A COMPARISON OF FEEDING PHYSIOLOGY IN CULTURED AND WILD BLUE MUSSELS MYTILUS EDULIS AND M. TROSSULUS

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A COMPARISON OF FEEDING PHYSIOLOGY IN CULTURED AND WILD BLUE MUSSELS *MYTILUS EDULIS* AND *M. TROSSULUS*

by

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Abstract

The objective was to improve carrying capacity models by providing standardized values for clearance, ingestion, filtration and oxygen uptake for cultured and wild, *Mytilus edulis* and *M. trossulus* from Newfoundland. Clearance and ingestion rates of small and large *M. edulis* and *M. trossulus* were also compared.

Measured physiological rates were not significantly different between cultured and wild mussels. *Mytilus trossulus* demonstrated significantly higher rates of clearance and ingestion compared with *M. edulis*. Rates of clearance and ingestion generally increased with an increase in food supply. Seasonal patterns were observed for all variables. Larger mussels had higher rates of clearance and ingestion than smaller mussels and should be socked at lower densities. Smaller mussels should be socked at a lower biomass per sock as they have higher clearance per unit biomass.

Stock size and species proportions, in addition to temperature variability and food availability, contribute to the overall stock food demand. Socking and stocking biomass and site layouts should be adjusted to minimize the risk of exceeding site carrying capacity.

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Section 1 Introduction

1.1 A Brief History of the Blue Mussel Industry

Based upon the discovery of blue mussel shells near primitive dwelling grounds, it is believed that blue mussels have been a part of the diets of coastal people since before recorded time (Scarratt 1993). The origin of the blue mussel industry in North America can been traced to the pickling and canning of wild mussels during the two world wars (Lutz 1980). During this time, Newfoundland was the most actively involved region in North America, with three commercial canneries in operation and annual landings of approximately 1,000 tonnes (Sutterlin *et al.* 1981). The Canadian blue mussel industry eventually crashed due to a variable supply of wild blue mussels and competition from other industries offering alternative sources of protein.

In Canada, the blue mussel aquaculture industry has shown a steady increase in production from only 2,062 tonnes in 1986 to 14,920 tonnes in 1998 (DFO 1999). The success of Canadian blue mussel aquaculture can be attributed to an abundant natural seed supply, exercising the longline culture method for commercial growout, developing markets and dedicated efforts by private owners and operators and various governmental support mechanisms (Mallet and Myrand 1995). Collaborative efforts of academia, industry and government have resulted in increased production, and a progressive blue

mussel industry. As a result, blue mussel aquaculture continues to be a profitable and expanding business venture in Canada.

1.2 The Economics of Aquaculture

1.2.1 Trends in Global Aquaculture Production

The global annual yield of the traditional capture fisheries is estimated to be approximately 135 thousand metric tonnes, live weight (DFO 1999). Canadian catch has decreased since 1990, and will conceivably continue to decline. Production capacity has peaked and many species are at risk. Whether or not the wild fishery can remain competitive in the face of advancing technology and increasing demand is questionable, but it is clear that the demand for fisheries-related products will continue to increase (Heggberget 1997). In 1986, it was estimated that fish contributed about 17 % of animal protein supplies, but in many countries, people may have derived as much as 50 % of their daily animal protein requirement from fish (e.g., Bangladesh, Indonesia, Japan, Philippines, Thailand) (Shang 1986). In 1997, food production experts from around the world gathered at the Food and Agricultural Organization of the United Nations (FAO) World Food Summit in Rome. A key conclusion of the Summit was that, given declines in wild fishery production and the production increases that can reasonably be expected from land-based agriculture, world food production will not keep pace with demand unless aquaculture production continues its rapid expansion (FAO 2000).

The aquaculture industry has become a profit and employment generating industry in a number of countries worldwide. In Canada, aquaculture production facilities now operate across the country, with activities in all provinces and territories. For instance, the rural-based aquaculture industry of Newfoundland, based primarily on steelhead trout, Atlantic salmon and blue mussels, demonstrated further growth in 1998 compared with the preceding year and attained an export value of $12.9 million, employing 461 people at peak employment (DFA 1999). In Newfoundland, total blue mussel production in 1999 was estimated to be 1,699 tonnes with a value of $3.7 million. Total blue mussel production in 1998 was estimated to be 946 tonnes with a value of $815,000. This represents almost a 56 percent increase in production with a 22 percent increase in value over one year (DFO 1999).

1.2.2 Present Status of Blue Mussel Industry

Today, commercial operations exist throughout the world and aquaculture has become one of the fastest growing food production systems on the planet. Between 1984 and 1996, total world aquaculture production more than tripled in weight, from 10.4 to 34.1 million metric tonnes (mmt), and in value, from US$13.1 billion to US$46.5 billion (FAO 2000). Since 1984, farmed fish and shellfish production has increased at an average annual rate of 10.4 percent, compared with only 2.8 percent per year for conventional livestock production. Moreover, the FAO has calculated that to maintain current global per capita consumption levels, world aquaculture production will need to increase to 62 mmt by 2035 (FAO 2000).

Canadian aquaculture is a growing industry. In 1998, total aquaculture farm-gate production from over 600 farms was worth C$443 million, representing close to 27 percent of the total landed value of Canadian fish and seafood. In the last decade, the growth rate has averaged 14 percent per year in value and 15 percent per year in volume. This rate exceeds the annual global rate by more than 40 percent but considerably lags the growth of leading countries.

Mytilus edulis is one of the major species of mussels cultivated worldwide. Currently, over twenty countries report regular harvests of farmed mussels. The majority of the farmed crop is composed of the various *Mytilus* species which occur in Europe, Asia and North and South America (Gosling 1992). *M. edulis* is the major molluscan species cultivated in Canada, and the most rapidly expanding shellfish sector in Canadian aquaculture.

Seafood consumers have a diverse range of products from which to choose, comprised of wild and cultured species, supplied by domestic production as well as imports (Wessells *et al.* 1995). Acceptance and selection are affected by economic factors such as price and income, socio-demographic factors such as nationality, household composition and location as well as preferences and opinions regarding seafood products and the quality of seafood products (Wessells *et al.* 1995). Therefore it is imperative that the aquaculture industry continue to provide premium seafood products. In order to provide premium

products at competitive rates, the industry must also learn to optimize production without compromising product quality or growth rates.

The mussel cultivation industry is currently undergoing a rapid expansion and faces a number of constraints ranging from planning and financing to a need for improved knowledge of species biology (Heggberget 1997). Rapid expansion has stimulated interest in estimating the carrying capacity of a specific culture area (Fréchette and Bacher 1998; Scholten and Smaal 1998; Newell *et al.* 1998; Carver and Mallet 1990). Carrying capacity is the highest stocking density at which production levels are maximized without inhibiting growth (Carver and Mallet 1990). There is concern that uncontrolled increases in stock density will eventually result in reduced growth rates and environmental disturbance. Continued research is needed in order to determine the most cost-effective and time-efficient method of achieving shorter production cycles while maintaining high quality meat yields. This is the key to becoming and remaining a competitive force in the world blue mussel aquaculture industry.

1.3 Ecological Role of Bivalves

Ecology may be defined as the scientific study of the interactions that determine the distribution and abundance of organisms (Krebs 1994). The adaptability of the organism may be defined by its capacity to optimize its physiological processes in a variable environment (Bayne *et al.* 1985). It is important to undertake ecological research to identify the significance of relative distribution patterns and abundance of organisms and

to quantify the effects of environmental variability on organisms. This knowledge will facilitate the application of ecological research.

1.3.1 Ecological Applications

Research directed towards elucidating physiological responses from animals offers a range of applications. For instance, bivalves are sedentary filter feeders and have the ability to concentrate a broad range of bacteriological pollutants, chemicals and naturally occurring toxins from the water column or sediment in which they live (Gosling 1992). These suspension feeding bivalves comprise a significant component of the inshore marine benthic ecosystems of the world. As a result, blue mussels have become important biological indicators. Programs such as the 'Mussel Watch' monitoring program have been developed to assess the spatial and temporal trends in chemical contamination of the environment (Gosling 1992). Many regions and countries of the world, including the United Kingdom, France, Canada, Australia, Japan, Taiwan, India, Mediterranean, South Africa and the former USSR have established similar monitoring programs (Gosling 1992).

An experimental approach to measuring the effects of changing environmental factors on organisms will not only provide insight on distribution and abundance but will also assist in the management of stocks in aquaculture. Bivalves are ideal candidates for ecological and physiological studies because there are many documented techniques that can be utilized to quantify food supply, food uptake and metabolic loss for these animals

(MacDonald and Thompson 1985). This, compounded with the wide range of applications for blue mussels, has resulted in a large body of literature investigating their biology.

1.3.2 Factors Affecting Production

Considerable research has been directed towards examining growth profiles of bivalves and the factors affecting their growth. Not only does growth vary according to size, age and genotype (Dolmer 1998), but environmental factors including temperature, salinity, water movement and seston quality and quantity also impact upon growth (Seed and Suchanek 1992). Despite the extraordinary volume of literature on bivalve biology, there are still many areas of bivalve physiology which are not completely understood. Further, bivalve physiology is strongly affected by season and locale, making it very difficult to identify consistent spatial/geographic trends in physiological behavior. For instance, Thompson (1984) found no clear relationship between oxygen consumption and the gametogenic cycle for *Mytilus edulis* in Newfoundland, whereas Widdows and Bayne (1971) observed high rates of oxygen consumption in *M. edulis* during the winter, and attributed the increased rate to gametogenesis. Smaal *et al.* (1997) suggested no relation between clearance rate and reproductive condition throughout the year. In gaining a better understanding of physiological processes, for instance, how oxygen consumption and feeding patterns relate to the gametogenic cycle, improved estimates of production will be attainable.

1.3.2.1 Mussel Origin

For the purpose of this work and throughout this thesis, mussel origin is defined as whether a mussel came from a wild or cultured population. There are a number of differences between wild and cultured mussels, e.g., the latter have a rapid growth and high meat yield, characteristics that significantly contribute to their quality (Gosling 1992). The fast growth of blue mussels held in suspension translates into a lighter, cleaner shell, and hence a greater number of mussels per unit weight (Lutz 1980). These features not only affect the site productivity and yield, but they also affect the acceptability of mussel products to buyers. In addition, cultivated blue mussels allocate less than half of their energy budget to reproduction than wild blue mussels in order to achieve their rapid growth (Rodhouse *et al.* 1984). Mallet and Carver (1993) found a positive correlation between shell growth and survival for a range of size classes. Fast growing blue mussels were found to have a lower risk of mortality compared with slow growing blue mussels. Camacho *et al.* (1995) observed that seed originating from collector ropes had higher growth rates than seed collected from intertidal areas, and suggest that this is due to a higher condition index and previous adaptation to rope culture conditions.

Mussels from collector ropes and the rocky shores experience very different feeding conditions. Food availability is often higher for mussels from collector ropes, and as a consequence they show higher condition indices (Camacho *et al.* 1995). Lower food

levels at the bottom compared to food levels in the water column (MacDonald 1986), differential food quality (Rodhouse *et al.* 1984), increased suspended sediment levels (MacDonald 1986) and increased vulnerability to predation pressures all contribute to the slower growth, lower meat yields and thicker shells of wild bivalves grown on the sea bottom compared to cultured bivalves grown in suspension.

1.3.2.2 Density

In Newfoundland, cultured mussels are grown out at densities that are often much higher than the densities of natural assemblages of wild mussels. Dense aggregations of bivalves can locally deplete the water of seston resulting in food limited growth (Pilditch *et al.* 1996). If a mussel sock is stocked too densely, there is an increased risk of mussel loss due to a depleting of food and oxygen. In addition, high stocking densities may result in reduced juvenile settlement due to a greater accumulation of biodeposits leaving relatively less surface area available for larval settlement (Mallet and Carver 1993). Mussel farmers must be able to show that they are benign users of coastal water, if they are to be allowed to expand to new areas or significantly increase production in existing areas (Gosling 1992). Also, pressure from nearby mussels may impair shell gaping. Shell gaping is a critical factor in controlling mussel pumping rate, which in turn affects food acquisition (Jørgensen *et al.* 1988).

Aquaculture sites should be designed to maximize food availability. It is likely that a decrease in the supply of seston will occur in the center of a lease if stocking density

and/or lease size are increased beyond optimal density (Pilditch *et al.* 1996). However, increased nutrient regeneration in the vicinity of mussel lines may actually enhance local primary production, given that increased stock densities have a positive effect on primary production (Carver and Mallet 1990). Such concerns strengthen the argument for continued research and development in aquaculture. The importance of the ratio of food supply to food demand per individual mussel for a particular site cannot be underestimated. Indices of energy acquisition and energy loss define the minimum needs for growth and are therefore critical to choosing potential cultivation areas. These physiological functions, when integrated into an ecosystem model, should allow predictive modeling of shellfish production of a bay (Bougrier *et al.* 1995).

The feeding behavior of cultivated mussels in response to natural particle assemblages is of particular interest for the selection of mussel farm sites and in the calculation of carrying capacities for these sites. The manipulation of density is a major tool for a mussel farmer to use to increase commercial production (Gosling 1992). Different stocking densities of mussels may take variable amounts of time to reach market size (Mallet and Carver 1993). For instance, deliberate overcrowding can also be used by a mussel farmer to slow growth rates for specific purposes such as to maintain a continuous supply of mussels of the desired size for marketing. The final market product must be taken into consideration when assessing the best or optimal stocking density as different products may necessitate a different initial stocking density (Parsons and Dadswell 1992). The manipulation of stocking density will become a more useful tool with increasing

diversification of the blue mussel market (e.g., mussel salads, individually-quick-frozen (IQF) products, vacuum-packed products and ready-made products).

1.3.2.3 Size

The market for seafood products demands a year round supply. In order to satisfy these demands, farmers must maintain several size classes of mussels. This will ensure availability of market size mussels for harvest throughout the year. Assuming that all size classes of animals respond in a similar manner to similar environmental conditions may jeopardize the reliability of models used to estimate production. For instance, a certain size class may have a higher overall food demand than another and will therefore take longer to reach market size given similar food availability conditions. Such mussels may also consume a disproportionate amount of the available food supply, depriving the other mussels. If different size classes of mussels consume different amounts of the available food, then this has implications for site design and site layout.

There is evidence within the literature that animals of different size classes do not always respond similarly to environmental conditions. Thiesen (1968) concluded that mortality in *Mytilus edulis* is size dependent with a mean annual mortality varying between 68 percent and 34 percent in mussels of 25 mm and 50 mm shell length, respectively. According to Suchanek (1978), Peterson (1979) and Tsuchiya (1983), smaller mussels are thought to be especially vulnerable to mortality at high temperatures. Thompson (1984) also reported size dependent mortality for *M. edulis* in Newfoundland.

Recent observations support these earlier findings. Temporal patterns of growth and survival were independently estimated for three size classes of mytilid mussels from a commercial aquaculture farm in Nova Scotia (Mallet and Carver 1993). Temporal variations in tissue weight in the two largest size groups were highly correlated, but were significantly different from those observed in the smallest size group. Mallet and Carver (1993) suggest that mussels of different sizes were responding differently to either endogenous and/or environmental cues. There have also been differences reported in the feeding behavior of small and large bivalves. Smaal *et al.* (1997) observed that clearance rates in smaller cockles (*Cerastoderma edule*) were reduced at low temperatures compared with larger animals. Lu and Blake (1997) observed that the weight specific clearance rates of juvenile bay scallops (*Argopecten irradians concentricus*) were independent of shell size at greater than 20,000 cells/mL, but decreased with increasing shell size at lower cell concentrations. Further, size-dependent bioaccumulation of hydrophobic organic contaminants in suspension feeding bivalves has been observed to be driven by size related differences in uptake rate (Gilek *et al.* 1996). However, others have observed no significant differences between small and large bivalves. For instance, Wildish and Saulnier (1992) observed no significant differences in growth rate between individual adult and juvenile giant scallops *Placopecten magellanicus* at a common water velocity of 10 cm/s.

It is important to understand the growth patterns of the different size classes of bivalves, as well as the underlying physiological and biochemical processes associated with growth. If small and large size classes of blue mussels respond differently to similar conditions, then this will affect production significantly. It is difficult to ascertain which of these processes or combinations thereof affect the performance of blue mussels, but it is still necessary to establish how different size classes respond to specific environmental conditions (Mallet and Carver 1993).

1.3.2.4 Species

Early genetic studies of *Mytilus* populations on the east coast of North America suggested that *Mytilus edulis* was the only species present (Koehn *et al.* 1976; Gartner-Kepay *et al.* 1980). Koehn *et al.* (1984) subsequently provided evidence that the *Mytilus* populations of Atlantic Canada consist of two genetically distinct forms that occur sympatrically at some locations, but with no evidence of interbreeding. These two genetically distinct forms, identified as groups II and III by Koehn *et al.* (1984) were later confirmed to belong to the species *M. edulis* and *M. trossulus*, respectively (Varvio *et al.* 1988; McDonald *et al.* 1991; Bates and Innes 1995; Mallet and Carver 1995; Comesaña *et al.* 1999). Mixed populations of the two species, with a range of proportions, commonly occur along the Atlantic coast of Nova Scotia, in Newfoundland and along the upper reaches of the Gulf of St. Lawrence (Mallet and Carver 1995).

The situation in Atlantic Canada is similar to that found in southwest England and the Atlantic coast of France, where *M. edulis* and *M. galloprovincialis* have overlapping ranges and are found at some locations to occur sympatrically (Cousteau *et al.* 1991). Gardner (1996) proposed that species of *Mytilus* adapt to different environments and thereby maintain their integrity, despite high dispersal potential and widespread hybridization.

There are very few sharply pronounced distributional differences in *Mytilus*. According to Gardner (1996), most differences occur as a shallow cline from one taxon to another. However, there is evidence of distributional differences between species on a global scale (Gosling 1984; Koehn 1991; Gardner 1992), as well of evidence supporting physiological and morphological adaptations to different environments (Tedengren *et al.* 1990; Gardner and Skibinski 1991; Willis and Skibinski 1992; Hilbish *et al.* 1994). For instance, in Europe *M. edulis* and *M. galloprovincialis* appear to be differentially distributed relative to the degree of wave exposure and the level of attachment in the intertidal zone (Gosling 1992; Comesaña and Sanjuan 1997). *M. galloprovinciallis* is more likely to be found in exposed environments than *M. edulis* (Gardner and Skibinski 1991; Willis and Skibinski 1992). In California, *M. galloprovincialis* and *M. trossulus* exhibit differential distribution patterns relative to temperature and salinity profiles (Sarver and Foltz 1993).

Bates and Innes (1995) sampled mussels from the intertidal zone of Newfoundland and found a higher frequency of *M. trossulus* at the more wave-exposed sites, and a higher frequency of *M. edulis* at the more sheltered sites. Comesaña *et al.* (1999) also sampled

from Newfoundland, but did not find a consistent pattern in the distribution of these species relative to wave exposure. However, these samples were collected subtidally (Comesaña *et al.* 1999). This is likely a complicating factor in attempting to detect differences in distribution related to wave exposure.

In general, *M. edulis* is characterized as a temperate cold-water mussel which can occur in brackish waters, and *M. trossulus* is a cold-water mussel, often found in areas which were ice-covered in previous Ice Ages, and is capable of withstanding very low salinities (Gardner 1996). If environmental variability plays an important role in maintaining the genetic integrity of the species, then it likely that two species may coexist in areas of environmental change (ecotones), since neither species is fully adapted to the changing (intermediate) environment (Gardner 1996). This is what is observed in Atlantic Canada. *Mytilus edulis* and *M. trossulus* in eastern Canada are located between the cooler Atlantic waters of higher salinity (the Boreal or Nova Scotian Province) and the cold sub-polar waters of lower salinity (the Arctic Province) (Varvio *et al.* 1988; McDonald *et al.* 1991).

The coexistence of *M. edulis* and *M. trossulus* in Atlantic Canada is also interesting from an aquacultural standpoint. Very little is known about the performance of the species relative to each other. Certain farm operators argue that higher production rates could be achieved if they could grow a stock of pure *M. edulis* (Mallet and Carver 1995). From the information collected at their study site on individual weight, survival and grading losses, Mallet and Carver (1995) estimated that the economic value of *M. edulis* was 1.7 times greater than its congener *M. trossulus*.

The literature suggests that similar species may display different adaptations to similar environmental conditions. Differential physiological adaptations may contribute significantly to the overall carrying capacity of a mussel culture site. Comesaña *et al.* (1999) have suggested that further studies be conducted to identify the factors responsible for maintaining the integrity of each species. Further studies are also needed to quantify the species-specific physiological responses of *M. edulis* and *M. trossulus* for incorporation into models used to predict blue mussel production.

1.3.2.5 Concentration of Available Food

Physiological responses such as changes in clearance rates, ingestion and particle selection may change with changing environmental conditions as suspension feeders are capable of regulating the quality and quantity of seston they consume (MacDonald and Ward 1994). Prins *et al.* (1994) observed that individual clearance rates of blue mussels decreased with increasing suspended particulate matter concentrations and showed a positive correlation with chlorophyll-*a*.

Food flux, defined as the amount of food per tidal cycle, must be studied in order to assess the impact of continually removing nutrients from water systems through harvesting (Thompson, 1984; Carver and Mallet 1990). Food flux varies temporally and spatially, fluctuating according to a number of factors such as current and phytoplankton blooms. Each of these factors affect the amount of food that is actually available to

bivalves for consumption. Establishing the relationship between the concentration and quality of suspended particulate matter and the uptake of this material by bivalves in specific environments is important to the understanding of energy flow, not only through this major group of marine primary consumers (Kiørboe *et al.* 1980), but also through the benthic community as a whole (MacDonald and Ward 1994).

1.3.2.6 Seasonal Variables

In order to understand the physiological ecology of suspension feeding animals, it is necessary to determine how they continue to meet their maintenance requirements from a diet that varies spatially and temporally in both availability and quality (Kreeger *et al.* 1995). The influence of temperature and food on the growth of bivalves is well documented within the literature, especially for mytilids (e.g., Widdows 1978; Bayne and Worrall 1980; Kautsky 1982; Sprung 1984). According to Hatcher *et al.* (1997), food availability is a significant control on the seasonally changing metabolism of mussels regardless of water temperature. They suggest that observed variability in growth rate of ice-covered *Mytilus edulis* is probably a response to differences in food availability rather than exposure to low temperatures. The higher temperature and food conditions associated with shallow waters in Sunnyside, Trinity Bay, NF have been shown to be more favorable for somatic growth and gamete production in the scallop *Placopecten magellanicus* than deeper waters (MacDonald and Thompson 1986).

