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Research article

Ecological interactions between the vase tunicate (*Ciona intestinalis*) and the farmed blue mussel (*Mytilus edulis*) in Nova Scotia, Canada

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Abstract

This study was undertaken to quantify the ecological interactions between blue mussels (*Mytilus edulis* Linnaeus 1758) and vase tunicates (*Ciona intestinalis* Linnaeus 1767) in the context of mussel farming. To quantify the extent of competition for food resources at varying temperatures, clearance rates for both species were calculated using *Tetraselmis striata* (Butcher 1959). Between 4-13°C, mussel clearance rates were at least three times higher than those of tunicates. At 16°C and 19°C, the mussel clearance rates fell to the same level as the tunicates. Clearance rates were also examined using different sized algal species, and a substantial overlap in mussel and tunicate particle size utilization was observed. To determine the effects of tunicate density on mussel productivity, size and condition indices were measured in the field under varying tunicate density. Mussel size and condition decreased with increasing tunicate densities. In addition, up to 50% mussel mortality was observed under heavy tunicate fouling (~2 $kg \bullet m^{-1}$). Mussels and tunicates have the potential for substantial food resource competition, and tunicates were found to have a negative effect on mussel productivity. Heavy tunicate fouling was associated with higher mussel mortality, lower overall size and condition. The cost effectiveness of removing the vase tunicate from mussel lines is also discussed.

Key words: aquaculture, aquatic invasive species, biofouling, *Ciona intestinalis*, impact, meat yield, *Mytilus edulis*

Introduction

Many sessile marine communities are increasingly dominated by non-native ascidians, and species such as the vase tunicate (*Ciona intestinalis* Linnaeus 1767) have been shown to decrease species richness (Blum et al. 2007). Vase tunicates have been recorded in most major harbors and ports around the world (McDonald 2004 and references therein) and in Canada, the first documented case of biofouling by the vase tunicate was reported in 1997 on a mussel farm in Lunenburg, Nova Scotia (Cayer et al. 1999). It has since spread to many locations and is particularly troublesome for long line mussel farms (Howes et al. 2007). The aquaculture industry produced 2,300 tonnes of mussels (*Mytilus edulis* Linnaeus 1758) in Nova Scotia in 2005, for a value of $3.06 million (Statistics Canada 2005). In addition to presenting serious operational challenges for mussel farmers due to the added stress placed on culture equipment, biofouling by the vase tunicate has been anecdotally linked to decreased mussel productivity because of depressed growth, although results have varied (Leblanc et al. 2003). Potential causes of lower growth rates include obstruction of water flow (Uribe and Etchepare 2002), competition for food at a local scale (Lesser et al. 1992) and through a reduction in the standing crop of phytoplankton at the bay scale (Petersen and Riisgard 1992). This has led to investigations into tunicate growth, reproduction and settlement patterns, as well as mitigation strategies to reduce the impact of tunicate fouling (Carver et al. 2003; Howes 2005; Howes et al. 2007). The New Zealand Mussel Industry Council has developed a Tunicate Treatment Technology that seems to be effective at treating the mussel lines, and this technology has been successfully applied in local Nova Scotia conditions (Mallet and Carver

2006). In order to determine the cost effectiveness of this potential mitigation strategy, it is important to quantify the impacts that tunicates have on the mussels and what factors mediate these impacts.

Mussels and tunicates are both suspension feeders and a first set of experiments were designed to quantify the degree to which mussels and tunicates might compete for food. A first laboratory experiment in the food competition series examined the effect of temperature on the clearance rates of *C. intestinalis* and *M. edulis*. Decreasing temperature affects clearance rate either through a general reduction in metabolic rates (Hawkins and Bayne 1992) or by increasing the viscosity of the water (Joergensen et al. 1990). It was thought that differences in the clearance rate at different temperatures would not only show the degree to which the two species compete for food at various water temperatures, but would also provide some insight into how well these two species are adapted to the cold waters of Nova Scotia. A second laboratory experiment compared the feeding rates of *C. intestinalis* and *M. edulis* when fed different species of algae of different sizes in an attempt to determine the extent of food resource competition.

To complement these laboratory experiments on clearance rates, field experiments were set up to evaluate the impact of tunicate density on mussel growth and mussel quality. Hawkins and Bayne (1992) have suggested that mussels can consume and metabolize up to seven times the energy required to maintain basic functions and most of this extra energy is directed towards shell and tissue growth. Concordantly, food supply is likely the most important factor that determines growth rate in mussels (Seed and Suchanek 1992). It is probable that tunicates and mussels compete for food at a local micro-circulatory scale (Lesser et al. 1992), and since tunicates can almost completely cover mussels, the amount of food that reaches the mussels could be severely reduced. Inhibition can also be a problem for mussels that have been completely or partially smothered by tunicates, as the large amount of biofouling can increase the flow resistance of the inhalant or exhalant currents (Uribe and Etchepare 2002). Increasing resistance or merging inhalant and exhalant currents is of particular importance because the mussel creates a pressure differential to pump the water (Joergensen et al. 1988). Therefore, it may be argued that as tunicate density increases, we should expect a concurrent decrease in size and condition of mussels. Food resource competition at the whole bay scale is also possible; benthic populations of tunicates (167 individuals m^{-2}) were theoretically shown to be able to filter the entire volume of the cove they inhabited once per day (Petersen and Riisgard 1992). However, the difficulties associated with testing at the scale of an entire bay precluded any observation of this magnitude in this study.

