DYNAMICS AND MANAGEMENT OF ANADROMOUS ALEWIFE (*ALOSA PSEUDOHARENGUS*) POPULATIONS

by

A. Jamie F. Gibson

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
March 2004

© Copyright by A. Jamie F. Gibson, 2004

National Library of Canada
Bibliothèque nationale du Canada

Acquisitions and Bibliographic Services
Acquisisitons et services bibliographiques

395 Wellington Street
Ottawa ON K1A 0N4
Canada

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-612-89804-0
Our file Notre référence
ISBN: 0-612-89804-0

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou aturement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this dissertation.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de ce manuscrit.

While these forms may be included in the document page count, their removal does not represent any loss of content from the dissertation.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

DALHOUSIE UNIVERSITY

To comply with the Canadian Privacy Act the National Library of Canada has requested that the following pages be removed from this copy of the thesis:

Preliminary Pages
- Examiners Signature Page (pii)
- Dalhousie Library Copyright Agreement (piii)

Appendices
- Copyright Releases (if applicable)

To my father, Merritt Gibson,
mother, Wilma Gibson,
and partner for life, Tracy Horsman

Table of Contents

List of Tables viii
List of Figures xi
Abstract xvii
Acknowledgements xviii

Chapter 1. Introduction 1

1.1 Objectives 1
1.2 Thesis Overview 2
1.3 About Alewife 6
1.4 Publications Resulting from this Thesis 8

Chapter 2. A Statistical, Age-Structured, Life History Based, Stock Assessment Model for Anadromous Alosa 11

2.1 Introduction 11
2.2 The Model 12
2.3 Example 1. Margaree River, NS Alewife 15
2.4 Example 2. The Gaspereau River, NS, Alewife Fishery 21
2.5 Estimation of SR Time Series, Maturity Schedules and Mortality Rates 24
2.5.1 Spawner-Recruit Time Series 33
2.5.2 Instantaneous Natural Mortality 33
2.5.3 Maturity Schedules 36
2.6 Discussion 36

Chapter 3. Effectiveness of a High-Frequency Sound Fish Diversion System at the Annapolis Tidal Hydroelectric Generating Station, Nova Scotia 40

3.1 Introduction 40
3.2 Methods 41
3.2.1 Study Area 41
3.2.2 The Fish Diversion System 42
3.3.3 Experimental Design 45
3.2.4 Field Methods 49
3.2.5 Data Analysis 49
3.2.6 Alternative models 53

3.3 Results 54

3.4 Discussion 66

Chapter 4. A Logistic Regression Model for Estimating Turbine Mortality at Hydroelectric Generating Stations. 71

4.1 Introduction 71

4.2 The Study Area 72

4.3 Methods 72
4.3.1 Field Methods 73
4.3.2 Statistical Analysis 74

4.4 Results 77

4.5 Discussion 83

Chapter 5. A Meta-Analysis of the Habitat Carrying Capacity and Maximum Reproductive Rate of Anadromous Alewife in Eastern North America 92

5.1 Introduction 92

5.2 Methods 93
5.2.1 The Data 94
5.2.2 Model Assumptions 94
5.2.3 The Spawner-Recruit Relationship 96
5.2.4 The Recruit-Spawner Relationship 97
5.2.5 Data Standardizations 99
5.2.6 The Statistical Models 101

5.3 Results 103

5.4 Discussion 105

Chapter 6. Reference Fishing Mortality Rates from Noisy Spawner-Recruit Data 113

6.1 Introduction 113

6.2 Estimating Reference Fishing Mortality Rates 119
6.2.1 Estimating F_{msy} 119
6.2.2 Reference Point Uncertainty 122
6.2.3 Incorporating SR Parameter Uncertainty when Estimating Reference F's 127
6.2.4 Comparison of F_{msy}, F_{marg} and $F_{maxE[Y]}$ 129

6.3 Including Information from Other Populations 132

6.4 Discussion 138

Chapter 7. Biological Reference Points for Anadromous Alewife (*Alosa pseudoharengus*) Fisheries in the Maritime Provinces **144**

7.1 Introduction 144

7.2 Methods 145
7.2.1 Reference Point Estimation 145
7.2.2 Effects of Variable Maturity on Reference Points for Alewife 148
7.2.3 Simulation-Based Reference Points 150
7.2.4 Relationship between turbine mortality and fishery reference points 150

7.3 Results 151
7.3.1 Reference Point Estimation 151
7.3.2 Effects of Variable Maturity on Reference Points for Alewife 154
7.3.3 Simulation-Based Reference Points 156
7.2.4 Relationship Between Turbine Mortality and Fishery Reference Points 165

7.4 Discussion 165

Chapter 8. Conclusions **172**

8.1 Summary 172

8.2 Future Research 177

Bibliography **182**

List of Tables

Table 2.1. The equations used for the Margaree River alewife model. 18

Table 2.2. The equations used for the Gaspereau River alewife model. 23

Table 2.3. Parameter estimates for the Gaspereau River alewife population obtained from the statistical life history model. While the standard errors for the recruitment deviates are large relative to their estimates, the mean asymptotic recruitment and spawning biomass at maximum sustainable yield are comparatively well estimated..... 25

Table 2.4. Datasets used to estimate spawner-recruit time series, mortality rates and maturity schedules for the spawning run reconstructions of four alewife populations in the Maritime Provinces. 27

Table 2.5. Statistical models used to estimate spawner-recruit time series, mortality rates and maturity schedules for four alewife populations in the Maritime Provinces. Notation is explained in the text. 29

Table 2.6. Estimates of instantaneous natural mortality rates (M^{adult}) and maturity schedules for four alewife populations in the Maritime Provinces. The maturity schedule gives the proportion of immature fish (m_a) that are alive at age a that mature at age a, for ages 2 to 6. The numbers in brackets are standard errors. 35

Table 3.1. Sound pressure levels measured in the turbine forebay at the Annapolis Tidal Generating Station, Nova Scotia, on September 8, 1999 (from Birmann 1999). Measurement locations are shown in Figure 3.3. 47

Table 3.2. The number of fish of each species captured at each sampling location the Annapolis Tidal Generating Station, Nova Scotia, while evaluating the effectiveness of an ultrasound fish diversion system during September and October 1999. The two columns for each location given the number of fish captured with the diversion activated (on) and deactivated (off). The "number of cycles" is the number of generation cycles during which fish of each species were captured. Species for which the data are modelled are marked with an asterisk..... 57

Table 3.3.Model coefficients and standard errors for clupeids captured at the Annapolis Tidal Generating Station, Nova Scotia while evaluating the effectiveness of an ultrasound fish diversion system during September and October 1999. Standard errors are corrected for overdispersion. The "site" coefficients are scaled against the tailrace (south side) site. The "diversion" coefficients are the difference ($\log N_{off}$-$\log N_{on}$). Asterisks indicate the level of statistical significance (two-tailed t-test): one, two and three asterisks indicating significance at 90, 95 and 99% confidence levels respectively (residual degrees of freedom = 169)..... 59

Table 4.1. The total number of specimens and number of live specimens of each species captured in 447 net sets during 48 randomly selected generation periods between September 7, 1999 and October 22, 1999 at the Annapolis Tidal Generating Station, Nova Scotia. Data for species in boldface was considered sufficient for analysis. 79

Table 4.2. A comparison of mortality estimates and log likelihoods for logit, probit and complementary log-log link functions for 12 species of fish at the Annapolis Tidal Generating Station, Nova Scotia. 80

Table 4.3. Logistic regression coefficients and estimates of turbine mortality for 12 species of fish at the Annapolis Tidal Generating Station. Numbers in brackets are standard errors. Estimates where the increase in mortality with increasing net deployment duration (β_1) is significantly different from 0 at a 95% confidence level after correcting for dispersion are marked with asterisks. Confidence intervals for mortality are calculated using normal approximations on the link scale and are corrected for over-dispersion. ... 84

Table 5.1. Spawner-recruit time series used for estimating random effects distributions for the maximum reproductive rate and the carrying capacity for alewife. Details of the life history modelling are provided in Chapter 2. 95

Table 5.2. Comparison of the fit of the Beverton-Holt and Ricker spawner-recruit for eight alewife populations. The models are Beverton-Holt: $R = \alpha S/(1+S/K)$ and Ricker: $R = \alpha S \exp(-\beta S)$, where S is the spawner biomass (kg) and R is the number of age-3 recruits. Parameter estimates were obtained using maximum likelihood assuming a lognormal error distribution. Fits are evaluated by comparison of the log likelihoods.... 98

Table 5.3. Values used for calculation of $SPR_{F=0}$. The weights-at-age are taken from the Margaree River population. Maturity probabilities (m_a) are calculated from the life history model output for the Margaree River, Gaspereau River, Miramichi River, and Mactaquac Headpond..... 100

Table 6.1. Summary of methods for estimating reference fishing mortality rates. Methods are presented in the context of the Beverton-Holt SR model, parameterized in terms the slope of the model at the origin of the SR model (α) and the asymptotic recruitment level (R_0). The maximum likelihood methods use the mode of the SR likelihood or probability surface as the estimate of α that is used to estimate F_{msy}. The marginal probability density for α is found by integrating over R_0 and the optimal F is estimated using the mode of the resulting distribution. The decision theoretic method finds the value of F that maximizes the expectation of the catch over α and R_0. 118

Table 6.2. Reference exploitation rates for two alewife populations in the Maritime Provinces, Canada, estimated using no SR data, population-specific SR data or data from other populations. Estimates are obtained using either the mode of joint likelihood or probability distributions (F_{msy}), the marginal likelihood or probability density for α (F_{marg}) or by finding the exploitation rate that maximizes the expectation of the catch ($F_{\mathrm{maxE[Y]}}$). 137

Table 7.1. Parameter estimates obtained from the assessment and SR models that were used as input parameters for the simulation models and to calculate reference points. . 146

Table 7.2. Weight-at-age for 3 alewife populations in the Maritime Provinces. Weights are the mean weights of alewife sampled between 1997 and 2000 in the Gaspereau River and between 1970 and 1999 for the Mactaquac Headpond, and the weights-at-age reported by Chaput et al. 2001 for the Margaree River. The Miramichi weights-at-age were used for the Miramichi River population. 147

Table 7.3. Biological reference points for the Margaree River, Gaspereau River Miramichi River and Mactaquac Headpond alewife populations. Values in brackets are the corresponding exploitation rates. Definitions of the reference points are explained in the text..... 152

List of Figures

Figure 2.1. Part of the observed (x's) and predicted (lines) catch-at-age arrays for the Margaree River alewife population. Catches are partitioned by cohort year (right column) and age at maturity (labels at the top). The year (bottom labels) is the year of capture.. 19

Figure 2.2. Observed (x's) and predicted (solid lines) total catches and larval indices, and predicted exploitation rates and spawning escapements for the Margaree River alewife population. The dashed lines show 95% confidence intervals for the estimated values based on normal approximations. 20

Figure 2.3. Observed (x's) and predicted (lines) total catches and spawner escapement counts, the exploitation rates (assumed known) and predicted number of age-3 recruits for the Gaspereau River alewife population. The dashed lines show the number of spawners at MSY (upper right panel) and the median asymptotic recruitment (lower right panel) for this population. The grey shaded areas are 90% confidence intervals for these reference points. 26

Figure 2.4. Part of the observed (x's) and predicted (lines) spawning escapement arrays for the Mactaquac Headpond alewife population (females only). Escapements are partitioned by cohort year (right column) and age at maturity (labels at the top). The year (bottom labels) is the year of capture. 31

Figure 2.5. Observed (x's) and predicted (solid lines) catches, spawning escapements and exploitation rates for the Mactaquac Headpond alewife population. 32

Figure 2.6. Times series of spawning biomass (solid line) and recruitment (dashed line) for four alewife populations in the Maritime Provinces. Recruitment is indexed by the cohort year resulting in zero lag between spawning and recruitment in these graphs..... 34

Figure 2.7. Variability in the age at maturity for the Margaree River, Miramichi River and Mactaquac Headpond alewife populations. Each point (or circle) represents the proportion of fish within a cohort that were alive at a given age and matured at that age. The size of the circle is proportional to the number of immature fish in the cohort at that age. Points are jittered slightly to facilitate display. 37

population that matures over four years). Assuming an adequate sample size, this increase improves the researcher's ability to estimate mortality rates or other parameters that are held constant across these categories. 38

Figure 3.1. A map of the Annapolis Tidal Generating Station, Nova Scotia, showing the location of the two fishways, sluice gates and sampling locations used during an assessment of an ultrasound fish diversion study during September and October 1999.. 43

Figure 3.2. A map of the turbine intake at the Annapolis Tidal Generating Station, Nova Scotia, showing the location of the sound field, the location of the new fishway relative to the turbine intake and the location of the sound pressure level measurements taken on September 8, 1999 (adapted from Birmann 1999)..... 44

Figure 3.3. Voltage spectrum of the signal applied to the transducers at the Annapolis Tidal Generating Station, Nova Scotia, during September and October 1999, measured using a bandwidth of 60 Hz (adapted from Birmann 1999). 46

Figure 3.4. The location, time and magnitude of clupeid catches at the Annapolis Tidal Generating Station, Nova Scotia, while evaluating the effectiveness of an ultrasound fish diversion system during September and October 1999. Generation periods sampled when fish were not captured are marked with "o". Note scale differences between axes. 61

Figure 3.5. A comparison of two estimates of the effectiveness of an ultrasound fish diversion system at the Annapolis Tidal Generating Station, Nova Scotia, during September and October 1999. The dark bars show the estimates obtained from a model that includes environmental variables and the light bars show the estimates from a model without the environmental variables. The left panel (tailrace) shows estimates of the deterrent effect based on changes in the rates of fish passage through the turbine tube, while the right panel (new fishway) shows the changes in the rates of passage of fish through a fishway that bypasses the turbine. 63

Figure 3.6. Estimates of the effectiveness of an ultrasound fish diversion system and the increase in fish passage in the new fishway with the diversion activated at the Annapolis Tidal Generating Station, Nova Scotia, during September and October 1999. Coefficients were estimated using the model with environmental variables. Error bars are one standard error: round brackets indicate standard errors estimated under the assumption of a Poisson error distribution, and square brackets indicate those estimated assuming a quasi-Poisson error distribution. 65

Figure 4.1. The relationship (solid line) between the mortality estimate ($M_{d=0}$) and lambda, a power parameter that determines the functional form of the relationship between mortality and net deployment duration for 12 species of fish at the Annapolis Tidal Generation Station, Nova Scotia. The dashed line shows the profile log likelihood for lambda, standardized by subtracting the maximum log likelihood from each estimate. The intersections between the dotted line and the dashed line show the 95% confidence interval for lambda. 81

Figure 4.2. Mortality (solid line) as a function of the duration of net deployment for 12 species of fish at the Annapolis Tidal Generating Station, Nova Scotia. Each point represents a fish that was either alive (0), or dead (1). Points are slightly jittered to facilitate display. The y-intercept is an estimate of acute mortality in the absence of any time in the net, interpreted as an estimate of acute turbine mortality. Error bars are 95% confidence intervals. 82

Figure 5.1. Spawner-recruit relationships for 8 alewife populations, plotted on different scales to show the variability around the fitted models for each population. The scale on the right is the number of age-3 recruits produced in each cohort. The scale on the left shows the number of subsequent spawners that would be produced by these recruits in the absence of anthropogenic mortality. The solid line is the spawner-recruit relationship obtained for each population individually, the dashed line is the spawner-recruit relationship for each stock from the mixed-effects model, and the dotted line is the replacement line. 106

Figure 5.2. Spawner-recruit relationships for 8 alewife populations, plotted on the same scale to show the variability between populations. Line symbolism is identical to Figure 5.1 107

Figure 5.3. A meta-analytic summary of the maximum lifetime reproductive rate (alpha) and the habitat carrying capacity for eight alewife populations. The light grey shaded regions are individual fits that depict the profile likelihood for each parameter, truncated to show the 95% confidence interval. The profile is used to gauge the relative plausibility of different values (wider is more plausible). The black dot is the maximum likelihood estimate for each parameter. Convergence of the nonlinear least squares algorithm was not obtained for the Miramichi and Long Pond stocks. Where convergence was obtained, approximate asymptotic 95% confidence intervals are shown (black line). The dark grey shaded regions show summaries of the mixed model results. The "mixed model mean" represents the estimated mean of the logarithm of each parameter with a 95% confidence interval. The "mixed model estimated random effects distribution" is the normal distribution for the logarithm of each parameter based on its mean and variance estimated with the mixed effects model. 108

Figure 5.4. A comparison of the estimates of the maximum lifetime reproductive rate and the habitat carrying capacity obtained from individual regressions on each alewife population and the empirical Bayes estimates obtained from the mixed model..... 109

Figure 5.5. A meta-analytic summary of the depensation parameter for eight alewife populations (see Figure 5.3 for details). A value of the depensation parameter greater than one is evidence of depensation, a value equal to one returns the Beverton-Holt model, whereas a value less than one suggests a model with a sharper bend than the Beverton-Holt may be appropriate. Data for five of the populations contain little or no information about depensation when analysed individually..... 110

Figure 6.1. Beverton-Holt spawner-recruit models (solid line) and production model reference points for the Miramichi River (bottom) and Gaspereau River (top) alewife populations. The dashed line labelled "SPRF0" is the replacement line in the absence of fishing mortality. The slope of the SR model at the origin was essentially infinite for the Miramichi population, and reference points could not be estimated for that population. 123

Figure 6.2. Profile log likelihoods (solids lines) for (a) the maximum reproductive rate, (b) the asymptotic recruitment level and (c) the fishing mortality rate at MSY for the Gaspereau River (top) and Miramichi River (bottom) alewife populations. The log likelihoods are standardized to a maximum of 0 by subtracting the maximum log likelihood from each estimate. The intersections between the dotted lines and the profile likelihoods show likelihood ratio based 95% confidence intervals for each parameter. Upper and lower bounds cannot be determined for all populations. The contour plots (d) show the joint log likelihood surface for the maximum reproductive rate and the asymptotic recruitment level. The black square indicates the point at which the log likelihood is maximized (not available for the Miramichi population). The contour interval is -1 moving away from this point. The grey-shaded region shows the likelihood ratio based 95% confidence region for the parameters. 125

Figure 6.3. A summary of the simulation results comparing reference fishing mortality rates estimated using maximum likelihood estimation (M.L.E.), the mode of the marginal probability density (M.P.D.) and a decision theoretic model (D.T.). The box plots show the distributions of the estimated reference fishing mortality rates for 500 simulated SR datasets for each combination of the alpha and sigma. The median value is indicated with a point and the grey shaded region shows the inter-quartile range. The whiskers are drawn to the nearest value within 1.5 times the inter-quartile range. The dotted line gives the true F_{msy} for the simulated dynamics. 131

Figure 6.4. A summary of the simulation results for the maximum reproductive rate of 50 and sigma=0.9. The solid line gives the known equilibrium yield, scaled to a maximum of one, as a function of the exploitation rate. The box plots show the distribution of the reference fishing mortality rates estimated from 500 simulated SR datasets using the three methods. For each method, the solid line is the median value and the grey shaded region shows the inter-quartile range. The whiskers are drawn to the nearest value within 1.5 times the inter-quartile range. Points beyond these limits are plotted as points. 133

Figure 6.5. The relationship between the mean equilibrium catch, mean spawner abundance, mean spawning biomass per recruit, and mean yield per recruit for three methods of estimating reference fishing mortality rates and the variability in the SR data (sigma), based on 500 simulated SR datasets for each combination of alpha and sigma. Mean equilibrium values were calculated by applying the estimated reference fishing mortality rates for each dataset to the known dynamics used to simulate the data. The dotted line shows equilibrium values that result when the MLE of the maximum reproductive rate (alpha) is used to estimate F_{msy}, the dashed line shows the values that result when the mode of the marginal probability is used to estimate a reference F (F_{marg}) and the solid line shows equilibrium values obtained by fishing at the decision theoretic reference point $F_{\mathrm{maxE[Y]}}$. 134

Figure 7.1. The relationship between the instantaneous rate of fishing mortality (F) and spawning biomass per recruit for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations. 153

Figure 7.2. Beverton-Holt spawner-recruit models (solid line) and production model reference points for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations. The dashed line labelled "SPRF=0" is the replacement line in the absence of fishing mortality. 155

Figure 7.4. Profile log likelihoods (solids lines) for the exploitation rate that produces maximum sustainable yield (left column) and the spawning biomass that produces maximum sustainable yield (right column) for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations. The log likelihoods are standardized to a maximum of 0 by subtracting the maximum log likelihood from each estimate. The intersections between the dotted lines and the profile likelihoods show a likelihood ratio based 95% confidence intervals for each parameter. Upper and lower bounds cannot be determined for all populations. 158

Figure 7.5. Comparison of simulation results for the Margaree River using constant (solid lines) and variable (dashed lines) maturity schedules. The lines give the means of the summary statistics (mean and standard deviation) for the catch and spawning escapement for a 50 year time period. The means are calculated from 100 simulations at each exploitation rate (0.0 to 0.99 with an increment of 0.01). The horizontal dashed line in the lower, left plot is the spawning escapement that gives maximum sustainable yield..... 159

Figure 7.6. A summary of the simulation results for the Margaree River alewife population. Each plot summarizes 100 population projections (50 year duration) at each exploitation rate,*u*, (0.0 to 0.99 with an increment of 0.01). The solid line in the upper two plots are the median catch and spawning escapements as a function of *u*. The dashed lines are the 10th to 90th percentiles (bottom to top lines) of the catch and spawning escapements. The middle two plots show the median (solid lines) and mean (dashed lines) catch and spawning escapement as a function of *u*. The points are the exploitation rates corresponding to 1: $F_{90\%max.med}$, 2: $F_{35\%}$, 3: $F_{max.E(C)}$, and F_{msy}. The bottom left plot shows the relationship between spawning escapement and catch. Each point represents the mean of 100 simulations at each exploitation rate (the uppermost point is $u = 0.00$, and u increases by 0.01 to a maximum of 0.99 in the lower left corner). The lower right plot shows the relationship between the standard deviation of the catch and the catch for each *u*. 160

Figure 7.7. A summary of the simulation results for the Miramichi River alewife population. Line and point symbolism are explained in the caption for Figure 7.6. 162

Figure 7.8. A summary of the simulation results for the Mactaquac Headpond alewife population. Line and point symbolism are explained in the caption for Figure 7.6. 163

Figure 7.9. A summary of the simulation results for the Gaspereau River alewife population. Line and point symbolism are explained in the caption for Figure 7.6. 164

Figure 7.10. The relationship between juvenile (left column) and adult (right column) and fishery reference points for Gaspereau River alewife. F_{msy}, S_{msy} and C_{msy} are the equilibrium fishing mortality rate, spawner biomass and catch at MSY. F_{col} is the fishing mortality rate that will drive the population to extinction. Juvenile turbine mortality was assumed to occur after compensatory mortality. Adult turbine mortality occurs after spawning. 166

Abstract

The objective of this thesis is to conduct basic research about the population dynamics of anadromous alewife and use the results to develop assessment and management models this species. This objective is met through the development of a population dynamics model based on the life history of anadromous *Alosa*. The two underlying themes throughout the thesis are the adaptation of the model to individual stocks and management questions, and parameter estimation for the model. I used the model to estimate fishing and natural mortality rates, maturity schedules and spawner-recruit (SR) time series that I used to derive fisheries reference points for alewife populations in the Maritime Provinces, Canada.

The effects of turbine mortality at hydroelectric generating stations on fishery yields and reference points were examined using the model. Based on experiments at the Annapolis Tidal Generating Station, I tested whether a modification to methods used to estimate turbine mortality could improve the resulting estimates and whether modelling of the process governing the rate of fish passage at hydroelectric generating stations could improve assessment of fish diversion systems.

Spawner-recruit relationships for alewife are poorly determined when estimated using population-specific data. I therefore carried out a meta-analysis of the dynamics of eight alewife populations to derive species-level probability distributions for the maximum lifetime reproductive rate and carrying capacity for alewife. I used the resulting distributions as Bayesian priors when estimating fishery reference points.

I evaluated methods of estimating fishery reference points from noisy SR data using simulated data. When the maximum likelihood estimates of the SR parameters are used to estimate the fishing mortality rate that produces maximum sustainable yield, the resulting estimates may lead to substantial under- or over-exploitation of the population. In contrast, the method of maximizing the expectation of the yield is less variable, produces larger yields and substantially reduces the risk of over-exploitation.

Acknowledgements

I completed this thesis with the assistance, support and encouragement of many people and organizations. Financial support was provided by Nova Scotia Power Inc. (NSPI), the Department of Fisheries and Oceans (DFO), the Nova Scotia Department of Environment and Labour, the Acadia Centre for Estuarine Research and NSERC.

Michael Allen, Gregor MacAskill, Samara Eaton, Trisha Holland, Lee Jamieson, Ken Meade, Nadine Thomas and Sean Gillis assisted with field work in Annapolis Royal and Mark Johnston, Alex Levy and Steve Murray with field work on the Gaspereau River. Terry Toner, Ken Meade, Greg Carlin, Paul MacKay and John James of NSPI provided advice, encouragement and logistical support when working around hydroelectric facilities. The fish diversion system tested at the Annapolis Tidal Generating Station was supplied by Alden Research Laboratory, and the acoustic modelling for the system, its deployment and measurement of its sound field were performed by Michael Birmann (Scientific Solutions, Inc.). Gerald Chaput (DFO) supplied data for the Miramichi River and Margaree River alewife populations, and Brian Jessop (DFO) provided data for the Mactaquac Headpond population. Nick Barrowman, Keith Bowen and Shelton Harley provided advice on statistics as well as bits of computer code.

Many colleagues at Dalhousie and Acadia Universities provided comments and discussions about earlier versions of thesis chapters and manuscripts that substantially improved these works, including Graham Daborn, Sonja Teichert, Shelton Harley, Keith Bowen, Kurtis Trzcinski, Ian Jonsen and Nell Denheyer. Additionally, I thank the members of the Myers Lab, in particular Shelton Harley and Dan Kehler, as well as Kurtis Trzcinski for making this component of my education the stimulating and enjoyable experience that it was. Jeff Hutchings and Chris Taggart, together with my supervisor Ransom Myers formed the supervisory committee for my degree program at Dalhousie University.

I would like to thank my partner, Tracy Horsman for being there, or not, as appropriate throughout the thesis and my father, Merritt Gibson, for instilling in me a life-long love for biology and our natural environment. This thesis would not have been possible without their support.

Finally, I would like to thank my supervisor, Ransom Myers, for accepting me as as a student, for many, many, stimulating discussions and ideas, and for fundamentally changing the way I think.

CHAPTER 1. INTRODUCTION

A fundamental challenge of fisheries science is to develop an understanding of the population dynamics of the species of interest and how human activities influence these dynamics. For many species of fish, human activities that influence population dynamics extend beyond fisheries. In the case of diadromous species, activities such as hydroelectric development, pollution, water withdrawals for agricultural or industrial applications and pollution from point or non-point sources can affect population dynamics either directly, by changing mortality, or indirectly by altering or restricting access to habitat. These activities may affect life stages differently depending on the location and timing of the activities and the requirements of organisms at the particular life stage. Given that the overall purpose of fisheries management is to ensure sustainable production from fish stocks over time, stock assessments and management should include all activities that may affect population size or productivity.

Alewife *Alosa pseudoharengus* is an anadromous species of fish whose dynamics are influenced by many human activities. It supports both directed and by-catch commercial fisheries during coastal migrations, and is fished both recreationally and commercially as they ascend natal rivers to spawn during the spring. Dams, hydroelectric development, and sewage and industrial outfalls are known to be responsible for declines in alewife population size (Rulifson 1994).

1.1 Objectives

The overall objective of this thesis is to provide a better understanding of the population dynamics of anadromous alewife, how human activities affect alewife populations, how their dynamics change in response to human activities and how this information can be used to manage these alewife populations. This objective is met through the development and parameterization of a population dynamics model for

alewife that includes several human activities that may influence their dynamics. In turn, this objective is met through the following series of projects:

- the development of a population dynamics model for anadromous *Alosa* to provide a basis for stock assessment and testing hypotheses about alewife life history (Chapter 2)
- parameter estimation for the model, including natural, fishing and turbine mortality rates, maturity schedules, reproductive rates and habitat carrying capacity (Chapters 2, 4 and 5)
- the development of decision theoretic methods for deriving fishery reference points and the evaluation of the methods by testing whether yield and conservation benefits can be improved simultaneously if the methods are used (Chapter 6)
- the comparison of several fishery reference points using life history based simulation models (Chapter 7)
- the development of methods for assessing the effects of hydroelectric development on alewife populations and fisheries (Chapters 3, 4 and 7).

1.2 Thesis Overview

I develop a life-history based, age-structured population dynamics model for anadromous *Alosa* in Chapter 2. The model is built around a four dimensional array that contains the number of adult fish within a population in each year, by sex, age and the number of previous spawnings. The previous spawning history determines the number of times that a fish has previously been exposed to riverine impacts that contribute to overall mortality rates. The model is designed to incorporate the kinds of data typically collected for anadromous *Alosa* stocks, such as catch-at-age, spawning escapement counts at fish ladders, larval and juvenile abundance indices, and turbine mortality estimates. Fournier and Archibald (1982) and Deriso et al. (1985) developed the general theory for statistical

catch-at-age models for stock assessment that allow auxiliary data to be incorporated into the model. Following their approach, I show how the model can be adapted to individual stocks and management questions, and how the model parameter estimates can be obtained by maximum likelihood using four alewife fisheries in the Maritime Provinces as examples. This approach is particularly useful when data for the population is sparse, as illustrated with the Gaspereau River data. In the last part of the chapter, I estimate fishing and natural mortality rates, maturity schedules and spawner-recruit time series for four alewife populations is the Maritime Provinces. These are analysed in detail later in the thesis.

Hydroelectric development has the potential to impact upon *Alosa* populations (or any migratory fish population) by limiting access to spawning areas upstream of dams, through mortality of fish passing through turbines when migrating downstream and by changes in habitat quality and quantity as a result of the changes in flow regimes associated with water management. In chapters 3 and 4, I describe experiments conducted at the Annapolis Tidal Generating Station, Nova Scotia, Canada, to assess survival of fish passing through the turbine at the station and to test the effectiveness of a behavioural fish guidance system installed at the station to reduce the incidence of fish passage through the turbine.

High-frequency sound has been demonstrated to elicit avoidance responses in anadromous *Alosa* (Dunning et al. 1992, Nestler et al. 1992, Mann et al. 1997), research that has lead to the development of fish deterrent and fish guidance systems that have subsequently tested at several electric generating stations with varying degrees of success (e.g. Nestler et al. 1992, Ross et al. 1996, Popper 1999, Ross 1999). In chapter 3, I describe an experiment to test the effectiveness of a high-frequency sound fish diversion system at the Annapolis Tidal Generating Station. The effectiveness of the diversion system was tested by comparing the rates of fish passage through the turbine and fishways with the diversion system turned on and off. Fish behaviour and rates of passage at hydroelectric stations vary considerably in response to environmental variables

(O'Leary and Kynard 1986, Jessop 1990b, Gibson 1996). In addition to testing the effectiveness of the fish diversion system, I examine the hypotheses that erroneous estimates of diversion effectiveness may arise if environmental variables are ignored and that the statistical significance of the effectiveness estimates may be overestimated if inappropriate statistical distributions are assumed.

In chapter 4, I present a method that allows separation of fish mortality caused by handling and capture techniques from that caused by passage through a turbine, an issue that may have confounded many turbine mortality studies (Mathur et al. 1994). By simply varying the duration of the deployment of nets used to capture fish downstream of the turbine, survival can be modelled as a function of the duration of the net deployment. The model is then used to predict the survival of fish that have not spent time in the net. In this chapter, I develop the methods and demonstrate the approach using data for 12 species captured at the Annapolis Tidal Generating Station. Hypotheses about the functional form of the relationship between time in the net and mortality are tested during the model development.

Spawner-recruit models are a widely accepted tool for analyzing population dynamics (Moussalli and Hilborn 1985; Myers et al. 1999), providing biological reference points for management (Myers et al. 1994) and a basis for the estimation of the long-term consequences of mortality caused by pollution, dams or other human activities (Barnhouse et al. 1988, Hayes et al. 1996). In Chapter 5, I provide a detailed analysis of the population dynamics of anadromous alewife using data for eight alewife populations in eastern North America. I modelled the datasets in two ways: fitting models to each dataset individually, and using meta-analytic methods to simultaneously estimate model parameters for the eight populations. The later method reduces among population variability, provides biologically realistic estimates and is used to derive probability distributions for the maximum reproductive rate at low population size and the habitat carrying capacity for alewife at the species level. These distributions are used as Bayesian priors in Chapter 6.

Biological reference points are indices based on the biological characteristics of a fish stock and the characteristics of its fishery. They play a central role in the implementation of management strategies by providing the link between stock assessment and management strategies (Caddy and McGarvey 1996), a basis for risk assessment (Punt and Hilborn 1997) and a gauge to determine whether management actions are being achieved (Caddy and Mahon 1995). Reference points are the topics of Chapters 6 and 7.

Biological reference points derived from alewife spawner-recruit relationships are typically not well determined. In Chapter 6, I review and evaluate methods of estimating reference fishing mortality rates from spawner-recruit data, including maximum likelihood, Bayesian and decision-theoretic methods. I use Monte Carlo simulations to examine the hypothesis that fishery and conservation objective can be better met using decision theoretic methods. I find that although the maximum likelihood method is the least biased of the methods of estimating F_{msy}, it is also the most variable. At times, the estimated F_{msy} exceeded the fishing mortality rate that would drive the population to extinction. In contrast, the method of maximizing the expectation of the yield (a decision-theoretic approach) is biased but much less variable. On average, it produced yields that are higher than the other methods while substantially reducing the risk of over-exploiting the population. In this chapter, I also demonstrate how these methods can be extended to include information from other populations using the priors developed in Chapter 5. The priors may be used to assess the plausibility of parameter estimates obtained for a single population, or combined with the data for the population of interest. Data from two alewife populations are used to demonstrate these methods.

Reference points used to manage alewife fisheries in the Gulf of St. Lawrence presently differ from reference points used for alewife fisheries in the Bay of Fundy. In Chapter 7, I evaluate whether life history differences between populations in these regions are sufficient to warrant different management targets. Using data from two alewife populations in the Gulf of St. Lawrence and two populations in the Bay of Fundy,

I calculate several fishery reference points for each population and evaluate reference point performance using population simulations. In this chapter, I also evaluate whether variability in age-at-maturity, which can have a marked influence on annual spawning run size, also affects reference fishing mortality rates. Additionally, I develop relationships between turbine mortality, fishery yields and reference points that can be applied to alewife fisheries on rivers developed for hydroelectric generation.

Key findings in this research are summarized in the final chapter of thesis.

1.3 About Alewife

Alewife is one of four species in the genus *Alosa* that are found on the eastern Coast of North America, together with American shad *Alosa sapidissima*, blueback herring *Alosa aestivalis* and hickory shad *Alosa mediocris* (Waldman 2003). The genus *Alosa* contains 10 other species found in the Gulf of Mexico, Europe, the Caspian Sea and Black Sea. These species in turn are members of the subfamily Alosinae. This subfamily, loosely referred to as shads, includes 7 genera and about 30 species (Waldman 2003). Together, these species support some of the world's most important fisheries.

Alewife is a diadromous fish species. Adults spawn in rivers during the spring and young-of-the-year alewife move downstream in the late summer and early fall to winter at sea. The fish mature at three to six years of age at which time they return to the rivers to spawn. Fidelity to their natal river has not been demonstrated for alewife, although a high degree of homing to the river of first spawning has been demonstrated for alewife (Jessop 1994) as well as the closely related American shad (Melvin et al. 1986). Additionally, meristic and morphometric differences exist among river populations of American shad (Carscadden and Leggett 1975, Melvin 1984) that are evidence of homing to natal rivers. Alewife are iteroparous and in non-impacted populations may spawn up to four to six times throughout their lives.

Alewives are sympatric with blueback herring throughout much of their range (Loesch 1987). Although their spawning periods overlap, alewives may begin to spawn 3

to 4 weeks earlier than bluebacks. In Bay of Fundy rivers, alewives typically begin to spawn in late April and may continue to do so over two months (Scott and Scott 1988), utilizing ponds, lakes or slow-flowing portions of streams and rivers as spawning habitat. In areas were spawning seasons overlap, the two species are isolated by the use of different spawning sites (Loesch and Lund 1977), with blueback herring spawning in areas with faster moving water (Loesch 1987).

Alewife juvenile ecology appears highly variable. When spawned in moving water, the eggs and larvae of both species are transported downstream. In Lake Ainslie, N.S., a non-tidal freshwater lake, juvenile alewives and small numbers of blueback herring are present in the lake until late August when they begin to move downstream to the estuary (O'Neill 1980). Young-of-the-year alewives and blueback herring are present in the non-tidal freshwater of the Mactaquac Dam headpond during July through September and at least to late October (Jessop and Anderson 1989). Migration from this headpond probably begins in late August, and increases rapidly through early September (Jessop 1990b). In the Chesapeake Bay area, juveniles are distributed throughout tidal fresh water during spring and early summer, and may move upstream in the summer with the encroachment of saline water (Warinner et al., in Loesch 1987). In the Annapolis River, NS, a river without lakes or impoundments, alewife are present in the estuary at salinities of about 30 in July (Gibson 1996).

Rulifson (1994) surveyed fisheries biologists to determine the distribution and status of anadromous *Alosa* in eastern North America. Within the Maritime Provinces, 141 of 145 rivers identified in the survey contained alewife. The majority of these populations (121 of 141) were thought to be in decline. Only one was listed as increasing, although few data exist about most of these populations. Causes of the declines were identified for 30 rivers, and included dams (29 rivers), chemical factors (2 rivers) and sewage (1 river). Over-fishing was not identified as a cause for the decline in the survey.

In-river alewife fisheries are of local economic value. Landings are typically reported for river herring, and include both alewife and blueback herring. Reported

landings for river herring in the Maritime Provinces (since 1960) peaked in 1980 at just less than 11,600 t, and averaged 6,231 t between 1997 and 1999 (DFO 2001). Several stocks in this region exhibit characteristics of over-exploited stocks (Robichaud-LeBlanc and Amiro 2001). Landings one hundred years ago were more or less similar: between 1892 and 1900 inclusively (Anon. 1892 - 1901), landing in the New Brunswick and Nova Scotia averaged roughly 5,050 t (minimum: 3,586 t ; maximum: 6,550 t)[1]. The Saint John and Miramichi Rivers in New Brunswick produce the largest river herring yields in North America (Schmidt et al. 2003).

Ecologically, alewife is a prey species at sea and in fresh water, and is an important predator that can alter zooplankton community composition within lakes (Mills et al. 1992, Gibson and Daborn 1998). They can also serve as a vector for nutrient transport from the oceans to inland waters (Durbin et al. 1979, Garman 1992, Garman and Macko 1998). As a result, human activities such as fishing and the construction of dams that impact upon alewife population size may indirectly alter the productivity and community structure within their natal watersheds (Freeman et al. 2003).

1.4 Publications Resulting from this Thesis

Some of the research undertaken as part of this thesis has been published prior to appearing here, resulting in the following list of articles and reports:

Gibson, A.J.F., and R.A. Myers. in press. Estimating reference fishing mortality rates from noisy spawner-recruit data. Canadian Journal of Fisheries and Aquatic Sciences.

Gibson, A.J.F., and R.A. Myers. 2003. A statistical, age-structured, life history based, stock assessment model for anadromous *Alosa*. p. 275-283. *In* K. E. Limburg, and J.R.

---

[1] Landings were reported in barrels. I assumed a barrel contained 500 fish and an average weight of 0.25 kg per fish for this comparison.

Waldman [ed.] Biodiversity, Status, and Conservation of the Worrld's Shads. American Fisheries Society Symposium 35. American Fisheries Society, Bethesda, MD.

Gibson, A.J.F., and Myers, R.A. 2003. A meta-analysis of the habitat carrying capacity and the maximum lifetime reproductive rate of anadromous alewife in eastern North America. p. 211-221. *In* K. E. Limburg, and J.R. Waldman [ed.] Biodiversity, Status, and Conservation of the World's Shads. American Fisheries Society Symposium 35. American Fisheries Society, Bethesda, MD.

Gibson, A.J.F., and R.A. Myers. 2002. Effectiveness of a high-frequency sound fish diversion system at the Annapolis Tidal Gererating Station, Nova Scotia. North American Journal of Fisheries Management 22: 770-784.

Gibson, A.J.F., and R.A. Myers. 2002. A logistic regression model for estimating turbine mortality at hydroelectric generating stations. Transactions of the American Fisheries Society 131: 623-633.

Gibson, A.J.F., and R.A. Myers. 2002. Meek's halfbeak (*Hyporhamphus meeki*) and flying gurnard (*Dactylopterus volitans*) captured in the Annapolis Basin, Nova Scotia. Canadian Field-Naturalist 116: 134-135.

Gibson, A.J.F., and R.A. Myers. 2003. Biological Reference Points for Anadromous Alewife (*Alosa pseudoharengus*) Fisheries in Atlantic Canada. Canadian Technical Report of Fisheries and Aquatic Sciences No. 2468.

Gibson, A.J.F., and R.A. Myers. 2003. Biological Reference Points for Bay of Fundy Alewife Fisheries. Proceedings of the 5th Annual Bay of Fundy Science Workshop. Wolfville, NS.

Gibson, A.J.F., and R.A. Myers. 2001. Gaspereau River Alewife Stock Status Report. DFO Canadian Stock Assessment Secretariat Research Document 2001/061. Department of Fisheries and Oceans, Ottawa, Ontario.

Gibson, A.J.F. 2000. The Gaspereau River alewife stock and fishery: 2000. Acadia Centre for Estuarine Research Publication No 58. Wolfville, NS. 25 p.

Gibson, A.J.F. 2000. Characteristics of the Gaspereau River alewife stock and fishery: 1999. Acadia Centre for Estuarine Research Publication No 56. Wolfville, NS. 52 p.

Gibson, A.J.F. 1999. Characteristics of the Gaspereau River alewife stock and fishery: 1998. Acadia Centre for Estuarine Research Publication No 49. Wolfville, NS. 91 p.

CHAPTER 2. A STATISTICAL, AGE-STRUCTURED, LIFE HISTORY BASED, STOCK ASSESSMENT MODEL FOR ANADROMOUS ALOSA

2.1 Introduction

The, biology, fisheries, and data for anadromous *Alosa* populations differ from those of marine fish. Consequentially, traditional fisheries models that are designed for marine species (e.g. virtual population analyses and biomass dynamic models that assume known catch-at-age or catch) are often not appropriate for *Alosa*, and do not fully utilize the available data. For example, riverine fisheries for *Alosa* target mature fish whose availability to the fishery depends not only with recruitment and mortality rates, but also with variable maturity schedules. Additionally, anadromous fish are often affected by other anthropogenic activities such as hydroelectric generation and barriers (Rulifson 1994), and survivorship differs depending upon whether or not a fish is sexually mature, and how many times it has previously spawned. A fishes' previous spawning history may be determined from its scales (Marcy 1969). This information can therefore also be included in a model and used to separate marine sources of mortality (a function of age), from riverine sources of mortality (a function of previous spawning history). Auxiliary data such as escapement counts at fish ladders, larval abundance indices, and counts of seaward migrating juveniles are often available and can also be incorporated into an assessment model.

Fournier and Archibald (1982) and Deriso et al. (1985) developed the general theory for statistical catch-at-age models for stock assessment that allow auxiliary data to be incorporated into the model. With the development of software that allows complex, nonlinear models to be fitted rapidly, these techniques are being used more frequently for stock assessment. Here, I present an age-structured, life history model for anadromous *Alosa* and show how it can be linked to the kinds of data typically collected for *Alosa*

stocks. This approach provides a flexible, dynamic method for *Alosa* stock assessment and can be used to address critical management issues. In the first example, I show how the model can be used to determine whether increased in-season closures have reduced fishing mortality rates to target levels for the Margaree River, NS, alewife fishery. In the second example, I show how spawner biomass reference points can be estimated using the limited data available for the Gaspereau River, NS, alewife fishery. In the last part of this chapter, I use the approach to estimate spawner-recruit time series, maturity schedules, and natural mortality for the Margaree River, Gaspereau River, Miramichi River, NB, and Mactaquac Headpond, NB alewife populations. The output from these analyses are used in a meta-analysis of the population dynamics of alewife (Chapter 5), in the estimation of reference points for alewife fisheries (Chapter 6 and 7) and in Monte Carlo simulations of alewife fisheries (Chapter 7).

2.2 The Model

The following model is based on the life cycles of the three species of anadromous *Alosa* that are indigenous to eastern North America: the American shad (*Alosa sapidissima*), blueback herring (*Alosa aestivalis*) and alewife (*Alosa pseudoharengus*). Although differences exist between species and between populations of the same species, the life cycles of anadromous *Alosa* have several shared characteristics. Adults of these species ascend rivers during the spring and spawn in lakes, pools or stillwaters within the watershed. Young-of-the-year remain in fresh water until mid-summer to late fall when they emigrate to the sea. Fish mature at 2 to 7 years of age, and maturity schedules vary between populations and between years. Most populations are iteroparous. Stocks are often fished during the spawning migration, although intercept fisheries exist in some regions. Leggett and Carscadden (1978) describe the life history of American shad in greater detail, while Loesch (1987) provides an overview of the life histories of blueback herring and alewife. I model this life history as follows:

Of primary interest is the number of fish returning to the river in year t, of sex s (indexed m or f), age a, that have spawned p times previously, denoted $N_{t,s,a,p}$. Assuming a non-selective fishery, the number of eggs produced in year t, Q_t, is a function of the number of females in year t, $N_{t,f,a,p}$, the exploitation rate in that year, u_t, and an age and previous spawning specific fecundity, $f_{a,p}$, and is given by:

$$Q_t = \sum_{a,p} N_{t,f,a,p}(1-u_t) f_{a,p} \,. \tag{2.1}$$

Density-dependent natural mortality within the spawning/nursery areas is thought to regulate *Alosa* population size (e.g. Crecco and Savoy 1988). This is to say that the rate of larval natural mortality, M_t^{larval}, varies between years: i.e., $M_t^{\text{larval}} = g(Q_t)$, where g is a function of Q_t that describes the nature of the density dependence. The effects of environmental variability, ε_t, can be incorporated into the model as deviates around the density dependent relationship. Given the sex ratio (υ_s), the number of offspring of each sex that survive to migrate seaward in year t ($O_{t,s}$) is then:

$$O_{t,s} = Q_t \mathrm{e}^{-g(Q_t)+\varepsilon_t} \upsilon_s \,. \tag{2.2}$$

Two equations are used to model the number of fish in the spawning run in each age, sex and previous spawning history category. In-river alewife fishing seasons are typically relatively short (about a month) with the majority of the catch being taken during a couple weeks. As a result, the effects of natural and fishing mortality occurring concurrently can be ignored. For fish that have not previously spawned (p=0), the number of fish entering the river to spawn (downstream of the fishery) in year t, of sex s and age a:

$$N_{t,s,a,0} = O_{t-a,s} e^{-T^{\text{juv}}} m_{t-a,s,a} e^{-M^{\text{juv}} a} \prod_{j=0}^{j=a-1} (1 - m_{t-a,s,j}) \,. \tag{2.3}$$

Here, T^{juv} is the instantaneous rate of turbine mortality for juvenile fish (zero for rivers that are not developed for hydroelectric generation) and M^{juv} is the instantaneous natural mortality rate for immature fish at sea. The maturity schedule, $m_{t-a,s,a}$, is the probability

that an immature fish of sex s that is alive at age a will mature at age a. The maturity schedule may vary between cohorts, where the cohort year is given by t-a. For fish that have spawned previously, the number of fish of sex s, age a, that spawned p times previously entering the river (downstream of the fishery) in year t is:

$$N_{t,s,a,p} = N_{t-p,s,a-p,0} e^{-\left(\sum_{k=t-p+1}^{t} F_k + T^{\text{adult}} p + M_{s,a}^{\text{adult}} p\right)} \tag{2.4}$$

where F is the instantaneous rate of fishing mortality, T^{adult} is the instantaneous rate of turbine mortality for adult fish, and $M_{s,a}^{adult}$ is the sex and age specific instantaneous rate rate of natural mortality for adults (the relationship between F and the annual exploitation rate u is: $F_t = -\log(1-u_t)$). Female spawner biomass (SSB) can be used as a proxy for the number of eggs if fecundity is directly proportional to weight:

$$SSB_t = \sum_{a,p} N_{t,f,a,p} w_{t,f,a,p} e^{-F_t} . \tag{2.5}$$

As will be shown in Chapter 5, overcompensation does not appear to be characteristic of *Alosa* populations. I therefore used a Beverton-Holt relationship between SSB_t and O_t (Hilborn and Walters 1992). This is a two-parameter spawner-recruit model where α is number of recruits produced annually per unit biomass of spawners (Myers et al. 1999) and K is the half-saturation constant. The full dynamical model becomes:

$$N_{t,s,a,p} = \begin{cases} \dfrac{\alpha SSB_{t-a}}{\left(1 + SSB_{t-a} / K\right)} e^{-T^{\text{juv}}} \upsilon_s m_{t-a,s,a} e^{-M^{\text{juv}} a} \prod_{j=0}^{j=a-1} (1 - m_{t-a,s,j}) & \text{if} \quad p = 0 \\ N_{t-p,s,a-p,0} e^{-\left(\sum_{k=t-p+1}^{t} F_k + T^{\text{adult}} p + M_{s,a}^{\text{adult}} p\right)} & \text{if} \quad p > 0 \end{cases} \tag{2.6}$$

Two examples of how this model can be adapted to different populations are given below. The model is adapted to produce estimates for variables corresponding to the data that exists for the population. Model parameters are then estimated through minimization of the value of an objective function that relates the model predictions to

the observed age structure and catch, and any auxiliary information (e.g. larval indices, escapement counts) that may exist for the population.

I programmed this model using AD Model Builder (Fournier 1996). AD Model builder uses the C++ auto-differentiation library for rapid fitting of complex non-linear models, has Bayesian and profile likelihood capabilities, and is designed specifically for fitting these types of models.

2.3 Example 1. Margaree River, NS Alewife

The Margaree River in Nova Scotia supports an *Alosa* fishery that is executed in-river using tip-traps installed along the bank (Chaput et al. 2001). Alewife make up the predominant component of the catch. Exploitation rates are controlled using within season closures that were first implemented in 1984, and have been subsequently modified. After 1995 it was evident that the population size had declined, and further closures were therefore introduced in 1996. Here, my objective was to use the model to determine whether this strategy successfully reduced exploitation rates to target levels of about 33 percent (Chaput et al. 2001).

