

**INFLUENCE OF ENVIRONMENTAL FACTORS ON SPAT
COLLECTION AND MUSSEL (*Mytilus edulis*) CULTURE IN
RAFT SYSTEMS IN TWO SCOTTISH SEA LOCHS**

**A Thesis Presented for the Degree of “DOCTOR OF
PHILOSOPHY” to University of Stirling**

by

SEDAT KARAYÜCEL

BSc & MSc (Aquaculture)

Institute of Aquaculture

University of Stirling

Stirling, Scotland, UK

SEPTEMBER, 1996

DECLARATION

I hereby declare that this was thesis composed by myself and is the result of my own research. It has neither been accepted or submitted for any other degrees.

All the sources of information have been duly acknowledged.

Sedat KARAYÜCEL (Candidate)

DEDICATION

TO MY FATHER, HASAN

TO MY MOTHER, SAFÍYE

TO MY WIFE, ÍSMÍHAN

TO MY SON, ANIL

FOR THEIR ENDLESS LOVE AND SUPPORT

ABSTRACT

Growth, mortality, production, spat collection, seasonal cycles of condition index, biochemical composition, carrying capacity of commercial raft culture systems and population genetic characteristics of blue mussel (*Mytilus edulis*) were studied at different sites in Loch Etive and Loch Kishorn on the west coast of Scotland between May 1993 and May 1995. The main objective of the study was to evaluate current suspended mussel culture production in raft systems and to obtain basic information on the biology and the genetic structure of the two mussel populations in the lochs.

There were some water quality differences between the sites in relation to seston, salinity and transparency but not to temperature, particulate organic matter and chlorophyll-a. When food is available (as particulate organic matter and chlorophyll-a), there was a clear seasonal cycle in mussel somatic growth and shell growth. Mussel growth was relatively high from mid-spring until late autumn, but very slow during the rest of the year. The spring-summer period of rapid shell length and somatic growth coincided with relatively optimum environmental conditions and positive relationships were indicated between growth rates, temperature and salinity, indicating the limiting effect of these two primary factors on growth from late-autumn to mid-spring when there is also a lack of available food.

Mussel growth was higher at 2 m depth on the raft-rope systems, but in lantern nets experimental growth did not show differences between depths. Growth was found to be similar in the lantern nets and on culture ropes in the two lochs in the first year of experiments (from May 1993 to May 1994). Overall, mean length increments were 31.01 mm in Loch Etive and 28.75 mm in Loch Kishorn over a 15 month period. The mussels reached marketable size (>50 mm) in two years from the known time of spat settlement. A cross-transplantation experiment showed that site rather than stock is the main factor explaining differences in mussel growth in Loch Etive and Loch Kishorn. The position of the mussels within a raft has a significant effect on their growth; mussels at the inflow of a

raft have a better growth than those near the outflow ($p < 0.05$) due to greater availability of food.

Mean mussel biomass was higher in Loch Kishorn while production was higher in Loch Etive, but there were seasonal and monthly fluctuations in both biomass and production at both sites. Biochemical composition and energy content were similar in both sites, while mussel meat yield and condition indices were significantly higher in Loch Kishorn than Loch Etive. Meat content, condition index and carbohydrate values were high during the summer and low from autumn to spring, reaching minimum values in March and April at the time of spawning.

Spat settlement occurred in June-July in Loch Etive and June-December in Loch Kishorn. Sea squirt, starfish and eider duck are problems effecting spat collection at the Loch Kishorn site, whereas spat collection in Loch Etive is unaffected by these pests/predators.

The carrying capacities for cultured mussels were found to be about 24 metric tons per raft for Loch Etive and 38 metric tons per raft for Loch Kishorn using a particulate organic matter based model; these are reasonable estimates in comparison to the known mussel production levels reported by producers. However, a seston-based model gave an overestimate of carrying capacity for both sites.

Cross-transplantation of mussels, electrophoresis and shell morphological measurements showed significant differences between the Loch Etive and Loch Kishorn mussel populations. Mortality rates were higher in transplanted mussels than in the native mussels ($p < 0.001$).

ACKNOWLEDGEMENTS

It gives me great pleasure in expression my deep and special gratitude and profound regard to my supervisor Dr. Donald J. Macintosh and my previous supervisor Dr. Hadrian Stirling for their help, encouragements, friendship, scholarly advice and guidance and constructive criticism throughout this research and during the writing up thesis and for everything they have done for me.

This study was carried out in the field throughout whole two years and has dependend on the co-operation, understanding, openness and support of Kishorn Shellfish Farm and Muckairn Mussel Farm operators and their staff without their help these experiments would be impossible. Therefore, I would like to express my particular and sincere thanks to them for everything they have done for me.

Many thanks also go to all members of staff of Institute of Aquaculture and in particular to Mr. Allan Porter, Mr. Ian Eliot, Miss. Anne Nimno, Mrs. Julia Farrington, Mr. Charlie Horrower, Mrs. Betty Stenhouse, Mrs. Shelia Frize for their ever help during this study.

In addition I am very grateful to my colleagues and friends at the Institute of Aquaculture for their friendship and helpful discussion. During my PhD programme, I have been founded by Turkish Government through University of Ondokuz Mayis of Turkey, I would like to thanks to the Rektor of this university, Dean of Faculty and Head of Department and all friends supported me and given me this opportunity. I would like to thanks my mother Safiye, my wife, Ismihan and my son, Anil, whose encouraged, helped and supported me during my PhD.

TABLE OF CONTENTS

	<u>Page</u>
ABSTRACT	i
ACKNOWLEDGEMENTS	iii
TABLE OF CONTENTS	iv
LIST OF TABLES	x
LIST OF FIGURES	xiv
LIST OF PLATES	xix
CHAPTER 1: GENERAL INTRODUCTION	1
1.1. General Background.....	1
1.2. Systematics and Distribution of <i>Mytilus edulis</i>	3
1.3. Biology and Life Cycle of the Common Mussel.....	3
1.4. General Features of Mussel Farming.....	7
1.4.1. Origins of Mussel Farming.....	9
1.4.2. Cultivation on Poles (Bouchet Systems).....	10
1.4.3. Cultivation on the Sea Bed (On-bottom System).....	11
1.4.4. Cultivation on Suspended Ropes (Off-bottom System).....	12
1.5. Status of Shellfish Farming in Scotland.....	12
1.6. Problems of Shellfish Farming.....	14
1.7. Mussel Culture in Scotland.....	16
1.7.1. Bottom Culture.....	17
1.7.2. Suspended Culture.....	17
1.7.2.1. Long-line Culture.....	17
1.7.2.1.1. Advantages and Disadvantages of Long-lines Over Raft system.....	20
1.7.2.2. Raft Culture.....	20
1.8. Oyster Culture.....	27
1.9. Scallop Culture.....	28
1.10. Study Areas.....	30

1.10.1. Climate of Scotland.....	30
1.10.2. Productivity of Scottish Sea Lochs.....	31
1.10.3. Loch Etive.....	34
1.10.4. Loch Kishorn.....	37
CHAPTER 2: LITERATURE REVIEW.....	40
2.1. Methods of Cultivation.....	40
2.2. Factors Affecting Growth.....	40
2.2.1. Salinity.....	42
2.2.2. Temperature.....	42
2.2.3. Food Quality and Quantity.....	43
2.3. Carrying Capacity.....	44
2.4. Spat Settlement.....	46
2.5. Mortality.....	48
2.6. Biochemical Composition.....	49
2.7. Condition Index.....	50
2.8. Genetics of <i>Mytilus</i>	53
2.9. Objectives of Study.....	56
CHAPTER 3: MATERIALS AND METHODS.....	57
3.1. Enviromental Parameters.....	57
3.1.1 Collection of Water Samples.....	57
3.1.2. Temperature and Salinity.....	57
3.1.3. Chlorophyll-a.....	57
3.1.4. Determination of Seston, Particulate Organic Matter and Particulate Inorganic Matter.....	59
3.1.5. Transparency or Secchi Disk Depth.....	60
3.1.6. Particle Number.....	60
3.2. Field Experiments.....	60
3.2.1. Experimental Mussels.....	60
3.2.2. Design of Experiments Materials and Sampling.....	61
3.2.2.1. Lantern Nets.....	61

3.2.2.2.	Culture Ropes.....	65
3.2.2.3.	Spat Collectors.....	66
3.3.	Growth.....	68
3.4.	Production and Biomass.....	69
3.5.	Survival and Losses.....	70
3.6.	Condition Index and Biochemical Compositi.....	70
3.6.1.	Biochemical Composition.....	71
3.6.1.1.	Moisture.....	71
3.6.1.2.	Ash.....	72
3.6.1.3.	Protein.....	72
3.6.1.4.	Lipid.....	72
3.6.1.5.	Carbohydrate.....	72
3.6.1.6.	Energy Content.....	73
3.7.	Carrying Capacity.....	73
3.7.1.	Preparation of Experimental Mussels.....	73
3.7.2.	Filtration and Assimilation.....	77
3.8.	Morphometric and Genetic Studies.....	78
3.8.1.	Measurements of Shell Dimensions.....	78
3.8.2.	Electrophoresis.....	79
3.8.2.1.	Sample Collection and Preparation.....	79
3.8.2.2.	Preparation of Starch Gels.....	79
3.8.2.3.	Running, Slicing and Staining Gels.....	80
3.9.	Statistical Analyses.....	80
CHAPTER 4: RESULTS.....		82
4.1.	Growth and Production of Mussels in Raft Cultured System in Loch Etive and Loch Kishorn.....	82
4.1.1.	Environmental Parameters.....	82
4.1.1.1.	Temperature.....	86
4.1.1.2.	Salinity.....	90
4.1.1.3.	Total Seston.....	90

4.1.1.4.	Particulate Organic Matter (M).....	92
4.1.1.5.	Percentage of Particulate Organic Matter (POM%).....	92
4.1.1.6.	Chlorophyll-a.....	94
4.1.1.7.	Transparency (Secchi Disk).....	94
4.1.1.8.	Particle Number.....	96
4.1.2.	Growth.....	96
4.1.2.1.	Shell Growth.....	96
4.1.2.2.	Somatic Growth.....	104
4.1.2.3.	Mussel Length- Weight Relationship.....	112
4.1.3.	Morphology of Mussels.....	115
4.1.4.	Survival and Losses.....	118
4.1.5.	Eliminated Biomass.....	120
4.1.6.	Mussel Biomass and Production.....	123
4.1.6.1.	Biomass.....	123
4.1.6.2.	Production.....	125
4.2.	Effects of Environmental Factors, Depth and Position on Raft on Growth and Mortality of Cultured Mussels.....	129
4.2.1.	Environmental Factors.....	129
4.2.2.	Growth.....	134
4.2.3.	Shell Characteristics.....	135
4.2.4.	Mortality.....	135
4.3.	Growth and Mortality of Mussels Reared in Lantern Nets in Loch Kishorn.....	144
4.3.1.	Growth.....	144
4.3.2.	Mortality.....	149
4.3.3.	Shell Characteristics.....	150
4.4.	The Effect of Environmental Factors on Condition Index and Meat Yield in Loch Etive and Loch Kishorn.....	153
4.4.1.	Condition Index.....	153
4.4.2.	Biochemical Analyses.....	159
4.4.2.1.	Energy (Calorific) Content.....	159

4.4.2.2.	Moisture.....	160
4.4.2.3.	Ash.....	160
4.4.2.4.	Lipid.....	162
4.4.2.5.	Protein.....	162
4.4.2.6.	Carbohydrate.....	162
4.5.	Spat Collection and Growth of Mussel Seeds.....	166
4.5.1.	Spat Collection and Associated Problems	166
4.5.2.	Shell Growth.....	172
4.5.3.	Growth in Live Weight.....	177
4.6.	Cross-transplantation of Mussels Between Loch Etive and Loch Kishorn.....	182
4.6.1.	Environmental Factors.....	182
4.6.1.1.	Temperature.....	182
4.6.1.2.	Salinity.....	182
4.6.1.3.	Seston.....	186
4.6.1.4.	Particulate Organic Matter (POM) and POM %.....	186
4.6.1.5.	Chlorophyll-a.....	186
4.6.1.6.	Transparency.....	188
4.6.2.	Growth.....	188
4.6.3.	Morphology of Transplanted Mussels.....	197
4.6.4.	Condition Index.....	200
4.6.5.	Mortality and Survival.....	203
4.7.	Carrying Capacity Estimation.....	206
4.8.	Morphometrics and Genetics.....	210
4.8.1.	Shell Morphometrics.....	210
4.8.2.	Allele Frequency.....	219
CHAPTER 5:	DISCUSSION.....	222
5.1.	Environmental Factors and Their Effects on Growth.....	223
5.1.1.	Temperature.....	223
5.1.2.	Salinity.....	226
5.1.3.	Total Seston and Particulate Organic Matter.....	227

5.1.4.	Phytoplankton and Chlorophyll-a.....	230
5.1.5.	Water Currents.....	232
5.1.6.	Transparency and Particle Concentration.....	234
5.1.7.	The Effect of Depth on Growth.....	234
5.2.	Growth.....	235
5.2.1.	Shell Growth.....	235
5.2.2.	Somatic Growth.....	237
5.2.3.	Growth and Morphological Differences Between Loch Etive and Loch Kishorn Populations.....	239
5.3.	Losses and Mortality.....	242
5.4.	Biomass and Production.....	245
5.5.	Condition Index and Biochemical Composition.....	246
5.5.1.	Condition Index.....	246
5.5.2.	Biochemical Composition and Energy Content.....	251
5.6.	Spat Settlement and Growth of Seed.....	253
5.7.	Carrying Capacity.....	256
5.8.	Morphometrics and Genetics.....	258
5.9.	Conclusions.....	261
5.10.	Recommendations for Future Research.....	265
	REFERENCES.....	266
	Abbreviations.....	293
	Appendices.....	296

LIST OF TABLES

	Page
Table-1. Summary of shellfish farming statistics for Scotland, 1986 - 1994.....	15
Table-2. Advantages and disadvantages of a long-line system over a raft system for mussel rearing.....	20
Table-3. Summary of the main physical parameters of Loch Etive and Loch Kishorn.....	39
Table-4. Mean (\pm SE) of monthly values of environmental parameters measured at 2 m and 6 m at each experimental site from May 1993 to August 1994.....	85
Table-5. Correlation matrix (r) between environmental factors, mussel meat yield and Specific Growth Rate (in length) in Loch Etive.....	87
Table-6. Correlation matrix (r) between environmental factors, mussel meat yield and Specific Growth Rate (in length) in Loch Kishorn.....	88
Table-7. Average shell lengths ($L \pm$ SE) at 2 m, 6 m and pooled (2+6 m) at each sampling date and monthly growth increments ($\Delta L = L_2 - L_1$ mm) of experimental mussels in Loch Etive between May 1993 and August 1994.....	99
Table-8. Average shell lengths ($L \pm$ SE mm) at 2 m, 6 m and pooled (2+6 m) at each sampling date and monthly growth increments ($\Delta L = L_2 - L_1$, mm) of experimental mussels in Loch Kishorn between May 1993 and August 1994....	100
Table-9. Effect of site and depth on length, live weight (LW), wet meat weight (WMW) and ash-free dry meat weight (AFDMW) of rope cultured mussels from Loch Etive and Loch Kishorn.....	102
Table-10. Monthly distribution of live weight (g) at depth of 2 m and 6 m in Loch Etive (LE) and Loch Kishorn (LK).....	105
Table-11. Monthly distribution of wet meat weight (g) at depth of 2 and 6 m in Loch Etive (LE) and Loch Kishorn (LK).....	106
Table-12. Monthly values of ash-free dry weight (g) at depth of 2 m and 6 m in Loch Etive (LE) and Loch Kishorn (LK).....	107
Table-13. Monthly length-weight equations ($\text{Log}_{10} W = a + b \text{Log}_{10} L$) relating dry (DMW) and ash-free dry meat weight (AFDMW) to shell length (L) for rope grown mussels at Loch Etive between May 1993 and August 1994.....	114
Table-14. Monthly length-weight equations ($\text{Log}_{10} W = a + b \text{Log}_{10} L$) relating dry (DMW) and ash-free dry meat weight (AFDMW) to shell length (L) for rope grown mussels at Loch Kishorn between May 1993 and August 1994.....	114
Table-15. Linear regressions ($y = a + bx$) between shell length, shell width and shell height for Loch Etive (LE) and Loch Kishorn (LK) mussels.....	118
Table-16. The mean shell characteristics of mussels from Loch Etive (LE) and Loch Kishorn (LK) in July 1994 with an adjusted mean shell length (52.92 mm)....	118
Table-17. Monthly eliminated biomasses, g ash-free dry weight and Kcal m^{-1} of rope cultured mussels in Loch Etive and Loch Kishorn.....	122

Table-18.	Monthly ash-free dry weight (shell + tissue) and computation of production of the rope cultured mussels in Loch Etive from May 1993 to August 1994....	127
Table-19.	Monthly ash-free dry weight biomass (\pm SE) (shell + tissue) and computation of production of the rope cultured mussels in Loch Kishorn from May 1993 to August 1994.....	128
Table-20.	Mean (\pm SE) values of environmental parameters in Loch Etive from May 1993 to August 1994, at the inflow and outflow of a mussel culture raft and at 2 m and 6 m depth.....	130
Table-21.	Average monthly shell lengths (mm) in Loch Etive from May 1993 to August 1994, at 2 m and 6m depth and at the inflow and outflow points of a culture raft.....	137
Table-22.	Mean (\pm SE), initial and final growth parameters and increments over a 15 months experimental period in Loch Etive.....	138
Table-23.	Two-way analysis of variance (ANOVA) for growth parameters of mussel reared in lantern nets in Loch Etive.....	139
Table-24.	Mean shell characteristics (\pm SE) of mussels in the lantern nets experiments in Loch Etive, at 2 m and 6 m depth and at the inflow and outflow points of the culture raft.....	141
Table-25.	Monthly mean shell lengths and growth increment of experimental mussels reared at depths of 2 and 6 m in lantern nets in Loch Kishorn.....	146
Table-26.	Mean, (\pm SE) initial and final growth parameters and increments at 2 m and 6 m in lantern nets experiment in Loch Kishorn from May 1993 to August 1994.....	147
Table-27.	Mean (\pm SE) shell characteristics of mussels from two different depths reared in lantern nets in Loch Kishorn over a 15 months experimental period.....	152
Table-28.	Minimum, maximum and mean values of condition indices and meat yield for Loch Etive and Loch Kishorn mussels over a 15 months experimental period.....	154
Table-29.	Two-way (ANOVA) results showing significance levels for mussel condition index and meat yield between the studied sites and depths.....	158
Table-30.	Minimum, maximum and mean (\pm SE) values for biochemical composition of mussels in Loch Etive (LE) and Loch Kishorn (LK).....	163
Table-31.	Correlation matrix between environmental factors, condition indices and biochemical composition in Loch Etive.....	164
Table-32.	Correlation matrix between environmental factors, condition indices and biochemical composition in Loch Kishorn.....	165
Table-33.	Mean monthly seed density (individuals m ⁻¹ rope) at 2 m and 6m depths, plus both depths pooled, in Loch Etive (LE) and Loch Kishorn (LK) from June 1993 to April 1994.....	169
Table-34.	Mean (\pm SE) monthly shell length (mm) and increment in shell length ($\Delta L = L_2 - L_1$) of mussel seed in Loch Etive (LE) and Loch Kishorn (LK) from June 1993 to April 1994.....	170

Table-35. Monthly average length specific growth rate (SGR%) of mussel spat after settlement on collector ropes at depth of 2 m and 6 m and plus pooled values for both depths from July 1993 to April 1994 in Loch Etive (LE) and Loch Kishorn (LK).....	171
Table-36. Mean (\pm SE) monthly live weight and monthly increment ($\Delta L = L_2 - L_1$, mm) of live weight of seed mussels in Loch Etive (LE) and Loch Kishorn (LK) from June 1993 to April 1994.....	180
Table-37. Correlation matrix between environmental factors and specific growth rate of mussels in Loch Etive.....	181
Table-38. Correlation matrix between environmental factors and specific growth rate of mussels in Loch Kishorn.....	181
Table-39. Mean (\pm SE) values of environmental parameters measured at Loch Etive (LE) and Loch Kishorn (LK) from May 1994 to May 1995.....	183
Table-40. Correlation matrix between environmental factors, condition indices and specific growth rate in length (SGR) in Loch Etive from May 1994 to May 1995.....	187
Table-41. Correlation matrix between environmental factors, condition indices and specific growth rate in length (SGR) in Loch Kishorn from May 1994 to May 1995.....	187
Table-42. Mean shell lengths ($L \pm$ SE) recorded at sampling and monthly growth increments ($\Delta L = L_2 - L_1$, mm) of two mussel stocks grown at native and transplanted sites during the experimental period (from May 1994 to May 1995).....	189
Table-43. Mean (\pm SE) live weight (LW), wet meat weight (WMW), dry meat weight (DMW) and ash-free dry meat weight (AFDMW) growth of native mussel stock in Loch Etive (LE) and Loch Kishorn (LK) and transplanted mussel stocks (LK-LE and LE-LK) four sampling dates (May 1994, October 1994, February 1995 and May 1995).....	195
Table-44. Two-way ANOVA results on shell length (L), live weight (LW), wet meat weight (WMW), shell weight (SW) and dry meat weight (DMW) in transplanted and native mussels.....	196
Table-45. The mean shell characteristics of native (LE and LK) and transplanted (LK-LE and LE-LK) mussels from Loch Etive (LE) and Loch Kishorn (LK) one year after transplantation.....	199
Table-46. Linear relationships ($y = a+bx$) between various combinations of morphological shell parameters for native (Loch Etive (LE) and Loch Kishorn (LK)) and transplanted (LK-LE and LE-LK) mussels.....	200
Table-47. Minimum, maximum and mean values of condition indices and meat yield in native and transplanted mussels in Loch Etive (LE) and Loch Kishorn (LK).....	202
Table-48. Estimates of carrying capacity based on seston concentration according to Incze <i>et al.</i> (1981) for the months of August 1994 (at the end of culture period) in the raft system in Loch Etive (LE) and Loch Kishorn (LK).....	208
Table-49. Estimates of volume of water (passing through the raft system), particulate organic matter (POM) supply, POM demand and carrying capacity	

	according to Carver and Mallet (1990) for the months of May and August 1994 in the raft systems in Loch Etive and Loch Kishorn.....	209
Table-50.	Mean, minimum and maximum of shell characteristics of Loch Etive and Loch Kishorn mussels used in this study.....	216
Table-51.	Mean, minimum and maximum ratios of shell characteristics of Loch Etive and Loch Kishorn mussels measured in this study.....	218
Table-52.	Allele frequencies of mussel (<i>Mytilus edulis</i>) from Loch Etive and Loch Kishorn populations.....	219
Table-53.	Observed distribution and expected Hardy-Weinberg equilibrium distribution of genotypes for phosphoglucomutase (PGM) and glucose 6-phosphate isomerase (GPI) loci in Loch Etive (LE) and Loch Kishorn (LK) mussel populations.....	221

LIST OF FIGURES

	<u>Page</u>
Fig. 1. Global distribution of mussels <i>Mytilus edulis</i> , <i>M. galloprovincialis</i> , <i>M. trossulus</i> and <i>M. californianus</i>	4
Fig. 2. Schematized development stages and life cycle of blue mussel from wild broodstock to spat ready for settlement on spat collectors.....	8
Fig. 3. Side view of a single long-line system.....	18
Fig. 4. View of a home-made raft system used for mussel culture on the West coast of Scotland.....	22
Fig. 5. A simplified two layer circulation system in sea lochs and fjords.....	32
Fig. 6. Map of Loch Etive (LE) showing the sites at which the study conducted.....	36
Fig. 7. Map of Loch Kishorn (LK) showing the sites at which study was conducted....	38
Fig. 8. Schematic representation of mussel raft showing the position of the lantern nets in relation to the water flow direction through the raft created by currents.....	63
Fig. 9. Schematic diagram of the system used for take water samples for carrying capacity experiment.....	75
Fig. 10. Model for estimating the impact of intensive mussel cultivation in raft system.....	76
Fig. 11. Shell measurements taken for morphological analysis of Loch Etive and Loch Kishorn mussels.....	78
Fig. 12. The annual sea water temperature cycle at experimental sites (A: Loch Etive, B: Loch Kishorn) at 2 m and 6 m depth at each month from May 1993 to August 1994.....	83
Fig. 13. The annual sea water temperature cycle at Loch Etive (A) and Loch Kishorn (B) at 0.2, 4 and 8m depth at each month from May 1993 to August 1994.....	84
Fig. 14. Monthly distribution of salinity at 0.2, 2, 4, 6 and 8 m depth in Loch Etive (A) and Loch Kishorn (B) from May 1993 to August 1994.....	89
Fig. 15. Monthly variation in total seston concentration (A: Loch Etive, B: Loch Kishorn), POM (C:Loch Etive, D: Loch Kishorn) and POM% (E: Loch Etive, F: Loch Kishorn) at 2 and 6 m depth between May 1993 and August 1994.....	91
Fig. 16. Monthly distribution of chlorophyll-a (Ch-a) concentration in Loch Etive (A) and Loch Kishorn (B) from May 1993 to August 1994.....	93
Fig. 17. Monthly secchi disk depth or transparency (A) and particle number (B) at Loch Etive (LE) and Loch Kishorn (B) from May 1993 to August 1994.....	95
Fig. 18. Changes in the size frequency distributions of experimental mussels in Loch Etive between May 1993 and August 1994.....	97
Fig. 19. Changes in size frequency distributions of experimental mussels in Loch Kishorn between May 1993 and August 1994.....	98

Fig. 20. Growth in mean shell length in Loch Etive (A) and Loch Kishorn (B) and growth in live weight (LW) in Loch Etive (C) and Loch Kishorn (D) from May 1993 to August 1994.....	103
Fig. 21. Monthly average length specific growth rate (SGR%) for mussels grown in Loch Etive(A) and Loch Kishorn (B) at 2 m, 6 m and pooled values between May 1993 and August 1994.....	108
Fig. 22. Monthly changes in wet meat weight (WMW) at 2 m, 6 m and pooled values in Loch Etive (A) and Loch Kishorn (B).....	109
Fig. 23. Monthly distribution of dry meat weight (DMW) in Loch Etive (A) and Loch Kishorn (B) during the experimental period.....	110
Fig. 24. Seasonal changes in ash-free dry meat weight (AFDMW) in Loch Etive (A) and Loch Kishorn (B) from May 1993 to August 1994.....	111
Fig. 25. Shell length-live weight relationship in Loch Etive (A) and Loch Kishorn (B)....	113
Fig. 26. Relationships between shell length-ash free dry shell weight (AFDSW) in Loch Etive (A) and Loch Kishorn (B) and shell length- dry shell weight of experimental mussels in Loch Etive (A) and Loch Kishorn (B).....	116
Fig. 27. Monthly distributions of shell weight (SW) at 2 m and 6 m depth and pooled values in Loch Etive (A) and Loch Kishorn (B) during experimental period.....	117
Fig. 28. Changes in cumulative survival (A), monthly survival (B) and losses (C) in Loch Etive (LE) and Loch Kishorn (LK) over the experimental period.....	119
Fig. 29. Monthly (A) and cumulative (B) eliminated biomass (EB) of experimental mussels in Loch Etive (LE) and Loch Kishorn (LK) from June 1993 to August 1994.....	121
Fig. 30. Monthly changes in density (A) and ash-free dry weight biomass (B) as grams per mussel in Loch Etive (LE) and Loch Kishorn (LK) during the experimental period.....	124
Fig. 31. Monthly (A) and cumulative (B) changes in production in Loch Etive (LE) and Loch Kishorn (LK) from June 1993 to August 1994.....	126
Fig. 32. The seasonal cycle of seston (A), particulate organic matter (POM) (B) and POM% (C) in Loch Etive at 2 m and 6 m depth and inflow and outflow of the mussel culture raft during experimental period.....	131
Fig. 33. The monthly changes in chlorophyll-a (A) and particle number (B) in the mussel culture system in Loch Etive.....	132
Fig. 34. Monthly distribution of length (A), live weight (B), wet meat weight (C), dry meat weight (D) and ash-free dry meat weight (AFDMW) (E) in lantern nets in Loch Etive at 2 m and 6 m depth and at the inflow and outflow of a culture raft.....	136
Fig. 35. Monthly specific growth rate in length (SGR%) in the lantern net experiment in Loch Etive from June 1993 to August 1994, at 2 m and 6 m depth and at the inflow and outflow points of the mussel culture raft.....	140
Fig. 36. Length-width (A) and height-width (B) relationship at 2 m and 6 m depth in the lantern net experiment in Loch Etive.....	142
Fig. 37. Cumulative (A) and monthly mortality (B) of mussels in lantern nets in Loch Etive	

from June 1993 to August 1994, at 2 m and 6 m depth and at the inflow and outflow points of the culture ropes.....	143
Fig. 38. Monthly distribution of shell length (A), live weight (B), wet meat weight (C), dry meat weight (D) and ash-free dry meat weight (AFDMW) (E) in lantern nets experiment in Loch Kishorn, at 2 and 6m depth from May 1993 to August, 1994.....	145
Fig. 39. Monthly specific growth rate in length (SGR%) (A), cumulative mortality (B) and monthly mortality (C) at 2 m and 6 m depth in the lantern nets experiment between May 1993 and August 1994.....	148
Fig. 40. Monthly distribution of shell weight at 2 m and 6 m depth in the lantern nets experiment in Loch Kishorn from May 1993 to August 1994.....	151
Fig. 41. Monthly distribution of wet meat volume condition index (CIV) (A) and dry meat weight condition index (CID) (B) at 2 m and 6 m and the pooled value for the two depths in Loch Etive from May 1993 to August 1994.....	155
Fig. 42. Monthly distribution of wet meat volume condition index (CIV) (A) and dry meat weight condition index (CID) (B) at 2 m and 6 m and the pooled value for the two depth in Loch Kishorn from May 1993 to August 1994.....	156
Fig. 43. Seasonal cycle of meat yield (MY) (A) at 2 m and 6 m depth and pooled values for the two depths; pooled values for mussel energy (B) in Loch Etive (LE) and Loch Kishorn (LK).....	157
Fig. 44. Monthly distribution of moisture (A), ash (B), lipid (C), protein and carbohydrate (D) values as percentage in the meat of mussels from Loch Etive (LE) and Loch Kishorn (LK).....	161
Fig. 45. Monthly distribution of mussel spat density at 2 m and 6 m in Loch Etive (A) and Loch Kishorn (B) from June 1993 to April 1994.....	168
Fig. 46. Mean shell length distribution at 2 m and 6 m depths in Loch Etive (A), Loch Kishorn (B) and pooled values for both depths (C) from June, 1993 to April 1994.....	173
Fig. 47. Monthly changes in Specific Growth Rate (SGR%) at 2 m and 6m in Loch Etive (A), Loch Kishorn (B) and pooled values for two depths (C) in Loch Etive (LE) and Loch Kishorn (LK) from July 1993 to April 1994.....	174
Fig. 48. Length- weight relationship in seed mussels in Loch Etive (A) and Loch Kishorn (B) during the experimental period.....	175
Fig. 49. Length- height relationship in seed mussels in Loch Etive (A) and Loch Kishorn (B) during the experimental period.....	176
Fig. 50. Monthly live weight distribution of seed at 2 m and 6 m depth in Loch Etive (A) from July, 1993 to April, 1994, Loch Kishorn (B) from August, 1993 to April, 1994 and pooled values for two depths (C) in Loch Etive (LE) and Loch Kishorn (LK).....	179
Fig. 51. Seasonal cycle of sea water temperature (A), salinity (B), seston (C) and particulate organic matter (POM) (D) at depth of 2 m in Loch Etive (LE) and Loch Kishorn (LK) from May 1994 to May 1995.....	184
Fig. 52. Monthly distribution of percentage of particulate organic matter (POM%) (A), chlorophyll-a (B) at 2 m depth and transparency (Secchi disk depth) (C) in Loch Etive (LE) and Loch Kishorn (LK).....	185

Fig. 53. Size frequency of experimental mussels in May 1994 (A and B), October 1994 (C and D) and May 1995 (E and F) in transplanted and native stocks.....	190
Fig. 54. Monthly changes in shell length (A), live weight (B), wet meat weight (C), dry meat weight (D), ash-free dry meat weight (E) and shell weight (F) in native (LK and LE) and transplanted (LK-LE and LE-LK) mussels at depth a of 2 m in Loch Etive and Loch Kishorn.....	191
Fig. 55. Monthly specific growth rate in length (SGR%) in transplanted (LK-LE and LE-LK) and native (LE and LK) mussels in Loch Etive (LE) and Loch Kishorn LK) from May 1994 to May 1995.....	193
Fig. 56. Linear relationships between width-length (A and B), height-length (C and D) and width-height (E and F) in native (LE and LK) and transplanted (LK-LE and LE-LK) mussels in Loch Etive and Loch Kishorn.....	198
Fig. 57. Monthly changes in wet meat volume condition index (CIV) (A and B), dry meat condition index (CID) (C and D) and meat yield (E and F) in native (LE and LK) and transplanted (LK-LE and LE-LK) mussels in Loch Etive and Loch Kishorn from May 1994 to May 1995.....	201
Fig. 58. Distribution of monthly mortality (A), cumulative mortality (B) and survival (C) in native Loch Etive and Loch Kishorn (LE and LK) and transplanted (LK-LE and LE-LK) mussel stocks in Loch Etive and Loch Kishorn respectively.....	204
Fig. 59. Frequency of shell characteristics of hinge plate (A), length of anterior retractor muscle scar (B), anterior adductor muscle scar (C), posterior adductor muscle scar (D), length of byssal retractor muscle scar (E), distance between ventral edge of posterior adductor muscle scar and ventral margin of shell (F) and ligament margin (G) in Loch Etive mussels.....	212
Fig. 60. Frequency of shell characteristics of hinge plate (A), length of anterior retractor muscle scar (B), anterior adductor muscle scar (C), posterior adductor muscle scar (D), length of byssal retractor muscle scar (E), distance between ventral edge of posterior adductor muscle scar and ventral margin of shell (F) and ligament margin (G) in Loch Kishorn mussels.....	213
Fig. 61. Frequency of hinge teeth in Loch Etive (A) and Loch Kishorn (B) mussel populations.....	214
Fig. 62. Mussel length- width in Loch Etive (A) and Loch Kishorn (B) length- height in Loch Etive (C) and Loch Kishorn (D) with linear regression lines fitted.....	215

LIST OF PLATES

	<u>Page</u>
Plate-1. Home made raft system for mussel culture in Loch Etive.....	23
Plate-2. Spanish raft system for mussel culture in Loch Kishorn.....	23
Plate-3. Tubing of mussel seeds for culturing.....	26
Plate-4. Working boat for mussel harvesting.....	26
Plate-5. Nansen type bottle was used for water sampling.....	58
Plate-6. One year old seed mussels from Loch Etive.....	62
Plate-7. One year old seed mussels from Loch Kishorn.....	62
Plate-8. Mussel spat and the method of dimension measurement under a microscope.....	67
Plate-9. Experimental set up to measure filtration rate of mussels in the field.....	67
Plate-10. Experimental spat collector in Loch Kishorn showing mussel seed settlement after three months.....	167
Plate-11. Experimental spat collector in Loch Etive showing mussel seed settlement after three months.....	167
Plate-12. Loch Etive (LE) mussels in Loch Kishorn (LK) after one year, transplantation.....	205
Plate-13. Loch Kishorn (LK) mussels in Loch Etive (LE) after one year, transplantation.....	205
Plate-14. Loch Etive mussels.....	217
Plate-15. Loch Kishorn mussels	217
Plate-16. GPI (Glucose phosphate isomerase) loci for Loch Etive mussels after staining.....	220

CHAPTER 1: GENERAL INTRODUCTION

1.1 General Background

World demand for food fish and shellfish is projected to rise by 19 million metric tons (mt) over the next 15 years, to reach 91 million mt a year. Most of this increase will have to come from aquaculture production (Anonymous, 1995). This estimate of increase is based on annual *per capita* fish consumption remaining at around 13 kilograms (kg), while the world population rises to 7 billion. Within this scenario, fish catches are not likely to show any sharp increases, whereas aquaculture will continue to progress.

FAO (1994) notes that world aquaculture production exceeded 19.3 mt. If seaweeds are included, farm production is already over 20 million mt. If aquaculture production can be doubled in the next 15 years, then seafood supplies should meet expected demand. This seems feasible, considering recent annual rates of expansion, and the interest of the private sector, governments and financing institutions in supporting aquaculture. However, the challenge is formidable. Proper planning, including environmental considerations, systems management and disease control, will have to play a more important role than at the present if crashes in production are to be avoided (Anonymous, 1995).

Many countries are trying to increase their present production by culturing new species (e.g. turbot, halibut, sturgeon, Australian silver perch, etc.), and competing in quality and price to find a place in the market. At present, the most popular fish for aquaculture is the Atlantic salmon (*Salmo salar*). Demand for salmon is increasing worldwide in response to massive marketing over the past decade, therefore some countries have attempted to increase their capacity, for example Norwegian farmed salmon production in 1994 rose by 15% over the previous year to a new record total of 207,000 mt out of total a world production of 420,000 mt (Anonymous, 1995). After Norway, the top producers were Scotland, Chile, Ireland and Canada.

Scotland has a big potential for aquaculture on the west coast, where conditions are very suitable for the development of salmon, trout and mussel farming due to the presence of many sea lochs, inlets and islands that offer shelter. The Scottish water is almost free

from pollution, parasites and disease (Drinkwater, 1987). Moreover, the North Atlantic drift keeps water temperature higher than in other areas of similar latitude. Scottish aquaculture is still dominated by salmon and trout farming, but shellfish culture, mainly of mussels, king scallops, queen scallops and oysters has also developed very significantly in the last decade.

Scottish farmed salmon production increased by more than 30% in 1994 to reach a new record total of 64,046 mt with 131 companies working 262 sites (Anonymous, 1995). The main reason for this increase in tonnage was the larger size of fish and better survival achieved by improvement in nutrition, a big reduction in mortality through vaccination and other good husbandry practices. Trout production also rose in 1994, from 4,023 mt to 4,262 mt from 56 companies working 72 sites (Anonymous, 1995).

There is no doubt that fish and shellfish industries make appropriate use of natural resources, create various job opportunities and play a vital economic role in many rural communities throughout the Highlands and Islands of Western Scotland. The shellfish industry in Scotland has a very short history and is still developing. Scottish shellfish production has showed considerable expansion over the last decade with total shellfish production reaching 957 mt in 1994.

The statistical data from 1993 to 1994 showed that Pacific oyster decreased in production from 207 mt to 168 mt (-19 %), but native oyster rose to 11.4 mt (20 % increase in production); queen scallop production was 38.2 mt (21% increase) and king scallop rose 21.1 mt to 23.9 mt (13 % increase). However mussel production was almost stable, with production of 716 mt (1 % increase over one year). Mussel farming has a great potential in Scotland. However it continues to perform below prediction due to the small-scale of mussel culture units, lack of corporate investment, unclear marketing image and lack of information on the best culture methods.

1.2. Systematics and Distribution of *Mytilus edulis*

Phylum : Mollusca
Class : Bivalvia
Subclass : Lamellibranchia
Superorder : Pteriomorpha
Order : Mytilida
Family : Mytilidae
Genus : *Mytilus*
Species : *edulis*, Linnaeus 1758 (Barnes, 1987).

The genus *Mytilus* is one of the most cosmopolitan of all marine genera, being widely distributed throughout the temperate latitudes of both hemispheres (Soot-Ryen, 1955; Seed, 1976, 1992). In the northern hemisphere *Mytilus edulis* occurs along the eastern seaboard of North America as far south as Cape Hatteras in North Carolina (McDougal, 1943; Dodge, 1952), but electrophoretic evidence now indicates that this species is absent from both Pacific coasts and has a more restricted distribution on the east coast of North America, extending from the Canadian Maritimes southwards to Cape Hatteras in North America (McDonald and Koehn, 1988; Varvio *et al.*, 1988; McDonald *et al.*, 1990). In Europe it extends from the Arctic waters of the White Sea and northern Norway and southwards to north Africa (Seed, 1976; Suchanek, 1985). In the north, it is also present in Iceland (Varvio *et al.*, 1988) and Hudson Bay (Canada) (Koehn, 1991). In the southern hemisphere, it occurs in the Falkland islands and along the east and west coasts of South America (Fig. 1).

1.3. Biology and Life Cycle of the Common Mussel

Effective management of cultivated animals mainly depends on understanding of the optimal conditions for their reproduction and growth especially their food requirements, feeding mechanisms, reproduction and the physiological ecology of the larvae and adults (Okumus, 1993). The following section describes the general biological and physiological characteristics of the *Mytilus edulis* (L.) the blue, common or European mussel.

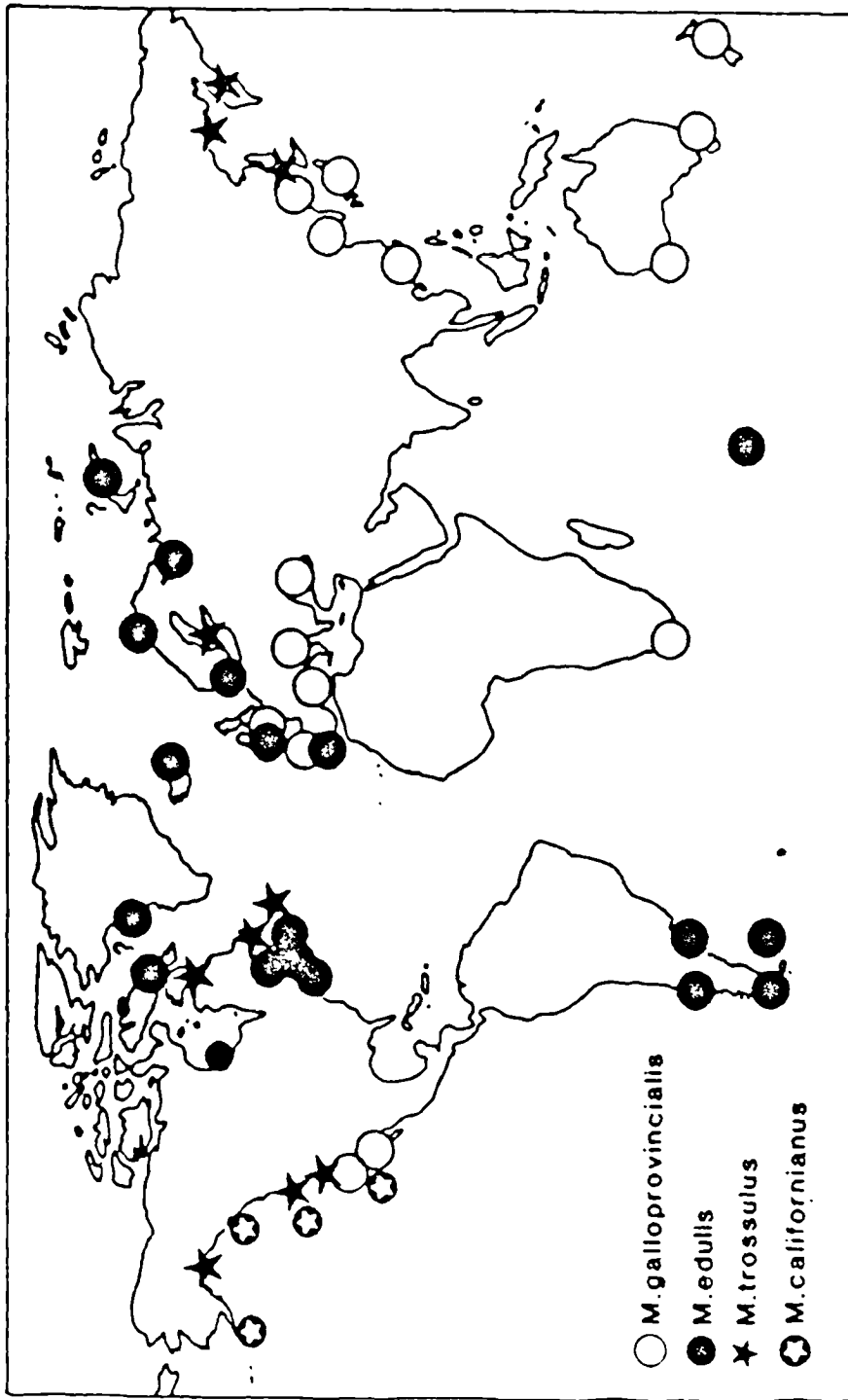


Fig. 1. Global distribution of mussels, *Mytilus edulis*, *M. galloprovincialis*, *M. trossulus* and *M. californianus* (After Seed, 1992).

Mussels are filter feeders, and are mainly herbivorous, eating phytoplankton, but they also eat some zooplankton and much organic detritus (Dare, 1980). The concentration of suspended food particles in the aquatic environment is mostly low, of the order 1 mg or less of organic matter per litre of water (Jørgensen, 1990), therefore, they need large amounts of water to meet their food requirements. A mussel can filter between 2 and 5 litres of water in an hour (Figueras, 1989), or 45-64 litres per day (Dare, 1980). Filtration rates of mussels depend on different factors (such as temperature, oxygen and food level), and have been studied by many researchers in the field and laboratory (Walne, 1972; Widdows, 1978a, b; Widdows *et al.*, 1979; Widdows and Bayne, 1971; Mohlenberg and Riisgard, 1979; Bayne *et al.*, 1989; Riisgård, 1991; Okumus and Stirling, 1994)

Age, size, genotype, light, temperature, depth, food, salinity and current velocity are the main factors influencing the growth of *Mytilus edulis* (Jamieson *et al.*, 1975). For more detail see Chalfant *et al.*(1980). The alimentary tract of *Mytilus edulis* consists of an anterior mouth, oesophagus, stomach, a long complicated intestine and a posterior anus. The mouth parts have two pairs of accessory structures-the labial palps, which serve to convey food into the mouth and a large digestive gland, or liver. The mouth is situated between the anterior retractor muscles of the byssus just posterior to the anterior adductor muscle. The labial palps arise as a prolongation of the lips on both sites of the mouth, forming a two-paired organ. The stomach is a small sac of irregular form, usually more or less elliptical in shape.

Water enters the pallial cavity through the inhalant siphon (which is continuous along the entire length of the ventral surface) before passing through the gill ostia into the suprabranchial chamber, and is expelled through the exhalant siphon. Food particles are bound into mucus strings on the gill lamellae and are carried to the labial palps via ciliated grooves on the lamella margins. The palps regulate the amount of food which enters the mouth and direct surplus material towards a rejection tract on the mantle surface. From the palps, food is directed into the mouth, passes through the oesophagus and enters the stomach, where the particulate material is sorted and directed, either towards the digestive tubule duct openings, or towards the intestine. Intracellular and extracellular digestion

occurs in the digestive gland, which also stores nutrient reserves and regulates their transfer to other tissues (Bayne *et al.*, 1976a, b).

In terms of reproduction, the mussel reaches sexual maturity at an age of six months to one year, depending on the growth rates in different latitudes (Yonge, 1976; Dare, 1980; Figueras, 1989, 1990). The sexes are separate. Mussels shed eggs and sperm directly from their genital ducts into the water, where fertilization takes place. The two sexes are distinguishable by the color of the gonad. As spawning approaches, females are pale orange, while males are white to pale yellow. Temperature is probably the single most important environmental parameter affecting sexual maturation (Dardinac-Corbeil, 1990), but salinity, tidal range exposure, daylength and chemical stimuli may all be involved. The frequency and seasonality of the reproductive cycle in *Mytilus* varies according to their geographical distribution (Herlin-Houtteville and Lubert, 1975). In Britain, populations living in the north spawn only once a year, that is in late spring (Seed, 1976) and March-April (Mason, 1991; Okumus, 1993), whereas those living in the south, an area of milder winter and warmer summers, may spawn twice a year, in spring and late summer (Seed, 1976). Bayne (1965) observed that fertilization of *Mytilus edulis* occurs successfully at temperatures from 5 to 22°C and salinities between 15 and 40 ‰. One *M. edulis* can lay up to 8 million eggs (Bayne *et al.*, 1978).

The early life history of mussel larvae is quite complex. Fertilized eggs range from 60-90 µm in diameter, having a vitelline coat between 0.5 and 1.0 µm thick. The initial cleavage division typically arises within one hour of fertilization (Lutz *et al.*, 1991). A ciliated trochophore stage is reached approximately 24-48 hours after fertilization. A fully formed shell of the "veliger" stage is present by 48 hours at 20°C, with length, height and hingeline dimensions of approximately 95, 70 and 70 µm, respectively. The planktonic veliger stage generally lasts approximately 2-4 weeks, during which time the larvae actively feed in the water column. A well defined foot is present by the time larvae achieve lengths of 195-210 µm. Upon reaching approximately 260 µm in length the pediveliger larvae are capable of metamorphosis (Lutz, 1985). However, in the absence of a suitable substrate, the organisms have the ability to delay metamorphosis for up to 40 days at 10°C (Bayne,

1965, 1976). Temperature, perhaps more than any other factor, influences the duration of metamorphic delay (Strathmann, 1987).

Mytilus larvae attach most readily to filamentous substrates, such as bryozoans, and filiform algae (Kiseleva, 1966; Davies, 1974; Lane *et al.*, 1985; Eyster and Pechenik, 1987). The use of artificial collectors, especially filamentous ones, deployed in the field has proven to be extremely effective in monitoring settlement of mussel larvae under natural conditions (King *et al.*, 1990). The final settlement stage is very significant in practice because spat collection is the first step in mussel farming. The life cycle of *M. edulis* is illustrated in Fig. 2.

1.4. General Features of Mussel Farming

In 1992 world aquaculture production exceeded 19.3 mt tonnes, of which mollusc production accounted for over 3.5 million mt, or 18.1% of total production, mainly from oyster (27.2 %), scallops (15.7 %), clams (21.9 %) and mussels (31 %) (FAO, 1994). As these figures show, mussels represented the highest production among the cultured bivalves. The total production of mussels exceeded 1.1 mt in 1992. The vast majority of this came from aquaculture. Over 20 countries report significant harvests of farmed mussels but world production is dominated by two countries, China with almost 50 % of the total and Spain with 13 %. France, Italy, Denmark, Holland, Germany and Ireland are the other main producers in Europe. Among the Asian countries, China, Korea and Thailand are leading producers, while in the New World, Chile, Canada and USA are major producers. During the last six years, production increased from nearly 0.8 mt in 1986 to 1.1 mt in 1992 corresponding to a 36 % increment in total production (FAO, 1994). There are 10 species of cultivated mussels. By far the majority of the farmed crop is the blue-type of mussel i.e. of the various *Mytilus* species which occur in the temperate waters of Europe, Asia and North and South America. Green mussels of the various *Perna* species are farmed in warmer waters, particularly in Thailand and Philippines, but also in China and New Zealand.

High fecundity and a mobile free-living larval phase are two characteristics which have contributed to the widespread distribution of the relatively few mussel species, and at

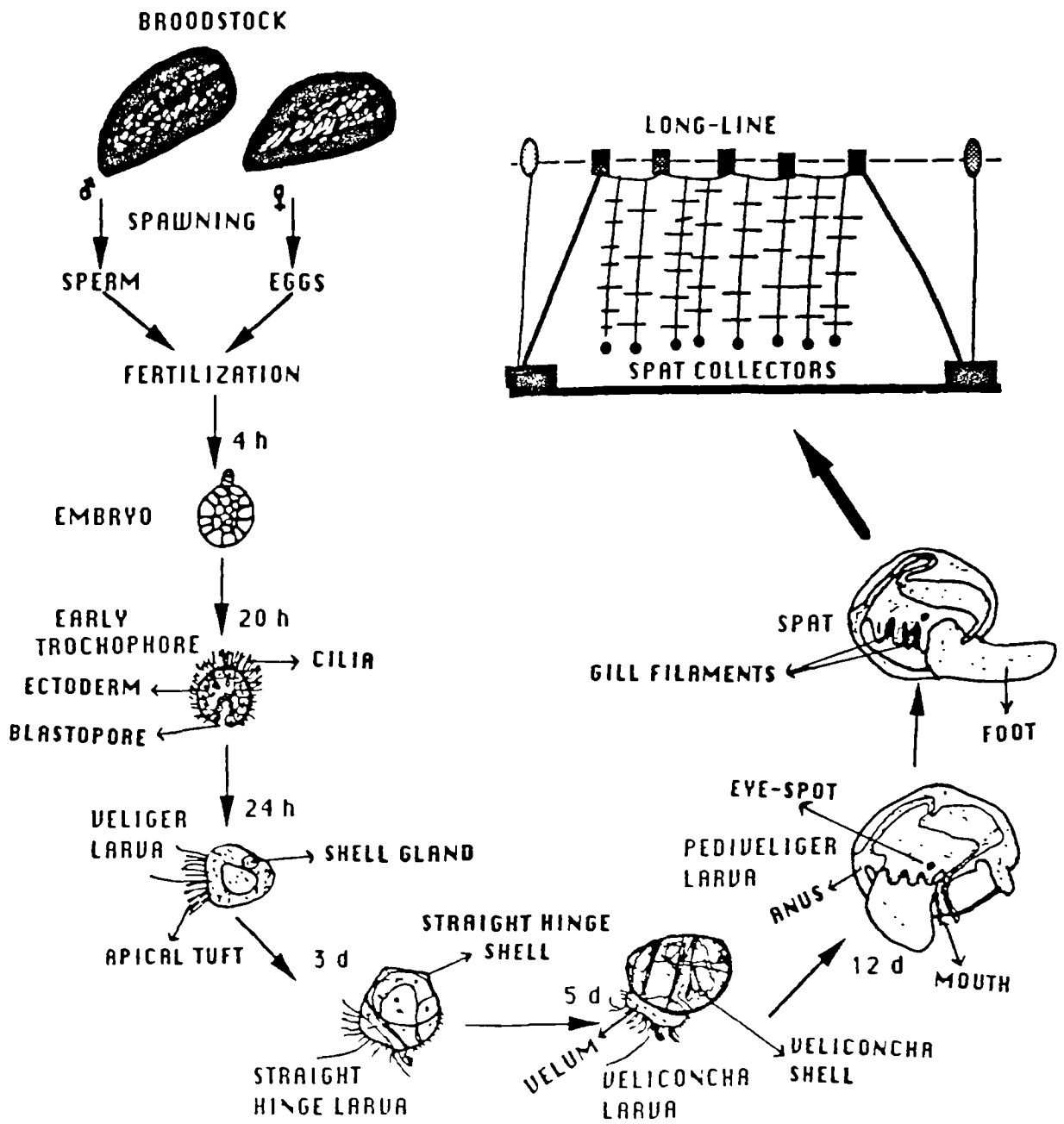


Fig. 2. Schematized development stages and life cycle of blue mussels from wild broodstock to spat ready for settlement on spat collectors (from Field, 1922; Bayne, 1976; Sutterlin *et al.*, 1981)

the same time have greatly influenced the technology and practice of mussel farming. The natural abundance of mussel larvae, particularly in temperate coastal waters, is reflected in the dominant position that the settled larvae, or mussel seeds, frequently attain on the hard substrata of intertidal and subtidal zones of many shorelines. Although mussel farmers may need to expend considerable effort to obtain sufficient seed to stock their farms, the natural availability of seed sources, without the need to resort to hatchery production, has been a significant positive factor in the development of mussel farming. The seed for culture are mainly derived from natural reproduction with settlement of spat on artificial substrata or “collectors”.

The mussel, as a filter feeder primarily utilizing phytoplankton and detrital food, requires only a supply of high productivity seawater to grow and fatten. The cultured mussel is one of the few animals that produces a superior product grown “naturally” and has a significantly higher market value than wild mussels. Mussels exhibit more rapid growth under cultivation, hence marketable size is reached at an age of 1.5-2.5 years. The yields and quality of meat are much better than those from traditionally exploited natural shore mussels (Mason, 1972a, b; Lutz, 1980).

Disease is an ever present risk in any intensive livestock production system and numerous pathogenic and parasitic organisms have been identified in mussels (Bower and Figueras, 1989). However, mussel growing in high densities, either in the wild or in a farming situation, seems to be relatively free from the risk of mass mortality. These characteristics have perhaps the greatest influence on the technical design and operational systems in practice for mussel culture throughout the world.

1.4.1. Origins of Mussel Farming

The huge expansion of mussel production in recent years, has arisen as a combination of the development of the existing culture industry in Asian countries, such as China, Thailand, Korea and Philippines and its emergence as a new industry in other countries, such as the USA, Chile, Sweden, Canada, Ireland and Scotland.

Mussel cultivation has a long history. It started accidentally in France during the 13th century when mussels were observed attached to wooden posts on the beach (Mason,

1976). This formed the basis of the actual cultivation method there (bouchot culture, using vertical wooden posts). Later in the middle of the 14th century, people in Holland started transferring mussel seed to zones where they could achieve better growth (Figueras, 1990). However, production in the Spanish rias, the world's leading region for suspended culture of mussels, started only in 1946 (Milne, 1979b; Pérez-Comacho *et al.*, 1991).

Each country has developed its own cultivation techniques in accordance with the quite specific environmental conditions of their coastal regions. One method can be more successful in a particular region, but all rely on either the ability of mussels to attach to collectors, or collecting of seed settled elsewhere and their transfer to the culture areas. The various methods are well documented (Mason, 1972a, 1976, 1991; Korringa, 1976; Dare, 1980; Lutz, 1980; Dijkema and van Stralen, 1989; Figueras, 1989, 1990; Muise, 1990; Quayle and Newkirk, 1989; Pérez-Comacho *et al.*, 1991; Lutz *et al.*, 1991; Rosell, 1991). Based on the adaptability and hardiness of mussels, three basic culture systems have been developed.

1.4.2. Cultivation on Poles (Bouchot System)

The cultivation of mussels on poles first developed in France as mentioned above. Basically wooden poles are set into the seabed in rows, or bouchots. The poles, usually 20-30 cm diameter oak tree trunks, protrude 2-3 m above the seabed and are spaced 20-50 cm apart. A bouchot may contain about 125 poles and be up to 50 m long. Bouchots are spaced 15-25 m apart at right angles to the shoreline. Several series of bouchots may extend across the intertidal zone. France's bouchot culture method produces about 50,000 mt mussels annually (Figueras, 1989).

The bouchot is used for both mussel seed catching and on-growing, although in recent years there has been increasing emphasis on catching the seed on horizontal ropes strung between poles, rather than on the vertical poles themselves (= 'hanging- bouchots'). Farming involves stripping the seed from the catching poles and transferring them to mesh tubes. The mussels are reattached by winding the tubes around the growing poles. Stripping, reattaching and harvesting by hand are the major operations in the labour intensive farming cycle. Seed caught on ropes are transferred to the bouchots by winding

short lengths (3 m) around the poles and nailing each end. Again this is done manually. Mussels reach marketable size (over 4 cm) after 12-18 months. Bouchot culture techniques produce about 5 mt live weight of mussels per acre per year (Hurlburt and Hurlburt, 1980) or about 1 kg m⁻² of seabed. An average of 25 kg of mussels are harvested from each pole annually (Korringa, 1976).

Pole or stake cultivation of mussels is also conducted on a simpler and less mechanized level in Asian countries such as Philippines (Rosell, 1991) and Thailand (Chalermwat and Lutz, 1989; Lutz *et al.*, 1991). Here bamboo poles, set into the seabed in shallow bays, provide the substrate for both catching the seed and on-growing to market size (over 5-10 cm). For green mussel (*Perna viridis*) this takes 6-10 months, the harvest from single poles averages 8-12 kg mussels.

1.4.3. Cultivation on the Sea Bed (On-bottom System)

On-bottom or seabed cultivation is based on the principle of transferring mussels from areas where they have settled in great abundance, to culture plots, where they can be spread at lower density in order to obtain much better growth and fattening. This method has been developed in the Netherlands into a highly sophisticated and mechanized industry producing 50,000-100,000 mt per year (Dijkema and van Stralen, 1989).

Much of the Dutch farming practice described by Korringa (1976), remains unchanged. One-year-old seed mussels, 10-30 mm in size, are dredged and relayed, either on intertidal plots, to produce thick-shelled adults with strong adductor muscles that are preferred for the fresh domestic and export markets, or on subtidal plots. Subtidally, the mussels grow faster and develop a high meat yield and thin shell that is preferred for processing. The mussels remain on the culture plots for 18-24 months before being harvested by dredging. The crop is spread on special plots for 10-14 days for the purpose of eliminating weak and damaged mussels. Dutch culture techniques produce about 22 mt of mussels for each acre per year, or about 5.5 kg m⁻² of mussel bed (Hurlburt and Hurlburt, 1980). On-bottom culture methods are also well-established in Thailand, Denmark and Germany, and recently have been developed in the USA (Lutz *et al.*, 1991)

1.4.4. Cultivation on Suspended Ropes (Off-bottom System)

The suspended mussel culture techniques first developed by using rafts as a floating platform in Galicia, Spain, have expanded rapidly to other countries (Figueras, 1989, 1990; Lutz *et al.*, 1991), sometimes using different installations, such as long-lines or racks. The best examples of suspended mussel culture have been practiced in Galicia, Spain. The young mussels which settle naturally on rocks are the most important source of seed, representing 60-70 % of the total used for mussel farming in Galicia. The remainder are collected from ropes hung from floating rafts. Mussel seed from coastal rocks or collectors hung from the raft are tied to the ropes using a fine mesh net, which decomposes a few days later. There are wooden pegs spliced at 40 cm intervals crosswise into the ropes, which help to support the weight of the mussels. After 5-6 months, when mussels have reached 4-5 cm, the ropes are taken up to redistribute the mussels onto longer pieces of rope. Each rope produces enough seed for about three new ropes (or thinning out ropes) where mussels remain until they reach marketable size (7-10 cm) (Perez-Comacho, 1987). The production reaches about 33-48 mt raft⁻¹ or 130 kg m⁻² or 14.5 kg m⁻² of rope in a year (Perez-Comacho *et al.*, 1991).

The Spanish system has provided the model for commercial raft culture of mussels all over the world, including China, Chile, Canada, USA, New Zealand Australia, Malaysia, India and Ireland. Differences between the regions in geomorphology, topography and environmental factors have led to different techniques being adopted. The most recent development has been the use of long line systems for suspending culture ropes. This method was probably first used in New Zealand for mussel culture, but nowadays, it is used in many countries such as Sweden, Scotland, USA, Canada and China.

1.5. Status of Shellfish Farming in Scotland

There is a continuing and growing interest in shellfish culture in Scotland, stemming from the advantages of cultivating of molluscs over other animals. The advantages are: (1) molluscs are non- motile or of limited motility, therefore they can be

kept in captivity without the need for constant attention and artificial feeding and are easy to harvest; (2) The various methods of shellfish cultivation lend themselves well to part time activities and thus can help considerably in places such as the Highlands and Islands of Scotland where employment opportunities are scarce; (3) Scottish waters, particularly on the West coast, are well suited to bivalve cultivation for the following reasons:

- a) They receive the benefit of the North Atlantic Drift current with higher temperatures than in many other areas of similar latitude.
- b) The geographical features include many inlets, lochs and islands which offer local shelter.
- c) Many inlets are partly cut off from the open sea by narrow entrances with shallow sills, helping to produce relatively high summer temperatures.
- d) They are almost entirely free from pests and diseases, and from bacterial and chemical pollution (Drinkwater, 1987).

Shellfish farming statistics in Scotland are recorded by the Scottish Office Agriculture and Fisheries Department (SOAFD). The main shellfish species currently cultured in Scotland are the common mussel (*Mytilus edulis*), native oyster (*Ostrea edulis*), Pacific oyster (*Crossostrea gigas*), king scallop (*Pecten maximus*) and queen scallop (*Chlamys opercularis*). Some experimental trials with the Manila clam (*Ruditapes philippinarum*) are being carried out, but there is no record that this species is being cultured commercially (SOAFD, 1993). Sea urchins and abalone are also other possibilities for Shellfish culture in Scotland (McLeod, 1994).

SOAFD produces an annual report on the state of the Scottish shellfish farming industry based on the annual returns of records by farms. By the end of 1994, the number of registered shellfish companies had risen to 348, an increase of around 8 % on the previous year, but only 196 of them were active. The farms range in size from very small ones, involving crofters supplementing their incomes, to large commercial scale operations. Active farm sites are intensively located in the Highland (45 %) and Strathclyde (34 %) regions. The shellfish farms employed 82 full time and 255 part time workers. Total production by species for the years 1986-1994 is shown in Table-1 (SOAFD, 1993, 1994, 1995).

Shellfish production has almost tripled in Scotland over the last 8 years (Table-1). There has been some decrease in mussel production from 1991 to 1994 due to the fact that some big companies reduced their market supply due to fouling, predation from starfish and eider duck, plus husbandry problems. For example Kishorn Shellfish Farm has about 300 mt capacity but produced only around 100 mt of mussels in 1994.

Although the shellfish industry is still very young and small at present it has been described as the sector in Scotland which has the largest potential for growth. Shellfish production from small businesses has expanded slowly, Scottish mussels and oysters are now supplied to supermarkets, thereby bringing Scottish shellfish to a wide range of customers. The demand and price for farmed mussels is at present very strong and, after several stagnant years, the oyster trade has also strengthened. The present poor prices for salmon have made a few salmon growers look again at the possibility of shellfish farming as a means of bolstering flagging incomes. After all, much of the capital investment of a salmon farm, e.g. shore access, slipway, boats, moorings, buildings, electricity, telephones are available immediately for shellfish farming.

1.6. Problems of Shellfish Farming

It is disappointing that the shellfish farming industry continues to perform less well than predicted. Compliance with the European Communities (EC) directives is a potential heavy burden on shellfish growers and suppliers. The EC regulations affecting the shellfish industry include food hygiene, disease control, financial aid, transport of animals, veterinary checks, product safety, frozen food, labeling and advertising, testing and certification, insurance, movement of capital, financial, services, company law and barriers to trade. Consequently, unclear market requirements, low/unstable prices, investment needs in equipment, lack of a producer organisation, lack of information and support from government to develop the Shellfish industry in Scotland.

At present, the following subjects are being investigated in Scotland by SOAFD;

- 1- Mollusc purification methods
- 2- Organic pollution of the sea

Table-1. Summary of shellfish farming statistics for Scotland, 1986- 1994: the number of farms, estimated production for market in metric tons calculated using the following average individual weights: Oysters (both species): 80 g; Queens: 40 g and Kings: 120 g (Modified from SOAFD, 1993, 1994 and 1995)

YEAR	NUMBER OF FARMS			PRODUCTION BY SPECIES					
	Registered	Active	Mussel	Pacific Oyster	Native Oyster	Queen Scallop	King Scallop		
1986	144	141	260.0	40.6	0.08	11.3	9.0		
1987	168	162	270.0	88.7	35.00	32.2	12.6		
1988	174	169	380.0	126.0	1.70	16.6	7.9		
1989	223	181	350.0	98.7	1.20	91.3	5.4		
1990	290	229	460.0	115.3	0.08	52.4	8.2		
1991	310	228	1024.0	184.0	10.00	61.2	38.0		
1992	321	214	898.0	204.8	15.50	61.5	58.6		
1993	332	205	708.0	207.0	9.50	31.5	21.1		
1994	348	196	716.0	168.0	11.40	38.2	23.9		

- 3- Detection of algal blooms
- 4- Culture of new species
- 5- Herpes virus in Pacific oyster
- 6- Scallop transportation studies
- 7- Heavy metal contamination in farmed molluscs

1.7. Mussel Culture in Scotland

The mussel is one of the commonest of all marine animals around Scottish coasts (Drinkwater, 1987). As far back as the early 19th century they were gathered from Scottish shores (such as the Dornoch Firth) as bait used in line fishing, as well as for human consumption. The fishing rights to these mussel beds were granted by Royal Charter in 1612 to the small town of Tain in the Dornoch Firth. Income from the sales of mussels are still paid into the Tain Common Fund and are used for the benefit of the local community (Edwards, 1992). Mussels occur in dense beds, particularly in estuaries, but these animals are usually of poor quality and grow slowly due to overcrowding. However if they are removed and transplanted to better growing areas, they grow well. Nowadays, considerable investment and effort is being made to increase mussel production, either by farming or by better utilisation of natural stocks.

Mussel culture has had a very short history in Scotland. The first report on commercial possibilities of suspended cultivation was produced by Mason (1969) for West coast sea lochs. The first commercial mussel farm was set up in Loch Sween in the 1970's (Holmyard, 1992). A mussel industry has since developed by trial and error; today, there are three different methods (one bottom and two suspended method) available (described below) and their usage is entirely site dependent. Moreover, each site has different characteristics with regard to spatfall, water exchange, availability of food, temperature, salinity, position (sheltered or exposed), depth of water, suitability of the sea bottom for anchorage and shore access and other infrastructure, all of which affect the operation and production features.

1.7.1. Bottom Culture

Bottom culture is used in a few areas on the East coast of Scotland (Holmyard, 1992). Basically, seed mussels are transplanted from natural beds, where growth and survival is poor, on to 'lays' in sheltered inshore waters with a silty sea bed, favorable water currents and richer food supplies. Optimum seed density per square meter, tide height and bottom structure are the most important factors for bottom culture. Large mussels are transplanted for a year to improve their meat quality before marketing. For best growth and fattening, mussels are relayed as low as possible in the intertidal zone preferably in the sublittoral zone.

1.7.2. Suspended Culture

Suspended mussel cultivation is practiced with long-line and raft culture in Scotland. Raft and long-line cultivation are being selected depending on site conditions such as degree of shelter or exposure, salinity and spatfall, characteristics. But sometimes they may even be set up side by side in the same loch, or even on the same farm as on the West coast of Scotland.

1.7.2.1. Long-line Culture

The long-line culture system itself consists of a series of buoyed horizontal polypropylene lines and head ropes or headlines. In Scotland, 100-200 m length of long-line is about 18-30 mm diameter and supported by 25-30 litre of plastic floats, at 0.5-1.5 m intervals depending on the quantity of mussels on the system. When the mussels grow to market size, head ropes need more support with additional floats, otherwise headlines might sink to the bottom and the whole crop be lost. The head ropes may be on the surface or suspended 1.5-3 m below it, especially in areas with excessive freshwater run-off. In this case, floats are connected to the headropes by a 1.5 to 3 m length of rope (about 12-16 mm in diameter) (see Fig. 3). Vertical culture ropes, or droppers, are about 14-18 mm diameter and 4-6 m in length hung from the head ropes. At every 40 to 50 cm, a wood or plastic peg 25 cm in length is inserted through the strands of each rope, which prevents the mussel clusters from sliding down the rope and being lost. For mussel cultivation, mussel

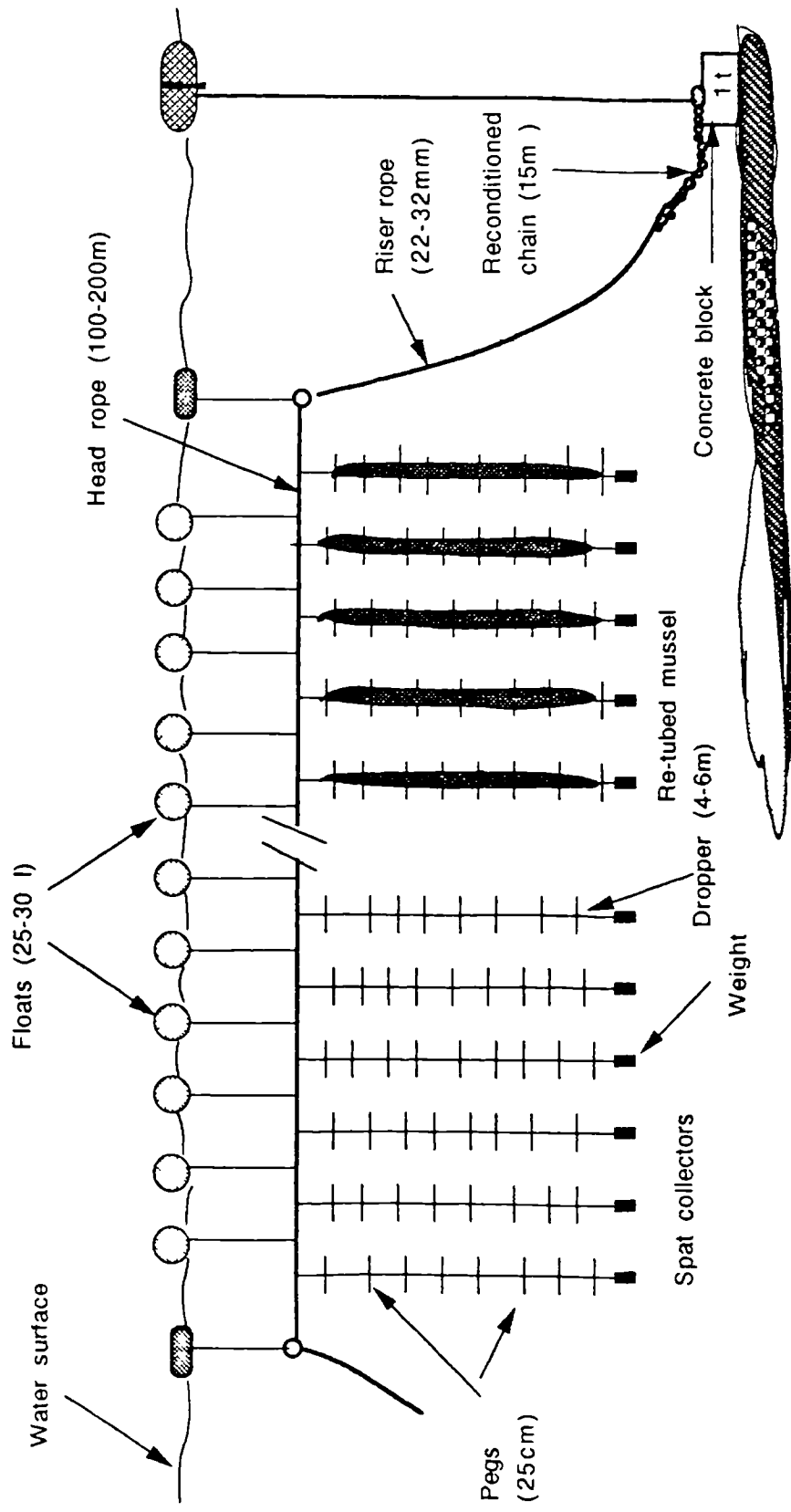


Fig. 3. Side view of a single long line system.

seeds are collected by hairy spat collector ropes from the sea coast, or after harvesting, small sized mussels are re-tubed again for grow on via the long-line method.

A concrete block anchor, about one mt in weight supports a long-line system depending on long-line size and bottom structure. A 200 m long-line costs around £1,500 and the annual return from this, assuming a conservative harvest of 10 mt, will be about £7,000 to £8,000 (Holmyard, 1992).

Recently the use of a double long-line head rope is being practiced in Scotland with the advantage that it requires only one concrete block instead of two. Adams Equipment Ltd. is producing a new barrel connector for floats which are designed to connect a standard 200 litre plastic "L" ring barrel to a double head rope long-line system. The long-line head ropes can be connected without knots by simply looping the rope to the barrel connector. This provides a simple and efficient method for removal or addition of barrels from the long-line. Each connector consists of one galvanized base bracket with 2 "A" horns and two galvanized barrel connecting bands complete with bolts. The specially designed long-line barrels cost, around £32 each, but plastic barrels are normally readily available second hand (washed) from agricultural and industrial users, thereby reducing the cost of the system. In this system, one double head rope long-line 100 m in length should normally have four 100 kg anchors (two each end). Each anchor has 15 m of 22 mm open link ground chain (reconditioned chain) and a 32 mm polypropylene riser.

1.7.2.1.1. Advantages and Disadvantages of Long-lines Over Raft Systems

As can be seen in Table-2, long-line and raft system have some advantages and disadvantages to each other.

Table-2. Advantages and disadvantages of a long-line system over a raft system for mussel rearing (from Herriot, 1984).

Advantages	Disadvantages
1- Lower cost	1- No working surface
2- All plastic, no corroding parts	2- More difficult to work
3- Flexes with the forces of the sea	in rough weather
4- Biologically more suitable (mussels feed better because spread out more)	3- Take up more surface area
5- Catches less wind	4- Worse tangling problems if mooring line breaks
6- Less hazard to navigation	5- More vulnerable to
7- Less scenic impact	malicious damage
8- Less shaking action on mussel ropes from waves than raft	
9- Quicker to harvest (with adequate boat)	

1.7.2.2. Raft Culture

Raft culture offers utilisation of three dimensional space in the water and allows large quantities of mussels to be grown in a relatively small amount of space. In recent years, there has been considerable and rapid development of raft cultivation of mussels on the West coast of Scotland. The rafts in use around Scotland range from tubular metal versions, through converted salmon cages to sophisticated purpose built rafts, but in general most farmers use small home made timber rafts, the main structure of timber mussel rafts are constructed from a timber frame, holding expanded polystyrene floating blocks and timber hanging beams 50-70 cm apart. These rafts carry about 100-200 droppers depending on raft dimension (6-12 m long and 4-8 m wide).

A new, technologically advanced home made raft system (Muckairn mussel rafts) is being produced by Walter Spiers in Loch Etive (Fig. 4) and is now used widely on the West coast of Scotland. The main structure is made from galvanized steel joists (10 cm * 10 cm) and the buoyancy comprises plastic floats (120 cm * 80 cm * 65 cm) filled with closed-cell foam. Wooden beams (11 m * 10 cm * 8 cm), placed 70 cm apart, provide space for a minimum of 200 droppers (culture ropes) (Plate-1). Droppers are 8 m long and 16 mm in diameter. Pegs (25 cm) are inserted at 40-60 cm intervals on the culture ropes, then a 1-2 kg weight is attached to the lower end each rope. The droppers are hung at 40-60 cm intervals from the wooden beams.

Before spat settlement sea algae settle on the rope. Each raft has more than 10 mt production capacity and over 20 mt floating capacity. Eight heavy duty mooring points ensure that the structure remains in place. They are inter-connected to each other by a 3.8 cm diameter * 5 m length of chain and are anchored at both terminals. The cost of each raft is around £6,000-7,000, a produce return over a year of £10,000.

Currently, Adams Equipment Ltd. is manufacturing a large sized mussel raft. Each raft is 12 m * 14 m complete with floating, hanging beam support steelworks and hanging beams with sufficient capacity to accommodate 580 on growing ropes and a mussel stock capacity of 30,000 mt. The cost of each raft is around £10,000. Floating deck sections 12 m * 1 m top surface of floating blocks provide a walking surface.

A Spanish raft system is being used at Kishorn Shellfish Farm in Loch Kishorn which is the largest mussel farm in Scotland, with around 250-300 t capacity based on six rafts. The technology and equipment for this farm has been imported from Galicia, Spain (Plate-2). Measuring 27 m * 20 m, the rafts are made from durable eucalyptus frames and cross beams, from which hang 850 ropes each 9-10 m long. Four large steel floating drums support each raft and one anchoring point, so the raft can turn around its anchor depending on flow direction; this provides an equal chance for the mussels to take up food around the raft. This is considered important for uniform growth. These rafts are quite expensive; costing £50,000 each for an annual expected return of £60,000 (Holmyard, 1992). The main problem is that there is not a built-in walkway on the Spanish raft system, but one can be attached.

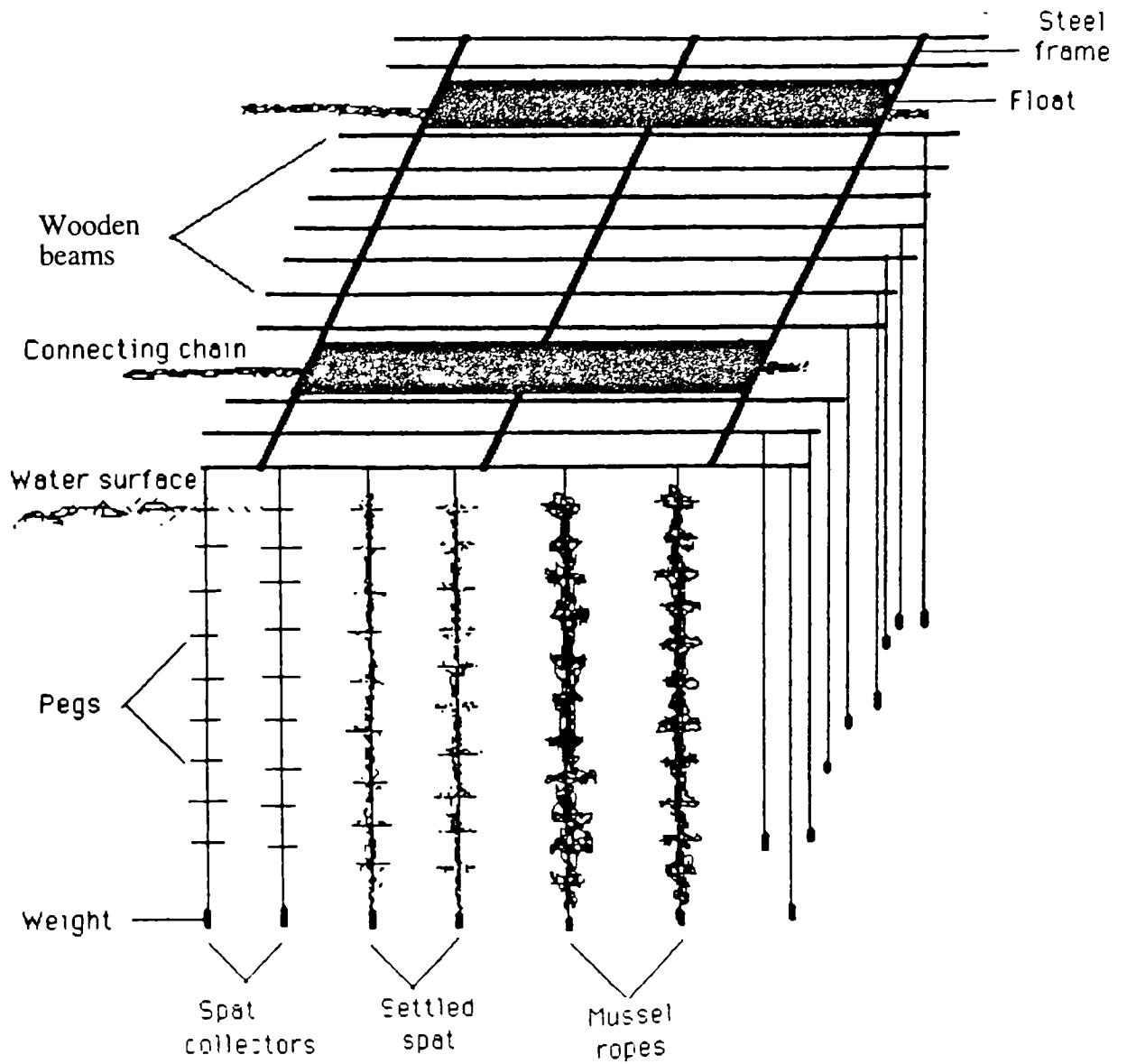


Fig. 4. View of a home made raft system for mussel culture used on the West coast of Scotland

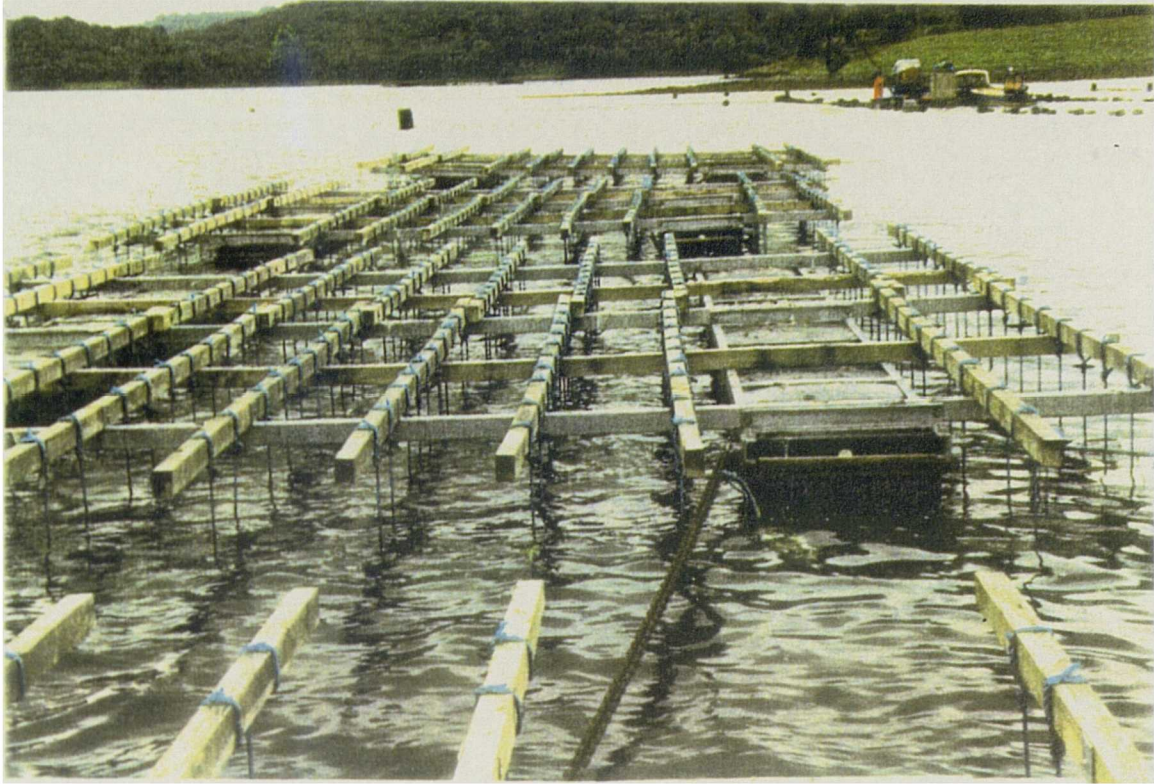


Plate-1. Home made raft system for mussel culture in Loch Etive



Plate 2. Spanish raft system for mussel culture in Loch Kishorn

Mussels have a strong tendency to settle on filamentous objects, making it necessary that algae and hydroids first settle on the substratum (Figueras, 1989). Therefore, the spat collectors are hung out at least one month before spatfall. However some farms (e.g. Kishorn Shellfish Farm) are using hairy spat collector ropes. In this case it is not necessary to hang the spat collectors before spatfall, but time of settlement varies somewhat from loch to loch, even between years in the same loch (personal observation). Therefore farmers do not take risks; they hang their spat collectors earlier than the expected spatfall time.

Spawning takes place around April and May when the water temperature reaches 8-10°C and spat settlement usually occurs around June-December depending on the particular Scottish sea loch. Seeds naturally settle on to the spat collectors. Seed density might change year to year depending on environmental factors at the spat collection sites. Therefore, in general mussel farmers have more than one spat collection site to minimize this risk. If there is not enough spat on the spat collectors, seeds are collected from natural beds and transferred to the raft after tubing in French socks (bio-degradable cotton). Naturally-settled spats on collectors can become overcrowded 9-12 months after spat settlement, which can reduce their growth, or cause layers to separate from the rope and fall off. Mussels are stripped off the ropes and retubed (thinned out) using bio-degradable (French) cotton tubing (Plate-3). Retubed mussels are hung from beams until they reach market size (over 50 mm).

Growth of mussels in Scottish waters is relatively slow and it takes approximately 2.5 to 3 years to reach market size from settlement. Harvest takes place from early summer until winter. Each culture rope (8-10 m) produces 50 to 70 kg mussels under West coast of Scotland conditions. When marketable mussels are harvested, small seeds are retubed for suspended culture. Every 100 mussel ropes provide another 150 retubes in Loch Etive, i.e. the harvested ropes can supply enough seed for future on-growing mussels, therefore the farmer does not need to use spat collectors in that site. This circumstance provides more rafts space for production i.e. spat collector rafts can be used for on-growing instead.

