Efficacy of high-pressure seawater spray against colonial tunicate fouling in mussel aquaculture: inter-annual variation

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Abstract

Invasive species such as ascidians have negative effects on aquaculture operations worldwide. Prince Edward Island, Canada, in particular has seen high fouling levels of non-native tunicates including the colonials Botryllus schlosseri and Botrylloides violaceus. Previous research indicated that high-pressure seawater spraying of mussel socks fouled with colonials is an effective mitigation strategy. Those results, however, were based on a year (2009) with unseasonably low water temperatures at the beginning of the colonial tunicate growing season in June and July; therefore, we repeated part of that study in the following year (2010) to determine whether typical (warm) early season water temperature affected tunicate fouling levels and how both treatment efficacy and fouling effect on mussel productivity differed between the two years. In 2010, Botryllus schlosseri fouling (in terms of biomass) was four-fold higher than in the colder year (2009), reaching an average biomass of 600-800 g per full-length mussel sock (up to 2.4 m long), but it still did not affect mussel productivity. B. violaceus was also present on mussel socks, but only in very low amounts (<50 g per mussel sock), so that results for this species were inconclusive. High-pressure water spraying was at least as effective in 2010 as in 2009 at removing B. schlosseri tunicate fouling from mussel socks, though in 2010, treatment also negatively affected mussel productivity by reducing mussel biomass by 30% in the frequently (5×) treated group. Considering these results along with the potential risk of increased tunicate spread (through fragmentation) and the cost of treatment, frequent application of high-pressure water spray is unnecessary.

Key words: tunicates; invasive species; aquaculture; Botryllus schlosseri; Mytilus edulis; mitigation

Introduction

Worldwide, marine invasions are on the rise (Ruiz et al. 1997; Cohen and Carlton 1998), including those that negatively affect aquaculture production (e.g. Lee and Gordon 2006; Ramsay et al. 2008; Carman et al. 2010). The Prince Edward Island (PEI) blue mussel (Mytilus edulis Linnaeus, 1758) aquaculture industry has faced multiple challenges in recent years due to the introduction and proliferation of several non-native tunicate species (Carver et al. 2003; Locke et al. 2007; Locke et al. 2009). These highly invasive tunicate species rapidly colonize the artificial substrates created by the suspension of mussel long lines within the water column (Lambert and Lambert 2003; Forrest et al. 2007; Tyrrell and Byers 2007). This rapid and heavy fouling of mussel socks has become a major problem for producers in PEI, leading to increased production and processing costs, and limiting the profitability of the industry (Locke et al. 2009). Of the four tunicate species present, the two colonial species (Botryllus schlosseri (Pallas, 1766) and Botrylloides violaceus Oka, 1927) have been the most prolific in their spread and colonization of new bays and estuaries within PEI waters. This can be attributed to the ability of these species to rapidly reproduce both sexually (free swimming larvae) and asexually (budding or fragmentation) (Bullard et al. 2007; Carver et al. 2006). The tunicates’ high reproductive capacity combined with other modes of dispersal such as rafting on dislodged seaweeds and attachment to boat and barge hulls (Lambert
and Lambert 2003; MacNair et al. 2006) has resulted in these species spreading to most of the major aquaculture-containing bays and estuaries on PEI.

Scientists and mussel growers have evaluated and field-tested many mitigation strategies in attempts to reduce the levels at which these organisms foul mussel socks and to minimize the regional spread of invasive species, however few studies have focused on the impacts of these species and subsequent mitigation techniques employed to control them on mussel productivity (e.g., LeBlanc et al. 2007; Locke et al. 2009; Arens et al. 2011). Of the methods tried by growers - freshwater, brine, lime, acetic acid immersion and high pressure water (Carver et al. 2003; MacNair et al. 2006; Forrest et al. 2007) - high pressure water has become the most commonly used treatment against solitary and colonial tunicates on PEI (authors’ pers. obs.). Previous work by our research group (Arens et al. 2011) showed that the use of high pressure water is effective at decreasing the biomass of both B. schlosseri and B. violaceus on mussel socks. However the reductions observed were only short-term, as both species quickly recolonized the socks. This recolonization may be attributed in part to the large amount of newly available (i.e., cleaned) substrate, and the settlement and growth of small fragments formed during the removal of the original colonies from the mussel socks, which drift in the water column, possibly settling on adjacent mussel socks (Edlund and Koehl 1998; Paetzold and Davidson 2010). Anecdotal evidence from mussel growers indicates a perceived decrease in mussel productivity as a result of heavy fouling by B. schlosseri and B. violaceus on mussel socks. No such decrease was observed in Arens et al.’s (2011) study, though tunicate fouling levels were not particularly high in the study year (see Discussion), which may have been a result of unusually cool water temperatures at the beginning of the tunicate growing season (June and July 2009; see Figure 2).