The data for the Margaree River alewife fishery consists of the total catch (C_t) for the years 1983 to 2000, an estimate of the number of fish captured in each age and previous spawning history category ($C_{t,a,p}$) for the years 1983 to 2000 and a larval abundance index (I) for the years 1983 to 1985, and 1989 to 2000. The larval index is based on the number of yolk-sac larvae captured using a plankton net and is assumed to be measured before compensation occurs in the population. Based on this assumption, it is used as an index of spawner escapement. I used only the second half (p>0) of the full dynamical model (equation 2.6). The model (Table 2.1) is set up as a combined sex model that estimates the number of virgin fish in each age class that enter the river in each year, $N_{t-a,a-p,0}$, the exploitation rate in each year, u_t, and a catchability coefficient for larval alewife, q, for a total of 108 estimated parameters. This approach is similar to traditional statistical catch-at-age models (Quinn and Deriso 1999), with the exception

that the previous spawning history is incorporated into the model by adding another dimension to the catch-at-age array. This increases the number of observations of total mortality rates in each year. I assumed a constant value of 0.6 for M^{adult} for all year and age classes. This value is within the range used by some other authors. For example, Crecco and Gibson (1990) used $M^{adult} = 1.0$ in an analysis of reference points for alewife fisheries, while Chaput and Alexander (1989) estimated the instantaneous natural mortality rate to be 0.44 between the first and second spawnings for alewife in the South River, NB. I assumed the larval index in year t, I_t, was linearly related to spawning escapement in year t through a catchability coefficient, q, (also assumed constant across years). I used a lognormal error structure for the catch (C_t^{obs} and C_t^{pred} are the observed and predicted catches in year t) and the larval index (I_t^{obs} and I_t^{pred} are the observed and predicted larval indices in year t). I used a multinomial error structure for the number of fish in each year, age and previous spawning category ($\pi_{t,a,p}^{obs}$ is the number of fish of age a that have spawned p times previously within a sample collected in year t, and $p_{t,a,p}^{pred}$ is the predicted proportion of fish in each age and previous spawning category in that year). I fit the model by minimizing the value of an objective function ($O.B.V.$) that is the sum of the non-constant portions of the negative log likelihoods for the catch, larval index and number of fish in each year-age-previous spawning category. The relative contribution of each likelihood to the objective function was controlled by a set of weighting values, λ_i, selected to keep any one part of the objective function from dominating the fit. Because of difficulties interpreting juvenile (Jessop 1994) and larval abundance indices, I weighted the larval index so that its contribution was about one half that of the other components.

The observed and predicted catch are shown in Figure 2.1. The catch is partitioned by cohort and age at maturity and the abundance of fish in each category is projected through time. As shown in this figure, cohort sizes and the proportions

maturing at each age vary between year classes. Exploitation rates and the number of virgin fish in each age category are estimated in the model, and predicted catches and spawning escapements (Figure 2.2) are calculated from model output. The fit to the larval index is not as good as to the catch or composition data because of the smaller weighting factor used for these data. The increased within season closures have reduced exploitation rates from an average of 0.79 (1991 to 1995 time period) to 0.39 (1996 to 2000). Spawning escapement has increased as a result of these closures.

Table 2.1. The equations used for the Margaree River alewife model.

Dynamics:

$$N_{t,a,p} = N_{t-p,a-p,0} e^{-\left(\sum_{k=t-p+1}^{t} F_k + M^{\text{adult}} p\right)}$$

$$C_{t,a,p} = N_{t,a,p} u_t$$

$$C_t = \sum_a \sum_p \left(N_{t,a,p} u_t\right)$$

$$I_t = q \sum_a \sum_p \left(N_{t,a,p} (1-u_t)\right)$$

Log Likelihoods (non-constant portions):

$$\ell_{catch} = -\sum_t (\ln C_t^{obs} - \ln C_t^{pred})^2$$

$$\ell_{composition} = -\sum_t \sum_a \sum_p \pi_{t,a,p}^{obs} \ln p_{t,a,p}^{pred}$$

$$\ell_{larval} = -\sum_t (\ln I_t^{obs} - \ln I_t^{pred})^2$$

Objective Function:

$$O.B.V. = -(\lambda_1 \ell_{composition} + \lambda_2 \ell_{catch} + \lambda_3 \ell_{larval})$$

Estimated Parameters:

$N_{t,a,0}$ (90 parameters)

u_t (17 parameters)

q (1 parameter)

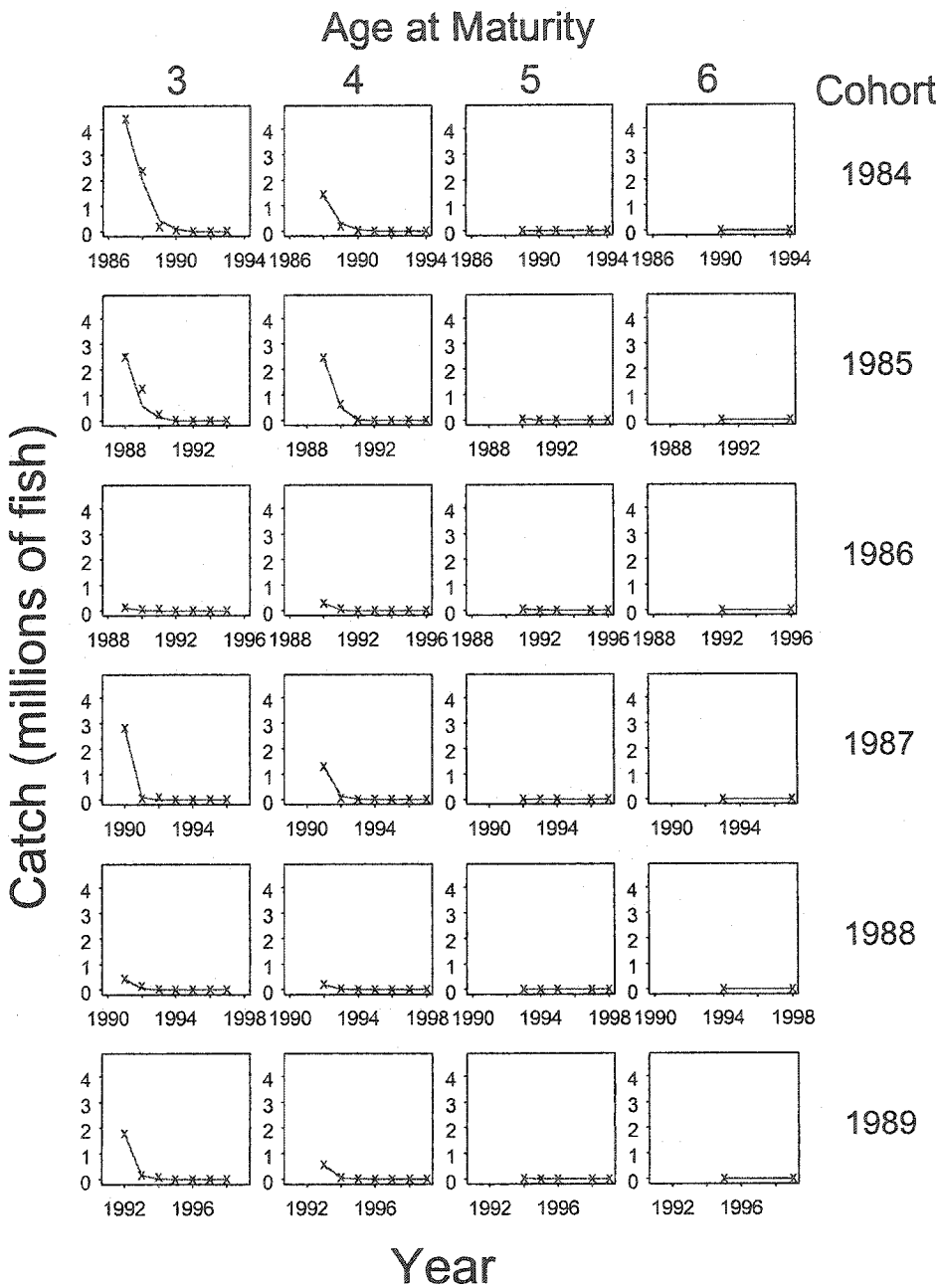

Figure 2.1. Part of the observed (x's) and predicted (lines) catch-at-age arrays for the Margaree River alewife population. Catches are partitioned by cohort year (right column) and age at maturity (labels at the top). The year (bottom labels) is the year of capture.

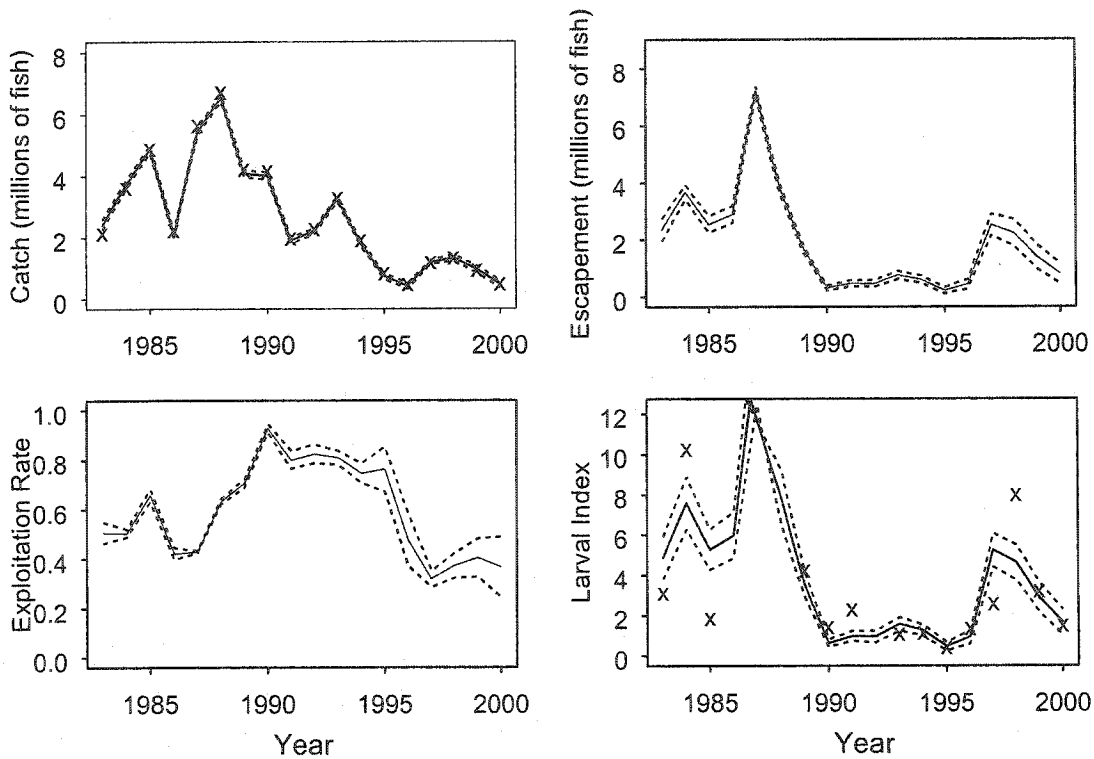

Figure 2.2. Observed (x's) and predicted (solid lines) total catches and larval indices, and predicted exploitation rates and spawning escapements for the Margaree River alewife population. The dashed lines show 95% confidence intervals for the estimated values based on normal approximations.

2.4 Example 2. The Gaspereau River, NS, Alewife Fishery

The Gaspereau River, also in Nova Scotia, supports an alewife population that shows the characteristics of a heavily impacted stock (Gibson and Myers 2001). The stock is fished commercially as fish ascend the river to spawn, and the watershed has been extensively modified for hydroelectric generation. Water management policies are being developed to reduce impacts on this population, including improvements to fish passage facilities. Here, my objective was to use the life history model to determine the biomass of fish that need to reach the spawning areas to produce maximum sustainable yield (SSB_{msy}) in the fishery.

Data for the Gaspereau River alewife stock and fishery are limited. The data consist of the catches for the years 1964 to 2000, spawning escapement counts (E_t) at a fish ladder just upriver from the fishery for the years 1982 to 1984, 1995, and 1997 - 2000, and the sex, age and spawning history composition for all years when counts were conducted except 1995 (Gibson and Myers 2001). I used data from 1979 to 2000 in this model because it is unclear whether or not some large catches in the mid-1970's were the result of the construction of a causeway on a nearby river. I set up the model (Table 2.2) to estimate the log of the mean asymptotic recruitment, R_0, and a recruitment deviate ε_t for each year around the spawner-recruit relationship. Recruitment deviates were constained to have a mean of zero. R_0 can be interpreted as the median carrying capacity of the nursery areas rescaled by survival to the age at recruitment, selected here as age-3. As such, all factors affecting survival from the egg to age-3 are incorporated into the spawner-recruit relationship. I used a logarithmic form of the Beverton-Holt model, parameterized in terms of R_0 by using the substitution $K = R_0 / \alpha$. The logarithmic form constrains recruitment to be positive during the estimation process and results in a multiplicative error structure for recruitment.

SSB_{msy} can be estimated from the spawner-recruit relationship. For semelparous species, given a spawner-recruit function $R=f(S)$, the spawning escapement at MSY

occurs where $f'(S)=1$ (Quinn and Deriso 1999). For an iteroparous species, if fishing occurs just before spawning, natural mortality during the fishing season is negligible, the fishery is non-selective and fish are fully grown when entering the fishery, the situation is analogous. SSB_{msy} occurs at the point where the first derivative of the spawner-recruit relationship equals the inverse of the rate at which recruits produce replacement spawners in the absence of fishing mortality (denoted $SPR_{F=0}$):

$$f'(S) = \frac{1}{SPR_{F=0}}. \tag{2.7}$$

When fishing occurs on fish that are not fully grown, this relationship underestimates the true SSB_{msy} (Deriso 1980). For the Beverton-Holt spawner-recruit model,

$$f'(S) = \frac{\alpha}{\left(1 + SSB_{msy} / K\right)^2}. \tag{2.8}$$

Thus,

$$SSB_{msy} = K\sqrt{SPR_{F=0}\alpha} - K. \tag{2.9}$$

Because the data for this population are very limited, a number of restrictive assumptions are made. Foremost, I treat the exploitation rate as known. For years where the catch and spawning escapement are known, the exploitation rate can be calculated directly. I use the mean exploitation rate for years that lack escapement counts. I also treat the maturity schedule as fixed across cohorts. While this assumption is not realistic, the data are insufficient to estimate a maturity schedule for each cohort (age data are only available for 7 of the 21 years). I fixed $\alpha = 60.7$ (at low spawner abundance, one kilogram of spawners can produce 60.7 age-3 recruits annually), a value taken from a meta-analysis of 5 other populations (Gibson and Myers 2001). As in the previous example, I fit the model to the data by minimizing an objective function value that is the sum of the non-constant portions of the negative log-likelihoods of the catches, escapement counts, and sex/age/previous spawning compositions of the spawning run.

Table 2.2. The equations used for the Gaspereau River alewife model.

Dynamics:

$$\log R_t = \log(\alpha) + \log(SSB_{t-3}) - \log(1 + \left(\frac{SSB_t}{(\mathrm{R}_0 / \alpha)}\right) + \varepsilon_t$$

$$N_{t,s,a,0} = R_{t-a+3} \upsilon_s m_{s,a} e^{-M^{\mathrm{juv}}(a-3)} \prod_{j=3}^{j=a-1} (1 - m_{s,j})$$

$$C_{t,s,a,p} = N_{t,s,a,p} u_t$$

$$C_t = \sum_s \sum_a \sum_p \left(N_{t,s,a,p} u_t\right)$$

$$E_{t,s,a,p} = N_{t,s,a,p}(1 - u_t)$$

$$N_{t+1,s,a+1,p+1} = E_{t,s,a,p} e^{-M^{adult}}$$

$$SSB_t = \sum_s \sum_a \sum_p (E_{t,s,a,p} w_{t,s,a,p})$$

Reference Point:

$$SSB_{msy} = K\sqrt{SPR_{F=0}\alpha} - K$$

Log Likelihoods (non-constant portions):

$$\ell_{catch} = -\sum_t (\ln C_t^{obs} - \ln C_t^{pred})^2$$

$$\ell_{composition} = -\sum_t \sum_s \sum_a \sum_p \pi_{t,s,a,p}^{obs} \ln p_{t,s,a,p}^{pred}$$

$$\ell_{escapement} = -\sum_t (\ln E_t^{obs} - \ln E_t^{pred})^2$$

Objective Function:

$$O.B.V. = -(\lambda_1 \ell_{composition} + \lambda_2 \ell_{catch} + \lambda_3 \ell_{escapement})$$

While the estimated recruitment deviates for each year have wide standard errors (Table 2.3), the mean asymptotic recruitment and the spawning biomass at MSY are well determined by the model. These reference points are consistent with those produced by a meta-analysis of alewife populations (Chapter 5). As weighted, the model tracks the count very closely (Figure 2.3), and fits the catch reasonably well except during the 1984 to 1988 time period. I believe the large residuals in this time period may be due to annual variability in the maturity schedules and the possibility that the mean exploitation rate may not be indicative of the exploitation rates in these years. However, I simply do not have the data to investigate these hypotheses; only the catch is known during this time period. The estimated SSB_{msy} implies that MSY occurs with an equilibrium spawner abundance of about 400,000 fish. Current spawner abundance is typically 10 to 40% of this level. The mean asymptotic recruitment for this population is about 1.7 million fish. The estimated recruitment is lower than this value in 14 of the 19 years that were included in the model.

2.5 Estimation of SR Time Series, Maturity Schedules and Mortality Rates

The population dynamics of anadromous alewife are analysed in the following chapters. Information about the reproductive rates (characterized by spawner-recruit models fit to SR time series), natural and anthropogenic mortality rates and maturity schedules are required for these analyses. In this section, I adapt the model to estimate SR time series, mortality rates and maturity schedules for four populations in the Maritime Provinces. Analyses have been presented for two of these populations; the others are the alewife native to the Mactaquac Headpond, NB and the Miramichi River, NB. The data available for each population are listed in Table 2.4. Details of the models, described below, are provided in Table 2.5.

Table 2.3. Parameter estimates for the Gaspereau River alewife population obtained from the statistical life history model. While the standard errors for the recruitment deviates are large relative to their estimates, the mean asymptotic recruitment and spawning biomass at maximum sustainable yield are comparatively well estimated.

Year	Recruitment Deviate	Standard Error
1979	-0.81	1.49
1980	-0.81	1.51
1981	-0.81	1.51
1982	-0.38	0.99
1983	0.93	0.61
1984	-0.81	2.12
1985	1.49	0.01
1986	0.29	0.93
1987	-1.43	0.16
1988	1.45	0.08
1989	-0.04	2.09
1990	-1.09	1.16
1991	0.43	0.60
1992	0.88	0.83
1993	0.56	1.17
1994	0.60	2.46
1995	1.07	1.36
1996	-0.82	1.04
1997	-0.35	1.50
1998	0.12	5.9
1999	0.32	1.50
2000	-0.81	0.59
R_0	1,647,800 fish	602,330
SSB_{msy}	91,939 kg	33,607

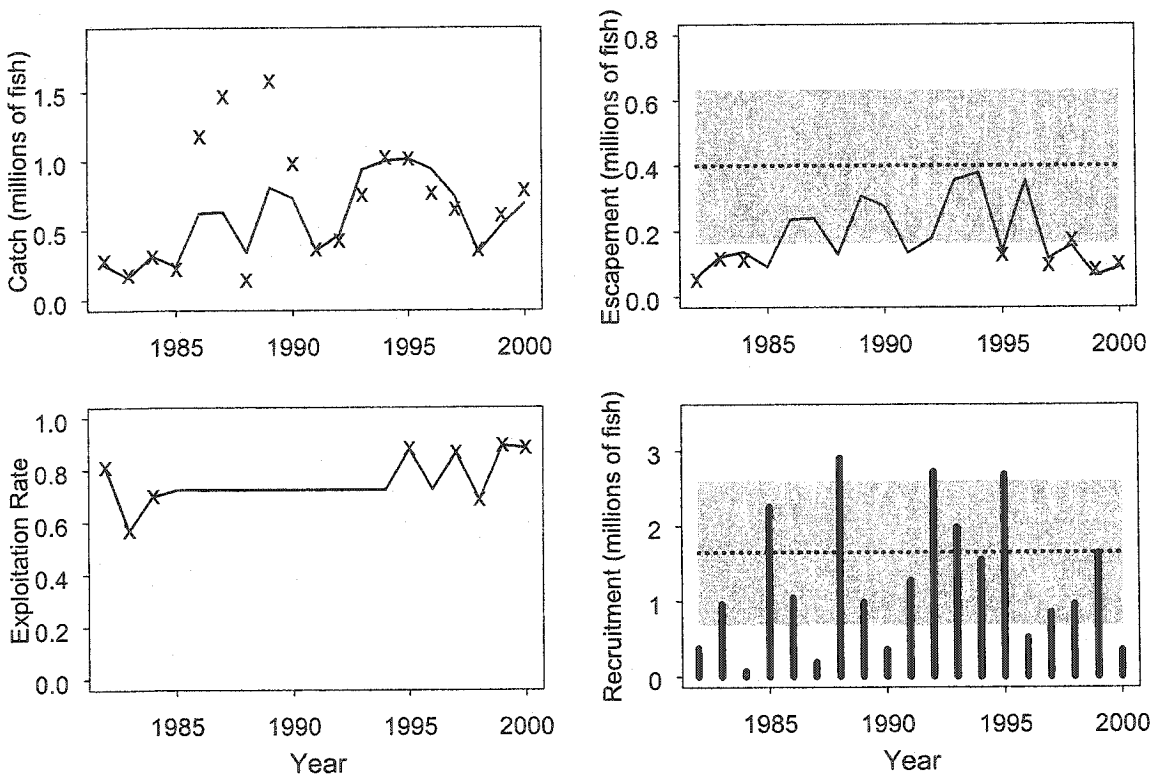

Figure 2.3. Observed (x's) and predicted (lines) total catches and spawner escapement counts, the exploitation rates (assumed known) and predicted number of age-3 recruits for the Gaspereau River alewife population. The dashed lines show the number of spawners at MSY (upper right panel) and the median asymptotic recruitment (lower right panel) for this population. The grey shaded areas are 90% confidence intervals for these reference points.

Table 2.4. Datasets used to estimate spawner-recruit time series, mortality rates and maturity schedules for the spawning run reconstructions of four alewife populations in the Maritime Provinces.

	Population			
Data Type	Gaspereau River	Margaree River	Miramichi River	Mactaquac Headpond
Catch	1982 to 2001	1983 to 2000	1982 to 2000	1973 to 1999
Escapement Counts	1982 to 1984 1995 1997 to 2001	not available	not available	1973 to 1999
Sex, Age and Previous Spawning	1982 to 1984 1997 to 2001	1983 to 2000 (age and p.s. only)	1982 to 2000 (age and p.s. only)	1973 to 1999
Larval Index	not available	1983 to 1985 1989 to 1991 1993 to 2000	not available	not available

Slightly different model formulations were used for the Gaspereau River and Margaree River populations than those presented in the previous sections. In the case of the Gaspereau River population, the primary difference is that the number of age-3 recruits in each cohort is estimated (the SR model is removed) so that the subsequent analyses of the SR relationship would not be influenced by an assumed SR relationship when estimating the SR time series. The two restrictive assumptions used in the previous analysis are retained for this model formulation: the exploitation rate was assumed known and maturity schedules were assumed constant from year to year. As in the previous example, I calculated the annual exploitation rate directly by dividing the catch by the sum of the catch and the escapement count. For years when no data other than the catch is available, I used the mean of the calculated exploitation rates (the fishery has been conducted in a similar manner throughout this time period). I set up the model to estimate the number of age-3 recruits in each year and a maturity schedule for each sex for ages ranging from 3 to 6. The instantaneous natural mortality rate was also estimated within the model.

For the Margaree River population, the model is identical to the model previously presented with the exception that the larval index was removed from the model. Comparison of the model output with and without the larval index indicated that estimated exploitation rates were slightly higher when the larval index was removed and that a retrospective pattern evident when the larval index was included was much less evident when the larval index was not included. Merritt and Quinn (2000) suggest that conservatism and the biological plausibility of parameter estimates are two criteria that can be used to select between alternative models and to assess auxiliary data. Additionally, the Margaree River population was the only population for which a larval index was available, so its exclusion contributed to the consistency of the modelling approaches among populations. I removed the larval index from the model for these

Table 2.5. Statistical models used to estimate spawner-recruit time series, mortality rates and maturity schedules for four alewife populations in the Maritime Provinces. Notation is explained in the text.

	Populations		
	Gaspereau River	Margaree and Miramichi Rivers	Mactaquac Headpond
Dynamics:	$N_{t,s,a,0} = R_{t-a+3} \upsilon_s m_{s,a} e^{-M^{juv}(a-3)} \prod_{j=3}^{j=a-1} (1-m_{s,j})$	$N_{t,a,p} = N_{t-p,a-p,0} \exp\left(-(\sum_{k=t-p+1}^{t} F_k + M^{adult} p)\right)$	$N_{t,s,a,p} = N_{t-p,s,a-p,0} \exp\left(-(\sum_{k=t-p+1}^{t} F_k + M^{adult} p)\right)$
	$C_{t,s,a,p} = N_{t,s,a,p} u_t$	$C_{t,a,p} = N_{t,a,p} u_t$	$C_{t,s,a,p} = N_{t,s,a,p} u_t$
	$C_t = \sum_s \sum_a \sum_p (N_{t,s,a,p} u_t)$	$C_t = \sum_a \sum_p (N_{t,a,p} u_t)$	$C_t = \sum_s \sum_a \sum_p (N_{t,s,a,p} u_t)$
	$E_{t,s,a,p} = N_{t,s,a,p}(1-u_t)$	$E_{t,a,p} = N_{t,a,p}(1-u_t)$	$E_{t,s,a,p} = N_{t,s,a,p}(1-u_t)$
	$SSB_t = \sum_s \sum_a \sum_p (E_{t,s,a,p} w_a)$	$SSB_t = \sum_a \sum_p (E_{t,a,p} w_a)$	$SSB_t = \sum_s \sum_a \sum_p (E_{t,s,a,p} w_a)$
	$R_t = \sum_s \sum_{a=3}^{6} \left(N_{t+a,s,a,0} / \exp\left(-M^{juv}(a-3)\right)\right)$	$R_t = \sum_{a=2}^{6} \left(N_{t+a,a,0} / \exp\left(-M^{juv}(a-3)\right)\right)$	$R_t = \sum_s \sum_{a=3}^{6} \left(N_{t+a,s,a,0} / \exp\left(-M^{juv}(a-3)\right)\right)$
Log Likelihoods (non-constant portions):	$\ell_{catch} = -\sum_t (\ln C_t^{obs} - \ln C_t)^2$	$\ell_{catch} = -\sum_t (\ln C_t^{obs} - \ln C_t)^2$	$\ell_{catch} = -\sum_t (\ln C_t^{obs} - \ln C_t)^2$
	$\ell_{composition} = -\sum_t \sum_s \sum_a \sum_p n_{t,s,a,p}^{obs} \ln p_{t,s,a,p}$	$\ell_{composition} = -\sum_t \sum_a \sum_p n_{t,a,p}^{obs} \ln p_{t,a,p}$	$\ell_{composition} = -\sum_t \sum_s \sum_a \sum_p n_{t,s,a,p}^{obs} \ln p_{t,s,a,p}$
	$\ell_{escape} = -\sum_t (\ln E_t^{obs} - \ln E_t)^2$		$\ell_{escape} = -\sum_t (\ln E_t^{obs} - \ln E_t)^2$
Objective Functions:	$O.B.V. = -(\lambda_1 \ell_{composition} + \lambda_2 \ell_{catch} + \lambda_3 \ell_{escape})$	$O.B.V. = -(\lambda_1 \ell_{composition} + \lambda_2 \ell_{catch})$	$O.B.V. = -(\lambda_1 \ell_{composition} + \lambda_2 \ell_{catch} + \lambda_3 \ell_{escape})$
Estimated Parameters:	R_{t-a+3} (20 parameters) $m_{s,a}$ (6 parameters) M^{adult} (1 parameter)	$N_{t,a,0}$ (Margaree: 90 parameters) (Miramichi: 76 parameters) u_t (Margaree: 18 parameters) (Miramichi: 19 parameters) M^{adult} (1 parameter)	$N_{t,s,a,0}$ (216 parameters) u_t (27 parameters) M^{adult} (1 parameter)

reasons. After its removal, the models for the Margaree River and Miramichi River populations are identical.

The data for the Mactaquac Headpond population consists of estimates of the catch and spawning escapement in each year, and estimates of the spawning run composition by sex, age and previous spawning history (Table 2.4). The model is similar to the Margaree and Miramichi populations, with the exceptions that I used a two-sex model, and added third log likelihood to the objective function to fit to the observed spawning escapements (E_t^{obs} and E_t are the observed and predicted spawning escapements respectively). I used a lognormal error structure for the escapement data.

The model output fit the observed data reasonably for all populations with the exception of the Mactaquac Headpond. For this population, the observed data shows increasing abundance through time for some sub-cohorts, particularly between the first and second spawnings (Figure 2.4). This pattern could arise if all the first-time spawning fish did not ascend the river to the base of the dam. This pattern is less evident in more recent years (only part of the escapement-at-age array is shown in Figure 2.4). During the mid 1970's and early 1980's the estimated spawning escapement is higher than the observed escapement count as a result (Figure 2.5), and the observed harvest fraction (calculated as the catch divided by the sum of the catch and the escapement count) is higher than the estimated exploitation rates during this period. This pattern is not evident in late 1980's and 1990's suggesting some non-stationarity in the process generating these data. The increase in the observed abundance within a sub-cohort through time was not evident in data for the Margaree, Gaspereau or the Miramichi rivers. These fisheries are executed much closer to the river mouths than the fishery for the Mactaquac Headpond population. This SR time series derived from this analysis differs from that derived by other authors from the same data. For example, Jessop (1990a) used the observed escapement count as a measure of spawner abundance and calculated the number of age-3 recruits from the observed number of first time spawners in each sub-cohort.

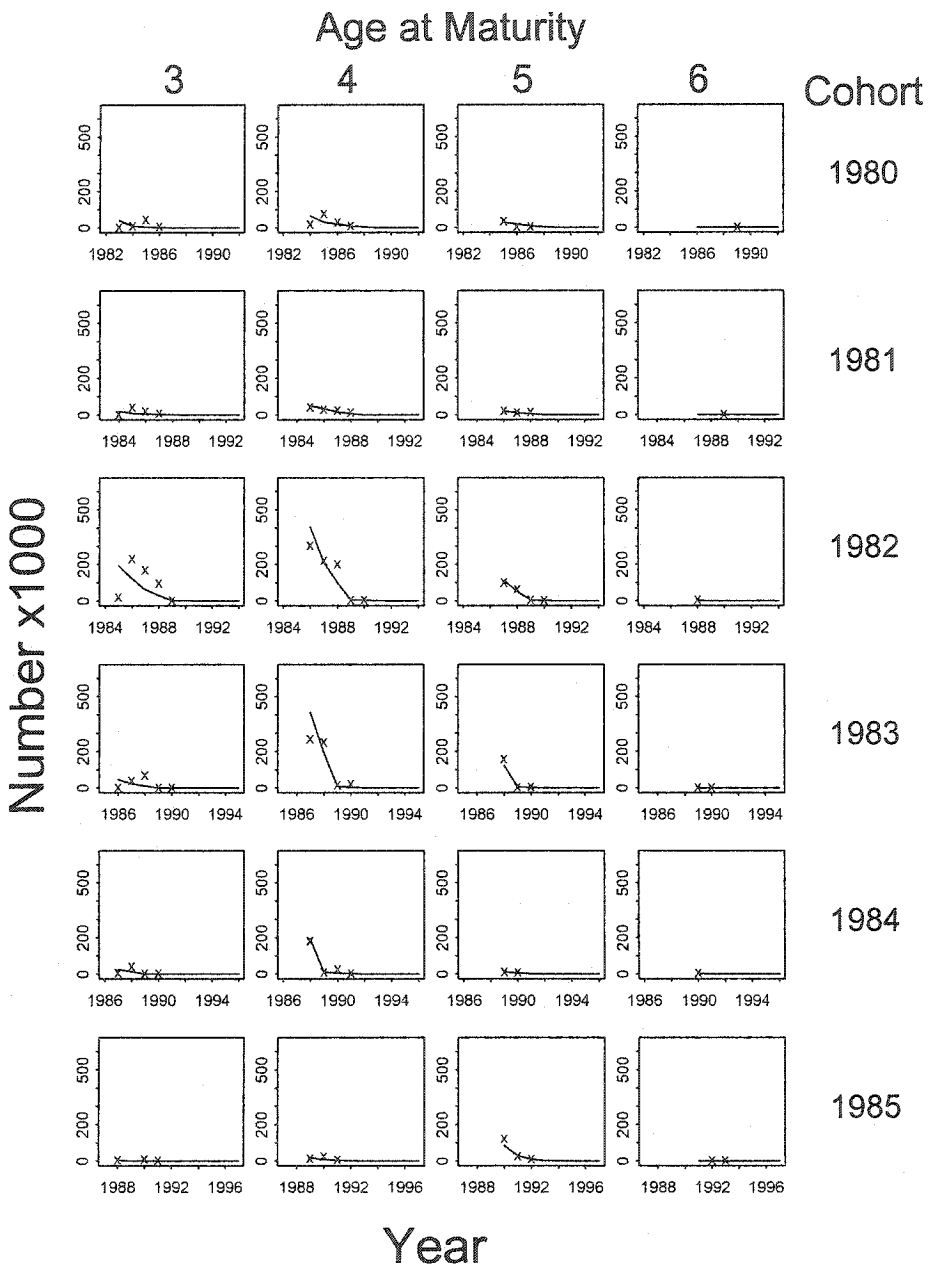

Figure 2.4. Part of the observed (x's) and predicted (lines) spawning escapement arrays for the Mactaquac Headpond alewife population (females only). Escapements are partitioned by cohort year (right column) and age at maturity (labels at the top). The year (bottom labels) is the year of capture.

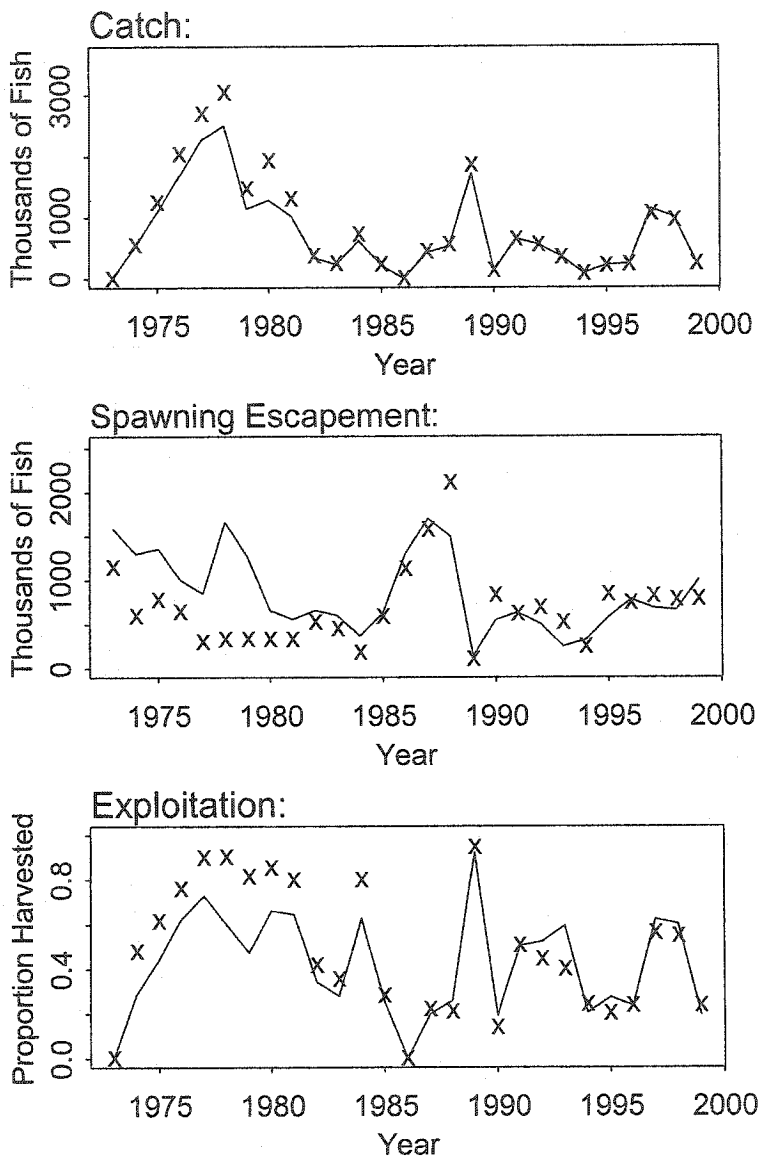

Figure 2.5. Observed (x's) and predicted (solid lines) catches, spawning escapements and exploitation rates for the Mactaquac Headpond alewife population.

2.5.1 Spawner-Recruit Time Series

The resulting spawner-recruit time series are shown in Figure 2.6. Recruitment tracked the spawner biomass for the Gaspereau River more closely than it did for the other three populations. A clear pattern is not evident for these other populations. These series will be analysed more fully in the following chapters.

2.5.2 Instantaneous Natural Mortality

Estimates of the instantaneous rate of natural mortality for adult fish ranged between 0.25 for the Mactaquac Headpond to 0.53 for the Gaspereau River (Table 2.6). The low estimate for the Mactaquac Headpond may be inaccurate due to the issues of increasing abundance within a sub-cohort that is not completely addressed within the assessment model. The estimates for the Gaspereau River and Mactaquac Headpond are further confounded because these rivers are modified for hydroelectric generation and estimates of turbine mortality are not available for these rivers. The standard errors (based on the assumption of asymptotic normality) for the Gaspereau River, Margaree River and Mactaquac Headpond suggest that these parameters are well estimated for these rivers. However, the profile likelihood for M^{adult} for the Margaree River (not shown) indicates that the asymptotic approximation is not very good for this river and that the lower bound for M^{adult} is not well determined. This is probably due to the confounding effects of simultaneously estimating u_t and M^{adult} without auxiliary data. However, the estimates of M^{adult} for both the Margaree and Miramichi River are similar to that obtained by Chaput and Alexander (1989) of 0.44 between the first and second spawnings for alewife in the South River. The standard errors obtained by asymptotic approximations closely matched the profile likelihoods for M^{adult} for the Gaspereau River and Mactaquac Headpond (auxiliary data is available in the form of escapement counts for these populations).

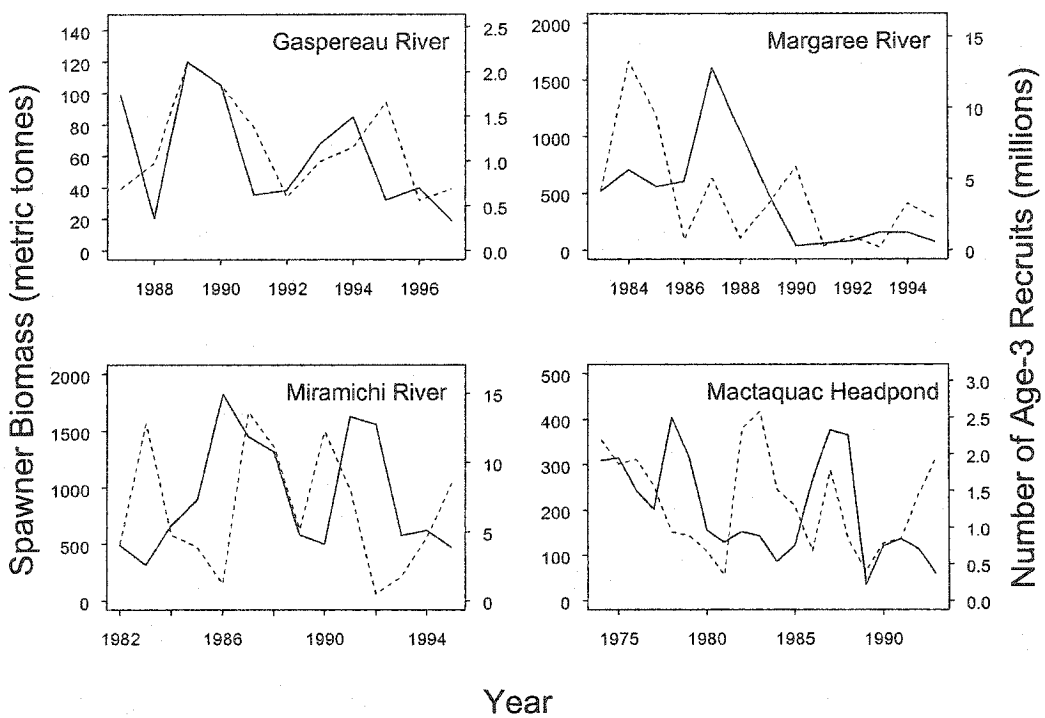

Figure 2.6. Times series of spawning biomass (solid line) and recruitment (dashed line) for four alewife populations in the Maritime Provinces. Recruitment is indexed by the cohort year resulting in zero lag between spawning and recruitment in these graphs.

Table 2.6. Estimates of instantaneous natural mortality rates (M^{adult}) and maturity schedules for four alewife populations in the Maritime Provinces. The maturity schedule gives the proportion of immature fish (m_a) that are alive at age a that mature at age a, for ages 2 to 6. The numbers in brackets are standard errors.

	Population			
Parameter	Gaspereau River	Margaree River	Miramichi River	Mactaquac Headpond
M^{adult}	0.53 (0.05)	0.44 (0.01)	0.49 (1.02)	0.25 (0.08)
m_2	<0.01	<0.01	<0.01	<0.01
m_3	<0.01	0.52	0.37	0.06
m_4	0.53	0.97	0.91	0.49
m_5	0.98	0.94	0.83	0.93
m_6	1.00	1.00	1.00	1.00

2.5.3 Maturity Schedules

Maturity schedules differ between alewife populations in the Gulf of St. Lawrence and the Bay of Fundy. Most alewife in the Gulf region mature at ages 3 or 4 (Table 2.6), and the majority of variability in age at maturity occurs at age-3 (Figure 2.9). Most alewife in the Bay of Fundy populations mature at ages 4 and 5 (Table 2.6), and most of the variability for the Mactaquac population occurs at age-4 (Figure 2.7). With the exception of the age-4 category for the Mactaquac Headpond population, age at maturity does not appear to be a function of cohort size (Figure 2.7). The Gaspereau River data is not sufficient to estimate a separate maturity schedule for each cohort.

2.6 Discussion

In this chapter, I presented a general, life history-based model for the population dynamics of anadromous *Alosa*, and shown how the model can be used for stock assessment by adapting it to the data collected for individual populations. This approach has several advantages, foremost being that the life history of interest is specifically modelled. For *Alosa*, data such as spawning escapement counts at fish ladders, larval and juvenile abundance indices, counts of emigrating juveniles, previous spawning history, indices of the number of post-spawning fish (Olney and Hoenig 2001), and information about other sources of mortality can be incorporated into the assessment process.

One of the most useful pieces of information often collected for *Alosa*, that is not typically available for marine species, is the number of times that a fish has previously spawned (available from a fishes' scales). Riverine impacts such as fishing or turbine passage do not affect immature fish at sea. When the number of previous spawnings is known, this variable can be used to determine the number of times that the fish has been exposed to riverine impacts by adding an extra dimension to the catch-at-age array. Additionally, when data are partitioned by sex and age-at-maturity as well as age, the number of observations of a cohort each year increases (from one to eight for a

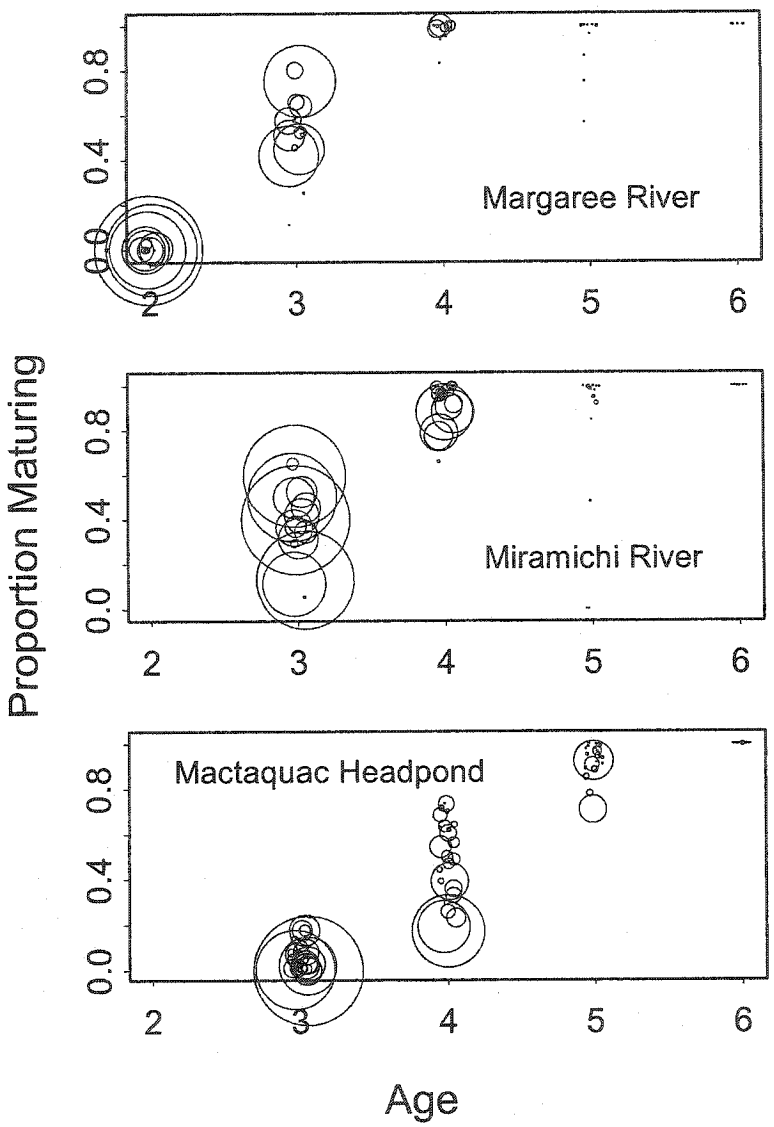

Figure 2.7. Variability in the age at maturity for the Margaree River, Miramichi River and Mactaquac Headpond alewife populations. Each point (or circle) represents the proportion of fish within a cohort that were alive at a given age and matured at that age. The size of the circle is proportional to the number of immature fish in the cohort at that age. Points are jittered slightly to facilitate display.

population that matures over four years). Assuming an adequate sample size, this increase improves the researcher's ability to estimate mortality rates or other parameters that are held constant across these categories.

While not specific to *Alosa* populations, statistical methods of fitting stock assessment models have a major advantage over virtual population analyses (VPA): models can be fit to intermittent datasets. For many smaller fisheries, such as the Gaspereau River example presented here, assessment data are not collected each year. VPA based methods use a backwards summation for which estimates of the numbers at age are required for each year (Hilborn and Walters 1992). While fitting through long periods when age data were not collected requires additional constraints be placed on the model, statistical methods can be used to estimate abundance when all that is known is the size of the catch.

The life history model presented here can be further generalized if appropriate for some populations. As presented, I treated *Alosa* fisheries as non-selective. When selective fishing gear such as gillnets are used, selectivity models (e.g., Millar and Holst 1997) can be incorporated into the model, allowing the error in the selectivity parameter estimation to be carried forward through the assessment. Similarly, when catchability varies with fish abundance (e.g. Harley et al. 2001), these relationships can also be included in the model.

Meta-analytic approaches to stock assessment and fisheries biology are becoming more common (e.g. Myers et al. 1999, Chapter 5 of this thesis). In order for these approaches to be successful, some standardization between datasets (e.g. a standard definition of recruitment for spawner-recruit meta-analysis) is required. When a general life history model is used for the assessments, a basis for these kinds of standardizations is provided.

Also within this chapter, I used the model to estimate spawner-recruit time series, maturity schedules and mortality rates for four alewife populations in the Maritime Provinces. Some differences between these populations are evident from these analyses,

most notably the differences in age at maturity between populations in Gulf of St. Lawrence and the Bay of Fundy. The effects of these differences on population dynamics and on the reference points for management will be evaluated later in this thesis.

CHAPTER 3. EFFECTIVENESS OF A HIGH-FREQUENCY SOUND FISH DIVERSION SYSTEM AT THE ANNAPOLIS TIDAL HYDROELECTRIC GENERATING STATION, NOVA SCOTIA

3.1 Introduction

During the last decade, behavioral guidance systems have come to the forefront of fish passage research (Popper and Carlson 1998). Stimuli such as light, sound and electric shock are used to elicit avoidance responses from fish that repel them away from structures such as the intake pipes at cooling water plants or turbine intakes at hydroelectric generating stations. Of these technologies, high-frequency sound, or ultrasound has been demonstrated to elicit avoidance responses in alewives *Alosa pseudoharengus* (e.g. Dunning et al. 1992), blueback herring *Alosa aestivalis* (e.g. Nestler et al. 1992) and American shad *Alosa sapidissima* (e.g. Mann et al. 1997) in tanks and enclosures. Results of these experiments have led to the development of fish deterrent and fish guidance systems that have subsequently been tested at several electric generating stations with varying degrees of success (e.g. Nestler et al. 1992, Ross et al. 1993, Ross et al. 1996, Popper 1999, Ross 1999).

Fish abundance, behaviour and rates of passage at hydroelectric stations vary considerably in response to environmental variables (O'Leary and Kynard 1986, Stokesbury and Dadswell 1989, Jessop 1990b, Gibson 1996), and failure to incorporate important covariates into the analysis may have confounded some previous assessments of fish guidance systems (Ross et al. 1993). Changes in the rate of fish passage in response to environmental conditions has the potential to lead to an under or overestimation of the effectiveness of a diversion system if these variables are not included in the analysis.

In this chapter, I describe an experiment to test the feasibility of using ultrasound to deter fish from passing through the turbine at the Annapolis Tidal Generating Station. Age-0 fish of three species of anadromous *Alosa* that utilize the Annapolis River and

Estuary as spawning and nursery habitat (American shad, blueback herring and alewife) were the target species for this study. The sound barrier was designed specifically for these species. Due to the uncertainty of the range of hearing of many species of fish, I did not know if any of the other species present in the Annapolis Estuary would respond to this signal. The diversity of the Annapolis Estuary fish community provided the opportunity to test whether the selected signal would produce a measurable response in several other species, albeit without anticipation of success for some of these.

My objectives were to evaluate the extent to which the diversion system reduced fish passage through the turbine, and to determine if deterred fish then moved seaward through the fishways. I also wanted to determine how environmental variability affected the precision and accuracy of the effectiveness estimates. Specifically, I wanted to evaluate whether a model of the process that determines the rate of fish passage (environmental conditions and diversion system status) would result in diversion effectiveness estimates that were more accurate and had smaller standard errors if the confounding effects of the environmental variables were removed.

