



National Library  
of Canada

Bibliothèque nationale  
du Canada

Acquisitions and  
Bibliographic Services Branch

Direction des acquisitions et  
des services bibliographiques

395 Wellington Street  
Ottawa, Ontario  
K1A 0N4

395, rue Wellington  
Ottawa (Ontario)  
K1A 0N4

Your file    Votre référence

Our file    Notre référence

## NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

## AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

**Habitat-dependence of population abundance and  
variability in juvenile Atlantic salmon (*Salmo salar*)**

by

**André J. Talbot**

**submitted in partial fulfilment of the requirements  
for the Degree of Doctor of Philosophy**

at

**Dalhousie University**

**Halifax, Nova Scotia**

**February 1994**



National Library  
of Canada

Acquisitions and  
Bibliographic Services Branch

395 Wellington Street  
Ottawa, Ontario  
K1A 0N4

Bibliothèque nationale  
du Canada

Direction des acquisitions et  
des services bibliographiques

395, rue Wellington  
Ottawa (Ontario)  
K1A 0N4

Your file     *Votre référence*

Our file     *Notre référence*

**The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.**

**L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.**

**The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.**

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

ISBN 0-315-93799-8

**Canada**

Name André J. TALBOT

Dissertation Abstracts International is arranged by broad, general subject categories. Please select the one subject which most nearly describes the content of your dissertation. Enter the corresponding four-digit code in the spaces provided.

ECOLOGY

**0329 U·M·I**

SUBJECT TERM

SUBJECT CODE

**Subject Categories**

**THE HUMANITIES AND SOCIAL SCIENCES**

**COMMUNICATIONS AND THE ARTS**

Architecture 0729  
 Art History 0377  
 Cinema 0900  
 Dance 0378  
 Fine Arts 0357  
 Information Science 0723  
 Journalism 0391  
 Library Science 0399  
 Mass Communications 0708  
 Music 0413  
 Speech Communication 0459  
 Theater 0465

**EDUCATION**

General 0515  
 Administration 0514  
 Adult and Continuing 0516  
 Agricultural 0517  
 Art 0273  
 Bilingual and Multicultural 0282  
 Business 0688  
 Community College 0275  
 Curriculum and Instruction 0727  
 Early Childhood 0518  
 Elementary 0524  
 Finance 0277  
 Guidance and Counseling 0519  
 Health 0680  
 Higher 0745  
 History of 0520  
 Home Economics 0278  
 Industrial 0521  
 Language and Literature 0279  
 Mathematics 0280  
 Music 0522  
 Philosophy of 0998  
 Physical 0523

Psychology 0525  
 Reading 0535  
 Religious 0527  
 Sciences 0714  
 Secondary 0533  
 Social sciences 0534  
 Sociology of 0340  
 Special 0529  
 Teacher Training 0530  
 Technology 0710  
 Tests and Measurements 0288  
 Vocational 0747

**LANGUAGE, LITERATURE AND LINGUISTICS**

Language 0679  
 General 0679  
 Ancient 0289  
 Linguistics 0290  
 Modern 0291  
 Literature 0401  
 General 0401  
 Classical 0294  
 Comparative 0295  
 Medieval 0297  
 Modern 0298  
 African 0316  
 American 0591  
 Asian 0305  
 Canadian (English) 0352  
 Canadian (French) 0355  
 English 0593  
 Germanic 0311  
 Latin American 0312  
 Middle Eastern 0315  
 Romance 0313  
 Slavic and East European 0314

**PHILOSOPHY, RELIGION AND THEOLOGY**

Philosophy 0422  
 Religion 0318  
 General 0318  
 Biblical Studies 0321  
 Clergy 0319  
 History of 0320  
 Philosophy of 0322  
 Theology 0469

**SOCIAL SCIENCES**

American Studies 0323  
 Anthropology 0324  
 Archaeology 0326  
 Cultural 0327  
 Physical 0327  
 Business Administration 0310  
 General 0272  
 Accounting 0272  
 Banking 0770  
 Management 0454  
 Marketing 0338  
 Canadian Studies 0385  
 Economics 0501  
 General 0501  
 Agricultural 0503  
 Commerce Business 0505  
 Finance 0508  
 History 0509  
 Labor 0510  
 Theory 0511  
 Folklore 0358  
 Geography 0366  
 Gerontology 0351  
 History 0578  
 General 0578

Ancient 0579  
 Medieval 0581  
 Modern 0582  
 Black 0328  
 African 0331  
 Asia Australia and Oceania 0332  
 Canadian 0334  
 European 0335  
 Latin American 0336  
 Middle Eastern 0333  
 United States 0337  
 History of Science 0585  
 Law 0398  
 Political Science 0615  
 General 0615  
 International Law and Relations 0616  
 Public Administration 0617  
 Recreation 0814  
 Social Work 0452  
 Sociology 0626  
 General 0626  
 Criminology and Penology 0627  
 Demography 0938  
 Ethnic and Racial Studies 0631  
 Individual and Family Studies 0628  
 Industrial and Labor Relations 0629  
 Public and Social Welfare 0630  
 Social Structure and Development 0700  
 Theory and Methods 0344  
 Transportation 0709  
 Urban and Regional Planning 0999  
 Women's Studies 0453

**THE SCIENCES AND ENGINEERING**

**BIOLOGICAL SCIENCES**

Agriculture 0473  
 General 0473  
 Agronomy 0285  
 Animal Culture and Nutrition 0475  
 Animal Pathology 0476  
 Food Science and Technology 0359  
 Forestry and Wildlife 0478  
 Plant Culture 0479  
 Plant Pathology 0480  
 Plant Physiology 0817  
 Range Management 0777  
 Wood Technology 0746  
 Biology 0306  
 General 0306  
 Anatomy 0287  
 Biostatistics 0308  
 Botany 0309  
 Cell 0379  
 Ecology 0329  
 Entomology 0353  
 Genetics 0369  
 Limnology 0793  
 Microbiology 0410  
 Molecular 0307  
 Neuroscience 0317  
 Oceanography 0416  
 Physiology 0433  
 Radiation 0821  
 Veterinary Science 0778  
 Zoology 0472  
 Biophysics 0786  
 General 0786  
 Medical 0760  
 EARTH SCIENCES 0425  
 Biogeochemistry 0425  
 Geochemistry 0996

Geodesy 0370  
 Geology 0372  
 Geophysics 0373  
 Hydrology 0388  
 Mineralogy 0411  
 Paleobotany 0345  
 Paleocology 0426  
 Paleontology 0418  
 Paleozoology 0985  
 Palynology 0427  
 Physical Geography 0368  
 Physical Oceanography 0415

**HEALTH AND ENVIRONMENTAL SCIENCES**

Environmental Sciences 0768  
 Health Sciences 0566  
 General 0566  
 Audiology 0300  
 Chemotherapy 0992  
 Dentistry 0567  
 Education 0350  
 Hospital Management 0769  
 Human Development 0758  
 Immunology 0982  
 Medicine and Surgery 0564  
 Mental Health 0347  
 Nursing 0569  
 Nutrition 0570  
 Obstetrics and Gynecology 0380  
 Occupational Health and Therapy 0354  
 Ophthalmology 0381  
 Pathology 0571  
 Pharmacology 0419  
 Pharmacy 0572  
 Physical Therapy 0382  
 Public Health 0573  
 Radiology 0574  
 Recreation 0575

Speech Pathology 0460  
 Toxicology 0383  
 Home Economics 0386

**PHYSICAL SCIENCES**

Pure Sciences 0485  
 Chemistry 0485  
 General 0485  
 Agricultural 0749  
 Analytical 0486  
 Biochemistry 0487  
 Inorganic 0488  
 Nuclear 0738  
 Organic 0490  
 Pharmaceutical 0491  
 Physical 0494  
 Polymer 0495  
 Radiation 0754  
 Mathematics 0405  
 Physics 0605  
 General 0986  
 Acoustics 0986  
 Astronomy and Astrophysics 0606  
 Atmospheric Science 0608  
 Atomic 0748  
 Electronics and Electricity 0607  
 Elementary Particles and High Energy 0798  
 Fluid and Plasma 0759  
 Molecular 0609  
 Nuclear 0610  
 Optics 0752  
 Radiation 0756  
 Solid State 0611  
 Statistics 0463  
 Applied Sciences 0346  
 Applied Mechanics 0346  
 Computer Science 0984

Engineering 0537  
 General 0537  
 Aerospace 0538  
 Agricultural 0539  
 Automotive 0540  
 Biomedical 0541  
 Chemical 0542  
 Civil 0543  
 Electronics and Electrical 0544  
 Heat and Thermodynamics 0348  
 Hydraulic 0545  
 Industrial 0546  
 Marine 0547  
 Materials Science 0794  
 Mechanical 0548  
 Metallurgy 0743  
 Mining 0551  
 Nuclear 0552  
 Packaging 0549  
 Petroleum 0765  
 Sanitary and Municipal 0554  
 System Science 0790  
 Geotechnology 0428  
 Operations Research 0796  
 Plastics Technology 0795  
 Textile Technology 0994

**PSYCHOLOGY**

General 0621  
 Behavioral 0384  
 Clinical 0622  
 Developmental 0620  
 Experimental 0623  
 Industrial 0624  
 Personality 0625  
 Physiological 0989  
 Psychobiology 0349  
 Psychometrics 0632  
 Social 0451



## TABLE OF CONTENTS

LIST OF FIGURES .....	vii
LIST OF TABLES .....	xiv
GENERAL ABSTRACT .....	xviii
ACKNOWLEDGEMENTS .....	xix
<b>CHAPTER 1</b>	
GENERAL INTRODUCTION .....	1
Population Estimation .....	10
<b>CHAPTER 2</b>	
SIMULTANEOUS ANALYSIS OF REMOVAL DATA FROM MANY SITES ..	12
INTRODUCTION .....	12
ESTIMATION AT SINGLE SITES .....	14
SIMULTANEOUS ANALYSIS OF MANY SITES WITH NO EFFECT OF CAPTURE SEQUENCE .....	16
VARIATION IN CATCHABILITY WITH CAPTURE SEQUENCES ....	18
VARIATION AMONG SITES ASSOCIATED WITH ENVIRONMENTAL VARIABLES .....	20
ALGORITHM .....	21
SIMULATION TESTS .....	22
TESTING THE MODELS WITH FIELD DATA .....	28
DISCUSSION .....	36
Strategies for bias and error variance minimization in field studies .....	39
<b>CHAPTER 3</b>	
DENSITY-DEPENDENT HABITAT USE AND POPULATION EXPANSION IN JUVENILE ATLANTIC SALMON .....	42
INTRODUCTION .....	42
MATERIALS AND METHODS .....	44
The species studied .....	44
Description of sampling .....	45
Adult data .....	51
Statistical models .....	53
ROBUSTNESS: Are the results robust to changes in statistical methods? .....	59
Hypotheses examined .....	60
Taylor's Power Law .....	61

<b>RESULTS</b> .....	<b>62</b>
Density and growth response at the population level .....	62
Estimated patterns of distribution .....	62
Site Invariant Response Hypothesis .....	67
<b>Variable Response Hypothesis</b> .....	<b>72</b>
Relationship of growth rate to population response .....	80
Population stability .....	83
<b>DISCUSSION</b> .....	<b>87</b>
Comparison with other studies .....	87
Implications for population regulation and population estimation ...	90
Density as an indicator of habitat quality .....	94
 <b>CHAPTER 4</b>	
<b>SCALES OF DENSITY-DEPENDENT GROWTH AND HABITAT</b>	
<b>RESPONSE IN ATLANTIC SALMON</b> .....	<b>96</b>
<b>INTRODUCTION</b> .....	<b>96</b>
<b>METHODS</b> .....	<b>100</b>
Statistical analysis .....	104
<b>RESULTS</b> .....	<b>105</b>
1) The growth of female 1+ parr is influenced by the local density of salmon parr. ....	108
2) The growth of female 1+ parr is influenced by the density of salmon parr of the tributary or river segment. ....	113
3) The growth of female 1+ parr is influenced by overall population density. ....	116
4) The growth response to changes in overall population abundance is tributary-specific. ....	122
5) The growth response to change in local population abundance is a function of the juvenile response to changes in overall population abundance. ....	130
<b>DISCUSSION</b> .....	<b>135</b>
Scale of density-dependent growth .....	135
A mechanism for understanding population expansion .....	139
Density-dependent habitat selection .....	144
 <b>CHAPTER 5</b>	
<b>GENERAL DISCUSSION</b> .....	<b>147</b>
<b>THE VARIABILITY OF POPULATION SIZE</b> .....	<b>147</b>
Should we study Open or Closed Populations? .....	148
<b>DENSITY-DEPENDENT HABITAT USE</b> .....	<b>149</b>
Processes controlling population expansion among habitats .....	152
<b>FURTHER CONSIDERATIONS</b> .....	<b>164</b>

<b>POPULATION STUDIES: THE IMPORTANCE OF ESTIMATES</b>	
<b>FROM ALL SITES</b> .....	<b>167</b>
<b>APPENDIX A: Figures for Chapter 2</b> .....	<b>170</b>
<b>Figure A-1</b> .....	<b>170</b>
<b>Figure A-2</b> .....	<b>183</b>
<b>BIBLIOGRAPHY</b> .....	<b>199</b>

## LIST OF FIGURES

**Figure 1-1: Theoretical graphical predictions of the expected local changes in population density in response to an increase in population abundance plotted as a function of distance from the centre of the population range. A: Population increases uniformly in all habitats (null hypothesis). B: Population increases in marginal habitats. C: Population concentrates in the primary habitats. 7**

**Figure 3-1: Topographic map of the Little Codroy River basin, showing the location of fish sampling stations, temperature and depth recorders, and watersheds comprising the drainage basin. 47**

**Figure 3-2: Plot of the relationship between slopes estimated from the Poisson model using upstream and downstream adult migrants independently. The regression line is shown with 95 % confidence intervals. The dotted line is the 1:1 relationship, which falls well within the confidence limits of the regression. 57**

**Figure 3-3: Plot of the number of spawners captured on the Little Codroy River ( $N_s$ ) against the average growth rate of 1+ female parr during their first year. The number of spawners is used as an indicator of total population abundance. The mean and standard errors are given for growth rate. 63**

**Figure 3-4: Bubble plot of the geographic distribution of the average density of 1+ female parr of Atlantic salmon in the Little Codroy River watershed. The radius of the circle is proportional to the density. Note that the highest densities are in the upper watershed below Little Codroy Pond. This figure can be compared to the slopes presented in Figure 3-7.**

**65**

**Figure 3-5: Taylor Power plots of the log of the variance of local abundance against the log of the mean density of local abundance. The dashed line represents the 1:1 relationship. a: Each point represents a site and the mean and variance are estimated over years (Temporal variability). The regression line is given by:  $\log(V(n_i)) = -1.87 + 1.312 \log(M(n_i))$ ,  $R^2 = 0.62$ ,  $n = 27$ ,  $P < 0.001$ . b: Each point represents a year and the mean and variance are estimated over sites (Spatial variability).**

**68**

**Figure 3-6: Bivariate plots of the relationship between the response to change in population abundance ( $\beta_j$ ) and the average station density ( $n_j$ ). Each point represents a tributary or river segment mean. The graphs represent densities estimated in a) the year of lowest adult returns and b) the absolute change in local density between the year of lowest and highest returns specific to stations.**

**73**

**Figure 3-7: Bubble plot of the geographic distribution of the slope ( $\beta_1$ ) of the regression of local to total abundance of 1+ female juvenile Atlantic salmon in the Little Codroy River watershed. Shaded circles indicate negative slopes. The magnitude of the slope is proportional to the radius of the circle. Note that the largest slopes are below the areas of highest density in the watershed or are areas with lower average densities (see Figure 3-4).**

**76**

**Figure 3-8: a) Variation in the mean station density of juvenile salmon as a function of the distance from the estuary along the main river segment. Higher densities are clearly near the headwaters of the river. The regression equation fitted to the data (for illustrative purpose of the tendency only) is shown ( $R^2 = 0.36$ ,  $n=21$ ). b) Variation in the response in local density of juveniles as a function of distance from the estuary along the main river segment. The more stable sites are at the headwaters of the river. Station 2 appears to be an exception. It had the highest mean water velocities of any station sampled in this study and may not have been an ideal habitat. The regression equation fitted to the data is shown ( $R^2 = 0.44$ ,  $n=14$ ).**

**78**

**Figure 3-9: Bivariate plot of  $\beta_1$  and the mean growth of 1+ female parr observed in the first year of sampling at individual stations. Each point represents tributary of river segment means and vertical bars are standard errors. The relationship is significant (see text).**

**81**

**Figure 3-10: Bivariate plot of the coefficient of variation in local female densities at sampling stations (over all years sampled) against a) the mean female density. The equation is given in the text; b) the size-at-age of 1+ female parr at stations; and c) the regression slope ( $\beta_i$ ) of the same stations. The relationships are significant in all cases (see text). All points are included in the regression analyses, including outliers (filled circles).**

**85**

**Figure 4-1: Plot of the relationship between first and second year growth of individual fish. Coefficients of determination and regression line are presented for each tributary (numbered 1 to 10 as in Chapter 3) separately. A small amount of random variation has been added to overlapping points in order to make them visible.**

**106**

**Figure 4-2: Plots of growth variables (first year growth, second year growth and total length) against estimates of density (local 1+ female juvenile density, local 1+ total juvenile density, average tributary 1+ female density, average tributary total 1+ juvenile density, average river 1+ female density, average river total 1+ juvenile density, spawner abundance). The densities are arranged in sequence of increasing spatial scale. Statistics are given in Table 4-1.**

**109**

**Figure 4-3: Relationship between the change in growth rate and local density for each of the 10 tributaries. Both variables are calculated from predicted values derived from their respective regressions slopes with spawner abundance within tributaries. 120**

**Figure 4-4: Regression plots of growth and local juvenile density against spawner abundance for all tributaries. The plots are for a) first year growth, and b) second year growth. The values of growth and density have been shifted slightly horizontally to reduce the amount of overlap. —●—: Growth; ---□---: Density. 124**

**Figure 4-5: Regression plots of growth and local juvenile density against average tributary 1+ female densities for all tributaries. The plots are for a) first year growth, and b) second year growth. —●—: Growth; ---□---: Density. 127**

**Figure 4-6: Plot of the first and second year small scale density-dependent growth response against the local juvenile density response to variation in spawner abundance. The relationships are significantly negative (see text). Each point represents a sampling site and is labelled by tributary number. —●— : First year growth response. ---□--- : Second year growth response. 131**

**Figure 4-7: Plot of the least squares means of density and growth after statistical control of the effect of spawner abundance and tributary (from the analysis of Table 4-6a). The negative slope indicates that a local effect of density on growth rate persists after removal of the effects of population abundance and tributary-specific response and provides evidence for local density-dependent growth. 136**

**Figure 5-1: Graphical representation of hypotheses concerning the distribution of animals across habitat types. Relative fitness is plotted as a function of local population density. Line type (solid, dashed and dotted) represent different habitats. A: Simple proportional negative density-dependent effect with habitats of variable initial fitness. B: Variable negative density-dependent effect with equal initial fitness among habitats. C: combination of A: and B: above. Note the crossing over of some of the lines, indicating that local densities in secondary habitat may exceed those of primary habitats under certain conditions. Units are arbitrary. 155**

**Figure 5-2: Three-dimensional plot of the effect of overall population abundance on the relationship between fitness and local habitat density for primary (solid line) and secondary (dotted line) habitats. Note that the slope increases with increasing population abundance. The scales are arbitrary. 162**

**Figure A-1: Histograms of the estimated population size (  $\hat{N}$  ) for the Maximum Likelihood (ML), Beta and combined Beta and ML models for the simulated data. The bar at the extreme right of the histograms represents extreme values and include cases where infinite estimates were predicted. The parameters used in the equation are indicated at the top of the figure page. The series of histograms presented is the entire simulation with  $N=50$ . It is apparent that the variance of the Beta estimator is lower than other methods at any combination of parameters. Note also the classic skewness of the distribution of the ML estimator, particularly at low probabilities of capture. While the combined estimator is less biased, its variance is large.** 170

**Figure A-2: Actual capture probabilities as a function of capture sequence for some species used, originating from Mahon's (1980) data. The value in the upper left corner is the actual population size ( $N_i$ ). It is apparent that the capture probabilities vary among species and decrease within the capture sequences for some of the species.** 183

## LIST OF TABLES

- Table 2-1: Mean square errors and bias of the exact maximum likelihood (ML), maximum weighted likelihood (MWL), and beta model estimates for 21 populations with the capture probability uniformly distributed between the limits  $L_1$  and  $L_2$ , and actual population size equal to  $N$ . Bias and RMSE are undefined for ML. The values reported here are from the subgroup of finite estimates. 23**
- Table 2-2: Mean square errors and bias of the exact maximum likelihood (ML), maximum weighted likelihood (MWL), and beta model estimates for 6 populations with the capture probability uniformly distributed between the limits  $L_1$  and  $L_2$ , and actual population size equal to  $N$ . 27**
- Table 2-3: The bias and root mean square error (RMSE) for Mahon's (1980) data. 31**
- Table 2-4: The actual probabilities of capture for Mahon's (1980) data calculated directly from the counts. The mean and  $\sigma_p$  are calculated over all capture sequences and sites. The other values are averaged over sites.  $p_1$  - first capture probability,  $p_j$  - mean of all subsequent capture events.  $\gamma$  - proportional change in probability. 34**

<b>Table 2-5: The estimated mean and standard deviations of the Beta distribution of the Beta and Beta-Gamma models for Mahon's (1980) data, as well as estimates of the proportional decrease parameter (<math>\gamma</math>) of the Beta-Gamma model. *Lower limit of the standard deviation as specified by the preset constant (Equation 9 in the algorithm section).</b>	<b>35</b>
<b>Table 3-1: Physical stream characteristics at sampled stations. Distance indicates distance of a station from the estuary.</b>	<b>49</b>
<b>Table 3-2: Atlantic salmon parr regression statistics by station and tributary.</b>	<b>55</b>
<b>Table 4-1: Pearson correlations of growth indicators with various juvenile and adult population abundance indicators. The values correspond to Figure 4-2 except for locally detrended first year growth.</b>	<b>111</b>
<b>Table 4-2: Analysis of covariance demonstrating a significant effect of local density on first year growth and non-significant effect on second year growth, with spawners abundance and tributary controlled statistically. A: <math>R^2=0.143</math>, B: <math>R^2=0.229</math>. See Figure 4-4a,b. The lines highlighted in bold letters are of particular interest (see text)</b>	<b>114</b>

**Table 4-3: Analysis of covariance demonstrating an important heterogeneity in the slopes between tributaries (the interaction term) on the relationship between growth and average tributary densities among years. A:  $R^2=0.049$ ; B:  $R^2=0.205$ . See Figure 4-5a,b. The lines highlighted in bold letters are of particular interest (see text). 115**

**Table 4-4: Analysis of covariance demonstrating the main effect of local density on first and second year growth, with tributary density and tributaries (and their interaction) controlled statistically. A:  $R^2=0.060$ ; B:  $R^2=0.206$ . Local density appears to be an important determinant of first year growth but not of second year growth. The lines highlighted in bold letters are of particular interest (see text). 117**

**Table 4-5: Nested analysis of variance demonstrating the significant effect of the number of adult migrants (spawners) within tributaries on the first and second year growth. A:  $R^2=0.131$ ; B:  $R^2=0.227$ . Growth response to changes in overall population abundance is thus tributary specific. The lines highlighted in bold letters are of particular interest (see text). 119**

**Table 4-6: Analyses of covariance demonstrating the effect of spawner abundance and tributaries on first and second year growth. A:  $R^2=0.131$ , B:  $R^2=0.227$ , C:  $R^2=0.194$ . The significant interaction indicates that response is tributary-specific. The lines highlighted in bold letters are of particular interest (see text). 123**

**Table 4-7: Multivariate ANOVA to test the effect of tributary and overall population abundance on first and second year growth. The corresponding univariate  $R^2$  are: First Year Growth  $R^2=0.131$  and Second Year Growth,  $R^2=0.227$  (from Table 4-6). Canonical correlations are: 1: 0.477, 2: 0.353. The line highlighted in bold letters is of particular interest (see text).**

134

## **GENERAL ABSTRACT**

**This thesis addresses local population consequences of variability in abundance, habitat use and catchability as expressed by Atlantic salmon (*Salmo salar*) juvenile and adult populations in a riverine system.**

**Ranges of abundance are extremely broad among different sampling sites, and classical methods of estimating population abundance lack generality, because they do not use all available information and, in combination with low catchability, often yield unreasonable estimates. A method that simultaneously uses all sampling information from several sites or sampling occasions is developed to estimate local population sizes. It is based on the reconstruction of a statistical (Beta) distribution function from observations within the population.**

**A mechanism is proposed of habitat use as a function of population expansion and contraction with changes in overall population abundance. Variation in local densities proves consistent with the hypothesis that response to fluctuation in population abundance occurs mainly in marginal habitats. Preferred habitats also provided the fastest and most stable growth rates. This accords with more general theories of density-dependent habitat use and on ranges of populations.**

**The scale of density-dependent growth is shown to be much greater than implied by local population density of juveniles, and is also affected by overall population abundance. Furthermore, the strength of density-dependent relationships increases downstream, indicating cumulative effects. Variability of density-dependent growth is shown to be habitat specific and offers further support to the population expansion-contraction mechanism.**

**Some general consequences of habitat-specific density-dependence are discussed.**

## **ACKNOWLEDGEMENTS**

**Ransom A. Myers (Fisheries and Oceans, St. John's, NFLD) was instrumental to the success of the thesis, from his scientific excellence and energy to his friendly support and unrelenting encouragement. He also provided the datasets used in the thesis.**

**My thesis supervisor, Ian McLaren provided timely and judicious scientific advice and encouragement. His calm and positive attitude soothed my internal turmoil.**

**There are several important people who have had a positive influence over the years, unbeknown to some of them. Nancy Shackell for the endless discussions, Nick Hill for letting me loosen up "After all, it's only a thesis", Toby Hay, Daniel Ruzzante, Beren Robinson, Titiek Matricia, Mike Paterson, Roger Doyle and many others. Jean-Marie Sévigny and Raymond Bourgeois were and are the best of friends and their encouragement was constant.**

**Thanks to William Warren and Noel Cadigan for statistical assistance. John Hoening, John Gibson, Daniel Ruzzante, Sandra Walde, Jeffrey Hutchings, Nancy Shackell, Steve Riley, and Mike Chadwick read various parts of the thesis and provided useful comments and suggestions.**

Nick Barrowman, Nick Payton, Stirling Bown and Chris Rendel helped with the programming of S-Plus and MATHEMATICA programs on UNIX-based systems at Fisheries and Oceans, St-John's, NFLD. Marie Harkin produced most of the artwork, checked references and corrected the manuscripts. Becky Field took care of most of the administrative problems while I was off campus.

I would like to pay tribute to my father, Lionel Talbot, autodidactic, who passed away in 1989 after having distinguished himself internationally in the development of electronic components, and my mother, Henriette Harvey, mother of three sons who owe her respect and admiration. They taught us that the only limits that exist are those that we impose on ourselves.

Finally, I would like to thank my wife, Marie Harkin, for helping, listening, and for encouraging me from the beginning. Our two children, Philippe and Marianne, my principal reason for being, I thank for their understanding towards my frequent, prolonged absences and also for the inspiration to continue.

# CHAPTER 1

## GENERAL INTRODUCTION

Habitat selection and the distribution of animals over a geographic range is one of the central themes in ecology (Andrewartha and Birch 1982). Yet, we know very little of the mechanisms controlling contraction and expansion of populations over their distributional range. In addition, although individual growth response to population abundance is an important element of productivity, population growth and fitness, it has received very little attention in this respect, perhaps because the data sets necessary to address this issue are extremely rare.

Density-dependent habitat selection (DDHS), or how population size and local density interact and influence the choice of habitat and hence the relative distribution of the population among habitats, has been the subject of much research over the last 50 years. Much of the work has centred on what is also called optimal foraging, since it has been primarily concerned with short-term exploitation of habitat or "patches" of different types and quality (for example, see reviews by Rosenzweig 1985, 1991; Milinski and Parker 1991; Kacelnik *et al.* 1992a). Many of the models developed assume depletion of the resources and a diminishing rate of return, and whose parameters are embodied in the marginal value theorem (for example, see review by Milinski and Parker 1991). Habitat selection is generally viewed as a special branch of optimal foraging theory (Rosenzweig 1985, 1991; MacArthur and Pianka 1966). These

theoretical developments all assume that animals have a partial or even a perfect knowledge of their environment and of other foraging patches.

Competition within a species forces individuals to use a wide variety of habitats. The Ideal Free Distribution (IFD; Fretwell and Lucas 1970) provides predictions for the optimal distribution of individuals among habitats in order to maximize individual fitness and population size. Again, in habitats of patches that can be depleted by foraging individuals, optimal foraging and the minimization of travel time are important elements of success. However, theoretical work such as that of Hastings (1983) and Holt (1985), using  $n$ -patch, single-species models, demonstrated that dispersal is selected against in a spatially varying, but temporally constant, environment similar to that of a riverine system, and that selection on dispersal rates in a population does not maximize total population size. Hastings (1983) and Holt (1985) provided arguments supporting the hypothesis that the absence of migration among patches is an evolutionarily stable strategy for a single species distributed across  $n$  patches. Atlantic salmon juveniles have particular features of distribution and abundance that facilitate tests of population expansion-contraction mechanisms. We may assume that juveniles know only their own "patch" or habitat, in a sense being "myopic" (Mitchell 1985, in Rosenzweig 1985). Mitchell argues that such myopic animals should discriminate between very different patch types (perhaps such as riffles and pools for juvenile salmon) and much less between similar patch types. In salmon, the habitat is selected by the parental generation through spawning activity and the

building of nests or "redds" in areas suitable for the hatching of eggs and the rearing of larvae and fry. In some populations, salmonid fry move very little from their hatching areas (Elliott 1986). Therefore, distribution of juveniles is in part a reflection of the density-dependent habitat selection by adults. In this thesis, "habitat selection" of parr therefore is more of a "fait accompli" than actual habitat selection or foraging behaviour among patches of variable quality.

Several other researchers have invoked density-dependent habitat selection in the quest of understanding community structure, i. e. multispecies assemblages. Early optimal foraging studies were aimed at understanding community structure of competing species (MacArthur and Connell 1966; MacArthur 1972; Levin 1976, 1986; Rosenzweig 1991), giving rise to, among other theoretical developments, isolog analysis favoured by Pimm *et al.* (1985) and isodars by Morris (1988). These authors and others have shown that competing species will cohabit in preferred habitats at low population densities but that habitat selection depends on the relative frequencies of each species in the species assemblages. A multitude of patterns of habitat selection depend on a very large number of correlated factors, and this complexity is demonstrated in the experimental approaches of Werner and collaborators (Werner and Hall 1976; Werner *et al.* 1983). Habitat selection is thus much more complex among than within species, particularly if the species are competitors of the same resource, or if a predator is modelled into the habitat selection criteria.

Thus, the analysis of multispecies habitat selection has been hampered by the difficulty in isolating and testing components of competition theory (Rosenzweig and Abramsky 1985), and by the application of detailed knowledge of the biology and interaction of a restricted number of species to complex species assemblages and habitat use (Gaston 1990). Direct test of patterns in simple systems may be the best recourse. Fish assemblages in northern rivers, which may provide ideal conditions for testing the population consequences of competition among species because of the relatively low species diversity, may be particularly well suited to these studies. In a series of papers, John R. Gibson and colleagues (Gibson 1966, 1973, 1978, 1981, 1988; Gibson and Dickson 1984; Gibson and Power 1975) demonstrated that Atlantic salmon at high densities can displace brook trout (*Salvelinus fontinalis*) in riffle habitat preferred by both species, although the two species can cohabit at low densities of Atlantic salmon. However, brook trout is not able to exclude Atlantic salmon parr from the preferred riffle habitat at any observed densities despite a size advantage within age-classes. These differences were attributed to the energetic and behavioural advantage of Atlantic salmon parr in the preferred riffle habitat (Gibson 1988).

This study does not deal directly with the reaction to changes in abundance at the edge of a distribution range (see reviews by Gaston 1990, Gaston and Lawton 1988), but draws elements from the theoretical background of such work. Atlantic salmon extend from Ungava Bay to Maine, and historically to New York. The present study is concerned with how a single species population distributes itself within an area that

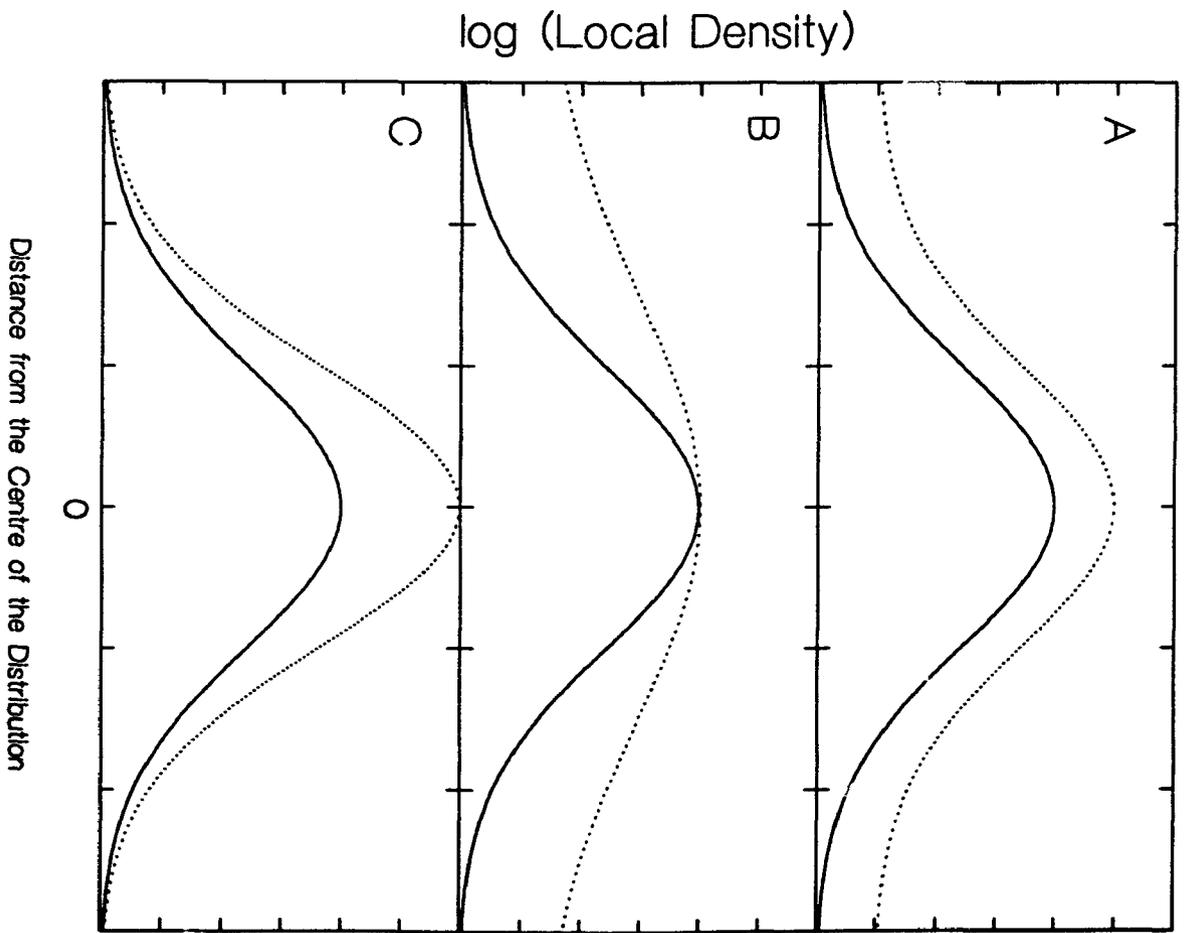
can potentially be surveyed by individuals before habitat selection takes place. Atlantic salmon re-invade their reproductive and juvenile habitat yearly, and spawning site selection is a function of environmental variables and competition among adults (Jones 1959). In this study, a population is defined as the total number of individuals in a river system, while the local population occurs at a sampling station.

Myers (1992) demonstrated that the temporal variability in abundance of three species of marine fish in the North Atlantic is greater at the northern and southern limits of the species range. The variability at the periphery has been attributed to density-independent factors. This has also been reported for non-fish species (Huffaker and Messenger 1964; Richards and Southwood 1968; Coulson and Whittaker 1978), but biological, sampling and analytical difficulties render firm consensus difficult (Gaston 1990; McArdle *et al.* 1990; McArdle and Gaston 1993). For example, temporal population variability depends on the temporal and spatial scale at which populations are sampled (Wiens 1981; Wiens *et al.* 1987; McArdle *et al.* 1990). Gaston (1990) adds that single measures of spatial population variability have little or no generality because of the dependence of the variance on the mean population density in animal populations, so that many forms of spatial comparison (within species, among species) are of little use without a time series covering a significant period of fluctuation in population abundance. Among local populations of species, temporal population variability may be a better predictor of the probability of local extinction than average population size (Karr 1982).

How a population expands and contracts over a geographical range can be represented graphically as it applies to the present study (Figure 1-1a,b,c). A hypothetical situation is shown in which the density of organisms is greatest in the centre of the distribution and declines gradually towards the extremes. I use a Gaussian curve to simplify the presentation as done elsewhere for comparative purposes (Whittaker 1965; Brown 1984), although here we are not dealing with the range of a species but rather the range of a population. In Figure 1-1a, the change in population abundance remains a constant proportion in all habitats, as would be predicted by the Ideal Free Distribution. In Figure 1-1b, the response to changes in population abundance is proportionally greater at the edge of the distribution, so that animals will occupy marginal habitats with an increase in population abundance. In Figure 1-1c, the population density concentrates in the best habitats as population increases, as might be expected if density-independent factors limit densities in marginal habitats.

The dependence of local density of juvenile salmon parr and other salmonids on environmental gradients has been well documented for several variables such as bottom types, water velocity and depth (Symons and Heland 1978; Baglinière and Champigneulle 1982; Egglshaw and Shackley 1982; Kennedy and Strange 1982, 1986; Alexander and Hansen 1986; Heggenes *et al.* 1990), stream discharge (Gibson and Myers 1988), organic load (Gibson and Haedrich 1988; Johnson *et al.* 1990), and stream characteristics (Gibson 1966; Gibson and Power 1975; Baglinière and Arribe-Moutounet 1985; Morantz *et al.* 1987; Gibson *et al.* 1990, 1993; Talbot and Gibson

**Figure 1-1: Theoretical graphical predictions of the expected local changes in population density in response to an increase in population abundance plotted as a function of distance from the centre of the population range. A: Population increases uniformly in all habitats (null hypothesis). B: Population increases in marginal habitats. C: Population concentrates in the primary habitats.**



**Figure 1-1**

1990). These relationships have been used to develop habitat classification systems (Binns and Eiserman 1979; Symons 1979; Coté *et al.* 1987; Kozel and Hubert 1989; Caron and Talbot 1993).

Density-dependent mortality and, to a lesser extent, growth, have been documented for several salmonid species (e.g. Elliott 1984b, 1987, 1988; Gee *et al.* 1978b; Prouzet 1978). There is general agreement that some form of density-dependence operates on juvenile salmonid populations, although some controversy persists as to the shape of stock-recruitment relationships (Solomon 1985). However, it is not known how density-dependence can be a mechanism for population expansion and habitat use. There is some evidence that site-specific response to population abundance may influence the dynamics of production. Gee *et al.* (1978a) found much variation in the production-to-biomass relationship among sampling sites, both in the magnitude and in the slope of the relationship.

Understanding the relationship between population abundance and the responses of local density and growth will contribute to several bodies of theory. Population density and growth rates are important components of productivity and biomass estimates, given by the equations  $B_i = D_i W_i$  and  $P_i = t G W_i B_i$ , and where  $B_i$  represents the biomass at site  $i$  ( $\text{g m}^{-2}$ ),  $D$  is the density ( $\text{no. m}^{-2}$ ),  $W$  is the weight (g),  $t$  is the time interval, and  $Gw$  is the growth rate of weight. Local variation in response produces greater variability in production than might be thought (Gee *et al.* 1978a). Production

estimates can be improved from knowledge of the mechanisms underlying habitat use and population expansion-contraction, but the extensive data sets required for such investigations are rarely available. Such knowledge can also be important in the management of populations. It has been the accepted practice to monitor fluctuations in populations in the best habitats (Hankin and Reeves 1988), but the present study indicates that, because of habitat-specific responses and a decrease in spatial variability with increases in population abundance, the monitoring of secondary sites might be more appropriate.

### **Population Estimation**

In addition to density-dependent habitat selection, other consequences of habitat-specific population abundance require attention. It has been shown that catchability of fish depends on habitat characteristics (Pollock *et al.* 1984; Routledge 1989). Conventional population estimation methods do not consider all the information available to estimate local population abundance, and sampling bias can lead to substantial errors in the estimation of population abundance. The statistical distribution of abundances however, can be estimated for a given spatial or temporal set of samples. Given that this sample distribution is known or approximated, then a substantial improvement in local population estimation is possible. In addition to the improved accuracy and reduced error variance of local population estimates, the large probabilities of infinite estimates in certain types of habitats are completely eliminated

by this method. This is particularly suited for studies of habitat use and for situations in which the captures are subdivided into several subgroups according to species, age or size-classes. It is therefore proposed that patterns of population variability and the statistical distribution of samples can improve population estimation where populations are relatively small and samples are a significant proportion of the population.

The present work consists of five chapters. A general introduction has been presented in this first chapter. Chapter 2 presents a population estimation technique for depletion sampling methods. It is based on the principle that variations in the catchability of animals among sites and sampling occasions provide useful information for estimating the population abundance at a particular site. Chapter 3 presents a statistical treatment of the interaction between adult abundance and local juvenile population density over 8 years among several sampling sites on a small river system in Newfoundland, the Little Codroy River. Chapter 4 presents a study of the scale of density-dependent growth. It also demonstrates habitat-specific density-dependent growth and relates it to mechanisms of density-dependent habitat selection. A general discussion (Chapter 5) studies the implication of the results of the thesis, and develops and integrates patterns observed in the present thesis into the existing theoretical framework of habitat selection.

## **CHAPTER 2**

### **SIMULTANEOUS ANALYSIS OF REMOVAL DATA FROM MANY SITES**

#### **INTRODUCTION**

**The estimation of population abundance in animal populations is an important element of any ecological study. Yet, methods developed to date often lack the rigour required for proper interpretation of distribution and abundance data. For example, habitat assessment studies depend intrinsically on reliable population estimation methods across all types of habitats encountered. The failure of estimation methods (e.g. Zippin 1958) to reach a solution (what is often called "estimator failure" in the literature) has often led to the substitution of the actual total count of captured animals for the estimated population size. This correction in effect assumes that the capture probability is 1 when in fact it is more likely to be near 0. Occasionally, the station is simply dropped from the analysis. Both of these methods of corrections result in serious bias in estimation of habitat use.**

**The importance of reliable population estimation methods to the study of patterns of habitat selection in animals must be emphasized. Ironically, it is precisely when population census incorporates heterogeneous habitats that traditional methods fail. Many species use micro-habitats in a manner that renders low capture probabilities. For example, darters of the genus *Etheostoma* hide under rocks in streams and are**

very difficult to capture, but are among the most abundant animals in many water bodies of North America and are an important component of biomass and production (Mahon 1980). It is also well known that the efficiency of electrofishing capture methods depend on environmental conditions such as water hardness, velocity, depth, work experience of the sampling team (Peterson and Cederholm 1984; Cowx 1990).

There are two major classes of population estimation methods commonly used for salmonids: 1) mark-recapture methods, where all members of a population captured on a given occasion are marked and released back into the population, and 2) removal without replacement methods. In removal methods for estimating population abundance, animals are sequentially removed from an area by electrofishing or trapping. Population size is estimated from the successive decreases in catches or catch per unit effort; only the case where effort is constant between each successive capture event is considered here, but both techniques are comparable. In this chapter, removal methods are considered.

The main difficulties of traditional maximum likelihood methods of analysing removal data are that 1) solutions do not always exist (Pollock 1991), 2) relatively low precision is achieved if capture probability is low, and 3) catchability may vary among the sequence of capture events. The first problem largely can be solved by adopting a Bayesian approach in which a non-informative prior distribution for capture probability is assumed (Carle and Strub 1978). The second problem is fundamental; improved

estimates are sought by examining the variability of capture probability among sites. The third problem can be approached by allowing the capture probability to vary with capture event (Otis *et al.* 1978; Schnute 1983). However, by estimating different capture probabilities, the confidence limits of the estimate of population size are increased. For example, Schnute (1983) found that 6 of the 17 Atlantic salmon datasets he analyzed had a significant decrease in capture probability with successive sampling. However, the 95 % confidence intervals for abundance calculated in each of these six cases extended to positive infinity. It frequently may be possible to estimate non-constant capture probability, but the resulting estimates of population may have too little precision to be useful. Although this can be partially overcome by increasing the number of capture events, this is often not practical.

The approach taken here is that the estimation for each site should not be considered in isolation. Very often, identical sampling techniques are used at a large number of sites. By considering these simultaneously it may be possible to estimate the variation in capture probabilities between sites and between capture events at a site.

### **ESTIMATION AT SINGLE SITES**

The assumptions of the removal method are: 1) changes in population size only occur through sampling, and 2) the probability of capture is the same for all individuals at each sampling occasion. The second assumption will later be modified.

Let  $C_{ij}$  be the number of animals caught at the  $i^{\text{th}}$  site on the  $j^{\text{th}}$  capture event. The sequence of capture events is referred to as a "capture sequence". There are  $J_i$  capture events at site  $i$ , and there are  $I$  sites. The number of animals at each site,  $N_i$ ,  $i=1,2,\dots,I$  must be estimated. The probability of capture at site  $i$  during capture event  $j$  is  $p_{ij}$ . The catch at any occasion (capture event)  $C_{ij}$  is assumed to be binomial, so that the joint probability of the  $J_i$  catches is multinomial. The likelihood derived from the joint probability of observing  $C_{ij}$  for  $j=1,2,\dots,J_i$  at site  $i$  is

$$L(C_{i1}, C_{i2}, \dots, C_{iJ_i} | N_i, p_{i1}, p_{i2}, \dots, p_{iJ_i}) = \frac{N_i!}{(N_i - T_{ij})!} \prod_{j=1}^{J_i} \frac{p_{ij}^{C_{ij}} (1-p_{ij})^{N_i - T_{ij}}}{C_{ij}!}, \quad (1)$$

$$\text{where } T_{ij} = \sum_{j=1}^{J_i} C_{ij}.$$

The most common assumption is that  $p_{ij}$  is constant across capture events ( $j$ ) at a given site. For a single site there are approximate solutions to finding the maximum of Equation (1) (Moran 1951; Zippin 1956; Soms 1985), and exact maximum likelihood solutions (Otis *et al.* 1978) which are analytic for  $J=2$  but must be obtained iteratively for other cases. A near-Bayesian approach is described by Carle and Strub (1978). They propose a maximum weighted likelihood (MWL) estimation of  $N_i$  by integrating over the range of  $p$  with a Beta prior; this represents a compromise between a Bayesian and non-Bayesian approach. They claim a smaller bias and mean square error than the maximum likelihood solution when  $J=3$  but they arbitrarily select values of  $\alpha$  and  $\beta$  for the Beta distribution, which could in theory be selected from visual

examination of the distribution of the capture probabilities estimated by maximum likelihood. The assumption is made initially that the capture probability at site  $i$  is constant during all capture events, i. e.  $p_{ij} = p_{i1}$  for  $j > 1$ , which will be called  $p_i$ , but this assumption will be relaxed in the section on variation in catchability with capture sequence.

### SIMULTANEOUS ANALYSIS OF MANY SITES WITH NO EFFECT OF CAPTURE SEQUENCE

Improvements in the estimation of population abundance can be made by assuming a prior weighting of capture probabilities. Improved estimator may be possible if the underlying distribution of capture probabilities are estimated from the data. This is done by assuming that the capture probability for any site is a random variable that does not change with capture event  $j$ , e.g. capture probability  $p_i$  at a site  $i$  is a random variable from a beta density function given by

$$f_{\alpha,\beta}(p_i) = \frac{(\alpha+\beta+1)!}{(\alpha-1)! (\beta-1)!} p_i^{\alpha-1} (1-p_i)^{\beta-1}, \quad (2)$$

where the first term of (2) is the beta function  $B(\alpha,\beta)$ , and  $0 \leq p_i \leq 1$ ,  $1 \leq \alpha$ ,  $1 \leq \beta$ .

Let  $N$  be the vector of the total population size to be estimated at the  $I$  sites, with elements  $N_i$  and  $C$  be the matrix of capture sequences at  $I$  sites and  $J$  capture events,

with elements  $C_{ij}$ . The joint density function for the  $i^{\text{th}}$  row of  $C$  and  $p_i$  with respect to  $\alpha$  and  $\beta$  becomes

$$P_{\alpha,\beta}(p_i | C_{i1}, C_{i2}, \dots, C_{ij}, N_i) \propto L(C_{i1}, C_{i2}, \dots, C_{ij} | N_i, \alpha, \beta) f_{\alpha,\beta}(p_i). \quad (3)$$

Thus, the joint likelihood of observing the matrix of captures  $C$  at  $I$  sites is the product over all sites of equation (3) integrated over the range of  $p_i$ , (0,1). The resulting likelihood is

$$\begin{aligned} L(C | N, \alpha, \beta) &= \prod_{i=1}^I \frac{N_i!}{(N_i - T_i)! \prod_{j=1}^{J_i} C_{ij}} \int_0^1 p_i^{T_i} (1-p_i)^{J_i N_i - X_i - T_i} p_i^{\alpha-1} (1-p_i)^{\beta-1} B(\alpha, \beta) dp_i \\ &= B(\alpha, \beta) \prod_{i=1}^I \frac{N_i!}{(N_i - T_i)! \prod_{j=1}^{J_i} C_{ij}} B(T_i + \alpha - 1, J_i N_i - X_i - T_i + \beta - 1), \end{aligned} \quad (4)$$

where  $X_i = \sum_{j=1}^{J_i} (J_i - j) C_{ij}$ . The parameters  $\alpha$  and  $\beta$  of the beta distribution and  $N_i$  for

each site can be estimated by maximizing the above likelihood. This model will be referred to as the Beta model.

The joint likelihood (4) is simply the product over sites of the single-site likelihood used by Carle and Strub (1978). However, they did not estimate the parameters of the Beta distribution but, rather, simply used  $\alpha = \beta = 1$ , i. e. a uniform prior for the capture probabilities equivalent to  $p=0.5$  and  $\sigma_p = 1/12$ .

### VARIATION IN CATCHABILITY WITH CAPTURE SEQUENCES

Empirical studies of stream fishes have shown the assumption of constant catchability is so badly violated as to make depletion methods often inapplicable (Mahon 1980; Cross and Scott 1975; Raleigh and Short 1981; Schnute 1983). Methods of dealing with heterogeneity in the capture probabilities among the capture events have been developed by several authors, but the most comprehensive is the CAPTURE program by Otis *et al.* (1978).

