Received: 4 August 2020 | Accepted: 22 February 2021

DOI: 10.1111/1365-2435.13788

RESEARCH ARTICLE

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

Resource allocation to a structural biomaterial: Induced production of byssal threads decreases growth of a marine mussel

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Funding information
National Oceanic and Atmospheric Administration, Grant/Award Number: NA14OAR4170078; National Science Foundation IGERT Program on Ocean Change Fellowship, Grant/Award Number: 1068839; University of Washington, Friday Harbor Laboratories; University of Washington, Department of Biology

Handling Editor: Anthony Herrel

Abstract

1. The biomechanics of specialized mechanical structures produced by organisms provides crucial fitness advantages. The energetic cost associated with producing these structural materials and the resulting energetic trade-off with growth, however, is rarely quantified. We integrate resource allocation to structural material production with an energetic framework by combining an experimental manipulation with an energetic model.
2. Mytilid bivalves produce byssus, a network of collagen-like threads that tethers individuals to hard substrate. We hypothesized that a manipulation that induces the production of more byssal threads would result in increased energetic cost and decreased growth of the species *Mytilus trossulus*.
3. In month-long field experiments in spring and autumn, we severed byssal threads across a range of frequencies (never, weekly, daily), and measured shell and tissue growth. We then quantified the costs associated with the production of byssal threads using a Scope for Growth model.
4. We found that byssal thread removal increased byssal thread production and decreased growth. The cost calculated per byssal thread was similar in the spring and autumn (~1 J/thread), but energy budget calculations differed by season, and depended on thread quantity and seasonal differences in assumptions of metabolic costs.
5. This work demonstrates that the cost of producing a structural material has a substantial effect on mussel energetic state. The energetic cost of producing byssal threads was 2%–8% percent of the energy budget in control groups that had low byssal thread production, and increased six to 11-fold (up to 47%) in mussels induced to produce threads daily.
6. We propose that characterizing the trade-off between the cost of biomaterial production and growth has implications for understanding the role of trade-offs in adaptive evolution, and improved natural resource management and conservation practices.

KEYWORDS
bioenergetics, byssus, ecomechanics, energetic cost, marine ecology, *Mytilus trossulus*, resource allocation, sensitivity analysis

1 | INTRODUCTION

The specialized mechanical structures that organisms produce, such as cactus spines, spider webs and bivalve shells provide a range of fitness advantages, including predator deterrence, resource acquisition and abiotic stress amelioration (Crofts & Anderson, 2018; Gosline, 2018; Vogel, 2013). The production of a structural biomaterial, however, requires an investment of energetic resources. The investment might result in energy allocation trade-offs that shift performance traits on the individual level, and affect population dynamics (Sebens et al., 2018) and spatial distributions of organisms (biomechanical ecotype, Read & Stokes, 2006). For example, the altered growth and development of plants in response to wind or mechanical perturbation (thigmorphogenesis) reduces plant size and fecundity (Chehab et al., 2008; Telewski & Pruyn, 1998). Similarly, the induction of dragline spider silk production reduces spider survival and fecundity (Bonte et al., 2016). For marine bivalves, a greater cost of shell production induced by low salinity conditions can affect energetic limitation (Sanders et al., 2018). In conditions of low food availability and/or high metabolic cost, such trade-offs could be greater and thus more evident; structural biomaterials would be prioritized at the expense of growth (Clarke, 1999) or their production and maintenance could decline altogether (Melzner et al., 2011).

Energy budget models provide a framework for investigating energy allocation trade-offs by explicitly quantifying energetic fluxes associated with consumption of food, maintenance of cellular tissues and growth of somatic and reproductive tissues, and reproduction. Examples of these types of models include Scope for Growth (SFG; Bayne et al., 1976; Thompson & Bayne, 1974; Widdows & Bayne, 1971), fish bioenergetics (Kitchell et al., 1977) and Dynamic Energy Budgets (DEB; Kooijman, 2010). This mechanistic approach has been used to study relationships between environmental factors (e.g. energy inputs and temperature- or salinity-dependent metabolic costs) and organismal processes (soft tissue growth and reproductive output; e.g. Kearney et al., 2010, 2012; Kooijman, 2010; Maar et al., 2010, 2015; Matzelle et al., 2015; Sarà et al., 2011, 2013). Different energy budget frameworks often yield similar biological predictions from environmental variables (e.g. Filgueira et al., 2011; Nisbet et al., 2012), but differ in complexity and in their handling of uncertainty (Boersch-Supan & Johnson, 2019). Energy budget models also provide a flexible framework with which to evaluate trade-offs with structural materials since structural material production costs correlate with well-described bioenergetic fluxes (Sanders et al., 2018; Sarà et al., 2013; Sebens et al., 2018), and can have different mass-specific costs (Brody, 1945; Sanders et al., 2018). SFG models provide a simple conceptual framework where tissue growth is represented as a function of consumption of food minus physiological costs (Bayne et al., 1976; Sebens, 2002; Widdows & Bayne, 1971, Figure 1). The combination of these models with experimental manipulations of the quality (Sanders et al., 2018) or quantity of structure produced by organisms provides an excellent opportunity to study energy allocation and trade-offs.

An example of a biomaterial known to be influenced by external conditions is byssus, a structural material made by bivalves that consists of a network of collagen-like threads that tethers each animal to hard substrate (Bell & Gosline, 1996; Waite et al., 1998). Marine mytilid mussels are a common organismal study system for energetic models (Kooijman, 2010; Sebens et al., 2018; van der Veer et al., 2006), in part due to their ecological and economic importance. The mechanical strength of byssus has consequences across multiple scales of biological organization, including life-history traits, mussel population dynamics and community structure (Carrington et al., 2015; Denny, 1995). For example, mussels act as ecosystem engineers (Borthagaray & Carranza, 2007), when they use their byssus to densely aggregate into mussel beds, a physical structure that provides refuge for associated species by limiting flow (O'Donnell, 2008). Byssal thread structure facilitates culturing of this species; mussels attach to collector ropes as larvae (Brenner & Buck, 2010), and as adults, form attachments to culture ropes without a surrounding net that would otherwise limit flow and increase fouling (Korringa, 1976).

Previous studies estimated byssal thread production as 8%–10% of the energy budget of mussels (Hawkins & Bayne, 1985; Lurman et al., 2013). An elemental balance method demonstrated that ~8% of both the carbon and nitrogen incorporated into *Mytilus edulis* organic tissues was incorporated into byssal threads during a summer period of net growth (Hawkins & Bayne, 1985). Lurman et al., (2013) found that respiration increases approximately 10% during periods of thread production. These findings provide estimates of the baseline cost of byssal thread production, but they do not account for the variable rate at which threads are produced or the potential energetic trade-off with other processes, such as growth. The production of byssus also requires a cascade of events that include animal activity, including animal movement, foot extension and chemotaxis of the foot to identify a suitable location to establish attachment. The quantification of carbon and nitrogen investment in byssus (~8%, Hawkins & Bayne, 1985), and the instantaneous increase in respiration (Lurman et al., 2013) may therefore account for only part of the full cost of production of byssus.

The energetic trade-off between thread production and tissue growth can be characterized with a SFG model (Figure 1). Mussels modulate their production of byssal threads in response to a range of environmental conditions, such as increased wave disturbance (Bell & Gosline, 1997; Carrington et al., 2008; Dolmer & Svane, 1994; Lee et al., 1990; Moeser et al., 2006; Van Winkle, 1970; Young, 1985),

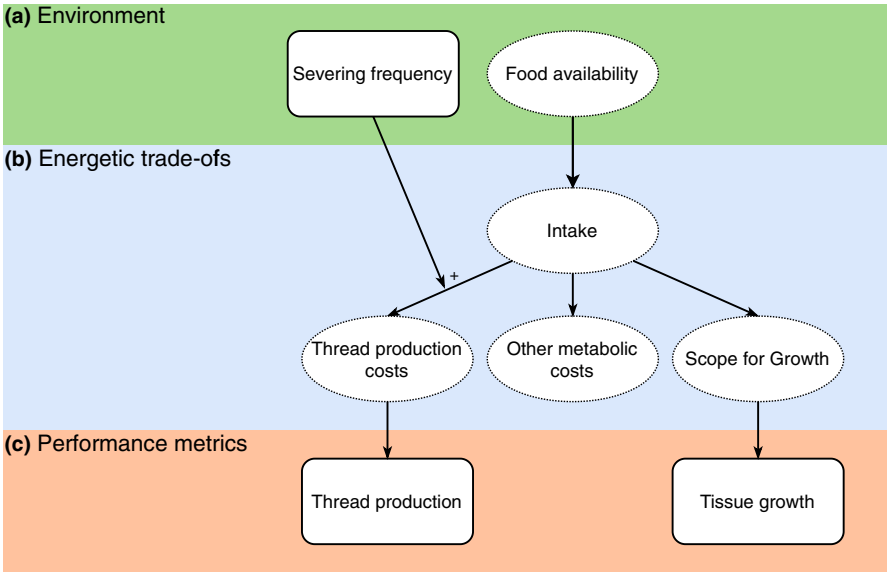

FIGURE 1 Schematic representation of possible energetic trade-offs between mussel byssal thread production and growth using a Scope for Growth framework. Environmental conditions (a), such as increased wave disturbance, predation pressure or, in the case of this study, experimental byssal thread removal by severing, can increase byssal thread production and affect other performance metrics (b, c). We hypothesized that energy allocation to byssal thread production is prioritized over tissue growth, which includes growth of new somatic and reproductive tissue. We considered tissue growth as an index of the theoretical Scope for Growth (b) since gamete production was minimal during these experiments. We used experimental observations of the relationship between thread production and growth to determine the cost of producing threads. 'Intake' indicates assimilated intake. Thread production is considered a metabolic cost separately from other metabolic costs, which includes respiration costs of somatic and reproductive tissue. Solid rectangles indicate empirical observations that were experimentally quantified, and dashed circles indicate model components. See text for details

seawater temperature and pH (George et al., 2018; Newcomb et al., 2019; O'Donnell et al., 2013), as well as seasonal and/or reproductive cycles in natural systems (Carrington, 2002; Moeser & Carrington, 2006; Newcomb, 2015; Zardi et al., 2007). Within the framework of a SFG model, the theoretical variable, SFG, can be used an index of tissue growth (including gonadal and somatic tissue growth), and is calculated as the difference between consumption minus physiological cost (Bayne et al., 1976; Sebens, 2002; Widdows & Bayne, 1971; Figure 1).

In natural environments, mussels modulate their production of byssal threads depending on environmental conditions, but in the laboratory the production of new byssal threads can be experimentally stimulated by severing the network of byssal threads (Young, 1985). Firstly, we hypothesize that experimental manipulation (severing) of byssal threads increases energy allocated to byssal thread production (Figure 1). We predict that mussels in treatments with greater byssal thread severing frequencies will produce more byssal threads. Secondly, we hypothesize that energy allocation to byssal thread production is prioritized over tissue growth (Figure 1). Byssal threads are produced even under starvation conditions (Clarke, 1999; Roberts, 2019), and starvation does not decrease the production of byssal threads of larger mussels with a large glycogen energetic reserve (Babarro et al., 2008; Babarro & Reiriz, 2010). We predict that mussels in treatments with greater byssal thread severing frequencies have decreased tissue growth. To test our hypotheses, we severed byssal threads at different frequencies and quantified the effect on byssal thread production and tissue growth. We combine the results of our manipulative experiments with a SFG model to evaluate how much energy mussels allocate towards byssal thread production, and away from tissue growth and reproduction, when a higher rate of thread production is necessary to maintain attachment. We used the growth data in a two-step optimization approach to determine the cost of producing threads by evaluating the relationship between tissue growth and thread production rate. The SFG model was then used to estimate the allocation of energy towards byssal threads relative to other costs and production across the range of quantity of structural material produced. We demonstrate an energetic trade-off of production of a structural material, mussel byssus, with growth, and show that enhanced production of mussel byssus can have a substantial metabolic cost, much higher than previous estimates.