Methods

Food resource competition

Both mussel and tunicate specimens were collected in November 2005 at Indian Point Marine Farms, Nova Scotia (NS) and stored in a flow through tank at the Bedford Institute of Oceanography (BIO) in Dartmouth, NS with unfiltered seawater from the Bedford Basin. The feeding trials were performed sequentially at 4, 7, 10, 13, 16 and 19°C on randomly selected animals from that source. All experimental animals were held in a single tank and experiments were conducted as the temperature was slowly increased. Heating was achieved through use of an immersion heater. The rate of temperature increase was no faster than 1°C every 48h and animals were given at least 48 h to acclimate to the desired temperature before any trials were performed. Since incoming water in November was cold (4°C) and phytoplankton poor, animals were given a mix of cultured algae twice daily to assure they were adequately fed. It is assumed that animals were of similar physiological condition throughout this experiment. The algae were cultured as described in Neima (1997).

For each temperature, 12 1.1 L feeding chambers (5 with tunicates, 4 with mussels and 3 controls) were used to measure clearance rates. Control chambers consisted of feeding chambers with no animals to account for the natural settling rate of the phytoplankton. Mussel sizes ranged from 15-25g and tunicates ranged from 12-20g in whole wet weight. Animals were placed on small-perforated platforms above a stir-bar, which assured homogeneity of the particle concentration. Acclimated mussels and tunicates were placed individually in feeding chambers filled with UV-sterilized seawater filtered to 1 µm. Animals were left to recover from handling stress for an hour before feeding trials commenced. An initial concentration of 20,000 cells/ml of *Tetraselmis* sp. was

administered after the recovery period. The concentration of the culture was determined with the use of a Coulter Counter Multisizer™ II with a 100 µm aperture tube, in a design similar to Montagnes et al. (1994).

A total of six 20 ml samples were drawn from each chamber at 15-min intervals for trials at 4-10°C and 10-min intervals for trials at 13-19°C as the animals consumed the algal particles faster at warmer temperatures. Clearance rates were calculated over entire period but using only cell concentrations above 2,000 cells•ml^{-1}, as concentrations below this number were considered depleted (Petersen and Riisgard 1992) and hence unreliable. Clearance rates were calculated using the formula from Coughlan (1969) and standardized by dividing by the wet weight of the individuals. This particular method was chosen for its simplicity and transferability across species. Cranford (2001) and Riisgard (2001) can be consulted for useful reviews on pros and cons of this and other methods for measuring clearance rates. Data were analyzed with the following general linear model: $m_{ijk} = Sp_i + t_j + Sp_i\ X\ t_j + \varepsilon_{ijk}$ where Sp = fixed effect of animal species (2 levels, mussel or tunicate), t = fixed effect of temperature (6 levels) and m = clearance rate. Normality was verified by visual inspection of the normal probability plot of the residuals. All statistical analyses in this manuscript were done using Minitab 14 (Minitab Inc., Austin, TX).

At a constant temperature of 19°C, mussels and tunicates were fed the diatom *Chaetoceros muelleri* (Lemmerman 1898) and the flagellates *Tetraselmis striata* (Butcher 1959), Tahitian *Isochrysis* sp, and a locally-isolated strain of *Prymnesium* sp. (Gouda et al. 2006). Algal concentrations and clearance rates were obtained as previously described above. Data were analyzed with the following general linear model: $m_{ijk}=Sp_i+Al_j+ Sp_i\ X\ Al_j + \varepsilon_{ijk}$ where Al = fixed effect of algal species (4 levels) and the other variables are defined above. Normality was verified by visual inspection of the normal probability plot of the residuals.

Effects of tunicate fouling density on mussel survival and growth

A New Zealand style (or continuous) mussel line was loaded with mussel seed and deployed at Indian Point Marine Farms, Nova Scotia in 2005. This site was chosen because it had been previously identified as having high tunicate fouling compared to other sites in NS (Clancey and MacLachlan 2004). Weekly recruitment in excess of 120 tunicates per Petri dish (or 1.5 tunicates cm^{-2} week^{-1}) had been recorded at this site (Howes et al. 2007). Divers collected mussel and tunicate samples by stripping 10 cm segments of mussel line and placing samples in collection bags. These samples were randomly obtained from one long-line in one lease between depths of 3-8 m and were taken from both high (~100% coverage) and low (~0-10% coverage) tunicate fouling areas, based on on-site visual assessment of the fouling intensity. In October 2006, a total of 5 high and 5 low tunicate fouling mussel line samples were taken. The collection was repeated in December 2006, and 4 samples obtained at each fouling density.