It is assumed that the capture probability at any site is a random variable, and that probabilities for subsequent capture events at that site are functions of the capture probability during the initial capture event. The simplest assumption is that the capture probability after the initial capture event at a site  $i$  is a fraction  $\gamma$  of the initial capture

probability, such that  $p_{ij} = \begin{cases} p_i & \text{if } j = 1 \\ \gamma p_i & \text{if } j > 1 \end{cases}$ . If the  $p_i$  is distributed as a beta random

variable, a straightforward modification of model (3) is obtained, in which one more parameter must be estimated. The resulting likelihood is

$$\begin{aligned}
L(C|N, \alpha, \beta, \gamma) &= \prod_{i=1}^I \frac{N_i!}{(N_i - T_{ij})! \prod_{j=1}^{J_i} C_{ij}!} \\
&\quad \cdot \int_0^1 p_i^{C_{ij}} (1-p_i)^{N_i - C_{ij}} \prod_{j=2}^{J_i} (\gamma p_i)^{C_{ij}} (1-\gamma p_i)^{N_i - T_{ij}} p_i^{\alpha-1} (1-p_i)^{\beta-1} B(\alpha, \beta) dp_i \\
&= B(\alpha, \beta) \prod_{i=1}^I \frac{N_i!}{(N_i - T_{ij})! \prod_{j=1}^{J_i} C_{ij}!} \\
&\quad \cdot \int_0^1 \gamma^{T_{ij} - C_{ij}} p_i^{T_{ij} + \alpha - 1} (1-p_i)^{N_i - C_{ij} + \beta - 1} (1-\gamma p_i)^{J_i - T_{ij} - (N_i - C_{ij})} dp_i
\end{aligned} \tag{5}$$

where  $0 \leq \gamma \leq 1$ . A numerical solution to the above equation is used. This model will be referred to as the Beta-Gamma model.

It is possible to generalize the above approach in a manner similar to that used by Otis *et al.* (1978). That is, a sequence of parameters can be fit to describe the change in catchability, and their significance determined by a likelihood ratio test. An alternative approach is to parameterize capture probability as a function of the capture sequence in a manner similar to that used by Schnute (1983). Schnute's method assumes that the change in probability of capture from event to event is a constant

fraction of the initial probability. The problem reduces to the Beta model when the  $\gamma$  parameter tends to 1.

### VARIATION AMONG SITES ASSOCIATED WITH ENVIRONMENTAL VARIABLES

If it is thought that environmental variables affect capture probability (Pollock *et al.* 1984; Routledge 1989), the mean of the beta function can be assumed to be a function of the environmental variable, e.g. a logistic function. This function can be

$$p' = \frac{e^{\alpha+\beta x}}{1+e^{\alpha+\beta x}}, \quad (6)$$

where  $x$  is an explanatory environmental variable and  $p'$  is the mean probability of capture. An alternative approach is to classify sites into discrete classes and estimate the parameters of the beta distribution separately for each class of sites. A simple approach is to keep the standard deviation of the distribution of  $p$  constant and fit different means for each discrete category. The  $\alpha$  and  $\beta$  parameters of the Beta function are estimated for each site independently. A likelihood ratio test can be used to determine the significance of new estimates.

## ALGORITHM

Although the approach adopted here greatly increases the number of parameters that have to be estimated simultaneously, the increase in computational complexity is not too great. For given  $\alpha$  and  $\beta$ , the parameters  $N_i$  which maximize (3) can be found independently for each site. The logarithms of these likelihoods are summed to obtain the overall likelihood. Thus a maximization problem with  $I+2$  parameters is changed to a two-parameter problem in which  $I$  single-parameter solutions are obtained for each pair of  $\alpha$  and  $\beta$ . In practice, it is best not to estimate  $\alpha$  and  $\beta$  directly but to estimate in terms of the mean and standard deviation of the beta distribution, which are easy to understand. The mean must be constrained between 0 and 1, and the standard deviation must be constrained to be greater than zero.

In none of the simulated and real data sets that were analyzed was there a problem with using an unconstrained minimization algorithm for the mean; however, the constraint on the standard deviation presents a problem because a solution of a constant  $p$  is often obtained. This can be solved by using a constrained minimization algorithm or by using a transformation. For example, the standard deviation  $\sigma$  can be set to a non-zero value by the transformation

$$\sigma = \sigma_0 + e^x \tag{9}$$

where  $x$  is the variable used by the minimization algorithm and  $\sigma_0$  is a small preset constant (0.05 in the presented estimates). In practice,  $\sigma = \sigma_0$  on seven occasions in tests with field data (see the section on "Testing the models with field data"). This indicates that the value of  $p$  is constant for all elements of the group.

The analysis was performed using the S-PLUS programming language, available from Statistical Sciences, Inc., 1700 Westlake Ave. N., Suite 500, Seattle, WA 98109 USA. Programs are available for use.

## SIMULATION TESTS

The Beta models were tested with simulated data. A series of sampling stations were defined with a fixed number of fish and capture events (Table 2-1). Probability of capture was constrained to be uniformly distributed between a lower limit ( $L_1$ ) and upper limit ( $L_2$ ) for each of the fish density and number of capture sequence combinations and for 21 sites; each combination was simulated 200 times. This distribution was selected as an extreme case within the restriction of unimodality for the capture data. The distribution of the capture probabilities was constrained for the different groups to be between 0.1-0.2, 0.2-0.4, 0.4-0.6 and 0.6-0.8. Probability of capture remained constant with time (capture sequences). Results for combinations when  $J$  and capture probability were both high are not shown, as all methods did

**Table 2-1: Mean square errors and bias of the exact maximum likelihood (ML), maximum weighted likelihood (MWL), and beta model estimates for 21 populations with the capture probability uniformly distributed between the limits  $L_1$  and  $L_2$ , and actual population size equal to  $N$ . Bias and RMSE are undefined for ML. The values reported here are from the subgroup of finite estimates.**

Parameters				ML			MWL			Beta			Combined		
J	N	$L_1$	$L_2$	Bias*	Median	RMSE*	Bias	Median	RMSE	Bias	Median	RMSE	Bias	Median	RMSE
3	20	0.1	0.2	-7.67	11	12.95	-10.61	9	11.44	-10.30	10	10.89	-8.08	12	9.24
3	20	0.2	0.4	-0.44	16	14.65	-4.36	15	6.45	-4.63	16	5.80	-0.31	19	5.42
3	20	0.4	0.6	0.51	19	11.00	-1.02	19	3.17	-1.61	19	2.49	0.59	20	3.20
3	20	0.6	0.8	-0.26	20	2.63	-0.34	20	1.17	-0.60	20	1.02	-0.26	20	1.03
3	50	0.1	0.2	-5.27	35	45.91	-20.86	27	24.21	-18.28	31	20.27	-5.94	42	15.90
3	50	0.2	0.4	7.10	46	53.49	-5.75	43	12.88	-6.54	44	10.21	8.22	56	17.89
3	50	0.4	0.6	0.24	49	13.47	-1.01	48	5.46	-2.10	48	4.23	0.42	50	4.99
3	50	0.6	0.8	-0.54	50	1.93	-0.57	50	1.86	-1.07	49	1.85	-0.53	51	1.61
3	200	0.1	0.2	13.61	178	147.27	-43.31	145	72.48	-45.12	155	55.23	16.04	210	58.21
3	200	0.2	0.4	8.18	194	70.58	-5.86	189	39.02	-14.54	187	30.39	12.28	213	35.98
3	200	0.4	0.6	-0.24	198	12.60	-0.96	198	11.84	-3.99	197	11.27	0.11	201	10.91
3	200	0.6	0.8	-0.55	199	3.57	-0.56	199	3.55	-1.27	199	3.45	-0.55	200	3.28

\*estimates > 1000 eliminated from series.

Table 2-1: continued

Parameters				ML			MWL			Beta			Combined		
J	N	L <sub>1</sub>	L <sub>2</sub>	Bias*	Median	RMSE*	Bias	Median	RMSE	Bias	Median	RMSE	Bias	Median	RMSE
5	20	0.1	0.2	-0.29	15	21.51	-6.53	13	8.05	-6.19	14	7.21	-0.47	19	6.67
5	20	0.2	0.4	1.14	19	17.63	-1.84	18	3.87	-2.21	18	3.34	1.36	21	5.04
5	20	0.4	0.6	-0.32	20	1.52	-0.45	20	1.21	-0.69	20	1.15	-0.32	20	1.03
5	50	0.1	0.2	10.26	43	81.59	-10.61	38	16.35	-10.38	40	13.22	10.92	56	24.83
5	50	0.2	0.4	1.64	48	29.59	-2.12	47	7.2	-3.36	47	6.24	2.29	52	9.74
5	50	0.4	0.6	-0.51	50	2.07	-0.64	49	1.98	-0.93	49	1.85	-0.50	50	1.71
5	200	0.1	0.2	18.53	193	108.03	-12.01	180	50.53	-21.34	181	35.03	22.24	221	47.62
5	200	0.2	0.4	0.1	198	21.83	-1.49	197	17.66	-6.63	196	16.72	1.77	204	16.50
5	200	0.4	0.6	-0.69	199	3.85	-0.79	199	3.83	-1.43	199	3.82	-0.68	200	3.64
7	20	0.1	0.2	1.11	17	23.34	-4.20	15	6.12	-4.15	16	5.32	1.21	20	6.89
7	20	0.2	0.4	-0.18	19	6.80	-1.03	19	2.44	-1.35	19	2.26	-0.08	20	2.53
7	50	0.1	0.2	6.67	46	56.04	-5.32	43	12.40	-6.51	44	9.45	7.82	54	19.21
7	50	0.2	0.4	-0.30	49	6.32	-1.13	49	4.28	-2.05	49	4.01	-0.17	50	3.78
7	200	0.1	0.2	7.42	197	60.16	-4.97	191	33.83	-19.79	182	27.92	9.66	211	28.86
7	200	0.2	0.4	-0.40	199	9.29	-1.11	199	8.79	-3.14	198	8.23	-0.35	201	7.80

\*estimates >1000 eliminated from series

equally well because virtually all fish were caught.

The fits of the various models were evaluated by comparison of the bias and root mean square error (RMSE). The bias is calculated as:  $BIAS = E(\hat{N}) - N$  and RMSE as  $RMSE = \sqrt{\sigma^2 + BIAS^2}$ . These were calculated for the 21 sites within the different combinations described above. If the maximum likelihood estimate of population was greater than 1000, the maximum likelihood result was not used in the computation of the bias and RMSE. This in effect eliminated estimates of infinity (estimator failure). The bias and RMSE for the Maximum Likelihood (ML) estimator are both technically undefined because its expectation and variance are infinite because of the finite probability of a population size estimate of infinity. The "bias" and "RMSE" estimates in Table 2-1 are thus dependent upon which cutoff value is used. The bias is not a very meaningful means of comparison in this context. The results for the ML and CAPTURE estimates are not directly comparable to MWL and the Beta models because of the above reasons. However, the median of the distribution of estimates is defined for all estimators since infinite estimates can be considered in the calculation.

The Beta model (Table 2-1) yielded the smallest RMSE, with biases similar to the MWL of Carle and Strub (1978). Nevertheless, the ML estimator usually has the smallest "bias", but this is achieved as a result of the very large positive skewness of the distribution, particularly with  $J=3$  (The figures for this chapter are given as an

appendix for convenience. Please refer to Figure A-1). The combined estimator is much less biased with respect to the true  $N$  than the Beta model but the variance is greater.

To examine the effect of number of sites on the Beta distribution function parameter estimates, the simulations were repeated with a small number of sites, i.e. 6 instead of 21 (Table 2-2). The results were similar to those reported in Table 2-1; the Beta model again provided the lowest RMSE although these were very slightly larger than those reported for 21 sites (Table 2-1). It appears that it is not essential to use a large number of sites to benefit from the prior estimation of the distribution of capture probabilities. Estimates are improved from simultaneous analysis of even a small number of sites.

The median of the simulated values of the ML and Beta estimators are similar for most cases, with the possible exception of a combination of small  $J$  (number of sampling events) and large  $N$  (Table 2-1). Interestingly, the MWL estimator is consistently the most biased, as might be expected from the use of a non-informative prior, except when probabilities of capture are high, in which case all methods do equally well.

The ML estimator is usually less "biased", and the Beta estimator always has a lower RMSE (Table 2-1). Could a low-bias and low-RMSE estimator be devised? An

**Table 2-2: Mean square errors and bias of the exact maximum likelihood (ML), maximum weighted likelihood (MWL), and beta model estimates for 6 populations with the capture probability uniformly distributed between the limits  $L_1$  and  $L_2$ , and actual population size equal to N.**

J	Parameters			ML		MWL		BETA	
	N	$L_1$	$L_2$	bias*	RMSE*	bias	RMSE	bias	RMSE
5	20	0.2	0.4	1.189	16.935	-1.886	4.084	-2.192	3.604
5	20	0.4	0.6	-0.342	2.585	-0.51	1.272	-0.741	1.232
5	50	0.2	0.4	0.691	15.702	-2.151	7.695	-3.384	6.996
5	50	0.4	0.6	-0.489	2.254	-0.628	2.134	-0.999	2.047
5	200	0.2	0.4	2.205	25.888	-0.922	19.132	-6.581	17.464
5	200	0.4	0.6	-0.625	4.112	-0.732	4.08	-1.417	4.163

\*estimates >1000 eliminated from series.

estimator which combined the ML and Beta estimator was evaluated.

The combined estimator was defined as

$$\hat{N}_{combined} = \hat{N}_{\beta} \frac{1}{n} \sum_1^n \frac{\hat{N}_{ML}}{\hat{N}_{\beta}} \quad (12)$$

where  $\hat{N}_{\beta}$  is the beta estimator,  $\hat{N}_{ML}$  is the maximum likelihood estimator, and  $n$  is the number of sites where the ML estimator converged. When the ML estimator does not converge, equation (7) yields simply the Beta model estimate. The average estimated bias is only calculated over sites where the ML estimator converged.

For low capture probability the combined estimator often has the lowest bias and the median closest to the true population size, but the error variance (RMSE) is greater than in the Beta model (Table 2-1, Figure A-1). The median is also closer to the real population size than for other methods.

### TESTING THE MODELS WITH FIELD DATA

The Beta and other published models were tested with data published in Mahon's (1980) Appendix 1. Mahon (1980) presented data from 11 sites. Sections of a stream were closed off and an electrofishing apparatus used to estimate population abundance.

Five to 8 passes (capture events) were made at each site. The fish were removed without replacement. All remaining fish were collected using rotenone as a piscicide.

The data for each species were analyzed separately but combined length classes are given in Mahon's Appendix 1. Two species were from 5 streams in Poland and 6 sites were in Ontario, Canada. Of those in Canada, four were done with 30 minutes between capture events and the rest were done with 90 minutes between capture events. This variation in the methods, sites and species surveyed presumably increased the heterogeneity of the capture probabilities in the data set.

Mahon's (1980) data are useful in the present context because the total number of fish at a sampling site and the true capture probabilities for each capture event are known. The capture sequences can be used to evaluate the accuracy and bias of the different models presented here. The capture probabilities vary widely among species and sites (Figure A-2). For several species, the probability of capture is very low, particularly for benthic species (e.g. *Etheostoma* spp.), and combinations of low catchability and low abundance are common. It is also evident that the capture probabilities are extremely heterogeneous within the capture sequence. These generally, but not always, decrease along the sequence, indicating that there may be a decrease in the probability of capture along the capture sequence ( $\gamma < 1$ ).

Heterogeneity in the capture probabilities within the capture sequence further increases the complexity in the data set. These data thus provide an extreme test of the models. The results of CAPTURE were compared, whenever available, to results from the models developed in this chapter as well as to the exact maximum likelihood (ML) and maximum weighted likelihood (MWL) models (Table 2-3). The initial model was used where  $\alpha$  and  $\beta$  was estimated, which is termed the Beta model, and the modified (Beta-Gamma) model, where the decrease in capture probability  $\gamma$  for capture events after the first is estimated. To accommodate the program CAPTURE, some of the capture sequences for Mahon's (1980) data were divided by 10 and truncated to the nearest integer value. This was necessary because of the abnormally large catches in some of the sequences that cannot easily be accommodated by some algorithms. These data however have much larger values than would normally be found in depletion survey methods. This transformation has no effect on the estimated parameters.

The estimated mean and standard deviations of the Beta distribution, corresponding to the probabilities of capture as well as the proportional decrease parameter (Beta-Gamma model) are highly variable among species. The true probability of capture, as calculated from the catch data, range from a low of 0.095 for a darter (*Etheostoma flabellare*) to a high of 0.335 for *Catostomus commersoni* (Table 2-4). In 13 of the 15 species studied the catchability decreases within the capture sequence ( $\gamma < 1$ ). This is comparable to a number of studies that have demonstrated that probabilities of capture decrease after the first sampling episode (Otis *et al.* 1978; Raleigh and Short 1981;

Table 2-3: The bias and root mean square error (RMSE) for Mahon's (1980) data.

<b>BIAS TABLE</b>					
<b>Species</b>	<b>ML</b>	<b>MWL</b>	<b>BETA</b>	<b>BETA-GAMMA</b>	<b>CAPTURE</b>
<i>Ambloplites rupestris</i>	-4.4	-7.2	-7.4	-6.0	-6.8
<i>Catostomus commersoni</i>	-10.5	-10.5	-6.7	-5.7	-3.7
<i>Etheostoma caeruleum</i>	-155.3	-156.7	-33.5	-85.8	-15.5
<i>Etheostoma flabellare</i>	-13.5	-31.2	195.5	-130.8	271.8
<i>Etheostoma nigrum</i>	-28.5	-28.7	-27.8	-25.0	-4.5
<i>Hypentelium nigricans</i>	-0.8	-0.8	-0.8	-0.8	-0.8
<i>Micropterus dolomieu</i>	-4.8	-4.8	-2.8	-2.5	-2.3
<i>Nocomis spp.</i>	-68.0	-68.2	-65.2	-63.5	-63.3
<i>Notropis cornutus</i>	-457.0	-457.5	-439.2	-467.0	-412.3
<i>Pimephales notatus</i>	-69.2	-179.4	33.6	-210.8	-88.2
<i>Rhinichthys atratulus</i>	-23.7	-23.8	-22.3	-20.8	-15.5
<i>Rhinichthys cataractae</i>	-25.3	-25.8	-17.8	-14.5	-12.8
<i>Semotilus atromaculatus</i>	-31.5	-32.2	-30.3	-29.2	-26.2
<i>Noemacheilus barbatulus</i>	-100.8	-101.0	-82.6	-77.6	-71.2
<i>Phoxinus phoxinus</i>	-363.6	-363.8	-326.2	-326.6	337.2
<b>Mean Absolute Bias</b>	<b>90.5</b>	<b>99.4</b>	<b>86.1</b>	<b>97.8</b>	<b>87.9</b>
<b>Percent Bias</b>	<b>-17.97</b>	<b>-21.69</b>	<b>-13.40</b>	<b>-17.96</b>	<b>-13.20</b>

Table 2-3: continued.

<b>RMSE TABLE</b>					
<b>Species</b>	<b>ML</b>	<b>MWL</b>	<b>BETA</b>	<b>BETA-GAMMA</b>	<b>CAPTURE</b>
<i>Ambloplites rupestris</i>	12.1	10.5	10.1	8.2	10.4
<i>Catostomus commersoni</i>	17.4	17.4	12.9	11.9	20.3
<i>Etheostoma caeruleum</i>	213.6	215.0	165.6	123.8	163.7
<i>Etheostoma flabellare</i>	1100.0	1071.9	893.7	371.1	1104.7
<i>Etheostoma nigrum</i>	51.8	52.2	53.3	46.6	14.5
<i>Hypentelium nigricans</i>	0.9	0.9	0.9	0.9	0.9
<i>Micropterus dolomieu</i>	6.7	6.7	3.6	3.2	3.0
<i>Notemigonus crysoleucas</i>	125.9	126.3	127.8	141.8	138.4
<i>Notropis cornutus</i>	870.5	871.0	862.2	899.4	761.8
<i>Pimephales notatus</i>	554.1	464.9	706.9	488.7	550.4
<i>Rhinichthys atratulus</i>	32.0	32.2	31.1	29.8	20.2
<i>Rhinichthys cataractae</i>	48.5	48.6	36.0	32.9	34.4
<i>Semotilus atromaculatus</i>	40.2	40.8	37.4	36.0	32.1
<i>Noemacheilus barbatulus</i>	112.0	112.2	96.0	90.0	84.6
<i>Phoxinus phoxinus</i>	660.2	660.3	590.4	585.6	615.3
<b>Mean RMSE</b>	<b>250.4</b>	<b>248.7</b>	<b>241.9</b>	<b>191.3</b>	<b>237.0</b>

Schnute 1983; Peterson and Cederholm 1984; Bohlin and Cowx 1990).

The estimated mean and standard deviation of the Beta distribution are generally greater than the true probabilities (Table 2-5), resulting in the negative bias characteristic of the maximum likelihood methods. The Beta-Gamma model has a significantly better fit to Mahon's (1980) data than the Beta model in 7 species (with one ambiguous case). The Beta-Gamma value for the initial probability is slightly greater than the overall mean estimated by Beta. The proportional decrease parameter  $\gamma$  is usually slightly greater than the actual value (Table 2-4).

The bias and RMSE were calculated for each species over all sites. It is apparent from Table 2-3 that the Beta model usually has lower RMSE than ML or MWL. The Beta estimator has the lowest overall bias and the Beta-Gamma estimator had the lowest RMSE overall for Mahon's data. The CAPTURE method ranked second overall for RMSE, closely followed by the Beta model. Both Beta-Gamma and CAPTURE estimators had 6 out of 15 lowest RMSE's, but Beta-Gamma was lower overall.

The CAPTURE estimator did well at reducing the bias, obtaining the smallest value in 10 out of 15 cases. However, this is only because the bias was large and positive for some species, which reduced the mean absolute bias.

Table 2-4: The actual probabilities of capture for Mahon's (1980) data calculated directly from the counts. The mean and  $\sigma_p$  are calculated over all capture sequences and sites. The other values are averaged over sites.  $p_1$  - first capture probability,  $p_j$  - mean of all subsequent capture events.  $\gamma$  - proportional change in probability.

species	Actual Probabilities					
	$\mu_p$	$\sigma_p$	$p_1$	$\sigma_{p1}$	$p_j$	$\gamma$
<i>Ambloplites rupestris</i>	.132	.140	.243	.113	.114	0.469
<i>Catostomus commersoni</i>	.335	.224	.394	.194	.325	0.825
<i>Etheostoma caeruleum</i>	.140	.070	.199	.067	.131	0.658
<i>Etheostoma flabellare</i>	.095	.038	.131	.033	.089	0.679
<i>Etheostoma nigrum</i>	.131	.133	.093	.088	.137	1.473
<i>Hypentelium nigricans</i>	.295	.277	.388	.270	.277	0.714
<i>Micropterus dolomieu</i>	.269	.213	.205	.174	.283	1.381
<i>Nocomis spp.</i>	.248	.169	.346	.078	.232	0.671
<i>Notropis cornutus</i>	.161	.168	.227	.195	.151	0.665
<i>Pimephales notatus</i>	.153	.159	.229	.175	.141	0.616
<i>Rhinichthys atratulus</i>	.211	.151	.310	.125	.194	0.626
<i>Rhinichthys cataractae</i>	.289	.125	.313	.113	.285	0.911
<i>Semotilus atromaculatus</i>	.178	.116	.284	.112	.162	0.570
<i>Noemacheilus barbatulus</i>	.186	.087	.271	.056	.169	0.624
<i>Phoxinus phoxinus</i>	.150	.095	.210	.092	.139	0.662

Table 2-5: The estimated mean and standard deviations of the Beta distribution of the Beta and Beta-Gamma models for Mahon's (1980) data, as well as estimates of the proportional decrease parameter ( $\gamma$ ) of the Beta-Gamma model. \*Lower limit of the standard deviation as specified by the preset constant (eq. 9 in the algorithm section).

species	BETA			BETA-GAMMA				Likelihood ratio	
	mean	s.d.	L	mean	s.d.	$\gamma$	L	2 $\Delta$ L	Prob
<i>Ambloplites rupestris</i>	0.311	0.062	6.76	0.375	0.05*	0.540	9.28	5.04	0.025
<i>Catostomus commersoni</i>	0.406	0.128	1173.46	0.422	0.135	0.902	1174.57	2.22	0.135
<i>Etheostoma caeruleum</i>	0.244	0.065	1009.94	0.265	0.073	0.647	1019.79	19.70	<0.001
<i>Etheostoma flabellare</i>	0.147	0.05*	1276.78	0.159	0.05*	0.730	1281.89	10.22	0.001
<i>Etheostoma nigrum</i>	0.251	0.05*	1097.83	0.249	0.05*	0.829	1099.05	2.44	0.118
<i>Hypentelium nigricans</i>	0.431	0.05*	15.95	0.504	0.05*	0.743	16.92	1.94	0.164
<i>Micropterus dolomieu</i>	0.357	0.05*	227.48	0.361	0.05*	0.951	227.50	0.04	0.833
<i>Nocomis spp.</i>	0.347	0.05*	763.70	0.371	0.05*	0.796	766.36	5.32	0.021
<i>Notropis cornutus</i>	0.331	0.139	1219.78	0.324	0.136	1.060	1220.16	0.76	0.385
<i>Pimephales notatus</i>	0.243	0.176	1975.85	0.255	0.093	0.964	1977.36	3.02	0.082
<i>Rhinichthys atratulus</i>	0.336	0.061	707.79	0.348	0.052	0.852	709.00	2.42	0.121
<i>Rhinichthys cataractae</i>	0.326	0.079	3347.76	0.338	0.084	0.889	3349.98	4.44	0.035
<i>Semotilus atromaculatus</i>	0.344	0.118	1417.56	0.355	0.123	0.924	1418.09	1.06	0.304
<i>Noemacheilus barbatulus</i>	0.331	0.05*	4404.50	0.340	0.05*	0.901	4406.36	3.72	0.054
<i>Phoxinus phoxinus</i>	0.282	0.05*	976.74	0.290	0.05*	0.893	977.38	1.28	0.264

## DISCUSSION

In general, maximum likelihood estimators are biased at low values of  $N$ ,  $p$  and  $J$ . In such instances, the distribution of ML estimates is highly positively skewed (Figure A-1), and the Beta estimator is slightly negatively skewed. The combined estimator had a larger variance than the Beta estimator but was less biased. The problem of estimator bias was not solved directly by estimating the distribution of capture probabilities among sites, but the reduction in error variance and the elimination of estimator failure addressed the more general problem of reliability for ecological studies.

The use of Bayesian methods to incorporate prior information on the probabilities of capture from sampling surveys is shown to be generally more robust than maximum likelihood (ML). Pollock (1991) has recognized the potential of Bayesian methods for capture-recapture and for removal data but deplored the lack of theoretical development and detailed robustness studies. This chapter addresses both these problems in the context of depletion studies.

If capture probability does not vary with capture event the beta method is a superior estimate, in terms of mean square error, to the alternatives, including the Maximum Weighted Likelihood (MWL) method of Carle and Strub (1978), which uses an unestimated Beta prior. This superiority results from using information from all sites to obtain a superior estimate of the possible variability in capture probability. It can be

viewed simply as an extension of the MWL in which the prior is better estimated. It also eliminates the loss of data as a result of infinite estimates that are obtained when classical methods are used, namely the approximate ML (Zippin 1956, 1958), the exact ML (Raleigh and Short 1981; Schnute 1983; Pollock 1991) and CAPTURE (Otis *et al.* 1978). When capture probabilities decrease significantly with time (as a function of the capture sequence), the CAPTURE method often gives better solutions (lower bias), but non-convergence is often a problem. Non-convergence may bias the evaluation of population abundance in comparative studies particularly if it is associated with environmental variables. For comparative studies such as those dealing with habitat use, the Beta-Gamma model is superior because it gave the lowest error variances. If the initial population estimator yields biased results, adoption of the Beta model will not necessarily improve the situation.

Inference concerning the distribution of the probabilities of capture simultaneously, as proposed here, is an extension of the method proposed by Carle and Strub (1978). They suggested using a uniform prior (a rectangular distribution) in a method similar to Bayesian inference, but in which prior information from other removal studies is not estimated or applied. Since prior information is often readily available in the same study, this information can be used to reduce the effect of sampling error. It is shown that information from as few as 6 sites is sufficient to render the Beta model estimates superior to the ML or MWL estimates.

The estimator developed in this chapter appears to be superior to existing methods. It gave smaller RMSE than MWL or ML methods in all simulations even though the assumption that capture probabilities were distributed according to a beta distribution was grossly violated. In the present analysis of Mahon's (1980) data, in which the true numbers of fish were known, the Beta-Gamma estimator gave an overall lower RMSE when capture probability was allowed to decrease after the first capture event. Again one of the assumptions was violated, as the method of capture was changed at some sites to improve capture probability. Although the purpose of the present work is to develop a method that eliminates estimator failure (infinite estimates) and to minimize the error variance of the estimates in depletion survey methods, the same approach can be used with mark-recapture methods when there are several similar population estimates to be made. For example, the Beta model is directly transferable to the Model  $M_{bh}$  of Otis *et al.* (1978).

Furthermore, Carle and Strub (1978) demonstrated by computer simulation that a large fraction of samples can result in estimator failure for combinations of relatively low  $N$  and  $p$ . These combinations, however, are not infrequent in stream samples, where depletion sampling is most appropriate, particularly if species or year-classes are treated separately. Talbot and Gibson (1991) found the proportion of estimator failure to be near 30 % in salmonid samples from Newfoundland streams. This problem can be avoided completely if information concerning the distribution of  $p$  is used as a prior probability of  $p$  in simultaneous population estimation (Carle and Strub 1978).

However, Carle and Strub's (1978) method does not estimate the distribution of capture probabilities from the data, thus reducing the robustness of the estimator, and possibly resulting in bias. In fact, Carle and Strub (1978) recommend the use of  $\alpha=\beta=1$ , as opposed to the Beta and Beta-Gamma model developed here. Carle and Strub's (1978) method was tested for catch-effort data by Helminen *et al.* (1993) and was found superior to Zippin's (1958) and regression-based methods (Ricker 1975).

The "bias" of classical methods of estimating population size, when infinite solutions are ignored, is usually considered to be in the 15 to 25 % range (Mahon 1980; Bohlin and Cowx 1990), but can be as high as 50 % for juvenile Atlantic salmon (Heggberget and Hesthagen 1979). The methods evaluated in the present study had biases ranging from 13 to 22 % using the highly heterogeneous data from Mahon (1980).

Interestingly, the MWL method had the highest average bias. This is perhaps due to the use of an uninformative prior. Estimating the distribution of the prior from the data appears to decrease the bias to 18%. More homogeneous studies might improve this figure even further.

### **Strategies for bias and error variance minimization in field studies**

Since the bias of the ML class of estimators cannot be eliminated by any of the existing methods, a sampling strategy can be devised to minimize its impact. This is

particularly necessary when the actual number of animals is required such as in studies of productivity.

It is demonstrated (e.g. Figure A-1) that the bias of the estimator is greatly reduced with (1) a high number of sampling events, (2) use of the combined indicator, and (3) high probability of capture. The latter obviously cannot be controlled very easily. A large number of sampling events (7 or more) should be done on a subset of the sites to be sampled. These will serve to estimate the mean and variance of the Beta distribution with greater accuracy. The more general survey can then be continued with 3 or 4 sampling events. The bias observed with the long series can be applied as prior probabilities to correct estimates from the short series.

The combined estimator is less biased than other methods and easily computed from the ML and Beta estimators, although it has a larger variance. If the level of repetition is high and capture sequences relatively short, this method might be the optimal compromise between existing estimators.

Finally, sampled populations are often subdivided into several subgroups representing species, age and size classes, sexes and other ecological considerations. Although more homogeneous subgroups are obtained, this technique is particularly subject to estimator failure, since the population size of the subgroups, and thus the probability of capture, are often very small. The Beta estimators are ideally suited for such data since the

**estimation of the Beta prior from the large number of replicate series will permit a more reliable estimation of the subgroup abundances and eliminate the risk of estimator failure.**

## **CHAPTER 3**

### **DENSITY-DEPENDENT HABITAT USE AND POPULATION EXPANSION IN JUVENILE ATLANTIC SALMON**

#### **INTRODUCTION**

A central question in population ecology can be expressed as follows: How does the distribution of animals change when the overall population size changes? Expansions of local populations can be categorized in three distinct patterns in time and space: 1) habitat use increases proportionately in all habitats, independently of density or quality; 2) habitat use increases more in marginal habitats than primary habitats; 3) habitat use increases proportionately more in primary habitats than secondary habitats. To detect the patterns that occur requires time-series data of local population abundances over the entire distribution range of a population. The purpose of this study is to examine the distribution of a well sampled population over eight years in order to test the hypothesis that the population spreads out mainly by expanding into marginal habitats.

Despite the importance of geographic range extension, very few studies have been able to address this issue directly. Examples of within-population dynamics of distribution are hard to find because they are beyond the scope of optimal foraging models of

distribution (Parker and Sutherland 1986; Sutherland and Parker 1991), but very different from the interspecific patterns of habitat use and community structure (e.g. Brown 1984; Gaston and Lawton 1988; Gaston 1990).

Density-dependent habitat selection models have dealt with habitat use and local densities of animals in relation to individual fitness (reviewed by MacCall 1990). Most of these models, however, have assumed habitats to be "patches" in an optimal foraging game (Milinski and Parker 1991; Parker and Sutherland 1986). Such microhabitat models may not be appropriate for longer term seasonal or yearly selection processes, and deal mainly with free-ranging foragers over a relatively restricted geographical range. The Ideal Free Distribution and its derivatives (Fretwell and Lucas 1970; Parker and Sutherland 1986) have been applied to habitat models (e.g. Fagen (1988)), but assume that individual competitive success can be evaluated in all "patches". This is clearly unlikely to be a mechanism of range extension on a large scale.

The expansion of habitat use has direct implications for the monitoring of population fluctuations since densities may remain relatively stable in primary parts of the range, either because of habitat saturation or territoriality (Grant and Kramer 1990). In such instances, variation in population abundance would be most easily detected in marginal habitats. For example, Myers (1992) has shown that variability in abundance of marine

fishes is greatest at the edge of a distribution and that population on the edge of the range are controlled by density-independent factors.

A population of Atlantic salmon (*Salmo salar*) that has been sampled throughout its population over 8 years, and in which there has been a relatively large variation in the total abundance, was analyzed. A fitness-correlated trait, growth rate, was also estimated for each fish. The overall objective of the present work is to analyze changes in the distribution of animals among sites as population abundance changes. Two hypotheses are considered: that local population response is invariant over all sites, and that the population fluctuates with greater amplitude in marginal habitats. The consequences of density-dependent habitat use are examined for the study of density-dependent phenomena in general. The implications of this work for theories of density-dependent habitat selection, population regulation, and abundance estimation are discussed.

## MATERIALS AND METHODS

### The species studied

The species studied is Atlantic salmon (*Salmo salar*). Adult salmon return from the sea in the fall to spawn in freshwater, essentially re-invading the reproductive habitat in which they were born. Yearly migrations are composed of mixed year-classes. The

adults actively search for good spawning sites, influencing their own local densities for given habitats as well as fry densities when the eggs hatch the following spring.

Therefore, a returning adult salmon should select a site that will provide good survival and growth for the egg (physical attributes) and also consider density-dependent factors associated with local conditions (biological variables). The resulting density and abundance of parr will thus depend on both habitat selection by adults and the local habitat effects on their offspring. Such within-population, density-dependent habitat selection has been demonstrated for brown trout (*Salmo trutta*) in streams (Elliott 1986).

### **Description of sampling**

Frequently used expressions in the text are as follows: parr are juvenile salmon in the freshwater stage of their lives (although males often mature at the parr stage), smolts are fish that have gone through a physiological change in preparation for sea life, anadromous animals inhabit the sea during part of their lives but must return to freshwater to reproduce; kelts are adult salmon that return to the sea the following spring after fall reproduction; adult migrants are mature salmon that move to the river spawning grounds, usually in the upper reaches of the river drainage system.

The data used in this chapter are drawn from records of parr sampled during a detailed demographic study of the Little Codroy River by A.R. Murray (1968a,b,c,d; Myers

1984). These data include the number of parr collected, sizes, ages and earlier sizes-at-age from scales, sex, maturity status, date of sampling, and physical stream characteristics, from each of 48 stations sampled annually throughout the watershed (Figure 3-1, Table 3-1). This chapter combines data from 1) the sampling program to estimate parr population densities in the river system, 2) climatic and geomorphic aspects of the river, and 3) the number of anadromous adults that were parents to each cohort. Parr were collected from each sampling station in the main river and tributaries in August-September of 1954 to 1963 using a powerful electrofishing apparatus (Murray 1958). Each station was fenced with a net upstream and downstream before electrofishing began. Multiple capture attempts were made with the electrofishing gear until no more fish were caught. The stream bed sampling was extensive; after 1957 1.7% of the stream bed area accessible from the sea was sampled.

Male parr were not used in estimates of temporal and spatial heterogeneity because most were mature (72 % at age 1 and 84 % at age 2, n=2574; Myers *et al.* 1986). Since mature males seek sites for spawning with anadromous females, their distribution will be associated with spawning rather than habitats used for growth, and their distribution and growth rates will be altered. Since no females were known to mature in the parr stage, it is assumed that they tend to remain in the habitat in which they grew (Jones 1959). For these reasons, only female parr were used to study distribution heterogeneity and growth rate. Rimmer *et al.* (1983) have noted autumnal microhabitat shifts of parr in small rivers. Parr do not leave given river areas or

**Figure 3-1: Topographic map of the Little Codroy River basin, showing the location of fish sampling stations, temperature and depth recorders, and watersheds comprising the drainage basin.**

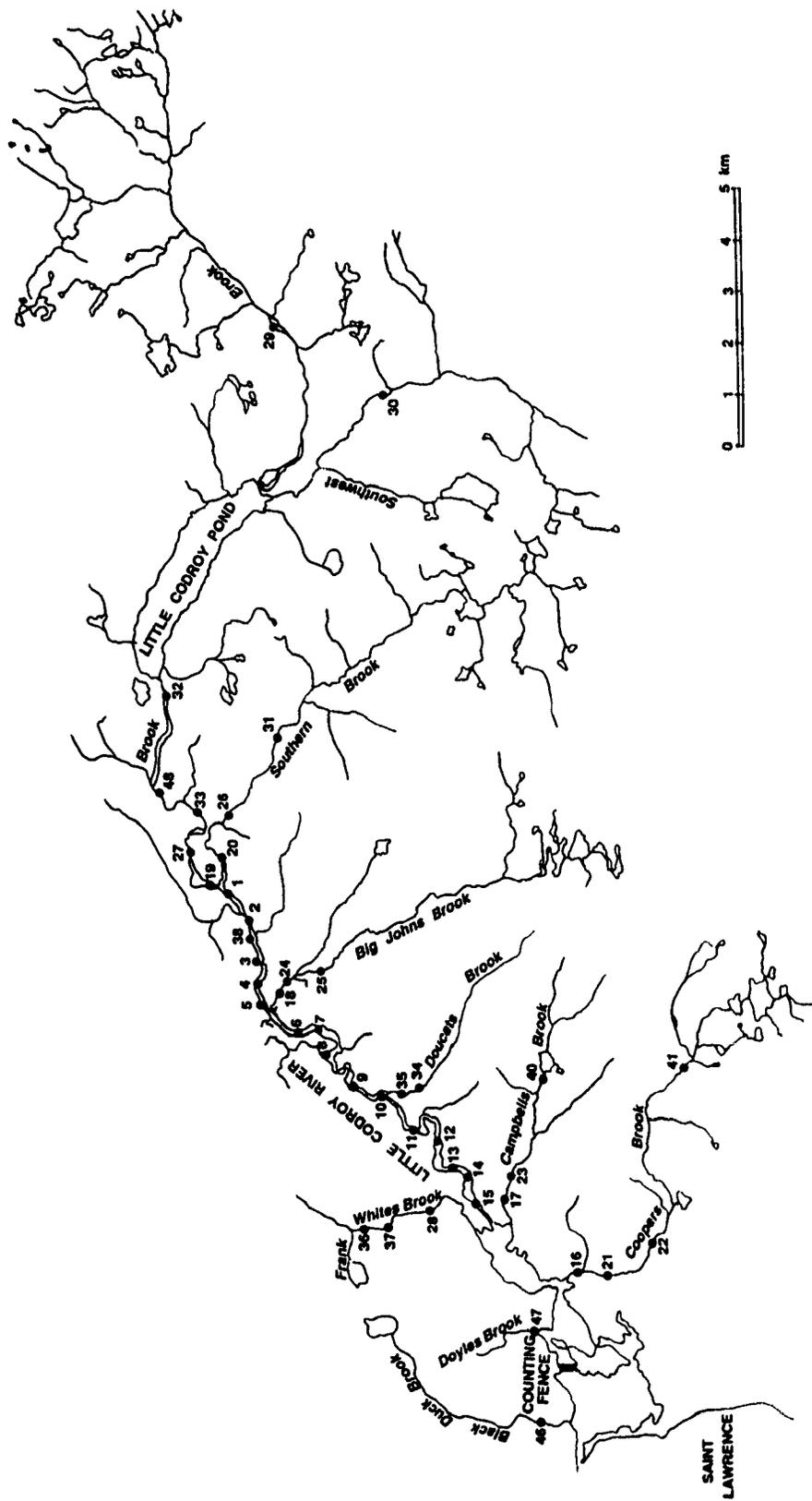


Figure 3-1

**Table 3-1: Physical stream characteristics at sampled stations. Distance indicates distance of a station from the estuary.**

Station	Tributary	river width (m)	river depth (m)	river velocity (m/s)	order	distance (km)	bedrock %	boulders %	coarse rock %	fine rock %	coarse gravel %	fine gravel %	sand %	mud %
16	1	6.58	0.18	0.64	3	0.25	0	0	0.2	0.5	0.3	0	0	0
21	1	6.50	0.20	0.45	3	0.62	0	0.33	0.4	0.25	0	0	0	0
22	1	7.74	0.16	0.39	3	1.23	0.6	0.25	0.15	0	0	0	0	0
17	2	5.11	0.14	0.50	2	0.60	0	0.25	0.5	0.25	0	0	0	0
23	2	4.47	0.12	0.52	2	0.97	0	0.53	0.32	0.1	0.05	0	0	0
40	2	6.07	0.06	0.34	2	1.92	0.5	0.3	0.2	0	0	0	0	0
28	3	2.72	0.09	0.26	2	0.57	0	0	0.5	0.5	0	0	0	0
36	3	2.43	0.07	0.20	2	1.32	0.5	0	0.5	0	0	0	0	0
37	3	2.35	0.09	0.27	2	1.05	1	0	0	0	0	0	0	0
11	4	25.44	0.30	0.36	4	2.14	0	0	0	0	0.5	0.45	0.05	0
12	4	18.38	0.28	0.30	4	1.29	0	0	0	0	0.1	0.65	0.2	0.05
6	5	16.84	0.20	0.65	4	4.73	0	0	0	0	0.5	0.5	0	0
8	5	21.11	0.28	0.64	4	3.99	0	0	0	0.05	0.55	0.4	0	0
9	5	14.87	0.29	0.57	4	3.28	0	0.05	0.15	0.25	0.55	0	0	0

Table 3-1: continued.

Station	Tributary	river width (m)	river depth (m)	river velocity (m/s)	order	distance (km)	bedrock %	boulders %	coarse rock %	fine rock %	coarse gravel %	fine gravel %	sand %	mud %
1	6	19.36	0.22	0.58	4	7.03	0	0	0	0.37	0.38	0.22	0.03	0
2	6	12.77	0.21	0.79	4	6.54	0	0	0	0.25	0.5	0.25	0	0
3	6	17.81	0.28	0.56	4	5.66	0	0.04	0.5	0.3	0.12	0.04	0	0
4	6	26.14	0.30	0.55	4	5.30	0.05	0.1	0.05	0.1	0.4	0	0.2	0
5	6	13.42	0.25	0.75	4	5.08	0.02	0.2	0.25	0.22	0.3	0	0	0
34	7	3.56	0.10	0.50	1	3.61	0	0.4	0.5	0.1	0	0	0	0
35	7	3.76	0.12	0.44	1	3.31	0	0.1	0.6	0.3	0	0	0	0
47	7	1.46	0.06	0.43	1	0.10	0.5	0	0.5	0	0	0	0	0
18	8	8.30	0.16	0.49	3	5.29	0	0.15	0.4	0.3	0.1	0.05	0	0
24	8	7.78	0.20	0.50	3	5.58	0	0.35	0.4	0.1	0.1	0.05	0	0
25	8	7.02	0.20	0.58	3	5.93	0	0.55	0.25	0.2	0	0	0	0
20	9	9.50	0.20	0.47	3	7.40	0	0	0	0.15	0.33	0.42	0.1	0
26	9	10.27	0.20	0.35	3	8.10	0	0.5	0.4	0.1	0	0	0	0
19	10	17.17	0.25	0.42	4	7.38	0	0.1	0.4	0.35	0.15	0	0	0
27	10	18.59	0.20	0.43	4	7.69	0	0.12	0.41	0.26	0.06	0	0.12	0
32	10	9.49	0.15	0.27	4	9.96	0	0.2	0.15	0.25	0.2	0.2	0	0
33	10	13.66	0.30	0.37	4	8.46	0	0	0	0.25	0.5	0.25	0	0
48	10	14.42	0.24	0.44	4	9.25	0	0.4	0.5	0.1	0	0	0	0
29	11	6.64	0.12	0.55	3	15.97	0	0.1	0.45	0.45	0	0	0	0
30	11	5.15	0.09	0.30	3	15.00	0	0.1	0.45	0.45	0	0	0	0

habitat types at low temperatures, but move from unsheltered summer stations to sheltered winter stations within their local stream bed. All parr captured at stations were measured and scales were collected. These scales were measured from the centroid to the annuli in order to estimate back-calculated length-at-age 1 of the 1+ fish caught. This was used to estimate first year growth (Ricker 1975). The use of back-calculated growth is preferable to length or weight at time of capture because times of sampling surveys varied by as much as two months. All analyses were done on scale measurements directly to avoid biases of back-calculation (Francis 1990) but were converted to metric units for graphs and tables throughout.

#### **Adult data**

A counting fence was erected annually in the estuary of the river in order to census salmon migrating into and out of the river. Every fish swimming through the fence was counted, measured, and its life history stage identified. An adult abundance index was obtained from the number of adult anadromous salmon associated with the corresponding cohort. Two measures were considered: the number of upstream migrants counted and the number of surviving adults returning to the sea. Both indicators are subject to error. The number of upstream migrants would be affected by variable recreational fishing pressure in the river, and possible incomplete counts if some fish migrated into the river before or after the counting fence was erected in the river. The seaward salmon (kelts) count is from census of fish returning to the sea in

general on the following spring. It is subject to variable post-spawning mortality and incomplete counts. The sources of error for both should be independent because they occurred in different years. The correlation between the two counts is 0.424 ( $n=8$ ). The counts of upstream migrants and of kelts the following spring were averaged as an index of the number of parents ( $N_t$ ) that gave rise to the cohort of interest. Although this index will underestimate the actual adult numbers, it is assumed here only that the index is proportional to the true abundance.

The errors in the estimation of the adult abundance index should be independent of estimation errors of local parr densities, avoiding biases in the estimates of the slopes (p. 578 in Sokal and Rohlf 1981). Several authors have demonstrated that the number of spawning adult salmon in a given area is directly related to egg deposition rates (e.g. Chadwick 1982; Solomon 1985).

In order to relate parr densities to the parental generation, the number of upstream anadromous migrants were time-lagged 2 years, the post-spawning downstream migrants (kelts) were time-lagged 1 year and local parr densities were not time-lagged (even though growth estimated from scales occurred in the previous year). Local densities therefore serve as a rough estimate of density in the previous year, in which the actual back-calculated growth occurred.

Stations were grouped for categorical analysis according to river tributaries, definable areas and/or river segments (Table 3-1, Figure 3-1). Stations 46 and 47 were ignored because they are tributaries directly off the estuary and were sampled only once. Stations 29 and 30 were also sampled only once and could only be used when presenting growth data (Regrouped as tributary no. 11). I use the term "tributary" in the present context as a convenient term although not all sections are actual tributaries but may represent sections of the main river (group 3 and 4). The abundance of 1+ female parr was averaged within tributaries for some analyses. The adult abundance index ( $N_t$ ) remains unchanged by these groupings.

Station dimensions were 23 m (75 ft) in length, except in 5 cases where the lengths were 30.6 m (100 ft; stations 17, 21, 28, 34 and 35) and 4 cases where station length was 15.3 m (50 ft; station 4 and 12) and 18.4 m (60 feet; station 23 and 25). The stream width varied from 2.1 m (station 37 in tributary 3) to 31.2 m (station 4 in tributary 6) with a mean width of 12 m. Parr densities were corrected for the occasional different station length.

### Statistical models

The basic model relating the number of adult migrants to fry density is:

$$n_{i_t} = \alpha_i N_t^\beta, \quad (1)$$

where  $n_{it}$  represents the local abundance of fry at site  $i$  and time  $t$ ,  $\alpha$  is a constant dependent on densities,  $N_t$  is the adult abundance index at time  $t$ , and  $\beta_i$  is the density-dependent response of local densities ( $i$ ) with respect to total population abundance.  $\beta_i$  is the parameter of greatest interest.

The model parameters could not be estimated using the traditional log transformation and linear regression because of the presence of zero catches. The parameters were estimated using an extra-Poisson model for the counts of age 1 females at each site. This corresponds to a log-linear model of counts of yearling females with log-transformed adult count with overdispersion (i.e.  $\text{Var}(Y_i) = \sigma^2 E(Y_i)$ ; GLIM: Generalized Linear Interactive Modelling, version 3.77, Payne 1986). The extra-Poisson variation was necessary because the Poisson distribution did not adequately describe the variability in counts. The extra Poisson model assumed that the variance in the counts is equal to the predicted count multiplied by a dispersion parameter, which is estimated from the data (McCullagh and Nelder 1989, chapter 6). The standard errors of the estimates are underestimated if the error is assumed to be Poisson, but specifying overdispersion does not alter the estimated slopes ( $\beta_i$ 's). Estimates for each station sampled for 3 years or more are given in Table 3-2. Station 36 is set to missing since no fish were caught in the four years it was surveyed and the theoretical slope is zero. The estimated response at station 11 was a negative outlier, and given that the average count was 0.5 females over four years, it was also dropped from further analyses.

Table 3-2: Atlantic salmon parr regression statistics by station and tributary.

Station	Tributary	No. of 1+ parr	No. of 1+ females	No. of years sampled	Slope ( $\beta_i$ )	S.E. ( $\beta_i$ )	Scale parameter ( $\hat{\sigma}_i$ )
16	1	18.17	10.17	6	0.216	0.7480	6.208
21	1	17.20	6.60	5	-0.503	0.8726	2.635
22	1	16.00	7.50	4	0.306	0.1122	0.041
17	2	16.78	9.50	8	1.225	0.6220	3.649
23	2	20.00	9.75	4	1.140	0.9655	2.572
40	2	6.00	2.00	1			
28	3	6.40	3.75	4	1.347	1.475	3.619
36*	3	0.00	0.00	4	0.000	1.4080	0.0001
37	3	4.25	2.25	4	0.074	1.7550	2.926
11*	4	0.67	0.50	6	-1.594	2.1080	1.497
12	4	1.67	1.00	6	1.486	1.3060	1.012
13	4	2.00	1.00	1			
15	4	4.00	2.00	1			
6	5	8.00	3.25	4	1.412	1.4040	2.824
8	5	9.00	4.00	6	1.255	0.8421	1.805
9	5	16.40	4.80	5	1.194	0.8914	0.561
10	5	2.50	0.83	6	1.485	1.9010	1.792
1	6	9.75	7.00	4	0.260	0.9020	2.472
2	6	18.67	8.21	7	1.936	0.7363	2.075
3	6	47.67	20.00	6	-0.111	0.9231	13.670
4	6	14.00	4.00	2			
5	6	29.04	10.67	6	-0.263	0.5431	2.614
38	6	3.75	2.50	2			
34	7	22.33	7.00	3	2.260	0.2736	0.113
35	7	26.50	8.50	4	2.167	0.1586	0.084
18	8	27.77	9.09	7	0.833	1.1610	8.713
24	8	32.40	9.00	5	1.717	1.3510	6.844
25	8	30.40	7.60	5	1.927	1.2300	4.506
20	9	6.24	3.88	6	-0.106	0.8813	1.908
26	9	50.60	19.80	5	-0.155	0.1997	0.423
19	10	40.00	18.17	6	-0.951	0.7535	7.894
27	10	24.00	11.80	5	0.129	0.6782	2.914
32	10	9.00	5.00	2			
33	10	13.67	7.00	3	0.019	1.6660	7.924
48	10	41.50	9.50	2			
29	11	5.00	1.00	1			
30	11	5.00	4.00	1			

\*Slopes not used in the analyses (see text).

