Population structure and grazing capacity of cultivated mussels in Prince Edward Island, Canada

L.A. Comeau, R. Filgueira, J.D.P. Davidson, A. Nadeau, T. Guyondet, R. Sonier, A. Ramsay, J. Davidson

Fisheries and Oceans Canada
Gulf Fisheries Centre
P.O. Box 5030
Moncton, New Brunswick
Canada, E1C 9B6

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Population structure and grazing capacity of cultivated mussels in Prince Edward Island, Canada

by

L.A. Comeau[1], R. Filgueira[2], J.D.P. Davidson[1], A. Nadeau[1], R. Sonier[1], T. Guyondet[1], A. Ramsay[3], J. Davidson[4]

[1] Fisheries and Oceans Canada, Gulf Fisheries Centre, P.O. Box 5030, Moncton, New Brunswick, E1C 9B6, Canada

[2] Dalhousie University, Marine Affairs Program, 1355 Oxford Street, PO Box 15000, Halifax, Nova Scotia, B3H 4R2, Canada

[3] Prince Edward Island Department of Agriculture and Fisheries, Aquaculture Division, 548 Main Street, Montague, Prince Edward Island, C0A 1R0, Canada

[4] Department of Health Management, Atlantic Veterinary College, University of Prince Edward Island, 550 University Avenue, Charlottetown, Prince Edward Island C1A 4P3, Canada

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ABSTRACT

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This report provides a comprehensive overview of cultivated mussel populations suspended from longlines in Prince Edward Island (PEI), Canada. From October 2015 to December 2016, leaseholders from six major mussel-producing embayments were interviewed on a monthly basis to capture information on the content of their leases. In addition, mussels were periodically sampled for laboratory measurements (shell length, tissue weight and condition index) and assessments of fouling invasive tunicates (*Styela clava*, *Ciona intestinalis*, *Botrylloides violaceus* and *Botryllus schlosseri*). Morphometric measurements were performed on 7229 mussels extracted from 114 collector ropes and 220 polyethylene socks. It was found that following their settlement, pediveliger larvae developed into commercial-size mussels (shell length 55 mm) over a period of approximately 25 months. Clearance rate (CR = volume of water cleared of suspended particles per unit time) was modelled as a function of mussel shell length and abundance on collector ropes and polyethylene socks. Model outcomes indicated that mussels attached to collector ropes had a collective potential of clearing particles twice as fast as those attached to polyethylene socks. Intensive competition for food particles at the collector rope scale may explain the outstanding quantity of seed falling off collectors. Specifically, the abundance of seed on collectors fell by 74.6% (~1.81% per day) as shell length increased from 1.2 mm to a socking size of 20.0 mm. At the lease scale, CR per unit lease area, termed CR_{Area} and scaled to $l\ h^{-1}$ leased m^{-2}, varied by a factor of nearly 40 over a production cycle. This variation was primarily driven by seasonal temperature acting on physiological rates. A low proportion (≤ 11.9%) of collector and sock samples contained invasive tunicates. This observation was consistent with the participant growers reporting intense mitigation (treatment) measures. It is anticipated that the information presented in this report will serve the parameterization of future carrying capacity models.

RÉSUMÉ

Comeau, L.A., Filgueira, R., Davidson, J., Nadeau, A., Sonier, R., Guyondet, T., Ramsay, A., and Davidson, J. (2017). Population structure and grazing capacity of cultivated mussels in Prince Edward Island, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 3228: viii + 23 p.

Ce rapport fournit un aperçu complet des populations de moules d'élevage sur filières à l'Île-du-Prince-Édouard (Î.-P.-É.), Canada. D'octobre 2015 à décembre 2016, six mytiliculteurs opérants dans des baies d'élevage intensif ont été interrogés mensuellement afin de répertorier le contenu de leurs baux. De plus, des moules furent périodiquement échantillonnées dans le cadre d'une évaluation en laboratoire (longueur de la coquille, poids du tissu et indice de condition) comprenant aussi le dénombrement des ascidies envahissantes (*Styela clava*, *Ciona intestinalis*, *Botrylloides violaceus* et *Botryllus schlosseri*). En somme des mesures morphométriques furent effectuées sur 7 229 moules extraites de 114 collecteurs de naissains et 220 boudins en polyéthylène. Les résultats suggèrent que les larves de moule en stade pédiveligère croissent pour atteindre la taille commerciale (longueur coquille 55 mm) sur une période d'environ 25 mois. Le taux de filtration (CR = volume d'eau dégagé de particules en suspension par unité de temps) a été modélisé en fonction de la longueur et l'abondance des moules présentes sur les collecteurs ainsi que les boudins. Selon les modèles, les naissains sur collecteurs auraient un potentiel de filtration deux fois supérieur à celui des moules sur boudins. Une compétition intense pour les particules alimentaires à l'échelle du collecteur pourrait expliquer la perte importante en naissains. Par exemple l'abondance des naissains sur les collecteurs a diminué de 74,6% (~ 1,81% par jour) lorsque la longueur de leur coquille est passée de 1,2 mm à une taille de boudinage de 20 mm. À l'échelle du bail le CR par unité de superficie concédée, appelé CR_{Area},fut présenté à l'échelle de l h^{-1} m^{-2} de bail. Ce dernier varia par un multiple d'environ 40 au cours d'un cycle de production. Cette variation s'explique principalement par la variation saisonnière de la température agissant sur les taux physiologiques des moules. Une faible proportion (≤ 11,9%) des échantillons de collecteur et de boudin présentait des ascidies envahissantes. Cette observation était cohérente avec les producteurs participants participant à l'étude, déclarant des mesures d'atténuation intenses (traitements). Il est attendu que les informations présentées dans ce rapport serviront à paramétrer les futurs modèles de capacité de charge.

INTRODUCTION

Blue mussel (*Mytilus edulis*) farming in PEI is carried out using a longline system of suspended polyethylene sleeves (Scarratt, 2000). Mussels are cultivated on the northern and the eastern sides of the island, where a total of 4351 ha of estuarine waters have been leased out to individuals and companies. Presently, there is a societal consensus that the PEI mussel industry is completing its developmental phase and entering into a management phase. This view is evidenced by a moratorium on the granting of new leases since 1999. The view is also supported by an increasing interest in Ecological Carrying Capacity (ECC), defined as the magnitude of aquaculture production that can be supported without leading to unacceptable changes in ecological process, species, populations, or communities in the environment (Byron and Costa-Pierce, 2013). Over the past decades the concept itself and its level of complexity have substantially evolved, prompting the creation of different ECC modelling approaches. Water-column ECC may be inferred from indicators such as the Dame index (Comeau, 2013; Comeau et al., 2015; Dame and Prins, 1998), box models (Filgueira and Grant, 2009; Grant et al., 2008) or spatially-explicit ecological models (Filgueira et al., 2014; Filgueira et al., 2015b). Moreover there is an emerging interest to quantify the influence of bivalve culture on the greater food web using Ecopath, Ecosim and related components (Byron et al., 2011; Kluger et al., 2016). These models, regardless of their complexity level, share one commonality: their predictions are heavily influenced by stock forcing variables, such as the abundance and size-frequency distribution of cultured bivalves within leases.

In this study, we conducted a comprehensive survey of cultured mussel stocks in PEI. The intent was to generate a quantitative overview of mussel lease utilization, especially in regards to seasonal trends in population structure, densities, and degree of fouling by invasive tunicates. Mussel size frequency distributions and allometries were of particular interest since these variables are required for computing rates of filtration and biodeposition at the lease scale. As a first step towards this goal, we focussed on calculating monthly estimates of filtration (clearance) rate per unit lease area, with the intent of determining if grazing pressure was constant throughout the production cycle. It is anticipated that the information presented in this paper will serve future carrying capacity models.

METHODS

Leaseholder interviews

In 2015, six mussel-producing bays (Figure 1), representing the major culture areas across PEI, were selected for study. Within each of these bays, an individual lease was selected for study. The main selection criterion was the willingness of the leaseholder to share private husbandry information, with the understanding that the data would not be divulged in a way that could be traced back to individual leaseholders. The PEI Aquaculture Alliance (PEIAA) was mandated to periodically interview each leaseholder over the October 2015—December 2016 period. On a monthly basis the PEIAA solicited the following information from each leaseholder participant: the number of socks with mussels that underwent larval development in the year 2013, 2014, or 2015; the number of socks that were treated for invasive tunicates (*Styela clava*, *Ciona intestinalis*, *Botrylloides violaceus* and *Botryllus schlosseri*) and the specific treatment that was applied (calcium hydroxide or high-pressure water).