2 | MATERIALS AND METHODS

2.1 | Field manipulation of byssal thread production

The effect of thread severing frequency on thread production rate and growth of *Mytilus trossulus* was investigated in a field setting over 1 month in autumn 2013 (mid-October to mid-November) and in spring 2014 (late April to late May). *Mytilus trossulus*, ranging approximately 2–3 cm length (~80–200 mg dry weight tissue), were collected from Argyle Creek on San Juan Island, WA (Lat

48.521652°N and Long 123.014061°W) and transported to Friday Harbor Laboratories (Lat. 48.525350°N, Long. 123.012521°W). The pre-existing byssal threads were severed from each mussel using scissors before the mussel was placed in a flexible mesh enclosure (10 cm × 22 cm, HDPE vexar plastic, 1 cm^2 mesh size) suspended from a floating dock at ~1 m depth. Seawater temperature and salinity were similar in both 2-month-long experiments (autumn—9.7 ± 0.4 C, 30.3 ± 0.4 psu; spring—9.4 ± 0.4 C, 30.6 ± 0.3 psu, means ± *SD*, BCO-DMO dataset, Carrington, 2019, Figure S4). The three treatments differed in the frequency at which the newly produced byssal threads were severed during the experiment: never, weekly or daily (or 0, 1 and 7 times per week respectively). Fifteen mussels were distributed evenly among three replicate enclosures for each treatment.

Mussels were labelled with numeric tags attached to their shell with cyanoacrylic acid. They were tethered with glue inside the enclosure using ~2 cm of fishing line epoxied to the shell to limit movement and provide isolation from other mussels. In the never-severed (control) treatment, mussels were attached such that they were unable to reach the cage surface with their foot, thus limiting their opportunity to attach byssus. This was done to ensure that this group of mussels achieved the lowest possible production by producing a minimum of threads. Mussels in this treatment did, however, attach byssal threads to their own shell and to their tether.

Mussels in the 'daily' treatment group were monitored for byssus production every day by counting and severing newly produced byssal threads. New byssal threads were also counted and severed for mussels in the 'weekly' treatment group, but at a lower frequency of once per week. New byssal threads of the mussels in the 'never' treatment group were not severed and were counted at the end of the 4-week experimental period. Thread production of each individual mussel was counted in all treatments; however, in the 'never' control group in spring only the total number of byssal threads produced by the group was recorded. This value was divided by sample size to obtain an average thread production for each individual in this single group.

2.2 | Mussel condition, length and weight measurements

Shell growth was calculated as the change in shell length, measured with calipers (±0.1 mm). Buoyant weight (±0.001 g) was determined in seawater at the beginning and end of the experiment (salinity ~30 psu). Buoyant weight was used as a measure of total animal wet weight, including shell and tissue. Since body tissue is a similar density to seawater, this non-destructive metric is representative of changes in shell weight of individual mussels. At the end of the experiment, the mussels were killed to obtain dry tissue and shell weight measurements. Specifically, gonad and somatic tissues were removed from the shell and dried at 60°C to a constant weight, and the dried shell weight was measured (±0.01 g). Condition index (CI) was calculated for each mussel by dividing dry tissue weight (g) by shell length cubed (mm^3; Crosby & Gale, 1990). Gonadal-somatic index (GSI) was calculated by dividing gonad weight (g DW) by total tissue weight (g DW; Carrington, 2002). Mortality during the month-long experiment was 17% in the spring and 4% in the autumn. As a result of mortality, sample sizes ranged from 11 to 5 per treatment. Two mussels in the autumn died just prior to the end of the experiment and final length was estimated from the growth rate, and tissue weight was estimated from the relationship between length and tissue mass of the sample population at the end of the experiment.

2.3 | Energetics and energy allocation to byssus

The allocation of energy towards byssus production was determined using a SFG framework following the general method of Bayne et al. (1976), with modifications suggested by Sebens et al. (2018) and Sanders et al. (2018). First, the cost per thread was calculated from the relationship between thread production and tissue growth. Then, this cost was incorporated into a SFG model and used to calculate the proportion of energy allocated to byssal thread production and the metabolic cost of byssus relative to baseline somatic costs. Model parameters are summarized in Table 1.

All energy budget calculations are expressed as daily fluxes (in J), and the calculations for each animal used normalized values from the 4-week experiment. Scope for Growth (SFG, J), the energy available for growth (somatic and gonad), is calculated as follows:

$$\mathrm{SFG} = E - \mathrm{cost}_{\text{non-byssus}} - \mathrm{cost}_{\text{byssus}}, \quad (1)$$

where E is the energy intake (J), $\mathrm{cost}_{\text{non-byssus}}$ is the cost of tissue maintenance (J) and $\mathrm{cost}_{\text{byssus}}$ is the cost of producing byssus (J). We assumed mussels were minimally reproductive because mussels were small and had a low proportion of tissue that was reproductive (length < 3 cm, GSI < 0.20). Gonadal and somatic tissue maintenance costs are included in the term, $\mathrm{cost}_{\text{non-byssus}}$ (Equation 1). Most of the gonad weight consisted of structural tissues, rather than gametes, in these small mussels, and thus, we did not calculate a separate allocation or cost for gamete production.

Individual energy intake (E) depends on initial tissue mass ($\mathrm{TM}_{\text{initial}}$, mg DW):

$$E = f \times a' \times \mathrm{TM}_{\text{initial}}^{d}, \quad (2)$$

where f is the relative food availability coefficient (unitless), a' is the energy intake coefficient (J/mg^d) and is described in more detail in equation 4, and d is the energy intake exponent (unitless). The relative food availability coefficient (f) is a scaling factor for the amount of food available during the experiment and was estimated from the experimental data for each season. Food availability was considered

TABLE 1 Summary of parameter calculations for the Scope for Growth model. The model had five input parameters, each estimated separately for each season using constants obtained from this and previously published studies. (*b*) SFG parameter values were derived from estimations of the energetic optimal size (W_{opt}), respiration, shape coefficient and the relationship between wet and dry mass. Error propagation was used to estimate parameter variance from data sources. Where possible, values were estimated from the studied subpopulation, rather than using a separate set of mussels or dataset (i.e. δ)

Parameter		Unit	Season	Value	SE	Equation	Source
Input parameter							
a'	Intake coefficient	J/(day × *f* × mgDW^d)	Aut	0.90	0.26	$a' = (b \times e)/(W_{opt}^{(d-e) \times d})$	Equation from Sebens (1982)
			Spr	1.76	0.55		
b	Cost coefficient	J/(day × mg DW)	Aut	0.081	0.019	$b = R \times (4.75\ \text{cal/ml}O_2)$	Calculation
			Spr	0.158	0.043		
d	Intake exponent	Unitless	All	0.69	0.01	Gill area = $(\text{len}^3)^d$	Jones et al. (1992) *M. edulis* (van der Veer et al., 2006–0.67)
E	Cost exponent	Unitless	All	1			van der Veer et al. (2006)
C.F.	Energetic conversion factor	J/mg DW	All	21.6	1.6		Table S1
Measured values used to calculate input parameters							
W_{opt}	Energetic optimum size	g DW	All	0.72	0.06	—	Unpublished data, E. Roberts
R	Respiration	ml O_2/hr	Aut	0.073	0.017	—	Fly and Hilbish (2013) (0.429 g DW in Autumn and 0.247 g DW in Spring)
			Spr	0.082	0.022	—	
*R*_g	Respiration	ml O_2/(hr × g DW)	Aut	0.170	0.040	*R*_g = *R*/g DW	Calculation
			Spr	0.332	0.089		
δ	Volumetric mass coefficient	mg DW/(cm^3)	Aut	8.2	0.3	Mass = $\delta \times (\text{length})^3$	This paper
			Spr	6.8	0.2		
Ratio	Conversion coefficient	mg WW/mg DW	All	3.98	0.07		This paper, separate sampling (n = 100)

equal for all mussels within each season since they were exposed to the same water mass. The energy intake exponent (*d*) is an allometric scaling factor for the relationship between tissue mass and gill area (the food capture surface for mussels), and has been well-described for *M. edulis* (Bayne & Newell, 1983; Jones et al., 1992; Table 1).

The metabolic cost of somatic and gonadal tissue for each experimental mussel is calculated as a function of initial tissue mass, $TM_{initial}$ (mg DW):

$$\text{cost}_{\text{non-byssus}} = b \times \text{TM}_{\text{initial}}^{e}, \quad (3)$$

where *b* is the mass-specific metabolic cost coefficient (J/mg^e) and *e* is the allometric cost exponent (unitless) that relates mass-specific metabolic cost and tissue mass. We assume that the cost relates directly to the amount of tissue (e = 1, Bayne et al., 1976), a value that has been shown to be well-conserved among bivalve species (Kooijman, 2010; Sarà et al., 2013), thus *b* has units of J/mg. *Mytilus* spp. respiration per unit tissue mass generally differs by season and follows reproductive cycles (Widdows, 1978), so *b* was determined from the spring and autumn measurements of mass-specific oxygen consumption of Fly and Hilbish (2013) for *M. trossulus* from WA. Respiration at 10°C was estimated from a linear regression of the respiration measurements from 5 to 20°C, and the standard error was estimated as the average standard error from each temperature: 0.170 ± 0.040 ml O_2/(hr × g DW) in autumn and 0.333 ± 0.089 ml O_2/(hr × g DW) in spring (Table 1). The spring and autumn values were then converted to daily values to yield the metabolic cost coefficient (*b*) for autumn (0.81 ± 0.019 J/mg) and spring (0.158 ± 0.043 J/mg; Table 1, Riisgård & Randløv, 1981).

The energy intake coefficient (a') is calculated as the average amount of food available over the course of the life span of a mussel to produce an individual of a given size, given optimal size theory (Table 1; Sebens, 2002):

$$a' = \frac{b \times e}{W_{\text{opt}}^{d-e} \times d}, \quad (4)$$

where W_{opt} is the energetic optimal size (mg DW), or the size at which the difference between intake and costs is maximized and the coefficients *b*, *d* and *e* are defined in Equations 2 and 3. By using this metric for the intake coefficient, we assume that mussels at their maximal size have a maximal surplus and that all surplus goes to reproduction rather than to growth. We assume a value of 720 ± 60 mg DW for W_{opt} (Roberts, 2019; Table 1). Note that the seasonal difference in respiration resulted in a reduced different metabolic cost coefficient and a

greater energy intake coefficient in spring compared to autumn (b and a', Table 1).

The cost of byssal thread production is calculated as the number of threads produced, N_{Th}, multiplied by the cost of each individual thread, h (J/thread):

$$\text{cost}_{\text{byssus}} = h \times N_{Th}. \quad (5)$$

Substituting the equations for intake (Equation 2), non-byssus cost (Equation 3) and byssus cost (Equation 5) into Equation 1 yields the following equation for SFG as a function of initial tissue mass and byssal thread production:

$$\text{SFG} = f \times a' \times \text{TM}_{\text{initial}}^{d} - b \times \text{TM}_{\text{initial}}^{e} - h \times N_{Th}. \quad (6)$$

This SFG model was then fit to the experimental tissue growth measurements using the two-step optimization method, described in the following sections.

