Seasonal changes in the metabolism of cultured mussels (*Mytilus edulis*) from a Nova Scotian inlet: the effects of winter ice cover and nutritive stress

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Abstract

This study examined the seasonal changes in standard respiration and ammonium excretion rates of mussels (*Mytilus edulis* L.) from suspended culture in Nova Scotia. The measurements included the harsh winter period when the mussel culture lines are held under a thick ice cover. In order to assess the role of short-term energy reserves, mussels were removed from the field and changes in metabolism in the absence of food were measured for up to 11 days. The time required to exhibit maintenance metabolism is a useful index of the magnitude of stored reserves serving as catabolic substrates and a measure of the degree of coupling of mussels to ambient food supplies. The experimental mussels were collected from commercial lines on an aquaculture farm in Upper South Cove, Nova Scotia. The winter mussels, which were collected from under the ice-covered cove, showed signs of nutritional stress, and respiration rates were less than or close to those required for maintenance metabolism. The standard summer and autumn metabolic rates were within the range expected due to the difference in water temperature from winter, with a Q10 of around 2.0. However, the rates measured during spring were much higher than expected based on water temperature, and decreasing rates during particle-starvation suggested that these mussels had accumulated metabolic reserves during the early spring phytoplankton bloom. High mantle index values during spring and their correlation with both respiration and ammonium excretion indicated that the energy demands of reproduction influenced metabolism in this season. These results demonstrate that food availability is a significant control on the seasonally-changing metabolism of mussels regardless of water temperature. It is proposed that low values for the O:N ratios in experimental mussels may reflect the metabolic acclimation of mussels in suspended culture to a high quality food source with a consistently low C:N ratio. © 1997 Elsevier Science B.V.

Keywords: Mussels; Metabolism; Seasonal; Ice-cover; Nutritive-stress

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1. Introduction

Much of the extensive literature dealing with the ecophysiology of the blue mussel *Mytilus edulis* L. arises from research done on European populations (Hawkins and Bayne, 1992). Although this species is circumpolar (Gosling, 1992), there are fewer studies of its adaptations to low temperature regimes. Mussel culture is important in areas such as Atlantic Canada (Mallet, 1989) and northern Russia (Sukhotin and Kulakowski, 1992) where there is seasonal ice cover. Various studies of northern climates (Kautsky, 1982; Thompson, 1984a,b; Loo and Rosenberg, 1989) have documented low winter growth and metabolic rates in boreal waters compared to rates in other seasons, with low temperatures and/or inadequate food proposed as limiting factors. Due to the frequent co-occurrence of low temperatures and reduced primary production, few studies have presented data that can resolve the relative importance of these two factors. Mallet et al., 1987 studied growth of *Mytilus edulis* in Nova Scotia and suggest that tissue growth is probably food-limited in bays that develop continuous ice cover during the winter period. They propose that ice cover may inhibit the development of a local spring phytoplankton bloom. Thus, they suggest that variability in growth rate is probably a response to differences in food availability rather than exposure to low temperatures.

The purpose of the present study is to examine aspects of metabolism of mussels (*Mytilus edulis* L.) taken from suspended culture under the ice (Upper South Cove, Nova Scotia) and to compare these to measurements made during the other seasons. The seasonal metabolic response of mussels to food deprivation is examined. The tested prediction is that during food-rich periods, mussels removed from particle sources are buffered against starvation by accumulated stored reserves. When removed from the food resource, these animals should exhibit decreasing metabolic rates until the short-term reserves are used up, and maintenance metabolism is approached. Maintenance metabolism is represented by a metabolic rate which is adequate to maintain life but not to support feeding, digestion and growth (Bayne et al., 1989).

