EVALUATION OF SUSPENDED MUSSEL (*Mytilus edulis L.*) CULTURE AND INTEGRATED EXPERIMENTAL MARICULTURE WITH SALMON IN SCOTTISH SEA LOCHS

A Thesis Presented for the Degree of "DOCTOR OF PHILOSOPHY" to University of Stirling

by

İBRAHİM OKUMUŞ

BSc & MSc (Agriculture; Animal Husbandry)

Institute of Aquaculture

University of Stirling

Stirling, Scotland \ U.K.

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DEDICATION

TO MY FATHER AND MOTHER

TO MY BROTHERS, WIFE AND SISTERS

TO MY DAUGHTERS GÜLŞAH AND BİLGEN

FOR THEIR ENDLESS LOVE AND SUPPORT

A B S T R A C T

Growth, mortality, production, physiology and seasonal cycles of condition index and proximate biochemical composition of experimental populations of blue mussels (*Mytilus edulis* L.) were studied at different sites in Loch Etive and Loch Leven on the West coast of Scotland between May 1990 and September 1992. The main objective of the study was to evaluate current suspended mussel culture practices and to establish the basis for their possible integrated cultivation with salmon cage farming. In addition, a preliminary investigation on employment of the 'Charm II' system as a rapid method for detecting residues of drugs used for treating cultured salmon in the tissues of mussels was carried out.

There were some differences between sites in salinity, seston and particulate organic matter, but not in chlorophyll-a. Food availability (as particulate organic matter and chlorophyll-a) showed a clear seasonal cycle and in consequence growth of mussels were relatively rapid from late-spring until mid-autumn (ca 6 months) and very slow or absent during the rest of the year. This period of rapid length and tissue growth coincided with relatively optimum environmental conditions and there were apparent positive relationships between monthly growth rates and temperature and chlorophyll-a values, indicating the limiting effect of these two primary factors on growth during autumn-winter and even in early spring.

Almost all growth parameters examined were showed significant differences between the lochs. Growth performance of both native and transplanted mussels in Loch Leven was quite poor. Overall annual length increments were 25.1-25.9 mm at sites in Loch Etive and Dunstaffnage Bay, but 20.1-22.8 mm in Loch Leven. A cross-transplantation experiment showed that site rather than stock is the main reason for differences in growth parameters between Lochs Etive and Leven. These observed growth differences between sites and stocks were also confirmed by physiological measurements and estimated growth potential or scope for growth.

Growth of mussels at salmon farms was faster than at neighbouring mussel farms during two annual experiments, but only meat weight at one salmon farm during experiment I, and length and live weight at the salmon farm in Loch Etive as well as

all growth parameters at the salmon farm in Loch Leven during experiment II were significantly greater (P≤0.05). These differences were most likely a result of high particulate organic matter levels at salmon farms.

Similar to growth, biomass and production, the condition index and biochemical composition of mussels showed a clear seasonal cycle. Meat content, condition index and glycogen values were high during summer, started to decline in late autumn and reached minimum values in April before showing maximum increases in May. This reflects the typical storage and reproductive cycle of mussels in Northern Europe: accumulation of reserves during summer and their utilization during winter and early spring as energy resources for metabolism and reproduction. This cycle clearly showed that the main spawning of mussels on the West coast of Scotland occurred during March-May, and primary spat settlement from June to August.

Heavy losses occurred from French socks, causing substantial amounts of eliminated biomass during experiment I, but when these fall outs were eliminated during experiment II by using lantern nets, it was clear that natural mortality rates were quite low and similar at all sites.

Apart from growth characteristics and physiological responses, there were persistent morphological differences between the Loch Etive and Loch Leven populations. Cross-transplantation and physiological measurements after various acclimatization periods showed that, while morphological differences might be related to genetic origin, all other differences between the two populations are governed by environmental factors.

The practical implications of these findings for developing suspended mussel culture on the West coast of Scotland and the possibility of a simple integrated salmon-mussel farming system, which could be effective in controlling potential eutrophication from intensive salmon cage farming and the removing large amounts of organic matter by mussels leading alterations in ecosystem, are discussed.

A preliminary study with the Charm II Test has showed that the system is not so appropriate method as expected for screening mussel tissue sampled straight from the field, since mussel tissues require purification due to interference from bacteria or microbial detritus, before screening.

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1. INTRODUCTION

1.1. General Background

With a dramatic expansion of production over the past decade "aquaculture", i.e. the cultivation of aquatic organisms, has become a world-wide major industry. Not only has the number of freshwater and marine finfish species successfully farmed increased, but there have also been rapid developments and expansion in the farming of finfish and shellfish species in the marine and estuarine environments of the many countries, as in the case of the Atlantic salmon (*Salmo salar*) and blue mussel (*Mytilus edulis*) culture in Scotland. The Atlantic salmon have been cultured commercially since 1970s and mussels since 1980s, and the main development area of mariculture of these species has been the Scottish Northwest Coast and offlying Islands, one of the least developed areas of the United Kingdom. Despite the slow growth and its present small scale structure, shellfish farming is becoming a well established industry in Scotland and there might be a great potential for further expansion. Unfortunately, so far, this industry could not use this potential largely due to small-scale ownership and lack of corporate investment (cf. salmon companies) - despite the entrance of large companies,e.g. Kishorn Shellfish, in general, difficulties in marketing image and distribution infrastructure have held back investors.

There is no doubt that both industries make appropriate use of natural resources and have created job opportunities and casting a vital economic lifeline to many rural communities throughout the Highland and Islands of Western Scotland. On the other hand, as a result of such rapid expansion and development, questions are being asked about the possible ecological impact of mariculture, especially salmon farming, on the coastal marine ecosystem which in some areas has become a risk factor to the

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industry itself (Rosenthal *et al.*,1988). Unlike intensive salmon farming, mussel culture represents a more or less self-regulated extensive system that is integrated with the natural marine ecosystem (Folke & Kautsky, 1989) and which might even be integrated with salmon farming and offer a unique opportunity to reduce probability of eutrophication (Officer *et al.*,1982; Larsson,1985), and increased production (Wallace,1980).

The main objective of this study is two fold: a) to evaluate suspended mussel culture in the West coast of Scotland, b) to investigate the growth of mussels in the immediate vicinity of salmon cages.

1.2. Biology and Life Cycle of Common Mussel

The section following describes the generalised biological and physiological characteristics of blue, common or European mussels (*Mytilus edulis* L.) because the effective management of the cultivated animals mainly depends on an understanding of the optimal conditions for their reproduction and growth, especially their food requirements and feeding mechanism, reproduction and the physiological ecology of larvae and adults. More detailed information can be found in Field (1922), Seed (1976), Barnes (1987) and Dardignac-Corbeil (1990).

While phytoplankton may be the principal component of the diet of mussels, like other filter feeders (Rodhouse *et al.*,1984b; Smaal & van Stralen,1990), however, it has been suggested that some bivalves can exploit non-phytoplanktonic carbon to meet their energy requirements (e.g. West *et al.*,1977; Dare, 1980; Héral, 1987; Lucas *et al.*,1987; Langdon & Newell,1990) and dissolved organic substances can provide up

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to half of the energy necessary for their metabolism (Héral,1987). The gills ensure the supply of food by filtering the water. They are well equipped to create a current of water (lateral cilia), to collect (eu-latero-frontal cirri) and to transport (frontal cilia) food (Winter,1978). According to Figueras (1989) an individual mussel can filter between 50-120 l of water per day. There are two gills, each made up of two rows of filaments and groups of cilia join each filament to its neighbour. The current enters between the mantle lobes, crosses the gills, and passes through the shell cavity, leaving through the exhalant siphon. The frontal cilia are covered in a layer of sticky mucus and particles are retained by adhering to the cilia.

The particles retained by the gills are conveyed via the labial palps towards the mouth where they are all ingested when the particle concentration is low, but excess particles are rejected as 'pseudofaeces' by the labial palps (Thompsom & Bayne, 1974; Widdows, 1978a&b). There is some disagreement as to whether mussels are able to select living particles such as phytoplankton. The absorption of dissolved organic substances mainly takes place at the gills before ingestion, but also through the stomach and middle intestine (Héral, 1987).

In terms of reproduction, sexual maturity might be reached at an age of 6 months to one year, depending on the latitude (Dare, 1980; Figueras, 1989, 1990). The sexes are separate, and usually distinguishable by the colour of the mantle flesh as spawning approaches; males are white to pale yellow, females a pale orange. The gonad, which is made up of a mass of follicles, extends throughout the mantle. The only factor appearing to affect gonad development and the time and length of the spawning period is temperature (Dardignac-Corbeil, 1990). In northern Europe the main

spawning takes place in spring, e.g. April - May in England and Wales (Dare, 1980), and March-April in Scotland (Mason, 1991; this study). Simplified development stages and life cycle of *M. edulis* are schematised in Fig.1. When the mussels are mature, gametes are released into the external environment and fertilization takes place. Each female *M. edulis* can lay up to 8 million eggs (Bayne *et al.*, 1978) with a mean diameter of 70 µm (Widdows, 1991). 4-5 h (at 18°C) after fertilization, cilia appear and the trochophore stage is reached within 2 days. The early life history is quite complex. The larva soon develops a fully formed shell of the 'veliger' stage which lasts approximately 1 to 4 weeks; when the larva reaches approximately 150 µm in length, first the umbo, later at around 210 µm the foot and the 'eyes', appear (Lutz *et al.*,1991). Larvae at this stage of development are called 'pediveligers' and are ready to metamorphose into a young mussel or spat; however, in the absence of suitable settling substrate, the larvae can delay metamorphosis for up to 6 weeks (Bayne, 1976). Upon contact with a suitable substratum, preferably filamentous materials such as spat collectors, the pediveligers attach themselves onto the substratum by a means of byssal threads, but young mussels detach and reattach elsewhere several times. Permanent settlement occurs within a month of first settlement and a sessile life-style begins (Bayne, 1964). This final settlement stage and onwards is of main interest to mussel aquaculture, because a basic requirement of all mussel culture practices is secure supply of spats and that is why big culture operations around the world have been located in areas traditionally as where natural seed mussels are readily available every year (Mason, 1976).
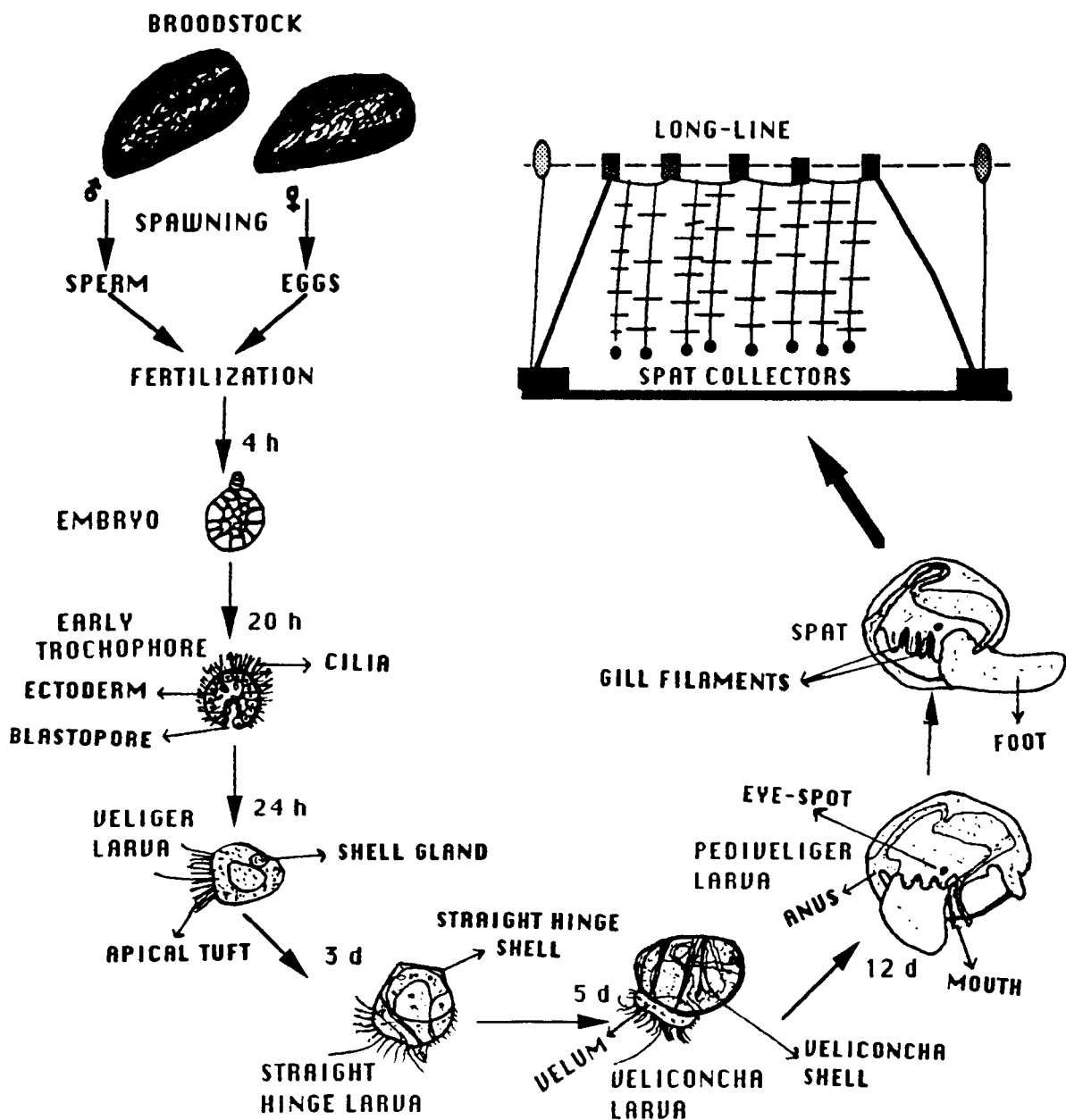
Fig.1. Schematised development stages and life cycle of blue mussels from wild broodstock to spats ready for settlement on spat collectors (From Field,1922; Bayne,1976; Sutterlin *et al.*,1981).

1.3. General Features of Mussel Culture

In 1990 world marine aquaculture produced 3.96 (excluding seaweeds) million tonnes corresponding to around 33% of the total aquaculture production and the cultivated mollusc production was 2.96 million tonnes, mainly from oysters (30%), mussels (37%), clams (17%) and scallops (11%) (FAO,1992). As these figures indicate mussels and oysters, which are possibly the first marine species to be cultivated, are the main cultivated bivalve species. Although there is increasing interest and activity in mussel culture, both in Asia and North America, the main centre of mussel culture and consumption has been western Europe which accounts for over half the world's production, with Spain, Denmark, Holland, Italy, France, Germany and Ireland the main producers. Among the Asian countries, China, Thailand and Korea are the leading producers, while in America, Chile, Canada and the USA are principal producers. During the last 6 years production increased steadily from 0.7 million tonnes in 1984 to 1.08 million tonnes in 1990 corresponding to a 55% increment, while during the same period oyster production was almost constant; 0.86 in 1984 and 0.88 million tonnes in 1991 (FAO,1992). There are about 10 species of cultured mussel, but the common or blue mussel and the Mediterranean mussel (*M. galloprovincialis* Lmk.) comprise 66% of world production (Nash, 1991).

The success of mussel, and the other bivalve mollusc as well, culture is mainly due to the advantages given by a combination of specific features of their biology and ecology which are of strategic significance for expanding mariculture in coastal waters and estuaries. In particular, the following features have played a major role in the expansion of mussel and other bivalve molluscan culture in various countries:

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- The larvae for culture are mainly derived from natural reproduction with settlement of the spat on collectors.

- Bivalve molluscs are secondary producers, consuming natural phytoplankton and detrital food at a low level of the trophic chain which is very efficient in energetic terms (Mason & Drinkwater,1981; Héral *et al.*,1990; Mason,1991). In this way, a lot of unutilized organic substances are consumed by mussels and converted to animal protein or mineralized very quickly and returned via nutrient cycles to the marine ecosystem.

- There are several constraints associated with utilisation of natural mussel beds that limits their commercial exploitation. Wild mussels allocate less resources to somatic growth and more to maintenance requirements than cultured mussels (Rodhouse *et al.*,1984a) due to factors such as overcrowding, excessive exposure to air or strong wave action and very silty water. Hence they grow slowly and tend to have poor meat quality. Cultured mussels, on the other hand, are one of the few animals that produce a superior product over those grown naturally and have a significant higher market value. These mussels exhibit more rapid growth under cultivation, hence a marketable size is reached at an age of 1.5-2.5 years, and the yield and quality of meat are much better than traditionally exploited natural shore mussels (Mason, 1972a; Lutz,1980). The terms "cultured, farmed or cultivated" improves the poor image of the shellfish in some conservative communities both in developed and underdeveloped countries, and makes it possible to market them as a cheap valuable animal protein resource.

- There are no reported catastrophic mass mortalities of mussels caused by

parasites and diseases, in contrast to oyster culture in Europe.

- The introduction of rearing systems like the long-line which is simple in design, easy to install, of low capital cost and aesthetically more acceptable for the public than a large raft. As a typical example of extensive aquaculture, shellfish farming is a small-scale business with low capital costs, so it can be undertaken by families with limited financial resources, whether in the first or third worlds. This applies especially to mussel farming.

Mussel culture, on the other hand, could be limited by several factors. For example, European mussel production has fluctuated at around 400,000 t over the last ten years and the possibilities for extension of mussel cultivation in leading countries (namely Spain, France and the Netherlands) are very limited, although there seems to be a large economic potential. Because mussel culture is an extensive aquatic production system in which farmers raise naturally settled or collected seeds to marketable size without feeding the animals, the whole culture system completely depends on the carrying capacity of the ecosystem, and the production increase requires enlargement of the cultivation areas, which may be very difficult to find in traditional producer countries. Sewage discharges, eutrophication and industrial pollution cause problems with pathogens, toxic algal blooms and pollutants. In addition there is high competition for coastal areas between fish farmers, fishermen, recreation tourism industry and more recently environmental groups. The extension of cultivation to the open sea or less sensitive off-shore sites requires new technological developments, such as flexible rafts or submersible long-lines, which may not be economical for the shellfish farming industry at present.

On the other hand, increasing demand and development of general aquaculture stimulated the industry in other countries which have suitable areas for shellfish culture. The huge expansion of mussel production in recent years, therefore, was probably due to development of the existing industry in some Asian countries, such as China, Korea and Thailand, and appearance of the industry in new countries, such USA, Chile, Ireland, Canada, Scotland and Sweden.

Mussels have been cultured in France since 13th and in the Netherlands since the 18th centuries, but in Spain only since 1946. These pioneering countries developed their own extensive cultivation techniques in accordance with quite specific environmental conditions of their coastal regions. Thus one method might more successful in a particular region than the others, but all these techniques rely on either the ability of mussels to attach to the spat collectors with the byssus or the gathering of spats settled elsewhere. Today these techniques are well documented (e.g. Mason,1972a, 1976, 1991; Korringa, 1976; Lutz, 1980; Dijkema & van Stralen, 1989; Figueras, 1989, 1990; Quayle & Newkirk, 1989; Dardignac-Corbeil, 1990; Lutz *et al*.,1991) and consist of three basic forms, with some local modifications in different areas. These are:

a) Bouchot or Pole (intertidal) culture (Atlantic Coast of France, Thailand and Philippines),

b) Bottom (sub- and intertidal) culture (The Netherlands, Denmark, Germany, England and Wales)

c) Suspended (subtidal) culture:

-Raft (Spain, China, Chile, USA, New Zealand, Scotland);

-Long-line (New Zealand, China, Korea, Italy, Ireland, Sweden, Scotland)

-Rack (Italy, Yugoslavia, France).

The main principles of these techniques have basically not changed much in the last decade (since the reviews of Mason,1972,1976; Korringa,1976) except possibly the development of the long-line system, construction of strong and larger rafts and introduction of mechanization to facilitate the handling of seed mussel strings and crop harvesting with transport to depuration and processing plants. These few recent developments have led to the establishment of modified mussel culture systems which are biotechnically and economically suited to diverse environmental conditions of the many countries from North Canada to China and New Zealand.

The *bouchot* method uses a series of wooden stakes driven into the sea bed around the low tide mark. Mussel spat is collected naturally either on those poles which are sited furthest offshore (spat bouchot) or along horizontally suspended hairy ropes and then transplanted onto poles nearer the shore (rearing bouchot) for grow out. Naturally settled spat take around 15 months to reach market size of 40-50 mm. Apart from being well known on the Atlantic coast of France, bouchot culture, usually in the form of long bamboo poles, is carried out in Thailand for green mussel cultivation (Chalermwat & Lutz,1989; Quayle & Newkirk, 1989).

Bottom culture of mussels mainly takes place in the North Sea area of Northwestern Europe and is mainly a subtidal operation. The best known example has been the culture practice in the Dutch Wadden Sea. The spats are collected from areas where survival and growth are poor and relaid on specially prepared growing plots. After spending 18 to 24 months on growing plots the mussels are harvested at a size

of around 70 mm. Recently, dam construction and dike heightening in Holland has had both positive and negative effects on bottom cultivation of mussel in recent years (Dijkema & van Stralen, 1989), and during 1990-1991 the Dutch mussel industry suffered a serious shortage caused by combination of severe gales, poor spatfalls and large eider duck stocks (Edwards, 1992).

The suspended mussel culture technique first developed by using rafts as a floating platform in Galicia, Spain, and expanded rapidly to other countries (see for example Figueras,1989,1990; Lutz *et al.*,1991; Mason, 1991), sometimes using different installations, such as long-lines or racks . The main principles of cultivation using one of these installation are exactly the same.

The best example of suspended mussel culture has been practised in Galicia, Spain since the late 1940's. The main source of seed in Galicia is naturally settled spats on rocks, representing 60-70% of that used for mussel farming. The remainder are collected on ropes hung from rafts. The Rias of Galicia, the deep, sunken river valleys, are very productive, and mussels reach marketable size (80-90 mm) in 12-18 months (Figueras, 1989, 1990). According to Pérez Camacho *et al.* (1991) the production per ha/year is around 33-48 tonnes/raft or 130 kg/m^2 or 14.5kg/m of rope. In the Galicia region, over a area of 3000 ha, nearly 200 000 tonnes of mussels are produced yearly (Figueras, 1989, 1990).

The geomorphology and topography of the Aiguillon (Atlantic coast) area of France, the rias of Galicia, Spain and the Dutch Wadden Sea are quite different, and this certainly had a major influence on the culture techniques that have developed. Therefore, one of the techniques can be more successful under specific environmental

and socio-economic conditions than the other and <u>vice versa</u>.

The most recent development in mussel culture has been the use of long-line systems for suspending culture ropes. This method had evolved in Japan for suspended oyster culture and was probably first used in New Zealand for mussel cultivation, but today it is used in Ireland, Canada, China, Sweden, USA and Scotland. The long-lines are low in capital cost, simple to design and aesthetically more acceptable for suspended mussel culture (Jenkins, 1979). This system has also been shown to better withstand the rigors of waves and currents than rafts and is therefore a very good candidate for open sea mariculture.

1.4. Mariculture in Scotland

The west coast of Scotland and many of the Islands are very suitable for development of shellfish and also salmon farming due to the presence of many long sea lochs, inlets and islands which offer shelter, depth and often some local heating during summer. The North Atlantic drift keeps water temperatures higher than in other areas of similar latitude, particularly during the winter. The water is almost free from all pollution and main parasites and diseases of shellfish (Drinkwater, 1987).

Aquaculture in Scotland is currently dominated by salmon and trout farming, but shellfish culture, mainly mussels and oysters, has also developed significantly. The experiments both for salmon and shellfish farming were started in 1960s. During 1970s the salmon farming industry overcame the main problems, such as cage design, nutrition, reproduction and diseases, with involvement of big companies, such as Unilever (Marine Harvest), and started to expand rapidly from the late 1970s onwards

(Institute of Aquaculture,1989). In spite of successful experimental results (Mason, 1969), development of shellfish farming was slower than salmon and there was no rapid expansion until the beginning of 1980s.

The development of both the salmon and shellfish farming industries has been welcomed and very substantially supported by public funds through the former Highlands and Islands Development Board (HIDB, now renamed Highland Enterprise,HE), which has played a significant role in the development of the industry, on the basis of its contribution to the economic and social welfare of remote parts of Scotland (Gowen *et al.*,1988; SWCL,1990).

1.4.1. Salmon Culture

The salmon cultured in Scotland is the Atlantic salmon (*Salmo salar*), which is an anadromous fish which spawns and offspring develops in freshwater before migrating to the sea to feed. The culture process is almost a carbon copy of the natural life-cycle and therefore salmon farming takes place in two different environments.

Broodstock fish are kept in sea cages and moved to freshwater and held there until spawning, in Scotland in November. The incubation period is approximately 520 degree days and the hatching takes place in January or February. The young fish are grown in tanks, raceways and freshwater cages until they are ready to go sea (smoltification). The smoltification starts 16-18 months after hatching and these fish (called S1) are transferred to sea cages. The rest of the young stock stays in freshwater for another year (S2). The smolts grow faster in sea water than freshwater. After 1 to 1.5 years some of them sexually mature at a weight of around 2 kg (grilse)

and are harvested, but most of the stock requires two years in sea cages to reach a marketable size which is around 2-5 kg (Institute of Aquaculture,1989).

In Scotland the main system employed for salmon farming is cage culture. Although there is a wide variety of cage designs, the main features are very similar; incorporating a floating collar, suspended net bag and a mooring system. The type and capacity of cages varies among farms and sites. The simplest and oldest type cages are the rectangular wooden cages with average dimension of 7x7 m with a 5 m deep and stocking capacity of approximately 5 tonnes at a density of 20 kg m^{-3}. These small cages are usually moored in rafts of up to 16 individual units arranged as a two-across rectangle. One farm may operate several rafts, spaced at least 100 m apart, at one site. The competitive use of the limited well sheltered sites has led to development of more robust new cages such as the Viking, High-Seas and Farmocean. The capacity of these cages vary from 15 t to 200 t. Although some of these cages are quite successful in moderately exposed sites (Institute of Aquaculture,1989), the vast majority of salmon farms are located in very sheltered and often shallow areas of sea lochs with very limited water movement (SWCL,1988). In all the cages, the feeding is generally automatic and dry pellets is given several times per day. Although in theory the feed conversion ratio in salmon farming is around 1.5:1, in practice it can be over 2:1 as the main aim of most salmon farmers is rapid growth rather than optimum utilization feed by fish and minimising wastage. Since high fish densities are maintained in such a small space, chemical treatment as well as vitamin supplements in feed are often necessary in salmon farming.

Salmon production in Scotland increased dramatically during the last 10 years.

This trend looks likely to continue as the production is increasing every year. According to the Scottish Office Agriculture & Fisheries Department (SOAFD) 1991 survey results, the industry produced 40,000 tonnes of salmon, worth approximately £120 million which is 94% of the total output value of Scottish aquaculture (salmon, trout and shellfish; Anonymous,1992a). The increase was about 25% over the year. Around 286 cage sites, with a total capacity of approximately 5.5 million m³, were in operation. Highland region is the biggest producer with 37%, followed by Shetland at 26.1%. The industry employs 1285 full-time and 351 part-time personnel, comprising 75% of total Scottish aquaculture sector employees. According to forecasts, Scottish salmon production will be static at around 40,000 tonnes until at least 1994. Table-1 summarises salmon farming statistics for 1986-1991.

Table-1. Salmon farming statistics (production, tonnes, employment and number of marine cage sites) for 1986-1991 (various source).

| YEAR | SITES | EMPLOYMENT | | PRODUCTION |
		F\T	P\T	
1986	157	527	206	10,333
1987	196	608	198	12,721
1988	244	991	329	17,951
1989	292	1102	316	28,553
1990	298	1165	326	32,350
1991	286	1285	351	40,593

1.4.2. Shellfish Culture

Main shellfish species currently cultured in Scotland are the common mussel

(*Mytilus edulis*) and the Pacific oyster (*Crassostrea gigas*). More recently cultivation

of the king scallop (*Pecten maximus*) and the queen scallop (*Chlamys opercularis*) has

commenced. Experimental trials for the Manila clam (*Ruditapes philippinarum*) are

being carried out by the Sea Fish Industry Authority and businesses, but only one

farm has started to ongrow (SOAFD,1991b).

The main statistics regarding the shellfish farming industry in Scotland comes from

annual survey of Scottish Office Agriculture and Fisheries Department (SOAFD). The

SOAFD produce an annual report on the state of the shellfish farming industry based

on the annual returns of questionnaires of all registered farms. The SOAFD (1992b)

annual report stated that by the end of 1992, the number of registered farms rose to

321, an increase of just around 4% on the previous years, but only 214 of them were

active, i.e. experimentally or commercially producing shellfish (Table-2).

Each farm may consist of one or more registered sites and so 321 registered farms

supported 498 sites, of which 311 were active. The farms range in size from very

small, involving crofters supplementing their incomes, to large commercial scale

operations. The number of active farm sites producing marketable shellfish consists

of 85% (265) of active farms; the remaining active farms held stock for ongrowing

but did not market shellfish for various reasons. The Table-2 shows the total

production by species for the years 1986-1992 as compiled by SOAFD. The data for

mussels include those bottom grown, which have subsequently been fattened in

suspended cultivation, but not dredged mussels from the Dornoch Firth (around 3,000

t in 1991).

There has been some increases in production of oysters, scallops and queens in

Table-2. Summary of shellfish farming statistics for Scotland, 1985-1992: number of farms, production for market in t and total value of production (Sources: SOAFD,1988,1990-92b; *: HIDB,1991 & Anonymous,1992a). N.A: not available, for conversion of numbers to weight the following average individual weights were used: Oysters (both species): 80g; Queens: 40g and Kings:120 g.

| YEAR | NUMBER OF FARMS | | PRODUCTION BY SPECIES | | | | | VALUE* £ |
	Registered	Active	Mussel	Pacific Oyster	Native Oyster	Queens Scallop	King Scallop	
1985	98	98	N.A	N.A	N.A	N.A	N.A	N.A
1986	144	141	260	40.6	0.08	11.3	9.0	227,869
1987	168	162	270	88.7	35.0	32.2	12.6	486,232
1988	174	169	380	126.4	1.7	16.6	7.9	600,380
1989	223	181	350	98.7	1.2	91.3	5.4	713,268
1990	290	229	460	115.3	0.08	52.4	8.2	750,000
1991	310	228	1024	184.0	10.0	61.2	38.0	1,498,937
1992	321	214	898		15.5	61.5	58.6	N.A

1992, with little increase in the number of active businesses, but production of mussels decreased by 12%. According to SOAFD, (1991b), the enormous increase in production during 1991 probably was led by some 12 large producers, followed by a general development of the industry as a whole. Cultivation and husbandry techniques have improved in what remains a developing industry, resulting in improved efficiency of operation. The other factors contributing to market development were efforts by the Association of Scottish Shellfish Growers (ASSG) and HE, the formation of cooperatives by small business to ensure a constant supply throughout the year, and a buoyant market.

The market value of the cultured Scottish shellfish industry has been estimated at around £1,498,937 (Table-2) of which £716,800 came from mussels, £690,000 oysters and £92,137 scallops (Anonymous,1992a). These figures show that the market value of farmed shellfish is still very small, compared to, for example, the £1.4 million market value of mussels dredged from the Dornoch Firth. During 1991, however, the industry has employed 87 full-time, 173 part-time and 93 casual staff, most of which go to family members.

Although the Scottish shellfish farming industry is very small at present, it has been described as the sector in Scotland which has the largest potential for growth (Anonymous, 1992a). The industry has a very short history and is still at an early stage of development. The other factors, including lack of information about "how to start a farm", unclear potential markets, lack of producer confidence, slow growth rates of the native flat oyster and king scallop, concern over introduced exotic species such as Pacific oysters or Manila clams and the small scale structure of industry itself

have played an important role in the slow growth rate. Although there are a few larger company farms, eg Salen Shellfish Scotland Ltd, Loch Fyne Oysters Ltd, Kishorn Shellfish Ltd and Scallop Kings Ltd, the shellfish farming industry in Scotland is still largely a small-scale family business whose turnover can be as little as £5,000 which would explain their large numbers. Therefore, it is unrealistic to expect the Scottish shellfish farming industry ever to become capital-intensive like the salmon farming industry, mainly because it has not been attractive to many big companies due to the relatively low level of profits (Gruer,1987 cited by Meikle & Spencer,1992). However, as producer confidence increases, market demand improves and economies of scale increase efficiency, shellfish farming could become a prime sector (Meikle & Spencer,1992).

1.4.2.1. Mussel Culture in Scotland

The mussel is one of the commonest of all marine species around the Scottish sea coasts (Drinkwater,1987). As far back as the early 19th century, mussels were collected from natural beds such as the Dornoch Firth, consumed by rural communities and used for bait (Edwards, 1992). The Dornoch Firth is the one of the Scotland's oldest exploited mussel beds. The fishing rights of these mussel beds were granted by royal charter to the small town of Tain and income from these mussels still goes to the local community fund.

In spite of the natural abundance and utilization of mussels as food around the Scotland for a long time, mussel culture in Scotland has a very short history. Mason (1969) first reported on the commercial possibilities of suspended cultivation of

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mussels in some West coast sea lochs. From these experimental rafts the first commercial mussel farm was set up in Loch Sween in the early 1970's and a new industry developed by trial and error methods to a point where it is now practised in many of the sea lochs on the West coast of Scotland. Mussel were the first shellfish species cultured commercially and today farming produces the largest amount of farmed shellfish in Scotland (Table-2). The main technique used is suspended culture by using long-lines and rafts.

Like the raft culture operations, the long-line method is based on suspended culture techniques, but unlike rafts long-lines are relatively cheap, simple and adaptable to mechanization and to wider environmental conditions. Although long-line specifications are modified according to site conditions, such as exposure, current and freshwater run-off, their general features do not change. As Fig.2 displays, the long-line culture system itself consists of a series of buoyed horizontal lines; usually polypropylene and called head ropes or headlines. The head ropes are attached to a number, depending on the kind of floats used and growth cycle, of plastic air-filled floats and securely anchored at each end using large concrete blocks or other suitable anchoring system. For, example, in a typical Scottish West coast sea loch a 1.5 tonne concrete block anchor can support a long-line system with a 150 m long double head-line. The type of flotation used varies from farm to farm, but most of the farmers are using 25 l black plastic oil drums (Plate-2), which are very cheap and easily available locally. The length of the long-lines varies between 100-200 m. During the growth period more and more floats are added to head ropes to compensate for the increasing weight of the growing mussels. The head ropes may be on the surface or suspended

TOP VIEW

├──────── 100-200m ────────┤

PLASTIC FLOATS (25 l oil drums)

SIDE VIEW   HEAD ROPES (∅ 20mm)   FLOATS

3-4 cm

PEGS (20cm)

4-8m

3-5cm   3-5cm   3-5cm

SPAT COLLECTORS   ROPES WITH MUSSELS   RE-TUBED MUSSELS

MOORING CHAIN

CONCRETE BLOCK (1-2t)
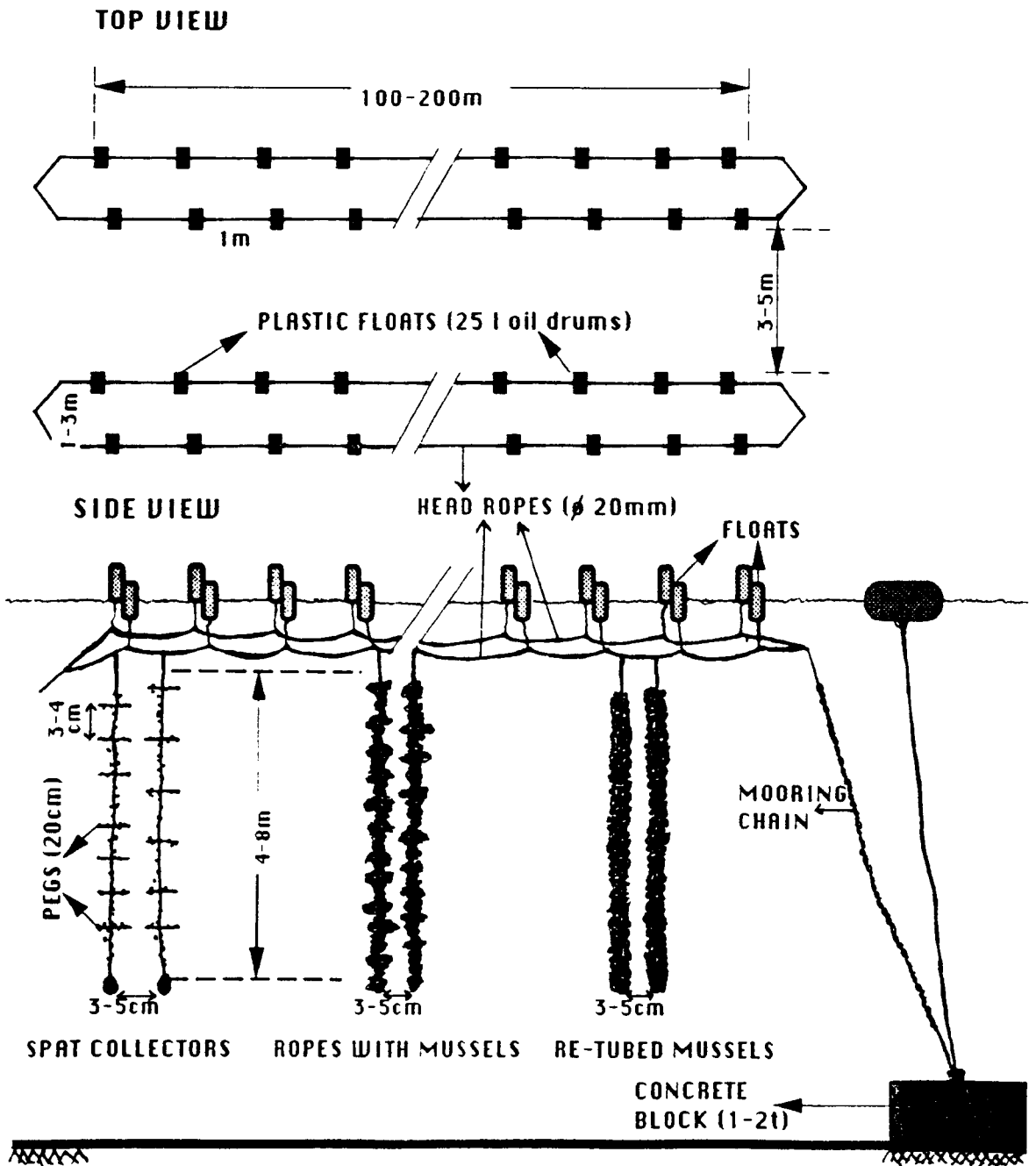
Fig.2. Schematic diagram depicting the configuration, with top and side views, of double long-line unit - a relatively primitive, but very cheap and widely used in West and Northwest coast of Scotland.

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1-3 m below it, especially in areas with excessive freshwater run-off. The distance between head ropes is around 1-3 m, but usually two head ropes are combined to create a single unit with a distance of 3-5 m between neighbouring units (Fig.2). From these head ropes are strung the vertical culture ropes or "droppers" which have a length of 4-8 m. The droppers are spaced at intervals of approximately 30-50 cm.

The main advantage of long-lines for the Scottish farmers is probably the cost. A 200 m long-line costs around £1500 and return from this, assuming a conservative harvest of 10 t per head rope, will be about £7000 to £8000 (Holmyard, 1992).Unfortunately some of these cheap long-lines might sink very easily during fast-growing summer periods and sometimes recovery may be very difficult or even impossible. Another problem with long-lines is the difficulty of protecting the stock against eider ducks since surrounding them with anti-predator net is almost impossible.

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 home- made small timber rafts (Plate-3) which are may be relatively primitive but cost effective; £2,500-5,000. These rafts are constructed from a timber frame, holding expanded polystyrene flotation blocks and timber hanging beams 0.5 m apart. Overall dimensions can vary between 6 to 12 m long and 4 to 8 m wide and the number of beams from 10 to 20. These rafts can carry about 100-200 droppers of about 6 m long. Only the largest mussel farm, Kishorn Shellfish in Loch Kishorn, is using large Spanish rafts. The company started with two rafts of 80 tonnes capacity and subsequently increased this number to six. The rafts, measuring 27 x 20 m, have

Plate-2. A long-line mussel farm (Glencoe Shellfish) in Loch Leven, also used as experimental site during the present study.

Plate-3. Home-made timber mussel rafts used by Loch Etive Farmed Shellfish in Loch Etive. This farm was one of the major experimental sites during present study.

durable eucalyptus frames and cross-members. This dense timber is buoyed by four large steel flotation drums per raft. Each raft can carry up to 850 ropes of 15m. These rafts are quite expensive: costs £50,000 each for an annual expected return of £60,000 (Holmyard,1992), and more importantly their durability and capacity under the Scottish West coast conditions are not tried and tested.

A new type of raft, the Muckairn mussel raft, has been designed by two mussel farmers using galvanised steel, timber and rotationally moulded plastic floats filled with closed- cell foam, and successfully tested in Loch Etive (Anonymous,1992; Holmyard,1992). Ten 11 m long wooden beams, 0.5 m apart, provide space for minimum of 200 culture ropes. Floatation capacity for mussels is over 20 tonnes and eight heavy duty mooring points ensure that the structure remains in place. A fleet of five fully equipped and moored rafts, with 100 tonnes total carrying capacity costs around £25,000 for a return of £75,000 (Holmyard,1992).

There are new projects working on developing submersible raft and long line systems which might help protect farms from storms, ducks (Holmyard,1992) and clear the way for open sea mussel farming.

The collectors and/or culture ropes are suspended from head ropes and beams at intervals of about 30-50 cm. During the preparation of collectors, a short piece of wood or purpose-built plastic "peg", about 20 cm long, is inserted horizontally at intervals of about every 30-40 cm between the strands of each rope to prevent the mussels from sliding down the ropes and to increase the surface area for spat settlement and mussel clumps during ongrowing (Fig.2). The collectors are hung out at least one month before the main spatfall. This enables them to receive a coating of

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small algae and hydroids on which the spats can settle more easily. The time of settlement varies somewhat from loch to loch and between years in the same loch. Although in some lochs there might be autumn spawning and settlement, the main spawning takes place around April when the water reaches a temperature of around 8-10°C and the main settlement usually occurs in June-July. Major source of seed is natural settlement of spat onto collectors. There is usually no shortage of spat settlement, but from year to year and place to place, the various phases of the reproductive cycle show degrees of variation which are normally due to variations in the natural environment. For this reason some farmers have more than one site and in case of spatfall shortage on one site they transfer spat from other side. Alternatively, naturally settled semi-grown juvenile mussels are gathered from where they have attached to the nets and floats of salmon cages or dredged from natural beds such as the Dornoch Firth and stocked into nylon mesh tubings, for growing or fattening. Mussels migrate out through the mesh and attach to the net or each other. Bio-degradable cotton mesh or "French socks" with a synthetic core are also increasingly used (see section 3.3.2 and Plate-7); the cotton eventually rots away, leaving the mussel attached to a central rope. Under-size mussels after harvest are also usually re-tubed and left to grow for another year. In most cases after spatfall the seed are simply left to grow until they reach market size (Plate-1). In a few operations the mussels are thinned out on the rope and the removed individuals are re-tubed.

Growth of mussels in Scottish waters is relatively slow and roughly it takes approximately 2.5-3 years to reach market size of 50-60 mm from settlement. Harvesting takes place from early summer to until late winter. During harvesting

mussel ropes are raised by a means of a crane which is generally fitted on a specially designed motorised floating work platform and brought on board. The mussels are separated and cleaned by machine and packed in 1, 2 or 5 kg sacks. Those of unmarketable size are re-tubed for further on-growing. Although most small farmers market their produce locally, Scottish mussels are now available regularly in British supermarkets, e.g. Tesco, famous restaurants and larger fish markets like Billingsgate, London (Edwards, 1992).

The Scottish shellfish farming industry is dependent on its quality image, associated with clean waters free from pollution, and uses the purity image of the west coast waters as a marketing advantage. At present, a large majority of the shellfish farmers do not purify their product since according to new EC shellfish hygiene site classifications, 90% of sites have been graded class "A", 9.4% "B" and the rest "C" (Anonymous,1993). Loch Etive, which is one of the largest mussel growing areas in Scotland, has been classified "A" for nine months of the year and "B" for the three remaining months during the summer. The areas designated as class B or lower, should purify mussels before marketing.

Perhaps the most dreadful fear of shellfish farming and fishing industries is the occurrence of a toxic phytoplankton bloom. Until recently the West and Northwest coasts of Scotland appeared to be free from such problems which may have been due to lack of a monitoring programme, and the first toxic bloom was recorded on the Scottish West coast in July 1990 and there was another outbreak of paralytic shellfish poisoning (PSP) in both the North West of Scotland and Orkney in 1991. The alga species responsible for the toxin in the shellfish on the West coast had not been

positively identified, but *Gonyaulux tamarensis* (Lebour) had been suspected (Anonymous,1992). Consequently, SOAFD issued a precautionary health based warning, advising against the consumption of shellfish taken from the area between Sleat on Skye and Ardnamurchan Point in 1990, and from an area stretching from Kyle of Lochalsh to Toscaig near Applecross in 1991. After the first incidence in 1990, SOAFD increased its monitoring programme significantly in scale, eg. sampling frequency doubled from fortnightly to weekly, and geographical coverage. There was no report on recurrence of the bloom in 1992. Although blooms were local, the shellfish farming industry suffered slightly as a result of the bad publicity associated with the shellfish warnings put out by SOAFD in summer 1990 and 1991. In addition the earlier (May,1990) reported major PSP incidence and following ban in Northeast England and East coast of Scotland automatically created a similar image, with little help from the media, for shellfish from all areas.

There were around 100 registered mussel farms in Scotland during 1991 and 1992, but only 38 of them produced mussels for the table and a further 10 for ongrowing, while the rest were inactive. Over 70 percent of these farms were very small family businesses and produce only around five tonnes each year in spite of static output in 1987 and 1989. Production more than doubled during 1991 as 1,024 tonnes were produced, the output of two farms being 39% of the total (Table-2), but dropped in 1992 to 879.8 tonnes due to decline in production of one of the two large farms. The Scottish mussel farming industry at present is still very small in European terms, with supplies dominated by Spain (200,000 t), France (55,000 t) and Holland (100,000 t). Production, however, is now increasing steadily and has trebled over the last five

years. Following approximately 20-25 years of experimentation, setbacks and problems, the technology or "know how" is available and, more importantly, confidence among farmers is increasing. According to Holmyard (1992) as a result of problems surrounding the salmon industry, Scottish development organisations such HE are encouraging salmon farmers to diversify into shellfish and there seems to be some response from salmon farms, for example Kishorn Shellfish is owned by a salmon producer.

Among the main bio-technical problems facing the industry are lack of expertise, losses of stock by storm damage, freshwater run-off and recent toxic blooms. Predators, mainly eider ducks and occasionally starfish, may be a problem. There are about 10,600 eider ducks in the farming area of the Scottish west coast (Institute of Aquaculture, 1989). According to Milne & Galbraith (1986, cited by SWCL,1988) losses at unprotected farms could be as high as 2.7 kg of mussels per day. Some farmers employing rafts are using predator nets against ducks, but, as mentioned above, this is nearly impossible for long-lines. Starfish, in areas with constant high salinity, occasionally settle in great quantities on the spat collectors during summer months and cause damage to juvenile mussels. The other problem is the heavy settlement of barnacles (*Balanus balanoides*) on shells in some locations, e.g. in Loch Etive, during summer months (Plate-1, page xvi).

1.4.2.2. Oysters

Most of the oyster production in Scotland comes from the Pacific oyster which was introduced from Canada and USA (Institute of Aquaculture,1989). It grows faster

than the native oyster (*Ostrea edulis*), reaching an average harvestable size of 80 g in 2-4 years, but due to low water temperatures, this species does not naturally spawn in Scottish waters, so farmers are dependent on hatchery produced seed. Currently practised ongrowing 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 rafts or long lines). The native oyster is susceptible to *Bonamia* (Protozoan) and grows very slowly, requiring five years to reach market size. The production of Pacific and native oysters in 1992 were 204.8 t million and 15.5 t respectively (Table-2).

1.4.2.3. Scallops

Although there seems to be much interest in scallop culture, only one company has been involved in scallop farming since 1975 with commercial production from 1983 (IOE,1990). The king scallop grows relatively slowly requiring 4 years to reach a size of 100 mm or 120 g, although it has been marketed after one year as a "princess scallop" at a mean size of 45 mm, while the queen scallop is marketable in 2-3 years at a size of 60-70 mm or 40 g. At present farmers rely on natural seed, which settles in monofilament mesh-filled bags. Cultivation usually takes place in lantern nets, but king scallops after reaching 45 mm may also be ongrown using ear hanging where a hole is drilled in of the ears of the scallop which is then suspended from a long-line. Trials are also being conducted by the Sea Fish Industry Authority (SFIA) to "ranch" 2 years old (60 mm) king scallop on licensed areas of sea bed where fishing is banned.

Production of king scallop for the table rose by 55% in 1992 as 24 farms sold 58.6 t (489,000 shells), of which approximately 41% came from two farms, while a total of 16 farms produced 61.5 t (1.5 million) queens (Table-2).

1.5. Ecological Implications of Salmon and Mussel Farming

In general both intensive fish and extensive shellfish farming can cause changes in marine ecosystems. These impacts of mariculture have been investigated or reviewed by several authors (e.g. Gowen & Bradbury,1987; Gowen *et al.*,1988; Rosenthal *et al.*,1988; Institute of Aquaculture,1989; Ackefors & Enell,1990; Gowen *et al.*,1990). The main potential environmental impacts of intensive aquaculture are: hypernutrification leading to eutrophication, organic enrichment of the benthos, increased biochemical oxygen demand and changes in benthic and bacterial populations.

Intensive culture of salmonids continuously generates large amounts of organic and inorganic waste (uneaten food, faeces and excretory material), and some dissolved organic material (nitrogen, carbon and phosphorus). The fate of the main components carbon, nitrogen and phosphorus in food fed to salmon in a typical cage farm is summarised in Fig.3. In general the recipient for particulate organic waste is the sediment and for dissolved waste the water column. Approximately 60-70% of the total nitrogen consumed by salmonids is excreted as soluble ammonia and urea (Gowen *et al.*,1988; Folke & Kautsky, 1989; Ackefors & Enell.,1990). In addition some ammonia is released from remineralization of organic nitrogen in uneaten food and faeces accumulated in sediments, but this ammonium released from sediment is
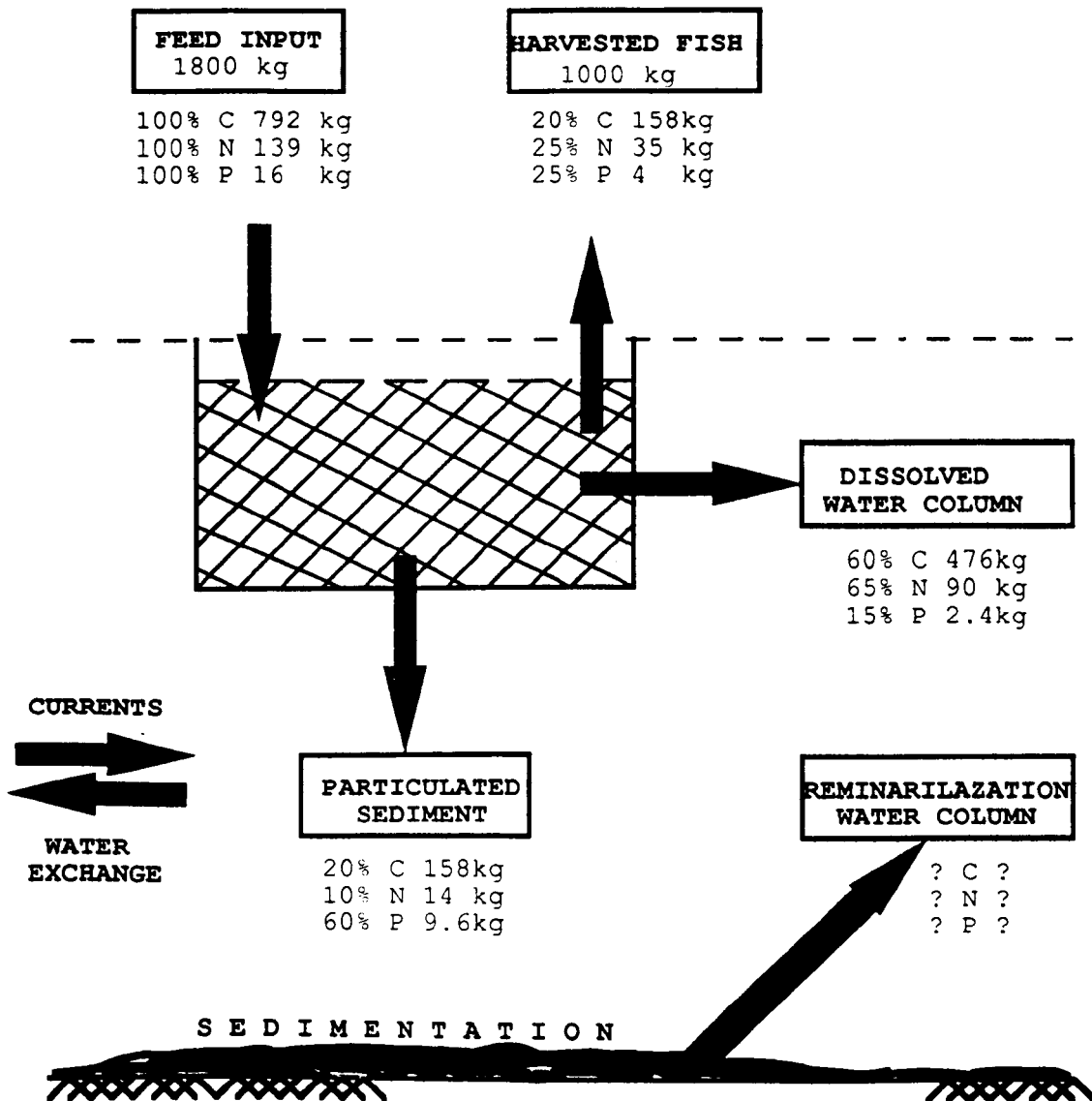
Fig.3. Average carbon (C), nitrogen (N) and phosphorus (P) loads to marine environment from a typical cage salmon farm, expressed in percentage and kg per tonne of fish produced per season. Presumed food conversion ratio is 1.8 and approximate C,N and P content of pellet feed is 44, 7.7 and 0.9% (data from Penczak *et al.*,1982; Gowen & Bradbury,1987; Gowen *et al.*,1988; Folke & Kautsky,1989; Ackefors & Enell,1990; and redrawn after Folke & Kautsky,1989).

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unlikely to be a significant contributor to hypernutrification (Gowen et al.,1990). Deposition of organic carbon, nitrogen and phosphorus waste in the form of uneaten food and faeces beneath cages can lead to major changes in sediment chemistry and ecology of the benthic organisms, while out-gassing of hydrogen sulphide from anoxic sediment could be harmful to fish in cages (Gowen & Bradbury, 1987; Gowen et al.,1988; Frid & Mercer,1989; Lumb,1989).

Any substantial and measurable increase in the concentration of dissolved nutrients has been termed hypernutrification and any increase in primary production resulting from hypernutrification has been defined as eutrophication (ICES,1984 cited by Rosenthal et al.,1988). In the marine environment, dissolved inorganic nitrogen rather than phosphorus is considered to be the nutrient most likely to limit growth of phytoplankton (Dugdale,1967). Both dissolved inorganic nitrogen and some forms of organic nitrogen can be assimilated by phytoplankton (Gowen & Bradbury,1987), so the discharge of these nutrients from fish farms, together with other soluble waste compounds such as vitamins, may lead to eutrophication. The extent of hypernutrification may depend on the size of the farm and the hydrography of water body within which the farm is located (Rosenthal et al.,1988; Gowen et al.,1988; 1990). Gowen et al. (1988) observed localised hypernutrification of the water column around a salmon farm, but did not find any significant effects on the phytoplankton. Eutrophication could lead to significant changes such as increase in phytoplankton growth and standing crop or changes in phytoplankton composition which may adversely affect the fish farming industry itself, such as appearance of toxic blooms (Rosenthal et al.,1988; Gowen et al.,1990).

Unlike salmon, shellfish farming requires no input of enriching food or polluting chemicals, therefore it is relatively benign. Studies, however, show that large scale mussel culture can cause environmental changes by removing essential nutrients, modifying nutrient cycles and sometimes the food web, accumulating organic wastes on the sea bed and aggregating fouling organisms and predators (e.g. Tenore & Gonzalez,1976; Dahlback & Gunnarsson,1981; Rosenberg & Loo,1983; Kaspar *et al.*,1985; Rodhouse *et al.*,1985; Tenero *et al.*,1985; Rosenthal *et al.*,1988; Gowen *et al.*,1990).

Like other bivalves, mussel culture relies on naturally available phytoplankton and large-scale cultivation, such as in the Spanish Ria de Arosa, will consume large quantities of phytoplankton and decrease the density of phytoplankton. According to Figueras (1989) one raft of mussels in the Ria de Arosa (Galicia, Spain), measuring 18x18 m with a approximate capacity of 80-100 tonnes at harvest, can filter 70 million litres of water in a day and ingest 180 tonnes of organic matter in a year. The amount of phytoplankton removed by mussel culture varies from 30-50% of total available biomass (Loo & Rosenberg,1983; Rodhouse *et al.*,1985; Figueras,1989). Rodhouse *et al.* (1985) estimated that in Killary Harbour (Ireland) with each tonne of mussels harvested, approximately 32.2 kg carbon, 6.6 kg nitrogen and 0.5 kg of phosphorus are removed from the ecosystem. So the loss of mainly nitrogen through mussel harvest and high deposition rates may limit the primary production in areas affected by mussel culture.

On the other hand, mussel farming can also stimulate primary production by speeding up the regeneration of the nutrients held in phytoplankton and other forms

of particulate organic material back into the water column and sediment, as faeces and pseudo-faeces and soluble excretion products, (Tenero & Gonzalez,1976; Kautsky & Wallentinus,1980; Kaspar *et al.*,1985; Tenero *et al.*,1985; Kautsky & Evans,1987; van der Veer,1989; Prins & Smaal,1990). In this way the mussels keep the nutrients circulating in the photic zone (Kautsky & Wallentinus, 1980) and this process acts as a driving force in the turnover of phytoplankton and nutrients in estuaries and coastal waters, but this stimulation process of phytoplankton production cannot change the fact that mussels are net removers of nutrients. On the contrary mussel farming could be helpful in reducing eutrophication in some coastal areas (Officer *et al.*,1982; Larsson,1985).

In general, the changes in the benthos beneath off-bottom mussel farms are similar to those resulting from organic waste from salmon farming (Gowen *et al.*,1990). Sedimentation rates of from 1 kg-C $m^{-2}yr^{-1}$ (Dahlback & Gunnarsson,1981; Rosenberg & Loo,1983) to 9.5 kg-C $m^{-2}yr^{-1}$, which is much less than salmon farming, and 1.1 kg-N m^{-2} yr^{-1} (Rodhouse *et al.*,1985) have been recorded beneath mussel rafts. Tenero *et al.* (1985) claimed that in Spanish Rias a significant proportion of mussel particulate organic waste is intercepted and consumed by enriched epifauna. They estimated that mussels can produce about 13 kg-C m^{-2} yr^{-1}, but only 0.2 to 0.9 kg-C m^{-2} yr^{-1} reaches the sediment.

From the present literature it is clear that the loss of nutrients due to harvesting and sedimentation might ultimately deplete primary productivity below critical threshold levels, and limit growth and further mussel production, so it is obviously important to assess the carrying capacity, i.e. the stock density at which production

levels are maximised without negatively affecting growth rate of animals and the ecosystem of the area before the establishment of large scale mussel cultivation. Recently there have been several attempts to develop and apply carrying capacity models (Incze *et al.*,1981; Rodhouse & Roden, 1987; Carver & Mallet,1990), and the main components in determination of carrying capacity have been reviewed by Deslous-Paoli (1987) and Héral (1987).

It is apparent from this short review that salmon and mussel farming can both affect the marine environment in different ways. Salmon farming, relying on artificial feeding, has a greater impact on the environment than mussel farming (SWCL,1988) and in general mussel culture represents a more or less self-regulated extensive aquaculture system (Folke & Kautsky,1989) and has positive effects on the ecosystem provided that it is of the proper dimensions and at the right location (Kaspar *et al.*,1985; Larsson,1985; Tenero *et al.*,1985). Folke & Kautsky (1989), who discussed the basis for salmon and mussel culture from a theoretical viewpoint, including support required from the marine ecosystem to sustain production and effects of these two culture system to environment, suggested that it would be environmentally, may be economically as well, advantageous to integrate salmon and mussel farming. Similarly, Rosenthal *et al.* (1988) proposed that in areas of dense bivalve culture, the development of polyculture systems which provide nutrients to extensive shellfish farming, could be considered as a possible beneficial side effect in a properly managed system combining intensive and extensive operations.

1.6. Literature Review

The growth of filter feeders like the mussel is affected by a number of environmental factors which have been studied by numerous of authors and reviewed by Seed (1976), of which food availability and temperature are predominant. Particularly quality and quantity of the available food may be the most important single factor regulating mussel growth (e.g. Seed,1976; Incze *et al.*,1980; Wallace,1980; Rodhouse *et al.*,1984; Skidmore & Chew,1985; Héral, 1987; Mallet *et al.*,1987a; Page & Hubbard,1987; Dardignac-Corbeil,1990). More detailed information on food and feeding habits of mussels and similar bivalves can be found in Bayne *et al.*,(1976a), Winter (1978), Héral (1987), Dardignac-Corbeil (1990).

The gills retain almost all particles of 3-5 µm diameter (Jorgensen, 1975) and even below 1 µm diameter (Winter,1978; Dardignac-Corbeil, 1990). Conversely, some workers found a close relationship between nanoplankton smaller than 20 µm and growth (Incze *et al.*,1980; Rosenberg & Loo, 1983). Héral (1987) suggested that the size range of particles retained by mussels is not constant and probably depends on the seston load of the system.

Temperature has been widely known as an important factor in controlling growth rate in aquatic animals. Temperatures in the range of 10°C to 20°C have been suggested as optimal for growth and physiological optima of mussels (Bayne *et al.*,1973 cited by Incze *et al.*,1980). According to Héral (1987), with exception of the spawning period, temperature is possibly the primary explanatory factor for shell growth and the third factor for meat production after food availability and reproductive cycle of the animals.

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Among the other factors salinity (Brenko & Calabrese,1969; Seed,1976), exposure to air and genotypic characteristics (Dickie *et al.*,1984; Skidmore & Chew,1985; Mallet *et al.*,1987a; Mallet & Carver,1989) may also influence growth and survival.

Variation occurs in the concentration and composition of available food and other environmental factors, namely temperature, current and salinity characterise coastal environments. Certain sites may support better growth than others because physiological studies have shown that growth may be regulated by the interaction of several such environmental factors (Thompson & Bayne,1974; Bayne, *et al.*1976b; Bayne & Widdows,1978; Widdows, 1978a&b).

The performance of wild and cultured mussels and other bivalves under different environmental conditions has been assessed through measurements of growth rate, biomass, production, physiological energetics, condition index and survival by many workers around the World. A few of them are briefly reviewed below and some of other recent studies are summarised in Table-3.

There are only two published studies of mussel culture in Scotland. The first one was carried by workers from SOAFD Marine laboratory (Aberdeen) during 1966-1969, mainly to investigate the growth of naturally settled spats and re-tubed wild mussels in Lochs Sween, Ewe, Ardvar and Beag, and the feasibility of suspended mussel culture in West coast of Scotland (Mason, 1969,1972a&b; Mason & Drinkwater, 1981). The second work by Jones (1981) was aimed at studying the relationship between primary productivity and growth of cultivated mussels in Loch Sween. Similarly, some research has been carried out around the British Isles, Ireland and Northern Europe, which has a similar climate. Dare & Davies (1975) carried out

Table-3. Summary of recent studies (particularly those experiment conducted in field conditions) on growth, mortality, biomass and production, seasonal cycle of condition index, approximate biochemical composition and physiological energetics of mussels (mainly cultivated) and other bivalves.

Author & Year of Publication	Species	Factors Studied	Geographical Region
Zwaan & Zandee,1972	*M. edulis*	Glycogen cycle	Dutch Wadden Sea
Seed,R.,1973	*M. edulis*	Absolute and allometric growth in natural mussels	N.E. England
Bayne & Widdows,1978	*M. edulis*	Physiological differences between two populations	S.W. England
Incze *et al.*,1978	*M. edulis*	Settlement, growth and survival	Maine, USA
Widdows,1978a,b	*M. edulis*	Body size, food, season, stress and physiology	Plymouth, England
Bayne *et al.*,1979	*M. edulis*	Physiological differences between populations	S.W. England
Hickman,1979	*P. canaliculus*	Allometry and growth	New Zealand
Pieters *et al.*,1979	*M. edulis*	Growth, biochemical composition, spawning and environment	Dutch Wadden Sea
Widdows *et al.*,1979	*M. edulis*	Seston, available food and feeding activity relations	S.W. England
Bayne & Worrall,1980	*M. edulis*	Growth and production of two natural populations	Plymouth, England
Hickman & Illingworth,1980	*P. canaliculus*	Condition cycle	N. New Zealand
Incze *et al.*,1980	*M. edulis*	Temperature, seston and growth, mortality	Maine,USA
Lutz *et al.*,1980	*M. edulis*	Seasonal cycle of condition index	Maine,USA
Pieters *et al.*,1980	*M. edulis*	Biochemical composition, reproduction and food	Dutch Wadden Sea

Table-3. continued..

Author & Year of Publication	Species	Factors Studied	Geographical Region
Seed,1980a	*G.demissa & B.exustus*	The relationship between shell shape and habitat	Carolina, USA
Zandee *et al.*,1980	*M.edulis*	Seasonal variations in biochemical composition	Dutch Wadden Sea
Sutterlin *et al.*,1981	*M. edulius*	Evaluation of mussels culture	Newfoundland
Ceccerelli & Barboni,1983	*M. galloprovincialis*	Growth, survival & biomass	Po River Delta, Italy
Ceccherelli & Rossi,1984	*M. galloprovincialis*	Settlement, growth & production	Adriatic Sea
Chatterji *et al.*,1984	*P. viridis*	Growth in re-circulation system	S. W. India
Dickie *et al.*,1984	*M. edulis*	Stock * site & growth, mortality	Nova Scotia
Thompson,1984	*M. edulis*	Reproductive cycle & physiological ecology	Newfoundland,Canada
Widdows *et al.*,1984	*M. edulis*	Environmental factors & physiology of populations	S.England & S.Wale
Bressan & Marin,1985	*M. galloprovincialis*	Seasonal cycle of biochemical composition & condition index	N. Adriatic Sea
Skidmore & Chew,1985	*M. edulis, M. californianus*	All aspects of mussels aquaculture	Puget Sound, USA
Craeymeersch *et al.*,1986	*M. edulis*	Secondary production of intertidal mussels	S.W. Netherlands
Tedengren & Kautsky,1986	*M. edulis*	The effect of physiological differences on size	N. Sea & Baltic Sea
Mallet *et al.*,1987a	*M. edulis*	Temperature, stock * site & growth	Nova Scotia
Page & Hubbard,1987	*M. edulis*	Growth & temperature, food	California,USA
Boromthanarat & Deslous-Paoli,1988	*M. edulis*	Production on bouchots	Marennes-Oléron,Fr.

Table-3. continued...

Author & Year of Publication	Species	Factors Studied	Geographical Region
Magnusson et al.,1988	M. edulis	Scope for growth	Sweden
Widdows & Johnson,1988	M.edulis	Physiological energetics: scope for growth	Norway
Brown, & Hartwick,1988a,b	C. gigas	Temperature, salinity, food & growth, condition index, survival	British Columbia
Bayne et al.,1989	M. edulis	Effects of seston concentration on feeding, digestion and growth	Plymouth, England
Mallet & Carver,1989	M. edulis	Stock * site & growth, mortality, secondary production	Nova Scotia
Deslous-Paoli et al.,1990	M. edulis	Energy budget	Marennes-Oléron,Fr.
Kautsky et al.,1990	M. edulis	Growth & morphology of reciprocal transplanted mussels	Baltic & North Sea
Page & Ricard,1990	M. edulis	Food & Growth	California, USA
Smaal & van Stralen,1990	M. edulis	Food & growth, condition index	Scheldt, Netherlands
Tedengren et al.,1990	M. edulis	Physiology	Baltic & North Sea
Grenz et al.,1991	M. galloprovincialis	Environment & energy budget	Mediterranean
Hickman et al.,1991	P.canaliculus	Food & condition index	New Zealand
Navarro et al.,1991	M. galloprovincialis	Physiological energetics	Galicia,Spain
Mallet & Carver,1991	M. edulis	Effects of various factors on growth and mortality	Nova Scotia
Robert et al.,1991	O. edulis	Growth and mortality	S.W. France
Ruiz et al.,1992	C. gigas	Environmental changes and the biochemical composition	Galicia, Spain

a four year suspended culture trial to investigate settlement, survival, growth and meat biomass in the Menai Straits (North Wales) using spat transplanted from Morecambe Bay (Eastern Irish Sea). The transplanted spats reached a marketable size of around 60 mm at between 1.5-2 years, but extremely heavy losses occurred soon after transplantation. In another work in the Conwy Estuary, N. Wales, Dare & Edwards (1975) investigated seasonal changes in flesh weight and biochemical composition of sublittoral mussels from natural mussel beds. In a detailed work by Dare (1976) settlement, growth and production of natural mussels was studied in Morecambe Bay. Rodhouse et al. (1984a&b) studied food resource and its allocation, gametogenesis and growth in natural and suspended cultured mussels in Killary Harbour, Ireland. In an another study Rodhouse *et al.*(1985) determined population structure, growth and survival of mussels, and estimated production and carbon and nitrogen flow. Condition index and variability in mussels from rafts, commercial subtidal beds and unexploited intertidal beds around Ireland were examined by Aldrich & Crowley (1986). There are three works from same area in Northern Europe: in Western Sweden, Loo & Rosenberg (1983) and Rosenberg & Loo (1983) studied growth, production and energy flow of mussels from settlement to harvest in a long-line system.