2.4 | Tissue growth calculation

Mussel tissue growth is calculated as the difference between final and initial tissue dry weight, where final dry weight is measured directly and initial dry weight is estimated (because direct measurement is destructive). Specifically, an estimate of initial tissue mass ($\text{TM}_{\text{initial\_fit}}$, mg DW) is calculated from shell length ($\text{length}_{\text{initial}}$, cm) as follows:

$$\text{TM}_{\text{initial\_fit}} = \delta \times \text{length}_{\text{initial}}^{3}, \quad (7)$$

where δ is the shape coefficient (mg DW/cm^3) that relates length and tissue mass and is estimated from final length and tissue weight for each season (Table 1). We assumed that the exponent relating length and tissue mass is 3 (Kooijman, 2010) and confirmed this assumption with a separate sampling (see Supplementary Methods in Supporting Information). The residuals of the final tissue mass ($\text{TM}_{\text{residual}}$, mg DW) are calculated as the difference between the measured final tissue mass (TM_{final}) and the final tissue mass value estimated from the shell length:

$$\text{TM}_{\text{residual}} = \text{TM}_{\text{final}} - \delta \times \text{length}_{\text{final}}^{3}. \quad (8)$$

The residuals ($\text{TM}_{\text{residual}}$, mg DW) are added to the estimate of the initial tissue mass ($\text{TM}_{\text{initial\_fit}}$):

$$\text{TM}_{\text{initial\_g}} = \text{TM}_{\text{initial\_fit}} + \text{TM}_{\text{residual}}. \quad (9)$$

An additional independently determined value of initial dry tissue weight ($\text{TM}_{\text{initial}}$) was calculated from the relationship between dry tissue weight and buoyant weight in each season. This initial tissue mass estimate was used in the equations for intake and cost (Equations 2, 3 and 6).

2.5 | The cost of byssus estimation using a two-step optimization

We used the experimental data to calculate two parameters, h (cost per thread, J/thread) and f (food scalar, unitless), using a sequential linear regression. This optimization method minimized the difference between the measured tissue growth rate (G_{TM}, joules/day) and predicted tissue growth rate calculated as SFG from the initial tissue mass ($\text{TM}_{\text{initial}}$) and thread production (N_{Th}) for each individual, and allowed for an estimate of population error from the data.

Step 1 of the two-step optimization was a calculation of the cost per thread from the relationship between growth and thread production. If the production of N_{Th} byssal threads decreases growth, then the cost of thread production can be calculated from the slope of this relationship. In other words, energy that would have been used for growth had to be diverted to production of N_{Th} byssal threads. Specifically, the cost per thread (h, joules/thread) is estimated as the magnitude of the coefficient B_1 in a linear regression relating thread production (N_{Th}, threads/day) and tissue growth (G_{TM}, joules/day):

$$G_{\text{TM}} = B_0 + B_1 x + \in, \quad (10)$$

where x is the rate of thread production (N_{Th}, threads/day), the intercept, B_0, is excess, unaccounted for energy, and $\in$ is a random noise variable.

Step 2 of the two-step optimization estimated relative food availability (f, unitless) as the coefficient B_1 from a linear equation (Equation 10), where B_1 multiplied by $\times$ is now the intake (E, J/day), and the intercept, B_0, is the negative sum of byssal thread cost ($\text{cost}_{\text{byssus}}$, J/day) and metabolic cost ($\text{cost}_{\text{non-byssus}}$, J/day) for each individual mussel. In this step, the intercept, B_0 is calculated from costs and is not estimated from the linear regression. $\in$ remains as the random noise variable relating the predicted and observed growth values for each individual.

The proportion of the energy budget allocated to byssus (proportion of cost, unitless) is then calculated by dividing $\text{cost}_{\text{byssus}}$ by E for each individual mussel:

$$\text{proportion of cost} = \frac{\text{cost}_{\text{byssus}}}{\text{cost}_{\text{byssus}} + (\text{cost}_{\text{non-byssus}} \times P_{\text{Som}})}, \quad (11)$$

where P_{Som} is the proportion of the total tissue that is somatic tissue. A proportion of cost of 1 indicates that all costs are byssus costs, and proportion of cost of 0.5 indicates that byssus and somatic costs are equivalent.

2.6 | Statistical analysis

All statistical analyses and model calculations were performed with R software for Mac OSX (version 3.4, R Development Core Team, 2017). Data were transformed to normalize distributions; thread production (count data) was square root transformed, gonad index

(proportional data) was arcsine square root transformed, and shell growth, buoyant weight change, tissue growth and condition index (all continuous data) were log-transformed for statistical analyses. All transformed data met assumptions of equal variances, with the exception of tissue growth. For this metric, variance differed among seasons but not within each season, limiting comparisons between seasons. The effect of experimental byssal thread manipulation on thread production, shell length and weight, tissue growth, gonad index and condition index was evaluated for autumn and spring separately using one-way ANOVAs with thread severing frequency as fixed factor. We used two separate one-way ANOVAs for each season as a more conservative approach where we evaluated the experiments as two repeated manipulations that spanned the two seasons rather than evaluating differences between the two seasons. Additional statistical analyses that evaluated model assumptions about organismal traits are described in the Supporting Information Methods. These are the effect of initial tissue mass and byssal thread production on tissue growth (multiple regression), and the relationship between tissue growth and byssal thread production with treatment as a fixed factor (ANCOVA). If any significant effects were present, a post hoc Tukey test was performed to evaluate differences between groups. Preliminary analyses of the effect of byssal thread manipulation on the metrics listed above were performed using linear mixed models (LME; Zuur et al., 2009), and these analyses confirmed that the random effect of the enclosure was not significant so we did not include this random effect in further analyses(data not shown).

We ran the model parameter estimations as linear regressions in R where each parameter was estimated as the coefficient in a linear equation of all individual mussel samples within each season, separately (Equation 10, Methods Section 3.5). Model sensitivity to the parameters used to estimate the cost of producing byssal threads and the proportion of the energy budget used for thread production for each season was determined with an individual parameter perturbation (IPP) analysis (Kitchell et al., 1977) using the estimated standard error for each parameter. A sensitivity of 1.1 indicates that a change in parameter by 1 *SE* causes a resultant change in simulated cost by 10%. We used parameter standard error in place of a nominal 10% change in each parameter to perturb the model in order to simulate a more realistic range of parameter values.

3 | RESULTS

3.1 | Field manipulation of byssal thread production

Byssus severing increased thread production by a factor of 5 in both seasons (Figure 2; Table 2). The effect of greater byssus severing frequency significantly decreased shell growth by 50% in the autumn and 25% in spring ($p < 0.001$ and $p = 0.01$ respectively; Figure 2; Table 2). Byssus severing frequency significantly decreased buoyant weight growth in the autumn, but this effect was only marginal in the spring ($p = 0.002$ and $p = 0.11$ respectively; Figure 2; Table 2). Byssus severing frequency significantly decreased tissue growth by 70% in autumn and 45% in the spring ($p < 0.001$ and $p = 0.01$ respectively; Figure 2; Table 2). GSI was overall 30% greater in the spring compared to the autumn, but there was no significant effect of byssus severing frequency on gonad index for either season ($p = 0.7$ to 0.9; Figure 2; Table 2), probably because gonad tissue was a small proportion. Condition index did not differ significantly among treatments ($p = 0.2$–0.7; Figure 2; Table 2). Since none of the treatments resulted in mass loss, the relationship of shell to tissue did not change radically.

There was a significant negative relationship between thread production and tissue growth across all treatment groups in both autumn and spring ($p = 0.02$ and $p = 0.3$ respectively; Table S2), but no significant relationship between initial mass and tissue growth for either season ($p = 0.43$–0.67; Table S2), and no interaction between these two effects on tissue growth ($p = 0.21$–0.88; Table S2). While there was an overall negative relationship between thread production and tissue growth, this effect was driven by the byssus severing manipulation. The range of growth and thread production was greatest in the autumn, and in this season, there was a negative effect of byssus severing frequency on growth ($p = 0.007$; Figure S1; Table S3), but within each treatment there was an overall positive relationship between byssal thread production and growth ($p = 0.04$; Figure S1; Table S3). In the spring, there was a similar trend, but both effects were only marginally significant.

3.2 | Cost of byssal thread production

Tissue growth predicted by the model had a smaller range (15–42 mg DW) than observed growth (10–80 mg DW) in autumn and spring, and at least 90% of the predicted growth rates had a percent error relative to observed growth of <40% (Figure 3; Figure S3e,f). The cost of byssal thread production was similar between the two seasons, ranging 1.0–1.2 J per thread (Table 3). Relative food availability (*f*, unitless) was 40% higher in the autumn than in the spring (Table 3).

The mussel energy budget components (intake, somatic cost, gonadal cost, cost of byssus and growth), as determined by the two-step optimization, are represented across the range of byssal thread production rates for each season in Figure 4. The daily cost of byssus production was proportional to the number of threads produced, and the predicted growth rate decreased as thread production increased, as observed in our experiments.

Metabolic costs of somatic and gonadal tissue were two times greater in spring than in autumn (Table 1), and the proportion of the energy budget allocated towards byssal thread production was two to four times greater in the autumn (Figure 4; Table 4). The proportion of the energy budget allocated towards thread production for mussels induced to produce threads daily was six to 11 times greater than the control group (up to 47%, Table 4). Mussels induced

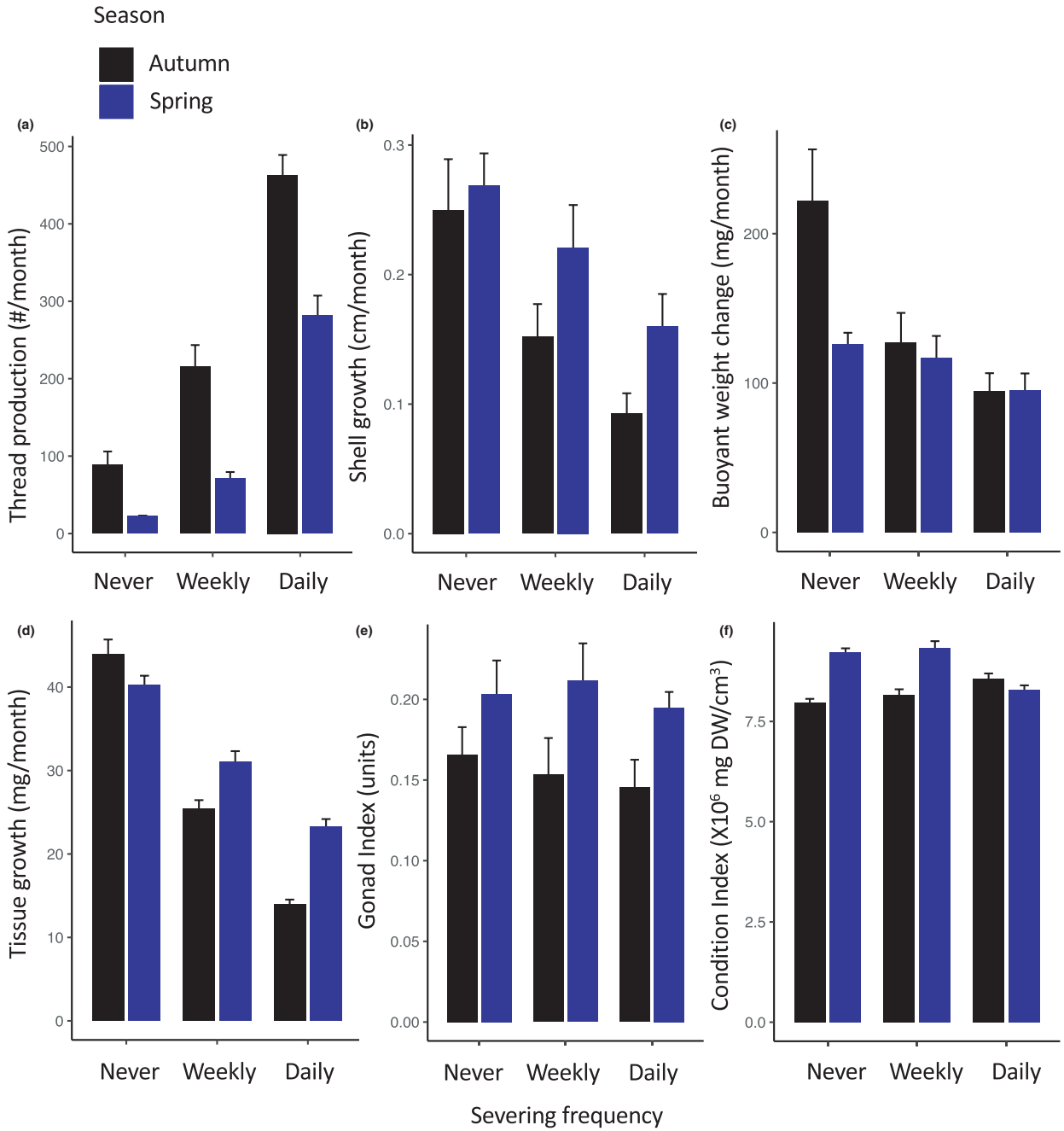

FIGURE 2 Summary of byssal thread production, growth and mussel condition across a range of byssus severing frequencies in autumn and spring. (a) Thread production, (b) shell growth, (c) buoyant weight change, (d) tissue dry weight growth, (e) final gonad index and (f) final condition index as a function of the frequency at which the byssus was severed in autumn (black bars) and spring (blue bars; means ± *SE*, $n = 15$ in autumn, $n = 11$–14 in spring). The byssus was severed at a range of frequencies: once at the start of the experiment ('never'), once per week ('weekly') and once per day ('daily'). The change in buoyant weight is the change in weight of the living mussel, inclusive of its shell