During harvesting, mussel ropes are raised by a means of a crane which is generally fitted on a specially designed motorized floating work platform and brought on board.

Recently, a more developed workboat (Molly Malone) was built (Plate-4) and is used by Walter Spier in Loch Etive. The design is based on a catamaran configuration, with a length of 12 m, beam of 5 m and a draft of 15 cm at the fore, increasing to 30 cm at the end and powered by a Ford FSD 80 marinised transit engine diving through a Castoldi waterjet; the vessel is capable of 8 knots. It was constructed from aluminium; the vessel has a bulkhead every 1.2 m which supports the 5 mm deck plates on stringers.

For grading of mussels, the most popular machine is hydraulically operated De-clumper (Model B1) which is imported from France or Spain. The de-clumper has a 4,000 kg h⁻¹ capacity per hours and its grid size is changeable from 9 to 27 mm manually, depending on mussel size. The price of the de-clumper is around £1,500. A French company (Cochon) is manufacturing more modern and larger washer-graders. The Cochon mussel grader has adjustable brushes which cope equally well with heavy barnacle or brittle star fouling; there is a choice of grid sizes. Mussel flow capacity is 600-5,000 kg h⁻¹. Equipped with diesel, petrol, electric or hydraulic motors, they are readily adaptable for use with tippers, conveyors and weighing machines. After grading, mussels are packed in 2-8 kg sacks depending on market demand.

The techniques of growing mussels by the suspended method has several advantages over bottom cultivation. The growth rates that can be achieved to produce stock which characteristically have a thin, attractive shell, high meat yields and which are completely free from grit and pearls as the mussels never come into contact with the sea bed. Although mussel prices have remained steady (£700-1,100 per mt) over a number of years, rope-grown mussels are able to attract a premium price. Scottish mussels are now available regularly in British supermarkets, large fish markets like Billingsgate London and in good restaurants (Edwards, 1992). Over the past two years the Scottish farmed mussel industry has seen a number of changes in work practices as EC legislation has required the updating of grading, handling and transport methods and the introduction of purification systems for farming molluscs in less than "A" class waters. Complying with the legislation has been costly for the farmers and some businesses have closed. Others farmers have risen to the challenge and have increased production levels to ensure that their new investments pay off.



Plate 3. Tubing of mussel seeds for culturing



Plate 4. Working boat for mussel harvesting.

Moreover, the natural problems of eider duck and starfish predation, fouling organisms and toxic algal blooms are still affecting farmers in some areas. For example Kishorn Shellfish Farm lost about 200 mt of their production due to a high eider duck predation and it could not collect spat due to sea squirt settlement in 1994. There are many strategies to keep birds from the valuable stock such as nets, balloons, loud noises and shooting, but the birds usually simply fly away, returning later.

Paralytic shellfish poisoning (PSP) and diaretic shellfish poisoning (DSP) are monitored at 68 sites in Scotland [by SOAFD] through April to September. Their programme showed that in the future there will be a need for the study of bacterial involvement in toxic events and an investigation into why these toxic events occurred. Depuration methods for toxic contaminated shellfish are also on the list for future studies in the industry (Buchanan, 1995a). Shellfish culture areas were classified 60 % "A" (Mussels can be collected for direct human consumption) and 40 % "B" (Mussels can be collected but only placed on the market for human consumption after treatment in a purification center, after relaying) in Scotland. Loch Etive, which is one of the largest mussel growing areas in Scotland, has been classified as category "B" from June to October inclusive instead of July to September as previously. The Loch retains its classification "A" status for the remainder of the year. All operators will therefore have to depurate a month earlier and later in the year (McLeod, 1995).

1.8. Oyster Culture

The following short sections on oyster and scallop farming in Scotland are included for comparison, to show why mussel culture is at present much more successful and significant in production terms.

Most of the oyster culture in Scotland comes from Pacific oyster (*Crassostrea gigas*) (see Table-1) which was introduced from Japan (Drinkwater, 1987). Pacific oysters reach market size (70-100 g) in three years in Scottish waters. The native oyster (*Ostrea edulis*) grows more slowly than the Pacific oyster which reaches market size in around 5 years. Seed production of Pacific oysters is much more developed. The main problem in oyster cultivation is the seed of the oyster, because the Pacific oyster does not spawn in

Scottish waters, so farmers depend on hatchery- produced and imported seeds. In 1994, high mortality occurred in the imported oyster seeds imported from France to Britain. Scotland must resist all attempts to import French *Crossestrea gigas* seed for growing. In this regard, the new draft EC Shellfish Health Directive is of some help in that it now requires:

- 1- All mollusc farmers within the EC to be registered
- 2- Recording and reporting of all abnormal mortalities on farms and natural beds
- 3- Immediate prevention of movements of stock from an affected area pending full investigation by the official service of the Member State (Buchanan, 1995b).

Currently practised on-growing methods are intertidal (in perforated trays or plastic mesh bags on trestles), subtidal (in stacks or trays), and suspended culture (in trays or lanterns hung from raft or long-lines). A new method of oyster cultivation is being tried in Loch Broom, which it is hoped will lead to earlier maturation and increased production. Already used in France, the method involves growing oysters on suspended ropes. Mainly, the oysters are cemented on to ropes which are then suspended from long-lines supported by buoys. The lines float five metres below the surface avoiding the most turbulent wave action and freshwater run-off. At present the main problems facing the oyster industry are fouling organisms (sea weeds, sea squirts, crabs and mussels), and *Polidora cliata* (Polychaeta). By far the most important affect of fouling organisms is that of blocking the mesh of the tray and thus impeding water exchange. However, crabs feed directly on oysters depending on size. Scotland has a great potential for oyster cultivation but better cultivation methods and purification systems must be developed.

1.9. Scallop Culture

The king scallop (*Pecten maximus*) and the queen scallop (*Chlamys opercularis*) are both present in sufficient quantities to support a culture industry for these species in a number of places in Scotland. The production of scallops has shown a significant increase from 1986 to 1994 (Table-1), but there were sharp decreases in queen scallop (49 %) and king scallop (64 %) production from 1992 to 1993, partly due to an increase in the

competition from wild stocks, as the catch figures were strong for the at year. Scallop cultivation methods and techniques are still developing (e.g. different ways of long-line culture, spat collection and optimum temperatures for transportation and net changing). A future development is that most farmers now cultivate their scallops on the sea bed from the age of two years to market size (110-120 mm for king scallop). Scottish Fisheries Investigation Association (SFIA) suggest that the way forward could be by ranching the scallops; on a suitable selected area of sea bed and scallop size important for planted sea bed in the right environment, king scallops do not migrate to any great degree.

Spat of both species might be obtained by putting out artificial collectors. The best kind of collector consists of an outer mesh bag with other fine mesh netting pushed inside. The larvae enter through the outer covering and settle on the inner material, where they remain attached for a time. By the time they are ready to release themselves from the attachment, they have grown too large to escape through the outer mesh (Drinkwater, 1987). At present, cultivation takes place in lantern nets or cages hung from long-lines or by the ranching method. The king scallop grows relatively slowly, requiring 4 years to reach market size (110-120 mm) while the queen scallop is marketable in 2-3 years at a size of 60-70 mm, or 40 g in Scotland. Scottish scallop farming is still a pioneering industry and relatively high risk because methods and equipment are still being improved. In summary, scallop farming has the following problems:

- 1- There are unacceptable spat mortalities during transportation to growing sites,
- 2- When there is a slower growth rate than anticipated, cash flow is a problem,
- 3- Lack of political and institutional support,
- 4- Expenses include up-front investment in equipment (boat, lanterns, etc.),
- 5- Predators, fouling and competitors,
- 6- Risks associated with long-lines and cost of rafts,
- 7- Low/unstable prices.

1.10. Study Areas

1.10.1. Climate of Scotland

Scotland has a temperate, maritime climate characterized by the absence of extremes in temperature and rainfall throughout the year. Ocean currents moderate the climate, the nature of the coastline allowing their effects to penetrate through the mainland (Anonymous, 1989).

In general, winters are mild and summers cold. Warm or even hot weather can and does occur in inland Scotland, but it is often accompanied by a very high daily range of temperature in valleys, especially in the spring and early summer. Sometimes temperatures fall below freezing point overnight, but rise to the mid-twenties during the day. In contrast, there are relatively small daily ranges in temperature on the coast of Scotland where the moderating influence of the sea limits the fall of temperature during the night, while sea-breezes limit the maximum temperatures on warm days during the summer. In winter, temperature in the British Isles is influenced to a very large extent by the surface temperature of the surrounding seas. In spring, summer and autumn the effect of latitude on the heat received from the sun is the dominant factor.

In general, Scotland's climatic conditions are mild in comparison to other regions at similar latitudes in the Northern hemisphere. The presence of the relatively warm waters of the North Atlantic Drift and the marine current that passes from the Irish Sea through the North Channel, near to the west coast of Scotland, plus the air currents passing across these warm waters, provides the west coast and indeed the whole of Scotland with a moderate climate.

The wind, which comes in off the Atlantic laden with moisture is moderate and with such a variety of topography, spatially very variable. Onshore winds can raise the sea level along large parts of the coast above that of the astronomic tides and offshore winds can similarly lower it. The range of these changes can be metres in extent, and the normal tidal current can in this way be significantly altered (Edwards and Edelsen, 1976).

One main misconception is that the whole of Scotland suffers from very high rainfall. In fact, the west coast of Scotland has an annual rainfall of about 1,000 mm on the

low islands to over 3,200 mm on the high hills, with an average of 2,500 mm (Green and Harding, 1983; Price, 1983) and seasonal distribution is essentially oceanic with a marked rainfall minimum in spring and maximum in winter, typical of all the European Atlantic coast (Green and Harding, 1983). Mean air temperature on the west coast of Scotland near to sea level is around 5 -5.5°C in January, which is 1.6°C higher than the east coast, and around 13 -15°C in summer (Murray, 1978; Price, 1983)

1.10.2. Productivity of Scottish Sea Lochs

In Scottish sea lochs an adequate supply of nutrients and light are essential as these are the most important limiting factor for phytoplankton productivity (Wood *et al.*, 1973; Tett and Wallis, 1978; Grantham, 1981). Both of these factors are directly or indirectly controlled by weather conditions so the effects of the wet and variable highland climate on the west coast of Scotland dominates the ecology of the phytoplankton in sea lochs (Wood *et al.*, 1973).

The concentration of nutrients, stability of the water column and transparency are all affected by the relative proportion of saline to river water. Many Scottish sea lochs are fjordic estuaries (Milne, 1972a) with two layer estuarine circulation driven by fresh water inflow (Fig. 5) (Dyer, 1973) and tidal mixing being important in determining their hydrography. The physical and chemical properties of the surface layers of partly enclosed areas of the sea are grossly affected by the degree of mixing of river water with offshore of coastal water. This, in turn, is largely the result of the input of freshwater, the tidal regime and to a lesser extent, the topography of the area (Solorzano and Grantham, 1975).

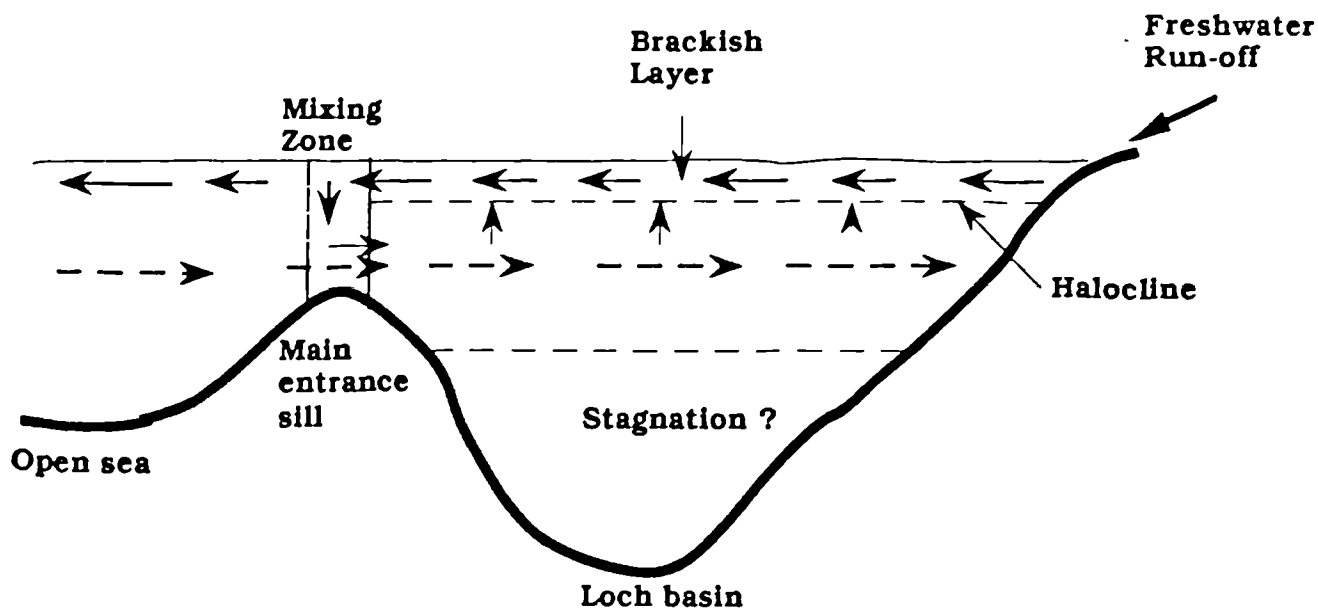


Fig.5. A simplified two layer circulation system in sea lochs and fjords. The current (solid arrows) discharge brackish water to sea. A compensation current (dashed arrows) flows in over the sill to replace water which is entrained (vertical arrows) into surface outflow. Mixing is strongest over the sills, where there may be recirculation of brackish water into the incoming current (after Okumus, 1993).

The addition of freshwater to such a basin gives a strong salinity gradient (halocline) in the surface layers and this results in a considerably vertical stability.

The main contributors to the nutrient budget of the lochs are river run-off and sea water from outside the loch and, as a result of uptake by phytoplankton, the concentration of main nutrients follows the seasonal cycle of phytoplankton with the highest values in autumn and winter and the lowest in summer. Among the principal nutrients, phosphate is mainly supplied by the incoming sea water, but variable amounts of nitrate, nitrite, silicate and ammonium are provided by freshwater run-off throughout the year. Therefore, the freshwater input to the lochs is the main factor in controlling the distribution of major

nutrients and hence the initiation and subsequent support of phytoplankton populations (Okumus, 1993).

Solarzano and Grantham (1975) and Solorzano and Ehrlich (1977) reported that the amount of dissolved organic nitrogen and dissolved organic phosphorus are markedly affected by freshwater run-off. In Loch Etive, the surface (1 m) concentration of the dissolved organic nitrogen and phosphorus was reported to be from 3.0-9.0 $\mu\text{g-at. NO}_3\text{-N l}^{-1}$ and 0.02-0.45 $\mu\text{g-at. PO}_4\text{-P l}^{-1}$, respectively (Solorzano and Ehrlich, 1977). Excretory products from marine organisms, decomposed biological matter and material introduced by land drainage and tidal flow provide the bulk of the soluble organic substances in the loch water.

The ecology of phytoplankton has been described for several Scottish sea lochs: Loch Striven (Marshall and Orr, 1927, 1930), Loch Sween (Marshall, 1947; Gould, 1950), Loch Etive (Wood *et al.*, 1973), Loch Creran (Tett and Wallis, 1978) and Loch Ardbrahir (Gowen *et al.*, 1983).

The timing of the spring increases in phytoplankton in various sea lochs has been reported Loch Creran: (56°31'N, 5°23'W) in early March (Tett and Wallis, 1978), Loch Etive (56°27'N, 5°19'W) in March (Wood *et al.* 1973), Loch Nevis (57°00'N, 5°41'W) in March (Marshall, 1947; Gould, 1950), Loch Striven and upper Firth of Clyde (55°56'N, 5°03'W and 55°51'N, 4°56'W) in late March (Marshall and Orr, 1927, 1930).

In general, the spring increase of phytoplankton production starts in sea lochs in March and reaches a maximum in late spring or early summer, declines in autumn and reaches a minimum in winter. Dinoflagellates and microflagellates are important in sea lochs. Loch Ardbhair is dominated by diatoms, in particularly *Thalassiosira decipiens*, *Skeletonema costatum* and *Ceratium lineatum*. Gowen *et al.* (1983) reported that throughout 1981, phytoplankton in Ardbhair was dominated by diatoms and small flagellates, as is the phytoplankton of other sea lochs, for example Loch Etive (Wood *et al.*, 1973). A low concentration of chlorophyll-a and high surface nitrate concentration suggests that phytoplankton growth is light-limited.

The concentration of the suspended matter in Loch Etive varies with river discharge, biological production and water movement (Solorzano, 1977). The contribution

from phytoplankton production shows a seasonal trend with the highest values in the spring and lowest in winter (Solorzano, 1977; Stirling and Okumus, 1994). The C:N ratios in the surface (1 m) of the loch throughout the year fluctuate between 6.5-20, being the highest in winter. The lowest ratios occur in early autumn and are associated with high levels of dissolved organic nitrogen and ammonium. Variation in the concentration of POM in the surface layer of the loch is mainly the result of the seasonal production in the loch and adjacent coastal water and the input of organic detritus of terrestrial origin. Environmental conditions during the spring and autumn blooms, such as light, temperature and nutrients, may have contributed to the differences in the value of the particulate organic nitrogen and chlorophyll-a. The occasional influx of denser water in to the deep basin (Edwards and Edelsen, 1977; Solorzano and Ehrlich, 1977) significantly affected the concentration and distribution of the particulate organic material in this section of Loch Etive.

The main feature of the phytoplankton in Loch Etive is a predominance of the diatom *Skeletomena costatum*, though small flagellates are also important. Solorzano and Ehrlich (1977) found that about 70 g C m⁻² year⁻¹ is a rough estimate of gross annual primary production in the euphotic zone of the lower basin. Light is the most important limiting factor in the loch, and the effects of the West Highland climate dominate the ecology of the phytoplankton. The amount of dissolved nitrogen and dissolved organic phosphorus are markedly affected by the freshwater run-off. The lowest values of organic nitrogen occurs during winter and spring, with a marked increase in the summer and autumn months, associated with high and low salinity respectively (Solorzano and Ehrlich, 1977).

1.10.3. Loch Etive (56° 33' 44" N, 005° 03' 52" W) :

There are 110 sea lochs around Scotland. Loch Etive is a west coast sea loch adjacent to the town of Oban; it opens into Loch Linnhe, an extension of the Firth of Lorne which separates Mull and Ardnamurchan from the main part of Argyll (Fig. 6). Among the Scottish sea lochs, Loch Etive has an exceptionally high run-off and small tidal range. (Edwards and Edelsen, 1977).

Loch Etive is the third longest loch in Scotland being 30 km in length and has the greatest ratio of length to width (30), and flushing time (14 days) of all Scottish sea lochs (Edwards and Sharples, 1986). The rainwater catchment of 1,400 km² is larger than that of any other Scottish fjord and 7 times the mainland mean. The average freshwater run-off, allowing for evaporation of 250 mm, is 3,037 million m³ per year (Edwards and Sharples, 1986). Contrary to regional south westerly drainage, water from the neighboring Loch Awe catchment drains north westward to enter Loch Etive at Inverawe.

Loch Etive is a fjord, with three basins, the innermost bottom water stagnates for months or years, with slowly changing temperature. A bottom water renewal is shown to be caused by low freshwater run-off. The renewal is a series of overflows of sill water during spring flood tides. During the overflows, dense water forms a turbular plume whose observed behaviour is similar to that expected from theory, an entrainment constant of 0.013 is found on a bottom slope of 6° (Edwards and Edelsen, 1977).

Loch Etive is connected to the sea by a sill 300 m wide, 4 km long and 10 m deep. Severe shoaling on the sill chokes currents so that the internal tidal range is 2 m, compared with an external range of 4 m. Wood *et al.* (1973) established the estuarine circulation in Airds Basin, and the possibility of a salinity control of the renewals of deep water in the inner basin is recognised by Gage (1972) and Solorzano and Grantham (1975). At the beginning of April, the temperature of water at the sill depth is 7°C, typical of coastal water, whose annual cycle is exemplified by Milne (1972a). Near the surface, the water warms in spring; the thermocline at 50 m separating the sill water from stagnant bottom water erodes, the deep thermocline deepens and the temperature of the sill water increases like that of coastal water. At the beginning of May a mass of water at sill temperature appears below the warm water. By mid-May there is a near uniform mass of sill water at all depths. Subsequently, bottom temperature changes little, the sill water warms like that of the coastal water and surface water warms more rapidly with terrestrial influence.

Edwards and Edelsen (1977) found that salinity of the surface waters increases in April. Below the primary halocline the salinity of sill water also increases. The comparison of coastal salinity of 33-34 ‰ with that of the stagnant water emphasizes the importance of

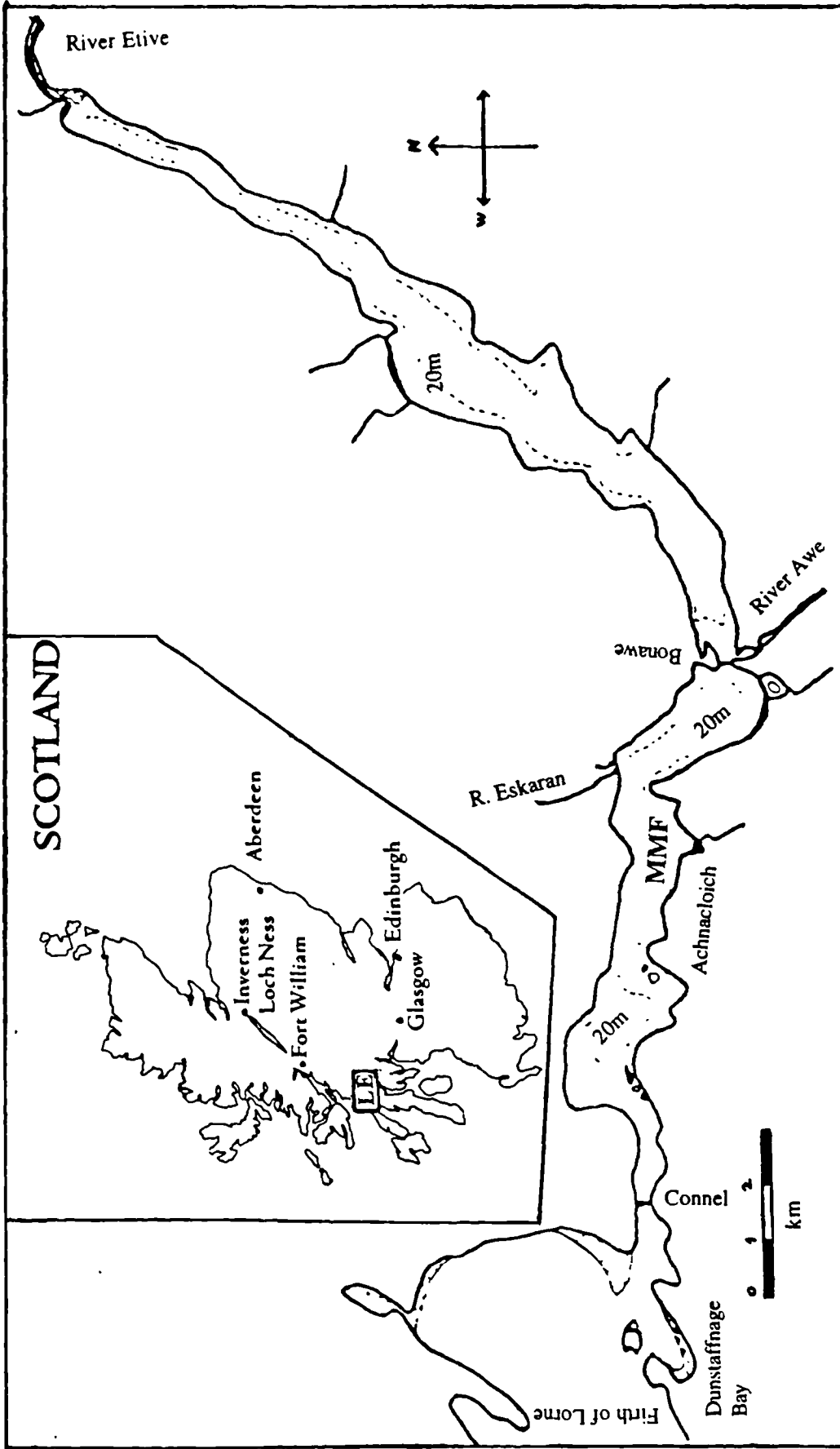


Fig. 6. Map of Loch Etive (LE) showing the sites at which the study was conducted. MMF: Muckkairm Mussel Farm.

freshwater in the fjord. The secondary halocline deepens until a third briefly appears to the separate rising stagnant water from intruding cool water at the bottom. By mid-May the haloclines disappear. At the end of May, the primary halocline returns, followed in June-July by a second one. (Edwards and Edelsen, 1977). A brief description of the geology and topography of these lochs, and their main physical parameters, are summarized in Table-3.

Field studies were carried out in Muckairn Mussel Farm (MMF) which consists of ten home made rafts and six single long line systems (Plate-1). MMF is located near to Achnacloich (Fig. 6) The site is just 30-40 m from the shore and the depth is around 20-25 m. There are eider ducks around the mussel farm. Production capacity of the mussel farm is around 100 mt which ranks it in second place in term of production after Kishorn Shellfish.

1.10.4. Loch Kishorn (57° 24' 50" N, 005° 34' 33" W)

Loch Kishorn is one of the simplest and smallest sea lochs in Scotland (Fig. 7). It is simply an arm of the sea, so it shows characteristics typical of coastal seawater. As seen in Table-3 , Loch Kishorn is one of the smallest sea lochs by ratio of length to width (3:1) and area (7.1 km²). There are no published data about this loch other than the main physical features (Table-3) given by Edwards and Sharples (1986) and one technical survey report prepared to monitor marine fish farms by Hunter and Scanlan (1988).

Hunter and Scanlan (1988) reported that *Cladophora rupestris* is common around some small shallow pools and a full furoid zonation is present, as is a *Laminaria* zone at the low water mark. In the intertidal zone, furoid algae dominate the horizontal surfaces while barnacles dominate the vertical ones. *Polisiphonia lanosa*, *Enteromorpha* and *Pilayella* are common epiphytes in the loch. Mussels, dog whelks, littorinids, barnacles and limpets are common animals in Loch Kishorn. There is a one large salmon farm and the largest mussel farm in Scotland in the Loch.

Field studies were carried out in Kishorn Shellfish Farm (KSF) which is a Spanish style mussel farm and located near to Kishorn Island in Loch Kishorn (Plate-2).

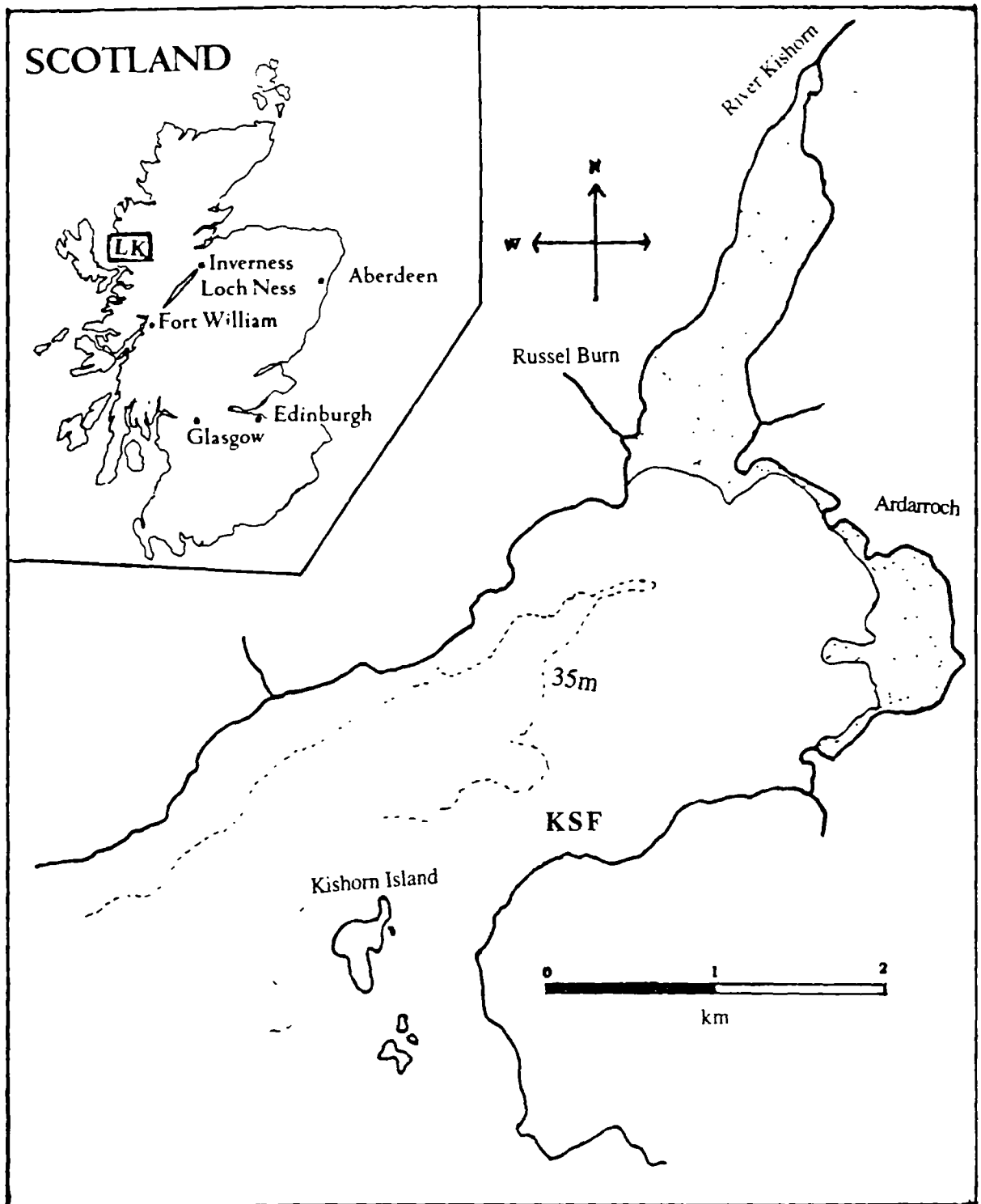


Fig. 7. Map of Loch Kishom (LK) showing the sites at which study was conducted. KSF: Kishorn Shellfish Farm.

Kishorn Shellfish Farm has about 250-300 mt production capacity based on six rafts. The main problem in that there is no fixed walk way on the rafts, but a mobile walk way can be used. Kishorn Shellfish Farm has serious eider duck and sea squirt fouling problems. Depth of the site is around 35 m and it is around 300-350 m away from the salmon farm.

Table-3 Summary of the main physical parameters of Loch Etive and Loch Kishorn
(from Edwards and Sharples, 1986)

Parameters	Loch Etive	Loch Kishorn
Length (km)	29.5	4.1
Tidal range (m)	1.8	4.7
Max. depth (m)	139.0	61.0
Mean depth at low water (m)	33.9	22.2
High water area (km ²)	29.5	7.1
Low water area (km ²)	27.7	5.4
5m area (km ²)	23.6	4.5
10m are (km ²)	20.6	3.6
Low water volume. (M m ³)	939.8	119.9
Watershed (km ²)	1350	66
Rainfall (mm y ⁻¹)	2500	2000
Run-off (M m ³ y ⁻¹)	3037.5	152.2

CHAPTER 2: LITERATURE REVIEW

2.1. Methods of Cultivation

All methods used in the cultivation of mussels can be assigned to one of two categories; they are either on-bottom cultivation or off-bottom cultivation. The various culture methods were described in Chapter 1. This section reviews the performance of mussel culture systems in relation to environmental conditions and introduces the objectives of the present study.

The Spanish system has provided the example for experimental and commercial raft culture of mussels all around the world, including China (Zhang, 1984), Chile (Chanley and Chanley, 1991), Canada (Heritage, 1983), the U.S.A. (Lutz, 1980), New Zealand (Jenkins, 1979), Australia (Maclean, 1972), Malaysia (Sivalingam, 1977), Singapore (Cheong and Lee, 1984), India (Nagabhushanam and Mane, 1991), Venezuela (Mandelli and Acuna, 1975) and Ireland (Anon, 1990). Submersible rafts have been proposed for utilizing more exposed situations in India (Rajan, 1980) and a self-buoyant bamboo raft submerged 1-1.5 m below the surface is a standard culture method used in the Philippines (Rosell, 1991). However, the more general approach to mussel farming in more exposed areas, or in areas where large floating structures, such as rafts, are considered aesthetically unacceptable, has been to adopt the long-line method of cultivation.

Culture of mussels (*M. edulis*) on ropes suspended from rafts or long lines is a well established practice in several countries (Andreu, 1958, 1968; Dare and Davies, 1975; Mason, 1972b, 1976; Lutz, 1980; Figueras, 1990; Muise, 1990). Basically, the suspended culture process is divided into four stages: (i) obtaining the seed (ii) growing the seed (iii) thinning out the ropes and transferring the seed on to new ropes and (iv) final harvest and sale (Perez-Comacho *et al.*, 1991).

2.2. Factors Effecting Growth

Jamieson *et al.* (1975) suggested that growth rate is affected by age, size, genotype, light, temperature, depth, food, salinity and current. Since the concept of allometric growth was first introduced it has been applied extensively to many bivalves, including *Mytilus*

(Richards, 1928; Coe and Fox, 1942; Coe, 1946; Genovese, 1965; Hancock, 1965; Seed, 1968, 1973; Sadykhova, 1970). The general growth pattern is that growth is fast in young mussels, but becomes slower as the mussels get older and larger. The reduction in growth rate in larger-sized mussels can be associated with reduced metabolic activity and decreased feeding efficiency. Filtration rate has been shown to correlate negatively with increases in meat weight of individual organisms (Theede, 1963; Walne, 1972). Bright light has been shown to have a negative effect on shell growth rate in *M. edulis*, while having a positive effect on meat yield (Coulthard, 1929; Jamieson *et al.*, 1975). Light seems to have a detrimental effect on growth in *Mytilus*. Continuous darkness, reduced levels of irradiance, wavelengths below 600-700 nm and photo periods of 7 h or less, all significantly increase the linear growth rate in *M. edulis* (Stromgren, 1976a, b).

Physical movements of water have been shown to affect metabolism and growth rate in *M. edulis*. Harger (1970) documented a reduction in growth rate of mussels exposed to wave action on open shores during the winter months.

M. edulis being a filter feeding animal, is dependent upon plankton, organic detritus, bacteria, and probably dissolved organic matter in the water as sources of food. Environmental parameters influencing growth rate can be divided into those of general action and those of local action. Factors of general action include water temperature and salinity, which may affect rates of biochemical reactions within an organism in temperate latitudes. Local factors determining nutritional conditions can influence greatly the growth rate of marine bivalves (Sukhotin and Maximovich, 1994). The most important factors are particulate organic matter concentration and quality (Essink and Bos, 1985; Wilson, 1987; Brown, 1988; Thompson and Nickols, 1988), duration of air exposure (Savilov, 1953; Baird, 1966; Seed, 1969), population density (Broom, 1982; Peterson and Beal, 1989), exposure to air and genotypic characteristics (Dickie *et al.*, 1984; Skidmore and Chew, 1985; Mallet *et al.*, 1987a; Mallet and Carver, 1989) and water current velocity (Harger, 1970; Grizzle and Morin, 1989). In addition, size, age, reproductive condition and genetic characteristics affect the growth of mussel.

Intraspecific competition for food and space can lead to extreme variation in growth rate (Seed and Suchanek, 1992). Strong wave action can significantly reduce the growth

rate in *M. edulis* (Harger, 1970; Suchanek, 1981) and storms and wave action can also be detrimental (Coe and Fox, 1944; Coe, 1945). Pollutants may also be detrimental to growth (Alyakrinskaya, 1967), although mussels are known to flourish near sewage outfalls (Nair, 1962; Bohle, 1965) possibly through an increase in the potential food supply.

2.2.1. Salinity

Mussels are extremely euryhaline and natural populations are found over a wide range of salinities (Bayne *et al.*, 1976a, b). Bohle (1972) suggested that mussels living in environments with strongly varying salinities have reduced growth rates. Salinity is known to affect the growth and survival of mussels (Brenko and Calabrese, 1969; Seed, 1976). Mussels have an extremely low growth rate at 4 to 5 ‰ salinity and attain maximum shell lengths of approximately 40 mm only (Remane and Schlieper, 1971). Numerous other workers have reported similar detrimental effects of lowered salinities on growth of mussel (Paul, 1942; Lubinsky, 1958; Bagge and Salo, 1967; Theisen, 1968; Jamieson *et al.*, 1975). Jamieson *et al.* (1975) noted a reduction in growth rate of *M. edulis* at salinities in excess of 40 ‰.

Brackish estuaries and lagoons are favorable habitats for mussel growth but this probably reflects the increased food level in those environments rather than any beneficial effects of reduced salinity. Low salinity may have a detrimental effect on growth and can even be lethal to mussels under extreme conditions (Almada-Villela, 1984). However, *M. edulis* can survive considerable reduced salinities and will even grow as dwarfed individuals in the inner Baltic, where salinities can be as low as 4-5 ‰ (Kautsky, 1982). Bohle (1972) found that under various steady state salinities, mussels gradually acclimated to lowered salinity levels. *M. edulis* can effectively isolate itself from transient low salinity by closing its valves and maintaining a relatively high osmotic concentration within the mantle fluid (Davenport, 1979; Aunaas *et al.*, 1988).

2.2.2. Temperature

Temperature has been widely acknowledged as an important factor in controlling growth rates. The environmental temperature range for *M. edulis* is fairly wide. Almada-

Villela *et al.* (1982) examined the effect of several constant temperatures on *M. edulis* and found that there are linear growth between 3°C and 20°C, while it proceeded only very slowly in low temperatures (3°C and 5°C). Loo and Rosenberg (1983) found that low temperatures (lower than 5°C) did not seem to limit growth whenever these coincided with the spring phytoplankton bloom. Coulthard (1929) reported that growth of *Mytilus* occurred between 3°C and 25°C, with an optimum between 10°C and 20°C. Physiological studies on *M. edulis* have also demonstrated that between 10°C and 20°C water temperature has little effect on scope for growth (Bayne *et al.*, 1976a). Mussels have been shown to be tolerant of temperatures of -15°C, when 60 % of the body water is frozen (Bayne *et al.*, 1976b). The upper thermal tolerance limit is given as 26°C by Jamieson *et al.* (1975), with filtration rates being affected negatively above 22°C.

Low temperature and low food levels have a negative relationship with growth rate (Kautsky, 1982; Loo and Rosenberg, 1983; Skidmore and Chew, 1985). At low temperatures feeding activity is slow and food intake is low. The rate at which shell material is manufactured by the mantle is less affected by temperature, so that fast growing individuals have thin shells, while animals which are growing slowly have relatively thick shells (Drinkwater, 1987). According to Heral (1987), with the exception of spawning period, temperature is possibly the primary explanatory factor for shell growth and the third factor affecting meat production after food availability and the reproductive cycle of the animals.

2.2.3. Food Quality and Quantity

Culture of mussels (*Mytilus* spp.) is an efficient method of converting marine phytoplankton into nutritious and palatable food (Korringa, 1979). The growth of benthic suspension feeders like the mussel *M. edulis* is influenced by a number of environmental factors (Seed, 1976) of which food availability and temperature are predominant. Quality and quantity of available food might be the most important factors regulating growth (Boje, 1965; Seed, 1976; Incze *et al.*, 1980; Pieters *et al.*, 1980; Wallace, 1980; Rodhouse *et al.*, 1984a; Heral, 1987; Page and Hubbard, 1987; Mallet *et al.*, 1987a; Dardinac-Corbeil, 1990).

In natural seston (total amount of particulate material present in suspension), phytoplankton is an important food component (Redhouse *et al.*, 1984b), which is selected from seston before ingestion (Kioborne and Mohlenberg, 1981). Large aggregations of shellfish may have a significant impact on nutrient and energy cycling in shallow marine ecosystems (Boyton *et al.*, 1980; Dame *et al.*, 1980). Natural beds of filter-feeding bivalves are known to deplete substantially particle concentrations in their overlying waters (Wright *et al.*, 1982; Carlson *et al.*, 1984; Cohen *et al.*, 1984) and are thought to act as a natural eutrophication control in shallow enclosed bays (Officer *et al.*, 1982). The relations between food quantity, temperature and scope for growth in *M. edulis* have been described by Thompson and Bayne (1974), Widdows (1978a, b) and Bayne and Worrall (1980). The effect of food concentration on growth has been measured in mussels by Winter and Langton (1976). Newell *et al.*, (1982) showed that quantitative and temporal differences between habitats, in the energy content of the mussels' food supply, have a marked influence on the timing of the gametogenetic cycle. Probably the single most important factor in determining growth rate is food supply, since this provides the necessary energy to sustain growth (Gosling, 1992). Mussels are efficient filter feeders removing particles down to 2-3 μm with 80-100 % efficiency (Mohlenberg and Riisgard, 1979). The total amount of particulate material present in suspension (seston) contains several potentially utilizable food types. These include bacteria, phytoplankton, fine organic detritus and material of organic origin, although the precise nutritional contribution that each of these makes to the diet varies seasonally, and among mussels of different size (Page and Hubbard, 1987). Dissolved organic matter may also contribute to the energy intake of *Mytilus* (Manahan *et al.*, 1983; Siebers and Winkler, 1984).

2.3. Carrying Capacity

Rapid expansion of the mussel culture industry has prompted considerable interest in the problem of estimating carrying capacity, i.e. the stock density at which production levels are maximized without negatively affecting growth rates (Carver and Mallet, 1990). The accelerated growth and superior condition of mussels in suspended culture systems is due to their maintenance under the optimal conditions available in the environment. Simply

stated, this involves maximizing exposure to food while minimizing physical trauma and predation. The rapid growth of this sessile organism is subsidized by physical energy flows in nature; mussels require considerable volumes of water to meet their metabolic demands, and these volumes are provided primarily by tidal circulation (Lutz, 1985). Although these free energy flows help to make mussel aquaculture an extremely efficient means of protein production, limits to the productivity of natural waters necessarily limit the amount of shellfish biomass that can be supported before competition for available nutrients limits overall growth (Lutz, 1985).

The success of suspended culture techniques is directly dependent on production of food and oxygen in the growing waters and upon adequate circulation (Incze and Lutz, 1980; Lutz, 1980; Incze *et al.*, 1981). A consideration of possible biological constraints to mussel aquaculture in an estuary or bay involves an extension of the ecological concept of “carrying capacity” to the culture or husbandry of mussels. By evaluating the ability of a body of water to support dense aggregations of shellfish, the optimal production density can be determined (Lutz, 1985).

The carrying capacity of coastal sites for suspended mussel culture should be modeled and criteria for site selection, stocking density and number of leases determined based on estimated production potential. A major consideration in the site selection process should be carrying capacity of the site, i.e. the maximum level of production that a site might be expected to sustain (Beveridge, 1987). Assessment of carrying capacity will lead to efficient use of finite lease space, will optimize mussel growth rates, permit financial planning through project yield, and allow informed regulation of inshore waters for aquaculture and competing interests such as traditional fisheries or leisure activities.

Modeling carrying capacity for bivalve molluscs in open, suspended culture systems was developed by Incze *et al.* (1981). Basically, the culture system used in this model is three-dimensional, having a depth, a width and a length, with a water surface area and a face area “facing” the current. For a number of areas where mussels are cultured, it has been shown that the feeding capacity of the area is related to phytoplankton dynamics (Tenore and Gonzales, 1976; Incze and Lutz, 1980; Rosenberg and Loo, 1983). Current velocity is also important for the availability of food to mussel rafts (Rosenberg and Loo,

1983) and dense mussel beds (Wildish and Kristmanson, 1985; Frechette and Bourget, 1985a, b). The potential yield of mussels and carrying capacity of mussel culture areas have been also calculated from the production and transport of carbon (Rosenberg and Loo, 1983; Rodhouse and Roden, 1987).

2.4. Spat Settlement

M. edulis is a dominant and widely distributed littoral mussel, whose life cycle is typical of intertidal marine invertebrates with an extended larval dispersal period and sedentary adulthood. The larvae appear capable of moving great distances (Koehn *et al.*, 1976). Adult females are remarkably fecund, liberating about 25 million eggs per season and as many as 12 million in a single spawning episode (Field, 1922). Spawning involves the liberation of gametes into the surrounding water mass where fertilization takes place (Chipperfield, 1953). Ontogeny proceeds from a trochophore larva through a variety of later larval stages each differing in response to light and gravity (Bayne, 1964). The most extended larval stage is the veliconcha, the feeding larva, lasting for a minimal period of twenty-two days. This time is required for complete development and growth of the foot, a necessary structure for settling (Bayne, 1965). In the absence of a suitable settling place, the veliconcha stage may be delayed for up to about fifty-five days from the time of fertilization (Bayne, 1965). Larvae appear to settle on a number of substrates (Engle and Loosanoff, 1944; Chipperfield, 1953), but Bayne (1964) reported that primary settlement occurred upon filamentous algae, thus avoiding the larvae pediveliger mortality that would occur if they settled upon adult mussel beds.

Good spat settlement, rapid growth and high survival are essential for successful mussel culture (Stirling and Okumus, 1994). Mussel populations differ in spat abundance, growth and survival performance even between very close sites, for example between the North sea and Baltic sea (Johannesson *et al.*, 1990; Kautsky *et al.*, 1990) and between surprisingly close (in order of kilometers or less) inlets, bays, fjords, or lochs within the same coastal waters (Widdows *et al.*, 1984; Skidmore and Chew, 1985; Mallet and Carver, 1989). Most of those differences are generally induced by environmental variables, namely, salinity, exposure to air, temperature and food availability, particularly in

geographically close stocks (Seed, 1976; Dickie *et al.*, 1984; Mallet and Carver, 1989; Kautsky *et al.*, 1990), but some may be caused by genetic variation (Mallet *et al.*, 1987a; Johannesson *et al.*, 1990).

Suspended cultivation relies upon natural mussel spat collection which, because of the abundance of *M. edulis* in UK waters, does not present too many problems. However, certain areas are far more favorable for settlement than others and if such conditions are not present at the cultivation site, spat have to be collected in a different area and transported.

The spat collectors used vary from purpose- built units of polyethylene mesh to salvaged pieces of frayed rope and old sacking material (Muisse, 1990). Smooth surfaces are generally unattractive to prospecting plantigrates and maximum settlement occurs on roughened, scarred or fibrous substrata (Seed, 1969; Dare *et al.*, 1983; King *et al.*, 1990). *Mytilus* species are known to settle on a wide variety of filamentous substrata, including the byssal filaments of nonspecific adults (Petraitis, 1978; Suchanek, 1981; Hosami, 1984; Eyster and Pechenik, 1987), filamentous algae (Paine, 1974; Suchanek, 1978; King *et al.*, 1990), fibrous ropes (Mason, 1976c; Lutz, 1980) and onto adult beds (Petersen, 1984a, b). Spat collectors are placed in seed collecting sites before the expected settlement time.

In temperate waters *Mytilus* larvae are generally abundant throughout the spring and summer months although several studies (Rodhouse *et al.*, 1985) have recorded *M. edulis* larvae in the plankton throughout much of the year. The onset, duration and intensity of settlement and recruitment exhibits considerable spatial and temporal variation (see reviews by Seed, 1976; Suchanek, 1985).

When the seed reach appropriate size, they are removed from the collectors by hand or with a stripping machine designed for the purpose; then they are filled into cotton socks for grow out. For rope culture, suggested optimum spat densities are 6,000, 10-20 mm seed or 300 40 mm seed per metre of rope for *M. galloprovincialis* in Spain (Figueras, 1989), or 200 10 mm seed per meter for *Perna canaliculus* in New Zealand (Jenkins, 1979). Seeding densities for *M. edulis* grown in mesh stockings in Irish long-line culture are based on the weight of the small (2-8 mm) seed. Recommended densities range from 0.5 kg of seed per meter of stocking (Roantree, 1986) to 1.5 kg m⁻¹ (Herriot, 1984).

Consistent and continuous recruitment of mussel seed to natural population is critically important for sustained harvests of quality mussels. The density of recently recruited juveniles in a population may also have an effect on the growth rate of those juveniles. Extremely high densities may provide limited opportunities for growth due to overcrowding and competition for available food. Also, it has been shown that growth of recently settled spat in populations of mixed ages is greatly reduced (Seed, 1969).

2.5. Mortality

Mytilus is highly adaptable and especially tolerant of a wide range of environmental conditions. However, extremes in physical factors such as storms, temperature and desiccation, and excessive deposition of silt are all known cause to mortality in mussels (Seed and Suchanek, 1992). These factors will vary seasonally and their combined and/or synergistic effect can occasionally result in spectacular mass mortalities.

Factors influencing mortality in *M. edulis* have been studied by many researchers and several factors have been identified as being responsible; these include predation, temperature, food, parasites and physical factors such as sedimentation, wave action, tidal scour and overcrowding (Wallis, 1975; Dare, 1976; Dare and Edwards, 1976; Walting and Maurer, 1976; Bayne *et al.*, 1977; Incze *et al.*, 1978, 1980; Freeman and Dickie, 1979; Kautsky, 1982). However, the possibilities of post-spawning mortality has largely been ignored. Incze *et al.* (1980) suggested that gametogenesis is a possible factor contributing to mortality. High levels of natural mortality have also been reported in some populations of *M. edulis* at times of metabolic stress (Emmett *et al.*, 1987).

Predation is undoubtedly the single most important source of natural mortality in *Mytilus*. Moreover, many mussel predators such as crabs (Jubb *et al.*, 1983), starfish (Menge, 1972; O'Neill *et al.*, 1983), gastropod molluscs (Hughes and Dunkin, 1984; Hughes and Burrows, 1990) and shorebirds (Incze *et al.*, 1980; Durrell and Gross-Custard, 1984; Feare and Summers, 1985; Meire and Eryvynck, 1986; Raffaelli *et al.*, 1990) are known to forage selectively on specific size ranges of *Mytilus*.

2.6. Biochemical Composition

The biochemical composition of mussels has been studied by several workers (e.g. Alvarez, 1968; Giese, 1969; Williams, 1969; Pavlovic *et al.*, 1970; Zwaan and Zandee, 1972; Dare, 1973; Gabbott and Bayne, 1973; Ruiz *et al.*, 1992). Most determination of the biochemical composition of marine bivalves have been concerned with the gross changes in protein, lipid and carbohydrate content. Methods of biochemical analysis for marine invertebrates have been reviewed by Giese (1967) and Holland and Gabbott (1971). Changes in biochemical composition are usually reported as differences in the level of a given constituent (% dry weight), or as changes in biochemical content (weight per animal) (Giese, 1967).

Typically, the biochemical composition of bivalves undergoes marked seasonal changes associated with the annual reproductive cycle (Giese, 1969; Walne, 1970; Sastry, 1979). This cycle has been well documented for *Crassostrea gigas* (e.g. Masumota *et al.*, 1934; Quayle 1964; Walne, 1970; Whyte and Englar, 1982; Briggs, 1983; Muniz *et al.*, 1986). In autumn-winter reserves of glycogen are accumulated; in spring, gametogenesis reaches a peak of activity so that by early summer oysters are fully ripe and spawning. During this phase glycogen drops, while lipid concentrations are low and the flesh has a high water content. Autumn fattening then begins again.

Most of the studies show that the changes in body weight are mainly due to changes in carbohydrate content or glycogen content. The seasonal cycles for storage and utilization of glycogen reserves reflect the complex interaction between food supply, temperature, growth and annual reproductive cycle (Gabbott, 1976). The seasonal cycle of storage and utilization of glycogen reserves is closely linked to the annual reproductive cycle. The seasonal changes in lipid content of *M. edulis* show an inverse correlation with the change in glycogen content (Williams, 1969). The lipid level falls rapidly after spawning and then increases again as the gametes mature.

The seasonality of gametogenesis and the cyclic nature of energy reserves in marine mussels have been investigated by several researchers. These studies (Pieters *et al.*, 1979; Zandee *et al.*, 1980; Lowe *et al.*, 1982; Bayne *et al.*, 1983) demonstrate a complex relationship between reproductive activity and energy storage cycles (Gabbott, 1983).

Glycogen reserves are used for energy requirements when food is scarce or poor (Zwaan and Zandee, 1972; Gabbott and Bayne, 1973; Emmett *et al.*, 1987) but there is some evidence that protein reserves are also used at this time (Pieters *et al.*, 1979). Egg and sperm in bivalves are composed primarily of protein and lipid (Pieters *et al.*, 1980), so the cyclic pattern of lipid and protein content is correlated with the accumulation and shedding of gonadal products.

Ruiz *et al.* (1992) reported that high variation in carbohydrate levels during storage and gametogenetic development suggests that carbohydrates are the main respiratory substrate. In contrast, protein and lipid are important for supporting energetic cost during winter when available food is scarce, as indicated by low chlorophyll-a levels. Gabbott and Bayne (1973) showed a marked seasonal shift from reliance on carbohydrate as the main energy reserve in the summer, to a greater reliance on protein as the main reserve in the winter in *M. edulis*. However glycogen is the primary energy storage substrate in oysters, providing energy for many physiological processes, and is stored when food is abundant and later utilized in the production of gametes (Bayne, 1976; Gabbott, 1976, 1983).

Many studies of British lamellibranchs have revealed a decline in dry flesh weight during winter when shell growth is greatly reduced or has ceased, and prior to spawning. Such declines have been reported for *Cardium edule* (Hancock and Franklin, 1972), *Mercenaria mercenaria* (Ansell *et al.*, 1964), *Tellina tenuis* (Ansell and Trevallion, 1967) and *Donax vittatus* (Ansell, 1972). Dare and Edwards (1975) reported that dry flesh weight is highest in summer and autumn, when protein and carbohydrate are maximal, then decreases through the winter to a post-spawning minimum in spring; weight loss in winter results from rapid utilization of carbohydrate reserves and depletion of both protein and lipid content.

2.7. Condition Index

Condition measurement is particularly important in aquaculture, where it is used to describe the quality and quantity of the marketable product. Its use in environmental monitoring has also been suggested because reduction in condition is associated with physiological stress (Widdows, 1985). Seasonal cyclic fluctuations in condition index (CI)

could be explained partially by changes in salinity and the number of days within various temperature regimes (Austin *et al.*, 1993). Seasonal and regional variation in indices have been related to changes in the carbohydrate (glycogen) and protein fraction, and to a lesser extent with the amounts of lipids and minerals present (Ingle, 1949; Walne, 1970; Walne and Mann, 1975; Mann, 1978). These changes are associated with the accumulation or storage of nutrients to be used during winter, a differentiation of gonadal material and differentiation of gametes, spawning and reproductive period (Haven, 1960; Giese, 1969; Quayle, 1969; Walne, 1970; Mann, 1978; Gabbott, 1975, 1983; Gabbott and Stephenson, 1978).

CI generally shows a gradual rise as a result of feeding and accumulation of glycogen and other food reserves prior to spawning (Austin *et al.*, 1993). Changes in condition index are attributable principally to fluctuations in glycogen at the polluted site and protein at the clean site (Roper *et al.*, 1991). Pridmore *et al.* (1990) studied marine pollution effects on *C. gigas* condition and suggested that measures of condition for oyster may be useful in environmental monitoring. The measurement of condition often involves the estimation of flesh weight of the shellfish, together with the capacity of its shell valves, but it is only an approximate quantitative test (Williams, 1969).

Measurement of condition is a well established technique for assessing the “health” or fatness of bivalve shellfish (Roper *et al.*, 1991). A variety of different methods have been used for assessing condition based on physical, biochemical and physiological measurements (Hickman and Illingworth, 1980; Lucas and Beninger, 1985; Davenport and Chen, 1987). The result has been that different workers have drawn diverging conclusions as to the effects of parasitism by *Mytilicola*. Korrynga (1952) shown that very small number of parasites did have an adverse effect on mussel condition while Hepper (1955) published results indicating that parasitism did not necessarily cause loss of condition. Hepper (1955) concluded that if environmental conditions for mussel were good, they could withstand fairly heavy infections without suffering loss of condition.

Condition indices are regarded as useful measurements of the nutritive status of bivalves (Crosby and Gale, 1990). Condition index may also be employed as an assay for monitoring various pollutant and disease. In the early 20th century, a qualitative index of

bivalve condition referred to as the degree of fattening was employed (e.g. Moore, 1908). Savage (1925) attributed the fattening of an oyster to the accumulation of glycogen reserves. Galtsoff (1964) credits the first quantification of condition index to Grave (1911). This index was based on the percentage of the internal shell volume occupied by the oyster soft body tissue. Walne (1970), however, attributes the first quantitative index to Milroy (1909) who used an index based on wet soft body tissue.

The first definable quantitative dry weight condition index (CID) equation, as described by Higgins (1938) was as follows;

$$\text{CID} = \frac{\text{dry soft tissue (g)} \times 100}{\text{Internal shell cavity volume (ml)}}$$

The internal shell cavity volume in the equation is the difference between the volume of water displaced by whole live animal and the volume of water displaced by the shell alone. Walne (1970) followed the technique of pooling samples for dry weight and volumetric assessment of internal shell cavity volume, but increased the condition index by an order of magnitude by altering the formula as follows;

$$\text{CID} = \frac{\text{Dry soft tissue (g)} \times 1000}{\text{Internal shell cavity volume (ml)}}$$

Walne and Mann (1975) further modified this formula such that dry soft tissue weight was a function of dry shell weight as follows;

$$\text{CI} = \frac{\text{Dry soft tissue (g)} \times 1000}{\text{Dry shell weight (g)}}$$

Lawrence and Scott (1982) followed several years later with yet another revision of the condition index formula presented as follows;

$$\text{CI} = \frac{\text{Dry soft tissue weight (g)} \times 100}{\text{Internal shell cavity capacity (g)}}$$

The shell cavity capacity in bivalves in gram is determined by subtracting dry shell weight (g), from the whole live animal weight (g).

Volumetric condition index (wet meat volumetric condition index) (CIV) was measured by Lutz *et al.* (1980) as follows;

$$\text{CIV} = \frac{\text{Volume of soft tissue (ml)} \times 100}{\text{Volume of shell cavity (ml)}}$$

Condition indices in *Mytilus* vary according to body size (Baird, 1958), season (Mason, 1976; Dix and Ferguson, 1984; Rodhouse *et al.*, 1984 b), level of parasitic infection (Kent, 1979; Theisen, 1987) and with a local environmental conditions, especially the availability of food and degree of aerial exposure (Baird, 1966; Seed, 1980; Yamada, 1989). Seasonal changes are due to a complex interaction of those factors such as temperature, food supply and salinity which are thought to influence somatic growth and reproductive development.

2.8. Genetics of *Mytilus*

In the genus *Mytilus*, the systematic position of *M. galloprovincialis* (Lmk.) has been the object of numerous controversies (Bayne, 1976), whereby it has either been accorded a specific status, or has been integrated into *M. edulis* (Soot-Ryen, 1955; Beaumont *et al.*, 1989). Even though the morphoanatomical (Beaumont *et al.*, 1989), physiological (Seed, 1971), and genetic differences are marked, several studies have demonstrated that hybridization occurs between the two taxons at their synoptic sites- the British coast (Lewis and Seed, 1969; Ahmad *et al.*, 1977; Skibinski *et al.*, 1978) and French coast (Cousteu *et al.*, 1991).

There is a significant genetic differentiation throughout the geographic range of *M. edulis*; this can be observed over distances from a few metres to many kilometres. Second, individual loci may each show very different patterns of spatial differentiation, ranging from little or no genetic differences over great distances to very sharp step clines. Third, observed patterns of spatial genetic differentiation are very often statistically correlated with patterns of environmental variation (Boyer, 1974; Koehn *et al.*, 1976; Lassen and Turano, 1978; Theisen, 1978; Gartner-Kepkay *et al.*, 1980; Gosling and Wilkins, 1981; Skibinski *et al.*, 1983). Comparisons of shell characters between *M. edulis* and *M. galloprovincialis* have concentrated on sites where both species and their hybrids co-occur (Lewis and Seed,

1969; Seed, 1972, 1974, 1978; Verduin, 1979; Ferson *et al.*, 1985; Beaumont *et al.*, 1989). Seed (1968) reported that shell characters of mussels are influenced by the environmental factors.

The use of enzyme electrophoresis to characterise individual and population differences in genetic composition, together with multivariate techniques applied to both enzyme and morphometric phenotypes, have assisted greatly in elucidating the systematics and taxonomic status of species (e.g. McDonald and Koehn, 1988; Varvio *et al.*, 1988; McDonald *et al.*, 1991). Electrophoresis is a technique that has been extensively used to address questions of geographic variation between population and species level systematics in bivalves (Buroker *et al.*, 1979; Gartner-Kepkay *et al.*, 1980; Buroker, 1983; Skibinski *et al.*, 1983; Gosling, 1984; Blot *et al.*, 1988; McDonald and Koehn, 1988; McDonald *et al.*, 1991; Sarver and Foltz, 1993). The study of allozyme variation has proved very useful in clarifying the complex biosystematics of the mussel genus *Mytilus* (Varvio *et al.*, 1988). Earlier studies involving laboratory-reared bivalves have produced evidence for direct or indirect selection at a number of loci (Beaumont *et al.*, 1989; Adamkewicz *et al.*, 1984; Graffney and Scott, 1984; Hvilson and Theisen, 1984; Mallet *et al.*, 1985, 1986). Despite the large number of enzymes that are potentially available for study, in practice only a few have a sufficiently high level of variation to be of significant taxonomic value (e.g. Ahmad *et al.*, 1977; Skibinski, 1983; Grant and Cherry, 1985; Varvio *et al.*, 1988, Beaumont *et al.*, 1989); for more details see Seed (1992) and Gosling (1992). The study of allozyme variation in different populations of *Mytilus* has gone some way in helping to resolve the systematics of the genus (Gosling, 1992).

Skibinski *et al.* (1983) reported that *Mytilus edulis* is present all around the Britain and Ireland but at low frequency in SW England. *M. galloprovincialis* is present in SW England, the south and west coast of Ireland and the north-east of Scotland and England. It appears to be absent from Wales, the Irish sea coast of England and SE England. These results confirm some of the findings of Seed (1978) based on morphological and anatomical characters.

The performance of wild and cultured mussels and other bivalves under different conditions has been assessed through measurements of growth rate, biomass, condition

index, production, mortality, physiologic energetic and biochemical composition by several workers throughout the world (Walne, 1972; Widdows, 1978a, b; Jamieson *et al.*, 1975; Mohlenberg and Riisgård, 1979; Lutz, 1985; Riisgård, 1991; Okumus and Stirling, 1994; Stirling and Okumus, 1994)

There have been only a few published experiments on mussel culture in Scotland. The first one was carried out by workers from SOAFD Marine laboratory (Aberdeen) during 1966-1969. They investigated the growth of natural settled spat and retubed wild mussels in Lochs Sween, Ewe, Ardvar and Beag, and the feasibility of suspended mussel culture on the west coast of Scotland (Mason, 1969, 1972a, b; Mason and Drinkwater, 1981). Jones (1981) studied, the relationship between primary productivity and growth of cultivated mussels in Loch Sween. Growth, mortality and shell morphology were investigated in Loch Leven and Loch Etive in a suspended system by Stirling and Okumus (1994).

Similarly, some research has been done around the England, Ireland and Northern Europe, which has a similar climate. In Sweden, Loo and Rosenberg (1983) and Rosenberg and Loo (1983) studied energy flow, growth and production of mussels from settlement to harvest in a long-line system. Dare and Davies (1975) carried out a four year suspended culture trial to investigate settlement, growth, survival and biomass in North Wales (Menai Strait) using spat transplanted from The eastern Irish Sea. The transplanted spats reached a marketable size of 60 mm at between 1.5-2 years, but heavy losses occurred soon after transplantation. Dare and Edwards (1975) investigated seasonal changes in biochemical composition and flesh weight from natural beds in the Conwy Estuary, North Wales. Settlement, growth and production of natural mussels was studied in Morecambe Bay (Eastern Irish Sea) by Dare (1976). Rodhouse *et al.* (1984 a, b) studied food resources, gametogenesis and growth in natural and suspended cultured mussels in Killiary Harbour, Ireland. In another study Rodhouse *et al.* (1985) determined population structure, growth and survival of mussels and estimated production and nitrogen flow. Aldrich and Crowley (1986) investigated condition index and variability in mussels from rafts, commercial subtidal beds and unexplored intertidal beds around Ireland.

2.9. Objectives of Study

1. To study the main factors determining growth of mussels in two sea lochs (Loch Etive and Loch Kishorn) on the west coast of Scotland, by determining the following environmental parameters: temperature, salinity, Chlorophyll-a transparency, total suspended particle number, particulate organic matter and transparency
2. To study the effect of depth and position (in relation to the inflow and outflow current of the raft) on mussel growth, and of other environmental factors and natural mortality in the raft system
3. To gather basic information about the seasonal cycle of mussel length increase and somatic growth, condition index, biochemical composition, spat settlement and growth of seeds, carrying capacity and to discuss, in the light of these findings, ways to improve current mussel culture practices on the west coast of Scotland.
4. To study the influence of site on the growth, natural mortality, condition index and shell morphology of mussels by conducting cross-transplantation experiments between two different lochs.
5. To undertake a preliminary genetic study to determine any differences in genetic structure of mussels from the two sea lochs.

CHAPTER 3: MATERIALS AND METHODS

3.1. Environmental Parameters

3.1.1. Collection of Water Samples

Standard depths of 2 m and 6 m were selected for the collection of the water samples to avoid surface fluctuations in salinity. Most Scottish sea lochs are affected by freshwater run off from the surrounding mountains or rivers. As a result of the variable salinity at the surface, mussel farmers suspend mussels 1-2 m below the surface in Loch Etive. Therefore experimental lantern nets were hung 2 m below the surface in both sea lochs for comparison of all parameters. Duplicate water samples were collected by a Nansen type (designed by U.K. National Institute of Oceanography) sampling bottle. Water sampling is shown in Plate-5. The sampler was dropped to the desired sampling depth and 1 l of water was sampled by pulling a rope to close the stopper. The water samples were stored in 1 l plastic bottles, and transported to the Institute of Aquaculture in cool boxes. Some 2-3 drops of 10 g l⁻¹ magnesium carbonate were added to samples as fixative which were used for chlorophyll-a measurement. The water samples were collected generally in the 3th or 4th week of every month from May 1993 to May 1995.

3.1.2. Temperature and Salinity

On each sampling date, salinity and temperature were measured with a salinity temperature bridge (M.C.5 manufactured by Kent Industrial Measurements Ltd.) at the surface (0 m) and at 2, 4, 6 and 8 m depth to represent different rope lengths at the experimental sites.

3.1.3. Chlorophyll-a

Chlorophyll-a was measured spectrophotometrically according to Strickland and Parsons (1972) and Stirling (1985) as follows; duplicate 1 l water samples were each filtered through a 4.7 cm diameter Whatman GF/C filter paper. The filter paper containing the residue was soaked in a corked 15 ml plastic tube containing 90% acetone for twenty



Plate 5: Nansen type bottle was used for water sampling

hours at 4°C in a refrigerator in the dark (achieved by wrapping it in a black plastic bag). Tubes were taken out from the refrigerator, left at room temperature for 3-4 hours and centrifuged for 8-10 minutes at 3000 rpm. The supernatant was saved for chlorophyll-a (Ch-a) determination. A sample of supernatant was poured into a 4 cm path-length spectrophotometer cuvette and its absorbances at 663 nm and 750 nm were read against 90 % acetone in a similar reference cuvette. Finally a water quality laboratory computer program was used to calculate Ch-a, and the result expressed as Ch-a in $\mu\text{g l}^{-1}$. (see Stirling, 1985).

3.1.4. Determination of Seston, Particulate Organic Matter and Particulate Inorganic Matter

A numbered, 4.7 cm diameter Whatman GF/C filter paper was used for sample filtration after the following treatment. It was ashed at 450-500°C for 12 hours in a muffle furnace. Then filter paper was rinsed with distilled water, dried in an oven at 105°C for 45-50 minutes, cooled in a desiccator containing silica gel and weighed to the nearest 0.1 mg (W1).

Duplicate 1 l water samples were filtered. The filter paper containing the residue was dried in a oven at 105°C for 45-50 minutes. Thereafter, this was cooled in a desiccator for 30 minutes and weighed (W2). This was later incinerated in a muffle furnace at 450°C for 12 hours, after which it was cooled in a desiccator and weighed again (W3). Particulate organic matter (POM), particulate inorganic matter (PIM) and seston (total particulate matter) were calculated using the following formulae;

$$\text{a) Seston (total suspended particulate matter in the sample) (mg l}^{-1}\text{) = (W2-W1)/V}$$

$$\text{b) Particulate inorganic matter in the seston (mg l}^{-1}\text{) = (W3-W1)/V}$$

Where, V is volume of filtered water sample = 1 l

$$\text{c) Particulate organic matter (mg l}^{-1}\text{) = a - b (where; a = seston, b = particulate inorganic matter)}$$

Percentage of POM (POM%) within seston was calculated as follows:

$$\text{POM (\%)} = [\text{POM} / \text{seston}] * 100$$

3.1.5. Transparency or Secchi Disk Depth

A black and white painted Secchi disk was used to measure the euphotic zone. The disk was lowered into the water and the depth at which it disappeared was recorded (D1). It was lifted up and the depth at which it first reappeared was measured (D2). Transparency (Tr) was calculated as follows and expressed in metres:

$$\text{Tr} = (D1 + D2) / 2$$

3.1.6. Particle Number

250 ml sea water samples from a depth of 2 m and 6 m, were taken by water sampler and passed through a 150 µm nylon mesh into pre-washed plastic bottles. Then 2-3 drops lugol's iodine solution were added immediately and the samples transferred to the laboratory in a cool box.

A quantitative analysis of particle counts and size frequency distributions was carried out by an electronic particle counter (Counter Multisizer, Coulter Electronics, Luton, Beds, U.K). Cuvettes containing 15 ml of Isoton and a 5 ml sub-sample of seawater were each placed in the counter. Each sample was counted three times and the mean number of particles calculated, taking account of the relative amounts of sea water and Isoton.

3.2. Field Experiments

Two main field experiments were conducted during this study between May 1993 and May 1995. The first year experiments (May 1993 - August 1994) were related to growth, mortality, survival, condition index, production, biomass, spat collection and carrying capacity. The second year experiments involved mussel cross-transplantations in Loch Etive and Loch Kishorn. A genetics analysis of the mussels was also conducted between May 1994 and May 1995. Experimental animals, design and sampling procedures for the first year and second year experiments are described below.

3.2.1. Experimental Mussels

Experimental mussels used for this study were one year old rope-grown mussel from Loch Etive (darker and bluish mussels) (Plate-6) and Loch Kishorn (brighter and

brownish mussels) (Plate-7). In the first year of study, mussels were reared experimentally in lantern nets. One year old mussels for the lantern net experiments were collected from ropes at a depth of 2 m from Loch Etive and Loch Kishorn. Empty shells and very small or large mussels were eliminated to obtain a uniform size of live experimental animals. Growth, biomass and production were monitored on the culture ropes to determine the performance of the commercial culture facilities at the experimental sites.

3.2.2. Design of Experiments Materials and Sampling

3.2.2.1. Lantern Nets

Mussel culture in lantern nets was conducted from May 1993 to August 1994 in Loch Etive (LE) and Loch Kishorn (LK). The aim of the lantern net study was to find out the degree of natural mortality in the raft system and to check differences either in growth parameters or environmental parameters depending on depth and position on the raft (inflow and outflow points of the raft relative to current direction). One year old mussels *Mytilus edulis* were collected by hand at a depth of 1-2 m from culture ropes suspended from mussel rafts in Loch Etive and Loch Kishorn. Extra large and small mussels were removed to leave a relative uniform size. The mean lengths were: 24.04 ± 0.47 mm in Loch Etive and 26.61 ± 0.91 mm (mean \pm SE) in Loch Kishorn. Mussels were stored in four lantern nets hung from the raft at two different points below 2 m and 6 m in Loch Kishorn. Each lantern net contained three experimental trays (40 cm diameter plastic tray) at a density of 150 mussels per tray, or 450 stocked mussels per lantern net. Two lantern nets were suspended in the inflow and the outflow of the raft depths of 2 m and 6 m below the surface in Loch Etive (Fig. 8).



Plate 6 One year old seed mussels from Loch Etive



Plate-7. One year old seed mussels from Loch Kishorn.

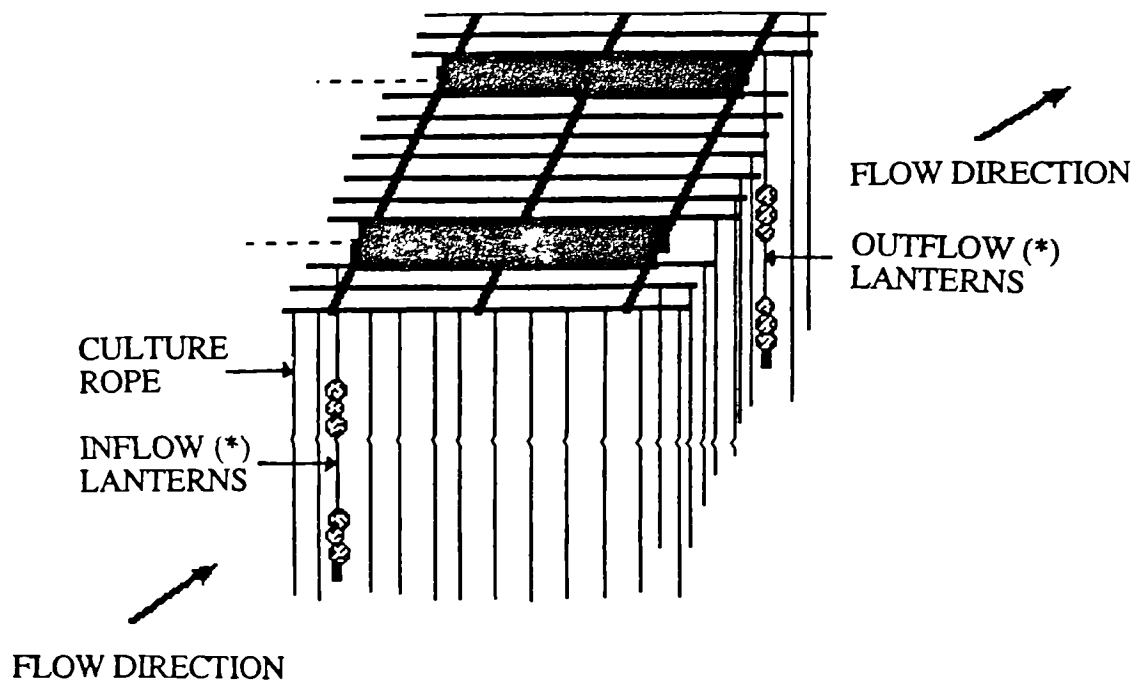


Fig. 8. Schematic representation of a mussel raft showing the position of the lantern nets in relation to the water flow direction through the raft created by currents; the water inflow and outflow points are indicated (*)

This system represented the condition found under commercial mussel culture and also allowed comparison of the effect of differences in salinity in relation to water depth.

Sampling was carried out monthly, 6-8 mussels from each experimental tray were randomly collected, at each of the inflow and outflow positions giving a total of 40-50 animals per sample from each loch. Inflow and outflow positioned mussels were combined to represent 2 m and 6 m of depths. In Loch Kishorn, in the lantern nets growth and mortality of mussels and comparison of the positions were ignored because a single mooring system was used to moor the raft.

A cross transplantation experiment was carried out between Loch Etive (LE) and Loch Kishorn (LK). The objectives were to monitor and compare, growth, condition index, natural mortality and changes in shell characteristics of native (LE: Loch Etive mussels and LK: Loch Kishorn mussels) and transplanted (LK-LE: mussels transferred from Loch Kishorn to Loch Etive and LE-LK: mussel transferred from Loch Etive to Loch Kishorn) mussel stocks. Two lantern nets were used to monitor mussels at each site, one for native stock, the other for transplanted stock. Each lantern net consisted of five 40 cm diameter plastic trays with an initial total of 1,600 mussels. All lantern nets were suspended 2 m below the surface and the nets were cleaned of fouling organisms during each sampling event. At each sampling, 60-70 mussels were taken for measurement of growth and condition factor (15 mussels were used for condition index every month for each stock).

On each sampling date at each site, empty shells were counted and removed to determine mortality and all lantern nets were brushed and cleaned of fouling organisms. All samples were placed in a labelled mesh bag and transported to the laboratory in a cool box. Mussel samples were kept in a cold room, with a temperature of $9\pm 1^{\circ}\text{C}$ in four aquarium tanks, each with 10 l capacity of seawater adjusted according to the site salinity, until the animals were measured.

3.2.2.2. Culture Ropes

Muckairn Mussel Farm and Kishorn Shellfish Farm were used to determine biomass, production and growth performance of mussels (*M. edulis*) under suspended culture (raft system) conditions in Loch Etive and Loch Kishorn respectively, from May 1993 to August 1994 (i.e. until marketable size). The experiments were carried out exactly under commercial conditions. Details about the raft culture set up were provided in Chapter-1.

One year old seed mussels were tubed into cotton “French socks” for culturing in late April 1993 and early May 1993 at the two site by the farmers. Polypropylene ropes (8-10 m) and plastic pegs (25 cm) were inserted into the socks while tubing was performed. Plate-3 shows ropes ready for tubing and the tubing process in Loch Etive and Loch Kishorn. The high tensile socks are made of cotton which decays after a few weeks in water, the mussels becoming attached to the ropes, pegs and to each other during this period. The mean number of mussel seeds per tube were 1,680 in Loch Etive and 1,615 in Loch Kishorn. Mean initial sizes were 25.70 ± 0.37 mm (mean+SE) at 2 m and 27.51 ± 0.53 mm at 6 m in Loch Kishorn, and 23.57 ± 0.39 mm at 2 m depth and 24.51 ± 0.47 mm at 6 m in Loch Etive.

Sampling was carried out at monthly intervals. On each sampling date at each site, three ropes were selected for sampling from the raft (one from inside, one from outside and one from in the middle of raft). Mussel ropes were lifted by hand and a 20 cm section each of rope was harvested from each depth. The samples from the three ropes were pooled to represent each depth. Each pooled sample was placed in a labelled mesh bag and transported to the laboratory in a cool box.

In the laboratory, mussels were counted and their shells scrubbed clean of encrusting organisms (e.g. barnacles, polychaetes, other epifauna and seaweeds). Subsamples were taken from these mussels for measurements of growth and condition index. They were stored in an aquarium in the cold room ($9 \pm 1^\circ\text{C}$) to prevent gonad release before measurement. The aquarium contents were aerated and the animals were fed algae (*Isocrysis galbana*) to keep them in normal condition. Mussels from the two depths were pooled to obtain the number of mussels per metre of culture ropes in the systems.

On each sampling date at each site, apart from sampling mussels for length, weight and condition index, temperature, salinity and transparency were also measured and water samples taken. In addition records were made of the general conditions, such as the prevailing weather and work on the raft; any heavy losses, predation by eider ducks, fouling by starfish and barnacles, or new spat settlement.

3.2.2.3. Spat Collectors

Spat collections and growth of spat were conducted monthly in Loch Etive and Loch Kishorn between April 1993 and April 1994. Polypropylene ropes 16 mm diameter and length 8 m were prepared at the Institute of Aquaculture. Plastic pegs (25 cm) were inserted into the ropes and at the end of each rope a 2-3 kg weight was attached to give strength to the spat collectors (ropes) against wave action. Six spat collectors were suspended from a spat collector raft in Loch Kishorn, three more from a mooring chain and another three from the inflow of the raft in Loch Etive in April 1993.

Samples were taken at monthly intervals from depths of 2 m and 6 m of water column to find out the effect of depth on spat settlement and spat growth. A 5 l capacity tank was filled with sea water then three spat collectors were lifted gently and spat from about 15-20 cm of rope from each depth were displaced into the tank by brush or hand depending on the spat size. Spat samples were transferred to 2 l plastic cups (pre-marked and filled by sea water) and placed inside an open cool box (without fitting the lids). Spat were transferred to the laboratory in a cool box and kept in a cold room. Counting of spat was done under a stereo microscope using different magnifications depending on the spat size. Spat length and height was measured under a microscope (Plate-8) to the nearest 0.01 mm. Shell length was determined by measuring the maximum anterior-posterior axis. Live weight was measured by weighing live animals with their shell closed after blotting them with tissue paper.



Plate 8. Mussel spat and the method of diameter measurement under a microscope.

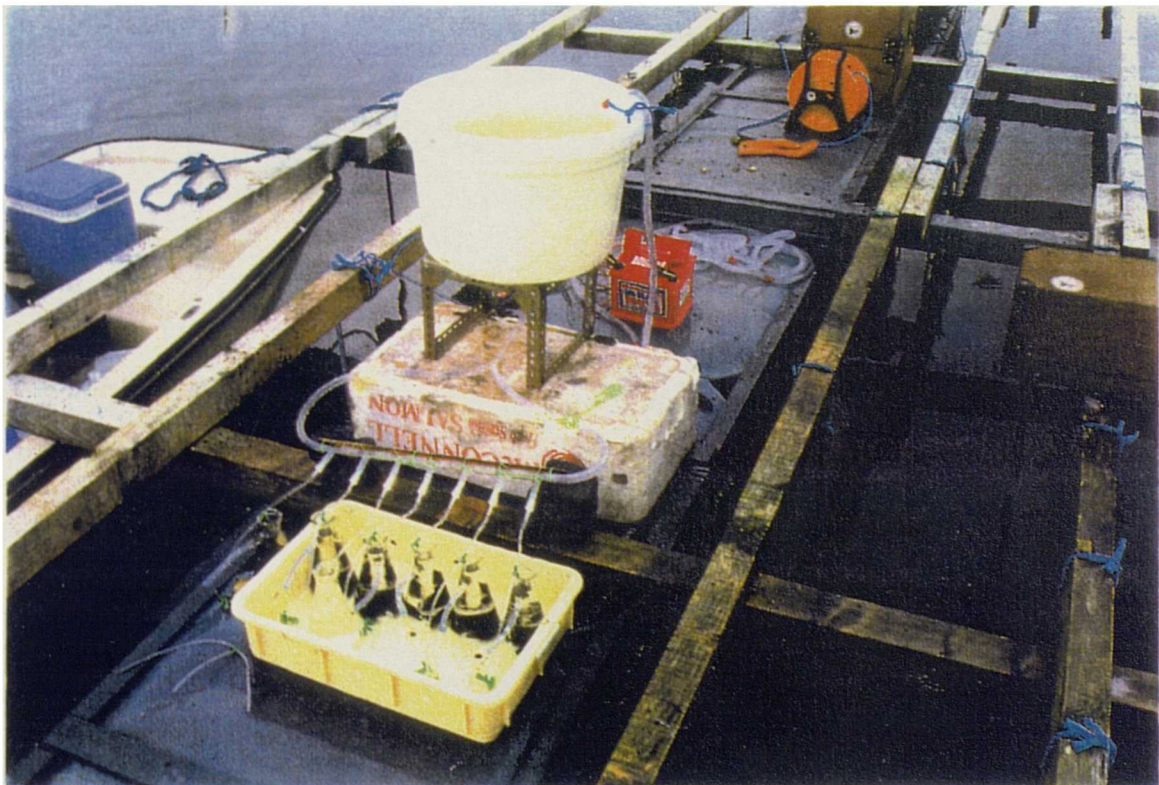


Plate 9. Experimental set up to measure filtration rate of mussels in the field.

Photograph shows a mussel raft at Loch Etive with apparatus used in the experiment (Fig 9 describes apparatus used)

3.3. Growth

Growth in bivalves is generally measured as the increase in shell length and height (oysters), but it can also be useful to measure growth in terms of shell and tissue weight increases. The growth parameters measured were: change in length (L), live weight (LW), wet meat weight (WMW), dry meat weight (DMW) and ash-free dry meat weight (AFDMW). The shell height (H) and width (W) of mussels were also measured during the experiment. LW and WMW were measured by weighing live animals and their meats after dissecting the mussels and blotting off excess water with tissue. DMW and AFDMW were measured after drying the meat (tissue) at 105°C for 20 hours in an oven and combusting at 500 C for 15 hours in a muffle furnace. Measurements of length, height and width were made to the nearest 0.1 mm by a means of vernier calipers.

Since all mussels were of the same approximate initial mean size ($P>0.05$) mussel size at each sampling date was considered an indication of the growth rate in relation to site and depth. Growth rates could then be followed in terms of change in the mean growth parameters over the time between each sampling date. From these data, a mean and standard error (\pm SE) were calculated for each sample and sampling month. The percentage increase in each parameter was calculated as the absolute growth estimate divided by its initial value.

Daily and monthly specific growth rate (SGR) were calculated from:

$$\text{SGR (\%)} = [(\ln L_2 - \ln L_1) / (T_2 - T_1)] * 100$$

where, L_1 and L_2 are mean shell length at time T_1 and T_2 in days (T_2-T_1 was an average 30 days) (Chatterji *et. al*, 1984).

Shell organic matter was estimated by two different methods:

- 1) The shells from each site were treated with concentrated hydrochloric acid (for 24-48 h) to remove calcareous matter and rinsed in distilled water. They were later transferred to an oven at 105 °C overnight and ash-free shell organic matter was determined after ignition in a muffle furnace at 550°C overnight (AFSW) (Rodhouse *et al.*, 1984a, b)
- 2) The ash- free shell organic matter (AFSOW) present in the shell was also estimated by igniting the dry shell (DSW) in a muffle furnace at 550°C overnight (Safae, 1992).

$$\text{AFSOW (\%)} = (\text{DSW} - \text{AFSW}) * 100$$

The amount of shell organic matter was used for estimation of biomass and production.

The relationships between total length and live mussel weight, shell length and dry meat, ash-free dry meat, dry and ash-free dry shell organic weights were determined by linear regression analysis according to the following formula:

$$W = a.L^b$$

or when written in logarithmic form

$$\text{Log}_{10} W = a + b \cdot \log_{10} L,$$

where; W is the weight in g, L is the shell length in mm, a and b are constants estimated by least squares regression.

In addition, the von Bertalanffy growth equation was fitted to the total length, using the following equation:

$$L_t = L_\infty (1 - e^{-k(t-t_0)})$$

$$k = \pm \log_e b$$

$$L_\infty = a / 1 - b$$

$$t_0 = (a - \log_e L_\infty) / k$$

where, L_t is the length at time t , L_∞ is the asymptotic (or maximum) length, e is the base of the natural logarithm, k is the rate at which the asymptotic length is approached, t is the time of observation and t_0 is the age at which $L_t = 0$ (Chatterji *et al.*, 1984).

3.4. Production and Biomass

Ash-free dry meat weight and shell organic weights were used to determine the biomass and production (Pr) on the rope grown mussels at both sites. The biomass is expressed as the mean ash-free dry weight (AFDW) of individual mussels g m^{-1} rope including shell organics, and production (Pr, in g m^{-1}) was calculated by using the following equations:

$$\text{Pr} = [(N_t + N_{t+1}) / 2] * (W_{t+1} - W_t)$$

and eliminated biomass (EB) due to natural mortality and losses:

$$\text{EB} = (N_t - N_{t+1}) * [(W_t + W_{t+1}) / 2]$$

where N is the number of mussels per metre of rope and W is the mean ash-free dry weight (including shell organic), at time t (Crisp, 1984).

The biomass was converted into energy units by multiplying energy values obtained from bomb calorimetry of dry mussel meat (see 3.6.1.6) by the ash-free dry weight values.

3.5. Survival and Losses

Cumulative survival, monthly survival and losses from the culture ropes were determined after the number of mussels on sampled rope sections were counted. In the lantern net experiments, the number of mussels stocked in each lantern net was known and it was possible to count and remove any empty shells on every sampling date.