Growth of mussels and a few other bivalves in and around fish farms has been investigated and as a result of these studies, the integrated culture of these two groups has been suggested by some authors (section 1.5). Wallace (1980) reported that mussels sampled from two fish farms, attached to fish cages, near Tromsø, Norway were found to have grown at a relatively high rate, and continuously during the

winter. In contrast, mussels taken from other populations far from cages in the same area had grown more slowly and had marked winter rings. After this first report Farias (1983) carried out a 3-month trial in a loch in West coast of Scotland during the spring. He suspended small seed mussels from a rainbow trout marine cage site and a control site, but he did not observe significant growth difference between the sites. More recently, Jones & Iwama (1991) compared the growth and condition index of one year old oysters, *C. gigas*, at commercial salmon farms and control sites in British Columbia, Canada. After over a 5 month experimental period, they found that the increase in shell heights of oysters suspended at the salmon farms were as much as three times greater than that at control stations. The condition index of oysters was also significantly better at salmon sites than at control sites. Shpigel & Blay (1991) studied the possibility of integration of intensive pond culture of gilthead seabream, *Sparus aurata* (L) with Pacific oyster culture in Israel. They designed an oyster culture system which utilizes the excess phytoplankton production in ponds and functions as a biological filter. The results showed that oyster growth was rapid and phytoplankton levels were sufficiently reduced.

1.7. The Objectives

This study was carried out mainly in ambient conditions in West coast of Scotland between May 1990 and September 1992. The study consisted of three main experiments:

1- Growth experiments: growth performance, mortality, biomass and production of experimental mussel populations were monitored in salmon and mussel farms. In

addition performance of stocks from two lochs were monitored in native sites and in the neighbouring loch by cross-transplantation.

2- Physiological energetics: physiological energetics of cultured mussels from different locations were carried out in the field.

3- Investigation of the 'Charm Test' as a rapid method for detecting antibiotic residues in cultured mussel tissue. The materials, methods, results and discussion about this part of the study is presented separately in Chapter 6.

Considering the importance of mariculture, i.e. the salmon and mussel industries for Scotland's Highlands and Islands rural economy and the impact of salmon culture on its valuable estuarine and coastal environment, the main aims of the present trials are (a) to evaluate the present suspended mussel culture practice by investigating growth and performance of cultivated mussels, *Mytilus edulis* L, at different sites in sea lochs in West coast of Scotland and (b) to establish the basis for potential integrated culture of salmon and mussels by testing the hypotheses claiming that mussels could utilize organic waste from salmon cages and/or potential enhanced phytoplankton growth and hence grow better than at reference sites.

The secondary objectives are:

- Determine relevant environmental parameters (temperature, salinity, transparency, particulate organic matter, particle size distribution and chlorophyll-a) and study the main factors governing growth in West Coast of Scotland,

- Gather basic information about seasonal cycle of length and somatic growth, condition index and biochemical composition and discuss, in the light of these

findings, improving current culture practice.

- Investigate, by conducting cross-transplantation experiments between different lochs, the influence of the site and stock on growth performance and survival of mussels.

- Study the physiology of native and transplanted cultured mussels in the field to determine effects of variable environmental conditions on physiological responses, and gather necessary data for predicting the scope for growth and compare with previously recorded trends in growth rates for different mussel populations.

- Carry out a preliminary investigation on employment of the 'Charm II' radio assay system as a rapid method for detecting residues of potentiated sulphonamides (Trimethoprim + sulphadiazine) residues derived from salmon farming in the tissues of mussels.

2. THE STUDY AREA

Background information on the study area is presented about the general climate, topography, hydrographic variables (salinity, temperature, current and oxygen) and phytoplankton production which directly or indirectly affect the growth performance of mussels and other shellfish species and so the culture techniques.

The broad features of Scottish sea lochs have been described by Craig (1959), and Milne (1972a) reviewed hydrographic characteristics of nearly all the West coast sea lochs. Edwards & Edelsten (1976) and Landless & Edwards (1976) discussed the distributions of salinity, temperature, current and dissolved oxygen in relation to fish farming in the Scottish West coast, and Edwards & Sharples (1986) have summarised the main physical features of the main sea lochs in a catalogue. In addition, hydrography of some individual lochs were studied by several authors, for example Loch Etive by Wood *et al.*(1973), Gage (1972, 1974), Loch Creran: Gage (1972; 1974), Lochs Eil and Linnhe: Pearson (1970) and Loch Ardbhair: Gowen *et al.* (1983). The lochs in vicinity of the Firth of Lorne have received more attention because they represent typical fjordic lochs with more than one sill (Milne, 1972a) and are near the Dunstaffnage Marine Laboratory of Scottish Marine Biological Association (SMBA).

2.1. Climate

In general, Scotland's climatic conditions are surprisingly 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 marine current that pass, from the Irish Sea through the North Channel, near to the west coast of Scotland, and the

air current across those warm waters, provides the West coast and the whole of Scotland with a moderate climate. Mean air temperature on the West coast 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°C to 15°C in summer (Murray, 1978; Price, 1983). Occasional interludes of more continental type weather can be seen and produce exceptional dry conditions in summer and cold conditions in winter (Green & Harding, 1983). Snowfall at sea level is light and infrequent. The temperature drops below freezing for at most a few days during January and February in some years, and ice occurs only on those lochs having excessive freshwater run-off and long extended inland arms. The West coast of Scotland has an annual rainfall of about 1000 mm on the low islands to over 3200 mm on the high hills, with an average of 2500 mm (Green & Harding, 1983; Price, 1983), and the seasonal distribution is essentially oceanic with a marked rainfall minimum in spring and maximum in winter, typical of all the European Atlantic coast (Green & Harding, 1983). 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 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 in metres, and the normal tidal current can in this way be significantly altered (Edwards & Edelsten, 1976).

2.2. Geopographical Features

The coastline of West Scotland is very complicated. In contrast with other British coastal regions, the notable feature of the bathymetry is the existence of glacially

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deepened valleys (Ellett & Edwards, 1983). Glaciation has produced a great number of islands and peninsulas, while many sounds and inlets now penetrate deep into the land and creating an indented, irregular coastline (Price, 1983). In general, these inlets, known as sea lochs, are deep, surrounded by high hills and so well sheltered. On the Scottish mainland there are about 50 of these lochs or inlets that extend inland for many kilometres and cover a total area of 1,000 km^2. These sea lochs provide the greatest potential for fish farming and today most of the salmon and shellfish farms are operating in these lochs rather than open coastal waters. Many of these lochs are fjordic estuaries (Milne, 1972a), being a glacially over-deepened valley, often with a sill near the mouth. Some of the lochs have no significant sills or basins and are oceanographically simple arms of the sea. However, in the majority, sills are important as barriers to the free exchange of bottom water and as regions of high current and mixing, and control the access of outside water to the deeps of the lochs (Edwards & Edelsten, 1976). The sills are quite shallow compared with deep water found inside and there may be several, forming many basins in a loch. The two-layer estuarine circulation system driven by freshwater inflow and tidal mixing is important in determining their hydrography. With exception of the inner or upper basin of Loch Etive, progressively shorter residence times and more frequent water renewals are the usual sequence in these lochs.

The present experiments were carried out in Loch Etive, Dunstaffnage Bay (in Firth of Lorne), Loch Leven and Loch Kishorn. Although Dunstaffnage Bay is situated just outside the main entrance sill of the Etive in Forth of Lorne, it has been accepted as part of the Etive system (Edwards & Sharples, 1986) and where there is

an obvious difference from Etive it is mentioned. Lochs Etive and Leven are typical

fjordic sea loch systems which are partially separated from the main coastal marine

waters by shallow turbulent entrance sills, near the well-defined Firth of Lorne -

Loch Linnhe estuarine system. Each loch is a double basin system interconnected and

linked to the Firth of Lorne through narrow and shallow sills and hence to the North

Atlantic. Both of them posses features typical of their origin from submerged lower

tracts of river valleys later subjected to the erosional effect of glaciation. A brief

description of geology and topography these lochs are given and the main physical

parameters are summarised in Table-4.

Table-4. Summary of the main physical parameters of the Loch Etive, Leven and
Kishorn (from Edwards & Sharples, 1986).

Parameter	Etive	Leven	Kishorn
Length (km)	29.5	13.4	4.1
Tidal range (m)	1.8	3.7	4.7
Max. depth (m)	139.0	62.0	61.0
Mean depth at LW (m)	33.9	16.9	22.2
HW area (km^2)	29.5	8.6	7.1
LW area (km^2)	27.7	7.5	5.4
5m area (km^2)	23.6	5.3	4.5
10m area (km^2)	20.6	4.3	3.6
LW vol. (M m^3)	939.8	126.7	119.9
Watershed (km^2)	1350	338	66
Rainfall (mm\y)	2500	2000	2000
Run-off (M m^3\y)	3037.5	591.5	115.2
Number of sills	6	5	0

- **Loch Etive** (56° 33' 44" N, 005° 03' 52" W; Fig.4): It is a glacially over deepened valley, with two main sills, one at the entrance (the Connel narrows) and the other at Bonawe (Woods *et al.*, 1973). The former sill, 300 m wide and 8-10 m deep and 4 km long, at Connel marks the seaward entrance with width varying from 0.5 to 1.2 km (Solórzano & Ehrlich, 1977b; Edwards & Edelsten, 1977), while the latter about 11 km farther inland at Bonawe (Gage, 1972) divides the loch into two main basins. The upper basin with a surface area of nearly 17 km^2 has a maximum depth of 153 m and the 11.35 km^2 lower basin has a maximum depth of 60 m and runs east to west in rather lower country (Gage, 1972; Wood et. al., 1973). The whole length of the loch is about 29.5 km. There are additional sills in the lower basin, but the effects of these upon hydrography and production are not so important (Wood *et al.*,1973).

Among Scottish sea lochs, Loch Etive has an exceptionally high run-off with a large catchment area of 1350 km^2, over which the average rainfall is about 2500 mm per annum (Milne, 1972a; Edwards & Sharples, 1986). Freshwater run-off from this area determines much of the hydrography of the loch. In the lower loch the drainage from the River Awe is particularly important. This river drains half the catchment and flows from Loch Awe, to enter Loch Etive at the Bonawe narrows (Wood et. al., 1973). Significant volumes of freshwater also enter the loch from the River Etive at the head and from many burns throughout the length of the loch. The average annual freshwater run-off, allowing for evaporation of 250 mm, is 3037.5 million m^3 (Edwards & Sharples, 1986). The typical two layer fjordic-estuarine circulation system can be seen in this loch (Wood *et al.*,1973).
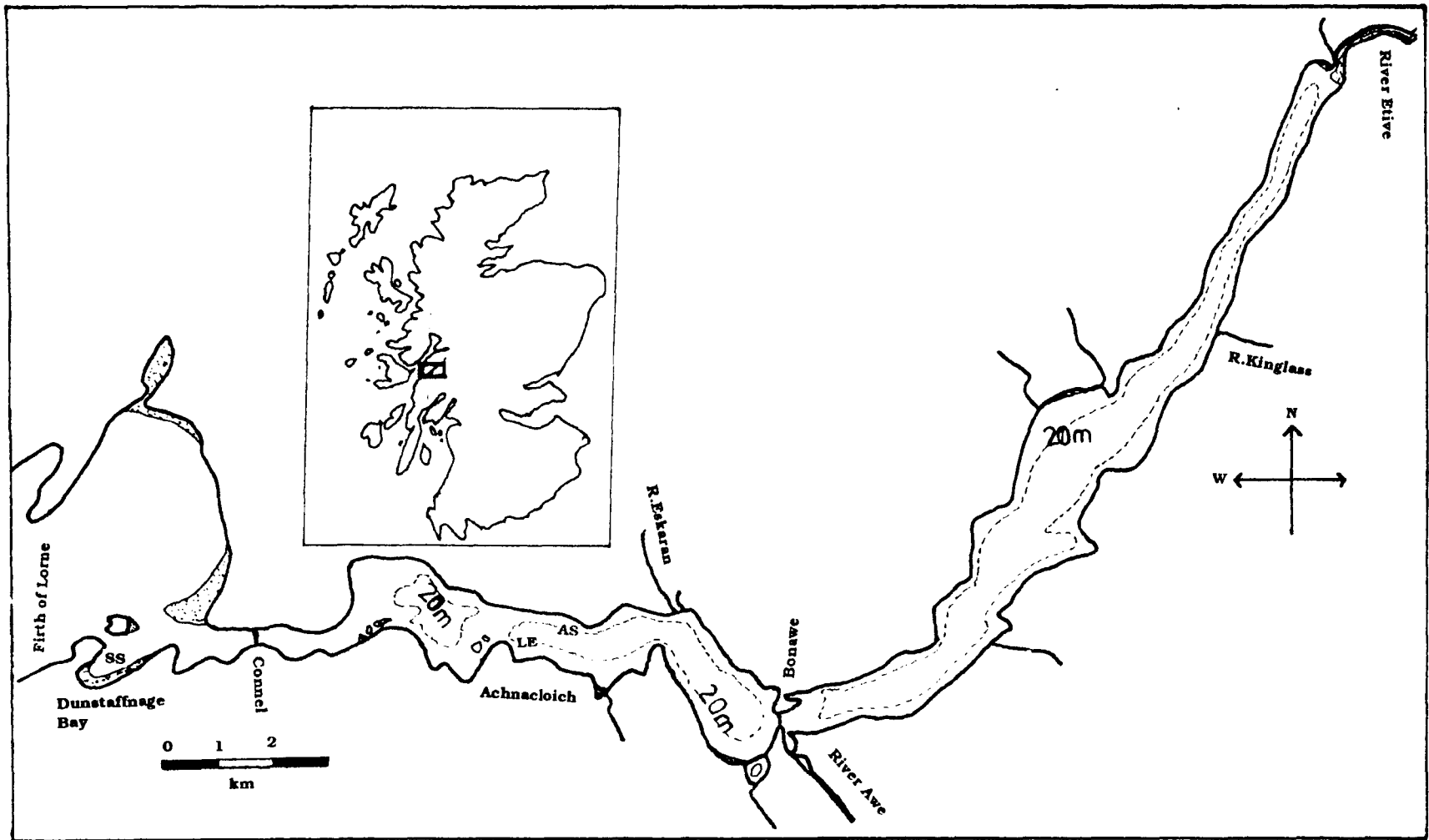
Fig.4. Map of Loch Etive, including Dunstaffnage Bay, showing the approximate positions of the experimental salmon and mussel farms, and the main freshwater supplies of the loch.

Although there are one salmon and one trout farm, the loch with around 13 shellfish farms is one of the largest mussel growing areas in Scotland.

- **Dunstaffnage Bay** (56° 27' 20" N, 005° 25' 54" W; Fig.4): It is a small bay located in Firth of Lorne, just after the entrance sill of the Loch Etive. The bay receives run-off water from Loch Etive, and during periods of high rainfall brackish water from Etive causes the salinity in Dunstaffnage Bay to fall, so that water in this bay is a mixture of coastal sea water of the Firth of Lorne and the brackish water of Etive. Out of the main current, during the ebb tide an eddy develops in the bay with low salinity (15-20‰) water from loch Etive and during flood tides the bay is flushed very easily and salinity rises to 30-35‰ (Edwards, per. com). There used to be just one salmon farm in this bay.

- **Loch Leven** (56° 42' 56" N, 004° 59' 40" W; Fig.5): It is 13.4 km long, varying in width from 0.2 km to 1.5 km with upper and lower basins. The entrance channel at Ballachulish Ferry is very narrow, 0.15 km wide and only 4 m deep. The lower basin has a mean depth of 60 m. The upper basin, 4.5 km long, has a mean depth of 48 m and is connected to the lower basin by a very narrow channel 27 m wide and 3.4 m deep (Milne, 1972a).

Although the catchment area of Loch Leven is only 338 km^2, which is very small compared with Etive, with an average annual rainfall of about 2000 mm, freshwater is constantly flowing from the British Aluminium plant at Kinlochleven at the head of the loch, so total freshwater run-off is 591.5 million m^3 per annum (Edwards & Sharples, 1986). This makes the surface water, especially in upper basin, naturally more brackish and the 20‰ isohaline varies from a depth of 6 m in winter
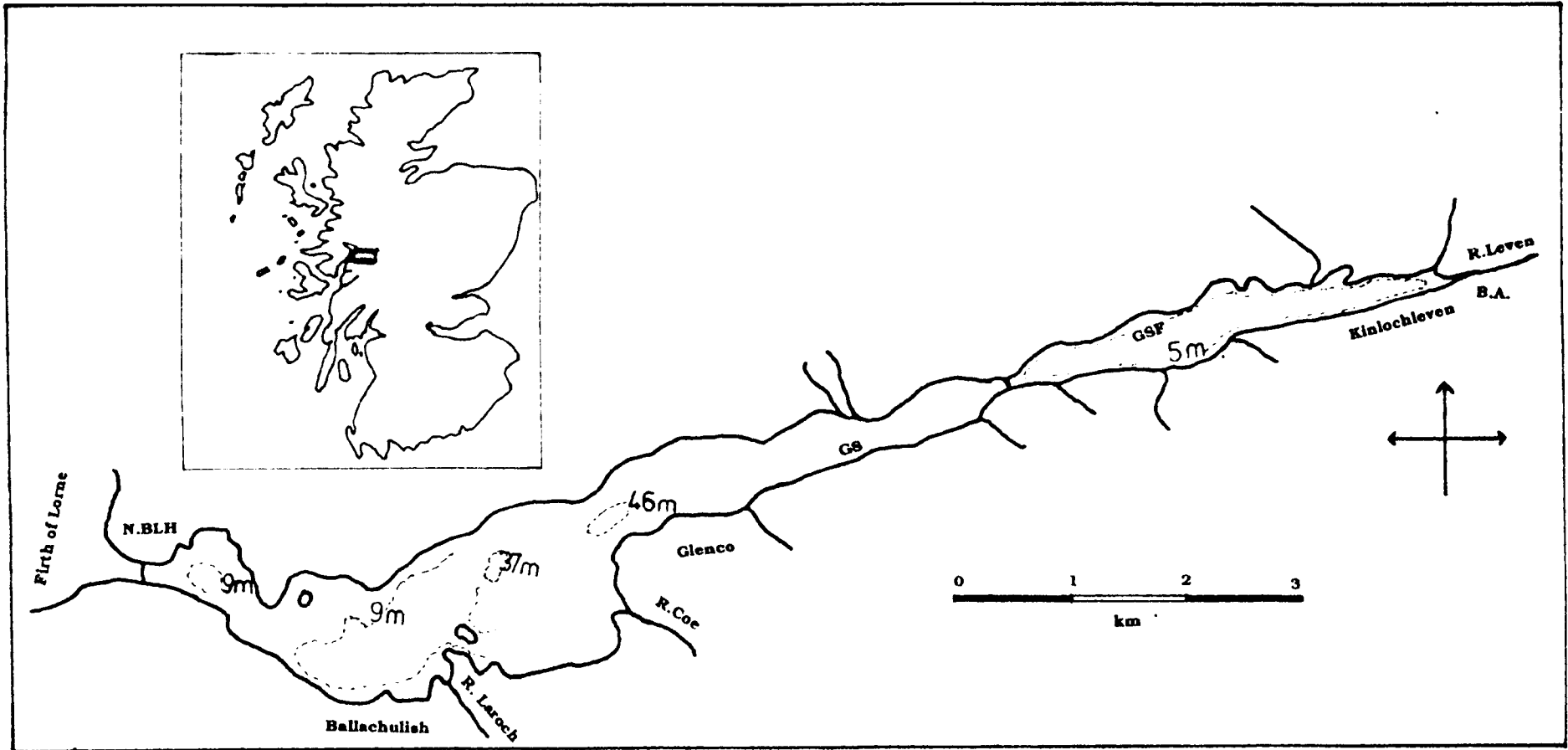
Fig.5. Map of Loch Leven indicating the relative positions of experimental salmon (GS) and mussel (GSF) farms, and the main freshwater supplies of the loch. The inset map shows the location of the Loch Leven (B.A.: British Aluminium Plant, N.BLH: North Ballachulish).

to 1 m in summer (Milne, 1972a).

There were two large salmon farms, but one of them closed down in spring 1992; there are two long-line mussel farms, one of them (Glencoe Shellfish Farm) is in upper part of the loch and the other near Ballachulish.

- **Loch Kishorn** (57° 24' 50" N, 005° 34' 33" W; Fig.6): Loch Kishorn, which has not got any sill, is one of the simplest sea lochs. It is simply an arm of the sea, thus it shows mainly characteristics of coastal seawater with a very thin brackish layer on the surface. As seen in Table-4, it is a very small loch with a length of 4.1 km, an area of 7.1 km^2 and quite a high tidal range. There is no published data about this loch other than the main physical features (Table-4) given by Edwards & Sharples (1986). There is one salmon and one large mussel farm in Loch Kishorn.

2.3. General Hydrography

General hydrographic characteristics of West coast sea lochs are summarised here based on background information. Some of these variables for experimental sites were also determined during the study.

- **Salinity**: The main water sources in lochs are the coastal high salinity (about 30‰-35‰) sea water at the seaward end and river run-off, which is a source of constant low salinity (0‰) at the landward end (Edwards & Edelsten, 1976). The brackish surface layer produced by freshwater run-off moves seawards and the salinity increases, while a layer of deeper water, flowing in over entrance sill, moves landwards.The interface between these two layers is the halocline, a zone where salinity changes rapidly with depth, the depth of which is usually between 0-5m
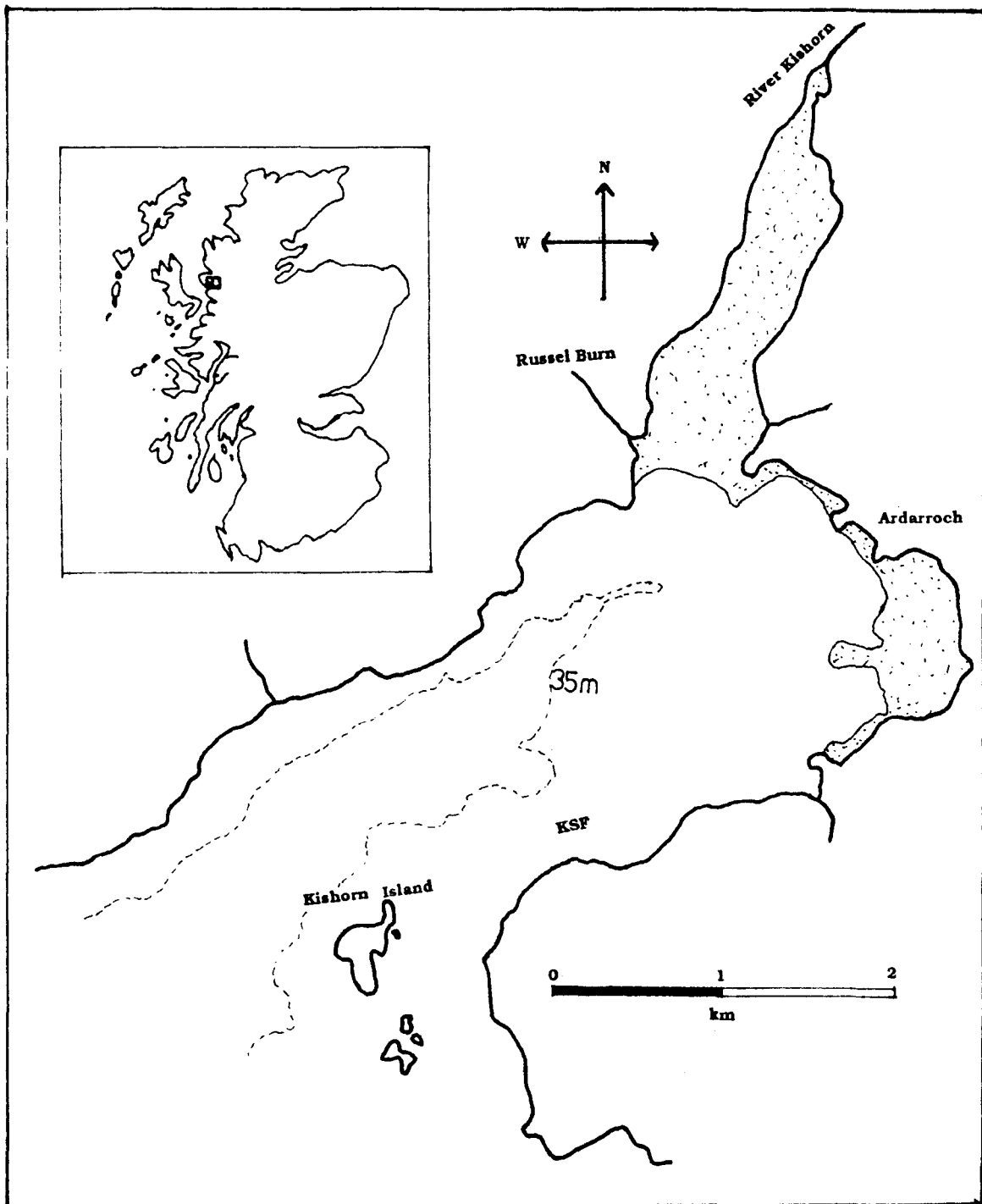
Fig.6. Map of Loch Kishorn showing the site of Kishorn mussel farm and freshwater entrances.

(Milne, 1972a; Edwards & Edelsten, 1976; Landless & Edwards, 1976). The Fig.7 shows the simplified estuarine or fjordic circulation. Apart from the rate of run-off, the salinity is influenced by tidal range, shape of the loch and the nature of the sills. The level of salinity, its horizontal extent and depth of the brackish layer fluctuates because of varying run-off, so that it is possible for a whole loch or part of it to be covered with a brackish layer of quite low salinity (Landless & Edwards, 1976); the upper basin of the Loch Leven is a good example. This surface layer of low and fluctuating salinity might be a constraint for shellfish growth, so most farmers suspend their stocks at 1-3 m depth. The salinity of the most of the West coast sea lochs at 2-4 m depth is around 32-34‰ (Milne,1972; Landless & Edwards, 1976), for example even the salinity of very brackish Loch Etive at 2m depth is around 20‰ (present study). The 20‰ isohaline varies from a depth of 10-14 m in winter to the surface in summer in Loch Etive, and 6m in winter to 1 m in summer in Loch Leven (Milne,1972).

- **Temperature**: Temperature of sea water on the West coast of Scotland varies between 6°C in late February and 14°C in July (Craig, 1959), while freshwater entering lochs from rivers has widely varying temperature, just above 0°C or even 0 °C sometimes in winter and near 20°C in summer (Edwards & Edelsten, 1976). The annual cycle of temperature, which is the lowest during January-February and highest during July-August, is similar in different lochs. Gage (1972) stated that there was very good resemblance in timing of the annual cycle in the lower Etive and Firth of Lorne, while deep water in the upper loch basin followed that of the lower basin with approximately a month's lag. This is very similar to surface water of Loch Leven
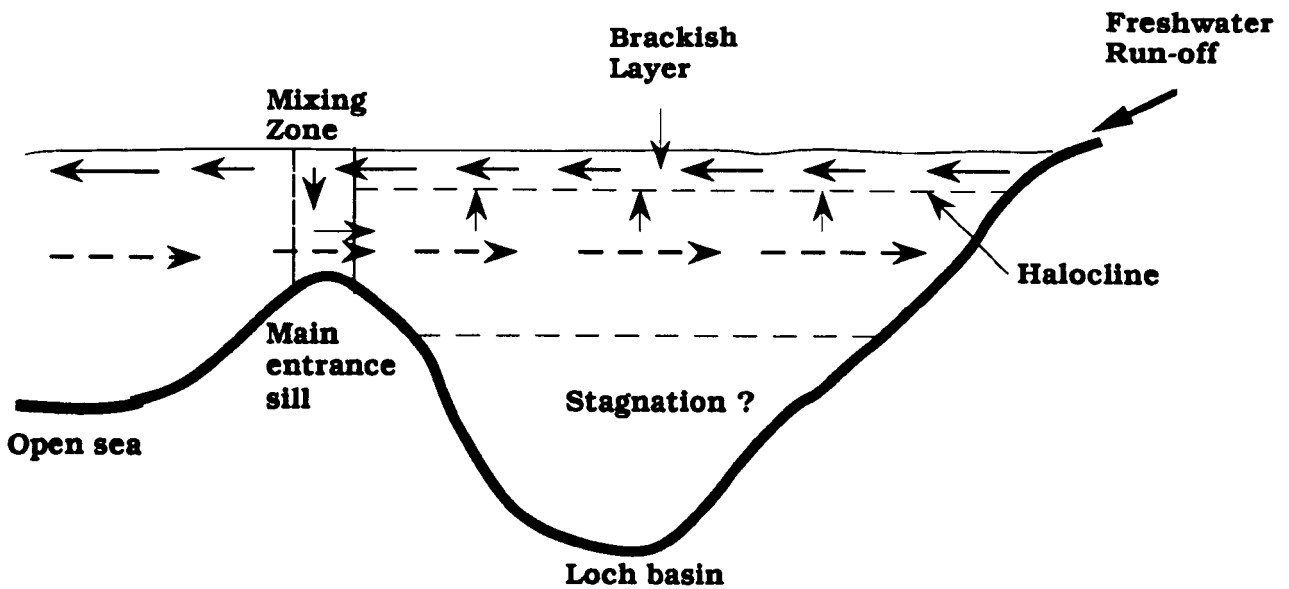
Fig.7. A simplified two layer circulation system in sea lochs and fjords. The current (solid arrows) discharge brackish water to sea. A compensation current (dashed arrows) flows in over the sill to replace water which is entrained (vertical arrows) into surface outflow. Mixing is strongest over the sills, where there may be recirculation of brackish water into the incoming current (redrawn from Edwards & Edelsten, 1976).

(Milne, 1972a), while in Loch Kishorn it probably follows the coastal cycle because freshwater run-off is very low and there is no sill which will modify the tidal regime.

- **Current:** The sources of current in sea lochs are tidal movements at the seaward end, run-off at the landward end and winds over the loch's surface. Of the all sources tides are the most persistent and, at the flood and ebb, usually predominant. The astronomic tide on the West coast is mainly semidiurnal, and the spring and neap tide range alters from place to place. The spring tide range varies from about 3.7 m in the Firth Lorne to 4.7 m in the lochs (e.g. Kishorn) opposite to Skye, and the neap range is near one third of this, i.e. just over 1 m and 2 m, respectively (Milne, 1972a; Edwards & Edelsten, 1976). The tidal range might be modified by sills or entrance

narrows of lochs, for example the tidal cycle in Etive shows an attenuation in amplitude and a lag in phase when compared with the just outside the Loch in the Forth of Lorne; the mean spring tide range of 3.7 m being reduced by the Connel narrows to 1.8 - 2 m (Wood *et al.*,1973; Edwards & Sharples, 1986) and the times of high and low water delayed by about 1.5 hours (Gage, 1972). The brackish layer on the surface as described above has a net water movement seawards, which is greatest at the surface, while deeper water moves landward reaching a maximum between the halocline and near or below sill depth in lochs around the Firth of Lorne such as Leven, Creran and Etive (Wood *et al.*,1973; Edwards & Edelsten, 1976 and Fig.7).

- **Oxygen:** According to Landless & Edwards (1976) water of Scottish sea lochs is usually at or near to 100% saturation with respect to oxygen. The exceptions only occur in deeper water in enclosed basins, such as upper basin of Loch Etive (Edwards & Edelsten, 1977). Therefore an oxygen shortage in water surrounding cultivated animals is very unlikely to be encountered.

2.4. Productivity of West Coast Sea Lochs

An adequate supply of nutrients and light is essential and the most important limiting factor for phytoplankton productivity (Wood *et al.*,1973; Tett & 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 in West coast of Scotland dominate the ecology of the phytoplankton in sea lochs (Wood *et al.*,1973).

The seasonal cycle, distribution and concentrations of the principal nutrients of some of the Scottish sea lochs have been comprehensively investigated by SMBA, for

example Solórzano & Grantham (1975; Etive, Creran, Linnhe), Solórzano & Ehrlich (1977a&b; Etive), Solórzano & Ehrlich (1979; Creran) and Gowen et al.(1988; Spelve). The main contributors to the nutrient budget of the lochs are river run-off and sea water from outside the loch. As a result of uptake by phytoplankton, the concentrations of main nutrients follow 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 the phytoplankton populations. Although freshwater run-off is deficient in phosphate (Solórzano & Ehrlich, 1977a; Solórzano & Ehrlich, 1979), nitrate rather than phosphate might be a critical factor in the productivity of some lochs depending on the freshwater input (Solórzano & Grantham, 1975). Apart from direct nutrient supply, freshwater run-off stabilises the brackish layer on the surface and thus allows phytoplankton to remain in the euphotic zone (Solórzano & Grantham, 1975). The stability also reduces the supply of nutrients from the deeper water, thereby limiting the phytoplankton growth. Excessive run-off might, however, lead to dilution of the phytoplankton and cause wash out (Grantham, 1981).

The ecology of phytoplankton has been described for several lochs: Loch Striven (Marshall & Orr, 1927,1930); Loch Sween (Marshall, 1947; Jones, 1981); Loch Etive (Woods et al., 1973); Loch Creran (Tett & Wallis 1978); Loch Eil (Grantham, 1981) and Loch Ardbhair (Gowen et al.,1983) and Loch Spelve (Gowen et al.,1988). In

general, the spring increase of phytoplankton production starts in sea lochs in March (Wood *et al.*,1973; Solórzano & Grantham,1975; *Tett & Wallis, 1978*; Solórzano & Ehrlich, 1979; Jones, 1981; Gowen *et al.*,1988), thus 1 or 2 months earlier than in similar coastal waters (Tett & Wallis, 1978), and declines in autumn as day length and the light intensity decrease (Tett & Wallis, 1978). The upper 8-10 m of the water column correspond approximately to both the brackish and the euphotic zone (e.g. Woods *et al.*,1973; Tett & Wallis 1978). Although dinoflagellates and microflagellates are important, diatoms (particularly *Skeletonema costatum*; e.g. Wood *et al.*,1973; Gowen *et al.*,1988), are the dominant phytoplankters in most sea lochs (Marshall & Orr, 1927; Marshall, 1947; Wood *et al.*,1973; Solórzano & Grantham,1975). There may be some exceptions, for example in Loch Ardbhair dinoflagellates were dominant (Gowen *et al.*,1983). It has been reported that average concentrations of diatoms over 10 m of water column can reach 10^6-10^7 cells l^{-1} during spring and summer (Marshall & Orr,1927; Marshall,1947; Wood *et al.*,1973). It is well known that many estuarine diatoms can tolerate a wide range of salinity. The gross annual primary production of the euphotic zone in Loch Etive was estimated as 70 g Cm^{-2} $year^{-1}$ during 1970-1971 (Wood *et al.*,1973).

3. MATERIALS AND METHODS

Selection of practical aspects of this study and choice of methods was based on the availability of facilities, various difficulties during more than two years of field studies and extreme weather conditions of the region. These and additional problems, such as site access difficulties and distance between study area and Stirling University contributed to limit the number of investigated lochs and sites. In addition, due to lack of seawater aquarium facilities, some work under laboratory conditions such as feeding of mussels with mixtures of phytoplankton and salmon feed, and detailed physiological energetics experiments, which were considered in the original project proposal, had to be abandoned. However, it is considered that the main objectives of the project could still be achieved despite these constraints.

3.1. Experimental Stations

As has been discussed in Chapter 1 (section 1.4.2.1), mussel farming is carried out all around the West coast sea lochs and Western Isles, some of which are quite different from each other with regard to hydrographic variables and primary production. Unfortunately, no detailed study on mussel culture had been carried out in this area, apart from the initial study of Department of Agriculture and Fisheries for Scotland during 1966-1970 in Linne Mhuirich (Loch Sween) and Lochs Ewe, Ardvar and Loch Beag (Mason, 1969). The lochs and sites for the present study were selected according to; a) presence of salmon and mussel farms in the same loch basin; b) willingness of farmers to cooperate with the research; c) presence of relevant background information about the loch (e.g. hydrography, nutrient cycle, production) and d) easy accessibility of sites by road from Stirling. Initially one salmon and

mussel farm in Loch Etive, another salmon farm in Dunstaffagne Bay (Firth of Lorne) and a mussel farm in Loch Leven were chosen: the operators of these commercial farms were approached in early 1990 and after a positive reply the experiment was started in May. A salmon site was not studied in Loch Leven during the first year because the loch was chosen mainly in order to compare the growth parameters with Etive, but during the second year a trial was also carried out on a salmon farm there. Loch Kishorn has been chosen only for the physiological energetic study because the farm was the largest unit mussel farm in Scotland.

The experimental sites, which are referred to by abbreviations of their commercial names, are briefly described below and relative positions are shown in Figs.4-6:

- LE (Loch Etive Farmed Shellfish): This is a mussel farm site, there are some suspended oyster trays and lantern nets as well and consists of several small rafts (10x6m with 10-16 horizontal beams; see home-made timber rafts Plate-3) and is located near to Achnacloich Pier in the lower basin of Loch Etive (Fig.4). The site is just 30-40 m from the shore and the depth is around 10-17 m. This site was used both as a control for the salmon farm sites, and the main experimental site for comparison between lochs and physiological energetic trials. There were eider ducks around the farm and so rafts were surrounded by anti-predator nets. In addition, there was an electronic multi-sound system to keep away the ducks.

- AS (Ardchattan salmon): A relatively small salmon farm with an approximate production capacity of around 50 tonnes which was using about 20 small (7x7x5m) wooden Kames type cages and situated at Ardchattan about 100 m from the shore opposite to LE (Fig.4). The approximate depth is about 20-30m. The site was used

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both for growth and physiological experiments.

- SS (Stirling Salmon): This was again a small salmon farm similar to AS in Dunstaffagne Bay adjacent to the Marine laboratory (Fig.4). The approximate capacity of farm was about 25-30 tonnes with 8 small cages. The cages were located about 200 m from the shore and the depth of the site was around 25 m. The farm was closed down at the end of the first experiment in spring 1991, so this site had to be abandoned.

- GSF (Glencoe Shellfish Farm): This is a newly founded long-line mussel farm in the upper part of the Loch Leven (Fig.5). The farm consisted of around 8 double long-line units, each anchored parallel to the shore, with length of 160 m (Plate-2 and Fig.2). The site was around 35 m to the shore with depth of 35 to 50 m. The head ropes were 1 m and rearing ropes 2.5 m below the surface due to high freshwater water run-off, particularly during the winter. This site was used during all experiments. There were occasional appearances of eider ducks.

- GS (Glencoe Salmon): A salmon farm site was located just inside the secondary sill dividing the loch near to the village of Glencoe (Fig.5). It was one of the largest single site salmon farms in Scotland, with a approximate production capacity of over 200 tonnes. The farm was employing 20 "Viking" type steel and 6 "Pollar Circle" cages. The site was situated just a few meter distance to south shore of the loch and the mean depth was 30 m. The site was used only during the second experiment.

- KSF (Kishorn Shellfish Farm): A Spanish style mussel farm was located near to Kishorn Island in Loch Kishorn (Fig.6). The farm was using 4 large (27x20m) rafts, anchored 8-10 m apart parallel to the shore, with a carrying capacity of 850

ropes of 15 m. The site was visited only twice, May and September 1992, to conduct two-day physiological trials on the rafts.

3.2. Environmental Parameters

3.2.1. Collection of water samples

Standard depths of 2m and 6 m were selected for the collection of the water samples. As a result of the variable salinity at the surface farmers suspend mussels from 1.5-2 m in Loch Etive and 2-2.5 in Loch Leven and therefore experimental mussels were suspended from 2 m. This made it desirable to exclude observations from 0-2 m. Duplicate water samples were collected with Nansen-type (designed by U.K. National Institute of Oceanography, N.I.O.) sampling bottle. The sampler was dropped into desired sampling depth and around 1 l of water was sampled by pulling the rope to close the stopper. The samples were stored in 1 l plastic bottles, and transported to laboratory in cooling boxes. The water samples were collected generally during second week of every month from May 1990 to May 1992, except January 1991 and 1992. All water samples were passed through a 0.3 mm nylon mesh to remove the large zooplankton and debris and 2-3 drops of 10 g l^{-1} magnesium carbonate suspension were added into samples for chlorophyll-a.

3.2.2. Temperature & Salinity

Salinity and temperature were routinely measured at the surface and other sampled depths (section 3.2.1). Temperature was determined by a means of a mercury-in-glass thermometer (Gallenkamp; -10 to 50±0.5°C), and the salinity (‰ part per thousand)

with a hand refractometer (Atago S\Mill; ± 1‰) as soon as water samples were taken from mentioned depths. Cumulative day-degrees (D°) were calculated for each site as the sum of monthly D° or average temperature between two measurement multiplied by the number of days separating the measurements.

3.2.3. Transparency

A black and white painted secchi disk was used to obtain estimates of the depth of the euphotic zone during the first growth experiment. Although for the best results it is necessary to calibrate the disc against a photometer and use it under standardised conditions, the disc used in this study was not calibrated, and was used under a variety of different lighting, weather and sea surface conditions. The results, therefore, give only a rough indication of the transparency of the water.

3.2.4. Chlorophyll-a

Phytoplankton biomasses were followed monthly by measuring chlorophyll-a according to the spectrophotometric method described by Strickland & Parsons (1972) & Stirling (1985). The samples of 1 1 sea water were filtered through 4.7 cm Whatman GF/C glass fibre filters soon after collection to remove and concentrate particulate material including phytoplankton from the water. These filters were wrapped in aluminium foil and stored in a deep-freezer until they were analysed. The green plant pigment, chlorophyll-a, was extracted from the particulate material retained on the filters by soaking the filters for at least 20 hours in 90% acetone and 10% water in 15 ml tubes at 4°C in dark. After extraction the tubes were warmed to

room temperature and centrifuged for 5-10 min, and the supernatant was poured into a 4 cm path-length spectrophotometer cuvette and the absorbances at 663 nm and 750 nm were measured against 90% acetone in a marked 4 cm reference cell.

Finally, calculations were carried out using absorbency values at 663 and 750 nm, the volume of water sample, volume of acetone extract and the path length of the spectrophotometer cuvette and operating a simple computer programme based on the equation given by Stirling (1985). The results are expressed as chlorophyll-a in µg/l which also includes phaeo-pigments.

3.2.5. Seston and Particulate Organic Matter (POM)

The amount of seston and particulate organic matter (POM) concentration were determined according to two different methods. During the first experiment the method described by Strickland and Parsons (1972) was exactly followed, but in the second experiment there was a small modification.

A known, generally 1 l, volume of water was filtered through numbered, pre-washed, ashed, at 500°C for 12 h and pre-weighed 4.7 cm Whatman GFC glass-fibre filters and the salts were washed out of the filters with distilled water. The filters were then oven dried for 1 h at 75°C, cooled in a desiccator and weighed in order to calculate the seston. During the second experiment the same filter papers were used first for chlorophyll-a analysis, after which the acetone was evaporated in an oven at 75°C overnight and then they were weighed for seston. The filters were then ashed at 500°C in a muffle furnace for 12 h, cooled and weighed again to determine the amount of combusted material. This value gives the particulate organic material

(POM, mg l^{-1}), while the difference between POM and the seston concentration is the particulate inorganic matter (PIM) (Strickland & Parsons,1972; Stirling,1985). Percent of POM (% POM) within the seston was calculated as :

POM (%) = [POM / seston] * 100

3.2.6. Particle Counts and Size Distribution

A quantitative analysis of particle counts (particles grater than 1 µm) and size - frequency distribution were carried out during the experiment II (May 1991 to May 1992), in addition to particle counts during the physiological energetics trials, by using a electronic particle counter (the Coulter Multisizer, Coulter Electronics, Luton, Beds, U.K.). A cuvette containing about 18-19 ml of ISOTON II with an approximate concentration of 0.85 NaCl (supplied by Coulter Electronics) and 1 or 2 ml of the water sample to be analysed is placed on the platform of the sampling stand. A stirrer ensures that the sample is well-mixed. When directed, a quantity of the sample is drawn by vacuum pressure created by the pump and regulated by the vacuum control unit through a small precisely drilled orifice into a glass tube. This glass tube is selected on the basis of particle size; a 70 µm orifice tube was selected. As each particle passes through the tube aperture it creates an electric pulse by changing the resistance of the sensing zone, the size of the pulse being related to the size of the particle and the signal is transmitted to the Multisizer unit where it is processed and displayed on the screen. The display gives information on N = particle count and Σ = channelizing count with particle size distribution. By manipulation of the displayed data it is possible to count only particles within a defined size range. Each sample is

counted three times and the mean number of particles of a desired size range is calculated by taking into account factors such as amount of water sample and size of tube aperture used.

3.3. Experimental Design

Three main field experiments were conducted during this study between May 1990 and September 1992. The first two experiments, called 'experiments I & II', were related to growth, survival, biomass, production, condition index and biochemical composition, and the third one 'Physiological Measurements'. During experiment I few spat collectors were set up in Loch Etive and Loch Leven. Experimental animals, design and sampling producer for experiments I & II are described here, while detailed information about physiological work is given in section 3.8. There was an experiment with the Charm System which is described in Chapter 6.

3.3.1. Experimental Mussels

All specimens of common mussels (*Mytilus edulis*) employed in these studies were obtained from suspended ropes in Lochs Etive and Leven. The seed mussels, 2 years old, for the experiment I were taken from site LE. After grading using a commercial grading machine, the damaged and empty shells were removed and the mussels were sampled for initial population structure. They had a mean length of 27.14 (SE±0.7739) mm and size range of 18 - 34 mm (Fig.8a and Plate-4).

Experimental animals for the experiment II were exactly one year old rope grown mussels from Lochs Etive (LE; Plate-5) and Leven (GSF; Plate-6). The size ranges

Plate-4. The rope grown seed mussels, with a size range of 18-34 (27.14±0.774 SE) mm, from Loch Etive used as original stock in experiment I.

Plate-5. One year old rope grown seed mussels with a size range of 19.1 - 26.5 mm and mean length of 22.07± 0.226 from Loch Etive (stock LE) used for the experiment II.

Plate-6. Cultivated juvenile mussels with a size range of 19.2 - 26.5 mm and means of 22.08 (± 0.232) mm during their second summer from Loch Leven (stock LL) used as experimental mussel at both site in Loch Leven and at the same time transplanted to LE.

Plate-7. High tensile French re-tubing socks, made of reinforced black polypropylene and cotton, filled with seed mussels of 884±64 per metre and used during experiment I.
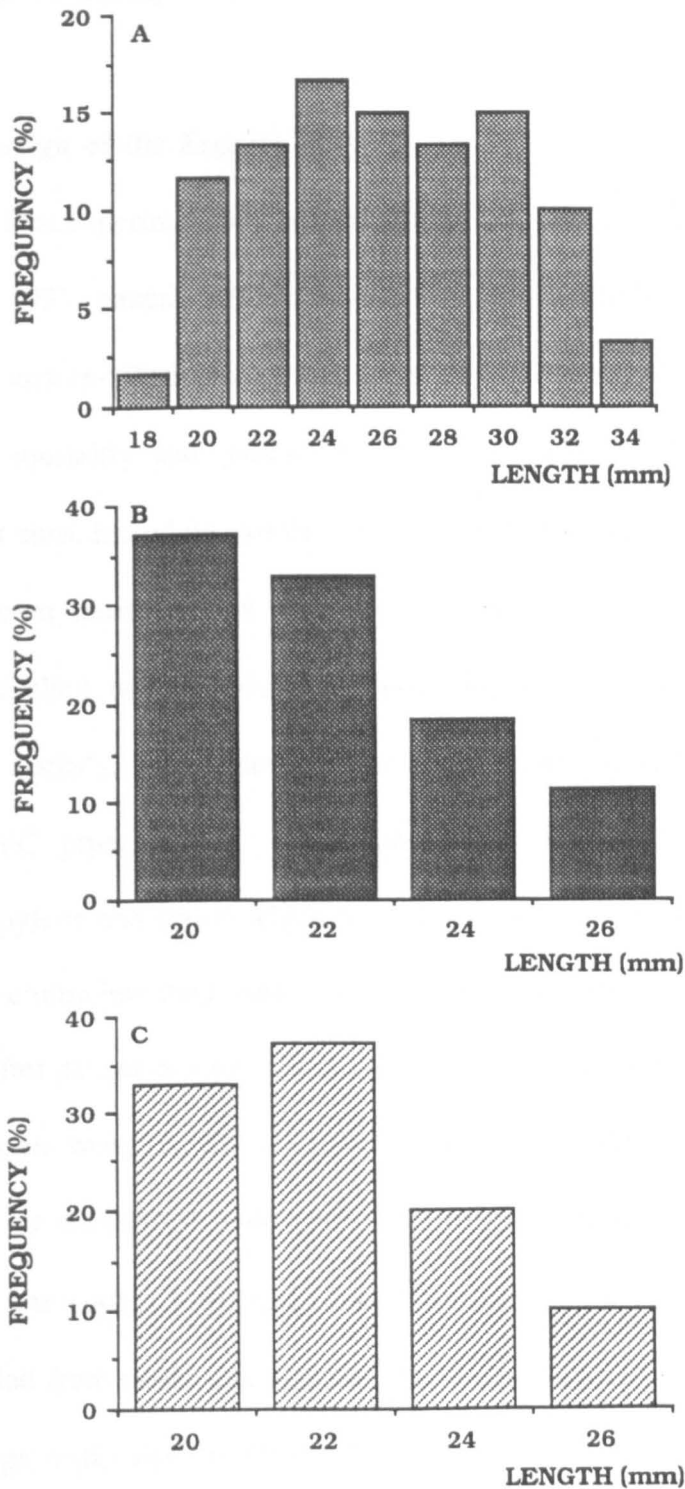
Fig.8. Initial population structure or length - frequency distribution of experimental
mussel stocks (a: experiment I, May 1990 - June 1991; b: stock LE and c: stock
LL for experiment II, May 1991 - May 1992).

and means were 19.1 - 26.5 mm and 22.07±0.226) mm for LE, and 19.2 - 26.5 mm and 22.08 (± 0.232) mm for LL (Loch Leven) stock (Fig.8b&c) respectively.

3.3.2. Design of the Experiments

The first experiment was performed at sites LE, AS, SS and GSF from May 1990 to June 1991, exactly 13 months, and mainly depended on monitoring measured, counted and re-tubed rope grown seed mussels. The main aim was to compare the growth, mortality and production of these mussel seeds on suspended ropes at different sites, including salmon cages and different depths or levels. The 2 years old rope grown mussels were sorted by a commercial grading machine, empty and damaged shell were removed by hand. The mussels then were re-tubed into 12 "French socks", with a mesh size of 20 mm and 5 m long (Plate-7), using a 1.5 m long PVC pipe (Ø6cm). This high tensile sock is made of reinforced black polypropylene and cotton which decays after a few weeks in water, during which the mussels clump into the former material which has been treated to withstand ultraviolet light. After all socks were filled, two of them were chosen at random, emptied and the mussels were counted in order to estimate, by means of simple proportion, the number of mussels in each sock. The mean number per meter was 884±64(SE). Finally, the socks, 3 for each site, were transported to the experimental sites and suspended from centre and both of end of a raft located in middle of the farm at LE, from cage walk- ways at AS and SS (one of them in the middle of four cages and the others on outer walk-ways), and from landward end of a long-line at GSF. The mesh tubes were suspended from 2 m below the surface to represent commercial mussel

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culture practices, because of fluctuating salinities at these mussel farms.

Experiment II was carried out in LE, AS, GSF and GS from May 1991 until May 1992, 12 months. The objectives were to monitor the growth and natural mortality more closely and to compare the stocks from Loch Etive (stock LE) and Loch Leven (stock LL). Lantern nets were used in this experiment in order to control losses through fall off. Each lantern net consisted of four 40 cm diameter plastic trays, but three trays in each lantern were used for stocking. The mussels from each stock were divided into three groups, one for its native site, one for the salmon farm in the same loch and the last one for transplanting to other loch, and stocked in 6 lantern nets, giving a total of 12 nets, at a density of 142 mussels per tray or 425 animals per lantern. The lanterns were distributed between sites as follows:

- Four at LE (2 native stock, called LE, and two with stock from Loch Leven, LL→LE), all lanterns suspended from a central beam of the raft.

- Two at AS (stock LE), suspended between two cages.

- Four at GSF (two with native stock, LL, and two with stock from Loch Etive, LE→LL), suspended from central-landward point of a double long-line unit, and

- Two in GS (stock LL), suspended between two cages.

All lantern nets were suspended 3 m below the surface and the nets were cleaned of fouling organisms during each sampling.

3.3.3. Sampling procedure

The sampling during the experiments I & II was started at the beginning of May 1990 and 1991, and carried out on a monthly basis, except January for both

experiment, until June 1991 and May 1992, respectively. On each sampling event at each site, apart from sampling of experimental mussels for length, weight and condition index, temperature, salinity and light intensity were measured and water samples were taken. In addition general conditions (e.g. heavy losses, predation by eider ducks, fouling by barnacles or new spat settlement) of experimental mussels were checked, and the number of dead mussels in lantern nets noted, empty shells and newly settled spats, if present, were removed and lantern nets were cleaned of fouling organisms. In experiment I, the first 2 m of French socks at 2-4 m water depth, of the 5 m long sock was considered "Level I" and the last 2 m at 5-7 m water depth, "Level II". The mussels from 20 cm of rope section, 10 cm from Level I and 10 cm from Level II, were stripped off from ropes at each site as the monthly sample. In experiment II, 6 mussels from each tray, i.e. 42 mussels from each site and/or stock, were randomly sampled. The number of these specimens removed at each date were each time summed up to adjust the estimate of survivors on the socks and lantern nets at the next count. Each sample was placed into a labelled mesh bag and transported to the laboratory in a cooling box. In the laboratory, mussels were counted and the shells were scrubbed clean of encrusting organisms, blotted dry and then the required measurements of length, weight and volume were taken immediately. During experiment I, the shell length of all mussels was measured for shell length growth and size - frequency distribution, and around 50 (25 from each level) from each site, spanning the available size range, were sub-sampled for determining other parameters such as live weight, meat weight, shell weight and shell organic content, and condition index (see next section for details).

3.4. Growth

Growth in bivalves is generally measured as increase in shell length and height (oysters), but it can be very useful sometimes to measure growth in terms of weight increases as well (somatic growth). The growth, therefore, was estimated from the change in shell length (L), live weight (LW), wet (WMW), and ash-free dry (AFDMW) meat weights of randomly sampled mussels over the sampling period. The shell length was determined by measuring the maximum anterior - posterior axis to the nearest 0.1 mm by a means of sliding vernier callipers. Live and wet meat weights were measured by weighing live animals with their shells closed (including shell cavity water), and the meats after dissecting the mussels and blotting off excess water with tissue, while ash-free dry meat weight was determined after drying meats in an oven and ashing in a muffle-furnace (section 3.7.2.1 & 3.7.2.2). The shell height (maximum dorsi-ventral axis) and width (maximum lateral axis) of the cross-transplanted mussels were also measured at the end of experiment II.

Since all the seed mussels were of the same approximate initial mean size, mussel size at each sampling date was considered an indication of the growth rate in relation to site, level or stock, so the growth rates were followed in terms of change in the mean growth parameters over the time between each sampling events. From these data a mean and standard error ($\pm$SE) were calculated for each sample and sampling month, and the percent increase in each character was calculated as the absolute growth estimate divided by its initial value.

The specific growth rate (SGR) of the experimental mussels were calculated from the following equation (Chatterji et al.,1984):

$$SGR(\%) = [(LnL_2 - LnL_1) / (T_2 - T_1)] * 100$$

where; L_1 and L_2 are the length at time 1 and 2; and T_1 and T_2 are time 1 and 2 (in days).

The shells from all sites in the experiment I were pooled in December 1990 and treated with concentrated hydrochloric acid to remove calcareous matter, rinsed in distilled water and the organic residue was determined (Rodhouse et. al.,1984a,b). The shell organic content for other months were derived from the relationship between shell length and organic matter content of shells. In experiment II, the percentage of organic matter in dry shell for each stock was determined at the beginning and end of the experiment. The amount of shell organic matter was used for estimation of biomass and production (experiment I), and comparing effect of site and stock on shell organic content (experiment II).

For experiment I, allometric (generally) relationships between shell length and dry meat, ash-free dry meat (every month), dry and ash-free dry shell organics (in December) weights were determined by linear regression analysis according to following equation:

$$W = aL^b$$

or when written in logarithmic form:

$$Log_{10}W = a + b*log_{10}L,$$

where; W is the weight (dry, ash-free dry meat, and dry and ash-free dry shell organics), L is the shell length, a and b are constants estimated by least squares regression.

In addition, every monthly size-frequency distribution values from experiment I

for each site was analysed by ELEFAN (Electronic Length-Frequency Analysis of Gayanilo, Soriano & Pauly, 1989) to compute the parameters of the von Bertalanffy length - growth equations for all the experimental periods. The equation is expressed as:

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

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 the rate at which the asymptotic length is approached, t is time of observation, and t_0 the age at which $L_t=0$ (Chatterji et al.,1984).

3.5. Mortality and Losses

In order to estimate mortality rates or losses in French socks during experiment I, the number of mussels in the socks were estimated at the beginning of the experiment and afterwards the number of mussels on sampled rope sections were counted, and so monthly and cumulative mortality rates were recorded until end of the experiment. During experiment II the number of mussels stocked in each lantern were known and it was possible to count and remove any empty shells on every sampling occasion.

Monthly calculations of percent survival and instantaneous mortality rates were corrected for population reduction caused by removals for measuring growth and condition parameters. The survival (S) was estimated by:

$$S\ (\%) = (N_t\ /\ N_0)\ *\ 100,$$

and the instantaneous total mortality rate (Z) by using the equation of Ricker (1975):

$$Z = Log_e\ (N_t\ /\ N_0),$$

where; N_o is the number of experimental mussels at the beginning and N_t is the corrected number of animals remaining after time t.

3.6. Production and Biomass

The monthly data on stock survival and ash-free dry meat and shell organic weights were used to estimate the biomass and production in each site. The biomass and production were estimated for experiment I and the methods of computing production and biomass follow those of Crisp (1984). The biomass is expressed as the mean ash-free dry weight (AFDW) of the individual mussels (g/mussel) or g m^{-1}, including shell organics, and the production (P, g m^{-1}) was calculated by using the following equation:

$$P = ((N_t + N_{t+1}) / 2) * (W_{t+1} - W_t)$$

and the eliminated biomass (EB):

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

where; N is the number of mussels m^{-1} and W is the mean ash-free dry weight, including shell organics, at time t (Crisp, 1984).

The biomass later was converted into energy units, in kcal kg^{-1} m^{-1} by multiplying monthly ash-free dry weight values with caloric content of meat and shell organics in that month.

3.7. Condition Index and Biochemical Composition

3.7.1. Condition Index

Condition index (CI) was monitored monthly throughout the year during both

experiments. The condition index was determined using three different methods. During experiment I following two methods were used as recommended by (Baird, 1958):

$CI_{vol} = [WMV / SCV] * 100$

where; WMV (ml) and SCV (ml) are wet meat and shell cavity volumes (whole volume of mussel-total shell volume), respectively.

$CI_{dry} = [DMW (g) / SCV (ml)] * 100$

where; DMW (g) is dry meat weight.

The condition index employed in experiment II was a modified version of a weight-based index recommended for use in the mussel farming industry (Hickman & Illingworth, 1980). The index:

$CI_{wet} = [WMW / (LW - SW) * 100$

where; WMW, LW and SW are wet meat, live and shell weights (g).

The CI_{vol} and CI_{dry} were determined as the mean of three replicate groups of 10 similar sized mussels, while for CI_{wet} mean of 5 replicate groups with 5 mussels in each was used. The measurements were made for each group separately, but the results were averaged to give mean CI value per month. Whole volume, the volume of all the mussels in each group, was measured by placing the live mussels into a 1000 ml measuring cylinder, containing a known volume of freshwater and measuring the amount of water displaced by the mussels. They were then dissected and the meat were blotted with paper towels to remove excessive water, weighed (WMW) and their volume (WMV) were determined by direct displacement in a 100 ml measuring cylinder. The shell volume (SV; volume of the empty shells) was determined in the

same way as the whole volume or meat volume. After weighing and measuring the volumes, the meats were dried in an oven and used for determining CI_{dry}.

The meat yield (MY) is another fundamental measure of meat quality and very closely related to condition index. The yield calculated as:

MY(%) = [Meat Weight/ Live Weight] * 100

The relationship between CI_{dry} and CI_{vol}, and between the all three condition and indices and yield were determined by linear regression.

3.7.2. Biochemical Composition

After determination of the condition index and dry meat weights, the dried meat were ground to powder, kept in stopper bottles in a refrigerator and used for biochemical analysis. All meat samples were re-dried before analysis.

3.7.2.1. Moisture

The moisture content was determined by drying the accurately weighed triplicate samples at 80°C for about 24 hours to a constant weight and the percentage of moisture was calculated as follows:

Moisture (%) = [(WMW - DMW) / WMW] * 100

where; WMW and DMW are wet and dry meat weights (g), respectively.

3.7.2.2. Ash

The ash content was obtained by combusting known weights of triplicate dry meat samples in pre-weighed porcelain crucibles in a muffle furnace at a temperature of

450°C for 12 hours, and was calculated as a percentage of dry meat weight:

Ash (%) = [ash weight (mg) / sample weight (mg)] * 100

3.7.2.3. Carbohydrate (Glycogen)

The anthrone-microdetermination method of Trevelyan & Harrison (1952) was used for determination of the glycogen in dry mussel tissue.

The anthrone reagent was prepared freshly by adding 500 ml of concentrated sulphuric acid (H_2SO_4) to 200 ml of water and dissolving 0.4 g of anthrone in 200 ml of the diluted acid solution.

Duplicate samples of about 0.1 mg were weighed into test tubes and 1 ml of distilled water was added. 5 ml of anthrone reagent was pipetted down the side of the test tubes, forming a two phase layer solution, and the test tubes were cooled in ice-water to stop the reaction. When all the samples were ready, the contents were mixed by rapid swirling and after covering with close-fitting bakelite bottle-tops the tubes were heated for exactly 10 min in a vigorously boiling water-bath. The tubes were then cooled in ice-water for about 2-3 min and mixed again to homogenise the colour. At the same time a stock solution of glucose (300 µg ml^{-1}) in fully saturated benzoic acid was prepared, and 3, 50, 100 and 150 µg ml^{-1}, standard glucose solutions were prepared by diluting the stock solution. 1 ml duplicate samples of each standard glucose solution were pipetted into test tubes, as well as duplicate blanks using 1 ml distilled water was prepared.

The samples were read in a spectrophotometer at 620 nm against a H_2SO_4 blank (2 vol H_2SO_4 : 1 vol water). A calibration curve was drawn for each set of samples

by plotting the absorbency of the standard glucose solutions against the concentration of glucose.

Finally, the absorbency values of the samples were converted into carbohydrate values using the standard curve and the glycogen (%) was calculated as follows:

Glycogen (%) = [WG / WS] * 100

where; WG and WS are weight of carbohydrate and sample in mg, respectively.

3.7.2.4. Lipid

The lipid content of tissues was determined following the chloroform-methanol method described by Bligh & Dyer (1959), modified by Ansell & Trevallion (1967) and has been recommended by Crisp (1984) as the most reliable method for molluscan tissues.

About 30 mg of dry sample was taken and homogenised with 19 ml of a chloroform-methanol mixture consisting of 5 parts chloroform, 10 parts methanol and 4 parts water. This extraction was carried out in two steps, firstly about 12 ml and then the remainder of the solvent. The homogenate was centrifuged to remove insoluble material and then diluted with 5 ml chloroform and 5 ml distilled water in a separating funnel. The mixture was shaken vigorously, allowed to separate, and the lower organic chloroform layer containing the purified lipid run into a weighed small beaker. The chloroform was removed by evaporating in a fan oven at around 75°C, the beakers containing the lipids were allowed to stabilise at room temperature for 30 min and weighed to the nearest 0.01 mg. The percentage of lipid was calculated as follows:

Lipid *(%)* **= [WL / WS] * 100**

where; WL and WS are the weights of lipid and sample in mg, respectively.

3.7.2.5. Protein

The standard micro-Kjeldahl method (Tecator, Kjeltec system, 1003 Distilling unit; Digestion system 40, 1016 Digestor) was used for protein analysis.

Approximately 200 mg triplicate dry samples were weighed into Kjeldahl tubes and after adding 2 mercury catalyst "Kjeltabs" and 5 ml concentrated sulphuric acid, the samples were digested at 420°C for 1 h. The tubes were allowed to cool and then 20 ml deionised water and 5 ml sodium thiosulphate solution were added. Finally, the samples were distilled after treatment with NaOH and titrated with standard hydrochloric acid solution for measuring nitrogen. Total nitrogen was calculated and converted to percent protein by applying the empirical factor of 6.25 (Kjeldahl factor for animal protein) as follows:

Total Nitrogen *(%)* **= [(V2 - V1) * N / WS] * 0.014 * 100**

Protein *(%)* **= Total Nitrogen** *(%)* **X 6.25**

where; WS is the weight of the sample (mg), V1 and V2 volume of hydrochloric acid solution required for the blank (ml), and for the test portion (ml), respectively, and N is normality of the hydrochloric acid solution.

3.7.2.6. Energy Content

The energy or caloric content of dry meat and shell organics were determined by bomb calorimetry (Gallenkamp Autobomb CBA-500). The material (meat and shell

organic content) was homogenised and then dried to a constant weight at 80°C for about 24 hours. At least three replicates of about 1.5 g material were weighed and made into pellets. Sample weight was chosen to give a heat release of about 7.2 Kcal (30,000J). During the pellet making a standard length of about 9 cm cotton thread was dipped inside the pellets.

Before combustion of the samples the heat capacity of the bomb was determined from the temperature rise in the bomb thermometer after the complete combustion of known quantities of AR benzoic acid (energy content of 6.35 Kcal g^{-1} 24.43 kJ g^{-1}). This value was then used in the determination of the energy value of the samples. Benzoic acid was a also used as a binding material for shell organics.

The pellet was placed into the bomb's crucible, the cotton was attached to the rod and the bomb cavity was filled with oxygen to a pressure of about 35 bar. The temperature was recorded initially and 10-12 minutes after bomb being fired. The increase in temperature after the bomb was fired, the heat capacity of the bomb which is determined by burning a known quantity of analytical grade benzoic acid, and the energy value of the cotton thread were then used to calculate the energy value of per gram dry mussel meat (kJ g^{-1}). Finally these values were transformed into Kcal g^{-1} by using the relationship; 1 Kcal = 4.1816 kJ.

3.8. Physiological Energetics

This study was carried in the field, except ammonia excretion rate, under ambient conditions of food availability, salinity and temperature, in Loch Kishorn (Kishorn Shellfish Farm, KSF, Spanish rafts), Loch Leven (Glencoe Shellfish Farm, GSF, long-

lines), Loch Etive (Loch Etive Farmed Shellfish, LE, rafts and Ardchattan Salmon

Farm ,AS, salmon cages) on two occasions, mid-May and mid-September 1992. In

addition to native mussels the physiological measurements were also carried out for

cross-transplanted (LL→LE and LE→LL from Loch Leven to Loch Etive and vice

versa) mussels between Loch Etive and Leven after 15 days, 4.5 months (transplanted

specifically for this experiment) and 1 year acclimatization (mussels transplanted for

experiment II; see section 3.3.1).

On two occasions, around middle of May and September, the sites were visited

and necessary data were collected.

In order to determine both total and organic particulate matter in seston during

each visit, duplicate samples of sea water were taken from depths of 2 m and 8 m,

and from three different points (front, centre and end) of the rafts, long lines and

cages.

An experimental flow-through system, which consisted of a battery operated

pump, a 30 l head or mixing tank and six experimental chambers (500 ml Buchner

flasks), one without animals as a "control", was used to determine clearance rate,

faeces production and respiration. The ammonia excretion rate was measured in the

laboratory under the ambient sea water temperature. In general, the physiological

procedures described by Widdows (1985a) were followed for measurements and

calculations (see below).

The mussels were detached from the ropes by scissors, cleaned of fouling

organisms and kept in individual chambers. On each sampling occasion at each site,

the physiological variables were measured over a size range (41.3 mm to 70.5 mm

shell length and 0.36 g to 2.33 g dry meat weight, DMW) of around 15 mussels. All experimental mussels were rope grown and approximately the same age, around 2-3 years old. The mean shell length and dry meat weight biomasses of these animals are given in Table-5.

After all the physiological measurements were completed, the dry meat weight of each mussel was determined and all physiological rates were standardised to weight-specific rates for 1 g mussels (DMW) using of the following equation:

$$Y_s = [(W_s \setminus W_e)^b] * Y_e$$

where Y_s is the physiological rate of the standard (1g DMW) mussel, W_s is 1 g, W_e is the dry meat weight of the experimental mussel, Y_e is the physiological weight to be corrected and b is the weight power,which is 0.4 for clearance rate, 0.65 for rate of oxygen consumption and 0.65 for rates of ammonia excretion (Widdows, 1978a; Winter,1978; Widdows & Johnson,1988).

3.8.1. Clearance Rate (CR)

Clearance rate, the volume of water cleared of particles per hour, was estimated by measuring the removal of natural suspended particles larger than 4 µm (Widdows,1985a) as water at a flow rate of 150 ml min^{-1} passed through experimental chambers containing the individual mussels. The head tank was continuously kept full by pumping the water from a of depth 3 m, aerated with a battery operated aerator and stirred manually. Water was distributed to experimental chambers through flexible transparent tubes with a diameter of 0.5cm connected to tank near bottom; flow rates were controlled with small individual taps. Individual mussels were placed in

Table-5. Size (mean ± SE for shell length, L, and dry meat weight, DMW), original stock and acclimatization period of mussels used in physiological energetics experiments. LL→LE1 & LE→LL1: mussels transplanted 1 year ago, and LL→LE & LE→LL: mussels transplanted at the end April 1992.