to produce threads daily also had a greater 'ramping up' of metabolism such that byssal costs were a greater percentage of total non-reproductive cost (41%–66%) than the control group (6%–24%, Table 4). The relationship between thread production and the proportion of non-reproductive costs going to thread production was nonlinear (Figure 5; Table S4). At greater thread production rates, the proportion of non-reproductive costs approached an asymptote of 50%–70%, and the byssal thread production rate that resulted in the half maximum cost was six to eight threads per day, depending on the season (Figure 5; Table S4).

3.3 | Model sensitivity analysis

The IPP analysis demonstrated that increasing the energetic conversion factor (C.F.) by 1 *SE* increased the cost per thread

TABLE 2 Summary of one-way ANOVAs evaluating the fixed effect of byssus severing frequency on byssal thread production, shell growth, buoyant weight change, tissue growth, final gonad index and final condition index. The autumn and spring manipulations were analysed separately. Bold font indicates a significant effect ($p > 0.05$) and pairwise comparisons (Tukey's HSD) identified significant differences between groups

		Thread production (#/week)				Shell growth length (mm)				Buoyant weight change (mg)			
Season	**Effect**	**SS**	***df***	***F* val.**	***p***	**SS**	***df***	***F* val.**	***p***	**SS**	***df***	***F* val.**	***p***
Autumn	Frequency	1,181	2	64.89	**<0.001**	0.02	2	8.74	**<0.001**	0.02	2	7.09	**0.002**
	Residuals	364	40			0.06	42			0.1	42		
	Freq.			**Group**				**Group**				**Group**	
Tukey's HSD	Never			a				a				a	
	Weekly			b				a				ab	
	Daily			c				b				b	
		Tissue growth (g)				**Gonad index (g DW/g DW)**				**Condition index (g DW/g DW)**			
Season	**Effect**	**SS**	***df***	***F* val.**	***p***	**SS**	***df***	***F* val.**	***p***	**SS**	***df***	***F* val.**	***p***
Autumn	Frequency	0.02	2	10.65	**<0.001**	0.01	2.00	0.35	0.70	0.03	2	0.33	0.72
	Residuals	0.05	42			0.4	40.0			1.8	42		
	Freq.			**Group**				**Group**				**Group**	
Tukey's HSD	Never			a				—				—	
	Weekly			a				—				—	
	Daily			b				—				—	
		Thread production (#/week)				**Shell growth length (mm)**				**Buoyant weight change (mg)**			
Season	**Effect**	**SS**	***df***	***F* val.**	***p***	**SS**	***df***	***F* val.**	***p***	**SS**	***df***	***F* val.**	***p***
Spring	Frequency	934	2	123.3	**<0.001**	0.01	2	4.90	**0.01**	0.001	2	2.34	0.11
	Residuals	132	35			0.04	35			0.008	35		
	Freq.			**Group**				**Group**				**Group**	
Tukey's HSD	Never			a				a				—	
	Weekly			b				ab				—	
	Daily			c				b				—	
		Tissue growth (g)				**Gonad index (g DW/g DW)**				**Condition index (g DW/g DW)**			
Season	**Effect**	**SS**	***df***	***F* val.**	***p***	**SS**	***df***	***F* val.**	***p***	**SS**	***df***	***F* val.**	***p***
Spring	Frequency	0.01	2	5.36	**0.01**	0.00	2	0.09	0.92	0.10	2	1.84	0.17
	Residuals	0.02	35			0.3	35			1.0	35		
	Freq.			**Group**				**Group**				**Group**	
Tukey's HSD	Never			a				—				—	
	Weekly			ab				—				—	
	Daily			b				—				—	

(*h*) estimate by 10%, and the error introduced by variability in the data was greater than the error introduced by the SE of the conversion factor (C.F.) in both seasons (36% in autumn, 34% in spring; Figure S2). The cost per byssal thread was independent of the parameter values of *b* and *d* (Figure S2; Equation 10).

Both of the byssus energy allocation metrics, the proportion of the energy budget allocated towards thread production and the proportion of cost allocated towards byssus (excluding reproductive costs), were sensitive to changes to *b* and C.F., and neither measure was more than marginally sensitive to *d*. The population error of the proportion of cost allocated towards byssus also differed by

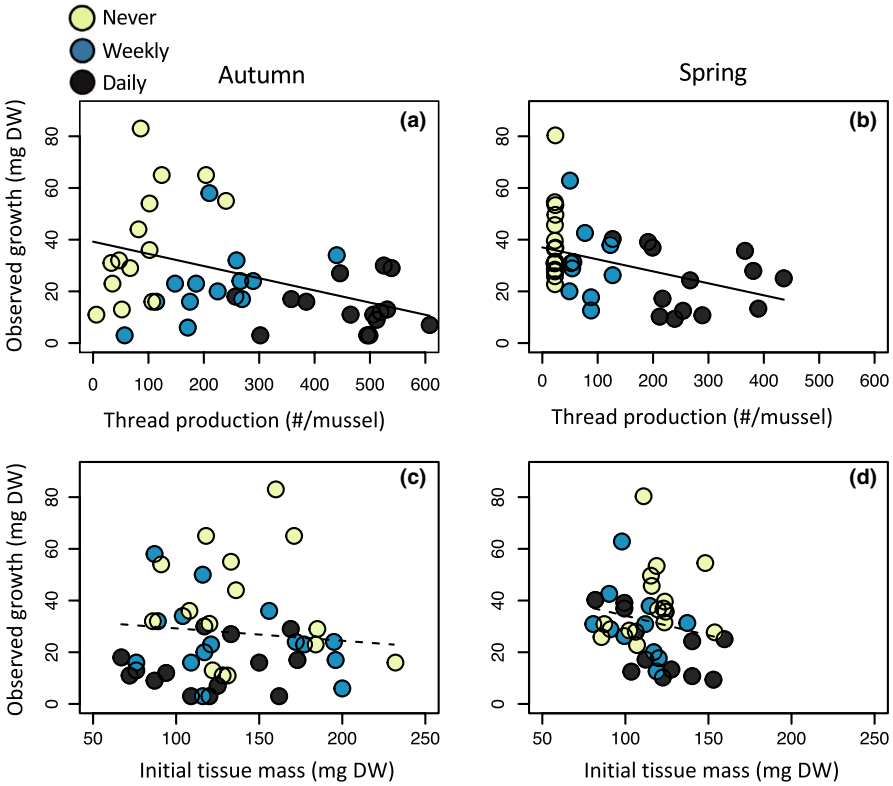

FIGURE 3 Mussel tissue growth as a function of thread production and initial tissue mass. Tissue growth as a function of (a, b) thread production and (c, d) estimated initial tissue mass in the autumn and spring. Symbols represent individual mussels in different severing frequency treatments (see inset for colour scheme) and data were pooled across treatments for regression analyses. There was a significant negative relationship between thread production and tissue growth (a, b), but not initial tissue mass in both seasons (c, d; Table S2). Observed growth (mg DW) divided by the energetic conversion factor (C.F.) is G_{TM}

TABLE 3 Summary of parameter estimations of the cost per thread (*h*) and the food scalar (*f*) using the two-step optimization for the autumn and spring datasets. Bolded statistical values indicate statistical significance

	Cost per thread (*h*; J/thread)		Food scalar (*f*, Proportion)	
Season	**Estimate ± *SE***	***p***	**Estimate ± *SE***	***p***
Autumn	1.01 ± 0.37	**0.01**	1.42 ± 0.09	**<0.001**
Spring	1.16 ± 0.39	**0.005**	1.00 ± 0.04	**<0.001**

treatment and was greatest for the control group that was never severed in the autumn (Figure S2). The error introduced by changing *b* by 1 *SE* was often similar to the magnitude of the population standard error (Figure S2). W_{opt} had no effect on these three model outputs in either season.

4 | DISCUSSION

4.1 | The cost of byssus as a component of a SFG framework

The 2-month-long experiments demonstrated that clipping byssal threads greatly increased byssus production and significantly decreased growth. This trade-off is consistent with reports of constitutive byssal thread production regardless of growth rate or energetic input (Clarke, 1999; Hawkins & Bayne, 1985; Roberts, 2019), depending on mussel size or glycogen reserve depletion (Babarro et al., 2008; Babarro & Reiriz, 2010). This result supports the concept that energy allocation is prioritized towards production of byssal threads over growth (Clarke, 1999), and that this trade-off is a fitness strategy that minimizes the risk of dislodgement and can maximize overall fitness (Sebens et al., 2018). Mussels that allocate too little energy to byssus production face an increased risk of dislodgement and mortality, those that allocate too much energy experience reduced growth and reproduction. Determining the optimum allocation requires a model that estimates population increase based on changes in life history, energy allocation and environmental conditions (Carrington et al., 2015).

Using this demonstrated trade-off between byssus production and growth, we were able to quantify the energetic costs associated with producing byssus (~1 J/thread). Mussels in the control group, where byssus was severed only once at the start of the experiment, produced fewer threads, and allocated 2%–8% of the energy budget towards threads. These results are consistent with previous estimates of up to 8% of each of the carbon and nitrogen budgets (Hawkins & Bayne, 1985), and consistent with an approximate 10% increase in respiration reported during periods of thread production (Lurman et al., 2013). In contrast, severing byssus daily stimulated byssal thread production and increased energy allocation to byssus six to 11-fold, such that the byssus represented 41%–66% of the total non-reproductive energetic costs.