Overdispersion is very common in biological data (McCullagh and Nelder 1989). The scale parameter used in combination with the Poisson error structure approximates the negative binomial error distribution (Payne 1986). The regression of local juvenile density with the adult spawner abundance was also repeated assuming an exact negative binomial error structure in which the negative binomial " $k$ " was assumed constant over all sites (Lawless 1987; Barnwal and Paul 1988; McCullagh and Nelder 1989). The  $\hat{k}$  for the Little Codroy River was 1.715. The parameter  $k$  has been used as a measure of aggregation in some studies (Pielou 1977), owing to its property of remaining constant with changes in abundance of a population if mortality is random within the population, but it is very sensitive to the actual statistical distribution, which diminishes its generality. The estimates of the slopes from the negative binomial model were found to be highly associated with the extra-Poisson model used here ( $R^2=0.97$ ,  $n=28$ ). I also examined the slopes estimated from the number of spawners alone and from the number of kelts alone as predictor variables. The estimated slopes are correlated ( $r=0.496$ ,  $n=27$ ,  $P=0.008$ , Figure 3-2). The estimated regression slope ( $N_u = 0.107 + 0.876 N_k$ ) is very close to the 1:1 relationship, although variance in the estimated slopes is greater than expected from local response to adult population abundance. A combined estimator of adult abundance is thus justified.

**Figure 3-2: Plot of the relationship between slopes estimated from the Poisson model using upstream and downstream adult migrants independently. The regression line is shown with 95 % confidence intervals. The dotted line is the 1:1 relationship, which falls well within the confidence limits of the regression.**

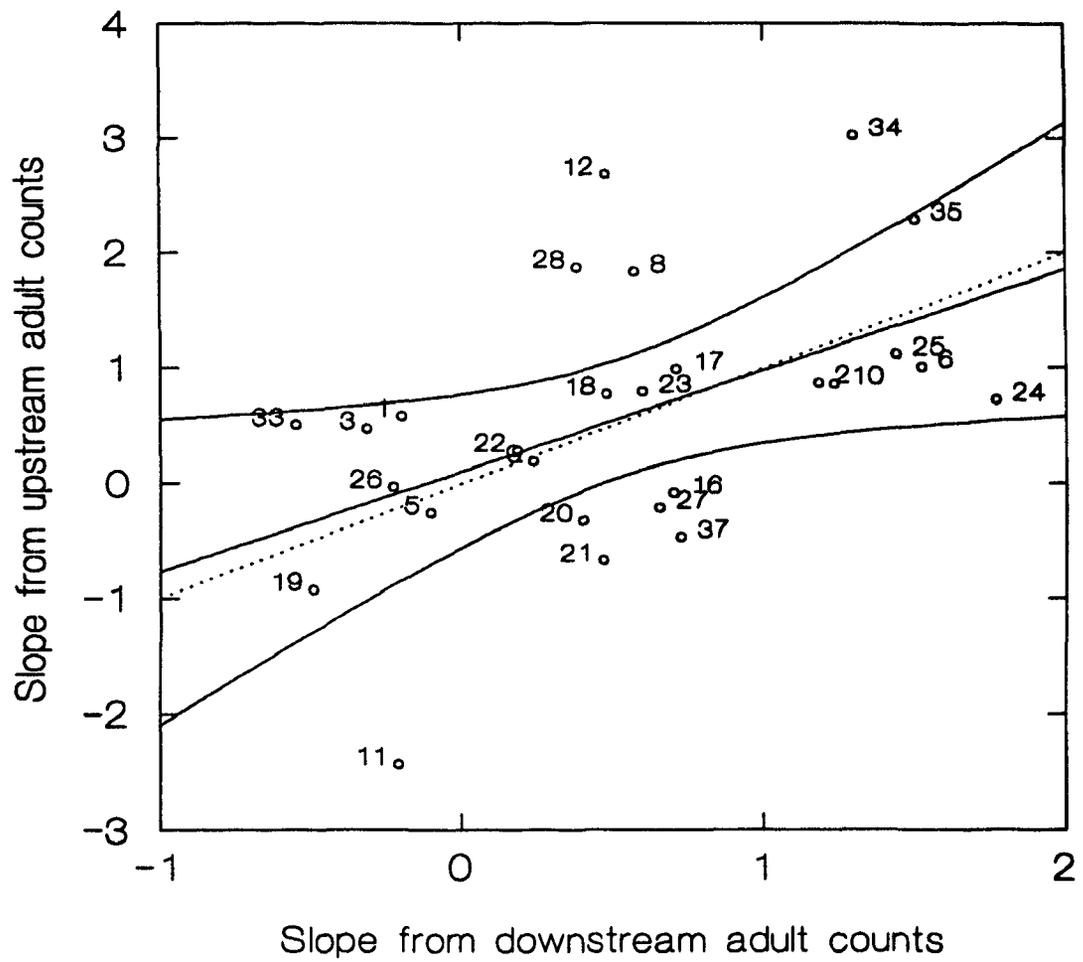


Figure 3-2

**ROBUSTNESS: Are the results robust to changes in statistical methods?**

A potential problem with using an estimate of the number of spawning adults to estimate the total number of parr is that there may be a nonlinear relationship between total number of spawners and total number of parr surviving to age 1 typical of general stock-recruitment relationships. For example, a doubling of parents may produce a doubling of egg or fry the following spring at low densities, but this is not expected at the highest densities. Such non-linearity could not be distinguished from other density-dependent factors controlling habitat utilization such as migration and other causes of mortality. If this was a serious problem in this river, the overall estimates of  $\beta_i$  would be expected to be significantly less than the predicted value of 1 (Solomon 1985). The unweighted mean  $\beta_i$  was 0.78 with s.e. = 0.18. This indicates that there may be density-dependence in survival of eggs or young parr, but the difference between the actual and predicted mean slope is not significant (df=1,25, F=1.518, P=0.23), and the variance in the slopes is quite large. I assume that the difference is not large enough to create a bias in the estimated effects among habitat.

Since the precision of the regression parameters increases with the number of years the site was surveyed, analyses of summary data were weighted by the number of years sampled where appropriate.

### **Hypotheses examined**

The Site Invariant Response hypothesis makes the prediction that the local response to changes in population abundance, i.e. the  $\beta_i$ 's, are homogeneous among sites and tributaries. This hypothesis represents a proportional increase in juvenile abundance at all sites in response to changes in adult population abundance (Figure 1-1a).

The Variable Response hypothesis assumes that fluctuation in local population abundance as a function of overall abundance is greatest in marginal habitats (Figure 1-1b). It is derived from the hypothesis that primary habitats of a given species will generally be filled to some optimum carrying capacity while fluctuations in population abundance affect the colonization of peripheral or marginal habitats (Fretwell and Lucas 1970; Andrewartha and Birch 1982). One testable prediction derived from this hypothesis is that  $\beta_i$  (the slope of local parr population density in relation to adult abundance) is negatively related to  $n_{ii}$  (local parr abundance). In such a case, local densities are assumed to be an indicator of habitat quality (McClendon and Rabeni 1987; Moreau and Legendre 1979; Frenette *et al.* 1984).

As a null hypothesis,  $\beta_i=1$  is expected if there is no density-dependent mortality (Myers and Pépin 1986). Habitats in which the parr density does not fluctuate as a function of total abundance will have  $\beta_i$  close to zero.

### Taylor's Power Law

The relationship between local population variability and abundance is examined using the Taylor "Power Law" (reviewed by Taylor 1986). This law defines the relationship between the variance of and the mean of local densities as

$$\log_{10}(s_x^2) = \alpha + \beta \log_{10}(\bar{x}) \quad (2)$$

Taylor power plots are usually approximately linear for animal distribution data.

Simple linear regression can be used to estimate the slope of the relationship. The technique can be used to examine both spatial and temporal heterogeneity (Taylor and Woiwod 1980; Taylor *et al.* 1978). The vast majority of observed relationships fall between the ranges of 1 and 2 (Taylor and Woiwod 1980; Taylor *et al.* 1978; Anderson *et al.* 1982). A slope of 1 indicates adherence to the Poisson distribution while slopes greater than 1 indicate overdispersion. Although this relationship has been used to demonstrate density-dependent processes (e.g. Taylor and Woiwod 1980; Elliott 1986), caution must be taken in order to avoid false interpretation (see Discussion). The estimates obtained are also critically dependent on the sample size, the range of densities over which the data is collected and the degree of environmental heterogeneity (Anderson *et al.* 1982). However, the technique might be a useful tool for comparison of populations and published studies.

## RESULTS

### **Density and growth response at the population level**

The response of numbers and growth of parr in the population is examined first when all sites are analyzed together. Over the sampling period the number of anadromous salmon returning to the river, as demonstrated by the adult abundance index, declined to less than one half of their original numbers (Figure 3-3), ranging from a high of 303 fish in 1956 to a low of 93 in 1962. A decrease in the density of parr was also observed, from an average capture of 30 parr per station in 1956 to 10.7 parr per station in 1963. The mean size of 1+ females increased quite dramatically over the same interval (Figure 3-3) and seemed to be associated with the change in density. Clearly, although growth in the first year can also be used as an indicator of habitat quality, it also incorporates density-dependent effects.

### **Estimated patterns of distribution**

The highest densities of 1+ female parr tended to occur in the upper reaches of the Little Codroy River below Codroy Pond and in the tributaries south of the main river (Table 3-2, Figure 3-4). Coopers Brook (group 1) also had a high density population, perhaps because it is the first main tributary directly off the estuary, and may be

**Figure 3-3: Plot of the number of spawners captured on the Little Codroy River ( $N$ ) against the average growth rate of 1+ female parr during their first year. The number of spawners is used as an indicator of total population abundance. The mean and standard errors are given for growth rate.**

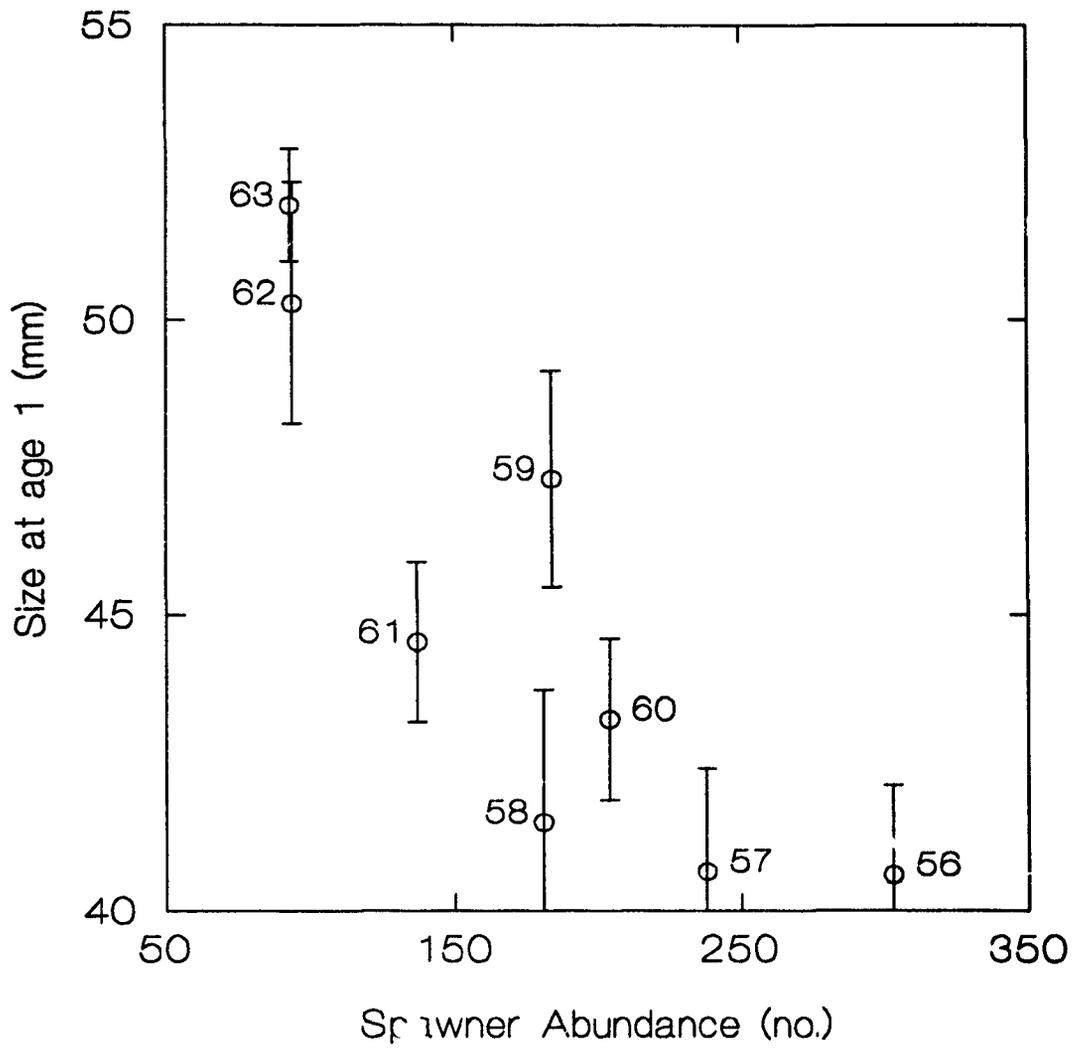
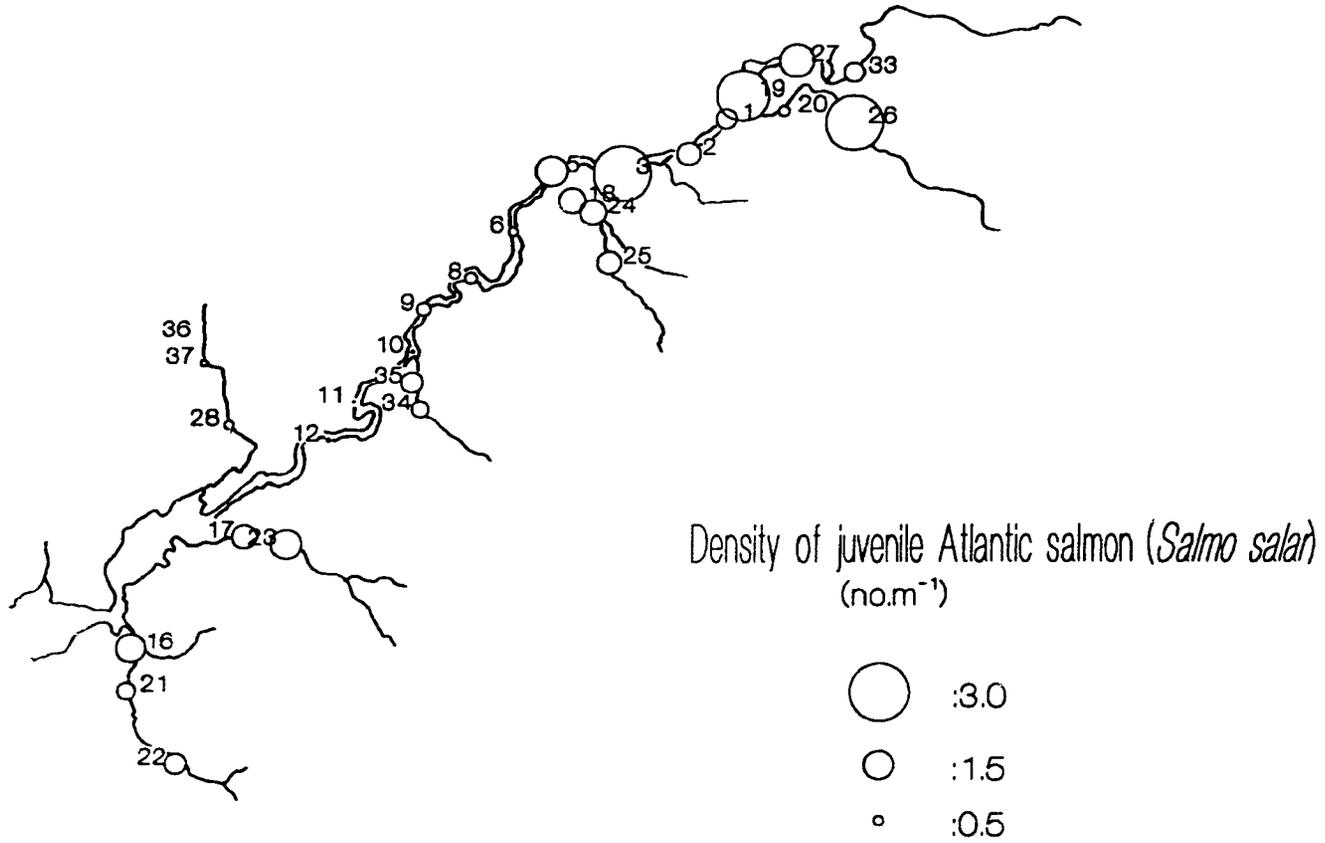


Figure 3-3

**Figure 3-4: Bubble plot of the geographic distribution of the average density of 1+ female parr of Atlantic salmon in the Little Codroy River watershed. The radius of the circle is proportional to the density. Note that the highest densities are in the upper watershed below Little Codroy Pond. This figure can be compared to the slopes presented in Figure 3-7.**

Figure 3-4



considered a separate river.

Plots of the Taylor "Power law" (Taylor 1986) indicate a strong positive correlation between the log of the variance of local abundance with the log of the mean station abundance when considered as both temporal and spatial variability (Figure 3-5a,b). The slope of the linear regression fitted to the temporal variability data of Figure 3-5a is equal to  $1.3 \pm 0.25$  s.e. ( $n=33$ ,  $R^2 = 0.473$ ). This slope is significantly less than 2 ( $df=1,30$ ,  $F=7.802$ ,  $P=0.009$ ) but not different from 1 ( $df=1,30$ ,  $f=1.438$ ,  $P=0.240$ ). The slope of the spatial variability data (Figure 3-5b) is  $1.09 \pm 0.53$  s.e. ( $n=7$ ,  $R^2=0.458$ ). This slope is not significantly different from 2 ( $df=1,5$ ,  $F=2.986$ ,  $P=0.145$ ) nor from 1, but only 7 years are used (only 2 stations were sampled in 1956). A slope greater than 1 indicates overdispersion with respect to the Poisson distribution. These results are classically interpreted to mean that variability at a site is proportionally greater at low abundance (Elliott 1986) and that distribution of parr among sites is primarily a result of density-dependent aggregation (Elliott 1986; Nachman 1981; Gaston 1990; McArdle *et al.* 1990). However, as stated previously, caution must be used in reaching such conclusions (see "Comparison with other studies" in the Discussion).

### **Site Invariant Response Hypothesis**

In this section, the spatial and temporal pattern in the variation of  $\beta$ , the response of local female density to changes in population abundance, among habitats is evaluated.

**Figure 3-5: Taylor Power plots of the log of the variance of local abundance against the log of the mean density of local abundance. The dashed line represents the 1:1 relationship. a: Each point represents a site and the mean and variance are estimated over years (Temporal variability). The regression line is given by:  $\log(V(n_i)) = -1.87 + 1.312 \log(M(n_i))$ ,  $R^2 = 0.62$ ,  $n = 27$ ,  $P < 0.001$ . b: Each point represents a year and the mean and variance are estimated over sites (Spatial variability).**

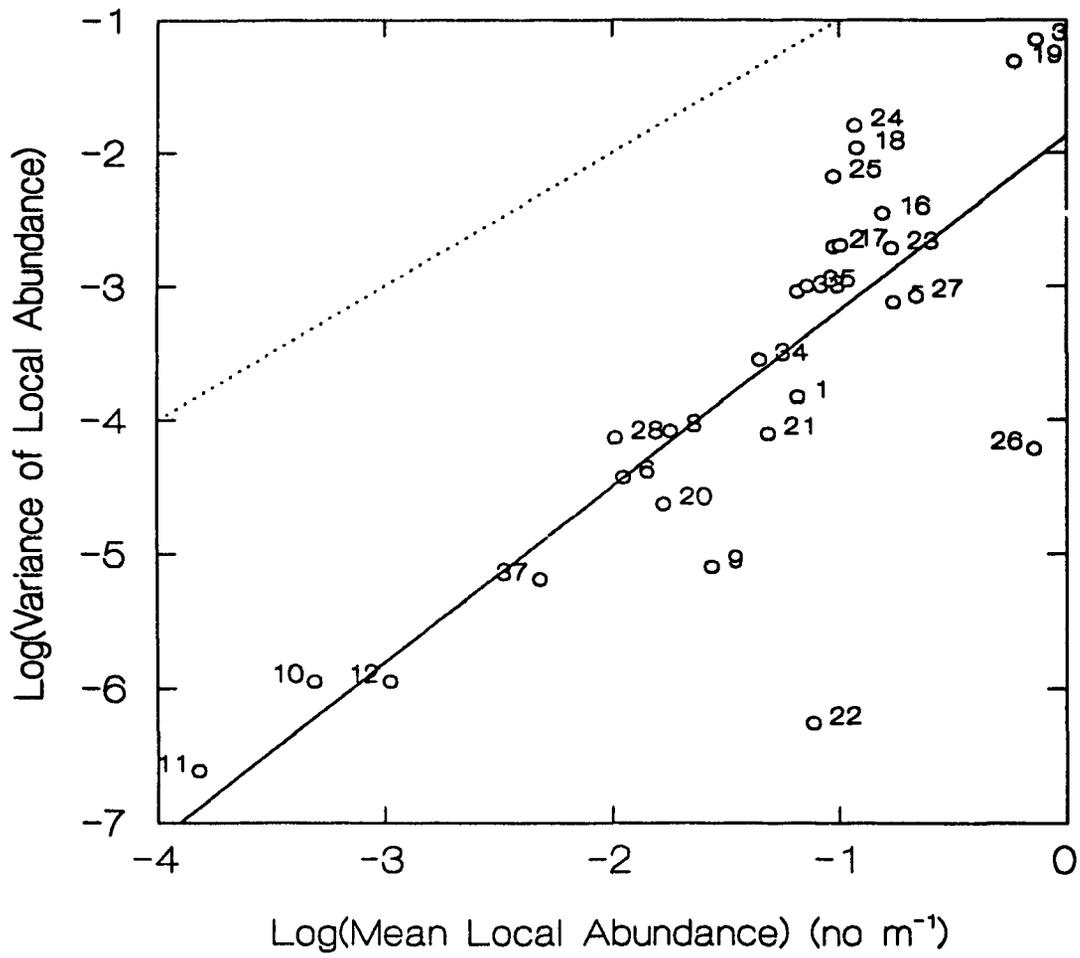
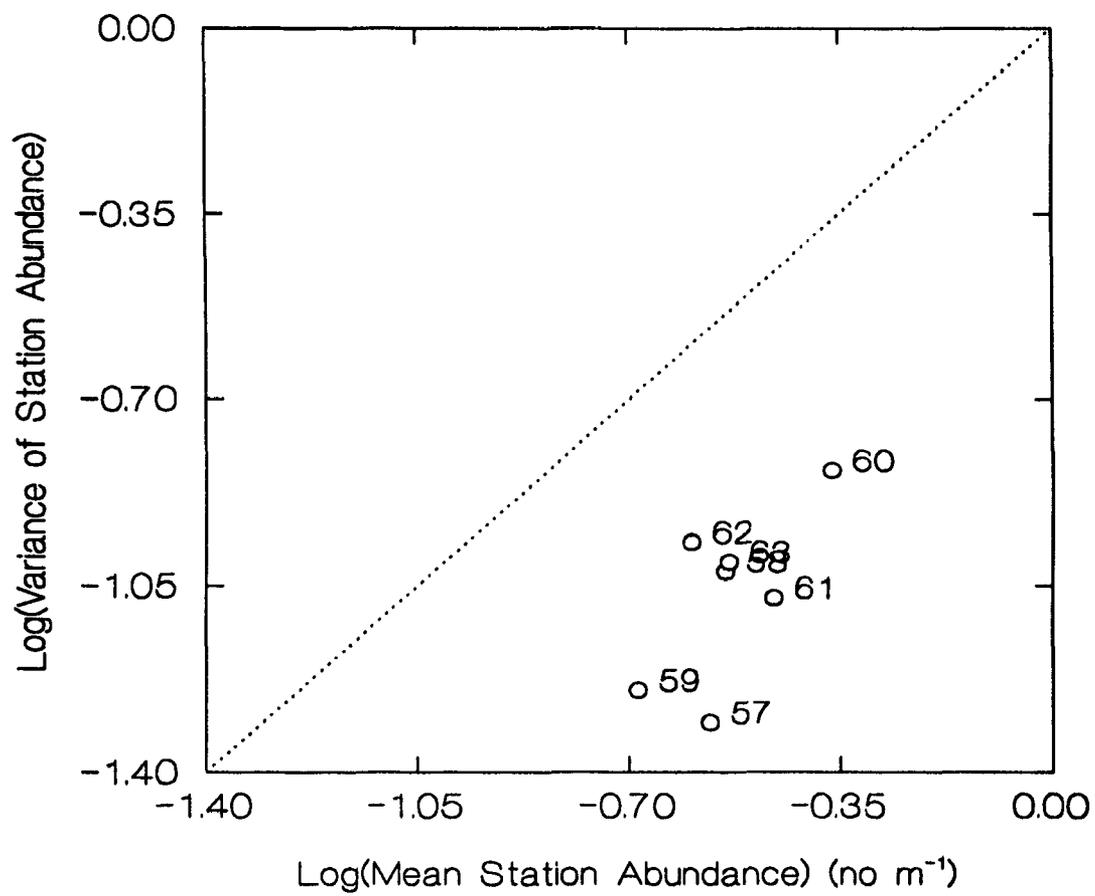


Figure 3-5a

**Figure 3-5b**

To test this hypothesis, we need to show that local response to changes in the overall population abundance was not the same throughout the river. To test for homogeneity of the slopes among sites, a likelihood ratio test was used to compare the residual deviance of a common slope model to the sum of the residual deviance of the separate slopes estimated above. The common slope was estimated at 0.398 (df=112). The residual deviance of 423.9 for the common slope model was larger than the sum of the residual deviances of the separate slopes (320.2, df=88). The log likelihood of the difference between the two models was highly significant ( $\Delta L=103.7$ , df=24,  $P<0.0001$ ), indicating that there is a high degree of heterogeneity of slopes among stations. Similarly, to test for heterogeneity of slopes among tributaries, a simple analysis of covariance with a Poisson error structure, with  $\log N_i$  as a continuous predictor variable, tributary as categorical predictor variable (Table 3-2), and individual site juvenile densities as dependent variable, explained 45.5 % of the variance in distribution and abundance. The difference in residual deviance between a common slope and the heterogeneity of slopes model is highly significant ( $\Delta L=63.3$ , df=9,  $P<0.0001$ ). Since sites as well as tributaries contribute significantly to the variance of slopes, this hypothesis is thus clearly rejected, implying that the habitats respond differently to overall population abundance.

### **Variable Response Hypothesis**

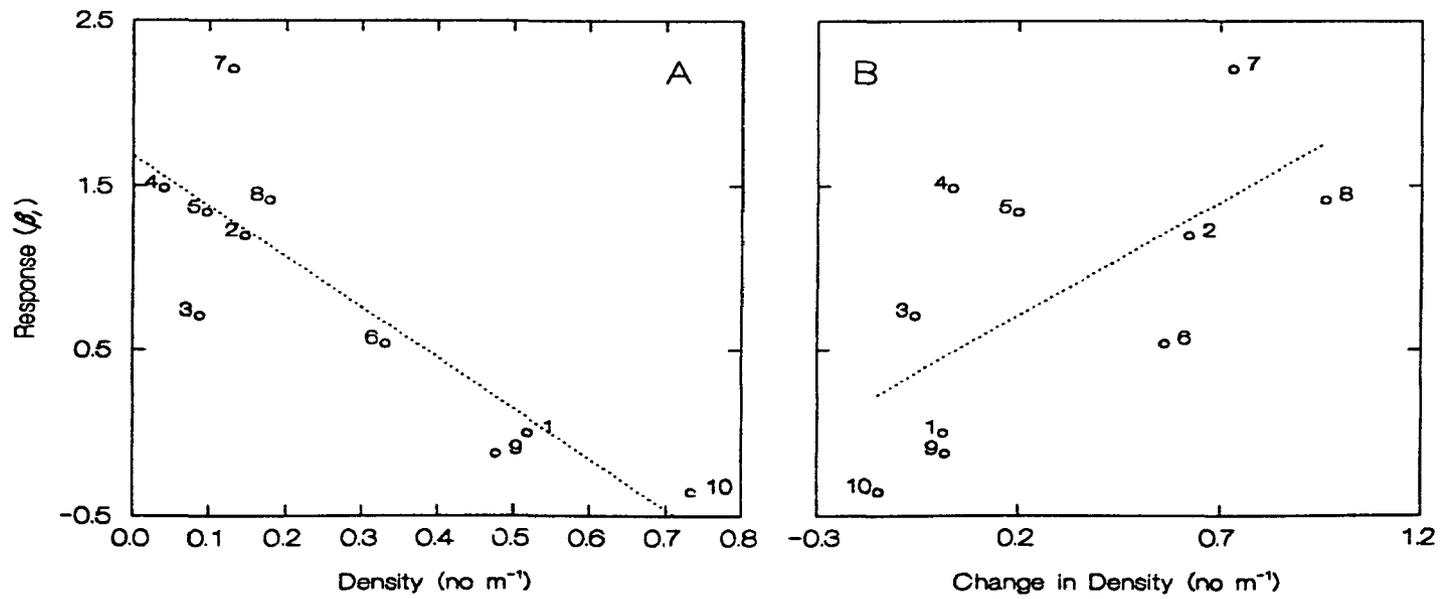
The hypothesis states that fluctuation in local population abundance as a function of overall abundance is greatest in marginal habitats. If this hypothesis is valid, then local density should not respond to changes in overall population abundance in the sites that have high densities when overall population abundance is low. The local population response, i.e. the  $\beta_i$ 's, were close to zero in sites with high density in the year in which  $N$  was lowest (Figure 3-6a). There was a negative correlation of the  $\beta_i$ 's with local density in the year of the smallest  $N$  ( $r=-0.86$ ,  $df=1,8$ ,  $F=22.23$ ,  $P=0.002$ ).

Although the data are consistent with the hypothesis, there are sections of the river in which the local population response was low and yet had low density (Figure 3-6a, section 3). However, these sites had relatively good growth rates (see below). This section of the river do not appear to be responding to changes in overall population abundance within the range observed.

It is also useful to examine the relationship of the  $\beta_i$ 's with the actual change in local density from the year of the smallest  $N$  to the year in which  $N_t$  was highest (Figure 3-6b). The relationship between slopes and absolute change in density is significantly positive as predicted ( $r=0.65$ ,  $df=1,8$ ,  $F=5.78$ ,  $P=0.043$ ). Note that some sections of the river with high  $\beta_i$ 's had among the highest local densities in the year of highest  $N_t$ . The population appears to "overrespond" in these sections. Clearly, local population density may not be the best indicator of habitat quality.

**Figure 3-6: Bivariate plots of the relationship between the response to change in population abundance ( $\beta_i$ ) and the average station density ( $n_i$ ). Each point represents a tributary or river segment mean. The graphs represent densities estimated in a) the year of lowest adult returns and b) the absolute change in local density between the year of lowest and highest returns specific to stations.**

Figure 3-6 a,b

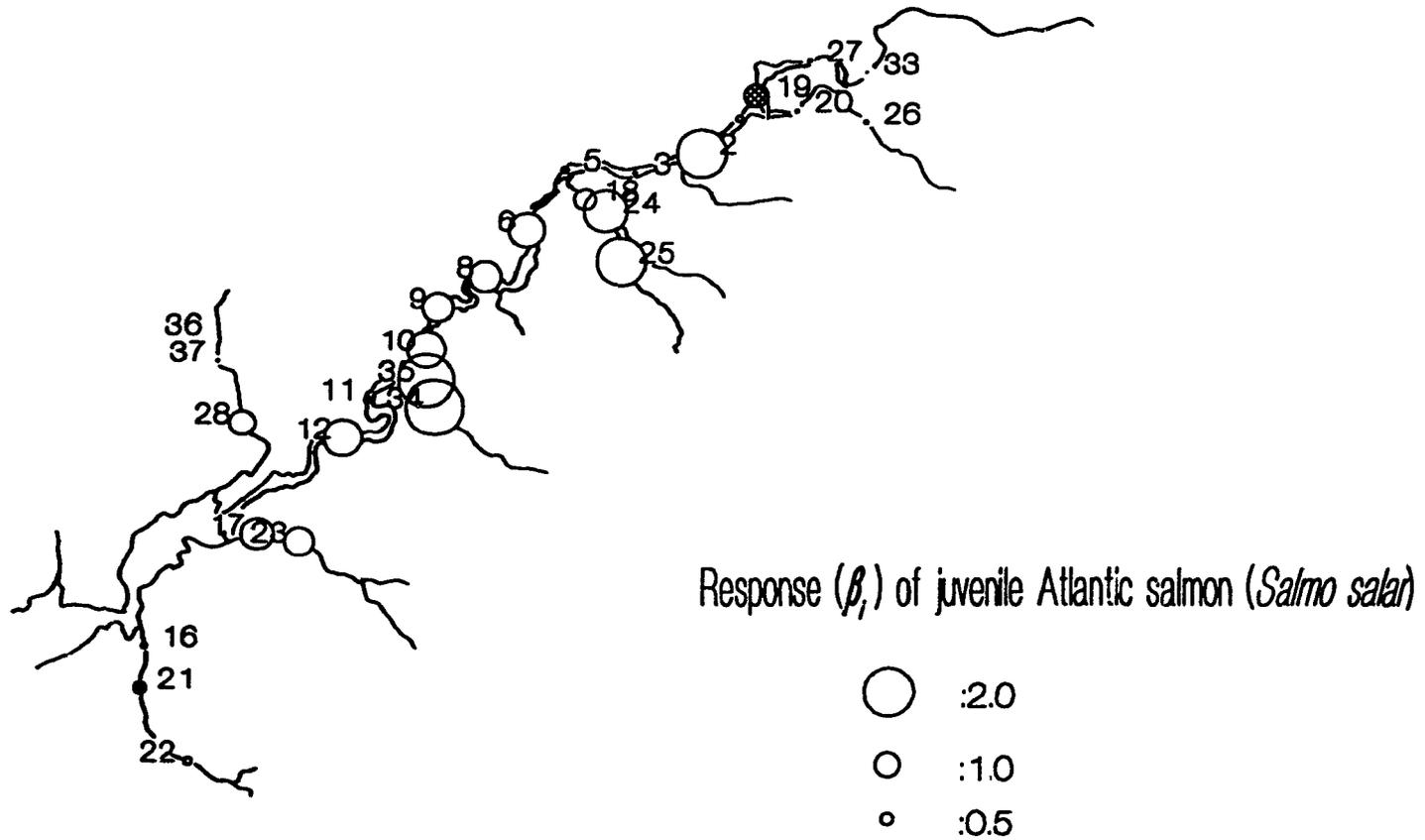


The individually estimated slopes of local densities ( $\beta_i$ ) in relation to adult migrants for each station with more than 2 years are plotted geographically using the bubble plot technique (Figure 3-7). Sites with the largest slopes do not correspond to those with the overall highest densities (Figure 3-4). The greatest slopes tend to occur at intermediate distances along the main river as well as in the tributaries off the main river. River group 1 (Coopers Brook) was stable over time ( $\beta_i$  near 0), but this river may represent a special case since it opens directly into the estuary of the Little Codroy River.

The main river segment was isolated to demonstrate the variable response of density to changes in population abundance. Figure 3-8a demonstrates that average juvenile densities were generally much higher in the upper reaches of the river. This is well represented by the linear regression  $\log(\bar{n}_i) = 0.013 + 0.017 * D_i$  ( $R^2=0.36$ ,  $df=1,19$ ,  $F=10.81$ ,  $P=0.004$ ). Response however, is far greater in the lower reaches of the main river segments. The slopes ( $\beta_i$ 's) decrease progressively upstream (Figure 3-8b). This relationship is also well described by a linear regression estimated as  $\beta_i = 1.812 - 0.228 D_i$  ( $R^2=0.44$ ,  $df=1,12$ ,  $F=9.29$ ,  $P=0.01$ ). Note that the fitted equations are used to illustrate the tendencies of the data only and are not meant to represent the most suitable model for the present data. Station 2 is an obvious outlier in the present case (Figure 3-8b). It is the station where the highest water velocities were recorded (Table 3-1), in association with poor substrate for salmon parr, and may be unsuitable for

■ **Figure 3-7: Bubble plot of the geographic distribution of the slope ( $\beta_j$ ) of the regression of local to total abundance of 1+ female juvenile Atlantic salmon in the Little Codroy River watershed. Shaded circles indicate negative slopes. The magnitude of the slope is proportional to the radius of the circle. Note that the largest slopes are below the areas of highest density in the watershed or are areas with lower average densities (see Figure 3-4).**

Figure 3-7



**Figure 3-8: a) Variation in the mean station density of juvenile salmon as a function of the distance from the estuary along the main river segment. Higher densities are clearly near the headwaters of the river. The regression equation fitted to the data (for illustrative purpose of the tendency only) is shown ( $R^2 = 0.36$ ,  $n=21$ ). b) Variation in the response in local density of juveniles as a function of distance from the estuary along the main river segment. The more stable sites are at the headwaters of the river. Station 2 appears to be an exception. It had the highest mean water velocities of any station sampled in this study and may not have been an ideal habitat. The regression equation fitted to the data is shown ( $R^2 = 0.44$ ,  $n=14$ ).**

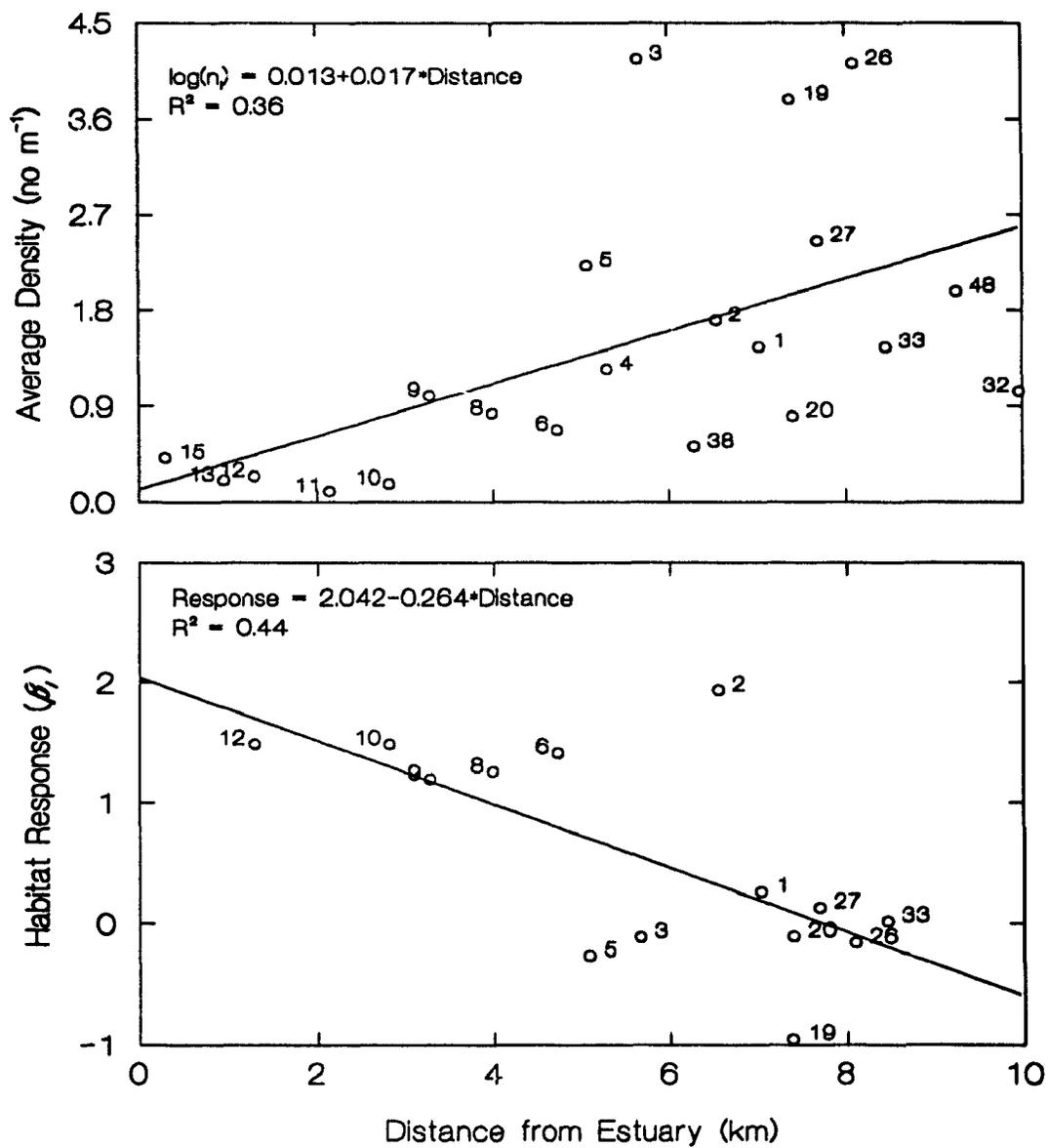


Figure 3-8 a,b

juvenile settlement in years of high discharge. The contrast between the distribution of the local juvenile densities and their population response is remarkable and represents strong evidence for a habitat-specific expansion of use in response to increasing population abundance.

### **Relationship of growth rate to population response**

Growth rate of salmon can be postulated to be a good indicator of habitat quality (Gibson and Haedrich 1988) and, with biomass, reflects the productive capacity of habitats. Areas with good growth rates are predicted to have  $\beta_i$ 's close to zero.

Conversely, in the Little Codroy data, the sections of the river which responded to changes in density had poor growth rates (Figure 3-9). Local density response,  $\beta_p$ , was significantly related to the size-at-age 1 of juveniles (Weighted Least Squares, with number of female parr as weight variable,  $R^2=0.254$ ,  $df=1,24$ ,  $F_s=6.10$ ,  $P<0.021$ ).

However, there is considerable scatter, particularly when using individual values ( $R^2=0.02$ ,  $df=1,1082$ ,  $F_s=20.05$ ,  $P<0.0001$ ). This result is not due to relatively lower densities in stable sites since there is a slight, although non-significant, positive association between local densities and growth rates ( $R^2=0.001$ ,  $df=1,1153$ ,  $F_s=1.58$ ,  $P=0.21$ ). Variation in growth rate is expected to be large because of local and larger-scaled density-dependent effects (Chapter 4). It is clear that different population control processes regulate densities in different tributaries. Stable populations were associated with faster growing parr than found in tributaries with fluctuating

**Figure 3-9: Bivariate plot of  $\beta_i$  and the mean growth of 1+ female parr observed in the first year of sampling at individual stations. Each point represents tributary of river segment means and vertical bars are standard errors. The relationship is significant (see text).**

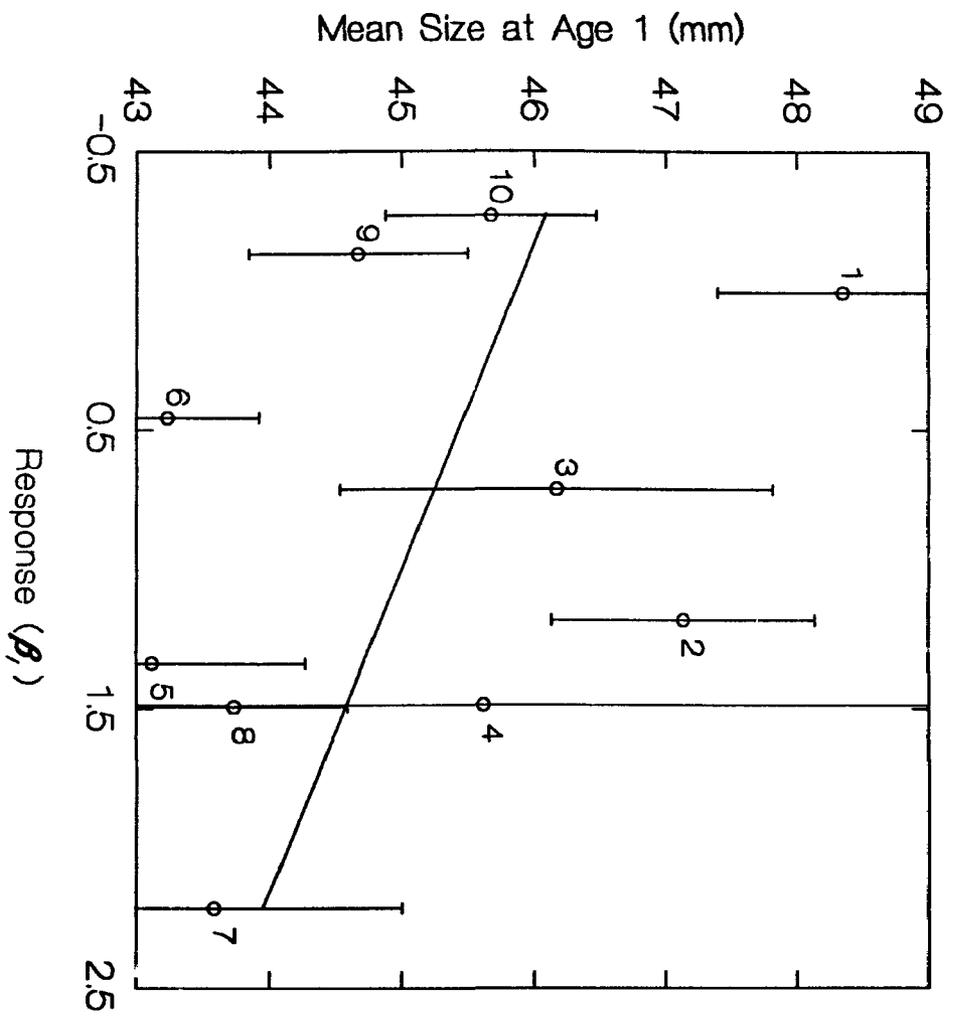


Figure 3-9



populations. Growth rate was high in the stable sites throughout the study even though the population abundance at different stable sites differed by more than an order of magnitude (Figure 3-6a). In particular, there was a section of the river with low mean density, good growth rate, and which did not respond to population fluctuations (groups 3, Figure 3-6a,b).

### **Population stability**

The variance in density at each site over time is also examined as an indicator of habitat quality, because population stability (i.e. low variance in density measured over time) has been associated with good habitats (Rice *et al.* 1986). Furthermore, it is necessary to investigate the variance in density to check the present conclusions about the local population response. That is, a zero regression slope does not necessarily imply that there is no variation in the dependent variable, but only that this variation is unexplained by the predictor variable. It is therefore necessary to consider purely stochastic effects by testing the within-station variance of density. Local density estimates were log-transformed ( $\log(n_i+1)$ ) to reduce the dependence of the coefficient of variation (C.V.) on the mean, and the C.V. of local densities was used in regression analyses. Despite the log transformation, the C.V. remained dependent on the mean in accordance with the power function  $CV(\log(n_i+1))_i = 0.124 \pm 0.016 \log(\bar{n}_i)^{-0.523 \pm 0.037}$  ( $R^2=0.84$ ,  $df=2,28$ ,  $F=311.4$ ,  $P<0.0001$ ). However, the very high values for low densities with the C.V. of the log-transformed densities may be due to a sampling bias

resulting from small sample sizes (Anderson *et al.* 1982; McArdle *et al.* 1990). Similar results were obtained with the untransformed densities

$(CV(n_{y_i}) = 0.416 \pm 0.053 \bar{n}_i^{-0.345 \pm 0.056}, R^2=0.51, df=2,28, F=139.5, P<0.0001; \text{Figure 3-10a}).$

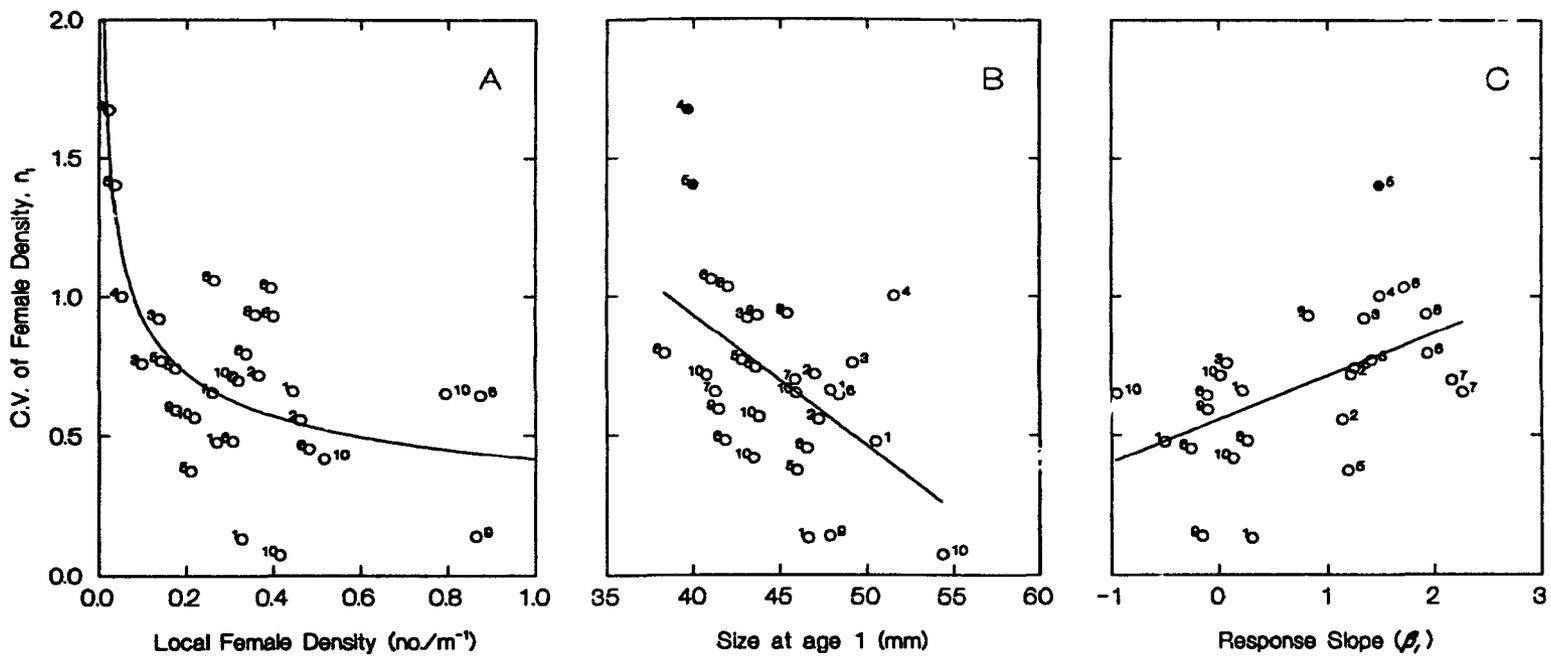
The coefficient of variation of the untransformed female density was negatively related to growth rate ( $n=30, r=-0.52, t=3.23, P=0.003; \text{Figure 3-10b}$ ) and positively associated with the response slopes ( $n=26, r=0.51, t=2.92, P=0.007; \text{Figure 3-10c}$ ).

