



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 *Voire 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

**TEMPERATURE AND THE DISTRIBUTION OF MATURE FEMALE
LOBSTERS (*Homarus americanus* Milne Edwards) OFF CANSO, N. S.**

by

Raúl Alejandro Ugarte

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

at

Dalhousie University
Halifax, Nova Scotia, Canada

September 1994

© Copyright by Raúl Alejandro Ugarte, 1994



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 *Voire 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 ACCORDE UNE LICENCE IRREVOCABLE ET NON EXCLUSIVE PERMETTANT A LA BIBLIOTHEQUE NATIONALE DU CANADA DE REPRODUIRE, PRETER, DISTRIBUER OU VENDRE DES COPIES DE SA THESE DE QUELQUE MANIERE ET SOUS QUELQUE FORME QUE CE SOIT POUR METTRE DES EXEMPLAIRES DE CETTE THESE A LA DISPOSITION DES PERSONNE INTERESSEES.

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 PROPRIETE DU DROIT D'AUTEUR QUI PROTEGE SA THESE. NI LA THESE NI DES EXTRAITS SUBSTANTIELS DE CELLE-CI NE DOIVENT ETRE IMPRIMES OU AUTREMENT REPRODUITS SANS SON AUTORISATION.

ISBN 0-315-98948-3

Canada

Name RAUL ALEJANDRO UGARTE

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.

E C O L O G Y

0329

U·M·I

SUBJECT TER: A

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 0316
 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
 General 0679
 Ancient 0289
 Linguistics 0290
 Modern 0291
 Literature
 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
 General 0318
 Biblical Studies 0321
 Clergy 0319
 History of 0320
 Philosophy of 0322
 Theology 0469

SOCIAL SCIENCES

American Studies 0323
 Anthropology
 Archaeology 0324
 Cultural 0326
 Physical 0327
 Business Administration
 General 0310
 Accounting 0272
 Banking 0770
 Management 0454
 Marketing 0338
 Canadian Studies 0385
 Economics
 General 0501
 Agricultural 0503
 Commerce-Business 0505
 Finance 0508
 History 0509
 Labor 0510
 Theory 0511
 Folklore 0358
 Geography 0366
 Gerontology 0351
 History
 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
 General 0615
 International Law and Relations 0616
 Public Administration 0617
 Recreation 0814
 Social Work 0452
 Sociology
 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
 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
 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
 General 0786
 Medical 0760
 EARTH SCIENCES
 Biogeochemistry 0425
 Geochemistry 0996

Geodesy 0370
 Geology 0372
 Geophysics 0373
 Hydraulics 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
 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
 Chemistry
 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
 General 0605
 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
 Applied Mechanics 0346
 Computer Science 0984

Engineering
 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
 Personal 0625
 Physiological 0989
 Psychobiology 0349
 Psychometrics 0632
 Social 0451



DALHOUSIE UNIVERSITY

FACULTY OF GRADUATE STUDIES

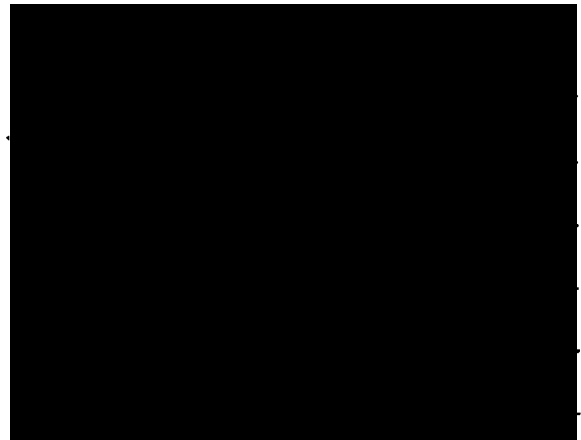
The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "Temperature and the Distribution of Mature Female Lobsters (*Homarus americanus* Milne Edwards) Off Canso, N.S."

by Raul A. Reyes Ugarte

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

Dated October 12, 1994

External Examiner
Research Supervisor
Examining Committee



DALHOUSIE UNIVERSITY

DATE: October 27th, 1994

AUTHOR: Raul Alejandro Ugarte

TITLE: Temperature and the Distribution of Mature Females


Lobsters (Homarus americanus Milne Edwards) off

Canso, N.S.

DEPARTMENT OR SCHOOL: Biology

DEGREE: Ph. D. CONVOCATION: Spring YEAR: 1995

Permission is herewith granted to Dalhousie University to circulate and to have copied for non-commercial purposes, at its discretion, the above title upon the request of individuals or institutions.



Signature of Author

THE AUTHOR RESERVES OTHER PUBLICATION RIGHTS, AND NEITHER THE THESIS NOR EXTENSIVE EXTRACTS FROM IT MAY BE PRINTED OR OTHERWISE REPRODUCED WITHOUT THE AUTHOR'S WRITTEN PERMISSION.

THE AUTHOR ATTESTS THAT PERMISSION HAS BEEN OBTAINED FOR THE USE OF ANY COPYRIGHTED MATERIAL APPEARING IN THIS THESIS (OTHER THAN BRIEF EXCERPTS REQUIRING ONLY PROPER ACKNOWLEDGEMENT IN SCHOLARLY WRITING) AND THAT ALL SUCH USE IS CLEARLY ACKNOWLEDGED.

**a Marisol,
Rocio y
Camila**

TABLE OF CONTENTS

Table of Contents.....	v
List of Figures.....	ix
List of Tables.....	xii
Abstract.....	xiii
Acknowledgements.....	xiv
General Introduction	1
CHAPTER I	
Female lobster distribution and reproductive condition in relation to the physical habitat of the Canso fishing ground.....	5
1.1 Introduction.....	5
1.2 General area description and fishery.....	7
1.3 Methods.....	9
1.3.1 Distribution evaluation.....	9
1.3.2 Ovary and embryo development.....	10
1.4 Results.....	11
1.4.1 Temperature regimes.....	11
1.4.2 Fishing depth.....	12
1.4.3 Ovarian females.....	12
Catch per trap.....	12
Size distribution.....	13
Ovary development.....	13
1.4.4 Berried females.....	14
Distribution and abundance.....	14
Embryo stage.....	15
1.4.5 Size at maturity.....	15

1.5 Discussion.....	16
1.5.1 Trapping as a sampling tool.....	16
1.5.2 Seasonal depth variation in the fishery.....	16
1.5.3 Physiological and reproductive condition of the females.....	18

CHAPTER II

A field study of late stage embryo development and ovigerous female lobster <i>Homarus americanus</i> movement in relation to temperature.....	36
2.1 Introduction.....	36
2.1.1 Embryonic cycle.....	37
2.2 Materials and methods.....	38
2.2.1 Caged females.....	38
2.2.2 Free ranging females.....	39
2.3 Results.....	40
2.3.1 Temperature.....	40
2.3.2 Embryo condition at the start of the study.....	41
2.3.3 Caged females.....	41
2.3.4 Free range females.....	43
2.3.5 Commercial fishing survey analysis.....	44
2.4 Discussion	44
2.4.1 Embryonic development and temperature regime.....	44
2.4.2 Berried female movement on the Canso ground.....	45
2.4.3 Comparisons with other inshore populations.....	46
2.4.4 Synchronization with other physiological and reproductive.....	
processes.....	48
2.5 Summary.....	49

CHAPTER III

Ovarian development and movement of mature female lobsters <i>Homarus americanus</i> in relation to temperature.....	63
3.1 Introduction.....	63
3.2 Materials and methods.....	65
3.2.1 Caged females.....	66
3.2.2 Free ranging females.....	67
3.3 Results.....	68
3.3.1 Temperature regimes.....	68
3.3.2 Cage experiments.....	68
Ovary development.....	68
Spawning Rate.....	69
Newly extruded embryos.....	70
3.3.3 Distribution and Movement of Tagged Females.....	70
Movement.....	70
Ovarian development.....	71
3.4 Discussion.....	72
3.4.1 Caged experiments.....	72
3.4.2 Female distribution and movement.....	74
3.4.3 Animal size and ovary maturation relationship.....	76
3.4.4 Ovarian maturation and larval development.....	77
3.5 Summary.....	78

CHAPTER IV

General discussion.....	93
4.1 Distribution, reproductive condition, and movement of female lobsters in Canso.....	94
4.2 Synchronization of reproductive and molting processes in the Canso area...98	

4.3 Descriptive model of the distribution of Canso lobster population.....	101
4.4 Lobster recruitment collapse and landing variability along Nova Scotia's eastern shore.....	104
4.4.1 Recruitment overharvesting.....	104
4.4.2 Canso Causeway effect.....	106
4.4.3 The Harding et al's (1983) Hypothesis - eastern shore bays as reproductive refuges?.....	107
APPENDIX 1	
Embryonic cycle of <i>Homarus americanus</i> incubated in situ.....	110
APPENDIX 2	
Newly extruded egg bearing female distribution on the Canso ground.....	114
APPENDIX 3	
Ovigerous Female <i>Homarus americanus</i> Distribution in Jeddore Area (44° 45' N, 63° 00' W), N.S. eastern shore.....	124
APPENDIX 4	
Winter trapping survey for berried females in the Canso ground and Chadabucto Bay..	134
APPENDIX 5	
Recruitment overharvesting in eastern Nova Scotia lobster <i>Homarus americanus</i> stock? Support for Robinson's (1979) hypothesis.....	136
APPENDIX 6	
Statistical tables.....	151
REFERENCES.....	161

LIST OF FIGURES

Fig. 1.1.	Map of Nova Scotia showing the Canso fishing ground location	8
Fig. 1.2.	Map of Canso showing different fishing areas	22
Fig. 1.3.	Temperature regimes of the different fishing areas in Canso ground	23
Fig. 1.4.	Mean fishing depth during the trapping survey spring/summer 1992	24
Fig. 1.5.	CPTH of ovarian females on the different fishing areas of Canso	25
Fig. 1.6.	CPTH (kg) of legal lobsters in relation to water temperature	26
Fig. 1.7.	Relationship between CPTH and three different bottom temperatures	27
Fig. 1.8.	Mean size (CL) of ovarian females captured on the different fishing areas	28
Fig. 1.9.	Size frequency of ovarian females on the different fishing areas	29
Fig. 1.10.	Ovary condition of lobsters on the different fishing areas of Canso	30
Fig. 1.11.	CPTH of berried females on the different fishing areas of Canso ground	31
Fig. 1.12.	CPTH of berried females in relation to temperature	32
Fig. 1.13.	Mean embryo maturity (PEI) during spring/early summer among the areas	33
Fig. 1.14.	Frequency of hatching females during early July on the shallow areas	34
Fig. 1.15.	Size at maturity on the inner and outer areas of Canso fishing ground	35
Fig. 2.1.	Map of the Canso lobster ground showing the cage sites	52
Fig. 2.2.	The design of the experimental cages in the field	53
Fig. 2.3.	Temperature regimes at the Canso study site	54
Fig. 2.4.	Mean seasonal profile on the Canso fishing ground during 1992	54
Fig. 2.5.	Daily variation in temperatures at the experimental site	54
Fig. 2.6.	Temperature and embryonic development in the cage experiment	55
Fig. 2.7.	Frequency of caged females with hatched embryos during 1991-92	56
Fig. 2.8.	Relationship between female size (CL) and embryo maturation in May	57
Fig. 2.9.	Movement of berried females in Canso ground	58
Fig. 2.10.	Mean depth of tagged and recaptured berried females in the Canso ground	59

Fig. 2.11. Rate of embryonic development of caged and free-ranging females	60
Fig. 2.12. Embryonid development of berried females from commercial catches	61
Fig. 2.13. Molt frequency of caged berried females in relation to temperature	62
Fig. 3.1. Map of the Canso ground showing the cages site	81
Fig. 3.2. Temperature regime at the 3 and 17 m caged sites during the study period	82
Fig. 3.3. Frequency of spawned females at 3 and 17 m	83
Fig. 3.4. Temperature regimes and spawning period at 3 and 17 m	83
Fig. 3.5. Development of newly extruded embryos at 3 and 17 m	84
Fig. 3.6. Development of newly extruded embryos and temperature regimes	84
Fig. 3.7. Depth of recapture of tagged ovarian females	85
Fig. 3.8. Movement of ovarian females tagged on the outer area of the Canso ground	86
Fig. 3.9. Relationship between tagging depth and rate of movement	87
Fig. 3.10. Relationship between depth of capture (commercial catch) and female size	88
Fig. 3.11. PTG condition of free-range lobsters at tagging (May 20 th - 27 th)	89
Fig. 3.12. Ovarian development of caged and free range lobsters in July	90
Fig. 3.13. Relationship between size and PTG stage of free range lobsters in July	91
Fig. 3.14. Relationship between depth of capture and PTG stage for free range lobsters in July	92
Fig. 4.1. Temperature regime differences between Canso and Bay of Fundy	96
Fig. 4.2. Reproductive cycle of a female lobster in relation to temperature in Canso area	99
Fig. 4.3. Descriptive model of lobster distribution during its life history in Canso area	103
Fig. A.1. Embryonic cycle and temperature regime in the Canso ground	113
Fig. A.2.1. Canso map showing trap set areas during charter in late July 1991	118
Fig. A.2.2. Capture composition during charter in late July 1991	119
Fig. A.2.3. Proportion of new and old egg bearing females during charter	120
Fig. A.2.4. Mean size (CL) of the different lobster stages captured during charter	121
Fig. A.2.5. Mean depth distribution of new and old egg bearing females during charter	122

Fig. A.2.6. Relationship between female size and depth distribution of newly extruded females	123
Fig. A.3.1. Map of Jeddore area and its location in Nova Scotia	128
Fig. A.3.2. Depth distribution of ovigerous females with old and newly extruded eggs	129
Fig. A.3.3. Bottom temperatures inside and outside of Jeddore Harbour	130
Fig. A.4.1. Map of Canso showing winter trapping locations	134
Fig. A.4.2. Temperature profile during February 18, 1992, in Canso area	135
Fig. A.5.1. Map of Nova Scotia showing study sites and their respective LFA	147
Fig. A.5.2. Size at 50% maturity of female lobsters at Canso and Jeddore	148
Fig. A.5.3. Size frequency of ovigerous females at Canso and Jeddore	149
Fig. A.5.4. Size frequency of ovarian females before and after the fishing season at both Jeddore and Canso	150

LIST OF TABLES

Table 1. Number of traps, berried and ovarian females and the average depth of fishing during the fishing surveys	21
Table 2.1. Mean PEI and female size of both the wild stock and cages females in May	50
Table 2.2. Pearson-r correlation matrix between variables of tagged berried females	51
Table 3.1. Lobster ovary development in caged lobsters	79
Table 3.2. Pearson-r correlation matrix between variables of tagged ovarian females	80
Table A.5.1. CPTH of ovigerous and legal lobsters from Canso and Jeddore areas	145
Table A.5.2. Number of potentially ovigerous females and egg production in Canso and Jeddore	146
Tables with statistical procedures and results for Chapters I, II and III	152-160

ABSTRACT

A study on the reproductive ecology of mature females lobsters (*Homarus americanus*, Milne Edwards) was carried out on Canso N. S. lobster grounds during 1991 and 1992. These waters are cold with six months at $< 4^{\circ}\text{C}$ and a brief period of three months or so, with temperatures $> 10^{\circ}\text{C}$. During the summer prevailing southwest winds produce upwelling events of variable intensity, which can drop surface temperatures to as low as 5°C . These events co-occur with important phases of lobster reproduction such as embryo maturation and hatching, larval development, adult molting and mating, ovary development and egg extrusion. In addition to the thermal instability of the warm water period, the Canso lobster ground has a highly variable bottom topography creating a range of habitats and thermal regimes over short distances.

Surveys made with the help of commercial fishermen showed that during late spring/early summer, mature females are not homogeneously distributed over the grounds, but associated with certain physical features and warm shallow waters. A tag/recapture study showed that females with maturing ovaries and embryos move rapidly in mid-to late spring to the shallows ($< 10\text{ m}$). Using the Perkins Eye Index and cement gland techniques on animals from the commercial survey, from the tag/recapture study and on animals caged at depth (3 m to 17 m) it was shown that the warm shallow waters accelerate both ovary and embryo maturation. The time available in a typical year to complete the reproductive and early recruitment processes is brief, thus this spring short-term movement reduces the risk of a year-class failure. The study's results are then used to model life history distribution in relation to spatial and temporal steady state variables, and to add new insights into the Canso Causeway closure and the collapse of the eastern shore lobster fishery during the 1970s.

ACKNOWLEDGMENTS

I am particularly grateful to Dr. John Pringle for his strong support beyond the duties of a supervisor. He encouraged me to carry out this research and provided guidance throughout the study. Finally, he reviewed (patiently) many drafts of my thesis. I extend my gratitude to the rest of the Pringles, especially Joan, who opened their home and heart to me and my family during our period in Canada. My arrival in Canada was made possible by an IDRC scholarship for a one year training program in the Department of Fisheries and Oceans. My gratitude is also extended to Dr. Bernabé Santelices for his initial support and encouragement in my trip to Canada. During my stay in the Halifax Lab, my life was also enriched with the friendship of other terrific people; Glyn Sharp, who as a Canadian brother, kept my sanity during the hard periods of my life as a graduate student; Bob Semple, my adventure buddy who was always ready for anything I needed; Rui Santos and Put Ang, who became part of my family; Christiane Hudon, who supported and refined my crazy ideas in the beginning of my study and John Tremblay, who also reviewed and commented on some of the chapters. This study was possible in great extent due to the technical assistance of Ron Duggan who facilitated the operation and interaction with the fishermen in Canso. The fishermen of Canso (especially Mike Newel, Steve Meade and Pat Parker) were instrumental in providing logistic support during the course of my study. Ernie Bond kept the tagged lobsters recaptured by the fishermen. Noel Lumsden helped me with some of the dives. The members of my committee were at all times encouraging and supportive. Drs. Ron O'Dor, Gary Newkirk, and Gareth Harding reviewed drafts and provided valuable feedback and support throughout all stages of the study. Stan Cobb (my external examiner) gave me valuable suggestions to improve the final draft. Computer and Statistical assistance were provided by Dave Swetnam, Chris Hunter and

Jerry Black, and by Bob Rodgers. Thanks to Vikki Clayton, Bettyann Field, Sheila Shellnutt and Michele Covey who were always ready to provide clerical help. Dave Aiken and Susan Waddy's technical advice were key to the second half of my work. I wish to express my appreciation to the Department of Fisheries and Oceans for providing me with financial support. Mrs. Karen McIntyre from Financial Services at Dalhousie spent days and days dealing with my scholarship. I also received financial support from Lett Bursary of Dalhousie University.

I would like to thank this wonderful country, Canada, that gave me freedom and peace as I never felt before and where I could experience the beauty of its nature so close to my home.

Finally, my eternal gratitude to Marisol who fulfilled my family role during my long absences in the field and while I was writing this thesis. My apologies to my daughters, Rocio and Camila for all these years stolen from their beautiful lives. Thank you all for your patience and love.

GENERAL INTRODUCTION

The American lobster, *Homarus americanus* (Milne-Edwards), is a long-lived (> 40 years) crustacean of the order Decapoda, Family Nephropidae. It is found along the east coast of North America, from North Carolina to southern Labrador, Newfoundland. Commercial fisheries extend from northern Newfoundland to northern New Jersey (Herrick, 1911). The major centers of commercial abundance, however, are located within the Gulfs of Maine and St. Lawrence, and along inner Scotian Shelf waters, where over 90% of the inshore landings occur (Wilder 1954). An offshore stock occurs along the outer edge and upper slope of the continental shelf between The Gully, Sable Island and the mouth of Delaware Bay (Shroeder 1959). *H. americanus* has been heavily exploited in the NW Atlantic for well over 100 years, but is yet one of the most economically important fisheries. Because of the lobster's commercial importance, interest in its biology has been growing steadily over time, and is one of the best understood of aquatic invertebrates. The bulk of the available information is in the fields of physiology, biochemistry, and neurobiology. A large information gap still exists in the area of ecology and natural behaviour of heavily exploited stocks.

Movement studies of the American lobster have been carried out for almost a century (Haakonsen and Anoruo 1994). Deep-shallow water seasonal migrations have been observed for mature lobsters on the continental shelf (Cooper and Uzmann 1971, Uzmann et al 1977, Lund 1979, Fogarty et al 1980, Campbell et al 1984, Pezzack and Duggan 1986), in the Bay of Fundy (Campbell and Stasko 1986) and for ovigerous females off Grand Manan Island (Campbell 1986). As lobsters are migrating into warmer waters, these movements have been linked to reproductive and growth events (Cooper and Uzmann 1971, Campbell and Stasko 1986). Campbell (1986), provided evidence to

support the hypothesis that deep/shallow migrations of ovigerous females are necessary for the completion of the embryonic cycle off Grand Manan Is., N.B., Canada.

Most inshore lobster stocks are considered non-migratory, typically moving < 12 km (Cooper and Uzmann 1980, Miller et al 1989). Some short seasonal movements observed for lobsters in Newfoundland (Ennis 1983, Ennis 1984a) were associated with storm turbulence. Magdalen Island lobsters moved into lagoons where a high incidence of molting animals were observed (Templeman 1936, Munro and Thierrault 1983). It has been argued that these short term movements of inshore lobsters are not associated with reproductive events.

Nova Scotia's eastern shore is one of the least studied areas in terms of lobster ecology (Pringle and Burke 1993). Landings are unstable when compared with nearby stocks (Duggan and Pringle 1988) and in the late 1970's the fishery was deemed collapsed (Robinson 1980). Four disparate hypotheses reflected the shallowness of understanding of lobster ecology by fisheries scientists (Pringle and Burke 1993). Low temperature was suggested as one of the causal mechanisms for the decline in recruitment (Harding et al 1983a). The eastern shore presents a cold and highly variable temperature regime (this study) as a consequence of mixing (El Sabh, 1977) and frequent upwelling during the warm water season (Petrie et al 1987). Though the stock has recovered since the collapse, it is still below 20% of the historical peak.

The eastern shore lobster stock exhibits considerable variability throughout its distribution. Pringle and Duggan (1984,1985) demonstrated the eastern shore not to be a homogeneous fishery as earlier portrayed (Robinson 1979; Campbell and Robinson 1983); catch per unit of effort (CPUE) is higher for the eastern portion of the stock. Moreover, log book data

kept by volunteer fishermen shows the abundance of berried females, based on catch per trap haul, decreases from northeast to southwest (¹ Duggan unpub. data).

In order to increase our knowledge of the ecology of the lobster along the eastern coast of Nova Scotia, a study was initiated in the early 1980's by Department of Fisheries and Oceans personnel. It was shown that most lobsters move < 12 km annually (Duggan and Pringle 1988, Jarvis 1989, Miller et al 1989). There was some anecdotal evidence of seasonal shoreward movement of lobster along the eastern shore. In some areas, fishermen begin trapping lobster during spring in waters 30-40 m deep and gradually move their traps shoreward (to depths < 10 m) until late spring/early summer. Many fishermen believe this progressive change in apparent location of lobsters is due to a spring inshore migration. Duggan and Pringle (1988) found a high incidence of ovigerous females inside the protected waters of Jeddore Harbour during late summer/early fall of 1987. They speculated the harbour may be an important area for spawning, egg development, and larval hatching. Following this hypothesis, Jarvis (1979) tracked berried females in the area, but found no obvious reproductive advantage for lobster to move inside the Harbour. His model suggested embryo development could be completed successfully in open areas given the prevailing temperatures of the open coast. Others workers showed there was sufficient degree-days for larval development in surface waters (Moore et al 1986).

The present study examines the reproductive ecology of mature female lobsters (*Homarus americanus*) along the eastern shore of Nova Scotia. It was designed to assess the effect of temperature on aspects of the reproductive process, in particular the behavioural component (e.g. movement) that has evolved apparently to enhance larval survival in this hypothesized marginal climate (Harding et al 1983).

¹ R. Duggan. Senior lobster technician, Fisheries and Oceans Canada, Halifax. N. S.

The Canso N.S. lobster fishing ground (45° 20'N, 61° 00' W) (Fig. 1.1A) was chosen for study for the following reasons: 1) the grounds have the highest density of ovigerous females within the eastern shore stock; 2) the physical habitat is highly variable, and 3) the fishermen welcomed scientific research and were cooperative.

Chapter I describes the spatial and temporal pattern of distribution of both mature and juvenile female lobsters on the Canso lobster ground. The data were obtained from at-sea monitoring of commercial catches. The ground is divided into three areas based on depth, bottom topography, and water temperatures. Female distribution is discussed in relation to animal size, reproductive condition and physical oceanographic conditions. Chapter II assesses the effect of water temperatures on embryo development in their last period of incubation (late stage embryos) by caging berried females at two depths (3 m and 17 m), each having significantly different temperature regimes. Recaptured ovigerous females were used to assess temporal and spatial distributions. Chapter III assesses the effect of temperature on development of both ovaries and young embryos of caged and free-ranging females. The results of the experimental work (Chapter II and III) are discussed in relation to the observed natural distributions reported in Chapter I. A general discussion, Chapter 4, brings together the findings of the study including a descriptive model of the life cycle of the Canso lobster in relation to temporal, physical and spatial factors. Attempts are then made to provide new insights on long standing resource management problems that have been troubling the resource management team for years.

CHAPTER I

FEMALE LOBSTER DISTRIBUTION AND REPRODUCTIVE CONDITION IN RELATION TO THE PHYSICAL HABITAT OF THE CANSO FISHING GROUND.

1.1 Introduction

In lobster, as well as most of the marine crustacean species, habitat suitability is a function of the animal's physiological tolerance to physical factors and the presence of food, adequate substrate, predators and competitors. Juvenile and adult lobsters have different tolerances for certain factors, thus their distribution changes during the life cycle. This is typical of Panulirids; juvenile *Panulirus argus* and *P. cygnus* live the first two to five years in shallow habitats then move deeper as adults to reproduce (Chittleborough 1970, Davis 1976). Different reproductive requirements appear to determine adult lobster distribution. Ovigerous *P. argus*, for example move to areas with offshore currents to release their larvae (Buesa Mas 1970). In comparison to spiny lobster species, the distribution of the different stages of the American lobster and their physical requirements are less well known (Whale and Steneck 1992).

During the last half of this century, a considerable amount of information has been compiled from laboratory experiments, on the effect of physical factors on the physiology and reproductive processes of the American lobster. Temperature plays a dominant role in the reproductive and growth processes (Aiken and Waddy 1980). Laboratory based evidence suggests that, in some marginal habitats, lobsters could optimize their physiological and reproductive functions by moving seasonally to warmer areas. For example, it has been demonstrated that lobsters from Georges Bank's offshore canyons maintain themselves in 10° - 17°C waters by seasonal deep-shallow migrations (Cooper and Uzmann 1971). The same has been observed for mature lobsters in the Bay of Fundy (Campbell and Stasko 1986), and for ovigerous females off both the Grand Manan

(Campbell 1986, 1990) and Magdalen Islands (Templeman 1936, Munro and Therriault 1983). The common factor of all these migrations is the movement of animals to warmer environments throughout the year. Perhaps the only field study directly relating a physiological function with temperature in the American lobster, was that reported by Campbell (1986) in which he argued the need for deep-shallow migratory movement of ovigerous females for the maturation of embryos (but see Appendix I). Favorable "brood" areas for final embryo maturation and larval release were also described (Campbell 1990).

Inshore stocks along Nova Scotia's eastern shore appear non-migratory based on recent studies of Duggan and Pringle (1988) (see also a review by Miller et al 1989), basically moving < 12 km. There is some anecdotal evidence of seasonal shoreward movement of lobster along the eastern shore. In some areas, fishermen begin trapping lobster during spring in about 30-40 m of water. The traps are gradually moved shoreward (≤ 10 m of water) until late spring-early summer. Many fishermen believe this apparent progressive change in apparent lobster location is due to a spring inshore migration. However, Wilder and Murray (1958) interpreted similar trends in fishing pattern on Nova Scotia's south shore to the removal of legal-sized lobsters from shallow areas during the previous season and to warmer temperatures in the deeper waters in early spring thereby enhancing catchability. In Connecticut inshore stocks, however, short-term movement was correlated to temperature changes (Steward 1972).

Duggan and Pringle (1988) found a high incidence of ovigerous females in late summer/early fall, inside the large, protected Jeddore Harbour, N.S. However, while studying berried female movement in the same area Jarvis (1979), found no difference in lobster numbers between the inside and outside of the harbour. He further suggested there was no reproductive physiological advantage for lobsters to move inside.

The objective of this Chapter is to determine the distribution of mature, female lobsters in the Canso N. S. area (eastern shore), in relation to their physiological and reproductive condition.

1.2 General description of the area and fishery

The study area is located on the Canso (45° 20'N, 61° 00' W), Nova Scotia fishing grounds (Fig. 1.1A). These grounds consist of rocky inlets, channels, and reefs covering approximately 100 km² (Fig. 1.1B) with a granitic bedrock bottom interspersed with algal-covered boulders, pebbles and bivalve shells (Moore et. al. 1986). Channel walls and some reefs consist of layers of boulders, the interstices of which provide lobster shelter. The bottom topography is irregular, with large variations in water depth over short horizontal distances (Fig. 1.1C). Basins 20 to 30 m deep are numerous in the Derabies Island archipelago and depths up to 100 - 200 m are within 300 m eastward in Chedabucto Bay (Fig. 1B). The Bay maintains a cold mass of water ($\approx 2^{\circ}$ - 5° C) below 40 m depth year around (Appendix II; Fig. 2.4).

The fishing grounds support a moderate, limited-entry lobster trap fishery with about 22 boats fishing a 63 d open season, which begins about May 1, depending on weather and ice conditions (Pringle and Duggan, 1991). Early season trapping is concentrated in deep water, in about 10 - 40 m depth. Most fishermen gradually move their traps shoreward (<10 m), over the season. Mean annual fishing production has varied markedly over the last 15 years, ranging from 24 t in 1979 to 261 t in 1989, dropping again to 127 t in 1993 (Pringle et al 1993).

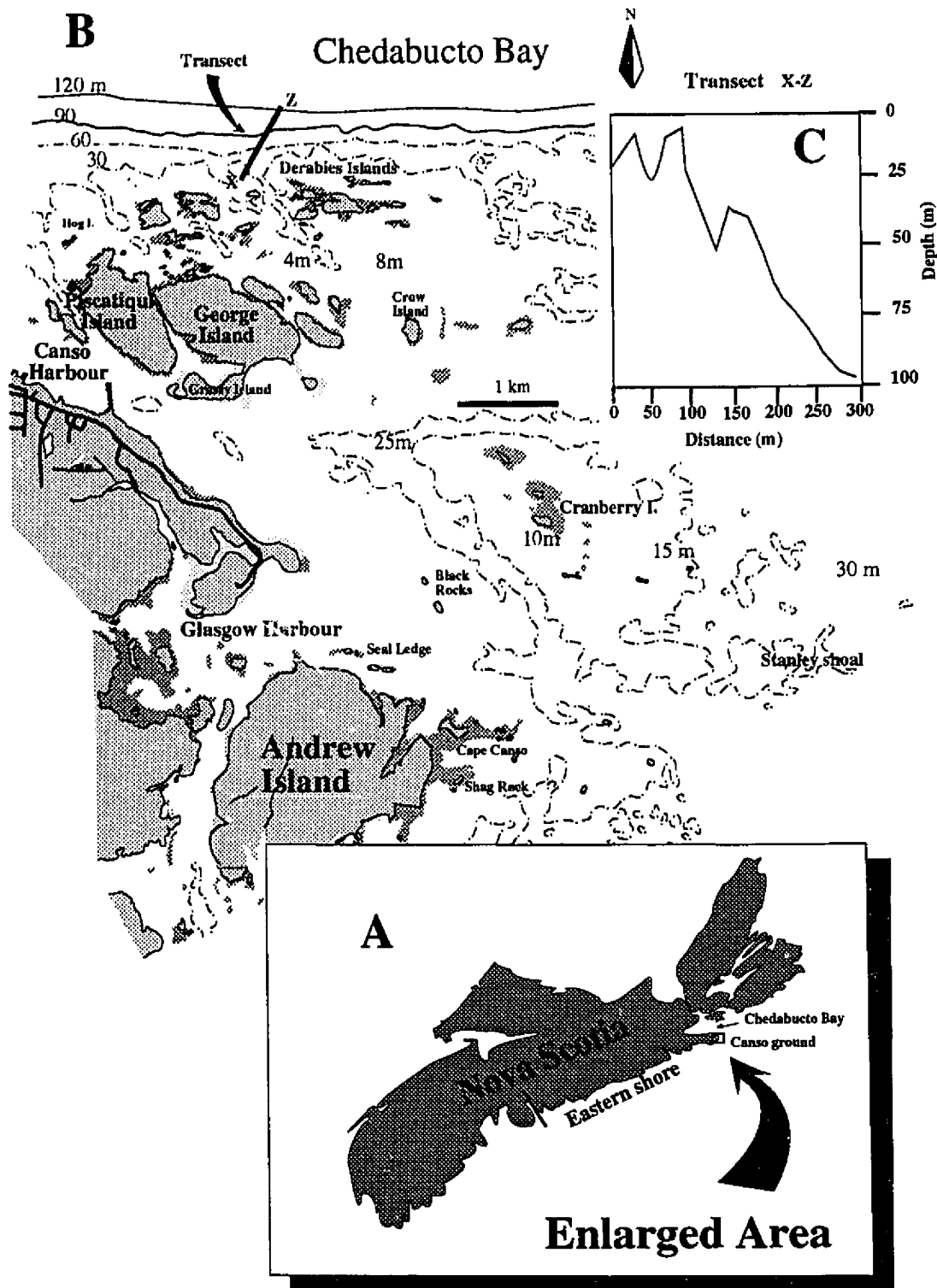


Figure 1.1. Chart of Nova Scotia (A), showing (B) the Canso ground and (C) a single profile of the bottom topography.

1.3 Methods

1.3.1 Distribution evaluation

The spring-summer distribution of the Canso area's lobster stock was assessed through at-sea observations on lobster fishing vessels. Trap capture was used to assess relative lobster abundance. Common methods for determining abundance such as trawl surveys (Alverson and Pereyra, 1969) used for other species, are inadequate for lobsters, which live in crevices mostly on irregular bottom. Though abundance estimation by trap has its limitations of both accuracy and precision as several environmental, physiological, and behavioural factors affect the attraction and the entering of traps by lobsters (Krouse 1989), it does offer the potential for making crude but inexpensive estimates of crustacean density (Miller 1975). Water temperature is one of the most important physical factors affecting lobster catchability (McLeese and Wilder 1958). Sexual gender, reproductive condition, and lobster size are also factors influencing the capture by traps (Miller 1990). This study did not require absolute density estimates of females on the grounds, but rather their general distribution with season.

The Canso fishing ground was divided into three areas, "inner", "middle" and "outer" based on depth and exposure (Fig. 1.2). "Inside" corresponds to the inlet system, which includes in the north the Derabies and Hog archipelagos, including Piscatiqui I., George I. and Crow I. and in the south, the Glasgow Harbour area. This area is characterized by shallow waters (8 m average) and low wind and wave exposure (Fig. 1.2). "Outside" corresponds to the eastern deep water area (22 m average), unprotected from winds and large seas. The main fishing locations are Eastern Rock, Sand Shoal, and Stanley Shoal (Fig. 1.2). The "Middle" ground has an average depth of 12 m; it corresponds mainly to the Cranberry Is. system, the most easterly group of islands and shoals outside the main inlet system

(Fig. 1.2). The northern boundary of the Canso fishing ground is the deep waters (>100 m) of Chedabucto Bay where lobstering is not carried out (Fig. 1.1 and 1.2).

Three vessels were chosen, one predominantly fishing in each of the areas. An observer went on board each vessel for over 30 boat-days and more than 4,800 traps were assessed over four periods during 1992; May 20th to 27th, June 3rd to 4th, June 23rd to 24th, and July 8th to 9th, the end of the season. Traps were baited with either frozen or fresh mackerel and perch, or fresh flat fish. Loran-C coordinates as well as depth were registered for each trap haul. Captured lobsters were measured (CL), sexed, and sampled for either ovary or embryo condition using the methods described below. Catch effort data were complemented with logbook data from four volunteer fishermen. They registered daily catches expressed in total weight, and one registered both total number of legal lobsters and number of berried females.

1.3.2 Ovary and embryo development

Ovary development was followed in each experiment using the Pleopod Tegumental Gland (PTG) technique described by Aiken and Waddy (1982). Though the function of the cement gland is not completely known, a good correlation exists between ovary development and cement gland development (Aiken and Waddy 1982). Four stages of cement gland development (learned from S. Waddy²) were employed; Stage 1 corresponding to the first stage of ovarian development and Stage 4 indicating imminent egg extrusion (within a few days). As there is some degree of subjectivity in delimiting these stages, intermediate values (e.g. stage 2.5) were included. It was also observed during the pleopod analysis that no difference could be made between PTG Stage 2 and undeveloped PTGs. This factor was considered during data analysis.

² Ms S. Waddy, lobster research scientist, Biological Station, St. Andrews N.B.

The proportion of mature lobsters, estimated as those bearing PTG's > 2.5 during July, was also calculated during this study, using the method described in Appendix 5.

The Perkins' Eye Index (PEI) was used to evaluate embryonic development in each berried lobster (Perkins, 1972; Helluy and Beltz, 1991). During sampling at sea, 40 -50 eggs were removed haphazardly from the berried females, and a pleopod was clipped from non-berried females (hereafter termed "mature" females). Eggs and pleopods from individual females were placed separately in a vial of cool salt water. The vials were placed on ice and brought to the laboratory to be examined with a stereo microscope. Ten live embryos were chosen randomly (this sample size reduced considerably the standard deviation around the mean). The eye index is the combination of the greatest width and length of an embryo's eye divided by two.

Water temperature (hereafter referred as temperature) for the inner, middle and outer areas was monitored continuously with Ryan thermographs (Fig. 1.2) from which a daily average was obtained.

Statistical analysis of the data³ were carried out using different modules of SYSTAT 5.2 for Macintosh (Wilkinson 1992). These analyses are given in Appendix 6 unless otherwise indicated.

1.4 Results

During the period, May 20th through July 9th, 1992, a total of 4,823 traps were sampled throughout the grounds. They yielded 1,513 mature and 343 berried females (Table 1).

³ Rough data for this and the following chapters and appendices are available in the computer room at the Halifax Benthic Fisheries Lab. Halifax, N.S. under the file "Ugarte Canso Lobster".

1.4.1 Temperature regimes

Mean daily temperatures and patterns varied with depth for the three fishing areas (Fig 1.3). Early in May temperatures were ≤ 0 °C at all depths, however, by mid-May, the shallower area warmed rapidly to between 4 and 6 °C; these temperatures were not observed at 17 m and 24 m depth. Temperatures at 24 m never attained 6 °C throughout the study (Fig. 1.3).

1.4.2 Fishing depth

Fishing depth varied significantly throughout the season and amongst the grounds (ANOVA, $F_{3,1279} = 27.333$; $p < 0.001$ and $F_{2,1279} = 336.67$; $p < 0.001$ respectively). At the beginning of the season (May 20th), fishing depths were 13.8 m, 18.6 m and 26.4 m for the inner, middle and outer areas respectively (Table 1). As the season progressed, fishermen fishing on the inner and middle areas moved gear to the shallows, and by July 8th fished at 7.2 m and 9.9 m depth respectively (Fig. 1.4, Table 1). However, fishermen on the outer area did not change depth, remaining at about 25 m throughout the season (Fig. 1.4, Table 1).

1.4.3 Mature females

1.4.3.1 Catch per trap

Capture of mature females varied significantly throughout the season (ANOVA; $F_{3,4389} = 9.605$; $p < 0.001$). The inner and middle areas showed a similar catch per trap (CPTH), which differed significantly (ANOVA; $F_{2,4389} = 3.361$; $p < 0.035$) to that of the outer area (Fig. 1.5).

Mature lobsters were caught throughout between May 20th to 27th (Table 1); CPTH was 0.26 individuals for the inner and middle areas and 0.33 individuals per trap for the outer area (Fig. 1.5). A significant increase ($p < 0.001$) in CPTH was observed in early June, being similar (~ 0.40 indiv/trap) for all grounds, and was the peak capture rate for the season (Fig. 1.5). This peak was also evident when expressed in weight of the legal catch

(see Fig. 1.6). Bottom temperatures at 17 m showed a strong correlation (Pearson $r = 0.73$; $p < 0.001$) with CPTH to June 10th (Fig. 1.7). Correlation between catch and temperature was weak ($r = 0.155$) after June 10th (Fig. 1.7). Catch sampling in late June, showed a decrease in number of females captured, especially on the outer area ($p < 0.05$), where, CPTH dropped by 45% (0.23 ind/trap haul) from early June (Fig. 1.5). During July 8th-9th, the mean number of females per trap haul dropped to 0.26 on the inner and middle areas, but a minor increase (t-test; $p < 0.18$) was observed (0.30 indiv/trap) on the outer grounds (Fig. 1.5).

1.4.3.2 Size distribution

During late May the mean size of ovarian females trapped averaged 89.5 mm and 87.5 mm CL on the inner and middle areas respectively; females on the outer ground were significantly smaller at 83.8 mm CL (ANOVA; $F_{3,1287} = 53.962$; $p < 0.001$). These differences in size among the grounds increased through the summer (Fig. 1.8). There was a striking increase in size (t-test; $p = 0.061$) of females from the inner area from May to July 8th-9th (94.3 mm CL) (Fig. 1.8). Size of females captured in the middle remained constant, and those from the outer area, though not significantly, tended to decrease (Fig. 1.8).

By July, females > 99 mm CL had totally disappeared from the outer area (Fig. 1.9), and were reduced in numbers from the middle area. The inner area however, showed an increase in frequency of larger animals; from 19% in May to 26% in July.

1.4.3.3 Ovary development

During late spring (May 22nd-June 4th) more than 80% of the females had ovaries in PTG stage ≤ 2 throughout the grounds (Fig. 1.10A). Ovary development of females in the inner area was more advanced than those from the middle and outer areas ($X^2 = 35.7$; $df = 2$; $p < 0.001$) (Fig. 1.10A). As the season progressed (July 8th-9th), females from the different

grounds showed a clear difference in ovary condition; more than 65% of the inner ground females were in PTG stage ≥ 3 (Fig. 1.10B), which suggests extrusion would occur within two to three weeks. A significant difference ($X^2 = 110.1$; $df = 2$; $p < 0.001$) was found between the outer area females and the remainder, with more than 80% of the former females with ovaries still in a PTG stage < 2 or undeveloped, and none > 2.5 (Fig. 1.10B); there had been no sign of development during this period. Females from the middle area presented an intermediate ovary development with 35.7% of the females in a PTG stage ≥ 3 , but also with more than 33% of the females with PTGs < 2 (Fig. 1.10B).

1.4.4 Berried females

1.4.4.1 Distribution and abundance

During the study period, there were significant differences in capture of berried females, both through the season and among the fishing areas (ANOVA; $F_{3,4414} = 14.47$; $p < 0.001$). Berried female CPTH increased from May through July in the inner and middle areas, but remained constant in the outer ground (Fig. 1.11). During May, berried females were captured in small numbers throughout the grounds; 0.043, 0.020 and 0.045 animals per trap haul for the inner, middle, and outer areas respectively (Fig. 1.11). By early June, their CPTH increased in the first two areas (≈ 0.08 ind/trap), but not in the outer area (Fig. 1.11). CPTH of both non-ovigerous and berried females was positively correlated with water temperature (Pearson $r = 0.683$; $P < 0.001$). However, unlike ovarian lobsters, this relationship held for berried females throughout the season (Fig. 1.12). CPTH of berried females in late June on the inner area reached 0.142. This number was over twice the rate from the middle area ($p < 0.001$) (Fig. 1.11). CPTH of berried females on the outer area decreased to 0.014, with only three animals captured (Fig. 1.11, Table 1). By early July, the CPTH of berried females on the middle area increased significantly ($p < 0.001$) to 0.135. This rate of capture was similar to the inner ground which did not present

a significant increase with the previous survey (Fig. 1.11). Female capture from the outer ground returned to the constant level of the first two samplings (0.046 ind/trap) (Fig. 1.11).