In contrast to the situation during food-rich periods, mussels removed from particle sources in the winter should have few short-term reserves against starvation and should show little change in metabolism in the absence of food. In addition, the relative influences of food and temperature on metabolic rates, integrated over seasonal time scales, are examined a posteriori by comparing seasonal changes in metabolic rates with seasonal changes in food availability (chlorophyll *a* concentrations) and water temperature. Although several studies (e.g., Kreeger, 1993) have examined various aspects of mussel metabolism during seasonal cycles, very few have dealt with populations which survive under conditions ranging from continuous ice cover during the winter to water temperatures as high as 26°C during the summer, as has been documented in Upper South Cove. Also, very few studies have examined metabolic conditions of mussels compared to continuously-recorded food conditions in situ. Because of continuous fluorometer deployment at this site (Hatcher et al., 1994), we have detailed records of food conditions in the culture area.
2. Methods

2.1. Study site

Upper South Cove is a long, narrow inlet on the Atlantic Coast of Nova Scotia, lying to the west of Lunenburg Bay (Fig. 1). During each tide, water is exchanged through a narrow entrance at the southern end of the cove. The tidal range is 1–2 m, with complete exchange at the mouth. From December to April a layer of ice approximately 30 cm thick covers much of the cove. The Corkum Island mussel farm is the site of many collaborative studies on the ecological role of cultured mussels (Mallet and Carver, 1993; Hatcher et al., 1994; Grant et al., 1995). Both *Mytilus edulis* and *Mytilus trossulus* are cultured on longlines in the upper 5–7 m of the water column at a local density of approximately 400 mussels·m$^{-2}$. For this study, mussels (*M. edulis*) were collected from a longline at a depth of approximately 5 m, in a water depth of 10 m. All samples were taken from the same mussel lease (Fig. 1).

2.2. Field collection and measurement of respiration and ammonium excretion

Ten sampling trips were conducted in 1990 (see Table 1). During each trip, adult mussels (53–57 mm in shell length) were collected from the same commercial array of

![Fig. 1. Study site for mussel metabolism experiments (X), Upper South Cove, Lunenburg Bay.](image-url)
Table 1
Sampling trips to Upper South Cove in 1990; four replicate mussels were collected for each set of respiration measurements

<table>
<thead>
<tr>
<th>Season</th>
<th>Dates</th>
<th>Days of particle-starvation after which respiration was measured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>Jan. 25-26</td>
<td>3, 4, 6, 10, 11</td>
</tr>
<tr>
<td></td>
<td>Feb. 8-9</td>
<td>3, 4, 6, 7, 10, 11</td>
</tr>
<tr>
<td></td>
<td>Feb. 22-23</td>
<td>3, 4, 7, 10</td>
</tr>
<tr>
<td>Spring</td>
<td>April 19-20</td>
<td>5, 7, 8, 11</td>
</tr>
<tr>
<td></td>
<td>May 3-4</td>
<td>3, 4</td>
</tr>
<tr>
<td>Summer</td>
<td>June 28-29</td>
<td>11, 15</td>
</tr>
<tr>
<td></td>
<td>Aug. 9-10</td>
<td>1, 7</td>
</tr>
<tr>
<td>Autumn</td>
<td>Nov. 1-2</td>
<td>3 (2 sets)</td>
</tr>
<tr>
<td></td>
<td>Nov. 15-16</td>
<td>3 (2 sets)</td>
</tr>
</tbody>
</table>

mussel-lines, by divers using SCUBA. Access holes were cut through the ice with a chain saw during the winter period (Dec. to March). Four mussels were used for metabolism measurements at an on-site field station (Fig. 1). Individuals were placed in respiration chambers 6–24 h after collection and incubated at the in situ temperature. The remaining mussels (approx. 30) were returned to the Aquatron laboratory at Dalhousie University and placed in a flow-through filtered seawater system at temperatures close to those at the site of collection (within 2°C). At varying periods after collection (from 3 to 15 days) metabolic rates were measured using the same incubation system that was used in the field. All experimental animals were open, with siphons extended during incubations. At the end of the incubation, mussels were blotted dry, weighed and the tissue separated from the shell. The tissues were divided into mantle and remainder, then dried separately. A mantle index is calculated as the mantle dry weight divided by the dry weight of the remainder of the soft tissues. The percent water is calculated as the total dry weight (tissue) divided by the animal fresh weight (blotted).

