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A Comparative Analysis of Lake Whitefish
(Coregonus clupeaformis)
Population Dynamics in Northeastern Lake Michigan

presented by

MARTIN ANTHONY SMALE

has been accepted towards fulfillment
of the requirements for

M.S. degree in Fisheries & Wildlife

William W. Taylor
Major professor

Date March 3, 1988

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A COMPARATIVE ANALYSIS OF LAKE WHITEFISH
(*Coregonus clupeaformis*)
POPULATION DYNAMICS IN NORTHEASTERN LAKE MICHIGAN

By

Martin Anthony Smale

A THESIS

Submitted To
Michigan State University
In Partial Fulfillment of Requirements for the Degree

MASTER OF SCIENCE

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1988

ABSTRACT

A COMPARATIVE ANALYSIS OF LAKE WHITEFISH (*Coregonus clupeaformis*) POPULATION DYNAMICS IN NORTHEASTERN LAKE MICHIGAN

Martin A. Smale

Three objectives were pursued for this project: 1) an analysis of sampling strategies for the commercial whitefish catch; 2) a comparison of statistics describing growth, mortality and reproduction in differentially exploited whitefish stocks and; 3) testing of available recruitment data for possible influences of winter and spring temperatures on year-class strength.

In the two areas most intensively sampled, composition of the Leland catch was influenced by seasonal variation, while the North Shore samples were subject to sample to sample variation of uncertain origin. Stratifying catch sampling by season and location were recommended to increase accuracy.

The North Shore fishery was based on a relatively large stock which decreased in abundance from 1.9 million to 0.8 million fish from November, 1980 to 1982. Annual mortality was high (A = 0.77/year) while growth was slow relative to Leland and to 1966-67 estimates for this stock. The Leland stock was sparser and also declined in abundance from 1980-82. Annual mortality was moderate (A = 0.55/year), growth was rapid and Leland fish matured at a relatively large size.

Slowest growth and lowest mortality were found for the commercially unexploited East Traverse area, where size at maturity was intermediate. Estimates of per capita reproductive output were lowest for East Traverse fish, and similarly greater for North Shore and Leland stocks due to more rapid growth and earlier maturation.

Adapting a stock-recruitment model to incorporate early winter severity and spring temperatures as additional factors in year-class strength greatly improved accuracy of the resulting hindcasts. Recruit per stock ratios were weakly correlated with stock size, increased ice-cover and mild springs. The combined factors model increased agreement between observed and hindcast recruitment values from r^2 = 0.04 to r^2 = 0.62 over a base stock-recruitment model. Trends of above and below average catch during the past 60 years were associated with episodes of cold and mild winters respectively in the Lake Michigan area.

ACKNOWLEDGEMENTS

This research was sponsored by the Michigan Sea Grant College Program, Grants No. NA-80AA-D-00072 and NA-85AA-D-SG045, Project No. R/GLF-16, from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce; as well as funds from the State of Michigan.

The opportunity for personal growth and knowledge provided during this study through encounters with a rich and diverse pool of opinions, expertise and experience was its most satisfying aspect for me. The appreciation I wish to express to individuals who have contributed to this study comes from both a personal and a professional point of view.

My advisor, Dr. William Taylor, earned special thanks both for having sufficient faith to provide this opportunity and for the effort to prod me through it. I would also like to thank the other members of my commitee, Dr. Niles Kevern and Dr. John Gill, for their encouragement and experience. Dr. Darrell King, the unofficial member, also gave many memorable hours of discussion and ideas.

The Michigan Fish Producers Association was instrumental to this study, and individual members are due special thanks. Ross Lang of Leland; the Frazier Brothers, Paul Van Landschoot and Cliff Bigelow of Naubinway; Don Cole of St. James and Ralph Cross Jr. of Charlevoix contributed time, effort, experience and the chance to participate briefly in their way of making a living from the Lake.

Cooperation and assistance from the Fisheries Division of the Michigan Department of Natural Resources was equally essential to this research. Myrl Keller, Ron Rybicki and the the R.V. Steelhead crew from Charlevoix, and also Don Nelson, Asa Wright and Doug Jester of Lansing contributed data, sampling assistance and experience for which I warmly thank them all. Several individuals from the U.S. Fish and Wildlife Service and the Sault Ste. Marie Tribe of Chippewa and Ottawa Indians also contributed essential information.

Fellow students and lab-mates gave time, frozen extremities, companionship and warm minds to idiot-proof ideas on. In particular, Mark Freeberg, Andy Loftus, Gary Whelan, Ann Livingstone, Mark Bagdovitz, Dan Hayes, Pat Marie Maher and Dave Dowling deserve special credit and a beer. Thanks also to Sue Plesko for help with typing.

I frequently encountered people of miscellaneous origin whose ideas or efforts were critical at some point in the study. Dr. Fred Copes and Mark Ebener of Wisconsin - Stevens Point, along with Paul Scheerer and Peter Jacobson, formerly of this Department, laid a strong foundation for this study. John MacKinney and Ron Kinnunen of the Sea Grant Extension Program earned thanks for their participation. Dr. Stephen Bowen of Michigan Technological University and Raymond Assel of GLERL provided important input at exactly the right times.

Acknowledgements but not necessarilly appreciation is due also to the makers of Merit cigarettes, several brands of coffee and Stroh's brewery, whose products enabled much of my

participation in these events. For the fine friends and significant others who put up with me lately, this was also appreciated. Last, but far from least, I would like to thank my parents, Jim and Margaret, not only for the usual parental duties but also for bailing me out of troubles. This one's for you.

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FOREWORD

The research described in this thesis is a continuation of an investigation into the population dynamics of lake whitefish in northeastern Lake Michigan which began in the fall of 1980. Scheerer (1982) and Scheerer and Taylor (1985) described population characteristics of certain stocks in the study area (Figure 1), and Jacobson (1983) and Jacobson and Taylor (1985) developed a model which simulated characteristics of yield from one stock under varying conditions of fishing. These studies provided fundamental information about whitefish stocks in the area and generated some of the questions addressed in this study.

This research was dependent on the commercial whitefish catch for data, therefore the first topic considered will be an analysis, in hindsight, of methods for obtaining the most reliable information from catch sampling with a minimum of redundancy. Determination of optimum sampling schedules, including size, frequency and timing of sampling is a sequential procedure in which previous samples are used to guide later sampling. A systematic analysis of differences and similarities amongst the samples used in this study was developed to test the reliability of information and to explore options for increasing the efficiency with which data for estimating vital population statistics were obtained.

In the initial studies, differences between the two principal study populations were sufficient that questions arose about which characteristics of the whitefish

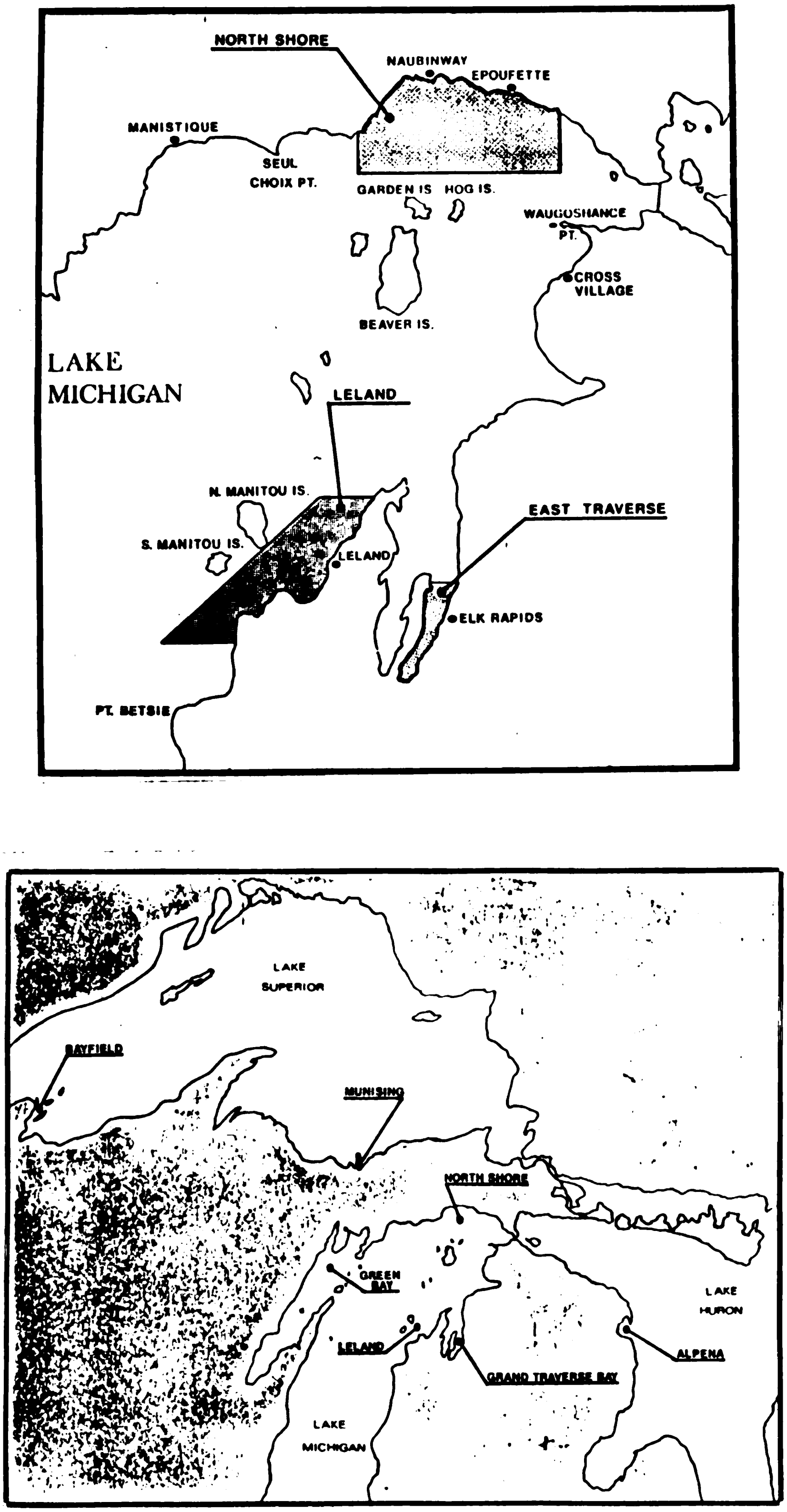

Figure 1. Maps of (A) the study area in northeastern Lake Michigan, including sampling boundaries of the three principal study populations and (B) locations of other upper Great Lakes whitefish studies used in comparisons.

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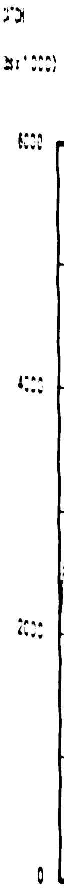
populations could be considered constant, either over time or between populations, and which characteristics vary both with time and place. The simplistic observation that population characteristics vary may be more useful than an assumption of equal and constant dynamics, but an objective of this research was to determine whether any discernible pattern of organization could be found to variations amongst and within whitefish populations.

Comparisons between the three principal populations at Leland, the North Shore, and in the East Arm of Grand Traverse Bay (East Traverse area), representing three different levels of fishing intensity, were made. Additionally, available information about the North Shore population over a 50-year time span enabled an evaluation of changes within a population. This portion of the study represented a large scale experiment, with fishing intensity a principal independent variable and characteristics of mortality, growth and reproduction the important dependent variables. This study design was supplemented by observations of whitefish dynamics obtained from the literature for certain critical characteristics and relationships.

Another topic considered was the factors influencing recruitment to Lake Michigan whitefish stocks. Strong fluctuations in the strength of individual year classes are one contributing factor to the highly variable catch record (Figure 2) of Lake Michigan stocks (Wells and McClain 1973, Patriarche 1977). Determining factors responsible for this



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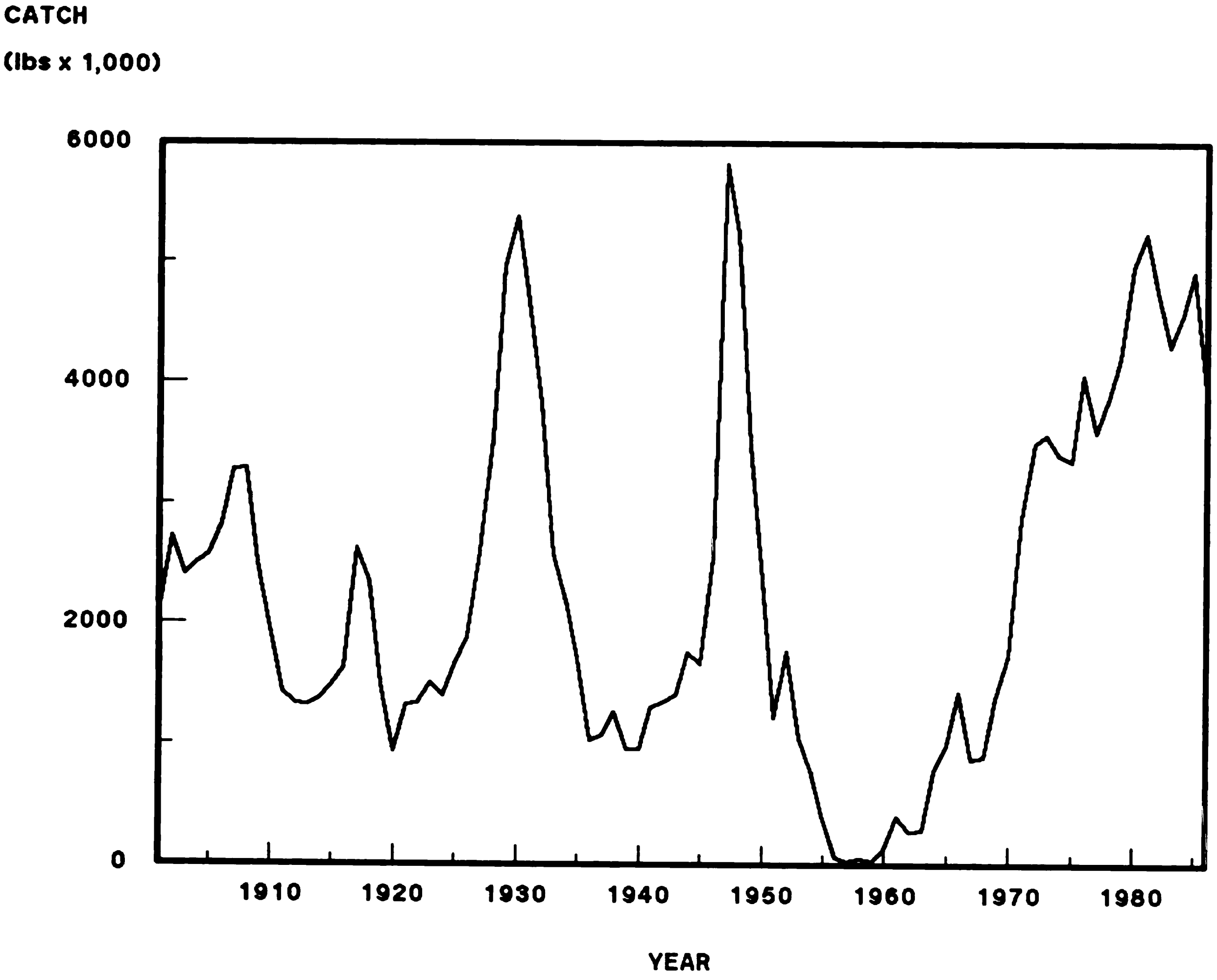

Figure 2. Lake Michigan whitefish catch, 1900-84.

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variation is likely to be useful in anticipating future changes in the stocks and minimizing the negative impacts of the fishery on yield and persistence. Recent studies by Freeberg (1986) and Taylor and Freeberg (1984) have suggested that both early winter ice cover and larval densities in proportion to the local abundance of zooplankton may be determinants of survival through the critical early life history stages of Lake Michigan whitefish. A section of this study analyzed available records of the catch and its age structure from the North Shore area to determine whether effects of these factors were detectable in past levels of recruitment.

Because of its length, this thesis was subdivided into three chapters, each of which deals with one of the above-mentioned topics. Each chapter consists of separate introduction, methods, results and discussion sections. These topics were by no means discrete, but each was dealt with somewhat independently in order to develop data and relationships in a more orderly fashion.

THE STUDY AREA AND FISHERIES

Sampling and tagging of whitefish in northeastern Lake Michigan was conducted within a study area rangeing along the north shore of the Lake from Point Patterson to the Straits of Mackinac; along the western shoreline of the Lower Peninsula to Point Betsie, and included areas around the Beaver Island archipelago and parts of Grand Travese Bay. There is a strong north to south shift in the morphology of the

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the Lake, with relatively little water deeper than 200 feet between the North Shore and the Beaver Islands, while the bottom drops rapidly to over 200 feet within less than a mile of much of the Leland and Grand Traverse Bay coastlines. The North Shore coastline is more indented with small bays and points than the Leland coast, and shoal areas are common in the area between the North Shore and the Beaver Islands and also around the Islands themselves.

The North shore fishery has historically been one of Lake Michigan's more productive. From 1981 through 1984, 29 percent of Michigan's yield from the Lake was from Whitefish Management Area 03 (WFM-03) which encompasses the North Shore stock. The area was fished by up to seven state-licensed trap-net fisheries and a variable number of tribal-authorized gill net operations. The treaty catch averaged 31 percent of WFM-03 catch during 1981-1984. Historically, this fishery suffered from the lakewide collapse of the whitefish stocks which led to negligible production by the late 1950's, but since 1960 yield steadilly increased with a recent decline following the peak year of 1981 (Figure 3).

By contrast, the Leland fishery supported a single trap-net operation, and the area (WFM-06) contributed an average of 2 percent of Michigan yield from the Lake during 1981 through 1984. The tribal fishery in this area was also reduced, producing an average of 22 percent of WFM-06 yield in recent years, with no full-time gill net fisheries operating during the study period. The Leland area was

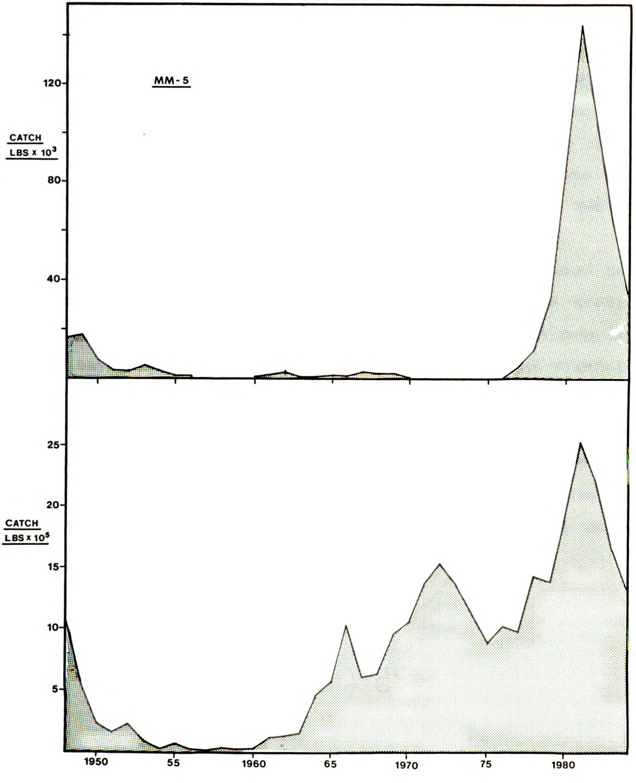

Figure 3. Whitefish catch in statistical districts MM-3 and MM-5 of Lake Michigan, 1948-84.

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closed to commercial fishing in 1970 and reopened for the current trap-net fishery in 1977. Statistical District MM-5, which includes the Leland fishery, had a typically low and erratic production record (Figure 3) with lowest yields also occurring at the end of the 1950's. In comparison to historical precedent, recent Leland yields were huge, but a strong year to year decline occurred during this study.

The East Arm of Grand Traverse Bay was closed to commercial fishing at the time sampling for this study occurred. A trap-net fishery began operating in both Arms of the Bay in the late summer of 1985, and commercial fishing for whitefish began in 1977 in the Outer Bay. A sport fishery for whitefish occured inside the East Arm but little is known about the amount of sports catch and its impact on the population. Although not strictly valid, for purposes of this study fish sampled from the East Traverse area were assumed to be from an unexploited population.

CHAPTER ONE

SAMPLING DESIGN

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INTRODUCTION

Commercial catch samples offer the advantage of cheap access to very large numbers of fish. This advantage is accompanied by restrictions due to minimum size limits and size-specific efficiencies of the gear such that only a portion of the population is sampled. Full vulnerability to the trap-net gear for whitefish may not be attained until a length of 489 mm (Eschenroder et. al. 1980). Although several samples included sub-legal whitefish, the analysis of commercial samples was limited to only recruited (> 432mm) whitefish.

The replicability of results is a possible limit to the utility of catch samples. During this study, occasional atypical samples were observed, and it became apparent that the frequency and extent of such deviations needed consideration. Single-shot samples, where one large sample is assumed to be representative of the fishable population, are reliable only if deviant samples are rare or absent. The alternate sampling strategy of frequent samples over a broad range of locations and times is both expensive and potentially redundant. An objective of this analysis was to find a strategy which minimized both the risk of unreliable information and redundancy.

If a population is at a dynamic equilibrium and therefore unchanging over time, one representative sample is sufficient to describe that population until some event disturbs the equilibrium. The problem of how frequently to

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sample is then determined by the rate of population change and the time span required before detectable population differences have accumulated. The problem of sampling frequency is different than the problem of the optimum timing to maximize the likelihood of obtaining a representative sample (Cochran 1977). Seasonal changes in the frequency distributions of size and age of the catch were apparent in the initial study. Distinguishing differences due to flux within the populations from seasonal changes in the range of sizes and ages sampled by the fishery was a second objective.

Thirdly, trawl samples of juvenile whitefish in the East Traverse area were taken to corroborate estimates of year-class strength from whitefish egg and larval mortality estimates (Freeberg 1986). The potential for forecasting recruitment to the fishery from enumeration estimates of juvenile age classes exists, but the extent of sampling effort and qualities of sampling design necessary are almost unknown. Statistics of age-specific catch rates and how they varied with timing, depth and location of East Traverse trawls were analyzed to determine whether juvenile sampling can be conducted within reasonable limits of effort.

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METHODS

Because several variables were measured to describe each fish, an analysis of every variable and how it changes from sample to sample, season to season and place to place would be overwhelming. In order to simplify the problem of sampling design, one variable described by one statistic and tested by one procedure was selected. The frequency distribution of lengths within individual and pooled samples was chosen as the statistic, and the Kolmogorov-Smirnov two-sample test (Steel and Torrie 1980) was the indicator of difference. The distribution of lengths was chosen rather than the distribution of ages to avoid complications caused by the approximately 20 percent error rate common to scale aging procedures and the shift in calendar age of the fish every January 1. It was assumed for the time being that if samples were representative of the length distribution in the catchable population, the sample was also representative of the distributions of age, weight and sex.

Table 1 lists sampling dates and locations for all areas. Length-frequency distributions for North Shore and Leland samples were tabulated for 10 mm length increments and converted to cumulative percent distributions. Comparisons were made first between individual samples collected within the same area and same 30-day period to test for the frequency of occurence of deviant samples. Individual samples were then pooled for each season in each year and compared sequentially to estimate the most common time-span between

Table 1. Whitefish sampling dates, locations, gear types and measurements taken, 1980-84.

DATE	NUMBER SAMPLED	GRID	GEAR	MEASUREMENTS*
		-North_Shore-		
10-23&29-1980	513	115-116	TN	1, 2, 3
6-29-1981	107	117	TN	1, 2, 3, 4, 5
8-24&25-1981	300	218	TN	1, 2, 3
10-17&24-1981	331	116-117	TN	1, 2, 3
5-17&18-1982	412	216-218	TN	1, 2, 3, 6
10-19-1982	189	117	TN	1, 2, 3, 6
4-27&28-1983	89	215-218	TN	1, 2, 3
6-8 & 9-1983	93	216-218	TN	1, 2, 3
6-27-1983	42	216	TN	1, 2, 3, 4
7-14&15-1983	49	217	TN	1, 2, 3, 4, 5
8-4-1983	96	216	TN	1, 2, 3
9-12-1983	64	216-217	TN	1, 2, 3
10-6-1983	56	X	TN	1, 2, 3
10-19-1983	103	115-116	TN	1, 2, 3, 4, 7
10-31-1983	64	115-117	TN	1, 2, 3, 4, 7
11-16-1983	32	116	GN	1, 2, 3, 4, 5
5-1-1984	100	215-218	TN	1, 2, 3, 4, 5
5-23-1984	31	216	TN	1, 2, 3, 4
7-11-1984	75	217	TN	1, 2, 3, 4, 5
8-9-1984	19	X	TN	1, 2, 3
9-10-1984	38	218	TRL	1, 2, 3, 4, 5
9-21-1984	59	217	TN	1, 2, 3, 4, 5
9-22-1984	41	213	TRL	1, 2, 3, 4, 5
10-8-1984	138	X	TN	1, 2, 3, 4
10-31-1984	20	116/117	TN	1, 2, 3, 4, 7
11-17-1984	54	116	GN	1, 2, 3, 4, 5
	2615			
		-Beaver_Island/Cross_Village-		
6-16-1981	219	316	TN	1, 2, 3
5-18-1982	169	317-418	TN	1, 2, 3
4-8-1983	69	315	TN	1, 2, 3
5-18-1983	123	317	TN	1, 2, 3
6-7-1983	64	419	TN	1, 2, 3
7-13-1983	32	317	GN	1, 2, 3
8-3-1983	63	418	TN	1, 2, 3
8-5-1983	38	315	TN	1, 2, 3, 4
8-11-1984	14	315	TN	1, 2, 3, 4
	791			

Table 1. (continued)

DATE	NUMBER SAMPLED	GRID	GEAR	MEASUREMENTS*
		-Leland-		
10-29&30-1980	114	714-814	TN	1, 2, 3
6-15-1981	81	812-912	TN	1, 2, 3
8-27-1981	94	812-912	TN	1, 2, 3
10-21&22-1981	244	812	TN	1, 2, 3, 4
5-20&24-1982	148	812-912	TN	1, 2, 3, 6
10-24-1982	186	812-912	TN	1, 2, 3, 4
2-14-1983	50	814	TN	1, 2, 3
4-7-1983	128	812-912	TN	1, 2, 3
5-10-1983	51	812-912	TN	1, 2, 3
6-13-1983	45	912	TN	1, 2, 3
6-29-1983	50	615	TN	1, 2, 3
6-30-1983	61	812-912	TN	1, 2, 3
7-21-1983	34	912	TN	1, 2, 3
8-2-1983	20	812-912	TN	1, 2, 3
8-25-1983	28	812-912	TN	1, 2, 3
10-4-1983	36	812-912	TN	1, 2, 3, 4
10-24-1983	53	812-912	TN	1, 2, 3, 4, 7
4-11-1984	41	812-912	TN	1, 2, 3
5-3-1984	33	812-912	TN	1, 2, 3
6-25-1984	58	812-912	TN	1, 2, 3, 4, 5
7-24-1984	22	813	TN	1, 2, 3
8-25-1984	53	714-812	TN	1, 2, 3, 4, 5
9-6-1984	12	814	TN	1, 2, 3, 4, 5
9-7-1984	4	814	TRL	1, 2, 3, 4, 5
9-23-1984	36	713-814	TN	1, 2, 3, 4, 5
10-15-1984	70	714-812	TN	1, 2, 3, 4, 7
	1752			
		-Grand Traverse Bay-		
6-14-1981	140	615	PS	1, 2, 3
6-7-1983	204	816-916	TRL	1, 2, 3, 5
6-3-1984	95	816-916	TRL	1, 2, 3, 4, 5
9-29-1984	622	816-916	TRL	1, 2, 3, 4, 5
6-21-1985	251	816-916	TRL	1, 2, 3, 4, 5
	1312			

*1 = length, 2 = weight, 3 = scales, 4 = sex and maturity, 5 = includes sublegal sizes, 6 = girth, 7 = fecundity

TN = Trap Net, GN = Gill Net, TRL = Trawl, PS = Purse Seine significant differences. Finally, samples from the same season in each area were pooled for all years in order to test for differences amongst average seasons and therefore seasonal effects.

In the East Traverse area, the Michigan Department of Natural Resources research vessel, the R.V. Steelhead, trawled for whitefish. Otter trawls with a 1.9 cm cod end mesh were fished along the bottom using 5 or 10 minute tows. Initial sampling sites were selected on the basis of previous experience of the Steelhead's crew. Loran-C coordinates were used to keep locations consistent each year, and depth profiles and water temperatures were recorded.

RESULTS

Commercial catch:

Grand total pooled length distributions from 1980-84 indicated a substantial size differential between the North Shore and Leland stocks (Table 2), with a North Shore median length (460 mm) smaller than the Leland median (503 mm). Samples matched by season and year from waters surrounding Beaver Island (Grids 315, 316 and 317) differed significantly (K-S test, $P < 0.05$) from samples taken in the Cross Village area (grids 418 and 419) for three out of four comparisons, while none of the four comparisons between matched samples within either area differed. Samples from these areas were therefore split into Beaver Island and Cross Village stocks. Pooled cumulative percent length distributions (Table 3) indicated a larger median length (482 mm vs. 470 mm) for

Table 2. Yearly and pooled total cumulative percent length-frequency distributions for North Shore and Leland samples, 1980-1984.

	NORTH SHORE						LELAND					
LENGTH (mm)	1980	81	82	83	84	Pool	1980	81	82	83	84	Pool
430	11	9	4	6	12	8.0	2	2	2	1	3	1.9
440	26	21	9	16	30	20.4	10	7	4	3	4	5.6
450	43	36	18	26	45	33.8	21	12	8	5	7	10.7
460	61	54	31	39	61	50.0	39	23	14	9	11	19.1
470	77	67	45	49	73	62.0	56	33	20	16	14	27.8
480	86	77	61	61	83	73.6	72	44	27	22	17	36.5
490	91	88	75	71	88	82.6	83	51	34	27	20	43.2
500	95	94	88	80	90	89.2	85	61	42	34	23	48.9
510	97	97	94	86	93	93.4	86	67	53	40	28	54.7
520	98	98	97	90	96	95.6	87	73	63	48	34	61.0
530	99	99	99	94	97	97.2	87	77	71	58	39	66.1
540	99	99	99	96	97	98.1	87	81	76	64	43	70.2
550	99	100	99	97	98	98.7	88	83	81	72	52	75.2
560	99	-	100	98	99	99.4	89	86	85	80	58	79.7
570	100	-	-	98	99	99.5	90	88	87	84	67	83.5
580	-	-	-	99	99	99.6	92	90	90	87	73	86.5
590	-	-	-	99	99	99.7	92	90	93	89	78	88.5
600	-	-	-	99	100	99.9	93	90	93	91	84	90.2
610	-	-	-	99	-	99.9	93	91	94	93	87	91.4
620	-	-	-	99	-	99.9	93	91	95	94	89	92.4
630	-	-	-	99	-	99.9	93	92	96	95	91	93.0
640	-	-	-	100	-	100	93	92	97	95	93	93.8
650	-	-	-	-	-	-	94	93	97	95	93	94.5
660	-	-	-	-	-	-	96	95	98	96	94	95.8
670	-	-	-	-	-	-	98	96	98	97	96	96.8
680	-	-	-	-	-	-	98	98	98	98	96	97.6
690	-	-	-	-	-	-	100	98	98	99	97	98.1
700	-	-	-	-	-	-	-	99	98	99	97	98.4
N	496	701	546	694	337	2774	112	405	403	518	205	1643

Table 3. Pooled total cumulative percent length-frequency distributions from the Beaver Island (grids 315, 316 and 317) and Cross Village (Grids 418 and 419) areas, 1981-84.

LENGTH (mm)	BEAVER ISLAND	CROSS VILLAGE
430	2	4
440	7	14
450	13	24
460	21	38
470	33	50
480	47	62
490	62	78
500	72	86
510	80	90
520	86	94
530	90	96
540	93	98
550	95	99
560	97	100
570	97	100
580	98	100
590	98	100
600	99	100
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Beaver Island samples and a broader distribution.

Yearly comparisons differed significantly ($P < 0.05$) at both Leland and the North Shore. The trend over time was for Leland median length to steadily increase from 467 mm in 1980 to 548 mm by 1984. The North Shore median increased from 454 mm in 1980 to 474 mm in 1982, then receded to 453 mm in 1984. Neither stock was at a stable equilibrium during the study. Changes in the size structure of both stocks were matched by parallel changes in age structure (see chapter 2), corroborating both the general reliability of the aging techniques used and the assumption that sampling of the length composition is indicative of the age composition.

Comparisons between pairs and trios of samples taken within a 30-day timespan in the North Shore area found 11 out of 32 samples differed ($p < 0.05$), using individual sample sizes from 32 to 226 fish. North Shore comparisons by specific location of capture were not attempted because locations were sometimes unidentified. Differences in median length between matched samples that were significantly different ranged from 31 mm to 7 mm, but the K-S test also responds to differences in distribution other than central tendency.

At Leland, 27 matchable samples were available and comparisons of pairs, one trio, one quartet and one quintet were made. Of these 27 comparisons, 5 were significantly different, with sample sizes ranging from 11 (from a single net) to 152 fish. Differences in median length ranged from 39 mm

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to 63 mm. Several location-specific comparisons were made and of these, the single Cats Head Bay (Grid 615) sample was different than 3 of the 4 matched samples from Grids south of Leland; 5 out of 6 comparisons between Good Harbour Bay samples (Grids 813 and 814) were different than Empire (Grid 912) samples while only 1 out of 6 comparisons from within these areas were different. Comparisons by location were only made during the 1983 summer, but spatial heterogeneity seemed to be an important consideration at Leland. Most Leland samples consisted of fish from more than one net and more than one location so that site-specific differences were usually homogenized out of individual samples.

With April 1 to June 15 designated the spring and October the fall sampling periods, seasonally pooled samples were examined sequentially to estimate the typical time span before detectable population change occured (Table 4). Significant differences between adjacent seasons occurred in 6 out of 10 Leland comparisons and 4 out of 10 North Shore comparisons. Two-season time spans differed in 7 of 9 Leland cases and 4 out of 9 North Shore cases, while comparisons spanning a full year differed 7 times out of 8 at Leland and 6 times out of 8 in the North Shore. No specific span of seasons showed a noticeably high or low frequency of change. This information alone, however, does not distiguish between differences due to changes in the population and those due to seasonal differences in the portion of the population sampled by the fishery.

Table 4. Sequential comparisons by season of the maximum difference (Kolmogorov - Smirnov D statistic) between cumulative percent length-frequency distributions, Leland and North Shore 1980-84. Significant differences (P < 0.05) are underlined.

LELAND

	FL 80	SP 81	SU 81	FL 81	SP 82	SU 82	FL 82	SP 83	SU 83	FL 83	SP 84	SU 84
SP81	0.28	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx
SU81	0.23	0.09	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx
FL81	0.44	0.23	0.24	xx	xx	xx	xx	xx	xx	xx	xx	xx
SP82	xx	0.22	0.24	0.04	xx	xx	xx	xx	xx	xx	xx	xx
SU82	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx
FL82	xx	xx	xx	0.13	0.16	xx	xx	xx	xx	xx	xx	xx
SP83	xx	xx	xx	xx	0.21	xx	0.13	xx	xx	xx	xx	xx
SU83	xx	xx	xx	xx	xx	xx	0.04	0.10	xx	xx	xx	xx
FL83	xx	xx	xx	xx	xx	xx	0.28	0.17	0.28	xx	xx	xx
SP84	xx	xx	xx	xx	xx	xx	xx	0.35	0.45	0.33	xx	xx
SU84	xx	xx	xx	xx	xx	xx	xx	xx	0.24	0.14	0.21	xx
FL84	xx	xx	xx	xx	xx	xx	xx	xx	xx	0.09	0.27	0.10

NORTH SHORE

	FL 80	SP 81	SU 81	FL 81	SP 82	SU 82	FL 82	SP 83	SU 83	FL 83	SP 84	SU 84
SP81	0.08	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx
SU81	0.05	0.13	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx
FL81	0.30	0.38	0.29	xx	xx	xx	xx	xx	xx	xx	xx	xx
SP82	xx	0.38	0.32	0.06	xx	xx	xx	xx	xx	xx	xx	xx
SU82	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx
FL82	xx	xx	xx	0.09	0.07	xx	xx	xx	xx	xx	xx	xx
SP83	xx	xx	xx	xx	0.09	xx	0.08	xx	xx	xx	xx	xx
SU83	xx	xx	xx	xx	xx	xx	0.11	0.04	xx	xx	xx	xx
FL83	xx	xx	xx	xx	xx	xx	0.20	0.16	0.16	xx	xx	xx
SP84	xx	xx	xx	xx	xx	xx	xx	0.25	0.26	0.14	xx	xx
SU84	xx	xx	xx	xx	xx	xx	xx	xx	0.26	0.10	0.07	xx
FL84	xx	xx	xx	xx	xx	xx	xx	xx	xx	0.20	0.12	0.17

Length distributions pooled for each season for all years found no difference between the average North Shore spring, summer and fall catch. However, very significant ($P < 0.01$) differences occurred between the length compositions of all three seasons at Leland. Large fish were most common in Leland spring samples, while North Shore samples were uniform. The median length of the sampled catch at Leland (Figure 4) changed consistently over the three years; with an increase in median length from fall to the following spring, a decrease by summer and another increase in the fall. The fall to spring increase was unexpected in that overwinter fishing and growth are minimal, therefore length distributions should remain static during this span. For North Shore median lengths, no seasonal pattern was apparent, with both increases and decreases observed over seasons in different years.

Generalizations about an ideal sample size are difficult because the degree of precision required and the distribution of the variable in the population are both factors in determining sample size. Considerations other than sheer size of the sample were determinants of accuracy for certain purposes. First, standardizing sample size was found, in hindsight, to be helpful when pooling samples in that balanced data meant that samples of equivalent precision were combined. Secondly, the random catch samples used to analyze frequency distributions of variables such as age, size and sex were not ideal for other analyses. In particular, samples

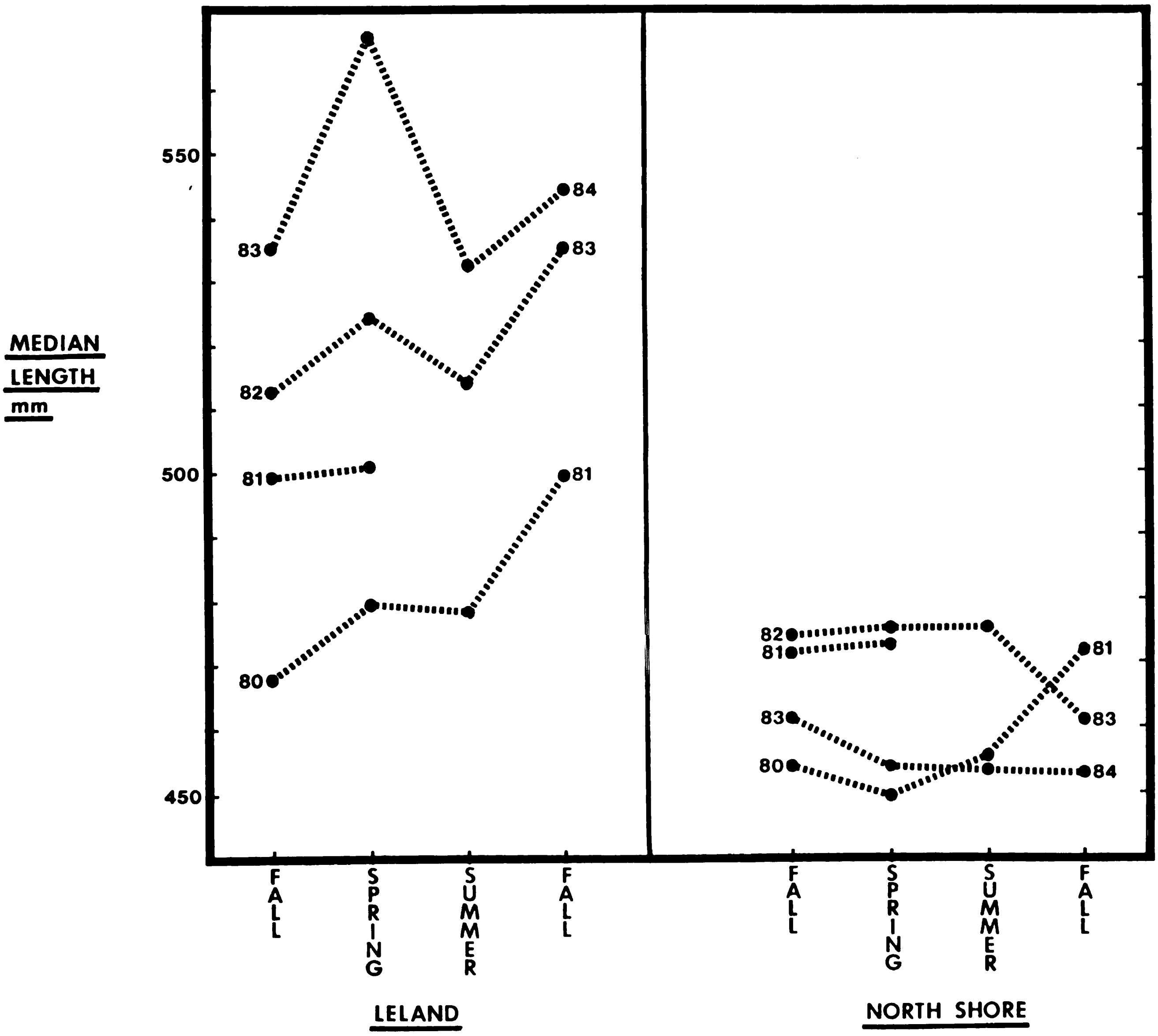

Figure 4. Seasonal changes in the median length of whitefish sampled at Leland and the North Shore, 1980-84.

stratified by size were more useful for estimating morphometric relationships such as those between length and weight or length and scale size. Random samples of the catch were strongly unbalanced towards intermediate sizes, and this imbalance contributed to uncertainty in estimating morphometric relationships.

In analyzing the distributions of age or size in the catch, the law of diminishing returns with increased sample size for binomial confidence intervals was relevant. For example (Figure 5), confidence interval width for an estimated frequency of 50 percent declines in negative exponential fashion from 44 to 10 percent as sample size increases from 25 to 400 individuals. Each doubling of N results in a smaller gain in precision, with a noticeable inflection circa 200 individuals.

Precision of the estimate of frequency in a class is also influenced by the frequency itself. Relative error, the width of the confidence interval divided by the frequency, decreases negative exponentially with increasing frequency (Figure 6). For example, with a sample N = 100, the confidence interval for a frequency of 10 percent represents 130 percent of the estimate. But with the same sample, a frequency of 80 percent is estimated with a precision of more than 20 percent of the frequency. Sample size determination is a tradeoff: each consecutive doubling of N produces a smaller gain in precision, and smaller frequencies are less precisely estimated than larger frequencies for a given N.

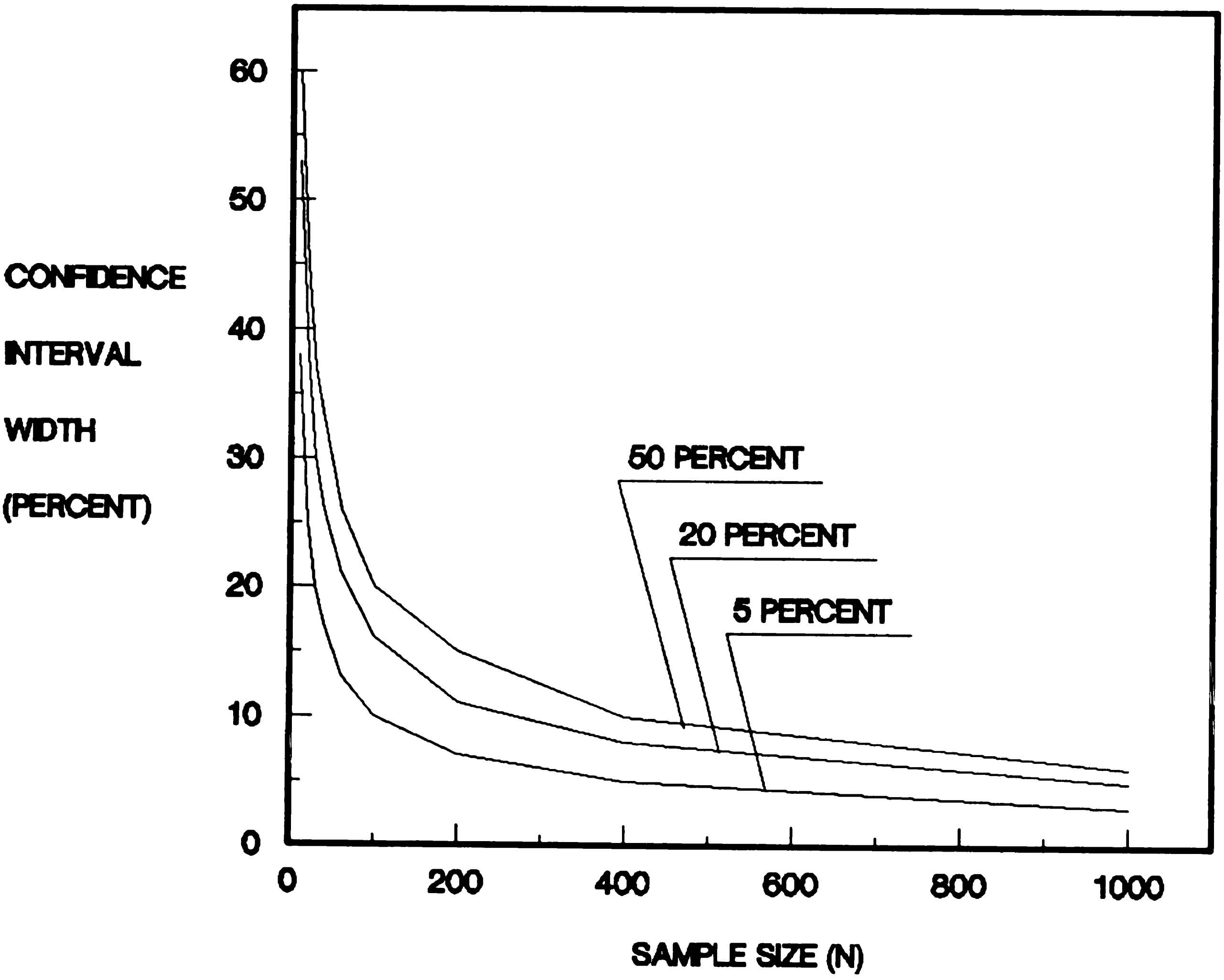

Figure 5. Binomial confidence interval width (0.95) as a function of sample size for classes representing 50, 20 and 5 percent of the total sample.

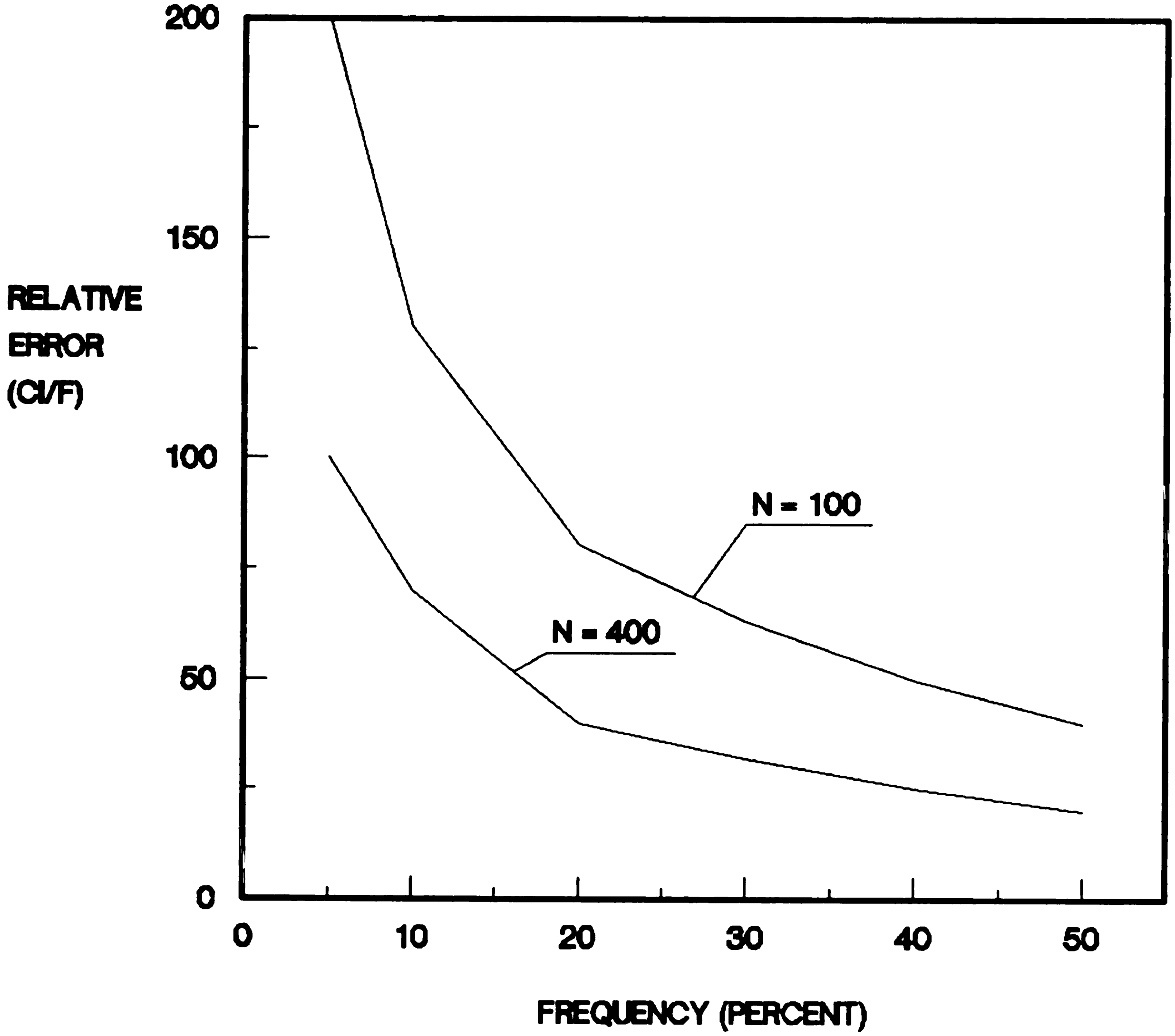

Figure 6. Relative error (confidence interval width divided by frequency in the sample) in relation to frequency in the sample for samples of N = 100 and N = 400.

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East Traverse Trawl Samples:

First year (1983) trawling results were modest (204 fish caught), and an even smaller catch in June 1984 (95 fish) prompted additional trawling in September 1984 which caught many more fish with similar effort (622), including young of the year. In the third year, June trawling was expanded from 5 to 12 trawls in order to search for more productive areas, but numbers caught (151) did not improve proportionally.

The distribution of spring catch per trawl followed a probable negative binomial distribution, with frequent small catches mixed with occasional very large catches, which is symptomatic of a clumped distribution of fish by location. Spring catch per trawl of yearling fish was even more negatively skewed, with zero catch the modal frequency. Mean catch per effort for 1983 and 1985 spring trawls combined was 21.2 fish per 10 minute trawl with a standard deviation of 30.1. Catch per effort of yearlings alone averaged 10.2 per trawl with a standard deviation of 15.8. The differences in spring CPE between 1983, 1984 and 1985 were not significant ($P > 0.10$) with this level of trawl to trawl variation.

Using Stein's two-stage sampling formula to estimate sample size for spring trawling (Steel and Torrie 1980), 124 trawls would be needed to estimate mean catch per effort within 10.6 fish per trawl (± 25 percent) and 31 trawls to estimate the mean within 21.2 fish per trawl (± 50 percent). For estimates of mean yearling catch per trawl, 147 trawls would be needed for an estimate within 5.1 fish per trawl (±

25 percent) and 37 trawls to within 10.2 per trawl (± 50 percent).