Mussel samples

In addition to the interviews, study leases were visited on a monthly basis. They collected two mussel socks for each year-class present at the time of sampling. Growers use a standard 2 m sock across PEI. Due to sample processing constraints, only a 30 cm section from the bottom part of each sock was removed, transported to the laboratory, and frozen (-40ºC) for later analysis. Field observations suggested that the 30 cm samples were representative of the entire socks. Mussels were counted in each 30 cm sample and thereafter extrapolated to a standard 2 m sock, thus yielding a sock-level mussel density for each year-class ($Nm_{sock,YC}$). A subsample of 22 mussels was randomly removed for shell length and dry weight measurements. Dry tissue weight for each mussel was obtained by placing soft tissues into a drying oven at 60 °C for a minimum of 12 h. A condition index (CI) was calculated according to a formula provided in Davenport and Chen (1987):

$$CI = \frac{\text{Dry tissue weight}}{\text{Dry shell weight}} \times 100$$

The age of mussels was estimated based on year-class information provided by leaseholders. The estimate was refined using the following equation:

$$Age\ (months) = \frac{\text{ND}_{S-P}}{30}$$

where $ND_{S\text{-}P}$ is the number of days between the sample date and the pediveliger date. Pediveliger larvae are those competent to settle and metamorphose after reaching a size of approximately 250 µm (Bayne, 1964). Published estimates of pediveliger dates for PEI mussels vary from June 11 to June 27 (Filgueira et al., 2015a). Thus, we fixed the pediveliger date to June 18th for the purpose of estimating the age of mussels in our study.

Clearance rates

Clearance rate (CR) is defined as the volume of water cleared of suspended particles per unit time. In our study, CR was estimated at the collector rope and polyethylene sock scales. Specifically, CR per meter of collector rope and polyethylene socking material was calculated as:

$$CR_{Structure} = \frac{(0.005 \times MSL^{1.688}) \times Nm}{1000}$$

where $CR_{Structure}$ represents the volume of water (m^3) cleared of particles per meter of available structure (rope or sock) per hour, *MSL* represents the mean shell length of mussels measured on the structure, and *Nm* the mussel count per meter of structure. The coefficients (0.005 and 1.688) were obtained from a clearance rate allometric equation previously reported for PEI cultivated mussels (Comeau et al., 2015).

CR estimates were also computed at the lease scale. CR per unit lease area, termed CR_{Area} and scaled to l h^{-1} leased m^{-2}, was calculated as:

$$CR_{Area} = \sum_{YC=1}^{3} \left(Nm_{sock,YC} \times CR_{ind,YC} \times SD_{Lease,YC} \right)$$

where $Nm_{sock,YC}$ is the number of mussels per 2 m sock of a given year-class (YC), $CR_{ind,YC}$ (l h^{-1} ind^{-1}) represents CR for an average-size (shell length) mussel in that particular year-class sock, and $SD_{Lease,YC}$ is the reported number of socks of a given year-class per leased m^{-2}. $CR_{ind,YC}$ was computed using the allometric equation CR = 0.005 × Shell length$^{1.688}$ reported for cultivated mussels (Comeau et al., 2015). CR_{Area} accounted for all three mussel year-classes that may have been present in the lease. For each of the six surveyed leases, CR_{Area} was computed on a month-per-month basis in accordance with the frequency of grower interviews and the collection of sock samples.

Given the effect of temperature on the physiological response of organisms, $CR_{Structure}$ and CR_{Area} were corrected according to the extended Arrhenius law (Kooijman, 2010):

$$\dot{k}(T) = \dot{k}_1 \times \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right) \times s(T)/s(T_1)$$

$$s(T) = \left(1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)\right)^{-1}$$

where T is the absolute temperature (K), T_1 is the reference temperature (K), $\dot{k}(T)$ is the physiological rate at temperature T, $\dot{k}_1$ is the physiological rate at temperature T_1, T_A is the Arrhenius temperature, T_L and T_H the lower and upper tolerance range, respectively, and T_{AL} and T_{AH} the rate of physiological rate decrease at lower and upper boundary, respectively. T represents monthly mean water temperature, computed from loggers (YSI Incorporated, OH, USA) moored in 5 culture embayments in 2016-2017 (PEI Department of Agriculture and Fisheries). This particular series was selected because it represents the most comprehensive temperature dataset for PEI mussel culture sites. T_1 during CR measurements was acquired from Comeau et al. (2015). Remaining parameters (T_{AL}, T_L, T_{AH}, T_H, T_A) were derived from van der Veer et al. (2006).

Statistics

Linear regression analysis was used to explore relationships between dependent variables, such as shell length, and plausible explanatory variables, such as age. Serial independence of the error terms was graphically assessed and further tested using the Durbin–Watson test; residuals were screened for normality using expected normal probability plots and the Kolmogorov–Smirnov test. Residuals were both graphically and quantitatively (Levene test) assessed for homogeneity of variances. Data were log-transformed where heteroscedasticity and/or non-normality were detected. When data transformations failed to stabilize the variance, weighted-least square regression analysis was applied, in which case, weights were estimated by examining the relationship of the variance of the dependent variable to various powers of values of the independent variable.

A primary goal was to assess whether lease-scale sock density (SD_{Lease}) and grazing rates (CR_{Area}) significantly vary over a production cycle. Differences between consecutive months were computed to remove autocorrelation and render series stationary. Monthly differences were compared using nonparametric statistics (Kruskal-Wallis) because data transformations failed to stabilise variances. The significance threshold was set at $\alpha = 0.05$. Adjusted *P* values were computed. All analyses were performed in SPSS v. 20 (IBM SPSS Inc., Chicago).

RESULTS

Size frequencies

Shell length frequency distributions were grouped according to the estimated mussel age. Figure 2 shows the length distributions of mussel seed (age 2 to 3 months) when they were still attached to collector ropes. Bimodal distribution patterns indicate distinct spawning events and / or the influence of heterogeneous growing conditions across seed collection sites. Seed were transferred into polypropylene socks in October when they were approximately 4 months of age. Figure 3 shows the length distribution of mussels attached to polypropylene socks, starting with a median length of 25 mm (age 4 months) and finishing with a median length of 60 mm (age 29 months). Minor and occasional discrepancies in shell length growth (e.g., 15-month vs 16-month mussels) are likely attributable to our sampling design (pooling of multiple sites) and sampling effort.

Abundances

Mussel seed abundance on collector ropes was highly variable, ranging from 63—32250 individuals per meter of collector with a CV of 80.1% (n = 110 collectors, mean 8716 ± 666 seed m^{-1} SEM). Mussel abundance on socks ranged from 197—1307 individuals per meter of sock material; it had a CV of 38.0% (n = 218 socks, mean 563 ± 14 individuals m^{-1} SEM). Abundances were inversely proportional to age and shell length (Figure 4). Relationships were highly significant ($P < 0.001$), although their capacity to explain mussel abundance was consistently weak. Independent variables (age or shell length) explained 22 to 36% of the variation in mussel abundance on the structures. Relationships had strikingly steep slopes, indicating a tendency towards massive crop loss over time. For instance the abundance of seed on a collector fell by 74.6% (~1.81% per day) as shell length increased from 1.2 mm to a socking size of 20.0 mm; similarly, mussel abundance on socks decreased by 45.8% (~0.08% per day) from deployment to a harvestable size (shell length 55 mm).

Allometries

Figure 5 summarizes relationships between the age of mussels, their shell length and tissue weight. Each data point represents the mean (or coefficient of variation) associated to a collector rope (▲) or polyethylene sock (●). Mean shell length within the structure (collector or sock) followed a clear logarithmic pattern (Figure 5a), with age of the mussels explaining 91% of the variation. Shell length was highly variable amongst individuals that had naturally settled on collectors (Figure 5b); the standardized measure of dispersion (CV) reached 90.4 % ($n = 113$ collectors, mean 35.6 ± 1.9 % SEM). However, during the growout phase shell length was relatively similar amongst individuals in polyethylene socks ($n = 220$ socks, mean 8.8 ± 0.2 % SEM).

A surviving pediveliger larva attained a commercial length of 55 mm approximately 25 months following its settlement onto a collector rope (Figure 5a); at this harvest point its dry tissue weight was approximately 0.48 g (Figure 5c). In our study, tissue weight measurements were limited to mussels sampled during the growout phase. Within the socks themselves tissue weight was noticeably more variable in comparison to shell length (Figure 5b versus 5d). For instance, when focussing on commercial-size mussels (≥ 55 mm SL), the CV associated to mean shell length was 5.7% compared to 39.8% for tissue weight. Enhanced variability associated to tissue weight, both amongst and within socks, is consistent with the periodic release of gametes during spawning events. Figure 6 shows that these spawning events occurred during spring (May—July).

Sock densities and clearance rates

Figure 7 shows clearance rates at collector rope and polyethylene sock scales, termed $CR_{Structure}$. Mussel shell length explained up to 35% of the variation in $CR_{Structure}$. The relationship was remarkably steep for collectors. Peak $CR_{Structure}$ estimates were 12.7 (collectors) and 7.1 (socks) cubic meter of water per meter of structure per hour.

At the lease scale, monthly SD_{Lease} and CR_{Area} estimates significantly differed across the production cycle (Kruskal-Wallis applied to differenced data, $P < 0.01$). SD_{Lease} ranged from 0.12 ± 0.02 to 0.21 ± 0.04 socks m^{-2} (Figure 8a). As expected SD_{Lease} tended to increase during the autumnal socking period and thereafter decrease as older socks were harvested. CR_{Area} was much more variable, ranging from 22 ± 5 to 841 ± 92 $l\ h^{-1}\ m^{-2}$ (Figure 8b). CR_{Area} strongly co-varied with water temperature (Figure 8c).