Monthly calculation of cumulative survival was determined using the following equation:

$$\text{Survival (\%)} = (N_t / N_o) * 100$$

where, N_t is the number of mussels remaining after time t and N_o is the number of mussels at the beginning.

3.6. Condition Index and Biochemical Composition

One year old mussels were collected from a suspended raft culture system (from 2 m and 6m depth on the ropes) from Loch Etive and Loch Kishorn. These animals were used for condition indices and meat yield (from May 1993 to August 1994). Samples were transferred to the laboratory in a cool box. Condition indices, measurement of shell length and meat yield were carried out one day later. Twenty five mussels were used to measure condition index for each depth of the raft culture system. The volume of whole mussels was found by using a 50, 100 or 250 ml measuring cylinder. They were then opened and blotted with tissue paper, put into a measuring cylinder and their meat and shell volume measured by direct water displacement. Shell volume was measured in the same way. The shell cavity volume was estimated as the difference between the whole animal volume and shell volume. Meats were dried in a pre-weighed aluminum foil cup at 105°C for overnight to obtain their dry weight and moisture content.

Condition index wet meat volume (CIV) was assessed by measuring the volume of the shell cavity and the volume of meat (Lutz *et al.*, 1980):

$$\text{Wet meat volumetric condition index} = \frac{\text{Volume of soft tissue (ml)}}{\text{Volume of shell cavity (ml)}} \times 100$$

Condition index dry meat weight (CID) was found after drying the wet meat (Baird, 1958; Austin *et al.*, 1993; Lutz *et al.*, 1980):

$$\text{Dry weight condition index} = \frac{\text{Weight of dry tissue (g)}}{\text{Volume of shell cavity (ml)}} \times 100$$

Meat yield was estimated from following formula :

$$\text{Meat yield (\%)} = \frac{\text{Wet meat weight (g)}}{\text{Total weight (g)}} \times 100$$

3.6.1. Biochemical Composition

After determination of condition index and dry meat weight, the dry meat samples from 2 m and 6 m depth were pooled and ground by coffee grinder, then kept in stoppered bottles in a deep-freeze (-20°C) to await biochemical analyses. The samples were re-dried before biochemical analyses.

The relationship between condition indices, meat yield, biochemical composition and environmental factors were determined by using a Correlation Matrix.

3.6.1.1. Moisture

The moisture content of mussels was determined by drying the mussels as triplicate samples in a pre-weighed aluminium foil cup in an oven at 105°C overnight (about 20 hours) to constant weight. Moisture was expressed as a percentage of initial sample weight and calculated from the following formula:

$$\text{Moisture (\%)} = [(\text{Wet meat weight} - \text{Dry meat weight}) / \text{Wet meat weight}] * 100$$

3.6.1.2. Ash

Ash weight was determined by combusting a known dry weight of tissue at 500°C overnight in a muffle furnace and re-weighing the tissue. Ash was calculated as a percentage of dry meat weight in triplicate samples from the following formula:

$$\text{Ash (\%)} = (\text{ash weight} / \text{sample weight}) * 100$$

3.6.1.3. Protein

The micro-Kjeldahl method according to AOAC (1990) was used for determination of protein. Around 200 mg dry tissue sample was digested in concentrated sulphuric acid. Ammonia from the digest was released when reacted with 40 % sodium hydroxide and distilled, trapped in 2 % boric acid and quantified by titration against 0.2 molar hydrochloric acid. An automated Kjeltex Auto 1030 Analyser was used; samples were run in triplicate. Percentage, protein was calculated using the titre values for blank and samples as follows:

$$\text{Protein (\%)} = \frac{(\text{Sample titre} - \text{blank titre}) * 0.2 * 14.007 * 6.25 * 100}{\text{Sample weight}}$$

3.6.1.4. Lipid

The method employed was that of solvent extraction using a soxhalet extractor according to AOAC (1990) and duplicate samples. Around 1 g of dry meat sample was weighed into a glass thimble and corked with cotton. 500 ml petroleum-ether (40-60°C) was added to a pre-weighed cup. Both thimble and cup units were coupled to the Soxtec System 1043 Extractor and run according to the specifications of the operation manual from the manufacturer. The extracted lipid in the cup was weighed and expressed as a percentage of the original sample from the following equation:

$$\text{Lipid (\%)} = (\text{Lipid weight} / \text{Sample weight}) * 100.$$

3.6.1.5. Carbohydrate

About 3 mg dry samples in triplicate were used to determine total carbohydrate according to Dubois' phenol sulphuric method. Duplicate glucose standard solutions were prepared to obtain a calibration curve. 1 ml phenol solution (5 %) was added to each tube (15 ml glass tube) and placed into an ice bath for 5 minutes. While in the ice bath, 8 ml

concentrated sulphuric acid solution was added quickly to each tube. The solutions were allowed to stabilise then the optical density of each sample was read at 520 nm against a 0 mg blank. Standard optical density was plotted on a computer (or graph paper) against standard concentration. From the resulting curve, the sample concentrations were obtained. Results were expressed as percentage of dry sample from the following equation:

$$\text{Total Carbohydrate (\%)} = (\text{mg glucose in sample} / \text{sample weight (mg)}) * 100$$

3.6.1.6. Energy Content

The energy content of dry meat was determined by bomb calorimetry (Gallenkamp Autobomb CBA-500). Approximately 1 g samples were combusted with oxygen following the procedures in the operation manual. Initial and final temperatures were recorded. The temperature rise was substituted into the equation below to evaluate the energy content. The energy value determined from a benzoic acid standard of known energy was used to check the calibration accuracy.

$$\text{Energy (Kcal g}^{-1}\text{)} = \frac{(\text{Temperature difference} * 10.82) - 0.0896}{\text{Sample weight} * 4.18}$$

3.7. Carrying Capacity

3.7.1. Preparation of Experimental Mussels

This experiment was carried out in the field on a raft system under ambient conditions of food availability (Plate-9). Mussel samples were collected by hand (from depth of 2 m) from the commercial mussel culture rafts in Loch Etive and Loch Kishorn. Clusters of mussels was detached from ropes and individuals immediately removed by cutting the byssus threads with scissors. Twenty five individuals were immediately cleaned of fouling organisms to avoid possible clearance of food by these other species. Every effort was made to reduce any variation caused by factors other than filtration by the mussels. All experimental mussels were rope grown and approximately the same age of 2.5-3 years old. The shell length ranged from 51 to 62 mm (56.36 ± 0.63) in Loch Etive and from 52 to 67 mm (58.32 ± 0.77) in Loch Kishorn (each 11-15 g weight or about 1 g dry meat weight).

Six 500 ml Pyrex conical flask were used: five contained five mussels each and the sixth was used as a control (see Fig. 9 and Plate-9). Duplicate 1 l water samples were taken outlet of the flask to measure the filtration rate, assimilation, seston and particulate organic matter.

In order to determine seston, particulate organic matter (POM) and filtration rate, the experiment was conducted in Loch Etive and Loch Kishorn on two occasions, May and September 1994. During each visit, duplicate water samples were taken and transported to the Institute of Aquaculture in a cool box. The determination of seston and POM were carried out according to Stirling (1985) as described earlier in section 3.1.4.

Current measurement was carried out over the ebb and flood tide periods of neap and spring tides using a Brystoke BMF 208 current meter, from an anchored boat. A mean value for the currents measured was used as a value for “flow rate”.

The carrying capacity model used in this study was that developed by Incze *et al.*, (1981). The culture system used (Fig. 10) is three-dimensional, having a depth (h), a width (w) and length (l), with a water surface area (a) and face area ($A=h*w$) “facing the current”. The model attempts to determine the concentration of seston as water enters each tier as a function of (a) water flow rates; (b) original seston concentration (before entering first tier of culture units) and (c) the filtration of particles by all mussels in the up-current waters. The model has following assumptions:

- 1) The concentration of particles per litre is homogeneous as it enters each tier.
- 2) Flow is normal to the face of the tier.
- 3) Flow through the system is laminar.
- 4) Each mussel filters 1.5 and 1.75 l h⁻¹ in Loch Kishorn and Loch Etive respectively (average values).

Carrying capacity was based on seston concentration and estimated according to Incze *et al.* (1981). Provided seston concentrations are not reduced by more than 50 %, the number of tiers which can be included in an ideal system (one which from each tier was found from the following equation:

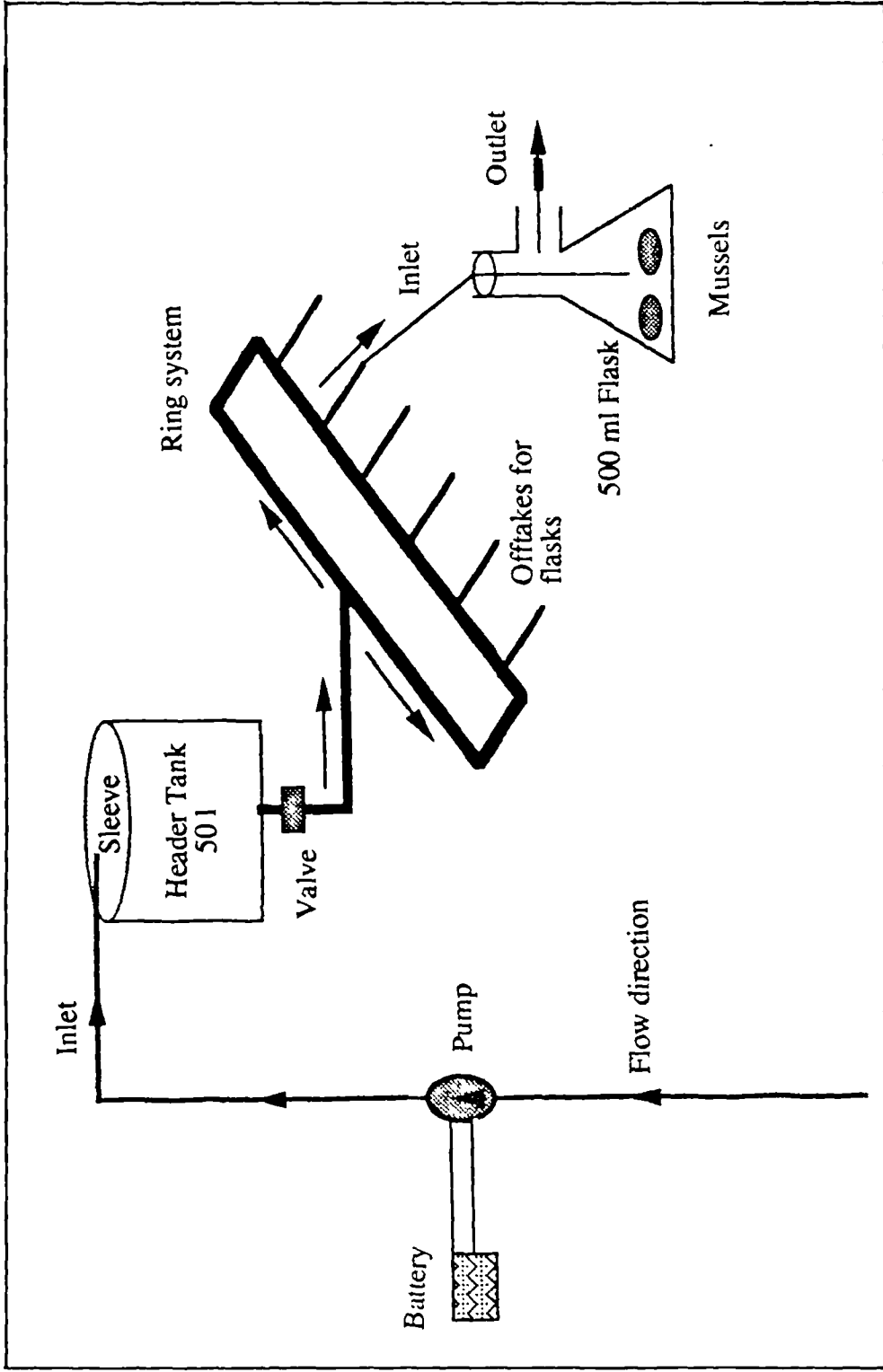


Fig. 9. Schematic diagram of the system used for taking water samples for the carrying capacity experiment.

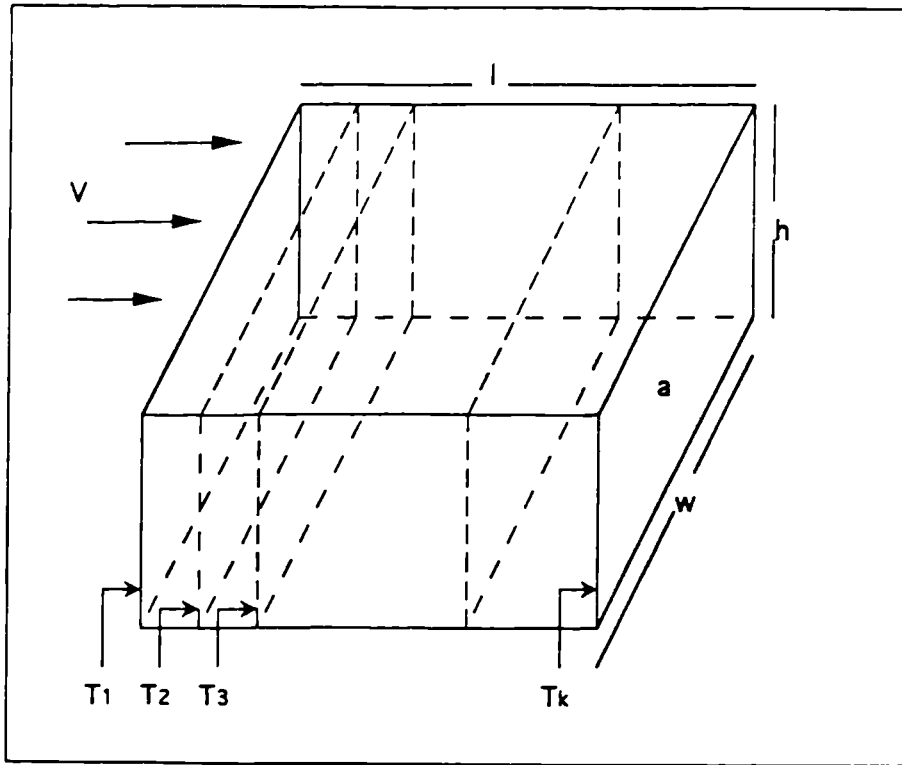


Fig. 10. Model for estimating the impact of intensive mussel cultivation in a raft system (after Incze *et al.*, 1981). T1, T2....Tk are tiers (=horizontal wooden beams, arranged in parallel, each supporting a row of mussel culture ropes, or droppers) of mussel culture unit; V is the flow of current.

$$n_2 = n_1 (N - \text{Filtration rate} \cdot M) / N$$

where

A: (m²), area of culture system normal to the flow, $a = w \cdot h$

V: (m h⁻¹), flow rate of water mass entering normal to face A

N: (l h⁻¹), volume of water entering through face A per unit time, $N = V \cdot A \cdot 10^3$

n_k : (mg l⁻¹), concentration of particles per litre flowing into tier T_k, K=1, 2,...

M: number of mussels suspended in each of the tiers

The second model for carrying capacity used was that according to Carver and Mallet (1990). The model is based on food supply (as POM) and food demand (as POM) by the mussels in the system. Multiplying the volume of water by the appropriate POM gives estimates of food supply. Multiplying the filtration rate (l h⁻¹) by the average of

concentration of POM gives daily ration (mg l^{-1}). Food supply (g POM week^{-1}) was divided by food demand (g POM kg^{-1} mussel) to obtain weekly estimates of carrying capacity for the system.

3.7.2. Filtration and Assimilation

The 30 l head tank was kept full continuously by pumping the water from a depth of 3 m and stirring. The outlet from the header tank fed six 500 ml Buchner flasks via a ring system controlled by a main valve (Fig. 9). Each off take from the ring was connected to a "T" adapter from which one tube ran vertically in to the flask. Flow rates were controlled with small individual taps. Mussels were placed in the experimental flask 5 with the in flow at the bottom and the out flow from the top of the flask. The mussels were allowed to acclimate for 30-40 minutes before water sampling. The system was covered by a paper carton to avoid effects from direct sunshine on the experimental mussels.

After all mussels had started active feeding, water samples were collected four times during a one hour period from the outflows of flasks including the control flask. At the end of the experiment mussel faeces were collected on to Whatman GF/C paper using a pipette, to calculate an assimilation rate.

Filtration rate (l h^{-1}) were calculated according to Carver and Mallet (1990) using the following formula;

$$\text{Filtration rate} = V * (\text{POM}_1 - \text{POM}_2 / \text{POM}_1)$$

where POM_1 is the average of POM concentration (mg l^{-1}) in the control chamber, POM_2 is the POM concentration (mg l^{-1}) in the experimental chambers and V is the flow rate ($\text{150 ml minute}^{-1}$) in the experimental chambers. Assimilation was calculated by comparing the POM to seston ratio in the faeces with the POM to seston ratio in the food (Conover, 1966).

3.8. Morphometric and Genetic Studies

3.8.1. Measurements of Shell Dimensions

After mussel tissue samples had been taken for electrophoresis, all remaining flesh was removed and the shell cleaned and dried. In total, 68 mussels from Loch Etive and 63 mussels from Loch Kishorn were used to measure shell characteristics. Shell length, height and width were measured by vernier caliper (to the nearest 0.1 mm), while the other shell traits were measured under a stereomicroscope (Fig. 11).

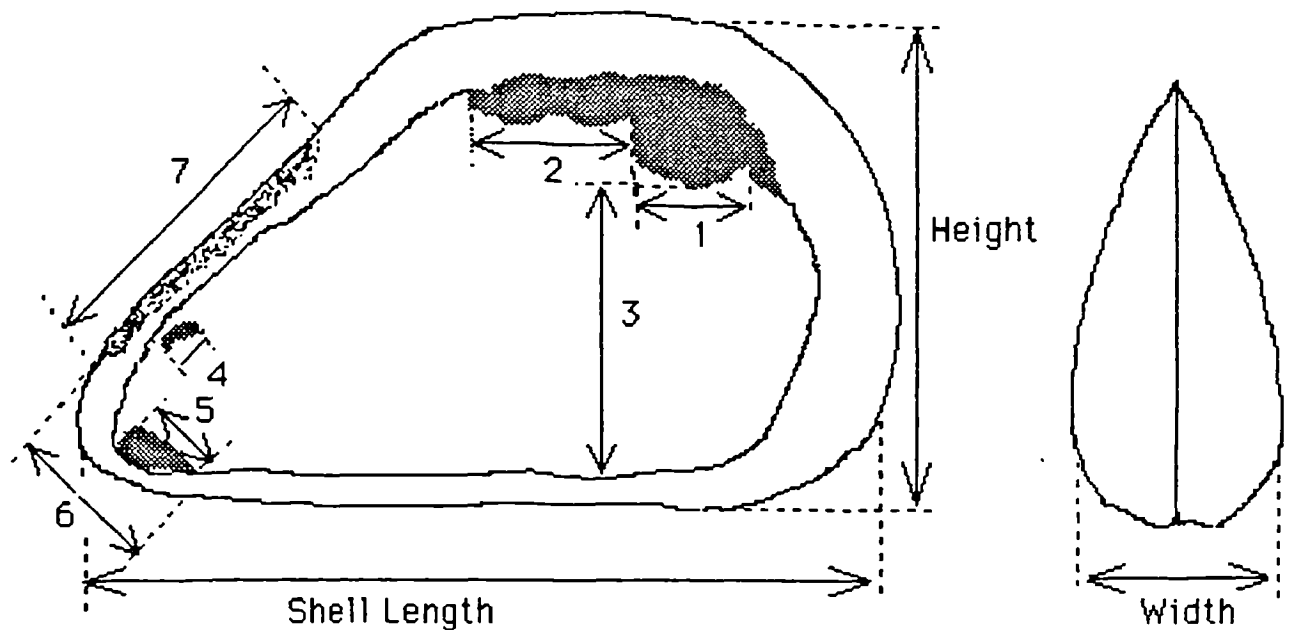


Fig. 11. Shell measurements taken for morphological analysis of Loch Etive and Loch Kishorn mussels.

Where,

- 1: length of posterior adductor muscle scar (pam).
- 2: length of posterior retractor muscle scar (lprs).
- 3: distance between ventral edge of posterior adductor muscle scar and ventral margin of shell (pam-vm).
- 4: length of anterior retractor muscle scar (arms).
- 5: length of anterior adductor muscle scar (aams).
- 6: length of hinge plate (hp).
- 7: ligament margin (lm).

3.8.2. Electrophoresis

Electrophoresis is now a very widely used technique to detect and measure biochemical genetic variation in animal populations (Ferguson, 1980). Horizontal starch gel electrophoresis was used as a technique to determine whether there has been any genotypic differentiation between Loch Etive and Loch Kishorn mussels. The general procedure for this technique is described below in three stages.

- i) Sample collection and preparation
- ii) Preparation of starch gels
- iii) Running, slicing and staining gels.

3.8.2.1. Sample Collection and Preparation

Mussel samples (2.5-3 years old) were collected from commercial raft cultured ropes by hand and transferred from Loch Etive and Loch Kishorn to the Institute of Aquaculture laboratory in a cool box. The valves were cleaned of fouling organisms (epibiotic growth). Each mussel was measured for shell length using calipers accurate to 0.1 mm and weighed to the nearest 0.01 g. Then the shells were kept until further measurement of other shell characteristics. A small piece of digestive gland and adductor muscle tissue was sampled from each mussel using a scalpel and scissors and put in small plastic tubes (Eppendorf). Samples were stored separately at - 70°C until needed.

For electrophoresis, tissues were taken from the deep freezer, thawed for a few minutes and then placed in ice. The samples were moistened with 0.5 ml of 0.1 molar buffer (pH: 8.0) buffer and purified sand was added to the tubes; the sample was then homogenized using a glass rod and centrifuged at 5,000- 6,000 rpm for 15 minutes. Samples were absorbed onto 10 x 2 mm pieces of Whatman No.1 filter paper.

3.8.2.2. Preparation of Starch Gel

About 66 g starch (Sigma Ltd.) was mixed with 500 ml of distilled water and 0.1 molar buffer (see Appendix 1) solution in a Buchner flask. The mixture was heated with constant rotation of the flask to an almost translucent jelly state, quickly degassed using a vacuum water pump and then poured into 6 mm thick gel frames. The gels, covered with a

glass plate, were allowed to set and cool overnight at room temperature, or for 1-2 hours at 4°C in a refrigerator.

3.8.2.3. Running, Slicing and Staining Gels

The gel was taken out of the frame and a parallel cut was made 3 cm from the edge to create an origin. The samples (filter paper) were placed along this cut with about 25-30 samples per gel and one tracking dye (0.1 % phenol blue) at the each end of the gel to indicate mobility through the gel. When all samples were correctly arranged, the frame was placed back on the gel and a perspex spacer positioned between the gel and frame to keep the sample slot closed (to keep the sample tight).

The gel was then placed in an electrophoretic bath with a buffer. A gauze wick soaked in the buffer was applied to either end of the gel to connect the gel and buffer. The gel was then covered with a polythene sheet to reduce evaporation and ice in a plastic bag was placed onto the polythene sheet to prevent heating of the gel. The bath tray was covered with a transparent lid and placed in a refrigerator at 4°C.

The gel was allowed to run for one hour with an electrical current of 45 mA. The filter papers were removed and the gel was run again overnight with a 30 mA current. The following morning, the gel was taken from the refrigerator and removed from the bath. It was then sliced horizontally into three slices, each of which could be stained for a different enzyme system. The appropriate stains (Appendix-1) for the enzyme system to be examined were weighed and mixed with staining buffer solution and 2 % agar (at approximately 50-60°C). This mixture was poured over the slice allowed to set and then incubated at 37°C until the banding patterns became visible. The electropherograms were then analyzed and scored for the respective genotypes and when necessary they were preserved in gel fixative solution (Appendix-2). Finally, they were dried to seal onto filter paper for storage.

3.9. Statistical analyses

Initial length differences between the sites were tested by one-way analysis of variance (ANOVA). The length-weight relationship were determined by using least squares

regression. Correlation matrix analysis was performed to evaluate the relationship between growth parameters, environmental factors, condition index and biochemical composition.

Two-way ANOVA was applied to determine the effect of depth and site on mussel growth and environmental factors. Two-way ANOVA was also used to determine effect of site and stock in cross-transplanted mussels. Student's *t* test was also applied to test differences between the depth in each site and between the sites. Both contingency table (Chi-squared) and ANOVA were used to test significance of variance in mortality.

Results from the biochemical composition analyses between the site were subjected to one way ANOVA at the 5 % probability level. Percentages were transformed by arc-sine transformation (Zar, 1984) prior to the ANOVA and reversed afterwards. One-way ANOVA was applied to test for differences in shell characteristics between the sites. All statistics were executed using a MINITAB software. Allele frequencies, heterozygosity and Hardy-Weinberg distribution were performed according to Ferguson (1980), while genetic identity and distance was calculated according to Nei (1972).

CHAPTER 4. RESULTS

In summary, the experiments conducted in year 1 (May 1993 to August 1994) and year 2 (May 1994 to May 1995) are listed below. Results from these studies are then presented in sections 4.1 to 4.7.

YEAR 1:

- a) Growth and production of mussels in raft cultured system in Loch Etive and Loch Kishorn.
- b) Effect of environmental factors, depth and position on raft on growth and mortality of cultured mussels
- c) Growth and mortality of mussels reared in lantern nets in Loch Kishorn.
- d) The effect of environmental factors on condition index and meat yield in Loch Etive and Loch Kishorn.
- e) Spat collection and growth of mussel seeds.

YEAR 2:

- f) Cross-transplantation of mussels between Loch Etive and Loch Kishorn.
- g) Carrying capacity estimation.
- h) Morphometrics and genetics.

4.1. Growth and Production of Mussels in Raft Cultured System in Loch Etive and Loch Kishorn

4.1.1. Environmental Parameters

The monthly changes in water temperature and salinity, seston, particulate organic matter (POM), POM %, chlorophyll-a (Ch-a), transparency (Secchi disk) and particle number (PN) were measured in Loch Etive and Loch Kishorn during the experimental period. Environmental factors were also measured at the inflow and outflow of the raft at depths of 2 m and 6 m in Loch Etive. Table-4 shows the average values of these environmental factors at 2 m and 6 m, plus pooled values for both depths in Loch Etive and

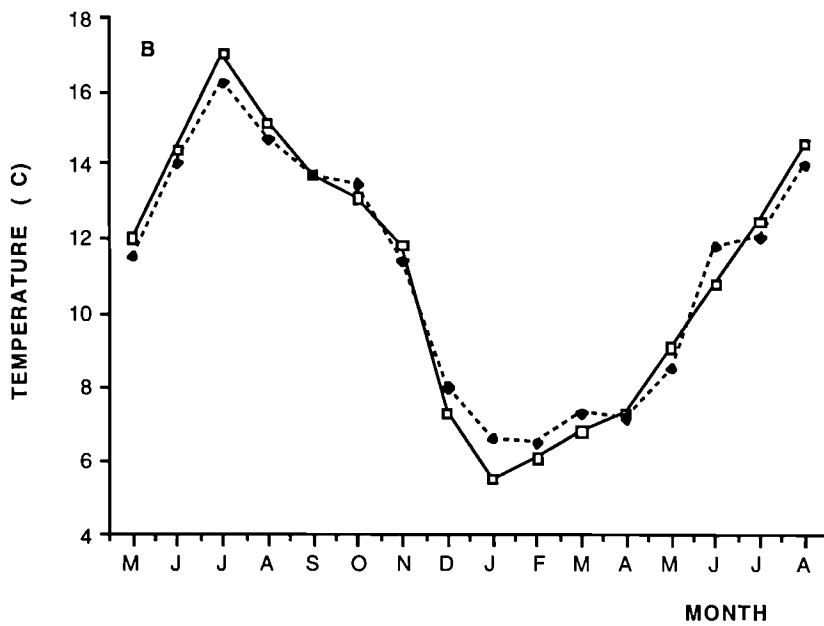
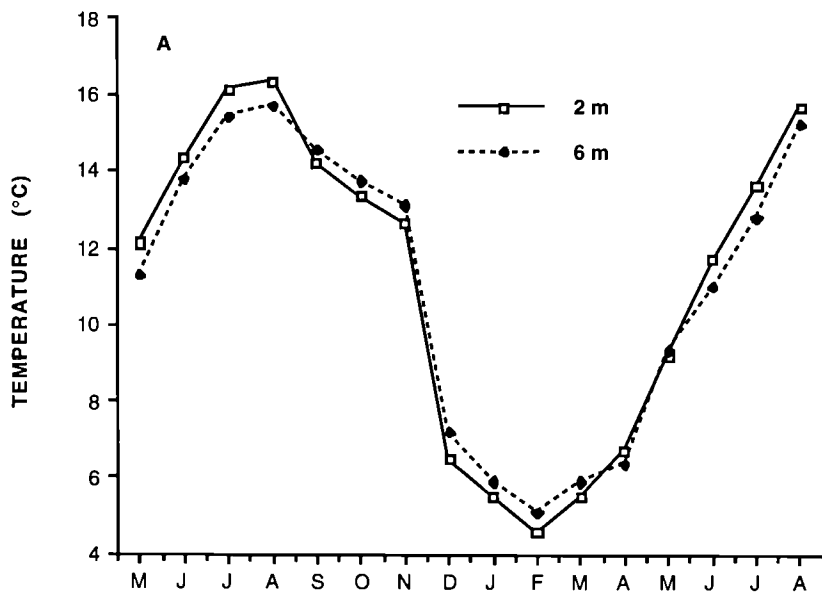


Fig.12. The annual sea water temperature cycle at experimental sites (A: Loch Etive, B: Loch Kishorn) at 2 m and 6 m depth at each month from May 1993 to August 1994.

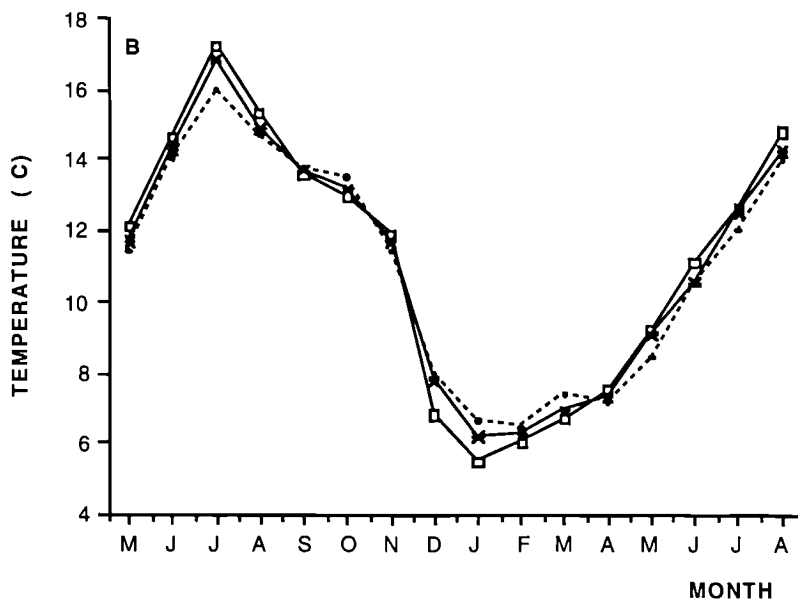
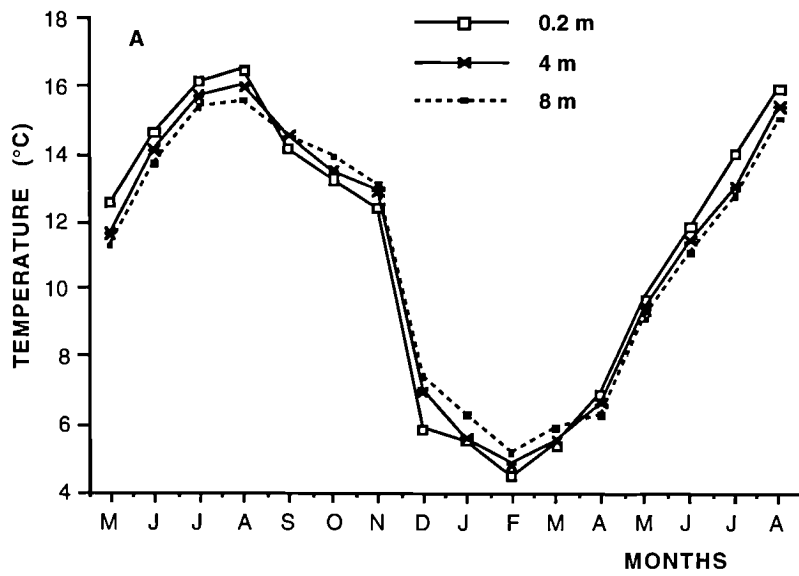


Fig.13. The annual sea water temperature cycle in Loch Etive (A) and Loch Kishorn (B); graphs show temperature at 0.2, 4 and 8 m depth in each month from May 1993 to August 1994.

Table 4. Mean (\pm SE) of monthly values of environmental parameters measured at 2 m and 6 m at each experimental site from May 1993 to August 1994. Superscript letters indicate one-way ANOVA comparisons between sites; those bearing different letters are significantly different at $P < 0.05$ or less. LE: Loch Etive, LK: Loch Kishorn.

Site	Temperature (°C)	Salinity (‰)	Seston (mg l ⁻¹)	POM (mg l ⁻¹)	POM% (µg l ⁻¹)	Ch-a (µg l ⁻¹)	PN	Transparency (m)
2 m	11.12 \pm 1.03	20.57 \pm 1.36	3.13 \pm 0.46	1.67 \pm 0.18	44.76 \pm 3.06	1.81 \pm 0.47		
6 m	11.02 \pm 0.96	22.68 \pm 1.18	2.93 \pm 0.41	1.41 \pm 0.14	43.13 \pm 3.06	1.81 \pm 0.54		
Mean	11.07 \pm 0.97 ^a	21.63 \pm 1.28 ^a	3.03 \pm 0.43 ^a	1.54 \pm 0.16 ^a	43.94 \pm 2.98 ^a	1.81 \pm 0.50 ^a	40098 \pm 2411 ^a	5.25 \pm 0.32 ^a
2 m	11.07 \pm 0.90	33.27 \pm 0.36	4.76 \pm 0.88	1.86 \pm 0.24	56.68 \pm 2.78	1.76 \pm 0.44		
6 m	11.06 \pm 0.81	33.79 \pm 0.25	4.91 \pm 0.90	1.80 \pm 0.21	51.91 \pm 2.65	1.68 \pm 0.50		
Mean	11.07 \pm 0.84 ^a	33.53 \pm 0.31 ^b	4.83 \pm 0.88 ^b	1.83 \pm 0.23 ^a	54.30 \pm 2.84 ^a	1.73 \pm 0.47 ^a	43761 \pm 4338 ^b	7.31 \pm 0.50 ^b

Loch Kishorn. Correlation matrices between the environmental factors for each site are shown in Tables 5 and 6.

4.1.1.1. Temperature

Fig. 12 show the monthly distribution of sea water temperature at depths of 2 m and 6 m in Loch Etive, while Fig. 13 show monthly values of sea water temperature recorded at the surface (0.2 m), 4 m and 8 m in Loch Kishorn. The seasonal cycle of temperature was very similar (not significantly different, $P < 0.05$) at all depths at both sites. Average values of environmental factors are given in Table-4. The average water temperature was 11.12 ± 1.03 at 2 m and 11.02 ± 0.96 at 6m in Loch Etive, while it was 11.07 ± 0.90 and 11.07 ± 0.81 at 2 m and 6 m, respectively in Loch Kishorn.

In Loch Etive, the lowest values were 4.6 and 5.1°C in February 1994, and the highest were 16.30-15.7°C at 2 m and 6 m, respectively in August 1993, while the lowest values of 5.5 and 6.6 °C in January 1994 and highest of 16.2 and 17.0°C at 2 m and 6 m, respectively were recorded in Loch Kishorn, in July 1993. The temperature of the surface (0.2 m) and at 2 m was slightly higher than that recorded at 6 m during the summer, but the temperature at 6 m was higher in winter compared to the surface temperature and at 2 m at both sites.

The relationships between temperature and other environmental factors are given in Tables 5 and 6. There was no evidence of any significant correlation between temperature, seston, POM and chlorophyll-a ($P > 0.05$) in Loch Kishorn. The lack of a clear relationship between temperature and these environmental factors might have been due to a high fluctuation in these parameters while temperature had clearly an annual cycle. However, temperature was correlated positively with salinity in Loch Etive ($r = 0.756$, $P < 0.001$) and Loch Kishorn ($r = 0.546$, $P < 0.05$). There was a sharp decrease in water temperature from November to December 1993 which was attributed to snow melting from the surrounding mountains.

Table-5. Correlation matrix (r) between environmental factors, mussel meat yield and Specific Growth Rate (in length) in Loch Etive. Degrees of freedom = 15. (* : $P < 0.05$, ** : $P < 0.01$, *** : $P < 0.001$). SGR: specific growth rate, SES: seston, POM: particulate organic matter, MY: meat yield in %, T: temperature, S: salinity, Ch-a: chlorophyll-a, PN: particle number, SEC: Secchi depth.

	SGR	MY	T	S	SES	POM	POM%	Ch-a	PN
MY	0.403								
T	0.625**	0.356							
S	0.486*	0.577*	0.756***						
SES	0.124	0.557*	0.057	0.307					
POM	0.094	0.045	0.060	0.267	0.932***				
POM%	0.174	-0.262	-0.264	-0.145	-0.120	-0.149			
Ch-a	0.187	0.251	0.211	0.154	0.547*	0.672**	-0.491*		
PN	0.096	0.342	0.428	0.207	0.307	0.243	-0.349	0.300	
SEC	0.105	0.069	0.232	0.332	-0.304	-0.362	0.134	-0.202	-0.396

Table-6. Correlation matrix (r) between environmental factors, mussel meat yield and Specific Growth Rate (in length) in Loch Kishorn. Abbreviations and superscripts are explained in Table-5.

	SGR	MY	T	S	SES	POM	POM%	Ch-a	PN
MY	0.843***								
T	0.691**	0.704**							
S	0.356	0.330	0.546*						
SES	0.099	0.2273	-0.098	0.093					
POM	0.197	0.323	0.015	0.108	0.940***				
POM%	-0.890	-0.227	0.064	-0.101	-0.745**	-0.634			
Ch-a	0.422	0.451	0.204	0.097	0.841***	0.792***	-0.546*		
PN	0.073	0.334	0.254	-0.62	0.348	0.468	-0.113	0.276	
SEC	-0.360	-0.197	0.216	0.353	-0.400	-0.368	0.107	-0.384	-0.284

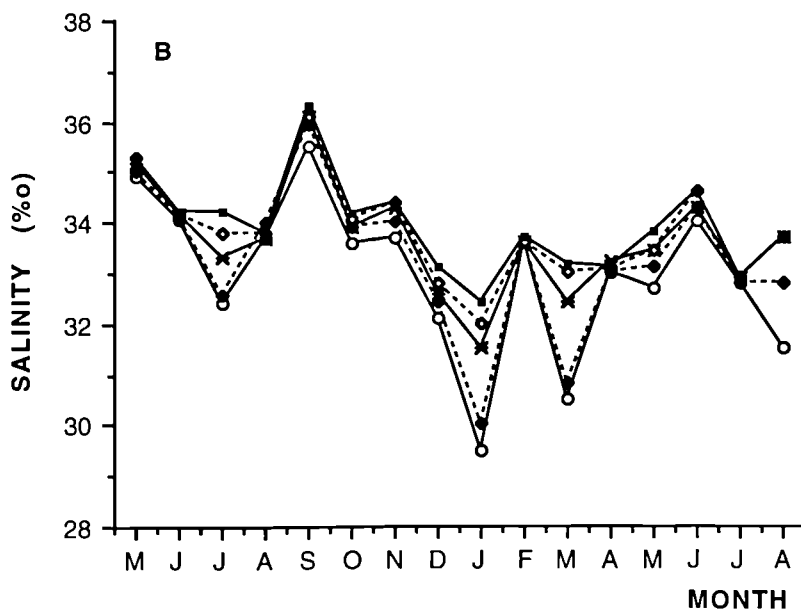
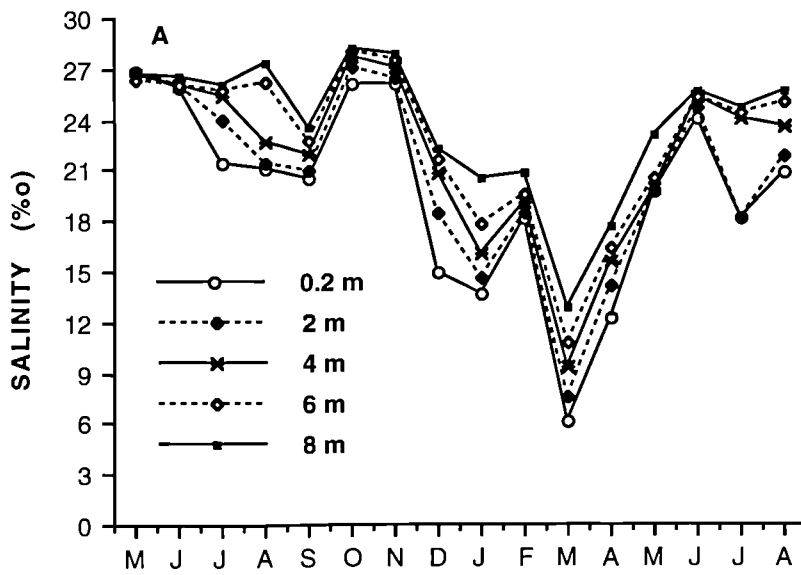


Fig.14. Monthly distribution of salinity at 0.2, 2, 4, 6 and 8 m depth in Loch Etive (A) and Loch Kishorn (B) from May 1993 to August 1994.

4.1.1.2. Salinity

Fig. 14 show the monthly distribution of salinity at five different depths (surface, 0.2, 2, 4, 6 and 8 m); mean salinity values at 2 m and 6 m are given in Table-4 for Loch Etive and Loch Kishorn. In general, the salinity, especially at the experimental depths (2 and 6 m) was higher in the summer and autumn than in spring and winter. However, there were high fluctuations between the months in the same season due to melting snow and freshwater run-off from the surrounding mountains. Very little variation was observed between different depths in Loch Kishorn ($P>0.05$) while the variation was significant between the surface and 6 m and 8 m in Loch Etive. Differences in the salinity values between the two sites was also significant ($P<0.05$).

Mean values of salinity are given in Table-4 for depths of 2 m and 6 m at both sites. The lowest salinity values were recorded with a mean of 7.5 ‰ at 2 m in Loch Etive, in April 1994 and with a minimum of 30 ‰ in Loch Kishorn, in January 1994. Salinity had a maximum value of 28 ‰ at 6m in Loch Etive in October 1993, and of 36.1 ‰ at 6m in Loch Kishorn in September 1993. Mean surface (0.2 m) salinities were found to be 19.64 ± 1.45 ‰ with a minimum 6 ‰ in Loch Etive and 33.0 ± 0.38 ‰ with a minimum 29.5 ‰ in Loch Kishorn ($P<0.001$).

4.1.1.3. Total Seston

The monthly distribution of seston is depicted in Fig. 15 and its relationship with other environmental factors in Loch Etive and Loch Kishorn is shown in Tables 5 and 6 respectively. In general, the seston had a similar pattern with POM and chlorophyll-a (Ch-a). It had a minimum value of 1.2-1.3 mg l^{-1} in December in Loch Kishorn and Loch Etive respectively, while maximum values were recorded of 8.5 mg l^{-1} in June and 15.20 mg l^{-1} in May 1994 in Loch Etive and Loch Kishorn respectively. There were great fluctuations in seston values between the sampling periods . The mean values for seston were 4.76 ± 0.46 mg l^{-1} at 2 m and 2.93 ± 0.41 mg l^{-1} at 6 m in Loch Etive. Seston reached a maximum value together with the peak in Ch-a in Loch Kishorn and one month later than Ch-a in Loch Etive. Seston values showed significant relationship with POM in Loch Kishorn ($r=0.940$,

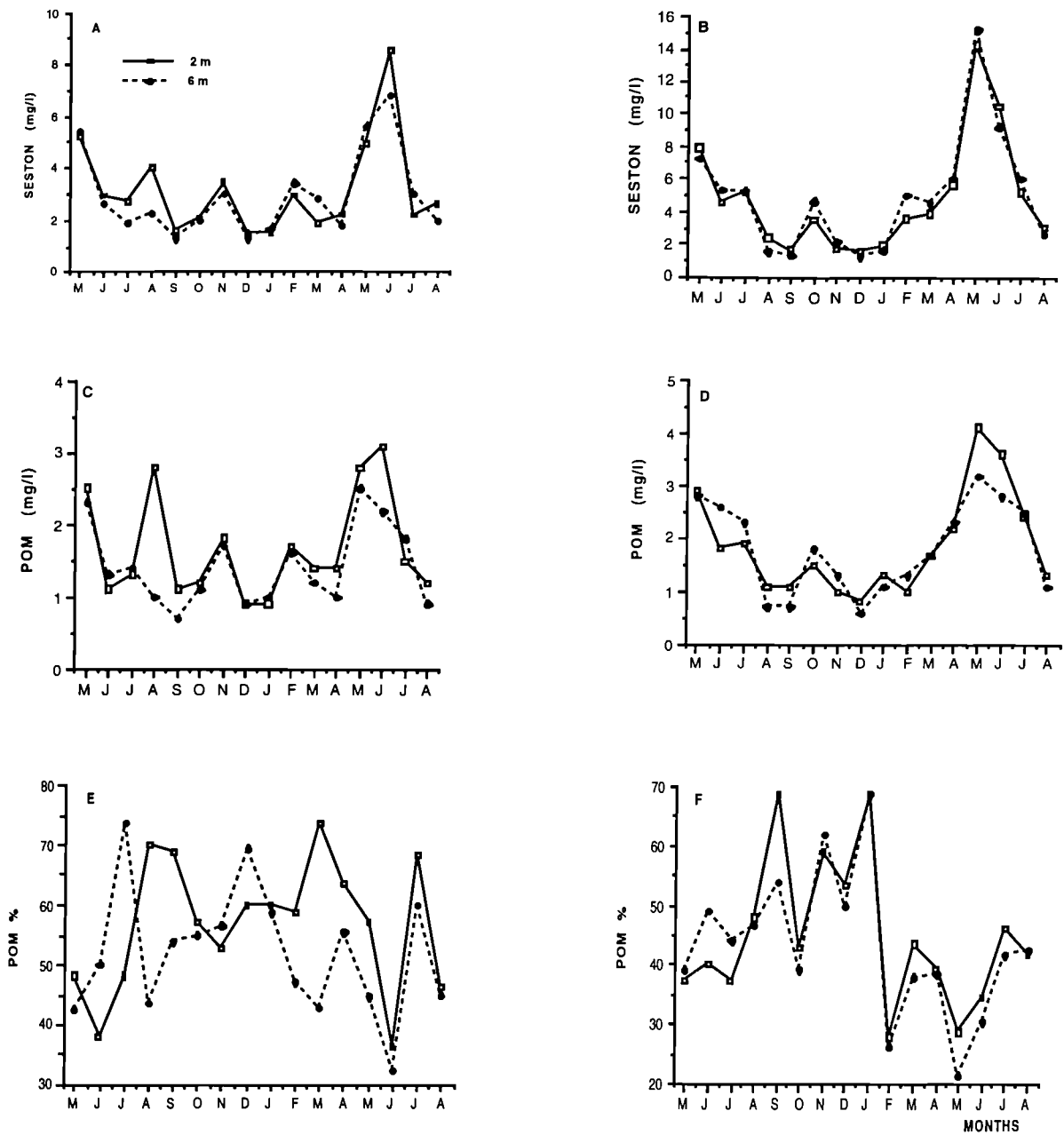


Fig.15. Monthly variation in total seston concentration (A: Loch Etive, B: Loch Kishorn), POM (C: Loch Etive, D: Loch Kishorn) and POM% (E: Loch Etive, F:Loch Kishorn) at 2 m and 6 m depth between May 1993 and August 1994.

$P < 0.001$) and Loch Etive ($r = 0.932$, $P < 0.001$). Seston had also a significant relationships with Ch-a in Loch Kishorn ($r = 0.841$, $P < 0.01$) and Loch Etive ($r = 0.547$, $P < 0.05$). Seston was mainly affected by the cycle of phytoplankton bloom and freshwater run-off from the surrounding mountains. The seston value was found to be significantly higher in Loch Kishorn than Loch Etive ($P < 0.05$), but depth had no effect on the seston level ($P > 0.05$).

4.1.1.4. Particulate Organic Matter (POM)

The monthly distribution of particulate organic matter (POM) and percentage of particulate organic matter in seston (POM%) values are shown in Fig. 14 and the relationship between POM and other environmental factors is shown in Tables 5 and 6. In general, POM was found to be higher in the spring and summer months compared with the winter period. In May 1994 it was affected by algal bloom and run-off. Neither site nor depth had a significant effect on POM. Mean values of POM at 2 m were higher than at 6 m at each site but not to a significant extent ($P > 0.05$). The amount of POM was significantly correlated with Ch-a and seston at both sites.

4.1.1.5. Percentage of Particulate Organic Matter (POM %)

Monthly distribution of POM % is shown in Fig. 15 and mean values are given in Table-4. Two-way ANOVA results show that neither site or depth had a significant effect on POM % ($P < 0.05$). However, mean POM % was found to be higher in Loch Etive (53.46 ± 2.84) than Loch Kishorn (44.93 ± 2.98) while in both sites POM % was higher at 2 m than 6 m. The relationship between POM % and the other environmental factors is given in Tables 5 and 6. It had a inverse relationship with Ch-a, seston and POM at both experimental sites. POM % ranged from 25.86 to 69 % in Loch Kishorn and from 24.91 to 65.61 % in Loch Etive. The organic matter in seston was observed to be very high in winter when Ch-a was almost absent. This result shows that freshwater run-off carries organic matter into the loch from the surrounding land and mountains.

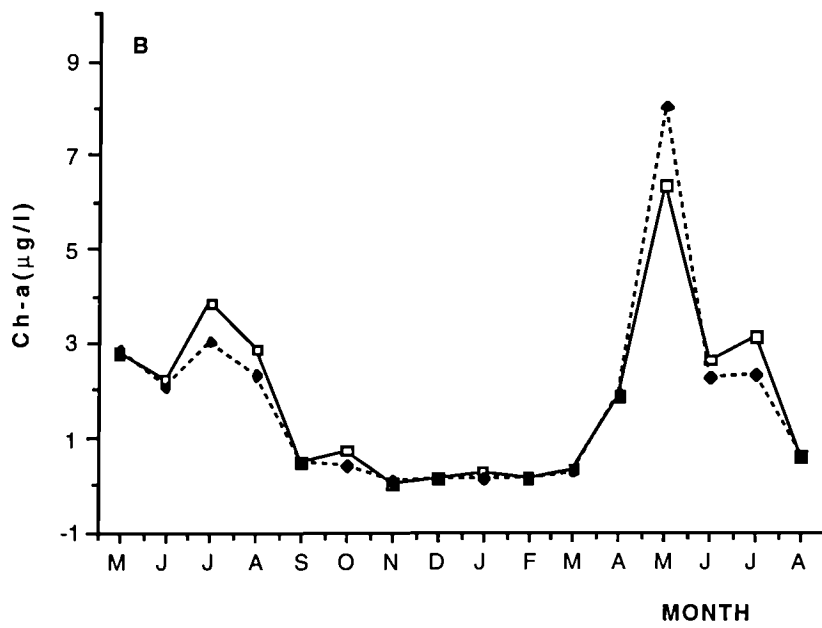
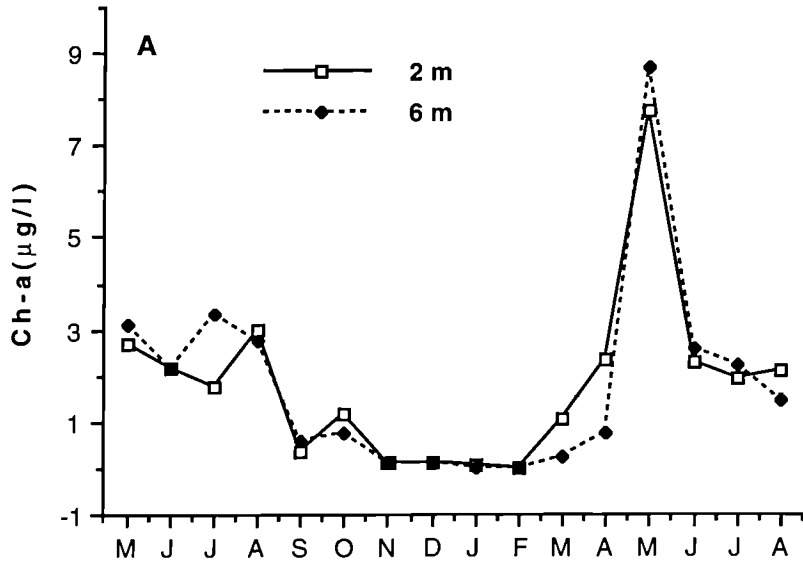


Fig.16. Monthly distribution of chlorophyll-a (Ch-a) concentrations in Loch Etive (A) and Loch Kishorn (B) from May 1993 to August 1994.

4.1.1.6. Chlorophyll-a

The monthly distribution of chlorophyll-a (Ch-a) is shown in Fig. 16 and the mean values for 2 m and 6 m and pooled values for both sites are given in Table-4. At both sites and depths the seasonal cycle of Ch-a distributions followed very similar patterns. Ch-a values were higher in spring and summer and low to almost absent values in winter. Ch-a content started to decline in August and reached a minimum $0.04 \mu\text{g l}^{-1}$ in November in Loch Kishorn and $0.02 \mu\text{g l}^{-1}$ in February in Loch Kishorn. A steady increase commenced at both sites in March-April 1993 and reached maximum values of $8.03 \mu\text{g l}^{-1}$ at 6 m in Loch Kishorn and $8.64 \mu\text{g l}^{-1}$ in Loch Etive. Mean Ch-a content was found to be $1.81 \pm 0.5 \mu\text{g l}^{-1}$ in Loch Etive and $1.73 \pm 0.47 \mu\text{g l}^{-1}$ in Loch Kishorn. Neither depth or sites had a significant effect on Ch-a ($P > 0.05$). As mentioned before, Ch-a had a positive relationship with seston ($r = 0.547$, $P < 0.05$) and POM ($r = 0.672$, $P < 0.01$) in Loch Etive, while Ch-a had an even stronger positive relationship with seston ($r = 0.841$, $P < 0.001$) and POM ($r = 0.792$, $P < 0.001$) in Loch Kishorn (Table-5).

4.1.1.7. Transparency (Secchi Disk)

Fig. 14 shows the monthly distribution of transparency in Loch Etive and Loch Kishorn. Transparency ranged from 3.5-8.75 m with a mean 5.75 ± 0.32 m in Loch Etive, while it ranged from 4.5 to 10.5 m with a mean 7.31 ± 0.5 m in Loch Kishorn. Differences between the sites were found to be significant ($P < 0.01$). There were some fluctuations between the sites during the same sampling month which was possibly due to changes in phytoplankton and weather conditions. Transparency was mainly affected by phytoplankton bloom and weather conditions over the experimental period. The relationships between transparency and the other environmental factors are depicted in Tables 5 and 6. Although slightly negative relationships were found between transparency, seston, POM, Ch-a and PN at both sites, these were not significant ($P > 0.05$).

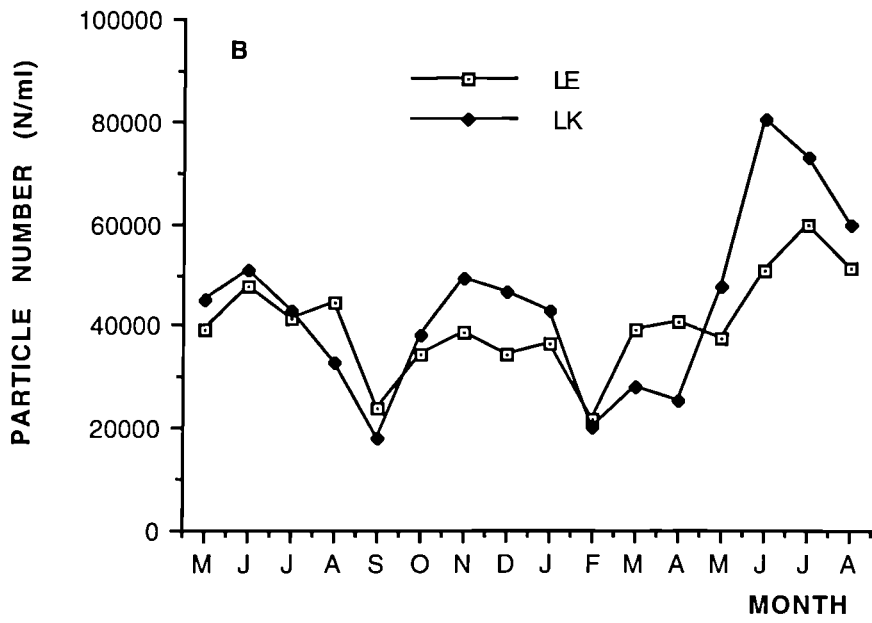
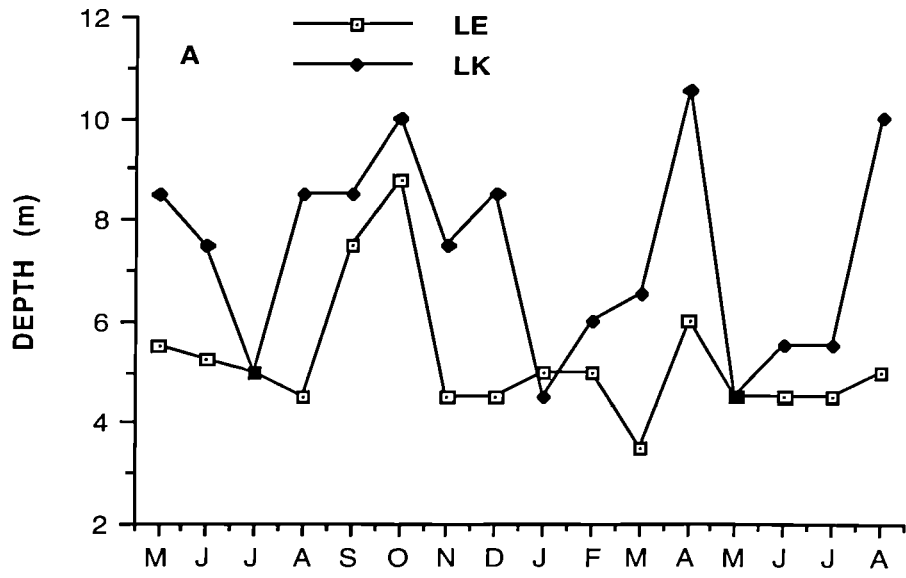


Fig.17. Monthly Secchi disk depth or transparency (A) and particle number (B) at Loch Etive (LE) and Loch Kishorn (LK) from May 1993 to August 1994.

4.1.1.8. Particle Number

Particle counts were carried out only during first year of experimentation. Monthly distribution of particle number (PN) is shown in Fig 17. The monthly variation in particle number was found to be significant ($P < 0.001$) within a single site. Average values for particle numbers were $40,098 \pm 2411$ number ml^{-1} and $43,761 \pm 4.338$ number ml^{-1} in Loch Etive and Loch Kishorn, respectively ($P < 0.01$). Particle number ranged from 21,464 to 59,536 number ml^{-1} in Loch Etive, while it ranged from 18,072 to 80,224 number ml^{-1} in Loch Kishorn. No significant correlation was found between PN and other environmental factors (Tables 5 and 6) but mainly it was affected by phytoplankton bloom, seston and POM in the both sites. In general when Ch-a was high, PN was also found to be high.

4.1.2 Growth

Shell length (L) and somatic (live weight: LW, wet meat weight: WMW, dry meat weight: DMW and ash-free dry meat weight: AFDMW) growth for rope cultured mussel populations were followed by monthly sampling in Loch Etive and Loch Kishorn from May 1993 to August 1994.

4.1.2.1. Shell Growth

The initial length and length frequency changes in distributions of the rope cultivated mussel populations are given in Figs. 18 and 19 for Loch Etive and Loch Kishorn. The main changes in the population structure took place during the summer (May-September 1993); size range shifted from around 16-34 mm to 34-54 mm in September in Loch Etive. However, changes in the population structure were small between September and January due to lack of food and low temperature, the shift being only from 34-54 mm to 40-56 mm.

When the water temperature increased and food was freely available from May 1994 to August 1994, growth rate increased and the size range measured increased to 46-62 mm with a mean of 55.05 ± 1.75 mm. Over a 15 month experimental period, the total mean length increase was 31.01 mm and the average monthly increase was 2.07 mm.

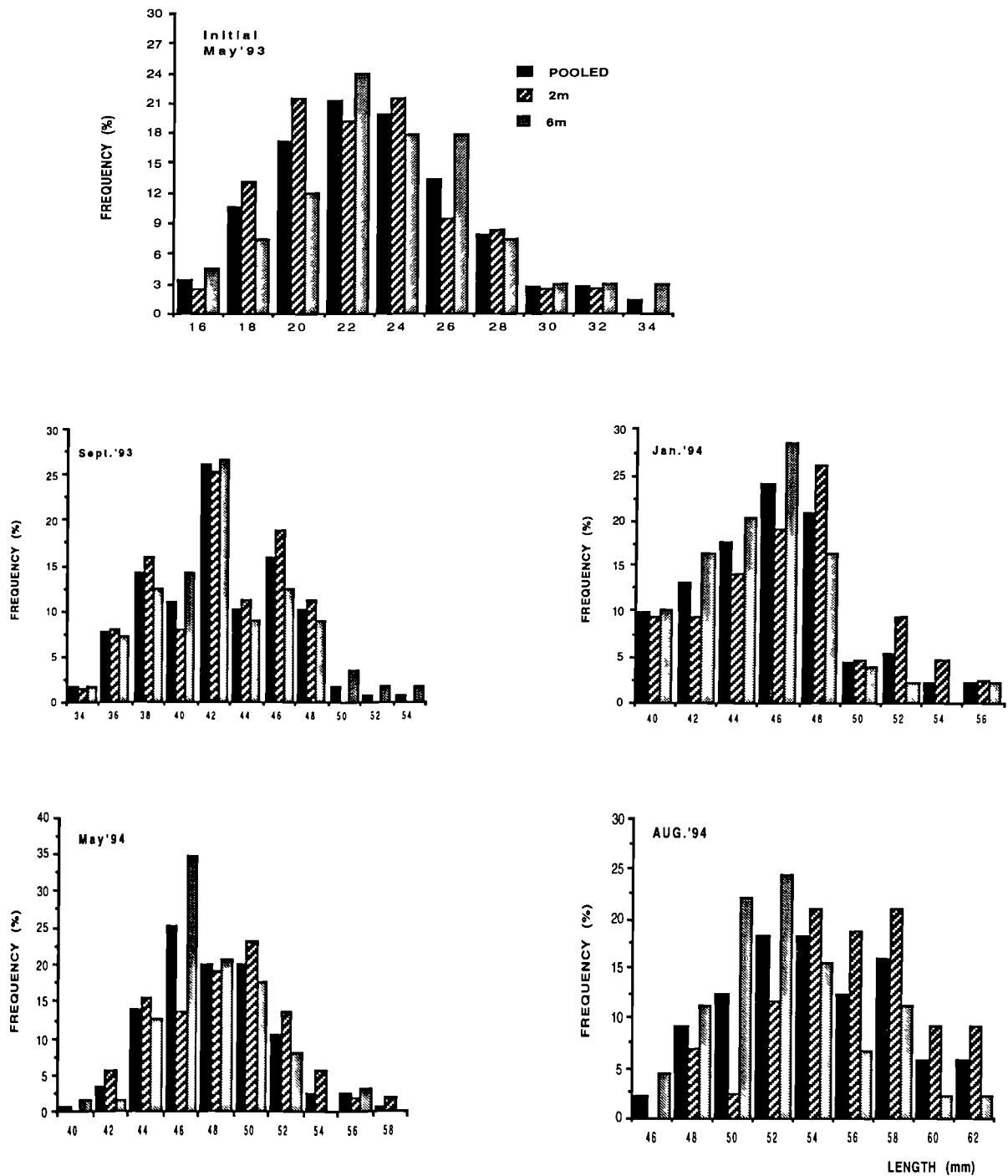


Fig.18. Changes in the size frequency distributions of experimental mussels in Loch Etive between May 1993 and August 1994.

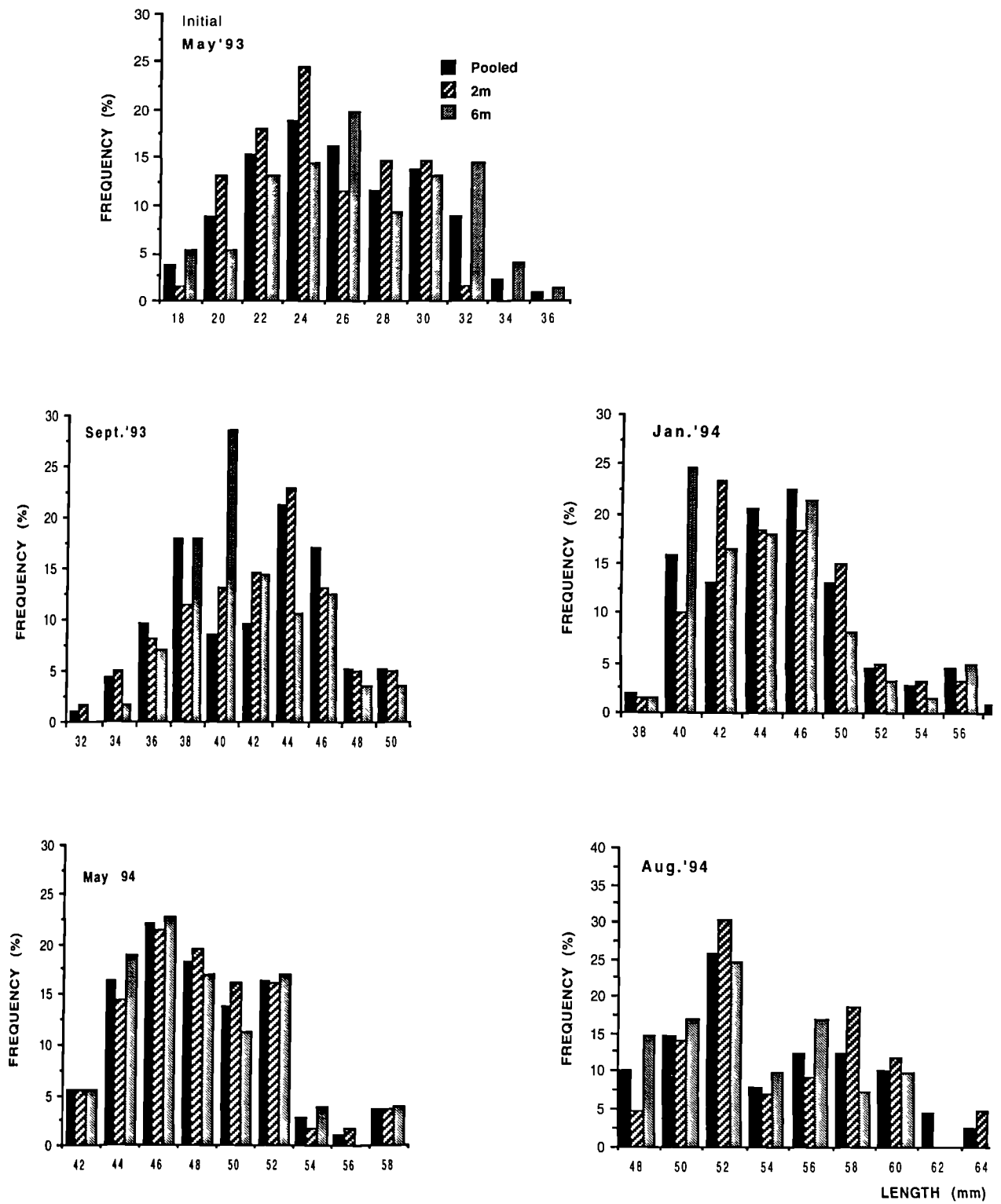


Fig.19. Changes in size frequency distributions of experimental mussels in Loch Kishorn between May1993 and August 1994.

Table-7. Average shell lengths (L±SE; mm) at 2 m and 6 m and pooled (2+6 m) at each sampling date and monthly growth increments ($\Delta L=L_2-L_1$; mm) of experimental mussels in Loch Etive between May 1993 and August 1994. N is monthly sample size, L is length of mussels.

Month	2 m			6 m			POOLED		
	L±SE	ΔL	N	L±SE	ΔL	N	L±SE	ΔL	N
May	23.57±0.39		84	24.51±0.47		74	24.04±0.47		158
June	26.19±0.41	2.62	65	26.53±0.43	2.02	58	26.36±0.17	2.32	123
July	33.93±0.51	7.74	58	33.56±0.56	7.03	58	33.75±0.19	7.39	116
August	37.91±0.56	3.98	61	37.93±0.49	4.37	62	37.92±0.1	4.18	123
September	43.17±0.49	5.26	63	43.52±0.58	5.58	57	43.34±0.17	5.42	120
October	44.78±0.58	1.61	58	44.60±0.39	1.09	65	44.69±0.09	1.35	122
November	45.28±0.46	0.50	51	45.22±0.49	0.62	55	45.25±0.03	0.56	106
December	46.29±0.43	1.01	56	45.71±0.37	0.49	57	46.00±0.29	0.75	113
January	46.68±0.60	0.39	44	46.05±0.46	0.34	51	46.37±0.32	0.37	95
February	46.91±0.52	0.23	58	46.62±0.44	0.57	53	46.77±0.15	0.40	111
March	47.61±0.49	0.70	56	47.37±0.62	0.75	40	47.49±0.12	0.73	96
April	48.16±0.34	0.55	57	47.65±0.45	0.78	63	47.91±0.26	0.67	120
May	49.45±0.50	1.29	53	48.46±0.37	0.81	62	48.96±0.50	1.05	115
June	53.51±0.54	4.06	52	51.21±0.51	2.75	60	52.36±1.15	3.41	112
July	54.77±0.66	1.26	51	52.19±0.53	0.98	44	53.48±1.29	1.12	95
August	56.80±0.55	2.03	44	53.30±0.52	1.11	45	55.05±1.75	1.57	89
Increment (mm)	33.23			28.79			31.01		

Table-8. Average shell lengths (L±SE; mm) at 2 m and 6 m and pooled (2+6 m) at each sampling date and monthly growth increments ($\Delta L=L_2-L_1$; mm) of experimental mussels in Loch Kishorn between May 1993 and August 1994. N is monthly sample size, L is length of mussels.

Month	2 m			6 m			POOLED		
	L±SE	ΔL	N	L±SE	ΔL	N	L±SE	ΔL	N
May	25.70±0.37		61	27.51±0.53		71	26.61±0.91		132
June	31.50±0.54	5.80	60	30.01±0.44	2.5	57	30.76±0.75	4.15	121
July	38.02±0.52	6.32	57	35.19±0.50	5.18	63	36.61±1.42	5.85	120
August	41.35±0.52	3.33	70	40.04±0.44	4.85	61	40.70±0.66	4.09	131
September	42.90±0.55	1.55	61	42.40±0.50	2.36	56	42.65±0.25	1.96	117
October	43.15±0.46	0.25	66	42.54±0.40	0.14	58	42.85±0.31	0.20	124
November	45.79±0.44	2.64	64	43.26±0.42	0.72	58	44.53±1.27	1.68	122
December	45.85±0.42	0.06	65	44.78±0.41	1.52	65	45.32±0.54	0.79	130
January	46.05±0.51	0.20	58	45.10±0.48	0.32	62	45.58±0.48	0.26	120
February	46.18±0.52	0.13	66	45.74±0.46	0.64	66	45.96±0.22	0.39	132
March	46.85±0.52	0.67	61	46.16±0.43	0.42	63	46.51±0.35	0.55	133
April	47.39±0.46	0.54	66	46.37±0.50	0.21	54	46.88±0.51	0.38	120
May	49.34±0.47	1.95	59	49.09±0.51	2.72	55	49.22±0.13	2.34	114
June	50.91±0.46	1.57	51	49.62±0.51	0.53	52	50.27±0.65	1.05	103
July	52.51±0.57	1.60	52	50.60±0.57	0.98	50	51.56±0.96	1.29	102
August	55.50±0.64	2.99	44	54.21±0.58	3.61	42	54.86±0.65	3.30	86
Increment	29.8			26.7			28.75		

(mm)

As can be seen in Tables 7 and 8, increase in length was found to be higher in the young mussels than older ones. Monthly length increment ranged from 0.37 to 7.39 mm in Loch Etive. In Loch Kishorn, in May 1993 the initial size frequency distribution ranged from 18 mm to 34 mm, and this increased to 32-50 mm in September. Over the 15 month experimental period, the final size frequency distribution obtained was 46 mm to 62 mm with a mean of 54.86 ± 0.65 mm, with 1.88 mm being the mean monthly increase in length.

The monthly length increase measured was a minimum 0.20 mm and a maximum 5.85 mm in Loch Kishorn. Site had no effect on length. Monthly length increment at depths of 2 m, 6 m and pooled values are depicted in Fig 20 and Tables 7 and 8 for Loch Etive and Loch Kishorn respectively. One way ANOVA results show that there was no difference in shell length increment between sites ($P > 0.05$) and it was found that the growth increment between the depths was insignificant in Loch Kishorn ($P > 0.05$), while it differed significantly in Loch Etive ($P < 0.05$).

Mainly, the length increments occurred in the early months of the experiment when the mussels were seeds. 62.3 % of the length increase was observed in Loch Etive from May 1993 to September 1993 while 56.8 % of the growth in length took place during the same period in Loch Kishorn. Monthly changes of specific growth rate for shell length (SGR %), ranged from 0.7 to 22.5 % in Loch Etive. The average monthly SGR was 5.9 % at 2 m and 5.1% at 6 m depth and the pooled value of the two depths was 5.5 % in Loch Etive. SGR values reached their maximum at the two sites in July 1993 and are shown in Fig. 18. SGR was found to be very low during the winter. This trend is reflected in the length growth curves of Fig. 20. Monthly changes in specific growth rate for shell length (SGR) ranged from 0.49 to 15.8 % in Loch Kishorn. Average SGR values were observed to be 4.8 % at 2 m and 4.2 % at 6 m, with a mean of 4.5 %. The result of a two-way ANOVA showed that depth had a significant effect ($P < 0.001$), but site did not ($P > 0.05$). The effects of depth and site on mussel length are given in Table-9 for July 1993, November 1993, May 1994 and August 1994.

Table-9. Effect of site and depth on length, live weight (LW), wet meat weight (WMW) and ash-free dry meat weight (AFDMW) of rope cultured mussels from Loch Eive and Loch Kishorn. Two-way ANOVA was conducted on four critical sampling dates. (ns: not significant, *; P<0.05; **, P<0.01 and ***, P<0.001).

Month	Factors	DF	LENGTH (mm)			LW (g)			WMW (g)			AFDMW (g)		
			SS	MS	P	SS	MS	P	SS	MS	P	SS	MS	P
July (1993)	Site	1	23.641	23.641	**	0.599	0.599	ns	9.807	9.807	***	6.75x10 ⁻⁶	6.75x10 ⁻⁶	ns
	Depth	1	7.462	7.462	ns	1.703	1.703	*	4.044	4.044	**	1.03x10 ⁻⁴	1.02x10 ⁻⁴	**
	Site*Depth	1	4.365	4.365	ns	0.197	0.197	ns	1.662	1.662	*	6.75x10 ⁻⁶	6.75x10 ⁻⁶	ns
	Error	8	14.680	1.835		1.721	0.215		1.955	0.244		7.05x10 ⁻⁵	8.81x10 ⁻⁶	
	Total	11	50.147			4.22			17.468			1.873x10 ⁻⁴		
November (1993)	Site	1	1.960	1.960	ns	19.915	19.915	***	0.398	0.398	ns	5.20x10 ⁻⁶	5.20x10 ⁻⁶	ns
	Depth	1	5.699	5.699	*	4.314	4.314	**	0.793	0.793	*	1.00x10 ⁻⁴	1.00x10 ⁻⁴	*
	Site*Depth	1	4.002	4.002	ns	0.422	0.422	ns	0.108	0.108	ns	5.59x10 ⁻⁵	5.59x10 ⁻⁵	*
	Error	8	6.970	0.871		3.109	0.389		0.626	0.078		8.10x10 ⁻⁵	1.01x10 ⁻⁵	
	Total	11	18.632			27.761			1.927			2.42x10 ⁻³		
May (1994)	Site	1	0.141	0.141	ns	10.718	10.718	*	2.424	2.424	**	2.59x10 ⁻³	2.59x10 ⁻³	***
	Depth	1	1.333	1.333	ns	1.549	1.549	ns	0.046	0.046	ns	2.21x10 ⁻⁵	2.21x10 ⁻⁵	ns
	Site*Depth	1	0.864	0.864	ns	1.346	1.346	ns	0.249	0.249	ns	3.89x10 ⁻⁴	3.89x10 ⁻⁴	**
	Error	8	0.864	0.864		9.368	1.171		1.225	0.153		2.31x10 ⁻⁴	2.31x10 ⁻⁴	
	Total	11	12.151			22.981			3.943			3.22x10 ⁻³		
August (1994)	Site	1	0.357	0.357	ns	18.693	18.693	**	3.091	3.091	*	2.67x10 ⁻³	2.67x10 ⁻³	***
	Depth	1	14.674	14.674**		29.588	29.588	***	6.539	6.539	***	1.79x10 ⁻³	1.79x10 ⁻³	***
	Site*Depth	1	3.193	3.193	ns	13.027	13.027	**	1.097	1.097	ns	1.50x10 ⁻⁵	1.50x10 ⁻⁵	ns
	Error	8	8.084	1.010		8.847	1.106		2.561	0.320		6.28x10 ⁻⁴	7.84x10 ⁻⁵	
	Total	11	26.308			70.155			12.287			5.099x10 ⁻³		

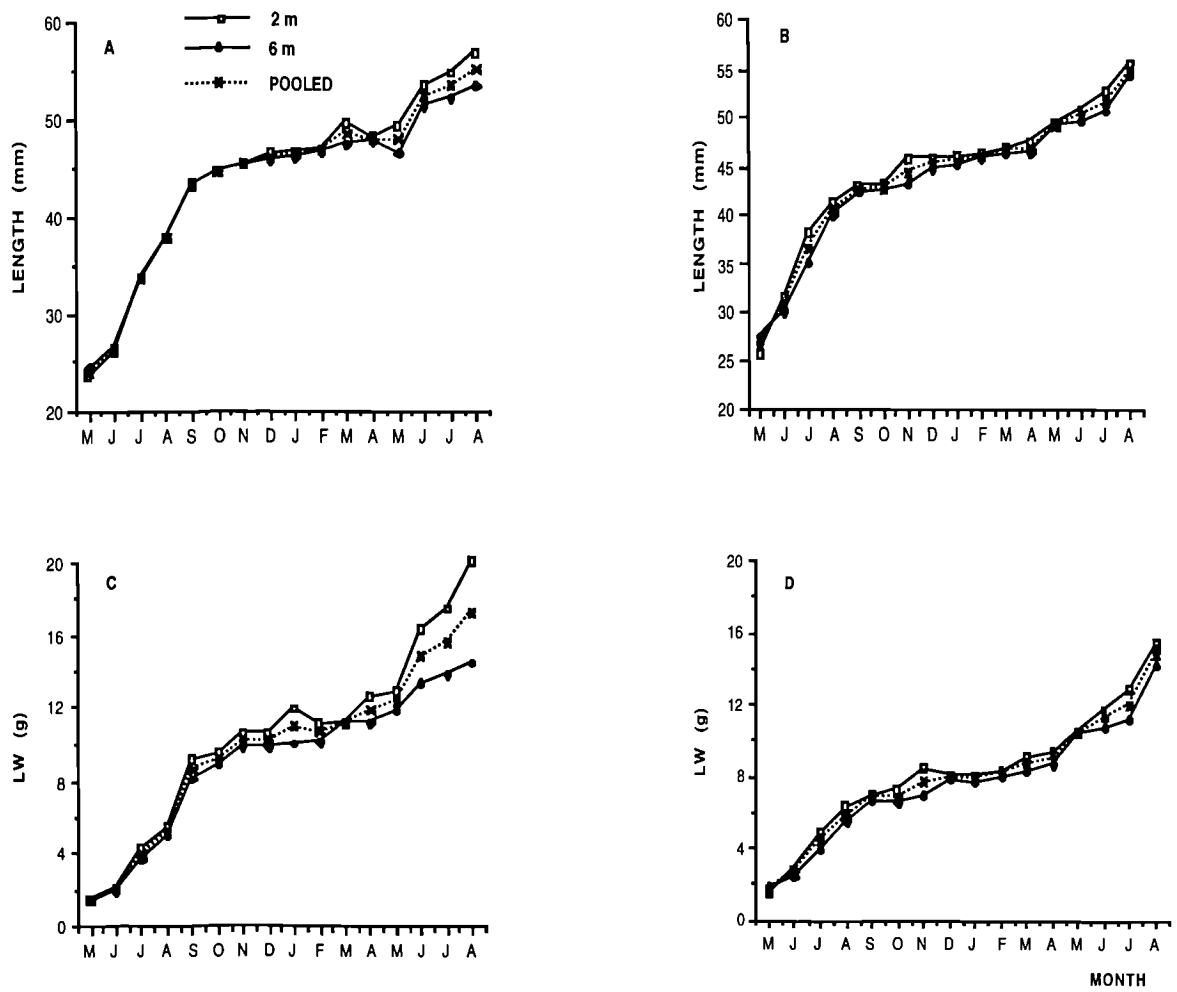


Fig.20. Growth in mean shell length of mussels at Loch Etive (A) and Loch Kishorn (B) and growth in live weight (LW) in Loch Etive (C) and Loch Kishorn (D) from May 1993 to August 1994.

4.1.2.2. Somatic Growth

Variation in the live weight growth (LW), wet meat weight growth (WMW), dry meat weight growth (DMW) and ash-free dry meat weight growth (AFDMW) were measured over the experimental period. Monthly values of live weight at 2 m and 6 m are given in Table-10.

There was a strong seasonal somatic growth, especially LW, WMW and DMW at both sites with positive growth in the summer and negligible or negative growth at the winter months. AFDMW was affected mainly by WMW and the condition index at both sites. At the end of the experiment, the mean live weight of the mussels was 14.24 g at Loch Kishorn and 17.2 g at Loch Etive. Both depth and site had a significant effect on LW.

The length - live weight relationship is shown in Fig 25. The effects of depth and site on L, LW, WMW and AFDMW were tested in July 1993, November 1993, May 1994 and August 1994 and significance levels are given in Table 9. The mean wet meat weight was 7.81 g and 6.93 g at 2 m and 6 m depth in Loch Kishorn compared to 7.35 g and 5.20 g at these depths, in Loch Etive. Pooled values for WMW were 7.37 g and 6.28 g in Loch Kishorn and Loch Etive, respectively ($P < 0.05$) (Fig. 20c). Wet meat weight had a highly significant positive relationship with condition index ($P < 0.01$).

DMW showed a clear trend, increasing during the summer and decreasing in the winter (Fig 23). DMW was affected by fluctuation in the condition index. The decreases in WMW were attributed to low temperature and a decline in available food from October to April and a sharp decrease in WMW indicates spawning at both sites in June. As can be seen in Fig 22, there was a quick recovery in wet meat weight, reaching a maximum in August 1994 due to recover in meat weight and growth during the summer. A sharp increase in WMW coincided with the main spawning period which took place in April in Loch Kishorn and in May in Loch Etive in 1993. Observations on gonad development and spat settlement supported this result at both sites. There was a one or two months recovery period in gonad development between successive spawnings.

Table-10 . Monthly distribution of live weight (g) at depths of 2 m and 6 m in Loch Etive (LE) and Loch Kishorn (LK). Superscript letters indicate one-way ANOVA comparisons; figures bearing different letters are significantly different at $P < 0.05$ or less on four sampling dates (July 1993, October 1993, May 1994 and August 1994).

Month	LE		LK	
	2 m	6 m	2 m	6 m
May	1.45±0.07	1.40±0.08	1.52±0.07	1.83±0.10
June	2.18±0.11	1.93±0.25	2.71±0.13	2.46±0.11
July	4.24±0.18 ^{ab}	3.62±0.15 ^a	4.86±0.20 ^a	3.91±0.17 ^{ab}
August	5.39±0.24	4.95±0.19	6.27±0.23	5.43±0.19
September	9.20±0.32	8.10±0.33	6.99±0.28	6.59±0.23
October	9.45±0.39 ^{cd}	8.79±0.22 ^{bc}	7.26±0.23 ^{abc}	6.49±0.19 ^{ab}
November	10.58±0.32	9.82±0.32	8.45±0.23	6.90±0.19
December	10.55±0.32	9.78±0.26	8.15±0.26	7.84±0.21
January	11.95±0.44	9.99±0.32	8.11±0.29	7.68±0.26
February	11.10±0.41	10.15±0.24	8.33±0.27	8.02±0.21
March	11.19±0.34	11.13±0.47	9.10±0.33	8.28±0.22
April	12.52±0.39	11.14±0.38	9.35±0.26	8.62±0.25
May	12.87±0.45 ^b	11.79±0.33 ^{ab}	10.55±0.32 ^a	10.38±0.33 ^a
June	16.27±0.50	13.30±0.42	11.69±0.31	10.78±0.32
July	17.49±0.69	13.88±0.39	12.83±0.40	11.12±0.36
August	19±96±0.66 ^b	14.43±0.41 ^a	15.34±0.53 ^a	14.24±0.48 ^a

Table-11. Monthly distribution of wet meat weight (g) at depth of 2 m and 6m in Loch Etive (LE) and Loch Kishorn (LK). Superscript letters indicate one-way ANOVA comparisons; figures bearing different letters are significantly different at $P < 0.05$ or less on four sampling dates (July 1993, October 1993, May 1994 and August 1994).

Month	LE		LK	
	2 m	6 m	2 m	6 m
May	0.71±0.034	0.698±0.041	0.73±0.04	0.90±0.05
June	0.86±0.42	0.68±0.040	1.48±0.08	1.32±0.06
July	1.59±0.07 ^a	1.14±0.05 ^a	2.81±0.12 ^b	2.18±0.11 ^a
August	1.61±0.08	1.43±0.06	2.93±0.12	2.48±0.10
September	2.52±0.11	2.52±0.11	3.05±0.14	2.85±0.12
October	3.35±0.14	3.03±0.08	2.97±0.11	2.68±0.09
November	3.47±0.11 ^b	3.21±0.11 ^{ab}	3.37±0.11 ^{ab}	2.66±0.99 ^a
December	3.26±0.11	3.09±0.10	3.32±0.11	2.96±0.10
January	3.42±0.16	3.04±0.11	3.33±0.12	3.00±0.10
February	3.15±0.13	3.11±0.01	3.30±0.12	3.28±0.10
March	3.17±0.11	3.56±0.19	3.62±0.15	3.06±0.10
April	3.58±0.13	3.36±0.11	3.12±0.09	3.13±0.11
May	4.18±0.12 ^{ab}	3.86±0.09 ^a	4.84±0.16 ^b	4.94±0.19 ^b
June	6.23±0.23	5.31±0.14	5.66±0.20	5.30±0.20
July	5.88±0.23	4.64±0.15	5.36±0.20	4.15±0.13
August	7.35±0.29 ^b	5.20±0.16 ^a	7.81±0.31 ^b	6.93±0.29 ^b

Table-12. Monthly values of ash-free dry weight (g) at depth of 2 m and 6m in Loch Etive (LE) and Loch Kishorn (LK). Superscript letters indicate one-way ANOVA comparisons; figures bearing different letters are significantly different at $P < 0.05$ or less on four sampling dates (July 1993, October 1993, May 1994 and August 1994).