Compounding this, blue mussels are ectothermic animals. With an increase in the environmental temperature, there is a corresponding increase in the metabolic rate. An increase in the metabolic rate of an organism implies an increase in the energy (food) requirement of that organism in addition to an increase in oxygen expenditure for fueling metabolic processes. Therefore it is important to incorporate seasonal differences into carrying capacity models.

1.3.2.7 Reproductive Condition

Since fecundity in mussels is age-dependent (Kautsky 1982), there will be differences in energy expenditure to growth and reproduction between adults and juveniles. Patterns of energy storage and usage associated with reproductive cycles in bivalves are well documented in the literature. MacDonald and Thompson (1986) observed a reduction in somatic weight as gamete development proceeded and an increase during periods of reduced gametogenic activity, suggesting a close relationship between energy available for growth and the reproductive cycle. Positive correlations between oxygen consumption and gametogenic activity have been reported for *Mytilus edulis* (Bayne and Widdows 1978) and *Cardium edule* (Newell and Bayne 1980). Respiration rates of cockles were observed to be significantly related to reproductive condition (Smaal *et al.* 1997). However, Newell *et al.* (1982) attributed observed differences in the gametogenic cycle of seven latitudinally separated populations of *M. edulis* to temporal and quantitative differences among habitats in the energy content of the mussels available food supply.

Changes in physiological status may also affect feeding. Newell and Thompson (1984) found reduced clearance rates in wild mussels for up to five days following prolonged periods of spawning. Smaal *et al.* (1997) found the respiration rates of *M. edulis* to be highest during the reproductive period.

1.4 Objective

In Newfoundland, *Mytilus edulis* inhabits a unique, subarctic environment that is dominated by the Labrador current and characterized by low water temperatures for several months of the year and low seston concentrations (Thompson 1984). Such systems have periods of very low water flow and therefore exhibit localized food depletion compared to estuaries, e.g., Carver and Mallet (1990).

The objective of this project was to contribute towards improved models for estimating the carrying capacities of blue mussel aquaculture sites in Newfoundland by providing empirical values for four physiological processes associated with feeding demand: clearance rate, ingestion rate, filtration rate and rate of oxygen consumption. Further, this project will provide a comparison of these four processes in two size classes of cultured and wild blue mussels, *M. edulis* and *M. trossulus*. Size and species proportions on a mussel aquaculture site may potentially affect the overall food demand of a particular stock of mussels. This, in turn, has direct implications for stocking density and stock

performance. Continued research and development in this field is crucial to the maintenance and expansion of the blue mussel aquaculture industry in Newfoundland.

1.4 Hypotheses

For *Mytilus edulis* and *M. trossulus* obtained from Reach Run, Newfoundland:

1. Weight-specific rates of clearance, ingestion, filtration and oxygen consumption differ between cultured and wild blue mussels.

2. *Mytilus edulis* and *M. trossulus* demonstrate different physiological responses to similar environmental conditions.

3. Rates of clearance, ingestion, filtration and oxygen consumption increase with an increase in the available food concentration in all blue mussels.

4. Rates of clearance, ingestion, filtration and oxygen consumption follow a seasonal cycle in all blue mussels.

Section 2 Methods

2.1 Site

Mussels used throughout this study were obtained from an aquaculture site (Farewell Mussel Farms Ltd.) at Reach Run, Newfoundland (49° 25′ N, 54° 42′ W (4531)) (Appendix 1). The site has been characterized as a flow-through system with currents averaging 3.4 cm/s (Struthers, A., pers-comm., Marine Institute, Memorial University). Longlines are anchored to the bottom with boulders and run parallel to the current flow. Average depth of the site is 24 m (MacNeil, G., pers-comm., Marine Institute, Memorial University). Average salinity from the surface to a depth of 15 m is 28 ppt (Clemens *et al.* 2000).

2.2 Mussel Stock

For the purpose of this study, the term 'blue mussels' encompasses the species *Mytilus edulis* and *M. trossulus*. Approximately 100 unprocessed cultured blue mussels were obtained monthly from suspended mussel socks. At the same time, approximately 100 wild blue mussels were collected along the shoreline of the cultivation site. Mussels were obtained from as large a size range of cultured and wild animals as possible, ranging 10-75 mm shell length (SL). Samples were obtained during the third week of almost every month for 17 months between March 1998 and August 1999. Mussels were transported

to the Ocean Sciences Centre (OSC), Memorial University of Newfoundland (MUN) in Logy Bay, Newfoundland within 12 hours.

2.3 Laboratory Conditions

At the OSC, cultured and wild mussels were placed in separate trays of a flow-through system; each tray was continuously supplied with coarsely filtered seawater at ambient temperature and salinity. Throughout the study salinity ranged between 32 and 34 ppt and temperature ranged between 4 °C and 16.5 °C (Figure 1). Dissolved oxygen was always above 80 percent saturation.

All mussels were maintained on a batch-fed diet of cultured algae. At the start of the project, the dry weight of a random sample of 25 mussels was recorded as well as the dry weight of algae per liter. Daily ration was approximately 3 percent of the dry soft body weight of the animals. The diet consisted of equal cell concentrations of two species of microalgae, the diatom *Chaetoceros muelleri* and the flagellate *Isochrysis galbana* (clone T-ISO), providing a balanced diet for the mussels. Cultures of these two species were maintained in logarithmic phase growth in autoclaved *f*/2 medium, at 20 °C, under constant illumination (fluorescent cool white lights) and were gently aerated with filtered air. Dissolved silica was added to *C. muelleri* cultures. It has been shown that particles approximately 5 μm diameter have an important role in the nutrition of mussels since particles of this size represent an important fraction of the total particulate organic matter naturally available to mussels (Vahl 1972). As well, *Mytilus edulis* has been shown to

retain all particles above 4 μm at close to 100 percent efficiency (Newell and Shumway 1993). Larger particles up to 110 μm have also been shown to possibly comprise a significant portion of the diet of *Mytilus edulis*, however, particles of this size were not available to the mussels used throughout the present study.

Mussels were acclimated to laboratory conditions for at least 7 days prior to experimentation.

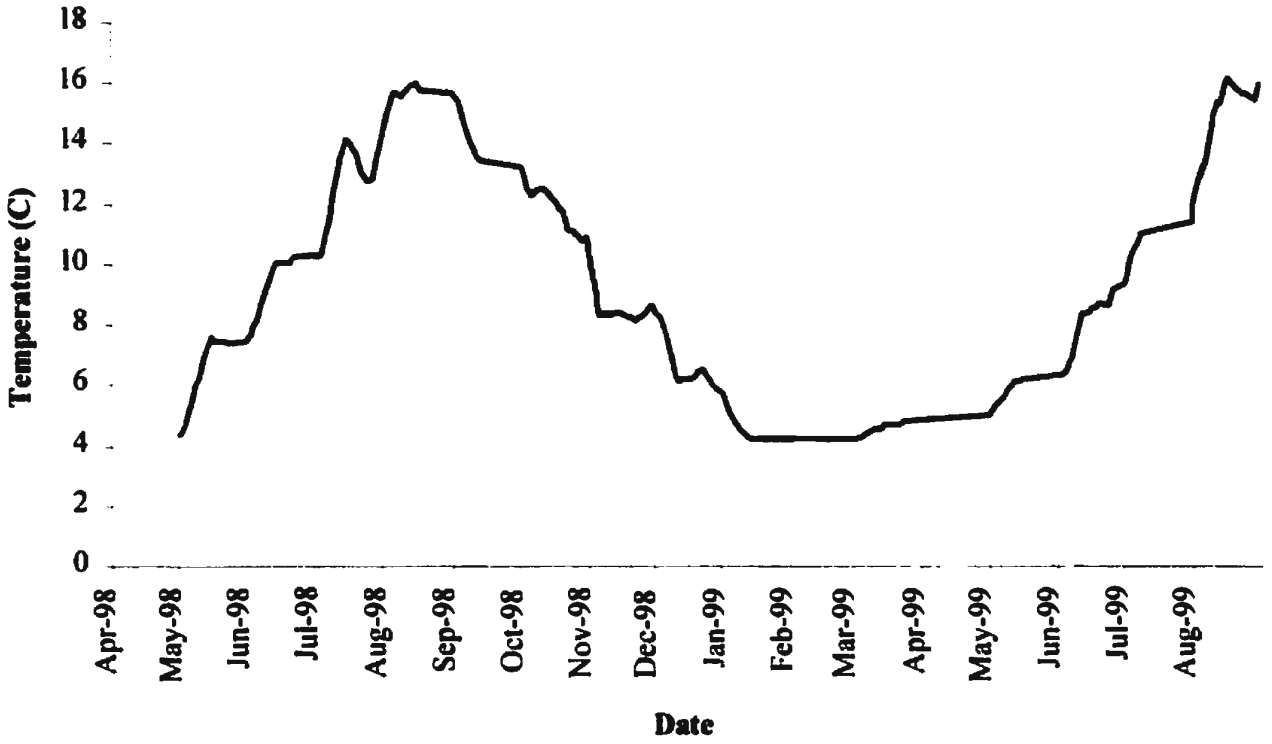

Figure 1: Ambient seawater temperature (degrees Celsius) in the flow-through holding trays.

2.4 Physiological Working Definitions

Four physiological variables were measured for all experimental mussels. Clearance rate (L/h) was defined as the volume of water cleared of suspended particles greater than 2 μm in diameter per unit time; in the absence of pseudofeces, ingestion rate (cells/h) was defined as the number of suspended particles greater than 2 μm in diameter removed per unit time; filtration rate (mg/h) was defined as the weight of total particulates filtered per unit time (Bayne 1976). Oxygen consumption (mL/h) was defined as the estimated rate of decrease of the volume of oxygen inside a respiration measurement chamber per unit time (Thompson 1984).

2.5 Experimental Apparatus

The experimental apparatus was an "octopus set-up", as per MacDonald (1985). The octopus set-up (Appendix 2) (octopus set-up A) consisted of a constant volume (7.7-L) header tank connected to eight individual feeding chambers. One mussel was placed in each of seven feeding chambers. One chamber was used as a control chamber. The size and shape of the oblong containers prevented recirculation of the experimental diet. This was verified by observing the patterns of colored dyes introduced into the containers. The header tank received seawater filtered through a linear arrangement of four filter cartridges, a coarse filter, a 10-μm filter, a 3-μm filter and a 1-μm filter. This effectively reduced potential variations in the experimental diets due to irregularities in the quantity

and quality of suspended seston in the incoming seawater. Seawater was maintained at ambient temperature and salinity. Three peristaltic pumps delivered a 50/50 percentage mixture by cell numbers of *Chaetoceros muelleri* and *Isochrysis galbana* from a 68-L food reservoir to the header tank, supplying the header tank with a known concentration of food and at known and constant rate. The food reservoir was gently aerated to ensure uniform mixing and to prevent particle settlement. In turn, the header tank, also aerated, supplied the eight feeding chambers with a known concentration of food at known and constant rates.

Inflow rates, maintained by calibrated flow restrictors into the individual feeding chambers, ranged from 130-180 mL/min. It has been determined that clearance rates are independent of water flow in this range for scallops (MacDonald 1985). Header inflow was such that water flowed continuously through the outflow, thereby providing a constant head, which ensured that the flow through each valve varied less than 10 % (MacDonald 1985). After the water passed through an inflow valve, it was delivered to the bottom of the feeding chamber. A mussel was positioned behind a baffle at the bottom of the feeding chamber. Baffles further ensured good mixing within the chambers. The overflow exited through a drain near the surface of the chamber. Samples were collected from this overflow to measure rates of clearance, ingestion and filtration. Mussels were then removed from the feeding chambers and placed in respiration measurement chambers to measure rate of oxygen consumption.

A second identical octopus set-up (octopus set-up B) was employed as well in order to increase sample size.

2.6 Experimental Design

About seven to ten trials were conducted per month with each trial lasting three days. For each trial, small and large cultured and wild mussels were used. Mussels with a shell length (SL) less than or equal to 35 mm were characterized as small and mussels with a SL greater than or equal to 50 mm were characterized as large. Mussels were exposed to low (<3,500 cells/mL), medium (>3,500 cells/mL, <7,500 cells/mL) or high (>7,500 cells/mL) food concentrations consisting of a 50/50 percentage mixture of *Chaetoceros muelleri* and *Isochrysis galbana*. Octopus set-ups A and B received the same experimental diet.

Day 1

On day 1 of each trial, 14 mussels were selected, 7 cultured (small and large) and 7 wild (small and large). All mussels were gently scrubbed to remove any dirt or epibionts. Shell lengths and shell heights were recorded (mm) using Vernier calipers. Mussels were then placed in the feeding chambers of the octopus set-up already supplied with filtered seawater. The food reservoir was prepared and food was pumped from the food reservoir to the header tank at a specific rate calculated according to algal density within the food reservoir and the flow rate of the incoming filtered seawater supplying the header tank.

Once the pumps had been activated, the mussels were left to acclimate to the experimental apparatus and diet for approximately 24 hours. Within an hour of placing the mussels in the individual feeding chambers, water samples were collected from each standpipe and timed the flow so that outflow rate (mL/min) could be determined.

Day 2

Clearance Rate

Any feces present in the feeding chambers were carefully removed with a pipette. This ensured that particle counts were representative of the actual number of algal cells that had been removed from the water. From octopus set-up A, 10-mL outflow water samples were collected from the drain of each of the eight feeding chambers and 10-mL inflow water samples were collected from the header tank. Particle concentrations were then quantified using a Model II Coulter Multisizer fitted with a 100-μm aperture tube. The final particle count was a minimum of three consecutive and consistent samples.
The number of cells/mL was quantified by measuring three 50-μL volumes from each 10-mL sample. Samples were taken at least three times over a time period of approximately 7 hours, and an average clearance rate was calculated.

Clearance rates were calculated according to:

$$CR = F(C_1 - C_2) / C_1 \quad \text{where:}$$

CR = clearance rate (L/h)

F = flow rate of individual feeding chamber (mL/min)

C_1 = particle concentration of inflow sample (cells/mL)

C_2 = particle concentration of outflow sample (cells/mL)

All measurements were corrected for the control chamber. However, there was no significant settlement in the control chamber.

Ingestion Rate

Ingestion rates were calculated according to:

$$IR = (CR * B) - PS$$ where:

IR = ingestion rate (cells/h)

CR = clearance rate (L/h)

B = Available food concentration (cells/L)

PS = rate of pseudofaeces production

All measurements were corrected for the control chamber. However, there was no significant settlement in the control chamber.

Filtration Rate

From the same octopus set-up, 4-L outflow water samples were collected from the drain of each of the eight feeding chambers and 4-L inflow water samples were collected from the header tank. Samples were taken at least three times over a time period of approximately 7 hours, and an average filtration rate was calculated The particulate material was gently vacuum filtered onto preweighed and precombusted GF/C filters. Filters were then rinsed with 10 mL of 3 percent (isotonic) ammonium formate.

The filters were then dried to constant weight at 60 °C, combusted in a muffle furnace at 450 °C for approximately 12 hours, cooled in a dessicator and reweighed. All filters were placed in a desiccation chamber for approximately 15 minutes prior to weighing to correct for any moisture uptake from the air.

Filtration rates were calculated according to.

$$FR = F(I-O) \quad \text{where:}$$

FR = filtration rate (mg/h)

F = flow rate of individual feeding chamber (L/h)

I = inflow seston (mg)

O = outflow seston (mg)

All measurements were corrected for the control chamber. However, there was no significant settlement in the control chamber.

Oxygen Uptake

Concurrently on Day 2, oxygen uptake rates were measured in those mussels previously maintained in octopus set-up B. Mussels were removed from the feeding chambers and placed immediately in Plexiglas oxygen uptake measurement chambers filled with a known volume (375 or 380 mL) of filtered (to 1 μm) and fully saturated seawater at ambient temperature and salinity (Appendix 3). Mussels did not feed in the respiratory chambers. A respiratory rather than a feeding pumping rate was maintained. Within the chambers, mussels were placed on perforated clear glass plates overlying a magnetic stir bar. The cover of the chambers had three openings. The center opening was for positioning an oxygen electrode. Two holes located on either side of this facilitated filling the chambers with seawater as well as expiration of any excess air bubbles. These two holes were sealed with rubber stoppers during the oxygen uptake experiments. Up to four oxygen uptake chambers were then placed in a temperature control bath (Neslab) maintained at ambient seawater temperature. Submersible magnetic stirrers gently circulated the water in the respiration chambers. Temperature was maintained within 0.5 °C of ambient temperature.

The oxygen uptake chambers were sealed with an oxygen electrode, and the decline in partial pressure of oxygen in the chambers was measured with an OM2000 oxygen meter (Cameron Instrument Company, Texas). The oxygen level was never allowed to drop below 75 % of saturation. Oxygen uptake experiments usually lasted from 1.5 to 3 hours per mussel, depending upon water temperature and animal size. Mussels were then returned to the octopus set-up.

Oxygen uptake was calculated using the following equation:

$$R = m * C * V$$ where:

R = oxygen uptake (L/h)

m = rate of decrease in oxygen (mm Hg/h)

C = conversion factor for converting mm Hg to oxygen solubility in mL/L based upon salinity and temperature

V = volume of the oxygen uptake measurement chamber (L)

Day 3

Clearance, ingestion and filtration rates were measured in mussels from octopus set-up B and oxygen uptake were measured in mussels from octopus set-up A.

Once all measurements had been made, the soft body tissues of the mussels were removed. A small piece was taken from the adductor muscle or the mantle of each

mussel and preserved in 95 % ethanol for allozyme and DNA analysis. The remaining tissues were dried to constant weight at 60 °C in preweighed aluminum foil boats.

2.7 Genetic Identification of Species

2.7.1 Allozyme analysis

Horizontal starch-gel electrophoresis was carried out on 11 % gels (Sigma starch) at 4 °C. The supernatant was used as the source for 5 enzyme loci that show different levels of diagnostic power for the 2 *Mytilus* taxa. Two loci were used to distinguish between the taxa. Esterase-D (*Est-D*) is a highly diagnostic locus for *Mytilus edulis* and *M. trossulus*, and mannose-6-phosphate isomerase (*Mpi*) is completely diagnostic between these 2 taxa. Electrophoretic procedures were conducted following Bates and Innes (1995) for *Est-D* and Väinolä and Hvilsom (1991) for *Mpi* (Comesaña *et al.* 1999).

2.7.2 DNA analysis

Total DNA extraction was performed following procedures outlined in Heath *et al.* (1995). Two nuclear markers (*Glu 5* and *ITS*) and 1 mitochondrial DNA marker (*COIII*) were analyzed after polymerase chain reaction amplification. *Glu 5* and *ITS* are co-dominant DNA markers producing 2 specific *Mytilus edulis* and *M. trossulus* patterns and distinct patterns for hybrids. Similar amplification conditions were provided for both

markers. The PCR products were run in a 3 % agarose gel (2 % Sigma and 1 % NuSieve GTG agarose). The 2 allozyme loci (*Est-D* and *Mpi*) and the 2 nuclear DNA markers (*Glu 5* and *ITS*) were used to classify the mussels as "pure" *edulis*, "pure" *trossulus* or hybrids (Comesaña *et al.* 1999).

2.8 Standardization of Physiological Rates

Each physiological rate was examined for each mussel. Sample sizes and weight ranges are listed in Tables 2a, 3a, 4a and 5a. The effects of body size can be excluded by selecting animals of equivalent size, but it is likely that there will be variation in the dry soft body weight (Bayne *et al.* 1985). For this analysis, the effects of body size were removed according to a standardization procedure described in Bayne *et al.* (1985). First, log value physiological rates were regressed against log value dry weights for each sample for each of clearance rate (L/h), ingestion rate (cells/h), filtration rate (mg/h) and oxygen uptake (mL/h).

The slopes of the individual regression equations were used as weight coefficients. These weight coefficients were then used to correct all physiological rates to a standard animal of one gram dry tissue weight using an allometric equation:

$$Y = aX^b \qquad \text{where:}$$

Y = physiological rate

X = dry body weight (g)

a = intercept

b = slope (weight exponent)

The weight exponent of each equation was then used to correct for differences in body weight. Rates of clearance, ingestion, filtration and oxygen consumption have been corrected to a standard 1 gram animal by means of the equation:

$$\log a = \log Y - b \log X \qquad \text{where:}$$

a = corrected physiological rate

Y = the uncorrected (measured) physiological rate

b = the weight exponent for the physiological rate function

X = the observed dry weight of the animal

For comparisons between small and large mussels, small mussels were standardized to 0.1 gram and large mussels to 1 gram dry weight using the same equation described above. For all other comparisons, all rates were standardized for a 1 gram mussel. If the weight coefficients obtained from the regressions analyses were significantly different from each other, then the standardization analysis was complete. If the slopes were not significantly different, then slope elevations were compared using an analysis of covariance (ANCOVA).

2.9 Statistical Analysis

According to Sokal and Rohlf (1995), multiway analyses of variance (ANOVAs) were performed to simultaneously test the significance of each of the independent factors on each of the four physiological rates examined. ANOVAs were used in order to test for differences among sample means as well as differences among linear combinations of the means (Sokal and Rohlf 1995).

All statistical procedures were carried out using the General Linear Model (GLM) procedure of SPSS 9.0 for Windows. The dependent variables were standardized rates of clearance (L/h/g), ingestion (cells/h/g), filtration (mg/h) and oxygen consumption (mL/h/g). The independent variables or factors were mussel origin (cultured or wild), mussel species (*Mytilus edulis* or *M. trossulus*), date and food concentration (low, medium or high). Although the relationship between date and temperature is not exactly linear, date was selected as an independent factor since the many temperatures would have complicated the ANOVA analyses, and as well, the measurements obtained from the mussels tested during one date period were subsequently used to develop weight exponents.

Small and large mussels were compared qualitatively and descriptive values only are provided, i.e. these groups were not compared in order to demonstrate a statistical significance since it is already known that larger mussels have higher feeding rates than smaller mussels.

Section 3 Results

3.1 Standardization of Physiological Rates

All mussels (cultured and wild, small and large, *Mytilus edulis* and *M. trossulus*) were pooled for the purpose of calculating slopes for each monthly sampling period because, individually, the sample sizes were not always large enough to perform regressions. Log clearance, log ingestion, log filtration and log oxygen uptake were significantly correlated with log dry weight, in most cases. The only exception was in July 1999, log filtration rate was not significantly correlated with log dry weight. Weight coefficients ranged from 0.130 to 0.529 for clearance rate, 0.194 to 0.578 for ingestion, 0.135 to 0.782 for filtration and 0.186 to 0.823 for oxygen uptake (Tables 2b, 3b, 4b and 5b). For each factor, the slopes for each sampling period were compared using an analysis of covariance (ANCOVA). All slopes were significantly different ($P<0.001$), therefore no further analyses were conducted at this point (Table 1). Elevations were not compared.