Logbook analysis also showed a decrease in capture of ovigerous females from June 18 through 24th, which was associated with the drop in temperature to ≤ 4 °C during that period (Fig. 1.12)

1.4.4.2 Embryo stage

Embryo development varied significantly, both through the study period (ANOVA, $F_{2,187} = 7.780$; $p < 0.001$) and amongst the lobster fishing areas (ANOVA, $F_{2,187} = 3.214$; $p < 0.042$). During May, no significant differences were found in embryo development amongst the areas (Fig. 1.13), however, by late June an increase in development was observed in embryos from the middle (PEI=433.5 μm) and inner areas (PEI=459.2 μm) ($P < 0.001$). No significant development was observed in the embryos of lobsters from the outer area (Fig. 1.13). Development continued through early July in embryos from the middle areas (PEI=463 μm); the inner area embryos showed no increase in development from late June (Fig. 1.13). However, 39.8% of the inner area females had either hatched or were hatching by July 8th-9th, versus 17.0% in the middle area (Fig. 1.14). Embryos from the outer area had not developed significantly from late May (Fig. 1.13)

1.4.5 Size at maturity

Mean lobster size at fifty percent female maturity was markedly different between the inner (75.6 mm CL) and the outer (98.8 mm CL) areas in July 8-9 (Fig. 1.15).

1.5 Discussion

1.5.1 Trapping as a sampling tool

Our trapping survey did not estimate real densities of lobsters on the Canso ground, but the relative abundance observed (CPTH) allowed us to discern a pattern in distribution in relation to size, sexual development and physical variables. Mature female lobsters in Canso fishing ground presented unique distribution patterns during spring/summer, which were associated with both physical conditions, such as substrate and temperature, and state of maturity and animal size. Most information about palinurid lobster movement and distribution comes from commercial catch monitoring (Herrnkind 1980). The main advantage of these data lies in the wide geographic coverage, the large quantity of data, and the low expense to the researcher, "Generally, major redistribution of migrant lobsters and their biological features (adult males, gravid females, etc.) appear clearly" (Herrnkind 1980). Miller (1989) demonstrated that, although there was bias in the capture in relation to size, density of lobsters in two different habitats was reflected in the capture by traps. Our trap surveys carried out during the spring-early summer period, presented seasonal variations in the capture of both mature and berried females. As well, there were clear differences in abundance and size composition of the capture among the grounds.

1.5.2 Seasonal depth variation in the fishery

A seasonal change in the mean depth of fishing was observed in both the inner and middle fishing areas, where trapping started at about 13.8 m and 18.6 m, respectively, in May, and ended up at about 7.2 m and 9.9m in the inner and middle areas respectively. Fishermen, kept a constant number of traps in each area, and the shoreward movement of gear was within each area (unpub. data , also Table 1). Fishing depth did not change, however, on the outer area (Fig. 1.4).

The activity level of lobsters appeared to increase once the temperature rose above 2 °C . McLeese and Wilder (1958) reported that *H. americanus* walking rate increased by a factor of 2.3 when water temperature increased from 2-10 °C; catch rate in the field increased by an order of magnitude when temperature went from 3-11 °C. In fact, on the Canso grounds in 1992, the seasonal peak in capture occurred at 4 °C in early June (Fig. 1.6), about one-quarter into the fishing season.

Capture of legal (≥ 81 mm CL) lobsters from logbook information (kg), showed a variable pattern which was associated with both changes in temperature and fishing pressure. Before June 10th, there was a good correlation between capture and water temperature (Figs. 1.6 and 1.7). This correlation was lost after June 10th, most probably due to a decrease in available lobsters. Exploitation rate in this area is estimated at about 0.52 (Miller et al 1987), therefore a strong reduction in recruits would be expected by mid-season. The number of lobsters captured during the fishing survey showed the same variation in pattern as the logbook data. Abundance of ovarian females, based on CPTH, was similar on the inner and outer areas throughout the season. The outer area showed a little more variable pattern but not significantly different from inner areas (Fig. 1.5). A totally different picture was evident when the mean size of capture was compared, with significantly larger females on the inner area than on the middle and, especially, the outer areas (Fig. 1.8). Larger animals are the fishermen's target and they are being constantly taken out of the grounds and, though a strong fishing pressure was acting on the ovarian females through to the end of the season, there was still a steady increase in the mean size on the inner area (Fig. 1.8). It is thus, reasonable to speculate that, during this period, large animals are being continuously supplied to the inner area from the deeper areas. The reduction in the middle area and the total disappearance from the outer area of larger lobster at the end of the season (Fig. 1.9) support this hypothesis and explains the change in trap location toward shallower water through the season.

The pattern of distribution and abundance of berried females, as reflected in the trapping surveys, was different from that of ovarian females. Capture of berried females increased steadily with the increase in temperature through the season, and there was a significant variation in trap capture among the areas (Figs. 1.12 and 1.11). At the study's beginning (May 20th-27th) ovigerous lobsters presented a similar density among the areas. This pattern changed drastically by late June when the inner area had abundances of two to three times as high as the middle and the outer areas, respectively (Fig. 1.11). The most variable pattern was observed in the middle area, with an increase in abundance to June 3th-4th, a small decrease in June 24th-25th, and a dramatic increase by July 8th-9th. The inner area, however, always had a lower, but almost constant density (Fig. 1.11). Different temperature regimes among the areas could be a possible explanation for these differences in the abundance, especially between the inner and outer areas. However, by late July temperature at 20 m was ≥ 5 °C, and this temperature showed a good correlation with a peak in berried captures over 0.15 indiv/trap haul by mid-June (see Fig. 1.12). Moreover, differences in trapability between ovarian and berried females for *H. americanus* and *H. gammarus* have been attributed to differences in rate of feeding rather than a different response to temperature (Templeman and Tibbo 1945, Brandford 1979). The same was reported for the crab *Carcinus maenas* (Ropes 1968). Therefore, the evidence appears to indicate that berried females are indeed less abundant in the outer area than in the inner area during the fishing season.

1.5.3 Physiological and reproductive condition of the females among the grounds

It was evident from our study that the location of females had an obvious impact on both their ovary and embryo development. A clear difference in the ovarian condition was evident among the areas as the season progressed. From a similar ovary maturity condition on May 20th-29th, PTG analysis carried out by July 8th-9th, indicated almost 50% of the females from the inner area would spawn within the next couple of weeks; whereas on the

outside grounds 80% of the females presented immature ovaries (Fig. 1.10). It seems that, due to the marginal conditions of the outside ground, size at maturity is being severely affected in this latter area. In fact, 50% size at maturity is reached at 98.5 mm CL, compared to 75.6 mm CL occurring on the inner area (Fig. 1.15). This dramatic difference in maturity within the same ground is similar to a finding by Squires et al (1971) for lobsters in Newfoundland. Here, lobsters of two arms of the same bay had different reproductive cycles and it was suggested the different temperature regimes were responsible. This phenomenon appears to occur in other invertebrates as well; MacDonald and Thompson (1981) reported that reproductive condition of *Placopecten magellanicus* along a depth gradient on a micro-geographical scale was equal or greater than variation on a latitudinal scale. Probably, this difference in maturation of the females between the inner and outer areas, produced a different catchability, which would thus explain why fishermen in that ground do not move their gear.

As was described for ovarian females, the shallow warmer waters of the inner area accelerates the rate of embryonic development of the berried lobsters, and consequently produces an earlier hatch (Fig. 1.11). The cold temperatures of the outer area, by contrast, appears to inhibit it (Fig. 1.3, 1.11). The seeming lack of increment in PEI of embryos in the inner area by July 8th-9th, was because 40% of the captured berried females were already hatching or had hatched versus 17% in the middle area (Fig. 1.14). Therefore, only females with less developed eggs were left to be sampled on the inner area.

It seems then, that the geographic and bottom topographic conditions of the Canso fishing ground appear to create a range of environments having a dramatic impact on the maturation process of ovaries and eggs. The habitat differences influence the distribution of the females. Are these animals seeking these shallower and warmer environments? What are the real benefits of being in the inner or middle area? If a movement to shallow water occurs, when are they moving? Answers to these questions are important to understand the

reproductive process of lobsters in nature and the associated behavioural strategies of the animals to support them. A combined program of tagging and experimental manipulation of animals in the field is required and follows in Chapter II and III.

Table 1. Number and depth (m) of sampled traps and number of ovarian and berried females captured during different periods through the fishing season May20 -July 9, 1992, on the Canso grounds.

Ground		Sample dates				Sub totals
		May 20-29	June 3-4	June 24-25	July 8-9	
Inner	Traps (no.)	423	350	520	281	1,574
	Mean depth (\pm SD)	13.8 (13.1)	10.9 (15.1)	7.1 (1.5)	7.2 (3.9)	
	Ovarian (no.)	109	138	166	73	486
	Berried (no.)	18	29	74	45	166
Middle	Traps (no.)	607	461	513	295	1,876
	Mean depth (\pm SD)	18.6 (5.3)	15.9 (5.4)	12.9 (4.6)	9.9 (3.8)	
	Ovarian (no.)	160	187	164	79	590
	Berried (no.)	12	37	32	40	121
Outer	Traps (no.)	399	315	219	440	1,373
	Mean depth (\pm SD)	26.4 (4.8)	23.1 (3.7)	22.2 (3.1)	24.2 (3.8)	
	Ovarian (no.)	130	129	48	130	437
	Berried (no.)	18	14	3	21	56

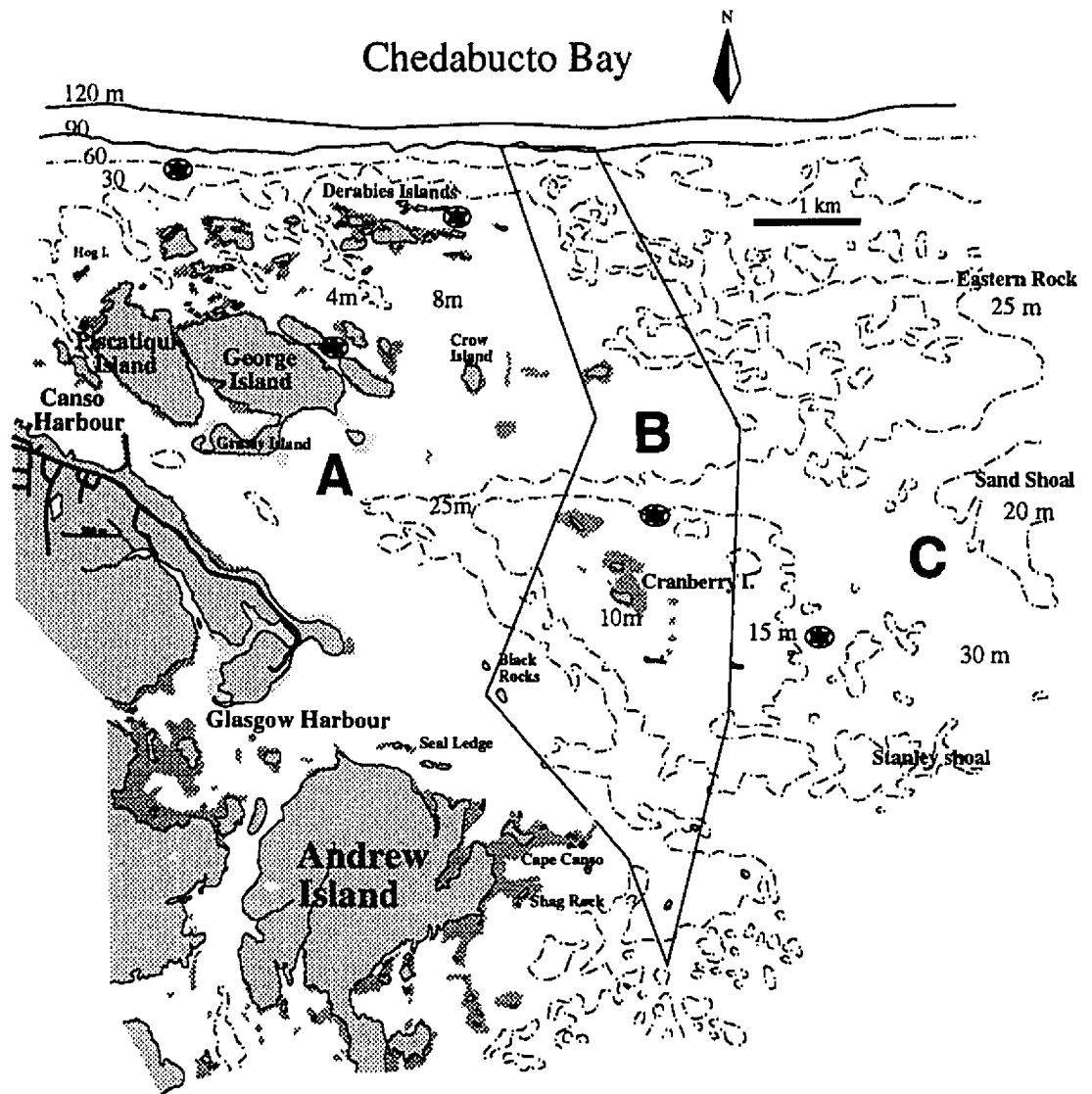


Figure 1.2. Chart of Canso showing the different fishing grounds. (A) Inner, (B) Middle and (C) Outer. ● Thermograph locations.

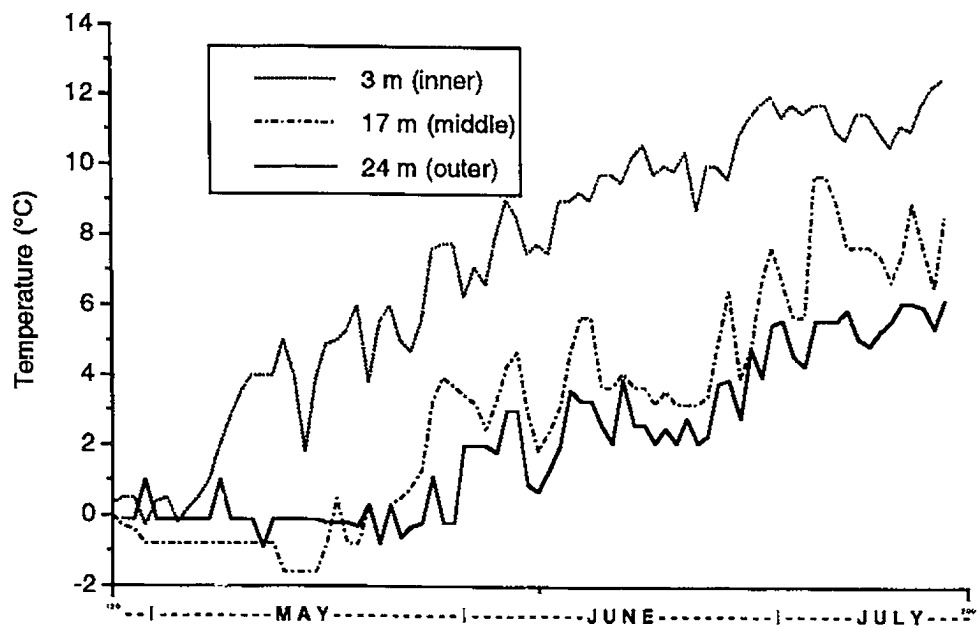


Figure 1.3 . Temperature regimes of the different Canso fishing areas during the trap survey (May 20th -July 9th, 1992).

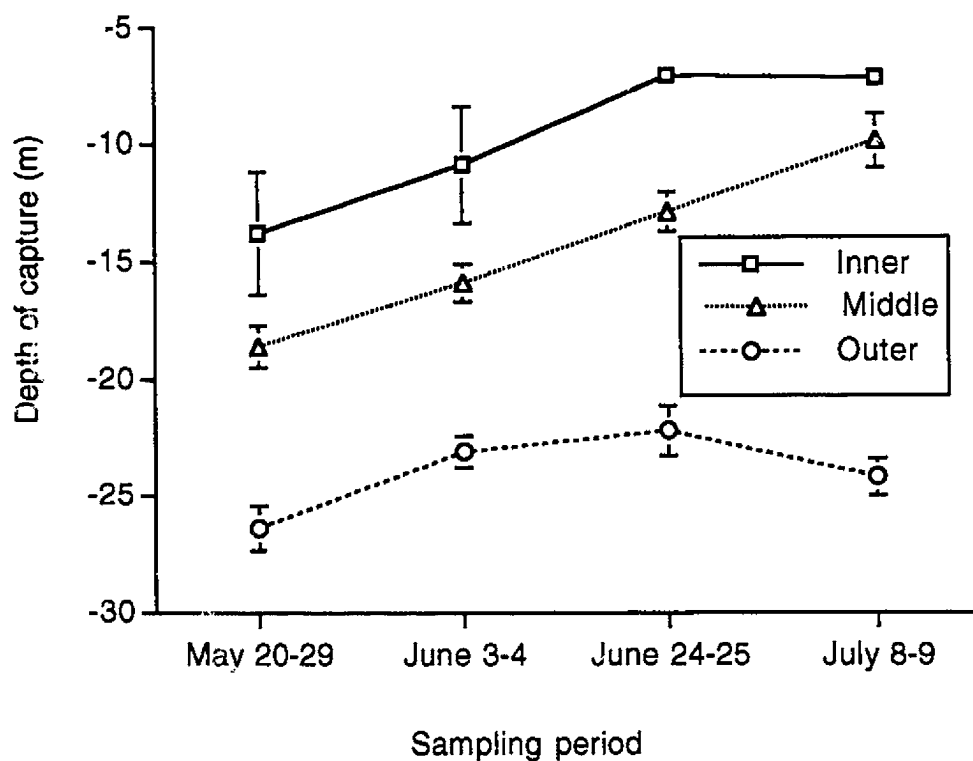


Figure 1.4. Mean depth (\pm 95% confidence intervals) of the commercial traps during spring and summer on the inner, middle, and outer areas of the Canso fishing grounds (1992).

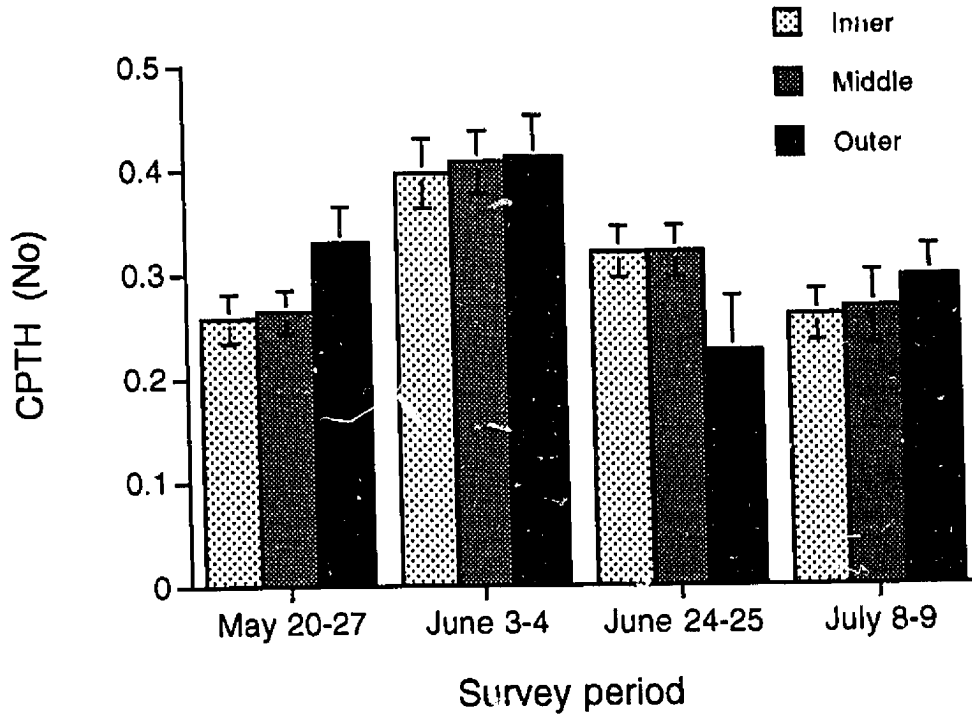


Figure 1.5. Catch per trap (CPTH ± 1 SE) of ovarian females extrapolated from trap captures, during spring-summer on the inner, middle, and outer areas of the Canso fishing grounds in 1992.

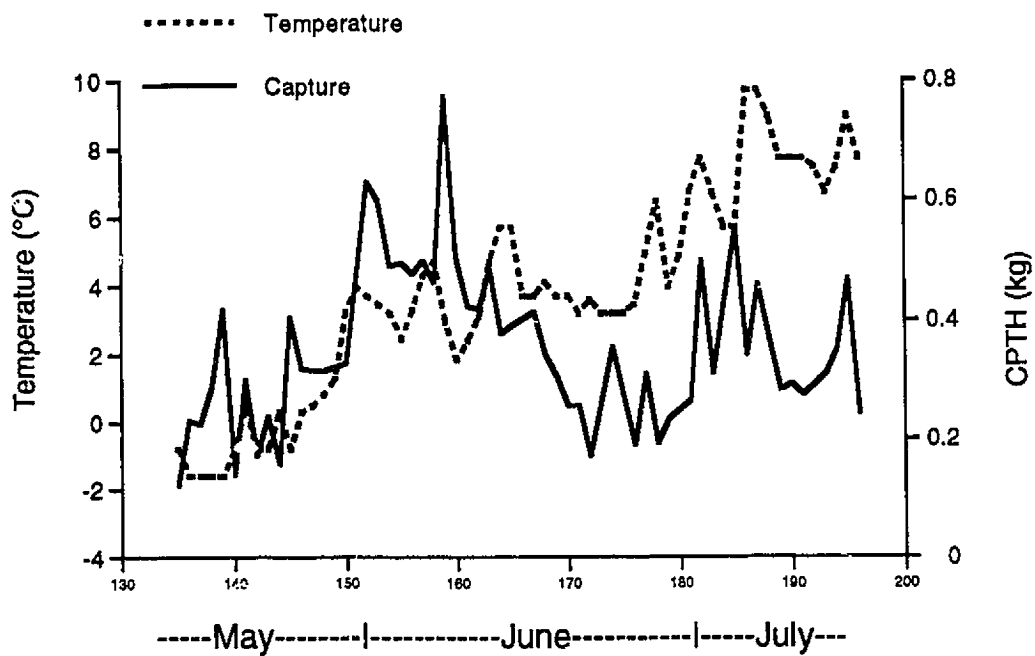


Figure 1.6. CPTH expressed as weight (kg) of legal size (81 mm CL) lobsters (males and females) and water temperature at 17 m on Canso's fishing grounds. Data obtained from log books submitted by volunteer fishermen.

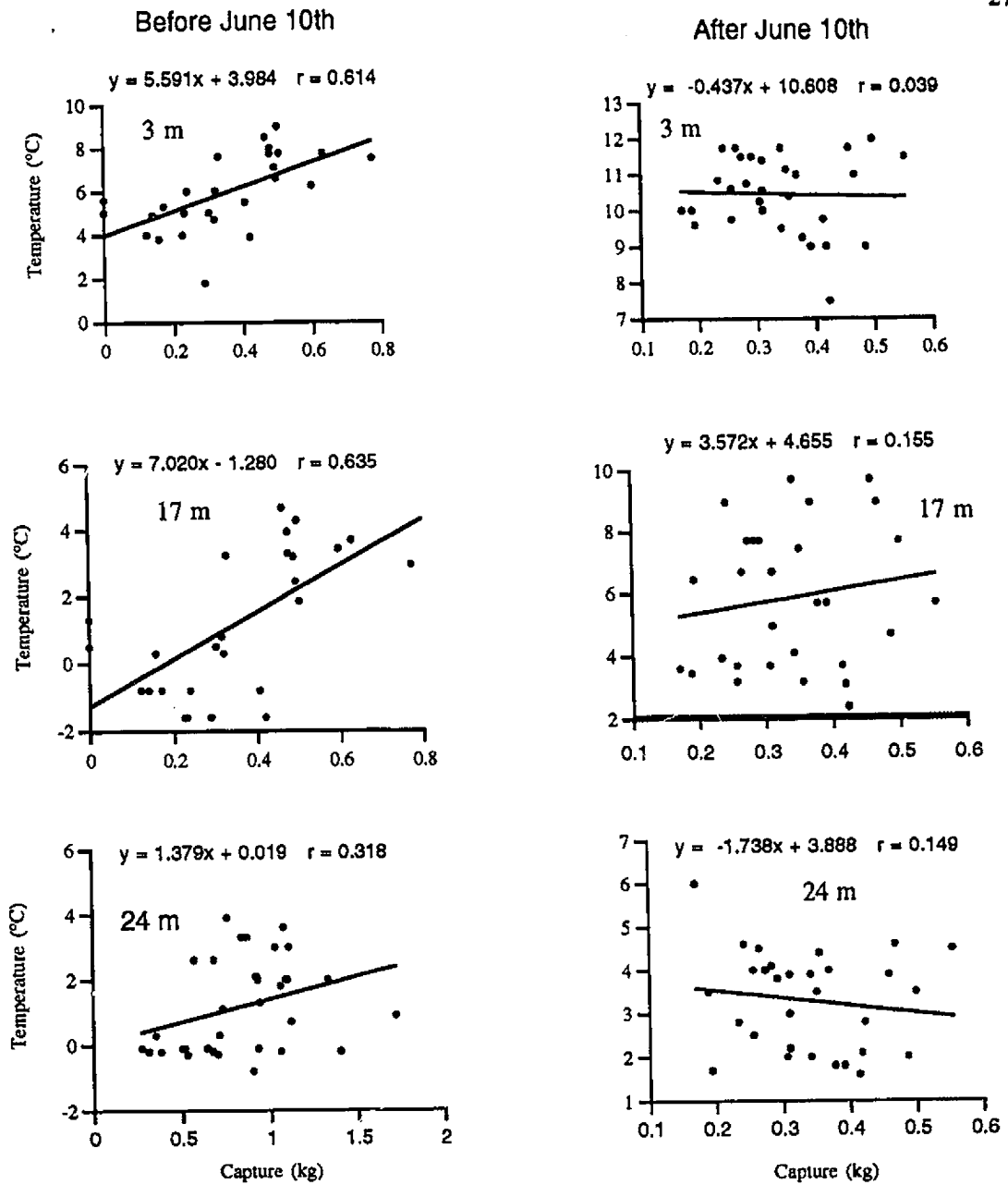


Figure 1.7. Relationship between temperature and CPTH of legal sized lobsters at three depths on the Canso N.S. grounds before and after June 10, 1992.

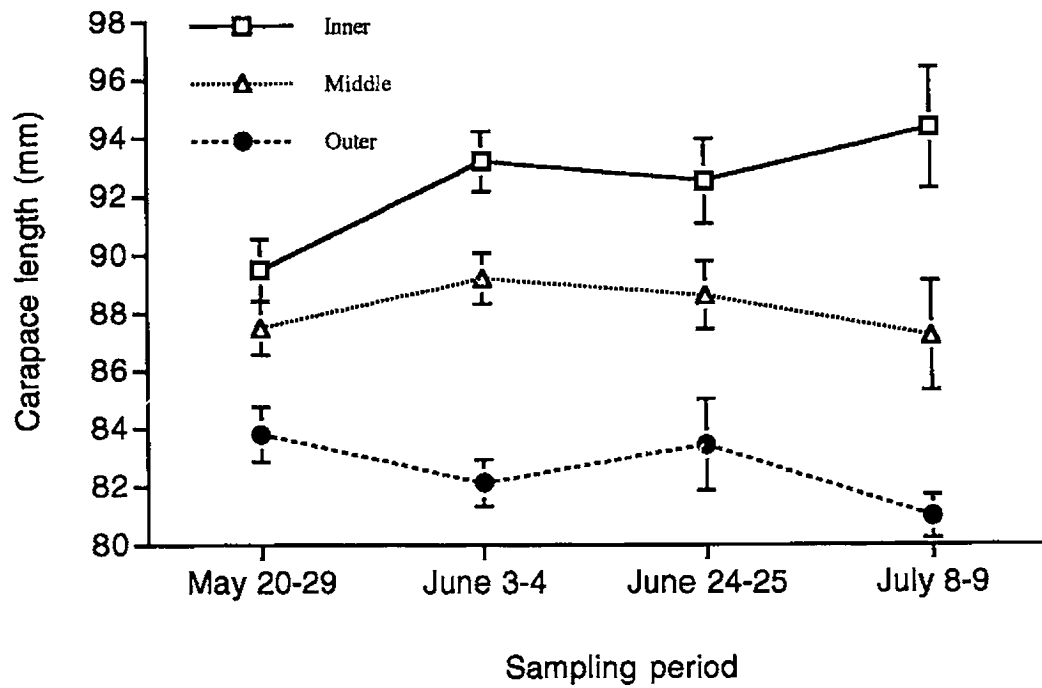


Figure 1.8 . Mean size (± 1 SE) of ovarian females on the inner, middle and outer areas of the Canso fishing ground during 1992.

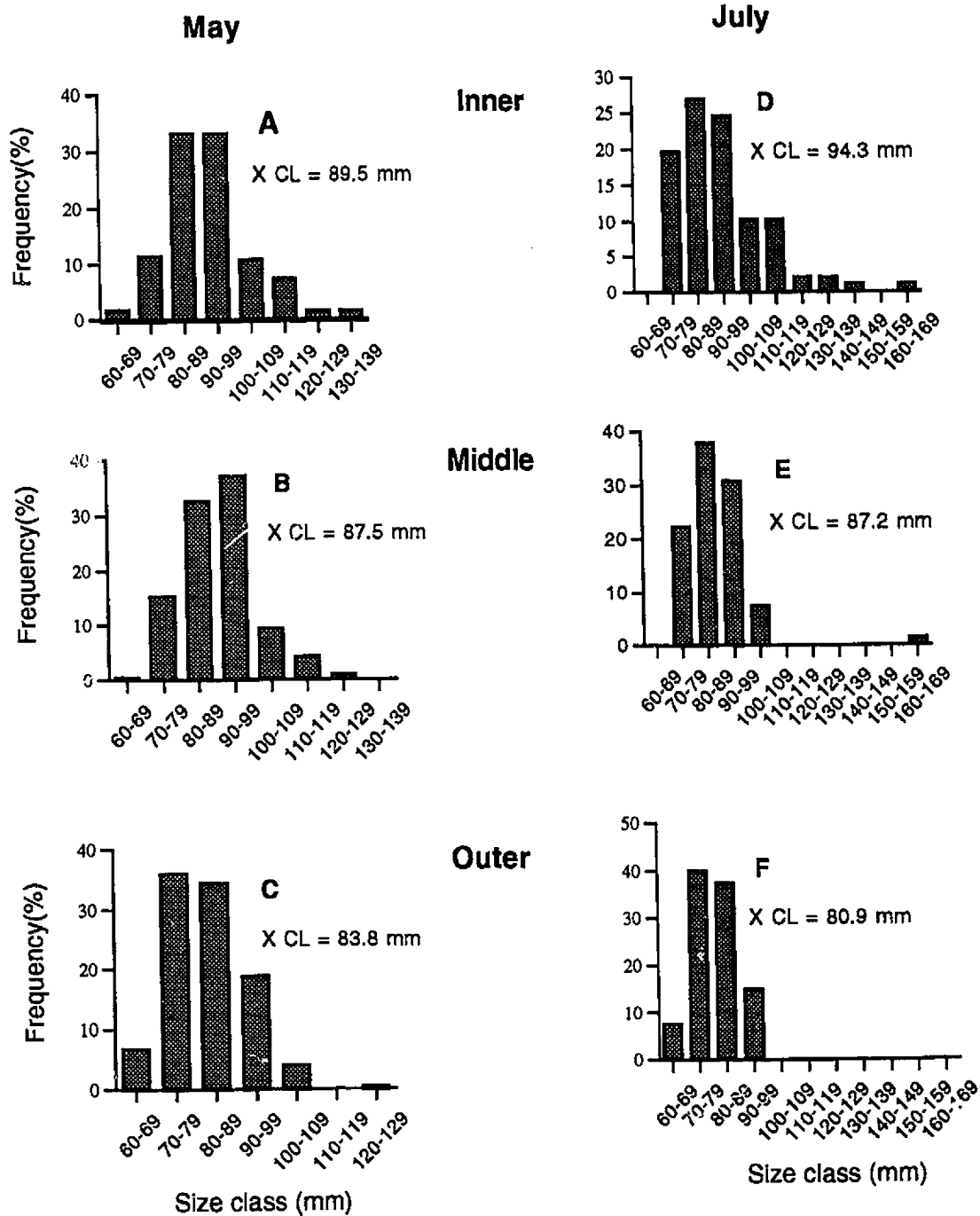


Figure 1.9. Size frequency of ovarian females on the inner, middle and outer areas of the Canso grounds during spring (May 29) and summer (July 9) of 1992.

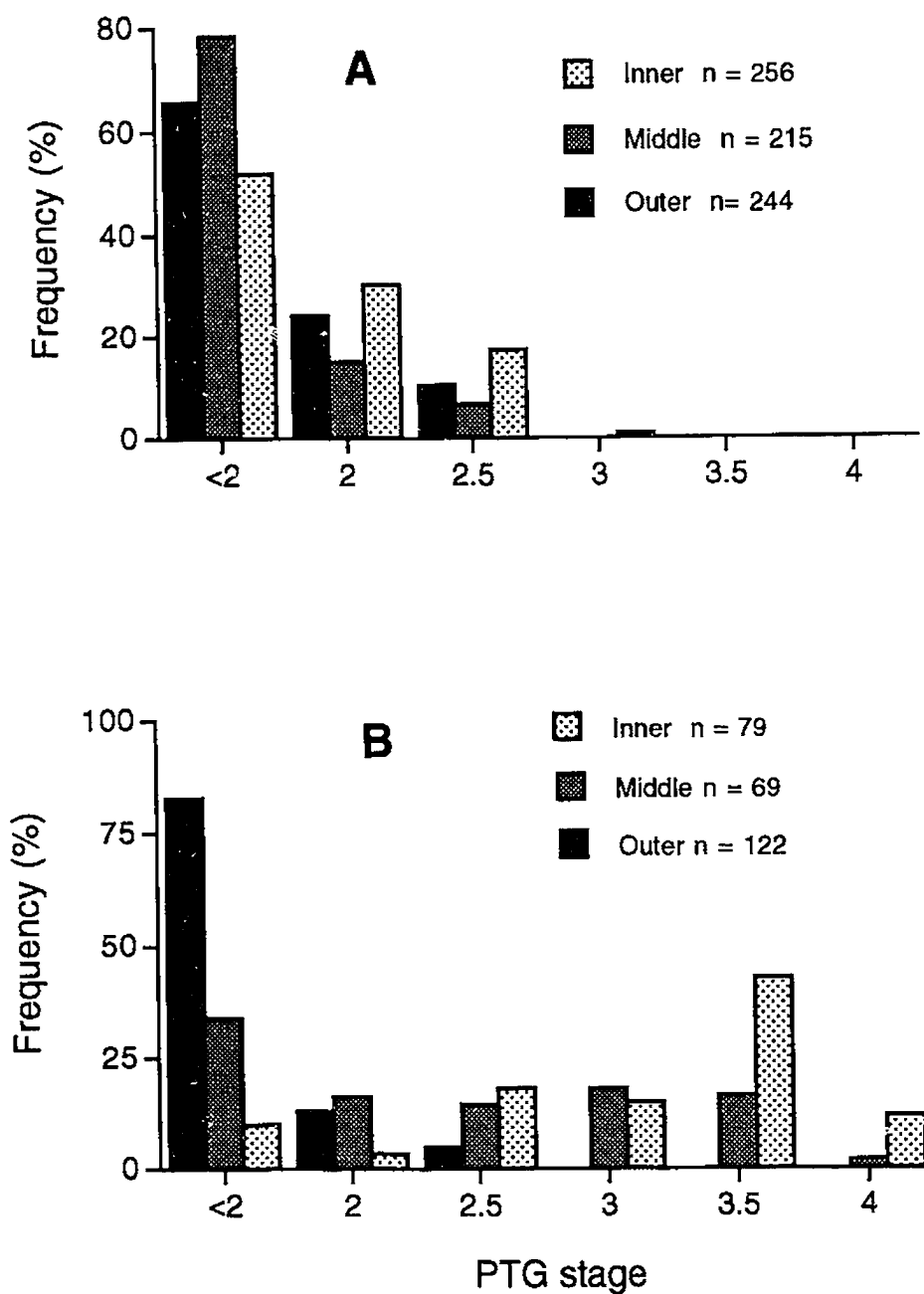


Figure 1.10 . Pleopod tegumental gland condition of lobsters for the inner, middle and outer areas of the Canso's fishing grounds during spring (May 20-June 4) (A) and summer (July 8-9) (B), 1992.

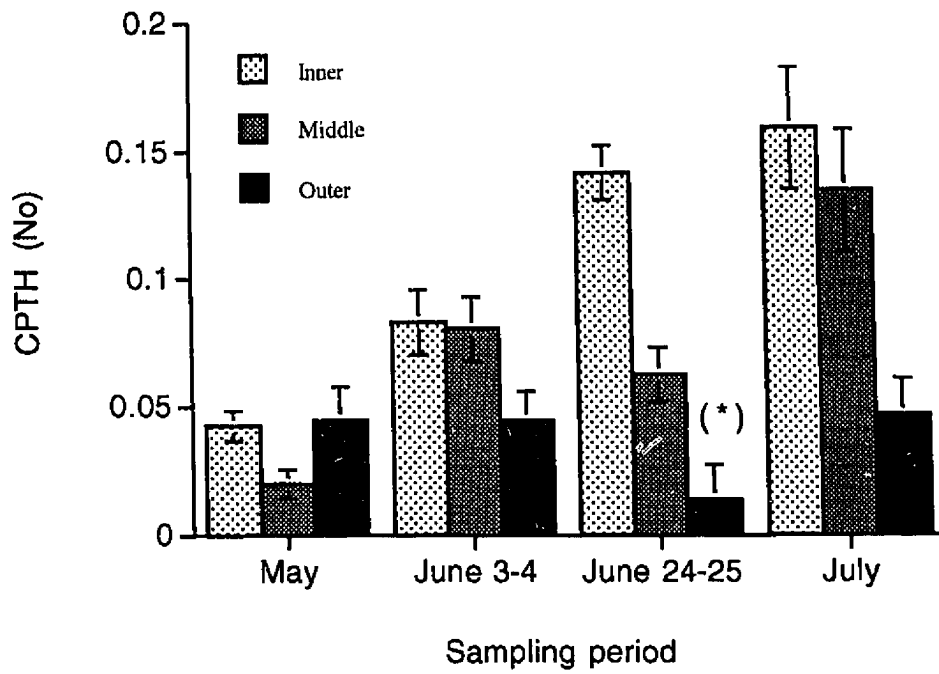


Figure 1.11. CPTH of berried females from May 29th to July 9th, 1992, on the inner, middle and outer areas of the Canso N.S. fishing ground. (* only three females sampled).

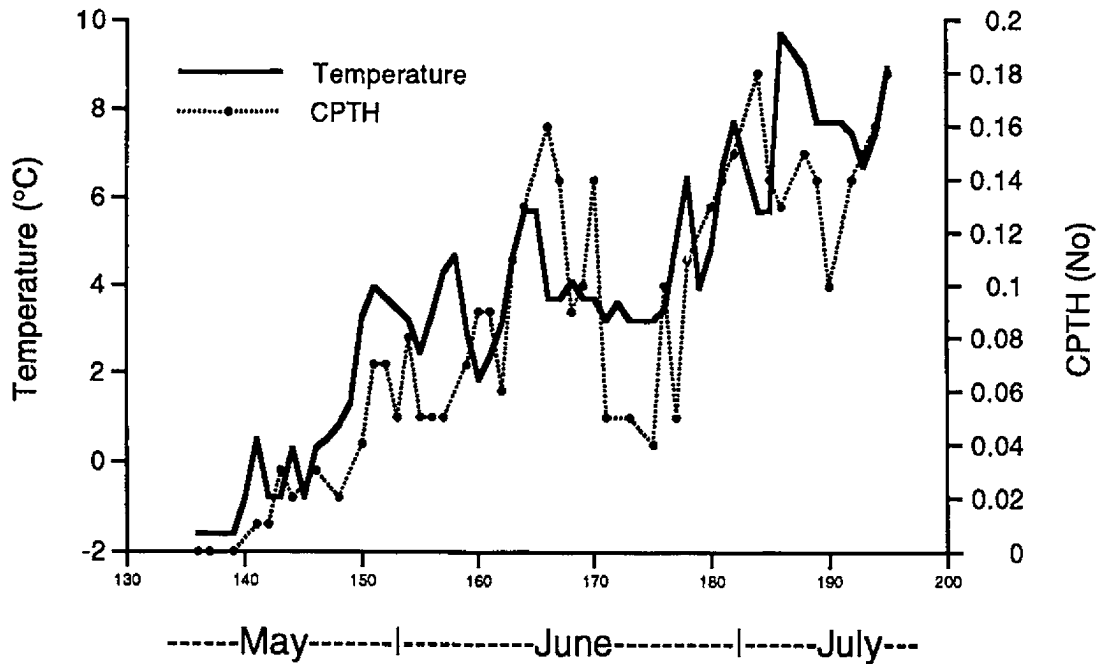


Figure 1.12. Water temperature at 17 m and commercial (logbooks) CPTH of berried lobsters during the 1992 fishing season on the Canso, N.S. fishing ground.

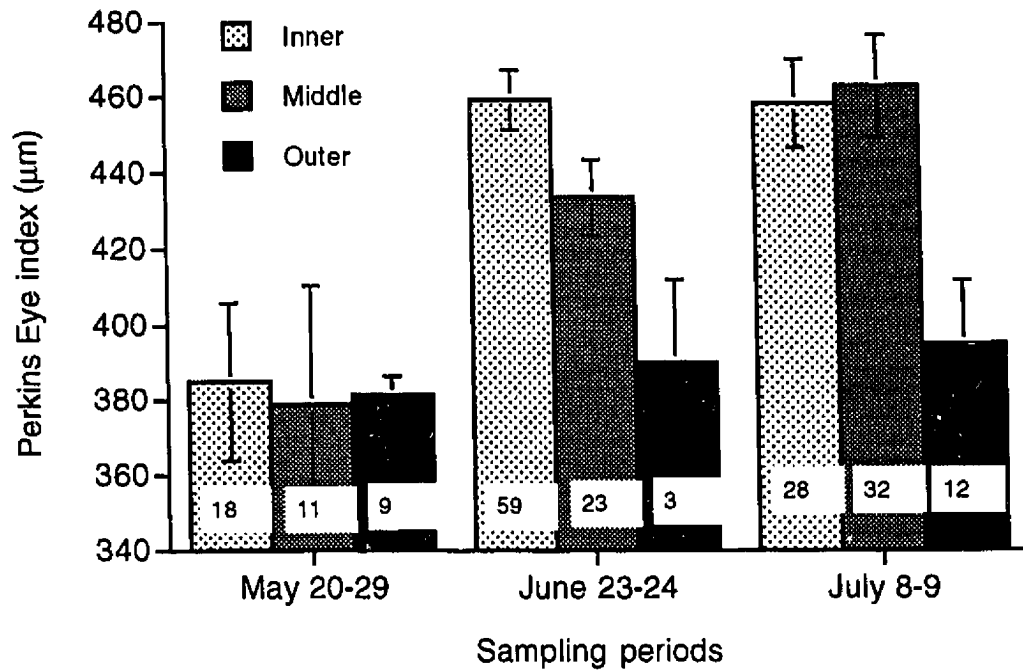


Figure 1.13 . Mean (± 1 SE) embryo maturity (PEI) during late spring/early summer of lobsters from the inner, middle and outer fishing areas of Canso N.S. (N_o within bars = sample size).