Note that the outliers in Figure 3-10 a and b are stations 9, 10 (Tributary group 5), and 11 (Tributary group 4), which are a series of highly variable, low-density stations in the lower reaches of the main river. Again, similar relationships were obtained with the C.V. of the log-transformed densities (Growth:  $n=30, r=-0.435, t=2.55, P=0.016; \text{Response slope: } n=26, r=0.47, t=2.59, P=0.016$ ).

Similar results are obtained with the scale parameter of the Poisson regression estimates (Table 3-2). The scale parameter  $\sigma_i$  is an estimator of over- or under-dispersion of a Poisson distribution (McCullagh and Nelder 1989). A strong negative association exists between the scale parameter and the growth rate of parr in the year of greatest adult abundance ( $R^2=0.33, df=1,24, F=11.59, P=0.002$ ). The relationship is slightly positive with growth rate in the year of lowest adult abundance ( $R^2=0.07, df=1,23, F=1.79, P=0.19$ ). Although the latter is not significantly different from zero, it is significantly different from the relationship between  $\sigma_i$  and growth in the year of highest abundance ( $df=1,23, F=18.53, P<0.001$ ). The difference between these two relationships and the general trends within each indicate density-dependence on a local

**Figure 3-10: Bivariate plot of the coefficient of variation in local female densities at sampling stations (over all years sampled) against a) the mean female density. The equation is given in the text; b) the size-at-age of 1+ female parr at stations; and c) the regression slope ( $\beta_1$ ) of the same stations. The relationships are significant in all cases (see text). All points are included in the regression analyses, including outliers (filled circles).**

Figure 3-10a,b,c



scale (See Chapter 4).

The presence of a relationship with simple variability corroborates the earlier definition of stability. It is possible to conclude that habitats with high densities, low variances and low  $\beta_i$  also provide better growth rates and are probably primary habitats for parr growth.

## DISCUSSION

### Comparison with other studies

Very few previous studies have quantified the local population response to the change in the total population abundance, and related these changes to fitness traits. In the present chapter, it is demonstrated that fish in primary habitats, as defined by high stable densities and superior growth rates, are less responsive to changes in population abundance than those in secondary habitats.

Elliott (1986) found that migration of brown trout (*Salmo trutta*) fry and parr was related to the local density. Inference was derived from a combination of small scale behavioural response and from the Taylor Power Law. Although Taylor's Power Law is sometimes a useful method of describing data, there are several problems in interpreting the results (Anderson *et al.* 1982). The slopes of the relationship between

variability and mean abundance in the present study were similar to those observed in Elliott's (1986), which were between 1.15 and 1.66. Anderson *et al.* (1982) demonstrated from a simulation study that slopes between 1 and 2 are a direct and inevitable consequence of demographic processes alone such as birth, death, immigration and emigration rates. Furthermore, Anderson *et al.* (1982) show that environmental heterogeneity in time or space is sufficient to generate overdispersion (slopes between 1 and 2) even for stable populations at carrying capacity. They conclude that it is not necessary to invoke complex behavioural mechanisms such as density-dependent migration rates and species-specific gregariousness. The results and conclusions emanating from such work must therefore be interpreted with caution. The power law relationship between population variability and average abundance may therefore be of little value simply because an understanding of the underlying mechanisms is required in order to interpret the results. Without this information, the density-dependent dispersion null model is unknown, and with this information at hand the Taylor Power Law is unnecessary. The estimation of the Taylor "Power Law" appears insufficient to explain patterns of distribution of natural populations.

Examination of the local population response is easier to interpret. Elliott (1986) clarified the mechanism responsible for density-dependent migration on a very small scale (his study area was a 60 m<sup>2</sup> section of a stream) in a small part of a population. Similar processes were noted on a much larger scale of the total population. Elliott (1987) concluded from his study of two populations of brown trout from neighbouring

streams that regulation of population size is by density-dependence in favourable habitats and density-independent limiting factors operate in unfavourable habitats. He also proposes that his data support Haldane's (1956) hypothesis that different genotypes will predominate in the two types of habitat, which will lead to different stable points in the dynamics of the populations. Even without genetic differentiation, I feel that the dynamics of population regulation is a function of habitat use across variable environments, and that a gradient of density-dependent effects is expected. Nevertheless, as in Elliott's (1986) study, population variability is relatively greater in low density stations, which supports Elliott's (1986) conclusion that habitat use is primarily density-dependent in salmonids.

Among other studies of local population response across many sites to migratory breeding site selection, Moser (1988) found that the wintering sites of grey plovers (*Pluvialis squatarola*) in British estuaries were filled sequentially as overall population abundance increased, which was presumed to indicate site preference by individuals. Furthermore, in Moser's (1988) study there was considerable variability in the rate of increase of the local populations as overall abundance increased. Low response was associated with the sites filled first while high rates of increase far above the population mean were associated with marginal sites.

Other studies have primarily examined response to population fluctuation on a much smaller scale than the level of a population, or have not related changes in distribution

to fitness-related traits (MacCall 1990). Whitham (1980) demonstrated that the selection of leaves within a tree by aphids was consistent with the Ideal Free Distribution (Fretwell and Lucas 1970), even though fitness was unequal within leaves.

### **Implications for population regulation and population estimation**

The spatial distribution of juvenile salmon in the Little Codroy River was highly variable. The among-site and among-year coefficient of variability in juvenile densities was 99.3 % overall, and ranged from 52.8 % (1959) to 127.5 % (1962) over the 8 years studied. The local density of juveniles did not change in proportion to the total population fluctuations. The site invariant response hypothesis, which predicts proportional changes in all habitats in response to population changes, is rejected. The results are consistent with density-dependent range expansion. Dynamic emigration (Taylor 1986) is a possible mechanism limiting density in primary habitats (Elliott 1986), although density-dependent mortality may predominate in some habitats (Prouzet 1978; Elliott 1987).

Sections of the river which had the best growth rates had the least change in local population abundance. This is consistent with the hypothesis that population abundance expands in the marginal parts of the range. That large sections of the river did not respond at all to the changes in population numbers is remarkable. This implies that

the study of population dynamics of Atlantic salmon (and perhaps most species) must be examined on a scale much smaller than previously thought. Atlantic salmon are somewhat unusual in that the entire population can be censused at two periods of the life-history, when anadromous adults return to spawn and when smolts return to the sea. It is clear from this study that the density-dependence that occurs between these two life stages is largely due to different utilization of the habitat. The response to local changes in density may be less important than those associated with habitat use.

There is a disturbing lesson in this work to those ecologists and resource managers who depend upon estimates of population abundance (see also Chapters 2 and 5). If the results for salmon in the Little Codroy River are typical of other species, then it is very difficult, in general, to infer changes in total population from sampling in just a few sites. Hankin and Reeves (1988) surveyed the density and habitat area of Pacific salmon in riffles and pools along several stations of a small stream. They noted marked density and size differences among habitats, and concluded that extrapolation of abundance estimation based on subsampling "representative reaches" would likely be unrepresentative of true fish abundance. They suggest that sampling effort should be distributed according to estimates of within-habitat variability. Their study did not incorporate temporal variation, but their sampling design did incorporate variability of densities within types of habitats. The selective sampling of primary habitats may have contributed to the historically poor relationship between stock size and juvenile densities.

The implications for population regulation are clear. Age of reproduction is correlated with growth rate in Atlantic salmon (Thorpe and Morgan 1980; Thorpe *et al.* 1982), and mortality will increase for longer residence in the river (Myers 1984). Population regulation may occur by range expansion into marginal habitats, producing lower growth rates, and result in decreases in survival.

It is likely that salmonids become non-territorial at high densities. Such a change has been observed in artificial streams and enclosures as well as in manipulated field conditions (Gibson and Dickson 1984). A breakdown of territorial behaviour is predicted at high densities because of the decreased benefits of territory defence in relation to the increased energy expenditures required with high numbers of competitors (Milinski 1988). However, the environmental conditions may play an important role in territorial defendability, and a shift to non-territoriality may only take place in secondary habitats (Grant and Kramer 1990).

The density in the sites varied by more than an order of magnitude (Figure 3-6a,b), and the average growth rates varied by 25%. If growth is closely correlated with fitness, it is clear that not all fish are equal and this violates the main assumptions of the Ideal Free Distribution (IFD, Parker and Sutherland 1986). There have been several models to describe Density-Dependent Habitat Selection (Milinski and Parker 1991; McCall 1990). The data presented here are consistent with predictions of models that describe animals of unequal fitness (Milinski and Parker 1991; Parker and

Sutherland 1986), for example the Ideal Despotic Distribution model (Milinski and Parker 1991) or, generally, Interference models (Parker and Sutherland 1986). These models hypothesize that animals defend a resource in short supply and that surplus individuals migrate to other habitats. However, in the present and most field studies conducted along the entire range in distribution of a population, the behaviour that results in the observed dynamics is unknown. In the present study, the Optimal Foraging models on which these distribution theories are based are unlikely to apply over such a large range, particularly since juvenile densities are based largely on parental breeding site selection. Models of source-and-sink habitat use (Wiens and Rottenberry 1981; Pulliam and Danielson 1991) may be more appropriate.

The principal limitation of this analysis is the relatively short time series (8 years or fewer). It is possible that some of the observed changes in the distribution may be caused by unknown environmental factors, rather than changes in population size. However, the high association between response slopes derived from independent measures of adult abundance reduces the likelihood of this argument. Thus, it would be useful to have the present results tested with an independent data set. Although the time series are relatively short, the sampling was extensive: 1.7% of accessible habitat was sampled each year. The effort required to reproduce this study would be extensive. In particular, the measurements of body size, and the determination of the age and sexes of the animals in this study are necessary because of the different behaviour of the sexes and age classes; the movement patterns of females are distinct

from mature male parr (Jones 1959; Myers and Hutchings 1986). In addition, back-calculated sizes-at-age needed to be estimated from scale samples for every fish captured over the 8 years of the survey.

### **Density as an indicator of habitat quality**

Brown (1984) proposed that the distribution of population density over a geographical range is much like a normal probability distribution surface. If this were so, local population densities could be predicted from a simple constant function of population abundance. It is shown that Brown's (1984) generalization is clearly insufficient to explain local abundances from overall population abundance and that habitat quality not only plays a role in determining the mean densities, but also population stability, and must be incorporated in a predictive model.

It has been argued that population density may not be a good indicator of habitat quality in birds (van Horne 1983; Rice *et al.* 1986). In a survey of the wildlife literature, van Horne (1983) found that the usual assumption that high densities reflect high habitat quality can be modified by three effects. 1) Seasonal changes in habitat use can be very large, for winter months are often critical and may mask any effect of summer habitats. 2) "Multi-annual variability" in the resource requirements of a species, including short term feeding, breeding, etc., may alter the distribution that would otherwise be reflected in longer-term habitat quality. 3) Thirdly, and perhaps

most important for juvenile salmon, are social interactions and territoriality that may limit the density in the best habitats (see also Grant and Kramer 1990). In this study, densities in some years were observed to be higher in unstable secondary habitats than in the stable "primary" habitats. This is expected if densities are limited in the best habitats as a result of territoriality (Grant and Kramer 1990). It is known that juvenile salmon are territorial in riffles, but tend to school in pools and slower sections of the rivers (Gibson and Coté 1982; Gibson 1988). Much experimental and observational information on the limitation of density by territorial behaviour exists in the literature, and its influence on habitat selection by fishes has been reviewed by Milinski (1988) and modelled by Talbot (1983), Parker and Sutherland (1986) and Sutherland and Parker (1991) and others. High densities in secondary habitats were also observed in a modelling exercise with data on birds by Rice *et al.* (1986), who concluded that the best avian habitats were not those with highest densities overall, but more likely those with the highest consistency of occurrence. They also found, as I did here, a positive association between abundance and stability, but the relationship is not axiomatic. It is proposed in this chapter that stability is the primary indicator of habitat quality.

**CHAPTER 4**  
**SCALES OF DENSITY-DEPENDENT GROWTH AND HABITAT RESPONSE**  
**IN ATLANTIC SALMON**

**INTRODUCTION**

What is the scale of density-dependent interaction within a population? Small scale density-dependent interactions are expected in most systems because of direct competitive interference among individuals, such as in territory defence and food acquisition (Allen 1969; Grant and Kramer 1990). It is generally believed that density-dependence on a small scale is the process that gives rise, through mortality, to the classic dome-shaped stock-recruitment curves whose magnitude is governed by some carrying capacity of the environment (Ricker 1975; Gee *et al.* 1978b; Solomon 1985). Although small-scale density-dependence may influence fitness components such as growth rates and mortality, it is possible that larger scale density-dependence operates as well, through mechanisms such as reduced prey abundance and physico-chemical modification of the environment (Egglshaw and Shackley 1978; Gibson and Haedrich 1988).

It is convenient to study density-dependence at discrete levels (see also Wiens *et al.* 1987, for a similar exercise with bird habitat selection). Density-dependent growth is

studied on three spatial scales: 1) The largest scale is the entire river population, calculated by two methods: a) the average number of juveniles over all stations, and b) the number of adult spawners. This level ignores variation of broad-scale river habitat characteristics such as depth, discharge, turbidity, bottom types and water velocity. 2) The second spatial scale is the tributaries. This scale is large enough to incorporate differences in local habitat characteristics, such as riffles, pools or flats. 3) The smallest spatial scale I study is at the sampling site, typically a 23 m length of river segment. At this scale, the habitat is relatively homogeneous. Two further levels are possible at the extremes, namely the space occupied by an individual fish, such as a territory, and the distributional range of the species, as exemplified by Atlantic salmon (*Salmo salar*) which ranges from the Labrador coast to Maine, Connecticut and Rhode Island (the biogeographic scale, Wiens *et al.* 1987). We are not concerned with these extremes since the focus of the present chapter is to determine the mechanisms of habitat expansion which operate when populations, represented at the adult stage by a migratory group of individuals returning to their river of birth, fluctuate in abundance. Minimum territory requirements of salmonids (e.g. Allen 1969; Elliott 1984b; Grant and Noakes 1987; Grant and Kramer 1990) and historical changes in the species range of Atlantic salmon (e.g. Saunders 1981, 1986) have been addressed in a different context. Nevertheless, spatial requirements of juveniles represents an important element of density-dependence, and its role will be discussed.

Small-scale density-dependent growth has been demonstrated for several fish species, including salmonids (Cushing and Harris 1973; Backiel and Le Cren 1978; Elliott 1988; Randall 1982; Gibson and Dickson 1984; Hanson and Leggett 1985). Other studies have shown population responses consistent with density-dependent hypotheses (see review by Goodyear 1980; MacCall 1990). However, understanding the scale at which density-dependence occurs is further complicated by the dynamics of growth variation in relation to habitat use. Several authors have shown or hypothesized that density regulation mechanisms differ among habitats (McNicol *et al.* 1985; Puckett and Dill 1985; Grant and Noakes 1988; Elliott 1987; Grant and Kramer 1990). For example, in shallow, fast moving streams, territoriality of juvenile salmonids is thought to limit density (Allen 1969; Grant and Kramer 1990), whereas no such mechanism may operate in flats or pools, where juvenile salmon are even known to school (Gibson 1988). The response of individuals to density might therefore differ markedly among different habitats. It might be predicted that the nature of the growth regulation of juvenile salmon is habitat-specific, and that the probability of observing a negative density-dependent growth response decreases in primary habitats (stable, high density sites as defined in Chapter 2). These issues have seldom been addressed directly in the scientific literature. This chapter therefore deals exclusively with density-dependent growth, although other factors, biotic and abiotic, may affect or control habitat use. For example, density-dependent mortality or migration may mask any density-dependent growth (Fraser 1969; Ricker 1975; Grant and Kramer 1990; Elliott 1984a,b, 1987; Gee *et al.* 1978b).

Density-dependent growth may also play an important role in habitat selection and population expansion and contraction. Growth is a fitness-correlated trait, and should be under strong selection pressures to maximize it. Habitats that can sustain high growth rates at high densities can be expected to be preferred to habitats with less support capacity and with a greater density-dependent response. Density-dependent habitat use has been inferred for Atlantic salmon juveniles in a river system where some sections and tributaries remained more stable than others despite a two-fold change in overall population abundance (Chapter 3). Furthermore, sites with good average growth rates, were more likely to have stable parr populations, irrespective of overall adult abundance, than sites with poorer growth rates. This variation in the response was also shown to be dependent on habitat type and location at the tributary level.

In this chapter, I examine the scale of density-dependent growth. Several hypotheses are examined to test the scale of dependence of growth, based on the assumptions that growth can be affected by the local population density, average population abundance in a tributary, or by the overall population abundance in the river (negative density-dependence on a large scale). Two further hypotheses are considered in an effort to provide additional evidence for the density-dependent habitat use model of Chapter 3. The heterogeneity of the large scale growth response is also examined for variation among tributaries. The importance of density-dependent growth is finally considered as an element of the mechanism for population expansion and contraction. This is

achieved by examining the results of the previous tests within the context of the proposed mechanisms.

## METHODS

The data used in this chapter are drawn from records of Atlantic salmon parr (juvenile salmon) sampled during a detailed demographic study of the Little Codroy River by A.R. Murray (1968a,b,c,d; Myers 1984). These data include the number of parr collected, sizes, ages and earlier sizes-at-age from scales, sex, maturity status, and physical stream characteristics, from each of 48 stations sampled annually throughout the watershed (Table 3-1, 3-2; Figure 3-1). This chapter also uses data from a sampling program to estimate parr population densities in the river system and the number of anadromous adults that were parents to each cohort. Details of the methodology used to capture parr and sample specimens are given in Chapter 3. The length, weight and stage of sexual maturation were recorded for each individual parr. Scales were sampled and analyzed to estimate age and to back-calculate growth rate. Back-calculated length-at-age 1 of the 1+ fish caught was used to estimate first year growth (Ricker 1975).

A counting fence was erected annually in the estuary of the river in order to enumerate adult salmon migrating into and out of the river (Murray 1968). Every fish

swimming through the fence was counted, measured, and its life history stage identified. An estimate of total population abundance (adult abundance index) was obtained from the number of adult anadromous salmon associated with the corresponding cohort. Two measures were considered: the number of upstream migrants counted and the number of surviving adults returning to the sea. Both indicators are subject to error. The number of upstream migrants would be affected by variable recreational fishing pressure in the river, and incomplete counts if some fish migrated into the river before or after the counting fence was erected. The census of fish returning to sea the following spring is subject to variable post-spawning mortality and incomplete counts. The sources of error for counts of upstream and downstream migrants should largely be independent because they occurred in different years, and the counts can be averaged as an index of the parental stock ( $N_t$ ) that gave rise to the cohort of interest. This abundance index may fall short of the actual adult numbers, but we are only interested in the covariance of the adult count and local parr densities, and not in the magnitude of the intercepts.

The adult abundance index has the advantage of being analytically independent of local parr densities, avoiding possible part-whole correlations with total parr counts. In order to relate parr densities to the parental generation, the number of upstream anadromous migrants were time-lagged 2 years, kelts were time-lagged 1 year and local parr densities were not time-lagged (even though growth estimated from scales

occurred in the previous year). Local densities therefore serve as an estimate of density in the previous year in which the actual back-calculated growth occurred.

To examine the variability among segments of the river system, stations were grouped for categorical analysis according to river tributaries or river segments (Table 3-1).

These are referred to as "tributaries" even though 2 of these are actually segments of the main river. The adult abundance index ( $N_t$ ) was used as a covariate in some analyses. The resultant local density response variable  $\beta$  is defined in Chapter 3.

Juvenile population densities were calculated for all 1+ fish and for 1+ females only. However, only the growth of females is used. Myers *et al.* (1986) found that 72% of age 1 and 84% of age 2 male parr were mature in the Little Codroy River. Since mature males seek sites for spawning with anadromous females, their distribution will be associated with spawning rather than with habitats used for growth, and their distribution and growth rate will be altered. Male parr density will be considered in some analyses, however, because of their potential influence on the growth of females.

Parr densities were calculated using two methods (Chapter 3): numbers per unit length of river at a station, and numbers per unit area of stream bottom at a station. Analyses were replicated for both "density" estimates. The objective was to avoid bias in the analyses by integrating a dimension of the river into the density estimates, since spurious correlations could result from the analyses of covariance among tributaries

(see also Chapter 3). When no important differences were detected, only the length-corrected results are reported in order to remain consistent with the analyses of Chapter 3.

Densities were estimated at 38 sites over a period of 8 years. Not all sites were sampled every year. Local density-dependent growth response could not be estimated for sites sampled fewer than 3 years. Since the precision of the regression parameters increases with the number of years the site was surveyed, all analyses of summary data were weighted by the square root of the number of years sampled per station in a weighted least squares design.

Growth variables consist of back-calculated size-at-age scale estimates for the first year of life (G1), the growth in the second year until the sampling date (G2), and total length (LT). First year growth was also detrended for differences between sampling stations by subtracting the mean station density from each estimate. To check for robustness of the growth/density relationship, the station mean was subtracted from the growth estimate of individual fish. Density was calculated using: local density, average yearly tributary densities, average yearly river densities and the indicator of adult spawner abundance as described previously.

## Statistical analysis

Factorial analysis of variance is a suitable method of analysis for the nested hierarchical nature of the environmental scaling described above (Wiens *et al.* 1987; Orians and Wittenberger 1991; McKone 1993). The models fitted to data are general linear hypotheses. The most common analysis of variance design used growth values from individual fish, so that the two-way design is given by

$$Y_{ij} = \mu_Y + \alpha_i A + \beta_t B + (\alpha\beta)_{it} AB + \varepsilon_{ij}$$

where  $Y_{ij}$  is the dependent variable of the  $j^{\text{th}}$  fish at the  $i^{\text{th}}$  site and  $t^{\text{th}}$  sampling occasion,  $\mu_Y$  is the mean of the population,  $\alpha_i$  is the fixed site effect,  $\beta_t$  is the fixed year effect,  $(\alpha\beta)_{it}$  is the interaction term and  $\varepsilon_{ij}$  is the residual error term. On occasion, the dependent variable used was a station inter-annual mean or a regression slope estimated elsewhere (e.g.  $\beta_i$ 's from Chapter 3). On several occasion, a covariate (variable on a continuous scale) was introduced in the above design, which becomes in the case of a one-way ANOVA

$$Y_{ij} = \mu_y + \alpha_i A + \beta_w (X_i - \mu_x) + \varepsilon_{ij}$$

where  $\beta_w$  is the within groups regression slopes and  $X_i$  is a continuous variable of a station-level characteristic (Winer 1971). In general, I was most concerned with testing

the assumption of homogeneity of slopes within groups. This was done using a homogeneity of slopes model as implemented by SAS v. 6.04 (SAS 1985). Analyses of covariance were also employed on more complex designs. For computational details, I referred to Snedecor and Cochran (1967). McKone (1993) demonstrated the importance of a large number of sites for the comparison of population across spatially variable environments. Mixed model ANOVA's were shown to be more powerful in studies with a large number of sites, while nested designs were more appropriate to studies with a small number of sites but many replicates within sites. In this thesis, the large number of sites distributed over the entire range of distribution of the population permits the use of both mixed and nested designs. In many tests, the interaction term is the parameter of interest, which is particularly well suited to the sampling program used on the Little Codroy River.

## RESULTS

First and second year growth are weakly correlated when all sites are combined ( $R^2=0.10$ ,  $n=1155$ ,  $P<0.0001$ ). When the analysis was repeated for each tributary (Figure 4-1), it was found that the slopes of the relationship varied among tributaries (analysis of covariance with first year growth regressed on second year growth; first year growth by tributary interaction,  $F=4.00$ ,  $df=9,1135$ ,  $P<0.0001$ , Figure 4-1). The correlation between first and second year growth varied among tributaries as well (Figure 4-1).

**Figure 4-1: Plot of the relationship between first and second year growth of individual fish. Coefficients of determination and regression line are presented for each tributary (numbered 1 to 10 as in Chapter 3) separately. A small amount of random variation has been added to overlapping points in order to make them visible.**

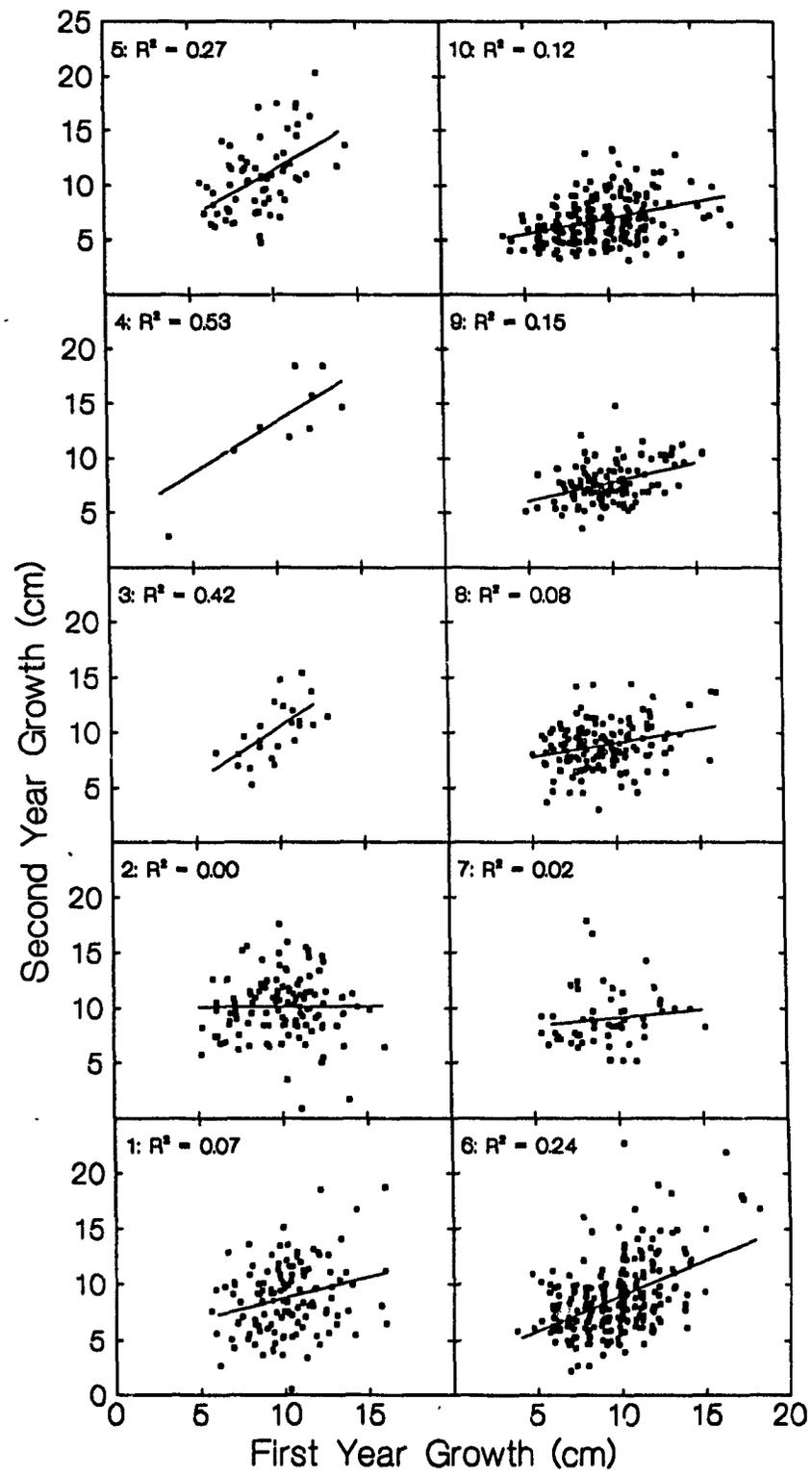


Figure 4-1

These two growth indicators can be used as separate estimators of response to growth, particularly when performing among-tributary comparisons. It is therefore reasonable to consider possible reasons for this variation among tributaries.

**1) The growth of female 1+ parr is influenced by the local density of salmon parr.**

The growth rate (first and second year growth (G1 and G2), length (LT)) of parr was related to population abundance as measured by local densities ( $n_u$ ), average tributary densities ( $\bar{n}_u$ ) and annual densities ( $\bar{n}_i, N_i$ ). There is generally strong evidence for negative density-dependent growth in juvenile populations (Table 4-1, Figure 4-2). However, the strength of the individual relationships varies considerably. Note that the variance in growth also decreases as a function of most indicators of population abundance but particularly with estimates of local density (Figure 4-2). Although this effect might be due to a reduction in the number of samples at high densities, Elliott (1984a) attributes a similar result in brown trout (*Salmo trutta*) fry (see Elliott's Figure 6b) to density-dependent effects. Note however that the relationship in this thesis is among sites while Elliott's (1984a) is among years but with sampling sites (quadrats) combined. It indicates that growth is much less constrained at low local densities than at high population densities, in accordance with some theoretical predictions of density-dependence (e.g. Anderson *et al.* 1982). Similar results were also obtained by Grant and Kramer (1990) who reported reductions in residual variance of the territory/size relationship as a consequence of density-dependence. It is likely that a

**Figure 4-2: Plots of growth variables (first year growth, second year growth and total length) against estimates of density (local 1+ female juvenile density, local 1+ total juvenile density, average tributary 1+ female density, average tributary total 1+ juvenile density, average river 1+ female density, average river total 1+ juvenile density, spawner abundance). The densities are arranged in sequence of increasing spatial scale. Statistics are given in Table 4-1.**

Figure 4-2

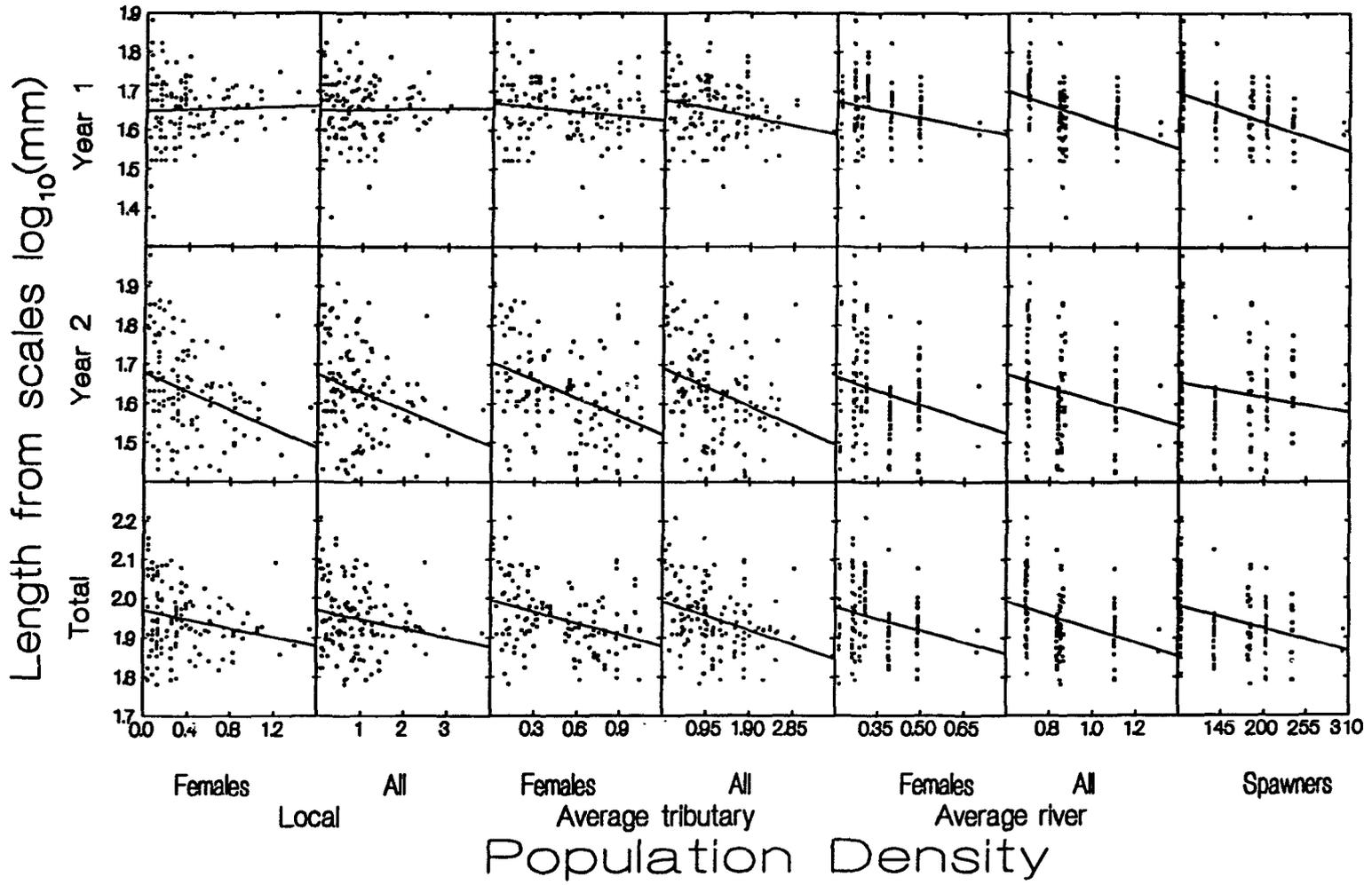


Table 4-1: Pearson correlations of growth indicators with various juvenile and adult population abundance indicators. The values correspond to Figure 4-2 except for locally detrended first year growth.

DENSITY VARIABLE	GROWTH VARIABLE							
	Total length		1 <sup>st</sup> year growth		Locally detrended 1 <sup>st</sup> year growth		2 <sup>nd</sup> year growth	
	r	P	r	P	r	P	r	P
local 1+ female density	-.216	.012	.009	.919	-.077	.374	-.306	<.001
local 1+ juvenile density	-.191	.027	.008	.876	-.098	.259	-.272	.002
Average Tributary 1+ female density	-.326	<.001	-.143	.100	-.115	.187	-.368	<.001
Average Tributary 1+ juvenile density	-.285	.001	-.155	.074	-.095	.273	-.305	<.001
Average river 1+ female density	-.271	.002	-.232	.007	-.274	.001	-.238	.006
Average river 1+ juvenile density	-.353	<.001	-.406	<.001	-.447	<.001	-.247	.004
Number of adult spawners	-.353	<.001	-.485	<.001	-.524	<.001	-.200	.021

significant fraction of high density samples are habitats where territoriality plays a role in limiting size variation and density, and where habitat characteristics are more suitable for certain size classes.

Overall, the strength of the correlation between indicators of density and growth in the first summer (G1) and total size increased progressively as the indicators of density integrated a larger area (Table 4-1). The reverse trend is evident with the second year of growth (G2), which is more closely related to local female density and female density averaged over the tributary (Table 4-1). These results seem to imply that density-dependence is a function of population density over a large area, refuting the hypothesis that growth is regulated only by local abundance. However, further analysis is required. Several factors may operate at the local station or tributary level that might be masked by the overall trend. For example, local productivity, habitat characteristics and territoriality may limit standing stock, growth and density. Growth and mean juvenile densities may differ greatly among stations, so that within-station covariance may be masked by overall heterogeneity. To circumvent this, growth of each individual fish was transformed by subtracting the overall station mean according to the formula  $DG_{ij} = G_{ij} - \bar{G}_i$ , where  $DG_{ij}$  is the detrended growth of the  $j^{\text{th}}$  fish at the  $i^{\text{th}}$  site. The station-detrended growth rate was regressed with the density variables. Generally the Pearson correlations are slightly higher but the basic pattern remains the same (Table 4-1), that is, the overall correlation of growth increases with the scale of density-dependence.

Within station, both the unweighted mean and median of the estimated relationship between growth and parr density are negative, as expected (median: -11.6, mean:  $-34.071 \pm 23.4$  s.e.,  $n=29$ ), but the slopes are extremely variable. Two further levels of noise can be controlled, and partial correlations examined. The effect of tributary and the number of spawners (and their interaction) was removed statistically from the growth/local density relationship. Under such control, the effect of local density (Table 4-2) becomes very important for first year growth (G1) but less so for second year growth (G2). Qualitatively, the sign of the local density-dependent growth regressions can be used as well. The number of stations with a negative and positive slopes was 21 and 9 respectively (G-test:  $\chi^2=4.86$ ,  $df=1$ ,  $P<0.05$ ). This is strong support for the small scale density-dependence hypothesis, which is accepted.

**2) The growth of female 1+ parr is influenced by the density of salmon parr of the tributary or river segment.**

Overall, the average tributary density of 1+ juveniles and 1+ female juveniles is significantly negatively related to first and second year growth; however, the effect is much more important for second year growth (Table 4-1, Figure 4-2). To determine if this intermediate scale of density-dependence is statistically significant when other factors are removed, an analysis of covariance with growth as dependent variable was used to determine the effect of average tributary density among years (Table 4-3). The analysis reveals that the interaction between average tributary densities and the

**Table 4-2: Analysis of covariance demonstrating a significant effect of local density on first year growth and non-significant effect on second year growth, with spawners abundance and tributary controlled statistically. A:  $R^2=0.143$ , B:  $R^2=0.229$ . See Figure 4-4a,b. The lines highlighted in bold letters are of particular interest (see text).**

**A: DEPENDENT VARIABLE- First Year Growth (G1)**

Source	DF	Mean Square	F Value	Pr > F
<b>Local density</b>	<b>1</b>	<b>72.1191658</b>	<b>15.91</b>	<b>0.0001</b>
Tributary	9	9.212	2.03	0.0330
Spawners	1	257.016	56.68	0.0001
Spawners*Tributary	9	13.929	3.07	0.0012
Error	1134	4.534		

**B: DEPENDENT VARIABLE- Second Year Growth (G2)**

Source	DF	Mean Square	F Value	Pr > F
<b>Local density</b>	<b>1</b>	<b>18.741</b>	<b>2.86</b>	<b>0.0911</b>
Tributary	9	46.833	7.15	0.0001
Spawners	1	147.089	22.45	0.0001
Spawners*Tributary	9	23.113	3.53	0.0003
Error	1134	6.552		

**Table 4-3: Analysis of covariance demonstrating an important heterogeneity in the slopes between tributaries (the interaction term) on the relationship between growth and average tributary densities among years. A:  $R^2=0.049$ ; B:  $R^2=0.205$ . See Figure 4-5a,b. The lines highlighted in bold letters are of particular interest (see text).**

**A: DEPENDENT VARIABLE - First Year Growth (G1)**

Source	DF	Mean Square	F Value	Pr > F
Tributary	9	15.298	3.04	0.0013
Avg Tributary densities	1	29.650	5.90	0.0153
<b>Avg Tributary densities*Tributary</b>	<b>9</b>	<b>20.208</b>	<b>4.02</b>	<b>0.0001</b>
Error	1135	5.025		

**B: DEPENDENT VARIABLE: Second Year Growth (G2)**

Source	DF	Mean Square	F Value	Pr > F
Tributary	9	55.141	8.17	0.0001
Avg Tributary densities	1	75.918	11.25	0.0008
<b>Avg Tributary densities*Tributary</b>	<b>9</b>	<b>32.921</b>	<b>4.88</b>	<b>0.0001</b>
Error	1135	6.747		

tributary grouping is significant, indicating that the slopes of the relationship varies among tributaries, thus supporting the hypothesis that the average tributary density is an important determinant of growth (Table 4-3), although its importance may vary among tributaries. Although the effect is highly significant, only 5% of the variance in first year growth is explained by this statistical model, whereas 21% of the variance of second year growth is explained (Table 4-3). With local density included as a covariate in the statistical model, the effect of average tributary density remains quite significant within tributary for both growth variables (G1 and G2) but more importantly for G2 (Table 4-4), indicating that tributary support of productivity varies considerably. Furthermore, local density remains significant for G1 but not for G2. It is concluded that average tributary density is an important element limiting growth, but that the effect is specific to tributaries and is somewhat less important than local population density. Hypothesis 2 cannot be rejected.

**3) The growth of female 1+ parr is influenced by overall population density.**

Growth rates (G1, G2, LT) are significantly correlated with all indicators of density based on overall averages (stations within years), namely the annual average female 1+ parr density and 1+ parr density of both sexes combined, as well as with the number of adult spawners (Table 4-1, Figure 4-2). This is strong support for this hypothesis since average parr densities and spawner abundance are independent

**Table 4-4: Analysis of covariance demonstrating the main effect of local density on first and second year growth, with tributary density and tributaries (and their interaction) controlled statistically. A:  $R^2=0.060$ ; B:  $R^2=0.206$ . Local density appears to be an important determinant of first year growth but not of second year growth. The lines highlighted in bold letters are of particular interest (see text).**

**A: DEPENDENT VARIABLE- First Year Growth (G1)**

Source	DF	Mean Square	F Value	Pr > F
<b>Local density</b>	1	65.292	13.13	<b>0.0003</b>
Tributary	9	15.235	3.06	0.0012
Avg Tributary density	1	37.785	7.60	0.0059
<b>Avg Tributary density*Tributary</b>	<b>9</b>	<b>20.153</b>	<b>4.05</b>	<b>0.0001</b>
Error	1134	4.972		

**B: DEPENDENT VARIABLE: Second Year Growth (G2)**

Source	DF	Mean Square	F Value	Pr > F
<b>Local density</b>	1	7.329	1.09	<b>0.2975</b>
Tributary	9	55.210	8.18	0.0001
Avg Tributary density	1	71.159	10.55	0.0012
<b>Avg Tributary density*Tributary</b>	<b>9</b>	<b>32.952</b>	<b>4.88</b>	<b>0.0001</b>
Error	1134	6.747		

measures of abundance and the strength of the relationships are quite similar. Within tributaries, the effect of the number of spawners on growth rate remains important (Table 4-5) even though G2 and LT are significantly correlated with average tributary densities and G1 is not. One further prediction on the basis of the above hypothesis is that change in growth should be negatively related to change in density when both are derived as a function of change in population abundance. The percent changes in growth and density, calculated from the within-tributaries regressions of growth or local density with adult population abundance, indicate that tributaries with greater temporal stability also have less variation in growth rate (Figure 4-3). However, there is considerable scatter about the regression line ( $r=-0.42$ ,  $n=10$ , 1-tailed  $P=0.11$ ), perhaps in part as a consequence of the tributary-specific growth response (Hypothesis (2)). Hypothesis (3) is supported from the evidence presented above.

To summarize the results of the first three hypotheses, it appears that large-scale population density has a strong effect on growth in the first year and local densities has a somewhat lesser effect. The density-dependent growth response of the second year growth is stronger at the local or tributary level. This may be a result of increased migration capabilities of parr in their second year, which would increase local competition in certain habitats.

**Table 4-5: Nested analysis of variance demonstrating the significant effect of the number of adult migrants (spawners) within tributaries on the first and second year growth. A:  $R^2=0.131$ ; B:  $R^2=0.227$ . Growth response to changes in overall population abundance is thus tributary specific. The lines highlighted in bold letters are of particular interest (see text).**

**A: DEPENDENT VARIABLE: First Year Growth (G1)**

Source	DF	Mean Square	F Value	Pr > F
Tributary	9	6.881	1.50	0.1435
<b>Spawners within Tributary</b>	<b>10</b>	<b>68.692</b>	<b>14.95</b>	<b>0.0001</b>
Error	1135	4.594		

**B: DEPENDENT VARIABLE: Second Year Growth (G2)**

Source	DF	Mean Square	F Value	Pr > F
Tributary	9	49.599	7.56	0.0001
<b>Spawners within Tributary</b>	<b>10</b>	<b>54.784</b>	<b>8.35</b>	<b>0.0001</b>
Error	1135	6.562		

**Figure 4-3: Relationship between the change in growth rate and local density for each of the 10 tributaries. Both variables are calculated from predicted values derived from their respective regressions slopes with spawner abundance within tributaries.**

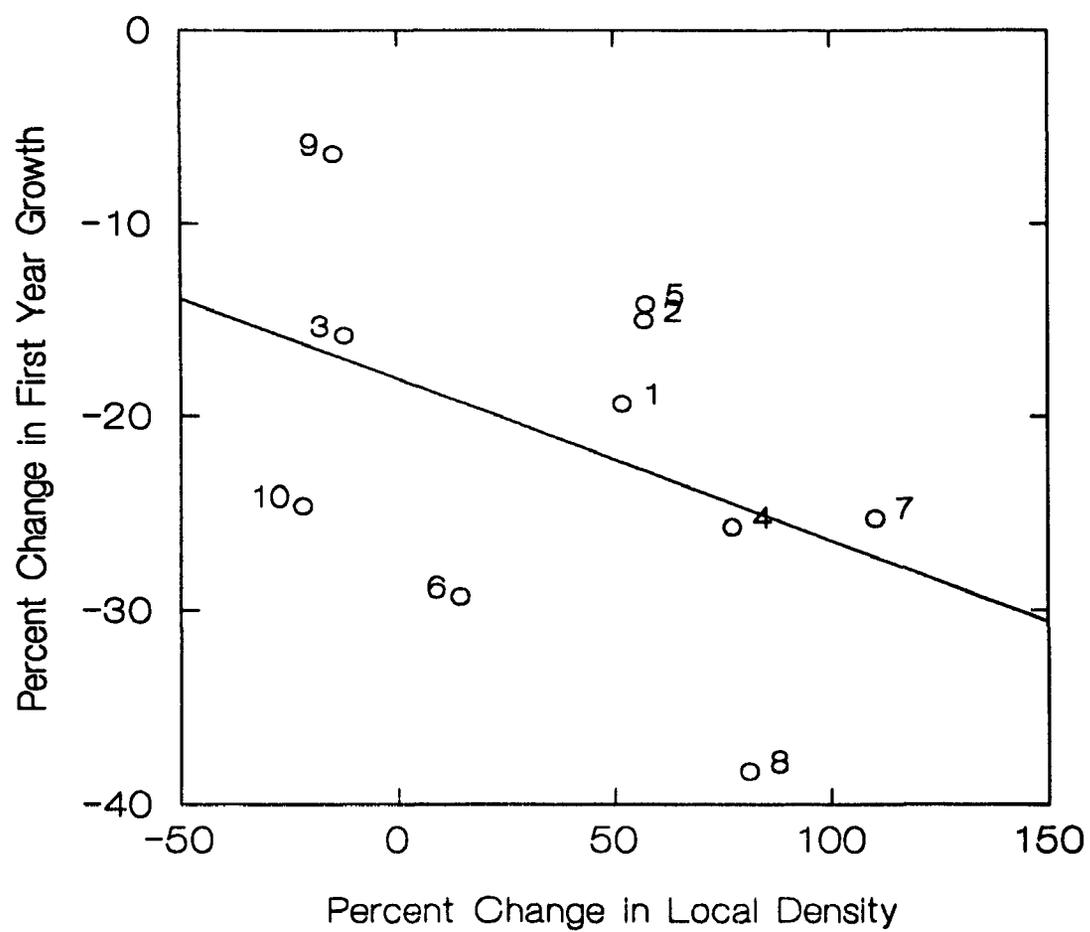


Figure 4-3

**4) The growth response to changes in overall population abundance is tributary-specific.**

Large-scale density-dependent growth response is hypothesized to differ among tributaries. This hypothesis differs from hypotheses (1) and (2) tested above where tributary effects were tested with local and average tributary parr densities. Whereas a test of homogeneity of slopes using parr densities is done at different mean parr densities among tributaries, potentially introducing a confounding factor in the analysis, a test using spawner abundance is achieved at a constant mean and variance of the predictor variable among groups and is a much more powerful test.