With the hypothesis that colonial fouling levels would be higher in a year with typical (warmer than 2009) water temperatures early in the growing season, we repeated part of the work from 2009 (Arens et al. 2011) to determine (1) whether increased colonial tunicate fouling affected mussel productivity and (2) whether efficacy of high-pressure ambient seawater spraying would be consistent in different years (repeatability).

Methods

Treatment application and sample collection

A trial using above-water, high-pressure seawater spray as a tunicate mitigation treatment was conducted on mussel socks in St. Peters Bay, on the north shore of PEI, Canada (Figure 1) at the same site that was used in 2009 by Arens et al. (2011). The colonial tunicate species B. schlosseri and B. violaceus are established at this site, while the solitary species C. intestinalis and S. clava, which could have affected treatment efficacy, were never detected.

In general, we followed methods as described in Arens et al. (2011), but rather than repeating their extensive study, we only used one of their 17 treatments, namely the most frequent treatment consisting of a total of five high-pressure water applications at three-week intervals between 19 July and 14 October 2010 (Treatment Group 5 in Arens et al. (2011), hereafter identified as the 5×-treated group). Out of 48 randomly chosen, uniform mussel socks on a mussel long-line which had been seeded in May 2010 (see Table 1 for sock characteristics), 15 socks were assigned to the 5×-treated group and 33 to the control (socks lifted from the water but not sprayed) group. The socks were divided into three blocks, each containing five treatment socks and 11 control socks to control for variability along the length of the mussel line. On 19 July, 11 August, 31 August, 24 September and 14 October 2010, treatment socks were sprayed for approx. 10 s with high-pressure (~700 psi) ambient seawater (~28 psu, 6.3-23.4°C), using a single rotary nozzle, gas-powered, hand-held pressure washer. On each of the five treatment dates, nine untreated sock sections (45 cm long) were collected (three per block) to evaluate seasonal changes in tunicate biomass and mussel productivity throughout the trial period. No sock was sampled more than twice to avoid sampling from different sections of the mussel sock, and socks at either end of each group (i.e. the 1st and 11th sock for controls, and the 1st and 5th sock of 5×-treated socks) were excluded to avoid possible edge effects (i.e. socks being affected by adjacent, differently treated socks). Upon completion of the trial on 16 November 2010, nine sock sections each were collected from the 5×-treated group and the control group (all 45 cm long, three per block for both treatment and control socks). Towards the end of the trial, we noted
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**Figure 1.** Prince Edward Island (PEI), Canada, with an inset showing the study site, St. Peters Bay, and a star indicating the study lease. Shaded regions within each bay indicate areas occupied by mussel leases.

**Figure 2.** (A) Average daily water temperatures in St. Peters Bay for the years 2000-2008 (grey lines), Arens et al.’s (2011) study year (2009) and the year of the present study (2010). Weekly data for 2000-2008 taken from Mussel Monitoring Reports (available from the PEI Department of Fisheries, Aquaculture and Rural Development (Charlottetown, PEI, Canada) and at [http://www.gov.pe.ca/fard/index.php?number=1038181&lang=E](http://www.gov.pe.ca/fard/index.php?number=1038181&lang=E)). (B) Temperature difference between Arens et al.’s study year and the rest of the decade calculated as $T_{2009} - \text{average}(T_{2000-2008}, 2010)$. 
that our control socks appeared to have less colonial tunicate fouling than an adjacent line that had been treated only once, on 17 August 2010. To meet one of our objectives (i.e. evaluate the effect of colonial tunicate fouling on mussel productivity), sampling a relatively heavily fouled line was necessary. Therefore, nine sock sections (all 45 cm long) were collected from this adjacent line (1×-treated) for comparison with our control and 5×-treated group. The 1×-treated socks were of the same seed source and had been deployed at the same time as the control and 5×-treated socks, but had not been sampled monthly over the summer. For comparison with these 1×-treated socks in 2010 we used data from Arens et al.’s (2011) Treatment Group 7 (treated on 6 August 2009).