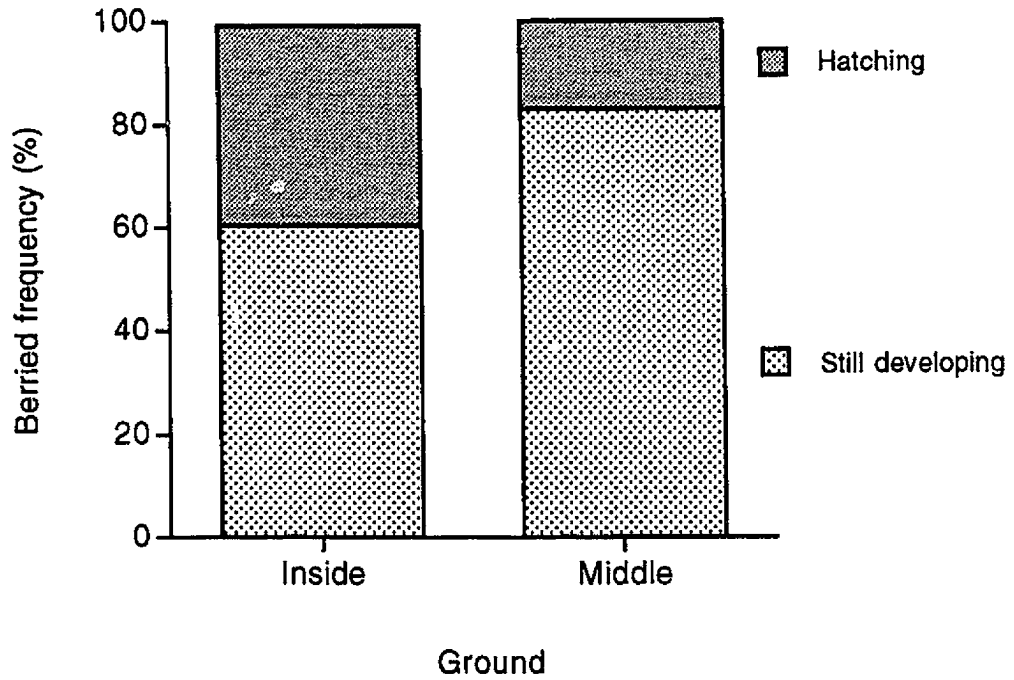


Figure 1.14. Frequency of hatched and hatching berried females condition during the trap survey of July 8th-9th, 1992 on Canso fishing grounds.

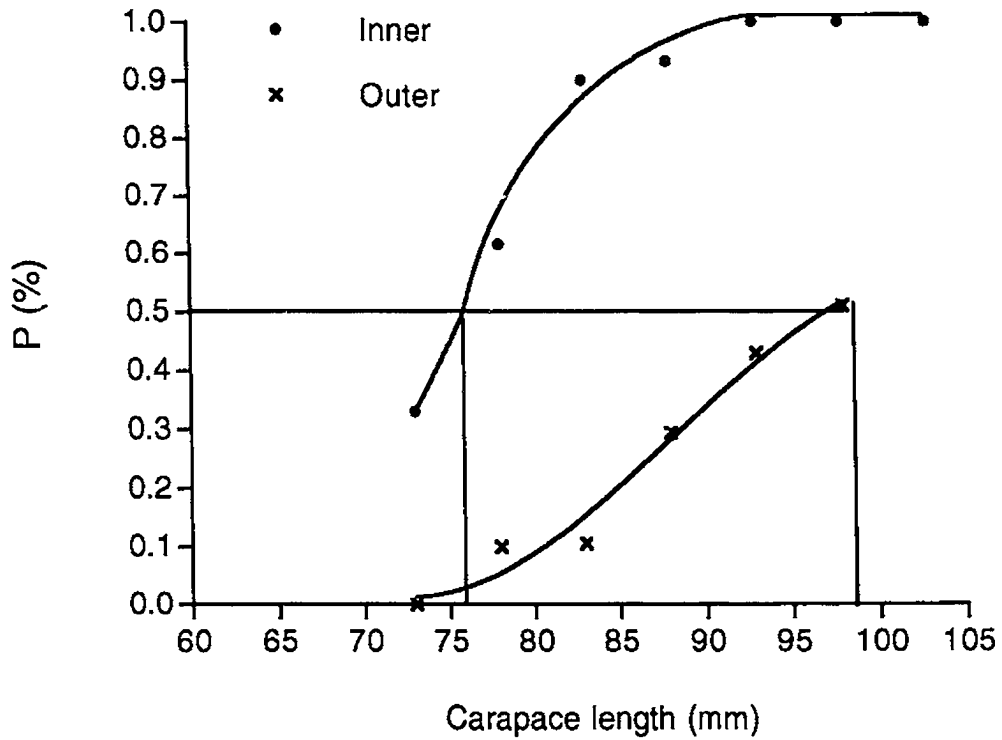


Figure 1.15. Relationship between female size (CL) and percent maturity for lobsters from Canso's inner and outer areas during the 1992 fishing season.

CHAPTER II

A FIELD STUDY OF LATE STAGE EMBRYO DEVELOPMENT AND BERRIED FEMALE LOBSTER MOVEMENT IN RELATION TO TEMPERATURE.

2.1 Introduction

Temperature is an important factor controlling the life history of crustaceans (Sastry 1983). For the American lobster, *H. americanus* Milne-Edwards, temperature plays a key role in the reproductive and growth processes (Aiken and Waddy 1980). This relationship has been observed on rate of embryo development (Templeman 1940, Perkins 1972, Brandford 1978), time to hatch (Templeman 1936a, Caddy 1976), and rate of larval development and survival (Templeman 1936b, Cobb 1968, Caddy 1979, Hudon et al 1986, MacKenzie 1988, Cobb et al 1989). Furthermore, temperature has been implicated in behaviour. For example, temperature is thought to be the factor regulating seasonal deep-shallow migrations of reproductively mature lobster in the Bay of Fundy (Campbell and Stasko 1986), of ovigerous females off Grand Manan Island (Campbell 1986) and of offshore (continental slope) lobsters (Cooper and Uzmann 1971, Uzmann et al 1977, Lund 1979, Fogarty et al 1980, Campbell et al 1984, Pezzack and Duggan 1986). These migrations increased degree-days and thus postulated to enhance rate of molting, growth, gonadal development, egg extrusion and embryo development (Cooper and Uzmann 1971, 1980, Uzmann et al 1977, Lund 1979, Munro and Therriault 1983, Campbell 1986, Campbell and Stasko 1986, Campbell 1990).

Mature inshore lobsters on Canadian grounds outside the Bay of Fundy exhibit reduced movements, typically less than 12 km between release and recapture (see reviews by Cooper and Uzmann 1980 and Miller et al 1989). Some workers have observed mature lobsters moving into deep water in autumn and back to shallow water during spring

(Corriveau and Tremblay 1948, Bergeron 1967, Lund 1979), while others demonstrated little seasonal movement (Wilder 1954, Wilder and Murray 1958). Cooper *et al* (1975) and Ennis (1983, 1984) suggested lobster movement to deeper waters was in response to storm turbulence, and did not equate this movement with a seasonal migration involving significant distances. Seasonal movement by Gulf of St. Lawrence lobsters was confirmed by Templeman (1936) and Munro and Therriault (1983). Here, they moved into Magdalen Island's shallow lagoons from mid-May through June and out to deeper water in October. Duggan and Pringle (1988) found a high incidence of ovigerous females inside the Jeddore Harbour. They speculated (based on Harding *et al*, 1983) that the harbour would be an important area for both hatching and larval development. Following this hypothesis, Jarvis (1979) tracked berried females in the area, but did not find an advantage for the lobster to move inside the harbour based on embryo development; this could be completed successfully in open areas. As well, DiBacco and Pringle (1992) demonstrated that flushing rate of the Jeddore Harbour was too high to allow larval development beyond Stage I within the Harbour.

In contrast, the trapping survey reported in Chapter I, showed clear differences in distribution of berried females along a gradient of depth and temperature, which appeared to have a direct influence on the rate of embryonic development in the Canso area.

The objectives of this study are:

- 1.- to evaluate the effect of *in situ* temperature regimes on late-stage embryo development, and
- 2.- to determine whether berried females are seeking shallow warmer water.

Specifically, this study is designed to answer the question, " Is there an advantage to accelerate embryonic development during the last part of the incubation period, and if so is there a movement of the berried females to achieve this?"

2.1.1 Embryonic cycle

On the Atlantic coast of Nova Scotia, the majority of mature females molt and mate from June through September and carry sperm over a 10-12 mo. ovarian maturation period; egg extrusion and fertilization follow. The embryos incubate on the abdominal ventral surface for approximately 10-12 mo., depending on water temperature (Perkins 1972, Aiken and Waddy 1986). In this study we term "late stage berried females" as those fecund spring females, which extruded eggs the previous summer (July -August). The newly extruded embryos of laboratory-held animals continue development until water temperatures drop to $\approx 4^{\circ}\text{C}$ (Perkins 1972). Development resumes the following spring and hatch that summer (Perkins 1972). During spring, a late stage berried female may have "advanced" (Perkins Eye Index [PEI] $> 400\ \mu\text{m}$ or less advanced (PEI $< 400\ \mu\text{m}$) embryos, depending upon time of extrusion and subsequent development rate.

2.2 Materials and methods

Two experiments were carried out with late-stage berried females during spring and summer, 1991 and 1992 on the Canso fishing grounds (Fig. 2.1). First, ovigerous females were caged (Fig. 2.2) at two depths until embryo-hatch, each with different spring/summer temperature regimes (Fig. 2.3). Secondly, free range animals were marked and recaptured to determine movement. Embryo development was followed in each experiment using Perkins' (1972) eye index. During 1992 the tracking method was refined and the study area extended to cover a deeper outer fishing area (Chapter I, Fig 1.2).

2.2.1 Caged females

Two study sites, 3 m and 17 m water depth (Fig. 2.1) were chosen based on 1990 temperatures. Temperature was monitored continuously at both sites throughout the study with Ryan thermographs from which daily averages were obtained. A one-in-10 year NE

storm moved the 17 m cage system approximately 100 m. The cages were re-secured in the same place during 1992. Each year at the beginning of the fishing season (May 10th-20th), trap caught, late-stage berried females were obtained from local fishermen. Forty animals were randomly selected, identified by number, and placed separately in compartments in one of ten wire cages (130 x 50 x 35 cm); five cages were located at each depth (Fig. 2.2). The females were fed a diet that alternated between either frozen mackerel or squid about every week. Sea urchins and crabs were also occasionally offered. The size of the mesh allowed the entrance of different invertebrates into the cages; lobsters were seen feeding on them on several occasions.

Each female's embryo mass was sampled about every 15 d from May 10th through June 20th and weekly thereafter until embryo hatch. The cages were located by divers at each observation, secured with a line and brought on board the vessel for 10 to 15 min. Each lobster was subjectively assessed for embryo mass quantity and 40 -50 eggs were chosen randomly, placed in a vial of ambient salt water and taken to the lab. The PEI was used to evaluate embryonic development (See Chapter I). Embryonic development was followed until hatch.

2.2.2 Free ranging females

Temperatures at the start of fishing season (in May 10th) are generally cold, thus catchability of ovigerous females is low (McLeese and Wilder, 1958, also Chapter I). In order to have adequate numbers, most fishermen saved their daily catch of ovigerous females. Their full cooperation allowed the tagging of 176 ovigerous females on May 21st to 23rd, and 50 on June 13th, 1991. Numbered carapace tags (*sensu* Wilder 1954, Stasko 1980) were applied, an egg sample removed, and each female released in the general area of capture. Thereafter, fishermen would contact research personnel via VHF radio upon capturing a tagged female. The vessel was boarded, the female recovered, and both the

capture location (Loran-C coordinates) and depth were recorded. Another egg sample (≈ 50 eggs) was removed and the female returned to the water. A \$ 5 reward was paid to the fisherman. A chartered vessel fished 100 traps daily for four days early in the closed season (July 28th to 31st) in an attempt to recover more of the tagged animals. During the charter, traps were set from 2 to 30 m depth scattered along the fishing ground, mostly in the inner and middle area (Chapter I; Fig 1.2).

To improve the accuracy of point-of-capture/point-of-return data during the 1992 season, research personnel participated in the fishery to gather the berried females for tagging. Eighteen boat-days provided 205 berried females between May 20th and June 7th. Our on-board participation allowed an animal to be tagged and released within 3 min. and 20 m of point-of-capture. Also, the study area was expanded to include the deeper fishing grounds in the "outer" fishing area (See Fig 1.2 Chapter I). Catch location and biological variables were recorded as in 1991. Variation in depth between tag and recapture as well as the female's movement rate (expressed as $m \cdot d^{-1}$) were calculated. Another fishing survey by the research team, was carried out the 24th-25th June and 8th-9th July, 1992, to extend information on berried female distribution.

Data analysis (parametric and non-parametric) were carried out using different modules of SYSTAT 5.2 for Macintosh (Wilkinson 1992). Statistical analysis are provided in Appendix 6.

2.3 Results

2.3.1 Temperature

Temperature patterns during 1991 and 1992, inter-or intra-year patterns differed from mid-spring to early fall (Fig. 2.3). Mean annual temperatures for these years were respectively 6.9 °C and 5.1 °C (3 m) and 5.1 °C and 4.8 °C (17 m). During the spring to summer/early fall, a strong thermocline developed to 15-20 m deep, during both years (Fig. 2.4).

Temperature at 3 m varied little from the upper 8-9 m (Fig. 2.4), whereas at 17 m it was both colder and fluctuated more markedly (Figures 2.4, 2.5). The wind and the deep cold waters of Chedabucto Bay influenced the thermocline depth on the Canso fishing grounds; variations in temperature of 7 to 9 °C may occur within hours at 17 m (Fig. 2.5). The average daily (daily maximum plus daily minimum divided by two) temperature during the experimental period (May 21st to September 30th, 1991) was 12.0 °C and 9.2°C at 3 m and 17 m, respectively; during 1992 they were, respectively, 11.1 °C and 7.6 °C. A difference of 0.9 °C and 1.6 °C was found in the mean daily temperatures at 3 m and 17 m, respectively, between the years. The average number of degree-days of both years (the sum of the daily average temperatures above 0°C) during the study period were, respectively, 1707 and 1151 at 3 m and 17 m, a difference of 556 degree days or 33%.

2.3.2 Embryo condition at the start of the study

The maturity of the embryos (PEI) and the size (CL) of both the caged and wild females at the start of the experiment in May 1991 and 1992 are shown in Table 2.1. Both the PEI and size of wild caught, but not for caged animals, was significantly different between years (ANOVA; $F_{1,541} = 9.175$; $p = 0.003$, and $F_{1,502} = 4.765$; $p = 0.030$; $n = 506$, respectively). Significant differences in embryo development between depths were not found at the beginning of each year's experiment.

2.3.3 Caged females

During both years (May to September), all caged females survived and, except for two small females (69 and 77 mm CL), egg masses appeared in good condition through to hatch.

Embryos at both 3 and 17 m depth remained without noticeable development well into spring for both 1991 and 1992 (Figs. 2.6C, 2.6D, 2.6G and 2.6H). Embryos resumed

development in early June at 3 m and in mid-June at 17 m, and developed rapidly through to hatch. Rate of embryonic development ($\mu\text{m} \cdot \text{d}^{-1}$) was significantly higher in 1991 than in 1992 (ANOVA; $F_{1,68} = 4.732$; $p = 0.033$), and was also significantly higher at 3 m than at 17 m (ANOVA; $F_{1,68} = 26.3$; $p = 0.000$; $n = 72$).

Females at 3m with more advanced embryos in early May, showed rapid development once water temperatures reached 7-8°C (June 5th-7th, 1991 and June 13th-19th, 1992; Figs. 2.6A and 2.6C respectively). All larvae were liberated 30 to 40 d later (July 3th-10th, 1991; July 3rd-25th, 1992) when water temperatures reached 13-14°C (Fig. 2.6A, 2.6C). The less mature embryos in 1991 resumed development almost two weeks after the advanced embryos and were (Fig. 2.6C) liberated 25 d later (August 2nd-5th) when water temperatures were ~ 17°-18°C (Fig. 2.6A). During 1992, the advanced embryos developed rapidly from the experiment's beginning (May 20th), when water temperature was ~ 5 °C (Figs. 2.6B and 2.6D). A marked increase in embryo development was evident around June 17th-19th, when the temperature was 9 °C; larval hatch began July 8th at a temperature of 11-12 °C (Figs. 2.6B and 2.6D). The less mature embryos resumed development along with the advanced embryos (Fig. 2.6D); however, mean hatching occurred about 20 d later (\approx July 28th) with some embryos hatching as late as August 25th (Fig. 2.6 D).

Advanced embryos held at 17 m during 1991, showed some development at temperatures < 5 °C, though development was greater when temperature were over 5 - 6 °C (late June) (Figs. 2.6E and 2.6G). Larval hatch began July 15th at water temperatures of 9-10°C (Figs. 2.6E and 2.6G). Delayed embryos began development in early July at a temperature of 9 °C (Figs. 2.6E and 2.6G). Larval hatch began August 10th at water temperatures of ~ 10 °C (Figs. 2.6E and 2.6G). The colder temperature regime at 17 m during July through mid-August 1992 (Fig. 2.6F), extended the embryonic period into late summer (Fig.

2.6H). Some of the advanced embryos developed rapidly during a brief period of warmer water (~ 8 °C) occurring the first week of July (Figs. 2.6F and 2.6H); some hatched shortly after (Fig. 2.6H). Temperatures dropped below 6-7 °C through the second half of July through to August 10-11 (Fig. 2.6F), retarding hatching, except for two well advanced clutches. Temperatures after August 15th, rose above 9 °C, initiating another major hatch (Figs. 2.6F and 2.6H). Some less mature embryos extended development well into September (Fig. 2.6H). In general, 75% of the clutches at 17 m hatched 20 d and 35 d later than those at 3 m depth for 1991 and 1992 respectively (Fig. 2.7). Also, hatching was later at both depths by 19 d (3 m) and 30 d (17 m) in relation to 1991 (Fig. 2.7). Furthermore, the difference in the 75% hatch rate between 3 m in 1991 and 17 m in 1992 was 45 d (Fig. 2.7).

2.3.4 Free range females

No relationship was found between the initial (May) depth of tagged (DT) females and their length (CL) or the maturation of their respective embryos (PEI) (Pearson $r = -0.065$; Table 2.2). During early Spring, more than 65% of the females presented advanced embryos (> 400 μm). This condition was always found in larger females, those >95 mm CL; < 95 mm CL carried both developed and undeveloped embryos (Fig. 2.8).

Of the 226 ovigerous females tagged in 1991, 76 (33.6%) were recaptured during the fishing season (closed July 6th), but only 67 (29.6%) were returned with useful information. During the charter of late July/early August, only two tagged females were recovered from 450 trap-hauls. During 1992, of the 205 tagged ovigerous females, 85 (41.5%) were returned with useful data on movement and 67 (32.7%) were assessed for embryo development.

Most of the berried females tagged and released in the inner and middle area showed

reduced movements (< 500 m), whereas females from the deeper outer area made longer (up to 10 km) movements toward the middle and inner areas (Fig. 2.9). Though little long-shore movement of berried females from the middle and inner area was detected, there was a clear movement of these animals to shallow waters (Fig. 2.10) within the same area.

During 1991, from the original depth of capture and release (12.6 m) May 20th-23rd, 12 lobsters were recovered at a mean depth of 7.3 m two weeks later (Fig. 2.10A). The group of 50 animals tagged June 13th, were captured and released at a mean depth of 9.0 m (Fig. 2.10A). Thirty one females were recovered at a mean depth of 8.4 m between June 15th and June 25th, and 24 females were recovered, July 1st to 5th, at 6.1 m. During the charter of early August, two June carapace-tagged females were recovered at 9.0 m (Fig. 2.10A). The mean depth of capture during the charter, of 20 non-tagged, late-stage berried females was 9.5 m. Mean depth of first-capture for the three areas in May/June 1992, averaged 15.7 m (Fig. 2.10B). The pattern of movement to shallow water was as in 1991, though in deeper waters due to the expansion of the study to deeper areas. The animals moved steadily to shallow water. Nineteen females were recovered in early July at a mean depth of 9.1m. During the last week of the experiment (July 7th to 15th), the end of the 1992 fishing season, the berried females were captured in deeper water (13.0 m) (Fig. 2.10).

During both years, the females from deeper waters showed both the largest depth change (DV) ($r = 0.682$; $p < 0.001$) (Table 2.2) and the fastest rate of movement (RM) to shallow waters ($r=0.85$; $p < 0.001$). No relation could be established between animal size and rate of movement (RM) ($r= 0.024$; $p < 0.001$), probably due to the reduced number of large animals (>100 mm CL) observed (< 5%) (Table 2.2).

Embryonic development rate of free ranging females was close to that of animals caged at 3 m during both 1991 (ANOVA; $F_{2,48} = 11.65$; $p < 0.0001$) and 1992 (ANOVA; $F_{2,44} = 10.596$; $p < 0.0001$) (Fig. 2.11). Between May 20th and June 19th, 1991, the rate of

embryo development was $0.55 \mu\text{m (PEI)/d}^{-1}$; this rate increased to $2.97 \mu\text{m/d}^{-1}$ in the period from June 19 to July 3-5 (Fig. 2.11 A). The same pattern was observed during 1992, although the rate of development appeared lower than in 1991 (Fig. 2.11 B).

2.3.5 Commercial fishing survey analysis

During the fishing survey carried out June 24th and July 8th, 1992, berried females showed the same distribution pattern as tagged animals (Fig. 2.10 C). On July 8th-9th, 23.9% of the berried females caught by the fishermen were already hatching (Fig. 2.12).

2.4 Discussion

2.4.1 Embryonic development and temperature regime

This study confirms that the natural development rate of late stage *H. americanus* embryos is affected by water temperatures (Perkins 1972). Embryonic development and hatching was delayed 20 to 35 d if ovigerous lobsters remained in temperatures averaging $8.5 \text{ }^{\circ}\text{C}$ (those occurring at 17 m) during the last phase of the incubation period (from May to July) (Fig. 2.7). This delayed development would be even greater in deeper (colder) water such as that of the outer area off Canso, where berried females were found during May. In fact, the previously reported trapping survey demonstrated no embryo development from May through early July in this area. Cage experiments also showed that embryos in advanced condition ($> 400 \mu\text{m EI}$) in spring, developed faster and hatched earlier than the less mature embryos ($\text{PEI} < 400 \mu\text{m}$), even when the former were under cold temperatures. These differences in development between embryos < 400 and $> 400 \mu\text{m PEI}$, is due to the meta-naupliar molt cycle occurring in the egg (Helluy and Beltz 1991). Embryos $> 400 \mu\text{m}$ are ready for the transition from D0 to the irreversible molt stage D1 once the temperature goes over $5 \text{ }^{\circ}\text{C}$ (Aiken 1973). Those embryos with a $\text{EI} < 400 \mu\text{m}$ have still to complete stage D0, which is characterized by a developmental arrest independent of temperature (see details of an *in situ* embryonic cycle in Appendix I).

2.4.2 Berried female movement on the Canso ground

The Canso fishing ground is surrounded by deeper water, especially the inner basin of Chedabucto Bay where underlying waters are permanently cold (Figs. 2.1 and 2.4). Strong northeast winds force these cold waters through channels to fill the basins of the Canso ground, producing sudden fluctuations of the temperature, especially evident at 17 m depth (Fig. 2.5).

Berried females move to shallow warmer water during mid-spring and this accelerates the rate of final embryo maturation. During the spring-summer period the difference in average temperature on the Canso grounds between 3 and 17 m depth is $\sim 3^{\circ}\text{C}$, with a net gain of 556 degree-days in the shallower water. Moving to shallow waters during spring allows the late stage berried females to maximize their environmental temperature and escape the greater fluctuations in temperature at intermediate depths (17m). Though, there was an homogenous layer from surface to at least 8 m depth (Fig. 2.4), the berried females appear to concentrate at about 7-9 m depth during this period (Fig. 2.10). This late spring-summer distribution near the thermocline allowed the eggs to accelerate embryonic development (Fig. 2.11), and produce an early hatch (Fig. 2.12). Under the prevailing conditions of the eastern shore, particularly the Canso area, an early larval release would provide the larvae more time in warmer temperatures to complete development and reduce mortalities (Templeman 1936, Caddy 1976, MacKenzie 1988), seek suitable substrate and settle as juveniles (Cobb, 1968, Cobb et al 1989). The late larval stages are less viable in cold water with high mortalities observed at 10°C (MacKenzie 1988). Laboratory studies show larvae hatched late in the season (fall, winter) take longer to become postlarvae and have higher mortality rates than those hatched in summer, even when temperatures are identical (Aiken et al 1982, Aiken and Waddy 1986). In Northumberland Strait, larval survival to Stage IV appeared to be greatest for larvae hatched early in the season (Caddy 1976).

2.4.3 Comparisons with other inshore populations

The dynamics of berried female movement on the Canso ground appear different to that observed for inshore females of the western Bay of Fundy, and Grand Manan, N. B. In the latter area, berried females make extensive seaward movements to take advantage of the warmer winter waters of the deep basins, compared to coastal shallows. Here in the basins, an important portion of the embryonic development is carried out (Campbell 1986, see his Figs. 6 and 10). These animals return to shallow water during spring/summer to complete embryo development and hatching. By contrast, on the Canso ground, berried females are caught down to 37 m depth during May where bottom temperatures fluctuate between 1.5 -2.5 °C. Low catch rates during the May tagging, suggest movement of berried females is just beginning. The cold, deep waters of nearby Chedabucto Bay, unlike the Bay of Fundy, do not present a physiological advantage to late-stage berried females, as it remains < 2 °C during the winter (Fig. 2.4). Trapping experiments during winter did not provide any lobsters beyond 40 m depth (Appendix 4). As well, the bottom topography in this portion of the Scotian shelf prevents direct communication with the warmer slope waters. In the northern Gulf of Maine and mouth of the Bay of Fundy, slope water enters the shelf basins through channels and gullies (McLelland 1954 a,b, Smith *et al* 1978). Thus, it is here hypothesized that berried females on the Canso ground overwinter at the same depth at which they are caught in early May. As the water warms and a thermocline develops in the upper 10-15 m, females move to shallow water during spring and concentrate between 7-9 m depth (Figs. 2.4 and 2.10). Most tagged lobsters in our study were recaptured within 1 km of the tagging site, except for some tagged in the deepest areas outside of the inlet system of Canso (Fig. 2.9). However, due to the bottom topography, these short movements allow females to find a variety of habitats, with a range of temperatures (Figs 2.1, 2.3). This is probably a common situation along the eastern shore, and is probably the reason for the short seasonal movements observed in nearby areas (Duggan and Pringle, 1988, Jarvis 1989, Miller *et al* 1989)

The reason for the apparent movement back to deep water (11-13 m) at the end of the embryonic period (Fig. 2.10), can only be speculated upon. Jarvis (1989), also observed a similar phenomenon when tracking late stage berried female lobsters with ultrasonic transmitters in Jeddore Harbour, N.S. He suggested these may be specific places where females move for larval hatch. In Grand Manan, berried females congregate in specific areas with strong tidal currents, which has been suggested to facilitate larval dispersion (Campbell 1990). This behavior is well known in other Caribbean lobsters such as *P. argus* (Buesa Mass 1970). The sequence of molting and mating may also play a role in this downward movement. Females seek out and choose males in the mating process (Atema *et al* 1979, Karnofsky *et al* 1989). Large males appears to concentrate in 10 to 15 m of water at this time of the year on the Canso grounds (unpub. data).

2.4.4 Synchronization with other physiological and reproductive processes

A berried female has to synchronize molting and mating following embryo maturation and hatching (Aiken and Waddy 1980). While tracking free-ranging females in the Jeddore area, Jarvis (1989) found a one month interval between hatching and molt. The same interval was observed in more than sixty lobsters in our cages during 1991 and 1992 (Fig. 2.13). Thus a late hatch, as observed for some females kept at 17 m, may leave a narrow margin for the molting process. Indeed, during both 1991 and 1992 lobsters with embryos initially < 300 μm at 17 m delayed hatch until September and hence did not molt. The reason for this phenomenon is unclear; the restrictive condition of the cages, which were reported to reduce the rate of molting, (Stewart and Squires 1968), were similar at both depths and thus not the problem. Also, temperatures were above 5 °C (the threshold for molting [Aiken 1973]) during late October, a month after the last hatch. Additional evidence for the critical time required between larval hatch and molt, those smaller marked females of 1992 with less mature embryos, were recovered at the same size in 1993. It appears then, that a proportion of the female population is unable to maximize embryo

development, hatching, and molting, under the prevailing conditions of the Canso ground.

Interannual variation in temperature may also influence this synchronization. It was observed in this study that small changes in average temperature (0.9 °C at 3 m and 1.6 °C at 17 m) between years produced a marked impact on embryonic development; the peak (75%) of the hatching period was delayed almost 25 d in the caged females during 1992 (Fig. 2.7). Therefore, it is reasonable to speculate that in a year with cold summer temperatures, as sometimes occur in this area (see Petrie et al, 1987), some of these reproductive or physiological processes will be extensively delayed or precluded.

2.4.5 Summary

This study showed that environmental temperature affects embryonic development. Cold deep water at 17 m reduces the rate of embryonic development and may delay hatching for almost a month. Berried females move from deep to shallow water during spring and remain close or above the thermocline. These movements involve short horizontal distances in the inner and middle areas, but females from the deep outer area make movements of up to 10 km to the shallower areas. Females remain in shallow water until embryos are ready to hatch, then move to deeper waters where probably hatching, molting, and mating take place. It was also observed that if a female arrived in spring with poorly developed embryos (PEI < 400 µm), hatch is later and so is molting. In some females with embryos with PEI < 300 µm, a late hatch precluded molting that year. Consequently, it seems that an alternative for coping with a short season of warm water on this ground is for females to arrive in spring with well developed embryos (PEI > 400 µm EI). On the Canso grounds, more than 65% of the berried females arrived in the springs of 1991 and 1992, with well developed embryos. Thus, it is suggested that mature females are probably maximizing temperatures in even earlier stages of the embryonic process, perhaps during ovarian maturation the previous summer.

Table 2.1. Mean (± 1 SD) embryo stage (PEI) and female size (CL) of both the wild stock and the caged females at the start of the experiment in spring of 1991 and 1992.

=====

	1991		1992	
	Wild	Caged	Wild	Caged
n	223	40	273	40
PEI	403.1 \pm 63.5	401.1 \pm 11.1	380.5 \pm 87.0	395.6 \pm 75.6
CL (mm)	88.8 \pm 9.4	89.8 \pm 11.1	86.4 \pm 9.7	89.8 \pm 11.0

Table 2.2. Pearson r correlation matrix between ln-transformed variables. Data from 1991 and 1992 are grouped. Underlined values are highly significant ($p < 0.001$).

=====

	CL	PEI	DT	DV	RM
Female size (CL)	1.000				
PEI	<u>0.231</u>	1.000			
Tag depth (DT)	-0.065	-0.044	0.000		
Depth variation (DV)	<u>0.486</u>	0.044	<u>0.682</u>	1.000	
Movement rate to shallow water (RM)	0.024	-0.040	<u>0.572</u>	<u>0.850</u>	1.000

=====

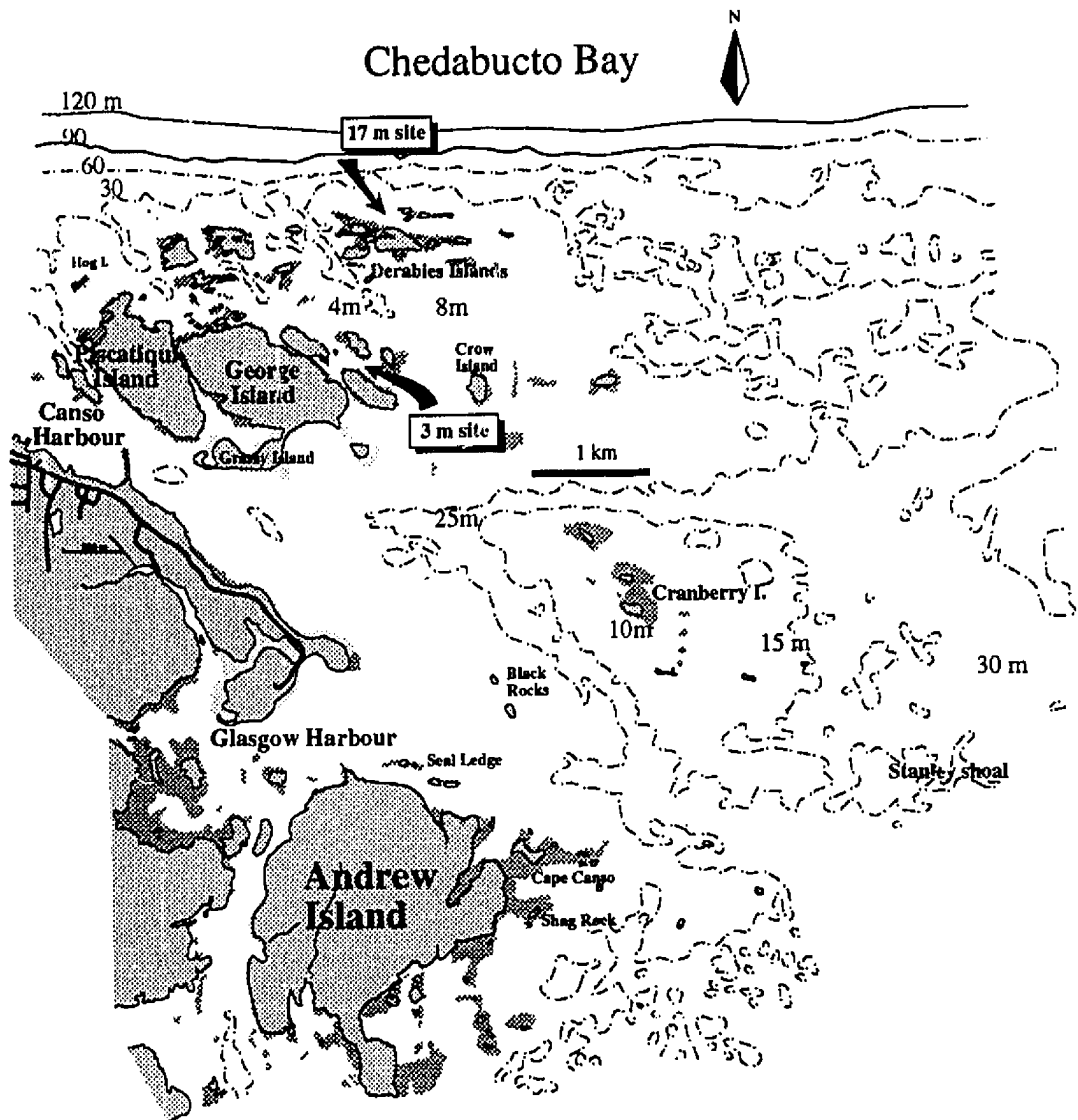


Figure 2.1. The Canso N.S. fishing ground with the two cage sites demarcated.

The depth isobars are in metres.

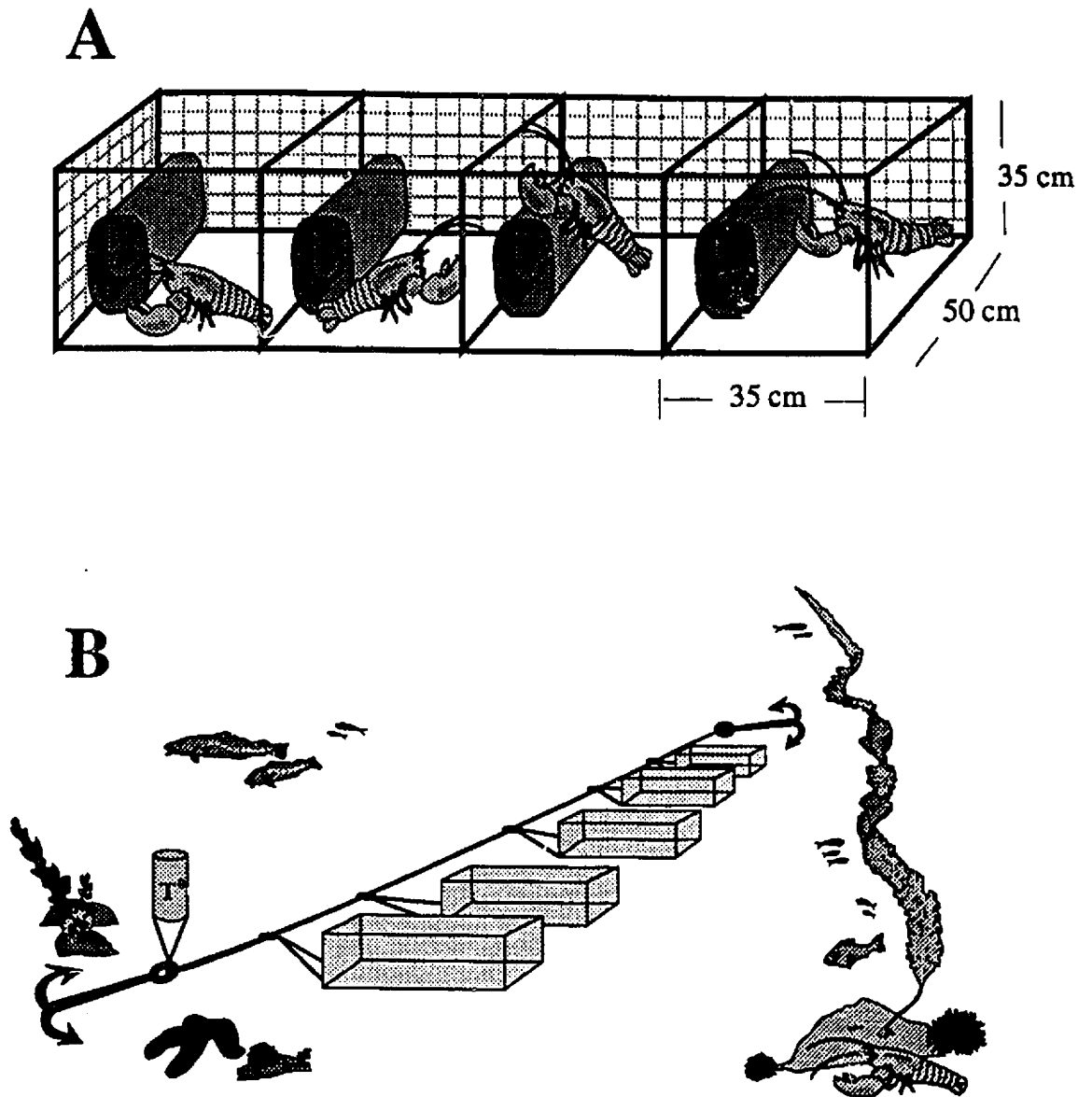


Figure 2.2. The design of the experimental cages; (A) detail of the cage with lobsters and individual shelters and (B) their arrangement on the bottom, using anchors. Note the the attachment of the thermograph.

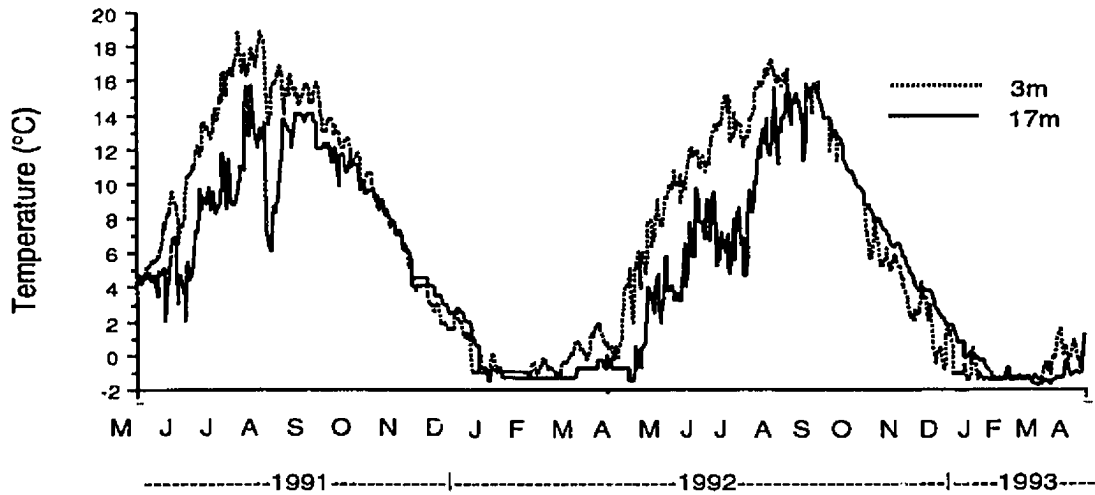


Figure 2.3. Temperature regimes (mean daily temperatures) at the Canso study site (Fig. 1)

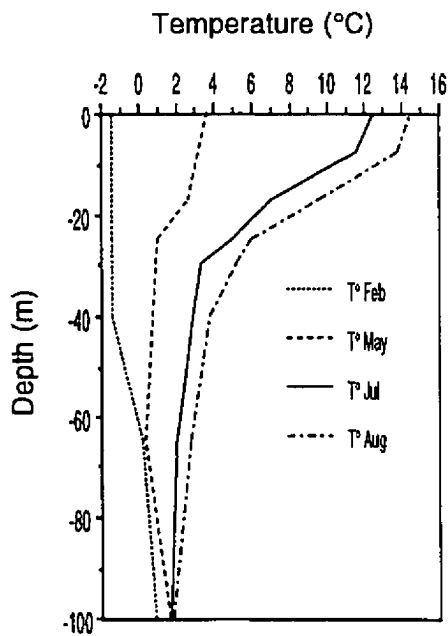


Figure 2.4. Mean seasonal temperature profile on the Canso fishing grounds during 1992.

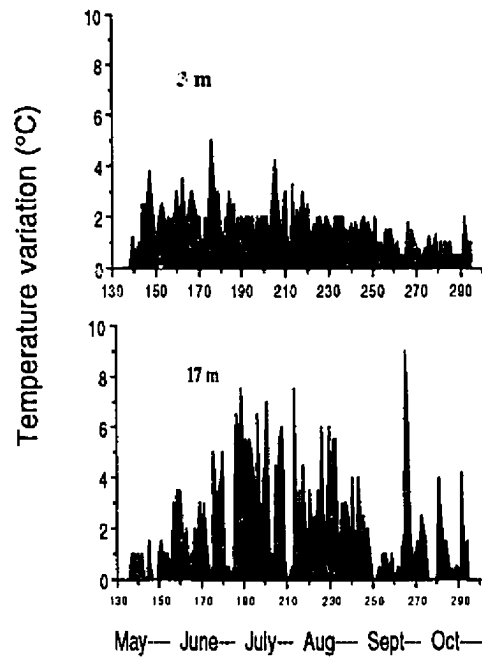


Figure 2.5. Daily variation (max-min) in water temperature at 3 and 17 m of the Canso fishing ground during 1992.