This hypothesis can easily be tested by examining the among-tributary variation in the slope of the relationship between growth and spawner abundance. To test this, an analysis of covariance of growth as dependent variable was performed with tributary as categorical variable and number of adult migrants as covariate. The main effects as well as the interaction terms were significant (Table 4-6, Figure 4-4a,b). The significance of the interaction term (Table 4-6) is evidence for a tributary-specific response. This is consistent with the results obtained with average tributary parr densities (Table 4-3, Figure 4-5a,b). It can be seen that the relationship of growth and density to spawner and tributary abundance is highly variable. The differences between the slopes of the growth and density regression lines are also highly variable among

**Table 4-6: Analyses of covariance demonstrating the effect of spawner abundance and tributaries on first and second year growth. A:  $R^2=0.131$ , B:  $R^2=0.227$ , C:  $R^2=0.194$ . The significant interaction indicates that response is tributary-specific. The lines highlighted in bold letters are of particular interest (see text).**

**A: DEPENDANT VARIABLE - First Year Growth (G1)**

SOURCE	DF	Mean-Square	F-RATIO	P
Tributary	9	6.881	1.498	0.144
Spawners	1	233.148	50.754	<0.001
<b>Tributary*Spawners</b>	<b>9</b>	<b>11.946</b>	<b>2.601</b>	<b>0.006</b>
ERROR	1135	4.594		

**B: DEPENDANT VARIABLE - Second Year Growth (G2)**

Source	DF	Mean-Square	F-RATIO	P
Tributary	9	49.599	7.558	<0.001
Spawners	1	159.164	24.254	<0.001
<b>Tributary*Spawners</b>	<b>9</b>	<b>22.420</b>	<b>3.417</b>	<b>&lt;0.001</b>
ERROR	1135	6.562		

**C: DEPENDANT VARIABLE: Total Length (LT)**

SOURCE	DF	Mean-Square	F-RATIO	P
Tributary	9	65.650	4.540	<0.001
Spawners	1	777.584	53.775	<0.001
<b>Tributary*Spawners</b>	<b>9</b>	<b>41.615</b>	<b>2.878</b>	<b>0.002</b>
ERROR	1135	14.460		

**Figure 4-4: Regression plots of growth and local juvenile density against spawner abundance for all tributaries. The plots are for a) first year growth, and b) second year growth. The values of growth and density have been shifted slightly horizontally to reduce the amount of overlap. —●—: Growth; ---□---: Density.**

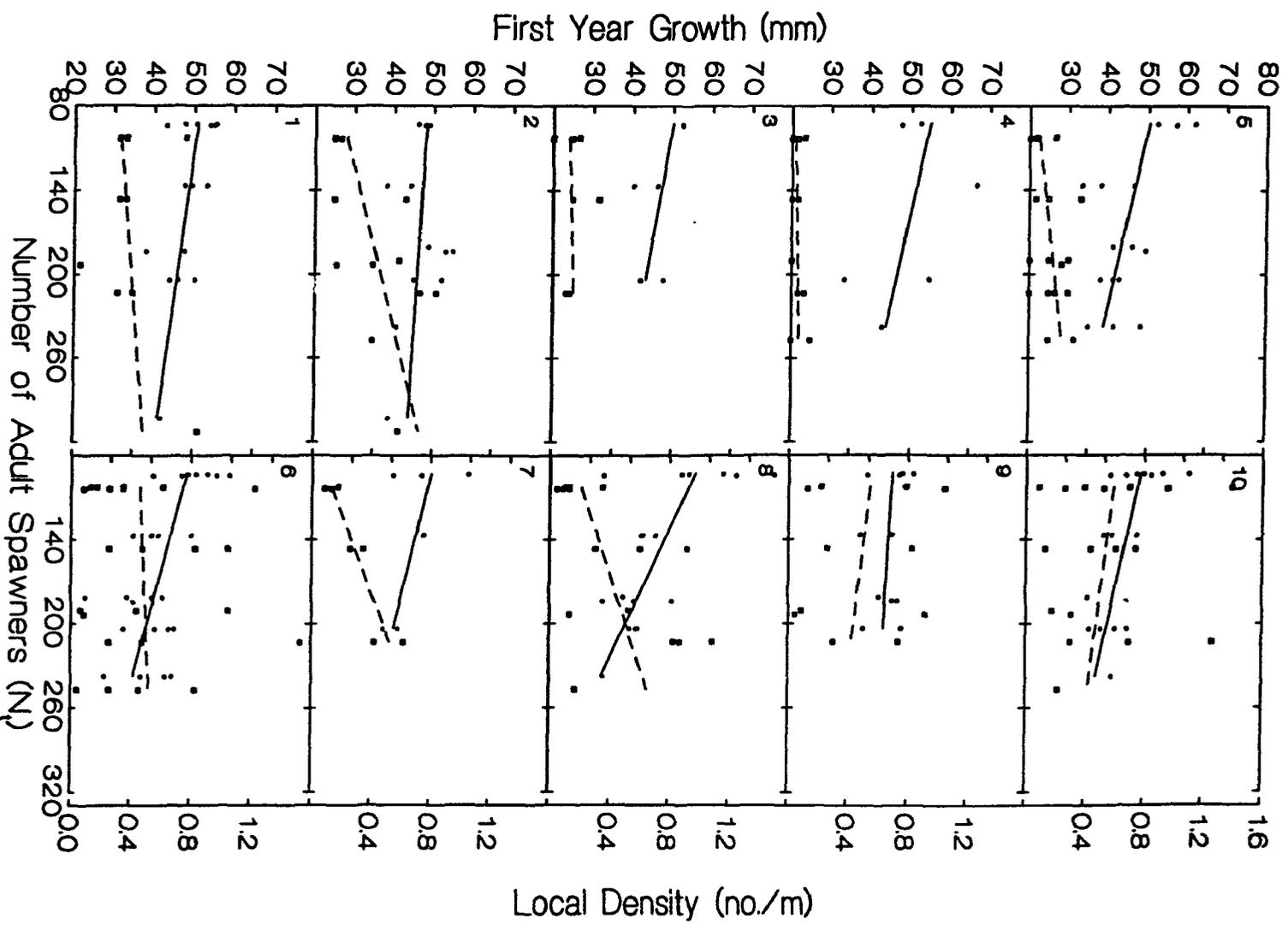


Figure 4-4a

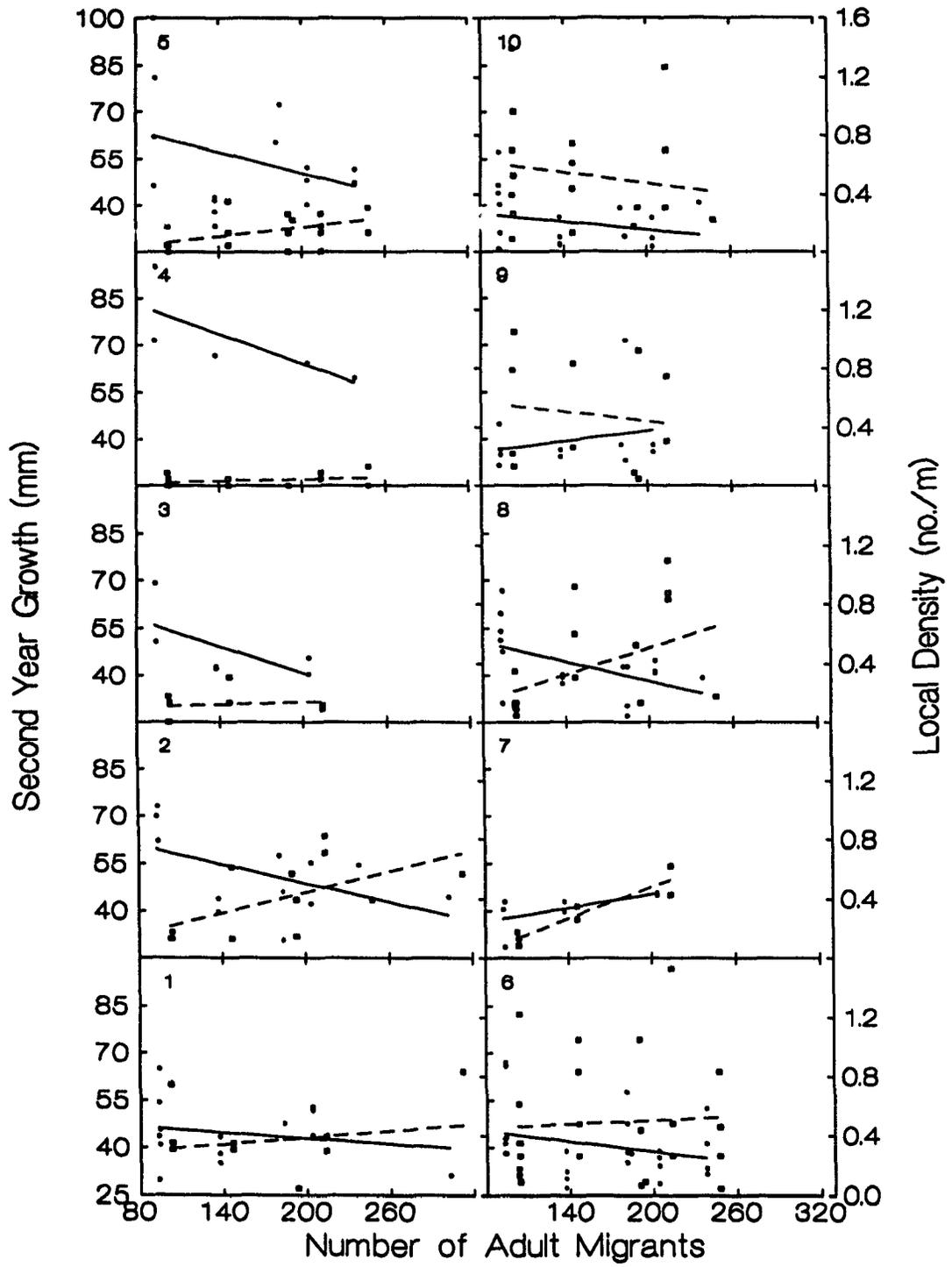


Figure 4-4b

Figure 4-5: Regression plots of growth and local juvenile density against average tributary 1+ female densities for all tributaries. The plots are for a) first year growth, and b) second year growth. —●—: Growth; ---□---: Density.

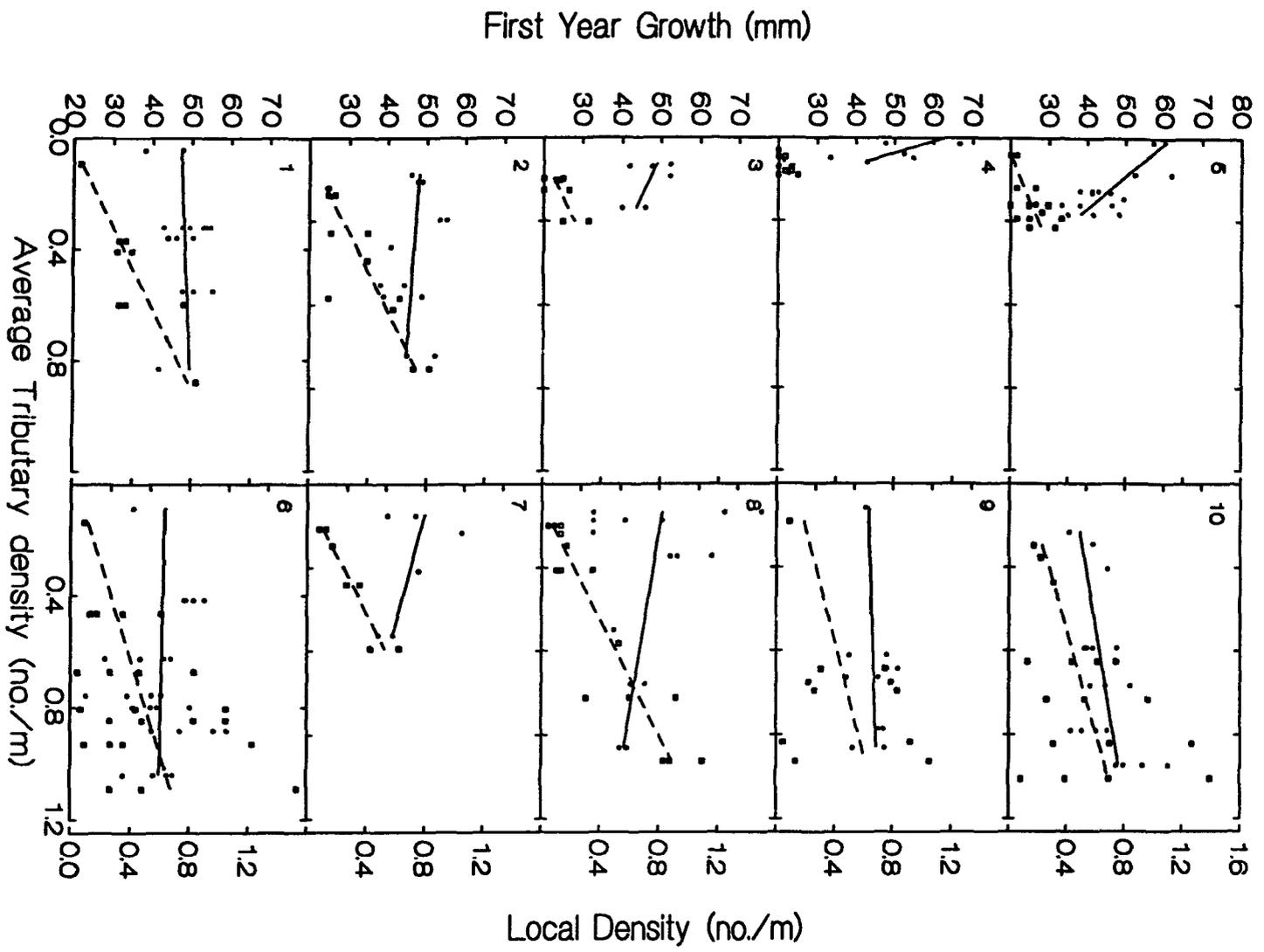


Figure 4-5a

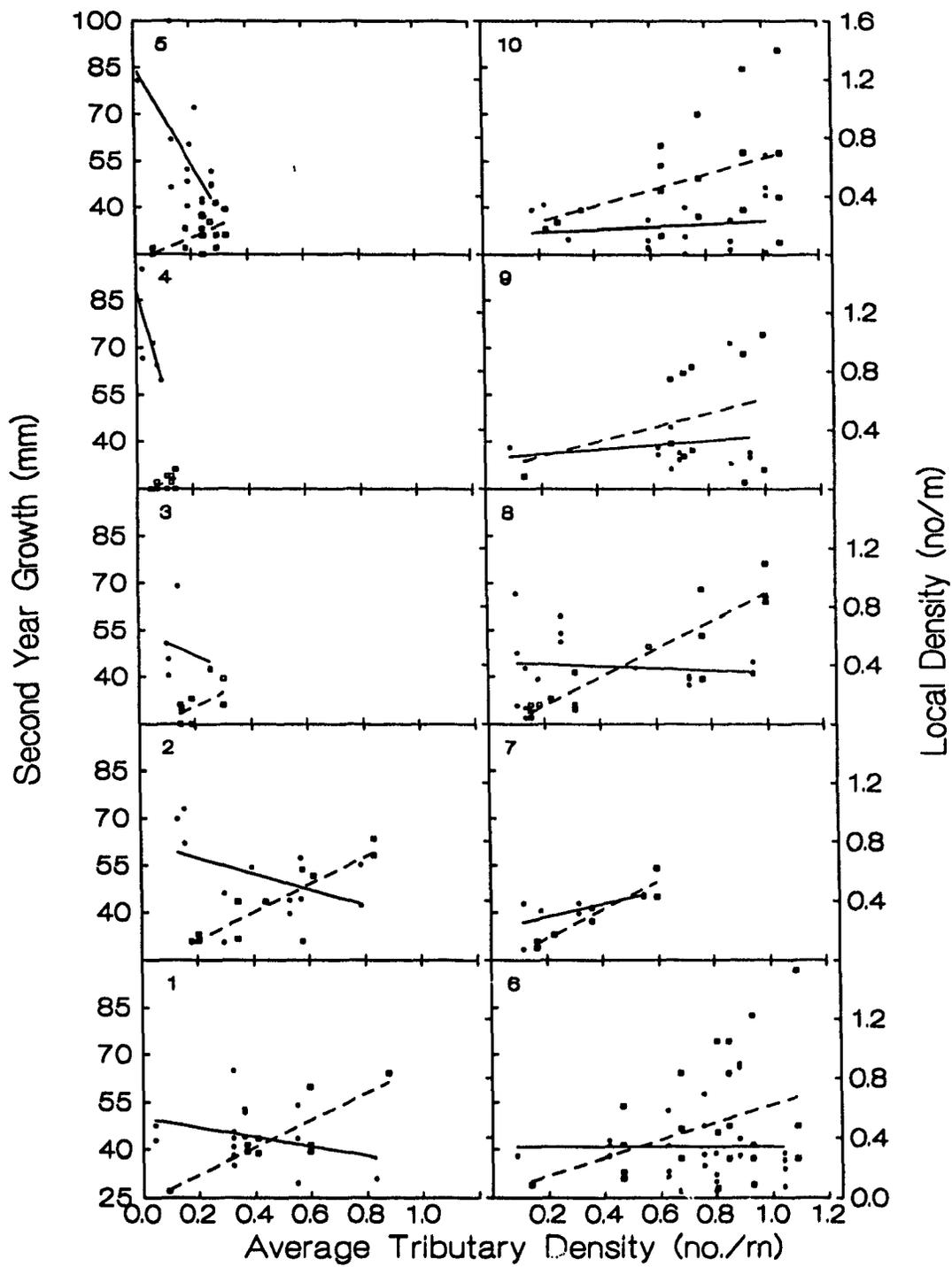


Figure 4-5b

tributaries. There is ample evidence for tributary-specific response to changes in population abundance. Hypothesis 4 has strong support.

**5) The growth response to change in local population abundance is a function of the juvenile response to changes in overall population abundance.**

In this section, I aim to demonstrate that growth response is related to density-dependent habitat use. Firstly, it can be shown that the variance of growth is heterogeneous among years (Bartlett's test of homogeneity of variance with the subgroup of stations sampled for more than 6 years,  $n=195$ ,  $df=7$ ,  $\chi^2=14.42$ ,  $P=0.044$ ).

First year (G1) and second year growth are regressed against local population density of 1+ female parr. These slopes are used as local response indicators. A negative slope indicates negative density-dependence of growth. The relationship between the first year growth response derived above and the density response (derived in Chapter 3) is significant and negative (Weighted Least Squares using square root of the number of years sampled per station as weight variable;  $R^2=0.154$ ,  $df=1,24$ ,  $F=4.363$ ,  $P=0.047$ , Figure 4-6), indicating that habitats that responded to changes in density as a function of total abundance also responded locally in growth rate. The linear model, however, does not fit the data very well. The problem with using the estimated relationship between growth and density in these analyses is that a 100% change in density at a station with only 1 fish is given as much weight in the analysis as a 100% change in

**Figure 4-6: Plot of the first and second year small scale density-dependent growth response against the local juvenile density response to variation in spawner abundance. The relationships are significantly negative (see text). Each point represents a sampling site and is labelled by tributary number. —●— : First year growth response. ---□--- : Second year growth response.**

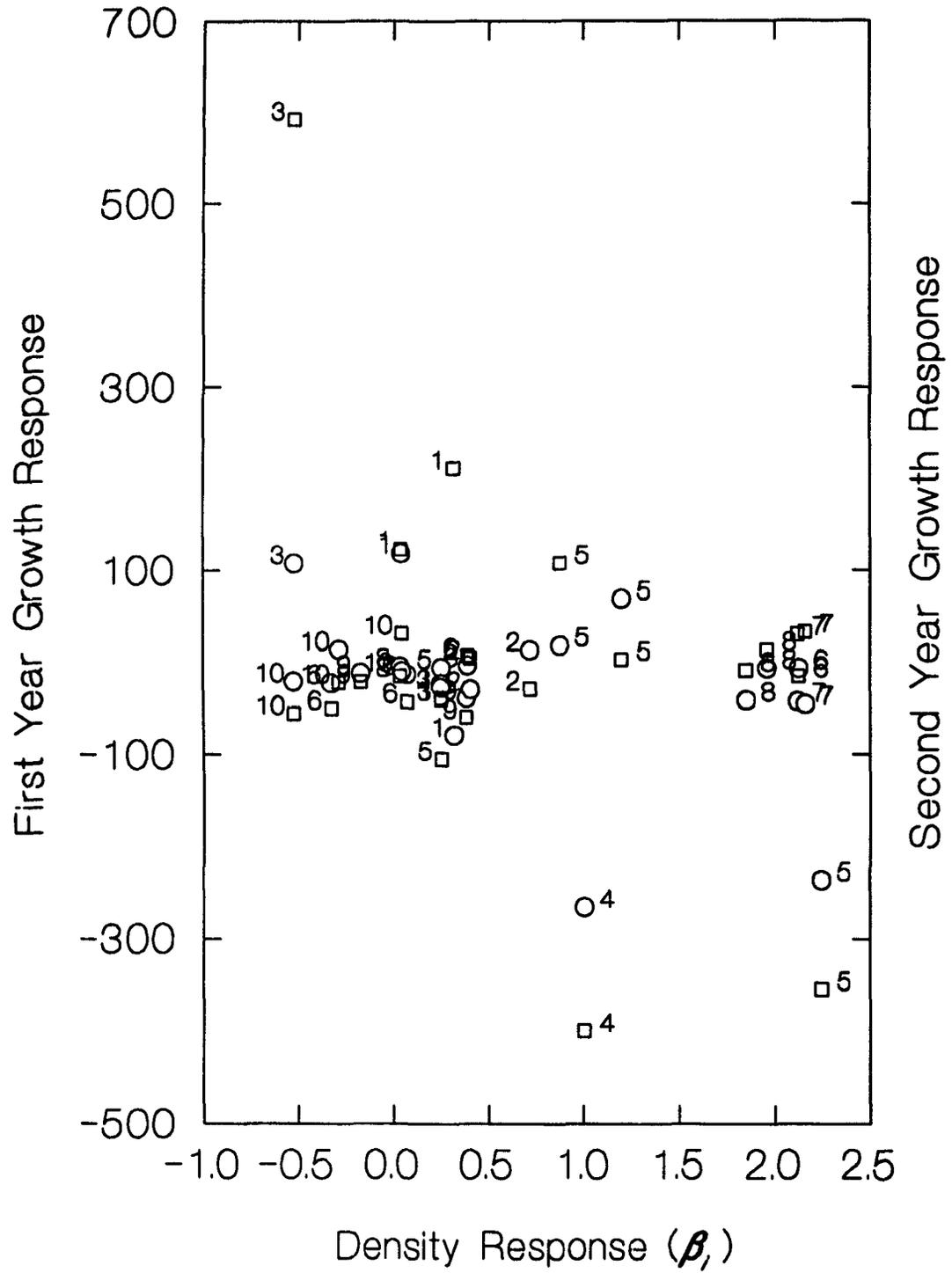


Figure 4-6

density at a station with, say, 60 fish, the latter being much more biologically meaningful. Nevertheless, this is evidence for a joint density-dependence at some sites to changes in population abundance and a joint stability of other sites to these same changes. Furthermore, the regression intercept does not depart significantly from the origin (0,0;  $F=0.0002$ ,  $df=1,24$ ,  $P=0.990$ ), indicating that some habitats tend to be stable both in density and in growth rate.

If habitat expansion and contraction occur in marginal habitats, one predicts that the relationship between changes in local abundance and changes in overall population abundance will differ markedly in different habitats (Chapter 3). Furthermore, if growth is considered an estimator of habitat quality, the relationship between growth rates and the overall population abundance is expected to differ among habitats (tributaries). A significant interaction term between tributaries and overall population abundance ( $N_t$ ) is apparent in analyses of covariance implicating either first year growth (G1), second year growth (G2) or total length (LT) as dependent variable (Table 4-6). The multivariate result, showing the effect of tributary and overall population abundance on G1 and G2 is also highly significant (Table 4-7). These results are strong evidence for differential effects of tributary on the relationship between population abundance and local growth. Several mechanisms are possible and are likely to vary in importance according to habitat characteristics. However, the variable growth response to increased overall population abundance (Figure 4-3), from strong (tributary 8, -32.9 % change in growth overall) to weak (tributary 9, -6.6 %

**Table 4-7: Multivariate ANOVA to test the effect of tributary and overall population abundance on first and second year growth. The corresponding univariate  $R^2$  are: First Year Growth  $R^2=0.131$  and Second Year Growth,  $R^2=0.227$  (from Table 4-6). Canonical correlations are: 1: 0.477, 2: 0.353. The line highlighted in bold letters is of particular interest (see text).**

<b>SOURCE</b>	<b>DF</b>	<b>Wilk's Lamda</b>	<b>F</b>	<b>Pr &gt; F</b>
Tributary	18,2270	0.930	4.659	0.0001
Spawners	2,1134	0.950	29.604	0.0001
<b>Tributary*Spawners</b>	<b>18,2268</b>	<b>0.953</b>	<b>3.086</b>	<b>0.0001</b>

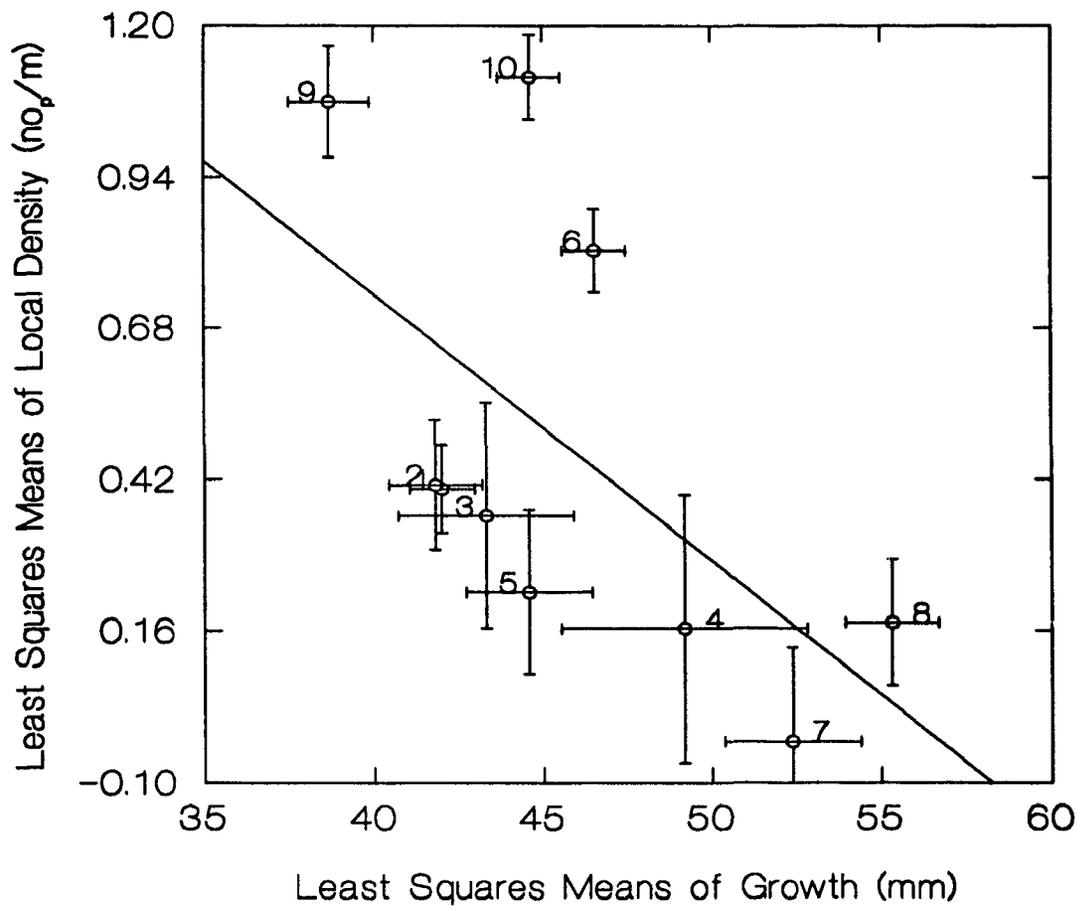
change in growth overall) would imply an additional variable cost to habitat selection. The corresponding changes in density corresponding to the changes in growth rate above were 57.7 % and -13.9 % in tributaries 8 and 9 respectively. Note that the decrease in growth rate in tributaries that also had a small decrease in density (such as tributary 9) is indicative of density-dependence on a larger scale than in the local or tributary scale (Hypotheses 1 to 3). Furthermore, the adjusted least squares means from the analysis of covariance for first year growth (Table 4-6) are negatively correlated with the equivalent least squares means for density ( $r=-0.596$ , 1-tailed  $P=0.035$ , Figure 4-7) even though the test is weak because of the relatively few data points. This is equivalent to the residual correlation of growth and density. Since the main effects of the number of migrants and tributaries, and the interaction term, have been removed statistically, the negative relationship between least squares means of growth and local densities represents small-scale interdependence. This further supports the hypotheses that density-dependent growth occurs on a small scale.

## DISCUSSION

### Scale of density-dependent growth

This chapter demonstrates that small (local) and large scale (overall population) density-dependent growth are important components of productivity in riverine environments. That the local density of juveniles influences local growth rates is not

**Figure 4-7: Plot of the least squares means of density and growth after statistical control of the effect of spawner abundance and tributary (from the analysis of Table 4-6a). The negative slope indicates that a local effect of density on growth rate persists after removal of the effects of population abundance and tributary-specific response and provides evidence for local density-dependent growth.**

**Figure 4-7**

surprising in itself and has been shown by several other authors (e.g. Egglisshaw and Shackley 1977; Gibson and Dickson 1984). However, it is also proposed that density-dependence operates at a larger spatial scale, i.e. at the scale of the tributary and whole river.

Growth dependence does not disappear with the integration of a progressively larger spatial scale and, in the case of first year growth rate, the relationship appears to strengthen. That a decrease in growth rates in local populations is found even though the local population density remains constant or decreases is further evidence for large scale density-dependent effects. This appears in tributary 3, 9 and 10 (Figure 4-3, 4-4).

There is very little literature available on the scale of density-dependent growth. Most of the literature deals with scales of habitat selection or avian censuses (Wiens 1981, Orians and Wittenberger 1991). Orians and Wittenberger (1991) reiterated the importance of measuring habitat selection and performing analyses on various scales because of the scale-dependence of the interpretation of behaviours. In particular, they stated that nesting site selection of female yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) was a function of vegetation density on the smallest scale (the territory) but a function of food supply on an intermediate scale. This and other examples (see Wiens 1981; Wiens and Rotenberry 1981; Wiens *et al.* 1987) are essentially sampling problems, whereas the present study demonstrate density-dependence over a wide range of scales of population abundance.

Growth in the first and second year are correlated. This is not surprising; Menzies (1927) long ago noted that growth of salmon parr in the first year is a good indicator of growth throughout life. Nevertheless, there is considerable variation in the strength of this relationship among tributaries. This invalidates the assumption used by Evans *et al.* (1984, 1985) that growth is fixed at an early age throughout life. It is probable that the poor fit of the models developed by Evans *et al.* (1984, 1985) to predict smolt production from parr growth was due to the failure of this assumption.

A possible weakness of the present approach to testing the scale of density-dependence is that whole river and tributary densities are not independent of local population densities, since the latter are used in the calculations of the former. However, this dependence should not affect the temporal variability observed with large-scale population abundance since these are independent measures. When performing tests using parr densities, growth response is always estimated within stations and tributary averages of the response are used to minimize this problem.

### **A mechanism for understanding population expansion**

Fitness of individuals, as measured by growth rate (Kacelnik *et al.* 1992a,b; Oksanen *et al.* 1992), is more stable in preferred habitats (with stable high densities) than in habitats with fluctuating densities. Any increase in the abundance of the population is

realized in secondary habitats in which densities are not upper-bounded by interference competition and where density-dependent growth is most important. However, there should be strong selection pressure for fish that can limit locally the impact of population abundance through mechanisms such as territory defence and habitat selection.

Several authors have noted that density-dependent population regulation operates in favourable habitats, whereas density-independent factors predominate in secondary habitats (e.g. Elliott 1987; Newton and Marquiss 1986; Reynoldson 1957). There is ample evidence demonstrating that not all individuals in a population of salmonids defend a territory (McNicol *et al.* 1985; Puckett and Dill 1985; Grant and Noakes 1988; Grant and Kramer 1990). Grant and Kramer (1990) suggest that territory defence is a mechanism for density-dependence in preferred salmonid habitats, but that territoriality, or more precisely the territory size hypothesis, does not predict maximum densities in pool habitats. It was postulated (Chapter 3) that most of the population expansion should take place in marginal pool habitats and that the preferred riffle habitat should retain a stable juvenile population at any population abundance. Populations are therefore expected to expand in areas where there is the least resistance to population pressure. Density-dependent fitness and per capita growth rate will determine productivity in each habitat.

This chapter demonstrates that density-dependent growth and habitat use are important aspects of population distribution. Several processes are involved. The repartition of animals among available habitats appears to be some function of density-limiting mechanism in preferred habitats. For example, where territoriality limits density, stability of growth and density prevail. However, where there are no direct mechanisms to limit density (as opposed to indirect mechanisms such as loss in growth potential, increased risk of mortality), the variation in density will generally be of larger amplitude and density-dependent growth will predominate. These habitats will tend to be secondary choices as a consequence of the passive effect of density-dependence on individual growth rates. Although I have no data on territoriality, the present results are consistent with those stating that territoriality is a density-limiting mechanism for particular habitats. Most studies, however, are not concerned with growth response nor do they take population abundance into consideration. This study is one of the first studies to investigate the dynamics by which a population adjusts to changes in abundance.

Density-dependent mortality, fecundity and growth are not independent and a mixture of correlated responses to changes in population abundance can be expected.

Furthermore, the response of these processes may not only be habitat-specific, but the compensation of other processes may also be variable. For example, density-dependent mortality or migration may reduce density-dependent growth response in preferred habitats (Elliott 1984b, 1986, 1987, 1988) but other types of density-dependence may

dominate in habitats where fish school. Elliott (1984a,b) reported important density-dependent mortality of trout fry in his study stream but little or no density-dependent growth. The early drop in density after hatching may have compensated for the original variation in egg and larval densities. Unfortunately, Elliott (1984a,b) analyzed his stream data by combining information from all river segments of his study area, and it is impossible to evaluate the data on a habitat-specific response level. Similarly, Prouzet (1978) found that density-dependent growth appeared to predominate as a factor limiting productivity on a river with a steep slope. However, on a stream with a lesser slope, local migration of parr was the chief factor controlling local production. Randall (1982) obtained a negative relationship between growth of fry and density among a number of sampling sites and rivers. Egglisshaw and Shackley (1977) concluded that growth of parr is controlled by water temperature and local population density. Gibson and Dickson (1984) reported that salmon fry stocked in fishless reaches of a river left pools if riffle habitat was available. It thus appears that density-regulating mechanisms are habitat-specific, and that behaviour may play an additional role depending on local environmental conditions.

There is very little information in the literature on growth response within the context of density-dependent habitat selection (DDHS). MacCall (1990) reviewed density-dependent habitat selection as it applies to marine fish population. MacCall (1990, Table 1.1) reports that 19 papers have been published demonstrating the expansion and contraction of population range or differential use of marginal habitats with changes in

population abundance, but none of these authors address growth response directly. Swain (1993) demonstrated density-dependence of cod in relation to age-classes but not within or among-habitat variability in individual growth. Fretwell and Lucas (1970)'s Ideal Free Distribution (IFD) assumes multiple discrete habitats and distribution proportional to habitat suitability. Although no explicit mention of growth response is made, equal growth rates among all individuals in all habitats is a consequence of the basic assumptions (see also Kacelnik *et al.* 1992a,b). This restrictive theoretical framework has been relaxed in the Ideal Despotic Distribution and other theoretical developments to allow for variation in individual success (Kacelnik *et al.* 1992a), but does not provide the theoretical framework for mechanisms of population expansion and contraction. Fretwell and Lucas' (1970) theory of distribution is based on fitness criteria, but most tests of the theory have used resource acquisition as a surrogate (Kacelnik *et al.* 1992a,b). Again, differential food acquisition rates among individuals within a patch has been very well documented (Milinski 1988; Kacelnik *et al.* 1992a,b), but not the density or growth response of animals within and among feeding patch in response to fluctuation in population abundance. In the general discussion, the applicability of the Ideal free Distribution theory to the task of prediction of habitat use with fluctuating population abundance will be addressed.

### **Density-dependent habitat selection**

Bowlby and Roff (1986) were able to predict salmonid biomass from the percentage of the stream area composed of pools, considered secondary habitats for juvenile salmon (Gibson 1966; Gibson and Power 1975; Baglinière and Arribe-Moutounet 1985; Morantz *et al.* 1987). Many physical and chemical variables have been shown to be good predictors of standing stock and production of river systems. These observed patterns have been used to develop habitat classification systems (Binns and Eiserman 1979; Symons 1979; Coté *et al.* 1987; Kozel and Hubert 1989; Caron and Talbot 1993). Talbot and Gibson (1990) found that standing stock of Atlantic salmon was correlated with the number of pools in a stream segment in a river with high juvenile salmon abundance. If the present population expansion hypothesis is correct, much of the variation in population abundance occurs in marginal habitats. Therefore whole-river production models based on the quantity of secondary habitat available may be more appropriate for predicting response to changes in population abundance than the class of models based on habitat preference (e.g. Binns and Eiserman 1979; Symons 1979; Coté *et al.* 1987; Kozel and Hubert 1989; Caron and Talbot 1993).

Gillis and Kramer (1987) used a laboratory experiment with zebrafish (*Brachydanio rerio*) to test predictions of the IFD at various population densities. They found that the fish were distributed significantly more evenly among the three continuous food sources at high population density than predicted by the IFD, and that the fish were

distributed according to the IFD at low densities. High levels of interference competition were observed at the point feeding sources. This supports the general hypothesis that interference competition limits population densities in the preferred habitats and that surplus individuals tend to occupy marginal habitats. However, there is a basic and important difference between Gillis and Kramer's (1987) study and the present work. The fish in Gillis and Kramer's (1987) experiments were free to move among feeding sites. While this assumption may be reasonable within sites in a river system, it seems insufficient to describe population-level changes in habitat use. In the Little Codroy River system, the distances are certainly too great for the juveniles to explore (Jones 1959; Rimmer *et al.* 1983), and local juvenile densities are generally a reflection of adult habitat selection.

Elliott (1987) provides arguments that populations near the carrying capacity of the ecosystem are genetically adapted to negative density-dependence, and that changes in population abundance are due to density-dependent factors in "favourable habitats" with high density and to a combination of density-dependent and density-independent factors in "unfavourable habitats". This conclusion is in accord with the findings of the present study. Earlier work on the same population by Elliott (1985) suggested that 1+ trout occupying territories in preferred habitats were able to maintain optimal growth rates while new migrants had sub-optimal growth. He postulated that fish had not immigrated to these habitats to improve their success since their growth rate only improved after the residents emigrated as smolts. This implies that territoriality can

limit population density if growth rates of new arrivals fall to a level below physiological requirements. Furthermore, reduced growth retards maturation or smoltification (Thorpe and Morgan 1980; Thorpe *et al.* 1982; Thorpe 1986; Herbinger 1987). Fraser and Sise (1980) postulated that responses of populations of minnows in pools are related to food and not to abiotic (e.g. shelter) factors, and that the search for food increased migration rates. They found that distributions of minnows tended to even out among pools as population size increased, probably because territoriality limited the upper densities within pools.

Although there are very few published accounts of within-habitat growth response to population abundance variation, the subject is of primary interest to ecologists who are attempting to understand the causes of range expansion and contraction. Reduced growth of animals in marginal habitats may lead to range contraction as a result of reduction in population abundance (Brown 1984). This chapter shows that density-dependent growth is an element of habitat use and could represent an important cost of habitat selection. The variable scale of density-dependent growth is consistent with the consequences of population expansion and contraction into marginal habitat. Further research should consider other density-dependent factors of habitat use, such as mortality.

## **CHAPTER 5**

### **GENERAL DISCUSSION**

I demonstrate in this thesis that heterogeneity in the local densities of juvenile Atlantic salmon (*Salmo salar*) among tributaries and sampling sites of a river system can be used to answer general questions of habitat use. It is also shown that the estimation of local population abundance can benefit from knowledge of the population variability among sampling sites. In this closing chapter, I will discuss the importance of studying population variability in closed systems, the applicability of distribution theories to the observed patterns in density-dependent habitat use, and conclude on the importance of Bayesian inference methods to local population estimation techniques.

#### **THE VARIABILITY OF POPULATION SIZE**

A large number of studies have recently attempted to describe intra and interspecific temporal variability in the size of animal populations (McArdle and Gaston 1993). These studies have been hampered by measurement problems of scale (Wiens *et al.* 1987) and the dependence of the variance of densities on the mean (Anderson *et al.* 1982; Taylor 1986; Gaston 1990; McArdle *et al.* 1990). Within species, the recent trend has been to make extensive use of Taylor's power law (Taylor and Woivod 1980; Taylor 1986), but possible problems with the interpretation of the results from this "law" have been discussed in Chapter 3.

### **Should we study Open or Closed Populations?**

Part of the difficulty in studying variability of the size of populations appears to be the lack of rigour at defining what exactly is meant by a population, as this is critical for understanding mechanisms controlling fluctuations in population abundance (McArdle and Gaston 1993). For example, some studies use the term to define a group of individuals that are separated from others by an arbitrary boundary, such as a series of mussels beds along a salinity gradient (see Goss-Custard 1993; McGrorty and Goss-Custard 1993) but where clear connections to a larger more extensive littoral population is obvious. These types of study permit only limited inference on population variability since many external variables will have a direct influence on local conditions (such as the effect of a particularly strong year class on overall population abundance and density-dependent habitat use).

Clearly the ideal population to study population dynamics is closed to migration (Wiens *et al.* 1987; McArdle and Gaston 1993). If inference on local response to changes in population abundance is required, then reliable estimates of population sizes are required, without the confounding influence of immigration and emigration. This is clearly the case of Atlantic salmon, where adults generally have a high stream fidelity (in the order of 90 %), and where little if any migration of juveniles among streams or tributaries is likely. In the present study, we have the added advantage of independent measures of population abundance in the adult counts at the counting

fence in the estuary and from mean juvenile densities over 38 sites throughout the river system. If we take the extreme case of a fully open population (for example sea birds nesting on a near-shore island) where migration rates are an important component of local densities, then what is actually being measured in such a study is the local variation in density of animals at a site, irrespective of the size of the sampling site (i.e. a quadrat or a whole "island"). Little can be said from this series of measurements on the variability in the abundance of the population. Unfortunately, closed or near-closed populations are extremely rare, and the spatial and temporal datasets required for the study of population variability are scarce (McArdle and Gaston 1993).

### **DENSITY-DEPENDENT HABITAT USE**

The population density of juvenile Atlantic salmon in the Little Codroy River varied considerably between sites and years. This variation can be described in large part by a model of density-dependent habitat use in relation to population abundance. Insight into population dynamics of Atlantic salmon may be obtained from long-term investigations of natural populations, particularly with respect to the causes of variation in local abundance, dispersion and growth rates. The large change in spawner abundance (a two-fold change over 8 years) in the Little Codroy River system, combined with detailed and repeated censuses of juvenile abundance at 38 widely

spaced sites and comprehensive biological, physical and edaphic data makes it one of the very few datasets suitable for the present studies.

This study is among the first to test specific hypotheses of local population response to changes in overall population abundance. The testing of formal hypotheses is important, because it is difficult to determine the response simply by examining range maps or contour maps of density without a statistical model. Many of the examples of range expansion reviewed by MacCall (1990) may not have been actual range expansions (e.g. Whitham 1980). However, some clear cases of range extension with increasing population size have been described for Northern anchovies (*Engraulis mordax*) off the Southern California coast (Kramer and Ahlstrom 1968) and the Japanese sardine (*Sardinops melanosticta*) in the Japan sea (Sharp 1980). In contrast, increases in local density of larvae without a range expansion was reported for the Peruvian anchoveta (*Engraulis ringens*), a species closely related to the Northern anchovy (Santander *et al.* 1982 in MacCall 1990).

Colonization of secondary habitats is generally characterized by decreased reproductive success, growth and increased probability of death (Brown 1969; Brown 1984; Elliott 1986, 1987; MacCall 1990). For this reason, overall population productivity might be thought to decrease below some theoretical maximum if some animals are forced to live and grow in secondary habitats. However, it was pointed out by Brown (1984) that the spreading of the population to secondary habitats should actually increase total

productivity, over the alternate hypothesis in which animals crowd into the best habitats, with a resultant decrease in growth and increase in mortality (see also Pulliam and Danielson 1991). Further support from empirical field studies have supported this idea. Dome-shaped stock-recruitment curves are typical of Atlantic salmon and other salmonids (Gee *et al.* 1978b; Elliott 1984b; Solomon 1985), but these are unexpected in primary habitats if territorial behaviour limits densities. Interestingly, the largest, deepest sites of the 16 samples by Gee *et al.* (1978b), sites where territorial behaviour might be least effective, also had the highest density-dependent mortality rates and were excluded from the analyses. Territorial defence appears to limit local population density and productivity in the primary salmonid habitats, but not in secondary habitats where densities can surpass those in primary habitats (Le Cren 1973; Mason and Chapman 1965; Slaney and Northcote 1974; Fausch 1984; Grant and Kramer 1990) even though the actual mechanism limiting density in primary habitats is not clear (Grant and Kramer 1990).

It appears that density-dependent habitat use is a mechanism that optimizes population growth when primary habitats have reached their saturation or carrying capacity " $K$ ". Average population density may therefore be a poor indicator of habitat quality (van Home 1983; Rice *et al.* 1986). This is corroborated by the present study, where the relative variability among sections of the river and the response to changes in total population abundance is greatest in secondary habitats. Since juveniles tend to spend most of their life cycle in the immediate area surrounding their birth site, the density-

dependent responses observed should reasonably reflect the local conditions. Habitat quality might be more related to population stability than to density itself. What then are primary and secondary habitats? Primary habitats may simply be defined as stable sites with high productivity and where densities are limited by some behavioural processes.

Of critical importance to developing a relationship between productivity and habitat use is the measurement of the carrying capacity of habitats. It could be estimated from the inflection point of habitat-specific dome-shaped stock-recruitment curves, but a large time series among identifiable habitat types would be required. Elliott (1993) suggested a simpler method. He tested the use of the relationship of mean weight to mean density among age classes of brown trout (*Salmo trutta*), and speculated that this relationship could be used to compare temporal and spatial variation in carrying capacity within streams.

### **Processes controlling population expansion among habitats**

The ability of animals to make discriminatory choices among types of habitats has been abundantly demonstrated in the behavioural ecology literature (e.g. Rosenzweig 1991; Orians and Wittenberger 1991; Pulliam and Danielson 1991; Jaenike and Holt 1991; Huey 1991). However, mechanisms of habitat selection and population interactions are still hotly debated (Rosenzweig 1991). L. R. Taylor and colleagues, in

a series of articles on the relationship between population variability and mean abundance (reviewed by McArdle *et al.* 1990 but see Anderson *et al.* 1982), suggest that the variability in local population density is greatest at sites of highest abundance. They proposed that the mechanism explaining this relationship is density-dependent migration rate, where a slope of the logarithm of the values above 2 indicates concentration of animals with increased population abundance and slopes less than 2 indicate a levelling out of local densities with increasing population abundance. Although the general nature of the variance to mean abundance ratio has been clearly demonstrated, the mechanisms underlying the phenomenon are open to debate (Anderson *et al.* 1982) and may lead to misinterpretation of ecological data (see Chapter 3).

The distribution theory of Fretwell and Lucas (1970) has received a lot of attention in the literature, perhaps because it makes clear predictions. However, it is not obvious whether their theory can predict changes in habitat use resulting from variable population abundance (Gillis and Kramer 1987). The following section examines the distribution theories in light of the findings of the present study. The geographic distribution of juveniles is likely a consequence of spawning site selection of adult migrants. It is likely that the dispersal of newly emerged fry will result in the colonization of the available stream area to a density level that is related to local spawning densities (Gee *et al.* 1978b). This must be considered throughout the

following discussion, as the juveniles probably do not make any active habitat choices but rather suffer the consequences of the selection made by their parents.

The fitness " $W$ " of individuals, as estimated by growth rate, has been shown to decrease with density of juvenile salmon; however, the resultant growth and densities emanating from density-dependent habitat use are not constant between habitats or at all spatial scales. According to habitat selection theory, primary habitats should be used preferentially until habitat saturation is reached or a density-dependent response reduces fitness in these habitats to a level below the expectation of success in other habitats. In this simplest of scenarios, the density-dependent response curves (or the slopes  $\beta_i$ 's, estimated at site  $i$ ) are equal among habitats, an assumption used in the Ideal Free Distribution theory of Fretwell and Lucas (1970) and the basic "basin" model of MacCall (1990; Figure 5-1a). This example can be called the "variable  $W_i$  - fixed  $\beta$ " model because only the initial habitat-specific fitness varies. This model finds wide ranging support in the literature (Milinski 1988; Milinski and Parker 1991; Kacelnik *et al.* 1992a) in that average densities appear to decrease from primary to secondary habitats.

Alternative scenarios to the "variable  $W_i$  - fixed  $\beta$ " model can be constructed. The average fitness of individuals among habitats may be equal as densities approach zero, reflecting the absence of competition for resources and the scope for growth of the population/species (Figure 5-1b). This model corresponds to a "fixed  $W$  - variable  $\beta_i$ "

**Figure 5-1: Graphical representation of hypotheses concerning the distribution of animals across habitat types. Relative fitness is plotted as a function of local population density. Line type (solid, dashed and dotted) represent different habitats. A: Simple proportional negative density-dependent effect with habitats of variable initial fitness. B: Variable negative density-dependent effect with equal initial fitness among habitats. C: Combination of A: and B: above. Note the crossing over of some of the lines, indicating that local densities in secondary habitat may exceed those of primary habitats under certain conditions. Units are arbitrary.**

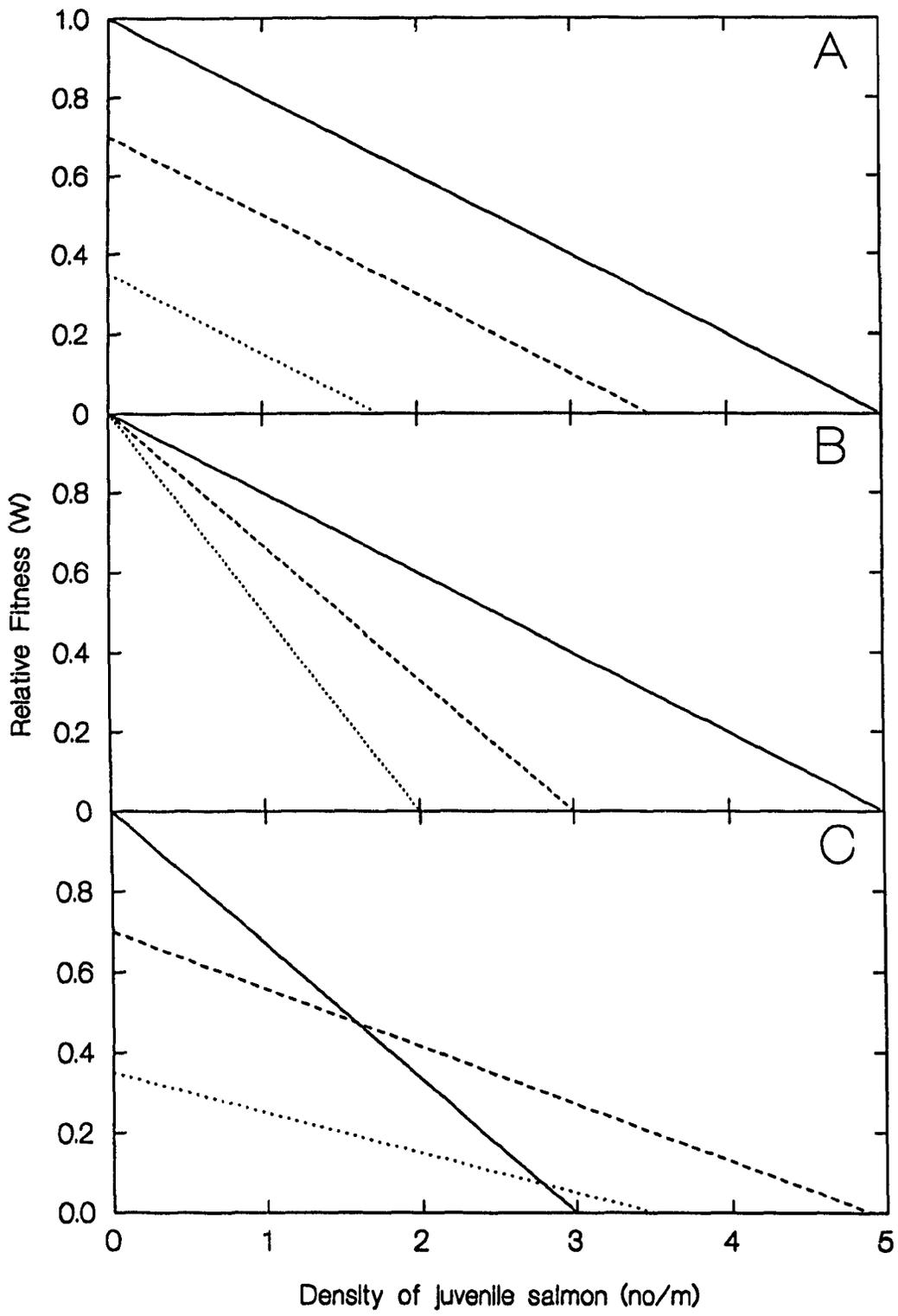


Figure 5-1

where  $W$  is only fixed at initial densities. This model originated with the idea that the intrinsic rate of increase of a population is a genetically fixed value (e.g. MacArthur and Wilson 1967), and that differences in resource availability and use among habitat control the carrying capacity  $K$ . Thus, unlike the previous model, this model predicts that all habitats will be used at any population abundance. Differential habitat use is a result of the faster drop in fitness in secondary habitats than primary sites as abundance increases.

A third alternative scenario is a "variable  $W_i$  - variable  $\beta_i$ " model, where both initial fitness and density-dependent responses are variable. In this model, it is possible for the fitness curves to cross at some density (Figure 5-1c), but secondary habitats will be used only as population abundance increases to a level where the realized fitness drops below the basic fitness of secondary habitats (as defined by the intersection of the line with the abscissa).

There are other families of models, in particular what are referred to as the first and second quadrat fixed points models (FQFP and SQFP respectively) and "variable  $W_i$  - fixed  $K$ " models (similar to the models reviewed by MacCall 1990), but these make similar predictions to the above and are not addressed here.