DATE	SITE	STOCK	Period of acclimati- zation	L (mm)	DMW (g)
10-18 May 1992	L.Etive (AS)	Native	-	50.8±4.83	1.17±0.34
" (LE)	"	-	48.8±4.29	1.17±0.27
" (LL→LE1)	L.Leven	1 year	49.6±3.87	1.13±.87
" (LL→LE)	"	15 days	52.3±5.83	0.97±0.52
	L.Kishorn (KSF)	Native	-	49.9±5.32	1.17±0.39
	L.Leven (GSF)	"	-	50.4±5.33	0.88±0.44
	" (LE→LL1)	L.Etive	1 year	49.8±4.84	0.83±0.49
	L.Leven (LE→LL)	"	15 days	47.7±5.10	1.06±0.79
7-17 Sept. 1992	L.Etive (AS)	As above	-	53.9±4.48	1.54±0.47
	" (LE)	"	-	57.5±2.99	1.01±0.34
	" (LL→LE)	"	4.5 months	52.3±3.23	1.13±0.53
	L.Kishorn (KSF)	"	-	62.2±5.41	1.59±0.42
	L.Leven (GSF)	"	-	57.6±4.65	1.29±0.46
	" (LE→LL)	"	4.5 months	55.2±4.01	1.23±0.61

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experimental chambers with the inflow at the bottom and the outflow from the top. After all mussels started feeding, water samples were collected four times during a 1 hour period from the outflow of all containers, including control, and few drops of Lugol's iodine solution were added to preserve the samples a few days prior to particle counts. Aliquots of water samples were used for particle count, by a means of a coulter counter (the Coulter Multisizer) using a 70 μm orifice tube as described in section 3.2.6. The "clearance rate" (CR 1 h^{-1}) was the calculated as flows (Widdows,1985a):

$$CR \ (1 \ h^{-1}) = [(C_1 - C_0) \ / \ C_1] \ * \ Flow \ rate \ (1 \ h^{-1})$$

where; C_1 and C_0 are particle concentrations of the control and each experimental (with mussels) chamber, respectively.

3.8.2. Absorption Efficiency (AE)

The absorption efficiency was measured by the ratio method of Conover which is based on organic contents of food and faeces and pseudofaeces and for reasons of practicability, simplicity and the cost has been widely used (e.g. Bayne & Widdows,1978; Bayne et al.,1979; Thompson,1984; Bayne, Hawkins & Navarro,1987; Tedengren et al.,1990; Navarro et al.,1991) and recommended (Widdows, 1985a). The amount of seston and particulate organic matter were determined as described in section 3.2.5. Faeces and pseudofeaces were collected during clearance rate measurements by pipeting them onto washed, ashed and pre-weighed glass fibre filters.

The Conover ratio for absorption efficiency (AE) was computed as follows:

$$AE = (F - E) / [(1 - E) * F]$$

where; F and E are ash-free dry weight:dry weight ratio of food, and faeces, respectively.

3.8.3. Respiration Rate (VO_2)

The respiration rates were also measured at the ambient conditions of the sea in closed chambers of 500 ml. After measurement of clearance rates, the initial oxygen concentrations in each chamber determined and water inflow of the experimental chambers were turned off immediately and after 60 min the oxygen concentrations was measured again by immersion an oxygen probe (Clandon Oxygen Meter, YSI Model 57) into water in flasks, while agitating probe and manually stirring the water. Before taking each batch of the measurements the probe was calibrated at ambient temperature and observed salinity by producing air-saturated water using small an aerator and following the manufacturer's instructions.

3.8.4. Ammonia Excretion Rate (VNH_4-N)

For measurements of ammonia excretion, each mussel was placed in a glass beaker containing 200 ml sea water, which had been filtered through Millipore membrane filters with a pore diameter of 0.45 μm and fully saturated with oxygen by aeration. After at least 2 hours incubation period, water samples were taken from experimental and control beakers without animals, and kept in a deep freezer. The determination of ammonia was carried out according to Phenol-hypochlorite method of Strickland & Parsons (1972) as follows:

2 ml phenol solution was added to 50 ml of water sample, mixed and then 2 ml sodium nitroprusside and 5 ml oxidising solution added. As standards 5, 10 and 25 μg NH_4-N l^{-1} concentrations were prepared from a stock solution of 1,500 μg NH_4-N l^{-1} (0.100 g of ammonium sulphate in 1000 ml distilled H_2O) and treated same as samples. The top of the flasks were covered and the absorbency in duplicate were read at 640 nm against distilled water after one hour at room temperature. Finally, in order to convert the spectrophotometer readings into μg NH_4-N l^{-1} a standard curve was constructed and then μg NH_4-N excreted per hour was calculated.

The rate of oxygen consumed to nitrogen excreted, O:N, was calculated by atomic equivalents according to Widdows (1985a):

$$O:N = [(O_2(ml\ h^{-1}) * 1.428) / 16] / [NH_4\text{-}N\ (mg\ h^{-1}) / 14]$$

where; 16 and 14 are the atomic weights of O and N respectively.

3.8.5. Scope for Growth (SFG)

The basic physiological responses of 1 g (DMW) mussels were first converted to energy equivalents (J h^{-1}) and used in the balanced energy equation to calculate 'scope for growth' (Crisp,1984; Widdows, 1985a&b; Widdows & Johnson,1988; Navarro *et al.*,1991). Calculation of C, A, R and U (all J h^{-1}) is:

$$C = CR\ (l\ h^{-1}) * POM\ (mg\ l^{-1}) * 20.78\ (J\ mg^{-1}),$$

$$A = C\ (J\ h^{-1}) * AE,$$

$$R = Vo_2\ (ml\ O_2\ h^{-1}) * 20.33,$$

$$U = NH_4\ excretion\ (\mu g\ NH_4\text{-}N\ h^{-1}) * 0.0249$$

The balanced energy equation is as follows:

$$C = P + R + U + F,$$

where C is total consumption of food energy; P is production of both somatic tissue and gametes; R is respiratory energy expenditure; U is energy lost as excreta, and F is faecal energy loss.

The absorbed ration (A) is the product of consumption (C) and the absorption efficiency (AE) of energy from the food, so the production (P) can be estimated from the difference between energy absorbed from the food and the energy losses via respiration and excretion:

$$P \ (J \ h^{-1} \ g^{-1} \ DMW) = SFG = A - (R + U)$$

As P is not measured directly, but is derived from other estimations, it is referred as "scope for growth (SFG)" (Widdows & Johnson, 1988). A positive SFG means that energy is available for growth and production and when SFG is negative the stored energy in the organism is utilised to maintain basal life functions.

In addition, the net growth efficiency (K_2), a measure of the efficiency with which food is converted into meat weight, was calculated from components of the balanced energy equation as: $K_2 = [A-(R+U)]/A$ or SGF/A.

3.9. Data Analysis

Prior to statistical analysis, all data were checked for heterogeneity of variance among groups in order to normalise the distribution curves. All environmental data were transformed to Log_{10} and the 'arcsine transformation' was used for all percentage data before any statistical analysis. The following analyses were performed:

- One-way analysis of variance (ANOVA) to determine statistical differences between sites in the data concerning shell length, weights and biomass. Data from October, end of the summer growth, and final two sampling were used to test the statistical significance of variance between the sites. One-way ANOVA was also applied to test the simultaneous effect of site on observed differences in environmental parameters, condition index and physiological rates (CR, AE, VO_2 and NH_4-N). Tukey's Multiple Range Test was applied to detect which particular factor(s) caused the significant F-ratio of the overall comparison between means.

- During the experiment II, two-way ANOVA was employed to test the effect of site and stock on growth parameters of cross-transplanted mussels.

- As two different stocks were used in experiment II, before any statistical significance test live and meat weights were adjusted for initial differences with an analysis of covariance. There was no significant difference in initial shell length between two stocks.

- Both contingency tables (Chi-squared) and ANOVA were used to test significance of variance between sites, depths and stocks in mortality.

- The length - weight relationships were determined by using least squares regression. Simple linear regression and correlation coefficient analysis were used to evaluate the relationships between various growth and environmental parameters.

All statistical analysis were performed using the Minitab statistical package and the results are reported at a significant level of $P \leq 0.05$, unless stated otherwise.

4. RESULTS

Observations of environmental parameters recorded during the experiments and the results of growth experiments I and II, and physiological measurements are presented here, while the trials with Charm system are given in Chapter 6. Interpretation of the results based on information derived from Figures 9-38 and Tables 6-31 (note: sampling was missed both in January 1991 and 1992 hence these months have been skipped in Figures and Tables).

4.1. Environmental Parameters

The seasonal changes in water temperature, salinity, transparency (secchi disk), chlorophyll-a, total seston and particulate organic matter and particle size distribution measured at sites in Loch Etive, Dunstaffnage Bay in Firth of Lorne and Loch Leven during the period from May 1990 - June 1991 at SS, May 1991 - May 1992 at GS and May 1990 to May 1992 at all other sites are summarised on a monthly basis, except January 1991 and 1992, in Figs.9-16 and May 1990 - May 1992 at all other sites, while overall average values for each growth experiment at different depths and sites are shown in Table-6. The correlations among environmental parameters are summarised in Table-7. In addition to depths and sites, statistical comparisons were also carried out between two lochs for each experiment.

4.1.1. Temperature

Fig.9 shows monthly values of sea water temperatures recorded at 0 m and 6 m and the mean values for each site are summarised in Table-6. The annual cycle of temperature was very similar at all sites with lowest values of 3.5 - 6.2°C in February
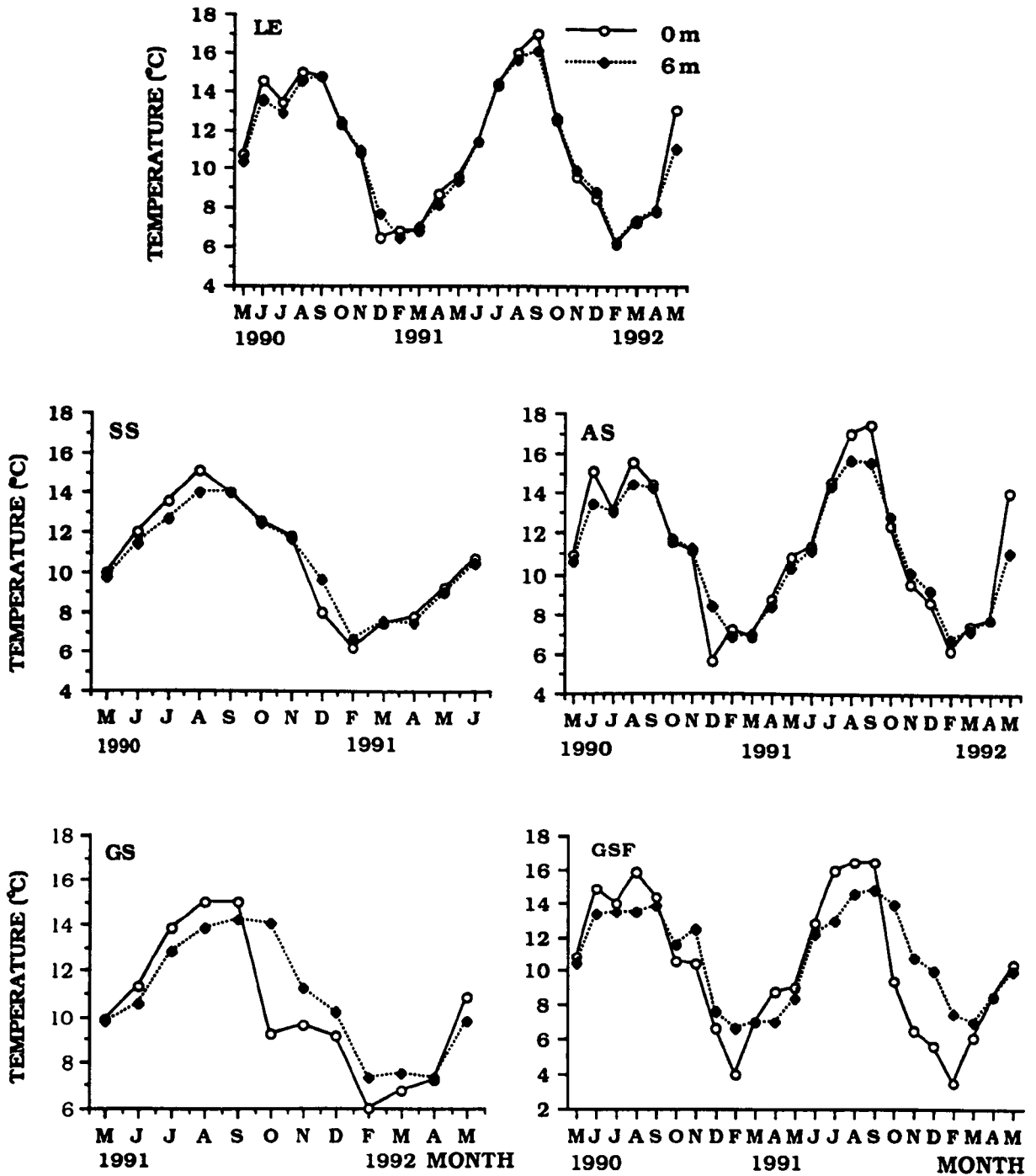
Fig.9. The annual sea water temperature cycle at experimental sites recorded at 0 m and 6 m at each month. LE (Loch Etive Shellfish, Loch Etive), AS (Ardchattan Salmon (Loch Etive), SS (Stirling Salmon, Dunstaffnage Bay), GS (Glencoe Salmon, Loch Leven), and GSF (Glencoe Shellfish Farm, Loch Leven). Note: sampling was missed in January 1991 and 92.

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Table-6. Overall mean (±SE) of monthly values of environmental parameters measured at 2 and 6 m at each experimental site from May 1990 to May 1992. Superscript letters indicate multiple range test comparisons between sites (one-way ANOVA Tukey and paired student's t test); those bearing different letters are significantly different at P≤0.05 or less. Superscript stars show (*P≤ 0.05, **P≤ 0.01, ***P≤0.001) significance levels between depths at same site.

Parameters		Experiment I (May 1990 - June 1991)				Experiment II (May 1991 - May 1992)			
		LE	SS	AS	GSF	LE	AS	GS	GSF
Temperature (°C)	Mean	10.8±0.57	10.6±0.51	10.9±0.56	10.7±0.62	11.0±0.68	11.2±0.69	10.5±0.37	10.5±0.75
Salinity(‰)	2m	20.8±1.34	29.5±1.19	21.2±1.61	26.1±1.17*	19.2±1.68	18.70±1.63	27.8±1.55	23.9±1.43
	6m	23.7±1.03	32.1±1.24*	23.9±1.62	29.2±0.58	22.0±1.58	22.0±1.62**	29.8±1.42	27.4±1.14
	Mean	22.2±0.88*	30.8±0.88ᶜ	22.5±1.15*	27.7±0.72ᵇ	20.6±1.17*	20.3±1.18*	28.8±1.05ᶜ	25.7±0.97ᵇ
Transparency (m)		6.4±46.7	6.0±42.2	5.8±46.4	6.3±45.7	6.2±51.7	6.1±51.9	5.2±53.7	6.3±53.7
Seston (mg l⁻¹)	2m	5.3±0.89	7.1±1.07	6.8±1.06	5.3±0.89	6.8±0.67	9.6±0.85	7.9±1.13	6.9±1.05
	6m	4.7±0.89	6.8±1.10	6.3±0.87	5.6±0.97	6.9±0.71	8.6±1.31	7.4±0.85	7.2±1.07
	Mean	5.0±0.62*	6.9±0.75ᵇ	6.6±0.68ᵇ	5.4±0.65*	6.8±0.48*	9.1±0.77ᵇ	7.6±0.69b*	7.1±0.73*
POM (mg l⁻¹)	2m	2.5±0.49	3.5±0.57	3.2 ±0.56	2.4±0.37	3.4±0.43	4.8±0.40	3.9±0.59	3.4±0.49
	6m	2.0±0.47	3.1±0.60	3.0 ±0.49	2.0±0.39	3.2±0.37	4.2±0.63	3.4±0.39	3.3±0.46
	Mean	2.2±0.34*	3.3±0.41ᵇ	3.1±0.37ᵇ	2.2±0.27*	3.3±0.28*	4.5±0.37ᵇ	3.6±0.35*	3.3±0.33*
POM (%)	2m	45.6±2.35	47.9±1.27*	45.8±1.94	45.6±1.79	51.0±2.59	51.2±0.82*	49.5±2.03	48.7±1.60
	6m	42.5±1.94	43.5±1.64	44.4±1.69	40.8±2.23	47.4±2.12	48.2±0.83	47.4±0.73	47.0±1.99
	Mean	44.1±1.53	45.7±1.11	45.1±1.27	43.2±1.48	49.2±1.68	49.7±0.65	48.5±1.08	47.9±1.26
Chl-a (µg l⁻¹)	2m	2.00±0.44	1.85±0.38	2.09±0.45	1.48±0.27	2.03±0.44	2.34±0.47	1.61±0.44	1.32±0.35
	6m	1.56±0.38	1.65±0.36	1.51±0.29	1.08±0.24	1.61±0.44	1.61±0.39	1.40±0.39	0.87±0.22
	Mean	1.78±0.29ᵇ	1.75±0.26ᵇ	1.80±0.27ᵇ	1.28±0.18*	1.82±0.31ᵇ	1.98±0.31ᵇ	1.51±0.29ᵃᵇ	1.10±0.21*
Particles(No.ml⁻¹)		-	-	-	-	30,012	30,991	30,821	31,782

and highest values of 16.1 - 17.5°C at 0 m and 6 m, respectively, in August - September of both years. Ice cover was reported in January 1991 in both Loch Etive and Leven but the sampling was missed in this month. Although the minimum values of 3.5-4.0°C were registered at 0 m at GSF in Loch Leven and the maximum recorded value was 17.5 °C at the surface at AS in Loch Etive, the mean maximum difference between the sites was as small as 0.58°C and the comparison of overall mean values showed no significant statistical differences between sites and depths (P>0.05; Table-6). The surface values recorded during the summer, up to September, however, tended to be very slightly higher than at 6 m and, as Fig.9 clearly displays during the winter they tend to be lower. This cycle was clearer at sites in Loch Leven than in Loch Etive and Firth of Lorne (Fig.9) and was presumably due to influence of high freshwater run-off from the melting snow of the surrounding mountains during the winter months in Loch Leven but, as has been mentioned, the overall mean differences between the depths were around 0.13 - 0.50°C and no statistical differences were observed (P>0.05). A significant relationship was found between mean monthly chlorophyll-a concentrations and temperature data from individual sites (P≤0.01 for LE and P≤0.05 for other sites) and from the combined data (P≤0.001; Table-7). There was no evidence of any significant correlation between temperature and seston, POM, %POM and the other environmental parameters.

4.1.2. Salinity

The Fig.10 shows the distribution of salinity at 0, 2 and 6 m and the means of monthly recorded values for each experimental period and site are given in Table-6.

Table-7. Correlation coefficients (r) between environmental parameters calculated from Pearson product moment correlation (ns: not significant *: P≤0.05, **: P≤0.01, ***: P≤0.001).

Parameters	Chlorophyll	Temp.	Seston	POM	%POM	Secchi
Temperature	0.458***					
Seston	0.319**	0.032ns				
POM	0.399***	0.000ns	0.959***			
%POM	0.562***	0.148ns	0.473***	0.622***		
Secchi Depth	0.584***	0.574***	0.333***	0.381***	0.392***	
Particle Number	0.274ns	0.265ns	0.276ns	0.321*	0.410**	0.198ns

In general, the salinity, especially at 2 and 6 m, was higher during the summer months than winter, but there were rapid changes from one sampling month to next. Very little variation was observed between sites in the same loch, especially in Loch Etive, but there were significant differences between sites in different lochs (Table-6). The highest salinities, which also showed uniformity between sampling months, were recorded at SS in Dunstaffagne Bay (Fig.10 and Table-6) with a minimum of 20 %o and maximum of 35%o. During experiment I, at SS and GSF mean salinity measured at 2 and 6 m was significantly (P≤0.001) higher than at the other sites, while there was also a significant (P≤0.05) difference in salinity between 0 and 6 m at the former site and similarly in experiment II mean values recorded at 2 and 6m at sites in Loch Leven were significantly higher than corresponding values obtained in Loch Etive (P≤0.001). The lowest salinity values, with a mean of 8.9 (experiment I) and 6.4%o (experiment II), were observed at 0 m at GSF in Loch Leven and the values at 2 and 6 m at this site were significantly higher (P≤0.001) than at 0 m (Fig.10). The mean salinity at LE and AS was very similar (Fig.10 and Table-6), but mean salinity at 6 m at AS was substantially higher (P≤0.05) than at the surface during experiment II.
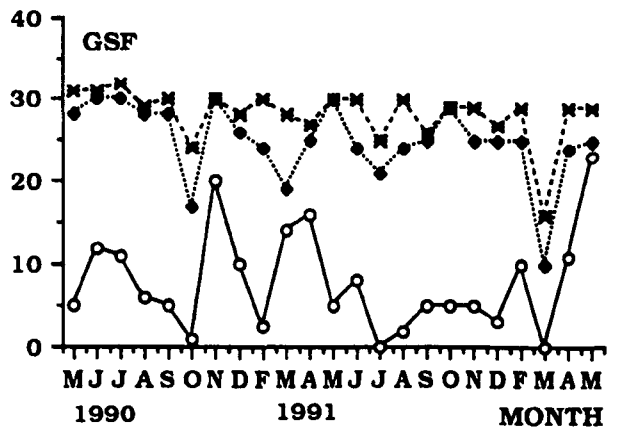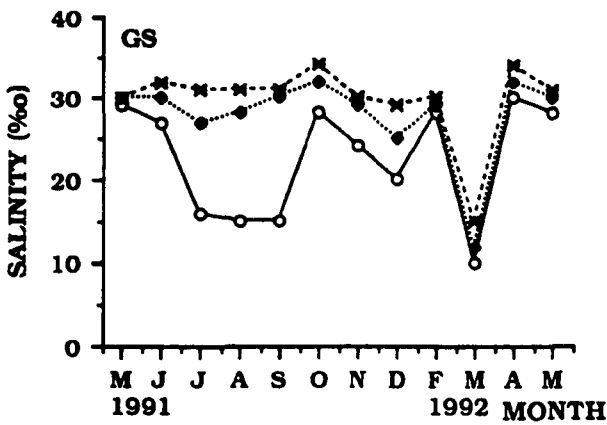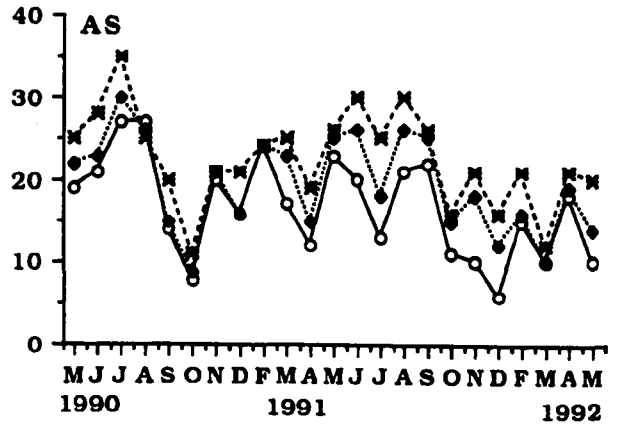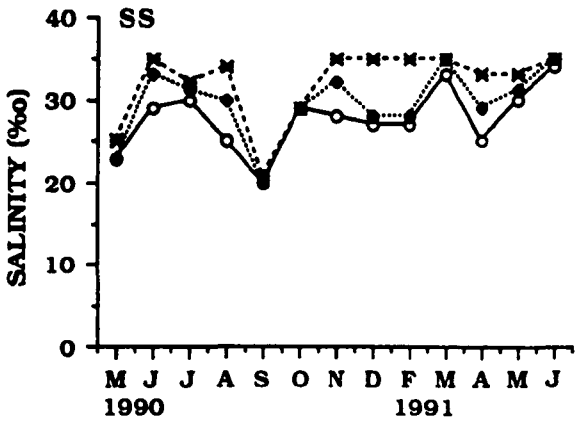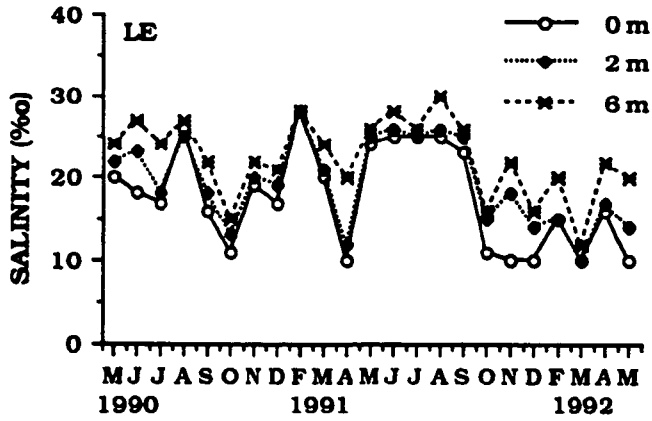
Fig.10. Monthly distributions of salinity at 0, 2, and 6 m depth at different sites over the experimental period of two years. Site codes as explained in Fig.9.

In contrast, the surface salinities at GS in the same loch (Leven) were considerably higher than GSF, but once again salinity at the surface was significantly ($P \leq 0.01$) lower than the other two depths at this site as well. In addition mean salinity at GS was higher ($P \leq 0.05$) than at GSF. Even when the surface values were excluded, variation between GSF and GS was still significant ($P \leq 0.05$) in favour of GS. When the two lochs are compared, general mean salinity in Loch Leven (22.99 ±1.120) was significantly higher than Loch Etive (18.95±1.04) during experiment II ($P \leq 0.01$).

4.1.3. Transparency (Secchi Disk)

The transparency showed marked seasonal fluctuations, reaching maximum values of 7.0 to 9.3 m in May to September; while the lowest values of 2.2 to 3.0 m were recorded during November to March of both years. The seasonal cycle was very similar at all sites as the monthly measurements were usually carried out at all sites on same day (Fig.11 and Table-6). There were some fluctuations between sites at the same sampling date which was possibly due to sudden changes in weather conditions, mainly cloud cover and rain and very small differences between salmon farm sites, mainly AS and GS, and nearest mussel farms, LE and GSF. There was no clear relationship between transparency and chlorophyll-a, seston and POM concentration at individual sites, except temperature at three sites but when data from all sites were combined, transparency significantly correlated with these parameters (Table-7). The relationship between chlorophyll-a, seston and POM, however, should be negative not positive as found during this study, which was possibly due to relationships between temperature (sunlight) and secchi disc, and temperature and seston rather than
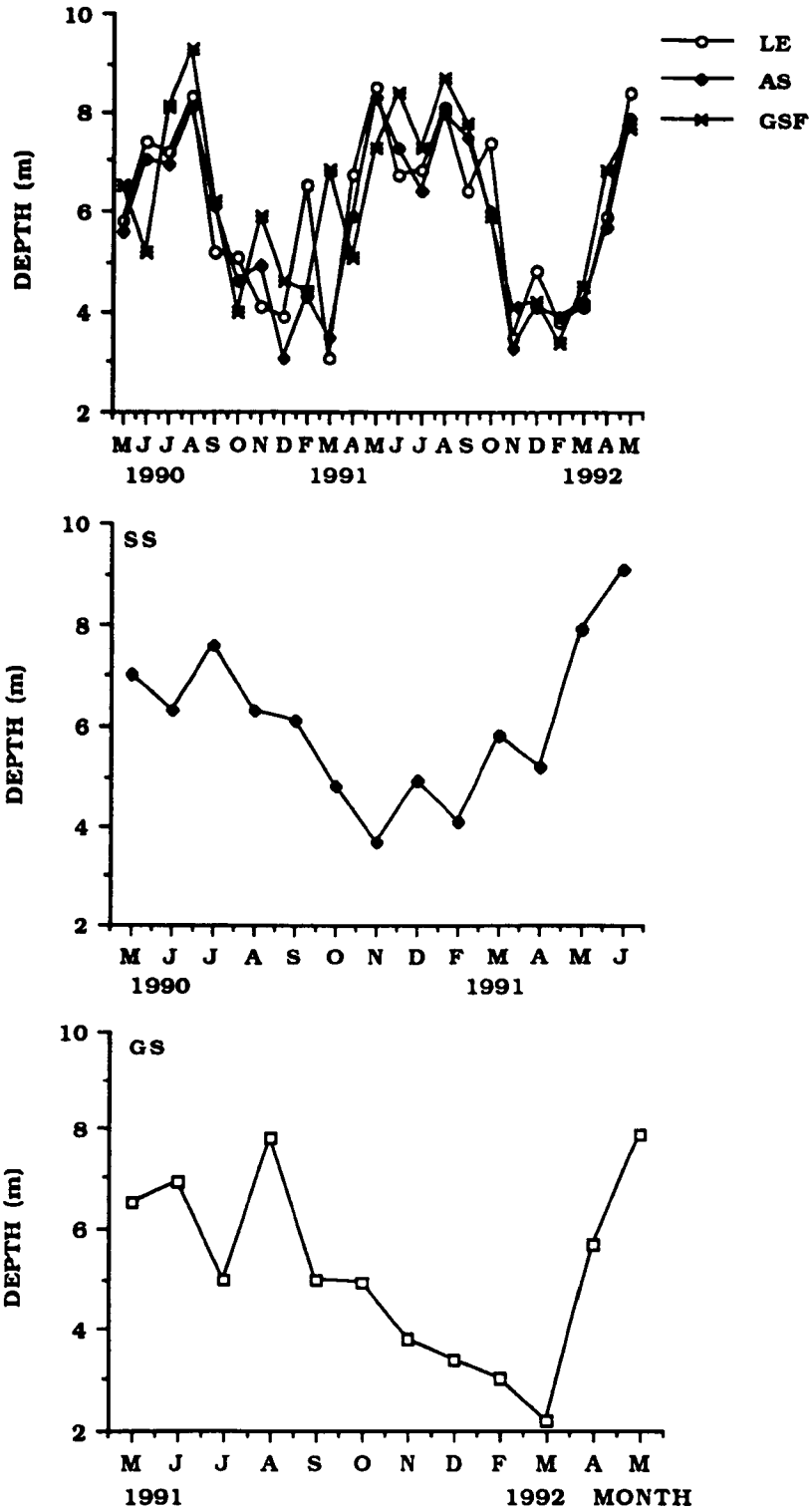
Fig.11. Monthly secchi disk depths or transparency at experimental sites measured during the experimental period of two years.

a true positive correlation between these parameters.

4.1.4. Total Seston and Particulate Organic Matter

Total Seston: Total seston or particulate matter values were generally high, 5-7 mg l^{-1}, at all sites during the summer months and dropped to a minimum in November before starting to increase in December and reach to highest values of 12.0-17.4 m l^{-1} at all sites in May 1991, which was almost one month before the chlorophyll-a maxima (Fig.12). After this peak the values were steady at around 4-7 mg l^{-1}, except at AS where concentrations were fluctuating, but high, particularly between May 1991 and February 1992.

Average seston concentration was significantly higher at the salmon farm sites (SS and AS) than at mussel farms during experiment I and in experiment II again seston concentrations at AS were higher than other sites (Table-6). Except at GSF, seston concentrations at 2 m were slightly higher than at 6 m at all sites. Overall combined seston values showed a significant relationship with other environmental variable, except number of particles (Table-7).

Particulate Organic Matter (POM): The values of POM showed the same annual cycle pattern as the seston. As Fig.13 displays, high values of around 2.9 - 4.9 mg l^{-1} were recorded in May-June in 1990 and May in 1992 at almost all sites, with minimum POM values of 0.25 to 2.2 mg l^{-1} during September - December in 1990 and 1991.

Mean POM concentrations at 2 m were higher than at 6 m at each site in both experiments, but no significant statistical differences observed between the sampling
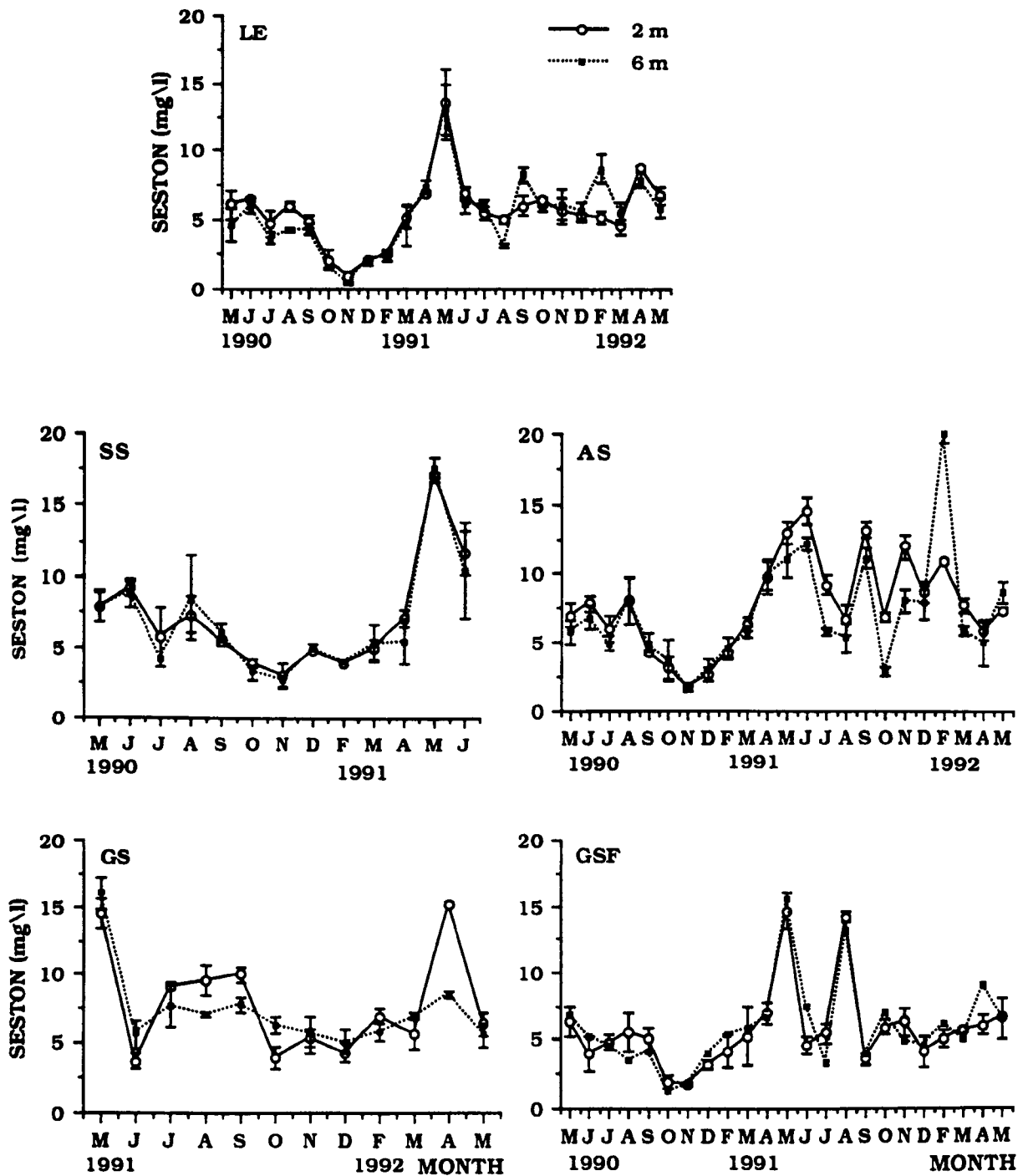
Fig.12. Variations in total seston concentrations at five experimental sites in two lochs during period of May 1990 to May 1992 (Error bars ±SE).
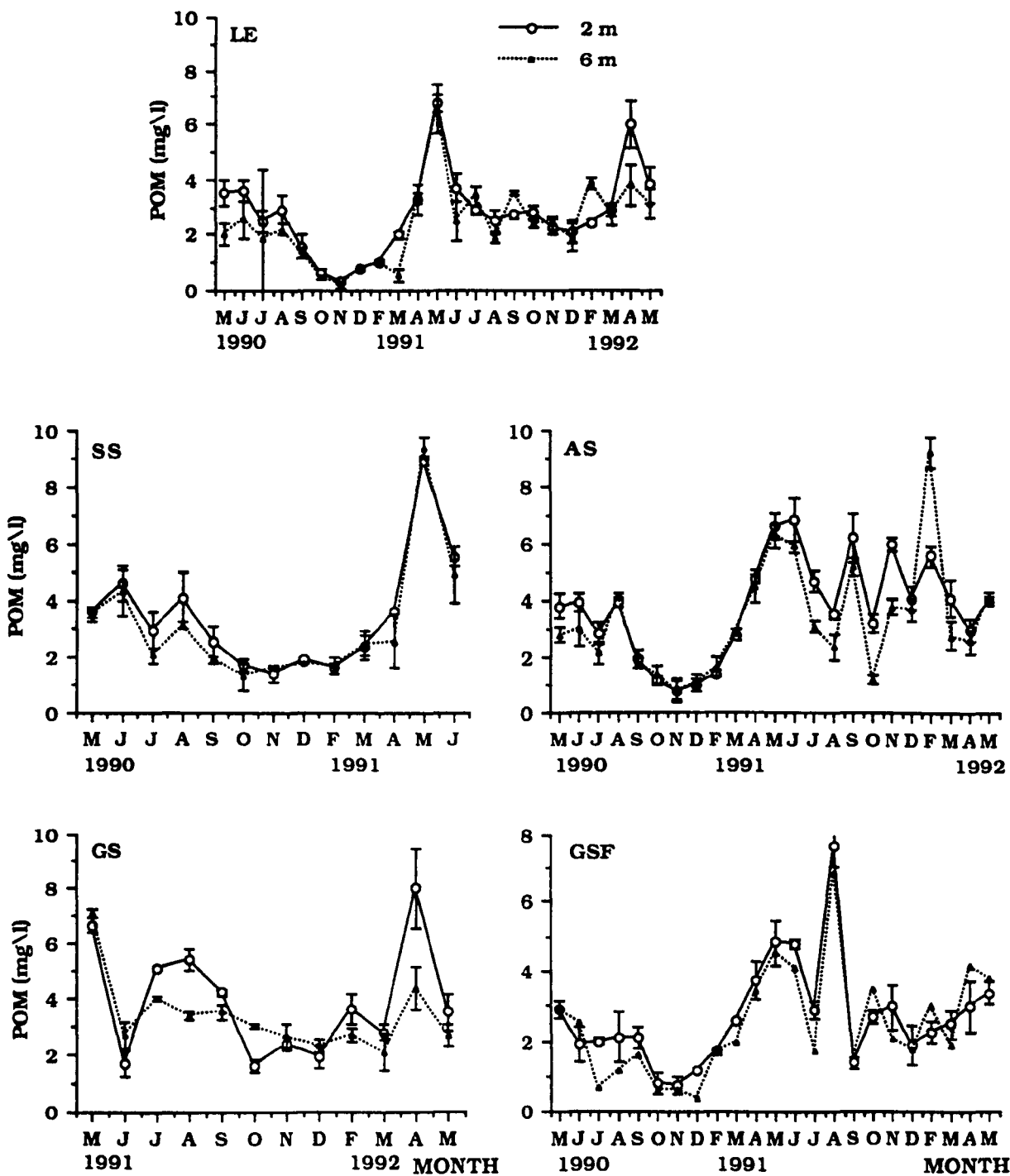
Fig.13. Monthly POM distributions at two sampling depths at experimental sites during May 1990 to 1992 (error bars ±SE).

depths at any of the sites (Table-6). The average of experiment I was highest at SS, similar to seston concentrations. POM values were also significantly higher at both salmon farm in experiment I and at only AS in experiment II ($P \leq 0.05$; Table-6).

%POM (percentage of POM in total seston) showed clear summer maxima and winter minima, especially at mussel farms, i.e. LE and GSF. At salmon sites, although, there was winter minima during December-February, the summer peak was not so clear, because values were steady at about 40-50% in other seasons (Fig.14). Like seston and POM, average values of %POM in both experiments were higher at 2 m than at 6 m, but there was no significant difference in %POM between sites (Table-6).

Significant correlation ($P \leq 0.001$) was found between chlorophyll-a and %POM (Table-7). Seston, POM and %POM data collected from each loch during the experiment II compared and no significant differences between lochs were noticed.

4.1.5. Particle Concentration and Size Distribution

Particle counts were carried out only during experiment II. Fig.15a exhibits particle number distribution, and Table-6 presents mean values. The variation in particle number between sites was not significant; in fact overall means of monthly samples were exactly the same for each site (Table-6).

Average size frequency distributions for the experimental period were calculated from analysis of monthly samples for each site. As can be seen in Fig.15b, size frequency distributions of suspended particles were almost identical at all sites, being dominated by smaller particles; just over 70% of the total detected particles was
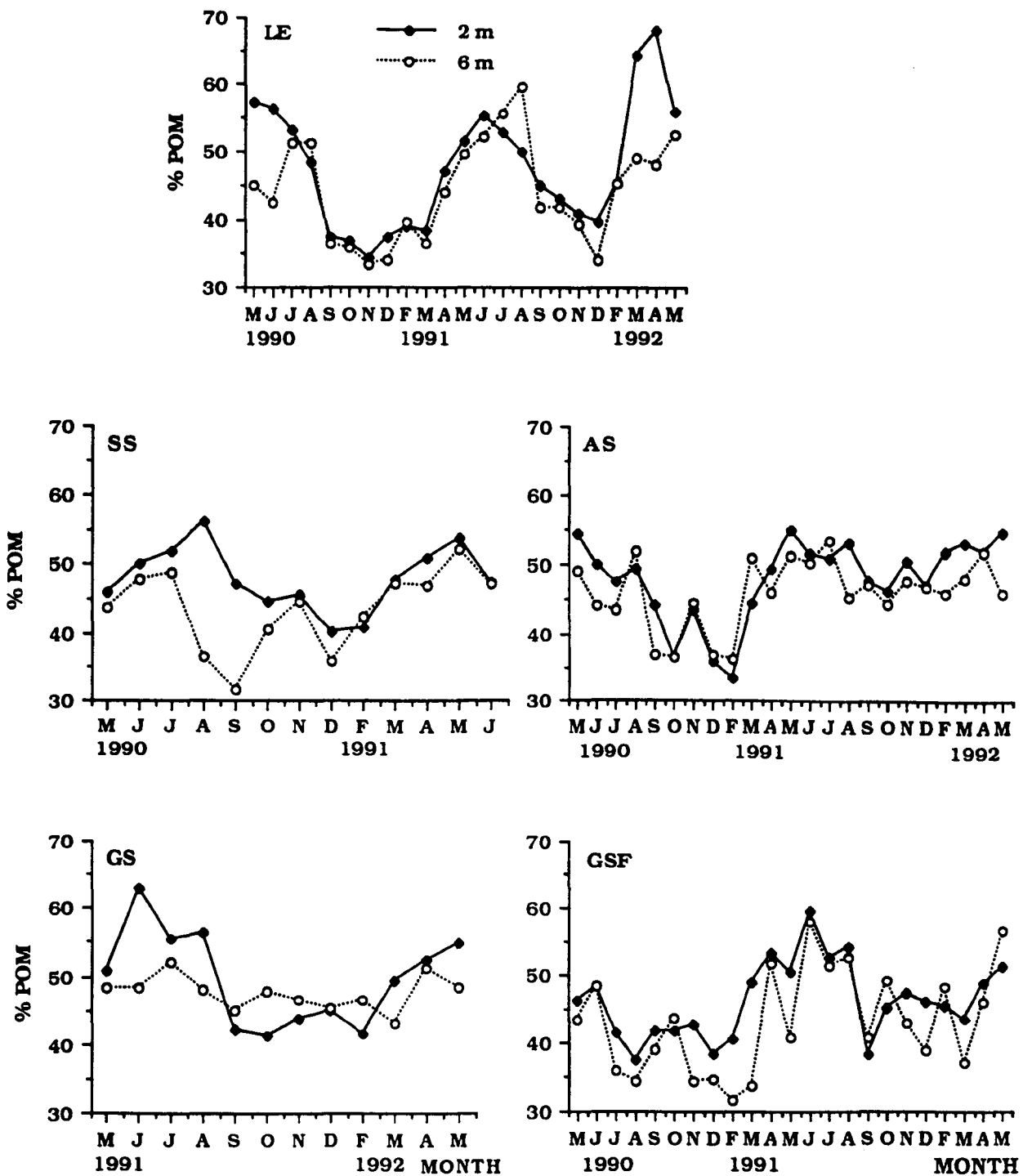
Fig.14. %POM distributions at two sampling depths at five experimental sites in Loch Etive and Leven.
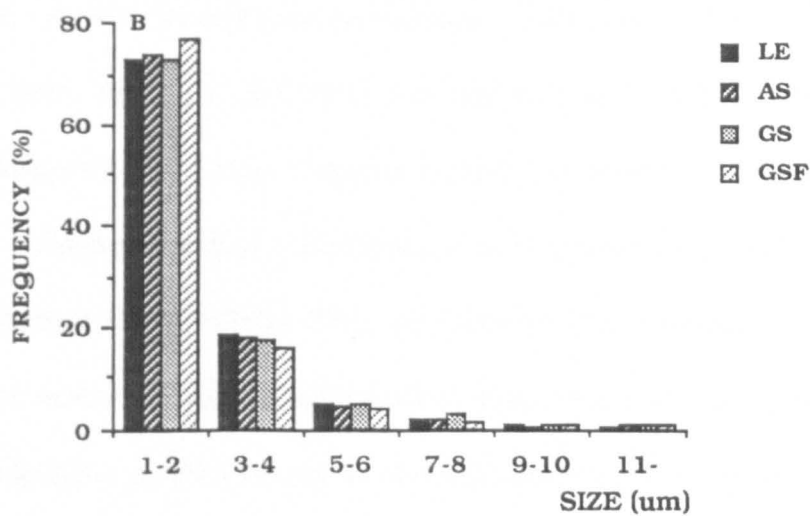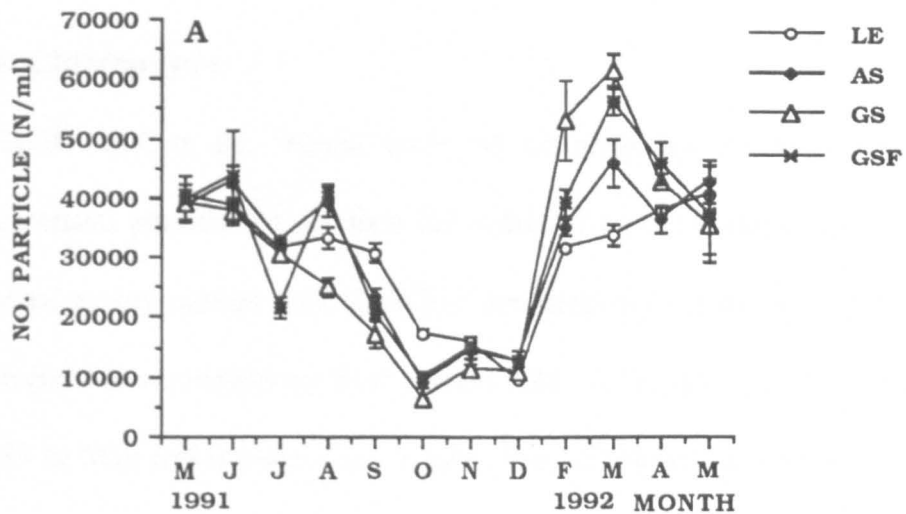
Fig.15. Particle number (a) and size-frequency distribution (b) at sites LE, AS, GS and GSF during the experiment II.

between 1-2 μm and around 18% was in size range of 3-4 μm, and the rest between 5-12 μm. No significant correlation was found between particle number and other environmental parameters, except POM at LE and temperature at GS (Table-7).

4.1.6. Chlorophyll-a

Fig.16 exhibits the annual cycle of chlorophyll-a concentrations during the experimental periods. At all sites the seasonal cycle of chlorophyll-a distributions followed a very similar pattern. When the sampling began in May 1990, the mean chlorophyll-a concentrations were around 1.95 - 2.78, μg l^{-1}, reaching that year's peak at GSF in May and at other sites in June. The chlorophyll-a content started to decline in July and continued until March 1991, dropping to minimum range of 0.11 - 0.40 μg l^{-1} during December-February (Fig.16). The steady increase commenced at all sites in March - April 1991 and reached maximum values of 4.5-4.8 μg l^{-1} at sites in Loch Etive in June, 2.92 μg l^{-1} at GSF in July and 4.23 μg l^{-1} at GS in August 1991. The values dropped under 2.0 μg l^{-1} during August - September and below 1.0 μg l^{-1} after October, reaching minimum concentrations in December 1991 -February 1992. When the experiment ended in May 1992, the chlorophyll-a concentration at sites in Loch Etive rose around 3.4 μg l^{-1}, but in Loch Leven it was still around 1.0 μg l^{-1} (Fig.16).

Chlorophyll-a profiles, which were tested separately for each experiment, showed that values recorded at all other sites were significantly higher than values from GSF. Overall mean concentrations were the highest at AS and lowest at GSF during both experimental periods and between the depths it was slightly higher at 2 m than at 6m at all sites despite of only 4 m differences between two level (Fig.16 and Table-6).
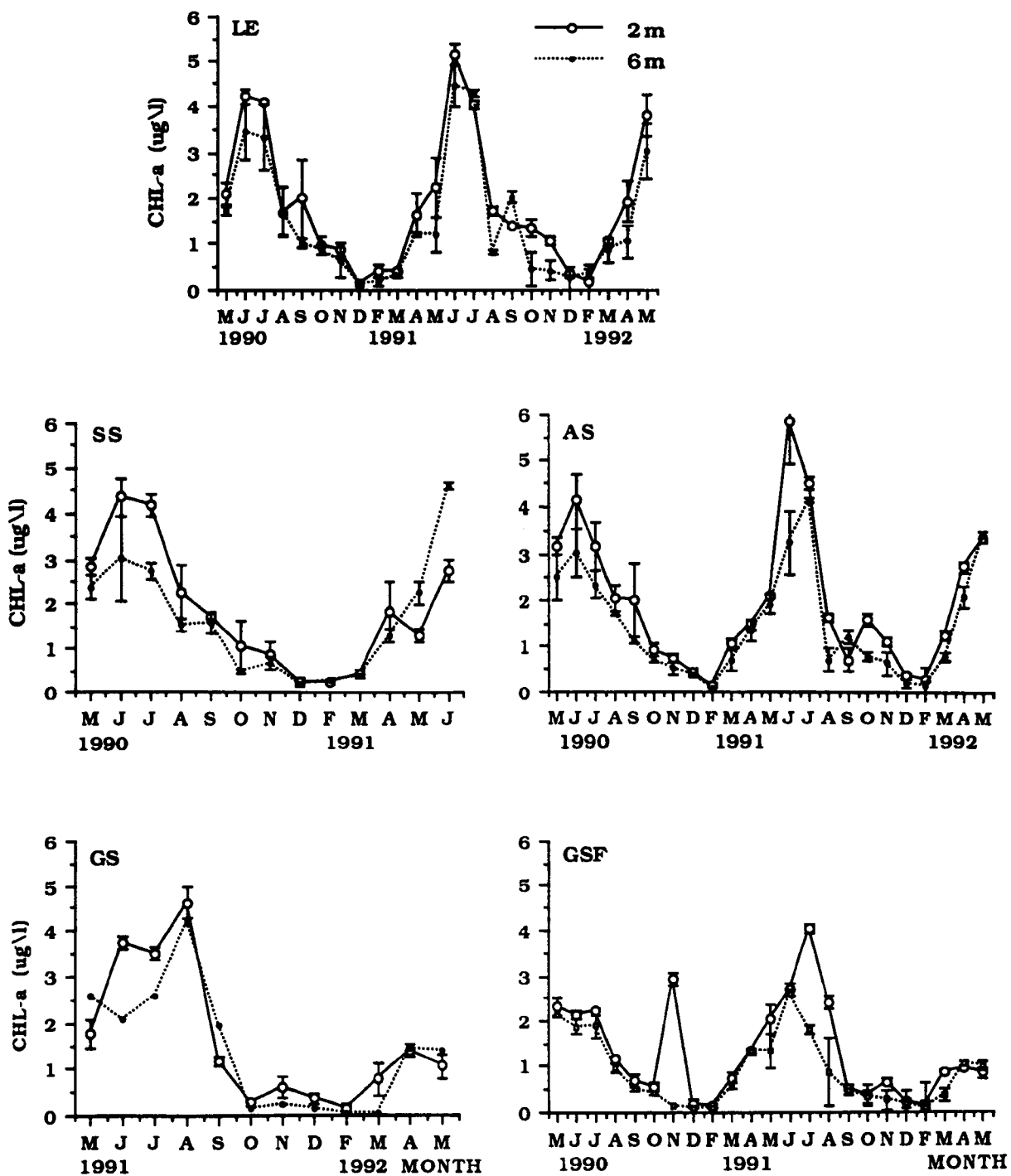
Fig.16. Monthly chlorophyll-a concentrations determined at 2 and 6 m at five experimental sites during May 1990 to 1992.

The variation in chlorophyll-a between the two lochs was compared only for data obtained during the experiment II and the overall mean for sites in Loch Etive was significantly higher than Loch Leven (P≤0.05). There was no detectable differences between overall values from salmon and mussel farms. Apart from particle concentrations, there were significant positive correlations between chlorophyll-a concentrations all other environmental parameters (Table-7).

4.2. Growth

4.2.1. Experiment I

Shell length (L) and somatic (live weight, LW, wet meat, WMW, and ash-free dry meat weight, AFDMW) growth rates for 2 years old cultivated mussel populations were followed by monthly sampling, except in January, at two mussel and two salmon farms, namely Loch Etive Shellfish (LE), Stirling Salmon (SS), Ardchattan Salmon (AS) and Glencoe Shellfish (GSF), over a period of 13 months (from first week of May 1990 to first week of June 1991), and the results are presented in Figs. 17-38, and Tables 8-31.

4.2.1.1. Shell Length

The initial length frequency distribution of the experimental mussel population is given Fig.8, and Figs.17(a-d) display the changes in size-frequency distributions through the experimental period. The main changes in population structure took place during summer (May-September 1990); size range shifted from around 18-34 mm to 24-52 mm in July and 28-56 mm in September. In addition to fast growth rates, heavy
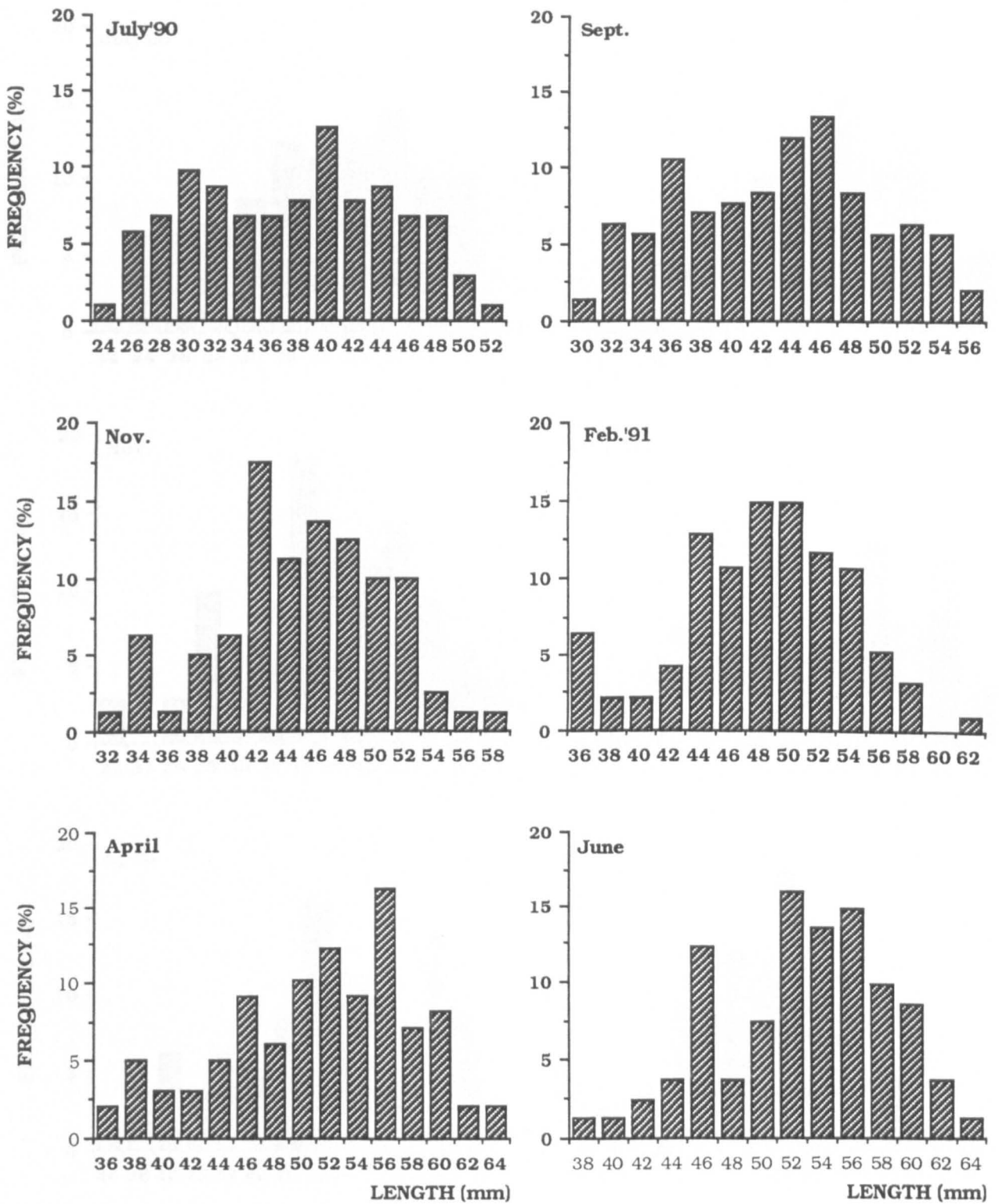
Fig.17(a). Changes in the size-frequency distributions of experimental mussels with an initial size range of 18-34 mm, at sites LE in Loch Etive from July 1990 to June 1991.
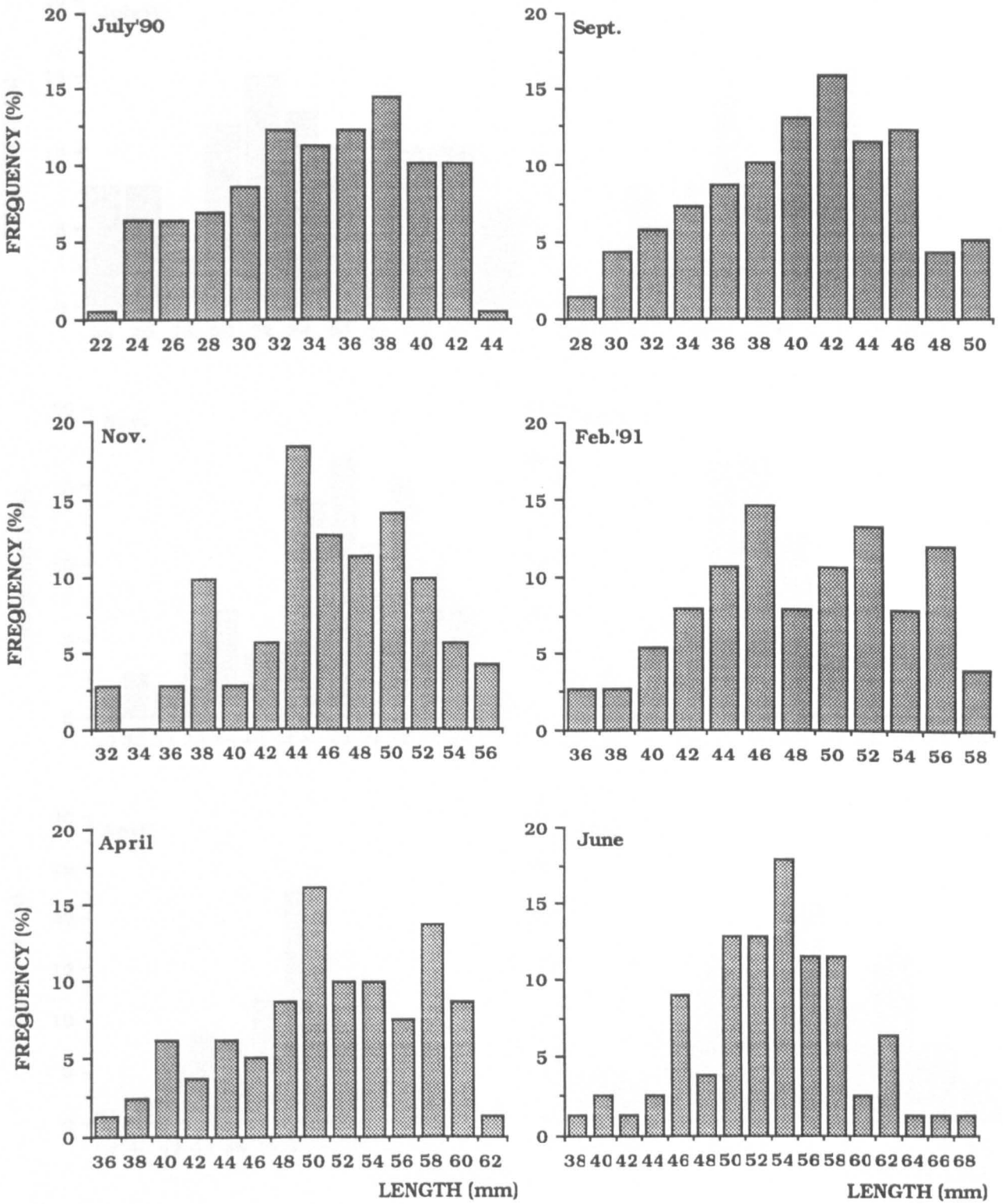
Fig.17(b). Size - frequency for site SS in Dunstaffnage Bay from July 1990 to June 1991.
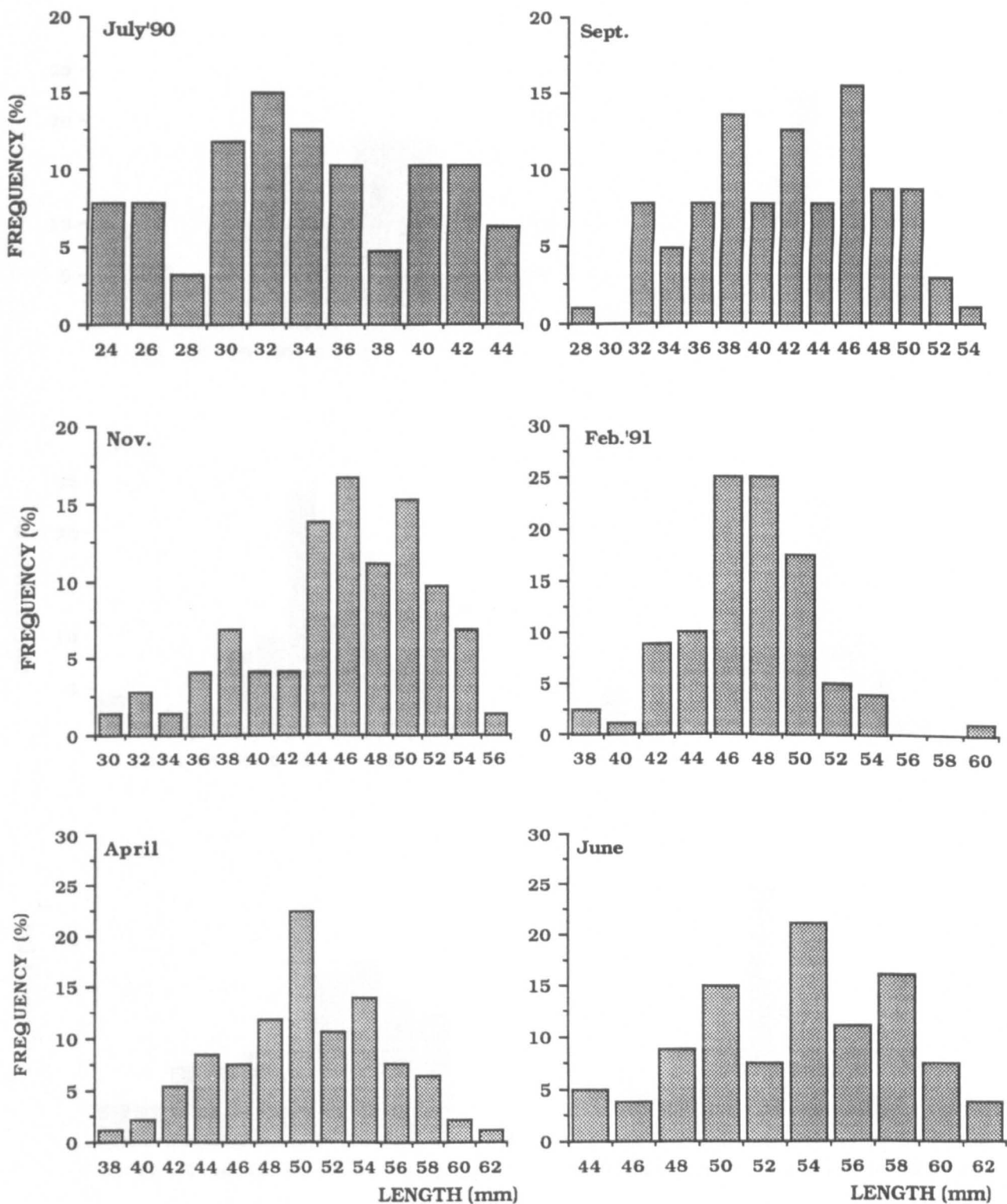
Fig.17(c). Size - frequency for site AS in Loch Etive from July 1990 to June 1991.
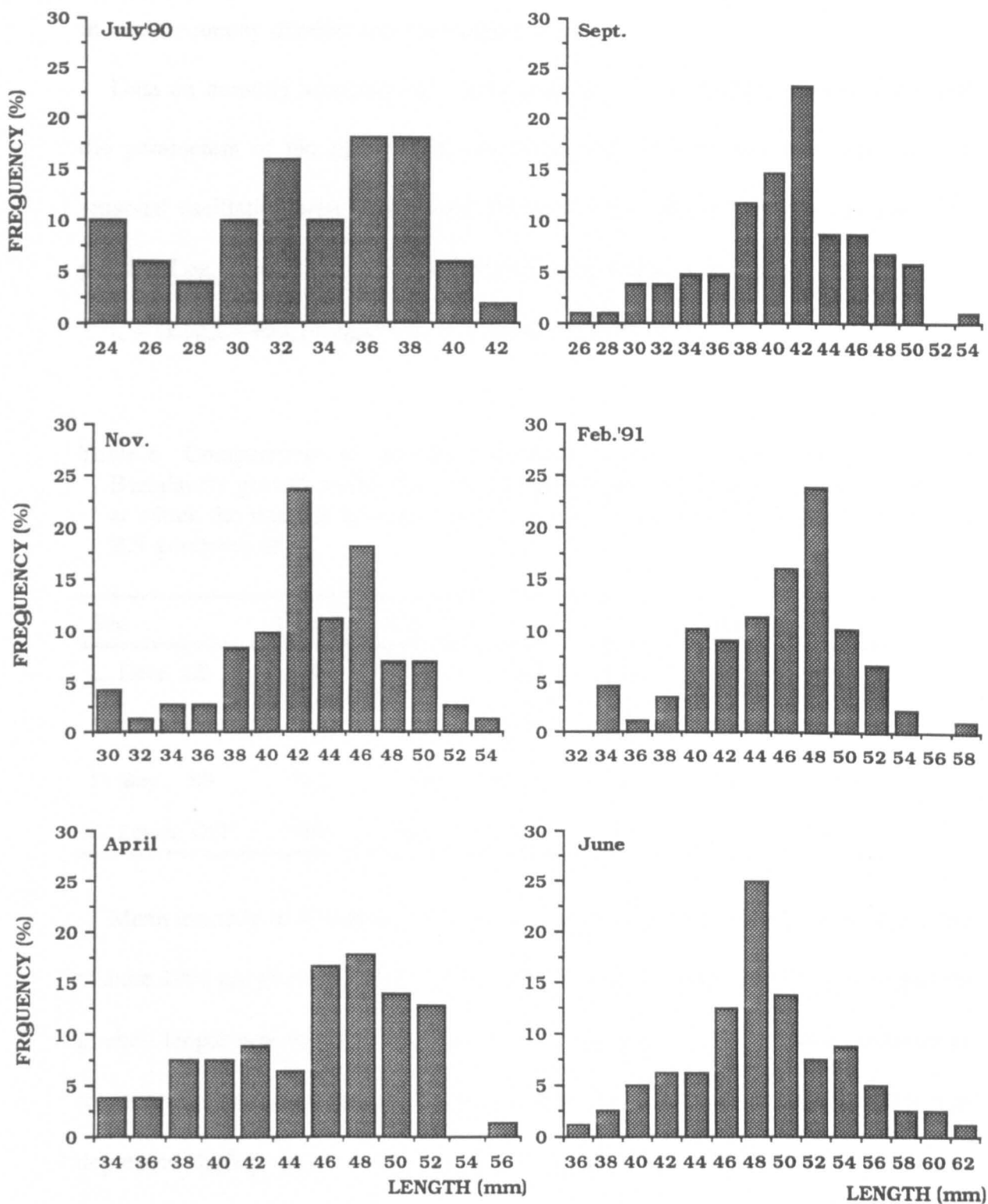
Fig.17(d). Size - frequency for GSF in Loch Leven from July 1990 to June 1991.

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losses and mortality during the first two months had an effect on these rapid changes in size-frequency distributions (see section 4.4).

Data on monthly size-frequency were analysed by the ELEFAN programme and the parameters of the generalised von Bertalanffy growth equations adjusted for seasonal oscillation were determined (Table-8). The values for t_0 are calculated by plotting $Log_e(L\infty-Lt)$ against mean monthly length and using the formula:

$t_0 = [Log_e L\infty + Kt_0) - Log_e L\infty]/K$ (Chatterji et al.,1984).

Table-8. Comparisons of growth parameters in the seasonally oscillating von Bertalanffy growth model. $L\infty$ is asymptotic length, K growth constant, t_0 the age at which the mussels belong to zero mm size, C amplitude, WP winter point and RN goodness of fit.