For the September trawls, catch per effort averaged 133.6 fish with a standard deviation of 75.3 and a coefficient of variance of 56 percent, less than half the spring coefficient of 142 percent. Fall yearlings averaged 9.8 per trawl with a standard deviation of 4.8 and a coefficient of variance of 49 percent, one-third the spring coefficient of 155 percent. Not only was the September trawling more productive, but trawl to trawl variation was considerably less.

Trawl to trawl variation was a considerable problem in using catch per trawl estimates as an index of abundance, especially considering 12 trawls represent a full day's effort. Initial sampling design was planned on a best guess basis, and results were tested to consider whether some stratifying procedure could minimize this variability. Since trawl sites were standardized, catch per effort consisistency was examined by site. Locations were determined by Loran-C coordinates and repeatability was no better than ±100 meters. Spring 1984 results were omitted due to uncertainty about the locations of some trawls.

With respect to all age classes (Table 5), location D, the deepest, produced the most or second most fish in all three years and location B, the shallowest, was always last. With respect to yearlings alone however, location D was always last and location A first in 1984 and 1985, but not 1983. Location B was unfavored by whitefish in general and

Table 5. Whitefish catch (N) per 10 minute trawl at standard sites in Grand Traverse Bay for combined age classes and for yearlings, 1983-1985.

SITE	DEPTH (FEET)	JUNE 1983	SEPTEMBER 1984	JUNE 1985
		- All Ages -		
A	100	11	125, 84*	8,12*
B	40-100	7	54	0
C	100-160	72	249	3
D	200-380	119	156	23
		- Yearlings -		
A	100	3	24, 58*	6,5*
B	40-100	4	13	0
C	100-160	28	0	2
D	200-380	0	0	0

*Replicate trawls from the same location a few hours apart.

Note: Trawls taken in June 1984 and trawls at non-standard sites in June 1985 were not included in these results.

at best a fair spot for yearlings, so trawling elsewhere seems advisable. Replicate trawls at site A taken a few hours later in the day produced catches more similar to the earlier catch than to other sites, however, length frequency distributions differed in the replicate trawls on two of three occasions.

Depth distributions (Figures 7 and 8) were estimated from catch at depth per effort at depth calculations for each sample. In June 1983, when water temperatures were near homothermous (40 degrees F surface - 37 degrees F below 130 feet), effort was concentrated at 100 feet but the bulk of the catch occurred between 120 and 280 feet. Segregation of age groups by depth was not severe although yearlings may have been more abundant in water shoaler than 200 feet. Only fish older than 2 were found below 300 feet. Depth distributions were not calculated for June 1984 when the water was also homothermous, but the low catch that year suggests that again the bulk of the effort was expended above the main concentrations of fish.

In September 1984, when water temperatures were stratified, the bulk of the catch was taken between 100 and 200 feet, and age groups were well segregated. Young of the year were found only at 100 feet and shoaler, yearlings at all depths and fish older than 3 only at depths greater than 100 feet. The apparent spike of abundance at 100 feet more likely represented a clumped distribution and concentrated effort at 100 feet rather than a concentration of fish at that depth.

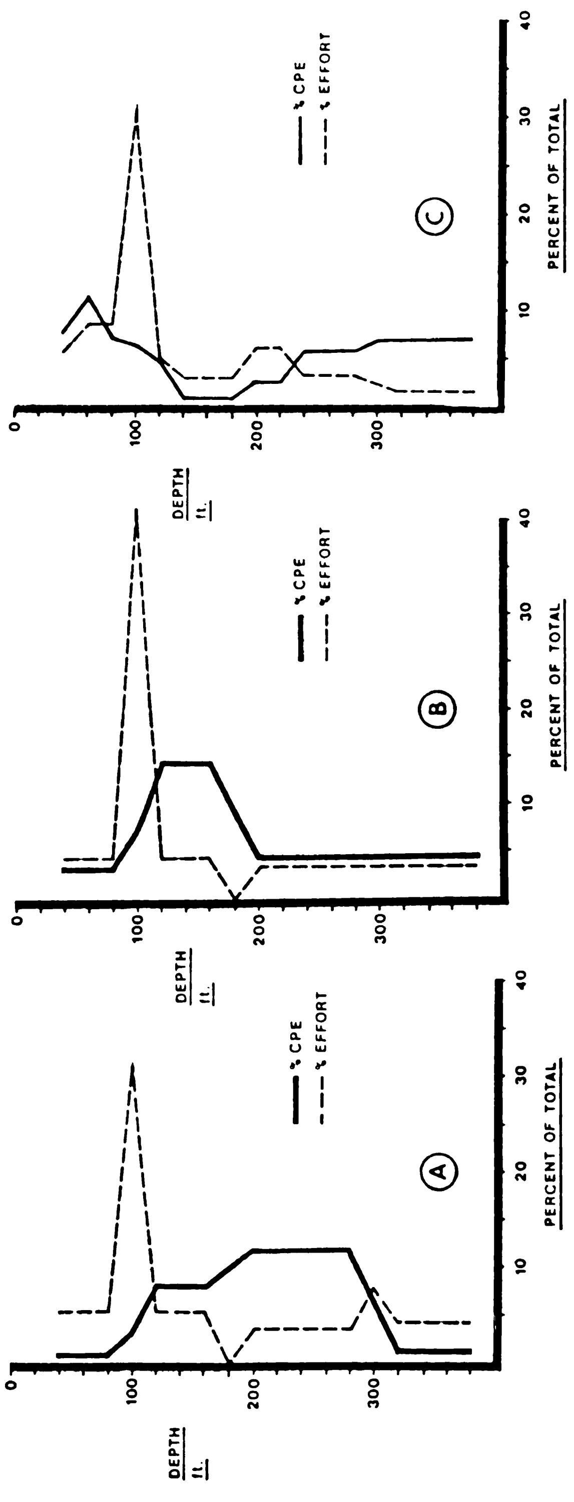

Figure 7. Depth distributions of effort expended and whitefish caught per trawl for all ages combined in East Traverse trawl samples for: A) June 1983; B) September 1984 and; C) June 1985.

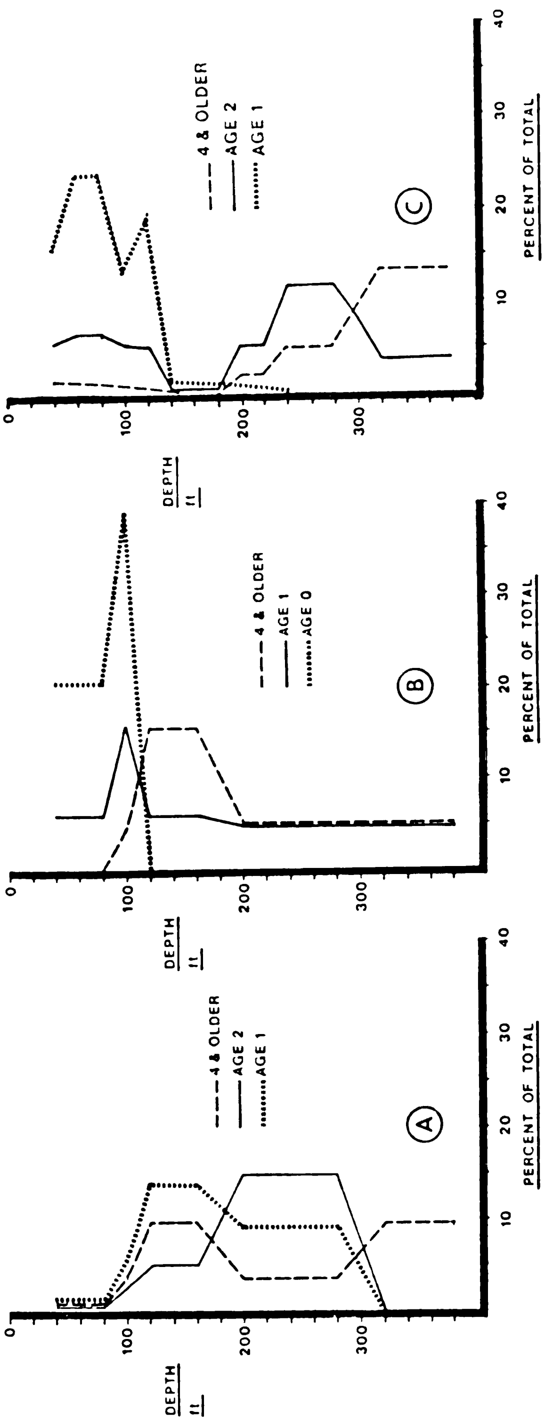

Figure 8. Depth distributions of whitefish catch per effort separated by age group in East Traverse trawl samples for: A) June 1983; B) September 1984 and; C) June 1985.

Trawling in June 1985 was conducted in thermally stratified water due to a milder spring and later trawling date. Surface temperatures were 61 degrees F with a thermocline present from 58 to 48 degrees F between 40 and 80 feet. Depth distributions were bimodal with most success between 40 and 120 feet or between 240 and 400 feet. Yearlings were common from 40 to 120 feet, scarce below 120 feet and absent below 240. Segregation of age groups was most pronounced when the Lake was stratified, with the youngest fish prefering depths near the thermocline.

DISCUSSION

Commercial catch sampling:

Certain characteristics of the Leland and North Shore catch were unique, suggesting that a uniform sampling strategy would give nonuniform results. The Leland size structure was broad and daily catches were low, while the North Shore catch was opposite in character. The increased variation in the Lealnd catch necessitated more intensive sampling, but the lower catch sometimes limited sampling options.

North Shore samples, in comparison to Leland, exhibited a greater frequency of matched sample-to-sample differences; a reduced frequency of differences between sequential seasons; no detectable seasonal shifts in composition; and a distribution of lengths which increased then receded during the study period. Characteristics of Leland samples included a known possibility of site-specific differences; less frequent matched-sample differences; more frequent season to season changes and a strong seasonal shift in composition for all three seasons.

The greatest single impediment to sampling accuracy in both fisheries was sample to sample variation between individual samples matched for general area and date. The frequency of differences was approximately 1 in 3 for North Shore samples and 1 in 5 for Leland. The design of the study was insufficient to pinpoint the cause of this variation, but three non-exclusive explanations are possible. First, sample deviations could be due to an affinity by the fish for others of the same size/age class, i.e. size selective aggregation. This effect, if present, would result in a relatively random distribution of deviant samples with no relationship to the spatial or temporal distribution of the fishing gear. Secondly, sample deviations could be due to an affinity by the members of different size/age groups for different habitat features such as depth. In this case, sample variations would be patterned by the distribution of gear with respect to depth or any other habitat feature. Thirdly, deviant samples could be due to spatial heterogeneity within the population; i.e. each fishery is based on several subpopulations of differing characteristics whose home ranges do not fully overlap. If so, sample variation would be patterned with respect to the spatial distribution of fishing effort.

The specific cause of sample variation is uncertain at this point, and all three possibilities need to be accounted for in designing a sampling strategy to compensate for the effect. If sampling variation was known to be structured, such as by depth or location, effort could be stratified across each factor to balance the samples. Size selective aggregations, which should be distibuted randomly amongst samples, cannot be compensated for by structured sampling, rather multiple samples would be necessary. Some evidence from this study suggests that sampling variations are indeed structured, but the possible presence of random deviations in catch samples also cannot be rejected.

East Traverse trawl samples indicated that different size/age classes of whitefish followed different depth preferences, and that this differential changed with thermal stratification. However, these samples included a much broader range of sizes than did the commercial samples, and whether commercially legal sizes of whitefish segregate by depth was not clear. The commercial samples themselves were an innappropriate tool for testing for differences in depth preferences because the gear was almost always fished at similar depths during any season.

The presence of spatial heterogeneity within the two areas is quite likely. Location specific differences at Leland were almost always significant when tested for, but this effect could not be investigated more extensively because of the decline in Leland catch during later years of the study. Location specific differences were not examined in North Shore samples, but Brown (1968) found consistent differences in characteristics of both the catch and the fish landed at Seul Choix, Naubinway and Brevort.

Experimental gill-netting on the North Shore spawning grounds in Novembers of 1983-84 provided a clue about the spatial organization of these whitefish. Both areas which appeared to be likely looking spawning grounds did contain spawning whitefish, and length frequency distributions from the two areas differed even though nets were set about 3 km apart on the same day. Many more likely looking spawning grounds were seen along the North Shore coast, and a very reasonable inference is that the fishery is based on multiple spawning stocks. Males from these nets were tagged and released to test for possible homing to the same spawning area, but results were unavailable at this time. Tag returns from November 1980-82 North Shore taggings were dispersed throughout the North Shore area, but recapture locations were not identified with enough certainty to test for incomplete homogenization during the fishing season. At Leland, very few whitefish were captured on a suspected spawning area at the north end of Good Harbor Bay in Novembers 1983-84, and no spawning ground was identified.

Sample to sample variation, for whatever cause, implies that single samples of the catch are inadequate for obtaining and testing reliable information. A single catch sample, regardless of the number of fish sampled, is a sample size of one. Given that sample to sample variation occurs, replicate samples are required in order to evaluate the reliability of the information gathered.

The intended use for catch sampling is an important criterion for designing a sampling stategy. If objectives of a study included the assessment of differences amongst local groupings within an area, sampling should be stratified consistently by location. If, on the other hand, objectives are concerned with statistics for the typical fish within an area (as was the case for most of this study), an opposite strategy of homogenizing samples over as many locations, depths etc. as possible is desirable. Even deviant North Shore and Leland samples were more like other samples from the same area than they were like samples from other areas, so the range of sample variation within an area is comparatively subtle. Whether or not spatial heterogeneity within an area should be addressed in assessment or management plans is not a sampling issue. But if sampling efforts are confined to a specific location within an area, either by intention or inadvertantly, samples can be considered representative only of that location, not the stock as a whole. Conversely, if sampling is homogenized over a broad range of locations, information will be representative of the area but not necessarilly of specific locations.

Assuming that descriptions of area-wide average characteristics are intended for most catch sampling regimes, steps can be taken to minimize the risk and effect of deviant samples by homogenizing sampling effort. The lower frequency of between sample differences found at Leland was not due to a greater homogeneity of characteristics in this stock, rather the opposite was the case. But the typical Leland sample more often than not consisted of fish from several nets and locations along the Leelenau coast, while North Shore samples were more often from a smaller number of nets often grouped near each other. The lower frequency of Leland sampling differences was a function of the difference in sampling strategy, and although inadvertant, the difference in results illustrates the effectiveness of dispersed rather than concentrated efforts at reducing variation between samples. Obtaining samples from one or a few nets increases the risk that a sample will be unrepresentative of whitefish in the area.

Planning sampling with cooperating fishermen could be used to ensure that samples are broadly distributed rather than obtained inadvertantly from only a few locations and habitats. Marking boxes of fish by location was also useful for homogenizing samples. Sampling the entire contents of a catch box was a common tactic in this and other studies, but was also an error in that the bulk of the sample is more likely to be from fewer nets. Subsampling boxes to disperse effort would increase efficiency because fewer samples would be needed due to an expected decrease in sample variation. In addition, replicating samples such as by collecting 3 homogenized samples from 3 fishermen, is necessary if the reliability of the information is to be known rather than assumed.

There are practical considerations which make sample homogenization difficult, but insufficiently homogenized efforts require more individual samples, thus homogenization should increase both efficiency and accuracy. Sampling the entire contents of a catch box is convenient for the sampler and fisherman alike in that the remainder of the catch can be processed while samples are taken. Subsampling from every box is more representative but also more awkward for both parties. Saving out boxes on the boat which contained several fish from each net was tried, but this also interfered with normal operations and risked non-random selection of fish for sampling. Subsampling from the entire catch was feasible and convenient when fish were being dressed (eviscerated) on the return trip to the dock, but other arrangements could be made with specific fishermen. Testing samples and subsamples for differences in length composition with the Kolmogorov - Smirnov test was also useful when collecting samples for deciding when a sufficient number of samples had been taken.

The optimum timing and frequency of sampling schedules depends also on the purpose of sampling as well as the pattern of temporal change in the composition of the catch and the stock. Two questions were considered: first, whether the catch is representative of the stock during any or all saesons and second, how rapidly each changes. Neither the Leland or North Shore stocks were at a stable dynamic equilibrium during the study, and the recruitment and subsequent decline of a very strong 1977 year-class was responsible for much of the change in the stocks (see Scheerer and Taylor (1985) or chapter 2). Because of more intensive exploitation, population flux and turnover was more rapid in the North Shore area than at Leland, even though Leland samples differed more frequently over time.

The presence of seasonal shifts in the composition of the Leland catch and the absence of this effect in North Shore samples can be explained by the greater homogeneity of the North Shore stock and/or the more uniform habitat. Whether various size/age groups of whitefish have an affinity for each other or for specific habitat features is largely a moot issue for North Shore sampling because the range of available sizes and ages in this area is limited. Similarly, the shallow slope of the bottom and comparatively uniform depth limit habitat selection options for the fish. At Leland, seasonally varying segregation of different groups should be more pronounced due to the greater heterogeneity of both the stock and the habitat. The Leland fishery was clearly sampling different segments of the stock in different seasons, and sampling effort was sufficiently distributed over the area in this study to discount the possibility that seasonal relocation of effort by the fishery was responsible for this effect.

The seasonal changes followed a consistent pattern in all 4 years, with a large median length in spring samples compared to the preceding fall. There was also a trend of increasing median length present so that changes in the composition of the stock and changes in the catch composition were occurring simultaneously. The most difficult feature of this seasonal shift is that there is no means to determine with certainty in which, if any, season the catch is representative of the stock. A best guess is that spring samples are most representative; water temperatures are unstratified and the catch is not predominantly male, as fall samples tended to be. But confirming this guess would require a determination of the actual composition of the stock by methods other than sampling of the commercial catch. The seasonal difference also was not trivial, for example catch curve mortality estimates based on spring and fall samples alone differed by over 15 percent.

The treatment of seasonal variation in samples depends on whether they are used to describe the composition of the catch or the composition of the population. For example, estimates of the median weight of the catch are used to convert weight of the catch to numbers caught, and for this purpose, median weights for each of the 3 seasons must be averaged to estimate median weight for the year. But because the median weight of the catch is not representative of the stock in at least 2 seasons out of three, averaging seasonal statistics together is an error for describing the distributions of the stock. If the validity of samples from any particular season could be established, seasonal shifts could be dealt with by ignoring samples from unrepresentative seasons. Without this validation, the only proper treatment of seasonal effects is to tabulate statistics independently by season, with the highest and lowest statistics representing the range of confidence in the estimates.

Seasonal shifts were not detected in the North Shore samples and samples were sufficiently powerful to detect any non-trivial difference. Descriptions of the size composition should be equally valid for any season, however the predominance of males in October samples could bias statistics other than length distributions. Temporal changes in length composition were less frequent than at Leland, but North Shore changes were due to population flux alone. Significant differences were detected for 40 percent of the comparisons from adjacent seasons, while 75 percent of the comparisons spanning a year were different. Sampling the North Shore catch in each season would result in redundancy for the majority of the information; sampling less frequently than annually could overlook important changes in the composition of the stock. The rate of population flux probably varies in the North Shore area during a span of many years, but annual sampling seems a reasonable compromise frequency. For most general purpose samples, late spring would be an optimum time since daily catch is high and scale margins have grown past the most recent annulus.

Requirements of precision may vary with the intention of the study, but binomial confidence intervals offer a useful technique for evaluating sample size. Although stock age and size compositions usually contain more than two classes, precision of the frequency estimate for any class can be estimated binomially by considering individuals either as members or not members of a specific class.

Regardless of frequency, there is a rapid decrease in the gain in precision per additional individual sampled above a size of N = 100, and gains after N = 200 are negligible. For single samples, 100 individuals may often be adequate, and more than 200 is clearly redundant. This is not to imply that such samples are absolutely precise, rather there is no further meaningful gain to be made by additional sampling, assuming the individual sample itself is representative. Using a standard sample size, when practical, would be useful in pooling data and making comparisons because data are then balanced.

The observation that precision of frequency estimates depends on the frequency itself, as well as sample size, implies that the least common class will also be the least precisely estimated. In analyzing discrete-class frequency distributions, this variation in precision with frequency is equivalent in effect to non-homogeneity of variance. Although technically sufficient grounds for rejecting the validity of procedures such as regression analysis of age structures, no feasible alternative currently exists. The precision of frequency estimates declines with smaller frequencies even following log transformation, thus some caution in interpreting regression based or ratio based age and size structure results is suggested.

Because Leland and Leland-like age/size distributions are broader, frequencies in any given class would typically be lower. Logically, broader distributions would seem to imply the need for larger samples in order to gain precision equivalent to estimates for less diverse stocks, but such is not entirely the case. The law of diminishing returns implies that gains in precision with samples beyond circa 200 individuals would be trivial, therefore there is an upper practical limit to precision. Above this limit, frequency estimates for single classes from broad distributions will be unavoidably less precise.

This analysis of sampling design has largely been concerned with obtaining reliable and representative information about the distribution of ages and sizes within the catchable stock. Characteristics of these random samples of the catch make them less than ideal for estimating other population traits. Tailoring sampling to satisfy the needs of each type of analysis would usually be more efficient than using one very large sample for all purposes. Samples stratified by length, even into coarse classes such as small, medium and large, would be more accurate than random samples for estimating morphological relationships. Analyses of sexual characteristics such as maturity and fecundity require sampling at specific times of the year (see chapter 2). The inclusion of sub-legal whitefish is useful in determining growth rates, and sampling these small fish can take some unique procedures. The disadvantage to special purpose t

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sampling is that more samples are necessary, but the advantage is that fewer fish on the whole would have to be sampled to gain the same precision for all statistics.

In summary, North Shore sampling would be most efficient and accurate with 3 samples of 100 fish taken in late June. Ideally, each sample should be dispersed throughout the area with a few fish sampled from as many nets or boxes as can be managed. A second sample which concentrates on small and large fish in order to stratify by lengths may also be taken concurrently. At Leland and areas where seasonal effects would be prominent, samples either need to be repeated each season and some degree of uncertainty to the statistics accepted, or further experimentation to validate the representativeness of a particular season should be undertaken.

East Traverse Trawl Samples:

This evaluation of juvenile trawling efficiency was a pilot study, and whether results from the Bay generalize to other areas of Lake Michigan is unknown. Characteristics of the trawl catch included a great deal of trawl to trawl variation in catch rates and age structure of individual trawls; an apparent clumping of fish by location; and depth segregation by size which apparently responded to thermal stratification. A completely randomized trawling design can be rejected as hopelessly inefficient. The skewed catch distributions indicated that the likely result for random trawling would be few or no fish, with a large variance.

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Avoiding locations where whitefish are absent and concentrating effort where they are found would reduce variance between trawls. The consistency in efficiency rankings for the four sites is encouraging. Whitefish seemed to prefer specific places rather than to migrate randomly around the Bay in groups. In developing plans for more widespread juvenile sampling, part of the process should include searching for and testing of reliable index sites.

A second problem in analyzing year-class strength from catch data is that sampling must include some reference standard by which cohort strength can be judged. There are two possible methods of comparison: catch per effort of a specific age group; and age structure analysis. Both methods require some number of years to calibrate. At this point, results have not been sufficient to justify choosing either strategy. Catch per effort of the 1983 year class, which Freeberg (1986) estimated to be in reduced abundance at the end of the larval stage, was less than CPE of both the preceding and following year classes as yearlings. This same cohort was less frequent in the age distribution than other year classes at the same age, thus either method detected the diminished abundance of the 1983 cohort.

But if water temperatures are stratified, age structure analysis would be the less reliable method due to increased segregation. The frequency of a specific age class in the sample would be a product of its abundance and the fraction of total effort expended at the depth at which it lived.

Conversely, the reliability of catch per effort analysis is dependent on the consistency of the spatial distibution of whitefish over the area. So far, random movements of whitefish have not been a grossly obvious problem, but this possibility has also not been thoroughly discounted.

For the time being it seems worthwhile to consider both CPE and age-structure sampling strategies and using one set of results to corroborate the other. For estimating yearling CPE, trawling at depths from 40 to 160 feet when the Lake is stratified appeared the most reliable. For comparing yearling frequencies to other age groups, stratifying sampling across a range of depths during periods of unstratified temperatures seems advised.

The single September trawl was 3 to 7 times more productive than any of the three spring trawls. This result is unexplainable, and a more thorough search the following spring failed to find whitefish in similar densities anywhere in the East Arm. Since the low spring catch contributed to uncertainty and imprecision in results, September trawling would be advised for CPE procedures. The strong depth segregation in September, however, would preclude any useful estimates of age structure.

Results of this study do not indicate that enumeration estimates of cohort strength from trawl sampling are infeasible, nor do they guarantee reliability. Results to date have been only partially adequate to evaluate reliability of the results themselves. Some methods for improving accuracy were apparent, but further trial and error will be needed to test the improvements. Distinguishing black from white in terms of forecasting cohort strength may be a reasonable goal, but reliably forecasting shades of grey may take a considerable effort. Some exploratory work will be necessary to find reliable sampling sites and times, and a minimum of two or three years to calibrate and interpret year-class estimates will be needed.

CHAPTER TWO

ABUNDANCE, MORTALITY, GROWTH AND REPRODUCTION

INTRODUCTION

A necessary step in the maturation of any scientific discipline is the progression from a strictly descriptive phase, in which variables are measured, tabulated and reported, to an analytical phase, which seeks to determine the difference which makes a difference amongst the variables of interest (Bateson 1979). This evolution in the study of exploited populations is often inhibited by the enormity of the task. For describing characteristics of a population, the unit of sampling is the individual fish, and the objective is to describe the average individual. But for analyzing population dynamics, the unit of sampling is the population, and inferences about the mechanisms by which populations change over time and location require consideration of a sufficient sample of populations and a range of differences amongst them.

Population dynamics has used three basic techniques for gaining and testing new knowledge. Natural experiments, which contast population traits under a range of conditions found in nature, can be broad in scope and powerful, but reliability can be hindered by uncontrollable extraneous factors. Controlled experiments, in which only factors of interest are intentionally manipulated while all others are held constant, are more reliable but are scarce in population dynamics. The limited scope and artificiality of typical controlled experiments inhibits the application of results to wild populations. Synthetic population models are a third type of

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experiment, in which the effect of intentionally manipulated variables is simulated by equations describing relationships amongst variables of concern. The drawback to synthetic models is that they are entirely dependent for validity on assumptions about relationships derived from natural and/or controlled experiments with real organisms.

Attempts to analyze whitefish populations and explain mechanisms of difference within and amongst them have been undertaken. Healey (1975) used the natural experiment approach to compare dynamics of numerous stocks and concluded that the reserve capacity for growth was an important indicator of an exploited population's ability to persist. Healey (1980) also adopted a semi-controlled experimental approach to show that whitefish populations respond to exploitation with accelerated growth and increased recruitment. Jensen (1976) also compared the dynamics of several populations, as well as using the synthetic model approach (1981) to identify accelerated growth, early maturation and density-dependent early life survival as potential mechanisms by which stocks compensate for exploitation.

Survivorship, growth and reproductive capacity clearly vary over a wide range within and amongst whitefish stocks, implying that such differences need to be accounted for on a case by case basis when assessing and prescribing management regimes for any stock. The intention in this chapter is to determine whether traits of different stocks vary in predictable and systematic patterns and to describe such patterns, if possible. Such knowledge could enable assessment and prescription to be conducted systematically, rather than individualistically. Both Healey and Jensen (op. cit.) focused on interactions between population density, exploitation, growth and reproductive capacity in order to assess the degree of exploitation which whitefish stocks can tolerate without a diminished productivity or persistence. Recapitulating and extending these studies, primarilly by developing and contrasting life tables for three differentially exploited stocks, was an objective of this study.

A second objective was to contrast and compare the "life program" (Gerking 1959) of whitefish with respect to two factors: chronological age and body size. The majority of the modes of analysis and synthesis used to evaluate population dynamics of fish are age-structured in nature, yet the majority of investigations into the topic have concluded that chronological age per se is an irrelevant determinant of basic biological processes. In this study, population traits of several whitefish stocks were compared with the objective of determining if any traits were fixed or constant in the life program, either by age or by size. If certain characteristics during the life history are invariant with time or location, comparisons amongst populations can be made relative to an equivalent point of reference. Secondly, the enormous range of plasticity in growth amongst different stocks enabled a contrast of traits of whitefish of equal age but unequal size versus traits of fish of equal size but

unequal age. The objective of such comparisons was to determine whether life history functions such as growth, sexual maturity, fecundity and life expectancy are determined by chronological age, size or some other factor.

Sufficient information from this and other Great Lakes whitefish studies were available that a systematic analysis of differences was possible. One type of comparison was between dynamics of three stocks in northeastern Lake Michigan at East Traverse, Leland and the North Shore which represented a range of commercial exploitation from none to moderate to intense respectively. A second contrast was between current North Shore whitefish dynamics and previous assessments of this stock dating back to 1932. Presumably, these fish shared a common genetic heritage, enabling a distinction of nature versus nurture effects. Thirdly, comparisons of male versus female whitefish were made because the sexes presumably share the same environment, therefore sexual dimorphism can be symptomatic of heritable differences.

The range and level of replication of these comparisons was extended by including previous studies of Great Lakes whitefish dynamics which included estimates of growth and sexual maturity. The range of difference was extended further by comparing whitefish traits and those of related Coregonid fishes, including bloater chubs _coregonus_ _hoyi_, ciscoes (or lake herring) _Coregonus_ _artedi_, and menominee _Prosopium cylindraceum_. Sources of data were numerous, and other studies will be refered to hereafter by time and location to avoid repetitious citation. Samples collected during this study were combined with those from Scheerer (1982) to provide observations of the Leland and North Shore stocks for 1980-84, more limited estimates of Beaver Island and Cross Village dynamics for 1981-84 and East Traverse characteristics for 1983-84. Historical trends in the North Shore stocks were evaluated with studies by Caraway (1951), Piehler (1967) and Brown (1968), supplemented by data from the Michigan Department of Natural Resources (MDNR) which is either unpublished or in Rybicki (1980) or Patriarche (1977). Other Great Lakes whitefish studies considered were from the Thunder Bay - Alpena area of Lake Huron (Van Oosten 1938), the Munising Bay (Edsall 1961) and Bayfield (Dryer 1963) areas of Lake Superior, and Green Bay in Lake Michigan (Mraz 1964). Other Coregonid studies included bloater chubs in Lakes Superior (Dryer and Beil 1964) and Michigan (Brown 1970), ciscoes from Birch Lake (Clady 1967) and Lake Superior (MDNR 1974) and Lake Michigan menominee (Mraz 1964, Armstrong et al 1977).

METHODS

A mark-recapture program with tagged whitefish began in the North Shore and Leland areas in November 1980 wih an objective of identifying home range areas and estimating abundance and mortality statistics. Whitefish from 2 trap-nets per area were tagged at the beginning of November in 1980 through 1982 (Table 6), which allowed tagged fish a full winter to disperse from the tagging site. Tags from recaptured fish were saved by the fishermen until they were collected during sampling trips. Information on the specific location and date of recapture was provided by most but not all fishermen. Tagging was discontinued after 1982, but recaptures were tabulated through 1984.

Biomass estimates were made using values of reported catch by known cooperating fishermen from November to November each year. Annual catch was corrected for recruitment during the season by subtracting an estimate of the fraction of the catch which grew to legal size (432 mm) during the year. Recaptures were corrected for tag loss at monthly intervals using Scheerer's estimated instantaneous rate of tag loss of 0.093. The biomass estimate equalled the number of marked fish times catch divided by recaptures. Biomass was converted to numerical abundance by dividing by the mean weight of the sampled catch during that year. Confidence intervals were estimated from standard Poisson distribution methods (Ricker 1975).

Table 6. Whitefish tagging dates and locations, 1980-84.

DATE	NUMBER TAGGED	TAGGING GRID
	North Shore	
11-4-1980	1683	116
11-3-1981	1024	117
11-5-1982	722	117
*11-16-1984	202	116
	3631	
	Leland	
11-7-1980	415	714
11-2-1981	117	812
11-3-1982	106	812
	638	
	Beaver Island	
**11-5-1980	19	316
	Grand Traverse Bay	
***6-14-1981	163	615

*Tagged from gill-nets; not used for abundance or mortality estimates.

**No recaptures reported.

***Sublegal (< 483 mm) fish from purse seine.

Age structure and survivorship:

Annual survival rates (S) were estimated from tagging recaptures as the ratio of the percentage of marked fish recaptured in their second year at large divided by the percentage recaptured in their first year at large. Percentages were adjusted for tag loss. Exploitation rates (E) were estimated as the percentage of recaptures in the first year at large, adjusted for non-cooperating fishermen by multiplying recaptures by the ratio of total catch to cooperator's catch. Instantaneous rates of total mortality (Z), fishing mortality (F) and non-fishing mortality (M) were estimated from these annual percentages. Catch curve estimates of total mortality (Robson and Chapman 1961) were used to supplement tagging estimates, and to estimate mortality in areas where tagging was not used.

Sampling and age determination:

Sampling of the commercial catch provided information about the size and age structure of the catchable population, maturation and sexual characteristics, and scales for growth analysis. Total length and weight to the nearest 10g were measured on all fish, and a patch of scales was taken from between the center of the dorsal fin and the lateral line. Fish were examined for sex and maturity whenever possible, but whitefish are usually sold in the round (uneviscerated) and this information was often unavailable.

Net-run samples, which included sublegal fish, were collected on some occasions. Trawls operated by the MDNR in the Leland and North Shore area and the U.S. Fish and Wildlife Service in the North Shore area supplemented pre-recruit sampling in these areas. Trawling was the principal method used to collect fish in the East East Traverse area, but some information on length at maturity was obtained from the recently opened trap-net fishery in October 1985.

Three scales from each fish were selected for reading on the basis of symmetry and non-regeneration. Scales were cleaned in an ultrasonic cleaner to remove skin and slime and read at 22X magnification on a microfiche reader. Annuli were identified principally by cutting-over of the circuli. Scale radius from the focus to the center of the anterior margin was measured on three scales, and annular radii were measured along the same line on at least one scale. Replicate scale age determinations were in agreement for at least 67 percent and at best 92 percent of the individuals. Older fish were aged less reliably, therefore specific ages greater than 10 were not assigned. All age assignments used were my own in order to maintain a consistent aging standard.

Growth:

Estimates of mean length at age of capture were biased by selectivity of the trap-net gear, therefore growth was estimated from back calculated lengths. The relationship between scale radii and fish length was fit by regressing mean scale radii for fish in consecutive 10mm length intervals against length. This procedure was more accurate than other common procedures (Smale and Taylor 1987).

Fish were grouped by stock, year, year-class and sex, and standard deviations and means were calculated for annular radii at each age, total scale radii, and length at capture for each group. Annular lengths were calculated from the standard intercept-corrected proportional back calculation formula (Carlander 1981), using group means rather than back calculating for individual fish. Since the coefficients of variance (C.V.) for scale radii at any length were constant, the standard deviations of annular scale radii were multiplied by the ratio of the C.V. of scale radii at length divided by the C.V. of lengths at a given scale radius in order to convert standard deviations of scale size to standard deviations in length.

Annual increments in length were plotted against both age and back calculated length of the fish in order to compare growth on a per age and per size basis. These plots as well as standard Walford plots (Bagenal and Tesch 1978) were used to assess the growth potential, or maximum attainable length, of different groups. Tests for growth compensation (increased growth of initially small fish later in life) subdivided groups into the smallest and largest thirds at ages 1 or 2, then compared average lenght increments of these groups at succesively older ages.

Initial estimates of the rate of growth in weight with respect to growth in length were confounded by non-homogenous variance, sample truncation and unbalanced size groups. Therefore, length-weight relationships were assessed by

averaging log transformed weights at consecutive 10mm increments in length. Running regressions with 50mm length spans of $\log_e$ mean weight versus length tested for changes in slope and intercept amongst different size classes of fish. Weights at length were converted to weights at age for each group considered, then weights at age were used to calculate instantaneous growth rates.

Maturity and fecundity:

Maturity was determined by examination of the gonads at the time of sampling. Since whitefish are not fractional spawners, determination was usually unambiguous, although some males were found with partially developed gonads and were judged to be in the process of maturing. Maturity and sex composition data were collected from North Shore fish throughout the season in order to make between-season comparisons. Other populations were usually examined in late summer and early fall.

Fecundity was estimated from dry-weight proportions, using whitefish ovaries collected in late October, approximately 2 weeks prior to spawning. Ovaries were rinsed gently and most extraneous ovarian tissue was separated out. A subsample of 200 eggs was counted and both the sample and subsample dried to constant weight at 95 degrees C. Both were then weighed and the numbers of eggs were estimated by proportional weights. Replicate subsamples from several indivduals were counted in order to assess reliability of the measurements.

Life tables:

Estimates of growth, maturation, survival and growth were assembled into life tables in order to estimate the production of eggs per average female whitefish per lifetime (R_O) for the North Shore (1967 and current), Leland, and East Traverse stocks. Estimates of means and standard deviations for age-specific female lengths were converted to frequency distributions using tables of the Z-distribution. From these distributions, the percentage of recruited fish (>430mm) at the time of annulus formation was calculated for each age. This percentage was multiplied by the estimate for fishing mortality, then averaged for successive ages in order to estimate age-specific fishing mortality. A baseline natural mortality rate of $M = 0.50$ was used for juvenile fish in all stocks, however this rate was increased by an annually compounded rate of 10 percent/year times the percentage of mature females to simulate spawning mortality. Age-specific fishing and non-fishing rates were added and the estimated numbers surviving from an initial cohort of 1000 age zero females was calculated for each age and stock.

Age-specific length frequency distributions were also used in conjunction with length schedules of female maturity to estimate the percentage of mature females at age. This estimate coincided with directly determined age schedules of maturation except for age groups when most females were unrecruited at the time of maturation. The mean weight of mature females at age was determined from fall samples. The regression of fecundity on weight for each stock was used to convert mean weights to fecundity. North Shore fecundity on weight relationships were used for the East Traverse stock because East Traverse fecundities were unavailable. Age-specific egg production was estimated by multiplying the number of mature survivors by the average fecundity at age. Reproductive output equalled the sum of egg production from all ages.

Reproductive output estimates were used for three purposes: first, a direct comparison amongst stocks of varying character; second, for sensitivity analysis, in which individual components of the estimates were varied and their impact assessed and third; stability analysis, in which the impact of annual variation in early life survival was simulated and assessed.

RESULTS

Abundance and Biomass Estimates:

Estimated abundance and biomass for the Leland and North Shore stocks declined between November 1980 and November 1982 (Table 7). The decrease in biomass in the North Shore area represented a loss of 60 percent of the 1980 value while the Leland stock declined by 55 percent. The declining abundances were reflected in decreasing catch in both areas (Figure 3). North Shore biomass estimates averaged 6.4 times the Leland values.

The relationship between biomass estimates and trap net catch per effort (CPE) in the fishing season following tagging in WFM-03 was linear (Figure 9) with an intercept at the origin. Effects such as gear saturation or capture efficiency which varied with abundance were not detectable at this level of precision. Trap-net CPE values in District MM-3 in 1981 were a record high for the period since 1948 when catch records by District began, thus the study period included high and varying levels of abundance.

Leland CPE per kg of catchable fish was higher in all 3 years, indicating that the lower Leland catch was not a product of a less efficient fishery. Confidence intervals on Leland abundance estimates averaged 57 percent of the estimates while North Shore estimates were precise within 23 percent. The smaller number of tagged fish in a similar sized area accounted for the lower precision of Leland estimates.

Table 7. North Shore and Leland estimates of abundance and biomass from November tagging, 1980-82.

YEAR	ABUNDANCE (Million fish)	BIOMASS (Million kg)
	NORTH SHORE	
1980	1.9 (1.7 - 2.1)	1.6 (1.4 - 1.8)
1981	1.2 (1.1 - 1.4)	1.2 (1.1 - 1.3)
1982	0.78 (0.70 - 0.88)	0.77 (0.69 - 0.86)
	LELAND	
1980	0.29 (0.22 - 0.37)	0.36 (0.28 - 0.46)
1981	0.14 (0.11 - 0.19)	0.21 (0.17 - 0.27)
1982	0.13 (0.10 - 0.18)	0.20 (0.15 - 0.26)

(0.95 Confidence Intervals)

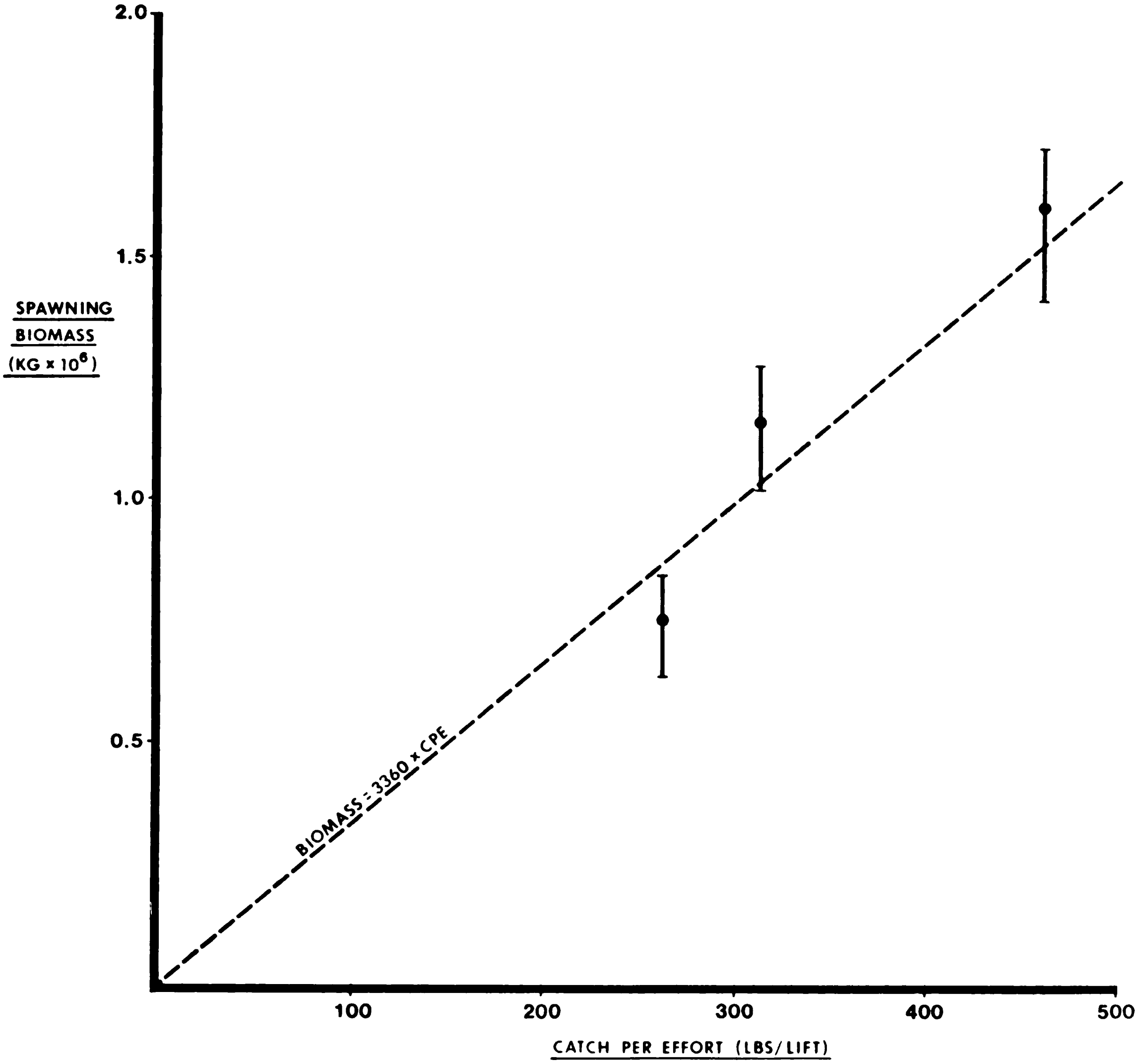

Figure 9. Trap net catch per effort in WFM-03 for 1981, 1982 and 1983 in relation to biomass estimates from tagging conducted in Novembers 1980-82.

Abundance at Leland in 1980 was probably overestimated. Whitefish were tagged north of Leland in 1980 but fishing effort during 1981 was concentrated south of Leland. Whitefish tagged south of Leland, near Empire, in 1981 and 1982 were not homogenized with the 1980 group as recapture rates per pound of catch differed from the two groups between northern and southern grids (Chi-square test, $P < 0.05$).

Efforts to trace the dispersal of North Shore whitefish by grid were discontinued after 1982 because of differences in the reliability of reported recapture locations amongst different fishermen. Ninety-four percent of the whitefish were recaptured in WFM-03, with most of the remainder recaptured to the east near Mackinac City or the west near the Garden Peninsula. Only one tagged North Shore fish in 4 years ventured south of Gray's Reef.

Mortality Estimates from Tag Returns:

Estimates of total, fishing and non-fishing mortality rates based on tag returns from recruited fish (Table 8) indicated that North Shore mortality and fishing rates exceeded Leland estimates. In comparison to other Lake Michigan tag return mortality estimates (Ebener and Copes 1985), North Shore total and fishing mortality rates ($Z = 1.49$ and $F = 0.87$) were slightly lower than Big Bay DeNoc ($Z = 1.84$ and $F = 1.44$). Leland rates ($Z = 0.80$ and $F = 0.42$) were both lower than rates in the North/Moonlight Bay stock ($Z = 1.04$ and $F = 0.53$). In comparison to the mean total

Table 8. Instantaneous and annual mortality estimates from 1981-84 tag returns.

		NORTH SHORE	LELAND
Instantaneous Total Mortality	Z	1.49 (1.39-1.56)	0.80 (0.73-0.89)
Instantaneous Fishing Mortality	F	0.87	0.42
Instantaneous Natural Mortality	M	0.62	0.38
Fraction of Total Due to Fishing	F/Z	0.59	0.53
Annual Percent Total Mortality	A	77% (75-79%)	55% (52-59%)
Annual Percent Exploitation	E	45% (43-47%)	29% (24-33%)

(0.95 Confidence Intervals)

mortality rate estimated for exploited stocks of Z = 1.02 (Healey 1975), North Shore mortality was high and Leland moderate.

Experimenting with different procedures for estimating mortality (Seber 1973, Ricker 1975, Youngs and Robson 1978), and for treating year vs. years at large effects, found little difference due to method and none that was significant. Recapture rates per pound of reported catch did not vary between years in either area, nor were there differences amongst cooperating fishermen. Precision of the estimates was limited principally by the number of tagged fish rather than by method or annual variation in recapture efficiency. Effects of non-homogenous dispersal patterns of tagged fish were detectable at Leland but not in North Shore results. Dispersing tagging effort over a broader area could be useful in obtaining more representative results.

Size of the fish at tagging was an influence on subsequent return rates, but the pattern of change with size differed in the two stocks. First-year at large percentage returns for North Shore whitefish increased with size at tagging from 21 percent (cooperating fishermen only) for legal fish under 480mm to 32 percent for fish over 520mm. Annual mortality increased from 72 percent to 91 percent for the two size groups. This increase in exploitation and mortality with size was probably due to increased vulnerability to the trap-net and gill-net gear for larger fish.

At Leland, return rates and annual mortality actually decreased with size at tagging. First-year returns decreased from 35 to 28 to 19 percent for size groups $\leq$ 480mm, 490-540mm and $\geq$ 550mm at tagging. Annual mortality for the same groups decreased from 82 to 70 to 55 percent per year. This effect could be due to larger Leland whitefish being out of range of the fishery for much of the year. This explanation is consistent with the seasonal changes in the size composition of the catch discussed in chapter 1.

Age Structure:

Age compositions of the samples by percent averaged over the years of sampling are listed in Table 9, with more detailed descriptions in the Appendix. Of the commercially exploited stocks, the broadest age structure was found at Leland, with ages 7-10+ commonly present. Beaver Island age composition ranked second in breadth, and North Shore and Cross Village samples were similarly narrow in age distributions with over 90 percent of the catch from the three youngest ages. Trawl-caught East Traverse samples were not comparable to the trap-net samples, but older fish were common in comparison to exploited areas.

Seasonal variation was present in the Leland age composition, with ages 7 and older comprising 32 percent of the spring samples but only 10 percent of the fall samples. No distinguishable seasonal differences in North Shore age structure were found.

A feature of the age compositions in all areas was variability in relative frequencies of the different age

Table 9. Age structure (percent) of the sampled study populations, averaged over seasons from 1980-84 with minimum and maximum percentages in parentheses.

AGE:	LELAND	NORTH SHORE	BEAVER ISLAND	CROSS VILLAGE	EAST TRAVERSE
0:	—	—	—	—	—
1:	—	—	—	—	22.5 (6-37)
2:	—	—	—	—	37.2 (33-41)
3:	8.8 (0-57)	13.8 (0-78)	—	—	19.8 (13-27)
4:	30.6 (7-67)	50.2 (17-84)	24.1 (9-68)	36.2 (20-52)	5.8 (2-9)
5:	24.1 (5-53)	25.9 (1-80)	43.8 (19-83)	51.8 (46-58)	4.1 (3-6)
6:	16.0 (0-28)	6.9 (0-22)	19.6 (6-40)	10.0 (2-18)	2.6 (0-6)
7:	10.1 (2-25)	1.9 (0-6)	8.4 (0-21)	2.1 (0-4)	3.1 (1-5)
8:	2.6 (0-10)	0.7 (0-3)	3.0 (0-7)	0	2.6 (2-5)
9:	2.3 (0-14)	0	0.3 (0-2)	0	0.8 (0-3)
10:	1.8 (0-7)	0	0.4 (0-1)	0	0.8 (0-1)
>10:	3.7 (0-11)	0	0	0	0.6 (0-1)
N:	1667	2670	583	207	871

Sampling Periods: Leland: Fall 1980-Fall 1984
NorthShore:Fall 1980-Fall1984
Beaver Island: Spr. & Summ. 1981-1983
Cross Village: Spr. & Summ. 1982-1983
East Traverse: Spr. 1983-1984, Summ. 1984

groups, indicating a dynamic cohort structure. Over the years of the study, the average range of variation in frequencies at age equalled 197 percent of the average frequency, with no detectable differences in variation amongst age groups or populations. A prominent feature of the age composition of the Leland and North Shore catch (Figures 10 and 11) was a strong 1977 year-class which was followed throughout the study. This cohort was more frequent than either preceding or following cohorts at the same age and was dominant in the catch at age 4 when both fisheries achieved record harvests. Although followed for a shorter time-span, the 1977 year-class also was dominant in Beaver Island and Cross Village samples. East Traverse samples were not analyzed with respect to cohort strength. Since population abundance also changed during the study, differences in relative frequencies of cohorts underestimated differences in absolute frequency.