Baseline byssal thread production rates measured in this experiment were likely lower than in rocky shore habitats. The experimental mussels were within a protected enclosure under a dock, without predators or wave forces, but were flushed by

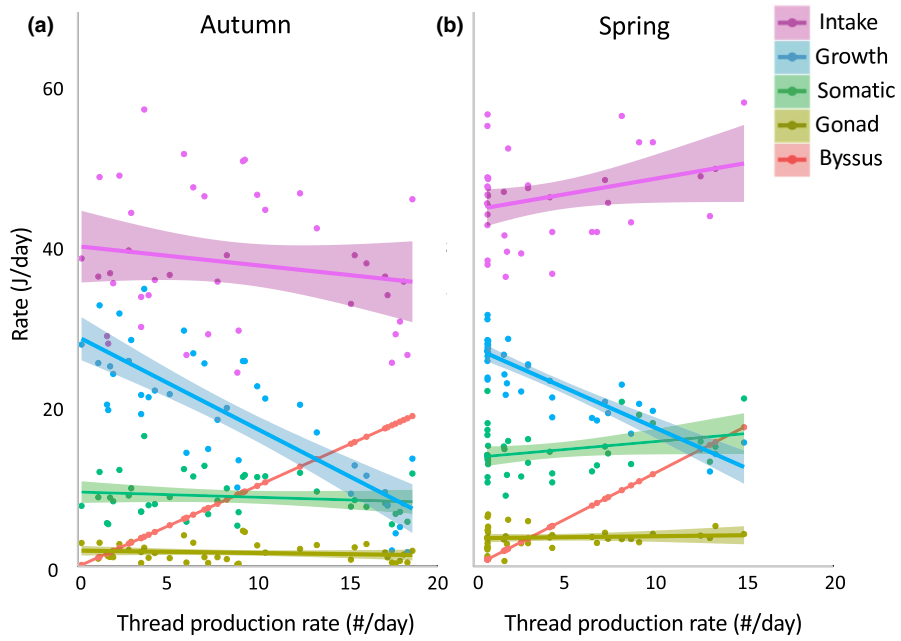

FIGURE 4 Model results for all components of a mussel's energy budget (J per day) as a function of byssal thread production rate (threads per day). Model results are presented for autumn (a) and spring (b) as determined by the two-step optimization. Circles represent calculated values of budget components (see inset for colour scheme) for each individual; lines are linear regressions ± 95% confidence intervals. Byssus production cost does not deviate from the regression line because it is calculated as directly proportional to the thread production rate measured during the experiment. Growth (blue) represents the SFG value determined for each mussel. Somatic (green) is the maintenance cost for somatic tissue, and Gonad (yellow) is the maintenance cost for gonad during this time period

TABLE 4 Summary of model outputs estimating energy budget allocations to producing byssus. Energy allocation to byssus as a proportion of the energy budget and as a proportion of metabolic cost (excluding reproductive tissue maintenance costs), for each of the byssal thread production treatments in the two field manipulations

	Autumn		Spring	
Treatment	**Estimate**	***SE***	**Estimate**	***SE***
Proportion of energy budget				
Never	0.08	0.01	0.02	0.001
Weekly	0.20	0.03	0.07	0.01
Daily	0.47	0.04	0.23	0.02
Proportion of cost				
Never	0.24	0.03	0.06	0.003
Weekly	0.44	0.04	0.18	0.02
Daily	0.66	0.02	0.41	0.02

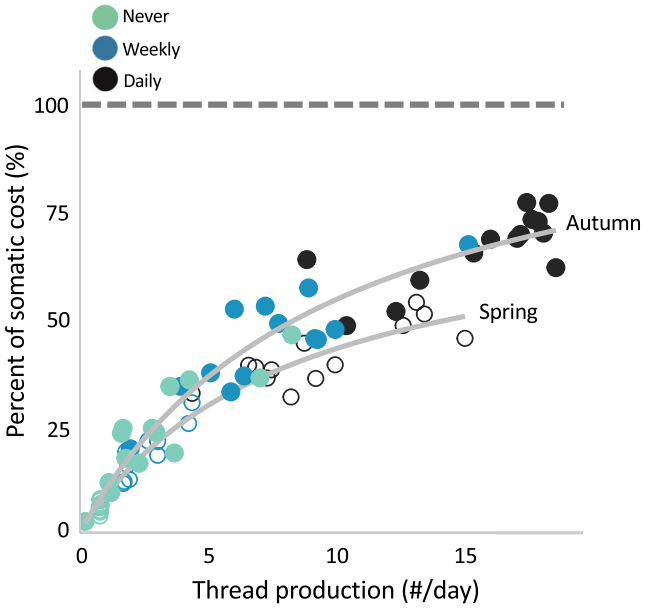

FIGURE 5 Energy allocation towards byssal threads, expressed as a proportion of metabolic costs of tissue maintenance (excluding reproductive costs), as a function of thread production in the autumn (closed circles) and spring (open circles). Symbol colours represent the frequency of severing in the treatment. Each curve is an exponential fit (proportion of cost $= V_{max}\left(1 - e^{\frac{-N_{Th}}{\tau}}\right)$, Table S4)

currents. Additionally, mussels that had the byssus severed at the lowest frequency ('never') were also tethered away from substrate to minimize byssal thread production. In natural wave-swept environments, greater hydrodynamic forces induce mussels to produce more byssus (Bell & Gosline, 1997; Carrington et al., 2008; Dolmer & Svane, 1994; Lee et al., 1990; Moeser et al., 2006; Van Winkle, 1970; Young, 1985), and high tide-pool temperatures can induce mussels to move to another location by sloughing off previous threads and producing more threads (Schneider et al., 2005). Predator cues can also induce thread production (*Mytilus edulis*—Garner & Litvaitis, 2013; *Ischadium recurvum*—Brown et al., 2011), and byssal thread production is greater at sites with high predation than at those with low predation risk (Leonard et al., 1999). Unsuccessful predation might

also cause thread breakage, and thus increase the production rate of new threads. Conditions that cause or require greater thread production can increase the cost of byssus to values high enough to equal the entire energy surplus (i.e. >50%) and limit growth or reproduction entirely. In contrast, stressful conditions that limit the production of threads, such as low pH conditions where mussels remain closed, might limit investment in thread production (George et al., 2019).

A lower proportion of energy was allocated towards byssus in spring than in autumn, reflecting both a lower byssal thread production rate and ~two times greater mass-specific respiration costs in this season (Fly & Hilbish, 2013). *Mytilus trossulus* matures and spawns in spring (Skidmore, 1983) and periods of spawning can decrease thread production (Babarro & Reiriz, 2010); byssus attachment strength decreases following seasonal reproductive periods (Carrington, 2002; Zardi et al., 2007). Greater spring mass-specific respiration costs likely reflect greater reproductive costs. For the congener species, *M. edulis*, mass-specific respiration costs are ~two times greater in the spring, corresponding to an increased reproductive status (Widdows, 1978).

Overall, increased severing frequency caused a significant decrease in growth (Table 2), and, overall, there was a trade-off between byssal thread production and growth when treatments were pooled (Table S2). After accounting for the effect of experimental treatment on growth, however, there was a significant positive relationship between thread production and growth in autumn but not in spring (Figure S1; Table S3). Within the same experimental population, variability in growth among individuals can depend on intrinsic genetic variance in growth trajectories (Dmitriew, 2011), size-specific intake and metabolic costs (Martin et al., 2012), and extrinsic factors such as microscale differences in flow and food availability (Denny & Gaylord, 2010). Although all mussels in these experiments were exposed to the same food concentration (within a season), genetic variation in food uptake (Dmitriew, 2011), individual mussel behaviour (gape, closure, pumping; Miller & Dowd, 2019) and the location of mussels in the cages might differ. The resulting variability in food intake could account for a range of growth rates among individuals in this study. On the one hand, these results support the hypothesis that both thread production and growth could be positively correlated across a broad range of energetic surplus, if individuals with increased growth also have greater resources with which to produce byssal threads (Roberts, 2019). On the other hand, however, when a large proportion of the energy budget is allocated towards byssal thread production, in this case induced by a greater severing frequency, there is a strong negative trade-off.

4.2 | Model sensitivity analysis and model limitations

Traditionally, sensitivity analyses (i.e. IPP) have been used to characterize the sensitivity of model results to a nominal change (i.e. 10%) in parameter values (Kitchell et al., 1977; Monaco et al., 2014; Sanders et al., 2018). Our sensitivity analysis compared population error due to variability among individuals to the influence of the error introduced by uncertainty in parameter values. The cost per byssal thread calculation was sensitive to the energy conversion factor (C.F., J/mg DW; Figure S2), the energy required to produce one unit of tissue mass. The value used for this parameter was consistent with SFG methodology (e.g. Sanders et al., 2018, caloric density of tissue), but this value differs depending on the bioenergetics theory employed (Kooijman, 2010; Rumohr et al., 1987, Table S1). A lower caloric density of the tissue would decrease the magnitude of the calculated energy budget and magnitude of the individual thread costs (Figure S2). The energy required to produce tissue mass includes both the overhead energy consumed in anabolism and catabolism as well as the cost (stored energy) of the building blocks of mass in the organism. We used the simplifying assumption that the energy required for growth is proportional to the change in mass and that mass and energy can thus be interconverted (e.g. DEB theory—Kooijman, 2010), but ultimately both energy and mass are required for growth. Further, mussel shell calcification is estimated to range between 30% and 60% of the energy budget for Baltic *M. trossulus* with the greatest cost at lower salinities (6–16 psu, Sanders et al., 2018). Salinities remained high (~30 psu) during this experiment, and thus calcification costs may be lower than estimated by Sanders et al. (2018). Previously, the cost of shell has been attributed solely to the cost of producing shell organic matrix. Not accounting for energy expenditure to the production of inorganic substance is a limitation of many energy budget models. Similarly, SFG models that do not account for the cost of byssus may overestimate the fractional contributions of other components of the organism relative to all energy assimilated (e.g. shell). The utility of a simple model, however, in answering a specific research question should not be minimized, especially when contributions of overhead costs are not known with much certainty.

Uncertainty in respiration and the resulting metabolic cost coefficient, *b*, contributed substantially to our uncertainty of our calculation of the proportion of the energy budget allocated towards thread production (Figure S2; Table 2). Respiration is variable even within individuals of the same population at the same temperature (Fly & Hilbish, 2013; Sanders et al., 2018), suggesting that the contribution of the uncertainty of respiration to energy budget calculations should be carefully considered (Boersch-Supan & Johnson, 2019). We used published respiration values for *M. trossulus* in the same season from the same site estimated for the environmental seawater temperature using a linear fit (10°C, Fly & Hilbish, 2013; Figure S4). These published respiration values were for smaller mussels than those in our experiments, so respiration values were scaled according to size (spring 0.25 g, autumn 0.47 g Fly & Hilbish, 2013; Table 1). We make the simplifying assumption that the cost of threads is not included in published respiration values (Fly & Hilbish, 2013), though thread production and feeding may increase respiration (Lurman et al., 2013). We assumed that respiration scaled linearly

with tissue mass (e = 1), based on the theory that maintenance costs scale with the volume of the individual (Kooijman, 2010; Sarà et al., 2013), but given empirical evidence from other organisms (Metabolic Theory of Ecology; Brown et al., 2004), this exponent is likely <1 (0.75 for *M. edulis*, Widdows, 1987). This model evaluated a 'snapshot' of growth for one size class (2–3 cm, juvenile mussels) over just 1 month. Within this small size range, we observed no significant relationship between mass and the actual observed growth (Figure 3; Table S2) but a positive relationship between the mass and predicted scope for growth (Figure S3). Investigations that include a wider range of organism sizes may more fully capture the relationship between SFG and mass for this species. Moreover, size can act as a confounding factor under conditions of stress, and it is possible that size could have affected the trade-off between size and thread production even within the small size range of our experiment. Experiments with a wider range of sizes would give a clearer picture of how an energetic trade-off to byssus is affected by mussel size. Smaller juvenile mussels can produce a greater number of threads than larger adults (30 vs. 90 mm *M. galloprovincialis*, Babarro et al., 2008), so adult mussels might have a lower energetic investment in thread production. Further, experiments performed over the longer term (>1 month) could elucidate the effect of byssus severing on mussel condition, which might reflect unequal energy allocation to volumetric size and tissue mass.