Site	$L\infty$,mm	$K (y^{-1})$	t_0	C	WP	Rn
L. Etive LE	71.6	1.32	-0.28	0.64	0.94	0.160
" " AS	72.4	1.66	-0.19	0.48	0.46	0.152
D. Bay SS	73.2	1.98	-0.23	0.46	0.81	0.152
L. Leven GSF	68.0	0.98	-0.42	0.75	0.25	0.151

Mean monthly shell lengths (mm) at the four sites and two depths from May 1990 to June 1991 are given in Table-9 and plotted in Fig.18. In general the growth pattern in shell length was similar at all sites. Growth appeared to be continuous throughout the year but the main increases occurred between May and November, and it was depressed during winter months. Average monthly growth during the first growth season, May-November 1990, was highest at SS (3.30 mm) followed by AS (3.27 mm), LE (3.08 mm) and GSF (2.79 mm) during the first growth season. The growth
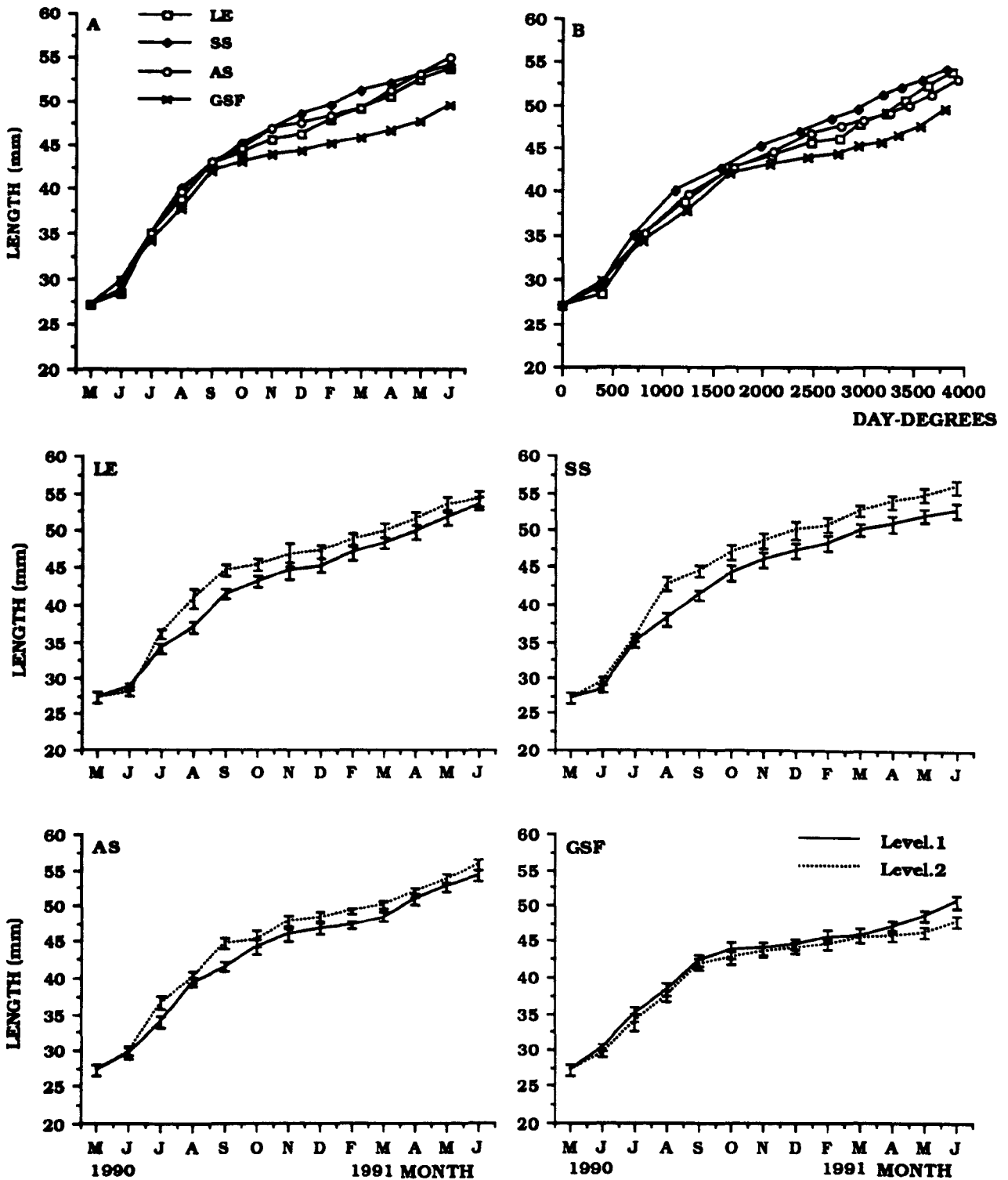
Fig.18. Growth in mean shell length of re-tubed experimental mussels grown in two
salmon and two shellfish farms during experiment I; May 1990 - June 1991.
Overall means compared in A against time and in B against cumulative day-
degrees, followed by comparisons at each site between mussels at 2-4 m (Level
1) and 5-7 m (Level 2); vertical bars indicate SE.

Table-9. Average shell lengths (L ±SE; mm) at each sampling date and monthly growth increments (ΔL,mm) of experimental mussels at four sites; LE= Loch Etive Shellfish, SS= Stirling Salmon, AS= Ardchattan Salmon (Loch Etive) and GSF= Glencoe Shellfish (Loch Leven) in two lochs between May 1990 and June 1991 (13 months). N is monthly sample size and superscripts as explained in Table-6.

| Month | LE | | | SS | | | AS | | | GSF | | |
	L ±SE	ΔL	N	L ±SE	ΔL	N	L ±SE	ΔL	N	L ±SE	ΔL	N
May	27.1 ±0.706		60	27.1 ±0.774		60	27.1 ±0.774		60	27.1 ±0.774		60
June	28.4 ±0.411	1.30	197	28.9 ±0.391	1.76	192	29.7 ±0.482	2.60	146	29.8 ±0.319	2.66	186
July	35.0 ±0.461	6.59	128	35.1 ±0.407	6.17	187	35.1 ±0.560	5.37	127	34.3 ±0.741	4.54	50
August	38.8 ±0.771	3.76	103	40.2 ±0.717	5.12	105	39.6 ±0.529	4.51	144	37.8 ±0.607	3.44	83
September	42.7 ±0.539	3.95	125	42.6 ±0.523	2.44	152	42.7 ±0.539	3.12	125	42.0 ±0.512	4.25	103
October	44.2 ±0.566	1.41	143	45.2 ±0.734	2.59	91	44.6 ±0.729	1.83	84	43.1 ±0.649	1.11	84
November	45.6 ±0.920	1.45	72	46.9 ±0.669	1.69	72	46.7 ±0.687	2.16	72	43.9 ±0.600	0.72	72
December	46.2 ±0.628	0.59	80	48.5 ±0.723	1.57	75	47.5 ±0.592	0.78	72	44.4 ±0.555	0.51	72
February	47.9 ±0.644	1.71	95	49.5 ±0.626	1.02	75	48.2 ±0.382	0.66	80	45.2 ±0.382	0.80	78
March	49.1 ±0.585	1.15	94	51.1 ±0.611	1.63	68	49.2 ±0.425	0.99	86	45.7 ±0.593	0.57	79
April	50.5 ±0.652	1.45	96	52.1 ±0.690	0.95	81	51.2 ±0.486	2.06	94	46.5 ±0.540	0.80	88
May	52.4 ±0.690[b]	1.89	99	53.0 ±0.670[b]	0.92	88	53.0 ±0.540[b]	1.80	94	47.6 ±0.577[a]	1.09	79
June	53.8 ±0.680[b]	1.40	81	54.2 ±0.720[b]	1.17	78	54.9 ±0.533[b]	1.85	80	49.5 ±0.594[a]	1.89	81
Increment												
Total (mm)	26.65			27.03			27.73			22.22		
(%) of												
initial L	98.10			99.59			102.1			81.80		
mm/month		2.05			2.08			2.13			1.71	

Note: there are no data for January 1991 therefore values in February include growth in January as well.

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was considerably slower at GSF than at other sites during the first summer growth season, although there were no significant differences between sites in October. The second growth season appeared to be resumed in March, but it was slow with a mean monthly increment of 0.73- 2.33 mm between March and June 1991 (Table-9 and Fig.18). At the end of experiment I, after 13 months, experimental populations reached an overall mean shell length of 53.04 mm by growing 1.99 mm per month. Changes in time of the monthly specific growth rate for shell length (SGR%), which ranged from 0.1 to 25 percent, are shown in Fig.19. SGR values reached maximum values at all sites in July 1990, decreased steadily until November and remained constant between November and March before slight recovery after March. This trend is reflected in the growth curves of Fig.18.

Statistically significant differences (P≤0.001) in final shell lengths (May and June 1991) were found between the sites (Table-11), and Tukey's Multiple Range test revealed that growth at site GSF was significantly slower than at the rest (Table-9). When overall monthly length increments and final mean shell lengths of sites in and around Loch Etive (LE, SS and AS) were compared, it was observed that mussels suspended at salmon farms (SS and AS) had grown slightly better than at mussel farm (LE), but the differences were not significant (Table-9).

Mussels at level 2 (4-6 m) in Loch Etive and Dunstaffnage Bay grew faster than mussels located at level 1 (2-4 m) and vice versa at GSF (Fig.18). The final shell length differences between depths ranged from 0.72 mm (LE) to 3.26 mm (SS) and depth had significant (P≤0.05) effect on shell length growth only at sites SS and GSF.

The concept of expressing age after settlement or beginning of the experiment
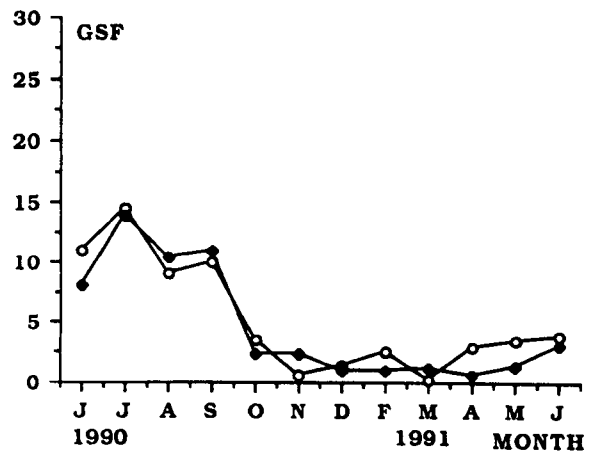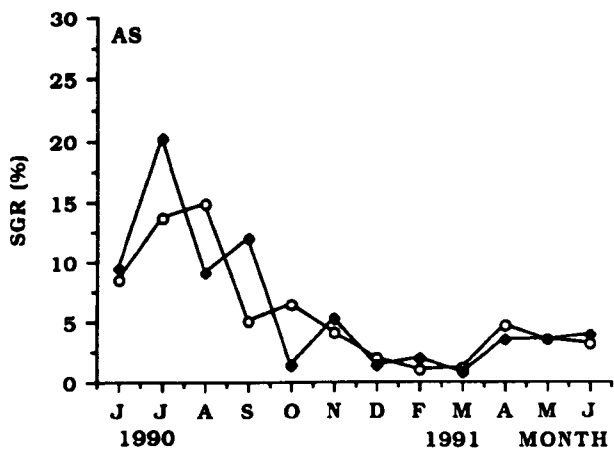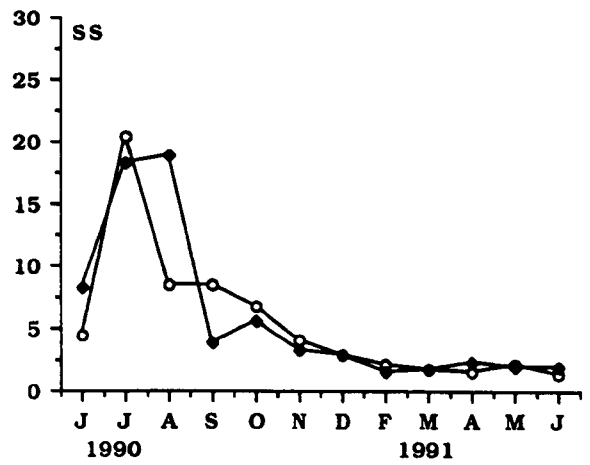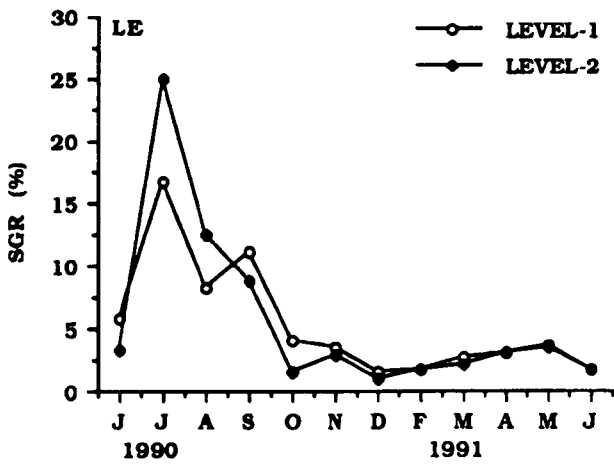
Fig.19. Monthly average length specific growth rate (SGR%) for mussels grown at four sites at two depths (Level.1&2) during the experiment I.

in terms of cumulative day-degrees (the number of days between sampling dates x mean temperature between two sampling date) has been applied to *Mytilus edulis* growth by several authors (e.g. Dare & Davies,1975; Hickman,1979: Wilson,1987). In Fig.18B, the information contained in Fig.18A has been re-drawn on a day-degree basis, which according to Dare & Davies (1975) smooths out seasonal variations due to main environmental variations, and also demonstrates dependence of growth on temperature. As Fig.18B shows, increments in shell length appeared to be linearly related to age in day-degrees ($L = 25.6 + 0.07D°$, $r=0.9733$).

4.2.1.2. Tissue Growth

Variations of LW, WMW and AFDMW are shown in Fig.20, and minimum, maximum and final mean weights recorded during the seasonal cycle are summarised in Table-10. A strong seasonality of tissue growth (total flesh including gonad material), especially WMW and AFDMW, at all sites was evident, with positive growth in the summer and negative growth in the winter months. The pattern of annual variation was as follows: all three, LW, WMW and AFDMW, body weight components continued to increase during the summer and WMW and AFDMW reached peaks in October (Fig.20). Tissue growth at GSF was highly significantly ($P \leq 0.01$ for LW and $P \leq 0.001$ for WMW and AFDMW) slower than at the other three sites, except LW at AS in October (Table-11) . Starting from November meat weights decreased until April and the mean losses of around 8.9 -28.2% WMW and 39.7-54.8% AFDMW were observed during winter period which also comprises main spawning. Tissue growth resumed at all sites after sampling in April and maximum
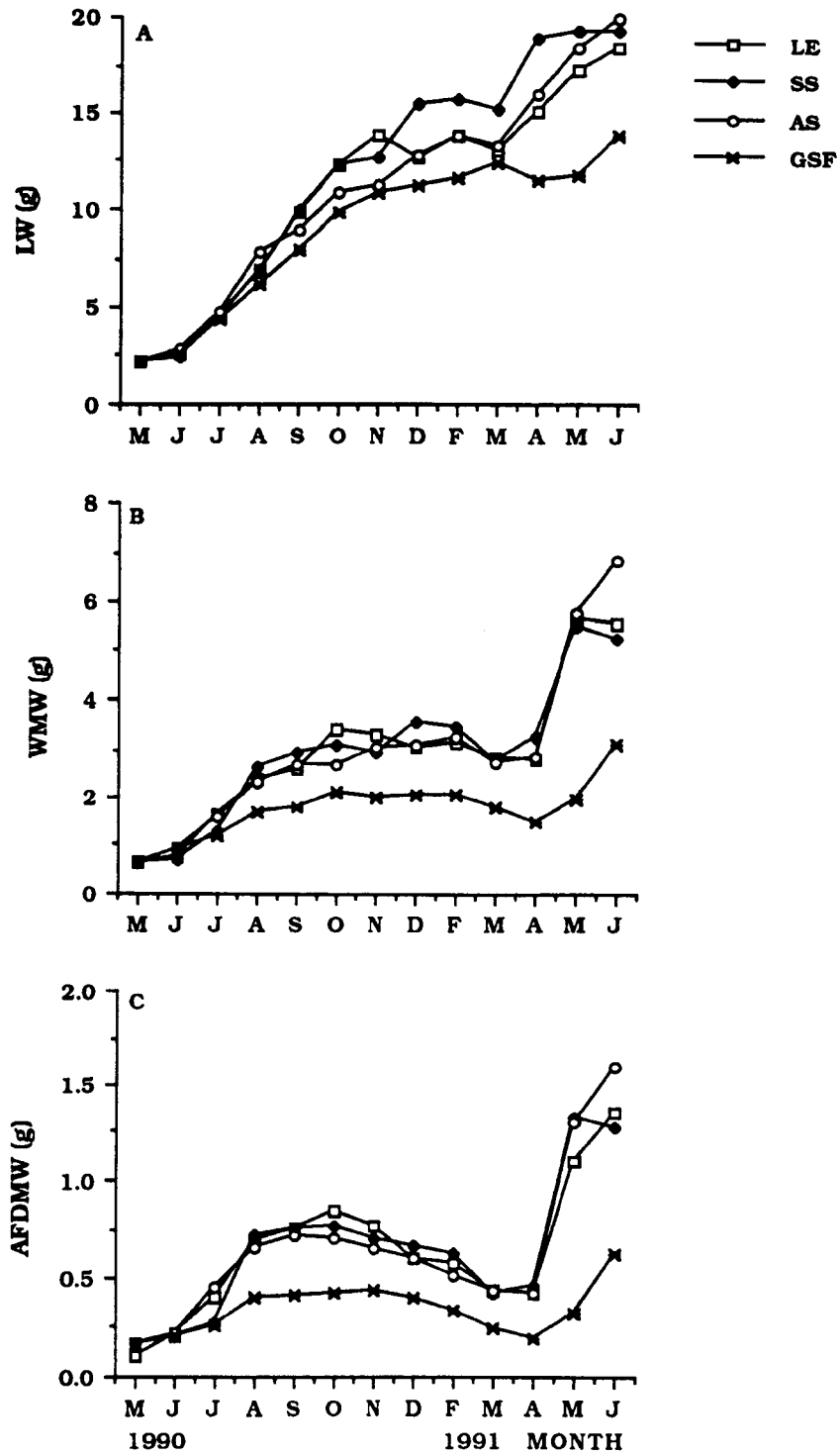
Fig.20. Seasonal changes in live weight (LW), wet (WMW) and ash-free dry meat weights (AFDMW) during experiment I.

Table-10. Mean (±SE) live weight (LW), wet (WMW) and ash-free dry meat weight (AFDMW) values (in g) of experimental mussels at critical sampling dates(October 1990, and April, May and June 1991). Initial weights in May 1990 were: LW=2.16±0.158; WMW=0.68±0.05 and AFDMW=0.16±0.012. Superscript letters as in Table-6.

Parameter	Month	LE ±SE	SS ±SE	AS ±SE	GSF ±SE
	October	12.3±0.681[b]	12.4±0.603[b]	10.8±0.576[ab]	09.9±0.501[a]
	April	15.1±0.729	19.0±0.685	16.0±0.469	11.5±0.498
LW	May	17.3±0.889[b]	19.4±0.769[b]	18.5±0.505[b]	11.8±0.471[a]
	June	18.4±0.815[b]	19.3±0.901[b]	20.0±0.525[b]	13.8±0.535[a]
	Increment	16.26	17.14	17.80	11.70
	October	3.40±0.198[c]	3.05±0.175[c]	2.67±0.165[b]	2.08±0.123[a]
	April	2.79±0.130	3.21±0.121	2.85±0.097	1.49±0.066
WMW	May	5.63±0.253[b]	5.48±0.189[b]	5.75±0.168[b]	1.97±0.098[a]
	June	5.52±0.233[b]	5.25±0.220[b]	6.80±0.186[c]	3.08±0.130[a]
	Increment	4.840	4.570	6.120	2.400
	October	0.85±0.050[b]	0.77±0.040[b]	0.71±0.040[b]	0.43±0.025[a]
	April	0.42±0.020	0.46±0.017	0.43±0.015	0.20±0.009
AFDMW	May	1.40±0.063[b]	1.33±0.048[b]	1.31±0.041[b]	0.32±0.016[a]
	June	1.36±0.056[b]	1.29±0.052[b]	1.60±0.044[c]	0.62±0.026[a]
	Increment	1.200	1.125	1.443	0.464

monthly increases occurred during April-May at sites in Loch Etive and one month later in Loch Leven (Fig.20 and Table-10).

These weight decreases were initiated by decline in available food and possibly secondary spawning in autumn and lasted throughout the winter owing to starvation, and very low values during March-April and sharp increases in May coincided with main spawning and recovery. Maximum absolute increment in weights was at AS and minimum at GSF (Fig.20 and Table-10). Statistical analysis of data from the last two samples showed that there were significant differences between not only GSF and the rest but also between sites in Loch Etive (Table-11). According to Tukey's Multiple

Table-11. Effect of site (factor) on length, LW, WMW and AFDMW of experimental mussels. One-way ANOVA was conducted in three sampling date. According to MRT the site(s) significantly differ(s) from the others is(are) indicated with P, (Tot. DF = 199 for weights), (NS = not significant; * = P≤0.05; ** = P≤0.01 and *** = P≤0.001).

Month (Year)	Source of variance	DF	LENGTH			LW			WMW			AFDMW		
			MS	F	P	MS	F	P	MS	F	P	MS	F	P
October (1990)	Factor	3	66.7	1.51	NS	71.2	4.03	**	15.9	11.4	***	1.78	17.2	***
	Error	398	44.0			17.7		(GSF)	1.40		(GSF)	0.10		(GSF)
	Total	401									(AS)			
May (1991)	Factor	3	556.0	16.0	***	584.1	25.1	***	166.81	95.7	***	14.6	107.1	***
	Error	356	34.8		(GSF)	23.2		(GSF)	0.74		(GSF)	0.14		(GSF)
	Total	359												
June (1991)	Factor	3	493.3	16.1	***	296.7	11.6	***	122.5	58.1	***	9.56	66.8	***
	Error	316	30.6		(GSF)	25.6		(GSF)	2.11		(GSF)	0.14		(GSF)
	Total	319									(AS)			(AS)

Range Test (MRT) all tissue growth parameters at GSF were significantly lower than the others, and WMW at site AS was lower than LE and SS in October 1990, caught up in May 1991 and even overtook the latter in June ($P \leq 0.05$). There was not any evidence suggesting significant differences between Level 1&2. WMW and AFDMW constituted on average 26.7% and 5.8% of live weight, while shell weight averaged 37.0% of live weight.

4.2.1.3. Length - Weight Relationships

Shell lengths were related to dry (DMW) and ash-free dry meat (AFDMW) weights according to the equation $W = a*L^b$. Linear relationships were established between $\log_{10}$ DMW and AFDMW, and $\log_{10}$ shell length (L) using experimental samples from site LE (Table-12). The relationships were determined every month so that the changing condition factor of mussels during the year relative to their reproductive status and starvation could be eliminated, and the tissue growth pattern in the cultivated populations could be predicted by measuring shell length and applying these length-weight regressions. Although the plots of meat weight against shell length showed departures from the regression due to considerably lower meat weight than average, it was generally observed that most of the individuals fitted the regressions well. All regressions of length - DMW and AFDMW were significant, and analysis of covariance demonstrated significance ($P \leq 0.05$).

The allometric relationships between shell length (L; in mm) and dry shell weight (DSW) and ash-free dry shell organic weight (AFDSOW; in g) were also determined and the best fitted lines are plotted in Fig.21. The allometric equation for dry shell

weight was:

$$Log_{10}DSW = -3.54 + 2.61*Log_{10}L \ (r=0.9632; \ 49 \ df),$$

and the equation for ash-free dry shell organic matter weight (AFDSOW) was:

$$Log_{10}AFDSOW = -5.48 + 2.83*Log_{10}L \ (r=0.9817; \ 49 \ df).$$

On average DSOW and AFDSOW were 2.92 ± 0.245% and 2.86 ± 0.256%, respectively, of whole dry shell weight, and the ash content of the shell organic residue after acid treatment was 2.58 ± 0.055%.

Table-12. Monthly length - weight allometric equations ($Log_{10}W = a+bLog_{10}L$) relating dry (DMW) and ash-free dry meat weight (AFDMW) to shell length (L) for experimental mussels grown at LE. a & b are constants, r is correlation coefficient. N = 50 for each month.

Month	DMW			AFDMW		
	a	b	r	a	b	r
May	-5.0306	3.0535	0.9704	-5.2106	3.0828	0.9532
June	-4.8537	2.5621	0.9224	-5.1670	2.7843	0.9456
July	-5.7376	3.1842	0.9627	-5.6403	2.8844	0.9780
August	-5.3624	3.1792	0.9831	-5.5124	3.2009	0.9723
September	-5.8507	3.2624	0.9747	-6.1320	3.3174	0.9168
October	-4.7522	2.9691	0.9817	-4.8265	2.7685	0.9814
November	-5.7789	2.7942	0.9300	-6.0554	2.6943	0.8930
December	-4.5283	2.8246	0.9651	-4.6142	2.6347	0.9841
February	-5.6418	2.8968	0.9068	-5.7413	2.9128	0.9368
March	-6.8316	3.3154	0.9606	-6.8474	3.2885	0.9583
April	-4.7424	2.7612	0.9891	-4.8503	2.5611	0.9890
May	-4.3879	2.7109	0.9498	-4.4565	2.8049	0.9107
June	-5.7377	2.7179	0.9712	-4.8782	2.7179	0.9638

4.2.2. Experiment II

4.2.2.1. Shell Length

The initial length-frequency distribution of stocks is shown in Fig.8 b&c, and Fig.22 presents the final population structures. Initial shell length of both stock had
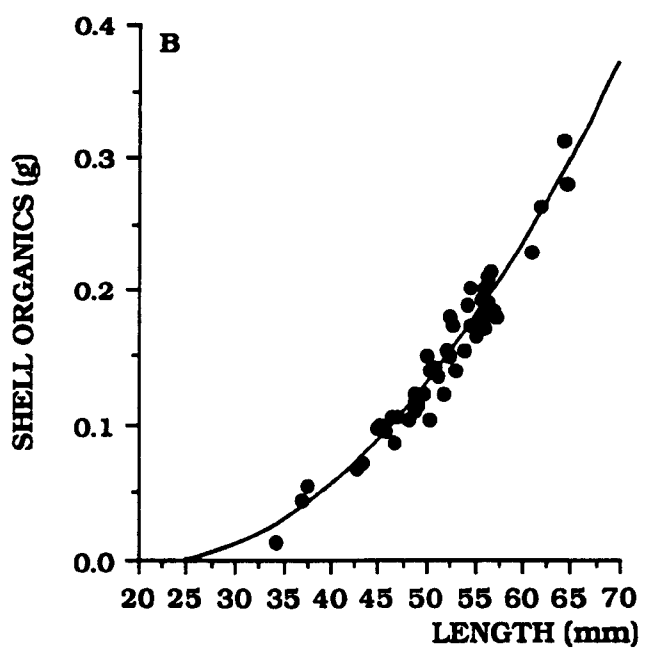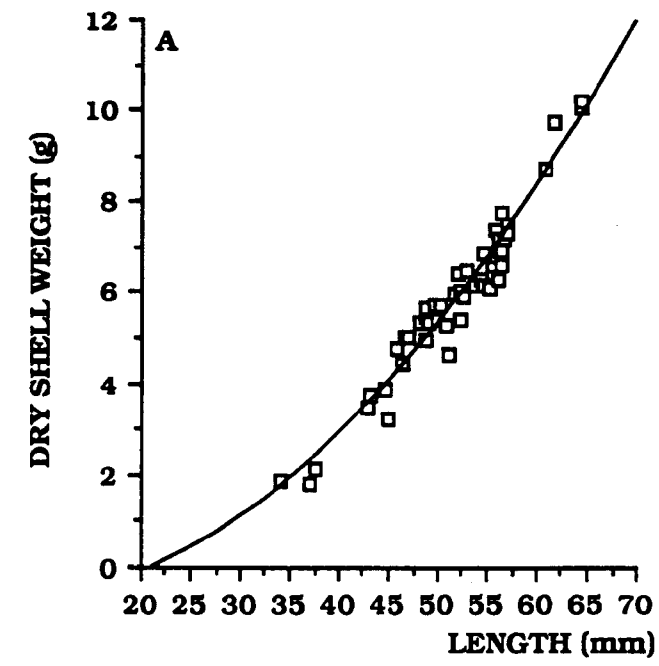
Fig.21. Relationships between shell length - dry shell weight (A) and ash-free dry
shell organic weight (B) fraction of experimental mussels.
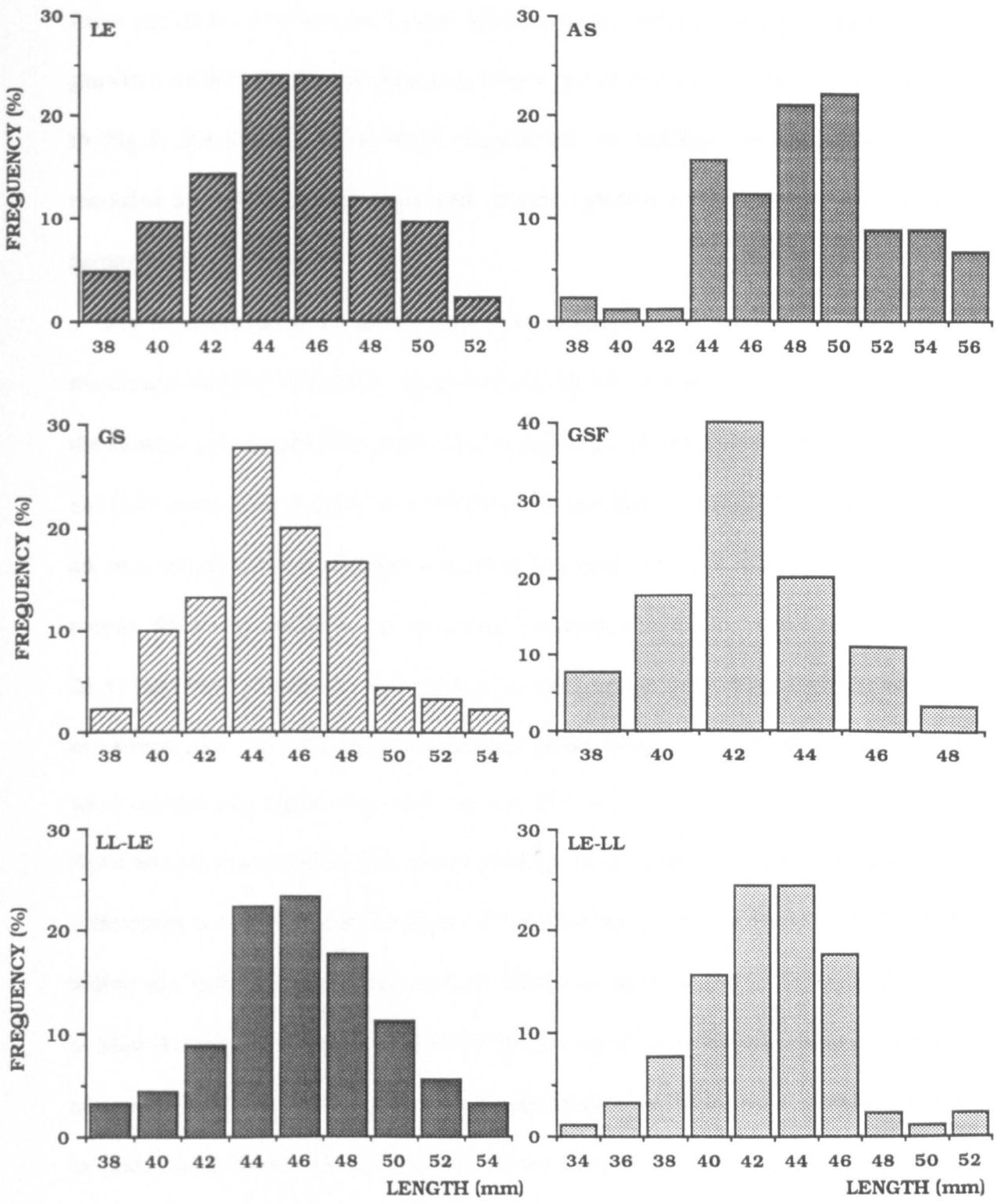
Fig.22. Final length-frequency distributions of experimental native and transplanted mussel stocks, experiment II.

a range of 20.0 - 26.0 mm and the final range was 38.0 - 56.0 mm at sites in Loch Etive and 38.0 - 54.0 in Loch Leven. Monthly mean shell lengths and length specific growth rates for experimental mussels over a period of 1 year at four sites are shown in Fig.23 A&B and Fig.24 A&B, respectively. In addition average shell lengths recorded at each sampling event and monthly growth increments at each site are summarised in Table-13.

As in experiment I, growth rate was temporally variable at all sites, with maximum monthly increments of up to 7 mm/month between May and October, and the slowest growth rate from November to April of 0.39 mm per month in Loch Etive and 0.57 mm/month in Loch Leven (Table-13). The mean increase in shell length over all sites during the experimental period of one year was 23.6 mm or 1.97 mm per month; there was considerable variability, however, ranging from 20.1 mm (GSF) to 26.51 mm (AS) (Table-13). The differences between the lochs were apparent as early as October and the shell length of mussels grown at sites LE and AS in Loch Etive were significantly higher than sites GS and GSF in Loch Leven in all three (October, April and May) analyses of the data (P≤0.001). There were no statistically significant differences between sites in the same loch in October, but the variance in shell length within the lochs was significant in Loch Leven in April (P≤0.05), and in both lochs in May (P≤0.01 for Loch Etive and P≤0.001 for Loch Leven); the shell length growth of mussels suspended from salmon cages was better than those grown at mussel farms in both lochs (Table-13 and Fig.23). When pooled data from salmon sites were compared with mussel sites, the differences were significant both in April and May 1992 (P≤0.001), but not in October 1991. Similarly growth in Loch Etive was

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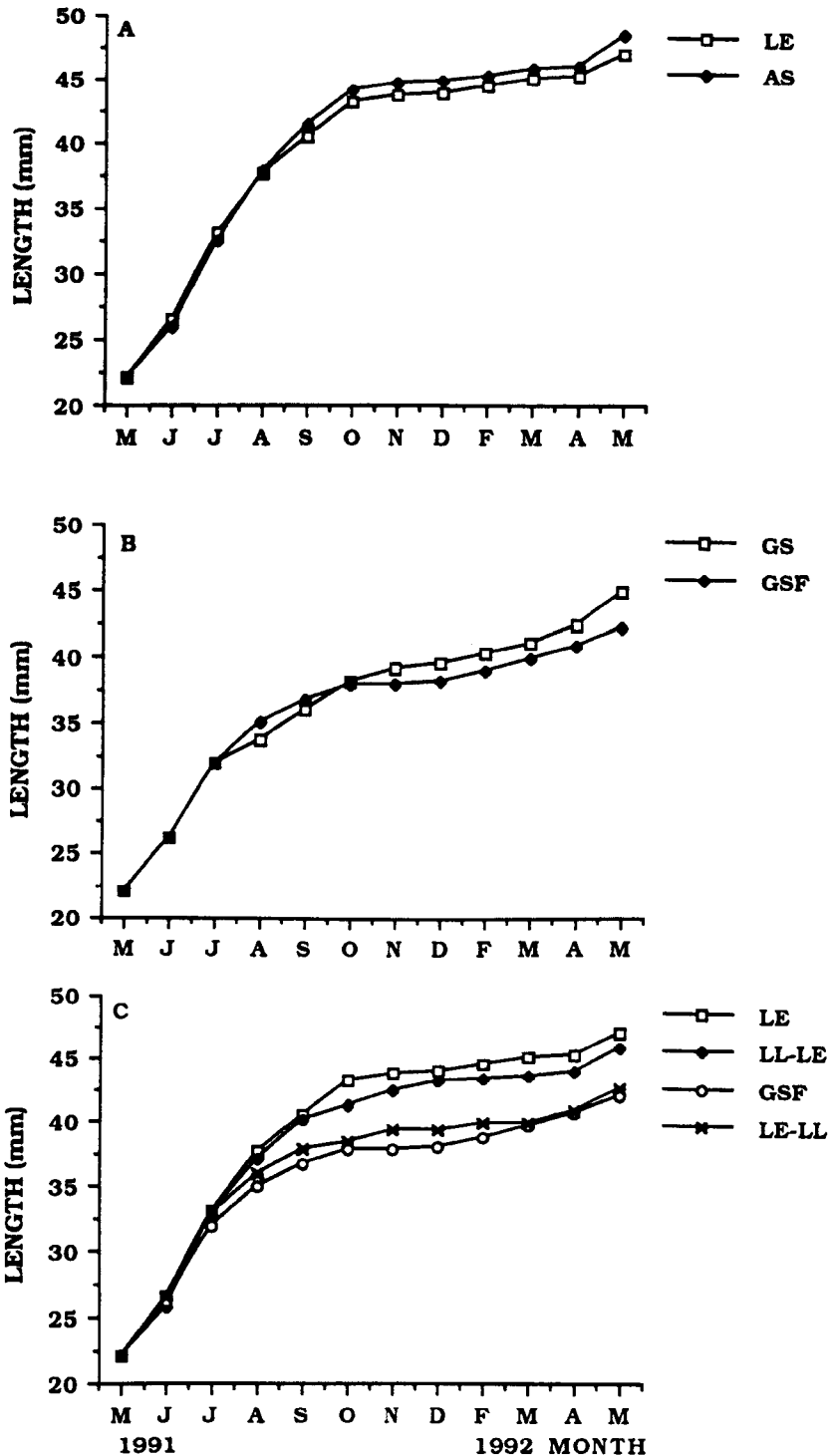
Fig.23. Mean shell length growth of two mussel stocks grown at native and transplanted sites during the experiment II (A: sites in Loch Etive; B: sites in Loch Leven and C: cross-transplanted stocks between Loch Etive and Leven and grown at LE and GSF; LL→LE stock LL, site LE and LE→LL vice versa).
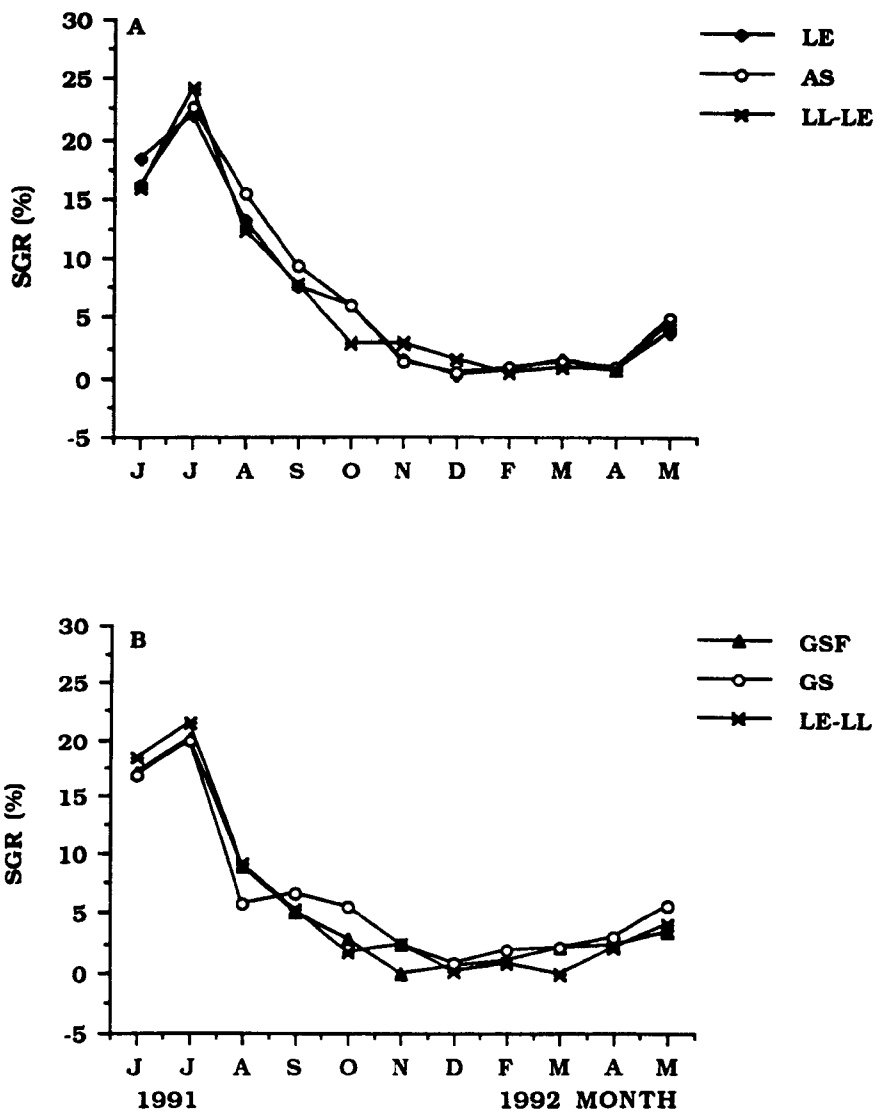
Fig.24. Length specific growth rates of mussels from two stocks grown at native and transplanted sites during the experiment II (A: sites in Loch Etive and B: sites in Loch Leven).

Table-13. Mean shell lengths (L ±SE; mm) recorded at each sampling and monthly growth increments (ΔL, mm) of two mussel stocks grown at native and transplanted sites during the experiment II May 1991-92, 12 months. LL→LE stock LL, site LE and LE→LL vice versa, N=70 in May 1991, 90 in May 1992 and around 42 all other sampling dates. Superscript letters as explained in Table-6.

Sites/Stocks	LE		AS		GS		GSF		LL→LE		LE→LL	
Month	L ±SE	ΔL	L ±SE	ΔL	L ±SE	ΔL	L ±SE	ΔL	L ±SE	ΔL	L ±SE	ΔL
May	22.1±0.23		22.1±0.23		22.1±0.23		22.1±0.23		22.1±0.23		22.1 ±0.23	
June	26.5±0.28	4.44	25.9±0.35	3.85	26.1±0.31	4.03	26.2±0.29	4.07	25.9±0.28	3.78	26.5±0.37	4.43
July	33.0±0.33	6.51	32.5±0.47	6.54	31.8±0.40	5.73	32.0±0.28	5.83	32.9±0.29	7.07	32.8±0.41	6.32
August	37.7±0.42	4.69	37.9±0.38	5.42	33.7±0.32	1.87	34.9±0.45	2.95	37.2±0.32	4.26	36.0±0.35	3.14
September	40.5±0.54	2.95	41.6±0.58	3.71	36.1±0.43	2.35	36.8±0.42	1.85	40.2±0.46	3.03	37.9±0.62	1.93
October	43.2±0.62[c]	2.52	44.2±0.56[c]	2.58	38.1±0.47[a]	2.07	37.8±0.36[a]	1.03	41.3±0.42[b]	1.12	38.5±0.47[a]	0.63
November	43.9±0.58	0.68	44.8±0.63	0.60	39.1±0.34	0.95	37.8±0.45	0.01	42.6±0.38	1.22	39.4±0.41	0.91
December	44.0±0.42	0.11	45.0±0.63	0.19	39.4±0.52	0.30	38.1±0.38	0.23	43.3±0.46	0.69	39.5±0.45	0.05
February	44.6±0.50	0.66	45.3±0.59	0.37	40.1±0.46	0.75	38.9±0.43	0.84	43.4±0.51	0.15	40.1±0.34	0.61
March	45.2±0.53	0.67	45.9±0.59	0.56	41.0±0.36	0.90	39.8±0.46	0.88	43.7±0.48	0.33	40.1±0.45	0.02
April	45.5±0.40[d]	0.24	46.3±0.39[d]	0.36	42.3±0.47[b]	1.29	40.8±0.46[a]	0.98	44.0±0.42[c]	0.22	41.0±0.45[a]	0.90
May	47.2±0.40[d]	1.69	48.6±0.42[e]	2.33	44.9±0.35[b]	2.56	42.2±0.24[a]	1.42	46.0±0.37[c]	2.00	42.8±0.34[a]	1.79
Total Increment (mm)	25.16		26.51		22.80		20.09		23.87		20.69	
(%)	113.7		120.1		103.3		90.99		108.1		93.75	
mm mo⁻¹		2.10		2.21		1.90		1.67		1.99		1.72

significantly higher than in Leven in all comparisons. The overall growth pattern in shell length were very similar in both experiment I & II. The length growth of transplanted mussels is described in a later section (4.2.3).

4.2.2.2. Tissue Growth

As has been described in section 4.2.1.2, there was a pronounced annual cycle in live and meat weights at all sites. Fig.25 clearly shows a rapid and continuous growth from early summer to through autumn up to October-November, especially at sites in Loch Etive. The meat weights reached maximum mean values of 1.60 - 2.70 g (WMW) and 0.37-0.66 g (AFDMW) around October with a mean increment of 0.28 and 0.09 g mo^{-1} WMW and AFDMW, respectively (Table-14), whereas increments in live weight continued at a less pronounced rate throughout the winter indicating the replacement of losses in meat content with water. In October 1991, WMW and AFDMW of samples from sites in Loch Etive were significantly higher, after the adjustment for initial differences, than those from Loch Leven (P≤0.001), and also AS was better than LE (P≤0.05). No marked changes took place in WMW from October to April when it dropped sharply to a minimum of 1.06-1.67 g. AFDMW, however, decreased gradually to minimal values (0.15 - 0.23 g) in April and then growth resumed very rapidly (Table-14 and Fig.25 E,F). The spring peaks in tissue growth coincided with the recovery period right after the main spawning and start of that year's shell growth. Since the WMW did not change as much during this period, the decrease of AFDMW must have been compensated by an increase in water content (see section 4.6.2.1). By the end of the experiment, the overall mean increases in
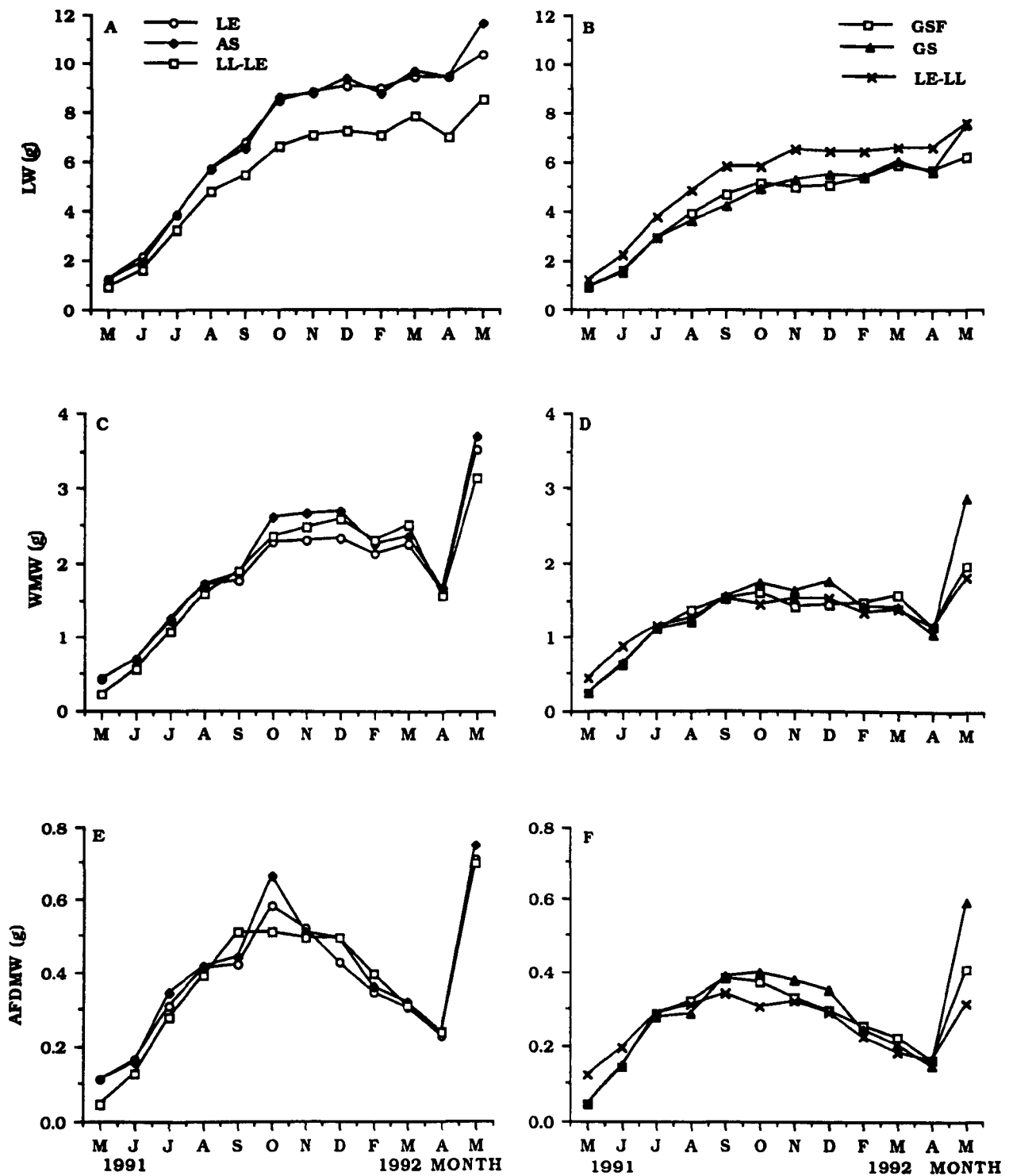
Fig.25. Seasonal variations in live weight (A&B), wet meat (C & D) and ash-free dry meat weights (E & F) (g) of mussels between May 1991 and May 1992, experiment II.

Table-14. Mean (±SE) live weight (LW), wet (WMW) and ash-free dry meat weight (AFDMW; in g) growth of experimental mussels at critical sampling dates (May 1991, October 1991, and April and May and 1992). K is instantaneous growth rates. Superscript letters explained in Table-6.

Character	Month	SITES / STOCKS					
		LE	AS	GS	GSF	LL→LE	LE→LL
LW	May (initial)	1.23 ±0.039	1.23 ±0.039	0.91 ±0.036	0.91 ±0.36	0.91 ±0.036	1.23 ±0.039
	October	8.45 ±0.335	8.61 ±0.311	4.95 ±0.178	5.17 ±0.161	6.60 ±0.220	5.82 ±0.186
	April	9.47 ±0.289	9.45 ±0.271	5.60 ±0.251	5.67 ±0.142	7.02 ±0.196	6.62 ±0.232
	May	10.40±0.412^d	11.70±0.405^e	7.57 ±0.261^b	6.24 ±0.172^a	8.52 ±0.299^c	7.64 ±0.292^b
	Increment (g)	9.18^d	10.47^e	6.66^b	5.33^a	7.61^c	6.41^b
	(%)	746.3	848.8	731.9	585.7	836.3	521.1
	K (mo^{-1})	0.178	0.188	0.177	0.160	0.186	0.152
WMW	May (initial)	0.43 ±0.015	0.43 ±0.015	0.24 ±0.008	0.24 ±0.080	0.24 ±0.008	0.43 ±0.015
	October	2.28 ±0.094	2.61 ±0.103	1.71 ±0.063	1.60 ±0.052	2.36 ±0.090	1.45 ±0.059
	April	1.61 ±0.047	1.67 ±0.062	1.06 ±0.038	1.15 ±0.034	1.55 ±0.045	1.16 ±0.042
	May	3.52 ±0.145^c	3.71 ±0.144^c	2.86 ±0.079^b	1.96 ±0.045^a	3.14 ±0.122^{bc}	1.83 ±0.060^a
	Increment (g)	3.09^d	3.28^d	2.620^c	1.72^b	2.90^{cd}	1.40^a
	(%)	718.6	762.8	1091.7	716.7	1208.3	325.6
	K (mo^{-1})	0.175	0.180	0.206	0.175	0.121	
AFDMW	May (initial)	0.11 ±0.004	0.11 ±0.004	0.05 ±0.002	0.05 ±0.002	0.05 ±0.002	0.11 ±0.004
	October	0.58 ±0.024	0.66 ±0.026	0.40 ±0.015	0.37 ±0.012	0.51 ±0.019	0.31 ±0.013
	April	0.23 ±0.006	0.23 ±0.009	0.15 ±0.005	0.16 ±0.005	0.23 ±0.007	0.14 ±0.005
	May	0.71 ±0.029^d	0.75 ±0.029^d	0.60 ±0.016^c	0.41 ±0.009^b	0.70 ±0.027^d	0.32 ±0.010^a
	Increment (g)	0.60^{cd}	0.63^d	0.55^c	0.36^b	0.65^d	0.21^a
	(%)	533.9	567.0	1100.0	720.0	1300.0	191.0
	K (mo^{-1})	0.155	0.160	0.207	0.175	0.220	0.089

weight components, excluding transplanted mussels, were higher at sites in Loch Etive than Loch Leven ($P \leq 0.001$). Final LW weight of mussels grown at AS was significantly heavier than those grown at LE ($P \leq 0.01$) which was the only site difference within Loch Etive, whereas within Loch Leven all three tissue growth parameters were considerably higher at GS than GSF in May 1992 ($P \leq 0.001$); thus the site associated with salmon farming had a considerable positive effect on tissue growth in Loch Leven, but not in Loch Etive except for live weight.

4.2.2.3. Growth of Transplanted Mussels

Seed mussels used for experiment I all came from Loch Etive (LE), including those at site GSF in Loch Leven (LL) and the performance of these mussels in LL was not as good as those in LE (section 4.2.1). In addition, mussel farmers who cooperated with us during this study suggested that there seemed to be some morphological differences between LE and LL 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 genetic. Reciprocal transplantations were, therefore, conducted using same age (one year old) and sizes of rope-grown mussels during experiment II in order to compare growth rate, mortality and morphology in transplanted mussels from LE and LL stocks with that of their native in situ stocks. Length and tissue growth results of transplanted mussels are given in this section, and morphology in section 4.3, while the other results such as mortality, condition index and biochemical composition are presented under the relevant

sections.

The growth rate of LL mussels transplanted to LE (called LL→LE) in May 1991 increased dramatically compared to the control population in LL, at site GSF, and nearly approached that of control (native) mussels in LE (Fig.23C and Fig.24). The rapid increase in growth rate after transfer resulted in characteristic growth marks on the shells, although the general shell shape and colour of the LL mussels remained unaltered.

The growth of LE mussels transplanted to LL (called LE→LL), on the other hand, was very slow compared to control stock grown in LE, but it was very similar to the native LL stock (Fig.23C and Fig.24). Table-13 shows mean shell lengths for transplanted (LL→LE and LE→LL) and control (LE and GSF) stocks recorded at each monthly sampling. At the end of the one year experiment average final shell length in Loch Etive (LE and LL→LE) was 46.56 mm and 42.47 mm in Loch Leven (GSF and LE→LL), and the mean final length attained by LE and LL stocks were 44.97 mm and 44.06 mm, respectively (Table-13).

Variations in live and meat weights for the transplanted mussels are plotted in Fig.25 and summarised in Table-14. The growth of both transplanted stocks followed the growth pattern exhibited by native stocks; LL→LE was similar to LE and LE→LL to GSF. The biggest difference between transplanted and native stocks was observed in live weight. Although live weight increment of LL→LE was faster than control stock in LL, as it was with length, the native LE stock had higher mean live weight (Fig.25A&B). The increase in mean live weight over all stocks were 7.80 (LE) and 6.47 g (LL), and for sites 8.40 (LE) and 5.87 g (GSF). The considerable live weight

differences between the stocks was a result of shell weight differences between the two stocks (see section 4.3). Unlike live weight, tissue growth of transplanted mussels was very similar to native stocks (Fig.26C-F). The tissue growth of both native and transplanted stock was better in LE than LL (Table-14 and Fig.26 C-F). However, comparisons of absolute growth rates between LE and LL stocks are difficult because initially LE was significantly heavier in LW, WMW and double the AFDMW. The comparisons of monthly instantaneous growth rates (Table-14) show that LL→LE have grown faster than LE and LL, and growth of LE→LL was the slowest.

The effect of site, stock and site*stock on growth was checked on three occasions (October 1991 and April and May 1992) by conducting 2-way ANOVA, after the adjustment for initial weight differences between stocks by using covariance analysis (ANCOVA), and the results are given in Table-15. Both site and stock significantly affected length growth (P≤0.001 for site and P≤0.01-0.05 for stock), but site differences, which accounted for nearly 30% of the variance, appear as the dominant factor, being about fifteen times as important as stock, which only accounted for less than 2% of total variance. The influence of both site and stock on live weight was highly significant (P≤0.001), and again the contribution of site to total variance (around 27%) was considerably higher than that of the stock (13%) with significant interaction in October and April (3.0%). Finally, most of the variance in WMW was explained only by site (44%) but in AFDMW by site (41%) and site*stock (3%). The effect of site on both meat weights was very highly significant (P≤0.001), but there was no significant effect of stock (Table-15).

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Table-15. Results two-way ANOVA on shell length, live weight (LW), wet (WMW) and ash-free dry meat (AFDMW) weights of transplanted mussels; where DF degree of freedom, Var is the variance component, %Var is the percent of the total variance explained by each factor, and P is the level significance (ns: not significant, *: P≤0.05, **: P≤0.01 and ***: P≤0.001).

Month (Year)	Factors	LENGTH				LW				WMW				AFDMW		
		DF	Var	%Var	P	DF	Var	%Var	P	Var	%Var	P	Var	%Var	P
	Site	1	705	29.8	***	1	172	27.3	***	26.7	40.2	***	1.95	35.8	***
October	Stock	1	68	2.9	**	1	66	10.4	***	0.60	0.90	ns	0.02	0.29	ns
(1991)	Stock*Site	1	14	0.6	ns	1	15	2.4	*	0.05	0.08	ns	0.22	4.01	***
	Error	164	1578			164	377			39.1			3.25		
	Total	167	2365			167	630			66.4			5.44		
	Site	1	625	31.8	***	1	186	27.8	***	7.6	38.3	***	0.36	27.9	***
April	Stock	1	33	1.66	*	1	122	18.2	***	0.05	0.26	ns	0.00	0.0	ns
(1992)	Stock*Site	1	18	0.91	ns	1	24	3.5	***	0.02	0.09	ns	0.04	3.23	**
	Error	164	1292			164	338			0.51			0.90		
	Total	167	1967			167	669			0.18			1.31		
	Site	1	1508	28.1	***	1	289	25.0	***	93.0	51.9	***	5.22	58.4	***
May	Stock	1	73	1.36	**	1	121	10.5	***	0.71	0.40	ns	0.07	0.79	ns
(1992)	Stock*Site	1	9	0.16	ns	1	2.9	0.24	ns	3.07	1.72	*	0.11	1.24	*
	Error	356	3786			176	744			82.0			3.54		
	Total	359	5376			179	1157			178			8.94		

4.2.3. Evaluation of Site, Salmon Farm and Stock Effects

In the light of findings during experiments I&II it is possible to rank lochs, sites including salmon effects, (LE, AS, SS, GS and GSF) and stocks (LE, LE→LL, LL and LL→LE) according to final shell length and mean increments in live weight, wet meat weight, ash-free dry meat weight, final AFDW biomass and cumulative net production. When sites and stocks within each loch are combined, the performance of all the above mentioned parameters at sites in Loch Etive (as loch) was significantly better than Loch Leven ($P \leq 0.01$) during both experiments. At the end of experiment I (June 1991) all tested parameters, i.e length, LW, WMW, AFDMW and final biomass in mussels grown at GSF (Loch Leven) were much lower than those grown at other sites ($P \leq 0.001$) (see also Tables-9,10&25). The only significant differences between other sites, namely LE, AS and SS, were higher meat weights (WMW and AFDMW) at AS ($P \leq 0.05$); the other growth, biomass and production values of mussels grown at AS were also slightly higher than the other two sites. Length and LW growth at SS were very slightly better than at LE but WMW, AFDMW, biomass and production were poorer. Thus the mussels at site AS exhibited the best performance during experiment I, followed by LE and SS, but when data from salmon sites are pooled and compared with LE, which is accepted as the control site for the salmon farm effect on growth, none of the above mentioned parameters were significantly different except for WMW ($P \leq 0.05$).

The results of experiment II are summarised in Table-16 (see also Tables-13-15) to illustrate the growth performance of experimental mussels at different sites in the two lochs, and also stock and salmon effects in order of to rank. As can be

Table-16. Mean final (in May 1992) shell length of experimental mussels with initial length of 22.1 mm in May 1991, and mean increments in live weight (LW), wet meat weight (WMW) and ash-free dry meat weight (AFDMW) over the same period arranged in rank order of sites and stocks according growth performance (1 is lowest and 6 is the best performance). Superscript letters indicate overall MRT comparisons of sites and stocks, and * significance level (*,** and *** = P≤0.05, P≤0.01 and P≤0.001 respectively) for salmon "effect" comparison within each loch.

Parameter	Loch / Rank	Loch Leven			Loch Etive			Comments
		1	2	3	4	5	6	
Site/Stock Shell Length (mm)		LL 42.17^a	LE→LL 42.76^a	GS*** 44.88^b	LL→LE 45.95^c	LE 47.17^d	AS** 48.58^e	Highly significant salmon, and stock (P≤0.01) effects LE>LL. No interaction
Site/Stock LW (g)		LL 5.33^a	LE→LL 6.41^b	GS*** 6.66^b	LL→LE 7.41^c	LE 9.17^d	AS** 10.47^e	Highly significant salmon, and stock (P≤0.001) effects LE>>LL. No interaction
Site/Stock WMW (g)		LE→LL 1.40^a	LL 1.72^b	GS*** 2.62^c	LL→LE 2.90^{cd}	LE 3.09^d	AS 3.28d	No stock effect and salmon effect only in Loch Leven. Significant (P≤0.05) site*stock interaction. Worst performance of LE→LL.
Site/Stock AFDMW (g)		LE→LL 0.21^a	LL 0.36^b	GS*** 0.55^c	LE 0.60^{cd}	AS 0.64^d	LL→LE 0.65^d	Best performance by LL→LE

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seen in Table-16, ranking orders of length and LW, and WMW and AFDMW are the same and significance levels are very similar. According to overall ranking for sites and stocks, mussels at salmon site (AS) in Loch Etive showed the best performance (although the site was 5th in AFDMW due to very slight differences).

Salmon farm (GS) in Loch Leven was the third in overall ranking, and the first within Loch Leven. The salmon site had a significant effect on all parameters in Loch Leven, but only on length and LW in Loch Etive. In site - stock comparisons, site was the main factor governing all growth parameters of mussels length ($P \leq 0.01$) and LW ($P \leq 0.001$), while only WMW and AFDMW were significantly affected by site*stock interaction and in AFDMW the best performance was LL→LE the best but differences between native LE and transplanted mussels were not significant.

4.2.4. Relationships between Growth Rate and Environmental Factors

Correlation coefficients relating the monthly length and tissue growth rates to temperature, chlorophyll-a and particulate organic matter were determined for all sites combined as well as for individual sites during the each experiment. The correlation coefficients and significance levels for all sites combined for each experiment are presented in Table-17, since there was no significant relationship between POM and growth parameters, this is not shown in that table. There was quite strong correlation between monthly shell length growth rate and temperature and chlorophyll-a concentrations during both experiments. LW also correlated significantly with temperature in both experiment and chlorophyll-a in experiment II, while meat weights were clearly related to chlorophyll-a.

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Table-17. Linear correlation coefficients (r) and significance levels of shell length and tissue growth rates against water temperature and chlorophyll-a for all sites combined (NS: not significant; *: P≤0.05; **: P≤0.01 and ***: P≤0.001).

Growth Parameters		Environmental Parameter					
		Temperature			Chlorophyll-a		
		n	r	P	n	r	P
Length	Exp.I	48	0.73	**	48	0.38	**
	Exp.II	66	0.70	***	66	0.67	***
LW	Exp.I	48	0.49	***	-	-	NS
	Exp.II	66	0.66	***	66	0.48	***
WMW	Exp.I	-	-	NS	48	0.29	*
	Exp.II	66	0.41	**	66	0.41	**
AFDMW	Exp.I	-	-	NS	48	0.32	*
	Exp.II	66	0.30	*	66	0.34	*

4.3. Morphology of Transplanted Mussels

The first apparent morphological difference between LE and LL cultured mussel populations was shell colour. Mussels from LE have a very dark bluish-black colour (Plate-5 and 8a) compared to the brighter brownish colour of LL mussels (Plate-6 and 9a). Although there seemed to be some colour changes in transplanted mussels (Plate-8&9), it was not uniform and might be a subjective observation.

The second morphological difference between mussels from the two lochs was the shape and weight or thickness of the shell. LE mussels had lower length: height and length : width ratios, i.e. a broader and wider body shape than LL mussels which were slender in shape. The mean values of shell morphological parameters for control (LE and LL) and transplanted (LL→LE and LE→LL) mussels measured in May 1992 (exactly one year after the transplantation) are given in Table-18 (see also Plates 6-9).

Plates-8. Shell colour and morphological appearance in Loch Etive mussels; LE: at
native site and LE→LL: one year after transplantation to Loch Leven.

LE

LE→LL

Plates-9. Shell colour and morphological appearance in Loch Leven mussels; LL: at native site and LL→LE: one year after transplantation to Loch Etive.

LL

LL→LE

Table-18. The mean shell characteristics (SW: shell weight, g; L: length; H: height and W: width, mm) of control (LE and LL) and transplanted (LL→LE and LE→LL) mussels from Loch Etive and Leven, one year after transplantation (N=45; W in g and L and H in mm). Superscript letters as explained Table-6.

Site/stock	Length	Weight	Height	Width	L:H	L:W	H:W
LE	47.0	3.51	25.2	17.6	1.78[a]	2.55[a]	1.43[a]
	±0.61	±0.14	±0.32	±0.23	±0.011	±0.015	±0.01
LE→LL	43.38	2.54	24.3	17.7	1.84[a]	2.53[a]	1.37[b]
	±0.53	±0.09	±0.28	±0.18	±0.008	±0.017	±0.01
LL	42.7	2.40	23.0	15.8	1.95[b]	2.84[b]	1.46[c]
	±0.35	±0.06	±0.15	±0.11	±0.007	±0.011	±0.006
LL→LE	46.0	3.00	22.9	16.1	1.95[b]	2.78[b]	1.42[c]
	±0.56	±0.08	±0.26	±0.19	±0.006	±0.009	±0.07

Although some authors (e.g. Seed,1968) suggested that ratios of length:height and width, and height:width decrease with increase in length, the height and width data in this study have not been adjusted for differences in mean lengths because all mussels used in this trial were of the same age and size differences were not so great. As can be seen in Table-18, mussels measuring 42.7 mm in length from LL had highest length:height, length:width and height:width ratios, followed by the same stock transplanted to LE, i.e. LL→LE, and LE mussels transferred to LL. According to the results of 2-way ANOVA, stock was the only significant factor affecting length:height, length:width and height:width ratios ($P \leq 0.001$) by accounting for 9-71% of total variance. Although length:height ratios were influenced both by stock ($P \leq 0.001$) and site ($P \leq 0.01$), the main factor once again was stock, accounting around 60% of observed variance in comparison to site with just over 2%. The relationships between length - height and width are illustrated in Fig.26, from which changes,
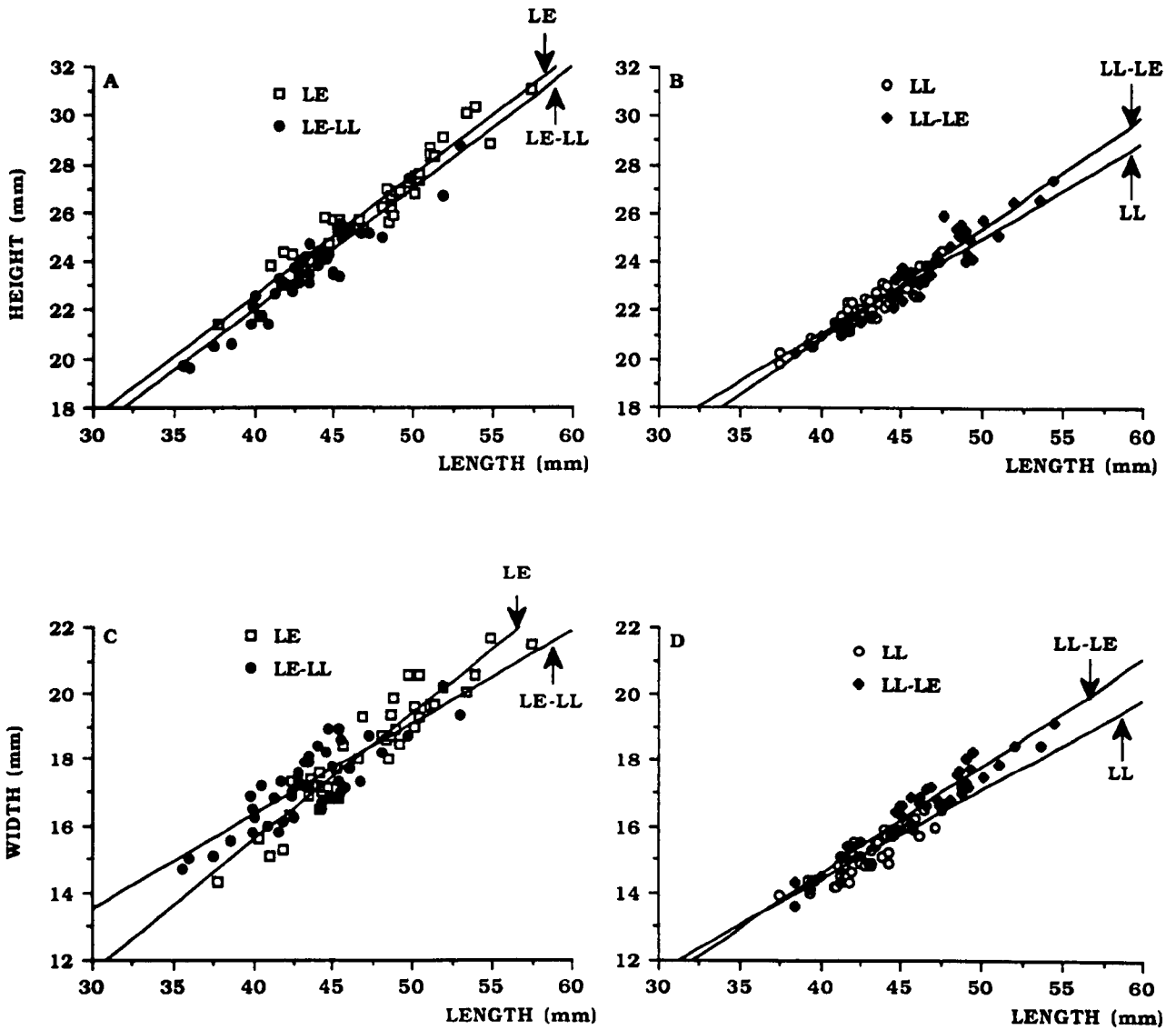
Fig.26. Linear regressions of shell height and width on shell length in mussels from LE and LL suspended in native (LE and LL) and cross-transplanted (LL→LE and LE→LL) environments.

particularly in shell width, in transplanted mussels can be seen and these data are summarised in terms of slope (b), intercept (a) and correlation coefficient (r) of the linear regression equations in Table-19. The regression slopes of both length - height and length - width between original stocks (LE and LL) were significantly different (P≤0.001). The slopes of length - height showed significant variation between LL and LL→LE (P≤0.05), but not between LE→LL.