3.2 Methods

3.2.1 Study Area

The Annapolis River Estuary is a macrotidal estuary in southwestern Nova Scotia. In 1960, a tidal dam was built across the estuary near Annapolis Royal. This dam transformed the estuary upriver of the dam from a vertically homogenous estuary with a tidal range of about 10 m, to a highly stratified salt wedge estuary with a tidal range of about 0.5 m (Daborn et al. 1979). The Annapolis Tidal Generating Station was constructed at this dam and has been in operation since 1984 (Dadswell et al. 1986). Operation of the generating station increased the flow of tidal water past the dam, thereby increasing the tidal range on the upstream side of the dam to between 0.5 m and 1.0 m. At least 35 species of fish are present in the vicinity of the tidal generating station at some time during the year.

The Annapolis Tidal Generating Station was designed as a prototype to test the StraFlo™ turbine for proposed, large-scale hydroelectric development in the upper Bay of Fundy (Douma and Stewart 1981). This unit is a low-head propellor turbine (7.6 m runner diameter) that rotates at 50 rpm, and generates only on the ebb tide (normal operating head range: 1.4 - 6.8 m). Output at a head of 5.5 m is 17.8 MW, with a corresponding discharge of 408 m^3/s. During an average tidal cycle the unit generates for 5.5 hours. During low neap tides it may spin freely when the turbine tube is opened to allow the headpond to fill more quickly, but otherwise is at a standstill for the remainder of the 12.5 hr tidal cycle. During most tidal cycles, the headpond is filled only through the 3 sluice gates located within the dam just south of the turbine (Figure 3.1). Two fishways have been constructed to augment fish passage at the dam (Stokesbury 1987). The "old fishway" is an open slot, 4 m wide, located beside the sluice gates about 300 m from the turbine forebay. The "new fishway" runs between the turbine forebay and the tailrace, is 3 m wide and is located about 12 m from the turbine intake. Water depth in both fishways varies between 1.5 m and 3 m depending on the stage of the tide. Discharges through the fishways are 42.7 m^3/s and 10.1 m^3/s for the old and new fishways respectively, for a 0.3 m head (Stokesbury and Dadswell 1991). The intake to the turbine is 40 m wide and 15.1 m in height. Water velocity at the entrance to this tube is 0.68 m/s at a flow of 408 m^3/s.

3.2.2 The Fish Diversion System

The fish diversion system tested during this assessment was a band-limited random noise signal projected into the turbine forebay by 4 International Transducer Corporation Model 3406 transducers mounted across the top of the turbine intake (Figure 3.2). Transducers were angled downward at 15 degrees, and sideways at 30 degrees of the centerline. The signal pulse was presented at a 33% duty cycle (0.5 seconds on, followed by 1 second off) with most energy focused between 122 and 128kHz (Figure

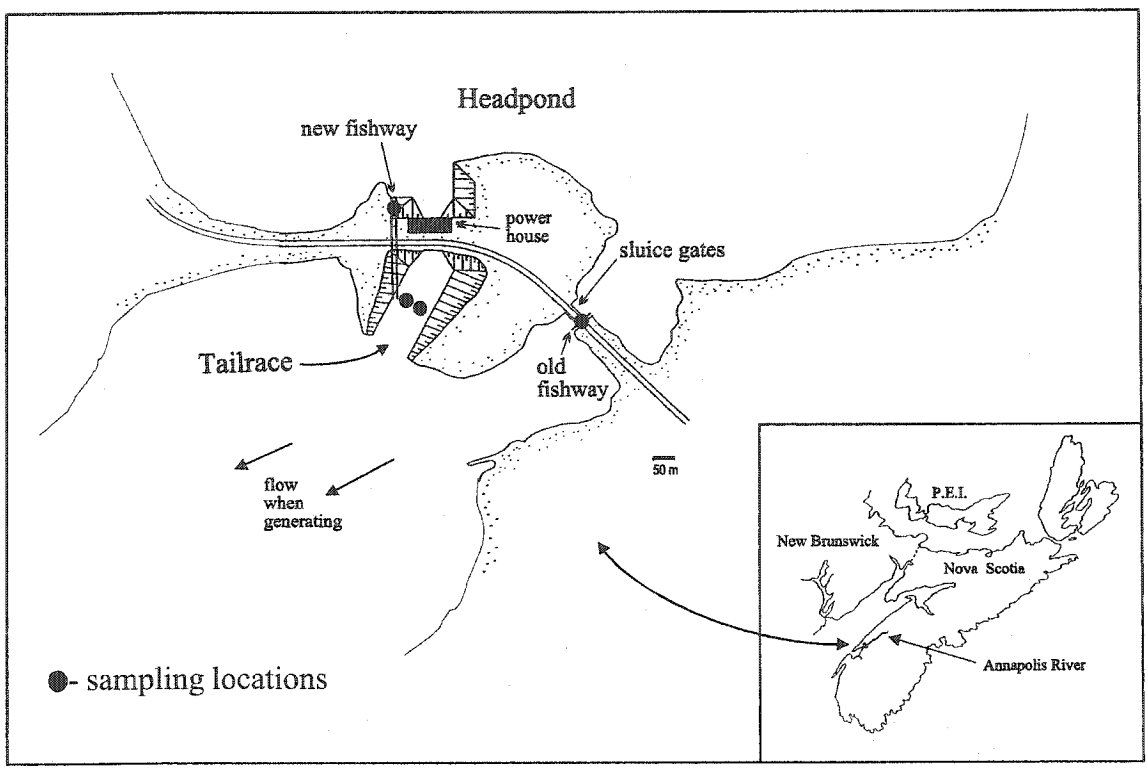

Figure 3.1. A map of the Annapolis Tidal Generating Station, Nova Scotia, showing the location of the two fishways, sluice gates and sampling locations used during an assessment of an ultrasound fish diversion study during September and October 1999.

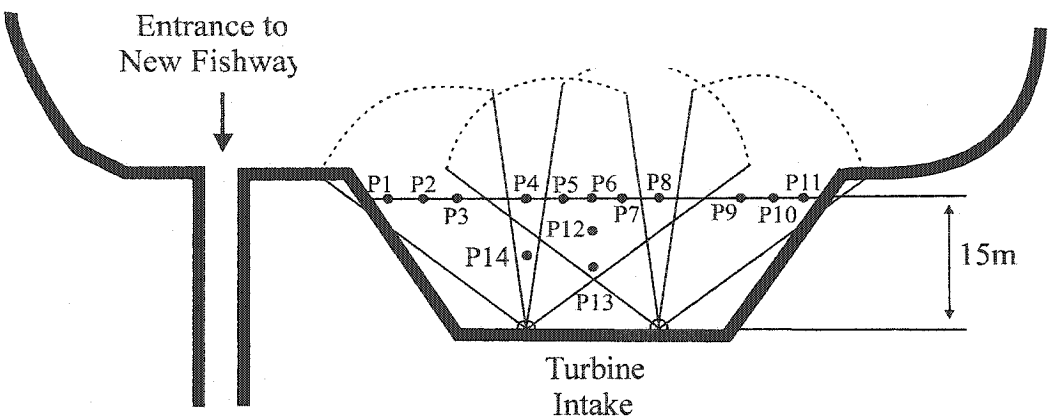

Figure 3.2. A map of the turbine intake at the Annapolis Tidal Generating Station, Nova Scotia, showing the location of the sound field, the location of the new fishway relative to the turbine intake and the location of the sound pressure level measurements taken on September 8, 1999 (adapted from Birmann 1999).

3.3). The sound pressure level one meter from the transducers was 181 dB re 1 uPa (Birmann 1999). Hydrophone measurements were made across the intake canal at depths of 1.6, 3.2 and 4.8 m to verify the acoustic output of the transducer array (Figure 3.2).

The measurements show a variation in sound pressure level of between 155 dB and 160 dB (Table 3.1). Based on these measurements, the sound pressure levels dropped below the 160 dB threshold (above which avoidance responses by *Alosa* are known to occur) at a distance of about 10 to 12 m from the intake face (Birmann 1999).

3.3.3 Experimental Design

Migratory species deterred from passing through the turbine have the option of moving seaward through either of the two fishways. Resident species also have the option of remaining on the landward side of the dam. The requirements for fish diversion therefore differ among species: deterrence from turbine passage is sufficient for resident species, whereas redirection (diversion) to the fishways is a necessary requirement for migratory species. I designed the experiment to evaluate the effectiveness of the system for both deterrence and diversion.

I conducted the evaluation by monitoring fish passage with nets deployed in the two fishways and at two locations in the tailrace below the turbine (Figure 3.1). An experiment was designed in which the diversion system was turned either on or off for the full generating period. While this decision limited the sample size, the alternative, to activate and deactivate the diversion system a number of times during a generation cycle, was rejected due to uncertainty about the independence of the samples and the difficulty of interpreting this type of experiment in the context of the actual operation of the plant. Additionally, migratory species tend to move past the turbine at the beginning of the generating cycle (Gibson 1996), so choosing this alternative would have substantially increased the complexity of the statistical model. I chose the catch of each species at each sampling location per generating cycle as my experimental unit. I did not weight the data by the volume of water filtered by a net or discharged through the turbine, because this

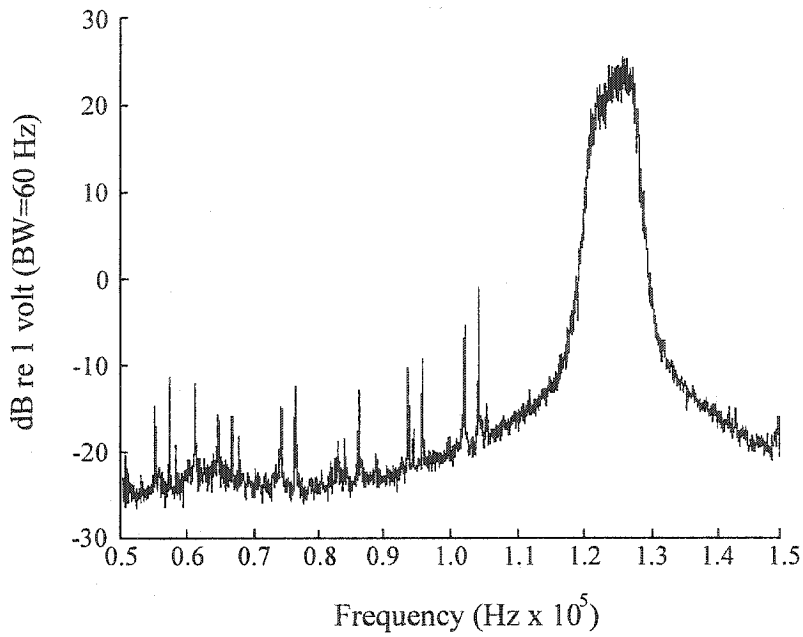

Figure 3.3. Voltage spectrum of the signal applied to the transducers at the Annapolis Tidal Generating Station, Nova Scotia, during September and October 1999, measured using a bandwidth of 60 Hz (adapted from Birmann 1999).

Table 3.1. Sound pressure levels measured in the turbine forebay at the Annapolis Tidal Generating Station, Nova Scotia, on September 8, 1999 (from Birmann 1999). Measurement locations are shown in Figure 3.3.

Location	Hydrophone depth (m)	Sound pressure level dB re 1 uPa
P1	3.2	155.2
P2	1.6	158.1
P2	3.2	157.0
P2	4.8	155.3
P3	3.2	157.5
P4	3.2	155.8
P5	3.2	157.9
P6	3.2	159.5
P7	3.2	156.3
P8	3.2	155.0
P9	3.2	158.0
P10	3.2	156.0
P12	1.6	160.0
P12	3.2	160.7
P12	4.8	161.3
P13	1.6	155.1
P13	3.2	163.1
P13	4.8	164.7
P14	3.2	167.4

standardization would only be applicable if the rate of passage was proportional to the volume of water. This assumption would not be suitable for species that stage between generation periods and then migrate early in the generation cycle. Additionally, the duration of generation and the discharge volume during each tidal cycle are relatively consistent because the volume of water available for generation is controlled as the headpond is filled.

Fish passage was monitored between September 7, 1999 and October 22, 1999. I used a stratified random sampling design to more or less evenly distribute the sampling effort throughout the study period while retaining randomization. I divided the generation cycles between these dates into consecutive pairs, and randomly chose one cycle from each pair to be sampled. I then took the series of generation cycles to be sampled, divided this series into consecutive pairs, and randomly chose to turn the diversion on during one cycle in each pair, and off during the other.

Based on previous studies of fish passage at the Annapolis causeway (Stokesbury and Dadswell 1989, Gibson 1996), I anticipated that environmental conditions (water temperature, salinity, tidal range and proportion of the generating period occurring at night) and seasonal migratory patterns would markedly influence the number of fish moving past the generating station during any given generation cycle. If the randomization procedure (through time) did not achieve complete randomization across the set of environmental variables that determine the rate of fish passage, the resulting estimates of the diversion effectiveness could be inaccurate. The experimental design allowed the detection of such errors by comparing the direction of the response between sampling locations. For example, with the diversion system activated, an increase in the rate of passage through a fishway that was accompanied by an increase in the rate of passage through the turbine would not be attributed to the diversion system, but rather to incomplete randomization across environmental variables that determine the rate of fish passage.

3.2.4 Field Methods

Nets used to monitor fish passage in the tailrace were 1.0 m in diameter and consisted of three sections: a 2.0 m long section, cylindrical in shape, made of 1 cm mesh nylon netting; a middle section made of 2 mm Nitex net, 3 m in length, tapering from 1 m to 0.18 m during the final meter, and the collector. The collectors were 1.75 m long, and were constructed with Spandex cloth fitted over 0.5 m diameter, aluminum cylinders (0.75 m in length). Entrances to the collectors were funnel-shaped to keep fish from escaping out of the collector. The tail ends of the collectors were designed so that they could be opened and closed with drawstrings. Nets deployed in the fishways were of similar design, but were 0.75 m in diameter. Nets in the tailrace were deployed for the full generation period (about 5.5 hr), while the fishway nets were deployed for the period of seaward flow (about 8 hr).

Temperature and salinity were measured at the start of each generating period using an YSI model 1000 SCT meter. The proportion of darkness during each sampling period was calculated using the time of sunrise and sunset predicted using ASTRONOMY LAB 1.13.Tide range was predicted using the computer program TIDES 3.05 using harmonic constants for Digby, Nova Scotia, at the mouth of the Annapolis Estuary.

3.2.5 Data Analysis

I defined the effectiveness of the sound barrier, E, for deterring fish from passing through the turbine as the mean proportion of fish deterred, and used the number of fish captured at each site in the tailrace during each generation cycle as a measure of the rate of passage through the turbine during that cycle. The effectiveness of the sound barrier was therefore defined as:

$$E = 1 - \frac{\overline{C}_{\text{on}}}{\overline{C}_{\text{off}}} \tag{3.1}$$

where $\overline{C}_{\text{on}}$ is the mean number of fish of a given species captured in the turbine tailrace with the diversion activated, and $\overline{C}_{\text{off}}$ is the mean number of fish of that species captured in the turbine tailrace with the diversion deactivated. This is the definition used by Popper (1999), although some other researchers have worked with totals rather than means.

To assess whether deterred fish then moved seaward through the fishways, I defined a "fishway factor", F_p, as the ratio of the mean rate of fish passage through a fishway p with the diversion activated to the rate of fish passage with the diversion deactivated. This factor was defined as:

$$F_p = \frac{\overline{C}_{p,\text{on}}}{\overline{C}_{p,\text{off}}} \tag{3.2}$$

where $\overline{C}_{p,\text{on}}$ is the mean number of fish of a given species captured in passage p with the diversion activated, and $\overline{C}_{p,\text{off}}$ is the mean number of fish of that species captured in passage p with the diversion deactivated.

For each species, the effectiveness of the diversion E, and the fishway factor F_p are therefore transformations of similar quantities for each passage: the ratios of the mean number of fish captured in a passage with the diversion activated to the mean number captured with the diversion deactivated. I discuss two models that were used to estimate these ratios: one that includes environmental variables, and a base model where these variables are not included.

For the base model, I assumed that the number of fish of each species captured in passage p during generation period t ($C_{p,t}$), was a random variable that is a function of the passage p, and the on/off status of the diversion system during generation period t (D_t). I expected the catches at the two tailrace sites would be different, although I expected the diversion effectiveness to be the same at both these sites. I accounted for differences in catchability among sites by including site as a factor in the model. I

assumed the effects of the diversion system and other factors that influence the rate of fish passage would act multiplicatively, and used log-linear models for this reason. In the base model, the expectation of the catch $\mathrm{E}(C_{i,t,d})$ of each species at site *i*, on generation cycle *t*, given diversion status *d* was modelled as:

$$\mathrm{E}(C_{i,t,d}) = e^{\mu+\beta_i+\beta_{p,d}D_t} \tag{3.3}$$

Here, μ is the grand mean of the natural logarithm of the catch of the given species, β_i is the coefficient for site *i*, and $\beta_{p,d}$ is the coefficient for the diversion status *d* at passage *p*.

To examine the influence of environmental variability on the resulting estimates, I developed a model to simultaneously estimate the effects of a set of environmental variables together with the effectiveness of the diversion system. This second model is an extension of the base model that includes the environmental variables: temperature (X_t), salinity (S_t), tidal range (R_t), and the proportion of the sampling period occurring at night (L_t). I postulated that an optimal value for fish passage existed for each species for each environmental variable, and that the rate of passage would decrease as the value deviated from the optimal. I therefore included quadratic terms for each of these variables in the model. The fitted model was therefore:

$$\mathrm{E}(C_{i,t,d}) = e^{\mu+\beta_i+\beta_r R_t+\beta_{r2}R_t^2+\beta_l L_t+\beta_{l2}L_t^2+\beta_{x1}X_t+\beta_{x2}X_t^2+\beta_{y1}S_t+\beta_{y2}S_t^2+\beta_{p,d}D_t} \tag{3.4}$$

where: β's not included in the base model correspond to the matching environmental variables.

In both models, the quantity $(\beta_{\mathrm{t,on}} - \beta_{\mathrm{t,off}})$ is an estimate of the difference in the natural logarithms of the mean catch in the tailrace (subscript t) with the diversion activated and deactivated. From this quantity, the ratio of the number of fish captured with the diversion turned on to the number captured with the diversion turned off can be calculated directly and transformed to provide estimates of the effectiveness of the

diversion system. Similarly, an estimate of the fishway factor for the new fishway (subscript n) follows directly from the quantity $\left(\beta_{\text{n,on}} - \beta_{\text{n,off}}\right)$.

I fit both models to the observed data using two methods within a generalized linear modelling context (McCullagh and Nelder 1989). First, I assumed a Poisson error structure, which is often used for count data and is appropriate when the passage of individual fish is independent of the passage of other fish. If fish passage is not independent, the precision of the resulting estimates will be under or overestimated using this distribution. I therefore also fit the models using quasi-likelihood, which allows estimation of a dispersion parameter, ϕ, simultaneously with the model coefficients. Overdispersion ($\phi > 1$) is a common characteristic of fish catches due a variety of factors that affect their distribution such as schooling behaviour, habitat preferences and deil variability and leads to an overestimation of statistical significance if a Poisson error structure is assumed. The dispersion parameter is used to rescale the variance of $C_{p,t}$ from the Poisson model. This quasi-likelihood approach does not change the parameter estimates, but results in more realistic estimates of their associated error than would be obtained under an assumption of a Poisson error distribution, which occurs if the estimate of $\phi = 1$. Here, I present standard errors estimated under the assumptions of Poisson and extra-Poisson errors to illustrate that the former can lead to substantial overestimates of statistical significance if the independence assumption is violated.

I tested the statistical significance of the model coefficients under the assumption of asymptotic normality of the response on the link scale (McCullagh and Nelder 1989). Model coefficients were considered statistically different than zero if the interval $\beta \pm z_{1-\alpha/2} s_\beta$, where s_β is the standard error of the coefficient and $z_{1-\alpha/2}$ is the critical value of a standard normal distribution for a given confidence level, did not include zero. Significance tests for the diversion effectiveness and fishway factor were carried out similarly using one-sided t-tests.

I used likelihood ratio tests (Venables and Ripley 1999) to compare the fits of the base model and the model with the environmental variables. Here, the difference in the residual deviances of the base model D_{base} and the model with the environmental variables D_{env} is assumed to be approximately chi-squared distributed. This difference is rescaled by the dispersion parameter to correct for overdispersion (Venables and Ripley 1999):

$$\frac{D_{base} - D_{env}}{\phi} \sim \chi^2_8 \tag{3.5}$$

where 8 is the number of degrees of freedom associated with the environmental component of the model.

3.2.6 Alternative models

To assess the robustness of my conclusions with respect to the models selected, several other models were fit to both the data and subsets of the data. First, I compared the means of the ratio of the tailrace catch to the new fishway catch with the diversion activated to that with the diversion deactivated using a Mann-Whitney *U* test. This approach standardizes the tailrace catch against the new fishway catch and can be used to test for the existence of a significant deterrent effect. The approach has the advantages that the environmental component of the model is not required (the fishway catch is used as an index of the rate of fish passage), and a statistical distribution is not assumed. The disadvantages are that when the data are standardized in this way, the magnitude of the diversion effect cannot be estimated because the deterrent and diversion characteristics of the diversion system cannot be separated. Additionally, zeros in the new fishway data are problematic because division by zero is not defined. I used a similar approach where I modelled the catch in the tailrace as a function of the catch in the new fishway and the status of the diversion system using log-linear models and quasi-likelihood. This approach allows zeros in the new fishway data to be included in the analysis, but otherwise has the same advantages and disadvantages as the approach above.

Other models that were fit to the data are modifications of the base model and the environmental models. I fit both models to the data for each sampling site individually to determine whether the environmental effects at any one site were substantially influencing the fit of the model. I also fit both models to the data after removing periods at the beginning and end of the time series if the species under investigation was not present throughout the study to determine if these zero catches were influencing the results. I also estimated the effectiveness of the diversion system after removing seasonal trends in abundance by including "generation cycle number" as a third order polynomial in the model, again using both the full data set and subgroups based on sampling site. Finally, for species present in adequate abundance, I fit the models after trimming subsets of the largest catches from the data, to determine if the effectiveness of the diversion changed as abundance increased.

3.3 Results

Sampling was conducted at the four locations during 48 generation cycles. Net failures (typically due to fouling with seaweed or other debris) reduced the number of valid samples to 47 for the north side of the tailrace, 45 for the south side of the tailrace, 45 for the new fishway, and 44 for the old fishway. Storm conditions and a diversion equipment malfunction near the end of the project resulted in the diversion being turned off during more periods (N=28) than it was on (N=20).

Over 53,000 fish representing 27 taxa were captured during this study (Table 3.2). Of these, Atlantic silversides *Menedia menedia* were by far the most abundant. I present the results for the 11 species that were captured during more than 20 generation cycles (Table 3.2). While some species (e.g. sea lamprey *Petromyzon marinus*) were captured in greater abundance than some of the species for which results are presented, a preliminary analysis for these species produced results that were sensitive to the model formulation and had very wide standard errors, and therefore could not be considered reliable. I

present a detailed analysis of the clupeid data and a summary of the results for the remaining 7 species.

The relative abundance of the clupeids varied throughout the study and between sampling sites. Blueback herring were captured most frequently in the tailrace (north side) and new fishway (Figure 3.4), and were most abundant at all four locations during the last week of September. Most alewives and American shad were captured in the new fishway, with peak abundances during the last week of September and mid-October. Very few clupeids were caught in the old fishway, regardless of whether or not the diversion was activated (Figure 3.4). Additionally, no significant diversion effect was detected for any species at the old fishway (clupeids: Table 3.3), although standard errors for the parameters estimates are very large. Consequentially, the data provide little indication about the effectiveness of the diversion at this site, other than it does not appear to be an important passage for most species either with or without the diversion system. I focus the remaining analysis on the rates of passage through the turbine and the new fishway for this reason.

When the catches in the tailrace are modelled as a function of the catches in the new fishway and the on/off status of the diversion system, significant deterrent effects were detected for American shad ($p = 0.03$; d.f. = 40) and alewife ($p = 0.06$; d.f. = 40), but not for the other species. No significant deterrent effects were detected using the Mann-Whitney *U* test.

With one exception, the other alternative modelling approaches resulted in only minor differences in the coefficient estimates and did not change the interpretation of the effectiveness of the diversion system from that described below. For blueback herring, the estimates for both the diversion effectiveness and the fishway factor changed when the largest catches were trimmed from the data. I have included an analysis of the blueback herring data with the three largest catches removed under the label "blueback herring trimmed", as well as the analysis for the full set of data for blueback herring.

Environmental variables affected the rate of fish passage at the Annapolis Tidal Generating Station. For *Alosa*, daylight (proportion of darkness) had the greatest influence of the environmental variables (Table 3.3), the largest catches occurring at night. Catches of all clupeid species except alewife increased with tidal range. Within the clupeids, salinity was a significant variable only for Atlantic herring *Clupea harengus harengus* (Table 3.3). Temperature was a significant variable for alewives and blueback herring. Comparison of the deviances for the base model with the model including environmental variables shows that the environmental component of the model was highly significant for all species (Table 3.4). The percentage of the null deviance explained by the base model ranged between 3.9% for windowpane *Scophtalmus aquosus* to 44.6% for American eels *Anguilla rostrata*, and was less than 30% for 8 of the 11 species. The percentage of the null deviance explained by the model with the environmental variables ranged from 36.6% for windowpane to 97.5% for Atlantic herring, and was greater than 50% for 8 of the 11 species.

Estimates of the effectiveness of the diversion system differed between the base model and the model including the environmental variables for all species (Figure 3.5). When estimated with the base model, a limited deterrent effect was detected for 8 of the 11 species (Figure 3.5). Fish passage in the new fishway increased with the diversion activated for all *Alosa*, Atlantic silverside, and blackspotted stickleback *Gasterosteus wheatlandi*. However, for the later two species, the rate of passage through the turbine also increased with the diversion activated (Figure 3.5), indicating that some factor other than the on/off status of the diversion was influencing their rate of passage. Similarly, the decreased rates of passage through the turbine with the diversion activated was accompanied by decreased rates of passage through the new fishway for Atlantic herring, American eels, pipefish *Syngnathus fuscus*, windowpane, hake *Urophycis spp.* and butterfish *Peprilus tricanthus* (Figure 3.5). These results also indicate that some factor other than the on/off status fish diversion system was influencing the rate of fish passage

Table 3.2. The number of fish of each species captured at each sampling location the Annapolis Tidal Generating Station, Nova Scotia, while evaluating the effectiveness of an ultrasound fish diversion system during September and October 1999. The two columns for each location given the number of fish captured with the diversion activated (on) and deactivated (off). The "number of cycles" is the number of generation cycles during which fish of each species were captured. Species for which the data are modelled are marked with an asterisk.

	Tailrace (north side)		Tailrace (south side)		New fishway		Old fishway			
Diversion status:	on	off	on	off	on	off	on	off		Number
Species									Total	of cycles
Atlantic silverside (*Menidia menidia*)*	479	304	464	115	17214	18706	4183	6534	47999	47
Atlantic herring (*Clupea harengus harengus*)*	232	387	107	165	317	561	50	38	1857	42
Pipefish (*Syngnathus fuscus*)*	55	75	27	55	89	343	57	346	1047	41
Blackspotted stickleback (*Gasterosteus wheatlandi*)*	18	28	19	11	260	341	78	95	850	44
Blueback herring (*Alosa aestivalis*)*	70	68	42	28	43	50	10	0	311	33
Mummichog (*Fundulus heteroclitus*)*	2	0	2	2	22	75	12	54	169	14
Alewife (*Alosa pseudoharengus*)*	8	12	3	11	85	39	2	0	160	23
Sea lamprey (*Petromyzon marinus*)	10	8	2	0	18	18	52	50	158	4
Hake spp. (*Urophycis spp.*)*	19	38	14	24	7	16	2	3	123	24
American eel (*Anguilla rostrata*)*	1	6	3	1	36	64	0	5	116	27
American shad (*Alosa sapidissima*)*	9	15	3	13	44	18	0	0	102	23
Butterfish (*Peprilus triacanthus*)*	12	18	0	4	8	39	2	5	88	26
Windowpane (*Scophthalmus aquosus*)*	7	9	4	10	8	14	2	7	61	23
Winter flounder (*Pseudopleuronectes americanus*)	11	9	5	12	1	2	0	2	42	16
Rainbow smelt (*Osmerus mordax*)	2	2	1	1	4	3	0	2	15	10
Atlantic mackerel (*Scomber scombrus*)	2	2	2	4	0	1	1	0	12	12

Table 3.2 (con't.)

	Tailrace (north side)		Tailrace (south side)		New fishway		Old fishway			
Diversion status:	on	off	on	off	on	off	on	off		Number
Species									Total	of cycles
Lumpfish (*Cyclopterus lumpus*)	1	2	0	0	2	1	0	0	6	6
Cunner (*Tautogolabrus adspersus*)	3	0	0	0	0	2	1	0	6	5
White perch (*Morone americana*)	0	0	0	0	0	2	1	0	3	1
Pollock (*Pollachius virens*)	0	0	0	0	1	2	0	0	3	3
Smooth flounder (*Liopsetta putnami*)	0	1	0	0	0	0	1	0	2	2
Bluefish (*Pomatomus saltatrix*)	0	0	0	0	2	0	0	0	2	1
Wrymouth (*Cryptacanthodes maculatus*)	0	0	0	0	0	0	0	1	1	1
Longhorn sculpin (*Myoxocephalus scorpioides*)	0	0	1	0	0	0	0	0	1	1
Meek's halfbeak (*Hyporhamphus meeki*)	0	0	0	0	0	1	0	0	1	1
Flying gurnard (*Dactylopterus volitans*)	0	0	0	0	0	1	0	0	1	1
Four-beard rockling (*Enchelyopus cimbrius*)	1	0	0	0	0	0	0	0	1	1

Table 3.3.Model coefficients and standard errors for clupeids captured at the Annapolis Tidal Generating Station, Nova Scotia while evaluating the effectiveness of an ultrasound fish diversion system during September and October 1999. Standard errors are corrected for overdispersion. The "site" coefficients are scaled against the tailrace (south side) site. The "diversion" coefficients are the difference ($\log N_{off} - \log N_{on}$). Asterisks indicate the level of statistical significance (two-tailed t-test): one, two and three asterisks indicating significance at 90, 95 and 99% confidence levels respectively (residual degrees of freedom = 169).

Variable	American shad	Blueback herring	Blueback herring (trimmed)	Alewife	Atlantic herring
Dispersion parameter	2.24	3.37	2.35	1.39	8.58
Intercept	6.70 (12.06)	-26.37 (10.10)***	-5.53 (9.51)	5.56 (8.21)	25.88 (5.06)***
Site (new fishway)	3.54 (5.61)	0.23 (0.27)	0.73 (0.25)***	2.27 (0.30)***	0.72 (0.18)***
Site (old fishway)	-6.67 (16.84)	-1.16 (0.45)**	-0.73 (0.40)*	-1.51 (0.65)**	-1.20 (0.32)***
Site (tailrace - north side)	1.76 (5.62)	0.80 (0.21)***	0.61 (0.21)***	-0.15 (0.34)	0.63 (0.16)***
Proportion of darkness	4.43 (3.29)*	5.76 (2.30)**	7.58 (2.09)***	11.38 (2.75)***	1.78 (1.54)
Proportion of darkness squared	-2.50 (2.81)	-3.74 (1.97)*	-5.53 (1.78)***	-8.03 (2.27)***	0.66 (1.28)
Tidal range	-2.40 (2.20)	1.60 (1.64)	-3.30 (1.60)**	-6.89 (1.75)***	-4.17 (1.23)***
Tidal range squared	0.19 (0.16)	-0.11 (0.12)	0.23 (0.12)**	0.48 (0.13)***	0.33 (0.09)***
Salinity	0.03 (0.50)	0.57 (0.38)	-0.28 (0.35)	-0.39 (0.40)	-0.59 (0.29)**
Salinity squared	-0.01 (0.01)	-0.01 (0.01)*	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)**
Temperature	-0.23 (0.98)	1.98 (1.01)**	2.78 (0.92)***	3.42 (0.92)***	-0.53 (0.43)
Temperature squared	0.01 (0.03)	-0.06 (0.03)*	-0.09 (0.03)***	-0.12 (0.03)***	0.01 (0.02)
Diversion (new fishway)	-1.20 (0.44)***	0.04 (0.39)	-0.45 (0.39)	-0.92 (0.27)***	0.31 (0.22)
Diversion (old fishway)	-0.18 (30.8)	-7.52 (13.81)	-7.47 (12.22)	-6.71 (13.99)	-0.51 (0.63)
Diversion (tailrace)	0.54 (0.54)	-0.22 (0.27)	0.68 (0.31)**	0.65 (0.48)	-0.01 (0.23)

Table 3.4. An analysis of the residual deviances for the base model and the model with the environmental variables for 11 species of fish captured at the Annapolis Tidal Generating Station during September and October 1999, while evaluating the effectiveness of an ultrasound fish diversion system. The mean dispersion parameter (ϕ) is mean of the parameter estimates from the two models. P-values are based on a likelihood ratio test, after correcting the differences in the residual deviances for overdispersion. Residual degrees of freedom are 166 and 174 for the models with and without the environmental variables respectively.

		Residual deviance				
Species	Null deviance	Base model	Environmental model	Difference	Mean ϕ	p-value
Atlantic silverside	182,871.9	111,997.8	56,370.6	55,627.2	899.8	<0.001
Atlantic herring	4,541.8	3,657.8	1,020.4	2,637.4	21.9	<0.001
Pipefish	2,428.1	1,766.9	706.5	1,060.4	9.2	<0.001
Blackspotted stickleback	2,290.0	1,352.8	1,007.3	345.5	8.7	<0.001
Blueback herring	1,003.8	848.1	459.5	388.6	6.6	<0.001
Blueback herring (trimmed)	628.3	487.4	281.2	206.2	3.2	<0.001
Alewife	688.4	430.6	184.7	245.9	2.3	<0.001
Hake (spp.)	409.1	353.7	150.2	203.5	2.4	<0.001
American eel	452.2	250.6	190.8	59.8	1.9	<0.001
American shad	436.2	317.5	237.6	79.9	2.6	<0.001
Butterfish	293.8	221.8	168.8	52.9	2.4	0.005
Windowpane	201.7	193.8	127.7	66.1	1.4	<0.001

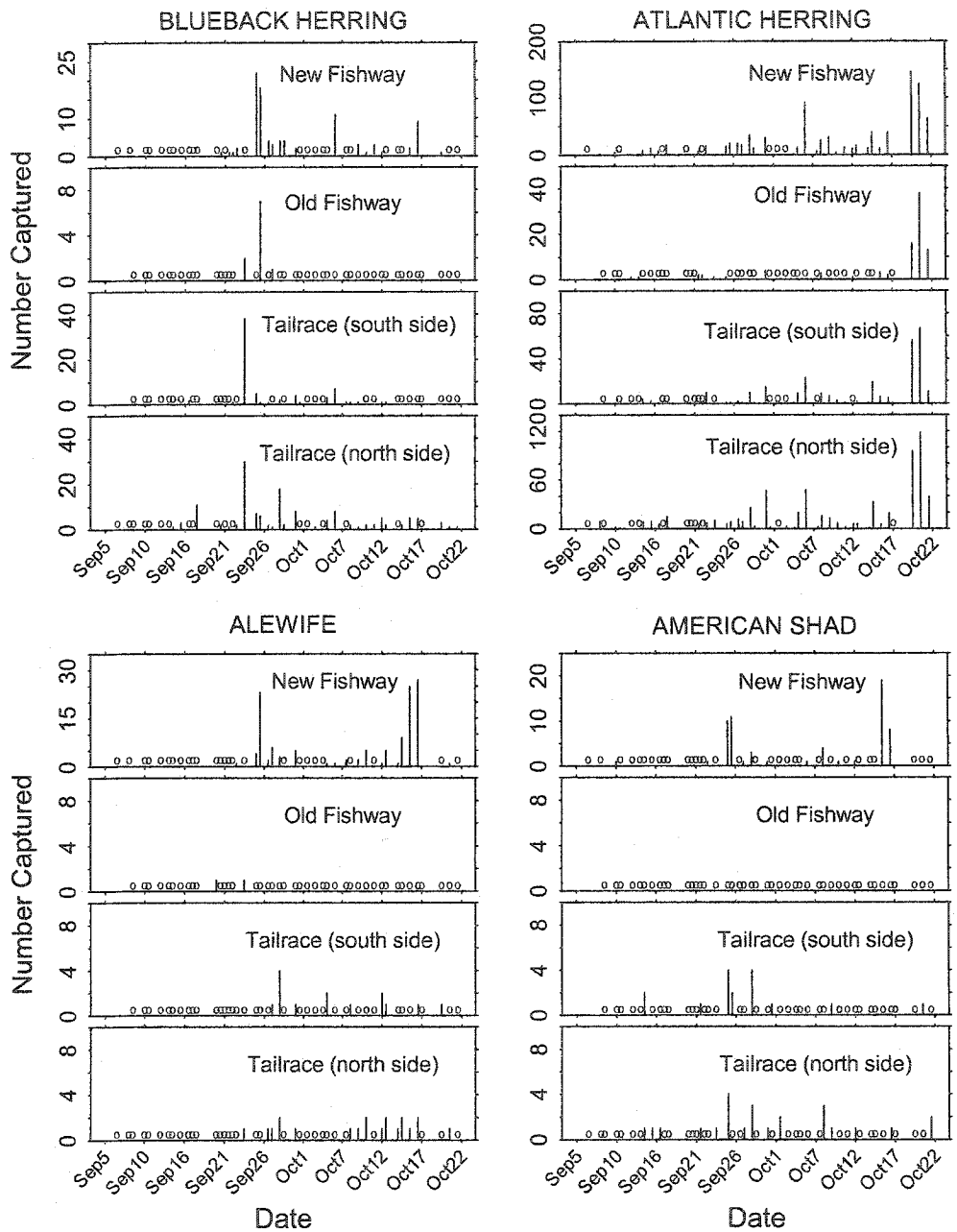

Figure 3.4. The location, time and magnitude of clupeid catches at the Annapolis Tidal Generating Station, Nova Scotia, while evaluating the effectiveness of an ultrasound fish diversion system during September and October 1999. Generation periods sampled when fish were not captured are marked with "o". Note scale differences between axes.

for these species. Hence, comparisons of the base model results for tailrace and new fishway indicate that the limited effectiveness implied from the examination of the results from a single sampling location may be erroneous for all non-*Alosa* species.

When the environmental variables were included in the model, the diversion effectiveness estimates for non-*Alosa* species were shifted closer to zero (Figure 3.5), and there was better consistency between the results for the new fishway and tailrace. This improved consistency, together with the highly significant improvement in the model fit, indicate that the model with the environmental variables provides better estimates of the effectiveness of the diversion system.

Dispersion parameters were greater than one for all species except winter flounder (Table 3.4), indicating that for a given species, the passage of fish at the generating station is not independent of other fish of the same species. As a result of this, the standard errors obtained from the quasi-likelihood model were larger than those obtained from the Poisson model for all species (Figure 3.6). Atlantic silverside catches had the highest dispersion parameter, which resulted from 54.8% percent of their catch occurring during four generation periods (even though Atlantic silversides were captures during all generation periods). This migratory pattern results in very wide standard errors for the effectiveness coefficient for Atlantic silversides when estimated using quasi-likelihood (Figure 3.6).

While the use of quasi-likelihood increased the standard errors of the effectiveness coefficients, the inclusion of the environmental variables in the model decreased these standard errors for 10 of the 11 species. When estimated using quasi-likelihood, the standard errors for the effectiveness coefficients for the environmental model ranged from 58.5% the size of those from the base model for Atlantic silverside to 115.7% for butterfish.

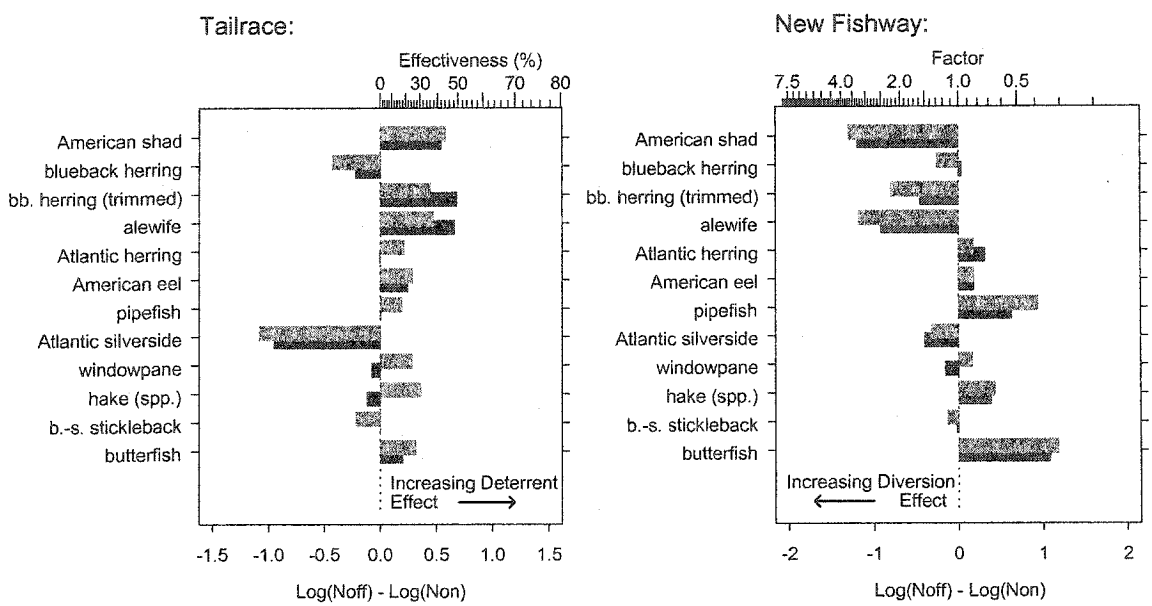

Figure 3.5. A comparison of two estimates of the effectiveness of an ultrasound fish diversion system at the Annapolis Tidal Generating Station, Nova Scotia, during September and October 1999. The dark bars show the estimates obtained from a model that includes environmental variables and the light bars show the estimates from a model without the environmental variables. The left panel (tailrace) shows estimates of the deterrent effect based on changes in the rates of fish passage through the turbine tube, while the right panel (new fishway) shows the changes in the rates of passage of fish through a fishway that bypasses the turbine.

Of these modelling approaches, the model with the environmental variables provided the best fit to the data, smaller standard errors for the effectiveness coefficients, the best consistency between sampling locations and is sensible because factors other than the status of the diversion system contribute to the rates of fish passage at this generating station. From this model, the results for the tailrace suggest an effectiveness of 42% for American shad and 48% for alewife (Figure 3.6), although these estimates are not significantly different from zero when the standard errors are calculated using quasi-likelihood (Table 3.3). However, the increases in the catch of these species in the new fishway with the diversion activated (3.3 and 2.5 times for American shad and alewife respectively) that are statistically significant are consistent with these estimates and enhance their credibility. For blueback herring, the catch did not decrease with the diversion activated when the model was fit to the full blueback herring dataset. However the system diverted about 49% for blueback herring after the generation cycles with the three largest catches were removed from the data (Figure 3.6). These findings are again consistent with the new fishway results: no increase in catch with the diversion activated using the full blueback herring dataset and an increase in catch of about 1.5 times when estimated using the trimmed blueback herring dataset (Figure 3.6).

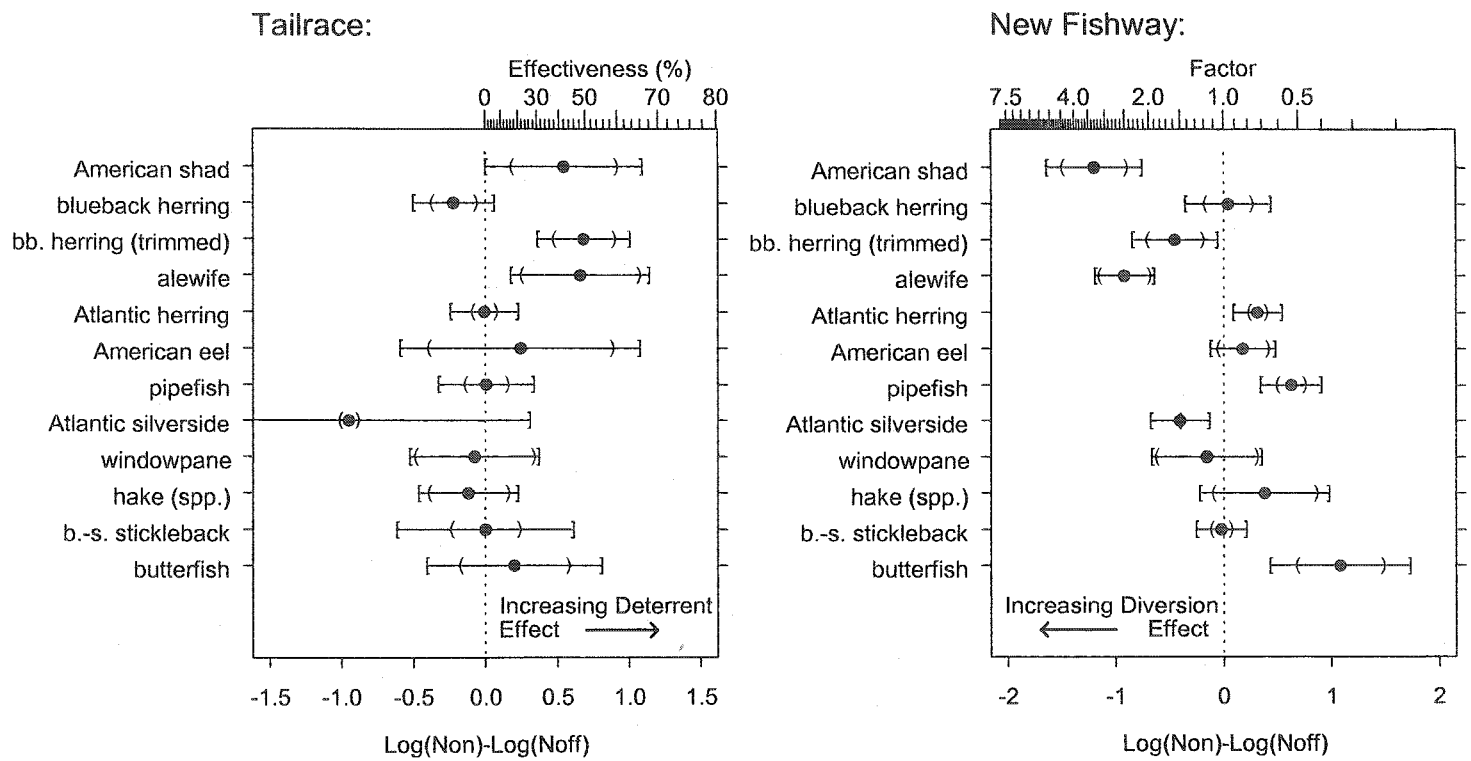

Figure 3.6. Estimates of the effectiveness of an ultrasound fish diversion system and the increase in fish passage in the new fishway with the diversion activated at the Annapolis Tidal Generating Station, Nova Scotia, during September and October 1999. Coefficients were estimated using the model with environmental variables. Error bars are one standard error: round brackets indicate standard errors estimated under the assumption of a Poisson error distribution, and square brackets indicate those estimated assuming a quasi-Poisson error distribution.

3.4 Discussion

In this chapter, I have provided the first evaluation of an ultrasonic fish diversion system at a tidal hydroelectric generating station, and have used a modelling approach that allows separation of the effects of environmental variables on the rate of fish passage from those of the diversion system. On the whole, these results indicate that the ultrasonic barrier was partially effective for *Alosa*, but not for the other species.

Comparisons of the results of the base model with the model including the environmental variables show that varying environmental conditions can affect both the accuracy and precision of the diversion effectiveness estimates. This problem may have confounded some other studies (Ross et al. 1993). By monitoring fish passage at two locations where the response to an effective diversion stimulus should be in opposite directions (decreased rates of passage through the turbine accompanied by increased rates of passage through the fishways), I was able to detect such errors by comparison of the consistency of the estimates at the two locations. When I included environmental variables in the model, the overall model fit was considerably improved, the resulting effectiveness estimates had smaller standard errors and the estimates were more consistent between the new fishway and tailrace sampling locations. This result shows that both the accuracy and precision of the effectiveness estimates can be improved if the diversion effectiveness is evaluated within a model of the process that determines the rate of fish passage.

The influence of environmental variables on the rate of passage or impingement is consistent with other studies at generating stations. For example, Ross et al. (1993) found that wind direction, temperature and time of day affected the rate of impingement at the James A. Fitzpatrick Nuclear Power plant cooling water intake. Nestler et al. (1992) found that the response of blueback herring to ultrasound varied between day and night at the Richard B. Russell dam. While not quantified during my study, environmental variables may also influence a fish's response to a stimulus, and hence the effectiveness of a diversion system. Additionally, the "motivational state" of fish has been shown to

vary throughout the year, as discussed by Popper and Carlson (1998). The timing of this study was appropriate for age-0 *Alosa*, the target species in this study, because they are only present at the Annapolis Tidal Generating Station during the fall. The response of other species that are present at this location at other times of the year and under different environmental conditions, as well as adult *Alosa* that are present in the late spring and summer, remains to be examined at this station.

When the movement of fish past generation stations is not independent of other fish (due to schooling behaviour or some other reason), estimates with a reasonable level of precision may be difficult to obtain. This problem is well illustrated in this study where the catches of all 11 species were overdispersed. As recognized by Popper (1999), the use of a Poisson error structure can lead to overestimation of statistical significance if fish passage is not random. The quasi-likelihood approach used herein corrects for this problem by rescaling the standard errors by the dispersion parameter. If fish catches are highly overdispersed, the resulting standard errors may be large relative to the parameter estimates, greatly reducing statistical significance. In this study, the distribution of the catch (characterized by the dispersion parameter) had a greater effect on the precision of the diversion coefficient estimates than did the number of fish captured. Atlantic silversides were by far the most abundant fish in this study, but had the second largest standard errors for the diversion coefficients at the tailrace site when the effects of overdispersion were included in the model. The catches of some the species for which I have not presented results were also clumped: sea lamprey were captured only during a six day period, a pattern is similar to that observed during other studies at this station (Gibson 1996), and 86.7% of mummichog were captured on 5 tides. When fish migrations occur during relatively short time periods, obtaining reliable diversion estimates may be problematic.

Comparisons of the results when the blueback herring data are modelled as a whole, and when the generation cycles with the three largest catches are trimmed from the data, suggest that the effectiveness of the diversion system may be partially dependent

on the abundance of target species. This pattern was observed at both the tailrace and the new fishway. While the reason for this observation at the Annapolis Tidal Generating Station is unknown, crowding may limit the ability of fish to respond to a signal. Alternatively, the increased abundance under favourable environmental conditions may be a result of increased motivation to move seaward.