Therefore temperature and not stocking density was the main factor contributing to the seasonal variability in grazing pressure.

Tunicates

A low proportion (≤ 11.9%) of samples contained invasive tunicates (Table 1). Tunicate infested samples were mainly collected in autumn and winter (Figure 9). *Ciona intestinalis* was the most densely aggregated of the tunicates, with an average count of 155 ± 63 individuals per meter of socking material; the maximum was 274 ± 119 individuals per meter of socking material in October. The average size of solitary tunicates was 32.1 ± 3.9 mm and 26.2 ± 1.7 mm for *Styela clava* and *Ciona intestinalis*, respectively.

DISCUSSION

Abundances

A high level of variability was detected with respect to seed. Amongst collectors mussel abundance ranged from 63—32250 individuals per meter of collector with a CV of 80.1%. The wide ranging estimates may be attributed to varying success of mussel larvae development and recruitment onto collectors, which presumably varies from year to year due to a wide range of natural factors, including hydrodynamics (flushing) and timing of the spring phytoplankton bloom in keeping with the match-mismatch hypothesis (Cushing, 1969; 1990).

Our results indicated a massive crop loss over time. The abundance of seed on collectors fell by 74.6% (~1.81% per day) over a 3-month growth period as shell length increased from 1.2 mm to a socking size of 20.0 mm; similarly, mussel abundance on socks decreased by 45.8% (~0.08% per day) from deployment to harvest (SL 55 mm). Some proportion of these losses may be attributed to predation, particularly from ducks, crabs, and sea stars. However, the bulk of the loss was likely driven by self-thinning processes, whereby a lack of space and intraspecific competition for food resources result in mussels falling off the socks (Fréchette et al., 1992; Lauzon-Guay et al., 2005). One concern with self-thinning is the efficient use of phytoplankton, the building block of the food web in an aquatic system. Phytoplankton provides sustenance to mussels as well as other filter feeding shellfish and zooplankton and largely determines the ecological and production carrying capacity of an estuary or bay. When mussels fall off and settle in or on the bottom during the grow-out period, the benefit of this valuable resource, which has fed the mussels since the seed stage, is lost from the standpoint of shellfish aquaculturists. From an ecological standpoint, the energy is transferred to benthic pathways with potential effects (positive or negative) on ecosystem components such as predators or scavengers. Inspections by SCUBA divers suggest that mussels which fall onto fine-silted bottoms eventually die from predation or clogging of their gill apparatus. This mortality has never been quantified and nothing is known about the amount of food resources (phytoplankton) that these detached mussels extract from the environment. In New Zealand, a large portion of the mussels falling from culture systems survive and colonize areas underneath leases (McKindsey et al., 2011). The overall benthic footprint of PEI mussel leases could be mitigated by reducing mussel fall offs. In Galicia Spain for instance, growers regulate self-thinning by redistributing half-grown mussels: mid-way in the production cycle they transfer mussels from 1 culture rope to two new ropes, thus reducing densities before the mussels fall to the bottom and become worthless.

Allometries

There were two notable observations relating to allometric relationships. The first observation concerns shell length, which was robustly (r^2 =0.91, P<0.001) correlated to mussel age. The relationship suggests that pediveliger larvae attain a commercial length of 55 mm approximately 25 months following their settlement onto collector ropes. The second noteworthy observation concerns tissue weight. Enhanced variability associated to tissue weight, both amongst and within socks, is consistent with the periodic release of gametes during spawning events. This observation is relevant because tissue weight parameterization can theoretically serve the computation of clearance rates, with the underlying rational that tissue weight is related to the water pumping apparatus and more specifically the surface area of gills. However, it is apparent from our dataset that this approach would inevitably introduce errors since tissue weight is unstable seasonally due to reproductive output. This complication with tissue weight was also highlighted by Filgueira et al. (2008) and Cranford et al. (2011).

Sock densities and clearance rates

This study provided new insight into the grazing capacity potential of cultivated mussels at the local scale. Based on modelling data, mussels attached to collector ropes had a potential of clearing particles twice as fast as those attached to socks. However, the validity of these estimates is uncertain since they were scaled up from measurements on individuals maintained under non-competitive conditions. In the field, intense competition for food resources at the local scale may lower individual CR through compensatory mechanisms. Intra-specific competition may also forcibly lead to mussels to fall off structures when energy demands are unmet. Hence the projected filtration potential of collectors in this study (maximum 12.7 $m^3\ m^{-1}\ h^{-1}$) may not actually occur in the field; rather, the remarkable potential may be indicative of intense food depletion at the local scale and consequently of unsustainable conditions at the collector scale. This interpretation is consistent with the massive seed loss indicated above for collectors (~1.81% per day). It also raises the concept of production carrying capacity (PCC) at the local scale. In theory the extractive capacity of the cultivated mussels is maximized at PCC, meaning that the crop is exploiting available food resources at an optimal rate from a productivity standpoint. Cultivating mussels beyond PCC thresholds may be counterproductive due to self-thinning processes mentioned earlier. Testing such hypotheses requires experimental work, specifically through the manipulation of mussel densities, spacing of individual structures along a longline, and measurements of food depletion and mussel productivity.

It was particularly striking in our study that grazing pressure varied seasonally by a factor of nearly 40 (CR_{Area} ~ 22 to 841 l h^{-1} m^{-2}), whereas stocking density varied by a factor of only 2 (SD_{Lease} ~ 0.12 to 0.21 socks m^{-2}). Our integration of water temperature in the computation of CR_{Area} was primarily responsible for the marked seasonal variation in grazing capacity of cultured mussel stocks. The dominant effect of temperature is not surprising considering the highly variable environmental conditions under which PEI mussels are cultivated. In winter, near-freezing (~ -1 °C) estuarine waters substantially curtail CR by lowering physiological rates (Comeau et al., 2008; Pernet et al., 2007) and increasing water viscosity (Podolsky, 1994). In future work, it would be valuable to compare seasonal trends in CR_{Area} with the timing of seasonal phytoplankton blooms. Current results suggest a mismatch, particularly during summer when CR_{Area} peaked; at temperate latitudes bloom events typically occur during autumn and spring with the turnover of the water column.

Tunicates

Comeau et al. (2015) reported that the presence of the solitary tunicate *C. intestinalis* or *S. clava* may increase CR_{Area} by 30–47% compared to non-infested scenarios, even with treatment measures in effect. These estimates were based on solitary tunicate counts ranging from 287 (treated) to 2034 (untreated) individuals per meter of socking material. In the present paper, tunicates were not integrated into CR_{Area} estimates. The reason is that a low proportion (≤ 11.9%) of samples contained invasive tunicates; moreover, when solitary tunicates were detected in autumn, their abundance was relatively low, averaging for instance 155 ± 63 *C. intestinalis* per meter of socking material; their body size was also relatively small, rendering difficult the computation of their clearance rates due to a lack of CR – body size equations for these tunicates in the literature. Overall, our observations on invasive tunicates during the study are consistent with the participant growers reporting intense mitigation (treatment) measures.

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REFERENCES

Bayne, B.L., 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). J. Anim. Ecol. 22, 513–523.

Byron, C., Link, J., Costa-Pierce, B., Bengtson, D., 2011. Calculating ecological carrying capacity of shellfish aquaculture using mass-balance modeling: Narragansett Bay, Rhode Island. Ecol. Model. 222, 1743-1755.

Byron, C.J., Costa-Pierce, B.A., 2013. Carrying capacity tools for use in the implementation of an ecosystems approach to aquaculture. in: Ross, L.G., Telfer, T.C., Falconer, L., Soto, D., Aguilar-Manjarrez, J. (Eds.), Site selection and carrying capacities for inland and coastal aquaculture. FAO/Institute of Aquaculture, University of Stirling, FAO Fisheries and Aquaculture Proceedings, Rome, pp. 87–101.

Comeau, L.A., 2013. Suspended versus bottom oyster culture in eastern Canada: Comparing stocking densities and clearance rates. Aquaculture 410–411, 57–65.

Comeau, L.A., Filgueira, R., Guyondet, T., Sonier, R., 2015. The impact of invasive tunicates on the demand for phytoplankton in longline mussel farms. Aquaculture 441, 95–105.

Comeau, L.A., Pernet, F., Tremblay, R., Bates, S.S., Leblanc, A., 2008. Comparison of eastern oyster (*Crassostrea virginica*) and blue mussel (*Mytilus edulis*) filtration rates at low temperatures. Can. Tech. Rep. Fish. Aquat. Sci. 2810.

Cranford, P.J., Ward, J.E., Shumway, S.E., 2011. Bivalve filter feeding, variability and limits of the aquaculture biofilter. in: Shumway, S.E. (Ed.), Shellfish Aquaculture and the Environment. Jon Wiley & Sons Inc, Chichester, UK, pp. 81–112.

Cushing, D.H., 1969. The regularity of the spawning season of some fishes. J. Cons. Int. Explor. Mer. 33, 81–92.

Cushing, D.H., 1990. Plankton production and year class strength in fish populations: An update of the match/mismatch hypothesis. Adv. Mar. Biol. 26, 249–293.

