MUSSEL CULTURE IN BRITISH COLUMBIA: THE INFLUENCE OF SALMON FARMS ON MUSSEL GROWTH AND BIOCHEMICAL COMPOSITION

by

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ABSTRACT

To realise the potential for mussel culture in British Columbia, mariculture research must identify specific environments and suitable locations which promote maximum growth in mussels. The present study investigates the possible advantages, through nutritional enrichment, of salmon farms as sites for mussel culture.

Mussels were cultured at different distances around two salmon farms on the east coast of Vancouver Island (Departure Bay and Genoa Bay). Three parameters of mussel growth: condition index, carbohydrate content, and crude protein content were monitored at 3-6 wk intervals from September 1988 to August 1989. Distinct seasonal differences in growth were observed, but distance from the farm did not substantially influence mussel growth. Adult mortality and larval settlement were similarly unaffected.

Contrary to prediction, the farms did not increase available food for mussels. Measures of seston and chlorophyll concentration, made concurrently with the mussel collections, indicated that neither a direct contribution of nutrients in the form of feed and fish faeces, nor an indirect contribution of waste ammonia to augment phytoplankton production, occurred. This was despite currents flowing, at least part of the time, in such a direction as to transport potential nutrients from the farms to the mussels.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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INTRODUCTION

Culture of mussels for food has extended over the past seven centuries (Bardach *et al.*, 1972), and the edible mussel *Mytilus edulis* has dominated the world harvest of these bivalves. This cosmopolitan species is endemic to British Columbia and is often abundant in intertidal and shallow subtidal zones. A potential thus exists for mussel culture in British Columbia but, to realise this potential, mariculture research must focus on identifying specific environments which promote maximum growth of mussels. Salmon farms are a potential location for mussel culture which warrant investigation. Wallace (1980) reported that mussels on fish-farm floats grew at twice the rate of those from sites without fish farms. The present study investigates the possible advantages, through nutritional enrichment, of culturing mussels in close proximity to salmon farms.

Nutritional enhancement for mussels growing close to salmon farms could be manifested as an increase in energy storage products, growth rate, and/or condition index. The latter is an assessment of tissue accretion relative to mussel size and will be explained in detail later. The following is a brief description of energy metabolism in mussels with an explanation of how nutritional status might be enhanced by food materials emanating directly or indirectly from a salmon farm.

Glycogen and protein are considered the primary energy storage products of mussels (Gabbott, 1983). In *Mytilus edulis* the digestive gland is the site of glycogen synthesis as well as some storage. The mantle, however, is the main site of glycogen

storage, specifically its vesicular cells which can store large amounts of this carbohydrate (Gabbott, 1983). Protein is also stored as granules in the adipogranular cells of the mantle's connective tissue matrix (Gabbott, 1983) and in the digestive gland (Thompson *et al.*, 1974). All body proteins can be regarded as secondary energy reserves, but it is unlikely that all have equal capacity to be mobilised as an energy source. For example, muscle proteins are likely mobilised before gill proteins because of the importance of the gill as a feeding structure. Slow protein turnover in essential tissues is known to exist in *M. edulis*, and protein degradation products are recycled for maintenance of essential protein components (Hawkins, 1985).

In *Mytilus edulis* the accumulation of energy storage products and their subsequent expenditure follows a seasonal cycle. Studies of seasonal changes in biochemical composititon of mussels are numerous (de Zwaan and Zandee, 1972; Gabbott and Bayne, 1973; Dare and Edwards, 1975; Widdows, 1978; Pieters *et al.*, 1979; Zurburg *et al.*, 1979; Pieters *et al.*, 1980; Zandee *et al.*, 1980; Hawkins and Bayne, 1985; Emmett *et al.*, 1987) with most work being done in Britain and Europe. The characteristics of mussel energetics identified in these studies have been generally applied to *M. edulis* in British Columbia, with only differences in the timing of the cycle being noted for local populations (Emmett, 1984; Emmett *et al*, 1987).

The seasonal cycle of accumulation and expenditure of energy storage products is closely linked to the annual gametogenic

cycle (Bayne, 1973; Gabbott and Bayne, 1973; Thompson *et al.*, 1974). In British and European populations the demand for metabolic energy decreases in summer as mussels switch from the energy-demanding gametogenesis of winter/spring to a period of reproductive inactivity (Widdows and Bayne, 1971; Bayne, 1973). Widdows (1973) and Thompson and Bayne (1974) have confirmed this decrease in metabolism in mussels during summer by showing evidence of decreased oxygen uptake by mussels in this season as compared with winter. Also, at this time, food is readily available in the form of abundant phytoplankton. Therefore, energy stores such as glycogen and proteins are accumulated during summer, and there is a concomitant rise in condition index. At this time, glycogen reserves are accumulated in both mantle and non-mantle tissues, with highest levels being present in the digestive gland and mantle (de Zwaan and Zandee, 1972; Gabbott and Bayne, 1973; Emmett, 1984).

Proteins also accumulate during summer through processes of tissue growth and granule storage (Bayne, 1973; Dare and Edwards, 1975; Pieters *et al.*, 1979; Emmett, 1984), with the majority of accumulation being through growth of non-mantle tissues (Gabbott, 1983). An increase in condition index at this time reflects increase in body mass relative to shell size.

Following summer's relatively low metabolic activity, metabolic rate gradually increases over autumn and winter due to high energy demands of gametogenesis (Widdows and Bayne, 1971; Bayne, 1973). The majority of stored glycogen is used up in

early winter. As this depletion is synchronous with oogenesis and vitellogenesis it is generally believed that during winter glycogen energy reserves are preferentially allocated to gametogenesis (Gabbott, 1975; Bayne *et al.*, 1982). Similarly, protein stored as granules in the mantle is used to support gametogenesis at this time (Hawkins, 1985).

Since food levels are low during winter, the energy required for high metabolic rate is met using energy reserves of proteins in the non-mantle tissues (Gabbott and Bayne, 1973; Dare and Edwards, 1975). The muscles, adductors and foot, show a greater decrease in percentage protein during winter months than do other organs (Zurburg *et al.*, 1978; Zandee *et al.*, 1980). The most conclusive evidence for a switch from carbohydrate metabolism in summer to dependence on protein metabolism in winter comes from Bayne (1973). This author reports seasonal differences in nitrogen excretion whereby winter mussels under temperature and nutritive stress excrete large amounts of ammonia, indicating extensive protein deamination. Mussel populations in British Columbia appear also to exhibit a winter dependence on proteins for energy metabolism. Lowered levels of total body protein during winter months (December to February) have been reported by Emmett (1984) for mussels growing in Departure Bay and Bamfield Inlet.

Thus, in winter, somatic growth in *Mytilus edulis* is minimal and somatic tissues may even be mobilised to supply energy for maintenance and gametogenesis. This decline is evident in lower

condition indices reported for this season (Gabbott and Bayne, 1973; Emmett *et al.*, 1987), and results in a lower yield of mussel meat from commercial culture operations during winter. In some B.C. mussel populations the level of energy reserves at the time of spring spawning is low and this may increase susceptibility of mussels to post-spawning mortality. A high summer mortality has been reported for B.C. mussels by Quayle (1978), Heritage (1983), Emmett *et al.* (1987), and Jamieson (1989). Insufficient food in the post-spawning period may therefore be a prime obstacle for mussel culture in British Columbia. Indeed, winter food quantity and quality have been identified as limiting factors for growth of mussels cultured on both sides of the Atlantic Ocean (Incze and Lutz, 1980; Wallace, 1980; Rosenberg and Loo, 1983).

Mussel-salmon polyculture warrants investigation because salmon farms represent a potential for constant food supply to mussels, even in the critical post-spawning months. Salmon farms provide two potential enrichment inputs to the environment. First, soluble waste such as ammonium and urea are excreted as the by-products of metabolism and these may serve as a nitrogen source for blooms of phytoplankton in the vicinty of the salmon farm. This represents an indirect nutritional contribution. Second, particulate organic waste made up of unconsumed fish meal and faeces, and containing proteins, carbohydrates, lipids, and carotenoid pigments, represents a direct nutritional contribution for mussels.

Excreted ammonium and urea can be used directly by phytoplankton and are, in fact, their preferred forms of nitrogen (McCarthy *et al.*, 1977). Alternatively, these compounds may be oxidised by blue-green algae into nitrites and nitrates before being taken up by phytoplankton (this nitrification is probably minimal because Cyanophyceae make up a very limited part of the marine phytoplankton; Lee, 1980). It is, therefore, reasonably certain that a salmon farm would generate an influx of nitrogen in several different forms to the surrounding seawater. Since nitrogen is the primary limiting nutrient for algal production in the marine environment (Ryther and Dunstan, 1971; Eppley *et al.*, 1979; Codispoti, 1989), it follows that salmon farming should augment phytoplankton production and thus increase the principal source of food for mussels.

Particulate organic materials from fish meal and faeces provide basic protein, carbohydrate, and lipid nutrients. Carbohydrates and proteins from particulate waste are readily consumed and digested. Mussels can even utilise cellulose (Crosby and Reid, 1971), a material often added to fish feed as a palatability enhancer, but one which is not digested by salmon. Some lipids, and soluble carbohydrates and protein, are likely lost as the food pellets and faeces break down in seawater. Thus, these nutrients have a reduced availability to mussels, but those obtained are readily utilised. All bivalves are capable of converting oils of the type commonly used in fish feeds (e.g., those containing a high percentage of essential w3 fatty acids) to glycogen (Castell and Trider, 1974), and mussels possess a

typical complement of enzymes for digesting carbohydrates and proteins.

Antibiotics and carotenoid pigments are lesser constituents of salmon meals, but may provide an important nutritional contribution to mussels. Carotenoid pigments are added to enhance flesh colour of salmon. Recent studies by Hertzberg *et al.* (1988) and Partali *et al.* (1989) have isolated 19-20 carotenoid compounds from the tissues of *Mytilus edulis*, including some varieties used in salmon diets, and have indicated a capacity for interconversion of carotenoids by mussels. Antibiotics are added to improve the health of salmon by curtailing the growth of pathogens, but little is known of their effect on mussels. There are, however, reports of antibiotics causing rapid shell growth in mussels (Dey and Bolton, 1978), but the effects of antibiotics on larval growth and survival appear to be highly variable and often contradictory (le Pennec and Prieur, 1977).

The amount and composition of food wastage in salmon culture varies depending upon feed composition and feed management practices employed by farm operators. Braaten *et al.* (1983) estimate that 20% of food goes uneaten by cage-reared salmon. Furthermore, digestibility figures from Gowen and Bradbury (1987) suggest that 26% of food eaten by salmon ends up as faeces. Thus, there is substantial particulate waste from salmon farms (equivalent to about 40% of all feed given), the bulk of which is organic compounds of nitrogen and carbon. These could be

directly utilised by many organisms, including mussels living in the vicinity of the farm. However, the effects of this form of enrichment are limited by the range of dispersal. Most food-wastage particles, being more dense than seawater, sink in the immediate vicinity of the farm. Gowen and Bradbury (1987), reviewing the ecological impact of salmonid farming, reported that the maximum range of dispersal for feed debris is about 120 m, but that the majority of particles settle immediately around the salmon farm.

In comparison, enrichment through metabolic by-products should be more widely dispersed since ammonium, urea, and of their oxidation products, nitrite and nitrate are soluble in seawater. Gowen and Bradbury (1987) estimate that 68-86% of the nitrogen consumed by salmon is excreted. Thus, a considerable influx of nitrogen exists to enhance phytoplankton quality or abundance in the vicinity of salmon farms.

If mussels are cultured close to salmon farms they may gain a continuous food supply, resulting in a higher "scope for growth" (energy available for growth and reproduction) throughout the year, and possibly decreased time to reach market size (50-75 mm). This could enhance the productivity of mussel culture operations and would reduce production costs with obvious benefit to commercial growers. This study investigated the potential of mussel-salmon polyculture in British Columbia from the perspective of enhanced mussel growth. Two salmon-farm sites were studied, and analyses of condition index, glycogen content, and crude protein content in mussels suspended at different

distances from the farms, as well as measures of chlorophyll and seston concentration at these same distances, were used to assess possible enhancement.

METHODS AND MATERIALS

Sites and Culture Technique

Mussels *(Mytilus edulis)* were cultured at two salmon farms on the east coast of Vancouver Island, one in Departure Bay near the Pacific Biological Station, and the other in Genoa Bay (Fig. 1). An identical investigation of the potential of mussel-salmon polyculture was carried out at each site, although no direct comparison was intended because of differences in environment and operation at the salmon farms. However, it was hoped that use of two sites would indicate between-site variation in mussel culture and provide more information on the practicality of polyculture with salmon. At the Departure Bay farm the water was 20-25 m deep and the current travelled at a mean speed of 2.7 $cm \cdot s^{-1}$ (in the period monitored). Temperatures ranged from 2.1 ^{o}C in February to 18.5 ^{o}C in August; salinities ranged from 19.0 ‰ in February to 32.0 ‰ in May. In Genoa Bay, water depth was 10-15 m in the vicinity of the farm and currents averaged 1.5 $cm \cdot s^{-1}$ (in the period monitored). Temperature and salinity data were not taken at this site. At both salmon-farm sites mussels were deployed at four stations: 3 m, 15 m, and 75 m from the perimeter of the farm, and at a control station (Fig. 2). The control station was located such that, as much as possible, the mussels were isolated from the farm but not subjected to markedly different environmental conditions. The stations were sited along a west-east axis in Departure Bay and a

Figure 1. Location of study sites at Departure Bay and Genoa Bay on the east coast of Vancouver Island, and location of source mussels in Indian Arm and Okeover Inlet.

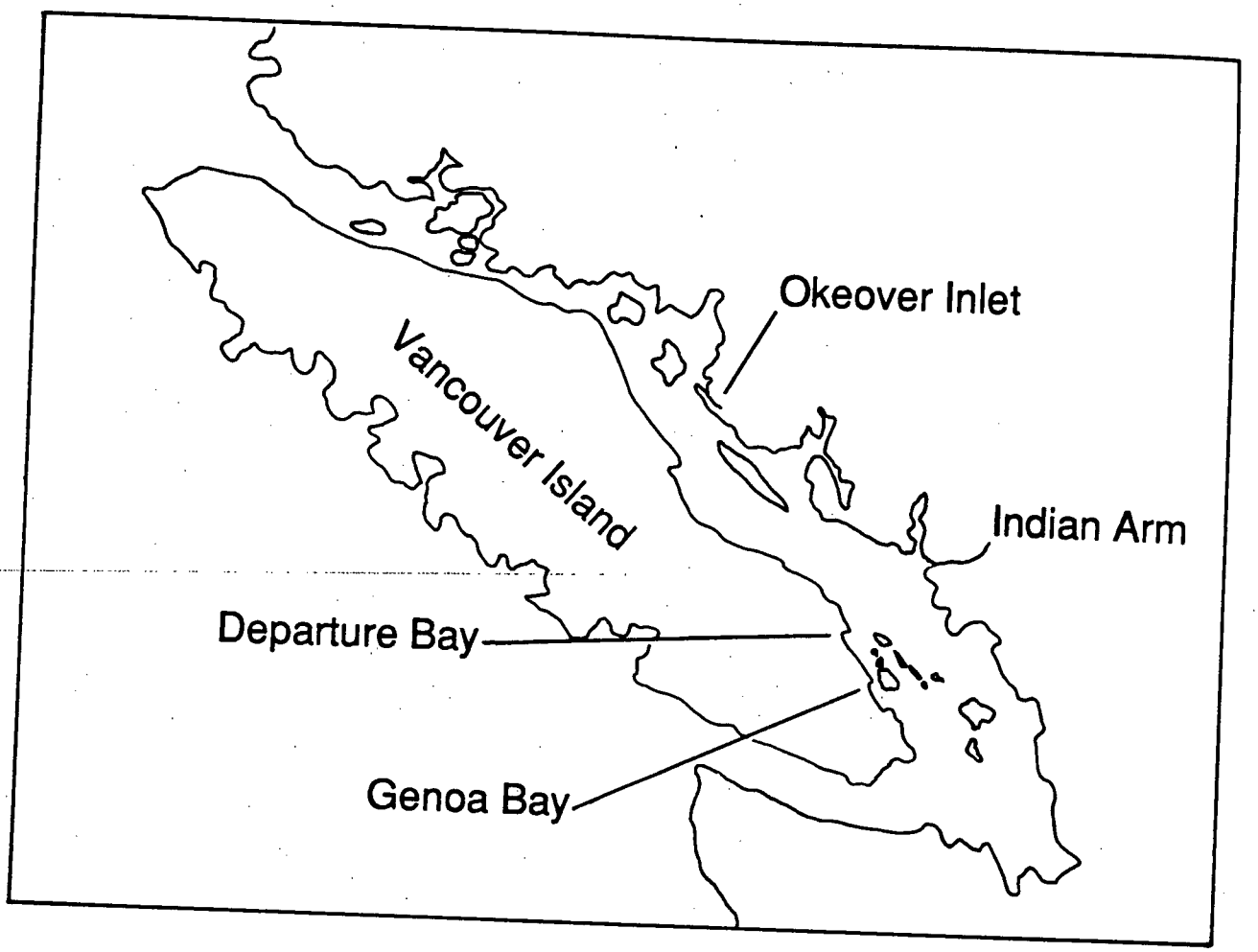
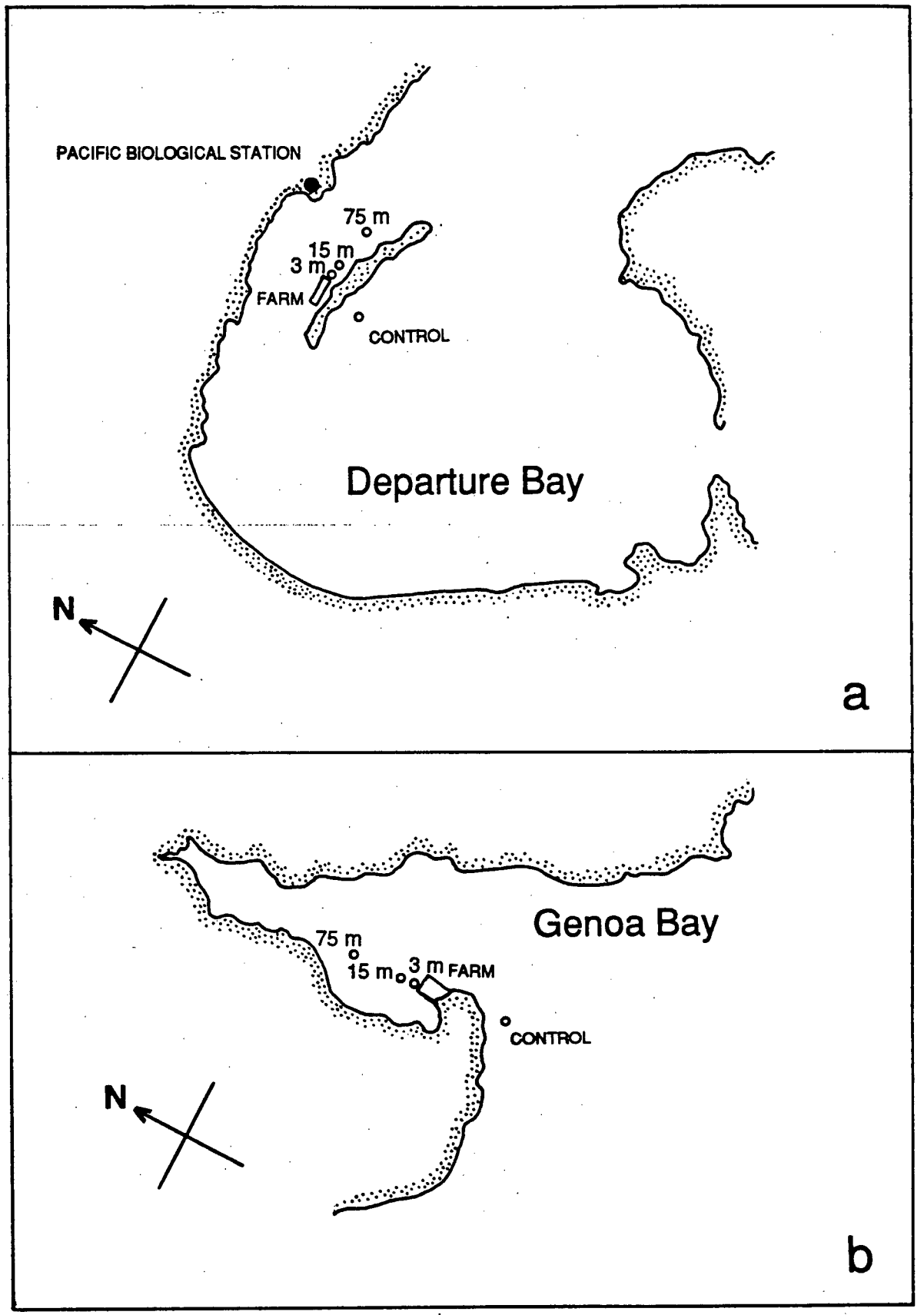

Okeover Inlet
Vancouver Island
Indian Arm
Departure Bay
Genoa Bay

Figure 2. Site-diagrams of a) Departure Bay and b) Genoa Bay showing the array of stations 3 m, 15 m, and 75 m from the farm, and a control station physically separated from the farm.