All physiological rates presented in this thesis are the calculated standardized rates for a one gram dry weight mussel, unless otherwise indicated. All residuals were examined graphically, and followed a normal distribution pattern.

Table 1: A summary of the analyses of covariance (ANCOVAs) performed to compare the weight coefficients (slopes) for each factor, clearance (L/h), ingestion (cells/h), filtration (mg/h) and oxygen uptake (mL/h) for each sampling period.

	Clearance (L/h)	**Ingestion (cell/h)**	**Filtration (mg/h)**	**Oxygen Uptake (mL/h)**
R Squared	0.489	0.400	0.622	0.643
Degrees of Freedom	15, 315	15, 315	15, 315	14, 313
F – Statistic	19.16	13.34	32.92	38.41
P-value	< 0.001	< 0.001	< 0.001	< 0.001

Table 2a: A summary of the sample size and the minimum and maximum dry weights (W) (g) of the animals (*Mytilus edulis* and *M. trossulus*) comprising each respective sampling period for clearance rate (L/h).

Month	n	W_{min}	W_{max}
April 98	11	0.02	1.17
May 98	25	0.03	2.51
June 98	21	0.02	1.91
July 98	25	0.03	2.82
August 98	19	0.02	1.29
September 98	14	0.03	1.70
October 98	30	0.03	1.91
November 98	30	0.10	3.63
December 98	28	0.09	2.69
January 99	13	0.03	2.75
March 99	24	0.02	2.95
May 99	15	0.02	3.72
June 99	21	0.02	2.09
July 99	9	0.02	1.45
August 99	31	0.01	2.19

Table 2b: Regression analyses for log value physiological rates and log value dry weights, following the allometric relationship $y = ax^b$, where y = clearance rate (L/h).

Month	a ±SE	b ±SE	r^2	F	p-value
April 98	0.556 ± .040	0.189 ± 0.057	0.50	11.03	0.00891
May 98	0.439 ± .076	0.310 ± 0.10	0.27	9.71	0.00486
June 98	0.424 ± 0.094	0.312 ± 0.091	0.35	11.65	0.00292
July 98	0.531 ± 0.033	0.130 ± 0.041	0.28	9.84	0.00479
August 98	0.400 ± 0.10	0.433 ± 0.10	0.50	19.29	0.000398
September 98	0.374 ± 0.084	0.339 ± 0.098	0.46	11.86	0.00487
October 98	0.427 ± 0.055	0.300 ± 0.058	0.47	26.56	<0.0001
November 98	0.160 ± 0.056	0.276 ± 0.10	0.18	7.53	0.0105
December 98	0.0232 ± 0.077	0.498 ± 0.13	0.33	14.51	0.000766
January 99	-0.0174 ± 0.99	0.378 ± 0.13	0.36	7.87	0.0171
March 99	0.190 ± 0.56	0.237 ± 0.073	0.29	10.57	0.00366
May 99	0.160 ± 0.086	0.379 ± 0.087	0.56	19.05	0.000766
June 99	0.247 ± 0.068	0.177 ± 0.078	0.17	5.20	0.0342
July 99	0.090 ± 0.13	0.529 ± 0.20	0.43	7.09	0.0323
August 99	0.554 ± 0.050	0.252 ± 0.055	0.40	21.12	<0.0001

Table 3a: A summary of the sample size and the minimum and maximum dry weights (W) (g) of the animals (*Mytilus edulis* and *M. trossulus*) comprising each respective sampling period for ingestion rate (cells/h).

Month	n	W_{min}	W_{max}
April 98	11	0.02	1.17
May 98	25	0.03	2.51
June 98	21	0.02	1.19
July 98	25	0.03	2.82
August 98	19	0.02	1.29
September 98	14	0.03	1.70
October 98	30	0.03	1.91
November 98	30	0.1	3.63
December 98	28	0.09	2.69
January 99	13	0.03	2.75
March 99	24	0.02	2.95
May 99	15	0.02	3.72
June 99	21	0.02	2.09
July 99	9	0.02	1.45
August 99	31	0.01	2.19

Table 3b: Regression analyses for log value physiological rates and log value dry weights, following the allometric relationship $y = ax^b$, where y = ingestion rate (cells/h).

Month	a ±SE	b ±SE	r^2	F	p-value
April 98	4.29 ± 0.086	0.276 ± 0.12	0.29	5.10	0.00503
May 98	4.05 ± 0.086	0.252 ± 0.11	0.15	5.08	0.0341
June 98	3.98 ± 0.13	0.350 ± 0.12	0.27	8.23	0.00984
July 98	4.12 ± 0.060	0.194 ± 0.073	0.22	7.11	0.0145
August 98	4.02 ± 0.18	0.467 ± 0.18	0.24	6.66	0.0194
September 98	4.05 ± 0.10	0.334 ± 0.12	0.35	8.14	0.0145
October 98	4.05 ± 0.12	0.335 ± 0.12	0.18	7.48	0.0107
November 98	3.84 ± 0.059	0.387 ± 0.11	0.29	12.88	0.00125
December 98	3.95 ± 0.097	0.509 ± 0.16	0.24	9.63	0.00458
January 99	3.53 ± 0.097	0.377 ± 0.13	0.37	8.20	0.0154
March 99	3.66 ± 0.079	0.221 ± 0.10	0.14	4.69	0.0414
May 99	3.85 ± 0.18	0.431 ± 0.19	0.24	5.35	0.0378
June 99	4.04 ± 0.081	0.258 ± 0.093	0.25	7.72	0.0120
July 99	3.57 ± 0.19	0.578 ± 0.28	0.28	4.15	0.0502
August 99	4. 42 ± 0.069	0.283 ± 0.071	0.33	15.80	0.000428

Table 4a: A summary of the sample size and the minimum and maximum dry weights (W) (g) of the animals (*Mytilus edulis* and *M. trossulus*) comprising each respective sampling period for filtration rate (mg/h).

Month	n	W_{min}	W_{max}
April 98	10	0.04	1.05
May 98	22	0.03	1.95
June 98	22	0.02	1.91
July 98	26	0.03	2.82
August 98	17	0.02	1.28
September 98	14	0.03	1.70
October 98	44	0.01	1.91
November 98	23	0.1	3.63
December 98	28	0.06	2.69
January 99	12	0.03	1.48
March 99	22	0.02	2.95
May 99	12	0.02	3.72
June 99	19	0.02	1.91
July 99	8	0.02	1.45
August 99	26	0.01	2.19

Table 4b: Regression analyses for log value physiological rates and log value dry weights, following the allometric relationship $y = ax^b$, where y = filtration rate (mg/h).

Month	A ±SE	b ±SE	r^2	F	p-value
April 98	0.622 ± 0.078	0.782 ± 0.31	0.34	6.31	0.0332
May 98	-1.90 ± 0.29	0.601 ± 0.38	0.13	4.63	0.0422
June 98	-2.41 ± 0.11	0.222 ± 0.11	0.14	4.48	0.0470
July 98	-2.47 ± 0.054	0.148 ± 0.063	0.23	5.52	0.0247
August 98	-2.63 ± 0.13	0.265 ± 0.12	0.18	4.51	0.0508
September 98	-2.47 ± 0.12	0.424 ± 0.15	0.36	8.38	0.0135
October 98	-2.41 ± 0.067	0.173 ± 0.071	0.10	5.94	0.0192
November 98	-2.47 ± 0.086	0.331 ± 0.14	0.36	5.07	0.0352
December 98	-2.66 ± 0.037	0.318 ± 0.059	0.50	28.60	< 0.0001
January 99	-2.56 ± 0.12	0.455 ± 0.16	0.40	8.21	0.0168
March 99	-2.60 ± 0.089	0.292 ± 0.11	0.38	6.81	0.0168
May 99	-2.50 ± 0.014	0.135 ± 0.014	0.89	95.57	< 0.0001
June 99	-2.86 ± 0.10	0.323 ± 0.11	0.30	8.80	0.00864
July 99	-1.11 ± 0.49	0.356 ± 0.93	-0.06	0.15	0.706
August 99	-2.75 ± 0.085	0.220 ± 0.087	0.34	6.32	0.0191

Table 5a: A summary of the sample size and the minimum and maximum dry weights (W) (g) of the animals (*Mytilus edulis* and *M. trossulus*) comprising each respective sampling period for oxygen uptake (mL/h).

Month	N	W_{min}	W_{max}
May 98	11	0.04	2.51
June 98	21	0.02	1.91
July 98	28	0.03	2.82
August 98	19	0.02	1.29
September 98	13	0.03	1.45
October 98	50	0.01	2.04
November 98	34	0.1	3.63
December 98	24	0.09	2.69
January 99	9	0.03	2.75
March 99	24	0.02	2.95
May 99	16	0.02	3.72
June 99	26	0.02	2.09
July 99	7	0.02	1.45
August 99	27	0.01	2.19

Table 5b: Regression analyses for log value physiological rates and log value dry weights, following the allometric relationship $y = ax^b$, where y = oxygen uptake (mL/h).

Month	a ±SE	b ±SE	r^2	F	p-value
May 98	0.367 ± 0.14	0.823 ± 0.24	0.43	12.31	0.00348
June 98	-0.246 ± 0.059	0.186 ± 0.060	0.30	9.48	0.00618
July 98	-0.274 ± 0.047	0.336 ± 0.053	0.60	40.74	< 0.0001
August 98	-0.516 ± 0.064	0.464 ± 0.063	0.75	54.30	< 0.0001
September 98	-0.172 ± 0.11	0.450 ± 0.12	0.50	13.02	0.00411
October 98	-0.188 ± 0.078	0.623 ± 0.082	0.54	57.91	< 0.0001
November 98	-0.876 ± 0.083	0.794 ± 0.16	0.41	24.20	< 0.0001
December 98	-1.18 ± 0.094	0.370 ± 0.17	0.14	4.78	0.0395
January 99	-1.63 ± 0.23	0.691 ± 0.28	0.38	5.89	0.0456
March 99	-1.29 ± 0.077	0.415 ± 0.10	0.41	17.32	0.000406
May 99	-0.431 ± 0.048	0.245 ± 0.045	0.65	29.06	< 0.0001
June 99	-0.477 ± 0.073	0.387 ± 0.081	0.46	22.63	< 0.0001
July 99	-0.324 ± 0.039	0.487 ± 0.053	0.93	84.33	0.000257
August 99	-0.647 ± 0.17	0.655 ± 0.17	0.34	15.28	0.000625

3.2 Mussel Origin

All measured physiological rates for each sample mussel were standardized to 1 gram dry tissue weight. Four-way analyses of variance (ANOVAs) were used to test the significance of mussel origin, species, available food concentration and date on standardized rates of clearance, ingestion, filtration and oxygen uptake. The analyses revealed no significant differences in the observed rates of clearance ($F = 1.387$, d.f. = 1, 315, $P = 0.240$) (Table 6), ingestion ($F = 3.290$, d.f. = 1, 315, $P = 0.071$) (Table 7), filtration ($F = 0.250$, d.f. = 1, 282, $P = 0.610$) (Table 8) and oxygen uptake ($F = 0.030$, d.f. = 1, 307, $P = 0.860$) (Table 9) between cultured blue mussels and wild blue mussels. Therefore, cultured and wild mussels were pooled and treated as a single group for all remaining analyses.

Table 6: ANOVA showing no significant difference in clearance rate between cultured and wild *Mytilus edulis* and *M. trossulus*.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	574.18	110	5.22	3.85	<0.001
Intercept	1268.50	1	1268.50	935.51	<0.001
Cultured or Wild	1.88	1	1.88	1.39	0.24
Species	39.75	1	39.75	29.32	<0.001
Food Concentration	7.78	2	3.89	2.87	0.06
Date	173.72	14	12.41	9.15	<0.001
Cultured or Wild * Species	0.31	1	0.31	0.23	0.63
Cultured or Wild * Food Concentration	0.79	2	0.40	0.29	0.75
Species * Food Concentration	5.19	2	2.59	1.91	0.15
Cultured or Wild * Species * Food Concentration	2.83	2	1.41	1.04	0.35
Cultured or Wild * Date	35.00	13	2.69	1.99	0.02
Species * Date	15.00	14	1.07	0.79	0.68
Cultured or Wild * Species * Date	5.54	10	0.55	0.41	0.94
Food Concentration * Date	41.99	20	2.10	1.55	0.07
Cultured or Wild * Food Concentration * Date	10.32	11	0.94	0.69	0.75
Species* Food Concentration * Date	15.10	13	1.16	0.86	0.60
Cultured or Wild * Species * Food Concentration * Date	0.48	2	0.24	0.18	0.84
Error	277.97	205	1.36		
Total	2998.71	316			
Corrected Total	852.15	315			
	R Squared = .674 (Adjusted R Squared = .499)				

Table 7: ANOVA showing no significant difference in ingestion rate between cultured and wild *Mytilus edulis* and *M. trossulus*.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	75748293044	110	688620845.86	11.37	<0.001
Intercept	64769637992	1	64769637991.93	1069.47	<0.001
Cultured or Wild	199275716	1	199275716.02	3.29	0.07
Species	1056741960	1	1056741959.73	17.45	<0.001
Food Concentration	17154486135	2	8577243067.26	141.63	<0.001
Date	9172240889	14	655160063.51	10.82	<0.001
Cultured or Wild * Species	5134037.854	1	5134037.85	0.08	0.77
Cultured or Wild * Food Concentration	154997326.6	2	77498663.30	1.28	0.28
Species * Food Concentration	90018557.4	2	45009278.70	0.74	0.48
Cultured or Wild * Species * Food Concentration	237686363.7	2	118843181.87	1.96	0.14
Cultured or Wild * Date	2793727553	13	214902119.46	3.55	<0.001
Species * Date	1089787069	14	77841933.51	1.29	0.22
Cultured or Wild * Species * Date	481258106.5	10	48125810.65	0.79	0.63
Food Concentration * Date	14522193685	20	726109684.23	11.99	<0.001
Cultured or Wild * Food Concentration * Date	3517716708	11	319792427.98	5.28	<0.001
Species * Food Concentration * Date	808754209.1	13	62211862.24	1.03	0.43
Cultured or Wild * Species * Food Concentration * Date	172066916.8	2	86033458.40	1.42	0.24
Error	12415335766	205	60562613.49		
Total	1.64468E+11	316			
Corrected Total	88163628811	315			
	R Squared = .859 (Adjusted R Squared = .784)				

Table 8: ANOVA showing no significant difference in filtration rate between cultured and wild *Mytilus edulis* and *M. trossulus*.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	931.47	99	9.41	1.33	0.05
Intercept	1759.18	1	1759.18	249.43	<0.001
Cultured or Wild	1.80	1	1.80	0.25	0.61
Species	0.19	1	0.19	0.03	0.87
Food Concentration	0.66	2	0.33	0.05	0.95
Date	163.06	13	12.54	1.78	0.05
Cultured or Wild * Species	20.00	1	20.00	2.84	0.09
Cultured or Wild * Food Concentration	29.63	2	14.82	2.10	0.13
Species * Food Concentration	45.86	2	22.93	3.25	0.04
Cultured or Wild * Species * Food Concentration	8.53	2	4.27	0.61	0.55
Cultured or Wild * Date	67.10	11	6.10	0.86	0.58
Species * Date	91.92	13	7.07	1.00	0.45
Cultured or Wild * Species * Date	27.91	10	2.79	0.40	0.95
Food Concentration * Date	116.05	17	6.83	0.97	0.50
Cultured or Wild * Food Concentration * Date	114.69	10	11.47	1.63	0.10
Species * Food Concentration * Date	92.92	11	8.45	1.20	0.29
Cultured or Wild * Species * Food Concentration * Date	5.48	3	1.83	0.26	0.85
Error	1290.69	183	7.05		
Total	5618.06	283			
Corrected Total	2222.16	282			
	R Squared = .419 (Adjusted R Squared = .105)				

Table 9: ANOVA showing no significant difference in oxygen uptake between cultured and wild *Mytilus edulis* and *M. trossulus*.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	76.06	100	0.76	3.93	<0.001
Intercept	49.41	1	49.41	255.57	<0.001
Cultured or Wild	0.01	1	0.01	0.03	0.86
Species	0.17	1	0.17	0.87	0.35
Food Concentration	1.64	2	0.82	4.23	0.02
Date	41.05	13	3.16	16.33	<0.001
Cultured or Wild * Species	0.01	1	0.01	0.05	0.82
Cultured or Wild * Food Concentration	1.89	2	0.94	4.89	0.01
Species * Food Concentration	0.98	2	0.49	2.53	0.08
Cultured or Wild * Species * Food Concentration	0.34	2	0.17	0.88	0.42
Cultured or Wild * Date	5.68	12	0.47	2.45	0.01
Species * Date	2.13	13	0.16	0.85	0.61
Cultured or Wild * Species * Date	1.64	11	0.15	0.77	0.67
Food Concentration * Date	7.95	15	0.53	2.74	<0.001
Cultured or Wild * Food Concentration * Date	3.02	11	0.27	1.42	0.17
Species * Food Concentration * Date	2.28	12	0.19	0.98	0.47
Cultured or Wild * Species * Food Concentration * Date	0.00	1	0.00	0.02	0.87
Error	40.02	207	0.19		
Total	198.95	308			
Corrected Total	116.08	307			
	R Squared = .655 (Adjusted R Squared = .489)				

3.3 Clearance Rate

A three-way ANOVA testing the simultaneous effects of mussel species, available food concentration and date on clearance rate was performed. Available food concentration did not significantly affect clearance rate ($F = 0.613$, d.f. = 2, 315, $P = 0.543$) (Table 10). Therefore, this variable was pooled for all further analyses involving clearance rate. A two-way ANOVA showed that mussel species ($F = 46.64$, d.f. = 1, 315, $P < 0.001$) and date ($F = 11.08$, d.f. = 14, 315, $P < 0.001$) each significantly affected the rates of clearance (Table 11). Therefore it was necessary to examine the combination of these variables over the duration of the study (Figure 2). Mean monthly clearance rates of *Mytilus trossulus* were consistently higher than those of *M. edulis*. *M. trossulus* had a mean overall clearance rate of 3.37 L/h and *M. edulis* had a mean overall clearance rate of 2.07 L/h. A seasonal pattern in clearance rate was apparent for both species. Clearance rates were generally higher during the summer compared with rates observed during the winter. For instance, *M. edulis* had an average clearance rate of 3.57 L/h in July 1998, compared to 0.97 L/h in December 1998 and 0.83 L/h in January 1999. In addition, clearance rates dropped in August 1998 to 2.65 L/h from 3.57 L/h in July 1998. For instance, *M. trossulus*, mean clearance rate decreased steadily from July 1998 to January 1999, and then began to increase during the spring and summer months. For a summary of the sample size, mean values and standard deviations for each of these groups, see Appendix 4.

Table 10: ANOVA showing no significant difference in clearance rate among low (<3,500 cells/mL), medium (>3,500 cells/mL, <7,500 cells/mL) and high (>7,500 cells/mL) food concentrations.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	494.58	68	7.27	5.02	<0.001
Intercept	1261.26	1	1261.26	871.24	<0.001
Species	43.86	1	43.86	30.29	<0.001
Food Concentration	1.77	2	0.89	0.61	0.54
Date	183.86	14	13.13	9.07	<0.001
Species * Food concentration	6.83	2	3.41	2.36	0.10
Species * Date	19.61	14	1.40	0.97	0.49
Food Concentration * Date	45.36	20	2.27	1.57	0.06
Species * Food Concentration * Date	23.30	15	1.55	1.07	0.38
Error	357.57	247	1.45		
Total	2998.71	316			
Corrected Total	852.15	315			
	R Squared = .580 (Adjusted R Squared = .465)				

Table 11: ANOVA showing a significant difference in clearance rate between *Mytilus edulis* and *M. trossulus* over time.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	397.49	29	13.71	8.62	<0.001
Intercept	1580.54	1	1580.54	994.21	<0.001
Species	74.14	1	74.14	46.64	<0.001
Date	246.58	14	17.61	11.08	<0.001
Species * Date	27.13	14	1.94	1.22	0.26
Error	454.67	286	1.59		
Total	2998.71	316			
Corrected Total	852.15	315			
	R Squared = .466 (Adjusted R Squared = .412)				

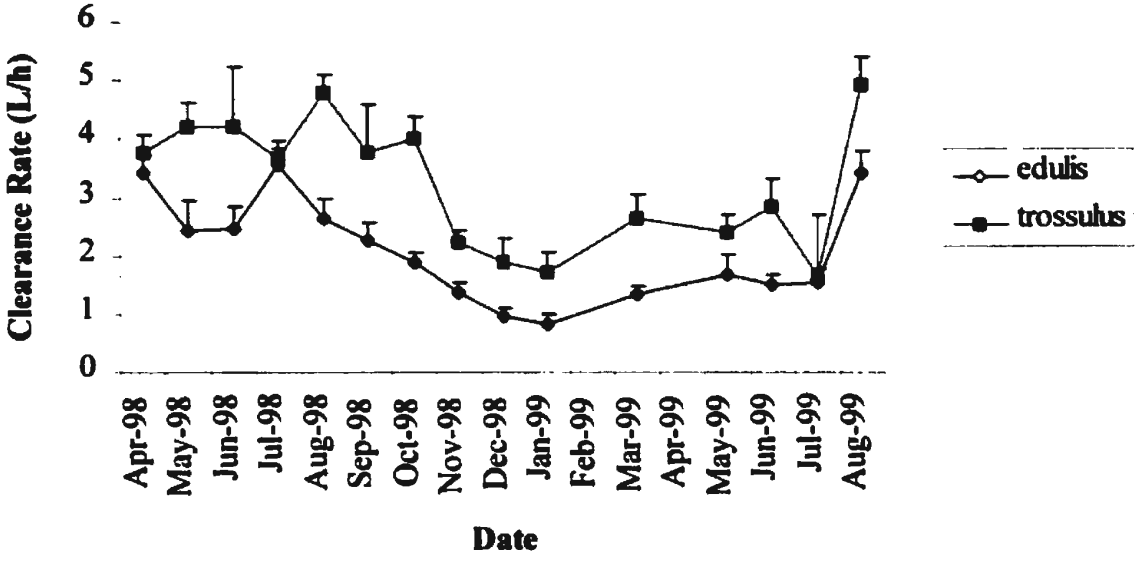

Figure 2: A comparison of clearance rate (L/h per one gram dry tissue mass) in *Mytilus edulis* and *M. trossulus* ($P < 0.0001$) over time ($P < 0.0001$). Vertical bars = 1 standard error.