Available records of the North Shore catch indicated a greater dynamic range in age composition during the past 50 years than was encountered in this study. Circa 1930 and circa 1950, the North Shore age structure (Table 10) was dominated by age 3, 4 and 5; with age 4 the typical modal age, as it was during this study. During 1960-65, age 2 was the modal age, with age 3 and older fish relatively scarce. Whitefish catch during 1930, 1950 and this study was at average to well above average levels, while yield and abundance circa 1960 were extremely low. A 3-year running mean of the mean age of the catch (Figure 12) indicated a

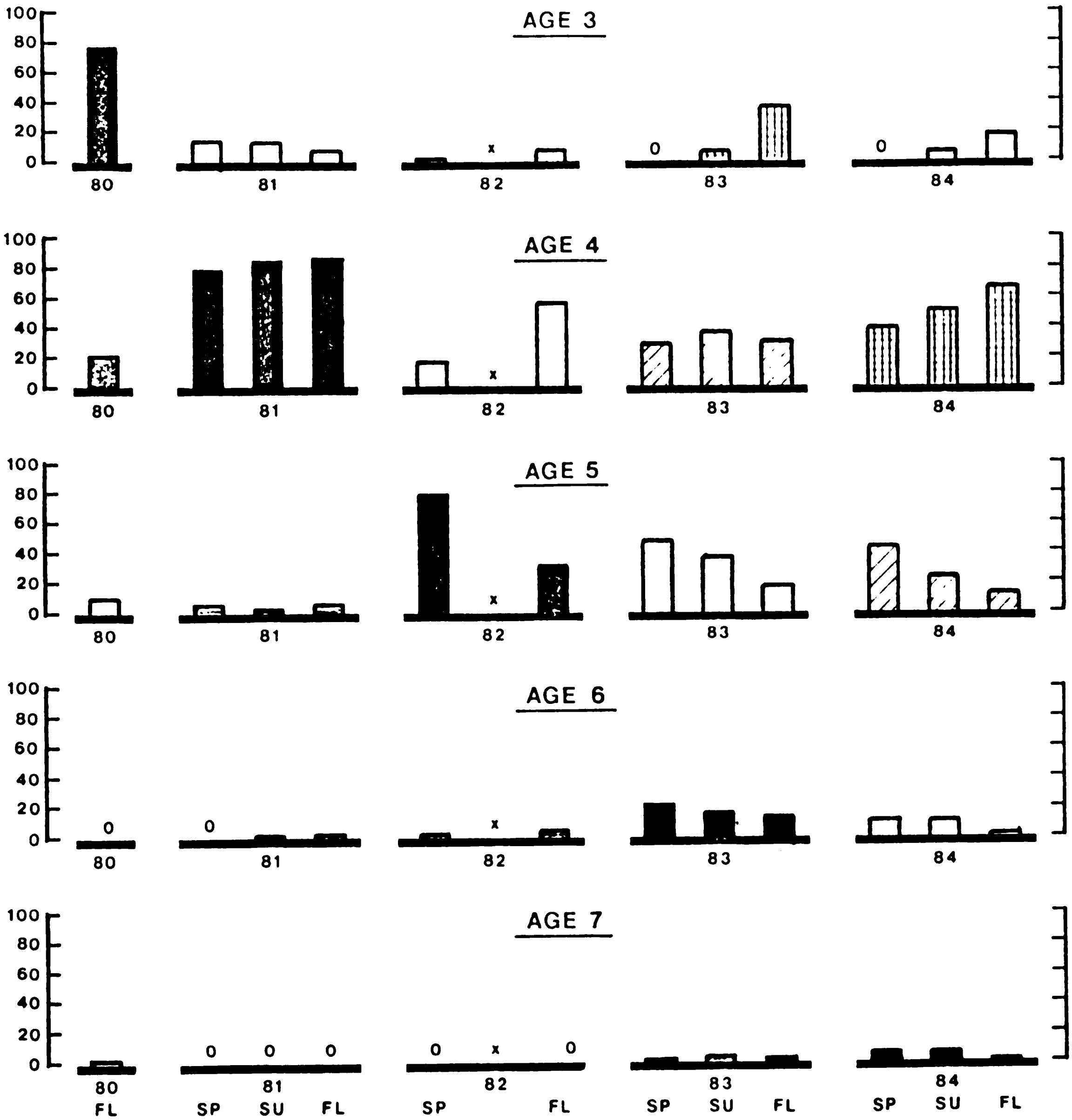

Figure 10. Percentages of the sampled North Shore catch in the 5 most common age classes by year from 1980-84.

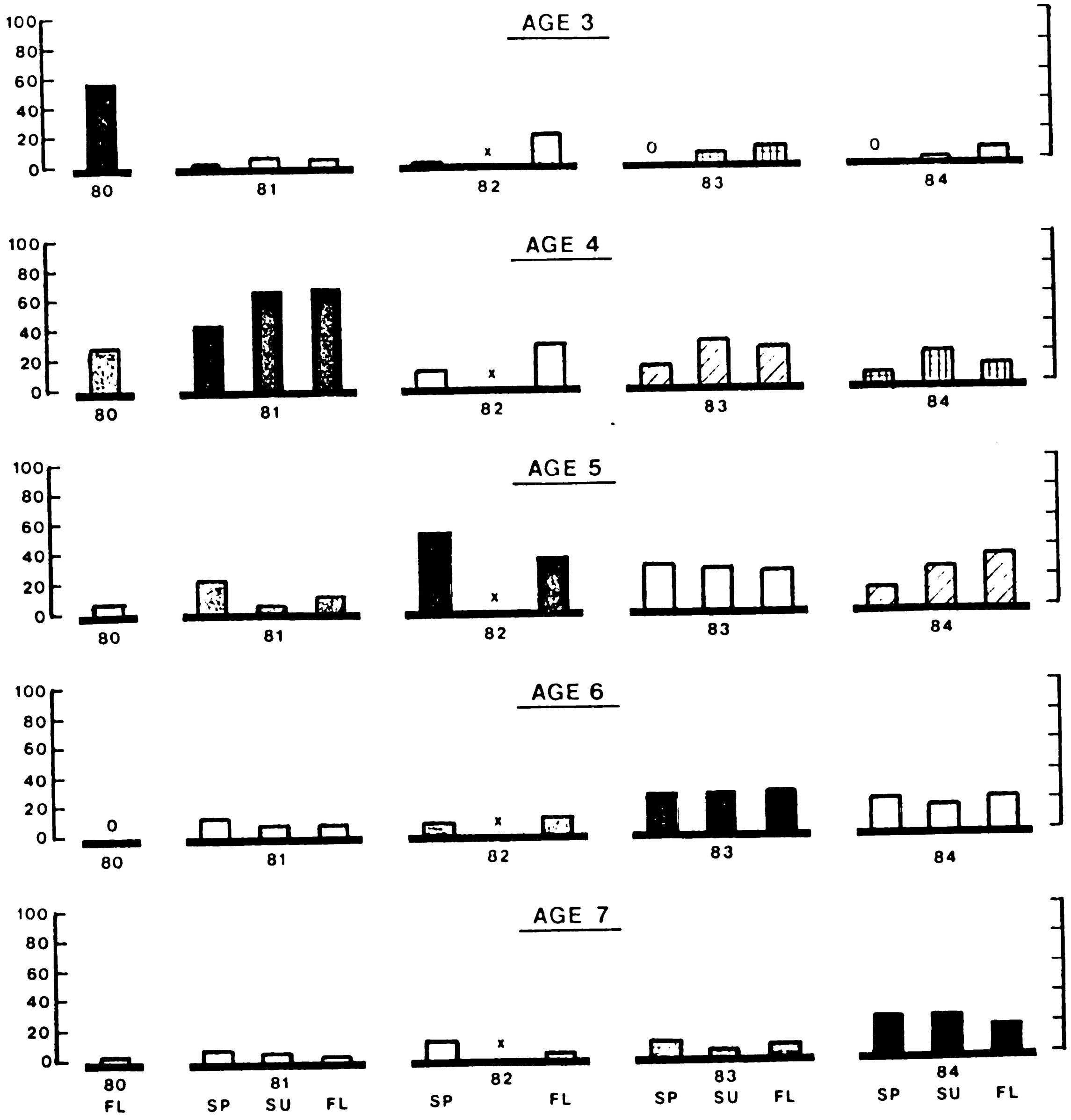

Figure 11. Percentages of the sampled Leland catch in the 5 most common age classes by year from 1980-84.

Table 10. Age structure estimates in percent from North Shore area samples, 1929 - 1979.

	AGE								
YEAR	**2**	**3**	**4**	**5**	**6**	**7**	**N**	**GEAR**	**SOURCE**
1929	0	20	70	7	3	0	30	GN	A
1932	1	8	77	5	7	2	674	TN	A
1948	0	38	48	12	2	0	102	PN	B
1950	0	60	28	9	0	2	45	PN	B
1950	0	38	14	10	14	24	21	GN	A
1960	84	14	1	1	0	0	151	PN	A
61	82	13	2	0	0	0	153	PN	A
62	55	40	4	0	0	0	109	PN	A
1965	99	1	0	0	0	0	77	TN,GN	C
66	11	84	5	0	0	0	637	TN	C
67	21	32	43	3	0	0	937	TN	A
68	9	74	8	8	8	1	611	GN	D
69	25	58	16	1	0	0	96	GN	D
70	44	54	2	0	0	0	169	TN	D
71	8	81	10	1	0	0	296	TN	D
72	28	68	2	1	0	0	141	TN	D
73	1	65	30	1	1	1	141	TN	D
74	0	15	69	8	8	0	13	TN	D
75	2	92	4	1	1	1	133	TN	D
76	2	83	14	1	0	0	184	TN	D
77	4	36	36	20	1	2	124	TN	D
78	0	44	36	12	7	0	586	TN	D
79	2	63	31	4	1	0	389	TN	D

Sources:
A: Brown, 1968
B: Caraway, 1951
C: Piehler, 1967
D: MDNR Data, some of which is in Rybicki (1980) or Patriarche (1977).

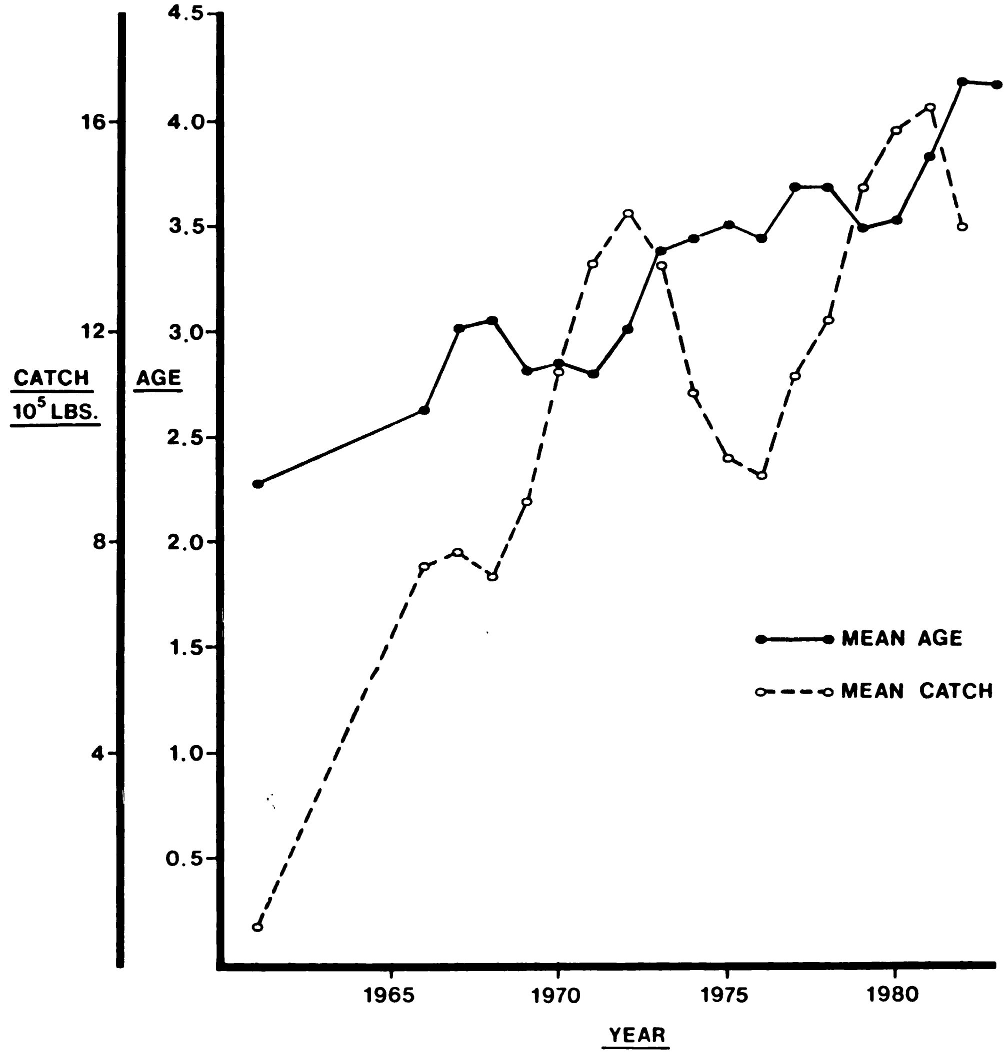

Figure 12. Three-year running means of District MM-3 whitefish catch and age of the sampled catch from 1961-84.

trend of increasing mean age from 2.3 years during 1960 to 4.2 years at the time of this study. This trend was paralleled by an increase in the 3-year running mean of District MM-3 catch. The length composition of the catch in samples from 1960-67 was not different than current distributions, therefore whitefish tended to become older, more abundant but not larger during the past 25 years.

Some caution is necessary in interpreting past records of the North Shore age composition because some samples were small, infrequent, from different gears or from areas peripheral to the North Shore stock. But some of the early samples were very reliable, and together with data from the other study stocks, it was apparent that age structures of northeastern Lake Michigan stocks were neither stationary nor stable. Both long term trends associated with changes in abundance and short term fluctuations due to year-class variation were observed.

A trend was noted for female whitefish to be commonly larger and older than males from the same samples. The possibility of a sexual difference in age structure and therefore life expectancy was tested for by treating male and female fish as independent samples and calculating age distributions for each. In contrast to the more common procedure of testing sex ratios at age, comparisons of age distributions by sex are not sensitive to the fluctuations in sex ratios common to many Coregonid populations.

Age distributions for Leland and East Traverse females (Table 11) were significantly older than for males from the same samples. There was no sexual difference in the spring North Shore age structure, but females were again older than males in September/October samples. The possibility that fall samples contained a disproportionate number of older, mature females is unlikely because immature females were common in these same samples.

Standardizing age distributions of the spring and fall samples to the same chronological age, rather than calendar age, by subtracting one year from the age of the spring fish (Figure 13) provided another explanation. Age distributions of male whitefish did not change from fall to the following spring, while median female age decreased by approximately a full year. This effect would occur if overwinter mortality of males was equal for all age groups, but female mortality was selective of older fish.

A sexual difference in age structure was common amongst populations of whitefish and other Coregonids. Out of 9 whitefish populations and 5 of other Coregonids, median female age exceeded that of males by an average of 0.35 years, with an older female median in 12 of the 14 comparisons and an equal median in 2. The 95th percentile of female age distributions averaged 0.46 years older than for males with 2 populations in which the male 95th percentile exceeded that of females slightly. Sex ratios in these studies ranged from over 80 percent male to over 80 percent female, and the

Table 11. Cumulative percent frequency at age comparisons for males and female whitefish in three study populations.

	LELAND				EAST TRAVERSE			
AGE	N	CUMULAT. PERCENT	N	CUMULAT. PERCENT	N	CUMULAT. PERCENT	N	CUMULAT. PERCENT
	MALES		FEMALES		MALES		FEMALES	
3	39	16	51	23	--	--	--	--
4	108	62	39	44	--	--	--	--
5	52	83	60	71	25	33	16	20
6	25	94	44	90	21	61	18	43
7	10	98	20	99	17	84	20	68
8	3	99	2	100	5	91	14	86
9	1	100	0	100	7	100	5	92
10	0	100	0	100	0	100	6	100

LELAND: -- $D = 0.173$ --
$P < 0.01$

EAST TRAVERSE: -- $D = 0.183$ --
$P < 0.05$

	NORTH SHORE - SPRING				NORTH SHORE - FALL			
AGE	N	CUMULAT. PERCENT	N	CUMULAT. PERCENT	N	CUMULAT. PERCENT	N	CUMULAT. PERCENT
	MALES		FEMALES		MALES		FEMALES	
3	13	9	17	9	73	38	30	18
4	68	54	94	61	85	82	84	67
5	39	80	49	88	18	92	36	88
6	17	91	13	96	9	96	13	96
7	7	96	7	99	4	98	6	99
8	5	99	0	99	3	100	1	100

NORTH SHORE - SPRING: -- $D = 0.084$ --
(Not signif.)

NORTH SHORE - FALL: -- $D = 0.204$ --
$P < 0.01$

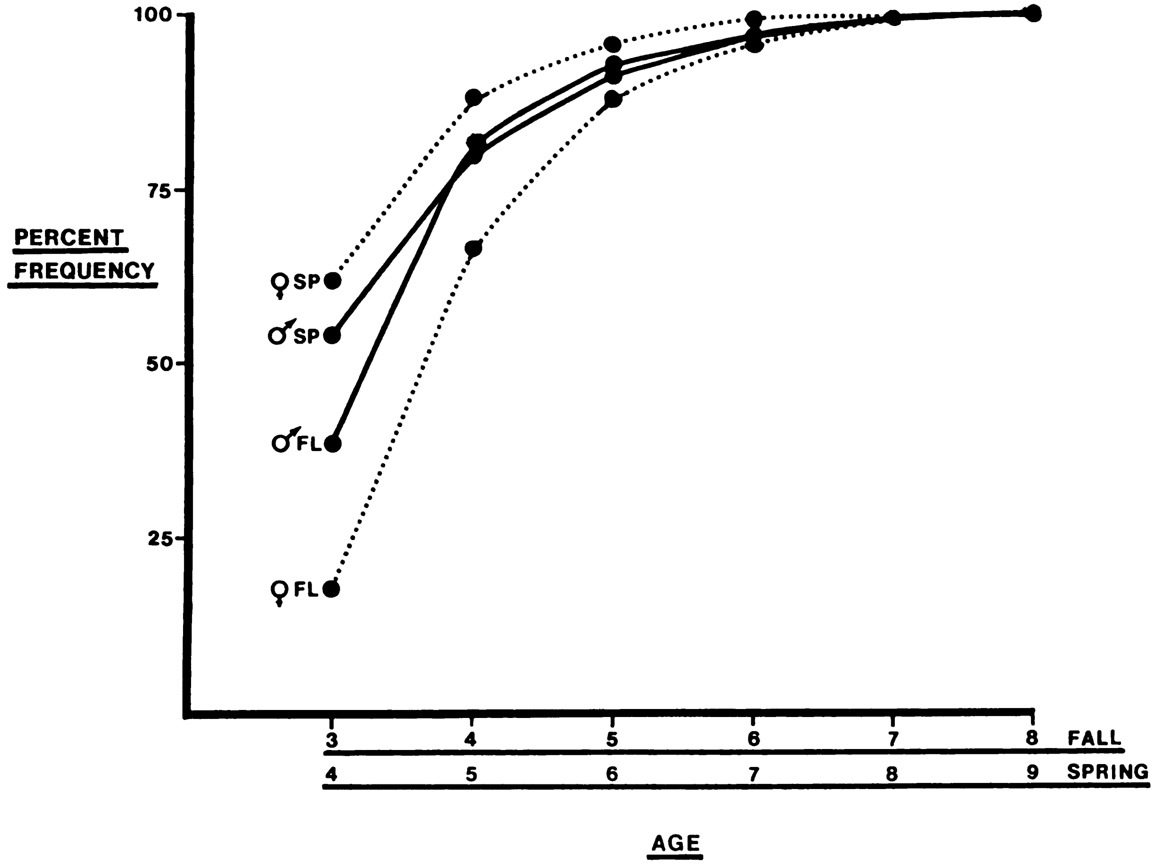

Figure 13. North Shore cumulative percent age composition for male and female whitefish, with a one year adjustment for chronological age for spring versus fall comparisons.

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and the difference in age distributions occurred regardless of sex ratios. Differences were also distinct in both unexploited stocks (East Traverse and Munising Bay) and it is unlikely this effect was due to a sexual difference in exploitation.

Year Class Indices:

Trap net catch per effort multiplied by the percent frequency of four year old fish in the same year was used as an index of year-class strength for the 1977-80 year classes. By this index, the 1977 North Shore year-class was slightly more than 3 times as abundant as the second largest 1980 year class and 4.6 times as large as the 1979 year class at the same age (Table 12). At Leland, each year class following the 1977 was successively weaker. The 1980 year class was moderate at the North Shore but poor at Leland, and was the only one of the four out of phase between the two areas. The range of difference in cohort strength exceeded 10-fold at Leland.

Age Structure Mortality Estimates:

Total mortality rates estimated from regression analysis and ratios of the age composition tended to be lower than estimates from tag returns. Unlike tag return estimates also, these rates were sensitive to the calculation procedures used. Regression slopes of the $\log_e$ percent frequency at age versus age (Table 13) pooled by season and averaged by percent over all years of record yielded instantaneous mortality estimates of $Z = 1.21$ for North Shore fish and $Z = 0.47$

Table 12. Relative abundance index (trap-net catch per effort times yearly average percent frequency at age 4) for the 1977-80 year-classes, North Shore and Leland.

Year Class	North Shore	Leland
1977:	386	140
1978:	102	33
1979:	84	23
1980:	123	12

for Leland, compared to 1.49 and 0.80 respectively from tag returns. Because of the seasonal shifts and strong dominance by the 1977 cohort, analyzing the accuracy of Leland age-frequency mortality estimates was considered pointless.

Accuracy of North Shore estimates was affected by two factors: variable year-class strength, and the decreasing precision of estimates of frequency with increased age. The effect of cohort variation was examined by successively deleting one, two then three year's data from the total sample. Annual mortality estimates from a single year varied by a range of 16 percent; a two year span reduced the range to 11 percent and three years to 6 percent.

In regression analysis of age-frequency data, the relatively rare older ages are weighted equally with the more common younger fish, even though their frequency estimates are less precise. In this regard, averages weighted by the number of fish per age of the ratios of successive $\log_e$frequency estimates would be more reliable. The weighted mean ratio estimate of North Shore mortality, $Z = 1.39$, was more in line with the tag return estimate. As discussed in chapter 1, the odds of including the older, larger fish in the population in any given sample were not fully random because of heterogeneity amongst samples. The oldest and largest North Shore fish found were from relatively few samples, and insufficiently homogenized samples would increase the risk of overlooking these scarcer groups. Some procedures are inordinately sensitive to small changes in

Table 13. Estimates of total annual (A) and instantaneous (Z) mortality rates from catch curves using 1980-84 agestructure averages forLeland, North Shore, Beaver Island, Cross Village and East Traverse whitefish.

AREA	AGES	INST. TOTAL (Z)	ANNUAL PERCENT (A)	r^2	YEARS
LELAND					
Fall	4-10	0.75	53	.978	1980-84
Summer	5-10	0.61	46	.859	1981-84
Spring	5-10	0.47	37	.904	1981-84
All seasons	5-10	0.58	44	.930	1980-84
NORTH SHORE					
All seasons	5-8	1.21	70	.996	1980-84
BEAVER ISLAND					
Spring & summer	5-10	1.06	65	.940	1981-84
CROSS VILLAGE					
Spring & summer	5-7	1.60	80	.999	1982-83
EAST TRAVERSE					
Spring & summer	3-12	0.44	35	.936	1983-84
	6-12	0.46	37	.905	1983-84
	2-3	0.50	39	--	1983-85

frequency of older ages and are most influenced by sampling design. These samples were insufficient for analyzing more subtle effects inherent in age structure analysis such as non-normal distributions of frequencies or unequal variance (Fournier and Archibald 1982) but the large influence of cohort strength on accuracy renders these considerations moot.

Tag returns and estimates of mortality from them varied with the size, and therefore age, of the fish in both stocks. The assumption of constant survivorship required for most age-frequency analyses of survivorship is not likely to be correct, and this factor should also be considered in interpreting results.

In areas where no tagging was conducted, Cross Village mortality ($Z = 1.60$) exceeded that in the Beaver Island ($Z = 1.06$) area (Figure 14). Both estimates were probably biased toward the high side by the inclusion of the strong 1977 cohort in only the 3 youngest age groups. East Traverse mortality was low ($Z = 0.44 - 0.50$) and the estimate was similar to that from an unexploited stock in the West Arm of the Bay of $Z = 0.42$ by Rybicki and Keller (1977). The estimateof juvenile mortality for ages 2 - 3 was based on average ratios from 1983 through 1985 data, while other ages were estimated from regressions with 1983 and 1984 samples.

Current North Shore catch curve plots were not as steep as those from early and mid-1960's data (Figure 15), but the most striking difference between the past and present catch

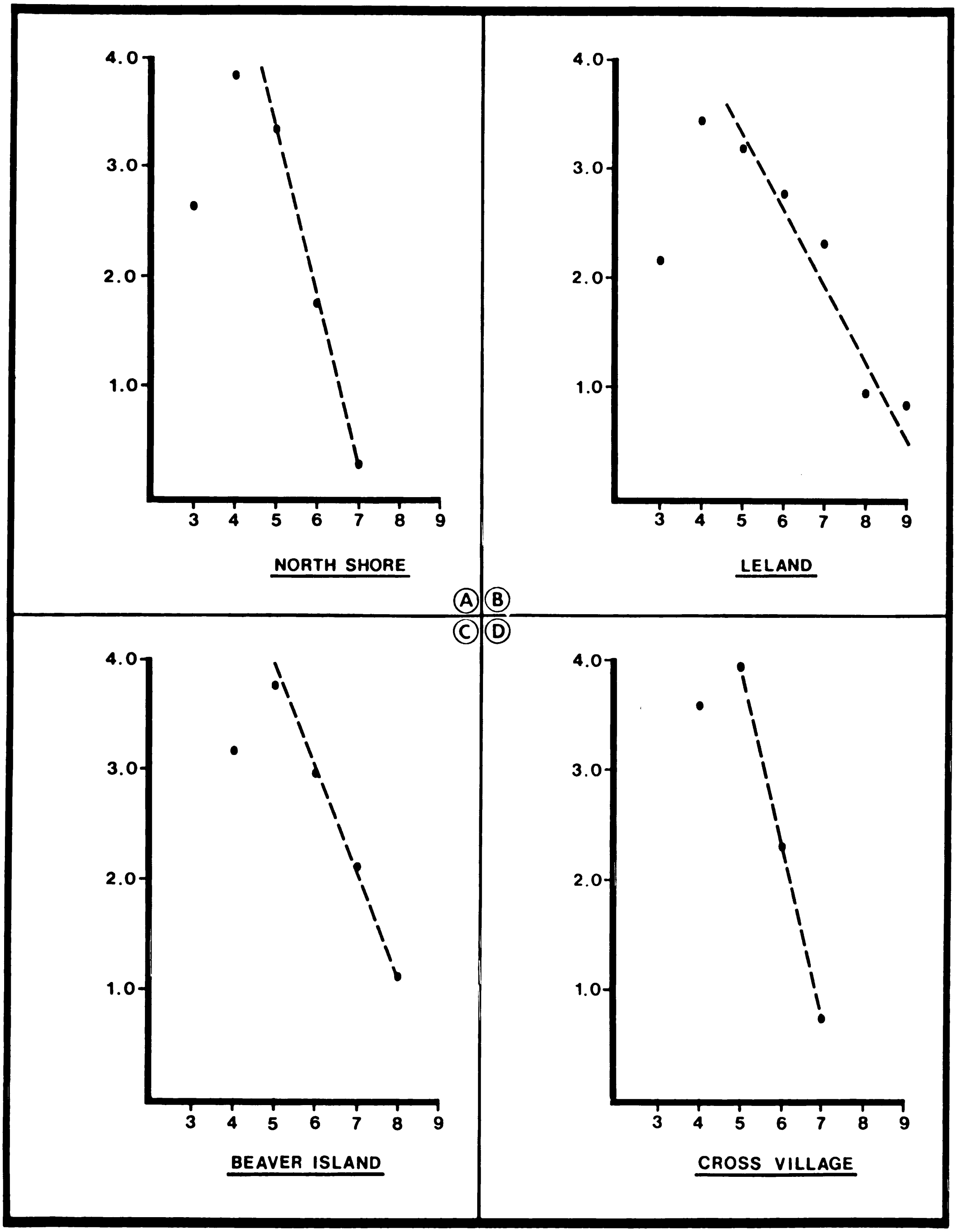

Figure 14. Catch curve plots ($\log_e$ percent frequency versus age) for: A) North Shore; B) Leland; C) Beaver Island and; D) Cross Village using pooled age structure data.

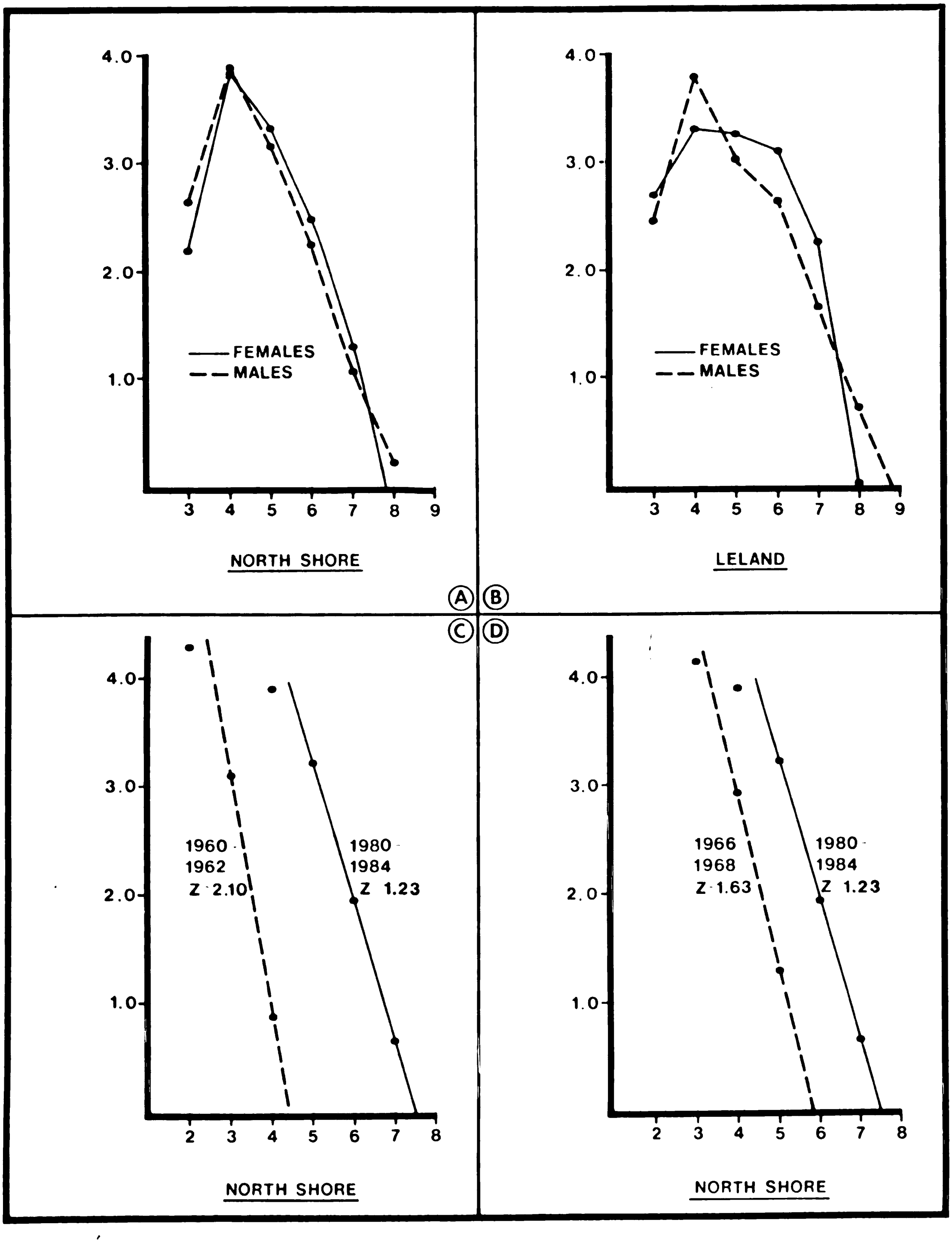

Figure 15. Comparisons of catch curves for (A) and (B): male versus female North Shore and Leland samples; (C) 1960-62 North Shore versus this study and (D) 1966-68 North Shore versus this study.

curves was the parallel shift towards older ages in the most recent plots. Whether these differences in slope were real and due, for example, to greater sea lamprey (*Petromyzon marinus*) predation; or were an artifact of an expanding population and an unstable age structure cannot be determined. But the shift indicated a considerable change in the structure of the North Shore stock over the past 25 years.

The sexual difference in age structure was reflected in catch curve plots by sex (Figure 15). Survivorship for males at both Leland and the North Shore was constant (i.e. linear descending limb) following the age of full recruitment while female mortality increased with age. Female survival at early ages past recruitment was high in comparison to males from the same samples, but female mortality apparently increased with age until it exceeded that of males at the older ages. This effect was most pronounced at Leland, where exploitation contributed the least to total mortality, suggesting this sex differential was due to non-fishing causes.

Growth in Length:

Because of the size-selective nature of the trap-net gear used to collect most samples, mean lengths at age of fish in the catch were not used for growth measurements. Back calculated lengths were estimated from the relationship between scale radius and measured length:

$$\text{LENGTH (mm)} = 48.6 + 3.54\ \text{(SCALE RADIUS)}$$

with scale radii measured at 22x magnification. This relationship did not vary amongst the study stocks.

Back-calculated lengths at age were considered from 9 different upper Great Lakes whitefish stocks plus 2 additional time periods from the North Shore with the objectives of determining the range of growth variation and analying patterns for suggested causes. Specific questions asked about growth in length were whether whitefish growth was determinate, whether population density influenced growth, whether sexual dimorphism in growth occured, and whether growth was age-dependent or size-dependent. Other whitefish growth data were available but did not include other stock characteristics such as sex or maturity, and some of the available data was not relevant to certain questions.

Variation in growth amongst these studies was considerable (Figure 16), with a timespan to reach 432mm rangeing from under 3 years to over 11 years. Munising Bay whitefish were the smallest at all ages, but the largest fish at age differed amongst stocks. Cross comparisons of fish at specific ages and sizes therefore included a broad range of each variable.

Lengths at age in the 4 study stocks (Table 14, Figure 17) were above average in 3 but well below average for East Traverse fish. Leland fish were the largest at all ages, and North Shore and Beaver Island fish were similar in length. Because of the relatively low sampling intensity and some uncertainty about how many stocks were being sampled at Beaver Island, these data will be less extensively analyzed.

Estimates of growth potential (L_{max}) were made from

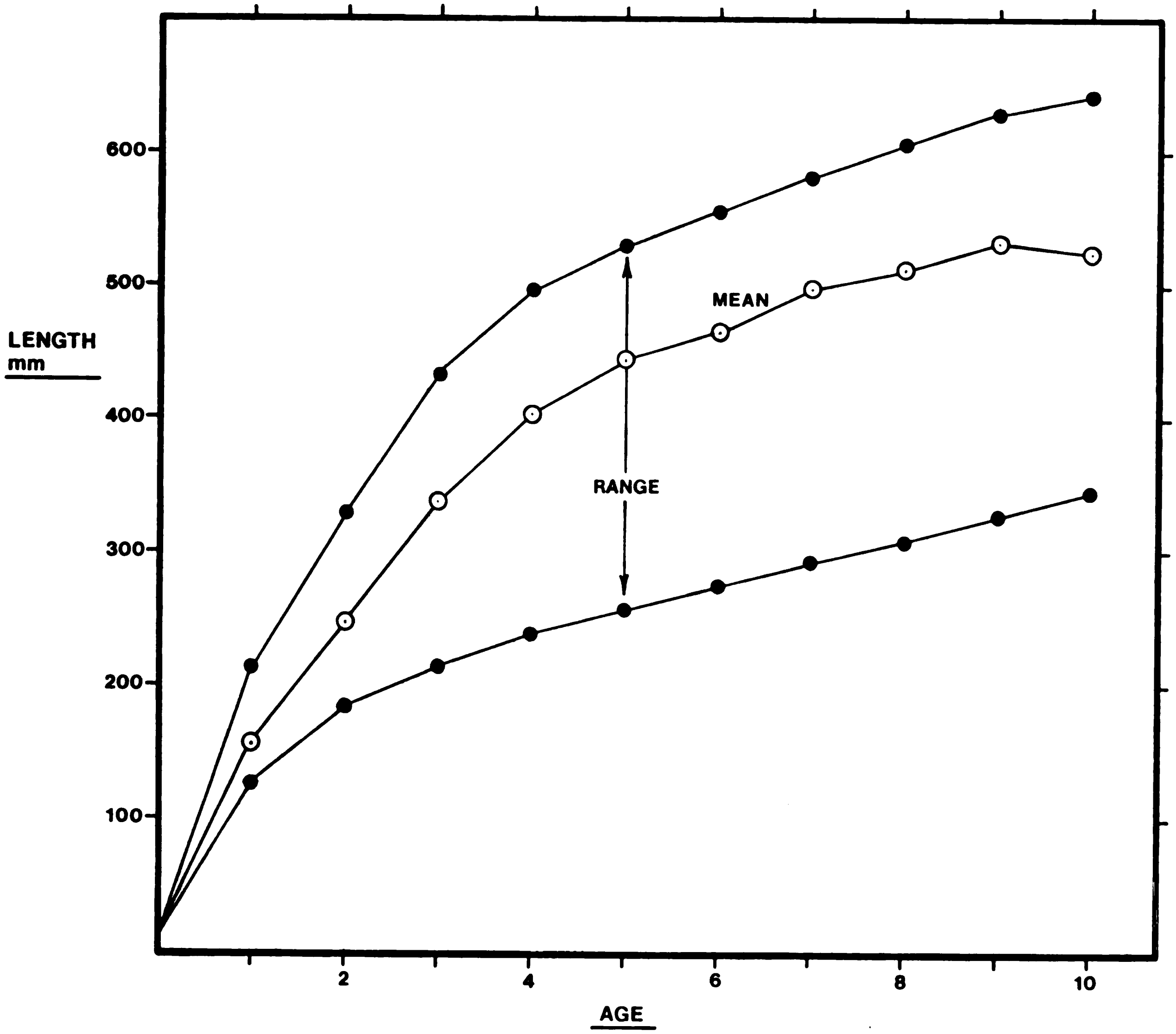

Figure 16. Minimum, maximum and mean lengths at age from eight upper Great Lakes whitefish populations.

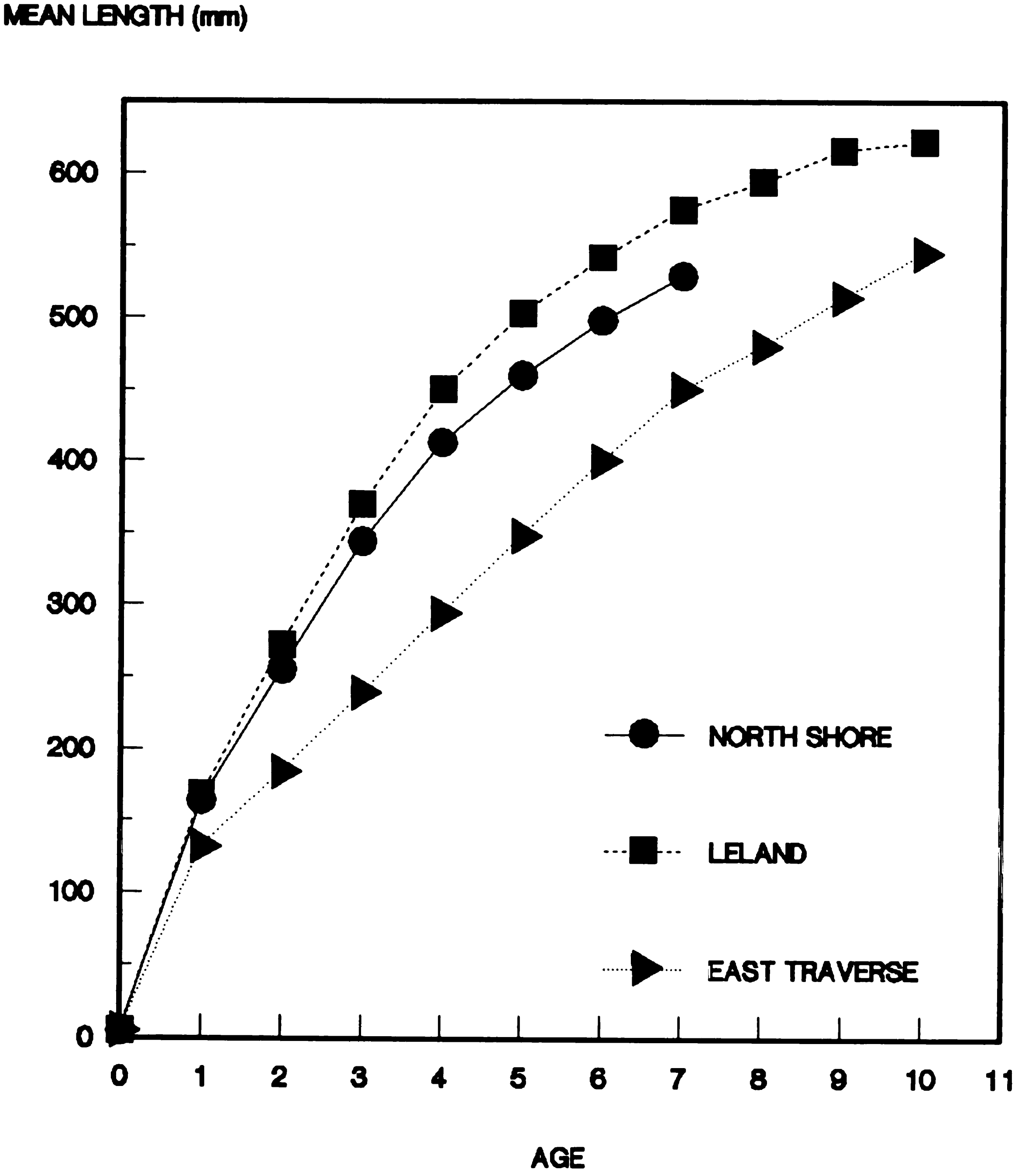

Figure 17. Mean back calculated lengths at age for Leland, North Shore and East Traverse whitefish, 1982-84.

Table 14. Back calculated lengths by age at capture, with averages, annual increments and standard deviations per age group, North Shore, Leland, East Traverse and Beaver Island, 1982-84.

NORTH SHORE
LENGTH AT AGE:

	1	2	3	4	5	6	7	8	9	10	N
1:	-	-	-	-	-	-	-	-	-	-	0
2:	165	253	-	-	-	-	-	-	-	-	44
3:	163	260	359	-	-	-	-	-	-	-	121
4:	159	253	345	422	-	-	-	-	-	-	203
5:	164	251	336	407	461	-	-	-	-	-	198
6:	170	260	343	411	461	499	-	-	-	-	129
7:	166	255	339	405	459	498	531	-	-	-	39
8:	166	249	341	398	447	488	522	553	-	-	13
9:	-	-	-	-	-	-	-	-	-	-	0
10:	-	-	-	-	-	-	-	-	-	-	0
	164	255	344	413	460	498	529	553	-	-	MEAN
	159	91	89	69	48	38	31	24	-	-	INC.
	13.5	22.5	25.9	26.9	25.4	27.2	34.7	31.0	-	-	S.D.

LELAND
LENGTH AT AGE

	1	2	3	4	5	6	7	8	9	10	N
1:	-	-	-	-	-	-	-	-	-	-	0
2:	172	293	-	-	-	-	-	-	-	-	26
3:	168	274	377	-	-	-	-	-	-	-	84
4:	167	272	373	457	-	-	-	-	-	-	163
5:	168	267	366	447	505	-	-	-	-	-	220
6:	168	274	368	446	500	541	-	-	-	-	186
7:	168	272	369	450	505	546	579	-	-	-	87
8:	168	279	375	457	507	543	571	598	-	-	28
9:	174	284	382	458	508	543	571	596	616	-	17
10:	173	266	367	442	493	525	552	578	616	622	9
	168	272	370	450	503	542	575	594	616	622	MEAN
	163	104	98	80	53	39	33	19	20	6	INC.
	13.2	22.3	28.1	29.3	28.4	28.4	28.8	29.7	31.9	33.6	S.D.

Table 14. (cont.)

EAST TRAVERSE
LENGTH AT AGE

	1	2	3	4	5	6	7	8	9	10	N
1:	140	-	-	-	-	-	-	-	-	-	42
2:	134	189	-	-	-	-	-	-	-	-	52
3:	132	190	248	-	-	-	-	-	-	-	74
4:	134	189	254	316	-	-	-	-	-	-	40
5:	133	184	240	306	371	-	-	-	-	-	39
6:	126	175	226	282	347	414	-	-	-	-	34
7:	128	175	228	285	337	398	460	-	-	-	43
8:	131	184	236	290	343	391	441	481	-	-	29
9:	130	178	226	277	337	390	436	475	512	-	13
10:	131	182	229	277	342	403	451	485	518	545	8
	132	184	239	294	348	400	450	480	514	545	MEAN
	127	52	55	55	54	52	50	30	34	27	INC.
	8.8	14.6	18.3	21.2	25.8	25.4	27.5	21.2	27.2	29.8	S.D.

BEAVER ISLAND
LENGTH AT AGE

	1	2	3	4	5	6	7	8	9	10	N
1:	-	-	-	-	-	-	-	-	-	-	0
2:	-	-	-	-	-	-	-	-	-	-	0
3:	-	-	-	-	-	-	-	-	-	-	0
4:	162	257	347	435	-	-	-	-	-	-	16
5:	166	249	332	403	467	-	-	-	-	-	31
6:	169	255	332	396	448	492	-	-	-	-	30
7:	175	258	336	395	444	487	526	-	-	-	12
8:	168	257	337	401	447	492	537	566	-	-	5
9:	-	-	-	-	-	-	-	-	-	-	0
10:	-	-	-	-	-	-	-	-	-	-	0
	168	254	335	405	455	491	529	566	-	-	MEAN
	163	86	81	70	50	36	38	37	-	-	INC.
	12.1	19.9	28.2	29.6	29.2	29.7	31.6	32.2	-	-	S.D.

Walford plots of length at the next age on length at the current age. Two examples of long-term Coregonid growth studies were found: North Shore whitefish from 1932 to present and Lake Michigan bloaters for which Brown (1970) reported growth data back to 1919. In both studies, lengths at age varied over time, particularly amongst younger fish. But Walford plots converged on a similar maximum length value for all time periods, tending to support the determinate growth concept (Figure 18). L_{max} estimates were not identical over time, but in both studies, maximum size did not increase with faster growth. Although there is no common method for testing the precision of L_{max} estimates, irregular deviations from linearity were common to all Walford plots, suggesting that variation in L_{max} over time was due to error. In several studies, the oldest fish were discarded from the data on the grounds that low sample size and high variance made these points relatively less precise, and that larger fish are commonly underaged (Beamish and McFarlane 1987).

Although within-stock variation in growth potential was small or absent, amongst-stock variation was large. L_{max} estimates ranged from a low of 450mm for Munising Bay fish to 685mm for Alpena whitefish (Table 15). Maximum size was largest for the 3 most southern stocks: Alpena, Leland and East Traverse and the two lowest estimates were for the 2 Lake Superior stocks: Munising Bay and Bayfield. The two Superior stocks were probably atypically small for this Lake, but nonetheless, there was a north to south trend of

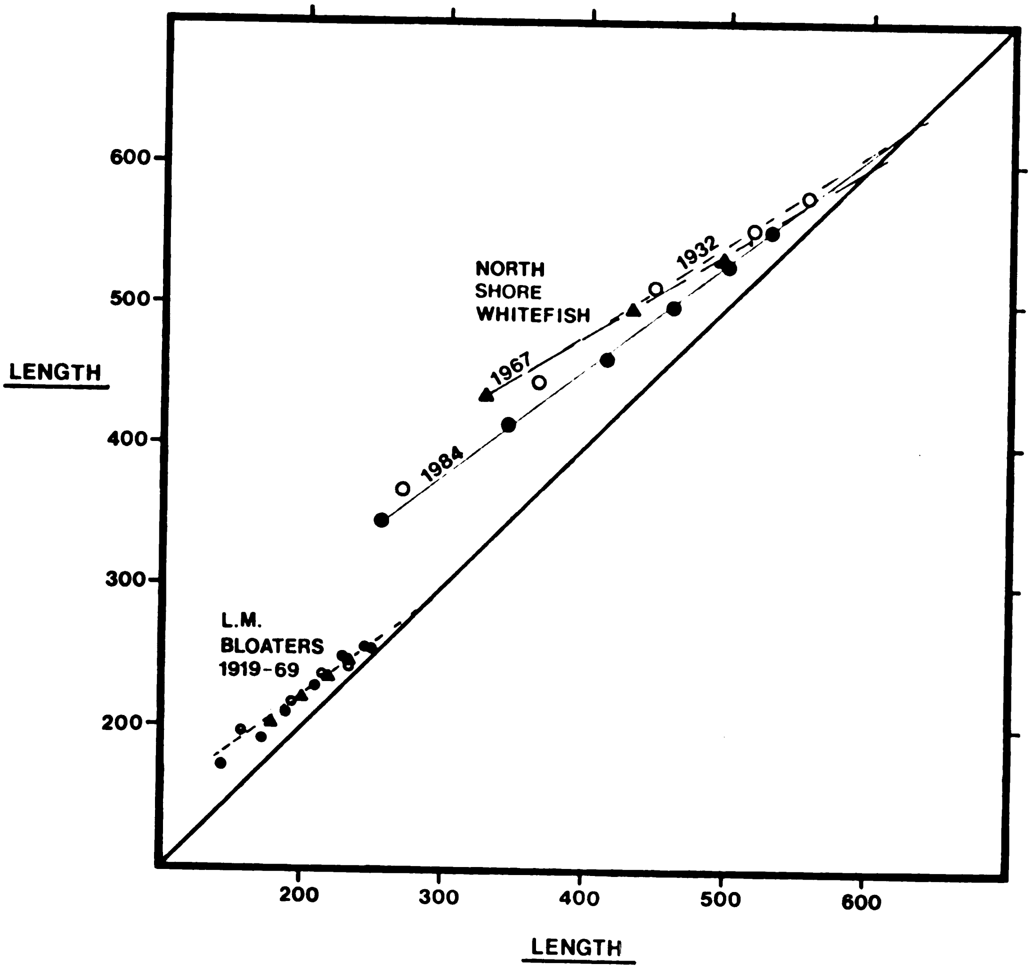

Figure 18. Walford plots and maximum lenght estimates for North Shore whitefish from 1932-84 and Lake Michigan bloaters from 1919-68 (Brown 1970).

Table 15. Maximum length estimates for several upper Great Lakes whitefish stocks, and typical estimates for other Coregonids.

LOCATION	YEARS	MAXIMUM LENGTH (mm)
ALPENA	1922-23	685
LELAND	1983-84	665
EAST TRAVERSE	1983-84	660
GREEN BAY	1952	640
NORTH SHORE	1932	640
	1966-67	625
	1983-84	630
BAYFIELD	1957	580
MUNISING BAY	1953	450
(ALSO)		
MENOMINEE		470-520
CISCOES		400-430
BLOATERS		290-310

decreasing maximum size.

Large L_{max} estimates were not necessarilly associated with rapid growth. Leland, Alpena and East Traverse whitefish grew to virtually the same size but at very different rates. To achieve 75 percent of their estimated maximum length, Leland fish required just over 3 years, Alpena fish required just over 4 years and East Traverse fish required over six years. The most rapid growth occurred in 1966-67 North Shore samples, but these fish grew to only an intermediate size. In other words, growth rates and growth potential varied independently of each other amongst stocks.

Within a given stock, maximum size also seemed to vary amongst individuals and sometimes between sexes. For Leland fish, the estimated average L_{max} for the population was considerably smaller than the largest fish sampled (750mm). Alternately, a number of North Shore fish exhibited the steadilly diminishing spacing between annuli that was normally symptomatic of old fish even though they were well below 500mm in length. Sexual dimorphism in growth was found only in the 3 southern stocks, where adult females were longer than adult males. Walford plots by sex in these stocks were parallel, indicating that females grew to a larger size than males rather than at a faster rate.

Taken as a whole, the pattern of variation in maximum length suggests that this trait is innate rather than environmentally determined. L_{max} varied amongst related species, amongst populations of the same species, sometimes between sexes in the same population but not significantly within a population with varying growth. Nor were the largest fish always the fastest growing. The observation that growth rate and growth expectancy can vary independently indicated that analyses of growth need to consider both characteristics, and that large size at older age is not necessarilly due to more rapid growth.