Table-19. Linear relationships (Y = a+bX) between various combinations of morphological shell parameters for control (LE and LL) and transplanted (LL→LE and LE→LL) mussels (N=45). Superscript letters as explained in Table-6.

Dependent - Independent	Site\Stock	Intercept(a)	Slope(b)	r
Height on Length	LE	2.61±0.961	0.498±0.020^b	0.966
	LE→LL	2.02±1.065	0.499±0.025^b	0.952
	LL	5.40±1.025	0.389±0.024^a	0.927
	LL→LE	2.62±0.969	0.453±0.021^b	0.957
Width on Length	LE	0.04±0.937^a	0.387±0.020^c	0.948
	LE→LL	5.07±1.208^b	0.280±0.028^a	0.839
	LL	3.26±0.913^b	0.277±0.021^{ba}	0.893
	LL→LE	1.46±0.661^a	0.327±0.014^b	0.961
Width on Height	LE	1.11±1.436^a	0.706±0.055^b	0.891
	LE→LL	5.40±1.433^b	0.500±0.060^a	0.784
	LL	1.50±1.370^a	0.618±0.062^{ba}	0.835
	LL→LE	1.05±1.030^a	0.659±0.044^b	0.917

Note: significance (t) test of slope (b=1) showed that slope of all variables are highly significant (P≤0.001).

LE mussels generally have heavier or thicker shells than LL mussels (Fig.27). In LE mussels, the shell constituted on average 85.8% of the total dry weight (dry shell weight + dry meat weight) compared to 84.5 % in LL and 81.5% in LL→LE and 87.3% in LE→LL. One year after transplantation both stock and site had significant

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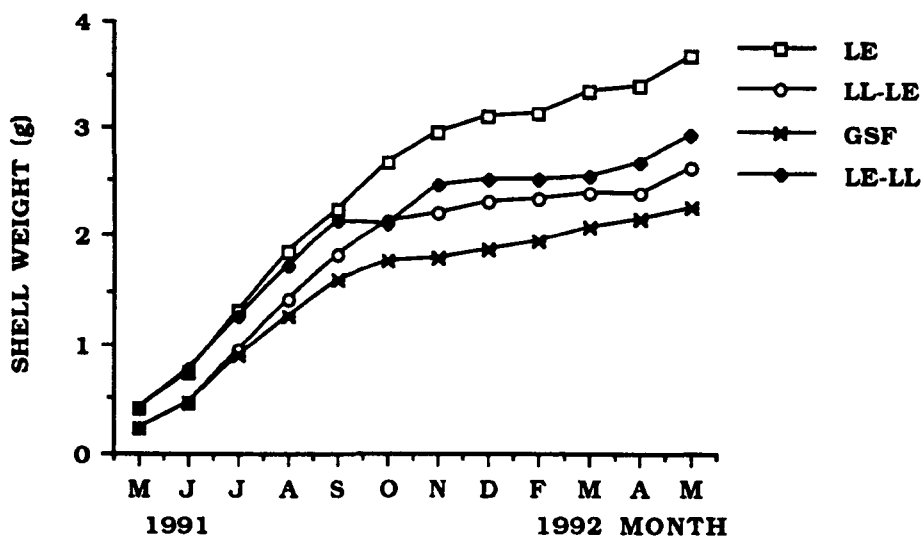
Fig.27. Monthly average shell weights (dry; in g) of control (LE and LL) and transplanted (LL→LE and LE→LL) mussels.

effects (P≤0.001) on shell weight which was adjusted for differences in initial weight and length. Site, however, accounted for only 4% of total variance in shell weight in comparison with 30% due to the stock. A comparison of ash-free organic content in the shells (AFDSOW) of LE, LL, and LL→LE and LE→LL at the end of the experiment was conducted. AFDSOW consisted of 3.25% (LE), 3.08% (LL), 3.16% (LL→LE) and 3.18% (LE→LL) of whole dry shell weight and the average ash content was 4.11% of acid treated dry shell weight. As the mean % values show, AFDSOW was very slightly higher in LE mussels than LL, with the intermediate values for transplanted mussels, but neither stock nor site had a significant affect on the organic matter content of shells (P>0.05).

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4.4. Mortality and Losses

Fig.28 shows computed changes in population density (expressed as mean number of mussels per meter), percent survival and monthly mortality rates of mussels on experimental ropes during experiment I (see also Tables 20-23). Survival, expressed mussels staying on the ropes as percent of initial stock number, was quite low at all sites; ranging from 27.8% to 38.5% by the end of the experiment (Fig.28). Severe losses occurred during the first 3 months and around 37% to 55% of the original stock was lost between May and August and 48-61% of it by October 1990, at the end of first summer growth season, i.e. before reaching 45 mm shell length (Fig.28B). Decline in density continued throughout the experiment but at a decreasing rate. Excluding the first three months, overall mean monthly rate of loss and mortality was around 5.2.% (Fig.28C). After 13 months, the density of mussels per m on experimental ropes dropped from 884±64 at all sites to 246±9 at GSF, 303±13 SS, 315±19 AS and 340±17 at LE (Fig.28A) with cumulative losses of 72.2%, 65.7%, 64.4 and 61.5%, respectively. As shown in Fig.28 survival of mussels at sites in Loch Etive was slightly higher than in Loch Leven, and within Loch Etive at LE, and it seemed to be better at Level 2 of LE, AS and SS and at Level 1 of GSF than at other levels, but no significant differences were detected neither between sites nor depths for individual sites (X^2 = 0.591 and 1-way ANOVA, P>0.05).

This very poor survival was partly as a result of natural mortality and partly fall off of mussels from ropes, due to lack of space, water currents and handling
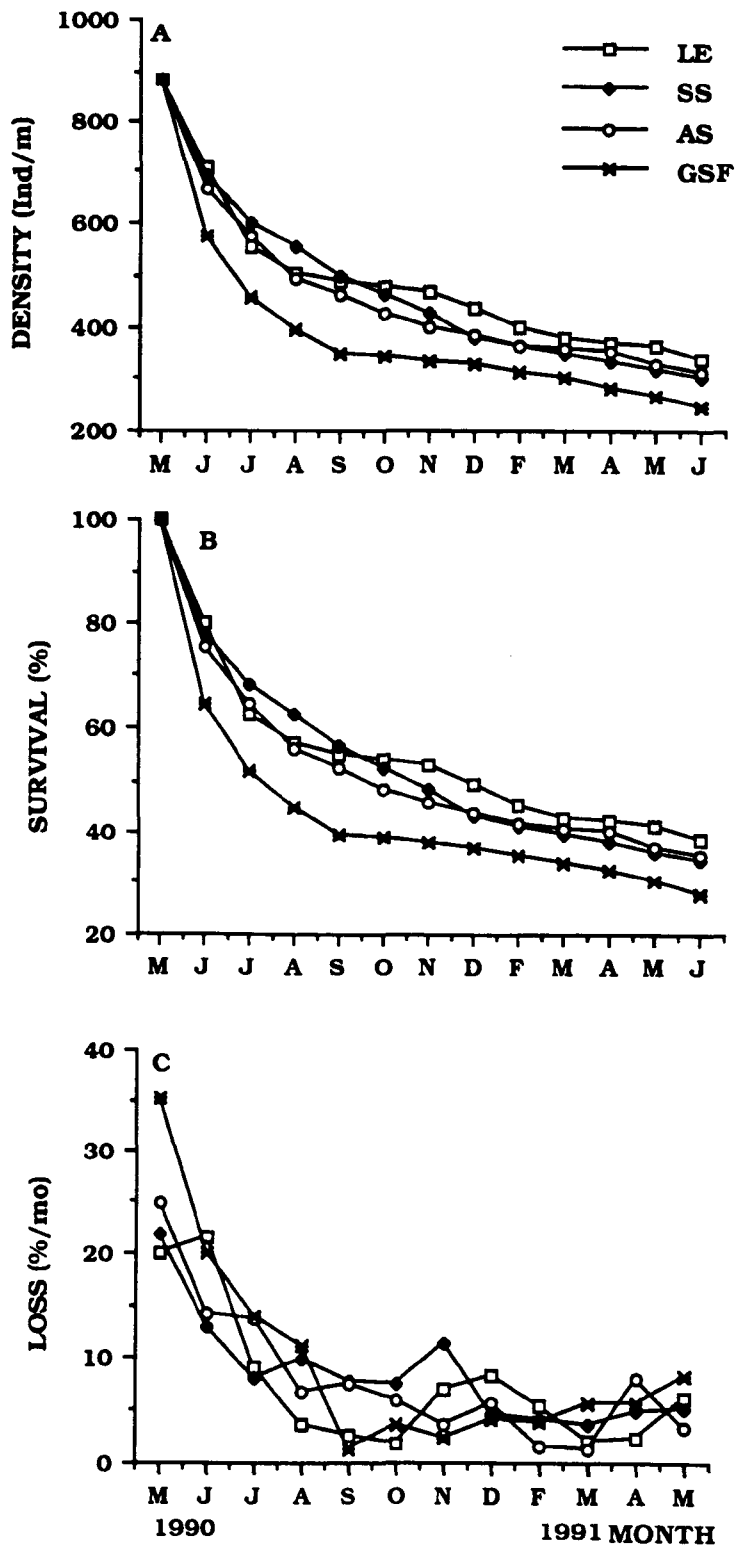
Fig.28. Changes in population density (A), percent survival (B) and monthly losses (C) of mussels during experiment I.

during sampling. It was observed during early sampling months that some of the mussels, especially small ones, stacked inside the socks and died, and large clumps of mussels frequently became detached from the ropes, with mussels forming unstable masses as they emerged from the sock meshes. Scattered mussels which had died in situ on ropes were also observed during each sampling. Since it was not possible to estimate separately rates of natural mortality and losses due to fall off, survival and loss were used here to define the presence of mussels on ropes and disappearance from them. Although losses from sampling were minimised by careful handling, there is no doubt that some of the losses can be attributable disturbance during sampling. There was no predation, however, either from eider ducks (*Someteria mollissima* L.) or from starfish (*Asterias rubens* L); the former especially is a common predator of cultivated mussels on the West coast of Scotland.

As losses due to fall off were eliminated by using lantern nets, percent survival was higher during experiment II (Fig.29) in comparison with experiment I. Although mortality rates seemed to be higher during the first few months after the experiment commenced, Fig.29B shows that there was a regularity, except at GS and LE→LL, in mortality throughout the experimental period. Mean cumulative mortality, excluding transplanted mussels, between May 1991 and 1992 was 6.6% at sites in Loch Etive and 10.7% in Loch Leven. Highest mortalities of 14.4% and 7.3% occurred at GS in Loch Leven and at AS in Loch Etive, respectively (Fig.29).

Averaged over all sites, stock LE, with a mean cumulative mortality of 7.4%, exhibited higher mortalities than stock LL, which had a 5.8% mean cumulative mortality. In contrast, when averaged for stocks, site LE (5.3%) was better than site
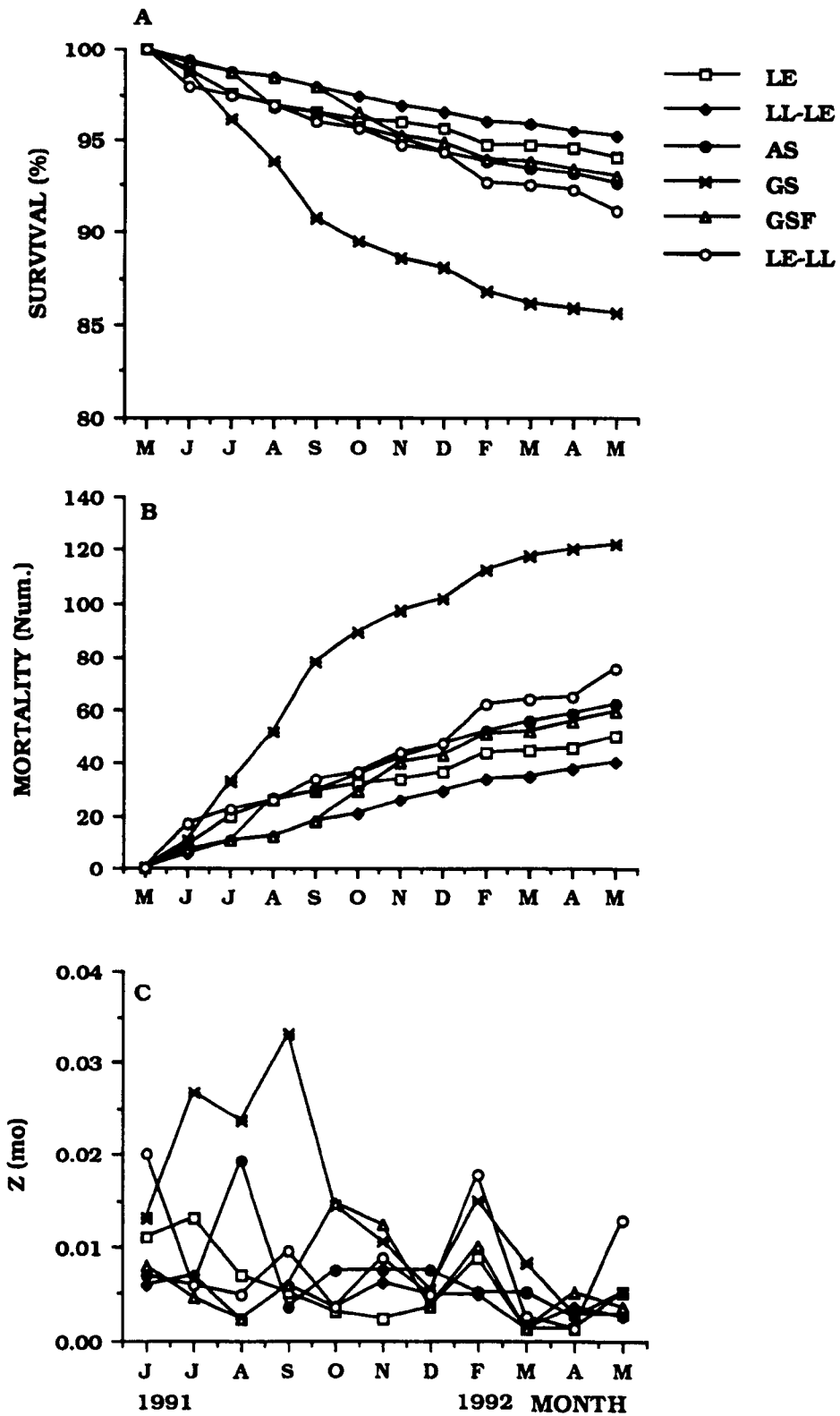
Fig.29. Percent survival (A), cumulative mortalities (B) and instantaneous mortality rates (C) in experiment II.

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LL (7.9%) (Fig.29). Neither site nor stock alone, however, had a significant effect on natural mortality rates (P>0.05). Site and stock accounted for only 10.7% and 2.7%, respectively, of mortality variance, and the rest of the variance explained by stock*site interaction. Instantaneous mortality (Z) rates were calculated for experiment II (Fig.29C) and monthly rates were somewhat higher for sites GS, GSF (both stock) and AS compared to LE, both native and LL→LE. There was no clear relationship between survival or mortality rates and environmental parameters, season and growth during both experiment.

4.5. Biomass and Production

The both biomass and production, which are the result of the interaction of growth and mortality, were estimated only for experiment I and expressed as ash-free dry weight, including shell organics. Biomass values are mainly presented and discussed as g ash-free dry weight (AFDW; ash-free dry meat weight + weight of shell organic) per mussel and per m, while production is expressed as g AFDW per m, but both were also converted to Kcal by multiplying values in g by the monthly energy value of AFDM and shell organic matter in order to facilitate comparisons with other research. The energy content of shell organic matter was determined as 4.793 Kcalg^{-1} in September 1990, while the energy content of AFDM was measured every month and ranged between 4.854 and 5.430 Kcalg^{-1} (see section 4.6.2.6).

4.5.1. Biomass

Tables 20-23 give monthly biomass values as g and Kcal AFDW/mussel and

Fig.30 illustrates changes in biomass g AFDW/mussel and per meter. Since meat weight comprises the major part of the organic biomass per mussel (including shell organics), the annual cycle was very similar to AFDMW values (Fig.30A and section 4.2.1.2 Fig.20). Mean biomass per mussel reached its first peak values of 0.55 to 0.964 g in October/November increasing to 0.36 g at GSF and 0.64-0.77 g at sites in Loch Etive and Dunstaffnage Bay over the summer growth season, with a steady decline from October 1990 to March-April 1991, and a rapid increase from April to May-June 1991. Total biomass increments over the experimental period were 0.59 g at GSF and 1.30-1.60 g at other sites. The differences in biomass between the sites were statistically analysed in October 1990, May and June 1991. The variation between GSF and the other sites were significant on all occasions ($P \leq 0.001$) and there was a significant difference between SS and AS in May 1991 only ($P \leq 0.05$). There was no significant differences between depth levels at any of the sites.

The biomass per meter was also calculated and plotted in Fig.30B. It followed mainly the temporal changes in AFDW and also population density. The initial biomass was estimated as 168.8 g m^{-1}. There was decline ranging from 1.1% to 16.9% at all sites, except LE, during the first month, then an increase of around 127-170% at sites in Loch Etive over the summer, and a 44-52% decline throughout the winter, from August-October 1990 and until April 1991. During the experimental period, the second biomass peaks of 487 to 578 g AFDW m^{-1} in Loch Etive and Dunstaffnage Bay were observed in May-June (Fig.30B). As Fig.30B shows, the biomass cycle at GSF was not marked and far lower in amplitude than the other sites ($P \leq 0.001$). The mean and final biomass, and increments at each site are summarised in Table-25.

Table-20. Monthly ash-free dry weight biomass and computation of production of the experimental mussels at site LE) in Loch Etive from May 1990 to June 1991 (403 days) (N: mean number live mussels per meter). * values for 2 months (January and February).

Month	Duration (Days)	N±SE (m)	AFDMW (±SE,g)	AFDSW (±SE,g)	Individual Biomass		Mean N (m)	Changes in Biomass (g/ind)	Production	
					g	Kcal			(g/m/mo)	(Kcal/m/mo)
May		884±64	0.160±0.012	0.031±0.003	0.191	0.924				
	33						796	0.056	44.50	272.9
June		707±52	0.212±0.017	0.035±0.003	0.247	1.267				
	30						631	0.208	131.2	690.9
July		555±33	0.394±0.025	0.061±0.004	0.455	2.362				
	31						530	0.313	165.9	879.3
August		505±21	0.687±0.052	0.081±0.007	0.768	4.021				
	31						496	0.094	46.60	193.9
September		487±36	0.755±0.035	0.107±0.006	0.862	4.412				
	30						481	0.102	49.10	172.7
October		475±31	0.848±0.050	0.116±0.009	0.964	4.771				
	33						471	-0.072	-33.9	-30.6
November		467±29	0.765±0.041	0.127±0.008	0.892	4.706				
	31						451	-0.152	-68.6	-374.8
December		435±22	0.608±0.033	0.132±0.007	0.740	3.875				
	70						417	-0.020	-8.30*	-30.4*
February		399±9	0.574±0.032	0.146±0.008	0.720	3.802				
	27						389	-0.127	-49.3	-266.1
March		378±17	0.437±0.022	0.156±0.007	0.593	3.117				
	30						374	-0.002	-0.70	-40.8
April		370±18	0.422±0.020	0.169±0.008	0.591	3.008				
	28						366	1.005	367.8	1837.7
May		362±09	1.404±0.063	0.192±0.009	1.596	8.029				
	29						351	-0.035	-12.3	-34.4
June		340±11	1.360±0.056	0.201±0.009	1.561	7.931				

Table-21. Ash-free dry weight biomass and computation of production of the experimental mussels in a salmon farm (SS) in Dunstaffnage Bay between May 1990 and June 1991; 403 days. * as in Table-20.

Month	Duration (Days)	N±SE (m)	AFDMW (±SE;g)	AFDSW (±SEg)	Individual Biomass (g)	Individual Biomass (Kcal)	Mean N (m)	Changes in Biomass (g/ind)	PRODUCTION (g/m/mo)	PRODUCTION (Kcal/m/mo)
May		884±64	0.160±0.012	0.031±0.003	0.191	.924				
	33						787	0.050	39.40	236.1
June		690±44	0.205±0.011	0.036±0.003	0.241	1.224				
	30						646	0.096	62.00	329.5
July		602±37	0.275±0.018	0.062±0.004	0.337	1.734				
	31						578	0.474	274.0	1446.2
August		554±41	0.720±0.049	0.090±0.007	0.811	4.236				
	31						527	0.048	25.30	85.40
September		500±24	0.753±0.042	0.106±0.007	0.859	4.398				
	30						481	0.030	14.40	-191.0
October		462±17	0.765±0.040	0.124±0.007	0.889	4.401				
	33						445	-0.041	-18.2	204.3
November		428±10	0.710±0.034	0.138±0.006	0.848	4.460				
	31						404	-0.031	-12.5	-72.30
December		380±26	0.666±0.032	0.151±0.008	0.817	4.281				
	70						372	-0.027	-10.0*	-38.70*
February		363±05	0.631±0.033	0.159±0.007	0.790	4.177				
	27						356	-0.190	-67.5	-365.0
March		348±08	0.426±0.026	0.174±0.006	0.600	3.150				
	30						342	0.045	15.40	45.40
April		335±15	0.462±0.017	0.183±0.008	0.645	3.283				
	28						327	0.882	288.4	1437.3
May		319±17	1.334±0.048	0.193±0.008	1.527	7.679				
	29						311	-0.037	-11.5	-35.00
June		303±13	1.285±0.052	0.205±0.010	1.490	7.566				

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Table-22. Ash-free dry weight biomass and computation of production of experimental mussels in a salmon farm (AS) in Loch Etive between May 1990 and June 1991; 403 days. * as in Table-20.

Month	Duration (Days)	N±SE (m)	AFDMW (±SE;g)	AFDSW (±SE;g)	Individual Biomass (g)	(Kcal)	Mean N (m)	Changes in Biomass (g/ind)	PRODUCTION (g/m/mo)	(Kcal/m/mo)
May		884±64	0.160±0.012	0.031±0.003	0.191	0.924				
	33						775	0.060	46.50	270.3
June		665±53	0.212±0.014	0.039±0.003	0.251	1.273				
	30						619	0.255	157.7	834.9
July		572±40	0.444±0.028	0.062±0.005	0.506	2.623				
	31						533	0.233	124.2	662.4
August		494±27	0.653±0.043	0.086±0.006	0.739	3.866				
	31						478	0.083	39.60	163.9
September		461±21	0.716±0.040	0.106±0.006	0.822	4.209				
	30						444	0.007	3.100	-46.60
October		427±30	0.710±0.040	0.119±0.007	0.829	4.104				
	33						415	-0.034	-14.90	26.70
November		402±36	0.657±0.036	0.136±0.006	0.793	4.168				
	31						395	-0.044	-17.40	-97.00
December		387±41	0.607±0.026	0.142±0.005	0.749	3.922				
	70						376	-0.087	-32.90	-163.7
February		365±32	0.514±0.021	0.148±0.004	0.662	3.487				
	27						362	-0.068	-24.60	-131.6
March		359±16	0.437±0.020	0.157±0.005	0.594	3.124				
	30						357	0.005	1.800	-26.00
April		354±23	0.428±0.014	0.171±0.006	0.599	3.051				
	28						340	0.893	303.6	1514.9
May		326±18	1.312±0.041	0.180±0.007	1.492	7.506				
	29						321	0.304	97.40	523.30
June		315±19	1.603±0.044	0.193±0.006	1.796	9.139				

Table-23. Ash-free dry weight biomass and computation of production of experimental mussels in a long-line mussel farm (GSF) in Loch Leven between May 1990 and June 1991; 403 days. * as in Table-20.

Month	Duration (Days)	N±SE (m)	AFDMW (±SE;g)	AFDSW (±SE;g)	Individual Biomass (g)	Individual Biomass (Kcal)	Mean N (m)	Changes in Biomass (g/ind)	PRODUCTION (g/m/mo)	PRODUCTION (Kcal/m/mo)
May		884±64	0.160±0.012	0.031±0.003	0.191	.924				
	33						729	0.054	39.30	234.2
June		573±37	0.206±0.011	0.039±0.002	0.245	1.245				
	30						516	0.065	33.50	181.6
July		458±29	0.252±0.014	0.058±0.003	0.310	1.598				
	31						427	0.162	69.10	365.0
August		395±23	0.396±0.021	0.076±0.004	0.472	2.453				
	31						373	0.045	16.80	66.10
September		351±11	0.415±0.020	0.102±0.005	0.517	2.631				
	30						349	0.017	5.900	1.200
October		346±17	0.425±0.024	0.109±0.006	0.534	2.634				
	33						340	0.020	6.800	91.30
November		334±14	0.440±0.018	0.114±0.005	0.554	2.903				
	31						330	-0.041	-13.50	-76.90
December		326±09	0.395±0.022	0.118±0.005	0.513	2.669				
	70						320	-0.050	-16.00*	-77.00
February		313±15	0.339±0.019	0.124±0.006	0.463	2.428				
	27						307	-0.091	-27.90	-150.4
March		301±08	0.244±0.010	0.128±0.006	0.372	1.938				
	30						293	-0.038	-11.1	-75.90
April		284±11	0.199±0.009	0.135±0.005	0.334	1.679				
	28						276	0.126	34.80	168.4
May		268±16	0.319±0.016	0.141±0.005	0.460	2.289				
	29						257	0.324	83.30	430.7
June		246±09	0.624±0.026	0.160±0.007	0.784	3.965				
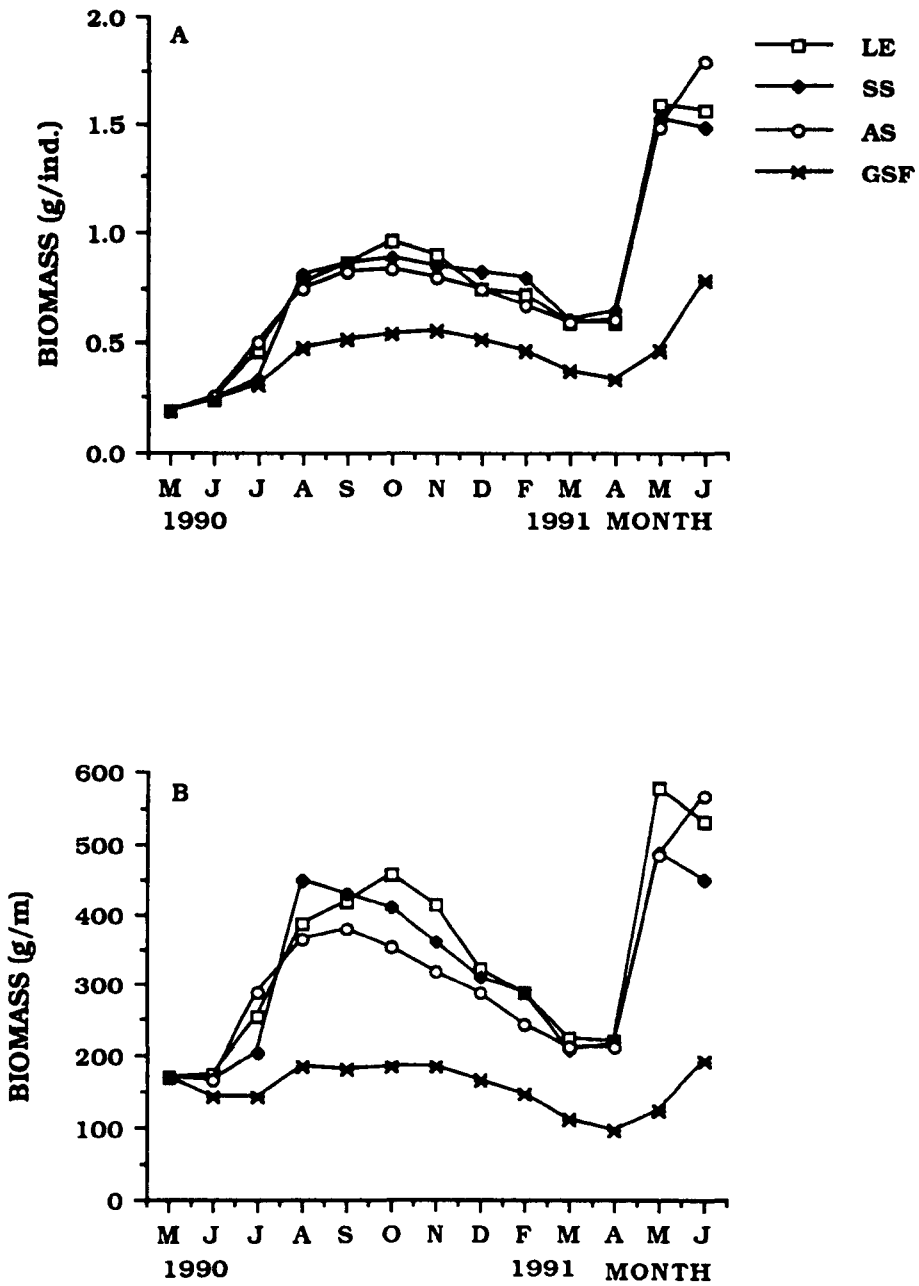
Fig.30. Monthly ash-free dry weight (meat + shell organics) biomass as g mussel^{-1} (A) and g m^{-1} (B). Values in February also include January.

4.5.2. Production and Eliminated Biomass

Tables-20-23 demonstrates the computation of monthly production while Table-24 summarises monthly eliminated biomass values, and some of these results are plotted in Figs.31&32. The temporal changes in production generally followed those of biomass in g per m. The highest production increments, excluding GSF, were observed between May and August 1990, ranging from 158-274 g m^{-1} mo^{-1}, and April-June 1991 (288-367 g m^{-1} mo^{-1}). The production was negative from November 1990 to April 1991, mainly related to decreases in meat weight and secondly to losses and mortality (Fig.31B). Accumulated net production over the experimental period is shown in Table-25. This gives a turnover ratio of net biological production to mean biomass (P:B) of 1.42 (GSF), 1.86 (LE), 1.88 (SS) and 2.20 (AS). Aquaculture production, expressed as overall biomass (AFDW) increment per m of rope as shown in Table-25, was 47-58% of net biological production at sites LE, AS and SS, but only 11% at GSF. Thus about 42-89% production was lost or eliminated during the experimental period due to stock losses, natural mortality, and utilization of stored reserves during winter and gamete production. The monthly eliminated biomass calculated from Tables-20-23 is given in Table-24; it was quite high during early months as a result of severe losses (Fig.32). Total eliminated biomass (including shell organics) is shown in Table-25. Table-25 also shows total lost in situ production of mussels remaining on the ropes during experiment I (mainly October - April). This represents losses due to utilization of reserved material for metabolism and reproduction, but not mortality. The result is very different from that of eliminated biomass, being greatest at site LE followed by SS, while still least at GSF and it is

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Table-24. Monthly eliminated biomasses, g and Kcal AFDW m^{-1}, of experimental mussels.

MONTH	SITE DAYS	LE (g/m)	LE (Kcal/m)	SS (g/m)	SS (Kcal/m)	AS (g/m)	AS (Kcal/m)	GSF (g/m)	GSF (Kcal/m)
May	33	38.8	193.9	41.9	208.4	48.4	240.6	67.8	337.4
June	30	53.4	275.8	25.4	130.2	35.2	181.2	31.9	163.5
July	31	30.6	159.6	94.9	143.3	48.6	253.1	24.6	127.6
August	31	14.7	75.90	45.1	233.1	25.8	133.2	21.8	111.8
September	30	11.0	55.10	33.2	159.6	28.1	141.3	2.60	13.20
October	33	7.4	37.90	29.5	143.8	20.3	103.4	6.50	33.20
November	31	26.1	137.3	40.0	209.8	11.6	60.70	4.30	22.30
December	70	26.3	138.2	13.7	71.90	15.5	81.50	6.30	33.10
February	27	13.8	72.60	10.4	55.00	3.80	19.80	5.00	26.20
March	30	4.7	24.50	8.10	41.80	3.00	15.40	6.00	30.70
April	28	8.7	44.10	17.4	87.70	29.3	147.8	6.40	31.70
May	29	34.7	175.6	24.1	122.00	18.1	91.50	13.7	68.80
June									

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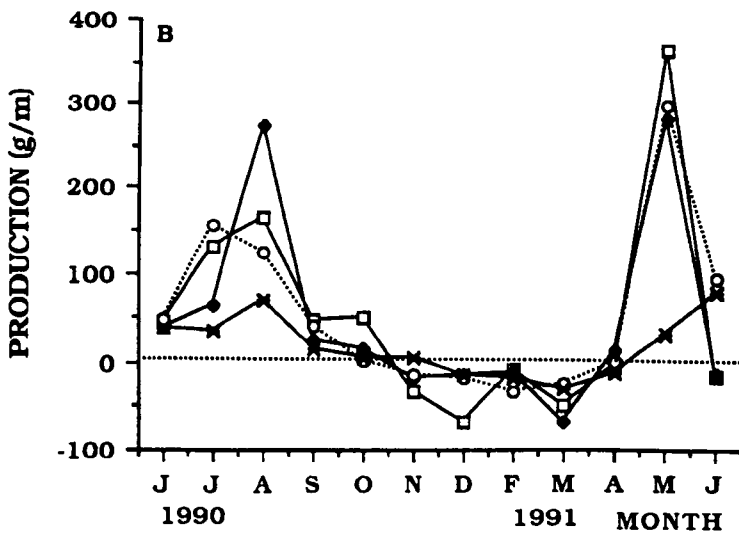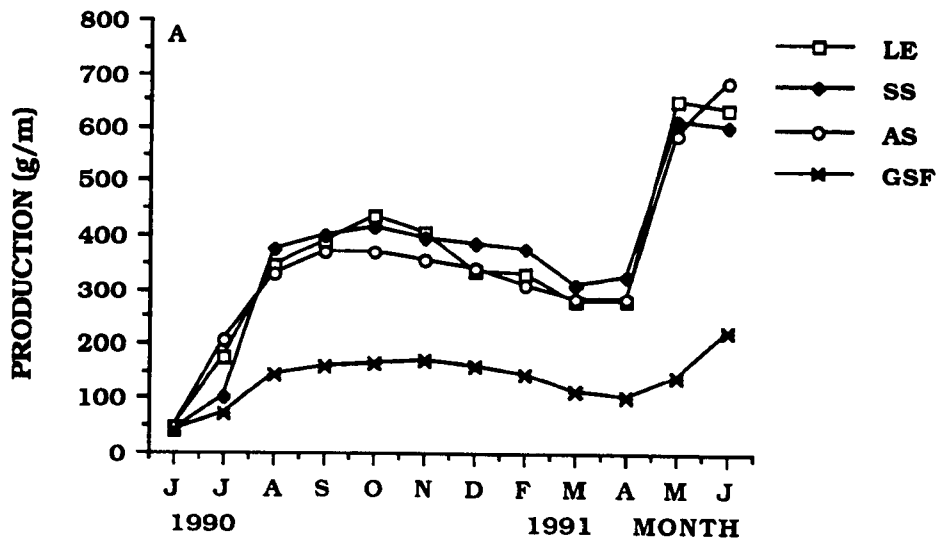
Fig.31. Cumulative (A) and monthly (B) production, g AFDW m⁻¹, of experimental mussels between May 1990 and June 1991. Values in February also include January.
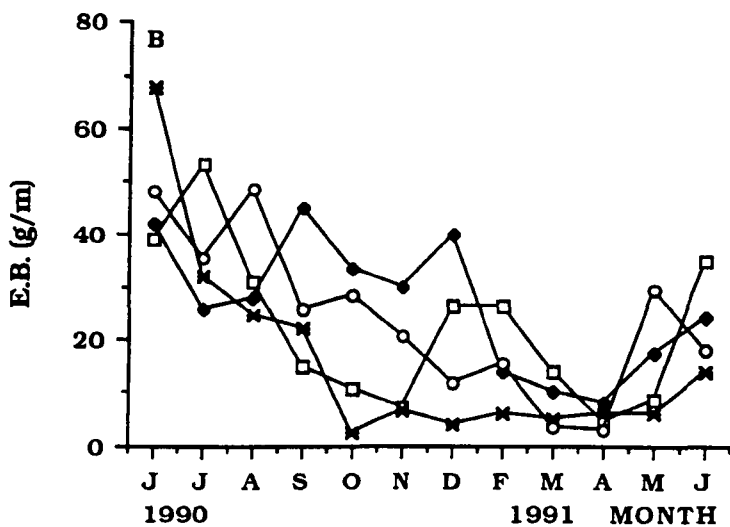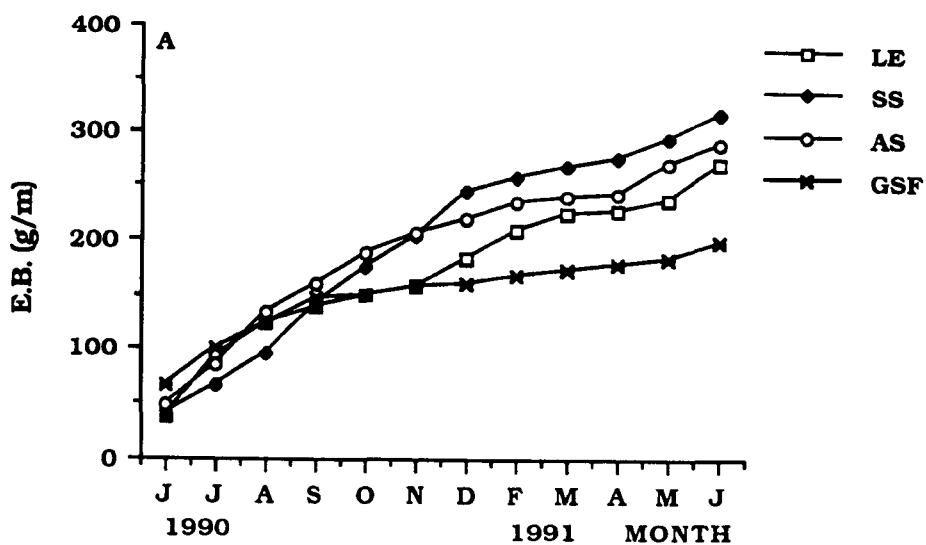
Fig.32. Cumulative (A) and monthly (B) eliminated biomass (g AFDW m^{-1}) of experimental mussels. Values in February also include January.

Table-25. Summary of biomass, production and eliminated biomass, as g AFDW per m of cultivation rope (socks or tubes), at four sites during experiment I (May'90-June'91). Initial biomass was 168.8 g m^{-1} at all sites.

| Location | Loch Etive | | Dunstaff. Bay | Loch Leven |
Site	LE	AS	SS	GSF
A) Mean Biomass	341.4	311.6	319.3	155.7
B) Final Biomass	530.7[b]	565.7[b]	451.5[b]	192.9[a]
C) Biomass Increment	361.9	396.9	282.7	24.1
D) Eliminated Biomass	270.1	287.2	316.5	196.9
E) Cumulative Net Production	632.0	684.1	599.2	221.0
F) P:B (E/A)	1.85	2.20	1.88	1.42
G) % Retained	57.3	58.0	47.2	10.9
H) Lost in situ Production	173.1	89.8	119.7	68.5
I) Gross Production	805.1	773.9	718.9	289.5
J) % in situ loss [(H/I)*100]	21.5	11.6	16.6	23.7

also quite small at AS. Adding this to net biological production gives gross biological production.

4.6. Condition Index and Biochemical Composition

4.6.1. Condition Index

The seasonal variations in condition index of experimental mussels for experiments I & II are depicted in Figs.33 & 34, respectively, and minimum, maximum and annual mean values are given in Table-26. The condition index is
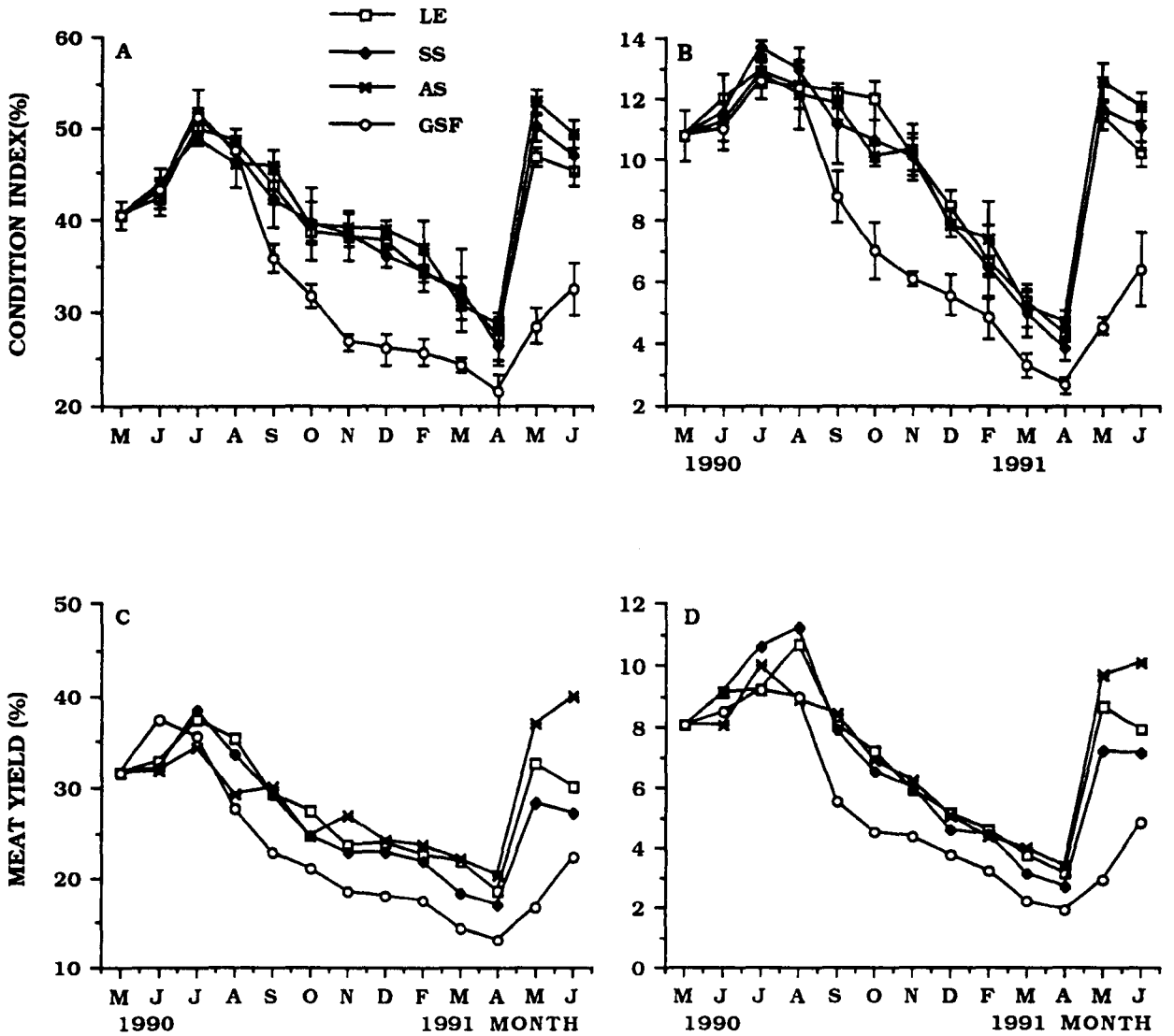
Fig.33. Seasonal variation in condition indices (CI_{vol}: A) and (CI_{dry}: B) meat condition index and meat yields (MY_{wet}:C and MY_{dry}: D) of mussels during experiment I.

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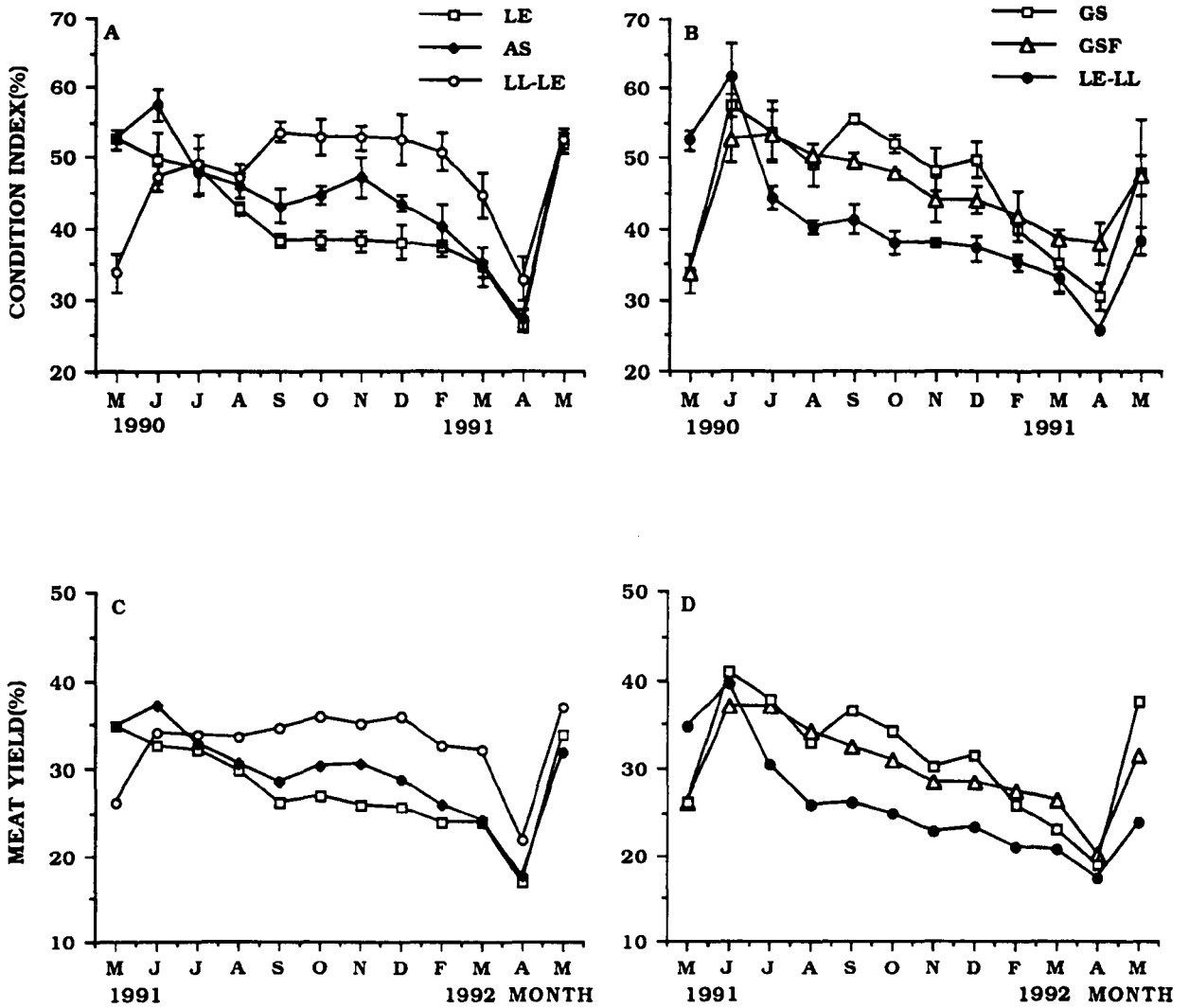
Fig.34. Annual cycle in weight based CI (CI_{wet}) and MY_{wet} of mussels from two lochs grown in native and cross-transplanted environments, (A) and (B) are CI, and (C) and (D) MY in Loch Etive and Loch Leven, respectively.

primarily affected by the accumulation and release of reproductive materials as well as the utilization of stored resources during the winter months. Changes in the two condition indices, CI_{vol} and CI_{dry}, were very similar in experiment I, as Fig.33 shows, and there was a clearly defined seasonal cycle. The maximum values occurred in May-August followed by a steady decline throughout the rest of the year to minimum levels in April and a subsequent increase in May. In general, the annual cycle of CI during experiment II was very similar, but the decline after the early summer peak was not so rapid, even remaining constant at some sites (AS, GS) and stocks (LL→LE) during the autumn and winter (Fig.34 A&B). The minimum values in April and rapid increase in May samples reflects the main period of spawning and recovery.

There was a substantial disparity in level of condition, apart from between months, between sites in different lochs as well (Fig.33). The annual mean CI_{vol} and CI_{dry} were around 40.5-41.7% and 9.8-9.9% at sites in Loch Etive, compared with 33.6% and 7.4% at GSF, respectively (Table-26), and this variation between the lochs in both indices was statistically significant ($P\leq0.05$). The situation in experiment II was slightly different, as two different stocks were employed and there were some morphological differences between the stocks, such as shell form and weight which affects condition index values (section 4.3). The mussels transplanted form LL to LE (LL→LE) had highest CI_{wet}, followed by native stock at native sites at GS and GSF, and the CI values of LE→LL and LE were the lowest in this experiment (Fig.34A&B; Table-26). When the transplanted mussels were excluded, however, neither the differences between sites in same loch nor between sites overall were significant ($P>0.05$). In site and stock comparisons, Loch Etive as a site was better than Loch

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Leven, but site and site*stock interaction had no significant effect on condition index. The stock LL, however, exhibited higher CI values than LE and it significantly affected the CI values (P≤0.05) by accounting for 12% of the total variance (Fig.34 and Table-26).

Correlations between CI_{vol} and CI_{dry} were determined for all sites combined as well as individual sites and a significant relationship was found between these indices. The regression equation for sites all combined:

CI_{dry} = -4.80 + 0.36*CI_{vol} (r=0.945; P≤0.001).

Meat yields (MY), which according to Hickman *et al.* (1991), might provide the most practical and meaningful measure of condition of mussels for the industry, were significantly correlated with all three corresponding condition indices and annual cycle of all three CI was confirmed by both wet (MY_{wet} for CI_{vol} and CI_{wet}) and dry (MY_{dry} for CI_{dry}) meat yields at each site and stock during both experiments (Fig.33 and Fig.34 C&D; Table-26). Using the pooled CI and MY data for all samples following regression equations was obtained:

CI_{vol} = 9.51+1.11*MY (r=0.917; P≤0.001),

CI_{dry} = 1.51+1.17*MY (r=0.959; P≤0.001) and

CI_{wet} = 11.5+0.70*MY (0.552; P≤0.001).

Monthly mean condition indices were also correlated with temperature, chlorophyll-a and particulate organic matter for each site separately and all sites combined, and highly significant correlations were detected between condition indices and temperature and chlorophyll-a (Table-27). There was no correlation between CI and POM at any of the individual sites, but when data from all sites were combined CI_{vol}

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Table-26. Maximum, minimum and annual mean condition indices and meat yield values during the experiment I and II (1:CI_{vol} and MY_{wet}, 2: CI_{dry} and MY_{dry}, and 3: CI_{wet}).

CI/MY	Site/Stocks	LE 1	2	3	LL→LE 3	SS 1	2	AS 1	2	3	GS 3	GSF 1	2	3	LE→LL 3
CI	Minimum	27.5	4.30	26.5	32.9	26.5	3.90	28.7	4.70	27.2	30.6	21.5	2.70	37.8	25.8
	Maximum	50.0	12.9	52.6	53.8	51.9	13.7	49.0	12.9	57.5	57.6	51.4	12.6	53.4	61.8
	Mean	40.5	9.90	41.4	47.6	40.8	9.80	41.7	9.90	44.9	46.1	33.6	7.4	45.2	40.4
MY	Minimum	18.5	3.10		21.9	16.9	2.70	20.3	3.40		19.1	12.9	1.90		17.6
	Maximum	37.5	10.7		36.8	38.4	11.2	40.0	10.1		40.9	37.4	9.20		34.9
	Mean	28.2	7.10		32.7	26.8	6.80	28.9	7.20		31.4	22.8	5.26		25.6

Table-27. Correlation coefficients (r) and significance levels (ns: not significant, *: P≤0.05, **: P≤0.01 and ***: P≤0.001) between three condition indices and some environmental variables at individual experimental sites (1: CI_{vol}, 2: CI_{dry} and 3: CI_{wet}).

Variable		LE 1	2	3	SS 1	2	AS 1	2	3	GS 3	GSF 1	2	3
CI_{dry}	r	0.89			0.94		0.94				0.98		
	P	***			***		***				***		
Temp	r	0.69	0.83	-	0.64	0.81	0.63	0.80	-	0.76	0.80	0.80	0.78
	P	**	***	ns	*	***	*	***	ns	**	***	***	**
Chl-a	r	-	-	0.66	0.65	0.59	0.58	0.57	-	-	-	-	-
	P	ns	ns	*	*	*	*	*	ns	ns	ns	ns	ns

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was significantly correlated with POM (P≤0.01; r=0.345). The multiple regression equations between CI and environmental parameters, all sites combined, in decreasing order of importance were:

$$CI_{vol} = 16.0+1.64Temp+1.33Chl-a+1.06POM \quad (r=0.752; P≤0.001),$$

$$CI_{dry} = -0.45+0.78Temp+0.39Chl-a \quad (r=0.804; P≤0.001) \text{ and}$$

$$CI_{wet} = 31.2+1.02Temp+1.26Chl-a \quad (r=0.531; P≤0.01).$$

4.6.2. Proximate Biochemical Composition

Proximate biochemical analyses for moisture, ash, protein, lipid and glycogen were carried out during experiment I for each site, and for transplanted and control mussels in experiment II and the results are presented as mean percentages of dry meat weight or wet meat weight in the case of moisture content. No statistical differences, except ash content during experiment II, were found when the various dry meat composition analyses were compared for mussels from two different stocks cultured at different sites in two lochs. In fact data for each component was very similar in experiment I, so all sites were combined and average values presented here, while results for experiment II are processed separately for each site and stock. The results indicated the clear seasonal changes in almost all the main biochemical compounds of the cultivated mussels (Figs.35 & 36). The data also demonstrated the inverse relationship between various biochemical components during both experiments: the increases and decreases in water, protein and ash values coincided with decreases and increases in glycogen values and vice versa (Figs.35-36).

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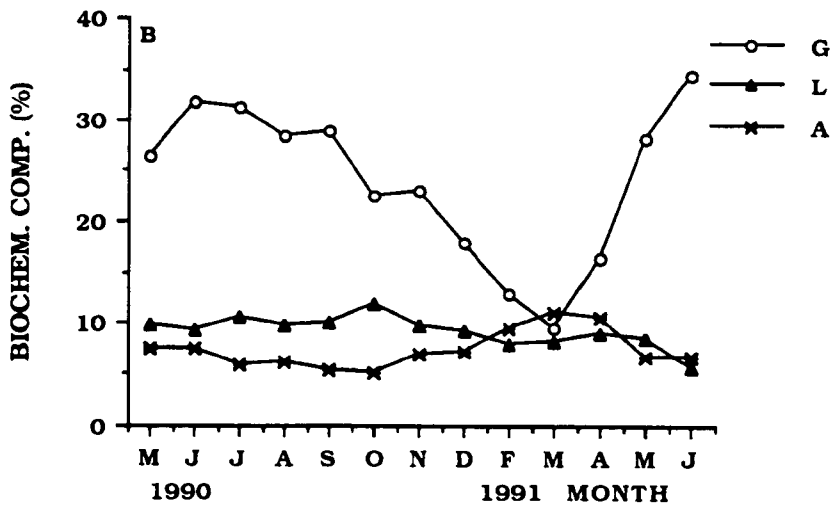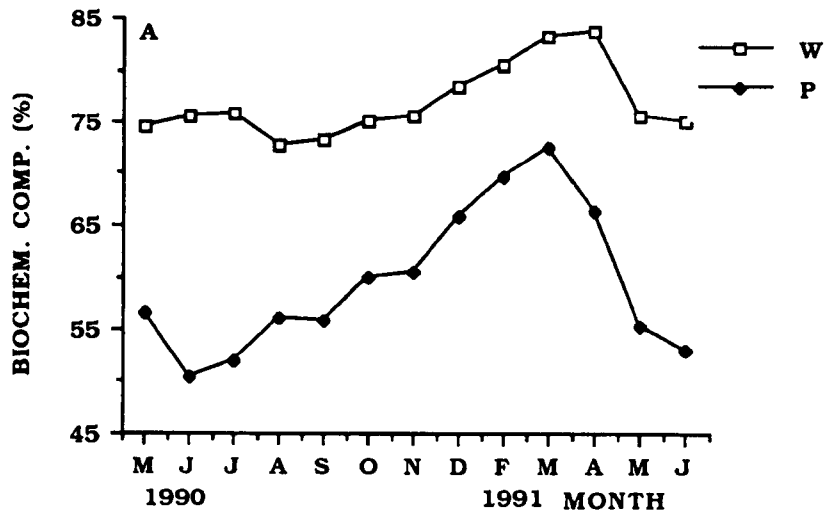
Fig.35. Seasonal variations in percentage biochemical composition of dry meat of experimental mussels with 27.14-54.87 mm mean length during May 1990-June 1991. A: water (W) and protein (P); B: glycogen (G), lipid (L) and ash (A).
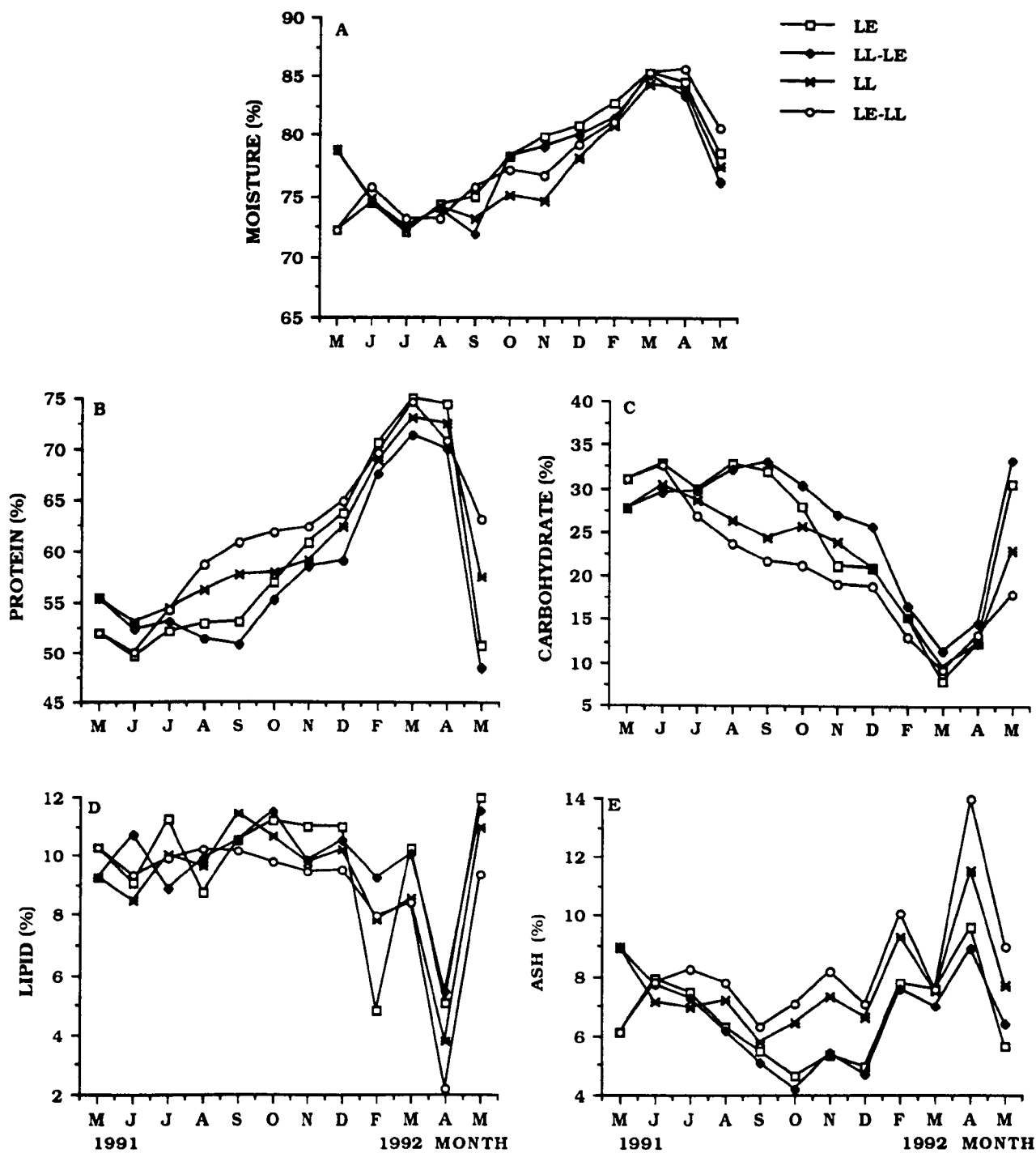
Fig.36. Seasonal variations in percentage biochemical composition of dry meat of experimental mussels from two populations grown in native and cross-transplanted sites over the experimental period of May 1991 to May 1992 (A:water, B: protein, C: glycogen, D: lipid and E:ash).

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4.6.2.1. Moisture

The moisture content of the meat showed fluctuations between 69.9 and 85.1% with an overall average of 76.6% and it was slightly higher, around 0.7%, in mussels from GSF than the other three sites during experiment I. During experiment II, the moisture content range, 71.9-85.7%, and the mean, 77.8%, were very similar to experiment I. The moisture content of LE, both as site and stock, mussels seemed to be hardly higher than the LL. In general, the values were minimum during summer (August) coinciding with the time of maximum meat weights (Figs.20,25 and 34-35) and increased steadily until April reaching maximum values, and dropped in May 1991 & 1992 (Figs.34A & 35A).

4.6.2.2. Protein

Average protein content was 59.9% during both experiments with minimum values of 48.7% and 49.6%, and a maximum of 73.2% and 75.1% during experiments I and II, respectively. Site LL mussels had a mean protein content of 61.3% and LE 58.6%, whereas as stock LE had 60.6% and LL 59.2%; the mean of LE→LL (Loch Etive mussels in Loch Leven) was the highest at 61.9% protein, and LL→LE (Loch Leven mussels in Loch Etive) was the lowest at 57.8%. However, neither site nor stock had a statistically significant affect on mean protein content of dry meat.

The annual cycle can be summarised from Figs.36A & 37B: a gradual increase, during both experiment I and II, was observed from minimum levels (50.7% and 49.6-53.1%) in June; this reached annual maximum values (72.6% and 71.3-75.1%) in March then declined again in May of both 1991 and 1992 (Fig.35A and 36B).

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4.6.2.3. Glycogen (Carbohydrate)

During both experiments glycogen reserves were quickly restored during the spring. The seasonal pattern of glycogen (Fig.35B and 36C) shows two main peaks during each experiment in June (1990 & 1991) then it declined through the winter to a minimum in March coinciding with minium meat weights and CI (Figs.20 and 25), and also with spawning. The average glycogen contents were 23.7% and 23.3%, with minimum and maximum values ranging from 8.5 to 36.1% and 7.9 to 33.2%, for experiments I and II, respectively. In stock-site comparisons site LE and stock LL with means of 25.1% and 24.0%, respectively, had the highest glycogen content (Fig.36C). The mean annual glycogen content of mussels transplanted to Loch Leven was lowest; 20.7%.

As has been mentioned, there was good agreement between glycogen and the annual CI cycle (Figs.32-35) and linear regression analysis showed that there is a strong and significant relationship between monthly glycogen and CI_{vol} (r=0.69, P≤0.001), CI_{dry} (r=0.74, P≤0.001) and CI_{wet} (0.55, P≤0.01) values.

4.6.2.4. Lipid

The lipid pattern (Fig.35B and 36D) is characterised by the absence of marked seasonal trends, especially during experiment I. The values fluctuated between 7.8-11.9% (mean 9.2%) in experiment I and 2.2-12.0% (mean of 9.8%) experiment II. As Figs.34 & 35 shows the lipid was quite high, around 8-11%, up to October 1990 with a peak in September over experiment I and March 1992 in experiment II, and minimum in June 1991 and April 1992 (Fig.35B and 36D). Lipid content, during

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experiment II, increased dramatically after April minima.

4.6.2.5. Ash

Ash values ranged from 6.0% to 11.2%, average 8.2%, during experiment I and 4.2% to 14.0% with a mean of 7.3% experiment in II. In case of site-stock comparison, both transplanted and control stock in Loch Leven had significantly higher, by an average 1.4%, ash contents than mussels in Loch Etive ($P \leq 0.01$) (Fig.36E). During both experiments one major peak was observed in spring 1991 and 1992, and over rest of experimental period ash fluctuated (Fig.35B and 36E).

4.6.2.6. Energy (Caloric) Content

The energy content of the meat was determined during each month for all sites combined during experiment I (Fig.37A) and separately for each site and stock during experiment II, which was combined in Fig.37B. The mean ash-inclusive energy content of dry meat ranged from 4.66 to 5.10 Kcal/g with a mean of 4.932±0.118 Kcal/g and the mean ash-free energy content was 5.248±0.191 (5.16-5.63) Kcal/g in experiment I. The caloric values during experiment II were very similar to experiment I; with a mean of 5.015 ±.230 (4.61-5.44) Kcal/g ash-inclusive and 5.417±0.177 Kcal/g ash-free (Fig.37B), and there was not any difference between mussels from different stocks and sites. As Fig.37 shows energy content of dry meat varied seasonally with steady values during summer and early autumn and maximum values coinciding with highest protein values just before spawning during early spring. The relationship between energy and lipid content was not clear.
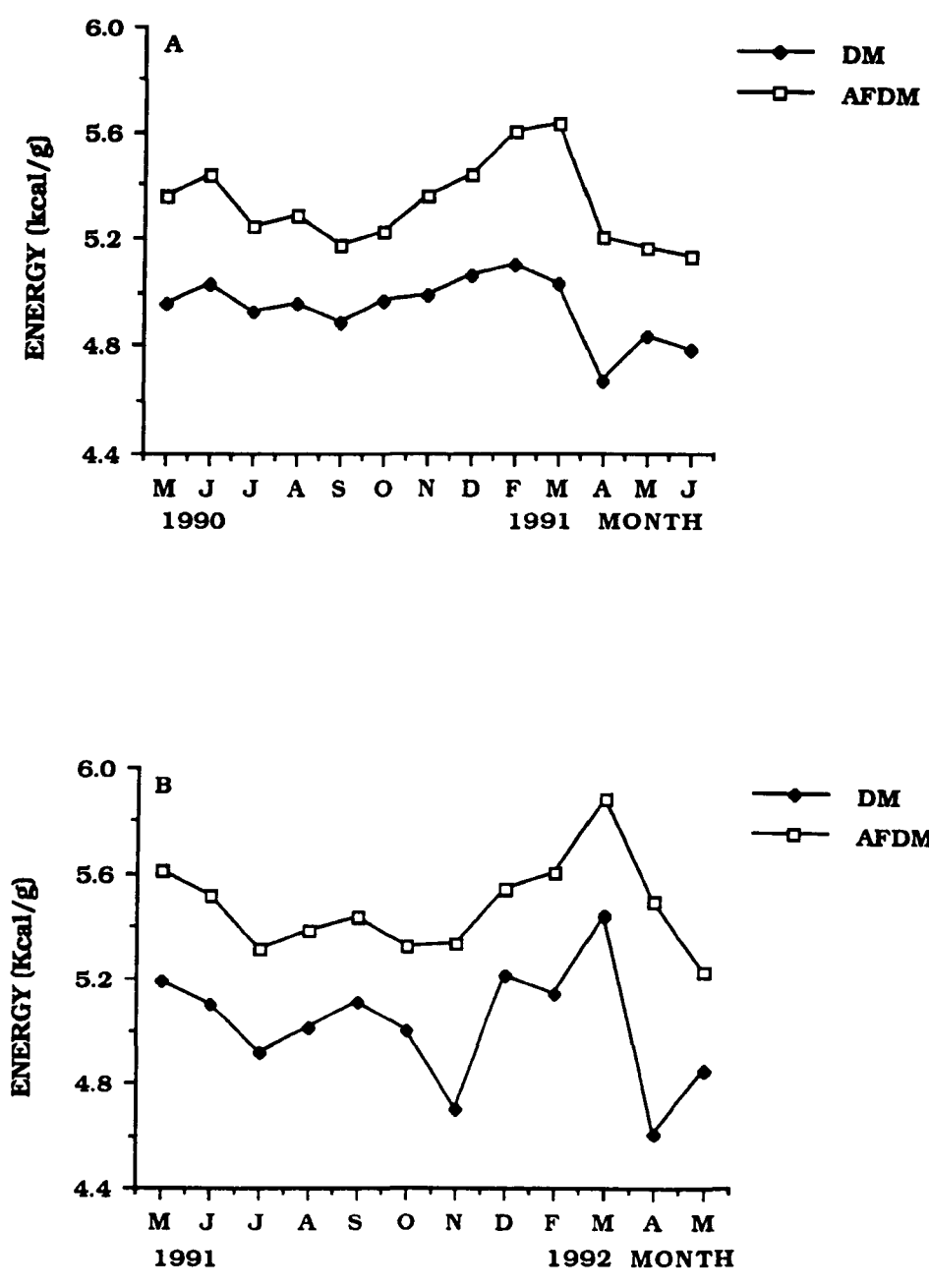
Fig.37. Seasonal changes in the ash-inclusive and ash-free mean caloric values (determined with a bomb calorimetry) of dry meat in cultivated mussels during May 1990- May 1992 (A: experiment I and B: experiment II).