Tunicates were counted and weighed immediately and mussels were kept in flow-through tanks with unfiltered ambient 4°C seawater until processed. Mussels were processed in a random order within a period of 1 week. Length, width and height of each mussel shell were measured with digital calipers accurate to 0.01 mm. Mussels were dissected and blotted with paper towel to reduce the excess water. Shells and tissue weights were measured separately in pre-weighed aluminum dishes, and dry tissue weights were obtained following a 48 h desiccation period at 80°C. All mussels were processed with the exception of those smaller than 1 cm in length.

Length, width and height of the mussel shell, as well as shell wet weight, tissue wet and dry weights were used as indicators of final size. The mussels deployed along the experimental sock were initially haphazardly drawn from a pool of small mussel seed (~1 cm), and the mean mussel size along the sock was assumed to be initially homogenous. Observed differences in final size among the segments of various fouling levels are assumed to reflect differences in growth rate or size specific mortality rather than small, random differences in initial size. Two condition indices were also computed. Meat yield (M_y) was calculated by taking the ratio of wet tissue weight (T_w) to wet tissue weight plus wet shell weight (S_w): $M_y = T_w / (T_w + S_w)$. The water content ratio (W_R) was calculated by taking the ratio of dry tissue weight (T_d) to wet tissue weight: $W_R = T_d / T_w$.

The effects of tunicate fouling intensity on mussel mortality and on abundance of market-size mussels were tested with likelihood ratio test and t test respectively. Size and condition

indices, as well as estimated total weight of all market-size products per m were related to tunicate density by linear regression. Throughout this study, mussels are considered to be of market size when ≥45 mm in length. The estimated total weight of market-size products per m is the sum of shell and wet tissue weight of all market-sized mussel in a 10cm segment, multiplied by 10. Condition indices were measured for a wide range of mussel sizes and reproductive stages, and were found to vary with size. To correct for potential size bias, condition indices were first regressed against shell length and the residuals were stored. The residuals were then averaged per segment and used in a linear regression against ln(segment tunicate density), to display the relationship between condition indices and tunicate density with size bias removed.

Results

Food resource competition

Tunicate clearance rates increased with temperature throughout the experimental range. Interestingly, the mussel clearance rates reached a peak around 10°C to 13°C and showed decreased performance above 13°C (Figure 1). At all experimental temperatures between 4°C and 13°C mussels exhibited substantially higher (up to 8 times higher) clearance rates than tunicates (Figure 1). Conversely, at higher experimental temperatures (16°C and 19°C) tunicate and mussel clearance rates were very similar. Not surprisingly, results from a general linear model analysis showed that there was a significant effect of species ($F = 129.73$, $df = 1$, $P = 0.000$), and temperature ($F = 9.90$, $df = 5$, $P = 0.000$) on clearance rate. The interaction term was also found to be significant ($F = 12.26$, $df = 5$, $P = 0.000$). This model fits the data very well ($R^2 = 0.85$).

Mussels and tunicates were found to feed on all algal species employed in these feeding trials. The mussels cleared the mid-sized phytoplankton species, *Isochrysis* sp. and *C. muelleri,* two times faster than the tunicates (Figure 2); however, similar clearance rates for both species were observed when the largest, *Prymnesium* sp., and smallest, *T. striata*, algal strains were used. Results from a general linear model showed that there was no significant effect of algal species on the clearance rate of the animals ($F = 0.80$, $df = 3$, $P = 0.510$), but that the tunicates and mussels did differ significantly in clearance rates ($F = 13.91$, $df = 1$, $P = 0.001$). The interaction term was not significant ($F = 2.37$, $df = 3$, $P = 0.103$). The model fit was lower than in the previous analysis but still fairly high ($R^2 = 0.53$).

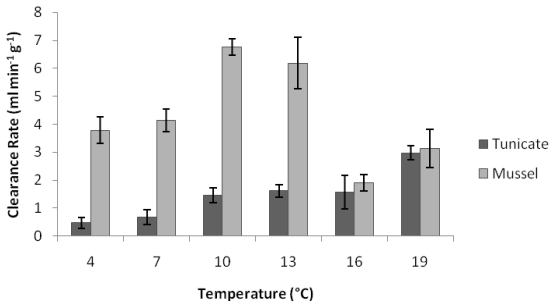

Figure 1. Mean wet weight-specific clearance rates of mussels (*M. edulis*) and tunicates (*C. intestinalis*) at different temperatures. Individual clearance rates were calculated for cell concentrations between 20,000 and 2,000 cells ml^{-1} of *T. striata*. Error bars indicate the standard error between replicates. At each temperature, 5 tunicates and 4 mussels were used to calculate means.