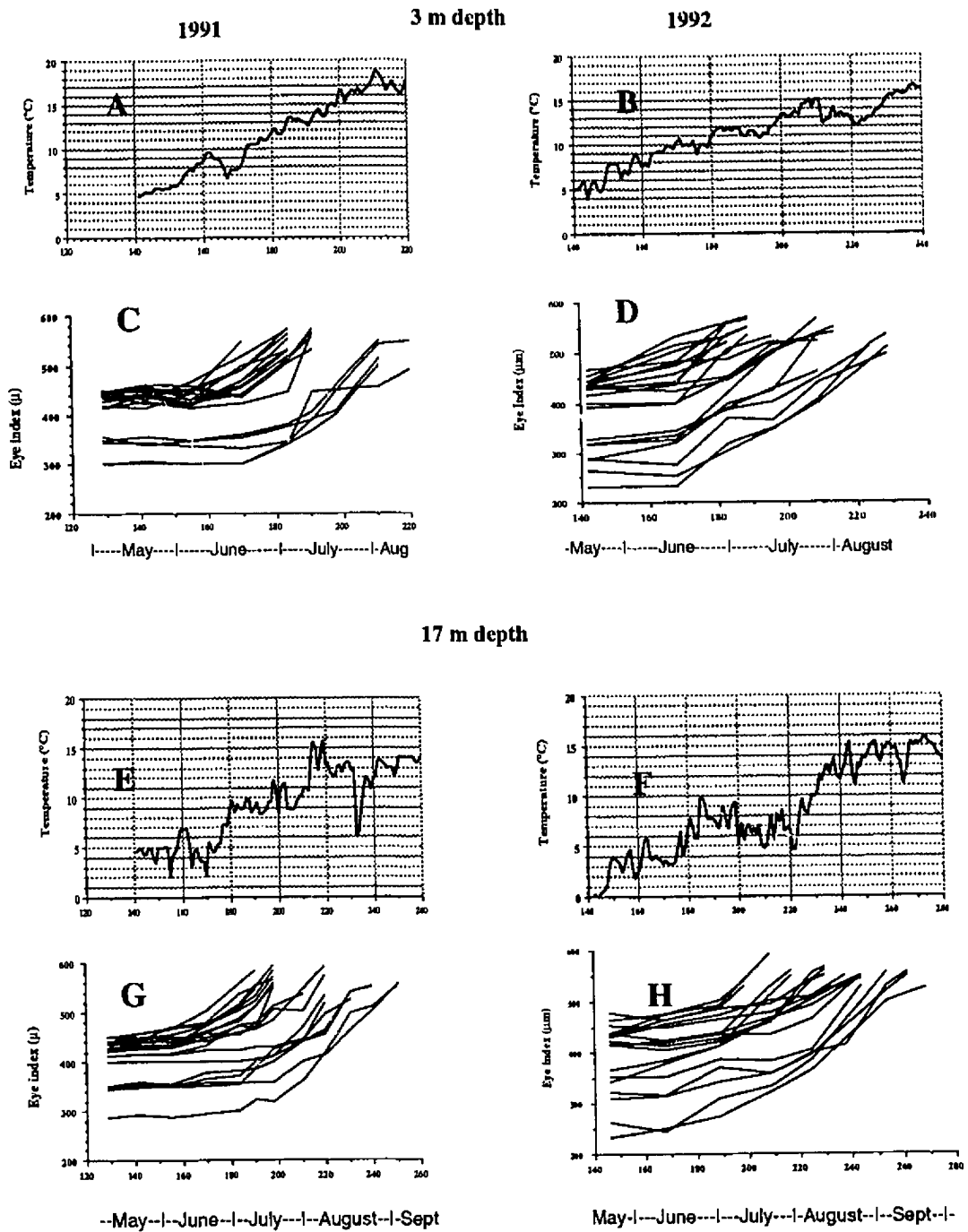


Figure 2.6. Mean daily temperature ($^{\circ}\text{C}$) regimes (A, B, E and F) and embryonic development expressed as PEI (C, D, G and H) at the Canso study sites (See Fig. 2.1) during 1991 and 1992. Each line represents the embryonic development of the clutch of a single female. The termination of each line represents the date of completion of hatch (± 3 days).

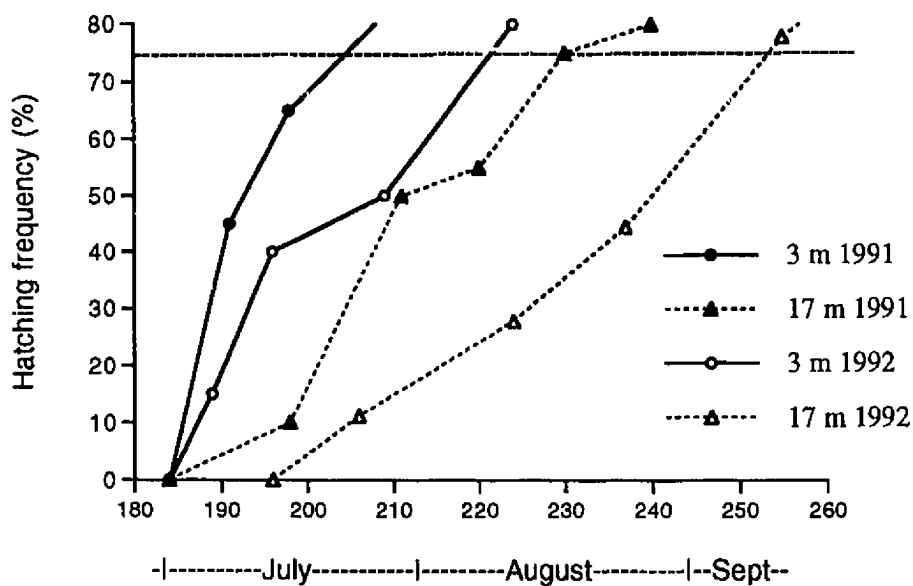


Figure 2.7. Frequency of caged (3 m and 17 m) females with hatched clutches in relation to time, during both 1991 and 1992 at Canso, N. S.. Horizontal broken line denotes the time when 75% of the clutches were hatched.

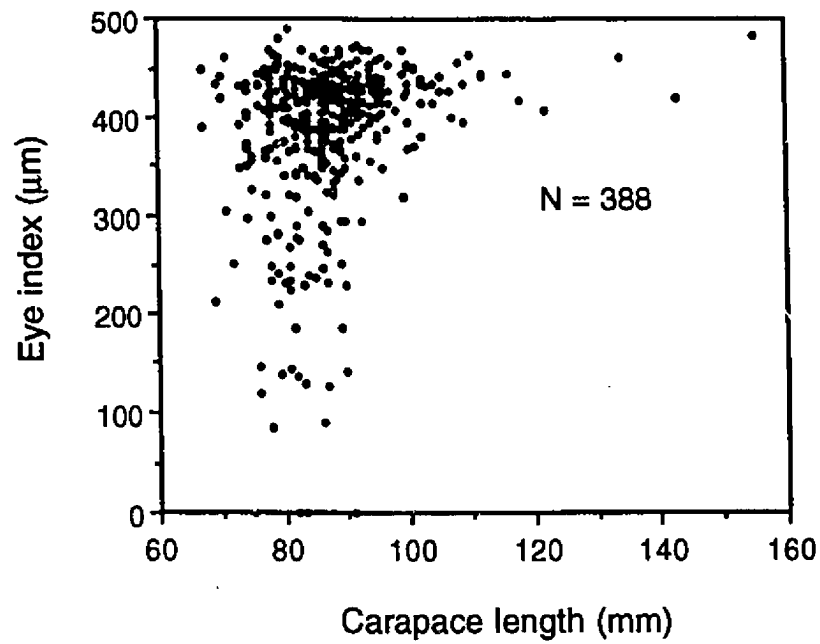


Figure 2.8. Relationship between female length (CL) and embryo maturation (PEI) during late May for 1991 and 1992.

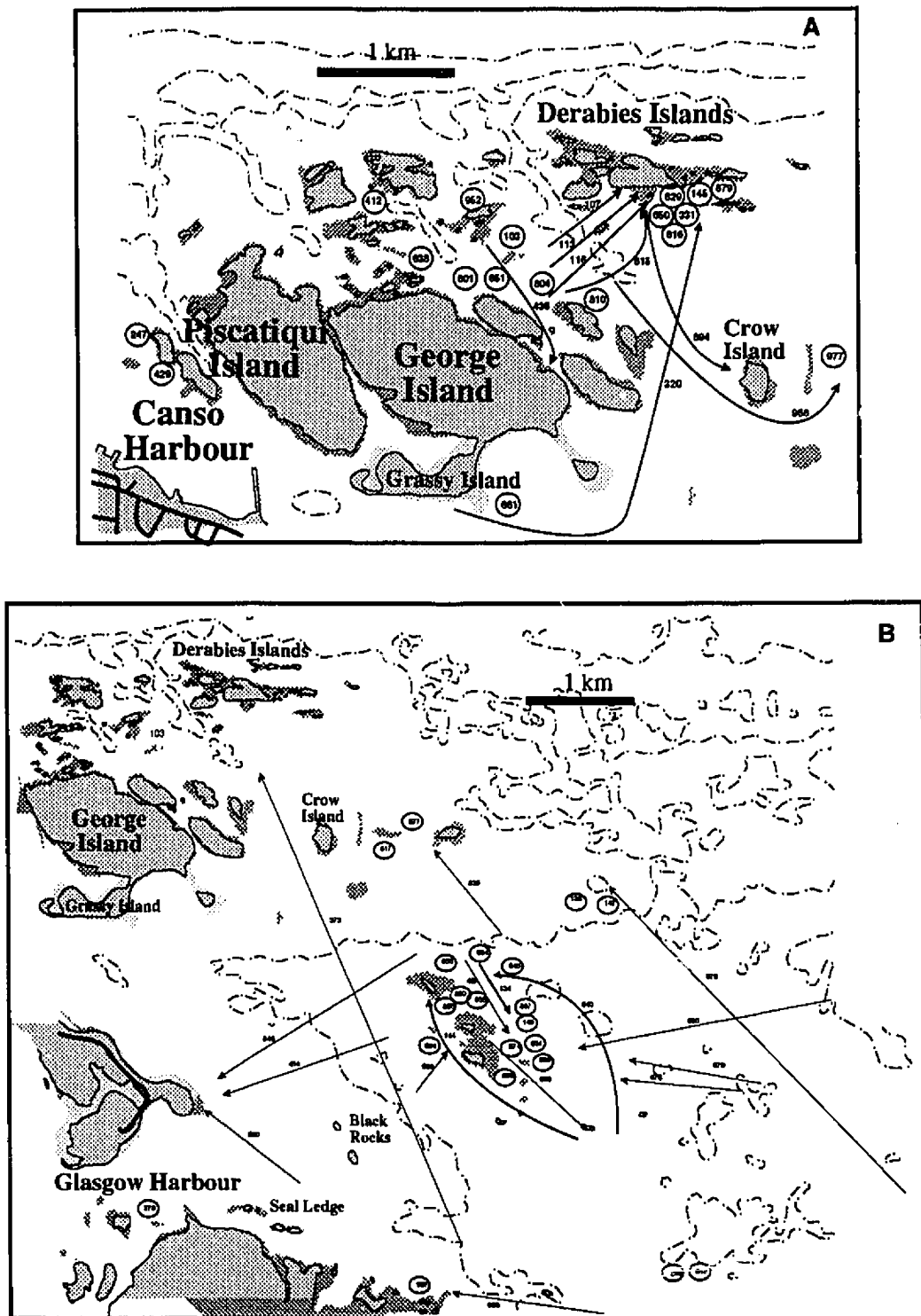


Figure 2.9. Movement of tagged berried females from the (A) inner and (B) middle and outer areas of the Canso fishing grounds. End of arrows are point of recapture; circles are lobsters moving less than 500 m; numbers are identification tags.

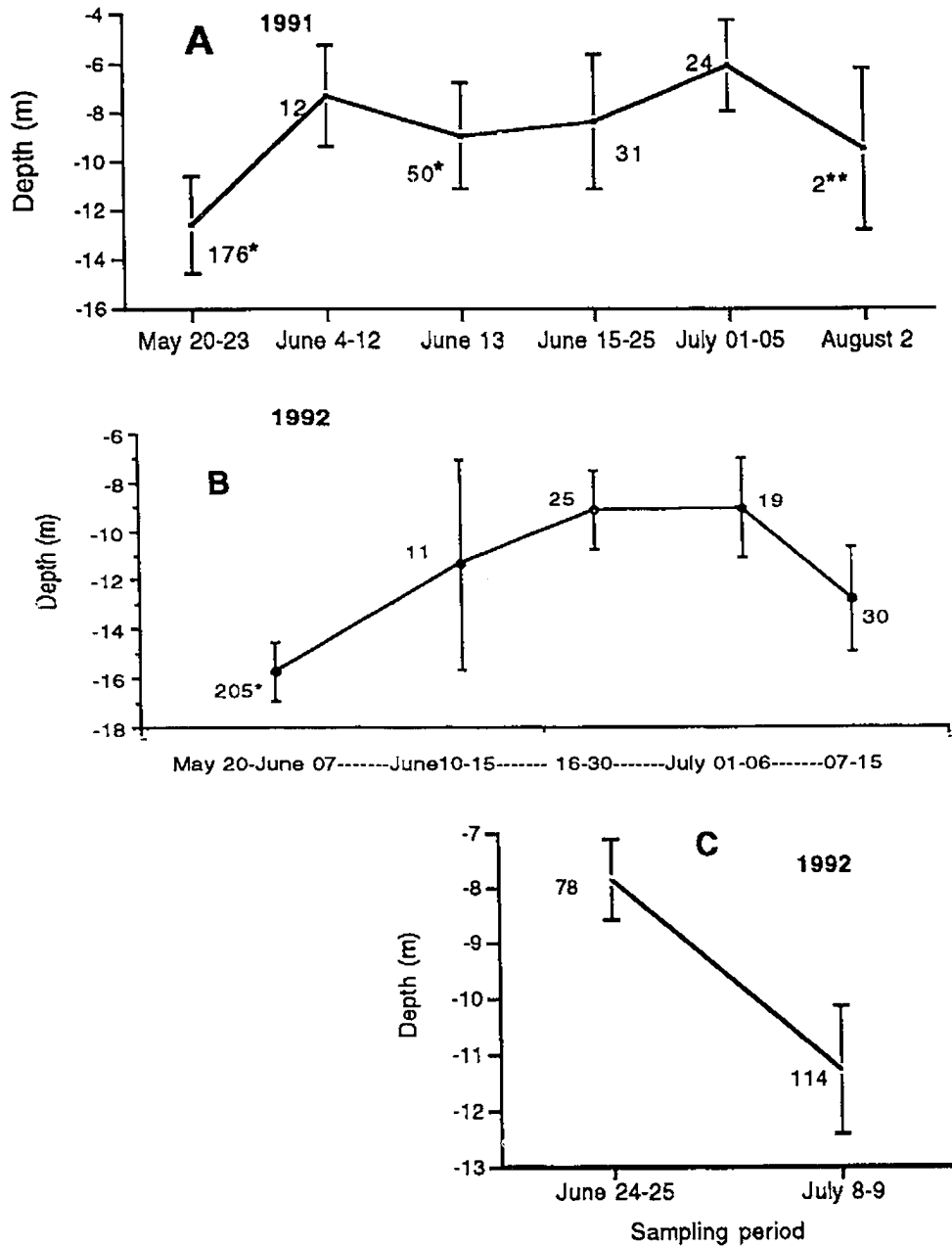


Figure 2.10. Mean depth of tagged and recaptured late-stage berried females during spring-summer 1991 (A) and 1992 (B) in the Canso area. (C) Mean depth of capture of berried females during two fishing survey periods in 1992: (*) indicates number of lobsters tagged in May 20-23 and June 13, 1991, and May 20 to June 7, 1992. Other numbers indicate recaptures. (**) indicates lobsters recaptured during charter (August 1-3) after the fishing season of 1991. Vertical bars = 95% confidence intervals.

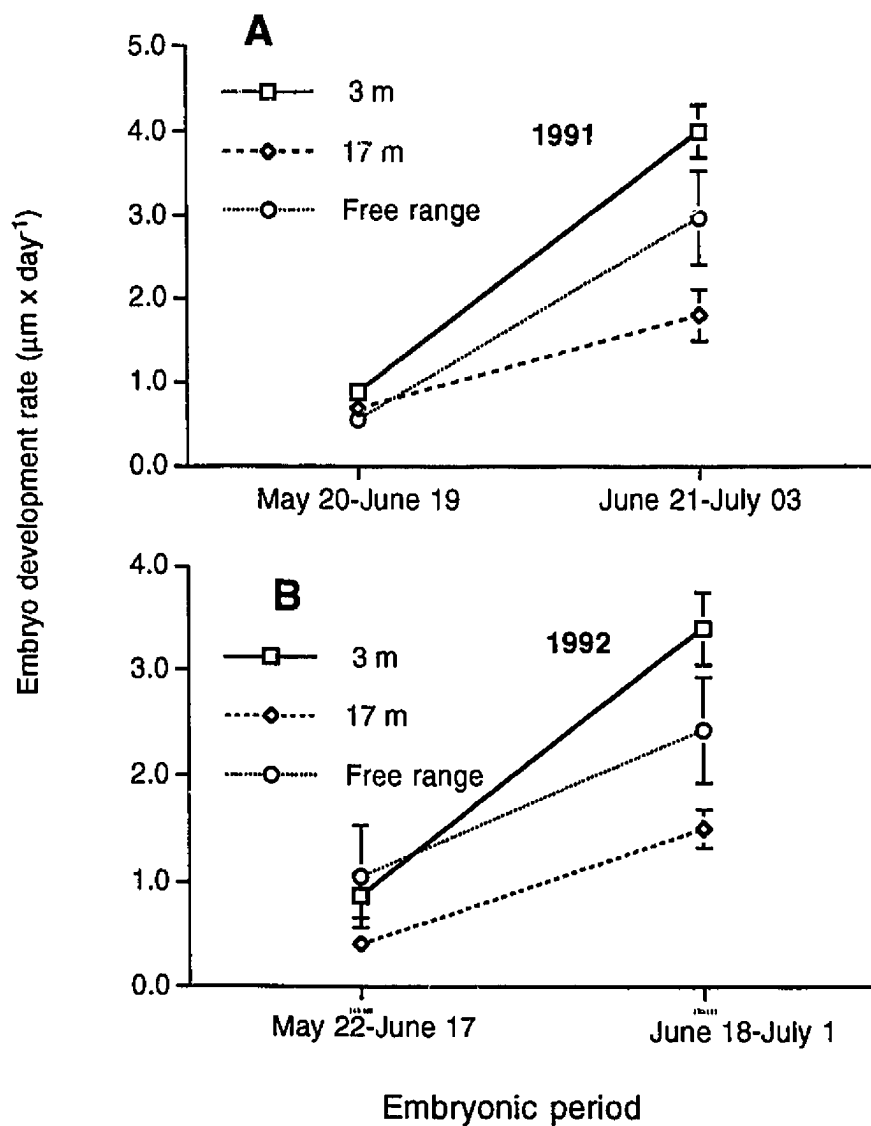


Figure 2.11. Rate of embryonic development (± 1 SE) of caged and free-ranging tagged females during 1991 and 1992 at Canso N.S.

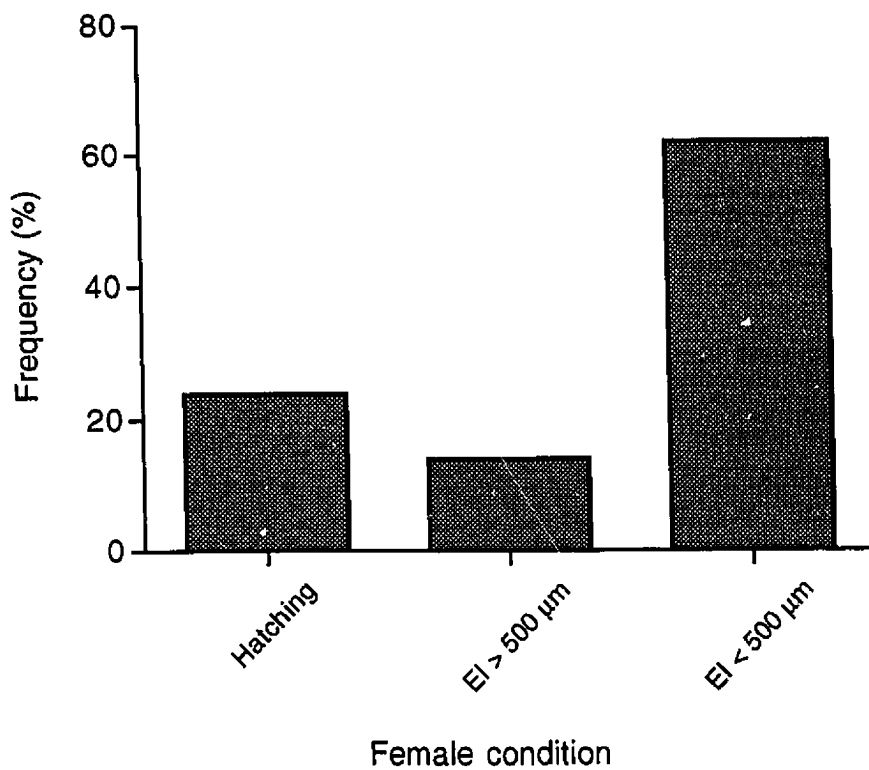


Fig. 2.12. Embryonic development of ovigerous females obtained from commercial fishermen on the Canso N.S. ground, July 8-9, 1992.

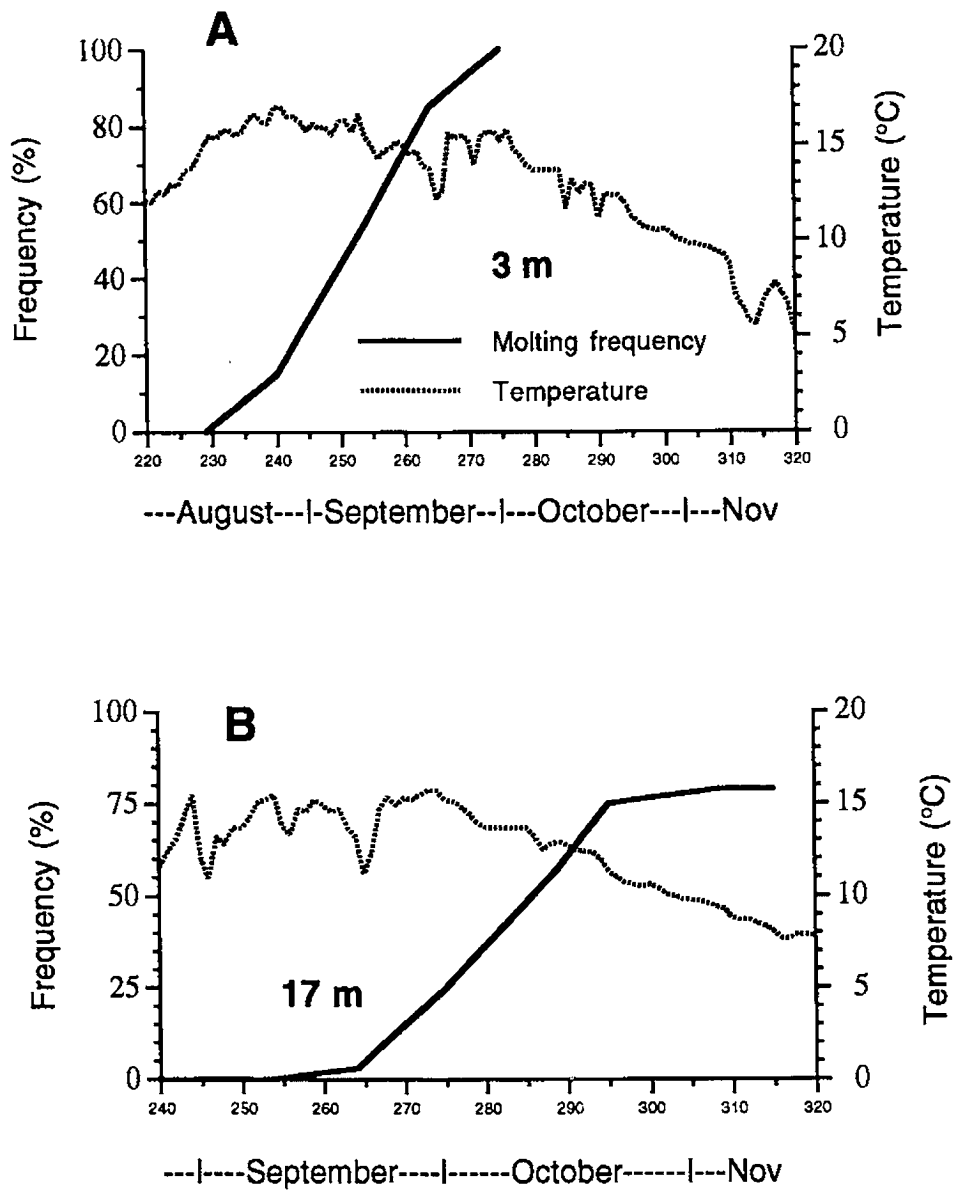


Figure 2.13. Molt frequency of late stage berried females in relation to temperature at the Canso experimental sites; (A) 3 m and (B) 17 m depth.

CHAPTER III

OVARIAN DEVELOPMENT AND MOVEMENT OF MATURE FEMALE LOBSTERS IN RELATION TO TEMPERATURE.

3.1 Introduction

Temperature is the main factor affecting the reproductive cycle of the American lobster, *Homarus americanus*, (Aiken and Waddy 1985, 1986, Waddy and Aiken 1986, 1991); low winter (<5 °C) and high spring-summer (> 10 °C) temperatures are necessary to synchronize final vitellogenesis and hence spawning. If the increase in temperature above 5 °C is delayed in spring, final oöcyte maturation and spawning will be delayed (Waddy and Aiken 1991). For example, low summer temperatures in areas such as Newfoundland may preclude spawning in a significant number of mature lobsters (Ennis 1971, 1982). Continuous low spring temperatures may cause the female to abort ovarian development through yolk re-absorption of the mature oöcytes (Ennis 1984b, Waddy and Aiken 1991). The laboratory-based information on the key role of temperature in the reproductive process, has lead to the suggestion that the seasonal deep/shallow water movements of lobsters observed in cold water habitats, such as the continental shelf's offshore canyons and in the Bay of Fundy, maximizes temperature to achieve molt and reproduction (Cooper and Uzmann 1971, Uzmann et al 1977, Lund 1979, Fogarty et al 1980, Campbell and Stasko 1986, Campbell 1986, Pezzack and Duggan 1986, and this study; Chapter II).

Most inshore lobsters do not make extensive migrations (Cooper and Uzmann 1980, Miller et al 1989), though small-scale, seasonal movement from shoal (5-20 m) to deep water (30-60 m) has been reported. These movements have not been associated with reproductive events; it has however been suggested they occur to avoid stormy waters and ice scouring (Cooper et al 1975, Ennis 1983). In areas such as the southern Gulf of St.

Lawrence, migration to maximize temperatures appears unnecessary since spring-summer water temperatures are likely sufficient for completion of reproduction (Campbell and Stasko 1986). Annual migration from outside to inside the Magdalen Is. lagoons, was observed when a temperature gradient inside/outside of the lagoons developed; molting occurred in the warmer lagoonal waters (Templeman 1935, Munro and Thierrault 1983).

Nova Scotia's eastern shore has been hypothesized as a marginal climate for lobster recruitment (Huntsman 1923, Harding et al 1983). Frequent summer upwelling events produce marked changes in temperature (Petrie et al 1987) during the season of major reproductive events. In portions of this area, late stage berried females may experience major changes in temperature by moving only short distances. This is due to irregular bottom topography and a strong thermocline which develops during late spring-summer. The rate of embryonic development, and hence the time of hatch could be advanced if the female ascends only a few meters to be above the thermocline during late spring.

Trapping surveys suggest mature (functionally reproductive) lobsters migrate seasonally in this area (Chapter I). Fishermen trap lobsters in early May in waters 14-24 m depth. Most traps are gradually moved shoreward, until by late May-early June, they are in less than 10 m depth. Fishermen by the end of the fishing season (late June-early July) know that large females are more abundant in shallow waters. This has led to a suggestion that lobsters are moving to shallow water during late spring coincidental with the fishing season.

Optimizing temperature to synchronize different biological functions, such as embryo development and hatching, molting and mating, appears to be a critical factor for the species along the Nova Scotia's eastern shore, where the warm water period is brief. As previously established, it seems that female arrival in the spring with well developed embryos (> 400 μm PEI) facilitates this synchronization. In fact, more than 60% of the

berried females carried well-developed embryos in the spring of 1991 on the Canso N.S. grounds (Chapter II).

The current study assesses movement of mature female lobsters in relation to temperature during spring/early summer, the period just prior to egg extrusion.

3.2 Materials and Methods

Two experiments were carried out with mature females in 1992: first, females were caged until after spawning (egg extrusion) at two depths with different temperature regimes; and second, free-range animals were tagged and recaptured. Ovary development was followed in each experiment using the Pleopod Tegumental Gland (PTG) technique (Aiken and Waddy 1982). Approximately 65% of the lobsters studied were adult-Ia animals (Aiken and Waddy 1982) that had molted and mated the previous summer and were thought to be ready to spawn for the first time. Fifteen percent were larger adult-III lobsters, likely having experienced one or more spawns. The remaining 20% were immature animals.

3.2.1 Caged females

The two experimental sites were in 3 m and 17 m water (Fig. 3.1), each having significantly different temperature regimes (Chapter II). Trap-caught, non-ovigerous females, were purchased from local fishermen between May 25th-29th, 1992. Forty animals, varying in size from 77 mm to 121 mm CL ($90.4 \text{ mm CL} \pm 10.1 \text{ SD}$), were randomly selected; each was assigned an identification number, and placed in separate compartment in one of ten wire cages (130 x 50 x 30 cm); five cages were located at each depth (see Chapter II). To maintain similar physical conditions to those of the related study on embryo maturation (Chapter II), the cages were secured in the same location.

Previous studies in the area (Chapter I and II) showed that at 17 m the temperature was both, colder and more variable than at 3 m. The Ryan thermographs are sometimes not sufficiently sensitive to respond to sudden temperature changes, therefore, a more sensitive electronic thermograph (Sea Log Temperature Recorder VEMCO Ltd.) was deployed at 17 m on June 15, 1992.

Ovary resorption has been associated with unfavorable holding conditions or handling stress in the weeks prior to spawning (Templeman 1940, Aiken and Waddy 1985).

Female handling was thus kept to a minimum; one pleopod only was clipped from each female monthly for three months. The cages were always diver located, secured with a line and brought on board the field vessel for no more than 10 to 15 min. Each clipped pleopod was placed in cool, salt water in separate vials. The vials were placed on ice and transported to the laboratory where each pleopod was examined with a stereo microscope within 2 d (more than three days caused PTG degeneration). Ovary development was followed through to spawning. Every 7-10 d from July 20th through September 10th, a visual non-physical inspection of each female was done underwater by SCUBA-equipped observers, which provided accurate time-of-spawning data. The caged females were fed a rotating diet of frozen mackerel and squid at each observation. As well, invertebrates moving through the cages were seen being consumed by the caged lobsters.

Caged females, after spawning, were kept at depth to assess development of newly extruded embryos throughout the winter to spring, when the experiment was terminated (May 23, 1993).

3.2.2 Free ranging females

Lobster catchability in May is likely reduced due to low water temperature (McLeese and Wilder 1958). Consequently, it took seven days to collect 340 females between May 20th

and 27th, 1992. Science personnel tagged lobsters aboard the fishing vessels on the Canso fishing ground between 5 and 40 m depth. The Canso fishing ground was divided into three release areas; "inner", "middle" and "outer" (Fig. 3.1). The whole process of removal from trap, tag and release was reduced to 3 min., and within 20 m of point-of-capture. Numbered carapace tags (sensu Wilder 1954, Stasko 1980) were applied to the females. Loran coordinates and depth were taken for each lobster released, lobster size recorded (CL), and a pleopod removed. As lobsters were captured during the fishing season, the fishermen were paid for each legal sized lobster captured and tagged.

Fishermen, upon capturing a tagged female, would immediately contact research personnel via VHF radio, who then boarded the vessel at-sea, recovered the female, recorded both capture location (Loran coordinates) and depth, removed a pleopod and returned the lobster to the fisherman along with a \$ 5.00 reward. A second release was not made because rate of second recapture was low during previous experiments (Chapter II). To complement information on female distribution and ovarian condition, additional data were obtained from at-sea observations aboard commercial boats during June 24th-25th and July 8th-9th, 1992.

Statistical analyses [regressions, Pearson (r) correlation indices, and contingency tables] of the different variables obtained from caged, tagged and recaptured, as well as commercially fished lobsters, were carried out using different modules of SYSTAT 5.2 for Macintosh (Wilkinson, 1992). They are provided in Appendix 6 unless otherwise indicated.

3.3 Results

3.3.1 Temperature regimes

Daily average temperatures at the beginning of the study (May 20th) were ~ 4-5 °C at 3 m; these increased steadily, reaching > 10 °C by June 18 (Fig. 3.2). Temperatures at 17 m

were more variable than at 3 m during the period (May 20th - Sept 6th), averaging ~ 0 °C at the beginning of the study and reaching 10 °C by early July (Fig. 3.2). However, by mid July temperatures dropped, hitting a low of 5 °C by July 20th and remaining < 10 °C through August to 12th; increase thereafter was steady, reaching 16 °C in late August (Fig. 3.2).

3.3.2 Cage experiments

Females appeared healthy during the study, with only one female resorbing her ovaries (Table 3.1). A clear effect of temperature on ovary maturation was observed in females caged at 3 m and 17 m.

Ovary development

Females at the beginning of the experiment had undeveloped ovaries with more than 59% of the females with a PTG value of < 2.5 at both depths (Table 3.1). Only 25% and 15% of the females respectively had a PTG stage of 2.5 at 3 m and 17 m respectively. Differences in ovary maturation between depths at the beginning of the experiment were not significant ($X^2 = 0.163$; $df = 1$; $p = 0.686$). By early July when temperatures averaged ~ 11.5 °C at 3 m (Fig. 3.2), the ovaries showed noticeable development, with 65% of the females at PTG stage 3 -3.5 (Table 3.1). By contrast, at 17 m in 7.5 °C water only 15% of the females were at these stages (Table 3.1). Differences in PTG stage with depth were significant ($X^2 = 9.53$; $df = 1$; $p = 0.002$). The last pleopod analysis on Aug. 13th, at 3 m showed that one female (5%) had resorbed her oöcytes, three small females (CL 75-78 mm) had undeveloped ovaries, and the remaining 16 (80%) had extruded eggs (Table 3.1). At 17 m, one female (5%) was in stage 3, two (10%) were in stage 3.5, four (20%) were in 4; 11 (55%) bore newly extruded eggs and two (10%) females (78 mm and 81 mm CL) bore undeveloped ovaries (Table 3.1).

Spawning Rate

In shallow water (3 m) the spawning process started on July 15 with an average temperature of 13.3 °C (Figs. 3.3 and 3.4 A). The spawning process accelerated and was completed by the end of July, when 10 females spawned between July 25th and 31st, at temperatures between 14-15 °C . Spawning was completed in 16 d (Fig. 3.3).

Water temperature at 17 m was colder and more variable than at 3 m during the last period of ovary maturation and spawning (Fig. 3.4 B). It remained around 5 °C well into June and rose to slightly over 10 °C only after July 4th, remaining at about 10 °C until July 16th when colder water returned and persisted to August 7th (Fig. 3.4 B). Females began spawning July 30th, and 60% had spawned by August 13th, (Figs. 3.3, 3.4 B). Egg extrusion proceeded at a low, but steady rate with all animals having spawned by August 31st, 1992; the process took a total of 32 d (Fig. 3.3).

Newly extruded embryos

Development rate of newly extruded embryos was significantly faster (t-test, $p < 0.001$) at 3 m than at 17 m (Fig. 3.5). Embryos of females caged at 3 m presented a fast and synchronous development immediately after extrusion (end of July), reaching an eye index (PEI) of $430 \mu\text{m} \pm 12.0$ (SD) by late November when water temperatures were ~ 7-8 °C (Fig. 3.6 A). Embryos at 17 m developed slower than those at 3 m, reaching a PEI of only $341 \mu\text{m} \pm 21.9$ (SD) when development stopped in early January at ~3 °C (Fig. 3.6 B). Mean PEI after the winter (in May 1993) was significantly higher (t-test, $p < 0.001$) at 3 m than at 17 m (Fig. 3.5).

3.3.3 Distribution and Movement of Tagged Females

Of the 330 ovarian animals tagged, 138 (41.8%) were recovered during the fishing season (until July 12th). Non-ovigerous females were initially distributed between 4 and 40 m

depth, May 20th - 27th. No relationship was found between depth at first capture (tagging) and lobster size (Pearson, $r = -0.244$; $p > 0.05$; Table 3.2).

Movement

Ovarian females moved to shallower water through the study period (Fig. 3.7), moving from a mean depth of $18.1 \text{ m} \pm 7.7$ (SD) in late May to $11.9 \text{ m} \pm 5.6$ (SD) by early June. The rate of movement to shallow water decreased to mid June, when they were recovered at a mean depth of $10.3 \text{ m} \pm 6.4$ (SD), and this rate continued to slow when in early July, the end of the fishing season, they were at a mean depth of $9.6 \text{ m} \pm 4.5$ (SD).

The movement of the tagged lobster on the fishing grounds was shoreward. These movements were $< 1 \text{ km}$ in those females tagged in the inner and middle areas. However, lobsters tagged on the outer area moved longer distances, some moving 8 km to the inner area (Fig. 3.8 A, B). Lobsters from the deepest waters moved significantly faster to shallow water than the rest of the tagged females ($r = -0.362$; $p < 0.001$; Table 3.2) (Fig. 3.9). No correlation was found between lobster size and depth of recapture at the end of the fishing season (July 8-9) (Table 3.2), however, the number of recaptured females was low (28) and larger tagged females ($> 100 \text{ mm CL}$) were rare. By contrast, a significant correlation ($r = 0.410$; $p < 0.001$; Table 3.2) between size and depth of capture was found in the commercially fished females; females $> 100 \text{ mm CL}$ were all recaptured shallower than 11 m , with all but three under 9 m (Fig. 3.10).

Ovarian development

Adult-Ib (molting and spawning in the same season) were rare in the study area, and less than 1% according to Robinson (1979) (see also Appendix IV). This was fortunate for, according to Aiken and Waddy (1982), adult-Ib reproductive class female complicate the PTG staging system, as they retain their undeveloped stage 1 cement glands until after the summer molt, resulting in pubertal year appearance in early summer. Therefore, the

prediction of spawning based on the PTG technique was not confounded by adult-1b females.

At tagging, 54 % of the females had immature ovaries (PTG stage < 2) (Fig. 3.11). There was no relationship between depth at tagging and ovary maturity ($r = -0.278$; $p > 0.05$; Table 3.2), but the larger lobsters had significantly ($r = 0.319$; $p < 0.001$, Table 3.2) more advanced ovaries than the smaller lobsters.

More than 60% of the tagged lobsters were recaptured before June 19th, only three week after release (Fig. 3.7) when the temperatures were still averaging 7-8 ° C at 3 m and under 4 °C at 17 m depth (Fig. 3.2); no noticeable ovary development occurred during this period. Only 28 females (21.4%) were recaptured in early July when temperatures between 3 m and 17 m were respectively 9 and 12 °C (Fig. 3.2). Fifty percent of these females had a PTG stage ≥ 3 , which did not differ significantly ($\chi^2 = 2.54$; $df = 2$; $p = 0.285$) from those females caged at 3 m (65% \geq stage 3) and those commercially fished (48% \geq stage 3) (Fig. 3.12); those observed at 17 m were significantly less mature (only 15 % stage ≥ 3) ($\chi^2 = 10.84$; $df = 3$; $p < 0.013$) (Fig. 3.12, Table 3.3).

There was a trend from the fishing data, that by early July larger females (CL > 100 mm) had more mature ovaries than smaller lobsters ($\chi^2 = 34.7$; $df = 1$; $p < 0.001$) (Fig. 3.13, Table 3.2). Also, deeper occurring (> 15 m) females had less developed ovaries than those from shallow warmer water (≤ 15 m) ($\chi^2 = 114.0$; $df = 1$; $p < 0.001$). In fact, animals captured in waters deeper than both 15 and 20 m had PTG reading ≤ 3 and ≤ 2 respectively (Fig. 3.14).

3.4 Discussion

3.4.1 Cage experiments

Laboratory studies have suggested that ovary maturation and the spawning processes of inshore populations of lobsters of the Canadian east coast are mainly regulated by temperature (Aiken and Waddy 1985b, 1986b). Photoperiod becomes important in the control of spawning only when winter temperatures remain over 9-15 °C (Waddy and Aiken 1991). It has been suggested that in certain offshore habitats, where mature lobsters remain between 10° and 17 °C (Cooper and Uzman 1971), photoperiod regulates spawning (Nelson 1986). By contrast, Canadian Atlantic inshore lobsters are never exposed to winter temperatures above 5°C.

Others factors, such as trapping, handling, and caging in the months prior to spawning, could cause degeneration and oöcite resorption (Templeman 1940, Aiken and Waddy 1985a). Lipid and protein deficiencies due to diet could also affect final vitellogenesis (Castell and Budson 1974, Castell and Kean 1986). In the current cage experiments, all factors (salinity, photoperiod, food) but temperature were similar at both depths. Depth itself appears not to have an influence on time of spawning as egg extrusion occurs during the same period in both the shallow (off Lower West Pubnico, N.S.) and deep (on the offshore Browns Bank) waters of the northern Gulf of Maine; both locations have the same temperature regime (Campbell and Pezzack 1986).

Temperature regimes at 3 m and 17 m depth off Canso, N. S. (Fig. 3.1) were clearly different during the study period, and all else being equal, were likely the cause of the variance in the rate of ovary development and subsequent spawning of the caged females. The rate of ovary maturation of females at 3 m, was faster than those animals kept at 17 m, especially at the end of June/early July (Table 3.1). As well, the spawning period in the shallow site was more synchronous and of a shorter duration, occurring over 16 d, from

July 15th to 31st. The rate of ovary maturation of females at 17 m was slower than for the animals at 3 m and consequently the spawning period was delayed and spread over 32 days, from July 30th to August 31st (Fig. 3.3), most likely due to the colder waters (Fig. 3.4).

Waddy and Aiken (1991) showed vitellogenesis and subsequent spawning requires exposure to temperatures $< 5^{\circ}\text{C}$, followed by temperatures $\geq 10^{\circ}\text{C}$ for about three weeks. The present work supports this laboratory observation as an increase in spring temperatures over 10°C was necessary to initiate spawning (Fig. 3.4 B). However, the present work shows a minimum period of only two weeks at 10°C is sufficient to initiate spawning as was seen for 60% of the mature lobsters at 17 m (Figs. 3.3 and 3.4). Following this period a cold period with temperatures between 5° and 7°C prevailed for 23 d, with only brief periods with temperatures $> 10^{\circ}\text{C}$ (Fig. 3.4 B). Nevertheless, ovary development continued showing that once a certain degree of ovary maturation has been reached, the spawning process does not stop.

3.4.2 Female distribution and movement

During mid-spring (May 20th-27th) ovarian female lobsters were caught from 5 to 40 m, with an average depth of 18 m. This distribution is probably close to the actual winter distribution as lobsters are scarce deeper than 40 m along Nova Scotia's eastern shore (Pezzack 1984, Pringle and Duggan personal comm.). As was previously discussed for berried females (Chapter II), possible reasons for the absence of deep water lobsters off Canso is the temperature depth profile and bottom topography of this area, which presents no temperature advantage for the lobsters to either immigrate to or emigrate from the Canso fishing grounds.

Mature female Canso lobsters began moving from deep (18 m average) to shallow waters when temperatures rose above 3.4 °C in the mid-spring (Fig. 3.2), which is the range of temperature in which laboratory animals become moderately active (McLesse and Wilder 1958). Campbell (1986) described a similar seasonal deep-to-shallow migration of ovigerous females in June-July, two months after the shallow waters warm off the Bay of Fundy's Grand Manan Island. As well, the seasonal migration of ovigerous females into Magdalen Island shallow lagoons occurs between mid-May and the end of June, following both lagoon warm-up and the establishment of a thermal gradient into the lagoon from waters beyond (Munro and Therriault 1983). The current tagging study began when bottom temperature were $\approx 0^{\circ}\text{C}$ (May 20), suggesting that it was prior to lobster movement and that the captured lobsters were not coming from deeper waters.