4.7. Settlement and Growth of Spats

In order to monitor the settlement and growth of spats, polypropylene ropes, about 6 m long and 16 mm in diameter with pegs every 30-40 cm, were hung from a raft in Loch Etive and long line in Loch Leven at the beginning of May 1990. As the head ropes of the long lines were suspended 1 m below water level (section 3.1), so were the collectors. Soon after setting up, the ropes and pegs became covered a film of brown filamentous algae (*Ectocarpus sp*).

Although the sexual cycle and spawning period of the mussel populations were not directly studied, the seasonal cycle of meat content, condition index and biochemical composition (section 4.6) suggests that main spawning takes place during March-May. The settlement in Loch Etive started from June onwards and by the end of July the ropes, especially upper parts, were completely covered by small spats with a density of approximately 19500 ind m^{-1}. In Loch Leven, however, main settlement took place nearly one month after Loch Etive. The density of spats on the upper part of ropes in Loch Leven was round about 21100 ind m^{-1} in August. In both lochs there was no appreciable settlement on the last 2 m section of the ropes. There were subsequent settlements at very low levels throughout the summer in Loch Etive and almost all year around in Loch Leven.

During the summer some of the spats fell off as the algal filaments died off while water currents carried away others which were attached to sea weeds, especially in Loch Etive. By November the densities dropped to 8600±800(SD) and 6350 ±560 ind m^{-1} at level 1 (0-2 m) and level 2 (2-4 m), respectively in Loch Etive, and 15300 ±1300 ind m^{-1} at level 1 (1-3 m) and 8500±640 at level 2 (3-5 m) in Loch Leven.

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The length- frequency distributions of juvenile mussels settled in early summer were determined in November 1990 and shown in Fig.38A&B. The mean length of spats reached 14.52 ±0.313 (SE) mm in Loch Etive and 11.74±0.234 mm in Loch Leven in November. This difference between the two lochs in shell length growth was statistically important (P≤0.001). There were also significant differences between levels in shell length growth in both lochs, i.e. the mean shell length of mussels at the first level (15.24±.46 in Loch Etive and 12.98±0.325 in Loch Leven) was better than the second level (13.96±0.423 L. Etive and 10.37±0.283 L. Leven) (P≤0.001 for Loch Leven and P≤0.05 for Loch Etive).

This experiment was terminated in spring 1991 because most of the 1990 settlement was lost in Loch Etive and there was a heavy new settlement on experimental ropes and therefore it would not be possible to follow the growth of mussels settled in summer 1990.

4.8. Physiological Energetics

4.8.1. Environmental Parameters

Environmental data, mainly total seston and particulate organic matter (POM) and also salinity, temperature and particle concentrations for experimental sites are presented in Table-28.

Seawater temperature was almost the same at all sites with slightly higher values in September, but salinity was much higher and more uniform in Loch Kishorn than both Loch Etive and Leven, where it was much lower in September.

Seston (total particulate matter) concentrations did not exhibit much variability

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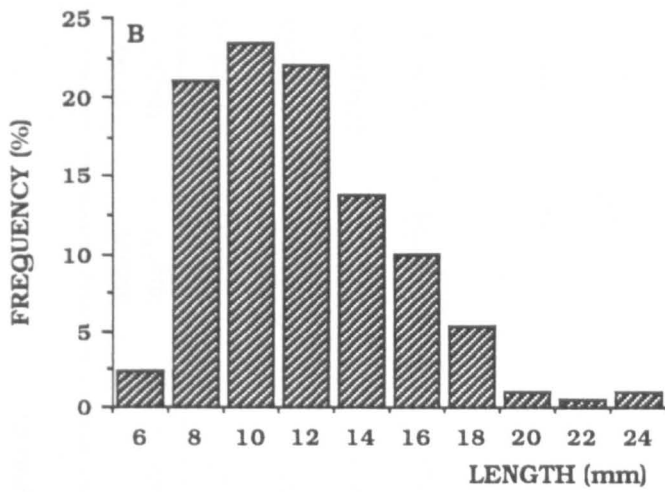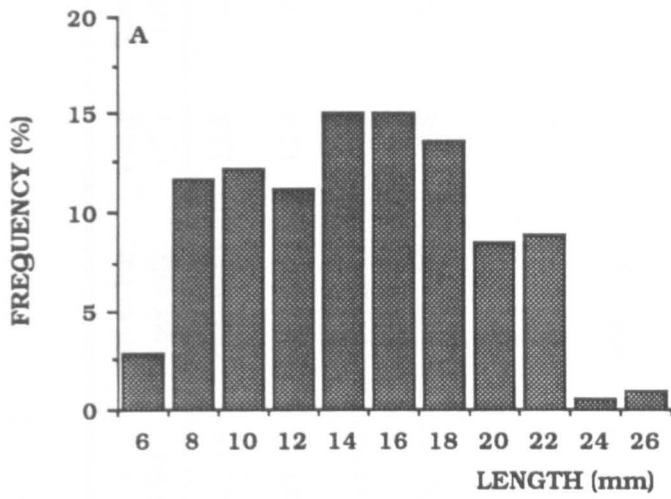
Fig.38. Length-frequency distributions in November 1990 for spats settled in June-August 1990 (A, Loch Etive and B, Loch Leven).

Table-28. Seston, POM and particle concentrations, salinity and temperature (means ±SE) at each site during physiological measurements. N is number of samples for seston and POM. KSF: Kishorn Shellfish, Loch Kishorn, and other site codes as in Fig.9 and superscript letters as in Table-6.

Date	Site	N	Seston (mgl⁻¹)	POM (mgl⁻¹)	%POM	No of Par. (per ml)	Temp. (°C)	Salinity (o%)
	LE	9	7.68±0.63	2.41±0.42	31.38±2.19[b]	4346±242	12.5	25
10-18 May 1992	AS	9	9.00±0.79	3.45±0.68	38.33±1.42[c]	6138±220	12.5	27
	GSF	9	8.51±1.17	2.04±0.56	23.97±1.88[a]	6874±343	12.0	21
	KSF	6	8.21±1.25	2.64±0.35	32.16±2.27[b]	5120±190	11.8	35
	LE	9	5.36±0.23a	1.93±0.39	36.00±1.77[b]	3650±148	13.0	17
7-17 Sept. 1992	AS	6	6.95±0.68[ab]	2.40±0.31	34.53±1.42[b]	3895±297	13.0	15
	GSF	6	7.96±0.97[b]	1.78±0.27	22.36±1.18[a]	4640±256	12.8	18
	KSF	9	8.77±0.88[b]	2.29±0.29	26.11±2.23[a]	3830±238	13.1	35

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among sites (range 4.40 to 18.0 mgl^{-1}), but mean concentration at LE was significantly lower than the other seston values observed at sites GSF and KSF ($P \leq 0.001$) in September (Table-28). As Table-28 shows high seston concentrations tended to coincide with high particle concentrations.

The food availability, expressed as particulate organic matter or POM, ranged between 0.81 and 8.35 mgl^{-1} in May and 1.09-3.59 mgl^{-1} in September with highest mean values at AS (salmon farm) followed by KSF (Loch Kishorn), and the lowest at GSF (Loch Leven) in both May and September (Table-28), but no significant differences in POM concentrations between the sites were detected ($P > 0.05$). As is shown in Table-28, however, there were differences in %POM between sites, with highest values at AS and LE. Water samples for POM were taken from three points (seawards, middle and landwards the farms) in shellfish farms. Although there was a detectable reduction in POM concentrations at GSF and KSF (see section 3.1), due to filtering activity of mussels, this decrease in POM was not found to be significant ($P > 0.05$). The other parameter used to define the nutritional value of seston was percent organic weight or %POM. %POM values were highest at AS followed by LE and KSF and lowest in GSF (Table-28) and differences between sites were significant both in May and September ($P \leq 0.001$).

4.8.2. Physiological Measurements

All physiological rates were corrected to a standard body size of 1 g dry meat, as described in section 3.8, which approximated the mean dry weight range of 0.83 to 1.59 g for mussels used in these measurements. The results of all physiological

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measurements are summarised in Table-29 for native and in Table-30 for transplanted mussels.

4.8.2.1. Clearance Rates

When the transplanted mussels are excluded, the native mussels in both Loch Etive (sites LE and AS) and Loch Kishorn (KSF) had significantly higher clearance rates than those in Loch Leven (GSF) in both the May and September trials ($P \leq 0.01$). In addition there were significant differences between AS and KSF in September ($P \leq 0.05$). Mussels at salmon farm AS had highest rates in May and overall values at AS were slightly higher than nearest mussel farm (LE), but it was vice versa in September. The clearance rates were significantly higher in May than September at all sites with higher values in May ($P \leq 0.05$ at GSF; $P \leq 0.01$ LE and AS; $P \leq 0.001$ KSF).

When data for each were combined, the stock or origin of mussels did not have any significant effect on clearance rates of transplanted mussels, while overall site had a highly significant effect on this physiological variable ($P \leq 0.001$). Mussels transplanted to Loch Etive had higher rates than those in Loch Leven ($P \leq 0.01$; Table-30). The clearance rates of mussels after 15 days acclimatization (in May) were significantly lower than native mussels in their new environment in both lochs ($P \leq 0.001$ at LE, and $P \leq 0.05$ at LL). Although Loch Leven mussels transplanted to Loch Etive (LL→LE) did not show any significant variation from the original stock in Loch Leven, the significant decline in clearance rates of Loch Etive mussels was apparent 2 weeks after transplantation. The clearance rates, however, for native and

Table-29. Physiological rates of 1 g (DMW) mussels in native stocks (LE, AS, GSF, KSF) at four sites in three lochs (Lochs Etive, Leven and Kishorn). All data are means (±SE) of 15 mussels.

Month (1992)	Site/Stock	CR (l h^{-1})	AE	VO$_2$ (ml h^{-1})	NH$_4$-N (µg h^{-1})	O:N index
	LE	2.43±0.131^b	0.616±0.047	0.538±0.035^a	9.52±2.07^{ba}	70.61
May	AS	2.58±0.302^b	0.542±0.055	0.591±0.057^a	10.86±0.80^b	68.06
	GSF	1.66±0.141^a	0.545±0.045	0.533±0.042^a	10.67±0.72^b	62.42
	KSF	2.78±0.170^b	0.543±0.040	0.501±0.021^a	7.71±0.92^a	81.19
	LE	1.76±0.158^{bc}	0.517±0.038	0.489±0.021^a	5.01±1.27^a	122.0
September	AS	1.61±0.146^b	0.477±0.042	0.544±0.041^a	7.62±0.37^a	89.20
	GSF	1.27±0.089^a	0.505±0.025	0.721±0.043^b	15.23±2.22^b	59.12
	KSF	2.02±0.133^c	0.422±0.038	0.496±0.041^a	8.26±1.62^a	75.03

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Table-30. Physiological rates of 1 g (DMW) mussels in native (LE, GSF) and cross-transplanted mussels between Lochs Etive and Leven (LL→LE and LE→LL, transplanted from Loch Leven to Loch Etive and vice versa), (LL→LE1 and LE→LL1 mussels transplanted 1 year before the trials). All data are means (±SE) of 15 mussels.

Month (1992)	Site/Stock	CR (l h⁻¹)	AE	VO₂ (ml h⁻¹)	NH₄-N (µg h⁻¹)	O:N index
	LE	2.43±0.131[c]	0.616±0.047[c]	0.538±0.035[b]	9.52±2.07[a]	70.61
	LL→LE1	2.55±0.175[c]	0.520±0.042[c]	0.512±0.047[b]	11.45±0.88[a]	55.87
	LL→LE	1.44±0.195[a]	0.475±0.037[b]	0.602±0.054[bc]	17.49±1.82[c]	43.01
May	GSF	1.66±0.141[b]	0.545±0.045[c]	0.533±0.042[b]	10.67±0.72[a]	62.42
	LE→LL1	1.59±0.140[b]	0.602±0.035[c]	0.499±0.035[a]	13.20±1.03[a]	47.23
	LE→LL	1.12±0.147[a]	0.298±0.027[a]	0.633±0.036[c]	14.75±1.36[b]	53.62
	LE	1.76±0.158[b]	0.517±0.038	0.489±0.021[a]	5.01±1.27[a]	122 .0
	LL→LE	1.68±0.160[b]	0.548±0.040	0.522±0.032[a]	9.95±1.04[b]	65.55
September	GSF	1.27±0.089[a]	0.505±0.025	0.721±0.043[b]	15.23±2.22[c]	59.12
	LE→LL	1.32±0.148[a]	0.475±0.042	0.528±0.038[a]	11.84±1.35[b]	55.72

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transplanted mussels in the same loch were very similar after 4.5 months (in September) and 1 one year acclimatization (Table-30).

4.8.2.2. Absorption Efficiency

Despite significant differences in percent POM concentrations between sites (Table-28), the food absorption efficiency with which the mussels assimilated material cleared from suspension was higher in spring than autumn, but this difference was significant only at KSF ($P \leq 0.05$). The efficiency values of native mussels, however, did not show any significant variation between sites/lochs, neither in May nor in September (Table-29).

Effect of site and stock on absorption efficiency was not so clear i.e. neither site nor stock affected absorption efficiency, as only newly transplanted mussels had significant absorption efficiency differences in May ($P \leq 0.01$). The absorption efficiency of both recently transplanted stocks were also significantly lower than native stock of host site in May ($P \leq 0.001$ at LL and $P \leq 0.01$ at LE), but not the efficiency of stocks transplanted one year previously and after 4.5 months acclimatization in September (Table-30).

4.8.2.3. Oxygen consumption

The weight specific oxygen consumption ranged between 0.489 and 0.721 ml O_2 g^{-1} h^{-1} (Table-29&30), and did not show any significant variation between sites in May but there were significant differences in September ($P \leq 0.001$) due to increased oxygen uptake by native mussels in Loch Leven (GSF). Apart from GSF, there was a very

slight decrease in oxygen consumption of native experimental populations in September in comparison to values determined in May.

In the case of native and transplanted mussels, although there were some significant differences both in May and September (Table-30), the effect of stock and\or site was not so apparent. For example, VO_2 values for mussels 15 days after transplantation was significantly higher than both their original populations and native stocks in the same environment, but after 4.5 months and 1 year O_2 consumption rates were very similar (Table-30).

4.8.2.4. Ammonia Excretion and O:N Ratio

There were significant differences between sites in ammonia excretion of native mussels in May ($P \leq 0.05$) and September ($P \leq 0.001$), particularly in September values for mussels at GSF were higher than the others (Table-29). In general, there was a significant drop in ammonia excretion rates of mussels at AS and LE, and increase at GSF between May and September ($P \leq 0.01$).

The ammonia excretion rates of all transplanted mussels increased in comparison to their original stock in native environments in May, and both site and stock had a significant effect on excretion rates ($P \leq 0.01$); i.e. both as site and stock, Loch Leven (GSF) mussels had higher values than that of Loch Etive (Table-30). Ammonia excretion of mussels transplanted to Loch Etive (LL→LE) at the beginning May'92 was considerably higher than native mussels (LE) both in May and September ($P \leq 0.001$), while in Loch Leven mussels which were transplanted 15 days and 1 year before the trials excreted more ammonia than native mussels ($P \leq 0.05$).

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The mean O:N or the ratio of oxygen consumed to nitrogen excreted constitutes a suitable measure of protein catabolism relative to both carbohydrate and lipids, acting as an index to evaluate nutritional status (Bayne & Newell,1983), and relatively high rate of protein catabolism results in a low O:N ratio which is generally recognised as a sign of stress condition (Widdows,1978b). O:N values calculated during present trials varied between 43.01 and 123 (Table-29&30). They appeared to be lower for native mussels at GSF than the other sites and for all transplanted mussels it was lower than native mussels at the same sites (Table-29&30).

4.8.3. Scope for Growth

The basic physiological measurements summarised in previous section were converted into energy equivalents (J g^{-1} h^{-1}) to calculate " scope for growth, SFG", which is an index of the energy available to the mussels for both somatic growth and production of gametes (Warren & Davis,1967, cited by Bayne & Widdows,1978). The resulting energy budgets and SFG are given in Table-31. In all native populations SFG values, which ranged from 8.89 to 87.9 J $g^{-1}h^{-1}$, were higher in May than September. The differences between native mussels at different sites were also significant in both trials ($P \leq 0.001$); SFG for mussels at GSF was lower than the other three sites. Although, mean SFG of mussels at AS was slightly higher than LE and KSF (Table-31), it was not substantial enough for statistical significance.

There were substantial decreases in SFG of transplanted mussels in May or after 15 days of acclimatization, particularly SFG of LE→LL was as low as 0.74 J g^{-1} h^{-1} (Table-31). Site or loch had a highly significant effect on SFG ($P \leq 0.001$) and values

Table-31. Components of the energy budget (J g⁻¹h⁻¹) in native and transplanted mussels from four sites in three lochs; means of 15 replications (±SE). C, total consumption of food energy; A, energy absorbed; R, energy respired; U, energy excreted; SFG, scope for growth and K2, net growth efficiency. Superscript stars indicates significant differences in SFG between sites (LE, AS, GSF and KSF), while superscript letters indicates differences between transplanted and native mussels (LE, LL→LE, GSF and LL→LE); those bearing same number of * or same letters are not different.

Month (1992)	Site/ stock	C	A	R	U	SFG	K2=SFG/A
	LE	121.8±9.56	73.45±6.15	10.94±0.708	0.237±0.022	62.28±6.18***ᶜ	84.79±0.014
	LL→LE1	127.93±8.79	69.28±7.45	10.40±0.752	0.280±0.020	58.61±7.74ᶜ	84.60±0.066
	LL→LE	72.15±9.75	34.59±5.16	12.21±1.100	0.435±0.045	21.91±5.35ᵇ	63.34±0.110
May	AS	185.1±21.7	100.2±13.9	12.04±1.150	0.270±0.020	87.90±13.9**	87.72±0.020
	GSF	70.43±6.02	38.70±4.13	10.84±0.861	0.266±0.018	27.55±4.13*ᵇ	71.19±0.041
	LE→LL1	67.55±5.92	40.46±3.98	10.14±0.718	0.329±0.026	29.99±4.32ᵇ	74.41±0.050
	LE-LL	47.52±6.22	13.97±2.42	12.86±0.731	0.367±0.034	0.740±2.53ᵃ	5.290±0.182
	KSF	152.8±9.35	83.61±7.63	10.19±0.430	0.192±0.019	73.20±7.09**	88.55±0.016
	LE	70.53±6.35	37.15±4.34	9.95±0.426	0.125±0.010	27.08±4.54**ᶜ	72.89±0.057
	LL→LE	67.49±6.42	36.92±4.29	10.60±0.656	0.248±0.026	26.06±4.13ᶜ	70.58±0.069
September	AS	80.54±7.29	38.47±4.33	11.07±0.815	0.190±0.009	27.23±4.41**	70.78±0.029
	GSF	47.24±3.17	23.92±1.95	14.65±0.867	0.380±0.055	8.89±1.57*ᵃ	37.16±0.052
	LE-LL	48.94±5.49	22.75±3.46	10.73±0.775	0.295±0.034	11.72±3.25ᵇ	51.52±0.062
	KSF	96.24±6.32	39.90±2.96	10.08±0.845	0.206±0.040	29.6±3.43**	74.42±0.036

of both native and transplanted mussels at LE were higher than GSF. Differences in SFG values between native and transplanted animals at the same sites were significant after 15 days of acclimatization in both Loch Etive and Leven ($P \leq 0.001$), but no significant differences could be shown after 4.5 months and 1 year of acclimatization. The SFG of native mussels significantly declined ($P \leq 0.001$) and increased for newly transplanted mussels between May and September ($P \leq 0.001$ for LE$\rightarrow$LL; ns for LL$\rightarrow$LE).

The rate of mean absorbed energy required for maintenance energy (SFG=0 or A=R+U) was estimated to be around 10.33-13.07 J g^{-1} h^{-1}; the minimum for mussels at KSF and the highest for mussels at GSF.

4.8.4. Growth Efficiency

The scope for growth, as a proportion of the absorbed ration (A), gives net growth efficiency (K_2) which is a measure of the efficiency with which food is converted into body tissues (Widdows,1978b). The K_2 estimated in this study ranged from 0.37 to 0.87 for native and 0.05 to 0.85 for transplanted mussels (Table-31). The K_2 values of native mussels determined in May were higher than September values, whereas for transplanted mussels they were minimum 15 days after transplantation and maximum after one year of acclimatization. Among the native populations GSF had lower mean K_2 values than the other three sites ($P \leq 0.001$). There were no significant differences between native and transplanted mussels in Loch Etive, whereas in Loch Leven native mussels had higher K_2 values than those transplanted in May ($P \leq 0.05$) but in September the latter was slightly better (Table-31).

5. DISCUSSION

The results of this study show that variability in growth, biomass, production and physiological energetics in mussels between sites in the same loch was far less than sites in different lochs, losses and natural mortality rates were similar at all sites and the effect of salmon farming on some of the growth parameters was significant. Reciprocal transplantation demonstrated that site rather than stock is the main factor affecting growth characteristics. Growth parameters in marine bivalves is principally affected by the interactions of several environmental parameters, particularly salinity, temperature and food availability (Bayne & Newell,1983). The effects of main environmental variables on growth characteristics, physiology and survival of bivalves have all been examined alongside in-situ and in-vitro experiments around the world (e.g.Incze et al.,1980; Jones,1981; Widdows et al.,1984; Page & Hubbard,1987; Brown & Hartwick,1988a&b; Page & Ricard,1990; Tedengren et al.,1990). The present findings were compared with similar previous studies and discussed in detail in the light of the main objectives of the study.

5.1. Environmental Parameters

5.1.1. Temperature

Water temperature 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 temperature has been extensively investigated for mussels (e.g. Bayne et al.,1976a&b; Seed,1976; Incze et al.,1980; Page & Hubbard,1987; Brown & Hartwick,1988).

Annual water temperature distribution (Fig.9) is mostly influenced by the season. At the seaward end of the lochs the coastal sea water is a source of temperature which varies smoothly through the year between narrow limits (7 to 14°C) which change little from year to year, and at the landward end, river run-off is a source of widely varying temperature (Edward & Edelsten,1976). Therefore, water temperature in lochs is influenced mainly by tidal range and quantity of freshwater run-off (Milne,1972a; Edwards & Edelsten, 1976). For example, according to Gage (1972) seasonal changes in temperature in Loch Etive appear to follow roughly the local coastal pattern but usually with a lag in timing that is possibly because of the restricting effect of the sills. This is also valid for Loch Leven which is very near to Loch Etive and also connected to the Firth of Lorne. The main hydrographic differences between the two lochs is high freshwater run-off in Loch Etive and high tidal range in Loch Leven, so the seasonal pattern of temperature in Loch Leven might follow the coastal pattern more closely than in Loch Etive. Water of low temperature is mainly due to the influence of cool freshwater run-off from surrounding mountains. By late spring, reduced freshwater flow and increase in solar radiation contribute to a rise in temperature of the freshwater entering the loch (Solórzano and Grantham,1975) and the temperature of whole loch gradually rises.

There is some evidence, particularly in Loch Leven, of vertical temperature stratification with slightly higher values at the surface than at 6 m during summer and vice versa during winter (Fig.9). Gage (1974) reported similar observations at the head of Loch Etive where the temperature range for the deeper waters resembles fairly closely the coastal pattern, while the range at the surface was somewhat higher. This

is mainly caused by direct solar warming of the surface brackish layer in summer. In winter, surface temperature is depressed lower than the normal coastal minimum by the considerable amount of cold freshwater entering the loch. This effect was most marked in Loch Leven where the greatest depression of surface salinity by run-off occurs. Growth was governed by seasonal temperature variation and this temperature difference between the surface and 6 m was not enough to have any impact on growth of mussels below a depth of 2 m.

5.1.2. Salinity

As briefly described in section 2.3 (Fig.7), freshwater run-off from rivers, which is less dense (1.0 g cm^3) than seawater (1.025 g cm^3), overflows the seawater and forms two layers: a surface brackish water layer and a saline deep water layer within which salinity is constant to the bottom. It is basically a broad interface between freshwater and seawater layers in which turbulence enables the transfer of seawater upwards and also allows the movement of freshwater downward (Kennish,1986). Thus, the salinity and dimensions of the brackish layer depend on freshwater run-off. This layer in lochs with high run-off such as Loch Etive might be very deep. Fish and shellfish farming in Loch Etive, for example, mainly takes place in this zone, and rapid salinity fluctuations, as well as constant low salinity, could have a negative effect on cultivated shellfish species.

Lochs such as Etive and Leven, with significant freshwater sources, are distinctly different in form and hydrographic character from those without such sources, for example Loch Kishorn. They have a well-defined vertical salinity stratification as

shown by significant differences in salinity values between the surface, and 2 and 6 m depths during the present study (Fig.10). The vertical salinity stratification was more profound in Loch Leven than Loch Etive and Dunstaffnage Bay. That is because the halocline occurs below 6 m (at 10 m; Wood *et al.*,1973) in Loch Etive due to very high run-off while in Loch Leven it is just above 2 m. In addition within Loch Leven the surface salinity values at site near the head of the loch (GSF) were much lower than at GS (Fig.10), which is one sill lower down the loch than GSF (Fig.5). Although the catchment of the loch is not excessive (Table-4), freshwater constantly flows from the River Leven and the British Aluminium Plant in Kinlochleven at the head of the loch. Since there is no sill, which would help mixing between the freshwater and brackish water layer, between site GSF and main freshwater entrance of the loch (Fig.5), surface water at this site is not well mixed with the underlying saline layer. On the other hand, as a result of relatively high (about 3.7 m) tidal range a large amount of seawater enters from Forth of Lorne and keeps the salinity over 25%o just below 2 m and around 30%o at 6 m.

Relative to its surface area Loch Etive has a considerably greater catchment area than Loch Leven (Table-4) and the constricting effect of the shallow main sill at Connel (Fig.4), reduces the external tidal range of 4 m to an internal one of 2 m. This is responsible for the relatively low but vertically quite uniform salinity distribution above the halocline in the lower part of the loch where experimental sites were located. The main sills at Connel and Bonawe and the secondary sills in the lower basin create a vertically and horizontally well-mixed basin. In the lower loch run-off from the River Awe, which is almost half the total catchment (Wood *et al.*,1973),

determines the hydrography of this basin and much of the whole loch. The ratio of mean river flow to mean tidal flow for the whole loch over a year is around 1:8 (Wood *et al.*,1973).

Dunstaffnage Bay is under the direct influence of coastal seawater from Firth of Lorne and, apart from brackish water run-off from Loch Etive during ebb tide, there is no freshwater entrance. Therefore, recorded salinity values were quite high with 35%o salinity at 6 m in most of the experimental period and uniform with season, except September 1990, in comparison to sites in Loch Etive (Fig.10).

Annual salinity measurements below 2 m where the culture ropes are suspended were usually above 20%o at sites SS (Dunstaffnage Bay), GSF, and GS (Loch Leven), while at LE and AS salinity levels below 20%o occurred over a substantial portion of the year. At these sites month to month fluctuations were greater than at the other sites. It has been widely acknowledged that blue mussels are euryhaline and poikilosmotic, i.e. they are capable of withstanding relatively great salinity ranges, from 4-5%o to fully oceanic conditions, but at the same time they are incapable of maintaining an inner osmotic concentration (Bayne *et al.*,1976a) during day-to-day salinity fluctuations. So they have to minimise the osmotic stress by isolating their tissues and body fluids from the surrounding water (Akberali & Trueman,1985). In *M. edulis* complete isolation from surrounding environment is achieved by siphon and shell valve closure. When the salinity drops from around 30-35% to 7%o (Akberali & Trueman,1985), firstly they close the exhalant siphon, which prevents pumping and isolates the mantle cavity from falling salinities, and then valve closure occurs for complete isolation if salinity continues to decline. 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 (Bernard,1983 cited by Brown & Hartwick,1988). In Scottish sea lochs with deep brackish layer, culture ropes are suspended 1-3 m the below surface, but as main spat settlement takes place in the upper 4 m section of the water column (section 4.7), this brackish layer still plays an important role in the culture cycle. The apparent advantage that low or fluctuating salinities might have on mussel culture practised in these areas is in the control of certain predators, such as starfish, and the type of biofouling competitors.

5.1.3. Total Seston and Particulate Inorganic Matter

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 & Widdows,1978; Incze *et al.*,1980; Rodhouse *et al.*,1984; Smaal *et al.*,1986; see also Table-32). Total seston concentrations determined at experimental sites during this study varied between 0.7 and 17.4 mg l^{-1} depending on season and sites (Fig.12). Mean seston concentrations at both salmon farms during experiment I and at AS in experiment II were higher than at mussel farms. In general, total seston concentration in lochs varies with river discharge, biological production (which shows a seasonal trend) with highest values in the spring and the lowest in winter, and water movement (Solórzano,1977). In the present study highest seston values were recorded during summer and lowest during late autumn at nearly all sites (Fig.12). This pattern reflects the effect of

phytoplankton production, and freshwater run-off during winter and early spring.

Mean particulate inorganic matter (PIM) values recorded during this study ranged

between 2.75 and 4.6 mg l^{-1}, which consisted of 41-66% of total seston, with

Table-32. Total seston, particulate organic matter (POM), %POM and chlorophyll-a
values reported in mussel growth and physiology studies (note: the chlorophyll-a
values are annual means and the others are ranges).

Location	Ses. (mg l^{-1})	POM (mg l^{-1})	%POM	Chl-a (µg l^{-1})	Reference
Ria de Arosa					Tenero &
(Spain)	-	-	-	7.9	Gonzales,1976
Cattewater (UK)	-	0.9-5.6	-	-	Bayne &
Lynher (UK	7-42[a]	1.2-4.8	19[a]	-	Widdows,1978
Lynher (UK)	4.5	1.1	2.5	1.4	Widdows et al.,1979
Killary Harbour					Rodhouse et al.,1984
(Ireland)	-	-	-	1.6&2.4	&1985
Tamar (UK)	4-19	-	10-20	-	Widdows et al.,1984
Swansea (UK)	3-7	-	24-44	-	Widdows et al.,1984
Bellevue					
(New Foundland)	3-6	1-3	43	-	Thompson,1984
Oosterschelde					
(The Netherlands)	15-28	1.7-3.2	10-12.5	5.9	Smaal et al.,1986
Whitehead					Carver &
(Nova Scotia)	0.9-2.8	0.3-1.1	33-55	-	Mallet,1990
Marennes-Oléron,					Deslous-Paoli et
(France)	10-95	2-20[b]	10-30	4-5	al.,1990
California Coast	2-30	0.5-10	10-70	2.0	Page & Ricard,1990
Boca del Rio-					
Mandinga,Mexico	8.7	5.1	59	12	Farias,1991
Northwest					
Mediterranean	3.2-38.2	0.82-23.0	26-60	2.4	Grenz et al.,1991
Jervis Inlet					
(B.Columbia)	-	0.70-15.0	-	4.1	Jones &Iwama,1991
Galicia (Spain)	0.7-2.7	0.35-1.10	35.8-54.7	-	Navarro et al.,1991
L.Etive(Scotland)					
site LE	0.7-13.3	0.3-6.7	34-58	1.8	This study
AS	1.7-14.5	0.8-7.4	43-56	1.9	"
D.Bay(Scotland)	2.9-17.4	1.5-9.15	38-53	1.8	"
L.Leven(")					
site GSF	1.6-15.1	0.7-7.3	36-59	1.2	This study
GS	4.7-15.3	2.1-6.9	43-56	1.5	"

a: Mean for Lynher and Cattewater estuaries; b: Approximate estimation from graph

maximum values from mid-autumn to early spring and the lowest during summer. These relatively high levels of PIM in autumn and winter are probably related to land drainage during the rainy season. The PIM concentrations measured during this work did not show apparent differences between experimental sites, and are very similar to values determined at some other locations where bivalve food resources have been examined (Widdows *et al.*,1979; Rodhouse *et al.*,1984b; Smaal *et al.*,1986; Farias,1991). In order of decreasing importance, PIM in estuaries is generally held to be derived from rivers, freshwater run-off, or from the sea by tidal transport, or comes from local re-suspension of bottom sediments by tidal currents and waves, and release of trapped fine sediments in the marginal areas of the system (Shubel,1971; Moore,1977; McLusky,1989). These materials are moved along the estuary generally in suspension at varying speeds by water movement and their ultimate fate in estuaries is sedimentation, which may be a lengthy process (Moore,1977). When considering growth and physiological energetics of filter feeders at relatively high seston levels, the effect of PIM should be taken into account (Kiørboe & Møhlenberg,1981), but studies of the effect of the PIM levels on physiology and growth of mussels have led to divergent conclusions. In some cases growth has been found to decrease with low seston quality, even at very low seston concentrations (Widdows *et al.*,1979; Bayne *et al.*,1987). Other results show either no net effect, or an increase of growth rate at low or moderate seston concentration ($\approx$1-25 mg l^{-1}), as filter feeding activity is highly stimulated by low quantities (5-12.5 mg l^{-1}) of PIM, resulting better growth per unit time (Winter,1976&1978; Kiørboe *et al.*,1981; Kiørboe & Møhlenberg,1981). Furthermore, according to Kiørboe *et al.*(1981), suspended bottom material may serve

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as an additional food source. The negative effect of PIM on growth rate is potentially to "dilute" the POM content of seston, and thus to decrease the energy value of seston rather than to reduce the amount of material filtered by the mussels (Widdows *et al.*,1979; Kiørboe & Møhlenberg, 1981; Héral.,1987). However, Kiørboe *et al.*(1981) found that mussels efficiently counteract the food diluting effect of PIM (silt in their experiment) by selective sorting of particles, by increasing their clearance and ingestion rates, and by utilizing some of the food originating from the silt. In any case, neither total seston nor PIM levels recorded during this study were too high to effect physiological parameters and limit growth (Widdows *et al.*,1979; Rodhouse *et al.*,1984b), but high enough to stimulate feeding activity.

5.1.4. Transparency

The mean transparency (secchi depth) in the sea lochs ranged between 5-7 m and did not show any significant variation between the sites, but it exhibited a regular seasonal pattern at all sites: high during spring-summer and low during autumn-winter (Fig.11; Table-6). These transparency values are lower than secchi disc values in Loch Eil (Grantham,1981) and the depth of the euphotic zone (the depth at which light was 1% of that above water surface) values recorded in Loch Etive by Wood *et al.*(1973). Gowen *et al.* (1988) reported that the euphotic zone was shallower at stations next to a fish farm than at a control station, and ascribed this into the effect of farm installations on light penetration. At salmon and shellfish farms, cages nets, rafts and ropes covered with mussels, combined with more particulate material (originating from the farms) could cause greater attenuation of light. According to the results of

this study, variations in secchi depths are related to firstly season, because of variation in radiation, and secondly particulate inorganic matter concentrations. Wood *et al.*(1973) reported large day-to-day fluctuations in irradiance at the surface, and a possible inverse relationship between the depth of the euphotic zone and amount freshwater entering the loch. Similarly, Grantham (1981) determined some relationships between rainfall and secchi depth. It appears that in the sea lochs large amounts of suspended matter and dissolved humic material are transported into the lochs with freshwater run-off, which is higher during autumn-winter months, and this reduces the transparency of the water. Limited transparency and the high proportion of cloudy days might cause light limitations (Wood *et al.*,1973) and light may become the limiting factor for primary production.

5.1.5. Particle Concentration

Particle measurements were carried out only during experiment II, and unfortunately it was not possible to analyse the fluorescence (phytoplankton - chlorophyll-a) characteristics of particles with the Coulter Counter. Total particle concentrations ranged between just over 9,000 and 60,000 number ml^{-1} with maximum numbers during spring-summer, and minimum during autumn-winter.

Although the size range of natural particles falls within the size range limit for *M. edulis* (Jorgensen,1975; Bayne *et al.*,1977; Héral, 1987), almost 70 percent of detected particles were between 1-2 μm which is a very unusual natural particle size range in comparison to studies in other estuaries (Bayne *et al.*,1977; Widdows *et al.*,1979; Newell *et al.*,1989). One possible explanation could be breakdown of cells

before counting, since samples were preserved in Lugol's iodine for a few days. This may have caused an increase in particle number and decrease in size range. Particle counting during physiological energetics work was carried out immediately, on the same or following day after sampling, so there was little possibility of cell breakage. A small percentage of larger particles, however, can still dominate seston in terms of weight per unit volume (as mg/l); for example if 1% of particles are a size of 10 µm and this comprise 90% of total weight. So the 5-12 µm size fraction at experimental sites dominates food availability for mussels.

5.1.6. Sources of Food for Mussels

Food for filter feeders has been described as the edible fraction of suspended organic material obtainable by animals (Herman & Scolten,1990). The quantity and quality of food, also known as food availability, in seston have significant effects on the physiology and growth of shellfish (e.g. Winter,1978; Widdows *et al.*,1979; Bayne & Newell,1983; Rodhouse *et al.*,1984b) and are the main criteria for site selection for a shellfish farm and carrying capacity estimations. The quality or availability of food in seston has been expressed as organic matter/unit volume of particles (Bayne *et al.*,1987), organic content of seston (Widdows *et al.*,1979; Smaal *et al.*,1986), percent fluorescent particles, i.e. phytoplankton (Newell *et al.*,1989) or the ratio of particulate inorganic (PIM) to organic matter (POM) (Wallace & Reinsnes, 1985; Wilson,1987).

5.1.6.1. Particulate Organic Matter

Although between 30% and 58.8% (overall mean of 46%) of total seston was

POM (Fig.13-14), average POM values of 2-4.8 mg l⁻¹ were comparable to values measured in other mussel studies generally in estuaries around the British Isles and elsewhere (Table-32). The mean POM content of seston was similar at all sites. Unfortunately, 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 (Widows *et al.*,1979; Wallace & Reinsnes, 1985). Especially in estuarine environments with high freshwater input, non-living organic matter (e.g. bacteria, dead organisms, food waste from salmon cages, faeces and pseudo-faeces from mussels, micro-zooplankton and other detritus) can constitute a significant proportion of the POM, sometimes being more abundant than living organic matter (Riley,1970; Kennish,1986). The weak correlation between chlorophyll-a and POM concentrations indicates the presence of non-phytoplankton organic particulates which may be estimated on the basis of particulate carbon and nitrogen. In such a study, Solórzano (1977) determined high values of particulate organic C:N ratios in Loch Etive in autumn and winter, and suggested that this was as a direct result of the large amount of non-living organic material.

There were significant differences in POM values recorded at salmon and mussels farms; POM was higher at both salmon farms in experiment I and at AS in experiment II than at neighbouring mussel sites, and %POM values at salmon farms were stable at around 40-50%. It is most likely that this was as a result of food wastage and faeces from salmon cages. In a similar study with the Pacific oyster, *Crassostrea gigas* (Thunberg), Jones & Iwama (1991) also found higher concentrations of POM at the stations associated with salmon farms than at control

stations.

Although phytoplankton can be the most important component of POM (Riley, 1970) and the main food for mussels, particularly during spring and summer, and the presence of non-living particulate matter reduces the quality of seston, there is strong evidence showing the utilisation by mussels and some other bivalves of non-phytoplanktonic sources, mainly organic detritus and bacteria, to meet their energy requirements when phytoplankton concentrations are seasonally low or where there are high concentrations of non-living particulate organic matter and bacteria (Seed,1976; Widdows et al.,1979; Rodhouse et al.,1984b; Lucas et al.,1987; Page & Hubbard,1987; Langdon & Newell,1990). Since phytoplankton production varies seasonally in most estuaries and coastal waters, the relative importance of phytoplankton in the diet of mussels most likely varies with location and time of the year as well. Rodhouse et al. (1984b), for example, suggested that cultured mussels on offshore rafts depended principally on phytoplankton for food, while inshore mussels utilised both phytoplankton and non-phytoplankton particles. Similarly, Widdows et al. (1979) estimated that phytoplankton food availability exceeded maintenance requirements only during June to August, and that non-phytoplankton particles must contribute substantially to the nutrition of mussels at other times of the year in the Lynher estuary. As a consequence of these variations in phytoplankton food, detritus acts as a stabilizing food source for filter feeders. Use of detritus by bivalves may take 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 (Héral,1987) since the digestive enzymes

of molluscs have the ability to utilise it (Bayne *et al.*,1976a). Salmon farm sites have higher POM levels than ordinary sites and may have high bacteria concentrations as well (Gowen *et al.*,1988; Rosenthal *et al.*,1988; Jones & Iwama,1990) since POM and DOM (dissolved organic matter) released from salmon farms would be available for heterotrophic organisms such as bacteria (Gowen *et al.*,1988). Langdon & Newell (1990) demonstrated that blue mussels living in marshes obtain around 30% of their nutrition from detritus material derived from the vascular plant *Spartina alterniflora*. Although there is no direct evidence suggesting the utilisation of salmon food particles as supplementary food source by bivalves, mussels could utilise particulate feed fragments from pellets as well (Wallace,1980; Jones & Iwama,1991). Bacterioplankton occurs in varied concentrations in all coastal and estuarine ecosystems, and the free-living bacterial resource could contribute only 4.2% to the carbon and 17% to the nitrogen budget of the Lynher estuary mussels (Lucas *et al.*,1987). Lack of experiments, however, makes it difficult to assess the effect of natural bacteria on growth. In addition, if there is enough phytoplankton source during spring and summer and mussels are quiescent during winter, when phytoplankton is minimum, they may not consume non-phytoplanktonic food sources at all. Apart from phytoplankton, detritus and bacteria, DOM (mainly free amino acids, sugars and fatty acids) may also serve as a food source for *M. edulis* (West *et al.*,1977; Héral,1987; Prieur *et al.*,1990), and fish farms may also contribute to natural concentrations of DOM, but little is known of the potential importance of DOM to the nutrition of bivalves and the energy contribution they represent has to date not been taken into account in growth studies of any bivalves. An exception is Manahan *et al.* (1983,

cited by Langdon & Newell,1990) who estimated that uptake of amino acids at ambient concentrations in seawater could meet 34% of the metabolic requirements of *M. edulis.*

5.1.6.2. Phytoplankton and Chlorophyll-a

There is no doubt that phytoplankton is the main food source for mussels (e.g.Incze *et al.*,1980; Rodhouse *et al.*,1984b; Langdon & Newell,1990). The usual way to follow changes in phytoplankton biomass is to determine chlorophyll-a (Héral.,1987).

5.1.6.2.1. Differences Between Sites and Lochs

There was no significant difference in chlorophyll-a levels between individual sites, but combined values for sites (LE and AS) in Loch Etive (comparison made during experiment II) was higher than those in Loch Leven (GSF and GS)(P≤0.05). Particularly at site GSF chlorophyll-a levels were much lower than sites in Loch Etive (Fig.16); for example during spring (April-May) 1992 concentrations in Loch Etive were around 2.0-3.5 µg l^{-1}, while in Loch Leven they were still just around 1.0 µg l^{-1}. The freshwater input to lochs is the most important factor determining the initiation and subsequent support of the phytoplankton population (Solórzano & 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. The nutrient status of Loch

Leven is unknown, but the limitation of nutrients is directly affected by the amount of freshwater entering into the loch, and it has been considered that nitrate depletion would limit the growth of phytoplankton in Lochs Linnhe and Creran (Solórzano & Grantham, 1975; Tett & Wallis,1978) adjoining Loch Leven. Thus the situation in Loch Leven with a similar run-off and catchment area is probably similar. In Loch Etive, on the other hand, freshwater run-off is extremely high and the concentrations of nutrients is directly affected by the amount of freshwater entering the loch (Solórzano & Grantham,1975; Solórzano,1977). In that case nutrient limitation during summer should not be such a problem in Loch Etive compared to Loch Leven, since salinity was hardly over 25‰ between 0-6 m in the former and there was not much seasonal variation. Thus, differences in nutrient concentrations might be one reason for variations in summer chlorophyll-a levels between the two lochs.

Another main difference between the lochs is the depth of the brackish layer or halocline. In Loch Etive the halocline generally occurs at around 10 m and the top 10 m also coincides with the euphotic zone (Wood *et al.*,1973), whereas in Loch Leven the halocline is just above 2 m, but the depth of the euphotic zone is around 6 m. Consequently, in Loch Leven phytoplankton would be either mixed to a depth below the halocline and diluted with incoming seawater from the Firth of Lorne, which in general has a lower biomass than waters in the lochs ((Solórzano & Grantham, 1975; Gowen *et al.*,1988;), or restricted to the top 2 m. If the first assumption is correct, light would be a limiting factor as well, and this would make the development of a phytoplankton bloom light and temperature dependent. This could also explain the delay in the spring increases. If the second assumption is true, which is less likely,

then this biomass cannot be utilised by cultivated mussels in this loch the since they are suspended 2 m below the surface. Finally, the flushing time of the lochs can create variations in chlorophyll-a concentrations by limiting the accumulation of biomass, since the flushing time of Loch Leven (cf 2.5 days) is much shorter than Loch Etive (8 days). In brief, it is more likely that the 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.

Water at 2 m contained very slightly higher chlorophyll-a than that at 6 m at almost all sites in all seasons. Solórzano & Ehrlich (1979) also found higher chlorophyll values at 1 m than at 5 m in Loch Creran but it was during autumn and winter, while during summer values at 5 m were higher than those at the surface. They suggested that this was as a result of shortage of light at 5 m in autumn-winter and very low levels of ammonium and nitrate at the surface during summer. The same explanation, however, is not exactly valid for this study. There would not be nutrient limitation at 2 m in Loch Etive during summer due to high freshwater run-off, but light and transport of the phytoplankton from 6 m to below the euphotic zone by the sinking with each flooding tide may be a possible explanation for slight, but regular, differences in chlorophyll-a between two levels. In Loch Leven, both light and the increasing dilution effect of seawater of poor algal content are possible factors affecting chlorophyll-a contents at 6 m.

5.1.6.2.2. Effect of Salmon Farms

The mean chlorophyll-a values did not show any significant variation between the

nearest salmon and shellfish farms. Jones & Iwama (1991), on the contrary, have observed significant increases in chlorophyll-a levels at all stations associated with a salmon farm compared to two control sites. As has been reviewed in section 1.5, the feed required to produce 1 tonne of fish contains around 100-140 kg N. Of this N, 25% is retained in the fish, and the remainder is either not ingested or converted to organic waste products (Fig.3) (Penczak *et al.*,1982; Gowen & Bradbury,1987; Gowen *et al.*,1988; Ackefors & Enell,1990). Since nitrogen is considered to be the limiting factor for production in most sea areas and some Scottish sea lochs, especially during the summer (Dugdale,1967; Solórzano & Grantham,1975; Solórzano & Ehrlich,1979; Jones,1981), this significant eutrophicating component should contribute to elevated levels of chlorophyll-a (i.e. an increase in phytoplankton biomass). No nutrient measurements were made during this study and it is, therefore, impossible to say whether nutrient availability was a limiting factor for phytoplankton growth during summer and nitrogen release from salmon cages has caused local hypernutrification around salmon farms. There have been some field studies of the effect of fish farms on marine phytoplankton and several have used chlorophyll-a concentration as an indicator of eutrophication. In general these studies so far are inconclusive or have shown little detectable increase in chlorophyll-a levels adjacent to fish cages. For example, Weston (1986a; cited by Institute of Aquaculture,1989) in Puget Sound and Institute of Aquaculture (1989) in Ireland failed to attribute any increased chlorophyll-a concentrations to salmon cage farming. According to Gowen *et al.* (1988), on the other hand, Mäkinenn & Pursianien (1987) found a two-fold increase in dissolved nitrogen concentration and five fold increase in primary production adjacent to a fish

farm compared to natural levels. Gowen *et al.* (1988) extensively investigated changes in the nutrient status and ecology of phytoplankton resulting from the release of dissolved and particulate material from a large salmon farm located in Loch Spelve, which is also adjacent to the Firth of Lorne and with a similar general hydrography to Lochs Etive and Leven. They reported that there was some evidence for localised increases in ammonium levels next to the fish farm which were considered to result from excretion by fish and sufficient enough to stimulate phytoplankton growth, but they could not detect any apparent increase in phytoplankton biomass (both in terms of chlorophyll-a and total cell volume). They concluded that light availability might have influenced the ability of the phytoplankton to utilise the additional nitrogen, or phytoplankton utilised the additional ammonium, but was transported beyond the fish farm before any significant growth had taken place, since the doubling time of phytoplankton populations is about 2-3 days (Tett & Wallis,1978). In the present study chlorophyll-a levels were slightly higher at the salmon farm (GS) than the nearest shellfish site (GSF) in Loch Leven during summer, but it is very difficult to draw any conclusion. There could be two possibilities; (a) chlorophyll-a levels might be reduced by the filtering activity of mussels at GSF, and (b) from autumn to spring the production is limited by light so there was no difference between the two sites, but during summer nutrients were limiting and nitrogen discharge from the salmon farm, which was a quite large farm, supported greater phytoplankton growth.

5.1.6.2.3. Seasonal Phytoplankton Cycles

Seasonal cycles of chlorophyll-a observed at experimental sites in Lochs Etive,

Leven and Dunstaffnage Bay were similar to the seasonal cycles determined previously in the same or similar West coast sea lochs (Table-33). The seasonal cycle of phytoplankton production in sea lochs and factors effecting it have been described elsewhere (e.g. Wood *et al.*,1973; Solórzano & Grantham,1975; Tett & Wallis,1978; Solórzano & Ehrlich,1979; Grantham,1981; Jones,1981; Gowen *et al.*,1983) so it is not going to be repeated here. The spring increase (defined by Tett & Wallis,1978 as the time when chlorophyll concentrations first exceed 1 µg l^{-1}) was in early April both in 1991 and 1992 (Fig.16), but the maximum values measured in Loch Etive and Dunstaffnage Bay were around 5.0 µg l^{-1} in June, and in Loch Leven 3-4 µg l^{-1} in July-August. As shown in Table-33 maximum spring values measured during this study are in agreement with the majority of previous studies, but the timing of the spring peak, which is generally in March, was very late in 1991 and 1992. There could be two possible explanations for this delay. Firstly, the spring bloom in Scottish west coast sea lochs only persists for 2 to 3 weeks (Gowen *et al.*,1988) and the sampling interval was one month, so it is likely that the peak of the bloom was missed both in 1991 and 1992. Secondly, the spring peak was delayed by combinations of several factors which control the initiation and magnitude of the spring increase and vary from year to year. Increasing solar energy input, resulting in increasing net production, is the main cause of the spring increase, but the timing is probably also affected by variations in the vertical and horizontal stability of the water column due to freshwater run-off (as higher run-off causes dilution), and tidal mixing. So light limitation might play an important role in years of poor spring increases (Wood *et al.*,1973; Gowen *et al.*,1983; Gowen *et al.*,1988). In any case it is not valid

Table-33. Seasonal chlorophyll-a (μg l^{-1}) values (range) determined at a depth range of 0-10 m in some Scottish west sea lochs (winter: December-February; spring; March-May; summer: June-September).

Loch	Winter	Ranges Spring	Summer	Spring Bloom Conc.	Month	Reference
L. Ardbhair	0.1-0.3	0.4-3.0	0.5-3.9	3.0	April-June	Gowen *et al.*,1983
L. Creran	-	0.5-2.6	-	4.5	March	Solórzano & Grantham,1975
	0.1-1.8	0.8-10.8	0.8-6.8	10.8	March	Solórzano & Ehrlich,1979
	0.05-2.3	0.4-37.2	1.2-7.8	37.2	March	Tett & Wallis,1978
Dunstaffnage Bay	0.2-0.3	0.5-2.6	2.0-4.5	2.6	June	This study
L. Eil	0.05	-	-	5.5	May	Grantham,1981
L. Etive	-	0.1-3.6	-	3.6	March	Solórzano & Grantham,1975
	0.1-0.4	0.4-5.0	0.9-3.7	5.1	April	Wood *et al.*,1973
	0.1-0.4	0.4-3.4	1.3-4.8	4.8	June	This study
L. Leven	0.1-0.2	0.7-2.9	1.1-4.4	2.9	June	This study
L. Linnhe	-	0.1-2.6	-	3.0	March	Solórzano & Grantham,1975
Lynn of Lorne	0.13	-	-	2.6	March	Grantham,1981
L. Spelve	-	3.0-4.5	4.0-6.0	10	April	Gowen *et al.*,1988
L. Sween	0.5-0.9	0.5-6.8	0.6-3.9	6.8	March	Jones, 1981

to compare peak chlorophyll-a values measured during this study with those previously reported for various lochs where the sampling has been more frequent. Annual surface chlorophyll-a concentrations Lochs Etive and Leven can, however, be compared to neighbouring Loch Creran and Loch Eil, and other lochs such as Lochs Spelve and Sween, and in spite of some hydrographic differences, overall chlorophyll-a values are quite similar (Table-33).

Compared to chlorophyll-a values measured in mussel growth sites around the world phytoplankton biomass in Scottish sea lochs is similar to sites around the British Isles (including Ireland), but lower than other locations (Table-32). This is mainly because the factors governing the growth and annual cycle of phytoplankton in sea lochs are different from the classical marine environment and other estuaries. The growth of phytoplankton in Scottish west sea lochs is governed mainly by freshwater run-off, water column stability, nutrient supply, and light intensity (Grantham,1981). These factors affecting phytoplankton production in sea lochs have been studied and discussed extensively by several authors (e.g. Wood *et al.*,1973; Solórzano & Grantham,1975; Tett & Wallis,1978; Solórzano & Ehrlich,1979; Grantham,1981; Jones,1981; Gowen *et al.*,1983; Gowen *et al.*,1988).

5.1.7. Water Currents

Finally, several studies have emphasized 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 & 1985; Larsson,1985; Carver & Mallet,1990). Unfortunately, current measurements were not carried at experimental sites during this

study, but approximate spring and neap tide current speeds values can be calculated using the following equation (Edwards & Edelsten,1976):

$$V_{max}(m/sec) = [(A*H)/B]*10^{-4}$$

where A: surface area (m^2) of the loch landward of the site, B: cross-sectional area (m^2) of the loch at the site, and H: range of the tide (m). Some of these values have been taken from Table-4 and some of them from Admiralty Charts. So the velocities during neap and spring tides are estimated to be around 0.06 and 0.15 m s^{-1} at the sites in Loch Etive (tidal ranges 0.7 and 1.8m neap and spring and neap respectively), and 0.03 and 0.10 ms^{-1}, respectively, at GSF (tidal ranges 1.2 and 3.7). The values in Dunstaffnage Bay are 0.05 and 0.1 m s^{-1} (Edwards, A. pers. comm) and at GS in Loch Leven possibly a little higher (around 0.03-0.16 m s^{-1}; Edwards & Edelsten,1976) than at GSF since, due to an additional sill between GS and GSF the upper basin would be subject to lower tidal exchange and hence current velocities than seaward. Similar values of 0.04-0.15 m s^{-1} in the lower basin of Loch Etive were determined between the surface and 5 m by Wood *et al.* (1973). These estimated values are also in agreement with other directly determined values around fish farming sites in sea lochs. All this data indicates that current speeds are generally low; a range of between 0.02 and 0.1 m s^{-1} is typical for the majority of fish farms in Scottish sea lochs (Edwards & Edelsten,1976; Lumb,1989).

So the current speeds at sites GSF and SS appear be less favourable for mussels than at the other sites. The current velocities at AS and LE, however, could be lower than values estimated for Achnacloich Basin, as the basin is quite wide and the sites are located outside the main stream. In addition, in 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). In brief, these differences in current speed between sites cause some differences in growth rates of mussels through food supply.

These current speeds are also comparable with reported values from other mussel culture sites; for example it is around 0.001-0.002 m s^{-1} in Northwestern Sweden (Rosenberg & Loo,1983) , 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 Ria de Arosa (Figueras,1990) and 0.2-2.2 m s^{-1} in the Dutch Wadden Sea (Korringa,1976). A typical moderate current velocity of 0.02 - 0.06 m sec^{-1} is 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, as also the ability of mussels to remain attached without spending extra energy on byssus production. Farming installations (rafts, long-lines, culture ropes with mussels and cages) reduce the current speed, so the current speed in the middle of a farm comprising several rafts could be considerably lower than at the ends and this would create growth differences within and between rafts, depending on the position. Long-lines do not cause large differences in current speed compared to rafts and cages. This factor was considered during the experimental design and experimental mussels were suspended from different points on experimental rafts and cages, but it still is possible that mussels at the salmon farms were exposed to a reduced current. A theoretical model dealing with current velocities and carrying capacity is provided by Incze et al. (1981) and Carver & Mallet (1990).

5.2. Growth

5.2.1. Shell Length

Growth in bivalves consists of increases in both the shell and the soft body or meat (somatic growth), but the measurement of shell length is most widely used and possibly the easiest way to measure growth (Quayle & Newkirk,1989). Several alternative methods (Seed,1976,1980b; Quayle & 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 own 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**, relying on measurements of shell growth of 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 growth only during the first 2-3 years of life is important. Experimental mussels can be stocked in various types of stockings (for example Pergolari, Norwegian tubes, French socks; Dare & Davies,1975; Mason & Drinkwater,1981; Mallet & Carver,1989; Farias,1983,1991) or into small cages, lantern nets and vexar baskets (Incze *et al.*,1980; Sutterlin *et al.*,1981; Kautsky,1982; Skidmore & Chew,1985; Mallet &

Carver,1989; Kautsky *et al.*,1990; Page & Ricard,1990).

In general, length growth in temperate waters is rapid between late spring and early autumn, and slow or absent during the colder season. During the present study, shell length growth commenced in mid-spring and the main growing season was May to October, with virtually very little or no growth from December to March. Over 90% of length growth in Loch Etive happened between May and October, and in Loch Leven between April and October during experiment II (Table-13). In spring shell growth appeared to start earlier in Loch Leven than Loch Etive, although the reason is not clear.

Comparable periods of growth and quiescence have been described by Mason & Drinkwater (1981) in Linne Mhuirich (Western Scotland), in Killary Harbour by Rodhouse *et al.* (1984b), Dare & Davies (1975) for raft cultivated mussels and Dare (1976) for intertidal mussels in Morecambe Bay (England). As Figs.9,10,13 & 16 show, in October chlorophyll-a levels dropped below 1 μg l^{-1}, POM 2 mgl^{-1}, temperature below 10 °C and salinity started to fluctuate; in spring (usually in April) the growth speeds up when chlorophyll-a concentrations exceed 1 μg l^{-1}, but temperature is still around 7-8 °C. These factors, i.e. temperature, salinity and food supply, are generally acknowledged as the main factors governing seasonal and overall growth rate in mussels and similar bivalves.

Annual rates of growth in length showed variations between sites, particularly between sites in different lochs (Tables-9&13; Figs.18&23). Overall shell length increment was higher in Loch Etive and Dunstaffnage Bay than Loch Leven; 5 mm during experiment I and 4.5 mm during experiment II and, additionally, it was 2.7

mm greater at GS (salmon farm) than at GSF (mussel farm). These variations in growth in mussels among sites that have similar temperature regimes can be attributed to defined variables, namely salinity and food availability. Food availability may have limited mussel growth at sites in Loch Leven compared to Loch Etive and Dunstaffnage Bay, because there were significant differences in chlorophyll-a concentrations between the lochs ($P \leq 0.05$), and some variation between sites in Loch Leven (Table-6).

5.2.1.1. Effect of Salmon Farming on Length Growth

During experiment I growth at both salmon farms (AS and SS) was slightly (0.4-1.1 mm) better than the nearest mussel farm (LE), but this variation was not significant (Table-9). At the end of the experiment II, however, the length differences (1.4 mm in Loch Etive and 2.7 mm in Loch Leven) between mussels suspended at mussel and salmon farms were significant in both lochs ($P \leq 0.01$ in Loch Etive, $P \leq 0.001$ in Loch Leven and $P \leq 0.001$ between overall salmon sites $\underline{vs}$ mussel sites). Similar results have been reported by a few authors who investigated growth of shellfish around salmon cages. Wallace (1980) investigated growth in a number of naturally settled mussel population around Tromsø and Senja, Norway, about 350 km north of Arctic Circle. Two of five populations were from sites associated with salmon cage farms and the author reported that mussels close to fish farms had grown at relatively high rates, almost twice the rate of other wild populations, and almost continuously, i.e. without any winter interruption, while those from other populations had been subjected to clear and relatively prolonged growth stoppages. In his

conclusion, he speculated that this rapid and continuous growth were as a result of organic waste from salmon farming. As has been discussed in section 5.1.6.1, although there is no direct evidence suggesting that detritus could make a substantial contributions to the ration of mussels (e.g. Widdows *et al.*,1979; Rodhouse *et al.*,1984b), it is possible that organic food wastage from fish farms can be utilised by mussels and might support extra growth. Alternatively, it is widely acknowledged that suspended mussels have higher growth rates than mussels in natural beds because they have more access to suspended organic matter. This might be the main reason for the rapid growth of mussels associated with fish farming sites studied by Wallace (1980). Continuation of summer growth rate throughout the Arctic winter, however, is very surprising. If temperature is not a limiting factor, then the growth of mussels suspended at salmon farms during the present study should have continued during winter which is much milder than winter in Northern Norway, but it almost stopped at both salmon and shellfish sites. Farias (1983), with mussels suspended from marine rainbow trout cages in Kames Bay (Loch Melfort) in Scotland, and Jones & Iwama (1991) with Pacific oysters (*C. gigas*) suspended from chinook salmon (*Oncorhynchus tshawytscha*) cages in Jervis Inlet (Northwest Vancouver, British Columbia, Canada) conducted more specific and controlled studies to compare growth of shellfish in the immediate vicinity of marine fish cages and control sites. Both studies were quite short; first one 3 and second one 5 months. Farias (1983) found somewhat higher surface POM values around cages than the control site, but higher growth rates at the fish farm site were not quite significant at the 5% level. Jones & Iwama (1991) found that, as a result of higher concentrations of chlorophyll-a and POM around salmon

farms (see section 5.1.6), increases in shell heights of oysters suspended at salmon farm were as much as three times greater than that at the control sites. According to Rodhouse *et al.* (1984b) cultured mussels are mainly dependent on phytoplankton for food. If this is true, then there would not be substantial growth differences between sites associated with salmon farms and controls, unless of course fish farming creates a considerable degree of local eutrophication. During the present study, nutrient release from salmon cages, with exception of slight chlorophyll-a differences between salmon and mussel sites in Loch Leven (section 5.1.6.3), did not cause the type of eutrophication (section 5.1.6) which could support extra growth, but the growth rates were higher during both experiment I (not significantly) & II at salmon farms than at neighbouring mussel farms and these results are in agreement with previous studies. The amount of POM, however, was significantly higher around salmon cages than mussel farms. Perhaps these extra POM levels were utilised by mussels when other factors (salinity, temperature and physiology of the animals) were favourable for growth, but phytoplankton production was not enough; this would have created variation in growth between mussel populations grown at salmon and mussel farms. Alternatively, nutrient release from salmon farming might have caused very slight increments in chlorophyll-a levels which was not detectable, but led better growth.

5.2.1.2. Comparison with the Literature

The results of this study can be compared with those Mason & Drinkwater (1981) from various lochs on the West coast of Scotland (Table-34). Growth during the

Table-34. Comparison of first and second year growth in shell length of mussels in suspended culture around Europe and America .

Locality	Length (mm)	Time from settlement (month)	Annual Growth (mm)		Temperature (°C)	Reference
			1.Year	2.Year		
France[1]	40-50	15-24	20-30	10-20	8-20	Figueras,1989; Mason,1991
Holland[2]	60-70	24-36	20-30	-	(-)1-21	Dijkema & Stralen,1989
Ireland (West Coast)	43.0	18.0	20-25	15-20	7-18	Rodhouse et al.,1984b
Maine, USA	50.0	12.0	-	-	4-24	Incze et al.,1978
Newfoundland, Canada	50-60	34-35	-	-	1-18	Sutterlin et al.,1981
Northern Norway (Oslofjord)	50-60	15.0	-	-	-	Loo & Rosenberg,1983
Spain (Galica)	80-90	12-18	70.0	-	9-21	Figueras,1989,1990
Sweeden (west coast)	60.0	17-18	35.0	25.0	0-20	Loo & Rosenberg,1983
Wales	60.0	18-24	47.5	10-20	5-18	Dare & Davies,1975
Scotland (West coast):						
Linne Mhuirich (L. Sween)	61-64	12-14	40-50	15-20	3-20	Mason & Drinkwater,1981
L. Thuirnaig (L. Ewe)	62.0	26.0	30-40	20-25	-	Mason & Drinkwater,1981
Loch Beag	60.0	26.0	30-35	20-25	-	Mason & Drinkwater,1981
Loch Ardvar[3]	52.4	13.0	-	21.5	-	Mason & Drinkwater,1981
Loch Etive[4]	54.4	13.0	-	25.6	7-17	This Study
Dunstaffnage Bay[4]	54.2	13.0	-	25.9	6-15	This Study
Loch Leven[4]	49.5	13.0	-	20.5	5-15	This Study

[1]) Bouchot culture (Atlantic Coast)
[2]) Bottom culture (Waddensea)
[3] Rope grown mussel seed with initial mean length of 30.9 mm transferred from another loch
[4]) Re-tubbed rope grown mussels with initial mean length of 27.1 mm.

second year appeared to be similar or higher than values reported by Mason & Drinkwater (1981). Whereas, growth of small mussels during their first year in Loch Etive and Leven, where the mean length of spat settled in June-July reached 14.5 and 11.7 mm, respectively, five months after settlement, is much lower than Linne Mhuirich (33 mm six months after settlement) but higher than Loch Beag (5.2 mm six months after settlement). In Scotland the most promising site for mussel culture to be found to date appears to be Linne Mhuirich, a small inlet of Loch Sween where some environmental parameters, notably salinity and temperature, and even possibly food supply, seem to be very favourable as the experimental site was quite shallow. For example salinity in Linne Mhuirich during Mason & Drinkwater (1981)'s study was mostly between 30 and 35%o and never fell below 25%o, which is the maximum salinity in central Loch Etive. In addition, temperature during that study, particularly during summer, seems to be higher in Linne Mhuirich than Lochs Etive and Leven. Unfortunately, there is no detailed data available on POM and phytoplankton biomass, but they were probably similar to other sea lochs. Jones (1981), on the other hand, did not observed the same growth rate reported by Mason & Drinkwater (1981) in Coal Scotnish, another inlet of Loch Sween.

Growth rates vary widely with both location and time on account of environmental factors influencing growth parameters. In consequence even spatially close populations may differ greatly in growth rate (Rodhouse et al.,1984b). In addition comparisons of the present results with previous studies are difficult because of differences in initial size, experimental duration or methods used in calculating growth rates. In spite of these facts rough comparisons might be helpful in

understanding the interaction between various populations and environmental variables. In the present investigation growth rates of rope grown seed during their second year varied between 20.5 and 25.9 mm year^{-1}. The growth rates of cultured mussels from settlement to a marketable shell length of 50-60 mm at different geographical areas is shown in Table-34. Even the maximum values observed during the present study appear to be much lower than the growth rates measured in mainly suspended cultivation in various parts of the world. There is no doubt that some of these areas, for example Northwest Spain, have optimum conditions for mussel growth, while others such as the West coast of Ireland are comparable to the West coast of Scotland. The results from some areas are very surprising; for example, Loo & Rosenberg (1983) claimed that the same daily growth rate reported from Ria de Arosa was also observed at Tjärnö, Sweeden. Another reason for the substantial variation in growth rates between this and other studies in Table-34 could be initial size differences of the experimental mussels. Growth rate declines with increasing size due to a greater energy allocation to gamete production than to somatic growth (Rodhouse *et al.*,1984b) and reduced relative metabolic activity in larger mussels (Seed,1976). Comparisons between second year growth rates might be more useful, for example the mean shell length reached one year after settlement can vary from 47.5 (Dare & Davies,1975) to 61 mm (Mason & Drinkwater,1981) in rope-cultivated mussels and from less than 6 mm on high exposed rocks (Seed,1969, cited by Dare,1976) to 34.5-37.7 mm in exploited intertidal mussel populations (Dare,1976), but growth during the second year is generally around 10-20 mm (Table-34) which is similar to the present results.

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5.2.1.3. Factors Effecting Shell Length Growth

5.2.1.3.1. Temperature

There is no doubt that temperature is generally accepted as a very important factor controlling growth rate (Seed,1976; Brown & Hartwick,1988a; Jones & Iwama,1991) in temperate regions. Good correlation between water temperature and growth rates showed that water temperature had a strong effect on the length growth rate of mussels during this study as well (Table-17). Physiological studies on *M. edulis* around the British Isles have shown water temperature to have little effect on the "scope for growth", the energy available for somatic growth and reproduction, between temperatures of 10 and 20°C (Bayne *et al.*,1976b). In an earlier study Coulthard (1929, cited by Seed,1976) reported that the optimum temperature for *Mytilus* is around 10-20°C. Recently, Kautsky (1982) obtained significant correlation between temperature and growth of mussels in small experimental cages in the Baltic Sea. This study shows that water temperature cannot be eliminated as a major factor regulating mussel growth rate in the West coast of Scotland. If the apparent growth and physiological temperature optimum is between 10 and 20°C, then there is a period of 6 months, roughly from May to October, for summer growth of mussels in Scottish sea lochs (section 5.1.1).

Since, in general, rates of growth of marine bivalves increase with rise in temperature over the ecological range of the species, Hickman (1979) suggested that some of the variation in growth in different localities can be explained by temperature differences, as demonstrated by calculating growth in length (mm) per 1000 day-degrees (D°). He made this calculation from various earlier studies of mussels grown

in suspended culture and values ranged from 8.9 to 15.2 mm per 1000 D°. Unfortunately, the non-linear relationship between rate of growth and D° makes the comparative use of such data difficult (Bayne & Worrall,1980). Furthermore, variations in other environmental factors (for example salinity in some Scottish sea lochs) could dramatically effect the day-degree growth rate. Therefore, temperature or cumulative D° accompanied by food availability might provide a more acceptable method of predicting mussel growth within the salinity limits of 20-35%o and within a temperature range of 0-20°C (Hickman,1979; Bayne & Worrall,1980; Sutterlin *et al.*,1981), and would certainly facilitate comparisons of different growth results.