3.4 Ingestion Rate

A three-way ANOVA testing the simultaneous effects of mussel species, available food concentration and date on ingestion rate was performed. Mussel species ($F = 6.206$, d.f. = 1, 315, $P = 0.013$), the available food concentration ($F = 99.922$, d.f = 2, 315, $P < 0.001$) and date ($F = 8.213$, d.f. = 14, 315, $P < 0.001$) each significantly affected the observed rates of ingestion (Table 12). Therefore it was necessary to examine each combination of these variables separately over the duration of the study (Figures 3 and 4).

Table 12: ANOVA showing a significant difference in ingestion rate between *Mytilus edulis* and *M. trossulus* as well as among low (<3,500 cells/mL), medium (>3,500 cells/mL, <7,500 cells/mL) and high (>7,500 cells/mL) food concentrations over time.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	67753905135	68	996380957.87	12.06	<0.001
Intercept	62625105655	1	62625105655	757.89	<0.001
Species	512844765.1	1	512844765.08	6.21	0.01
Date	9500707494	14	678621963.83	8.21	<0.001
Food Concentration	16513226121	2	8256613060.3	99.92	<0.001
Species * Date	2295399863	14	163957133.09	1.98	0.02
Species * Food Concentration	100116181.3	2	50058090.66	0.61	0.55
Date * Food Concentration	12389530652	20	619476532.62	7.50	<0.001
Species * Date * Food Concentration	1894233118	15	126282207.85	1.53	0.10
Error	20409723676	247	82630460.23		
Total	1.64468E+11	316			
Corrected Total	88163628811	315			
	R Squared = .769 (Adjusted R Squared = .705)				

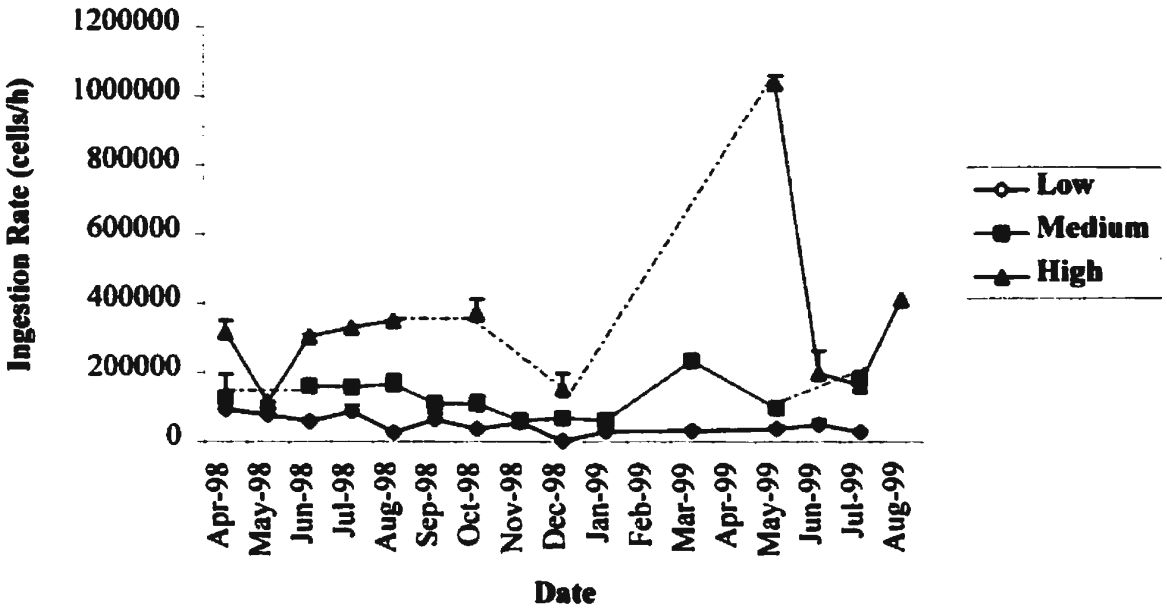

Figure 3: A comparison of ingestion rate (cells/h per one gram dry tissue mass) in *Mytilus edulis* ($P = 0.013$) at low (<3,500 cells/mL), medium (>3,500 cells/mL, <7,500 cells/mL) and high (>7,500 cells/mL) food concentrations ($P < 0.0001$) over time ($P < 0.0001$). Vertical bars = 1 standard error.

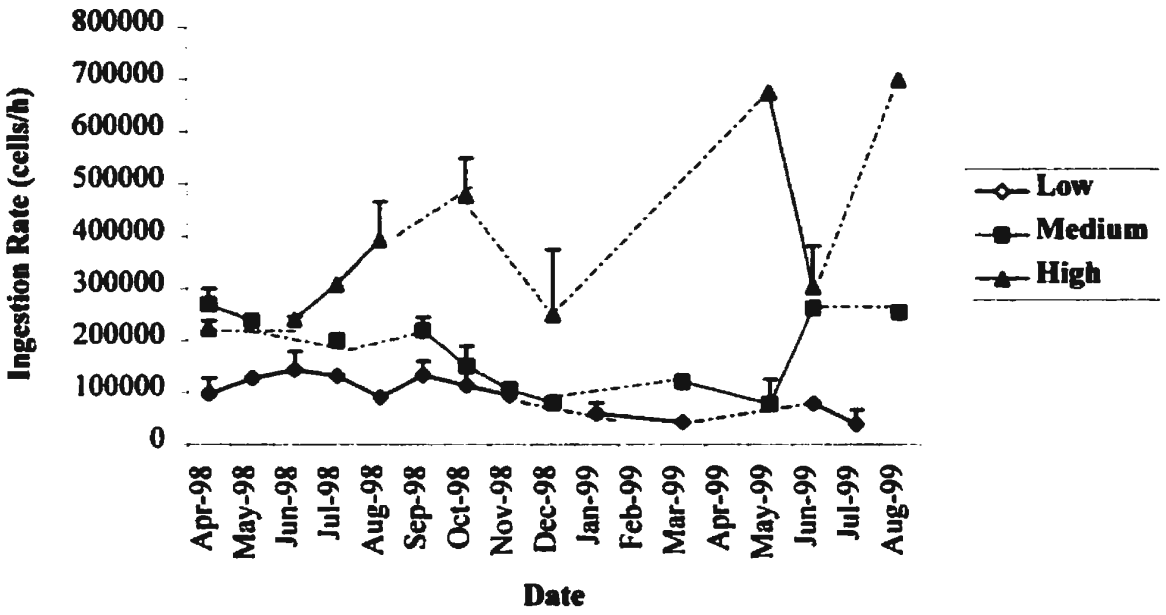

Figure 4: A comparison of ingestion rate (cells/h per one gram dry tissue mass) in *Mytilus trossulus* ($P = 0.013$) at low (<3,500 cells/mL), medium (>3,500 cells/mL, <7,500 cells/mL) and high (>7,500 cells/mL) food concentrations ($P < 0.0001$) over time ($P < 0.0001$). Vertical bars = 1 standard error.

Mytilus trossulus demonstrated higher mean rates of ingestion (Figure 4) than *M. edulis* (Figure 3) at each food concentration. In addition, a positive relationship was observed between rate of ingestion and available food concentration. *M. edulis* ingested an average of 48,497 cells/h at low food concentrations, 124,613 cells/h at medium food concentrations and 323,169 cells/h at high food concentrations. Comparatively, *M. trossulus* ingested an average of 101,958 cells/h at low food concentrations, 183,609 cells/h at medium food concentrations and 370,844 cells/h at high food concentrations. Average rates of ingestion generally increased as the available food concentration increased. Rates of ingestion observed at medium and/or high food concentrations were consistently higher than rates observed at low food concentrations. However, during April 1998 for *M. trossulus* the mean rate of ingestion observed at medium food concentrations was higher than the rate observed at the higher food concentration.

A seasonal pattern in ingestion rate was observed for *M. edulis* and *M. trossulus*. Ingestion rates were generally higher during the summer compared with rates observed during the winter. For instance, *M. trossulus* exposed to high food concentrations had an average ingestion rate of 700,237 cells/h in August 1999, compared to 250,113 cells/h in December 1998. In addition, ingestion rates were lower in June 1998 averaging 132,038 cells/h compared to 158,261 cells/h in July 1998 and 178,406 in August 1998. For a summary of the sample size, mean values and standard deviations for each of these groups, see Appendix 5.

3.5 Filtration Rate

A three-way ANOVA testing the simultaneous effects of species, available food concentration and date on filtration rate showed that mussel species ($F = 0.111$, d.f. = 1, 282, $P = 0.739$) and the available food concentration ($F = 0.024$, d.f. = 2, 282, $P = 0.977$) did not significantly affect filtration in blue mussels (Table 13). Date, according to this three-way ANOVA is not significant ($P = 0.075$). Since date was significant for all other physiological rates, a separate one-way ANOVA was performed to test date again. There was a high amount of variability associated with filtration rate, and it is likely that this interfered with the effect of seasonality on filtration rate. Therefore, mussel species and food concentrations were pooled for all further analyses involving filtration. A one-way ANOVA showed that date ($F = 3.136$, d.f. = 13, 282, $P < 0.001$) significantly affected filtration rate in blue mussels (Table 14). However, it is necessary to note that date was not a significant factor according to the initial three-way analysis performed.

Table 13: ANOVA showing no significant difference in filtration rate between *Mytilus edulis* and *M. trossulus* or among low (<3,500 cells/mL), medium (>3,500 cells/mL, <7,500 cells/mL) and high (>7,500 cells/mL) food concentrations.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	0.0006	59	1.05E-05	1.47	0.025
Intercept	0.0016	1	1.62E-03	226.32	0.0001
Species	0.0000	1	7.98E-07	0.11	0.74
Date	0.0002	13	1.18E-05	1.64	0.075
Food Concentration	0.0000	2	1.69E-07	0.02	0.98
Species * Date	0.0001	13	5.93E-06	0.83	0.63
Species * Food Concentration	0.0001	2	2.77E-05	3.86	0.02
Date * Food Concentration	0.0001	17	4.41E-06	0.61	0.88
Species * Date * Food Concentration	0.0001	11	8.53E-06	1.19	0.30
Error	0.0016	223	7.18E-06		
Total	0.0056	283			
Corrected Total	0.0022	282			
	R Squared = .280 (Adjusted R Squared = .089)				

Table 14: ANOVA showing a significant difference in filtration rate of blue mussels (*Mytilus edulis* and *M. trossulus*) over time.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	0.00029	13	2.25E-05	3.14	0.0002
Intercept	0.00270	1	2.70E-03	376.13	<0.001
Date	0.00029	13	2.25E-05	3.14	0.0002
Error	0.00193	269	7.17E-06		
Total	0.00562	283			
Corrected Total	0.00222	282			
	R Squared = .132 (Adjusted R Squared = .090)				

A seasonal pattern was observed in the overall mean filtration rates in this study (Figure 5), although this trend may not be significant. Filtration rates were generally higher during the summer compared with rates observed during the winter. For instance, mussels (*M. edulis* and *M. trossulus*) demonstrated an average filtration rate of 4.17 mg/h in June 1998 and 3.78 mg/h in July 1998, compared to 2.57 mg/h in November 1998 and 2.40 mg/h in December 1998. For a summary of the sample size, mean values and standard deviations, see Appendix 6.

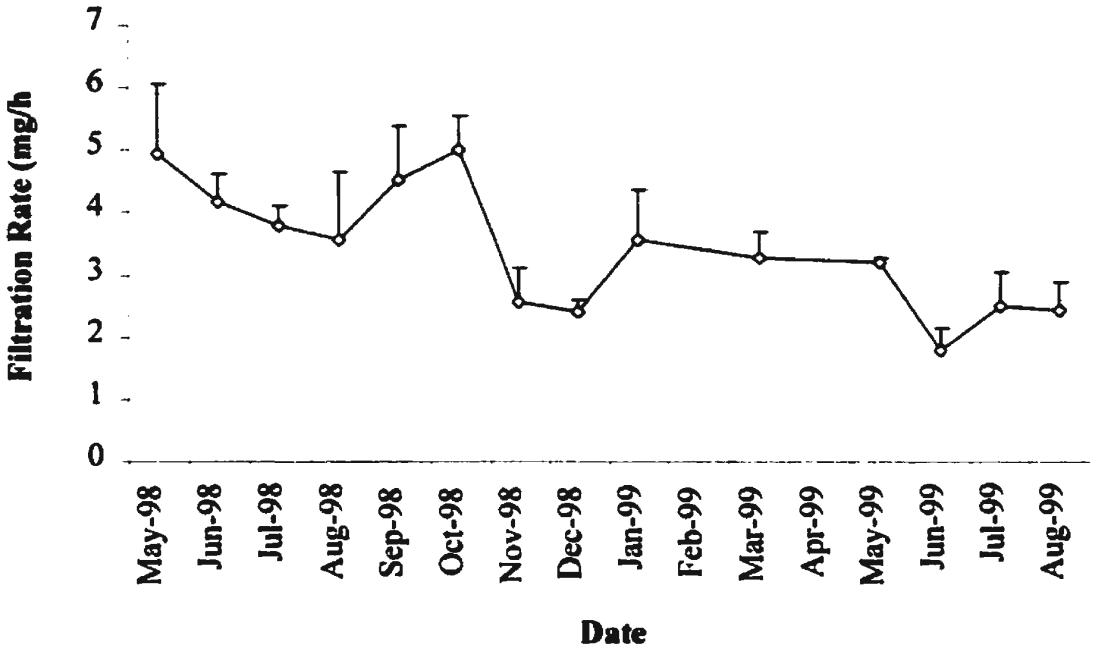

Figure 5: A comparison of filtration (mg/h per one gram dry tissue mass) in *Mytilus edulis* and *M. trossulus* over time (P = 0.0002). Vertical bars = 1 standard error.

3.6 Oxygen Uptake

A three-way ANOVA showed that mussel species ($F = 0.01$, d.f. = 1, 308, $P = 0.92$) and the available food concentration ($F = 0.52$, d.f. = 2, 308, $P = 0.60$) were not significant factors affecting oxygen uptake in blue mussels (Table 15). Therefore, mussel species and food concentrations were pooled for all further analyses involving oxygen uptake. A one-way ANOVA showed that date ($F = 15.77$, d.f. = 13, 308, $P < 0.001$) significantly affected the rate of oxygen uptake in blue mussels (Table 16).

Table 15: ANOVA showing no significant difference in oxygen uptake between *Mytilus edulis* and *M. trossulus* or among low (<3,500 cells/mL), medium (>3,500 cells/mL, <7,500 cells/mL) and high (>7,500 cells/mL) food concentrations.

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Corrected Model	65.22	59	1.11	5.38	<0.001
Intercept	54.29	1	54.29	264.44	<0.001
Date	46.39	13	3.57	17.38	<0.001
Food Concentration	0.21	2	0.11	0.52	0.60
Species	0.00	1	0.00	0.01	0.92
Date * Food Concentration	2.55	15	0.17	0.83	0.65
Date * Species	2.96	13	0.23	1.11	0.35
Food Concentration * Species	0.80	2	0.40	1.94	0.15
Date * Food Concentration * Species	8.45	13	0.65	3.17	<0.001
Error	51.12	249	0.20530937		
Total	198.95	309			
Corrected Total	116.35	308			
	R Squared = .561 (Adjusted R Squared = .456)				

Table 16: ANOVA showing a significant difference in oxygen uptake of blue mussels (*Mytilus edulis* and *M. trossulus*) over time.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	47.70	13	3.67	15.77	<0.001
Intercept	67.01	1	67.01	287.98	<0.001
Date	47.70	13	3.67	15.77	<0.001
Error	68.65	295	0.23		
Total	198.95	309			
Corrected Total	116.35	308			
	R Squared = .410 (Adjusted R Squared = .384)				

A seasonal pattern in oxygen uptake was observed in the mean values for oxygen uptake. Rates of oxygen uptake were generally higher during the summer compared with rates observed during the winter (Figure 6). Mean oxygen uptake rates generally increased from May 1998 through to November 1998, decreasing to 0.097 mL/h in December 1998, 0.043 mL/h in January 1999 and 0.063 mL/h in March 1999. Rates then proceeded to increase, corresponding with the seasonal increase in water temperature. For a summary of the sample size, mean values and standard deviations for each of these groups, see Appendix 7.

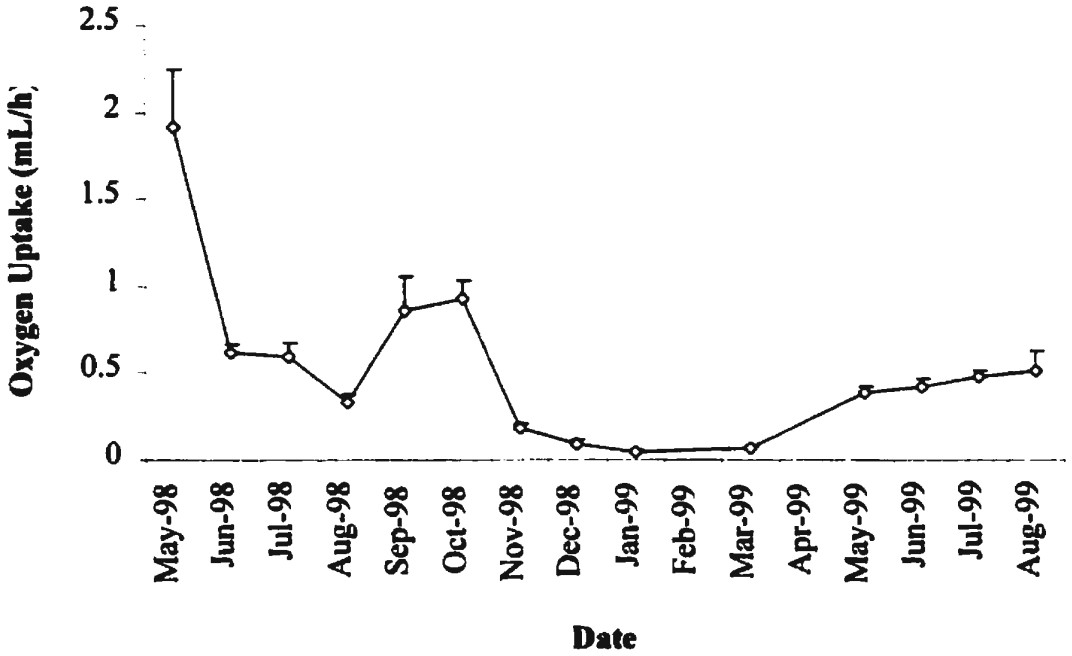

Figure 6: A comparison of oxygen uptake (mL/h per one gram dry tissue mass) in *Mytilus edulis* and *M. trossulus* over time ($P < 0.0001$). Vertical bars = 1 standard error.

3.7 Interactions

For all the analyses performed, there were no consistent interactions among any of the variables. The interaction between mussel origin and date was significant for clearance rate ($F = 1.99$, d.f. = 1, 13, $P = 0.02$) (Table 6), ingestion rate ($F = 3.55$, d.f. = 1, 13, $P = < 0.001$) (Table 7) and oxygen uptake ($F = 2.45$, d.f. = 1, 12, $P = 0.01$) (Table 9). This interaction was not significant for filtration rate. Although the interactions for clearance, ingestion and oxygen uptake were significant, no trend of any sort was obvious after plotting cultured and wild rates together according to date.

3.8 Dry Weight Comparison

Log dry soft tissue weight was regressed against log shell length. Regression analyses showed that dry weight was significantly, and positively correlated with shell length (Table 17). A four-way ANOVA showed that mussel origin ($F = 0.68$, d.f. = 1, 361, $P = 0.41$), mussel species ($F = 1.76$, d.f. = 1, 361, $P = 0.19$) and the available food concentration were not significant factors affecting the dry weight of the mussels (Table 18). A one-way ANOVA showed that date did significantly affect the dry weight of the mussels (Table 19, Figure 7). For a summary of the sample size, mean values and standard deviations for each of these groups, see Appendix 8.

Table 17a: A summary of the sample size and the minimum and maximum dry weights (W) (g) of the animals (*Mytilus edulis* and *M. trossulus*) comprising each respective sampling period.

Month	n	W_{min}	W_{max}
April 98	24	0.02	1.17
May 98	41	0.03	2.51
June 98	22	0.02	1.91
July 98	31	0.03	2.82
August 98	19	0.02	1.29
September 98	14	0.03	1.70
October 98	53	0.01	2.04
November 98	39	0.1	3.63
December 98	29	0.06	2.69
January 99	13	0.03	2.75
March 99	24	0.02	2.95
May 99	17	0.02	3.72
June 99	26	0.02	2.09
July 99	19	0.02	1.45
August 99	32	0.01	2.19

Table 17b: Regression analyses for log value dry weight and log value shell length (mm), following the allometric relationship $y = ax^b$, where y = dry weight of soft body tissues (g) and x = shell length (mm).