Because the water temperature at the collection site was often < 0°C in the winter, the incubation chambers were cooled in a circulating bath filled with non-toxic plumbing antifreeze. Each respiration chamber (12 cm I.D., 1 l volume) was fitted with a pre-calibrated Orion oxygen electrode which downloaded data to a computer via an Orion pH meter (model SA720). Filtered water (< 2 µm) in the chamber was slowly circulated from above with a magnetically-driven impeller at a speed of approximately 80 rpm. Incubations were terminated when the oxygen consumption rate was steady and linear (usually 3–4 h), and the oxygen concentration was approximately 80% of the initial values (which were all close to saturation). Ammonium excretion rates were calculated as the difference in ammonium concentration in subsamples of the stirred chamber water before and after respiration measurement, analysed using the techniques of Parsons et al. (1984). A chamber containing only water was used to correct for respiration and ammonium fluxes in contained water as well as consumption by the oxygen electrode. Oxygen consumption due to the probe and the overlying water never exceeded 10% of the mussel respiration, and ammonium changes in the water-only
chamber were insignificant compared to the chambers containing the experimental mussels.

2.3. Water column characteristics

A moored instrument array placed 3.5 m above the sediment surface at the reference site provided hourly estimates of temperature, concentrations of suspended particulate matter (seston) and chlorophyll $a$. These data have been published elsewhere (Grant et al., 1993; Emerson et al., 1994; Hatcher et al., 1994). The seasonal daily temperature means are given in Table 2. Daily means of chlorophyll $a$, calculated from continuously-recorded fluorescence measurements, as described in Hatcher et al. (1994), are presented in Fig. 2. Highest mean daily temperatures occurred in summer, and low winter temperatures extended well into the spring. The spring phytoplankton bloom, with chlorophyll $a$ concentrations up to $6 \mu g \cdot l^{-1}$ occurred in March, when the cove was still ice-covered, due to advection from open bay waters. Chlorophyll $a$ values were low in late spring and early summer ($2-4 \mu g \cdot l^{-1}$), high and variable in late summer and early autumn ($3-8 \mu g \cdot l^{-1}$) and they dropped rapidly to $2 \mu g \cdot l^{-1}$ in late autumn (Hatcher et al., 1994).

![Fig. 2. Chlorophyll $a$ concentration (daily means) at reference site in Upper South Cove. This figure was originally published in Hatcher et al. (1994), and is reproduced here with the permission of the publishers, Inter-Research.](image-url)
3. Results

3.1. Size relationships

The range in mean shell length of experimental mussels between seasons was small, from 53 to 56 mm (Fig. 3A). Despite the small range in shell length the range in tissue dry weights was 22% of the mean, from 0.99 to 1.31 g. (Fig. 3B). The lowest water content was in the spring, corresponding to the highest mantle index (0.59) (Fig. 3C, D).

![Graphs showing seasonal characteristics of Mytilus edulis](image-url)
Mussel metabolism experiments: analysis of covariance and a posteriori comparison of adjusted means using a Tukey test on seasonal differences in log-transformed metabolic rates

### Table 3

<table>
<thead>
<tr>
<th>Metabolic rate</th>
<th>Season MS</th>
<th>F</th>
<th>P</th>
<th>Dry weight MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Analysis of covariance</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oxygen consumption (log (x))</td>
<td>2.89</td>
<td>7.40</td>
<td>0.00</td>
<td>4.14</td>
<td>10.63</td>
<td>0.00</td>
</tr>
<tr>
<td>Ammonium excretion (log (x + 1))</td>
<td>4.55</td>
<td>11.66</td>
<td>0.00</td>
<td>8.25</td>
<td>21.14</td>
<td>0.00</td>
</tr>
</tbody>
</table>

(b) Tukey test (P ≤ 0.05) on adjusted means (based on average tissue dry weight of 1.2 ± 0.1 (SE) g) using MSE from models above; means presented are untransformed values