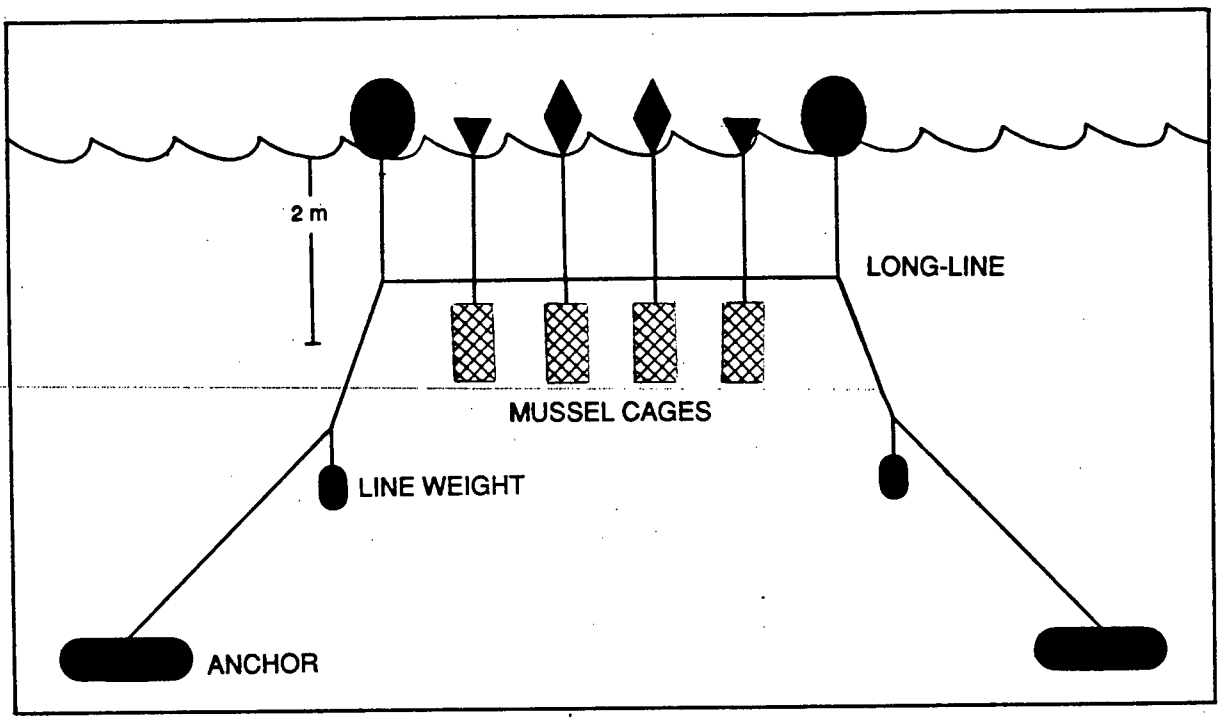

PACIFIC BIOLOGICAL STATION
75 m
15 m
3 m
FARM
CONTROL
Departure Bay
N
a
Genoa Bay
75 m
15 m
3 m
FARM
CONTROL
N
b

south-north axis in Genoa Bay. This difference was obligatory due to the topographical features of the two sites.

Four groups of mussels were hung in separate cages at each station at each site. The cages were closed cylinders (0.8 X 0.4 m diameter) of vexar mesh (2 cm). Suspended culture is known to eliminate benthic predators (e.g., crabs and starfish) and enhance growth since the mussels are afforded continuous access to food. In British Columbia use of protective enclosures is also necessary to exclude pelagic predators such as pile perch (when the mussels are small; e.g., < 14 mm), and scoter ducks (when the mussels are larger). Cage treatment was replicated four times at each station to obtain a measure of intra-station variability and to provide back-up in the event that a cage might be lost to storms, boats, or in other ways. Each cage was suspended from the floats of an anchored long-line set out parallel to the perimeter of the farm at the appropriate distance, and with its centre approximately 2 m beneath the surface (Fig. 3). By culturing at 2 m, fouling on the cages and mussels by algae, barnacles, bryozoans, mussels, sponges, tunicates and other organisms was reduced.

The initial intent was to use mussel spat collected from the bay around each salmon farm. To this end, mussels were obtained at the early juvenile stage in June 1988 by suspending traditional "collectors" from the floats of the salmon farms. The collectors were 3-m lengths of well-weathered, 2-cm diameter polypropylene rope which had been coiled and weighted such that

Figure 3. Long-line system for culture of mussels suspended within protective cages. This system was used at all stations at both sites.


2 m
LONG-LINE
MUSSEL CAGES
LINE WEIGHT
ANCHOR

they hung in the top 0.5 m of the water where settlement is heaviest (Chipperfield, 1953). However, these mussel spat were consumed by predators at both sites before the need to enclose them in protective cages was recognized. The lost animals were replaced with mussels from two sites on the mainland coast (see Fig. 1). The mussels ultimately cultured in Genoa Bay came from Indian Arm, and these were collected by the same method described above. In September 1988, 16 of these collectors with attached mussels were enclosed in the cages and deployed at the Genoa Bay site. The Departure Bay mussels were replaced in October 1988 with animals purchased from a commercial grower in Okeover Inlet. These mussels had settled during summer 1988, and had been stripped from the long-lines of an oyster farm and placed in 3-m lengths of net tubing known as "socks". Sixteen of these socks were coiled inside cages and deployed at the stations in Departure Bay. Thus, the mussel stocks at the two sites differed both in source and in attachment substrate within the cages.

Mussel Sampling

Sampling of experimental animals began when the mussels were deployed at each site (September 1988 in Genoa Bay and October 1988 in Departure Bay), and continued at 3-6 wk intervals until August 1989. The more frequent sampling occurred in the summer of 1989 when mussel growth was anticipated to be most active. Samples were always taken during daytime low tide. At each sampling time, approximately 15 cm of rope or sock were removed from the stock within each cage (for some samples later in the

study it became necessary to use mussels which had migrated to the sides or bottoms of the cages, but these appeared to be healthy, firmly attached, and of a size comparable to ones sampled from other cages at the same station). All mussels were handled as gently and as quickly as possible during sampling to minimise stress. At sampling times the mussel cages remained out of water for 2-10 min depending upon whether or not fouling growth had to be removed from the cages. Following sampling the mussels were taken to the laboratory and kept frozen at -40 ^{o}C until analysed.

Data Collection

Four growth parameters were monitored in the cultured mussels: 1) shell length, 2) condition index, 3) carbohydrate content, and 4) crude protein content.

1. **Shell Length**

Shell length (maximum anterio-posterior dimension) was likely a less useful measure of total body size than other measures because of variability in the allometric relationships between length and other shell dimensions. However, it provided a quick overview of growth among mussels in any given sample as well as a convenient means to get standardised subsamples from the 15-cm samples taken from each cage. The shell lengths of all mussels obtained from each cage were measured using electronic calipers. A length-frequency histogram generated from these data identified the modal length-class of the sample; mussels of this

length-class were then used for further analyses. Concurrent with measuring shell lengths, a semiquantitative measure of mortality was taken for each sample. Moribund and dead mussels were counted, and their shell lengths measured to determine both seasonal pattern of mortality and whether or not mortality was evenly distributed throughout the size range of a given sample. The mortality censuses were, however, not completely accurate because: a) breakdown and loss of empty shells was rapid, and b) identification of dead but not yet decaying mussels in the frozen state was difficult. These factors may have caused an underestimation of mortality.

2. **Condition Index**

Condition index was used to relate amount of shell to living tissue in the mussels, thus indicating their market quality and apparent health. Condition index was assessed as:

$$\text{CONDITION INDEX} = \text{DRY TISSUE WT } (\text{DRY SHELL WT})^{-1}(100)$$

The above was chosen because Davenport and Chen (1987), in a comparison of various methods used to assess condition index, found it to be accurate and to employ stable and easily measured parameters. Condition index was assessed for each of 10 mussels of modal length from the samples taken from each cage at each station and site. The shell and tissue of each mussel were separated and dried to constant weight at 90 ^{o}C in pre-weighed aluminum weighing pans. Prior to drying, shells were stripped of all fouling growths (e.g., byssus threads, barnacles, and

bryzoans) and all byssus threads were removed from the body. This was done for the sake of consistency because threads were inadvertently removed from some mussels during sampling.

Because mussels were frozen immediately after sampling, some food remnants regularly remained in the gut and were included as tissue weight. A separate investigation was undertaken to assess the magnitude of this error source. Twenty mussels ranging in length from 26-59 mm were suspended near the Departure Bay site and allowed to feed for 24 hrs. These mussels were then placed in individual 400 ml beakers in the laboratory and kept without food for 18 hr to allow them to void their guts. The faeces were filtered onto pre-weighed filter papers (Whatman GF/C) and dried to constant weight at 60 ^{o}C. The dry weight of gut contents in the mussels was then estimated from the measured weight of faeces using an absorption efficiency of 76% (mean of reported values for *M. edulis* at 5-15 ^{o}C: Widdows and Bayne, 1971; Vahl, 1973). Each animal's tissues were also dried to allow comparison of estimated dry weight of gut contents to its dry tissue weight. Results showed that gut contents accounted for only 5 $\pm$ 4 S.D.% of the dry tissue weight for the range of animals used (which encompasses the size range of most mussels analysed over the course of the study). This does not account for the soluble components of the faeces, however, even if these amounted to 25% of the total faecal weight this would only increase the gut contents to 8.2% of the dry tissue weight. Thus, inclusion of gut contents in the dry tissue weights of mussels probably represented only a small error source throughout the course of

the experiment, and no correction was applied to account for this non-tissue weight.

3. **Carbohydrate**

Carbohydrate, predominantly glycogen, is the primary energy storage compound in mussels (Gabbott, 1976) and, as noted previously, a measure of carbohydrate content is a good indication of metabolic state in bivalves (Gabbott and Stephenson, 1974). Carbohydrate was assessed as percentage dry tissue weight in each of 10 mussels from the identified modal length-class of the samples from each cage at the 3-m (closest to the salmon farm) and control stations at each site. It was expected that any influence of the salmon farm on mussel growth or energy reserve would be most evident in a comparison of these widely spaced stations. For carbohydrate analysis the tissues of each mussel (with byssus threads removed) were homogenized with a Brinkman Polytron tissue grinder and then lyophilised. Carbohydrate content was measured using the phenol-sulfuric test of Dubois *et al.* (1956). The colourimetric assay was done in triplicate for each mussel.

4. **Crude Protein**

Measurement of crude protein content afforded an assessment of bioaccumulation of the mussel's secondary energy storage product. The lyophilised mussel tissue remaining after carbohydrate analysis was used to determine crude protein content (thus, only mussels from the 3 m and control stations at each

site were analysed). To have sufficient lyophilised tissue for crude protein analysis, the tissues of all 10 mussels sampled per cage were combined. Each combined sample was analysed in duplicate using a modified selenium-catalyst Kjeldahl method (Williams, 1984). Nitrogen in the tissue was converted to ammonium sulfate by wet-acid digestion using a mixture of H_2O_2, H_2SO_4, and a $LiSO_4$/Se catalyst which aided in decomposition of more resistant organic molecules. Ammonia in the acid digest was reacted in series with salacylate/nitroprusside and a sodium hypochlorite solution to yield a green colour reaction which was read at 660 um in a Technicon Autoanalyser II. The nitrogen content of the tissue was converted to crude protein content by:

$$\% \text{ CRUDE PROTEIN} = \% \text{ NITROGEN} \quad (6.25)$$

and expressed as percentage dry tissue weight.

5. **Spat Density**

Settlement of mussel spat at each site was used as a further measure of salmon-farm influence on mussel vitality. In May 1989 spat were stripped from 5-cm lengths of 2-cm diameter polypropylene rope. These ropes were part of the support structure of the mussel long-lines and the salmon farms, rather than being specifically designed collectors. Three replicate samples were taken at each station and from within a salmon pen at each farm-site. The mussels in these samples were counted and density data compared with respect to distance from the farm.

6. **Chlorophyll and Seston**

Concurrent with each 3-6 wk mussel sample, 6 seawater samples of 0.5 L were taken at each station using a Van Dorn sampling bottle. The samples were taken from 2 m below the surface, the same depth at which the mussels were cultured. These samples were used to determine chlorophyll and seston concentrations at each station at both sites.

Chlorophyll analyses were performed in triplicate using a technique adapted from Parsons *et al.* (1984). Modifications to the technique included: 1) storing phytoplankton-bearing filters at -15 ^{o}C in glass vials containing silica gel as a desiccant for up to 6 wk, 2) shortening the time required for acetone-extraction of the pigments by sonicating the samples, and 3) measuring pigment concentrations using a Perkin-Elmer Spectrophotometer with a path length of 1 cm. Admittedly, chlorophyll is not a precise measure of the amount of food available to filter feeders since the ratio of chlorophyll to carbon varies considerably with the type and nutritional state of phytoplankton. Generally, however, the dry weight of phytoplankton is considered to be an order of magnitude greater than the weight of chlorophyll.

Determinations of total seston concentration (total suspended particulate matter) were also done in triplicate using a technique adapted from Strickland and Parsons (1972). Seawater samples were passed through a 120 um screen and then

vacuum-filtered onto pre-weighed millipore filters of 0.22 um porosity. The combination of pore size in screen and filter excluded zooplankton and large seston, but retained bacteria (although there is some debate as to whether mussels can feed on bacteria). Thus, all particles within the size range for feeding by mussels were measured, as were some possible non-food items. The filters were dried to constant weight at 60 ^{o}C and the dry weight of seston measured. Change in weight due to hygroscopicity of the filters was eliminated by including 3-5 blank filters (wetted with distilled water and dried) with each sample group.

Seston consisted of the total suspended particles in a seawater sample and likely included some non-food items (inorganic particles, and organic particles which were, by virtue of size, inedible for mussels). Therefore, the measured seston concentration presumably over-estimated available mussel food. In contrast, the chlorophyll concentrations likely under-estimated available food because mussels can feed on detritus and possibly bacteria in addition to the phytoplankton.

To obtain a more detailed estimate of the contribution to seston concentration made by salmon meal, a series of water samples were taken from the 3-m station at Departure Bay every 2 hrs for 24 hrs. These samples were collected in November when phytoplankton was scarce. Chlorophyll and seston were measured as above.

7. **Currents**

For a salmon farm to contribute nutrients directly to polycultured mussels, the water current would have to flow first past the salmon farm and then to the mussels. Current patterns were monitored at the two salmon-farm sites using an Interocean Systems Model 135 current meter at the Genoa Bay farm (February, April, July, and August 1989) and an AANDERAA temperature/salinity/current meter at the Departure Bay farm (March-June 1989). The model 135 meter recorded continuously for 4-5 d after each deployment, whereas the AANDERAA meter made recordings every 15 min throughout its deployment. The current meters were sited between the salmon farm and the mussel long-lines. The model 135 meter was kept at 2 m depth (the same as mussel culture) while the AANDERAA meter was installed at 10 m (in accordance with the pre-emptive needs of a scallop culture programme being conducted by the Pacific Biological Station).

8. **Statistical Analyses**

Growth data, except crude protein content, were analysed with 3-way Analyses of Variance (ANOVA) using the General Linear Models program of SAS (Statisical Analysis System) at the Pacific Biological Station. Crude protein content was analysed with a two-way ANOVA with cage treatment omitted since samples from the cages were pooled for protein analysis. A separate ANOVA was run for each growth parameter at each farm. Arcsine transformed data were used for the growth parameters which were measured as

percentages (i.e., condition index, carbohydrate content, and crude protein content). No statistical comparisons were made between mussels grown at the different sites owing to environmental differences between Departure Bay and Genoa Bay (e.g., water temperature, freshwater run-off, flushing rate, phytoplankton blooms), and owing to differences between the culture programmes at each salmon farm (e.g., feed type, feeding regime, as well as number, size, and species of fish). Chlorophyll and seston data were analysed using the same SAS package but with 2-way ANOVA's.

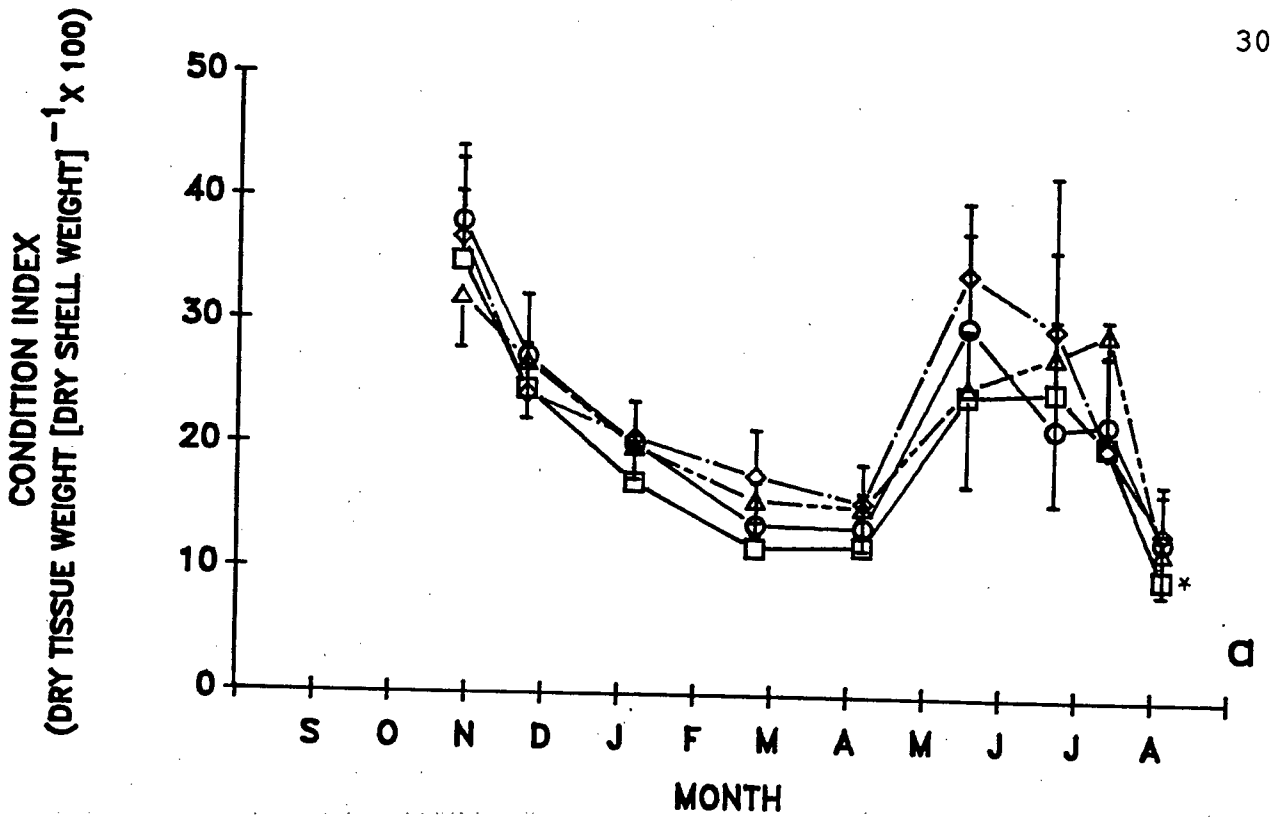
A multiple regression analysis of dry tissue weight, dry shell weight, and shell length was done using the MIDAS programme at UBC. Simple one-way ANOVAs for spat density and for the 24-hr seston series were done using the UBC Genlin programme.