Month	LE		LK	
	2 m	6 m	2 m	6 m
May	0.0105±0.0005	0.0101±0.0005	0.0161±0.001	0.0167±0.001
June	0.0185±0.009	0.0129±0.043	0.0235±0.001	0.0213±0.001
July	0.0304±0.002 ^b	0.0228±0.001 ^a	0.0304±0.001 ^b	0.0257±0.001 ^{ab}
August	0.0259±0.012	0.0212±0.001	0.0579±0.002	0.0448±0.002
September	0.0357±0.001	0.0409±0.001	0.0500±0.002	0.0371±0.002
October	0.0376±0.002	0.0342±0.001	0.0378±0.001	0.0408±0.001
November	0.0382±0.001 ^{ab}	0.0374±0.001 ^{ab}	0.0419±0.001 ^b	0.0317±0.001 ^a
December	0.0545±0.002	0.0596±0.002	0.0586±0.002	0.0470±0.002
January	0.0626±0.003	0.0572±0.002	0.0734±0.003	0.0610±0.002
February	0.0627±0.002	0.0612±0.002	0.0644±0.002	0.0518±0.002
March	0.0455±0.006	0.0566±0.003	0.0547±0.002	0.0478±0.002
April	0.0505±0.002 ^b	0.0500±0.002 ^a	0.0617±0.002 ^c	0.0629±0.002 ^c
May	0.0509±0.002	0.0373±0.001	0.0695±0.002	0.0771±0.003
June	0.0749±0.003	0.0649±0.002	0.0733±0.002	0.0712±0.003
July	0.0780±0.003	0.0626±0.002	0.1033±0.004	0.0786±0.002
August	0.0974±0.004 ^b	0.0696±0.002 ^a	0.1259±0.005 ^c	0.1031±0.004 ^b

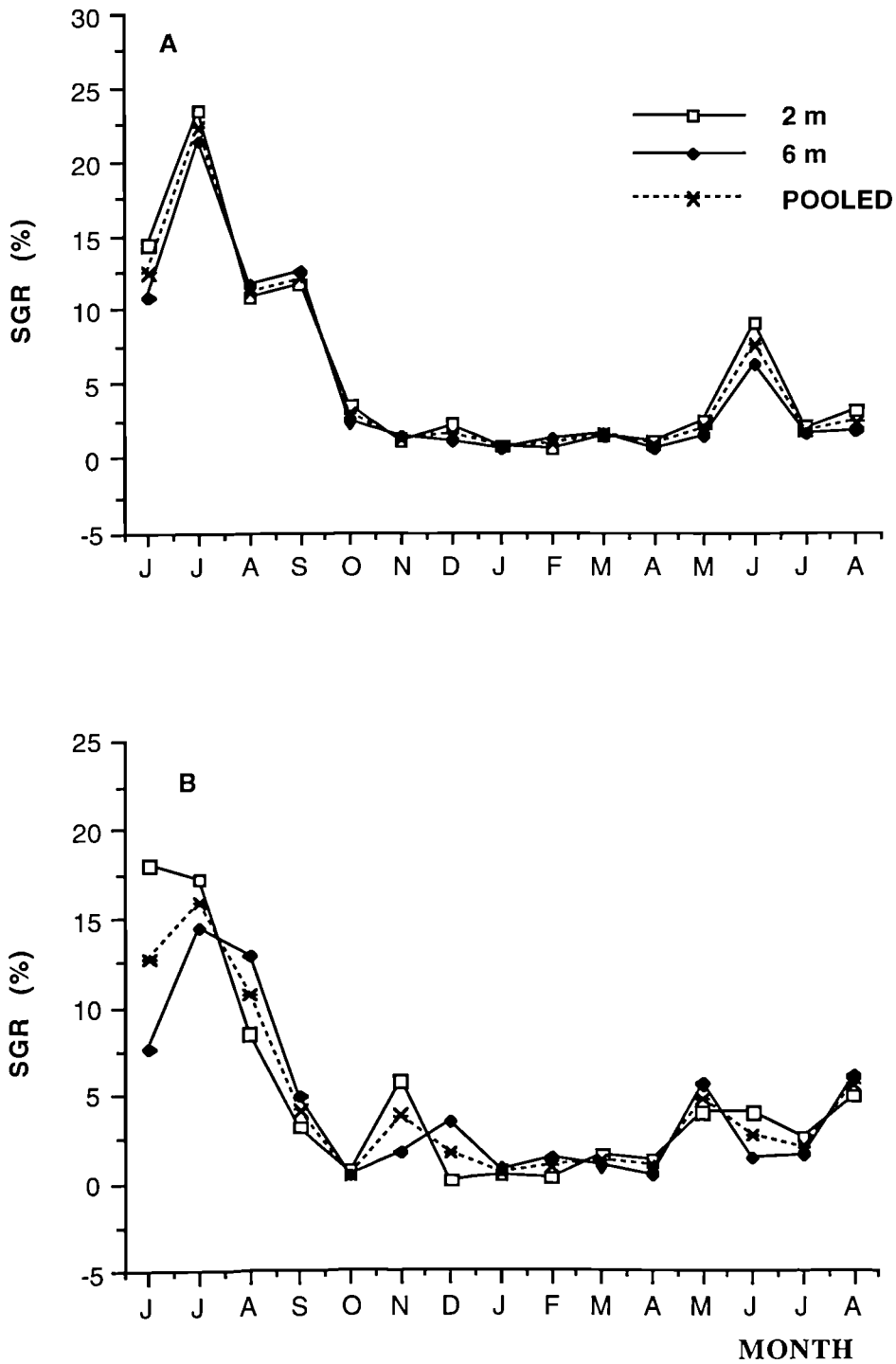


Fig.21. Monthly average length specific growth rate (SGR%) for mussels grown in Loch Etive (A) and Loch Kishorn (B) at 2 m and 6 m and pooled values between May 1993 and August 1994.

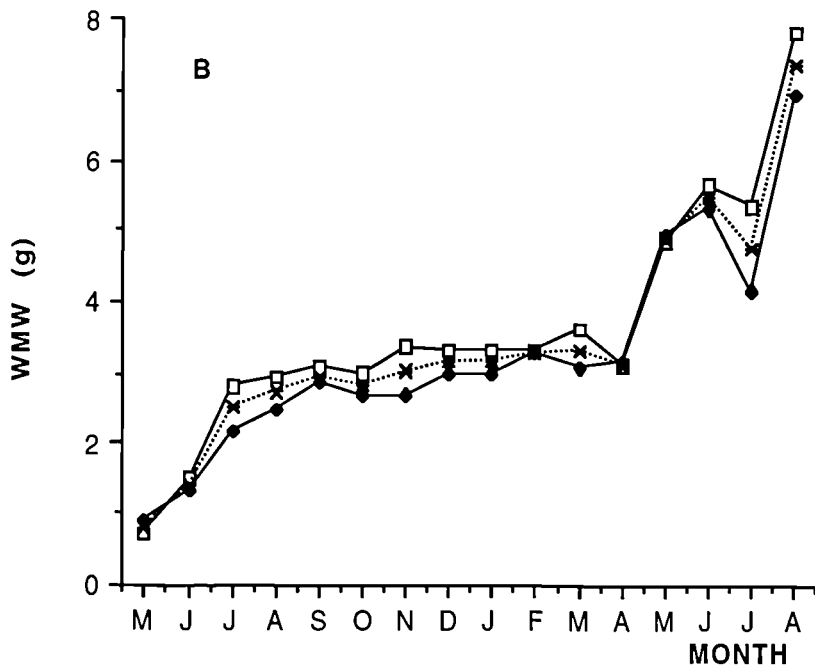
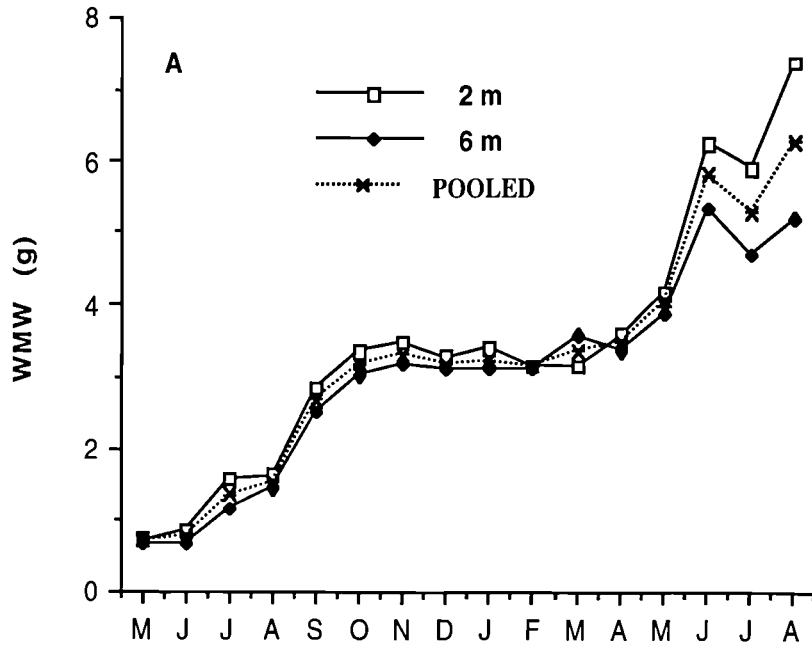


Fig.22. Monthly changes in wet meat weight (WMW) at 2 m and 6 m and pooled values in Loch Etive (A) and in Loch Kishorn (B).

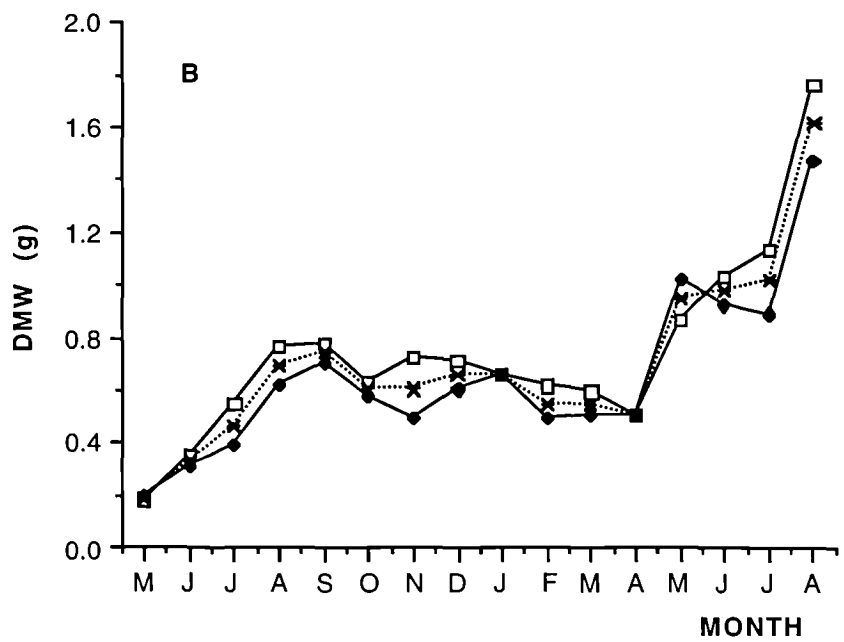
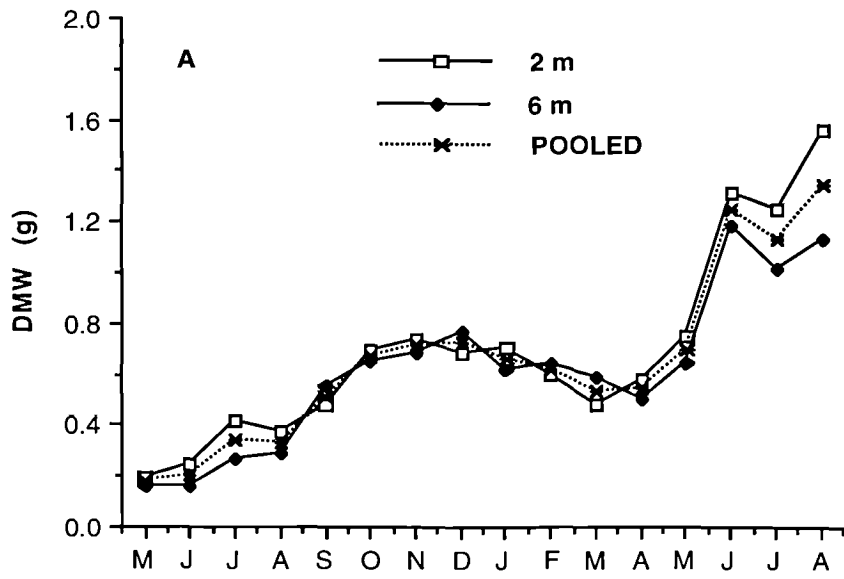


Fig.23. Monthly distribution of dry meat weight (DMW) in Loch Etive (A) and Loch Kishorn (B) from May 1993 to August 1994.

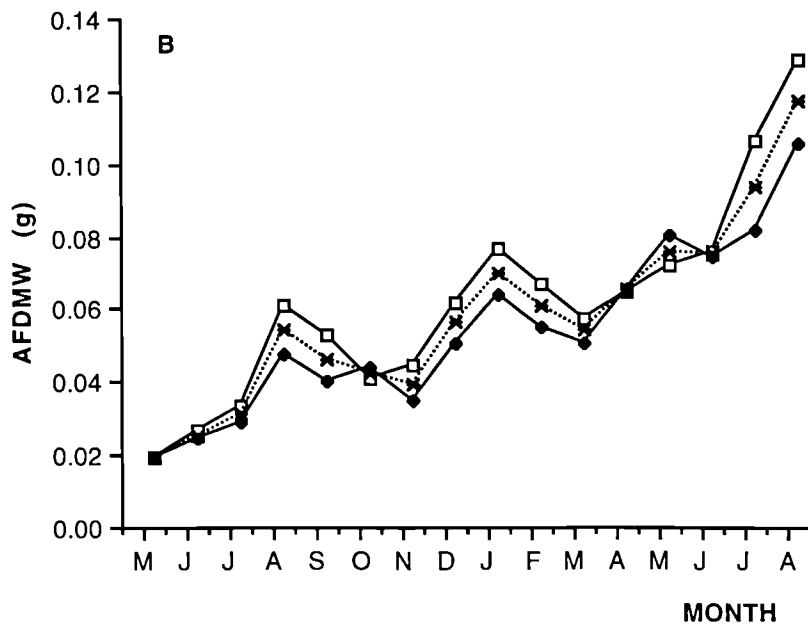
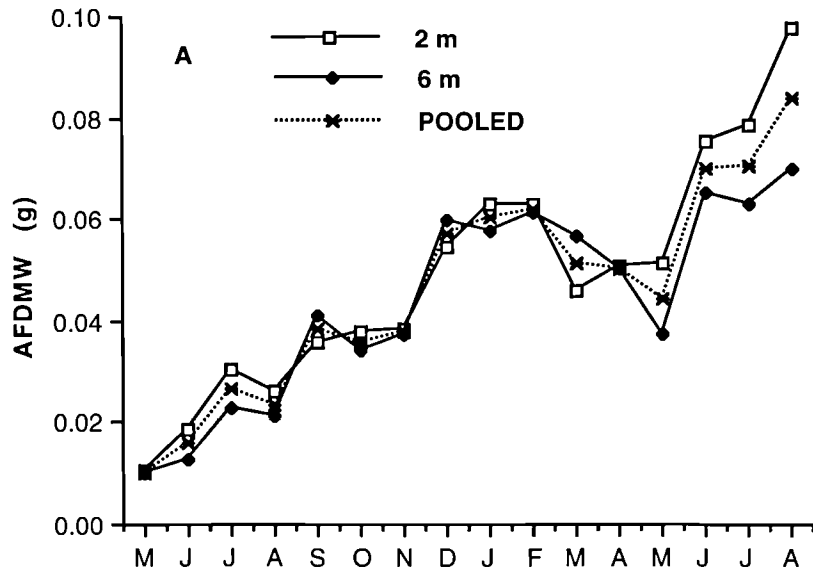


Fig.24. Seasonal changes in ash-free dry meat weight (AFDMW) in Loch Etive (A) and Loch Kishorn (B) from May 1993 to August 1994.

SGR had a highly positive correlation with temperature in Loch Etive ($r=0.625$, $P<0.01$) and Loch Kishorn ($r=0.691$, $P<0.01$). A Correlation Matrix between the SGR and environmental factors in each loch is given in Tables 5 and 6.

4.1.2.3. Mussel Length-Weight Relationship

A linear relationship was established between \log_{10} DMW and AFDMW, and \log_{10} shell length for both sites (Table -13). Relationships were determined monthly so that the changing condition factor of mussels during the year relative to their reproductive status and starvation could be eliminated, and somatic growth pattern in the cultivated populations could be predicted by measuring shell length and applying these weight-length regressions equations. All regressions of length-DMW and length-AFDMW were significant.

The size to weight relationships between shell length (L, in mm) and dry shell weight (DSW, in g) and shell length and ash free dry shell weight (AFDSW, in g) were also determined and the best fitting lines were plotted; their equations are given in Fig. 26. All the regressions of length and DSW, and length and AFDSW were highly correlated ($P<0.001$). The shell length to weight relationship was plotted for over 800 mussels randomly collected to avoid of the effect of spawning on live weight (Fig 25). The corresponding equations for mussels in Loch Etive and Loch Kishorn were as follows:

Loch Etive mussels:

$$\log_{10} W = -4.0505 + 3.0302 \log_{10} L \quad r=0.992$$

$$W = 0.000089 L^{3.0303}$$

Loch Kishorn mussels:

$$\log_{10} W = -4.1365 + 3.0421 \log_{10} L \quad r=0.997$$

$$W = 0.000073 L^{3.0421}$$

The von Bertalanffy equations $L_t = L_\infty (1 - e^{-k(t - t_0)})$ were:

a) for Loch Etive mussels $L_t = 63.25 (1 - e^{-0.267(t + 1.30)})$

b) for Loch Kishorn mussels $L_t = 53.26 (1 - e^{-0.644(t + 0.629)})$

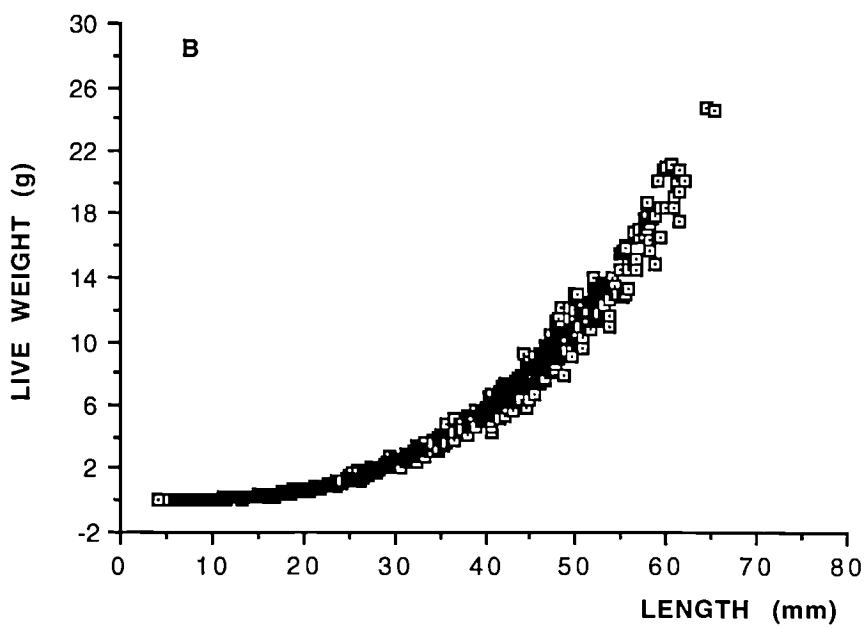
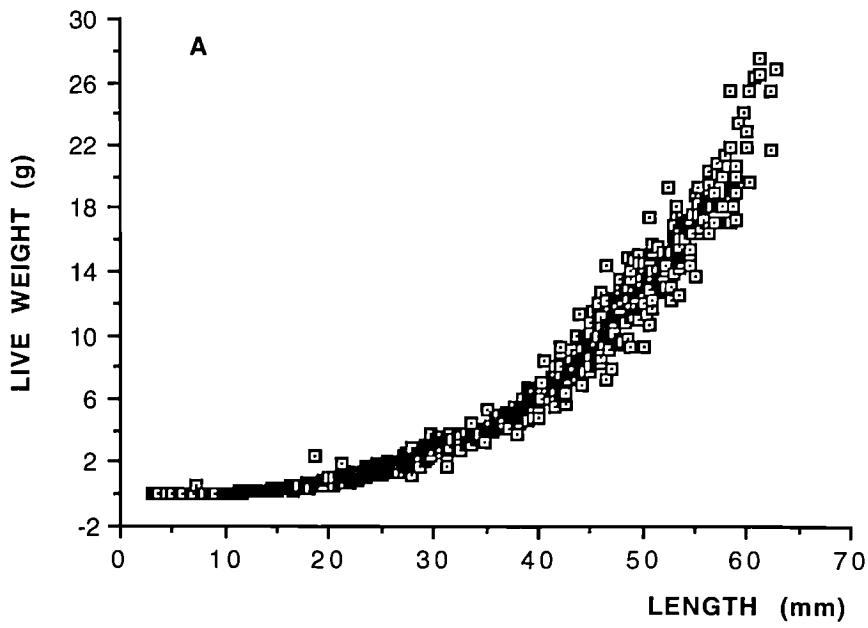


Fig.25. Shell length - live weight relationship for mussels in Loch Etive (A) and Loch Kishorn (B).

Table-13 Monthly length - weight equations ($\text{Log}_{10} W = a + b \text{Log}_{10} L$) relating dry (DMW) and ash-free dry meat weight (AFDMW) to shell length (L) for rope grown mussels at Loch Etive between May 1993 and August 1994. a and b are constants, r is correlation coefficient.

Month	DMW			AFDMW		
	a	b	r	a	b	r
May	-4.6346	2.8392	0.936	-5.89.81	2.8350	0.936
June	-4.9472	3.0401	0.926	-6.0606	3.0352	0.926
July	-4.9848	2.9902	0.788	-6.1117	2.9881	0.789
August	-5.6536	3.2929	0.942	-6.8053	3.2914	0.942
September	-5.7699	3.3195	0.770	-6.8938	3.3199	0.770
October	-5.3453	3.1298	0.884	-6.6025	3.1264	0.884
November	-4.5280	2.6492	0.756	-4.8126	2.6481	0.756
December	-5.2248	3.0315	0.740	-6.3253	3.0336	0.740
January	-4.6642	2.6759	0.462	-5.7113	2.6746	0.461
February	-5.0759	2.8954	0.725	-6.0544	2.8952	0.725
March	-4.9027	2.7256	0.656	-5.9277	2.7269	0.656
April	-5.7005	3.2387	0.741	-6.7600	3.2394	0.741
May	-4.6659	2.6736	0.818	-5.8331	2.6757	0.818
June	-3.6068	2.1503	0.617	-4.8714	2.1513	0.617
July	-4.7813	2.7984	0.783	-5.9831	2.7975	0.782
August	-5.0915	3.0056	0.645	-6.2964	3.0063	0.645

Table-14 .Monthly length-weight equations ($\text{Log}_{10}W = a + b \text{Log}_{10}L$) relating dry (DMW) and ash-free dry meat weight (AFDMW) to shell length (L) for rope grown mussels at Loch Kishorn between May 1993 and August 1994. a and b are constants, r is correlation coefficient. N is given in Table-8 for each month.

Month	DMW			AFDM		
	a	b	r	a	b	r
May	-4.6966	2.79.36	0.814	-5.7569	2.7949	0.815
June	-4.6346	2.8392	0.936	-5.8981	2.8350	0.946
July	-5.1570	3.0889	0.852	-6.4178	3.0902	0.853
August	-4.3119	2.5837	0.576	-5.4357	2.5841	0.576
September	-5.5905	3.3452	0.919	-6.7817	3.3429	0.919
October	-3.6210	2.1160	0.538	-4.8426	2.1158	0.538
November	-5.5068	3.2231	0.835	-6.7411	3.2225	0.834
December	-5.1826	3.0237	0.737	-6.2659	3.0231	0.737
January	-4.9332	2.8489	0.729	-5.8844	2.8491	0.728
February	-4.9269	2.8249	0.716	-5.9042	2.8240	0.716
March	-5.6757	3.2533	0.836	-5.7138	3.2542	0.836
April	-4.2207	2.3360	0.527	-5.1386	2.3385	0.528
May	-4.9486	2.8828	0.706	-6.0467	2.8813	0.706
June	-4.7993	2.8134	0.608	-5.9478	2.8144	0.608
July	-4.8274	2.8332	0.665	-5.8727	2.8340	0.665
August	-4.6390	2.7966	0.742	-5.7878	2.7966	0.742

4.1.3. Morphology of Mussels

Shell morphology and appearance was compared between the Loch Etive and Loch Kishorn mussels. The most apparent difference between the Loch Etive and Loch Kishorn rope cultured mussel populations was shell color. Mussels from Loch Etive have a very dark bluish-black color and are more striped compared to the brighter, brownish or brownish-black color of Loch Kishorn mussels.

The second difference between mussels from the two lochs was related to the shape and weight or thickness of the shell. Loch Etive mussels had greater height : length, width : length and width : height ratios, i.e. they had a broader and wider body shape than these from Loch Kishorn (Tables 15 and 16). Some authors (e.g. Seed, 1968) have suggested that these body ratios decrease with increase in length, height and width, therefore to avoid errors in the comparisons, all the ratios were obtained on standard length of mussels (with a mean length of 52.92 mm) from Loch Etive and Loch Kishorn in July 1994. One-way ANOVA showed that there was a significant site response concerning these ratios ($P < 0.001$) (Table-16). The slope (b), intercept (a) and correlation coefficient (r) of the linear regression equations are summarized in Table- 15. The monthly distribution of shell weights are depicted in Fig. 27. Ash-free dry shell organic weight (AFDSOW) was equivalent to 3 % of whole dry shell weight in Loch Kishorn mussels and 3.2 % in the Loch Etive population after treatment with hydrochloric acid, while it was found to be 2.7 % and 3 % for Loch Kishorn and Loch Etive, respectively after direct combustion of whole dry shells in a furnace at 550°C. Length-ash free dry shell weight (AFDSW) and length-dry shell weight relationships are shown in Fig. 26.

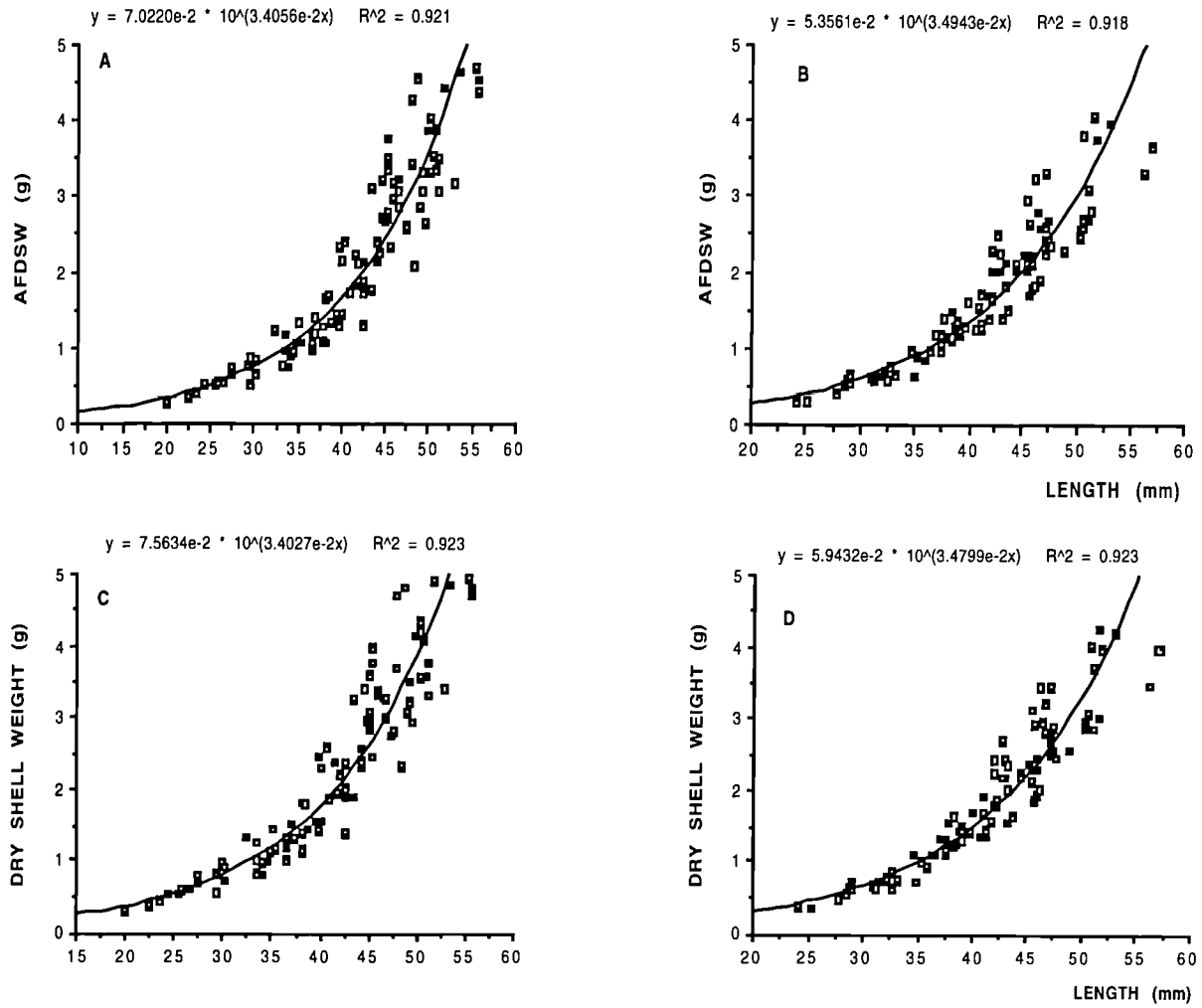


Fig.26. Relationships between shell length-ash free dry shell weight (AFDSW) in Loch Etive (A) and Loch Kishorn (B) and shell length-dry shell weight of experimental mussels in Loch Etive (C) and Loch Kishorn (D).

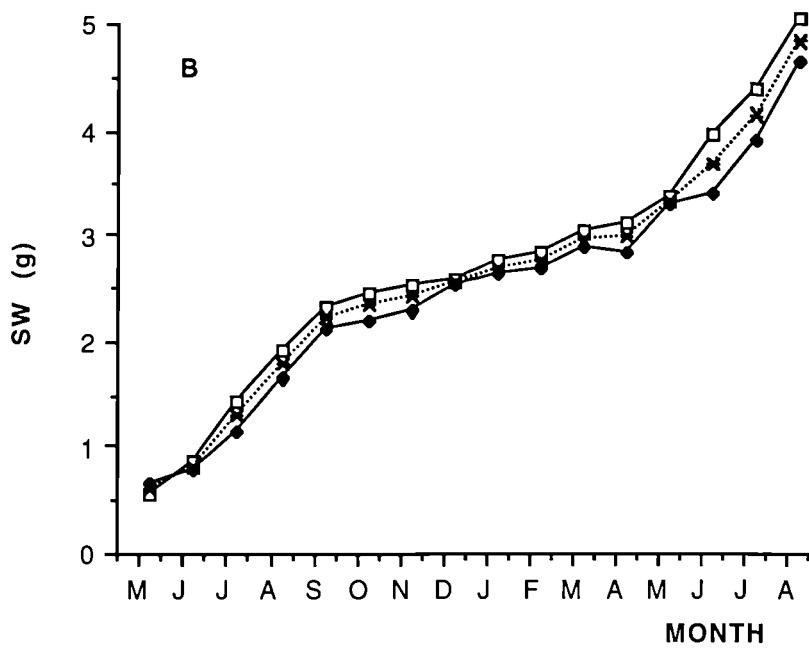
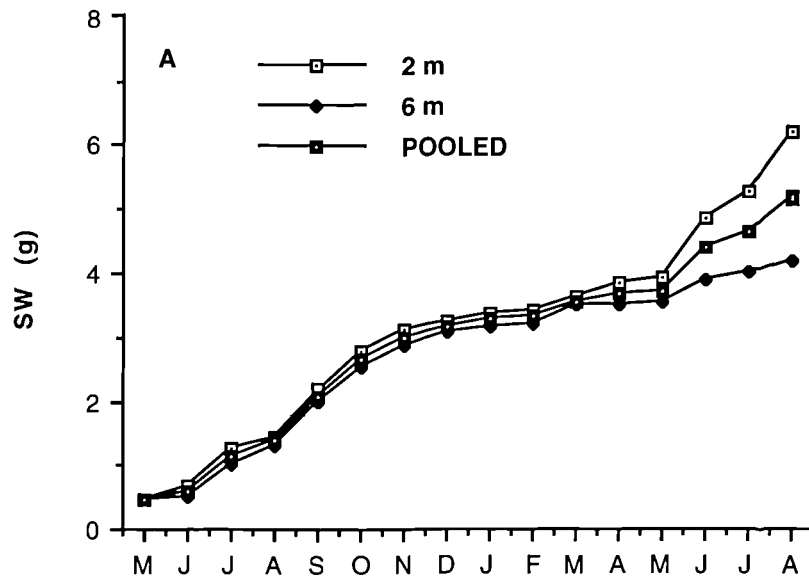


Fig.27. Monthly distribution of shell weight (SW) at 2 m and 6 m depth and pooled values in Loch Etive (A) and Loch Kishorn (B) during the experimental period.

Table-15. Linear regressions ($y = a + bx$) between shell length, shell width and shell height for Loch Etive (LE) and Loch Kishorn (LK) mussels.

	Site	Intercept (a)	Slope (b)	r
Height on Length	LE	-5.4182	2.1006	0.990
	LK	-4.2753	2.2139	0.989
Width on Length	LE	1.0122	2.4576	0.980
	LK	3.2322	2.6305	0.999
Width on Height	LE	3.1576	1.1644	0.981
	LK	3.6033	1.1744	0.988

Table-16. The mean shell characteristics of mussels from Loch Etive (LE) and Loch Kishorn (LK) in July 1994 with an adjusted mean shell length (52.92 mm). (N= 84 in LE and 78 in LK). Superscript letters indicate one-way ANOVA comparisons between sites; those bearing different letters are significantly different at $P < 0.05$ or less.

Site	Length (mm)	Weight (g)	Height (mm)	Width (mm)	H:L	W:L	W:H
LE	52.92	4.47	28.36	20.86	0.54 ^b	0.39 ^b	0.74 ^b
LK	52.92	4.09	26.67	18.83	0.50 ^a	0.36 ^a	0.71 ^a

4.1.4. Survival and Losses

Fig. 28 shows cumulative survival, monthly survival and monthly distribution of losses for rope cultivated mussels from Loch Etive and Loch Kishorn. Survival, expressed as the number of mussels staying on the ropes as percentage of initial stock number was quite low. Fig. 28 shows computed changes in population density (expressed as

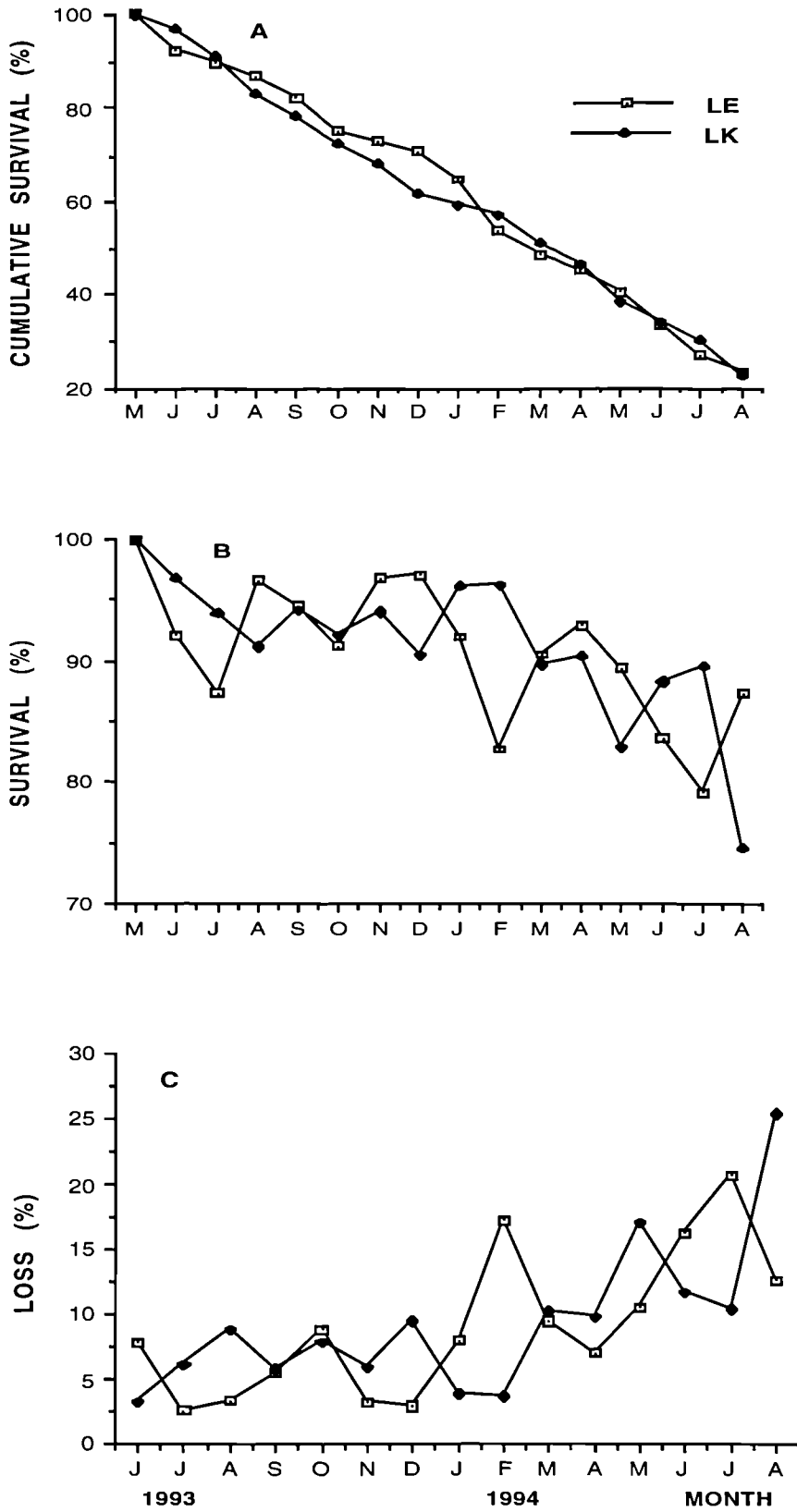


Fig.28. Changes in cumulative survival (A), monthly survival (B) and losses (C) in Loch Etive (LE) and Loch Kishorn (LK) over the experimental period.

mean number of mussels per linear meter of rope). The initial population density was 1,680 ind m⁻¹ rope and 1,590 ind m⁻¹ rope in Loch Etive and Loch Kishorn, respectively. Cumulative survivals were 23.4 % in Loch Etive and 22.6 % in Loch Kishorn of initial number. Monthly survival ranged from 82.8 % to 97.1 % in Loch Etive and 74.7 % to 96.9 % in Loch Kishorn while monthly losses ranged from 2.6 % to 20.8 % in Loch Etive and from 3.1 % to 25.3 % in Loch Kishorn.

4.1.5. Eliminated Biomass

Monthly eliminated biomass values were calculated from Tables 18 and 19 and are given in Table-17 for both sites. Monthly eliminated biomass ranged from 1.81 g m⁻¹ to 12.44 g m⁻¹ in Loch Etive (while it had a range of 1.05-13.98 g m⁻¹ in Loch Kishorn). Eliminated biomass was lowest in the early months of the experiment due to low values of ash-free dry weight and mussel size in both sites. However, eliminated biomass was higher for bigger sized mussels due to their high AFDW.

The mean eliminated biomass was found to be 4.52 g m⁻¹ of rope (equal to 24.29 Kcal m⁻¹) and in Loch Etive while it was calculated as 26.84 Kcal m⁻¹ and 5.06 g m⁻¹ in Loch Kishorn. There were significant differences between the sites depending on monthly values ($P < 0.001$), but site had no significant influence on mean eliminated biomass ($P > 0.05$). A decline in mussel density continued throughout the experiment with a low increasing rate. The monthly mean losses obtained were 9.1 % in Loch Etive and 9.3 % in Loch Kishorn, while monthly survival was found to be 90.9 % and 90.6 % in Loch Etive and Loch Kishorn respectively. Low survival and heavy losses were more apparent in the older mussels than younger mussels at both sites. Maximum losses were recorded in Loch Etive in July 1994 (20.8 %) and in Loch Kishorn in August 1994 (23.3 %). The minimum losses occurred in July and June in Loch Kishorn and Loch Etive respectively (2.6 % and 3.1 %). The high losses and poor survival at both sites was due to several factors: a) natural mortality after spawning; b) falling off the ropes (detached) due to lack of space and weak byssus during the summer; c) water current and handling when lifting the cultivation

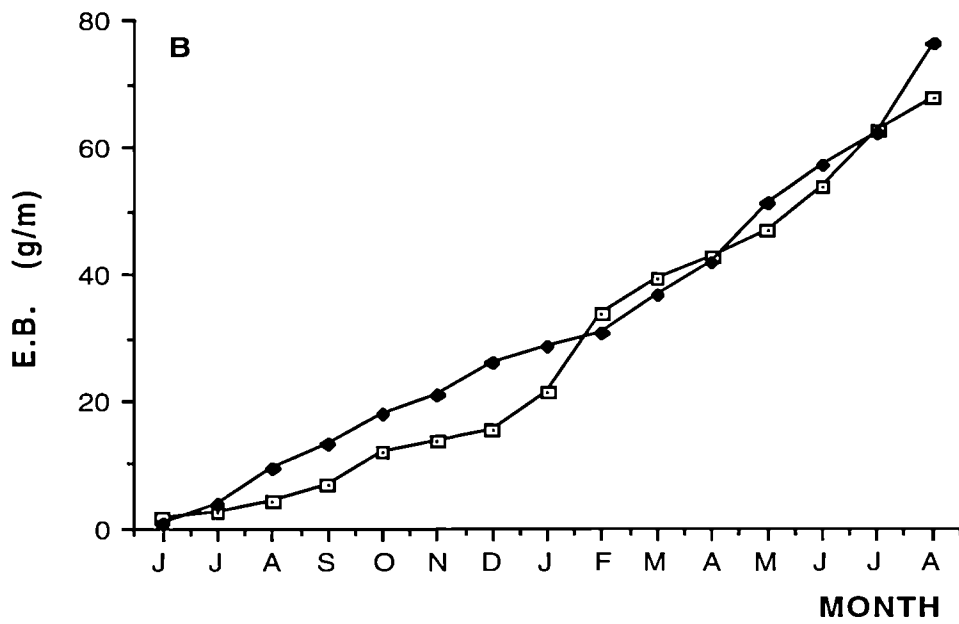
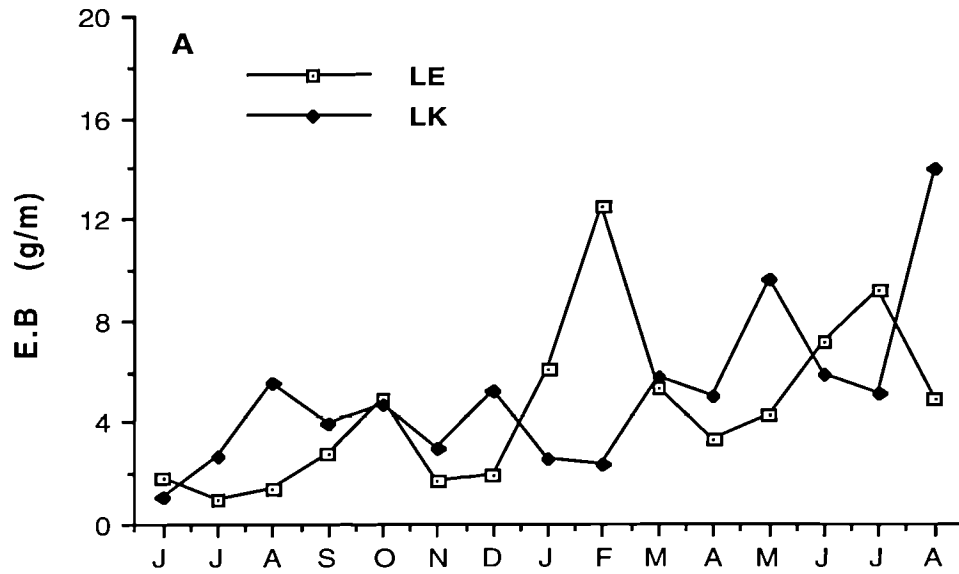


Fig.29. Monthly (A) and cumulative (B) eliminated biomass (EB) of experimental mussels in Loch Etive (LE) and Loch Kishorn (LK) from June 1993 to August 1994.

Table-17. Monthly eliminated biomasses, gram ash-free dry weight and Kcal m⁻¹ of rope cultured mussels in Loch Etive (LE) and Loch Kishorn (LK). N is monthly sample size

Month	SITE		LE		LK			
	Days	N	EB (g m ⁻¹)	EB (Kcal m ⁻¹)	Days	N	EB (g m ⁻¹)	EB (Kcal m ⁻¹)
May	22	130	1.807	9.386	34	50	1.055	5.580
June	33	40	0.906	4.752	33	94	2.614	14.020
July	31	50	1.365	7.178	30	126	5.487	28.608
August	33	80	2.716	14.120	35	75	3.945	20.074
September	31	120	4.944	26.004	28	98	4.635	24.774
October	28	40	1.67	8.954	31	67	2.958	16.191
November	29	36	1.91	10.224	30	102	5.248	27.810
December	34	94	6.025	32.515	31	38	2.548	13.302
January	29	188	12.436	67.727	30	34	2.372	12.529
February	28	85	5.27	29.151	28	93	5.780	31.978
March	30	58	3.306	18.169	27	78	5.031	27.975
April	32	80	4.292	23.624	31	126	9.576	51.458
May	26	111	7.110	38.711	24	71	5.518	29.909
June	35	118	9.198	48.563	37	56	5.1464	26.057
July	35	57	4.871	25.288	34	122	13.981	72.267
August								

ropes. Site had no effect on survival and losses ($P>0.05$). It was observed during the early sampling months that some of the mussels, especially small ones, stacked inside the larger mussels and died. There were heavy mussel losses due to heavy eel population in two sites. There was no clear relationship between survival, or mortality rates and environmental parameters, seston or growth during the experimental period.

4.1.6. Mussel Biomass and Production

Biomass and production, which are the result of interaction between growth and mortality, were estimated for the culture ropes on the raft systems in Loch Etive and Loch Kishorn from May 1993 to August 1994. Biomass values are presented in Tables 18 and 19 and discussed as g ash free dry weight (including shell organic content) per mussel and per meter of rope, while production is expressed as g ash free dry weight (AFDW) per meter (Tables 18 and 19). However, both biomass and production were also converted to Kcal by multiplying values in g by a monthly energy value for AFDW. The energy content of mussels was measured every month as described in materials and methods (see section 3.6.1.6).

4.1.6.1. Biomass

Monthly values of biomass as grams and Kcal AFDW mussels⁻¹ and changes in biomass gram AFDW per mussel are given in Tables 18 and 19 and whole cumulative biomass is illustrated in Fig 30. The differences in biomass between the sites were highly significant in May 1994 and August 1994 ($P<0.001$). Biomass (g ind⁻¹) ranged from -0.0089 to 0.0254 g ind⁻¹ from January 1994 to February 1994 and from July to August 1994 in Loch Kishorn. In Loch Etive it ranged from -0.0104 g ind⁻¹ (from February to March) to 0.0269 g ind⁻¹ from May to June 1994. The annual cycle of biomass was quite similar to AFDW values. Three main peaks were observed at each site, the first peak in

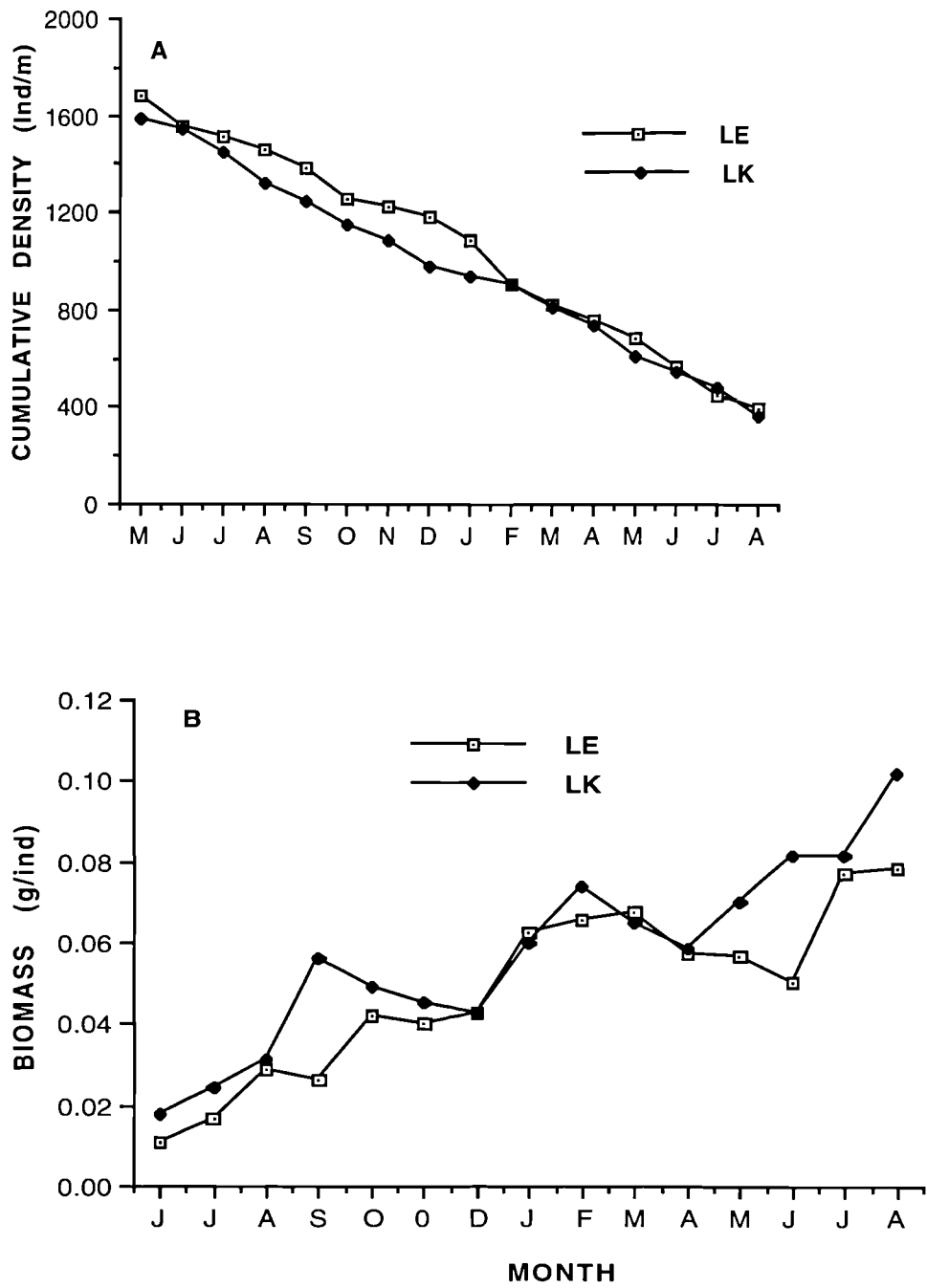


Fig.30. Monthly changes in cumulative density (A) and ash-free dry weight biomass (B) as grams per mussel in Loch Etive (LE) and Loch Kishorn (LK) during the experimental period.

August 1992 ($0.0312 \text{ g ind}^{-1}$), a second peak in January ($0.0742 \text{ g ind}^{-1}$) and a third peak in August 1994 with a final value of $0.1273 \text{ g ind}^{-1}$ in Loch Kishorn, while three peaks were also observed in Loch Etive, in September 1993, January 1994 and August 1994 (with values of 0.0419 , 0.0656 and $0.0925 \text{ g ind}^{-1}$, respectively).

4.1.6.2. Production

Tables 18 and 19 show the monthly production values while monthly and cumulative production data are plotted in Fig. 31. The minimum production values recorded were : -8.94 g m^{-1} and $-38.99 \text{ Kcal m}^{-1}$ in Loch Etive from February to March 1994 and -8.21 g m^{-1} and $-29.35 \text{ Kcal m}^{-1}$ in Loch Kishorn from January to February 1994. The negative values obtained result from an apparent decrease in production and energy values compared to the previous month (see Tables 18 and 19) Production was affected by AFDW and losses in the both sites. The maximum value for production were calculated as 34.16 g m^{-1} and $155.86 \text{ Kcal m}^{-1}$ in Loch Kishorn from July 1993 to August 1993, whereas in Loch Etive maximum values were recorded as 59.50 g m^{-1} from July to August 1994. There were high fluctuations between the sampling months ($P < 0.001$) and highly significant differences between the site at the end of the experiment ($P < 0.001$).

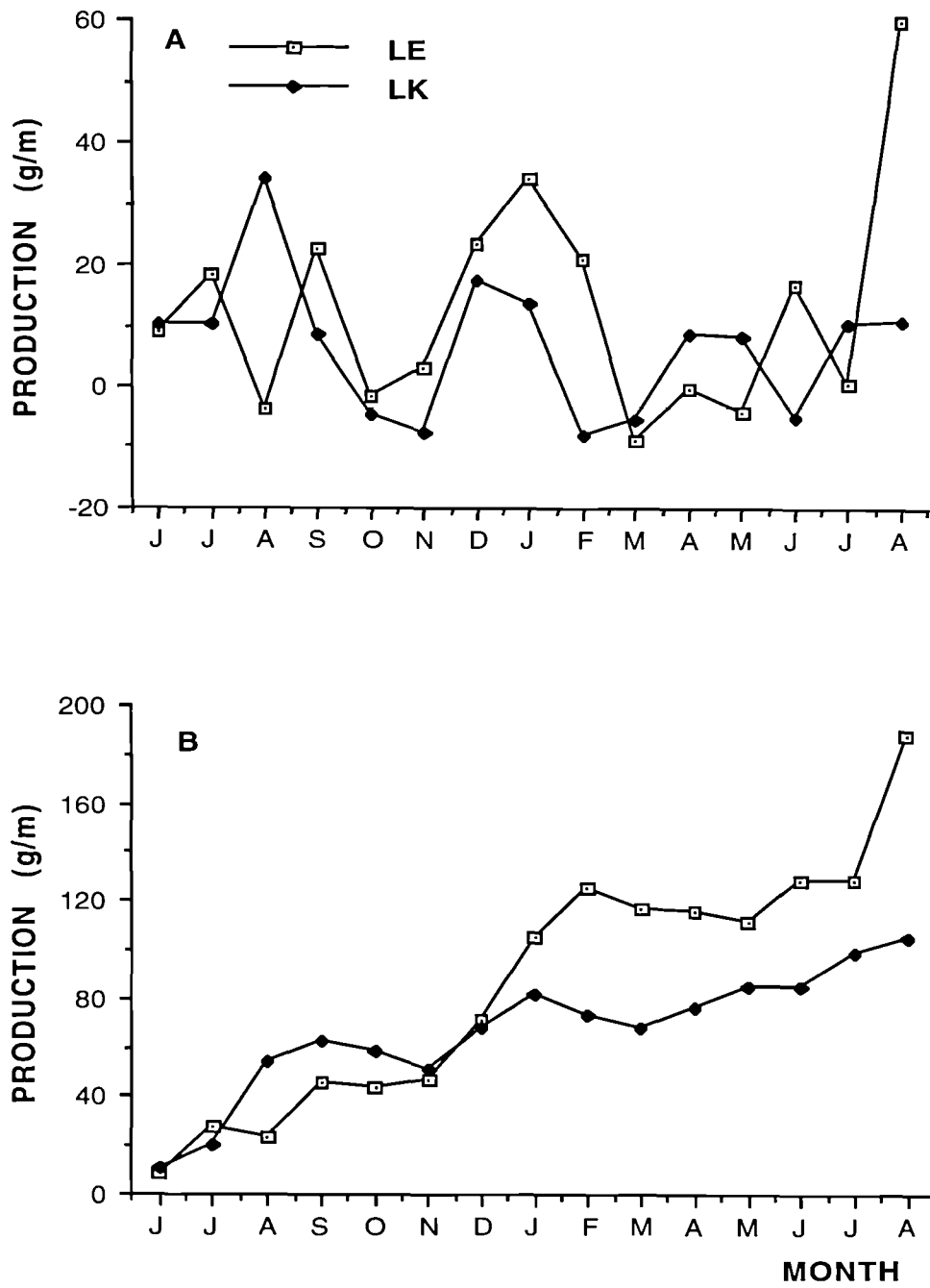


Fig. 31. Monthly (A) and cumulative (B) changes in production in Loch Etive (LE) and Loch Kishorn (LK) from June 1993 to August 1994.

Table-18. Monthly ash-free dry weight (shell + tissue) and computation of production of the rope cultured mussels in Loch Eive from May 1993 to August 1994. (N: mean number live mussels per meter)

Month	Duration (Days)	N	Energy value (Kcal)	Individual Biomass		Changes in Biomass (g ind ⁻¹)	Mean number	Production	
				AFDW (g)	Kcal			(g m mo ⁻¹)	(Kcal m mo ⁻¹)
May		1680	5.26	0.0111±0.005	0.0584				
June	22	1550	5.15	0.0167±0.026	0.0860	0.0056	1615	9.044	44.574
July	33	1510	5.30	0.0286±0.002	0.1516	0.0119	1530	18.207	10.368
August	31	1460	5.21	0.0260±0.007	0.1355	-0.0026	1485	-3.861	-23.909
September	33	1380	5.19	0.0419±0.001	0.2175	0.0159	1420	22.578	116.44
October	31	1260	5.33	0.0405±0.002	0.2159	-0.0014	1320	-1.848	-2.112
November	28	1220	5.39	0.0430±0.001	0.2318	0.0025	1240	3.10	19.716
December	29	1184	5.37	0.0626±0.002	0.3362	0.0196	1202	23.56	125.489
January	34	1090	5.41	0.0656±0.003	0.3549	0.0030	1137	34.11	21.262
February	29	902	5.40	0.0677±0.002	0.3656	0.0021	996	20.916	10.657
March	28	817	5.59	0.0573±0.005	0.3203	-0.0104	860	-8.944	-38.958
April	30	759	5.40	0.0567±0.002	0.3062	-0.0006	788	-0.4728	-11.111
May	32	679	5.62	0.0506±0.002	0.2844	-0.0061	719	-4.386	-0.0218
June	26	568	5.33	0.0775±0.003	0.4131	0.0269	624	16.786	80.309
July	35	450	5.23	0.0784±0.003	0.4100	0.0009	509	0.458	-1.578
August	35	393	5.16	0.0925±0.003	0.4773	0.0141	422	59.502	28.401

Table-19. Monthly ash-free dry weight (shell + tissue) and computation of production of the rope cultured mussels in Loch Kishom from May 1993 to August 1994. (N: mean number live mussels per meter)

Month	Duration (Days)	N	Energy value (Kcal)	Individual Biomass		Mean number	Changes in Biomass (g ind ⁻¹)	Production (g m ⁻¹)	Production (Kcal m ⁻¹)
				AFDW (g)	Kcal				
May	34	1590	5.37	0.0178±0.001	0.0956	1565	0.0066	10.379	50.08
June	33	1540	5.23	0.0244±0.001	0.1276	1493	0.0068	10.1524	64.348
July	30	1446	5.47	0.0312±0.001	0.1707	1383	0.0247	34.1601	155.864
August	35	1320	5.07	0.0559±0.002	0.2834	1283	0.0066	8.4678-4	0.415
September	28	1245	5.11	0.0493±0.002	0.2519	1196	-0.0040	-4.7840	2.153
October	31	1147	5.60	0.0453±0.001	0.2537	1194	-0.0063	-7.5222	-28.823
November	30	1080	5.34	0.0430±0.001	0.2296	1029	0.0169	17.3901	88.597
December	31	978	5.27	0.0599±0.002	0.3157	959	0.0143	13.7137	0.65.883
January	30	940	5.18	0.0742±0.003	0.3844	923	-0.0089	-8.2147	-29.351
February	28	906	5.40	0.0653±0.002	0.3526	860	-0.0063	-5.4180	-15.05
March	27	813	5.68	0.0590±0.002	0.3351	774	0.0110	8.5140	36.455
April	31	735	5.46	0.0700±0.002	0.3822	672	0.0120	8.0640	35.213
May	24	609	5.30	0.0820±0.003	0.4346	574	-0.0001	-0.0574	-15.326
June	37	538	4.98	0.0819±0.003	0.4079	510	0.0199	10.149	58.548
July	37	482	5.13	0.1019±0.003	0.5227	421	0.0254	10.6934	58.645
August		360	5.20	0.1273±0.005	0.6620				

4.2. Effects of Environmental Factors, Depth and Position on Raft on Growth and Mortality of Cultured Mussels

A lantern net experiment was conducted in Loch Etive from May 1993 to August 1994 to check natural mortality and mussel growth within the raft cultivated mussel system and as a control of growth without natural problems under suspended culture condition such as eider duck predation or losses by wave action. As can be seen in Fig. 8, lantern nets were hung from 2 m and 6 m at water inflow and outflow points of the raft.

4.2.1 Environmental Factors

The average environmental conditions during the experimental period are summarized in Table-20. Monthly distribution of temperature and salinity at 2 m and 6 m depths are depicted in Figs. 12 and 14, respectively in Loch Etive. Water temperature decreased very rapidly by 6°C from November to December 1993 which was attributed to snow thawing on nearby mountains. There were minor differences in temperature between the depths, but these were not significantly different ($P>0.05$). At 2 m, temperature ranged from 4.6°C in February to 16.3°C in August 1993 with a mean of $11.12\pm 1.03^\circ\text{C}$ whereas at 6 m, temperature ranged from 5.1°C in February 1994 to 15.7°C in August 1993 with a mean of $11.02\pm 0.96^\circ\text{C}$. Temperature was slightly higher at 2 m than 6 m during summer and vice versa in winter.

Salinity showed significant differences between the depths ($P<0.05$). In general, higher salinity was recorded during the summer months than winter, being affected by rainfall and snow thawing from the surrounding mountains. The minimum salinity at 2 m was 7.5 ‰ in March, with a maximum of 26.8 ‰ in August 1993, while it ranged from 10.75 ‰ to 28.0 ‰ at 6 m. The upper part (0.2 m) of the water column experienced the highest range in salinity from 6 to 26.8 ‰ on the surface. Mean salinity was found to be 20.57 ± 1.36 ‰ and 22.68 ± 1.18 ‰ at a depth of 2 m and 6 m, respectively.

Table-20. Mean (\pm SE) values of environmental parameters in Loch Etive from May 1993 to August 1994, at the inflow and outflow of a mussel culture raft and at 2 m and 6 m depth. POM: particulate organic matter; Ch-a: chlorophyll-a, PN: Particle number.

Parameters		Inflow	Outflow	2 m	6 m
Temperature ($^{\circ}$ C)	Mean	-	-	11.12 \pm 1.03	11.02 \pm 0.96
	Min.			4.6	5.1
	Max.			16.3	15.7
Salinity (‰)	Mean	-	-	20.57 \pm 1.36	22.68 \pm 1.18
	Min.			7.5	10.75
	Max.			26.8	28.0
Seston (mg l^{-1})	Mean	3.00 \pm 0.43	3.00 \pm 0.48	3.20 \pm 0.45	2.80 \pm 0.45
	Min.	1.40	1.10	1.30	1.20
	Max.	7.70	7.70	8.30	7.10
POM (mg l^{-1})	Mean	1.60 \pm 0.15	1.3 \pm 0.13	1.51 \pm 0.15	1.40 \pm 0.13
	Min.	1.00	0.70	0.80	0.90
	Max	2.70	2.20	2.40	2.40
POM %	Mean	54.84 \pm 2.32	50.80 \pm 3.33	51.96 \pm 2.50	54.71 \pm 3.18
	Min.	34.64	22.08	29.09	27.46
	Max.	71.43	66.67	62.16	70.83
Ch-a ($\mu\text{g l}^{-1}$)	Mean	1.81 \pm 0.50	1.34 \pm 0.4	1.81 \pm 0.47	1.81 \pm 0.54
	Min.	0.02	0.00	0.04	0.01
	Max.	8.18	6.49	6.70	7.97
PN	Mean	40098 \pm 2411	31780 \pm 1898	-	-
	Min.	21464	17480		
	Max.	59536	45104		

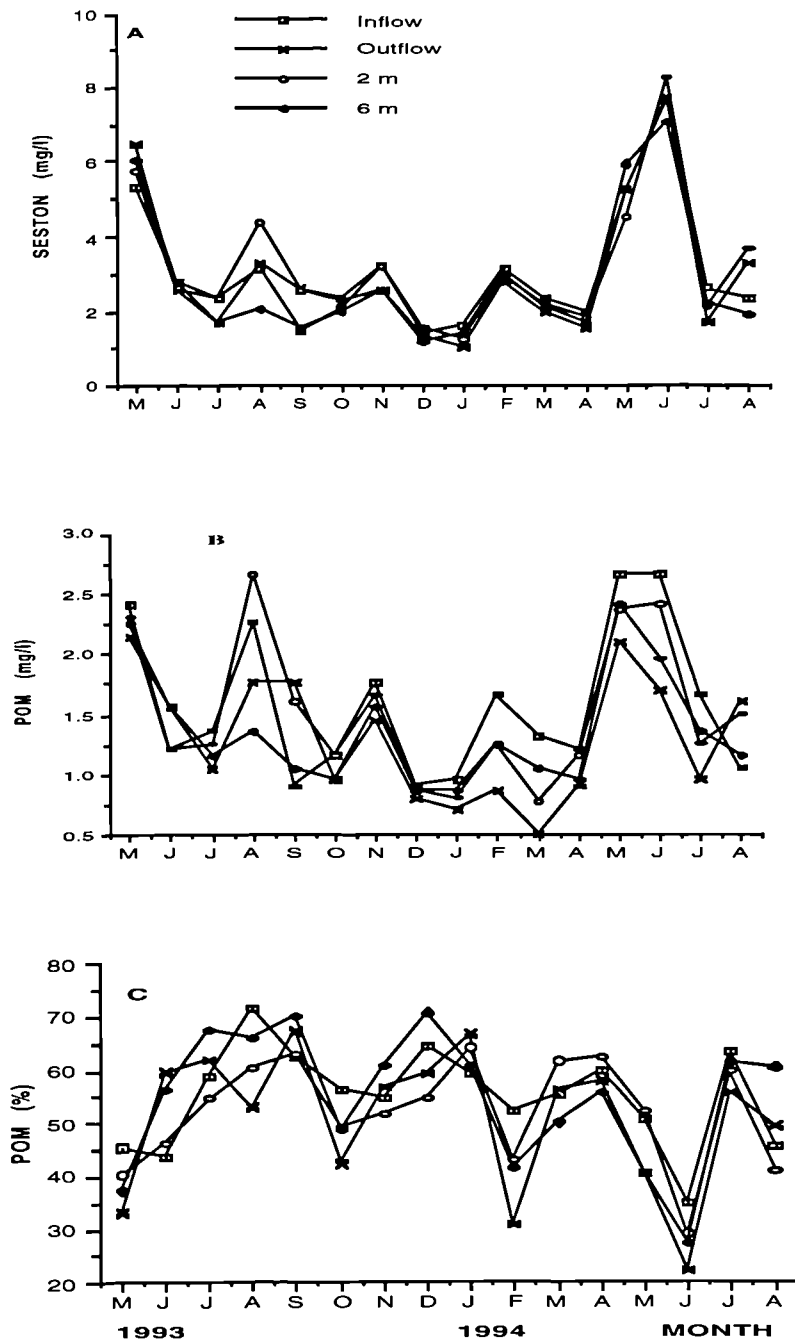


Fig.32. The seasonal cycle of seston (A), particulate organic matter (POM) (B) and POM% (C) in Loch Etive at 2 m and 6 m depth and inflow and outflow of the mussel culture raft during the experimental period.

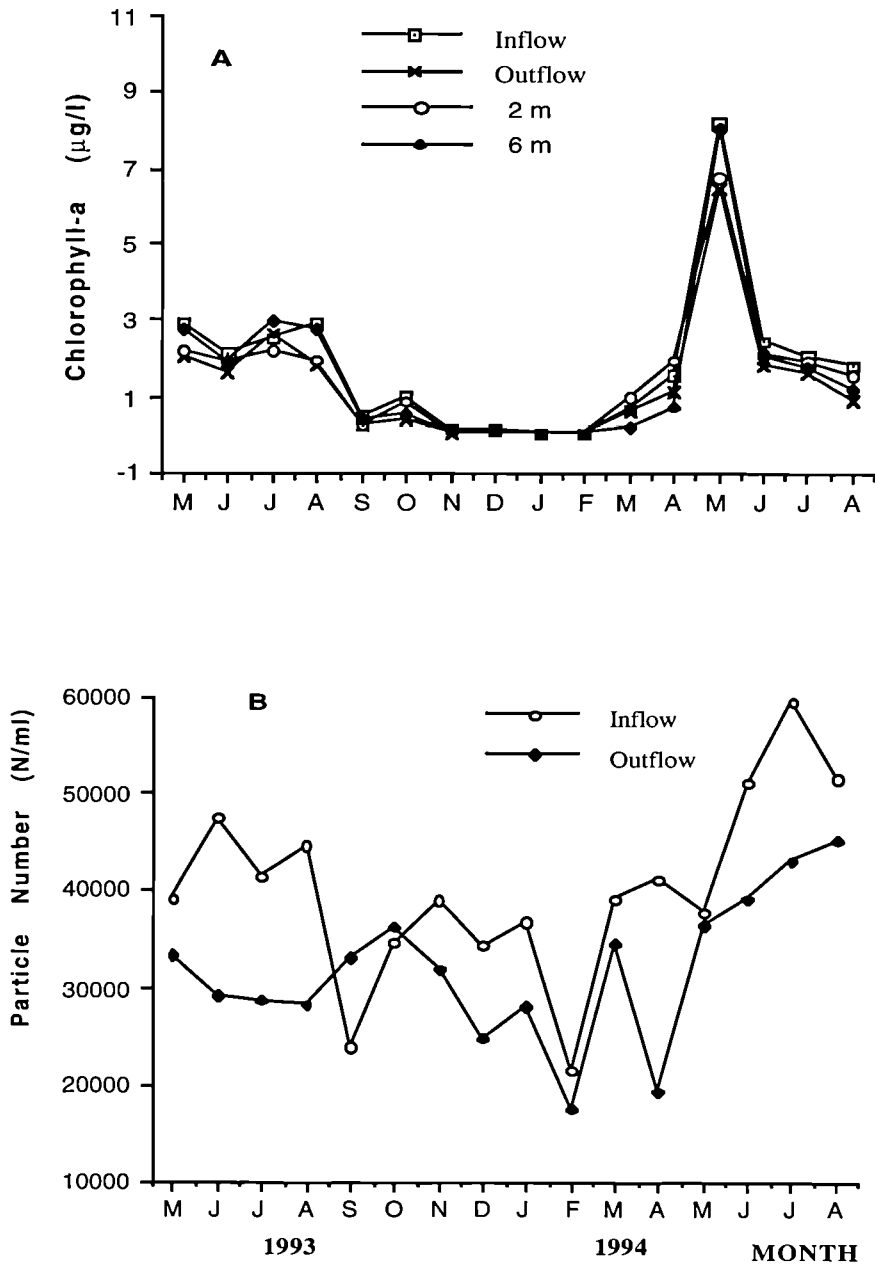


Fig. 33. The monthly changes in chlorophyll- a (A) and particle number (B) in the mussel culture raft system in Loch Etive.

The mean value of seston was $3.20 \pm 0.45 \text{ mg l}^{-1}$ and $2.80 \pm 0.45 \text{ mg l}^{-1}$ at 2 m and 6 m depth respectively, while the values were also similar at the inflow ($3.00 \pm 0.43 \text{ mg l}^{-1}$) and outflow ($3.00 \pm 0.48 \text{ mg l}^{-1}$); i.e. neither depth or position had a significant effect on seston distribution in the raft system. Minimum values of seston were observed during the winter and maximum values in late spring and early summer (Fig. 32).

In general, particulate organic matter (POM) was found to be higher in the summer and spring months than during the winter. It was affected by algal bloom and freshwater run-off into the loch. Minimum, maximum and mean values of POM are depicted in Table 20 and the monthly distribution of POM is shown in Fig. 32. POM varied from 0.7 mg l^{-1} in January at the outflow point to 2.65 mg l^{-1} at 2 m depths inside the raft in August 1993. There were significant differences in POM values between the positions ($P < 0.05$) but not between the depths ($P < 0.05$). Overall POM values averaged $1.60 \pm 0.15 \text{ mg l}^{-1}$ at the inflow and $1.30 \pm 0.13 \text{ mg l}^{-1}$ at the outflow point while POM was recorded as $1.51 \pm 0.15 \text{ mg l}^{-1}$ and $1.40 \pm 0.13 \text{ mg l}^{-1}$ at 2 m and 6 m, respectively inside the raft. POM values were affected significantly by Ch-a and seston concentration.

POM was found to be 19 % higher at the inflow than at the outflow of the raft. Percentage of POM (POM %) in seston was found to be $54.8 \pm 2.3 \%$ at the inflow and $50.8 \pm 3.3 \%$ at the outflow. Percentage of POM (POM %) in seston ranged from 34.6 % to 71.43 % at the inflow and from 22.1 % to 68 % at the outflow, while it ranged from 29.1 % to 62.2 % at 2 m and from 27.5 % to 70.8 % at 6 m inside the raft. Percentage of POM was not statistically different between positions or depths ($P > 0.05$). There was no clear seasonal pattern in distribution of POM% values (Fig. 32).

Monthly distribution of Ch-a values is given in Fig. 33 and Table-20 shows minimum, maximum and mean values of Ch-a. It ranged from $0.02 \mu\text{g l}^{-1}$ to $8.18 \mu\text{g l}^{-1}$ at the raft inflow point and from zero in January to $6.49 \mu\text{g l}^{-1}$ at the outflow from the raft in May 1994. Mean Ch-a values did not differ between the depths, but had a significant response to the position of the raft ($P < 0.05$). Ch-a values were found to be 35 % higher at the inflow than at the outflow of the raft. The low concentrations of the Ch-a, POM and PN at the raft outflow point can be attributed to food consumption by mussels. The number of particles counted was $40,098 \pm 2,411 \text{ number ml}^{-1}$ and $31,780 \pm 1,890 \text{ number ml}^{-1}$ at the

inflow and outflow points of the raft, respectively and these differences were highly significant ($P < 0.001$).

4.2.2. Growth

Mussels with a mean shell length of 22.65 ± 0.68 mm were placed inside the lantern nets in May 1993. Average monthly shell lengths and increments are given in Table -21. Initial, final and incremental length over the experimental period are summarized in Table-23. Monthly average changes recorded in length (L), live weight (LW), wet meat weight (WMW), dry meat weight (DMW) and ash-free dry meat weight (AFDMW) are plotted in Fig. 34. Additionally, the effect of mussel depth and position on their growth was tested by a multifactor analyses of variance (Two-way ANOVA) and results are given in Table 22. Fig. 34 shows that small mussels had a higher growth rate than older mussels. 69.97 % at 2 m and 68.67 % of total increments in shell length occurred from May until October at a depth of 6 m while 69.43 % and 67.59 % of total increments in shell length of mussels occurred at inflow and outflow, respectively from May to October 1993. Animals reached over 45 mm at both depths inside the raft whereas shell length was only 42.84 mm at the outflow point, compared to 47.16 mm at the inflow of the raft. During the winter, the mussel length increments were depressed significantly due to the low amount of available food and low temperature.

Growth rate was increased by algal bloom and increase in temperature, therefore specific growth rate was very low or zero over the winter period, but recovered from April to May 1994. At the end of the experiment, shell length results show that depth had no significant effect on mussel growth ($P > 0.05$), but the position of the raft had a significant effect on growth at the suspended raft system in Loch Etive. As can be seen in Fig. 35, specific growth rate in length (SGR) was found to be higher in young mussels than in older mussels. In June 1993, the highest SGR values were 30.6 %, 33.95 %, 30.95 % and 33.55 % at 2 m, 6 m, and the inflow and outflow points of the raft, respectively. Neither depth nor position had any significant effect on SGR ($P > 0.05$).

4.2.3. Shell Characteristics

Shell characteristics at the end of the experiment are summarised in Table-24. Neither position nor depth on the raft had any significant effect on the mussel height : length ratio, but there was a significant effect of depth on width : height and width : length ratio ($P < 0.05$). Linear regression analyses of shell length : height and length : width are shown in Fig. 36, for 2 m and 6 m depths. A significant positive relationship was found between length : width and length : height ($P < 0.05$).

4.2.4. Mortality

Monthly mortality and cumulative mortality are plotted in Fig. 37. Neither depth nor position had a significant effect on mortality ($P > 0.05$). Mortality rate was found to be higher in the younger mussels. Over the experimental period, cumulative mortality was 13.54 %, 12.87 %, 12.57 % and 14.03 % at the 2 m, 6 m, and inflow and outflow points of raft respectively. The highest monthly mortality was found to be 3.11 % and 2.53 % at 2 m and 6 m in June 1993 while it was 2.65 % and 2.99 % at the inflow and outflow points of the raft. These high mortality rates were attributed to the handling of the mussels necessary at the start of the experiment.

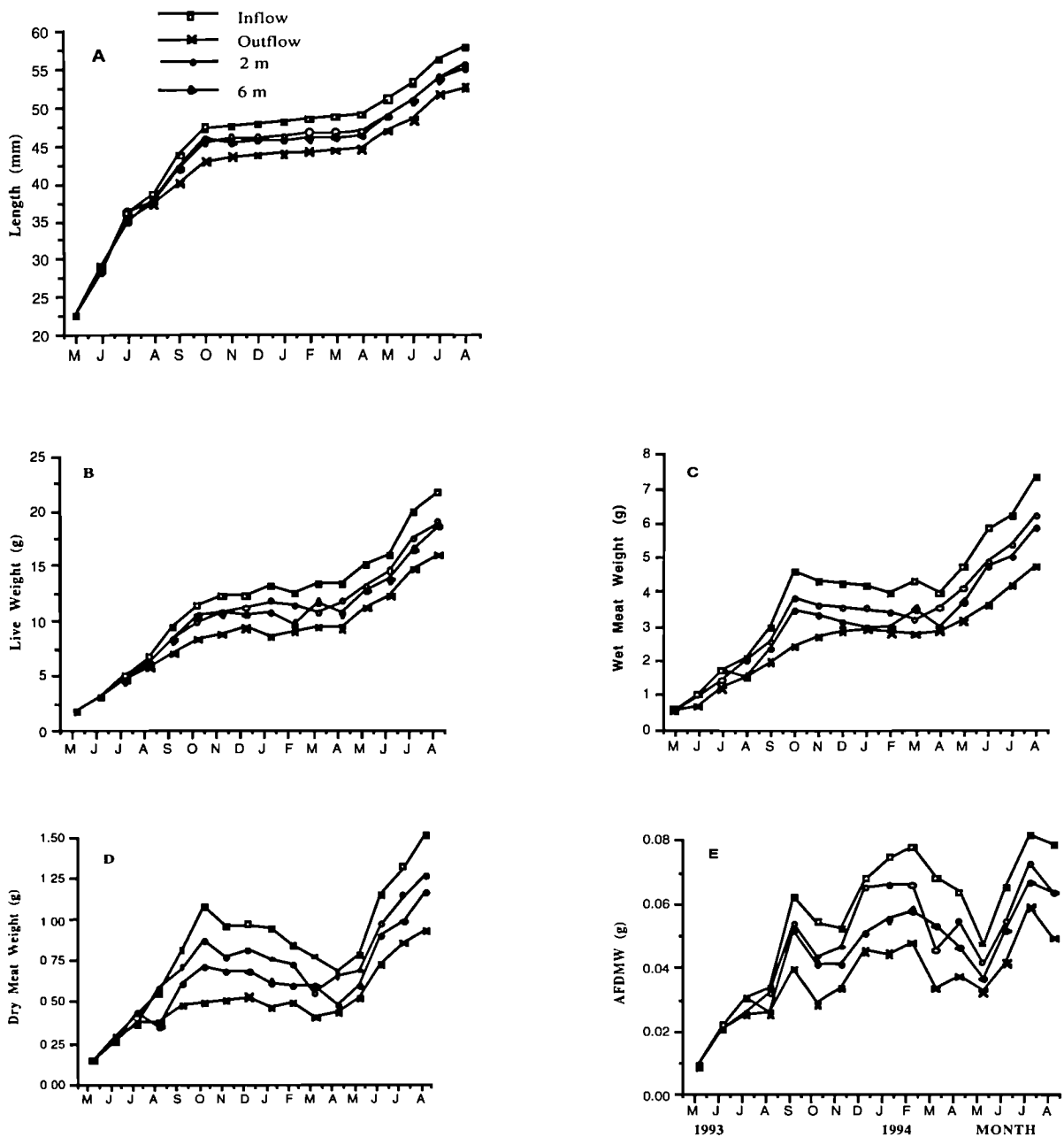


Fig. 34. Monthly distribution of length (A), live weight (B), wet meat weight (C), dry meat weight (D) and ash-free dry meat weight (AFDMW) (E) in lantern nets in Loch Etive at 2 m and 6 m depth and at the inflow and outflow points of a culture raft.

Table-21. Average monthly shell lengths (mm) in Loch Etive from May 1993 to August 1994, at 2 m and 6 m depth and at the inflow and outflow points of a culture raft. ($\Delta L=L_2-L_1$, mm).

Month	2 m	ΔL	6 m	ΔL	Inflow	ΔL	Outflow	ΔL
May	22.65		22.65		22.65		22.65	
June	28.35	5.7	29.05	6.4	28.43	5.78	28.97	6.32
July	36.21	7.86	34.96	5.91	36.01	7.58	35.16	6.19
August	37.7	1.49	38.17	3.21	38.59	2.58	37.28	2.12
September	41.61	3.91	42.10	3.93	43.65	5.06	39.98	2.70
October	45.3	3.69	45.23	3.13	47.16	3.51	42.84	2.86
November	45.90	0.60	45.41	0.18	47.50	0.34	43.35	0.51
December	45.98	0.08	45.44	0.03	47.65	0.15	43.54	0.19
January	46.23	0.25	45.60	0.16	48.12	0.47	43.93	0.39
February	46.57	0.34	45.81	0.21	48.31	0.19	44.10	0.17
March	46.64	0.07	45.91	0.10	48.62	0.31	44.29	0.19
April	46.82	0.18	46.09	0.18	48.99	0.37	44.37	0.08
May	48.64	1.82	48.81	2.72	50.98	1.99	46.83	2.46
June	50.75	2.11	50.79	1.98	53.24	2.26	48.38	1.55
July	53.91	3.16	53.66	2.87	56.16	2.92	51.79	3.41
August	54.94	1.03	55.53	1.87	57.95	1.79	52.52	0.73

Table-22 Mean (\pm SE) initial and final growth parameters and increments over a 15 months experimental period in Loch Etive. Superscript letters indicate one-way ANOVA test comparisons of mean values, those with letters in common are not significantly different at $P < 0.05$. LW: live weight; WMW: wet meat weight; DMW: dry meat weight and AFDMW: ash-free dry meat weight, SW: shell weight.

Parameter	2 m	6 m	Inflow	Outflow
L (mm)				
Initial	22.65 \pm 0.68	22.65 \pm 0.68	22.65 \pm 0.68	22.65 \pm 0.68
Final	54.94 \pm 1.23	55.53 \pm 1.13	57.95 \pm 1.16	52.52 \pm 0.71
Increment	32.29 ^b	32.88 ^b	35.30 ^c	29.87 ^a
LW (g)				
Initial	1.16 \pm 0.11	1.16 \pm 0.11	1.16 \pm 0.11	1.16 \pm 0.11
Final	18.36 \pm 0.45	18.13 \pm 0.89	21.07 \pm 1.06	15.43 \pm 0.63
Increment	17.2 ^b	16.97 ^b	19.91 ^c	14.27 ^a
WMW (g)				
Initial	0.55 \pm 0.06	0.55 \pm 0.06	0.55 \pm 0.06	0.55 \pm 0.06
Final	6.18 \pm 0.53	5.84 \pm 0.36	7.27 \pm 0.46	4.75 \pm 0.23
Increment	5.63 ^b	5.29 ^b	6.72 ^c	4.20 ^a
DMW (g)				
Initial	0.11 \pm 0.01	0.11 \pm 0.01	0.11 \pm 0.01	0.11 \pm 0.01
Final	1.23 \pm 0.46	1.13 \pm 0.28	1.47 \pm 0.37	0.9 \pm 0.17
Increment	1.12 ^b	1.02 ^b	1.36 ^c	0.78 ^a
SW (g)				
Initial	0.33 \pm 0.03	0.33 \pm 0.03	0.33 \pm 0.03	0.33 \pm 0.03
Final	5.90 \pm 0.29	5.56 \pm 0.28	6.71 \pm 0.31	4.74 \pm 0.19
Increment	5.57 ^b	5.23 ^b	6.38 ^c	4.41 ^a
AFDMW (g)				
Initial	0.0074 \pm 0.001	0.0074 \pm 0.001	0.0074 \pm 0.001	0.0074 \pm 0.001
Final	0.0623 \pm 0.006	0.0615 \pm 0.004	0.0768 \pm 0.005	0.0475 \pm 0.002
Increment	0.0546 ^b	0.0541 ^b	0.0712 ^c	0.040 ^a

Table-23. Two-way analysis of variance (ANOVA) for growth parameters of mussel reared in lantern nets in Loch Etive. (Pos: position, ns : not significant, P<0.05 : *, P<0.01: ** and P<0.001 :**)

Parameters	Source	DF	SS	MS	F	P
Length	Pos	1	755.15	755.15	51.83	***
	Depth	1	6.86	6.85	0.47	ns
	Pos*Depth	1	17.31	17.31	1.19	ns
	Error	96	1398.60	14.57		
	Total	99	2177.92			
LW	Pos	1	794.51	794.51	68.78	***
	Depth	1	1.33	1.33	0.12	ns
	Pos*depth	1	72.91	72.91	6.31	*
	Error	96	1108.86	11.55		
	Total	99	1977.62			
WMW	Pos	1	159.09	159.09	82.23	***
	Depth	1	2.846	2.846	1.47	ns
	Pos*Depth	1	17.098	17.098	8.84	**
	Error	96	185.721	1.935		
	Total	99	364.753			
DMW	Pos	1	8.4629	8.4629	109.57	***
	Depth	1	0.129	0.129	1.67	ns
	Pos*Depth	1	0.6755	0.6755	8.75	***
	Error	96	7.4149	0.0772		
	Total	96	16.6823			
AFDMW	Pos	1	0.021447	0.021447	102.76	***
	Depth	1	0.000384	0.000384	1.84	ns
	Pos*Depth	1	0.001669	0.001669	7.99	**
	Error	96	0.020034	0.000209		
	Total	96	0.043531			

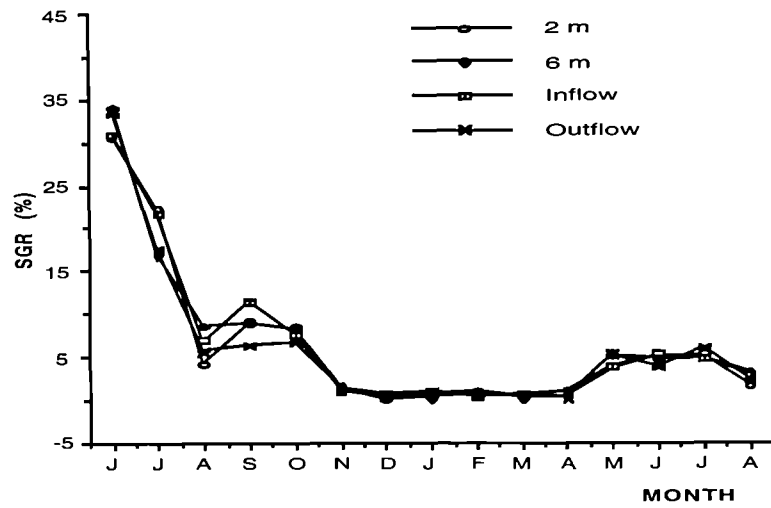


Fig. 35. Monthly specific growth rate in length (SGR %) in the lantern net experiment in Loch Etive from June 1993 to August 1994, at 2 m and 6 m depth and at the inflow and outflow points of the mussel culture raft.