Dame, R.F., Prins, T.C., 1998. Bivalve carrying capacity in coastal ecosystems. Aquat. Ecol. 31, 409–421.

Davenport, J., Chen, X., 1987. A comparison of methods for the assessment of condition in the mussel (*Mytilus edulis* L.). J. Molluscan Stud. 53, 293-297.

Filgueira, R., Grant, J., 2009. A box model of ecosystem-level management of mussel culture carrying capacity in a coastal bay. Ecosystems 12, 1222–1233.

Filgueira, R., Labarta, U., Fernández-Reiriz, M.J., 2008. Effect of condition index on allometric relationships of clearance rate in *Mytilus galloprovincialis* Lamarck, 1819. Rev. Biol. Mar. Oceanogr. 43, 391–398.

Filgueira, R., Guyondet, T., Comeau, L.A., Grant, J., 2014. A fully-spatial ecosystem-DEB model of oyster (*Crassostrea virginica*) carrying capacity in the Richibucto Estuary, Eastern Canada. J. Mar. Syst. 136, 42–54.

Filgueira, R., Brown, M.S., Comeau, L.A., Grant, J., 2015a. Predicting the timing of mussel larval development based on ocean temperature. J. Molluscan Stud., 1-5.

Filgueira, R., Comeau, L.A., Guyondet, T., McKindsey, C.W., Byron, C.J., 2015b. Modelling carrying capacity of bivalve aquaculture: a review of definitions and methods. Encyclopedia of Sustainability Science and Technology Springer Science+Business Media New York 2015, DOI 10.1007/978-1-4939-2493-6_945-1.

Fréchette, M., Aitken, A.E., Page, L., 1992. Interdependence of food and space limitation of a benthic suspension feeder: consequences for self-thinning relationships. Mar. Ecol. Prog. Ser. 460, 55–62.

Grant, J., Bacher, C., Cranford, P.J., Guyondet, T., Carreau, M., 2008. A spatially explicit ecosystem model of seston depletion in dense mussel culture. J. Mar. Syst. 73, 155–168.

Kluger, L.C., Taylor, M.H., Barriga Rivera, E., Torres Silva, E., Wolff, M., 2016. Assessing the ecosystem impact of scallop bottom culture through a community analysis and trophic modelling approach. Mar. Ecol. Prog. Ser. 547, 121-135.

Kooijman, S.A.L.M., 2010. Dynamic energy budget theory for metabolic organization. Cambridge University Press. 419 pp.

Lauzon-Guay, J.-S., Dionne, M., Barbeau, M.A., Hamilton, D.J., 2005. Effects of seed size and density on growth, tissue-to-shell ratio and survival of cultivated mussels (*Mytilus edulis*) in Prince Edward Island, Canada. Aquaculture 250, 652–665.

McKindsey, C.W., Archambault, P., Callier, M.D., Olivier, F., 2011. Influence of suspended and off-bottom mussel culture on the sea bottom and benthic habitats: a review. Can. J. Zool. 89, 622–646.

Pernet, F., Tremblay, R., Comeau, L., Guderley, H., 2007. Temperature adaptation in two bivalve species from different thermal habitats: energetics and remodelling of membrane lipids. J. Exp. Biol. 210, 2999–3014.

Podolsky, R., 1994. Temperature and water viscosity: physiological versus mechanical effects on suspension feeding. Science 265, 100–103.

Scarratt, D.J., 2000. Development of the mussel industry in eastern Canada. Bulletin of the Aquaculture Association of Canada 100, 37–40.

van der Veer, H.W., Cardoso, J.F.M.F., van der Meer, J., 2006. The estimation of DEB parameters for various Northeast Atlantic bivalve species. J. Sea Res. 56, 107–124.

Table 1 Occurrence and density of invasive tunicates on collector ropes (mussel seed) and polyethylene socks (grow out crop). Occurrence represents the proportion of samples infested with the tunicate species. Values are means ± SEM.

	Collector ropes		**Polyethylene socks**	
Species	Occurrence (%)	Count per meter of structure	Occurrence (%)	Count‡ per meter of structure
B. violaceus, *B. schlosseri*	0	0	11.9	3.5±1.1
S. clava	0.9	6.7†	5.0	6.6±0.1
C. intestinalis	13.3	97.5±27.7	6.8	155.2±63.1

† *represents a single sample, no SEM calculated.*

‡ represents grams per meter for colonials *Botrylloides violaceus*, *Botryllus schlosseri*

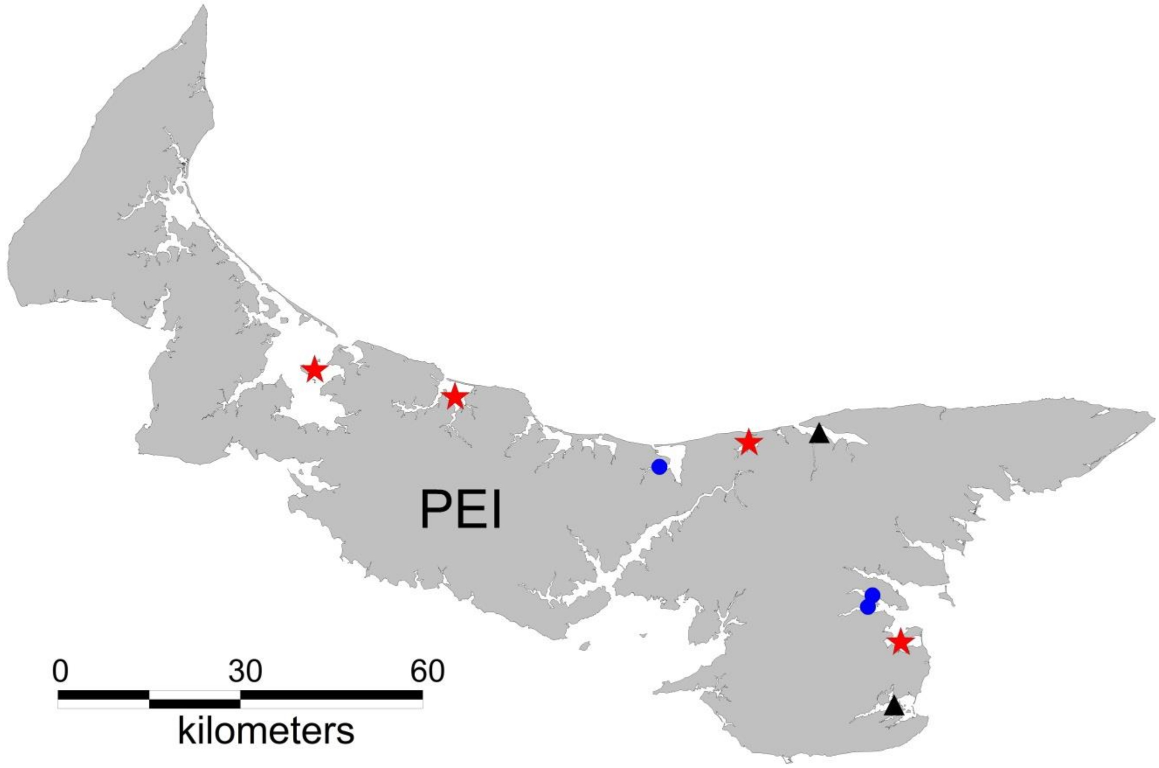


Figure 1 Location of sampling sites for mussel collectors (●), polyethylene socks (★) or both (▲). Grower interviews relate to all sites except collector sites.