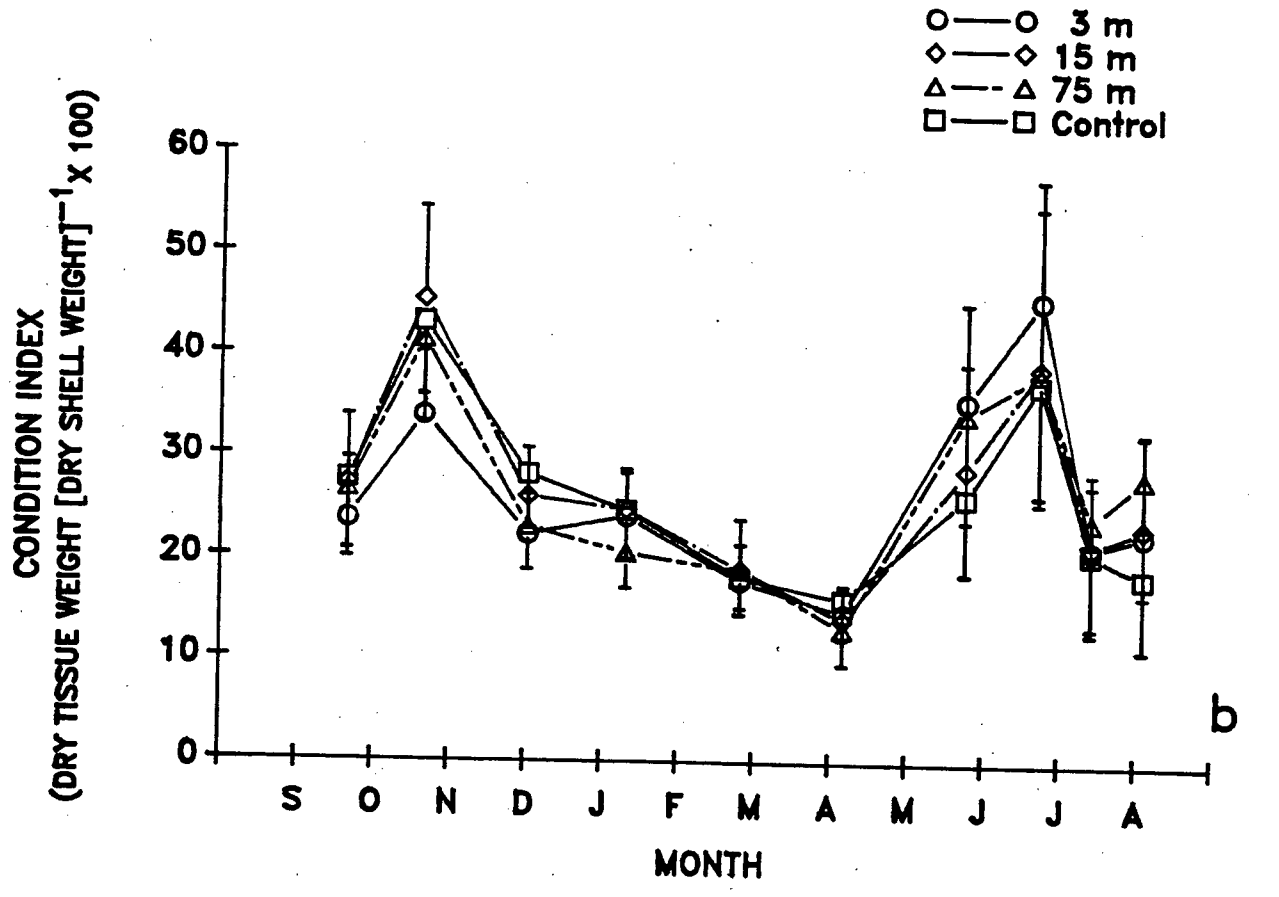
RESULTS AND DISCUSSION

1. Condition Index

Condition index was similar in magnitude and seasonal pattern at both sites. Fig. 4 illustrates monthly fluctuation of condition indices in mussels cultured at each of the four stations for both sites. Individual cages at each station have not been depicted; rather, the cage data were combined for each station because there were no significant differences between mussels cultured in separate cages at the stations (ANOVA: Departure Bay $F_{0.05(2),3,1274} = 1.2$, $p=0.62$; Genoa Bay $F_{0.05(2),3,1428} = 2.1$, $p=0.20$). Condition indices were not significantly influenced by distance from the salmon farm in Genoa Bay (ANOVA: $F_{0.05(1),3,1428} = 1.0$, $p=0.39$) but were in Departure Bay (ANOVA: $F_{0.05(1),3,1274} = 27.7$, $p<0.001$). However, the latter influence was contrary to that hypothesized. Mussels cultured at the control station had the lowest mean condition index (20.3 $\pm$ 9.4 SD%), but those at the 3-m station (22.3 $\pm$ 9.9 SD%) were significantly lower than at both 15 m (23.7 $\pm$ 10.0 SD%) and 75 m (22.7 $\pm$ 9.1 SD%) ($p<0.05$, Tukey Multiple Comparison Test: TMCT). Despite the significant distance-effect on condition index, it will be seen that other parameters of mussel growth were not similarly influenced, nor was survival. Mortality rates were similar at all stations within a site. Virtually no mortalities were recorded before June 1989 and, after this time, mortality counts rose rapidly, reaching almost

Figure 4. Monthly fluctuations in condition indices of mussels cultured in a) Departure Bay and b) Genoa Bay at different distances from salmon farms (3 m, 15 m, 75 m, and control stations) during 1988-89. Data are expressed as means $\pm$ SD, combining values for all mussels at a given station since cages comprised an homogenous set. N = 40 for all points except as indicated (*), where N = 30 due to loss of a cage.


CONDITION INDEX
(DRY TISSUE WEIGHT [DRY SHELL WEIGHT]$^{-1}$ X 100)
50
40
30
20
10
0
S O N D J F M A M J J A
MONTH
*
a


3 m
15 m
75 m
Control
CONDITION INDEX
(DRY TISSUE WEIGHT [DRY SHELL WEIGHT]$^{-1}$ X 100)
60
50
40
30
20
10
0
S O N D J F M A M J J A
MONTH
b

50% of mussels sampled in Departure Bay and 40% in Genoa Bay by August 1989.

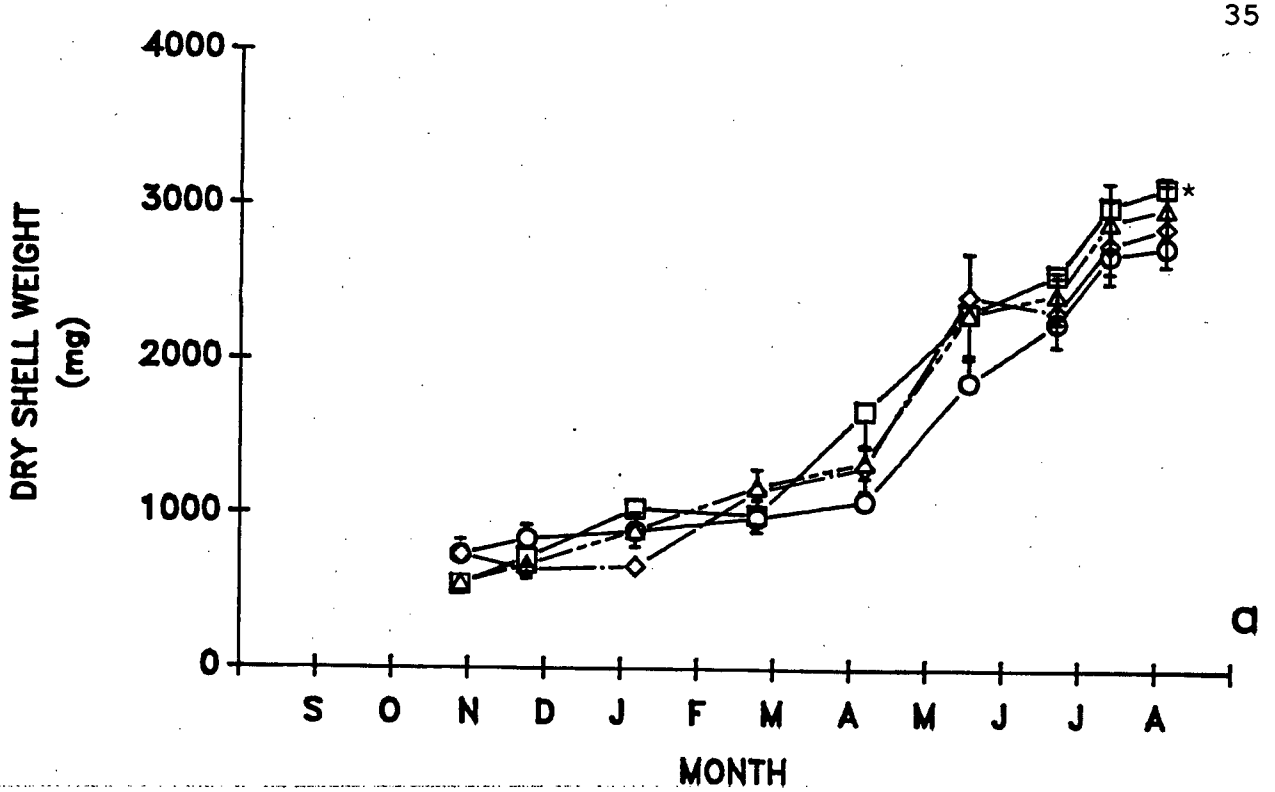
All interactive effects, with the exception of station-cage at both sites, and month-cage at Departure Bay, were highly significant, e.g., month-station (ANOVA: Departure Bay $F_{0.05(2),24,1274} = 14.6$, $p<0.001$; Genoa Bay $F_{0.05(2),27,1428} = 14.0$, $p<0.001$), month-cage (ANOVA: Genoa Bay $F_{0.05(2),27,1428} = 3.6$, $p=0.01$), month-station-cage (ANOVA: Departure Bay $F_{0.05(2),71,1274} = 4.0$, $p<0.001$; Genoa Bay $F_{0.05(2),80,1428} = 4.5$, $p<0.001$). Month-station effects may have resulted from positioning of the stations since this may have generated station differences which were more pronounced in certain months. For example, at Departure Bay, the 3 m and 15 m stations were sited close to the north shore of an island and were usually shadowed by it, the 75 m station was further off the north shore and was less shadowed, while the control was sited on the south side of the island and received the most sunlight. An influence on mussel growth generated by a differential exposure to sunlight would be most pronounced in summer. Similarly, the 3 m, 15 m, and 75 m stations at Genoa bay were sited closer to a marina than the control station. With boat traffic being heaviest in the summer, any effect of boat pollution on mussel growth would have been experienced primarily by the 3 m, 15 m, and 75 m, mussels, and to the greatest degree in summer. Station position was determined by topography and the necessity to avoid boat traffic. Topographical features of the two study sites almost certainly led to differences in current flow (speed and direction) between

stations. For instance, at Departure Bay the difference in proximity to the island likely caused a difference in current flow at the stations since current near the rock wall of the island would be slower. A difference in current flow among stations in Genoa Bay was evidenced by the fact that the 3 m, 15 m, and 75 m stations were iced-over in February 1989, but the control station was not. It was not possible to monitor current flow at each station since only two current meters were available for use and one remained fixed at the salmon farm in Departure Bay. Month-cage effects may have been due to the interaction of cages with regard to current flow. Mussels in cages on the outside of the long-line may have had access to a greater water flow and therefore more food, because they were in "filtering-competition" with a mussel population on only one side whereas the two inner cages had a competing population on both sides (positioned 1 m away). This filtering competition and any resulting changes in growth parameters due to decrease in food would have been most pronounced at times when current flow was slower (perhaps in summer when there was less wind to drive currents) or when the cages were more occluded by fouling growth (barnacles, bryozoans, caprellids, macrophytes, encrusting sponges, and tunicates settled most heavily in May-July 1989). While all fouling growth was removed at each sampling time in an attempt to minimise the effects of fouling on the cages, occlusion of the mesh may have somewhat hindered mussel feeding and thus may have adversely affected mussel growth. Month-station-cage effects may reflect a difference in the month-cage interaction at different stations. Owing to patchiness of

fouling growth, stations may have exhibited differences in filtering competition in late spring and summer when fouling organisms settled and grew on the cages. Filtering competition between mussels within a cage may also have been an important influence on mussel growth. Mussel density within each cage would have been ever-changing as mussels moved, sloughed off ropes and socks, died, or were collected, and these changes would have affected the filtering efficiency of mussels. The month-station-cage interaction would have been most pronounced for the inside cages which may have experienced greater filtering competition at times of low food concentration or when water flow through the cages was impeded by fouling growth. These are the most probable explanations for the significant interactive effects identified for condition index, and they likely apply to interactive effects on other growth parameters, such as dry tissue weight, dry shell weight, carbohydrate content, and crude protein content (see later).

Monthly changes in condition indices were highly significant for mussels at both sites (ANOVA: Departure Bay $F_{0.05(2),8,1274} = 269.9$, $p<0.001$; Genoa Bay $F_{0.05(2),9,1428} = 218.4$, $p<0.001$). Mussels in Departure Bay (Fig. 4a) exhibited a significant month-to-month decline during autumn 1988 and winter 1989 ($p<0.05$, TMCT). Condition index declined from an extreme high for all stations in October (36%) to a low in February (15%). This decline actually resulted from growth of shell (Fig. 5) while body tissue remained constant (Fig. 6). Shell weight of the Departure Bay mussels (Fig. 5a) showed significant

Figure 5. Monthly fluctuations in dry shell weights of mussels cultured in a) Departure Bay and b) Genoa Bay at different distances around salmon farms (3 m, 15 m, 75 m and control stations) during 1988-89. Data are expressed as means $\pm$ SD, combining values for all mussels sampled at a given station since cages comprised an homogenous set. N = 40 for all points except as indicated (*), where N = 30 due to loss of a cage.