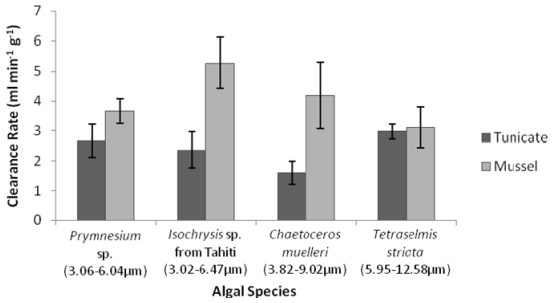

Figure 2. Mean wet weight-specific clearance rates of mussels (*M. edulis*) and tunicates (*C. intestinalis*) feeding on various algal strains at 19°C. Individual clearance rates were calculated for cell concentrations between 20,000 and 2,000 cell ml^{-1}. Error bars indicate the standard error between replicates. For each algal strain, 5 tunicates and 4 mussels were used to calculate means.

Effects of tunicate fouling density on mussel survival and growth

In October 2006, the occurrence of substantial recent mussel mortality was recorded, as empty shells were found still attached to the mussel line. Severe mortality was observed in the high tunicate fouling group; almost half of the mussel shells were empty while only 1 in 26 was found dead in the low tunicate density group (Figure 3a). Such an association between tunicate

density and mussel mortality was highly significant (χ^2 = 75.618, P-value < 0.0001). There were proportionally much fewer live mussels in the high tunicate density group. When dead mussels were included in the totals, there were still more mussels overall on the low tunicate density segments but the apparent difference in mussel abundance between groups was lessened. There was also a significant difference in numbers of large market size mussels in the high and low tunicate density sections (t = 3.49, df = 4, P-value = 0.025). The large market-size mussels were about three times more abundant in the low tunicate density sections of the mussel line than in the high tunicate density sections (Figure 3b).

The same overall trends could be seen in December 2006. There was a significantly higher mortality in high tunicate density section (χ^2 = 24.259, P-value = 0.000) and overall higher number of live mussels or total mussels in low tunicate density segments. However, the observed rate of recent mortality was not as high as in October 2006. There was again a significantly higher number of large market-size mussels in the low tunicate section density than in the high tunicate density sections (t = 3.16, df = 5, P-value = 0.025).

In October 2006, all the size indices of the sampled mussels followed the same decreasing trend with increasing tunicate density (Figures 4a to f). However, only the regression of mussel tissue dry weight with tunicate density was found to be significant (R^2 = 0.52, P = 0.019, Figure 4f). A significant negative linear regression of mussel meat yield with tunicate density and a significant positive linear regression of mussel water content with tunicate density were also observed (Figures 5a and b). Mussel condition indices (meat yield and water content) were also significantly correlated with mussel length, with smaller mussels displaying lower meat yield and higher water content (Figures 6a and b). The mean residuals from the regressions on mussel size were then plotted against ln(segment tunicate density) (Figures 6c and d). Meat yield residuals decreased rapidly for the first 500 g•m^{-1} of tunicates and water content increased sharply in the same range. Increases in tunicate density in excess of 500 g•m^{-1} only resulted in a slight additional decrease in meat yield residuals and a similar slight additional increase in the water content residuals (Figures 6c and d).

Not surprisingly, there was a strong and significant negative relationship in October 2006 between the amount of marketable mussel product and tunicate density (Figure 7). This model accounts for approximately half of the variability observed in the data (R^2=0.47, P = 0.028) and predicts a decrease in the amount of mussel product by almost 1.4 kg•m^{-1} for an increase of 1 kg•m^{-1} of tunicate density.

In December 2006, the same trends of decreasing size indices of the sampled mussels with increased tunicate density could be seen as in October 2006, but none of the regressions with size were significant (data not shown). The