The movement of mature females to shallow waters was particularly evident for the females tagged on the outer area (Fig. 3.8). The recaptured animals presented an east-west movement to the shoal areas, some being captured in the inner area. Unfortunately, fishing activity rapidly removed these animals from the grounds (more than 60% being recaptured before June 19th), making it difficult to assess their final destination. However, given the few that remained at the end of the fishing season, it appeared there would have been a continued movement to shallow water (Fig. 3.7). In fact, newly spawned lobster were found at an average depth of 6.6 m in this area in 1991 (see Appendix II). As was also observed for berried females (Chapter II), females in the inner and middle areas moved shorter distances than those from the outer area, but always to shallow water within their respective area.

An increased activity level in lobsters immediately after handling and release has been reported in studies with tagged lobsters (Jernakoff et al 1987 for *Panulirus cygnus*; Lund et al 1973, Maynard and Conan 1984, and Jarvis 1989 for *H. americanus*). In our tagging

experiment with mature females, we observed rapid movement to the shallow waters immediately after tagging in May. However, due to the unidirectional pattern of these movements, they were probably induced more by an environmental cue (Cooper and Uzmann 1980) rather than by a response to handling.

It is clear lobster movement to shallow warmer water accelerated ovary maturation rate, which is the first verification of such behavior influencing this important physiological function in nature. Temperatures at depths > 15 m appeared too cold to allow ovary maturation (Fig. 3.14). Though some low PTG stages (≤ 1) were found in shallow water, they were probably immature animals (Fig. 3.10). This work confirms the long standing hypothesis that migration is enhancing reproductive capability of the American lobster in marginal climatic areas (Cooper and Uzmann 1980, Campbell and Stasko 1986). Ovarian maturity of both tagged and wild-caught females during July was similar to that of females caged at 3 m (Fig. 3.12). Though the spawning process was not followed in the tagged females (commercial season ended July 12th, preventing further sampling), the similarity of the PTG pattern with those females caged in shallow water, suggests the normal spawning period in the wild stock of lobster in this area is similar to that of animals caged at 3 m. A 1991 study using a commercial vessel under charter showed the spawning process was well advanced by August 1st (Appendix II).

3.4.3 Animal size and ovary maturation relationship

During early July on the Canso grounds, large mature females (>100 mm CL) concentrated in shallow water (Fig. 3.10), and when they did they had more mature ovaries than the smaller mature females of deeper waters. (Fig. 3.14). Tagging studies in Maine waters (Dow 1974), off Cape Cod, Massachusetts (Morrisey 1971) off Southwestern Nova Scotia (Stasko 1978), and in the Bay of Fundy (Campbell and Stasko 1986) have

demonstrated that mature females tend to move sooner and further, either to deep or shallow water depending on the season, than smaller mature animals.

In the present study there was not a clear pattern of movement with size, probably because the short extent of the movement masked the size effect. It was clear though, that larger females were always more abundant in the inner area, at least through to July 9th. Previous surveys carried out in August 1991 in this study site (Appendix II), suggest that this segregation of size is maintained during the summer. As temperature would have the same effect for all mature females, this segregation of size through depth is difficult to explain. Lobsters are closely associated with shelters during all life history stages (Herrick 1911, Cobb 1971, O'Neill and Cobb 1979) and an increase in shelter availability increases the density of lobster in a particular area (Scarrat 1968, Stewart 1972, Sheehy 1976). Diving surveys on the Canso ground by the author showed a paucity of shelters in the granitic bedrock of the shallow inner area. Indeed, some females with newly extruded eggs (see appendix II) were utilizing every crevice available in the rocks. Due to the solid nature of the substrate in this area, shelters cannot be modified or increased as may occur on soft bottom (Cobb 1971, Stewart 1972). Thus, it is probable that shelters are a limiting resource in the inner area and large females are probably outcompeting the smaller females for prime location (Scrivener 1971). Though, small lobsters have been observed to successfully defend their shelters against larger lobsters in nature (O'Neill and Cobb 1979, Karnofsky et al 1989), most of these observations have been done on small immature animals. There is evidence supporting the fact that large females outcompete small females for access to dominant males (Atema 1986, Lee 1992) supporting the hypothesis that larger mature lobsters may outcompete smaller lobsters for prime brood location on the Canso ground.

3.4.4 Ovarian maturation and larval development

It was observed in Chapter II, that if berried females bore advanced embryos (PEI > 400 μm) in spring, they would hatch earlier, thus allowing the female to synchronize molting and mating during the summer-fall period. Though the duration of warm surface waters appears sufficient for larval development along the eastern shore (Moore et al 1986, Jarvis 1989), laboratory studies have shown larvae hatched late in the season (late summer-fall) take longer to reach Stage IV than those hatching in summer (Aiken and Waddy 1982). In Northumberland Strait, larval survival to Stage IV appears greatest for larvae hatched early in the season (Caddy 1976), and it is probably also true for the postlarval stage, which would have more time for substrate selection before settling (Cobb 1968, Botero and Atema 1982). Larval hatching during the warm period may be also synchronized to when peak food is abundant, as has been suggested for capelin (*Mallotus villosus*) larvae (Frank and Leggett 1983), although no similar data appear available for the American lobster.

It was hypothesized in Chapter II that the migratory behaviour of mature females would account for the embryonic stage found during the next spring. More than 60% of the ovigerous females carried advanced embryos (PEI >400 μm) during early spring (Chapter II). The present study of mature females shows that by moving to shallow waters during the spring the rate of ovarian development is accelerated and allows for an early spawning period. By remaining in shallow water during the summer the embryos attain the optimal maturity (PEI >400 μm) before the cold winter waters stops development (Figs. 3.5, 3.6, see also Appendix I). The greater frequency of the larger lobsters in the best micro-climatic conditions, will enhance the frequency of late stage embryos early in the summer. The study with late-stage berried females (Chapter II), confirms previous observations that larger females were carrying more mature embryos during the spring (Attard and Huddon 1987).

3.5 Summary

The present study shows that mature females move to shallow warm waters during spring-summer, and that this movement significantly accelerates rate of ovarian development, thus producing an early and more synchronous spawning period. By remaining in shallow water after spawning, a fast development of the newly extruded embryos occurs, reaching the "ideal eye index" of $> 400 \mu\text{m}$ and hence maturity before winter arrives. This behavior allows the advanced embryos to more readily exploit the warmer spring waters and to allow an earlier hatch. The females of early hatched embryos, will be able to better synchronize molting and mating before the temperature drops in late fall.

It is suggested that size segregation with depth among mature females, may be the result of lack of sufficient number of shelters in the inner area ; thus large females outcompete small mature lobsters and forcing them to deeper water.

Table 3.2. Pearson r correlation matrix between variables of tagged and recaptured animals. Some data analysis from the commercial fishery (*) on July are also included. Underlined values are significant ($p < 0.001$).

	CL	PTGT	DT	DC	PTGC	RBCH
Female size (CL)	1					
Pleopod tegumental gland at tagging (PTGT)	<u>0.319</u>	1				
Depth at tagging (DT)	-0.244	-0.278	1			
Depth at capture (DC)	-0.227 <u>-0.410*</u>	-0.122	<u>0.397</u>	1		
Pleopod tegumental gland at capture (PTGC)	<u>0.551</u>	<u>0.684</u>	<u>-0.580</u>	<u>-0.440</u> <u>-0.640*</u>	1	
Rate of bathymetric change (RBCH)	-0.215	-0.245	<u>-0.362</u>	---	-0.208	1

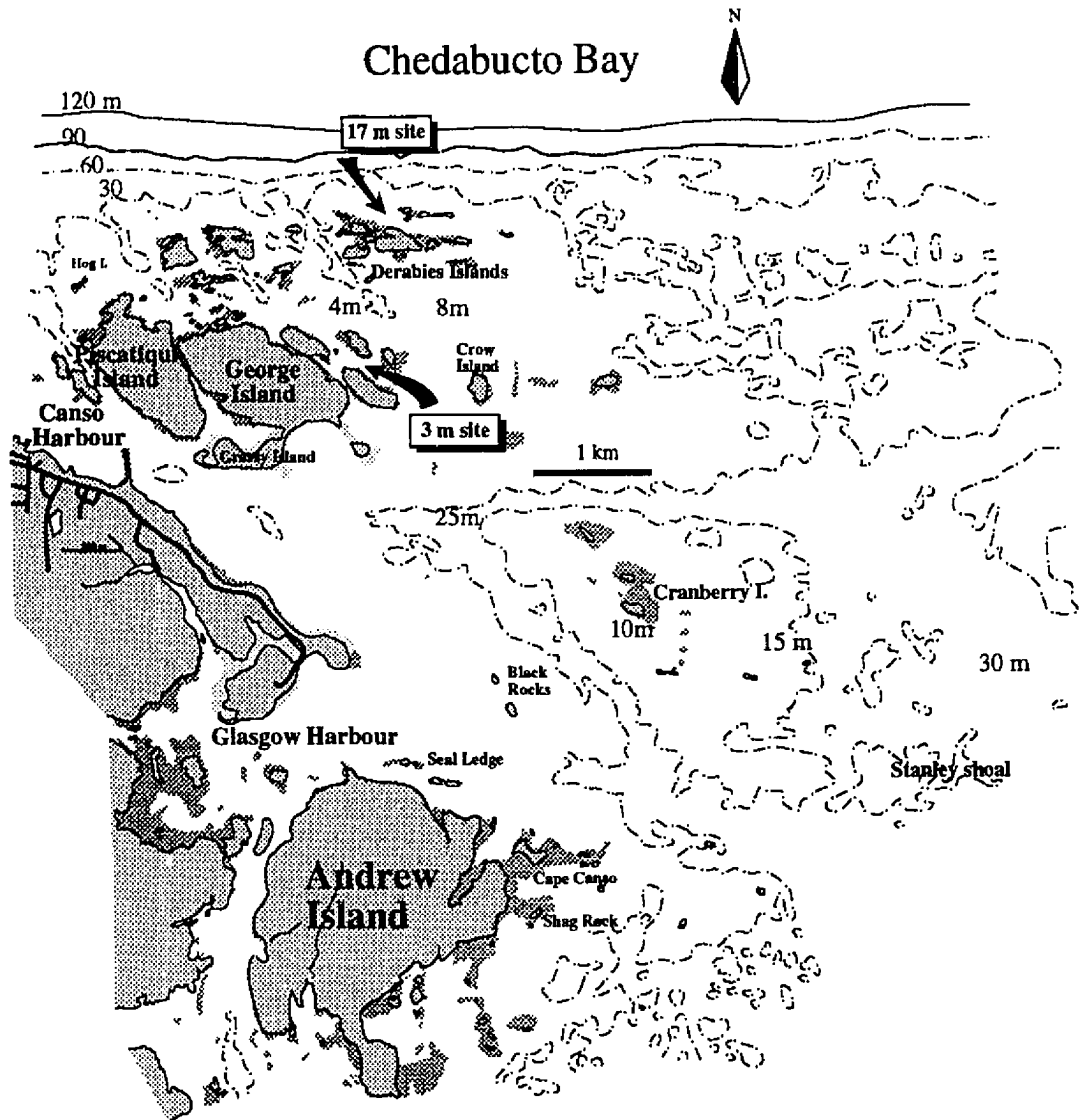


Figure 3.1. The Canso N.S. fishing ground with the two cage sites demarcated.

The depth isobars are in metres.

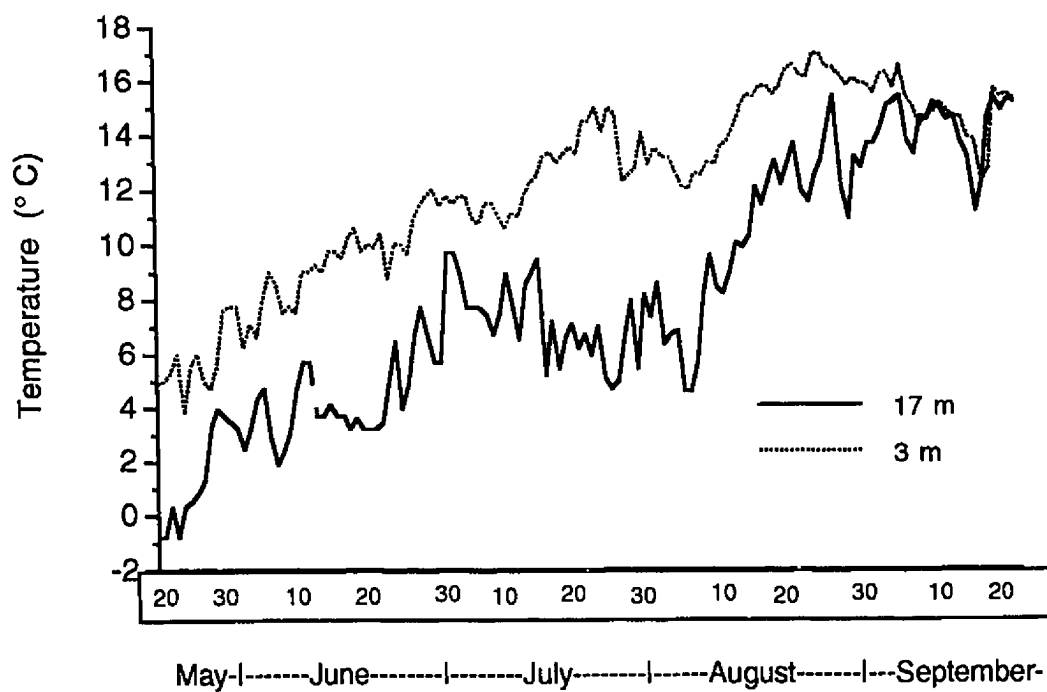


Figure 3.2. Temperature regimes at the 3 m and 17 m cages sites of the Canso, N.S. fishing grounds, during the study period

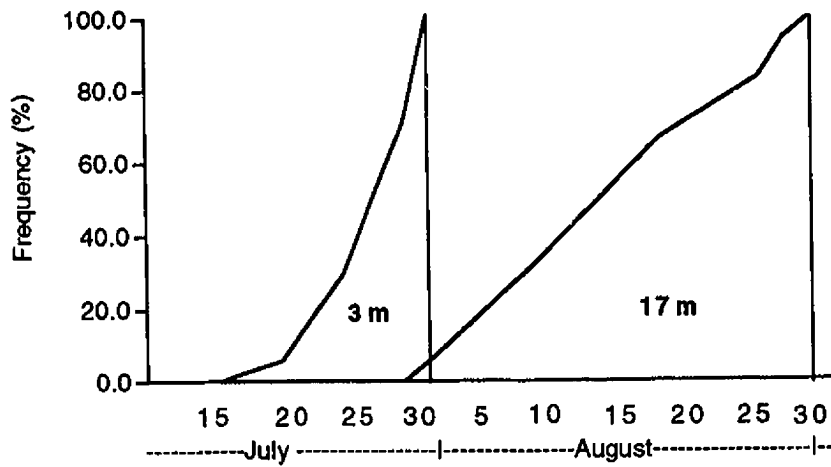


Figure 3.3. Percent spawned females over time while caged at 3 m and 17 m depth on the Canso N. S. lobster grounds in 1992.

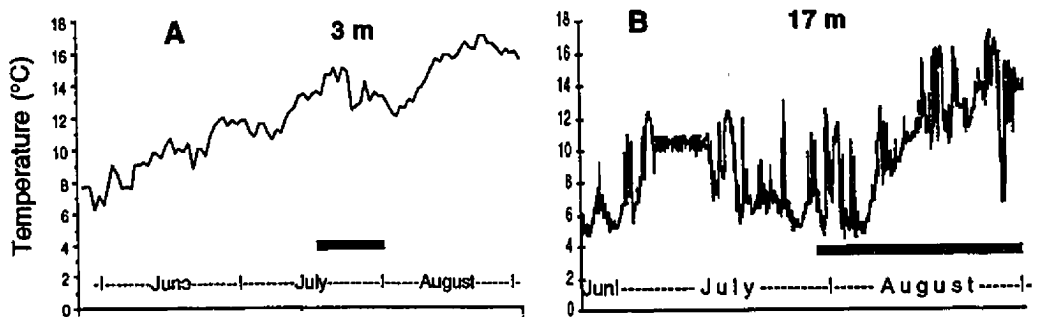


Figure 3.4. Temperature regimes for 1992 at the 3m and 17 m cage sites on the Canso, N. S. lobster grounds. Horizontal bars indicate the spawning period.

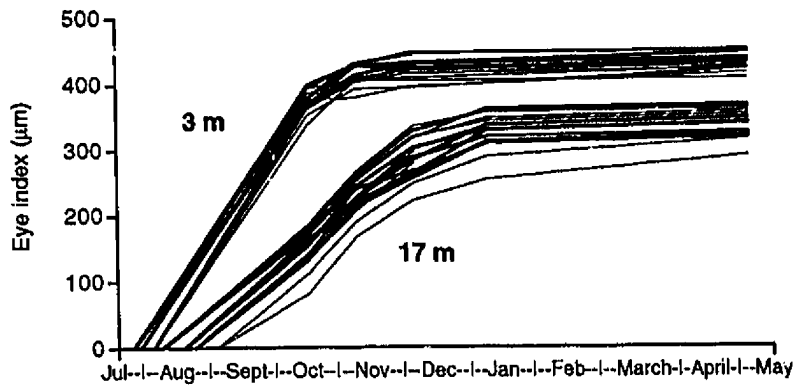


Figure 3.5 . Development of newly extruded embryos at both 3 and 17 m cage sites on the Canso, N. S. lobster ground (Each line represent the average of ten embryos of a single clutch).

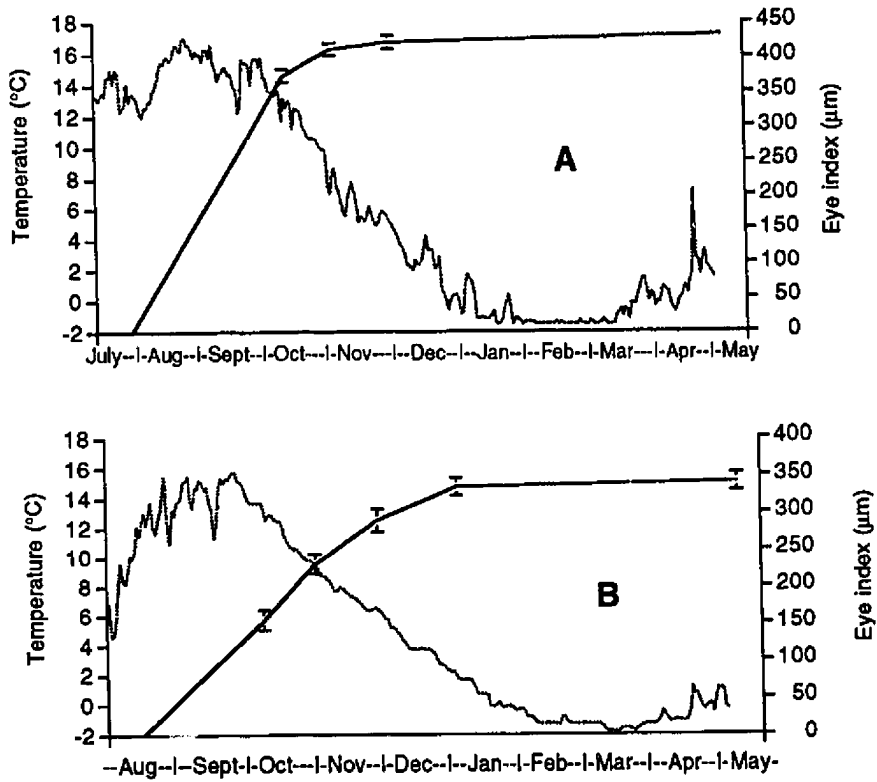


Figure 3.6. Mean development rate of newly extruded embryos (solid lines) and water temperature at 3 m(A) and 17 m (B) on the Canso N.S. lobster ground during 1992.

Vertical lines are 95% confidence intervals.

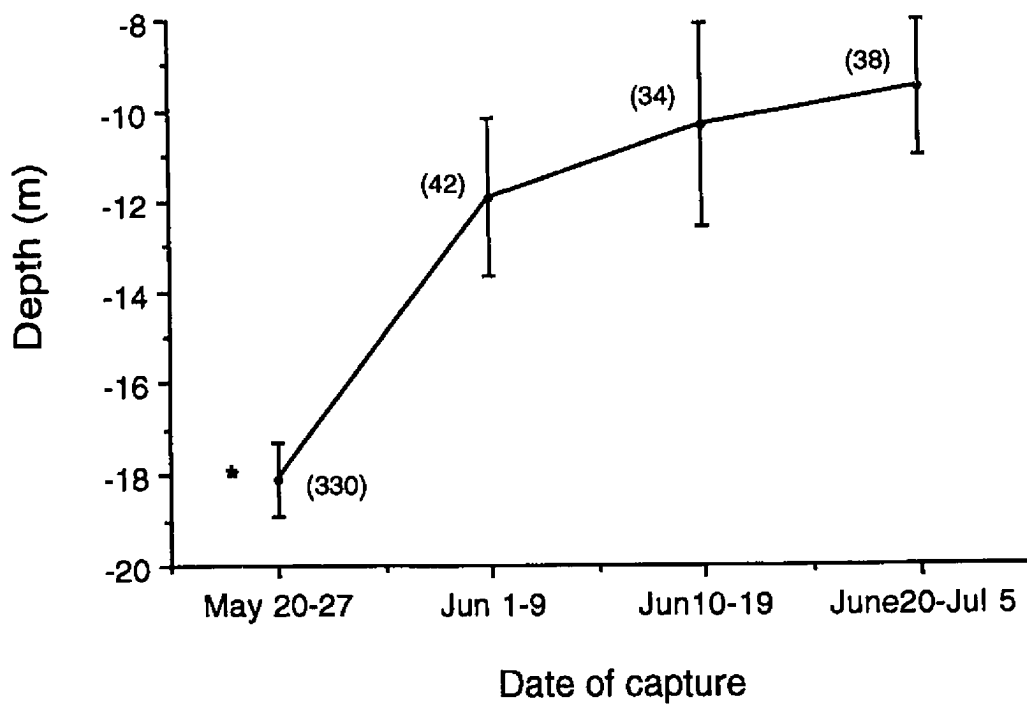


Figure 3.7 . Mean water depth ($\pm 95\%$ confidence interval) of lobsters at first recapture (*) and for subsequent recaptures between May and July 1992, on the Canso N. S. lobster grounds. Indicated in parenthesis number of recaptured lobsters.

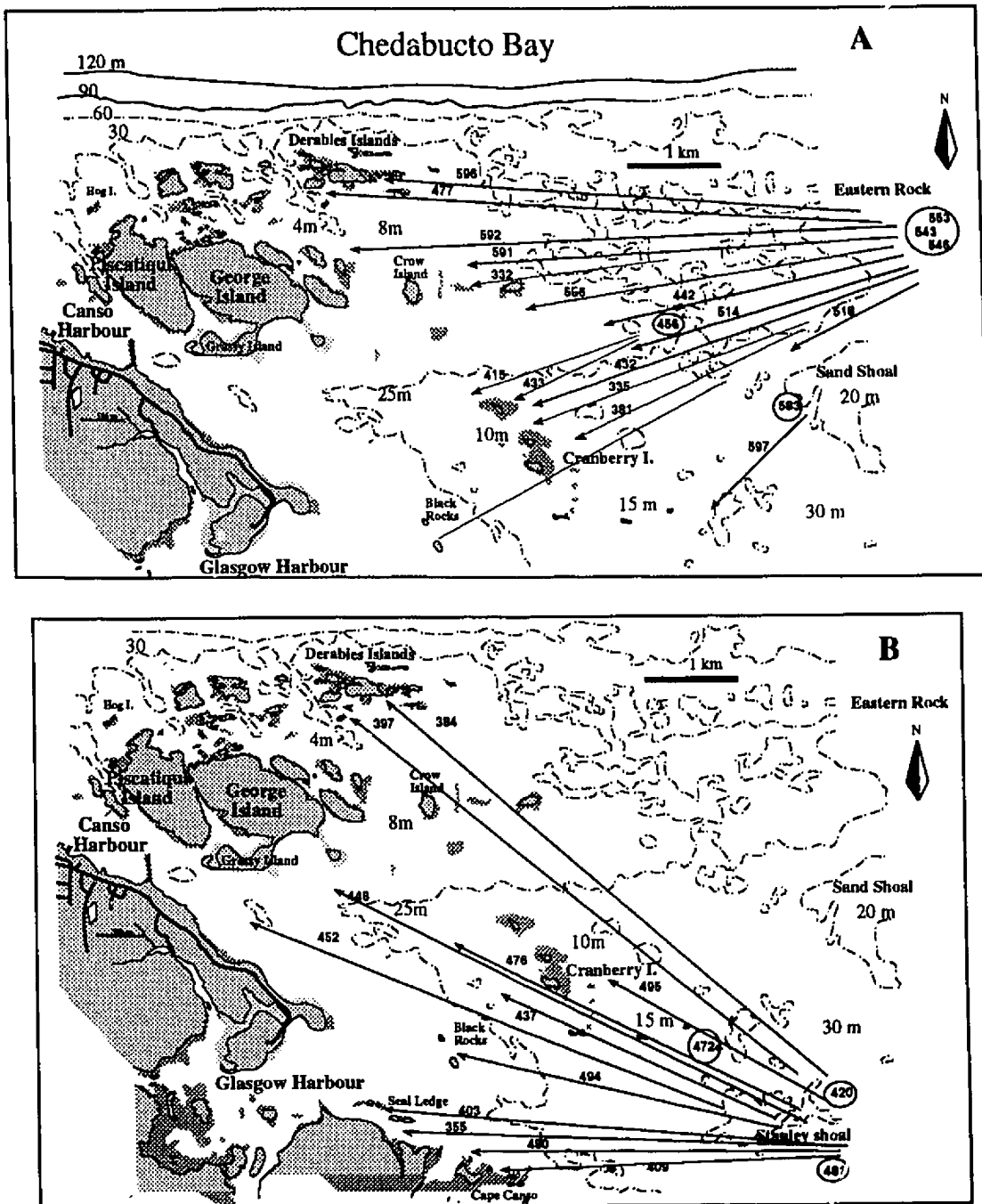


Figure 3.8. Movement of mature females tagged in the northeast (A) and southeast (B) side of the outer area of the Canso fishing ground during 1992.

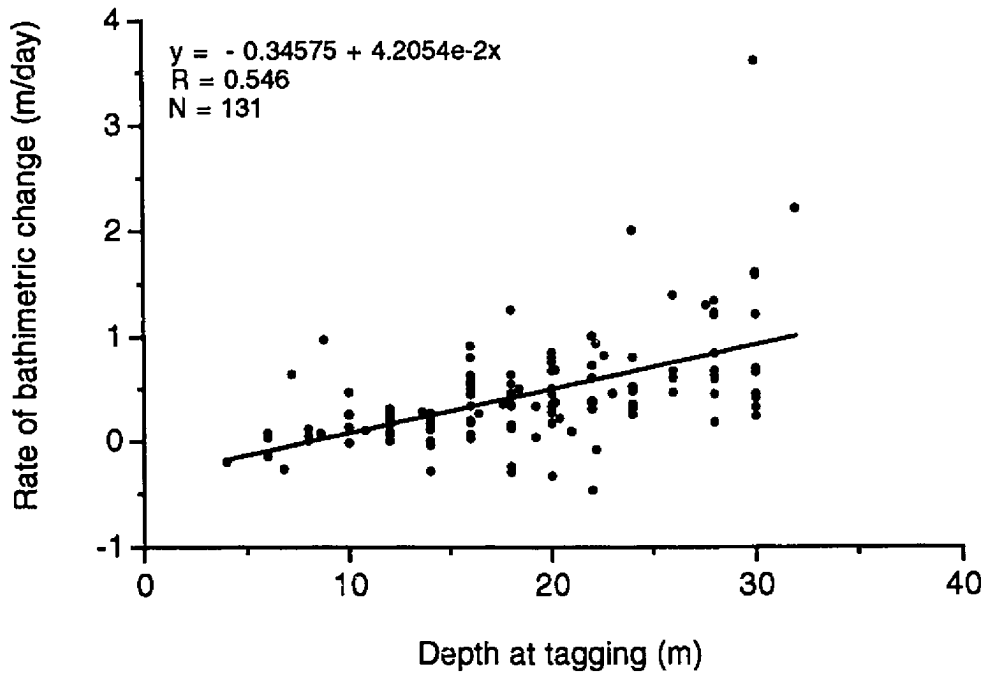


Figure 3.9. Relationship between tagging depth and the rate of movement to shallow water (bathymetric change) of lobsters recaptured during June-July, 1992.

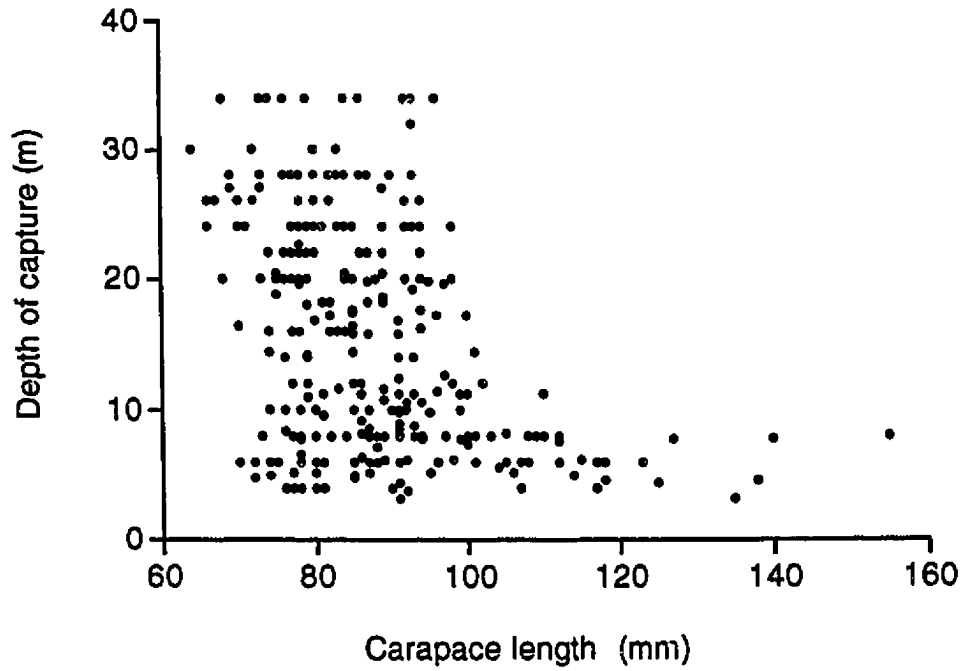


Figure 3.10. Relationship between depth of capture and female (mature and immature) size during early July for commercially fished lobsters. Note the distribution of animals > 100 mm CL.

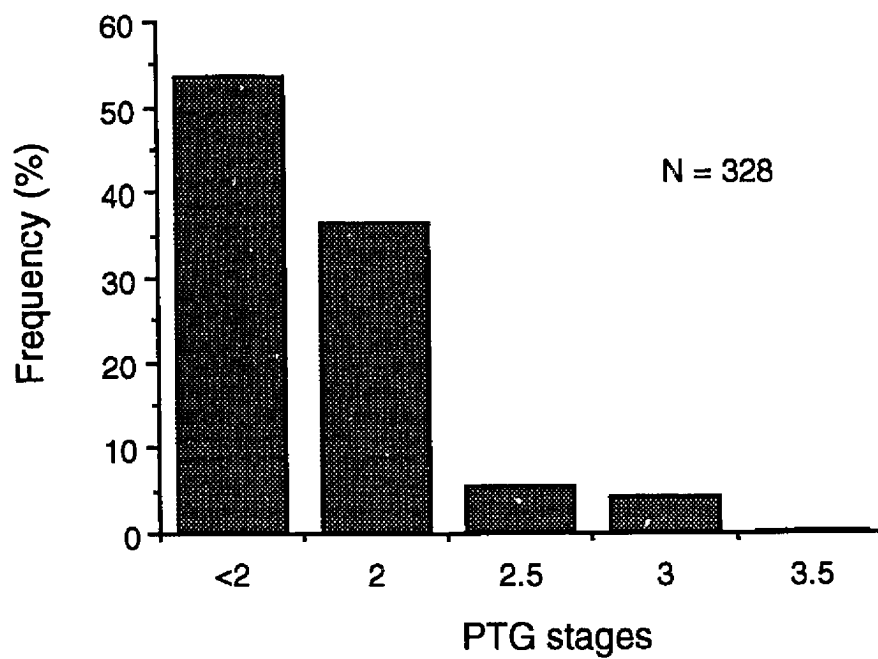


Figure 3.11 . Pleopod tegumental gland (PTG) condition of free range lobsters at tagging (May 20th-27th, 1992) on the Canso N.S. lobster ground.

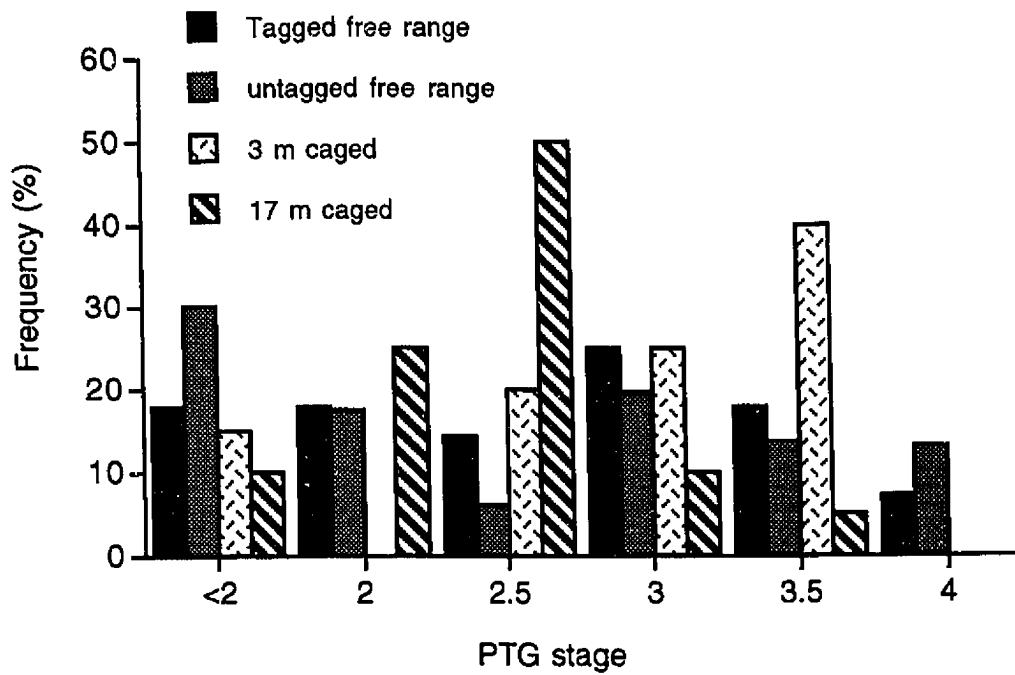


Figure 3.12. Ovarian development of caged and free ranging lobsters (both tagged and untagged-boat survey) during early July, 1992 on the Canso N. S. lobster grounds.

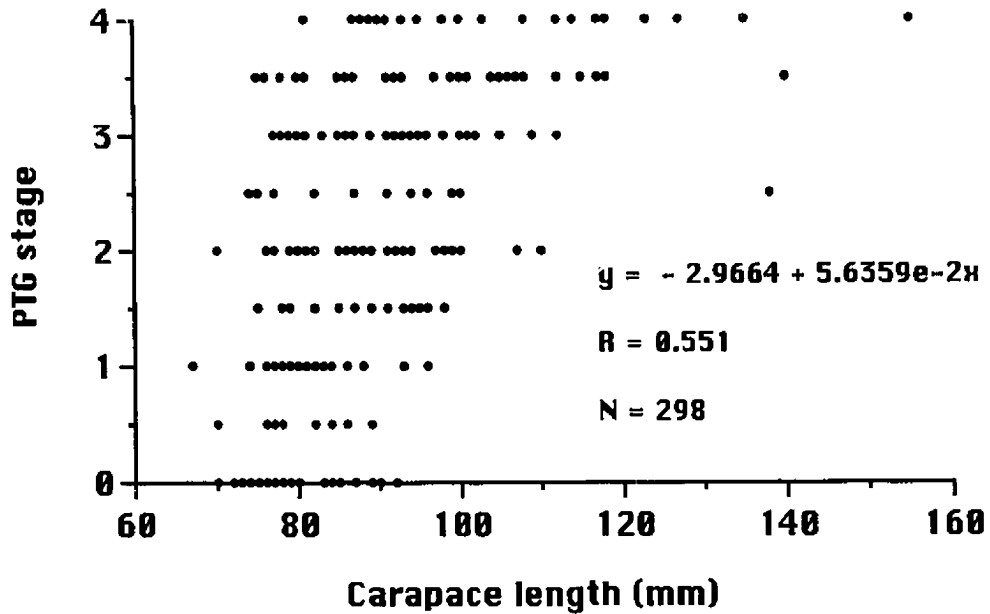


Figure 3.13 . Relationship between lobster size and ovarian development (PTG stage) during early July on the Canso lobster ground for commercially fished lobsters.

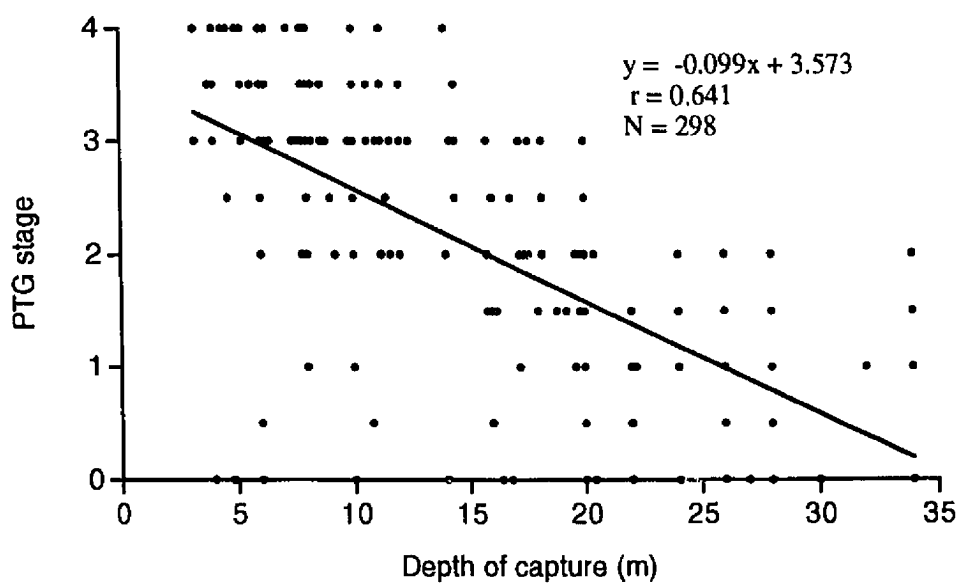


Figure 3.14 . Relationship between depth of capture and the PTG condition for commercially fished lobsters during early July, 1992, in Canso ground.

CHAPTER IV

GENERAL DISCUSSION

The main conclusions of the present study on the Canso lobster ground of Nova Scotia's eastern shore are that: (1) mature female lobsters are not homogeneously distributed over the ground, but distributed in association with benthic topography and physical oceanographic features; (2) from late spring through late summer the inner shallow area is warmer than the deeper outer area and during this period, large females are significantly more abundant in the shallow inner area than in the middle and outer areas and the former could be deemed a "brood" area; (3) the outer area carries mostly small, immature animals; (4) mature females move rapidly in mid-to late spring to the brood area where reproductive physiology is accelerated; and (5) the time available in a year with typical weather to complete the reproductive and early recruitment processes is short thus this movement enhances the chances of success.

The concepts and conclusions derived from this study are utilized to describe the causal factors and mechanisms underlying the distribution of mature females; to describe the synchronizing mechanisms for the reproductive processes near Canso; to present a descriptive model of life history stage distributions in relation to temporal and physical factors and, to provide insights into long standing questions of concern to lobster resource management of the eastern shore.

4.1 Distribution, reproductive condition, and movement of female lobsters in Canso.

Nova Scotia's eastern shore has a cool annual average temperature of 5.5 °C; six months with temperatures < 4°C and a narrow period of three months or so, with temperatures > 10 °C (Fig. 2.3). Prevailing long-shore summer winds blow from the southwest producing upwelling (Petrie et al 1987). These upwelling events can cause periods of cooler near-shore water with temperatures as low as 5 °C, in July (Petrie et al 1987). These events are of frequent and variable intensity and can co-occur with important phases of lobster reproduction such as embryo maturation and hatching, larval development, adult molting and mating, ovary development and egg extrusion. In addition to the thermal instability of the warm water period, the Canso lobster ground has an irregular bottom topography, with large variations in water depth over short horizontal distances (Fig. 1.1C). Basins 20 to 30 m deep are numerous among the islands of the inner and middle areas and depths up to 100 - 200 m are within 300 m eastward, in Chedabucto Bay (Fig. 1.1B). The Bay water below 40 m is cold ($\approx 2^{\circ}$ - 5 °C) year round . The Scotian Shelf waters off Canso has three main layers delimited by temperature and salinity (Hachey 1942, McLelland 1954a). The bottom layer, formed from intermediate and deep slope waters laying along the continental slope, is warm ($\geq 5^{\circ}$ C year round) with salinities $\geq 33.5\%$. This layer enters the shelf basins through channels and gullies (McLelland 1954a, Smith et al 1978). Over eastern portions of the shelf (Sable Island Bank and eastward [offshore to Canso]), there are no channels and gullies through which the warm slope waters can move (Hachey 1942). Thus, the cold intermediate layer, between 0°C and 3°C year round, extends to the bottom (McLelland 1954a, b), thereby providing no thermal advantage to lobsters either immigrating or emigrating from the Canso grounds. Consequently Chedabucto Bay, unlike the Bay of Fundy (Campbell and Stasko 1986, Campbell 1986), does not provide a thermal advantage (< 2 °C, Appendix 4) to mature females during the winter. Trapping experiments during winter provided no lobster deeper than 40 m

(Appendix IV). Movement studies on N.S.'s eastern shore with conventional tags (Duggan and Pringle 1988, Miller et al 1989) and electronic transmitters (Jarvis 1989) have demonstrated few long shore or deep water movement of adult animals. It is concluded that mature animals off Canso have a limited range of movement.

Despite the marginal thermal conditions of the Canso ground and adjacent waters, the reproductive process did occur successfully during the study years 1991 to 1993, because the female lobster's behavioural repertoire includes a seasonal migration to optimize local warm-water conditions.

Short-term, seasonal movements of inshore stocks, though following a temperature gradient, have not been shown empirically to result in accelerated egg development or hatching (Wilder 1954, Cooper 1970, Ennis 1984a, b, Munro and Thierrault 1983, Duggan and Pringle 1988). The irregular bottom topography of the Canso grounds and range of temperatures, due in part to the strong summer thermocline, produce a gradient of habitat similar to those found by only moving long distances in the northern Gulf of Maine and Bay of Fundy. For example, less than 300 degree-days are gained by moving from surface to 180 m depth in a year round, long distance migration in the Bay of Fundy (Campbell 1986); in Canso, a difference of 546 degree days exist from June-September between 17 m and 3 m (Fig. 4.1). Therefore, a female lobster on the Canso grounds can gain a large change in thermal habitat by moving a short horizontal distance.