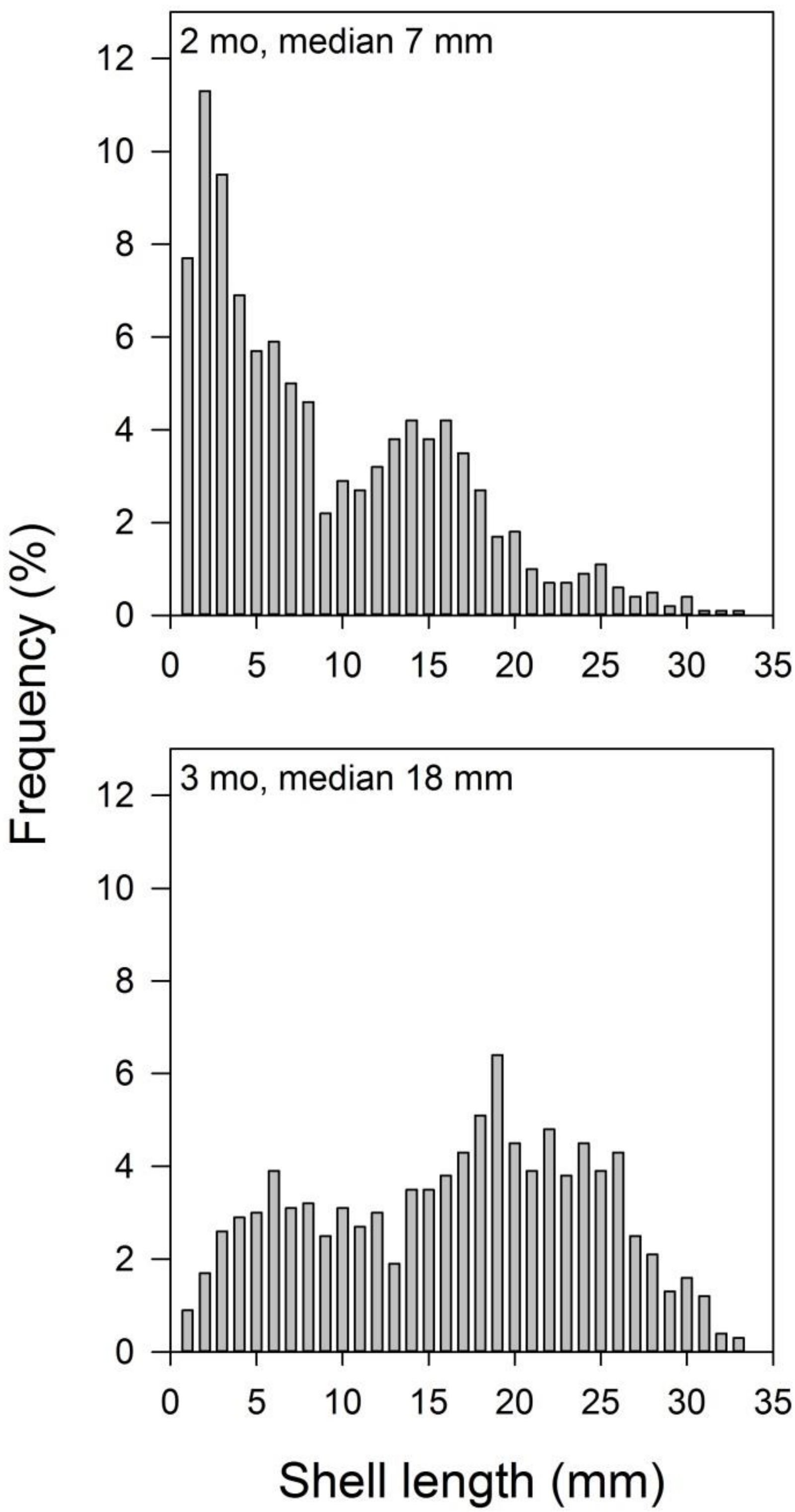


Figure 2 Shell length frequency distribution of mussels on collector ropes. Data grouped by estimated mussel age (months) at time of sampling.

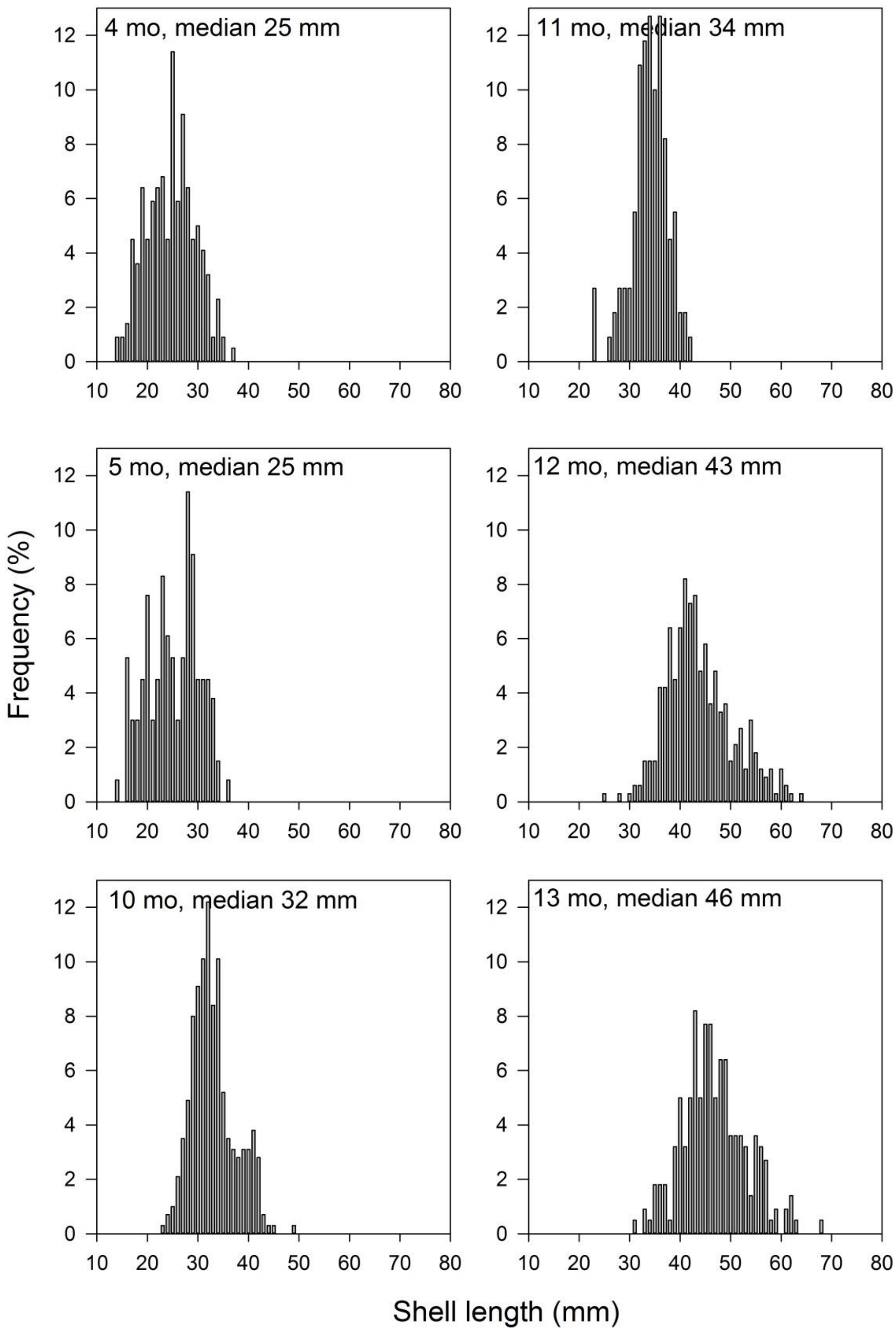


Figure 3 Shell length frequency distribution of mussels in polypropylene socks. Data grouped by estimated mussel age (months) at time of sampling. Age categories with relatively few measurements (n < 100) were excluded from presentation.