The estimates of the diversion effectiveness at Annapolis are similar to those reported by some authors, but are lower than those reported by others. Popper (1999) reported the results of a comprehensive project to divert fish away from the cooling water intake at the Salem Nuclear Power Plant. As part of that project, a composite sound signal that included an ultrasound component was found to reduce impingement of blueback herring (11.6 - 33.2%), alewife (9.2 - 14.7%), bay anchovy (33.1 - 35.7%) and Atlantic silversides (23.5 - 24.7%). Their estimates and statistical significance also varied depending on their modelling approach. For *Alosa*, these estimates are similar to my results at the Annapolis station. Another similarity between these studies was the apparent increase in impingement or turbine passage of some species when the diversion was activated. Both studies suggest that randomization of the on/off status of the diversion through time does not ensure randomization across the set of variables that determine abundance or the rate of fish passage. In my study, the better model fit, smaller standard errors and better compatibility between the tailrace and new fishway results when environmental variables were included in the model, demonstrate that this problem can at least partially be alleviated by evaluating the effectiveness of the diversion system in a model of the process that determines the rate of fish passage.

Other authors have reported better success when attempting to divert fish with ultrasound. Ross et al. (1993) reported that ultrasound reduced impingement of alewives by as much as 87% at James A. Fitzpatrick (JAF) Nuclear Power Plant cooling water intake, but also found that environmental variables affected the rate of impingement and the effectiveness estimates. Ross et al. (1996) conducted a follow-up study that utilized an improved deterrent system, and concluded that the system should be 87% effective in

most years. However, comparisons of the effectiveness of the ultrasound at Annapolis with the effectiveness at the JAF may not be appropriate, given the differences between the locations. Diversion at a cooling water intake requires only that fish are deterred from the vicinity of the intake. Fish do not need to be directed towards a fishway, as is the case of migratory species at the Annapolis generating station.

Ross (1999) reported good success when testing the use of ultrasound to divert blueback herring at the Vischer Ferry and Crescent hydroelectric stations. At the Vischer Ferry site, over 90% of blueback herring used the by- pass. At the Crescent site, the system was effective for age-0 blueback herring, but was ineffective for adults. Ross (1999) suggested the effectiveness for adult blueback herring could be increased by moving the sound field. Hydrology, time of day and condition of the fish were found to influence both the abundance of fish and the effectiveness of the ultrasonic barrier at part of his study.

This study, as well as others, shows that ultrasound can be used to reduce power plant impacts on *Alosa* populations, although the extent of the achieved reduction varies between studies. Undoubtedly, the effectiveness of a diversion system depends on many site and system specific variables, and had I tested a different system (range of frequencies, signal strength, number and orientation of transducers) I probably would have obtained a different result. However, the effectiveness of a behavioural guidance systems also depends on the time of year, time of day, fish age, flow field, environmental conditions and "motivational state" of the fish (see review: Popper and Carlson 1998), and the signal tested in this study may simply have been less effective under the conditions present at the Annapolis station during the fall. The Annapolis Tidal Generating Station and the Salem Nuclear Generating Station cooling water intake are both estuarine facilities. Comparison of the results at the Annapolis station with those obtained at the Salem plant may therefore be more valid than comparisons with riverine hydroelectric systems or cooling water intakes in the Great Lakes. However, the partial effectiveness of the diversion system for *Alosa* at Annapolis does imply a response by

these fish to the ultrasound signal under the conditions at Annapolis. Therefore, the effectiveness of the diversion could possibly be enhanced through the redeployment or the addition of transducers, or an increase in signal strength. Additionally, the system may be most effective when used in conjunction with other strategies. At Annapolis, migratory species tend to move just after the start of generation (Gibson 1996). Providing an alternate passage before the start of generation, by keeping an extra sluice gate open prior to the onset of generation, might reduce the number of fish upstream of the turbine at the start of generation, leading to an overall reduction of turbine passage.

CHAPTER 4. A LOGISTIC REGRESSION MODEL FOR ESTIMATING TURBINE MORTALITY AT HYDROELECTRIC GENERATING STATIONS.

4.1 Introduction

Accurate estimates of turbine mortality at hydroelectric generating stations are fundamental for assessments of fish-related impacts of these facilities. While turbine mortality studies at hydroelectric stations are numerous, the results of these studies are often conflicting (Mathur et al. 1994), making it difficult to generalize about species or make comparisons between locations. When estimating turbine mortality, separation of mortality resulting from turbine passage from that resulting from capture and handling is a fundamental problem that may have lead to the overstatement of turbine mortality in some studies (Mathur et al. 1994).

Turbine mortality studies can be loosely divided into two groups: those that use fish released into the turbine intake (e.g. Hogans 1987; DuBois and Gloss 1993; Mathur et al. 1994) and those that use naturally entrained fish captured in nets in the turbine tailrace (e.g. Stokesbury and Dadswell 1991; Navarro et al. 1996). When naturally entrained fish are used to estimate turbine mortality, capture and handling mortality is a confounding issue because mortality increases with time in the net (Stokesbury and Dadswell 1991). Determination of an appropriate duration for the control experiments is problematic because the length of time the entrained fish are in the net is unknown (Gibson 1996).

Here, I suggest that the problem of control experiment duration can be overcome with a slight modification to the methods used in many studies. By varying the duration of net deployment, the probability that a captured fish is alive can be modelled as a function of the duration of the net deployment. The intercept of the resulting model can be interpreted as an estimate of the survival of fish that have not spent time in a net, i.e. turbine mortality. To demonstrate this method, I present preliminary estimates of turbine mortality for several species of fish passing through the STRAFLO turbine at the

Annapolis Tidal Generation Station, Annapolis Royal, Nova Scotia, and suggest a modification to the model to include a correction for handling mortality resulting from other components of the capture process.

4.2 The Study Area

This study was carried concurrently with the assessment of the effectiveness of a fish diversion at the Annapolis Tidal Generating Station, presented in Chapter 3. Readers are referred to that chapter for a description of the site. Previous fish mortality studies at this site suggest that 21.3 % ± 19.8 % (95 % C.I.) of adult, post-spawning American shad *Alosa sapidissima* do not survive passage through the turbine Hogans (1987) and that age-0 clupeid turbine mortality is 46.3% (Stokesbury and Dadswell 1991). While accuracy of these estimates has been debated (Dadswell and Rulifson 1994; Gibson 1996), no studies exist that conclusively support or disprove these estimates. Survival of other species through this turbine has not been studied.

4.3 Methods

When naturally entrained fish are used to estimate turbine mortality, selection of an appropriate duration for control experiments is problematic because the length of time that a captured fish is in the net is unknown and varies between fish within a net deployment and between net deployments. As the duration of the net deployment increases, this variability and uncertainty also increase. In the limiting case, that of a deployment duration of zero length, the duration of the net deployment and length of time that a fish is in the net are the same. While a net cannot be deployed for a time period of zero, survival at this limit can be estimated by varying the duration of the net deployment and using the statistical methods described below.

4.3.1 Field Methods

Sampling for this study was integrated into an assessment of the effectiveness of an ultrasound fish diversion system at the Annapolis Tidal Generating Station during the fall of 1999 (Chapter 3). As such, fish that were captured in the tailrace during the assessment of the fish diversion system were used as test specimens for modelling mortality.

I captured naturally entrained fish using modified ichthyoplankton nets at two locations in the turbine tailrace (Figure 3.1). These nets were 1.0 m in diameter and consisted of three sections: a cylindrical section, 2.0 m long, made of 1 cm mesh nylon netting; a middle section made of 2 mm Nitex net 3 m in length, tapering from 1 m to 0.2 m during the final meter; and the collector. The collectors were 1.75 m long, and were constructed with Spandex cloth fitted over 0.5 m diameter, aluminum cylinders, 0.75 m in length. Entrances to the collectors were funnel-shaped to keep fish from escaping from the net and the tail ends of the collectors designed so that they could be opened and closed with drawstrings. Nets were fished for the full generation period (about 5.5 h), but the catch was removed from the nets and placed in buckets at pre-determined intervals ranging from 0.25 h to 5 h throughout the generation period. The catch was identified, enumerated and the live/dead status of each fish recorded about 10 minutes after removing the fish from the net. The resulting data set was used to estimate acute mortality (dead at the time of removal from the net) for each species for which sufficient numbers were captured.

Sampling was conducted during 48 randomly chosen generating cycles between September 7th and October 22nd, 1999, covering over 50% the generating time between these dates. The time of day or night varied with the precession of the tides. The interval at which nets were emptied was held constant throughout a generating cycle, in order to evenly distribute the number of fish captured over the time intervals. Nets were deployed a total of 447 times during this period.

Fish that were in very poor condition (e.g. not swimming and bleeding badly) were counted as dead. While an element of subjectivity is introduced by this decision, the effect of any resulting bias would be to increase the mortality estimate providing a more precautionary estimate as a result.

4.3.2 Statistical Analysis

I assumed that fish captured that were dead, either at the time of capture, or shortly thereafter, died either as a result of turbine passage, capture in the net, or some interaction of these variables. For each species, I treated the live/dead status of each fish (Y) as a binomial response (0 = alive, 1 = dead), and used the logistic model (Collett 1991):

$$E(Y) = \frac{\exp(\beta_0 + \beta_1 d)}{1 + \exp(\beta_0 + \beta_1 d)} \tag{4.1}$$

to model $E(Y)$, the expectation of the probability that a captured fish is dead as a function of d, the duration of the net deployment. Within this model, β_0 and β_1 are the linear regression coefficients on a logistic scale, and an estimate of the probability that a fish that has not spent time in a net is dead ($M_{d=0}$) can be calculated as:

$$M_{d=0} = \frac{\exp(\beta_0)}{1 + \exp(\beta_0)} \tag{4.2}$$

This approach to estimating turbine mortality requires extrapolation outside the range of observed data, which is potentially hazardous with binary data if the model formulation is inappropriate (McCullagh and Nelder 1989). I examined the robustness of my estimates in relation to model selection in two ways: by adding a power parameter that controls the degree of nonlinearity in the model, and by examining two other transformations as outlined below.

An assumption of the model (equation 4.1) is that mortality is linearly related to the duration of the net deployment on the logistic scale. Equation 4.1 is the specific case, λ=1, of the general model:

$$E(Y) = \frac{\exp(\beta_0 + \beta_1 d^{\lambda})}{1 + \exp(\beta_0 + \beta_1 d^{\lambda})}. \tag{4.3}$$

I examined the linearity assumption by using maximum likelihood to fit equation 4.3 to the acute mortality dataset for λ ranging from 0.01 to 3, and using profile log likelihoods as a guide for selecting an appropriate λ. The log likelihood for λ, β_0 and β_1 is given by:

$$\ell(\lambda, \beta_0, \beta_1) = \sum_i \left[y_i \log\left(\frac{\exp(\beta_0 + \beta_1 d_i^{\lambda})}{1 + \exp(\beta_0 + \beta_1 d_i^{\lambda})} \right) + (1 - y_i) \log\left(1 - \left(\frac{\exp(\beta_0 + \beta_1 d_i^{\lambda})}{1 + \exp(\beta_0 + \beta_1 d_i^{\lambda})} \right) \right) \right] \tag{4.4}$$

and the log profile likelihood for λ ($\ell_p(\lambda)$) is:

$$\ell_p(\lambda) = \max_{\beta_0, \beta_1} \ell(\lambda, \beta_0, \beta_1) \tag{4.5}$$

The maximum likelihood estimate of λ occurs where $\ell_p(\lambda)$ achieves its maximum value, and the plausibility of other possible values of λ was evaluated by comparing their log likelihoods with the maximized log likelihood. A likelihood ratio based 95% confidence interval for λ is calculated as:

$$\{\lambda : 2\left[\ell_p(\lambda^{\mathrm{MLE}}) - \ell_p(\lambda)\right] \le \chi_1^2(0.95)\} \tag{4.6}$$

where λ^{MLE} is the maximum likelihood estimate of λ (Kalbfleisch 1985). The profile log likelihoods suggested that λ=1 was appropriate (see results), and I therefore retained equation 4.1 as the model.

The logistic model (equation 1) has the advantage it can be fit as a generalized linear model (McCullagh and Nelder 1989) with the components:

random component: Y is a binomial random variable with

$$E(Y) = u \tag{4.7}$$

and

$$\mathrm{var}(Y) = u(1-u)\,. \tag{4.8}$$

systematic component: $g(u) = g(E(Y \mid d)) = \beta_0 + \beta_1 d$ (4.9)

link function: $g(E(Y)) = \mathrm{logit}(E(Y)) = \log\left(\frac{E(Y)}{1-E(Y)}\right)$ (4.10)

This model also has the advantage that the model parameters can be interpreted directly as the log odds-ratio, so that the mortality estimate can be easily calculated from the parameter estimates. However, to ensure its suitability as the link function and for extrapolation to the intercept, I also modelled the data using two other link functions (McCullagh and Nelder 1989): the probit or inverse Normal function:

$$g(E(Y)) = \Phi^{-1}(E(y)) \tag{4.11}$$

and the complementary log-log function:

$$g(E(Y)) = \log(-\log(1-E(Y)))\,. \tag{4.12}$$

Maximized log likelihoods (Collett 1991) were used as a guide to choose between these models (higher values imply better fits). The logistic model provided a slightly better fit (see results), and was therefore retained as the model.

The generalized linear models have the advantage that it is easy to calculate confidence intervals based on the assumption of asymptotic normality. These intervals were used for the turbine mortality estimates. Confidence limits were calculated on the logistic scale as $\beta_i \pm z_{1-\alpha/2}s$, where s is the standard error of β_i and $z_{1-\alpha/2}$ is the critical value of a standard normal distribution for a given confidence level. Estimates of β_1 were considered statistically different from 0 if their confidence interval did not include zero. Confidence limits for β_0 were transformed using the inverse of the link function (equation 2) to obtain confidence intervals for the rate of turbine mortality ($M_{d=0}$). I compared these confidence intervals to likelihood ratio based intervals. When not corrected for overdispersion (see below), the intervals based on the normal approximation for β_0 were slightly larger than the likelihood ratio based intervals.

If the survival of a fish within a net is not independent of other fish in the net, there would be greater variability in survival than predicted by binomial sampling error. I therefore also modelled the data grouped by net deployment, and looked for systematic deviations in the relationship between the expectation and variance of the mortality probability that would occur if the data were under or overdispersed. I calculated a dispersion parameter (ϕ) as the sum of the squared Pearson residuals divided by the residual degrees of freedom (McCullagh and Nelder 1989). A dispersion parameter much greater than one indicates that either the data is overdispersed or that the model fit is not good for some data points. For most species ϕ was near one (see results). Examination of residual plots (e.g. deviance residuals versus fitted values, normal quantile plots of the Pearson residuals) suggested the fits were reasonable. I therefore rescaled the standard error of β_0 by ϕ, and used the rescaled values for confidence interval calculations. This approach does not affect the turbine mortality estimate, but provides a more realistic estimates of the variance than would be obtained by under the assumption that mortality was independent for all fish. Overall, of the three methods used to produce confidence intervals, this method produced the widest intervals. I choose to report these intervals because, as the widest intervals, they provide the most precautionary estimate of the precision of the turbine mortality estimates.

4.4 Results

In total, 2,784 fish, belonging to 21 species, were captured during these experiments (Table 4.1). Atlantic silversides, *Menidia menidia*, were the most abundant species (1160 captured). Of the 21 species, the catches of 12 species were sufficiently large to warrant detailed analysis.

The choice of the link function had only minor effects on the resulting mortality estimates. The estimates from the complementary log-log model were slightly higher than those of the logistic and probit models (Table 4.2). With the exception of Atlantic

herring, *Clupea harengus*, maximized log likelihoods were similar between the three models. Overall, the fit of the logistic model was slightly better than the probit and complementary log-log models, a difference that was not statistically significant except for Atlantic herring. For Atlantic herring, the mortality estimate from the complementary log-log model was 5% higher, but the fit of the model was significantly worse. I concluded that the logistic model was the most suitable choice for modelling these data.

When λ is included in the model (equation 3), the turbine mortality estimate ($M_{d=0}$) is sensitive to the choice of λ (Figure 4.1). As λ approaches 0, the estimate of $M_{d=0}$ also approaches 0. As λ increases, $M_{d=0}$ approaches the proportion of dead fish within the sample. The log likelihood was maximized at $\lambda \approx 1$ for most species (Figure 4.2), with the exceptions being species with small sample sizes (American shad and alewife, *Alosa pseudoharengus*) and species where very few dead fish were captured (sea lamprey, *Petromyzon marinus*, blackspotted stickleback, *Gasterosteus wheatlandi*, winter flounder, *Pseudopleuronectes americanus*, and windowpane, *Scophthalmus aquosus*). For these exceptions, the profile log likelihood is almost flat or ramped, showing that there is little or no information about λ in these datasets. For species where λ could be estimated, λ was not statistically different from 1. I concluded that the specific case, λ=1, was reasonable for most species and used this model for the remaining analysis.

The probability that a captured fish was dead increased rapidly with net deployment duration for clupeids, but more slowly for other species such as Atlantic silverside, pipefish, *Syngnathus fuscus*, and blackspotted stickleback (Figure 4.2). This increase was statistically significant at $\alpha = 0.05$ for all species except American shad, winter flounder, windowpane and sea lamprey (Table 4.3). For the latter three species, very few dead fish were captured at any deployment duration (Figure 4.3). Figure 4.2 also shows that if turbine mortality was estimated using fixed duration net deployments, the resulting estimates would be very sensitive to the length of time that the net was deployed. For example, alewife mortality was about 18% for a one hour net deployment

Table 4.1. The total number of specimens and number of live specimens of each species captured in 447 net sets during 48 randomly selected generation periods between September 7, 1999 and October 22, 1999 at the Annapolis Tidal Generating Station, Nova Scotia. Data for species in boldface was considered sufficient for analysis.

	Mortality Experiments:	
Species	total number	number alive
sea lamprey (*Petromyzon marinus*)	20	20
American eel (*Anguilla rostrata*)	10	9
age-0 blueback herring (*Alosa aestivalis*)	206	144
age-0 alewife (*Alosa pseudoharengus*)	33	20
age-0 American shad (*Alosa sapidissima*)	39	22
age-0 Atlantic herring (*Clupea harengus*)	840	441
rainbow smelt (*Osmerus mordax*)	5	3
hake spp. (*Urophycis spp.*)	88	69
Atlantic silverside (*Menidia menidia*)	1160	1054
blackspotted stickleback (*Gasterosteus wheatlandi*)	68	65
pipefish (*Syngnathus fuscus*)	202	175
cunner (*Tautogolabrus adspersus*)	3	3
butterfish (*Peprilus triacanthus*)	32	22
longhorn sculpin (*Myoxocephalus scorpioides*)	1	1
lumpfish (*Cyclopterus lumpus*)	1	1
smooth flounder (*Liopsetta putnami*)	1	1
winter flounder (*Pseudopleuronectes americanus*)	31	28
windowpane (*Scophthalmus aquosus*)	28	24
mummichog (*Fundulus heteroclitus*)	6	6
Atlantic mackerel (*Scomber scombrus*)	9	4
fourbeard rockling (*Enchelyopus cimbrius*)	1	1
TOTAL	2784	2092

Table 4.2. A comparison of mortality estimates and log likelihoods for logit, probit and complementary log-log link functions for 12 species of fish at the Annapolis Tidal Generating Station, Nova Scotia.

	Acute Mortality Estimate			Log Likelihood		
Species	logit	probit	c. log-log	logit	probit	c. log-log
Atlantic herring	15.7	15.9	21.6	-500.6	-501.4	-505.6
alewife	7.7	6.6	11.6	-17.2	-17.1	-17.3
blueback herring	8.0	7.4	11.1	-108.2	-108.4	-109.2
American shad	23.4	22.8	24.1	-25.5	-25.5	-25.5
Atlantic silverside	2.2	1.7	2.4	-312.7	-312.4	-313.1
bs. stickleback	<0.1	<0.1	<0.1	-8.2	-8.1	-8.3
sea lamprey	<0.1	<0.1	<0.1	-0.0	-0.0	-0.0
hake (spp.)	8.7	8.1	9.6	-41.6	-41.6	-41.6
butterfish	8.7	7.7	10.2	-16.1	-16.0	-16.0
pipefish	2.2	1.7	2.8	-64.3	-64.3	-65.0
winter flounder	5.8	5.8	5.8	-9.4	-9.4	-9.4
windowpane	8.8	8.1	9.1	-11.3	-11.3	-11.3
			totals:	-1115.6	-1116.0	-1122.8

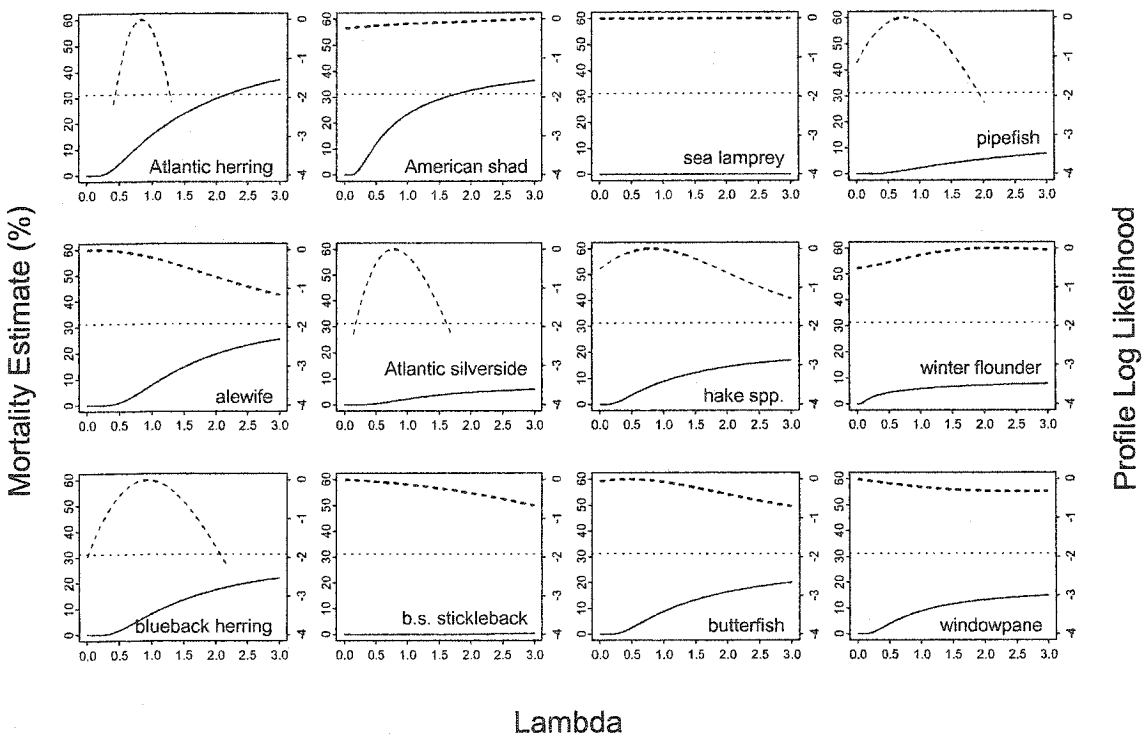

Figure 4.1. The relationship (solid line) between the mortality estimate ($M_{d=0}$) and lambda, a power parameter that determines the functional form of the relationship between mortality and net deployment duration for 12 species of fish at the Annapolis Tidal Generation Station, Nova Scotia. The dashed line shows the profile log likelihood for lambda, standardized by subtracting the maximum log likelihood from each estimate. The intersections between the dotted line and the dashed line show the 95% confidence interval for lambda.

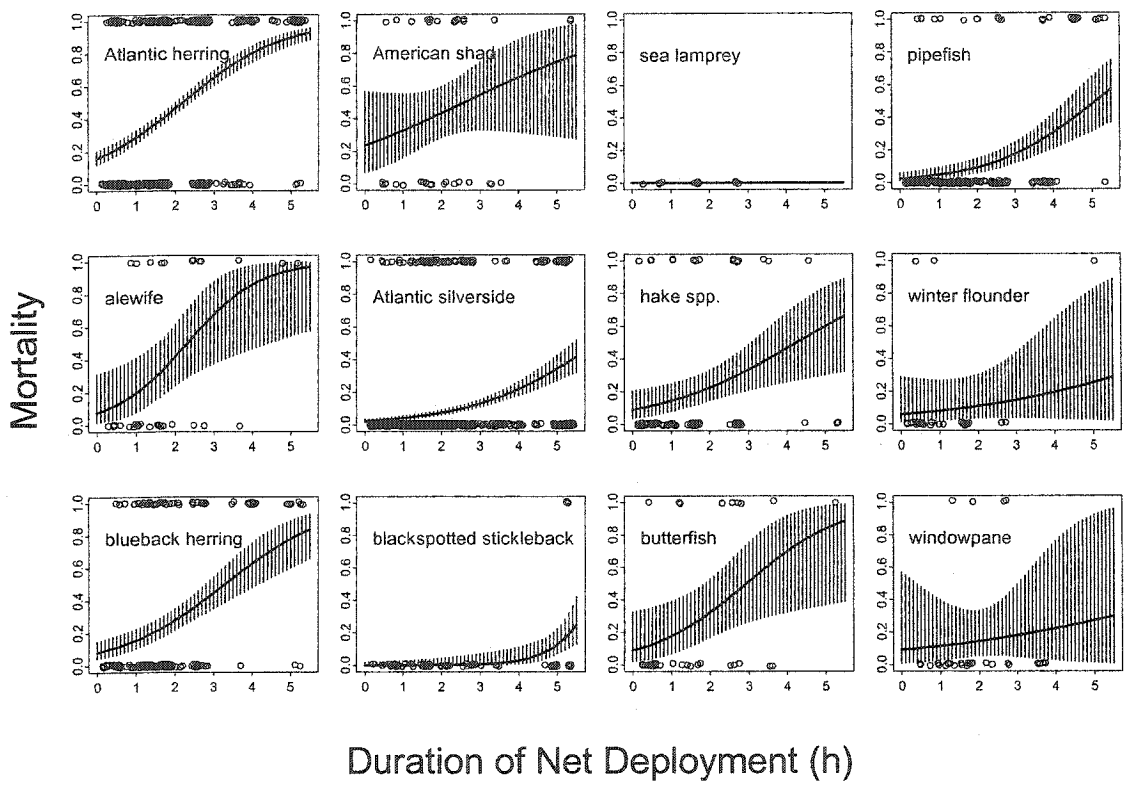

Figure 4.2. Mortality (solid line) as a function of the duration of net deployment for 12 species of fish at the Annapolis Tidal Generating Station, Nova Scotia. Each point represents a fish that was either alive (0), or dead (1). Points are slightly jittered to facilitate display. The y-intercept is an estimate of acute mortality in the absence of any time in the net, interpreted as an estimate of acute turbine mortality. Error bars are 95% confidence intervals.

and about 62% for a three hour net deployment. Regressing to a net deployment of zero length provides an estimate of 7.7%. Estimates of the rates of mortality ranged from 0.0% for sea lamprey to 23.4% for American shad (Table 4.3).

4.5 Discussion

In this chapter, I've demonstrated that with a slight change in the methods used in many studies, estimates of turbine mortality obtained using naturally entrained fish can be improved by modelling the probability that a captured fish is dead as a function of the duration of the net deployment. When net deployments of fixed duration are used to estimate turbine mortality, the resulting estimate is not only a function of the rate of turbine mortality, but also the duration of the net deployment (Stokesbury and Dadswell 1991, their Figure 2; my Figure 3). The duration of control experiments to correct for handling mortality cannot be chosen without knowledge of the length of time that fish are in the net, which varies both between deployments and within individual net deployments. By varying the duration of the net deployments, regression methods can be used to estimate the mortality for a net deployment of zero duration, providing a method to estimate the mortality attributable to turbine passage or passage via other structures.

A number of methods have been developed to estimate turbine mortality. These methods can be divided into two categories: those that use naturally entrained fish (e.g. Stokesbury and Dadswell 1991; Navarro et al. 1996) and those that use fish released into the turbine intake (e.g. Hogans 1987; Mathur et al. 1994). In the first case, fish are captured using nets in the turbine tailrace, and turbine mortality is estimated using either live/dead criteria (e.g. Navarro et al. 1996) or by conducting autopsies on dead fish (e.g. Stokesbury and Dadswell 1991; Sorenson et al. 1998). In the second case, fish released into the turbine tube may be recaptured in nets in the turbine tailrace (e.g. Ruggles et al. 1990 in part; Dubois and Gloss 1993), followed via radio tags (e.g. Hogans 1987),

Table 4.3. Logistic regression coefficients and estimates of turbine mortality for 12 species of fish at the Annapolis Tidal Generating Station. Numbers in brackets are standard errors. Estimates where the increase in mortality with increasing net deployment duration (β_1) is significantly different from 0 at a 95% confidence level after correcting for dispersion are marked with asterisks. Confidence intervals for mortality are calculated using normal approximations on the link scale and are corrected for over-dispersion.

Species	Regression Coefficients			Mortality (%)	
	β_0	β_1	ϕ	mean	95% C.I.
age-0 American shad	-1.18 (0.73)	0.45 (0.32)	1.17	23.4	6.1 - 58.8
age-0 blueback herring	-2.43 (0.35)	0.74 (0.14)*	1.59	8.1	3.5 - 17.2
age-0 alewife	-2.48 (0.88)	1.07 (0.42)*	0.96	7.7	1.5 - 31.4
age-0 Atlantic herring	-1.67 (0.16)	0.77 (0.07)*	1.80	15.7	10.8 - 22.1
sea lamprey	n/a	n/a	n/a	0.0	n/a
blackspotted stickleback	-9.99 (5.73)	1.61 (1.11)*	0.40	<0.1	<0.1 - 5.6
Atlantic silverside	-3.78 (0.21)	0.62 (0.07)*	2.23	2.2	1.1 - 4.1
pipefish	-3.77 (0.50)	0.73 (0.14)*	1.23	2.2	0.7 - 6.4
butterfish	-2.34 (0.81)	0.79 (0.34)*	1.15	8.7	1.7 - 34.5
winter flounder	-2.78 (0.91)	0.34 (0.36)	1.24	5.8	0.8 - 31.2
windowpane	-2.32 (1.29)	0.26 (0.56)	1.14	8.8	<0.1 - 59.4
hake (spp.)	-2.34 (0.49)	0.55 (0.19)*	1.10	8.7	0.3 - 20.9

detected downstream via PIT-tags (e.g. Skalski et al. 1998) or recaptured using some other method (e.g. Heisey *et al.* 1992). Estimates are reported either corrected for handling and capture mortality (e.g. Stokesbury and Dadswell 1991; Mathur et al. 1994) or not (Navarro et al. 1996). The resulting mortality estimates from both methods are often reported as acute (or immediate or short term: the proportion dead at or near the time of capture) or delayed (or long term: the proportion dead after holding the fish for some time period, typically 12, 24 or 48 h).

Each of these methods has its relative strengths and disadvantages, based on both scientific and practical considerations. When fish are abundant, estimation of acute mortality using naturally entrained fish captured with nets in the tailrace is a relatively easy and cost effective method of obtaining data. Handling of fish is reduced and the method can be applied in situations where test fish are not readily available (e.g. flatfish in this study). Estimates can be obtained for several species simultaneously without an increase in the required effort (e.g. Navarro et al. 1996, this study). The method can be easily integrated into sampling for other purposes (e.g. Stokesbury and Dadswell 1991; Navarro et al. 1996; this study). However, if controls are used to correct for capture and handling mortality, determination of an appropriate duration for the control experiments is difficult because the length of time the entrained fish are in the net is unknown (Gibson 1996). The regression methods presented herein provide a possible solution to this problem by estimating turbine mortality for a net deployment duration of zero length.

Releasing fish into the turbine tube provides better experimental control than the use of naturally entrained fish, but increases the stress to the fish associated with handling. Where the effects of stress are cumulative and culminate in increased mortality, the individual effects of handling, turbine passage and recapture can be difficult to distinguish (Ruggles et al. 1990). Improved handling and recapture methods, such as the HI-Z Turb'N tag-recapture technique (Heisey et al. 1992), have substantially reduced handling mortality, leading to improved mortality estimates over studies where handling mortality was high (Mathur et al. 1994). The experimental and statistical methods

described herein provide a tool that can be used to detect and reduce biases in turbine mortality estimates, although as discussed below, they do not completely alleviate problems when handling mortality is high.

Two aspects of turbine mortality not considered here are delayed mortality and mortality resulting from capture and handling other than time in the net. If delayed mortality is high, acute mortality may not be a sufficient measure of the overall effect of a turbine on a fish stock (Kostecki et al. 1987; Dubois and Gloss 1993). The importance of delayed mortality has varied between studies and locations. Dubois and Gloss (1993) reported differences in acute and 24-hour turbine mortality of up to 45% for striped bass (*Morone saxatilis*) passed through Ossberger crossflow turbines, although delayed mortality may have been overestimated because of high control mortality. Mathur et al. (1996) reported differences in acute and 48-hour turbine survival estimates of less than one percent for chinook salmon smolts (*Oncorhynchus tshawytscha*) at a dam on the Columbia River. The approach of modelling the mortality process can be used to estimate delayed mortality if fish are held in pens for a period of time prior to evaluating their live/dead status. The regression methods can be applied directly to the resulting dataset. However, holding facilities and handling protocols must not be a significant source of mortality if delayed mortality is to be reliably estimated (Ruggles et al 1990; Dubois and Gloss 1993; Mathur et al. 1994).

The second aspect, mortality resulting from capture and handling other than time in the net, can lead to an overestimate of turbine mortality. Mortality that is the result of the capture process can be separated into three components: the proportion of fish that die while entering the net (e.g. fish that are impinged or abraded against the net), the proportion of fish that die as a result of time in the net (e.g. due to crowding or suffication), and proportion of fish that die while being removed from the net (e.g. as a result of handling). The regression model (equation 1) estimates $M_{d=0}$, where the mortality that is a result of time in the net is zero. If $M_{d=0}$ is interpreted as turbine mortality without estimation of the other components, the resulting turbine mortality

estimate will be biased high. In instances where the resulting estimate of $M_{d=0}$ is small (and its confidence interval is small), these other components must also be small (less than $M_{d=0}$), and hence the effect of their bias on the estimate must be small. If $M_{d=0}$ is low enough that mitigation or remediation is not required, mortality can reasonably be attributed to the turbine without quantification of this bias, because correction for this bias would not alter management decisions. Where the resulting mortality estimate is high relative to the compensatory capacity of the stock, the estimate should not be interpreted as turbine mortality without quantification of mortality from other components of the capture process.

My approach can be extended to incorporate mortality from these other components of the capture process. Controls for handling mortality typically involve placing marked fish that have not passed through the turbine into the net for some period of time (e.g. Stokesbury and Dadswell 1991). If this type of control experiment is to be incorporated into the regression model, the duration of these experiments should also be varied to allow extrapolation to zero time in the net. The results of the control experiments can then be modelled simultaneously with those from the naturally entrained fish. A logistic model incorporating the results of the control experiments is

$$E(Y) = \frac{\exp(\beta_0 + \beta_1 d)}{1+\exp(\beta_0 + \beta_1 d)} t + \frac{\exp(\beta_0' + \beta_1' d')}{1+\exp(\beta_0' + \beta_1' d')} t' \tag{4.13}$$

where β_0, β_1 and d are the terms for the naturally entrained fish, β_0', β_1' and d' are the terms for the control fish, and t and t' are factors with two levels, either zero or one, that state whether or not a fish passed through the turbine. Turbine mortality can be calculated from β_0 and β_0' by combining equation 4.2 and the model of Burnham et al. (1987) based on competing risk theory:

$$M_{d=0} = 1 - \left(\frac{\exp(\beta_0)\exp(1-\beta_0')}{\exp(\beta_0')\exp(1-\beta_0)} \right) \tag{4.14}$$

The standard error of $M_{d=0}$ can be calculated from the standard errors of β_0 and β_0' using the rules for calculating the standard errors of functions of random variables (Kendall et al. 1983). This model structure has the advantage that it can be fit as a generalized linear model. Therefore, it can be easily modified to test assumptions about the functional form of the model by changing the link function. However, the calculation of confidence intervals for $M_{d=0}$ requires the assumption of normality for $M_{d=0}$ and as such can produce intervals that include values less than 0% or greater than 100%. An alternative approach, outside the generalized linear models family, is estimate $M_{d=0}$ directly within the model using maximum likelihood (the functional form of the model is obtained by solving equation 4.14 for β_0 and substituting the result in equation 4.13). This method has the advantage that confidence intervals that do not require the normality assumption can be derived from the profile likelihood.

The regression methods described in this chapter require extrapolation beyond the range of the data. The success of this extrapolation depends heavily on the correctness of the assumed model (McCullagh and Nelder 1989). With these data, I found that the logistic model provided a slightly better fit than the probit or complementary log-log models and that the resulting estimates were not very sensitive to the choice of the link function. The estimates were sensitive to the degree of non-linearity (λ) in the model, although the linear, logistic form was most appropriate. The best model could potentially vary between locations, and I recommend that researchers that employ these methods perform similar diagnostics to ensure the selected model is appropriate.

The estimates of the dispersion parameter ranged between 0.40 for blackspotted sticklebacks (most sticklebacks were captured alive) and 2.23 for Atlantic silversides, and were greater than one for all but two species. These results suggest that survival of individual fish within a net deployment was not independent of other fish captured at the same time. This situation could arise, for example, if mortality rates varied with operating efficiency (which varies with the stage of the tide) or if crowding with the net affected

survival. The dispersion parameter is used to rescale the standard errors of parameter estimates (on the logistic scale) and can therefore significantly change estimates of statistical significance and confidence intervals. Where possible, the binomial assumption should be tested to ensure that the precision of the resulting estimates is not overstated.

As discussed, the use of naturally entrained fish to estimate turbine mortality entails a loss of experimental control relative to the use of experimentally released fish. When regression methods are used, designing an experiment to achieve a specified confidence interval width requires consideration of a number of factors, including prior knowledge (or guesses) of capture rates and the slope and intercept of the regression equation, and the dispersion parameter. Small perturbations in the parameter estimates can markedly affect experimental design efficiency (Chaloner and Larntz 1989). Confidence intervals for the turbine mortality should be smallest when all sampling effort is at very short or very long durations (Sebastiani and Settimi 1997), although given this type of design, the researcher is not able to test the functional form of the model (i.e. determine whether the linear logistic model is appropriate). Selection of an appropriate design requires balancing the relative costs and benefits of these requirements. In this study, the relationship between net deployment duration and mortality varied substantially among species. If a pilot study showed that mortality does not increase with the length of the net deployment below some duration, these results could be used to select appropriate deployment durations for fixed duration experiments, substantially simplifying the experimental design.

Turbine mortality of clupeids has been previously studied at the Annapolis Tidal Generating Station. Stokesbury and Dadswell (1991) estimated that 46.3% of age-0 clupeids do not survive turbine passage. The estimates reported here of acute turbine mortality for American shad (23.4%), Atlantic herring (15.7%), alewife (7.7%) and blueback herring (8.1%) are all lower than 46.3%, differences that are statistically significant at a 95% confidence level with the exception of American shad. Two possible explanations exist for these discrepancies. The duration of the control experiments used

by Stokesbury and Dadswell (1991) was short relative to the length of the net deployments and the expected length of time that fish would have been in the nets (Gibson 1996). Turbine mortality could therefore have been overestimated in their study. Alternatively, the majority of turbine induced injuries reported by Stokesbury and Dadswell (1991) were pressure induced, such as eye haemorrhage or gas bladder damage (Dadswell and Rulifson 1994). If mortality resulting from pressure-induced injuries is not acute, it would not have been detected in my study. The results of these studies are therefore not directly comparable without further information about the timing of pressure-induced mortality. Estimates of acute turbine mortality for other species in my study ranged from 0.0% for sea lamprey to 8.8% for windowpane, and are the first turbine mortality estimates for these species.

While considerable effort has been focused on the estimation of turbine mortality, the interpretation of mortality estimates has received less attention. A turbine mortality estimate should be interpreted as the probability of an individual fish surviving turbine passage. As such, it affects the life expectancy of a fish and its lifetime fecundity. When fish are removed from a population, their removal may elicit a compensatory response such as increased growth and survival of other members of the population. The effect at the population level is the combined effects from all fish and will vary depending on factors such as the proportion of fish passing through the turbine, when turbine passage occurs relative to reproduction, when it occurs relative to compensatory processes and the life history characteristics of the species. A species with a short life span, high fecundity and that reproduces prior to passing through the turbine could potentially withstand a comparatively high turbine mortality rate with little impact at the population level. Conversely, for a species that has a long life span, low fecundity, reproduces late in life and passes through the turbine several times prior to reproducing, a comparatively low turbine mortality rate could mean extinction. With increasing interest in the development of tidal hydroelectric generation, an increasing number of species are being exposed to turbines. Models should be developed that allows not only estimation of turbine mortality

for a given species based on turbine design, but to allow prediction of the population response based on the general biology of the fish. Turbine mortality studies have traditionally focused on commercially important groups such the salmons and shads. Development of these models requires estimates for a wide range of species and turbine designs.

CHAPTER 5. A META-ANALYSIS OF THE HABITAT CARRYING CAPACITY AND MAXIMUM REPRODUCTIVE RATE OF ANADROMOUS ALEWIFE IN EASTERN NORTH AMERICA

5.1 Introduction

Spawner-recruit models are a widely accepted tool for analyzing population dynamics (Moussalli and Hilborn 1985; Myers et al. 1999), providing biological reference points for management (Myers et al. 1994) and a basis for the estimation of the long-term consequences of mortality caused by pollution, dams or other human activities (Barnhouse et al. 1988, Hayes et al. 1996). In this paper, I provide a detailed analysis of the population dynamics of anadromous alewife, *Alosa psuedoharengus*, using a two-parameter spawner-recruit model. One of these parameters, the maximum reproductive rate at low population size, is fundamental for determining the intrinsic growth rate r_{max} (Cole 1954), for the calculation of many biological reference points for management (Mace 1994), for population viability analyses (Lande et al. 1997) and is the biological limit to overfishing and other sources of anthropogenic mortality (Crecco and Gibson 1990, Myers and Mertz 1998a). The other parameter, the habitat carrying capacity, is needed to determine the potential long-term yield for a fishery, the target spawning escapement for management (Mousalli and Hilborn 1985), the size of fish passage facilities (Clay 1995) and can be used to compare habitat quality (Hayes et al. 1996). Together, the two parameters provide a basis for evaluating the status of a population, and assessing the changes to the population resulting from habitat alterations or other human activities.

Traditionally, fisheries biologists have relied upon data only from the population of interest to assess the effects of pollution, fishing and other activities. Unfortunately, the long and detailed time series that are required to arrive at firm conclusions simply do not exist for the majority of fish populations (Myers and Mertz 1998b). Fortunately, many populations of the same species (or closely related species) share similar life

history strategies. For this reason, parameter estimates from several populations can be combined, providing a probability distribution for the parameter estimates at some higher organizational level, such as the species (Myers et al. 1999, Myers et al. 2001). The resulting probability distributions can be combined with comparatively limited population-specific data to make inferences at the level of the specific population. In this way, the uncertainty of biological parameters used in fisheries management is reduced (Myers and Mertz 1998b). This approach, known as meta-analysis, allows conclusions to be reached by drawing upon data from many populations.

I therefore approached my analysis of alewife population dynamics in two ways: I modelled the datasets for each population individually, and used meta-analytic methods to simultaneously estimate model parameters for the eight populations. In so doing, I was were able to determine how well spawner-recruit parameters are determined for individual populations, and were also able provide estimates of the reproductive rate and habitat carrying capacity for alewife at the species level.

I primarily used compensatory spawner-recruit models for this analysis. Implicit in their use is the assumption that per capita survival from the egg to the age of recruitment is a decreasing monotonic function of the number of eggs, and that the maximum reproductive rate occurs at the origin. If there exists a spawner abundance threshold, below which survival is an increasing function of the number of eggs, these models would overestimate the limits of exploitation. I therefore also examined the data for evidence of this phenomenon, which is known as depensation (Clark 1976).

5.2 Methods

I adapted the methods of Myers et al. (2001) and Barrowman (2000) for this meta-analysis. As discussed below, I began by standardizing the data so that estimates of spawner-recruit parameters among populations are comparable. After standardizing the data, I fit spawner-recruit models to the data for each population individually, and assessed how well the parameter estimates are determined for each population. I then fit

the model to all datasets simultaneously using a mixed effects model. This model provided parameter estimates for each population that is weighted by the information contained in the data for other populations, and a probability distribution for the parameter estimates for alewife at the species level.

5.2.1 The Data

I used spawner-recruit time series for 8 alewife populations in eastern North America (Table 5.1). A statistical, age-structured, life history model designed specifically for *Alosa* (Chapter 2) was used construct the spawner-recruit time series for four of these populations. This model was adapted to the data available for each population (catch at age and previous spawning data for each population, larval indices for the Margaree River population, and escapement counts for the Mactaquac Headpond and Gaspereau River populations). Existing spawner-recruit series were used for the other four populations.

5.2.2 Model Assumptions

Some assumptions about population regulation in alewife are necessary for the following analyses. I assumed that year class strength of anadromous alewives is regulated primarily hrough intra-specific competition occurring during the pre-migratory larval and juvenile life stages. As such, the carrying capacity of freshwater nursery habitat is the factor that ultimately limits the size of an alewife population. This assumption consistent with the concentration hypothesis (Beverton 1995), which implies that density dependent processes should be greatest during life stages that are most concentrated in space, and with population regulation in American shad, *Alosa sapidissima* (Savoy and Crecco 1988). The carrying capacity of the nursery habitat may fluctuate from year to year about its median, as environmental conditions within the nursery areas vary, contributing to the variability about the spawner-recruit relationship. While it is the carrying capacity of nursery habitat that ultimately limits the size of an alewife stock, I report the carrying

Table 5.1. Spawner-recruit time series used for estimating random effects distributions for the maximum reproductive rate and the carrying capacity for alewife. Details of the life history modelling are provided in Chapter 2.

River	Spawning Area (km^2)	Time Series	Data Source
Annaquatucket River RI	1.0	1945 - 1989	Crecco and Gibson 1990
Long Pond ME	3.9	1950 -1955	Havey 1961
Damariscotta River ME	18.1	1977 -1984	Crecco and Gibson 1990
Lamprey River NH	0.2	1972 - 1985	Crecco and Gibson 1990
Saint John River NB	87.3	1968 - 1994	life history model
Margaree River NB	57.4	1983 - 1995	life history model
Miramichi River NB	75.0	1982 - 1995	life history model
Gaspereau River NS	22.9	1981 - 1997	life history model

capacity as the size of the spawning run that would result at high spawner abundance in the absence of anthropogenic mortality. This makes the results directly comparable with stock assessments that provide estimates of year class size or estimates of the size of the spawning run for populations that are exploited or impacted by other human activities. Additionally, the majority of the available data is about the adult portion of the population.

I modelled the population dynamics of alewives using two equations, a spawner-recruit relationship that expresses recruitment as a density dependent function of spawner biomass, and the replacement line, the slope of which is the inverse of the rate at which recruits produce replacement spawners. Here, an implicit assumption is made that all density-dependent processes occur between spawning and recruitment. I therefore choose the age of recruitment to be 3 (the earliest age of maturity for most stocks and the latest age that could reasonably be chosen), and defined recruitment for year class t, R_t, as:

$$R_t = \sum_{a=3}^{6} \left(N_{t+a,a} / e^{-M_{juv}(a-3)} \right). \tag{5.1}$$

Here, $N_{t+a,a}$ is the number of fish of age a, in year $t+a$, that are returning to the river to spawn for the first time, and M_{juv} is the instantaneous natural mortality rate of immature alewife while at sea. I assumed $M_{juv} = 0.4$ for all populations in my analysis, based on the empirical relationship between natural mortality and longevity (maximum age of 11 years) derived by Hoenig (1983).

5.2.3 The Spawner-Recruit Relationship

The Beverton-Holt and Ricker models are the most commonly used two parameter spawner-recruit models (Hilborn and Walters 1992). These models differ fundamentally in their assumptions of the underlying biology, the later showing a decline in recruitment at higher spawner abundance, a phenomenon known as overcompensation. While this does not appear to be a characteristic of alewife populations (see Figure 5.1), I used a formal model selection criterion, the Akaike information criterion (Quinn and

Deriso 1999), to choose between these models. The Beverton-Holt model provided the better fit for all eight populations (Table 5.2). I therefore choose a Beverton-Holt spawner-recruit function for the remaining analysis, and modelled the relationship between the spawning biomass in year t, S_t, and R_t as:

$$R_t = \frac{\alpha S_t}{1 + (\alpha S_t / \mathrm{R}_0)}. \tag{5.2}$$

Here, α is the slope at the origin, and in the deterministic model is the maximum annual reproductive rate which occurs at low population sizes (Myers et al. 1999) and R_0 is the asymptotic recruitment level, which is the carrying capacity expressed as the number of fish that survive to age-3.

5.2.4 The Recruit-Spawner Relationship

I modelled the rate at which recruits produce spawners (the inverse of the replacement line) using a spawning biomass per recruit ($SPR_{F=0}$) calculation (Mace 1994) that I have adapted for alewife life history:

$$SPR_{F=0} = \sum_{a_{rec}}^{a_{max}} SS_a w_a$$

where SS_a is given by:

$$\begin{aligned}
SS_3 &= p_3 \\
SS_4 &= SS_3 e^{-M_{ad}} + (1-m_3)e^{-M_{juv}} m_4 \\
SS_5 &= SS_4 e^{-M_{ad}} + (1-m_3)(1-m_4)e^{-2M_{juv}} m_5 \\
SS_6 &= SS_5 e^{-M_{ad}} + (1-m_3)(1-m_4)(1-m_5)e^{-3M_{juv}} m_6 \\
&\cdot \\
&\cdot \\
SS_{a_{\max}} &= SS_{a_{\max}-1} e^{-M_{ad}} + (1-p_3)(1-p_4)\ldots(1-p_{a_{\max}-1})e^{-(a_{\max}-3)M_{juv}} p_{a_{\max}}
\end{aligned} \tag{5.3}$$

Table 5.2. Comparison of the fit of the Beverton-Holt and Ricker spawner-recruit for eight alewife populations. The models are Beverton-Holt: $R = \alpha S/(1 + S/K)$ and Ricker: $R = \alpha S \exp(-\beta S)$, where S is the spawner biomass (kg) and R is the number of age-3 recruits. Parameter estimates were obtained using maximum likelihood assuming a lognormal error distribution. Fits are evaluated by comparison of the log likelihoods.