Table-24. Mean shell characteristics (\pm SE) of mussels in the lantern net experiment in Loch Etive, at 2 m and 6 m depth and at the inflow and outflow points of the culture raft. Data in the same column carrying the same superscript are not significantly different from each other at $P>0.05$. (L is the shell length, W is the shell width and H is the shell height).

Depth and Position	Weight (g)	Length (L, mm)	Height (H, mm)	Width (W, mm)	W:L
Initial	0.33 \pm 0.03	22.65 \pm 0.68	13.27 \pm 0.42	8.76 \pm 0.31	
	0.39 \pm 0.007 ^a	0.66 \pm 0.015 ^a	0.59 \pm 0.011 ^a		
2 m	5.90 \pm 0.42	54.94 \pm 1.23	28.27 \pm 0.66	22.62 \pm 0.67	
	0.41 \pm 0.008 ^{bc}	0.79 \pm 0.015 ^c	0.52 \pm 0.005 ^a		
6 m	5.60 \pm 0.28	55.53 \pm 1.13	29.45 \pm 0.52	21.79 \pm 0.45	
	0.39 \pm 0.008 ^a	0.74 \pm 0.015 ^a	0.53 \pm 0.008 ^a		
Inflow	6.70 \pm 0.31	57.95 \pm 1.15	30.43 \pm 0.56	23.57 \pm 0.53	
	0.41 \pm 0.008 ^{bc}	0.78 \pm 0.018 ^{bc}	0.53 \pm 0.008 ^a		
Outflow	4.70 \pm 0.19	52.52 \pm 0.73	27.80 \pm 0.43	20.84 \pm 0.39	
	0.40 \pm 0.008 ^{ab}	0.75 \pm 0.013 ^{ab}	0.53 \pm 0.005 ^a		

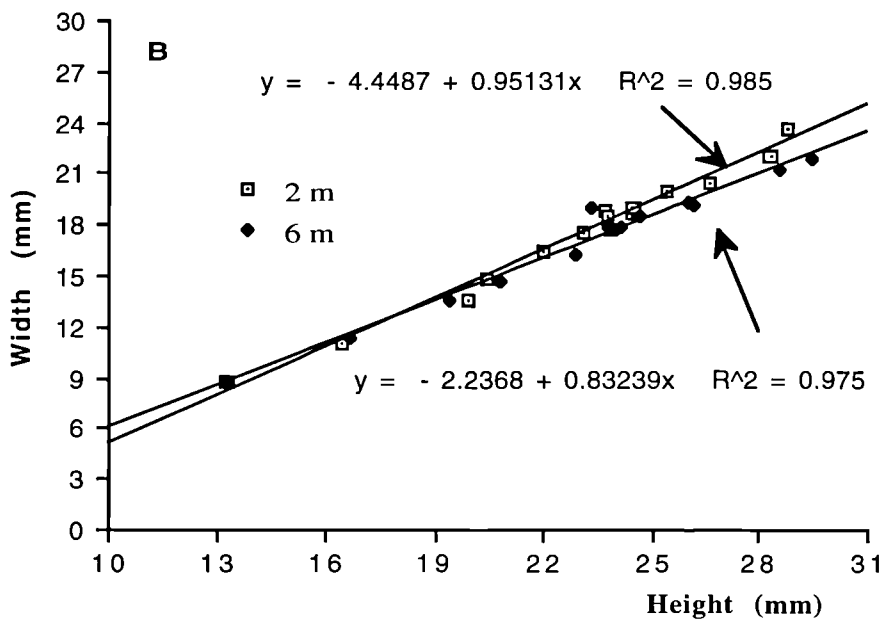
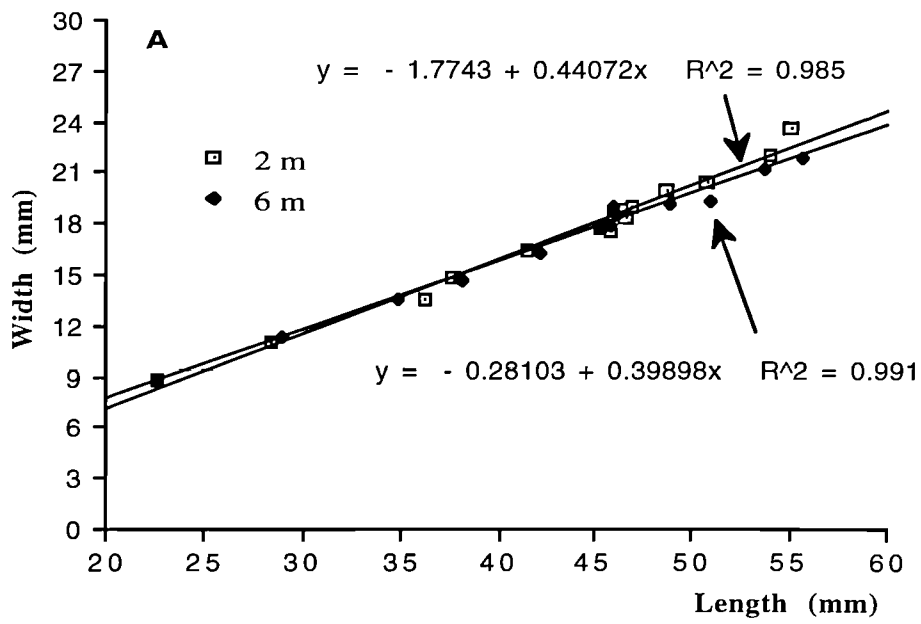


Fig. 36. Length-width (A) and height-width (B) relationships at 2 m and 6 m depth in the lantern net experiment in Loch Etive.

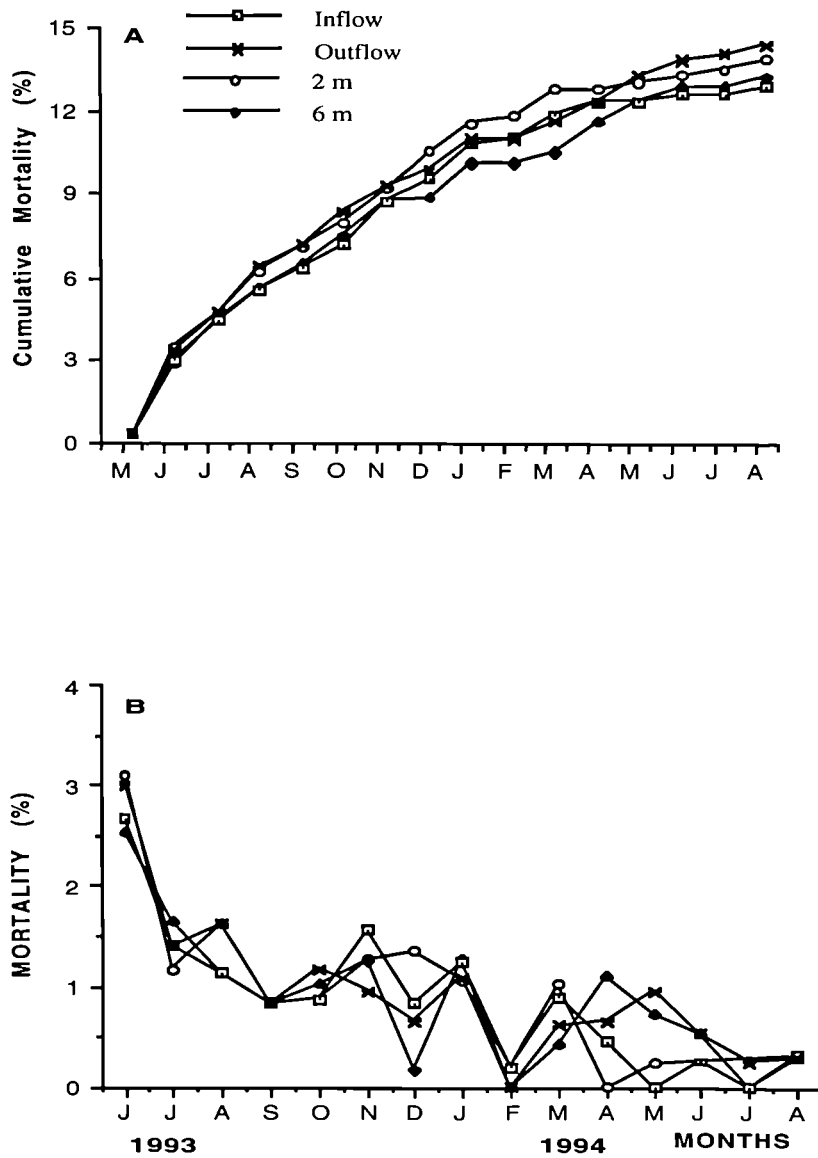


Fig. 37. Cumulative (A) and monthly mortality (B) of mussels in lantern nets in Loch Etive from June 1993 to August 1994, at 2 m and 6 m depth and at the inflow and outflow points of the culture rafts

4.3. Growth and Mortality of Mussels Reared in Lantern Nets in Loch

Kishorn

A lantern net experiment was carried out to monitor growth and natural mortality of mussels in comparison to rope cultured mussels in Loch Kishorn from May 1993 to August 1994. Four lantern nets (two from 2 m and two at 6 m depth) were suspended from a mussel raft at two different points to monitor growth in the system. Monthly records of environmental parameters, their mean values and the effects on mussel growth are presented in Chapter 4.1.1.

4.3.1. Growth

The initial mussel size ranged from 18.4 mm to 30.5 mm, with a mean of 24.14 ± 0.40 mm (\pm SE). These animals were stocked in lantern nets. Monthly shell distribution is depicted in Fig. 38 and the values of shell length and monthly increments are given in Table-25. One-way ANOVA comparisons between the depths and mean values for 2 m and 6 m are given in Table-26. At the end of the experiment, mussel length ranged from 47 mm to 62.9 mm at 2 m depth and from 46.2 mm to 57.1 mm at 6 m depth. Growth rate was observed to be higher in the small mussels compared with larger ones. Length increments of 28.78 mm and 26.89 mm occurred at 2 m and 6 m, respectively. The increment in shell length was higher at 2 m than 6 m but the difference was not significant ($P > 0.05$). At 2 m, 67.62 % of the increase in length occurred from May to September 1993 while at 6 m, the length increase was 62.85 % over the same period. Shell growth was almost absent during winter because of low available food and low temperature.

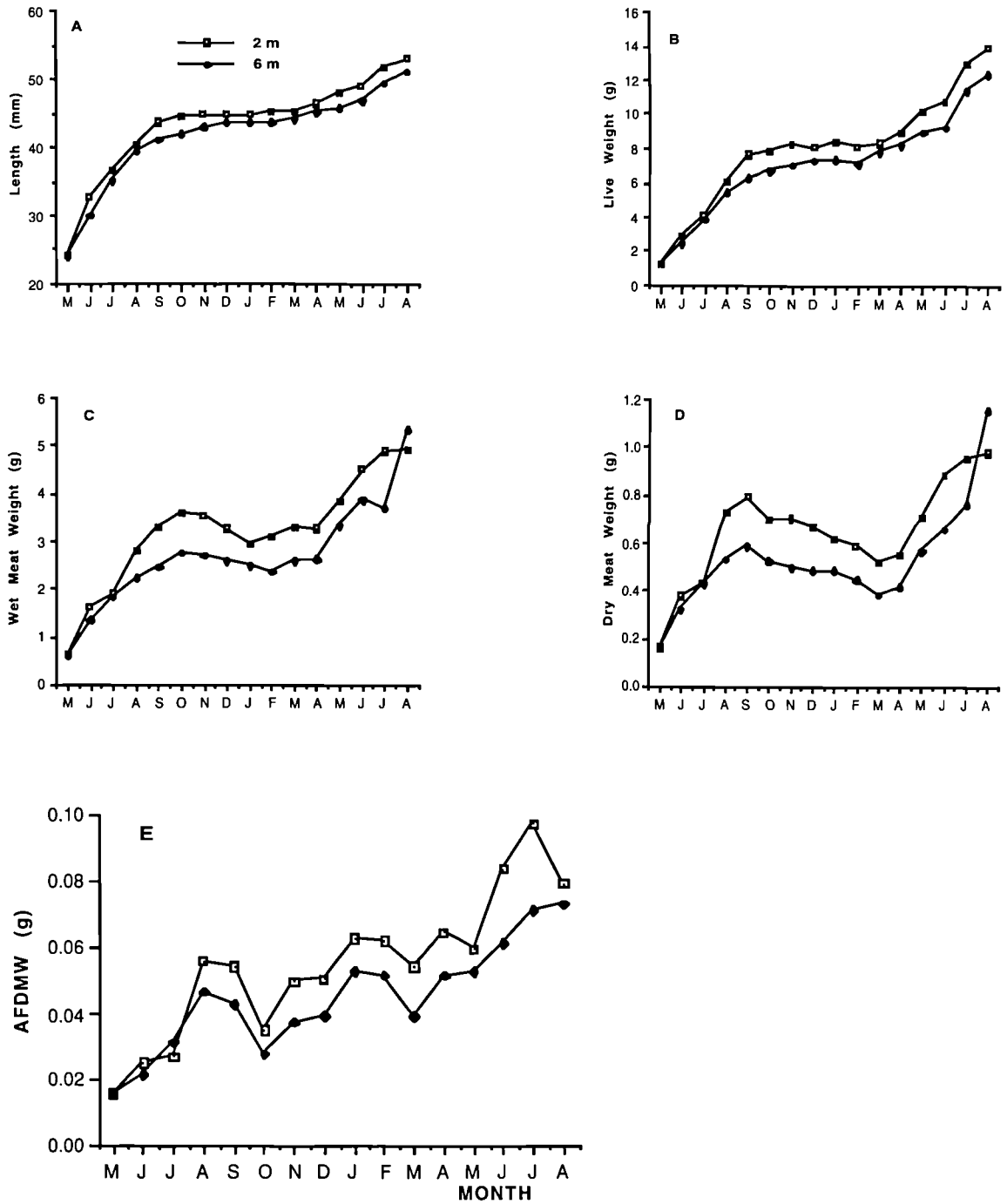


Fig. 38. Monthly distribution of shell length (A), live weight (B), wet meat weight (C), dry meat weight (D) and ash-free dry meat weight (AFDMW) (E) in the lantern nets experiment in Loch Kishorn, at 2 m and 6 m depth from May 1993 to August 1994.

Table-25. Monthly mean shell length and growth increment ($\Delta L=L_2-L_1$, mm) of experimental mussels reared at depths of 2 m and 6 m in lantern nets in Loch Kishorn.

	2 m	ΔL	6 m	ΔL
May	24.14		24.14	
June	32.69	8.55	29.99	5.85
July	36.55	3.86	35.15	5.16
August	40.46	3.91	39.36	4.21
September	43.60	3.14	41.04	1.68
October	44.43	0.83	41.86	0.80
November	44.59	0.16	42.98	1.14
December	44.71	0.12	43.55	0.57
January	44.73	0.02	43.64	0.09
February	45.05	0.32	43.69	0.05
March	45.38	0.33	43.96	0.27
April	46.38	1.00	45.06	1.10
May	47.82	1.44	45.72	0.60
June	48.89	1.07	46.81	1.09
July	51.75	2.86	49.27	2.46
August	52.92	1.17	51.03	1.76

The monthly distribution of specific growth rate in length is depicted in Fig. 39. Specific growth rate ranged from 0.04 % to 26.75 % at a depth of 2 m, while it ranged from 0.12 mm to 19.15% at 6 m depth. Average SGR values were 4.83 % and 4.65 % at 2 m and 6 m, respectively over the 15 months experimental period. Maximum values for SGR were obtained in June 1993 at both sites, while minimum value of SGR occurred in December at 2 m whereas it was minimum at 6 m in February 1994. High SGR values reflected available food and temperature conditions, with minimum values coinciding with low temperature and low food supply in winter.

Monthly live weight (LW) changes are shown in Fig. 38 and final values are given in Table-26. The mussels which were used for the lantern net experiment ranged from 0.65 g to 2.33 g in total weight (live weight). Initial mean live weight was 0.58 g and reached 13.89 ± 0.56 g at 2 m and 12.30 ± 0.39 g at 6 m after 15 months. Increments in LW were slightly higher at 2 m (13.31 g) than 6 m (11.72 g), but this difference was not significant

($P>0.05$). At the end of the experiment live weight ranged from 9.25 g to 23.65 g at 2 m depth compared to 8.57 g to 17.66 g at 6 m. Live weight was affected by gonadal development and gamete release, as well as by growth changes in tissue and in shell weight. Some negative increments in wet meat weight were recorded due to low gonadal development, spawning, or consumption of reserved energy in winter. Initial, final weight and ash-free dry meat weight is given in Table-26. Monthly changes in WMW, DMW and AFDMW are shown in Fig. 38.

Table-26. Mean, (\pm SE) initial and final growth parameters and increments at 2 m and 6 m in the lantern net experiment in Loch Kishorn from May 1993 to August 1994. Superscript letters indicate one-way ANOVA test comparisons of mean values. Those letters in common in the same row are not significantly different at $P<0.05$.

Parameters		2 m	6 m
Length (mm)	Initial	24.14 \pm 0.40	24.14 \pm 0.40
	Final	52.92 \pm 0.72	51.03 \pm 0.60
	Increment	28.78 ^a	26.89 ^a
LW (g)	Initial	0.58 \pm 0.06	0.58 \pm 0.06
	Final	13.89 \pm 0.56	12.30 \pm 0.39
	Increment	13.31 ^a	11.72 ^a
WMW (g)	Initial	0.62 \pm 0.03	0.62 \pm 0.03
	Final	4.91 \pm 0.19	5.33 \pm 0.19
	Increment	4.29 ^a	4.71 ^a
DMW (g)	Initial	0.158 \pm 0.08	0.158 \pm 0.08
	Final	0.974 \pm 0.038	1.167 \pm 0.41
	Increment	0.816 ^a	1.009 ^a
AFDMW (g)	Initial	0.0154 \pm 0.001	0.0154 \pm 0.001
	Final	0.0798 \pm 0.003	0.0735 \pm 0.003
	Increment	0.0644 ^a	0.0581 ^a

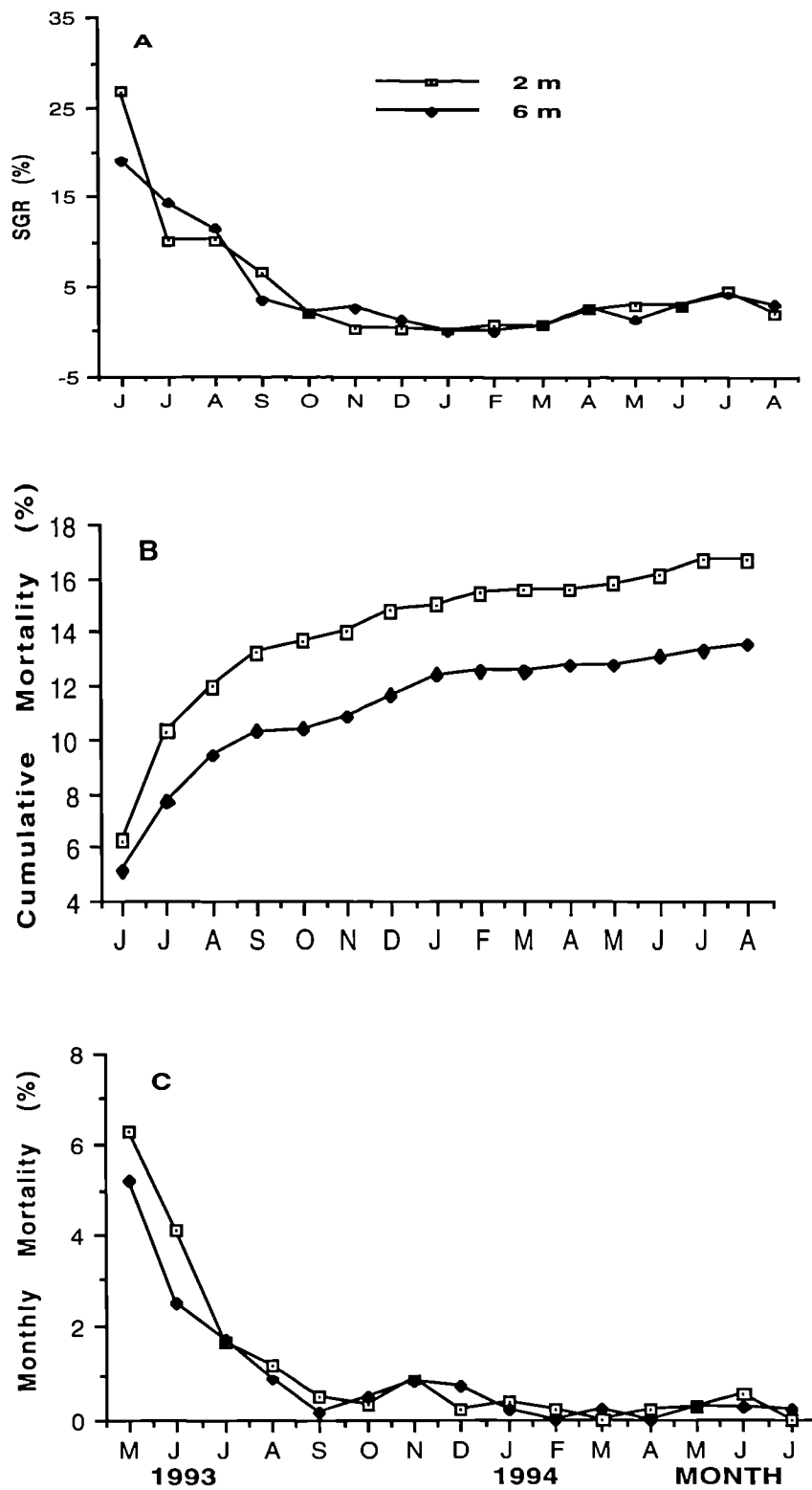


Fig. 39. Monthly specific growth rate in length (SGR%) (A), cumulative mortality (B) and monthly mortality (C) at 2 m and 6 m depth in the lantern nets experiment between May 1993 and August 1994.

were slightly higher at 2 m (13.31 g) than 6 m (11.72 g), but this difference between the depths was not significant ($P>0.05$). At the end of the experiment live weight ranged from 9.25 g to 23.65 g at 2 m depth compared to 8.57 g to 17.66 g at 6 m. Live weight was affected by gonadal development and gamete release, as well as by growth changes in tissue and in shell weight. Some negative increments were recorded due to low gonadal development, spawning, or consumption of energy reserves in winter.

In general, there were clear seasonal trends in mussel WMW and DMW, with both values being high in summer and decreasing over winter in 1993. A quick recovery was observed in WMW and DMW in early spring and these values reached a maximum at the end of the summer at both depths in 1994. There were no significant differences between the depths ($P>0.05$) at the end of the experiment, but the values of WMW and DMW were generally higher at 2 m than at 6 m, except in the final months. There was no clear seasonal cycle in AFDMW in Loch Kishorn. AFDMW was higher at 2 m than at 6 m over the experimental period, but not significantly different ($P>0.05$).

4.3.2 Mortality

Mortality rate was higher in the younger mussels than the older ones. The trends in monthly mortality and cumulative mortality are depicted in Fig.39. Cumulative mortality was found to be 16.73 % at 2 m, compared to 13.55 % at 6 m. Overall monthly mortality was 1.12 % and 0.9 % at 2 m and 6 m depth, respectively. Monthly mortality reached a maximum of 6.26 % at 2 m and 5.17 % at 6 m in June 1993 ($\chi^2=0.834$, $P>0.05$), however mortality was found to be zero at 2 m in April and August 1994 while it was zero at 6 m in March 1994. 37.4 % of the total mortality was recorded from May 1993 to June 1993 at 2 m while 38.15 % of the total mortality at 6 m occurred in June. The highest mortality rate was observed in the young mussels just after stocking them into the lantern nets which can be attributed to handling stress. The differences in mortalities with depth were not significant over the 15 months experimental period ($\chi^2=3.841$, $P>0.05$).

4.3.3 Shell Characteristics

Monthly changes in shell weight are shown in Fig. 40. The effect of depth on mean values and ratios of shell characteristics analysed by one-way ANOVA is given in Table-27. The initial shell weight was 0.39 ± 0.02 g and length 24.14 ± 0.40 mm. Mussels reached 4.56 ± 0.18 g and 52.92 ± 0.72 mm at 2 m and 3.96 ± 0.13 g and 51.03 ± 0.60 mm at 6 m by the end of the lantern net experiment. Shell length differed insignificantly ($P>0.05$), but shell weight showed a significant difference between the two depths over the 15 month experimental period ($P<0.05$). Shell height and width were noted to be slightly higher at 2 m than at 6 m, but were not significantly different ($P>0.05$).

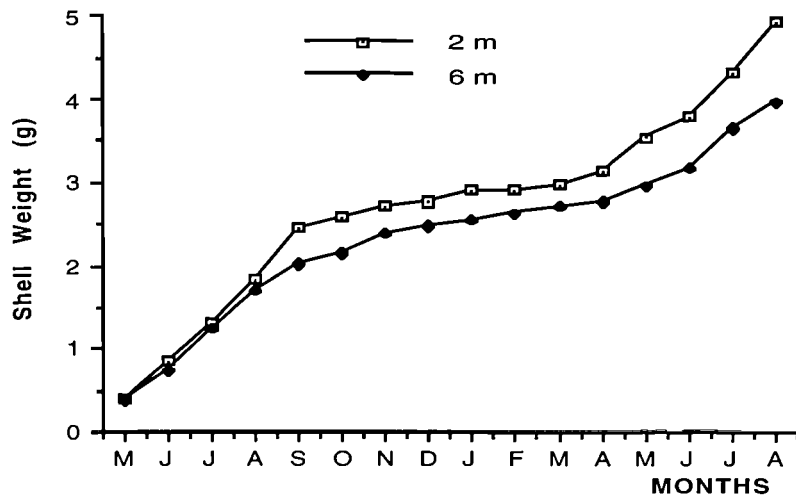


Fig. 40. Monthly distribution of shell weight at 2 m and 6m depth in the lantern nets experiment in Loch Kishorn from May 1993 to August 1994.

Table-27. Mean (\pm SE) shell characteristics of mussels from two different depths reared in lantern nets in Loch Kishorn over a 15 months experimental period. Superscript letters indicate one-way ANOVA test comparison. Values in the same column with the same superscript are not significantly different ($P>0.05$).

	Depth	Length (mm)	Weight (g)	Height (mm)	Width (mm)	W:L	W:H	H:L
Initial		24.14 \pm 0.40	0.39 \pm 0.02	13.04 \pm 0.19	8.16 \pm 0.15	0.34 \pm 0.004	0.63 \pm 0.008	0.54 \pm 0.005
Final	2 m	52.92 \pm 0.72 ^a	4.56 \pm 0.18 ^b	25.79 \pm 0.32 ^a	19.88 \pm 0.34 ^a	0.38 \pm 0.004 ^a	0.77 \pm 0.009 ^a	0.49 \pm 0.004 ^a
	6 m	51.03 \pm 0.60 ^a	3.96 \pm 0.13 ^a	25.12 \pm 0.30 ^a	18.77 \pm 0.26 ^a	0.37 \pm 0.004 ^a	0.75 \pm 0.009 ^a	0.49 \pm 0.003 ^a

4.4. The Effect of Environmental Factors on Condition Index and Biochemical Composition in Raft Cultured Mussels

4.4.1. Condition Index

Length distributions of mussels which were used for condition index (CI), meat yield (MY) and biochemical composition are given in Fig. 20. Seasonal variations in CI of experimental mussels at 2 m and 6 m are depicted in Figs. 41 and 42 and minimum maximum and mean values are given in Table-28.

Correlation matrices between condition index, MY, shell length, biochemical composition and environmental factors are shown in Tables 31 and 32. The monthly distributions of MY at depths of 2 m and 6 m are depicted in Fig. 43 for Loch Etive and Loch Kishorn. The results of two-way ANOVA are given in Table-29.

The condition index is mainly affected by accumulation and release of reproductive materials as well as the utilization of stored energy resources during the winter months. Changes in the two condition indices, CIV and CID, had similar patterns, were highly correlated in both Loch Etive ($r=0.815$, $P<0.001$) and Loch Kishorn ($r=0.707$, $P<0.01$) and showed a clearly defined seasonal cycle. The maximum CIV value occurred in July in Loch Kishorn and in May 1993 in Loch Etive. Gonad release occurred more than once in Loch Kishorn and in May 1993 in Loch Etive. The trend in condition index in 1993 and 1994 showed that spawning time is variable year to year.

The minimum CIV values for Loch Etive and Loch Kishorn mussels occurred in March and April, respectively and, together with the quick recovery in the May and June samples reflected the main period of first spawning and recovery. A second spawning occurred in July, with a rapid recovery in August 1994 at both sites. Average CIV in Loch Etive was found to be $42.37\pm 1.69\%$ at 2 m and $41.36\pm 1.23\%$ at 6 m, while at Loch Kishorn values were $58.03\pm 2.28\%$ at 2 m and $56.03\pm 2.2\%$ at 6 m. The mean CID at Loch Etive was $10.21\pm 0.64\%$ at 2 m and 9.57 ± 0.58 at 6 m and at Loch Kishorn it was $12.82\pm 0.7\%$ at 2 m and $12.53\pm 0.73\%$ at 6 m. The CI was slightly higher at 2 m than 6 m

Table-28. Minimum, maximum and mean values of condition indices and meat yield for Loch Etive and Loch Kishorn mussels over a 15 months experimental period.
 LE: Loch Etive; LK: Loch Kishorn; CIV: Wet meat volume condition index;
 CID: Dry meat weight condition index and MY: Meat yield in percentage.

SITE		CIV	CID	MY
LE	Minimum	35.00	5.89	29.4
	Maximum	51.96	13.95	49.5
	Mean	41.87	9.89	33.9
LK	Minimum	42.11	7.63	34.8
	Maximum	69.34	17.45	56.8
	Mean	57.03	12.68	44.2

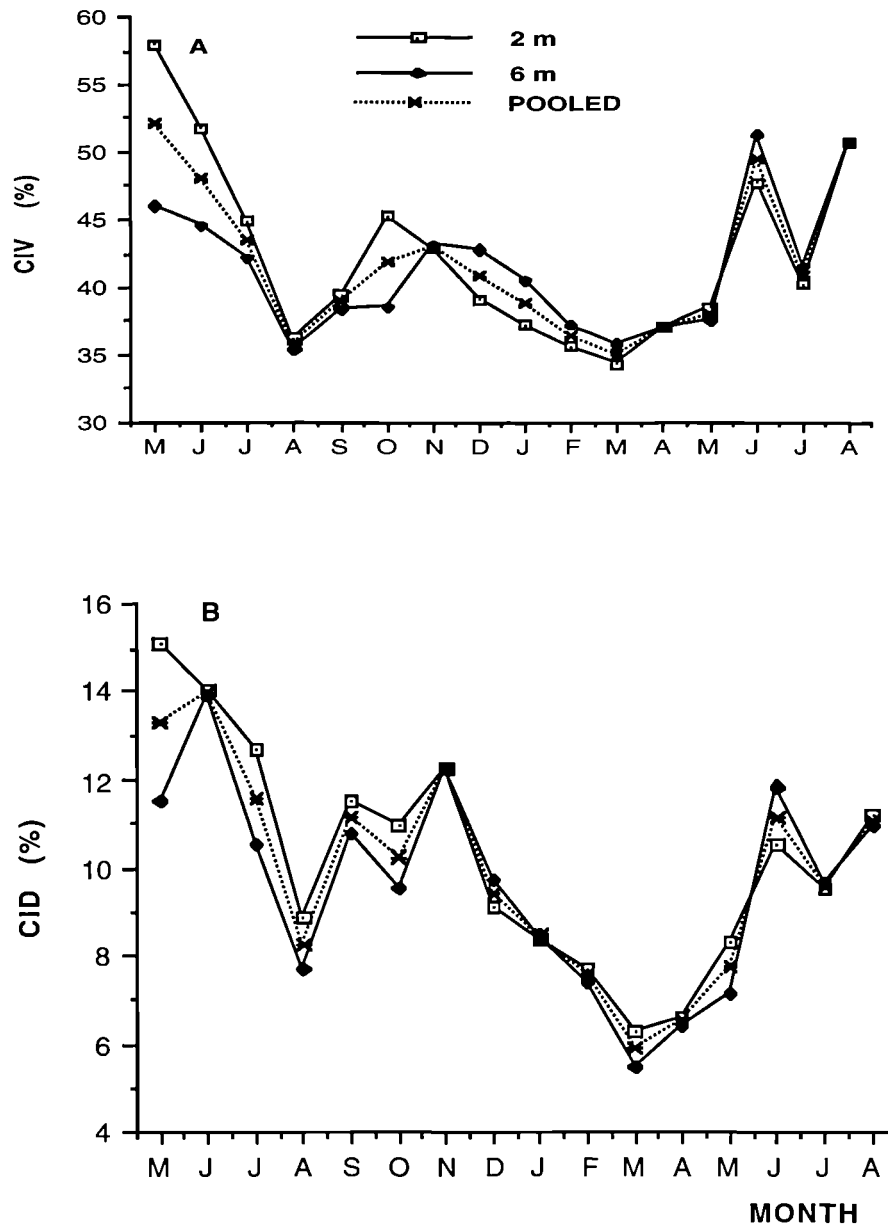


Fig. 41. Monthly distribution of wet meat volume condition index (CIV) (A) and dry meat weight condition index (CID) (B) at 2 m and 6 m and the pooled value for the two depths in Loch Etive from May 1993 to August 1994.

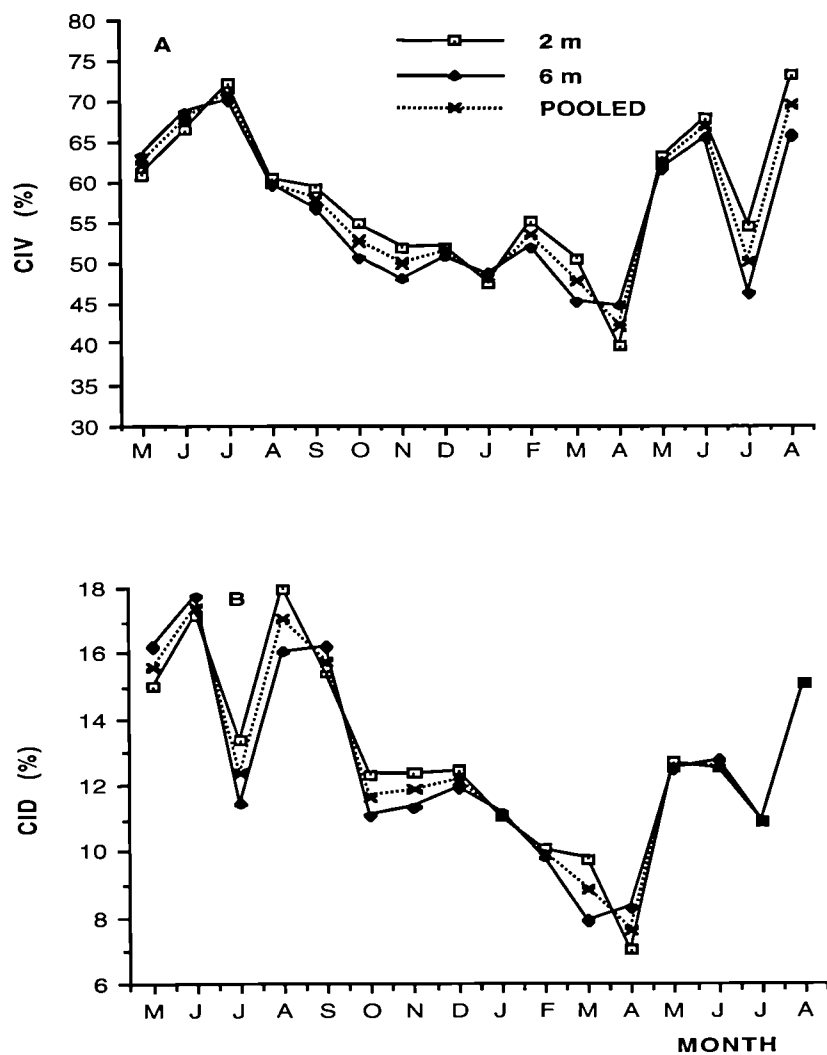


Fig. 42. Monthly distribution of wet meat volume condition index (CIV) (A) and dry meat weight condition index (CID) (B) at 2 m and 6 m and the pooled value for the two depths in Loch Kishorn from May 1993 to August 1994.

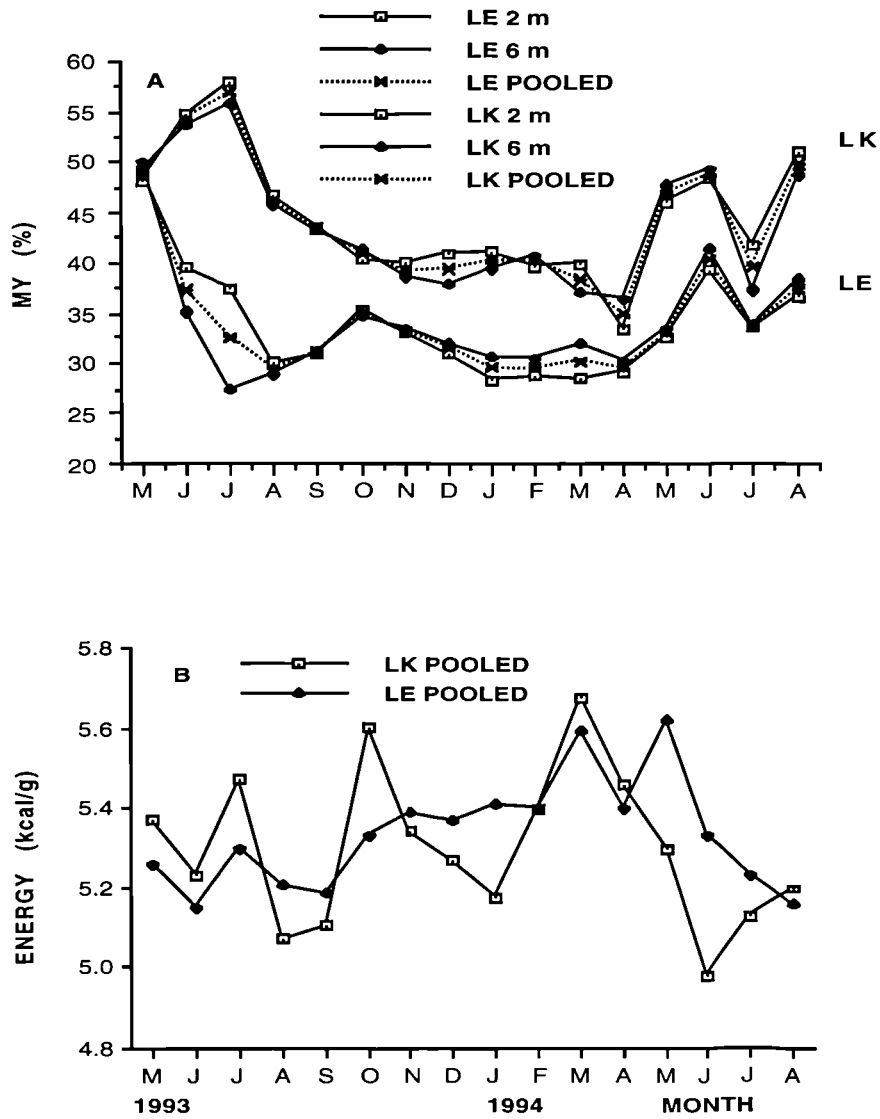


Fig. 43. Seasonal cycle of meat yield (MY) (A) at 2 m and 6 m depth and pooled values for the two depths; pooled values for mussel energy (B) in Loch Etive (LE) and Loch Kishorn (LK).

Table-29. Two-way ANOVA results showing significance levels for mussel condition index and meat yield between the studied sites and depths. CI: condition index; CIV: wet meat volume condition index; CID: dry meat weight condition index; MY: meat yield in percentage; ns: not significant. *: P<0.05; **: P<0.01 and ***: P<0.001.

CI	Source	DF	SS	MS	F	P
	Site	1	1243.71	1243.71	63.38	***
	Depth	1	12.33	12.33	0.63	ns
CIV	Site*Depth	1	1.43	1.43	0.07	ns
	Error	60	1177.3	19.62		
	Total	63	2434			
	Site	1	102.237	102.237	17.16	***
	Depth	1	2.818	2.818	0.47	ns
CID	Site*Depth	1	0.418	0.418	0.007	ns
	Error	60	357.517	5.959		
	Total	63	462.99			
	Site	1	652.29	652.29	44.48	***
	Deth	1	0.20	0.20	0.01	ns
MY	Site*Depth	1	4.39	4.39	0.30	ns
	Error	60	879.96	14.67		
	Total	63	1536.85			

at both experimental sites, but these differences were not significant ($P>0.05$). However, condition index was found to be different between the sites ($P<0.001$) and was higher in Loch Kishorn than Loch Etive. Morphological differences (i.e. wider, longer or higher shell shape) in mussels can affect the condition index between the sites, therefore MY was used as an indicator for CI in both lochs although MY exhibited a similar annual cycle (Fig. 43) to CIV at both sites. MY showed significant site response ($P<0.001$) but little depth effect. All environmental factors had a positive effect on CIV but only CIV was affected significantly by salinity ($r=0.965$, $P<0.01$) and temperature ($r=0.895$, $P<0.001$) in Loch Etive, while only temperature had a significant positive relationship with CIV ($r=0.689$, $P<0.01$) in Loch Kishorn. Wet meat volumetric condition indices were related positively to lipid and carbohydrate. However, CIV had a negative relationship with ash, moisture and protein at both sites. Degrees of relationship between condition indices and biochemical composition are given in Tables 31 and 32. These results show that the main energy sources in gonad development before spawning are lipid and carbohydrate.

4.4.2. Biochemical Analyses

4.4.2.1. Energy (Calorific) Content

The monthly distribution of energy is exhibited in Fig. 43. The energy content of mussels at Loch Etive and Loch Kishorn were similar with a mean of 5.33 ± 0.03 Kcal g^{-1} at Loch Etive and a mean of 5.3 ± 0.05 Kcal g^{-1} at Loch Kishorn. The monthly value of energy ranged from 5.15 to 5.59 Kcal g^{-1} in Loch Etive while it ranged from 4.98 to 5.68 Kcal g^{-1} in Loch Kishorn. There were no clear seasonal variations in energy values at either site. Proximate biochemical analyses for moisture, ash, lipid, protein and carbohydrate were carried out only in the first year experiment for rope cultivated mussels (from May 1993 to August 1994) and the results are presented as mean percentages of dry meat weight or wet meat weight in the case moisture content. No statistical differences were found when the various dry meat composition analyses were compared for mussels in the two lochs.

4.4.2.2. Moisture

Seasonal variation in moisture values are depicted in Fig. 44 and minimum and maximum and mean values are given in Table-30. Correlation matrices between moisture, biochemical parameters and environmental factors are shown in Table 31 and 32 and it was found that site had no effect on body moisture ($P>0.05$). The moisture content of wet meat ranged from 74.42 % to 84.77 % with a mean of 79.17 ± 0.78 % in Loch Etive, while it ranged from 74.43 to 83.42 % with a mean 79.39 ± 0.74 % in Loch Kishorn. In general, the moisture values were minimum during the summer while increasing steadily to a maximum in March and April, coinciding with the time of minimum carbohydrate content, meat weights and maximum protein value. Moisture had an inverse relationship with CI and MY, while it had a negative relationship with lipid, carbohydrate and a positive relationship with protein and ash in both sites. The differences are expressed statistically in Tables 31 and 32.

4.4.2.3. Ash

Ash values in Loch Etive ranged from 5.28 % to 10.43 %, averaging 7.36 ± 0.43 % and in Loch Kishorn ranged from 6.11 to 12.22 % with a mean of 8.05 ± 0.44 %. Ash related inversely with lipid, carbohydrate and CI, while it had a positive relationship with moisture in the two lochs. Ash content was highly correlated ($P<0.01$) with protein at both sites. The monthly distribution of ash is given in Fig. 44 and mean values in Table-30 while correlation matrices with other biochemical parameters, CIV and environmental factors are presented in Tables 31 and 32. The ash content of dry meat weight reached a peak in February in Loch Etive but in Loch Kishorn the peak was observed in April. However, ash and moisture had significant positive relationships with protein at both sites. When protein reached its maximum value, carbohydrate was at a minimum at both sites.

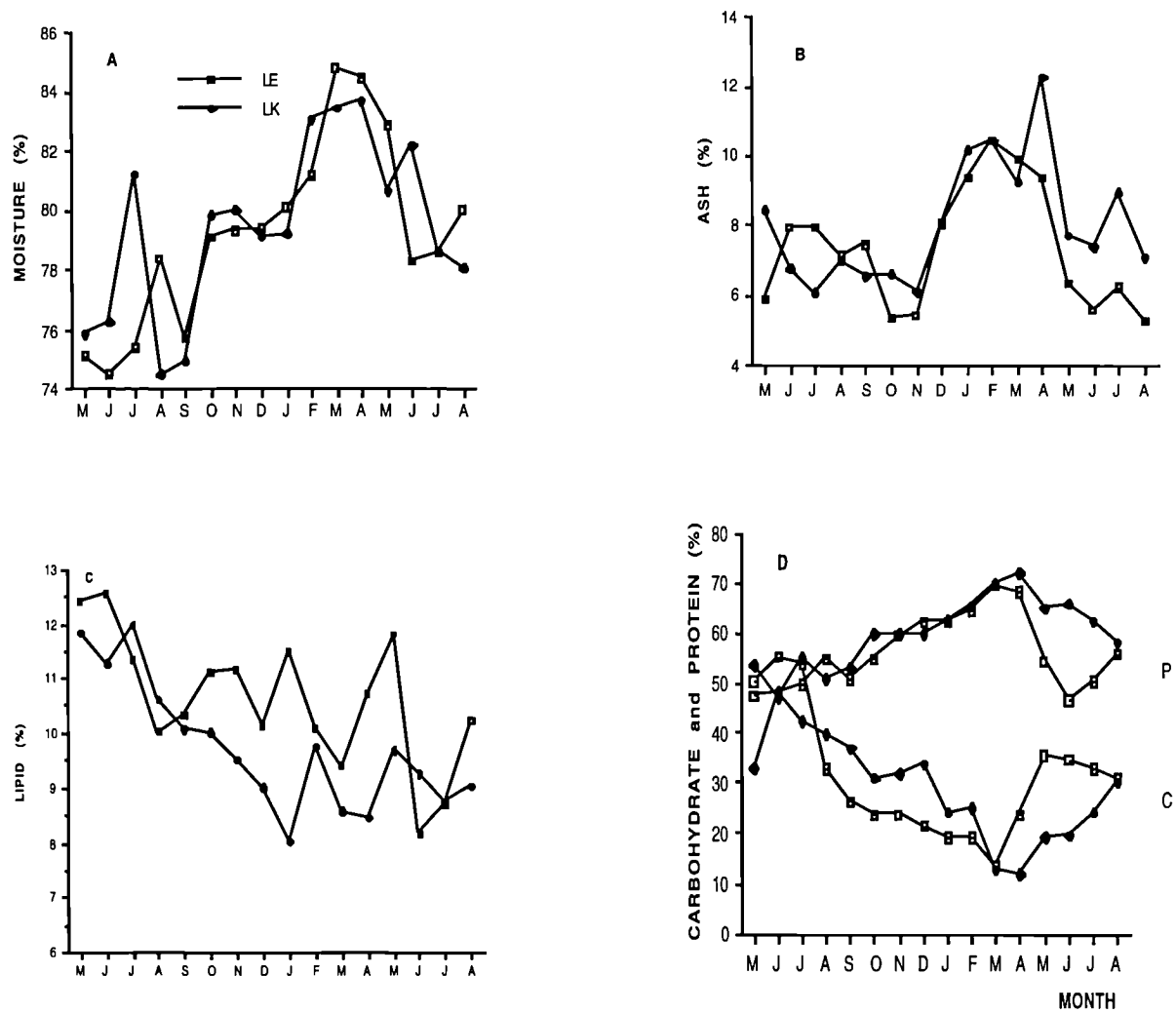


Fig. 44. Monthly distribution of moisture (A), ash (B), lipid (C), protein and carbohydrate (D) values in the meat of mussels from Loch Etive (LE) and Loch Kishorn (LK). P: protein, C: carbohydrate.

4.4.2.4. Lipid

The pattern of lipid content (Fig. 44) is characterized by an absence of marked seasonal trends, especially in Loch Etive. The values fluctuated between 8.16-12.53 % with a mean 10.60 ± 0.31 % in Loch Etive while they ranged from 8.01 % to 11.12% with a mean of 9.74 ± 0.30 % in Loch Kishorn. Lipid level was found to be higher in Loch Etive compared to Loch Kishorn, although the difference was not significant ($P < 0.05$). Lipid content was mainly related to gonad development and spawning. However lipid content was positively related to protein content and moisture at both sites. The correlation matrices between condition indices, environmental factors and condition index are given in Tables 31 and 32. Site had no effect on lipid content of dry meat ($P < 0.05$).

4.4.2.5. Protein

Average protein content was 56.16 ± 1.85 % with a minimum 46.81 % and maximum 69.57 % in Loch Etive mussels, while it ranged from 46.95 % to 71.97 % with a mean of 59.99 ± 1.73 % in Loch Kishorn. Monthly distribution of protein content is given Fig. 44 and mean values in Table-30. Site had no statistically significant effect on mean protein content of dry meat. A gradual increase in protein content of dry meat was observed from summer 1993 to March and April 1994 and then decreased with spawning. Protein had a significant inverse relationship with carbohydrate in Loch Etive ($r = 0.787$, $P < 0.001$) and in Loch Kishorn ($r = 0.947$, $P < 0.001$). Protein had a negative correlation with lipid at both sites.

4.4.2.6. Carbohydrate

The monthly distribution of carbohydrate is presented in Fig. 44 and mean values are given in Table-30. The carbohydrate content of dry meat ranged from 13.74 % to 55.19 % with a mean of 31.16 ± 3.14 % in Loch Etive, while it ranged from 12.08 % to 48.59 % with a mean 29.07 ± 2.58 % in Loch Kishorn. Carbohydrate had a very clear inverse relationship with protein content in Loch Etive ($r = 0.787$, $P < 0.01$) and in Loch Kishorn ($r = 0.947$, $P < 0.001$).

Table-30. Minimum, maximum and mean (\pm SE) values for biochemical composition of mussels in Loch Etive (LE) and Loch Kishorn (LK). Moisture values of mussels in wet meat weight and lipid, protein, carbohydrate and ash values in dry meat weight are given as percentages.

Site		Moisture	Lipid	Protein	Carbohydrate	Ash
LE	Min.	74.42	8.16	46.81	13.74	5.28
	Max.	84.77	12.53	69.57	55.19	10.43
	Mean	79.17 \pm 0.78	10.60 \pm 0.31	56.16 \pm 1.85	31.16 \pm 3.14	7.36 \pm 0.43
LK	Min.	74.43	8.01	46.95	12.08	6.11
	Max.	83.42	11.82	71.97	48.59	12.22
	Mean	79.39 \pm 0.74	9.74 \pm 0.30	59.99 \pm 1.73	29.07 \pm 2.58	8.05 \pm 0.44

There was good agreement between carbohydrate and the annual condition index cycle. A positive relationship was also observed with lipid, while a negative relationship with ash and moisture content was found at both sites.

Table-31. Correlation matrix between environmental factors, condition indices and biochemical composition in Loch Etive: CIV: condition index volumetric, CID: condition index dry, Ch-a: chlorophyll, SES: seston, POM: particulate organic matter, T: temperature, S: salinity, MY: meat yield, Li: lipid, P: protein, C: carbohydrate, A: ash, M: moisture, L: length of mussel in the Loch Etive. Significance levels: *: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$

	CIV	CID	Ch-a	SES	POM	T	S	MY	Li	P	C	A	M	E
CIV	0.815***													
CID	0.208,	-0.018												
Ch-a	0.244	0.208	0.547*											
SES	0.218	0.078	0.672**	0.932***										
POM	0.895***	0.663**	0.211	0.057	0.060									
T	0.965***	0.832***	0.152	0.310	0.264	0.747***								
S	0.508*	0.687**	0.249	0.596*	0.477	0.325	0.560*							
MY	0.241	0.370	0.238	-0.141	-0.071	0.081	0.304	0.240						
Li	-0.812***	-0.779***	-0.389	-0.455	-0.387	-0.751***	-0.762***	-0.638**	-0.116					
P	0.657**	0.703**	0.492	0.349	0.328	0.606*	0.611*	0.600*	0.451	-0.787***				
C	-0.773***	-0.587*	-0.344	-0.420	-0.398	-0.691**	-0.740**	-0.591*	0.012	0.658**	-0.345			
A	-0.768***	-0.873***	0.045	-0.084	-0.005	-0.683**	-0.752***	-0.497*	-0.288	0.830***	-0.721**	0.375		
M	-0.673**	-0.663**	0.235	0.150	0.252	-0.719**	-0.595*	-0.334	-0.010	0.608*	-0.476	0.351	0.758***	
E	-0.390	-0.540*	-0.088	-0.046	-0.073	-0.286	-0.414	-0.426	-0.689**	0.389	-0.689**	-0.054	0.644**	0.319
L														

Table-32. Correlation matrix between environmental factors, condition indices and biochemical composition in Loch Kishom (Superscript are as given in Table 31).

	CIV	CID	Ch-a	SES	POM	T	S	MY	Li	P	C	A	M	E
CID	0.707**													
Ch-a	0.435	0.181												
SES	0.310	-0.092	0.841***											
POM	0.305	-0.070	0.792***	0.940***										
T	0.689**	0.692**	0.204	-0.098	0.015									
S	0.411	0.578*	0.097	0.093	0.108	0.546*								
MY	0.963***	0.686**	0.453	0.274	0.322	0.697**	0.327							
Li	0.664**	0.628**	0.349	0.132	0.184	0.670**	0.596*	0.745***						
P	-0.578*	-0.912***	-0.041	0.306	0.227	-0.740**	-0.507*	-0.636**	-0.729**					
C	0.554*	0.786***	-0.040	-0.381	-0.321	0.721**	0.432	0.625**	0.737**	-0.947***				
A	-0.650**	-0.671**	-0.124	0.076	0.072	-0.792***	-0.497*	-0.614*	-0.555*	0.673**	-0.699**			
M	-0.355	-0.881***	-0.037	0.308	0.247	-0.576*	-0.471	-0.359	-0.443	0.877***	-0.715**	0.500*		
E	-0.338	-0.530*	-0.143	0.000	-0.008	-0.247	-0.258	-0.251	0.059	0.351	-0.245	0.210	0.517*	
L	-0.314	0.456	-0.122	0.053	-0.082	-0.366	-0.374	-0.491	-0.841***	0.647**	-0.641**	0.266	0.402	-0.204

4.5. SPAT COLLECTION AND GROWTH OF MUSSEL SEEDS

4.5.1. Spat Collection and Associated Problems

An experiment was conducted to provide data about mussel spat settlement density, growth of young seed mussels and problems of spat collection in the two Scottish sea lochs. A spat collection experiment was started by suspending six collectors (polypropylene ropes of 16 mm diameter) at each site in May 1993. The spat collector ropes were hung from a mussel culture raft at each site. Spat settlement started from June at both sites.

Plates 10 and 11 show that there was a uniform settlement of high quality seed after three months spatfall in Loch Etive, while there were fouling organisms (starfish and sea squirts) on the spat collectors in Loch Kishorn. Observations showed that the sea squirts and starfish settle on the spat collector ropes after their planktonic stages and their development occurs on the spat collectors thereafter. Starfish are easily dislodged by handling and environmental factors (such as currents) about 4-5 months after settlement, but sea squirts reach maturation on the collectors; they compete for space with the mussel stock and can eventually occupy 90 to 95 % of the available space. The density of sea squirts was observed to be from 3 m⁻¹ to 10 ind m⁻¹ rope in first the four months of mussel spat settlement.

Mussel spat settlement occurred in June and July 1993 in Loch Etive and from June to December 1993 in Loch Kishorn. In terms of spat abundance, there was a single peak (over 35,000 ind m⁻¹ rope) in Loch Etive in July 1993 and two peaks (over 48,000 and 16,500 ind m⁻¹ rope) in Loch Kishorn in July and November. The monthly distribution of spat density is shown in Fig. 45 and mean values at depths of 2 m and 6 m, plus pooled values for both depths are given in Table-33. Primary settlement of mussel spat was noted to be always high on seaweeds especially, *Laminaria* spp. and *Fucus* spp., followed by dense settlement on the polypropylene collector ropes.



Plate-10. Experimental spat collector in Loch Kishorn showing mussel seed settlement after three months



Plate-11. Experimental spat collector in Loch Etive showing mussel seed settlement after three months.

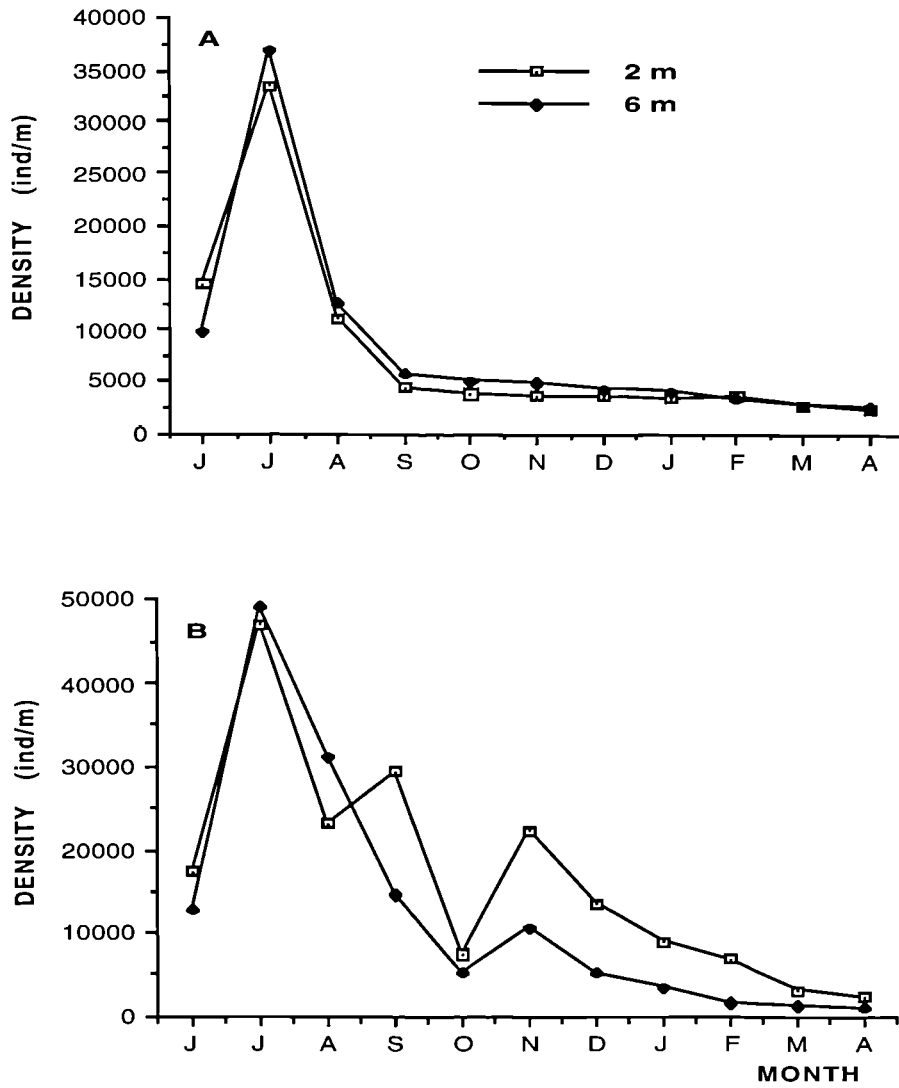


Fig.45. Monthly distribution of mussel spat density at 2 m and 6 m in Loch Etive (A) and Loch Kishorn (B) from June 1993 to April 1994.

Table-33. Mean monthly seed density (ind m⁻¹ rope) at 2 m and 6 m depth, plus both depths pooled, in Loch Etive (LE) and Loch Kishorn (LK) from June 1993 to April 1994.

Months	LE			LK		
	2 m	6 m	Pooled	2 m	6m	Pooled
June	14164	9740	11953	17412	12860	15137
July	33456	36908	35183	47040	49256	48149
August	11112	12624	11869	23040	31140	27091
September	4448	5768	5109	29368	14604	21987
October	3748	5016	4383	7472	5416	6445
November	3648	4788	4219	22440	10564	16503
December	3596	4276	3937	13456	5256	9357
January	3488	3984	3737	8924	3368	6147
February	3551	3336	3444	7004	1660	4333
March	2672	2855	2764	3164	1424	2295
April	2296	2467	2382	2348	996	1673

Table-34. Mean (\pm SE) monthly shell length (mm) and increment in shell length ($\Delta L=L_2-L_1$) of mussel seed in Loch Etive (LE) and Loch Kishorn (LK) from June 1993 to April 1994.

Months	LE			LK			
	2 m	ΔL	6 m	2 m	ΔL	6 m	ΔL
June	0.38 \pm 0.01		0.38 \pm 0.01	0.49 \pm 0.02		0.49 \pm 0.02	
July	3.61 \pm 0.04	3.23	3.51 \pm 0.05	2.12 \pm 0.38	1.63	1.49 \pm 0.18	1.00
August	5.31 \pm 0.04	1.70	4.03 \pm 0.03	2.96 \pm 0.031	0.84	2.99 \pm 0.03	1.50
September	11.98 \pm 0.59	6.67	13.2 \pm 0.50	7.64 \pm 0.47	4.68	6.31 \pm 0.23	3.32
October	18.73 \pm 0.77	6.75	17.48 \pm 0.65	14.24 \pm 0.49	6.60	12.00 \pm 0.4	5.69
November	20.51 \pm 0.56	1.78	19.87 \pm 0.61	12.79 \pm 0.68	-1.45	9.52 \pm 0.48	-2.48
December	20.58 \pm 0.73	0.07	20.13 \pm 0.67	11.54 \pm 0.37	-1.25	9.33 \pm 0.38	-0.19
January	20.83 \pm 0.63	0.25	20.27 \pm 0.62	13.31 \pm 0.57	1.77	10.64 \pm 0.46	1.31
February	21.34 \pm 0.51	0.51	20.96 \pm 0.60	14.27 \pm 0.59	0.96	11.21 \pm 0.43	0.57
March	23.59 \pm 0.52	2.25	22.55 \pm 0.39	15.79 \pm 0.45	1.52	12.20 \pm 0.42	0.99
April	25.27 \pm 0.51	1.68	23.81 \pm 0.41	17.97 \pm 0.59	2.18	12.63 \pm 0.43	0.43

Table-35. Monthly average length specific growth rate (SGR%) of mussel spat after settlement on collector ropes at depth of 2 m and 6 m, plus pooled values for both depths from July 1993 to April 1994 in Loch Etive (LE) and Loch Kishorn (LK).

Months	LE			LK		
	2 m	6 m	Pooled	2 m	6 m	Pooled
July	307.00	303.16	305.08	129.24	98.13	113.69
August	35.08	12.56	23.82	30.34	63.32	46.83
September	78.74	114.82	96.78	94.82	74.69	84.75
October	40.63	25.53	33.08	53.37	55.10	54.23
November	8.78	12.40	10.59	-11.51	-24.81	-18.16
December	0.37	1.39	0.88	-9.95	-1.95	-5.95
January	1.25	0.72	0.98	14.27	13.14	13.70
February	2.13	2.95	2.54	6.74	5.05	5.81
March	10.37	7.56	8.97	10.12	8.46	9.29
April	7.37	5.83	6.60	13.86	3.71	8.78

It has been considered that a seed density of over 1,200 ind m⁻¹ rope is necessary to produce high yields of rope cultured mussel in Scotland (Okumus, 1993). In comparison, a mean spat settlement of over 2,000 ind m⁻¹ rope was obtained at 2 m and 6 m depth in Loch Etive, even after high losses following settlement peaks in July (Table 33). In Loch Kishorn, seed mussel densities remained high at 2 m depth, being still above 2,000 ind m⁻¹ rope in April 1994, whereas at 6 m depth only 996 ind m⁻¹ rope remained by April 1994 (Table 33). The higher losses of seed mussels in Loch Kishorn at 6 m was caused mainly by fouling organisms (sea squirt and star fish).

4.5.2. Shell Growth

Spat settlement started at both sites in June 1993 and samples were first taken from Loch Etive on 20.7.1993 and from Loch Kishorn on 27.6.1993. Newly settled spat were counted under a stereoscopic microscope and photographs were taken at 10* magnification. Newly settled spat have a more rounded shape and brighter shell color than older spat. In June 1993, the Height : Length (H:L) ratios recorded was 85.5 % in Loch Etive whereas it was 79.6 % in Loch Kishorn. However, the H:L ratios decreased to 55.3 % and 54.9 % respectively by the end of the experiment (April 1994). Neither site nor depth had a significant effect on the H:L ratio in the seed mussels ($P>0.05$). The length to height relationship is shown in Fig. 49 for the Loch Etive and Loch Kishorn mussel seeds.

Seasonal changes in mussel seed shell length are depicted in Fig. 46 and mean (\pm SE) values of shell length and monthly increment in length ($\Delta L=L_2-L_1$) are given in Table-34. Their initial length was 0.38 ± 0.01 mm in Loch Etive and 0.49 ± 0.02 mm in Loch Kishorn. There were clear seasonal patterns of shell growth. High growth rate was observed from June to November in Loch Etive where seeds reached 20.51 ± 0.56 mm and 19.87 ± 0.61 mm at 2 m and 6 m depth, respectively. There was little growth in shell size in the winter period and an increase in growth rate occurred in March and April at both depths in Loch Etive.

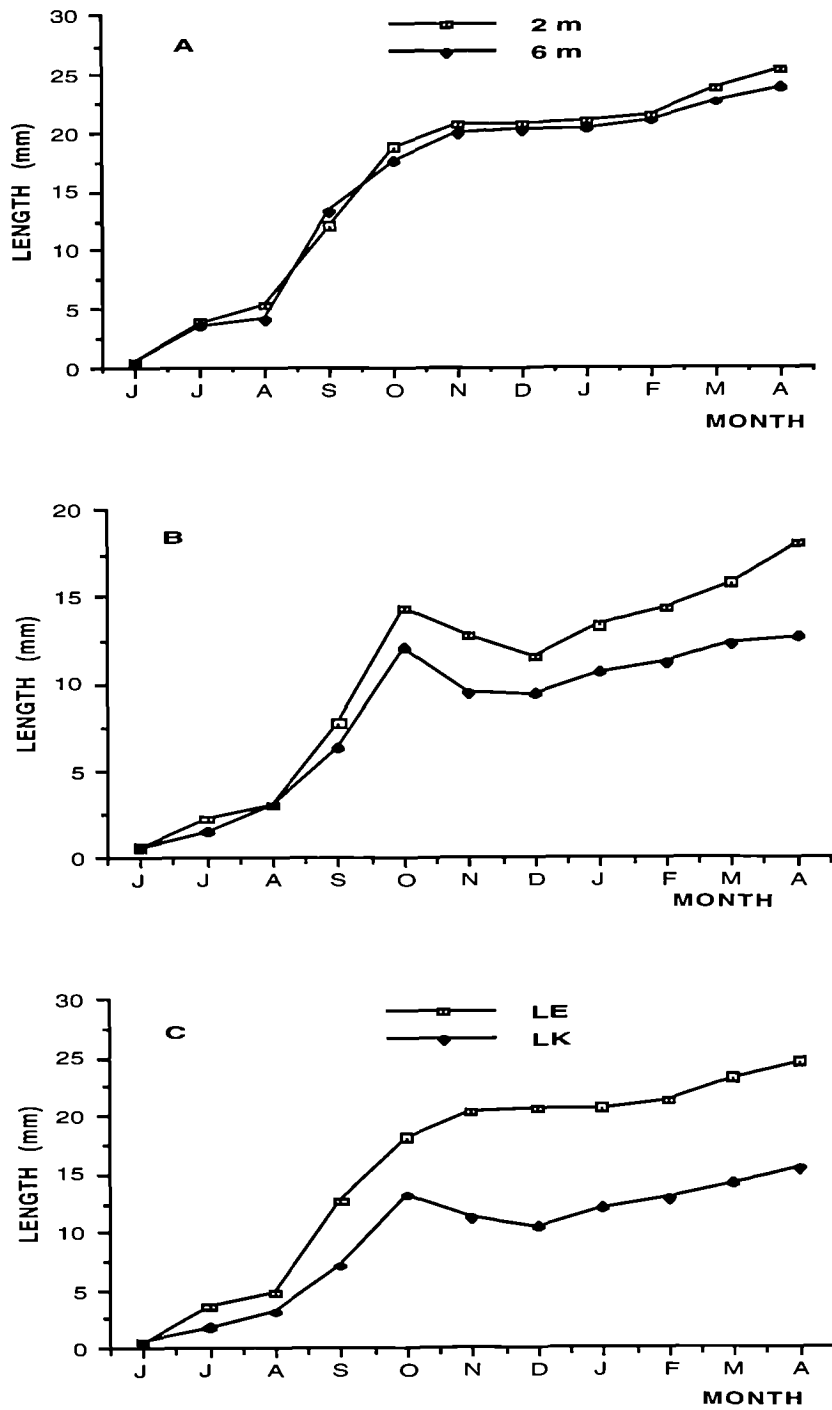


Fig. 46. Mean shell length distribution at 2 m and 6 m depths in Loch Eive (A), Loch Kishorn (B) and pooled values for both depths (C) from June 1993 to April 1994.

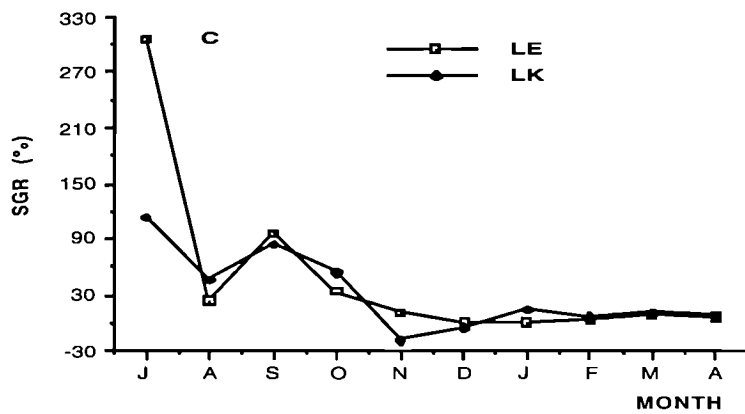
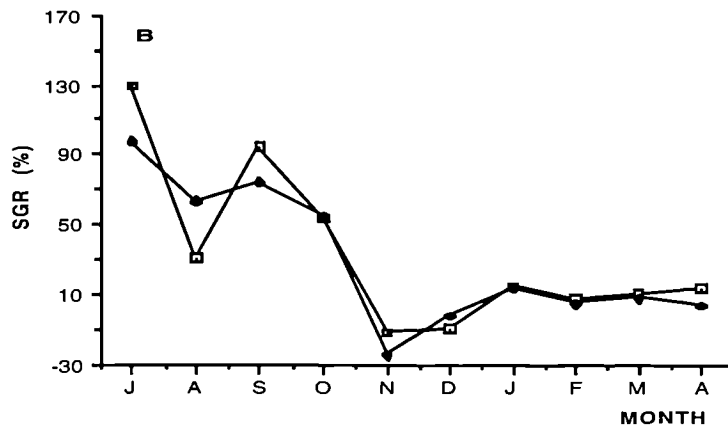
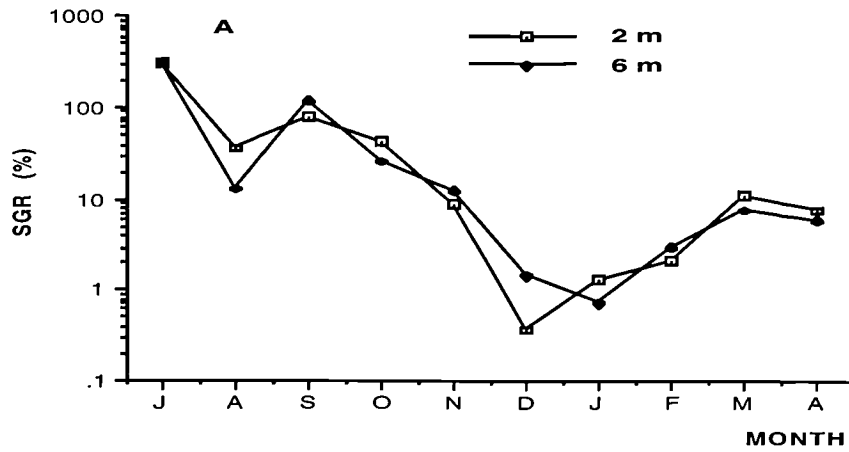


Fig.47. Monthly changes in specific growth rate (SGR%) at 2 m and 6 m in Loch Etive (A), Loch Kishorn (B) and pooled values for the two depths (C) in Loch Etive (LE) and Loch Kishorn (LK) from July 1993 to April 1994.

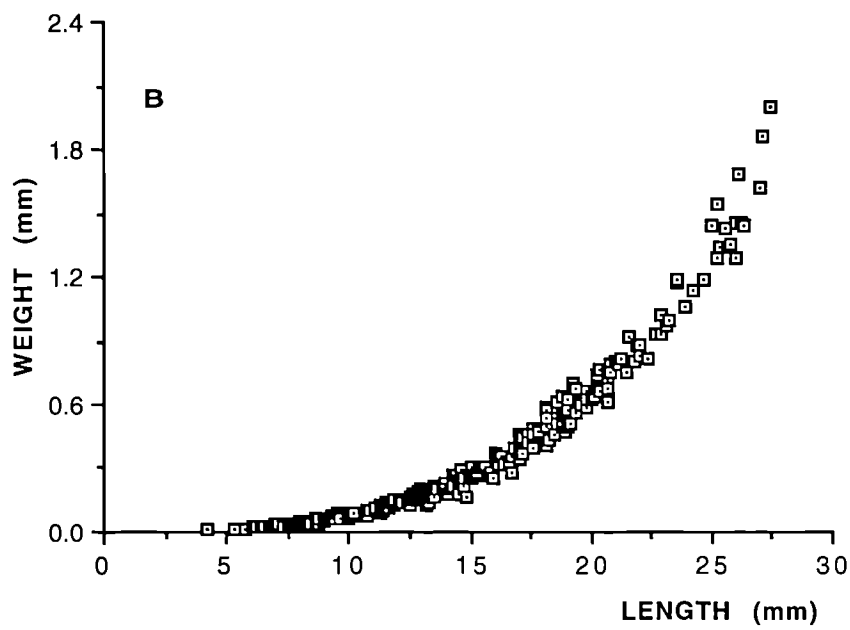
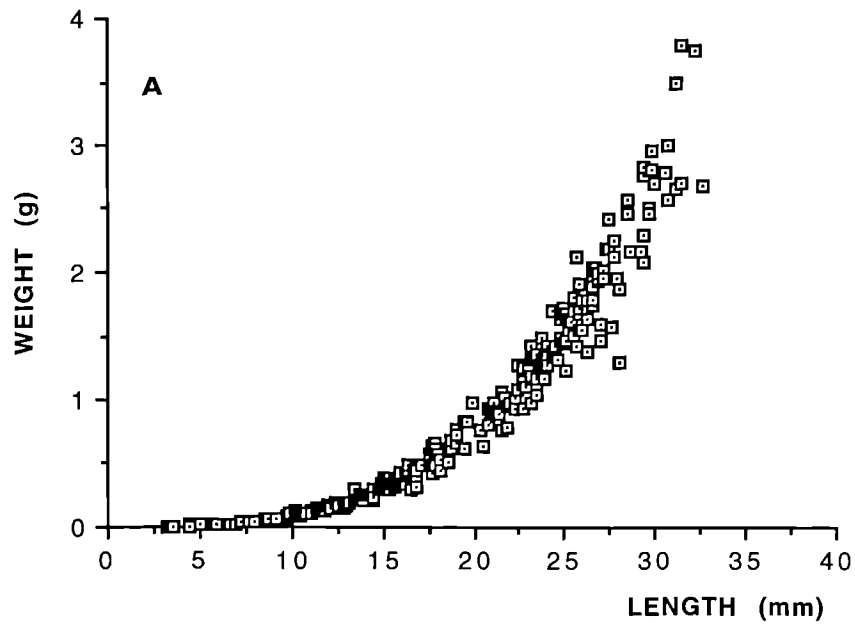


Fig. 48. Length-weight relationship in mussel seed in Loch Etive (A) and Loch Kishorn (B) during the experimental period.

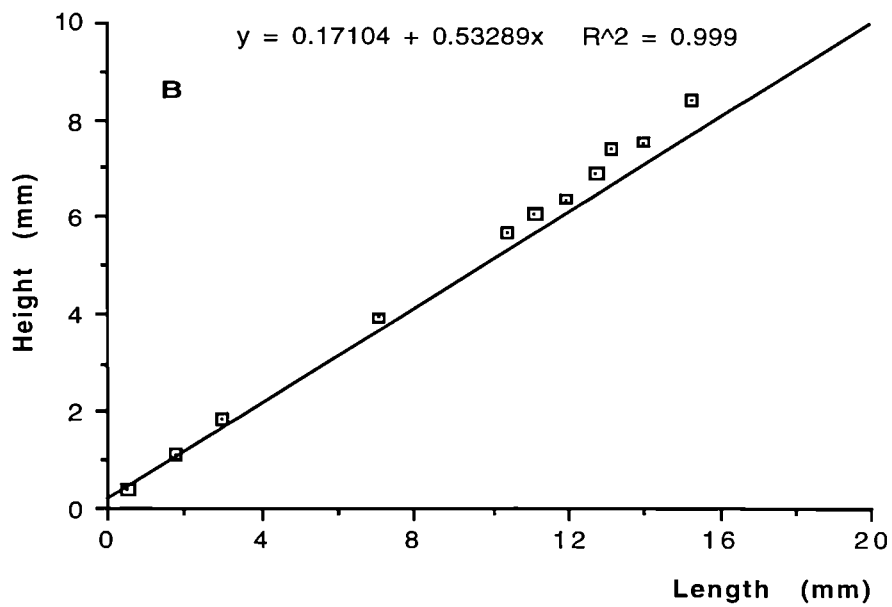
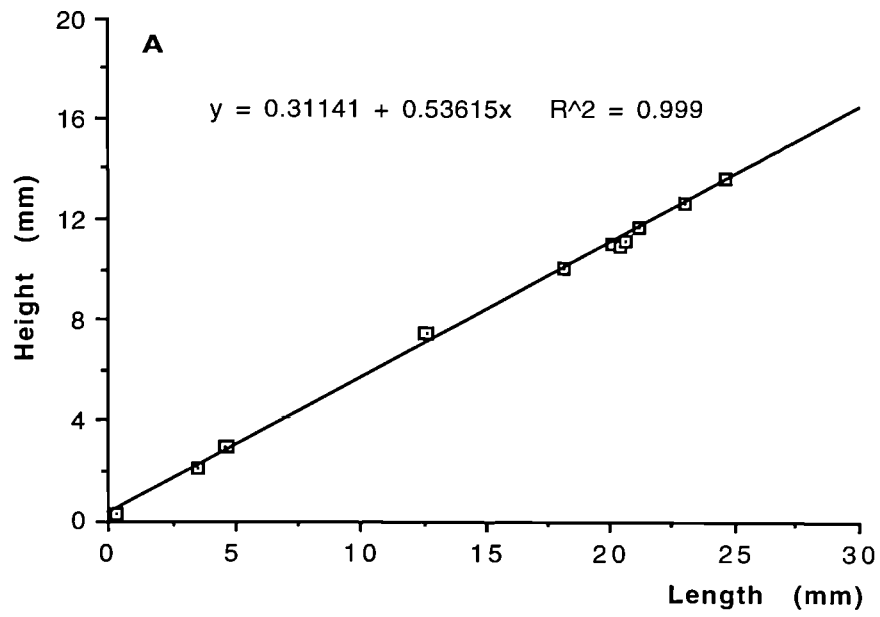


Fig. 49. Length-height relationship of seed mussels in Loch Etive (A) and Loch Kishorn (B) during the experimental period June to April 1994.

By April 1994, the seed mussels had reached mean shell lengths of 25.27 ± 0.51 mm and 23.81 ± 0.41 mm at 2m and 6m, respectively in Loch Etive. Depth had no significant affect on shell growth in this loch ($P > 0.05$). Seed mussel growth in Loch Kishorn was strongly influenced by heavy losses from fouling and predation (as noted in section 4.5.1). Shell length reached 14.24 ± 0.49 mm and 12.00 ± 0.40 mm at 2 m and 6 m respectively in October 1993, but these values decreased to 11.54 ± 0.37 mm and 9.33 ± 0.38 mm respectively from October to December 1993 (Table 34), implying that it was the larger mussel seed which were most affected by fouling and predatory organisms. By April 1994, mussel seed shell length was significantly higher at 2 m compared to 6 m depth (17.96 mm and 12.63 mm, $P < 0.001$). Overall, shell growth was significantly higher in Loch Etive compared to Loch Kishorn over the experimental period ($P < 0.001$)

Monthly specific growth rate (SGR %) is shown in Fig. 47 and Table-35. SGR % ranged from 0.88 to 305 in Loch Etive and from -18 % to 114 % in Loch Kishorn. In Loch Etive, SGR values reached a maximum in July 1993 due to rapid growth of the newly settled spat, then decreased through autumn and winter, before recovering again in March 1994. In Loch Kishorn, a maximum SGR value was also recorded in July 1993, but the minimum value obtained was negative (-18.16 %) due to heavy losses of seed mussels experienced in November 1993.

Length to weight relationships for the Loch Etive and Loch Kishorn seed mussels were as follows:

$$\text{Loch Etive: } \log_{10} \text{LW} = -4.0357 + 3.0081 \log_{10} \text{L}, r = 0.988 \text{ or } (\text{LW} = 0.000092 \text{ L}^{3.0081})$$

$$\text{Loch Kishorn: } \log_{10} \text{LW} = -4.0863 + 2.994 \log_{10} \text{L}, r = 0.990 \text{ or } (\text{LW} = 0.000082 \text{ L}^{2.994})$$

The values used to obtain the above regression equations are plotted in Fig. 48

4.5.3. Growth in Live Weight

The average live weight distribution of the seed mussels is shown in Fig. 50 and monthly live weight values and increments at the two depths are given in Table-36. There was a clear seasonal cycle in incremental weight change with a pronounced peak from July to November followed by growth cessation over winter. The increment was positive over the experimental period in Loch Etive, probably due to the absence of significant losses.

Final live weight was found to be 1.72 ± 0.09 g at 2 m and 1.41 ± 0.07 g at 6 m depth with a pooled mean of 1.57 ± 0.08 g in Loch Etive, compared 0.610 ± 0.056 g and 0.226 ± 0.023 g at 2 m and 6 m, respectively and a pooled mean of 0.418 ± 0.04 g in Loch Kishorn. Live weight did not differ significantly between the depths in Loch Etive. However the differences between the depths was significant in Loch Kishorn ($P < 0.001$). Comparing the two sites, the mean live weight of seeds was significantly higher in Loch Etive than Loch Kishorn ($P < 0.001$), reflecting the effect of heavy fouling and predation losses at the latter site.

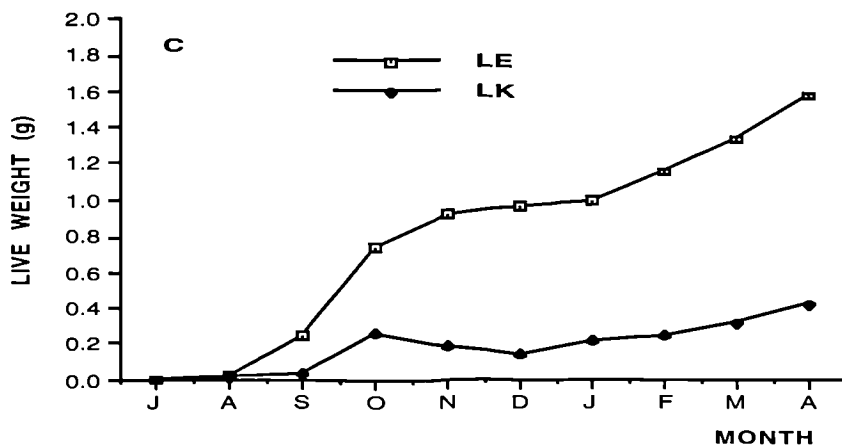
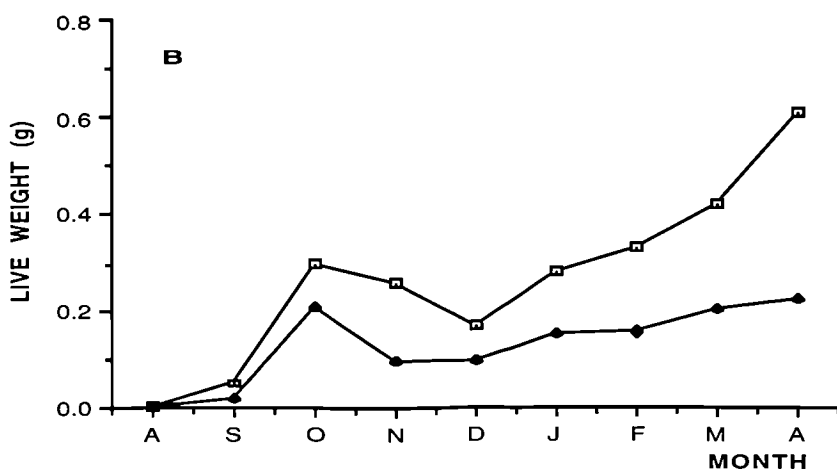
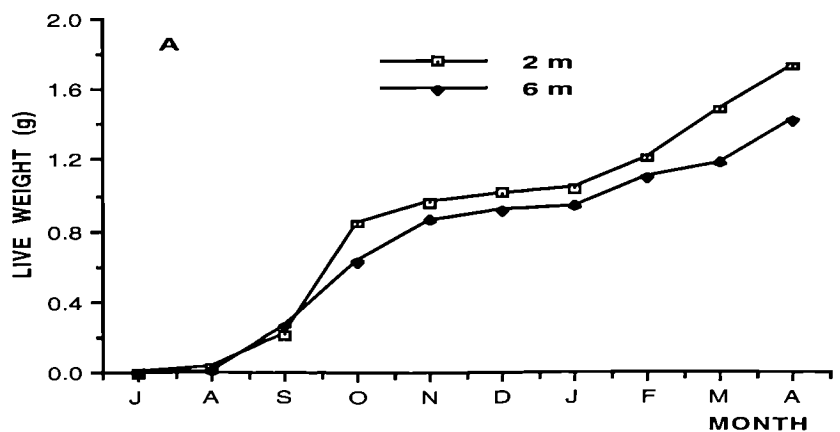


Fig. 50. Monthly live weight distribution of seed mussels at 2 m and 6 m depth in Loch Etive (A) from July 1993 to April 1994, Loch Kishorn (B) from August 1993 to April 1994 and pooled values for two depths (C) in Loch Etive (LE) and Loch Kishorn (LK).