In terms of environmental variables, only salinity (measured on every sampling date) and water temperature (continuously logged using a Vemco Minilog) were recorded. Since salinity was constant (27-28 psu) throughout the study, only temperature data are reported here.

Laboratory analysis
Sock sections were analyzed for mussel weight, abundance, length and condition index (CI), and weight of Botryllus schlosseri, Botrylloides violaceus and epifauna (non-ascidian epibionts including barnacles, algae and mussel spat) as described in Arens et al. (2011), with the exceptions that sections were trimmed to 30 cm instead of 15 cm and mussel spat was not recorded separately (due to very low amounts of spat being observed).

Data analysis
Weight and abundance data were standardized to a 15 cm length of sock to be comparable to results presented in Arens et al. (2011). Treatment effect was evaluated using data from all three treatment groups (control, 1×-treated, and 5×-treated) collected in November. Each of the parameters (mussel weight, abundance, length and CI, Botryllus schlosseri, Botrylloides violaceus weight and epifauna weight) was compared between control and 5×-treated socks using two-way ANOVAs with Treatment as fixed factor and Block as random factor. Assumptions for ANOVA were checked using z-scores for skew and kurtosis as well as normality plots (normality) and Levene’s test (homoscedasticity). Botryllus schlosseri and Botrylloides violaceus weight data were square root-transformed to normalize the data. Since no significant effect of Block or the Block*Treatment interaction term was found for any of the parameters, data from the three different blocks were pooled for control and 5×-treated socks for each parameter, and the three treatment groups (control, 1×- and 5×-treated) were compared by one-way ANOVA with Treatment as factor. However, since 1x-treated socks were collected from a different line (without corresponding blocks so that the location effect could not be tested statistically), Student’s t-test results are presented for the two block-design treatment groups (control and 5×-treated socks) in addition to ANOVA results.

Data from samples collected in November in the control, 1×- and 5×-treated groups was compared between 2009 and 2010 (both in terms of absolute values and treatment efficacy, i.e. percent difference relative to control) using Student’s t-tests. Significance level for all tests was $\alpha = 0.05$. All analyses were performed using SPSS 13.0.

Results
Water temperature
Water temperatures between June and November 2010 followed the patterns of 2000-2008, especially in the first two months (Figure 2). By contrast, during Arens et al.’s (2011) study (in 2009), water temperatures between late June and late July were on average (±SD) 4.0 ± 2.3°C colder than 2010 and 2000-2008 (Figure 2). In particular, there were three cold spells (5, 9 and 9 d long) during which water temperatures were on average 6.7, 4.6 and 6.2°C, respectively, colder than the rest of the decade, with a maximum 8.2°C difference on 26 July 2009 (Figure 2). During those same periods in 2010, temperatures differed from the 2000-2008 average by only -0.92, -0.34 and -0.35°C.

Seasonal changes of mussel and biofouling parameters
Mussel weight and length increased between mid-July and mid-November, while mussel abundance decreased slightly (~16% or about 11 mussels per 15 cm of sock) (Figure 3). Mussels grew between 1.7 and 4.7 mm in every three-week interval for a total growth of 14.6 mm between mid-July and mid-November, reaching an average (±SD) of 50.1 ± 1.1 mm in length. Mussel CI data were lost for July, late August
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Figure 3. Seasonal development of (A–D) mussel parameters and (E–G) biofouling weights on mussel socks. Epifauna includes mostly mussel spat, algae and barnacles. Sock sections (30 cm) were collected on 19 July, 11 August, 31 August, 24 September, 14 October and 16 November 2010. Data are mean ± SE. CI = condition index.
and September. CI increased between early August and mid-October, and remained unchanged by the last sampling in November (Figure 3).