Mature female lobsters are not homogeneously distributed on the 100 km² of Canso ground. Their distribution is linked to physical factors. Trapping surveys in late spring-early summer showed large females were significantly more abundant and with ovaries and embryos of advanced maturity in the inner warmer area than in the middle and outer areas of the ground. The cage experiments demonstrated that temperature regimes

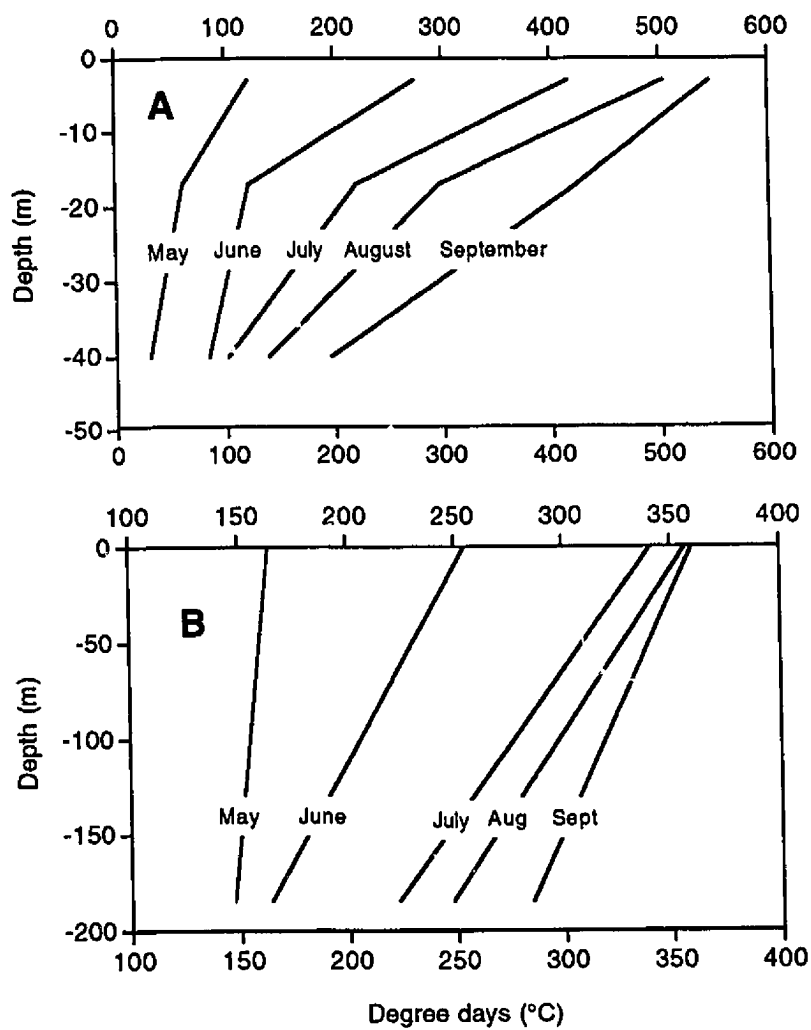


Figure 4.1. Temperature regimes during spring-summer in (A) Canso and (B) Grand Manan area. Data from the later were extrapolated from Campbell 1986 (his figure 8).

prevalent at 17 m are marginal for successful completion and synchronization of the various reproductive processes; both embryo and ovarian maturation were delayed compared to animals caged at 3 m. For example, though summer spawning was initiated at 17 m, the process was delayed and took twice as long to complete as animals at 3 m. The adverse impact on maturation was even more marked below 25 m on the outer ground with no ovary development observed in the wild animals surveyed here.

The seminal work of Campbell (1986) provided empirical evidence for the benefits of migratory movements on embryo development for Grand Manan Island berried females. The present study provides similar evidence for ovarian maturation. Although the environmental cues controlling the seasonal movement in the American lobster are not known, the present study suggests a high correlation to temperature occur. Animals were trapped once temperatures rose above 2 °C and the peak in catch rates occurred at 4 °C. The directed movement of the females from the deeper to the shallower areas suggest that this is not a random movement in search of food (Templeman 1935).

The data presented here concerns mature females however, we do know that immature animals are fished throughout the season in the outer area through to early July. A similar disparate distribution of immature and mature lobsters in such a small ground as Canso's has been described for other lobster stocks such as in Grand Manan Is. (Campbell 1990).

The term migration has not been clearly defined for the American lobster and it has been used loosely by many writers. Migration has been used to defined directed movement over long distances (Morrisey 1971, Cooper and Uzmann 1971, Campbell and Stasko 1986, Campbell 1986). Movement over shorter distances by inshore populations has been defined as non-migratory (Cooper and Uzmann 1980). Migration is a periodic phenomenon involving a round trip that may be of seasonal occurrence, or take a life time to complete (Orr 1970). Herrnkind (1980), used migration for *Panulirus argus* when

movement was temporally coordinated and spatially oriented, and when the lobster moved from one environment to another where various biological functions were optimized. Under this definition, the short-term movement of mature female American lobster observed in the present study are deemed migratory.

4.2 Synchronization of reproductive and molting processes in the Canso area

Photoperiod appears to play an important role in the reproductive process of the American lobster from the deep slopes of the continental shelf and for spiny lobsters of lower latitudes (Nelson, 1986, Lipcius and Herrnkind 1987). Temperature, however, is the main factor regulating final vitellogenesis and spawning, embryo development and hatching (Waddy and Aiken 1991), and probably molting (Stewart 1977) for the inshore American lobster. The extent and frequency of reproduction and molting varies according to the temperature regime affecting the indigenous stock (Templeman 1940b, Aiken and Waddy 1980, 1986). The colder temperatures affecting some stocks, such as those studied here on the Canso ground, force these processes into a short period (Fig. 4.2).

For Canso ground stocks, under the conditions of 1992, the spawning process occurred over a period of 16 d during the last half of July (Fig. 4.2). A brief spawning period of 17-20 days, from mid-July to early August, was also observed in the Bay of Fundy (Templeman 1940a). In warmer waters, the reproductive process starts earlier in the season, but is spread over a longer period. For example, egg extrusion starts in mid-June and extends to mid-July in southern areas of the Gulf of St. Lawrence (Templeman 1940a). These warm waters also allow a second spawning period during fall (Attard and Huddon 1987) for small adult *Ib* females, which molt and spawn during the same season (Aiken and Waddy 1982).

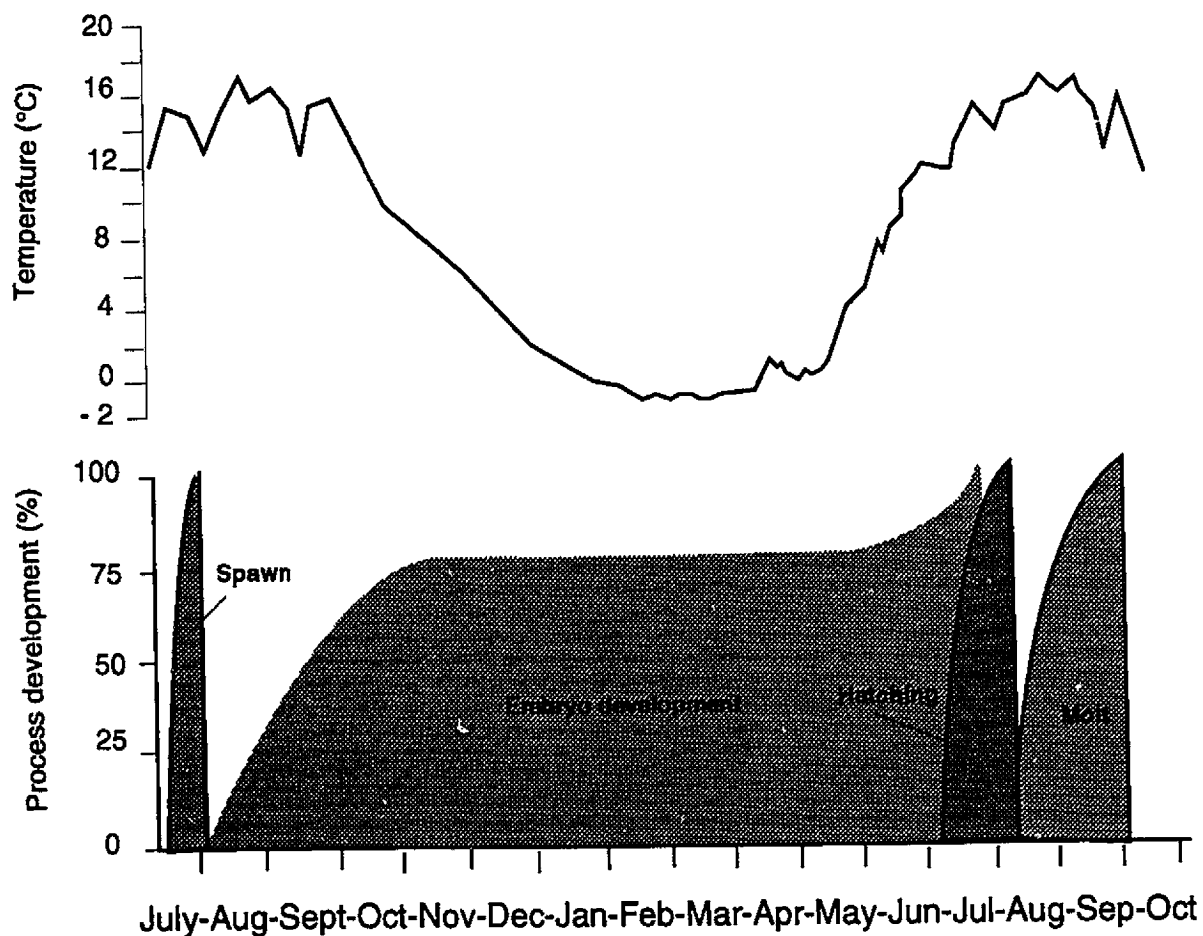


Figure 4.2. Occurrence of reproductive and molt events in relation to temperatures for a typical mature female lobster on the Canso N. S. lobster grounds during 1992.

The embryonic cycle was completed in 11.5 months for lobster on the Canso, N.S. ground. Embryos developed rapidly after extrusion in late July, reaching a PEI $\geq 420 \mu\text{m}$. Embryo development stopped in late November, enduring temperatures of $-1.5 \text{ }^\circ\text{C}$. Development continued as temperature rose over $4\text{-}5 \text{ }^\circ\text{C}$ late in May, and was completed by early July. Perkins (1972), under laboratory conditions, estimated 1,832 degree-days (above $3.4 \text{ }^\circ\text{C}$) were required to complete egg development in lobsters. Campbell (1986), using Perkins estimates, justified the deep-shallow migrations of berried females on the Grand Manan lobster grounds. He suggested that berried females remaining in shallow water year around, would receive 1,739 degree days, which was insufficient to complete the embryonic cycle in one year. The present study, shows the embryonic cycle of animals caged in shallow water (3 m) took 11.5 mo at only 1,665 degree days (Appendix I). A similar period of 11.5 mo was reported for the embryonic cycle in Newfoundland waters (Templeman 1939) and surprisingly, for the warmer waters of the Gulf of St. Lawrence (Templeman 1940). Whether embryos of marginal areas with no access to deep, warmer winter waters have been selected for faster development during the warm period, and to resist lower temperatures during winter, remains to be demonstrated.

Mature Canso lobsters molt once during the summer (Robinson 1979), unlike warmer water areas, which can have two molting periods (spring and fall) (Stewart 1972). Though, the molting process of mature males was not followed, the trapping surveys provided no lobsters in the soft shell condition during mid-spring-early summer suggesting a single molting as well.

The molting period of mature females on the Canso ground occurs about four to five weeks after hatching, similar to that period described by Jarvis (1989) for another eastern shore stock, which extended from mid-August to late September, a 45-50 d period. The failure of molting in late hatching lobsters, as noted in the current study though temperatures were $> 5 \text{ }^\circ\text{C}$ (the threshold for inhibition of molting [Aiken 1973]), requires

further attention. It is known that lobsters captured in autumn and held at 10°C during winter do not molt (Aiken 1980). Waddy and Aiken (1991) have suggested that the molt occurs during the warm water period to allow for cuticle mineralization prior to temperature decline.

The present study demonstrates that all physiological events occurring in a female lobster are well synchronized with adverse conditions affecting the timing of later processes. It is clear from this work that the timing of next summer hatch depends on the embryo stage reached the previous fall. Therefore, a late spawning will not produce well developed embryo before the winter arrives and consequently they will hatch late the following summer; given that the female molt occurs a month or so after embryo hatch, a late hatching will affect the time of molting and may not occur at all .

Larval maturation and post larval settlement are also processes that must be synchronized with the warm water period. Under the prevailing conditions of the eastern shore, particularly on the Canso ground, an early larval release would provide the larvae more time in warmer temperatures to complete development and reduce mortalities (MacKenzie 1988, Caddy 1976), seek suitable substrate and initiate the benthic phase (Cobb, 1968, Cobb et al 1989). The later larval stages are less viable in cold temperatures (Templeman 1936, MacKenzie 1988). As well, laboratory studies show larvae hatched late in the season (fall, winter) take longer to become post larvae and have higher mortality rates than those hatched in summer, even under similar temperatures (Aiken et al 1982, Aiken and Waddy 1986). In Northumberland Strait, larval survival to Stage IV was greatest for larvae hatched early in the season (Caddy 1976).

4.3 Descriptive model of the distribution of Canso lobster population

Information about the ecology, physiology, and behavior of the lobster gathered during this study, allows the construction of a descriptive model (Fig. 4.3) integrating season, water depth, bottom topography and temperature with the distribution of the life history stages of the Canso lobster stock. Females ovaries mature, complete vitellogenesis and spawn in late July on the inner grounds. They remain in this shallow warm environment until the water column mixes in late September/ early October. If water temperatures are within 15-18 °C, the new embryos will have attained more than 70 % of their development at a PEI $\geq 420 \mu\text{m}$ (Helluy and Beltz 1991). By the end of October, as temperature homogenizes in the water column, berried females move deeper, to the basins of the inner, middle and outer areas where they overwinter. The inner area becomes very unstable during fall due to continuous storms. When temperatures rise above 2 °C in late May, berried females move shoreward to the inner and middle areas where temperatures (10-15 °C) allow rapid embryo maturation. The female, at time of hatch, moves from the shoals, to deeper waters of the inner and middle areas. The reasons for this downward movement is unclear but, evidences suggest that she moves to waters with some current movement (Jarvis 1989) and discharges the larvae over two to three evenings (Jarvis 1989, pers. obs.). Within a month of hatch she chooses a male, molts and mates (Atema et al 1979, Karnofsky et al 1989).

The lobster size distribution obtained from fishing surveys provides indirect evidences of a main nursery grounds located in the outer area. The larvae released from the inner and middle areas, likely settle as postlarvae throughout the grounds. The high incidence of immature animals on the outer ground, is probably due to postlarval settlement, survival and growth rather than juvenile immigration, as a reduced range of movement has been suggested for juveniles (Cooper and Uzmann 1980). The reduced number of small

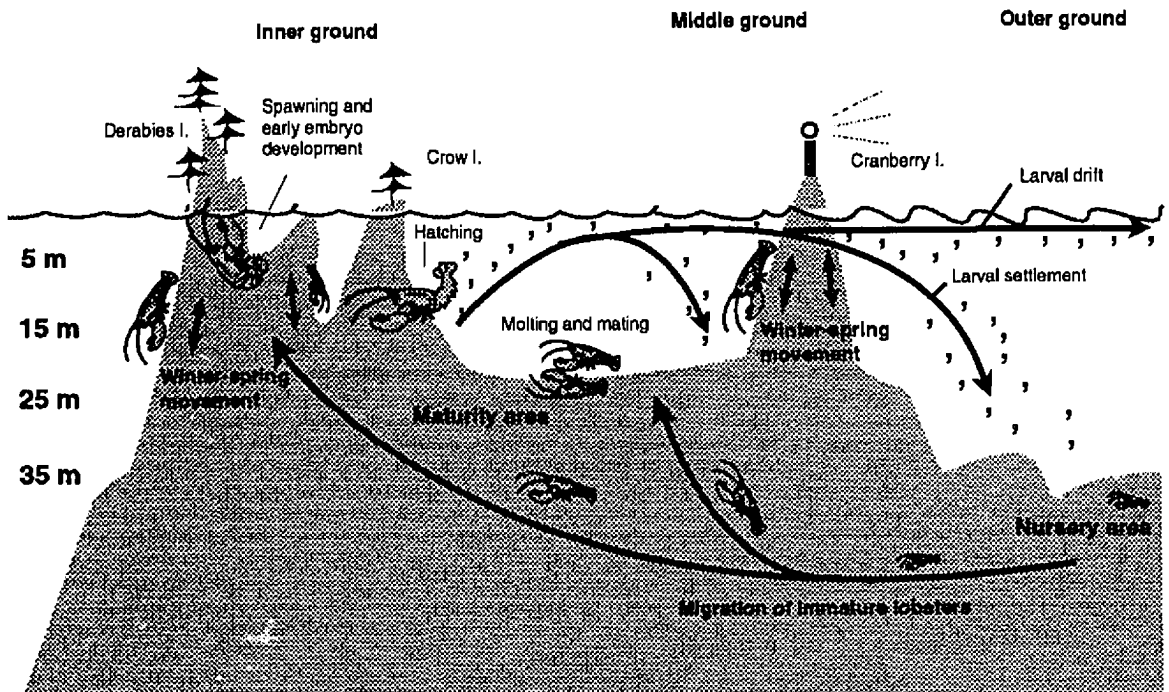


Figure 4.3 . Descriptive model of lobster distribution during its life history in the Canso area.

animals in the inner ground is difficult to explain; severe storms during late fall and ice scouring during winter make this area an unsuitable habitat for lobsters during the winter. Predation rate of juvenile lobsters has been reported high in some shallow, benthic areas (Richards and Cobb 1986, Wahle and Steneck 1992) and thus may be another factor responsible for the low density in the inner area. Mature females move directly and rapidly to the shallows during late spring. Females remaining in the outer area will mature at a larger size than those migrating to the shallows. Thus, the model depicts a directed movement from the nursery areas of the outer ground, towards the reproductive zones of the inner and middle areas.

4.4 Lobster recruitment collapse and landing variability along Nova Scotia's eastern shore

Nova Scotia's eastern shore lobster stock has, through the fishery's history, presented a cyclicity in the pattern of annual landings with peaks in the 1900's, 1930's, 1950's and 1990's. Nearby stocks recovered after the general declines of the late 1960's and early 1970's (Pringle and Burke 1993), but the eastern shore stock continued to decrease, and during the late '70's collapsed, with annual landings, between 1978 and 1981 at about 5% of peak levels. Landings increased by 1150% through 1989, but were yet only 25% of peak catch rates and have since declined (Pringle et al. 1993). A number of hypotheses were put forward (Ennis 1986) as responsible for the decline; recruitment overharvesting (Robinson 1979), reductions in larval recruits due to the Canso Causeway closure in 1954 (Dadswell 1979), marginal pelagic habitat of cold water temperatures for larval recruitment (Harding et al 1983), and habitat degradation (Wharton and Mann 1981).

4.4.1 Recruitment overharvesting

Robinson (1979), following an in-depth assessment of eastern Nova Scotia lobster stocks, conceded a role for environmental state variables in the fishery collapse. Nevertheless, by

using the historical approach, and considering factors such as increased effort levels; enhanced fishing effectiveness; minimum legal size in relation to reproductive maturity; he garnered considerable support for his recruitment overharvesting hypothesis. For the period Robinson (1979) covered, it must be noted, there was a paucity of data from the eastern shore lobster fishery.

Pringle and Duggan (1984; 1985) demonstrated that the eastern shore was not a homogeneous fishery as earlier portrayed (Robinson 1979; Campbell and Robinson 1983). Effort is concentrated at the western and eastern ends of the fishery, and CPUE and abundance is lower by about a factor of two to three in the western (LFA 32) than in the eastern stocks (LFA 31) (Pringle and Duggan 1985). As well, log books analysis (Duggan unpub. data) showed a higher capture of berried females in the eastern portion of the stock.

Previous research in the area (Watson 1989) and the current study have shown a larger size at maturity in the western fishery (Jeddore); 50% maturity is found at 98.1 mm CL in Jeddore compared with 82.6 mm CL in Canso (Appendix 5). Colder temperatures on the Jeddore ground than on the Canso ground are probably the reason for this difference in size at maturity (Templeman 1936 b). When the significant difference in size at maturity between the two stocks is considered, the proportion of mature females escaping the two fisheries to become fecund is dramatically different; 56 % in Canso versus 6 % for Jeddore. The difference in egg production per 100 females is 770,000.

Thus, this analysis, based on information derived from the work in Appendix 5, provides further support for the premise the eastern shore stock requires more eggs-per-recruit (Campbell and Robinson 1983) to both sustain and rebuild the fishery than is currently being produced.

4.4.2 Canso Causeway effect

There was a major habitat change with the closing of Canso Strait (Dadswell 1979) in 1955, which was coincidental with the last major peak in lobster landings for the eastern shore fishery. The warmer waters of St. Georges Bay previously may have supplied $\geq 60\%$ of the larvae to Chedabucto Bay (Harding et al 1979).

A decrease in temperature of $\sim 3\text{ }^{\circ}\text{C}$ from July through September in the sub-surface water (5-15 m) was observed after closure of the Strait (Dadswell 1979). However, when average temperatures from May to October showed no significant differences before and after the strait closure, it was concluded that lobster production was not affected significantly (Dadswell 1979). Reduction in larval flux from the Gulf was considered the most significant effect of the Causeway on the lobster fishery of the Chedabucto Bay area (Dadswell 1979).

The current study of the Canso ground, shows that most of the lobster brood stock is distributed between 5 and 20 m depth during late spring- summer. During these months, as reported above, several important physiological processes take place either, in the eggs, embryos or in spawning, molting and mating of the females. Considerable delay in the hatching process occurs when embryos are reared in a cold temperature regime such as those experienced at 17 m (Fig. 2.3). As well, important interannual differences in time of hatch was observed when average temperatures, from May to September, changed $1.5\text{ }^{\circ}\text{C}$ or less, as occurred between 1991 and 1992 (Fig. 2.7). The same effect was observed in the molting process; molt was delayed by a month, when the average temperature decreased by $0.5\text{ }^{\circ}\text{C}$ from one year to another in the Bay of Fundy (Stewart and Li 1969) and in Newfoundland (Templeman 1940b).

Size at maturity is most sensitive to local temperature regimes (Templeman 1936a). It was demonstrated above (Fig. 1.15) that a large difference in size at maturity occurs between the inner and outer areas of the Canso fishing ground correlated with different thermal regimes. The same effect was noted between the eastern and western ends of the eastern shore stock (Watson 1988, also Appendix 5). Thus, a decrease of 3 °C in the mean sub-surface water temperature in Chedabucto Bay, between July and September, because of the Canso Strait closure, would increase size at maturity reduce egg production, and thus likely reduce recruitment.

4.4.3 The Harding et al's (1983) Hypothesis - eastern shore bays as reproductive refuges?

Harding et al (1983) (after Huntsman 1923) characterized Nova Scotia's eastern shore waters as a "fringe habitat" for lobster, as summer temperatures are usually too cold on the open coast to allow for larval maturation to the post-larval stage. They further hypothesized that "larval refuges exist in protected embayments where a strong thermocline can be developed". Duggan and Pringle (1988), found a high incidence of ovigerous females inside the eastern shore's Jeddore Harbour. They speculated, that this harbour may be an important area for both embryo development and larval hatch. Jarvis (1989) then tracked ovigerous females from May to July, 1988, both in the harbour and in the outer waters. He found little direct evidence of directed movement of late stage berried females into the harbour. Furthermore, he found little physiological advantage for females to migrate inside, since there were sufficient degree days in the nearshore waters outside the harbour for late stage embryo maturation and larval development.

Parallel studies on larval distribution in the area (DiBacco and Pringle 1992) found only Stage I larvae inside Jeddore Harbour and no post-larvae; these workers suggested the harbour flushing rate was too high (4.4 tides) to retain larvae for more than two and half

days. Since Jeddore has a typical flushing rate for the eastern shore, it was concluded that the bays are not an important factor in contributing to larval recruitment along this coast; Harding's et al (1983) hypothesis on the role of the bays was rejected.

A more detailed analyses of the several fishing surveys carried out during 1987 and 1988 on the Jeddore N.S. lobster grounds, showed a clear pattern in berried female distribution associated with embryo maturation (Appendix 3). Of the newly extruded ovigerous females (NEF), at least 90% were found in shallow waters (< 9 m) of the Harbour. By contrast, old egg bearing females (OEF) were found down to 33 m, both inside and outside the Harbour (Appendix III, Fig. 2). This differential distribution may well explain the differences in the densities of berried females found by Duggan and Pringle (1988) and Jarvis (1989). The former authors carried out their study in October when only NEFs were present; Jarvis, however, tagged OEF in May. His conclusion of no physiological need for OEFs to migrate inside the Harbour as embryo development could be completed outside, supports one of the conclusions of Chapter II; final embryogenesis could be completed in a colder temperature regime. As well, the distribution pattern of NEFs inside the Harbour can be explained by the threshold of temperature required for final vitellogenesis. It was evident in Chapter III, and as noted by Waddy and Aiken (1991), that a minimum period of two weeks at temperatures $\geq 10^{\circ}\text{C}$ are required to induce spawning. Additionally, the spawning process is well synchronized amongst females, after at least four weeks at this temperature. When analyzing the pattern of temperature inside and outside Jeddore Harbour in 1988, it is evident that during July-August, a minimum period of two weeks at 10°C is found inside the Harbour only (Appendix III, Fig. 3). Temperatures $\geq 10^{\circ}\text{C}$ outside the Harbour are found only at August's end, and they drop rapidly through September (Appendix III, Fig. 3). Indeed, a strong southwest wind will decrease temperatures by 10°C in a few days (Petrie et al 1987) or sometimes in hours (Chapter III, Fig. 3.4). Therefore, in order for females to complete vitellogenesis,

spawn and carry well developed embryos into winter, they must migrate inside the Harbour. Consequently, Harding et al's (1983) hypothesis is confirmed; protected embayments along Nova Scotia's eastern shore are important in key aspects of lobster recruitment.

This integrated analysis of previous studies and the physiological/ecological factors gathered during the current study, leads to the conclusion that the decline from 1955 to the late 1970's was a combination of several variables, with temperature being the key steady state variable. The variability in landings of this stock, both before and after the collapse, is also probably a consequence of several factors. The annual "window" of warm temperature needed to fulfill and synchronize the reproductive and molting processes along this shore is narrow. The high incidence of wind driven upwelling along the eastern shore during the summer, makes this an area even more marginal for lobster recruitment. The reproductive and molting processes vary markedly with even small thermal changes between years. Consequently, a combination of a cold water year with extended upwelling events, could result in a total year class loss or a high mortality. Heavy fishing pressure during a similar period of harsh conditions could decimate the brood stock. A similar scenario has been suggested responsible for the high interannual variation in the Newfoundland broodstock (Ennis 1991). Thus, it could be hypothesized that the Canso Causeway in combination with the highly variable marginal environment may be the factors that has kept stocks at low levels along the eastern shore in the 1980's and 90's.

This study has provided some quantitative information about the relationship between the reproductive process and the physical habitat for the Canso lobster stock, and those of Nova Scotia's eastern shore. The information gathered here should form the basis for a quantitative model, which could be used to predict abundances in relation to wind and temperature events along this shore.

APPENDIX 1

EMBRYONIC CYCLE OF *Homarus americanus* INCUBATED *in situ*.

A.1. 1 Introduction

The relationship between temperature and embryonic development rate in *H. americanus* was demonstrated by Perkins (1972) in a laboratory study. Under the seasonal water conditions of this study, 50 wk and ~ 1,830 degree-days (above 3.4 °C) are required to complete the embryonic cycle. His study also showed that embryos of different ages developed at different rates when under identical temperatures. Older embryos showed no appreciable development < 2 °C, whereas, younger ones did. This process appears to be associated with the molt cycle of the nauplius into the metanauplius that occurs inside the egg (Helluy and Beltz, 1991), where a development arrest occurs at the transition from Do to D1 of the molt stage (Aiken, 1973).

The aim of this experiment was to determine the temperature requirements for the complete embryonic cycle of Canso ground lobsters.

A.1. 2 Materials and methods

Ten females bearing newly extruded eggs were caged at 3 m on July 1991. They were fed a rotating diet of frozen mackerel and squid. Each egg mass was examined monthly through May 1992, and every 10 d thereafter until embryo hatch. The Perkins' eye index (PEI) was used to evaluate embryonic development (fully described in Chapter I).

Embryonic development was observed until hatch.

Temperature at the cages was monitored continuously throughout the study period with Ryan thermographs from which a daily average was obtained.

A.1.3 Results

A rapid embryonic development occurred immediately after egg extrusion (July 24-28) in our caged females experiment (Fig. A.1A). Development stopped suddenly in early November when the embryos had an PEI of $\sim 430 \mu\text{m}$ (Fig. A.1A); temperature was $\sim 10^\circ\text{C}$ (Fig. A.1B). Embryos remained without further noticeable development for at least seven months, during which both the females' brood and their embryos weathered water temperatures below -1.5°C during the winter (Fig. A.1B). No single clutch died as a consequence of these low temperatures. Embryos resumed development the following spring (late May) at temperatures of $\sim 7^\circ\text{C}$ (Fig. A.1B). Embryos hatched between July 5th-15th when the temperature was 11°C (Fig. A.1B). The embryonic cycle was completed in 50 wk with a total number of degree days (over 3.4°C) of 1665 (Fig. 1.A.C).

A.1.4 Discussion and Conclusions

The embryonic cycle was completed successfully in a fifty week development period in caged females kept at 3 m in Canso. The same embryonic development (49.7 weeks) was reported by Perkins (1973) when incubating embryos at ambient temperatures. A value of 1665 degree-days (above 3.4°C) were necessary to complete the cycle in our study. This number is lower than that (1832) calculated to complete the embryonic cycle in Grand Manan lobsters (Campbell 1986).

More than 70 % of the embryonic cycle was completed during the first three months after extrusion in this study. Embryos reached an eye index of $\sim 430 \mu\text{m}$ before development stopped during mid-fall, allowing the embryos to develop faster and hatch earlier the following spring (also Chapter II).

Interesting is the observation that, though temperature was still high ($> 9^\circ\text{C}$) during late November, embryos stopped their development. This arrest in the embryonic development has been associated with the transition from D0 to D1 of the metanaupliar molt cycle

occurring in the egg (Helluy and Beltz 1991). According to these authors, embryonic metanauplius goes through the same molt cycle as juvenile lobsters (Aiken 1973). During the lobster molt cycle, temperature $< 5^{\circ}\text{C}$ arrests the molting process at D0 until spring conditions raise water temperatures and transition to the irreversible D1 stage (Aiken, 1973). In the present study, it appears the transition from D0 to D1 (and consequently the development arrest) started when embryos reached $\sim 430\ \mu\text{m}$ PEI, which was lower than the $470\ \mu\text{m}$ PEI reported by Helluy and Beltz (1991). This developmental arrest during the fall, when temperatures are still high, likely evolved to preclude hatching during the late fall/winter.

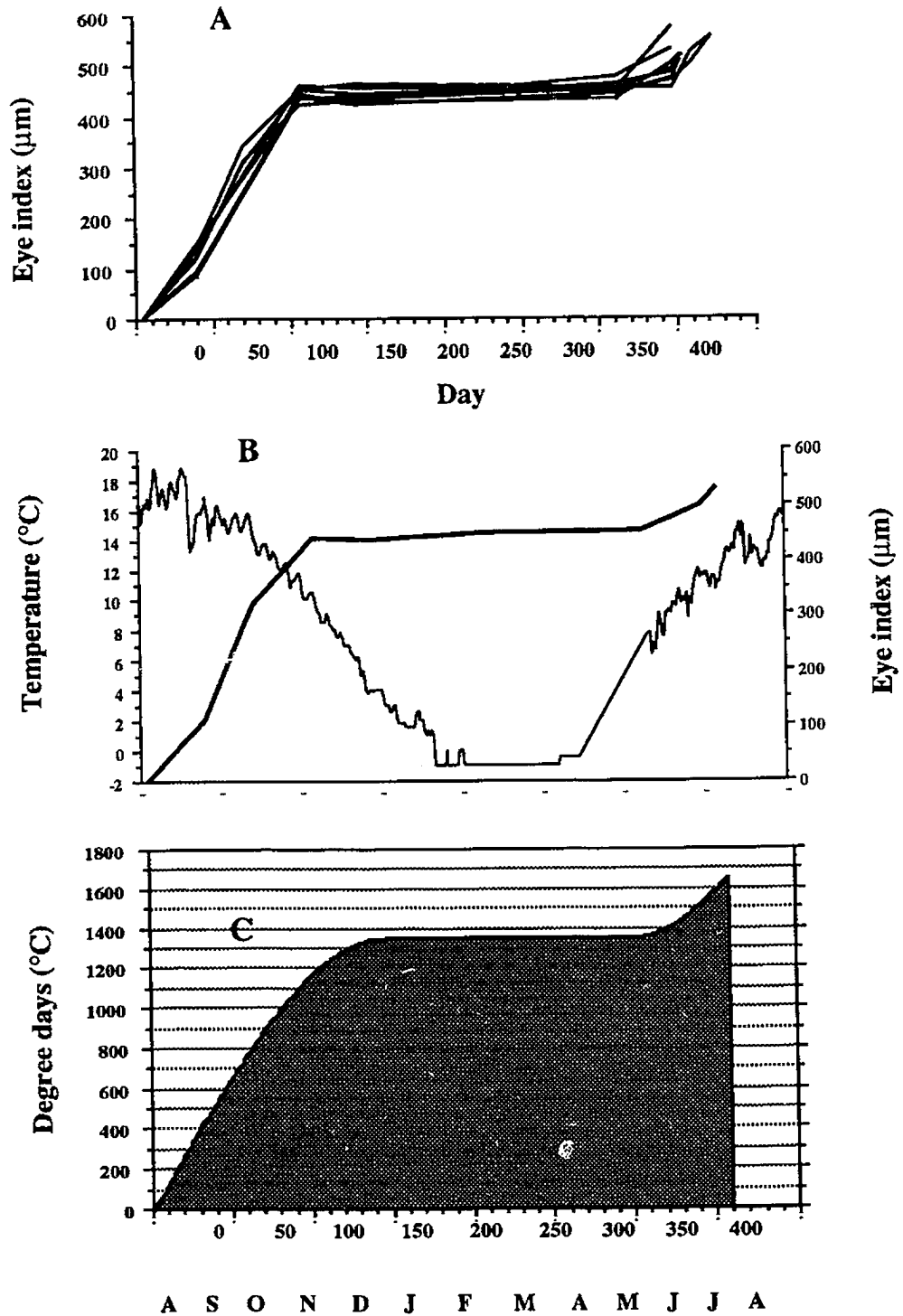


Fig. A.1.A. Embryonic development cycle of *H. americanus* at 3 m depth (Day 0 = July 21, approximate day of first extrusion).
 B. Embryonic cycle (curve = average size of 8 clutches) and temperature regime at 3 m depth.
 C. Cumulative degree days (> 3.4 $^{\circ}\text{C}$) required to complete the embryonic cycle

APPENDIX 2

NEWLY EXTRUDED EGG BEARING FEMALE DISTRIBUTION ON THE CANSO GROUND

2.1 Introduction

Distribution and movement of late stage ovigerous (OEF) and mature or non-ovigerous (NOF) lobsters has been described in this study. Both female components move to shallow water during spring-summer, allowing enhanced development of either embryos or ovaries. OEF and NOF are trapped during the fishing season (May-June) in the Canso area, consequently, many biological factors (e.g. movement, distribution, embryo and ovary stage, etc.) can be estimated with the fishermen's help. Unfortunately other stages, such as females with newly extruded eggs (NEF), occur during the closed season and are thus difficult to access. Because spawning occurs almost a month after the last assessment (late June/early July) of the distribution of the NOFs (Chapter I and III), and due to the dynamic behavior of the females during the spring-summer (fast movements and changes in distribution within days), the distribution of the new spawners can only be estimated from the location of the NOFs.

Here, the hypothesis that NEF's in late July occur at the same depth as NOFs in early July is rejected.

2.2 Methods

A three day fishing survey was carried out on the Canso fishing grounds from July 29th to 31st, 1991, using a chartered fully equipped (traps, bait and crew) fishing boat. A total of 450 traps were set and pulled between Cranberry I. and the main inlet system (Fig. A.2.1).

Each lobster was sexed, sized, and the reproductive stage recorded. Ovigerous females were classified as either newly extruded (NEF) or old egg (OEF) females. Depth and geographical position of capture was registered.

2.3 Results

Sex proportion, abundance, and mean size.

A total of 345 lobsters were trapped (0.77 animals per trap haul) and of these, 145 (42%) were males, 132 (38.3%) were non-ovigerous females (NOF), and 68 (19.7%) were ovigerous females (Fig. A.2.2). Of the ovigerous females, 51 (74.1%) and 16 (25.9%) were NEF and OEF respectively (Fig. A.2.3). Average carapace length was 85.7 mm (\pm SD = 15.9) for males, 85.5 mm (\pm SD = 14.1) for NOF and 93.6 mm (\pm SD = 11.8) and 79.1 mm (\pm SD = 6.3) for NEF and OEF respectively (Fig. A.2.4). NEF were significant larger ($p \leq 0.05$) than the other stages.

Ovigerous females distribution

Most (80.3%) of the NEF were caught in the inner area; the remainder 19.7% were around Cranberry I (Fig. A.2.1). Depth of capture varied from 2 m to 11m (average 6.8 m \pm 2.3 m SD), while (OEF) were caught deeper (t-test; $p < 0.05$) throughout the grounds between 5 m and 18 m depth (average 9.1 m \pm 3.3 m SD) (Fig. A.2.5). The larger NEFs tended to be captured in shallower waters ($r = 0.4$) than the smaller females (Fig. A.2.6), but this relationship did not hold ($r = 0.05$) for OEFs.

Most NEFs were caught in the inner area, and there were two particular places where concentrations were at least double than the other areas; a narrow channel between George I. and Oliver I. and in the Derabies group (Fig. A.2.1). Both places were surveyed by SCUBA divers. The Oliver Is. channel, formed from glacial till, was 2-3 m deep, with sandy bottom. The juxtaposition of the boulders created shelters for female lobsters. Most incubating females at Derabies Is. were found in a rocky wall, 9 m x 250 m, on the

island's south side. The females were inside the wall's crevices between 3 to 8 m deep at a density of approx. 1 animal per 25 m⁻². Only 6 OEF were observed during the diving survey, and they were deeper than 8 m. No males were discovered, and no NEF were observed deeper than 10 m. Diving surveys continued irregularly in these areas of larger concentrations, until late October when no NEF were observed.

2.4 Discussion

This late July 1991 fishing survey, showed a clear distribution pattern for ovigerous lobsters, especially NEF. The latter had an average distribution of about 6.8 m depth, shallower than the other stages measured (Fig. A.2.5). This is of particular interest because by early July, mature NOF moving from deep to shallow water to spawn, appear to be concentrated at about 9 m (Chapter III). Thus, either they spawn at the latter depth and then move to shallow waters to incubate the eggs or they both spawn and incubate at the shallower depth.

The behavior of NEFs to seek shallow waters during the summer has likely evolved to maximize degree days and hence enhance embryo maturation (Chapter III). This distribution contrasts that of OEF, which appear to move to deeper waters in July (Chapter II and III). One hypothesis for these two distribution is that of optimal use of the prime, nearshore habitat; that the Pre-NEFs can make better use of the warmer waters for both ovarian maturation and spawning than can the OEFs (Chapter III). It was demonstrated (Chapter II) that once an embryo reaches a certain development stage (PEI > 400 μ m), it can complete final maturation and hatch at low temperatures (< 10 °C). However, mature NOF need a certain period (\approx three weeks) with temperatures over 10 °C for final vitellogenesis and subsequent spawning (Chapter III, also Waddy and Aiken 1991). NEF's emaining in the warmer microenvironments until after spawning, allows their

embryos to reach a well developed stage before winter arrives, as observed in the cages experiment (Chapter III).

Average size for ovigerous females in the Canso area is 89.3 mm CL as estimated in Appendix 5. However, NEF in late July (onset of spawning) had a mean CL of 93.6 mm, significantly larger than the other components of the population (Fig. A.2.4). The larger mean size supports the hypothesis that larger females spawn earlier than smaller ones. Also, the shallow distribution of the larger females (Fig. A.2.6) may account for earlier extrusion, as observed in our shallow cages of Chapter III, and for the more advanced embryos found during spring (Chapter II, also Attard and Huddon 1987). These warmer microenvironments used by the larger females are likely scarce and are likely competed for, thus relegating the smaller and less dominant females to deeper waters (Fig. A.2.6). Consequently, these small females will spawn later in the summer, will present a less developed embryo during the next spring, and will hatch later that summer, as observed in July survey (Fig. A.2.4).

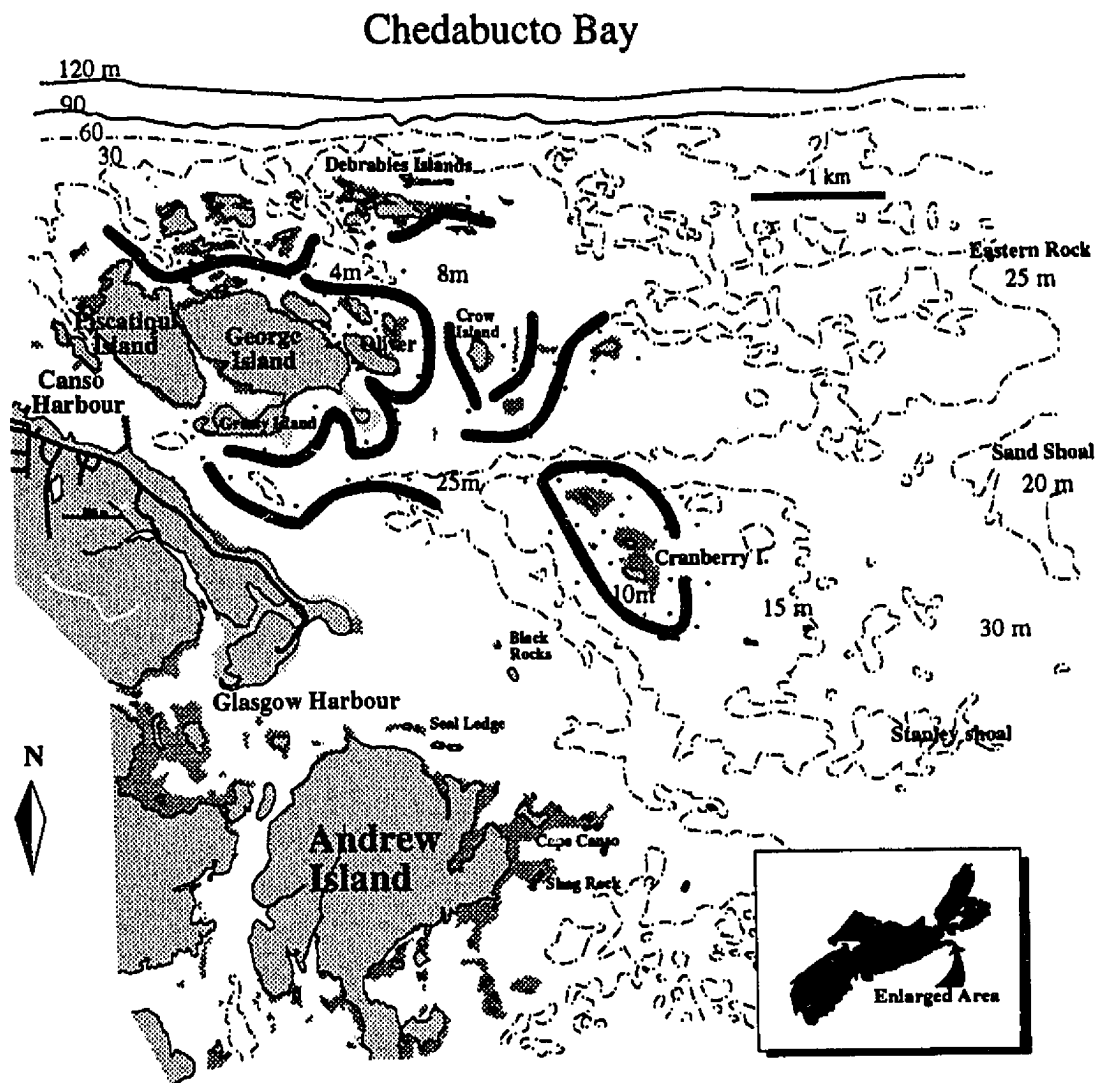


Figure A.2.1. Canso fishing ground. Dark traces represent trap set areas during the survey carried out in late July/early August, 1991.