According to our model, intake (E) was 33% greater in spring than autumn, reflecting the magnitude of f multiplied by a'. In spring, the greater intake counteracted greater mass-specific respiration costs when compared to autumn experiments (Fly & Hilbish, 2013). Phytoplankton blooms often occur in the spring in the Salish Sea (Lowe et al., 2016; Murray et al., 2015). The congener species, *M. edulis*, depends on a nutrient reserve during and after spawning (Gabbott, 1976), and across US East Coast latitudinal gradients, spawning corresponds with the timing of greater nutrition for adults and larvae, rather than temperature cues (Newell et al., 1982). In bioenergetics models, the relative food availability, f, is typically estimated for each site from the data and site differences are attributed to differing food quality (DEB, Kooijman, 2010). Our energetics model demonstrates that if parameters (e.g. metabolic cost, the shape coefficient) are not temporally or spatially explicit (e.g. measured for each season and/or population), the explanatory power of the model may be limited if it does not account for these differences (non-stationarity; Monaco & McQuaid, 2018, Monaco et al., 2019). We demonstrated the use of optimal size theory to calculate a scalar for lifetime average intake, a', representing lifetime average food consumption necessary to arrive at an asymptotic (maximal) size typical for the environment they were grown in (Sebens, 1982, 1987, 2002). The value obtained for a' differed by season, reflecting different assumptions about lifetime metabolic costs, given differing measurements of respiration, in each season (Sebens, 1982, 1987, 2002). In other words, to achieve a specific asymptotic size, the average value of a' during growth to that size can be calculated even when actual food availability is not known.

4.3 | Consequences in rocky shore systems and mussel aquaculture

An understanding of the energetics of byssal thread attachment has potential consequences in rocky shore systems, mussel aquaculture and in how we conceptualize the effects of climate change on mussels. Our findings of a trade-off between byssal thread production and growth suggest that dynamic changes in byssal thread production may impact mussel condition and growth in the field, consistent with the reciprocal transplant studies Babarro and Carrington (2011) with *M. galloprovincialis*. Decreased SFG might be a disadvantage if mussels do not grow fast enough to escape predation, if feeding or energetic reserves are limited by size, or if mussel energetic investment in reproduction is limited. There may be an advantage to staying small, however, when flow forces are limiting. Small mussels experience lower drag forces, and mussels that stay small could have a lower risk of becoming dislodged (Bell & Gosline, 1997). Further, in exposed environments, there are often fewer predators that might selectively consume smaller prey, and so it is possible that size escape from predation may be less necessary for survival in more wave-exposed environments. The formation of aggregated mussel beds may decrease hydrodynamic forces on a local scale (Carrington et al., 2008), and solitary mussels can produce more threads than those in an aggregation (Bell & Gosline, 1997; Carrington et al., 2008). Greater mussel bed density may also decrease food availability and feeding (Frechette et al., 1992), and increase the likelihood of low pH and DO conditions within an aggregation of mussels (George et al., 2019), suggesting there are ecological trade-offs to forming densely aggregated mussel beds that may mirror these organismal physiological trade-offs.

An understanding of the energetics of byssal thread attachment also has implications for mussel aquaculture practices. Mussels grown in suspension culture are often redistributed, or 'resocked', to reduce line density and competition for food (Gosling, 1992; Korringa, 1976). This practice presents a trade-off between inducing greater byssus production costs, with potentially more food, and either increased or decreased growth or survival (Roberts, 2019). Energetic limitations can thus inform mussel culture practices; redistribution of *M. trossulus* might be more successful in seasons with reduced mass-specific respiration and reproductive costs (i.e. not during the spring), or prior to stressful periods when costs are high, either due to reproduction (spring) or due to microscale low pH and DO due to respiration within mussel aggregations (late summer, George et al., 2019).

Mytilus spp. occur in coastal ecosystems and aquaculture farms globally (Gosling, 1992) and thus a promising direction for future work is to evaluate physiological trade-offs of byssal thread production costs in the context of climate change. Our expanded framework of organismal energy allocation, inclusive of byssus costs, may be used to develop new hypotheses of cascading effects of local and global anthropogenic changes on organismal processes, growth, reproduction and species distributions (SFG—Fly

et al., 2015). On the US west coast, buoy observations indicate that wave heights have increased 0.03 m/year (Allan & Komar, 2006). Climate change is expected to increase US west coast storm surge (Cheng et al., 2015) and wave heights in high-latitude coastal ecosystems around the globe (Semedo et al., 2013), which might directly lead to dislodgement and/or increase byssal thread costs and decrease growth. In our study region, ocean-estuarine circulation models predict ocean warming and acidification will be +1.5 C, pH −0.18, in year 2095 relative to year 2000 (Salish Sea, RCP8.5 scenario; Khangaonkar et al., 2019). Local pH and oxygen conditions within mussel conglomerates experience intermittent declines in summer to levels that strongly affect byssal thread production and attachment strength (pH of 5, George et al., 2019). Under these conditions, mussel stay can closed for multiple days, limiting byssal thread production (George et al., 2019). In the short term, greater seawater temperatures may decrease thread production (Newcomb et al., 2019), potentially affecting byssus cost and SFG, but long-term exposure to greater temperatures may not affect the number of byssal threads produced (Roberts, 2019).

Our work also suggests that a dynamic cost of byssus may compound or counteract the effects of climate change on intake or non-byssus costs. Warming in this region will likely decrease energetic resources available for growth for *M. trossulus* (Roberts, 2019), by lowering intake rates and increasing metabolic costs for this species (Fly & Hilbish, 2013). In contrast, for the non-native mussel species present in this region, laboratory experiments suggest that ocean warming will increase growth (Roberts, 2019) and SFG (Fly & Hilbish, 2013), potentially leading to changes in the distribution of these two competitor species in the region (Elliott et al., 2008). In the N.E. Atlantic, SFG models predict that ocean warming will cause range shifts (*M. edulis*—Fly et al., 2015). The effect of ocean warming on phytoplankton, the primary food source for bivalves, however, differs by region (Dunstan et al., 2018). In the Salish Sea, phytoplankton biomass may increase (Lowe et al., 2016, ~23%—Khangaonkar et al., 2019). While greater food availability might ameliorate negative effects of climate change on SFG, this 'buffering' effect would depend on the capacity of organisms to feed, which is a function of temperature.

We manipulated the production of a structural material to evaluate the trade-off between its production and growth and used an energetics model to evaluate the energetic cost of variable structural material production. There can be an energetic cost of many traits that exhibit phenotypic plasticity (Padilla & Savedo, 2013), and our approach may be applied to other inducible structural traits. Examples include organisms with inducible defences, such as herbivore-induced thorn production (Young, 1987) and predator cue-induced shell thickening (Brookes & Rochette, 2007). Phenotypic plasticity of structural materials can also occur as a result of environmental conditions such as wind exposure and trees, where some trees allocate energy to development and thickening of structural roots in response to wind gust direction (Nicoll & Dunn, 2000) and altered development due to wind exposure can reduce plant size and fecundity (Chehab et al., 2008; Telewski & Pruyn, 1998). Energetics models can include thermal performance curves and additional energy allocation 'compartments' such as energetic reserve as part of the model framework (Kitchell, 1977, Kooijman, 2010). Such mechanistic models that incorporate energy allocation to structural material production and other functional traits may be used to address specific research questions relating to energetic trade-offs between functional traits and organism growth in the context of environmental variability and change.

In summary, this study showed that the cost of producing byssal threads ranged from 2% to 47% of the energy budget depending on season and thread production rate, and that allocation of energy to byssus was 6%–66% of somatic metabolic costs. Further, this study demonstrated a methodology for quantifying the costs associated with producing a structural biomaterial by manipulating its production. This general approach can be applied to other organisms with inducible biomaterial production to evaluate the energetic cost of producing these structures. Energetic constraints from decreased food availability or greater metabolic costs at greater temperatures (Bennett & Lenski, 2007) could also strengthen the trade-off between biomaterial production and growth, affecting the degree to which structural biomaterials necessary for survival are prioritized by organisms over other processes (Koehl, 1996; Walker, 2007). Future work demonstrating the effect of energetic limitations on functional trade-offs will be needed to increase our understanding of adaptive evolution of structural materials, and to inform improved practices for natural resource management and conservation.

ACKNOWLEDGEMENTS

The authors thank Timothy Essington, Lauren Buckley, Jaqueline Padilla-Gamiño, Dave Beauchamp, Hilary Hayford and Lyda Harris for insightful discussions that improved the quality of this manuscript. They also thank Alex Lowe, Megan Dethier and Kevin Turner for their involvement in the experiments. E.A.R. was supported by a National Science Foundation IGERT Program on Ocean Change Fellowship (1068839), and several grants from UW Friday Harbor Laboratories and UW Biology (Edmondson Award, Richard and Megumi Strathmann Fellowship, Kohn Fellowship and Carrington Student Travel Fellowship). Additional support was provided by the National Sea Grant College Program, National Oceanic and Atmospheric Administration, US Department of Commerce, under project number NA14OAR4170078 (to EC and CS Friedman) through the Washington Sea Grant Program. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. The US government is authorized to reproduce and distribute this paper for governmental purposes.

AUTHORS' CONTRIBUTIONS

K.P.S. and E.C. conceived the ideas and designed the experiments; E.A.R. and K.P.S. designed the mathematical model; L.A.N., M.M.M., K.J.H. and S.A.L. collected the data; E.A.R. analysed the data and led the writing of the manuscript; E.C. and K.P.S. contributed critically to manuscript drafts, and all the authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.612jm641f (Roberts et al., 2021).

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REFERENCES

Allan, J. C., & Komar, P. D. (2006). Climate controls on US West Coast erosion processes. *Journal of Coastal Research*, *22*, 511–529. https://doi.org/10.2112/03-0108.1

Babarro, J. M. F., & Carrington, E. (2011). Byssus secretion of *Mytilus galloprovincialis*: Effect of site at macro- and micro-geographical scales within Ría de Vigo (NW Spain). *Marine Ecology Progress Series*, *435*, 125–140. https://doi.org/10.3354/meps09200

Babarro, J. M. F., Fernández Reiriz, M. J., & Labarta, U. (2008). Secretion of byssal threads and attachment strength of *Mytilus galloprovincialis*: The influence of size and food availability. *Journal of Marine Biological Association of the United Kingdom*, *88*, 783–791. https://doi.org/10.1017/S0025315408001367

Babarro, J. M., & Reiriz, M. J. (2010). Secretion of byssal threads in *Mytilus galloprovincialis*: Quantitative and qualitative values after spawning stress. *Journal of Comparative Physiology B*, *180*, 95–104. https://doi.org/10.1007/s00360-009-0392-y

Bayne, B. L., & Newell, R. C. (1983). Physiological energetics of marine molluscs. In K. M. Wilbur & A. S. M. Salenddin (Eds.), *The Mollusca*, Vol 4. Physiology, Part 1. Cambridge, MA (pp. 407–515). Academic Press. https://doi.org/10.1016/C2013-0-11705-9

Bayne, B. L., Thompson, R. J., & Widdows, J. (1976). Physology 1. In B. L. Bayne (Ed.), *Marine mussels: Their ecology and physiology* (Vol. 10, pp. 262–292). Cambridge University Press.

Bell, E. C., & Gosline, J. M. (1996). Mechanical design of mussel byssus: Material yield enhances attachment strength. *Journal of Experimental Biology*, *199*, 1005–1017.JEB0249.