_B. schlosseri_ and _B. violaceus_ were not found on mussel socks until early August and then only at very low levels (<3 g and <0.001 g, respectively; Figure 3). Biomass of both species increased by an order of magnitude by late August, but while _B. schlosseri_ increased overall by mid-November (almost doubling its fouling weight again), _B. violaceus_ biomass decreased to <1g. The maximum _B. schlosseri_ biomass per 15 cm on any sock section was 63 g (in November). In contrast, the level of _B. violaceus_ fouling stayed very low (on average <3 g) throughout the trial (Figure 3). Epifauna was the highest fouling category on all sampling dates, increasing steadily from 17.3 ± 4.7 g in July to 63.9 ± 26.2 g in November (Figure 3).

**Treatment effect**

When comparing the two blocked treatments (controls and 5×-treated socks), treatment had a significant effect on all variables (_t_-test: _p_ < 0.005 for all comparisons; Table 2) while location on the mussel line (i.e. block) did not (two-way ANOVA: _p_ > 0.2 for all analyses; data not shown). Spraying mussel socks with high-pressure seawater every three weeks on five dates decreased mussel biomass and abundance by 34% and 30%, respectively (Figure 4A,B). Mussels on 5×-treated socks were 4% shorter but had 11% higher CI than control mussels (Figure 4C,D).

Including mussels from 1×-treated socks in the comparison showed that spraying socks only once (in mid-August) had no effect on mussel biomass, abundance, or length compared to control mussels (Tukey’s test: _p_ > 0.7 for all comparisons; Figure 4A-D). However, mussel CI on 1×-treated socks was 6% lower than on controls (Tukey’s test: _p_ = 0.01) and 12% lower than on 5×-treated socks (Tukey’s test: _p_ < 0.0001).

Average weight of all three fouling categories was significantly lower on 5×-treated socks than on control socks (_t_-test: _p_ ≤ 0.001 for all comparisons; Table 2), with reductions of 98, 94 and 59% for _B. schlosseri_, _B. violaceus_ and other epifauna, respectively (Figure 4). Despite our estimates of less fouling on our control socks compared to 1×-treated socks on an adjacent line (the reason why these socks were included in the analysis), spraying mussel socks once with high-pressure water in mid-August significantly decreased the biomass of _B. schlosseri_ and epifauna (Tukey’s test: _p_ < 0.0001 for both), but not that of _B. violaceus_ (Tukey’s test: _p_ = 0.099), compared to control socks. Compared to 5×-treated socks, treating only once left significantly more _B. schlosseri_ and _B. violaceus_ biomass on the socks (Tukey’s test: _p_ < 0.0001 for both) but worked equally well against other epifauna (Tukey’s test: _p_ = 0.815) (Figure 4).

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**Table 1.** Stocking characteristics for mussel socks deployed in St. Peters Bay in May 2010. Data were obtained from 9 untreated mussel socks sampled on 19 July 2010. For mussel length, 20 randomly selected mussels from each sock were measured.

<table>
<thead>
<tr>
<th>Stocking characteristics</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean mussel density per 30 cm (SD)</td>
<td>143.1 (8.3)</td>
</tr>
<tr>
<td>Mean mussel length (SD)</td>
<td>35.5 mm (0.9)</td>
</tr>
<tr>
<td>Mean mussel weight per 30 cm (SD)</td>
<td>611.6 g (39.1)</td>
</tr>
<tr>
<td>Sock length</td>
<td>1.8 m</td>
</tr>
<tr>
<td>Socking material</td>
<td>Go Deep 6XL</td>
</tr>
</tbody>
</table>

**Table 2.** Student’s _t_-test results for comparisons of mussel and fouling parameters on untreated and 5×-treated (high-pressure seawater spray) mussel socks.