4000
3000
2000
1000
0
DRY SHELL WEIGHT (mg)
*
a
S O N D J F M A M J J A
MONTH

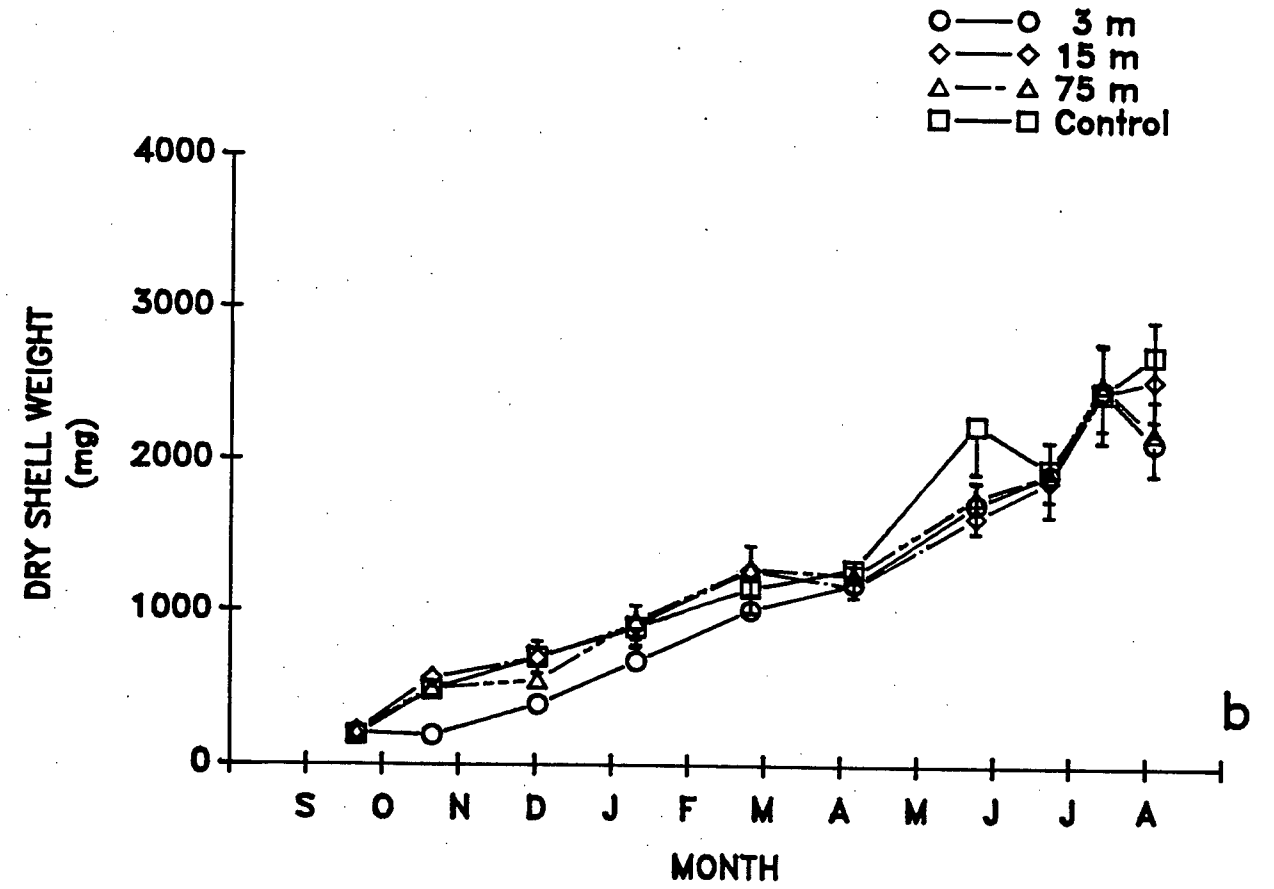
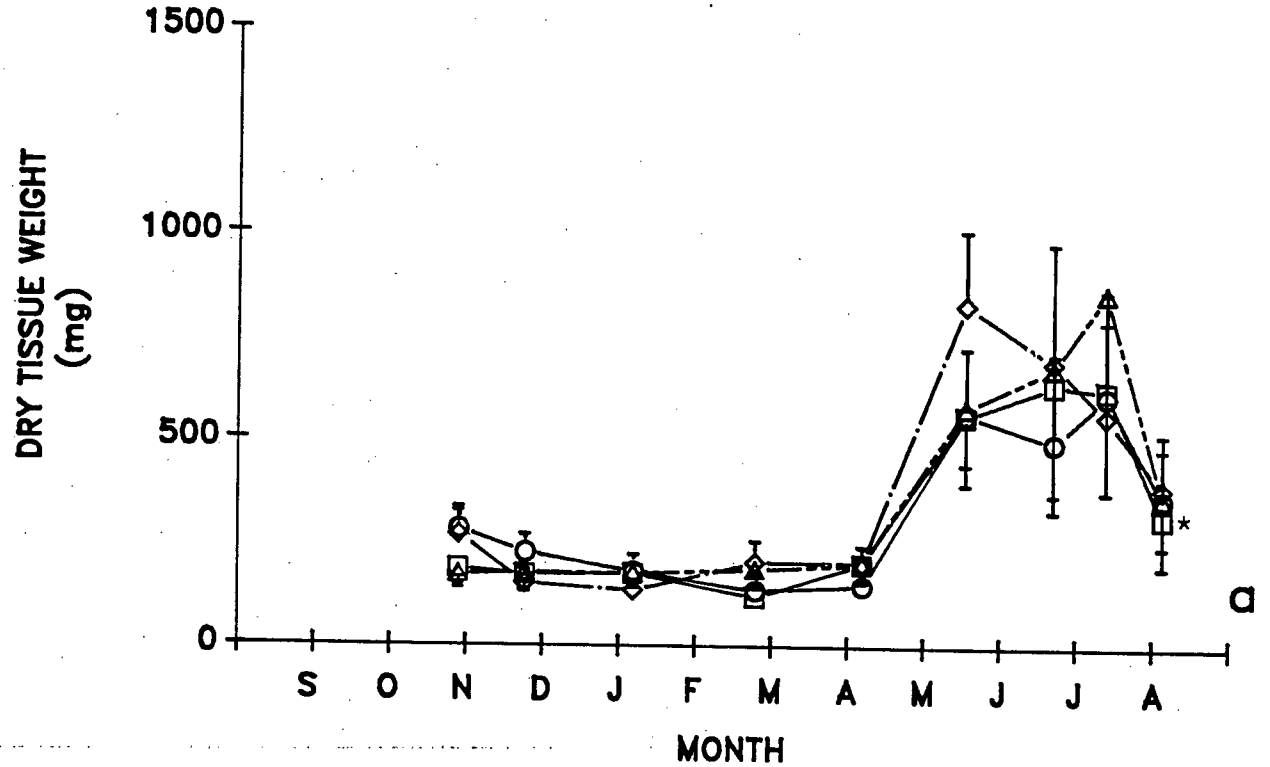
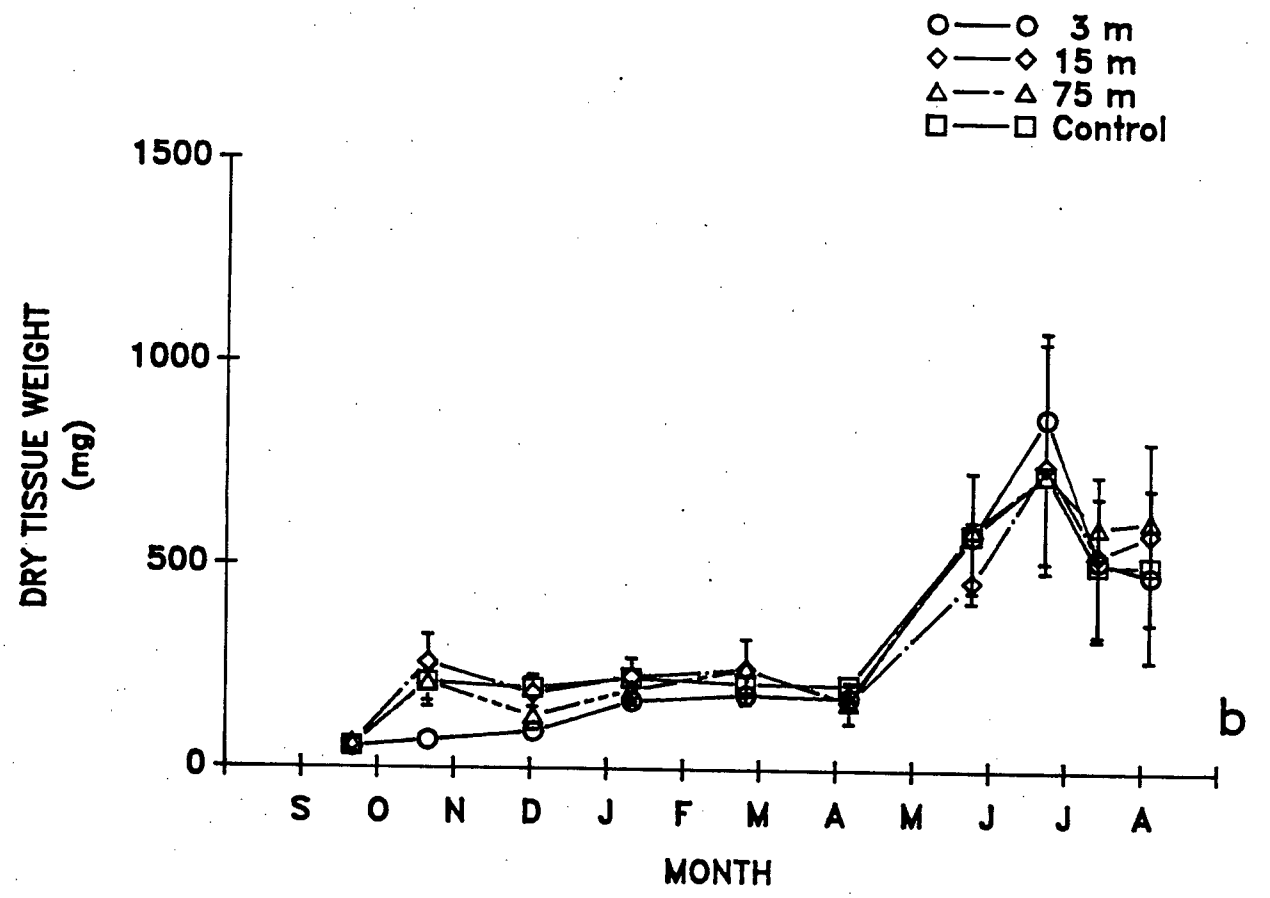

3 m
15 m
75 m
Control
4000
3000
2000
1000
0
DRY SHELL WEIGHT (mg)
b
S O N D J F M A M J J A
MONTH

Figure 6. Monthly fluctuations in dry tissue weights of mussels cultured in a) Departure Bay and b) Genoa Bay at different distances from salmon farms (3 m, 15 m, 75 m and control stations) during 1988-89. Data are expressed as means $\pm$ SD, combining values for all mussels sampled at a given station since cages comprised an homogenous set. N = 40 for all points except as indicated (*), where N = 30 due to loss of a cage.


1500
1000
500
0
DRY TISSUE WEIGHT (mg)
S O N D J F M A M J J A
MONTH
*
a


3 m
15 m
75 m
Control
1500
1000
500
0
DRY TISSUE WEIGHT (mg)
S O N D J F M A M J J A
MONTH
b

seasonal fluctuations (ANOVA: $F_{0.05(2),8,1274} = 2403.9$, $p<0.001$), with month-to-month significance during autumn and winter ($p<0.05$, TMCT), while dry tissue weight (Fig. 6a) remained constant for the same period (ANOVA: $F_{0.05(2),8,1274} = 378.7$, $p<0.001$) before increasing significantly later in spring 1989 ($p<0.05$, TMCT). Condition index then remained constant from February-April 1989 as shell growth slowed slightly (even though shell weight had increased significantly, $p<0.05$ TMCT) and dry tissue weight again remained constant. From February-April 1989 shell weight increased relative to tissue weight, but without a significant decrease in condition index. Condition index was thus only coarsely responsive to relative changes in shell weight and tissue weight during these periods, suggesting that it may be less useful as an indicator of mussel health than its common usage might imply.

Condition indices of mussels cultured in Departure Bay rose sharply in the spring, during April-May 1989, as tissue growth (seen as a significant increase in dry tissue weight, Fig. 6a; $p<0.05$, TMCT) outpaced shell growth (Fig. 5a; $p<0.05$, TMCT). Following peak spring/summer condition indices (in May for 3-m and 15-m stations, 30% and 34%, respectively; in June for control, 25%; and in July for 75 m, 30%) all treatment groups once again displayed significant month-to-month declines extending to the end of the study. The greatest decline at all stations occurred July-August 1989, and lowest mean condition indices for all sites (12%) were recorded in August. During May-August, shell weight (Fig. 5a) was still increasing significantly

($p<0.05$, TMCT), while dry tissue weight (Fig. 6a) first held constant in May-July and then dropped significantly in July-August 1989 ($p<0.05$, TMCT). Thus, Departure Bay mussels entered a wasting period in summer (recall also that mortality had reached almost 50% by August). Some of the weight loss in early summer (May-June) may have been due to spawning. Thick gamete-filled mantles were observed in mussels at both sites until June, indicating that mussels were in spawning condition until this time. After June the majority of mussels had shed their gametes.

The seasonal pattern of condition indices for mussels cultured in Genoa Bay (Fig. 4b) deviated only slightly from that described for those in Departure Bay. Initially, in September-October 1988, there was a significant increase, but from October-April there was a significant month-to-month decline ($p<0.05$, TMCT). This decline was from a mean (for all stations) of 41.0 $\pm$ 8.8 SD% in October 1988, to 14.4 $\pm$ 3.5 SD% in April 1989, and resulted from dry tissue weight (Fig. 5b) remaining constant (ANOVA: $F_{0.05(2),9,1426} = 492.7$, $p<0.001$) while shell weight was increasing significantly (ANOVA: $F_{0.05(2),9,1425} = 2641.3$, $p<0.001$). In April-June 1989 there was a significant month-to-month rise in condition index and dry tissue weight, and both peaked in June. Dry shell weight (Fig. 5a) also increased significantly over these months but peaked in July. Condition indices dropped dramatically from 40.1 $\pm$ 13.3 SD% to 21.8 $\pm$ 8.2 SD% in July, and remained at this level until the end of sampling in August 1989. It was interesting to note that the August condition index (22.9 $\pm$ 9.9 SD%), despite about a 40% decrease in

number, was significantly higher than the extreme low of April (14.4 $\pm$ 3.5 SD%) when mortality was virtually nil. This again raises the question of usefulness of condition index as a measure of market quality and apparent health of mussels.

The merit of condition indices which compare amount of body tissue to shell size and which are popularly used to assess product quality in bivalves can be assessed by the degree of correlation between dry tissue weight and either of two measures of shell size: dry shell weight and shell length. The question has been raised as to whether dry shell weight (as used in this study) or shell length is a better correlate with dry tissue weight, since both have been used for mussels (Davenport and Chen, 1987). Data were collected from 20 mussels randomly selected at the 3-m station in Genoa Bay. A regression of the log-transformed values was highly significant (ANOVA of Multiple Regression: $F_{0.05(2),3,198} = 442.6$, $p<0.001$) and was best described by the multiple regression equation:

$$\text{LOG TISS WT} = -1.165+0.250(\text{LOG SHELL WT})+0.186(\text{LOG SHELL LENGTH})$$

Considering dry shell weight and shell length separately, it is apparent that dry shell weight is the slightly more accurate predictor of dry tissue weight (dry shell weight $t_{0.05(2),1,198} = 3.6$, $p<0.001$; shell length $t_{0.05(2)1,198} = 2.7$, $p = 0.009$). Thus, either parameter could be reliably used to estimate body size in mussels and given the ease of measurement, shell length may be preferable.

The coefficient of determination for the multiple regression was high (r^2 = 0.82), suggesting that year-round, amount of tissue will be reflected with reasonable accuracy, by shell size. However, seasonal fluctuations in condition index, which became apparent during the study, indicate that the accuracy of predicting dry tissue weight based on either dry shell weight or shell length is likely to be seasonally influenced, to the point of being unreliable for comparisons between seasons.

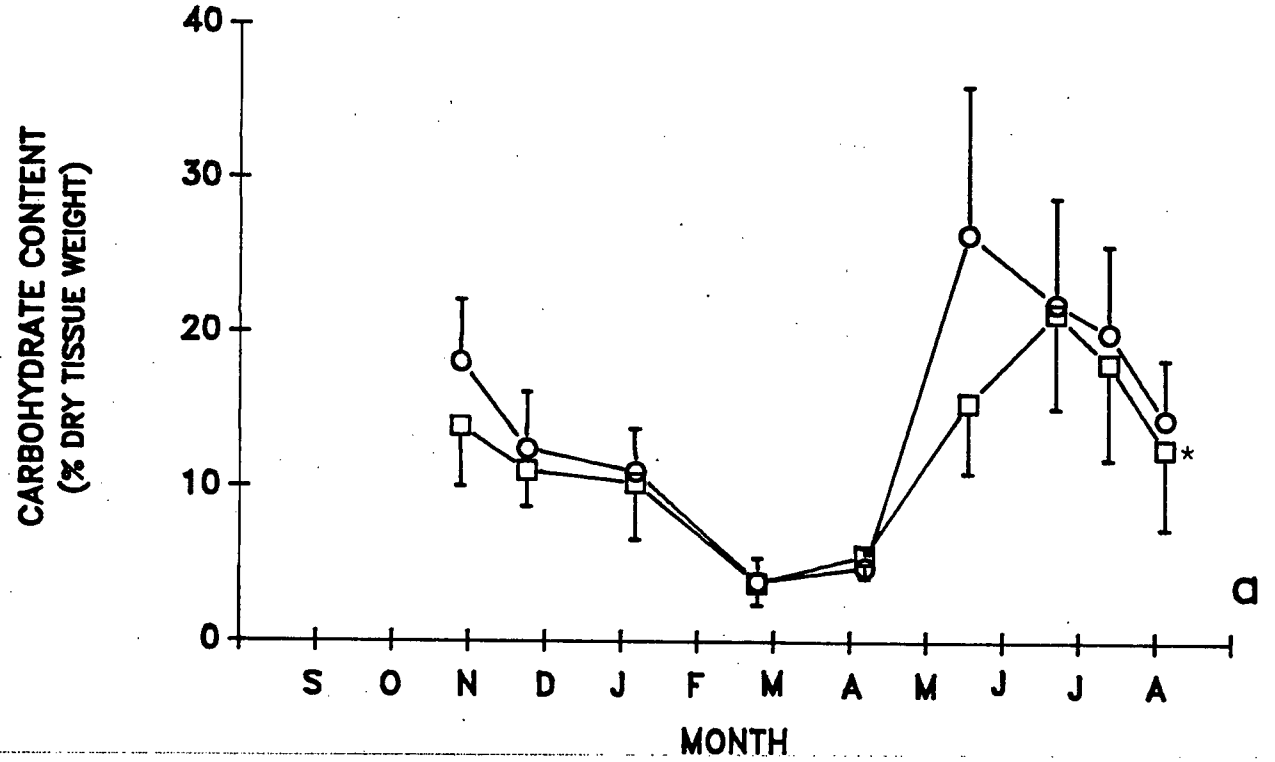
The nature of interactive effects of month, station, and cage on dry tissue and dry shell weight at both sites supports this notion of seasonal inconsistency. In all cases the month-station interaction was significant (ANOVA for dry tissue weight: Departure Bay $F_{0.05(2),24,1274} = 21.6$, $p<0.001$; Genoa Bay $F_{0.05(2),27,1426} = 10.1$, $p<0.001$; ANOVA for dry shell weight: Departure Bay $F_{0.05(2),24,1274} = 30.2$, $p<0.001$; Genoa Bay $F_{0.05(2),27,1425} = 33.6$, $p<0.001$). Other interactive effects showed a disparate degree of influence on these two growth parameters. In Departure Bay, dry tissue weight was also significantly influenced by the month-station-cage interaction (ANOVA: $F_{0.05(2),71,1274} = 3.2$, $p=0.01$) but not month-cage (ANOVA: $F_{0.05(2),24,1274} = 1.4$, $p=1.00$) or station-cage (ANOVA: $F_{0.05(2),9,1274} = 3.6$, $p=0.12$). Contrastingly, the station-cage interaction significantly influenced dry shell weight (ANOVA: $F_{0.05(2),9,1274} = 4.6$, $p=0.03$) but month-cage (ANOVA: $F_{0.05(2),24,1274} = 1.6$, $p=1.00$) and month-station-cage (ANOVA: $F_{0.05(2),71,1274} = 2.4$, $p=0.16$) did not. In Genoa Bay, dry tissue weight was significantly influenced by month-station-cage

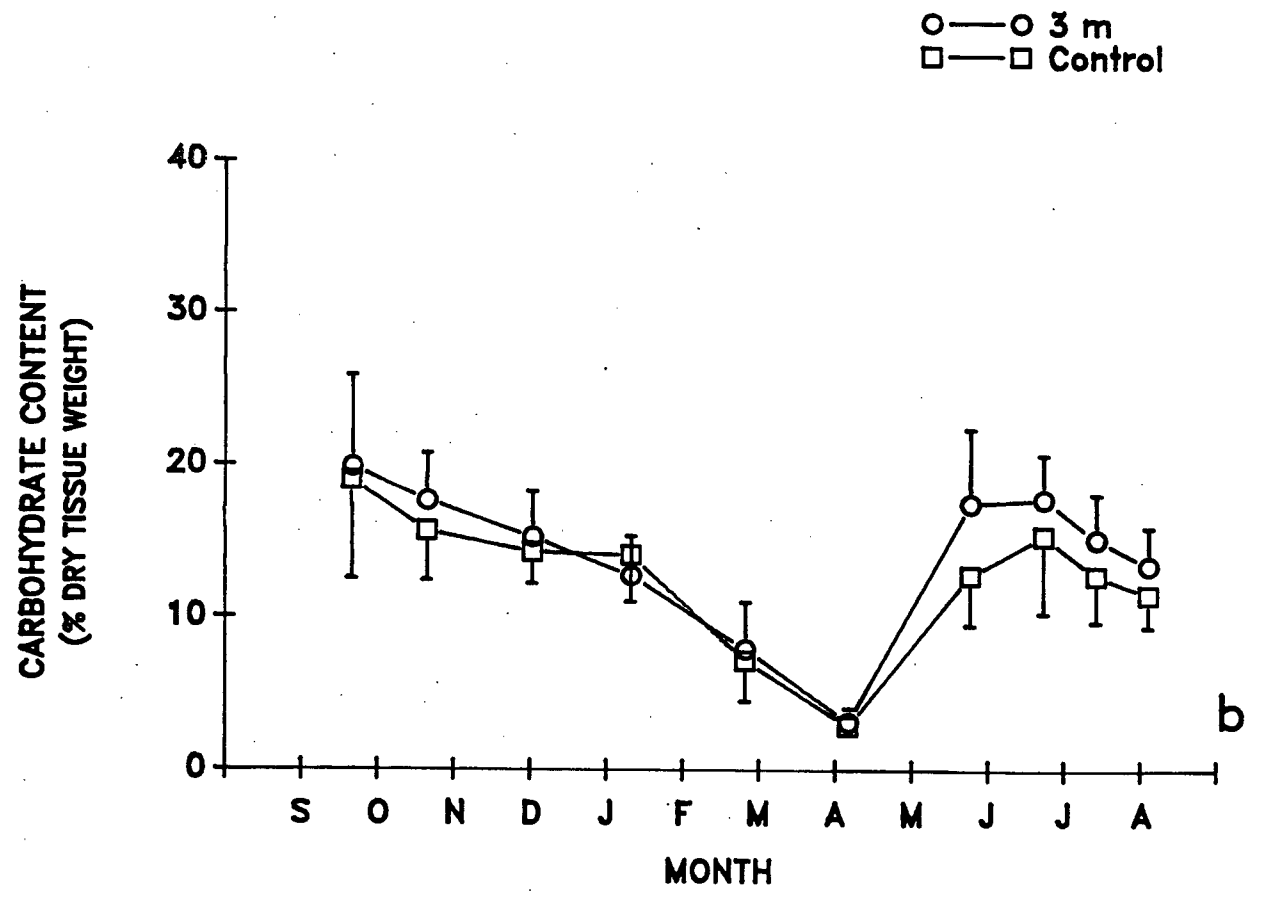
(ANOVA: $F_{0.05(2),80,1426} = 3.2$, $p=0.004$) and month-cage (ANOVA: $F_{0.05(2)<27,1426} = 3.4$, $p=0.03$) but not station-cage (ANOVA: $F_{0.05(2),9,1426} = 3.4$, $p=0.14$). Dry shell weight, however, was significantly influenced by the month-station-cage interaction (ANOVA: $F_{0.05(2),80,1425} = 2.8$, $p=0.03$) and station-cage (ANOVA: $F_{0.05(2),9,1425} = 5.4$, $p=0.01$), but not month-cage (ANOVA: $F_{0.05(2),27,1425} = 2.2$, $p=0.78$). Tissue and shell growth responded differently, or at least to different degrees, to food availability as affected by the interactions of time and location (see explanations for condition index). Thus, the relationship of tissue to shell exhibited temporal and spatial inconsistencies.