Month	a ±SE	b ±SE	R^2	F	p-value
April 98	-3.19 ± 0.70	1.81 ± 0.45	0.40	16.39	0.000535
May 98	-4.24 ± 0.34	2.53 ± 0.22	0.76	128.27	< 0.0001
June 98	-3.89 ± 0.40	2.18 ± 0.27	0.75	64.09	< 0.0001
July 98	-3.52 ± 0.45	2.03 ± 0.29	0.61	48.23	< 0.0001
August 98	-4.47 ± 0.14	2.51 ± 0.093	0.97	701.35	< 0.0001
September 98	-4.22 ± 0.61	2.49 ± 0.40	0.74	37.98	< 0.0001
October 98	-4.83 ± 0.32	2.83 ± 0.21	0.78	180.65	< 0.0001
November 98	-4.07 ± 0.31	2.41 ± 0.20	0.79	148.21	< 0.0001
December 98	-4.21 ± 0.18	2.49 ± 0.11	0.95	530.57	< 0.0001
January 99	-3.88 ± 0.89	2.14 ± 0.54	0.55	15.70	0.00223
March 99	-4.03 ± 0.78	2.29 ± 0.47	0.50	23.60	< 0.0001
May 99	-4.88 ± 0.11	2.90 ± 0.073	0.99	1597.64	< 0.0001
June 99	-5.41 ± 0.096	3.16 ± 0.061	0.99	2708.97	< 0.0001
July 99	-4.85 ± 0.28	2.81 ± 0.17	0.94	261.58	< 0.0001
August 99	-4.58 ± 0.42	2.59 ± 0.27	0.74	89.20	< 0.0001

Table 18: ANOVA showing no significant difference in dry weight between cultured and wild, *Mytilus edulis* and *M. trossulus* or among low (<3,500 cells/mL), medium (>3,500 cells/mL, <7,500 cells/mL) and high (>7,500 cells/mL) food concentrations.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	127.51	114	1.12	1.89	<0.001
Intercept	149.71	1	149.71	252.39	<0.001
Cultured or Wild	0.40	1	0.40	0.68	0.41
Species	1.04	1	1.04	1.76	0.19
Food Concentration	0.11	2	0.05	0.09	0.91
Date	23.23	14	1.66	2.80	<0.001
Cultured or Wild * Species	0.01	1	0.01	0.02	0.89
Cultured or Wild * Food Concentration	4.64	2	2.32	3.91	0.02
Species * Food Concentration	1.35	2	0.68	1.14	0.32
Cultured or Wild * Species * Food Concentration	0.40	2	0.20	0.33	0.72
Cultured or Wild * Date	17.29	13	1.33	2.24	0.01
Species * Date	10.51	14	0.75	1.27	0.23
Cultured or Wild * Species * Date	14.69	12	1.22	2.06	0.02
Food Concentration * Date	18.14	20	0.91	1.53	0.07
Cultured or Wild * Food Concentration * Date	8.29	11	0.75	1.27	0.24
Species * Food Concentration * Date	9.31	15	0.62	1.05	0.41
Cultured or Wild * Species * Food Concentration * Date	5.48	4	1.37	2.31	0.06
Error	146.51	247	0.59		
Total	542.52	362			
Corrected Total	274.02	361			
	R Squared = .465 (Adjusted R Squared = .219)				

Table 19: ANOVA showing a significant difference in dry weight in blue mussels (*Mytilus edulis* and *M. trossulus*) over time.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	24.45	14	1.75	2.67	<0.001
Intercept	245.44	1	245.44	374.95	<0.001
Date	24.45	14	1.75	2.67	<0.001
Error	253.98	388	0.65		
Total	557.88	403			
Corrected Total	278.43	402			
	R Squared = .088 (Adjusted R Squared = .055)				

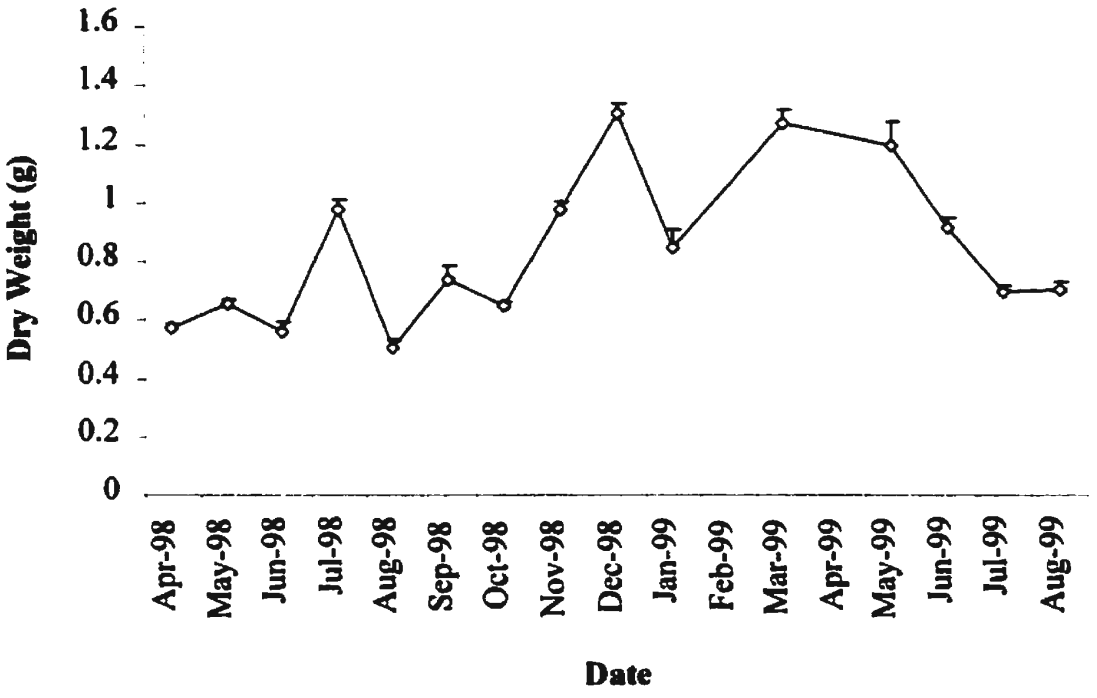

Figure 7: A comparison of dry weight in blue mussels (g) over time ($P < 0.001$). Vertical bars = 1 standard error.

3.9 Shell Analysis

The weights of eighty-five sets of blue mussel shells were compared. This random sample was comprised of 35 cultured *Mytilus edulis*, 31 wild *M. edulis*, 11 cultured *M. trossulus* and 8 wild *M. trossulus* (right and left valves). A one-way analysis of covariance (ANCOVA) was performed in order to determine whether mussel type, defined as cultured *M. edulis*, cultured *M. trossulus*, wild *M. edulis* or wild *M. trossulus*, significantly affected the relationship between shell weight and shell length. The analysis revealed that mussel type ($F = 230.49$, d.f. = 3, 84, $P < 0.001$) significantly affected the relationship between shell weight and shell length (Table 20). From this analysis, mean shell weight was lowest for cultured *M. trossulus*, and second lowest for cultured *M. edulis*. Wild *M. trossulus* had the highest mean shell weight, and wild *M. edulis* had the second highest mean shell weight. Overall, cultured *M. edulis* and *M. trossulus* had significantly lower mean values for shell weight compared with wild *M. edulis* and *M. trossulus* (Figures 8, 9, 10 and 11). For a summary of the sample size, mean values and standard deviations for each of these groups, see Appendix 9. A two-way ANOVA testing the significance of mussel origin and mussel species could not be performed due to a limiting number of degrees of freedom. A one-way ANCOVA showed that mussel origin is a significant factor affecting shell weight ($F = 63.515$, d.f. = 1, 84, $P < 0.0001$) (Table 21). For a summary of the sample size, mean values and standard deviations for each of these groups, see Appendix 10. A separate one-way ANCOVA showed that mussel species is also a significant factor affecting the relationship between shell weight and shell length ($F = 63.515$, d.f. = 1, 84, $P < 0.0001$) (Table 22). For a summary of the

sample size, mean values and standard deviations for each of these groups, see Appendix 11.

Table 20: ANCOVA showing a significant difference in the relationship between shell weight and shell length according to mussel species, *Mytilus edulis* and *M. trossulus*.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	50.56	4	12.64	438.05	<0.001
Intercept	22.12	1	22.12	766.57	<0.001
Log Shell Length	28.80	1	28.80	998.14	<0.001
Species	19.95	3	6.65	230.49	<0.001
Error	2.31	80	0.03		
Total	67.25	85			
Corrected Total	52.87	84			
	R Squared = .956 (Adjusted R Squared = .954)				

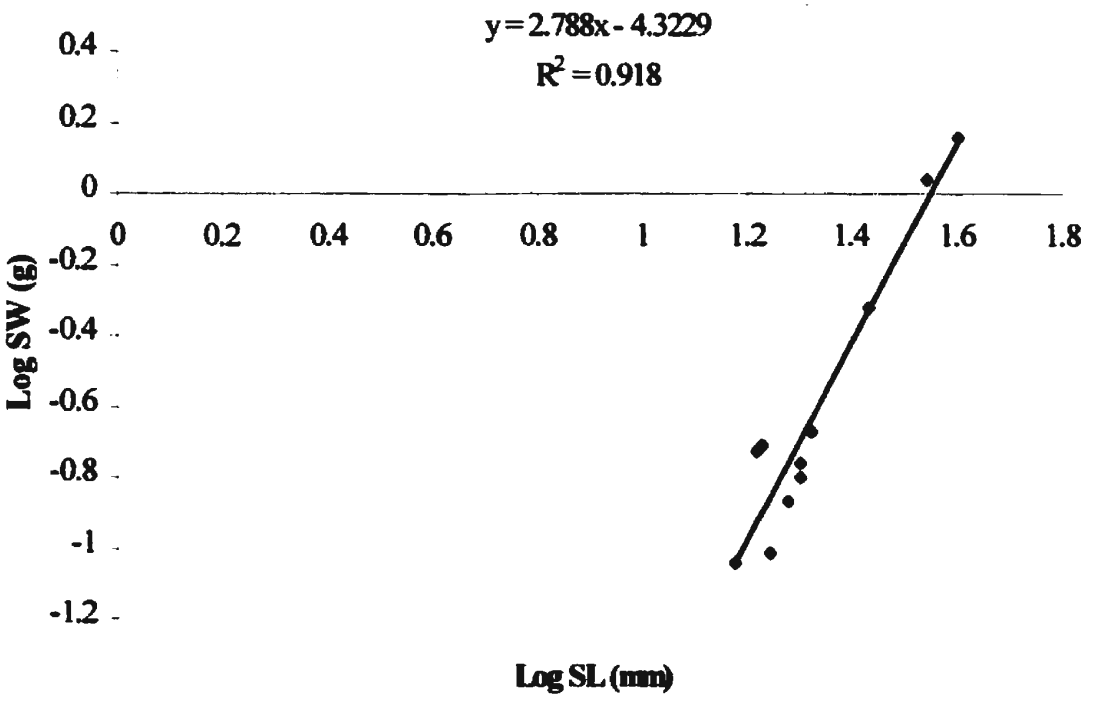

Figure 8: A comparison of the relationship between log shell weight (g) and log shell length (mm) for cultured *Mytilus trossulus* ($P < 0.0001$).

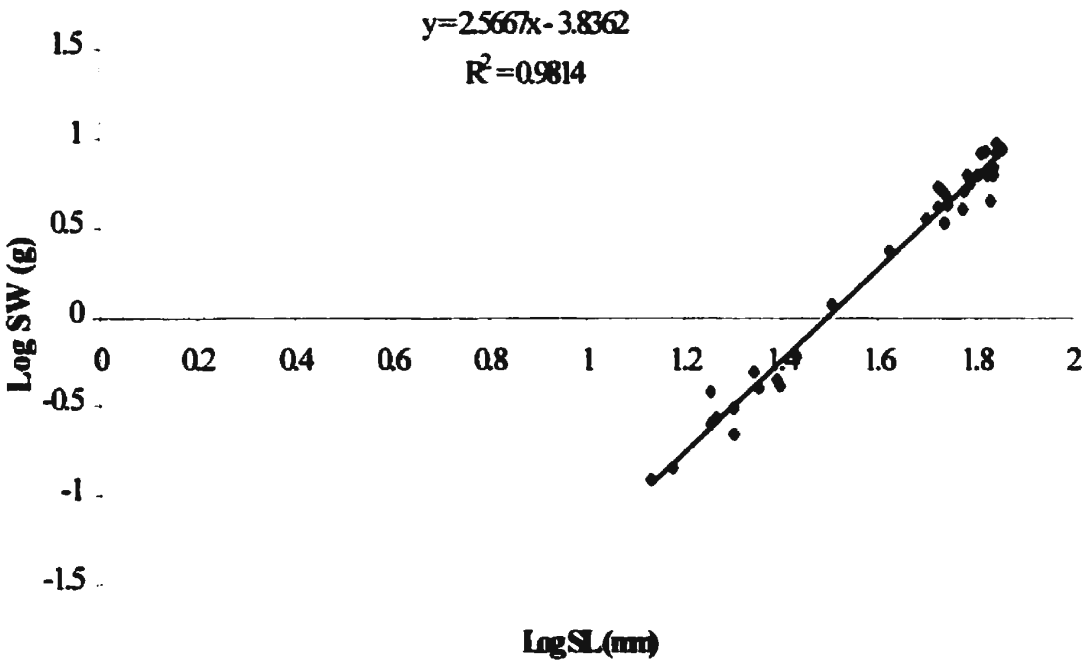

Figure 9: A comparison of the relationship between log shell weight (g) and log shell length (mm) for cultured *Mytilus edulis* ($P < 0.0001$).

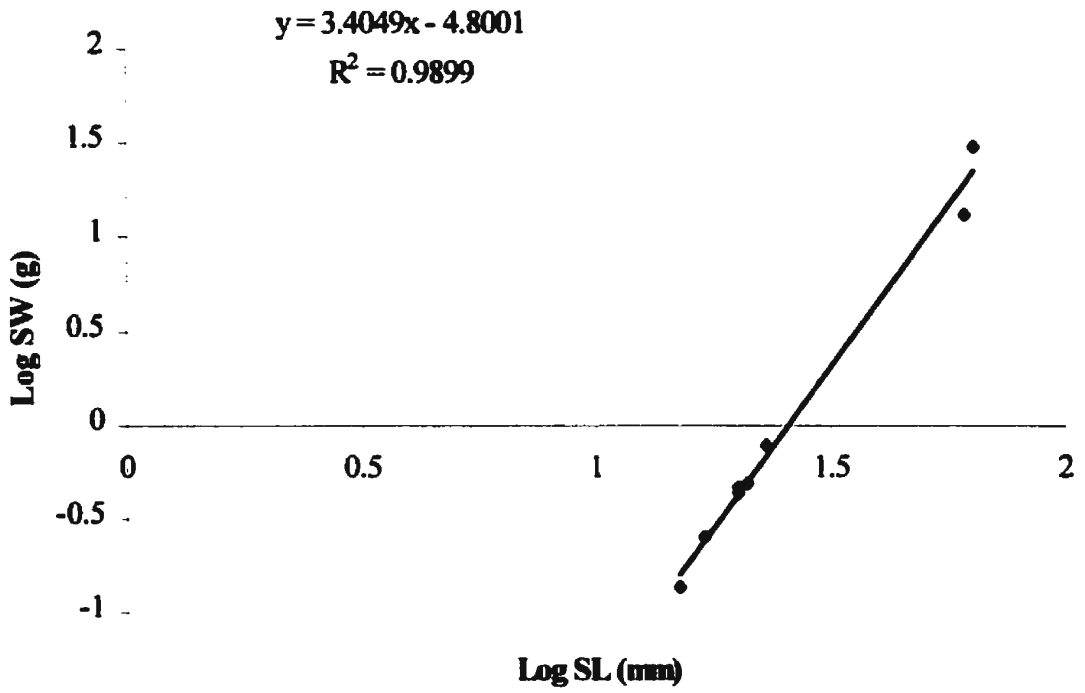

Figure 10: A comparison of the relationship between log shell weight (g) and log shell length (mm) for wild *Mytilus trossulus* ($P < 0.0001$).

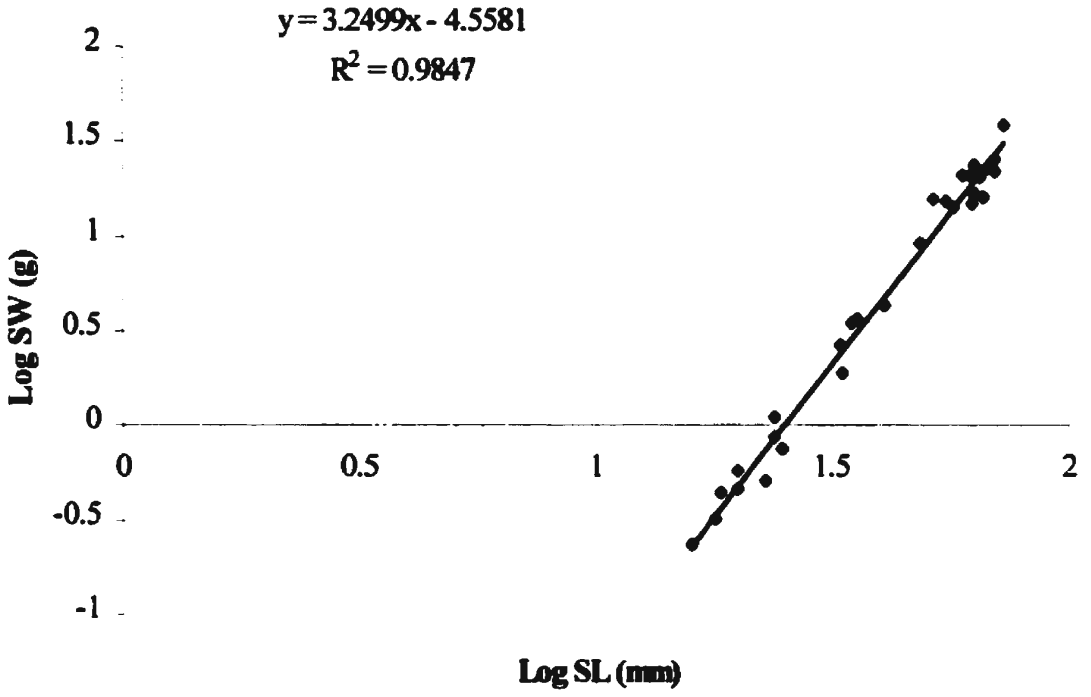

Figure 11: A comparison of the relationship between log shell weight (g) and log shell length (mm) for wild *Mytilus edulis* ($P < 0.0001$).

Table 21: ANCOVA showing a significant difference in the relationship between shell weight and shell length according to mussel origin.

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Corrected Model	40.32	2	20.16	131.80	<0.001
Intercept	22.10	1	22.10	144.44	<0.001
Log Shell Length	29.04	1	29.04	189.81	<0.001
Cultured or Wild	9.72	1	9.72	63.51	<0.001
Error	12.54	82	0.15		
Total	67.25	85			
Corrected Total	52.87	84			
	R Squared = .763 (Adjusted R Squared = .757)				

Table 22: ANCOVA showing a significant difference in the relationship between shell weight and shell length according to mussel species, *Mytilus edulis* and *M. trossulus*.

Source	Type III Sum of Squares	Df	Mean Square	F	Sig.
Corrected Model	40.32	2	20.16	131.80	<0.001
Intercept	22.10	1	22.10	144.44	<0.001
Log Shell Length	29.04	1	29.04	189.81	<0.001
Species	9.72	1	9.72	63.51	<0.001
Error	12.54	82	0.15		
Total	67.25	85			
Corrected Total	52.87	84			
	R Squared = .763 (Adjusted R Squared = .757)				

3.10 Size Comparison

Standardized physiological rates were compared in small and large *Mytilus edulis* and *M. trossulus*. Small mussels were characterized as having a shell length less than or equal to 25 mm and large mussels were characterized as having a shell length of greater than or equal to 50 mm. Most physiological rates are scaled to dry tissue weight. As the animals grow, physiological rates such as feeding and oxygen consumption change in relation to the dry weight with varying exponents (Newell and Shumway 1993). In order to compare mean rates of clearance and ingestion, physiological rates of small mussels were standardized for a 0.1 gram dry weight mussel and those of large mussels for a 1.0 gram dry weight mussel. These theoretical values are realistic estimates of the average size of the small and large mussels used throughout this study.

Standardized rates of clearance and ingestion, in both species, were higher for large mussels than for smaller mussels (Table 23, Figures 12, 13, 14 and 15). For small *M. edulis*, clearance rate was 1.1 L/h compared to 2.06 L/h for large *M. edulis*. For small *M. trossulus*, clearance rate was 1.66 L/h compared to 3.01 L/h for large *M. trossulus*. For small *M. edulis*, ingestion rate was 55,273.6 cells/h compared to 101,964.6 cells/h for large *M. edulis*. For small *M. trossulus*, ingestion rate was 92,044.0 cells/h compared to 194,720.5 cells/h for large *M. trossulus*.

Table 23: A summary of the mean standardized clearance rates (L/h) **(CR)** and ingestion rates (cells/h) **(IR)** for small (0.1 g) and large (1.0 g) *Mytilus edulis* and *M. trossulus* over time.

	Small *Mytilus edulis*		Large *Mytilus edulis*		Small *Mytilus trossulus*		Large *Mytilus trossulus*	
Date	**CR**	**IR**	**CR**	**IR**	**CR**	**IR**	**CR**	**IR**
Apr-98	0.35	12213.4	0.75	26419.9	0.72	24718.1	1.93	266090.1
May-98	0.78	25369.6	1.40	47524.5	1.54	60719.9	1.88	128837.1
Jun-98	2.21	114898.3	4.07	93325.4	2.45	112386.4	3.52	173389.1
Jul-98	1.18	54654.9	1.61	87937.1	2.07	107475.8	4.11	189628.4
Aug-98	1.21	44276.3	2.56	112819.8	2.05	78472.6	3.55	240123.1
Sep-98	2.65	78361.4	3.44	140641.2	2.71	118702.3	3.81	114815.4
Oct-98	0.98	53686.6	2.77	168476.2	1.76	101279.2	5.02	300742.1
Nov-98	1.03	58282.0	2.06	88969.9	1.72	71654.3	3.31	96189.1
Dec-98	0.95	37639.9	1.91	57374.5	2.01	129501.0	3.94	171278.0
Jan-99	0.73	32011.4	1.26	68920.7	1.17	39764.3	2.14	67463.1
Mar-99	0.31	27560.2	0.90	76331.2	0.60	62453.1	1.64	67518.3
May-99	0.70	73439.0	1.36	123803.6	1.01	140014.5	2.39	376853.8
Jun-99	1.01	65598.2	1.65	114095.3	1.88	93110.3	2.78	212020.2
Jul-99	0.45	19254.4	1.61	60315.2	0.48	10237.0	0.55	11631.0
Aug-99	1.92	131859.1	3.51	262514.1	2.76	230170.7	4.60	504228.6
Mean	**1.10**	**55273.6**	**2.06**	**101964.6**	**1.66**	**92044.0**	**3.01**	**194720.5**

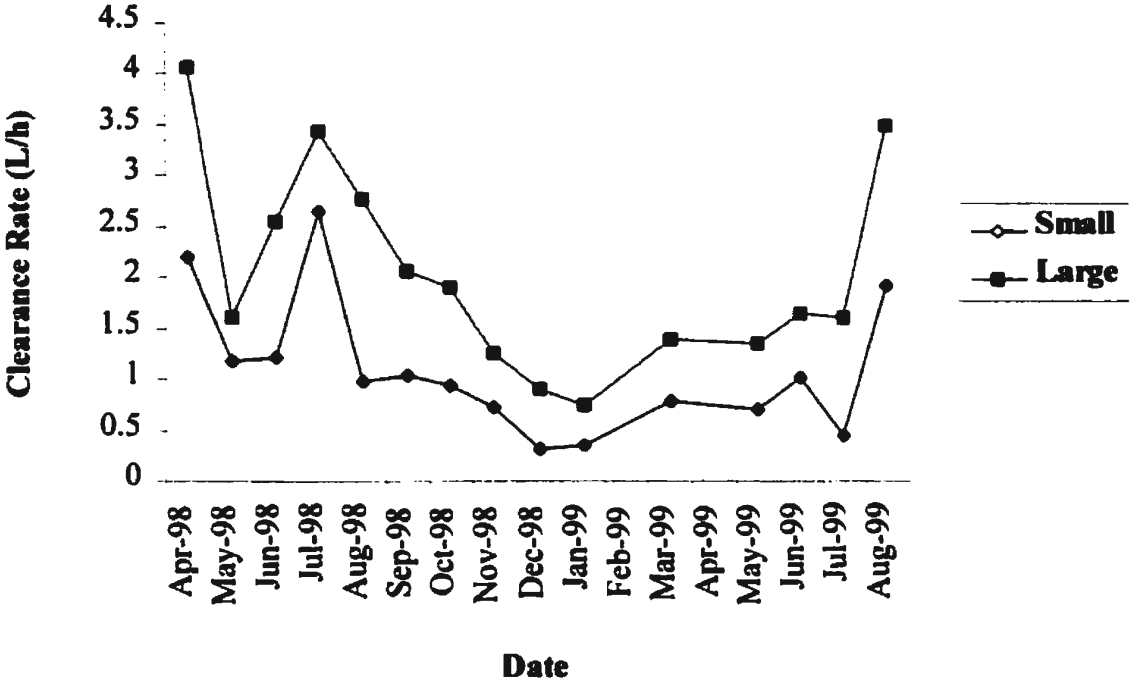

Figure 12: A summary of the mean clearance rates in small (L/h per 0.1 gram dry tissue mass) and large (L/h per one gram dry tissue mass) *Mytilus edulis* over time.