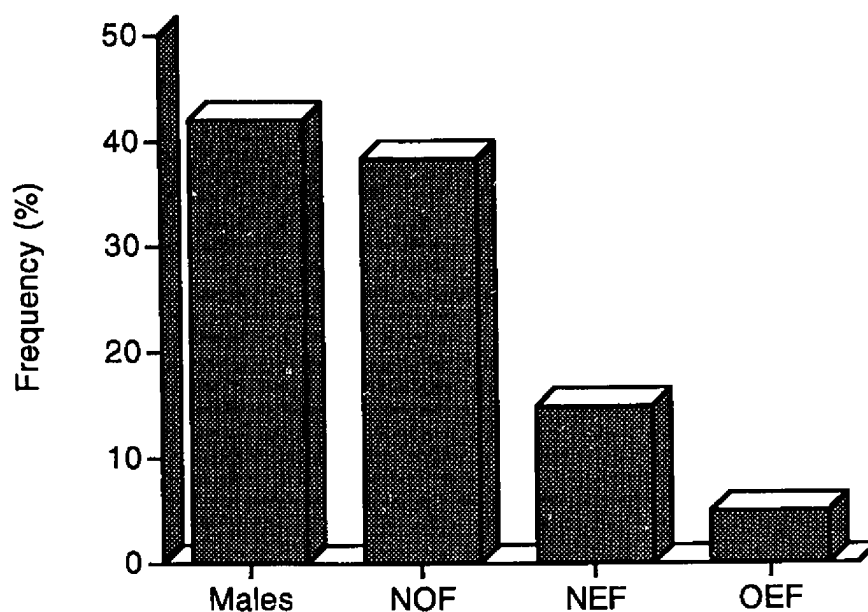


Figure A.2.2. Capture composition during July 28th-31st, 1991 on the Canso, N.S. lobster ground. NOF = non-ovigerous females, NEF and OEF are respectively new eggs and old eggs females.

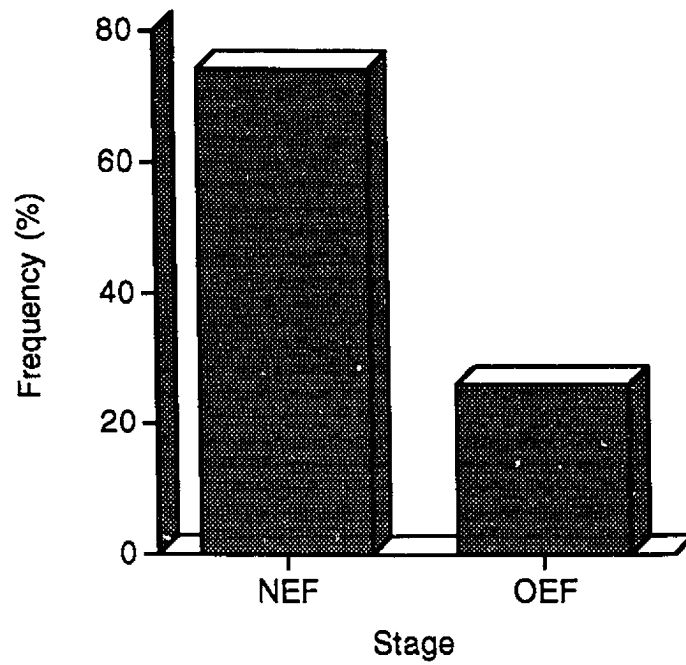


Figure A.2.3. Proportion of ovigerous females according to their embryonic stage. NEF and OEF are newly extruded and old eggs bearing females respectively.

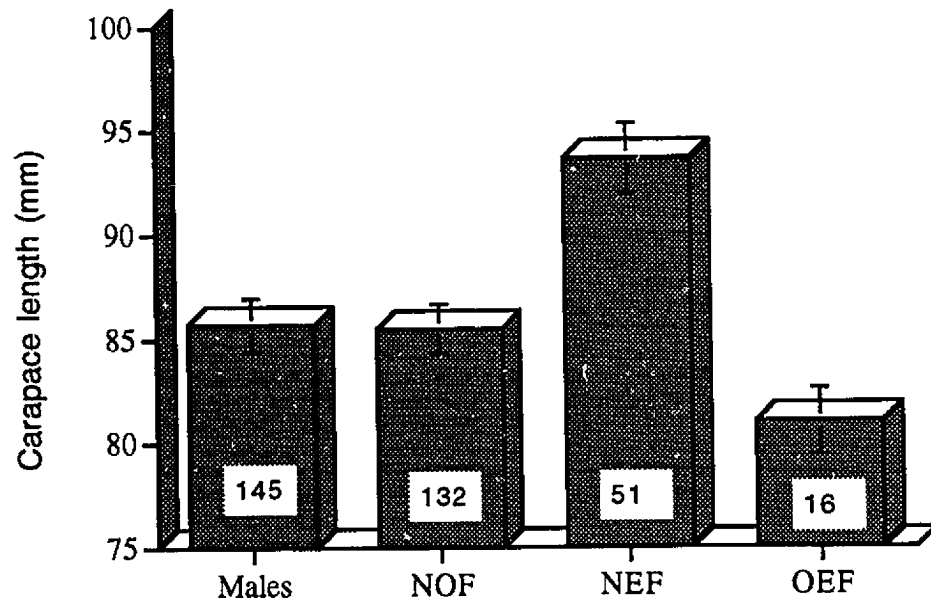


Figure A.2.4. Mean size (CL) (± 1 SE) of the different lobster stages captured during July 28-31, 1991, on the Canso lobster ground.

Numbers in columns are sample size. (NOF = non-ovigerous females; NEF and OEF are new and old egg females respectively).

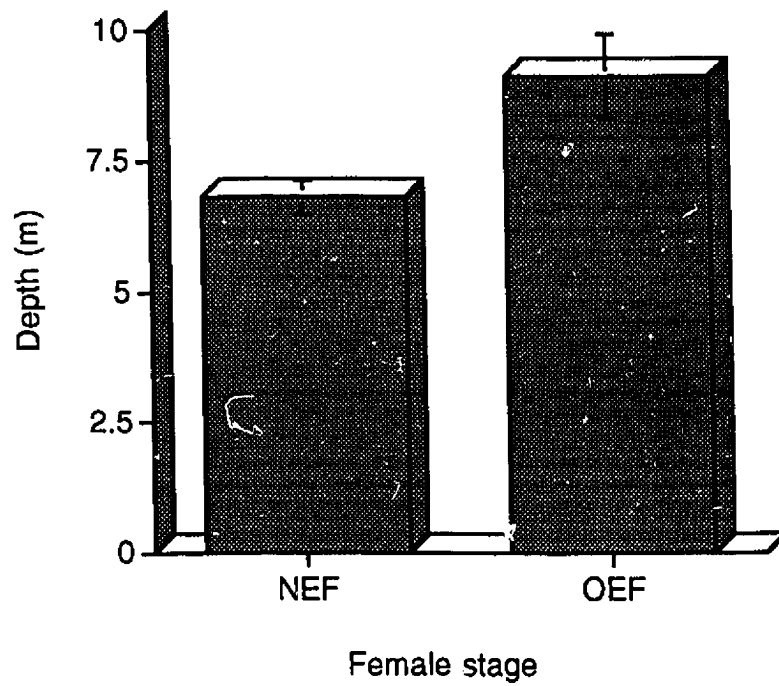


Figure A.2.5. Mean depth distribution (± 1 SE) of new eggs (NEF) and old egg bearing (OEF) females during the survey of July 28-31, 1991, on the Canso lobster ground.

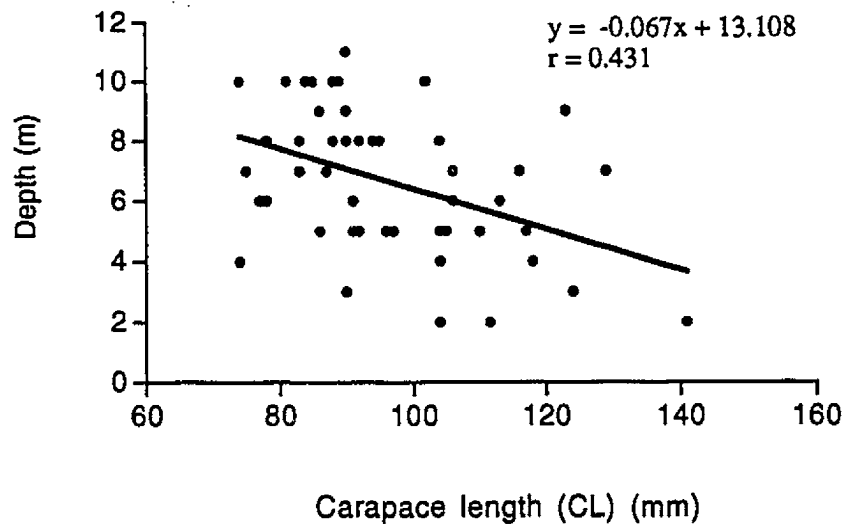


Figure A.2.6. Relationship between female size and depth distribution for NEF (newly extruded females).

APPENDIX 3

Ovigerous Female *Homarus americanus* Distribution in Jeddore Area

(44° 45' N, 63° 00' W), N.S. eastern shore.

3.1 Introduction

Harding et al (1983) characterized Nova Scotia's eastern shore waters as "fringe habitat" for lobster as temperatures are generally too cold on the open coast to allow for larval maturation to the post larval stage. They further hypothesized that "larval refuges exist in protected embayments where a strong thermocline can be developed". Duggan and Pringle (1988), found a high incidence of ovigerous females inside Jeddore Harbour. They speculated, that the harbour may be an important area for both embryo development and larval hatch. Investigating this hypothesis, Jarvis (1989) tracked ovigerous females from May to July both in the harbour and in the open coastal waters. He found no directed movement of late stage berried females inside the harbour. Furthermore, there was little physiological advantage for females to migrate inside, since there were sufficient degree days in outer waters to complete late stage embryo and larval development.

Jarvis's (1989) data were reviewed in light of new knowledge acquired from our Canso research. It is conclude that rejection of Harding's et al (1983) hypothesis was premature.

3.2 Method

The berried female distribution data was obtained by Duggan and Pringle (1988) from fishing surveys in Jeddore Harbour and in the outside waters of Clam Bay (44° 45' N, 63° 00' W) (Fig. A.3.1). The surveys were carried out on October 1986, May-June 1987, and August 1988 for a total of 28 fishing days. During the closed fishing season in July-

October, fishing boat and crew were chartered. The sex, presence of eggs, CL and depth and geographical position of each lobster captured was recorded. Ovigerous females were classified according to whether their embryos were "new" (NEF) or "old" eggs (OEF); "new" and "old" females were those with embryos < 3 mo. old and those with embryos within three month of hatching respectively.

Temperature at both sites were monitored continuously with Ryan thermographs.

3.3 Results

The fishing surveys in the Jeddore area during 1986 and 1987 provided a total of 87 ovigerous females with a different pattern of distribution for new (NEF) and old embryo carrying females (OEF) clearly in evidence. Ninety percent of the NEFs were caught in shallow water inside the harbour at depths varying from 1-9 m (mean = $4.0 \text{ m} \pm \text{SD } 1.7 \text{ m}$). Whereas OEFs (including a few in hatch) were distributed both outside and inside the Harbour from 3.5 to 33 m depth (average = $9.1 \pm \text{SD } 7.1$) (Fig. A.3.2).

Temperature regimes at the same depth in and outside the Harbour were different. A stable thermocline developed inside the Harbour with surface temperatures over $10 \text{ }^\circ\text{C}$ by the end of June (Fig. A.3.3). The temperature outside was colder and more variable (Fig. A.3.3) with relatively stable temperatures over $10 \text{ }^\circ\text{C}$ reached by mid-August.

3.4 Discussion

It is reported in Appendix 5 that the Jeddore area had a low density of ovigerous females. The reasons appear to be a combination of low temperatures and high fishing pressure (Appendix 5). Indeed, only 87 ovigerous females were captured in 3,161 traps hauls over 27 fishing days. There was, however, a clear pattern of female distribution which was associated with embryo maturation level. At least 90% of the newly extruded ovigerous females were found in shallow waters (less than 9 m) inside the harbour, whereas OEF

were found deeper (down to 33 m), at both inside and outside the Harbour (Fig. A.3.2). This differential distribution with embryo maturation, may well explain the difference in findings between Duggan and Pringle (1988) and Jarvis (1989). The former authors carried out their study in October when only NEFs were present, whereas Jarvis tagged OEF in May. His conclusion that, there was no physiological need for OEFs to migrate inside the harbour as embryo development could be completed outside, supports the conclusion reached for the Canso stock where it was confirmed that final embryogenesis could be completed in cold temperature regimes. The distribution pattern of NEFs inside the Harbour can be explained by the threshold of temperature required for final vitellogenesis. It was evident (Waddy and Aiken 1991) that a minimum of two weeks at temperatures of 10 °C are required to induce spawning, and that this process is well synchronized amongst females after at least four weeks at this temperature.

When analyzing the pattern of temperature inside and outside of Jeddore Harbour, it must be appreciated that, during July-August, a minimum period of two weeks at 10 °C is found inside the Harbour only (Fig. A.3.3). Temperatures ≥ 10 °C outside the Harbour are found only at the end of August, with temperatures dropping rapidly through September (Fig. A.3.3). Therefore, females must migrate inside the harbour in order for females to spawn and attain well developed embryos before winter water temperatures occur, they

Only Stage I larvae were found inside Jeddore Harbour (DiBacco and Pringle 1992), which was interpreted that the harbour flushing rate was too high (4.4 tides) to retain larvae for more than two and half days. As Jeddore is a typical harbour along the eastern shore, it was concluded that larval refuges were not important in larval recruitment and Harding's et al (1983) hypothesis was rejected.

It was also confirmed (Chapter II) that if a female arrives in winter with a well developed embryo ($PEI \geq 400 \mu\text{m}$), they hatch earlier in the summer, allowing the larvae with enough time to develop and settle before temperatures drop during the fall.

Harding et al's (1983) hypothesis, that protected embayments along Nova Scotia's eastern shore are important in key aspects of lobster stock recruitment is confirmed.

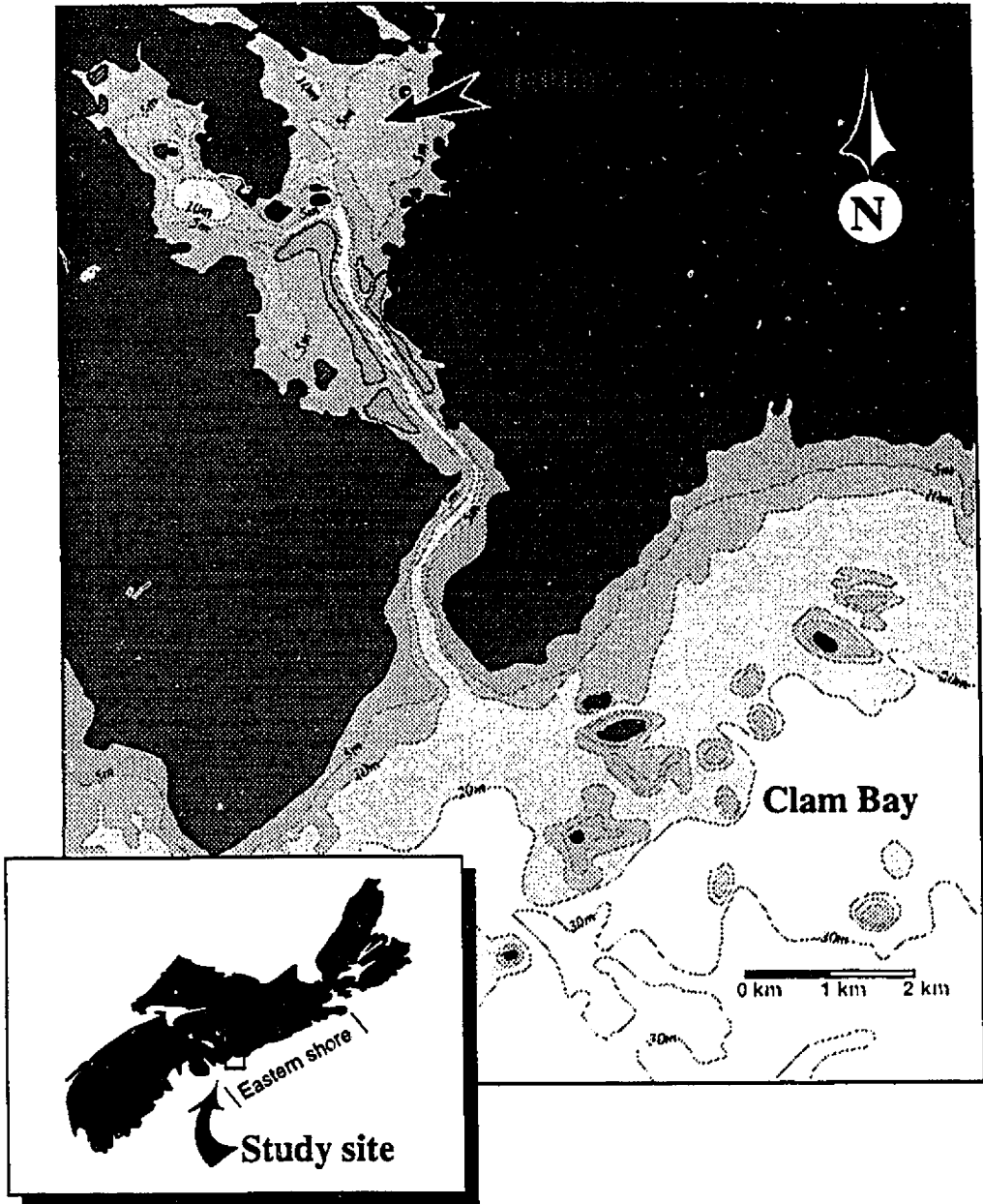


Figure A.3.1. Map of study area and its location in Nova Scotia

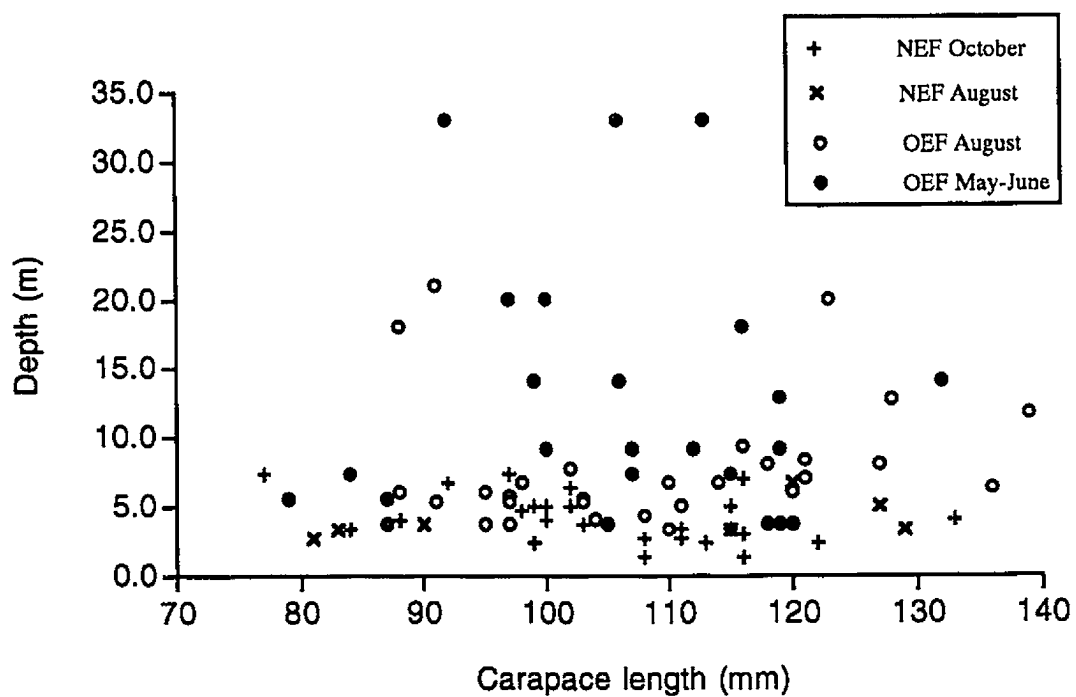


Figure A.3.2 . Depth distribution of ovigerous females with old and newly extruded eggs in Jeddore area.

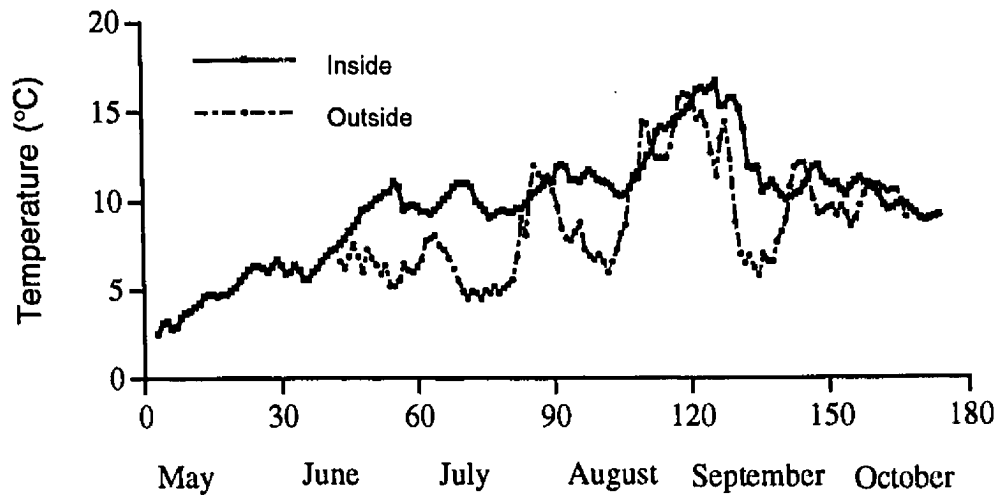


Figure A.3.3 . Bottom (9 m) temperatures inside and outside of Jeddore harbour. (Day 1= May 1).

APPENDIX 4

WINTER TRAPPING SURVEY FOR BERRIED FEMALES ON BOTH THE CANSO GROUNDS AND IN CHEDABUCTO BAY

A.4.1 Introduction

Mature female lobsters on the Canso fishing ground, move to shallow waters to complete final vitellogenesis, spawn and speed up embryo development (Chapter III). These newly extruded females remain in the shoals until mid to late October when they begin to disappear. During the same period, berried females off Grand Manan Island begin to migrate to deep water (180-200 m) of the nearby basin to take advantage of warmer waters during the winter (Campbell 1986). Female lobsters on the Canso ground, have easy access to deep water (160-180 m) in nearby Chedabucto Bay (Fig. A.4.1), however, it is not known whether the bay offers thermal advantage to the lobsters during the winter.

The present experiment was designed to assess; first, the thermal condition of Chedabucto Bay and second, to assess the depth distribution of berried females during the winter.

A.4.2 Materials and methods

Temperature Data

A profile of temperature was carried out from surface down to 200 m depth using an expendable bathythermograph on February 18, 1992 (Fig. A.4.2).

Lobster assessment

A chartered lobster fishing vessel and crew fished 20 traps daily from February 18 through 21, 1992, along a gradient of depths down to 200 m to detect lobster presence

in the deep water basins of Chedabucto Bay during the winter. Traps were set in groups of five and moved each day trying to cover the maximum fishing area within the four days of survey (Fig. A.4.1).

Diving observations (up to 20 m depth) complemented the trapping survey in the shallow water area.

A.4.3 Results

During February, 80 traps were hauled over a range of depths varying from 10 m to 200 m, the deepest spot in Chedabucto Bay. Only five animals were caught during the survey and they were at depths ranging from 14 to 28 m, near the steepest depth contours (Fig. A.4.1). The traps captured toad (*Hyas araneus*) and snow crab (*Chionoecetes opilio*) at depths below 70 m but no lobsters were caught. A two-day diving survey (up to 20 m depth) during the winter reported only three small males (CL ~ 78 - 85 mm) at about 15 m depth.

Water temperatures during February were below -1.0 °C from surface to ~ 40 m depth. Below 50 m the water temperature increased slightly up to 1.1 °C at the deepest location surveyed (200 m) (Fig. A. 4.2).

A.4.4 Discussion

Even though the embryonic cycle can be completed in the shallow waters of the Canso ground (Appendix 1), both diving survey and winter trapping, indicate the lobsters move to deeper water during fall. Moving deeper than 40-50 m, gave waters 2.6 °C warmer than the surface waters (1.1° vs -1.5 °C). This movement would provide no thermal advantage for embryos, as development stops at about 3 °C for less mature embryos and about 7 °C for more mature embryos (Chapter III, Appendix 1). Therefore, the downward movement of berried females during fall-winter may be controlled by

different factors. During the three years of study in this area, severe effects of late fall storms and ice scouring during the winter have been observed. Thus, it may be that females escape from these adverse conditions by moving deeper, probably no more than 30-40 m into the basins of the Canso grounds or to the slope of the Bay. Movement to deep water presumably to escape winter adverse conditions, has been reported for other populations of lobsters (Ennis, 1983, 1984). Lobsters move back to shallow water during mid-spring when water temperatures start to rise to complete embryonic development and hatching (Chapter II, III). In several instances during spring berried female lobsters have been observed walking through channels that connect the Bay and the basins with the shallows of the Canso ground.

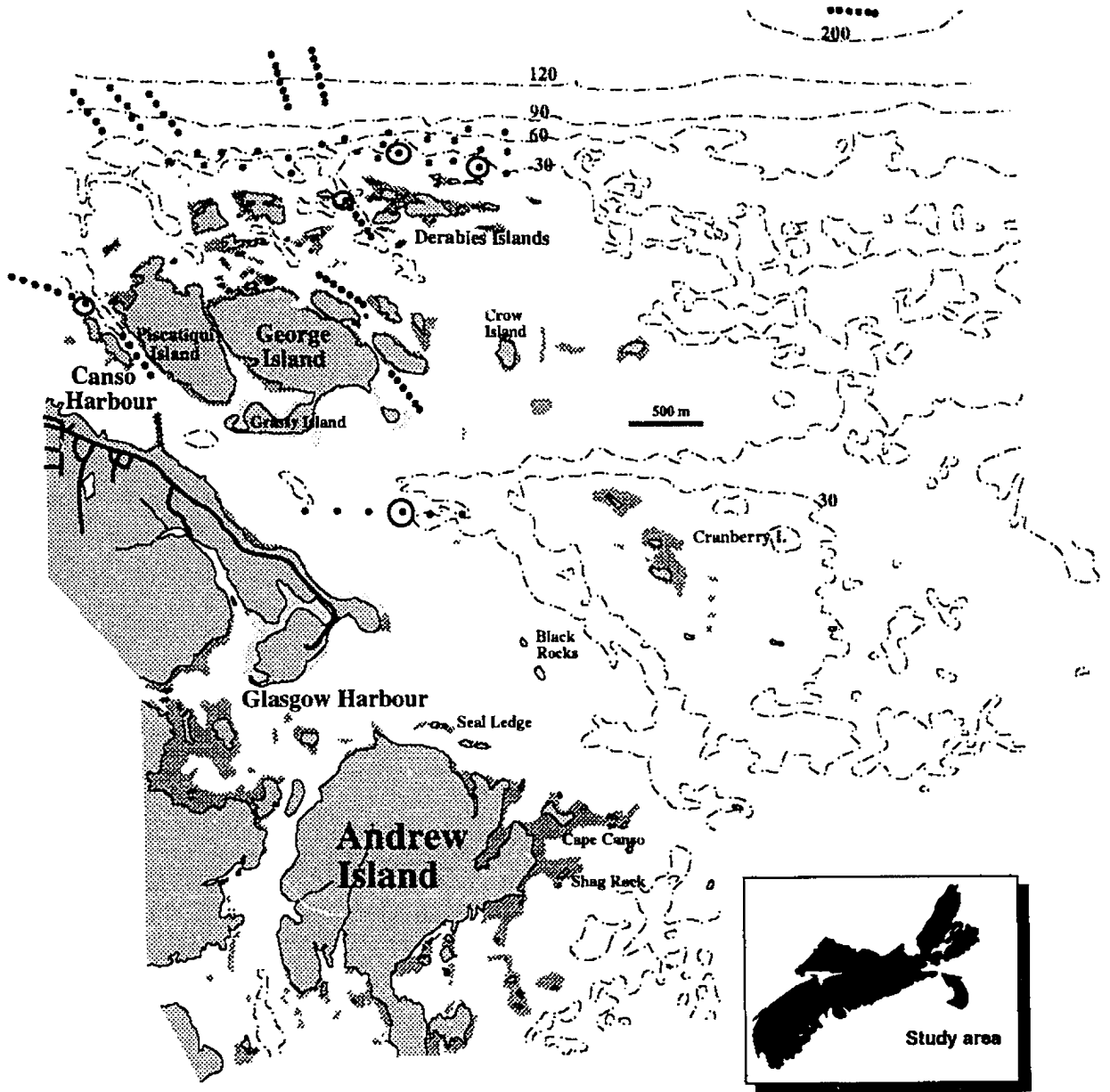


Fig. . Map of Canso area showing winter trapping spots (each dot represent a trap and circles represent captures)

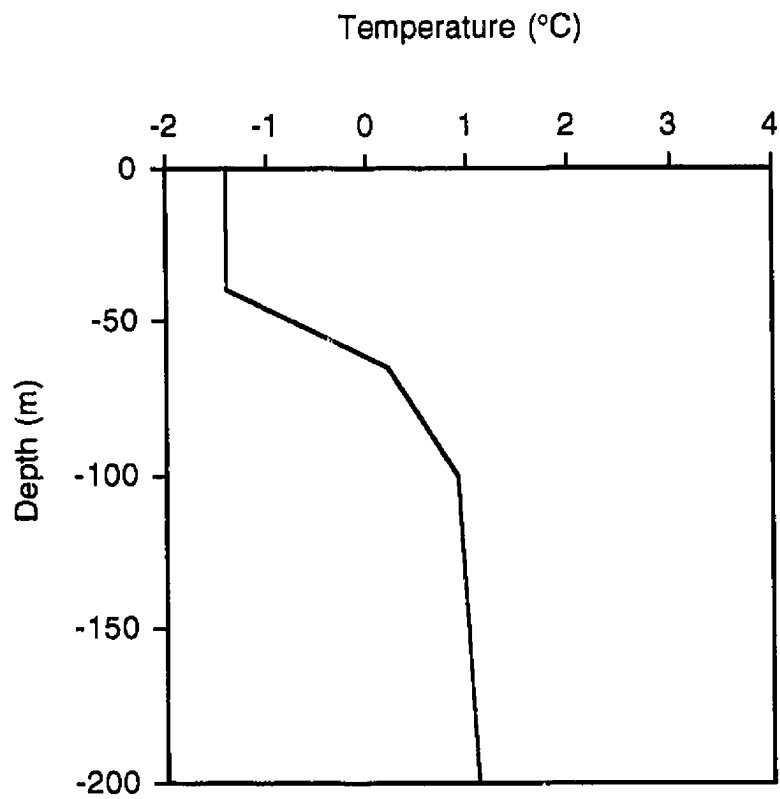


Figure A.4.2. Temperature profile during February 18, 1992, in Canso area.

APPENDIX 5

Recruitment Overharvesting in an eastern Nova Scotia Lobster (Homarus americanus) Stock ? Support for Robinson's (1979) Hypothesis.

Abstract

An inductive approach, based on analysis of commercial fishing pressure and size at reproductive maturity for an American lobster (Homarus americanus) stock along Nova Scotia's eastern shore, provides evidence for recruitment overharvesting, especially in the western part of this stock. This stock has been commercially harvested for over 100 years and the annual landings cycled downward, collapsing in the late 1970's. In this paper we examine and support Robinson's recruitment overharvesting hypothesis (Robinson, 1979. Fish. Mar. Serv. Tech. Rep. 834 [part 3]:77-99) as a cause of stock instability. Two lobster grounds were examined within this stock; Canso (45° 29' N, 61° 00' W) and Jeddore (44° 45' N, 63° 00' W) in the east and west parts of the stock respectively. Mean carapace length (CL) at fifty percent female maturity was 82.6 mm for Canso and 98.1 mm for Jeddore. Catch-per-trap-haul (CPTH) of ovigerous females was 0.1 for Canso and 0.01 for Jeddore. The annual fishery has a large impact on female mean size in Jeddore; dropping from 87 mm CL prior to the fishery to 74.5 mm CL after the season. No such difference in female mean size was observed in Canso. It was thus estimated that, only 6.2 out of 100 females left after the season became ovigerous in Jeddore, compared to 57.1 in Canso. Consequently, egg production per 100 mature females was only about 132,000 and 902,000 for Jeddore and Canso respectively. Therefore, it is recommended the management plan be substantially modified to increase egg production in the western part of the stock.

Introduction

The American lobster (Homarus americanus Milne Edwards) has been harvested commercially along Nova Scotia's eastern shore (Fig. 1), by nearshore trap fishers for over 100 years (Robinson 1980). The interannual fluctuations in landings and the stock collapse (annual landing less than 5% of peak landings) of the 1970's prompted federal fisheries personnel to discern cause (Robinson 1979). Four disparate hypotheses developed by four fishery department scientists attempted to explain the collapse (Pringle and Campbell 1988; Pezzack 1992). Robinson (1979) hypothesized recruitment overharvesting as the cause following assessment of historical catch rates, fishing effort and some biological data; size at reproductive maturity, fecundity and maturation of ovaries, embryos and larvae, all strongly influenced by temperature.

Recruitment overharvesting is most difficult to demonstrate, particularly in open marine systems (Cushing 1981). First, it is most difficult to develop a strong tie between a parent stock and subsequent recruits. Secondly, recruitment failure may be due to any one of a myriad of state variables acting on the pre-recruits at one or more of a number of development stages, thus rendering "cause and effect" difficult. The system's complexity and size eliminates the use of an experimental approach, consequently comparisons and induction are used.

Few biological data were available for the eastern shore lobster stock in the 1970's, nor were there traditional fisheries science data available on the fishery beyond annual landings and number of licensed fishers (Robinson 1979). The stock from Canso west to Halifax (Fig. 1) was considered homogeneous (Campbell and Robinson 1983; Robinson 1979). The paucity of data and the dire stock conditions prompted the initiation of ecological studies on lobster brood stock and larvae (Pringle and Duggan 1985; Jarvis 1989; DiBacco and Pringle 1992; Ugarte, unpub. data) at Canso and Jeddore, two fishing grounds at the stock's east and west borders respectively (Fig. 1). Furthermore, certain local fishers logged

daily catch data as part of a volunteer program run by Department of Fisheries and Oceans personnel (Pringle and Burke 1993). This paper provides support for Robinson's recruitment overharvesting hypothesis, particularly in the western portion of the stock.

Study Area Description

The study sites were located at Canso (45° 29' N, 61° 00' W) and Jeddore (44° 45' N, 63° 00' W) on the Atlantic coast of Nova Scotia in Lobster Fishing Area (LFA) 31 and LFA 32, respectively (Fig. 1). Twenty and 23 licensed boats operate in each study site respectively, beginning April 20 and extending for 63 days.

Materials and Methods

Size at Sexual Maturity

Sexual maturity (may also be referred to as "mature") determination involves the assessment of cement gland development (stages 3 and 4) in a lobster's pleopod (Aiken and Waddy 1982). This technique permits the delineation of ovigerous (capable of extruding eggs the next season) from non-ovigerous females. It was employed by Watson (1988) on trap-caught lobsters from Jeddore, and by the authors on both trap-caught and cage-held lobsters from the Canso grounds (Ugarte, unpubl. data). More than 250 females (distributed in 5 mm carapace length [CL] intervals) were analyzed per study. The proportion of mature females (p) from each area were transformed as follows:

$$p = \ln \frac{1-p}{p}$$

and plotted against lobster CL (X). The slope and regression intercept, yield the empirical constants a and b respectively, which when used in the following logistic function give a least square fit to the relationship between CL and the proportion of sexually mature females (Y) (Campbell and Robinson 1983; Neter et al. 1983; Watson 1988):

$$Y = \frac{1}{1 + e^{-(a + bX)}}$$

Size Distribution

Fisheries and Oceans Canada's lobster stock assessment program includes port sampling (500 lobsters, haphazardly removed from the catch from selected ports at the start and end of each season, are sexed and the CL determined to the nearest mm) and volunteer log book data (daily fishing logs kept by volunteer fishermen from key ports). These data were complemented with trap fishing by DFO-funded fisher contractors in October, 1987 and June, 1988 in Jeddore and July, 1991 and May, 1992 in Canso. The females' CLs before and after the fishery, were compared using a t-test for data from Canso and Jeddore.

Catchability

Catchability of lobsters varies with size (Miller 1989), therefore population estimates based on commercial sampling are probably not an exact representation of these parameters on the grounds. However, we have assumed constant catchability for both study sites.

Egg production

Egg production for both Canso and Jeddore was calculated based on Campbell and Robinson's (1983) carapace length-fecundity relationship for the eastern shore. A single function was estimated by these authors for this stock as follows:

$$Y = 0.000057X^{4.279}$$

where the \log_e transformed values for Y and X are the number of eggs and CLs respectively.

Results

Mean lobster size at fifty percent female maturity was markedly different (Fig. 2) between Canso (82.6 mm CL) and Jeddore (98.1 mm CL). The smallest fecund lobsters captured on these respective grounds were 66 and 75 mm CL. The mean size for trap-caught fecund lobsters at Canso and Jeddore were respectively 89.3 and 108.3 mm CL (Fig. 3).

Frequency of female lobster size classes trapped before and after the fishing season at Jeddore and Canso are given in Figures 4a and 4b. The range at Canso extended from the 61 / 65 mm CL to 136 / 140 mm CL; at Jeddore it went from 45/50 mm CL to 126/130 mm CL, nevertheless the preseason mean size was identical (Fig. 4a, 4b) for both sites (87 mm). There was no difference in mean size before and after the fishing season at Canso ($p > 0.05$); at Jeddore, however, the mean size was different ($p < 0.001$), decreasing by 13 mm to 74.5 mm CL.

Catch-per-trap-haul (CPTH) of ovigerous females was lower at Jeddore (0.01) than Canso (0.1) during the 1989 and 1990 fishing seasons (Table 1). Legal sized lobster CPTH at

Jeddore did not vary between years, and was about one-half that at Canso in 1989; in 1990 it was about two-third the Canso yield due to a drop in CPTH at the latter site (Table 1). The size distribution of non-ovigerous females in the commercial catch at seasons end is markedly different between Jeddore and Canso. About 83% of the animals in Jeddore were pre-recruits, whereas only 36 % were pre-recruits on the Canso grounds (Table 2, compare columns 2 and 6).

The proportion of ovigerous lobsters remaining on both the Canso and Jeddore grounds following the fishery, can be estimated from 1) the frequency of non-ovigerous females per size class (port sample data), and 2) the predicted percent maturity per size class using Watson's (1988) data for Jeddore and our data (1992) for Canso (It should be noted that size at maturity amongst years did not vary significantly for these ports [F. Watson and R. Miller, DFO, Halifax lab. Halifax. unpubl. data]). For example, size at first maturity at Jeddore occurred in the size class 76-80 mm CL, for which there would be about 21 animals out of 100 (Table 2). Of these, 5.4% are predicted to become ovigerous (Watson, 1988). These calculations, made for each size class (Table 2), predict only 6.2 of 100 animals at Jeddore would become ovigerous prior to the next fishing season; these animals would produce about 132,000 eggs. The same calculation made for Canso predict 57 of 100 to become ovigerous (Table 2); they would produce about 902,000 eggs.

Discussion

Robinson (1979), following an in-depth assessment of eastern Nova Scotia lobster stocks, conceded a role for environmental state variables in the fishery collapse. Nevertheless, by using the historical approach, and considering parameters such as increased effort levels; enhanced fishing effectiveness; minimum legal size in relation to reproductive maturity; the lack of brood stock refuges in both space and time, as are available in southwestern Nova Scotia and Northumberland Strait respectively (Campbell and Robinson 1983); and an

environment minimal for larval survival (Harding et al. 1983), he garnered considerable support for his recruitment overharvesting hypothesis. For the period Robinson (1979) covered, it must be noted, there was a paucity of data from the eastern shore fisheries. It has since been shown the catch declines of the late 1960's/1970's ended in 1982 for Nova Scotia's eastern shore. Landings increased by 1150% through 1989, but have since declined (Pringle et al. 1993).

Pringle and Duggan (1984; 1985) demonstrated the eastern shore not to be a homogeneous fishery as earlier portrayed (Robinson 1979; Campbell and Robinson 1983). First, effort (Pringle and Duggan 1984) was concentrated at the western and eastern ends of the fishery. Secondly, CPUE was greater by a factor of three in the eastern (LFA 31) than in the western (LFA 32) end of the stock and thirdly, lobster abundance was estimated to be greater by a factor of two in LFA 31 (Pringle and Duggan 1985). It is important to note that more extensive lobster movement data (Miller et al. 1989) support Robinson's (1979) claim that eastern Nova Scotia stocks tend not to migrate long distances.

Because of differences in ocean climate along the eastern shore, LFA 31 was recently divided into two management units (Fig. 1). This may be fortuitous for future management plans, given the large differences in both size class distribution and size at maturity we have found for Canso and Jeddore. Difference in size class distribution is no doubt due to fishing pressure in relation to production. Data for the Canso and Jeddore fisheries per se are not available, though estimates are available for both LFA 31 (location of Canso) and LFA 32 (location of Jeddore). In the late 1970s / early 1980's, Pringle and Duggan (1985) estimated yield per unit area of fishing ground in the former to be about double the latter when trap density was about the same for the two grounds. If these data accurately reflect the current two study sites then this unequal fishing pressure in relation to abundance could account for the difference in mean lobster size between the catches. We know mean size of animals captured in a fishery is often inversely related to mortality rate (Ricker 1975). Egg production should then be greater in Canso than in Jeddore, all else being equal, because

there are a greater number of mature females escaping the fishery (Fig. 4a, 4b). Campbell and Robinson (1983) demonstrated a decrease in egg production with increasing fishing mortality. In fact, we show a greater frequency of ovigerous females in Canso than in Jeddore (Table 1). When the significant size at maturity difference between the two stocks is considered (Table 2), the proportion mature females escaping the two fisheries to become fecund is dramatically different; 56 % in Canso vs 6 % for Jeddore (Table 2). The difference in egg production per 100 females is 770,000.

How many ovigerous lobsters are required to sustain or indeed enhance the current fishery and are these stocks recruitment overharvested ? Without a stock/recruit relationship it is most difficult to demonstrate definitively, recruitment overharvesting. We do know since the early 1980's recruitment pulse, many eastern Canadian stock yields have surpassed former historic high values (Pezzack 1992), whereas eastern shore stocks, at their 1989 peak, were only about 20% of historic high annual landings. And this from a fishery with mean fishing mortalities of only 0.6 (Miller et al. 1987) during the period 1977-1980 compared to 1.4 and 1.7 for those of the Bay of Fundy and Northumberland Strait (Campbell and Robinson 1983). As well, through the 1980's, exploitation rates (50%-60%) were modest (Miller et al. 1987; Pringle and Duggan 1991) compared to those (70%-85%) of many other Canadian stocks (Miller et al. 1987). Consequently, requests to increase exploitation rates have been resisted (Pringle and Duggan 1991). We thus provide further support for the premise the eastern shore stock requires more eggs-per-recruit (Campbell and Robinson 1983) to both sustain and rebuild the fishery than is currently being produced.