The day-degree growth rate of two-year-old rope grown mussels determined during this study ranged from 4.9 to 6.5 mm/1000 D°, which is very low compared to values calculated by Hickman (1979) for Venezuela, Spain, New Zealand, Spain, Wales and Canada, but the latter values were obtained mainly from annual growth rates during the first year when mussels generally grow very fast. For example, day-degree growth rate calculated for this study is roughly similar to the growth rate in Killary Harbour, Ireland, (Rodhouse *et al.*,1984b) and almost twice the growth rate (3 mm/1000 D°) of mussels in Wales during their second year (Dare & Davies,1975), but part of this difference is most likely due to size differences (initial mean lengths were 47.5 mm in Wales and 22.1-27.1 mm in the present study). Dare & Davies (1975) also carried out growth experiments with Norwegian tubes and trays, which were in general similar to the method of the present study, and seeds of 14-16 mm initial size reached 51-55 mm after one year, which is certainly much higher than annual growth increments recorded during the present and previous study carried out

by Mason & Drinkwater (1981), excluding Linne Mhuirich. The results reported by Dare (1976) for exploited intertidal and Dare & Davies (1975) for raft cultivated mussels clearly show that the Conwy estuary and Morcambe Bay are possibly the most favourable sites for the growth of mussels around the British Isles.

5.2.1.3.2. Food Availability

It has been shown previously that food availability can have the greatest influence upon bivalve growth rate (Seed,1976; Bayne & Newell, 1983; Brown & Hartwick,1988b) since if there is not enough food, growth will be retarded regardless of all other factors. In a number of studies including the present one (section 4.2.4; Table-17), a good correlation was found between growth rate and chlorophyll-a levels, especially on a seasonal basis (e.g. Sutterlin et al.,1981; Kautsky,1982; Rosenberg & Loo,1983; Page & Hubbard,1987; Brown & Hartwick,1988a; Jones & Iwama,1991). Incze et al. (1980) reported that chlorophyll-a levels of above 2 μg l^{-1} during the summer are accompanied by acceptable mussel growth rates in Maine estuaries in the USA. During this study the highest monthly growth increments of 5-7 mm occurred during June-July when chlorophyll-a content was between 3-4 μg l^{-1}. Similarly, comparison with the findings of Widdows et al. (1979) indicates that during summer, roughly May-September, chlorophyll-a concentrations in the experimental lochs exceed the maintenance ration of M. edulis ($\approx$2.4 μg l^{-1} chlorophyll-a). This certainly supports the main growth in shell length, but the data from the present work showed that chlorophyll-a concentrations of around 1.0 μg l^{-1} can still support considerable growth (over 2 mm/month). Perhaps mussels utilised the non-living part of POM as

a supplementary diet during autumn when temperatures are still around 8-10 °C. Lack of significant correlation between POM concentrations and growth rates, however, shows that non-living POM alone cannot support the apparent growth or when phytoplankton availability declines temperature drops as well and limits the growth because, apart from, a decline in quantity, the quality of seston during winter is very low. From October on, mainly low chlorophyll-a concentrations slow down the growth and falling temperatures in late autumn possibly limit the utilization of the non-living fraction of POM, but during spring higher water temperatures combined with elevated levels of food supply may stimulate rapid resumption of growth. Thus, in addition to temperature, the quantity and quality of food were also limiting factors for mussel growth in Scottish sea lochs.

High growth rates for mussels grown by suspended cultivation relative to growth of wild mussels have been recorded for several mussel populations around the world (Mason,1972a; Rodhouse *et al.*,1984b). For example it takes approximately six years in Killary Harbour, West coast of Ireland, for the fastest growing wild mussels, at 0% aerial exposure, to attain a shell length of 43 mm and AFDW, equal to that attained in 1.5 years in suspended culture. This is firstly because they are freely suspended in water column and therefore receive a superior food resource secondly, cultivated mussels allocate less energy for gamete output and shell deposition, and more to somatic growth than wild mussels (Rodhouse *et al.*,1984a) (Fig.39).

5.2.1.3.3. Salinity

As reported earlier by Newell (1976, cited by Parulekar *et al.*,1982), of all the
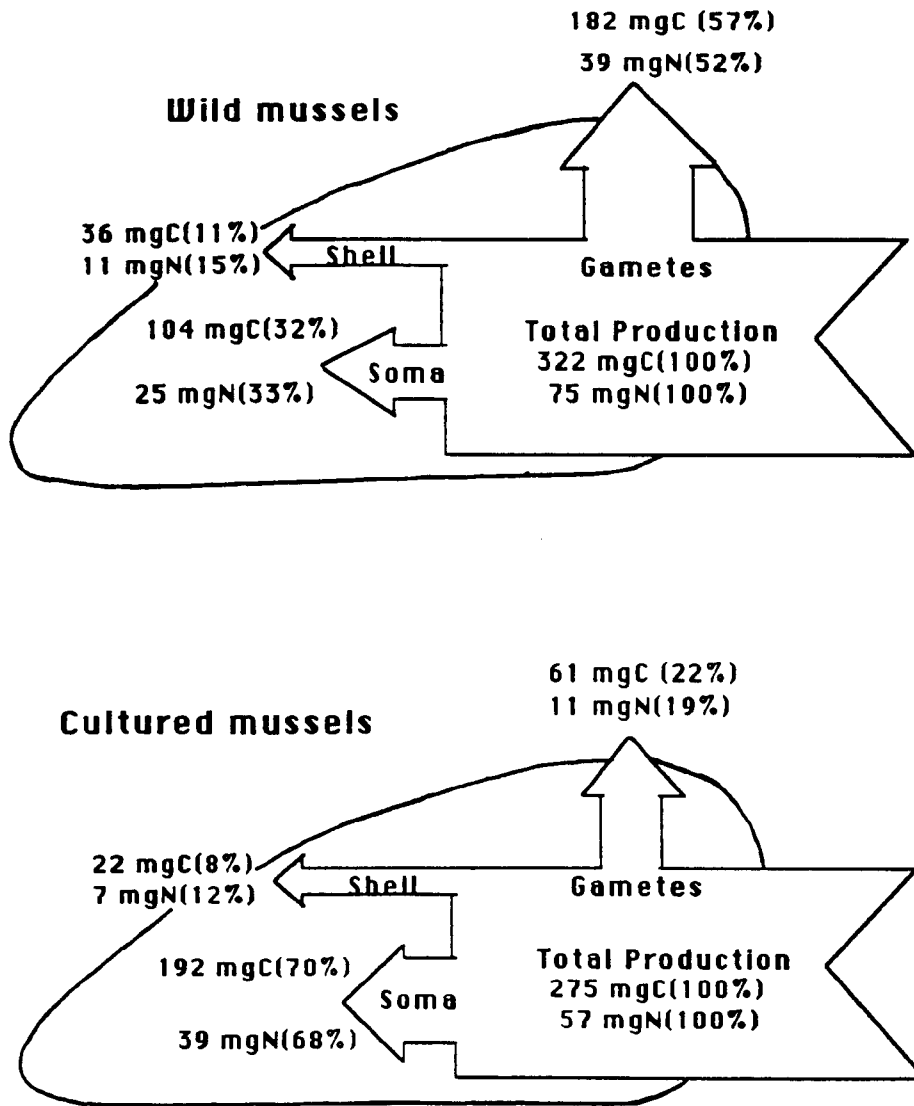
Fig.39. Allocation of carbon and nitrogen resources in wild and suspended cultured mussels (*M. edulis*) in Killary Harbour, Ireland (after Rodhouse *et al.*,1984a).

environmental variables, salinity, because of its wide seasonal variations and its relevance to osmo-regulation in aquatic organisms, also sometimes plays a dominant role in the growth of bivalves (Brown & Hartwick,1988a). For example in the Baltic sea stable low salinity (e.g.7%o in Sweden) is the main factor controlling growth rate and maximum attainable size in mussels (Kautsky,1982). Although salinity in the experimental lochs was not as low as the Baltic Sea, high fluctuations, particularly during spring when temperature and food conditions relatively favourable, could delay resumption of growth. As the cultivated and experimental mussels in Loch Leven were suspended below 2 m where salinity never dropped below 25%o, the effect of salinity on growth should be very limited and this factor can be eliminated. In Loch Etive (at sites LE and AS), however, salinity between 2-6 m was always below 25%o and sometimes as low as 10%o. Any sudden changes in salinity would subject these mussels to osmotic stresses to which they would continually be attempting to adapt. The resulting increased osmotic work load would be expected to reduce the amount of energy available for growth. Bayne (1976) measured the growth of *M. edulis* larvae from two populations at different salinities. Larvae from North Wales did not grow at 19%o and showed retarded growth at 24%o; at 30-32%o growth was normal. In larvae from a population in Oresund, however, where the ambient salinity was lower than in North Wales, growth occurred even at 14%o. This shows that although larvae can acclimatise themselves to possibly stable low salinity, fluctuations in salinity could retard growth.

5.2.1.3.4. The Effect of Depth

The effect of depth on growth rate in the literature is highly variable (Hickman,1979; Sutterlin *et al.*,1981; Kautsky,1982; Page & Hubbard,1987) and, unlike several studies which have reported a general decrease in growth rate with depth (Kautsky,1982, Loo & Rosenberg, 1983; Rodhouse *et al.*,1984b), during this study growth at level 2 (4-6 m) was better than level 1 (2-4 m) at site(s) in Loch Etive and Dunstaffnage Bay and <u>vice versa</u> at GSF in Loch Leven (Fig.18). There were no temperature differences between these depths, but there was some variation in chlorophyll-a levels (see section 5.1.6.2). Growth rates, however, increased with depth and decreasing chlorophyll-a and POM levels at the majority of sites. Rapid salinity fluctuations near the surface at sites in Loch Etive and Dunstaffnage Bay, and comparatively high salinity below 2 m but quite low food availability below 4 m (level 2) in Loch Leven are the most likely explanations for growth variations between depths. Growth of spat settled in June-July 1990, on the other hand, was better at level 1 than level 2 in both Lochs Etive and Leven. Mason & Drinkwater (1981) checked the effect of depth (0-2 m) on growth in Linne Mhuirich and did not find any significant difference.

5.2.1.4. Conclusions on Growth in Shell Length - Practical Implications

Although temporal variation in the growth rate of mussels is correlated with water temperature or degree-days, it may strongly covary with phytoplankton production. It is thus difficult to generalise about the importance of temperature or food availability alone in regulating growth rate. Nevertheless, when salinity conditions are

right, particularly in more northerly countries such as Scotland, Norway, Sweeden and Atlantic Canada, seawater temperature is probably more important than food availability (Mason, 1991), as it reduces optimum feeding and the growing season. For example, in the Oostershelde and Wadden Sea (The Netherlands), despite the very high chlorophyll levels (50-250 μg l^{-1} during spring), mussels reach marketable size in 2.5-3 years because chlorophyll-a does not always necessarily mean good feeding and growth, for it may coincide with temperatures so low that mussels are able to filter only a maintenance ration. So growth in marine bivalves is possibly governed by the interactions of temperature and food availability, especially in northern latitudes (Kautsky,1982; Bayne & Newell,1983), and during the present study the chlorophyll-a and temperature values were significantly correlated as well.

Since growth rate is governed by environmental parameters, the main factors considered during site selection for shellfish culture operations are the physical factors (temperature, salinity, current speed, shelter and depth), food supply and settlement. Although in general shelter and food supply are often considered major factors, in many Scottish sea lochs freshwater run-off or salinity might be the main environmental variable determining suitability of sites for mussel culture. Optimum salinity range alone, however, does not mean that a site is suitable for mussel culture. For example, during the present study at GSF, Loch Leven, salinity below 2 m where mussels were suspended was almost constant over at 25‰ all year round compared to fluctuating low salinities in Loch Etive, yet growth in Loch Etive was much better. Previous studies indicate that productivity values of sea lochs as a whole are very similar, but there might be differences even between basins or bays of the same loch.

As a result of these variations during the site selection process, if there is no established farm and no available data on environmental variables, a trial of at least one year should be carried out. During this trial spat settlement, both length and somatic growth of re-tubed mussels (preferably just over one-year-old rope grown mussels from the same loch) and some environmental parameters, for example salinity and temperature, are quite easy for shellfish farmers to measure. Food supply could be difficult, but growth observations can be used as an indicator for food supply. This kind of trial also helps to determine unknown environmental factors which might have considerable effects on growth and performance of mussels (see next section). Measurements of shell length, meat weight and condition index are quite easy, and a simple ruler, kitchen scale and measuring cylinder are enough. Sampling for shell growth and density of spat can be carried out at the end of first growth season (i.e. in October or November) and when the mussels are one year old, whereas growth of second year mussels should be measured possibly every three months; for example May, September, December and March. A length growth of around 25-30 mm during the first year (from settlement) and 20-25 mm during second year is normal for the majority of West sea lochs. Since shell growth may not always reflect meat growth, as was the case in Loch Leven during this study (see next section), meat and condition index of the year mussels should be determined every month or every 1-2 months.

If 50-60 mm shell length is accepted as the marketable size for cultivated mussels, and it is presumed that growth during the first year is slightly higher or the same as the second year, it is obvious that mussels cultured at experimental sites in

Loch Etive will take around 24 months to reach marketable size, which agrees with the findings of Mason & Drinkwater (1981) in Lochs Thuirnaig and Beag and is comparable with those obtained in other temperate localities (Table-34), but possibly even longer in Loch Leven. Although some mussels are ready for harvest during the second autumn, in practice harvest is generally carried out during the third summer and autumn when mussels are 24-30 months old or over 60 mm. Perhaps Scottish mussel farmers need a new common harvesting and marketing strategy which will bring harvesting forward and shorten the turnover time coupled with a campaign to make smaller (but in good condition) mussels acceptable. This view has also been shared by Dare and Davies (1975) and Mason & Drinkwater (1981).

5.2.2. Tissue Growth

A widely used method for estimating meat or tissue growth in bivalves is to employ regression to adjust dry or ash-free dry meat weights to an individual of standard length (Dare & Edwards,1975; Bayne & Worral,1980; Rodhouse *et al.*,1984b; Hilbish,1986). Since in mussels and most other bivalves there appears to be a significant relationship between length and meat weight, dry and/or ash-free dry weights are usually regressed against shell length, as has been done in this study (Table-12) and analysis of covariance used to estimate the mean meat weight (Crisp,1984). Sometimes it is not possible, however, to measure changes in meat weight from shell length because there is no apparent tight coupling between shell length and tissue growth; i.e. rates of growth in length and tissues do not occur synchronously. For example, 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, and a very similar pattern was observed during this study; there was a great increase in ash-free dry meat weight between April and May (Fig,20 & 25), but maximal shell length growth took place during summer (Table-9 & 13). This clearly suggests that growth in shell length and meat weight are influenced by different factors and uncoupled (Mallet *et al.*,1987a). For instance, as mentioned before Héral (1987) suggested that temperature is the primary explanatory factor for shell growth, but possibly the third factor for meat production. This might explain the later resumption of length growth in spring compare with somatic growth. The other reason for uncoupled length - somatic growth is the decline in meat weight during periods of negative energy balance due to food supply, spawning, stress etc.. This uncoupled length and somatic growth could be a general phenomenon in bivalves (Hilbish,1986). In addition, due to some other reasons such as stress, sometimes growth in length might not reflect the growth in soma as well, as appeared to be the case at GSF in Loch Leven. Even if both types of growth show very similar patterns in that particular year and site, it might vary with time and space even between very close localities. For example, length-weight equations determined for Loch Etive mussels during this study cannot be used for mussels from neighbouring Loch Leven. As a consequence of these reasons, there might be certain advantages in determining somatic growth by measuring directly, particularly if there was no similar previous study in that locality.

After all, the weight of farmed bivalves in practice would seem to be more important than shell length both for 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 in April-May, with increments gradually declined during summer and autumn before becoming zero in October-November, after which the mean weights decreased through the winter to a post-spawning minimum in spring (Fig.20 & 25). This growth pattern resembles the pattern of growth found in Linne Mhuirich in 1966-67 (Mason & Drinkwater,1981), Coal Scotnish and Sailean Mhór, Loch Sween, in 1980 (Jones,1981), and Killary Harbour, West coast of Ireland (Rodhouse et al.,1984b). This seasonal change in meat weight, according to Dare & Edwards (1975) who observed very similar patterns in sublittoral mussels in the Conway Estuary, results from rapid utilization of carbohydrate reserves and a depletion of both protein and lipid content (see section 5.6) in relation to the complex interactions of food availability and temperature with growth and reproductive cycles. During severe food shortage, when demands for the basal metabolism are not met by food uptake, the mussel will have a "negative scope for growth" (Bayne et al.,1976) and will utilise its stored energy reserves, resulting in the negative somatic growth (Kautsky,1982) (see section 5.8).

Some workers (e.g. Mason & Drinkwater,1981; Dare & Davies,1975) have used live weight to express harvestable yield. When the experimental mussels reached marketable size of 50-60 mm, mean live weight on French socks reached 6.1 kg m^{-1}, which is equivalent to a wet meat weight of 1.87 kg m^{-1} at all sites but GSF.

Although the testing of re-tubing material was not among the objectives of the study, these results are comparable to other studies. Almost the same values (maximum 6.2 kg m^{-1}, approximately equivalent to 1.54 kg m^{-1} wet meat) from mussels grown on ropes were obtained by Mason & Drinkwater (1981) in Linne Mhuirich and Loch Beag and in Killary Harbour by Rodhouse et al.(1985). Dare & 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}. When site is GSF excluded, low harvestable crops in present study were due to poor survival, but not to poor meat content or performance of mussels. During the experimental period live weight increased steadily by replacing depletion in meat content with water, but there was a small decline in February-March when meat contents were minium. Because of this decline in meat weight, this steady increase in live weight almost the whole year round shows that using live weight as a criterion for harvesting and production performance is certainly misleading. The wet meat weight and ash-free dry meat weight consisted of 17-38 % and 4.2-8.2 % of the live weight respectively with lowest values at GSF, while shell weight was 35-38% and the rest made up by shell cavity water (48-76%).

There were significant differences in somatic growth between salmon and mussel sites; in Loch Etive only WMW during experiment I and LW at AS during experiment II were higher than LE (P≤0.05) while in Loch Leven (experiment II) all three weights were higher at GS than at GSF (P≤0.01). There is not doubt all these values are comparable with values in the literature (e.g. Dare & Davies,1975; Mason & Drinkwater,1981; Grenz et al.,1991).

Although short term somatic growth rates appeared to be higher during spring and

summer there was no clear and significant positive correlation between meat increments and chlorophyll-a. As a matter of fact meat weights seemed to be more related to POM concentrations than chlorophyll-a. Several factors might account for the lack of a clear relationship between meat growth rate and amount of chlorophyll-a. Firstly, as has been discussed in section 5.1.6.2, the spring bloom in phytoplankton biomass in Scottish west coast sea lochs resumes generally in March, so it is possible that a spring peak missed during this study might have stimulated the maximum increments during April-May. Secondly, although phytoplankton provides a greater part of the mussel's diet, other organic matters could have provided a significant part of it (Jones,1981). Another important feature of meat growth, as mentioned above, is that it started in spring before shell length growth.

Mussels grown in Loch Leven had lower values for annual growth in live and meat weight than those from the Loch Etive and Dunstaffnage Bay (Table-10 & 14; Fig.20 & 25), but there were no differences between sites in the timing and duration of the annual periods of weight increase and decrease. The most important difference between the two lochs was the significantly lower tissue growth of mussels in Loch Leven and, in consequence, very low biomass and production. Although shell length growth was also slow in Loch Leven, meat weight and condition index were extremely low. There is no doubt that food availability is the main factor affecting meat growth, but available food levels (indicated by chlorophyll-a and POM) were not drastically low, particularly during spring and summer, and supported appreciable growth in shell length, so there could be some additional negative environmental factor(s) in this loch.

Apart from relatively low chlorophyll-a concentrations, environmental problems appear to be two-fold in Loch Leven: continuously fluctuating surface salinities and noticeably higher levels of zinc and copper. As just discussed above, experimental mussels were not exposed to rapidly fluctuating surface salinities in Loch Leven, so the direct effect of this factor on meat growth can be eliminated. Huchzermeyer (1985) carried out a short study in this loch to investigate the poor growth rate in farmed atlantic salmon (*S. salar*) and an outbreak of an ulcerative skin condition. He found raised levels of zinc (0.02-0.09 mg l^{-1}) and copper (0.02-0.04 mg l^{-1}) in loch water, apart from marked salinity fluctuations at the surface. Similar Zn (0.02-0.4 mg l^{-1}) and Cu (0.03-0.05 mg l^{-1}) levels were also found by the Forth River Purification Board in March 1985 (Huchzermeyer,1985). A proportion of these two metals is reaching the loch from freshwater inflows. Zn and Cu were also the only heavy metals detectable in the digests prepared from the mussels; Zn: 58-339 µg g^{-1} and Cu: <10-32 µg g^{-1} dry meat weight (Huchzermeyer,1985).

As mentioned before there is a British Aluminium Plant in Kinlochleven (Fig.5), but Huchzermeyer (1985) reported that although aluminium levels in the mouth of the River Leven, which receives the effluent from this plant, were slightly higher than in the other samples, even this level was not enough to constitute a danger for farmed salmon. He also reported considerably low fluoride levels and did not find any detectable heavy metal pollution originating from the British Aluminium Plant reaching the loch.

An indication of environmental quality in terms of these two metals may be obtained by comparing Zn and Cu in water and mussel tissues detected by

Huchzermeyer (1985) with those reported in the literature. Data in the literature show that concentrations of both metals appear to be higher in Loch Leven in both seawater and mussel tissues than in clean environments. Thurston *et al.* (1979) recommended "safe" levels of 0.05 mgl⁻¹ Zn and 0.02-0.06 mgl⁻¹ Cu in seawater while dry mussel tissues with Cu values of <6-13.7 µg g⁻¹ and <100-120 µg g⁻¹ Zn have been described as "clean or normal" (Segar *et al.*,1971; Davies & Pirie, 1980; Widdows *et al.*,1984).

The capacity of bivalve molluscs to accumulate heavy metals in their tissues far in excess of environmental levels is well known (Akberali & Trueman,1985). Widdows & Johnson (1988) found a clear and significant relationship between declining scope for growth and increasing Cu concentration in mussel tissue, and suggested that Cu appears to exert sublethal effects on feeding and growth rates of mussels over a relatively narrow range of water concentrations with a threshold effect at ca 0.005 to 0.01 mg l⁻¹ and a marked inhibition at 0.02 mg l⁻¹, which is lower than mean values detected in Loch Leven.

In general it is well known that heavy metals can play an important role as anthropogenic stressors and mussels can respond to Zn and Cu stress by valve closure, inhibition of byssal thread production, respiration, filtration rate, and in consequence poor growth and decline in organic body weight (Akberali & Truemen,1985), but it is not clear whether these Zn and Cu levels detected in Loch Leven could cause stress and the observed depression of growth. Some of these signs, e.g. very weak byssal threads, poor length and tissue growth, have been observed in this loch. However, without additional information on the physiological, cytological and biochemical stress responses, together with more detailed environmental data (Widdows, 1985a), it is

very difficult and unwise to relate these differences in meat weights to Zn and Cu levels in sea water or tissues. Moreover, this data should be taken cautiously, since Davies & Pirie (1980) did not find either Zn nor Cu levels in intertidal mussels from Loch Leven to be higher than at other clean sites around Scotland and Huchzermeyer (1985) himself found large variations between sampling dates. In addition, mussels from Loch Leven has been found completely clean and safe for human consumption by Environmental Health Services of Lochaber District Council in 1989. Therefore, additional studies that investigate poor meat content and environmental factors, including heavy metals, in Loch Leven are needed to determine whether poor growth in mussels results from environmental stress and/or low food supply. It has been suggested that shell growth is less susceptible to environmental variability than tissue growth due to the more or less constant presence of dissolved calcium in seawater (Brown *et al.*,1976). This might be true for comparisons between the Loch Etive and Loch Leven populations.

5.3. Growth and Morphological Differences Between Loch Etive and Leven Populations

M. 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 quite different environments, for example between the North sea and Baltic Sea, (Johannesson *et al.*,1990; Kautsky *et al.*,1990), between surprisingly close (in order of kilometres or less) inlets, bays, fjords or lochs of the same coastal waters (Widdows *et al.*,1984; Skidmore &

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Chew,1985; Mallet & Carver,1989), and between habitats in the same locality (Seed,1968).

Both native and transplanted mussels in Loch Leven exhibited slower length growth rate than those in Loch Etive; i.e. shell length growth in the transplanted mussels from both Loch Etive and Leven populations were similar to that of the native populations (Table-13&16; Fig.23C & 26B). There were slight (around 1 mm in 13 months) but nevertheless significant differences in final length between native (LE) and transplanted (LL→LE) mussels in Loch Etive, but the growth of transplanted mussels from Loch Etive was hardly better than control mussels (GSF) in Loch Leven. This small growth variation at LE was possibly a result of slow adaptation of transplanted mussels to the relatively lower salinity environment and/or LL→LE required time to recover from suspected persistent sublethal concentrations of Zn and Cu in tissues. Hence, both site and stock had significant effect on growth in shell length ($P \leq 0.001$ and $P \leq 0.01$ respectively), but site alone accounted for about 30% of the overall variance compared with only 2% for stock (Table-15&16). The effect of stock cannot, however, be explained in terms of environmental stress alone because in terms of LW increment Loch Etive stock (LE→LL) outgrows native stock in Loch Leven by May'92 as well as easily outgrowing transplanted Loch Leven stock (LL→LE) at site LE. Hence 10.5% of the variance was explained by stock with no interaction effect. The only possible environmental explanation might be the long-term influence of Zn and Cu accumulation in tissues of Loch Leven mussels. Unlike growth in shell length and live weight, the stock factor had no significant effect on tissue growth but site by stock interaction accounted for around 1.7% of the variance

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in wet meat weight in May'92 and 1.2-4.0% of the variance in ash-free dry meat weight on all three occasions (Table-15). This clearly shows that part of the differences in LW between stocks is due to differences in shell weight as Loch Etive mussels a have heavier shell than Loch Leven mussels (see below). This might be explained by the similarity between growth in shell length and LW, as WMW accounts for only 20-40% of LW with the rest due to the shell (35-38%) plus shell cavity water (ca 30%-40), so LW would surely reflect shell increments rather than meat changes. Hence high correlation between shell length and LW is to be expected and the 'uncoupling hypothesis' between shell length and tissue growth is not valid for LW. Another point worth mentioning is the underperformance of LE→LL in terms of meat weight which was reflected in exceptionally low %WMW/LW of 24% in May'92 (cf. 31-38% in other experimental populations) and %AFDMW/WMW of 17.5% (cf.20-22% in the others). This was most likely a result of both high water content of both the shell cavity and the meat.

These results clearly demonstrate that growth in length and more particularly tissue parts is to a major extent regulated by environmental (non-genetic) factors, likely to be salinity, temperature or food supply, rather than genotype. This is in agreement with the observation of Widdows *et al.* (1984) that environmental rather than genetic factors are primarily responsible for the physiological differences among populations. Since there are no temperature differences between the lochs and salinity values to which cultured mussels were exposed were higher in Loch Leven than Loch Etive, food availability, together with a suspected environmental stress factor due to high Zn and/or Cu concentrations in the seawater, were probably the main reasons for

growth rate differences. These findings are in accordance with the conclusions of various authors (e.g. Dickie *et al.*,1984; Mallet & Carver,1989; Johannesson *et al.*,1990; Kautsky *et al.*,1990) who found that site and its interactions are major determinants of variation in growth in populations of *M. edulis*. This could have important implications in practice because, for various reasons, growers are transferring considerable amounts of seed between sites in the same loch or between lochs and sometimes rely wholly on these seeds. It appears that the probability of finding better growing and surviving stocks for aquaculture or a stock that has the ability to adapt to a wider range of estuarine environmental conditions, although potentially important, is not very high. In addition, since there are no regular buyers and suppliers of mussel seed, at least at present, it is almost impossible to test the performance of a stock when, for example, spat settlement fails in a loch. On the other hand, it is relatively easy to find areas suitable for better growth and even if there is shortage of seed, this site could be exploited without worrying about the genotype of the stock to be transferred. Transferring seed from one site to another, however, results in extra seed loss (Paul,1987) and could be very labour intensive. Therefore, there is no doubt that a site suitable for both good settlement and growth is always preferable.

As discussed above, the shell length and tissue growth in transplanted mussels after 1 year acclimatization became very close to those of the native stocks of the recipient sites, but major differences in shell morphology, namely height, width, length:height, length:width and height:width, and the more narrow and elongated shape of the Loch Leven stock, did not change at all (Fig.26; Table-19), showing the

dominant effect of stock differences.

Various reasons have been suggested as possible causes of morphological differences between mussel populations relatively in close proximity. According to Seed (1968 & 1976), for example, shell morphology of wild mussels is influenced mainly by age, growth rate and population density; mussels from areas of high density have generally higher length:height ratios or narrow elongate shells. None of these factors, however, are valid for cultivated populations of the same age, similar density and growth rate. The same author has commented, based on the 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 eastern North America (Koehn & Gaffney,1984; Koehn *et al.*,1984), the Canadian Maritimes (Gartner-Kepkay *et al.*,1980) and between North Sea and Baltic Sea (Johannesson *et al.*,1990; Kautsky *et al.*,1990). Although there is no such evidence as allozyme frequency analysis from the present study, and despite the fact that during an average planktonic larval stage of about 3 weeks larvae could travel considerable distances facilitating genetic exchange between spatially separated populations, these two (Loch Etive and Leven) mussel populations may be isolated from each other in that there is little or no exchange of gametes between them. Consequently these morphological differences which remain almost unchanged after 1 year acclimatization could be a result of some kind of genetic variation. Surprisingly, a substantial amount of variation in some allozyme loci between populations over relatively short distance has

been reported around North America and Canada (e.g. Koehn *et al.*,1984). Another explanation, as suggested by Kautsky *et al.* (1990), would be the possibility of a very slow adaptation process. If the latter was the main reason, then there might be some slight changes over a one year period, but no significant changes in morphological characteristics of transplanted mussels occurred.

The shell weights of transplanted mussels in Loch Etive seemed to increase in comparison to the original stock in Loch Leven, but the contribution of the stock factor to total variance in shell weight was much greater than site. The shells of Loch Etive mussels were higher and appeared thicker, having a higher $CaCO_3$ content and a more darkish-blue colour, while Loch Leven mussels were thinner with brown, translucent shells. In this respect Loch Leven mussels seem to very similar to Baltic Sea mussels, while mussels from Loch Etive are typical of North Sea populations (Kautsky *et al.*,1990). Rate of shell formation is partially dependent upon supply of calcium to the mantle by the blood or external medium (Wilbur & Saleuddin, 1983) and the thinner shell structure of Baltic Sea mussels has been attributed to lower calcium content (Schlieper 1971; cited by Kautsky *et al.*,1990), low salinity and genetic factors (Kautsky *et al.*,1990). As has been mentioned several times, although surface salinity in Loch Leven was very low, these experimental mussels settled on spat collectors and were never exposed salinity below 25‰. So it is unlikely that salinity would have had a significant effect on shell thickness. Lochs Leven and Etive share the same coastal water source, so the calcium content of coastal seawater entering the lochs should be the same or very similar, but there might be some differences in catchment geology and in consequence the large amount of freshwater

entering Loch Etive could bring extra calcium which could explain slight effect of site. That these differences in shell thickness were also maintained in Loch Leven mussels that had been transplanted into Loch Etive would indicate that either genotypic differences or a very slow acclimatization process might be the main factor (Kautsky *et al.*,1990).

5.4. Mortality and Losses

The proportion of mussels lost (natural mortality plus fall-off) from the French socks ranged from 60 to 70%, being highest at site GSF and lowest at LE. Unlike pergolari tubes, losses from French socks did not occur just after immersion. Severe losses, however, followed immediately after disintegration of the cotton material due to lack of space for settlement. Disintegration of cotton material took 2-3 weeks and during this time mussels produce new byssus and attach to the netting and each other. Weak byssal thread formation observed in mussels in Loch Leven possibly resulted in extra losses from French socks. The reason for weaker byssus threads, as mentioned above, could be stress caused by sublethal Zn and Cu levels and low salinity (Sutterlin *et al.*,1981). Very heavy losses from ropes (up to 98% from ropes with initial density of 17,000-28,000 and 90-95% with 6,000-7,000 spat m^{-1} after one year) and Norwegian tubes were also reported by Dare & Davies (1975) in Conwy. After 13 months density dropped from 884±64 to a final of density ranging from 246 to 340 of over 50 mm length mussels m^{-1}. Under normal circumstances the mussel farm in Loch Etive usually yields around 280 mussels with a mean length of over 50 mm per m of unpegged rope (Paul,1987). As final live weight figures show, densities

of market size mussels in Linne Mhuirich (Mason & Drinkwater, 1981) were probably similar to those in the present trial. In a similar study Dare & Davies (1975), who stocked 1 m long Norwegian net tubes with diameters of 3.0 and 3.8 cm with 2,600 and 1,550 14 mm seed m^{-1}, respectively, recorded 200 mussels m^{-1} at 55 mm mean shell length after one year. They concluded that final density was governed by available attachment area, rather than by initial stock density or tube size. Certainly observations during the present study supports such a conclusion because the attachable surface area of socks was smaller than commonly used culture ropes.

Re-tubing of mussels has been quite a common practice amongst mussel farms since on harvestable ropes there are a lot of under-size mussels which settled later or grew slowly, and re-tubing is possibly the best way to utilise these mussels. The most commonly used tubes are nylon pergolari, but recently French socks as used during the present experiment and another French made bio-degradable cotton sock are widely employed. The latter version of the French sock is used with a pegged culture rope. The mussels re-attach themselves onto this rope before the cotton completely disintegrates and in this way heavy losses from pergolari and the earlier type of French sock can be reduced to minimum.

The only predator around experimental sites was eider duck, but certainly none of the experimental ropes was attacked. If mortality rates determined during experiment II (with prevention of losses) were normal natural mortality rates due to bio-physical factors, then natural mortality must have accounted for a very small part of total losses, and 50-60% of the loss during experiment I was actually due to fall-off. Natural mortality rates from French socks, however, had to be more than in

lantern nets for two main reasons; (a) population density on the socks was much higher than the lanterns in experiment II, increasing competition for space and available food; (b) although, losses from French socks could be less during the tubing process and early stages in water than widely used nylon mesh tubings such as pergolari, observations during the present and previous studies with similar re-tubing materials (Dare & Davies,1975; Mallet & Carver, 1991) suggest that there is a tendency for mussels, particularly small ones, to remain trapped in the centre of the socks, eventually resulting high mortalities. Additional losses possibly occurred as a direct result of handling during sampling events.

The natural mortality rates in lantern nets were extremely low in comparison to losses from French socks, varying between 4.7 and 14.4% per year, again with highest values in Loch Leven. Mortality caused by bio-physical factors rather than fall-off and predation has been determined by several authors using Vaxer mesh cages or similar trays or containers which would eliminate fall-outs and predation. For example, Mallet et al. (1987) found a total annual mean cumulative mortality of 19% (7-57%) at nine sites along the coast of Nova Scotia, Canada; Dare & Davies (1975) 53.1% in Morecambe Bay; and in Maine (USA) Incze et al. (1978) from just around 4% to over 90% in a period of 8 months, all of which are much higher than the mean annual mortality rate of 7.7% recorded during experiment II. The mortality rate (4.7%) of Loch Leven mussels in Loch Etive (LL→LE) was the lowest. 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 unfavourable environmental conditions may be more tolerant

of a wide range of environmental variables, and can show better performance in relatively favourable environments. This might also be the case for mussels in the LL→LE during experiment II.

Some authors (e.g. Dickie *et al.*,1984; Mallet *et al.*,1987b; Mallet & Carver,1989; Johannesson *et al.*,1990) found that, unlike growth rate, stock and its interactions were mainly responsible for variation in mortality. My cross-transplantation experiment, however, showed that mortality of transplanted mussels was quite low, and neither site nor stock alone had a significant effect on mortality rate, but the effect of site again appeared to be higher than that of stock. Another important feature worth mentioning was the slightly higher mortality rates at sites associated with salmon sites. This was particularly obvious during experiment II at salmon farms in both lochs. This could be as a result of high suspended matter concentrations around salmon cages.

In general natural mortality in mussel populations results from an interaction of many biological and physical factors (Dare,1976). Predators such as crabs, fishes, starfish and ducks are among the common causes of mortality in wild mussel populations. Two of these common enemies of the mussel, namely starfish (*A. rubens*) and eider ducks (*S. mollissima*) also cause mortalities in cultivated mussels in this area but, apart from starfish predation on spats during summer in one of the lochs, there was no detectable mortality as a result of predation. Other possible mortality factors might be salinity fluctuations, competition for food and space and disease or parasites although none of them alone caused mass mortality. Extremely low salinities have been reported to have caused mass mortalities in some estuarine bivalves species such as oysters (Farias,1991), but there is no evidence suggesting any relationship

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between mortality rates of mussels and low salinity values during this study.

5.5. Biomass and Production

Production in cultivated mussels is the net result of increases in biomass due to growth and losses in biomass as a result of natural mortality and fall-off. As discussed in sections 5.2 and 5.4 both growth and mortality, and consequently biomass and production, were affected by location or site due to environmental variables and population density. Therefore, both growth and losses were important factors in determining production but growth was probably the primary determinant since, despite substantial losses, production reached maximum values in April-May 1991. During this time shell organic production did not change much because shell length growth started later on, so a very rapid increase in AFDM was responsible for maximum production. If production is positive, as it was during summer, it means that there is growth in both length and meat (AFDMW) and a net energy gain in the animal, but under unfavourable conditions production is generally negative due to a mobilization of reserves (see section 5.6). Although mortality of suspended cultivated mussels, particularly due to both bio-physical factors and predation, can be far less than wild or bottom cultivated mussels, production losses due to fall-off can still be substantial. These losses due to fall-off and mortality make up the eliminated biomass (EB) which can be of the same order of magnitude as total tissue production (Table-25). As in intertidal mussels (Dare,1976) much of the eliminated production of suspended mussels can be utilised by decomposers following the massive falls and consumed by vertebrate and invertebrate predators. The amount of production utilised

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by the mussels themselves during the winter period of food scarcity for metabolic energy, during the gametogenesis stage and spawning for reproductive energy (called in Table-25 in situ production) also make up a substantial part of total or gross production. These two factors, i.e. higher EB and in situ production, could explain drops in overall production and the negative values of production from October 1990 to April 1991. Thirdly, the organic material stored in the shells accounts for part of gross production. Total annual organic shell production was 12.5-16.3 % of AFDM production at sites LE, AS and SS, and 29.4% at GSF. These values are less than half of figures determined by Dare (1976) for bottom grown intertidal mussels in Morecambe Bay, but similar to values reported by Deslous-Paoli et al. (1990) for bouchot-grown mussels. As mentioned in section 5.2.1.3.2, this is because of differences in resource allocation between wild and cultured mussels. Rodhouse et al. (1984a) compared the resource allocation in wild and cultivated mussel populations, when the total cumulative production was equal (Fig.39). They found that the wild population allocated more energy to the shell than the cultured one. This is not surprising because harsher environmental conditions on the shore and predators cause wild mussels to develop thicker shells than cultured ones. In addition, these two populations exhibit considerable differences in resource allocation for gamete, tissue and shell growth (Rodhouse et al.,1984a). In the cultivated population, all the mussels are young (under 18 months old) with very low reproductive effort, whereas the wild populations are dominated by old mussels with very high gamete production and low tissue growth, reversing the resource allocation to production. In addition to shell organic matter, byssus production (mainly composed of proteins) could account for

a substantial proportion of total production. For example, Hawkins & Bayne (1985) reported that byssus production in an open-shore mussel population consisted 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.

As can be seen in Table-25, final biomass and overall biomass increments (g AFDW m^{-1}) at sites LE, AS and SS are very similar and much higher than at GSF (P$\leq$0.001) which had very little (24.1 g m^{-1}) biomass increment. About 47-58% of cumulative net production at sites LE, AS and SS, which is slightly lower than values of 64% and 67% estimated by Rosenberg & Loo (1983) and Deslous-Paoli *et al.* (1990), and 11 % at site GSF, remained as biomass of mussels in the culture system, i.e. retained production (Table-25). Gross production at LE appears to be higher than both salmon farms, but net cumulative production at AS is the highest of the three sites. In addition in situ lost production as a % of gross production is far less at both salmon sites (at AS and SS; 12 and 17% or 89.8 and 119.7 g AFDW m^{-1} respectively), while % lost at site LE is almost as high as at GSF (21.5 and 23.7% or 173.1 and 68.5 g AFDW m^{-1}, respectively). This clearly shows that experimental mussels grown at salmon sites used less reserved energy (as % of gross production) than those at mussel farms. It is very unlikely that there could be differences in resource allocation for reproduction between populations, so these mussels should have got some extra food, possibly organic wastes from salmon farms, and obtained energy from late autumn to early spring. As with previous ranking according to growth results of experiment II (section 4.2.3, Table-16), AS appears to be the most

productive site if the sites are ranked according to data in Table-25, followed by LE, SS and GSF. Although there are no significant differences, growth, biomass and production of mussels at SS are slightly less than AS and even LE. Since the environmental variables are very similar, even the salinity regime at SS being more favourable for mussels, it very difficult to explain this slight difference. Part of the difference in production values is due to relatively high eliminated biomass (316.5 g m^{-1}) and in situ production lost (119.7g m^{-1}) at SS. The net production (g AFDW m^{-1}) determined at sites LE, SS and AS during this study is comparable roughly with that in Western Sweden during second year of growth (Loo & Rosenberg,1983). At site, GSF however, it was very low due to poor growth, especially AFDM, and high losses.

Much interest has been shown in turnover ratio of net production to mean biomass (P:B) and this has been used to estimate the production of mussel populations (e.g. Hibbert,1976, cited by Craeymeersch et al.,1986) as well as to compare the turnover time of different populations (Mallet & Carver,1989). The overall mean P/B ratio was around 1.86-2.20 for sites in Loch Etive and Dunstaffnage Bay (Table-25). This P/B ratio was similar those previously recorded for cultivated mussels; 2.2-2.7 in Western Sweden (Rosenberg & Loo,1983), 1.79 in the Bay of Marennes (Boromthanarat & Deslous-Paoli,1988), 1.18-1.97 in Northwest Mediterranean (Grenz et al,1991) and higher than values determined for wild populations on the Adriatic coast of Italy (Cerccherelli & Rossi,1984) and the Eastern Scheldt, S.W. Netherlands (Craeymeersch et al.,1986), but the ratio for mussels grown in Loch Leven (1.42) was even lower than in wild populations. Annual production from mussels at sites LE, AS and SS was higher than from mussels at GSF because of higher growth rate, meat

content and survival. Nevertheless, the eliminated biomass reached a mean of around 45% of the total production, as was described by Loo & Rosenberg (1983) and Boromthanarat & Deslous-Paoli (1988). This shows that with rope culture and even on bouchots, eliminated biomass can be very high due mainly to lost mussels. Thinning to control density can be one way of minimizing eliminated biomass but it is labour intensive and in reality can increase overall mortality and losses.

Considering the figures of biomass (Fig.30) and production (Fig.31), it could be suggested that mussels should be harvested starting from May up to November - December when mussels are just over two years old. After that time the AFDMW drops very sharply and a significant increase could not justifiably be expected until after spawning occurred in following spring. A similar optimum marketing period is apparent from condition index and meat cycle data.

5.6. Condition Index and Biochemical Composition

5.6.1. Condition Indices

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 shell

and meat, there are at least 6-7 condition index formulae in use at present (Davenport & Chen,1987; Crosby & Gale,1990), and employment of different formulae can make it difficult to compare the results of various studies. In addition some of these methods have more measuring errors than others (Davenport & Chen,1987; Crosby & Gale,1990). The methods used in this study, particularly CI_{vol} and CI_{dry}, have been well accepted and widely used for assessing condition index of mussels and other bivalves around the world (e.g. Baird, 1958 & 1966; Hickman & Illingworth,1980; Lutz *et al.*,1980; Aldrich & Crowley,1986). CI_{dry} is perhaps the best formula to express condition factor fluctuations 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 shell cavity volume or shell weight, comparisons will be difficult even if the same method has been used. As shell weights were markedly affected by habitat, employment of CI_{wet} formula in experiment II, for example, made it impossible to compare condition indices in Loch Etive and Leven stocks.

Baird (1958) emphasised that in order to compare the condition of mussel samples "the mussels should be approximately the same size", and he showed from individual condition measurements a curvilinear relationship between shell length and condition in mussels, with optimum condition index in *M. edulis* at between 50 and 60 mm length. Similarly, Hickman & Illingworth (1980) have observed an inverse relationship between condition index and size of *P. canaliculus*, resulting from changes in body proportions. There were no large size differences between mussels grown at different sites during this study so the values can be compared, but comparisons of the present

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results with those for larger mussels (80-120 mm), such as *M. galloprovincialis* from Spain and *P. canaliculus* from New Zealand, may not be so accurate. As far as "optimum size" is concerned, although it may not be optimum, the condition index of cultivated mussels in general has been observed throughout the growth period, particularly during their second year (Mason & Drinkwater,1981; Bressan & Marin,1985; Aldrich & Crowley, 1976; Emmett *et al.*,1987).

In general, condition indices recorded in Loch Etive and Dunstaffnage Bay during this study, with annual mean values of $CI_{vol} = 41.1$ and $CI_{dry} = 9.9$, are similar to those reported in the literature for wild and cultivated *M. edulis*, *M. edulis chilensis*, *P. Perna* and *P. canaliculus* species (e.g. Baird,1966; Hickman & Illingworth,1980; Zandee *et al.*,1980; Mason & Drinkwater,1981), but it seems to be slightly lower than the index measured by Mason & Drinkwater (1981). Seasonal cycles in condition, on the other hand, appeared to be somewhat different from those observed in Linne Mhuirich (Scotland) determined by Mason & Drinkwater (1981), who recorded maximum values during autumn and winter which is similar to the general cycle of condition index in Northern European waters (Baird,1966). 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), but not within a few hundred miles. This difference in amplitude and timing of the condition index cycle, therefore, resulted either from the fast growth rate of mussels in Linne Mhuirich during that study, or interannual fluctuations. During the present study, condition index increased very sharply immediately after annual minima in April and started to decline gradually after August. In Linne Mhuirich and other localities in Northern

Europe, the timing of spring minima is very similar to these Scottish sea lochs (Baird, 1958 & 1966; Gabbott & Bayne, 1973; Mason & Drinkwater,1981), but not the peaks (in December-February). When the tissue growth cycle is compared, the condition index cycle observed during this study appears to be more similar to that of mussels in the Conwy Estuary (Dare & Edwards,1975) and Dutch Wadden Sea (Pieters *et al.*,1979) than that in Linne Mhuirich.

All condition indices showed a similar seasonal cycle, with minimum values in early spring (March-April) and rising to peak levels in late spring and early summer (May-July), at all sites (Fig.33a,b & 34a,b). These seasonal changes result from the complex interaction of a variety of factors, including factors controlling length and tissue growth such as food, temperature and even salinity (section 5.2), on the metabolic activities of the mussels and most significantly, the reproductive cycle (Hickman & Illingworth,1980; Ceccherelli & Barboni, 1983; Hickman *et al.*,1991).

Although the seasonal pattern of the cycle at all sites was similar during both experiments, both condition indices in Loch Etive and Dunstaffnage Bay were higher than those in Loch Leven during experiment I (Fig.34). During experiment II, however, as mentioned above, due to substantial differences in shell weight between the stocks (section 5.3), the condition index values of mussels from Loch Leven appeared to be better than LE mussels (Fig.34a,b). The highest values were displayed by LL→LE the lowest by LE and LE→LL, which shows the effect of both site and morphology on condition index. In fact meat content of mussels grown in Loch Leven was significantly lower than those in Loch Etive (Fig.25 & Table-14). CI_{wet} values of mussels associated with salmon farms were slightly higher than at corresponding

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mussel farms in both lochs.

In Loch Leven the lower food supply which is, after the reproductive cycle, the most important factor affecting the condition of mussels (Skidmore & Chew,1985; Small & van Stralen,1990) could be the main reason for low condition indices all year around. When the site in Loch Leven (GSF) is excluded, the strong positive correlation between both condition indices and chlorophyll-a values for combined data during experiment I (CI_{vol}: r=0.5523, P≤0.001; CIdry: r=0.4806, P≤0.01) also demonstrates the effect of food supply on condition index. As discussed in section 5.2, there might be over-riding negative environmental factors in Loch Leven.

The fluctuations in condition index and meat weight have important implications for cultivation and harvesting strategy. For optimum exploitation the harvesting season should be timed according to the peak period for condition index. As a result of their observations, Mason & Drinkwater (1981) suggested that autumn and winter is the best time for marketing cultivated mussels from Scotland, but findings during the present study are not entirely in agreement with that marketing strategy. Both condition indices, assuming that a CI_{vol} of around 40 (corresponding to a CI_{dry} of 10) are acceptable for marketing (Mason,1969), and meat weight and biochemical composition values recorded during this study make it possible to conclude that the mussels were suitable for marketing during May-December in Loch Etive and Dunstaffnage Bay (Fig.33 & 34). In any case mussels remain in sufficiently good condition for marketing for up to 8-9 months in Scotland. Similar trends in condition index are likely to prove general all around Scottish coasts but there might be some differences in timing and amplitude between the south and far north or between lochs

resulting from stock differences and environmental conditions.

5.6.2. Biochemical Composition and Energy Content

The biochemical composition of the mussels varied predictably, with loss of water and accumulation of reserve materials. During summer and early autumn the contents of protein, glycogen and lipids (in terms of mean weight per animal) steadily increased to maximum values in September-October, although percentage values display a different picture. After this all three constituents declined during winter and minima were reached in early spring. Accumulation and depletion of these 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 & Stephenson,1974; Pieters *et al.*,1979; Bayne & Newell,1983). Gabbott & Bayne (1973) demonstrated a marked seasonal shift in mature mussels from a reliance on carbohydrate as the main energy reserve in summer and autumn to a greater reliance on protein as the major reserve in winter. This could be one reason for the significant loss of protein and small quantity of lipid between February (possibly including January) and April, when glycogen reserves were minimum. Very similar changes were observed by Dare & Davies (1975) in sublittoral mussels in North Wales.

In general carbohydrate, which has been shown to be mainly glycogen (Ansel & Trevallion,1967; Gabbott & Bayne,1973), is the main source of energy in bivalves (Zwaan & Zandee,1972; Gabbott & Bayne,1973; Pieters *et al.*,1979). As in the majority of bivalves from temperate waters (Zwaan & Zandee,1972; Dare &

Edwards,1975; Pieters *et al.*,1979), here the annual percentage glycogen cycle consisted of a rapid increase in spring and early summer (to maximum values of 35%), followed by small fluctuations in the late summer, while in autumn and winter there was a gradual decline reaching a minimum of about 5-10% in March and April. The maximum percentage glycogen level coincided with both the minimum protein and water levels and in consequence the seasonal glycogen cycle alternates with the protein and water content cycles. In addition, a simple positive relation between seasonal changes in dry meat weight and percentage glycogen has been observed during this and previous studies (Zwaan & Zandee,1972; Dare & Edwards,1975; Hickman & Illingworth,1980) since the period of both meat increments and the glycogen accumulation coincides with the main growth season and changes in dry meat weight result mainly from changes in glycogen content (Dare & Edwards,1975).

As far as lipid content is concerned, it was small fraction (2-12%) and showed no clear seasonal trends. Gabbott & Bayne (1973) and Dare & Edwards (1975) agree that there is a summer maximum and winter minimum, as observed during this study with maximum values during summer-autumn followed by a fall in winter to a minimum in spring at about spawning time (Fig.35b & 36d,e). This cycle was obvious during both experiments I and II.

Protein content showed a clear cyclical of pattern. Like glycogen, protein reserves are also built up but, similar to lipid, mainly in non-mantle tissues. Percentage values followed an inverse pattern with respect to glycogen. Many authors (Gabbott & Bayne,1973; Pieters *et al.*,1979; Zandee *et al.*,1980; Gabbott,1975; Pieters *et al.*,1980) agree on the importance of proteins as a source of energy during periods of limited

food supply, reduced glycogen levels and gonad maturation. Data referring to protein (Fig.35a & 36b) certainly justify this interpretation.

Ash content fluctuated slightly and did not exhibit any clear seasonal cycle. It was also slightly higher in native (LL) and transplanted (LE→LL) mussels in Loch Leven than mussels in Loch Etive (Fig.36e). The values were similar to those determined by Zandee *et al.* (1980) in Dutch Wadden Sea, but lower than in mussels from North Wales (Dare & Edwards,1975).

Caloric content was determined directly with an auto-bomb. The mean dry meat caloric content was around 4.97 Kcal g^{-1} (20.8 kJ) which agrees with values found for Conwy mussels (4.9 Kcal or 20.6 kJ) by Dare & Edwards (1975) and for Wadden Sea mussels (4.2 Kcal g^{-1} or 17.7) by Zandee *et al.* (1980). The highest value of about 5.4 Kcal g^{-1} dry meat weight was found during February-March (Fig.37) when gonads were full and lipid and protein contents were relatively high, and values were minimum just after spawning (April-May). Since lipid (9.5 Kcal g^{-1}) and protein (5.7 Kcal g^{-1}) both make higher contributions to caloric content than glycogen (4.2 Kcal g^{-1}), this pattern would be expected.

In the present study fairly good agreement can be 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 utilization of reserves (Gabbott & Bayne,1973; Dare & Edwards, 1975). According to Seed (1975 & 1976) several stages of the reproductive cycle can be distinguished in European mussel populations. In summer the gonads are in a state of rest (stage 0), during which there is no sexual

activity and reserves accumulate in the tissues. Gonadal development begins in autumn and continues during winter (stages 1-5) at the expense of glycogen reserves (Fig.35 & 36). In the final stage (stage 6- or spawning) release of gametes is induced by external factors. The seasonal cycle of biochemical constituents observed during this study can be matched with this reproductive cycle. In summer when food is abundant and mussels are in the resting stage, glycogen is very rapidly accumulated in tissues and starts to decrease gradually after September due to decline in food supply and gametogenesis (stages 1-5). The spawning stage (March-April) is characterised by minimal glycogen content and a rapid decrease of lipid and protein (in weight). After spawning the glycogen content recovers quickly (Fig.35b & 36c). There appears to be good agreement with the hypothesis of a 'storage cycle' (Gabbott,1975) : it is assumed that glycogen reserves, accumulated in summer and early autumn, are possibly converted into lipids during gametogenesis, which are stored in ripening eggs and used subsequently in the larvae as an energy reserve during the first life stages. This has been considered as a 'storage cycle' analogous to the glucose-fatty acid cycle in vertebrates (Gabbott,1975). Egg and sperm in bivalves are composed primarily of protein and lipid (Pieters et al.,1980) and thus some kind of relation is expected between the cyclic pattern of lipid and protein, and accumulation and release of gonadal products. Some authors (e.g. Pieters et al.,1979) observed an increase in lipid content during gametogenesis and a decline after spawning. This was somewhat in agreement with findings in this study.

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 cited by Emmett *et al.*,1987). Whatever the main factor controlling reproductive cycles, indirect evidences from this study such as minimum condition indices, meat weight and glycogen values suggest that spawning occurs during March-May in this area. Moreover, direct inspection of the mantle of sampled mussels showed a greater number of specimens with full orange gonads in mid-March, but mostly empty in April. This is in agreement with previous findings around UK (Seed,1975,1976; Mason, 1969).

5.7. Spat Settlement

The essential aspects of mussel culture are seed availability, a suitable ongrowing site and cost-effective technique (Mason,1976; Dare,1980; Mason & Drinkwater,1981). Despite successful controlled production of *M. edulis* larvae (Brenko & Calabrese,1969; Skidmore & Chew,1985), success in mussel aquaculture still depends on natural settlement of spats on collectors. This is mainly because, unlike oysters and scallops, production of mussel larvae artificially is not economic due to the low market price of mussels. The timing of settlement in this study is in agreement with observations by Mason & Drinkwater (1981) in Linne Mhuirich, Loch Beag and Loch Thuirnaig; in Loch Etive the settlement started in May-June and reached a maximum in July, but in Loch Leven main settlement took place almost one month later, but several months later than in Morecambe Bay (Dare & Davies,1975).

Dare (1976) compared his own findings on settlement and spawning cycle of mussels with literature around Britain, and concluded that settlement periods cannot be predicted from a knowledge of the spawning cycle alone. Spawning occurred during March-May, with a peak predicted from condition index cycle possibly in late March-early April when temperatures were still around 7-8°C. As *M. edulis* larvae first attach after about 36 days at 11 °C (Dare, 1976), there was a delay in settlement rather than 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 & Rossi,1984).

Seed (1976) revealed that in some localities marked seasonal settlement can be detected while in others settlement occurs more or less throughout the year. On the West coast of Scotland, settlement seems to be show a well defined seasonal pattern.

A variety of substrates have been used for spat collection (e.g. Dare & Davies,1975; Sutterlin *et al.*,1981; Dare & Edwards,1983; Farias, 1991), but synthetic polypropylene rope is widely used and has advantages over other materials from a practical viewpoint in that it is durable, relatively inexpensive and can be used both for spat collection and grow- out periods (Sutterlin *et al.*,1981). Dare & Davies (1975) found that very few, if any, would settle on polypropylene ropes in Morecambe Bay, Northwest of England. During this study, however, settlement on polypropylene ropes (19500 spat m^{-1} in Loch Etive and 21100 spat m^{-1} in Loch Leven) was as good as settlement (17000-28000 spat m^{-1}) on coir ropes used by Dare & Davies (1975).

Mason & Drinkwater (1981) found higher settlement on coir ropes compared to courlene (polythene) and sisal ropes, but settlement even on coir ropes appeared to be very poor (10,000-20,000 spat per 3 m rope). Perhaps the settlement of filamentous algae on collectors put into the water one month before settlement plays an important role on attracting the spats.

It is well known that in general spats are strongly influenced by water level and upper surfaces are preferred for settlement (Sutterlin et al.,1981; Farias,1991) and during this study settlement on the upper part of collectors was much higher than the lower in both lochs. Farias (1991) claimed that the initial surface-dwelling behaviour 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‰) necessary for better larval development. Brenko & Calabrase (1969), however, found that growth of *M. edulis* larvae decreases drastically below 20‰. Mussel larvae are pelagic until development of the pediveliger and tend to remain near the surface (Dare,1980), after which negative phototaxis and a failure to respond to pressure stimuli should encourage them to move towards bottom (Bayne,1976). Perhaps a combination of factors such as depth, water stratification and high current speeds could prevent them migrating to deep layers.

Almost 40% (in Loch Leven) and 60% (in Loch Etive) of the original stock was lost by November before reaching a mean length of 15 mm which was higher than losses reported by Dare & Davies (1975) in Wales and possibly elsewhere. As mentioned in section 4.7. main losses occurred in Loch Etive as a result of heavy algal and seaweed settlement on collectors before spat settlement. In addition some

losses can be attributed to very low surface salinity values, which probably cause weak byssall thread formation (Sutterlin *et al.*,1981) and fall-off of seed mussels from ropes, particularly in Loch Leven. Other possible causes are relatively high current speeds, severe overcrowding on the upper part of collectors during early stages (especially in Loch Etive) and predation on the lower part of collectors by starfish (*A. rubens*) in Loch Leven. Extremely high losses occurred during this study mainly due to heavy settlement of algae and seaweeds and starfish predation, which are both unusual for these lochs according to farm operators, and both farms rely on natural spat settlement in situ.

In general spat settlement is greater in protected areas such as lochs, bays and inlets, where newly settled spat are less likely to be swept away by wave action, tides and currents (Skidmore & Chew, 1985). My own observations during 1991 and 1992 also showed that the site in Loch Etive appeared to be especially favourable for natural settlement and Mason & Drinkwater (1981) found good settlement in three of four lochs investigated; Linne Mhuirich, Loch Thuirnaig and Loch Beag, but not in Loch Ardvar. The upper layer (0-10 m) of Loch Etive is more stable, flushing rate and current speed at LE are low whereas water just below 2 m in Loch Leven is relatively well mixed, flushing time is short and site GSF is located within main stream. So a great proportion of larvae in Loch Etive are able to remain in the surface layer and so long enough in the loch to settle.

5.8. Physiological Energetics

The techniques of physiological energetics allow one to understand the adaptation

of the energy balance in bivalve molluscs and to calculate the complete energy budget all over the seasonal variations of the field (Deslous-Paoli,1987). Thus measurement of the various components of the energy budget provide an estimate of growth potential or scope for growth. In addition physiological estimates of growth allow comparisons of populations and sites. Such physiological studies include measurements on both individuals and whole populations, and have been performed on mussels (e.g. Bayne & Widdows,1978; Widdows,1978a,b; Rosenberg & Loo,1983; Thompson,1984; Widdows *et al.*,1984; Deslous-Paoli,1990). The main aim of the present physiological study, however, was not determine the complete annual energy budget but to compare physiological responses of cultivated mussels to different environmental variables during the main growth season, and to confirm observed growth trends at different sites with physiological estimates of scope for growth.

All measurements during the present study, except ammonia, have been carried out in the field under conditions as close as possible to the natural environment, so some of the values determined in field could not be as accurate as those obtained in a laboratory. On the other hand, the application of laboratory studies to field conditions presents various problems (Bayne & Newell,1983), hence this field study should be more reliable than laboratory-based experiments.

Field measurements of mussels living in three different lochs, Loch Etive (two sites), Loch Leven and Loch Kishorn showed that, in addition to the morphological characteristics between native Loch Etive and Leven populations already described in section 4.3, population in Loch Leven differed markedly from Loch Etive and Kishorn populations in physiological responses (CR, AE, VO_2, SFG and K_2) (Table-

29,30 & 31). Reciprocal transplantation of mussels between Loch Etive and Loch Leven was used to examine the phenotypic plasticity of the physiological measurements.

Clearance rates of both native and transplanted mussels (after 4.5 months and 1 year) in Loch Leven were lower than at the other three sites. Some authors (Bayne & Widdows,1978; e.g. Widdows *et al.*,1979; Bayne & Worral,1980) found a negative relationship between clearance rate (CR) and seston concentrations, but seston concentration at GSF (Loch Leven) was not higher than at other sites and there was no such negative correlation between these two parameters. This was possibly due to relatively low total seston concentrations at all experimental sites (Table-28), since under estuarine conditions clearance rates are partially dependent upon the weight of seston (Bayne & Widdows,1978). %POM values, however, were significantly lower at this site and there was positive correlation between CR and POM values ($P \leq 0.01$, r=7629). This might also explain the differences in CR values between May and September.

According to Widdows *et al.* (1979) at very low seston concentrations, almost all suspended material (>2μm diameter- based on the hypothesis that *M. edulis* is a non-selective species) is filtered by the gills, passes through the mouth (ingested) and is transported to the digestive gland for digestion but at a decreasing rate. Following absorption, the remaining unabsorbed and excessive material is rejected as faeces. Consumption rate increases with increasing seston concentration until a threshold is reached, at which pseudofaeces are first produced which coincides with maximum consumption rates, and above which further material filtered by the gills is rejected

as pseudofaeces (Winter,1978; Widdows *et al.*,1979; Bayne *et al.*,1989). The pseudofaeces production alone was not estimated during this study, but according to Widdows *et al.* (1979) it occurs significantly when a threshold concentration of seston of around 5 mg l^{-1} is reached. If this threshold concentration is accepted, then at all sites, particularly in May, the concentrations of seston exceeded the threshold for pseudofaeces production (Table-28). These relationships between seston concentration, pseudofaeces and faeces production, ingestion and digestion have been reviewed by Winter (1978), discussed in detail by Widdows *et al.* (1979) and summarised in Fig.40. The material rejected as pseudofaeces before ingestion and as faeces before absorption (both combined as F in this study and also called biodepositon) can represent 40-71% of consumption and can be as high also 93% (Deslous-Paoli *et al.*,1990) in cultured mussels. Similarly, Hawkins & Bayne (1985) found that 48-62% of both the carbon and nitrogen consumed could be rejected as faeces and pseudofaeces. During the present study losses due to faeces and pseudofaeces have been estimated as 45.3-50.4% of consumed energy (Fig.41), which is similar to the above values.

As a consequence of the relationship briefly described above and schematised in Fig.40, the amount of absorbed food and the efficiency with which the mussels absorbed material cleared from seston depend on not only seston concentration but also the amount and proportion of POM (%POM), i.e. on the quality and quantity of food. Although during this study there was no detectable relationship between AE and either total seston, POM or %POM, it might have been expected to increase with
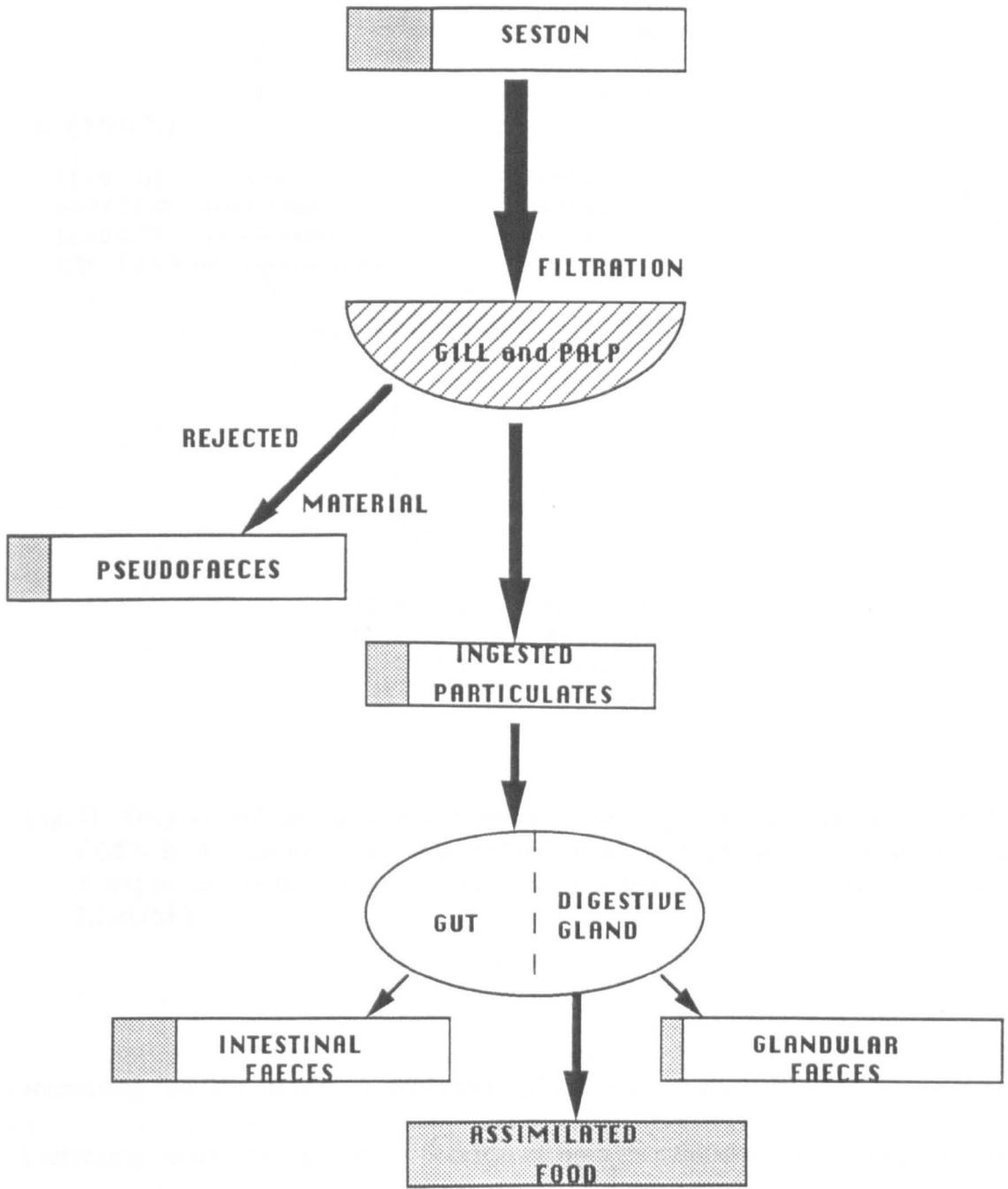
Fig.40. A schematic diagram of feeding, pseudofaeces and faeces production, ingestion and assimilation in *M. edulis*. Shaded areas, utilizable fraction (food); clear areas, non-utilizable fraction; and width of arrows roughly shows amount of seston and/or food transferred from one stage to next one (redrawn after Widdows *et al.*,1979).
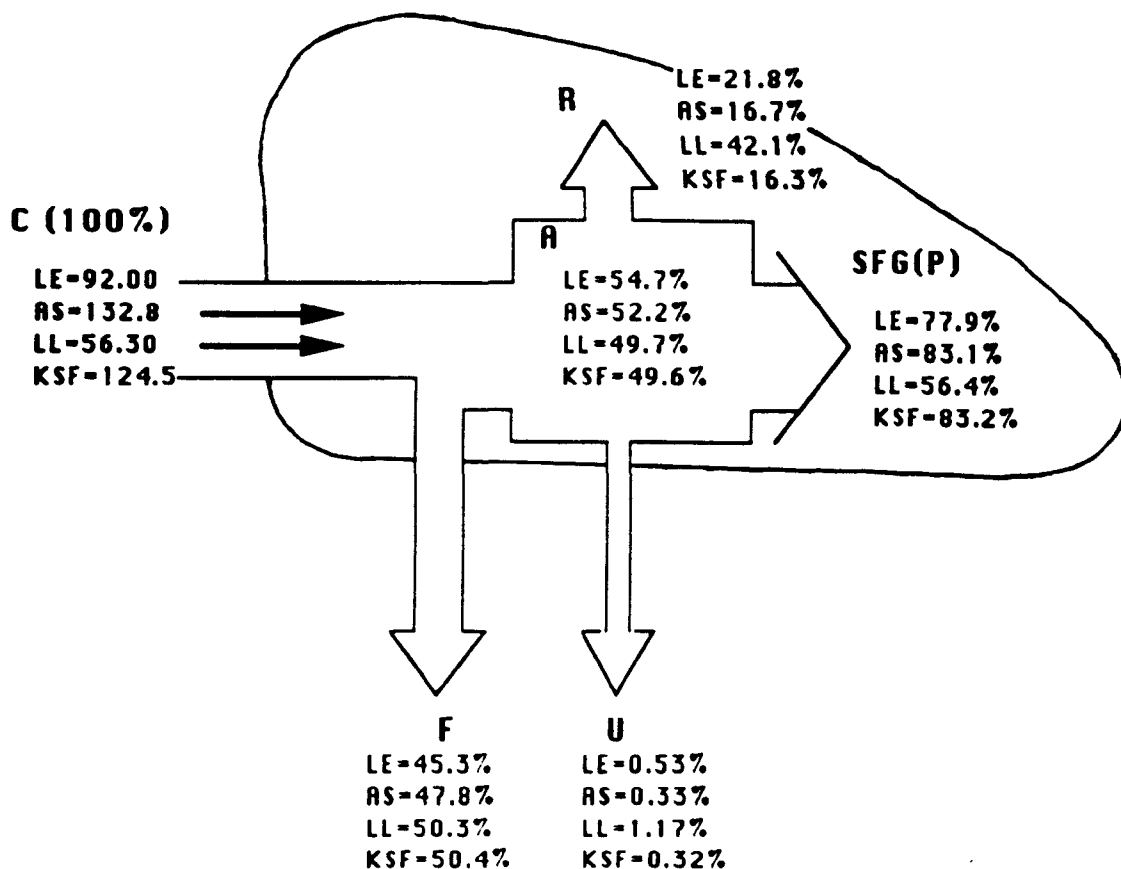
Fig.41. Diagram of the estimated distribution of the energy consumed (C) in J g⁻¹
DMW h⁻¹ by standard size (1 g DMW) cultivated mussels in three lochs. A and
F expressed as percent of C, and R, SFG and U as percentage of A. (note
LL=GSF).

increasing %POM (Bayne & Widdows,1978; Bayne et al.,1979) and decrease with

increasing seston concentrations because of both pseudofaeces and glandular faeces

production, and with extremely high POM concentrations (Deslous-Paoli et al.,1990)

as a result of increasing intestinal faeces production (Fig.40). There is a no evidence,

however, suggesting such a relationship between AE and these food parameters in

many field experiments (Bayne et al.,1989; Navarro et al.,1991).