Bell, E. C., & Gosline, J. M. (1997). Strategies for life in flow: Tenacity, morphometry, and probability of dislodgment of two *Mytilus* species. *Marine Ecology Progress Series*, *159*, 197–208. https://doi.org/10.3354/meps159197

Bennett, A. F., & Lenski, R. E. (2007). An experimental test of evolutionary trade-offs during temperature adaptation. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 8649–8654. https://doi.org/10.1073/pnas.0702117104

Boersch-Supan, P. H., & Johnson, L. R. (2019). Two case studies detailing Bayesian parameter inference for dynamic energy budget models. *Journal of Sea Research*, *143*, 57–69. https://doi.org/10.1016/j.seares.2018.07.014

Bonte, D., Verduyn, L., & Braeckman, B. P. (2016). Life history trade-offs imposed by dragline use in two money spiders. *Journal of Experimental Biology*, *219*, 26–30. https://doi.org/10.1242/jeb.132191

Borthagaray, A. I., & Carranza, A. (2007). Mussels as ecosystem engineers: Their contribution to species richness in a rocky littoral community. *Acta Oecologica*, *31*(3), 243–250. https://doi.org/10.1016/j.actao.2006.10.008

Brenner, M., & Buck, B. H. (2010). Attachment properties of blue mussel (*Mytilus edulis* L.) byssus threads on culture-based artificial collector substrates. *Aquacultural Engineering*, *42*, 128–139. https://doi.org/10.1016/j.aquaeng.2010.02.001

Brody, S. (1945). Energetic efficiencies of growth and work processes. In *Bioenergetics and growth with special reference to the efficiency complex in domestic animals* (pp. 37–58). Hafner Publishing Company Inc.

Brookes, J. I., & Rochette, R. (2007). Mechanism of a plastic phenotypic response: Predator-induced shell thickening in the intertidal gastropod *Littorina obtusata*. *Journal of Evolutionary Biology*, *20*(3), 1015–1027. https://doi.org/10.1111/j.1420-9101.2007.01299.x

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789. https://doi.org/10.1890/03-9000

Brown, K. M., Aronhime, B., & Wang, X. (2011). Predatory blue crabs induce byssal thread production in hooked mussels. *Invertebrate Biology*, *130*, 43–48. https://doi.org/10.1111/j.1744-7410.2011.00223.x

Carrington, E. (2002). Seasonal variation in the attachment strength of blue mussels: Causes and consequences. *Limnology and Oceanography*, *47*, 1723–1733. https://doi.org/10.4319/lo.2002.47.6.1723

Carrington, E. (2019). *UW FHL Temperature & Salinity data taken at Friday Harbor, WA between January 1, 2010 and January 1, 2016*. Biological and Chemical Oceanography Data Management Office (BCO-DMO). Version Date 2019-08-20. https://doi.org/10.1575/1912/bco-dmo.775732

Carrington, E., Moeser, G. M., Thompson, S. B., Coutts, L. C., & Craig, C. A. (2008). Mussel attachment on rocky shores: The effect of flow on byssus production. *Integrative and Comparative Biology*, *48*(6), 801–807. https://doi.org/10.1093/icb/icn078

Carrington, E., Waite, J. H., Sará, G., & Sebens, K. P. (2015). Mussels as a model system for integrative ecomechanics. *Annual Review of Marine Science*, *7*, 443–469. https://doi.org/10.1146/annurev-marine-010213-135049

Chehab, E. W., Eich, E., & Braam, J. (2008). Thigmomorphogenesis: A complex plant response to mechano-stimulation. *Journal of Experimental Botany*, *60*, 43–56. https://doi.org/10.1093/jxb/ern315

Cheng, T. K., Hill, D. F., Beamer, J., & García-Medina, G. (2015). Climate change impacts on wave and surge processes in a Pacific Northwest (USA) estuary. *Journal of Geophysical Research: Oceans*, *120*, 182–200. https://doi.org/10.1002/2014JC010268

Clarke, M. (1999). The effect of food availability on byssogenesis by the zebra mussel (*Dreissena polymorpha* Pallas). *Journal of Molluscan Studies*, *65*, 327–333. https://doi.org/10.1093/mollus/65.3.327

Crofts, S. B., & Anderson, P. S. (2018). The influence of cactus spine surface structure on puncture performance and anchoring ability is tuned for ecology. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 20182280. https://doi.org/10.1098/rspb.2018.2280

Crosby, M. P., & Gale, L. D. (1990). A review and evaluation of bivalve condition index methodologies with a suggested standard method. *Journal of Shellfish Research*, *9*, 233–237.

Denny, M. (1995). Predicting physical disturbance: Mechanistic approaches to the study of survivorship on wave-swept shores. *Ecological Monographs*, *65*, 371–418. https://doi.org/10.2307/2963496

Denny, M. W., & Gaylord, B. (2010). Marine ecomechanics. *Annual Review of Marine Science*, *2*, 89–114. https://doi.org/10.1146/annurev-marine-120308-081011

Dmitriew, C. M. (2011). The evolution of growth trajectories: What limits growth rate? *Biological Reviews*, *86*, 97–116. https://doi.org/10.1111/j.1469-185X.2010.00136.x

Dolmer, P., & Svane, I. (1994). Attachment and orientation of *Mytilus edulis* L. in flowing water. *Ophelia*, *40*, 63–74. https://doi.org/10.1080/00785326.1994.10429551

Dunstan, P. K., Foster, S. D., King, E., Risbey, J., O'Kane, T. J., Monselesan, D., Hobday, A. J., Hartog, J. R., & Thompson, P. A. (2018). Global patterns of change and variation in sea surface temperature and chlorophyll a. *Scientific Reports*, *8*, 14624. https://doi.org/10.1038/s41598-018-33057-y

Elliott, J., Holmes, K., Chambers, R., Leon, K., & Wimberger, P. (2008). Differences in morphology and habitat use among the native mussel *Mytilus trossulus*, the non-native *M. galloprovincialis*, and their hybrids

in Puget Sound, Washington. *Marine Biology*, *156*, 39–53. https://doi.org/10.1007/s00227-008-1063-3

Filgueira, R., Rosland, R., & Grant, J. (2011). A comparison of scope for growth (SFG) and dynamic energy budget (DEB) models applied to the blue mussel (*Mytilus edulis*). *Journal of Sea Research*, *66*, 403–410. https://doi.org/10.1016/j.seares.2011.04.006

Fly, E. K., & Hilbish, T. J. (2013). Physiological energetics and biogeographic range limits of three congeneric mussel species. *Oecologia*, *172*, 35–46. https://doi.org/10.1007/s00442-012-2486-6

Fly, E. K., Hilbish, T. J., Wethey, D. S., & Rognstad, R. L. (2015). Physiology and biogeography: The response of European mussels (*Mytilus* spp.) to climate change. *American Malacological Bulletin*, *33*(1), 136–149.

Frechette, M., Aitken, A. E., & Page, L. (1992). Interdependence of food and space limitation of a benthic suspension feeder: Consequences for self-thinning relationships. *Marine Ecology Progress Series. Oldendorf*, *83*(1), 55–62. https://doi.org/10.3354/meps083055

Gabbott, P. A. (1976). Energy metabolism. In B. L. Bayne (Ed.), *Marine mussels: Their ecology and physiology* (pp. 293–355). Cambridge University Press. https://doi.org/10.1113/expphysiol.1976.sp002367

Garner, Y. L., & Litvaitis, M. K. (2013). Effects of injured conspecifics and predators on byssogenesis, attachment strength and movement in the blue mussel, *Mytilus edulis*. *Journal of Experimental Marine Biology and Ecology*, *448*, 136–140. https://doi.org/10.1016/j.jembe.2013.07.004

George, M. N., Andino, J., Huie, J., & Carrington, E. (2019). Microscale pH and dissolved oxygen fluctuations within mussel aggregations and their implications for mussel attachment and raft aquaculture. *Journal of Shellfish Research*, *38*(3), 795–809. https://doi.org/10.2983/035.038.0329

George, M. N., Pedigo, B., & Carrington, E. (2018). Hypoxia weakens mussel attachment by interrupting DOPA cross-linking during adhesive plaque curing. *Journal of the Royal Society Interface*, *15*, 20180489. https://doi.org/10.1098/rsif.2018.0489

Gosline, J. M. (2018). *Mechanical design of structural materials in animals* (p. 400). Princeton University Press. https://doi.org/10.23943/9781400889839

Gosling, E. (1992). *The mussel* Mytilus*: Ecology, physiology, genetics and culture*. (p. 590). Elsevier Science.

Hawkins, A. J. S., & Bayne, B. L. (1985). Seasonal variation in the relative utilization of carbon and nitrogen by the mussel *Mytilus edulis*: Budgets, conversion efficiencies, and maintenance requirements. *Marine Ecology Progress Series*, *7*, 181–188. https://doi.org/10.3354/meps025181

IPCC. (2019). Technical summary. In H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, E. Poloczanska, K. Mintenbeck, M. Tignor, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, & N. M. Weyer (Eds.), *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. In press.

Jones, H. D., Richards, O. G., & Southern, T. A. (1992). Gill dimensions, water pumping rate and body size in the mussel *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology*, *155*, 213–237. https://doi.org/10.1016/0022-0981(92)90064-H

Kearney, M. R., Matzelle, A., & Helmuth, B. (2012). Biomechanics meets the ecological niche: The importance of temporal data resolution. *Journal of Experimental Biology*, *215*, 922–933. https://doi.org/10.1242/jeb.059634

Kearney, M., Simpson, S. J., Raubenheimer, D., & Helmuth, B. (2010). Modelling the ecological niche from functional traits. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*, 3469–3483. https://doi.org/10.1098/rstb.2010.0034

Khangaonkar, T., Nugraha, A., Xu, W., & Balaguru, K. (2019). Salish sea response to global climate change, sea level rise, and future nutrient loads. *Journal of Geophysical Research*, *124*, 3876–3904. https://doi.org/10.1029/2018JC014670

Kitchell, J. F., Stewart, D. J., & Weininger, D. (1977). Applications of a Bioenergetics Model to Yellow Perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada*, *34*(10), 1922–1935. https://doi.org/10.1139/f77-258

Koehl, M. A. R. (1996). When does morphology matter? *Annual Review of Ecology and Systematics*, *27*, 501–542. https://doi.org/10.1146/annurev.ecolsys.27.1.501

Kooijman, S. A. L. M. (2010). *Dynamic energy budget theory for metabolic organization*. (p. 514). Cambridge University Press. https://doi.org/10.1017/CBO9780511805400

Korringa, P. (1976). *Farming marine organisms low in the food chain: A multidisciplinary approach to edible seaweed, mussel and clam production* (p. 264). Elsevier.

Lee, C. Y., Lim, S. S. L., & Owen, M. D. (1990). The rate and strength of byssal reattachment by blue mussels (*Mytilus edulis* L.). *Canadian Journal of Zoology*, *68*, 2005–2009. https://doi.org/10.1139/z90-282

Leonard, G. H., Bertness, M. D., & Yund, P. O. (1999). Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. *Ecology*, *80*, 1–14.