<table>
<thead>
<tr>
<th>Oxygen consumption</th>
<th>Winter</th>
<th>Autumn</th>
<th>Summer</th>
<th>Spring</th>
<th></th>
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</thead>
<tbody>
<tr>
<td>Winter</td>
<td>3.77</td>
<td>&lt;</td>
<td>8.12</td>
<td>=</td>
<td>11.42</td>
</tr>
<tr>
<td>Autumn</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.98</td>
</tr>
<tr>
<td>Spring</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Ammonium excretion</th>
<th>Winter</th>
<th>Autumn</th>
<th>Summer</th>
<th>Spring</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>0.59</td>
<td>=</td>
<td>0.94</td>
<td>&lt;</td>
<td>1.98</td>
</tr>
<tr>
<td>Autumn</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td></td>
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<tr>
<td>Spring</td>
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Log-transformed tissue dry weight was used as a co-variate for mussels collected from the field before the measurements of rates; preliminary models indicated that slopes between the two variates were homogeneous among seasons; to homogenize variances for ammonium excretion, the $x + 1$ transform was used. There were three degrees of freedom for season, one for the covariate and 37 for the error term in both analyses.
Due to the large ranges, the seasonal differences in mean tissue dry weights were not significant (Table 3B: one-way ANOVA, \( P > 0.05 \)). Metabolic rates were analysed using analysis of covariance with tissue dry weight as the covariate.

### 3.2. Seasonal changes in metabolism

For the among-season comparison, the metabolic rates of mussels collected from the field less than four days previously were used. Analysis of covariance (ANCOVA) indicated that there was a significant effect of the factor Season and the covariate Size (dry tissue weight) on both oxygen consumption and ammonium excretion rates of these recently-collected mussels (Table 3). The winter adjusted mean oxygen consumption rate was less than in the other three seasons, which did not differ significantly from each other (Tukey test, \( P < 0.05 \); Table 3b). There was a factor of \(-3\) difference between the lowest adjusted mean oxygen consumption rate in winter and the highest in spring. In the spring, there was a significant correlation between the mantle index and the adjusted mean respiration rates (Pearson \( r = 0.60, P < 0.01, n = 45 \)), but not in the other seasons.

The winter and autumn adjusted mean ammonium excretion rates were not statistically different, but were significantly less than the summer and spring rates (Table 3b). There was a factor of \(-5\) difference between the lowest adjusted mean ammonium excretion rate in winter and the highest in spring. As was the case with the oxygen consumption rates, there was a significant correlation between the mantle index and adjusted mean ammonium excretion rates in spring mussels (Pearson \( r = 0.66, P < 0.01, n = 45 \)), but not in other seasons. Atomic O:N ratios were calculated from the adjusted mean oxygen consumption and ammonium excretion rates. These O:N ratios in freshly collected mussels ranged from 9.3 in the spring to 17.4 in the autumn.

Using the average temperature differences between seasons, and the adjusted mean rates presented in Table 3, it is possible to calculate average \( Q_{10} \) values for metabolic rate measurements. The difference in the daily mean temperatures between spring and winter was \( 5^\circ C \), between summer and winter \( 15^\circ C \) and between autumn and winter \( 10^\circ C \) (Table 2). The \( Q_{10} \) for oxygen consumption and ammonium excretion in summer and autumn, based on the temperature increase from winter values is approximately 2. However, the calculated \( Q_{10} \) for oxygen consumption rate is 7 and for ammonium excretion 10 from winter to spring. These very high values calculated for the \( Q_{10} \) are probably due to reproductive activity, as discussed below.

### 3.3. Seasonal changes in metabolic rate with progressive particle-starvation

The oxygen consumption rates of winter mussels were low three days after collection, and did not change significantly over the next eight days without food (One-way ANCOVA, \( F_t = 0.213, \ P = 0.955 \), Fig. 4). In contrast, the higher oxygen consumption rates of newly-collected spring mussels decreased significantly over the eight day period without added food (One-way ANCOVA, \( F_t = 23.122, \ P = 0.000 \)) (Fig. 4). The oxygen consumption rate decreased with particle deprivation during the summer, but the decrease was not significant (One-way ANCOVA, \( F_t = 2.522, \ P = 0.065 \)) (Fig. 4). As an overall comparison, after 11 days of particle
deprivation in the laboratory, mean oxygen consumption rates did not differ significantly among the three seasons, despite temperature differences (One-way ANCOVA, $F_s$ (season) = 0.303, $P = 0.744$). The time course of metabolic rate change was not examined in autumn mussels.