2. **Carbohydrate**

Total carbohydrate content, as a percentage of dry tissue weight, was similar in magnitude and seasonal pattern in the mussels at both sites (Fig. 7). Again only station means are shown because no significant differences were indicated among cage means (ANOVA: Departure Bay $F_{0.05(2),3,624} = 2.4$, $p=0.12$; Genoa Bay $F_{0.05(2),3,709} = 2.2$, $p=0.18$). Carbohydrate content followed the same seasonal trend as condition index, and monthly fluctuations were again highly significant (ANOVA: Departure Bay $F_{0.05(2),8,624} = 212.0$, $p<0.001$; Genoa Bay $F_{0.05(2),9,709} = 229.1$, $P<0.001$). At both sites, mussels cultured 3 m from the salmon farm had, on average, significantly higher percent carbohydrate than those at the control station (ANOVA: Departure

Figure 7. Monthly fluctuations in carbohydrate as percentages of dry tissue weight of mussels cultured in a) Departure Bay and b) Genoa Bay during 1988-89. A comparison is made between mussels cultured 3 m from the farm and at the control station. Data are expressed as means $\pm$ SD, combining values for all mussels sampled at a given station since cages comprised an homogenous set. N = 40 for all points except as indicate (*), where N = 30 due to loss of a cage.


CARBOHYDRATE CONTENT
(% DRY TISSUE WEIGHT)
40
30
20
10
0
S O N D J F M A M J J A
MONTH
*
a


3 m
Control
CARBOHYDRATE CONTENT
(% DRY TISSUE WEIGHT)
40
30
20
10
0
S O N D J F M A M J J A
MONTH
b

Bay $F_{0.05(1),1,624} = 43.2$, $p<0.001$; Genoa Bay $F_{0.05(1),1,709} = 39.7$, $p<0.001$). However, despite this, it is questionable whether differences in mean percent carbohydrate significantly influenced mussel growth. Means, which include all months, differed by less than 3% at both sites: Departure Bay 14.7 $\pm$ 8.8 SD% at 3-m versus 12.3 $\pm$ 6.7 SD% at the control station; and Genoa Bay 14.1 $\pm$ 5.9 SD% at 3 m versus 12.6 $\pm$ 5.6 SD% at the control station. If this greater store of carbohydrate energy was important to mussel production, then greater vitality and hence lower mortality of the mussels at the 3-m stations would have been expected. This was not the case. Also, note that at both sites, during summer when mortality was high the variation in carbohydrate content within mussel groups was much higher than during winter.

Increased carbohydrate levels of mussels grown at 3 m relative to those at the control occurred May-August 1989 at both sites. In B.C. waters, summer is normally a time of low phytoplankton levels but of high energy requirements for mussels. Therefore, it may be that during the low natural food levels of summer the salmon farm contributed sufficient nutrients to enhance the carbohydrate content of mussels grown close to the farm, but that during times of higher natural food concentration (i.e., during autumnal phytoplankton blooms) this minimal contribution did not generate a significant contribution to mussel nutrition. The significance of the month-station interactive effect (ANOVA: Departure Bay $F_{0.05(2),8,624} = 19.5$, $p<0.001$; Genoa Bay $F_{0.05(2),9,709} = 8.4$, $p<0.001$) was likely due

to the increased carbohydrate content of mussels cultured at the 3-m station as compared to those at the control station. Carbohydrate content was also significantly influenced by the interactive effects of month-cage in Genoa Bay (ANOVA: $F_{0.05(2),27,709} = 5.4$, $p<0.001$), and month-station-cage (ANOVA: Departure Bay $F_{0.05(2),23,624} = 4.6$, $p<0.001$; Genoa Bay $F_{0.05(2),27,709} = 3.6$, $p=0.01$), but not for station-cage, nor month-cage in Departure Bay. The significant interactive effects on carbohydrate content likely result from the same phenomena as have been postulated for differences in condition index, since these growth parameters are inter-related.

Mussels in Departure Bay (Fig. 7a) demonstrated a similar seasonal pattern of change in carbohydrate content regardless of distance from the farm. The 3-m and control stations exhibited a significant month-to-month ($p<0.05$, TMCT) decline in percent carbohydrate through autumn and early winter 1988. In February 1989, carbohydrate reached extreme lows of 3.9 $\pm$ 1.5 SD% at 3-m and 3.8 $\pm$ 1.4 SD% at the control station. After April 1989 carbohydrate levels rebounded to highs of 26.4 $\pm$ 9.6 SD% at the 3-m station in May, and 21.2 $\pm$ 6.1 SD% at the control station in June. Following this, levels rapidly declined to 14.5 $\pm$ 3.8 SD% at 3-m and 12.5 $\pm$ 5.2 SD% at the control station in August 1989.

The monthly pattern of total carbohydrate levels of mussels in Genoa Bay (Fig. 7b) resembled that of mussels in Departure Bay. Again, percent carbohydrate declined from the start of the study in September 1988 and reached extreme lows of 3.2 $\pm$ 0.9 SD%

at 3-m and 2.9 ± 0.6 SD% at the control station in April 1989. Thus, the decline was slightly more protracted in Genoa Bay as compared with Departure Bay. As in Departure Bay, following the spring low, carbohydrate content rebounded and peaked in June (17.8 ± 2.9 SD% at 3 m, and 15.4 ± 5.1 SD% at the control station). This summer high, however, was secondary to the initial carbohydrate level recorded in September which presumably reflected a high level in the juveniles in summer 1988. Following the June 1989 peak, carbohydrate content declined at both stations reaching 13.5 ± 2.5 SD% at 3 m, and 11.6 ± 2.1 SD% at the control, in August 1989.

Two further points can be made with respect to carbohydrate contents. First, at both sites the percent carbohydrate of mussels 3 m from the farm was significantly higher than the control group in October (Departure Bay: $t_{0.05(2),78} = 4.8$, $p<0.001$; Genoa Bay: $t_{0.05(2),78} = 2.8$, $p<0.01$). However, in February 1989 there was no difference between stations (Departure Bay: $t_{0.05(2),78} = 0.4$, $p>0.50$; Genoa Bay: $t_{0.05(2).78} = 1.2$, $p>0.20$) and it was only later in spring that mussels at the 3-m stations outpaced their control counterparts. This suggests that the difference between stations at each site was unlikely to have been the result of a difference which existed prior to experimental manipulation. Second, the mean percent carbohydrate of all mussels at both sites was significantly higher ($p<0.05$ TMCT) at the end of the study in August than during the spring-time low but, as already noted, mortality was almost 50% higher.

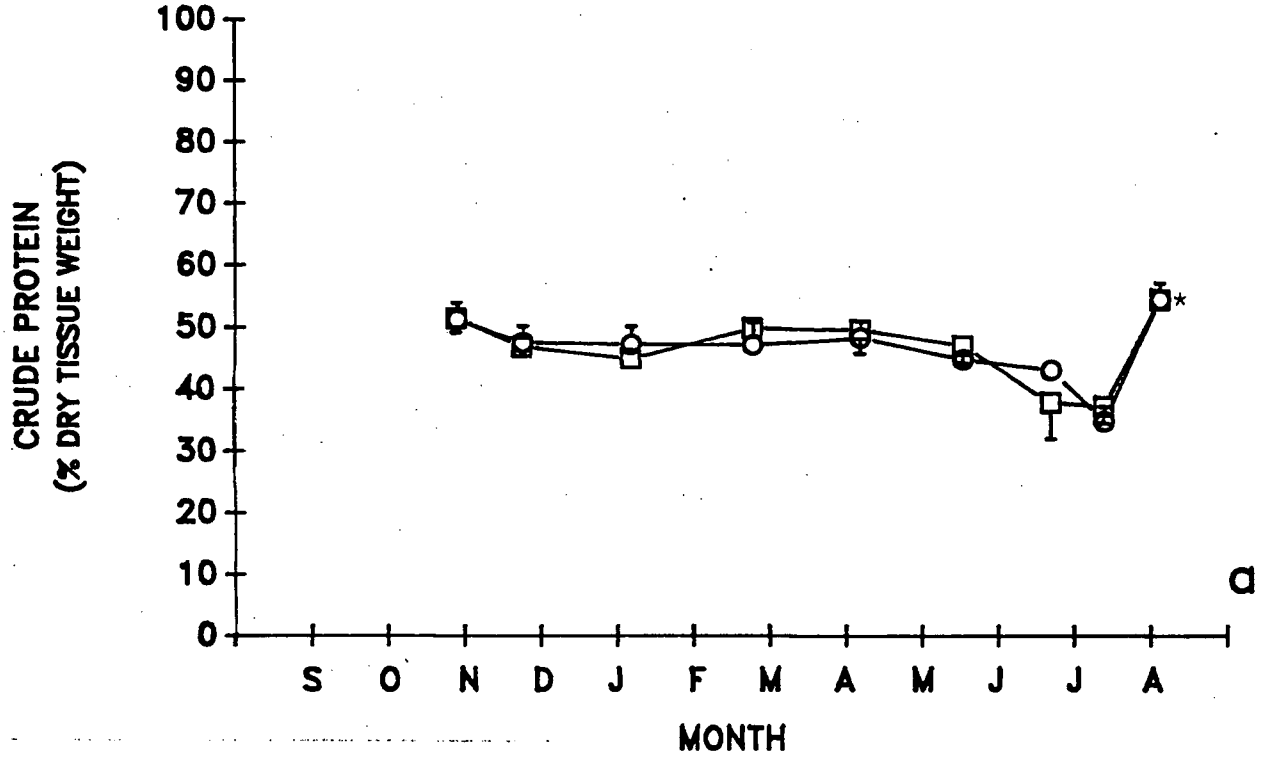
Thus, the mussels were dying despite containing an energy store in excess of 15% of their body weight.

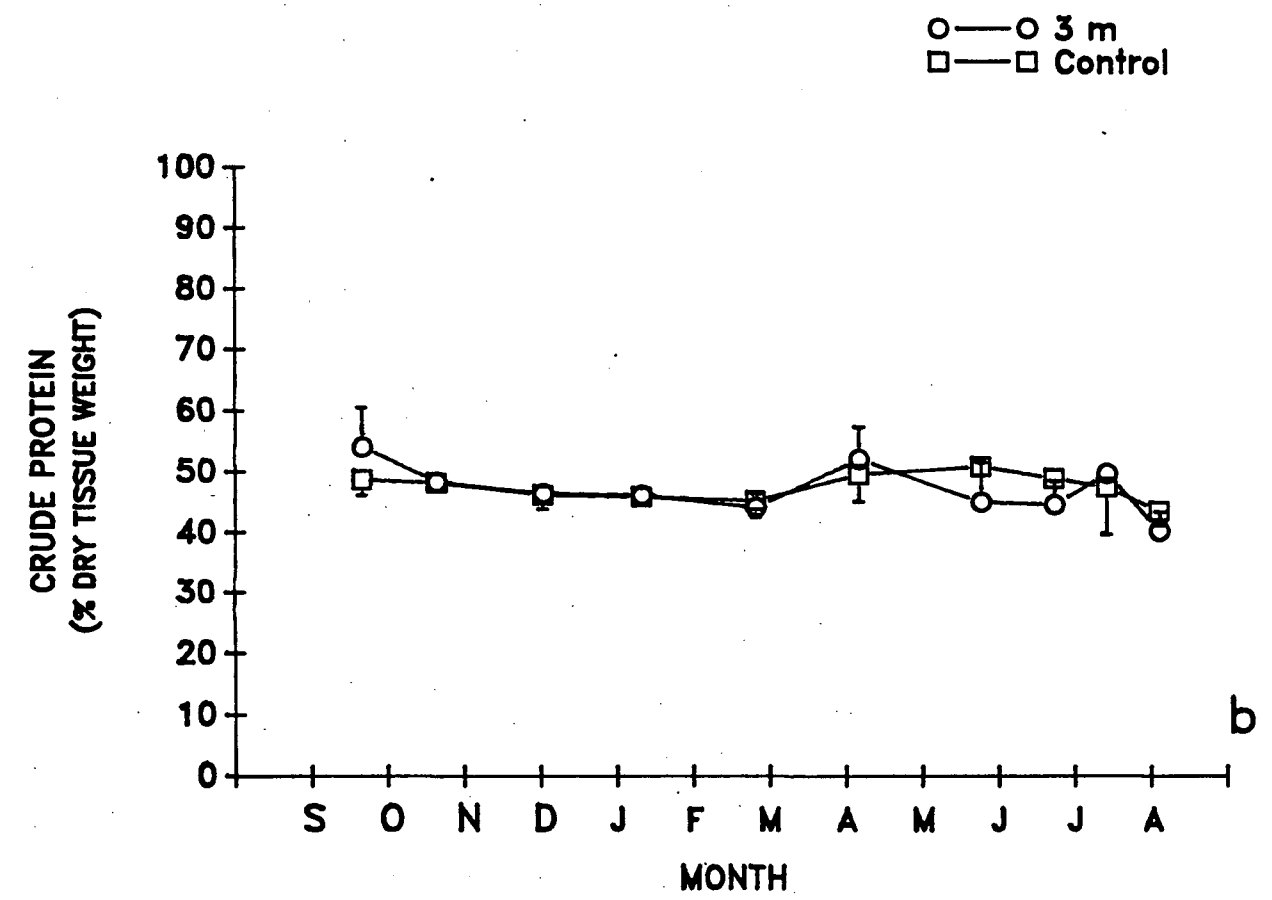
3. **Crude Protein**

In contrast to condition index and percent carbohydrate, crude protein content showed a less pronounced seasonal variation and the seasonal pattern differed between sites (Fig. 8). Since mussels from the four cages at each station were pooled for analysis, only mean values for replicate analyses on each sample are presented. There appears to have been no influence of distance from the salmon farm on percent crude protein at either site (ANOVA: Departure Bay $F_{0.05(1),1,70} = 0.00$, $p=0.97$; Genoa Bay $F_{0.06(1),1,80} = 1.48$, $p=0.23$). Monthly differences, however, were significant at both sites (ANOVA: Departure Bay $F_{0.05(2),8,70} = 128.3$, $p<0.001$; Genoa Bay $F_{0.05(2),9,80} = 27.1$, $p<0.001$). The interaction of month-station was also significant at both sites (ANOVA: Departure Bay $F_{0.05(2),8,122} = 6.8$, $p=0.003$; Genoa Bay $F_{0.05(2),9,140} = 7.0$, $p<0.001$). This interaction likely results from the same phenomena as have been postulated for growth parameters in general (see section on condition index).

Percent crude protein in Departure Bay mussels (Fig. 8a) remained almost constant at 48% from autumn 1988 to spring 1989 at the two stations. Recall that during this time dry tissue weight (Fig. 6a) was also constant, but carbohydrate was declining (Fig. 7a). This seems indicative of a conversion of carbohydrate to gametes. A significant decline in percent crude

Figure 8. Monthly fluctuations in crude protein as percentages of dry tissue weight of mussels cultured in a) Departure Bay and b) Genoa Bay during 1988-89. A comparison is made between mussels cultured 3 m from the salmon farm and at the control station. Data are expressed as means $\pm$ SD. N = 4, with each value representing analysis on the combined tissues of 10 mussels (where indicated, *, N = 3 due to loss of a cage).


CRUDE PROTEIN
(% DRY TISSUE WEIGHT)
100
90
80
70
60
50
40
30
20
10
0
S O N D J F M A M J J A
MONTH
*
a


3 m
Control
CRUDE PROTEIN
(% DRY TISSUE WEIGHT)
100
90
80
70
60
50
40
30
20
10
0
S O N D J F M A M J J A
MONTH
b

protein occurred May-July 1989 ($p<0.05$, TMCT), such that crude protein content reached a low of 36.0 $\pm$ 2.7 SD% in July 1989. This may have been a reflection of gamete release as well as some wasting as mussel condition declined. By August there was a significant rise in crude protein to 54.4 $\pm$ 2.2 SD% ($p<0.05$, TMCT). This apparent late summer increase in crude protein content may be misleading, however, based on the relatively greater loss of non-protein tissues such as carbohydrate, which have already been noted.

Genoa Bay mussels exhibited even less monthly variation in percent crude protein (Fig. 8b) than their Departure Bay counterparts. However, there was a significant drop in overall means for mussels at this site ($p<0.05$, TMCT), from 51.3 $\pm$ 5.5 SD% in September 1988 to 44.7 $\pm$ 2.5 SD% in February 1989. During autumn and winter, as with mussels cultured in Departure Bay, dry tissue weight remained steady (Fig. 6b), but percent carbohydrate dropped significantly (Fig. 7b). Presumably, the carbohydrate energy reserve was being depleted at the expense of gametogenesis, since it was not fueling protein anabolism and material was not being lost from the body. After April crude protein rose to 50.8 $\pm$ 4.9 SD% and then dropped steadily to an extreme low of 41.9 $\pm$ 3.1 SD% in August. This decline may have reflected shedding of gametes as well as a summertime wasting seen in the decreased dry tissue weight (Fig. 6b).