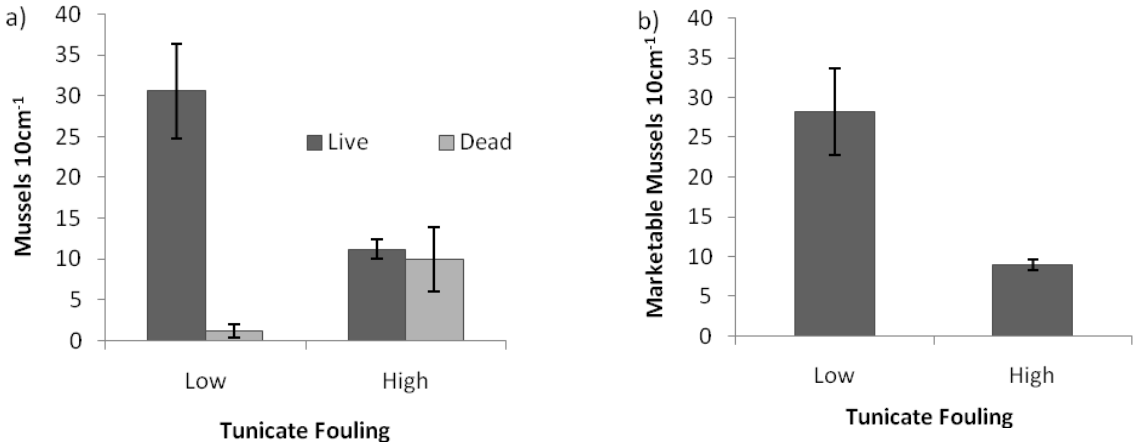

Figure 3. Mean number of mussels (*M. edulis*) collected per 10 cm segment (a) alive or dead and (b) of market size (>45mm) at high and low tunicate (*C. intestinalis*) densities (n = 5 at each density); data from October 2006. Tunicate densities are as defined by initial sampling scheme (low = 0-10% coverage, high = 100% coverage).

significant negative relationship between mussel meat yield and mussel length, and positive relationship between mussel water content and mussel length were still seen but were weaker than in October (R^2 = 0.177, P= 0.000 and R^2 = 0.253, P= 0.000 respectively). As in October 2006, there was a negative relationship between meat yield and tunicate density and a positive relationship between water content and tunicate density, but these were no longer significant. Finally, the negative relationship between the amount of marketable product and tunicate density was still present and was nearly significant (R^2 = 0.46, P= 0.063).

Discussion

Food resource competition

As expected, low clearance rates were observed in both *M. edulis* and *C. intestinalis* at 4°C and 7°C. These low temperatures correspond with lower mussel growth rates and metabolic activity (Almada-Villela 1982; in Hawkins and Bayne 1992), and high water viscosity (Joergensen et al. 1990). The tunicate clearance rates increased in an approximately linear relationship with increasing temperature. This is consistent with the trend seen in *C. intestinalis* from a natural population in Denmark (Petersen and Riisgard 1992). The Danish population clearance rate ranged from 4.6 $ml \bullet min^{-1} \bullet ind^{-1}$ at 4°C to 29 $ml \bullet min^{-1} \bullet ind^{-1}$ at 19°C, whereas the Nova Scotia population showed values of 6-10 $ml \bullet min^{-1} \bullet ind^{-1}$ at 4°C to 19.2-32 $ml \bullet min^{-1} \bullet ind^{-1}$ at 19°C (0.5 to 1.6 $ml \bullet min^{-1} \bullet g^{-1}$, standardized to individual tunicate weight of 12-20g). The clearance rates at 19°C were comparable between the two tunicate populations but at 4°C, the clearance rates for the Nova Scotia population were slightly higher. Also, the apparent proportional increase observed at 10°C was not detected in the Danish tunicate population. This discrepancy between populations could be linked with pre-spawn conditioning since the Nova Scotian tunicates have been found to start spawning between 8 and 11°C (Carver et al. 2003, Howes 2005).

It is clear that mussels are more efficient filter feeders than tunicates at low temperatures, but this advantage tends to disappear at higher temperature. To decrease competition, it may thus prove advantageous to select mussel leases that are subject to colder temperatures year round. The large decrease in mussel clearance rate observed at 16°C (Figure 1) may have been linked to spawning events. Bayne and Widdows (1978) also observed a pre-spawn increase in clearance rate followed by a post-spawn decrease, but did not provide possible explanation for the decrease. Indeed, one mussel actually spawned during a feeding trial at 13°C (which was then terminated) and other mussels may have spawned in the holding tank undetected. Mussels in Nova Scotia usually start spawning in late May-early June when the water temperature reaches 12°C (Seed and Suchanek 1992). It is thus possible that the lower clearance rates at the higher temperatures in the present study reflected such post-spawning decrease, since optimal feeding rates in sexually immature mussels have been shown to occur between 10-25°C and 10-20°C in mussels taken from the Mediterranean and Baltic Sea, respectively (Schulte 1975).

Overall, the data presented here suggest that there is an overlapping range of particle size preference suggesting that mussels and tunicates compete to some extent for the same food resource. It is difficult to draw definite conclusions about the particle size preferences of mussels and tunicates but it is clear that they are able to feed on the same particle sizes. The tunicates exhibited higher clearance rates when fed the smallest and largest algal strains and lower clearance rates with the mid-size strains, which was an unusual particle size preference distribution. However, it may be of importance to note that *Prymnesium* sp. was a local isolate while others are non-local species issued from laboratory cultures. Chemical cues can act to mediate the clearance rate of tunicates (Petersen and Riisgard 1992) or mussels (Ward and Targett 1989) and either species might have recognized that *Prymnesium* sp. is a local isolate and regulate clearance rate accordingly. When omitting the results from *Prymnesium* sp., mussels seemed to prefer smaller particles, while tunicates preferred the larger algal strain, *T. striata*. Dissolved organic matter was not considered here but should be considered in future studies, as it may account for 34-40% of the mussels' energy needs (Hawkins and Bayne 1992). Also, *C. intestinalis* and *M. edulis* have been shown to have very similar amino acid (glycine) uptake abilities (Stephens and Schinske 1961); however, to the best of our knowledge, no data is available on the possible importance of dissolved organic matter for *C. intestinalis*.