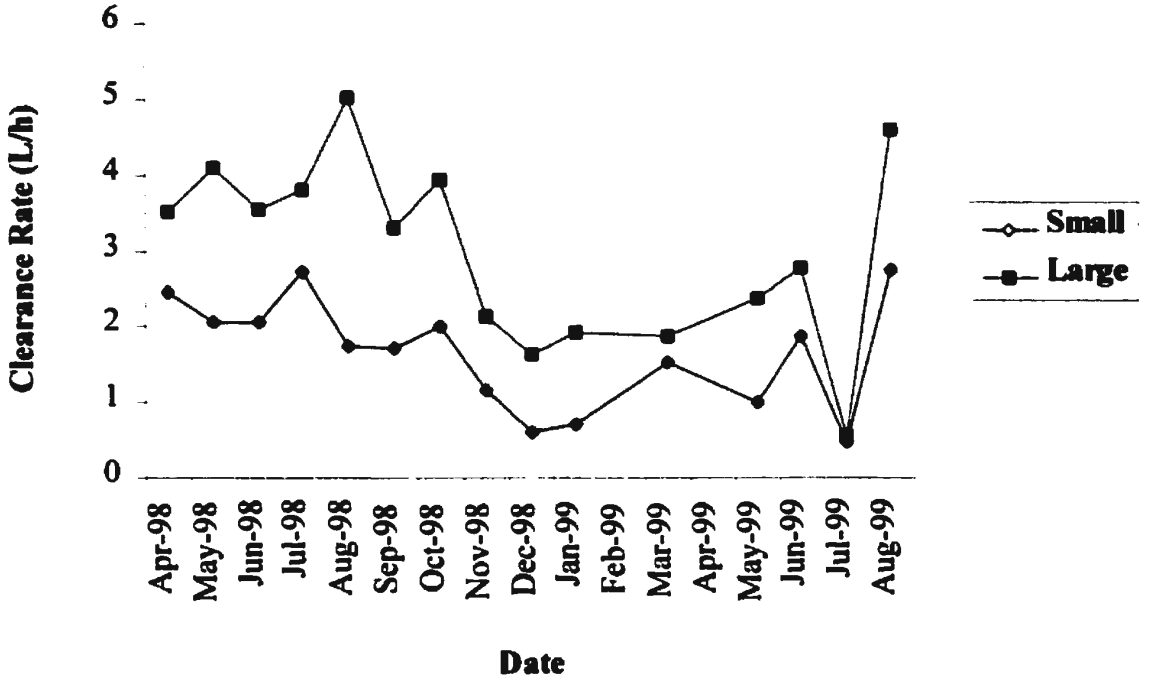

Figure 13: A summary of the mean clearance rates in small (L/h per 0.1 gram dry tissue mass) and large (L/h per one gram dry tissue mass) *Mytilus trossulus* over time.

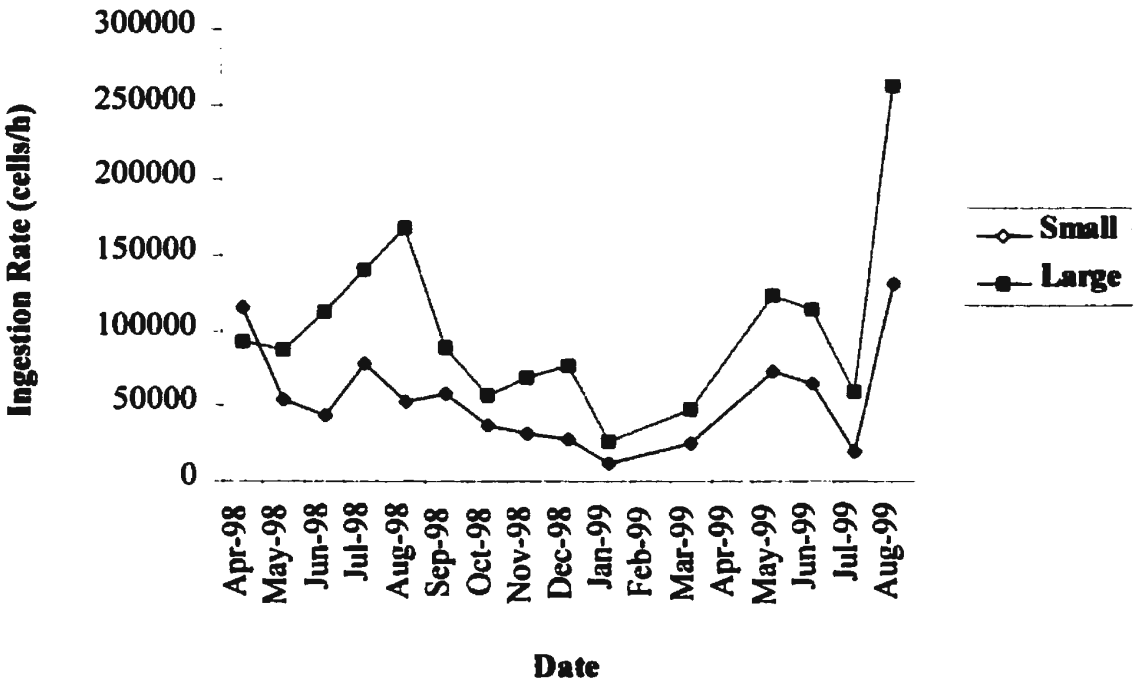

Figure 14: A summary of the mean ingestion rates in small (cells/h per 0.1 gram dry tissue mass) and large (cells/h per one gram dry tissue mass) *Mytilus edulis* over time.

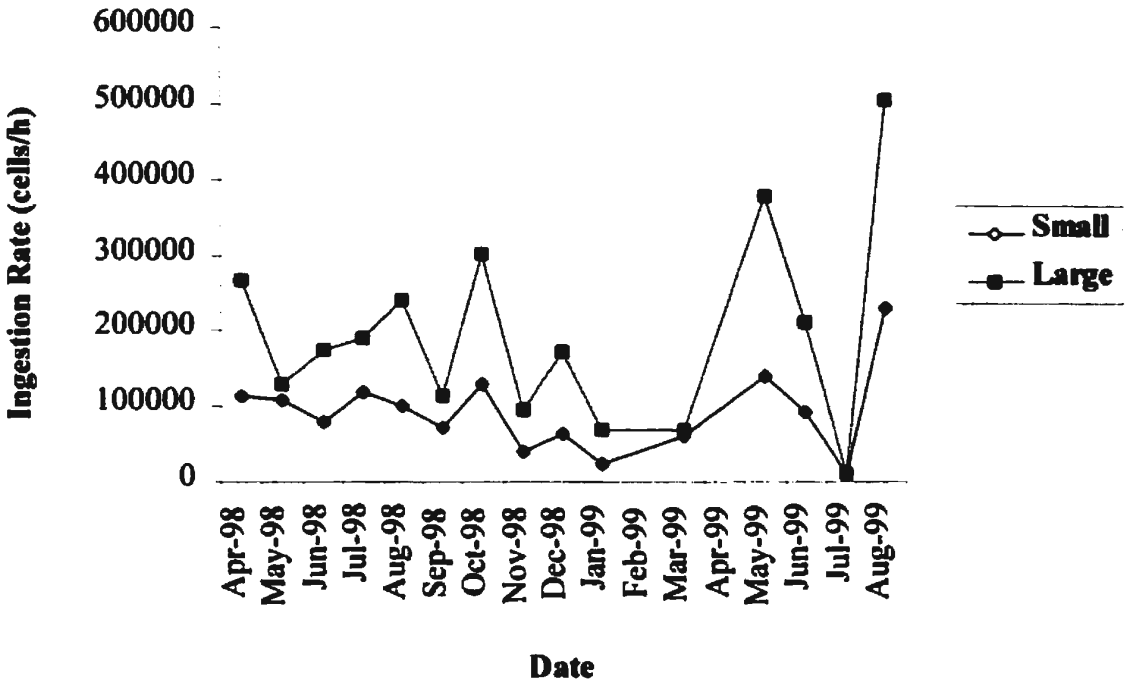

Figure 15: A summary of the mean ingestion rates in small (cells/h per 0.1 gram dry tissue mass) and large (cells/h per one gram dry tissue mass) *Mytilus trossulus* over time.

Section 4 Discussion

4.1 Comparison of Weight Exponents

Weight exponents for physiological rate functions for the present study were comparable with values reported in the literature (Thompson 1984; Bayne *et al.* 1989; Bougrier *et al.* 1995; Smaal *et al.* 1997), although reported weight coefficients are quite variable (Smaal *et al.* 1997; Jørgensen 1990; Jones *et al.* 1992). Thompson (1984) reported weight coefficients ranging from 0.233 to 0.512 for clearance rate in wild *Mytilus edulis*. Newell and Thompson (1984) reported weight exponents ranging from 0.413 to 0.514 for clearance rate in *M. edulis*. Bayne *et al.* (1989) reported a weight coefficient of 0.67 for all measures of feeding and Smaal *et al.* (1997) reported allometric weight coefficients of 0.5 for clearance rate in both *M. edulis* and *Cerastoderma edule*. MacDonald and Ward (1994) obtained a weight exponent of 0.68 for feeding in *Placopecten magellanicus*. In the present study, weight coefficients ranged from 0.13 to 0.53 for clearance rate, 0.19 to 0.58 for ingestion and 0.14 to 0.78 for filtration. Weight coefficients for oxygen uptake are, in general, higher than the coefficients reported for feeding. Smaal *et al.* (1997) reported values of 0.7 for respiration in both *M. edulis* and *C. edule*. Bayne *et al.* (1989) obtained weight coefficients of 0.75 for respiration in blue mussels. Thompson (1984) published weight coefficient values of 0.280 to 1.109 for oxygen uptake in *M. edulis*. For the present study, weight coefficients for oxygen uptake were, generally, higher than the weight coefficients for clearance rate, ingestion rate and filtration rate, ranging from 0.19

to 0.82, but were comparable with published values. The lower weight exponents were observed during the spawning period of these mussels. Spawning may have affected the rate of oxygen consumption, thereby affecting the weight exponents. Thompson (1984) reported weight coefficients ranging from 2.51 to 3.34 for shell length (versus dry weight) in wild *M. edulis*. Similar values were observed for the present study, ranging from 1.81 to 3.16 for both cultured and wild blue mussels. All rates discussed are standardized rates.

4.2 The Influence of Investigated Factors on Production

4.2.1 Mussel Origin

The results did not support the hypotheses that rates of clearance, ingestion, filtration, and oxygen consumption differed between cultured and wild blue mussels. These findings imply that cultured and wild mussels demonstrate similar feeding patterns, as well as respiration patterns, if they are exposed to similar environmental conditions. This is supported by previous studies that suggest that variation in the ingestion rate of mussels results from adaptations to distinct regional differences in quantitative and qualitative seston conditions (Bayne *et al.* 1984; Navarro *et al.* 1991). Mallet and Carver (1989) also found that spatial distribution (site) was the main factor accounting for differences in growth in transplanted juvenile Nova Scotian mussels. This again supports the observation that wild and cultured blue mussels display similar physiological responses when maintained in similar environments.

Although increased rates of growth and higher meat yields have been observed in cultured blue mussels compared with wild mussels (Gosling 1992), this is likely an environmental influence. Cultured and wild blue mussels normally occur in different microenvironments. Cultivated blue mussels are commonly grown in suspension culture, which offers a three-dimensional food supply, whereas wild blue mussels inhabit the subtidal and intertidal zones, which offers only a two-dimensional food supply. It is likely that the surrounding water flow patterns are also different for these two groups of mussels. In addition, blue mussels growing in the subtidal or intertidal zone are subject to an increased risk of predation. As a defensive response to this increased risk of predation, blue mussels have to direct more energy towards shell thickness (Rodhouse *et al.* 1984). According to this study, wild *Mytilus edulis* and wild *M. trossulus* have significantly higher mean values for shell weight than cultured *M. edulis* and cultured *M. trossulus*. The intertidal zone is also a high-energy environment requiring an increased amount of energy being directed towards byssal attachment. Finally, periodic aerial exposure in the intertidal zone causes mussels to close their valves in order to prevent desiccation. Periodic aerial exposure also means that mussels have to deal with a reduced feeding period, "repayment" of an oxygen debt and continual readjustments between aerobic and anaerobic metabolism (Thompson 1984). In response to their ambient environment, it is likely that wild blue mussels direct more energy towards survival, rather than meat growth. Similarly, MacDonald and Bayne (1993) have observed that wild scallops "sacrifice" fecundity for maintenance when food resources are limited. This implies that the redirection of energy flow is a natural response of bivalves, regardless of being wild

or cultivated. In Nova Scotia, mussel growers have experienced problems with eider ducks, which can strip mussel lines bare during their migration seasons. It would be interesting to test whether shell thickness will increase, over time, in these mussels as a natural response to predation.

According to Rodhouse *et al.* (1984), cultivated blue mussels allocate less than half of their energy budget to reproduction as do wild blue mussels. Again, this may be a consequence of environmental circumstances. The results of the present study showed that there were no significant differences in feeding demand or oxygen consumption between cultured and wild blue mussels, but it is possible that cultured and wild blue mussels demonstrate differential patterns of energy allocation, which was not investigated in this study.

Further, in Newfoundland the blue mussel culture industry relies upon wild spat collection, so the initial larval blue mussel population is largely comprised of wild blue mussels. Therefore, it is reasonable to conclude that observed differences between cultivated and wild blue mussels are due to adaptations to environmental factors rather than to genetic differences between these two groups. A one-way ANOVA ($P<0.001$) showed that the species composition between cultured and wild mussels was not significantly different. The continued success of the blue mussel industry in Newfoundland, based upon wild spat collection, validates the argument that observed differences between cultured and wild mussels are primarily the result of adaptations to environmental conditions.

The results obtained from the present study are based upon observations of cultured and wild blue mussels from only one location in Newfoundland. Caution should be exercised in extrapolating these results to other mussel cultivation sites within Newfoundland. It is important to conduct additional research to compare the responses of cultured and wild blue mussels from other locations in Newfoundland.

4.2.1.1 Shell Analysis

According to the shell analyses performed, cultured mussels have lower shell weight to shell length ratios than wild mussels. Cultured *Mytilus trossulus* had a lower shell weight to shell length ratio than *M. edulis*. Wild mussels probably have much heavier shells since they live in a more extreme environment than do cultured mussels, directing more energy towards shell thickness, which offers protection from high energy wave action and from predation pressures. In addition, the increased rate of growth observed in cultured mussels results in a thinner and lighter shell.

4.2.2 Species

The results support the hypothesis that *Mytilus edulis* and *M. trossulus* demonstrate different physiological responses to environmental circumstances. *M. trossulus* displayed higher rates of clearance and ingestion than *M. edulis*. This result corresponds with recent observations in the literature which suggest that different mytilid species exhibit

different physiological and morphological adaptations to similar environmental conditions (Tedengren *et al.* 1990; Gardner and Skibinski 1991; Willis and Skibinski 1992; Hilbish *et al.* 1994). For instance, Shumway *et al.* (1997) found significant differences in the rate at which individual algal species were cleared among three species of scallops. *Patinopecten yessoensis* had the highest overall rate and *Placopecten magellanicus* the lowest. Clearance rates for *Argopecten irradians* were intermediate compared with *P. yessoensis* and *P. magellanicus*.

Species-specific differences have also been observed within a genus. In *Mytilus*, for instance, Bates (1992) found an increased frequency of *M. edulis* in the larger size classes, and an increased frequency of *M. trossulus* in the smaller size classes in eastern Newfoundland. This observation is supported by Comesaña *et al.* (1999) who found higher growth and survival of wild *M. edulis* compared with *M. trossulus*. They postulated that higher growth and survival rates of *M. edulis* might explain the increase in frequency of *M. edulis* with increased shell length observed in Newfoundland populations. Different genotypes have been associated with various fitness levels (Koehn *et al.* 1984). It is reasonable to assume that *M. edulis* and *M. trossulus*, although obviously similar in appearance and even sympatric, employ different biological strategies to maximize survival.

The results of the present study suggest that *M. edulis* and *M. trossulus* are physiologically distinct species. Specifically, the results show that *M. trossulus* has a significantly higher rate of clearance and ingestion than *M. edulis*. This result has direct

implications for socking density and stocking density on a blue mussel culture site, analogous to the observed differences in small and large size classes of blue mussels. Since *M. trossulus* displays a higher overall food demand relative to *M. edulis*, the species proportions of a mussel stock of these two species need to be considered when calculating optimal stocking density. The adequacy of site food flux should also be considered if there is a higher percentage of *M. trossulus* stock. With an increase in the ratio of *M. trossulus* to *M. edulis*, there should be a correspondent decrease in the socking and stocking density to compensate for the elevated food demand of the *M. trossulus* portion of the stock. Consider the following example based upon the present study and the observed differences between clearance rates for *M. edulis* and *M. trossulus*:

Example 1A:

Average clearance rate for 1 gram dry tissue weight of *M. edulis*: **2.07 L/h**

Sock dimensions: diameter = 0.10 m; height = 2.5 m

Assume velocity of 0.10 m/s

Volume = $\pi r^2 h$

= $\pi(0.05\ m)^2(2.5\ m)$

=$0.0196\ m^3$

Thus, $0.0196\ m^3$ is the volume of water passing through the sock every second.

Assume a constant food concentration of 5,000,000 cells/L, and that this entire food concentration is available to the mussels for clearance, then:

5,000,000 cells/L x 1000 L/m^3 = 5,000,000,000 cells/m^3

0.0196 m^3/sec x 5,000,000,000 cells/m^3 = 98,000,000 cells/sec moving through the sock.

If *M. edulis* have an average weight-specific clearance rate of 2.07 L/h, then:

2.07 L/h x 5,000,000 cells/L = 10,350,000 cells/h = 2,875 cells/s

Assuming 50 % clearance, then:

98,000,000 cells/s x 0.50 / 2,875 cells/s = 17,043 individual 1 g mussels

Thus, for a given sock diameter and height and a given available food concentration and current, approximately 17 kg of 1 gram *M. edulis* can be supported.

Example 1B:

Average clearance rate for 1 gram dry tissue weight of *M. trossulus*: **3.37 L/h**

Sock dimensions: diameter = 0.10 m; height = 2.5 m

Assume velocity of 0.10 m/s

Volume = $\pi r^2 h$

= $\pi(0.05\ m)^2(2.5\ m)$

$=0.0196\ m^3$

Thus, $0.0196\ m^3$ is the volume of water passing through the sock every second.

Assume a constant food concentration of 5,000,000 cells/L, and that this entire food concentration is available to the mussels for clearance, then:

5,000,000 cells/L x 1000 L/m^3 = 5,000,000,000 $cells/m^3$

0.0196 m^3/s x 5,000,000,000 $cells/m^3$ = 98,000,000 cells/s moving through the sock.

If *M. trossulus* have an average weight-specific clearance rate of 3.38 L/h, then:

3.38 L/h x 5,000,000 cells/L = 16,900,000 cells/h = 4,694 cells/s

Assuming 50 % clearance, then:

98,000,000 cells/sec x 0.50 / 4,694 cells/sec = 10,439 individual 1 g mussels

Thus, for a given sock diameter and height and a given available food concentration and current, approximately 10.4 kg of 1 gram *M. trossulus* can be supported.

Therefore, all other factors being equal, 1.63 times more *M. edulis* can be supported than *M. trossulus*. Similarly, Mallet and Carver (1995) estimated the economic value of *M. edulis* to be 1.7 times higher than *M. trossulus*.

Very little is known about the performance of *M. edulis* relative to *M. trossulus*. Certain mussel farm operators argue that higher production rates could be achieved if they could grow a stock of pure *M. edulis*. Mallet and Carver (1995) observed that *M. trossulus* had a significantly lower tissue weight during the summer than *M. edulis* and was eliminated at a significantly higher rate during commercial grading trials than *M. edulis*. From this, they estimated that the economic value of *M. edulis* was 1.7 times higher than *M. trossulus*. The results of the present study agree with the observations of Mallet and Carver (1995). Blue mussels are cultivated extensively, so there is no increased food cost associated with the elevated food demand observed in *M. trossulus*. However, there would be greater space requirements to meet the elevated food demand of *M. trossulus*. Since higher rates of growth and survival in *M. edulis* compared with *M. trossulus* have been observed (Comesaña *et al*. 1999), *M. edulis* may direct more energy towards growth and survival than *M. trossulus*. However, *M. trossulus* may simply be an easier prey target with thinner shells or have lower thermal tolerance. Further research in this area is necessary for a more complete understanding of the observed patterns.

As expected, the results of the present study also showed that dry weight was significantly correlated with shell length. With an increase in shell length, there was a corresponding increase in dry weight. Therefore, if, as according to the present study, *M.*

edulis does have an overall greater shell length than *M. trossulus*, it is possible that it will also have a higher meat yield. Observations of an increased frequency of *M. edulis* in the larger size classes of mussels and an increased frequency of *M. trossulus* in the smaller size classes of mussels (Bates 1992) support the idea that *M. edulis* may have a higher economic value than *M. trossulus*. If *M. edulis* displays a higher overall rate of growth and survival than *M. trossulus*, even though *M. trossulus* displays a higher feeding rate, then it is possible that *M. edulis* is a more efficient feeder than *M. trossulus*. However, it is important to note that shell growth and meat yields are not necessarily coupled. Hilbish (1986) observed that rates of growth in shell and soft tissue do not occur simultaneously.