	Beverton-Holt			Ricker		
Population	α	*K*	log like.	α	β	log like.
Annaquatucket River	835.7	257.5	-589.8	62.3	5.85e-5	-597.5
Damariscotta River	52.4	56,603.8	-509.8	43.7	7.31e-6	-510.3
Lamprey River	56.1	1,066.4	-146.2	36.4	1.89e-4	-150.1
Mactaquac Headpond	35.7	62,562.0	-300.6	13.3	1.47e-6	-302.4
Gaspereau River	96.1	16,271.2	-158.3	46.8	1.17e-5	-159.2
Long Pond	>10e4	<1.0	-64.9	68.1	2.39e-4	-67.8
Margaree River	73.9	93,602.3	-210.1	35.8	4.91e-5	-210.5
Miramichi River	>10e4	<1.0	-232.5	30.2	1.30e-6	-232.6
		sum =	-2212.6		sum =	-2230.8

Here, a is the age of the fish, M_{juv} and M_{ad} are the instantaneous mortality rates for immature and mature fish, m_a is the probability that an immature fish that is alive at age a will mature at that age, and w_a is the age-specific weight. Note that this model can be used to calculate SPR-based reference points (Mace and Sissenwine 1993) by changing the mortality rates to include fishing mortality. Values used in this calculation of $SPR_{F=0}$ are shown in Table 5.3, and are calculated from the life history model output (Chapter 2) for the Margaree River, Miramichi River, Gaspereau River and Mactaquac Headpond. In the absence of fishing mortality, one age-3 recruit in the Gaspereau River population can produce 0.360 kg of spawner biomass throughout its life. This value is similar to the value for the Mactaquac Headpond population (0.353 kg), but lower than the $SPR_{F=0}$ values for the Gulf of St. Lawrence populations (Margaree River: 0.652 kg; Miramichi River: 0.584 kg). I used the mean of the Gaspereau River and Mactaquac Headpond $SPR_{F=0}$ values for the other four stocks on the basis of geographic proximity.

5.2.5 Data Standardizations

The eight spawner-recruit time series are not directly comparable for two reasons. First, the sizes of the spawning and nursery areas, and hence the quantity of habitat, differ between the eight populations. I therefore standardized both the spawner and recruit time series for each population by dividing by the amount of the nursery habitat in each watershed. This standardization allows the productivity of different populations to be compared on a per unit area basis. Second, the rate at which recruits produce spawners differs among populations, which implies that the size the spawning run that would result from identical numbers of age-3 recruits also differs among populations. A second standardization corrects for this problem. I defined $\widetilde{R}_t$ as the spawner biomass per unit area of nursery habitat that is produced by members of year class t throughout their lives in the absence of anthropogenic mortality, calculated as $\widetilde{R}_t = R_t \cdot SPR_{F=0}$. After this standardization, the slope of the replacement line is one for all populations, all

Table 5.3. Values used for calculation of $SPR_{F=0}$. The weights-at-age are taken from the Margaree River population. Maturity probabilities (m_a) are calculated from the life history model output for the Margaree River, Gaspereau River, Miramichi River, and Mactaquac Headpond.

	Age (yr)						
	3	4	5	6	7	8	9+
Weight (g):	213	267	312	351	394	415	441
Margaree River m_a:	0.52	0.97	0.94	1	1	1	1
Miramichi River m_a:	0.37	0.91	0.83	1	1	1	1
Mactaquac Headpond m_a:	0.06	0.49	0.93	1	1	1	1
Gaspereau River m_a:	0.01	0.53	0.98	1	1	1	1
M_{juv}	0.4	0.4	0.4	0.4	-	-	-
M_{adult}	1.0	1.0	1.0	1.0	1.0	1.0	1.0

differences in the population dynamics are in the spawner-recruit portion of the model, and data and parameter estimates are directly comparable among populations.

In the spawner-recruit model, I denote the standardized parameters as $\tilde{\alpha}$ and $\tilde{R}_0$; $\tilde{\alpha}$ is now the maximum lifetime reproductive rate (Myers et al. 1999), and is the number of offspring (that survive to subsequently spawn) produced by a fish throughout its lifetime at low population sizes in the absence of anthropogenic mortality. As such, it is the biological limit for fishing and other sources of anthropogenic mortality. $\tilde{R}_0$ is the carrying capacity (the size the spawning run in the absence of anthropogenic mortality) per unit area of nursery habitat.

5.2.6 The Statistical Models

I used this framework to set up the statistical model. Assume data are available for several alewife populations, and for each population i, there are n_i observations of the form $(S_{ij}, \tilde{R}_{ij}), j = 1....n_i$. These observations are modelled as:

$$\tilde{R}_{ij} = \frac{\tilde{\alpha}_i S_{ij}}{1 + \tilde{\alpha}_i S_{ij} / \tilde{R}_{0i}} e^{\varepsilon_{ij}} \tag{5.4}$$

where $\tilde{\alpha}_i > 0$, $\tilde{R}_{0i} > 0$ and $\varepsilon_{ij} \sim N(0, \sigma_i^2)$. As specified, error variance differs among populations, and errors are multiplicative. Taking the natural logarithms of both sides yields:

$$\log \tilde{R}_{ij} = \log(\tilde{\alpha}_i) + \log(S_{ij}) - \log(1 + \frac{\tilde{\alpha}_i S_{ij}}{\tilde{R}_{0i}}) + \varepsilon_{ij}. \tag{5.5}$$

Let $\log \tilde{\alpha}_i = a + b_i$ and $\log \tilde{R}_{0i} = c + d_i$; then:

$$\log \tilde{R}_{ij} = a + b_i + \log(S_{ij}) - \log(1 + \left(\frac{\exp(a + b_i) S_{ij}}{\exp(c + d_i)} \right) + \varepsilon_{ij}. \tag{5.6}$$

I fit this model under two assumptions about a, b_i, c and d_i. First I treated a, b_i, c and d_i as fixed effects. This is the equivalent to fitting to each spawner-recruit series

individually, and does not take advantage of similarities between model parameters among populations of a taxonomic group. The second method takes advantage of these similarities. I assumed that $\log\tilde{\alpha}_i$ and $\log\tilde{\mathrm{R}}_{0i}$ are normally distributed random variables and fit the model treating a and c as fixed, and b_i and d_i as random effects. Here, a and c are the means of $\log\tilde{\alpha}_i$ and $\log\tilde{\mathrm{R}}_{0i}$ respectively, and b_i and d_i are the random deviates for each population, such that:

$$\begin{pmatrix} b_i \\ d_i \end{pmatrix} \overset{iid}{\sim} \mathrm{N}\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma^2{}_b & 0 \\ 0 & \sigma^2{}_d \end{pmatrix}\right]. \tag{5.7}$$

Note that when estimated using this model, $\tilde{\alpha}_i$ and $\tilde{\mathrm{R}}_{0i}$ are the median maximum lifetime reproductive rates and median carrying capacities.

I used a sigmoidal Beverton-Holt model (Thompson 1993) to look for evidence of depensation:

$$\tilde{R}_{ij} = \frac{\tilde{\alpha}_i S_{ij}^{\delta_i}}{1+\tilde{\alpha}_i S_{ij}^{\delta_i} / \tilde{\mathrm{R}}_{0i}} e^{\varepsilon_{ij}}. \tag{5.8}$$

Here, a value of $\delta > 1$ gives a depensatory model, $\delta = 1$ is the original Beverton-Holt model, and $\delta < 1$ is a model with a sharper bend than the Beverton-Holt. I fit this model to the data for each stock individually, and to all stocks simultaneously using a mixed effects model as above.

The mixed effects model is an alternative to the hierarchical Bayes approach that does not require the specification of a joint prior distribution for the fixed effects and variance components. Estimates are obtained using maximum likelihood, and are identical to empirical Bayes estimates, in that the priors are obtained from the data (often referred to as MLE priors). As such, they can be used as priors for Bayesian analyses of population dynamics for stocks where little data exists about the stock under investigation (see Chapter 6). Here, I obtain estimates for the models using the approximate maximum

likelihood algorithm of Lindstrom and Bates (1990), using the S-Plus nonlinear mixed effects library of Pinheiro and Bates (1999).

5.3 Results

Figures 5.1 and 5.2 show two views of the data and fitted models for each population. The Lamprey River data shows little scatter around the fitted models (Figure 5.1), although the other populations show considerable variability about the model. For populations such as the Miramichi River, Mactaquac Headpond, and Long Pond, the slope at the origin for the individual models is very steep (unrealistically), suggesting almost no relationship between spawner abundance and recruitment (Figure 5.1). The mixed model provides much lower slopes at the origin for these populations. Figure 5.2 is similar to Figure 5.1, but shows the data for each population on the same scale. For the five populations where the maximum observed spawner abundance exceeds 10 t/km^2, the patterns are very similar, and the carrying capacity ranges from 27 to 86 t/km^2. Two of the other populations, the Mactaquac Headpond and Long Pond are distinctly dissimilar from the other populations, and their maximum observed spawner abundance is very low in comparison with the others populations. These populations resulted by providing access to impoundments. The data for Long Pond was collected during the first few years of re-colonisation, and escapement is controlled at the Mactaquac Headpond. The eighth population, the Gaspereau River, is impacted by fishing and hydro-electric development and spawner abundances are low relative to not only to the other populations, but also to the estimated carrying capacity for that watershed.

Figure 5.3 is a meta-analytic summary of the individual fits for each population and the mixed model results for alewife at the species level. The raindrop plots (Barrowman 2000) for each population (light grey shaded region) show the profile likelihood for each parameter, the width of which can be used to gauge the relative plausibility of different values. When estimated for each stock individually, the maximum lifetime reproductive rate was well determined for only two of the eight

populations. The lower bounds of the confidence intervals are determined for the other populations, but no upper limit can be determined from the data, as shown by the ramped profiles. For the Long Pond and Miramichi River populations, the estimates of the maximum lifetime reproductive rates are essentially infinite. Note that for stocks where the likelihoods are not approximately normal, the conventional, symmetric 95% confidence intervals are not adequate approximations of the uncertainty of the estimates. Overall, the individual datasets contained more information about the habitat carrying capacity than the maximum lifetime reproductive rate, although carrying capacities varied widely between populations (Figure 5.3).

I estimated random effects distributions two ways: using the data from all eight alewife populations and using all data excluding the Mactaquac Headpond. The results are sensitive to whether or not these data are included. When all data are used, the mixed model random effects distribution for $\log\tilde{\alpha}$ has a mean of 3.03 and a standard deviation of 0.1, suggesting that at low abundance and in the absence of anthropogenic mortality, alewives can produce about 20.6 replacement spawners throughout their lives. When the Mactaquac Headpond data is excluded, the random effects distribution for $\log\tilde{\alpha}$ mean of 2.96 and a standard deviation of 0.1, suggesting a median maximum lifetime reproductive rate of 19.2 replacement spawners per spawner. When all data are used, the mixed model random effects distribution for $\log\tilde{R}_0$ has a mean of 3.35 and a standard deviation of 1.06. The median habitat carrying capacity for alewife populations (in terms of the biomass of fish in the spawning run) is therefore 28.5 t/km^2, or assuming a mean weight of 0.23kg/fish, about 124,000 fish/km^2. When the Mactaquac Headpond data are excluded, the random effects distribution for $\log\tilde{R}_0$ has a mean of 3.94 and standard deviation of 0.42. These estimates suggest a median carrying capacity of about 51 t/km^2 of nursery area.

The estimates of the maximum lifetime reproductive rate for the individual stocks resulting from the mixed effects model showed considerably less variability than those

from the individual fits (Figure 5.4). Because the habitat carrying capacities were better determined by the individual fits than the maximum reproductive, their variability showed less "shrinkage" when estimated with the mixed model than did the maximum reproductive rates (Figure 5.4). Median habitat carrying capacity ranged from a low of 3.0 t/km^2 for the Long Pond population to 86.1 t/km^2 for Lamprey River.

I did not find evidence of depensation in these datasets at the observed levels of abundance. Five of the eight data sets contain little or no information about depensation (Figure 5.5), and for two of the remaining data sets, the depensation parameter was very close to one. The mixed effects model median (0.66) is not significantly different from one (Figure 5.5).

5.4 Discussion

This analysis of the population dynamics of anadromous alewife has uncovered a number of interesting factors about the biology of this species and shows how information about a single population can be evaluated using meta-analysis. Even if one ignores the modelling, when the data for several populations are simply standardized and plotted on the same scale (Figure 5.2), patterns become evident and populations that are different are easily identified. For example, looking only at the plot for the Mactaquac Headpond in Figure 5.1, one sees a plot that is similar to many other spawner-recruit plots for other populations and species: there is scatter around the fitted spawner-recruit relationship and what looks to be a reasonable range of spawner abundances relative to the predicted equilibrium abundance. Parameter estimates can be obtained for this stock based on an individual fit, which exemplifies the traditional approach to spawner-recruit modelling. However, when the data are standardized and plotted in a way that they can be compared to other populations (Figure 5.2), it is immediately apparent that either this population, or its data, is different from the five populations where the range of observed spawner abundances is larger. For populations such as the Mactaquac Headpond, where the spawner abundance is low relative to the other populations, carrying capacity is

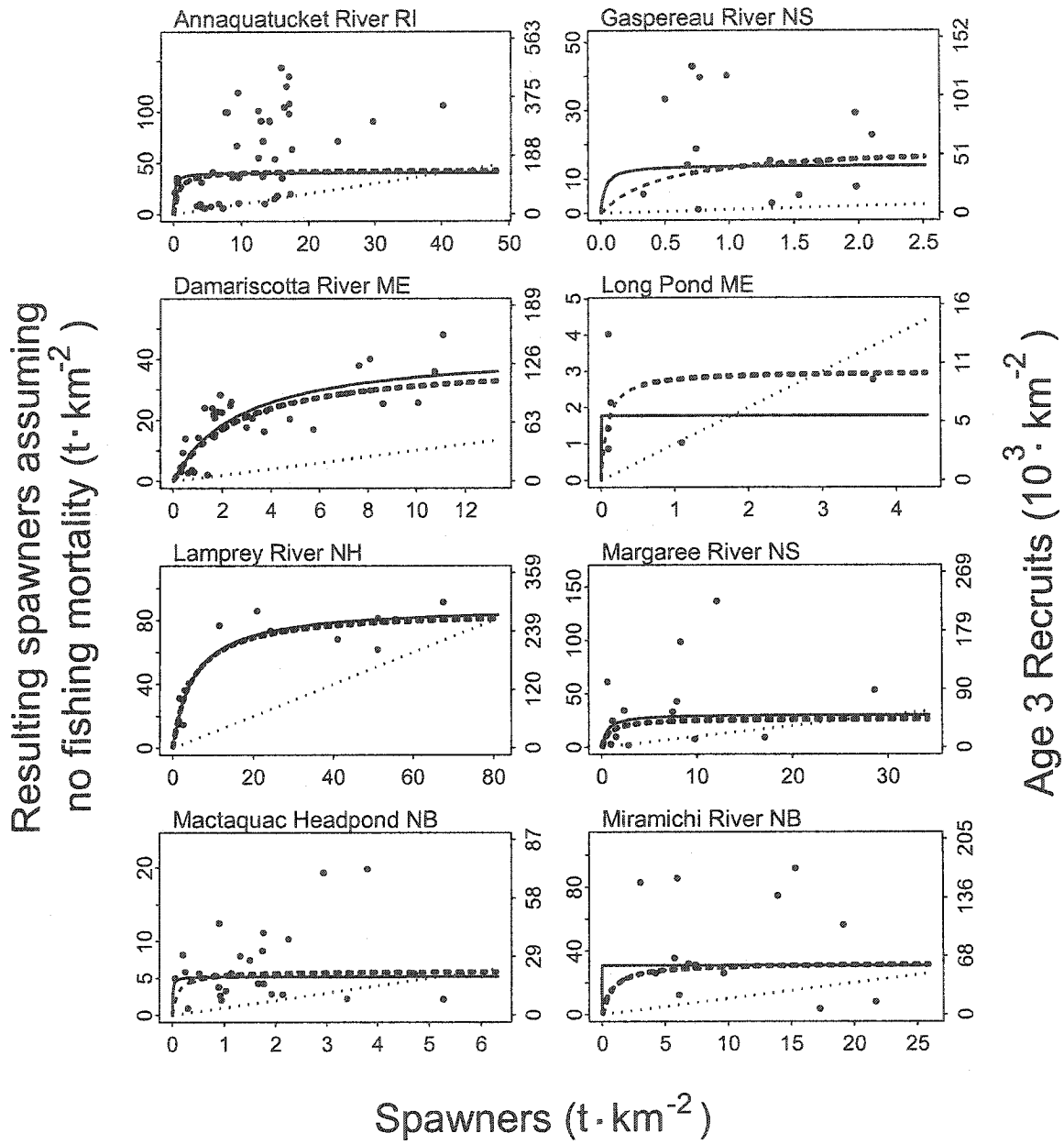

Figure 5.1. Spawner-recruit relationships for 8 alewife populations, plotted on different scales to show the variability around the fitted models for each population. The scale on the right is the number of age-3 recruits produced in each cohort. The scale on the left shows the number of subsequent spawners that would be produced by these recruits in the absence of anthropogenic mortality. The solid line is the spawner-recruit relationship obtained for each population individually, the dashed line is the spawner-recruit relationship for each stock from the mixed-effects model, and the dotted line is the replacement line.

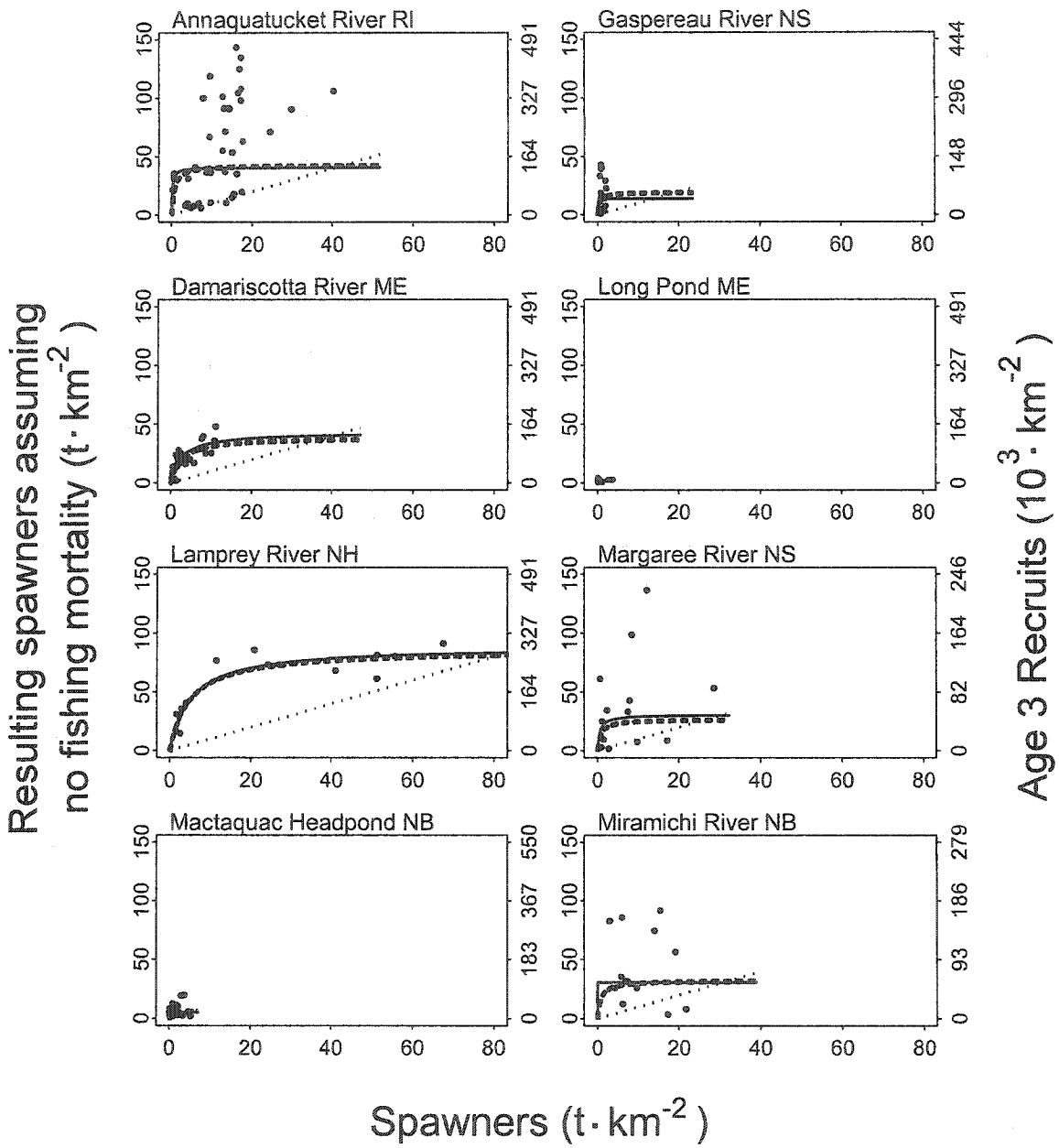

Figure 5.2. Spawner-recruit relationships for 8 alewife populations, plotted on the same scale to show the variability between populations. Line symbolism is identical to Figure 5.1.

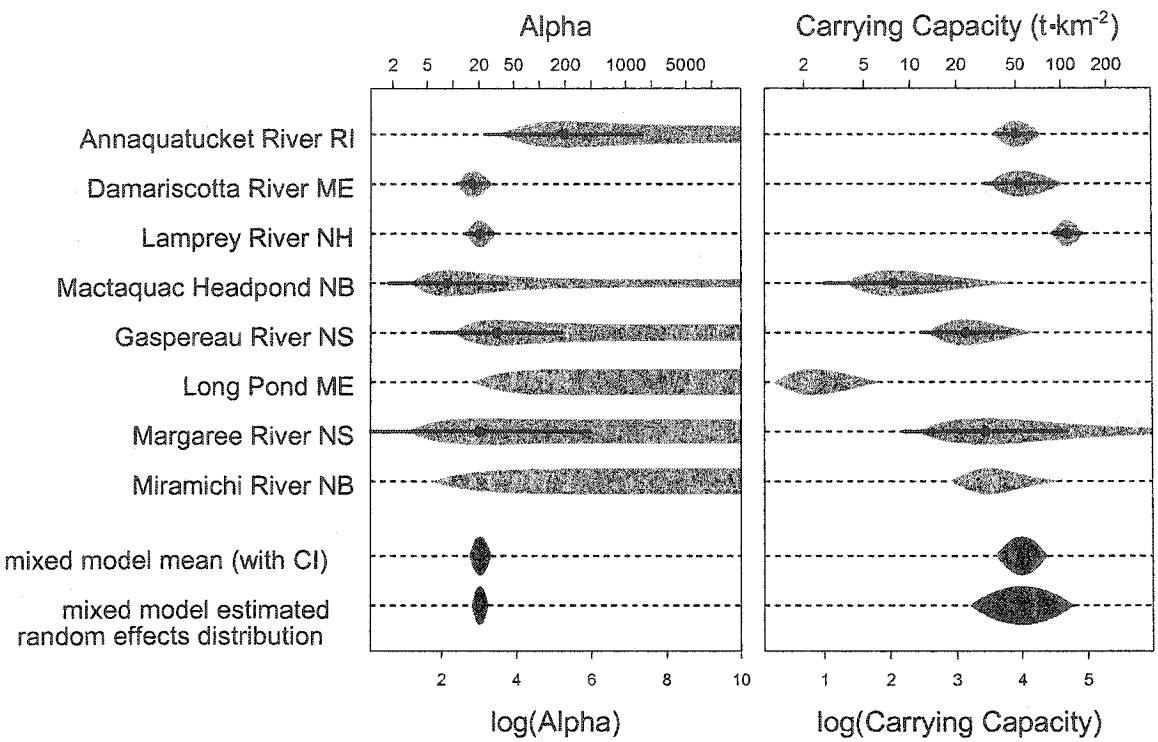

Figure 5.3. A meta-analytic summary of the maximum lifetime reproductive rate (alpha) and the habitat carrying capacity for eight alewife populations. The light grey shaded regions are individual fits that depict the profile likelihood for each parameter, truncated to show the 95% confidence interval. The profile is used to gauge the relative plausibility of different values (wider is more plausible). The black dot is the maximum likelihood estimate for each parameter. Convergence of the nonlinear least squares algorithm was not obtained for the Miramichi and Long Pond stocks. Where convergence was obtained, approximate asymptotic 95% confidence intervals are shown (black line). The dark grey shaded regions show summaries of the mixed model results. The "mixed model mean" represents the estimated mean of the logarithm of each parameter with a 95% confidence interval. The "mixed model estimated random effects distribution" is the normal distribution for the logarithm of each parameter based on its mean and variance estimated with the mixed effects model.

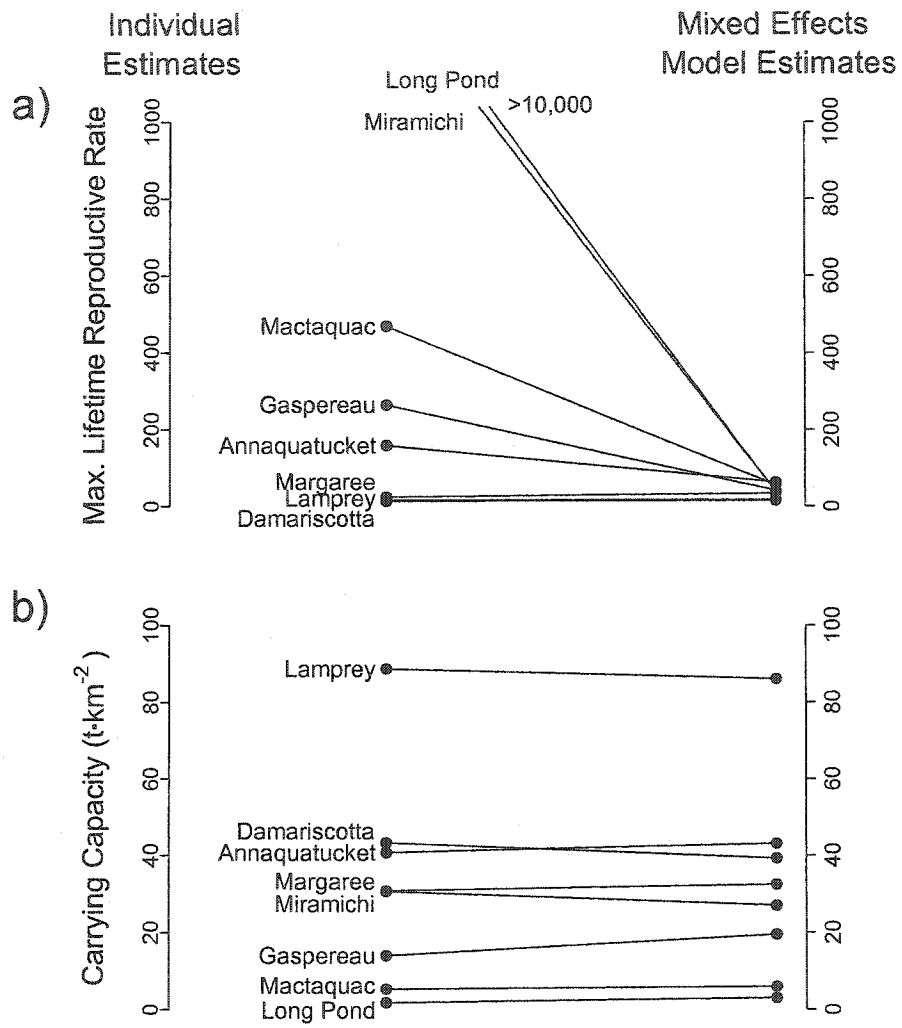

Figure 5.4. A comparison of the estimates of the maximum lifetime reproductive rate and the habitat carrying capacity obtained from individual regressions on each alewife population and the empirical Bayes estimates obtained from the mixed model.

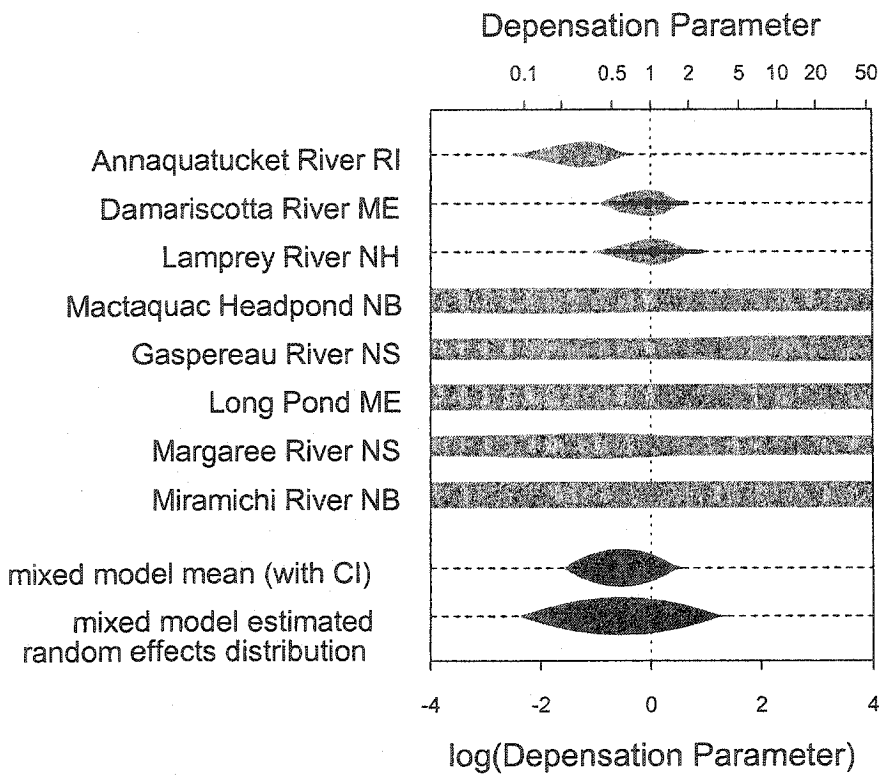

Figure 5.5. A meta-analytic summary of the depensation parameter for eight alewife populations (see Figure 5.3 for details). A value of the depensation parameter greater than one is evidence of depensation, a value equal to one returns the Beverton-Holt model, whereas a value less than one suggests a model with a sharper bend than the Beverton-Holt may be appropriate. Data for five of the populations contain little or no information about depensation when analysed individually.

probably being underestimated. This is not evident from an individual graph such as that shown in Figure 5.1. For these populations, spawner abundance would need to be increased to confirm whether the range of data is insufficient to accurately estimate spawner-recruit parameters, or whether the population is indeed different from other alewife populations. The experimental manipulation of spawner abundance to meet data requirements for management, has been strongly advocated (Walters 1986), and artificial reservoirs where spawner escapement is already controlled provide the ideal location for this kind of experimentation. However, this active approach to fisheries management has proven difficult to implement in practice (Jessop 1990a).

One of the most interesting factors to come out of this analysis is the relative constancy of the maximum lifetime reproductive rate of alewife among populations. When analysed individually, the maximum lifetime reproductive rate was well determined for only two of the eight populations. The maximum likelihood estimates for the other six populations were highly variable, had wide confidence intervals, and for the Long Pond and Miramichi River populations, were biologically unrealistic. When estimated using the mixed effects model, the variability among populations was greatly reduced, and realistic estimates were obtained for all populations.

The estimate of the maximum lifetime reproductive rate for alewife (19.3) is near the upper end of the range observed for other species. In a meta-analysis of 239 fish populations, Myers et al. (1999) found that the maximum lifetime reproductive rate of a fish species ranged from about 2 to 25. These results are not directly comparable because Myers et al. (1999) used a Ricker model for their analysis, which produces estimates of the maximum reproductive rate that are lower than those of the Beverton-Holt model (Myers et al. 1999). While the Beverton-Holt model provided a better fit to alewife data than the Ricker model, these results are not precautionary with respect to model selection because the estimated maximum reproductive rates are higher from the Beverton-Holt model. While my estimate of the maximum lifetime reproductive rate may be high

relative to other species, these results confirm that recruitment is related to spawner abundance in alewife, and that spawner abundance targets must be met to ensure adequate recruitment in this species.

When estimated using the mixed effects model, habitat carrying capacity still varied by a factor of about 25 times. This variability is similar to that determined for Atlantic cod, *Gadus morhua*, of more than 20 times (Myers et al. 2001) and coho salmon, *Onchorhynchus kisutch*, of about 10 times (Barrowman et al. 2003). However, as discussed above, I cannot discount the possibility that some of this variability may result from the carrying capacity being underestimated for some populations.

I did not find evidence of depensation in the data I examined. I was only able to estimate the depensation parameter for two of the eight populations I examined. These results, together with those of the mixed effects model, suggest that the use of purely compensatory models is appropriate for alewife. However, this finding may also reflect the limits of the data. Given that the slope at the origin is not well determined in several of the datasets, detection of an inflection point in the spawner-recruit relationship near the origin is not very feasible for these populations. A precautionary approach to the application of this result is therefore recommended.

The meta-analysis of the dynamics of fish stocks can be readily extended to the estimation of biological reference points or other management parameters and provides a basis to evaluate the plausibility of the resulting estimates. Mixed effects models, such as those used in this analysis provide probability distributions for model parameters that can be incorporated into the assessment process using Bayesian methods. When information about a population under study is compared with as many similar populations as possible, the resulting analysis and conclusions about the population under study are considerably enhanced.

CHAPTER 6. REFERENCE FISHING MORTALITY RATES FROM NOISY SPAWNER-RECRUIT DATA

6.1 Introduction

Biological reference points (BRP's) are indices based on the biological characteristics of a fish stock and the characteristics of its fishery. They are used to gauge whether specific management objectives are being achieved and provide both the link between stock assessment and management objectives (Caddy and Mahon 1995), and a basis for risk analysis of management actions (Punt and Hilborn 1997). Fishery reference points play a central role in the implementation of the precautionary approach advocated in initiatives such as the UN Straddling Fish Stocks and Highly Migratory Fish Stocks Agreement (Richards and Maguire 1998).

As the use of biological reference points becomes more prevalent in fisheries management, assessment of the precision of BRP estimates and development of methods that incorporate uncertainty into BRP estimation become more crucial (Caddy and McGarvey 1996; Overholtz 1999; Richards and Maguire 1998; Brodziak 2002). When the uncertainties surrounding the parameters used to calculate BRP's are explicitly included, "optimal" harvest policies may differ markedly from policies based on the best point estimates of these parameters (Ludwig and Walters 1982; Thompson 1992; Walters and Pearse 1996).

The most important source of uncertainty in estimating the long-term productivity of a fishery is the degree of density-dependence in the spawner-recruit (SR) relationship (Getz et al. 1987, Myers et al. 1999). However, many SR data sets contain only limited information about SR parameters for the population of interest (Myers et al. 1999). When estimated using only data from an individual population, SR parameter estimates are at times biologically implausible (e.g. estimates of the maximum rate at which spawners produce recruits that are infinite), or are poorly determined by the data (Barrowman and Myers 2000, Bradford et al. 2000, this thesis). Despite this uncertainty, the maximum

likelihood estimates (MLE) of the SR parameters are often taken to be the "best" estimates and used to calculate the fishing mortality rate that produces maximum sustainable yield (F_{msy}).

Several methods have been proposed to deal with uncertainty in the SR relationship, including methods that do not require a specification of the functional form of the SR model, methods that explicitly include uncertainty in the SR parameter estimates or model choice, and reference points that do not include an SR component. For example, the reference fishing mortality rate $F_{x\%}$ is the fishing mortality rate that reduces the spawning biomass per recruit (SPR) to x% its unfished level (Goodyear 1977, Shepherd 1982, Gabriel et al. 1989, Mace and Sissenwine 1993, Rochet 2002). This reference point is based on the premise of protecting spawning biomass, but does not require an SR relationship for its estimation. However, the selection of an appropriate value of x is problematic, and may be obtained only with reference to the productivity of a population (the SR relationship) or based on experience (Mace and Sissenwine 1993, Mace 1994, Clark 2002). Reference points based on yield per recruit (YPR) analyses (Beverton and Holt 1957) may also require adjustment based on stock productivity. Experience has shown that F_{max}, the fishing mortality rate that maximizes the yield per recruit within a cohort, advocated fishing mortality rates that were too high. As a result, the reference point $F_{0.1}$ (Gulland and Boerema 1973), which is the fishing mortality rate where the marginal gain in yield per recruit is an arbitrary 10% of that at the origin, is now more widely used. In conclusion, while reference points that do not explicitly include the reproductive capacity of the stock exist, most have one thing in common: the appropriate reference F values are chosen somewhat arbitrarily based on either experience with the stock or by comparison with F_{msy}.

Reference points that include the reproductive capacity of a population may be estimated within specification of a functional SR relationship. Getz and Swartzman (1981) used a stock- recruitment Markov transition matrix, first described by Walters (1975), to estimate the fishing effort that maximized yield without specification of the

functional relationship between spawning biomass and recruitment. Evans and Rice (1988) compared methods predicting recruitment using both a functional relationship and algorithms that did not require specification of the relationship and parameter estimation methods worked best in cases where the true functional form was known, but did not believe that the exact form of the real SR relationship could be known. Sissenwine and Shepherd (1987) proposed a reference point, F_{rep}, that is the fishing mortality rate that produces a replacement line with a slope that equals the average survival ratio (or median survival ratio, in which case it is referred to as F_{med}). It is the level of fishing mortality where recruitment has been more than sufficient to balance losses to fishing mortality in half the observed years (Jakobsen 1993). While F_{med} does not require estimates of the SR parameters, it is particularly sensitive to the range of observed spawner abundances, and is not conservative for a population that has been overexploited throughout the time period for which data are available (Jakobsen 1993, Quinn and Deriso 1999).

Bayesian and decision theoretic methods have been used to explicitly include parameter uncertainty in reference point estimation models. Clark (1991) suggested that a production-based reference fishing mortality rate could be estimated without knowledge of the true SR model by finding the fishing mortality rate that maximizes the minimum yield (F_{mmy}) over two SR models and a range of model parameters. Thompson (1992) provided an analytical solution to the problem of addressing uncertainty for single SR parameter. Ianelli and Heifetz (1995) integrated over the likelihood surface for two SR parameters to obtain the marginal probability density for the slope at the origin of the SR relationship while treating the other SR parameter as a nuisance parameter. Ianelli and Heifetz do not directly calculate a reference F from the marginal probability density for the slope at the origin, although their method does directly incorporate uncertainty in this parameter into their risk assessment. Chen and Holtby (2002) used the marginal probability density for the SR slope at the origin to estimate the probability density for F_{msy}. This approach has the advantage that uncertainty in the half saturation constant is explicitly included and that the marginal probability density for α can be used to assess

the precision of the resulting reference F. Its disadvantage is that all possible values of the SR parameters are considered equally favourable. If some points in the SR parameter space produce equilibrium yields at MSY that are higher than at other points, these points may be considered more favourable. A decision theoretic approach to estimating a reference point combines the probability for the model parameters with management objective criteria such as maximizing yield (Frederick and Peterman 1995). Brodziak (2002) used a decision theoretic approach to estimate a reference F that maximizes the expectation of the yield over two SR models (the Ricker and Beverton-Holt) and three values of the maximum reproductive rate for each model. This reference point, $F_{\mathrm{maxE[Y]}}$, is analogous to F_{msy} with the exception that uncertainty in the SR parameters is included in its estimation.

A major problem with reference point estimation based on SR analyses is that the long SR time series spanning a range of stock sizes required for the analyses are simply unavailable for many populations (Caddy and Mahon 1995, Myers and Mertz 1998a). Drawing upon the idea that populations of the same species (or closely related species) share similar life history strategies, meta-analytic methods have been developed that allow SR parameter estimates from several populations to be combined (Myers and Mertz 1998b, Myers et al. 1999, Myers et al. 2001, Myers et al. 2002). The mixed effects models used in these analyses are an alternative to a fully Bayesian approach. Estimates are obtained using maximum likelihood, and are identical to empirical Bayes estimates (Efron 1996), in that the priors are obtained from the data (often referred to as MLE priors). The analyses provide probability distributions for the parameter estimates at some higher organizational level, such as the species. These may be used as priors for Bayesian analyses (Hilborn and Walters 1992, Carlin and Louis 1996) of population dynamics for stocks where little or no data exist about the stock under investigation. When these priors are combined with data for the population of interest, the resulting Bayes posterior distribution for the population-specific SR parameters include information about the population under investigation as well as information based on experience with similar

populations. The posterior distribution can then be used to estimate a reference F, using either its mode (analogous to the MLE of F_{msy} from single species data), the marginal distribution for the slope at the origin, or by finding the fishing mortality rate that maximizes the expectation of the catch over the posterior distribution for the SR parameters.

In summary, fisheries biologists have several options for estimating a reference F depending upon the available data (Table 6.1). In the absence of sufficient data for a production model, the researcher may choose to use an alternative reference point (e.g. $F_{x\%}$), or may use a decision theoretic approach by assuming all parameter values within some bounds are equally plausible. When the researcher has sufficient population specific data for a production model, other alternatives are available. The researcher may calculate F_{msy} using either the maximum likelihood estimates of the SR parameters or the mode of the marginal probability distribution for slope at the origin (I will refer to this reference point as F_{marg} to distinguish it from the MLE-based estimate of F_{msy}.) Alternatively, the researcher may use a decision theoretic approach such as finding the fishing mortality rate that maximizes the expectation of the catch based on the likelihood surface for the SR parameters. If the researcher does not have population specific SR data, but has priors for the SR parameters obtained from other populations, reference fishing mortality rates may be found in similar ways. The researcher may estimate a reference F using either the mode of the joint prior distribution for the SR parameters, the mode of the marginal probability distribution for the maximum reproductive rate, or by finding the fishing mortality rate that maximizes the expectation of the yield given the joint prior distribution for the SR parameters. Finally, when both population specific data and data from other populations are available, the joint posterior distributions for the SR parameters may be obtained and used to estimate a reference F. In the following sections, I apply these methods, and address the question of which is best for estimating a reference fishing mortality rate.

Table 6.1. Summary of methods for estimating reference fishing mortality rates. Methods are presented in the context of the Beverton-Holt SR model, parameterized in terms the slope of the model at the origin of the SR model (α) and the asymptotic recruitment level (R_0). The maximum likelihood methods use the mode of the SR likelihood or probability surface as the estimate of α that is used to estimate F_{msy}. The marginal probability density for α is found by integrating over R_0 and the optimal F is estimated using the mode of the resulting distribution. The decision theoretic method finds the value of F that maximizes the expectation of the catch over α and R_0.

Data Requirements	Maximum Likelihood and Alternatives	Marginal Probability Density for α	Decision Theoretic Methods
Insufficient data for a production model	Alternatives: F_{med}, $F_{x\%}$, $F_{0.1}$		F_{mmy} $F_{\max E[Y]}$ (uniform bounded prior)
Population specific data only	F_{msy} from the M.L.E. of α and R_0	Integration of the likelihood over R_0 (F_{marg})	$F_{\max E[Y]}$ (likelihood only)
Data from other populations only	F_{msy} from the mode of the prior for α and R_0	Integration of the prior for α and R_0 over R_0 (F_{marg})	$F_{\max E[Y]}$ (priors only)
Combined data	F_{msy} from the mode of posterior for α and R_0	Integration of the posterior for α and R_0 over R_0 (F_{marg})	$F_{\max E[Y]}$ (priors and likelihood)

6.2 Estimating Reference Fishing Mortality Rates

In this section, I review and compare three methods of estimating reference F's when only population specific data is available. I use data from two anadromous alewife, *Alosa pseudoharengus*, populations as examples: the Gaspereau River, NS, and Miramichi River, NB. Both populations are exploited commercially as they ascend their natal rivers to spawn (DFO 2001). Descriptions of the fisheries and data collection are provided by Chaput and Atkinson (2001) and Gibson and Myers (2001). The SR time series, maturity rates and natural mortality rates for these populations were estimated in Chapter 2.

6.2.1 Estimating F_{msy}

F_{msy} may be estimated using surplus production models, spawner-recruit models for semelparous species, delay difference models, and age-structured production models (Quinn and Deriso 1992). Here, I estimate F_{msy} using a production model for alewife consisting of three parts: a spawner-recruit relationship, a spawning biomass per recruit model, and a yield per recruit model. In chapter 5, I showed that the Beverton-Holt SR model provided a consistently better fit to alewife spawner-recruit data than did the Ricker model. The Beverton-Holt spawner-recruit model gives the number of recruits (defined here as the number of offspring that survive to age-3) in year t+3, R_{t+3}, as a function of the spawning biomass in year t, SSB_t:

$$R_{t+3} = \frac{\alpha SSB_t}{1 + (\alpha SSB_t / R_0)}. \tag{6.1}$$

Here, α is the slope at the origin and in the deterministic model is the maximum rate at which spawners can produce recruits at low population sizes (Myers et al. 1999). R_0 is the asymptotic recruitment level, and is the limit approached by R_t as SSB_t approaches infinity (note that the Beverton-Holt model is often written in terms of the half saturation constant, K, which is related to R_0 by: $R_0 = \alpha K$). Parameter estimates may be obtained

using maximum likelihood assuming a lognormal error structure (Hilborn and Walters 1992, Myers et al. 1995). Denoting the Beverton-Holt spawner-recruit function as $g(SSB_i)$, the log-likelihood is given by:

$$\ell(\alpha, R_0, \sigma) = -n \log \sigma\sqrt{2\pi} - \sum \log R_i - \frac{1}{2\sigma^2} \sum \log\left(\frac{R_i}{g(SSB_i)}\right)^2 \tag{6.2}$$

where SSB_i and R_i are the observed spawner biomass and recruitment data, σ is the standard deviation of a normal distribution prior to exponentiation and n is the number of paired SR observations.

The second model component is the SPR model which gives the rate at which recruits produce spawners as a function of fishing mortality (Shepherd 1982, Mace and Sissenwine 1993, Mace 1994). For in-river alewife fisheries, this is:

$$SPR_F = \sum_{a_{rec}}^{a_{max}} SS_a w_a e^{-F}$$

where SS_a is given by:

$$\begin{aligned}
SS_3 &= m_3 \\
SS_4 &= SS_3 e^{-(M^{adult}+F)} + (1-m_3)e^{-M^{juv}} m_4 \\
SS_5 &= SS_4 e^{-(M^{adult}+F)} + (1-m_3)(1-m_4)e^{-2M^{juv}} m_5 \\
SS_6 &= SS_5 e^{-(M^{adult}+F)} + (1-m_3)(1-m_4)(1-m_5)e^{-3M^{juv}} m_6 \\
&\cdot \\
&\cdot \\
SS_{a_{\max}} &= SS_{a_{\max}-1} e^{-(M^{adult}+F)} + (1-m_3)(1-m_4)\ldots(1-m_{a_{\max}-1})e^{-(a_{\max}-3)M^{juv}} m_{a_{\max}}
\end{aligned} \tag{6.3}$$

Here, a is the age of the fish, m_a is the probability that an immature fish that is alive at age a will mature at that age, M^{adult} and M^{juv} are as the instantaneous natural mortality rates for adult and juvenile alewife respectively and w_a is the weight at age. These values are fixed constants in this analysis, although the decision theoretic methods presented herein could be extended to include uncertainty in these parameters.

For a given value of F, the spawning biomass produced by a given number of recruits in year t (throughout their lives) is $SSB = SPR_F \cdot R_t$. Equilibrium spawning biomass and recruitment levels (denoted with asterisks) may be found by solving this equation for R_t, and substituting the result in the spawner-recruit model (Quinn and Deriso 1999):

$$\frac{SSB^*}{SPR_F} = \frac{\alpha SSB^*}{1 + \frac{\alpha SSB^*}{R_0}}. \tag{6.4}$$

The equilibrium spawning biomass (SSB^*) is then:

$$SSB^* = \frac{(\alpha SPR_F - 1)R_0}{\alpha}, \tag{6.5}$$

and the equilibrium number of recruits (R^*) is found by substituting SSB^* in the spawner-recruit model:

$$R^* = \frac{\alpha SSB^*}{1 + \frac{\alpha SSB^*}{R_0}}. \tag{6.6}$$

In-river alewife fishing seasons are typically relatively short (about a month) with the majority of the catch being taken during a couple weeks. As a result, the effects of natural and fishing mortality occurring concurrently can be ignored when estimating the yield per recruit. The yield per recruit for a given F (YPR_F) is thus found analogously to the spawning biomass per recruit:

$$YPR_F = \sum_{a_{rec}}^{a_{max}} SS_a w_a (1 - e^{-F}) \ . \tag{6.7}$$

The equilibrium yield (Y^*) is then R^* multiplied by the yield per recruit for the given value of F:

$$Y^* = R^* \cdot YPR_F. \tag{6.8}$$

For a given α and R_0 pair, Y^* can be calculated for each value in a set of F's, and F_{msy} can be found using a search over the set to find the fishing mortality where Y^* is

maximized. If the maximum likelihood estimates of α and R_0 are used, the maximum likelihood estimate of F_{msy} is obtained. This is the most common method of estimating F_{msy}, but does not include uncertainty in the SR parameters in the selection of a reference F.

The data for both alewife populations show considerable variability about the fitted SR model (Figure 6.1). For the Gaspereau River population, all observed *SSB*'s are low relative to the estimated equilibrium unfished spawner biomass, and all but three are below SSB_{msy}. The SR parameter estimates ($\alpha = 96.1$, $R_0 = 1.6\,\text{million}, \sigma = 0.42$) obtained from these data appear biologically realistic, although given the limited range of the observed spawner biomasses, at least the estimate of the asymptotic recruitment level is questionable. The *SSB*'s for the Miramichi alewife population have a greater range than for the Gaspereau River, but the data exhibit greater variability about the fitted SR relationship. The SR parameter estimates for this population ($\alpha > 1\,\text{billion}$, $R_0 = 7.4\,\text{million}, \sigma = 0.94$) are biologically unrealistic: the estimate of α exceeds the fecundity of the fish, and the parameter estimates suggest that a spawner biomass of ten grams can produce half the recruitment of a spawner biomass of a million kilograms. Estimates of F_{crash} (the fishing mortality rate that drives the population to extinction) and F_{msy} from the Miramichi data exceed 5.0 suggesting that the population cannot be overfished and are simply not believable.

6.2.2 Reference Point Uncertainty

These examples illustrate some of the problems that may be encountered when deriving reference fishing mortality rates from noisy SR data. In the case of the Miramichi River population, the SR parameter estimates and resulting reference points are clearly unrealistic. Nonetheless, management advice often has to be provided when only data of this type is available. Plausible estimates are obtained for the Gaspereau River population, although they may be questionable given the limited range of the data.