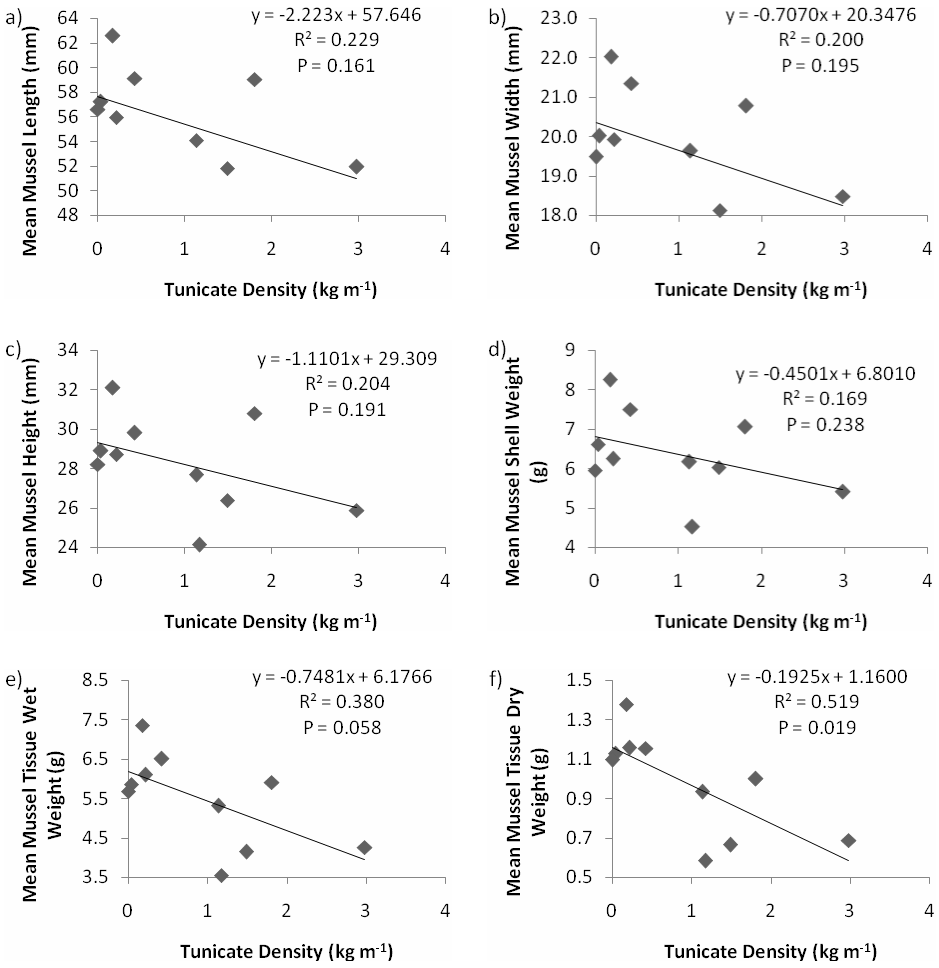

Figure 4. Various indices of mean mussel (*M. edulis*) size plotted against tunicate (*C. intestinalis*) density for each 10cm segment of mussel line; data from October 2006, n=10.

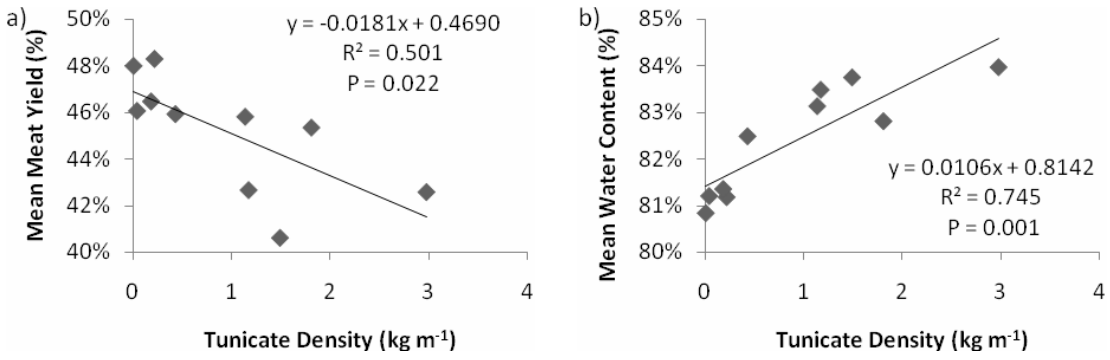

Figure 5. Various indices of mean mussel (*M. edulis*) condition plotted against tunicate (*C. intestinalis*) density of each 10cm segment of mussel line; data from October 2006, n=10.