Two types of comparisons were used to test for effects of population density on growth: between exploited and unexploited stocks; and within the North Shore stock during periods of varying abundance. Lengths at age for the 3 unexploited stocks (Figure 19) were considerably different from each other, with older West Traverse fish amongst the largest and Munising Bay fish consistently the smallest. The only common feature of these stocks was that fish were below average in length for the first 2 annuli. East Traverse and Munising Bay stocks were both slow growing, but fish grew to very different sizes. Walford plots for the West Traverse stock were too erratic for a reliable L_{max} estimate and it was uncertain whether they were a relatively giant stock or grew rapidly. Older Leland fish, which grew during a closure of the fishery, did not grow differently than age-classes which followed reopening of the fishery, but it was unlikely that Leland fish were at high densities during the closure. The relationship between growth and exploitation was inconsistent: the 2 slowest growing stocks were unexploited but not all unexploited stocks grew slowly.

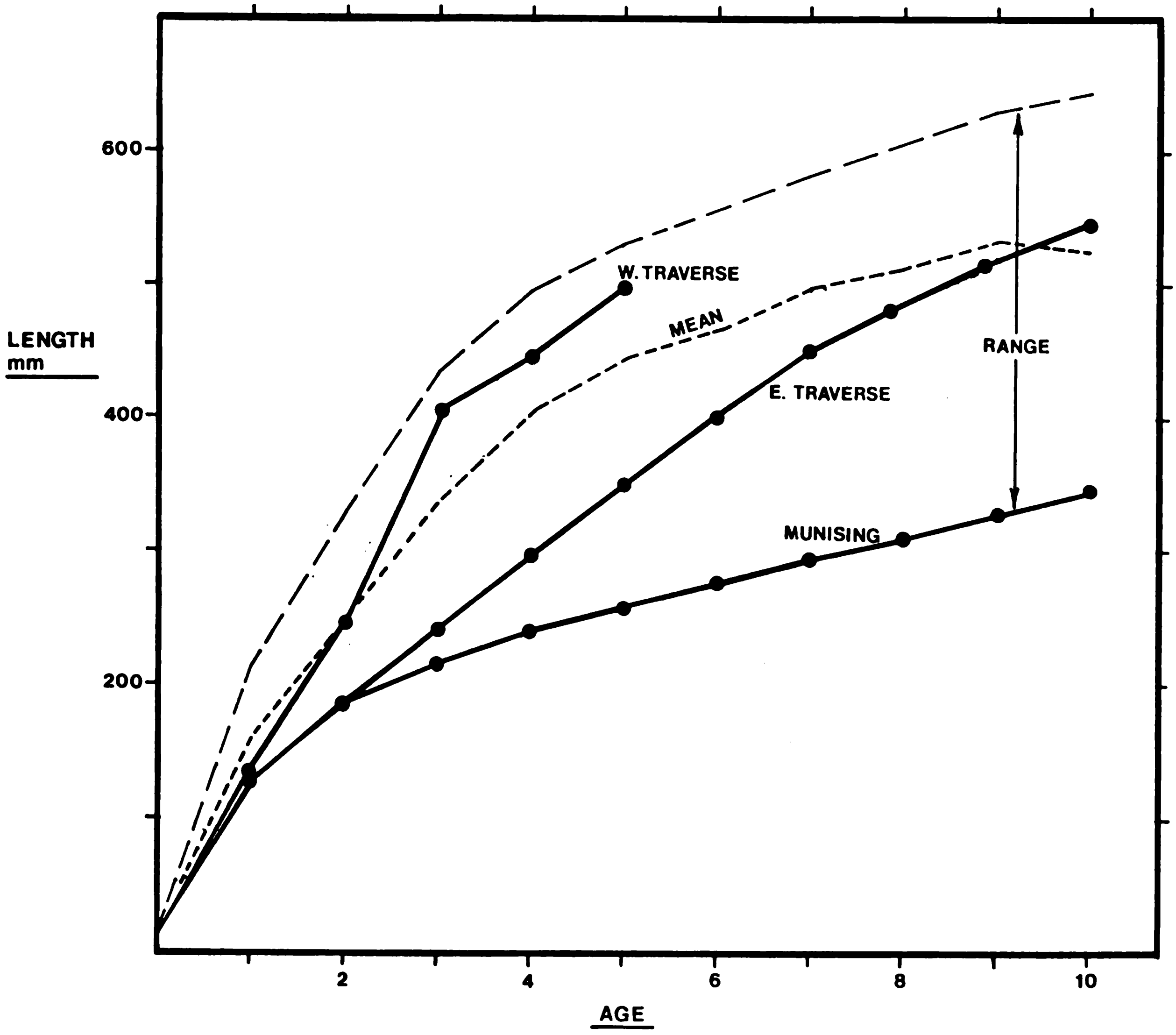

Figure 19. Mean lengths at age from 3 commercially unexploited whitefish stocks at Munising and the East and West arms of Grand Traverse Bay.

North Shore growth, however, did vary with changes in abundance. In 1966-67, when whitefish were recovering from the collapse of the stocks circa 1960, growth in length exceeded growth in 1932 and current growth, when whitefish catch was above average (Table 16, Figure 20). In 1966-67, whitefish required less than 3 years to reach 432mm, but at present 4.2 years is required for the average fish to reach legal size. In 1966-67, annual increments after the 3rd annulus were smaller than for recent fish at the same age, but this effect was likely due to the larger size at age of these fish. Annual increments plotted in relation to length rather than age indicated that 1966-67 whitefish grew faster than current fish of the same size throughout most of their growth history (Figure 21). Because this comparison did not depend on the assumption that exploited stocks are at low densities compared to unexploited stocks, it was a less ambiguous example of changing growth with changing abundance.

The phenomenon of growth compensation, where the growth of initially fast growing fish is inhibited at an earlier age by their larger size, is considered symptomatic of size-dependendent rather than age-dependent growth. Growth rates of fishes consistently diminish as fish become older and larger (Ricker 1975). If increased size inhibits growth, fish which attain a larger size relatively early in life would experience this inhibition sooner in the same fashion as a long distance runner who sets a fast pace at the beginning of

Table 16. North shore lengths at age averaged over ages at capture for 1932, 1950 and 1966-67.

	1932		1950		1966-67	
AGE	MEAN LENGTH	N	MEAN LENGTH	N	MEAN LENGTH	N
1:	181	63	174	43	212	1426
2:	270	63	283	43	329	1409
3:	365	63	398	43	432	992
4:	444	60	473	17	497	192
5:	517	13	519	5	530	14
6:	556	9	-	-	-	-
7:	581	5	-	-	-	-

1932 Data from Brown (1968)
1950 Data from Caraway (1951) for the St Helena Island area
1966-67 Data averaged from Piehler (1967) and Brown (1968)

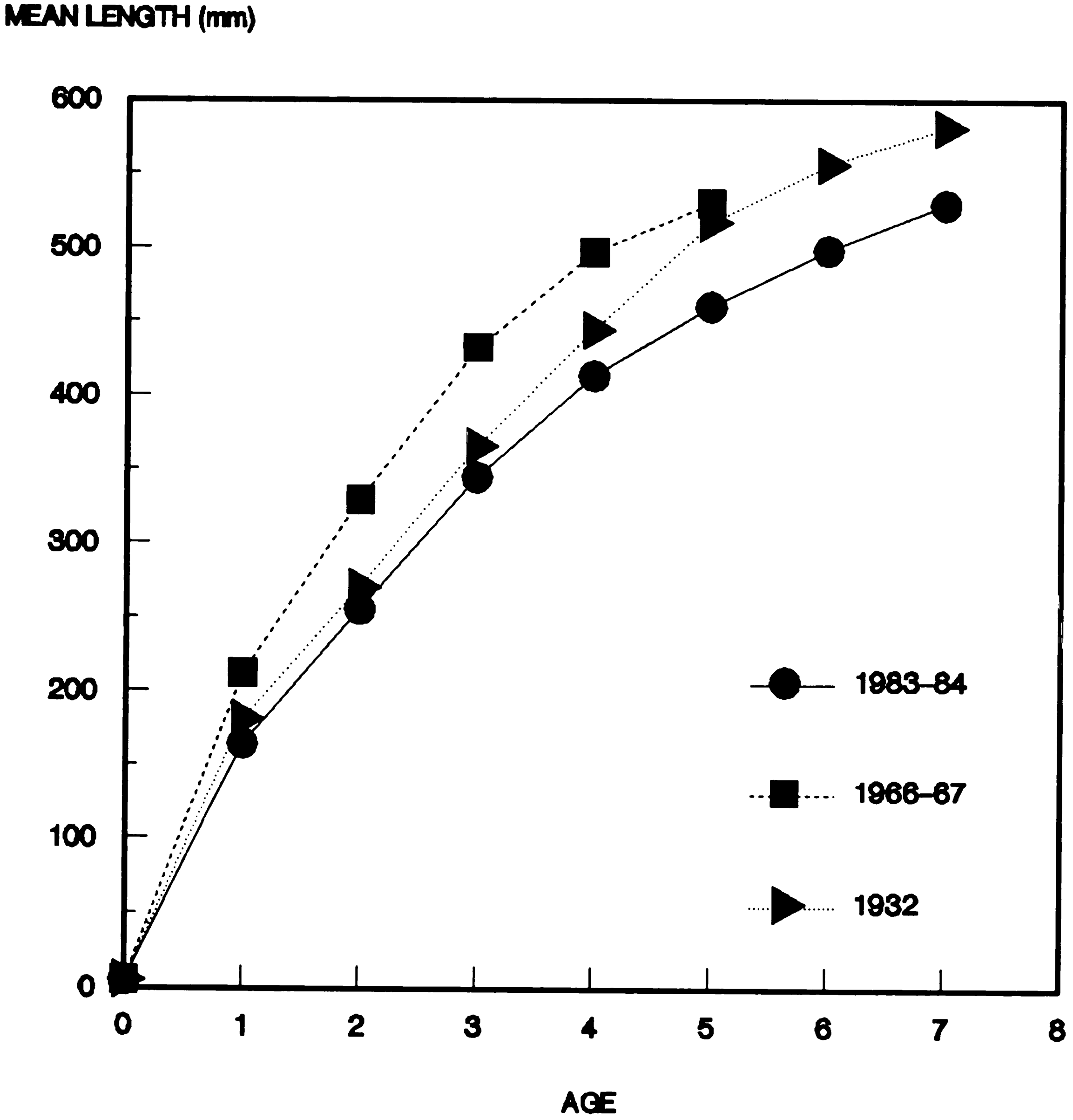

Figure 20. Mean back calculated lengths at age for North Shore whitefish from 1932, 1966-67 and 1982-84 samples.

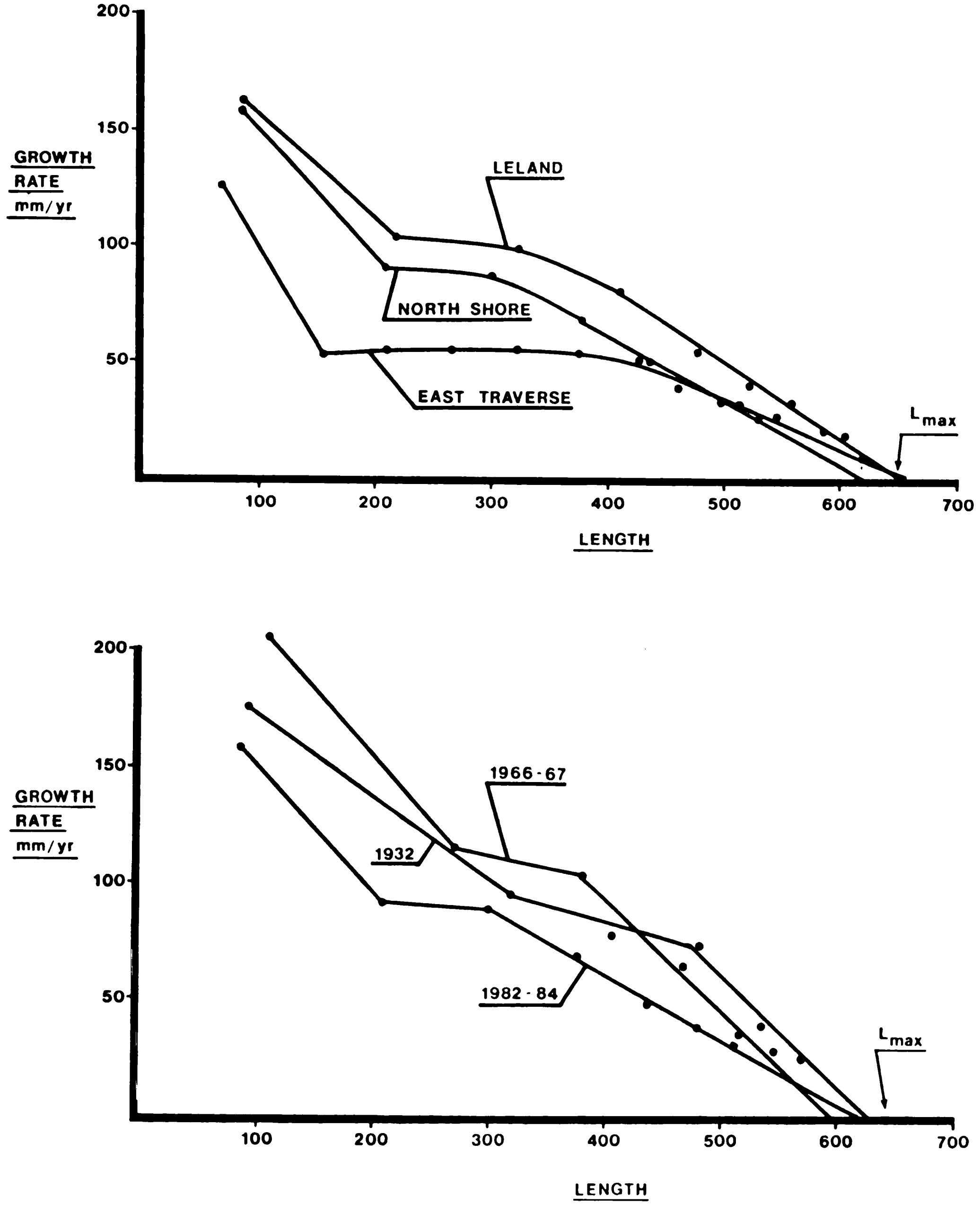

Figure 21. Annual growth increments in length in relation to mean length at age for (A) Leland, North Shore and East Traverse samples and (B) North Shore samples from 1932, 1966-67 and 1982-84.

a race tires sooner than those who set an initial moderate pace. Growth compensation is tested for by comparing the growth of initially large and small individuals at later ages, and was reported by Van Oosten for Lake Huron ciscoes (1929) and whitefish (1938), and also by Van Oosten and Hile (1949) for Lake Erie whitefish.

The clearest example of growth compensation occurred in the comparison between Leland and East Traverse fish, which grew to a similar maximum size. Leland fish were larger at all ages, but after the 5th annulus, East Traverse annual increments were larger than for Leland fish of the same age. But when increments were plotted in relation to length of the fish (Figure 21), East Traverse fish grew more slowly than Leland fish of the same size. Older East Traverse fish apparently grew more rapidly simply because they were smaller.

Growth compensation also occurred amongst individuals from a balanced sample of Leland and North Shore year-classes. Growth increments from the 2nd annulus to the 4th and 5th annuli were smaller (t-test, $P < 0.05$) on the average for the 33 largest individuals at age 1 than for the 33 smallest individuals taken from a sample of 100 fish in both stocks. Growth compensation was also present amongst East Traverse fish, but diminished increments for initially large individuals were not detectable until fish had passed the 6th annulus, suggesting that growth inhibition by size increased

Table 17. Back calculated lengths at age for the North Shore and Leland year-classes of 1977, 1978 and 1979 averaged over ages at capture of 3 through 5.

	---1977---- COHORT		---1978---- COHORT		---1979---- COHORT	
AGE	LENGTH	N	LENGTH	N	LENGTH	N
	NORTH SHORE					
1:	172	152	165	229	160	256
2:	266	152	251	229	257	256
3:	346	152	337	229	342	256
4:	410	130	407	203	409	247
5:	464	110	463	183	460	92
	LELAND					
1:	177	272	172	229	167	209
2:	290	272	273	229	274	209
3:	380	272	371	229	372	209
4:	457	257	445	204	458	172
5:	507	164	508	172	511	65

after fish attained a certain length.

Thirdly, growth compensation occurred amongst different year-classes within both the Leland and North Shore stocks (Table 17). In both areas, members of the extremely large 1977 cohort were 6 to 7 percent larger at the first annulus than members of the successively weaker 1978 and 1979 cohorts. Increments from the 1st or 2nd annuli to the 4th or 5th annuli were consistently larger for the weaker 1978 and 1979 cohorts, and similar results were reported by others investigating relationships between cohort strength and growth (Hile 1941, Mraz 1964, Henderson et al 1983). But this comparison was between fish that were the same age but unequal size. When growth increments were plotted in relation to length rather than age, the only consistent growth difference amongst cohorts was the increased first-year growth of the large 1977 cohort. This result, along with the similarity to previous studies, indicated that the formation of strong year-classes was associated with above normal growth during the first year of life. Other studies have interpreted similar data as implying that large cohorts grow more slowly because of greater density. But these studies did not account for differences in the initial length of the fish, and a more valid interpretation would be that members of large cohorts grow more slowly at older ages because they are larger.

Plots of annual length increments against length exhibited a common pattern of 3 stanzas in growth. Below 200mm, annual increments were very large relative to later growth; from 200mm to approximately 450mm increments were constant and growth reached a plateau stanza; after 450mm, annual increments diminished steadilly with increasing size, approaching zero growth at the maximum length. The transition from the plateau phase to the diminishing phase occurred at very dissimilar ages; 4 at Leland and the North Shore but not until age 7 for East Traverse. This inflection occurred at a slightly smaller size for North Shore fish and also at a smaller size for males than females in stocks where growth varied by sex. The size at which growth increments began to decrease was also similar to the size at which fish in each area began to mature.

Standard deviations in length at age exhibited no consistent relationship with age of the fish: lengths of fish of the same age in different stocks varied by different amounts (Table 14). But for cohorts of the same mean length, regardless of their age, standard deviations in length were virtually equal. Coefficients of variance (CV) in length at age decreased with increasing mean length in all stocks (Figure 22) from approximately 8 percent below 200mm to 5 or 6 percent past 500mm. But CV's were at least very similar for fish of the same mean size in all stocks. This consistency of patterning between variation in size and size itself was additional evidence that growth was size-dependent rather than age-dependent.

Growth in length differed by sex (Table 18) only at Alpena, Leland and East Traverse but in other areas, sexual

Table 18. Back calculated lengths at age for male and female whitefish, averaged over ages at capture, for North Shore, Leland and East Traverse whitefish, 1981-84.

	LELAND				EAST TRAVERSE			
	MALE		FEMALE		MALE		FEMALE	
	L	N	L	N	L	N	L	N
1:	169	158	166	186	128	101	128	94
2:	268	158	267	186	181	101	180	94
3:	362	145	365	176	240	101	232	94
4:	436	113	449	135	294	79	288	72
5:	486	72	503	110	348	53	342	59
6:	526	33	541	59	398	44	401	53
7:	558	12	581	19	448	31	450	35
8:	565	3	630	2	474	12	484	18
9:	-	-	-	-	493	5	523	5

	NORTH SHORE			
	MALE		FEMALE	
	L	N	L	N
1:	162	183	162	170
2:	253	183	253	170
3:	343	161	340	148
4:	409	117	409	119
5:	457	73	456	83
6:	494	33	498	39
7:	532	11	529	13

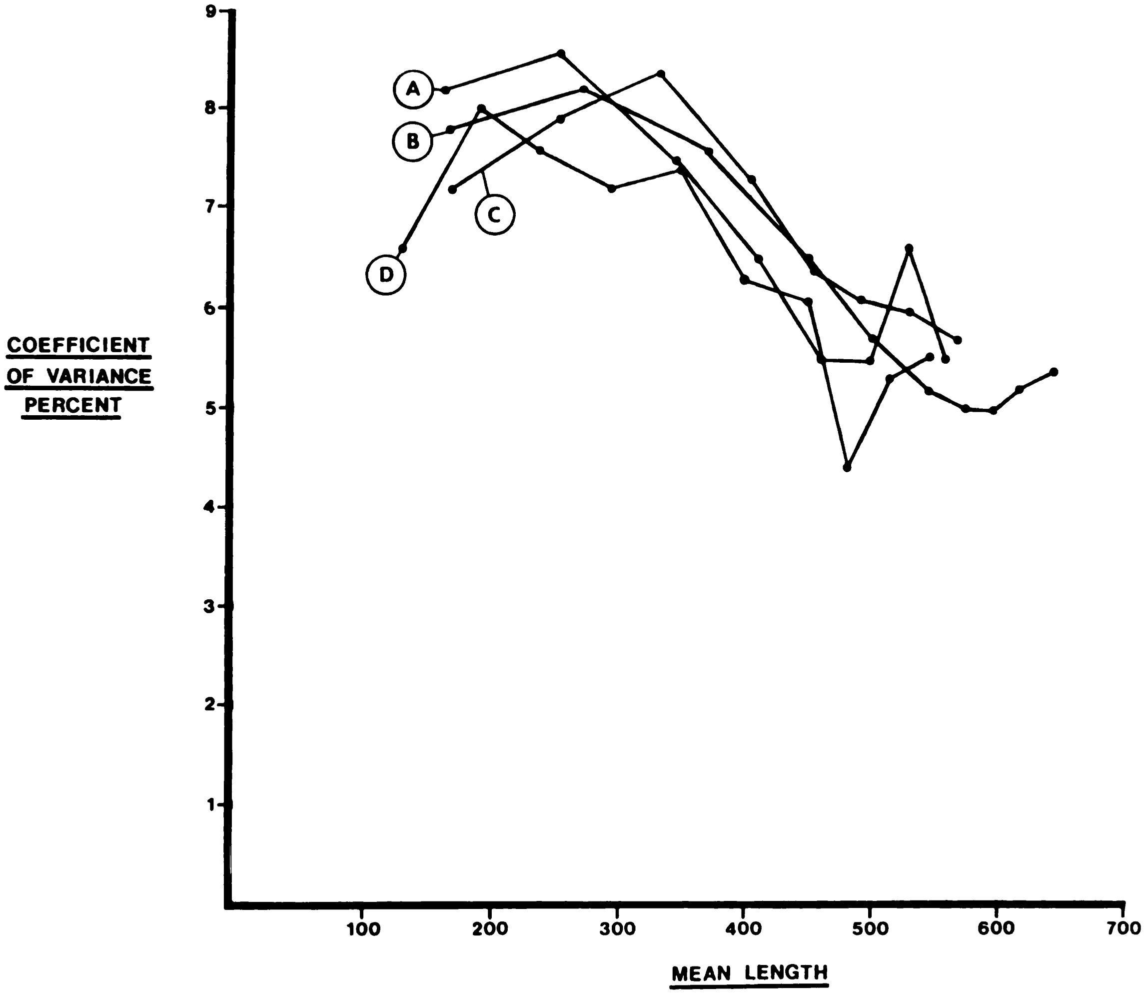

Figure 22. Coefficients of variance in length at age in relation to mean lengths at age from 1982-84 samples for (A) North Shore (B) Leland (C) Beaver Island and (D) East Traverse samples.

dimorphism was absent or undetectable. Juvenile males and females were equal in length and only adult females were longer than adult males of the same age. Dimorphism occurred only after maturity when it did occur, indicating that females continued to grow at the typically higher juvenile rates until they had attained a larger size.

Lee's phenomenon, which is symptomatic of size selective mortality and/or sampling bias (Ricker 1969), was small or absent in most of the previous growth studies. The larger sample size and timespan of this study provided clearer resolution of changes in mean length with increasing age at capture, and both Lee's phenomenon and the reverse effect were present in the growth data. Plots of mean annular scale radii in relation to age at capture (Figure 23) indicated that Lee's phenomenon varied between stocks and also with the size of the fish.

In North Shore samples, the radii of the 3rd and 4th annuli diminished with age at capture from 3 to 5 and then levelled off. When samples included sublegal fish, Lee's phenomenon diminished but not completely, indicating that both sampling bias and size-selective mortality influenced the results. A similar effect was present in the Leland growth data, but after age of capture 6, annular radii began to increase with increasing age of capture. This reverse Lee's phenomenon, present after age 8 in the East Traverse data as well, suggested that larger fish enjoyed an advantage in survival at older ages. The degree of suppression in mean

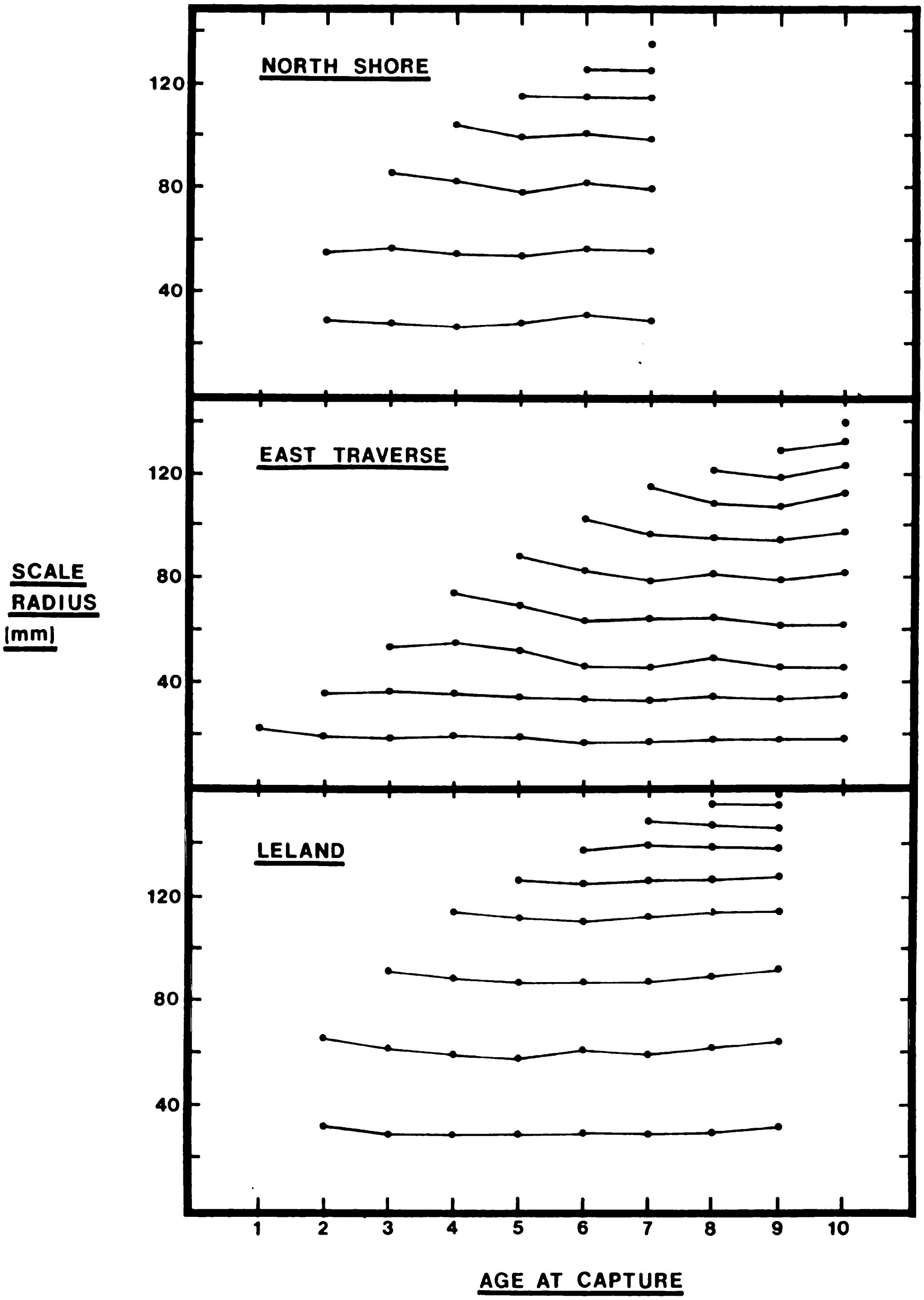

Figure 23. Mean annular scale radii (22X magnification) in relation to age at capture for averages of each age class, 1982-84.

length at age equalled approximately 15-20mm at the 4th annulus in each stock. Lee's phenomenon was also evident in the East Traverse growth record even though the trawling gear was clearly not selective for larger fish and the size-selective mortality due to fishing was reduced or absent. Growth suppression for East Traverse fish also did not occur until the 6th annulus, perhaps indicating that natural mortality was also size-selective after fish reached a particular size.

Growth in Weight:

Analyses of growth rates in terms of weight gain were restricted to the Leland, East Traverse and North Shore stocks in order to keep procedures consistent. These 3 stocks were assumed exemplify differences in growth due to varying maximum size and varying growth rate.

Variation in weight at length amongst all stocks in general was large enough that individuals were sometimes more than double the weight of other fish of the same length. Leland fish were the heaviest at all lengths (Table 19); North Shore juveniles outweighed East Traverse juveniles but East Traverse whitefish longer than 450mm were heavier than North Shore fish. Juvenile weights at length did not differ by sex in any area, but mature females outweighed mature males of the same length by an average of 7 to 12 percent (Table 20). Adult females were frequently identifiable by their plumper morphology, and were heavier than males of the same length in both spring and fall samples.

Table 19. Grand average weights at consecutive 10 millimeter increments of length, 1981-84, for North Shore, Leland, East Traverse and Beaver Island whitefish. Weight is in grams, numbers of fish are in parentheses.

LENGTH	NORTH SHORE	LELAND	EAST TRAVERSE	BEAVER ISLAND
400:	563 (15)	730 (2)	535 (8)	--
410:	623 (18)	723 (8)	554 (2)	--
420:	687 (47)	741 (16)	633 (5)	703 (4)
430:	723 (116)	844 (30)	682 (13)	748 (11)
440:	777 (131)	918 (39)	687 (9)	805 (18)
450:	824 (145)	959 (48)	813 (12)	860 (19)
460:	886 (139)	1024 (77)	863 (18)	905 (19)
470:	935 (127)	1111 (77)	962 (24)	941 (19)
480:	1002 (126)	1170 (77)	1003 (26)	1056 (19)
490:	1066 (104)	1234 (65)	1090 (21)	1078 (19)
500:	1156 (83)	1299 (70)	1202 (27)	1118 (19)
510:	1232 (80)	1390 (65)	1250 (28)	1286 (19)
520:	1280 (46)	1463 (80)	1366 (23)	1322 (19)
530:	1390 (32)	1556 (70)	1428 (26)	1424 (19)
540:	1501 (17)	1687 (59)	1547 (25)	1492 (10)
550:	1566 (12)	1710 (71)	1660 (12)	1600 (10)
560:	1647 (13)	1872 (64)	1748 (14)	1795 (9)
570:	--	2016 (56)	1830 (7)	1939 (5)
580:	1865 (4)	2118 (45)	1970 (13)	1980 (5)
590:	--	2280 (33)	2094 (9)	2041 (2)
600:	--	2392 (24)	2298 (2)	2092 (3)
610:	--	2573 (19)	2287 (3)	--
620:	--	2697 (16)	--	--
630:	--	2999 (14)	--	--
640:	--	3109 (15)	--	--
650:	--	3285 (14)	--	--
660:	--	3470 (18)	--	--
670:	--	3572 (18)	--	--
680:	--	3948 (11)	--	--
690:	--	3960 (8)	--	--
700:	--	3956 (3)	--	--

Table 20. Comparisons of mean weight at length between male and female whitefish in North Shore, Leland and East Traverse samples, 1982-84.

	NORTH SHORE		LELAND		EAST TRAVERSE	
LENGTH	MALE	FEMALE	MALE	FEMALE	MALE	FEMALE
350:	335	312	372	373	321	---
360:	403	388	435	492	345	369
370:	398	354	467	466	402	442
380:	440	420	549	524	405	491
390:	491	501	621	560	474	---
400:	529	545	669	---	515	525
410:	557	635	---	667	554	---
420:	648	696	748	664	647	590
430:	719	753	777	836	681	684
440:	768	792	1050	822	677	725
450:	800	874	916	937	755	808
460:	877	915	988	993	819	822
470:	918	975	1077	1068	884	1034
480:	1003	995	1149	1193	960	981
490:	1012	1133	1215	1156	1046	1093
500:	1093	1165	1256	1316	1093	1163
510:	1149	1261	1327	1405	1219	1256
520:	1277	1327	1421	1511	1284	1402
530:	1289	1325	1491	1639	1379	1437
540:	1471	1485	1612	1735	1441	1620
550:	1615	---	1704	1828	1538	1615
560:	1633	1575	1774	1933	1647	1792
570:	---	---	1830	2137	1694	1699
580:	---	---	2094	2210	1865	1984
590:	---	---	2301	2329	2141	2099
600:	---	---	2246	2441	2200	2208

No seasonal or year to year variation in mean weights at length were found in any area, with the exception of the fall North Shore catch where fish shorter than 480mm tended to be slimmer than at other times of year. This result was due to an increased preponderance of short males in the fall catch rather than any change in the morphology of the fish. The much higher than normal relative abundance of short, slender males in fall samples tended to depress weights at the shorter lengths, but this effect dissappeared when weights were averaged by sex rather than for the catch as a whole.

Slopes of the relationship between log transformed lengths and weights for whitefish have typically ranged from 3.1 to over 3.5, suggesting growth in weight relative to length is commonly well above isometric rates. The typical procedure has been to assume the relationship is linear over all lengths and obtain a best fit estimate of slopes through least-squares regression. The large sample size and broader than usual span of lengths considered in this study enabled a more detailed examination of length-weight relationships by averaging weights at length to reduce variance and breaking the relationship into segments of varying spans and ranges.

Length-weight exponents varied amongst stocks, amongst different ranges and spans of length from the same stock, and with the sex and apparently the maturity of the fish (Table 21). For East Traverse samples, which included lengths from 100 to 600mm, three stanzas of weight gain relative to length were identified. Below 200mm, weight gain was well below

Table 21. Slope (b) and intercept (a) estimates of the natural log transformed weight on length regressions using mean weights at 10 mm length increments.

AREA	RANGE OF LENGTHS	REGRESSION a	REGRESSION b	REGRESSION r^2	SEXES
NORTH SHORE	180-400	-12.434	3.118	0.997	Combined
	400-560	-12.193	3.096	0.998	Combined
	350-430	-16.055	3.731	0.981	Males
	430-560	-10.751	2.857	0.989	Males
	350-450	-17.444	3.965	0.998	Females
	450-560	-11.242	2.945	0.983	Females
LELAND	200-400	-12.925	3.230	0.989	Combined
	400-700	-12.975	3.245	0.994	Combined
	350-470	-14.066	3.424	0.966	Males
	470-570	-10.571	2.852	0.994	Males
	350-520	-14.884	3.553	0.987	Females
	520-620	-13.662	3.306	0.989	Females
EAST TRAVERSE	120-400	-12.649	3.152	0.999	Combined
	400-600	-15.091	3.565	0.997	Combined
	350-470	-14.090	3.393	0.990	Males
	470-600	-15.072	3.054	0.993	Males
	360-500	-15.784	3.677	0.981	Females
	500-600	-11.983	3.074	0.958	Females
BEAVER ISLAND	420-600	-12.792	3.197	0.994	Combined

isometric and gains in length outpaced gains in weight, resulting in slender fish. Past 200mm, weight gains accelerated to above isometric levels and fish became progressively endomorphic with increasing length. The 3rd stanza occurred at approximately the lengths at which fish matured, with the inflection at a larger length for females than males. Exponents for mature males and females were lower than for immature fish, but mean weights of mature fish averaged heavier than immatures of the same length.

Similar non-linearities in $\log_e$ length-weight relationships were found in Leland and North Shore samples. Intercepts and exponents for the standard length-weight equation ($W = aL^b$) listed in Table 21 for different ranges of lengths and by sex were chosen to give the best fit over the largest span of lengths in each stock. Length-weight statistics for juvenile fish did not differ between sexes in any area, but exponents for each sex separately were lower than for both sexes combined. For ranges of lengths above the size at which fish matured in a given area, exponents decreased to near or below isometric rates for each sex. Regressions which included all lengths and both sexes tended to overestimate both the mean weight of longer whitefish and the rate of weight gain relative to length. This effect, on more detailed examination, was due to both inflections inthe rate of weight gain and the increased predominanace of the heavier females at longer lengths in many samples.

Calculated mean weights at age (Table 22, Figure 24)

Table 22. Calculated mean weights at age and annual weight increments; North Shore, Leland, East Traverse and Beaver Island, 1982-84.

	NORTH SHORE		LELAND		EAST TRAVERSE		BEAVER ISLAND	
	WT. (gm)	INCRE-MENT	WT. (gm)	INCRE-MENT	WT. (gm)	INCRE-MENT	WT. (gm)	INCRE-MENT
1:	32	32	38	38	16	16	32	32
2:	127	95	178	140	33	17	125	93
3:	323	196	481	303	95	62	297	172
4:	637	314	943	329	189	94	603	306
5:	889	252	1353	410	336	147	875	272
6:	1136	247	1725	372	528	192	1117	242
7:	1370	234	2089	364	803	275	1417	300
8:	1607	237	2322	233	1010	207	1759	342
9:	--	--	2612	290	1290	280	--	--
10:	--	--	2696	84	1589	299	--	--

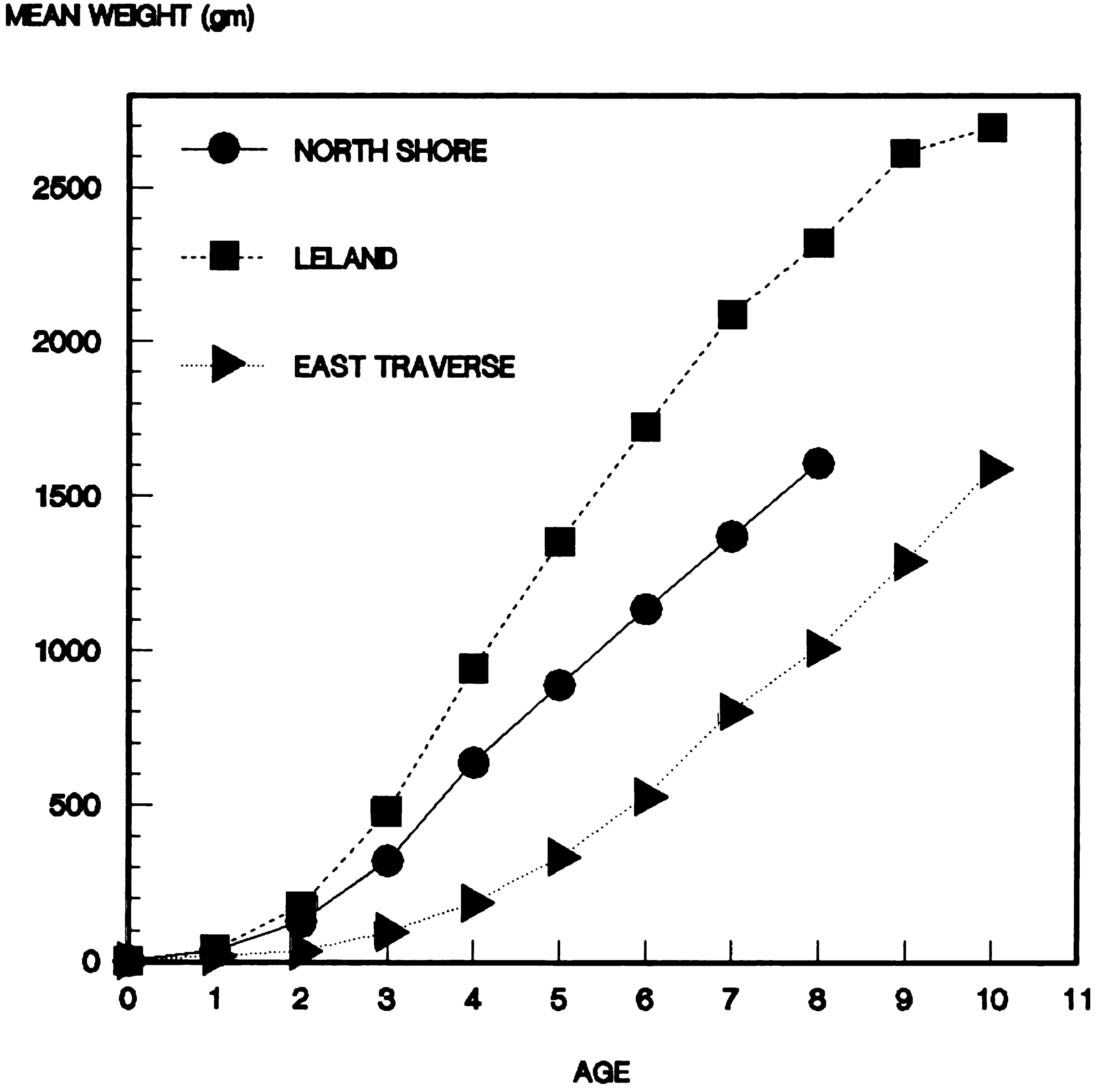

Figure 24. Calculated mean weights at age for (A) Leland (B) North Shore and (C) East Traverse whitefish 1982-84 in relation to chronological age.

reflected the disparity in growth between stocks. By age 5, Leland fish were 52 percent heavier than North Shore fish and 4-fold larger than East Traverse fish. Although growth in weight approximated the sigmoid shape of the Von Bertalanffy (1938) equation, good fits to this equation were not obtained. Equations which described juvenile growth accurately tended to overestimate growth of older fish, but curves which fit adult growth well underestimated juvenile growth.

Annual weight increments increased with age through the juvenile ages, peaked and then diminished. Leland growth peaked at age 5, North Shore growth at age 4, but East Traverse growth displayed no distinct peak even by age 10. In relation to length (Figure 25), weight increments peaked circa 400mm for North Shore fish and 500mm for Leland fish. The lack of any clear East Traverse growth maximum seemed to occur because the oldest fish included in the growth measurements had still not attained an average size at which growth would be expected to diminish.

Because of the plumper female morphology, growth in weight was sexually dimorphic, even in the North Shore where lengths were equal. Juvenile increments were the same for both sexes (Table 23) but females increments continued to increase for another year and another 60mm in length (Figure 26) past the point at which male growth peaked and began to decline. Female growth maxima occured at a larger size than for males, suggesting again that dimorphism in size

Table 23. Calculated mean weights at age for male and female whitefish; North Shore, Leland and East Traverse.

AGE:	NORTH SHORE		LELAND		EAST TRAVERSE	
	FEMALE	MALE	FEMALE	MALE	FEMALE	MALE
1:	31	31	33	38	14	14
2:	124	124	168	170	41	42
3:	311	307	436	449	92	102
4:	602	591	911	849	181	194
5:	923	852	1363	1179	312	319
6:	1151	1064	1735	1477	521	504
7:	1375	1315	2204	1748	796	753
8:	--	--	2892	1811	1041	911
9:	--	--	--	--	1421	1059

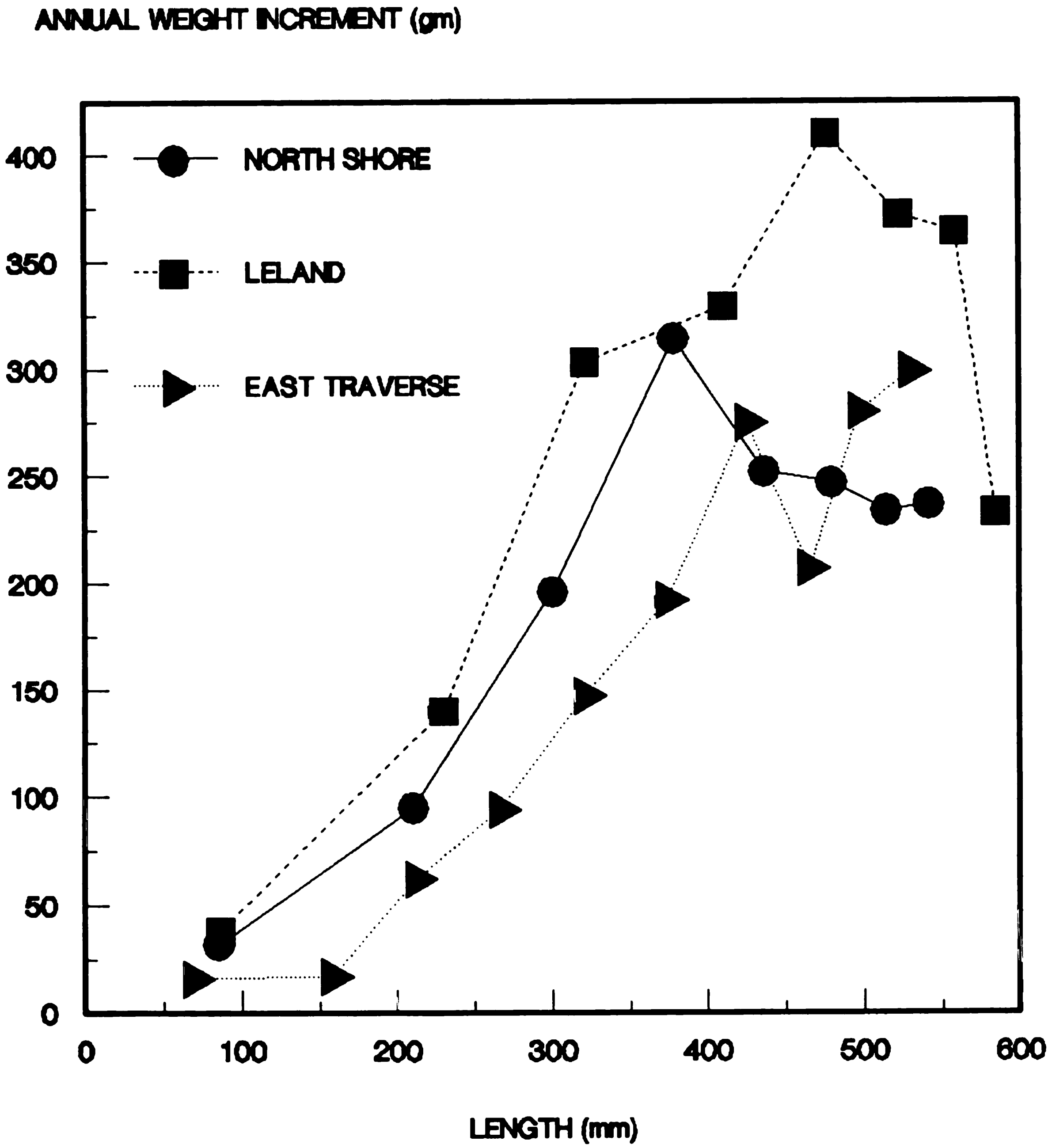

Figure 25. Mean annual increments in weight for Leland, North Shore and East Traverse whitefish in relation to length of the fish.

Figure

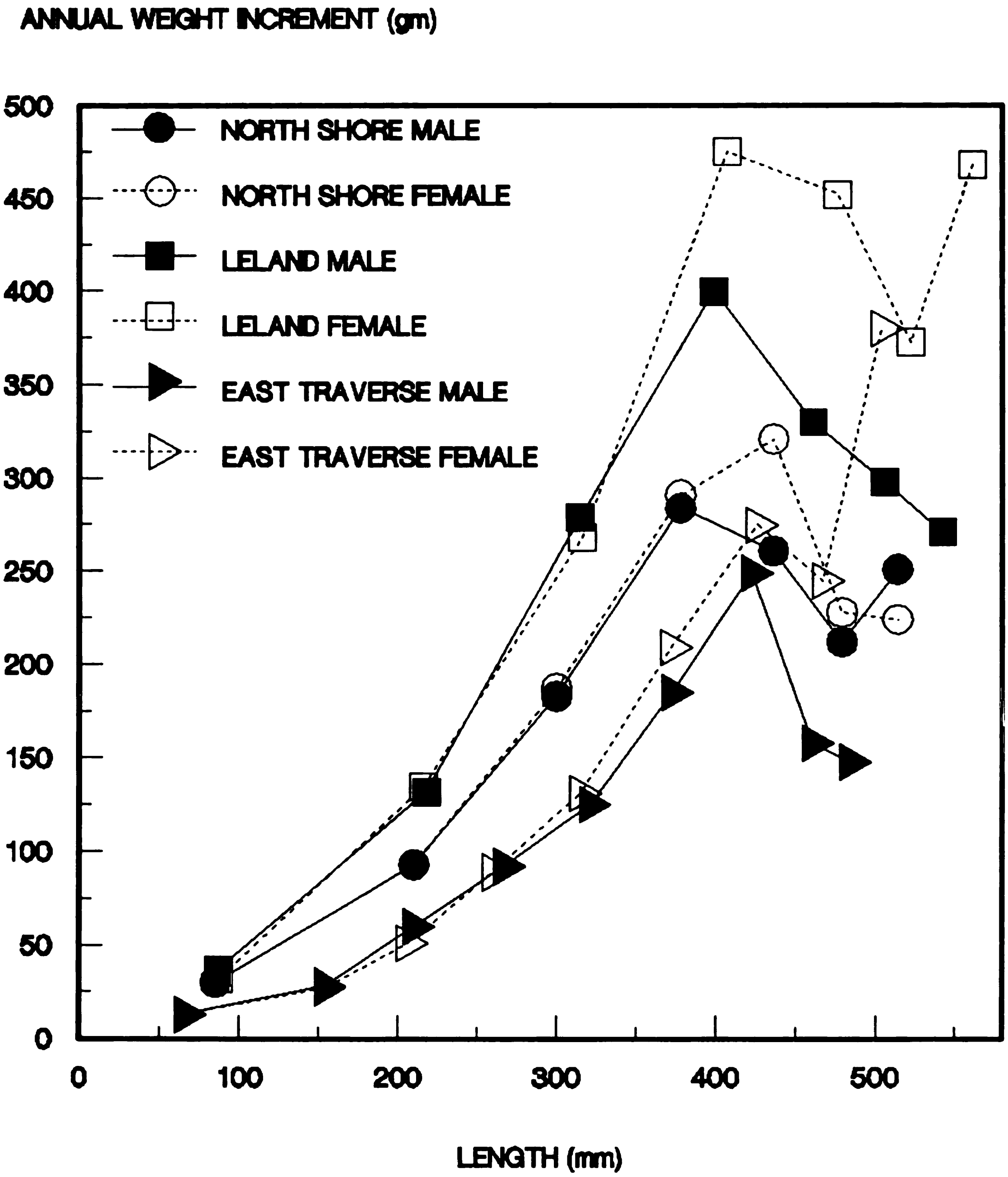

Figure 26. Mean annual increments in weight calculated for male and female whitefish in relation to length; Leland, North Shore and East Traverse samples, 1982-84.