Table-36. Mean (\pm SE) monthly live weight and monthly increment ($\Delta L=L_2-L_1$, mm) of live weight of seed mussels in Loch Etive (LE) and Loch Kishorn (LK) from June 1993 to April 1994.

Months	LE				LK			
	2 m	ΔL	6 m	ΔL	2 m	ΔL	6 m	ΔL
June	-	-	-	-	-	-	-	-
July	0.001 \pm 0.000	-	0.001 \pm 0.000	-	-	-	-	-
August	0.033 \pm 0.007	0.032	0.011 \pm 0.002	0.010	0.006 \pm 0.002	-	0.006 \pm 0.003	-
September	0.210 \pm 0.023	0.177	0.270 \pm 0.025	0.259	0.050 \pm 0.001	0.044	0.023 \pm 0.003	0.017
October	0.843 \pm 0.09	0.630	0.630 \pm 0.055	0.360	0.300 \pm 0.027	0.250	0.208 \pm 0.019	0.185
November	0.962 \pm 0.07	0.120	0.860 \pm 0.075	0.230	0.260 \pm 0.043	-0.04	0.096 \pm 0.013	-0.112
December	1.01 \pm 0.09	0.050	0.91 \pm 0.10	0.050	0.170 \pm 0.017	-0.09	0.099 \pm 0.015	0.003
January	1.03 \pm 0.10	0.020	0.94 \pm 0.08	0.030	0.280 \pm 0.036	0.110	0.153 \pm 0.022	0.054
February	1.20 \pm 0.14	0.170	1.10 \pm 0.08	0.160	0.330 \pm 0.038	0.050	0.158 \pm 0.017	0.005
March	1.48 \pm 0.10	0.280	1.18 \pm 0.06	0.080	0.420 \pm 0.037	0.090	0.204 \pm 0.023	0.046
April	1.72 \pm 0.09	0.240	1.41 \pm 0.07	0.230	0.610 \pm 0.056	0.190	0.226 \pm 0.023	0.022

Table-37. Correlation matrix between environmental factors and specific growth rate of mussels in Loch Etive. df: 10, SGR: Specific Growth Rate, T: temperature, S: salinity, SES: seston, POM: particulate organic matter, POM%: percentage of POM in seston, Ch-a: chlorophyll-a, PN: particle number and SEC: Secchi depth. (Significance level; *: P<0.05; **: P<0.01 and ***: P<0.001).

	SGR	T	S	SES	POM	POM%	CH-a	PN
T	0.391							
S	0.276	0.762**						
SES	0.043	0.160	0.368					
POM	-0.081	0.201	0.344	0.960***				
POM%	-0.552	-0.171	-0.402	-0.759**	-0.592*			
Ch-a	0.420	0.665*	0.471	0.560	0.553	-0.456		
PN	0.518	0.415	0.234	0.253	0.236	-0.327	0.645*	
SEC	-0.043	0.351	0.449	-0.222	-0.285	0.001	-0.058	-0.366

Table-38 Correlation matrix between environmental factors and specific growth rate of mussels in Loch Kishorn. Superscripts and abbreviations as given in Table- 37.

	SGR	T	S	SES	POM	POM%	CH-a	PN
T	0.540							
S	0.242	0.609*						
SES	-0.044	0.195	0.202					
POM	0.034	0.310	0.181	0.935***				
POM%	0.017	-0.043	-0.130	-0.717**	-0.449			
Ch-a	0.528	0.723**	0.277	0.573	0.629*	-0.323		
PN	0.018	0.174	-0.198	0.162	0.374	0.225	0.280	
SECC	-0.011	0.342	0.619*	-0.036	-0.049	-0.082	-0.022	0.001

4.6. Cross-transplantation of Mussels Between Loch Etive and Loch Kishorn

4.6.1. Environmental Factors

The following information refers to environmental parameters which were measured in Loch Etive and Loch Kishorn from May 1994 to May 1995.

4.6.1.1. Temperature

Sea water temperature varied from 5.3°C to 15.7°C with a mean of 9.64±0.93°C at a depth of 2 m in Loch Etive. In Loch Kishorn, temperature ranged from 7°C to 14.6°C with a mean of 9.78±0.63°C at depth of 2 m (Fig. 51 and Table-39). There was a clear seasonal pattern in temperature change at both sites which increased from May to August and then decreased gradually reaching a minimum value in February.

The mean temperatures did differ significantly ($P>0.05$). A sharper decrease in temperature in Loch Etive from November to December was attributed to snow melting and freshwater run-off to the loch from the surrounding mountains. Correlation matrices between temperature and other environmental factors for both sites are given in Tables 40 and 41. A high positive correlation occurred between temperature and salinity in Loch Etive ($P<0.01$) but not in Loch Kishorn ($P>0.05$).

4.6.1.2. Salinity

The monthly distribution of salinity is shown in Fig. 51 and mean values are given in Table-39. The salinity range in Loch Kishorn was only 30.2 ‰ to 34.3 ‰ compared to a much greater fluctuation in Loch Etive (8.4 ‰ to 24.5 ‰). Minimum values of salinity were recorded in December while maximum values were measured in June 1994 at the both sites. Mean salinity was significantly higher in Loch Kishorn (32.23±0.30) than Loch Etive (17.75±1.65) ($P<0.001$). In general, salinity was observed to be higher in summer and lower in winter and spring. Salinity had a positive relationship with the other measured environmental factors, but was only significantly correlated with temperature and seston in

Table-39. Mean (\pm SE) values of environmental parameters measured at Loch Etive (LE) and Loch Kishorn (LK) from May 1994 to May 1995.

Superscript letters indicate one-way ANOVA comparison between the sites at $P < 0.05$ or less. Common superscripts in the same column indicate that the superscripted values do not differ significantly ($P > 0.05$).

Site	Temperature (°C)	Salinity (‰)	Seston (mg l ⁻¹)	POM (mg l ⁻¹)	POM%	Ch-a (µg l ⁻¹)	Transparency (m)
LE	Minimum	8.4	1.2	0.7	36.5	0.077	4
	Maximum	24.5	8.5	3.1	70.6	7.72	5
	Mean	9.64 \pm 0.93 ^a	17.75 \pm 1.65 ^a	2.78 \pm 0.54 ^a	1.35 \pm 0.21 ^a	51.37 \pm 3.4 ^b	1.63 \pm 0.56 ^a
LK	Minimum	30.2	1.5	0.4	22.2	0.039	4.5
	Maximum	34.3	14.3	4.1	57.7	6.32	10
	Mean	9.78 \pm 0.63 ^a	32.23 \pm 0.30 ^b	4.6 \pm 1.02 ^a	1.72 \pm 0.29 ^a	40.64 \pm 2.62 ^a	1.76 \pm 0.58 ^a

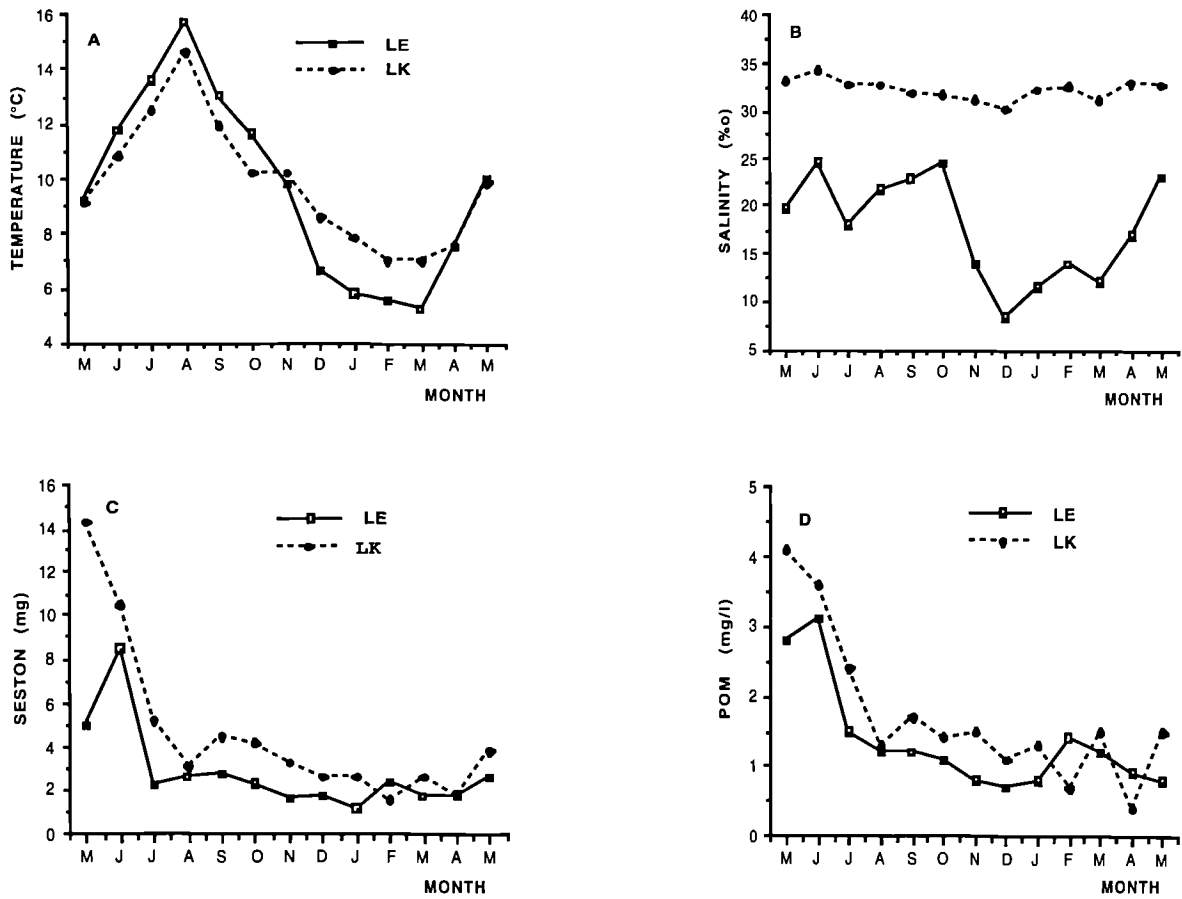


Fig. 51. Seasonal cycle of sea water temperature (A), salinity (B), seston (C) and particulate organic matter (POM) (D) at a depth of 2 m in Loch Etive (LE) and Loch Kishorn (LK) from May 1994 to May 1995.

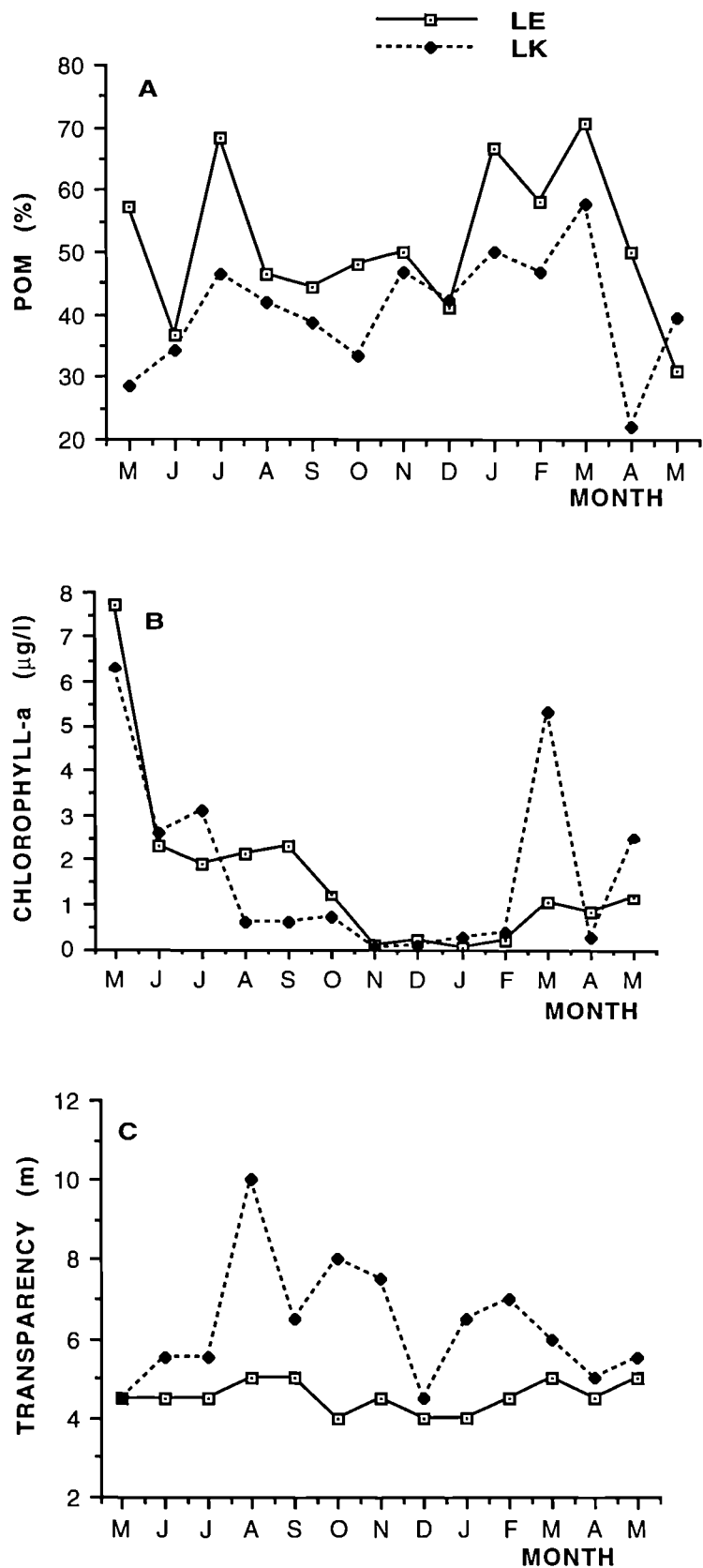


Fig. 52. Monthly distribution of percentage of particulate organic matter (POM%) (A), chlorophyll-a (B) at 2 m depth and transparency (Secchi disk depth) (C) in Loch Etive (LE) and Loch Kishorn (LK).

Loch Etive (LE), and only with seston in Loch Kishorn (LK). (Tables 40 and 41).

4.6.1.3. Seston

Seasonal distribution of seston is depicted in Fig. 51 and average results are given in Table-39. Average seston values were $4.6 \pm 1.02 \text{ mg l}^{-1}$ in Loch Kishorn and $2.78 \pm 0.54 \text{ mg l}^{-1}$ in Loch Etive ($P > 0.05$). Seston reached a maximum of 14.3 mg l^{-1} in Loch Kishorn in May 1994 and 8.50 mg l^{-1} in Loch Etive in June 1994. Minimum values of seston were 1.5 mg l^{-1} in February and 1.2 mg l^{-1} in March in Loch Kishorn and Loch Etive, respectively. Seston was observed to be high in summer and low in winter and early spring. Seston had a significant positive relationship with POM, Ch-a and salinity at both sites.

4.6.1.4. Particulate Organic Matter (POM) and POM %

The seasonal distribution of particulate organic matter (POM) and POM% (percentage of organic matter in seston) are shown in Fig. 51 and 52 respectively and their mean results are given in Table-39. The mean values of POM were $1.72 \pm 0.29 \text{ mg l}^{-1}$ in Loch Kishorn and $1.32 \pm 0.21 \text{ mg l}^{-1}$ in Loch Etive ($P > 0.05$), with ranges of 0.4 to 4.1 mg l^{-1} and 0.7 to 3.1 mg l^{-1} respectively. The maximum value of POM coincided with the peak in seston at both sites. However, in Loch Kishorn a minimum value of seston was recorded in April while it was recorded in December in Loch Etive. In general, POM was positively affected by chlorophyll-a ($P < 0.01$) and seston ($P < 0.001$) in the two experimental sites (Tables 40 and 41). The mean value of POM % was significantly higher in Loch Etive ($51.37 \pm 3.4 \%$) than Loch Kishorn ($40.64 \pm 2.62 \%$) ($P < 0.05$) with ranges of 22.2 to 57.7 in Loch Kishorn and 36.5 to 70.6% in Loch Etive, but without showing any regular seasonal trend (Fig. 52).

4.6.1.5. Chlorophyll- a

Mean Ch- a was $1.76 \pm 0.58 \mu\text{g l}^{-1}$ in Loch Kishorn and $1.63 \pm 0.56 \mu\text{g l}^{-1}$ in

Table-40. Correlation matrix between environmental factors, condition indices and specific growth rate in length (SGR) in Loch Etive from May 1994 to May 1995. CIV: condition index volumetric, CID: condition index dry, T: temperature, S: salinity, Ch-a: chlorophyll-a, POM: particulate organic matter, SEC: Secchi disk (Significance levels: *: P<0.05; **: P<0.01 and ***: P<0.001).

	SGR	CIV	CID	T	S	Ch-a	Seston	POM
CIV	0.531*							
CID	0.531*	0.669**						
T	0.846***	0.626*	0.680**					
S	0.466	0.727**	0.622*	0.750**				
Ch-a	0.051	0.652**	0.101	0.296	0.415			
Seston	0.337	0.795***	0.397	0.302	0.559*	0.519*		
POM	0.246	0.739**	0.169	0.224	0.438	0.723**	0.913***	
SEC	0.354	0.290	0.230	0.337	0.357	0.190	0.091	0.066

Table-41. Correlation matrix between environmental factors, condition indices and specific growth rate in length (SGR) in Loch Kishorn from May 1994 to May 1995. CIV: condition index volumetric, CID: condition index dry, T: temperature, S: salinity, Ch-a: chlorophyll-a, POM: particulate organic matter, SEC: Secchi disk (Significance levels: *: P<0.05; **: P<0.01 and ***: P<0.001).

	SGR	CIV	CID	T	S	Ch-a	Seston	POM
CIV	0.592*							
CID	0.506	0.771***						
T	0.813***	0.741**	0.813***					
S	0.281	0.573*	0.358	0.263				
Ch-a	-0.116	0.311	0.176	-0.101	0.260			
Seston	-0.063	0.528*	0.472	0.189	0.530*	0.666**		
POM	0.072	0.617*	0.514*	0.265	0.490	0.698**	0.964***	
SEC	0.509	0.039	0.005	0.487	-0.078	-0.425	-0.348	-0.308

Loch Etive ($P>0.05$). Ch-a values were high in spring and gradually reached a minimum in late autumn and winter (Fig. 52). Maximum Ch- a was recorded as $6.32 \mu\text{g l}^{-1}$ in Loch Kishorn and $7.72 \mu\text{g l}^{-1}$ in Loch Etive in May 1994 at both sites (Table- 39). Ch-a had a significant positive relationship with POM and seston in both sites. Chlorophyll-a was strongly affected by the development of algal blooms in the lochs.

4.6.1.6. Transparency

The monthly distribution of transparency is shown in Fig. 52 and mean values are given in Table- 39. Transparency was mainly affected by the presence of an algal bloom and the weather conditions. Transparency was found to be significantly lower in Loch Etive (6.27 ± 0.44 m) than Loch Kishorn (4.54 ± 0.11 m) ($P<0.01$), with ranges from 4 m to 5 m and from 4.5 m to 10 m, respectively.

4.6.2. Growth

Mussel farmers who cooperated in this study suggested that there are morphological differences between Loch Etive and Loch Kishorn mussels which might be genotypic as well. Seed (1968) and Kautsky *et al.*, (1990) suggested that reciprocal transplantations could be one way to examine the extent to which stock differences in growth and morphology may be environmentally induced or which are genetic in origin. This approach was applied by comparing rope-grown mussels of similar sizes and age (one year old) in terms of growth rate, mortality and morphology, using mussels transplanted between Loch Etive and Loch Kishorn stocks. Fig. 53 shows shell length frequency In May 1994 (initial), in October 1994 and May 1995 for both sites.

The growth rate of Loch Kishorn mussels (LK) transplanted to Loch Etive (denoted LK-LE) in May 1994 was similar to that of the native stock (LE) in Loch Etive (Table-42). At the end of the experiment, mussels from the native stock in Loch Etive (LE) were 50.30 ± 0.59 mm (mean length \pm SE), while transplanted stock in Loch Etive (LK-LE) attained 48.18 ± 0.55 mm.

Table-42. Mean shell lengths ($L \pm SE$) recorded at sampling and monthly growth increments ($\Delta L = L_2 - L_1$, mm) of two mussel stocks grown at native and transplanted sites during the experimental period (from May 1994 to May 1995). Common superscripts in the same row indicate that the superscripted values do not differ significantly ($P > 0.05$)

Month	LE	ΔL	LK-LE	ΔL	LK	ΔL	LE-LK	ΔL
May	27.35 \pm 0.33	-	26.08 \pm 0.35	-	26.66 \pm 0.38	-	25.82 \pm 0.40	-
June	30.65 \pm 0.48	3.30	28.60 \pm 0.45	2.52	27.99 \pm 0.37	1.33	26.99 \pm 0.45	1.17
July	35.95 \pm 0.45	5.30	33.31 \pm 0.54	4.50	31.96 \pm 0.43	3.97	29.72 \pm 0.44	2.73
August	42.58 \pm 0.41	6.63	40.41 \pm 0.47	7.31	35.16 \pm 0.55	3.20	35.02 \pm 0.48	5.30
September	45.64 \pm 0.45	3.06	42.88 \pm 0.47	2.47	36.41 \pm 0.53	1.25	36.86 \pm 0.54	1.84
October	47.02 \pm 0.52	1.38	43.80 \pm 0.49	0.92	37.31 \pm 0.72	0.90	37.00 \pm 0.54	0.14
November	47.22 \pm 0.41	0.20	44.00 \pm 0.58	0.20	40.45 \pm 0.58	3.14	38.42 \pm 0.49	1.42
December	47.92 \pm 0.46	0.70	44.23 \pm 0.58	0.23	40.59 \pm 0.49	0.14	38.66 \pm 0.42	0.24
January	48.11 \pm 0.40	0.19	44.64 \pm 0.54	0.41	41.63 \pm 0.49	1.04	39.36 \pm 0.44	0.70
February	48.24 \pm 0.53	0.13	44.78 \pm 0.44	0.14	41.81 \pm 0.53	0.18	39.48 \pm 0.37	0.12
March	48.87 \pm 0.44	0.63	45.42 \pm 0.53	0.64	42.38 \pm 0.51	0.56	40.72 \pm 0.56	1.24
April	49.27 \pm 0.45	0.40	46.18 \pm 0.45	0.76	43.94 \pm 0.51	1.60	42.62 \pm 0.42	1.90
May	50.30 \pm 0.59 ^c	1.11	48.18 \pm 0.55 ^{bc}	1.96	45.07 \pm 0.59 ^{ab}	1.10	43.71 \pm 0.59 ^a	1.10
Total Increment (mm)	23.03		22.06		18.41		17.89	
Monthly Increment (mm)		1.92		1.84		1.53		1.49

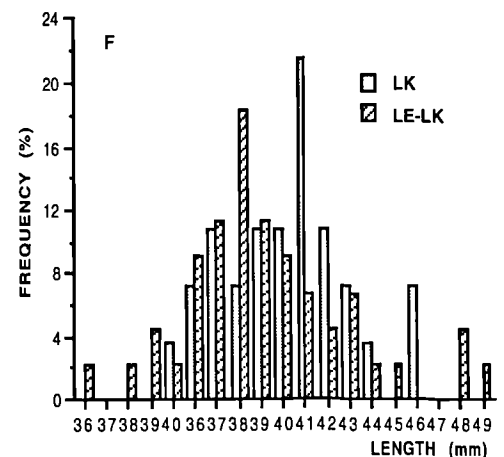
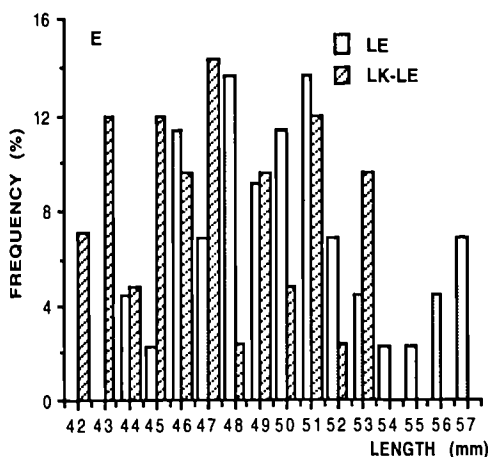
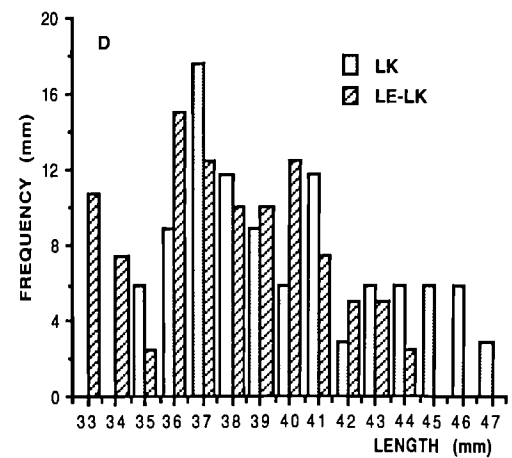
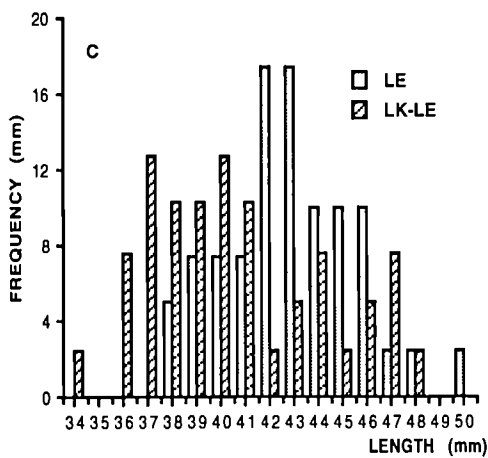
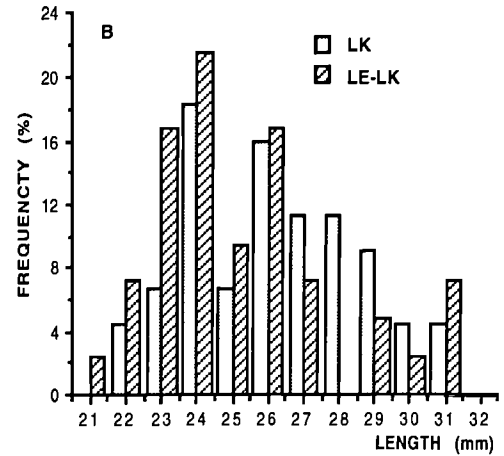
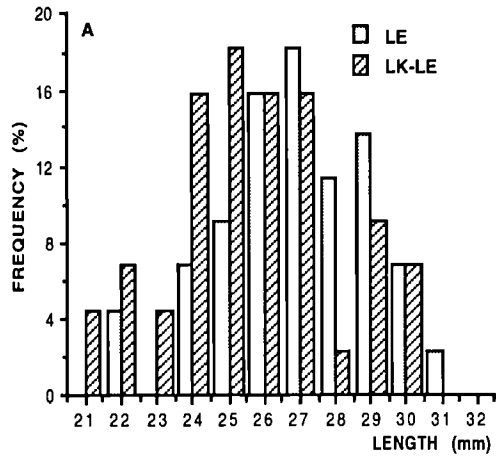


Fig. 53. Size frequency of experimental mussels in May 1994 (A and B), October 1994 (C and D) and May 1995 (E and F) in transplanted and native stocks. LE: Loch Etive, LK: Loch Kishorn

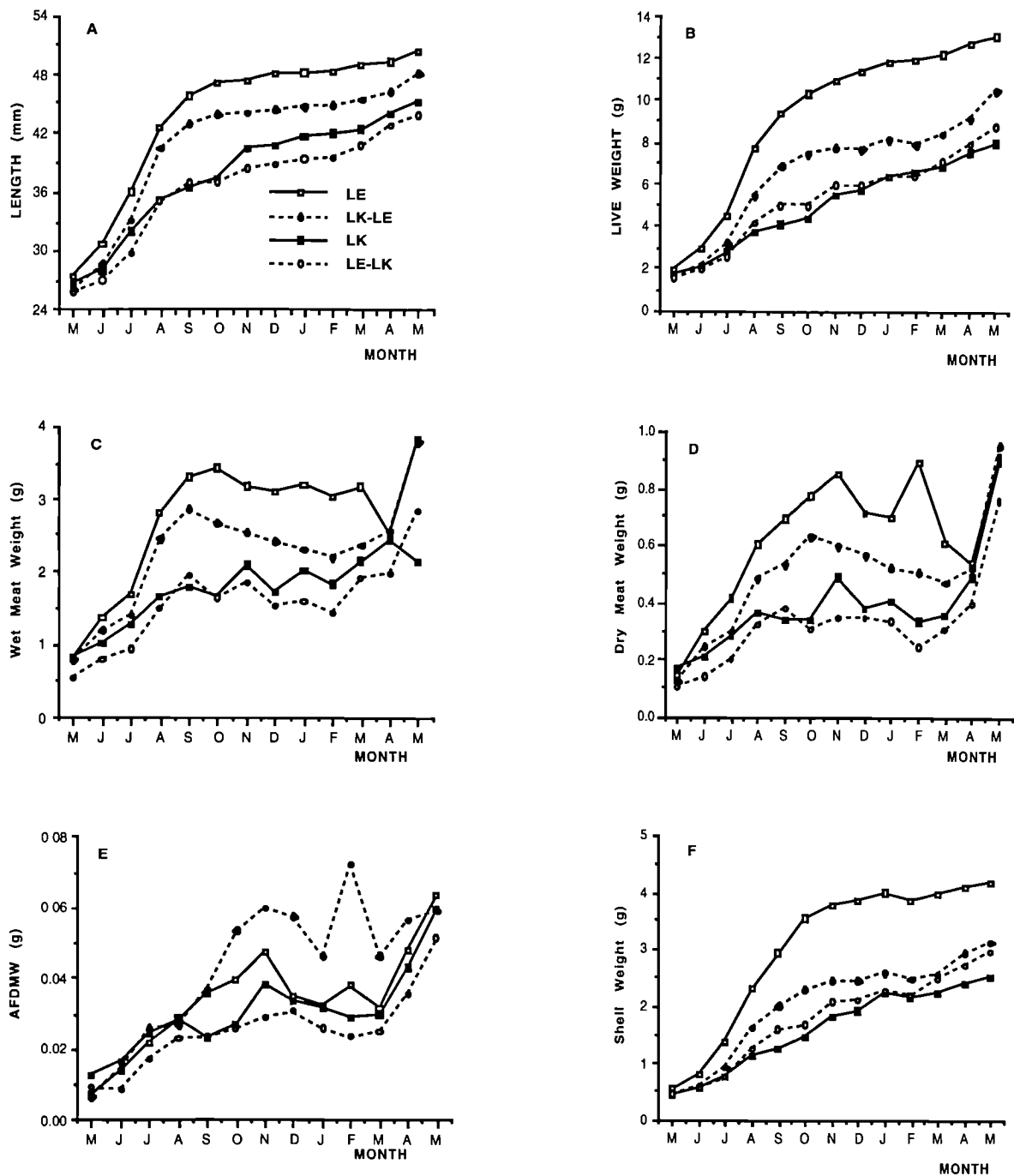


Fig. 54. Monthly changes in shell length (A), live weight (B), wet meat weight (C), dry meat weight (D), ash-free dry meat weight (E) and shell weight (F) in native (LE and LK) and transplanted (LK-LE and LE-LK) mussels at depth a of 2 m in Loch Etive and Loch Kishorn.

Over the 12 month experimental period increases in shell lengths were 23.03 mm and 22.06 mm for LE and LK-LE mussels, respectively (Table-42). Monthly increment was found to be 1.92 mm in LE and 1.84 mm in LK-LE mussels. One-way ANOVA results show that increment in shell length did not differ significantly between native stock (LE) and transplanted stock (LK-LE) in Loch Etive ($P>0.05$).

In the native stock (LE), 85.41 % of total increment in shell length occurred from May to October while length of transplanted mussels (LK-LE) increased by 80.33 % from May to October in Loch Etive.

In Loch Kishorn, native mussels (LK) reached 45.07 ± 0.59 mm and transplanted mussels (LE-LK) reached 43.71 ± 0.59 mm shell length at the end of experiment (Fig. 54 and Table-42). Increment in shell length was 18.41 mm in native stock (LK) compared with 17.89 mm in the transplanted stock (LE-LK) over the 12 months experimental period. 57.85% of total increment occurred from May to October in the native stock (LK) while it was 62.49 % in transplanted mussels (LE-LK) in Loch Kishorn. At the end of the one year experiment, average final shell length in Loch Etive (mean of LE and LK-LE) was 49.24 mm and 44.39 mm in Loch Kishorn (mean of LK and LE-LK). Two-way ANOVA results (Table-43) show that site (Loch Etive and Loch Kishorn) had a significant affect on shell length ($P<0.001$). However, stocks (native and transplanted) and site *stocks did not affect shell length ($P>0.05$)

The rapid increase in growth rate after transfer resulted in characteristic growth marks on the shell length although the general shell shape and color of the transferred stocks (LK-LE and LE-LK) mussels remained unaltered in the short term. Monthly specific growth rate in length (SGR %) is depicted in Fig. 55. In Loch Etive, specific growth rate ranged from 0.78 % to 14.51 % in native stock (LE) and from 0.33 % to 17.1 % in the transplanted stock (LK-LE). Monthly mean SGR was found to be 4.84 % and 4.79 % in LE and LK-LE, respectively. Maximum values of SGR were recorded from July to August in Loch Etive.

In Loch Kishorn, SGR ranged from 0.35 % to 10.75 % in native stock (LK) and from 0.29 % to 14.48 % transplanted stock (LE-LK). Monthly mean SGR was

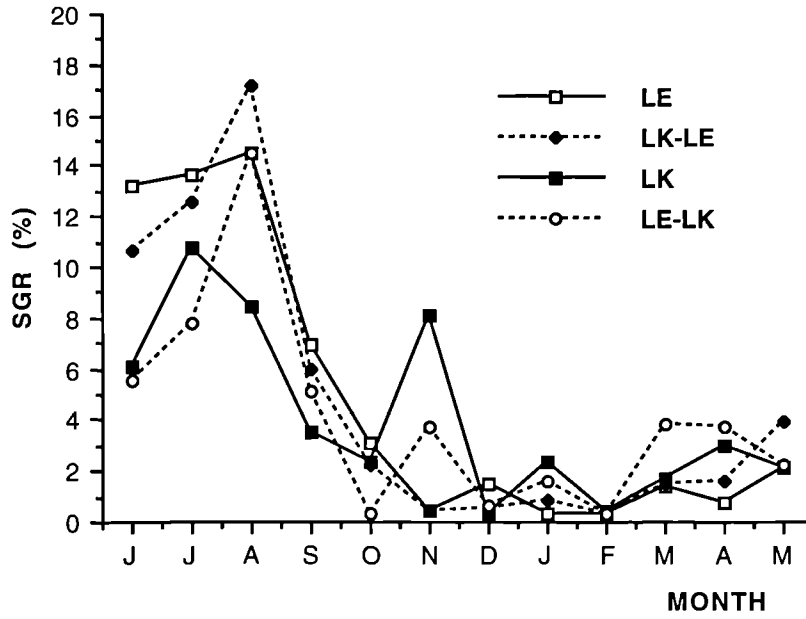


Fig. 55. Monthly specific growth rate in length (SGR%) in transplanted (LK-LE and LE-LK) and native (LE and LK) mussels in Loch Etive (LE) and Loch Kishorn (LK) from May 1994 to May 1995.

4.09 % and 4.12 in LK and LE-LK respectively. SGR reached a maximum from June to July in the native stock and from July to August in the transplanted stock in Loch Kishorn. In general SGR was high from spring to autumn and low in winter. Correlation matrices between SGR, condition indices and environmental factors are given in Tables 40 and 41. SGR had a strong positive relationship with temperature at both experimental sites ($P < 0.001$).

Variation in live weight (LW) wet meat weight (WMW), dry meat weight (DMW) and ash-free dry meat weight (AFDMW) for native stocks (LE and LK) and transplanted stocks (LK-LE and LE-LK) are plotted in Fig. 54 and summarised in Table-43. The effects of site stock and site stock on length (L), LW, WMW, shell Weight (SW) and DMW were tested by two-way ANOVA (shown in Table-44). The growth of both translated stocks followed the growth pattern exhibited by the native stocks; LK-LE was similar to LE and LE-LK to LK. The biggest difference between transplanted and native stocks was observed in live weight. The live weight increment of LE-LK mussels was greater than that of the native stock (LK) in Loch Kishorn while in Loch Etive, live weight increment was higher in the native stock (LE) than the transplanted stock (LK-LE). The increases in mean live weight for all stocks (native and transplanted) were 9.94 g and 6.73 g in Loch Etive and Loch Kishorn respectively ($P < 0.001$).

The best performance of growth in live weight was obtained for mussels in Loch Etive which grew from 1.95 ± 0.06 g to 13.05 ± 0.44 g (native stock) and from 1.63 ± 0.07 g to 10.41 ± 0.37 g (transplanted stock) ($P < 0.05$) over the 12 month experimental period. In Loch Kishorn, LW increased from 1.68 ± 0.07 g to 7.97 ± 0.27 g (native stock) and from 1.56 ± 0.08 to 8.73 ± 0.34 g (transplanted mussels). The difference in live weight was not significant between the native and transplanted stock in Loch Kishorn ($P > 0.05$). The considerable live weight differences between the native and transplanted stocks was a result of shell weight differences between the two stocks (see Table-45) The effect of site and site *stock on live weight was significant ($P < 0.05$), but there was no significant effect of stock (native and transplanted) on live weight (Table-44).

Table-43. Mean (\pm SE) live weight (LW), wet meat weight (WMW), dry meat weight (DMW) and ash-free dry meat weight (AFDMW) growth of native mussel stocks in Loch Etive (LE) and Loch Kishorn (LK) and transplanted mussel stocks (LK-LE and LE-LK) on four sampling dates (May 1994, October 1994, February 1995 and May 1995). Common superscripts in the same row indicate that the superscripted values do not differ significantly ($P>0.05$)

Parameter	Month	LE	LK-LE	LK	LE-LK
LW	May (initial)	1.95 \pm 0.06	1.63 \pm 0.07	1.68 \pm 0.07	1.56 \pm 0.08
	October	10.26 \pm 0.35	7.42 \pm 0.23	4.43 \pm 0.25	4.98 \pm 0.23
	February	11.87 \pm 0.40	7.91 \pm 0.23	6.57 \pm 0.25	6.32 \pm 0.17
	May	13.05 \pm 0.44 ^c	10.41 \pm 0.37 ^b	7.97 \pm 0.27 ^a	8.73 \pm 0.34 ^{ab}
	Increment (g)	11.1	8.78	6.29	7.17
WMW	May (initial)	0.79 \pm 0.03	0.79 \pm 0.04	0.82 \pm 0.04	0.53 \pm 0.03
	October	3.42 \pm 0.13	2.67 \pm 0.10	1.67 \pm 0.10	1.63 \pm 0.08
	February	3.02 \pm 0.11	2.19 \pm 0.08	1.83 \pm 0.09	1.42 \pm 0.06
	May	3.80 \pm 0.19 ^b	3.78 \pm 0.15 ^b	3.13 \pm 0.16 ^a	2.83 \pm 0.16 ^a
	Increment (g)	3.01	2.99	2.31	2.30
DMW	May (initial)	0.14 \pm 0.004	0.13 \pm 0.006	0.17 \pm 0.007	0.10 \pm 0.005
	October	0.77 \pm 0.03	0.63 \pm 0.02	0.34 \pm 0.02	0.31 \pm 0.01
	February	0.89 \pm 0.03	0.51 \pm 0.02	0.36 \pm 0.01	0.24 \pm 0.01
	May	0.91 \pm 0.05 ^{ab}	0.95 \pm 0.04 ^b	0.90 \pm 0.04 ^{ab}	0.75 \pm 0.04 ^a
	Increment (g)	0.77	0.82	0.73	0.65
AFDMW	May (initial)	0.006 \pm 0.0002	0.007 \pm 0.0003	0.012 \pm 0.0005	0.009 \pm 0.0004
	October	0.057 \pm 0.002	0.039 \pm 0.001	0.027 \pm 0.001	0.026 \pm 0.001
	February	0.073 \pm 0.003	0.038 \pm 0.001	0.029 \pm 0.001	0.023 \pm 0.001
	May	0.059 \pm 0.003 ^a	0.064 \pm 0.003 ^a	0.060 \pm 0.003 ^a	0.052 \pm 0.003 ^a
	Increment (g)	0.053	0.054	0.048	0.043

Table-44. Two-way ANOVA results on shell length (L), live weight (LW), wet meat weight (WMW), shell weight (SW) and dry meat weight (DMW) in transplanted and native mussels. (ns: not significant, *: P<0.05, **: P<0.01 and ***: P<0.001)

	Source	DF	SS	MS	F	P
L	Site	1	74.157	74.157	26.34	***
	Stock	1	9.632	9.632	3.45	ns
	Site*Stock	1	0.577	0.577	0.21	ns
	Error	8	22.351	2.794		
	Total	11	106.717			
LW	Site	1	35.398	35.398	36.07	***
	Stock	1	2.871	2.871	2.93	ns
	Site*Stock	1	9.205	9.205	9.38	*
	Error	8	7.852	0.981		
	Total	11	55.326			
WMW	Site	1	2.0584	2.0584	28.40	***
	Stock	1	0.0547	0.0547	0.75	ns
	Site*Stock	1	0.0520	0.052	0.72	ns
	Error	8	0.5800	0.0725		
	Total	11	2.745			
SW	Site	1	2.539	2.539	38.37	***
	Stock	1	0.295	0.295	4.45	ns
	Site*Stock	1	1.81	1.81	27.35	***
	Error	8	0.529	0.066		
	Total	11	5.172			
DMW	Site	1	0.0381	0.0381	8.05	*
	Stock	1	0.0055	0.0055	1.15	ns
	Site*Stock	1	0.0229	0.0229	4.84	ns
	Error	8	0.0379	0.0047		
	Total	11	0.104			

The mean value and one way ANOVA results of LW, WMW, DMW and AFDMW are given in Table-44 for four sampling dates (May 1994, October 1994, February and May 1995). Table-43 shows the effect of site, stock and site *stock on L, LW, WMW, SW and DMW. Site had a significant affect on wet meat weight ($P < 0.001$) but there was no affect of stock and site *stock ($P > 0.05$). As can be seen in Table-43, WMW and DMW growth at Loch Etive were better than at Loch Kishorn but AFDMW was similar at both sites. In general there were loses in WMW from October to February and good recovery from February to May due to the availability of food, plus high temperature during the latter period.

4.6.3. Morphology of Transplanted Mussels

The mussels in Loch Etive and Loch Kishorn differ in shell color, shell shape and shell weight. Mussels from Loch Etive have a very dark bluish-black color (Plate-14) compared to the brownish or brownish-black color of Loch Kishorn mussels (Plate-15). Although, there seemed to be some color changes in transplanted mussels, this was not uniform and might be a subjective observation. Mussels from Loch Etive have a higher height : length ($P < 0.001$) and width : length ratios ($P < 0.05$) i.e. they have a broader and wider body shape than Loch Kishorn mussels. Width : height ratio was found to be higher in Loch Etive than Loch Kishorn mussels ($P < 0.05$).

The mean values of shell morphological parameters for Loch Etive and Loch Kishorn native stock (LE and LK) and transplanted stocks (LK-LE and LE-LK) (Plates 12 and 13) mussels measured in May 1995 (exactly one year after the transplantation) are given in Table-45. Shell weight was found to be significantly higher in Loch Etive native stock (LE) than transplanted stock (LK-LE) ($P < 0.01$).

According to the results of two-way ANOVA, site ($P < 0.01$) and site *stock ($P < 0.001$) had significant effects on width : length ratios while stocks (native and transplanted) had no effect ($P > 0.05$). Height : length was only affected by site *stock ($P < 0.001$), while width : height ratio was affected only by site ($P < 0.001$).

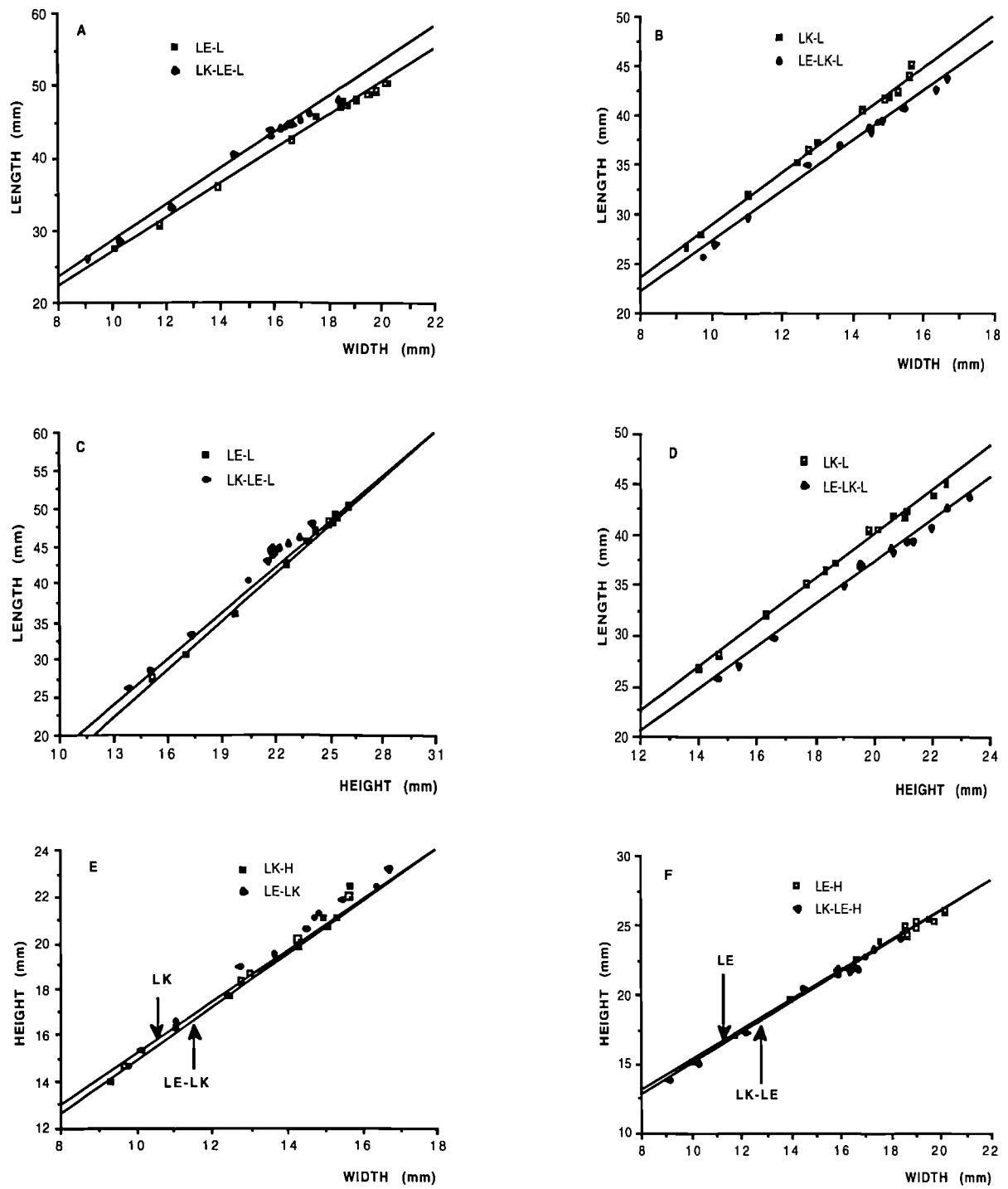


Fig. 56. Linear relationships between width-length (A and B), height-length (C and D) and width-height (E and F) in native (LE and LK) and transplanted (LK-LE and LE-LK) mussels in Loch Etive and Loch Kishorn.

Table-45. The mean shell characteristics of native (LE and LK) and transplanted (LK-LE and LE-LK) mussels from Loch Etive (LE) and Loch Kishorn (LK) one year after transplantation. Common superscripts in the same column indicate that the superscripted values do not differ significantly ($P>0.05$).

Site\Stock	Length (L) (mm)	Weight (g)	Height (H) (mm)	Width (W) (mm)	W:L	H:L	W:H
LE	50.38±0.59	4.18±0.12	26.08±0.29	20.19±0.26	0.40±0.003 ^c	0.52±0.005 ^{bc}	0.77±0.009 ^b
LK-L	48.14±0.55	3.11±0.11	26.06±0.27	18.39±0.26	0.38±0.007 ^{bc}	0.50±0.003 ^a	0.76±0.01 ^{ab}
LK	45.07±0.59	2.51±0.10	22.45±0.25	15.98±0.21	0.36±0.007 ^a	0.50±0.002 ^a	0.72±0.013 ^a
LE-LK	43.71±0.59	2.96±0.12	23.26±0.29	16.71±0.23	0.38±0.002 ^{bc}	0.53±0.003 ^c	0.72±0.009 ^a

The relationships between shell height, width and length are shown in Fig. 56 and relationships equations summarised in terms of slope (b), intercept (d) and correlation coefficient (r) are provided in Table-46. Monthly distribution of shell weight is illustrated in Fig. 54.

Table-46. Linear relationships ($y = a + bx$) between various combinations of morphological shell parameters for native (Loch Etive (LE) and Loch Kishorn (LK)) and transplanted (LK-LE and LE-LK) mussels.

Dependent (y)	Independent (x)	Site\Stock	Intercept (a)	Slope (b)	r
Length on Width		LE	3.700	2.333	0.996
		LK-LE	3.540	2.478	0.994
		LK	1.994	2.685	0.994
		LE-LK	1.798	2.533	0.992
Length on Height		LE	-5.975	2.167	0.997
		LK-LE	-4.477	2.207	0.995
		LK	-3.797	2.189	0.996
		LE-LK	-5.119	2.114	0.995
Height on Width		LE	4.511	1.074	0.994
		LK-LE	3.693	1.119	0.992
		LK	2.710	1.222	0.990
		LE-LK	3.310	1.195	0.993

4.6.4. Condition Index

The seasonal variations in wet condition index (CIV), dry condition index (CID) and meat yield (MY) for native (LE and LK) and transplanted mussels (LK-LE and LE-LK) are depicted in Fig. 57 and minimum, maximum and annual mean values are given in Table-47. Condition indices and meat yield are mainly affected by the accumulation and release of reproductive materials. Changes in two condition indices (CIV and CID) were very similar. Correlation matrices between condition indices and environmental factors are given in Tables 40 and 41.

CIV and CID showed a significant relationship ($r=0.699$, $P < 0.01$) and ($r=0.771$, $P < 0.001$) in Loch Etive and Loch Kishorn, respectively. As can be seen from Table-40, temperature, salinity, chlorophyll- a seston and particulate organic matter had a significant positive relationship with CIV in Loch Etive. CIV had a significant relationship with temperature, salinity seston and POM in Loch Kishorn (Table-41).

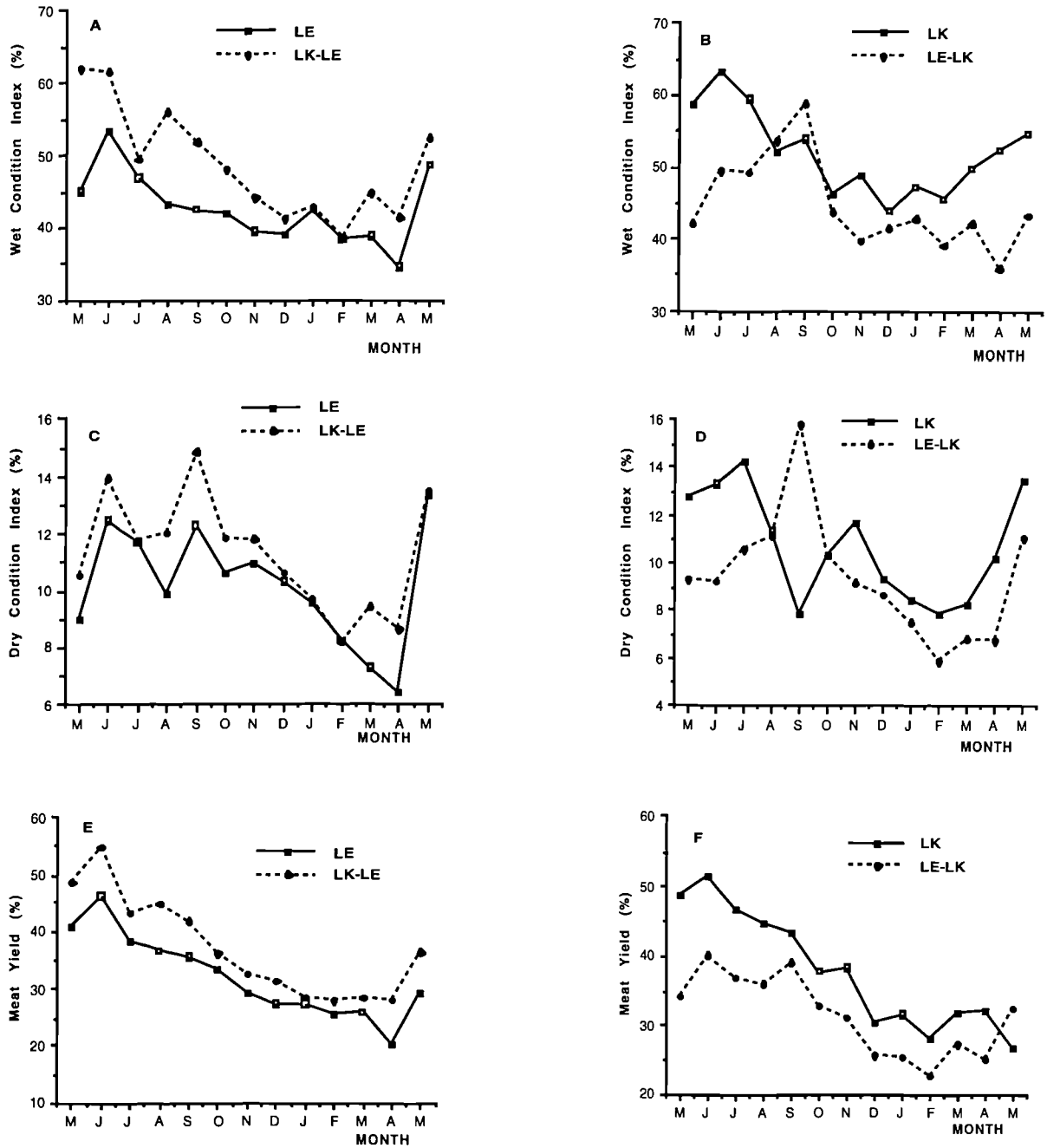


Fig. 57. Monthly changes in wet meat volume condition index (CIV) (A and B), dry meat condition index (CID) (C and D) and meat yield (E and F) in native (LE and LK) and transplanted (LK-LE and LE-LK) mussels in Loch Eive and Loch Kishorn from May 1994 to May 1995.

After combining the native and transplanted stocks, the annual mean CIV and CID were 45.63 % and 10.7 % respectively at Loch Etive, compared with 48.38 % and 10.7 % at Loch Kishorn. Neither CIV nor CID differed significantly by site ($P>0.05$). Moreover, meat yield was found to be quite similar with a mean of 34.07 % in Loch Etive and 34.53 % in Loch Kishorn ($P>0.05$).

Sharp increases from April to May in condition indices and meat yield show that spawning occurred in April. Meat yield in native and transplanted mussels had a similar seasonal cycle at both sites (Fig. 57). CIV was higher in Loch Kishorn than Loch Etive while MY was almost the same at the two sites (Table-47). These results show that meat yield was affected by morphological differences between the mussels at the two sites.

Table-47. Minimum, maximum and mean values of condition indices and meat yield in native and transplanted mussels in Loch Etive (LE) and Loch Kishorn (LK). CIV: wet meat volume condition index; CID: dry meat weight condition index and MY: meat yield. Superscripts show one-way ANOVA results. Common superscripts in the same row indicate that the superscripted values do not differ significantly ($P>0.05$)

Parameter		LE	LK-LE	LK	LE-LK
CIV	Minimum	34.52	38.52	43.85	36.00
	Maximum	53.15	61.83	63.25	58.77
	Mean	42.59±1.37 ^a	48.66±2.12 ^{ab}	51.97±1.63 ^b	44.78±1.75 ^a
CID	Minimum	6.45	8.19	7.81	5.88
	Maximum	13.33	14.85	14.28	15.83
	Mean	10.15±0.57 ^a	11.25±0.54 ^a	10.70±0.64 ^a	9.40±0.71 ^a
MY	Minimum	20.00	28.10	27.90	22.50
	Maximum	46.30	54.60	51.30	40.10
	Mean	31.87±2.01 ^a	36.26±2.58 ^a	37.71±2.32 ^a	31.36±1.60 ^a

4.6.5. Mortality and Survival

Monthly mortality, cumulative mortality and survival are illustrated in Fig. 58. Survival was expressed as the number of the live mussels staying in the lantern nets as a percentage of the initial stock number. Severe losses occurred during the first three months after transplantation due to handling and physiological responses to the different environment. Over the twelve month experimental period, cumulative mortality reached 7.3 % in LE mussels and 17.1 % in LK-LE mussels ($\chi^2= 71.8$, $P< 0.001$), while it was found to be 10.8 % in LK and 16.5 % in LE-LK stocks ($\chi^2= 18.2$, $p<0.001$). However mortality in the first three months accounted for 54.7 % and 79.4 % of the total in native stock (LE) and transplanted stock (LK-LE), respectively in Loch Etive from May to August 1994, while they were 56.9 % of the total mortalities in native (LK) and 64 % in transplanted stock (LE-LK) in Loch Kishorn. After combined native and transplanted stock, cumulative mortality was not differed significantly between Loch Etive and Loch Kishorn ($\chi^2= 1.34$, $P> 0.05$).

Maximum monthly mortalities were 2.1 %, 5.7 % , 4.1 % and 8.2 % in LE, LK-LE, LK and LE-LK, respectively. Mortality rate was higher in transplanted mussels than native mussels at two sites ($P<0.001$). Mortality in mussels continued throughout the experiment but at a decreasing rate. As shown in Fig. 58 survival of mussels at Loch Etive (87.5 %) was similar with Loch Kishorn (86.3 %). Survival was found to be 92.7 % in native stock (LE) and 82.9 % in transplanted stock (LK-LE) in Loch Etive. Whereas it was 89.2 % in native and 83.6 % in transplanted mussels in Loch Kishorn.

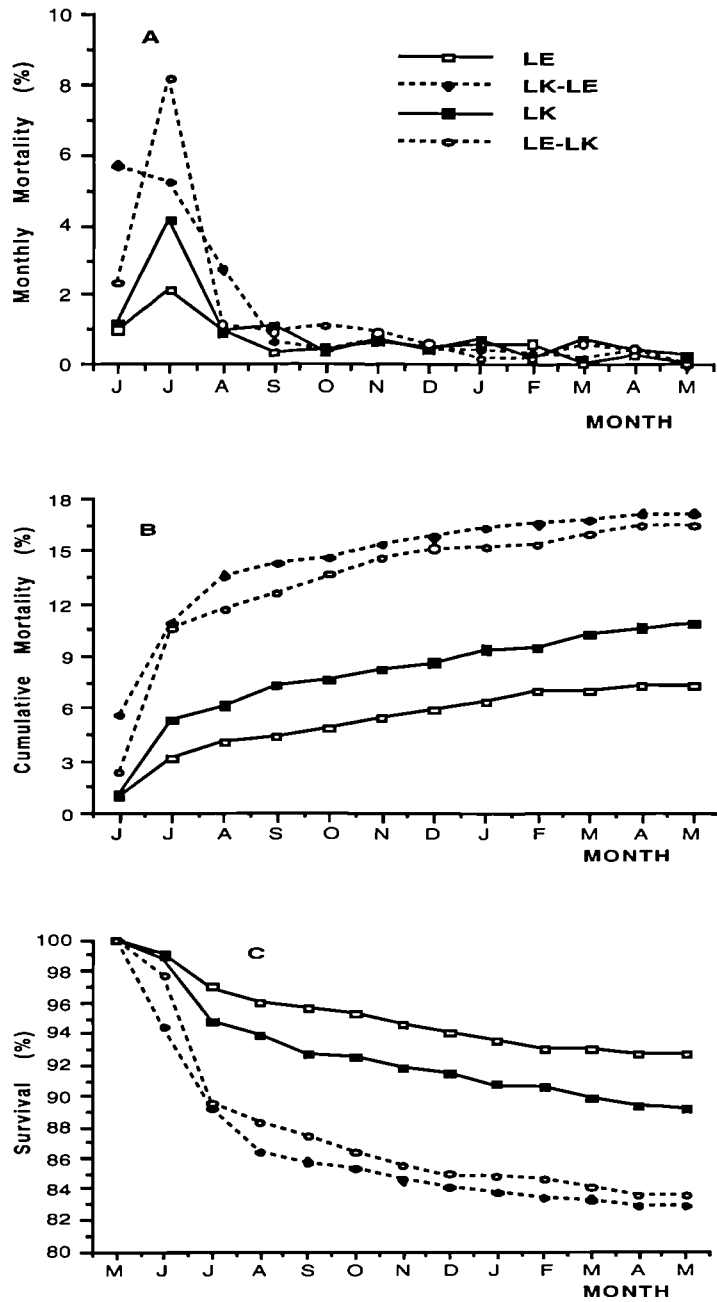


Fig. 58. Distribution of monthly mortality (A), cumulative mortality (B) and survival (C) in native Loch Etive and Loch Kishorn mussels (LE and LK) and transplanted (LK-LE and LE-LK) mussel stocks in Loch Etive and Loch Kishorn respectively.



Plate 12. Loch Etive (LF) mussels in Loch Kishorn (LK) after one year transplantation



Plate 13. Loch Kishorn (LK) mussels in Loch Etive (LE) after one year transplantation.

4.7. Carrying Capacity Estimation

Current measurements were carried out at a depth of 5 m in the water column to represent the mussel culture ropes. Actual rope lengths were 8 m in Loch Etive and 10 m in Loch Kishorn. The currents ranged from 0.01 m s^{-1} to 0.20 m s^{-1} , with a mean of 0.052 m s^{-1} in Loch Etive, and from 0.01 to 0.18 m s^{-1} , with a mean of 0.05 m s^{-1} in Loch Kishorn.

The system of mussel culture rafts used in this study consisted of a series of horizontal wooden beams in parallel (tiers), each supporting a row of droppers (ropes with attached mussels). The system is represented diagrammatically in Fig. 10. The surface area of the system facing the current was 80 m^2 in Loch Etive and 200 m^2 in Loch Kishorn. Mussel filtration rate ranged from 0.54 to 2.26 l h^{-1} in Loch Kishorn and 0.93 to 2.07 l h^{-1} in Loch Etive; these values were not significantly different between the sites ($P>0.05$). Filtration rate was higher in August (1.7 l h^{-1}) than May (1.1 l h^{-1}) in Loch Kishorn ($P<0.05$). In Loch Etive filtration rate was found to be lower in August (1.5 l h^{-1}) than in June (1.7 l h^{-1}), but the difference was not significant ($P>0.05$).

Assimilation efficiency varied from 8 to 39 % in Loch Kishorn and from 1 to 31% in Loch Etive. Mean values of assimilation efficiency were 19.85 ± 2.89 % in Loch Kishorn and 25.02 ± 1.84 % in Loch Etive. Differences in assimilation efficiency between the sites were not significant ($P>0.05$). In Loch Kishorn, assimilation efficiency was found to be 19.64 % in May and 20.09 % in August ($P>0.05$). However, assimilation efficiency was significantly higher in June (28.23 %) than August (21.17 %) in Loch Etive.

An estimate of carrying capacity was derived from the concentration of seston as water entered mussel raft system. Seston concentration was calculated as a function of water flow rate, the original seston concentration (before entering the first tier of the culture unit) and the filtration of particles by all mussels in the up-current tiers. Mean monthly estimates of seston concentration outside and inside the raft system were used to calculate a theoretical carrying capacity for each side. The calculations were based on the apparent requirement that seston concentrations must not be reduced by more than 50%

in an ideal mussel culture system (Incze *et al.*, 1981). This assumption allows the maximum number of mussel tiers to be calculated and forms the basis for the estimates of carrying capacity shown in Table 48.

In Loch Etive, average seston concentration was 6.6 mg l^{-1} in the sea water before it entered the first tier. When the water passed through the system (10 tiers, supporting 200 culture ropes) seston concentration was reduced from 6.6 mg l^{-1} to 5.9 mg l^{-1} , which was less than expected. Based on the method used by Incze *et al.* (1981), carrying capacity is estimated to be 5.7 times greater in Loch Etive than the present mussel culture system utilises, i.e. the loch could support a system with 57 tiers in a raft (see Table 48), rather than the 10 tiers currently used.

In Loch Kishorn, seston concentration was 6 mg l^{-1} in the water before the entering first tier. When water passed through the system (consisting of 27 tiers), seston concentration was reduced from 6 mg l^{-1} to 4.72 mg l^{-1} . In this case the estimation suggests that the loch could support 75 tiers per raft system (Table 48)

A second method was used to estimate carrying capacity for mussel culture rafts, based on Carver and Mallet (1990). This method uses food supply and food demand as particulate organic matter (POM) and relevant calculations for Loch Etive and Loch Kishorn are shown in Table 49. Daily food ration per mussel was estimated to be $129.0 \text{ mg POM day}^{-1}$ in May and $79.7 \text{ mg POM day}^{-1}$ in August 1994 in Loch Etive. In Loch Kishorn, daily food ration per mussel was calculated as $50.6 \text{ mg POM day}^{-1}$ in May and $147.7 \text{ mg POM day}^{-1}$ in August 1994. These estimates suggest a daily carrying capacity of 15,721 kg mussel in May and 24,428 kg mussel in August in Loch Etive, while it was 41,269 kg mussel in May and 38,040 kg mussel in August in Loch Kishorn. These estimates compare with actual mussel production capacity values in the raft systems in the two lochs as follow:

Loch Etive: 10,000 kg mussel per raft system.

Loch Kishorn: 50,000 kg mussel per raft system.

Table-48. Estimates of carrying capacity based on seston concentration according to Incze *et al.* (1981) for the months of August 1994 (at the end of culture period) in the mussel raft system in Loch Etive (LE) and Loch Kishorn (LK).

Number of tiers in raft system	Seston Concentration (mg l ⁻¹)	
	Loch Kishorn	Loch Etive
1	6.00	6.60
10	5.54	5.90
20	5.05	5.22
27	4.72	4.79
30	4.59	4.61
40	4.18	4.07
50	3.81	3.60
57	3.56	<u>3.30*</u>
60	3.46	-
70	3.15	-
75	<u>3.00*</u>	-

*: Renotes the 50% reduction level for seston, equivalent to an estimated 57 tiers in the Loch Etive and 75 tiers in the Loch Kishorn raft systems.

Table.-49. Estimates of volume of water (passing through the raft system), particulate organic matter (POM) supply, POM demand and carrying capacity according to Carver and Mallet (1990) for the months of May and August 1994 in the raft systems in Loch Etive and Loch Kishorn. (LE: Loch Etive, LK: Loch Kishorn, Aug: August)

Site	Date	Volume (m ³ week ⁻¹)	POM (mg l ⁻¹)	Food Supply (kg POM week ⁻¹)	Filtration rate (l h ⁻¹)	Food ration per mussel (mg POM day ⁻¹)	Food demand (g POM week ⁻¹)	Carrying capacity per raft* (kg mussel day ⁻¹)
LE	May	2 515 968	3.2	8,051	1.68	129.02	73.16	15,721
	Aug	2 515 968	2.2	5,535	1.51	79.73	32.37	24,428
LK	May	5 171 040	1.9	9,825	1.11	50.62	34.81	41,269
	Aug	5 171 040	3.6	18,616	1.71	147.74	69.91	38,040

*: Raft dimensions: Loch Kishorn = 27 m * 20 m * 10 m and Loch Etive = 11 m * 10 m * 8 m.

4.8. Morphometrics and Genetics

4.8.1. Shell Morphometrics

Percentage of frequency distributions for the morphometric characteristics measured on *Mytilus* are illustrated in Figs. 59, 60, 61 and 62 while mean, minimum and maximum values for the measurements for Loch Etive (LE) and Loch Kishorn (LK) mussels are given in Table-50 while ratios of shell characteristics (internal and external) are given in Table-51.

Generally, visual observation of shell color and shape between the Loch Etive and Loch Kishorn mussels showed distinguishable differences between the sites. Thus, it was not surprising that the measured shell parameters also revealed clear differences between the two lochs.

Retractor muscle (lbrs) and ligament margin (lm) than Loch Kishorn mussels ($P < 0.05$). Distribution of tooth frequency is given in Fig. 61. The average tooth number was found to be higher in Loch Kishorn mussels (7.71 ± 0.41) than Loch Etive mussels (2.56 ± 0.36) ($P < 0.001$). The number of teeth was higher on the right valve of Loch Kishorn mussels (4.0 ± 0.21) than on the left valve (3.71 ± 0.21). The number of teeth was also higher on the right valve (1.56 ± 0.24) than left valve (1.0 ± 0.15) of Loch Etive mussels.

Mean ratios of shell characteristics show significant differences between the sites (Table-50). The distribution of shell width (W) : shell length (L) ranged from 0.34 to 0.47 % in Loch Etive and from 0.32 to 0.43 % in Loch Kishorn. The mean value of W:L was significantly higher in Loch Etive (0.40 ± 0.0004 %) than Loch Kishorn (0.37 ± 0.004 %) ($P < 0.001$). The shell height (H) : shell length (L) ratio was also higher in Loch Etive (0.53 ± 0.001 %) than Loch Kishorn (0.49 ± 0.0001 %) ($P < 0.01$). However width : height was not significantly different between sites ($P > 0.05$). Thus the results show that mussels from Loch Etive have a higher and wider shell than Loch Kishorn mussels.

There were also significant differences in internal shell characteristics between the two lochs. The hinge plate (hp) : shell length (L) ($P < 0.001$), anterior adductor muscle scar

(aams): shell length (L) ($P < 0.001$) and posterior adductor muscle (pam)-ventral margin of shell (vm) : shell length (L) ($P < 0.05$) ratios were higher in Loch Etive than Loch Kishorn mussels. However ligament margin (lm) : shell length (L) ratio was higher in Loch Kishorn than Loch Etive mussels ($P < 0.05$). In contrast, posterior adductor muscle (pam) : shell length (L) and length of the byssal retractor muscle scar (lbrs) : shell length ratios (L) were not significantly different between the sites ($P > 0.05$).

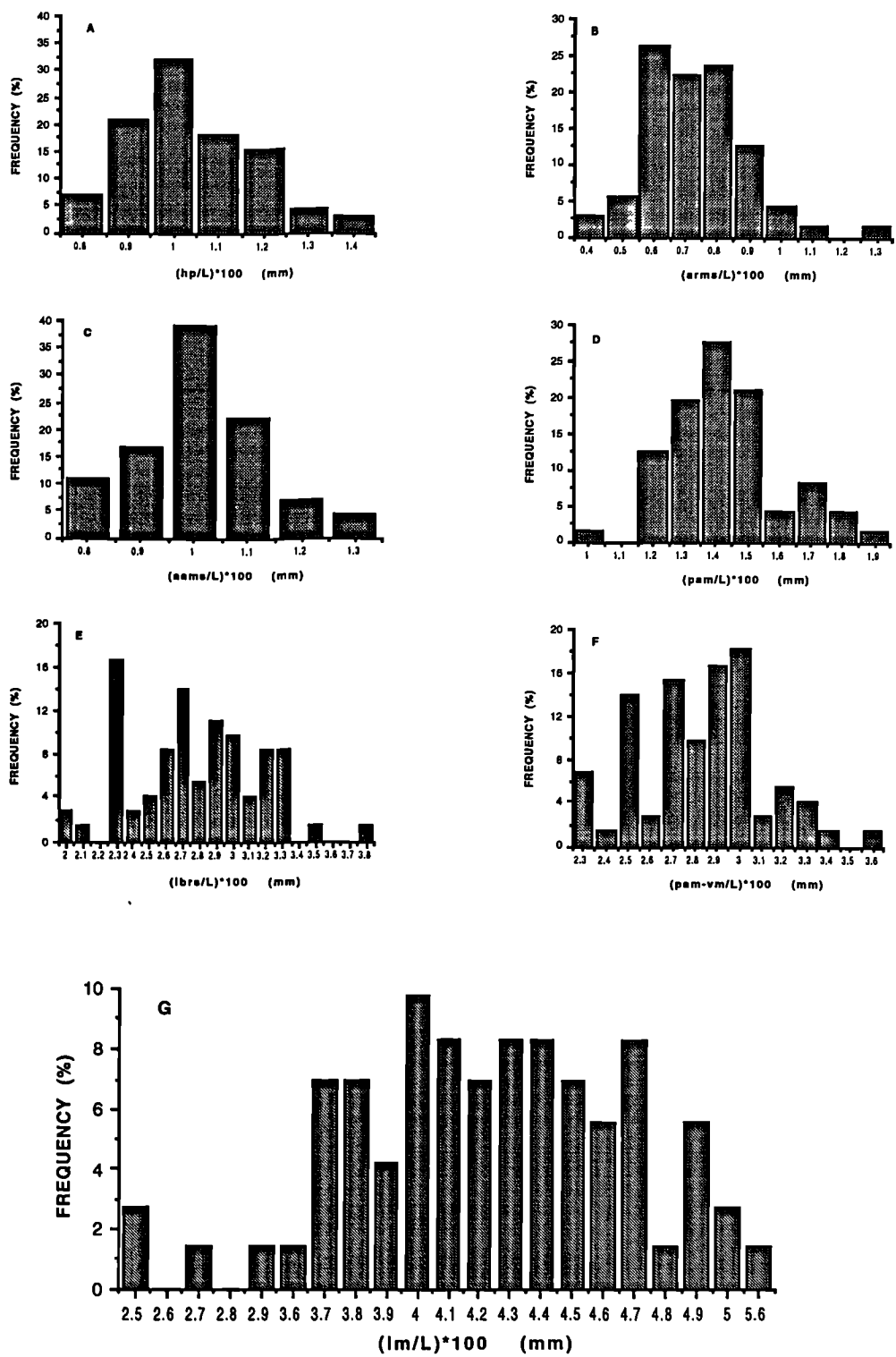


Fig.59. Frequency of shell characteristics of hinge plate (A), length of anterior retractor muscle scar (B), anterior adductor muscle scar (C), posterior adductor muscle scar (D), length of byssal retractor muscle scar (E), distance between ventral edge of posterior adductor muscle scar and ventral margin of shell (F) and ligament margin (G) in Loch Etive mussels.

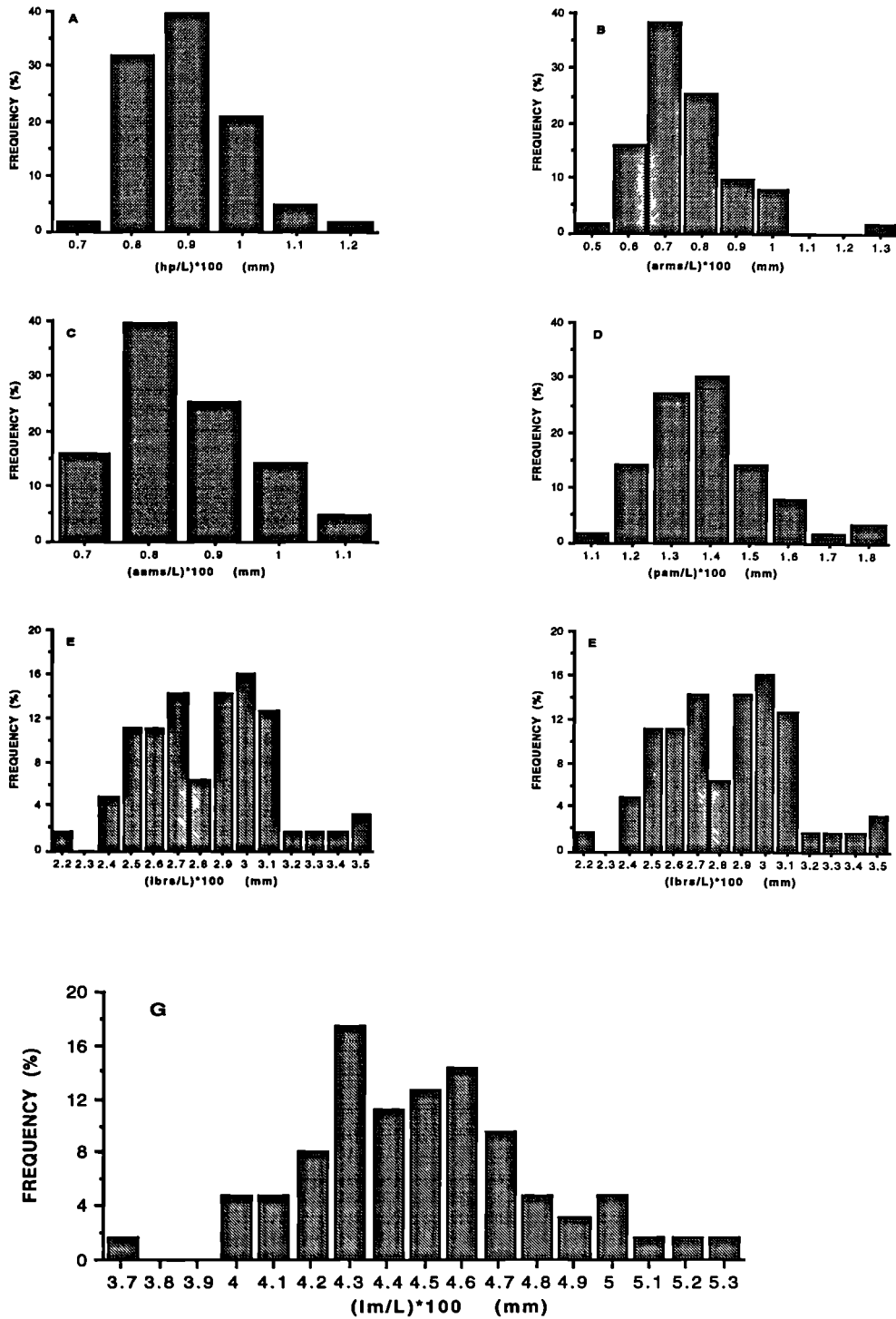


Fig.60. Frequency of shell characteristics of hinge plate (A), length of anterior retractor muscle scar (B), anterior adductor muscle scar (C), posterior adductor muscle scar (D), length of byssal retractor muscle scar (E), distance between ventral edge of posterior adductor muscle scar and ventral margin of shell (F) and ligament margin (G) in Loch Kishorn mussels .

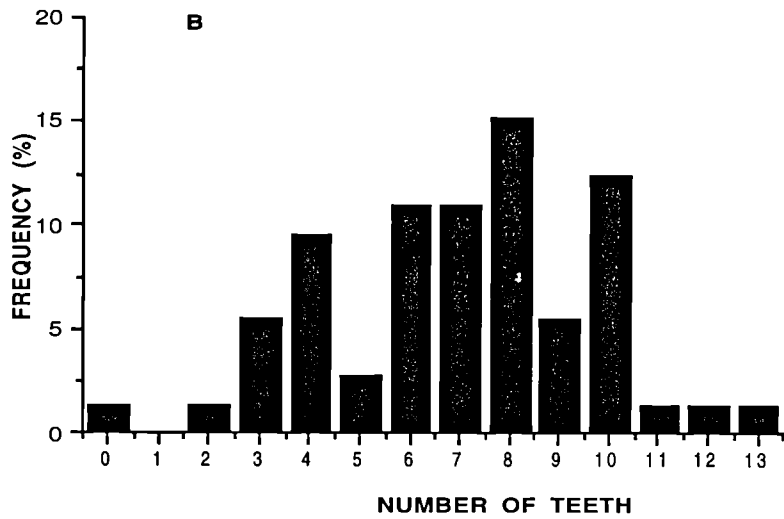
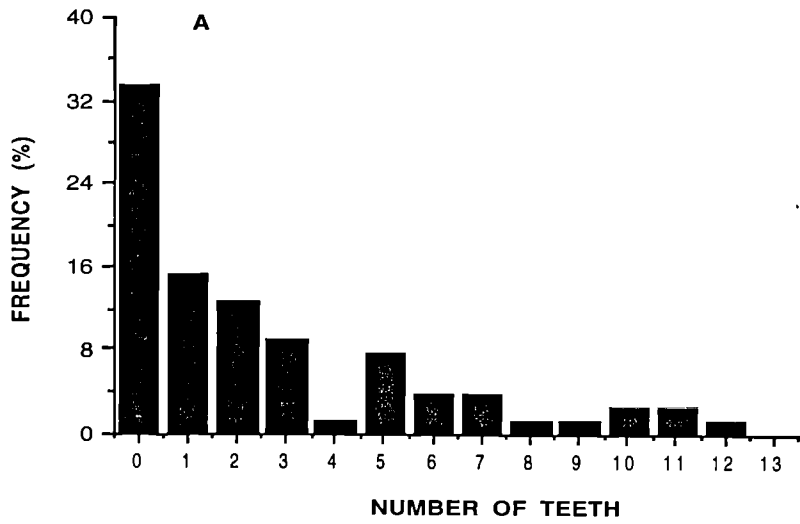


Fig.61. Frequency of hinge teeth in Loch Etive (A) and Loch Kishorn (B) mussel populations.

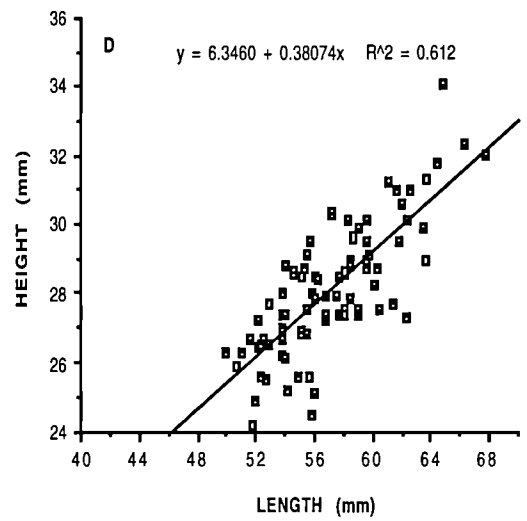
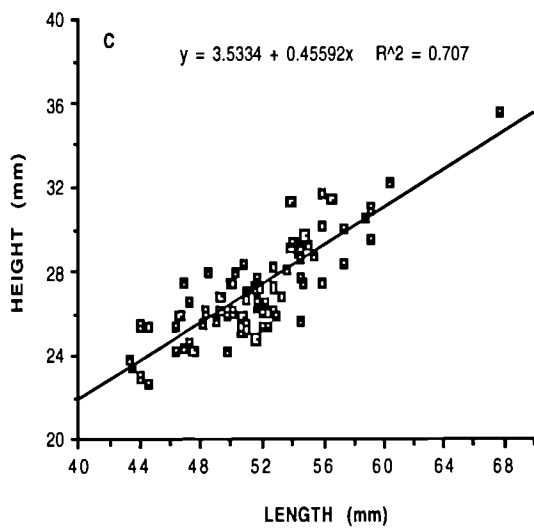
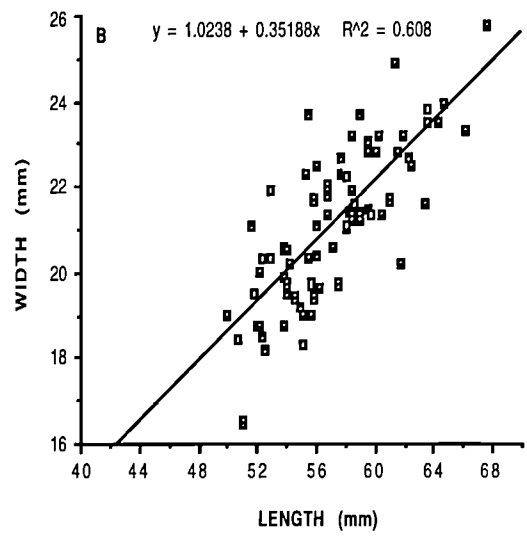
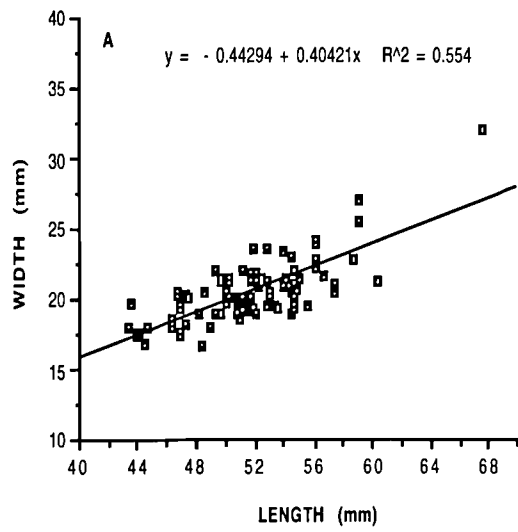


Fig.62. Mussel length-width in Loch Etive (A) and in Loch Kishorn (B) and length-height in Loch Etive (C) and in Loch Kishorn (D) with linear regression lines fitted.

Table-50. Mean, minimum and maximum of shell characteristics of Loch Etive and Loch Kishorn mussels used in this study. L: shell length (mm); W: shell width (mm); H: shell height (mm); hp: hinge plate; arms: length of anterior retractor muscle scar; aams: anterior adductor muscle scar; pam: posterior adductor muscle scar; lbrs: margin; To: number of teeth on hinge plate. LE: Loch Etive; LK: Loch Kishorn. Common superscripts in the same column indicate that the superscripted values do not differ significantly ($P>0.05$).

Site	L	W	H	hp	arms	aams	pam	lbrs	pam-vm	lm	To
LE	Mean	52.0	20.5	27.2	5.59 ^a	3.98 ^a	5.58 ^a	7.65 ^a	14.86 ^a	21.96 ^a	2.56 ^a
	Min	43.3	16.5	22.7	4.30	2.10	4.00	5.70	11.2	212.4	0.00
	Max	67.7	32.1	35.5	7.50	7.00	7.00	10.2	2.23	3.17	12.0
LK	Mean	57.16	21.14	28.11	5.42 ^a	4.61 ^b	5.16 ^a	8.18 ^a	15.26 ^a	25.97 ^b	7.71 ^b
	Min	49.9	16.5	24.2	4.30	3.00	3.70	6.30	12.8	20.5	0.00
	Max	67.7	25.8	34.0	6.80	7.30	7.00	11.7	18.3	32.0	16.0

Note: All units in the table are mm.