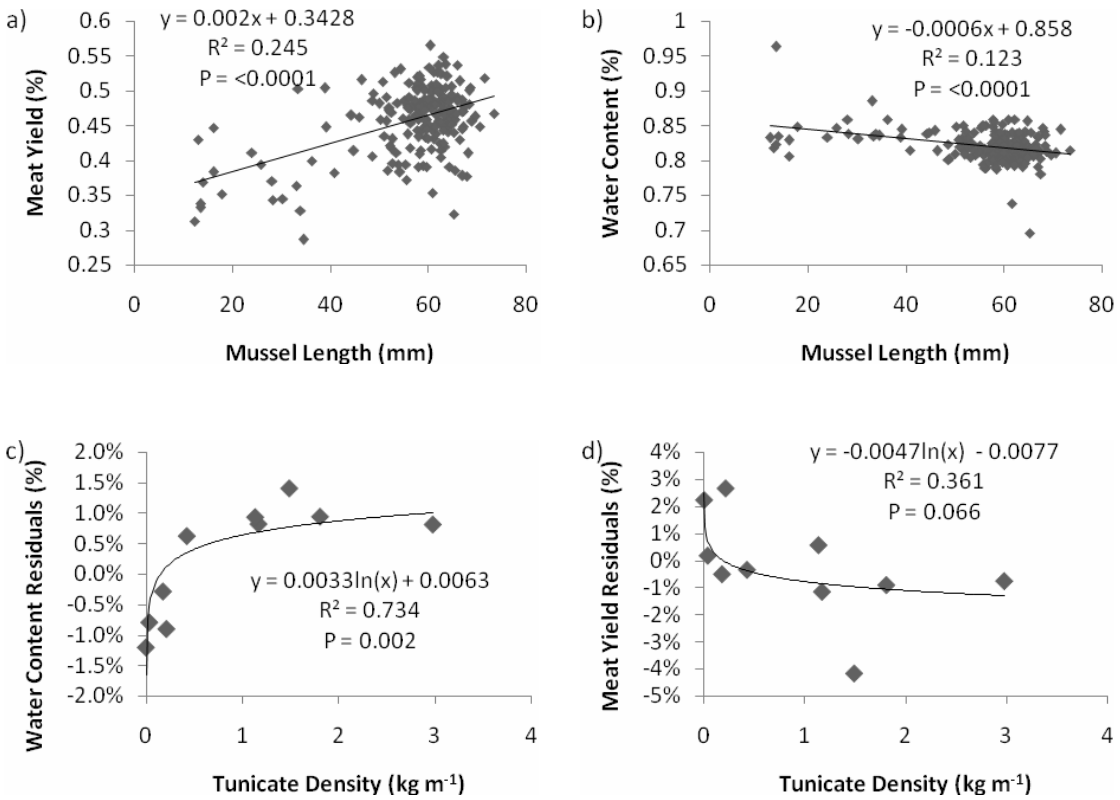

Figure 6. Linear regression of a) meat yield and b) water content as a function of mussel (*M. edulis*) shell length. The mean residuals from a) and b) above were calculated for each 10 cm segment and were plotted against the natural log of tunicate (*C. intestinalis*) density (kg•m^{-1}). This is shown in c) water content residuals and d) meat yield residuals respectively. Data is from October 2006, n= 209 for a) and b) and n=10 for c) and d). Results from a regression (regression equation, R^2 and p-value) are shown on each plot.

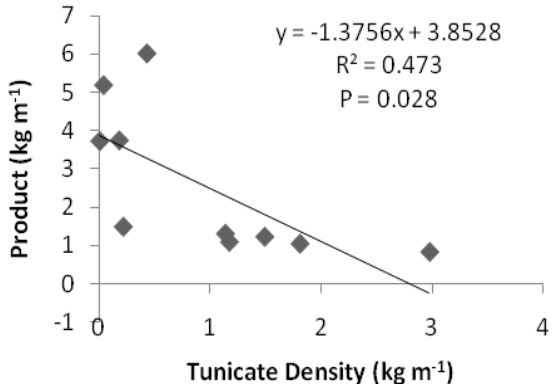

Figure 7. Estimated total weight (kg•m^{-1}) of marketable (≥ 45 mm) mussels (*M. edulis*) plotted against tunicate (*C. intestinalis*) density (kg•m^{-1}); data from October 2006, n=10. Results from a linear regression (regression equation, R^2 and p-value) are shown on the plot.