In general, *M. edulis* has been characterized as a temperate cold-water mussel which can occur in brackish waters, and *M. trossulus* has been characterized as a cold-water mussel, often found in areas which were ice-covered in previous Ice Ages, and is capable of withstanding very low salinities (Gardner 1996). Newfoundland has been characterized as a sub-arctic marine environment. This implies that *M. trossulus* may actually be better adapted to Newfoundland waters than *M. edulis*. However, additional research directed towards identifying how *M. trossulus* allocates the additional food energy will be instructive in determining which species, if either, is actually a superior candidate for aquaculture in Newfoundland. This is especially true since no significant difference was observed in the rates of filtration or oxygen uptake between *M. edulis* and *M. trossulus*. A simple growth study with the two species grown out side by side would also be very helpful in determining whether one species is more suitable for culture.

Mytilus edulis and *M. trossulus* did not differ in the rates of filtration or oxygen uptake. Although the same trends were observed, there was a higher degree of variability associated with these two variables. A larger sample size and further experimentation is necessary in order to determine whether the trends observed with these variables would correspond with the observations for clearance and ingestion in *M. edulis* and *M. trossulus*.

The results of the present study support the suggestion in the literature that *M. edulis* and *M. trossulus* are physiologically distinct. Differential physiological adaptations may significantly contribute to the overall carrying capacity of a blue mussel cultivation site. Efforts should be made to ascertain species proportions of a stock. Allozyme and DNA markers are the most reliable methods of species determination. If the species proportions of a stock are unknown, estimates of secondary production may be biased. According to Dickie *et al.* (1984), genotype is a major determinant of mortality effects in blue mussels. If more than one species is present in a stock of mussels, species proportions and associated physiological differences should be incorporated into models used to predict blue mussel production. Species-specific physiological differences will affect the overall food demand and performance of a stock of blue mussels. Incorporating this information into such models will greatly improve the reliability of predicted production estimates.

4.2.2.1 Shell Analysis

There are significant differences in the shell weight to shell length ratio between cultured *Mytilus edulis* and cultured *M. trossulus*. If *M. trossulus* has a lighter shell weight (for a given size), then it is possible that this species will be more easily damaged during harvesting and processing procedures. This suggests that *M. trossulus* may be an inferior candidate for aquaculture and agrees with the findings of Mallet and Carver (1995) stating that *M. edulis* has a higher economic value than *M. trossulus*. However, it is also possible that a lighter shell weight for a comparable size of mussel may be due to morphometric differences rather than shell thickness. In this case, such a mussel may not be more susceptible to breakage. Therefore it is important to compare shell morphometrics as well as shell thickness in order to determine with confidence which shells would be more susceptible to damage or breakage during processing.

4.2.3 Food Availability

Clearance rate was not significantly affected by the available food concentration. Low food availability was characterized as a food concentration of <3,500 cell/mL, and medium food availability was characterized as >3,500 cells/mL, <7,500 cells/mL. The narrow range of the available food concentration used in this study likely does not affect clearance rate, since clearance rate eventually peaks in relation to increasing food concentration, whereas ingestion plateaus in relation to increasing food concentration, until very high concentrations are reached (Dabinett, P., pers-comm., Memorial

University). The results of the present study support the hypothesis that rates of feeding (ingestion) increase with an increase in the available food concentration for all blue mussels. Mean ingestion rates were consistently higher at the high food concentrations compared to the mean rates of ingestion observed at the low food concentration. For April 1998, the overall mean ingestion rate at medium food concentration was higher than the mean rate at the high food concentration. There was a relatively small gap separating these two levels of food availability. More distinct levels of food availability may have allowed for more consistency among the months. Despite this, overall mean ingestion rates of increased rates of feeding with an increased available food supply were observed. The results of this study support recent published studies. Larval and juvenile bay scallops (*Argopecten irradians concentricus* (Say)) showed higher ingestion rates of *Isochrysis galbana* at higher algal concentrations (Lu and Blake 1997). Furthermore, Hatcher *et al.* (1997) studied the effects of winter ice cover and nutritive stress on the metabolism of cultured *M. edulis*. They observed that food availability is a significant control on the seasonally changing metabolism of mussels, regardless of water temperature. MacDonald and Ward (1994) reported that clearance rates in *Placopecten magellanicus* were positively correlated with the total amount of chlorophyll-containing particles in the surrounding water and ingestion increased with increasing concentration of total suspended particulate matter. Bayne *et al.* (1993) report similar observations for *M. edulis*.

Filtration rates were not significantly affected by food availability. Again, there was a higher amount of variability associated with this variable, which may explain why

filtration results were not consistent with the other measures of feeding. Oxygen consumption was not significantly affected by food availability. Likewise, Widdows *et al.* (1979) found that rates of oxygen consumption were not significantly affected by changes in seston concentration. However, metabolic rate is controlled by a number of interrelated variables. It is difficult to quantify the interacting effects of temperature, reproductive condition and food availability.

In addition, there are several references in the literature to the effect of food quality on bivalve feeding physiology. In this study, mussels were fed a diet that consisted of equal amounts of two species of microalgae, the diatom *Chaetoceros muelleri* and the flagellate *Isochrysis galbana* (clone T-ISO). The purpose of providing a diatom and a flagellate was to try to provide a balanced diet for the mussels. Physiological acclimation has been observed in *M. edulis* across several levels of experimental food quality. Relevant mechanisms of compensation include increased rates of ingestion, increased absorption efficiency and an apparent increase in digestive capacity (gut fullness) (Bayne *et al.* 1984). Mussels were observed to increase absorption rates for organics primarily by increasing absorption efficiency. Therefore, it is not likely that the type of food provided to the mussels throughout this study inhibited feeding activity.

4.2.4 Seasonal Variables

The results of this study indicate that rates of clearance, ingestion, filtration and oxygen uptake follow a seasonal cycle in all blue mussels examined. The influence of

temperature and food on the growth of bivalves is well documented within the literature, especially for mytilids (e.g., Widdows 1978; Bayne and Worrall 1980; Kautsky 1982; Sprung 1984). Seasonal variation in bivalve physiology is usually related to intrinsic factors such as body size and reproductive condition as well as to extrinsic factors such as temperature and food availability (Smaal *et al.* 1997). Rates of clearance, oxygen uptake (Foster-Smith 1975) and filtration (Winter 1978) have been observed to exhibit endogenous and exogenous controls. Jørgensen *et al.* (1990) showed a relation between reduced pumping rates of blue mussels and the higher water viscosity at low temperatures. However, according to Thompson and Newell (1985) it is inappropriate to define, absolutely, a particular set of physiological responses to temperature as characteristic of a given species, in a species as ubiquitous and diverse of habitat as *Mytilus edulis*.

Bayne and Widdows (1978) have demonstrated in *M. edulis* and *Cerastoderma edule* that reproductive condition (defined by a complex interaction among temperature, food availability and hormonal cycles) can explain the seasonal variation in oxygen consumption to a greater extent than temperature. Widdows (1985) found that oxygen consumption in blue mussels was independent of temperature. MacDonald and Thompson (1986) observed that oxygen uptake and clearance rate in scallops varied seasonally in relation to ambient temperature and food conditions, which appeared to be intricately connected with the energy demands of gametogenesis. Spawning is stressful for mussels (Bayne *et al.* 1978), and mussels have often been observed to resort to protein

catabolism for energy because their carbohydrate reserves have been exhausted by vitellogenesis (Bayne *et al.* 1976).

Significant seasonal cycles were associated with rates of clearance, ingestion, filtration and oxygen consumption in the present study. Physiological rates seemed to be affected by ambient seawater temperatures. Physiological rates generally corresponded to ambient seawater temperatures, increasing during the spring and summer, and decreasing during late autumn and winter. Reproductive condition also significantly affected blue mussel physiology. In the present study, rates of clearance, ingestion, filtration and oxygen consumption were depressed during spawning, which corresponds to Newell and Thompson's (1984) observation of a decrease in clearance rates in *M. edulis* following gametogenesis.

The interactive effects of season and reproductive condition on the seasonal cycles of blue mussels were evident. Throughout late spring and early summer of 1998 and 1999, intermittent spawning patterns were observed, however, most of the spawning occurred in June. Newell and Thompson (1984) observed depressed clearance rates in *M. edulis* during an extended, late summer period of spawning. During this extended spawning, mussels were observed to have a very pronounced shell gape that prevented the formation of siphons. This effectively reduced efficiency in the formation of feeding currents and therefore feeding efficiency. The decreases in clearance, ingestion, filtration and oxygen consumption during the late spring and summer months observed in this study correspond to the mussel spawning periods. The sharp increases sometimes observed following

depressed feeding activity agree with the observations of Smaal *et al.* (1997), who have suggested that feeding rate may increase to provide energy for gametogenesis. The spawning period also corresponds to the observed spawning in mussels from Trinity Bay, Newfoundland, which takes place during late July (Thompson 1984).

The effect of food availability on physiological rates further complicates the interpretation of the seasonal and reproductive condition data obtained from this study. Experimental mussels were fed predetermined diets (low, medium or high food concentrations) which did not match ambient seasonal food levels. Winter and Langton (1975) observed that growth (defined as an increase in the dry tissue weight) is a direct function of the quantity of food ingested up to an optimal level. Similarly, Riisgård (1991) observed that clearance rate (mL/min) peaks and gradually decreases at very high algal concentrations (>15,000 cells/mL). He proposed that unnaturally high algal concentrations commonly used in laboratory studies may lead to valve closure, reduced metabolism and reduced growth. Food concentrations used in this study were generally not unnaturally high, although, experimental mussels were exposed to low, medium and high food concentrations. Exposure to high food concentrations during some of the colder winter months may have not been representative of what the mussels would have experienced in their natural environment during colder periods.

It is important to acknowledge the inherent difficulty associated with separating the effects of temperature, reproductive condition and food availability. These variables are intricately related and it is very difficult to establish the exact effect of either temperature,

reproductive condition or food availability on rates of clearance, ingestion, filtration or oxygen consumption in blue mussels. Since there is a strong interaction among these variables, the overall effect of temperature and reproductive condition should be considered in blue mussel cultivation. These effects will likely have less influence on socking and stocking densities and carry more weight in deciding upon the optimal time to harvest or handle market-size mussels. If food intake is elevated prior to spawning, better meat yields may be achieved if mussels are harvested just prior to spawning, as long as harvesting does not result in gamete release prior to consumption. It is definitely best not to harvest immediately after spawning since mussel meat yields at that time will be minimal.

4.2.5 Size and Density

To consider the relative feeding rates of small and large mussels, standardized rates of clearance and ingestion were examined for small mussels standardized to 0.1 gram dry tissue weight and large mussels to 1.0 gram dry tissue weight. The implications of socking densities for the two size classes are illustrated in the following example based upon the observed differences between clearance rates for small and large blue mussels from the present study.

Example 2A:

Average clearance rate for 0.1 gram dry tissue weight of small blue mussels: 1.51 L/h

Sock dimensions for small blue mussels: diameter = 0.10 m; height = 2.5 m

Assume a current velocity of 0.10 m/s

Volume = $\pi r^2 h$

= $\pi(0.05\ m)^2(2.5\ m)$

=0.0196 m^3

Since the velocity is equal to 0.10 m/s, it will take one second for water to be replaced in the sock. Thus, 0.0196 m^3 is the volume of water passing through the sock every second.

Assuming a constant food concentration of 5,000,000 cells/L and that this entire food concentration is available to the mussels for clearance, then:

5,000,000 cells/L x 1,000 L/m^3 = 5,000,000,000 cells/m^3

0.0196 m^3/s x 5,000,000,000 cells/m^3 = 98,000,000 cells/s

Thus 98,000,000 cells are passing through the sock every second.

If small blue mussels have an average clearance rate of 1.51 L/h, then:

1.51 L/h x 5,000,000 cells/L = 7,550,000 cells/h = 2,097 cells/s

If 98,000,000 cells pass through the sock every second and 2,097 cells are consumed every second by 0.1 gram dry weight of small blue mussels, and assuming 50 % clearance, then:

98,000,000 cells/s x 0.50 / 2,097 cells/s = 23,367 individual 0.1 g mussels

Thus, for the given sock dimensions and a given available food concentration and current, approximately 2.3 kg dry weight of 0.1 g (small) blue mussels can be supported.

Example 2B:

Average clearance rate for 1 gram dry tissue weight of large blue mussels: **2.32 L/h**

Sock dimensions for large blue mussels: diameter = 0.10 m; height = 2.5 m

Volume = $\pi r^2 h$

= $\pi(0.05\ m)^2(2.5\ m)$

=$0.0196\ m^3$

Assume a velocity of 0.10 m/s and a flux equal to that for the smaller mussels of 0.0196 m^3/s.

Assuming a constant food concentration of 5,000,000 cells/L and that this entire food concentration is available to the mussels for clearance, then:

5,000,000 cells/L x 1,000 L/m^3 = 5,000,000,000 cells/m^3

0.0196 m^3/sec x 5,000,000,000 cells/m^3 = 98,000,000 cells/s

Thus 98,000,000 cells are passing through the sock every second.

If large blue mussels have an average clearance rate of 2.32 L/h, then:

2.32 L/h x 5,000,000 cells/L = 11,600,000 cells/h = 3,222 cells/s

If 98,000,000 cells pass through the sock every second and 3,222 cells are consumed every second by 1 gram dry weight of large blue mussels, and assuming 50 % clearance, then:

98,000,000 cells/sec x 0.50 / 3,222 cells/s = 15,208 individual 1 g mussels

Thus, for the given sock dimensions and a given available food concentration and current, approximately 15 kg dry weight of 1 gram (large) blue mussels can be supported.

Therefore, the values obtained from the present study indicate that larger mussels should be maintained at a much lower stocking density than smaller mussels, but can be maintained at a higher biomass per sock compared to smaller mussels. This is illustrated

in the following example. An equivalent dry weight, e.g., 1 kg dry weight of small mussels will clear (and ingest) more than 1 kg dry weight of large mussels.

Example 3:

Mean dry weight of one small mussel = 0.1 g

Mean dry weight of one large mussel = 1.0 g

1 kg = 10,000 small mussels

1 kg = 1,000 large mussels

Given the mean clearance rate of small mussels is 1.51 L/h and the mean clearance rate of large mussels is 2.32 L/h, then 1 kg of small mussels will clear 15,100 L/h and 1 kg of large mussels will clear 2,320 L/h.

If a mussel sleeve is beyond optimal biomass, then growth rates may become depressed due to competition for food (Fréchette and Bourget 1985; Mallet and Carver 1993). Dense aggregations of bivalves can locally deplete the water of seston resulting in food-limited growth (Pilditch *et al.* 1996). With such dense aggregations, the literature suggests that there is an increased risk of mussel drop-off due to an insufficient availability of oxygen, as well as reduced juvenile settlement due to a greater accumulation of biodeposits which effectively leaves less surface area for larval settlement (Mallet and Carver 1993).

Also, pressure from other mussels may impede shell opening and the formation of siphons. Shell opening is a critical factor in controlling mussel pumping rate, which, in turn, will affect acquisition of food (Jørgensen *et al.* 1988). Socking at optimal density will lessen the risk of food and oxygen deprivation, and ultimately mussel loss.

Similarly, it is important to consider the size distribution of a mussel stock when deciding upon optimal site stocking density and longline placement. Strategic density management can be a major tool for a mussel farmer to use to increase commercial production (Gosling 1992). For instance, if the goal is to attain market-size mussels in the shortest time, then smaller size classes should be stocked in an area with maximal accessibility to the available food resources. This will be dependent upon site characteristics including site type (flow-through or embayment) and site-specific food flux patterns. Food supply is influenced by a number of factors, varying temporally and spatially, such as season, water flow, mixing of the water column, upwellings, wind speed and direction, sedimentation/erosion characteristics and depletion by benthic filtration (Smaal and Haas 1997). Tidally dominated systems, for example, have periods of very low water flow and are therefore more vulnerable to localized food depletion, whereas in other systems food supply may not be as closely coupled to the tidal cycle (Carver and Mallet 1990). In large bays, primary production may constitute the primary food source (Carver and Mallet 1990). In Newfoundland, most of the available food supply is from primary production.

Several studies have emphasized the importance of currents in maintaining a constant supply of food to suspension feeders (Incze *et al.* 1980; Rosenberg and Loo 1983;

Fréchette and Bourget 1985). However, too strong a current may actually limit food acquisition. Filtration by blue mussels may be inhibited at flow rates exceeding 25 cm/s (Wildish and Miyares 1990). Wildish and Miyares (1990) hypothesize that as ambient seawater pressure at the inhalant siphon exceeds the mussel's ability to effectively remove food particles from the water, the ciliary pumping rate is decreased, and pumping becomes intermittent, exploratory and/or concerned with basal respiration. Although current flow rates rarely exceed 25 cm/s in Newfoundland, it is still important to consider flow rates. In addition, mussel orientation will also affect food intake. Wild mussels are benthic, and are generally perpendicular in orientation to current flow, whereas socked cultured mussels range in orientation from perpendicular to parallel to directly facing a current. Food flux and all factors affecting food flux must also be given due consideration when calculating optimal stocking density.

In Mutsu Bay, Japan, overstocking in the mid-seventies resulted in substantial growth reduction and mortality in the scallop, *Patinopecten yessoensis* (Ventilla 1982). In Newfoundland, Atlantic Ocean Farms (AOF) was one of the first commercial blue mussel cultivation companies, incorporated in 1981. AOF chose their sites based upon the abundance of natural mussel beds (Ward, J. pers-comm., AOF, St. John's, NF). However, the first 25,000 socks of mussels placed in the harbour did not grow. "It was years before we discovered we had overstocked the site, and it also had poor flushing and was unable to circulate nutrients" (DFA 1999). Identification and quantification of differences in the feeding demand and oxygen consumption patterns of small and large blue mussels is critical. When applied to an ecosystem model, such values will

strengthen the reliability of models used to predict carrying capacity and site production, thereby minimizing the possibility of overstocking.

The final market product should also be considered when evaluating optimal stocking density, since different end products may require a different initial stocking density (Parsons and Dadswell 1992). For instance, deliberate overcrowding can be used by a mussel farmer to slow growth rates for specific purposes such as to maintain a continuous supply of mussels of the desired size for marketing (Gosling 1992). This will become a more useful tool with increasing diversification of the blue mussel market (e.g., mussel salads, individually-quick-frozen (IQF) products, vacuum-packed products and ready-made products).

In addition to adjusting stocking density, a mussel farmer has other options to accommodate the observed differences in feeding and oxygen consumption between small and large blue mussels. Small and large mussels can be maintained on separate sites. Ideally, larger mussels should be maintained in an area offering maximal food flux. This will optimize growth for both the small and large mussels. Furthermore, whether separate sites are available or not, mussel lines should be oriented so that they are parallel to the current, instead of perpendicular. A parallel orientation will also optimize the available food supply to the mussels.

Section 5 Conclusion

5.1 Conclusions

With respect to the mussels used throughout this study, obtained from Reach Run, Newfoundland:

1) There were no significant differences in the observed rates of clearance, ingestion, filtration or oxygen uptake between cultured and wild blue mussels, *M. edulis* and *M. trossulus*.
2) *Mytilus trossulus* had, on average, higher rates of clearance and ingestion than *M. edulis*.
3) Ingestion rates increased with an increase in the available food concentration for *M. edulis* and *M. trossulus*.
4) Rates of clearance, ingestion, filtration and oxygen consumption varied seasonally for *M. edulis* and *M. trossulus*.

5.2 Recommendations Pertaining to Blue Mussel Cultivation

1) Ideally, small and large mussels should be maintained on separate sites in order to maximize the available food concentration for large blue mussels.
2) If it is not possible to maintain different size classes on separate sites, then larger mussels should be maintained in an area offering maximal food flux, or a larger number of smaller mussels can be grown out.

3) For any site, mussel lines should be oriented so that they are parallel to the current, not perpendicular, thereby optimizing the food supply to the mussels.

4) The adequacy of site food flux should also be reconsidered if there is a higher percentage of *Mytilus trossulus* stock, in which case the overall sock and site density should be lowered in order to ensure that there is a sufficient supply of food available to each mussel.

5) In designing carrying capacity models for blue mussel cultivation, it is important to incorporate size and species proportions, as well as food flux and season into the models, since each of these factors affect blue mussel feeding and respiratory physiology.