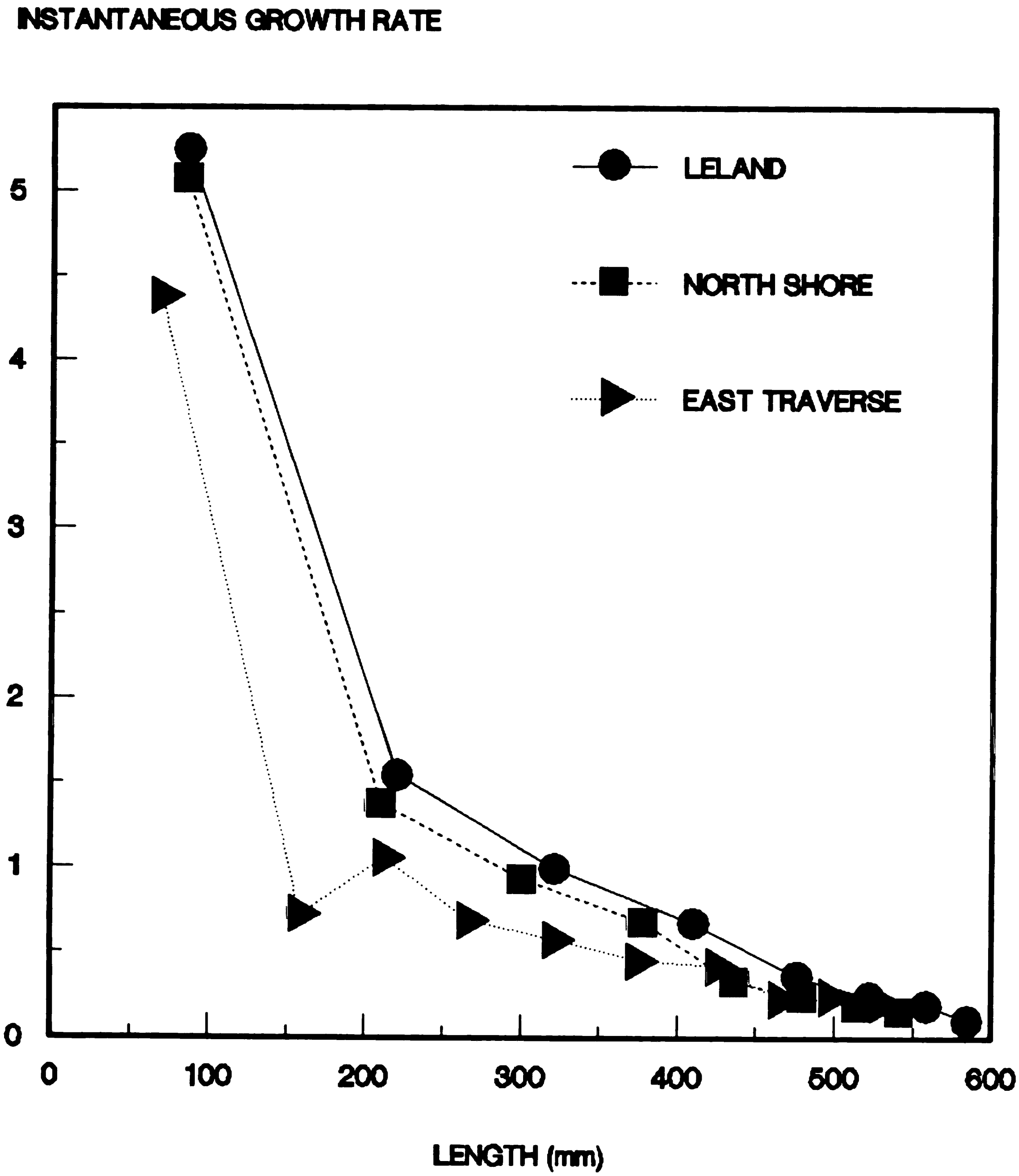

Figure 27. Mean instantaneous growth rates in relation to mean lengths at age; Leland, North Shore and East Traverse samples, 1982-84.

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occurred because females sustained the rapid growth characteristic of juvenile fish further than did males. For males, North Shore growth peaked at 370mm while Leland and East Traverse males peaked after 400mm. North Shore female growth peaked at 460mm, Leland at 510mm, and too few ageable East Traverse females over 500mm in length were evaluated to detect a distinct peak. The size at which growth maxima occurred was not dependent on growth rates, but did vary by sex. They also occurred at lengths similar to those at which fish matured.

Instantaneous growth rates (Figure 27) decreased with increasing fish length in all 3 stocks, with the most rapid rates of decrease at Leland and the North Shore. Leland and North Shore growth rate curves were also parallel, and presumably diminished to zero growth at the maximum length. When these rates were plotted in relation to percentage of the maximum length rather than true length, North Shore growth rates were equal to or slightly higher than Leland rates. This observation suggested that North Shore growth rates were equal to Leland rates when considered in proportion to the smaller growth potential. East Traverse growth rates were lowest in comparison to the other stocks for the smallest fish, and eventually surpassed North Shore rates after 420mm in length. After 500mm, East Traverse and Leland growth rates were virtually identical, indicating that growth differences between the fastest and slowest growing stocks affected juvenile fish only.

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Sexual Maturity:

The expectation that whitefish matured at a constant age was easily rejected when data were considered from all stocks (Figure 28). Female whitefish were mature as early as age 2 and immature females as old as 11 were reported, and age at maturity varied much less within a stock than amongst stocks. The percentages of mature males were equal to those for females at typically just under a year less in age. There was a tendency for late maturity in slow growing stocks such as Munising Bay, East Traverse and Bayfield while the fastest growth (North Shore 1966-67) was associated with the earliest maturity. But the association between growth and maturity was not wholly consistent: Leland fish were larger at all ages but matured at both a later age and larger size than North Shore fish.

Female whitefish also did not mature at a constant size in all stocks (Figure 29). Immature females as large as 540mm and mature females as small as 320 were reported, with no overlap between the schedules of small and large maturing stocks. Male maturation schedules typically lagged female schedules by 30-60mm, with most of the samples in other studies coming from the summer months.

The one association between growth characteristics and maturation which was consistent over the full range of studies was that between maximum length and the size at maturation. Whitefish and other Coregonids which matured at relatively large sizes grew to larger sizes (Table 24), and

Figure

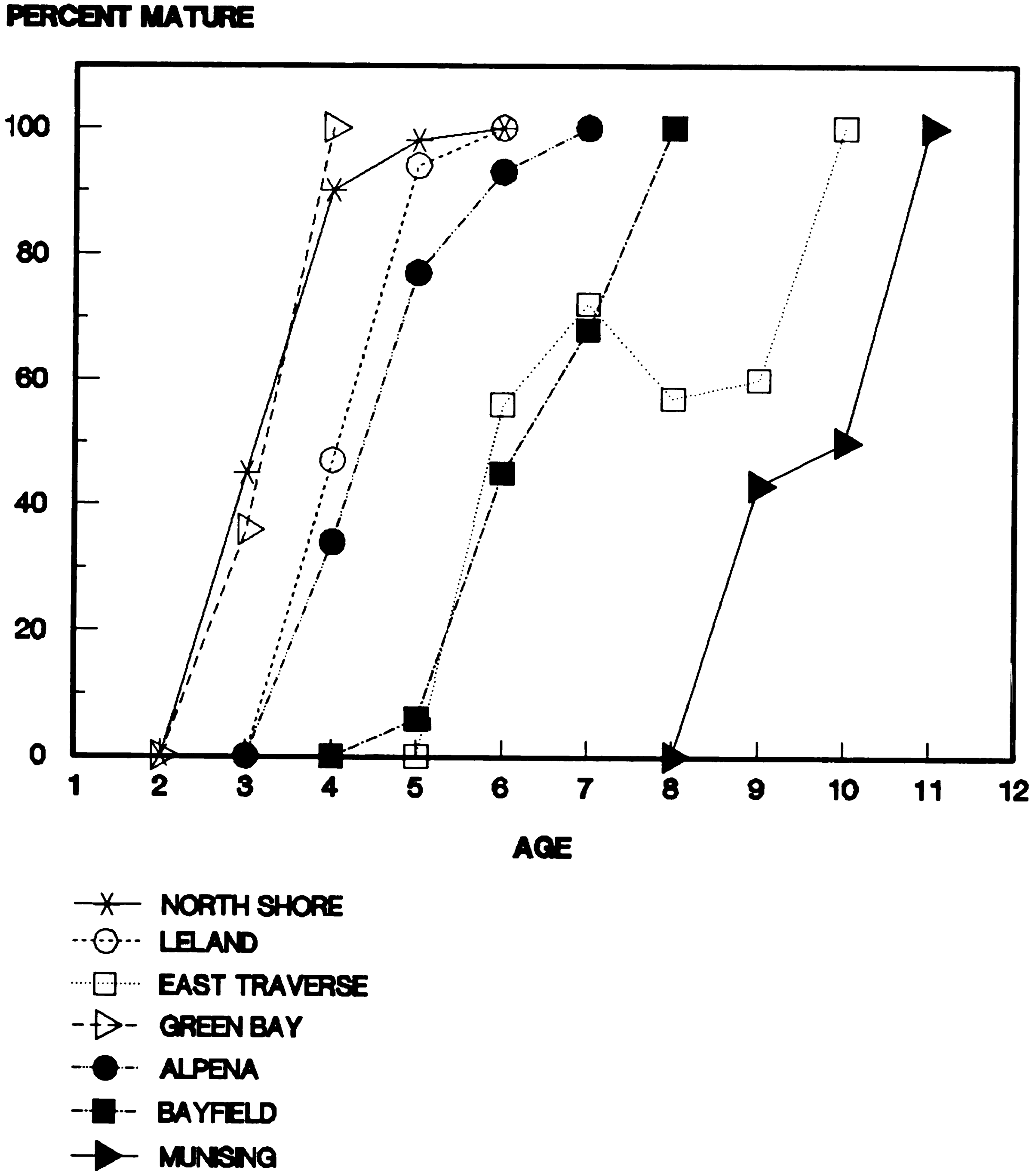

Figure 28. Age schedules of female whitefish maturation for several upper Great Lakes stocks.

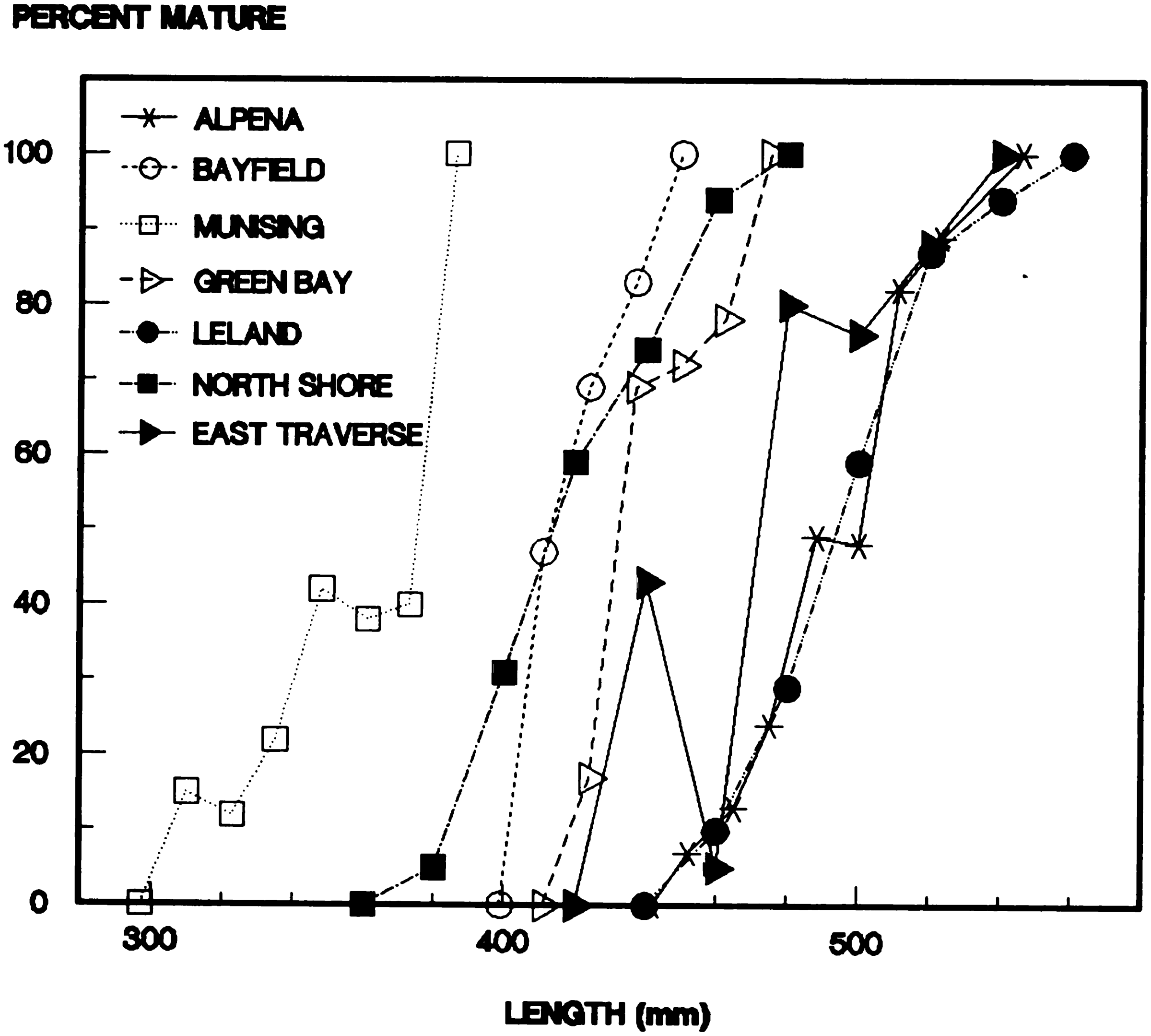

Figure 29. Length schedules of female whitefish maturation for several upper Great Lakes stocks.

Table 24. Maximum length estimates for several upper Great Lakes Coregonids and lengths at which 90 percent of the females were mature.

LOCATION	YEARS	MAXIMUM LENGTH (mm)	LENGTH OF 90 PERCENT FEMALE MATURITY (mm)
ALPENA	1922-23	685	535
LELAND	1983-84	665	525
EAST TRAVERSE	1983-84	660	510
GREEN BAY	1952	640	470
NORTH SHORE	1932	640	480
	1966-67	625	450
	1983-84	630	450
BAYFIELD	1957	580	420
MUNISING BAY	1953	450	385
(ALSO)			
MENOMINEE		470-520	~340
CISCOES		400-430	~285
BLOATERS		290-310	~210

as a rough approximation, maturity occurred at two-thirds the maximum length. This relationship held for differences between sexes within a stock: where growth potential was dimorphic, females matured at larger sizes than males. It also held for differences amongst whitefish stocks, with rankings of stocks by maximum length the same as the rankings by the size at which 90 percent of the females became mature. Other Coregonid species followed the same pattern, with the smallest species, bloaters, maturing at the smallest size followed by ciscoes, menominee and whitefish. Amongst sexes, populations and related species, neither life history trait was constant in relation to age or size, but the relationship of one to the other in terms of proportions by size was constant within allowances for error.

Spring and fall North Shore samples were examined to consider the effect of season on maturation schedules. For males (Tables 25 and 26, Figure 30) there was no significant seasonal difference (Chi-square, $P < 0.05$) in length schedules but much younger mature males were found in fall samples than in the spring. For females, the opposite pattern occurred, with no shift in age schedules from spring to fall but with much larger immature females found in the fall samples. Males were occasionally found throughout the sampling season whose maturity was ambiguous: only segments of the gonads were developed. These fish were assumed to be in the process of maturing. But no partially mature females were found; eggs were at the same stage of development or the

Table 25. Age schedules of male and female maturation, 1982-84; North Shore, Leland, East Traverse and Beaver Island. For each age, the percent mature and numbers sampled (in parentheses) are listed.

MALES

AGE:	NORTH SHORE SPRING	NORTH SHORE FALL	LELAND	EAST TRAVERSE	BEAVER ISLAND
2:	0 (6)	0 (20)	35 (17)	--	--
3:	50 (18)	92 (62)	67 (39)	--	--
4:	89 (70)	100 (75)	89 (108)	0 (18)	50 (4)
5:	100 (40)	100 (18)	94 (53)	38 (21)	64 (11)
6:	--	--	100 (26)	67 (18)	100 (9)
7:	--	--	--	95 (20)	--
8:	--	--	--	100 (7)	--

FEMALES

AGE:	NORTH SHORE SPRING	NORTH SHORE FALL	LELAND	EAST TRAVERSE	BEAVER ISLAND
2:	0 (11)	0 (14)	0 (11)	--	--
3:	48 (25)	50 (28)	0 (50)	--	--
4:	86 (97)	96 (54)	47 (47)	0 (17)	0 (2)
5:	96 (47)	100 (25)	94 (62)	0 (8)	50 (8)
6:	100 (13)	100 (11)	100 (44)	56 (18)	100 (10)
7:	--	--	--	72 (18)	100 (4)
8:	--	--	--	57 (14)	--
9:	--	--	--	60 (5)	--
10:	--	--	--	100 (3)	--

Table 26. Length schedules of male and female maturation, 1982-84; North Shore, Leland, East Traverse and Beaver Island. For each length interval, the percent mature fish and numbers sampled (in parentheses) are listed.

MALES

	NORTH SHORE		----LELAND----		EAST	BEAVER
LENGTH:	SPRING	FALL	1981-83	1984	TRAVERSE	ISLAND
311-330	0 (4)	0 (5)	--	50 (4)	0 (8)	--
331-350	33 (6)	0 (4)	--	25 (4)	0 (5)	--
351-370	38 (8)	29 (7)	--	50 (8)	0 (9)	--
371-390	57 (7)	50 (8)	--	60 (5)	0 (5)	--
391-410	50 (12)	86 (7)	0 (1)	100 (3)	29 (7)	--
411-430	93 (14)	94 (16)	50 (4)	100 (3)	60 (10)	0 (1)
431-450	100 (33)	100 (59)	50 (12)	50 (2)	57 (14)	67 (3)
451-470	100 (34)	100 (41)	70 (20)	75 (4)	79 (24)	86 (7)
471-490	--	--	89 (28)	100 (3)	100 (18)	88 (8)
491-510	--	--	87 (38)	100 (12)	100 (16)	100 (5)
521-530	--	--	98 (40)	100 (4)	100 (12)	100 (1)

Table 25. (continued)

	FEMALES				
	NORTH SHORE		LELAND	EAST TRAVERSE	BEAVER ISLAND
	SPRING	FALL			
371-390	12 (8)	0 (6)	0 (4)	0 (4)	--
391-410	67 (12)	0 (7)	0 (5)	0 (4)	--
411-430	89 (19)	36 (11)	0 (7)	0 (3)	0 (1)
431-450	89 (53)	79 (29)	0 (12)	43 (7)	100 (1)
451-470	95 (40)	93 (27)	10 (20)	5 (11)	67 (9)
471-490	100 (24)	100 (28)	29 (17)	80 (15)	83 (6)
491-510	100 (14)	100 (15)	59 (17)	76 (21)	100 (4)
511-530	--	--	87 (38)	88 (16)	100 (1)
531-550	--	--	94 (27)	100 (11)	--
551-570	--	--	100 (22)	100 (7)	--

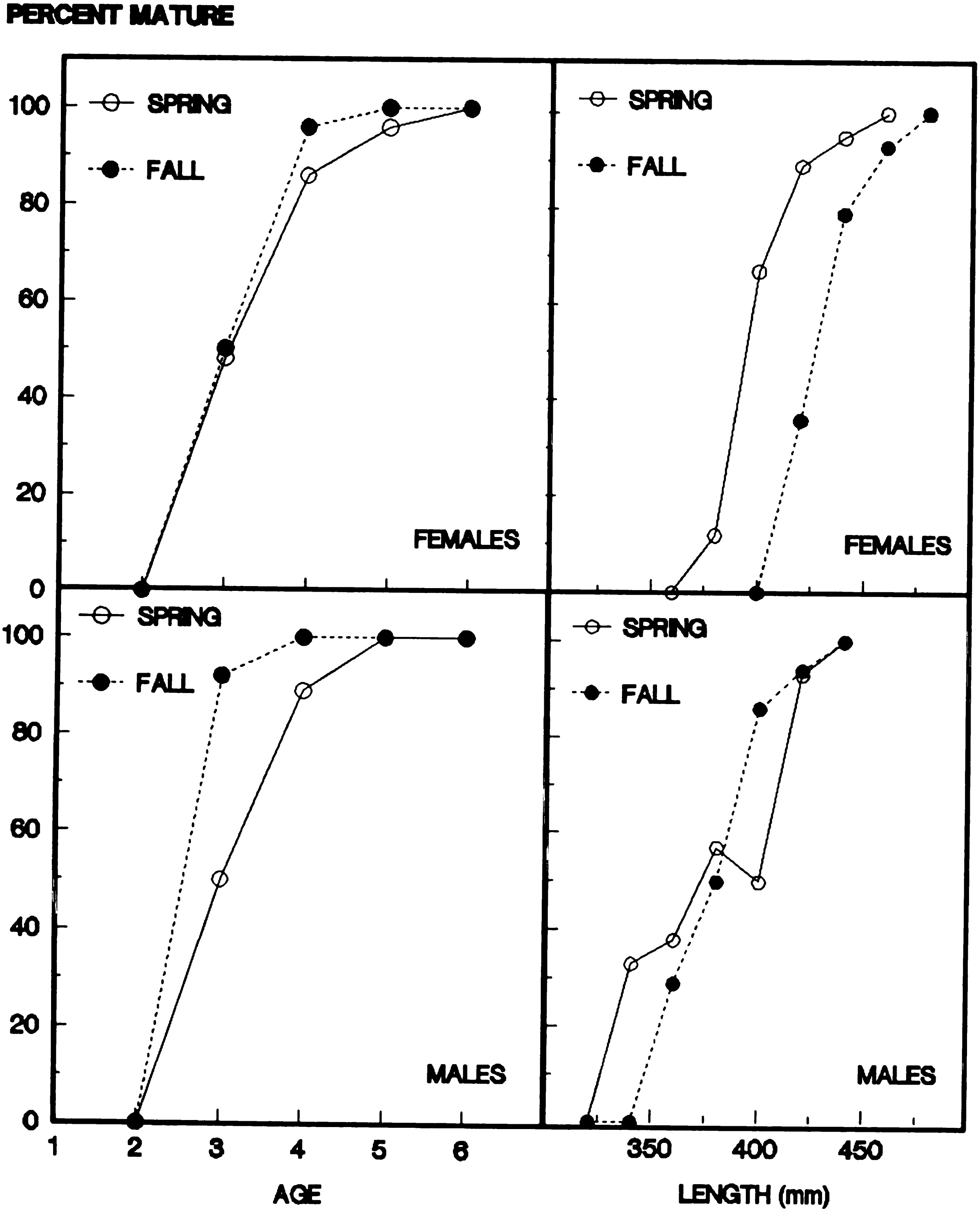

Figure 30. Schedules of maturation for North Shore whitefish by age and length for males and females from spring and fall samples.

fish was immature. Taken together, these two observations implied that males matured throughout the spring and summer whenever they reached a particular size, but females which reached a size at which they could become mature during the sampling season did not display visible characteristics of maturity until sometime during the following winter. During the spring, size schedules for North Shore males and females exhibited little if any difference, thus the observation that immature females were larger than immature males later in the season was due to the difference in seasonality of maturation. Sexual dimorphism in size at maturity was apparent only in spring samples from the Leland and East Traverse areas.

Between 1932 and 1983-84, North Shore age schedules of maturity tracked changes in growth (Figure 31). Both male and female immature whitefish were considerably older in 1932 and currently than they were in 1966-67 when growth was exceptionally rapid. In comparing maturity for the 3 time periods, seasonal differences amongst samples were accounted for by splitting data from this study such that male age schedules and female length schedules matched the seasonality of the previous studies to the extent that this was possible.

Length schedules of maturity also changed over time, with a trend toward steadilly decreasing size at maturation over time (Figure 31). The only non-significant difference was between current and 1967 male size schedules, but both males and females matured at a smaller size currently than in

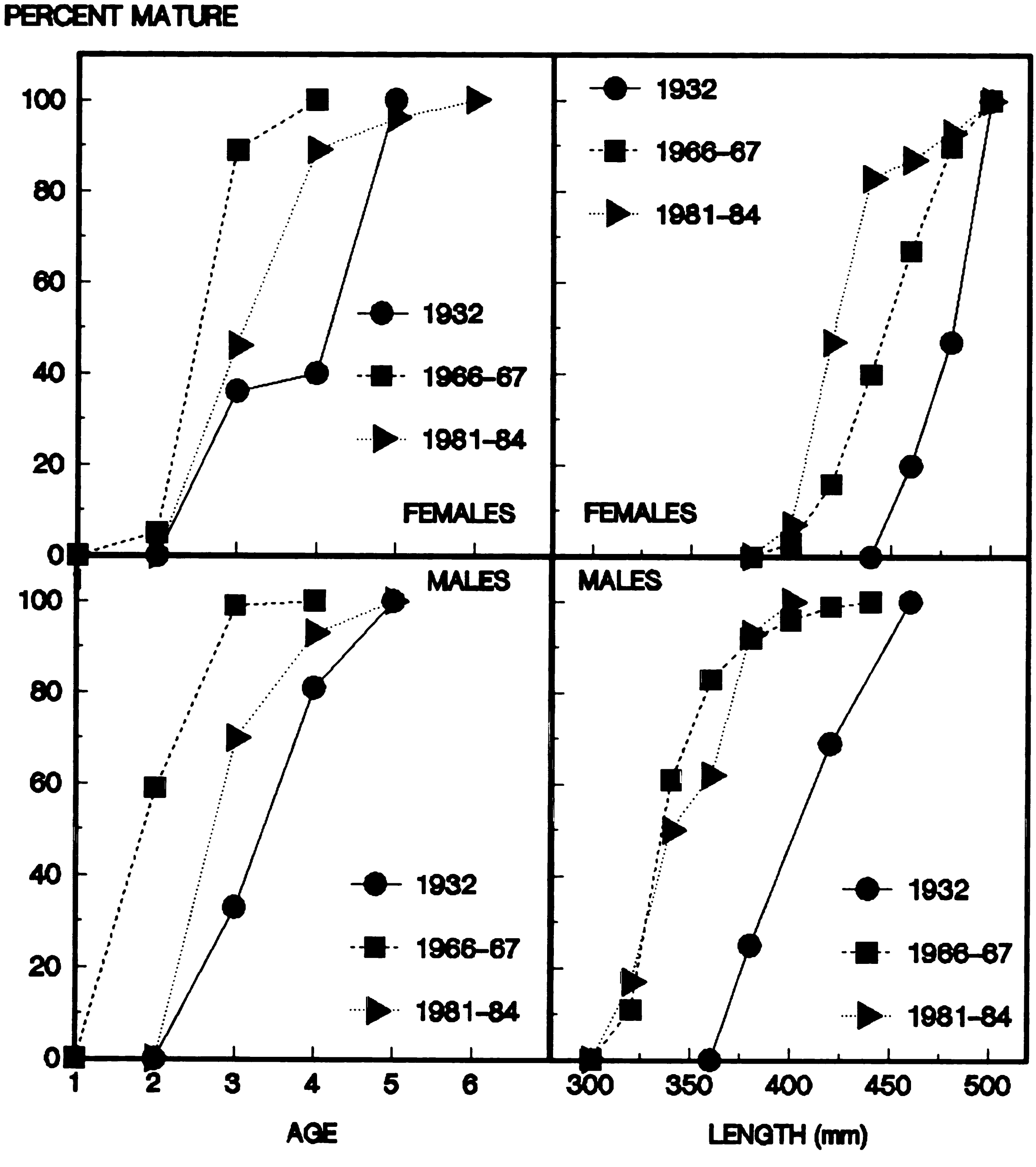

Figure 31. Schedules of maturation for North Shore whitefish by age and length from samples taken in 1932, 1967 and 1981-84.

1932 depsite the limited 1932 sample size. In comparison to the full range of variation in sizes at maturity amongst all stocks, this shift in maturity for North Shore fish was small. Whether it represented a true change in the population or resulted from an imperfect match for season or location amongst samples is uncertain.

Of the 4 study stocks, North Shore whitefish matured at both the smallest size and youngest age; Leland fish matured at an intermediate age but the largest size; and East Traverse fish matured at an intermediate size but the latest age. Another feature of the East Traverse data was the extended period of maturation: 5 partially mature ages were found compared to 2 or 3 in most other stocks. Beaver Island samples were too small for any thorough comparisons but did exhibit a slightly older age and larger size than the neighboring North Shore whitefish.

Within North Shore and Leland samples from the same season, partially mature age classes were tested to determine whether immature fish were smaller, on the average, than mature fish of the same age. Additionally, partially mature size classes of 20mm span were tested to determine whether mature fish were older than immatures of the same size. For North Shore males and females and Leland females, immature fish were significantly smaller (t-test, $P < 0.05$) than mature fish of the same age but no significant or apparent differences in age were found between mature and immature fish of similar size.

With one exception, Leland males, neither size or age schedules exhibited any apparent change during the study. Although few Leland males were sampled below 410mm prior to 1984, size schedules indicated that few if any males would be mature below 400mm. In 1984, sublegal Leland fish were more intensively sampled and mature males as small as 320mm were found. This result was probably the least expected observation during the study. These mature males were also younger than any previously found, but no corresponding change in the size or age schedules of female whitefish was found. The 1984 male size schedule was roughly bimodal (Figure 32), with half the population completing maturity by 400mm but others still immature at 470mm. These apparently precocious males were found only in Good Harbor Bay, as were most of the sublegal fish that year, were heavier than immature sublegals of the same length and seemed to have grown faster than the Leland norm.

Fecundity:

Fecundity versus weight relationships were analyzed for North Shore and Leland whitefish from ovaries collected in late October of 1983-84. A small sample (N = 11) was also analyzed from fish taken in the Alpena area of Lake Huron, but the small sample made this result inconclusive.

Fecundity estimates based on dried and weighed replicate subsamples of 200 eggs differed by an average of 2.9 percent for the 9 individuals tested. Reliability of wet weight estimates of fecundity for the same 9 fish varied by an

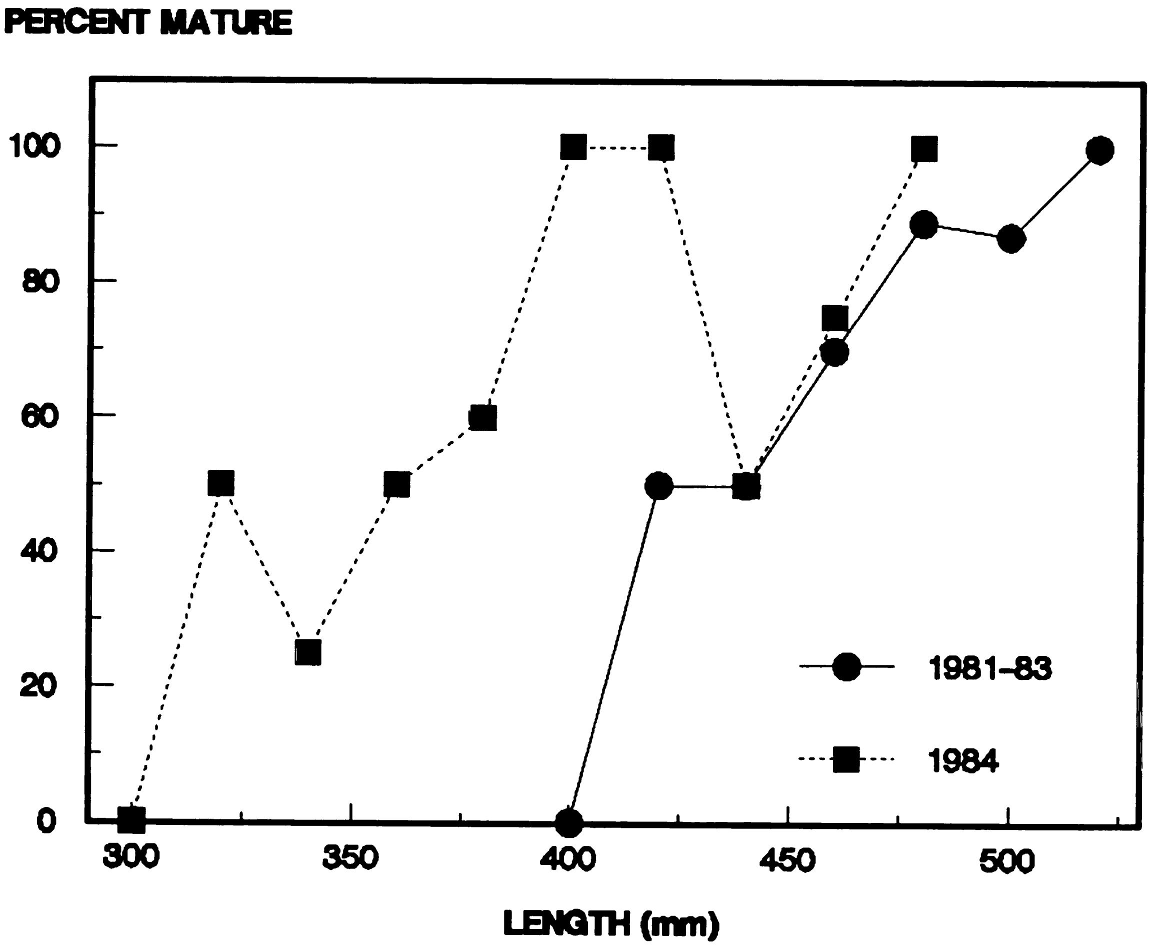

Figure 32. Length schedules of male maturation from Leland samples taken in 1981-83 and in 1984.

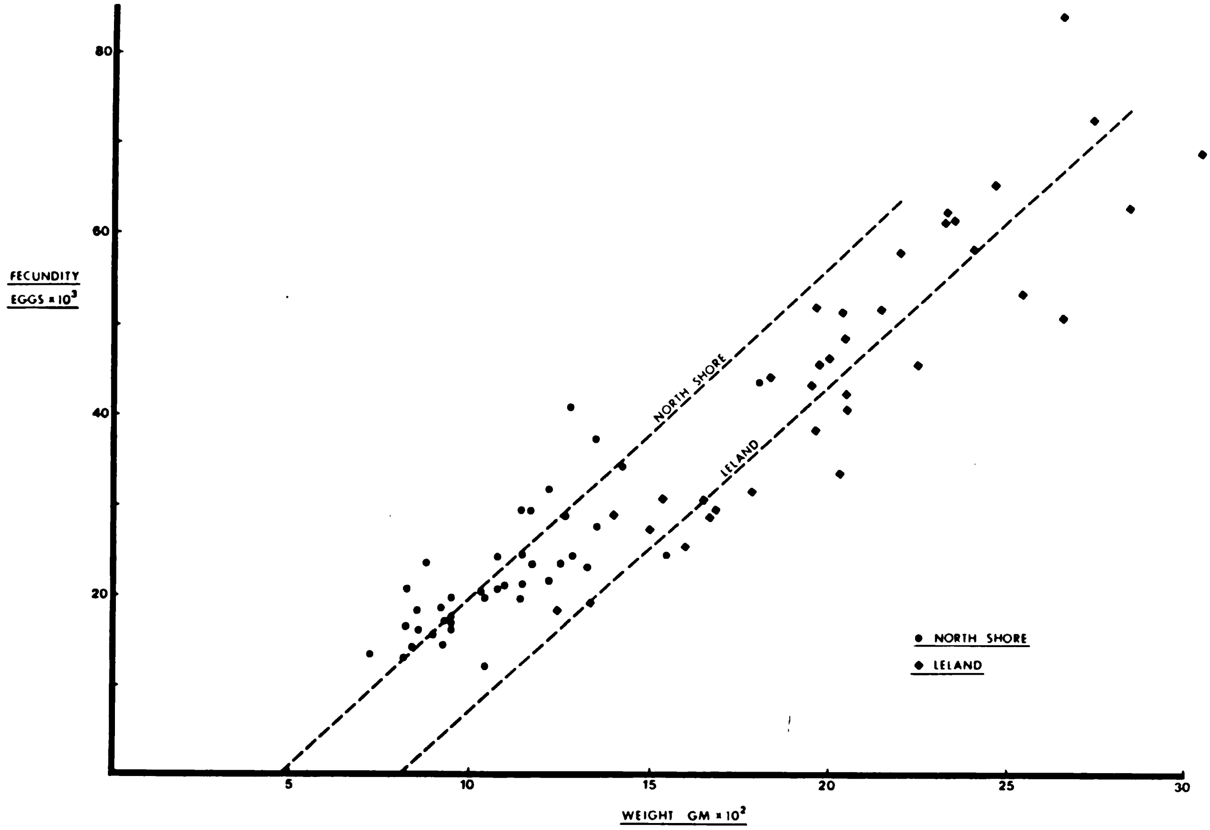

Figure 33. Scatter plots of fecundity versus weight for North Shore and Leland whitefish.

average of 11.2 percent, indicating that dry weight proportions were a more reliable technique.

Mean dry weight of Leland whitefish eggs collected during the last week of October was 7 percent greater than North Shore eggs collected at the same time, but the percent water in the eggs was equal in both groups. Leland eggs either ripened earlier than those in North Shore fish or were characteristically slightly larger.

Both stocks were characterized by considerable variation in fecundity between individuals of similar weight, but on the average, fecundity increased rapidly with weight in both areas (Figure 30). Eggs per female ranged from approximately 12,000 for a 750gram North Shore female to over 80,000 for a 2500gram Leland fish. The slope of geometric mean regressions between fecundity and weight was virtually identical in both areas, but the intercepts differed significantly both from each other and from zero. Regression equations for each area were:

(1). North Shore:

$$\text{FECUNDITY} = (\text{WEIGHT (gm)} \times 33) - 13{,}600$$

(2). Leland

$$\text{FECUNDITY} = (\text{WEIGHT (gm)} \times 36) - 29{,}300$$

Regression lines for the two stocks were parallel, and the x-axis intercept (weight at which fecundity equals zero) was similar to the weight at which female maturation began in each stock. The Alpena regression was also virtually parallel to the other two, with a higher weight axis intercept, but this difference was not significant.

The implication of the non-zero intercept is that for the average female, fecundity was not directly proportional to weight, instead relative fecundity (F/W) should increase with size of the fish. Within each stock, this increase in eggs per weight was clearly evident: mean relative fecundity (eggs/gm) of North Shore females increased from 16.1 at 800 ±100gm to 22.2 at 1300 ±100gm, and Leland relative fecudity increased, on the average, from 16.8 at 1500 ±100gm to 24.2 at 2500 ±100gm.

The wet weight of the ovaries from the Leland, North Shore and Alpena samples averaged 15 percent of female wet body weight for all 3 areas, with a range from 11 to 23 percent. Although this percentage did not differ by area, it did differ by size within an area. Ovary weight per body weight increased from an average of 13 percent to an average of 19 percent for the 15 lightest to the 15 heaviest individuals in both North Shore and Leland samples.

Age-specific effects on fecundity were tested for by calculating the average weight and average fecundity of fish at each age, then calculating the percent deviation from the expected fecundity for fish of that average weight from the fecundity on weight regressions. The calculated percent deviation was not significantly different from zero for any age group in either area, nor were any trends for this deviation to increase or decrease with age apparent.

Sex ratios:

As seems common for Great Lakes whitefish, sampled sex ratios varied strongly with season within an area. North Shore sex ratios for spring and summer samples in 1981-84 averaged 45 percent (151/337) male while October sex ratios averaged 61 (209/340) percent male. In samples taken in gill nets set on the spawning grounds in mid-November of 1983 and 1984, 80 percent (225/283) were male, but 54 percent of the 72 fish age 5 and older in these samples were female.

Leland sex ratios became increasingly feminine during the study. In October samples, when ratios were expected to be predominately male, the percent males declined from 63 percent in 1981-82 to 41 percent in 1983-84. Sex ratios of Leland juveniles were even in 1984 (29/57 were males), and the increase in the relative frequency of females occurred for recruited ages only. As the average age of the Leland stock increased from 1980 through 1985, it apparently became increasingly feminine.

Reproductive Output:

Per capita per lifetime reproductive output values, also referred to as cohort fecundity and reproductive expectancy, were calculated for current and 1966-67 North Shore whitefish and for the Leland and East Traverse populations. This statistic reflects the number of eggs expected from the average female over its lifetime past some given initial age, in this case equal to age zero fish during the fall of their first year of life. Reproductive output differs from population fecundity in that it standardizes gamete production on a per fish basis, enabling comparisons between relatively dense and sparse populations. Because this statistic integrates data on growth, survival, maturity and fecundity into one value, it offers a general description of the influence of all these characteristics on reproduction.

Reproductive output calculations used mean length and standard deviations to estimate the percentages of a given cohort which was recruited at the time each annulus was formed, and also to convert size schedules of maturity into age schedules for incompletely sampled age classes. Some smoothing of East Traverse age schedules of maturity was done and because fecundity estimates were unavailable for this stock, North Shore fecundity data were used. This substitution gave the most conservative estimate of difference. Calculations assumed that juvenile mortality ($Z = 0.50$) was constant and equal for all areas.

Cohort fecundity amongst the 4 estimates (Table 27, Figure 34) varied by over 3-fold, with the typical East Traverse female producing the fewest eggs per lifetime (1,740) followed by current North Shore females (4,784), Leland (5,429) and 1966-67 North Shore fish (5,814). The relatively low East Traverse reproductive expectancy was due to the delayed maturation in this area, resulting in fewer survivors from the initial cohort of age zero females even at the comparatively low juvenile mortality rate used. Age at maturity rather than life expectancy was the principal

Table 27. Age specific values of survivorship, maturity and fecundity used to calculate reproductive output for the North Shore, Leland and East Traverse stocks.

EAST TRAVERSE

AGE:	Z	N	MATURE WEIGHT	% MATURE	FECUNDITY	EGGS PER AGE	% OF TOTAL
0:		1000	--	0	0	0	0
	0.50						
1:		607	--	0	0	0	0
	0.50						
2:		368	--	0	0	0	0
	0.50						
3:		224	--	0	0	0	0
	0.50						
4:		136	--	0	0	0	0
	0.50						
5:		82	780	5	12,100	49,970	3
	0.50						
6:		50	840	45	14,120	317,509	18
	0.51						
7:		30	950	65	17,750	332,164	19
	0.51						
8:		18	1070	80	21,710	298,209	17
	0.52						
9:		11	1230	90	26,990	247,768	14
	0.52						
10:		6	1450	100	34,250	207,212	12
	0.53						
11:		4	1600	100	39,200	139,944	8
	0.54						
12:		2	1700	100	42,500	89,675	5
	0.56						
13:		1	1800	100	45,800	7,250	3
					SUM	= 1,739,705	

Table 27. (continued)

LELAND

AGE:	Z	N	MATURE WEIGHT	% MATURE	FECUNDITY	EGGS PER AGE	% OF TOTAL
0:		1000	--	0	0	0	0
	0.50						
1:		607	--	0	0	0	0
	0.50						
2:		368	--	0	0	0	0
	0.50						
3:		224	--	0	0	0	0
	0.53						
4:		133	1350	47	19,300	1,207,259	22
	0.76						
5:		62	1700	94	31,900	1,865,729	34
	0.88						
6:		26	2200	100	49,900	1,286,921	24
	0.94						
7:		10	2600	100	64,300	647,501	12
	0.95						
8:		4	2900	100	75,100	292,139	5
	0.95						
9:		2	3200	100	85,900	129,709	2
					SUM =	5,429,258	

Table 27. (continued)

NORTH SHORE, 1982-84

AGE:	Z	N	MATURE WEIGHT	% MATURE	FECUNDITY	EGGS PER AGE	% OF TOTAL
0:		1000	--	0	0	0	0
	0.50						
1:		607	--	0	0	0	0
	0.50						
2:		368	--	0	0	0	0
	0.50						
3:		224	780	38	12,140	1,031,189	22
	0.55						
4:		129	920	96	16,760	2,083,281	44
	0.94						
5:		51	1150	98	24,350	1,209,377	25
	1.49						
6:		11	1375	100	31,775	363,188	8
	1.49						
7:		3	1550	100	37,550	96,879	2
					SUM =	4,783,914	

NORTH SHORE, 1966-67

AGE:	Z	N	MATURE WEIGHT	% MATURE	FECUNDITY	EGGS PER AGE	% OF TOTAL
0:		1000	--	0	0	0	0
	0.50						
1:		607	--	0	0	0	0
	0.50						
2:		368	780	5	12,140	223,570	4
	0.67						
3:		188	1130	89	23,690	3,957,486	68
	1.50						
4:		42	1380	100	31,940	1,337,647	23
	1.66						
5:		8	1540	100	37,220	295,527	5
					SUM =	5,814,230	

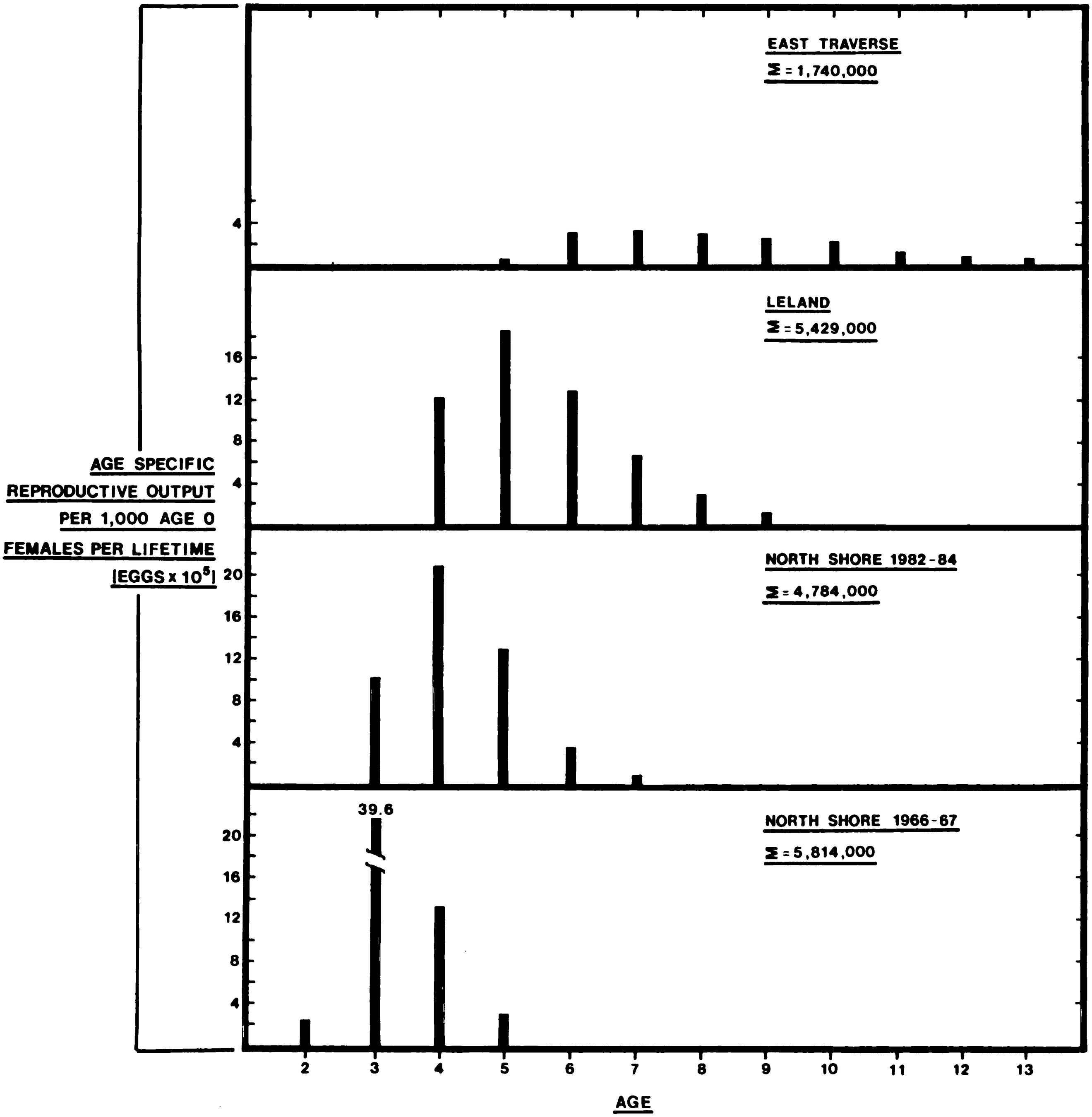

Figure 34. Estimates of the average production of eggs per female per lifetime, with contributions from each age group for East Traverse, Leland, North Shore (1982-84) and North Shore (1966-67) whitefish.

determinant of cohort fecundity in these 4 comparisons. The longest life expectancy was associated with the lowest output, while the shortest life expectancy but earliest maturity yielded the greatest reproductive output.

Presumably some thinning out of natural stocks would be necessary to stimulate accelerated growth and early maturation, and these comparisons were between a population at high density relative to its carrying capacity and exploited populations at lower relative densities. But to sustain a stationary age structure and no population growth, an equilibrium survival rate from egg deposition to age zero of 2 per 1740 eggs, or 0.115 percent, would be required for the East Traverse stock. Under steady state conditions, this early life survival rate would result in population growth rates of 22 and 25 percent per year for North Shore and Leland fish. For these stocks, 0.042 and 0.037 percent of the eggs in the females prior to spawning would have to be alive after one year to maintain the population at equilibrium.

East Traverse survivorship schedules were substituted into the North Shore and Leland life tables to provide estimates of cohort fecundity in the absence of fishing mortality. Assuming that eliminating exploitation would lead to no depensatory changes in growth or survival, the maximum reprodoductive expectancies were 11,600 eggs/female and 9,800 eggs/female for Leland and North Shore fish respectively. Current outputs therefore equalled 46 and 49 percent of the potential Leland and North Shore values, and the maximum leverage that changes in exploitation could exert on equilibrium reproductive rates would be a doubling of capacity. The same doubling could also be attained if survival from egg to age zero increased by 0.4 percent. In general, small changes in survivorship early in life had an impact on egg production equal to large changes later in life.

Even though Leland fish relative to the North Shore enjoyed the advantages of roughly 20 percent per year less adult mortality, a larger size, and greater age specific fecundity, reproductive output was only slightly higher and was a lower percentage of the unexploited maximum. Two factors contributed to this effect: the delayed maturity of Leland fish and the onset of exploitation a year before fish began to reproduce. With other variables held constant, increasing the Leland size limit to 500mm, equal to the mean length of females at the 5th annulus, would increase equilibrium cohort fecundity to 7,450 eggs/female, a 37 percent increase and equal to 64 percent of the unexploited maximum. Leland somatic growth peaks near 500mm, suggesting that such a gain could be achieved with at least no penalty in yield and perhaps even an increase. A 500mm size limit for North Shore fish would increase output to 84 percent of the maximum, but because somatic growth peaks well before 500mm at the North Shore, such a change would also strongly inhibit yield.

Stocks differed not only in the amount of reproductive

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output but also in the distributions amongst age-classes. Single age-classes produced at most 19 percent of the total output for East Traverse, 34 percent for Leland, 44 percent for current and 68 percent for 1966-67 North Shore fish. Two ages were responsible for 37, 58, 69 and 91 percent of the total output in these same stocks. Increased mortality and compressed age structures were associated with increased output but also with increased dependence on fewer ages. Under steady state conditions, reproduction was favored in the exploited stocks, but the effect of one or two year-class failures would be a rapid drop in reproductive capacity compared to much less effect on East Traverse output.

To test for this buffering effect of extended reproductive life expectancy on non-equilibrium dynamics, life tables were extended over a 100 year timespan with stochastic variation in early life survival simulated and carried through the tables. In order to avoid extending this report further, more detailed results of these simulations will be reported elsewhere. But in effect, extended reproduction decreased coefficients of variance in population size and egg production, stabilizing the populations under comparable conditions of early life survival. This stability was a double-edged sword in that extended age structures reduced the ability of populations to increase when early life survival was above average for any period. The degree of buffering also depended on the extent of annual variation in early life survival. Increased variation tended to diminish the differences in coefficients between broad and compressed reproductive age structures.

Whether or not stochastic simulations are realistic and worth pursuing further is debatable. Stochasticity assumes that early life survival is independent of the number of eggs deposited and that influential factors are randomly distributed through time. These assumptions are addressed in chapter 3. There seemed to be little point to devoting a large effort to analyzing population responses to stochastic non-equilibrium effects until there was some certainty to whether or not early life survival was truly stochastic.

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DISCUSSION

The objective of this chapter was to compare vital statistics from a broad array of upper Great Lakes whitefish populations. Exploitation rates ranged from nominal to intensive and the wide variation in somatic growth enabled cross comparisons between different age and size groups. Some data also included sufficient timespan that within-stock changes were distinguishable from amongst-stock differences. Although the certainty of conclusions which can be drawn from such large scale natural experiments is limited by the lack of control over independent variables, replication over either time or location increases the degree of certainty. Natural experiments can also reject hypotheses: if populations behave in unexpected fashion, expectations need to be modified.