Plate-14. Loch Etive mussels



Plate 15. Loch Kishorn mussels

Table-51. Mean, minimum and maximum ratios of shell characteristics of Loch Etive and Loch Kishorn mussels measured in this study. L: shell length; hp: hinge plate; arms: length of anterior retractor muscle scar; aams: anterior adductor muscle scar; pam: posterior adductor muscle scar; lbrs: length of byssal retractor muscle scar; pam-vm: distance between ventral edge of posterior adductor muscle scar and ventral margin of shell; lm: ligament margin; W: shell width; H: shell height. LE: Loch Etive; LK: Loch Kishorn. Common superscripts in the same column indicate that the superscripted values do not differ significantly ($P>0.05$). (After Beamont *et al.*, 1989, modified from McDonald *et al.*, 1991)

Site	hp: L	arms: L	aams: L	pam: L	lbrs: L	pam-vm: L	lm: L	W:L	H:L	W:H
LE	Mean	0.0108 ^b	0.0077 ^a	0.0108 ^b	0.0148 ^a	0.0285 ^a	0.0424 ^a	0.396 ^b	0.525 ^b	0.756 ^a
	SE	0.0002	0.0002	0.0002	0.0002	0.0004	0.0006	0.0004	0.001	0.002
	Min	0.0084	0.0037	0.0081	0.011	0.0208	0.0252	0.34	0.47	0.63
	Max	0.0142	0.0133	0.0137	0.0192	0.0383	0.0562	0.47	0.59	0.92
LK	Mean	0.0095 ^a	0.0081 ^a	0.0090 ^a	0.0143 ^a	0.0288 ^a	0.0453 ^b	0.369 ^a	0.492 ^a	0.752 ^a
	SE	0.0001	0.0002	0.0001	0.0002	0.0004	0.0004	0.004	0.0001	0.001
	Min	0.0079	0.0059	0.0071	0.0120	0.0226	0.0378	0.32	0.44	0.63
	Max	0.0125	0.0136	0.0115	0.0181	0.0359	0.0537	0.43	0.53	0.9

2.8.2. Allele Frequency

Allele frequencies at each of two loci examined for Loch Etive and Loch Kishorn mussels are given in Table-52. The allele frequencies are given in order of decreasing anodal mobility; 110 is the fastest and 75 is the slowest (Plate-16). The most common allele was GPI¹⁰⁰ (Glucose phosphate isomerase) with 60 % occurrence in Loch Etive and 33 % in Loch Kishorn. Whereas the most common alleles were PGM⁹⁰ (Posphoglucomutase) and PGM⁹⁵ with a 33 % occurrence in Loch Etive, while PGM⁹⁰ was the most common allele with a 42 % in Loch Kishorn.

Table-52. Allele frequencies of mussel (*Mytilus edulis*) from Loch Etive and Loch Kishorn populations. GPI: Glucose phosphate isomerase, PGM: Posphoglucomutase, LE: Loch Etive; LK: Loch Kishorn.

		ANODAL MOBILITY							
		110	105	100	95	90	85	80	75
<u>LOCUS</u>	<u>SITE</u>								
GPI	LE	0.00	0.02	0.60	0.02	0.32	0.02	0.02	0.00
	LK	0.06	0.12	0.33	0.28	0.17	0.06	0.00	0.00
PGM	LE	0.00	0.056	0.139	0.334	0.334	0.083	0.056	0.00
	LK	0.00	0.00	0.073	0.122	0.415	0.146	0.146	0.098

The calculated heterozygosity was found to be 0.50 for PGM in Loch Etive and Loch Kishorn while it was 0.47 and 0.50 for GPI loci in Loch Etive and Loch Kishorn respectively. The observed heterozygosity was 0.33 in Loch Kishorn and 0.40 in Loch Etive for PGM loci. However for GPI loci, observed heterozygosity was 0.38 in Loch Kishorn and 0.45 in Loch Etive. The Hardy-Weinberg distribution for frequencies of genotypes is given in Table-53. The similarity of the observed and expected values supported the hypothesis that the populations are in Hardy-Weinberg equilibrium.

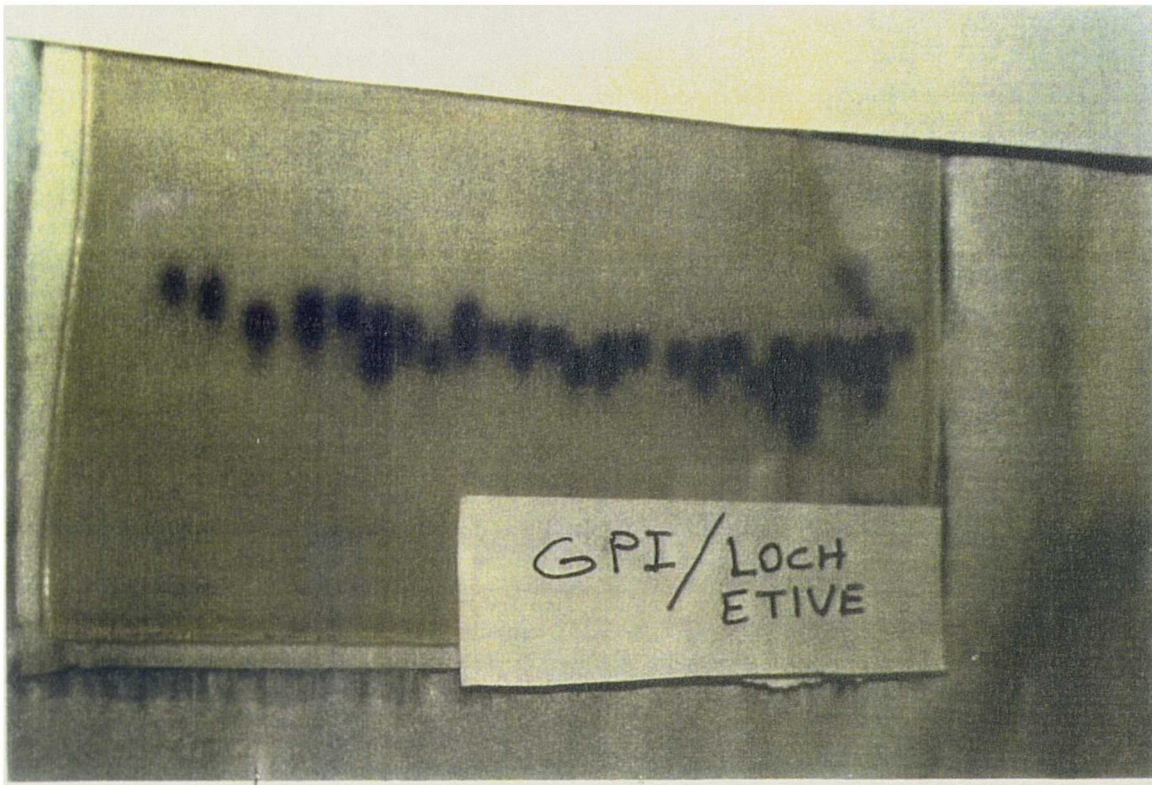


Plate-16. GPI (Glucose phosphate isomerase) loci for Loch Etive mussels after staining.

Nei's (1972) index for genetic identity was used to measure similarity among the populations. The genetic identity between Loch Etive and Loch Kishorn mussels is 0.69.

Table-53. Observed distribution and expected Hardy-Weinberg equilibrium distribution of genotypes for phosphoglucosmutase (PGM) and glucose phosphate isomerase (GPI) loci in Loch Etive (LE) and Loch Kishorn (LK) mussel populations.

Loci	Site		GENOTYPES			χ^2	p
			AA	AB	BB		
PGM	LE	Observed	30.55	44.44	25.0	0.727	0.695
		Expected	27.86	49.84	22.3		
PGM	LK	Observed	26.47	41.18	32.35	1.485	0.476
		Expected	22.15	49.83	28.03		
GPI	LE	Observed	45.71	42.86	11.43	0.222	0.989
		Expected	45.02	44.18	10.79		
GPI	LK	Observed	35.00	32.50	32.50	6.226	0.046
		Expected	26.26	49.96	23.77		

CHAPTER 5 : DISCUSSION

The results of this study show that variability in growth, biomass, production and condition index of *Mytilus edulis* and stock losses and natural mortality rates were similar at two mussel farming sites (Loch Etive and Loch Kishorn). However, the effect of transplantation between the two lochs had a significant effect on mortality. Mortality rate was found to be significantly higher in transplanted mussels than native mussels ($P < 0.05$).

Seed and Suchanek (1992) reported that several environmental factors can modulate growth in *Mytilus*. Of these, perhaps the availability of a suitable food resource is the most important since, without this, sustained growth cannot occur. Given adequate food, several factors particularly temperature, salinity and aerial exposure may interact, sometimes synergistically, resulting in various rates and seasonal patterns of growth. Such interactions and the tendency of some variables to vary together, makes it extremely difficult to identify the precise influence of any single factor in a natural mussel population.

Growth parameters in marine bivalves are mainly affected by interactions of several environmental parameters, particularly temperature and food availability (Bayne and Newell, 1983). The effects of these main environmental variables on growth, physiology and survival of bivalves have all been examined, using both alongside in-situ and in-vitro experiments around the world (e.g. Incze *et al.*, 1980; Jones, 1981; Widdows *et al.*, 1984; Page and Hubbard, 1987; Brown and Hartwick, 1988a, b; Page and Richard, 1990; Tedengren *et al.*, 1990; Stirling and Okumus, 1994; Okumus and Stirling, 1994; Loo and Rosenberg, 1983). Growth in mussels is affected principally by seasonal temperature, age and size, light, population structure, food supply, tidal exposure, salinity, waves and pollutants, as well as genotype (Seed, 1976; Seed and Suchanek, 1992).

The present results are compared below with findings of similar studies and the relevant information discussed in the light of the main objectives of this study.

5.1. Environmental Factors and Their Effects on Growth

5.1.1. Temperature

Water temperature in sea lochs is influenced mainly by tidal range and the quantity of freshwater run-off (Milne, 1972a). Many Scottish sea-lochs are fjordic estuaries (Milne, 1972b) and the two-layer estuarine circulation driven by freshwater inflow (Dyer, 1973) combined with tidal mixing are important in determining their hydrography (Gowen *et al.*, 1983).

According to Gage (1972) seasonal changes in temperature in Loch Etive appear to follow roughly the local coastal patterns but usually with a lag in timing that is possibly because of the restricting effect of the sill. Edwards and Edelsen (1977) reported that bottom temperature changes little, while sill water warms like coastal water and surface water warms more rapidly, with terrestrial influence in Loch Etive. Mean temperature was similar in Loch Etive and Loch Kishorn (Table 4). There was no clear evidence in Loch Kishorn and Loch Etive of vertical temperature stratification. However temperature was slightly higher at 2 m than 6 m during the summer and vice versa during the winter (Fig. 12). Gage (1974) reported that the temperature range for deeper waters resembles closely the coastal pattern, while the range at the surface was somewhat greater. This is caused mainly by direct solar warming of the surface brackish layer in summer in Loch Etive.

The main hydrographic differences between the two lochs is the higher freshwater run-off in Loch Etive and greater tidal range in Loch Kishorn. Thus, the seasonal pattern of temperature and salinity in Loch Kishorn is likely to follow the coastal pattern more closely than in Loch Etive. The present study showed that temperature has a positive relationship with salinity at both sites. Neither depth nor site has any significant effect on temperature. The sharp decrease in water temperature from November to December 1993 was attributed to snow melting from the surrounding mountains. In winter, surface temperature is depressed to lower than the normal coastal minimum by the considerable amount of cold freshwater entering the loch. By late spring, reduced freshwater flow and increase in solar radiation contribute to a rise in temperature of freshwater entering the

loch (Solórzano and Grantham, 1975) and temperature of whole loch gradually rises. Consequently annual water temperature distribution is mostly affected by season and freshwater run-off from nearby mountains at the two sites. At the seaward end of the lochs the coastal seawater is a source of temperature which varies smoothly through the year between narrow limits which change little from year to year, and at the landward end, river run-off is a source of widely varying temperature (Edwards and Edelsen, 1976).

Water temperature is one of the most important factors in the general dynamics of the estuarine ecosystem. It has been widely acknowledged as one of the major environmental factors that influence the abundance, distribution and growth of aquatic organisms, and the chemical and physical processes of estuarine waters.

The dependence of growth and physiology on water temperature has been extensively investigated, and well documented for mussels (e.g. Bayne *et al.*, 1976a, b; Seed 1976; Incze *et al.*, 1980; Page and Hubbard, 1987; Brown and Hartwick, 1988a, b; Almada-Villela *et al.*, 1982; Jamieson *et al.*, 1975; Kautsky, 1982; Loo and Rosenberg, 1983).

According to Héral (1987), with the exception of the spawning period, temperature is probably the primary explanatory factor for shell growth and the third factor affecting meat production (after food availability and the reproductive cycle of the animals).

Temperature is accepted as a very important factor controlling mussel growth rate (Seed, 1976; Brown and Hartwick, 1988a; Jones and Iwama, 1991) in temperate regions. High positive correlation ($P < 0.01$) between water temperature and specific growth rates showed that water temperature had a strong effect on the shell growth rate of mussels in Loch Etive and Loch Kishorn during this study. Coulthard, (1929), (cited by Seed, 1976) reported that the optimum temperature for *Mytilus* is around 10-20°C. Recently, Kautsky (1982) obtained a significant correlation between temperature and growth of mussels in small experimental cages in the Baltic Sea. This study is in agreement with Okumus (1993) that temperature one of the major factors regulating mussel growth in the west coast of Scotland.

Physiological studies on *Mytilus edulis* around the British Isles have shown water temperature to have a little effect on the "scope for growth" i.e. the energy available for somatic growth and reproduction between temperatures of 10 and 20°C (Bayne *et al.*, 1979). If the growth and physiological temperature optimum is between 10 and 20°C, then this corresponds to a period of 6-7 months (roughly from May to November) in Loch Kishorn and period 5-7 months (from May to November) in Loch Etive. Water temperature reached 10°C in June 1994 in Loch Etive with a one month delay compared to the same condition in 1993, due to snow melting from the surrounding mountains.

Mussel growth at the study sites was governed by seasonal temperature variation, but generally temperature differences between depths was not enough to have any impact on growth of mussels. Sukhotin and Kulakowski (1992) reported that seasonal changes of growth rate were mainly influenced by sea water temperature in the White Sea. Almada-Villela *et al.* (1982) examined the effect of several constant temperatures on *M. edulis* and found that between 3°C and 20°C normal growth; above 20°C growth declined sharply, while at lower temperatures (3 and 5°C) it proceeded very slowly.

The temperature range for *M. edulis* is fairly wide. Mussels have been shown to tolerate -15°C, when 60 % of the body water is frozen (Jamieson *et al.*, 1975). The upper tolerance limit is given as 26°C by Jamieson *et al.*, (1975), with filtration rates being reduced above 22°C. Loo and Rosenberg (1983) found that low temperatures (lower than 5°C) did not seem to limit growth whenever these coincided with the spring phytoplankton bloom. Along the northern California coast, where the annual temperature range is quite narrow, there was no obvious seasonal variation in *Mytilus* shell growth rate. This is in contrast to other areas in North America where the temperature range is wide and growth varies markedly, peaking between May and September depending on the specific locality (Loosanoff and Engle, 1943; Harger, 1970; Jameison *et al.*, 1975; Incze *et al.*, 1978). Seasonal variations in filtration rates of mussels (Walne, 1972), and availability of food (Incze *et al.*, 1980), are highly correlated with temperature and result in marked seasonal variations in mussel growth rates.

5.1.2. Salinity

Loch Etive, with significant freshwater sources, is distinctly different in form and hydrographic characters from Loch Kishorn. Monthly salinity fluctuation and salinity difference between the surface and 6 m and 8 m depth is significant in Loch Etive, but not in Loch Kishorn. This monthly fluctuation and differences between the depths is attributed to melting snow and freshwater run-off into Loch Etive from the surrounding mountains (Okumus, 1993 and this study). The occasional influx of denser water into Deep Basin, Loch Etive was recorded by Edwards and Edelsen (1977) and Solórzona and Ehlich (1977). Mean salinity in the Loch Etive during winter is about 25 ‰, compared with 33-34 ‰ in the sea outside. The density profile of the water column is largely determined by the salinity profile, which therefore determines the distribution of water masses in the water column. Salinity in the upper 10 m is very variable, in both time and space (Wood *et al.*, 1973).

Salinity and the dimensions of the brackish layer depend on freshwater run-off. Freshwater run-off from rivers, which is less dense (1.0 g cm³) than sea water (1.025 g cm³), flows over the seawater and so two layers are formed: a surface brackish water layer and a saline deep water layer within which salinity is constant to the bottom. Rapid salinity fluctuations, as well as constant low salinity, have a significant negative effect on cultivated shellfish species, especially on oysters (Okumus, 1993). Loch Etive has a considerably greater catchment area than Loch Kishorn. It has been widely acknowledged that blue mussels are euryhaline and poikilosmotic, i.e. they are capable of withstanding relatively great ranges at salinity, from 4-5 ‰ to fully oceanic conditions, but at the same time they are incapable of maintaining stable inner osmotic concentration (Bayne *et al.*, 1976a) during day to day salinity fluctuations.

Brackish estuaries and lagoons are favorable habitats for mussel growth, but this probably reflects the increased food levels in these environments rather than any beneficial effects of reduced salinity (Seed and Suchanek, 1992). Indeed, lowered salinity may have a detrimental effect on growth and can even be lethal to mussels under extreme conditions (Almada-Villela, 1984). Kautsky *et al.*, (1990) suggested that differences in growth rate are mainly due to physiological adaptations to environmental salinity.

Wide seasonal variations in salinity and its relevance to osmo-regulation in aquatic organism, also sometimes plays a dominant role in the growth of bivalves (Brown and Hartwick, 1988a). For example in the Baltic Sea, stable low salinity (e.g. 7 ‰) is the main factor controlling growth rate and maximum attainable size in mussels (Kautsky, 1982). Mussels are extremely euryhaline and natural population are found over wide a range of salinities (Bayne *et al.*, 1977). Bohle (1972) suggested that mussels living in environments with strongly varying salinities have reduced growth rates. Remane and Schlieper (1971) observed that mussels growing at 4 to 5‰ salinity had extremely low growth rates and attained a maximum shell length of approximately 40 mm. Several workers have reported similar detrimental effects of lowered salinities on growth of mussel species (Paul, 1942; Lubinsky, 1958; Bagge and Salo, 1967; Theisen, 1968; Jamieson *et al.*, 1975). Jamieson *et al.* (1975) noted a reduction in growth rate of *M. edulis* at salinities in excess of 40 ‰. In the present study salinity had a significant positive relationship with growth rate ($r=0.486$; $P<0.05$) in Loch Etive, while it had no significant relationship ($r= 0.356$; $P>0.05$) in Loch Kishorn. This is probably a result of the great fluctuations in salinity in Loch Etive compared with Loch Kishorn.

In addition, rapid fluctuations in salinity levels can reduce tolerance to changes in other environmental variables, such as temperature and food availability, and recovery may take several days (Brown and Hartwick, 1988a). High fluctuation in surface water salinity has more impact on spat collection than on mussel culture. However low salinities can control mussel predators such as starfish. Consequently, starfish were almost absent in Loch Etive, while there was heavy starfish settlement in Loch Kishorn. Low salinity in surface waters had no significant effect on growth of spat or mussels at either site. Results from reciprocal transplantation experiments suggest that differences in growth rate and maximum size between North Sea and Baltic mussels are mainly due to physiological adaptations to environmental salinity (Kautsky *et al.*, 1990).

5.1.3. Total Seston and Particulate Organic Matter

Probably the single important factor in determining growth rate is food supply, since it provides the necessary energy to sustain growth. Mussels are filter feeders

removing particles down to 2-3 μm with 80-100 % efficiency (Mohlenberg and Riisgård, 1979).

Mussels mainly live in estuarine and coastal environments where the concentration of seston or suspended particulate matter (organic, living and nonliving and inorganic matter) is often high and variable (Bayne and Widdows, 1978, Incze *et al.*, 1980, Rodhouse *et al.*, 1984b; Small *et al.*, 1986).

Several authors have identified seasonal and regional variations in both the quantity and quality of utilizable food as important determinants of mussel growth (Ceccherelli and Rossi, 1984; Fréchette and Bourget, 1987).

In general, total seston concentration in sea lochs varies with river discharge, biological production (which shows a seasonal trend) with highest values in spring and the lowest in winter, and with water movement (Solorzano, 1977). Growth has been found to decrease with low seston quality (Widdows *et al.*, 1979; Bayne *et al.*, 1987). According to Kiøborne *et al.* (1981), suspended bottom material may serve as an additional food source.

The total amount of particulate material present in suspension (=seston) contains several potentially utilizable food types; these include bacteria, phytoplankton, fine organic detritus and material of inorganic matter, although the precise nutritional contribution that each of these makes to the diet varies seasonally, and among mussels of different size (Rodhouse *et al.*, 1984a; Page and Hubbard, 1987).

Jones and Gowen (1985) reported that variation in the particulate organic matter content of the surface waters in the Loch Etive is caused mainly by seasonal production in the loch and adjacent coastal waters and by the input of organic detritus of terrestrial origin. Suspended matter with living and dead cells from the lower basin and coastal area, together with sediment from the basin slope, are probably the origin of the increases of organic detritus in the water column. The occasional influx of denser water in to deep basin (Edwards and Edelsen, 1977; Solorzano and Ehrlich, 1977) significantly affects the concentration and distribution of particulate organic material of the loch. Heavy rainfall and run-off (Table 5) bring large quantities of particulate detritus and dissolved humic material into Loch Etive (Wood *et al.*, 1973)

Wood *et al.*, (1973) reported that it is not possible to say whether the freshwater input to the loch affects production through reduced salinities or through effects on nutrient supply. Although nutrient levels are reduced in the surface waters of the loch, it seems possible that this is of only secondary importance as a limiting factor.

Seston concentration and particulate organic matter were slightly higher at 2 m than 6 m in Loch Etive, but not significantly. However in Loch Kishorn the amount of seston was found to be higher at 6 m than 2 m depth while POM was similar. This could be the result of current movement around Kishorn Island which is located about 70-80 m beyond Kishorn mussel farm.

The positive relationship between chlorophyll and seston shows that the amount of seston was clearly affected by phytoplankton blooms in both lochs over the two year experimental period. There was no clear seasonal pattern in the amount of seston and POM in Loch Etive (as a result of river discharge and heavy rainfall), but seston and POM had a clearer seasonal pattern in Loch Kishorn. Seston concentration had a significant positive correlation with the amount of particulate matter in both sites. Seston also had a significant relationship with chlorophyll-a concentration the Loch Etive and Loch Kishorn.

Food for filter feeders has been described as the edible fraction of suspended organic material obtainable by animals (Herman and Scolten, 1990). Seston has significant effects on the physiology and growth of shellfish (Winter, 1978; Widdows *et al.*, 1979; Bayne and Newell, 1983; Rodhouse *et al.* 1984b) and is a main criteria for site selection for a shellfish farm and for carrying capacity estimations. The amount of POM alone does not necessarily provide sufficient information on food availability and growth conditions due to the proportion of non-utilisable POM in seston (Widdows *et al.* , 1979; Wallace and Reinsnes, 1985). Especially in estuarine environments with high freshwater inputs, nonliving organic matter can constitute a significant proportion of the POM, sometimes being more abundant than living organic matter (Riley, 1970; Kennish, 1986). An inverse relationship between POM % and seston may result from a large amount of non-living material of terrestrial origin.

POM and seston had a significant positive relationship with Ch-a value at both sites. Phytoplankton might be the most important component of POM (Riley, 1970) and the main food for mussels, particularly during spring and summer. However, there is strong evidence showing that utilization by mussels and some other bivalves of non-phytoplanktonic sources, mainly organic detritus and bacteria, to meet their energy requirements when phytoplankton concentrations are low (Seed, 1976; Widdows *et al.*, 1979; Rodhouse *et al.*, 1984b; Lucas *et al.*, 1987; Page and Hubbard, 1987; Langdon and Newell, 1990).

Use of detritus by bivalves takes place in two ways; either only the microorganisms attached to the detritus are digested and the detritus rejected in the faeces; or part of the detritus is digested along with the associated bacteria (Heral, 1987) since the digestive enzymes of molluscs have the ability to utilize it (Bayne *et al.*, 1976a). Langdon and Newell (1990) demonstrated that blue mussels living in marshes obtained around 30 % of their nutrition from detritus material derived from the vascular plant *Spartina alterniflora*.

5.1.4. Phytoplankton and Chlorophyll-a

Jones and Gowen (1985) reported that in slowly flushed lochs (e.g. Loch Etive, Loch Striven and Loch Nevis) the potential phytoplankton growth is limited by the rate of replenishment of “internal cellular pools” (water exchange in the loch).

The freshwater input to lochs is the most important factor determining the initiation and subsequent support of the phytoplankton population (Solorzano and Grantham, 1975). It is the main source of nitrate and gives rise to an increase in the stability of the water column and keeps the cells in the euphotic zone by creating a two layer system, while upwelling of entrained seawater brings additional nutrients to the euphotic zone and disperses phytoplankton cells vertically. It has been considered that nitrate depletion would limit the growth of phytoplankton in Lochs Linne and Creran (Solorzano and Gratham, 1975; Tett and Wallis, 1978) adjoining Loch Leven.

Flushing time can create variations in chlorophyll-a concentrations by limiting the accumulation of biomass, since the flushing time of Loch Kishorn (three days) is much

shorter than Loch Etive (14 days). Consequently, it is more likely that differences in chlorophyll-a between the two lochs are due to differences in nutrient concentrations, water column stability and illumination, all of which are related to the freshwater run-off characteristics.

The amount of chlorophyll-a was found to be similar in Loch Etive between different depths whereas chlorophyll-a value was slightly higher at 2 m than 6 m in LK. Okumus (1993) reported that chlorophyll-a was very slightly higher at 2 m than 6 m in Loch Etive and Loch Leven. Solorzano and Ehrlich (1979) also found higher chlorophyll-a values at 1 m than at 5 m in Loch Creran but only during autumn and winter, since summer values at 5 m were higher than those at the surface.

Temporal changes in chlorophyll-a observed in Loch Etive and Loch Kishorn were similar to the general seasonal cycles. The spring increase (defined by Tett and Wallis, 1978 as the time when chlorophyll-a concentrations first exceed $1 \mu\text{g l}^{-1}$) was in April 1994 and in March 1995 at both experimental sites. Maximum values were $8.18 \mu\text{g l}^{-1}$ in LE and $7.18 \mu\text{g l}^{-1}$ in Loch Kishorn in May 1994. As shown in Table-33, the spring bloom (algal bloom) occurred at time in agreement with the majority of previous studies, i.e. March and April. The spring bloom in Scottish west sea lochs only persists for 2 or 3 weeks (Gowen *et al.*, 1988).

Several studies, including the present one, report a positive correlation between mussel growth rate and chlorophyll-a especially on a seasonal basis (spring and summer) (e.g. Sutterlin *et al.*, 1981; Kautsky, 1982; Rosenberg and Loo, 1983; Page and Hubbard, 1987; Brown and Hartwick, 1988a; Jones and Iwama, 1991; Okumus 1993). Incze *et al.*, (1980) reported that chlorophyll-a levels of above $2 \mu\text{g l}^{-1}$ during the summer are accompanied by acceptable mussel growth rates in marine estuaries in the USA. During this study the highest monthly growth increment of about 2-8 mm occurred May-September 1993 in Loch Kishorn and Loch Etive when Chlorophyll-a content was 2-3 $\mu\text{g l}^{-1}$. Comparison with the findings of Widdows *et al.*, (1979) indicate that during summer, roughly May-September, chlorophyll-a concentrations in the lochs exceed the maintenance ration of *M. edulis* (= $2.4 \mu\text{g l}^{-1}$ chlorophyll-a). However Okumus (1993) reported that chlorophyll-a concentrations of around $1.0 \mu\text{g l}^{-1}$ can still support

considerable growth (over 2 mm mo^{-1}) in Loch Etive and Loch Leven. He suggested that perhaps mussels utilize the non living part of POM as a supplementary diet during autumn when temperatures are still $8\text{-}10^{\circ}\text{C}$. However lack of significant correlation between mussel growth rates and POM (Tables 4 and 5) shows that non living POM alone cannot support the apparent growth. When phytoplankton availability declines and temperature also decrease this limits mussel growth in any event. In the second year experimental period, a high correlation was found between seston, POM and chlorophyll-a.

Phytoplankton is the main food source for mussels (e.g. Incze *et al.*, 1980; Rodhouse *et al.*, 1984b; Langdon and Newell, 1990). The usual way to follow changes in phytoplankton biomass is to determine chlorophyll-a (Heral, 1987).

Wood *et al.* (1973) reported that chlorophyll-a value decreased from 3.15 mg l^{-1} to 1.97 mg l^{-1} in Loch Etive over a four days interval. Phytoplankton growth in Loch Ardbhair (West coast of Scotland) is light-limited (Gowen *et al.*, 1983). Jones and Gowen (1985) reported that horizontal exchange transfers phytoplankton between a loch and its adjacent sea area, whilst stratification, by controlling average illumination experienced by phytoplankton and their nutrient supply, influences the rate of phytoplankton growth. Gowen *et al.*, (1983) reported that differential time scales of exchange and phytoplankton growth are likely to control the maximum achievable biomass within a loch.

5.1.5. Water Currents

Physical movements of water have been shown to effect metabolism and growth rate in *M. edulis*. Nixon *et al.* (1971) observed a marked increase in consumption of oxygen by a natural mussel bed when the current increased from 0 to 0.01 m s^{-1} . Walne (1972) recorded an increase in both pumping and growth of mussels at higher flow rates under laboratory conditions. Several studies have emphasised the importance of water movements in maintaining a constant supply of food to mussels (Incze *et al.*, 1981, Rosenberg & Loo, 1983; Rodhouse *et al.*, 1984b and 1985; Larsson, 1985; Carver and Mallet, 1990).

Current values of 0.04-0.15 m s⁻¹ in the lower basin of Loch Etive were measured between the surface and 5 m by Wood *et al.*, (1973), indicating, that current speeds are generally low. Loch Leven sea water currents just below 1.5-2.0 m are probably stronger than in Loch Etive while surface waters remain fairly static (Huchzermeyer, 1985). These differences in current speed between sites cause some differences in growth rates of mussels through the regulation of food supply. Current speeds higher than 0.06 m s⁻¹ are categorised as strong (Dare and Davies, 1975).

In Loch Etive and Loch Kishorn, the recorded current speeds are also comparable with values reported from other mussel culture sites; for example it is 0.1 m s⁻¹ in Killary Harbour (Rodhouse *et al.*, 1985), 0.05-0.3 m s⁻¹ in Birterbuy, Ireland (Wilson, 1987), 0.05-0.9 m s⁻¹ in the Rio de Arosa (Figueras, 1990) and 0.2-2.2 m s⁻¹ in the Dutch Wadden Sea (Korringa, 1976).

A moderate current velocity of 0.02-0.06 m s⁻¹ is typically suggested to be adequate for suspended mussel culture (Sutterlin *et al.*, 1981; Larsson, 1985), as a higher velocity makes both mooring of rafts and long-lines difficult and undermine the ability of mussels to remain attached without spending extra energy on byssus production (Okumus, 1993).

In the present study, mean current velocity was found to be 0.052 m s⁻¹ in Loch Etive and 0.05 m s⁻¹ in Loch Kishorn (P>0.05) which are good values for mussel culturing areas. However farming installations (rafts and long-lines) reduce water velocity, so the current speed in the middle of farms comprising several rafts can be considerably lower than those at the inflow; this can create mussel growth differences within and between rafts, depending on their size and position.

Currents in the lower basin of Loch Etive are derived both from tidal movements and from circulation. The latter is driven by the freshwater inflow; it comprises a relatively thin brackish layer moving seawards in the top 10 m of the water column and a slower, compensatory flow, landwards at greater depths. (Wood *et al.*, 1973).

5.1.6. Transparency and Particle Concentration

The mean transparency (Secchi depth) in the sea lochs studied by Okumus (1993) (Loch Etive and Loch Leven) ranged between 5 m and 7 m, but he reported that it exhibited a regular seasonal pattern at all sites: high during the spring-summer and low during autumn-winter. These values are lower than Secchi disc values for Loch Eil (Grantham, 1981) and the depth of the euphotic zone recorded in Loch Etive by Wood *et al.* (1973). In the present study, transparency ranged from 3.5 to 8.5 m in Loch Etive and from 4.5 to 10.5 m in Loch Kishorn. The mean value of transparency was significantly higher in Loch Kishorn than Loch Etive ($P < 0.05$). Large day to day fluctuations in light intensity were experienced in the irradiance recorded at Dunstaffnage Loch Etive due to variations in cloud cover. In Loch Etive, the high value of light intensity is related to the smaller volume of freshwater entering the loch during the summer period (Wood *et al.*, 1973).

According to results of this study, variation in Secchi depth values are related to weather conditions (e.g. sunny, cloudy, windy season) because of variation in radiation and particulate inorganic matter concentrations. Grantham (1981) determined some relationship between rainfall and Secchi depth. Large amounts of suspended matter may cause light to become the limiting factor for primary production in the sea lochs. Dissolved humic materials are transported into the loch with freshwater run-off and this reduces the transparency of the water. Limited transparency and a high proportion of cloudy days contribute to light limitation (Wood *et al.*, 1973).

5.1.7. The Effect of Depth on Growth

Reports on the effect of depth on mussel growth rate show high variation (Hickman, 1979; Sutterlin *et al.*, 1981, Kautsky, 1982; Page and Hubbard, 1987). Several studies have reported a general decrease in growth rate with depth (Kautsky, 1982; Loo and Rosenberg, 1983; Rodhouse *et al.*, 1984 b). However Okumus (1993) reported that mussel growth was better at 4-6 m than 2-4 m in Loch Etive and Dunstaffnage Bay; and vice versa in Loch Leven. This difference was attributed to rapid salinity fluctuation near the surface in Loch Etive and Dunstaffnage Bay, and comparatively high salinity below 4

m in Loch Leven. There were no significant differences in temperature and chlorophyll-a values with depth. If salinity had an important effect on growth in Loch Etive and Dunstaffnage Bay, growth in mussel spat should be better at 4-6 m than 2-4 m in these sites. Mason and Drinkwater (1981) did not find any significant difference due to depth in Linne Mhuirich (West coast Scotland).

In this study mussel growth was not significantly different between 2m and 6m depth in Loch Kishorn, while growth was better at 2m than at 6m ($p < 0.05$) in the rope culture experiments in Loch Etive. Such differences due to depth were not expected; they may have been due to heavy losses at 6m in the early stage of growth caused by duck predation and currents. However the lantern net experiments showed that depth had no effect on growth in Loch Etive and Loch Kishorn.

5.2. Growth

5.2.1 Shell Growth

Growth in bivalves consists of increase in both the shell and soft body parts. The measurement of shell length is the most widely used indicator of growth because it is the easiest to measure (Quayle and Newkirk, 1989). However, several alternative methods (Seed, 1976, 1980; Quayle and Newkirk, 1989) have been developed for growth analyses of bivalve molluscs: a) measurements of individuals from random samples of the population; b) successive measurements of marked individuals, and c) measurement of annual growth rings. All these techniques have been used to study growth in mussels, but each has its particular advantages and disadvantages.

Seed (1976) suggested that probably the most reliable estimates of growth have been obtained by using a combination of methods, such as a combination of (a) and (b) above, where the measurements are made on mussels from random samples of populations of known initial mean shell length and size range, and where there is no recruitment. In this method, measurements are made for only a small part of the mussel's life history and these measurements reflect growth only during that particular time interval. Therefore, the method might not be so reliable in population dynamic studies,

but in aquaculture operations this method is widely used since only growth during the first 2-3 years of life is important.

Experimental mussels have been stocked in various types of enclosures for example; pergolari tubing, Norwegian tubes or French socks (Dare and Davies, 1975; Mason and Drinkwater, 1981; Mallet and Carver 1989; Farias, 1983, 1991); or into small cages, lantern nets or exar baskets (Incze *et al.*, 1980; Sutterlin *et al.*, 1981; Kautsky, 1982; Skidmore and Chew, 1985; Mallet and Carver, 1989; Kautsky *et al.*, 1990; Okumus, 1993). Lantern nets were used in the present study.

Mussel shell length growth commenced in mid-spring and the main growing season was April to November in Loch Kishorn and from May to October in Loch Etive. There was very little growth from December to March in both sites. Spring shell growth appeared to start one month earlier in Loch Kishorn than Loch Etive. This difference was attributed to the lower salinity and lower concentrations of food in Loch Etive in April (Figs. 15 and 16). In general, mussel length growth in temperate waters is rapid during spring and summer, and slow or absent during the colder seasons (Craeymeersch *et al.*, 1986). Le Gall (1970) recorded high length growth between April and October and Seed (1968) showed that over 90 % of total annual growth occurred between April and September.

Comparable periods of mussel growth and quiescence have been described by Mason and Drinkwater (1981), Okumus (1993) in Western Scotland, in Killary Harbour by Rodhouse *et al.* (1984 b), Dare and Davies (1975) for raft cultivated mussels and Dare (1976) for intertidal mussels in Morecambe Bay (England).

As Figs. 12, 14, 15 and 16 show, in December temperature dropped below 10 °C at both sites, salinity decreased, POM level dropped to around 1 mg l⁻¹ and the chlorophyll-a value was very low from November to March. Therefore growth was very limited from December to March in the both sites. In spring (usually in April) mussel growth faster when chlorophyll-a concentrations exceed 1 mg l⁻¹, but temperature is still around 7°C. These factors, i.e. temperature, salinity and food supply, are generally acknowledged as the main factors governing seasonal and overall growth rate in suspended cultivated mussels and similar bivalves.

Over the experimental period, average shell length increment was higher in Loch Etive (31.01 mm) than Loch Kishorn (28.25 mm), but not significantly different ($P > 0.05$). These variations in growth in mussels between sites that have similar temperature regimes can be attributed to food quality. As expected, growth rates were higher in younger mussels than older ones. The combined effect of reduced feeding rate, plus an increased production of gametes in older mussels, may be responsible for their lower rate of growth. Older mussels show reduced metabolic activity and filtration rate (Jorgensen (1976), but increased gamete production (Thompson, 1984a).

5.2.2. Somatic Growth

Seasonal changes in flesh weight (for a given shell size) result from the storage and utilization of food reserves in relation to the complex interaction of food availability and temperature with growth and reproductive processes (Dare and Edwards, 1975). These processes differ considerably between mussels of different ages. Older mussels have a reduced growth rate (Seed, 1969), but also an increased gamete production (Thompson, 1984 b). All this will cause differences in the seasonal cycle between smaller and larger mussels. In the present study, the loss of weight in larger animals ($> 35\text{mm}$) between March and mid-April is attributable to spawning. From May to late June the meat content dropped in connection with the spring (May) spawning. The dry weight increased again later in the summer and in the autumn when new gonad and nutrient reserves were built. These findings are identical to those of other reports, both the UK and Holland (Dare and Edwards, 1975; Zandee *et. al.*, 1980)

Kautsky (1982) and Hilbish (1986) found that shell and meat increments exhibit different seasonal patterns of growth without any correlation between them. Similarly Dare (1976) reported that the meat weight of intertidal mussels exhibited a pronounced annual cycle independent of shell growth but related to spawning and other factors, possibly temperature and food availability. A very similar pattern was observed during this study; there was a great increase in meat weight and dry meat weight between April and June (Figs. 22 and 23), but maximum shell length growth took place during summer

(Fig. 20 and Tables 8-9). This clearly suggests that growth in shell length and meat weight are influenced by different factors and are uncoupled (Mallet *et al.*, 1987a).

Heral (1987) suggested that temperature is the primary explanatory factor for shell growth, but possibly only the third most important factor for meat production. This might explain the observed later resumption of shell growth in spring compared with onset of somatic growth. The other reason for uncoupled shell and somatic growth is a decline in meat weight during periods of negative energy balance due to poor food supply or spawning. In addition, due to other reasons such as stress, growth in length may not always reflect the growth in somatic tissues, as appeared to be the case in Loch Leven (Okumus, 1993).

In practice, the weight of farmed bivalves would seem to be more important than shell length, both for the producer and consumer; live weight is probably more important for the producer, while for the consumer the main concern is meat weight. It would appear that the maximum rate of increase in somatic growth occurred May-June in Loch Etive and April-May in Loch Kishorn (Fig. 22); this was followed by negative growth from June to July, and then recovery from July to August in both sites. Growth in somatic tissues declined from autumn until the post-spawning minimum in spring. A similar pattern of growth was found in mussels in Linne Mhuirich in 1966-1967 (Mason and Drinkwater, 1981), Loch Sween in 1980 (Jones, 1981), Killary Harbour, West coast of Ireland (Rodhouse *et al.*, 1984b), and Loch Leven and Loch Etive in 1990-1992 (Okumus, 1993).

The seasonal changes in meat weight, according to Dare and Edwards (1975) who observed similar patterns in sublittoral mussels in the Conway Estuary, result from rapid utilization of carbohydrate reserves and a depletion of both protein and lipid content in relation to the complex interaction of food availability and temperature with growth and reproductive cycles. During severe food shortage, when energy demands from the basal metabolism are not met by food uptake, the mussel will have a “negative scope for growth” (Bayne *et al.*, 1976b) and will utilize its stored energy reserves, resulting in negative somatic growth (Kautsky, 1982) as observed.

Some workers (e.g. Mason and Drinkwater, 1981; Dare and Davies, 1975) have used live weight to express harvestable mussel yield. In the present experiments, mussels reached a marketable size range of 50-60 mm (Tables 7 and 8), with a mean live weight (in French socks) of 5.4 kg m⁻¹ rope in Loch Kishorn and 6.8 kg m⁻¹ rope in Loch Etive. Similar values (6.2 kg m⁻¹) for mussel grown on ropes were obtained by Mason and Drinkwater (1981) by Okumus (1993) on west coast of Scotland (6.1 kg m⁻¹)

Dare and Davies (1975) recorded the best yield of 10-15 kg m⁻¹ live weight on ropes, but values on Norwegian tubes were only 3-4 kg m⁻¹. In Loch Kishorn low harvestable crops recorded in the present study were caused by heavy losses and poor survival, but were not due poor meat content or growth performance of the mussels. Meat weight were measured at 7.37 g ind⁻¹ in Loch Kishorn and 6.27 g ind⁻¹ in Loch Etive.

Although short term somatic growth rates appeared to be higher during spring and summer there was no clear and significant positive correlation between meat yield, chlorophyll-a and particulate organic matter at both sites. However, meat yield had a significant positive relationship with temperature in Loch Kishorn and with salinity in Loch Etive.

5.2.3. Growth and Morphological Differences Between Loch Etive and Loch Kishorn Populations

Mytilus edulis populations frequently differ in growth rates and in the morphology of their shells (Kautsky *et al.*, 1990). Growth, mortality and morphological differences have been reported between mussel populations from (a) quite different environments, for example between the North Sea and Baltic Sea (Johannesson *et al.*, 1990; Kautsky *et al.*, 1990); (b) from close (in order of kilometers or less) inlets, bays, fjords or lochs within the same coastal waters (Widdows *et al.*, 1984; Skidmore and Chew, 1985; Mallet and Carver, 1989) and (c) between habitats in the same locality (Seed, 1968).

Reciprocal transplantations could be one way to examine the extent to which stock differences in growth and morphology may be environmentally induced or genetically based. This approach was applied by comparing mussels of similar status in terms of growth rate and morphology using transplanted mussels from the Loch Etive and

Loch Kishorn stocks. The growth rate of Loch Kishorn mussels (LK) transplanted to Loch Etive (LK-LE) was similar to that of the native stock (LE) in Loch Etive. Studies of *Mytilus edulis* in temperate waters have consistently documented lower growth rates from November to April than during the warmer months. This pattern has been observed in *Mytilus* populations from Sweden (Kautsky, 1982; Loo and Rosenberg, 1983), the Netherlands (Pieters *et al.*, 1980), Canada (Freeman and Dickie, 1979), and Long Island Sound, U.S.A. (Hilbish, 1986).

Correlation analysis between environmental parameters and SGR showed that shell growth of mussels was mainly affected by salinity in Loch Etive ($P < 0.001$) and temperature ($P < 0.05$), while it was affected by temperature ($P < 0.001$) in Loch Kishorn. There were no significant effects of chlorophyll-a and POM on shell growth at either site. Similar findings were obtained by Okumus (1993). Mussels transplanted from Loch Leven to Loch Etive had a lower growth than native mussels and this was related to lower salinity. However, the condition index of mussels was affected by temperature, salinity, chlorophyll-a seston and particulate matter in Loch Etive, while condition index was affected by temperature, salinity, seston and particulate matter in Loch Kishorn.

These results clearly demonstrate that mussel growth in length and more particularly in somatic weight is largely regulated by environmental factors (these are most likely to be salinity, temperature and food supply) rather than by genotypic differences between populations. This is in agreement with the observation of Widdows *et al.* (1984) and Okumus (1993) that environmental rather than genetic factors are primarily responsible for the physiological differences observed among populations. These findings are also in accordance with the conclusion of various authors (e.g. Dickie *et al.*, 1984; Mallet and Carver, 1989; Johannesson *et al.*, 1990; Kautsky *et al.*, 1990; Okumus 1993) who found that site conditions are the major determinants of variation in growth in populations of *M. edulis*. This could have important implications in practice because, for various reasons, e.g. poor spat collection at the production site, growers are transferring considerable amounts of mussel seed between sites in the same loch, or between the lochs, and sometimes rely wholly on these seeds. Transferring seed from one site to another, however results in extra seed loss (Paul, 1987) and could be very labor

intensive . Therefore, there is no doubt that sites suitable for both good mussel settlement and growth will always be preferable.

Various reasons have been suggested to explain morphological differences between mussels produced in relatively close proximity. According to Seed (1968 and 1976), for example, shell morphology in wild mussels is influenced mainly by age, growth rate and population density. Mussels from areas of high density have generally narrow, elongate shells. However, none of these factors are valid for cultivated populations of the same age, similar density and growth rate. The same author has commented, based on suggestions of other workers and his own findings, that variation in shell morphology is essentially due to different environmental factors. Recently electrophoretic techniques have revealed that genetic differentiation might account for differences in growth rate and morphological features in several mussel populations; for example in eastern North America (Koehn and Gaffney, 1984; Koehn *et al.*, 1984), the Canadian Maritimes (Gartner-Kepkay *et al.*, 1980) and between the North Sea and Baltic Sea (Johannesson *et al.*, 1990; Kautsky *et al.*, 1990). Consequently the morphological differences observed after one year transplantation could be result of both environmental and genetic variation. Mallet *et al.* (1987b) reported that the blue mussel adapts to variable environments by maintaining both physiologically flexible and genetically variable population characteristics.

The results show that width: length ratio was similar in native and transplanted mussels in Loch Etive, while it was significantly different in native and transplanted mussels in Loch Kishorn. Height: length ratio was different in native and transplanted mussels in both sites, while width: height was the same in both native and transplanted mussels in the two Lochs.

The shell weight of transplanted mussels in Loch Etive seemed to increase in comparison to the original stock in Loch Kishorn. The shells of Loch Etive mussels were higher and appeared thicker, with a higher CaCO₃ content and more darkish-blue color, while Loch Kishorn mussels were thinner with brownish-black or brownish shells. In these respects Loch Kishorn mussels seem to be similar to Baltic Sea mussels, while mussels from Loch Etive are typical of North Sea populations (Kautsky *et al.*, 1990). The

rate of shell formation is partially dependent upon the supply of calcium to the mantle by the blood or external medium (Wilbur and Saleuddin, 1983) and the thinner shell structure of Baltic Sea mussels may be attributed to a lower calcium content (Schlieper 1971; cited by Kautsky *et al.*, 1990).

6.3. Losses and Mortality

The monthly proportion of mussels lost (natural mortality plus fall-off) from the culture ropes ranged from 2.58 % to 20.77 % in Loch Etive and from 3.14 % to 25.31 % in Loch Kishorn. Over the experimental period, total losses were 76.6 % in Loch Etive and 77.4 % in Loch Kishorn ($p > 0.05$). Most of these losses were caused by current forces due to weak byssal thread attachment and partly to massive fall-off observed from the ropes, particularly in Loch Etive, due to space competition. The reason for *Mytilus* having weak byssus threads can include salinity (Sutterlin *et al.*, 1981) or sublethal Zn and Cu levels (Okumus, 1993). However metal concentrations in the two lochs were not determined in the present study. Mortality might also occur after a period of extensive spawning and a significant decrease in meat yield would occur in the period immediately preceding death (Jamieson, 1989).

Very heavy losses from collector ropes (up to 98 %) was reported after one year after spat settlement by Okumus (1993) on west coast of Scotland. Similar losses from Norwegian tubes were also reported by Dare and Davies (1975) in Conway. Okumus (1993) reported around 30 % losses over a 13 month experimental period from French socks in Loch Etive. Under normal circumstances the mussel farm in Loch Etive usually yields around 280 mussels with a mean length of over 50 mm per metre of unpegged rope (Paul, 1987). In this study 393 ind m⁻¹ rope were obtained (over 50 mm shell length) from ropes in Loch Etive and 360 ind m⁻¹ rope from French socks in Loch Kishorn.

In a similar study, Dare and Davies (1975) recorded 200 ind m⁻¹ rope of 55 mm mean shell length one year after . They concluded that final density was governed by the available attachment area, rather than by the initial stock density or tube size. Certainly the present study supports such a conclusion because heavy cumulative losses from the ropes were observed.

Re-tubing of mussels has been quite a common practice on farms since harvestable ropes support a lot of under-size mussels which settled later, or grew more slowly; re-tubing is possibly the best way to utilize these smaller mussels. Re-tubing is widely employed at Loch Etive and Loch Kishorn mussel farms where the experimental studies were carried out.

The main predators around the experimental sites were eider duck (*Somateria mollissima*) and starfish (*Asterias rubens*). Eider ducks attacked spat collectors and culture ropes. Kishorn Shellfish farm lost around 200 mt of mussels due to a high eider duck population on the loch. Mussel farmers reported that one eider duck can consume 2.5 kg mussel per day. They feed mostly on mussels of length 10-50 mm which they swallow whole (Galbraith, 1992). Eider ducks occur all year around throughout Scottish coastal waters and peak numbers appear in sea lochs during spring and autumn. There are many strategies to keep birds from farms such as, nets, balloons, loud noises and killing by gun but usually birds fly away and return later. Starfish are mostly found on spat collectors. They eat mussel spat but when culture rope handled they drop off from the suspended mussel culture system. However, control of starfish is very difficult in the bottom culture of mussels.

Sea squirts are another major problem for Scottish mussel farmers as they compete with mussels for available space on the ropes. Sea squirts are a very big problem if salinities are around 25-35 ‰ at culture sites, but many Scottish sea lochs are nearer 20 ‰ salinity; in this case sea squirts are not serious pests. Consequently, Loch Etive is not affected by sea squirts, whereas they are an important problem in Loch Kishorn. During the 1994 spat collection season, there was a heavy sea squirt settlement on spat collectors and culture ropes in Loch Kishorn which ruined spat settlement. Potential predators of the intertidal mussels are oystercatchers (*Haematopus ostralegus*), herring gulls (*Larus argentatus*) and shore crabs (*Carcinus maenas*). Craeymeersch *et al.* (1986) reported that in SW Netherlands, oystercatchers can consume 40 % of mussel production in bottom cultured and intertidal mussel populations. Although herring gulls and oystercatchers are present on the west coast of Scotland, their effect on mussel production by suspended culture is unknown.

In the cross-transplantation experiment, cumulative mortality was 10.8 % in the native stock in Loch Kishorn (LK) and 16.45 % in the transplanted stock (LE-LK) in Loch Kishorn ($P < 0.001$). The results show that the stock type had a significant effect on mortality, but site did not. Over 50 % of total mortality occurred in the first three months after transplantation. This shows that mussels had a negative response to the different salinity and other environmental factors, and to the handling involved. The first year experiments in the lantern nets (from May 1993 to August 1994) showed that site did not significantly affect mortality ($P > 0.05$). The average losses were 12.57 to 14.03 % in Loch Etive and 13.55 to 16.73 % in Loch Kishorn over a 15 months period being slightly higher at 2 m depth compared to 6 m at both sites.

Mortality caused by bio-physical factors rather than fall-off and predation of mussels has been determined by several authors using vaxer mesh cages or similar trays or containers which eliminate fall-outs and predation. For example, Mallet *et al.*, (1987a) found a total annual mean cumulative mortality of 19 % (5-57 %) at nine sites along the coast of Nova Scotia, Canada; Dare and Davies (1975) recorded 53.1 % in Morecambe Bay; and in Maine (USA) Incze *et al.*, (1978) give a range from only 4 % to over 90 % in a period of eight months. Okumus (1993) reported 4.7 and 14.4 % in lantern nets per year in Loch Etive and Loch Leven on the West Coast Scotland. According to Mallet *et al.* (1987b) stocks originating from more stressful environments tend to exhibit lower mortalities than those originating from less stressful environments. This is because those animals adapted to unfavorable environmental conditions may be more tolerant of a wide range of environmental variables, and can show better performance in relatively unfavorable environments.

In general, natural mortality in mussel populations results from an interaction of many biological and physical factors (Dare, 1976). Predators such as crabs, fish, starfish and ducks are among the common causes of mortality in wild mussel populations. Extremely low salinities have been reported to have caused mass mortalities in some estuarine bivalves species such as oysters (Farias, 1991).

5.4. Biomass and Production

In natural populations of mussels, production may be limited by physiological stress (Koehn and Bayne, 1989), food availability (Jorgensen, 1976; Newell *et al.*, 1989), primary space (Navarrete and Castillo, 1990), and predation (Dare, 1976; Gardner and Thomas, 1987). Ardisson and Bourget (1991) reported that the suspended systems of mussel culture maximize food availability and reduce predation and physiological stress considerably. They suggested that at high density, space is the factor most limiting production; moreover, production can vary considerably from one region to another depending both on the number of recruits to a given area and the carrying capacity of the environment.

Fuentes *et al.* (1994) reported that the location of culture ropes within raft culture systems is the main factor controlling the increase in mussel biomass. The differences in the increase of biomass per rope between the fore and aft-parts of rafts are due to both differences in growth and differences in mortality. In the present study, growth rate, ash-free dry meat weight and the amounts of food were also found to be higher at the inflow of the raft than at the outflow (based on the lantern net experiment in Loch Etive).

Production in cultivated mussels is the net result of increase in biomass due to growth and losses in biomass as a result of natural mortality and fall-off. As discussed before, both mussel growth and mortality, and consequently biomass and production, were affected by location or site due to the environmental variables operating and population density. Therefore, both growth and losses were important factors in determining production, but growth appears to be the primary factor since, despite substantial losses, production reached a maximum in July - August 1994 in Loch Etive and in June - July 1993 in Loch Kishorn. During these periods, rapid increase in mussel ash-free dry meat weight (AFDMW) was responsible for boosting production.

Although mortality of suspended cultivated mussels, particularly due to both bio-physical factors and predation can be far less than that of wild or bottom cultivated mussels, production losses due to fall-off can still be substantial. Such losses make up the eliminated biomass (loss of mussels plus any decrease in stock ash-free dry meat weight) which can be of the same order of magnitude as total somatic production. As in intertidal

mussels (Dare, 1976), much of the eliminated production of suspended mussels can be utilised by decomposers, or consumed by vertebrate and invertebrate predators. The amount of production utilised by the mussels themselves during the winter period, when food is scarce, also makes up a substantial part of total or gross production.

The organic material stored in the mussel shell accounts for part of gross production. Total annual organic shell production was 7.9 % in Loch Kishorn and 5.9 % of ash-free dry weight (ash-free shell + ash-free meat) in Loch Etive. Higher values were reported by Okumus (1993), who found 12.5 % in Loch Etive and 16.3 % in Loch Leven mussels. Rodhouse *et al.* (1984a) compared the resource allocation in wild and cultivated mussel populations when the total cumulative production was equal. They found that the wild population allocated more energy to the shell than did the cultured mussels. This is not surprising, because harsher environmental conditions on the shore plus high predator risk cause wild mussels to develop thicker shells than cultured ones. In addition, these two population exhibited considerable differences in resource allocation for gamete, somatic and shell growth (Rodhouse *et al.*, 1984a). In the cultivated population, all the mussels were young (under two years old) with very low reproductive effort, whereas the wild population was dominated by older mussels with high gamete production and low somatic growth. In addition to shell organic matter, byssus production (mainly comprised of protein) could account for a substantial proportion of total production. For example, Hawkins and Bayne (1985) reported that byssus production in an open-shore mussel population made up of 44 % of total carbon and 21 % of nitrogen production, but unfortunately this fraction of production has been ignored in almost all biomass and production studies, including the present one.

5.5. Condition Index and Biochemical Composition

5.5.1. Condition Index

Condition index has been used for nearly half a century for biological and commercial purposes (Baird, 1958). In practice it can be considered a measure of fatness and marketability of commercially exploited species. It is also probably the most

practical and simplest method of monitoring reproductive activity (Farias, 1991). The amount of shell has been assessed by weight, volume or the volume of space which it encloses, while the quantity of meat has been measured variously as fresh, dried or cooked meat; drying and cooking have been performed upon fresh or frozen samples. As a result of differences in measuring the amount of shell and meat, there are at least 6-7 condition index formulae in use at present (Davenport and Chen, 1987; Crosby and Gale, 1990), and employment of different formulae can make it difficult to compare the results from various studies. The methods used in this study, i.e. wet meat volume condition index (CIV) and dry meat condition index (CID) have been well accepted and widely used for assessing the condition index of mussels and other bivalves (e.g. Baird, 1958 and 1966; Hickman and Illingworth, 1980; Lutz *et al.*, 1980; Aldrich and Crowley, 1986). CID is perhaps the best formula to express condition factor, because it is not influenced by loss of water and it is therefore more accurate. In addition, if there are considerable morphological differences between species or stocks, for example in shell cavity volume or shell weight, comparisons will be difficult even if the same method has been used .

The condition index of cultivated mussels has, in general, been observed throughout the growth period, particularly during their second year (Mason and Drinkwater, 1981; Bressan and Marin 1985, Aldrich and Crowley, 1986, Emmett *et al.*, 1987, Okumus 1993). The average, condition indices recorded in Loch Etive and Loch Kishorn during this study, (mean values over the 15 month experimental period) were CIV= 9.89 % in Loch Etive and CIV= 57.0 % and CID= 12.7 % in Loch Kishorn. Similarly, Okumus (1993) reported CID= 9.9 % in Loch Etive and Dustaffnage Bay mussels over a one year experimental period. Condition indices and meat yield showed a quite similar pattern at the two depth studied. Condition index was slightly higher at 2 m than 6 m. but not significantly. However, the site itself had a very significant affect on both condition index and meat yield.

Two peaks were observed in condition index and meat yield at each site , and there were time differences between sites and years for these maxima. Variation between very distant regions is expected since the timing and duration of phytoplankton production and reproductive cycles vary (Lutz *et al*, 1980; Ruiz *et al*, 1992). The meat

yield (i.e. soft-tissue) yield from mussels is dependent on seasonal growth and reproductive cycles, physical morphometry of the shell and maximum size achievable during a mussel's life expectancy (Jamieson, 1989). The main differences in condition index were an observed peak in February in Loch Kishorn, while it was close to a minimum value in Loch Etive.

Fluctuations in condition index and meat weight have important implications for mussel cultivation and harvesting strategies. For optimum exploitation, the harvesting season should be timed according to the peak period for condition index (around CIV=40 %). Mason and Drinkwater (1981) suggested that autumn and winter is the best time for marketing cultivated mussels from Scotland, while Okumus (1993) suggested the most suitable season for marketing should be between May and December in Loch Etive and Dunstaffnage Bay. These differences reflect seasonal differences between north west and west Scotland.

In any case, mussels remain in sufficiently good condition for marketing for around eight months of the year in Scotland. However, as noted above, there are differences in timing and amplitude of condition, especially between the south and far north, or between lochs as a result of stock differences or varying environmental conditions.

The distinct seasonal cycle of tissue growth (particularly dry meat weight) should also be taken into account when marketing mussels. Harvesting one month either side of the expected spawning date should be avoided (mid-March to mid-May on the west coast of Scotland), while a gradual decline in condition and hence meat quality will occur during late autumn and winter (Stirling and Okumus, 1995 for Loch Leven mussels). The optimum harvesting period is late summer-mid-autumn (August to October) of the second year at a shell length of 40-50 mm. This is traditionally the favored size for consumption of mussels in UK; the data obtained in this study strongly supports this practice. Encouraging market acceptance of this smaller size (instead of 60 mm mussels) would greatly increase the economic efficiency of suspended mussels cultivation and ensure optimum quality.

The observed fluctuation in condition indices and meat yields of cultured mussels was clearly related to the storage and release of gonadal material or spawning. This result agrees with Dolah *et al.* (1992). The condition indices and meat yield of mussels exhibited quite similar patterns at depth of 2 m and 6 m at both sites. Condition indices were found to be higher in Loch Kishorn than Loch Etive and were mainly affected by temperature and salinity. The changes in condition indices and meat yield had a positive relationship with carbohydrate and lipid, while they had a significant but negative relationship with protein in both sites.

The condition indices recovered quickly after spawning, which took place more than once in a year. The peak in spawning is changeable year to year depending on environmental factors in a particular area. When food is available, condition indices increase with the combination of temperature and salinity. In the present study, harvesting of mussels in Loch Etive and Loch Kishorn should be stopped in March- April and July-August, as these are periods of spawning and recovery. The remaining periods of the year are suitable for mussel harvesting, but there may be differences year to year due to environmental factors (such as food, temperature, or salinity).

Gabbott and Bayne (1973) reported that high temperature and low food level result in a decline in the body condition of mussels, in agreement with this study. Austin *et al.* (1993) suggested that the seasonal cyclic fluctuations in condition index could be explained by changes in salinity and temperature. Mussel condition correlates strongly with average annual primary productivity but not with Ch-a concentration (Small and van Stralen, 1990). During the winter there is long period of sexual inactivity and gonad development does not begin until spring. During the reproductive period abundant food is available so that growth and gametogenesis can take place at the same time (Williams, 1969). Bayne *et al.* (1978) reported that a simultaneous regression and resorption of previously formed gametes occurred in *Mytilus edulis* under conditions of temperature stress or a lack of food. For this reason condition index is often used to assess the apparent health of mussels (Taylor *et al.*, 1992).

Abbe and Sanders (1988) reported that high condition index values in oysters generally indicate that they are in good physiological condition, but low values do not

necessarily indicate poor health because condition decreases whenever tissue is lost; spawning for example results in a short term loss in condition. Long term loss, however, may indicate stress from other sources such as pollutants, hypoxia or disease. Temperature is the principal environmental factor affecting gonadal development in marine bivalves, but not the only determinant of the gonadal cycle (Ruiz *et al.*, 1992).

Chipperfield (1953) reported that ripening of gonads in *Mytilus* takes place within a few weeks of the onset of spawning, in general commencing when the sea temperature has risen above 7 °C; there is no correlation between nutritional condition and ripening of gonads or subsequent spawning. Lauckner (1983) suggested that a reduction in the condition of several bivalve species was associated with parasitism with the indication that parasites stress their host, affecting a wide variety of their biochemical and physiological functions.

Rajas and Ruiz (1972) and Walne (1970) found a significant relationship between condition index and glycogen content in oysters. Taylor *et al.* (1992) reported that carbohydrate followed the same seasonal trend as condition index in *Mytilus edulis*. These results are in agreement with the present study, where carbohydrate correlated significantly with condition index. Condition index is changeable depending on mussel size and year to year trends (Baird, 1966).

It is well documented that water temperature is the principal environmental factor controlling the broader aspects of the reproductive cycle, so spawning in *Mytilus* occurs earlier in the year in warmer waters and becomes progressively later in cooler waters (Seed, 1975). There is evidence, however, that endogenous factors might have a greater influence on reproductive cycles than water temperature or latitude (Newell *et al.*, 1982). Whatever the main factor controlling reproductive cycles, indirect evidence from this study, such as the observed minimum condition indices and carbohydrate values suggest that first spawning occurs March-April in Loch Etive and Loch Kishorn.

5.5.2. Biochemical Composition and Energy Content

The biological composition of mussels varied predictably with loss of water and accumulation of reserve materials. Accumulation and depletion of the stored reserves in bivalves depends on the stage of gonadal development, environmental influences on metabolic activities and the quantity and quality of available food (Ansell, 1972; Gabbott and Stephenson, 1974; Pieters *et al.*, 1979; Bayne and Newell, 1983). Gabbott and Bayne (1973) demonstrated a marked seasonal shift in mature mussels from a reliance on carbohydrate as the main energy reserve in winter. A similar result was obtained from the present study. Gabbott and Bayne (1973) concluded that, in summer, all energy loss is accounted for by the breakdown of carbohydrate, but in autumn, during more prolonged starvation, a marked increase in the utilization of lipid reserves occurs. Glycogen reserves are used to meet energy requirements during periods of low food availability (Pieters *et al.*, 1979). Egg and sperm in bivalves are composed primarily of protein and lipid and thus the cyclic pattern of lipid and protein is correlated with the accumulating and shedding of gonadal products (Pieters *et al.*, 1980).

In general carbohydrate, which has been shown to be mainly glycogen in bivalves (Ansell and Trevallion, 1967; Gabbott and Bayne, 1973), is the main source of energy in bivalves (Zwaan and Zandee, 1972; Gabbott and Bayne 1973; Pieters *et al.*, 1979). As in the majority of bivalves from temperate waters (Zwaan and Zandee, 1972; Dare and Edwards, 1975; Pieters *et al.*, 1979). In the present study, the carbohydrate cycle consisted of a rapid increase in spring, a peak in summer, then a gradual decrease from autumn to winter, reaching a minimum of about 12-13 % in April at both sites. Lipids are utilised principally in gametogenesis and are lost by adult female bivalves during spawning (Gabbott, 1983). Lipid may be used also to provide energy during the winter when carbohydrate reserves are depleted (Beukema and Bruin, 1979). The present study showed that there is a changeover during the winter from carbohydrate to protein as the main energy reserve. Carbohydrate was most abundant in summer at both sites, while lipid as a source of energy was used principally in gametogenesis and was lost during the spawning. Seasonal variations in glycogen and condition index are closely correlated, which reflects the interaction between food availability, temperature, growth and the

reproductive cycle (Zandee *et al.*, 1980; Gabbott and Stephenson, 1974; Valera, 1981). The rapid decline of glycogen content in November could be partly caused by the known rapid production of byssus threads (Pieters *et al.*, 1979), while Ansel (1972) attributed the loss of protein and glycogen to food scarcity, and the metabolic demands for gametogenesis (Widdows and Bayne, 1971). Jamieson (1989) reported that carbohydrate (glycogen), protein and lipid reserves are usually synthesized during periods of nutrient surplus and these are then used in somatic maintenance and gametogenesis during periods of relative nutrient scarcity.

The minimum percentage carbohydrate level coincided with both the maximum protein and water levels and in consequence the seasonal carbohydrate cycle alternates with the protein and water content cycles. In addition, a simple positive relation between seasonal changes in dry meat weight and percentage carbohydrate has been observed during this and previous studies (Zwaan and Zandee, 1972; Dare and Edwards, 1975; Hickman and Illingworth, 1980; Okumus, 1993).

As far as lipid content is concerned, it fluctuated within a small range in Loch Etive (8-13 %) and Loch Kishorn (8-12 %) mussels and showed no clear seasonal trends. Ash content showed a similar pattern in Loch Etive and Loch Kishorn, being high over winter up to late spring and low in summer. Ash ranged from 5 to 10 % with a mean 7.36 % and from 6 to 12 % with a mean 8.05 % in Loch Etive and Loch Kishorn respectively. Ash, protein and moisture correlated negatively with condition index while lipid and carbohydrate showed a positive relationship. Lipid correlated positively with carbohydrate while it had a negative relationship with protein at the both sites. Carbohydrate had an inverse correlation with protein, a finding in agreement with those of Dare and Edwards (1975) and Valera (1981). With release of gametes there was a fall in protein, ash and moisture content levels, coinciding with a rapid increase in the proportion of carbohydrate as found by Williams (1969). Lipid as a source of energy is used principally in gametogenesis and lost during spawning. When mussels spawn, their lipid levels fall and increase again with gonadal development. Barber *et al.* (1988) reported that the primary metabolic substrate in marine bivalves is glycogen and condition index is representative of general health of an individual oyster.

The mean mussel dry meat caloric content was around 5.33 Kcal g⁻¹ in Loch Etive and 5.3 Kcal g⁻¹ in Loch Kishorn ($P>0.05$). Similar values were reported for Conway mussels (4.9 Kcal g⁻¹) by Dare and Edwards (1975), for Wadden Sea mussels (4.2 Kcal g⁻¹) by Zandee *et al.* (1980) and for west coast of Scotland mussels (4.97 Kcal g⁻¹) by Okumus (1993).

In the present study, fairly good agreement was found between the pattern of biochemical composition, the condition index and reproductive cycle, since seasonal cycles of both condition index and biochemical composition can be indicators of the reproductive cycle as a result of the storage and utilisation of reserves by *Mytilus* (Gabbott and Bayne, 1973). According to Seed (1975 and 1976) several stages of the reproductive cycle can be distinguished in European mussel populations. In summer the gonads are in a stage of rest (stage O), during which there is no sexual activity and reserves accumulate in the tissues. Gonadal development begins in autumn and continues during winter (stage one - five) at the expense of glycogen reserves. The final stage (stage six - or spawning release of gametes) is induced by external factors. The spawning stage in Loch Etive and Loch Kishorn (March-April) was characterized by minimal carbohydrate content and rapid decrease in protein from spawning. After spawning the carbohydrate content recovery was rapid. These findings are in agreement with Okumus (1993).

5.6. Spat Settlement and Growth of Seed

The essential aspects of mussel culture are seed availability, a suitable on-growing site and cost-effective production technique (Mason, 1976; Dare, 1980; Mason and Drinkwater, 1981). Despite successful controlled production of *M. edulis* larvae (Brenko and Calabrese, 1969; Skidmore and Chew, 1985), success in mussel aquaculture still depends on natural settlement of spats on collectors. Spat settlement occurred in June and July in Loch Etive, whereas it was observed from June to December in Loch Kishorn. There was only one peak in Loch Etive in July, but two peaks occurred in Loch Kishorn.) in July and November.

Primary settlement of spat is always noted to be higher on the seaweeds especially *Laminaria* spp. and *Fucus* spp. Okumus (1993) reported that spat settlement started in May -June and reached a maximum one month later in July in Loch Leven. Dare (1976) compared his own findings on settlement and spawning cycle of mussels with literature from studies around Britain and concluded that settlement periods cannot be predicted from knowledge of the spawning cycle alone. In Loch Leven and Loch Kishorn spawning occurred during March-April, with a peak predicted from the condition index cycle when temperature was lower than 10°C. As *M. edulis* larvae first attach after about 36 days at 11°C (Dare, 1976), there was a delay in settlement, rather than a primary and secondary settlement as described by Bayne (1964).

At lower temperatures, veligers of *M. edulis* can prolong their planktonic existence chiefly by delaying metamorphosis, e.g. by up to 40 days at 10°C (Bayne, 1976), and a similar pattern of temperature dependent settlement delay for *M. galloprovincialis* larvae has been reported (Cerccherelli and Rossi, 1984).

Since 1980, a number of studies have been undertaken to assess the endogenous and exogenous factors that affect the development and settlement of mytilid larvae (Bayne *et al.*, 1983). Among exogenous factors, temperature, salinity and food have received the greatest attention (Riisgård *et al.*, 1980; Jespersen and Olsen, 1982; Manahan *et al.*, 1983; Sprung, 1984). Temperature, perhaps more than any other factor, influences the duration of metamorphic delay (Strathmann, 1987). The planktonic larvae of *Mytilus* depend mainly on a ration of phytoplankton cells for successful growth and development (Bayne *et al.*, 1983). *Mytilus* larvae attach most readily to filamentous substrates such as bryozoans, hydroids and filiform algae (Bayne, 1965; Kiseleva, 1966; Davies, 1974; Lane *et al.*, 1985; Eyster and Pechenik, 1987). When salinity, temperature food supply and other factors are optimal, larval development of *M. edulis* may be completed in less than 20 days (Bayne, 1965; Sprung, 1984). However, growth to metamorphosis in the plankton during spring and early summer at temperatures of about 10°C normally occurs in approximately one month (Seed, 1976; Lane *et al.*, 1985). It is not unusual for the duration of planktonic life to extend beyond two months when experimental conditions are less than optimal and suitable settlement surfaces are lacking

(Bayne, 1965, 1976). The pelagic life of *Mytilus* larvae can be prolonged, by even more than six months, due to delayed growth and metamorphosis (Lane *et al.*, 1985).

Seed (1976) revealed that, in some localities, marked seasonal settlement can be detected, while in others settlement occurs more or less throughout the year. For example, in White Sea mussels spawning occurs twice in a year and spat settlement take place in autumn and spring (Sukhotin and Kulakowski, 1992). Cheung (1993) reported that there were two recruitments per year, the first from July to September, the second from November to March in Hong Kong. Mortality was high in summer, especially among large individuals, during the post spawning period in *Perna viridis*.

Dare and Davies (1975) found that very few, if any, mussels would settle on polypropylene ropes in Morecambe Bay, northwest of England. During the present study, however, settlement on polypropylene ropes (35,183 spat m⁻¹ rope Loch Etive and 48,159 spat m⁻¹ rope in Loch Kishorn) was higher than that reported by Okumus (1993), who counted 1,950 spat m⁻¹ rope in Loch Etive and 21,100 spat m⁻¹ rope Loch Leven, and by Dare and Davies (1975) who studied settlement on coir ropes (17,000 - 28,000 spat m⁻¹ rope). Mason and Drinkwater (1981) found higher spat settlement on coir ropes compared with polythene and sisal ropes, but settlement even on coir ropes appeared to be very poor (3,300 - 6,600 spat m⁻¹ rope). It is concluded that the settlement of filamentous algae on collectors put into the water one month before mussel spat settlement played an important part in attracting spat to the ropes in Loch Etive and Loch Kishorn.

It is well known that upper surfaces of water are preferred for settlement (Sutterling *et al.*, 1981; Farias, 1991). During this study, settlement was higher at 2 m than at 6 m depth in both sites. Farias (1991) claimed that the initial surface-dwelling behavior of *Brachidontes recurvus* (Rafinesque) larvae in the Gulf of Mexico was perhaps influenced by the fact that the upper layer has low salinity conditions (18-20 ‰) which are necessary for better larval development *Brachiodontes recurvus*. In Loch Etive, there was fluctuation in surface salinity, but at 2 m mean salinity was over 20 ‰ therefore spat settlement at 2 m should not be affected by salinity. Brenko and Calabrese (1969) found that growth of *M. edulis* larvae decreases drastically below 20 ‰.

Consistent and continuous recruitment of mussel seed to natural populations is critically important for sustained harvests of quality mussels. The density of recently recruited juveniles in a population may also have an effect on the growth rate of those juveniles. Extremely high densities may provide limited opportunities for growth due to overcrowding and competition for available food. It has been shown that growth of recently-settled spat in populations of mixed ages is greatly reduced (Seed, 1969).

In Loch Etive, there was a clear seasonal cycle in shell growth, which was high from June to November, with mussel seeds reaching about 20 mm in November. Over the winter period, there was little growth in shell length and final shell length reached 25.27 mm at 2 m and 23.81 mm at 6 m depth ($P > 0.05$) in April due to low salinity.

5.7. Carrying Capacity

Rapid expansion of the mussel culture industry in Britain has prompted considerable interest in the problems of carrying capacity. Carrying capacity, in the context of mussel culture, may be defined as the stock density at which production levels are maximized without negatively affecting growth rates (Carver and Mallet, 1990). Heral (1987) reported that uncontrolled increases in stock density will eventually result in reduced growth rates and environmental disruption.

Several studies have emphasized the importance of water movement in maintaining a constant supply of particles to suspension feeders (e.g. Incze *et al.*, 1981; Rosenberg and Loo, 1983, Wildish and Kristmanson, 1984; Frechette and Bourget, 1985). The pattern and rate of particle renewal varies, however, depending on the hydrography of the system; in estuaries for example, particle movement may be dominated by river out flow, whereas in coastal inlets, particle movement may be dominated by tidal currents (Carver and Mallet, 1990). Food supply depends not only on the rate of water movement, but also on the quantity and quality of the particles in the water.

Rodhouse and Roden (1987) recommended that only 50 % of the food supply in Killary Harbour should be diverted towards mussel culture, otherwise they predicted severe modifications of the environment and decreasing mussel yields per unit area.

Similarly, Incze *et al.* (1981) specified in their carrying capacity model that the mussels should deplete only 50 % of the available food supply. Widdows (1978) calculated that a 1 g dry weight mussel requires only 0.6 mg l⁻¹ POM to achieve maximum growth efficiency; at a filtration rate of 2.5 l h⁻¹, this is equivalent to 36 mg POM day⁻¹, which is less than the value found in this study. If this is so in this case carrying capacity was underestimated. Therefore, more specific information is needed on the quantity and quality of food required to maintain maximum growth efficiency of *Mytilus* under various environmental conditions. Doering and Oviatt (1986) suggested that without good field data attempts to predict carrying capacity may be misleading.

Incze *et al.* (1981) developed a carrying capacity model which is based on maintaining critical levels of particle flow through culture areas. The application of this alternative model depends on prior knowledge regarding seasonal patterns in seston composition and the other environmental conditions conducive to growth of the cultivated species.

Incze *et al.* (1981) reported that the estimation of carrying capacities for bivalves in open systems is complicated by several factors: 1) seasonal and size related changes in the energy demands of the cultured organism; 2) seasonal changes in the abundance and nature of potential food substrates found in the nature waters; 3) a general lack of knowledge concerning the degree to which bivalves utilize various particles in the seston; and 4) the difficulty of quantifying water mixing and flow through in most culture areas.

The present model is offered as an approach, not a solution. According to the carrying capacity model developed by Incze *et al.* (1981) and used in the present study, the number of tiers should be 57 which is almost six times higher than the number of tiers on the existing raft system in Loch Etive, while the number of tiers should be 75 in Loch Kishorn which is three times higher than the existing value. There is a big difference in estimated carrying capacity of systems when we compare the filtration model (filtration of POM) used by Carver and Mallet (1990) and the seston clearance model used by Incze *et al.* (1981). Also it is not possible to compare our finding with those from other studies due to several different factors which affect the carrying capacity in a particular site such as seston, particulate organic matter, temperature, filtration rate and raft size. However

Incze *et al* (1981) found that in a Spanish raft system the number of tiers should be twice that actually operating in the raft.

Incze *et al.* (1981) accepted that current velocity should be the same in all parts of the raft system, but in fact it will decrease from the front to the back of the system. As a result, carrying capacity will be lower than the calculated value. Unfortunately measuring the current decrease across the raft was ignored in the present study.

Different times of the year will affect the carrying capacity because winter is known to be a period of stress to mussels because of low energy reserves in the tissues and high metabolic demand due to gametogenetic activity, but the degree to which external energy sources can be used during this season is unknown.

According to the model, based on food supply and food demand in the present study, the carrying capacity is estimated to be 15-25 mt in Loch Etive and 38-41 mt in Loch Kishorn. However small size (<50 mm) mussels were ignored in the estimations. According to the mussel farmers, a raft system can achieve 10-15 tons production in Loch Etive and 40-45 mt in Loch Kishorn. According to the present findings, there are about 11 mt of mussels in a single raft in Loch Etive and 49 mt in Loch Kishorn.

In conclusion, these results show that the Loch Kishorn farm is producing more mussels than the estimated carrying capacity of the system (by a factor of 20-40 %), while in contrast mussel production in Loch Etive is considerably below carrying capacity (by about 40 to more than 100 %)

5.8. Morphometrics and Genetics

The electrophoretic technique makes it possible to compare allele frequencies and levels of genetic variability within and between different populations of a species and between different species. Allele frequencies were shown to be different between the sites and loci. Ferguson (1980) reported that samples of species taken from different areas may differ significantly in their allelic frequencies. This could be due to selection for different homozygotes under varying environmental conditions or to genetic drift in isolated populations. In a study of five alleles at a leucine aminopeptidase locus in the mussel *Mytilus edulis*. Murdock *et al.* (1975) found that two populations only 100 m

apart had quite different allelic frequencies, while some widely separated populations (350 km apart) had almost identical allelic frequencies. In this case a significant correlation was found between allelic frequencies and the relative amount of wave action (exposure) at the site investigated. Ferguson (1980) suggested that in a widespread panmictic population, selection may produce differential survival in different regions and result in allelic frequency variation. In Ireland and the U.K., geographic variation has been interpreted as resulting from the mixing of *M. edulis* and *M. galloprovincialis* (Gosling and Wilkins, 1977; Skibinski and Beardmore, 1979; Gosling and Wilkins, 1981). However some areas e.g. North-west Europe and the east coast of U.S.A, south of Cape Cod, where only pure population of *M. edulis* have been analysed, allele frequencies within each region are remarkably homogeneous over large geographic distances (Ahmad *et al.*, 1977; Gosling and Wilkins, 1981; Skibinski *et al.*, 1983; Koehn *et al.*, 1984; Bulnheim and Gosling, 1988; Varvio *et al.*, 1988; Johannesson *et al.*, 1990; McDonald *et al.*, 1991)

At the GPI locus, six alleles were observed in *Mytilus edulis* in Loch Etive and Loch Kishorn and the two most common alleles were dominant. In contrast, at the GPI locus up to nine alleles have been observed in populations of *Mytilus edulis* on the east coast of North America.

In the present study, genetic identity was 0.69 and genetic distance was 0.37. These results show that there is high similarity between the mussels at the two sites, but genetic distance between the sites shows that the populations are not pure *Mytilus edulis*. This observation suggests that west coast of Scotland mussel populations are not pure; there has been some polymorphism and hybridization. Unfortunately there are no published data on the genetics of mussels on the West coast of Scotland. However, Okumus (1993) also reported that there are some morphological differences between Loch Etive and Loch Leven mussel populations.

Mean ratios of the shell characteristics showed significant differences between the sites. Similar shell characteristics were reported by Kautsky *et al.* (1990) from the Baltic Sea and North Sea *Mytilus* populations. They reported that Baltic Sea mussels have a more narrow and elongated shape than North Sea mussels. Baltic Sea mussels also have a

thinner shell and brownish color, while North sea mussels have a thicker shell and a bluish-white coloration. Similar results were reported by several researchers for Baltic Sea and North Sea populations (i.e. Remane and Schlieper, 1971; Theisen, 1978, 1982; Kautsky, 1982). Kautsky *et al.* (1990) reported that 1 year after transplantation of mussels some shell differences were maintained. Similar results were obtained in the present study.

Gosling (1992) reported that in South-West England hybridization, but little integration, is occurring between *M. edulis* and *M. galloprovincialis*, but at other localities e.g. parts of Scotland, North-East England and at exposed sites on the Atlantic coasts of Ireland, integration between these species is extensive (Skibinski and Beardmore, 1979; Gosling and Wilkins, 1981). This finding is supported by the present study of two Scottish West coast lochs.

5.9. Conclusions

1) Annual water temperature distribution ranged from 4.6-15.7°C in Loch Etive and from 5.5 to 17°C in Loch Kishorn. Temperature is mainly influenced by the seasonal climate and possibly also by tidal range and the quantity of freshwater run-off. The mean temperature was quite similar at both sites.

2) Salinity also fluctuated seasonally, being low in winter and spring and high in summer and autumn. In Loch Etive salinity was reduced by freshwater run-off and snow melting from the surrounding mountains. Overall, salinity was significantly higher and less fluctuating in Loch Kishorn (monthly mean 33.53 ‰, range 30 ‰ to 36.1 ‰) than in Loch Etive (monthly mean 21.63 ‰, range 7.5 ‰ to 28 ‰).

3) There were no significant differences in suspended particulate organic matter (POM) between the sites, but concentrations were slightly higher in Loch Kishorn than Loch Etive. In general, POM was affected by seston and chlorophyll-a concentration. POM% was similar in 1994 at the two sites, while it was significantly higher in Loch Etive than Loch Kishorn in 1995.

4) The amount of seston was higher in Loch Kishorn (range 1.2 mg l⁻¹ to 15.2 mg l⁻¹) than Loch Etive (range 1.3 mg l⁻¹ to 8.5 mg l⁻¹). This was correlated with chlorophyll-a and particulate organic matter levels.

5) Chlorophyll-a concentration was similar in both sites and was not significantly affected by depth. Chlorophyll-a values were higher in spring and summer (8.64 µg l⁻¹ in Loch Etive and 8.03 µg l⁻¹ in Loch Kishorn) and fell to very low levels in winter (0.02 µg l⁻¹ in Loch Etive and 0.04 µg l⁻¹ in Loch Kishorn). Chlorophyll-a concentration was mainly affected by the onset of algal blooms.

6) Mean particle numbers and transparency were significantly higher in Loch Kishorn than in Loch Etive (40,098 in Loch Etive and 43,761 in Loch Kishorn)

7) In response to the environmental conditions, the growth of mussels was relatively rapid from mid-spring until mid-autumn (April-October, or approximately seven months), but very slow during the rest of the year, as noted similarly with the growth pattern of mussels

in other regions of Northern Europe. The apparent positive relationship between SGR and temperature and salinity in Loch Etive and temperature in Loch Kishorn indicates that these are the two main limiting factors controlling mussel growth from late-autumn to mid-spring.

8) The average monthly SGR was 5.51 % in Loch Etive and 4.51 % in Loch Kishorn. Mussels reached marketable size (over 50 mm) after 2-2.5 years from spat settlement.

9) Somatic growth and shell growth were uncoupled. Maximum increase in wet meat weight and dry meat weight was observed between April and June, then meat weights decreased, whereas growth in shell length continued from mid-spring to mid-autumn.

10) The growth rate of cultured mussels was affected by depth in Loch Etive because more seed mussels were lost from the culture ropes at 6 m compared to 2 m. Growth was not affected by depth in lantern net experiments. Overall, mean growth in length appeared to be similar to that of mussels in other west coast sea lochs, but lower than some other culture areas in temperate regions as a result of a shorter growth season.

11) Somatic growth was significantly higher in Loch Kishorn than Loch Etive and was affected mainly by season, gonadal development and spawning.

12) Transplantation results (mussels exchanged between Loch Etive and Loch Kishorn) showed that growth in somatic and shell length was significantly higher in Loch Etive than Loch Kishorn for both native and transplanted mussels. This result shows that site characteristics control growth. For example, heavy fouling settlement onto the lantern net culture units had a negative effect on mussel growth in Loch Kishorn.

13) Similar growth and physiological responses in transplanted (after three months) and native mussels showed the dominant effect of site, but shell morphology of the transplanted mussels showed little change after one year's acclimatization. This may have been due to a secondary, slower adaptation process, or possibly to genetic differences between the two mussel stocks.

14) In the first year (1994) experiment, mussel mortality did not show differences between sites, or between 2 m and 6 m depths, or according to their position on the raft (in relation to the water inflow and outflow points). Average survival on the culture ropes was 23.39 % in Loch Etive and 22.64 % in Loch Kishorn, but when losses were discounted, by

rearing mussels in lantern nets to eliminate predation and fall-off, mean cumulative mortality was 13.32 % in Loch Etive and 15.14 % in Loch Kishorn.

15) About 79 % of total mortality in transplanted mussels (Loch Etive-Loch Kishorn) occurred in the first three months in Loch Kishorn, while about 64 % of total mortality occurred in the transplanted mussels (Loch Kishorn-Loch Etive) in Loch Etive. Mortality was significantly higher in the transplanted mussels (Loch Etive-Loch Kishorn and Loch Kishorn-Loch Etive) than in native mussels (Loch Etive and Loch Kishorn) ($P < 0,001$).

16) Ash-free dry weight biomass was higher in Loch Kishorn than Loch Etive due to high somatic growth in Loch Kishorn. Biomass was mainly affected by tissue growth, utilization of body reserves and losses. However, mussel production was higher in Loch Etive than Loch Kishorn because of other factors, including growth and spawning differences.

17) The condition index (CI) of rope cultured mussels reached a minimum in March in Loch Etive and in April in Loch Kishorn, then quick recovered at both sites. Mussels with a high CI can be harvested for about 8-9 months of the year in both lochs. CI did not vary significantly with culture depth.