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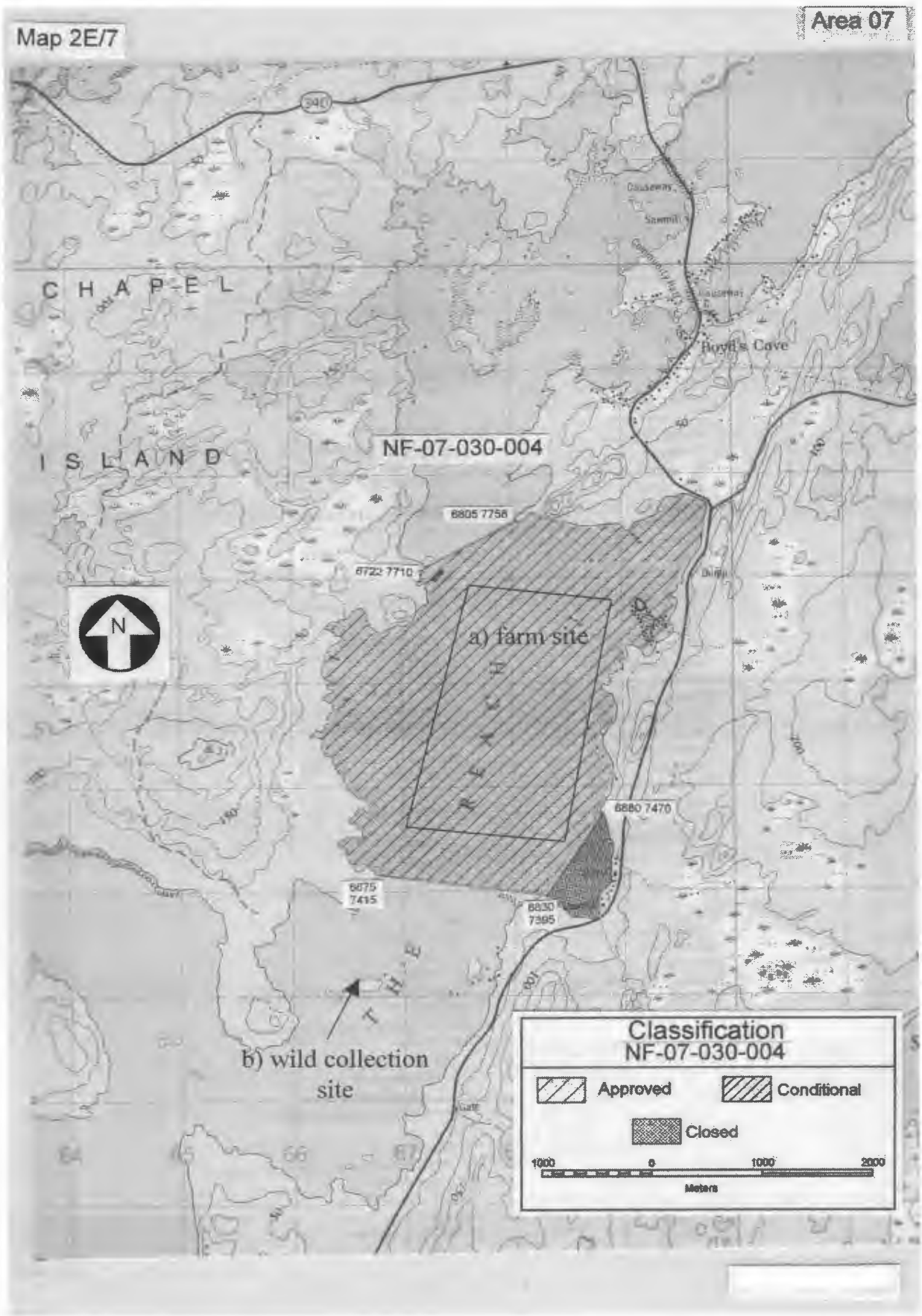
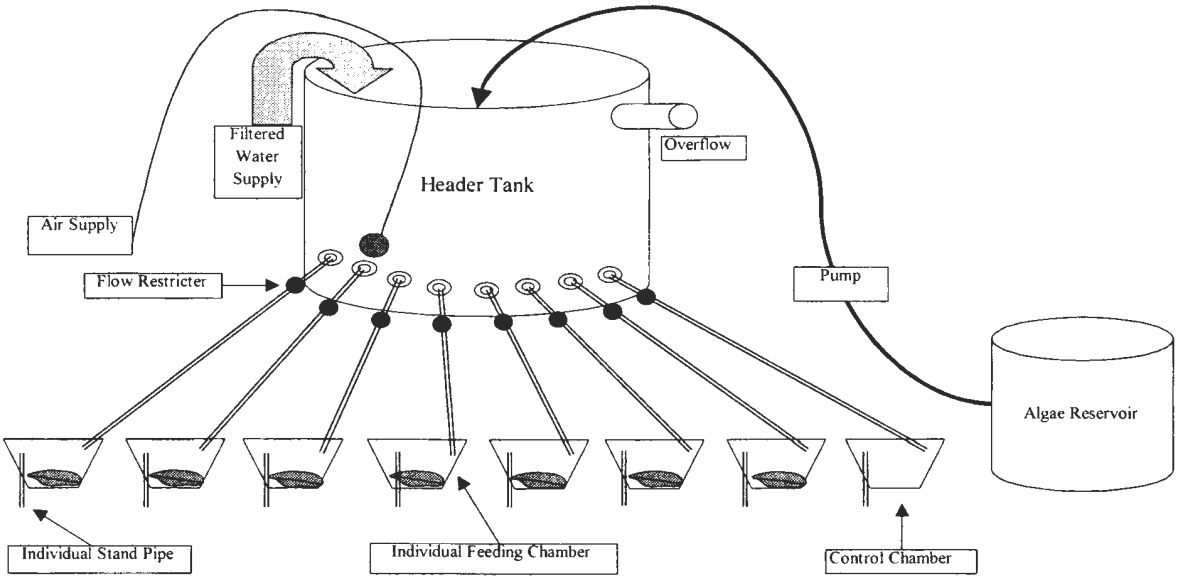
Appendix 1: A map of Reach Run, Newfoundland (49° 25′ N, 54° 42′ W (4531)) obtained from the Environment Canada Shellfish Classification internet site (1999).

Web address:

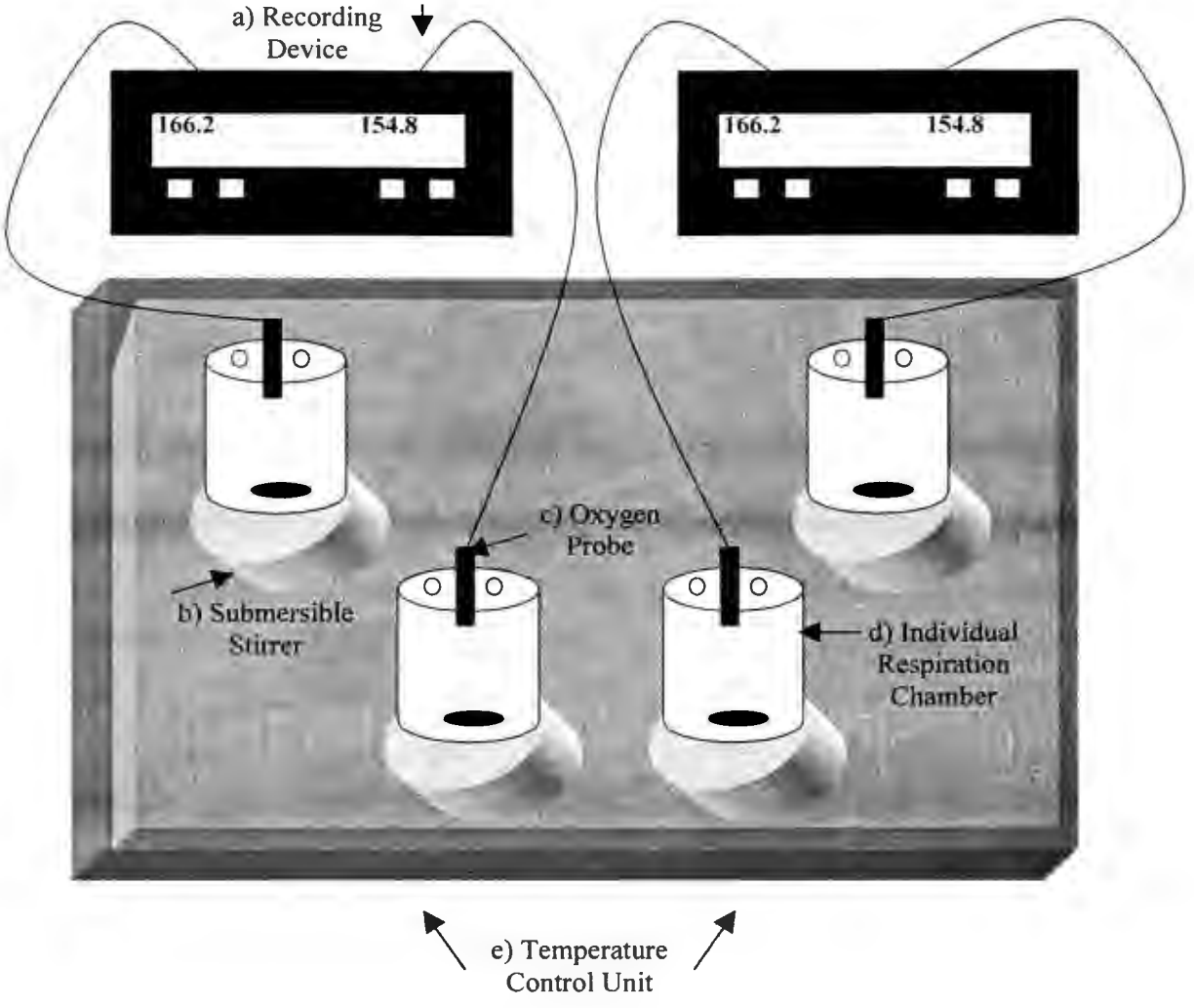
http://www.atl.ec.gc.ca/epb/sfish/maps/nf/high/f070304h.jpg


Map 2E/7
Area 07
CHAPEL
ISLAND
NF-07-030-004
Boyd's Cove
6805 7758
6722 7710
6880 7470
6875 7415
6830 7395
a) farm site
b) wild collection site
N
Classification
NF-07-030-004
Approved
Conditional
Closed
1000
0
1000
2000
Meters

Appendix 2: A schematic drawing of the octopus set-up as per MacDonald (1985).


Filtered
Water
Supply
Header Tank
Overflow
Air Supply
Flow Restricter
Pump
Algae Reservoir
Individual Stand Pipe
Individual Feeding Chamber
Control Chamber

Appendix 3: A schematic drawing of the respiration set-up.


a) Recording Device
166.2
154.8
166.2
154.8
c) Oxygen Probe
b) Submersible Stirrer
d) Individual Respiration Chamber
e) Temperature Control Unit

Appendix 4: A summary of the mean values, standard deviations and sample sizes for the standardized values of clearance (L/h) for *Mytilus edulis* and *M. trossulus* over time.

Species	Date	Mean	Std. Deviation	Sample Size
Mytilus edulis	Apr-98	3.42	0.57	3
	May-98	2.44	1.84	13
	Jun-98	2.48	1.25	12
	Jul-98	3.57	0.83	11
	Aug-98	2.65	1.28	16
	Sep-98	2.26	1.01	10
	Oct-98	1.89	0.57	14
	Nov-98	1.39	0.72	19
	Dec-98	0.97	0.51	14
	Jan-99	0.83	0.46	8
	Mar-99	1.34	0.47	16
	May-99	1.67	1.25	13
	Jun-99	1.52	0.58	12
	Jul-99	1.53	0.62	6
	Aug-99	3.43	1.60	19
	Total	2.07	1.32	186
Mytilus trossulus	Apr-98	3.77	0.91	8
	May-98	4.23	1.35	12
	Jun-98	4.23	3.08	9
	Jul-98	3.65	1.19	14
	Aug-98	4.80	0.51	3
	Sep-98	3.77	1.67	4
	Oct-98	4.00	1.52	16
	Nov-98	2.22	0.72	11
	Dec-98	1.89	1.54	14
	Jan-99	1.71	0.78	5
	Mar-99	2.65	1.08	8
	May-99	2.39	0.43	2
	Jun-99	2.84	1.45	9
	Jul-99	1.63	1.89	3
	Aug-99	4.94	1.62	12
	Total	3.38	1.76	130
Total	Jan-99	1.17	0.73	13
	Mar-99	1.78	0.95	24

Species	Date	Mean	Std. Deviation	Sample Size
	Apr-98	3.68	0.82	11
	May-98	3.30	1.83	25
	Jun-98	3.23	2.33	21
	Jul-98	3.62	1.03	25
	Aug-98	2.99	1.43	19
	Sep-98	2.69	1.36	14
	Oct-98	3.02	1.58	30
	Nov-98	1.69	0.81	30
	Dec-98	1.43	1.22	28
	May-99	1.77	1.19	15
	Jun-99	2.08	1.22	21
	Jul-99	1.56	1.07	9
	Aug-99	4.01	1.75	31
	Total	2.61	1.64	316

Appendix 5: A summary of the mean values, standard deviations and sample sizes for the standardized values of ingestion (cells/h) for *Mytilus edulis* and *M. trossulus* at low (<3,500 cell/mL), medium (>3,500 cells/mL, <7,500 cell/mL) and high (>7,500 cells/mL) food concentrations over time.

Species	Food Concentration	Date	Mean	Std. Deviation	Sample Size
Mytilus edulis	Low	Apr-98	93325.4		1
		May-98	78226.8	39576.2	7
		Jun-98	58147.0	24580.0	10
		Jul-98	87957.0	46532.2	8
		Aug-98	25788.4	19115.7	6
		Sep-98	64521.9	33844.8	4
		Oct-98	36379.2	15477.2	9
		Nov-98	54633.1	31966.9	11
		Dec-98	1698.2		1
		Jan-99	29180.2	16193.1	8
		Mar-99	31440.1	20710.2	10
		May-99	36162.5	27658.0	8
		Jun-99	48970.0	25109.1	3
		Jul-99	27939.0	11492.8	4
		Total	48497.1	33273.3	90
	Medium	Apr-98	234422.9		1
		May-98	126023.1	140015.8	4
		Jul-98	160845.5	18292.3	2
		Aug-98	158796.2	33215.8	6
		Sep-98	166606.4	68172.2	6
		Oct-98	110529.5	32510.9	4
		Nov-98	109474.0	65591.3	8
		Dec-98	60305.0	9769.8	8
		Mar-99	61015.9	26576.8	6
		May-99	68315.5	29200.5	3
		Jun-99	97469.2	12273.9	5
		Aug-99	181010.7	81796.5	13

Species	Food Concentration	Date	Mean	Std. Deviation	Sample Size
		Total	124613.6	73880.0	66
	High	Apr-98	316227.8		1
		May-98	115681.9	31616.9	2
		Jun-98	303998.8	49278.7	2
		Jul-98	331131.1		1
		Aug-98	350963.3	14210.4	4
		Oct-98	371535.2		1
		Dec-98	152884.7	90898.3	5
		May-99	1037951.3	672614.1	2
		Jun-99	198593.5	89016.2	4
		Jul-99	163731.2	31788.0	2
		Aug-99	411800.4	157719.0	6
		Total	323169.1	266386.5	30
	Total	Apr-98	214658.7	112757.8	3
		May-98	98695.7	79429.0	13
		Jun-98	99122.3	99363.7	12
		Jul-98	123316.2	84556.2	11
		Aug-98	156960.1	132099.6	16
		Sep-98	125772.6	75780.9	10
		Oct-98	81504.7	92362.8	14
		Nov-98	77724.0	54905.9	19
		Dec-98	89183.0	72500.8	14
		Jan-99	29180.2	16193.1	8
		Mar-99	42531.0	26673.4	16
		May-99	197703.7	421356.0	13
		Jun-99	119052.5	78628.1	12
		Jul-99	73203.1	72101.0	6
		Aug-99	253891.6	153356.3	19
		Total	119808.1	150872.8	186
Mytilus trossulus	Low	Apr-98	97723.7		1
		May-98	127573.5	50524.8	5
		Jun-98	143496.0	122971.4	6

Species	Food Concentration	Date	Mean	Std. Deviation	Sample Size
		Jul-98	131062.8	41942.0	6
		Aug-98	91201.1		1
		Sep-98	133789.9	67677.7	3
		Oct-98	113457.9	47117.5	6
		Nov-98	93803.7	23429.7	8
		Jan-99	59203.8	26692.9	5
		Mar-99	43213.3	9765.8	2
		Jun-99	78830.0	30721.6	5
		Jul-99	38862.5	47354.5	3
		Total	101958.3	60629.9	51
	Medium	Apr-98	269153.5		1
		May-98	237147.7	79580.5	7
		Jul-98	199628.2	85341.1	6
		Sep-98	218776.2		1
		Oct-98	150351.1	45144.2	3
		Nov-98	105430.6	65415.5	3
		Dec-98	79308.4	20268.0	4
		Mar-99	119955.4	49425.8	6
		May-99	77624.7		1
		Jun-99	261412.9	67340.1	2
		Aug-99	253925.6	73272.3	7
		Total	183609.1	88717.4	41
	High	Apr-98	223053.2	84308.9	6
		Jun-98	240784.2	25784.1	3
		Jul-98	307945.2	54859.7	2
		Aug-98	393576.2	6407.8	2
		Oct-98	477934.0	189597.4	7
		Dec-98	250113.0	225397.7	10
		May-99	676083.0		1
		Jun-99	302203.7	175893.9	2
		Aug-99	700236.5	175564.1	5
		Total	370843.6	228327.9	38

Species	Food Concentration	Date	Mean	Std. Deviation	Sample Size
	Total	Apr-98	213149.6	86675.1	8
		May-98	191491.8	86984.0	12
		Jun-98	175925.4	109470.0	9
		Jul-98	185716.9	86462.0	14
		Aug-98	292784.5	174635.1	3
		Sep-98	155036.5	69707.8	4
		Oct-98	279833.7	219385.2	16
		Nov-98	96974.7	35631.4	11
		Dec-98	201311.7	204153.8	14
		Jan-99	59203.8	26692.9	5
		Mar-99	100769.9	54959.6	8
		May-99	376853.8	423173.9	2
		Jun-99	169042.6	128680.1	9
		Jul-99	38862.5	47354.5	3
		Aug-99	439888.5	258753.1	12
		Total	206307.0	176809.9	130
Total	Low	Apr-98	95524.6	3110.1	2
		May-98	98787.9	49277.5	12
		Jun-98	90152.9	84995.8	16
		Jul-98	106430.9	48296.4	14
		Aug-98	35133.1	30261.7	7
		Sep-98	94208.2	58909.8	7
		Oct-98	67210.7	49573.0	15
		Nov-98	71126.0	34292.8	19
		Dec-98	1698.2		1
		Jan-99	40727.7	24931.8	13
		Mar-99	33402.3	19508.9	12
		May-99	36162.5	27658.0	8
		Jun-99	67632.5	30956.2	8
		Jul-99	32620.5	29113.9	7
		Total	67834.1	51780.6	141
	Medium	Apr-98	251788.2	24558.2	2
		May-98	196738.8	113245.2	11

Species	Food Concentration	Date	Mean	Std. Deviation	Sample Size
		Jul-98	189932.5	74648.0	8
		Aug-98	158796.2	33215.8	6
		Sep-98	174059.2	65281.6	7
		Oct-98	127595.9	40754.0	7
		Nov-98	108371.2	62217.0	11
		Dec-98	66639.5	16134.5	12
		Mar-99	90485.7	48773.8	12
		May-99	70642.8	24292.2	4
		Jun-99	144310.3	85180.0	7
		Aug-99	206530.9	84819.2	20
		Total	147219.4	84543.1	107
	High	Apr-98	236363.9	84637.7	7
		May-98	115681.9	31616.9	2
		Jun-98	266070.0	46242.1	5
		Jul-98	315673.8	41036.5	3
		Aug-98	365167.6	24771.0	6
		Oct-98	464634.1	179518.6	8
		Dec-98	217703.6	193057.7	15
		May-99	917328.5	519475.1	3
		Jun-99	233130.3	117493.6	6
		Jul-99	163731.2	31788.0	2
		Aug-99	542907.7	217844.9	11
		Total	349810.7	245099.4	68
	Total	Apr-98	213561.1	88329.9	11
		May-98	143237.8	94134.1	25
		Jun-98	132037.9	108353.7	21
		Jul-98	158260.6	89598.0	25
		Aug-98	178406.0	143247.2	19
		Sep-98	134133.7	72700.1	14
		Oct-98	187280.1	197094.9	30
		Nov-98	84782.6	48969.2	30
		Dec-98	145247.4	160804.3	28
		Jan-99	40727.7	24931.8	13

Species	Food Concentration	Date	Mean	Std. Deviation	Sample Size
		Mar-99	61944.0	46581.1	24
		May-99	221590.4	411026.4	15
		Jun-99	140476.8	103277.9	21
		Jul-99	61756.2	64066.6	9
		Aug-99	325890.4	217121.4	31
		Total	155393.1	167297.5	316

Appendix 6: A summary of the mean values, standard deviations and sample sizes for the standardized values of filtration (mg/h) in blue mussels (*Mytilus edulis* and *M. trossulus*) over time.

Date	Mean	Std. Deviation	Sample Size
May-98	4.94	3.89	10
Jun-98	4.17	2.20	22
Jul-98	3.78	1.73	26
Aug-98	3.56	4.53	17
Sep-98	4.52	3.27	14
Oct-98	4.99	3.78	44
Nov-98	2.57	2.65	23
Dec-98	2.40	1.10	28
Jan-99	3.57	2.79	12
Mar-99	3.27	1.99	22
May-99	3.20	0.31	12
Jun-99	1.81	1.43	19
Jul-99	2.50	1.54	8
Aug-99	2.45	2.22	26
Total	3.46	2.81	283

Appendix 7: A summary of the mean values, standard deviations and sample sizes for the standardized values of oxygen uptake in blue mussels (*Mytilus edulis* and *M. trossulus*) (mL/h) over time.

Date	Mean	Std. Deviation	Sample Size
May-98	1.91	1.33	11
Jun-98	0.62	0.25	21
Jul-98	0.60	0.39	28
Aug-98	0.34	0.16	19
Sep-98	0.86	0.71	13
Oct-98	0.93	0.75	50
Nov-98	0.18	0.12	34
Dec-98	0.10	0.07	24
Jan-99	0.04	0.04	9
Mar-99	0.07	0.05	24
May-99	0.39	0.13	16
Jun-99	0.42	0.28	26
Jul-99	0.48	0.09	7
Aug-99	0.52	0.58	27
Total	0.52	0.61	309

Appendix 8: A summary of the mean values, standard deviations and sample sizes for the standardized values of log dry weight (g) of blue mussels (*Mytilus edulis* and *M. trossulus*) over time.

Date	Mean	Std. Deviation	Sample Size
Apr-98	-0.38	0.44	24
May-98	-0.38	0.49	41
Jun-98	-0.73	0.71	22
Jul-98	-0.45	0.75	31
Aug-98	-0.71	0.74	19
Sep-98	-0.50	0.72	14
Oct-98	-0.64	0.71	53
Nov-98	-0.27	0.50	39
Dec-98	-0.16	0.61	29
Jan-99	-0.38	0.66	13
Mar-99	-0.27	0.74	24
May-99	-0.56	0.94	17
Jun-99	-0.47	0.78	26
Jul-99	-0.29	0.43	19
Aug-99	-0.62	0.76	32
Total	-0.45	0.68	403

Appendix 9: A summary of the mean values, standard deviations and sample sizes for log shell weight (covariate log shell length) comparing cultured and wild *Mytilus edulis* and *M. trossulus*.

Mussel Type	Mean	Std. Deviation	Sample Size
Cultured *Mytilus edulis*	0.291	0.625	35
Wild *Mytilus edulis*	0.651	0.727	31
Cultured *Mytilus trossulus*	-0.610	0.399	11
Wild *Mytilus trossulus*	1.410	0.245	8
Total	0.411	0.793	85

Appendix 10: A summary of the mean values, standard deviations and sample sizes for log shell weight (covariate log shell length) comparing cultured and wild blue mussels.

Cultured or Wild	Mean	Std. Deviation	Sample Size
Cultured	0.0758	0.693	46
Wild	0.8071	0.725	39
Total	0.4113	0.793	85

Appendix 11: A summary of the mean values, standard deviations and sample sizes for log shell weight (covariate log shell length) comparing *Mytilus edulis* and *M. trossulus*.

Species	Mean	Std. Deviation	Sample Size
Mytilus edulis	0.0758	0.693	46
Mytilus trossulus	0.8071	0.725	39
Total	0.4113	0.793	85