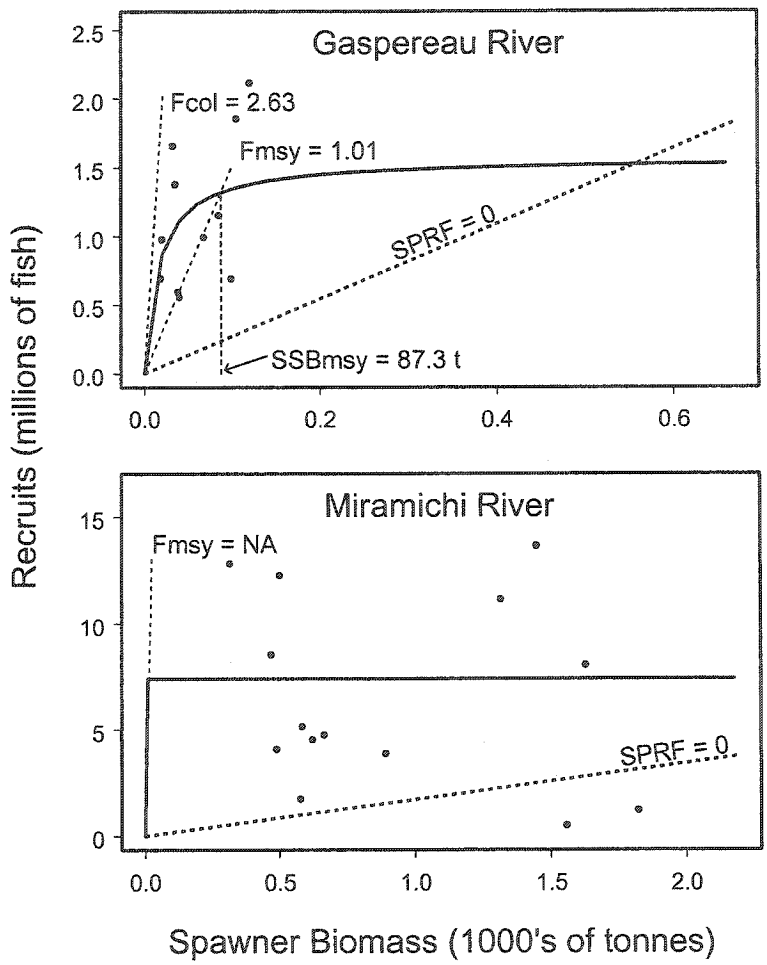

Figure 6.1. Beverton-Holt spawner-recruit models (solid line) and production model reference points for the Miramichi River (bottom) and Gaspereau River (top) alewife populations. The dashed line labelled "SPRF0" is the replacement line in the absence of fishing mortality. The slope of the SR model at the origin was essentially infinite for the Miramichi population, and reference points could not be estimated for that population.

The plausibility of an individual parameter estimate can be assessed by examining its log profile likelihood (Davison and Hinkley 1997). The log profile likelihood for α, $\ell_p(\alpha)$, is:

$$\ell_p(\alpha) = \max_{R_0\sigma} \ell(\alpha, R_0, \sigma). \tag{6.9}$$

The maximum likelihood estimate for α occurs where $\ell_p(\alpha)$ achieves its maximum value. The plausibility of other possible values of α is evaluated by comparing their log likelihoods with the maximized log likelihood. A likelihood based 95% confidence interval for α is:

$$\{\alpha : 2\left[\ell_p(\alpha^{\mathrm{MLE}}) - \ell_p(\alpha)\right] \le \chi_1^2(0.95)\}. \tag{6.10}$$

The profile likelihood and the associated 95% confidence interval for R_0 were found similarly, and for F_{msy} by mapping from the profile likelihood for α to F_{msy} using the production model.

The log profile likelihood for α for the Miramichi population is ramped: the lower bound of the 95% confidence interval for α is determined, but the maximum likelihood estimate and its upper bound are essentially infinite (Figure 6.2). For the Gaspereau River population, the MLE of α and the lower bound of its 95% confidence interval may be estimated, but $\ell_p(\alpha)$ decreases only very slightly above the MLE. The asymptotic recruitment level is better determined by the data although the upper and lower 95% confidence limits differ by a factor of about 5 times. The pattern for F_{msy} is similar to that of α; only the lower bound is determined by the data. Clearly, for data sets similar to these, the MLE of the SR parameters and the associated estimates of F_{msy} are not good reference points for fishery management.

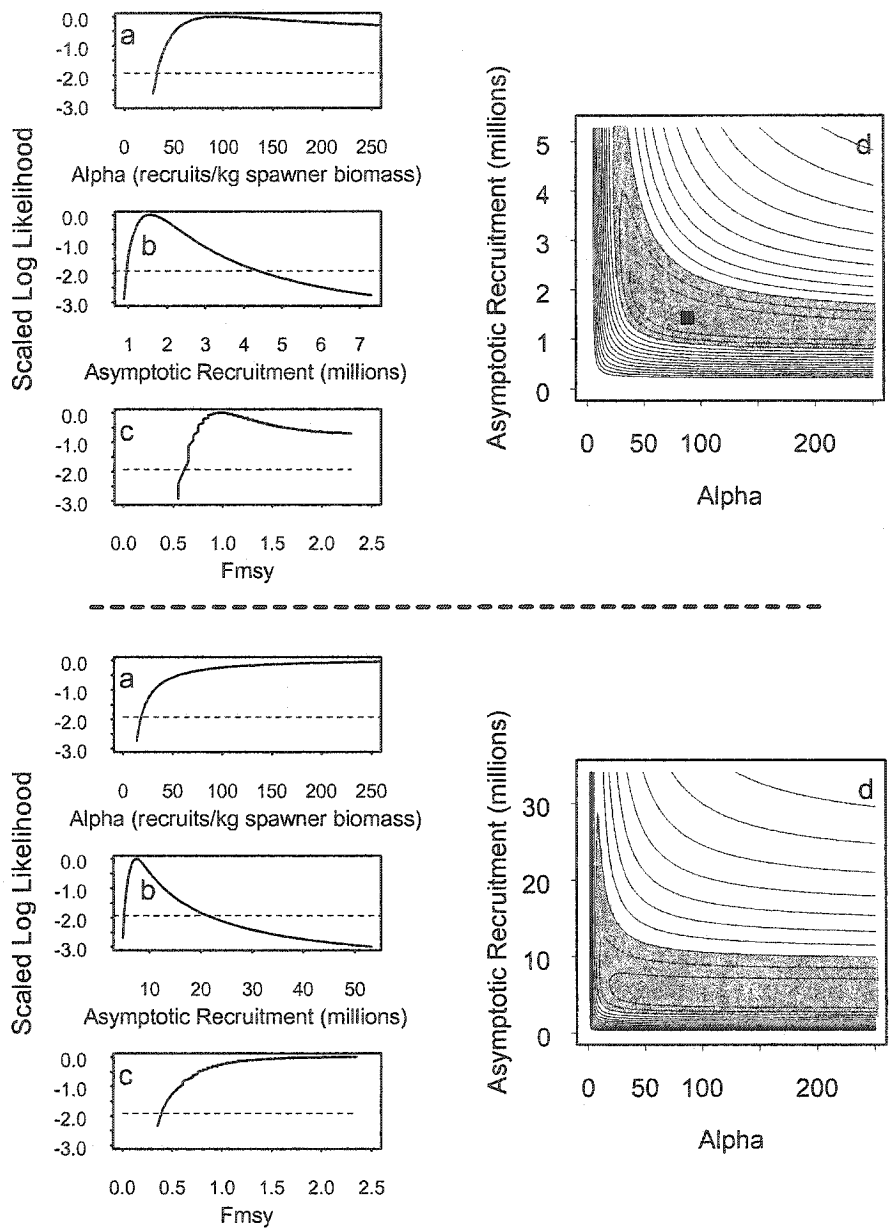

Figure 6.2. Profile log likelihoods (solids lines) for (a) the maximum reproductive rate, (b) the asymptotic recruitment level and (c) the fishing mortality rate at MSY for the Gaspereau River (top) and Miramichi River (bottom) alewife populations. The log likelihoods are standardized to a maximum of 0 by subtracting the maximum log likelihood from each estimate. The intersections between the dotted lines and the profile likelihoods show likelihood ratio based 95% confidence

intervals for each parameter. Upper and lower bounds cannot be determined for all populations. The contour plots (d) show the joint log likelihood surface for the maximum reproductive rate and the asymptotic recruitment level. The black square indicates the point at which the log likelihood is maximized (not available for the Miramichi population). The contour interval is -1 moving away from this point. The grey-shaded region shows the likelihood ratio based 95% confidence region for the parameters.

The log likelihood surfaces for α and R_0 (Figure 6.2) provide a basis for assessing the plausibility of pairs of parameter values. The surfaces for both the Gaspereau River and Miramichi populations show an "L"-shaped ridge, along which the likelihood changes only slightly. This implies that the probability of observing the data is similar, given either low values of α and high values of R_0, or high values of α and low values of R_0. One cannot choose between these scenarios on the basis of the data, and these surfaces again show the considerable uncertainty associated with the MLE of F_{msy}.

6.2.3 Incorporating SR Parameter Uncertainty when Estimating Reference F's

For both the Miramichi and Gaspereau River alewife populations, there are plausible values of α (not significantly different from the MLE of α at a 95% confidence level) for which there is the possibility that the asymptotic recruitment level is substantially higher than its MLE. The data therefore do not preclude the possibility of larger recruitments, suggesting that the subsequent catch could potentially increase if the fishing mortality rate was set below the MLE for F_{msy}. The data also suggest that larger recruitments are less plausible at the MLE for α than at lower values. An appropriate reference fishing mortality rate should not preclude the possibility of achieving larger catches, particularly if the reference rate is not significantly different from the MLE of F_{msy}. In this section, I demonstrate the two alternative methods of deriving reference fishing mortality rates that include SR parameter uncertainty: the use of the mode of the marginal probability density for α to determine F_{marg} and finding the fishing mortality rate that maximizes the expectation of the catch, $F_{\max E[Y]}$.

I begin by selecting a parameter space, Ω, for the SR model with two dimensions: α and R_0. Any point in this parameter space may be viewed as a separate hypothesis about the SR relationship for each population. I used $\alpha = \frac{1}{SPR_{F=0}}$ as the lower limit for α for each population. Below this limit, reproduction would not be sufficient to offset natural mortality and the population would go extinct. I set the upper

bound for α at 250. I used the 1st and 99th percentiles of the random effects distribution of R_0 derived in Chapter 5 for the bounds on R_0. The joint Bayesian posterior distribution is given by:

$$p(\alpha, R_0) = \left\{ \begin{array}{ll} \dfrac{L(\mathbf{R} \mid \mathbf{S}, \alpha, R_0) \cdot p(\alpha) \cdot p(R_0)}{\iint_{\Omega} L(\mathbf{R} \mid \mathbf{S}, \alpha, R_0) \cdot p(\alpha) \cdot p(R_0) d\alpha dR_0}, & \alpha, R_0 \in \Omega \\ 0 & \text{otherwise} \end{array} \right\} \tag{6.11}$$

where $L(\mathbf{R} \mid \mathbf{S}, \alpha, R_0)$ is the probability of observing the data for a given pair of parameter values, and $p(\alpha)$ and $p(R_0)$ are the prior probabilities that are the probabilities for alternative values for the parameters, before considering data for the population under consideration. In this section, I assume uniform priors over the intervals above; more informative priors are considered in a later section. The marginal probability distribution for α is calculated from the posterior distribution as:

$$p(\alpha \mid p(\alpha, R_0)) = \int p(\alpha, R_0) dR_0 \tag{6.12}$$

The mode of the resulting probability density provides an alternative estimate of α that is used to calculate F_{marg}.

For a given F, the expectation of the equilibrium yield is given by:

$$E[Y^*(F)] = \iint Y^*(F, \alpha, R_0) p(\alpha, R_0) dR_0 d\alpha \tag{6.13}$$

where $Y^*(F, \alpha, R_0)$ is the equilibrium yield as a function of the fishing mortality rate, α and R_0, and $p(\alpha, R_0)$ is the posterior density evaluated at α and R_0. The fishing mortality rate that maximizes the expectation of the yield is then:

$$F_{\max \mathrm{E}[\mathrm{Y}]} = \underset{F}{\operatorname{argmax}} \ \mathrm{E}[Y^*(F)]. \tag{6.14}$$

The estimates of F_{marg} and $F_{\max \mathrm{E}[\mathrm{Y}]}$ are less than the estimates of F_{msy} for both the Gaspereau and Miramichi River alewife populations (Table 6.2). While the estimate of F_{msy} for the Miramichi River population was essentially infinite, plausible estimates of

F_{marg} and $F_{\mathrm{maxE[Y]}}$ could be obtained. For the Gaspereau River population, the exploitation rate corresponding to F_{marg} was 7% lower than that corresponding to F_{msy}.

6.2.4 Comparison of F_{msy}, F_{marg} and $F_{maxE[Y]}$

Both F_{marg} and $F_{\mathrm{maxE[Y]}}$ provided estimates of reference fishing mortality rates that were lower than F_{msy} for Gaspereau River alewife. These reference points could also be calculated for the Miramichi River population, for which the estimate of F_{msy} was essentially infinite. Additionally, these reference points are intuitively appealing, because uncertainty in the SR relationship is explicitly included in their estimation. In this section, I compare the performance of these 3 reference points using a Monte Carlo simulation model.

The simulation model is based on the production model used to estimate F_{msy}. I ran simulations for 25 combinations of α (values: 10, 25, 50, 100, 250) and σ (0.1, 0.3, 0.5, 0.7, 0.9). A constant K was used for all simulations. For each combination, I simulated 500 SR data sets, randomly choosing 20 spawner biomasses between zero and the unfished equilibrium spawner biomass for each simulation. Recruitments were assigned to each spawner biomass by randomly selecting a value from a lognormal distribution with its mean determined by the SR function:

$$R_i = \frac{\alpha SSB_i}{1+\frac{SSB_i}{K}} \exp\left(\varepsilon_i \sigma - \frac{\sigma^2}{2}\right), \quad where\ \varepsilon_i \sim N(0,1). \tag{6.15}$$

The same random numbers were used for each set of 500 simulations to ensure that any differences detected were not an artefact of the random number generation. The reference points F_{msy}, F_{marg}, and $F_{\mathrm{MaxE[Y]}}$ were calculated for each dataset as described in the previous sections.

At low levels of recruitment variability, the three references points performed similarly (Figure 6.3). However, both F_{marg} and $F_{\mathrm{maxE[Y]}}$ consistently underestimated the true F_{msy} at higher levels of σ, whereas the MLE of F_{msy} was the least biased estimator of

the true F_{msy}. However, the maximum likelihood estimate was the most variable estimator, at times substantially overestimating or underestimating the true F_{msy}. At higher levels of α and σ, $F_{\mathrm{maxE[Y]}}$ had the least variability.

Do the benefits of least biasness outweigh the cost of high variability when choosing a method of estimating a reference F? I addressed this question by comparing the equilibrium yield, spawner biomass, yield per recruit and spawning biomass per recruit that would result if the estimated reference F's were applied to a population with the dynamics used to simulate the data. Using the case of α =50 and σ =0.9 as an example, about 25% of the populations would be highly overexploited if fished at the estimated MLE of F_{msy}, and 13.4% of the populations would be fished to extinction at this rate (Figure 6.4). None of the populations would be highly overexploited when fished at F_{marg} or $F_{\mathrm{maxE[Y]}}$ (Figure 6.4). Differences in mean equilibrium yield, spawner biomass, yield per recruit and spawning biomass per recruit resulting from the three reference F's were small at low levels of recruitment variability, but increased as variability increased (Figure 6.5). On average, $F_{\mathrm{maxE[Y]}}$ produces higher yields than either F_{msy} or F_{marg} while maintaining spawner biomasses that are on average higher than F_{msy}, but slightly lower than F_{marg} (Figure 6.5). In the example of α =50 and σ =0.9, the mean equilibrium catch obtained using $F_{\mathrm{maxE[Y]}}$ as a reference F exceeded the mean equilibrium catch obtained using F_{msy} as a reference F by a factor of 1.19, while maintaining spawner biomasses that were higher by a factor of 1.34. $F_{\mathrm{maxE[Y]}}$ typically produced YPR values between those of F_{msy} and F_{marg}, although these differences were small (Figure 6.5). F_{marg}, the most conservative reference point maintained the highest SPR levels.

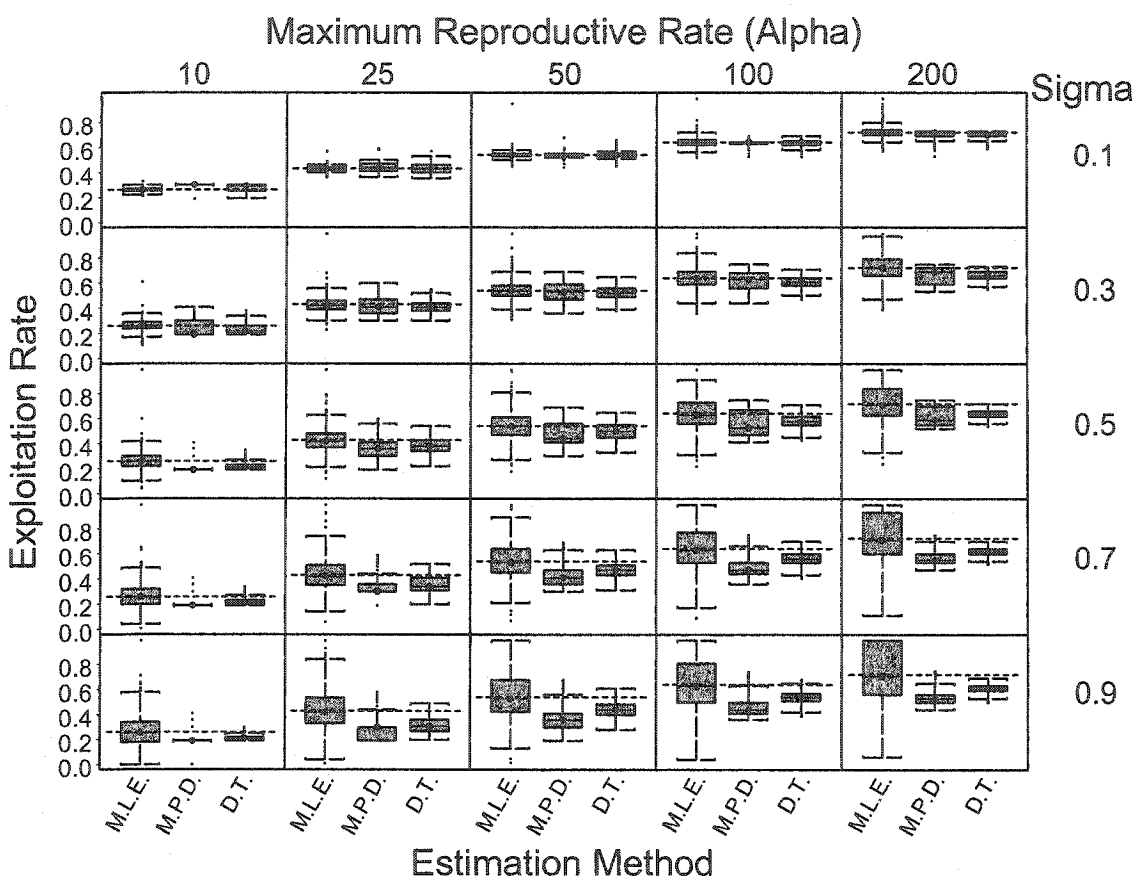

Figure 6.3. A summary of the simulation results comparing reference fishing mortality rates estimated using maximum likelihood estimation (M.L.E.), the mode of the marginal probability density (M.P.D.) and a decision theoretic model (D.T.). The box plots show the distributions of the estimated reference fishing mortality rates for 500 simulated SR datasets for each combination of the alpha and sigma. The median value is indicated with a point and the grey shaded region shows the inter-quartile range. The whiskers are drawn to the nearest value within 1.5 times the inter-quartile range. The dotted line gives the true F_{msy} for the simulated dynamics.

6.3 Including Information from Other Populations

The decision theoretic approach of maximizing the expectation of the catch is easily extended to include information from other populations. I used the random effects distribution for the log of the maximum lifetime reproductive rate and for the log of the carrying capacity (this thesis, Chapter 5) to derive priors for the SR for α and R_0. These priors contain the information about the distribution of these parameters at the species level obtained by analyzing data from other alewife populations.

The resulting prior probability densities for α and R_0 for alewife are shown together with the likelihood surface for these parameters for Gaspereau River alewife in Figure 6.6, providing a basis for assessing the plausibility of the estimates of α and R_0 for the Gaspereau River alewife population. The maximum likelihood estimate of α is high relative to the mode of the prior for α at the species level, whereas the prior for R_0 suggests that I may be underestimating R_0 using only the population specific data. The priors also suggest that the potentially very high asymptotic recruitment levels not precluded by the data are not very plausible given the species level information.

During the estimation of $F_{\mathrm{maxE[Y]}}$ in the preceding section, uniform bounded priors were assumed for $p(\alpha)$ and $p(R_0)$. The priors distributions for α and R_0 obtained from the meta-analysis are more informative alternatives for $p(\alpha)$ and $p(R_0)$, and enter directly into the estimation of $F_{\mathrm{maxE[Y]}}$ through the calculation of the Bayesian joint posterior distribution, $p(\alpha, R_0)$, shown in equation 13. When the informative priors are used, the estimates of the exploitation rate corresponding to $F_{\mathrm{maxE[Y]}}$ for Gaspereau River alewife are reduced from 61% (uniform bounded prior) to 56% (Table 6.2). For the Miramichi River population, the estimate is reduced from 68% to 53%. For both populations, the prior for α has the greatest influence on the estimates of the reference F's. As a result the estimates obtained using only the data from the other populations and using the combined data are the same (Table 6.2).

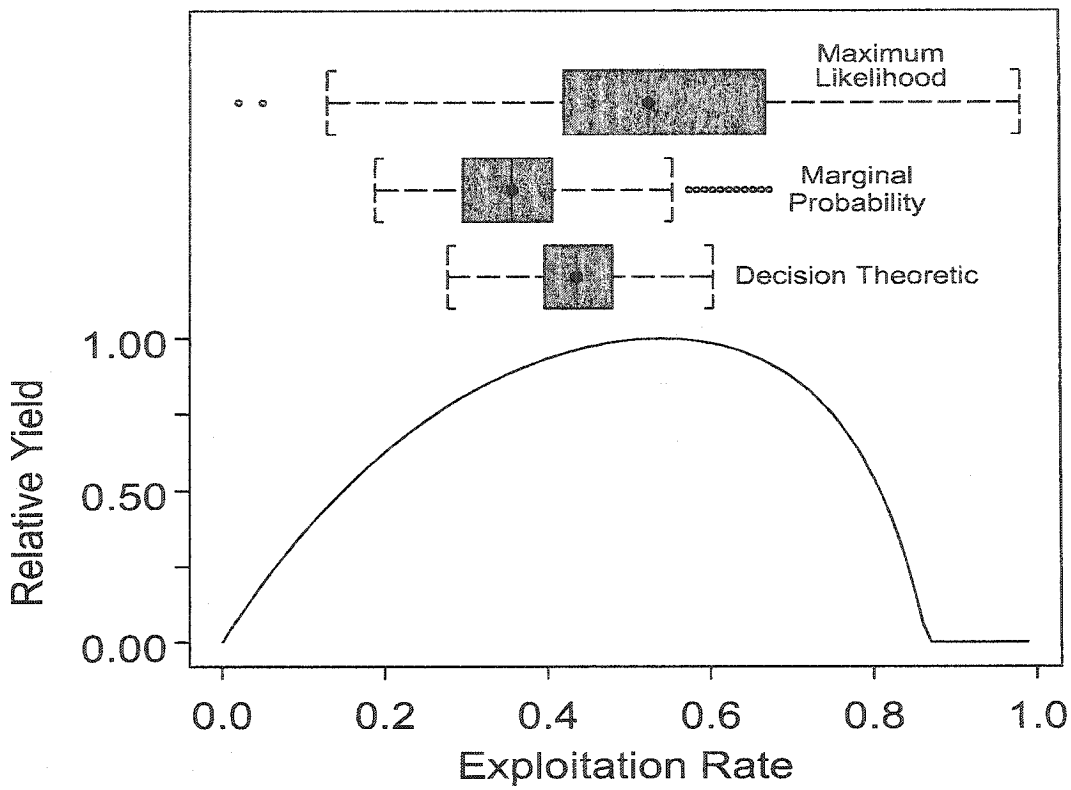

Figure 6.4. A summary of the simulation results for the maximum reproductive rate of 50 and sigma=0.9. The solid line gives the known equilibrium yield, scaled to a maximum of one, as a function of the exploitation rate. The box plots show the distribution of the reference fishing mortality rates estimated from 500 simulated SR datasets using the three methods. For each method, the solid line is the median value and the grey shaded region shows the inter-quartile range. The whiskers are drawn to the nearest value within 1.5 times the inter-quartile range. Points beyond these limits are plotted as points.

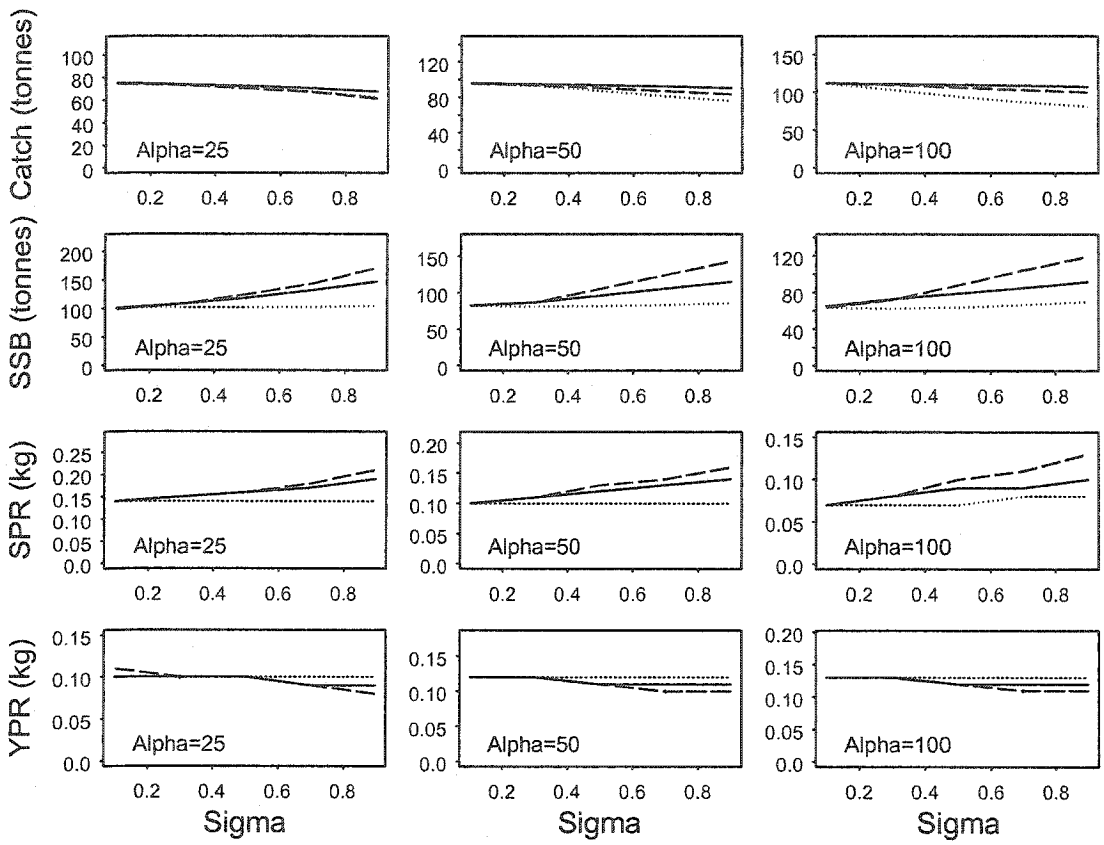

Figure 6.5. The relationship between the mean equilibrium catch, mean spawner abundance, mean spawning biomass per recruit, and mean yield per recruit for three methods of estimating reference fishing mortality rates and the variability in the SR data (sigma), based on 500 simulated SR datasets for each combination of alpha and sigma. Mean equilibrium values were calculated by applying the estimated reference fishing mortality rates for each dataset to the known dynamics used to simulate the data. The dotted line shows equilibrium values that result when the MLE of the maximum reproductive rate (alpha) is used to estimate F_{msy}, the dashed line shows the values that result when the mode of the marginal probability is used to estimate a reference F (F_{marg}) and the solid line shows equilibrium values obtained by fishing at the decision theoretic reference point $F_{\mathrm{maxE[Y]}}$.

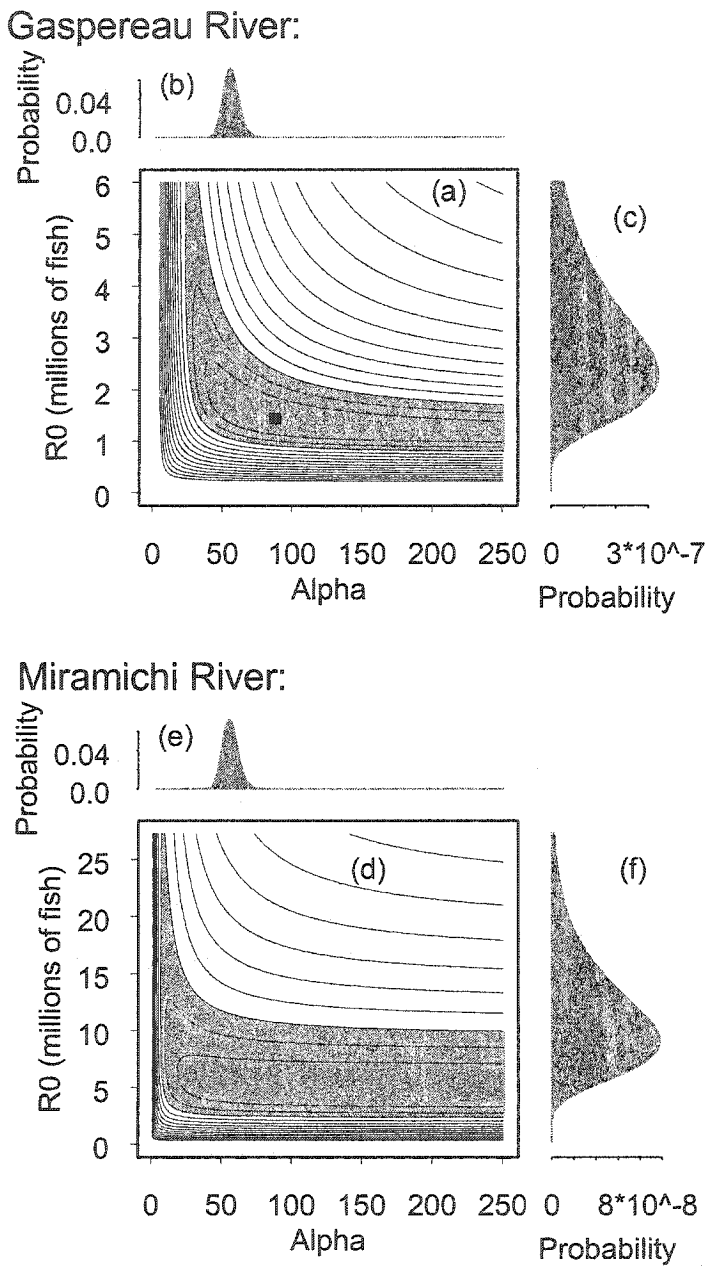

Figure 6.6. A comparison of the joint log-likelihood surface (a,d) for the slope at the origin and the asymptotic recruitment level with the random effects distributions for the slope at the origin (b,e) and the asymptotic recruitment level (c,f) for 2 alewife (*Alosa pseudoharengus*) populations. The random effects distributions are derived from a meta-analysis of eight alewife populations and

depict the distribution of the spawner-recruit parameters for alewife at the species level, and are scaled by the amount of nursery area available for these populations. The black square in the log-likelihood surface shows the point where the log-likelihood is maximized. The contour interval is -1 moving away from this point. The grey-shaded region shows the likelihood ratio based 95% confidence region for the parameters.

Table 6.2. Reference exploitation rates for two alewife populations in the Maritime Provinces, Canada, estimated using no SR data, population-specific SR data or data from other populations. Estimates are obtained using either the mode of joint likelihood or probability distributions (F_{msy}), the marginal likelihood or probability density for α (F_{marg}) or by finding the exploitation rate that maximizes the expectation of the catch ($F_{\mathrm{maxE[Y]}}$).

Reference Point	Gaspereau River	Miramichi River
No Data:		
$F_{\mathrm{maxE[Y]}}$ (uniform bounded probability surface)	0.61	0.63
Population-Specific Data Only:		
F_{msy} (maximum likelihood estimate)	0.63	>0.99
F_{marg} (mode of the marginal likelihood for α)	0.56	0.77
$F_{\mathrm{maxE[Y]}}$ (joint likelihood for α and R_0)	0.61	0.68
Data From Other Populations Only:		
F_{msy} (mode of joint prior distribution for α and R_0)	0.56	0.53
F_{marg} (mode of the marginal probability density for α based on the joint prior distribution)	0.56	0.53
$F_{\mathrm{maxE[Y]}}$ (joint prior distribution for α and R_0)	0.56	0.53
Combined Data:		
F_{msy} (mode of joint posterior distribution for α and R_0)	0.56	0.53
F_{marg} (mode of the marginal probability density for α based on the joint posterior distribution)	0.56	0.53
$F_{\mathrm{maxE[Y]}}$ (joint posterior distribution for α and R_0)	0.56	0.53

6.4 Discussion

Despite being embedded in the management objectives of many organizations and countries (Quinn and Deriso 1999; Mace 2001), the concept of MSY has been the target of much criticism (e.g., Larkin 1977; Sissenwine 1978; Mace 2001). These criticisms typically fall into three categories: problems with its implementation, its appropriateness as a management goal, and problems with its estimation (Punt and Smith 2001). Implementation problems are not specific to MSY, but apply to any management objective. In recent years, the role of MSY as a management objective has undergone a shift as a result of the development of precautionary and ecosystem-based approaches to fisheries management (Mace 2001). While the difficulty with the estimation of F_{msy} remains a valid criticism of MSY, in this chapter I have demonstrated that better reference fishing rates can be obtained by using the decision theoretic approach of maximizing of the expected yield and by including data from other populations when estimating a reference F.

When choosing any model-based reference point, an underlying mathematical model that reflects the fish population dynamics is also selected. Caddy and Mahon (1995) suggest that when selecting a reference point, rather than simply choosing the one with the best theoretical underpinnings, a more appropriate criterion may be picking the reference point that provides conservative advice under conditions of uncertainty. Francis (1997) uses a similar appeal to the precautionary principle to accept the paradigm that recruitment is related to spawner biomass. In my examples, although maximum likelihood was the least biased of the methods examined here, it provided the highest estimates for a reference F and lower average yields than the method of maximizing the expected yield, particularly when the SR data are noisy. The method of maximizing the expected yield is therefore more precautionary than the maximum likelihood method from both a conservation perspective (lower fishing mortality rates and higher spawner biomasses) and from that of maximizing yield.

In my simulations, the fishing mortality rate that maximized the expectation of the yield could be reasonably estimated from all datasets and showed much lower variability than the maximum likelihood estimate of F_{msy}. In the case of the Miramichi River alewife, the MLE of F_{msy} was essentially infinite, whereas the exploitation rate that maximized the expected yield was 0.68. This estimate is slightly higher than the average exploitation rate at MSY for alewife (0.65) reported by Crecco and Gibson (1990), and is within the range of values reported here in Chapter 7. However, using a life history based simulation model, the latter authors found that an exploitation rate of about 0.40 for in river alewife fisheries produced more than 90% of MSY, and suggested this to be a reasonable limit given that no allowances were made for factors such as implementation uncertainty. The inclusion of information from other populations through the use of informative priors lowered the estimated reference F's to 0.53 for the Miramichi population, providing a more conservative but reasonable reference F given the above results. Additionally, I did not obtain infinite estimates of the reference F's obtained from the mode of the marginal probability density or by maximization of the expected yield in any of the 12,500 simulated datasets in this study, although the estimates of infinite slopes at the origin (and the MLE of F_{msy}) were obtained for many of the simulated datasets. These results illustrate the problems with estimating F_{msy} using maximum likelihood, indicate that reasonable reference F's may be obtained by maximizing the expected yield even when the SR data exhibits considerable variability and shows that inclusion of information from other populations can also improve the resulting estimates.

While maximization of the yield performed well in my simulations, caution is warranted when using data with a limited spawner biomass range. For the Miramichi River population, the exploitation rate that maximized the expectation of the yield from the population-specific data was higher than when information from other populations was included. As shown in Figure 6.6, R_0 appears reasonably estimated for this population, but is low in comparison with other populations. While it is possible that Miramichi alewife have a higher maximum reproductive rate and lower carrying capacity

than other alewife populations, a more precautionary explanation is that this result reflects limitations of the data not overcome by maximizing the expected yield using only the population specific-data. When SR data have a limited range of spawner biomasses, R_0 may appear reasonably well estimated when in fact the estimate only reflects the average recruitment in the data series. This is the case with the Miramichi alewife data as evidenced by the infinite estimate of the maximum rate that spawners produce recruits. In these instances, the resulting reference F obtained by maximizing the expected yield may still be high relative to the true F_{msy}. Comparison with parameter estimates from similar populations (e.g. Figure 6) provides a method to detect this problem. Alternatively, SR data from several populations can be standardized so that it can be plotted on the same scale. When this is done, populations with data that are dissimilar to other populations are immediately evident (Myers et al. 2001; this thesis, Chapter 5). This method can also be used to detect populations for data is insufficient to estimate R_0.

At least in my examples, the method of maximizing the expectation of the yield clearly outperformed the maximum likelihood method of estimating F_{msy}. This finding leads to the suggestion that model fitting criteria based on management objectives may outperform those based solely on statistical criteria such as least biasness. However, in my examples, reference F's obtained from the mode of the marginal probability for the SR slope at the origin (F_{marg}) also produced higher average yields and spawner biomasses than reference F's obtained by maximum likelihood even though the F_{marg} showed the greatest bias. Also using simulations, Neilson and Lewy (2002) found that a Bayes estimate of spawning biomass in an age-structured assessment model outperformed the maximum likelihood estimate. In their example, the Bayes estimate showed less bias, but was based on the posterior mean rather than the mode. Both these analyses demonstrate the advantages of obtaining parameter estimates from the marginal probability density as opposed to maximum likelihood.

One of the most striking outcomes of my analyses is the observation that when F_{msy} was estimated from noisy SR data using maximum likelihood, a portion of the

populations could be fished to extinction if the reference F was implemented. In 13.4% of the $\alpha = 50$ and $\sigma = 0.9$ simulations, the estimate of F_{msy} exceeded the fishing mortality rate that would drive the population to extinction, and would have serious consequences for the population if used as a management target. In instances where the estimate of F_{msy} is essentially infinite, the estimate is obviously wrong and would not be used as a basis for management advice. The more serious problem occurs at low α 's when it may not be obvious when the MLE of F_{msy} exceeds the productive capacity of the population. Based on my simulations, this problem is alleviated by changing the optimization criteria for estimating the reference F: none of the simulated populations would be fished at a rate that cause extinction if fished at the rate obtained by maximizing the expectation of the yield.

Monte Carlo simulations provide a decision theoretic method to evaluate reference points or management plans (Clark et al. 1985, Francis 1993, Frederick and Peterman 1995, Hilborn 2001). For example, Clark et al. (1985) showed how decision theory could be used to choose optimal fishing mortality rates by maximizing the expectation of the yield given variability about a mean recruitment, and a known slope at the origin for the SR function. The expectation for a given F was approximated using Monte Carlo simulation, and the optimal F selected using a grid search over F. Here, SR parameter uncertainty is included via a probability surface, and I used the equilibrium yield for each combination of α , R_0 and F as a basis for evaluating the expectation of the catch. Using the equilibrium yield eliminates the need for Monte Carlo simulations to evaluate the expectation. This approach is useful for estimating BRP's for long term objectives, but is not applicable for evaluating decisions based on shorter term objectives such as recovery of an overexploited fishery (Overholtz et al. 1986, Rosenburg and Brault 1991, Rosenburg and Brault 1993).

The use of meta-analysis is becoming more common in fisheries science (e.g., Harley and Myers 2001; Chen and Holtby 2002; Dorn 2002; Millar and Methot 2002). For many species of fish, probability distributions for the maximum reproductive rate

have been derived at the species and family levels (Myers et al. 1999), and for categories based on life history strategies (Myers et al 2002). In this paper, I have shown how these distributions can be used to evaluate reference points based on stock-specific analyses, to place bounds on the range of plausible values for the SR parameters (see also Brodziak 2002), and be incorporated directly into reference point estimation. In my analyses, the priors for α and R_0 were much more informative than the data for either population, and therefore dominated the reference point estimation procedure. In Chapter 5, I did not preclude the possibility that the variance for α was underestimated in the analysis. Increasing the variance on the prior for α without changing its mean decreases the resulting reference F obtained by maximizing the expected yield.

The idea that reference points are more conservative when uncertainty is included in their estimation is not new. Ludwig and Walters (1982) found that in an active adaptive policy, inclusion of parameter uncertainty lead to higher target spawning escapements, although lower escapements could also lead to higher long term yields if they resulted in a reduction in parameter uncertainty. Walters and Pearse (1996) concluded that uncertainty in stock size estimates would significantly lower allowable catches as low-risk management policies are adopted. Decision theory provides a method for incorporating uncertainty into the decision analysis through the use of a loss function. Finding the fishing mortality rate that maximizes the expected yield provides a decision theoretic reference point with a risk neutral loss function because the magnitude of the equilibrium catch is used in its calculation. Risk adverse approaches may also be implemented without substantial modifications to the method by weighting or transforming the yield prior to maximizing the expected yield.

Both the Miramichi and Gaspereau River alewife populations have yield per recruit relationships that are ramped (see Chapter 7). The method of maximizing the expected yield given uncertainty in the SR parameters is most appropriate for fisheries similar to the fisheries on these rivers (a non-selective fishery on fish that are relatively full grown prior to recruiting to the fishery). For populations with a well determined F_{max}

(typically a fishery that catches fish over a wider size range), assumptions about the selectivity pattern, growth and survival will have greater influence on F_{msy} than in my examples. If the uncertainly associated with these parameters is quantified, it can also be included in when estimating a reference F using the method of maximizing the expected yield.

In summary, the analyses presented herein indicate that using decision theoretic methods that evaluate the quantities of interest, i.e. fishing mortality and yield, outperform more indirect methods, i.e. using maximum likelihood estimates of SR parameters to derive the fishing mortality rate that produces maximum sustainable yield. The decision theoretic reference fishing mortality rate was more conservative, produced higher yields and spawner biomasses a while reducing the probability of under- or over-exploiting the population in comparison with the maximum likelihood estimate of F_{msy}. Additionally, when data from other populations is available, they can be used either to assess the plausibility of parameter estimates, or incorporated directly into the reference point estimation process. In these ways, the use of fishery reference points as guide to fishery management can be improved.

CHAPTER 7. BIOLOGICAL REFERENCE POINTS FOR ANADROMOUS ALEWIFE (*ALOSA PSEUDOHARENGUS*) FISHERIES IN THE MARITIME PROVINCES

7.1 Introduction

Management strategies for anadromous alewife currently differ within the Maritime Provinces. In the absence of stock specific biological and fisheries information, the management objective is to maintain harvests at about their long-term mean levels (DFO 2001). Where information is available, populations in the Gulf Fisheries Management Region are managed on the basis that fishing mortality rates should not exceed the natural mortality rates, based on a review of several reference points (Chaput and Atkinson 1997). For the Margaree River, the instantaneous fishing mortality rate (F) is targeted not to exceed 0.4 (Chaput et al. 2001), whereas on the Miramichi River, the fishing mortality for alewife is targeted in the range of 0.4 to 0.5 (Chaput and Atkinson 2001). In the Scotia-Fundy Fisheries Management Region, exploitation rates (u) are targeted not to exceed the average u_{msy} (0.65, corresponding to $F = 1.0$) calculated by Crecco and Gibson (1990) for 9 alewife stocks. Whether the biology of the Gulf and Scotia-Fundy stocks is sufficiently different to warrant these different management strategies is unknown.

Here, my purpose is to evaluate reference points for alewife fisheries in the Gulf and Scotia-Fundy regions through an analysis of the population dynamics of four alewife populations in the Maritime Provinces. Two of these populations, spawn in watersheds that flow into the Gulf of St. Lawrence (the Margaree River and Miramichi River populations), and two spawn in watersheds that flow into the Bay of Fundy (the Mactaquac Headpond and Gaspereau River populations).

Process variability (variability around the SR relationship and variability in maturity schedules) can substantially alter the size of in-river spawning migrations from year to year. In this chapter I use a Monte Carlo simulation model to evaluate the

relationship between target fishing mortality rates and the performance of the fisheries when stochastic variability is added to the recruitment process (Hilborn 2001). Additionally, I compare simulations with stochastic variability in the maturity schedule with simulations using constant maturity schedules to determine whether failure to consider variability in age at maturity can lead to over-exploitation of these stocks.

7.2 Methods

7.2.1 Reference Point Estimation

I estimated reference points for the alewife populations using yield per recruit, spawning biomass per recruit and production models, using the SR time series, maturity schedules, exploitation rates and natural mortality rates estimated in Chapter 2 as a basis for the analysis. Parameter values used for reference point estimation are provided in Table 7.1. Weight-at-age vectors are provided in Table 7.2. Alewife in the Gulf of St. Lawrence populations are larger at age than alewife in Bay of Fundy populations.

I estimated five reference points using the production model presented in Chapter 6. The equilibium spawning biomass in the absence of fishing, SSB_{eq}, was estimated directly from the production model. A spawning biomass of 20% SSB_{eq} is sometimes used as a minimum threshold population size (Beddington and Cooke 1983, Goodyear 1993). $SSB_{20\%}$ was calculated as 20% the equilibrium spawner abundance in the absence of fishing. Grid searches were used to find the fishing mortality rate that produces maximum sustainable yield (F_{msy}) the corresponding spawner biomass that produces maximum sustainable yield (SSB_{msy}) and the fishing mortality rate that drives the population to extinction (F_{col}). I estimated F_{msy} by calculating C^* for each value of F, and selecting the value where C^* was maximized. SSB_{msy} was the value of S^* corresponding to this fishing mortality rate. The equilibrium fishing mortality rate at which the

Table 7.1. Parameter estimates obtained from the assessment and SR models that were used as input parameters for the simulation models and to calculate reference points.

	Population			
Parameter:	Gaspereau River	Margaree River	Miramichi River	Mactaquac Headpond
SR Model:				
α	96.10	73.88	>10,000[1]	32.79
R_0	1,563,665	6,915,954	7,400,447	2,296,051
K	16,217	93,603	<1	36,888
σ	0.42	1.26	0.94	0.65
Assessment Model:				
M^{adult}	0.53	0.44	0.49	0.25[2]
m_2	<0.01	<0.01	<0.01	<0.01
m_3	<0.01	0.52	0.37	0.06
m_4	0.53	0.97	0.91	0.49
m_5	0.98	0.94	0.83	0.93
m_6	1.00	1.00	1.00	1.00
			[1]73.88 used in simulations	[2]0.53 used in simulations and BRP calculations

Table 7.2. Weight-at-age for 3 alewife populations in the Maritime Provinces. Weights are the mean weights of alewife sampled between 1997 and 2000 in the Gaspereau River and between 1970 and 1999 for the Mactaquac Headpond, and the weights-at-age reported by Chaput et al. 2001 for the Margaree River. The Miramichi weights-at-age were used for the Miramichi River population.

	Weight (g)		
Age	Margaree River	Mactaquac Headpond	Gaspereau River
2	185	-	-
3	213	126	193
4	267	190	219
5	312	241	264
6	351	285	304
7	394	326	330
8	415	362	347
9	441	372	356
10	-	405	-
11	-	423	-
12	-	423	-

population goes extinct, F_{col}, is determined by the slope of the SR relationship at the origin α , and is the value of f where $1/SPR_{F=f} = \alpha$.

Reference points from the spawning biomass per recruit (SPR) and yield per recruit (YPR) analyses were also found using a grid search across a set of F's. I calculated YPR_F and SPR_F for each value of F, and reference points were then estimated by selecting the fishing mortality rate corresponding to the appropriate reference point criterion. The yield per recruit reference point, F_{max} was found by selecting the fishing mortality rate where YPR_F takes it largest value, and $F_{0.1}$ was found by selecting the fishing mortality rate where the marginal gain in yield was 10% that at F=0. The $F_{x\%}$ reference points were found by selecting the fishing mortality rate where the SPR_F was x% that of $SPR_{F=0}$. I estimated F_{med}, F_{high} and F_{low} by calculating the slope of the replacement line through each point in the SR time series, selecting the 10th, 50th and 90th percentiles of these slopes and selecting the fishing mortality rates that produce replacement lines with these slopes from the SPR_F vector. The decision-theoretic reference point, $F_{\text{max.E[Y]}}$, was found using the methods described in Chapter 6. Finally, reference points were calculated using the simulation model described below. These reference points include the fishing mortality rates that maximize the mean catch ($F_{\text{max.mean[Y]}}$), maximize the median catch ($F_{\text{max.median[Y]}}$), obtain 90% the mean catch ($F_{\text{90\%.mean[Y]}}$) and obtain 90% the median catch ($F_{\text{90\%.median[Y]}}$).

7.2.2 Effects of Variable Maturity on Reference Points for Alewife

The size of alewife spawning runs, and hence their availability to in river fishing is a function not only of recruitment and survival, but also of their maturity schedules, which can vary from year to year. A constant exploitation rate strategy, selected only on the basis of recruitment and survival, could substantially reduce spawner abundance in some years if maturity variability is a key determinant of run size. I investigated this possibility using a Monte Carlo simulation model based on the analysis for the Margaree

River. Random variability was introduced into the model through the recruitment process, and simulations using constant and variable maturity schedules were compared to determine whether variability in age at maturity affected the resulting reference points. The model equations are:

$$R_{t+3} = \frac{\alpha SSB_t}{1+\frac{SSB_t}{K}} \exp\left(\varepsilon_t \sigma - \frac{\sigma^2}{2}\right), \quad where\ \varepsilon_t \sim N(0,1) \tag{7.1}$$

$$N_{t,a,0} = R_{t-a+3} m_a e^{-M^{juv}(a-3)} \prod_{j=0}^{j=a-1} (1-m_j) \tag{7.2}$$

$$E_{t,a,p} = N_{t,a,p}(1-u_t) \tag{7.3}$$

$$N_{t+1,a+1,p+1} = E_{t,a,p} e^{-M^{adult}} \tag{7.4}$$

$$C_{t,a,p} = N_{t,a,p} u_t \tag{7.5}$$

$$C_t = \sum_a \sum_p \left(N_{t,a,p} u_t\right) \tag{7.6}$$

$$SSB_t = \sum_a \sum_p (E_{t,a,p} w_a) \tag{7.7}$$

For each population, the parameters α , R_0, σ were obtained from the SR model, M^{adult} and the mean maturity schedules, m_a, from the assessment model. I did not find evidence of autocorrelation in the residuals of the SR models for any of the populations, and therefore treated the deviates around the SR relationship as uncorrelated. I mapped the probability that a fish that is alive at age a matures at age a to the real line using a logistic transformation:

$$\text{logit}(m_a) = \log\left(\frac{m_a}{1-m_a}\right). \tag{7.8}$$

For each cohort, logit(m_a) was calculated for age classes 2 to 5, and the mean and standard deviations of m_a for each age class were calculated to describe the maturity process. For simulations with variable maturity schedules, a random component was

introduced on the logistic scale by drawing a random number from a normal distribution with the mean and standard deviation above. This value was back-transformed to obtain the random m_a:

$$m_a = \frac{\exp(\text{logit}(m_a) + \varepsilon_a)}{1 + \exp(\text{logit}(m_a) + \varepsilon_a)}, \text{ where } \varepsilon_a \sim N(0, \text{var}(\text{logit}(m_a))). \quad (7.9)$$

To find the exploitation rate (u) that produces maximum sustainable yield, I carried out simulations for u's ranging from 0 to 0.99 at an increment of 0.01. I assumed that the management strategy (fixed exploitation rate) was implemented without error. For each u, I carried out 100 simulations with maturity schedules that were constant and 100 simulations with maturity schedules that were random. The same set of random numbers was used for each exploitation rate and maturity schedule combination to ensure that any differences were not an artefact of the random number selection. I started each simulation at the equilibrium spawner biomass and age composition for the given exploitation rate and projected the population for 50 years.