18) The biochemical composition of mussels was similar in both sites. All indirect evidence, e.g. seasonal cycle of condition index, biochemical composition and observation of mantle conditions, suggested that first spawning occurs during March-April, with a second spawning in July.

19) Spat settlement takes place in June to July in Loch Etive and from June to December in Loch Kishorn. Uniform, high quality spat fall and very good growth occurred in Loch Etive, while in Loch Kishorn, starfish, sea squirt and eider duck caused problems for spat collection.

20) Estimates of carrying capacity for cultured mussels were made for both lochs using two different models. A particulate organic matter-based model gave reasonable estimates of carrying capacity in comparison to the actual mussel production levels. However, a seston-based model gave an over estimate of carrying capacity for both sites.

21) A preliminary study on the morphometrics and genetics of Loch Etive and Loch Kishorn populations have mussels from Loch Etive and Loch Kishorn have some significant differences and the genetic distance of the two populations is 0.37.

5.10. Recommendations For Furture Research

A substantial amount of information was obtained relevant to the main objectives of this research study, but it is certainly not enough for a complete evaluation of the bio-technical aspects of mussel culture. Further research on the following aspects is recommended:

- 1) Further assessment of mussel farm carrying capacity, with collection of more data over a longer time period. Also a carrying capacity model should be developed to better suit the particular environments being studied (i.e. Loch Etive and Loch Kishorn, and similar sea lochs).
- 2) More study should be made on condition index and bio-chemical condition of *Mytilus* using a standard size of mussel, and extending the work to include more sites on the west coast of Scotland and inclusion of histological methods for tissue analysis.
- 3) Studies on the effect of sea loch conditions on the distribution and morphology of larvae, and on spat collection. Due to the heavy sea squirt problem in some sea lochs, a study on efficient transport of spat between sites would be of great practical and economic value.
- 4) Detailed genetic studies from all around Scotland to examine hybridization of *Mytilus galloprovincialis* and *Mytilus edulis* on the west coast of Scotland.
- 5) Detailed investigation should be made on eider duck and ways of trying to reduce their population size since heavy losses caused by eider duck predation on mussels.
- 6) An environmental impact study on shellfish and antibiotics released during treatment of farmed salmon and the potential hazard that this practice may represent to shellfish consumers.

REFERENCES

- Abbe, C.R. and Sanders, J.G., 1988. Rapid decline in oyster condition in the Patuxent river, Maryland. *J. Shellfish Res.*, 7(1): 57-59.
- Adamkewicz, L.S., Taub, R. and Wall, J.R., 1984. Genetics of the clam *Mercenaria mercenaria* II. Size and genotype. *Malacologia*, 25 (2): 525-533.
- Ahmad, M., Skibinski, D.O.F. and Beardmore, J.A., 1977. An estimate of the amount of genetic variation in the common mussel *Mytilus edulis*. *Biochem. Genet.*, 15: 833-846.
- Akberali. H.B. and Trueman, E.R., 1985. Effects of environmental stress on marine bivalve molluscs. *Adv. Mar. Biol.*, 22: 101-198.
- Aldrich, J.C. and Crowley, M., 1986. Condition and variability in *Mytilus edulis* L. from different habitats in Ireland. *Aquaculture*, 52: 273-286.
- Almada-Villela, P.C., 1984. The effects of reduced salinity on the shell growth of small *Mytilus edulis*. *J. Mar. Biol. Ass., U.K.*, 64: 171-182.
- Almada-Villela, P.C., Davenport, J. and Gruffydd, LL.D., 1982. The effects of temperature on the shell growth of young *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.*, 59: 275-288.
- Alvarez, J.B., 1968. Variacion mensual de la composicion quimica del mejillon, *Perna perna* (L.). *Bol. Inst. Oceanog. Univ. Oriente, Venezuela*, 7: 137-47.
- Alyakrinskaya, I.O., 1967. Distribution of mussels and some data on their chemical composition in connection with the pollution of the Bay of Novorossiisk. *Trud. Ins. Okean.*, 85: 66-76.
- Andreu, B., 1958. Sobre el cultivo del mejillon en Galicia. *Biologia, crecimiento y produccion. Invest. Presq.* 745-746: 44-47.
- Andreu, B., 1968. The importance and possibilities of mussel culture. Working Paper 5. Seminar on Possibilities and Problems of Fisheries Development in Southeast Asia, German Foundation for Developing Countries, Berlin, 15 pp.
- Anonymous., 1990. Mussels. *Aquacult. Ir.*, 45: 36-37.
- Anonymous., 1995. Harvest tops 100m tonnes. *Fishing News Int.*, 34: 2
- Anonymous., 1989. The climate of Scotland: Some facts and figures. The Meteorological Office, London, 22pp
- Ansel, A.D., 1972. Distribution, growth and seasonal changes in biochemical composition for the bivalve *Donax vittatus* (Da Costa) from Kames Bay, Millport. *J. Exp. Mar. Biol. Ecol.*, 10: 137-150.
- Ansel, A.D. and Trevallion, A., 1967. Studies on *Tellina tenuis* Da Costa. 1. Seasonal growth and biochemical cycle. *J. Exp. Mar. Biol. Ecol.*, 1: 220-235.
- AOAC., 1990. Official Methods of Analysis. 15th. edition. Heldrich, K.(Ed.). Association of Official Analytical Chemists. Arlington, Virginia, U.S.A., 1298p.

- Ardisson, P.L. and Bourget, E., 1991. Abundance, growth and production estimation of the blue mussel *Mytilus edulis* on moored navigation buoys in the estuary and Northwest Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.*, 48:2408-2419.
- Aunaas, T., Denstad, J.-P. and Zachariassen, K.E., 1988. Ecophysiological importance of the isolation response of hibernating blue mussels (*Mytilus edulis*). *Mar. Biol.*, 98: 415-419.
- Austin, H., Haven D.S, and Moustafa, M.S., 1993 The relationship between trends in a condition index of American oyster, *Crassostrea virginica* and environmental parameters in three Virginia Estuaries. *Estuaries*, 16 (2): 362-374.
- Bagge, P. and Salo, A., 1967. Biological detectors of radioactive contamination in the Baltic. Report SFL-A9, Institute of Radiation Physics, Helsinki.
- Baird, R. H., 1958. Measurement of condition in mussels and oysters. *J. Cons. Perm. Inter. Exp. Mer.*, 23: 249-257.
- Baird, R. H., 1966. Factor effecting the growth and condition of mussels (*Mytilus edulis*). *Fish. Invest.*, 25 (2): 1-33.
- Barber, B.J., Ford S.E. and H.H. Haskin, 1988. Effect of the parasite MSX (*Hoplosporidium nelsoni*) on oyster (*Crassostrea virginica*) energy metabolism. I. Condition index relative fecundity. *J. Shell. Res.*, 7 (1): 25-31.
- Barnes, R.D., 1987. Invertebrate zoology. USA CBS College Publ. 883 pp.
- Bayne, B.L., 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *J. Anim. Ecol.*, 33:513-523.
- Bayne, B.L., 1965. Growth and delay of metamorphosis of the larvae of *Mytilus edulis* (L.). *Ophelia*, 2: 1.
- Bayne, B. L., 1976. The biology of mussel larvae. In : *Marine Mussels: their Ecology and Physiology*. B. L. Bayne, (Ed.). Cambridge University Press. pp 81-120.
- Bayne, B. L., Thompson, R.J. and Widdows, J., 1976a. Physiology: I. In: *Marine Mussels: Their Ecology and Physiology*. B.L. Bayne (Ed.). Cambridge: Cambridge University Press. pp. 121-206
- Bayne, B. L., Widdows, J. and Thompson, R.J., 1976b. Physiological integrations. In: *Marine Mussels: Their Ecology and Physiology*. B.L. Bayne (Ed.). Cambridge: Cambridge University Press. pp. 261-291
- Bayne, B. L., Widdows, J. and Newell, R.I.E., 1977. Physiological measurements on estuarine bivalve molluscs in the field. In: *Biology of benthic organisms*. Keegan, B.F., O'Ceidigh, P. and Boaden P.J.S. (Eds.). Proc. 11th European Symposium on Marine Biology, Galway, October 1976. Pergamon Press, Oxford and New York. pp. 57-68.
- Bayne, B. L. and Widdows, J., 1978. The physiological ecology of two populations of *Mytilus edulis* L. *Oecologia*, 37: 137-162.

- Bayne, B. L., Holland, D.L., Moore, M.N., Lowe, D.L. and Widdows, J., 1978. Further studies on the effects of stress in the adult on the eggs of *Mytilus edulis*. J. Mar. Biol. Ass. U.K., 58: 825-841.
- Bayne, B. L., Moore, M.N., Widdows, J. and Livingstone, D.R., 1979. Measurements of the responses of individuals to environmental stress and pollution: studies with bivalve molluscs. Phil. Trans. Roy. Soc. Lond. B. 286: 563-581.
- Bayne, B.L., Salkeld, P.N. and Worrall, C.M., 1983. Reproductive effort and value in different populations of the mussel, *Mytilus edulis* L. Oecologia, 59: 18-26.
- Bayne, B.L. and Worrall, C.M., 1980. Growth and production of mussels, *Mytilus edulis*, from two populations. Mar. Ecol. Prog. Ser., 3: 317-328.
- Bayne, B. L. and Newell, R.C., 1983. Physiological energetics of marine molluscs. In: The Mollusca, Vol. IV: Physiology Part 1, Saleuddin, A.S.M. and Wilbur, K.M. (Eds.) Academic Press, pp. 407-515.
- Bayne, B.L., Hawkins, D.W. and Navarro, E., 1987. Feeding and digestion by mussel *Mytilus edulis* L. (Bivalvia, Mollusca) in mixtures of silt and algal cells at low concentrations. J. Exp. Mar. Ecol., 111: 1-22.
- Bayne, B. L., Hawkins, A.J.S., Navarro, E. and Iglesias, I.P.R., 1989. Effects on seston concentration on feeding, digestion and growth in the mussel *Mytilus edulis*. Mar. Ecol. Prog. Ser., 55: 47-54.
- Beaumont, A.R., Seed, R. and Garcia-Martinez, P., 1989. Electrophoretic and morphometric criteria for the identification of the mussels *Mytilus edulis* and *M. galloprovincialis*. In: J. Ryland and P.A. Tyler (Eds.). Proc. 23rd Eur. Mar. Biol. Symp., Swansea, UK., 1988. Olsen and Olsen, Fredensberg, Denmark, pp. 251-258.
- Beukema, J.J. and Burin, W. D., 1979. Calorific values of the soft part of the tellinid bivalve *Macoma balthica* (L.) as determined by two methods. J. Exp. Mar. Biol. Ecol., 37: 19-30.
- Beveridge, M.C.M., 1987. Cage Aquaculture. Fishing News Books. Great Britain. 352 pp.
- Blot, M., Thiriot-Quievreux, C and Soyer, J., 1988. Genetic relationship among populations of *Mytilus desolationis* from Kerguelen, *M. edulis* from the North Atlantic and *M. gallprovincialis* from the Mediterranean. Mar. Ecol. Prog. Ser., 44: 239-247.
- Bohle, B., 1965. Undersokelser av bläskjell (*Mytilus edulis* L.) Oslofjorden . Fisk. Gan., 51: 388-394.
- Bohle, B., 1972. Effects of adaptation to reduced salinity on filtration activity and growth of mussels (*Mytilus edulis*). J. Exp. Mar. Biol. Ecol. 10: 41-49.
- Boje, R., 1965. Die Bedeutung von Nahrungsfaktoren fur das Wachstum von *Mytilus edulis* L. in der Kieler Forde und im Notd-Ostsee-Kanal. Kiel. Meer., 21: 82-100.

- Bower, S.M. and Figueras, A.J., 1989. Infectious diseases of mussels, especially pertaining to mussel transplantation. *World Aquaculture*, 20(4): 89-93.
- Boyer, J.F., 1974. Clinal and size-dependent variation at the LAP locus in *Mytilus edulis*. *Biol. Bull. Mar. Biol. Lab., Woods Hole* 147: 535-549.
- Boyton, W.R., Kemp, W.M. and Osbourne, C.G., 1980. Nutrient fluxes across the sediment-water interface in the turbid zone of a coastal plain estuary. In: V.S. Kennedy, (Ed.), *Estuarine Perspectives*. Academic Press, New York, pp. 93-109.
- Brenko, M. HRS. and Calabrese, A., 1969. The combined effects of salinity and temperature on larvae of the mussel, *Mytilus edulis* L.. *Mar. Biol.*, 4 : 224-226.
- Bressan, M. and Marin, M.G., 1985. Seasonal variations in biochemical composition and condition index of cultured mussels, *Mytilus galloprovincialis* (Lmk.), in the Lagoon of Venice (North Adriatic). *Aquaculture*, 48: 13-21.
- Briggs, R.P., 1983. Meat condition of the Pacific oyster *Crassostrea gigas* Thunberg grown in Strangford Lough, Northern Ireland. *J. Life. Sci. R. Dubl. Soc.*, 4: 225-30.
- Broom, M.J., 1982. Analyses of growth of *Anadara granosa* (Bivalve: Arcidae) in natural, artificially seeded and experimental populations. *Mar. Ecol. Prog. Ser.*, 9: 69-79.
- Brown, J.R., 1988. Multivariate analyses of the role of environmental factors in seasonal and site-related growth variation in the Pacific oyster *Crassostrea gigas*. *Mar. Ecol. Prog. Ser.*, 45: 225-236.
- Brown, J.R. and Hartwick, E.B., 1988a. Influences of temperature, salinity and available food upon suspended culture of the Pacific oyster, *Crassostrea gigas*, I. Absolute and allometric growth. *Aquaculture*, 70: 231-251.
- Brown, J.R. and Hartwick, E.B., 1988b. Influences of temperature, salinity and available food upon suspended culture of the Pacific oyster, *Crassostrea gigas*, II. Condition index and survival. *Aquaculture*, 70: 253-267.
- Buchanan, J., 1995.a. How are priorities decided for publicity funded R and D to assist our industry to be efficient? *Scot. Fish Farm.*, No: 78.
- Buchanan, J., 1995.b. Major catastrophe strikes French oyster growers is it disease? *Scot. Fish Farm.*, No: 75.
- Bulnheim, H.P. and Gosling, E.M., 1988. Population genetic structure of mussels from the Baltic Sea. *Helgolander. Wiss. Meeresunters.*, 42: 113-129.
- Buroker, N.E., 1983. Population genetics of the American oyster *Crassostrea virginica* along the Atlantic coast and the Gulf of Mexico. *Mar. Biol.*, 75: 99-112.
- Buroker, N.E., Hershberger, W.K. and Chew, K.K., 1979. Population genetics of the family *Ostreidae*. II. Inter-specific studies of the genera *Crassostrea* and *Saccostrea*. *Mar. Biol.* 54: 171-184.

- Carlson, D.J., Townsend, D.W., Hilyard, A.L. and Eaton, J.F., 1984. Effect of an intertidal mudflat on plankton of the overlying water column. *Can. J. Fish. Aquat. Sci.*, 41: 1523-1528.
- Carver, C.E.A. and Mallet, A.L., 1990. Estimating the carrying capacity of a coastal inlet for mussel culture. *Aquaculture*, 88: 39-53.
- Ceccherelli, V.U. and Rossi, R., 1984. Settlement, growth and production of mussel, *Mytilus galloprovincialis*. *Mar. Ecol. Prog. Ser.*, 16:173-184.
- Chalermwat, K and Lutz, R.A., 1989. Farming the green mussel in Thailand. *World Aquaculture* 20(4): 41-46.
- Chalfant, J.S., Archambault T., West, A.E., Riley, J.G. and Smith, N., 1980. Natural stocks of Mussels: Growth, Recruitment and Harvest Potential. In: A North American Prospective. Lutz R.A. (Ed.) Elsevier, Amsterdam. pp. 38-68
- Chanley, M.H. and Chanley, P., 1991. Chilean mussel culture: *Mytilus edulis chilensis* (Hupé, 1854), *Choromytilus chorus* (Molina, 1782), *Aulacomya ater* (Molina, 1782). In: W. Menzel (Ed.), *Estuarine and Marine Bivalve Mollusk Culture*, CRC Press, Boca Raton, Florida, pp. 135-143.
- Chatterji, A., Ansari, Z.A., Ingole, B.S. and Parulekar, A. H., 1984. Growth of the green mussel, *Perna viridis* L., in a sea water circulating system. *Aquaculture*, 40: 47-55.
- Cheung, S.G., 1993. Population dynamics and energy budgets of green-lipped mussel *Perna viridis* (Linnaeus) in a polluted harbour. *J. Exp. Mar. Biol. Ecol.*, 168: 1-24.
- Cheong, L. and Lee, H.B., 1984. *Mussel Farming*. Safis Extension Manual No.5. Southeast Asian Fisheries Development Centre, Bangkok, 51pp.
- Chipperfield, P.N.J., 1953. Observation on the breeding and settlement of *Mytilus edulis* (L.) in British waters. *J. Mar. Biol. Assoc., U.K.* 32: 449-476.
- Cloern, J.E. 1982. Does benthos control phytoplankton biomass in south San Francisco Bay? *Mar. Ecol. Prog. Ser.* 9: 191-202.
- Coe, W.R., 1945. Nutrition and growth of the Californian bay mussel (*Mytilus edulis diegensis*). *J. Exp. Zool.*, 99: 1-14.
- Coe, W.R., 1946. A resurgent population of the Californian bay mussel *Mytilus edulis diegensis*. *J. Morp.*, 78: 85-103.
- Coe, W.R. and Fox, D.L., 1942. Biology of the Californian sea mussel *Mytilus californianus*. I. Influence of temperature, food supply, sex and age on the rate of growth. *J. Exp. Zool.*, 90: 1-30.
- Coe, W.R. and Fox, D.L., 1944. Biology of the Californian sea mussel *Mytilus californianus*. III. Environmental conditions and rate of growth. *Biol. Bull.*, 87: 58-72.

- Cohen R.H., Dressler, P.V., Phillips, E.J. and Cory, R.L., 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnol. Oceanogr.*, 29: 170-180.
- Conover, R.J., 1966. Assimilation of organic matter by zooplankton. *Lim. Oceanogr.*, 11: 338-354.
- Coulthard, H.S., 1929. Growth of the sea mussel. *Can. Biol. Fish.*, 4: 123-36.
- Cousteu, C., Renaud, F., Delay, B., Robbins, I. and Mathieu, M., 1991. Mechanism involved in parasitic castration: in vitro effects of the trematode *Proisorhynchus squamatus* on the gametogenesis and the nutrient storage metabolism of the marine bivalve *Mytilus edulis*. *Exp. Zool.*, 73(1): 36-43.
- Craeymeersch, J.A., Herman, P.M.J. and Meire, P.M., 1986. Secondary production of an intertidal mussel (*Mytilus edulis* L.) population in the Eastern Scheldt (S.W. Netherlands). *Hydrobiologia*, 133: 107- 115.
- Crisp, D.J., 1984. Energy flow measurements. In: N.A. Holme and A.D. McIntyre (Eds.), *Methods for Study of Marine Benthos*, 2nd Ed. IBP 16, Blackwell, Oxford, pp. 284-386.
- Crosby, M.P. and Gale, L.D., 1990. A review and evolution of bivalve condition index methodologies with a suggested standard method. *J. Shell. Res.* 9 (1): 233-237.
- Dame, R., Zingmark, R., Stevenson, H. and Nelson, D., 1980. Filter feeder coupling between the estuarine water column and benthic subsystem. In: V. Kennedy (Ed): *Estuarine perspectives*, Academic Press, New York. pp. 521-526.
- Dardinac-Corbeil, M.J., 1990. Traditional Mussel Culture. In: *Aquaculture*, Vol. 1, G. Barnabè (Ed.), Eng. Trans. by L. Laird. Ellis Horwood. pp. 285-341.
- Dare, P.J., 1973. Seasonal changes in meat condition of sublittoral mussels (*Mytilus edulis* L.) in the Conwy Fishery, North Wales., I.C.E.S., C.M. 1969, *Shell. Comn.*, 31: 1-6.
- Dare, P.J., 1976. Settlement, growth and production of the mussel, *Mytilus edulis* (L.), in Morecambe Bay, England. *Fish. Invest., Lond. Series II*, 28(1). Her Majesty's Stationery Office, London. 25 pp.
- Dare, P.J., 1980. Mussel Cultivation in England and Wales. *Fish. Res. Tech. Rep.*, MAFF Direct. Fish. Res., Lowestoft, 56. 18 pp.
- Dare, P.J. and Davies, G., 1975. Experimental suspended culture of mussels, *Mytilus edulis* (L.), in Wales using spat transplanted from a distant settlement ground. *Aquaculture*, 6: 257-274.
- Dare, P.J. and Edwards, D.B., 1975. Seasonal changes in flesh weight and biochemical composition of mussels, *Mytilus edulis* (L.), in the Conwy Estuary, North Wales. *J. Exp. Mar. Biol. Ecol.*, 18: 89-97.
- Dare, P.J. and Edwards, D.B., 1976. Experiments on the survival, growth and yield of relaid seed mussels (*Mytilus edulis* L.) in the Menai Straits, North Wales. *J. Con. Int. Mer*, 37 (1): 16-28.

- Dare, P.J., Edwards, D.B. and Davies, G., 1983. Experimental collection and handling of spat mussels (*Mytilus edulis* L.) on ropes for intertidal culture. Fish. Res. Tech. Rep., MAFF Direct. Fish. Res., Lowestoft 74:1-23.
- Davenport, J., 1979. The isolation response of mussels (*Mytilus edulis* L.) exposed to falling sea water concentration. J. Mar. Biol. Ass. U.K., 59: 124-132.
- Davenport, J. and Chen, X., 1987. A comparison of methods for the assessment of condition in the mussel, *Mytilus edulis* L. J. Moll. Stud., 53: 293-297.
- Davies, G., 1974. A method for monitoring the spatfall of mussels (*Mytilus edulis* L.). J. Con. Int. Exp. Mer., 36: 27-34.
- Dickie, L.M., Bordeu, P.R. and Freeman, K.R., 1984. Influence of stock and site on growth and mortality in blue mussel, *Mytilus edulis*. Can. J. Fish Aquat. Sci., 41: 134-141.
- Dijkema, R. and van Stalen, M., 1989. Mussel cultivation in the Netherlands. World Aquaculture, 20(4): 56-62.
- Dix, T.G. and Ferguson, A., 1984. Cycles of reproduction and condition in Tasmanian blue mussels *Mytilus edulis planulatus*. Aust. J. Mar. Freshw. Res., 35: 307-313.
- Dodge, H., 1952. A historical review of the mollusk. I. The classes Loricata and Pelecypoda. Bulletin of the American Museum of Natural History, 100: 1-264.
- Doering, P.H. and Oviatt, C.A., 1986. Application of filtration rate models to field populations of bivalves: an assessment using experimental mesocosm. Mar. Ecol. Ser., 31: 265-275.
- Dolah, R.F.V., Bobo, M.Y., Levisen, M.V., Wendh, P.H. and Manzi, J.J., 1992. Effect of marina proximity on the physiological condition, reproduction and settlement of oyster populations. J. Shell. Res., 11(1): 41-48.
- Drinkwater, J., 1987. Shellfish Cultivation in Scotland. Scot. Fish. Inf. Pamphlet, 13. DAFFS, Aberdeen, 20 pp.
- Durrell, S.E.A. and Gross-Custard, J.D., 1984. Prey selection within a size-class of mussels. Anim. Behav., 32: 1197-1203.
- Dyer, K.R., 1973. Estuaries: a physical introduction. John Wiley and Sons, Toronto, Canada. pp. 109-110.
- Edwards, A. and Edelsen, D.J., 1976. Marine fish cages. The physical environment. Proc. Roy. Soc. Edinb., 75: 207-221.
- Edwards, A. and Edelsen, D.J., 1977. Deep water renewal of Loch Etive: a three basin Scottish fjord. Est. Coas. Mar. Sci, 5: 575-595.
- Edwards, A. and Sharples, F., 1986. Scottish Sea-Lochs: A Catalogue. Scottish Marine Biological Association and Nature Conservancy Council. 110 pp.
- Edwards, E., 1992. Mussels could be export earners. Fish Farm. Inter., 19(2): 6.

- Emmett, B., Thompson, K., and Popham, J. D. 1987. The reproductive and energy storage cycles of two populations of *Mytilus edulis* (L.) from British Columbia. *J. Shell. Res.*, 6(1): 29-36.
- Engle, J.B. and Loosanoff, V.L., 1944. On season of attachment of larvae of *Mytilus edulis* L. *Ecology*, 25: 433-40.
- Essink, K. and Bos, A.H., 1985. Growth of three bivalve molluscs transplanted along the axis of the Ems estuary. *Neth. J. Sea Res.*, 19: 45-51.
- Eyster, L.S. and Pechenik, J.A., 1987. Attachment of *Mytilus edulis* L. larvae on algal and byssal filaments is enhanced by water agitation. *J. Exp. Mar. Biol.*, 114: 99-110.
- FAO., 1994. Aquaculture production (1986-1992). FAO Fisheries Circular No. 815, Rev. 6.
- Farias, S.J.A., 1983. Experimental trial on the growth of mussels, *Mytilus edulis*, on ropes suspended from marine fish cages. M.Sc. Thesis, University of Stirling.
- Farias, S.J.A., 1991. Ecology, culture and utilisation of the mussel, *Brachidontes recurvus* (Rafinesque), in the context of an integrated management approach to Boca Del Rio-Mandinga estuarine system, Veracruz, Mexico. PhD, Thesis. University of Stirling. 234pp.
- Feare, C.J. and Summers, R.W., 1985. Birds as predators on rocky shores. In; P.G. Moore and R. Seed (Eds.), *The Ecology of Rocky Coasts*. Hodder and Stoughton, Sevenoaks, U.K., pp. 249-264.
- Ferguson, A., 1980. *Biochemical Systematics and Evolution*. Thompson Litho Ltd., East Kilbride, Scotland. 194 pp.
- Ferson, S., Rohlf, F.J. and Koehn, R.K., 1985. Measuring shape variation of two-dimensional outlines. *Syst. Zool.*, 34(1): 59-68.
- Field, I.A., 1922. Biology and economic value of sea mussel, *Mytilus edulis*. *Bull. Bur. Fish. Wash.*, 38: 125-259.
- Figueras, A.J., 1989. Mussel culture in Spain and France. *World Aquacult.*, 20(4):8-17.
- Figueras, A.J., 1990. Mussel culture in Spain. *Mar. Behav. Physiol.*, 16:177-207.
- Fréchette M. and Bourget, E., 1985a. Energy flow between the benthic and pelagic zones: Factors controlling particulate organic matter availability to an intertidal mussel bed. *Can. J. Fish. Aquat. Sci.* 42: 1158-1165.
- Fréchette, M. and Bourget, E., 1985b. Food limited growth of *Mytilus edulis* (L.) in relation to the benthic boundary layer. *Can. J. Fish. Aquat. Sci.* 42: 1166-1170.
- Fréchette, M. and Bourget, E. 1987. Significance of small-scale spatio-temporal heterogeneity in plankton abundance for energy flow in *Mytilus edulis*. *Mar. Biol.* 94: 231-240.
- Freeman, K.R. and Dickie, L.M., 1979. Growth and mortality of blue mussel, *Mytilus edulis*, in relation to environmental indexing. *Can. Fis. Res. Board.* , 36: 1238-1249.

- Fuentes, J., Reyero, I., Zapata, C. and Alvarez, G., 1994. Production of the mussel, *Mytilus galloprovincialis*, cultured in Galicia (NW of Spain): relative effects of source seed and growing environment. *Aquaculture*, 122: 19-31.
- Gabbott, P.A., 1975. Storage cycles in marine bivalve molluscs: A hypothesis concerning the relationship between glycogen metabolism and gametogenesis. In: Proc. 9th Europ. Mar. Biol. Symp., H. Barnes (Ed.). Aberdeen University Press. pp. 191-211.
- Gabbott, P.A., 1976. Energy metabolism. In: Marine mussels; their ecology and physiology, B.L. Bayne (Ed.). Cambridge Uni. Press, pp. 293-355.
- Gabbott, P.A., 1983. Development and seasonal activities in marine molluscs. In: *Mollusca Vol. 2*, Hochackha P.W. (Ed.), Academic press. New York. pp. 165-217.
- Gabbott, P.A. and Bayne, B.L., 1973. Biochemical effect of temperature and nutritive stress on *Mytilus edulis* (L.), *J. Mar. Biol. Ass. U.K.* 53: 269-286.
- Gabbott, P.A. and R.R. Stephenson, 1974. A note on the relationship between the dry weight condition index and the glycogen content of adult oysters (*Ostrea edulis* L.) kept in the laboratory. *J. Cons. Int. Exp. Mer.*, 35 (3) : 359-361.
- Gage, J., 1972. A Preliminary survey of the benthic macrofauna and sediments in Loch Etive and Crean, sea-lochs along the west coast of Scotland. *J. Mar. Biol. Ass. U.K.*, 52: 237-276.
- Gage, J., 1974. Shallow water zonation of sea benthos and its relation to hydrographic and other physical features. *J. Mar. Biol. Ass. U.K.*, 54: 223-249.
- Galbraith, C., 1992. Mussel farms their management alongside eider ducks. *Scottish Natural Heritage*, 21p.
- Galtsoff, P.S., 1964. The American oyster *Crassostrea virginica* (Gmelin), U.S., Fish Wildl. Serv., Fish. Bull. 64: 480 p.
- Gardner, J.P.A., 1996. The *Mytilus edulis* species complex in southwest England: effect of hybridization and introgression upon interlocus associations and morphometric variation. *Mar. Biol.* 125: 385-399.
- Gardner, J.P.A. and Thomas, M.L.H., 1987. Growth, mortality and production of organic matter by a rocky intertidal population of *Mytilus edulis* in the Quoddy region of the Bay of Fundy. *Mar. Ecol. Prog. Ser.*, 39: 31-36.
- Gardner, J.P.A. and Skibinski, D.O.F., 1990. Genotype-dependent fecundity and temporal variation of spawning in hybrid mussel (*Mytilus*) populations. *Mar. Biol.*, 105: 153-162.
- Gardner, J.P.A. and Skibinski, D.O.F., 1991. Mitochondrial DNA and allozyme variation in a hybrid mussel population. *J. Exp. Mar. Biol. Ecol.* 149: 45-54.
- Gartner- Kepkay, K.E., Dickie, L.M., Freeman, K.R. and Zouros, E., 1980. Genetic differences and environments of mussel populations in the Maritime Provinces. *Can. J. Fish. Aquat. Sci.*, 37: 775-782.

- Genovese, S., 1965. Ulteriore contributo alla sistematica del genere *Mytilus*. Analisi biometrica di due popolazioni proveniente dal Canale di Leme e da Boulogne. Bolletino di Zoologia, Fasc. II, 32: 247-62.
- Giese, A.C., 1967. Some methods for study of the biochemical constituents of marine invertebrates. Oceanog. and Mar. Biol. Ann. Rev. 5: 159-186.
- Giese, A.C., 1969. A new approach to the biochemical composition of the molluscan body. Oceanogr. Mar. Biol. Ann. Rev., 7: 175-229.
- Gosling, E.M., 1984. The systematic status of *Mytilus galloprovincialis* in western Europe: a review. Malacologia 25: 551-568.
- Gosling, E.M., 1992. Genetics and evolution. In: The Mussel *Mytilus*: Ecology, Physiology, Genetics and Culture, Gosling, E.M. (Ed.) Elsevier, Amsterdam. pp. 589
- Gosling, E. M. and Wilkins, N.P., 1977. Phosphoglucosomerase allele frequency data in *Mytilus edulis* from Irish coastal sites: its ecological implications. In: B.F. Keegan, P.O. C  idigh and P.S. Boaden (Eds), Biology of Benthic Organisms. Proc. 11th Eur. Mar. Biol. Symp., Galway, Ireland, 1976. Pergamon Press, London, pp. 297-309.
- Gosling, E.M. and Wilkins, N.P., 1981. Ecological genetics of the mussels *Mytilus edulis* and *M. galloprovincialis* on the Irish coasts. Mar. Ecol. Prog. Ser., 4:221-227.
- Gould, D.T., 1950. A fish cultivation experiment in an arm of a sea-loch. III. The plankton of Kyle Scottish. Proc. R. Soc. Edinb., Sect. B, 64: 36-64.
- Gowen R.J., Tett, P. and Jones, K.J., 1983. The hydrography and phytoplankton ecology of Loch Ardbhair: a small sea loch on the west coast of Scotland. J. Exp. Mar. Biol. Ecol., 71: 1-16.
- Gowen, R., Brown, J., Bradbury, N. and McLusky, D.S., 1988. Investigations into benthic enrichment, hypernutrification and eutrophication associated with mariculture in Scottish waters (1984-1988). Report to the Highlands and Islands Development Board, Crown Estates Commissioners, Countryside Commission for Scotland, Nature Conservancy Council and Scottish Salmon Growers Association. 289 pp.
- Graffney, P.M. and Scott, T.M., 1984. Genetic heterozygosity and production traits in natural and hatchery populations of bivalves. Aquaculture, 42: 289-302.
- Grant, W.S. and Cherry, M.I., 1985. *Mytilus galloprovincialis* Lmk. in southern Africa. J. Exp. Mar. Biol. Ecol., 90: 179-191.
- Grantham, B., 1981. The Loch Eil Project: Chlorophyll-*a* and nutrients in the water column of Loch Eil. J. Exp. Mar. Biol. Ecol., 55: 283-297.
- Grave, 1911. Anatomy and physiology of the Wingshell *Atrina rigida*. Bull. Bur. Fish., Wash., 29: 409-439.

- Green, F.H.W. and Harding, R.J., 1983. Climate of the Inner Hebrides. Proc. Royal Soc. Edinb. Sect. B, 83: 121-140.
- Grizzle, R.E. and Morin, P.J., 1989. Effect of tidal currents, seston and bottom sediments on growth of *Mercenaria mercenaria*: results of a field experiment. Mar. Biol., 102: 85-93.
- Hancock, D.A., 1965. Adductor muscle size in Danish and British mussels in relation to starfish predation. Ophelia, 2: 253-67.
- Hancock, D.A. and Franklin, A., 1972. Seasonal changes in the condition of the edible cockle (*Cardium edule* L.). J. Appl. Ecol., 9: 567-579.
- Harger, J.R.E., 1970. Comparisons among growth characteristics of two species of sea mussel *Mytilus edulis* and *Mytilus californianus*. Veliger, 13: 44-56.
- Haven, D. S., 1960. Seasonal cycle of condition index of oysters in the York and Rappahannock rivers. Proc. Nat. Shell. Ass. 51: 42-66.
- Hawkins, A.J.S. and Bayne, B.L., 1985. Seasonal variation in the relative utilization of carbon and nitrogen by the mussel *Mytilus edulis*: budgets, conversion efficiencies and maintenance requirements. Mar. Ecol. Prog. Ser., 25: 181-185.
- Hepper, B.T., 1955. Environmental factors governing the infection of mussels, *Mytilus edulis*, by *Mytilicola intestinalis*. Fish. Invest., Lond., Ser.II, 20 (3): 21pp.
- Héral, M., 1987. Evaluation of the carrying capacity of molluscan shellfish ecosystems. In: Working Group on Technology, Growth and Employment, Shellfish Culture Development and Management. INFRAMER, France. pp. 297-312.
- Heritage, G.D., 1983. A blue mussel, *Mytilus edulis* Linnaeus, culture pilot project in South Coastal British Columbia. Can. Tech. Rep. Fish and Aqua. Sci., 1174. British Columbia. 27 pp.
- Herlin-Houtteville, P. and Lubert, P.E., 1975. The The sexuality of pelecypod molluscs. In: Intersexuality in the animal kingdom. R. Reinboth (Ed). Berlin, Heidelberg, New York: Springer-Verlag. pp. 179-187
- Herman, P.M.J. and Scholten, H., 1990. Can suspension-feeders stabilise estuarine ecosystems? Proc. 24th Europ. Mar. Biol. Symp. pp 104-116.
- Herriott, N., 1984. A guide to longline mussel cultivation. Aquaculture Technical Bulletin, 9. National Board for Science and Technology, Dublin. 97pp.
- Hickman, R.W., 1979. Allometry and growth of the green-lipped mussel, *Perna canaliculus*, in New Zealand. Mar. Biol., 51:311-327.
- Hickman, R.W. and Illingworth, J., 1980. Condition cycle of the green lipped mussel, *Perna canaliculus*, in New Zealand, Mar. Biol., 60: 27-38.
- Higgins, E., 1938. Progress in Biological Enquiries, 1937. U.S. Bureau of Fisheries, Washington, D.C. Report of the Commissioner of Fisheries for the Fiscal Year 1938, Appendix 1. Adm. Rep., 30: 1-70.
- Hilbish, T.J., 1986. Growth trajectories of shell and soft tissue in bivalves; seasonal variations in *Mytilus edulis* (L.). J. Exp.Mar. Biol. Ecol., 96: 103-113.

- Holland, D.L. and Gabbott, P.A. 1971. A micro-analytical scheme for the determination of protein, carbohydrate, lipid and RNA levels in marine invertebrate larvae. *J. Mar Biol. Ass.U.K.*, 51: 659-668.
- Holmyard, N., 1992. The Scottish way to mussel success. *Fish Farm. Inter.*, 19(8): 18-21.
- Hosami, A., 1984. Ecological studies on the *Mytilus galloprovincialis* (Lamarck): rise and fall of recruited cohorts in adult mussel bed. *Venus*, 43:157-171.
- Huchzermeyer, K.D.A., 1985. An investigation into problems associated with the farming of Atlantic salmon (*Salmo salar* L.) in Loch Leven, Highland Region, Scotland. MSc Thesis. Institute of Aquaculture, University of Stirling. 104 pp.
- Hughes, R.N. and Dunkin, S.B., 1984. Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.) feeding on mussels, *Mytilus edulis* L. in the laboratory. *J. Exp. Mar. Biol. Ecol.*, 77: 45-68.
- Hughes, R.N. and Burrows, M.T., 1990. Energy maximization in the natural foraging behaviour of the dogwhelk *Nucella lapillus* (L.). In: M. Barnes and R.N. Gibson (Eds), *Trophic Relationships in the Marine Environment*. Aberdeen University Press, Aberdeen . pp. 517-527.
- Hunter, J. and Scanlan, C., 1988. Highland River Purification Board. Technical Report, TR6/88. Monitoring Marine Fish Farms. 17 pp.
- Hurlburt, C.G. and Hurlburt, J.A., 1980. European mussel culture technology and its adaptability to North American waters. In: *Mussel culture and Harvest: A North American Perspective*, R. A. Lutz (Ed). Elsevier, Amsterdam. pp. 69-98
- Hvilsom, M. and Theisen, B.F., 1984. Inheritance of allozyme variations through crossing experiments with the blue mussel, *Mytilus edulis*. *Heredity*, 101: 1-7.
- Incze, L.S., Porter, B., and Lutz, R.A. 1978. Experimental culture of *Mytilus edulis* in a Northern estuarine gradient: Growth, survival and recruitment. *Proc. World Maric. Soc.* 3: 523-541.
- Incze, L.S. and Lutz, R.A., 1980. Mussel culture: an east coast perspective. In: R.A. Lutz (Ed), *Mussel culture and harvest: A North American Perspective*, Elsevier Scientific Publishing Company, Amsterdam, pp. 99-140.
- Incze, L. S., Lutz, R.A. and Watling, L., 1980. Relationships between effects of environmental temperature and seston on growth and mortality of *Mytilus edulis* (L.) in a temperature Northern Estuary. *Mar. Biol.*, 57: 147-156.
- Incze, L.S., Lutz, R.A. and True, E., 1981. Modelling carrying capacities for bivalve molluscs in open, suspended-culture systems. *J. World Maric. Soc.*, 12(1): 143-155.
- Ingle, R.M. 1949. A comparative study of oyster condition. *Science* 109: 593.
- Jamieson, G.S., 1989. Growth, reproduction, and longevity of blue mussels (*Mytilus edulis*): Implications to northeastern Pacific mussel culture. *World Aquacult.*, 20(4): 94-100.

- Jamieson, G.S., Neish, I.C. and Clarke, C.S.L., 1975. Perspectives and development prospects of mussel cultivation in Maritime Provinces of Canada. Preference AMRL 74-11, Applied Marine Research Ltd., Marine Ecology Laboratory, Halifax, Nova Scotia, 75pp.
- Jenkins, R., 1979. Mussel Cultivation in the Marlborough Sounds (New Zealand). New Zealand Fishing Industry Board, Wellington, 2nd Edition, 77pp.
- Jespersen, H. and Olsen, K., 1982. Bioenergetics in veliger larvae of *Mytilus edulis* L. *Ophelia* 21: 101-113.
- Johannesson, K., Kautsky, N. and Tedengren, M., 1990. Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplantation. II. Genetic variation. *Mar. Ecol. Prog. Ser.* 59: 211-219.
- Jones, K.J., 1981. Phytoplankton biomass and growth of mussels in Coal Scottish and Sainen Mhor, Loch Sween in 1980. SMBA Internal Reports, 39: 28pp.
- Jones, K.J. and Gowen, R.J., 1985. The influence of advective exchange on phytoplankton in Scottish fjordic sea lochs. In: Toxic Dinoflagellates. Anderson, White and Baden (Ed). pp. 207-212.
- Jones, T.O. and Iwama, G.K., 1991. Polyculture of the Pacific oyster, *Crassostrea gigas* (Thunberg), with chinook salmon, *Oncorhynchus tshawytscha*. *Aquaculture*, 92: 313-322.
- Jørgensen, C.B., 1976. August Putter, August Krogh and modern ideas on the use of dissolved organic matter in aquatic environments. *Biol. Rev.*, 51: 291-328.
- Jørgensen, C.B., 1990. Bivalve filter feeding: Hydrodynamics, bioenergetics, physiology and ecology. Olsen and Olsen, Fredensborg, Denmark. 223 pp.
- Jubb, C.A., Hughes, R.N. and Rheinallt, T., 1983. Behavioural mechanism of size selection by crabs, *Carcinus maenas* (L.) feeding on mussels *Mytilus edulis* (L.). *J. Exp. Mar. Biol. Ecol.*, 140: 121-134.
- Kautsky, N., 1982. Growth and size structure in a Baltic *Mytilus edulis* L. population. *Mar. Biol.*, 68: 117-133.
- Kautsky, N., Johannesson, K. and Tedengren, M., 1990. Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplantations. I. Growth and morphology. *Mar. Ecol. Prog. Ser.*, 59: 203-210.
- Kennish, M.J., 1986. *Ecology of Estuaries*, Volume, 1: Physical and Chemical Aspects. CRC Press, 254 pp.
- Kent, R.M.L., 1979. The influence of heavy infestations of *Polydora ciliata* on the flesh content of *Mytilus edulis* L. *J. Mar. Biol. Ass. U.K.*, 59: 203-210.
- King, P.A., McGrath, D. and Britton, W., 1990. The use of artificial substrates in monitoring mussel (*Mytilus edulis* L.) settlement on an exposed rocky shore in the west coast of Ireland. *J. Mar. Biol. Ass. U. K.*, 70: 371-380.

- Kiøborne, T., Moglenberg, F., and Nohr, O. 1980. Feeding, particle selection and carbon absorption in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. *Ophelia*, 19(2): 193-205.
- Kiøborne, T., Mohlenberg, F. and Nøhr, O., 1981. Effect of suspended bottom material on growth and energetics in *Mytilus edulis*. *Mar. Biol.* 61:283-288.
- Kiøborne, T. and Mohlenberg, F., 1981. Particle selection in suspension - feeding bivalves. *Mar. Ecol. Prog. Ser.*, 5: 291-296.
- Kiseleva, G.A., 1966. Factors stimulating larval metamorphosis of the lamellibranch *Brachodontes lineatus* (Gmelin). *Zoologicheskii Zhurnal*, 45: 1571-1573.
- Koehn, R.K., 1991. The genetics and taxonomy of species in the genus *Mytilus*. *Aquaculture*, 94(2/3): 125-145.
- Koehn, R.K., Milkman, R. and Mittin, J.B., 1976. Population genetics of marine pelecypods. IV. Selection, migration and genetic differentiation in the blue mussel *Mytilus edulis*. *Evolution*, 30: 2-32.
- Koehn, R.K. and Gaffney, P.M., 1984. Genetic heterozygosity and growth rate in *Mytilus edulis* L. *Mar. Biol.*, 82: 1-7.
- Koehn, R.K., Hall, J.G., Innes, D.J. and Zera, A.J., 1984. Genetic differentiation of *Mytilus edulis* L. in eastern North America. *Mar. Biol.*, 79: 117-126.
- Koehn, R.K. and Bayne, B.L., 1989. Towards a physiological and genetical understanding of the energetics of the stress response. *Biol. J. Lim. Soc.*, 37: 157-171.
- Korringa, P., 1952. Epidemiological observations on the mussel parasite *Mytilicola intestinalis* Steuer, carried out in the Netherlands, 1951. *An. Biol., Copenh.*, 8: 182-185.
- Korringa, P., 1976. *Farming Marine Organisms Low in the Food Chain*. Elsevier Scientific Pub. Comp., Amsterdam. 264 pp.
- Korringa, P., 1979. Economic aspects of mussel farming. In: *Advances in Aquaculture*, T.V.R. Pillay and W.M.A. Dill (Eds.). Fishing News Books Ltd., England. pp. 371-379.
- Lane, D.J.W., Beaumont, A.R. and Hunter, J.R., 1985. Byssus drifting and the drifting threads of the young post-larval mussel *Mytilus edulis*. *Mar. Biol.*, 84: 301-308.
- Langdon, C.J., and Newell, R.I.E., 1990. Utilization of detritus and bacteria as food sources by two bivalve suspension-feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa*. *Mar. Ecol. Prog. Ser.*, 58: 299-310.
- Larsson, A.M., 1985. Blue mussel sea farming-effects on water quality. *Vatten*, 41: 218-224.
- Lassen, H.H. and F.J. Turano, 1978. Clinal variation in heterozygote deficit at the *Lap*-locus in *Mytilus edulis*. *Mar. Biol.* 49: 245-254.

- Lauckner, G., 1983. Disease of mollusca: bivalves. O. Kinne (Ed.), Disease of Marine Animals. Vol. II. Hamburg, West Germany: Biologische Anstalt Helgoland. pp. 477-962.
- Lawrence, D.R. and Scott, G.I., 1982. The determination and use of condition index of oysters. *Estuaries*, 5: 23-27.
- Le Gall, P. 1970. Etude des moulières Normandes: renouvellement, croissance. *Vie et milieu (ser B)*, 21: 545-590.
- Lewis, J.R. and Seed, R., 1969. Morphological variations in *Mytilus* from southwest England in relation to the occurrence of *M. galloprovincialis* Lamarck. *Can. Biol. Mar.* 10: 231-253.
- Loo, L.O. and Rosenberg, R., 1983. *Mytilus edulis* culture: growth and production in Western Sweden. *Aquaculture*, 35: 137-150.
- Loosanoff, V.L. and Engle, J.B., 1943. Growth, increase in weight, and mortality of mussels, *M. edulis* Linn., living at different depth levels. *Anat. Rec.* 87(4):27.
- Lowe, D.M., Moore, M.N. and Bayne, B.L., 1982. Aspects of gametogenesis in the marine mussels *Mytilus edulis* L. *J. Mar. Biol. Ass. U.K.*, 62: 133-145.
- Lubinsky, I., 1958. Studies on *Mytilus edulis* L. of the "Calanus" expeditions to Hudson Bay and Ungava Bay. *Can. J. Zool.* 36: 869-881.
- Lucas, A. and Beninger, P.G., 1985. The use of physiological condition indices in marine bivalve aquaculture. *Aquaculture*, 44: 187-200.
- Lucas, M. I., Newell, R.J., Shumway, S.E. Seiderer, L.J. and Bally, R., 1987. Particle clearance and yield in relation to bacterioplankton and suspended particle availability in estuarine and open coast populations of the mussel *Mytilus edulis*. *Mar. Ecol. Prog. Ser.* 36: 215-224.
- Lutz, R.A.(Ed.), 1980. *Mussel Culture and Harvest: A North American Perspective*. Elsevier Scientific Pub. Comp., Amsterdam. 350 pp.
- Lutz, R.A., 1985. Mussel aquaculture in the United States. In: J.V. Hunter and E.E. Brown (Eds), *Crustacean and Mollusk Aquaculture in the United States*. AVI Publishers, Westport, Connecticut, pp. 311-363.
- Lutz, R.A., Incze, L.S., Porter, B. and Stotz. 1980. Seasonal variation in condition of raft cultivated mussels (*Mytilus edulis* L.). *Proc. World. Mar. Soc.*, 11 : 262-268.
- Lutz, R.A., Chalermwat, K., Figureas, A., Gustafson, R.G. and Newell, C., 1991. Mussel aquaculture in marine and estuarine environments throughout the world. In: Menzel, W. (Ed), *Culture of Estuarine and Marine Bivalve Mollusks in Temperature and Tropical Regions*. CRC Press, Inc. Boca Raton, Florida, pp. 57-97.
- Maclean, J.L., 1972. Mussel culture: methods and prospects. *Aust. Fish. Pap.*, No, 20, 13pp.

- Mallet, A.L., Zouros, E., Gartner-Kepkay, K.E., Freeman, K.R. and Dickie, L.M., 1985. Larval viability and heterozygote deficiency in populations of marine bivalves: evidence from pair matings. *Mar. Biol.* 87: 165-172.
- Mallet, A.L., Freeman, K.R., and Dickie, L.M., 1986. The genetics of production characters in the blue mussel *Mytilus edulis*. I. A preliminary analysis. *Aquaculture*, 57: 133-140.
- Mallet, A.L., Carver, C.E.A., Coffen, S.S. and Freeman, K.R., 1987a. Winter growth of the blue mussel *Mytilus edulis* L.: Importance of stock and site. *J. Exp. Mar. Biol. Ecol.*, 108: 217-228.
- Mallet, A.L., Carver, C.E.A., Coffen, S.S., and Freeman, K.R., 1987b. Mortality variations in natural populations of the blue mussel, *Mytilus edulis*. L. *Can. J. Fish. Aquat. Sci.* 44: 1589-1594.
- Mallet, A.L. and Carver, C.E.A., 1989. Growth, mortality, and secondary production in natural populations of the blue mussel, *Mytilus edulis* L. *Can. J. Aquat. Sci.*, 46: 1154-1159.
- Manahan, D.T., Wright, S.J. and Stephens, G.C., 1983. Simultaneous determination of net uptake of 16 amino acids by a marine bivalve. *Am. J. Physiol.*, 244: 832-838.
- Mandelli, E.F. and Acuna, A.C., 1975. The culture of the mussel, *Perna perna* and the mangrove oyster, *Crassostrea rhizophorae*, in Venezuela. *Mar. Fish. Rev.*, 37: 15-18.
- Mann, R., 1978. A comparison of morphometric, biochemical and physiological indexes of condition in marine bivalve molluscs. In: *Energy and Environmental Stress in Aquatic Systems*. J.H. Thorp and J.W. Gibbons (Eds) D.O.E. Symposium Series (Conf. 771114) 854pp.
- Marshall, S.M., 1947. An experiment in marine fish cultivation: III. The plankton of a fertilized loch. *Proc. Roy. Soc. Edinb.*, B, 63: 21-33.
- Marshall, S.M. and Orr, A.P., 1927. The relation of the plankton to some chemical and physical factors in the Clyde Sea Area. *J. Mar. Biol. Ass. U.K.*, 14:837-868.
- Marshall, S.M. and Orr, A.P., 1930. A study of the spring diatom increase in Loch Striven, *J. Mar. Biol. Ass. U.K.*, 16: 853-878.
- Mason, J., 1969. Mussel raft trials succeed in Scotland. *World Fishing*, 18(4): 22-24.
- Mason, J., 1972a . The cultivation of the European mussel, *Mytilus edulis* L.. *Oceanogr. Mar. Biol. Ann. Rev.*, 10: 437-460.
- Mason, J., 1972b. Molluscs culture in Scotland. *World Fish.*, 21(9): 42-44.
- Mason J., 1976. Cultivation. In: *Marine Mussels; their ecology and physiology*, B.L. Bayne (Ed.). IBP 10. Cambridge University Press. pp. 385-410.

- Mason, J., 1991. Production of mussels. In: Production of Aquatic Animals; Crustaceans, Molluscs, Amphibians and Reptiles, C.E. Nash (Ed). ElsevierSci. Pub. pp. 121-138.
- Mason, J. and Drinkwater, J., 1981. Experiments on suspended cultivation on mussels in Scotland. Scot. Fish. Inf., Pamphlet, 4. DAFS, Aberdeen. 15 pp.
- Masumoto, B., Masumoto, M. and Hibino, M., 1934. The biochemical studies of magaki (*Ostrea gigas* Thunberg). II: The seasonal variation in the biochemical composition of *Ostrea gigas* Thunberg. J. Sci. Hir. Univ. Ser. A, 4: 47-56.
- McDonald, J.H. and Koehn, R.K., 1988. The mussels *Mytilus galloprovincialis* and *M. trossulus* on the Pacific coast of North America. Mar. Biol., 99: 111-118.
- McDonald, J.H., Koehn, R.K., Balakirev, E.S., Manchenko, G.P., Pudovkin, A.I., Sergiyevskii, S.O. and Krutovskii, K.V., 1990. Species identity of the "common mussel" inhabiting the Asiatic coasts of the Pacific Ocean. Biol. Morya, 1: 13-22.
- McDonald, J.H., Seed, R. and Koehn, R.K., 1991. Allozyme and morphometric characters of three species of *Mytilus* in the Northern and Southern hemispheres. Mar. Biol., 111: 323-335.
- McDougal, K.D., 1943. Sessile marine invertebrates of Beaufort, North Carolina. Ecol. Monog., 13:321-74.
- McLeod, D., 1994. Innovation and novelty to the fore. Scot. Fish Farm. No:70
- McLeod, D., 1995. Classification gradings announced. Scot. Fish Farm. No:77.
- Meire, P.M. and Eryvynck, A., 1986. Are oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*) Anim. Behav., 34: 1427-1435.
- Menge, B.A., 1972. Competition for food between two intertidal starfish species and its effect on body size and feeding. Ecology, 53: 635-644.
- Meredith-Young, J.L., 1983. World beating technology in Sounds. Catch (N.Z. Minist. Agric. Fish.) 10: 17-18.
- Milne, P.H., 1972a. Hydrography of Scottish West Coast Sea Lochs. Mar. Res., 3.
- Milne, P.H., 1972b. Fish and shellfish Farming in Coastal Waters. Fishing News Books Ltd. England. 208pp
- Milne, P.H. 1979. Fish and Shellfish Farming in Coastal Waters. Fishing News Books, Farnham, UK. 208 pp.
- Milroy, J. A., 1909. Seasonal variations in the quantity of glycogen present in samples of oysters. Sci. Invest., Lond., Ser. 2:17: 6.
- Mohlenberg, F. and Riisgård, H.U., 1979. Efficiency of particle retention in 13 species of suspension feeding bivalves. Ophelia, 17: 239-246.
- Moore, H. F. 1908. Volumetric studies of the food and feeding of oysters. Bull. U. S. Bur. Fish. 28: 1297-1308.
- Muise, B., 1990. Mussel culture in Eastern Canada. Wor. Aqua., 21 (2): 12-23.

- Muniz, E.C., Jacob, S.A. and Helm, M.M., 1986. Condition index, meat yield and biochemical composition of *Crassostrea brasiliiana* and *Crassostrea gigas* growth in Cabo Frio, Brazil. *Aquaculture*, 59: 235-50.
- Murdock, E.A., Ferguson, A. and Seed, R., 1975. Geographical variation in leucine aminopeptidase in *Mytilus edulis* L. from the Irish Coasts. *J. Exp. Mar. Biol. Ecol.*, 19:33-41.
- Murray, W.H., 1978. The Island of Western Scotland: The Inner and Outer Hebrides. Eyre Methuen Ltd. 328 pp.
- Nagabhushanam, R. and Mane, V. H., 1991. Mussels in India. In: W. Menzel (Ed), *Estuarine and Marine Bivalve Mollusc Culture*. CRC Press, Boca Raton, Florida, pp. 191-120.
- Nair, N.B., 1962. Ecology of marine fouling and wood-boring organisms of Western Norway. *Sarsia*, 8: 1-88.
- Navarrete, S.A. and Castilla, J.C., 1990. Barnacle walls as mediators of intertidal mussel recruitment: effects of patch size on the utilization of space. *Mar. Ecol. Prog. Ser.*, 68: 113-119.
- Nei, M., 1972. Genetic distance between populations. *Am. Nat.*, 106: 283-292.
- Newell, R.I.E., Hilbish, T.J., Koehn, R.K. and Newell, C.J. 1982. Temporal variation in the reproductive cycle of *Mytilus edulis* from localities on the east coast of the United States. *Biol. Bull.* 162: 299-310.
- Newell, C.R., Shumway, S.E., Cucci, T.L. and Selvin, R., 1989. The effects of natural seston particle size and type on feeding rates, feeding selectivity and food resource availability for the mussel *Mytilus edulis* Linnaeus, 1758 at bottom culture sites in Maine. *J. Shell. Res.*, 8: 187-196.
- Nixon, S.W., Oviatt, C.A., Rogers, C. and Taylor, K., 1971. Mass and metabolism of a mussel bed. *Oecologia* 8: 21-30.
- O'Neil, S.M. Sutterlin, A.M. and Agget, D., 1983. The effect of size-selective feeding by starfish (*Asterias vulgaris*) on the production of mussels, *Mytilus edulis* cultured on nets. *Aquaculture*, 35: 211-220.
- Officer, C.B., Smayda, T.J., and Manu, R., 1982. Benthic filter feeding: a natural eutrophication control. *Mar. Ecol. Prog. Ser.* 9: 203-210.
- Okumus, I., 1993. Evaluation of suspended mussel (*Mytilus edulis* L.) culture and integrated experimental mariculture (Salmon-Mussel) trials in Scottish sea lochs. PhD thesis, University of Stirling. 336pp.
- Okumus, I. and Stirling, H.P., 1994. Physiological energetics of cultivated mussel (*Mytilus edulis*) populations in two Scottish west coast sea lochs. *Mar. Biol.* 119: 125-131.
- Page, H.M. and Hubbard, D.M., 1987. Temporal spatial patterns of growth in mussels *Mytilus edulis* on an offshore platform: relationships to water temperature and food availability. *J. Exp. Mar. Biol. Ecol.*, 111: 159-179.

- Page, H.M. and Richard, Y.O., 1990. Food availability as a limiting factor to mussel *Mytilus edulis* growth in California coastal waters. *Fish. Bull.*, 88(4): 667-686.
- Paine, R.T., 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, 15: 93-120.
- Paul, M.D., 1942. Studies on the growth and breeding of certain sedentary organisms in Madras Harbour. *Proceedings of the Ind. Acad. Sci., Sect. B.*, 15: 1-42.
- Paul, J.D., 1987. Losses of seed mussels from spatting ropes following their transfer between sites. 1985-1986. Sea Fish Industry Authority Tech. Rep., 290. 14 pp.
- Pavlovic, V., Kekic, H. and Mladenovic, O. 1970. Glycogen in hepatopancreas and in muscles in *Ostrea edulis* L. and in *Mytilus galloprovincialis* Lmk. in the season summer-winter. *Bulletin scientifique. Cons. Acad.*, 15: 76-7.
- Pérez-Camacho, A., 1987. El cultivo del mejillón (*Mytilus edulis*) ostra (*Ostrea edulis*) en España. In: J.A.J. Verreth, M. Carrillo, S. Zanuy, and E.A. Huisman (Eds), *Investigación Acuicola en America Latina*. Pudoc, Wageningen, pp. 243-260.
- Pérez-Camacho, A., González, R. and Fuentes, J., 1991. Mussel culture in Galicia (N.W. Spain). *Aquaculture*, 94: 263-278.
- Petersen, J.H., 1984a. Establishment of mussel bed: attachment behaviour and distribution of recently settled mussels (*Mytilus edulis*) Veliger, 27: 7-13.
- Petersen, J.H., 1984b. Larval settlement behaviour in competing species: *Mytilus californianus* Conrad and *M. edulis* L. *J. Exp. Mar. Biol. Ecol.*, 82: 147-159.
- Peterson, C.H. and Beal, B.F., 1989. Bivalve growth and higher order interactions importance of density, size and time. *Ecology*, 70: 1390-1404.
- Petratis, P.S., 1978. Distributional patterns in juvenile *Mytilus edulis* and *Mytilus californianus*. *Veliger*, 21: 288-292.
- Pieters, H., Kluytmans, H.J., Zurbung, W. and Zandee, D.I., 1979. The influence of seasonal changes on energy metabolism in *Mytilus edulis* L., I. Growth rate and biochemical composition in relation to environmental parameters and spawning. In: 13th European Marine Biology Symposium: Cyclic Phenomena in Marine Plants and Animals. Naylor, E. and Hartnoll, R. G., (Ed.) Pergamon Press, New York, pp. 285-292.
- Pieters, H., Kluytmans, H.J., Zandee, D.I. and Gadee, G.C., 1980. Tissue composition and reproduction of *Mytilus edulis* in relation food availability. *Neth. J. Sea Res.*, 14: 349-361.
- Pieters, H., Kluytmans, H.J., Zandee, D.I., and G.C. Gadee, 1980. Tissue composition and reproduction of *Mytilus edulis* in relation food availability. *Neth. J. Sea Res.*, 14 : 349-361.
- Price, R.J., 1983. Scotland's environment during the last 30,000 years. Scottish Academic Press, 224 pp.

- Pridmore, R.D., Roper, D.S. and Hewitt, J.E., 1990. Variation in composition and condition of the Pacific oyster, *Crassostrea gigas*, along a population gradient in Manukau Harbour, New Zealand, Mar. Environ. Res., 30: 163-177.
- Quayle, D.B., 1964. Distribution of introduced marine molluscs in British Columbia. J. Fish. Res. Bd. Can., 21: 1155-1181.
- Quayle, D.B., 1969. Pacific oyster culture in British Columbia. Can. Bull. Fish. Res., 169:1-192.
- Quayle, D.B. and Newkirk, G.F., 1989. Farming Bivalve Molluscs: Methods for Study and Development. The World Aquaculture Society and The International Development Research Centre, 294 pp.
- Raffaelli, D., Falcy, V. and Galbraith, C., 1990. Eider predation and dynamics of mussel bed communities. In: M. Barnes and R.N. Gibson (Ed), Trophic Relationship in the Marine Environment. Aberdeen University Press, Aberdeen, pp. 157-169.
- Rajan, S.J., 1980. Experiments on submerged rafts for open sea mussel culture. In: K.N. Nayar, K. Mahadevan, K. Alagarswami, and P.T. Meenakshisundaram (Eds), Coastal Aquaculture: Mussel Farming, Progress and Prospects. Bull. Cent. Mar. Fish. Res. Inst., India, 29: 46-51.
- Rajas, A.V. and Ruiz, J.B., 1972. Variación estacional del engorde del ostión *Crassostrea rhizophorae*, de Bahía de Mochima Laguna Grande, Bol. Inst. Oceanog. Univ. Orienta., 11: 39-43.
- Remane, A. and Schlieper, C., 1971. Biology of Brackish Water. New York: Wiley-Interscience, 372p.
- Richards, O.W., 1928. The growth of the mussel *Mytilus californianus*. Nautilus, 41: 99-101.
- Riisgård, H.U., 1991. Filtration rate and growth in the blue mussel, *Mytilus edulis* Linnaeus, 1758: dependence on algal concentration. J. Shell. Res., 10(1): 29-35.
- Riisgård, H.U., Randlov, A. and Kristensen, P.S., 1980. Rates of water processing, oxygen consumption and efficiency of particle retention in veligers and young post- metamorphic *Mytilus edulis*. Ophelia, 19: 37-47.
- Riley, G.A., 1970. Particulate and organic matter in seawater. Adv. Mar. Biol., 8:1-118.
- Roantree, V., 1986. Plastic drums and tractor tyres. Aquacult. Ir., 24: 8-9.
- Rodhouse, P.G., Roden, C.M., Burnel, G.M., Hensey, M.P., McMahon, T., Ottway, B. and Ryan, T.H. 1984a. Food resource, gametogenesis and growth of *Mytilus edulis* on the shore and in suspended culture in Killary Harbour, Ireland. J. Mar. Biol. Ass. U.K., 64: 513-530.
- Rodhouse, P.G., Roden, C.M and Ryan, T.H., 1984b. Resource allocation in *Mytilus edulis* on the shore and in suspended culture. Mar. Biol., 84: 27-34.

- Rodhouse, P.G., Roden, C.M., Hensey, M.P. and Ryan, T.H., 1985. Production of mussels, *Mytilus edulis*, in suspended culture and estimates of carbon and nitrogen flow: Killary Harbour, Ireland. J. Mar. Biol. Ass. U.K. 65: 55-68.
- Rodhouse, P.G., McDonald, J.H., Newell, R.I.E. and Koehn, R.K., 1986. Gamete production, somatic growth and multiple-locus heterozygosity in *Mytilus edulis*. Mar. Biol., 90: 209-214.
- Rodhouse, P.G. and Roden, C.M., 1987. Carbon budget for a coastal inlet in relation to intensive cultivation of suspension-feeding bivalve molluscs. Mar. Ecol. Prog. Ser., 36: 225-236.
- Roper, D.S., Pridmore, R.D., Cummings, V.J. and Hewitt, J.E., 1991. Pollution related differences in the condition cycles of Pacific oysters *Crassostrea gigas* from Manukau Harbour, New Zealand. Mar. Environ. Res., 31: 197-214.
- Rosell, N.C., 1991. The green mussel (*Perna viridis*) in the Philippines. In: W. Menzel (Ed), Estuarine and Marine Bivalve Mollusk Culture. CRC Press, Boca Raton, Florida, pp. 298-305.
- Rosenberg, R. and Loo, L.O., 1983. Energy-flow in a *Mytilus edulis* L. culture in Western Sweden. Aquaculture, 35: 151-161.
- Ruiz, C., Abad, M., Sedano, F., Garcia-Martin, L.O. and Sánchez López, J.L., 1992. Influence of seasonal environmental changes on the gamete production and biochemical composition of *Crassostrea gigas* (Thunberg) in suspended culture in El Grove, Galicia, Spain. J. Exp. Mar. Biol. Ecol., 155: 249-262.
- Sadykhova, I.A., 1970. On the allometry of growth of *Crenomytilus grayanus* (Dunker) from the Gulf of Peter the Great. *Trudy molodykh uchenykh VNIRO*, 3, 108-115.
- Safae, M. S. 1992 Production estimate of a mussel population *Perna picta* (Born) on the atlantic coast of Morocco. J. Exp. Mar. Biol. Ecol., 163: 183-197.
- Sarver, S.K. and Foltz, D.W., 1993. Genetic population structure of a species complex of blue mussels (*Mytilus* spp.). Mar. Biol., 117: 105-112.
- Sastry, A.N., 1968. Relation among food, temperature and gonad development of the bay scallop, *Aegapeecten irradians* Lamarck, Physiol. Zool., 41: 44-53.
- Sastry, A.N., 1979. Metabolic adaptations of *Cancer irroratus* development stages to cyclic temperatures. Mar. Biol., 51: 243-250.
- Savage, R. E. 1925. The food of the oyster. Min. Agric. Fish., Fish. Invest., Ser. 2. 7: 1.
- Savilov, I.A., 1953. The growth and variations in growth of the White Sea invertebrates *Mytilus edulis*, *Mya arenaria* and *Balanus balanoides*. *Trudy Instituta Okeanologii. Akademiya nauk SSSR, Moskow*, 7: 198-259.
- Schlieper, C., 1971. Physiology of brackish water. In: Biology of Brackish Water. A. Remane and C. Schlieper (Eds). Wiley-Interscience, New York. pp. 211-350.

- SOAFD (Scottish Office Agriculture and Fisheries Department), 1993. Report of the SOAFD shellfish farms.
- SOAFD (Scottish Office Agriculture and Fisheries Department), 1994. Report of the SOAFD shellfish farms.
- SOAFD (Scottish Office Agriculture and Fisheries Department), 1995. Report of the SOAFD shellfish farms.
- Seed, R., 1968. Factor influencing shell shape in the mussel, *Mytilus edulis*. J. Mar. Biol. Ass. UK. 48: 561-584.
- Seed, R., 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. 2. Growth and mortality. Eocologia, 3: 317-50.
- Seed, R., 1971. A physiological and biochemical approach to the taxonomy of *Mytilus edulis* L. and *M. galloprovincialis* (Lmk.) from S.W. England. Cah. Biol. Mar., 12: 291-322.
- Seed, R., 1972. Morphological variations in *Mytilus* from French coasts in relation to the occurrence and distribution of *Mytilus galloprovincialis* (Lmk.). Cah. Biol. Mar., 13:357-384.
- Seed, R., 1973. Absolute and allometric growth in the mussel, *Mytilus edulis* L., (Mollusca: Bivalvia). Proc. Malac. Soc. Lond., 40: 343-357.
- Seed, R., 1974. Morphological variations in *Mytilus* from the Irish coasts in relation to the occurrence and distribution of *M. galloprovincialis* Lmk. Cah. Biol. Mar., 15: 1-25.
- Seed, R., 1975. Reproduction in *Mytilus* (Mollusca: Bivalve) in European waters. Pub. Stazz. Zool. Nap., 39: 317-334.
- Seed, R., 1976. Ecology. In: Marine mussels; their ecology and physiology, B.L. Bayne(Ed). IBP 10. Cambridge University Press, Cambridge. pp. 13-65.
- Seed, R., 1978. The systematics and evolution of *Mytilus galloprovincialis* (Lmk.) In: B. Battaglia and J.A. Beardmore (Eds), Marine Organisms: Genetics, Ecology and Evolution. Plenum Press, London, pp. 447-468.
- Seed, R., 1980. Shell growth and form in the bivalvia. In: Skeletal Growth of Aquatic Organisms; Biological Records of Environmental Change, D.C. Rhoads and R.A. Luzz (Eds.). Plenum Press. pp. 23-676.
- Seed, R., 1992. Systematic evolution and distribution of mussels belonging to the genus *Mytilus*: an overview. Am. Mar. Bull., 9(2): 123-137.
- Seed, R. and Suchanek, T.H., 1992. Population and community ecology of *Mytilus*. In: E. M. Gosling (Ed).The mussel *Mytilus*: ecology, physiology, genetic and culture. Elsevier Sci. Pub., Amsterdam, Netherland. pp. 87-169.
- Siebers, D. and Winkler, A., 1984. Amino acid uptake by mussels, *Mytilus edulis*, from natural seawater in a flow-through system.. Wiss. Meers., 38: 189-199.
- Sivalingam, P.M., 1977. Aquaculture of the green mussel, *Mytilus viridis* L. in Malaysia. Aquaculture, 11: 297-312.

- Skibinski, D.O.F, Ahmad M. and Beardmore J.A., 1978. Genetic evidence for naturally occurring hybrids between *Mytilus edulis* and *Mytilus galloprovincialis*. *Evolution*, 32: 354-364.
- Skibinski, D.O.F. and Beardmore, J.A., 1979. A genetic study of intergradation between *Mytilus edulis* and *M. galloprovincialis*. *Experientia*, 35: 1442-1444.
- Skibinski, D.O.F., Beardmore, J.A. and Cross, T.F., 1983. Aspects of the population genetics of *Mytilus* (*Mytilidae*: Molluscs) in the British Isles. *Biol. J. Lim. Soc.*, 19: 137-183.
- Skidmore, D. and Chew, K.K., 1985. Mussel Aquaculture in Puget Sound. Washington Sea Grant, Technical Report. University of Washington, Seattle. 57 pp.
- Small, A.C. and van Stralen, M.R., 1990. Average annual growth and condition of mussels as a function of food source. *Hydrobiologia*, 195: 179-188.
- Small, A.C., Verhagen, J.H.G., Cosen, J. and Hass, H.A., 1986. Interaction between seston quantity and quality and benthic suspension feeders in the *Oosterschelde*, The Netherlands. *Ophelia*, 26: 385-399.
- Solórzano, L., 1977. Chemical investigations of Loch Etive, Scotland. III. Particulate organic carbon and particulate organic nitrogen. *J. Exp. Mar Biol. Ecol.*, 29: 81-89.
- Solórzano, L. and Grantham, B., 1975. Surface nutrients, chlorophyll *a* and phaeopigment in some Scottish sea lochs. *J. Exp. Mar. Biol. Ecol.*, 20: 63-76.
- Solórzano, L. and Ehrlich, B., 1977. Chemical investigations of Loch Etive, Scotland. I. Inorganic nutrients and pigments. *J. Exp. Mar. Biol. Ecol.*, 29: 45-64.
- Solórzano, L. and Ehrlich, B., 1979. Chemical investigations of Loch Crean, Scotland. I. Inorganic nutrients, dissolved organic compounds and pigments. *J. Exp. Mar. Biol. Ecol.*, 40: 1-25.
- Soot-Ryen, T., 1955. A report on the family *Mytilidae* (Pelecypoda). *Allan Hancock Pasif. Exped.*, 20: 1-175.
- Sprung, M., 1984. Physiological energetics of mussel larvae (*Mytilus edulis*). I. Shell growth and biomass. *Mar. Ecol. Prog. Ser.* 17: 283-293.
- Stirling, H.P., 1985. Chemical and Biological Methods of Water Analyses for Aquaculturist. Institute of Aquaculture, University of Stirling. 119 pp.
- Stirling, H.P. and Okumus, I., 1994. Growth, mortality and shell morphology of cultivated mussel (*Mytilus edulis*) stock cross-planted between two Scottish sea lochs. *Mar. Bil.*, 119: 115-123.
- Stirling, H.P. and Okumus, I., 1995. Growth and mortality of mussels (*Mytilus edulis* L.) suspended at salmon cages and shellfish farms in two Scottish sea lochs. *Aquaculture*, 134: 193-210.
- Strathmann, M.F., 1987. Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast. University of Washington Press, Seattle, 670 pp.

- Strickland, J.D.H. and Parsons, T.R., 1972. A Practical Handbook of Seawater Analysis. Fish. Res. Brd., Can. Bull., 167. 310pp.
- Stromgren, T., 1976a. Growth patterns of *Mytilus edulis* in relation to variation, light conditions, feeding and starvation. Sarsia, 60: 25-40.
- Stromgren, T., 1976b. Length growth of *Mytilus edulis* (Bivalvia) in relation to photoperiod, irradiance and spectral distribution of light. Sarsia, 61: 31-40.
- Suchanek, T.H. 1978. The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. J. Exp. Mar. Biol. Ecol. 31: 105-120.
- Suchanek, T.H., 1981. The role of disturbance in the evolution of life history strategies in the intertidal mussels *Mytilus edulis* and *Mytilus californianus*. Oecologia, 50: 143-152.
- Suchanek, T.H., 1985. Mussels and their role in structuring rocky shore communities. In: P.G. Moore and R. Seed (Eds), Ecology of Rocky Coasts. Hodder and Stoughton, Sevenoaks, Kent, pp.70-96.
- Sukhotin, A.A. and Kulakowski, E.E., 1992. Growth and population dynamics in mussels (*Mytilus edulis* L.) cultured in the White Sea. Aquaculture, 101: 59-73.
- Sukhotin, A.A. and Maximovich, N.V., 1994. Variability of growth rate in *Mytilus edulis* L. from the Chupa Inlet (the White Sea). J. Exp. Mar. Biol. Ecol. 176:15-26.
- Sutterlin, A., Aggett, D., Couturier, C., Scaplen, R. and Idler, D., 1981. Mussel Culture in Newfoundland Waters. Mar. Sci. Res. Lab. Tech. Rep., 23. Newfoundland, 82 pp.
- Taylor, B.E., Jamieson, G. and Garefoot, T.H., 1992. Mussel culture in British Columbia: the influence of salmon farms on growth of *Mytilus edulis*. Aquaculture., 108: 51-56.
- Tedengren, M., Andre, C., Johannesson, K. and Kautsky, N., 1990. Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplantations. III. Physiol. Mar. Ecol. Prog. Ser., 59: 221-227.
- Tenore, K.R. and Gonzalez, N., 1976. Food chain patterns in the Ria de Arosa, Spain; an area of intense mussel aquaculture. In: Proceedings of the 10th European Symposium on Marine Biology, Vol. 2: population Dynamics; G. Persoone and E. Jaspers (Eds.). Universa Press, Wetteren. pp. 601-619.
- Tett, P. and Wallis, A., 1978. The general annual cycle of chlorophyll standing crop in Loch Crean. J. Ecol., 66: 227-239.
- Theede, H., 1963. Experimentelle Untersuchungen über die Filtrationsleistung der Miesmuschel *Mytilus edulis* L. Kieler Meeresforsch. 19: 20-41.
- Thiesen, B.F. 1968. Growth and mortality of culture mussels in the Danish Wadden Sea. Medd. Danm. Fisk. Hav., 6:47-78.
- Theisen, B.F., 1978. Allozyme clines and evidence of strong selection in three loci in *Mytilus edulis* L. (Bivalvia) from Danish water. Ophelia 17: 135-142.

- Theisen, B.F., 1982. Variation in size of gills, labial palps and adductor muscle in *Mytilus edulis* L. (Bivalvia) from Danish waters. *Ophelia*, 21: 49-63.
- Theisen, B.F., 1987. *Mytilicola intestinalis* Steuer and the condition of its host *Mytilus edulis* L. *Ophelia*, 27: 77-86.
- Thompson, R.J. and Bayne, B.L., 1974. Some relationship between growth, metabolism and food in the mussel, *Mytilus edulis* L.. *Mar. Biol.*, 27: 317-326.
- Thompson, R.J., 1984a. Production, reproductive effort, reproductive value and reproductive cost in a population of blue mussel, *Mytilus edulis* from a subarctic environment. *Mar. Biol. Prog. Ser.*, 16: 249-257.
- Thompson, R.J., 1984b. The reproductive cycle and physiological ecology of the mussel *Mytilus edulis* in a subarctic non-estuarine environment. *Mar. Biol.*, 79: 277-288.
- Thompson, J.K. and F.J. Nickols, 1988. Food availability controls seasonal cycle of growth in *Macoma baltica* (L.) in San Francisco Bay, California. *J. Exp. Mar. Biol. Ecol.*, 116: 43-61.
- Valera, G., 1981. Mussel possibilities in human nutrition. In: Food the from sea (Mahrung aus dem meer). International Symp. Bremerhaven (FGR) 8-9 Oct. 1980. Noel, H. (Ed) pp. 60-76.
- Varvio, S.L., Koehn, R.K. and Vainola, R., 1988. Evolutionary genetics of the *Mytilus edulis* complex in the North Atlantic region. *Mar. Biol.*, 98: 51-60.
- Verduin, A., 1979. Conchological evidence for the separate specific identity of *Mytilus edulis* L. and *M. galloprovincialis* Lamark. *Basteria*, 43: 61-80.
- Wallace, J.C., 1980. Growth rates of different populations of the edible mussel, *Mytilus edulis* L., in North Norway. *Aquaculture*, 19: 303-311.
- Wallace, J.C. and Reinsnes, T.G., 1985. The significance of various environmental parameters for growth of the Iceland scallop, *Chlamys islandica* (Pectinidae), in hanging culture. *Aquaculture*, 44: 229-242.
- Wallis, R.L., 1975. Thermal tolerance of *Mytilus edulis* of eastern Australia. *Mar. Biol.*, 30: 183-191.
- Walne, P.R., 1970. The seasonal variation of meat and glycogen content of seven populations of oysters, *Ostrea edulis* L. and a review of the literature. *Fish. Inves.*, London., Ser. 2, 26: 3
- Walne, P.R., 1972. The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. *J. Mar. Biol. Ass. U.K.* 52: 345-374.
- Walne, P.R. and Dean, G.D., 1972. Experiments on predation by the shore crab *Carcinus maenas* L. on *Mytilus* and *Mercenaria*. *J. Cons.*, 34: 190-199.
- Walne, P.R. and R. Mann., 1975. Growth and Biochemical Composition in *Ostrea edulis* and *Crassostrea gigas*. In Proceedings of the Ninth European Marine Biology Symposium, H. Barnes (Ed), pp. 587-607.

- Whyte, J.N.C. and Englar, J.R. 1982. Seasonal variation in the chemical composition and condition indices of Pacific oyster, *Crassostrea gigas*, grown in trays or on the sea bed. *Can. J. Fish. Aquat. Sci.* 39: 1084-94.
- Widdows, J. and Bayne, B.L., 1971. Temperature accumulation of *Mytilus edulis* with reference to its energy budget. *J. Mar. Biol. Ass. U.K.*, 51: 827-843.
- Widdows, J., 1978a. Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis* L. *J. Mar. Biol. Ass. U.K.*, 58: 109-124.
- Widdows, J., 1978b. Physiological indices of stress in *Mytilus edulis* L. *J. Mar. Biol. Ass. U.K.*, 58: 125-142.
- Widdows, J., 1985. Physiological procedures. In: B.L. Bayne, D.A., Brown, K. Burns, D.R. Dixon, A. Ivanovici, D.R. Livingstone, D.M. Lowe, M.N. Moore, A.R.D. Stebbing and J. Widdows (Eds), *The Effects of Stress and Pollution on Marine Animals*. Praeger Press, New York, pp. 161-178.
- Widdows, J., Fieth, P. and Worrall, C.M., 1979. Relationship between seston, available food and feeding activity in the common mussel *Mytilus edulis*. *Mar. Biol.*, 50: 195-207.
- Widdows, J., Donkin, P., Salkeld, P.N., Cleary, J.J., Lowe, D.M., Evans, S.V. and Thompson, P.E., 1984. Relative importance of environmental factors determining physiological differences between two populations of mussels (*Mytilus edulis*). *Mar. Ecol. Ser.*, 17: 33-47.
- Wilbur, K.M. and Saleuddin, A.S.M., 1983. Shell formation. In: *The mollusca*, Vol 4; *Physiology Part 1*, Saleuddin, A.S.M. and Wilbur, K.M. (Eds). Academic Press. pp. 235-287.
- Wildish, D.J. and Kristmanson, D.D., 1984. Importance to mussels of the benthic boundary layer. *Can. J. Fish. Aquat. Sci.*, 41: 1618-1625.
- Wildish, D.J. and Kristmanson, D.D., 1985. Control of suspension feeding bivalve production by current speed. *Helgolander wiss. Meeresunters.* 39: 237-243.
- Wilkins, N.P., Fujino, K. and Gosling, E.M., 1983. The Mediterranean mussel *Mytilus galloprovincialis* Lmk. in Japan. *Biol. J. Linn. Soc.*, 20: 365-374.
- Williams, C.S., 1969. The effect of *Mytiloca intestinalis* on the biochemical composition of mussels. *J. Mar. Biol. Ass. U.K.*, 49: 161-173.
- Wilson, J.H., 1987. Environmental parameters controlling growth of *Ostrea edulis* L. and *Pecten maximus* L. in suspended culture. *Aquaculture*, 64: 119-131.
- Winter, J.E., 1978. A review on the knowledge of suspension- feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture*, 13: 1-33.
- Winter, J.E. and Langton, R.W., 1976. Feeding experiments with *Mytilus edulis* L. at small laboratory scale. I. The influence of the total amount of food ingested and food concentration on growth. In: *Proceeding of 10th European*

- Symposium on Marine Biology, 1; G. Persoone and E. Jaspers (Eds).
Universa Press, Wetteren. pp. 565-581.
- Wood, B.J., Tett, P.B. and Edwards, A., 1973. An introduction to the phytoplankton, primary production and relevant hydrography of Loch Etive. *Journal of Ecology*, 61: 569-585.
- Wright, R.T., Coffin, R.B., Persing, C. and Pearson, D., 1982. Field and laboratory measurements of bivalve filtration of natural marine bacterio-plankton. *Limnol. Oceanogr.* 27: 91-98.
- Yamada, S.B., 1989. *Mytilus californianus*, a new aquaculture species. *Aquaculture*, 81: 275-284.
- Yonge, C.M., 1976. The " mussel" form and habit. In: B.L. Bayne (Ed), *Marine Mussels: their ecology and physiology*. Cambridge University Press, Cambridge, pp. 1-12.
- Zandee, D.I., Kluytmans, J.H. and Zurburg, W., 1980. Seasonal variations in biochemical composition of *Mytilus edulis* with reference to energy metabolism and gametogenesis. *Nether. J. Sea Res.* 14:1-29.
- Zar, J.H., 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ. 718 pp.
- Zhang, F.S., 1984. Mussel culture in China. *Aquaculture*, 39: 1-10.
- Zwaan, A. D., and Zandee, D.I., 1972. Body distribution and seasonal changes in the glycogen content of the common sea mussel *Mytilus edulis*. *Comp. Biochem. Physiol.*, 43: 53-58.

ABBREVIATIONS

a	: intercept
A	: Ash
AFDMW	: Ash-free dry meat weight
AFDSOW	: Ash- free dry shell organic weight
AFDSW	: Ash- free dry shell weight
AFDW	: Ash-free dry weight
Aug	: August
b	: Slope
°C	: Degree centigrade
C	: Carbohydrate
CI	: Condition index
CID	: Dry meat weight condition index
Ch-a	: Chlorophyll-a
CIV	: Wet meat volume condition index
D	: Depth
DMW	: Dry meat weight
DSW	: Dry shell weight
EB	: Eliminated biomass
EC	: European community
Fig	: Figure
g	: Gramme
h	: hour
H	: Shell height
Jan	: January
ind	: Individual
Kcal	: Kilocalorie
kg	: Kilogram
l	: Litre
L	: Length of mussel

Li	: Lipid
LE	: Loch Etive
LE-LK	: Mussels transferred from Loch Etive to Loch Kishorn.
LK	: Loch Kishorn
LK-LE	: Mussels transferred from Loch Kishorn to Loch Etive
LW	: Live weight
m	: Metre
M	: Moisture
mA	: milliamper
Max.	: Maximum
Min.	: Minimum
mm	: Millimetre
mo	: Month
mt	: Metric ton
MY	: Meat yield
N	: sample size
nm	: nano metre
ns	: Not significant
µg	: Microgramme
P	: Protein
PN	: Particle number
POM	: Particulate organic matter
POM %	: Percentage of particulate organic matter
Pos	: Position
Pr	: Production
r	: Correlation coefficient
rpm	: Round per minute
s	: Second
S	: Salinity
SD	:Standard deviation

SE	: Standard error
SEC	: Secchi depth
Sep	: September
SES	: Seston
SGR	: Specific Growth Rate
SOADF	: Scottish Office Agriculture and Fisheries Department
SW	: Shell weight
T	: Temperature
Tr	: Transparency
U.K	: United Kingdom
U.S.A	: United States of America
V	: Flow rate
W	: Shell width
WMW	: Wet meat weight

APPENDIX : 1

Loci used for staining were as follows:

1) GPI : Glucose phosphate isomerase (5.3.1.9)

MgCl₂ . 6H₂O.....5 mg
NADP.....5 mg
Fructose 6 phosphate....20 mg
Glucose 6 phosphaaate DH.....10 µl
MTT.....1 µl
PMS.....1 µl
Agar.....25 ml
Buffer (pH=8).....25 ml

2)PGM : Phosphoglucomutasse (2.7.5.1)

MgCl₂ . 6H₂O.....5 mg
NADP.....5 mg
Glucose 1 phosphate.....50 mg
Glucose 6 phosphaaate DH.....10 µl
MTT.....1 µl
PMS.....1 µl
Agar.....25 ml
Buffer (pH=8).....25 ml

APPENDIX : 2

Buffer (for 2.5 liter)

Tris.....30.25 g

EDTA.....29.0 g

Boric acid.....7.30 g

MgCl₂ . 6H₂O.....5.08 g

Dissolved in distilled water to make volume 2500 ml adjusted pH=8

The buffer for electrode was undiluted, but for the gel a dilution of 1 : 10 with distilled water was used.

Fixing solution used for fixing starch gels

Ethil alcohol.....4 units

Distille water.....1 unit

Acetic acid.....5 units