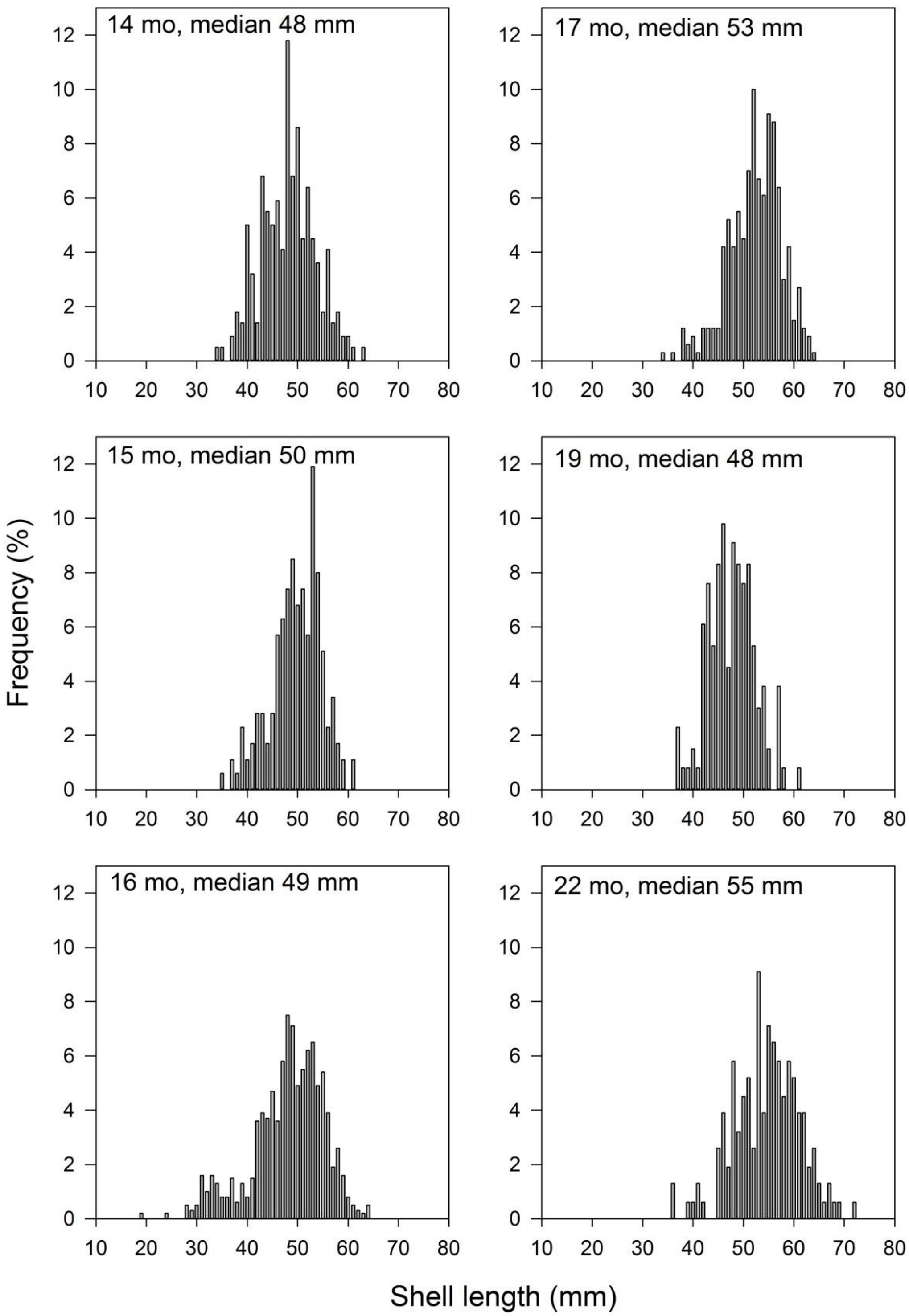
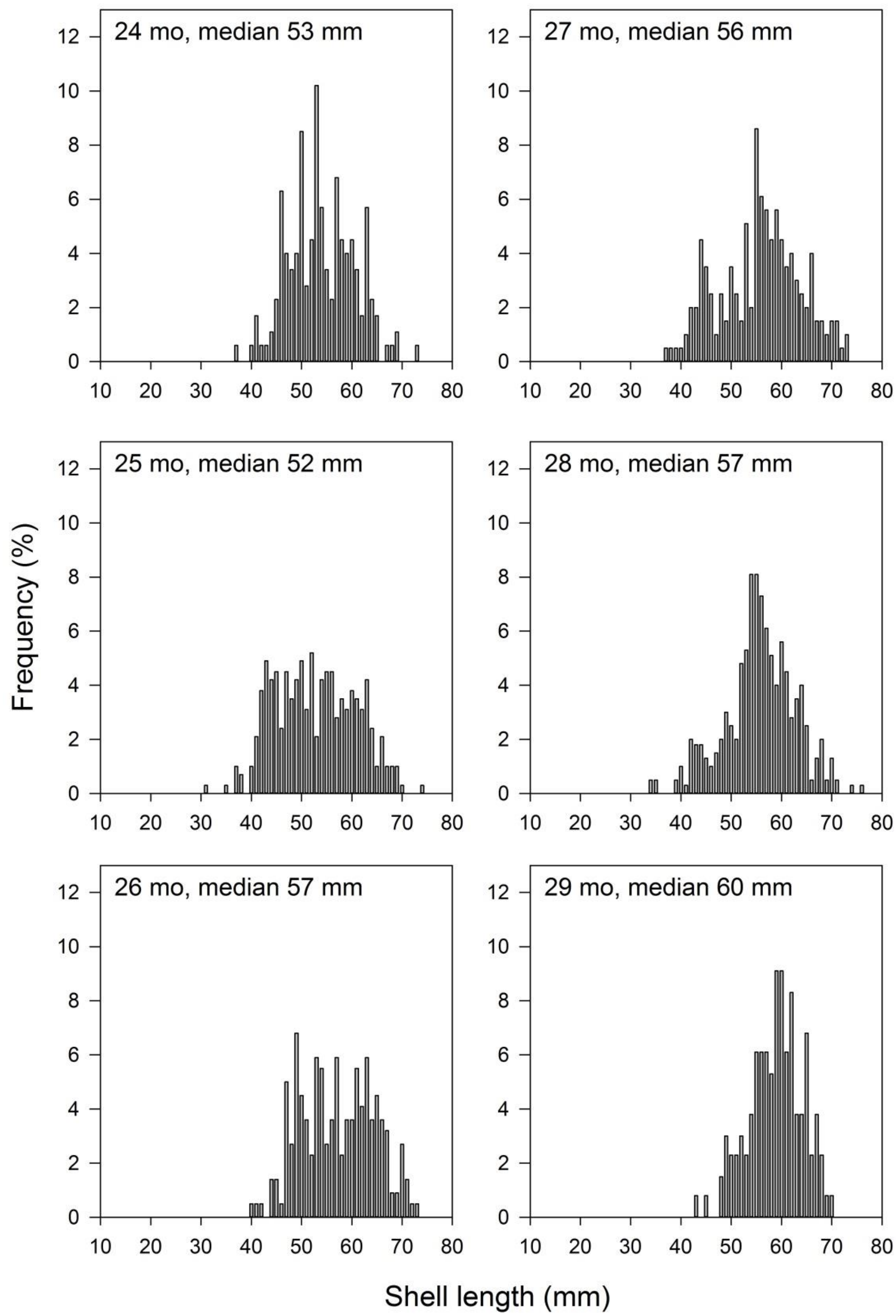


Figure 3 (continued)



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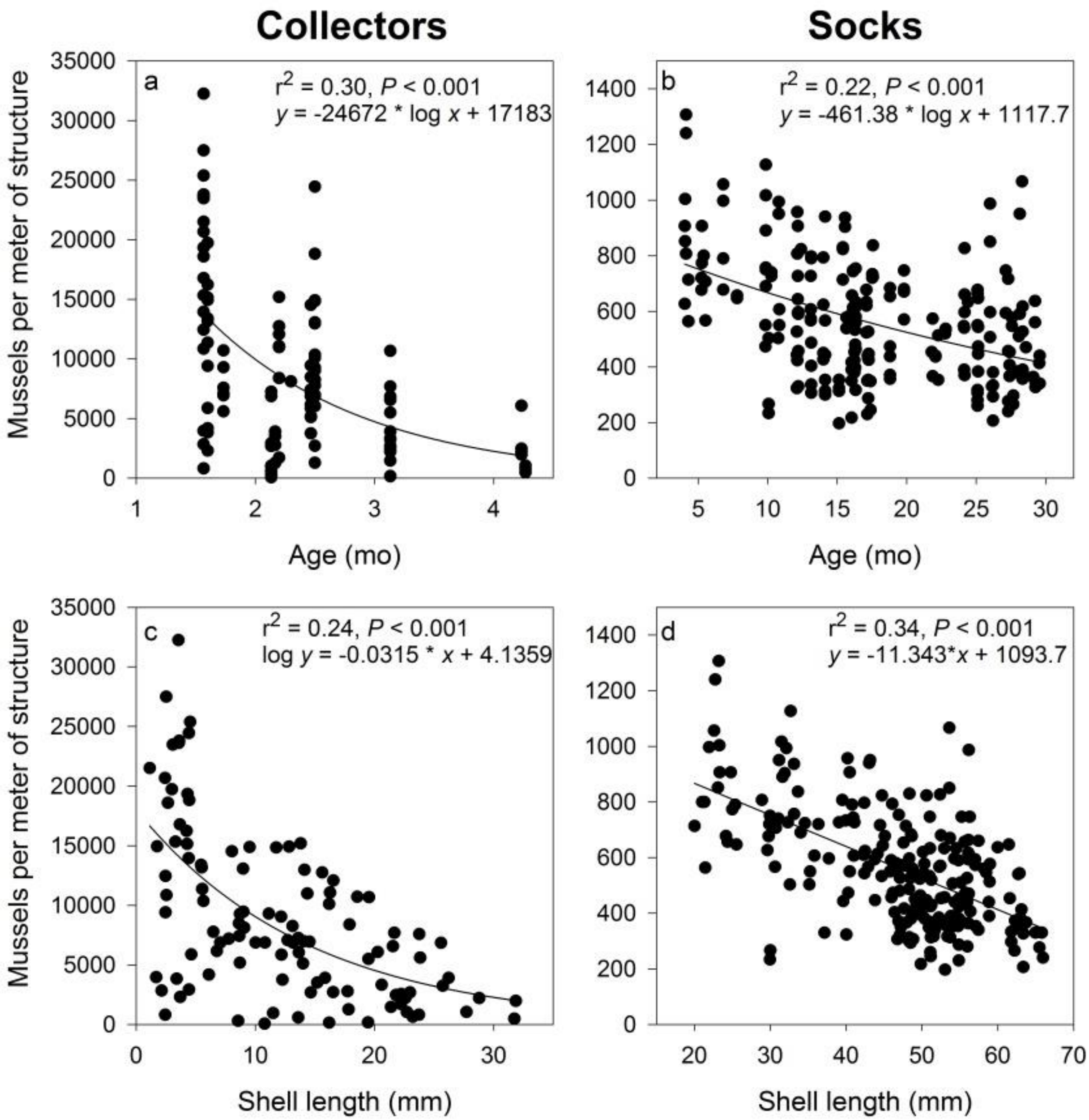

Figure 4 Mussel abundance on collector ropes (a, c) and polyethylene socks (b, d) as a function of mussel age and shell length. A weighted-least squares regression model was applied to panel a because data transformations failed to stabilize the variance.