So, which of these basic models fits the data best, if any? In the present study, very high heterogeneity among estimated slopes ( $\beta_i$ 's) violate the equality of slopes

assumption. There is also ample evidence from the literature that density-dependent processes are also habitat-dependent (e.g. Prouzet 1978; Mason and Chapman 1965; the present thesis). In this respect, the approach of MacCall (1990) appears to be inappropriate. MacCall's (1990) model predicts that an individual added to the population would have the same effect independently of where it was placed, in their analogy much like adding a drop of water to a bowl. This does not appear to be the case with salmonids (Grant and Kramer 1990; this study), where a density-dependent response is much more likely to occur in secondary habitats and where a mixture of habitat-specific behavioural strategies seem to exist. Unlike the pattern observed in the Little Codroy River, densities higher in some secondary habitats than in primary habitats at high population abundance are not possible with this model. The "fixed  $\beta$ " assumption is rejected.

There is some evidence to support the "fixed  $W$  - variable  $\beta_i$ " model. Growth rates at low population abundance are comparable in most tributaries (Chapter 3 and 4). However, several observations suggest otherwise. There is very little supporting evidence from the literature since it is generally assumed that fitness cannot be taken out of context of local physical characteristics, and that habitats are heterogeneous for many key variables; MacCall (1990) dismissed these assumptions as not plausible. Furthermore, the "fixed  $W$  - variable  $\beta_i$ " model predicts proportional changes in densities as population size changes. This is clearly not the case in most empirical field studies reviewed, including the present thesis. Density-independent population

regulation must also be considered. A flat fitness curve is consistent with density-independence. If density-independent processes operate in secondary sites and initial fitnesses are equal, all fish should be found in these habitats. This is also clearly not the case.

The "variable  $W_i$  - variable  $\beta_i$ " model does permit higher densities in secondary habitat than in primary habitat, but only if average fitness becomes proportionally greater in secondary habitats. The findings of the present thesis indicate that the negative effect of density-dependent growth was strongest in secondary habitats and thus contradicts this prediction. Density-dependent processes have been observed in primary habitat in several studies (riffles: Le Cren 1973; Fraser 1969; Mason and Chapman 1965; Prouzet 1978) but evidence for the absence of density-dependence in secondary habitats is weak. Prouzet (1978) noted that regulation of density in fast flowing waters was primarily through reduced growth rate and through emigration in slow flowing water, but migration is potentially another manifestation of density-dependence. Densities above those found in primary habitats at high population abundance supports a density-limiting mechanism in primary habitats. The "variable  $W_i$  - variable  $\beta_i$ " model is thus inadequate for describing the observed distribution, although realized fitness could be altered by other unmeasured density-dependent factors, such as the risk of mortality.

The above models fail to adequately represent the observed patterns in distribution of juvenile Atlantic salmon. Fretwell and Lucas (1970) proposed the Ideal Despotism Distribution (IDD) for cases in which territoriality limits densities in habitats, so that residents of primary habitats are able to maintain high fitness at any population abundance. This has given rise to a general class of interference models where asymmetric feeding success of dominant individuals is achieved through direct competitive interactions (Harper 1982; Parker and Sutherland 1986; Sutherland and Parker 1992). In the present study, although territorial behaviour may limit habitat use at some sites, it is unlikely to be the case for all sites. Schooling behaviour has been observed in pool habitats for Atlantic salmon, where territories are much harder to defend due to the height of the water column, in which the rationale of territorial defence for a drift-feeding species is doubtful (Grant and Noakes 1987; Grant *et al.* 1989), and where food distribution may be more clumped in space and time in pools than in riffles, reducing the advantage of dominance hierarchies and territory defence (Grant and Kramer 1992). The present data are consistent with interference models if temporal variation in habitat use is ignored or averaged out. However, these models predict decreasing densities of individuals across feeding patches even though the best competitors are located in the superior habitats. The applicability of this model to habitat use of juveniles resulting from the spawning site selection of adults is limited.

That the realized fitness must decline monotonically with increasing density (i.e.

$W_i = K/n_i$ ) in all habitats (e.g. Milinski and Parker 1991; Sutherland and Parker 1992)

seems unlikely in light of the variable behavioural response to crowding in different habitats (e.g. territorial behaviour in primary habitat and schooling in secondary habitat, floaters). If territoriality limits densities in primary habitats, a density-dependent response is not predicted before reaching habitat saturation because densities are limited by space and not food supply, and fitness curves may therefore be convex. In marine systems, the relationship between growth and density is thought to be a concave function for fishes because the growth compensation is greatest at low densities (Cushing and Harris 1973; Stubbs 1977; Garrod and Knights 1979; Fowler 1981). Extreme low densities probably do not have any effect on growth in any habitat. Finally, as shown in Chapter 4, density-dependent growth operates on different spatial scales. It is not solely a function of local density but also of the tributary and overall river population levels. This relationship is further complicated by habitat-specific sensitivity to population abundance. Density-dependence on a large scale will decrease fitness in all habitats in addition to any local effect. It must be concluded that the slope of all habitat-specific curves becomes more negative with increasing population abundance. How this might look is represented for a primary and secondary habitat in Figure 5-2.

Most importantly, it appears that none of the distribution models reviewed above can predict higher densities in secondary habitats. Source/sink models (Wiens *et al.* 1981; Pulliam 1988; Pulliam and Danielson 1991), where annual recruitment is said to exceed annual mortality in source habitats and the reverse pattern occurs in sink

**Figure 5-2: Three-dimensional plot of the effect of overall population abundance on the relationship between fitness and local habitat density for primary (solid line) and secondary (dotted line) habitats. Note that the slope increases with increasing population abundance. The scales are arbitrary.**

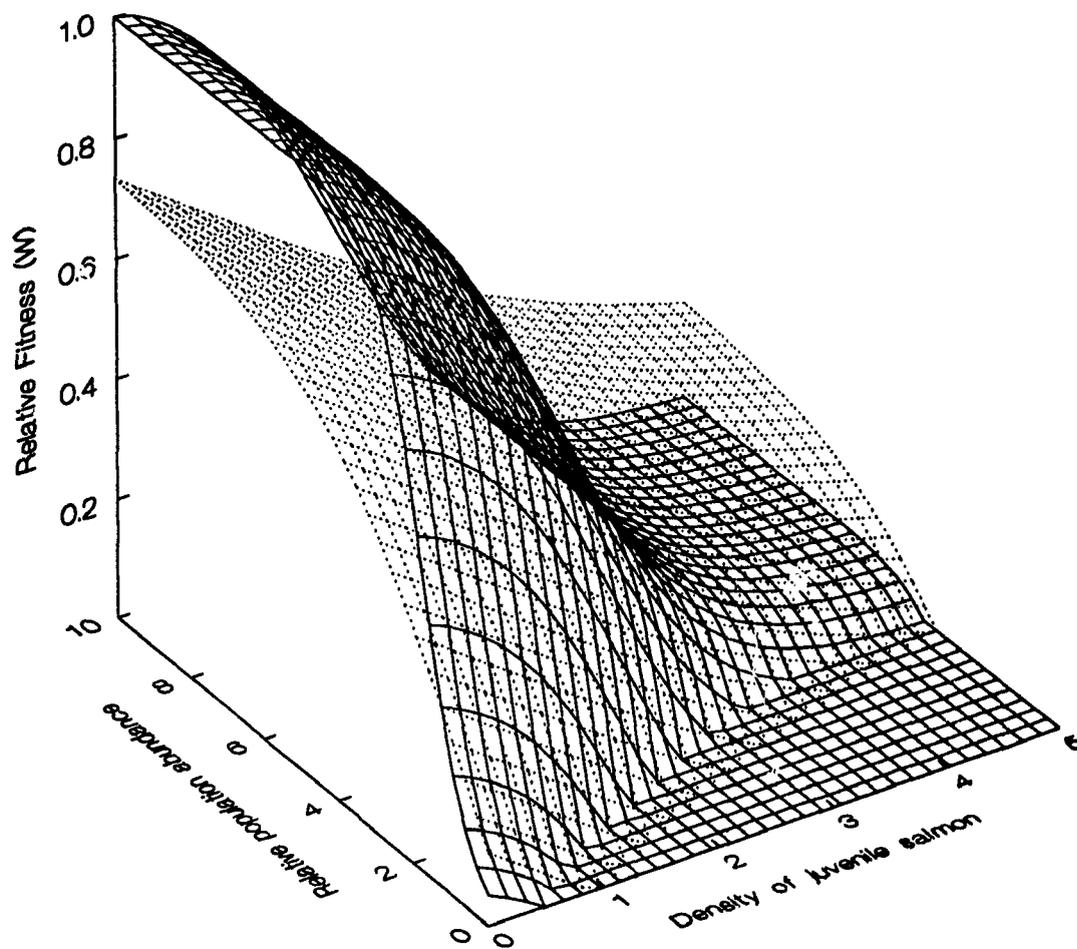


Figure 5-2

habitats, are also unable to predict the patterns observed with Atlantic salmon juveniles. An alternative, simpler hypothesis that has yet to be tested might assume that fry migrate away from the hatching site and settle in the first free territory or site that is encountered (Waser 1985; Caley 1991; Rees 1993). Densities would decrease as distance from spawning sites, usually in riffle habitat, increased. This hypothesis would predict greater variability of density with changes in population abundance as distances away from spawning sites increased. Such a model may also be made to incorporate territorial defence, mortality as a function of travel distance and growth variability among habitats.

#### **FURTHER CONSIDERATIONS**

Perhaps the greatest difficulty with a more realistic model incorporating several parameters is that they are difficult to introduce into a habitat-based production or Lotka-Volterra logistic growth models. Monotonically decreasing functions violate certain assumptions of habitat-specific responses, but these violations have been ignored and "faith in the heuristic value of the theory" (p. 142 in Milinski and Parker 1991) has been invoked in order to simplify the specification of parameters. Although this makes modelling easier, this thesis shows that these assumptions are unrealistic, and some form of habitat-specific response to population variation at small to large spatial scales will have to be introduced into production models.

The present mechanism of habitat use requires further testing, and environmental variables should be integrated in the hypothesis testing to make more realistic comparisons. Of the many environmental variables that are often routinely collected with field surveys, several may be correlated by chance alone, especially if the time series is short, to some parameter of population dynamics (Flack and Chang 1987).

The temptation to add an environmental variable to the model that correlates with the residual of habitat use may be difficult to resist but dangerous because of the risk of Type 1 error (the rejection of the null hypothesis when it is true). This type of exploratory approach must be accompanied by a rigorous hypothesis-testing methodology (see Flack and Chang 1987; Chapter 7 in Hilborn and Walters 1992).

It is possible that life-history characteristics other than growth, such as mortality, and maturation and migration to the sea (smolting), differ among habitats, and that fitness estimates based on growth alone are insufficient to describe habitat use criteria.

Further studies should consider these other density-dependent life-history parameters as well as migration of juvenile among habitat-types. These results should help to refine our understanding of density-dependent habitat use in Atlantic salmon, and perhaps contribute to the determination of the causes of the variable scales of density-dependent growth.

The shape as well as changes in the shape of the habitat-specific response curves will have important consequences on habitat management practices. Monitoring of the

population should consider secondary habitat because they are better indicators of fluctuations in population abundance. Habitats with stable growth rates and densities are desirable in enhanced production in natural systems such as in seeded streams, but artificial habitats that discourage density-dependent response and density-regulating mechanisms are best for aquaculture environments.

Although exploitation may not be of concern with juvenile Atlantic salmon, the general consequences of habitat-specific responses are interesting with regards to other fisheries. Presumably, the greatest amount of exploitation of a species occurs in the primary habitat where constant high densities tend to occur. These habitats are largely insensitive to changes in population abundance, and catches may not drop until a critical stock size is reached, whereas a management decision should have been implemented to protect the stock well before reaching this point. A similar conclusion has been reached with California anchovies and other schooling marine fishes (MacCall 1990). The implication of density-dependent habitat use is that fishing mortality will tend to increase as stock size decreases as a result of the dynamics of fishing fleets (Hilborn and Walters 1992). A geographically-based monitoring program of fisheries stocks with primary and secondary habitats clearly defined may prevent such a situation from occurring.

## **POPULATION STUDIES: THE IMPORTANCE OF ESTIMATES FROM ALL SITES**

A new approach to the estimation of population size from removal data is presented in Chapter 2. Models assuming a constant probability of capture in the sweep sequence and assuming a proportional change in the probability of capture after the first capture are compared to published methods and models. It is shown that the simultaneous use of information from all sites results in an important reduction in the error variance of the estimates. This has important consequences for comparative studies. Population estimates with lower variances increase the discriminatory power of subsequent analyses.

It has also been shown that maximum likelihood (ML) estimation methods are biased. There are two principal reasons for this. Firstly, there is bias arising from the failure to meet the assumptions of the methodology, such as equal catchability of all animals in a closed population. The probabilities of capture of fish are not likely to be constant in nature. The most susceptible fish are likely to be captured early and it appears that there is a small fraction of the population with capture probability near zero. It is impossible to know in a regular survey what this proportion is or how the individual capture probabilities vary, unless drastic measures are taken (e.g. using piscicide to kill all remaining fish (Mahon 1980)), but relaxing the assumption of constant probability of capture within a sequence solves this problem in part. Secondly, there is an inherent

bias in the estimation methodology. The general ML theory requires that the number of captures  $K$  and the population size  $N$  be large. In fact,  $K$  is usually less than 4 and  $N$  is frequently less than 100 (Carle and Strub 1978). It is also assumed that the catches are independent events with identical distributions, which is not possible in reality. As a consequence, the distribution of  $\hat{N}$  increases in skewness and bias as  $N$  and  $p$  become small.

There is a final consideration. Exclusion of samples as a result of the failure of the estimation method to reach a solution (estimator failure) can severely bias the geographical representation of distribution and abundance. This bias is further accentuated if the probability of estimator failure is linked to some environmental variable. Some studies have shown that the proportion of estimator failures can be as high as 50% in juvenile Atlantic salmon populations. The methods developed as part of this study solve these problems by obtaining estimates in all possible situations. However, it has frightening consequences. It questions the validity of any study that used Zippin's (1958) population estimation method, unless a careful examination demonstrated that the assumptions of the method were met.

These methods will be particularly useful to surveys of small populations over a broad geographic scale, to multiple species surveys where the relative abundance of an important fraction of the species is low as is common in most ecosystems (Preston

1948; MacArthur 1960; Hughes 1986), or when population estimation is subdivided among age or size classes.

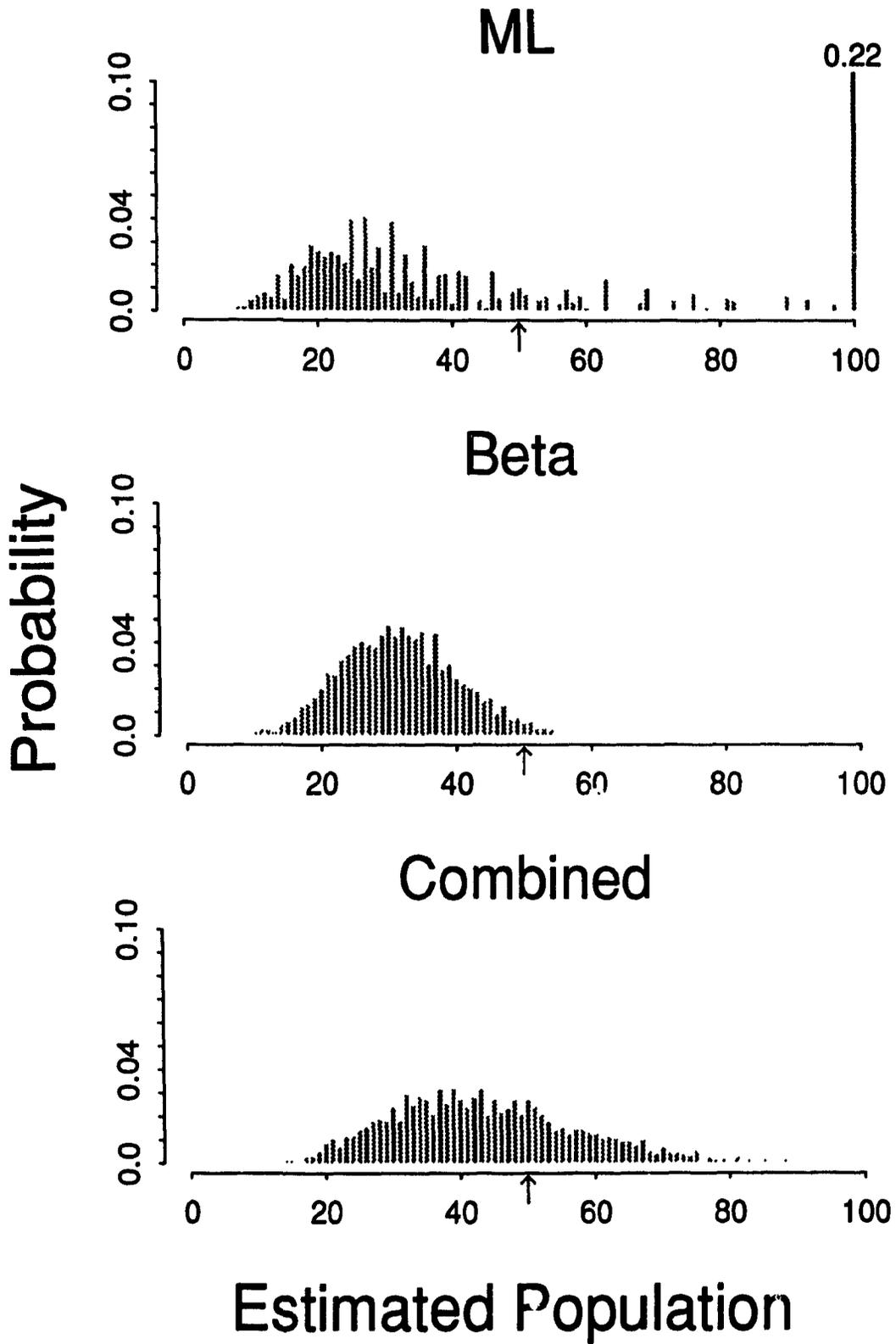
A Bayes-like method of incorporating information from all sites is used in the estimation process developed. Methods of Bayesian inference are useful tools for population estimation techniques because they provide information as to the likelihood of finding given densities in a particular system. This is important. If a biologist samples a sequence of {2,2,2,2,2} fish from a particular site, he knows that the population size is very unlikely to be several thousands for that section of the river, but classical estimation methods do not and may yield such unlikely figures. Bayes-like and Bayesian inference methods permit this type of information to be incorporated into the estimation technique based on observed mean and variance of the probabilities of capture for a particular set of samples.

In Chapter 2, we have therefore used the variability of densities among several sites distributed throughout the distributional range of a population to make inference on the density at a single site, which is in essence the inverse of making inference about population variability from the study of density-dependent habitat use (Chapter 3 and 4).

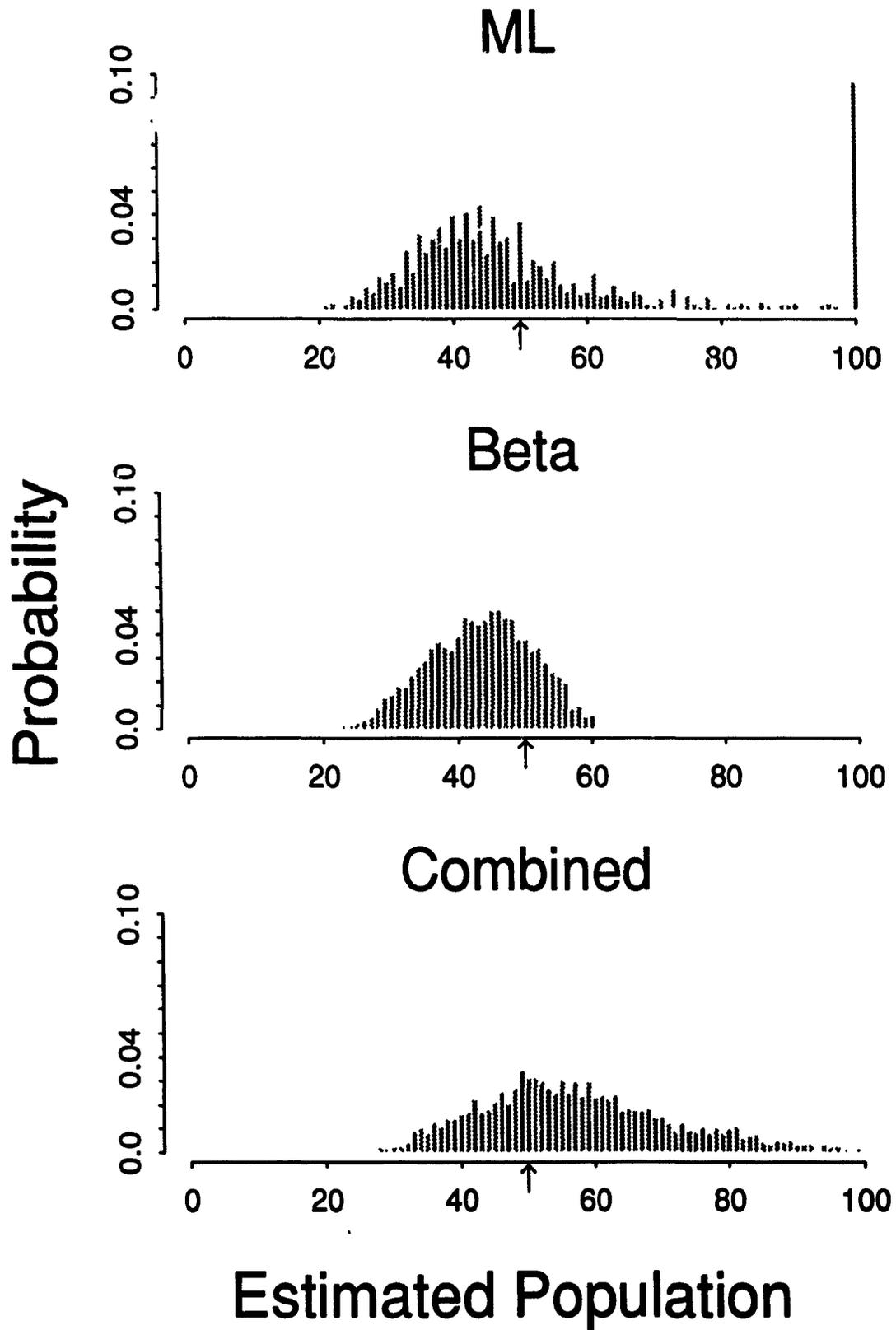
## **APPENDIX A: Figures for Chapter 2**

**Figure A-1: Histograms of the estimated population size ( $\hat{N}$ ) for the Maximum Likelihood (ML), Beta and combined Beta and ML models for the simulated data. The bar at the extreme right of the histograms represents extreme values and includes cases where infinite estimates were predicted. The parameters used in the equation are indicated at the top of the figure page. The series of histograms presented is the entire simulation with  $N=50$ . It is apparent that the variance of the Beta estimator is lower than other methods at any combination of parameters. Note also the classic skewness of the distribution of the ML estimator, particularly at low probabilities of capture. While the combined estimator is less biased, its variance is large.**