Most fish population studies, particularly with large populations inhabiting large bodies of water, are by necessity descriptive rather than analytical. The upper Great Lakes stocks included in this analysis represented a sample size of 10 populations at most, fewer for some variables, despite the probably hundreds of thousands of individual fish measured and the thousands of hours of work involved. Considering the effort needed, it is not surprising that a number of the fundamental hypotheses about mechanisms governing fish population behavior are still relatively untested for populations in the natural state, and that current debates over processes of growth, survival and reproduction have existed without formal resolution since the inception of fisheries science.

The ultimate goal of population dynamics is to develop models, usually explicit ones, which describe the behavior of populations and predict useful properties such as yield, persistence and stability of the populations. Various such models have been developed and proposed (i.e. Graham 1935, Beverton and Holt 1957, Ricker 1975, Deriso 1980) and each has been implemented for making management decisions. But is such model development a matter of putting the cart before the horse? Is the understanding of the basic mechanisms of growth, survival and reproduction sufficient that these processes can be simulated without risking invalid assumptions or incorrect descriptions of relationships between variables?

During their lifespan, fish undergo several ontogenic changes in behavior, morphology and physiology. While differing from the discontinuous metamorphoses typical of animals such as Crustaceans, the difference between a larval fish and the oldest fish in a population is equally profound. Chronological age has been the foundation variable for measuring, describing, analyzing and forecasting population behavior, but at least several authors (Alm 1959, Gerking and Raush 1977, Werner 1986) have concluded that size rather than chronological age determines the progression of fish through the life cycle. The objective of this part of the research was determine whether age-specific or size-specific life histories were detectable in whitefish populations in their natural state, and to incorporate this information into population theory.

The question is whether the biological age of whitefish is equivalent to their chronological age, their size or neither. For an exactly average individual in a population, there will a given life expectancy or lifespan, a given growth expectancy or potential size, and a given reproductive expectancy or gamete production. At a given point in the life cycle, an individual will have reached a particular fraction of its life, growth and reproductive expectancies, and by definition, fish of the same biological age will have attained equal fractions of their given expectancies. Two fish of the same age or same size will be equal in biological age if life history traits are either age or size dependent. A second question is whether life expectancies, growth expectancies or reproductive expectancies are independent traits or are codependent such that long life, large growth potential and high gamete production occur together.

In general, the chronological age of whitefish was found to be a biologically inert variable with only a coincidental relationship to the biological age. Processes of growth, maturity, fecundity and quite possibly survival were not detectably age specific in nature and variation in biological age independent of chronological age occurred both within and amongst stocks. This determination was not unexpected in that age-specific results seemed rare in the literature and limited to unusual circumstances, even under more rigidly controlled conditions.

But biological age was also not strictly equivalent to size either. For example, adult whitefish smaller than 350mm and juveniles larger than 500mm were found. Biological age and size seemed to be equivalent only within a stock and on the average. Members of a given stock seemed to undergo changes in characteristics of growth and maturity at similar sizes. But size alone did not account for variation amongst stocks or between individuals.

Results of this study were sufficient to reject both of the initial hypotheses that life history characteristics were either age dependent or size dependent. But traits did seem to be patterned rather than random or dependent on some other unmeasured variable. The life history of whitefish describes the series of metamorphoses from egg to senescence. As an alternative to age- or size-dependent metamorphoses, a hypothesis of proportional metamorphosis (PM) would be more inclusive. Three points in the life cycle seemed to be fixed and innate in character: size at birth, size at maturity and the maximum size an individual will attain. Each of these sizes varied amongst individuals and amongst stock-wide averages, but each seemed to occur at the same proportion in relation to the other.

Whitefish stocks exhibited a continuum of characteristics from the relatively dwarf type exemplified by Munising Bay fish to the giant type exemplified by Alpena (Figure 35).

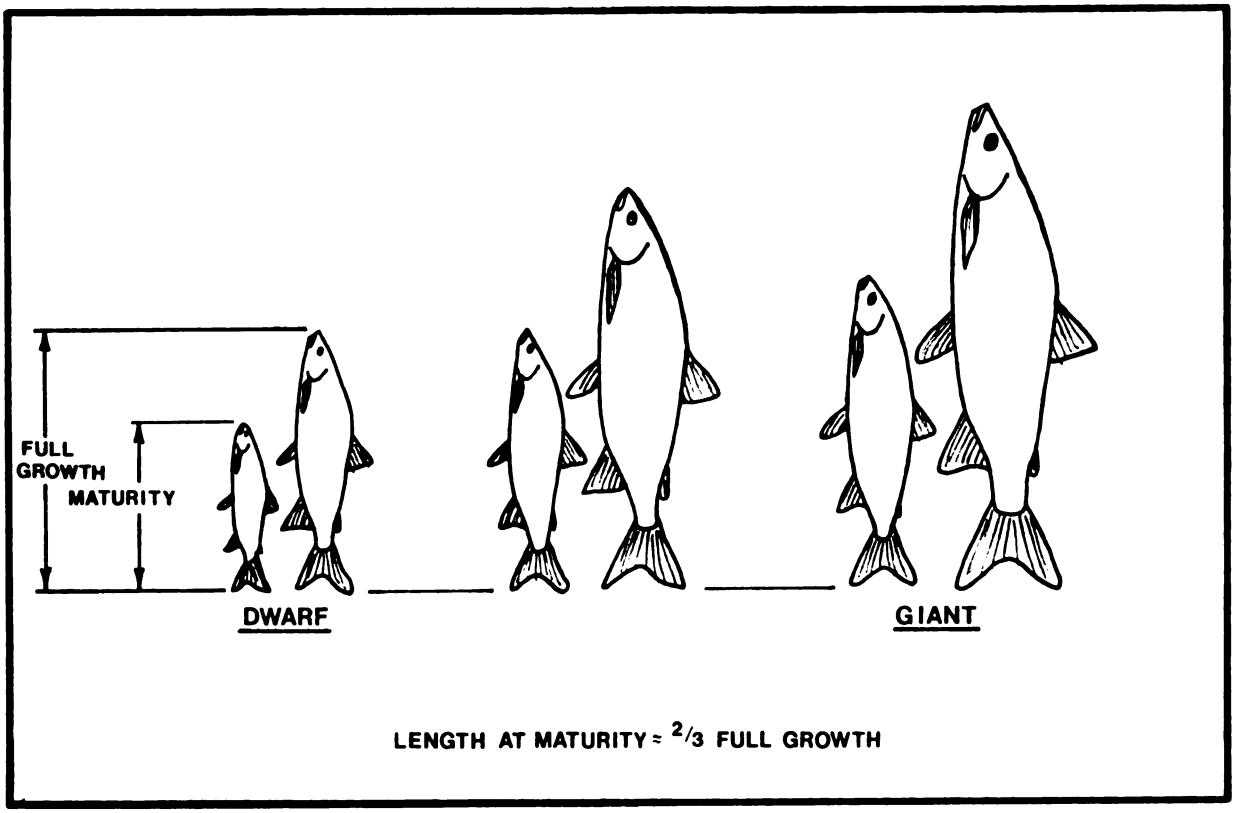

Figure 35. Expected proportions between size at maturity and maximum size of dwarf versus giant Coregonids.

Similarly, Great Lakes Coregonid species ranged in potential size from the bloater through most whitefish, thus the same kind of variation which occurred amongst populations of a species also occurred amongst species. The potential degree of genetic plasticity, both within and amongst Coregonid species can be large. But a common pattern seems to be that different individuals, sexes, populations or species represent "downsized" or "upsized" versions of each other with optional features, i.e. fin placement, mouthpart morphology etc., lending additional variation to a similar basic design pattern. Changes in growth, fecundity, morphology and perhaps survival seemed to accompany the transition from juvenile to adult. This transition did not occur at a specific age or size but occurred in proportion to the growth potential. Based on these observations, the most supportable predictor of biological age for whitefish would be its size in proportion to the size at which it matures and/or its ultimate size.

Proportional metamorphosis is an alternate hypothesis about the structure of the whitefish life history, and its potential value is that it enables traits to be predicted from each other. For example, stocks with small sizes at maturity should reach a smaller maximum size, peak in growth at or near maturation, be relatively slender in morphology and produce a high ratio of eggs per body weight. During this discussion, evidence related to age-, size- and proportion-dependent processes will be considered and compared to results from the literature. Finally, an effort to integrate this study into population theory and analysis will be developed.

Growth Potential:

Three types of observations supported the conclusion that whitefish growth was determinate, with a fixed average maximum length for fish in each stock. Maximum length estimates remained stable over time, larger maximum length estimates were not associated with increased growth rates, and maximum length varied between individuals and sometimes sexes within a stock. The conclusion that growth was determinate is not in agreement with a concensus opinion from the literature (i.e. Knight 1969), but the alternate conclusion, that increased size followed increased growth, was unsupported.

In the two available long-term Coregonid growth studies, North Shore whitefish and Lake Michigan bloaters, most of the growth variation occurred amongst smaller fish but annual increments converged towards a similar maximum length as the fish increased in size. Older age classes of fish were absent from the North Shore data and were intentionally excluded from the bloater growth record. The exclusion of old fish from the Walford plots, whether intentional or not, was justified in that smaller samples of old fish decreased the reliability of the plots, and older fish are commonly underaged (Mills 1980, Beamish and MacFarlane 1987). Although maximum length estimates in both studies were not identical over time, Walford plots are not absolutely precise and the deviations can be attributed to error. The variation in maximum length estimates within either group of Coregonids was much less than the variation amongst different stocks of the same species, and the largest maximum lengths in both cases did not occur at times when fish were growing most rapidly.

Healey (1975) reported a 3rd example from Great Slave Lake in which changes in whitefish growth did not result in increased maximum size of the fish. Examples of dwarf whitefish which were sympatric with normal whitefish and in which dwarfism was maintained over time have also been reported (Kennedy 1943, Fenderson 1964). The range of variation in maximum length amongst upper Great Lakes whitefish was by no means the most extreme example which was found for this species. Nor was the observation of a stable maximum length unprecedented.

Maximum length did not vary with growth rate amongst the several stocks considered. The most rapidly growing fish were found in the North Shore area during 1966-67, but these fish grew to a relatively moderate size. The 3 largest maximum length estimates occurred in slow (East Traverse), moderate (Alpena) and fast (Leland) growing stocks, indicating also that accelerated growth does not necessarily lead to a larger maximum size. It would seem more likely that maximum length was an innate character of the particular fish in each stock, while the time required to attain a particular fraction of the maximum length varied with environmental conditions.

The observation that maximum length varied amongst individuals and sometimes sexes from the same population was also consistent with the expectation that growth expectancy was an innate characteristic. Leland fish often outgrew the average maximum length for the population while North Shore individuals sometimes exhibited diminished annual increments at relatively small lengths. Individuals and sexes within a population shared a similar environment and presumably, if the environment determined the growth ceiling for a particular area, all members of a stock would eventually reach a common maximum size although at a varying rate. Individual variation was patterned more like variation in growth amongst humans, with some individuals growing towards a Kareem Abdul Jabbar-like stature and others reaching a more Bill Taylor-like size. The overall pattern of variation amongst maximum lengths was that this trait varied amongst individuals, sometimes between the sexes, amongst but not within widely different populations, and also amongst related species. This pattern of variation would be expected from a genetically determined trait rather than one which was environmentally determined.

Maximum length estimates also tended to increase from north to south within the region considered. Giant stocks were found at Alpena, Leland and East Traverse while the most dwarfish stocks were found in Lake Superior. Since maximum size was also associated with size at maturity, the trend may reflect a difference in reproductive characteristics as well as growth. Possibly, dwarfism was an adaptation to the more oligotrophic character or shorter growing season of the more northern areas, with fish responding to a greater potential delay in maturation by maturing at a smaller size. Alternately, if spawning success is influenced by winter conditions (see chapter 3) and reproductive life expectancy is influenced by maturity, the giantism of southern stocks could represent a bet-hedging strategy by the fish. Increased iteroparity due to the smaller fraction of eggs per weight of giant fish could enable them to reproduce more often and compensate for the more variable spawning success in southern areas by placing fewer eggs in more baskets. But whatever the ultimate cause, the observation that life history traits varied geographically should enable some general predictions about stock behavior in different areas of the region.

If growth expectancy within a stock is an innate character, it is necessary when comparing growth measurements amongst stocks to distinguish between differences due to growth potential and those due to growth rate (Figure 36). Conceivably, the smaller of two fish of the same age could actually be faster growing relative to its potential size than a larger fish. Growth measurements can be standardized to compensate for differences in maximum size simply by expressing growth in terms of the fraction of the maximum size which fish in each group attain in a given time. For

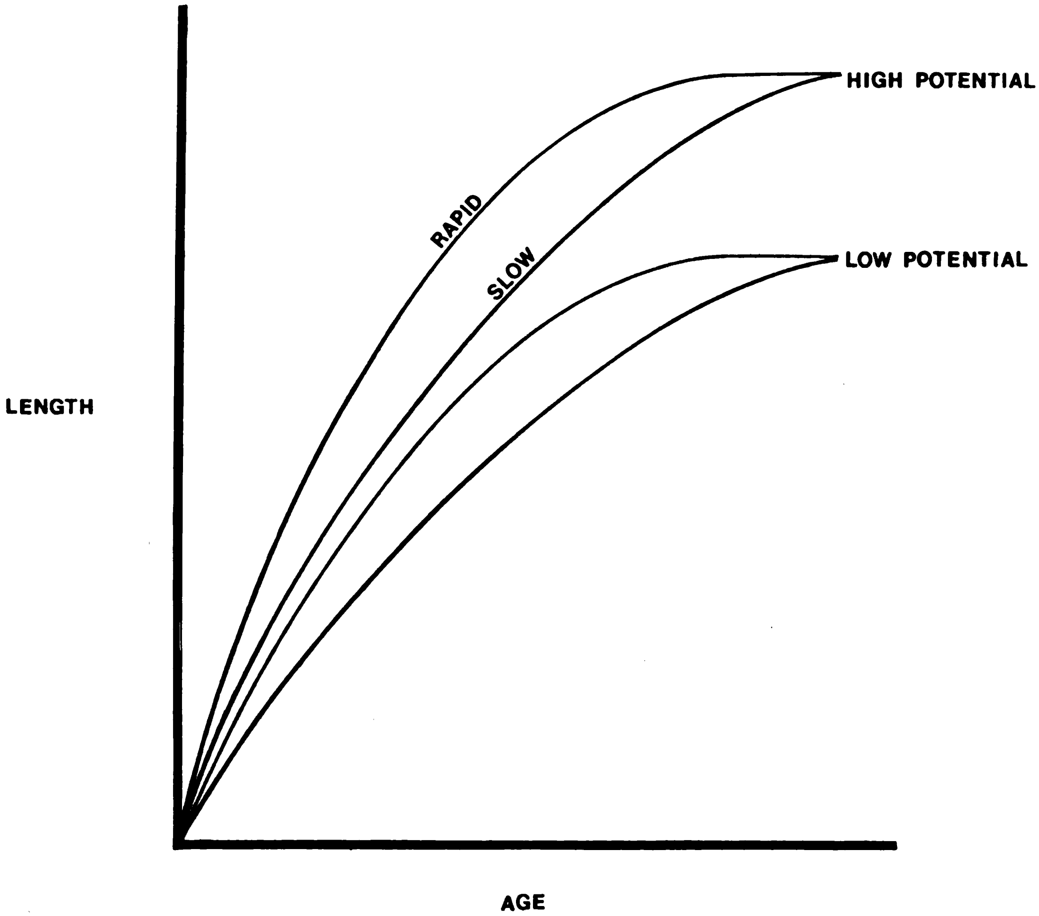

Figure 36. An illustration of the effects of differences in growth expectancy versus differences in growth rate on measured lengths at age.

example, Leland fish were larger than North Shore fish at the first annulus but fish in both areas had reached 26 percent of their maximum size during the same timespan. Differences in size at age could be due to differences in potential growth or to differences in growth rate, but treatment of the second difference as a fixed trait allows for comparisons amongst growth rates alone.

The conclusion that fish growth is indeterminate and that increased growth results in larger fish rather than fish which become large sooner was more common in the literature. This conclusion was based largely on observations that maximum size seems to vary amongst individuals and populations and that stunted fish can resume normal growth (Alm 1946 and others). The Von Betalanffy (1938) growth equation also predicts that maximum length would increase with improved rations per individual (Gulland 1977), but this expectation has not been reliably confirmed. Variation in growth expectancy within a species can be attributed to genetic variation amongst individuals, populations or races as easilly as it can to environmental variation. Recovery from stunting also does not exclude determinate growth: stunted fish may simply occur when food per fish ratios prohibit growth at sizes well below the maximum the fish could have attained.

Studies of fish growth almost always are able to only measure the presence of growth but not its absence. If spaces between annuli are absent or too small to be detected, the lack of measurable growth will not be seen. The illusion that fish continue to grow throughout their life could be an artifact of biased aging techniques. Mills (1980) illustrated how aging errors in whitefish could lead to the false conclusion that growth was continuous. Edsall (1960) reported that annuli of many of the larger Munising Bay whitefish were too closely spaced to be read, indicating that growth increments too small for measurement can also be found in Great Lakes stocks. Perhaps the expectation of finite whitefish growth has been overlooked because few fish in exploited stocks reach their full growth expectancy and because there is no method for measuring the absence of growth in fish which have.

Growth and Density:

Of the two comparisons relevant to density dependent growth, the accelerated North Shore growth during 1966-67 was a clearer example of this effect than the comparisons between exploited and unexploited stocks. This comparison was not influenced by differences in stock-specific characteristics of the fish, and the low catch during the period indicated that the abundance of whitefish in the area was definitely suppressed. In 1932 and 1983-84, whitefish catch was well above the Lakewide mean and growth was relatively slow. This growth differential affected the youngest fish to the greatest extent: age 1 whitefish differed in length by 29 percent between 1966-67 and this study, but this difference had actually decreased to 20 percent in length by age 4.

Healey (1975) found a relationship between increased exploitation and increased growth when many locations were considered, but both his study and this one found considerable growth variation from stock to stock within both the exploited and unexploited groups. Differences in growth expectancy could explain some variation amongst unexploited stocks. For example both East Traverse fish and Munising fish grew to very different sizes but both took over 10 years to achieve 90 percent of their maximum length. The relationship between exploitation and density was also apparently quite ambiguous. North Shore stock densities varied considerably despite a high rate of exploitation. At Leland, the catch record indicated that whitefish were most abundandant in 1981 due to the large 1977 year-class, 5 years after the fishery was reopened. Because population density varies independently of exploitation rate, growth cannot be reliably forecast from exploitation rates.

First-year growth of both Leland and North Shore year-classes exhibited an inverse relationship with the abundance of each cohort. Freeberg (1986) found that larval growth and survival both increased in Grand Traverse Bay when zooplankton per larvae ratios were high. Perhaps this growth advantage during the larval stage was maintained throughout the first year of life. Other studies (Mraz 1964, Henderson et al 1983) concluded that because members of large cohorts grew more slowly after age 1, their growth was density dependent. But this conclusion was reached by comparisons

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amongst groups of equal age but unequal size. Given the typically size-dependent but age-independent nature of most fish growth (Larkin et al 1957, Alm 1959, Gerking 1971), such comparisons cannot be considered valid. The differences in growth amongst cohorts argue more strongly that increased early life growth leads to greater survival and density.

Growth and Size:

As fish become older and larger, endogenous influences on growth such as the conversion efficiency of protein to tissue, metabolic rates, surface area to volume relationships and gut surface area to weight relationships change, creating a process of feedback which inhibits growth. In most cases, this inhibition was found to be influenced by the size of fish rather than their age. Gerking (1959) concluded that relationships between size and chronological age were used to assess growth only because of habit and conformity rather than because of any documented relationship between the two variables. Whitefish growth rates definitely diminish through the life cycle: larvae double in weight in a few weeks while adults require years for doubling. Instantaneous growth rates decreased with size and age in all 3 study stocks, and several observations indicated this deceleration of growth was size-dependent rather than age-dependent.

First of all, growth compensation was prevalent in comparisons between individuals from the same stock, between year-classes and time periods, and also between stocks. Secondly, variation in length amongst individuals in an age group was at least very similar for cohorts which were the same mean length regardless of their age or location. Thirdly, whitefish of similar growth potential reached peak growth increments in weight at similar sizes but very different ages.

If growth was age-dependent, growth would decrease by the same amount for fish of the same age and growth curves would steadilly diverge with increasing age. Growth would cease at the same age, even though fish were a different size. But if growth was size dependent, the feedback of size on growth would be least for the smallest fish and slower growing fish would continue to grow even though larger fish of the same age had ceased growth because of their large size (Figure 35). Size-dependent growth and determinate growth are therefore mutually complimentary effects because the effect of size on growth should be equal for fish of the same size. Assuming rations are above maintenance levels, small fish should continue to grow until they reach a size at which their physiology cannot sustain further growth even though they take much longer to reach this size.

In cases where the estimated maximum length of the whitefish were similar, fish which grew slowly initially grew more rapidly than others of the same age. But when growth was plotted in relation to length of the fish, they were found to be growing more slowly than fish of the same length at an earlier age. In order to make valid growth comparisons, only the length of time to grow from one size to another can be compared but the amount of growth between two ages cannot. But in cases such as North Shore versus Leland comparisons where fish differed in their growth expectancy, growth decreased by the same amount but at a smaller size for those fish with the smaller maximum length. The effect of size on growth was therefore not equal for fish of the same size and increments diminished in proportion to the maximum length. North Shore and Leland growth rates were equal when expressed as fractions of the maximum length, suggesting that the feedback which size exerts on growth is the same for fish which have attained the same fraction of their maximum size rather than for fish which are the same absolute size.

Growth in length exhibited 3 discrete stanzas in all stocks when plotted in relation to length. Very rapid growth below 200mm was followed by a stanza of constant increments until adult lengths were attained and then by a 3rd stanza of consecutively diminishing increments. The presence of discrete stanzas rather than a smoothly continuous rate of change in growth would complicate standard growth models, but this effect was consistent enough that it needs to be addressed before accurate models could be developed. Transitions from one stanza to another did not occur at specific ages, i.e. East Traverse increments did not exhibit the diminishing phase characteristic of adult fish until after the 7th annulus but North Shore and Leland fish reached this inflection after the 3rd and 4th annuli. Transitions did not occur at an equal length either: the more dwarfish North

Shore fish exhibited adult growth characteristics circa 400mm in length while the giant Leland fish delayed this inflection until after 470mm.

The changes in mean annular scale radius with increasing age at capture indicated that the growth data were influenced by size-selective mortality (Ricker 1969). But the effect of size-selective mortality on growth measurements may be much different than is typically expected. If growth was age dependent, selective mortality of the largest fish would also result in the earliest death of the fastest growing individuals. But the size-dependency of growth implies that selective mortality of larger fish would leave smaller fish, which are faster growing than larger fish, behind. For this reason, size-selective mortality should bias growth results such that growth prior to recruitment will be underestimated and growth following recruitment will be overestimated if larger fish are selectively harvested at younger ages. Mortality was size selective in this study, even in the unexploited East Traverse stock, and growth estimates were presumably biased by this effect. But size-selectivity was present in all cases, making results comparable even though juvenile growth was underestimated relative to adult growth by some undetermined amount.

The size-dependency of somatic growth leads to an apparent paradox in "age and growth" studies. For purposes of analysis and comparison, the chronological age of whitefish was irrelevant to growth but the size was important. An annual increment of 50mm would be slow growth for a 200mm fish and rapid growth for a 500mm fish. But whether this growth occurred at age 3 or age 5 was unimportant because age per se had no effect on growth. But measurements of the age of fishes is usually necessary in order to measure growth: annuli must be identified and spaces between them measured. Annuli therefore provide a measurement of the timespan required for a specific amount of growth to occur, but to interpret the biological meaning of this amount, comparisons must be made between fish of the same size rather than the same age. No determination can be made of whether one growth rate is more rapid than another unless the amount of time taken to grow between the same two sizes is compared.

There is an alternate method for calculating the relationship between size and timespan which seems rarely used but offers some advantages over traditional methods. Given a scatter plot of size versus age measurements from a sample of fish, there is no reason that mean growth cannot be estimated by averaging the ages of all fish of the same size to give a relationship between mean age at size and size. The traditional method of averaging sizes at specific ages encounters problems with sample truncation, or size-selective bias, because only the larger members of partially vulnerable age groups are included in the sample. Since most if not all sampling gears are size-specific but not age specific, estimates of the mean age of fish at any given size would be unbiased by selectivity. There seems to be a general assumption throughout the literature that because plots of size on the independent variable of age are referred to as growth measurements, there must be some biological relationship between these variables. But there is little in the literature or in this study to support this assumption. Even though the identification of annuli is necessary to measure the growth process, the assumption that a biological relationship between age and growth exists has probably inhibited the overall understanding of the growth process.

Growth in Weight:

When whitefish were sampled over a full span of lengths from early juveniles to older adults, inflections in the rate of weight gain relative to length were found. In East Traverse samples, which included the largest range of lengths, two transitions in the length-weight relationship occurred. Both transitions occurred at lengths similar to those at which growth in length changed from one stanza to another. For juveniles in all areas, length-weight exponents increased with increasing length until fish reached adult lengths, when exponents declined to isometric rates or below. This inflection occurred at a smaller length for males than females, and mature fish were heavier on the average than immatures of the same length. There was a consistent relationship between maturity and growth in weight relative to length, indicating that the metamorphosis from juvenile to adult was accompanied by changes in body morphology.

Least-squares regression analysis of length-weight data was complicated by several factors. Non-linearities in weight gain resulted in variation in exponent estimates due to the inclusion of different spans and ranges of lengths, particularly when both juveniles and adults were included in the regression sample. Statistics were also influenced by unbalanced samples, sample truncation and the choice of dependent and independent variables. These problems were mainly overcome by averaging weights at specific length increments from large samples but not all studies used this technique.

Samples which were not segregated by sex commonly overestimated exponents because of the increasing frequency of heavier females at longer lengths. Some of the apparent growth in weight in stocks would be due to the increasing depletion of slenderer members of the stock with increasing length rather than to actual growth of the fish if this shift in morphology was not accounted for. Since small errors in length-weight exponents can have relatively large impacts on growth estimates, variation in weight gain deserves careful attention.

For adult whitefish, no difference in the mean instantaneous growth rates were found between members of the overall fastest growing stock (Leland) and members of the slowest growing stock (East Traverse). Variation in growth occurred only amongst prerecruits, with the most pronounced difference in growth of fish of thesame length occurring amongst the smallest fish. The lower growth rates of adult North Shore fish seemed more a result of the lower growth expectancy of fish in this stock than of any environmental factor: North Shore fish attained similar percentages of their maximum length and weight during the same amount of time as did Leland fish. The absence of any true growth variation amongst adult fish might occur because their growth is regulated more by physiological restraints or because growth is limited by the amount of time which can be spent in feeding habitats. Prerecruits were the only phase of the life cycle which exhibited growth variation which could be considered density dependent.

Plotting annual weight increments in relation to length of the fish was suggested by Ricker (1945) as a means to set length limits which maximized yield. In the three stocks for which this method was applied, the peaks in growth were independent of growth rates but did vary with growth expectancy. In the two largest-growing stocks, weight increments peaked at similar lengths even though growth rates were entirely dissimilar. North Shore growth peaked at a shorter length despite faster growth than East Traverse fish, indicating that growth maxima occurred at a given point in the life history. Although these results applied to 3 stocks, each was quite different in character, and the implication is that the size at which growth peaks in a population is constant for that population and also predictable from other life history traits.

Sexual Maturity:

Several studies of maturation in fish have concluded that maturity is size-dependent and age-independent, and that inter-population and racial differences in size at maturity within a species are due to genetic differences (Alm 1959, Gerking 1959, Nikolsky 1963, Wydoski and Cooper 1966, Wolfert 1969, Ennis 1970). The expectation that maturity of whitefish was determined by size independently of age was consistent with most of the results from this study, as was the observation that size at maturity varies amongst but not within different populations. Some observations from this study however, suggested that male maturation may be a more complex process than a simple size-dependent event.

Seasonality of maturation differed between the sexes in North Shore samples. For males, apparently maturing fish were found during the growing season and size schedules of maturity remained fixed while the ages of mature males decreased from spring to fall. Males appeared to mature during the growing season whenever they reached a specific size. Female egg development was synchronous during the sampling season and age schedules remained fixed while larger immatures were present in fall samples compared to spring. Females may have become mature during the sampling season, but if they did, no visible signs of sexual maturity were apparent until after the following winter. This observation made sense in that females which matured in late summer would have less time to ripen and develop eggs by November, therefore delaying egg development until winter would allow for synchronous development the following year.

An implication of this difference in seasonality is that comparisons between male age schedules of maturity would differ depending on the time of year of sampling, as would length schedules for female whitefish. Conversely, age schedule comparisons amongst females and length schedules amongst males should be valid for any season. From visual determinations of maturity, females tended to overshoot the size of maturity determined from spring schedules. Even though immature females were larger than immature males in summer and fall samples, this effect was due to the difference in seasonality and sexual dimorphism in length at maturity was actually negligible for North Shore whitefish. The limited spring samples from East Traverse and Leland did display distinct dimorphism, and these were also the only stocks in which growth was also dimorphic.

The ages at which female whitefish matured varied from 2 to 12, and along with the general trend of earlier maturation with accelerated growth, enabled a definite rejection of age dependent maturity of whitefish. But variation in size schedules of maturity amongst stocks was too large to be explained by seasonal effects on sampling, which indicated clearly that different populations reached maturity at different sizes. Similar variation in length schedules has been found with other species and attributed to racial differences, in which case size at maturity may differ amongst populations but should remain constant for any given population.

Ages at maturity in the North Shore stock tracked changes in growth between 1932 and 1984. For example, nearly 90 percent of the age 3 females were mature in 1967 compared to approximately 40 percent in 1932 and 1981-84. But size schedules of North Shore maturation from different times also differed significantly with a trend of decreasing size at maturity for both sexes since 1932 and for females only between 1967 and this study. This result could be discounted as due to differences in either the location or timing of sampling amongst the studies. The 1932 sample was a single shot sample landed at Naubinway in October and could have been from a sub-stock with characteristics atypical of the North Shore area. Sampling locations in both this and the 1967 study were well homogenized by location, but the reported dates of maturity sampling in 1967 enabled only an approximate match with current sampling. Male size schedules are insensitive to seasonality and these did not differ from 1967 to now. The only size-specific difference was amongst females, which are sensitive to seasonality, and this may have been due simply to a failure to match the timing of previous measurements.

An alternate explanation of the apparent shift in North Shore length schedules would be that over the approximately 15 generations since 1932, the fishery has selectively culled the larger maturing fish and selected for characteristically smaller maturing brood stock. Previous examples of selection by sustained commercial fisheries for size-specific traits such as growth include Pacific salmon (Ricker 1981) and whitefish (Handford et al 1977). Given the relationship found in this study between growth and maturation characteristics, a selective advantage due to the ability to reproduce before becoming vulnerable to exploitation should be a favored trait in intensely exploited areas. Such selection should be accompanied by a selection for a smaller growth potential. The 1932 sample also exhibited a larger estimated maximum length than more recent samples but whether these effects can be taken at face value is not certain. In any case, the shift in length schedules within the North Shore stock was small relative to the entire range of differences in maturation in the region and does not allow a rejection of the hypothesis that length at maturity is fixed and stock specific.

Other results also supported the size dependent maturity hypothesis. Immature fish were consistently smaller than matures of the same age, but there was some overlap in size of the two groups. This would tend to indicate that different individuals within a population are programmed to mature at slightly different sizes. Secondly, maturation appeared to be extended over a broader span of ages in the East Traverse area and this slow rate of maturation would be consistent with a size dependent window of maturation (Figure 37). With coefficients of variance in length at age which are equal for cohorts of the same mean length, the timespan needed for fish

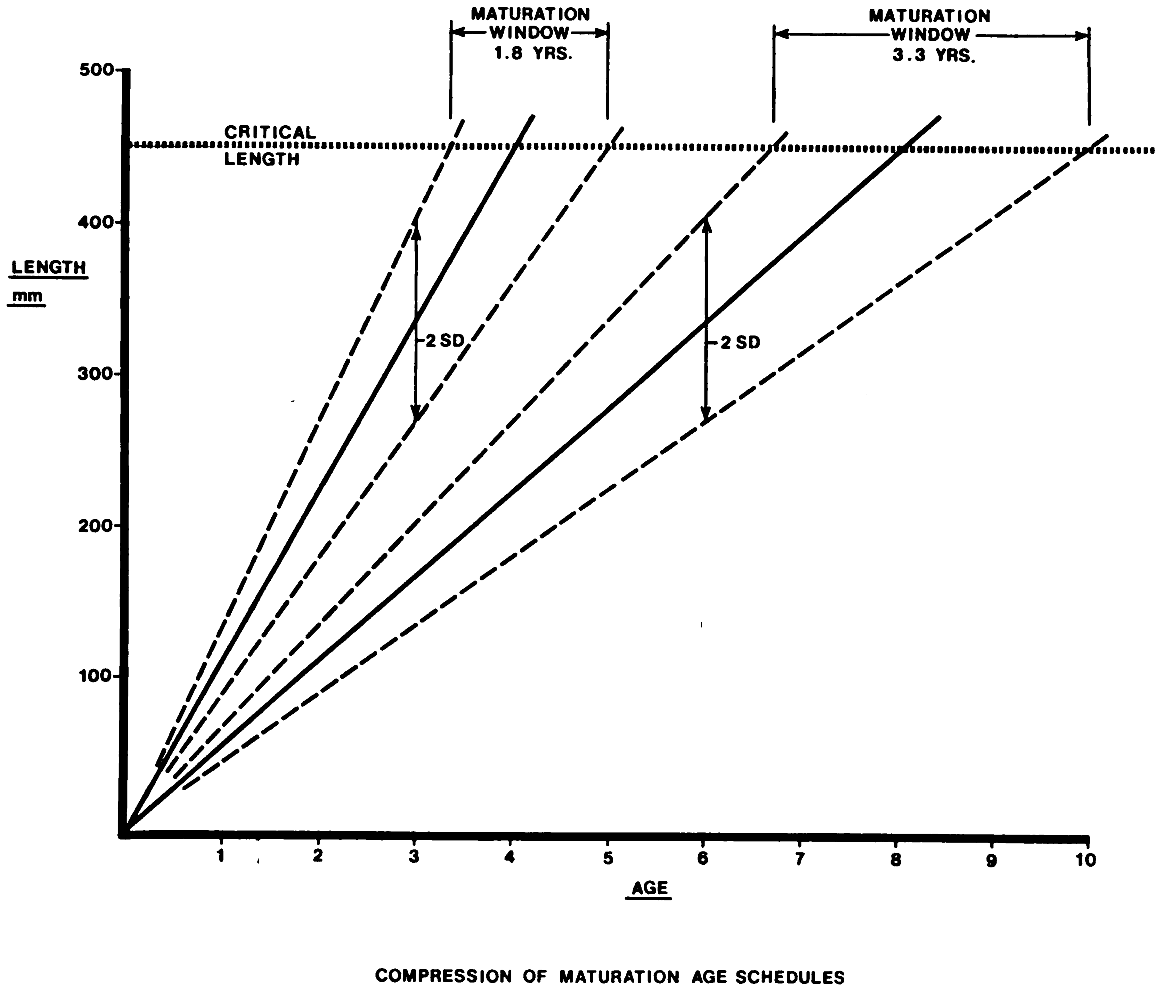

Figure 37. Effects of slow and rapid growth on the number of partially mature age groups in a population given a specific length at maturity and constant coefficients of variance in length.

which are 2 standard deviations apart in length to intercept a given length at maturity should increase with decreased growth. In most stocks, only 2 or 3 age classes were partially mature but slower growing stocks tended to exhibit extended maturation by age.

The Leland males, however, were one very puzzling example of size independent maturation. Since few prerecruited fish were sampled prior to 1984 at Leland there is no certainty that small mature males were not present beforehand. But so few mature males less than 450mm were found before 1984 that the presence of mature males as small as 320mm was completely unexpected. Other examples of stocks which included such a wide range of sizes for juvenile and adult fish were not in the literature. No counterpart small maturing female whitefish were found, and these sublegal males were mature at an earlier age as well as a smaller size than those previously sampled at Leland. This precocisity affected only males as female length schedules did not change during 1984. Bowen (1987) recently reported precocious maturation occurring amongst male ciscoes in Lake Superior thus this effect was not entirely novel.

The only example of variation in the size of male maturation obtained under controlled conditions was reported by Sohn (1975) who found that maturation of male platyfish was influenced by social factors. Males reared in tanks with larger males matured at a larger size than those which were not. These fish were programmed to mature over a range of sizes in that there was a length below which they could not mature and a length beyond which maturation could no longer be delayed. But within this range, maturity was determined by the presence or absence of larger males. At the time these apparently precocious males were found at Leland, the stock was declining rapidly and recruited ages were becoming increasingly female. Possibly, Leland males were responding to the relative scarcity of larger males by maturing earlier and at a smaller length than normal. For whitefish at least, this effect has been previously unobserved,

Maturation and Growth:

Three associations between growth characteristics and maturation characteristics were found within and amongst stocks. First, the stanza of constant increments in length ended at lengths near those at which fish matured in each stock regardless of whether this length was reached at 3 or 8 years of age. Second, maximum increments in weight occurred at lengths near the maturation length typical for each sex and stock. Thirdly, species, sexes and individuals which matured at smaller sizes exhibited reduced growth potential. Associations between accelerated growth and early maturation have been commonly reported but an apparent influence of maturity on growth characteristics is an unusual observation. But then few studies have related growth to the size of the fish, and this observation would not be possible if growth was evaluated in relation to age.

Decreasing growth following maturity would be a sensible expectation for female fish in that they are burdened with the extra bioenergetic demand of egg production. Eggs comprised an average of 15 percent of the female body weight and are especially calorie rich in comparison to normal body tissue (Bagenal 1978). Relative fecundity, or eggs per gram of weight also increased with fish size therefore the burden of egg production should increase with size.

But for males, the direct bioenergetic costs of reproduction should be lower than for females because of the lower relative weight and caloric value of the gonads. Male growth decreased with maturity as sharply as female growth which is not necessarilly consistent with a strict bioenergetic interpretation. Reproductive costs for males might include indirect effects such as aggressive behavior and courtship, but alternately it may be that growth of adult fish is more closely regulated by the endocrine system than is normally considered. It would be interesting to know whether the precociously maturing Leland males continued to grow to normal size or if their growth was dwarfed by their precocisity. The association between growth traits and maturity was quite consistent but this type of study is unable to elucidate the physiological mechanisms responsible.

If somatic growth is analogous to interest on an investment, the observations that growth is size dependent and related to maturity should be useful in developing harvest regimes which avoid growth overfishing or underfishing. Small whitefish grew very rapidly and their growth represented high rates of return on a nickel and dime investment. Large fish grew relatively slowly and were equivalent to a low return rate on a large capital. To maximize profit, fish cannot be harvested too soon because too little capital has accumulated. But when fish have grown relatively large, the return becomes so small that there is no gain to be made from continuing the investment, particularly when it is being taxed by natural mortality. Several models address the issue of the optimum age of harvest but this age would vary with growth (Jacobson and Taylor 1985). However, the optimum size of harvest appeared not only to be independent of growth rate but also predictable from other life history traits such as maturity.

In summary, whitefish growth was found to be influenced by the stock specific potential for growth, the size (but not age) of the fish in proportion to its growth potential, and the sex of the fish. These characters were endogenous to the fish rather than exogenous. Growth was also apparently influenced by the density of the overall population but only juvenile growth was affected.

Fecundity:

Cross-comparisons of fecundity at age and fecundity at weight found no age specific effects on fecundity either amongst or within the two stocks for which data were obtained. The absence of any independent effect of age on fecundity was consistent with other studies (Svardson 1949, Bagenal 1978) and not unexpected. But additionally, expected mean fecundities for whitefish of the same weight from the two stocks were also unequal, indicating that fecundity was not a direct function of size.

In the Leland and North Shore fecundity samples, the regression between fecundity and weight intercepted the weight axis at a weight similar to that at which fish matured in each stock. This was also true for the small Alpena sample which was examined but the number of fish was too small to attachany significance to the relationship, and the maturity determination had been made 60 years previously. Slopes of the regression were equal between the stocks, but the non-zero intercept implied that fecundity per weight should increase with increasing weight. Healey and Nicol (1975) noted that whitefish fecundity from several stocks and lakes increased with length faster than weight increased with length, which is an equivalent observation.

The smaller maturation of North Shore females gave them a head start relative to Leland females but mean weight specific fecundities increased at the same rate relative to weight in both stocks. North Shore females were more fecund than Leland females of the same weight, but because Leland females were larger they were more fecund on the average than North Shore females of the same age. North Shore fish also had a higher relative fecundity than Leland fish of the same weight and this difference was maintained as weight increased. These relationships enabled a calculation of expected fecundity for a 2 meter long whitefish, and for such a hypothetical fish the weight of the gonads exceeded the predicted weight of the fish, implying she would consist of a bag of skin surrounding two giant ovaries. This extrapolation possibly illustrates limitations to the data, but on the other hand it might be useful in understanding why whitefish of this length have been nonexistent.

Because fecundity was not directly proportional to weight, population fecundity can potentially vary independently of spawning biomass with changes in the size structure of a given stock. Larger females produced more eggs per gram of weight than smaller females, therefore an increase in median weight of a stock should produce a disproportionate increase in egg production. Spawning biomass may be a decent estimator of population fecundity when fluctuations in median size are small, but in some cases estimates of egg deposition would need to take the size structure of the stock into account.

Although fecundity was measured from 2 stocks, with limited observations from a third, the pattern implied by the results was that fecundity to weight relationships should vary with size at maturity. The rate at which fecundity increases with weight should remain constant but the intercept should increase with size at maturity. If this relationship does hold true across all or most stocks, the implication is that fecundity can be predicted from other life history traits, in particular, weight at maturity.

Life Expectancy:

Fishing mortality is clearly a size specific rather than age specific influence on whitefish population dynamics. Nets are size selective but do not select for fish of particular ages independently of their size. North Shore tag returns increased with the size of the fish when tagged, presumably because of increased vulnerability to the trap-nets and gill-nets used in the fishery. Leland exploitation rates decreased for larger fish, but the shifts in the size distribution of fish in the catch indicated that the largest whitefish were accessible to the fishery mostly during the spring.

The possibility that the natural life expectancy of at least some fish is dependent on their growth history rather than being a fixed span of years has been part of the literature for some time (Nikolsky 1963). This issue has not been fully resolved but the observation that faster growing fish die sooner than those who grow slowly is not uncommon (Gerking 1959). In the context used here, the question is whether the natural life expectancy of whitefish is age-dependent i.e. they live to a particular median age; or is size specific, in which case lifespan and natural mortality vary with growth. Evidence collected for this study was not conclusive, but several observations suggested that spawning mortality was a principal source of natural mortality amongst adult whitefish, in which case life expectancy would depend on both growth and maturity.

Approximately 35 percent of the adult whitefish in each stock died each year from non-fishing causes. Sources of non-fishing mortality are difficult to determine but it seems unlikely these fish were vulnerable to predators. North Shore natural mortality was higher than for Leland fish, but this would be expected if North Shore fish were biologically older relative to maturity than Leland fish.

Regardless of the sampled sex ratios, which fluctuated seasonally in many studies, females were consistently older than males throughout a number of studies of Coregonid age distributions. This effect was prominent in unexploited stocks and was not therefore an artifact of a differential in exploitation. The sometimes larger size of females should actually make them more vulnerable to fishing, in which case survival of females to an older age would be masked by exploitation.

When North Shore samples were pooled from all seasons, there was no detectable difference between the sexes in age distribution, but then these fish exhibited relatively little difference in maturation. However, from fall to spring there was a decrease in the median age of females but not of males, which would occur if overwinter mortality increased with age of the females. Catch curves for Leland and North Shore females were convex, indicating accelerating mortality with age, but male catch curves were linear, indicating a constant mortality rate. If the biological age of whitefish is equivalent to the time past maturity, many of the females do not reach this point until after recruitment while most of the sampled males are mature at an earlier chronological age. The difference in age distributions between the sexes seemed to occur because female mortality increased at a later age than male mortality.

For older age classes in Leland and East Traverse samples, there was an increase in the length of the fish at age of capture for annuli past the 6th to 8th year. This reverse Lee's phenomenon could be due to survival which favored fish which matured at a larger than normal size and therefore grew to an atypically large size. The Lee's phenomenon at younger ages could be due to sampling selectivity or size-selective mortality, but the effect was also present in East Traverse samples where neither factor applied. An inference from this observation is that natural mortality is highest for fast growing, early maturing fish and is delayed for large-maturing, high growth expectancy individuals. Collectively, these observations would be consistent with spawning mortality of whitefish

Extremely skewed sex ratios of over 90 percent females are not uncommon amongst Coregonids, especially the smaller species such as ciscoes and bloaters (Clady 1967, Brown 1970). These ratios seemed to be associated with decreasing population size and accelerated growth. The Leland population became increasingly female during the study but to a less exaggerated extent and only amongst the recruited age classes. The Leland stock also decreased as the abundant 1977 cohort was fished out, and apparently precocious males were found when abundance had decreased substantially.

An explanation for the skewed sex ratios of Coregonid stocks can be developed from spawning mortality, precocious male maturation and a brief series of recruitment failures. If males typically die at an earlier age due to spawning mortality, females would predominate the older ages in the stock. If one or two very poor year-classes are recruited into the stock, and males respond by maturing at a smaller size and younger age, and then die shortly thereafter, the bulk of the stock would soon consist of mostly old females. This effect would be even more prominent if the few precocious males present segregated themselves from the remainder of the stock and were therefore not included in normal catch samples. Recruitment failures combined with early and accelerated male mortality due to precocisity would result in female predominance, thus the skewed sex ratios sometimes found amongst Coregonids could be considered further evidence that spawning mortality occurs.

Spawning mortality has been reported for several species, including the related trout and salmon (Scott and Crossman 1979), rainbow smelt (Schaeffer et al 1982) and plaice (Wallace 1925). In arctic lakes, where growth is slow and fish reproduce perhaps every second or third year, whitefish life expectancy seems to be greatly extended in comparison to the Great Lakes region (Power 1978). The greater life expectancy of arctic fish argues also that natural mortality is influenced by growth and maturity, and that the rate of physiological aging varies independently of the rate of chronological aging.

These several observations about patterns of mortality amongst whitefish populations are circumstantial and based on inferences which could be explained by alternate mechanisms. Direct observations of whitefish spawning mortality would be precluded by the difficulty of finding fish in a large lake in the winter, therefore more conclusive evidence was unobtainable. But the assumptions of constant and equal mortality and life expectancy in the absence of fishing, although convenient to measure and model, were even more difficult to support. Other characteristics which described the biological age of whitefish such as growth and maturity were independent of chronological age, and it is reasonable that other aging processes would focus on size relative to maturity of the fish. The relative fecundity of females increased with size, implying that each successive spawning placed a greater demand on the average fish. The explanation of spawning as a source of natural adult mortality is consistent with other expectations about the structure of the whitefish life program in that it is neither an age-dependent or size-dependent explanation. Instead, life expectancy would vary with maturation.

Reproductive Output:

The estimate that fish in an unexploited population produced only a third as many eggs per female per lifetime as did fish in exploited stocks might seem surprising. It would seem that fish which lived to a greater age should produce more eggs, but this is true only if biological age and chronological age are equivalent. The principal difference between East Traverse and other whitefish was that they took twice as long to become as old as fish in other areas if age is defined by the metamorphosis from juvenile to adult. The relatively delayed East Traverse maturation resulted in an extended juvenile period with fewer fish surviving to adulthood. The bimodal size distribution reported by Johnson (1976) for arctic whitefish may simply be a more exaggerated example of this apparent stockpiling of fish in juvenile classes when somatic growth is slow.

Previous investigators (Healey 1975, Jensen 1981, Clark 1984) have analyzed some of the expected impacts of variation in growth, mortality, fecundity and maturation on reproductive expectancy. These studies were somewhat limited in application in that the extent and interdependency of variation was fairly ambiguous for whitefish on the whole. Amongst the study populations, accelerated juvenile growth seemed to be an important response by which exploited stocks compensated for losses to the fishery. In some respects, the exploited stocks actually overcompensated. It seems unlikely to suppose that reproduction in the Leland and North Shore stocks would be gamete limited under normal circumstances if the East Traverse stock can maintain itself at a much lower rate of reproduction. The lower somatic growth rates in this stock seem also to be a buffering mechanism which stabilizes the population. Poor year-classes should deplete the stock of juveniles, resulting in accelerated growth, earlier maturity and a larger cohort fecundity to replace losses due to diminished recruitment.

Another surprising outcome of the cohort fecundity calculations was that Leland output was only slightly higher than for North Shore fish despite overall lower mortality and greater growth at Leland. This result illustrated that the point at which fishing mortality occurs in the life cycle is at least as important to determining its effect on reproduction as the actual rate of mortality. Even though Leland fish were both typically larger and chronologically older than North Shore fish, at the time of their recruitment they were biologically younger. Leland fish were exposed to exploitation for approximately a year prior to first reproduction for females, cancelling most of the gain in reproductive output from reduced mortality. In comparison to North Shore whitefish, the Leland stock illustrates that whitefish of the same size are not necessarilly of the same biological age either, and that mortality early in the life cycle has a larger impact on reproduction than mortality at a later biological age.

Van Oosten (1938) recommended a 21 inch (533mm) length limit for Alpena, whitefish which matured at a slightly larger size than Leland. Increased length limits could simultaneously reduce growth and recruitment overfishing by delaying harvest until fish had reached a larger fraction of their growth and reproductive expectancies. Size limits which are too large reduce yield because for larger fish mortality exceeds growth, and the expected increase in egg production diminishes the further length limits are extended. Setting limits based upon either the age or the size of the fish would have different impacts on yield and reproduction in different stocks, but the relationship between size at maturity and growth seemed to indicate that limits set in proportion to the size at maturity would have equivalent impacts under any conditions.

The calculations of cohort fecundity and any predictions about population behavior made from them assume that steady state conditions apply. Variation in the strength of year-classes of whitefish in the Great Lakes ranged from approximately 8-fold to 20-fold (Christie 1963, Lawler 1965, Henderson et al 1983, Hastreiter 1984), which is moderate compared to the up to 200-fold range of recruitment variation reported for some fish stocks (Cushing 1982). The observation that stocks in which somatic growth is relatively slow are buffered by extended reproduction and the latent capacity for accelerated growth may be more important under such conditions than the equilibrium properties of each stock.

Christie (1963) noted that increased fishing pressure on Lake Ontario stocks had little effect on yield averaged over time, but that oscillations in the catch increased. The North Shore and Leland stocks were apparently susceptible to boom and bust conditions, with rapid expansion following recruitment of the large 1977 year-class and a sharp contraction thereafter. The classical explanation of collapses in exploited stocks through recruitment overfishing and gamete limited reproduction did not seem to apply to these stocks. Instead, vulnerability to a short run of poor recruitments would be a more likely mechanism for stock failure.

Life History Traits and Population Behavior:

The issue with which this study was concerned was whether the life program of upper Great Lakes whitefish was age-dependent, size-dependent or neither. There is an apparent dilemna in that the discipline of population dynamics is age-dependent in nature. Relationships between chronological age and the relative abundance, size aand reproductive status of fish are used to describe the processes of survival, growth and reproduction. But there is little evidence in the literature, and none from this study, to support the supposition that age per se influences any of these underlying biological mechanisms. Given just the age of a Great Lakes whitefish, no other predictions about the growth, maturity, fecundity or life expectancy could be made about that fish. Similarly, given just the age distribution of whitefish in a population, characteristics such as yield, productivity or persistence cannot be predicted.

It seems that because plots of relative abundance, size and age specific fecundity against the independent variable of age are used to measure survival, growth and reproduction, it has been assumed, almost by default, that there must also be a biological relationship with chronological age. But such an assumption can be misleading. For example, growth variation amongst cohorts which appeared density dependent from an age-dependent viewpoint was actually the opposite from the viewpoint of size-dependent growth. Additionally, the expectation that increased life expectancy in terms of age leads to increased reproductive capacity was untrue because reproductive age is size-dependent.