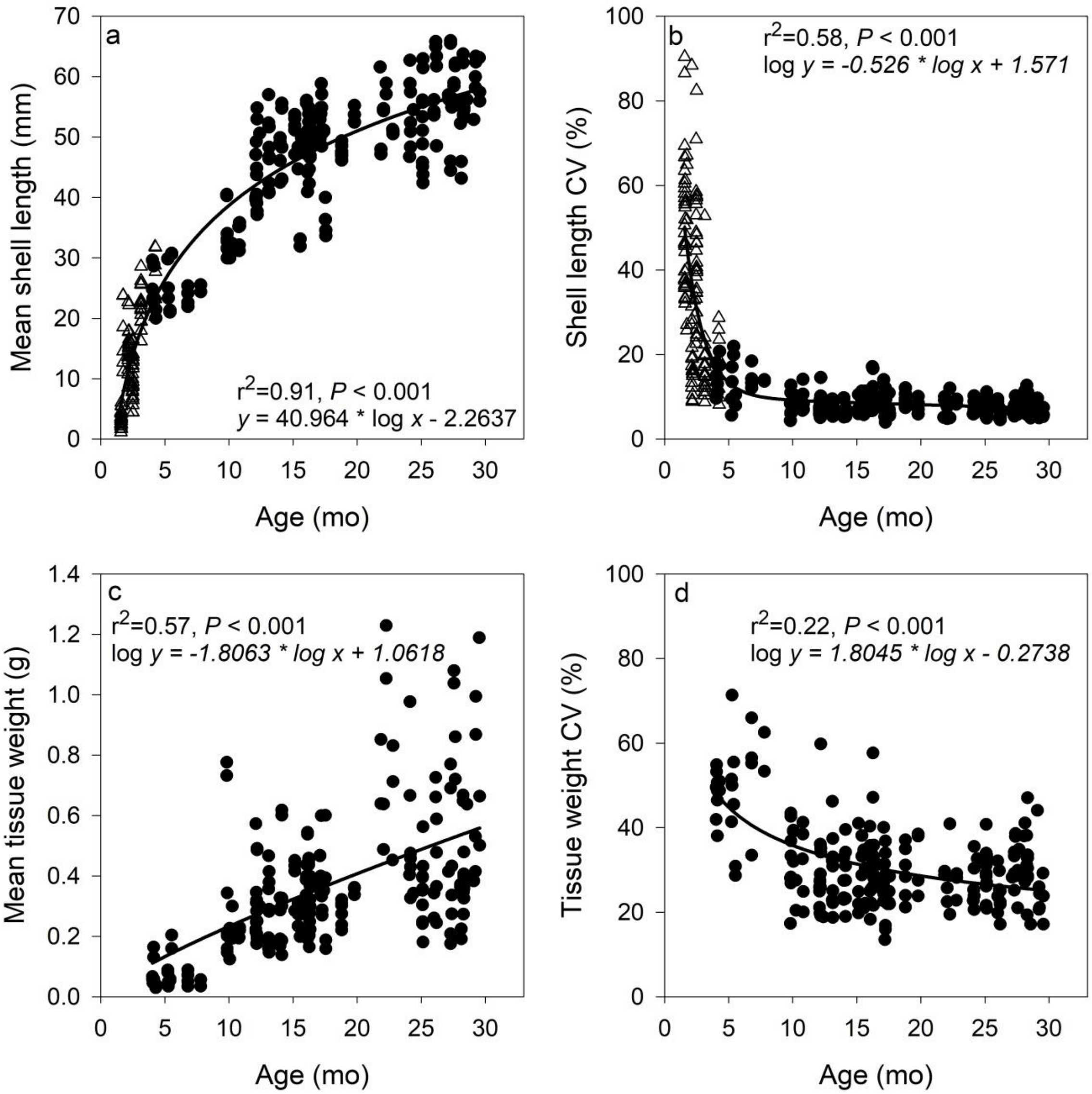

Figure 5 Mean (a, c) and coefficient of variation (b, d) of shell length and tissue weight as a function of age at the collector rope (∆) and polyethylene sock (●) scales. A weighted-least squares regression model was applied to panel b because data transformations failed to stabilize the variance.

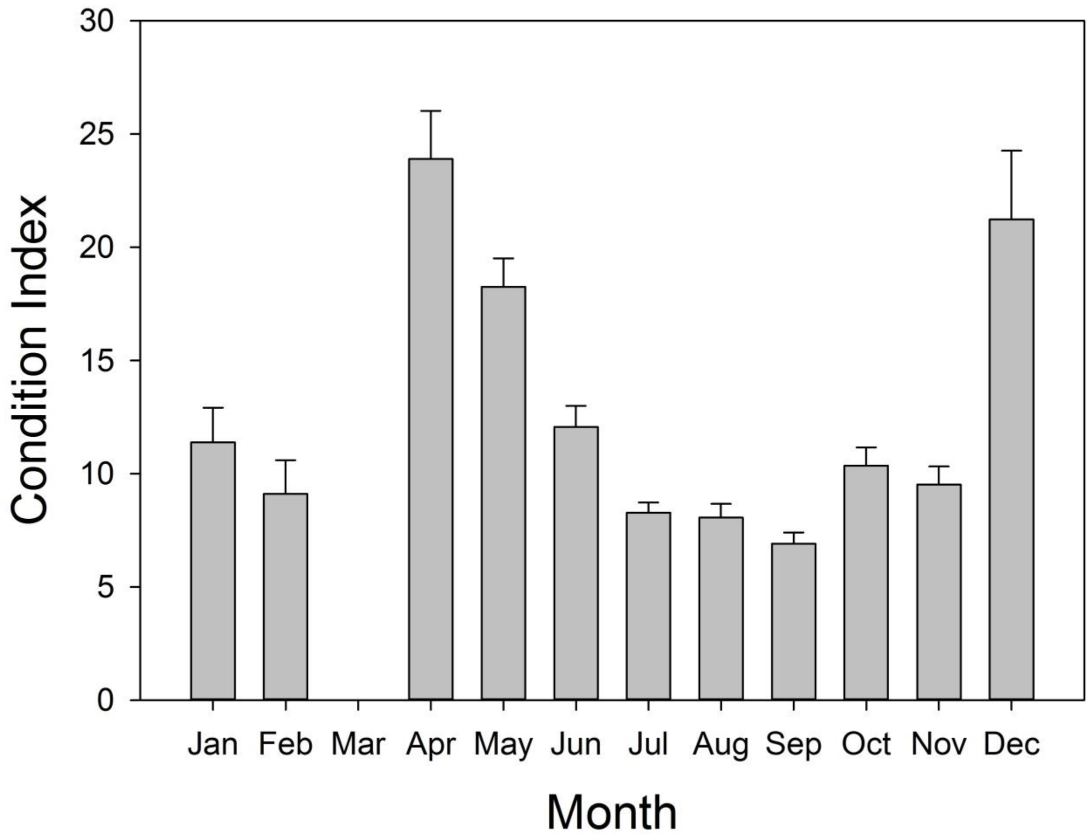

Figure 6 Mean (±SEM) condition index of cultivated mussels as a function of time. Mussels were sampled from polyethylene socks; dataset covers October 2015 to December 2016.

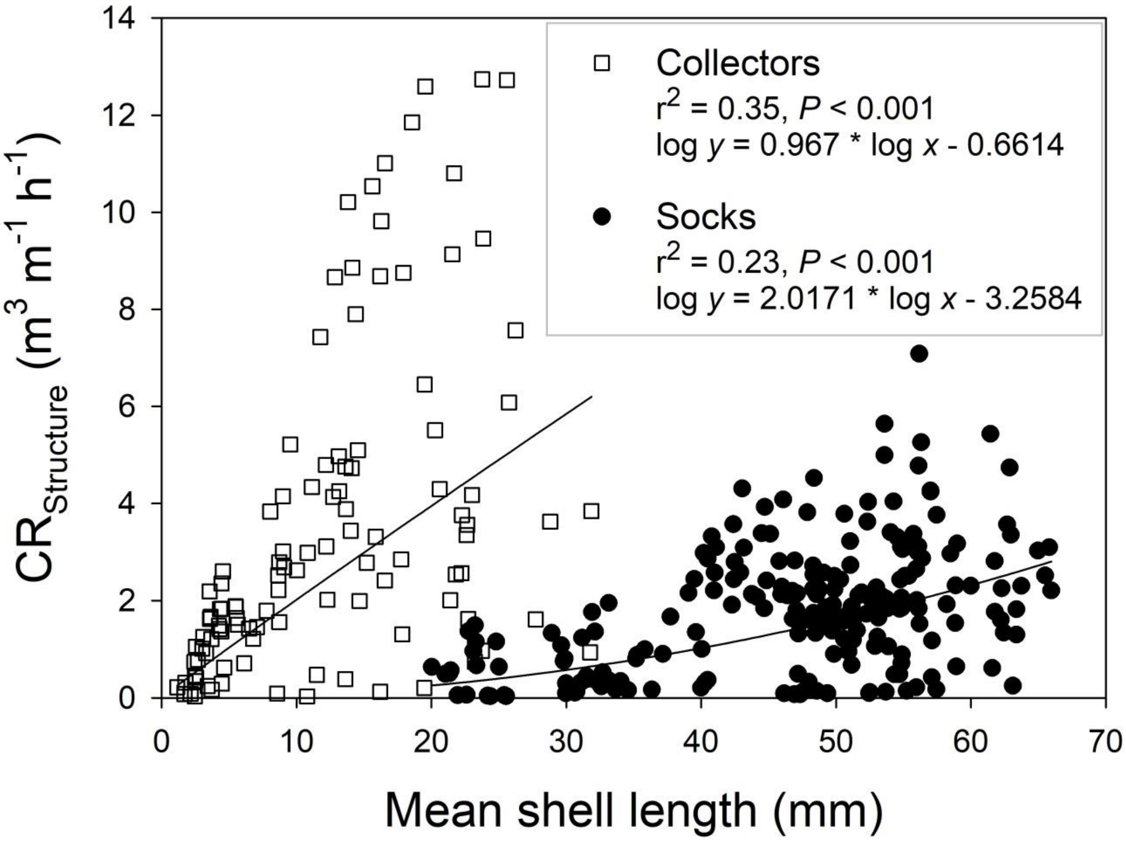

Figure 7 Modelled clearance rate ($CR_{Structure}$) as a function of mean shell length (MSL) of *M. edulis* found on collector ropes and polyethylene socks. $CR_{Structure}$ represents the volume of water (m^3) cleared of particles per meter of structure per hour.