<table>
<thead>
<tr>
<th>Parameter</th>
<th><em>t</em></th>
<th><em>df</em></th>
<th><em>p</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mussel weight</td>
<td>5.744</td>
<td>16</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Mussel abundance</td>
<td>3.805</td>
<td>16</td>
<td>0.002</td>
</tr>
<tr>
<td>Mussel length</td>
<td>4.147</td>
<td>16</td>
<td>0.001</td>
</tr>
<tr>
<td>Mussel condition index</td>
<td>-3.402</td>
<td>16</td>
<td>0.004</td>
</tr>
<tr>
<td>Epifauna weight</td>
<td>4.180</td>
<td>16</td>
<td>0.001</td>
</tr>
<tr>
<td><em>Botryllus schlosseri</em> weight</td>
<td>19.065</td>
<td>16</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><em>Botryloides violaceus</em> weight</td>
<td>4.369</td>
<td>16</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
Figure 4. Effect of a single (1×) or frequent (5×, at three-week intervals) high-pressure seawater treatment on (A-D) mussel parameters and (E-G) biofouling weights on mussel socks compared to untreated (Con) socks. Sock sections were collected on 16 November 2010. Treatments occurred in mid-August (1×-treated) or on 19 July, 11 August, 31 August, 24 September, and 14 October (5×-treated). Epifauna includes mostly mussel spat, algae and barnacles. Data are mean + SE. CI = condition index. Lines above bars connect treatment groups without significant differences (Tukey’s post hoc test p ≥ 0.05). Note y-axes for (C) and (D) do not start at zero in order to provide more detail.
Comparison with 2009 data

Generally, control, 5×- and 1×-treated socks sampled in November differed significantly between 2009 and 2010, with mussel parameters such as weight, length and CI higher in the warmer year (2010) than in 2009, especially on control and on 1×-treated socks (Figure 5). Mussel length was the only parameter that was similar between the two years on control and 1×-treated socks, and mussels on 5×-treated socks were shorter in 2010 than in the colder year, 2009 (Figure 5B). Botryllus schlosseri mass differed significantly between the two years for all three treatment groups, with approximately three-fold higher mass on controls in 2010, half the mass on 1×-treated socks in 2010 compared to 2009, and one sixth the mass on 5×-treated socks in 2010 compared to 2009 (though in that group, <6g of Botryllus schlosseri were found on average on sock sections in both years). Mass of Botrylloides violaceus was negligible (<2.5 g on average) in all treatment groups in 2010, as it had been in 2009 (two-way ANOVA, p = 0.535; Figure 5F).

The effect of high-pressure water spray on mussel weight, count and length but not mussel CI differed significantly between 2009 and 2010 in the 5×-treated group (Figure 6A-D). In the 1×-treated group, only the change in mussel weight and CI differed between the two trial years. Treatment was significantly more effective against Botryllus schlosseri in 2010 than in 2009, whether applied once or five times (Figure 6E), while it was less effective against Botrylloides violaceus in the 1×-treated group, and comparable in the 5×-treated group (Figure 6F).

Discussion

As hypothesized, colonial tunicate biomass was lower in 2009 (when early growing season temperatures were below the decadal average) than in 2010 (Figures 2 and 5E). This difference in fouling was due only to *B. schlosseri*, which reached an average biomass of 50.1 g per 15 cm on control sections – over three-fold higher than the fouling level of <16 g per 15 cm observed at the same site in the previous year by Arens et al. (2011). *B. schlosseri* colonies tend to start growing and sexually reproducing above 10-15°C, whether in situ or in the laboratory (Sabbadin 1955; Brunetti 1974; Brunetti et al. 1980; Epelbaum et al. 2009). Thus the prolonged period of unusually cold (<15°C; compared to the rest of the decade, Figure 2) water temperatures in St. Peters Bay between late June and late July 2009 likely played a role in the low level of *B. schlosseri* fouling observed by Arens et al. (2011). In contrast, *B. violaceus* fouling was negligible in both study years, more likely due to its low level of invasion in St. Peters Bay than to differences in temperature; while *B. violaceus* has been established in St. Peters Bay since 2001 (MacNair 2005), it has not yet reached the fouling level of *B. schlosseri*.