Although age was found to be an inert biological variable, the alternate supposition that biological processes are strictly size-dependent was also found to be false. Whitefish were found which were the same size but differed in growth, maturity and fecundity from stock to stock. The size at which metamorphoses in growth, maturity and morphology occurred seemed to be constant for a given population but variable amongst populations. Given the length of a whitefish alone, the only prediction which could be made about that fish would be its approximate vulnerability to fishing gear of a particular mesh size. Similarly, the distribution of sizes alone in a population would not enable forecasts of productivity, yield or persistence.

Even though life history traits were patterned on neither age or size, there was an apparent organization to characteristics amongst individuals, populations and even species. Events in the life cycle occurred at neither a specific age or size, but they did occur at similar proportions of size in relation to each other. Life history traits were also apparently interdependent; small maturation was associated with a low growth expectancy, growth which peaked at a small size, relatively slender adult morphology, a high fecundity to weight ratio and a potentially shorter reproductive life expectancy.

Assuming these relationships can be replicated across other stocks, the paradigm of proportional metamorphosis would enable predictions of any of these life history characteristic to be made to be made from another. Additionally, relationships amongst life history traits would enable the construction of both simpler and more realistic population models. Specific relationships between growth, fecundity, maturation etc. could be built into equations describing one trait in terms of another without unnecessary concern about combinations of variables which are biologically "out of bounds." For example, if fecundity to weight relationships are generally described by a constant slope and an intercept equal to the weight at maturity, equations can assume these relationships to be fixed and that only variation in weight within a stock will alter fecundity. The general advantage to understanding the structure of the life program is that the potential array of combinations of descriptive variables needed to simulate population behavior becomes simultaneously simpler and more realistic.

Whether the proportions and relationships found for this relatively small sample of whitefish populations will generalize further to all or most populations will require further examination. The original hypotheses which were tested were that events in the life cycle were either age- or size-dependent, and neither was supported throughout this study. Proportional metamorphosis was proposed as an alternative and so far has worked to describe the structure of the life program amongst a wide variety of Coregonid stocks, particularlly when a degree of allowance is made for differences in technique and measurement error amongst the numerous studies from which data were borrowed.

Although chronological age was not a biologically active variable, measurements of age are still extremely useful in describing population behavior. Rather than discarding age measurements, as has been suggested (Anderson 1980), there is a need to use this information in a more appropriate manner. The biological age of a whitefish varies independently of its biological age and one age cannot necessarilly be determined from the other. But measurements of chronological age do describe the timespan required for fish to reach a particular biological age. The size of a fish in proportion to its maturity describes how old a fish is, but the chronological age describes how long fish take to reach a given age. East Traverse fish, for example, took roughly 8 years to reach the same age that Leland fish reached in 4.

In order to measure rates at which biological relationships occur, some measurement of timespan, either discrete or continuous, is required for the denominator of any rate estimate. Measurements of mortality rates, growth rates or reproductive rates cannot be made without a measurement of time which the annuli of bony structures so conveniently provide. Rates of growth, mortality and reproduction should be assessed, analyzed and compared in relation to proportional size rather than age, but aging of fish is still needed to enable these measurements.

Two distinct types of models which forecast population behavior have been used. The surplus production type of model (Gulland 1977) depends on curves fit to observed values of yield and fishing intensity. Whether or not the assumptions of equilibrium behavior are justified, this type of model is empirical rather than analytical and mechanisms of growth, survival and recruitment which respond to changes in the fishery are not explicitly considered. At best, equilibrium models enable predictions of population behavior without understanding.

The second type of model is the age-structured model developed by Beverton and Holt (1957) and Deriso (1980), which can be adapted to analyses of reproductive behavior (Jensen 1981, Clark 1984). These models simulate the growth, survival and yield from a cohort of fish as they progress in age through the fishery. In theory, they identify the combination of exploitation rate and age of recruitment which gives the best yield per recruit, and can be adapted for more extensive analyses (i.e. Jacobson and Taylor 1985). But is it reasonable to make predictions about age dependent dynamics when age is unimportant to the biology of the fish, and are there simpler alternatives?

One alternate possibility would be to develop models based on Allen (1951) curves which are used to estimate production from size-frequency distributions. Rather than treating a cohort as all fish of the same chronological age, a cohort could be defined as all fish of the same size (Figure 38) and the average age of fish of any given size calculated or measured. By treating size as an independent variable and age as a dependent variable, the rate of time for a cohort to advance from one cohort interval to another can be determined. Size specific rates of growth, fishing mortality and natural mortality could be used to calculate yield at each increment, and the model could be parameterized from either observed size-frequency and age-frequency distributions or distributions could be calculated from equations of growth and survival. This suggestion is simply a sketch of a method for constructing a size dependent model which uses age to measure rates of change, and further development of the arithmetic is required.

A second alternative would be to make use of the concept of critical size. The timing of harvest in relation to the life cycle is at least as critical as the rate of harvest. For small fish, instantaneous rates of mortality and growth both tend to be relatively high (Figure 39), but rates decrease with size as growth slows and fish become less vulnerable to predators and starvation. Because growth exceeds mortality, production to biomass ratios are above

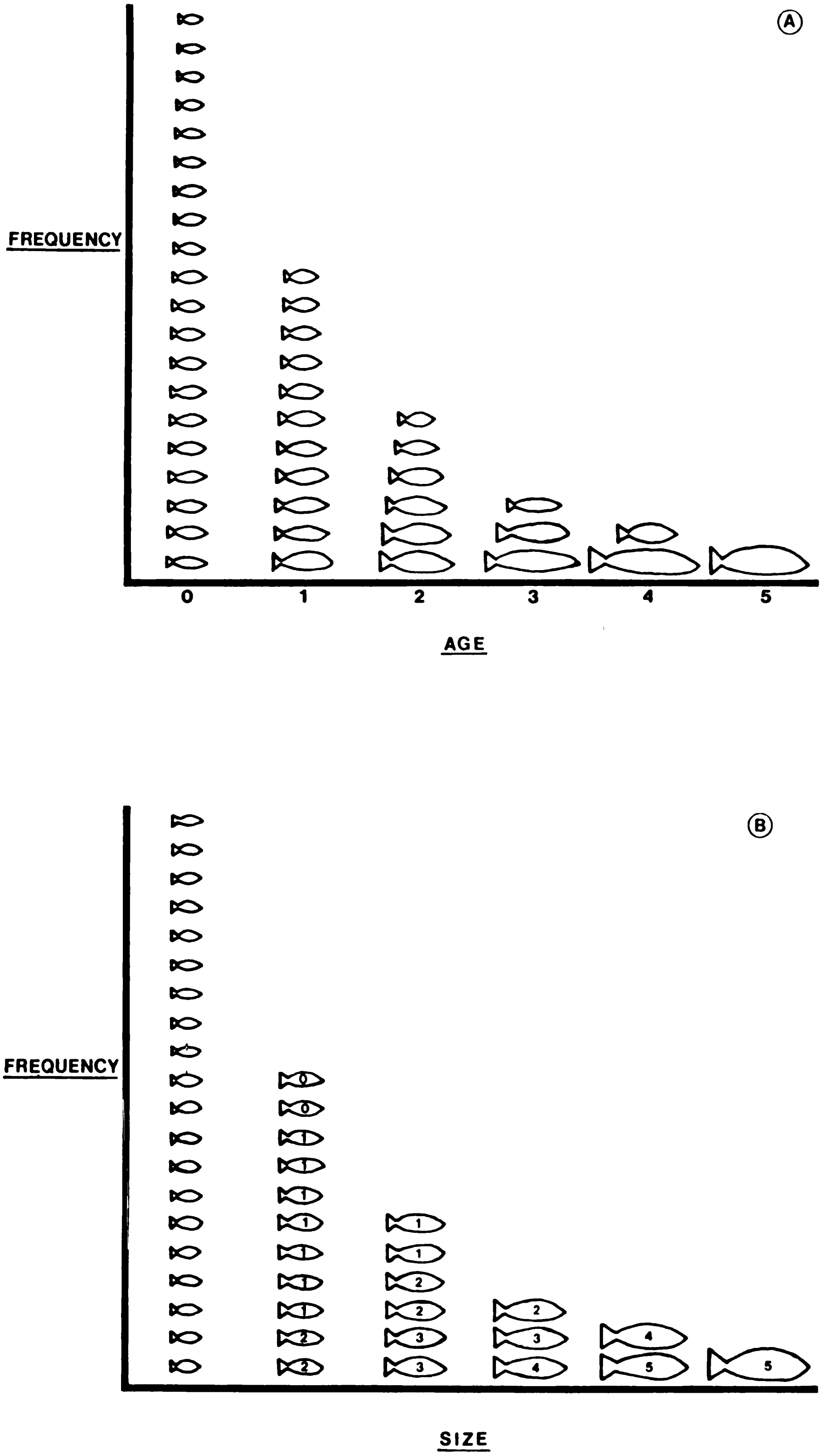

Figure 38. Cohort production based on age classes and on size classes.

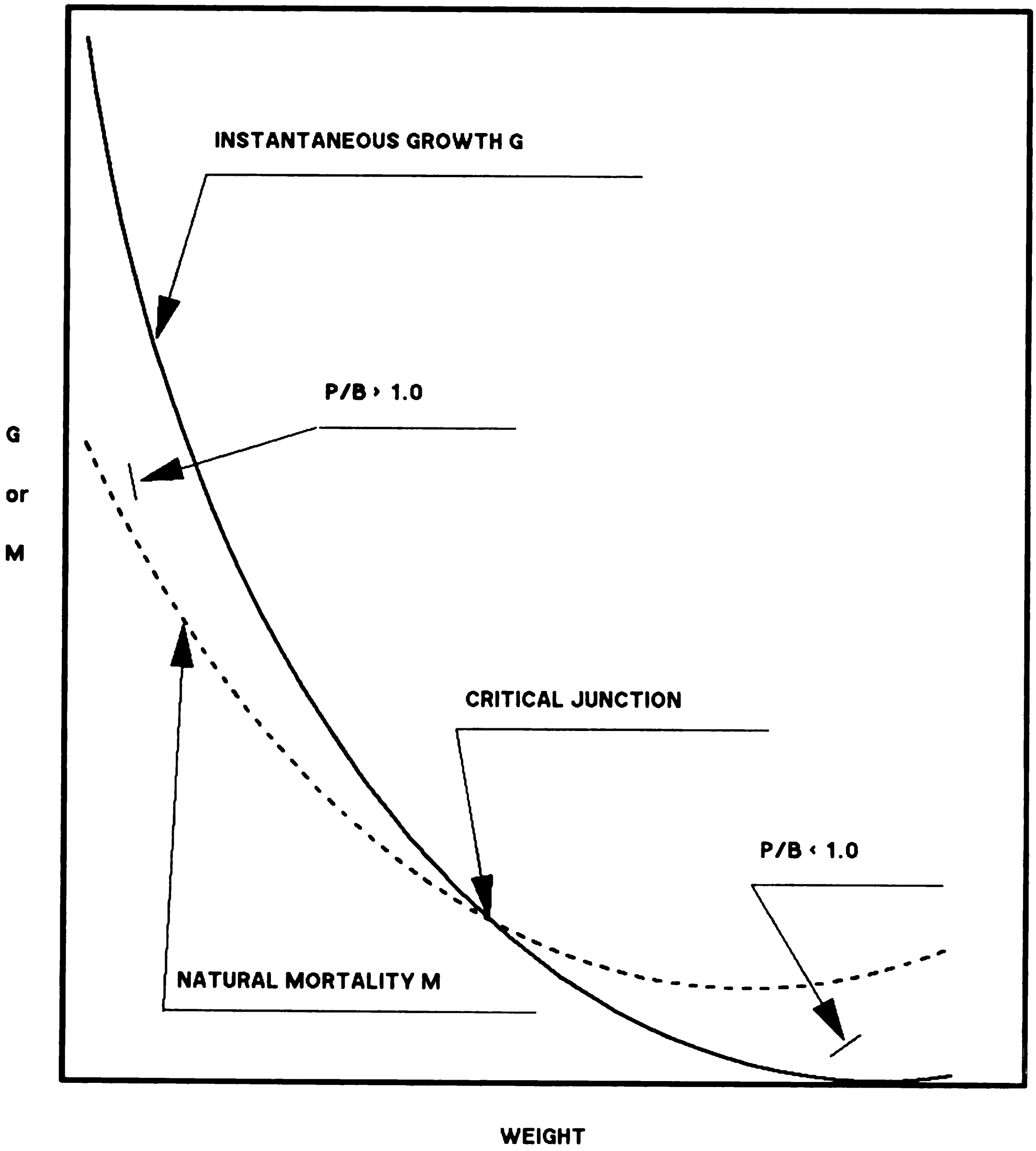

Figure 39. Critical length for harvest based on the intersection of instantaneous growth and natural mortality rates.

1.0 and the fish are contributing to an increase in the biomass of the population. But because mortality exceeds growth at some critical size, particularly when mortality is expressed in units of weight rather than numbers, fish above that size are contributing to a net loss in biomass of the population. Harvesting fish below the critical size diminishes yield below its potential because the production those fish would have contributed is lost. Harvesting fish well above the critical size diminishes yield because fish are lost to natural mortality before they can be caught. Proper length limits might be the most powerful tool for regulating the fishery, but this possibility tends to be overlooked when population dynamics are assessed from an age structured viewpoint.

A third and simpler alternative would be simply to consider the structure of the life history of the fish and how exploitation functions in the context of that structure. Both yield and the impact of exploitation on reproductive dynamics were dependent on the size at which whitefish were harvested in relation to the size at which other events in the life program occurred. The critical lenght for North Shore fish seemed to occur at 400mm, while Leland and East Traverse growth and natural mortality rates intersected closer to 500mm. Because the life history of whitefish was so closely focused on size at maturity, it is unlikely that the critical length estimates in these 3 very different stocks were similar to the maturation size by coincidence alone.

Simple measurements of life history traits may be sufficient information to design a regulated fishery which is both productive and conservative, and complex models may turn out to be superfluous when we have sufficient knowledge of biological relationships which govern the response of fish in the stocks to exploitation. A prediction which can be made from the proportional metamorphosis relationship is that the optimum age of harvest for whitefish will vary within a stock with fluctuations in growth and recruitment; the optimum size at harvest will vary from stock to stock with differences in maturity; but the optimum size at harvest as a fraction of the size at maturity should be constant and equal.

CHAPTER 3

RECRUITMENT IN RELATION TO STOCK SIZE AND CLIMATE

INTRODUCTION

The assumption that populations of fish behave in steady state, equilibrium fashion is common to a variety of fishery assessment and forecasting models. Stable age structure dynamics may successfully imitate actual population behavior in cases where annual fluctuations in recruitment are minimal or where the population age structure is sufficiently broad to dampen fluctuations introduced by single cohorts. But in other cases, the extent and causes of variations in the strength of successive cohorts may be unknown. Here, the default assumtion of equilibrium conditions may mislead and result in false predictions about population behavior and management decisions.

Cushing (1982) found that annual variation in cohort size ranged from a low of 3-fold to a high of 200-fold amongst different populations of fish. Variation at even the low end of this range could, under some circumstances, confound predictions of stock behavior made from stable age-structure models. For most exploited fish stocks, the required knowledge to forecast variation in recruitment is lacking, and an understanding of factors which influence reproductive success in or amongst different stocks is likely to be useful. The intention is to analyze factors which influenced recruitment to a stock of whitefish (Coregonus clupeaformis) in Lake Michigan, and to integrate them into a biologically sensible forecasting model.

The catch record (Baldwin et al 1979) of the Lake

Michigan whitefish fishery (Figure 2) does not inspire confidence in the utility of equilibrium based models to describe population behavior. Since at least 1920, whitefish yield has followed a series of peaks and valleys with a 250-fold range of variation. At least one peak, circa 1947, can be attributed to the effects of a single year-class (Hile et al 1953). The collapse of whitefish populations throughout Lake Michigan by 1960 was largely blamed on high adult mortality due either to overexploitation or lamprey (Petromyzon marinus) predation (Smith and Tibbles 1980). Stocks began to recover after 1960 and since the mid-1970's, the fishery has supported an unprecedented level of sustained high yields.

The influence of trends in recruitment on historical trends in this fishery received little consideration due to a lack of information. But explaining successes and failures of the fishery on the basis of adult dynamics alone seemed difficult to justify in our opinion. Adult mortality rates in productive areas of northern Lake Michigan (Ebener and Copes 1985, Smale 1987) have remained high enough to provoke alarm (Patriarche 1977) over the future of these stocks. Yet if high mortality resulted in stock collapses circa 1960, why have stocks expanded in recent years? Whitefish in Lake Michigan are near the southern extreme of their range where unstable dynamics are more likely. It was suspected that previous explanations of stock dynamics were incomplete, and that recruitment variation was responsible for at least some of the past fluctuations in whitefish yield.

Explanations of variation in whitefish recruitment have frequently focused on climatic variables. Miller (1952) found that year-classes were largely in phase in several Alberta lakes, and that wind vectors following spawning were well correlated with cohort size. Year-class strength in a Lake Ontario stock was correlated with combined effects of November and April temperatures (Christie 1963), and Lawler (1965) found that cold winters followed by delayed springs resulted in the strongest Lake Erie cohorts.

Neither Cucin and Regier (1966) or Henderson et al (1983) found any relationship between whitefish recruitment in South Bay, Lake Huron and Christie's November - April temperature index. But recruit per stock (R/S) ratios in this stock were negatively correlated with stock size, implying that densities of pre-recruited fish influenced recruitment. Healey (1980) observed an increase in recruitment following exploitation of previously unfished lakes, again suggesting an influence of density on pre-recruit survival. But in Lake Michigan, neither Walter and Hoagman (1975) or Hastreiter (1984) found a relationship between parental spawning stock size and recruitment to stocks in the northwestern part of the Lake.

Although most investigators presumed that whitefish year-class strength was determined at either the egg or larval stage, previous studies relied on inferences and associations between environmental conditions and cohort size during given years. A recent study by Freeberg (1986) in Grand Traverse Bay (GTB) of Lake Michigan provided the first known measurements of variation in survival for whitefish eggs and larvae. Results from this early life history study were applied to recruitment records for a neighboring stock along the North Shore of Lake Michigan in order to test for conformity of results with the early life study.

In summary, Freeberg found that whitefish egg survival in GTB varied with winter severity and ice cover over the spawning grounds, while larval survival varied with the density of larvae relative to the number of zooplankton in the Bay. Overwinter egg survival during the relatively cold winter of 1983-84, when spawning grounds were sheltered by ice throughout most of the winter, was 4 times higher than during the exceptionally mild, ice-free winter of the previous year. Several observations indicated that without a protective ice cover, egg mortality is high due to mechanical effects such as wind and wave action and shifting substrate.

But higher larval densities following the colder winter did not survive as well as the lower densities of the previous year. Starvation appeared to be the main source of larval mortality, particularly during the 5th week after emergence when zooplankton per fish ratios fell below levels a previous laboratory study had determined to be critical to survival (Taylor and Freeberg 1984). These results suggested that winter ice cover, larval densities and perhaps variation in the timing of annual zooplankton pulses would be likely influences on whitefish recruitment.

The hypothesis was that recruitment variation would be determined by differences in egg deposition, egg survival and larval survival. Egg deposition would increase linearly with increasing spawning biomass while egg survival would increase with earlier and more extensive ice cover. Larval densities would therefore be a function of stock size and winter ice cover. Larval survival would decrease with increasing densities of larvae relative to zooplankton abundance during the early spring emergence. Zooplankton abundance during the larval phase was expected to vary from year, with rapid spring warming stimulating a more synchronous "match" (Cushing 1982) between larval requirements and the limiting food supply. Strong year classes should result from spawning stocks which are large enough and winters which are cold enough to saturate inshore zones of the Lake with whitefish larvae, followed by mild springs to stimulate early bursts of zooplankton production. Poor to fair cohorts could result from either an inadequate deposition of eggs, poor egg survival due to a lack of ice cover or high larval densities during cold springs with inadequate zooplankton.

To test this three stage recruitment hypothesis, catch and age structure data from the North Shore area of Lake Michigan was used to estimate year-class strength and spawning biomass for 20 cohorts between 1958 and 1980. A series of models was developed in which the factors of egg deposition, winter ice cover, larval density and temperature dependent zooplankton densities were added in succession to an initial stock-recruitment equation. Recruitments were hindcast from each successive model and the coefficient of determination (r^2) between predicted and observed recruitments measured the accuracy and reliability of the model. By proceeding in stepwise fashion, the influence of each factor on the predictive power of the model was analyzed in turn.

Because winter conditions were found to be an important influence on recruitment, temperature records were examined for 3 northern Lake Michigan stations between 1900 and 1980. The question was whether yearly variation in early winter severity was uniformly distributed during the 20th century, or if trends in winter conditions were apparent. Finally, because predation by rainbow smelt (Osmerus mordax) has long been suspected of influencing whitefish recruitment (Wells and MacClain 1980), catch records for smelt were compared to whitefish catch records to look for possible associations in abundance between the two species.

METHODS

Spawning Biomass and Recruitment Estimates:

From 1981-83, a tagging program in cooperation with the North Shore fishermen provided mark-recapture estimates of North Shore spawning biomass. Biomass estimates during this portion of the study declined in direct proportion to a decline in trap-net catch per effort (CPE) in the area. The relationship between trap-net CPE and biomass was:

SPAWNING BIOMASS (kg) = 3300 x CPE (lbs/lift)

and trap-net CPE figures (Table 28) provided biomass estimates for most years. Between 1958 and 1964, trap-net effort in District MM-3 was too low for reliable biomass estimates. A regression between gill-net CPE and trap-net CPE during years when both gears were in common use calibrated the two gears with respect to each other, then biomass estimates were made from weighted mean CPE values for both gill-nets (the dominant gear during these years) and trap-nets between 1958 and 1964 only.

Cohort analysis procedures partitioned biomass estimates during each year into individual cohorts. Frequency at age estimates for the North Shore catch were available for most years between 1960 and 1984 from several sources including Piehler (1967), Brown (1968), Michigan Department of Natural Resources catch monitoring data (Patriarche 1977, Rybicki 1980), Scheerer and Taylor (1985) and this study. But the cohort analysis was complicated by two effects. First, as the North Shore stock increased in abundance from extremely low levels during the early 1960's, somatic growth slowed, the mean age at recruitment increased by nearly 2 years and the age structure of the catch shifted to progressively older ages. The mean age of the catch increased by 2 years between 1960 and 1984, which had to be compensated for in the cohort analysis. Secondly, the frequency at age estimates were of inconsistent quality, particularly in the middle years when sampling frequency and size were marginal. Because of doubt about the accuracy of some age structure estimates, standard cohort analysis procedures were modified to enable an estimate of the precision of year-class strength values.

Each cohort was detectably abundant in the catch for at least 3 years: first, when it began to recruit and only the larger fish were available to the fishery; second, when it was typically the dominant, or modal age group in the catch; and third, when it had passed the modal age and was relatively less abundant in the catch. At each of these 3 ages, abundance at age in the catch was estimated, then the abundance estimates for the pre- and post-modal age groups were corrected to their expected abundance at the modal age (Figure 40).

Annual biomass estimates were multiplied by the percentage of each age group in the sampled catch, yielding abundance at age in the catch. These figures were arranged in an array of year-class by age, $\log_e$ transformed, and then the difference between values at the modal age and the pre-modal and post-modal ages were calculated. Irregularities amongst these differences were smoothed by calculating a 3-year running mean across all years, yielding a correction factor for estimating abundance at the modal age from abundance at other ages. In effect, this correction factor estimated that (for example) on the average, a cohort was twice as abundant in the catch at its modal age than at either the previous or following age. Therefore, in order to fore-calculate or back-

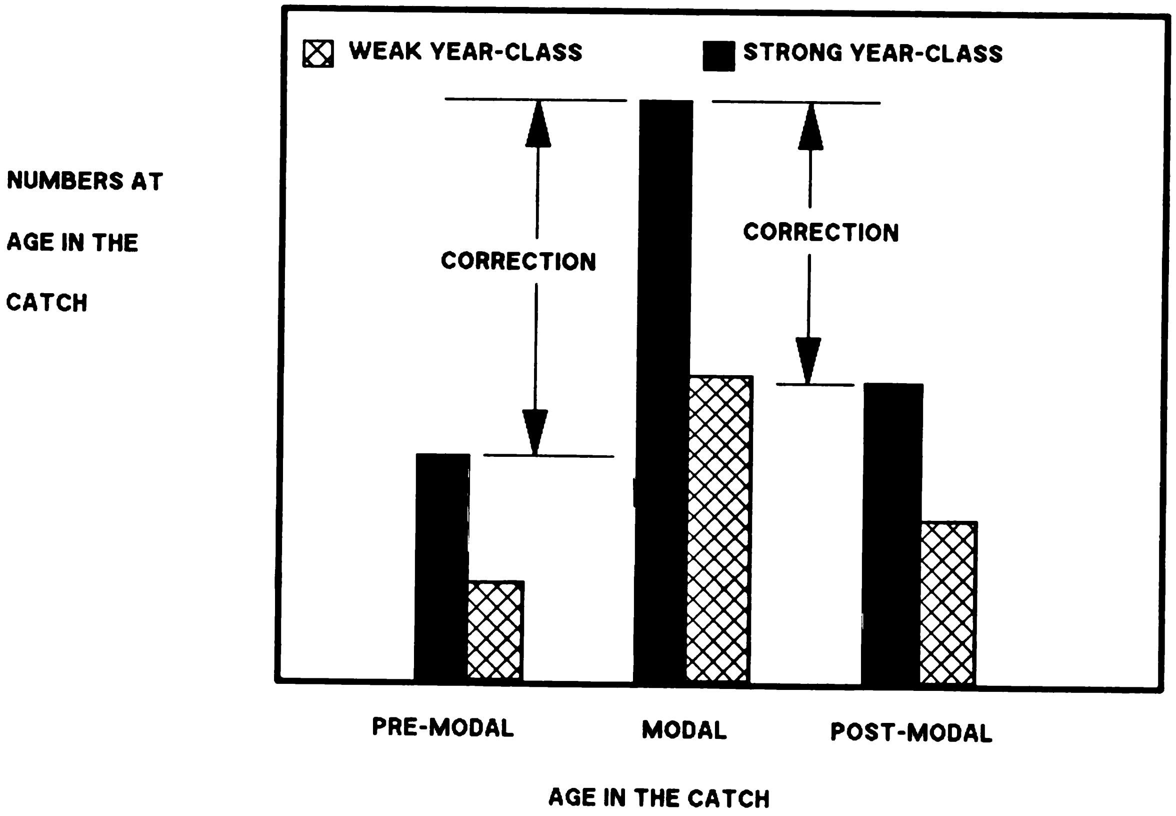

Figure 40. The estimation of cohort strength from catch at age estimates using different age groups corrected to the modal age in the catch.

calculate its abundance at the modal age, its abundance at either age should be doubled.

This procedure resulted in three estimates of the abundance of a cohort at its modal age in the fishery, and the average of these was used as the recruitment index for each cohort. Additionally, analysis of variance (ANOVA) with the 3 $\log_e$ transformed estimates enabled a calculation of variance amongst individual estimates relative to variance amongst the cohorts, and to place confidence intervals on the precision of the cohort estimates.

Model Construction:

The null model:

Assuming that egg deposition was proportional to stock biomass, constant survival rates from egg to recruit would result in recruitment which was proportional to stock size. To test this null hypothesis of constant survival, the null model consisted of the best fit line passing through the origin with recruitment increasing linearly with stock size. Recruitment hindcasts were calculated from this equation and the r^2 between the predicted and observed recruitments measured the accuracy of the predictions.

Stock recruitment model:

Assuming again that egg deposition (E) was proportional to spawning biomass, the terms $\log_e$(Recruits/Stock) and $\log_e$(Stock) in the Ricker (1954) stock-recruitment equation are proportional to $\log_e$(Recruits/Egg) and $\log_e$(Egg). The term $\log_e$(R/E) is equivalent to the survivorship from egg to

Table 28. North Shore gill-net and trap-net catch per effort (CPE) values and percent frequency at age for the sampled North Shore catch, 1958-84.

YEAR	GILL-NET CPE (LBS/1000FT)	TRAP-NET CPE (LBS/LIFT)	PERCENT IN AGE CLASS:					
			2	3	4	5	N	
1958	14.8	94.2	x	x	x	x	0	
1959	15.3	58.6	x	x	x	x	0	
1960	13.8	33.8	84	14	1	1	151	(a)
1961	15.4	150.4	82	13	2	0	153	(a)
1962	11.3	102.8	55	40	4	0	109	(a)
1963	15.3	168.9	x	x	x	x	0	
1964	17.1	168.4	x	x	x	x	0	
1965	x	156.1	100	0	0	0	72	(b)
1966	x	274.7	25	68	4	0	681	(b)
1967	x	205.9	29	31	35	2	1232	(a)
1968	x	147.2	9	74	8	8	611	(c)
1969	x	174.7	25	58	16	1	96	(c)
1970	x	214.9	44	54	2	1	169	(c)
1971	x	302.4	8	81	10	1	296	(c)
1972	x	355.1	28	68	2	2	141	(c)
1973	x	225.1	1	65	30	1	141	(c)
1974	x	230.0	0	15	69	8	13	(c)
1975	x	239.3	2	92	4	1	133	(c)
1976	x	209.4	1	60	38	0	339	(c)
1977	x	178.4	4	36	36	1	133	(c)
1978	x	251.9	0	44	36	7	586	(c)
1979	x	216.6	2	63	31	0	399	(c)
1980	x	312.5	0	78	21	0	513	(d)
1981	x	460.0	0	12	83	5	738	(d)
1982	x	311.9	0	4	37	55	452	(d)
1983	x	261.0	0	14	37	33	606	(e)
1984	x	227.0	0	8	52	26	361	(e)

1958-71 CPE data was from Statistical District MM-3, 1972-84 data was from whitefish management area WFM-03.

Sources: (a) Brown 1968, (b) Piehler 1967, (c) MDNR data, see Patriarche (1977) or Rybicki (1980), (d) Scheerer and Taylor 1985, (e) Smale 1987.

recruit, and the stock-recruitment equation predicts that this survivorship rate decreases as a negative exponential function of increasing egg deposition. Therefore, density is the only influence on survival in this model.

North Shore $\log_e(R/S)$ ratios were regressed on $\log_e(S)$ to obtain an empirical fit to the Ricker type stock-recruitment eqation. This equation was used to hindcast recruitments from stock size, and the r^2 between calculated and observed values measured the accuracy of the hindcasts.

Winter ice cover model:

This model simulated egg deposition which was proportional to stock size, egg survival which increased by a range of 4.6-fold as Lake Michigan ice cover increased, and survival from the larval stage to recruitment which was strictly density dependent. The maximum extent of Lake Michigan ice cover ranged from 13 percent to 100 percent during the period (DeWitt et al 1980), and for 3 years of missing data (1958, 1959 and 1980), ice extent was estimated from freezing degree day (FDD) accumulations at 3 northern Lake Michigan stations.

Spawning biomass was multiplied by 0.06 times the percent ice extent to simulate egg survival which increased from 1.3 percent during years of the lowest ice cover to 6.0 percent when the Lake was fully frozen over. This range of increase in survival was slightly broader than measured in the GTB study, but then the range of ice extent was also broader. This product was considered as proportional to the expected larval density (L) for each year. We then fit a larvae-recruitment curve rather than a stock-recruitment curve to simulate density dependent larval survival.

Log_e recruit per larvae (R/L) ratios were regressed on $\log_e(L)$ to obtain an empirical fit between larval densities and survival rates. The regression equation calculated hindcast recruitments from expected larval densities, and the r^2 between hindcast and observed values again tested the accuracy of the model.

Spring temperature model:

Based on results from the GTB study and an initial examination of the North Shore data, spring warming rates were expected to have little impact on larval survival at low larval densities. Regardless of zooplankton dynamics, low larval densities should be below the carrying capacity defined by zooplankton per fish ratios. However, as larval densities increased, spring warming, through its influence on zooplankton dynamics, should become increasingly influential to larval survival. Cold springs when larval densities were high would amplify the negative effects of density on survival while warm springs should increase recruit per larvae ratios.

To simulate this hypothetical interaction between densities and temperature, a series of larvae-recruitment curves was fit in which density dependent effects softened as spring warming rates increased. Since the term $\log_e(R/L)$ describes the survival rate from larvae to recruitment, the slope, beta, of the larvae-recruitment equation in linear form (Figure 41) describes the rate at which survivorship decreases with increasing density. To model survivorship which varied with both density and warming, the intercept, alpha, of the larvae-recruitment equation was held constant while the slope, beta, was made increasingly negative as spring temperatures decreased.

To do this, the deviation from the mean number of heating degree days (HDD) averaged from 3 northern Michigan stations (Escanaba, Sault Ste. Marie and Muskegon) was used as an index of spring warming. Years were grouped into cold, normal and warm spring with 6 or 7 years in each, then larvae-recruitment equations were calculated separately for each group. The three beta values were regressed against the mean HDD deviations of each group to estimate the amount of change in beta per HDD. Then the HDD deviation for individual springs was used to calculate an expected beta. Hindcasts were calculated from expected larval densities, the alpha value estimated from the initial larvae-recruitment equation and beta values calculated from each spring's HDD deviation. Hindcast values were again compared to observed recruitments.

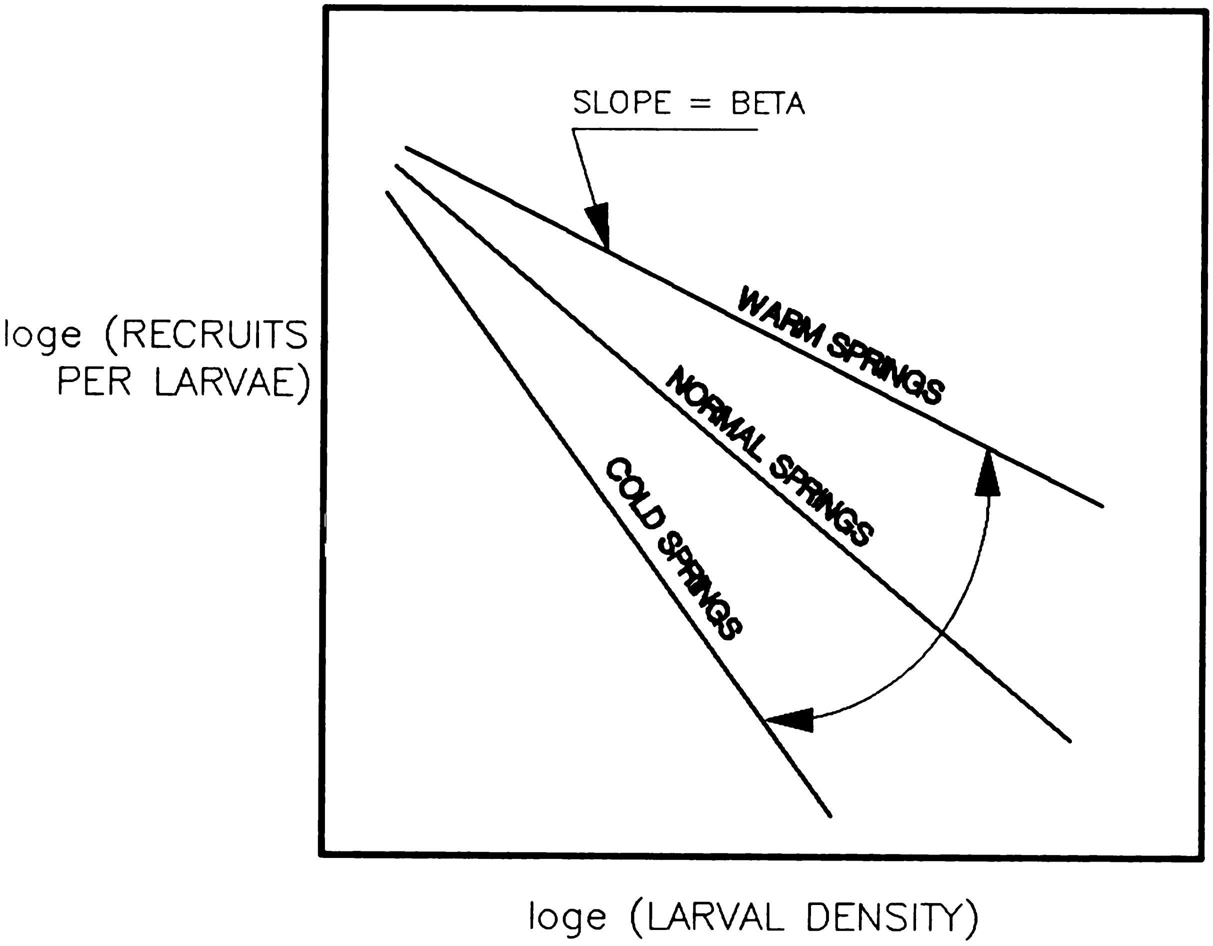

Figure 41. A proposed effect of a larval carrying capacity which varies with spring temperatures on stock-recruitment relationships.

RESULTS

Precision of the Recruitment Estimates:

The three estimates of cohort strength were each based on catch per effort at age, corrected to the modal age of a cohort in the catch. Variance between the 3 estimates of cohort strength, using $\log_e$ values, was small relative to the variation amongst cohorts. Year-class effects were highly significant ($F = 10.9$, $P < 0.01$) indicating that the cohort analysis procedures were able to discriminate between small, medium and large cohorts.

ANOVA table for the cohort strength estimates.

SOURCE	df	SUM OF SQUARES	MEAN SQUARE	F
TOTAL	62	40.55	-----	-----
AMONGST COHORTS	20	33.98	1.699	10.87
WITHIN A COHORT	42	6.57	0.156	-----

Confidence intervals (0.95) on the grand mean recruitment estimate equalled (+200,000 -139,000) recruits, but (+59 -37) percent of the individual cohort strength estimate was used as a working confidence interval during further procedures. Cohort strength estimates ranged from 104,000 recruits to 1,216,000 recruits: an 11-fold difference. Even though confidence limits for each year-class were fairly large, the magnitude of the variation in cohort size was still much larger than the degree of error. The estimated precision of cohort sizes represented the average degree of error across all cohorts, thus about half the cohorts were estimated with more and half with less precision than the confidence interval given.

Model Fitting:

The null model:

This model tested the null hypothesis that survivorship from egg to recruit was constant between 1958 and 1980. The best fit direct proportion equation between stock size and recruitment (Table 29) was:

$$R = 0.67 \times (S)$$

Recruitment hindcasts from this equation (Table 30) exhibited a minimal degree of agreement with observed values. The coefficient of determination (r^2) equalled 0.025 and only 7 of the 20 hindcasts fell within 0.95 confidence limits of the observed recruitments. Variation in recruitment from similar stock sizes was as high as 11-fold (1971 vs. 1977), indicating that pre-recruit survival was not constant.

Stock-recruitment model:

The relationship between spawning biomass and recruitment (Figure 42) was ambiguous. Both the smallest and the largest spawning stocks produced small to fair year-classes, while the largest cohorts and the greatest degree of variation occurred at intermediate stock sizes. Between 1958 and 1984 the fishery produced both record low and record high catches for this area, indicating a substantial range of stock sizes was included in the analysis.

Table 29. Estimated North Shore spawning biomass; recruitment indices; the extent of Lake Michigan ice cover; deviations from the mean number of April-May heating degree days averaged at 3 northern Michigan stations; and calculated larval density indices, 1958-1980.

YEAR	SPAWNING BIOMASS (kg)	RECRUITMENT INDEX (kg)	MAXIMUM ICE EXTENT (PERCENT)	MEAN HDD DEVIATION (DEG F)*	LARVAL DENSITY INDEX
1958	240,000	138,000	15**	+11	216,000
1959	171,000	353,000	90**	+26	924,000
1963	509,000	725,000	80	+11	2,444,000
1964	524,000	213,000	13	+76	409,000
1965	923,000	506,000	40	+20	2,215,000
1966	692,000	173,000	15	-77	623,000
1967	495,000	658,000	46	-75	1,365,000
1968	587,000	720,000	30	+31	1,057,000
1969	722,000	624,000	15	-1	650,000
1970	1,016,000	987,000	30	+49	1,829,000
1971	1,193,000	104,000	27	-52	1,933,000
1972	756,000	784,000	45	+11	2,042,000
1973	773,000	438,000	20	-39	927,000
1974	804,000	296,000	20	-45	965,000
1975	704,000	234,000	25	-31	1,091,664
1976	599,000	447,000	20	-8	719,000
1977	846,000	1,216,000	90	+107	4,570,000
1978	728,000	509,000	52	+9	2,271,000
1979	1,050,000	273,000	100	-67	6,299,000
1980	1,546,000	616,000	15**	+64	1,391,000

* = Positive heating degree day deviations are equivalent to milder than average springs.

** = Ice cover estimated from freezing degree day accumulations.

Table 30. Recruitment estimates in comparison to hindcasts made from each of the four recruitment models.

		PREDICTED FROM:			
YEAR	OBSERVED RECRUITMENT	NULL MODEL	STOCK-RECRUITMENT MODEL	WINTER ICE MODEL	WINTER/SPRING MODEL
1958	138,000	161,000	322,000	210,000	222,000
1959	353,000	114,000	296,000	367,000	436,000
1963	725,000	341,000	387,000	532,000	574,000
1964	213,000	351,000	390,000	268,000	384,000
1965	506,000	617,000	448,000	512,000	591,000
1966	173,000	463,000	417,000	315,000	184,000
1967	658,000	331,000	384,000	426,000	245,000
1968	720,000	393,000	401,000	386,000	476,000
1969	624,000	483,000	421,000	320,000	315,000
1970	987,000	680,000	458,000	476,000	678,000
1971	104,000	798,000	476,000	486,000	284,000
1972	784,000	506,000	426,000	497,000	535,000
1973	438,000	517,000	429,000	367,000	276,000
1974	296,000	538,000	433,000	373,000	268,000
1975	234,000	471,000	419,000	391,000	310,000
1976	447,000	401,000	403,000	333,000	312,000
1977	1,216,000	566,000	438,000	676,000	1,559,000
1978	509,000	487,000	422,000	517,000	549,000
1979	273,000	702,000	462,000	764,000	410,000
1980	616,000	1,034,000	508,000	429,000	676,000

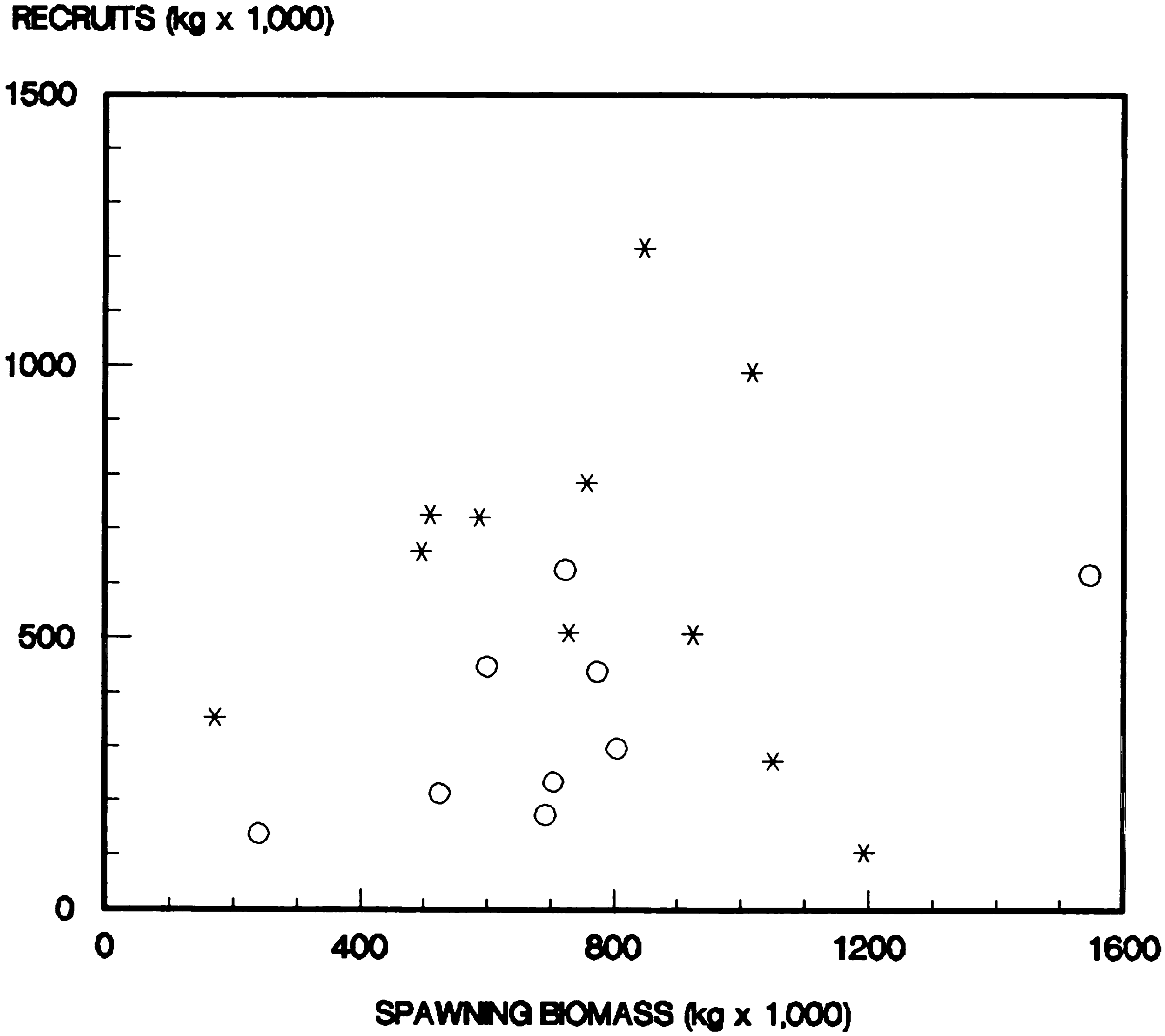

Figure 42. The North Shore recruitment index, 1958-80 year-classes, in relation to spawning biomass of the parent stock. Asterisks represent years of more than 25 percent ice cover, circles are years with less than 25 percent ice.

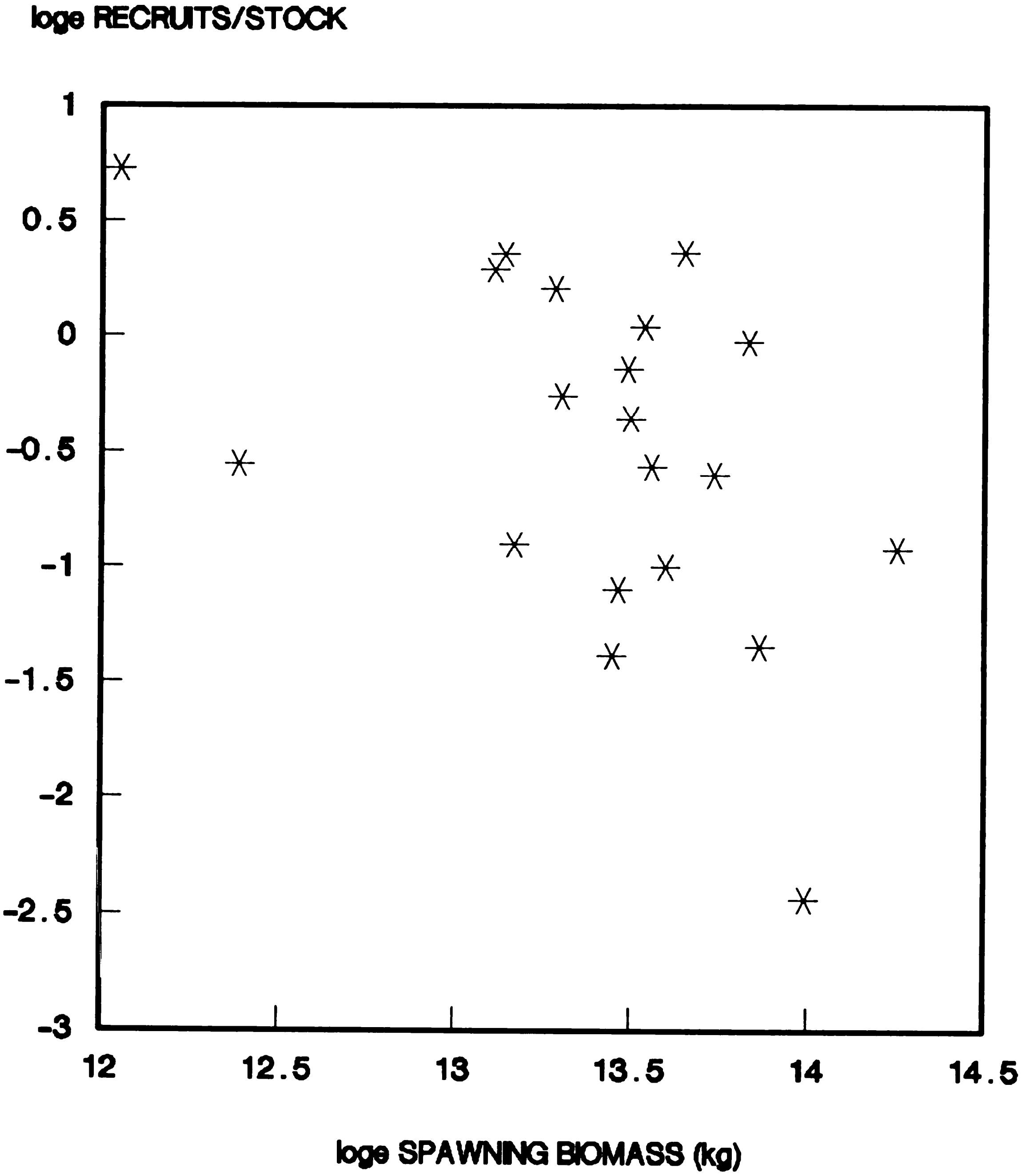

Figure 43. North Shore $\log_e$ recruit per stock ratios in relation to $\log_e$ stock size.

There was a significant ($r = -0.50$, $P < 0.05$) negative correlation between $\log_e(R/S)$ ratios and $\log_e(S)$, indicating that on the average, larger stocks produced fewer recruits per parent than did smaller stocks (Figure 43). The resulting stock-recruitment equation, in linear form, was:

$$\log_e(R/S) = 9.655 - 0.756 \times \log_e(S)$$

Recruitment hindcasts calculated from this equation were only slightly more accurate than those predicted from the null model. The r^2 increased to 0.043, with 8 of 20 hindcasts within the confidence range of observed values.

To test whether this low predictive power for the stock-recruitment function was an atypical result, the same comparison was made between hindcast and observed recruitments using data and a stock-recruitment equation from the South Bay study (Henderson et al 1983). Here also there was a significant negative correlation between $\log_e$ (R/S) ratios and $\log_e(S)$, but accuracy of the hindcasts was lower than for the North Shore stock. Hindcast and observed recruitments agreed with an r^2 of 0.004 for the South Bay study. Results from both studies were similar enough to suggest that density negatively influenced pre-recruit survival, but on the whole, measurements of stock size alone were sufficient to predict recruitment only within approximately an order of magnitude.

Winter ice model:

The expectation that egg survival, and therefore recruitment, would increase during cold winters with extensive ice was supported by an initial examination of the data. The 7 largest (R/S) ratios occurred during winters when Lake Michigan ice cover exceeded 25 percent, and (R/S) ratios were positively correlated ($r = 0.557$, $P < 0.05$) with ice extent without $\log_e$ transformation. But the relationship between ice extent and (R/S) ratios was not a simple linear increase. While all high (R/S) ratios occurred during colder than average winters, not all cold winters produced above average recruitments or (R/S) ratios (Figure 44).

Stock-recruitment curves were different for years of extensive ice (> 25% coverage) than for low ice years (Figure 42). When ice coverage was below normal, recruitment increased slowly with increasing stock size. But for years of extensive ice, the stock-recruitment curve was strongly domed with small cohorts produced by the combination of large stocks and cold winters. This effect was consistent with the expectation that extremely high larval densities resulting from both above normal egg deposition and survival would experience high mortality due to their density.