7.2.3 Simulation-Based Reference Points

I also used Monte Carlo simulations to examine the relationships between exploitation rates, catch and spawning escapement for each population, under the assumption of a fixed maturity schedule. Using the method above, for each simulation, I calculated the minimum, maximum, mean, median, standard deviation, and 10th through 90th percentiles (increment of 10) of the catch and spawning escapement to summarize the projection. I then used the mean of these summary statistics for each exploitation rate to evaluate the effect of fishing at that rate on the population size and catch.

7.2.4 Relationship between turbine mortality and fishery reference points

I examined the relationship between juvenile and adult turbine mortality using small modifications to the production model and input parameters for Gaspereau River

alewife. I assumed that juvenile turbine mortality occurred after compensation within the population. Given this assumption, the production of recruits (given by the SR component of the model) is reduced in direct proportion to the rate of juvenile mortality. Adult mortality is incorporated into the SPR component of the model after spawning and before fishing the following year. Using this modified production model, I calculated reference points of turbine mortality ranging from 0 to 100% at steps of 1%.

7.3 Results

7.3.1 Reference Point Estimation

Reference points for the 4 alewife populations are shown in Table 7.3. The fishing mortality rate that maximized the yield per recruit, F_{max}, was greater than 3.0 for all populations. $F_{0.1}$ was ranged between 0.61 for the Margaree River population and 0.86 for the Mactaquac Headpond population.

Because of differences in the maturity schedules and weights -at-age, the spawning biomass per recruit in the absence of fishing for the Gulf populations is almost twice that of the Scotia-Fundy populations (Figure 7.1). However, the fishing mortality rates that reduced spawning biomass per recruit to 35% the level without fishing mortality was similar for all populations (range: 0.47 to 0.54). The reference points F_{med}, F_{high} and F_{low} varied between populations (Table 7.3), potentially as a result of the different ranges of spawner abundances for each population (Figure 7.2). F_{low} equalled 0.0 for three of the four populations, indicating that recruitment was insufficient for replacement more than 10% of the time in these populations.

The fishing mortality rate that produces maximum sustainable yield, F_{msy}, estimated from the production model using the maximum likelihood estimates (M.L.E.'s) for α , ranged from 0.68 for the Mactaquac Headpond to >4.0 for the Miramichi River. The fishing mortality rate that drives the population to extinction, F_{col}, ranged from 1.82 for the Mactaquac Headpond to >4.0 for the Miramichi River. The spawning biomass that

Table 7.3. Biological reference points for the Margaree River, Gaspereau River Miramichi River and Mactaquac Headpond alewife populations. Values in brackets are the corresponding exploitation rates. Definitions of the reference points are explained in the text.

Theoretical Basis	Reference Point	Margaree River	Gaspereau River	Miramichi River	Mactaquac Headpond
Yield/Recruit	$F_{0.1}$	0.61 (0.50)	0.86 (0.58)	0.76 (0.53)	0.76 (0.54)
	F_{max}	>3.0 (>0.99)	>3.0 (>0.99)	>3.0 (>0.99)	>3.0 (>0.99)
Spawner/Recruit	$F_{35\%}$	0.47 (0.37)	0.54 (0.42)	0.50 (0.39)	0.51 (0.40)
	$F_{25\%}$	0.67 (0.49)	0.77 (0.54)	0.71 (0.51)	0.72 (0.52)
	F_{med}	0.86 (0.58)	1.12 (0.67)	0.79 (0.54)	0.42 (0.34)
	F_{high}	1.88 (0.85)	1.98 (0.86)	1.61 (0.80)	1.03 (0.64)
	F_{low}	0.00 (0.00)	0.93 (0.60)	0.00 (0.00)	0.00 (0.00)
Production Model	F_{col}	2.72 (0.93)	2.60 (0.92)	4.61 (>0.99)	1.82 (0.84)
	F_{msy}	0.98 (0.62)	1.01 (0.63)	4.61 (>0.99)	0.68 (0.41)
	SSB_{msy}	622.3 t	85.8 t	14.1 t	123.0 t
	$SSB_{20\%}$	883.8 t	109.3 t	865.3 t	112.5 t
Decision Theoretic Simulation Based	$F_{\mathrm{max.E[Y]}}$	0.75 (0.53)	0.82 (0.56)	0.75 (0.53)	0.75 (0.53)
	$F_{\mathrm{max.mean[Y]}}$	0.78 (0.55)	0.94 (0.61)	0.86 (0.58)	0.53 (0.41)
	$F_{\mathrm{max.median[Y]}}$	0.71 (0.51)	0.91 (0.60)	0.84 (0.57)	0.53 (0.41)
	$F_{\mathrm{90\%.mean[Y]}}$	0.44 (0.36)	0.52 (0.41)	0.47 (0.38)	0.33 (0.28)
	$F_{\mathrm{90\%.median[Y]}}$	0.37 (0.31)	0.51 (0.40)	0.43 (0.35)	0.31 (0.27)

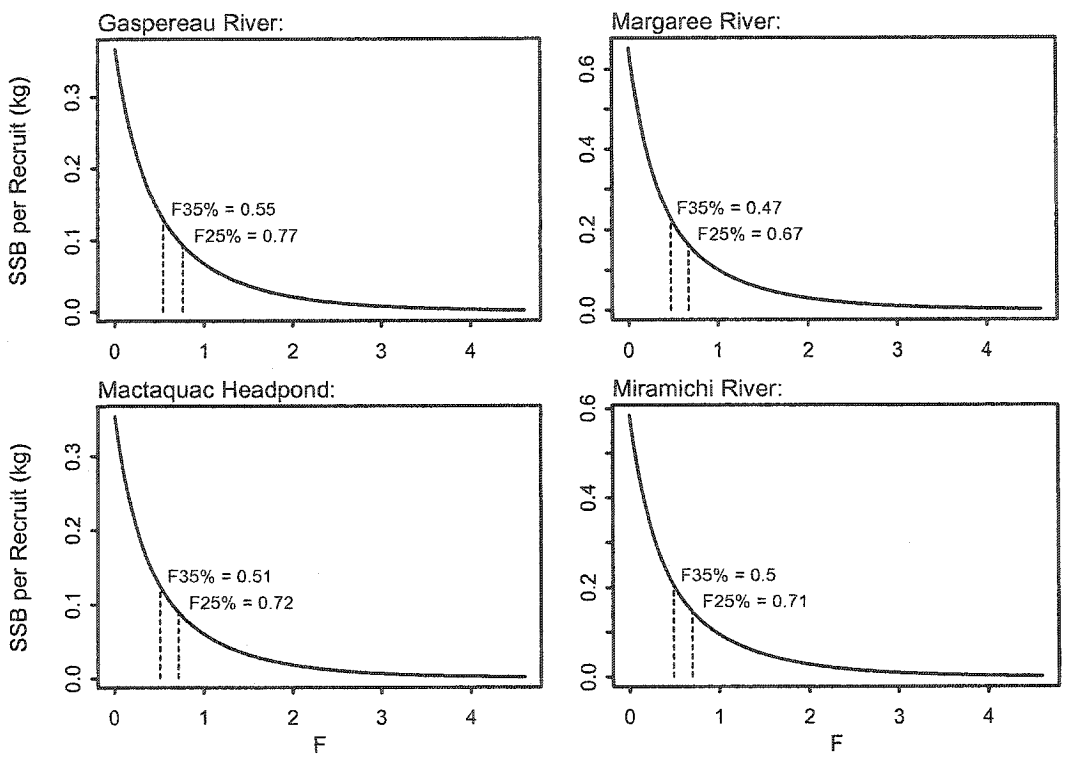

Figure 7.1. The relationship between the instantaneous rate of fishing mortality (F) and spawning biomass per recruit for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations.

produces maximum sustainable yield, SSB_{msy}, was less than $SSB_{20\%}$ for all populations except the Mactaquac Headpond (Table 7.3).

The relationships between the reference points from the production model are shown together with the SR data in Figure 7.2. The data for all populations show considerable variability about the fitted SR model. For the Gaspereau River, all spawner abundances are below $SSB_{20\%}$ and all but three observations are below SSB_{msy}. The pattern is similar on the Margaree River, where all but three spawner abundances are below SSB_{msy}.

The production model reference points were calculated using the maximum likelihood estimates from the SR model, and the resulting reference points are therefore only as good as the SR parameter estimates. Profile likelihoods (Figure 7.3) show that the while lower bound for a 95% confidence interval for alpha is determined for all populations, the upper bound is not determined for all populations except the Mactaquac Headpond (the profiles are ramped). Similarly, the 95% confidence interval for the asymptotic recruitment level is very wide for all populations. Profile likelihoods for the exploitation rate at MSY and SSB_{msy} are shown in Figure 7.4. Lower bounds on the 95% percent confidence interval for u_{msy} range from 0.24 (Margaree River and Mactaquac Headpond) to 0.32 for the Miramichi River. The upper bound for the 95% confidence interval (0.83) was only determined for the Mactaquac Headpond. Similarly, the lower bound on 95% confidence interval for SSB_{msy} could only be determined for the Mactaquac Headpond population.

7.3.2 Effects of Variable Maturity on Reference Points for Alewife

Comparison of the simulation results with variable and constant maturity schedules for the Margaree River show that variability in the maturity schedule has little effect on either the mean catch or spawning escapement (Figure 7.5), and hence little effect on the reference points. Standard deviations of the catch and spawning escapement are only slightly higher when stochastic variability in the maturity schedules is included

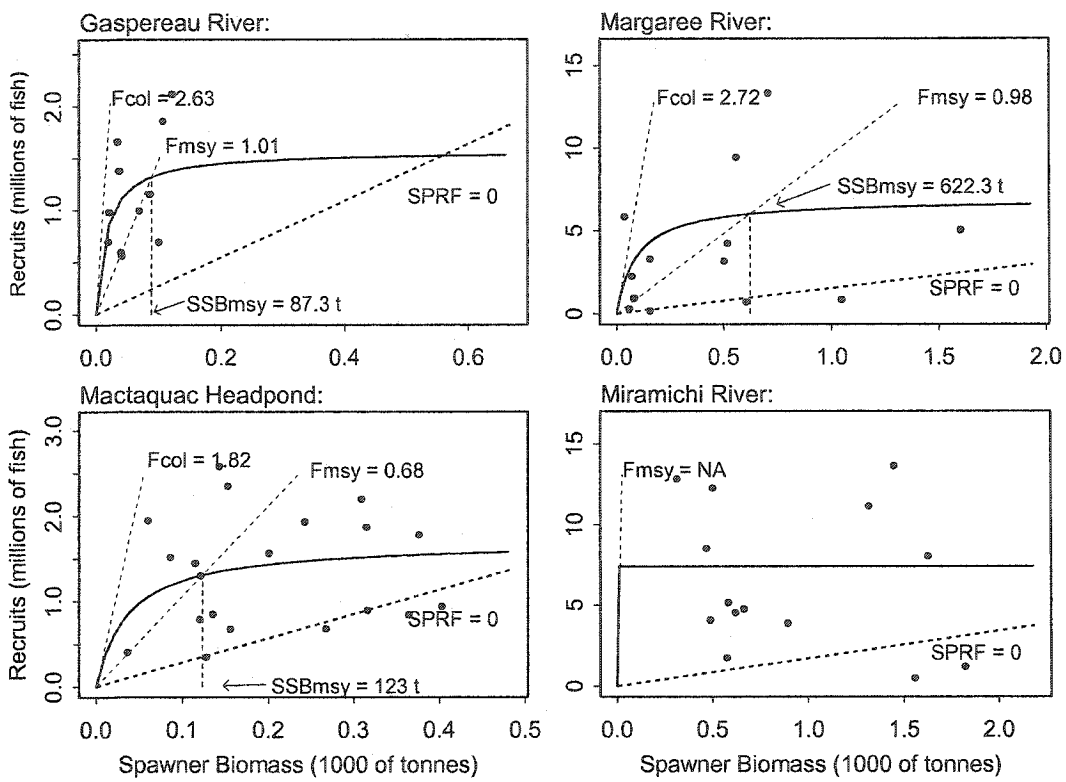

Figure 7.2. Beverton-Holt spawner-recruit models (solid line) and production model reference points for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations. The dashed line labelled "SPRF=0" is the replacement line in the absence of fishing mortality.

in the simulations (Figure 7.5). Comparison of the percentiles of the catch (not shown) indicates that the distribution of the catch is only slightly more skewed when variability in the maturity schedule is included. Simulations with a range of α's and σ's indicate that the variability around the SR model together with the high maximum reproductive rate have a much greater influence on spawning run size than does variability in the maturity schedule.

7.3.3 Simulation-Based Reference Points

Summaries of the simulation results are shown for the Margaree River (Figure 7.6), Miramichi River (Figure 7.7), Mactaquac Headpond (Figure 7.8) and Gaspereau River (Figure 7.9). The fishing mortality rate that maximizes the mean catch, $F_{\text{max.mean[Y]}}$, ranged from 0.53 for the Mactaquac Headpond to 0.94 for the Gaspereau River (Table 7.3). The fishing mortality rate that maximized the median catch, $F_{\text{max.median[Y]}}$, ranged from 0.53 for the Mactaquac Headpond to 0.91 for the Gaspereau River. For all populations, the median catch curve is relatively flat over the middle part of the curve. The fishing mortality rates that produce 90% of the maximum of the median catch, $F_{\text{90\%.median[Y]}}$, ranged between 0.31 for the Mactaquac Headpond to 0.51 for the Gaspereau River population. These results show that exploitation rates can be reduced by nearly 20% from the rate that maximizes the mean catch with only a 10% reduction in the average yield of the fishery.

Francis (1993) proposed that a level of harvesting could be considered "safe" if it maintained the spawning stock biomass above 20% its mean virgin level at least 90% of the time. The 10th percentile of the simulation results can be used to find this level. Assuming a mean weight of 0.25 kg/fish, the exploitation rates that match this criterion are: 0.18 for the Margaree River, 0.42 for the Gaspereau River, 0.41 for the Mactaquac Headpond, and 0.27 for the Miramichi River. These rates are sensitive to the coefficient of variation assumed for the SR simulations (the Margaree River had the highest coefficient of variation, while the Gaspereau River had the lowest).

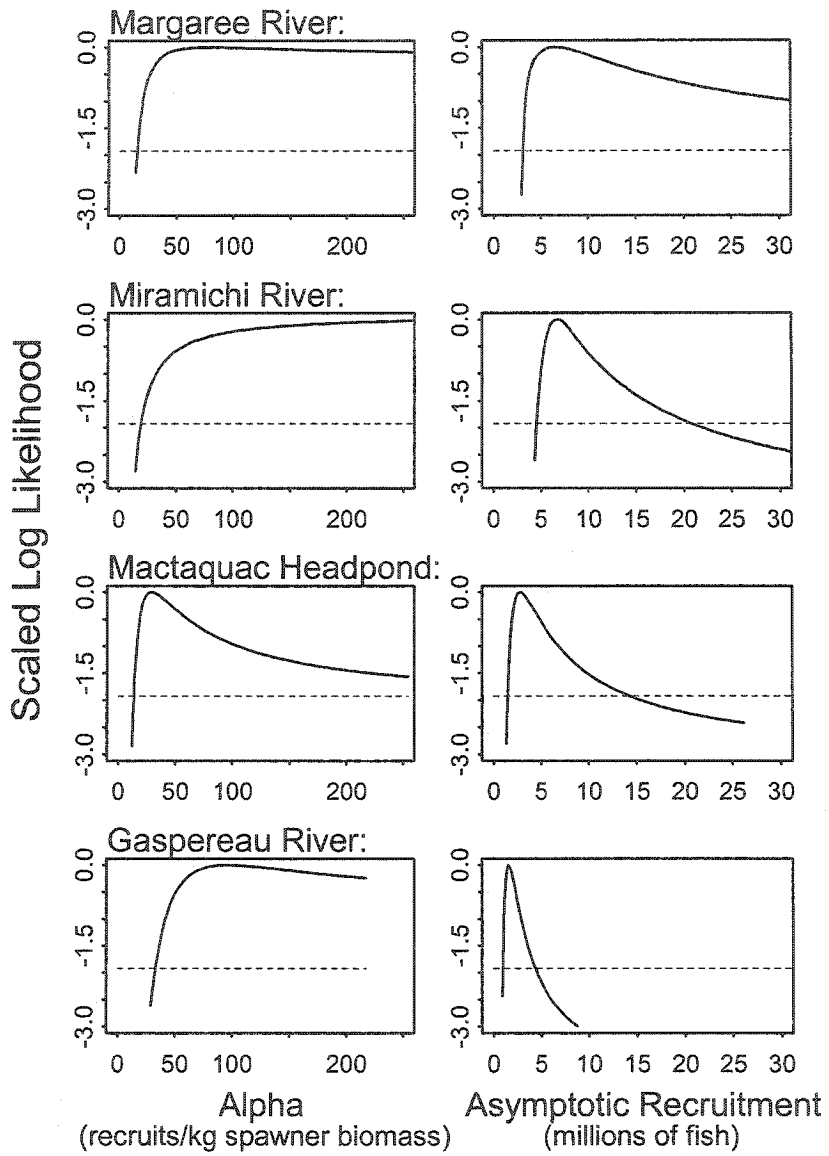

Figure 7.3. Profile log likelihoods (solids lines) for alpha (left column) and the asymptotic recruitment level (right column) for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations. The log likelihoods are standardized to a maximum of 0 by subtracting the maximum log likelihood from each estimate. The intersections between the dotted lines and the profile likelihoods show a likelihood ratio based 95% confidence intervals for each parameter. Upper and lower bounds cannot be determined for some populations

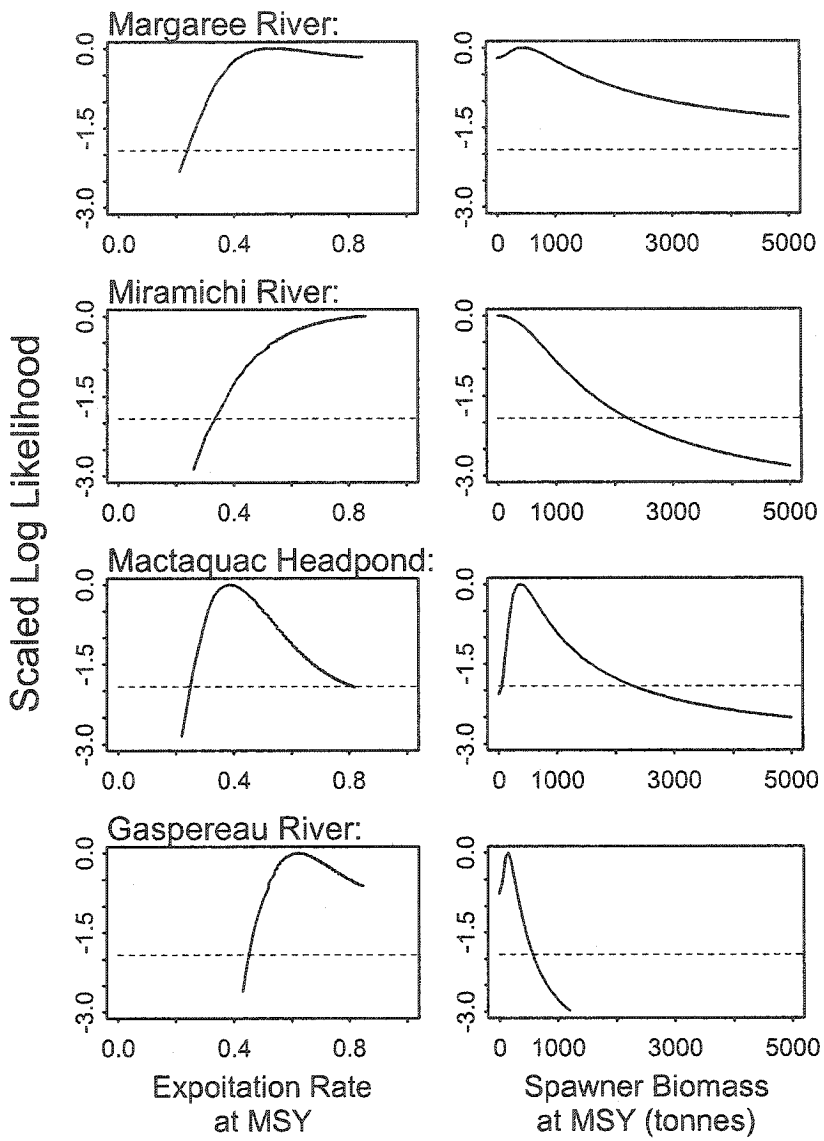

Figure 7.4. Profile log likelihoods (solids lines) for the exploitation rate that produces maximum sustainable yield (left column) and the spawning biomass that produces maximum sustainable yield (right column) for the Margaree River, Miramichi River, Mactaquac Headpond and Gaspereau River alewife populations. The log likelihoods are standardized to a maximum of 0 by subtracting the maximum log likelihood from each estimate. The intersections between the dotted lines and the profile likelihoods show a likelihood ratio based 95% confidence intervals for each parameter. Upper and lower bounds cannot be determined for all populations.

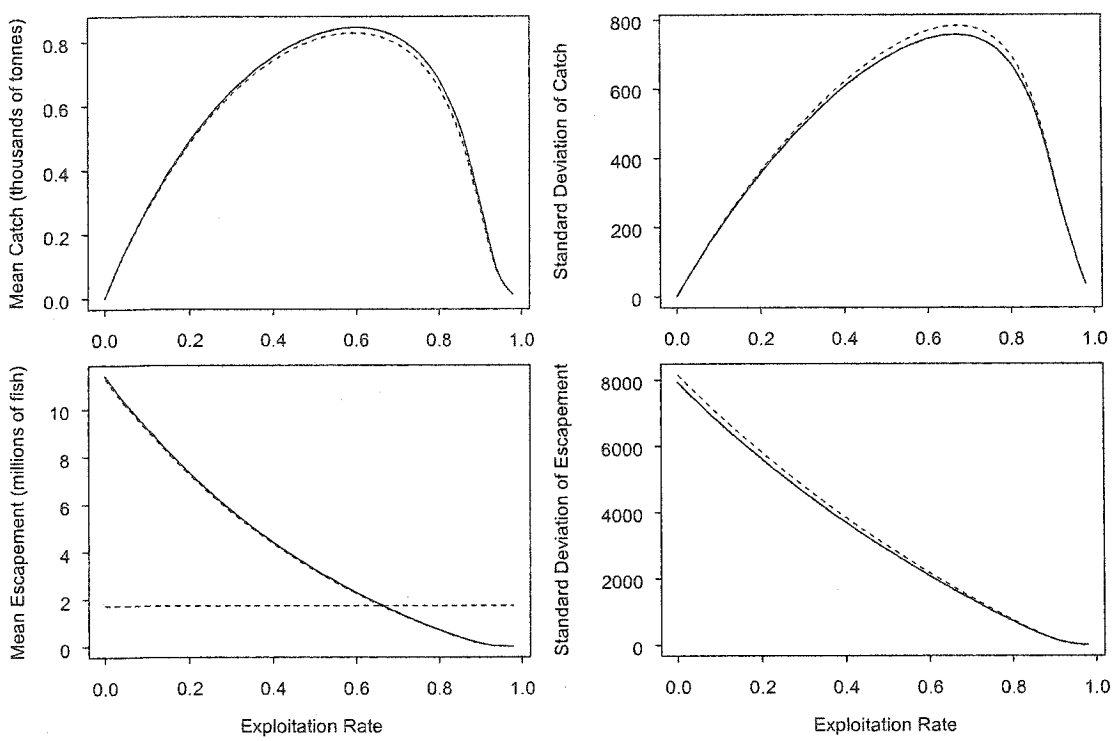

Figure 7.5. Comparison of simulation results for the Margaree River using constant (solid lines) and variable (dashed lines) maturity schedules. The lines give the means of the summary statistics (mean and standard deviation) for the catch and spawning escapement for a 50 year time period. The means are calculated from 100 simulations at each exploitation rate (0.0 to 0.99 with an increment of 0.01). The horizontal dashed line in the lower, left plot is the spawning escapement that gives maximum sustainable yield.

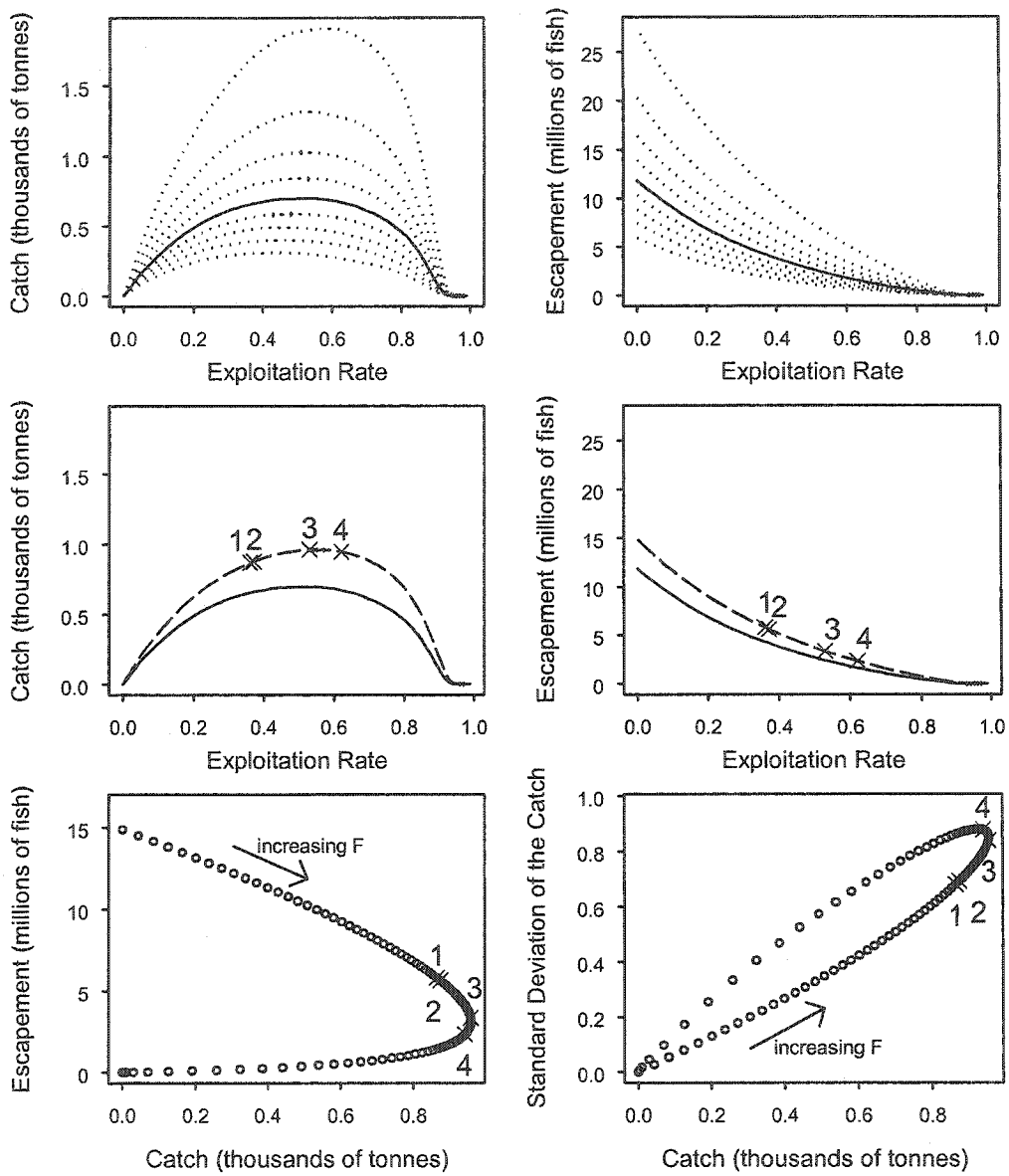

Figure 7.6. A summary of the simulation results for the Margaree River alewife population. Each plot summarizes 100 population projections (50 year duration) at each exploitation rate,u, (0.0 to 0.99 with an increment of 0.01). The solid line in the upper two plots are the median catch and spawning escapements as a function of u. The dashed lines are the 10th to 90th percentiles (bottom to top lines) of the catch and spawning escapements. The middle two plots show the median (solid lines) and mean

(dashed lines) catch and spawning escapement as a function of u. The points are the exploitation rates corresponding to 1: $F_{90\%max.med}$, 2: $F_{35\%}$, 3: $F_{max.E(C)}$, and F_{msy}. The bottom left plot shows the relationship between spawning escapement and catch. Each point represents the mean of 100 simulations at each exploitation rate (the uppermost point is $u = 0.00$, and u increases by 0.01 to a maximum of 0.99 in the lower left corner). The lower right plot shows the relationship between the standard deviation of the catch and the catch for each u.

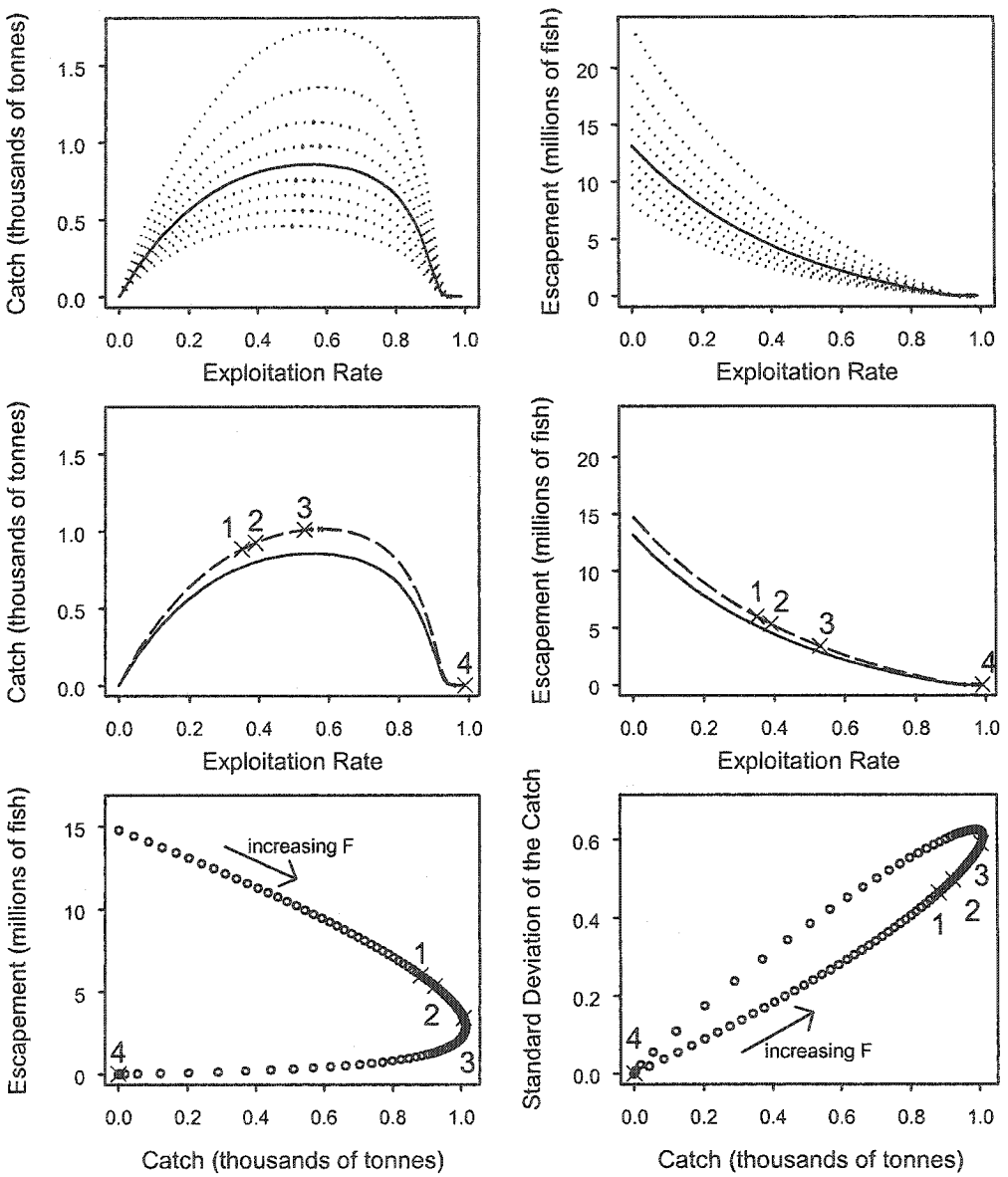

Figure 7.7. A summary of the simulation results for the Miramichi River alewife population. Line and point symbolism are explained in the caption for Figure 7.6.

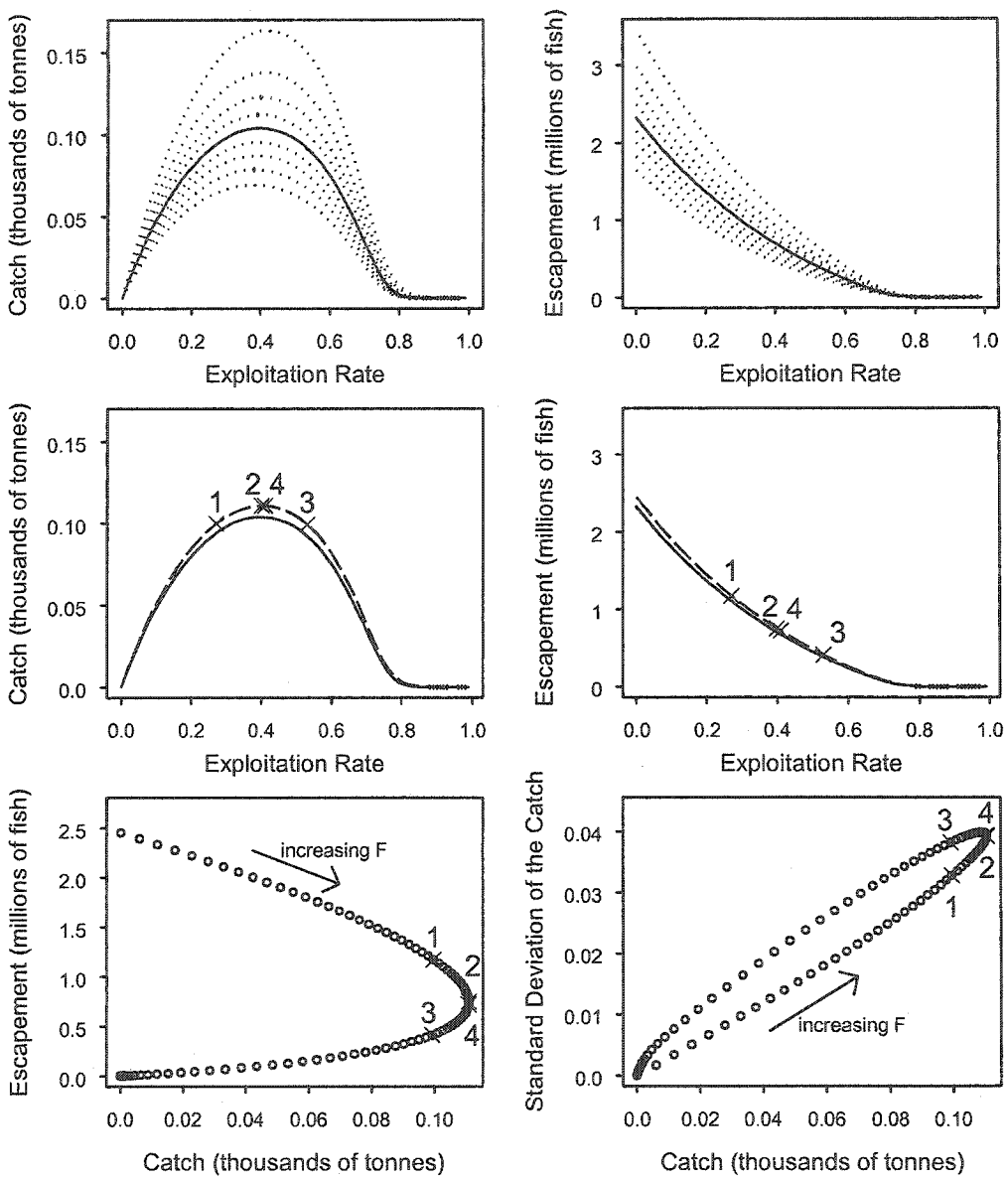

Figure 7.8. A summary of the simulation results for the Mactaquac Headpond alewife population. Line and point symbolism are explained in the caption for Figure 7.6.

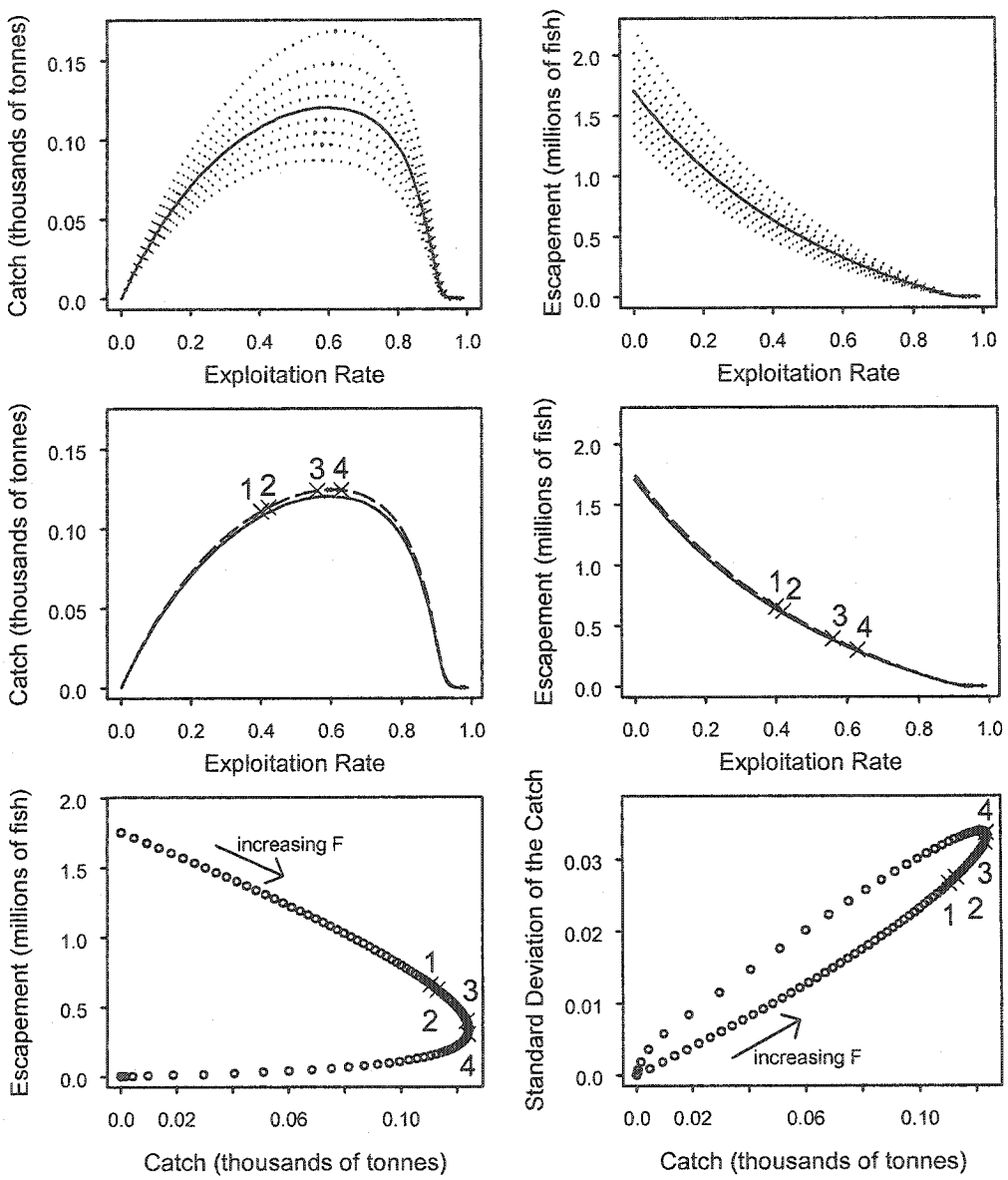

Figure 7.9. A summary of the simulation results for the Gaspereau River alewife population. Line and point symbolism are explained in the caption for Figure 7.6.

7.2.4 Relationship Between Turbine Mortality and Fishery Reference Points

Where watersheds are developed for hydroelectric generation, reference points will vary with the level of turbine mortality (Figure 7.10). Because juvenile turbine mortality occurs prior to reproduction, equilibrium catches and spawning escapements at MSY decrease with increasing mortality, and in the case of Gaspereau River alewife, the population is not sustainable at levels of juvenile turbine mortality that exceed 97%. Because adult turbine mortality occurs after reproduction, sustainable fisheries may exist even if all adult fish die during turbine passage. In the case of 100% adult turbine mortality, equilibrium yield at MSY are reduced to 75.3% from its level in the absence of turbine mortality, whereas 100% turbine mortality reduces the spawner biomass at MSY is reduced to 49.0% its level in without turbine mortality.

7.4 Discussion

In this chapter I have estimated biological reference points for alewife fisheries in four rivers in the Maritime Provinces. The results show that although there are some differences in the biology of Gulf of St. Lawrence and Bay of Fundy alewife (primarily age-at-maturity), the differences are not sufficient to warrant different reference fishing mortality rates between to two regions. Annual variability in the maturity schedules has little effect on the mean catch and for a species such as alewife (with a high maximum reproductive rate and variability around the SR model), and does not need to be considered when selecting a reference F.

The current reference point for the Scotia-Fundy region (exploitation rates targeted not to exceed 65%) is based on the analysis of Crecco and Gibson (1990), and is approximately the mean of the MLE of u_{msy} for eight alewife populations (64%). In my study, F_{msy} (and the corresponding u_{msy}) is not well determined for any population, but was lower than this target for all populations except the Mactaquac Headpond. The exploitation rate that produces maximum sustainable yield is a function of α . In the meta-analysis of eight alewife stocks (Chapter 4), the estimates of α were lower for

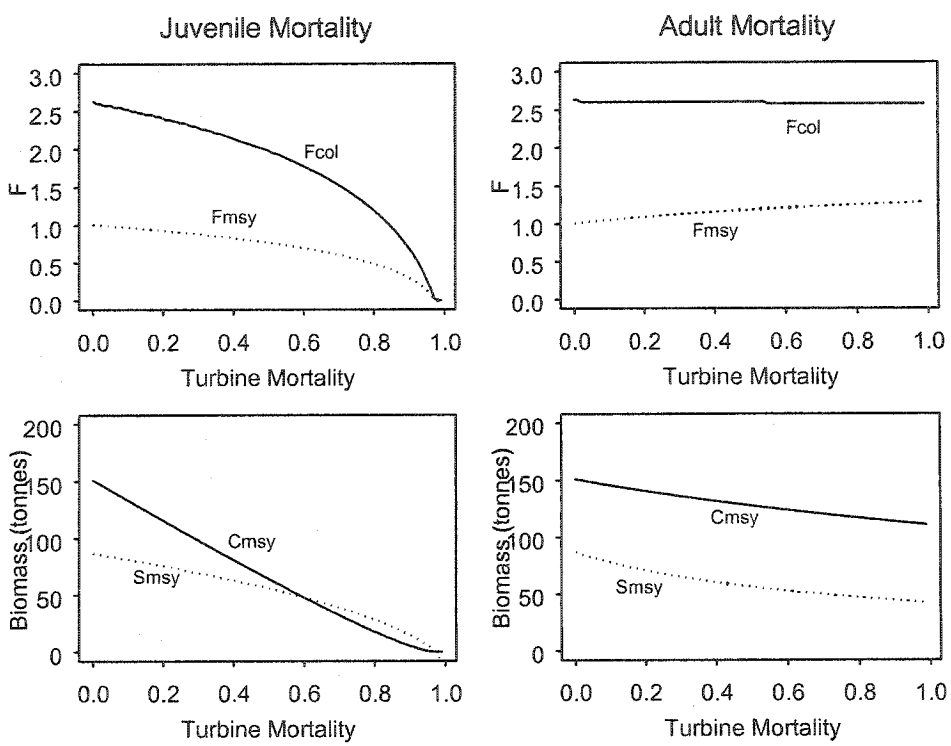

Figure 7.10. The relationship between juvenile (left column) and adult (right column) and fishery reference points for Gaspereau River alewife. F_{msy}, S_{msy} and C_{msy} are the equilibrium fishing mortality rate, spawner biomass and catch at MSY. F_{col} is the fishing mortality rate that will drive the population to extinction. Juvenile turbine mortality was assumed to occur after compensatory mortality. Adult turbine mortality occurs after spawning.

populations with smaller confidence intervals than for those larger confidence intervals for α . This suggests that α is potentially overestimated for populations where it is not well determined. Additionally, time series bias (Walters 1985, Myers and Barrowman 1995) and measurement errors in the spawner abundance time series (Walters and Ludwig 1981, Ludwig and Walters 1981) can cause α to be overestimated, although, in later case, the direction of the bias may actually depend on the range and distribution of the observed spawner abundances (Kehler 2001). When α is over-estimated, the exploitation rates that produce maximum sustainable yield or stock collapse are also over-estimated. Given that α is not well determined for any of the populations in this study, the resulting MLE of u_{msy} is probably not a good management target, given that most biases lead to its over-estimation.

These results show that fishing mortality rates that maximize the expectation of the catch for these populations are lower than the MLE's for F_{msy}. $F_{\text{max.E[Y]}}$ is therefore precautionary in the sense that it is less likely to lead to overexploitation of the populations. The simulation results show that even if the MLE's for α and R_0 are the "true" values, fishing at $F_{\text{max.E[Y]}}$ instead of at F_{msy} will only have a small effect on either the mean or median catch. Additionally, the simulation results suggest that an exploitation rate of about 40% will produce 90% the yield of fishing at the rate that produces the maximum yield (an exploitation rate of about 55 to 60% for populations other than the Mactaquac Headpond).

The Mactaquac Headpond population has the lowest maximum reproductive rate of any of the alewife populations for which I have data. The reference points for this population indicate that it should be fished at a lower rate as a result. However, I do not know why this population is less productive than others. Juvenile turbine mortality could potentially reduce recruitment in this population, although I do not have estimates of the rates of turbine mortality for this population. Alternatively, fish could be straying to other parts of the St. John River, are not completing the migration as far as the Mactaquac Dam (as suggested by the analysis in Chapter 2) or are being harvested in the lower river prior

to reaching the dam (Jessop 1994). Most likely, all factors are acting concurrently, and it is also likely that fish are straying from downstream into the headpond (it was colonized from populations downstream). Therefore, while these analyses suggest that the population dynamics of this population differ substantially from other alewife populations, the analysis should be not be considered conclusive until these issues are resolved.

Based on the results of the Monte Carlo simulations, fishing rates targeted at $F_{35\%}$ are probably reasonable strategies for alewife in the Maritime Provinces. For all populations, this rate was less than F_{msy}, but still produced greater than 90% the maximum median catch. In this sense, it precautionary if α is over-estimated in this study, but is not overly conservative because it produces a catch close to MSY if the estimated α 's are close to their true values. This finding is similar to those of Clark (1991) and Mace and Sissenwine (1993). Clark found that $F_{35\%}$ would achieve at least 75% of the MSY yield when the SR relationship was unknown. In a meta-analysis of 91 SR datasets, Mace and Sissenwine found that $F_{30\%}$ was a reasonable threshold reference point for 80% of the populations included in the analysis, whereas Mace (1994) suggested that $F_{40\%}$ be adopted when the SR relationship is unknown. In my study, $F_{35\%}$ ranged between 0.47 (Margaree River) and 0.54 (Gaspereau River), with a corresponding average exploitation rate of 39.5%.

Myers et al. (1994) suggested that the stock size corresponding to 50% the maximum average recruitment (the K parameter in the Beverton-Holt SR model) could be interpreted as a minimum biomass level at which recruitment to a fish stock is seriously reduced. For these populations this threshold is well below SSB_{msy} or $SSB_{20\%}$. For example, for the Gaspereau River population, these values are 16.2t, 85.8t and 109.3t for K, SSB_{msy}, and $SSB_{20\%}$ respectively. Myers et al. (1994) warn that for populations with an estimated slope at the origin that is high, the use of K as a threshold could produce population sizes that are very low. For the Gaspereau River, only one observed spawner abundance is below K, although all observed spawner abundances are below SSB_{msy}, and

harvest rates at times have exceeded 85%. As discussed earlier, many of the biases in the estimation of α , lead to its overestimation and hence to an underestimation of K. In these instances, biomass thresholds based on a percentage of virgin biomass may be preferable, although the selection of an appropriate percentage remains problematic (Myers et al. 1994). The alewife populations in this study have been heavily exploited. For the Gaspereau River, all predicted spawner abundances are below $SSB_{20\%}$ and all but two predicted spawner abundances are below $SSB_{20\%}$ for the Margaree River. The Mactaquac Headpond appears to be at low levels relative to the carrying capacity of alewife habitat (this thesis, Chapter 5), and reasonable estimates of K cannot be estimated from the stock specific data for the Miramichi River. Given these issues, the biomass thresholds presented herein should be treated as preliminary until further data at higher spawner abundances is collected for each population. However, the estimated carrying capacities of habitat for these four populations are lower than the mean of the empirical Bayes prior distribution for carrying capacity for alewife at the species level, suggesting that I am not overestimating the biomass thresholds for these populations. If this is true, these populations have been at or below $SSB_{20\%}$ during the period for which I have data.

Spawner-recruit model selection affects the resulting reference point estimates. In Chapter 4, I found that the Beverton-Holt model produces better fits to alewife SR data than the Ricker model, and did find evidence of depensation in alewife SR data. The Beverton-Holt model generally produces higher estimates of the slope at the origin than the Ricker model, and is not a precautionary selection as a result (Myers et al. 1999, Myers et al. 2002). Barrowman and Myers (2000) present an alternative SR model, the hockey-stick model, based on territoriality in the pre-recruit life stages (applicable for salmon). This model also produces estimates of the slope at the origin that are lower than those from the Beverton- Holt model. The hockey stick model can be used for estimating threshold biomass estimates (Bradford et al. 2000) because one of the parameters, S^*, is the threshold spawner biomass at which recruitment begins to decline. While not analyzed in detail here (alewife are not territorial), this model produces threshold biomass

estimates (S^*) that slightly higher than K for these populations. SSB_{msy} equates to S^* when estimated using the hockey stick model, producing an estimate 26.1t for SSB_{msy} (at $u = 0.85$) for the Gaspereau River (in comparison with 85.8t, at $u = 0.63$, from the Beverton-Holt model). This example shows that model selection not only has consequences for limit fishing mortality rates (Barrowman and Myers (2000), but for biomass thresholds as well.