The adjusted mean ammonium excretion rates showed similar patterns to those of oxygen consumption, i.e., significantly decreasing rates during eleven days without added food in spring mussels (One-way ANCOVA, $F_t$ (time since capture) = 5.275, $P = 0.005$) but not summer (One-way ANCOVA, $F_t = 2.594, P = 0.061$) nor winter (One-way ANCOVA, $F_t = 1.403, P = 0.245$) (Fig. 5). Similarly, after 11 days without added food, there was no significant difference among adjusted mean ammonium excretion rates in the three seasons (One-way ANCOVA, $F_s$ (season) = 0.441, $P = 0.653$) despite seasonal temperature differences.

Because the O:N ratio is a composite variable, made up from two measured variables with independent variances, regression analysis using adjusted means instead of ANCOVA is used to examine the changes over time. The O:N ratio (Fig. 6) did not show a significant increase or decrease as a result of lab retention in winter mussels (Type I Regression, $P = 0.731$). In spring and summer mussels, maximum O:N ratios were evident after five days of particle deprivation. An increase in O:N with time was
noted in spring mussels (Type I Regression; $P = 0.215$) but not in winter or summer. Although none of these trends were statistically significant, the regression between adjusted mean O:N and time since capture explained some of the variance in O:N in spring mussels and none in other seasons (adjusted $r^2 = 0.000$ in winter and summer, 0.215 in spring).

4. Discussion

4.1. Types of metabolism

Metabolic rates in bivalve molluscs have been classified by Bayne (1973), based on earlier work with fish (Fry, 1947). Various categories of metabolism have been described ranging from active metabolism, when the animal is actively feeding to maintenance metabolism, which is adequate to maintain life but not to support feeding, digestion and growth (Bayne et al., 1989). Standard metabolism is indicated by negligible feeding activity, and is considered to be a resting state. The use of standard metabolic rate measurements eliminates variance due to short-term changes in quality and quantity of
Fig. 6. Three-dimensional plot of atomic O:N ratios ($Y$) based on adjusted means presented in Figs. 3 and 4 as a function of time since collection from the field ($X$) and season ($Z$); no time course measurements were made during the Autumn season.

food in the gut, and provides a picture of metabolic function based on the integrated response of the animal to seasonally-changing conditions (Hatcher, 1991). In the present study, during the course of lab retention, the standard rates of metabolism approached maintenance rates.

The comparison of metabolic rates with the data of other studies is complicated by the tight relationship between food supply and metabolism and the lack of a standard approach. The standard metabolic rate can be only 50% of the routine rate, and an even smaller percentage of the active rate (Bayne et al., 1989). Therefore, comparisons must be made with groups of animals which are exhibiting the same category of metabolism. The category of metabolism measured in many studies is often not easy to assess because of a lack of information on the feeding status of experimental animals. The approach used in this study, an assessment of the rate of decline in metabolism with food deprivation, is superior to the standard approach of taking only one set of metabolism measurements. The use of standard metabolic rates eliminates variance due to short-term changes in quality and quantity of food, and the rate of decline to maintenance metabolism provides a picture of metabolic function based on the integrated response of the animal to its food supply.
4.2. Nutritional stress under the ice

Low respiration of winter mussels was probably caused by inadequate food rather than the low temperatures, as detailed below. Winter respiration was much lower than rates measured by Loo (1992) (approximately $5.4 - 7.1 \mu$mol·ind$^{-1}$·h$^{-1}$ for 40 mm long mussels) at similar temperatures ($-1.0\pm1.5 ^\circ C$) in Sweden. Significantly, mussels from under the ice in Upper South Cove respired at a rate which was well below the rate considered to represent maintenance metabolism for this species (approx. $5.26 \mu$moles·ind$^{-1}$·h$^{-1}$ for an individual of 1 g dry weight; Bayne et al., 1989). These low rates persisted after 11 days of particle deprivation.