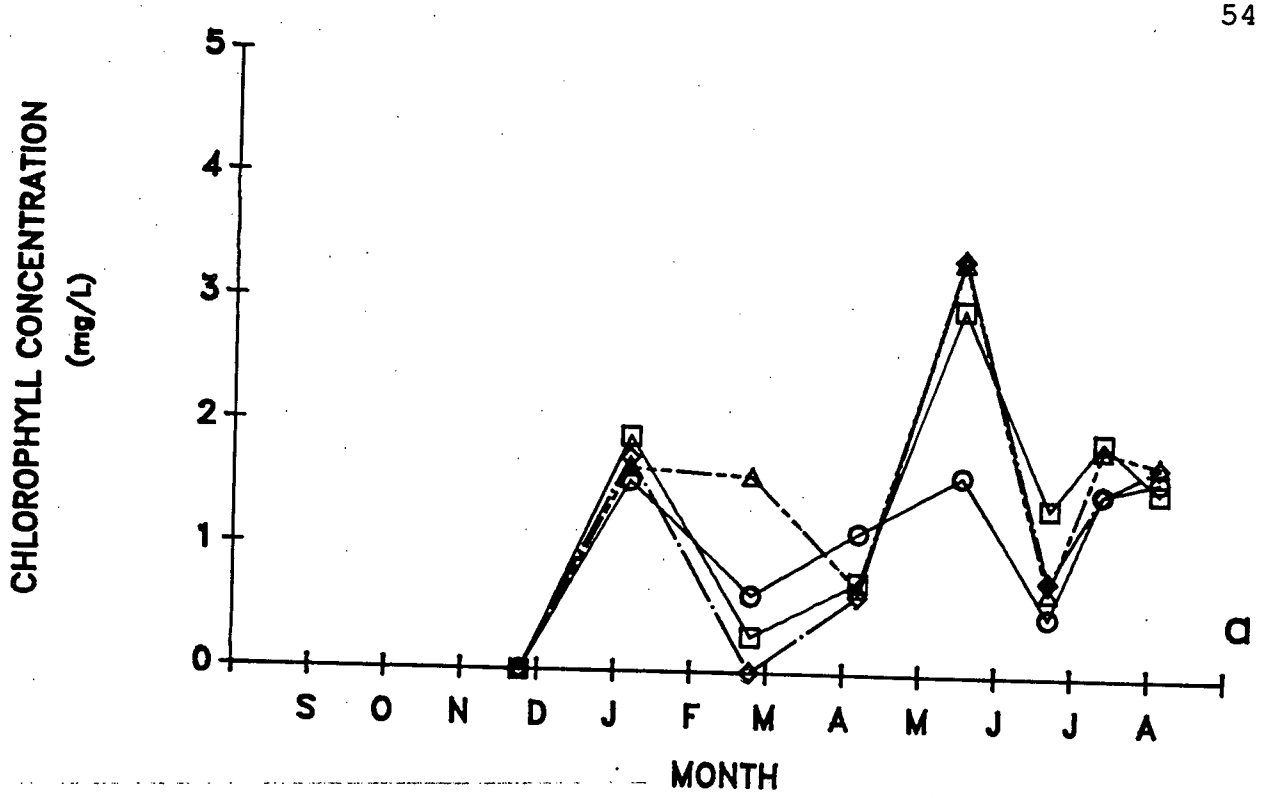
4. **Spat Density**

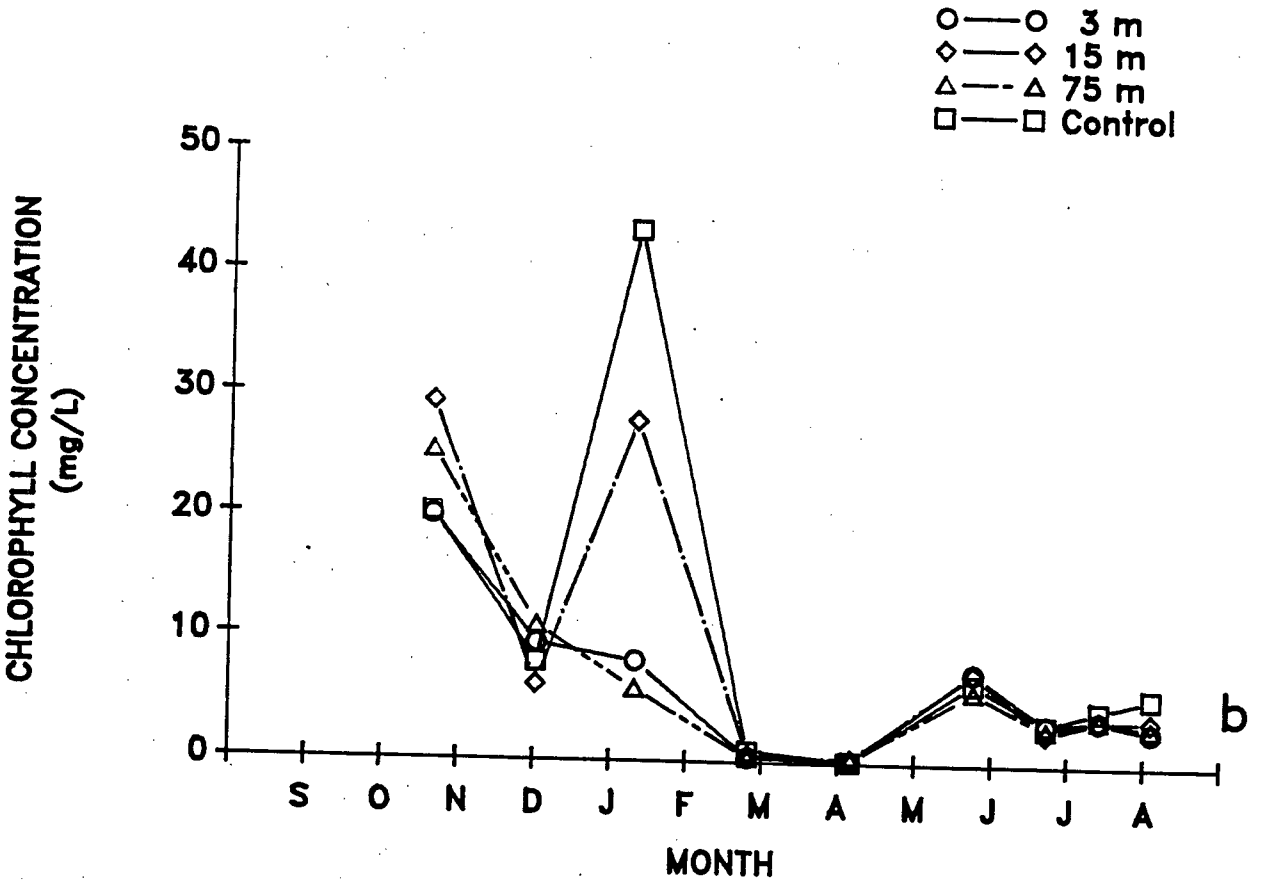
Spat samples taken at each site were not significantly different with respect to density in relation to distance from the salmon farm (ANOVA: Departure Bay $F_{0.05(1),4,10} = 2.9$, $p=0.08$; Genoa Bay $F_{0.05(1),4,10} = 2.6$, $p=0.10$). Thus, distance from a salmon farm did not influence spat settlement.

5. **Chlorophyll**

As with all the parameters related to mussel growth already considered, chlorophyll concentration in sampled water (Fig. 9) showed a significant monthly variation at both sites (ANOVA: Departure Bay $F_{0.05(2),7,53} = 90.5$, $p<0.001$; Genoa Bay $F_{0.05(2),8,62} = 129.3$, $p<0.001$). Distance from the salmon farm was also significant (ANOVA: Departure Bay $F_{0.05(1),3,53} = 3.9$, $p=0.01$; Genoa Bay $F_{0.05(1),3,62} = 12.1$, $p<0.001$) with the differences being characterized as follows: Departure Bay 3 m $\leq$ 15 m $\leq$ 75 m and control, and Genoa Bay 3 m and 75 m < 15 m and control (statistically homogenous subsets: $p<0.05$, TMCT). However, scrutiny of the data suggests that station differences may be largely due to "outliers" at the Departure Bay 75-m station in February 1989 and the 3-m station in May 1989, and at Genoa Bay for the 75-m and 3-m stations in January 1989. In keeping with this, the month-station interaction was also significant at both sites (ANOVA: Departure Bay $F_{0.05(2),21,53} = 8.9$, $p<0.001$; Genoa Bay $F_{0.05(2),24,62} = 29.5$, $p<0.001$. The reason for such an interaction is unclear; however, patchiness in phytoplankton distribution may have been a contributing factor.

Figure 9. Monthly fluctuations in chlorophyll concentrations at the 3 m, 15 m, 75 m, and control stations at a) Departure Bay and b) Genoa Bay during 1988-89. Data are expressed as means. N = 3.


CHLOROPHYLL CONCENTRATION
(mg/L)
5
4
3
2
1
0
S O N D J F M A M J J A
MONTH
a

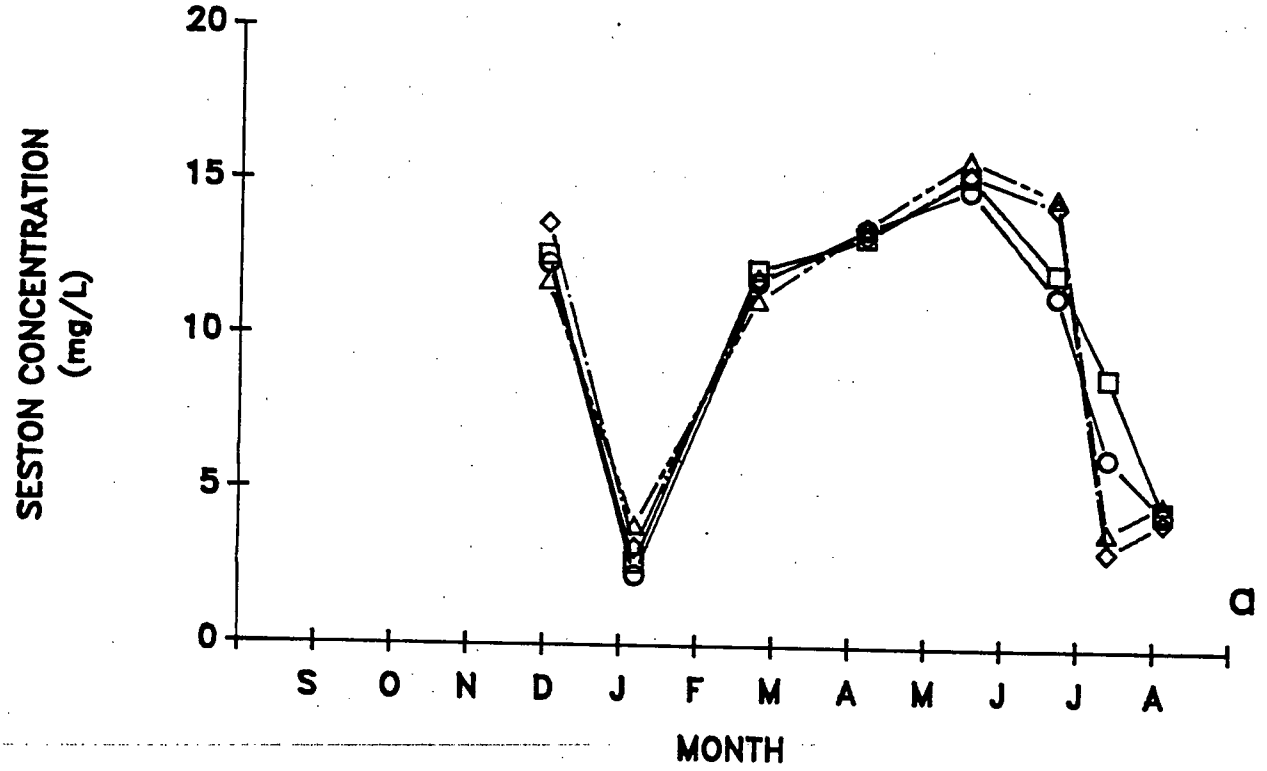

3 m
15 m
75 m
Control
CHLOROPHYLL CONCENTRATION
(mg/L)
50
40
30
20
10
0
S O N D J F M A M J J A
MONTH
b

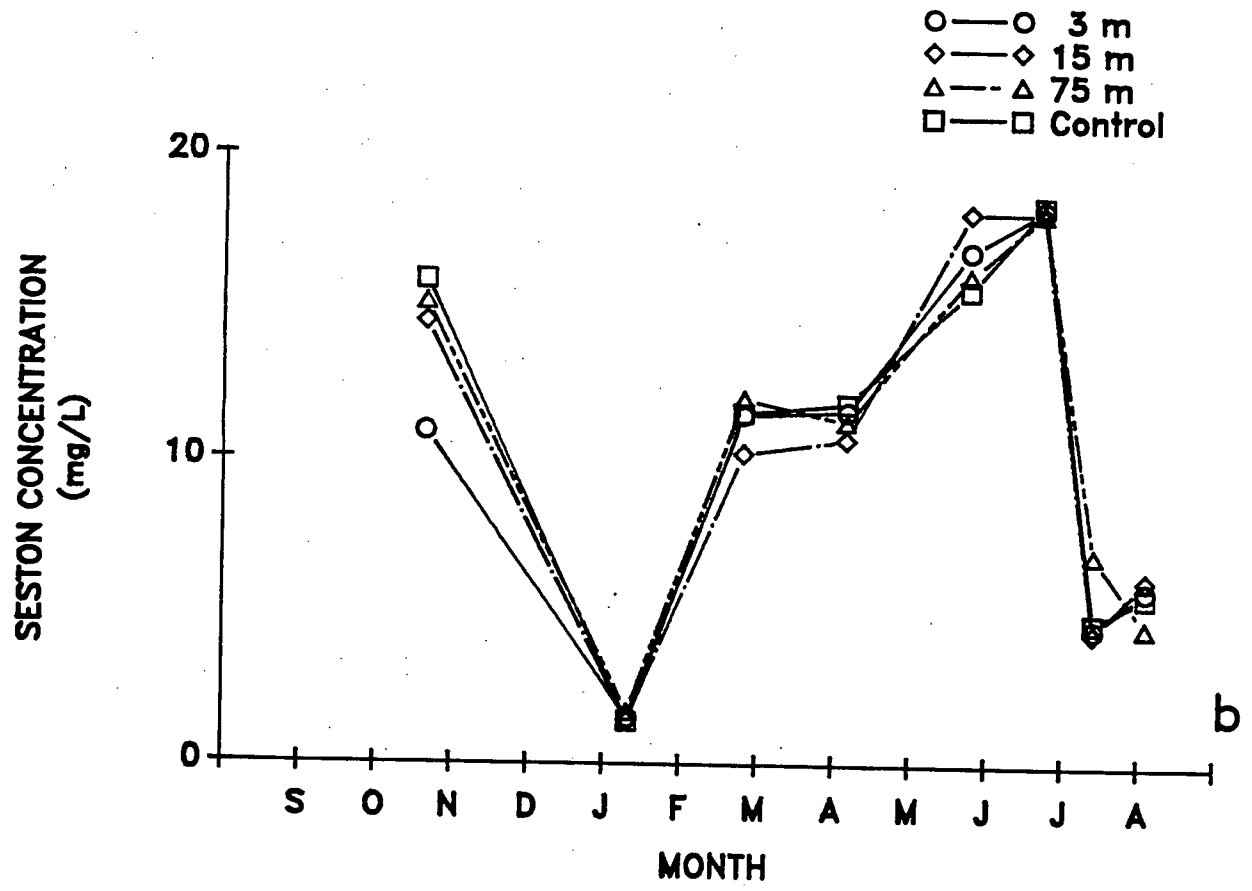
6. **Seston**

The concentration of seston at both sites (Fig. 10) was not significantly influenced by distance from the salmon farms (ANOVA: Departure Bay $F_{0.05(1),3,62} = 1.0$, $p=0.39$ Genoa Bay $F_{0.05(1),3,59} = 0.7$, $p=0.53$). There was, however, a significant month effect (ANOVA: Departure Bay $F_{0.05(2),7,62} = 187.5$, $p<0.001$; Genoa Bay $F_{0.05(2),7,59} = 255.3$, $p<0.001$) which was similar at the two sites. Month-station interaction was also significant at both sites (ANOVA: Departure Bay $F_{0.05(2),21,62} = 5.9$, $p=0.001$; Genoa Bay $F_{0.05(2),21,59} = 4.2$, $p=0.03$). As with chlorophyll concentration, the reason for such an interaction is unclear but, again, patchiness of seston distributions may have been a factor.

Seston concentrations in Departure Bay were similar at about 13 $mg.L^{-1}$ in all months except January (overall mean = 3.0 $mg.L^{-1}$), July (overall mean = 5.4 $mg.L^{-1}$), and August (overall mean = 4.4 $mg.L^{-1}$), and these excepted months comprise a statisically homogenous subset ($p<0.05$, TMCT). The seston concentrations in Genoa Bay (Fig. 10b) demonstrated greater monthly variability but had the same seasonal distribution of highs and lows as noted for Departure Bay. From 14.4 $mg.L^{-1}$ at the start of the study, seston dropped significantly ($p<0.05$, TMCT) to a low of 1.5 $mg.L^{-1}$ in January, and then rose with almost month-to-month significance to 18.2 $mg.L^{-1}$ in June before substantially dropping to about 2.7 $mg.L^{-1}$ in July-August.

Figure 10. Monthly fluctuations in seston concentrations at the 3 m, 15 m, 75 m, and control stations at a) Departure Bay and b) Genoa Bay during 1988-89. Data are expressed as means. N = 3.


SESTON CONCENTRATION (mg/L)
20
15
10
5
0
S O N D J F M A M J J A
MONTH
a

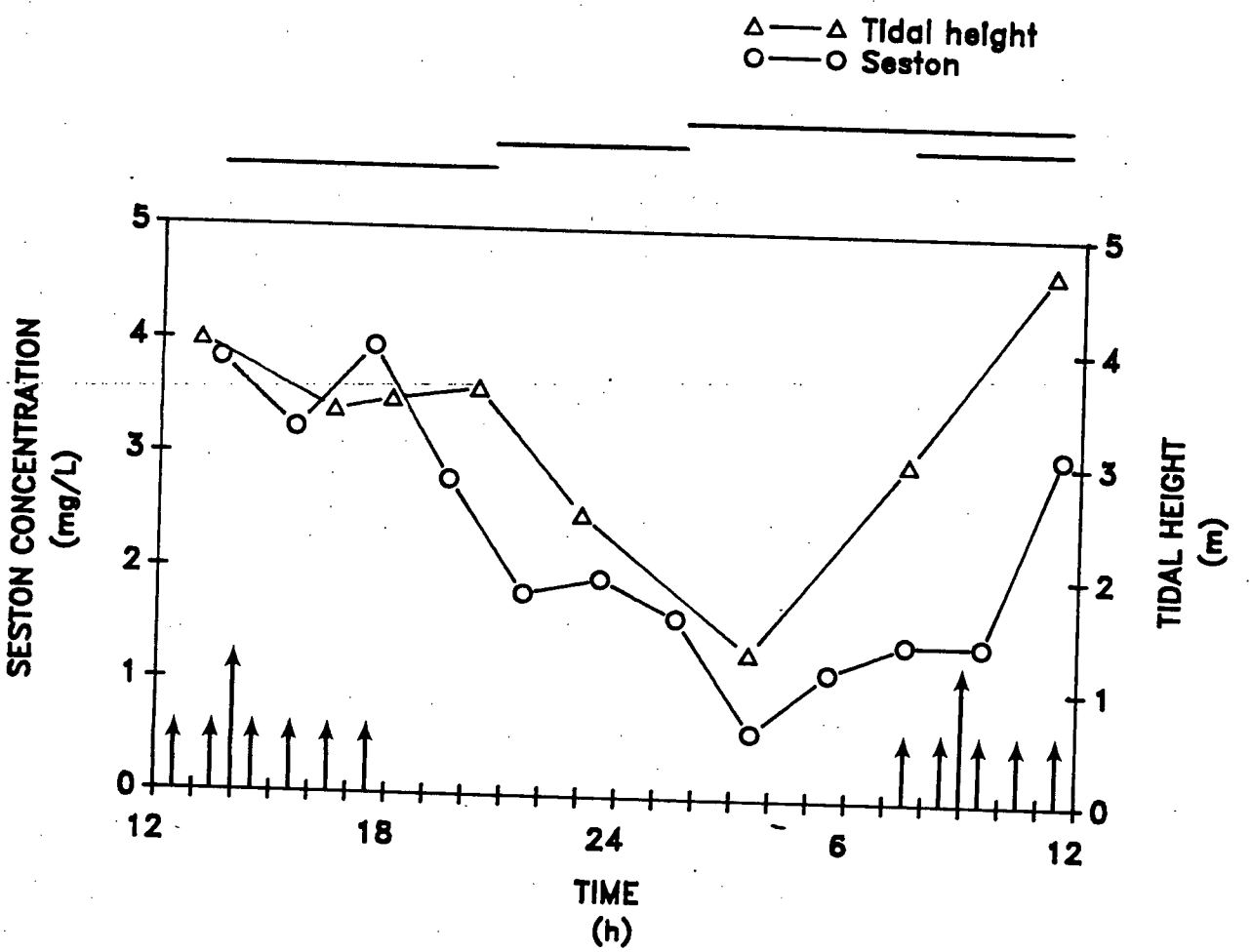

3 m
15 m
75 m
Control
SESTON CONCENTRATION (mg/L)
20
10
0
S O N D J F M A M J J A
MONTH
b

The 24-hr seston series, carried out in late November when phytoplankton was scarce (chlorophyll concentration was essentially zero), was an attempt to measure the seston component derived from the particulate organic waste of salmon culture without excessive background influence from phytoplankton as would exist in summer. The results of sampling over a complete tidal and feeding cycle are presented in Fig. 11.

Daily fluctuation in seston was highly significant (ANOVA: $F_{0.05(2),11,23} = 10.8$, $p<0.001$) and seemed to parallel both the tidal and salmon-feeding cycles. However, it is likely that the seston fluctuations were responding to effects of the feeding cyle and not the tidal cycle for the following reason. A comparison of current velocity collected over a 4-d period with the AANDERAA meter (see next section) and tidal cycle showed an absence of correlation between the two. Therefore, since any influence of tide on seston would presumably have operated through tidally derived changes in current speed, an influence of tide on seston can likely be dismissed.

Seston concentration thus appears to have fluctuated in tandem with feeding at the salmon farm which occurred hourly during daylight. However, the several-hour lag in decline of seston concentration after cessation of feeding in the evening appears incongruous with the rate of water flow away from the farm. The entire volume of water into which the feed was added would have passed the sampling station within one hour after feeding (based on mean current speed of 2.7 $cm \cdot s^{-1}$ for Departure

Figure 11. Fluctuation in tidal height and seston concentration as measured 3 m from the salmon farm in Departure Bay. Arrows at the bottom of the graph represent (by position) feeding times at the farm and (by size) the relative input of feed (tall arrows represent approximately 50% more feed), while horizintal lines at the top of the graph indicate statistically homogenous subsets of seston concentrations ($p<0.05$, TMCT).