Despite the relatively low organic ratio of the food in Loch Leven (Table-28) there were no detectable differences in AE values between sites. AE values were slightly higher in May when both POM and %POM were also high. These relationships between season, available food, the clearance rates and absorption efficiency combine to result in higher values for the physiologically useful ration in summer than winter (Bayne & Widdows,1978) and at those sites with higher food quality than at other sites.

The oxygen consumption of newly transplanted mussels was higher than in both native mussels and those transplanted one year ago, and VO_2 values of native mussels at GSF were significantly higher in September; otherwise values were quite uniform with a slight decrease in September. Bayne & Widdows (1978) and Bayne *et al.*(1989), who also found higher VO_2 in spring and summer, claimed that this correlates with both reproductive activity and rates of absorption. During this study mussels had just spawned and were inactive both in May and September, so any relation between the reproductive cycle and oxygen consumption is unlikely, and although in May both absorption rate and VO_2 values were relatively higher than values recorded in September, there was not any significant relationship.

Overall NH_4-N values at site GSF were higher than other sites and in both Lochs Etive and Leven, NH_4-N excretion rates of transplanted mussels even after 1 year of acclimatization were higher than that of native mussels. Except in native mussels at GSF, which is significantly higher than other native stocks in September, there was a significant drop in ammonia excretion in September. Tedengren & Kautsky (1986) and Tedengren *et al.* (1990), in a similar study in the Baltic Sea and North Sea, found

much higher NH_4-N excretion rates for Baltic than North Sea mussels at ambient salinities and also reported that excretion was very sensitive to changes in salinity due to changes in amino acid metabolism. As mentioned several times, surface salinity in Loch Leven fluctuates very frequently, but salinity of the water column surrounding the culture ropes was more stable than Loch Etive. Hence if this difference in NH_4-N excretion was due to differences in the salinity regime, values for Loch Etive mussels should be higher than Loch Leven.

Oxygen to nitrogen (O:N) ratios, which result from respiration and NH_4-N excretion, were lower both for native Loch Leven and all transplanted mussels, indicating that these have less favourable energy metabolism; i.e. a relatively high rate of protein utilization from both accumulated body reserves and available food (Widdows et al.,1984; Tedengren & Kautsky,1986), most likely as a result of a stressed condition (Bayne et al.,1976b; Widdows,1978b). It is well known that the catabolic balance between protein, carbohydrate and lipid varies also with season and gonadal development (see section 5.6). In May both populations had recently spawned and they were reproductively inactive but very active in tissue growth. In September mussels were still in the resting stage or gonadal development had just started. In any case the storage and reproductive cycles of the populations were exactly the same and there should not be any differences between experimental populations. O:N ratios were not very low compared to reported values from completely stressed environments, for example the Baltic Sea (Tedengren & Kautsky,1986), but substantial differences between sites still indicate that mussels in Loch Leven were under some degree of stress. The possibility of a stressed condition due to relatively

high Cu and Zn concentrations in Loch Leven has been mentioned in section 5.2.2, but there could be another unknown stressor or combination of several unfavourable conditions causing stress. Unfortunately, like some morphological differences remaining almost unchanged one year after transplanting, it is difficult, to explain why NH_4-N and O:N values for transplanted mussels were higher than for native mussels even after one year, while all other measured physiological parameters showed that there was complete acclimatization to the new environment within 4.5 months (between beginning of May and middle of September) which could be shorter (Widdows et al.,1984; Tedengren et al.,1990). As suggested before in section 5.3, it is possible that this was due to a very slow adaptation process, such as osmotic adjustments, or there could be some degree of genotypic difference between the stocks, although this is very unlikely.

Taking energy consumption as 100%, the distribution of total consumed and absorbed energy is summarised in Fig.41. About 45.3-50.4% of consumed energy is rejected as biodeposits, 49.6-54.7% is absorbed and 56.4-83.3% of absorbed or 28.0-43.4% of consumed energy allocated for Scope for Growth (SFG or production, P). The contribution of NH_4-N excretion to energy losses, 0.2-0.6% of C or 2.0-2.8% of R, was lower than the values reported by Bayne et al. (1979) and Bayne & Widdows (1978). The amount of energy allocated for respiration ranged between 8.1 and 21% of C which is comparable to estimations by Deslous-Paoli et al. (1990), and total loss of energy (U+F+R) accounted for 57-72% of consumption.

The scope for growth (SFG) measured at sites LE, AS and KSF was significantly higher, which simply reflects high food quality and better feeding conditions at these

sites in Loch Etive and Kishorn than at GSF, and confirmed empirical evidence on length and tissue growth rates at LE, AS and GSF. There were no significant differences in POM levels between sites, but at GSF seston levels were higher and %POM values were significantly lower than at other sites. In consequence mussels at GSF had filtered less particles and consumed less energy and this coupled with high oxygen consumption reduced energy allocated for SFG at this site. Although the transplanted mussels had a lower SFG than native mussels it was only apparent after 15 days acclimatization, while after 4.5 months it was very similar to native stocks (Table-31). As a consequence of low CR and AE values, energy consumed by these animals was considerably lower than the native mussels and higher VO_2 values caused further decline in energy available for growth during the acclimatization process.

Highly significant ($P \leq 0.001$) correlation between SGF and POM indicates that despite differences in physiological response both food quantity and quality are fundamental parameters influencing SFG, but at least half the variation in SFG was most likely due to differences in CR. Apart from seston and POM, temperature and salinity were also determined during the field work (Table-28). There was no difference in temperature between sites likely to effect the measured physiological parameters. Although the salinity to which mussels were exposed in Loch Kishorn was higher than in Lochs Etive and Leven, the effect of this differences in salinity is not clear. The mussels at site AS had very slightly higher SFG than at neighbouring site LE and again this is in agreement with observed growth and production parameters. There is no observed growth data from KSF (Loch Kishorn), but all measured physiological data, particularly SFG, indicate that actual growth at this site

is possibly very similar to AS and LE.

The value of SFG should be positive when surplus energy is available for tissue growth and reproduction; or SFG may be negative, in which case weight is lost due to utilisation of energy reserves (Thompson & Bayne,1974). Negative SFG which was due to the experimental acclimatization process was determined only for newly transplanted mussels in Loch Leven. The main period of growth in late spring and early summer reflected high values for SFG and K_2 in May and a considerable decline at all sites in September, which confirmed previous direct observations that growth had already started to decline then. This also confirms previous reports on seasonal variations of energy balance in mussels (Bayne & Widdows, 1978; Navarro *et al.*,1991).

Almost complete acclimatization (except for NH_4-N excretion) of transplanted mussels to their new environments within 4.5 months demonstrates that the measured physiological differences between populations are to a major extent regulated by environmental factors, which confirmed the results of two years of shell length and meat growth observations. As indicated by higher NH_4-N excretion and lower O:N ratios, the estimated lower SFG and probably the observed lower growth rate of native and transplanted mussels in Loch Leven are caused by a less favourable energy metabolism. This conclusion is in accordance with Widdows *et al.* (1984), who reported that physiological differences between morphologically and physiologically different Tamar and Swansea populations of *M. edulis*, were largely determined by environmental rather than genotypic factors as both transplanted populations were completely acclimatised within 2 months. Similarly, Bayne & Widdows (1978) and

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(Bayne *et al.*,1979) have also recorded considerable physiological and growth differences between different mussel populations and attributed these differences to environmental variables. Another study has been conducted by Tedengren & Kautsky (1986) and Tedengren *et al.* (1990) with North sea and Baltic populations and they found that differences in physiological responses of Baltic and North Sea mussels were mainly due to osmotic stress in the Baltic Sea. As mentioned above, however, it is difficult to define the exact unfavourable environmental factor(s) in Loch Leven. Tedengren *et al.* (1990) further suggested that part of the recorded differences between these two populations, e.g. the unchanged morphology of Baltic mussels after one year of acclimatization, was due to genotypic factors which can also affect physiological responses, e.g. causing lower CR because of a relatively smaller gill area due to an elongated shape, and hence lower SFG. There appear to be certain similarities, e.g. morphology and slow growth, between Baltic and Loch Leven populations but as has been discussed, there is no evidence except maybe from morphology, suggesting the possibility of genotypic differences between Loch Etive and Loch Leven mussels. Although the elongate shape of Loch Leven mussels did not change one year after transplantation, the clearance rates were exactly the same as the native mussels in Loch Etive after 4.5 months, which rules out any influence of shell morphology caused by genetic factors on physiology as suggested by Tedengren *et al.* (1990).

The physiological parameters for *M. edulis* measured under ambient condition in spring-summer during the present and previous studies in temperate regions are summarised in Table-35 to facilitate approximate comparisons. In general, the range

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Table-35. Clearance rate (CR) and absorption efficiency (AE), respiration (VO_2), ammonia excretion (NH_4-N), scope for growth (SFG) and net growth efficiency (K_2) values reported for *M. edulis* (1 g DMW) measured under ambient conditions during summer months. (see also Table-28 for other environmental parameters).

Location	POM (mg l⁻¹)	%POM	CR (l h⁻¹)	AE (%)	VO_2 (ml h⁻¹)	NH_4-N (µg h⁻¹)	SFG (J g⁻¹ h⁻¹)	K_2 (%)	Reference
Cattewater,UK	2.3-5.6	19	1.1-2.1	11-75	0.41-0.81	7.9-34.5	(-)11-40	54-80	Bayne & Widdows,1978
Lynher,UK	1.8-3.5	19	1.3-2.6	18-50	0.35-0.70	7.9-36.7	(-)4.9-28	(-)69-76	Bayne & Widdows,1978
Swansea,UK	-	13.3	1.59	24	0.70	29.3	1.8	11.0	Bayne *et al.*,1979
Lynher,UK	1.1	25	2.3-2.4	-	-	-	-	-	Widdows *et al.*,1979
Tamar,UK	0.6-1.8	20-25	4.2-5.0	39-42	0.48-0.70	28-65	8-25	32-62	Widdows *et al.*,1984
Swansea,UK	1.8-2.4	40-45	1.5	62-65	0.37-0.60	20-35	(-)1-25	(-)6-76	Widdows *et al.*,1984
Bellevue,Nfld	2.0-3.0	40-50	1.4-2.0	39-75	0.23-0.45	6-12	9.5-16	61-77	Thompson,1984
Whitehead,N.S.	0.3-1.1	33-55	1.2-2.5	3-34	-	-	-	-	Carver & Mallet,1990
North Sea*	-	-	2.1-2.4	60-67	0.95-1.55	10.7-106	63-73	74-84	Tedengren *et al.*,1990
Galicia, Spain	0.4-1.1	49-55	1.3-3.2	21-76	0.44-0.50	12.4-13.8	4.7-18.1	17-64	Navarro *et al.*,1991
L.Etive (LE)*	1.9-2.4	31-36	1.7-2.6	48-62	0.49-0.54	5.0-11.5	26.1-62.3	73-85	Present study
L.Etive (AS)	2.4-3.5	34-38	1.6-2.6	52-62	0.54-0.60	7.6-10.9	27.2-87.9	71-88	Present study
L.Leven (GSF)*	1.8-2.0	22-24	1.3-1.7	48-60	0.50-0.72	10.7-15.2	8.9-30.0	37-71	Present study
L.Kishorn (KSF)	2.3-2.6	26-32	2.0-2.8	42-54	0.50	7.7-8.3	29.6-73.2	74-88	Present study

*: carried out in a laboratory
a: excluding newly transplanted mussels in May.

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of CR, AE and VO$_2$ values for mussel populations from different locations are very similar during spring and summer. The AE values, at least the lower limit, for native mussels in the Cattewater and River Lynher (Bayne & Widdows,1978) and Swansea (Bayne *et al.*,1979) appeared to be lower than the values estimated in this study. This is most likely due to the low organic content of the seston over mussel beds in those locations. When values of mean assimilation efficiency (=(P+R/C)x100, which is very similar to AE but excludes U) for cultivated populations are compared, the estimated present values appeared to be lower (47.7-53.6) than those reported by Rosenberg & Loo (1983) in North West Sweden (60-80%) and that by Cabanas *et al.* (1979, cited by Rosenberg & Loo,1983) in Ria de Arosa, Spain (79%), but much higher than that given by Deslous-Paoli *et al.* (1990) in Marennes-Oléron (23%). Unfortunately, available food values for Sweden and Spain are not available, but POM concentrations in Marennes-Oléron were extremely high and this factor is likely to decrease the assimilation efficiency (Deslous-Paoli *et al.*,1990). In addition, it has been suggested that the ratio method of Conover, is not a very reliable index of absorption particularly at low food levels, due to losses of metabolically-derived organic material (mucus, metabolic enzymes, etc) from the intestinal tract (Hawkins & Bayne,1984 cited by Carver & Mallet,1990). Some other authors (e.g. Carver & Mallet,1990) have made similar comments about this method and in comparative studies, the ratio method has repeatedly indicated very low or negative efficiencies where other methods have indicated very high values (Bayne *et al.*,1987). Ammonia excretion values are very similar to those reported by Thompson (1984), Tedengren *et al.* (1990) and Navarro *et al.* (1991), but much lower than values for mussels in the

South of England. Relatively low O:N values indicate that mussels in these estuaries could be under some kind of environmental stress.

Almost all the measured physiological parameters were very similar to values reported by Navarro *et al.* (1991) for raft cultured mussels in Galicia, but SFG estimates were very low. This was due to very low POM values measured during their experiments, although quality of this food in Galicia might be better than that in Scottish sea lochs. With the exception of the SFG reported for North Sea mussels, which was conducted in a laboratory with mussels fed on cultured phytoplankton, all the other reported SFG estimates are also much lower than present values. K_2 could also be a indicator of quality of food (POM) and physiological condition of the mussels, as it is a measure of the efficiency with which food is converted into tissue growth. In fact it could be more meaningful than SFG in comparisons between sites with unknown food quality; for instance, in Table-35 although SFG values show wide variations, with a few exceptions, K_2 values are roughly similar. When newly transplanted mussels are excluded the mean net growth efficiency (37-88) appeared to be higher than that estimated by Rosenberg & Loo (1983) of 42-47% and Deslous-Paoil *et al.*(1990) (48%) for cultured populations.

Some of the differences in SFG between populations (Table-35) can be explained by variations in POM and %POM, while others are due to differences in physiological responses, mainly CR and AE. In addition the stage of the reproductive and storage cycles also play an important role. For example, on the West coast of Scotland maximum tissue growth in cultivated mussels occurs in May. This could partly explain the very high SFG in May. The energy content of POM in almost all

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physiological studies has been derived from the use of constant conversion factors rather than determined directly. Therefore, even the amount of phytoplankton present relative to non-living organic matter may differ considerably among sites so sites with high POM values will cause high SFG estimation when other physiological responses are similar. Thus comparisons of SFG values between very distant locations and of food availability, which could be transient in quantity and quality, could not be confirmed with empirical growth rates. For example, SFG values reported by Navarro *et al.* (1991) are much lower than values determined in this study, but in reality, it is well known that growth rates of mussels in Galicia are much better than that on the West coast of Scotland.

The main aim of this physiological study was to analyses the physiological responses and make comparisons between experimental sites rather than to obtain factual values of SFG for comparison with other locations. The good agreement between observed growth rates during experiment I and II and estimates physiological measurements at sites in Lochs Etive and Leven suggests that some of the features of growth might be explained by a closer analysis of physiological data (Bayne & Worral,1980). From the ecological standpoint, SFG could be the most useful of the integrations, since it represents the energy balance at any given time, under specified and well known conditions. Changes in SFG are, therefore, likely to be more significant and more easily interpreted than changes in the rates of single physiological variables (Thompson,1984). Similar physiological studies (e.g Bayne & Widdows,1978; Bayne & Worral,1980; Tedengren *et al.*,1990) illustrate the advantages of exploring difference in the production potential by individuals of the

same population at different sites. The present physiological study has been unable to identify clearly the cause of measured physiological differences between mussels in Loch Leven and the other two lochs, but it has demonstrated that even the limited data obtained during only the main growth season can be used to measure the effects of prevailing environmental condition on growth and production of mussels.

5.9. Salmon - Shellfish Farming: Integrated Mariculture ?

Like all other commercial businesses, the main aim of commercial salmon and shellfish farming enterprises is to produce the maximum quantity of good quality product in a short time with minimum expense. For this aim, both mariculture systems use and require resources from the marine ecosystem; salmon farming uses resources indirectly through wild fish caught for fish meal production while mussel farming uses phytoplankton directly. Therefore the production capacity of the systems depend on the productivity of the aquatic ecosystem; for mussel culture on local primary production and for salmon culture on overall world pelagic fish production which indirectly depends on primary production. Thus, increasing mussel production might cause local depletion in phytoplankton, while farmed salmon production may lead to wide spread ecological changes by increasing fishing pressure on pelagic fish species (e.g. herring, anchovy and capelin) widely used for fish meal production (Folke & Kautsky,1989).

Since both mariculture systems are directly dependent on the aquatic ecosystem, they ought to be completely "green". However, it is not easy to confirm that they perfectly fit into the aquatic ecosystem since it has been shown that they are not only

using the resources of the ecosystem, but are also discharging waste materials into the environment. The review of the literature (section 1.5) revealed that the rapidly developing salmon farming industry in unique coastal environments, such as Scottish sea lochs and Norwegian fjords, might have potential ecological impacts on the coastal ecosystem and that in some areas it had become a risk factor to the industry itself (Rosenthal et al.,1988). It has been widely acknowledged that the main impact of salmonid farming in marine environment is the release of carbon and nitrogen into the water column which can easily create hypernutrification (Gowen et al.,1988) leading, if nitrogen is the limiting factor, to a local or widespread eutrophication covering a whole inlet, bay, fjord or loch depending on the size of the farm and the hydrography of water body within which the farm is located. In addition, nutrient release from salmon farms could stimulate the toxic algal blooms which can be harmful to farmed salmon and shellfish and may even cause conflict between salmon and shellfish growers.

On the contrary, extensive mariculture represented by shellfish farming in Europe and North America is relatively better integrated with the coastal ecosystem (Folke & Kautsky, 1989) than salmonid cage farming. Of course, as is apparent from the literature review, it does not mean that large-scale mussel culture has no negative environmental effects but it means in general that mussel culture has less unfavourable effects on the ecosystem, provided that it is of the proper dimensions and at the right location (Kaspar et al.,1985; Larsson,1985; Tenero et al.,1985). Mussel culture, as a net nutrient remover, can thus counteract eutrophication and large-scale mussel cultivation may even lead to local nutrient depletion.

There might be a technique of preventing the potential eutrophication effect of salmon and the nutrient depletion effect of mussel farming. This technique, as has been suggested by a few authors (Rosenthal *et al.*,1988; Folke & Kautsky,1989; Stirling, 1990; Jones & Iwama,1991), involves integration of the two systems which are different in so many ways. In this integrated system salmon could be the main and mussels the secondary product which will use and re-cycle the pelleted feed wastage (the by-product) and faeces from salmon cages. This potential integrated mariculture system could have the following advantages:

a) Control of the potential eutrophicating (Officer *et al.*,1982; Larsson,1985: Folke & Kautsky,1989) effect of intensive salmon farming, as mussels filter large amounts of particulate organic matter, e.g. one raft of mussels (18x18 m with an approximate capacity of 80-100 tonnes at harvest) can filter 70 millon litres of water in a day and ingest 180 tonnes of organic matter in a year (Figueras,1989).

b) Better growth and increase in shellfish production through re-cycling some of the organic waste from salmon cages (Wallace,1980; Stirling,1990; Jones & Iwama,199; Presm study),

c) Better utilization (high production per unit area or volume) of these well sheltered coastal waters, for example the production of one ton of harvested farmed salmon is indirectly dependent on solar fixation by marine plankton from a water area of about 1 km^2, while the same amount of cultured mussels needs about 1/1000 of this area (Folke & Kautsky,1989).

d) The possibility of using excess mussel meat as salmon feed instead of for human consumption (Folke & Kautsky,1989), at least partly replacing expensive fish

meal as mussel meat is a good source of protein and has a favourable lipid composition and has been proven to be good ingredient in salmonid feed giving very favourable colour to the flesh (Farias,1991; Berge & Austreng,1989). If this were possible, the production of salmon could be ecologically more efficient than the present process, as salmon would be produced at a lower trophic level (phytoplankton → mussel → salmon) instead of the shortest possible alternative food chain of phytoplankton → zooplankton → small pelagic fish → salmon.

e) Better utilization of manpower and infrastructure facilities, e.g. shore building, boats, marketing process etc.

In short, this approach should eliminate the main negative environmental impacts of both salmon (nutrient release) and mussel (nutrient depletion) farming and in doing so optimise the energy flow in the ecosystem.

Although the evidence for a eutrophication effect of salmon culture and the reason for better growth of mussels next to salmon cages are not complete at this stage, salmon farming certainly can cause organic enrichment (Jones & Iwama 1991; present study). The particulate organic matter appears to be used directly by mussels as a food resource (section 5.1.6) if the availability of phytoplankton food is limited, while hypernutrification can cause an increase in phytoplankton biomass which can lead to rapid growth of shellfish as reported by Jones & Iwama (1991). The transfer, however, of this extra POM from salmon feed and faeces and phytoplankton to accelerate growth in shellfish depends largely on physical environmental factors, such as current speed, salinity, temperature, etc: as well as the absence of stressors such as pollution. If any of these environmental variables are sub-optimal then the extra

food might not lead to growth.

The economics of a possible integrated mariculture system suggested here have not been addressed in this study. It is well known, however, that a major expense in the mussel culture industry is that of main culture installations such as rafts and long-lines, but a few of these will not significantly increase the financial load of larger salmon companies. Even if such an integrated system is not so profitable in terms of economics, it should reduce the negative environmental impacts of these two mariculture systems. Present knowledge suggests that integration is possible so it is time to switch from focusing on a single aim of maximizing production and considering the importance of the environment and ecosystems in general.

The practicability of such a large-scale system including utilization of mussel meat as feed input for salmon needs considerable evaluation. On a small scale, however, a few lantern nets with on-growing oysters can be suspended from cage walk-ways and used for consumption by stock workers or marketed for extra income by the company or stock workers. This small-scale system will be of course far from any eutrophication control, but can help the better utilization of space, manpower and environment. The practicability of a large-scale salmon-mussel culture system should not be so difficult and can be worked out. For example, in Loch Kishorn salmon and mussel culture are being conducted by the same company. Although the rafts and cages are quite close to each other, when there is a consideration of possible eutrophication effect, cages and rafts can be re-located to channel the extra phytoplankton production into mussels. Similar to this, when there is a will, it is possible that the other established salmon farms can just add a few rafts or long lines

to their cages. Of course, the size, design and management of this system will depend on, apart from financial capacity of company and market demand, site specifications together with detailed environmental variables and also the main purpose of integration, whether simply as a precaution against potential eutrophication or additional production. If the latter then how this secondary product will be utilised, whether for human consumption or as an ingredient of salmon feed will need to be considered. At present some mussel farmers in West coast of Scotland are using spat settled on cage walk-ways and nets by re-tubing during their second year and this could be lead a complete integrated approach.

Apart from the feasibility and applicability of such an operation there are, however, potential problems such as the possible accumulation of feed antibiotics (section 6.2) and organo-phosphates (Egidius & Møster,1987), mainly trichlorophan and dichlorvos used to control sea lice parasites in salmon cages, in tissues of cultivated mussels as pointed out by Stirling (1990), which might increase the unfavourable environmental impact of mariculture.

The environmental issues associated with use of antibiotics in the fish farming industry have increasingly been raised (e.g. Solbé, 1982; Beveridge, 1984; Rosenthal et al.,1988; Brown, 1989; Institute of Aquaculture, 1989; Ackefors et al.,1990; Lunestad, 1992; Spencer,1992) and related literature has been reviewed in section 6.2 (see also 6.1). Antibiotics, largely oxytetracycline, oxolinic acid and sulphonamides in Europe and North America are given to fish through medicated feed. Since a substantial proportion (up to 20%) of the administered feed in salmon farming may be wasted directly (Gowen & Bradbury, 1987), some part of the medicated feed may

not be eaten by the fish and falls from the cages and dissolves in the water column and/or accumulates on the sea bed. Furthermore, the drugs may be egested in faeces or excreted by the fish. There is no doubt that some degree of potential exists for these antibiotics to reach the environment either directly from the feed or via fish faeces (Institute of Aquaculture, 1989) and some fraction of these drugs entering the environment could be taken up by wild fish, shellfish and crustaceans, resulting in concentrations that exceed those acceptable in food for human consumption (Lunestad, 1992). So the potential hazards that intensive use of chemotherapeutics could represent for human health should be considered as well, quite apart from the possibility of toxicity to non-target hosts including mussels. The possible occurrence and even bioconcentration of therapeutic agents in mussels from farms where salmon are receiving treatment is covered in the next chapter (6).

Environmental changes associated with salmon cage and suspended mussel farming, and of potential changes after system integration are summarised in Table-36. As shown in that table, in general the changes in the benthos beneath mussel farms are very similar to those resulting from organic waste from salmon farming (Gowen et al.,1990), but in magnitude it is likely to be much less than salmon farming and a significant proportion of mussel particulate organic waste is intercepted and consumed by the enriched epifauna (Tenero et al.,1985). Sedimentation rates under a 40 tonne salmon cage farm has been found to be 20 times higher than at control site (Folke & Kautsky,1989), while sedimentation rate below a 100 tonne mussel farm was only three times higher than at a nearby reference site (Dahlback & Gunnarsson,1981). Thus it appears that the impact of salmon farming should be on sea bed and benthos

Table-36. Summary of changes in the aquatic environment associated with intensive salmon cage and suspended mussel farming and potential changes after a possible integration of the two systems.

Farming system Environment	Salmon Farming	Mussel farming	After Integration
Water Column	- Increase in nutrients leading to eutrophication - Potential modifications in phytoplankton composition and possibility of algal blooms	- Depletion in essential nutrients - Modification of nutrient cycle (e.g. rapid regeneration of nutrients) -Increase in macro algae and epifauna - Modification of zooplankton community	- Counter-act against potential eutrophication and modifications in phytoplankton composition - Possibility of restoring natural nutrient balance
Benthos	- Increase in sedimentation rate - Organic enrichment - Reduction in redox potential - Generation of methane and hydrogen sulphide - Increase in BOD - Reduction in macrofauna biomass, abundance and species composition, and increase in the biomass of opportunistic species	- Increase in sedimentation rate - Organic enrichment - Reduction in redox potential - Generation of methane and hydrogen sulphide - Increase in BOD - Decrease in original community and domination of opportunistic species - Accumulation of empty shells under the long-lines or rafts	- Since both system has similar effect on benthos, certainly there will be increases in all these impacts which appears to be unavoidable - And unless site and capacity of salmon and mussel production properly selected all these changes could double when two system integrates and site could be abandoned after a few years.

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as could be suspended mussel farming. This relatively small impact of mussel culture on benthos could easily be resolved by rotating mussel rafts or long-lines around cages every few years, or relocating both the cage and mussel systems.

In brief, although the suggested integration of salmon and mussel cultivation systems may not find the necessary support for application from farmers at present, in the long term, the aquaculture industry should consider a system better integrated with the environment, aimed at achieving an equilibrium between the production capacity of farming systems and that of the ecosystem. Otherwise, with increasing production and public awareness on environmental issues, mariculture or aquaculture in general might loose its green image and become one of the latest contributors to environmental degradation despite its direct dependence on a clean environment.

6. PRELIMINARY INVESTIGATION OF THE 'CHARM II' SYSTEM AS A METHOD FOR DETECTING RESIDUES OF THERAPEUTIC AGENTS IN CULTURED MUSSELS

6.1. Introduction

One of the greatest challenges in intensive aquaculture is the increasing disease problem. The cultured species are especially subject to diseases caused by bacteria, fungi, protozoa and viruses exacerbated by high stocking density and adverse environmental conditions which impose stress on organisms and lead to disease outbreaks (Jacobsen & Berglind, 1988). Preventive methods, such as better husbandry techniques, vaccines and genetic selection are very important and improving day by day. When disease occurs, however, treatment of fish with chemotherapeutics, such as antibiotics, is still the main and most widely applied method. There are two principal methods for application of therapeutic treatments in aquaculture - either enteral administration of pharmaceutical products which are incorporated within the fish diet, or topical applications of compounds administrated as a dip or bath treatment, in a known concentration for a known time.

A wide variety of chemicals is used in aquaculture, such as therapeutics (parasiticides, fungicides, bactericides), disinfectants, anaesthetics, herbicides, antifoulants, hormones, dyes and lot more chemicals for other purposes (Anonymous, 1989). In some countries, there are hundreds of such chemical compounds in use, while in other countries, only a restricted number of chemicals is registered or approved for use in fish culture. For example, in 1988 there were 39 chemicals registered or approved for use in aquaculture in USA (Schnick, 1988), although less than a dozen of them have achieved widespread use in the United Kingdom (Austin, 1985). Table-37 is a compilation of chemotherapeutics which are widely used in aquaculture. All these chemicals themselves present a potential risk to the cultured

Table-37. Major chemotherapeutics used in aquaculture (from Institute of Aquaculture, 1989; Alderman & Michel, 1992).

ANTIBIOTIC	USE	ENVIRON.	METHOD	NOTES
Formalin	Ectoparasite	FW\SW	Dip	Use in cages as bath common
Acriflavin	Ectoparasite Fungus Bacteria	FW	Dip	Mostly for surface bacteria
Nuvan (dichlorvos)	Sea lice	SW	Bath	1 ppm for 1 hour, canvas around sea cage
Buffered Iodine	Bactericide	FW	Bath	Use to disinfect eggs
Oxytetracycline	Bactericide	FW\SW	Oral	Antibiotic widely used for systemic disease
Oxolinic acid (& Flumequine)	Bactericide	FW\SW	Oral	Antibiotic widely used for systemic disease
Sulphonamides (Sulphamethazine, sulphadimethoxine, sulphaguandine)	Bactericide	FW\SW	Oral	Antibiotic for systemic disease
Potentiated sulphonamides (Trimethoprim + sulphadiazine)	Bactericide	FW\SW	Oral	Third most widely used antibiotic for systemic disease
Erythromycin	Bactericide	FW	Oral	Antibiotic for bacterial kidney disease
Nitrofurans (furazolidone, furaltadone, nifurpirinol)	Bactericide	FW\SW	Oral\bath	Systemic disease
Hayamine 3500	Bactericide	FW	Add to water	Quaternary ammonium compound used for bacterial gill disease
Benzalkonium Chloride	Bactericide	FW	Add to water	Surface antibacterial (similar to above)
Chloramine	Bactericide	FW	Add to water	As above(also effective for some protozoa)

FW=Freshwater; SW=Sea water

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organisms and the environment if not used in a sensible way.

Very great attention has been paid to the usage of antibiotics among these chemicals by the aquaculture industry, but a few countries have provided information on the amount of antibiotics applied in the industry. For example, in 1988, the Norwegian aquaculture industry used 18220 kg of oxytetracycline, which corresponds to 0.21 kg t^{-1} of fish produced, whereas Finland used 0.115 kg t^{-1} (Anonymous, 1989). This level of usage of chemotherapeutic agents have induced regulations on a national level in some countries. In order to protect the consumer it was necessary to introduce withdrawal periods after treatment with such compounds before the fish and shellfish can be marketed. According to Swedish law, for example, the approximate withdrawal periods are 360 degree-days (°D) for oxytetracycline, 540°D for sulphamerazine and 720°D for trimethoprimasulfa (Ackefors et al.,1990).

Oxytetracycline, oxolinic acid and sulphonamides are probably the most widely used antibiotics in intensive fish farming in Europe and North America (Institute of Aquaculture, 1989). Almost all these antibiotics are administered enterally, by mixing the drug with the feed. They have found extensive use for the control of furunculosis, haemorrhagic septicaemia, bacterial gill disease, columnaris, generalised septicaemia, vibriosis and enteric redmouth (Austin, 1985). A large proportion (up to 20%) of the administered feed in salmon farming may be wasted directly (Gowen & Bradbury, 1987), so some part of the medicated feed is not eaten by the fish and falls from the cages and dissolves in the water column and/or accumulates on the sea bed. Therefore, the potential exists for the antibiotic to reach the environment directly from the feed or via fish faeces (Institute of Aquaculture, 1989). Austin (1985) predicted

that if all the antibiotic in feeds used in a typical land based fish farm was leached into the water supply (the worst scenario), the concentration of the drug in the effluent water would be:

Oxolinic acid;   1:50 000 000,

Oxytetracycline; 1:6 666 666,

Sulphonamide;   1:16 666 666.

The author concluded that the quantities of drugs likely to leach into the aquatic environment are very small.

The environmental issues associated with use of these therapeutic chemicals have increasingly been raised (e.g. Solbé, 1982; Beveridge, 1984; Rosenthal *et al.*,1988; Brown, 1989; Institute of Aquaculture, 1989; Ackefors *et al.*,1990; Lunestad, 1992), but, little is known about their environmental fate and effects on aquatic ecosystems and, with few exceptions, field data are still absent. In addition some of the drugs entering the environment will be taken up by wild fish, shellfish and crustaceans, resulting in concentrations that exceed those acceptable in food for human consumption (Lunestad, 1992). So the potential hazards that intensive use of chemotherapeutics could represent for human health should be considered as well.

6.2. Literature Review

A review of the relevant literature showed that there is very limited information concerning the effect of antibiotic residues on neighbouring fauna. Unfortunately, there was not any information in the literature concerning the environmental fate of sulfa drugs at the time of this study. Oxytetracycline (OTC), which has been a widely used antibiotic for a quarter of century (Jacobsen, 1989), has received most attention.

Some studies (Salte & Liestøl, 1983; Ackefors *et al.*,1990) show that withdrawal periods of OTC and sulphonamides (sulphamerazine, sulfadiazine - trimethoprim) from cultured fish after treatment are quite similar, so the degradation, persistence and possible effects of these antibiotics on the surrounding environment may be similar as well.

Only 20-30 % of the OTC administered in the form of medicated food pellets is actually taken by the fish whereas the rest, 70-80 %, reaches the environment (Samuelsen, 1989) and the most it is bound to particles and sediments under the farm (Jacobsen,1988; cited by Samuelsen, 1989). Jacobsen & Berglind (1988) investigated the persistence of OTC in sediments from fish farms and found a half-life of approximately 10 weeks and detectable concentrations up to 12 weeks after administration. In a similar study of degradation of OTC in seawater and its persistence in fish farm sediments, Samulsen (1989) found that the degradation of OTC in seawater is very rapid and most of this antibiotic disappears during the first few weeks, but the half-life of OTC in sediment is about 32 days and it remains in low concentrations for quite some time after feeding the antibiotic. He also showed that the degradation of OTC in seawater is influenced by both temperature and light intensity. Concerning the aquatic fauna, Austin (1985) monitored antibiotic resistance of bacteria isolated from trout farm effluent. He found that during treatment with oxytetracycline, 90% of the bacteria strains examined showed antibiotic resistance but the increased resistance level was reduced soon after termination of the treatment. Björklund *et al.*(1990) studied the residues and persistence of OTC in wild fish and sediments from fish farms after chemotherapy, and they detected residues of OTC in

wild fish up to 13 days after medication. There is very little information on the accumulation of antibiotics, mainly OTC, in shellfish. Yndestad (1986; cited by Björklund *et al.*,1990) claimed that residues of antibiotics were found in wild fish and in molluscs in the vicinity fish farms in Norway . Similarly, according to Samuelsen (1989), detectable concentrations of OTC were found in mussels (*M. edulis*) by Møster (1988) 80 m from a farm using the antibiotic. Lunestad (1992), who investigated oxolinic acid in wild fauna and examined a total of 250 fishes, 50 crabs and 30 samples of mussels, found average (maximum 10 000 ppb) 3800 ppb oxolinic acid concentration in the muscle of wild fish at the day of termination of treatment. He detected residues even in fish caught 400 m away from the cages. However, twelve days after termination of the treatment, detectable drug could not found in any species examined (detection method high-performance liquid chromatography, HPLC, and limit 5 ppb). Unfortunately Lunestad (1992) did not give results for mussel samples. Tibbs *et al.*(1988 & 1989) studied the accumulation of antibiotics in tissues of market-size oysters, clams and mussels suspended in mesh bags within coho salmon net pens during the time that food medicated with OTC was being administrated. The experimental shellfish were kept in pens for 10 days and specimens of each species were removed from bags each day and sent to the laboratory for analysis. The limit of detection in their first publication was around 50 ppb (part per billion) and in their second one 30 ppb, the rest of the experimental description being exactly the same. In their first paper they suggested that, according to preliminary results, the tissues contained OTC concentrations equivalent ranging up to 500 ppb. However, Tibbs *et al.*(1989) later claimed that no specimens of any

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species of shellfish contained detectable amounts of OTC and their conclusion is that antibiotic leaching from medicated food does not contaminate the tissues of shellfish in the immediate area.

6.3. Rationale and Objective

Salmon and mussel farming are practised side by side in most of the Scottish sea lochs. The mussel (*Mytilus edulis*) naturally settles on salmon cages (walk-ways, nets and ropes) and grow better than those which settle on the bottom. This is mainly because they are suspended like cultivated mussels, get more food and grows very fast. Therefore, some small scale mussel farmers are collecting and using these mussel as seed or marketable product after sorting according to size. However, the review of the literature suggests that there may be environmental effects of antibiotics and chemotherapeutic agents used in treatment of salmon diseases. More detailed research is necessary to determine the effects of antibiotics on macro-fauna, especially on sessile filter feeders such as mussels, near fish farming sites.

The main objective of this study was to carry out a preliminary investigation of the 'Charm II' system as a rapid method for detecting residues of potentiated sulphonamides (Trimethoprim + sulphadiazine) in the tissues of mussels naturally settled on salmon cages where the fish were being treated with these drugs.

6.4. Materials and Methods

6.4.1. The Principle of the Technique

The Charm II Test was chosen, mainly because it is available at the Institute and

has been used successfully for detecting antibiotics, generally oxytetracycline, in salmon (Inglis, 1992) and shrimp tissues (Higuare-Ciapara *et al.*,1990 & 1992). In addition, the technique has AOAC (Action Association of Official Analytical Chemists) approval for screening of sulphonamides and other antibiotics in milk (Charm & Chi,1988). It is also used for detecting sulphonamide residues in meat and the results were consistently in good agreement with the results of thin-layer chromatography (TLC) and HPLC (Hogg *et al.*,1989).

The Charm II Test is a rapid microbial receptor assay. For the detection of any antimicrobial drug, the Charm II uses a radioactively-labelled antimicrobial drug (labelled with ^{14}C or ^{3}H) which competes for specific binding sites on a cell or ribosome (binding reagent) with the contaminating 'target' drug. When the binding reagent is added to tissue or milk contaminated with antimicrobial drugs, the target drug binds to receptors in the cell. This prevents the [^{14}C] or [^{3}H] antimicrobial drug from binding to these sites. Thus the more radioactively - labelled antibiotic bound, the less contaminating antibiotic there is in the sample and the counts per minute (cpm) are inversely proportional to the amount of antibiotic present in the sample (Charm Sciences Inc.,1991). The reagents are sold in kits and detailed information about them is not provided with the kits, presumably for commercial reasons. Since the functional chemical group of the antimicrobial drug is involved with the binding side, not a specific side chain, a single receptor detects all members of a drug family as a whole, for example sulphonamides, but the test does not identify which sulphonamides are present; to identify a specific drug in a family an additional test must be performed. A calibration curve of cpm <u>vs</u> concentration is prepared by

spiking a negative sample with increasing concentrations of antimicrobial drug supplied by manufacturer. Finally, quantitative test results are expressed as positive or negative using a predetermined control point. The control point is determined by testing at least 6 spiked tissue samples and adding two standard deviations to the mean cpm of these samples. Samples with cpm greater than the control point are considered to be negative, while samples having cpm less than or equal to this point are regarded as positive and need to be retested to validate the positive results (Charm Sciences Inc.,1991).

6.4.2. Experimental Mussels

Market-size mussels (> 50 mm) were collected from cage walk-ways of a salmon farm which had undergone 2 weeks sulfatrim (83.3 g trimethoprin B.P. and 416,7g sulphadiazine) administration (positive samples). As a control, mussels from an experimental shellfish farm at Ardtoe, which is far from any effluent of salmon farms and agricultural residues, were collected for determination of a standard control point (negative samples). These mussels were shucked immediately after transportation to the laboratory and tissues were kept frozen until the analysis. Before the test the tissues were thawed overnight in a refrigerator. Additional mussels from a mussel farm in Loch Etive were taken and kept about 24 hours in a tank with recirculated seawater supply from a bacterial filtering unit. Fresh tissues of mussels were also used as control samples during initial work with mussels from the salmon farm.

After having problem with unpurified mussels, some purified mussels were brought from Conwy laboratory of the Ministry of Agriculture, Fisheries and Food, and used

these mussels immediately after arriving at Stirling. These mussels had been purified for at least 48 hours by keeping them in tanks filled with sea water sterilised for about 8 hours with chlorine dosed at the rate of 3 ppm (part per million) (Wood,1969). Naturally the stomachs of mussels were completely empty. The whole tissues of these mussels were used both as control or negative and positive after fortifying with sulfamethazine according to the manufacturer's recommended procedure (Charm Sciences Inc.,1991).

6.4.3. Antibiotic Detection

The procedure, which had been recommended by Charm Sciences Inc. (Scheemaker,1991) and was same as that used for detection of sulphonamides in fish, followed during the sample preparation and screening process is summarised in Fig.42. As the figure shows, tissue extracts were prepared by high-speed homogenization of about 20g mussel tissue for 20 seconds in MSU extraction buffer provided by the company, incubation at 60 °C for 30 min, centrifugation for 10 min at 1600 G and collection of the clear supernatant for the test. The pH of the extract was checked and, when necessary, was brought to 7.5 - 8.5, for maximum sensitivity, by adding M2 Buffer, which was also supplied by the company, drop by drop. A standardised binding tablet (of microbial cells) was pushed into a clean test tube, 300 µl of water added and incubated for 2 min at 35 °C, before adding 2 ml of sample extract diluted 1:1 with MSU Extraction Buffer and incubating the mixture for a further 2 min at 35 °C. Then an excess of radio -labelled antibiotic (probably tritium labelled sulphadimidine; Hogg *et al.*,1989) was added and the mixture incubated again

RAW TISSUE

Homegenize in MSU buffer 30 min @ 60°C

Centrifuge 10 min @ 1600 G

SUPERNATANT

Ensure extract pH is 7.5-8.5

TISSUE EXTRACT　　　　　　　　　　　**BINDING REAGENT**

Activated by
incubation with
300 ul water 2
min @ 35°C

2 ml + 2 ml MSU buffer

EXCESS　　　Incubate 2 min at 35°C

**Radio-labelled
Drug**

Binding of target drug
to receptor sites on reagent

Binding of 3H-drug to
vacant receptor sites

Incubation 2 min @ 35°C

Centrifuge 3 min @ 1600 G

PELLET

Scintillation
Fluid ——— 3 ml ———▶

Resuspend

COUNT 1 min IN "LIQUID SCINTILLATION" COUNTER
(Measurement of 3H bound to reagent)

Fig.42. Flow - chart of procedure for 'Charm II' screening of mussel tissues.

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for 2 min at 35 °C, followed by centrifuging for 3 min at high speed to obtain a solid pellet containing the bound drugs. This pellet was resuspended in 300 µl of water and 3 ml of 'Optiflour$^{R'}$ scintillation fluid, also supplied with the company test kit. Finally the sample was counted for 1 min and the cpm read on the ^{3}H channel of a scintillation counter.

Sufficient reagents were available for only 100 tests in all, including the establishment of a consistent drug-free control giving sufficient sensitivity combined with low standard error, plus the spiking of this control with standard additions of the target drug. Problems with establishing the control prevented us carrying out full investigation as was intended.

6.5. Results

All the cpm readings obtained during the process of establishing a control and later a suitable pre-treatment method are given in Table-38.

Firstly, to set a standard reference point to determine whether a sample was positive or negative, about 10 samples of whole tissues of control mussels (from Ardtoe) were run and the mean (±S.D) cpm (count per minute) was 620 ±58. Then 10 samples from salmon cages were screened to find out the response of the system to positive samples and the mean cpm was 600±46.

As can be seen in Table-38, the cpm values of both control and exposed samples from the salmon farm were very similar. More importantly these values were much too low (by a factor of 4-5) in comparison with previous work on salmon and shrimp tissues at the Institute indicating a marked loss of sensitivity, so it was certainly

Table-38. Cpm (count per minute) values of mussel tissues without\with pre-treatments, and unspiked\spiked with three concentration of sulfamethazine.

	Control[a] (Ardtoe)	Exposed[a] (Salmon cages)	Control[b] (Ardtoe)	Control[c] (L.Etive)	Charm Sciences		Conwy (Purified & Spiked)			
					Control	50ng\g	Control	20ng\g	50ng\g	100ng\g
	642	596	1557	1791	3731	2220	3474	2497	2088	1294
	509	594	1460	1710	3423	1829	3274	2507	2093	1324
	562	645	1423	1348	3259	2023	3311	2399	1887	1455
	611	641	1761	1712			3399	2388	1955	1204
	593	590					3505	2389	1984	1335
	655	522					3224	2465	1764	1219
	624	556					3462	2550	1896	1248
	637	564					3583	2481	1907	1318
	730	675					3518	2390	1985	1174
	633	615					3436	2514	2121	1301
N	10	10	4	4	3	3	10	10	10	10
Mean	620	600	1550	1640	3471	2024	3419	2458	1900	1287
S.D.	58	46	151	198	240	195	116	59	111	81

a: whole tissues,
b: excluding gills and stomach
c: starved

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impossible to draw any conclusion regarding possible drug contamination from these readings. A thick layer, probably a mixture of lipid and stomach contents, was formed at the top of the supernatant during the extraction procedure. This layer, which was preventing clear extraction, was suspected as a possible reason for such low counts from the scintillation counter and in order to get rid of this layer, the extract was centrifuged a second time. Although a very clear extract was obtained as a result of this treatment, there was no significant change in cpm. Consultation with Charm Sciences also confirmed that the results of these tests were much too low and we were reminded that there are some substances, such as high fat content, high bacteria or yeast contamination and somatic cells, which may interfere with the Charm test (Scheemaker,1992). As a result of this consultation with the manufacturer, bacterial contamination and/or the stomach contents of the mussels were considered to be more likely causes of extremely low cpm's. As a solution stomachs and gills were excluded, and the rest of the tissues of control mussels were rinsed in de-ionised water before analysis. In addition fresh mussels were starved in filtered re-circulating sea water for about 36 hours, gills and stomachs were separated, rinsed and screened. The readings improved slightly and the mean cpm rose to 1550±151 and 1640±198 after the latter two pre-treatments, respectively, but the counts were still very low.

In a third trial, tissues of purified mussels, which would be relatively free of bacteria, were used. The fresh mussels were dissected and whole tissues were used for extraction. The results of 10 samples were over 3000 with a mean cpm of 3419 ±116 (Table-38). After these improved results, tissues of purified mussels were spiked with sulfamethazine (supplied in the Charm test kit) at a concentration of 20 ng\g, 50

ng\g and 100 ng\g and screened. All the concentrations of sulfamethazine gave a suitable response. At the same time, the Charm Sciences informed us that they had tested some mussel samples in the USA and the results of control and spiked samples received from them were in very good agreement with those obtained in this study (Table-38). The mussels used by Charm Sciences were taken from a fish monger and it is unknown whether or not these mussels had been purified but most of the mussel production in the USA comes from natural beds and in general purification with ultraviolet light is compulsory (Dore,1991).

Finally, a calibration curve of counts per minute (cpm) vs drug concentration was determined by using these spiked tissues, as shown in Fig.43. This shows a clear
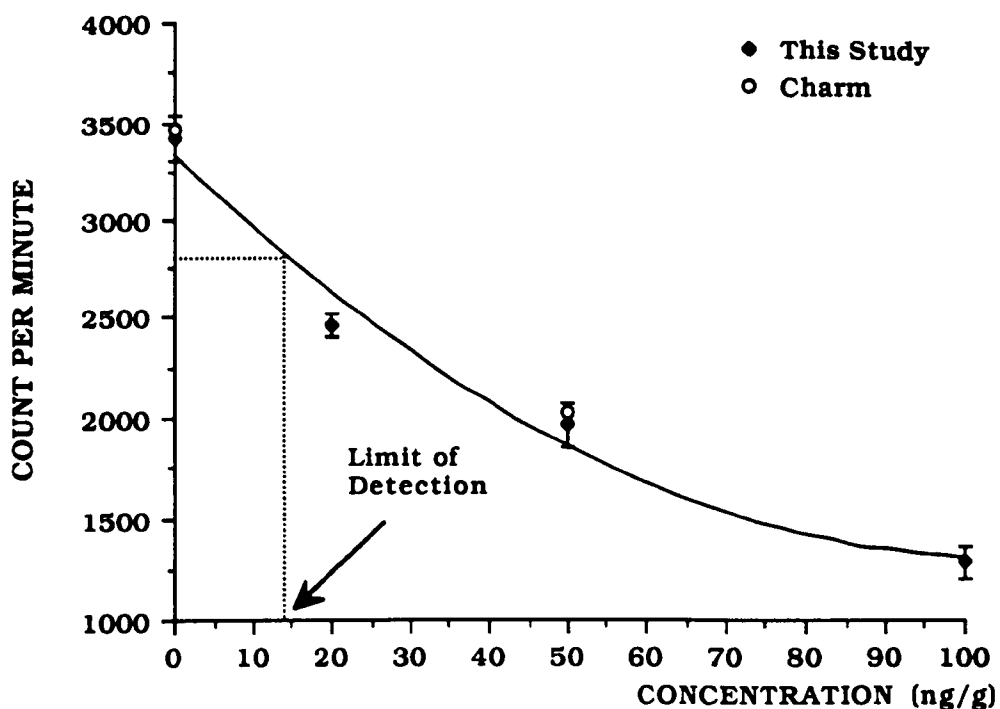
Fig.43. Sulfamethazine concentration vs cpm (count per minute) in control and spiked tissues of purified mussels from Conwy with standard deviations and limit of detection.

dose/response relationship with very small standard deviations. The limit of detection (the minimum significant quantity) is calculated from the standard deviation of the control, s_b, as explained in Stirling, (1985):

$$2\sqrt{2}* \; t_{0.1} \; (=1.833 \text{ for df}=9)*s_b.$$

So the critical cpm value for detection of sulfamethazine is 2,818 or less, corresponding a concentration of 14 ng/g.

Insufficient reagents were left by this stage to reexamine whether sulphonamide residues could be detected in mussels sampled from treated salmon farms and then purified to remove microbial contamination.

6.6. Discussion and Conclusions

The Charm II Test is a very simple and rapid method, taking about 3-4 hours for one person to analyse a batch of 10 samples and 2 reference controls, including sample preparation (Hogg *et al.* (1989), and therefore it is very suitable especially for analysing large number of samples of milk and animal tissues. The very low counts obtained with unpurified mussels from 'clean' control sites indicate that there is massive interference of bacteria or possibly microbial detritus concentrated on the surface of the gills or within the digestive organ. That this interference is overcome by subjecting mussels to standard purification procedures (using chlorine or UV light) supports this hypothesis, but one can only speculate at this stage as to the mechanism of this interference. Two possibilities come to mind: either microbial degradation products (these might be metabolites of the folic acid pathway with which sulpha drugs are known to compete) bind non-specifically with receptor sites on the binding

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reagent, thus simulating the target drug, or the radio - labelled drug binds preferentially to some low molecular weight (i.e. non-centrifugable) fraction, possibly lipoidal, which is derived from microbial contamination, leaving much of it in the supernatant and unavailable to bind with sites on the binding reagent. Both explanations would give low counts in controls.

Consultation with people who have worked with the Charm Test, and good agreement between results of these trials and the those of the manufacturer on purified mussel tissues convinced us that the mean cpm readings of the control and spiked purified mussel tissues were consistent and might be reliable. Hence the method should be reliable to detect sulphonamide residues in purified mussels. So it is obvious that before screening the tissues with the Charm II Test, filter-feeding molluscs should be kept in a purification system and certainly there is also a need to compare the results of Charm II test with alternative techniques, such as TLC, HPLC or bioassay.

According to the new EEC classification of shellfish farming sites based on faecal coliform levels, most of the Scottish West Coast sea lochs meets class A, where purification of shellfish prior to sale is not necessary. Thus if the Charm test is limited to testing purified material with a minimal bacterial load, it does not appear to be an appropriate technique for screening mussel tissues for drug residues arising from salmon farming in the West Coast and an alternative method, such as HPLC or bioassay will have to be used.

7. SUMMARY AND CONCLUSIONS

7.1. Summary of Methods

The present study was mainly conducted to investigate growth of cultured mussels during their second year (2 years old) at different sites, including salmon farms, in sea lochs (Loch Etive, Dunstaffnage Bay and Loch Leven) on the West coast of Scotland between May 1990 and September 1992.

During the first year of the study (experiment I), mussels with a shell length range of 18-34 (mean 27.1) mm from a raft farm in Loch Etive were stocked into French socks and suspended from salmon cage walk-ways (2 sites), mussel rafts and long lines (2 sites). Two of these sites, one salmon and one mussel, were in Loch Etive, a third salmon farm was in Dunstaffnage Bay and a second mussel farms, in Loch Leven. This experiment lasted from May 1990 until June 1991 (13 months) and the growth of mussels at salmon farms was compared with that at mussel farms together with mortality and losses, biomass, production, condition index and approximate biochemical cycle, as well as spat settlement. In experiment II (May 1991-May 1992), very similar size (20.0-26.0 mm) 1^+ year-old mussels from Lochs Etive and Leven were stocked into lantern nets and these are suspended at the same sites in Loch Etive and at a new salmon farm site in Loch Leven, in addition to the mussel farm used during experiment I. In this experiment the parameters examined were similar to the previous experiment, except production, but apart from adding another salmon farm site and using native mussels in each loch, losses due to fall-off from ropes (socks) were eliminated so it was possible to determine exact natural mortality rates, excluding predation. In addition, since size variation among individuals was very small, it was possible to follow growth more closely. During the same period, a

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cross-transplantation experiment was carried out between mussel farms in Loch Etive and Leven in order to study the effect of site, stock and stock*site interactions on growth, mortality, physiologic responses and morphology of mussels.

During these field studies all sites were visited monthly (except January) and mussel samples were brought to the laboratory to obtain necessary measurements. In addition, water temperature, salinity and transparency were measured at all sites and water samples were taken for particulate organic matter, chlorophyll-a content and particle size distribution determinations. In May and September 1992 the physiological responses of native mussels at both sites in Loch Etive, the mussel site in Loch Leven and at an additional mussel farm site in Loch Kishorn, and of mussels cross-transplanted between Loch Etive and Loch Leven after 15 days, 4.5 months and 1 year acclimatization periods, were measured fully under ambient conditions. Finally, a study was planned to carry out a preliminary investigation of the 'Charm II' system as a rapid method for detecting residues of potentiated sulphonamides (Trimethoprim + sulphadiazine) in the tissues of mussels naturally settled on the salmon cages and exposed to drug treatment of the salmon. As it was later realised that it was not possible to screen tissues of unpurified mussels in the 'Charm II' system this main objective was abandoned, and the suitability of this system for screening whole mussel tissues before and after purification was tested.

The main aim of this study was to evaluate the present mussel culture practice and to teste the hypothesis of "mussel around salmon farm can utilise organic waste from cages and potential enhanced phytoplankton growth and hence grow better than reference sites". The following conclusions are summarised and recommendations

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made from the two year field study.

7.2. Conclusions

1- Annual water temperature distribution (3.5 -17.5°C) is mostly influenced by the season and possibly by tidal range and quantity of freshwater run off.

2- Like temperature salinity also fluctuated seasonally with lowest values in winter and highest in summer, but in addition there were rapid monthly fluctuations. Values were highest at Stirling Salmon site in Dunstaffnage Bay, followed by Glencoe Salmon and Shellfish farm (excluding surface) in Loch Leven.

3- There were significant differences in particulate organic matter between salmon and mussel farms, and % particulate organic matter values at salmon farms were steady around 40-50%. It is most likely that it was a result of food wastage from salmon cages.

4- Chlorophyll-a concentrations ranging from 0.1 to 4.8 µg l^{-1} showed that phytoplankton production in Loch Etive was higher than in Loch Leven. Salmon farming did not cause any substantial increase in chlorophyll-a concentrations.

5- As a result of seasonal variations in environmental variables, growth of mussels was relatively rapid from late-spring until mid-autumn (May-October, approximately 6 months) and very slow or absent during the rest of the year which is very similar to seasonal growth of mussels in other regions of Northern Europe. The apparent positive relationships between monthly growth rates and temperature and chlorophyll-a values indicate the limiting effect of these two main factors on growth during autumn-winter and even until late spring. Moreover the negative effect of

rapidly fluctuating salinity values on growth and performance of cultivated mussels in sea lochs cannot be ignored. Overall annual length increments were 25.1-25.9 mm at sites in Loch Etive and Dunstaffnage Bay, and 20.1-22.8 mm in Loch Leven.

6- Maximum tissue growth (as live, wet meat and ash-free dry meat) occurred in April-May and shell growth in June-August, reflecting an uncoupled growth pattern.

7- Both length and tissue growth were significantly higher in Loch Etive and Dunstaffnage Bay than in Loch Leven; tissue growth in particular was very low at site Glencoe Shellfish Farm. Lower chlorophyll-a concentration in Loch Leven was the most likely cause, but previously noticeably high levels of Zinc and Copper concentrations have been recorded in this loch and the possibility of an environmental stress condition has been considered.

8- In spite of lack of important differences in chlorophyll-a concentrations, shell length growth of mussels at salmon farms during both experiments were slightly (1.4 mm in Loch Etive and 2.7 mm in Loch Leven) higher than at neighbouring mussels farms, but these differences were significant only during experiment II. In addition live weight at salmon farm in Loch Etive and all tissue growth parameters at salmon site in Loch Leven were significantly higher than corresponding mussel farms. Furthermore, in situ production losses at salmon sites during winter were less than mussel farms, indicating that mussels at salmon farms did not use energy reserves as much as those at mussel farm sites. The actual reason for differences in growth rates between sites, however, is not exactly known at this stage, but micro-environmental similarities between salmon and mussel sites in Loch Etive indicates that these differences could result from differences in particulate organic matter values. In Loch

Leven, however, there were some micro-environmental differences between the sites (in chlorophyll-a and currents), so part of these growth differences might be attributed these variations.

9- Length growth of mussels at site(s) in Loch Etive and Dunstaffnage Bay were higher at depths of 4-6 m than at 2-4 m and vice versa in Loch Leven.

10- Overall mean growth in length appeared to be similar to other West coast sea lochs in Scotland, except Linne Mhuirich, in Scotland, but lower than values from other mussel culture areas in temperate regions as a result of a shorter growth season.

11- Transplantation results showed that site was the main factor governing all growth parameters, i.e. Loch Etive was a better site than Loch Leven. Stock also had a significant effect on length and live weight, while wet meat and ash-free dry meat weights significantly affected by site*stock interaction. Similar growth and physiological responses of transplanted (after a few months of acclimatization period) and native mussels indicate the dominant effect of site but morphology of these mussels did not show any changes even after one year acclimatization, which was most likely as a result of slow adaptation process and/or possible genetic difference.

12- During the first experiment survival was very low, ranging from 27.8 to 38.6%, but when losses are eliminated mean cumulative natural mortality of mussels was as low as 6.6% at sites in Loch Etive and 10.7% in Loch Leven. Mortality rates at salmon farms in both lochs were slightly higher than that at mussel farms.

13- Ash-free dry weight biomass decreased and production were negative during winter reflecting utilization of body reserves accumulated during summer. As a consequence of very low tissue growth and slightly higher losses, the biomass and

production of mussels in Loch Leven were lower than Loch Etive. A substantial proportion (46% in Loch Etive and 89% in Loch Leven) of production was eliminated as a consequence of losses and utilization of reserves. The latter was the lowest at salmon farm.

14- The seasonal variations in condition index followed the pattern of tissue growth or biomass, increasing during summer, particularly May-August and declining after November to minimum in April. This suggests that from May to December (8-9 months) at sites around Loch Etive is the optimum time for harvesting and marketing. Biochemical composition showed clear seasonal cycles, similar to growth and condition index and which was very similar to the storage cycle described for mussels from temperate regions, namely a rapid increase in glycogen content after spawning during spring and utilization of this reserve during winter and early summer, and inverse relationships between glycogen, and protein and water contents.

15- All indirect evidence (seasonal condition index, biochemical composition, examination of mantle) suggest that spawning occurs during March-April and spat settlement starts in June.

16- Native and trans-transplanted mussels, as well as mussels at salmon farm in Loch Etive and at new site in Loch Kishorn, were also used to measure physiological rates and estimate the growth potential or scope for growth. In general the results of physiological measurements and scope for growth estimation confirmed observed length and tissue growth. Both native and transplanted mussels at site in Loch Leven differed markedly from sites in Loch Etive (namely Loch Etive Shellfish Farm and Ardcahattan Salmon) and Kishorn Shellfish Farm in physiological rates (clearance

rate, absorption efficiency, oxygen consumption, ammonia excretion, scope for growth and net growth efficiency) and the mussels at site Ardchattan Salmon had slightly higher scope for growth than neighbouring mussel farm site. It is estimated that actual growth in Loch Kishorn is probably very similar to sites in Loch Etive. This experiment also demonstrated that measurement of physiological rates in the field and estimated scope for growth during the main growth season can be used to compare sites and stocks or populations

17- There appeared to be no potential constraints on suspended mussel culture, despite fluctuating salinities near the surface and relatively slow growth of mussels as a result of low temperature values which closely covary with phytoplankton growth in lochs such as Etive and Kishorn. Environmental differences between lochs and between sites in the same loch might have favourable or unfavourable effects on the performance and growth of mussels. Therefore, site selection is possibly the single most important factor under the control of farmers. Potential osmotic stress caused by rapidly fluctuating salinities can be solved by avoiding the topmost few meters, but only solution for the generally slow growth rate due to climate could be shifting the marketing size from 50-60 (even 70) mm to 40-50 mm and so reducing the turnover time.

18- Although the Charm II Test is a very simple and rapid method of detecting drug residues in tissues, interference of bacteria or similar microorganisms with the system creates problems so mussels have to be purified before screening. Thus the system does not appear to be an appropriate technique for screening mussel tissues for drug residues arising from salmon farming on the West Coast where purification

is not necessary at majority of mussel farm sites, and an alternative method, such as high performance liquid chromatography or bioassay, has to be used.

7.3. Recommendations for Further Research

A substantial amount of information was obtained to relevant to the main objectives of this research, but it is certainly not enough for a complete evaluation of the bio-technical aspects of mussel culture and the results appeared to be conclusive for tested hypotheses. Further research on the following areas, however, should be conducted:

a) Further evaluative studies on, for example, energy flow and carrying capacity in lochs occupied by a large shellfish farm; culture strategies, i.e. optimum length of culturing ropes (possibility of using deeper water bodies), distance between ropes, efficiency of re-tubing and materials used, effect of control of density (thinning) on growth and survival etc..

b) Continuation of the study associated with environmental impact on shellfish of antibiotics released during treatment of farmed salmon and the potential hazard to public health hazard.

c) More studies on the environmental impact of intensive salmon farming on invertebrate populations, and preferably controlled feeding experiments in the laboratory with mussels and possibly oysters to investigate whether these filter feeders can utilise organic wastes (particulate and/or soluble from salmon cages and if so, whether this organic waste can supports considerable growth in the absence of sufficient phytoplankton food.

d) Detailed investigation of the unfavourable environmental factors in Loch Leven causing slow length and poor tissue growth.

e) Effect of sea loch system on distribution and morphology of mussels and larvae, and possibility of genotypic differences between populations from different lochs.

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APPENDIX

ABBREVIATIONS AND ACRONYMS

The abbreviations and acronyms used in this thesis are listed here in alphabetical order and the sections particular acronyms defiened are given in parenthesis.

A: Absorbed energy or ration (section 3.8.5)
AE: Absorption efficiency (section 3.8.2)
AFDMW:Ash-free dry meat weight (section 3.4)
AFDSOW: Ash-free dry shell organic weight (section 3.4)
AFDM: Ash-free dry meat
AFDW: Ash-free dry weight (section 3.6)
ANOVA: Analysis of variance
AS: Ardchattan Salmon farm (experimental site, section 3.1 and Fig.4)
ASSG: Association of Scottish Shellfish Growers
C: Consumed energy or ration (section 3.8.5)
ca: Approximately
cf: Compare
cm: Centimetre
CI: Condition index (section 3.7)
Chl-a: Chlorophyll-a
cpm: Count per minute (chapter 6)
CR: Clearance rate (section 3.8.1)
D°:   Day-Degree (section 2.2.2)
°C: Degree centigrade
DMW: Dry meat weight
DSOW: Dry shell organic weight
DSW: Dry shell weight
EB: Eliminated biomass (section 3.6)
EEC: European Economic Community
ELEFAN:Electronic Length-Frequency Analysis (section 3.4)
F: Faecel energy loss
Fig: Figure
g: Gramme
GS: Glencoe Salmon farm (experimental site, section 3.1 and Fig.5)
GSF: Glencoe Shellfish farm (experimental site, section 3.1 and Fig.5)
h: Hour
HE: Highland Enterprise
HIDB: Highlands and Islands Development Board
HPLC: High-performance liquid chromatography (section 6.4.1)
ICES: International Council for Exploitation of the Sea
J: Joule
K_2:   Net growth efficiency (section 3.8.5)
Kcal: Kilocalorie
kg: Kilogramme

km:	Kilometre
KSF:	Kishorn Shellfish farm (experimental site, section 3.1 and Fig.6)
L:	Shell length (section 3.4)
l:	Litre
LE:	Loch Etive Shellfish farm (experimental site and stock, section 3.1 and Fig.4)
LE→LL:	Mussels transferred from Loch Etive to Loch Leven (section 3.2.2)
LL:	Loch Leven (used to indicate stock)
LL→LE:	Mussels transferred from Loch Leven to Loch Etive (section 3.3.2)
LW:	Live Weight (section 3.4)
m:	Meter
μm:	Microgramme
μm:	Micrometer
min:	Minute
ml:	millilitre
mm:	Millimetre
mon:	Month
MY:	Meat yield (section 3.7)
NH$_4$-N:	Ammonia excretion (section 3.8.4)
nm:	Nanometre
ng:	Nanogram
O:N:	Oxygen to nitrogen ratio (section 3.8.4)
OTC:	Oxytetracycline
P:	Production (section 3.6)
PIM:	Particulate inorganic matter (section 3.2.5)
POM:	Particulate organic matter (section 3.2.5)
PSP:	Paralytic shelfish poisoning
R:	Respiratory energy expenditure (section 3.8.5)
s:	Second
SE:	Standard error of mean
SGR:	Specific growth rate (section 3.4)
SFIA:	Sea Fish Industry Authority
SFG:	Scope for growth (section 3.8.5)
SMBA:	Scottish Marine Biological Association
SOAFD:	Scottish Office Agriculture and Fisheries Department
SS:	Stirling Salmon farm (experimental site, section 3.1 and Fig.4)
SWCL:	Scottish Wildlife and Countryside Link
t:	Tonnes
TLC:	Thin-layer chromatography (section 6.4.1)
U:	Energy lost as excreta (section 3.8.5)
VO$_2$:	Respiration rate (section 3.8.3)
vs:	Versus
W:	Weight
WMW:	Wet meat weight (section 3.4)
yr:	Year
Z:	Instantaneous mortality rate (section 3.5)