Expected larval density indices were calculated from stock size and winter ice extent, then fit to a larvae-recruitment equation to incorporate this density dependent effect. Recruitments were hindcast from the equation:

$$\log_e(R/L) = 7.554 - 0.617 \times \log_e(L)$$

The correlation between survival rates from larvae to recruitment ($\log_e(R/L)$ and larval densities ($\log_e(L)$ was

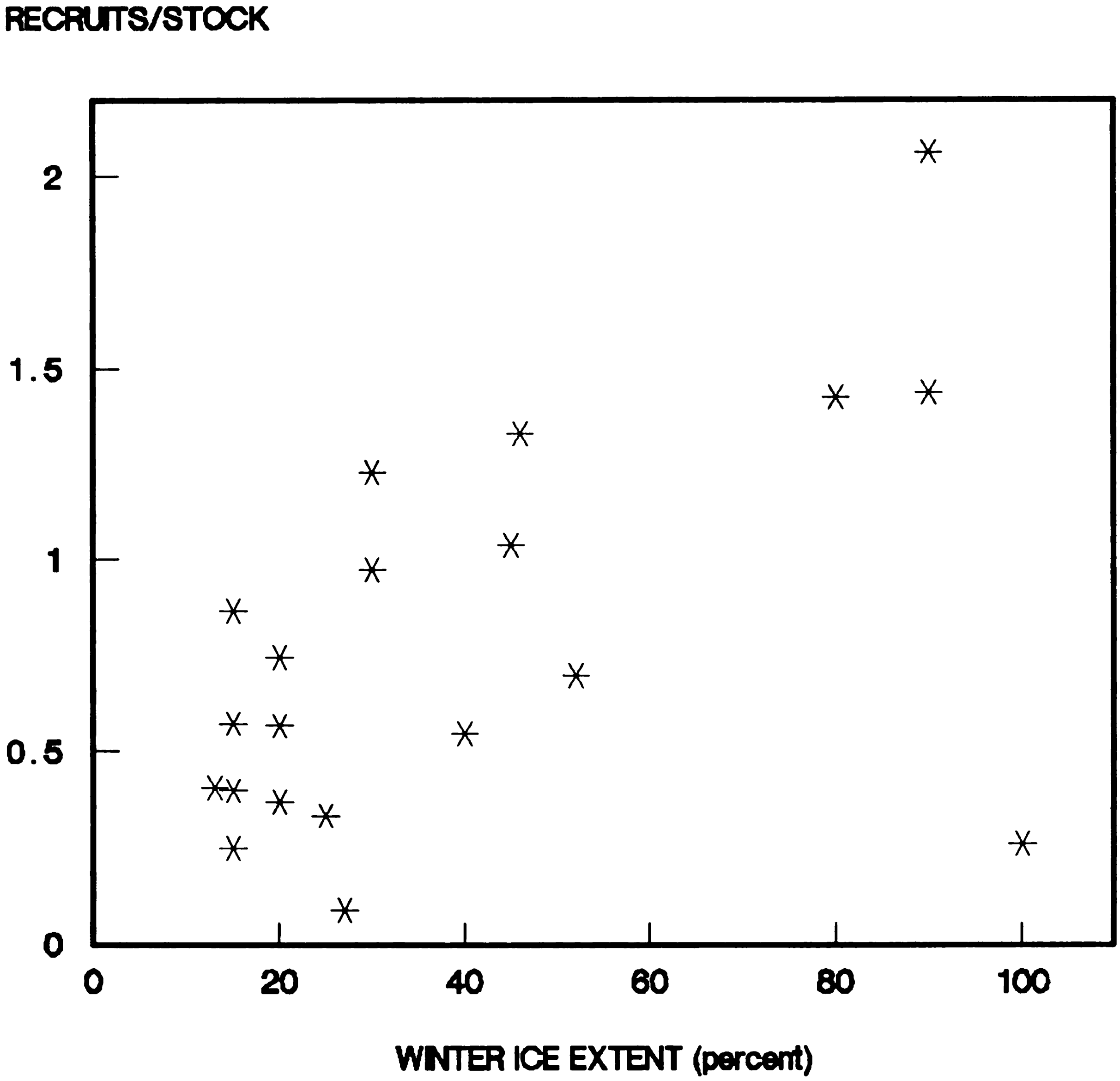

Figure 44. North Shore recruit per stock ratios in relation to the percent of Lake Michigan ice cover at its maximum extent.

stronger ($r = 0.632$ $P < 0.05$) than the equivalent correlation for the stock-recruitment relationship. Agreement between hindcast and observed values increased to an r^2 of 0.186, a fourfold increase from the stock-recruitment model, and 12 of 20 hindcasts were within the confidence range of the observed estimates.

Winter/spring model:

Deviations from the mean April-May accumulation of heating degree days were not, by themselves, correlated with either (R/S) ratios ($r = 0.379$ $P > 0.05$) or larval survival ($r = 0.273$ $P > 0.05$). But based on the Grand Traverse Bay study, it was expected that spring warming would influence larval survival only when densities were sufficiently high that zooplankton per fish ratios became limiting to survival. When years of expected high larval densities were isolated (Figure 45), a much stonger apparent relationship between spring temperatures and (R/S) ratios emerged. Cold springs apparently amplified the negative effects of density on survival while warm springs and high larval densities resulted in large year-classes and above average (R/S) ratios.

To simulate this interaction between larval density and spring warming, we varied the slope, beta, of the larvae-recruitment equation such that it became more negative during increasingly cold springs. Estimated betas were most negative for cold springs, least negative for the warm spring group, and a regression of betas on mean HDD accumulations for the 3

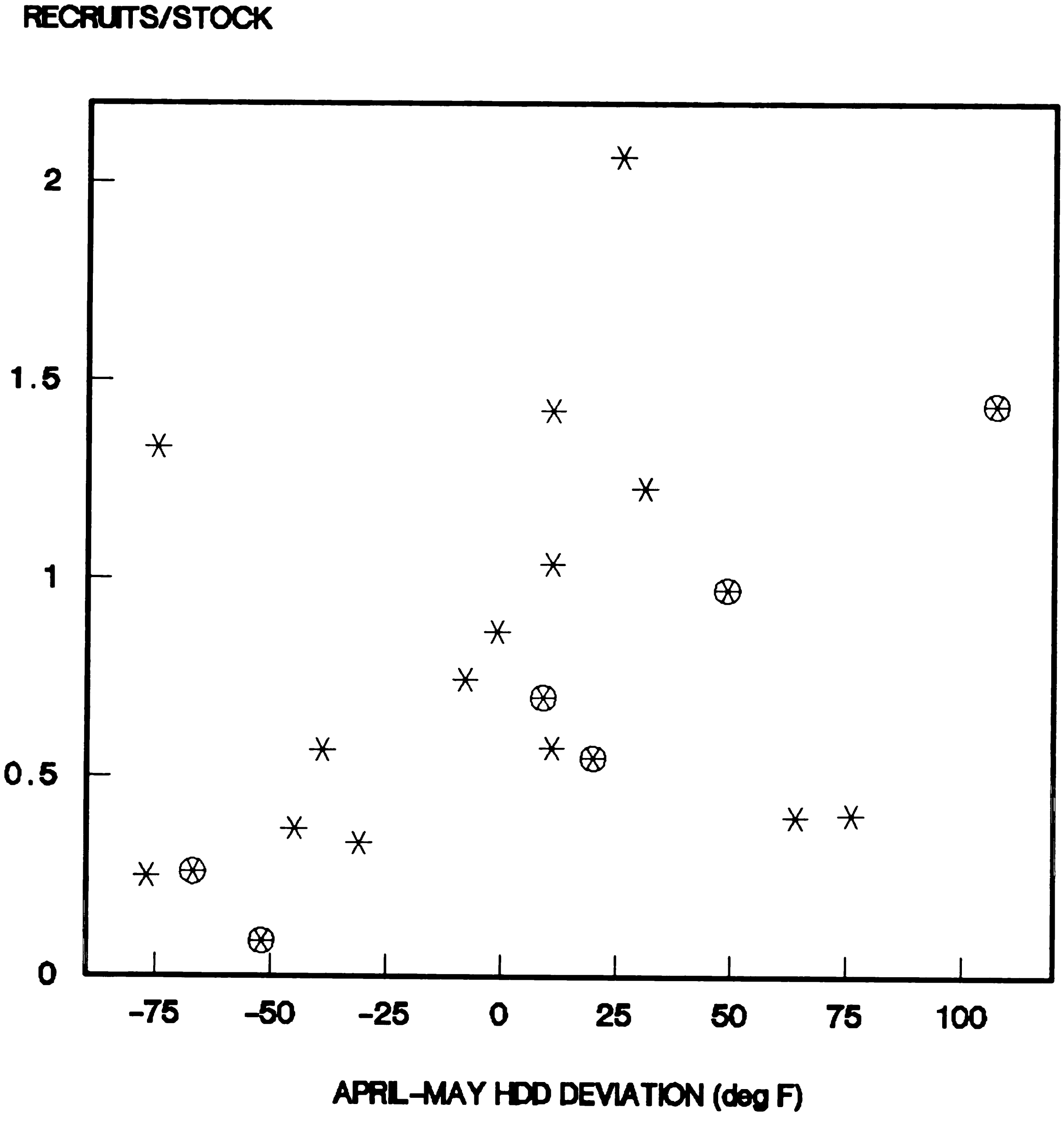

Figure 45. North Shore recruit per stock ratios in relation to deviations from the mean April-May heating degree day accumulation, with circled years representing expected high larval densities.

groups yielded the equation:

$$\mathrm{BETA} = -0.614 + 0.000513 \times (\mathrm{HDD})$$

Substituting this equation for beta into the larvae-recruitment model to compensate for spring temperature effects yielded the equation:

$$\log_e(R) = 7.554 + 0.386(\log_e L) + 0.000513(\mathrm{HDD})(\log_e L)$$

Recruitment hindcasts in this model were made from expected larval density indices and spring HDD deviations for each year. Larval densities had been calculated previously from stock size and winter ice.

Agreement between hindcast and observed recruitments with this model increased to an r^2 of 0.601, a 3-fold increase over the larvae-recruitment model and a near 15-fold increase over the initial stock-recruitment model. Seventeen of the 20 hindcasts were within the confidence range of the observed recruitments. Although agreement was less than 100 percent, at least some of the remaining recruitment variation can be attributed to error in the initial estimates. Even if hindcasts were perfect, some discrepancies between predicted and observed values remained because the observed values themselves were imprecise.

Climatic variation:

Given an apparent influence of climate on recruitment, the uniformity of the distribution of climatic events through time became a crucial question. If favorable and unfavorable years occurred with equal frequency during a given period, the fishery should be pseudo-stable and oscillate about a nearly stable equilibrium. If, on the other hand, favorable and unfavorable years were grouped, trends in climate should be reflected in trends in the fishery.

The concensus among previous investigators has been that climate in the Great Lakes region during the past 50 years has not been uniform in distribution. Eichenlaub (1978) reported a general warming trend for the Great Lakes which began circa 1930 and ended during the 1950's. Ayers (1965) also found that mean temperatures in the Lake Michigan basin were warmer than average during the same period and that shifts in temperature were associated with shifts in cloud cover, precipitation, wind vectors and storm frequencies. With respect to winter severity, Assel (1980a) found a high frequency of warm winters between circa 1930 and 1960, while winters from 1960 through 1979 were colder than the long term mean. Winter coldness and ice cover on Lake Michigan during the period of this recruitment analysis exceeded the 20th century norm (Assel and Quinn 1979).

We expected that the onset of freezeup for inshore whitefish spawning areas of northern Lake Michigan would be the most critical single influence on recruitment. Freezeup dates were unavailable therefore we analyzed freezing degree day accumulations during the first half of winter as the closest substitute. The percent deviation from the mean accumulation of freezing degree days (FDD) through mid-

January was calculated for each year from 1898-1984 (Assel 1980b) and averaged for 3 northern Lake Michigan stations: Green Bay, Escanaba and Traverse City.

The warming and cooling trends for general climatic events also applied to early winter severity for northern Lake Michigan. The cumulative departure from the mean FDD accumulation (i.e. the running summation) revealed distinct mild and cold periods during the past 50 years (Figure 46). From 1900-1920, the cumulative deviation oscillated about the mean without any apparent trend. A brief cold period during the 1920's was followed by a sustained period of milder than normal winters beginning in 1931 and lasting through 1958. A brief period of relatively normal winters interrupted this trend during the mid-1940's. Beginning with the severe winter of 1959, this warming was reversed and winters through 1984 were, on the average, much colder than the 20th century mean.

If abnormal winters are defined as those which deviate from the mean FDD accumulation by more than 25 percent, then 26 percent of the winters from 1898-1984 would be considered abnormally cold and 22 percent abnormally mild. A plot of these abnormal winters exhibited the uneveness of their distribution (Figure 47). From 1898-1930, 10 of 33 early winters were cold and 7 were warm for a fairly even distribution. But from 1931-58, only 2 cold winters occurred while 9 were abnormally warm. More recently, 10 of the 26 winters from 1959-84 were cold and only 3 were warm. Two of these 3 warm winters occurred after 1979.

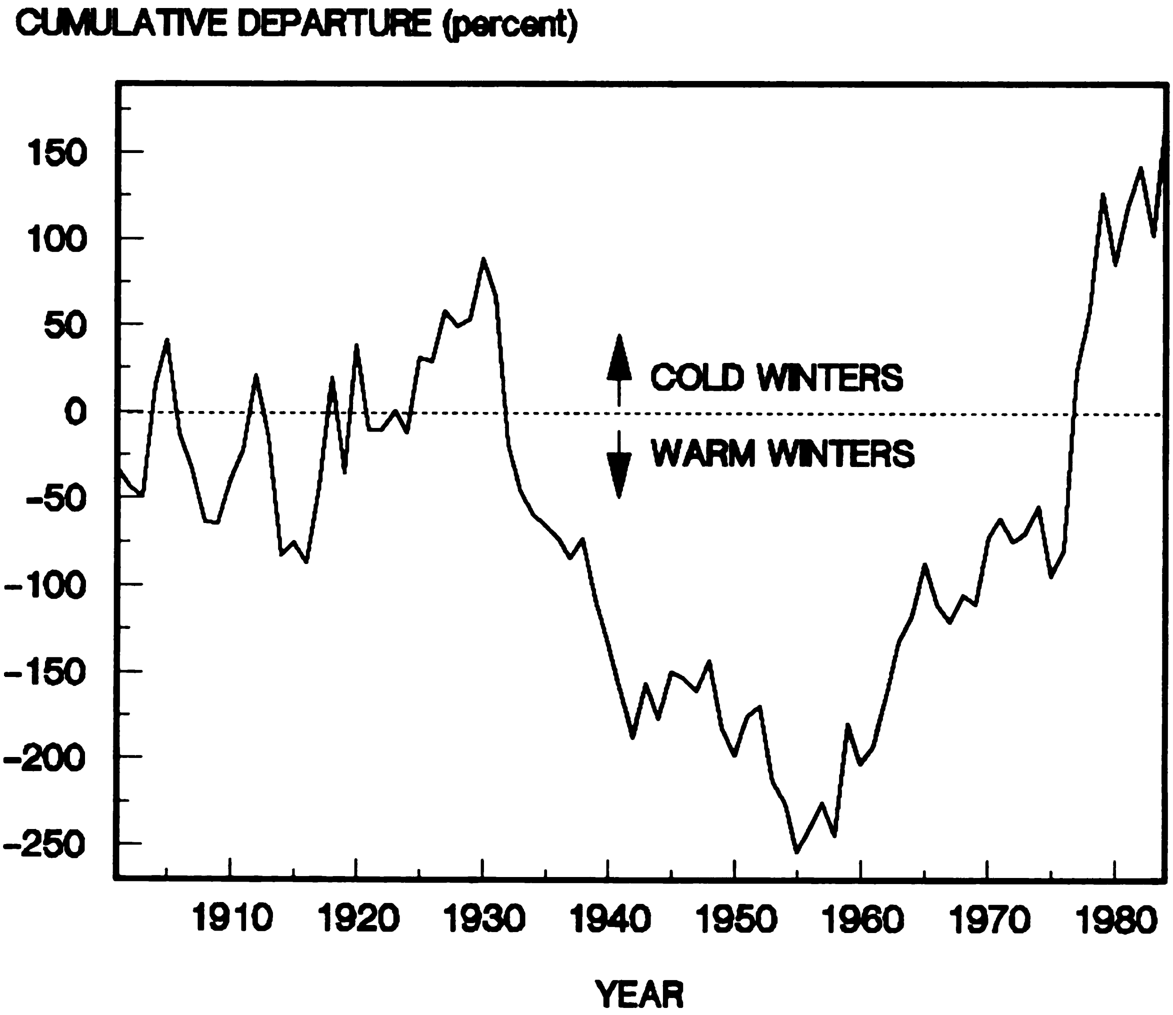

Figure 46. Cumulative departure from the mean mid-January accumulation of freezing degree days for northern Lake Michigan, 1900-84.

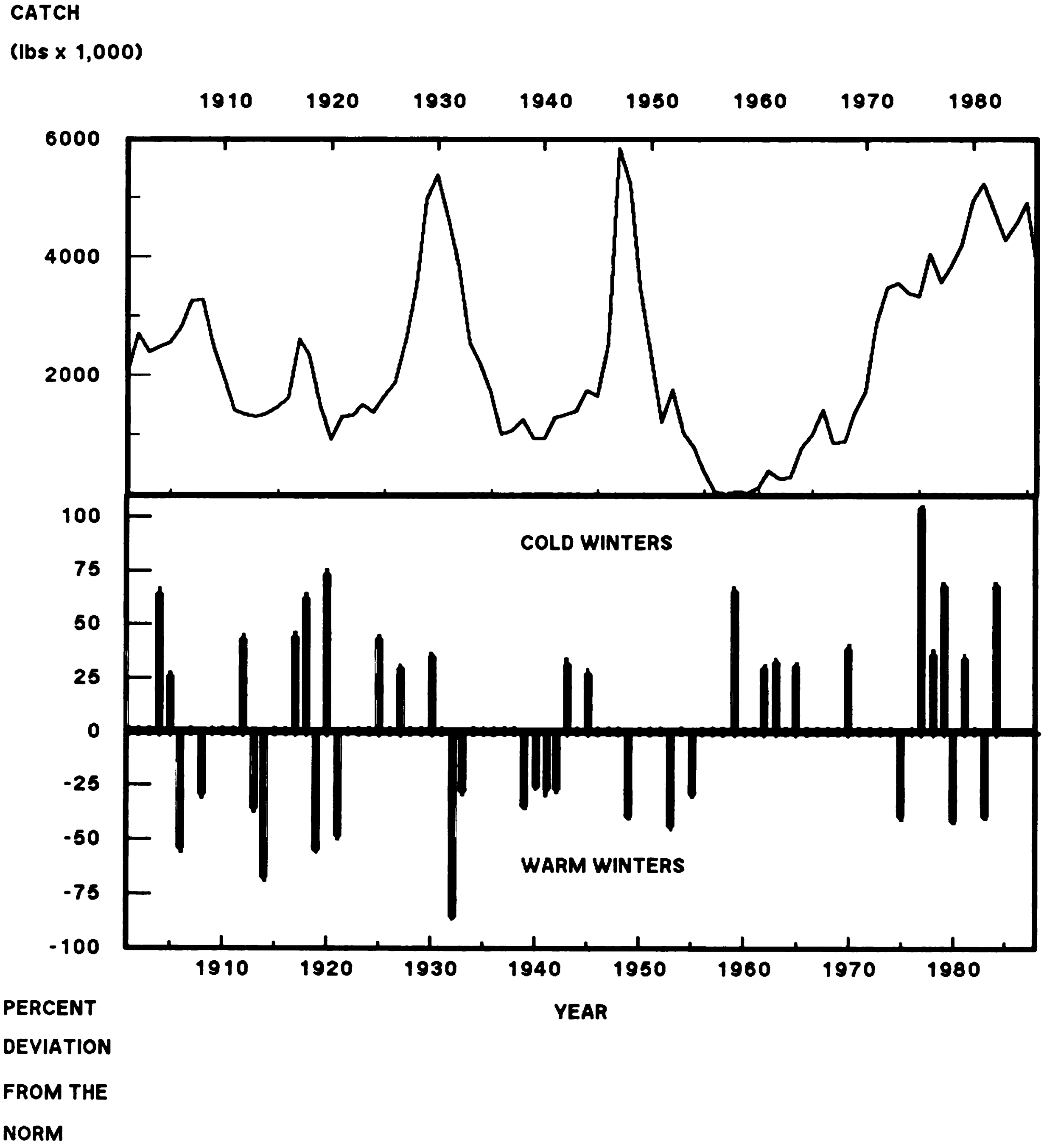

Figure 47. Lake Michigan whitefish catch 1900-84, and the distribution of abnormally mild and cold winters (deviating by ±25 percent or more from the mean) during the period.

The association between trends in early winter severity and trends in the fishery was striking. Cold winters during the 1920's were followed by peak whitefish yields circa 1930. Of the 2 cold winters between 1931-58, one was associated with the 1943 year-class of whitefish which was responsible for most of the large peak in catch circa 1947 (Hile et al 1953). Excepting effects of the 1943 year-class, whitefish catch from 1930-60 tended consistently downward, parallelling the trend of consistently warm to average winters during the same period. The beginning signs of recovery followed cold winters in 1959 and 1963, and the high sustained yields since the early 1970's were associated with the coldest 15 year period in recorded Great Lakes climatic history.

Rainbow smelt and whitefish:

The possibility that whitefish recruitment has been inhibited by predation from the introduced rainbow smelt has attracted consideration since it was noticed that a massive dieoff of smelt in Lakes Huron and Michigan in 1943 (Van Oosten 1944) was followed by huge year-classes of both whitefish and ciscoes (<u>Coregonus</u> <u>artedi</u>). We entertained this smelt hypothesis as an alternative to the climatic influences on recruitment by comparing catch records of smelt to those for whitefish.

Lake Michigan smelt and whitefish catches (Baldwin et al 1979) were converted to percentages of the mean and smelt catch was plotted in relation to whitefish catch 3 years later to allow for recruitment to the fishery. Despite the crudeness of catch figures as an index of abundance, the association between smelt catch and whitefish catch 3 years later was strong (Figure 48). Years of above average smelt catch were never followed by years of above average whitefish catch (1st quadrant), while years of above average whitefish catch only followed years of below average smelt yield (2nd quadrant). However, roughly one-third the years fell in the 3rd quadrant when both species were below average in yield, suggesting that low smelt numbers did not always predict high whitefish yields.

A time series plot of Lake Michigan smelt yield (Figure 49) suggested an explanation for this association other than a direct relationship between the 2 species. The sawtooth trend to smelt yield indicated that smelt abundance declined precipitously on occasion, then built up to higher levels over several years. Of 4 distinct years of peak smelt abundance; 1942, 1958, 1969 and 1976, all 4 preceded an abnormally cold winter, with rapid declines following. Not all cold winters were followed by declines. Apparently the combination of high smelt density and severe early winters triggered smelt collapses. Perhaps smelt populations behaved like northern deer herds, where cold winters result in high mortality only if numbers are unusually high.

The association between smelt and whitefish yields is more likely to result from 2 species reacting in opposite fashion to winter severity than from a direct biological relationship. The correspondence between diminished smelt

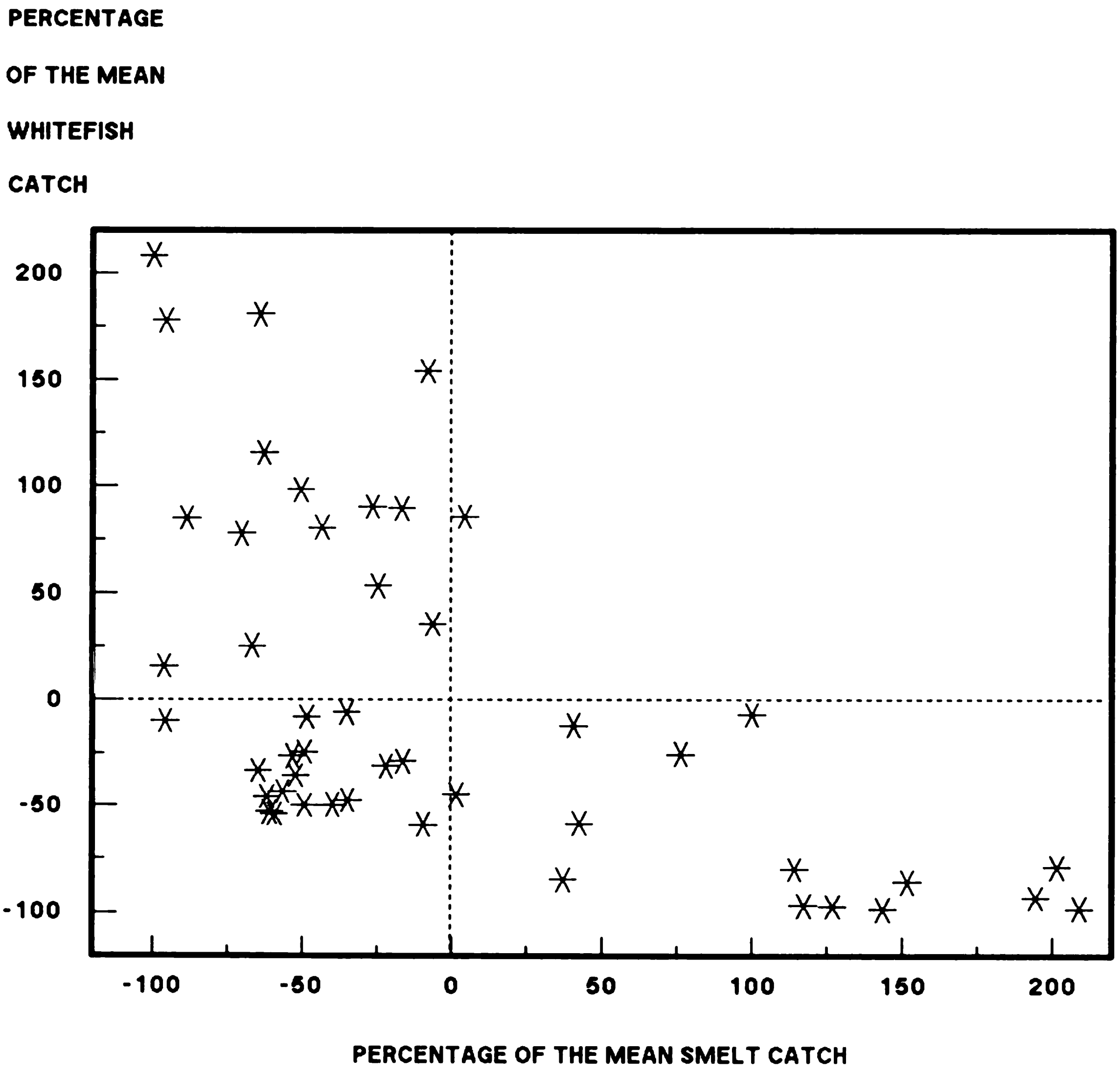

Figure 48. Percent deviation from the mean Lake Michigan whitefish catch in relation to the percent deviation from the mean rainbow smelt catch 3 years earlier, during 1932-77.

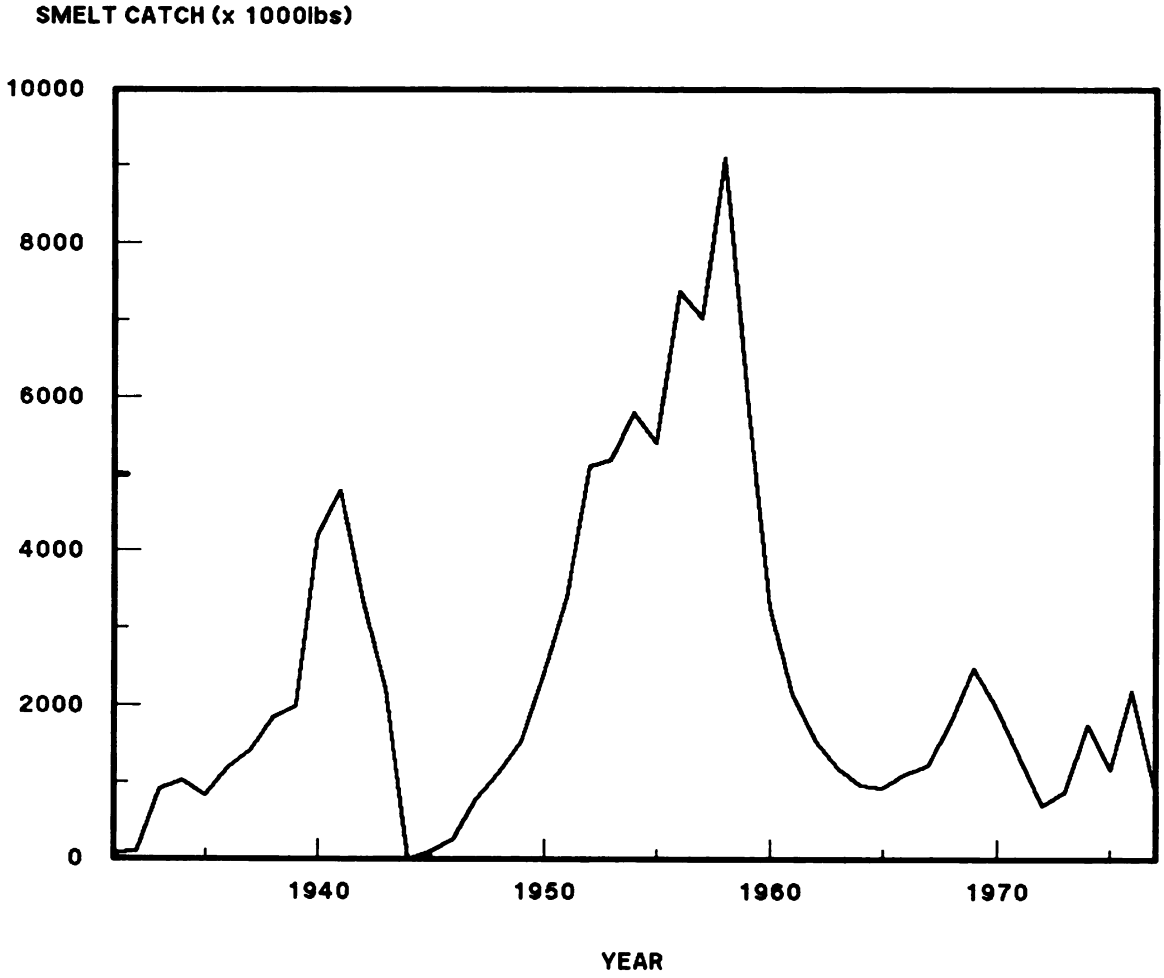

Figure 49. Lake Michigan smelt catch, 1932-77.

abundance and stong year-classes of whitefish was not wholly reliable. For example, low levels of smelt catch in 1944-47 did not precede strong whitefish year-classes comparable to the 1943 cohort, indicating that smelt alone cannot be responsible for diminished whitefish recruitment. Segleby et al (1978) found no evidence to support a relationship between ciscoe recruitment and smelt predation in Lake Superior even though smelt were consuming larval ciscoes. The apparent strong association between abundances of the 2 species can be explained on the basis of opposite responses to climatic stimuli without invoking a direct relationship. However, the association is strong enough to be useful as a forecasting index: changes in Lake Michigan smelt abundance would likely predict future changes in whitefish abundance.

DISCUSSION

Based on Freeberg's (1986) early life survival measurements, on stock-recruitment theory and on a modification of Cushing's (1982) match-mismatch hypothesis, we developed a hypothesis to explain variation in North Shore whitefish recruitment by considering 3 stages: egg deposition, egg survival and larval survival. Egg deposition was assumed proportional to spawning biomass. Egg mortality was expected to be from mechanical effects: wind and wave action as well as shifting substrate, which would be canceled by the blanketing action of ice over the spawning area. Larval mortality was expected to be principally from starvation and therefore predictable from densities of larvae relative to densities of zooplankton. The synchronicity between larval emergence and the spring outbursts of zooplankton typical of northern temperate lakes would be regulated by the rate of spring warming.

From this hypothesis, large cohorts would occur when stock size and egg deposition was adequate, winter ice formation was early and extensive to permit good egg survival, and a warm spring generated sufficient food to support an abundant larval crop. The 1977 year-class, the strongest of the 20, resulted from a benchmark vintage year: 1977 was the coldest early winter of the 20th century while the spring was the warmest of the 20 years considered. Poor year classes could result from either a low egg deposition, insufficient ice to protect the eggs or larval densities far in excess of the available zooplankton supply.

To test this hypothesis, a series of models was developed in which the expected effect of each factor on recruitment was simulated and added in sequence to an initial stock-recruitment model. Estimates of stock size and recruitment from the North Shore stock were used to calibrate the equations, and the degree of agreement between predicted and observed recruitments tested the reliability of each successive model. The models themselves however, were not simply derived from an empirical fit to observed data. Equations to describe survival through early life stages were derived independently of the North Shore data, with observed measurements used only to calibrate survival relative to environmental variables.

As each factor was added to the model, there was a progressive increase in agreement between hindcast and observed cohorts, supporting the general recruitment hypothesis. Although accuracy of the hindcasts was less than 100 percent, the verification of the final winter/spring recruitment model depended on the degree of improvement in hindcasting accuracy rather than its absolute accuracy. We expect that the accuracy of this model could be improved, but still, the degree of hindcasting power exceeded that of any existing formal whitefish recruitment model.

Although climatic differences amongst years were sufficient to generate an 11-fold difference in cohort size from intermediate spawning stocks, the influence of egg deposition on recruitment was far from negligible. In early years when stock sizes were small, even the most ideal years such as 1959 produced only an average cohort despite an exceptionally high recruit per parent ratio. Even though the relatively low larval densities expected from small spawning stocks should provide some measure of compensation for reduced egg deposition, reproduction from small stocks was clearly gamete limited. On the other hand, large spawning stocks do not necessarilly influence recruitment positively. In the South Bay study, the 4 largest spawning stocks produced the 4 smallest cohorts, and in this study the 3 largest stocks produced the 8th, 15th and 20th ranked year-classes. The strong negative effects of larval density on larval survival would explain the reduced (R/S) ratios and diminished recruitments apparently common to larger spawning stocks.

Evidence for an influence of early winter climate on recruitment was the strongest of those factors considered. First, the 4-fold difference in egg survival between 2 distinctly different winters in the Grand Traverse Bay study implied that winter ice is equivalent in effect to at least a 4-fold difference in egg deposition. Second, in the North Shore recruitment analysis, cold ice-extensive winters were a prerequisite, but not a guarantee, for larger than average cohorts and (R/S) ratios. Third, historical trends in early winter severity were strongly associated with historical trends in the whitefish fishery. In its effect on North Shore recruitment, extensive ice appeared to act in the same manner as increased egg deposition. Recruitment from small stocks was enhanced by cold winters but larger stocks benefitted only if the following springs were warm.

The expectation that warm springs created a closer match between zooplankton pulses and larval emergence was not confirmable from the Grand Traverse Bay study. Springs in both years were delayed and zooplankton outbursts did not occur until near the end of the zooplanktivorous larval phase. This study did document a clear relationship between larval survival and zooplankton per larvae ratios, but the supposition that early spring zooplankton dynamics were temperature driven was supported principally by the improvement in North Shore recruitment hindcasts when spring temperatures were added to the model. Information on early spring zooplankton dynamics in Lake Michigan seems to be absent from the literature. Hall (1964) found an influence of temperature on reproductive rates of Daphnia galeata in an inland Michigan lake, lending some support to the possibility of temperature dependent spring zooplankton pulses.

The winter/spring recruitment hypothesis is not without precedent. The model was based on Ricker's (1954) stock-recruitment relationship which we modified to include density independent egg mortality and a larval carrying capacity which varied with spring warming. The negative influence of higher pre-recruit densities on recruitment was observed previously in the South Bay study and the influence of climate on egg mortality was important in Miller's (1952) study in Alberta. Christie's (1963) use of November and April temperatures to explain recruitment variation is not inconsistent with the North Shore results. In effect, the winter/spring recruitment model is a reconciliation between stock-recruitment theory and the more empirically based indices such as Christie's November-April temperature index. The only unique aspects to this study are that factors were integrated into a comprehensive model derived from theory, and that their use was justified from an early life history study.

This model should not be directly applicable to other whitefish stocks, but there does seem to be enough common ground amongst the several existing whitefish recruitment studies to suggest that common factors may explain cohort variation to some degree in many cases. For example, North Shore recruitment for the year-classes of 1976-80 was roughly in phase with year-classes in at least 2 other northeastern Lake Michigan whitefish stocks, but these cohorts were not in phase with those in the northwestern part of Lake Michigan (Ebener and Copes 1985). Northwest Lake Michigan is a wind-ward shore, shallower and with less year to year variation in ice formation, therefore a different response to early winter conditions would be likely. In Lake Superior, as another example, whitefish yield has varied by only a 3-fold range compared to 250-fold in Lake Michigan. Perhaps the enormous volume and large thermal mass of Superior dampens the effects of climatic oscillations, stabilizing physical characteristics of the Lake and ultimately the fishery. In any case, even though climate may commonly influence egg and larval survival, it seems likely that the strength of climatic influences on each of these stages will be modulated by both the morphological characteristics of a location and the degree of climatic variation within a particular region.

It was uncertain whether the residual variance in cohort strength not explained by the winter/spring model was a result of incompleteness of the model or of error in the initial data used to construct it. Three of 20 hindcasts fell outside confidence limits of the observed cohort estimates, but the confidence limits represented the average degree of error rather than error for any single year-class. Even if the hindcasts had been perfect, the same result could have occurred. On the other hand, confidence limits were sufficiently wide that we would be unable to determine whether even fairly large differences between observed and predicted recruitments were real or simply due to error in the initial estimates.

Sources of error in the stock and recruitment estimates included variation in yearly catch per effort which was not due to changes in whitefish abundance, and error in the age structure estimates due to low sample size or frequency. Catch sampling procedures were not uniform during the period of record, therefore some year-classes were probably well estimated and other estimates were probably poor. Error in the estimates of stock size was not addressable, but error in

(R/S) ratios, the principal dependent variable in stock-recruitment analysis, would be influenced by imprecision in both the numerator and denominator. Error in the initial data was therefore carried through the fitting procedures and there was reason to suspect that hindcasts could have been more accurate had the initial estimates themselves been more precise. In practice, the hindcasts might have been as accurate as the initial estimates, but the margin of error was large and there is also a real possibility that the model could be further improved. Imprecision in the initial data did not inhibit model development, instead it limited the ability to evaluate the reliability and accuracy of the final model. Put more simply, if this much could be done with sometimes sloppy data, how much could be done with precise data?

If the residual error in recruitment variation is taken at face value, there are some likely choices for improving accuracy of the model. Each independent variable used in the model was a surrogate measurement of the actual biologically important variable. Spawning biomass was substituted for egg deposition, ice extent for mechanical stresses in the spawning substrate, and spring temperatures for zooplankton densities after larval emergence. Verification of the reliability of each substitution and more direct measurements of actual conditions would likely result in better reliability.

North Shore whitefish fecundity was not proportional to female body weight, therefore correcting population fecundity for shifts in the size composition of the spawning stock could be useful. Secondly, the use of maximum ice extent as an index of mechanical stresses could be misleading in some years. North Shore whitefish spawn approximately 2 to 8 weeks before ice forms over their spawning grounds, and this lag time, along with the frequency and intensity of storms in the area is likely to more accurately predict egg destruction than ice cover over the entire Lake. These data were unavailable for most years of this study, but this type of measurement would seem well suited to remote sensing applications. An alternative model using freezing degree day accumulations through mid-winter rather than ice extent was developed in order to consider another possible index variable, but hindcasts were no more accurate than those from the ice extent model.

The substitution of spring warming rates for zooplankton densities should be tested more directly. In the GTB study, larval emergence occurred shortly after ice-out, which occurs in the North Shore area between late March and early May. A more reliable model might predict the lag time between larval emergence and zooplankton pulses from climatic variables. But spring temperatures were influential enough that even the probably crude index used was able to detect their effect. Given the numerous species of Great Lakes fish dependent on early spring zooplankton, the lack of information about factors influencing both sides of this relationship seems to be a large gap in current knowledge.

The association between historical trends in early winter severity and trends in the whitefish fishery implies that diminished recruitment contributed to the collapse of stocks during the 1950's, while the recovery and unexpectedly high yields during recent years were due to an atypically favorable period for reproductive success. The near absence of cold winters prior to the collapse and their uncommon frequency since then enables an explanation of both the failures and the successes of the fishery. Prior explanations of historical trends were unable to consider influences on recruitment and were therefore based on factors influencing adult mortality: exploitation and predation by sea lampreys. But as the recent expansion of northern Lake Michigan stocks despite high mortality illustrates, stock dynamics are not reliably predictable from adult mortality alone.

Exploitation seems the least likely primary cause for the contraction of stocks during the 1950's. At least one study prior to the collapse (Caraway 1951) found enough differentiation in age structures amongst Lake Michigan stocks to indicate that mortality was not uniform throughout the Lake. But the contraction of stocks during the 1950's occurred throughout the Lake, indicating that some ubiquitous factor was responsible. Recent concern that stock failures were imminent due to excessive exploitation has yet to materialize. Although compensatory factors such as density dependent growth and early maturity have contributed to the persistence of these stocks (Taylor et al, in press), the abnormal frequency of cold early winters has likely been the principal cause of this unexpected success. Whether this fortune will persist cannot be predicted, but climatic anomalies of both short term duration and over a century's span are known.

Although the synchronicity between the lamprey invasion of the upper Great Lakes and the widespread contraction of whitefish stocks seems to be a clearer example of the catastrophic effects of high mortality, there are also cases where whitefish dynamics were not fully explained by lamprey predation. The current recovery in Lake Michigan began after 1960 even though treatment of tributaries with lampricide was not completed until 1968 (Smith and Tibbles 1980). Current mortality rates in productive areas of the Lake are also similar to those reported from Lake Huron during the lamprey infestation (Spangler 1970). Additionally, lampreys and whitefish have coexisted since the early 19th century or longer in Lake Ontario (Lark 1973) and lampreys were common during peak years of the Ontario fishery circa 1920 (Christie 1963). But in Lake Erie, which did not develop a serious infestation, whitefish became commercially extinct by 1960 even though this Lake once produced the highest yields of any Great Lake. The 4 western Great Lakes all produced their lowest yields circa 1960 (Figure 50), with the highest degree of contraction in the most southerly Lake and the lowest in Superior, the most northerly Lake. Considering the Great Lakes as a whole, examples can be found of whitefish stocks which persisted despite lamprey predation and of stocks which failed in its absence. There has been enough uniformity to trends in yield to suggest that climate, which is widespread in distribution, has influenced dynamics of a great many stocks.

The principal implication of this study is that the level of harvest which can be sustained from northeast Lake Michigan stocks without exceeding their capacity for replenishment through growth and recruitment varies sharply from year to year. The range of annual recruitment variation exceeded an order of magnitude, which is consistent with previous studies. But the novel result of this study was that influential factors were not evenly distributed through time. Annual fluctuations in recruitment are sufficiently large to confound predictions of stock dynamics based on stable age structure equilibrium conditions, and it is unlikely that these fluctuations would average themselves out over a short timespan because influential factors tended to clump together.

There is an inherent dilemna in managing harvest from a volatile, fluctuating resource. If the level of harvest is held constant, then the population level will oscillate in proportion to changes in replenishment. But if the population is maintained at a stable level, harvest must vary. Annual exploitation rates in northern Lake Michigan are near 50 percent and some fisheries are currently supported by as few as two age-classes. In the event of even a short term series

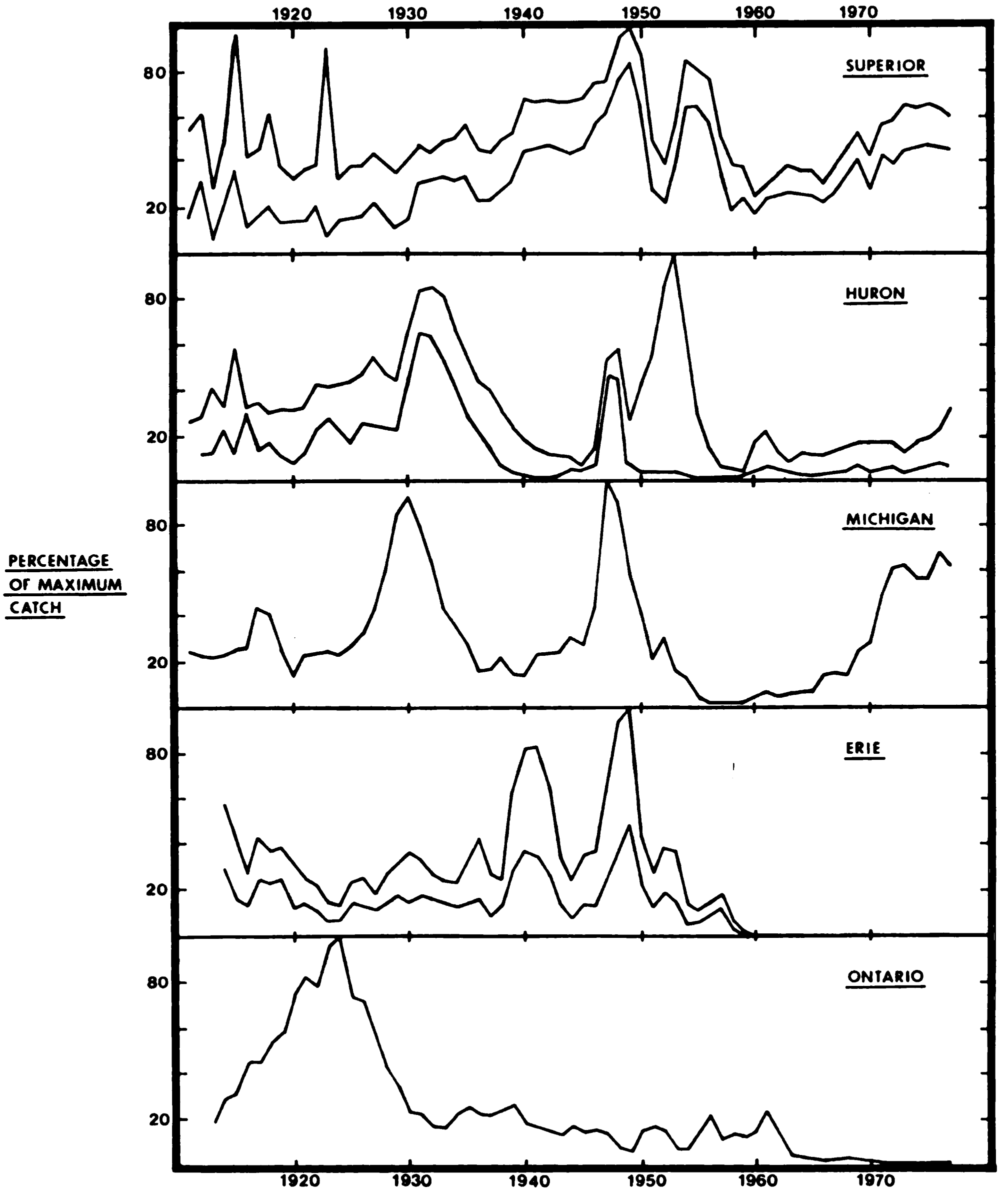

Figure 50. Great Lakes whitefish catch, 1910-77, expressed as percentages of the record catch in each Lake and with U.S. (bottom line) and total catch for some Lakes.

of recruitment failures, the potential capacity for the fishery to rapidly deplete the stocks is substantial. Even though stocks are presently abundant, a rapid decline to levels of the 1950's within a few years is not inconceivable.

Attempting to counteract this potential catastrophe by building up spawning stocks and stockpiling fish would likely be counterproductive given the commonly observed negative influence of large stocks on recruitment. A more conservative strategy would be to set a minimum level below which the fishery would not be allowed to deplete the spawning stocks. Putting such a strategy into practice would require the ability to anticipate recruitment variation and would increase stability of the stocks at the expense of increased variation in the fishery. Because whitefish in Lake Michigan are near the fringe of their range, we would expect volatile dynamics to be an inherent feature of this resource. Recognizing the tradeoffs between stable yield or stable populations and understanding the root causes of this dilemna should enable informed decisions about how to harvest the resource in a manner which maximizes both the conservation of stocks and long term yield.

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Appendix A. Percent frequency of age groups in the sampled catch by season and year from 1980-84.

NORTH SHORE

	N	3	4	5	6	7	8	9	10	>10
FL80	513	77.6	20.9	1.0	0	0	0	0	0	0
SP81	107	14.0	79.4	5.6	0	0	0	0	0	0
SU81	300	13.0	83.7	3.0	0.3	0	0	0	0	0
FL81	331	7.9	85.8	6.0	0.3	0	0	0	0	0
SP82	263	0.4	17.1	79.5	0.3	0	0	0	0	0
FL82	189	7.4	56.6	31.2	4.2	0	0.5	0	0	0
SP83	174	0	28.7	46.6	21.8	2.3	0.6	0	0	0
SU83	214	5.6	37.4	35.5	15.9	4.2	0.5	0	0	0
FL83	155	36.7	30.3	17.4	13.3	1.8	0.5	0	0	0
SP84	110	0	38.2	42.7	10.9	6.4	1.8	0	0	0
SU84	96	6.2	51.0	22.9	10.4	5.2	3.1	0	0	0
FL84	155	18.1	67.7	12.9	0.6	0.6	0	0	0	0

LELAND

	N	3	4	5	6	7	8	9	10	>10
FL80	114	57.0	28.9	7.0	0	2.6	1.8	1.8	0	0.9
SP81	81	2.5	44.4	22.2	12.3	6.2	2.5	0	1.2	8.6
SU81	94	6.4	67.0	5.3	7.4	5.3	1.1	1.1	4.3	2.1
FL81	244	6.6	67.2	11.1	7.4	1.2	0.8	0.8	2.0	2.4
SP82	232	1.7	12.9	53.0	7.8	11.6	0.4	3.9	3.9	4.8
FL82	184	20.1	29.9	35.3	10.9	2.2	0.5	0.5	0.5	0
SP83	222	0.5	14.4	29.7	27.5	9.0	9.5	1.8	0.5	7.2
SU83	162	6.2	29.6	27.2	26.5	3.7	1.2	1.2	1.2	3.1
FL83	76	10.5	26.3	25.0	27.6	6.6	2.6	1.3	0	0
SP84	74	0	6.8	13.5	21.6	24.3	2.7	13.5	6.8	10.8
SU84	120	1.7	20.8	27.5	16.7	25.0	4.2	1.7	0	2.5
FL84	64	7.8	12.5	34.4	23.4	18.8	3.1	0	0	0

BEAVER ISLAND

	N	3	4	5	6	7	8	9	10	>10
SP81	219	0	68.0	18.7	5.5	2.3	2.3	0.5	0	0
SP82	81	0	9.9	82.7	6.2	0	0	0	1.2	0
SP83	181	0	9.4	39.8	36.5	12.2	2.8	1.7	0.6	0
SU83	38	0	13.2	36.8	39.5	7.9	2.6	0	0	0
SU84	14	0	7.1	35.7	28.6	21.4	7.1	0	0	0

Appendix A.(continued)

CROSS VILLAGE

	N	3	4	5	6	7	8	9	10	>10
SP82	88	0	52.3	45.5	2.3	0	0	0	0	0
SU83	119	0	20.2	58.0	17.6	4.2	0	0	0	0

EAST TRAVERSE TRAWLS

	N	1	2	3	4	5	6	7	8	9	10	>10
SP83	204	36.8	40.7	12.7	2.5	3.4	0	1.0	2.0	0	0.5	0.5
SP84	94	6.4	33.0	25.5	8.5	6.4	3.2	5.3	5.3	3.2	3.2	0
FL84	573	8.6	33.7	27.1	9.2	4.5	5.6	5.2	3.0	1.4	0.9	0.8