Currently, a formal definition of risk has not been adopted for alewife in the Maritime Provinces. Francis (1993) suggested that a level of harvesting could be considered "safe" if it maintained the spawning stock biomass above 20% its mean virgin level at least 90% of the time. $F_{35\%}$ estimated in my analyses corresponds roughly with this definition for the Gaspereau River and Mactaquac Headpond population simulations, but did not meet this objective in the Margaree and Miramichi River simulations. When estimated using a simulation model, the level of harvesting that is considered "safe" depends largely on the amount of random variability introduced during the simulations. If the coefficient of variation (CV) estimated for the SR models is greater (due to measurement error) than the true variability in the SR process, the resulting "safe" level of fishing will be underestimated. The estimates of a "safe" level of harvesting for the Margaree and Miramichi Rivers are lower than any of the other reference points for these populations and their CV is higher than for the Scotia-Fundy populations. Measurement error is not separated from process error in the models, and it is therefore probable that the CV is overestimated for the Gulf Region stocks. I would therefore not recommend reducing the reference point below $F_{35\%}$ on the basis of this analysis until accuracy of the CV estimates is evaluated.

Based on the analyses presented herein, the limit reference points adopted alewife fisheries in the Scotia-Fundy region exceed the rate that produces MSY, whereas the limits adopted in the Gulf region are slightly lower than the rate that produces MSY. However, based on the simulations, the Gulf fisheries limit rates should produce about 90% to 95% the median yield when fishing at F_{msy} and are therefore not unrealistically

low. During the 1997 to 2000 time period, the exploitation rates on the Gaspereau River and Miramichi River (estimated in Chapter 2) are close to the level that threatens population persistence. Exploitation rates on the Margaree River are close to the rate that produces MSY. The Mactaquac Headpond population is managed using a constant escapement strategy, although the exploitation rate on this river also exceeds the rate that produces MSY. In 2002, the open period for the alewife fishery on the Gaspereau Riverwas reduced from five days per week to four days per week. As a result of this reduced fishing time, exploitation rates have been in the range of 60% to 65% during 2002 and 2003 and spawning escapements are two to three times greater than they were in the 1990's. It remains to be determined whether the increased spawning escapements will result in more lucrative fisheries on these rivers.

CHAPTER 8. CONCLUSIONS

The overall objective of this thesis was to contribute to our understanding of the population dynamics of alewife and the effects of human activities on these populations. This objective was met through a series of projects including the development of a population dynamics model based on the life-history of anadromous *Alosa*, estimation of natural, fishing and turbine mortality rates, maturity schedules, reproductive rates and habitat carrying capacity, development of methods for estimating turbine mortality and the effectiveness of fish diversion facilities at hydroelectric generating stations, development of assessment models and the estimation of fishery reference points. In Section 8.1, I summarize key findings in this thesis and in Section 8.2, I discuss key issues and directions for future research resulting from this research.

8.1 Summary

In the second chapter of this thesis I presented a life-history based, age-structured population dynamics model for anadromous *Alosa* that is the core of this thesis. The model structure is very flexible and can be adapted to the dynamics of individual populations, as well as their data and management issues. A major advantage of this type of model over virtual population analysis (Quinn and Deriso 1999) is the ability to fit to intermittent data. For many anadromous populations, data are collected during some years, and not others, and the kinds of data vary among years depending on the question under investigation. For example, Gibson and Amiro (2003) and Gibson et al. (2003b) used a similar approach to estimate abundance of two inner Bay of Fundy Atlantic salmon populations over a 30 year time period from intermittent data including juvenile abundance indices (obtained by electrofishing), recreational catch and effort, numbers of adults observed at counting fences, mark-recapture data, count of adults observed while diving and counts of redds in the rivers. Many of the individual data series spanned only a few years. These kinds of data are not readily incorporated in traditional fisheries models, but can be modelled using the approach used in Chapter 2. Because of its

flexibility, the approach emphasises basic data analysis by forcing the researcher to focus on what has been measured in the various data collections and how it relates to the dynamics of the population.

Also in this Chapter 2, I used the approach to estimate natural mortality rates, fishing mortality rates and maturity schedules for four alewife populations. When the number of dimensions in the catch-at-age array is increased (e.g. by adding sex or previous spawning history) and simplifying assumptions are made (e.g. fishing is not selective on the basis of sex), the number of data points is increased which may result in more precise estimates of the model parameters.

Hydroelectric development has the potential to impact upon *Alosa* populations both directly via mortality of fish passing through turbines when migrating downstream, or indirectly by limiting access to spawning areas upstream of dams or through changes in habitat quality and quantity as a result of the changes in flow regimes associated with water management. The experiments described in Chapters 3 and 4 provide ways to estimate survival of fish at hydroelectric generating stations through estimation of the survival of fish passing through the turbine at the station and by estimating the proportion of the population diverted fish guidance system installed at the station to reduce the incidence of fish passage through the turbine. Additionally, using the random effects distribution for carrying capacity estimated in Chapter 5, changes in equilibrium population size associated with the construction of impoundments or by providing fish passage may be evaluated. Finally, when this information is available, it can be incorporated into fisheries management through appropriate adjustments to management targets or limits as illustrated in Chapter 7. These models can also be used to assess losses or gains associated with watershed development as well as to evaluate where the greatest gains may be achieved if mitigation is to be attempted. For example, the analysis in Chapter 7 indicates that juvenile turbine mortality will have a greater impact on population size and viability that adult turbine mortality and therefore should receive greater attention.

Several practical and theoretical advancements came out of the evaluation of the ultrasound fish diversion system at the Annapolis Tidal Generating Station (Chapter 3). Foremost is the effect that varying environmental conditions can have on effectiveness estimates. From a practical perspective, errors resulting from varying environmental conditions can be detected by monitoring fish passage at two locations where the response to the diversion stimulus should be in opposite directions (e.g. turbine intakes and fishways) and comparing the consistency of the resulting estimates at the two locations. When environmental variables were included in the model, the overall model fit was considerably improved, the resulting effectiveness estimates had smaller standard errors and the estimates were more consistent between the new fishway and tailrace sampling locations, demonstrating that both the accuracy and precision of the effectiveness estimates can be improved if the diversion effectiveness is evaluated within a model of the process that determines the rate of fish passage. A somewhat disturbing result is the effect of overdispersion on the precision of the effectiveness estimates. The quasi-likelihood approach used in Chapter 5 corrects for this problem by rescaling the standard errors by the dispersion parameter, but when fish catches are highly overdispersed, the resulting standard errors may be large relative to the parameter estimates, greatly reducing statistical significance. In this study, the distribution of the catch (characterized by the dispersion parameter) had a greater effect on the precision of the diversion coefficient estimates than did the number of fish captured. When fish migrations occur during relatively short time periods, obtaining reliable diversion estimates may be problematic.

The meta-analysis of the maximum reproductive rate and carrying capacity for alewife is informative for several reasons. First, if data from several populations is simply standardized so it can be plotted on the same scale, populations with data that differs from others is immediately evident, as was the case with the Mactaquac Headpond population. Other than a basis for standardization, models are not required for these comparisons. Second the mixed effects model used to fit the model to all data sets

simultaneously is similar to an empirical Bayes analysis in the sense that the "information content" of a dataset is evaluated via the likelihood and the resulting empirical Bayes point estimate for the parameter is derived from that likelihood and the random effects distribution (equivalent to the empirical Bayes prior), which contains the "information" from the other datasets. This is a very useful method for analysis of multiple data sets because not all data sets are considered equally informative. As another example, Gibson et al. (2003a) found that when analysing mark-recapture data for small populations obtained by electrofishing, that the probability of catching a fish appeared highly variable. However, the variance estimate was substantially reduced when empirical Bayes methods were used estimate a random effects distribution for the probability of catching a fish because many of the data sets were essentially uninformative about electrofishing catchability because the number of marked fish was so few.

One of the most interesting factors to come out of this analysis is the relative constancy of the maximum lifetime reproductive rate of alewife among populations. The estimate of the maximum lifetime reproductive rate for alewife (19.3 spawners per spawner) is near the upper end of the range observed by Myers et al. (1999) for 238 other species, illustrating the high productivity of alewife populations. Habitat carrying capacity varied by a factor of about 25 times among populations. This variability is similar to that for Atlantic cod of more than 20 times (Myers et al. 2001) but higher than for coho salmon of about 10 times (Barrowman et al. 2003). Although, I did not find evidence of depensation in the datasets examined, only two of the data sets were informative about the depensation parameter. While this result suggests that the use of purely compensatory models is appropriate for alewife, a precautionary approach to the application of these models is recommended until the issue of depensation is resolved.

The most striking outcome of the comparison of methods of deriving reference points for fisheries management from spawner-recruit data (Chapter 6) is how poorly determined reference points can be when the maximum likelihood estimates of the spawner recruit parameters are used to estimate the reference points. The simulated data

used to evaluate the methods were relatively long SR time series (20 SR data points), randomly distributed between zero and carrying capacity, with each point drawn independently of the others. Even under these conditions, the estimated fishing mortality rate at MSY exceeded the true fishing mortality rate that would drive the population to extinction in some datasets. In contrast, the decision theoretic reference fishing mortality rate was more conservative, produced higher yields and spawner biomasses a while reducing the probability of under- or over-exploiting the population in comparison with the maximum likelihood estimate of F_{msy}. These results indicate that evaluating the quantities of interest, i.e. fishing mortality and yield, outperform more indirect methods, i.e. using maximum likelihood estimates of SR parameters to derive the fishing mortality rate that produces maximum sustainable yield. In the examples presented, the priors obtained by meta-analysis were more informative than the SR data from the individual populations, demonstrating again that biological parameters estimated for fisheries management can be improved if data from other populations are also take into consideration.

The comparison of reference points for Gulf of St. Lawrence and Bay of Fundy alewife populations (Chapter 7) demonstrates that although there are life history differences between the populations (e.g. age-at-maturity), these differences are not sufficient to warrant the difference management targets used in the two regions. The simulations used for the comparisons show relatively flat yield curves such that exploitation rates of about 40% produce yields that are only about 10% less than those obtained at the maximum likelihood estimate of F_{msy} (from 55 to 65% in these examples). For the four populations investigated in this chapter, the fishing mortality rate used as a management target for the Gulf populations appears reasonable, whereas the rate used for Bay of Fundy populations is high. The fishing mortality rates estimated for the Miramichi River and Gaspereau River populations (Chapter 2) are in some years are near the rates that could threaten the persistence of the populations. Since the start of the 2002 fishing season, alewife fishing on the Gaspereau River is has been restricted to 4 days a week

(rather than 5 days), and escapement counts during 2002 and 2003 have been in the range of 350,000 to 400,000 (in comparison with c.80,000 to 180,000 fish from 1997 to 2001). It remains to be seen if this reduction in exploitation will result in larger yields although irrespective of that outcome, the risk of over-exploitation has been reduced as a result of the reduced amount of fishing time. In the case of the Mactaquac Headpond population, the constant escapement policy in place for that population limits population growth by keeping the spawning biomass well below the carrying capacity of that headpond based on the results presented in Chapter 5.

Reference points used to manage alewife fisheries in the Gulf of St. Lawrence presently differ from reference points used in for fisheries in the Bay of Fundy. In chapter 7, I evaluate whether life history differences between populations in these regions are sufficient to warrant different management targets. Using data from two alewife populations in the Gulf of St. Lawrence and two populations in the Bay of Fundy, I calculate several fishery reference points for each population and evaluate reference point performance using population simulations. In this chapter, I also evaluate whether variability in age-at-maturity, which can have a marked influence on annual spawning run size, also affects reference fishing mortality rates. Additionally, I develop relationships between turbine mortality, fishery yields and reference points that can be applied to alewife fisheries on rivers developed for hydroelectric generation.

8.2 Future Research

The life history model presented in Chapter 2 is a useful and flexible tool that can be adapted to specific situations and questions. The model formulation used in any specific situation reflects the researcher's beliefs about the dynamics of the population and how the dynamics are linked to the available data. Model results are sensitive to model formulation, which remains a key source of uncertainty in the approach. For example, a Beverton-Holt model was used here as the functional relationship between spawner biomass and subsequent recruitment. This model provided a better fit to alewife

data, than did a Ricker model, but as was shown in Chapter 5, the alewife SR data analysed here are not informative about the shape of the SR relationship near the origin. Many of the results presented herein are conditional on this assumed form. An alternative approach to determining whether a critical population size exists below which population dynamics fundamentally change is discussed later in this section.

Another, key aspect of model formulation is the timing of events. For example, as presented (equation 2.6) all density dependent processes occur in freshwater during the first four or five months after hatching. If compensatory, over-compensatory or depensatory processes occur later in life, the model formulation presented would be inappropriate. The fundamental question of when and how year class size is determined is a fundamental question in fisheries biology that spans a time period of nearly 100 years (e.g. Hjort 1914, Myers and Cadigan 1993) that has key implications not just for this type of modelling but for most questions in fisheries dynamics. This question can best be addressed though the meta-analysis of data from multiple populations given the uncertainty associated with estimates of age specific abundance in data for most individual populations.

In Chapter 2, I used maximum likelihood to obtain parameter estimates using the model. In Chapter 6, I found that from a management perspective, decision theoretic methods of fitting population dynamics models performed better than maximum likelihood by specifically analysing the activity under investigation together with the management objectives. Uncertainty in the SR time series, mortality rates and maturity schedules was not included in models used in Chapter 6. Integration of the assessment models, dynamics models and management objectives in a decision theoretic context is a logical next step for improving the utility of these models for management purposes.

As shown in Chapter 3, over-dispersion presents a difficult problem when evaluating the effectiveness of behavioural fish guidance systems at hydroelectric generating stations, particularly for statistical inference. This problem is further exacerbated if the guidance system effectiveness is density dependent. Unlike turbine

mortality estimation, comparison with similar applications at other locations is not an alternative if the effectiveness is sensitive to configuration at the specific site. One approach to reducing over-dispersion could be to distribute the on/off status of the diversion system over the set of environmental variables that determine the rate of passage rather than through time (as done in my study). This approach might work for single species studies but would be less effective for multiple species if responses to the environmental cues differ among species. Additionally, a better understanding of the mechanisms that determine when fish migrate would be required to achieve randomization over these variables, and is an area that requires further research.

The method presented in Chapter 4 provides a simple way of correcting turbine mortality estimates for mortality associated with capture and handling. It also provides a method for estimating turbine mortality that is easily integrated into fish passage monitoring programs at hydroelectric stations. However, the method entails a loss of experimental control relative to the use of experimentally released fish. Controlled experiments may be difficult at large facilities or when test fish are difficult to obtain and tend to be focused on only single species. As the number of turbine mortality studies increases, models of turbine mortality rates as a function of the design parameters of the facility (turbine type, head, size and load) as well as the biological characteristics of the effected species could be developed and used to predict expected levels of turbine mortality at the facility of interest. These, together with pre-determined management objectives (acceptable levels of mortality based on analyses like those in Chapter 7) could be used to determine the rigor required in a turbine mortality study or the extent to which mitigation is required.

The shape of the spawner-recruit relationship near the origin, i.e. whether or not the relationship is depensatory, remains a fundamental uncertainty in fisheries biology and is a key determinant of fisheries reference points. As shown in Chapter 5, alewife data are not very informative about the shape of the spawner-recruit function near the origin. Barrowman et al. (2003) did not find evidence of depensation for coho salmon.

Myers et al. (1995) did not find evidence of depensation in 125 of 128 spawner-recruit time series they examined. Liermann and Hilborn (1997) conducted a similar analysis with a different depensatory model and concluded that depensation may be more common that suggested by Myers et at. (1995). Populations that undergo large declines often do not rapidly recover (Hutchings 2000, Hutchings 2001b), possibly indicating that depensatory population dynamics may be quite common. If so, the use of purely compensory models, such as was used throughout much of this thesis, would be inappropriate and would provide an overly optimistic assessment of the impacts of human activities. Hutchings (2001a) analysed whether or not populations recover as a function of how far (and fast) a population had declined over the range of the data, and found that population recovery was correlated with the extent of the decline. Despite the correlation, population recovery was quite variable. A logical next step might be to analyze similar data using models such as those used in this thesis to determine how far a population has declined below carrying capacity (rather than the data range). This approach would attempt to estimate the location of an inflection point in the SR model based on the response of populations to low population size, rather than by trying to estimate the shape of an SR function near the origin using relatively uninformative data (as done here in Chapter 5).

Data standardizations are often required for meta-analysis and these standardizations and the resulting model formulations reflect the researchers beliefs about the characteristics that populations have in common. For example, in the meta-analysis presented in Chapter 5, the maximum lifetime reproductive rate and carrying capacity for adults were assumed to be random variables at the species level. For anadromous species, the carrying capacity of freshwater habitat and the maximum rate at which spawning biomass produces recruits annually could also be considered random variables resulting in a different data standardization prior to conducting the meta-analysis (I did this for alewife and the resulting random effects distributions were very similar to the ones presented in Chapter 5). If meta-analyses are be effective, appropriate characteristics

need to choosen, and this area requires further research. An empirical approach to addressing this question is the comparison of the fits of models based on differing assumptions for many populations.

BIBLIOGRAPHY

Anon. 1890-1899 (10 documents). Annual Report of the Department of Marine and Fisheries, Bureau of Marine and Fisheries, Ottawa.

Barnthouse, L. W., R. J. Klauda, D. S. Vaughan and R. L. Kendall. 1988. Science, law, and the Hudson River power plants: a case study in environmental assessment. American Fisheries Society Monograph 4. American Fisheries Society, Bethesda, Maryland.

Barrowman, N. J. 2000. Nonlinear mixed effects models for meta-analysis. PhD thesis. Department of Mathematics and Statistics, Dalhousie University, Halifax, Nova Scotia.

Barrowman, N. J., and R. A. Myers. 2000. Still more spawner-recruitment curves: the hockey stick and its generalizations. Canadian Journal of Fisheries and Aquatic Sciences 57: 665-676.

Barrowman, N. J., R. A. Myers, R. Hilborn, D. G. Kehler, and C. A. Field. 2003. The variability among populations of coho salmon in the maximum reproductive rate and depensation. Ecological Applications 13: 784-793.

Beddington, J. R., and J. G. Cooke. 1983. The potential yield of fish stocks. U.N. FAO Fisheries Technical Paper 242. Rome, Italy.

Beverton, R. J. H. 1995. Spatial limitation of population size; the concentration hypothesis. Netherlands Journal of Sea Research 34: 1-6.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. MAFF Fisheries Investigations Series II 19: 533p.

Birmann, M. 1999. Sound system installation and sound field measurements. *In* Gibson A. J. F. and R. A. Myers. 1999. Assessment of a high frequency sound fish diversion system at the Annapolis tidal Generating Station with notes about the survival of fish moving seaward at the Annapolis causeway. Acadia Centre for Estuarine Research Publication No. 55. Acadia University, Wolfville, Nova Scotia.

Bradford, M. J., R. A. Myers and J. R. Irvine. 2000. Reference points for coho salmon (*Oncorhynchus kisutch*) harvest rates and escapement goals based on freshwater production. Canadian Journal of Fisheries and Aquatic Sciences 57: 677-686.

Brodziak, J. 2002. In search of optimal harvest rates for west coast groundfish. North American Journal of Fisheries Management 22: 258-271.

Burnham, K.P., D.R. Anderson, G.C. White, C. Brownie and K.H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5. American Fisheries Society, Bethesda, Maryland.

Caddy, J. F., and R. Mahon. 1995. Reference points for fisheries management. FAO Fisheries Technical Paper 347. Rome, Italy.

Caddy, J. F., and R. McGarvey, R. 1996. Targets or limits for management of fisheries. North American Journal of Fisheries Management 16:479-487.

Carlin, B. P., and T. A. Louis. 1996. Bayes and Empirical Bayes Methods for Data Analysis, Volume 69 of Monographs on Statistics and Applied Probability. Chapman and Hall, London.

Carscadden, J. E., and W. C. Leggett. 1975. Meristic differences in spawning populations of American shad, *Alosa sapidissima* (Wilson), spawning in tributaries of the St. John River, New Brunswick. Journal of the Fisheries Research Board of Canada 32: 653-660.

Chaloner, K., and K. Larntz. 1989. Optimal Bayesian design applied to logistic regression experiments. Journal of Statistical Planning and Inference 21: 191-208.

Chaput, G. J., and D. R. Alexander. 1989. Mortality rates of alewife in the Southern Gulf of St. Lawrence. CAFSAC Research Document 89/38. Department of Fisheries and Oceans, Ottawa, Ontario. 23p.

Chaput, G., and G. Atkinson. 1997. The gaspereau fisheries (*Alosa pseudoharengus* and *A. aestivalis*) of the Miramichi River with updates on the fisheries of the Pokemouche, Tradadie and Richibucto River of Gulf New Brunswick. CSAS Research Document 97/75. Department of Fisheries and Oceans, Ottawa, Ontario. 32 p.

Chaput, G., and G. Atkinson. 2001. The gaspereau fisheries (*Alosa pseudoharengus* and *A. aestivalis*) of the Miramichi River with updates on the fishery of the Richibucto River of Gulf New Brunswick. CSAS Research Document 2001/047. Department of Fisheries and Oceans, Ottawa, Ontario.

Chaput, G., P. LeBlanc and R. Crawford. 2001. Assessment of the Margaree River gaspereau fishery, 1997 to 2000. CSAS Research Document 2001/046. department of Fisheries and Oceans, Ottawa, Ontario.

Chen, D. G., and L. B. Holtby. 2002. A regional meta-model for stock-recruitment analysis using empirical Bayesian approach. Canadian Journal of Fisheries and Aquatic Sciences 59: 1503-1514.

Clark, C. W. 1976. Mathematical Bioeconomics. Wiley, New York.

Clark, C. W., A. T. Charles, J. R. Beddington and M. Mangel. 1985. Optimal capacity decisions in a developing fishery. Marine Resource Economics 2: 25-53.

Clark, W. G. 1991. Groundfish exploitation rates based on life history parameters. Canadian Journal of Fisheries and Aquatic Sciences 48: 734-750.

Clark, W. G. 2002. $F_{35\%}$ revisited ten years later. North American Journal of Fisheries Management 22: 251-257.

Clay, C. H. 1995. Design of fishways and other fish facilities. 2nd edition. CRC Press, Boca Raton, Florida.

Cole, L. C. 1954. The population consequences of life history phenomena. Quarterly Review in Biology. 29: 103-137.

Collett, D. 1991. Modelling Binary Data. Chapman and Hall/CRC Press, London.

Crecco, V. A., and M. Gibson. 1990. Stock assessment of river herring from selected Atlantic coast rivers. Special Report No. 19 of the Atlantic States Marine Fisheries Commission. 75p.

Crecco, V., and T. Savoy. 1988. Effects of climatic and density-dependent factors on intra-annual mortality of larval American shad. Pages 69-81 *In* R. D. Hoyt, editor. 10th annual larval fish conference. Proceedings of a conference held in Miami, Florida, USA, May 18-23, 1996. American Fisheries Society, Bethesda, Maryland.

Daborn, G. R., R. R. G. Williams, J. S. Boates and P. S. Smith. 1979. Limnology of the Annapolis River and Estuary: I. Physical and chemical features. Proceedings of the Nova Scotia Institute of Science 29:153-172.

Dadswell, M. J., and R. A. Rulifson. 1994. Macrotidal estuaries: a regional of collision between migratory marine animals and tidal power development. Biological Journal of the Linnaean Society. 51: 93-113.

Dadswell, M.J., R.A. Rulifson and G.R. Daborn. 1986. Potential impact of large-scale tidal power developments in the upper Bay of Fundy on fisheries resources of the Northwest Atlantic. Fisheries 11: 26-35.

Davison, A. C., and D. V. Hinkley. 1997. Bootstrap methods and their application. Cambridge University Press. Cambridge, U.K.

Deriso, R. B. 1980. Harvesting strategies and parameter estimation for an age-structured model. Canadian Journal of Fisheries and Aquatic Sciences 37: 268-282.

Deriso, R. B., T. J. Quinn II and P. R. Neal. 1985. Catch-age analysis with auxiliary information. Canadian Journal of Fisheries and Aquatic Sciences 42: 815-824.

DFO 2001. Gaspereau Maritime Provinces Overview. DFO Science Stock Status Report D3-17 (2001). Department of Fisheries and Oceans, Ottawa, Ontario.

Dorn, M. W. 2002 Advice on west coast rockfish harvest rates from Bayesian meta-analysis of stock-recruit relationships. North American Journal of Fisheries Management 22: 280-300.

Douma, A., and G. D. Stewart. 1981. Annapolis STRAFLO turbine will demonstrate Bay of Fundy tidal power concept. Hydro Power 1: 1-8.

Dubois, R. B., and S. P. Gloss. 1993. Mortality of juvenile American shad and striped bass passed through Ossberger crossflow turbines at a small-scale hydroelectric site. North American Journal of Fisheries Management 13: 178-185.

Dunning, D. J., Q. E. Ross, P. G. Geoghegan, J. J. Reichle, J. K. Menezes and J. K. Watson. 1992. Alewives avoid high-frequency sound. North American Journal of Fisheries Management 12: 407-416.

Durbin, A. G. S., S. W. Nixon and C. A. Oviatt. 1979. Effects of the spawning migration of the alewife on freshwater ecosystems. Ecology 60: 8-17.

Efron, B. 1996. Empirical Bayes methods for combining likelihoods. Journal of the American Statistical Association 91: 538-565.

Evans, G. T., and J. C. Rice. 1988. Predicting recruitment from stock size without mediation of a functional relation. Journal du Conseil International pour l'Exploration de la Mer 44: 111-122.

Fournier, D. 1996. An introduction to AD Model Builder for use in nonlinear modelling and statistics. Otter Research Ltd., Nanaimo, BC, Canada.

Fournier, D. A., and C. P. Archibald. 1982. A general theory for analyzing catch at age data. Canadian Journal of Fisheries and Aquatic Sciences 39: 1195-1207.

Francis, R. I. C. C. 1993. Monte Carlo evaluation of risks for biological reference points used in New Zealand Fishery Assessments. p. 221-230. *In* S. J. Smith, J. J. Hunt and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Canadian Special Publication of Fisheries and Aquatic Sciences 120.

Francis, R. I. C. C. 1997. Comment: How should fisheries scientists and managers react to uncertainty about stock-recruit relationships. Canadian Journal of Fisheries and Aquatic Sciences. 54: 982-983.

Frederick, S. W., and R. M. Peterman. 1995. Choosing fisheries harvest policies: when does uncertainty matter? Canadian Journal of Fisheries and Aquatic Sciences 52: 291-306.

Freeman, M. C., C. M. Pringle, E. A. Greathouse and B. J. Freeman. 2003. Ecosystem-level consequences of migratory faunal depletion caused by dams. pages 255-266 *In* K..E. Limburg and J. R. Waldman, editors. Biodiversity, status and conservation of the world's shads. American Fisheries Society, Symposium 35, Bethesda, Maryland.

Gabriel, W. L., M. P. Sissenwine and W. J. Overholz. 1989. Analysis of spawning stock biomass per recruit: an example for Georges Bank haddock. North American Journal of Fisheries Management 9: 383-391.

Garman, G. C. 1992. Fate and potential significance of postspawning anadromous fish carcasses in an Atlantic coastal river. Transactions of the American Fisheries Society 121: 390-394.

Garman, G. C., and S. A. Macko. 1998. Contribution of marine-derived organic matter to an Atlantic coast, freshwater, tidal stream by anadromous clupeid-fishes. Journal of the North American Benthological Society 17: 277-285.

Getz, W. M., R. C. Francis and G. L. Swartzman. 1987. On managing variable marine fisheries. Canadian Journal of Fisheries and Aquatic Sciences 44: 1370-1375.

Getz, W. M., and G. L. Swartzman. 1981. A probability transition matrix model for yield estimation in fisheries with highly variable recruitment. Canadian Journal of Fisheries and Aquatic Sciences 38: 847-855.

Gibson, A. J. F. 1996. Distribution and seaward migration of young-of-the-year American shad (*Alosa sapidissima*), blueback herring (*A. aestivalis*) and alewives (*A. psuedoharengus*) in the Annapolis River Estuary. Master's thesis. Acadia University, Wolfville, Nova Scotia.

Gibson, A. J. F. and P. G. Amiro. 2003. Abundance of Atlantic salmon (*Salmo salar*) in the Stewiacke River, NS, from 1965 to 2002. CSAS Research Document 2003/108. Department of Fisheries and Oceans, Ottawa, Ont.

Gibson, A.J.F. and G. R. Daborn. 1998. The Ecology of young-of-the-year alewives in Gaspereau Lake with reference to water management strategies in the Black River - Gaspereau River Watershed. Acadia Centre for Estuarine Research Publication No. 45. Wolfville, N.S.

Gibson, A. J. F., and R. A. Myers. 2000. Assessment of a high-frequency sound fish diversion system at the Annapolis Tidal Generating Station with notes about the survival of fish moving seaward at the Annapolis causeway. Acadia Centre for Estuarine Research Publication No. 55. Acadia University, Wolfville, Nova Scotia.

Gibson, A. J. F., and R. A. Myers. 2001. Gaspereau River alewife stock status report. CSAS Research Document 2001/061. Department of Fisheries and Oceans, Ottawa, Ontario.

Gibson, A. J. F., P. G. Amiro and K. A. Robichaud-LeBlanc. 2003a. Abundance of juvenile Atlantic salmon (*Salmo salar*) in inner Bay of Fundy River during 2000 and 2002 with reference to past abundance inferred from recreational catch data. CSAS Research Document 2003/XXX. Department of Fisheries and Oceans, Ottawa, Ont.

Gibson, A. J. F., R. A. Jones, P. G. Amiro and J. J. Flanagan. 2003b. Adundance of Atlantic salmon (*Salmo salar*) in the Big Salmon River, NB, from 1951 to 2002. CSAS Research Document 2003/219. Department of Fisheries and Oceans, Ottawa, Ont.

Goodyear, C. P. 1977. Assessing the impact of power plant mortality on the compensatory reserve of fish populations. p. 186-195. *In* W. VanWinkle [ed.] Proceedings of a conference on assessing the effects of powerplant induced mortality on fish populations. Pergamon Press, NY.

Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. p. 67-82. *In* S. J. Smith, J. J. Hunt and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Canadian Special Publication of Fisheries and Aquatic Sciences 120.

Gulland, J. A., and L. K. Boerema. 1973. Scientific advice on catch levels. Fisheries Bulletin 71: 325-335.

Harley, S. J., R. A. Myers and A. Dunn. 2001. Is catch-per-unit-effort proportional to abundance? Canadian Journal of Fisheries and Aquatic Sciences 58: 1705-1772.

Harley, S. J., and R. A Myers. 2001. Hierarchical Bayesian models of length-specific catchability of research trawl surveys. Canadian Journal of Fisheries and Aquatic Sciences 58: 1569-1584.

Havey, K. A. 1961. Restoration of anadromous alewives at Long Pond, Maine. Transactions of the American Fisheries Society 90: 281-286.

Hayes, D. B., C. P. Ferreri and W. W. Taylor. 1996. Linking fish habitat to their population dynamics. Canadian Journal of Fisheries and Aquatic Sciences 53 (supplement 1): 383-390.

Heisey, P.G., D. Mathur and T. Rineer. 1992. A reliable tag-recapture technique for estimating turbine passage survival: application to young-of-the-year American shad (*Alosa sapidissima*). Canadian Journal of Fisheries and Aquatic Sciences. 49: 1826-1834.

Hilborn, R. 2001. Risk analysis of salmon spawning escapement levels. p. 177-193. *In* E. Provost and G. Chaput [ed]. Stock, recruitment and reference points: assessment and management of Atlantic salmon. INRA, Paris.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Hjort, J. 1914. Fluctuation in the great fisheries of northern Europe reviewed in the light of biological research. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 20: 1-228.

Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fisheries Bulletin 81: 898-902.

Hogans, W. E. 1987. Mortality of adult American shad (*Alosa sapidissima*) passed through a STRAFLO turbine at the low-head tidal power generating station of Annapolis Royal, Nova Scotia. T.P.H. Applied Fisheries Research Inc., Wolfville, Nova Scotia.

Hutchings, J.A. 2000. Collapse and recovery of marine fishes. Nature (Lond.) 406: 882-885.

Hutchings, J.A. 2001a. Influence of population decline, fishing, and spawner variability on the recovery of marine fishes. Journal of Fish Biology 59 (Suppl. A): 306-322.

Hutchings, J.A. 2001b. Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk. Canadian Journal of Fisheries and Aquatic Sciences 58: 108-121.

Ianelli, J. M., and J. Heifetz. 1995. Decision analysis of alternative harvest policies for the Gulf of Alaska Pacific perch fishery. Fisheries Research 24: 35-63.

Jakobsen, T. 1993. The behaviour of F_{low}, F_{med} and F_{high} in response to variation in parameters used for their estimation. p. 119-125. *In* S. J. Smith, J. J. Hunt and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Canadian Special Publication of Fisheries and Aquatic Sciences 120.

Jessop, B. M. 1990a. Passage and harvest of river herring at the Mactaquac Dam, Saint John River: an attempt at active fishery management. North American Journal of Fisheries Management 10: 33-38.

Jessop, B.M. 1990b. Diel variation in density, length composition, and feeding activity of juvenile alewife, *Alosa pseudoharengus* Wilson, and blueback herring, *A. aestivalis* Mitchill, at near surface depths in a hydroelectric dam impoundment. Journal of Fish Biology 37: 813-822.

Jessop, B. M. 1994. Homing of alewives (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) to and within the Saint John River, New Brunswick, as indicated by

tagging data. Canadian Technical Report of Fisheries and Aquatic Sciences 2015. 26p.

Jessop, B. M. 1994. Relations between stock and environmental variables, and an index of abundance, for juvenile alewives and blueback herring. North American Journal of Fisheries Management 14: 564:579.

Jessop, B. M., and W. E. Anderson. 1989. Effects of heterogeneity in the spatial and temporal pattern of juvenile alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*) density on estimation of an index of abundance. Canadian Journal of Fisheries and Aquatic Sciences 46: 1564-1574.

Kalbfleisch, J. G. 1985. Probability and statistical inference volume 2: statistical inference, 2nd edition. Springer-Verlag New York Inc., New York.

Kehler, D. 2001. Bias in Spawner-Recruitment Models. Masters Thesis, Dalhousie University, Halifax, NS. 91p.

Kendall, M, A. Stewart and J. K. Ord. 1983. Kendall's advanced theory of statistics, Volume 1, 5th edition. MacMillan Inc., New York.

Kostecki, P. T., P. Clifford, S. P. Gloss and J. C. Carlisle. 1987. Scale loss and survival in smolts of Atlantic Salmon (*Salmo salar*) after turbine passage. Canadian Journal of Fisheries and Aquatic Sciences. 44: 210-214.

Larkin, P. A. 1977. An epitaph for the concept of maximum sustained yield. Transactions of the American Fisheries Society 106: 1-11.

Lande, R., S. Eigen and B. E. Saether. 1997. Optimal harvesting, exonomic discounting and extinction risk in fluctuating populations. Nature 372: 88-90.

Lane, D. E., and R. L. Stephenson. 1997. A framework for risk analysis in fisheries decision making. ICES Journal of Marine Science 55: 1-13.

Leggett, W. C., and J. E. Carscadden. 1978. Latitudinal variation in the reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. Journal of the Fisheries Research Board of Canada 35: 1469-1478.

Liermann, M., and R. Hilborn. 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. Canadian Journal of Fisheries and Aquatic Sciences 54: 1976-1985.

Lindstrom, M. J., and D. M. Bates. 1990. Nonlinear mixed effects models for repeated measures data. Biometrics 46: 673-687.

Loesch, J. G. 1987. Overview of the life history aspects of anadromous alewife and blueback herring in freshwater habitats. Pages 89-103 *In* M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. Common strategies of anadromous and catadromous fishes. Proceedings of an international symposium held in Boston, Massachusetts, USA, March 9-13, 1986. American Fisheries Society, Bethesda, Maryland.

Loesch, J.G., and W. A. Lund. 1977. A contribution to the life history of the blueback herring, *Alosa aestivalis*. Transactions of the American Fisheries Society 106: 583-589.

Ludwig, D., and C. J. Walters. 1981. Measurement errors and uncertainty in parameter estimates for stock and recruitment. Canadian Journal of Fisheries and Aquatic Sciences 38: 711–720.

Ludwig, D., and C. J. Walters. 1982. Optimal harvesting with imprecise parameter estimates. Ecological Modelling 14: 273-292.

Mace, P. M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. Canadian Journal of Fisheries and Aquatic Sciences 51: 110-122.

Mace, P. M. 2001. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. Fish and Fisheries 2: 2-32.

Mace, P. M., and M. P. Sissenwine. 1993. How much spawning per recruit is enough? p. 101-118. *In* S. J. Smith, J. J. Hunt and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Canadian Special Publication of Fisheries and Aquatic Sciences 120.

Mann, D. A., Z. Lu and A. N. Popper. 1997. A clupeid fish can detect ultrasound. Nature (London) 389:341.

Marcy, B. C., Jr. 1969. Age determinations from scales of *Alosa pseudoharengus* (Wilson) and *Alosa aestivalis* (Mitchill) in Connecticut waters. Transactions of the American Fisheries Society 98: 622-630.

Mathur, D., P.G. Heisey and D.A. Robinson. 1994. Turbine-passage mortality of juvenile American shad at a low-head hydroelectric dam. Transactions of the American Fisheries Society 123: 108-111.

Mathur, D., P. G. Heisey, E. T Huston, J. R. Skalski and S. Hays. 1996. Turbine passage survival estimation for chinook salmon smolts (*Oncorhynchus tshawytscha*) at a large dam on the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 53: 542-549.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models, 2nd edition. Chapman and Hall, London. 511p.

Melvin, G. D. 1984. The usefulness of meristic and morpometric characters in discriminated populations of American shad (*Alosa sapidissima*) inhabitating Cumberland Basin, New Brunswick. Doctoral dissertation. University of New Brnswick, Frederiction, NB.

Melvin, G. D., M. J. Dadswell and J. D. Martin. 1986. Fidelity of American shad, *Alosa sapidissima* (Clupeidae), to its river of previous spawning. Canadian Journal of Fisheries and Aquatic Sciences 43: 640-646.

Merritt, M. F., and T. J. Quinn II. 2000. Using perceptions of data accuracy and empirical weighting of information: assessment of a recreational fish population. Canadian Journal of Fisheries and Aquatic Sciences 57: 1459-1469.

Millar, R. B., and R. Holst. 1997. Estimation of gillnet and hook selectivity using log-linear models. ICES Journal of Marine Science 54: 471-477.

Millar, R. B., and Methot, R. D. 2002. Age-structured meta-analysis of U.S. West Coast rockfish (Scorpaenidae) populations and hierarchical modelling of trawl survey catchabilities. Canadian Journal of Fisheries and Aquatic Sciences 59: 383–392.

Mills, E. L., R. O'Gorman, J. DeGisi, R. F. Heberger and R. A. House. 1992. Food of the alewife (*Alosa pseudoharengus*) in Lake Ontario before and after the establishment of *Bythotrephes cederstroemi*. Canadian Journal of Fisheries and Aquatic Sciences 49: 2009-2019.

Moussalli, E., and R. Hilborn. 1986. Optimal stock size and harvest rate in multistage life history models. Canadian Journal of Fisheries and Aquatic Sciences 43: 135-141.

Myers, R. A., and N. J. Barrowman. 1995. Time series bias in the estimation of density-dependent mortality in stock-recruitment models. Canadian Journal of Fisheries and Aquatic Sciences 52: 223–232.

Myers, R. A., and N. G. Cadigan. 1993. Density-dependent juvenile mortality in marine demersal fish. Canadian Journal of Fisheries and Aquatic Sciences 50: 1591-1598.

Myers, R. A., and G. Mertz. 1998a. The limits of exploitation: a precautionary approach. Ecological Applications 8: S165-S169.

Myers, R. A., and G. Mertz. 1998b. Reducing uncertainty in the biological basis of fisheries management by meta-analysis of data from many populations; a synthesis. Fisheries Research 37: 51-60.

Myers, R. A., K. G. Bowen and N. J. Barrowman. 1999. The maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences 56: 2404-2419.

Myers, R. A., J. Bridson and N. J. Barrowman. 1995. Summary of worldwide stock and recruitment data. Canadian Technical Report of Fisheries and Aquatic Sciences 2024. iv + 327p.

Myers, R. A., N. J. Barrowman, Hilborn, R. and Kehler, D. G. 2002. Inferring Bayesian priors with limited direct data: applications to risk analysis. North American Journal of Fisheries Management 22: 351-364.

Myers, R. A., N. J. Barrowman, J. A. Hutchings and A. A. Rosenberg. 1995. Population dynamics of exploited fish stocks at low population levels. Science 269: 1106-1108.

Myers, R. A., B. R. MacKenzie, K. G. Bowen and N. J. Barrowman. 2001. What is the carrying capacity of fish in the ocean? A meta-analysis of population dynamics of North Atlantic cod. Canadian Journal of Fisheries and Aquatic Sciences 58: 1464-1476.

Myers, R. A., A. A. Rosenberg, P. M. Mace, N. J. Barrowman and V. R. Restrepo. 1994. In search of thresholds for recruitment overfishing. ICES Journal of Marine Science 51: 191-205.

Navarro, J. E., D. J. McCauley and A. R. Blystra. 1996. Turbine passage at four low-head hydroelectric facilities in northeast Michigan. North American Journal of Fisheries Management 16: 182-191.

Nestler, J. M., G. R. Ploskey, J. Pickens, J. Menezes and C. Schilt. 1992. Responses of blueback herring to high-frequency sound and implications for reducing entrainment at hydropower dams. North American Journal of Fisheries Management 12: 667-683.

Nielson, A., and P Lewy. 2002. Comparison of the frequentist properties of Bayes and the maximum likelihood estimators in an age structured model. Canadian Journal of Fisheries and Aquatic Sciences 59: 136-143.

O'Leary J. A., and B. Kynard. 1986. Behavior, length, and sex ratio of seaward-migrating juvenile American shad and blueback herring in the Connecticut River. Transactions of the American Fisheries Society 115: 529-536.

Olney, J. E., and J. M. Hoenig. 2001. Managing a fishery under moratorium: assessment opportunities for Virginia's stocks on American shad. Fisheries 26: 6-11.

O'Neill, J.T. 1980. Aspects of the life histories of anadromous Alewife and Blueback herring. M. Sc. thesis, Department of Biology, Acadia University, Wolfville, N.S. 306 p.

Overholtz, W. J. 1999. Precision and uses of biological reference points calculated from stock recruitment data. North American Journal of Fisheries Management 19: 643-657.

Overholtz, W. J., M. P. Sissenwine and S. J. Clark. 1986. Recruitment variability and its implication for managing and rebuilding the Georges Bank Haddock (*Melanogrammus aeglefInus*) stock. Canadian Journal of Fisheries and Aquatic Sciences 43: 748-753.

Pinheiro, J. C., and D. M. Bates. 1999. Mixed effects methods and classes for S and S-Plus, Version 3. Bell labs, Lucent Technologies and University of Wisconson - Madison.

Popper, A. N. 1999. Feasibility study on the use of sound to deter fish from the vicinity of the Salem Generating Station circulating water intake structure. PS&G Renewal Application, Appendix G, Exhibit G-7. Public Service Electric & Gas Company. Salem Permit Program. 44 South Clinton Avenue, Station Plaza 3, First Floor - MC/104, Trenton, New Jersey 08609.

Popper, A. N., and T. J. Carlson. 1998. Application of the use of sound to control fish behavior. Transactions of the American Fisheries Society 127: 673-707.

Punt, A., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Reviews in Fish Biology and Fisheries 7: 35-63.

Punt, A. E., and A. D. M. Smith. 2001. The gospel of maximum sustainable yield in fisheries management: birth, crucifixion and reincarnation. In: Conservation of Exploited Species (eds J. D. Reynolds, G. M. Mace, K. R. Redford and J. J. Robinson), Cambridge University Press, UK.

Quinn, T. J. II, and R. B. Deriso. 1999. Quantitative Fish Dynamics. Oxford University Press. New York.

Richards, L. J., and J. J. Maguire. 1998. Recent international agreements and the precautionary approach: new directions for fishery management science. Canadian Journal of Fisheries and Aquatic Sciences 55: 1545-1552.

Robichaud-LeBlanc, K. A., and P. G. Amiro (editors) 2001. Assessments of Gaspereau and Striped Bass Stocks of the Maritime Provinces, 2000. CSAS Proceedings Series 2001/11, Department of Fisheries and Oceans, Ottawa, Ontario.

Rochet, M. -J. 2000. Does the concept of spawning per recruit make sense? ICES Journal of Marine Science 57: 1160-1174.

Rosenberg, A. A., and S. Brault. 1991. Stock rebuilding strategies over different time scales. Northwest Atlantic Fisheries Organization Scientific Council Studies 16: 171-181.

Rosenberg, A. A., and S. Brault. 1993. Choosing a management strategy for stock rebuilding when control is uncertain. p. 243-249. *In* S. J. Smith, J. J. Hunt and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Canadian Special Publication of Fisheries and Aquatic Sciences 120.

Ross, Q. E. 1999. Studies of the feasibility of using high frequency sound in conjunction with by-passes located outside of the sound field to provide protection for young-of-the-year and adult blueback herring at the Cresent and Vischer Ferry Hydroelectric Projects. New York Power Authority, White Plains, New York.

Ross, Q. E., D. J. Dunning, J. K. Menezes, M. J. Kenna Jr. and G. Tiller. 1996. Reducing impingement of alewives with high frequency sound at a power plant on Lake Ontario. North American Journal of Fisheries Management 16: 548-559.

Ross, Q. E., D.J. Dunning, R. Thorne, J. K. Menezes, G. W. Tiller and J. K. Watson. 1993. Response of alewives to high-frequency sound at a power plant intake on Lake Ontario. North American Journal of Fisheries Management 13: 291-303.

Ruggles, C. P., T. H. Palmeter and K. E. Stokesbury. 1990. A critical examination of turbine passage fish mortality estimates. Report prepared for the Canadian Electrical Association, Research and Development. Montreal, Quebec.

Ruggles, C. P., and K. D. E. Stokesbury. 1990. Juvenile Alosid study at the Annapolis tidal power station. Report for Tidal Power Corporation by Monenco Maritimes Ltd.

Rulifson, R. A. 1994. Status of anadromous *Alosa* along the east coast of North America. Pages 108-112 *In* J. E. Cooper, R. T. Eades, R. J. Klauda, and J. G. Loesch, editors. Anadromous *Alosa* Symposium, Tidewater Chapter, American Fisheries Society, Bethesda, Maryland.

Savoy, T., and V. Crecco. 1988. Effects of climatic and density-dependent factors on intra-annual mortality of larval American shad. American Fisheries Society Symposium 2: 69-81.

Schimdt, R. E., B. M. Jessop and J. E. Hightower. 2003. Status of river herring stocks in large rivers. Pages 171-182 *In* K. E. Limburg, and J.R. Waldman [ed.] Biodiversity and Conservation of Shads Worldwide. American Fisheries Society Symposium Series. American Fisheries Society, Bethesda, MD.

Scott, W.B., and M.G. Scott. 1988. Atlantic Fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences 219: 731 p.

Shepherd, J. G. 1982. A versatile new stock-recruitment relationship of fisheries and construction of sustainable yield curves. Journal du Conseil Perm. International pour l'Exploration de la Mer 40: 67-75.

Sissenwine, M. P. 1978. Is MSY an adequate foundation for optimum yield? Fisheries 3: 22-24.

Sissenwine, M. P., and J. G. Shepherd. 1987. An alternative perspective on recruitment overfishing and biological reference points. Canadian Journal of Fisheries and Aquatic Sciences 44: 913-918.

Skalski, J. R., S. G. Smith, R. N. Iwamoto, J. G. Williams and A. Hoffman. 1998. Use of passive integrated transponder tags to estimate survival of migrant juvenile salmonids

in the Snake and Columbia rivers. Canadian Journal of Fisheries and Aquatic Sciences 55:1484–1494.

Sorenson, K. M., W. L. Fisher and A. V. Zale. 1998. Turbine passage of juvenile and adult fish at a warmwater hydroelectric facility in northeastern Oklahoma: monitoring associated with relicensing. North American Journal of Fisheries Management 18: 124-136.

Stokesbury, K. D. E. 1987. Downstream migration of juvenile alosids and an estimate of mortality caused by passage through the STRAFLO low-head hydroelectric turbine at Annapolis Royal, Nova Scotia. Masters thesis. Acadia University, Wolfville, Nova Scotia.

Stokesbury, K. D. E., and M. J. Dadswell. 1989. Seaward migration of juveniles of three herring species, *Alosa*, from an estuary in the Annapolis River, Nova Scotia. Canadian Field-Naturalist 103: 388-393.

Stokesbury, K. D. E., and M. J. Dadswell. 1991. Mortality of juvenile clupeids during passage through a tidal, low-head hydroelectric turbine at Annapolis Royal, Nova Scotia. North American Journal of Fisheries Management 11: 149-154.

Thompson, G. G. 1992. A Bayesian approach to management advice when stock-recruitment parameters are uncertain. Fisheries Bulletin 90: 561-573.

Thompson, G. G. 1993. A proposal for a threshold stock size and maximum fishing mortality rate. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S. J. Smith, J. J. Hunt and D. Rivard. Canadian Special Publication of Fisheries and Aquatic Sciences 120: 303-320.

Venables, W. N., and B. D. Ripley. 1999. Modern applied statistics with S-PLUS, 3rd edition. Springer-Verlag New York Inc., New York.

Waldman, J. R. 2003. Introduction to the shads. pages 3-9 *In* K..E. Limburg and J. R. Waldman, editors. Biodiversity, status and conservation of the world's shads. American Fisheries Society, Symposium 35, Bethesda, Maryland.

Walters, C. J. 1975. Optimal harvest strategies for salmon in relation to environmental variability and uncertain production parameters. Journal of the Fisheries Research Board of Canada 32: 1777-1784.

Walters, C. J. 1981. Optimum escapements in the face of alternative recruitment hypotheses. Canadian Journal of Fisheries and Aquatic Sciences 38: 678-689.

Walters, C. J. 1985. Bias in the estimation of functional relationships from time series data. Canadian Journal of Fisheries and Aquatic Sciences 42: 147–149.

Walters, C. J. 1986. Adaptive management of renewable resources. MacMillan, New York.

Walters, C. J., and D. Ludwig. 1981. Effects of measurement errors on the assessment of stock-recruitment relationships. Canadian Journal of Fisheries and Aquatic Sciences 38: 704–710.

Walters, C. J., and P. H. Pearse. 1996. Stock information requirements for quota management systems in commercial fisheries. Reviews in Fish Biology and Fisheries 6: 21-42.