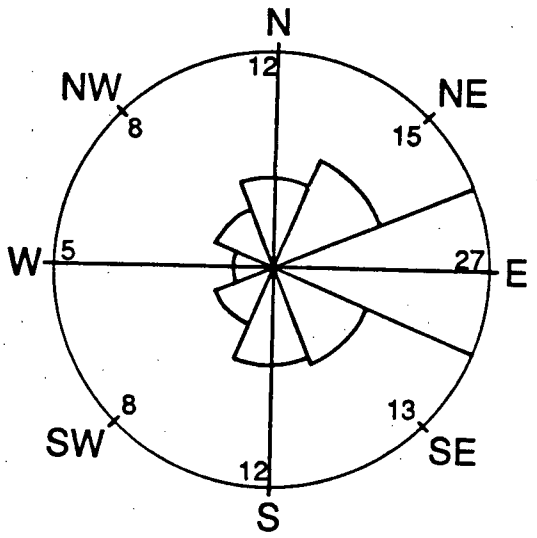

Tidal height
Seston
SESTON CONCENTRATION (mg/L)
TIDAL HEIGHT (m)
TIME (h)
0
1
2
3
4
5
12
18
24
6
12

Bay over the monitored period). Yet, seston did not reach a low until 8-10 h after feeding had stopped at 1730h. In this regard, it should be noted that the farm's seston contribution would have been comprised of all particulate organic waste of salmon culture (i.e., feed particles and faeces). Thus, given a gut-passage time of 24 h for salmon eating typical pelletted diets (Fange and Grove, 1979), the protracted decline in seston was reasonable, since it may have reflected the presence of faeces in the water. The steep increase in seston which occurred after feeding resumed at dawn may have, in turn, reflected the presence of particles of salmon meal in the water.

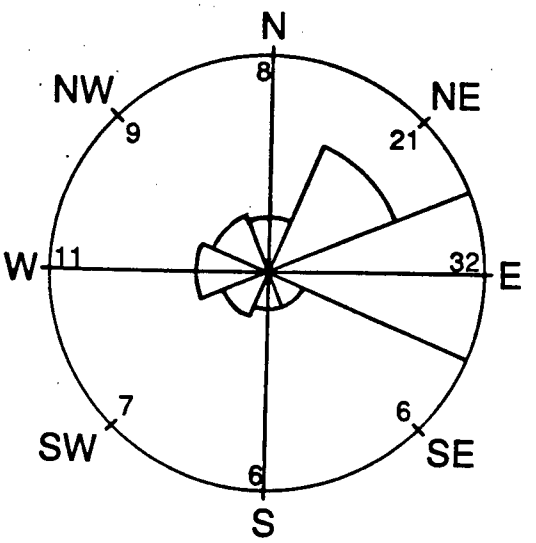
7. **Currents**

Data on current direction at both farms are presented in Fig. 12. These pie-diagrams show the aportioning of current flow among the four primary and four secondary compass directions. In Departure Bay (Fig. 12a), current direction was most frequently eastward, with northeastward being the next most frequent direction of flow, in all months. The frequency at which current flowed in these two directions was greater than all other directions combined in April and May. The existence of such a predominant eastward flow, rather than a counterbalanced current flow (with respect to frequency of direction), suggests that current flow in Departure Bay was not directed primarily by tidal changes. Basin topography and winds must have operated to maintain the eastwardly flow. The eastwardly flow, however,

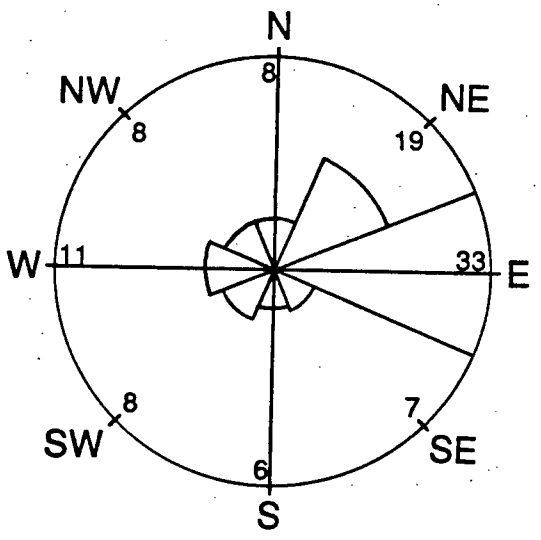
Figure 12. Diagramatic presentation of the aportioning of current flow (as percentage of the monitored period) to the four primary and four secondary compass directions at the two farm sites. Currents in Departure Bay (a) were monitored continuously from March-June 1989 while those in Genoa Bay (b) were monitored intermittently over 4-d periods in each of February, April, July, and August 1989. Insets indicate the positioning of treatment stations (3 m, 15 m, and 75 m) around the farms: Departure Bay stations extended in a line 10^{o} north of east; Genoa Bay stations were in a line extending north from the farm.



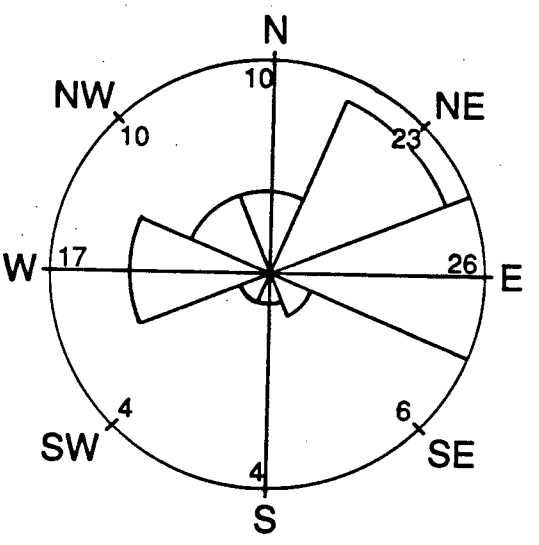
MARCH



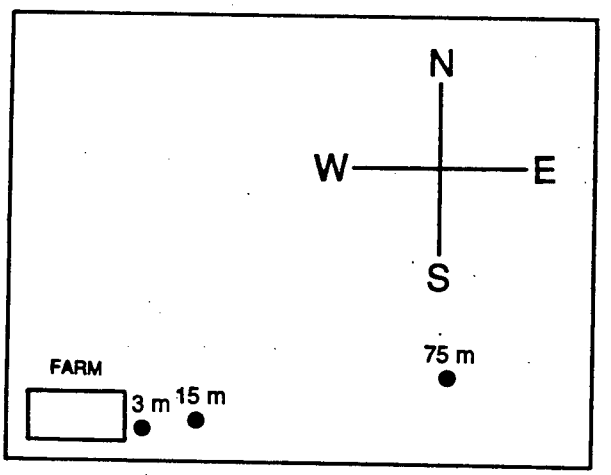
APRIL



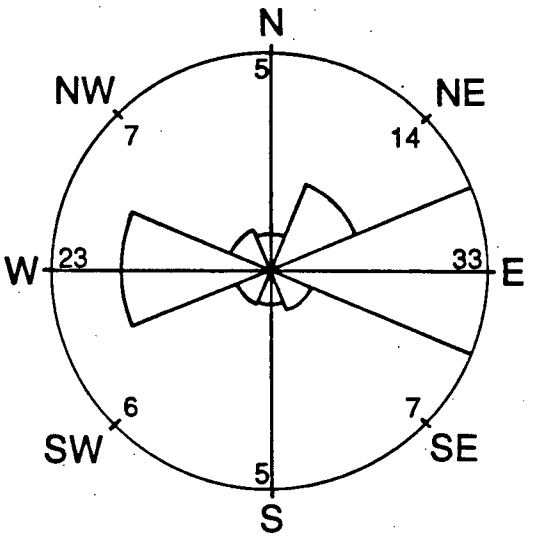
MAY



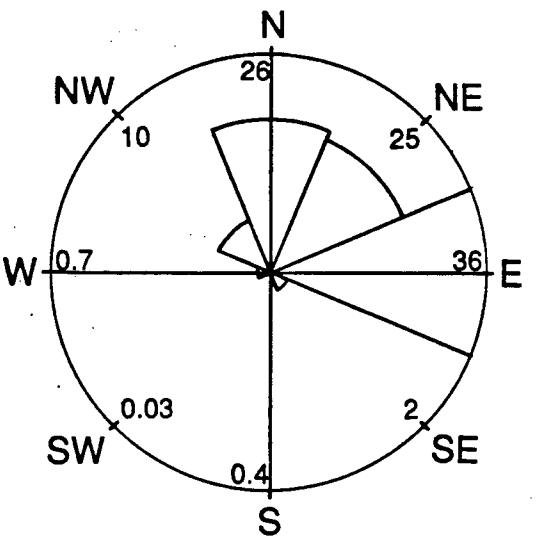
JUNE



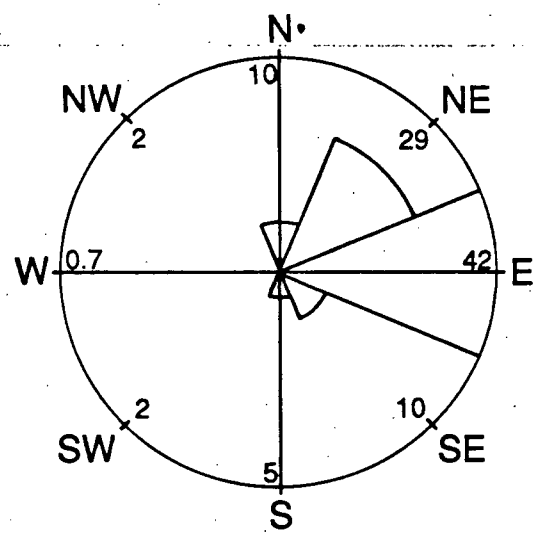
a



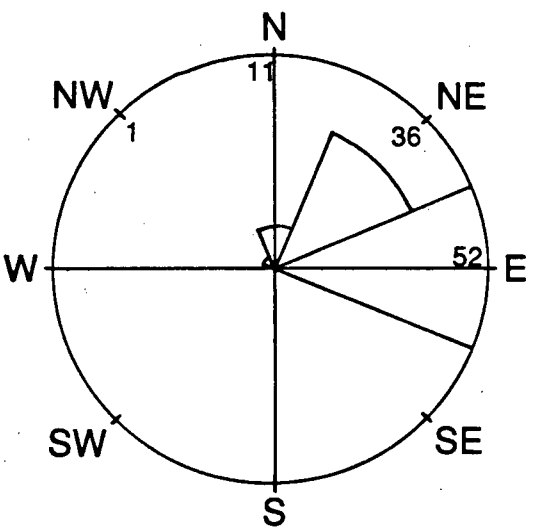
FEBRUARY



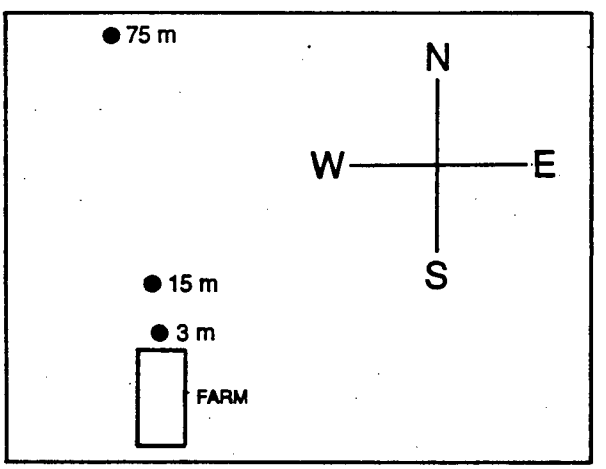
APRIL



JULY



AUGUST



b

should have been beneficial to mussel-salmon polyculture at this site, since long-lines were sited almost due east of the farm.

At Genoa Bay (Fig. 12b), current also flowed most frequently eastward in all monitoring periods. However, during the February period of monitoring, eastwardly flow was counterbalanced by a westward flow for 23% of the time. During all other monitoring periods the combined frequency of east, northeast, and north currents was over 80%. Also, eastward flow seemed to become increasingly more frequent during April-August 1989. It again seems apparent that, as in Departure Bay, tidal changes in Genoa Bay were not the primary force influencing the frequency of current direction. Note, however, that unlike Departure Bay, the predominance of eastward and northeastward flow in Genoa Bay was not ideal for mussel-salmon polyculture, since long-lines were sited almost directly north from the farm.

GENERAL DISCUSSION

Salmon farming is the most extensive form of aquaculture in British Columbia. In 1989, 217 salmon leases were held, with 125 being active (B.C. Ministry of Agriculture and Fisheries: Licensing Statistics March, 1990), and these produced 12,385 tonnes of cage-reared salmon (B.C. Salmon Farmer's Annual Report, 1989). Intensive culture of salmon in coastal waters generates substantial amounts of waste (Gowen and Bradbury, 1987), a form of organic enrichment comparable with domestic sewage and effluent from wood pulp and seaweed processing, as well as duck farming, which are known to provide nutrients to organisms in the surrounding waters (Pearson and Rosenberg, 1978). Such provision of nutrients has raised the issue of potential polyculture of mussels and salmon. However, in the present study growth, condition index, carbohydrate content, protein content, and spat settlement, all showed no consistent or substantial increase with decreasing distance of mussels from a salmon farm. Thus, availability of enrichment from salmon culture with regard to mussels comes into question.

For particles to be eaten by mussels they must be less than 120 um dia; particles larger than this are rejected (Reid, 1982). The 24-h seston sampling series in Departure Bay indicated that salmon-feeding increased the concentration of particles (in the range for feeding mussels: 0.2-120 um) from 1 to 4 mg.L-1. Thus, addition of farm-generated seston would appear to have doubled the available food for mussels. However, seston

concentrations in the present study were never above 20 mg.L-1, and an order of magnitude less than seston concentrations which can be efficiently filtered by mussels (Widdows *et al.*, 1979). In the present study, then, salmon farms probably could not have greatly enhanced the mussels' nutrition through addition of seston food as predicted.

The low increase in seston concentration associated with salmon-feeding noted in the present study seems anomalous to reported production of organic waste by other salmon farms. In reviewing studies on the ecological impact of salmon farming, Gowen and Bradbury (1987) indicated that 40% of the administered feed became organic waste in the form of uneaten pellets and faeces. Furthermore, Brown *et al.* (1987) showed that settlement of particulate organic waste strongly influenced species number, biomass, and diversity of benthic fauna in the first 15 m around a fish farm, and were altered, albeit to a lesser degree, for up to 120 m. The salmon farm selected for study by Brown *et al.* (1987) was located in a Scottish sea loch where mean current speed was 4 $cm \cdot s^{-1}$ and depth was 20 m. These site characteristics are comparable with those of Departure Bay and Genoa Bay, and with most salmon farms in B.C.. The study of Brown *et al.* (1987) indicated that mean size of sediment particles deposited around the salmon farm was within the range for feeding by mussels, corroborating that some farms, at least, generate seston available to feeding mussels. A possible explanation for the apparently low seston increase despite salmon-feeding may be that the water samples were taken 3 m

outside, rather than from within, the farm. Perhaps particulate organic wastes were filtered out by mussels on the nets of the farm and, thus, never reached the experimental animals. Based on known pumping rates of mussels (Vahl, 1973) and the density of mussels on the net-pens of, for example, the Genoa Bay farm (estimated to be $2 \cdot cm^{-2}$), the entire volume of a typical salmon pen (5.0 m X 5.0 m X 6.0 m) could theoretically be filtered every 3 minutes by the mussels on the net-pens. Because each pen within a farm is encircled by a curtain of net and the entire farm is encircled by a predator net, and depending upon the density of mussels on these, salmon farm nets may represent a screen with substantial capacity for filtering particulate organic waste. In fact, the population of mussels on some net-pens can be similar in density to a typical mussel bed, and Dame and Dankers (1988) urge that such populations be viewed as systems responsible for substantial uptake of suspended sediments, phytoplankton, organic carbon, and fixed nitrogen, as well as excretion of significant amounts of ammonium and organic phosphate.

Any influence of the salmon farm in terms of seston concentration would, in any event, have been overshadowed by seasonal influences on this parameter. Seasonal changes in seston concentration were similar in some respects to those of the measured growth and energy-storage parameters. Winter and summer lows in seston corresponded with declining condition index and carbohydrate content in the same season at both farm-sites (although it is notable that these declines continued for three

months after seston concentrations had begun to rise in spring, see Figs. 4-7). Dry shell weight, however, increased over winter despite the seston low. Thus, only the summer lows in seston corresponded with strict fidelity to a metabolically poor state in the mussels. Possibly the winter "low" in seston actually represented a concentration of food that was sufficient to sustain mussels at this time of year, when metabolic activity was low.

Phytoplankton production, like seston, apparently was not augmented by the salmon farms, despite an expectation that it would be based on nitrogenous excretion by salmon. Since approximately 68% of nitrogen consumed by farmed salmon is excreted (Gowen and Bradbury, 1987), and the majority of this excretion is ammonium (Rychly, 1979), there should have been ample potential for phytoplankton enrichment by the farms. Ammonium and urea excreted by cultured salmon may be oxidised or, as a preferred route, directly utilised by phytoplankton (M^{c}Carthy *et al.*, 1977; Gilbert *et al.*, 1982a; 1982b). Ammonium can also be absorbed rapidly by marine phytoplankton (Gilbert and Goldman, 1981). It seems clear that salmon farming should enhance the growth potential of phytoplankton by making nitrogen available to primary producers and, through this, enhance growth of mussels.

There are several possible explanations for lack of increased chlorophyll concentration despite a nitrogen influx generated by the salmon farms. For example, Gowen and Bradbury

(1987) have suggested that primary production can be enhanced but not lead to increased phytoplankton concentration because of quick removal by grazers. Yet, there would be no *a priori* reason to think that in the present study experimental mussels were somehow excluded from such grazing. Another possibility is that utilisation of ammonium and urea excreted by salmon may be limited by rapid flushing time (Gowen *et al.*, 1983). At farm sites where flushing is rapid, phytoplankton may not remain in the vicinity long enough to capitalise on the high concentrations of nitrogenous nutrients. Alternatively, despite high concentrations of nitrogenous nutrients, phytoplankton may be limited by other environmental characteristics such as low temperature, low light intensity, or low levels of other required nutrients (such as minerals, vitamins, and organic compounds of nitrogen and carbon). The existence of seasonal changes in chlorophyll concentration during the study (see Fig. 9) suggests that phytoplankton populations were probably more influenced by seasonal characteristics than by salmon farms since there would have been no seasonal fluctuation in production of nitrogenous waste by salmon.

The monthly fluctuations in chlorophyll concentration corresponded only slightly with monthly fluctuations in growth and energy reserves of the mussels. In Departure Bay the lowest chlorophyll concentration (November 1988) was synchronous with declining condition index and carbohydrate content. However, it was noted that at this time shell growth occurred and dry tissue weight was constant. Therefore, despite scarcity of

phytoplankton in November, the mussels were metabolically active, producing shell and converting carbohydrate. In general, from their deployment in autumn 1988 to spring 1989, Departure Bay mussels were apparently unaffected by fluctuations in phytoplankton, but this was reversed in summer 1989 when condition, growth and energy reserves did seem to correlate with summer fluctuations in phytoplankton. In Genoa Bay there was only slight correlation of chlorophyll concentration with condition, growth, and energy reserves, but here it was in winter. In summer, mussel growth at Genoa Bay appeared to be less related to phytoplankton fluctuations, although chlorophyll concentration rose in May 1989, coincidental with a spring rise in all growth parameters.