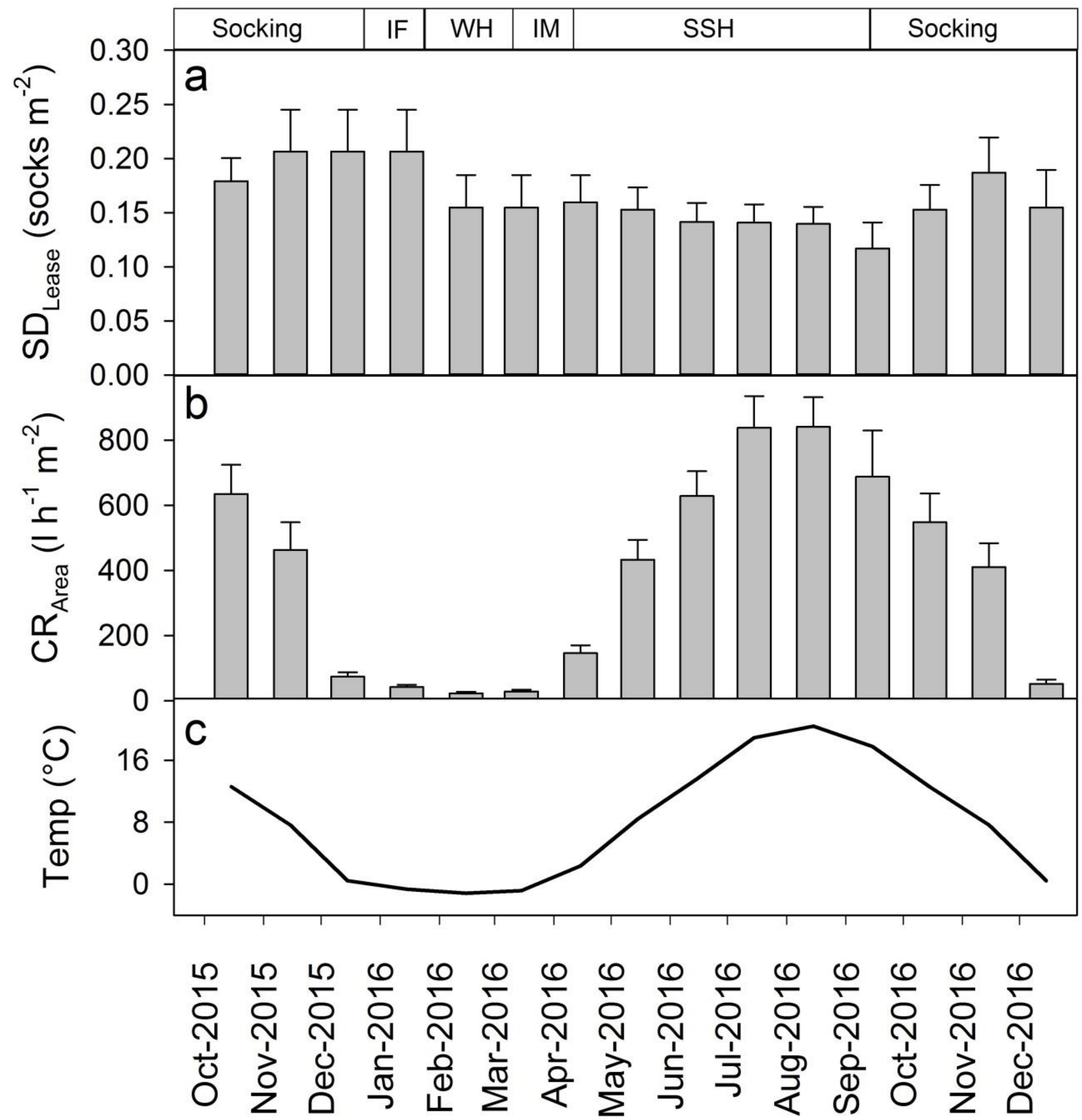

Figure 8 SD$_{Lease}$ (a) and CR$_{Area}$ (b) as a function of time. Results represent means ± 1 SEM derived from six PEI mussel growers interviewed on a monthly basis between October 2015 and December 2016. Husbandry phases are identified as “socking” when new crop (seed) was added to the lease, winter ice formation (IF), winter harvesting (WH), ice melting (IM), and spring and summer harvests (SSH). Monthly mean water temperature (c) applied in the calculation of CR$_{Area}$ (see methods).

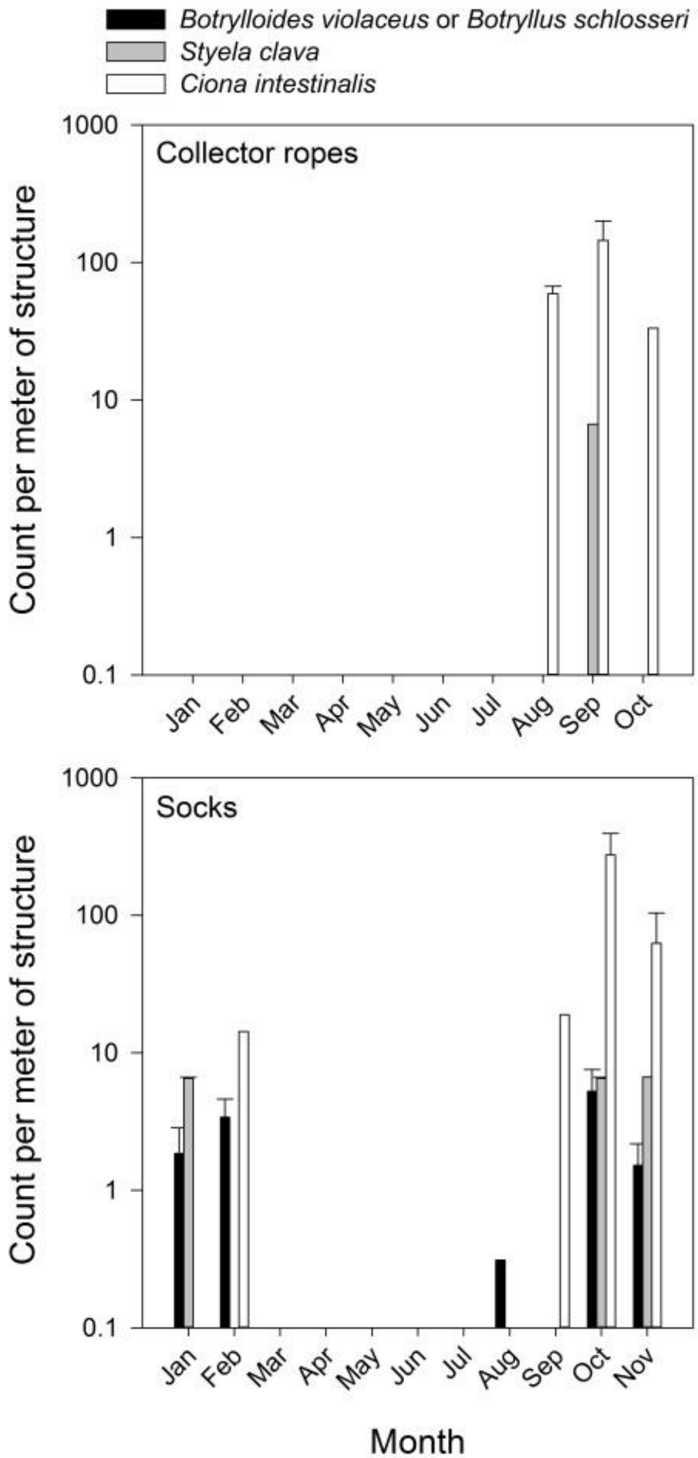

Figure 9 Mean (±SEM) tunicate abundance on collector ropes (top) and polyethylene socks (bottom) as a function of sampling month. Dataset covers October 2015 to December 2016; years were pooled due to low number of positive counts.