In contrast to low respiration, the ammonium excretion rates of winter mussels were relatively high. Bayne and Scullard (1977) found seasonally varying rates for U.K. Mytilus edulis ranging from about 0.64 in January to 2.42 $\mu$mol·h$^{-1}$ in July for well-fed individuals of $\sim 1$ g dry weight. This compares with adjusted mean rates of 0.59 for mussels collected in winter and 2.80 in summer from Upper South Cove. Rates of ammonium excretion were much higher in mussels from Upper South Cove than in mussels from Trinity Bay, Newfoundland. Thompson (1984a) measured rates of approximately 0.18 $\mu$mol·h$^{-1}$ in December to 0.68 in September in Trinity Bay mussels of about 1 g dry weight.

The lack of change in metabolism of mussels with particle-starvation and the low O:N ratios resulting from low winter respiration and high ammonium excretion indicate starvation. Starvation is also indicated by the low chlorophyll concentration at the site during winter (Hatcher et al, 1994), weight losses measured on mussels from this site by Mallet and Carver (1993) and a carrying capacity model of Upper South Cove by Grant et al. (1993). Further support for the dominant effect of low food availability rather than low temperatures in causing low winter respiration comes from the study of Loo (1992), who has shown that M. edulis at low temperatures ($-1.0 ^\circ C$) can respire at high rates if they have adequate food.

4.3. Respiration

In contrast to the winter period, the significant decreases in respiration with particle-starvation in the spring are probably a result of depletion of short-term stored reserves (Diehl et al., 1986). There was a distinct spring bloom in Upper South Cove which began before the ice broke up (Hatcher et al., 1994) and could have provided the energy through short-term storage for increased metabolic demands in the spring. These increased metabolic demands and higher respiration rates were probably due to the increased energy requirements of gametogenesis, reflected in rapid tissue weight gains between early March and early April in 1990 in Upper South Cove mussels (Mallet and Carver, 1993). DeVooy (1976) found that gametogenesis in mussels caused high respiration rates, irrespective of water temperature. In mussels, gametogenesis occurs in the mantle tissue (Bayne and Thompson, 1970), which may explain the positive relationship between the mantle index and respiration which was observed in spring but not in other seasons.

The relative importance of temperature on seasonally-varying respiration rates can be assessed by a preliminary calculation of average $Q_{10}$ values. The increase in respiration
rates from winter to spring was much higher than would be expected by the slight increase in average water temperature. For such a difference to be related to water temperature alone, an unrealistic $Q_{10}$ of ~10 would have to be invoked. It is clear that the metabolic demands of reproductive tissue account for this spring increase in respiration. In contrast, the increase in metabolic rates of newly-collected mussels from winter to summer and autumn are within the range expected because of the increased water temperature and a $Q_{10}$ of 1.5–2.0. This is a reasonable value for $Q_{10}$ in *Mytilus edulis*, as documented by Bayne et al. (1973); DeVooy (1976). Bayne et al. (1973) identified a $Q_{10}$ of 1.58 for acute response of standard metabolic rate and 2.7 for the routine rate over the temperature range of 10–20°C. DeVooy found a $Q_{10}$ of 2.36 in mussels from the Dutch Wadden Sea. The mussels in Upper South Cove undergo gametogenesis in the autumn as well as in the spring (Mallet and Carver, 1993), but the rates of oxygen consumption and ammonium excretion are not as high in autumn mussels. The reasons for the difference between the spring and autumn rates may be related to the fact that the spawning peak is much smaller in the autumn (Mallet and Carver, 1993).