Thus, even though salmon farms have the potential to augment nutrition of polycultured mussels via liberation of wastes, other factors such as temperature, light intensity, presence of nutrients other than nitrogen compounds, presence of competing filter feeders, and type of salmon feed, may operate to reduce the effect. Clearly, increased growth of mussels cannot be insured simply by siting mussel cultures close to salmon farms.

The importance of site to the success of mussel culture has been repeatedly emphasised in investigations of the influence of environment and genetics on mussel growth and survival (Freeman and Dickie, 1979; Dickie *et al.*, 1984; Widdows *et al.*, 1984; Mallet *et al.*, 1986; 1987a; 1987b; Swarbrick *et al.*, 1990). Reciprocal transplants of mussels by Mallet *et al.* (1987b) have

indicated that genotype is primarily responsible for mortality. This contradicts the results of Dickie *et al.* (1984) who have reported that growth rates of mussels from the same stock in two environments differ only slightly, while mortality differences are marked and are the principal determinants of net production. Therefore, whether through an effect on growth rate or mortality, the result is the same: environment substantially influences production of mussels. Thus, to reap benefit from mussel-salmon polyculture, both salmon-farm site and source of mussels should be carefully selected. Trial culture studies may be the only effective means to establish the potential growth rate of a specific mussel source in a given area (Jamieson, 1989). Furthermore, as a trial effort, the experiments at Departure Bay and Genoa Bay may be indicative of a problem associated with mussel source, since mortality of the transplanted stocks was high, and of site, since the farms did not fulfill their predicted potential to augment mussel growth.

Although present results cannot advocate mussel-salmon polyculture on the basis of any nutritional advantage for mussels, there still may be logistical advantages to this pairing. For example, salmon farms may provide structural support for deploying long-lines for mussel suspension. There may also be economic advantages to harvesting two crops from one lease. Conversely, other sometimes negative aspects of coupling of mussel and salmon culture should be investigated before such polyculture is commercially implemented. A primary concern is potential transfer of pathogens and parasites between mussels and

salmon. Disease is an important concern in all culture operations because spread of pathogens is enhanced by increased density which is a hallmark of animal husbandry. Disease concerns take on new dimension in polyculture because the species might respond differently to potential pathogens. Such differential response has been noted with bacteria, *Vibrio* spp., which are potentially harmful to salmon and known to be harboured in the hind-guts of mussels, *Mytilus edulis desolationis*, in higher concentration than in either stomach or surrounding seawater (Bouvy and Delille, 1987). Contact with mussel faeces may increase the risk of *Vibrio*-infection in salmon. Another potential risk is the possibility for mussel diseases to be transmitted to salmon. At least one disease has been identified for northeast Pacific mussels (Jamieson, 1989), a tumorous condition of blood cells known as hemic neoplasia which can be found in 60% of post-spawning mussels in B.C. (Bower, 1989) and 70% of mussels from Puget Sound (Elston *et al.*, 1988). As of yet there has been no investigation of this disease with respect to salmon. A contrasting consideration is the potential for differential response which may actually benefit salmon; that is, mussels may be able to filter and digest bacteria responsible for BKD (bacterial kidney disease) (Evelyn *et al.*, unpubl. data), thus possibly reducing risk of infection. In any case, thorough investigation of disease risks is necessary to assess the potential coupling of mussel and salmon culture. Thorough investigation of parasitic risks is also necessary. *Mytilocola intestinalis*, a parasitic copepod, is occasionally found within digestive tissues, and unidentified protozoans and *Nematopsis* sp.

have been observed in the lumen of kidneys in B.C. mussels. Although Emmett (1984) reported that low frequency of occurrence of these parasites tended to reduce their effect on mussel populations, there have been no studies of their possible effect on salmon. Similarly, the effect of salmon parasites on mussels has not been investigated.

Interest in aquaculture has also been shadowed by concerns of water quality effects. Both salmon culture (reviewed in Gowen and Bradbury, 1987) and mussel culture (Galkina *et al.*, 1982; Larsson, 1985; Dame and Dankers, 1988) have been studied in this regard, but never in the context of polyculture. In this context, the chief concern regarding salmon culture has been one of eutrophication, and the possibility that this process would favour mussel culture formed the basis of the present study. Reciprocal effects of this type of polyculture can be extrapolated from Larsson's (1985) investigation of influence of mussel culture on water quality. This 21-month-long study showed that long-lines of *Mytilus edulis* (about 160 tonnes wet-weight of mussels) did not give rise to measurable changes in concentration of inorganic nutrients and oxygen in the water mass passing through the culture, but ammonia-nitrogen sometimes doubled and phosphorus quadrupled. Dame and Dankers (1988) also reported significant release of ammonium and phosphorus from natural mussel beds. Thus, since salmon are known to be highly sensitive to ammonia (International Programme on Chemical Safety, 1986), it may be necessary to site mussel-salmon polycultures in areas with

high flushing rates to prevent extensive mussel culture from negatively influencing water quality for salmon.

The present study has provided information not only on the practicality of mussel-salmon polyculture, but also on the seasonal cycle of accumulation and expenditure of energy storage products by B.C. mussels. Particularly of interest are apparent differences with respect to energy metabolism, growth, and condition between B.C. mussels and their much-studied European counterparts. These differences may be important to the success of mussel culture operations in B.C..

A primary difference between energy storage in mussels cultured in the present study and that reported for European populations relates to the cycling of glycogen. In the present study, glycogen was represented in the measure of total carbohydrate. Since the majority of carbohydrate in mussels is stored as glycogen, and since practically all other carbohydrates are accounted for as blood sugars (whose level represents the balance between mobilisation of glycogen from the digestive gland and mantle and utilisation of glucose by body tissues), the obtained measure of total carbohydrate was thought to provide a useful assessment of carbohydrate energy reserve. In support of this, Dare and Edwards (1975) reported that values for glycogen content in *Mytilus edulis* were in close agreement with indirect estimates of total carbohydrate.

In European populations of *Mytilus edulis* described by Dare and Edwards (1975), Pieters *et al.* (1979), Zurburg *et al.* (1979),

and Zandee *et al.* (1980), glycogen was lowest in April, rose in April-June to 30-40% dry weight, and remained at this level before declining slowly to an April low in the following year. In B.C. populations, both in the present study and those of Emmett (1984) and Emmett *et al.* (1987), glycogen was again lowest late winter, rose steeply in spring reaching 15-30% dry weight, remained elevated through summer, and then began a steep decline with some slight counteraction in October. Thus, where European mussels apparently spend 5 months at 30-40% glycogen content before slowly expending their glycogen store (likely during gametogenesis: Bayne *et al.*, 1975; Bayne *et al.*, 1982; Peek *et al.*, 1989), B.C. mussels peak at only 15-30% glycogen content and maintain this level for only 3 months before rapidly exhausting their store in August, months before the onset of gametogenesis (Emmett *et al.*, 1987 reported this as beginning in December).

The early decline and resulting extreme low of carbohydrate content exhibited by B.C. mussels is not indicative of a lack of carbohydrate metabolism during autumn and winter, nor of an inability to undergo gametogensis because energy reserves are insufficient. Rather, it may be that a carbohydrate reserve is not accumulated because the energy acquired through autumn-winter feeding is used up in maintenance requirements and gametogenesis. Recall that winter mussels in the present study (Fig. 7) depleted their carbohydrate content without changing dry tissue weight or protein content. At this time they were likely producing gametic tissues (Emmett *et al.* (1987) have also reported gametogenic activity in mussels during autumn-winter). This pattern

contrasts with that of energy accumulation and allocation noted for European mussels. In these mussels, usually the entire body is involved in accumulation of glycogen during summer (de Zwaan and Zandee, 1972) and this energy reserve is heavily relied upon to meet metabolic demands during this season (Bayne, 1973). Then, in autumn-winter, remaining energy reserves (glycogen and protein) are converted to the lipid and protein consituents of the gametes (Gabbott, 1975; Pieters *et al.*, 1979; Zandee *et al.*, 1980; Kluytmans *et al.*, 1985). Thus, despite notable differences in seasonal cycles of energy reserves, B.C. and European mussels engage in gametogenesis and spawning at about the same time. This similarity in timing is not surprising since mussels are capable of wide adjustments in their spawning times. By virtue of their ability to alter gametogenic rate (Bayne, 1975) and spawning pattern (Newell *et al.*, 1982) in response to environmental conditions, mussels can apparently synchronise their reproduction with optimal conditions for larval growth and survival. Reproductive strategy is known to be a plastic characteristic in mussels (Lowe *et al.*, 1982; Newell *et al.*, 1982; Bayne *et al.*, 1983; Rodhouse *et al.*, 1984; Hawkins *et al.*, 1985). These authors reported that most populations of *Mytilus edulis* exhibited a "conservative" reproductive strategy where energy storage products were first accumulated then expended in gametogenesis but that increased food quality and quantity, as well as increased age, led to a change to an "opportunistic" strategy where gametogensis was fueled directly by nutrient intake. B.C. mussels, however, seem to exhibit a more opportunistic strategy in that energy storage seems to be

synchronous with gametogenesis (carbohydrate content increased in May-June which is generally a time of spawning for B.C. mussels).

A comparison of B.C. mussels with their European counterparts with respect to protein (reported to be the second most important energy storage product: Gabbott, 1983), shows less difference than noted for carbohydrate. In European populations, protein content fluctuates over the course of the year (40-60%, Thompson *et al.*, 1974; 45-75%, Dare and Edwards, 1975; and 30-52%, Zandee *et al.*, 1980). Protein content of B.C. mussels showed similar fluctuations (36-54% in Departure Bay and 40-54% in Genoa Bay, present study; 33-65%, Emmett, 1984). Thus, both degree of variation and actual value of protein content are similar in European and local mussels.

The cycling of energy reserves has an obvious influence on growth and, through this, on condition index. There seems to be a common pattern in both Europe and B.C.. Condition index, like glycogen content, remains high for a longer period after its increase in the spring (April) in European mussels than is the case in B.C. ones. In fact, Zandee *et al.* (1980), in a study of mussels in the Dutch Wadden Sea, recorded highest condition indices in July and August. In contrast, mussels cultured in Departure Bay and Genoa Bay had lowest condition indices in late summer. Regardless of geographic location, temperate mussels are generally in poorest condition during February-April. At this time, European mussels are completing gametogenesis (Bayne *et al.*, 1975; Bayne *et al.*, 1982; Peek *et al.*, 1989) as are B.C.

ones (Emmett *et al.*, 1987). Thus, to summarise, B.C. mussels differ from those of Europe in that they exhibit two lows in condition index: one occurring in early spring, presumably concurrent with gametogenesis, and a second in late summer, concurrent with high mortality.

Notwithstanding the extended period of low carbohydrate content, poor condition index, and similar protein content, B.C. mussels have a faster growth rate than their counterparts in temperate European waters. Mussels cultured in Departure Bay and Genoa Bay reached market size (50 mm) in 14 months. This compares favourably with 8-15 months required in Spain (Korringa, 1976) and 12-14 months required in New England (Incze and Lutz, 1980), slightly improves on the "two summer seasons" required in most of the North Sea (Wallace, 1980) as well as Atlantic Canada (Incze and Lutz, 1980), and is much faster than the "3-6 summer seasons" required within the Arctic circle (Wallace, 1980; Theisen, 1973). Such differences must, to some extent, be due to geographic variations in seasonal temperature, salinity, and availability of food; nonetheless, it remains clear that, despite short-comings in terms of energy reserves, B.C. mussel culture compares favourably with that in other areas of the world: the time to harvest is one of the shortest anywhere.

Market size for cultured mussels is defined by shell length, and growth-rate data are most often presented as increase in shell length over time. However, since relative tissue weight governs the market quality of mussels, it is important to know

the relationship of these two parameters. Hilbish (1986) has indicated a high degree of correlation between monthly increase in dry tissue weight and shell length (r^2=0.97) in Atlantic mussels, as has the present study for B.C. mussels (r^2=0.82). From this it is apparent that growth rate can be equally well-defined by dry tissue weight or shell length. However, this high correlation must be qualified in light of observations of uncoupled growth of tissue and shell (Kautsky, 1982; also present study). Kautsky (1982) reported that tissue growth sometimes preceded shell growth in Baltic Sea populations of *Mytilus edulis*, while the present study showed that shell growth sometimes preceded tissue growth (for example, October-April mussels in Departure Bay increased from 32-43 mm without a concommitent rise in dry tissue weight, and over the same period Genoa Bay mussels increased from 28-40 mm without a significant change in dry tissue weight). Despite this qualification, which may pertain only in autumn-winter, the point remains that, based on rate of increase in shell length and the correlation between shell length and dry tissue weight, B.C. mussels grow faster than mussels studied and cultured in Europe.

Another difference between European and B.C. mussels which relates to culture, is that European mussels increase in dry tissue weight in spring and summer, and then lose tissue in autumn and winter, but without suffering the high mortality seen in B.C. populations. Mussels in the present study increased in dry tissue weight in spring and began to waste in late summer, suffering about 50% mortality by summer's end. The magnitude of

tissue loss was similar in both European and B.C. populations, but high mortality seems specific to the Pacific northeast and represents a serious obstacle for culture in this region. With respect to tissue loss and mortality, Kautsky (1982) reported that *M. edulis* in the Baltic Sea routinely survived 30-50% loss of dry tissue weight (an extreme individual survived 78% loss) and Bayne and Worrall (1980) reported that recovery from a 25% loss of tissues was routine for 3-yr-old mussels in the English Channel, while 6-yr-old mussels regularly recovered from a 68% loss. In comparison, Departure Bay mussels lost 43% of their dry tissue weight and recovered poorly (50% mortality), while Genoa Bay mussels showed almost as poor a recovery (40% mortality) from a 29% loss of tissue. Some of this loss represents the emission of gametes, but another portion must owe to mobilisation of non-reproductive tissue to meet energy demands of maintenance metabolism. Such mobilisation first becomes necessary during spawning in spring and carries through to autumn. Mussels cease filtration during spawning which usually spans a 3-4 wk period (Chipperfield, 1953). This "fasting" necessitates mobilisation of body tissues since it occurs when carbohydrate reserve is at a low and metabolism is high (increased temperature in summer induces metabolic stress in mussels: Widdows and Bayne, 1971; Bayne *et al.*, 1978; Incze and Lutz, 1980). Therefore, mussels likely enter a period of negative "scope for growth" during spawning, a state which continues through summer and which possibly imposes mortality such as that observed in the present study.

Summer mortality is well-documented for mussels in the northeast Pacific (Quayle, 1978; Heritage, 1983; Emmett, 1984; Skidmore and Chew, 1985; Emmett *et al.*, 1987), the northwest Atlantic (Incze *et al.*, 1980), and the northeast Atlantic (Worrall and Widdows, 1984). Summer mortality was investigated by Worrall and Widdows (1984) in a mussel population from the English Channel which exhibited reduced scope for growth following spring spawning. Non-predatory mortality peaked one month after spawning when metabolic costs were high and energy reserves were at a minimum. There may have been a correlation between incidence of mortality and reproductive effort in this population, since mussels in larger size classes exhibited both higher mortality and higher reproductive effort. In another investigation by Incze and Lutz (1980), mortalities on raft-cultured *M. edulis* in Maine were thought to have been caused by reduced food ration during metabolic stress caused by high temperatures.

In the present study, summer mortalities occurred when the mussels' mean carbohydrate content was at an intermediate level. Thus, it appeared that mussels died despite being energetically competent. This prompted questioning of the relationship between energy reserves and energy budgets in mussels at the time of worst mortality in August, as compared with April when carbohydrate reserves were lowest and mortality was insignificant. A comparison of April and August mussels in this regard was made by combining physiological characteristics and environmental parameters, some measured in this study and some

taken from the literature (data shown in Table 1). The main points of interest from the table are: 1) mussels cultured at the 3-m station of both sites possessed a potentially longer-lasting carbohydrate reserve in April as compared with August, 2) August mussels exhibited a negative scope for growth (with energy deficits of 2-3 $kJ \cdot h^{-1}$), but in April Departure Bay mussels had a positive scope for growth, and Genoa Bay mussels were only marginally negative in this regard, and 3) therefore, although the mussels had a greater proportion of carbohydrate in August relative to April, they were energetically deficient for reasons of increased metabolism due to high temperature and possibly low food concentration. The results of the present study thus accord with those of Worrall and Widdows (1984), and Incze *et al.* (1980), who attributed summer mortality in English Channel and northwest Atlantic mussels, respectively, to energy deficiency. However, summer mortality cripples the production of mussels in B.C. to a much greater extent than in either Atlantic region.

Another difference between local and European mussels relates to maximum size: *M. edulis* cultured in B.C. rarely exceed 60 mm (Heritage, 1983; Emmett *et al.*, 1987), but in the northwest Atlantic commonly reach 70 mm (Freeman and Dickie, 1979), and on the Atlantic coast of Spain attain 80-90 mm (Korringa, 1976). In Spanish waters increased growth may be due to warmer temperatures, but the northwest Atlantic and northeast

Table 1. Energy reserves and energy budgets of mussels cultured in Departure Bay and Genoa Bay at the 3-m station. Data presented are for mussels of the mean weights and carbohydrate contents for April and August 1989.

Culture Characteristic	Departure Bay April	Departure Bay August	Genoa Bay April	Genoa Bay August
Total dry tissue weight (mg)	149	360	173	480
CHO content (% dry wt)	4.8	15.5	3.2	13.5
Equivalent CHO reserve (kJ)[1]	0.117	0.934	0.927	1.085
Water temperature (°C)	10	17	10	17
Seston concentration (mg/L)	13.4	4.4	11.4	5.4
Energy Metabolism				
Estimated VO_2 (ml O2/h)[2]	37	283	43	354
Longevity of CHO reserve (h)[3]	1.00	0.44	0.59	0.31
Energy Budget				
ENERGY IN (kJ/h)[4]	0.137	0.135	0.115	0.194
ENERGY OUT (kJ/h)[5]	0.112	2.147	0.158	3.561
SCOPE FOR GROWTH (IN - OUT, kJ/h)	0.025	-2.012	-0.043	-3.367

[1] The energy content of known weight of carbohydrate reserve was calculated from a generalized heat of combustion of carbohydrates, 1.68 $kJ \cdot kg^{-1}$ (Church and Pond, 1982).

[2] VO_2 was calculated using summer and winter equations for oxygen consumption based on dry tissue weight from Bayne (1973) corrected to the appropriate temperature using Q_{10} values from Widdows (1973).

[3] These values were calculated using a generalized oxycalorific conversion for carbohydrate of 20.9 $kJ \cdot L\ O_2^{-1}$ (Church and Pond, 1982).

[4] Values for "ENERGY IN" are derived from the present data on seston concentration converted to estimated energy content from data in Widdows *et al.* (1979), and calculated from estimates of absorption efficiency at varying food concentration and of filtration rate based on animal size from data in Widdows (1978).

[5] Values for "ENERGY OUT" are calculated using VO_2 values from generalized oxycalorific conversion, formulated for *M. edulis* eating a mixed algal diet (Widdows and Hawkins, 1989) of 20.1 $kJ \cdot L\ O_2^{-1}$.

Pacific are similar in temperature. Thus, variability in growth is not caused by temperature alone. Some of the identified differences between European and B.C. *Mytilus edulis* (Heritage, 1983; Emmett *et al.*, 1987; Swarbrick *et al.*, 1990; present study) may relate to differences in life history strategy. In comparison to *M. edulis* in Europe, local populations seem to have a shorter life span and higher reproductive output at an earlier age (gonad development occurs as early as 1-2 months after settlement in local mussels: Suchanek, 1981).

Many points of distinction between populations of *Mytilus edulis* in B.C. and other geographic regions have been made; such differences may be critical to the overall success of local culture operations. Notably, production of *M. edulis* in B.C. seems potentially more limited by summer mortality, and the relationship between spawning and seasonal changes in energy reserves in local populations is also distinct (Emmett *et al.*, 1987). Although polyculture has been shown in the present study to confer no particular advantages with respect to mussel growth, mussels in B.C. are fast-growing, potential culture sites are plentiful, and mussel culture in B.C. remains a viable prospect.

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