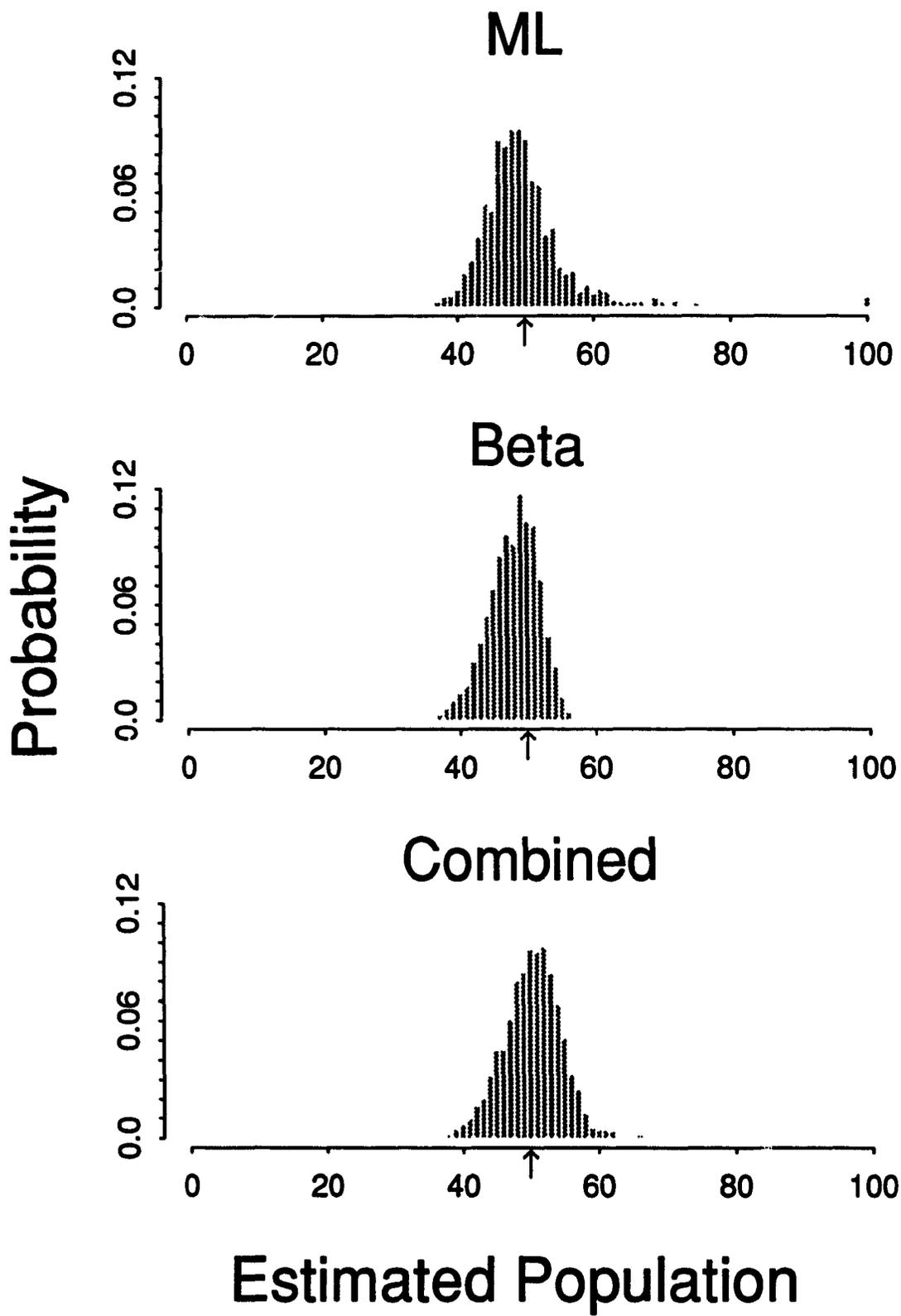
$N=50, K=3, 0.1 \leq p \leq 0.2$



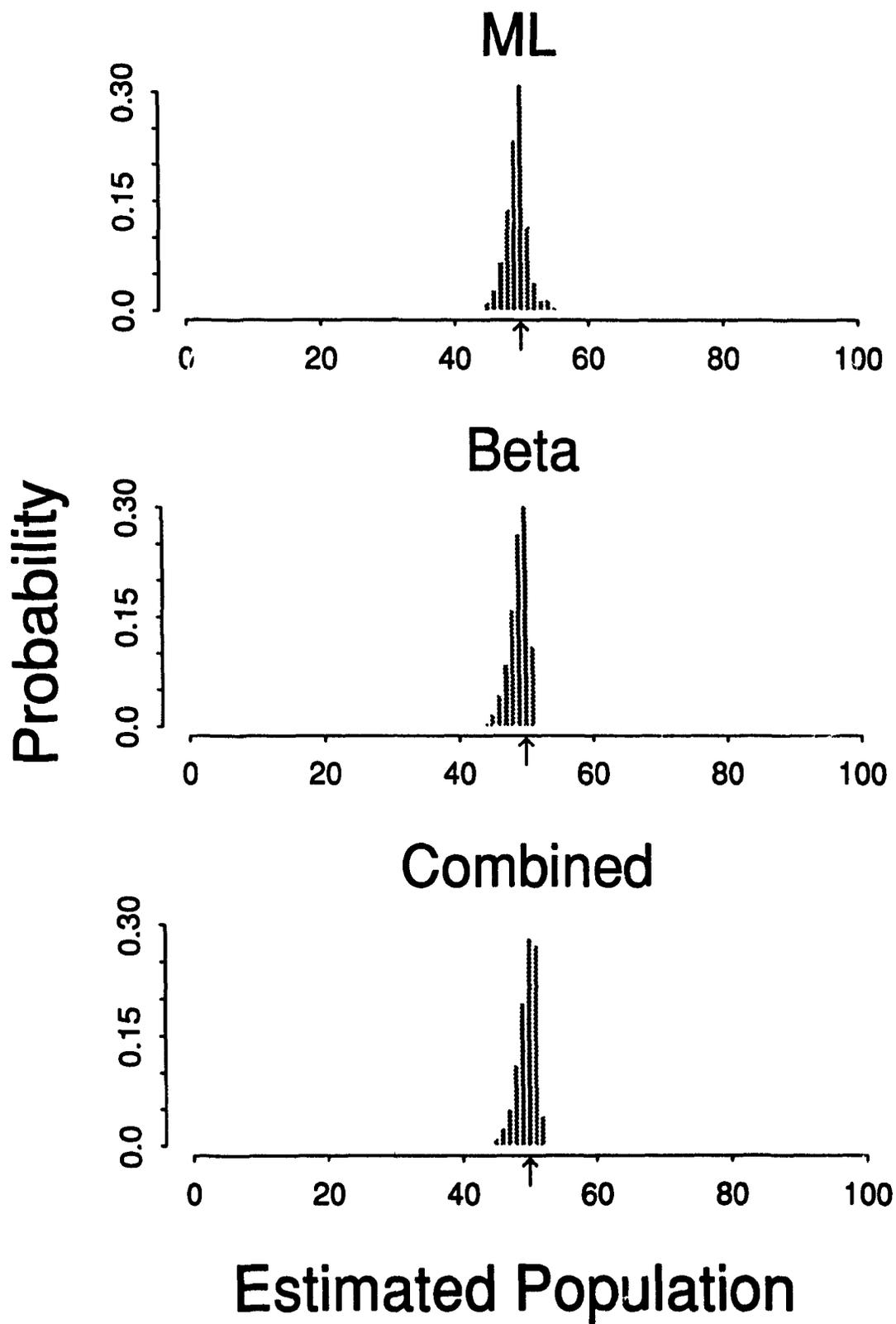
$N=50, K=3, 0.2 \leq p \leq 0.4$



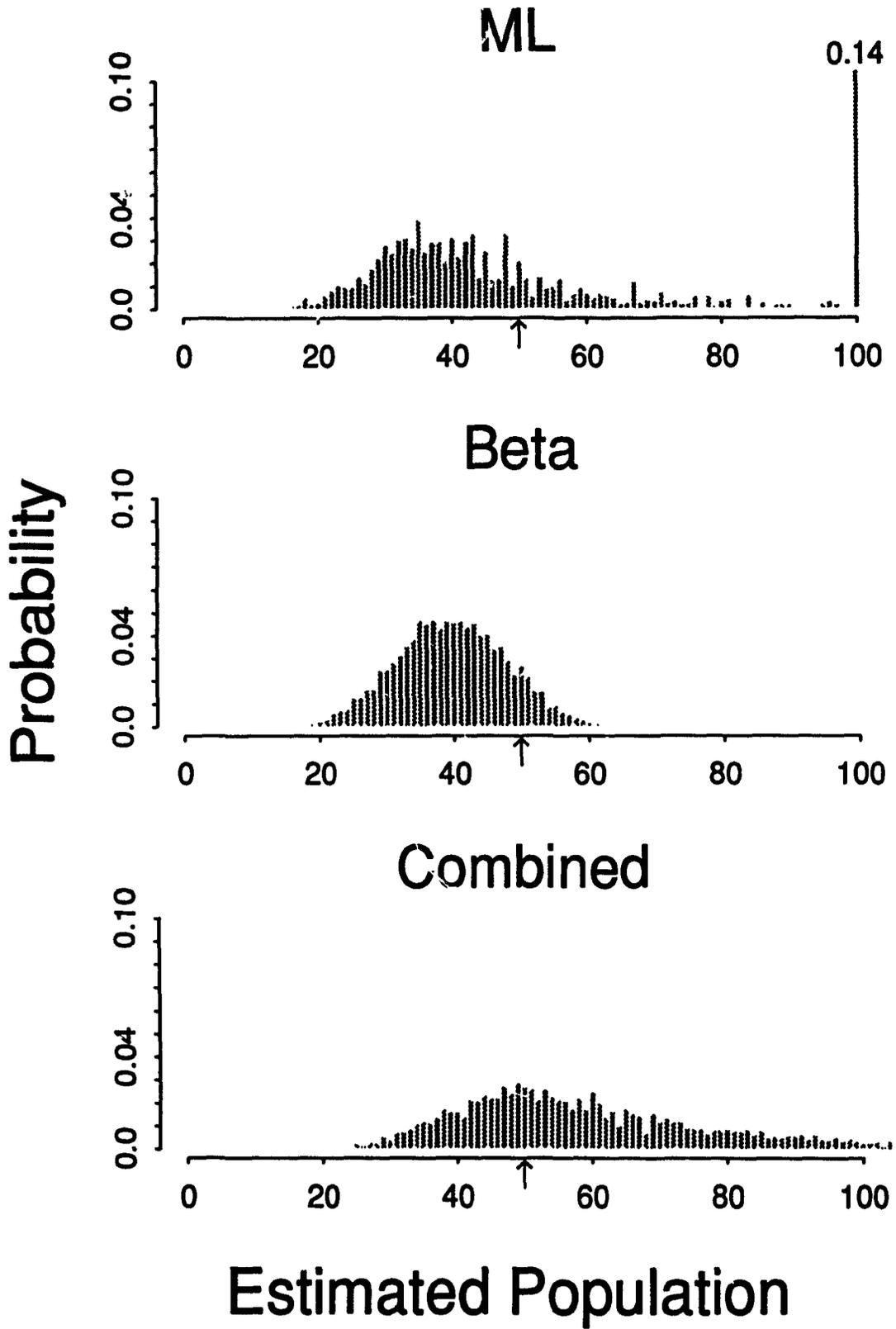
$N=50, K=3, 0.4 \leq p \leq 0.6$



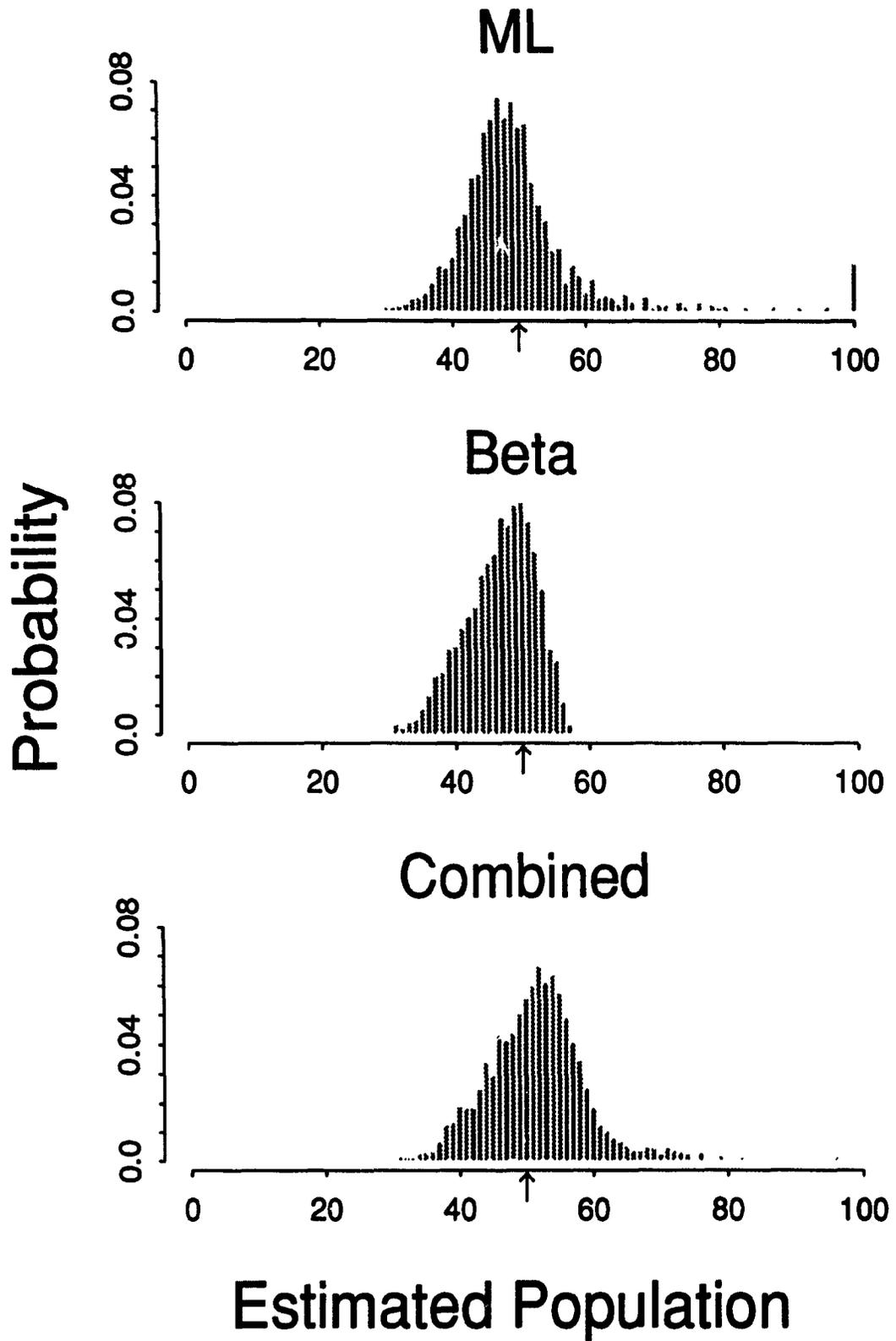
$N=50, K=3, 0.6 \leq p \leq 0.8$



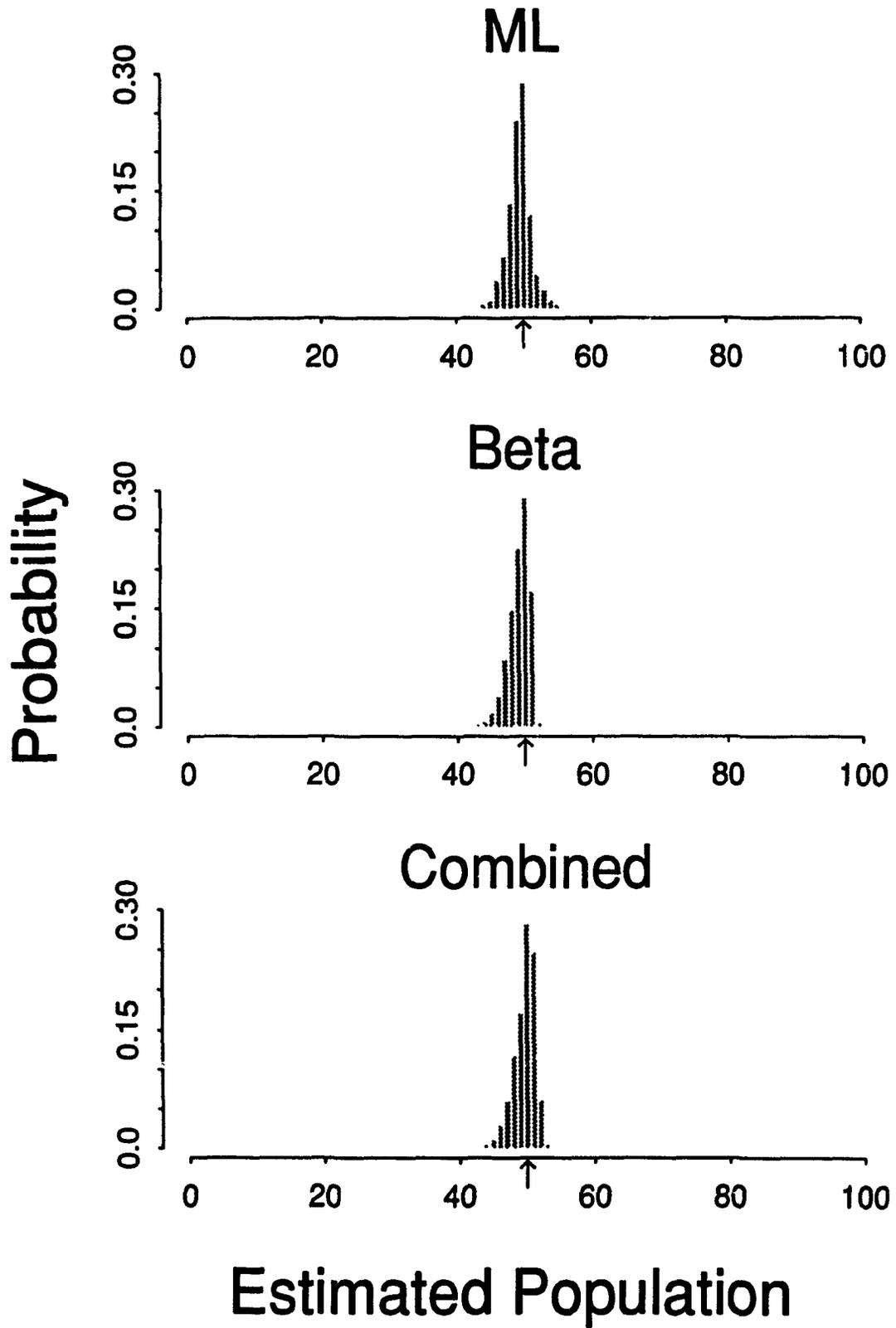
N=50, K=5,  $0.1 \leq p \leq 0.2$



$N=50, K=5, 0.2 \leq p \leq 0.4$

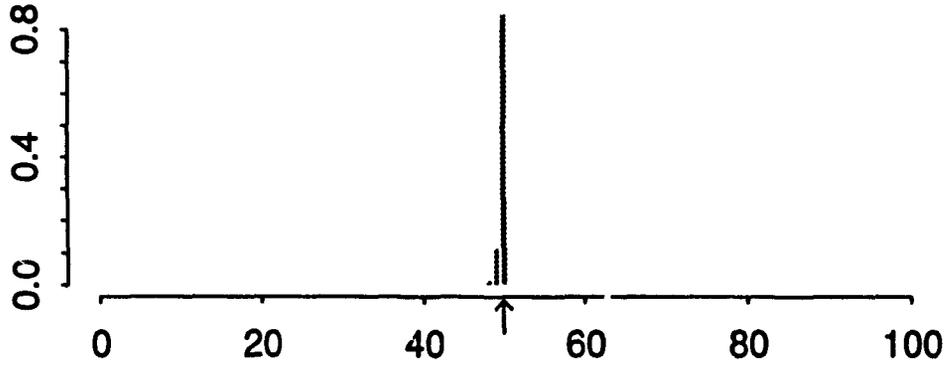


N=50, K=5,  $0.4 \leq p \leq 0.6$

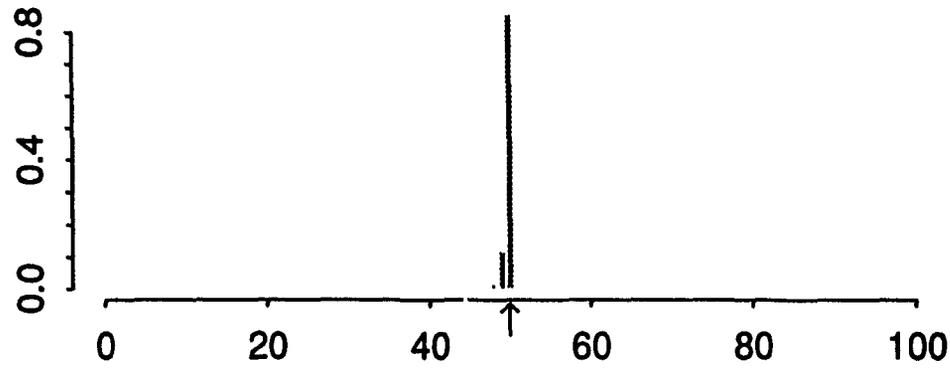


$N=50, K=5, 0.6 \leq p \leq 0.8$

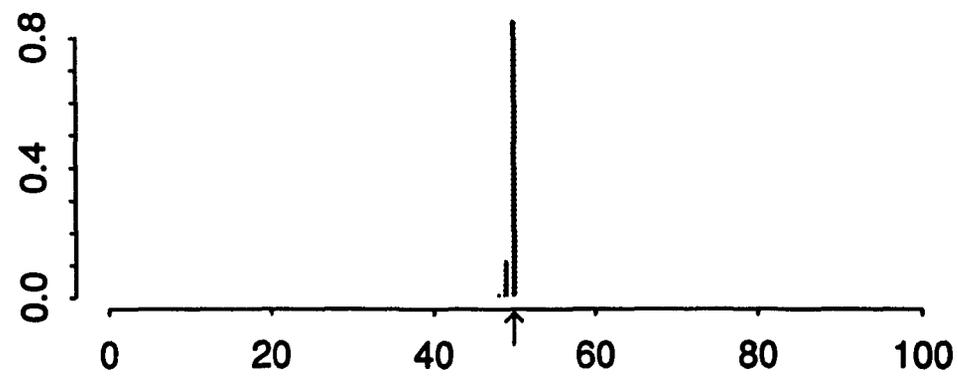
ML



Beta



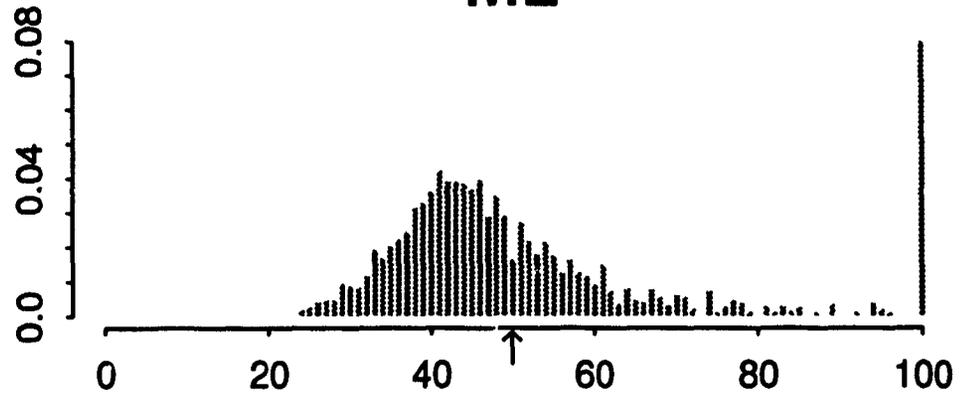
Combined



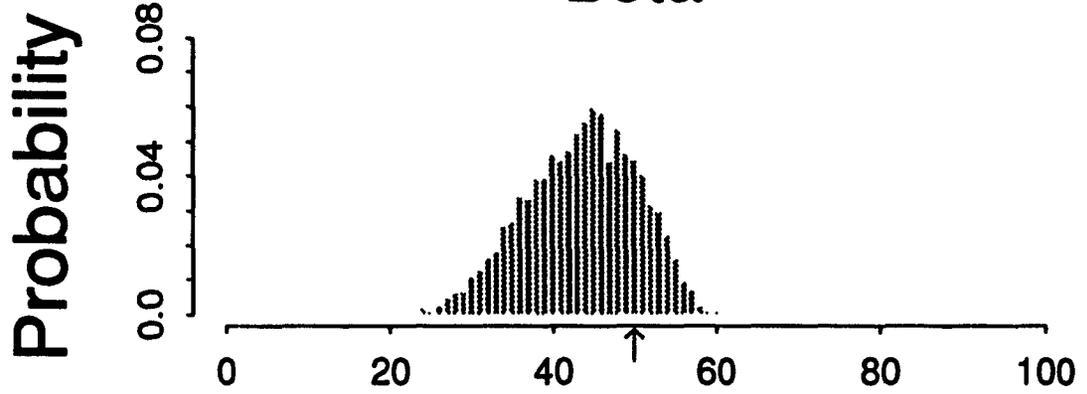
Estimated Population

$N=50, K=7, 0.1 \leq p \leq 0.2$

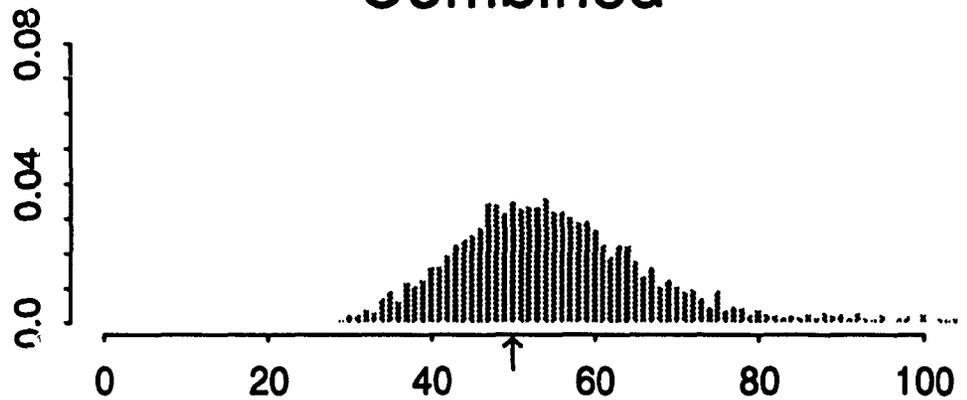
ML



Beta

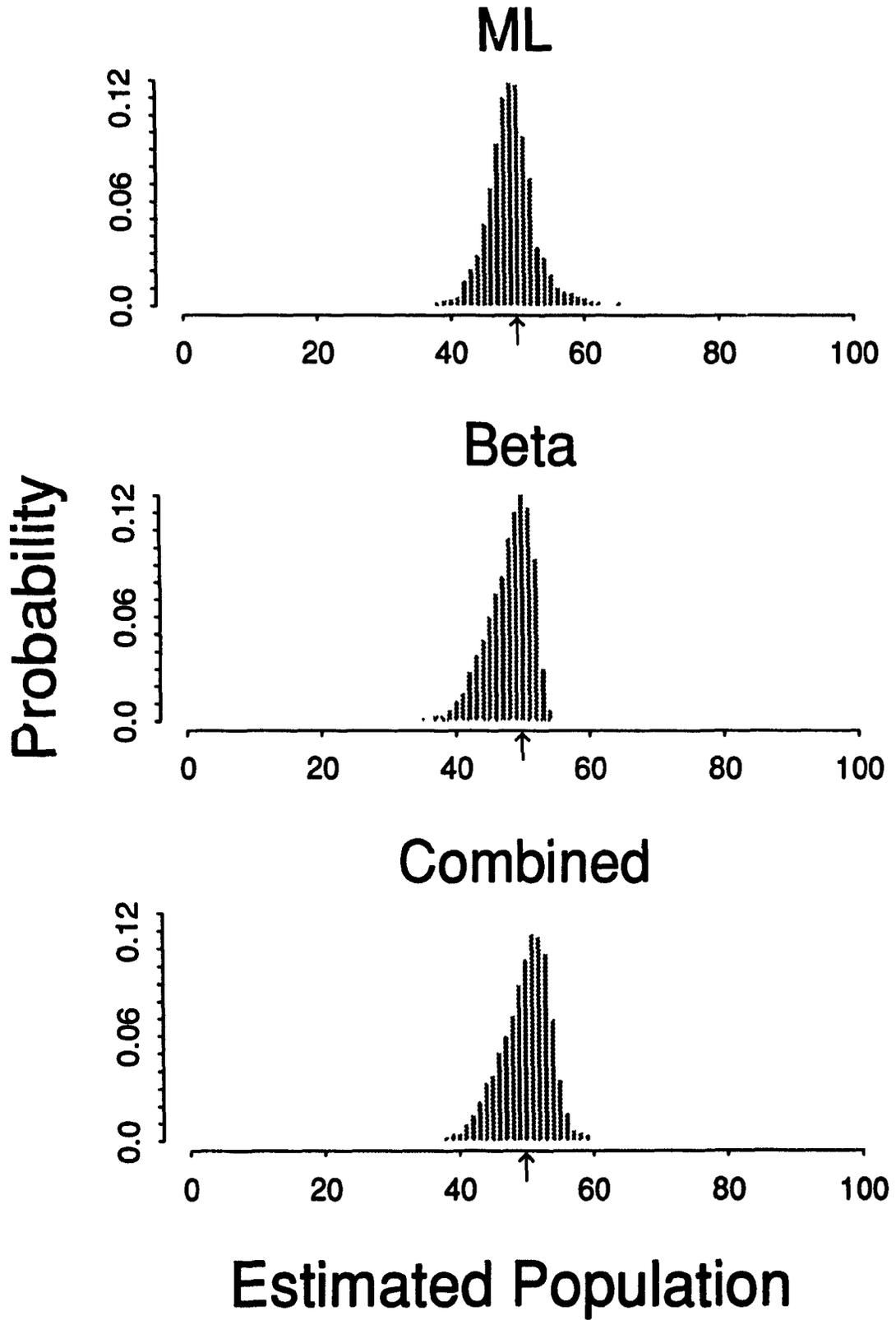


Combined

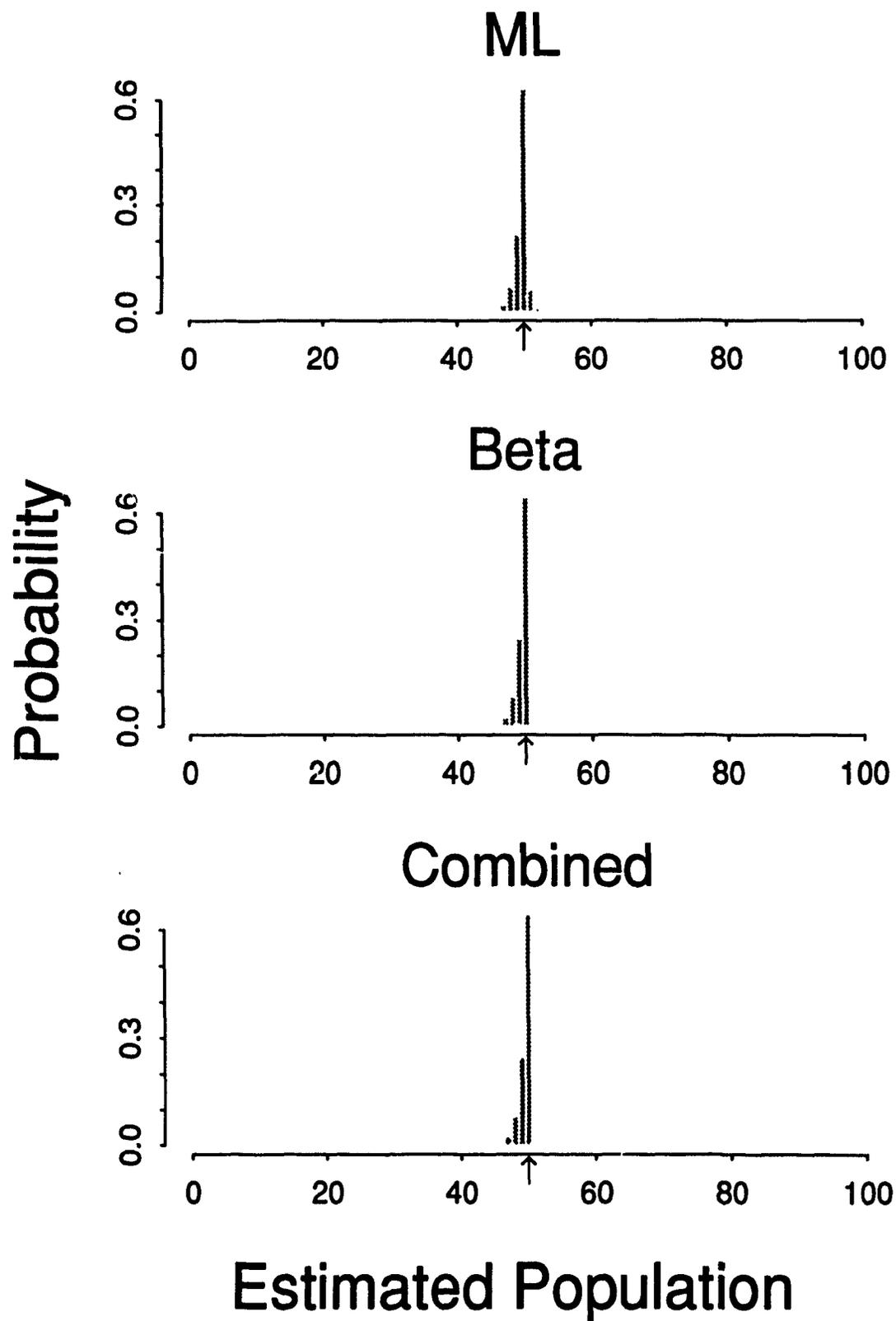


Estimated Population

$N=50, K=7, 0.2 \leq p \leq 0.4$

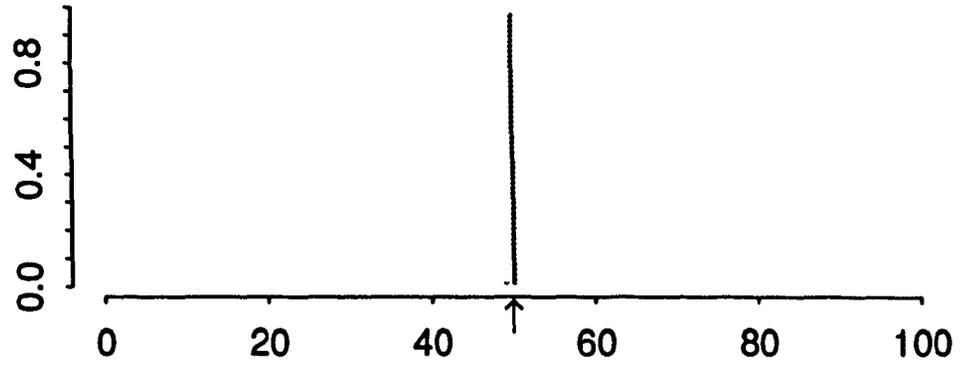


$N=50, K=7, 0.4 \leq p \leq 0.6$

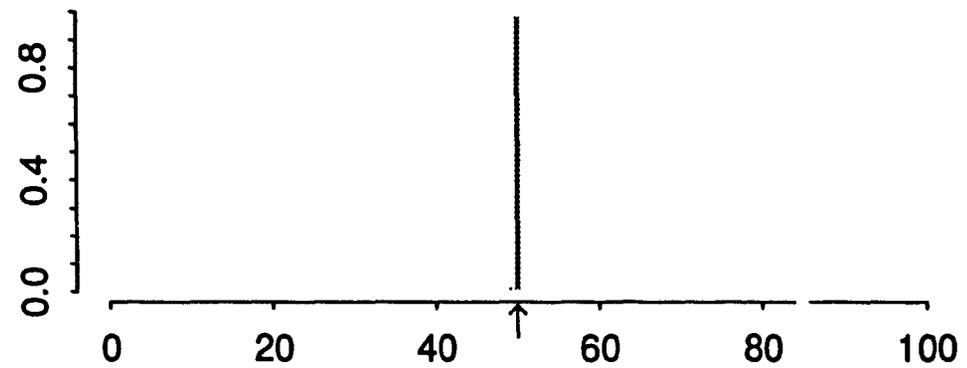


$N=50, K=7, 0.6 \leq p \leq 0.8$

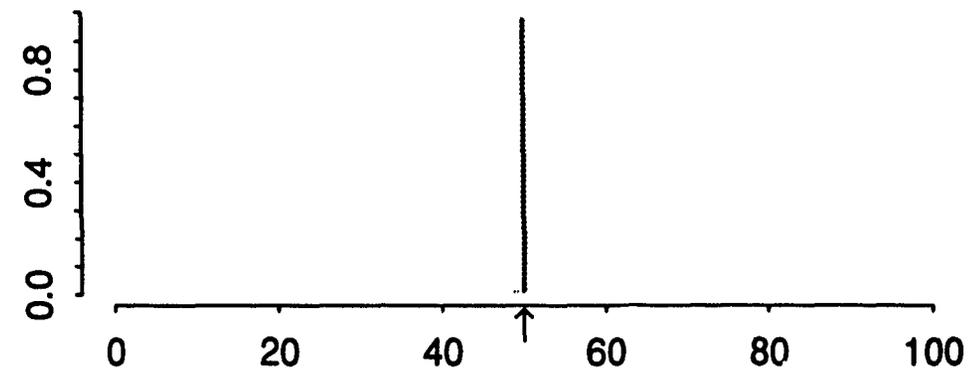
ML



Beta



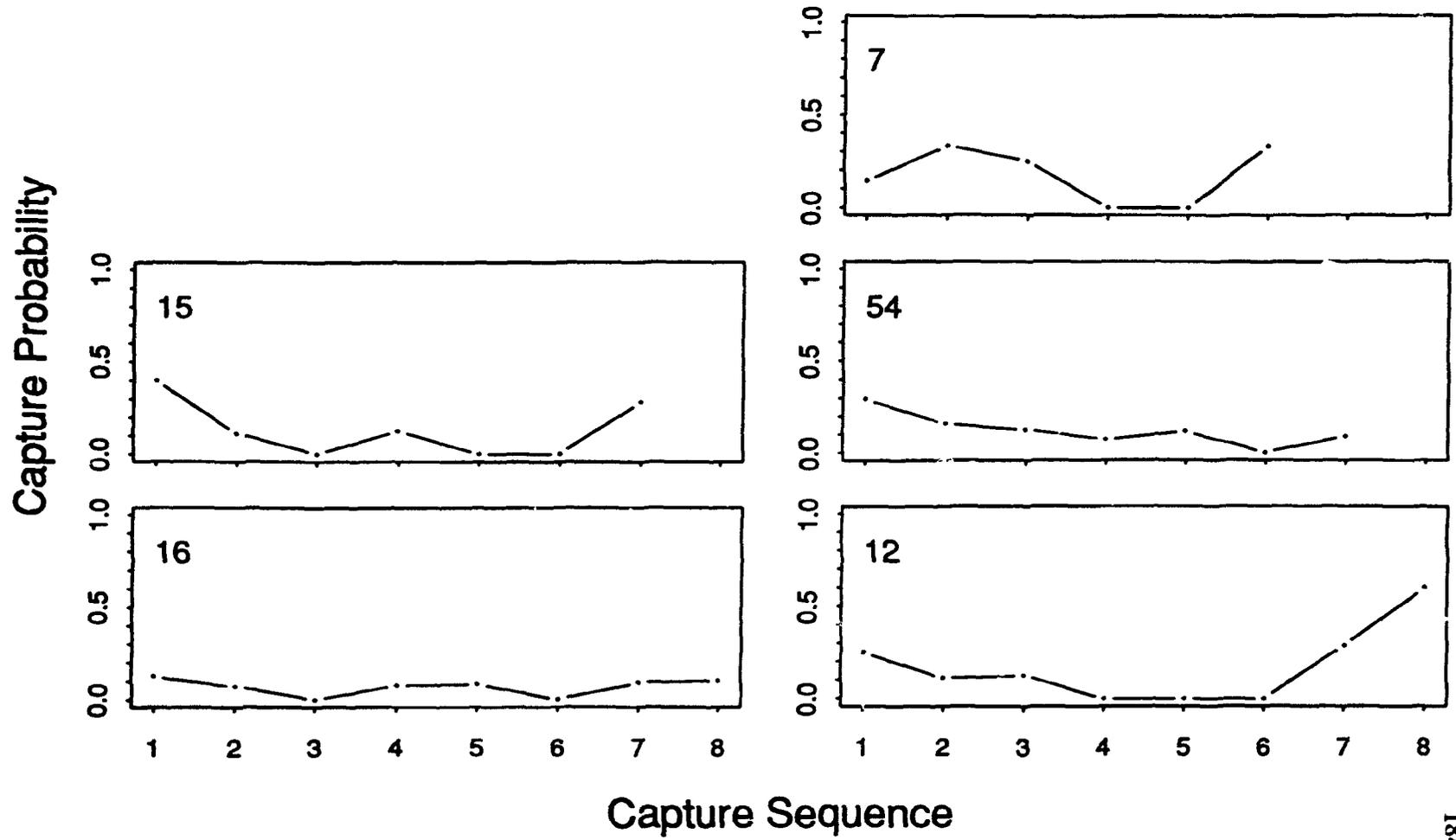
Combined



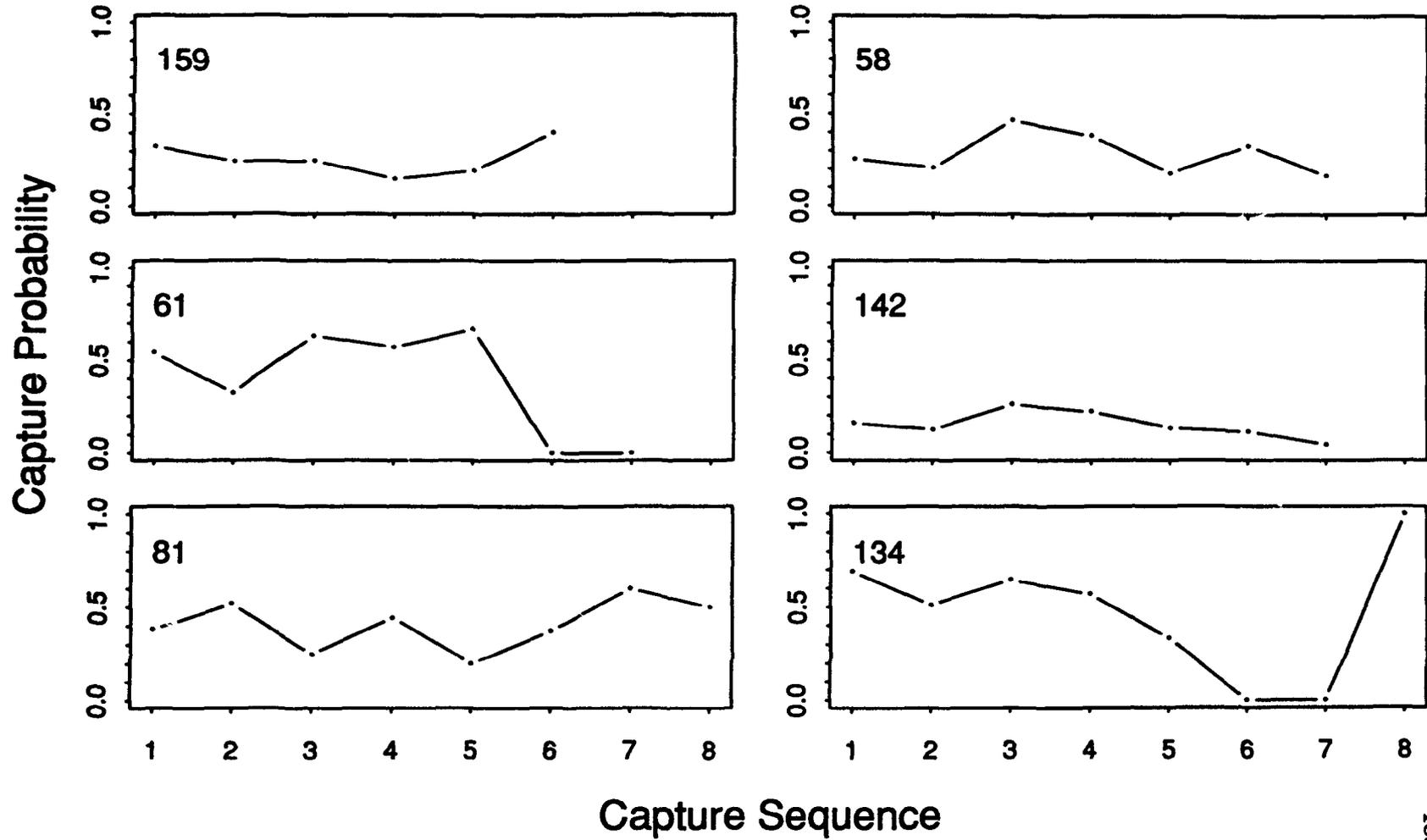
Estimated Population

**Figure A-2: Actual capture probabilities as a function of capture sequence for some species used, originating from Mahon's (1980) data. The value in the upper left corner is the actual population size ( $N_i$ ). It is apparent that the capture probabilities vary among species and decrease within the capture sequences for some of the species.**

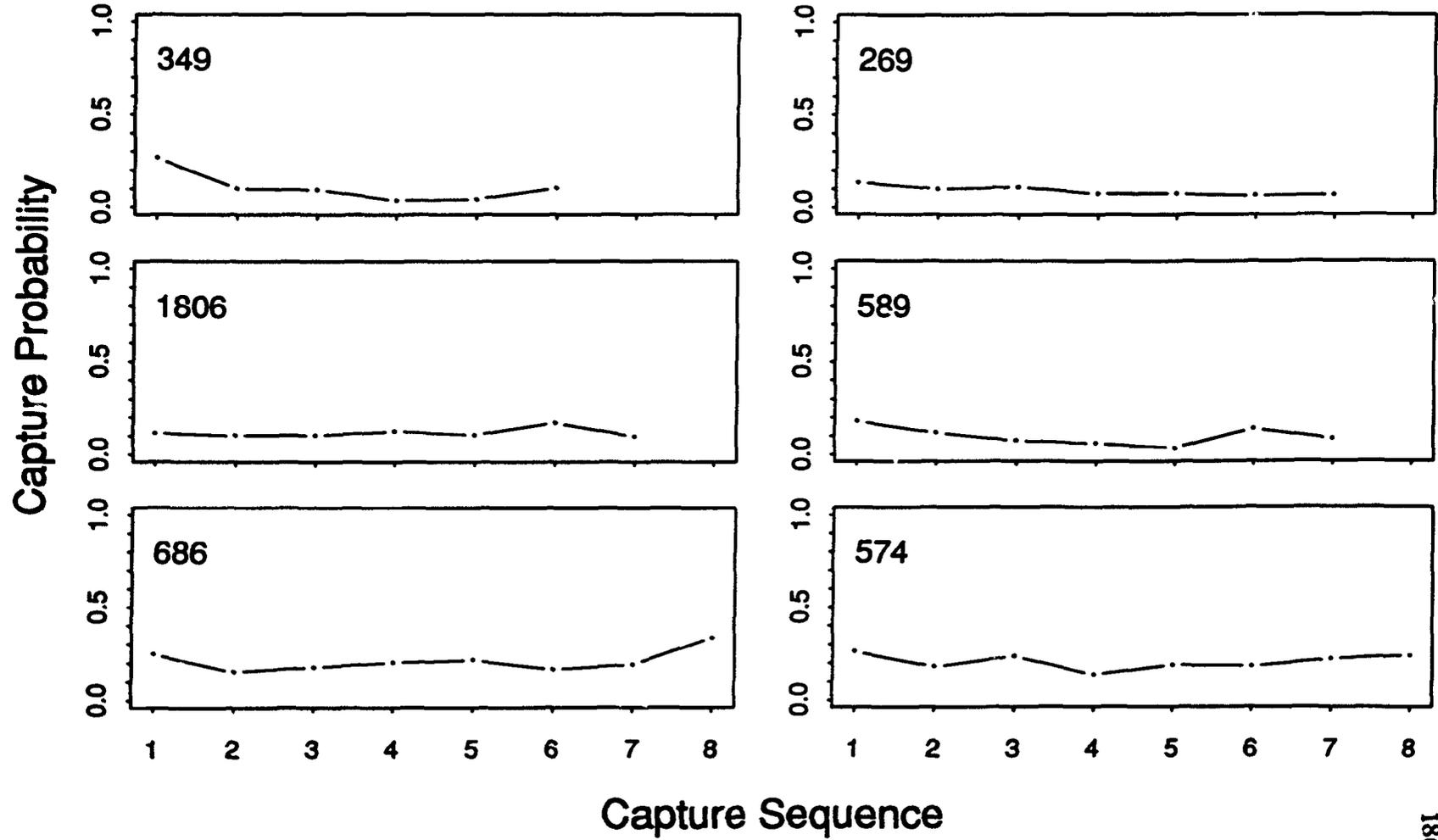
*Ambloplites rupestris*



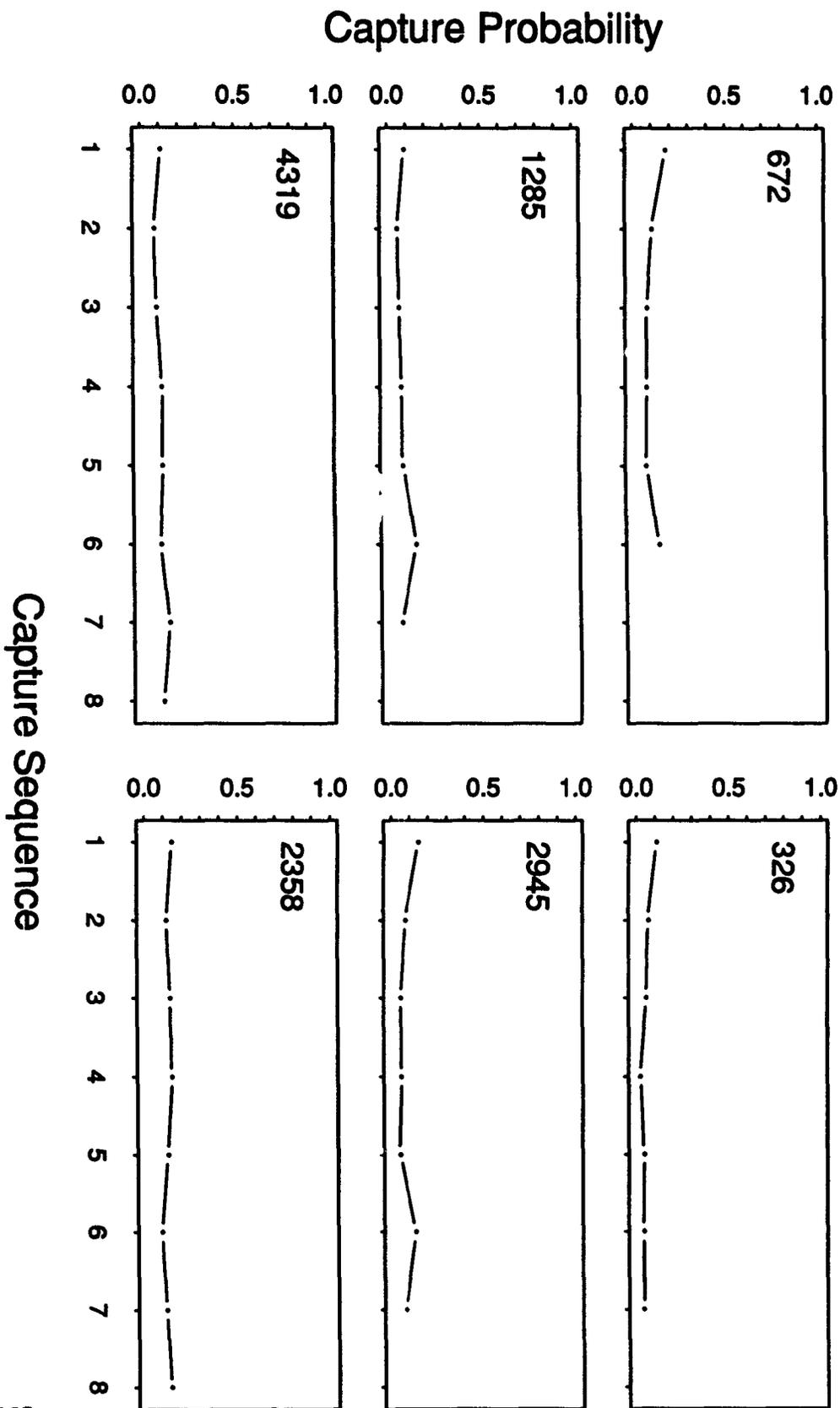
*Catostomus commersoni*



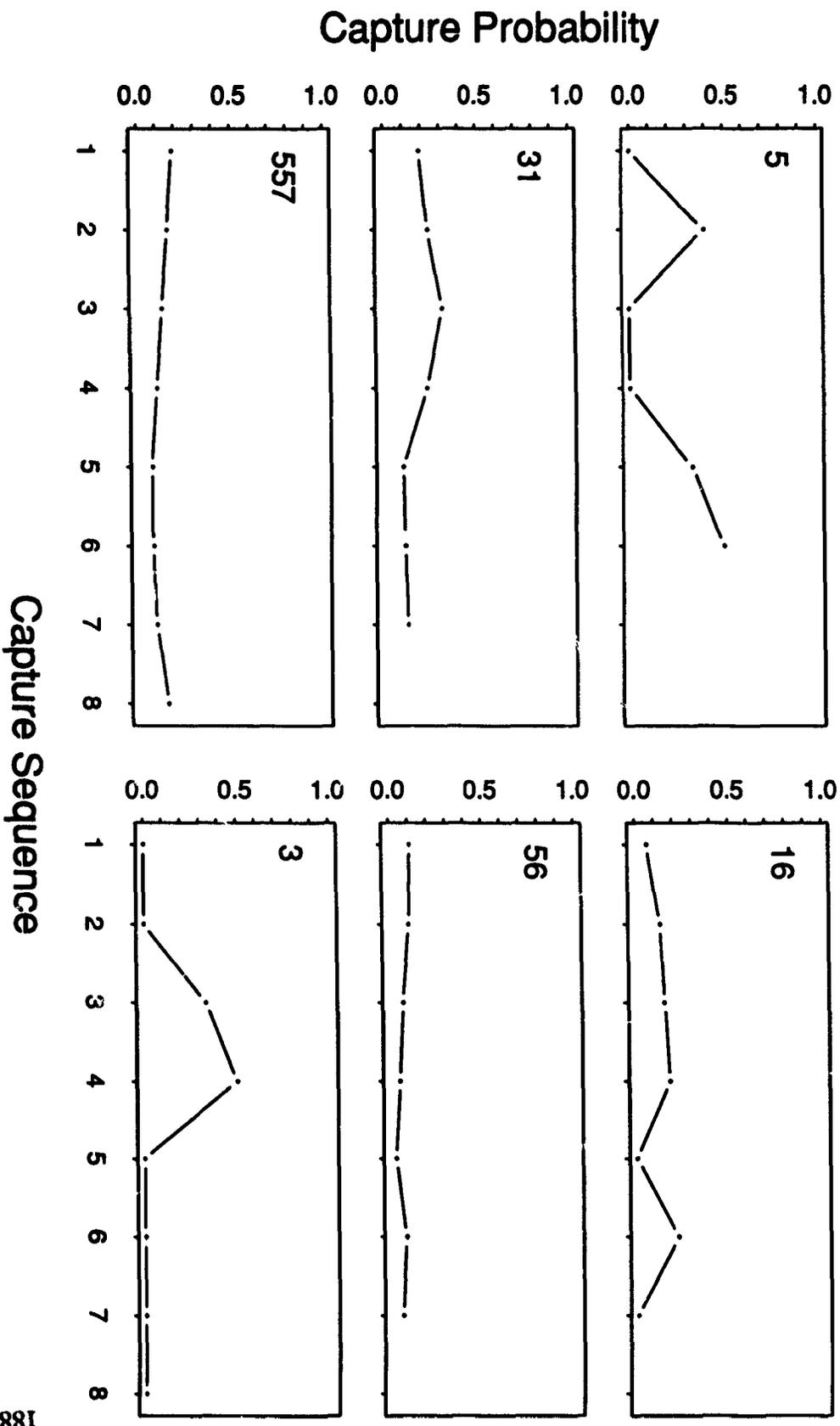
*Etheostoma caeruleum*



*Etheostoma flabellare*

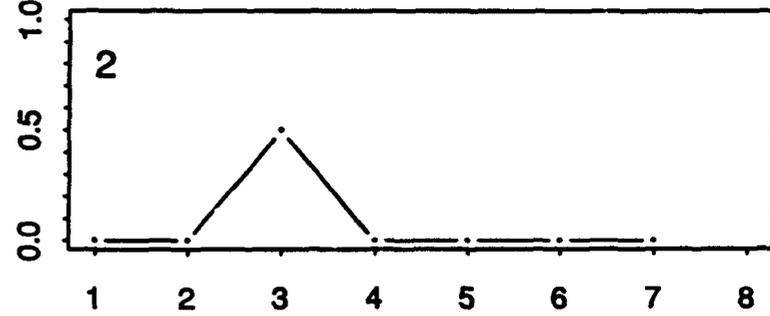
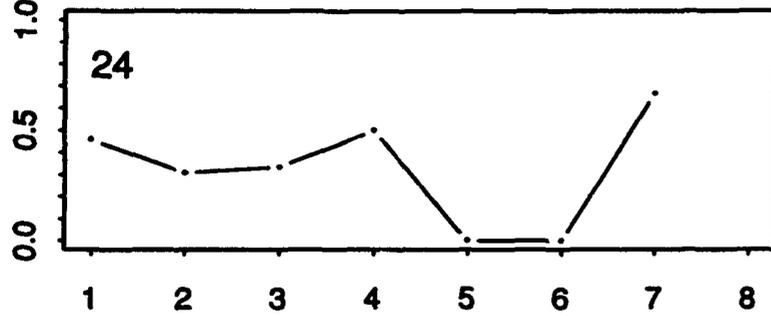
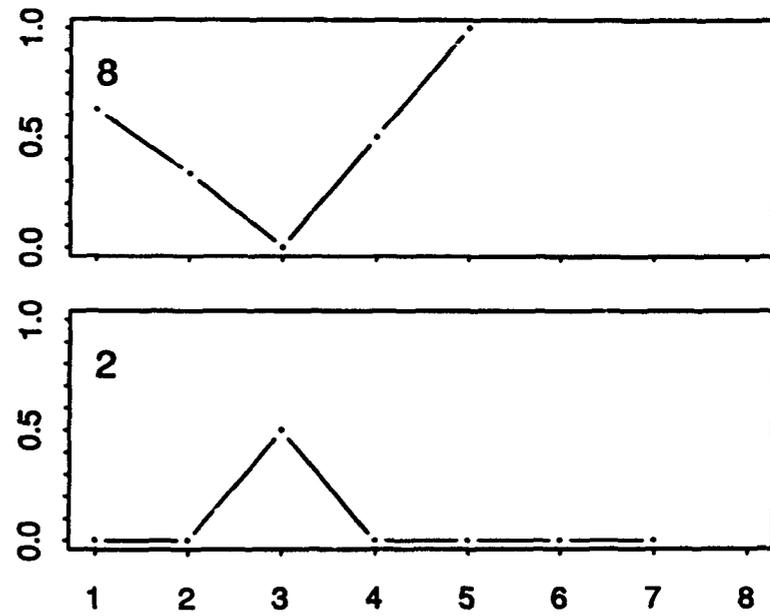
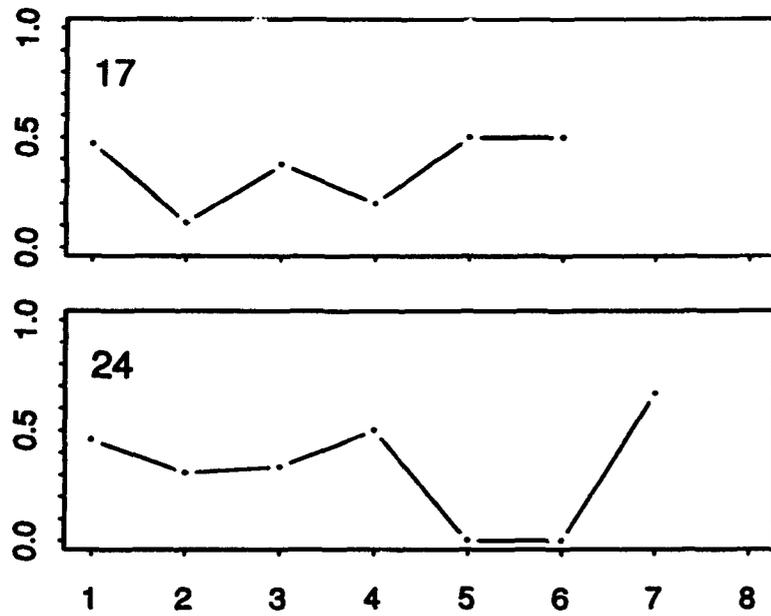


*Etheostoma nigrum*



*Hypentelium nigricans*

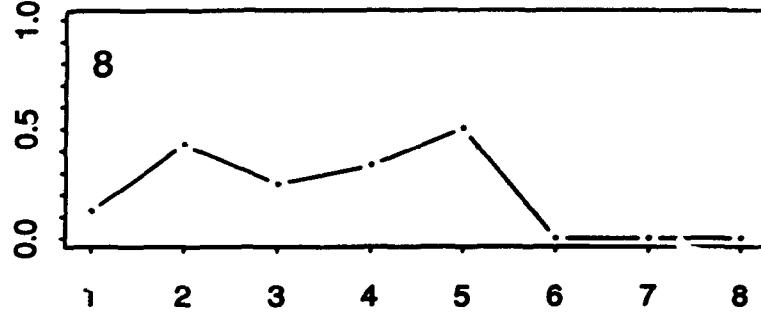
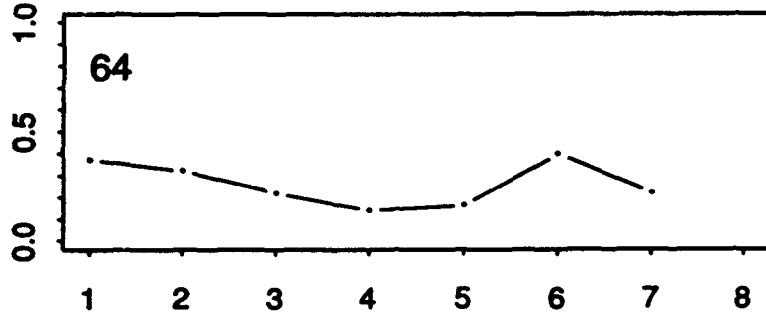
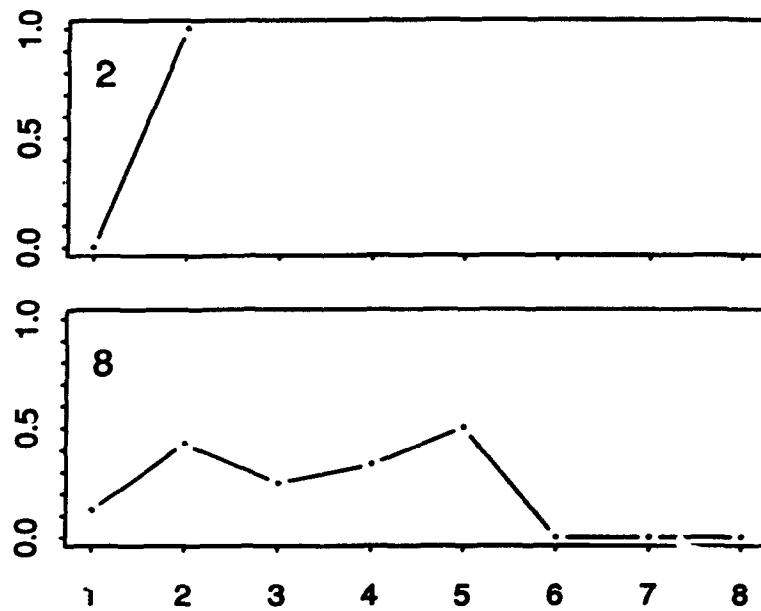
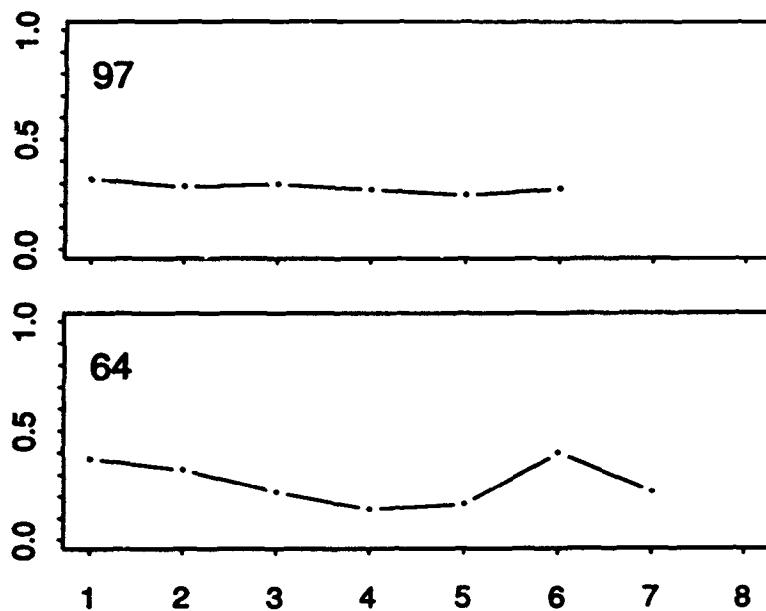
Capture Probability