Effects of tunicate fouling density on mussel survival and growth

Significantly higher recent mortality (detected by the presence of empty shells) was observed in the high tunicate density sections both in October and December 2006. Since dead mussels rapidly fall off the mussel line (P. Darnell, Indian Point Marine Farms, pers. comm.), the fact that so many dead mussels were found still attached to the line indicated that these mortalities were fairly recent. Although it cannot be ruled out that dead shells were simply better retained in heavily fouled sections of the mussel lines, it is more likely that this reflects a direct relationship between high tunicate density and higher mussel mortality. Indeed, in both October and December 2006, there were considerably more mussels overall (live plus dead shells) in the low tunicate fouling sections than in the corresponding high tunicate fouling sections, indicating that many dead mussels had already fallen off the heavily fouled sections of mussel lines and were not detected. Hence actual mortality rate over the growing season was greater than the recent mortality rate inferred from the presence of dead shells. One possible mechanism leading to the observed mussel mortality could be that the dense aggregation of tunicates reduced food accessibility to the point where the mussels could no longer meet their basic metabolic needs. In natural habitats, mortality has been linked to periods of metabolic stress, such as during spawning (Worrall and Widdows 1984). This suggests that tunicate induced mortality was more severe in the larger-sized mussels who expend high amounts of energy through reproductive effort.

When mussel size was examined, the various size indices consistently decreased with increasing tunicate density in both October and December; although this was only significant for dry weight in October. This is not surprising since the other size indices are related to shell size (shell length, shell width, shell height and shell weight). Because of the cumulative nature of shell growth, these indices are not very sensitive to the recently prevailing growing conditions compared to dry weight. Food competition and flow inhibition were likely the principal factors in decreasing mussel tissue weight. Decreases in shell length were likely due to a combination of (a) reduced growth and (b) disproportionally higher large mussel mortality from increased reproductive effort. The data collected in this study did not quantify the magnitude of (a) and (b), but rather their combined effect.

There were, as expected, a decrease of mussel meat yield and an increase in water content with increasing tunicate density, although this was only significant in October 2006. This indicates that higher tunicate density likely negatively affected mussel quality, in addition to inducing higher mortality and/or fall-off. The strong relationship between the condition indices and tunicate density observed in October suggested that food was a limiting factor for mussel growth. Smaller meat yields (R^2 = 49.3%, P = 0.023) and higher water content (R^2 = 74.5%, P = 0.001) observed in the high tunicate density socks implied that these mussels had little surplus energy to invest in somatic growth and reproduction. Poor condition is also often associated with high mortality in wild populations (Worrall and Widdows 1984).

In December, the trends that were seen in October (both for size and condition indices) were weaker. This could be due to several reasons. Firstly, as was demonstrated in this study, the tunicates have lower clearance rates than mussels in cold water, thus reducing the competition for food. Secondly, a fall bloom of phytoplankton could have allowed the mussels to recover by December from any impacts that were still evident in October. Lastly, there was a dramatic rise in the biomass of the tunicates between the sampling dates (up to an order of magnitude) and this might have decoupled the apparent high tunicate fouling areas in December from the areas that had been previously affected by high tunicate fouling. As a result, the recent increase in tunicate biomass might not have had time to have an impact on the mussels sampled in December.

Interestingly, the condition indices were found to vary with length. Correcting for the size-specific condition relationships (Seed and Suchanek 1992), it was possible to visualize how the condition indices varied with tunicate density without having size-induced bias. Meat yield decreased and water content increased drastically for the first 500 $g \bullet m^{-1}$ of tunicates and above this level of density there was very little change in condition. This suggests that below the critical level of tunicate density (500 $g \bullet m^{-1}$) the mussels reacted to tunicate fouling by allocating energy away from processes that improve condition,

such as somatic growth or gonad storage but the effect on size (or length) would be minimal. Any increase beyond the critical level would essentially decrease mean size through a decrease in growth rate or increased mortality of large individuals.

This study indicates that tunicate fouling on mussel lines affected both the amount of product directly and its quality. Either way, this will translate into a loss in revenue for the mussel growers. Although in North America, condition indices such as meat yield or water content do not directly influence the price per kg, it does affect how much meat the customer buys per dollar and thus it could affect the customer's ultimate perception of the product quality. In contrast, meat yield directly influences price per kg in Europe; an increase of approximately 7% in terms of meat yield leads to a doubling in price per kg (van Stralen and Dijkema 1994).

With a mussel value of $\$1.33 \bullet kg^{-1}$ (Statistics Canada 2005) and tunicate density estimated at 1.44 $kg \bullet m^{-1}$ (based on tunicate counts and mean wet weights in October 2006, Mallet and Carver, unpublished data), the loss of product of 1.4 $kg \bullet m^{-1}$ associated with an increase of 1 $kg \bullet m^{-1}$ in tunicate density would translate into a loss of $\$2.68 \bullet m^{-1}$of mussel line. Considering the minimal cost of using the Tunicate Treatment Technology ($0.04 to $\$0.11 \bullet kg^{1}$ of mussel) estimated by Mallet and Carver (2006), this mitigation strategy would be cost effective. A reduction in tunicate biomass would also make the harvesting/processing much easier for the growers thereby further increasing cost effectiveness. Finally, removing the tunicates could also reduce the potential demand on the food resources at an ecosystem level as suggested in Petersen and Riisgard (1992).

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