Neither in 2009 nor 2010 did we observe the high levels of colonial tunicates (including finger-like, lobe-shaped colonies hanging off mussel socks; cf. Figure 5 in Brunetti 1974) reported by mussel growers in St. Peters Bay. A possible reason for this is that both Arens et al.’s (2011) and our study were conducted using spring-socked mussel socks from the same year (favoured for their uniformity and lack of all fouling), rather than mussel socks from the previous year, while mussel growers may have been referring to crop that had been in the water for a year or longer. However, during our field visits, we did not observe any lobe-like growths, even on older crops on nearby mussel lines (authors’ pers. obs.).

Alternatively, colonial tunicate fouling levels may have been perceived to be higher than they actually were. In the present study, qualitative observations in October 2010 suggested that mussel socks on an adjacent, 1×-treated mussel line were much more heavily fouled by colonial tunicates than those socks used in the original experimental design. When we quantified tunicate mass, however, *B. schlosseri* fouling was four-fold lower on these 1×-treated socks than on control socks. We can only speculate why the 1×-treated socks appeared more heavily fouled in the field. Possible reasons are mussel sock variability and tunicate growth patterns. For example, natural variability of mussel socks can be a limitation in studies dealing with this type of suspended mussel culture since mussels are a live substrate: tunicate settlement can often be patchy with heavily fouled sections in between nearly unfouled mussels (authors’ pers. obs.). Thus a sock with a prominent, heavily fouled line were much more heavily fouled by colonial tunicates than those socks used in the original experimental design. When we quantified tunicate mass, however, *B. schlosseri* fouling was four-fold lower on these 1×-treated socks than on control socks. We can only speculate why the 1×-treated socks appeared more heavily fouled in the field. Possible reasons are mussel sock variability and tunicate growth patterns. For example, natural variability of mussel socks can be a limitation in studies dealing with this type of suspended mussel culture since mussels are a live substrate: tunicate settlement can often be patchy with heavily fouled sections in between nearly unfouled mussels (authors’ pers. obs.). Thus a sock with a prominent, heavily fouled section can give the impression of overall heavier fouling levels. It is also possible that *B. schlosseri* may utilize available substrates differently when undisturbed for a long time, e.g., colonies might extend into less visible surfaces such as crevices between mussels and
thus be overlooked when fouling levels are gauged qualitatively. However, the control socks’ undisturbed period was only about three weeks longer than that of 1×-treated socks, and it seems unlikely that such a short period of time would make a four-fold difference in *B. schlosseri* biomass. Regardless of the reason, our results emphasize that qualitative evidence, whether from anecdotal reports or field observations, needs to be treated with caution and verified by quantitative methods.

As in 2009, we observed no effect of colonial tunicate fouling on mussel growth, length, abundance or CI: despite increasing colonial fouling, these mussel parameters steadily increased throughout the season, not showing any sudden slowing of the rate of increase (Figure 3). While some studies have speculated

Figure 5. Comparison of treatment groups in terms of (A-D) mussel and (E and F) colonial tunicate (*Botryllus schlosseri* and *Botrylloides violaceus*) parameters between 2009 (data from Collins et al. 2011) and 2010 (this study). Data are mean ± SE. CI = condition index. Groups connected by horizontal bars are not significantly different from each other (t-tests, p ≥ 0.05).
Figure 6. Comparison of the effect of treating mussel socks once (in early or mid August) or 5× (every three weeks between mid-July and mid-October) between 2009 (data from Collins et al. 2011) and 2010 (this study) on (A-D) mussel parameters and (E and F) colonial tunicate weight. Values are the % difference of the mean value for each parameter and treatment group relative to the control mean value. CI = condition index. Groups connected by horizontal bars are not significantly different from each other (t-tests, p ≥ 0.05).