Capture Sequence

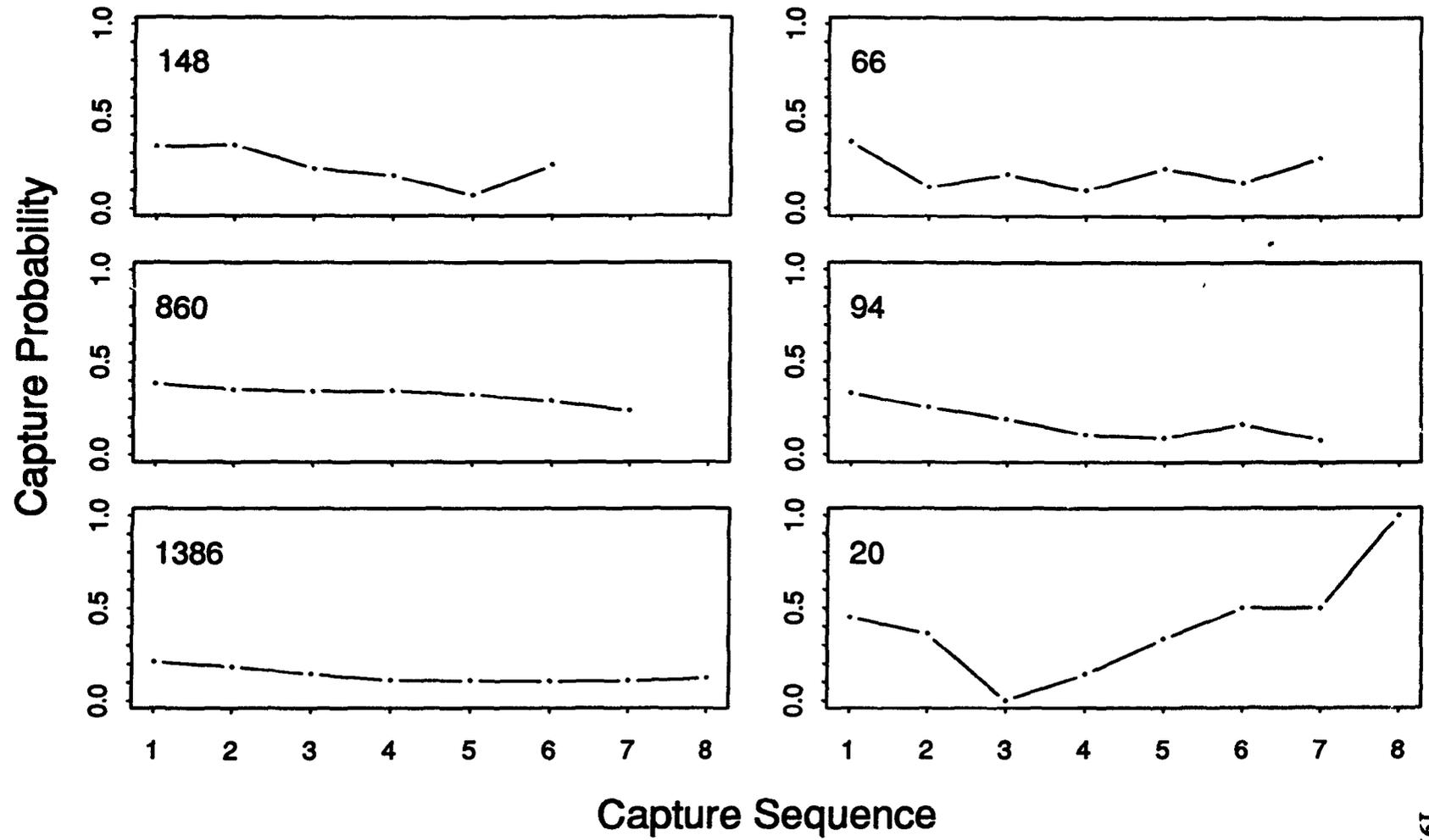
# *Micropterus dolomieu*

Capture Probability

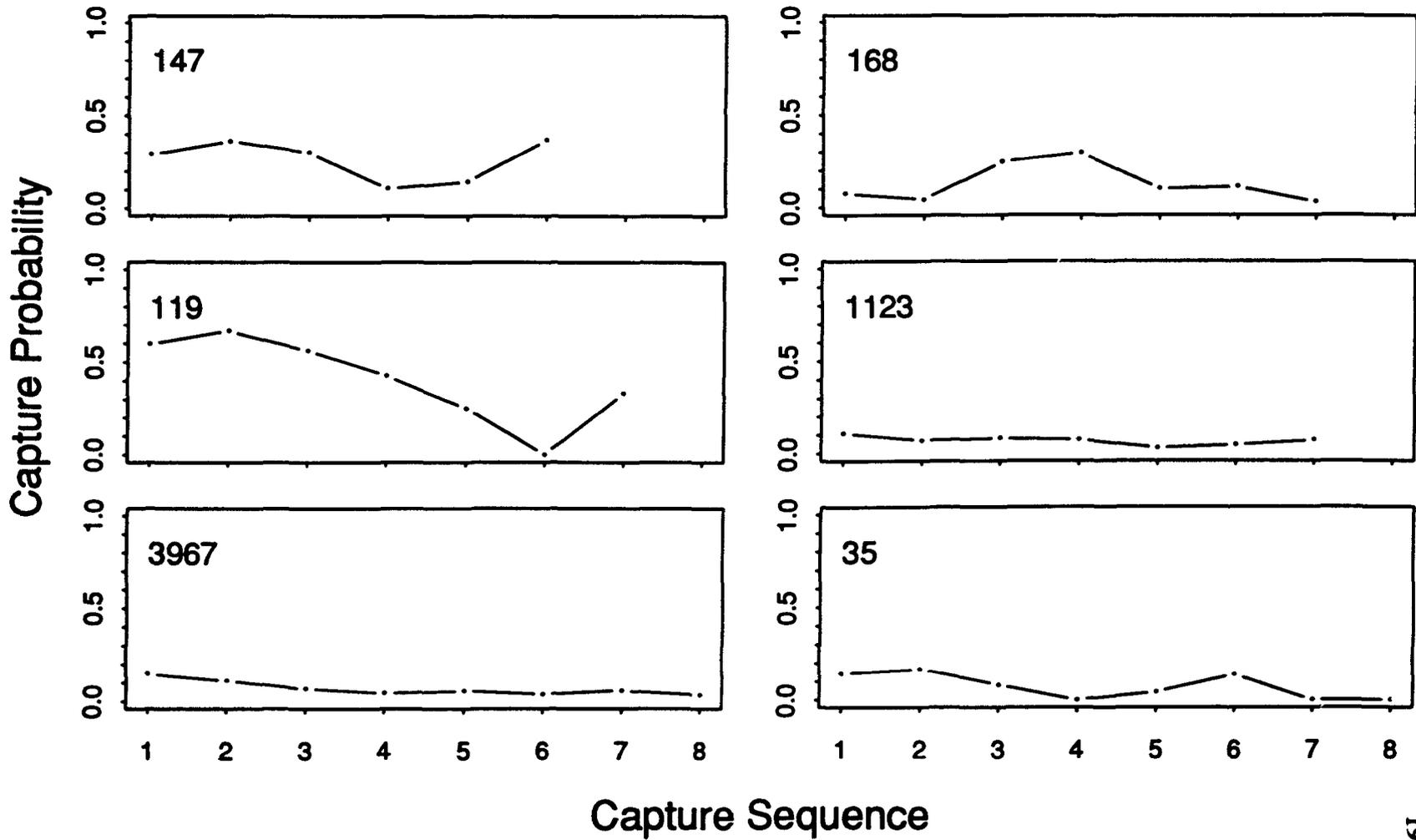


Capture Sequence

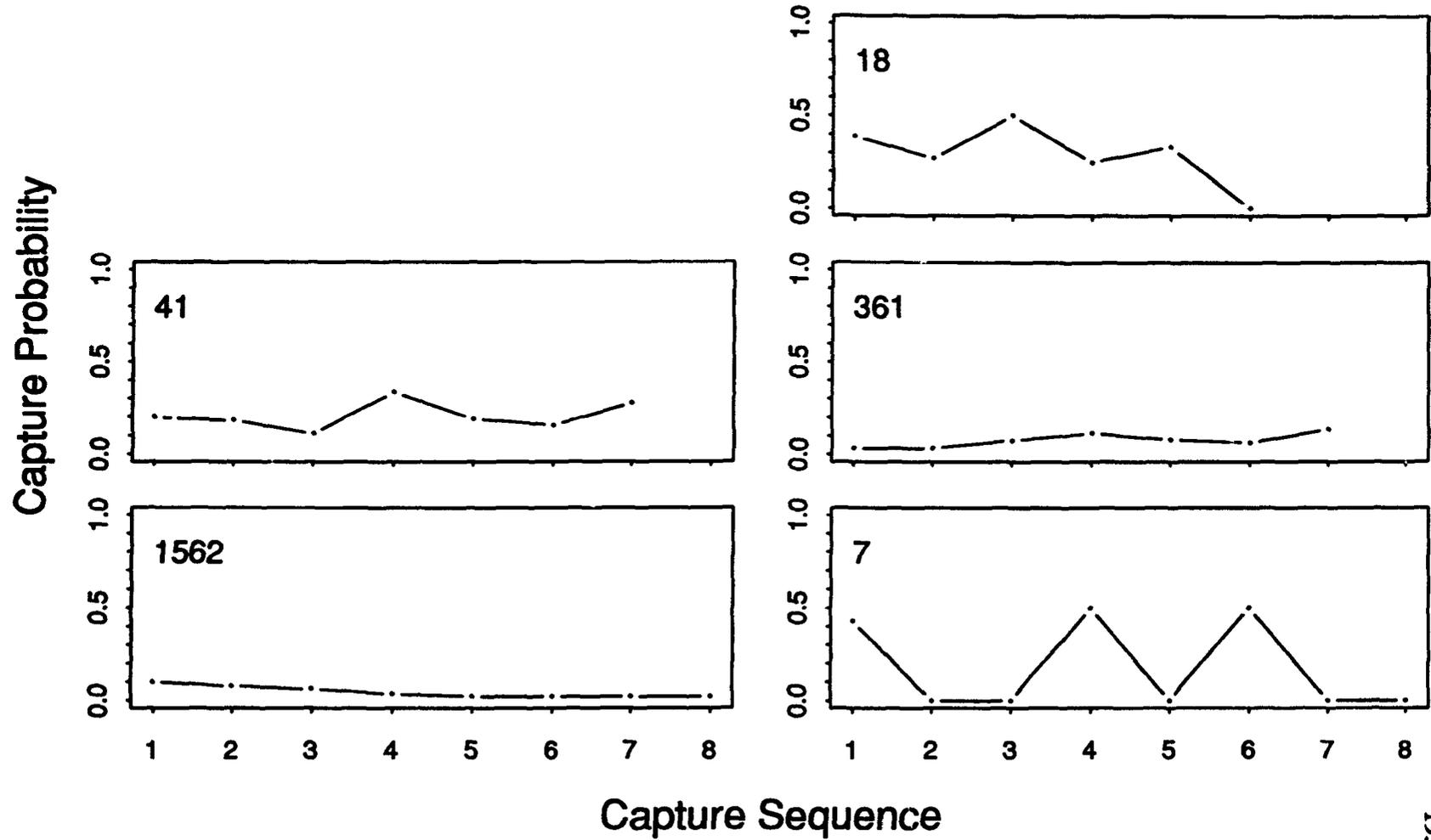
*Nocomis spp.*



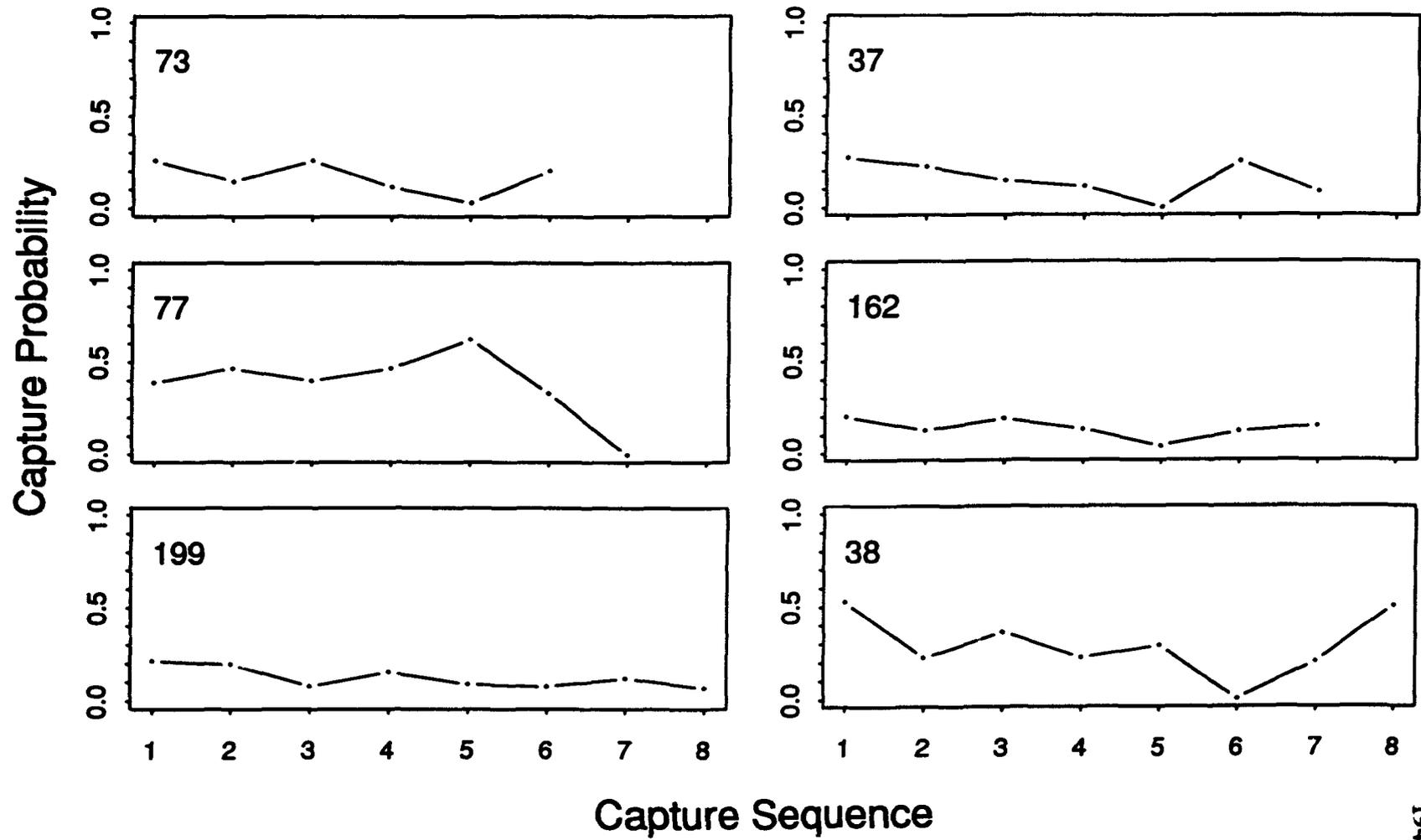
*Notropis cornutus*



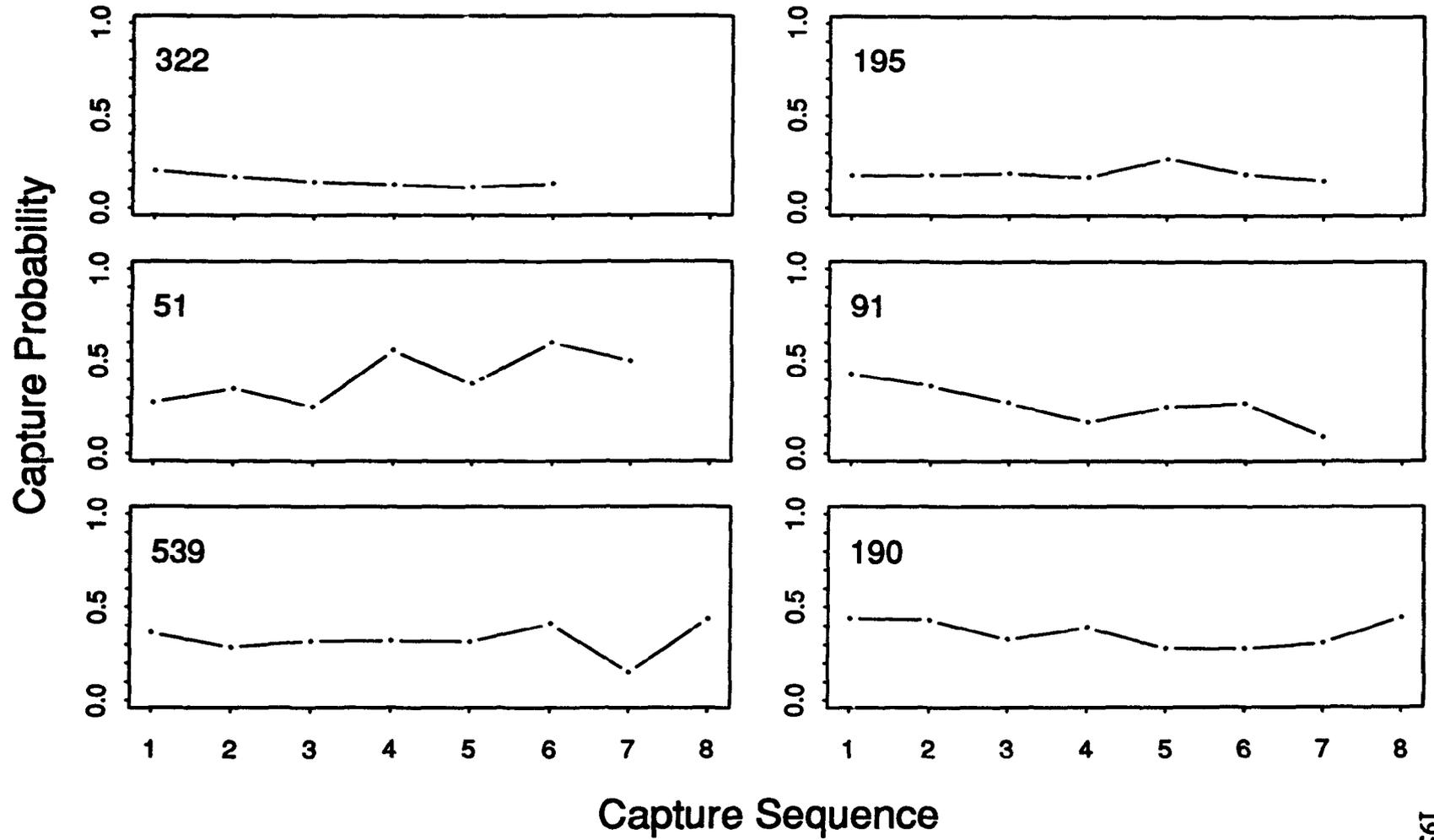
*Pimephales notatus*



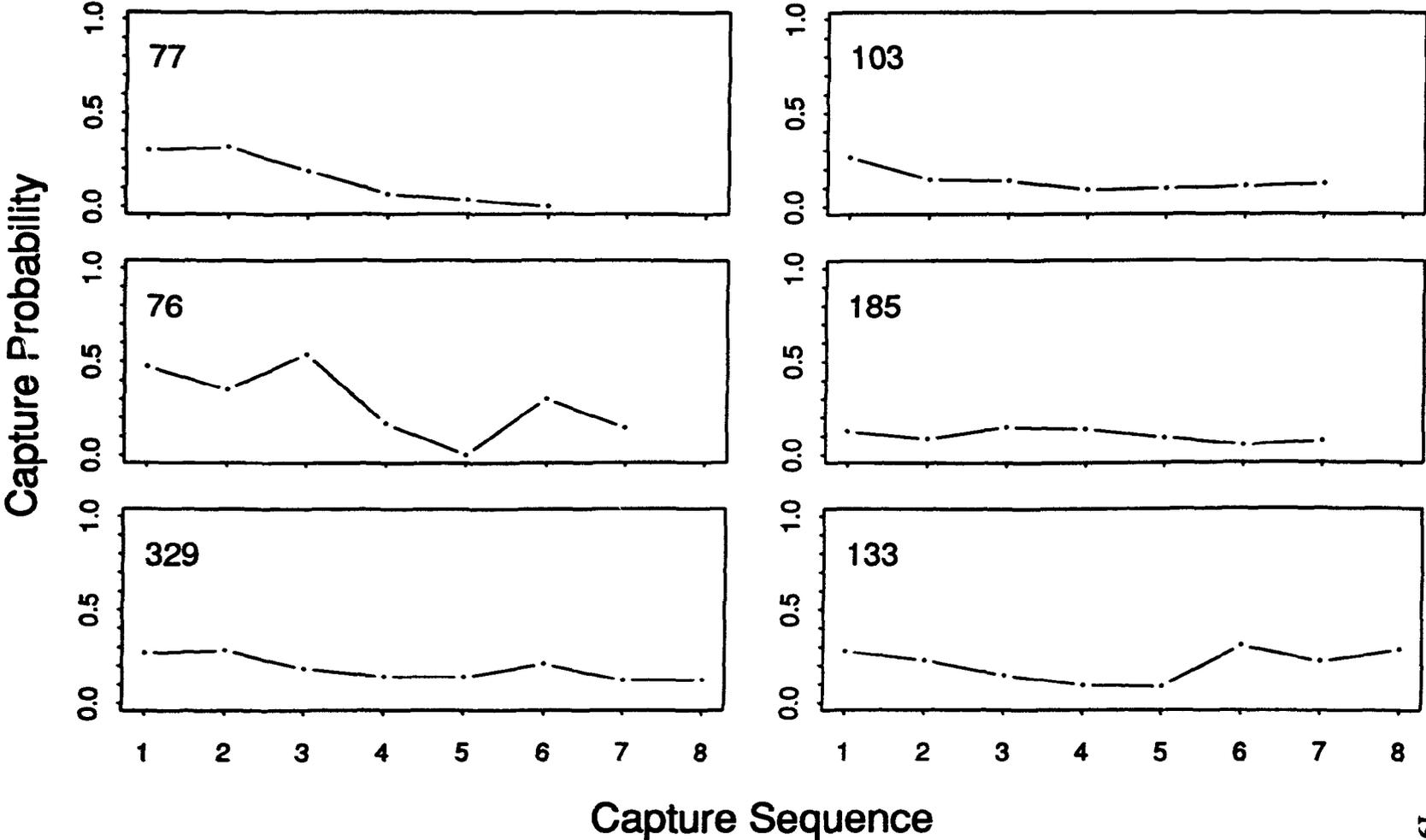
*Rhinichthys atratulus*



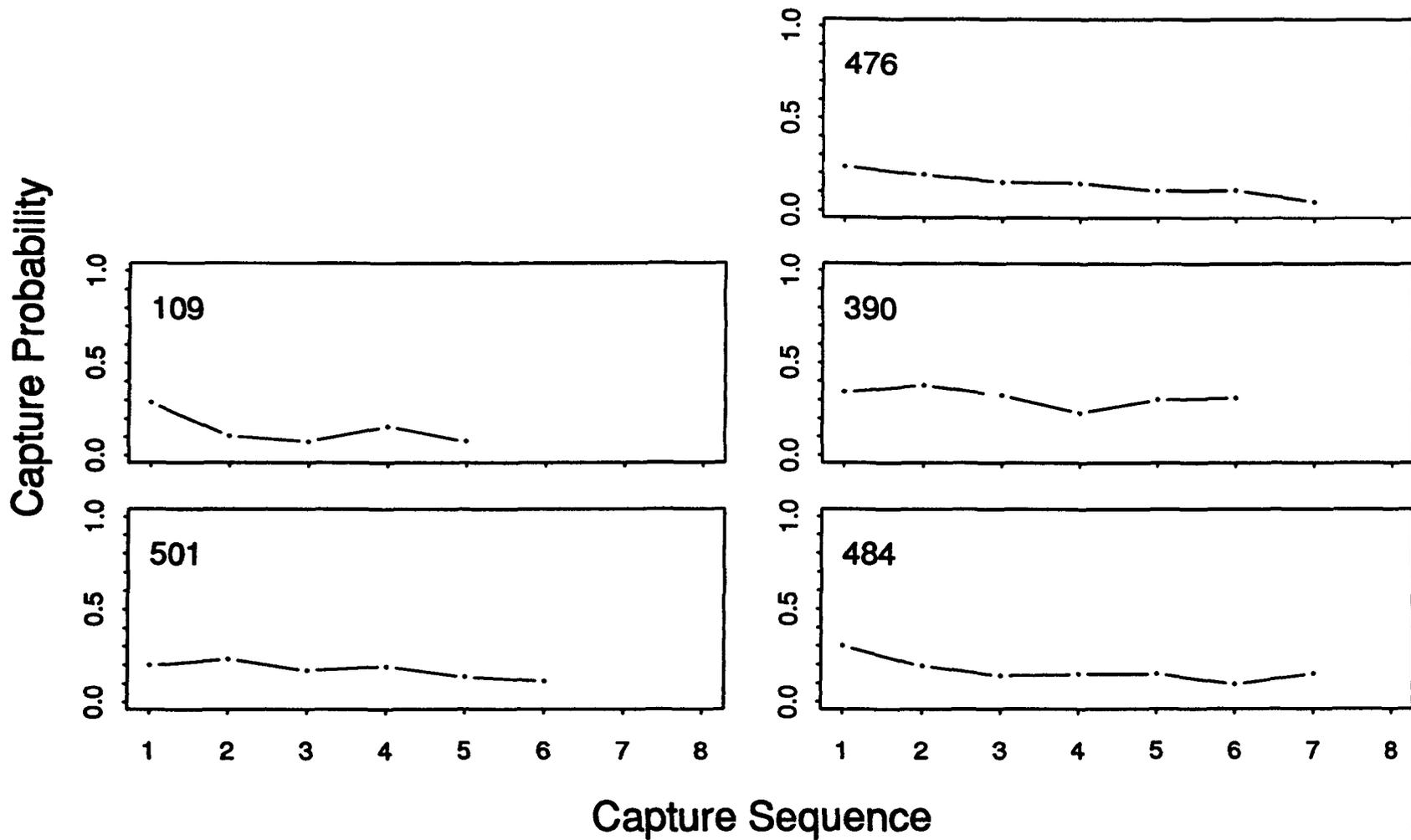
*Rhinichthys cataractae*



*Semotilus atromaculatus*

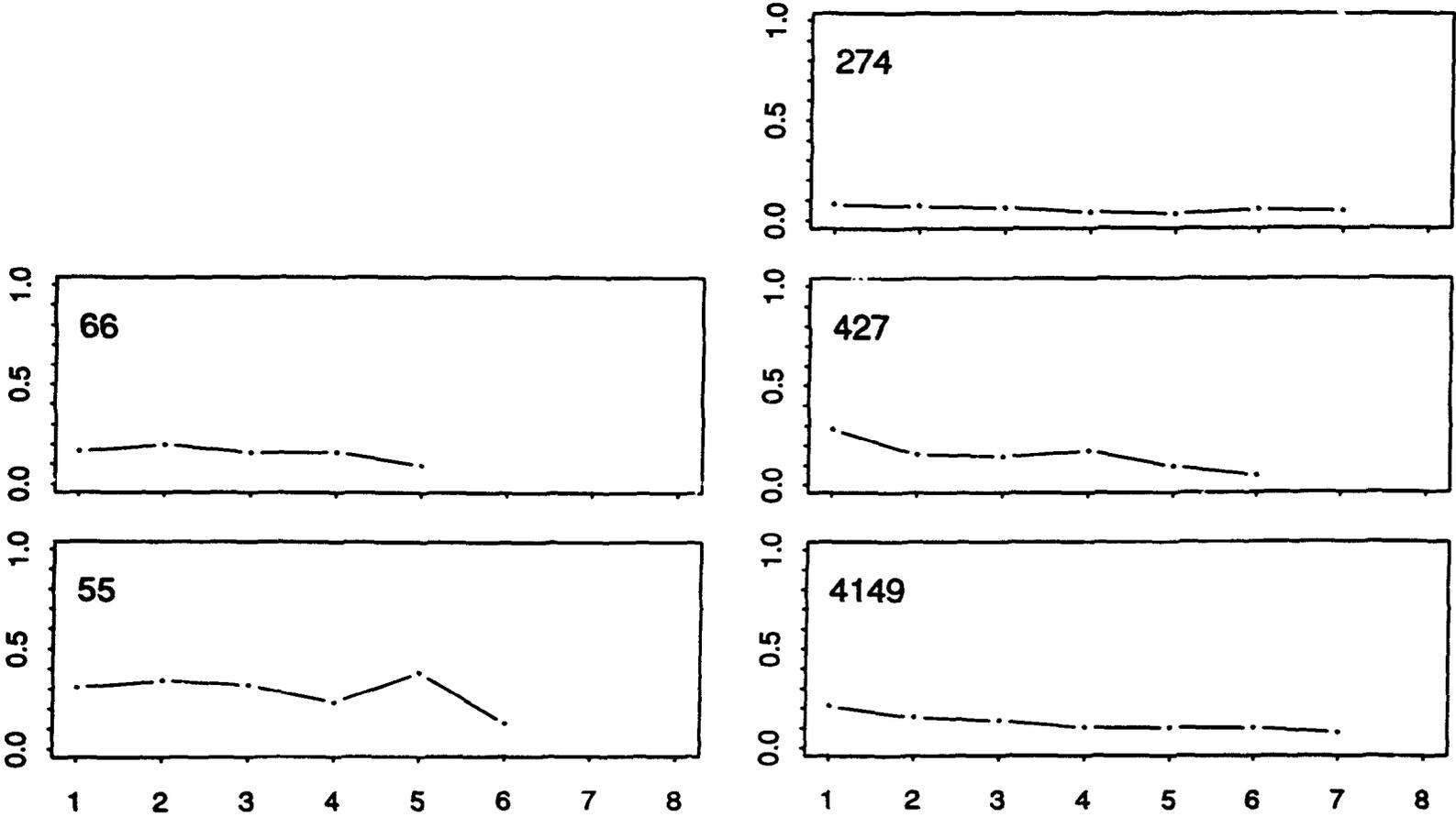


# *Noemacheilus barbatulus*



*Phoxinus phoxinus*

Capture Probability



Capture Sequence

## BIBLIOGRAPHY

- ALLEN, K. R. 1969. Limitations on production in salmonid populations in streams, p. 3-18. *In* T.G. Northcote [ed.] Symposium on Salmon and Trout in Streams. Institute of Fisheries, University of British Columbia, Vancouver, B.C.
- ALEXANDER, G. R., and E. A. HANSEN. 1986. Sand bed load in a brook trout stream. *N. Am. J. Fish. Manage.* 6: 9-23.
- ANDERSON, R. M., D. M. GORDON, M. J. CRAWLEY, and M. P. HASSELL. 1982. Variability in the abundance of animal and plant species. *Nature* (London), 296: 245-248.
- ANDREWARTHA, H. G., and L. C. BIRCH. 1982. The distribution and abundance of animals, 2nd ed. Univ. Chicago Press, Chicago, Ill.
- BACKIEL, T., and E. D. LE CREN. 1978. Some density relationships for fish population parameters. p. 279-302. *In* S.D. GERKING, [ed.] Ecology of freshwater fish production. Blackwell Scientific Pub., Oxford.
- BAGLINIÈRE, J. L., and D. ARRIBE-MOUTOUNET. 1985. Microrépartition des populations de truite commune (*Salmo trutta* L.) de juvénile de saumon atlantique (*Salmo salar* L.) et des autres espèces présentes dans la partie haute du Scorff (Bretagne). *Hydrobiologia* 120: 229-239.
- BAGLINIERE, J. L., and A. CHAMPIGNEULLE. 1982. Densité des populations de truite commune (*Salmo trutta* L.) et de juvéniles de saumon atlantique (*Salmo salar* L.) sur le cours principal du Scorff (Bretagne): préférendums physiques et variations annuelles (1976-1980). *Acta Oecologia* 3(3): 241-256.
- BARNWAL, R. K., and S. R. PAUL. 1988. Analysis of one-way layout of count data with negative binomial variation. *Biometrika*. 75: 215- 222.
- BAZZAZ, F. A. 1991. Habitat selection in plants. *Am. Nat.* 137 (Suppl.): S116-S130.
- BINNS, N. A., and F. M. EISERMAN. 1979. Quantification of fluvial trout habitat in Wyoming. *Trans. Am. Fish. Soc.* 108 (3): 215-228.
- BOHLIN, T., and I. G. COWX. 1990. Implications of unequal probability of capture by electric fishing on the estimation of population size, p. 145-155 *In* I.G. Cowx [ed.] Developments in electric fishing. Fishing News Books, Blackwell Scientific Pub., Oxford.

- BOWLBY, J. N., and J. C. ROFF.** 1986. Trout biomass and habitat relationships in southern Ontario streams. *Trans. Am. Fish. Soc.* 108: 215-228.
- BROWN, J. H.** 1984. On the relationship between abundance and distribution of species. *Am. Nat.* 124(2): 255-279.
- BROWN, J. L.** 1969. The buffer effect and productivity in tit populations. *Am. Nat.* 103: 347-354.
- CALEY, M. J.** 1991. A null model for testing distributions of dispersal distances. *Am. Nat.* 138: 524-532.
- CARLE, F. L., and M. R. STRUB.** 1978. A new method for estimating population size from removal data. *Biometrics* 34: 621-630.
- CARON, F., and A. J. TALBOT.** 1993. Re-evaluation of habitat classification criteria for juvenile salmon. p.139-148. *In* R. J. Gibson and R. E. Cutting [eds.] Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. NRC Can. Spec. Publ. Fish. Aquat. Sci. 118(1993).
- CHADWICK, E. M. P.** 1982. Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. *Can. J. Fish. Aquat. Sci.* 39: 1496
- COTÉ, Y., D. CLAVET, J.-M. DUBOIS, and A. BOUDREAULT.** 1987. Inventaire des habitats à saumon et estimation de production par photographie aérienne, p. 85-94 *In* M. Thibault and R. Billard [eds.] Restauration des rivières à saumon. INRA (Paris).
- COULSON, J. C., and J. B. WHITTAKER.** 1978. Ecology of moorland animals. p. 52-93. *In* O. W. Heal and D. F. Perkins [eds.] Production Ecology of British Moors and Montane Grasslands. Springer-Verlag, Berlin.
- COWX, I. G.** 1990. Developments in electric fishing. Fishing News Books, Blackwell Scientific Pub., Oxford. 358 p.
- CROSS, D. G., and B. SCOTT.** 1975. The effect of electric fishing on the subsequent capture of fish. *J. Fish. Biol.* 7: 349-357.
- CUSHING, D. H., and J. G. K. HARRIS.** 1973. Stock and recruitment and the problem of density dependence. *Rapports et Procès-verbaux des Réunions, Conseil international pour l'exploitation de la mer.* 164: 142-155.

- EGGLISHAW, H. J., and P. E. SHACKLEY. 1977. Growth, survival and production of juvenile salmon and trout in a Scottish stream, 1966-75. *J. Fish. Biol.* 11: 647-672.
- EGGLISHAW, H. J., and P. E. SHACKLEY. 1982. Influence of water depth on dispersion of juvenile salmonids, *Salmo salar* L. and *Salmo trutta* L., in a Scottish stream. *J. Fish. Biol.* 21: 141-155.
- ELLIOTT, J. M. 1984a. Growth, size, biomass and production of young migratory trout *Salmo trutta* in a lake district stream, 1966-1983. *J. Anim. Ecol.* 53: 979-994.
- ELLIOTT, J. M. 1984b. Numerical changes and population regulation in young migratory trout *Salmo trutta* in a lake district stream, 1966-1983. *J. Anim. Ecol.* 53: 327-350.
- ELLIOTT, J. M. 1985. Growth, size, biomass and production for different life-stages of migratory trout *Salmo trutta* in a Lake District stream, 1966-1983. *J. Anim. Ecol.* 54: 985-1001.
- ELLIOTT, J. M. 1986. Spatial distribution and behavioural movements of migratory trout *Salmo trutta* in a lake district stream. *J. Anim. Ecol.* 55: 907-922.
- ELLIOTT, J. M. 1987. Population regulation in contrasting populations of trout *Salmo trutta* in two lake district streams. *J. Anim. Ecol.* 56: 83-98.
- ELLIOTT, J. M. 1988. Growth, size, biomass and production in contrasting populations of trout *Salmo trutta* in two lake district streams. *J. Anim. Ecol.* 57: 49-60.
- ELLIOTT, J. M. 1993. The self-thinning rule applied to juvenile sea-trout, *Salmo trutta*. *J. Anim. Ecol.* 62: 371-379.
- EVANS, G. T., J. C. RICE, and E. M. P. CHADWICK. 1984. Patterns in growth and smolting of Atlantic salmon (*Salmo salar*) parr. *Can. J. Fish. Aquat. Sci.* 41: 783-797.
- EVANS, G. T., J. C. RICE, and E. M. P. CHADWICK. 1985. Patterns of growth and smolting of Atlantic salmon (*Salmo salar*) parr in a Southwestern Newfoundland river. *Can. J. Fish. Aquat. Sci.* 42: 539-543.
- FAGEN, R. Population effects of habitat change: A quantitative assessment. *J. Wildl. Manage.* 52(1): 41-46.

- FAUSCH, K. D.** 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Can. J. Zool.* 62: 441-451.
- FLACK, V. F., and P. C. CHANG.** 1987. Frequency of selecting noise variables in subset regression analysis: A simulation study. *Am. Statistician.* 41(1): 84-86.
- FOWLER, C.** 1981. Density dependence as related to life history strategy. *Ecology* 62: 602-610.
- FRANCIS, R. I. C. C.** 1990. Back-calculation of fish length: a critical review. *J. Fish. Biol.* 36: 883-902.
- FRASER, F. J.** 1969. Population density effects on survival and growth of juvenile coho salmon and steelhead trout in experimental stream channels, p. 253-265. *In* T.G. Northcote [ed.] *Symposium on Salmon and Trout in Streams.* Institute of Fisheries, University of British Columbia, Vancouver, B.C.
- FRASER, D. F., and T. E. SISE.** 1980. Observations on stream minnows in a patchy environment: A test of a theory of habitat distribution. *Ecology* 61(4): 790-797.
- FRENETTE, M., M. CARON, P. JULIEN, and R.J. GIBSON.** 1984. Interaction entre le débit et les populations de tacons (*Salmo salar*) de la rivière Matamec, Québec. *Can. J. Fish. Aquat. Sci.* 41: 954-963.
- FRETWELL, S. D., and H. L. LUCAS.** 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19: 16-36.
- GARROD, D. J., and B. J. KNIGHTS.** 1979. Fish stocks: Their life-history characteristics and response to exploitation. p. 361-382. *In* P.J. Miller [ed.] *Fish Phenology: Anabolic adaptiveness in teleosts.* Academic Press, New York, NY.
- GASTON, K. J.** 1990. Patterns in the geographical ranges of species. *Biol. Rev.* 65: 105-129.
- GASTON, K. J., and J. H. LAWTON.** 1988. Patterns in the distribution and abundance of insect populations. *Nature* 331: 709-713.
- GEE, A. S., N. J. MILNER, and R. J. HEMSWORTH.** 1978a. The production of juvenile Atlantic salmon, *Salmo salar*, in the upper Wye, Wales. *J. Fish. Biol.* 13: 439-451.

- GEE, A. S., N. J. MILNER, and R. J. HEMSWORTH. 1978b. The effect of density on mortality in juvenile Atlantic salmon (*Salmo salar*). *J. Anim. Ecol.* 47: 497-505.
- GIBSON, R. J. 1966. Some factors influencing the distribution of brook trout and young Atlantic salmon. *J. Fish. Res. Board Can.* 23: 1977-1980.
- GIBSON, R. J. 1973. Interactions of juvenile Atlantic salmon (*Salmo salar* L.) and brook trout (*Salvelinus fontinalis* [Mitchill]). *IASF Spec. Publ. Ser.* 4(1): 181-202.
- GIBSON, R. J. 1978. The behaviour of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) with regard to temperature and to water velocity. *Trans. Am. Fish. Soc.* 107: 703-712.
- GIBSON, R. J. 1981. Behavioural interactions between coho salmon (*Oncorhynchus kisutch*), Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*) and steelhead trout (*Salmo gairdneri*), at the juvenile fluvial stages. *Can. Tech. Rep. Fish. Aquat. Sci.*, 1029, 116 p.
- GIBSON, R. J. 1988. Mechanisms regulating species composition, population structure, and production of stream salmonids: a review. *Pol. Arch. Hydrobiol.* 35: 469-495.
- GIBSON, R. J., and Y. COTÉ. 1982. Production de saumonceaux et recaptures de saumons adultes étiquetés à la rivière Matamec, Côte-Nord, golfe du Saint-Laurent, Québec. *Naturaliste Can.* 109: 12-25.
- GIBSON, R. J., and T. DICKSON. 1984. The effects of competition on the growth of juvenile Atlantic salmon. *Nat. Can.* 111: 175-191.
- GIBSON, R. J., and R. L. HAEDRICH. 1988. The exceptional growth of juvenile Atlantic salmon (*Salmo salar*) in the city waters of St. John's, Newfoundland, Canada. *Pol. Arch. Hydrobiol.* 35(3-4): 385-407.
- GIBSON, R. J., and R. A. MYERS. 1988. A comparative review of juvenile Atlantic salmon production in North America and Europe. p. 14-18. *In* W. W. Crosier and P. M. Johnston [eds.] *Proc. 17th Ann. Study Course, Inst. Fish. Manage.* 1986, University of Ulster at Coleraine.
- GIBSON, R. J., and G. POWER. 1975. Selection by brook trout (*Salvelinus fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) of shade related to water depth. *J. Fish. Res. Board Can.* 32: 1652-1656.

- GIBSON, R. J., R. R. PORTER, and K. G. HILLIER. 1987. Juvenile salmonid production in the Highlands River, St. George's Bay, Newfoundland. *Can. Tech. Rep. Fish. Aquat. Sci.*, 1538: v + 109 p.
- GIBSON, R. J., D. E. STANSBURY, and B. L. DOOLEY. 1993. The freshwater habitat of Atlantic salmon: A review of spawning and rearing habitat, mechanisms of dispersion, and some effects of competition. (in press).
- GILLIS, D. M., and D. L. KRAMER. 1987. Ideal interference distributions: Population density and patch use by zebrafish. *Anim. Behav.* 35(6): 1875-1882.
- GOODYEAR, C. P. 1980. Compensation on fish populations. p. 253-280. *In* C. H. Hocutt and J. R. Stauffer, Jr. [eds.] *Biological monitoring of fish*. Lexington Books, Lexington, Mass.
- GOSS-CUSTARD, J. D. 1993. The effect of migration and scale on the study of bird populations. 1991 Witherby Lecture, *Bird Study*. 40: 81-96.
- GRANT, J. W. A., and D. L. KRAMER. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. *Can. J. Fish. Aquat. Sci.* 47(9): 1724-1737.
- GRANT, J. W. A., and D. L. G. NOAKES. 1988. Aggressiveness and foraging mode of young-of-the-year brook charr, *Salvelinus fontinalis* (Pisces:Salmonidae). *Behav. Ecol. Sociobiol.* 22: 435-445.
- GRANT, J. W. A., D. L. G. NOAKES, and K. M. JONAS. 1989. Spatial distribution of defence and foraging in young-of-the-year brook charr (*Salvelinus fontinalis*). *J. Anim. Ecol.* 58: 773-784.
- GRANT, J. W. A., and D. L. G. NOAKES. 1987. A simple model of optimal territory size for drift-feeding fish. *Can. J. Zool.* 65: 270-276.
- GRANT, J. W. A., and D. L. KRAMER. 1992. Temporal clumping of food arrival reduces its monopolization and defence by zebrafish, *Brachydanio rerio*. *Anim. Behav.* 44: 101-110.
- HALDANE, J. B. S. 1956. The relation between density regulation and natural selection. *Proc. Roy. Soc. B, London*, 145: 306-308.
- HANKIN, D. G., and G. H. REEVES. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. *Can. J. Fish. Aquat. Sci.* 45: 834-844.

- HANSON, J. M., and W. C. LEGGETT. 1985. Experimental and field evidence for inter and intraspecific competition on two freshwater fishes. *Can. J. Fish. Aquat. Sci.* 42 (2): 280-286.
- HARPER, D. G. C. 1982. Competitive foraging in mallards: "Ideal Free" ducks. *Anim. Behav.* 30: 575-584.
- HASTINGS, A. 1983. Can spatial variation alone lead to selection for dispersal? *Theor. Pop. Biol.* 24: 244-251.
- HEGGBERGET, T. G., and T. HESTHAGEN. 1979. Population estimates of young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., by electrofishing in two small streams in north Norway. *Rep. Inst. Freshwater Res. Drottningholm.* 58: 27-33.
- HEGGENES, J., A. BRABRAND, and S. J. SALTVEIT. January 1990. Comparison of three methods for studies of stream habitat use by young brown trout and Atlantic salmon. *Trans. Am. Fish. Soc.* 119 (1): 101-111.
- HELMINEN, H., K. ENNOLA, A. HIRVONEN, and J. SARVALA. 1993. Fish stock assessment in lakes based on mass removal. *J. Fish. Biol.* 41: 255-263.
- HERBINGER, C. M. 1987. Study of Atlantic salmon (*Salmo salar*) maturation using individually identified fish. Ph.D. thesis, Dalhousie University, Halifax, NS. 285 p.
- HILBORN, R., and C. J. WALTERS. 1992. Quantitative fisheries stock assessment: Choice, dynamics and uncertainty. Chapman and Hall, NY. 570 p.
- HOLT, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theor. Pop. Biol.* 28: 181-208.
- HUEY, R. B. 1991. Physiological consequences of habitat selection. *Am. Nat.* 137(Suppl.): S91-S115.
- HUFFAKER, C. B., and P. S. MESSENGER. 1964. The concept and significance of natural control. p. 74-117. *In* P. De Bach [ed.] *Biological Control of Insect Pests and Weeds*. Chapman and Hall, London.
- HUGHES, R. G. 1986. Theories and models of species abundance. *Am. Nat.* 128: 879-899.
- JAENIKE, J., and R. D. HOLT. 1991. Genetic variation for habitat preference: evidence and explanations. *Am. Nat.* 137(Suppl.):S67-S90.

- JOHNSON, N. T., C. J. PERRIN, P. A. SLANEY, and B. R. WARD. 1990. Increased juvenile salmonid growth by whole-river fertilization. *Can. J. Fish. Aquat. Sci.* 47 (5): 862-872.
- JONES, J. W. 1959. *The Salmon*. Collins, London. 192 p.
- KACELNIK, A., J. R. KREBS, and C. BERNSTEIN. 1992a. The ideal free distribution and predator-prey populations. *Trends in Ecol. Evol.* 7(2): 50-55.
- KACELNIK, A., C. BERNSTEIN, and J. R. KREBS. 1992b. Reply from Kacelnik, Bernstein and Krebs. *Trends in Ecol. Evol.* 7(9): 313-314.
- KARR, J. R. 1982b. Avian extinction on Barro Colorado Island, Panama: A reassessment. *Am. Nat.* 119: 220-239.
- KENDALL, M., and A. STUART. 1979. *The advanced theory of statistics. Vol 2. Inference and relationship.* 4th ed. MacMillan, NY. 748 p.
- KENNEDY, G. J. A., and C. D. STRANGE. 1982. The distribution of salmonids in upland streams in relation to depth and gradient. *J. Fish. Biol.* 20: 579-591.
- KENNEDY, G. J. A., and C. D. STRANGE. 1986. The effects of intra- and inter-specific competition on the distribution of stocked juvenile Atlantic salmon, *Salmo salar* L., in relation to depth and gradient in an upland trout, *Salmo trutta* L. stream. *J. Fish. Biol.* 39: 199-214.
- KOZEL, S. J., and W. A. HUBERT. 1989. Testing of habitat assessment models for small trout streams in the Medicine Bow National forest, Wyoming. *N. Am. J. Fish. Manage.* 9: 458-464.
- KRAMER, D., and E. AHLSTROM. 1968. Distributional atlas of fish larvae in the California current region: Northern Anchovy, *Engraulis mordax* Girard, 1951 through 1965. *California Cooperative Oceanic Fisheries Investigations Atlas*, vol. 9, 269 p.
- LAWLESS, J. F., 1987. Negative binomial and mixed Poisson regression. *Can. J. Statistics.* 15: 209-225.
- LE CREN, E. D. 1973. The population dynamics of small trout (*Salmo trutta*) in relation to density and territorial behaviour. *Rapp. P.-V. Reun. Int. Explor. Mer* 164: 241-246.
- LEVIN, S. A. 1976. Population dynamic models in heterogeneous environments. *Ann. Rev. Ecol. Syst.* 7: 287-310.

- LEVIN, S. A.** 1986. Population models and community structure in heterogeneous environments. p. 295-320. *In* T. G. Hallam and S. A. Levin [eds.] *Mathematical ecology*. Springer-Verlag, Berlin.
- MacARTHUR, R. H.** 1960. On the relative abundance of species. *Am. Nat.* 94: 25-36.
- MacARTHUR, R. H.** 1972. *Geographical ecology: Patterns on the distribution of species*. Harper and Row, New York, NY
- MacARTHUR, R. H., and J. H. CONNELL.** 1966. *The biology of populations*. J. Wiley and Sons, New York, NY
- MacARTHUR, R. H., and E. R. PIANKA.** 1966. On optimal use of a patchy environment. *Am. Nat.* 100: 603-609.
- MacARTHUR, R., and E. WILSON.** 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ. 203 p.
- MacCALL, A. D.** 1990. Dynamic geography of marine fish populations. *Books in recruitment fishery oceanography*, Washington Sea Grant Program. U. Washington Press, Seattle, WA. 124p.
- MAHON, R.** 1980. Accuracy of catch-effort methods for estimating fish density and biomass in streams. *Env. Biol. Fish.* 5(4): 343-360.
- MASON, J. C.** 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. *J. Wildl. Manage.* 40: 775-788.
- MASON, J. C., and D. W. CHAPMAN.** 1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. *J. Fish. Res. Board Can.* 22: 173-190.
- McARDLE, B. H., K. J. GASTON, and J. H. LAWTON.** 1990. Variation in the size of animal populations: Patterns, problems and artifacts. *J. Anim. Ecol.* 59: 439-454.
- McARDLE, B. H., and K. J. GASTON.** 1993. The temporal variability of populations. *Oikos* 67:1 187-191.
- McCLENDON, D. D., and C. F. RABENI.** 1987. Physical and biological variables useful for predicting population characteristics of smallmouth bass and rock bass in an Ozark stream. *N. Am. J. Fish. Manage.* 7: 46-56.

- McCULLAGH, P., and J. A. NELDER. 1989. Generalized linear models. Second ed., Monographs on Statistics and Applied Probability 37. Chapman and Hall, New York, NY 511 p.
- McGRORTY, S., and J. D. GOSS-CUSTARD. 1993. Population dynamics of the mussel *Mytilus edulis* along environmental gradients: spatial variations in density-dependent mortalities. *J. Anim. Ecol.* 62: 415-427.
- McKONE, M. J. 1993. Statistical analysis of experiments conducted at multiple sites. *Oikos* 67:1 184-186.
- McNICOL, R. E., E. SCHERER, and E. J. MURKIN. 1985. Quantitative field investigations of feeding and territorial behaviour of young-of-the-year brook charr, *Salvelinus fontinalis*. *Environ. Biol. Fishes* 12: 219-229.
- MENZIES, W. J. M. 1927. Some aspects of the growth of salmon in river and sea as observed from scale examination of Dee (Aberdeen) and Spey salmon 1921 to 1923 inclusive. *Salmon Fisheries (Fishery board of Scotland)* 1: 1-23.
- MILINSKI, M. 1988. Games fish play: Making decisions as a social forager. *Trends in Ecol. Evol.* 3(12): 325-331.
- MILINSKI, M., and G. A. PARKER. 1991. Competition for resources. p. 137-168. *In* J. R. Krebs and N. B. Davies [eds.] *Behavioural Ecology. An Evolutionary Approach*. 3rd edition. Blackwell Scientific Pub., Oxford.
- MORAN, P. A. P. 1951. A mathematical theory of animal trapping. *Biometrika*, 38: 307-311.
- MORANTZ, D. L., R. K. SWEENEY, C. S. SHIRVELL, and D. A. LONGARD. 1987. Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 44: 120-129.
- MOREAU, G., and L. LEGENDRE. 1979. Relation entre habitat et peuplements de poissons: essai de définition d'une méthode numérique pour des rivières nordiques. *Hydrobiologia* 67: 81-87.
- MORRIS, D. W. 1988. Habitat-dependent population regulation and community structure. *Ecol. Evol.* 2: 253-269.
- MOSER, M. E. 1988. Limits to the numbers of grey plovers *Pluvialis squatarola* wintering on British estuaries: An analysis of long-term population trends. *J. Applied Ecology* 25: 473-485.

- MURRAY, A. R. 1958. A direct-current electrofishing apparatus using separate excitation. *Can. Fish Cult.* 23: 27-32.
- MURRAY, A. R. 1968a. Smolt survival and adult utilization of Little Codroy River, Newfoundland, Atlantic salmon. *J. Fish. Res. Board Can.* 25: 2165-2218.
- MURRAY, A. R. 1968b. Estuarine net counting fence for trapping Atlantic salmon. *Trans. Am. Fish. Soc.* 97: 282-286.
- MURRAY, A. R. 1968c. Numbers of Atlantic salmon and brook trout captured at the Little Codroy River, Newfoundland, counting fence and auxiliary traps, 1954-1963. *Fish. Res. Board Can. Tech. Rep.* 84: 135 p.
- MURRAY, A. R. 1968d. Some climatic and geomorphic aspects of the Little Codroy river, Newfoundland. *Fish. Res. Board Can. Tech. Rep.* 98: 185 p.
- MYERS, R. A. 1984. Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 41(9): 1349-1353.
- MYERS, R. A. 1992. Population variability and the range of cod, haddock and herring in the North Atlantic. Manuscript.
- MYERS, R. A., and P. PÉPIN. 1986. The estimation of population size from research surveys using regression models. *ICES C.M.*1986/D:9
- MYERS, R. A., and J. A. HUTCHINGS. 1986. Selection against parr maturation in Atlantic salmon. *Aquaculture*, 53: 313-320.
- MYERS, R. A., J. A. HUTCHINGS, and R. J. GIBSON. 1986. Variation in male parr maturation within and among populations of Atlantic salmon, *Salmo salar*. *Can. J. Fish. Aquat. Sci.* 43: 1242-1248.
- NACHMAN, G. 1981. A mathematical model of the functional relationship between density and spatial distribution of a population. *J. Anim. Ecol.* 50: 453-460.
- NEWTON, I., and M. MARQUISS. 1986. Population regulation in the sparrowhawks. *J. Anim. Ecol.* 55: 463-480.
- OKSANEN, T., L. OKSANEN, and S. D. FRETWELL. 1992. Habitat selection and predator-prey dynamics. *Trends in Ecol. Evol.* 7 (9): 313.
- ORIAN, G. H., and J. F. WITTENBERGER. 1991. Spatial and temporal scales in habitat selection. *Am. Nat.* 137 (suppl.):S29-S49.

- OTIS, D. L., K. P. BURNHAM, G. C. WHITE and D. R. ANDERSON. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monograph 62. The Wildlife Society, Inc. Washington, DC. 135 p.
- PARKER, G. A., and W. J. SUTHERLAND. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. Anim. Behav. 34: 1222-1242.
- PAYNE, C. D. 1986. The GLIM system, Release 3.77. Royal Statistical Society. London, UK.
- PETERSON, N. P., and C. J. CEDERHOLM. 1984. A comparison of the removal and mark-recapture methods of population estimation for coho salmon in small streams. N. Am. J. Fish. Manage. 4: 99-102.
- PIELOU, E. C., 1977. Mathematical ecology. John Wiley and Sons, New York, NY. 385 p.
- PIMM, S. L., M. L. ROSENZWEIG, and W. MITCHELL. 1985. Competition and food selection: field tests of a theory. Ecology 66: 798-807.
- POLLOCK, K. H. 1991. Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: Past, present and future. J. Am. Stat. Ass. 86(413): 225-238.
- POLLOCK, K. H., J. E. HINES and J. D. NICHOLS. 1984. The use of auxiliary variables in capture-recapture and removal experiments. Biometrics 40: 329-340.
- PRESTON, F. W. 1948. The commonness and rarity of species. Ecology 29: 254-283.
- PROUZET, P. 1978. Relationship between density and growth of Atlantic salmon reared in nursery streams in natural conditions. ICES, C.M. 1978/M:13, 14 p.
- PUCKETT, K.J. and L. M. DILL. 1985. The energetics of territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Behaviour 92: 97-111.
- PULLIAM, H. R., and B. J. DANIELSON. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am. Nat. 137(Suppl.): S50-S66.
- RALEIGH, R. F., and C. SHORT. 1981. Depletion sampling in stream ecosystems: Assumptions and techniques. Prog. Fish-Cult. 43(3): 115-120.

- RANDALL, R. G. 1982. Emergence, population densities, and growth of salmon and trout fry in two New Brunswick streams. *Can. J. Zool.* 60: 2239-2244.
- REES, M., 1993. Null models and dispersal distributions: a comment on an article by Caley. *Am. Nat.* 141(5): 812-815.
- REYNOLDSON, T. B. 1957. Population fluctuations in *Urceilaria mitra* (peritricha) and *Enchytraeus albidus* (oligochaeta) and their bearing on regulation. *Cold Spring Harbour Symposia on Quantitative Biology*, 22: 313-327.
- RICE, J. C., R. D. OHMART, and B. W. ANDERSON. 1986. Limits in a data-rich model: Modelling experience with habitat management on the Colorado River. p. 79-86 *In* J. Verner, M. L. Morrison, and C. J. Ralph [eds.] *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. U. Wisconsin Press, Madison.
- RICHARDS, O. W., and T. R. E. SOUTHWOOD. 1968. The abundance of insects: Introduction. p.1-7. *In* T. R. E. Southwood [ed.] *Insect abundance*. Symposium of the Royal Entomological Society No. 4. Blackwell Scientific Pub., Oxford.
- RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fish. Res. Board Can. Bull.* 191, 382 p.
- RIMMER, D. M., PAIM, U., and R. L. SAUNDERS. 1983. Changes in the selection of microhabitat by juvenile Atlantic salmon (*Salmo salar*) at the summer autumn transition in a small river. *Can. J. Fish. Aquat. Sci.* 41: 329-332.
- ROSENZWEIG, M. L. 1985. Some theoretical aspects of habitat selection. p. 517-540 *In* M. L. Cody [ed.] *Habitat Selection in Birds*. Academic Press Inc., Orlando, FL.
- ROSENZWEIG, M. L. 1991. Habitat selection and population interactions: the search for mechanism. *Am. Nat.* 137(Suppl.): S5-S28.
- ROSENZWEIG, M. L., and Z. ABRAMSKY. 1985. Detecting density-dependent habitat selection. *Am. Nat.* 126: 405-417.
- ROUTLEDGE, R. D. 1989. The removal method for estimating natural populations: Incorporating auxiliary information. *Biometrics* 45: 111-121.
- SANTANDER, H., P. E. SMITH, and J. ALHEIT. 1982. Determination of sampling effort required for estimating egg production of anchoveta, *Engraulis ringens*, off Peru. *Instituto del Mar del Peru, Bull* 7, 18 p.

- SAS INSTITUTE INC. 1985. SAS User's guide: Statistics, Version 5 Edition. Cary, NC, USA.
- SAUNDERS, R. L. 1981. Atlantic salmon (*Salmo salar*) stocks and management implications in the Canadian Atlantic Provinces and New England, USA. *Can. J. Fish. Aquat. Sci.* 38: 1612-1625.
- SAUNDERS, R. L. 1986. The thermal biology of Atlantic salmon: influences of temperature on salmon culture with particular reference to constraints imposed by low temperature. *Rep. Inst. Freshwater Res. Drottningholm*, 63: 77-90.
- SCHNUTE, J. 1983. A new approach to estimating populations by the removal method. *Can. J. Fish. Aquat. Sci.* 40: 2153-2169.
- SHARP, G. D. 1980. Colonization: Modes of opportunism in the ocean. p. 143-166 *In* G. D. Sharp [ed.] Workshop on the effects of environmental variation in the survival of larval pelagic fishes. UNESCO Intergovernmental Oceanographic Commission, Workshop Report 28.
- SLANEY, P. A., and T. G. NORTHCOTE. 1974. Effects of prey abundance on density and territorial behavior of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. *J. Fish. Res. Board Can.* 31: 1201-1209.
- SOKAL, R. R., and F. J. ROHLF. 1981. *Biometry*. W. H. Freeman and Company. 2nd edition. San Francisco, CA. 859 p.
- SOLOMON, D. J. 1985. Salmon stock and recruitment and stock enhancement. *J. Fish. Biol.* 27 (Suppl. A): 45-57.
- SOMS, A. P. 1985. Simplified point and interval estimation for removal trapping. *Biometrics* 41: 663-668.
- SNEDECOR, G. W., and W. G. COCHRAN. 1967. *Statistical Methods*. 6th ed. Iowa State Univ. Press, Ames, Iowa. 593 p.
- STUBBS, M. 1977. Density-dependence in the life-cycles of animals and its importance in K- and r- strategies. *J. Anim. Ecol.* 46: 677-688.
- SUTHERLAND, W. J., and G. A. PARKER. 1992. The relationship between continuous input and interference models of ideal free distributions with unequal competitors. *Anim. Behav.* 44(2): 345-355.

- SWAIN, D. P. 1993. Density-dependent variation in the depth and temperature distribution of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. CAFSAC Working Paper 93/60.
- SYMONS, P. E. K. 1979. Estimated escapement of Atlantic salmon (*Salmo salar*) for maximum smolt production in rivers of different productivity. J. Fish. Res. Board Can. 36: 132-140.
- SYMONS, P. E. K., and M. HELAND. 1978. Stream habitats and behavioral interactions of underyearling and yearling Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 35: 175-183.
- TALBOT, A. J. 1983. A test of habitat selection theory using the response of guppies, *Poecilia reticulata* (Pisces: Poeciliidae), to food and oxygen availability. M.Sc. thesis, McGill University, Montréal, QC.
- TALBOT, A. J., and R. J. GIBSON. 1990. Habitat utilization by juvenile Atlantic salmon in Newfoundland rivers. CAFSAC Research Document 90/118.
- TALBOT, A. J., and R. J. GIBSON. 1991. Production of juvenile Atlantic salmon in Newfoundland rivers: Test of habitat models using a structural approach. CAFSAC Working Document 91/22.
- TAYLOR, L. R. 1986. Synoptic dynamics, migration and the Rothamsted insect survey. J. Anim. Ecol. 55: 1-38.
- TAYLOR, L. R., and I. P. WOIWOD. 1980. Temporal stability as a density-dependent species characteristic. J. Anim. Ecol. 49: 209-244.
- TAYLOR, L. R., I. P. WOIWOD, and J. N. PERRY. 1978. The density dependence of spatial behaviour and the rarity of randomness. J. Anim. Ecol. 47: 383-406.
- THORPE, J. E. 1986. Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period influences and conflicts with smolting. p. 7-14. In D. J. Meerburg [ed.] Salmonid age at maturity. Can. Spec. Pub. Fish. Aquat. Sci. 89.
- THORPE, J. E., and R. I. G. MORGAN. 1980. Growth rate and smolting-rate of progeny of male Atlantic salmon parr, *Salmo salar* L. J. Fish. Biol. 1: 451-460.
- THORPE, J. E., C. TALBOT, and C. VILLAREAL. 1982. Bimodality of growth and smolting in Atlantic salmon, *Salmo salar* L. Aquaculture 28: 123-132.

- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47(4): 893-901.
- WASER, P. M. 1985. Does competition drive dispersal? *Ecology* 66: 1170-1175.
- WERNER, E. E, J. F. GILLIAM, D. J. HALL, and G. G. MITTELBACH. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 191: 1540-1548.
- WERNER, E. E., and D. J. HALL. 1976. Niche shifts in sunfishes: experimental evidence and significance. *Science (Washington, D.C.)* 191: 404-406.
- WHITHAM, T. G. 1980. The theory of habitat selection: Examined and extended using *Pemphigus* aphids. *Am. Nat.* 115(4): 449-466.
- WHITTAKER, R. H. 1965. Dominance and diversity in land plant communities. *Science* 147: 250-259.
- WIENS, J. A. 1981. Scale problems in avian censusing. *Studies in Avian Biol.* 6: 513-521.
- WIENS, J. A., and J. J. ROTENBERRY. 1981. Censusing and the evaluation of avian habitat occupancy. *Studies in Avian Biol.* 6: 522-532.
- WIENS, J. A., J. T. ROTENBERRY, and B. VAN HORNE. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effect of spatial scale. *Oikos* 48: 132-147.
- WILKINSON, L. 1988. SYSTAT: The system for statistics. Systat Inc., Evanston, IL.
- WINER, B. J. 1971 *Statistical principles in experimental design.* McGraw-Hill Book Company, 2nd edition. New York, NY. 907 p.
- ZACKS, S. 1971. *The theory of statistical inference.* John Wiley and Sons, New York, NY.
- ZIPPIN, C. 1956. An evaluation of the removal method of estimating animal populations. *Biometrics* 12: 163-189.
- ZIPPIN, C. 1958. The removal method of population estimation. *J. Wildlife Manage.* 22(1): 82-90.