The relationship between respiration and water temperature was observed only in animals from the field. After 11 days of particle-starvation in the laboratory, respiration rates did not differ among the three seasons, despite seasonally-changing temperatures. A similar independence of routine oxygen consumption rate and temperature was noted for *Mytilus edulis* by Bayne et al. (1973). The independence of routine oxygen consumption and temperature and the strong influence of gametogenesis on metabolism of spring mussels lead to the conclusion that seasonal differences in food availability interacting with reproductive state of mussels are a stronger control on respiration than water temperature.

### 4.4. Ammonium excretion

The ammonium excretion of spring mussels follows the usual pattern for mussels (Bayne, 1976) which is a measurable decrease in ammonium excretion with particle-starvation, sometimes stabilising after an initial short increase. As was discussed with respect to respiration, the high ammonium excretion rates of spring mussels are probably fuelled by the catabolism of short-term reserves to support the demands of reproduction (Kreeger, 1993). Bayne and Widdows (1978) found that ammonium excretion rates of mussels collected from the Lynher River were significantly correlated with the gametogenic index. A significant positive correlation between the mantle index and ammonium excretion rates was found in Upper South Cove mussels in spring, but not in the other three seasons. Because gametogenesis occurs in the mantle tissues, this relationship indicates the close coupling between the two functions, supporting the earlier observations of Kreeger (1993); Bayne and Widdows (1978).

### 4.5. O:N ratio

Variations in the O:N ratio are an integrated result of variations in the rates of oxygen consumption and ammonium excretion. Although Kreeger (1993) calculated O:N ratios for *Mytilus trossulus* comparable to those in the present study, the majority of O:N ratios
of mussels are above 100, substantially higher than the maximum of 30 in Upper South Cove mussels. Low O:N ratios in mussels have been considered to be characteristic of low food availability by some authors (Kreeger, 1993). The respiration rate is diet-dependent, and drops dramatically after the food is removed, when the gut is clear (Bayne et al., 1989). In contrast, the ammonium excretion rate may increase immediately after food is removed as a consequence of increased catabolism of protein (Gabbott and Bayne, 1973; Bayne and Scullard, 1977). Thus, the O:N ratio is expected to drop dramatically after the animal stops feeding. According to some authors, the O:N ratio can be a useful indicator of the balance between protein, lipid and carbohydrate catabolism (Bayne, 1976) or the nutritional state of the animal (Grant and Thorpe, 1991). However, because of the dynamic interaction between the food supply and the O:N ratio, comparisons should be made with caution, as pointed out previously in relation to other benthic invertebrates (Hatcher, 1991).

Spring mussels exhibited high rates of respiration and ammonium excretion which declined with particle-starvation. These results suggest that metabolism of spring mussels was fuelled by short-term reserves which declined during the period of lab retention. The increase in O:N of spring mussels with particle-starvation was probably due to increased catabolism of glycogen, a short-term reserve, perhaps as a result of re-absorption of reproductive tissue (Bayne et al., 1982). The O:N ratios of summer mussels exhibited significant variability over the fifteen day period of particle-starvation, and no increasing or decreasing trend was obvious. As catabolism proceeds, fuelled by short-term reserves, the O:N ratio is a reflection of the composition of the mussels' food source over the longer term, as pointed out by Hatcher (1991); Ikeda (1977); Gaudy and Boucher (1983). Upper South Cove mussels are cultured in the euphotic zone of the water column, unlike their intertidal counterparts most often studied. Perhaps an increased N turnover with respect to C (i.e., a low O:N ratio) is a result of a catabolism acclimated to a rich phytoplanktonic food source, with a lower C:N ratio than the range of seston that is available to intertidal populations. Rodhouse et al. (1984) identified phytoplankton as the main food of mussels in suspended culture in contrast to the large range of seston that is utilised by intertidal populations. As pointed out by Rodhouse et al. (1984), the production of mussels in suspended culture can be three times that of intertidal mussels. Thus, the low overall O:N ratios of Upper South Cove mussels may be indicative of a high quality food source, rather than starvation. The range of the O:N ratio under nutritionally-controlled conditions is more informative than its absolute value, as has been pointed out previously (Hatcher, 1991).

Acknowledgments

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