about mussels and other bivalves being smothered by colonial tunicates (reviewed in Carver et al. 2006), we found no evidence for this phenomenon in the case of B. schlosseri in either 2009 (Arens et al. 2011) or 2010. Likewise, we did not observe mussel slippage (fall-off) that was reported by some mussel growers in colonial tunicate-infested bays. Mussel growers may have been referring to older socks (one or more years in the water), which may have had better established and higher tunicate fouling levels as well as higher mussel biomass with weaker byssal attachment and thus increased risk of mussel fall-off. However, we did not observe any such socks during our visits to the sampling site, and under regular
harvesting schedules, mussels would not remain in the water beyond two years (PEIDAFA 2003; Drapeau et al. 2006). In contrast to the 2009 results (Arens et al. 2011), the high-pressure water spraying negatively affected mussel productivity in 2010: mussel weight, count and length were significantly lower on 5×-treated socks than on controls (Figure 4A-C). The difference in weight was due to loss of mussels rather than reduced weight gain since mussel loss was noticed during each treatment (authors’ pers. obs.). The decreased length in the 5×-treated group could either be the result of loss of mainly large mussels during each treatment, leaving behind smaller mussels, or of slowed growth throughout the experimental period. Treated socks would have to be sampled throughout the experiment alongside the seasonal (untreated) samples to determine whether growth is affected by high-pressure water, or whether the treatment is simply selective with regard to the size of removed mussels. Mussel CI was significantly higher on 5×-treated socks, probably due to a combination of two factors: 5×-treated socks had significantly smaller mussels (which generally have a higher CI since their shells are thinner, thus affecting the meat:shell ratio of the CI), and the remaining mussels likely had less competition for available resources. However, this increase in the meat:shell ratio did not make up for the >30% loss in mussel weight from a commercial point of view. Losing one third of the crop is not economical, especially when not treating the mussel socks at all seems to have no negative effect on mussel growth within the first growing season. Our results also highlight the necessity of more than one study season when evaluating mitigation treatments. The causes of the mussel loss in just one of the two study years are unclear, but knowing that about 30% of mussels may be lost during high-pressure water spraying is important for growers deciding whether to apply a treatment or not.

While high-pressure spraying had no effect on mussel weight and length in 2009, values in the 5×-treated group still ended up at the same level for both years by November (Figure 5A). Without further study, it is impossible to conclude whether the colder early-summer temperatures in 2009 slowed mussel growth or if other factors played a role. Treatment is unlikely to play a role in the observed inter-annual differences since the same grower applied the treatments in both years.

Thus, while high-pressure water treatment was effective at reducing all fouling categories (colonial tunicates and other epifauna), with significant reductions of almost 100% of the colonial tunicate biomass and about 60% of other epifauna, it is inadvisable to treat mussel socks with little colonial tunicate fouling (i.e., <50 g per 15 cm, or approx. 600-800 g on a full length sock of 1.8-2.4 m); not only do the tunicates not affect mussel productivity, but mitigating such low fouling levels, especially using a frequent treatment regime, leads to high crop losses. The additional risk of increasing the spread of colonial tunicates through fragmentation during the spray application (Bullard et al. 2007; Paetzold and Davidson 2010; Arens et al. 2011) also supports minimizing the number of spray treatments applied to mussel socks. Lastly, the extensive treatment trial from 2009 showed that timing rather than frequency affected treatment efficacy the most, i.e. spraying socks shortly before harvesting provided the greatest commercial benefit in terms of tunicate fouling reduction (Figures 2 and 3 in Arens et al. 2011), which again suggests that fewer, well-timed treatment applications are preferable, both in saving effort and cost on the part of the grower and in preventing adverse effects on the mussel crop.

Conclusion

While tunicate fouling appears to be overall higher when water temperatures exceed 15°C early in the growing season (June, July), no negative effect on mussel productivity was apparent by the end of the same growing season (November). High-pressure seawater spray was effective at removing colonial tunicate fouling as well as other epifaunal organisms (mostly algae, barnacles and mussel spat) but negatively affected crop yields (30% reduction in mussel biomass on 5×-treated socks). Thus, pressure-washing mussel socks in colonial tunicate-infested bays is unnecessary unless colonial tunicates reach fouling levels that negatively affect mussel productivity or the crop needs to be cleaned of fouling prior to harvesting.

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