With regard to the eastern shore fishery, it appears there are significant production differences between LFA's 31 and 32 and the respective management plans should reflect this. There appears a need to enhance egg production throughout the eastern shore, but even more urgently in LFA 32 where, if our estimates are correct, egg production will be less by about a factor of seven compared to those in LFA 31. This could be accomplished by

either reducing fishing effort or increasing minimum legal size (Campbell and Robinson 1983); choices that should now be presented to industry.

Campbell and Robinson (1983), prior to the recruitment pulse, were prophetic in their suggestion egg per recruit, to sustain any future recruitment pulse, may need to be higher along the eastern shore than either in the Bay of Fundy or Northumberland Strait. In fact, the subsequent pulse fell far of that recorded for many other stocks (Pezzack 1992).

Population abundance is rarely controlled by a single state variable, although uncontrolled fishing pressure has been shown to extirpate certain marine species. The LFA 31/32 fishery was not uncontrolled; it was regulated with similar regulations to other Canadian lobster fisheries, and yet collapsed when others, under greater fishing pressure (Campbell and Robinson 1983) did not. There was a major habitat change with the closing of Canso Strait (Dadswell 1979) in 1955, coincidental with the last significant peak in lobster landings for the eastern shore fishery. The Canso Causeway blocked the flow of much warmer Gulf of St. Lawrence water, rich in larvae (Harding et al. 1979). Current studies (R. Ugarte, unpubl. data) suggest these warmer waters could have played a significant role on lobster ovarian, embryo and larval maturation.

Table A.5.1. Catch per trap haul (CPTH) of ovigerous females and of all lobsters from Jeddore and Canso area (n=number of traps sampled).

<u>Year</u>	<u>CPTH (ovigerous females)</u>		<u>CPTH (all lobsters)</u>	
	Jeddore	Canso	Jeddore	Canso
1989 & 1989 (combined)	<0.01 (n=20,795)	.122 (n= 21,447)	0.35 (n=20,795)	0.62 (n=21,447)

Sources of data

R. E. Duggan (unpublished data), from fisherman logbook

Table 2. Estimates of both the number of potentially ovigerous females per 100 females remaining on the grounds following the season's fishery at both Canso and Jeddore and their respective egg production.

		Jeddore				Canso			
1		2	3	4	5	6	7	8	9
Size class		Non-ovigerous ^a	Mature ^b	Potentially ovigerous ^c	Egg production ^d	Non-ovigerous ^a	Mature ^e	Potentially ovigerous ^f	Egg production ^g
CL (mm)		(No)	(%)	(No)	(No)	(No)	(%)	(No)	(No)
Pre-recruits	61 - 65	17.8	0.0	0.0	0	0.3	0.0	0.0	0
	66 - 70	16.9	0.0	0.0	0	4.7	7.5	0.3	1,187
	71 - 75	27.3	0.0	0.0	0	8.3	31.3	2.6	13,932
	76 - 80	20.9	5.4	1.1	7,826	23.0	32.7	7.5	53,359
Recruits	81 - 85	6.1	12.2	0.7	6,497	15.0	44.4	6.7	62,185
	86 - 90	3.2	8.6	0.3	3,576	15.7	70.0	11.0	131,132
	91 - 95	2.5	21.7	0.5	7,551	15.0	85.4	12.8	193,296
	96 - 100	1.8	28.7	0.5	9,447	7.0	90.0	6.3	119,034
	101 - 105	1.1	63.3	0.7	16,364	2.7	100.0	2.7	63,120
	106 - 110	1.1	89.3	1.0	28,635	2.7	100.0	2.7	77,314
	111 - 115	0.7	91.7	0.6	20,852	1.7	100.0	1.7	59,081
	116 -	0.8	100.0	0.8	31,102	3.3	100.0	3.3	128,294
Total		100		6.2	131,850	100		57.1	901,934

^aDerived from port sample data taken at the end of the fishing season

^bFrom Watson (1988)

^c(col. 3 x col. 2)/100

^d($y = 0.000057X^{4.279}$) x col. 4 (Formula from Campbell and Robinson [1979])

^e(R. Ugarte and J. Pringle, unpubl. data)

^f(col. 6 x col. 7)/100

^g($y = 0.000057X^{4.279}$) x col. 8 (Formula from Campbell and Robinson [1979])

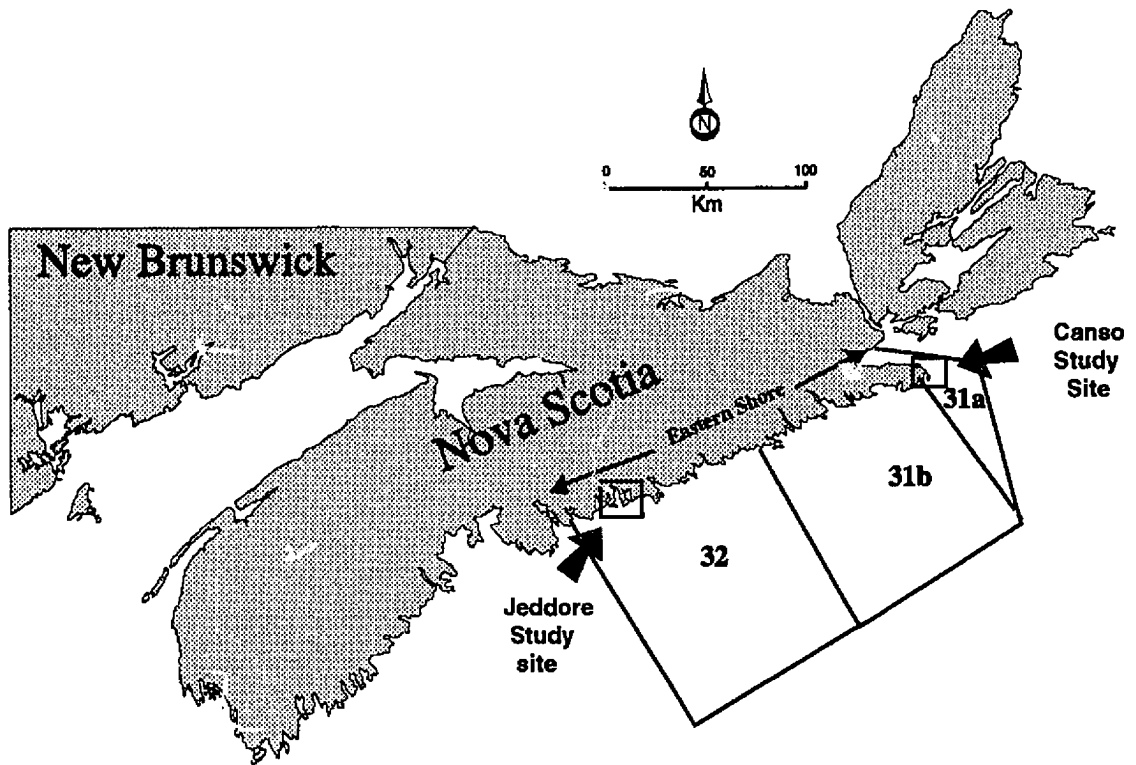


Figure A.5.1. Chart of Nova Scotia's Atlantic shore showing the study sites and their respective Lobster Fishing Area (LFA).

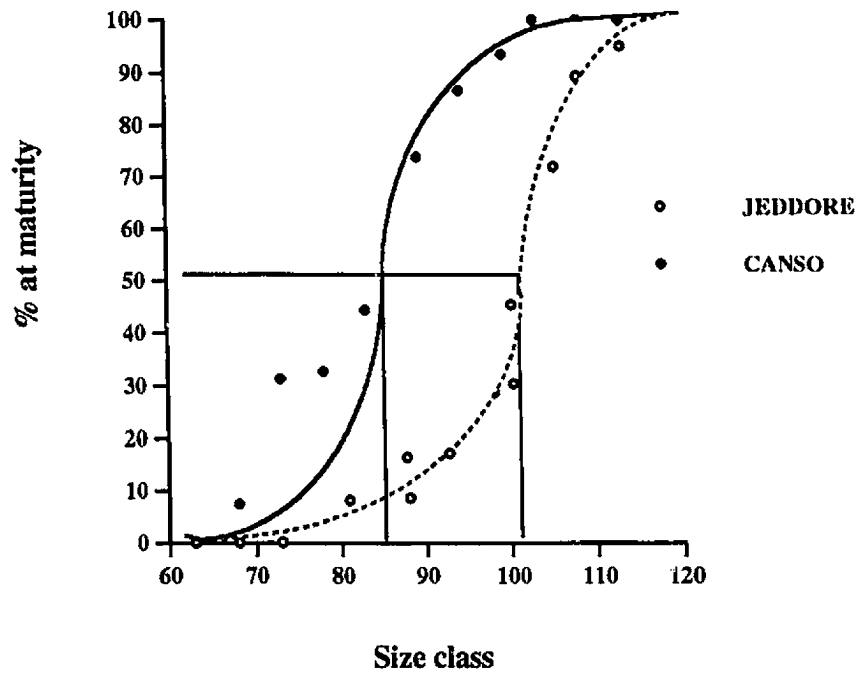


Figure A.5.2. Size at 50% maturity of female lobsters at Canso and Jeddore area, based on the examination of the pleopod tegumental gland (Aiken and Waddy 1982).

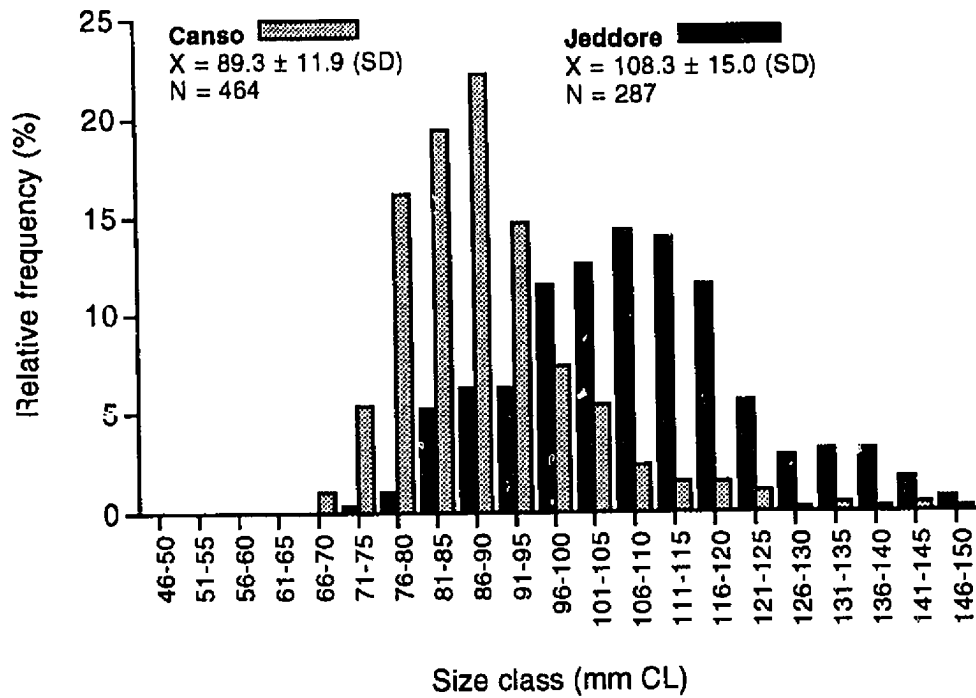


Fig. A.5.3. Size frequency of ovigerous females at Canso and Jeddore. Data obtained from fishing surveys and charters during 1987-88 in Jeddore and 1992 in Canso.

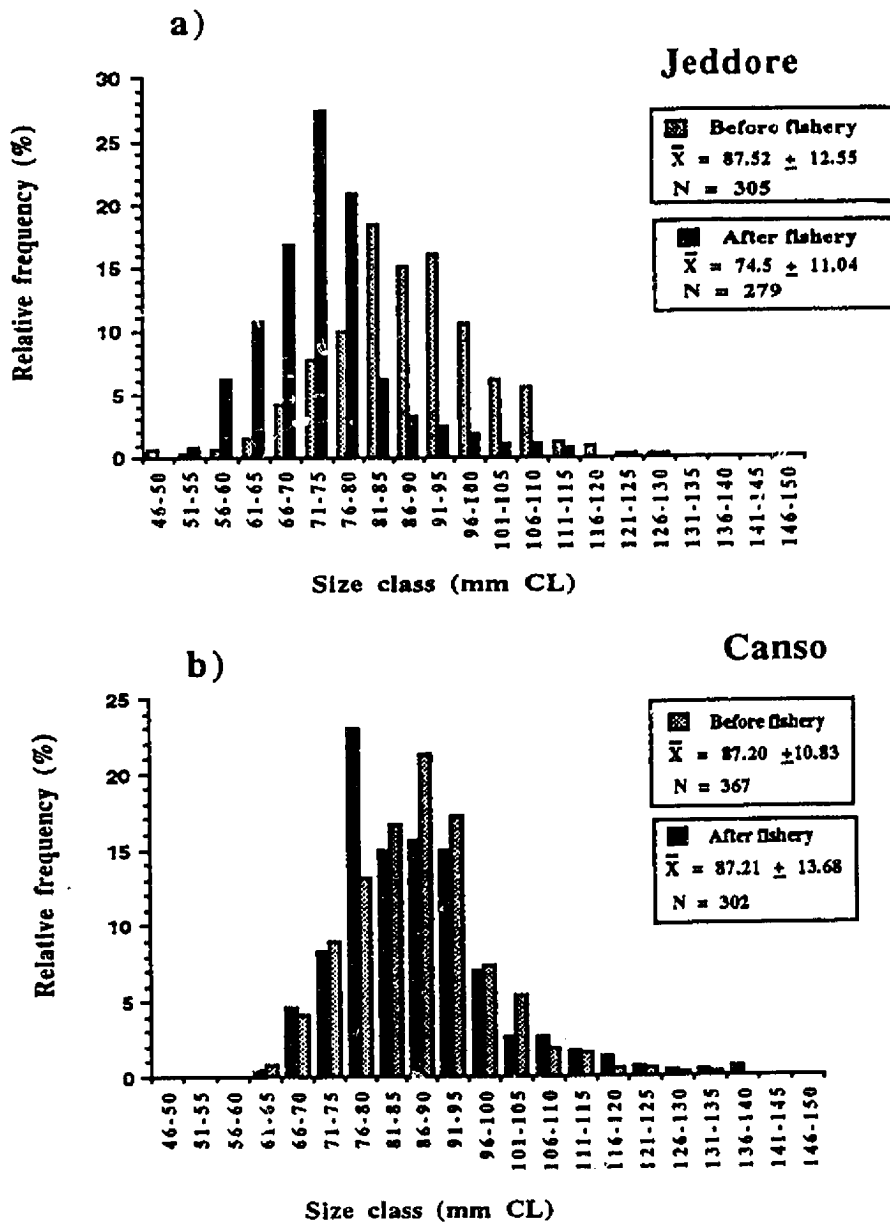


Figure A.5.4. Size frequency of non-ovigerous female lobsters before and after the fishing season at both (a) Jeddore and (b) Canso.

APPENDIX 6

STATISTICAL ANALYSIS TABLES

Statistical Analysis Tables for Chapter 1

Table I.2. Analysis of variance for fishing depth among the grounds during four periods from May 20 to July 9, 1992.

Source of variation	SM	DF	MS	F	P
Periods	1183.734	3	394.578	27.333	0.000
Ground	9720.155	2	4860.078	336.665	0.000
Period * Ground	357.802	6	59.634	4.131	0.000
Error	18463.587	1279	14.436		

Table I.3. Analysis of variance for abundance of ovarian females captured by traps in the different grounds during four periods from May 20 to July 9, 1992.

Source of variation	SM	DF	MS	F	P
Periods	9.299	3	3.100	9.605	0.000
Ground	2.169	2	1.085	3.361	0.035
Period * Ground	5.474	6	0.912	2.827	0.010
Error	1416.284	4389	0.323		

Table I.4. Analysis of variance for ovarian females size captured by traps in the different grounds during four periods from May 20 to July 9, 1992.

Source of variation	SM	DF	MS	F	P
Periods	335.656	3	11.885	0.786	0.502
Ground	15352.88	2	7676.440	53.916	0.000
Period * Ground	1456.194	6	242.699	1.705	0.116
Error	183241.692	41287	142.379		

Table I.5. Contingency table comparing PTG stages of ovarian females among grounds.

Period	Ground	PTG stage		Total
		< 2	≥2	
May 20-29	Inner	132	122	254
	Middle	167	46	213
	Outer	159	82	241
	Total	458	250	708
	Test χ^2	Value 35.707	DF 2	Prob 0.000

Period	Ground	PTG stage		Total
		< 2	≥2	
July 8-9	Inner	21	56	77
	Middle	34	33	67
	Outer	117	3	120
	Total	172	92	264
	Test χ^2	Value 110.091	DF 2	Prob 0.000

Table I.6. Analysis of variance for abundance of berried females captured by traps in the different grounds during four periods from May 20 to July 9, 1992.

Source of variation	SM	DF	MS	F	P
Periods	2.921	3	0.974	14.470	0.000
Ground	2.360	2	1.180	17.533	0.000
Period * Ground	2.119	6	0.353	5.248	0.000
Error	297.061	4414	0.067		

Table I.7. Analysis of variance for embryo stage of berried females captured in the different grounds during four periods from May 20 to July 9, 1992.

Source of variation	SM	DF	MS	F	P
Periods	71087.664	2	35543.832	7.780	0.001
Ground	29368.733	2	14684.367	3.214	0.042
Period * Ground	23974.820	4	5993.705	1.312	0.267
Error	854326.080	187	4568.589		

Statistical Analysis Tables for Chapter II

Table II.3. Analysis of Variance for embryo maturity (A) and female size (B) at (locations) 3 m, 17 m, and wild stock at the start of the experiment in May 1991 and 1992.

=====

A)					
DEP VAR: Embryo stage					
Source	SS	DF	MS	F	P
Year	76716.745	1	76716.745	9.175	0.003
Location	9859.789	1	9859.789	1.179	0.278
Year x Location	3498.164	1	3498.164	0.418	0.518
ERROR	4523536.312	541	8361.435		

B)					
DEP VAR: Size					
SOURCE	SS	DF	MS	F	P
YEAR	446.693	1	446.693	4.765	0.030
LOCATION	18.803	1	18.803	0.201	0.654
YEAR* LOCATION	76.223	1	76.223	0.813	0.368
ERROR	47063.163	502	93.751		

Table I I.4. Analysis of Variance for the development rate of embryos caged at 3 m and 17 m during 1991 and 1992.

Source	SS	DF	MS	F	P
Year	57.61	1	257.610	4.732	0.033
Depth	1433.88	1	1433.88	26.34	0.000
Year x Depth	226.319	1	226.319	4.157	0.045
Error	3701.684	68	54.437		

Statistical Analysis Tables for Chapter III

Table III.3. Contingency table between ovarian development (PTG) and lobster origin (tagged, caged, and fishery surveyed) on July 8-9, 1992. (A) excluding 17 m and (B) including 17 m.

A.-		PTG stage		Total
		< 3	≥3	
Origin		<hr/>		
	Fishery surveyed	98	85	183
	Tagged	14	14	28
	Caged at 3 m	7	13	20
		<hr/>		
	Total	119	112	231
Statistic		Value	df	Prob.
Pearson Chi-square		2.54	2	0.285
B.-		PTG stage		Total
		< 3	≥3	
Origin		<hr/>		
	Fishery surveyed	98	85	183
	Tagged	14	14	28
	Caged at 3 m	7	13	20
	Caged at 17 m	17	3	20
		<hr/>		
	Total	136	115	251
Statistic		Value	df	Prob.
Pearson Chi-square		10.84	3	0.013

Table III.4. Contingency table on the effect of depth (3m vs 17 m) on ovarian development (PTG) in May (A) and July 8-9 (B), 1992.

A.-		PTG stage		Total
		< 2	≥2	
Depth				
3 m		12	5	17
17 m		14	3	17
Total		26	8	34
Statistic		Value	df	Prob.
Pearson Chi-square		0.654	1	0.419
Yates corrected Chi-square		0.163	1	0.686

B.-		PTG satge		Total
		< 3	≥3	
Depth				
3 m		4	14	18
17 m		13	3	16
Total		17	17	34
Statistic		Value	df	Prob.
Pearson Chi-square		11.806	1	0.001
Yates corrected Chi-square		9.563	1	0.002

REFERENCES

- Aiken, D.E. 1973. Proecdysis, setal development, and molt prediction in the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 30: 1337-1344.
- Aiken, D. E. and S. L. Waddy. 1980. Reproductive biology, p. 215-276. In J.S. Cobb and B.F. Philips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.
- Aiken, D. E. and S. L. Waddy. 1982. Cement gland development, ovary maturation, and reproductive cycles in the American lobster *Homarus americanus*. J. Crust. Biol. 2(3): 315-327.
- Aiken, D.E. and S. L. Waddy. 1985a. Production of seed stock for lobster culture. Aquaculture. 44: 103-114.
- Aiken, D.E. and S. L. Waddy. 1985b. The uncertain influence of spring photoperiod on spawning in the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 194-197.
- Aiken, D.E. and S. L. Waddy. 1986a. Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective. Can. J. Fish. Aquat. Sci. 43: 2258 - 2270.
- Aiken, D.E. and S. L. Waddy. 1986b. Oöcyte maturation and spawning in wild American lobsters (*Homarus americanus*): lack of evidence for significant regulation by photoperiod. Can. J. Fish. Aquat. Sci.43: 1451-1453.
- Aiken, D. E., W. J. Rowe, D. J. Martin-Robichaud, and S. L. Waddy. 1982. Seasonal differences in the effect of photoperiod on survival and development of larval American lobsters (*Homarus americanus*). J. World Maricult. Soc. 13: 287-293.
- Alverson, D. L. and W.T. Pereyra. 1969. Demersal fish exploration in the northeastern Pacific Ocean - an evaluation of exploratory fishing methods and analytical

- approaches to stock size and yield forecasts. *J. Fish. Res. Board Can.*, 26: 1985-2001.
- Attard, J., and C. Hudon. 1987. Embryonic development and energetic investment in egg production in relation to size of female lobster (*Homarus americanus*). *Can. J. Fish. Aquat. Sci.* 44: 1157-1164.
- Atema, J., Jacobson, S., Karnofsky, E., Olesko-Szuts, S., and Stein, L. S. 1979. Pair formation in the lobster, *Homarus americanus* : Behavioral development, pheromones and mating. *Mar. Behav. Physiol.* 6, 277-296.
- Atema, J. 1986. Review of sexual selection and chemical communication in the lobster, *Homarus americanus*. *Can. J. Fish. Aquat. Sci.* 43: 2283 - 2390.
- Bergeron, T. 1967. Contribution a la biologie du homard (*Homarus americanus* Milne-Edwards) des Iles-de-la-Madeleine. *Naturaliste Can.* 94: 169-207.
- Bottero, L., and J. Atema. 1982. Behavior and substrate selection during larval settling in the lobster *Homarus americanus*. *J. Crustacean Biol.* 2: 59-69.
- Brandford, J.R. 1978. Incubation period for the lobster *Homarus gammarus* at various temperatures. *Mar. Biol.* 47: 363-368.
- Brandford, J.R. 1979. Locomotory activity and food consumption by the lobster *Homarus gammarus*. *Mar. Behav. Physiol.* 6: 13-24.
- Buesa Mas, R. J. 1970. Migration of the lobster (*Panulirus argus*). *Mar Pesca* 60, 22-27.
- Caddy, J. F. 1976. The influence in variation in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in the Southern Gulf of St. Lawrence. ICES Special Meeting Population assessment of Shelfish Stock, Paper No. 10:44 p.
- Caddy, J. F. 1979. The influence of variations in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in the

- southern Gulf of St. Lawrence. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 204-216.
- Campbell, A. 1986. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, Eastern Canada. Can. J. Fish. Aquat. Sci. 40: 1667-1675.
- Campbell, A. 1990. Aggregation of berried lobsters (*Homarus americanus*) in shallow waters off Grand Manan, eastern Canada. Can. J. Fish. Aquat. Sci. 47:520-553.
- Campbell, A., and D.G. Robinson. 1983. Reproductive potential of three American lobster (*Homarus americanus*) stocks in the Canadian Maritimes. Can. J. Fish. Aquat. Sci. 40: 1958-1967.
- Campbell, A., and D. S. Pezzack. 1986. Relative egg production and abundance of berried lobsters, *Homarus americanus*, in the Bay of Fundy and off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 43: 2190-2196.
- Campbell, A., and A.B. Stasko. 1986. Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy. Mar. Biol. 92: 393-404.
- Campbell, A., D.E. Graham, H.J. MacNichol, and A.M. Williamson. 1984. Movements of tagged lobsters released on the continental shelf from Georges Bank to Baccaro Bank, 1971-1973. Can. Tech. Rep. Fish. Aquat. Sci. 1288: 16 p.
- Castell, J.D. and S. D. Budson. 1974. Lobster nutrition: the effect on *Homarus americanus* of dietary protein levels. J. Fish. Res. Board Can. 31: 1363-1370.
- Castell, J.D. and J. C. Kean. 1986. Evaluation of the role of nutrition in lobster recruitment. Can. J. Fish. Aquat. Sci. 43: 2320-2327.
- Chittleborough, R.G. 1970. Studies on recruitment in the Western Australian rock lobster *Panulirus longipes cygnus* George: density and natural mortality of juveniles. Aust. J. Mar. Freshw. Res. 21: 131-148.
- Cobb, J. S. 1968. Delay of moult by the larvae of *Homarus americanus*. J. Fish. Res. Board Can. 25: 2251-2253.

- Cobb, J. S. 1971. The shelter-related behavior of the American lobster, *Homarus americanus*. Ecology. 52: 108-115.
- Cobb, J. S., D. Wang, and D.B. Campbell. 1989. Timing of settlement by postlarval lobster (*Homarus americanus*): field and laboratory evidence. J. Crustacean. Biol. 9: 60-66.
- Cooper, R.A. and J.R. Uzmann. 1971. Migrations and growth of deep-sea lobsters, *Homarus americanus*. Science 171: 288-290.
- Cooper, R.A. and J.R. Uzmann. 1980. Ecology of juvenile and adult *Homarus*. p. 97-142. In J.S. Cobb and B.F. Philips [ed.] The biology and management of lobsters. Vol. 2. Academic Press, New York, NY. 390 p.
- Cooper, R.A., R.A. Clifford, and C.D. Newell. 1975. Seasonal abundance of the American lobster, *Homarus americanus*, in the Boothbay region of Maine. Trans. Am. Fish. Soc. 4: 669-674.
- Corriveau, G. V. and J. L. Tremblay 1948. Contribution a la biologie du homard (*Homarus americanus*) dans la Baie-des-Chaleurs et la golfe du St. Laurent. Contr. Sta. Biol. St. Laurent. 19: 222 p.
- Davis, G.E. 1976. " U.S. National Park Service Spiny Lobster Study, "Interim Rep. U.S. Natl. Park Serv., Washington, D.C.
- DiBacco, C. and J. D. Pringle. 1992. Larval lobster (*Homarus americanus*, H. Milne Edwards, 1837) distribution in a protected Scotian shelf bay. J. Shell. Res. Vol 11. No 1, 81- 84.
- Dow, R. L. 1974. American lobsters tagged by Maine commercial fishermen, 1957-59. Fish. Bull., U.S. 72: 662-623.
- Duggan, R.E., and J.D. Pringle. 1988. Lobster size structure and seasonal distribution in the Clam Bay area of Halifax County, Nova Scotia. C.A.F.S.A.C. Res. Doc. 88/13: 25 p.

- El-Sahb, M. 1977. Oceanographic features, currents, and transport in Cabot Strait. J. Fish. Res. Board Can. 34: 516-528.
- Ennis, G. P. 1971. Lobster (*Homarus americanus*) fishery and biology in Bonavista Bay, Newfoundland 1966-70. Fish. Res. Bd. Can. Tech. Rep. 289:1-46.
- Ennis, G.P. 1982. Fishery and population biology of lobsters (*Homarus americanus*) at Comfort Cove, Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 1116:45 pp.
- Ennis, G.P. 1983. Observations on the behavior and activity of lobsters (*Homarus americanus*) in nature. Can. Tech. Rep. Fish. Aquat. Sci. 1165: 26 p.
- Ennis, G.P. 1984a. Small-scale movements of the American lobster *Homarus americanus*. Trans. Am. Fish. Soc. 113: 336-338.
- Ennis, G.P. 1984b. Comparison of physiological and functional size-maturity relationships in two Newfoundland populations of lobsters, *Homarus americanus*, US Dept. Comm. Fish. Bull. 82:244-249.
- Ennis, G.P. 1986. Stock definition, recruitment variability, and larval recruitment process in the American lobster, *Homarus americanus*, a review. Can J. Fish. Aquat. Sci. 43: 2072-2084.
- Ennis, G.P. 1991. Annual variation in egg production in a Newfoundland population of the American lobster, *Homarus americanus*. In, A. Wenner and A. Kuris [ed.] . Crustacean issues 7, Crustacean egg production, p 267-290. A. A. Balkema, Rotterdam, Brookfield.
- Fogarty, M. J. and R. Lawton. 1983. An overview of larval American lobster, *Homarus americanus*, sampling program in New England during 1974-79. U. S. Dep. Commer. NOAA Tech. Rep. NMFS SSRF-775: 9-14.
- Fogarty, M.J., D.V.D. Borden, and H.J. Russell. 1980. Movements of tagged American lobster, *Homarus americanus*, off Rhode Island. U.S. Dep. Commer. Fish. Bull. 78: 771-780.

- Frank, K. I., and W. C. Leggett. 1983. Survival value of an opportunistic life-stage transition in capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* 40: 1442-1448.
- Hachey, H. B. 1942. Waters of the Scotian Shelf. *J. Fish. Res. Board Can.* 5: 377-397.
- Haakonsen, H. O., and A. O. Anoruo. 1994. Tagging and migration of the American lobster *Homarus americanus*. *Reviews in Fisheries Science*, 2(1): 79-93.
- Harding, G.C., K.F. Drinkwater, and W.P. Vass. 1983. Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Gulf of Maine: a new synthesis. *Can. J. Fish. Aquat. Sci.* 40(2): 168-184.
- Harding, G.C., W.P. Vass. and K.F. Drinkwater. 1982. Aspects of larval American lobster (*Homarus americanus*) ecology in St. Georges Bay, Nova Scotia. *Can. J. Fish. Aquat. Sci.* 39: 1117-1129
- Helluy, S.M. and B.S. Beltz. 1991. Embryonic development of the American lobster (*Homarus americanus*): quantitative staging and characterization of an embryonic molt cycle. *Biol. Bull.* 180: 355-371.
- Herrick, F. H. 1911. The natural history of the American lobster. *Bull. U. S. Bur. Fish.* 29: 150-408.
- Herrnkind, W.F. 1980. Spiny lobsters: patterns of movement. p. 349-407. *In* J.S. Cobb and B.F. Philips [ed.] *The biology and management of lobsters*. Vol. 1. Academic Press, New York, NY. 463 p.
- Hudon, C., P. Fradette et P. Legendre. 1986. La répartition horizontale et verticale des larves de homard (*Homarus americanus*) autour des Iles de la Madeleine, golfe du Saint-Laurent. *Can. J. Fish. Aquat. Sci.* 43:2164-2176.
- Jarvis, C. 1989. Movement patterns of late-stage ovigerous female lobsters (*Homarus americanus*) at Jeddore, Nova Scotia. Ms Sci. Thesis. Dalhousie University, Halifax, N.S.

- Jernakoff, P., B.F. Phillips, and R.A. Maller. 1987. A quantitative study of nocturnal foraging distances of the western rock lobster *Panulirus cygnus* George. J. Exp. Mar. Biol. Ecol. 113: 9-21.
- Karnofsky, E. B., Atema, J., and R. H. Elgin. 1989. Field observations of social behavior, shelter use, and foraging in the lobster, *Homarus americanus*. Biol. Bull. 176: 239-246.
- Krouse, J. S. 1989. Performance and selectivity of trap fisheries for crustaceans. p 307-326. In J. F. Caddy [ed.] Marine invertebrate fisheries: Their assessment and management. Wiley and Sons. New York.
- Lee, T. C. 1992. Molting and mating behaviour in *Homarus americanus*, a field experiment. BSc Honours Thesis, Dalhousie University, Halifax, Canada.
- Lipcius, R. N., and W. F. Herrnkind. 1987. Control and coordination of reproduction and molting in the spiny lobster *Panulirus argus*. Maine Biology. 96: 207-214.
- Lund, W.A. 1979. Lobster investigations. Completion Report, Comm. Fish. Res. Devel. Act, Project 3-203-R, Univ. Conn. (Storrs). 24 p.
- Lund, W.A., L.L. Stewart, and C.J. Rathbun. 1973. Investigations on the lobster. Completion Report, Comm. Fish. Res. Devel. Act, Project 3-130-R, Univ. Conn. (Storrs). 189 p.
- MacDonald, B.A. and R. J. Thompson. 1988. Intraspecific variation in growth and reproduction in latitudinally differentiated populations of the Giant Scallop *Placopecten magellanicus* (Gmelin). Biol. Bull. 175:361-371.
- Maynard, D.R., and G.Y. Conan. 1984. Preliminary monitoring of short term movements for lobsters (*Homarus americanus*) in the Bideford River, Prince Edward Island, using ultrasonic telemetry. C.A.F.S.A.C. Res. Doc. 84/99. 21 p.

- McKenzie, B. R. 1988. Assessment of temperature effects on interrelationships between stage durations, mortality, and growth in laboratory-reared *Homarus americanus* Milne-Edwards larvae. *J. Exp. Mar. Biol. Ecol.* 116: 87-98.
- McLeese, D.W., and D.G. Wilder. 1958. The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. *J. Fish. Res. Board Can.* 15: 1345-1354.
- McLelland, H.J. 1954a. T,S relations and mixing on the Scotian Shelf. *J. Fish. Res. Board Can.* 11: 419-430.
- McLelland, H. J. 1954b. Bottom temperatures on the Scotian Shelf. *J. Fish. Res. Board Can.* 11: 404-418.
- Miller, R.J. 1975. Density of the commercial spider crab, *Chionoecetes opilio*, and calibration of effective area fished per trap using bottom photography. *J. Fis. Res. Board. Can.* 32: 761-768.
- Miller, R.J. 1989. Catchability of american lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) by traps. *Can. J. Fish. Aquat. Sci.* 46: 1652-1657.
- Miller, R. J. 1990. Effectiveness of crab and lobster traps. *Can. J. Fis. Aquat. Sci.* 47: 1228-1251.
- Miller, R.J., D.S. Moore, and J.D. Pringle. 1987. Overview of the inshore lobster resources in the Scotia-Fundy region. *C.A.F.S.A.C. Res. Doc.* 87/85. 10 p.
- Miller, R.J., R.E. Duggan, D.G. Robinson, and Z. Zheng. 1989. Growth and movement of *Homarus americanus* on the outer coast of Nova Scotia. *Can. Tech. Rep. Fish. Aquat. Sci.* 1716 : 17p.
- Moore, D.S., Miller, R.J., and L.D. Meade. 1986. Survey of shallow benthic habitat: Eastern shore and Cape Breton, Nova Scotia. *Can Tech. Rep. Fish. Aquat. Sci.* 1546: v + 49 p.

- Morrissey, T.D. 1971. Movement of tagged American lobsters, *Homarus americanus*, liberated off Cape Cod, Massachusetts. Trans. Am. Fish. Soc. 100: 117-120.
- Munro, J., and J.C. Therriault. 1983. Migrations saisonieres du homard (*Homarus americanus*) entre la cote et les lagunes des Iles-de-la-Madelaine. Can. J. Fish. Aquat. Sci. 40: 905-918.
- Nelson, K. 1986. Photoperiod and reproduction in lobster (*Homarus*). Amer. Zool. 26: 447-457.
- O'Neill, D. J. and J. S. Cobb. 1979. Some factors influencing the outcome of shelter competition in lobsters (*Homarus americanus*). Mar. Behav. Physiol. 6: 33-45.
- Orr, R. T. 1970. Animal in migration. The Macmillan Company, Collier-Macmillan LTD., London. 303 pp.
- Perkins, H. C. 1972. Developmental rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne-Edwards). Fish. Bull. 70: 95-99.
- Petrie, B., B. J. Topliss, and D.G. Wright. 1987. Coastal upwelling and eddy development off Nova Scotia. J. Geophys. Res. 29: 12,979-12,991.
- Pezzack, D.S. 1984. Lobster distribution on the Scotian Shelf and implications to the Jonah crab fisheries. C.A.F.S.A.C. Res. Doc. 84/44. 17 p
- Pezzack, D.S., and D.R. Duggan. 1986. Evidence of migration and homing of lobsters (*Homarus americanus*) on the Scotian Shelf. Can. J. Fish. Aquat. Sci. 43: 2206-2211.
- Pringle, J. D., and R. E. Duggan. 1984. Latent effort along Nova Scotia's Atlantic coast. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 84/102: 16 p.
- Pringle, J. D., and R. E. Duggan. 1985. An estimate of yield for oceanic Nova Scotia lobster grounds. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 85/102: 16 p.

- Pringle, J. D., and R. E. Duggan. 1991. Lobster stock assessment for LFA 31. CAFSAC Res. Doc.91/21. 15 pp.
- Pringle, J. D., and D. L. Burke. 1993. The Canadian lobster fishery and its management, with emphasis on the Scotian Shelf and the Gulf of Maine, p. 21-122. In L.S. Parson and W. H. Lear [eds.] Perspectives on Canadian marine fisheries management. Can. Bull. Fish. Aquat. Sci. 226.
- Pringle, J. D., R. Ugarte, R. Duggan, and P. Koeller. 1993. Review of request for an extension to the lobster fishing season in LFA 31A. DFO Atlantic Fisheries Research Document 93/67. 20 pp.
- Robinson, D. G. 1979. Consideration of the lobster (*Homarus americanus*) recruitment overfishing hypothesis; with special reference to the Canso Causeway. Fish. Mar. Serv. Tech. Rep. 834: 77-99.
- Robinson, D. G. 1980. History of the lobster fishery on the eastern shore of Nova Scotia, p. 8-23. In J. D. Pringle, G. J. Sharp and J. F. Caddy [ed.]. Proceedings of the workshop on the relationship between sea urching grazing and commercial plant/animal harvesting. Can. Tech. Rept. Fish. Aquat. Sci. 954.
- Ropes, J. W. 1968. The feeding habits of the green crab *Carcinus maenas* (L.). Fish. Bull 67: 183-203.
- Sastry, A. N. 1983. Ecological aspects of reproduction. p. 179-255. In F.J. Vernberg and W. B. Vernberg [ed.] The biology of crustacea. Vol. 8. Environmental adaptations. Academic Press, New York, NY.
- Scarratt, D. J. 1964. Abundance and distribution of lobster larvae (*Homarus americanus*) in Northumberland Strait. J. Fish. Res. Bd. Can. 21: 661-680.
- Scarratt, D. J. 1968. An artificial reef for lobsters (*Homarus americanus*). J. Fish. Res. Board. Can. 25: 2683-2669.

- Scrivener, J. C. E. 1971. Agonistic behaviour of the American lobster *Homarus americanus* (Milne-Edwards). Fish. Res. Board. Can. Tech. Rep. No 235.
- Sheehy, D. J. 1976. Utilization of artificial shelters by the American lobster (*Homarus americanus*). J. Fish. Res. Board. Can. 33: 1615-1622.
- Shroeder, W. C. 1959 The lobster, *Homarus americanus*, and the red crab, *Geryon quinquedens*, in the offshore waters of the western North Atlantic. . Deep Sea Res. 5: 266-82.
- Smith, P. C., B. Petrie, and C. R. Mann. 1978. Circulation, variability, and dynamics of the Scotian Shelf and slope. J. Fish. Res. Board Can. 35: 1067-1083.
- Squires, H. J., G.E. Tucker and G.P. Ennis. 1971. Lobsters (*Homarus americanus*) in Bay of Islands, Newfoundland, 1963-65. Fish. Res. Board. Can. Tech. Rep. 1151-1158 pp.
- Stasko, A.B. 1978. Inshore-ofshore SW Nova Scotia lobster stock interaction: a hypothesis. CAFSAC Res. Doc. 78/37, 10 p.
- Stasko, A.B. 1980. Lobster larval surveys in Canada, p. 157-165. In V.C, Anthony and J.F. Caddy [ed.] Proceedings of the Canada - U.S. workshop on status of assessment science for N.W. Atlantic lobster (*Homarus americanus*) stocks, St. Andrews, New Brunswick, Oct. 24-26, 1978. Can. Tech. Rep. Fish. Aquat. Sci. 932.
- Stewart, L. L. 1972. The seasonal movement, population dynamics, and ecology of the lobster, *Homarus americanus*, off Ram Island, Conn. Ph. D. thesis, University of Connecticut, Storrs.
- Stewart, J. E., and M. F. Li. 1969. A study of lobster (*Homarus americanus*) ecology using serum protein concentration as an index. Can. J. Zool. 47: 21-28.
- Stewart, J. E., and H. J. Squires. 1968. Adverse conditions as inhibitors of ecdysis in the lobster *Homarus americanus*. J. Fish. Res. Board. Can. 25(9): 1763-1774.

- Templeman, W. 1936a. Local differences in the life story of the lobster on the coast of the Maritime provinces of Canada. *J. Biol. Board Can.* 2: 41-88.
- Templeman, W. 1936b. The influence of temperatures, salinity, light, and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). *J. Biol. Board Can.* 2: 485-497.
- Templeman, W. 1940a. Embryonic developmental rates and eggs laying of Canadian lobsters. *J. Fis. Res. Bd. Can.* 5: 71-83.
- Templeman, W. 1940b. The life history of the lobster. *Nfld. Dep. Nat. Res. Serv. Bull.* 15:42 p.
- Templeman, W., and S.N. Tibbo. 1945. Lobster investigations in Newfoundland 1938 to 1941. *Nfld. Dept. Nat. Resour., Res. Bull. (Fish.)* 16: 98 p.
- Uzmann, J.R., R.A. Cooper, and K.J. Pecci. 1977. Migration and dispersion of tagged American lobsters, *Homarus americanus*, on the southern New England continental shelf. *NOAA Tech. Rep., NMFS, SSRF* 705.
- Waddy, S.L. and Aiken, D.E. 1986. Multiple fertilization and consecutive spawning in large American lobsters, *Homarus americanus*. *Can. J. Fish. Aquat. Sci.* 43: 2291-2294.
- Waddy, S.L. and Aiken, D.E. 1991. Egg production in the American lobster *Homarus americanus*. In, A. Wenner and A. Kuris [ed.]. *Crustacean issues 7, Crustacean egg production*, p 267-290. A. A. Balkema, Rotterdam, Brookfield.
- Wahle, R. A., and R. S. Steneck. 1992. Habitat restrictions in early benthic life: Experiments in substratum selection and in situ predation with the American lobster. *J. Exp. Mar. Biol. Ecol.* 157: 91-114.
- Watson, F.L. 1988. Size of functional reproductive maturity of female lobsters, (*Homarus americanus*, along the eastern coast of Nova Scotia, Canada. BSc Honours Thesis, Dalhousie University, Halifax, Canada.

- Wharton, W. G. and K. H. Mann. 1981. Relationship between destructive grazing by the sea urching, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic coast of Nova Scotia. Can. J. Fish. Aquat. Sci. 38: 1339-1349.
- Wilder, D.G. 1954. The lobster fishery of the southern Gulf of St. Lawrence. Fish. Res. Board Can., Gen. Ser. Circ. 24: 3-16.
- Wilder, D.G., and R.C. Murray. 1958. Do lobsters move offshore and onshore in the fall and spring? Fish. Res. Board Can., Prog. Rep. Atl. Coast Sta. 69: 12-15.
- Wilkinson, L. 1992. SYSTAT: the system for statistics. Evanston, IL: SYSTAT, Inc.