Lowe, A. T., Roberts, E. A., & Galloway, A. W. (2016). Improved marine-derived POM availability and increased pH related to freshwater influence in an inland sea. *Limnology and Oceanography*, *61*, 2122–2138. https://doi.org/10.1002/lno.10357

Lurman, G. J., Hilton, Z., & Ragg, N. L. (2013). Energetics of byssus attachment and feeding in the green-lipped mussel *Perna canaliculus*. *The Biological Bulletin*, *224*, 79–88. https://doi.org/10.1086/BBLv224n2p79

Maar, M., Saurel, C., Landes, A., Dolmer, P., & Petersen, J. K. (2015). Growth potential of blue mussels (*M. edulis*) exposed to different salinities evaluated by a Dynamic Energy Budget model. *Journal of Marine Systems*, *148*, 48–55. https://doi.org/10.1016/j.jmarsys.2015.02.003

Maar, M., Timmermann, K., Petersen, J. K., Gustafsson, K. E., & Storm, L. M. (2010). A model study of the regulation of blue mussels by nutrient loadings and water column stability in a shallow estuary, the Limfjorden. *Journal of Sea Research*, *64*, 322–333. https://doi.org/10.1016/j.seares.2010.04.007

Martin, B. T., Zimmer, E. I., Grimm, V., & Jager, T. (2012). Dynamic Energy Budget theory meets individual-based modelling: A generic and accessible implementation. *Methods in Ecology and Evolution*, *3*, 445–449. https://doi.org/10.1111/j.2041-210X.2011.00168.x

Matzelle, A. J., Sarà, G., Montalto, V., Zippay, M., Trussell, G. C., & Helmuth, B. (2015). A bioenergetics framework for integrating the effects of multiple stressors: Opening a 'black box' in climate change research. *American Malacological Bulletin*, *33*, 150–161. https://doi.org/10.4003/006.033.0107

Melzner, F., Stange, P., Trübenbach, K., Thomsen, J., Casties, I., Panknin, U., Gorb, S. N., & Gutowska, M. A. (2011). Food supply and seawater pCO_2 impact calcification and internal shell dissolution in the blue mussel *Mytilus edulis*. *PLoS ONE*, *6*(9), e24223. https://doi.org/10.1371/journal.pone.0024223

Miller, L. P., & Dowd, W. W. (2019). Repeatable patterns of small-scale spatial variation in intertidal mussel beds and their implications for responses to climate change. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *236*, 110516. https://doi.org/10.1016/j.cbpa.2019.06.016

Moeser, G. M., & Carrington, E. (2006). Seasonal variation in mussel byssal thread mechanics. *Journal of Experimental Biology*, *209*, 1996–2003. https://doi.org/10.1242/jeb.02234

Moeser, G. M., Leba, H., & Carrington, E. (2006). Seasonal influence of wave action on thread production in *Mytilus edulis*. *Journal of Experimental Biology*, *209*, 881–890. https://doi.org/10.1242/jeb.02050

Monaco, C. J., & McQuaid, C. D. (2018). Applicability of Dynamic Energy Budget (DEB) models across steep environmental gradients. *Scientific Reports*, *8*, 16384. https://doi.org/10.1038/s41598-018-34786-w

Monaco, C. J., Porporato, E. M. D., Lathlean, J. A., Tagliarolo, M., Sarà, G., & McQuaid, C. D. (2019). Predicting the performance of cosmopolitan species: Dynamic energy budget model skill drops across large

spatial scales. *Marine Biology*, *166*, 14. https://doi.org/10.1007/s00227-018-3462-4

Monaco, C. J., Wethey, D. S., & Helmuth, B. (2014). A dynamic energy budget (DEB) model for the keystone predator *Pisaster ochraceus*. *PLoS ONE*, *9*, e104658. https://doi.org/10.1371/journal.pone.0104658

Murray, J. W., Roberts, E., Howard, E., O'Donnell, M., Bantam, C., Carrington, E., Foy, M., Paul, B., & Fay, A. (2015). An inland sea high nitrate-low chlorophyll (HNLC) region with naturally high pCO_2. *Limnology and Oceanography*, *60*, 957–966. https://doi.org/10.1002/lno.10062

Newcomb, L. A. (2015). *Elevated temperature and ocean acidification alter mechanics of mussel attachment* (Doctoral dissertation; p. 116). University of Washington. Retrieved from http://hdl.handle.net/1773/35134

Newcomb, L. A., George, M. N., O'Donnell, M. J., & Carrington, E. (2019). Only as strong as the weakest link: Structural analysis of the combined effects of temperature and pCO_2 on mussel attachment. *Conservation Physiology*, *7*, coz068. https://doi.org/10.1093/conphys/coz068

Newell, R. I. E., Hilbish, T. J., Koehn, R. K., & Newell, C. J. (1982). Temporal variation in the reproductive cycle of *Mytilus edulis* (*Bivalvia*, *Mytilidae*) from localities on the East Coast of the United States. *Biological Bulletin*, *162*, 299–310. https://doi.org/10.2307/1540985

B. C. Nicoll, & A. J. Dunn (2000). The effects of wind speed and direction on radial growth of structural roots. In A. Stokes (Ed.), *The supporting roots of trees and woody plants: Form, Function and Physiology. Developments in Plant and Soil Sciences* (Vol 87). Springer. https://doi.org/10.1007/978-94-017-3469-1_21

Nisbet, R. M., Jusup, M., Klanjscek, T., & Pecquerie, L. (2012). Integrating dynamic energy budget (DEB) theory with traditional bioenergetic models. *Journal of Experimental Biology*, *215*, 892–902. https://doi.org/10.1242/jeb.059675

O'Donnell, M. J. (2008). Reduction of wave forces within bare patches in mussel beds. *Marine Ecology Progress Series*, *362*, 157–167. https://doi.org/10.3354/meps07435

O'Donnell, M. J., George, M. N., & Carrington, E. (2013). Mussel byssus attachment weakened by ocean acidification. *Nature Climate Change*, *3*, 587–590. https://doi.org/10.1038/NCLIMATE1846

Padilla, D. K., & Savedo, M. M. (2013). A systematic review of phenotypic plasticity in marine invertebrate and plant systems. In *Advances in marine biology* (Vol. 65, pp. 67–94). Academic Press. https://doi.org/10.1016/B978-0-12-410498-3.00002-1

R Development Core Team. (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Read, J., & Stokes, A. (2006). Plant biomechanics in an ecological context. *American Journal of Botany*, *93*, 1546–1565. https://doi.org/10.3732/ajb.93.10.1546

Riisgård, H. U., & Randløv, A. (1981). Energy budget, growth and filtration rates in *Mytilus edulis* at different algal concentrations. *Marine Biology*, *61*, 227–234. https://doi.org/10.1007/BF00386664

Roberts, E. A. (2019). *Resource allocation to growth and structure: The cost of mussel attachment in a dynamic coastal environment* (Doctoral dissertation, p. 188) University of Washington. Retrieved from http://hdl.handle.net/1773/45118

Roberts, E. A., Newcomb, L. A., McCartha, M. M., Harrington, K. J., LaFramboise, S. A., Carrington, E., & Sebens, K. P. (2021). Data from: Resource allocation to a structural biomaterial: Induced production of byssal threads decreases growth of a marine mussel. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.612jm641f

Rumohr, H., Brey, T., & Ankar, S. (1987). *A compilation of biometric conversion factors for benthic invertebrates of the Baltic Sea. Baltic Marine Biologists Publication*, *9*. 56 pages. Opulus Press.

Sanders, T., Schmittmann, L., Nascimento-Schulze, J. C., & Melzner, F. (2018). High calcification costs limit mussel growth at low salinity. *Frontiers in Marine Science*, *5*. https://doi.org/10.3389/fmars.2018.00352

Sarà, G., Kearney, M., & Helmuth, B. (2011). Combining heat-transfer and energy budget models to predict thermal stress in Mediterranean intertidal mussels. *Chemistry and Ecology*, *27*, 135–145. https://doi.org/10.1080/02757540.2011.552227

Sarà, G., Palmeri, V., Montalto, V., Rinaldi, A., & Widdows, J. (2013). Parameterisation of bivalve functional traits for mechanistic ecophysiological dynamic energy budget (DEB) models. *Marine Ecology Progress Series*, *480*, 99–117. https://doi.org/10.3354/meps10195

Schneider, K. R., Wethey, D. S., Helmuth, B. S. T., & Hilbish, T. J. (2005). Implications of movement behavior on mussel dislodgement: Exogenous selection in a *Mytilus* spp. hybrid zone. *Marine Biology*, *146*, 333–343. https://doi.org/10.1007/s00227-004-1446-z

Sebens, K. P. (1982). The limits to indeterminate growth: An optimal size model applied to passive suspension feeders. *Ecology*, *63*, 209–222. https://doi.org/10.2307/1937045

Sebens, K. P. (1987). The ecology of indeterminate growth in animals. *Annual Review of Ecology and Systematics*, *18*, 371–407. https://doi.org/10.1146/annurev.es.18.110187.002103

Sebens, K. P. (2002). Energetic constraints, size gradients, and size limits in benthic marine invertebrates. *Integrative and Comparative Biology*, *42*, 853–861. https://doi.org/10.1093/icb/42.4.853

Sebens, K. P., Sarà, G., & Carrington, E. (2018). Estimation of fitness from energetics and life-history data: An example using mussels. *Ecology and Evolution*, *8*, 5279–5290. https://doi.org/10.1093/icb/42.4.853

Semedo, A., Weisse, R., Behrens, A., Sterl, A., Bengtsson, L., & Günther, H. (2013). Projection of global wave climate change toward the end of the Twenty-First Century. *Journal of Climate*, *26*, 8269–8288. https://doi.org/10.1175/JCLI-D-12-00658.1

Skidmore, D. (1983). *Settlement, growth, and survival of* Mytilus edulis *L. in Puget Sound and Assessment of* Mytilus Californianus *for Aquaculture*. (Thesis MS). University of Washington.

Telewski, F. W., & Pruyn, M. L. (1998). Thigmomorphogenesis: A dose response to flexing in *Ulmus americana* seedlings. *Tree Physiology*, *18*, 65–68. https://doi.org/10.1093/treephys/18.1.65

Thompson, R. J., & Bayne, B. L. (1974). Some relationships between growth, metabolism and food in the mussel *Mytilus edulis*. *Marine Biology*, *27*, 317–326. https://doi.org/10.1007/BF00394367

van der Veer, H. W., Cardoso, J. F., & van der Meer, J. (2006). The estimation of DEB parameters for various Northeast Atlantic bivalve species. *Journal of Sea Research*, *56*, 107–124. https://doi.org/10.1016/j.seares.2006.03.005

Van Winkle, W. (1970). Effect of environmental factors on byssal thread formation. *Marine Biology*, *7*, 143–148. https://doi.org/10.1007/BF00354918

Vogel, S. (2013). *Comparative biomechanics: Life's physical world*. (p. 50). Princeton University Press.

Waite, J. H., Qin, X. X., & Coyne, K. J. (1998). The peculiar collagens of mussel byssus. *Matrix Biology*, *17*, 93–106. https://doi.org/10.1016/S0945-053X(98)90023-3

Walker, J. (2007). A general model of functional constraints on phenotypic evolution. *The American Naturalist*, *170*, 681–689. https://doi.org/10.1086/521957

Widdows, J. (1978). Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom*, *58*, 109–124. https://doi.org/10.1017/S0025315400024449

Widdows, J. (1987). Application of calorimetric methods in ecological studies. In A. M. James (Ed.), *Thermal and energetic studies of cellular biological systems* (pp. 182–215). https://doi.org/10.1016/C2013-0-06478-X

Widdows, J., & Bayne, B. L. (1971). Temperature acclimation of *Mytilus edulis* with reference to its energy budget. *Journal of the Marine Biological Association of the United Kingdom*, *51*, 827–843. https://doi.org/10.1017/S0025315400018002

Young, G. A. (1985). Byssus-thread formation by the mussel *Mytilus edulis*: Effects of environmental factors. *Marine Ecology Progress Series*, *24*, 261–271. https://doi.org/10.1007/978-3-7091-0286-2_18

Young, T. P. (1987). Increased thorn length in *Acacia depranolobium* - an induced response to browsing. *Oecologia*, *71*(3), 436–438. https://doi.org/10.1007/bf00378718

Zardi, G. I., McQuaid, C. D., & Nicastro, K. R. (2007). Balancing survival and reproduction: Seasonality of wave action, attachment strength and reproductive output in indigenous *Perna perna* and invasive *Mytilus galloprovincialis* mussels. *Marine Ecology Progress Series*, *334*, 155–163. https://doi.org/10.3354/meps334155

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media. https://doi.org/10.1007/978-0-387-87458-6

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Roberts EA, Newcomb LA, McCartha MM, et al. Resource allocation to a structural biomaterial: Induced production of byssal threads decreases growth of a marine mussel. *Funct Ecol*. 2021;35:1222–1239. https://doi.org/10.1111/1365-2435.13788