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Effects of wave exposure, temperature and epibiont fouling on byssal thread production and growth in the blue mussel, *Mytilus edulis*, in the Gulf of Maine

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ABSTRACT

Blue mussels (*Mytilus edulis*) need a strong byssal attachment to remain anchored on wave swept shores. Byssogenesis and mussel growth can be affected by abiotic factors, as well as by biotic interactions. Using short- and long-term field deployments of artificially-fouled mussels in coastal New Hampshire, we determined the effects of wave exposure, temperature and epibiont cover on the number and attachment strength of byssal threads produced and on mussel growth. In a factorial experiment, more byssal threads were produced by epibiont-covered mussels located at sheltered sites during summer. With each additional byssal thread that a mussel produced, its total attachment strength to the substrate increased by 3.8%. Furthermore, attachment strength increased by 6.7% when mussels were artificially fouled and by 17.1% during winter. Mussel growth was higher during summer at high wave exposure sites, presumably due to a seasonal increase in nutrients. Epibiont cover had no influence on mussel growth. Our results indicate that wave exposure, temperature, and epibionts influence byssal thread production, whereas wave exposure and temperature affect mussel growth. This study incorporates several different factors simultaneously in a series of field experiments which affect mussel byssal thread production, growth and survival and have an important implication for their population dynamics.

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1. Introduction

Blue mussels (*Mytilus edulis* Linnaeus, 1758) have adapted to life in the rocky and sedimentary intertidal and subtidal zones by secreting collagenous byssal threads that anchor them to the substrate on rocky shores or to conspecifics. Byssal thread production occurs within a couple of hours, and has become a model system for studies of bioadhesion (Waite, 2002). The process is intermittent, allowing for continued mobility of mussels, especially in juveniles (Wiegemann, 2005). Proteins are secreted and molded in the ventral groove of the foot, prior to being released as a newly formed byssal thread (Waite, 2002).

Mussels live in the intertidal environment, which is subjected to high water motion from breaking waves, resulting in the necessity of a strong attachment (Bell and Gosline, 1997). The strength of byssal attachment is altered by water flow conditions, often marked by an increase in thread numbers under high flow rates (Bell and Gosline, 1997; Carrington, 2002). Moeser et al. (2006) found that byssal thread production of *M. edulis* in a flume peaks at ambient flows of 11 cm/s and declines at higher velocities. Carrington et al. (2008) extended these findings to include *M. trossulus* (Gould, 1850), *M. galloprovincialis* (Lamarck, 1819), *M. californianus* (Conrad, 1837), and *Modiolus modiolus* (Linnaeus, 1758) and found that byssal thread formation declines at flow velocities above ~25 cm/s. They attribute their findings to an inability of the foot to extend to the substrate, without which byssal threads cannot form.

Seasonality, and therefore temperature, also affects attachment strength of mussel byssal threads. *M. edulis* changes between two alternative physiological states during the year: high reproduction/low attachment strength in summer and high attachment strength/low reproduction in winter, with spring and fall serving as transitional periods (Carrington, 2002). Carrington (2002) found that the strongest attachment occurs during the winter/early spring, which then allows for energetic requirements to shift to the production of gametes. The summer and fall proved to be the seasons with the weakest attachment strength, likely due to an elevated decay rate. Byssal thread degradation was attributed to environmental conditions such as increased evaporation and temperature changes resulting from daily tidal variation, along with biofouling activity by marine bacteria. Zardi et al. (2007) and Carrington (2002) suggest that *M. galloprovincialis* in South Africa, and *M. edulis* in Rhode Island allocate energy towards gamete production and potentially away from byssal thread production even in the presence of high wave action or stressful conditions.

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Mussels form dense aggregations in intertidal and subtidal environments providing structure for a diverse assemblage of organisms that often attach directly onto the mussel shells. Plant and animal epibionts may reduce the growth and survival of mussels (Thieltges and Buschbaum, 2007), and increase the potential for dislodgement (Witman and Suchanek, 1984). Mussel epibionts that increase the surface area exposed to water flow, such as kelp and barnacles, increase the chance of mussel dislodgement as compared to thin epibionts, such as colonial tunicates or encrusting bryozoans. The more likely dislodgement of mussels with protruding epibionts is due to an increase of hydrodynamic forces exerted on mussels, specifically a higher drag-induced loading (Dittman and Robles, 1991; O'Connor et al., 2006; Thieltges, 2005; Thieltges and Buschbaum, 2007; Witman and Suchanek, 1984). Thieltges and Buschbaum (2007) have identified the slipper shell, *Crepidula fornicata* (Linnaeus, 1758) as an epibiont that increases byssal thread production as compared to unfouled mussels. Additionally, larger hydrodynamic forces exerted on mussels fouled by epibionts may ultimately translate to a greater energy allocation to byssogenesis (Thieltges and Buschbaum, 2007). Naturally occurring epibionts on *M. edulis* in New Hampshire include barnacles, colonial and solitary tunicates, bryozoans, the slipper limpet *C. fornicata*, *Ulva* spp., and kelp, with coverage varying between seasons.

The overall goal of the present study was to determine the production of byssal threads, and growth in relation to epibiont presence, wave exposure, and water temperature in *M. edulis*. Because byssogenesis occurs rapidly, whereas changes in mussel length require an extended period, we designed two sets of field studies. Byssal thread production, as measured by number and strength of threads was determined after 24 h; mussel growth, as measured by changes in length was determined after 11 weeks.

2. Material and methods

2.1. Sample collection and preparation

Mussels (1417 total) of 50–70 mm shell length were collected from the University of New Hampshire (UNH) Atlantic Marine Aquaculture Center (42.942433° N, 70.633228° W) or from the UNH Coastal Marine Laboratory Pier (43.071971° N, 70.711465° W). After manual removal of all epibionts, mussels were measured for length, depth and height using digital calipers (General Tools and Instruments, New York, NY, USA), weighed, and labeled with queen bee tags (The Bee Works, Orillia, Ontario, Canada). To avoid variability introduced by different biotic and abiotic characteristics of epibionts of diverse species, we standardized epibiont simulation by attaching small pieces of high-pile carpet (~36 cm^2) to both valves of 708 mussels (i.e. fouled) (Fig. 1a) with cyanoacrylate glue; 709 mussels remained unfouled (i.e. no carpet attached).

2.2. Field deployments

Specimens were maintained in flowing seawater tanks at the UNH Coastal Marine Laboratory, New Castle, NH until experimentation, and were then placed into individual compartments of wire mesh cages. The cages (outer dimension 61 cm × 22.9 cm × 11.4 cm) were constructed from vinyl coated wire mesh (Gilbert and Bennett, Midwest Air Technologies, Inc., Lincolnshire, IL, USA), mesh size 1.7 cm^2, with individual compartments for each mussel. Each compartment (4.8 cm × 4.5 cm × 4.5 cm; L × W × H) contained a piece of slate (104 cm^2) (MS International, Inc., Orange, CA, USA) to serve as substrate for the mussels. In addition, individual plastic mesh

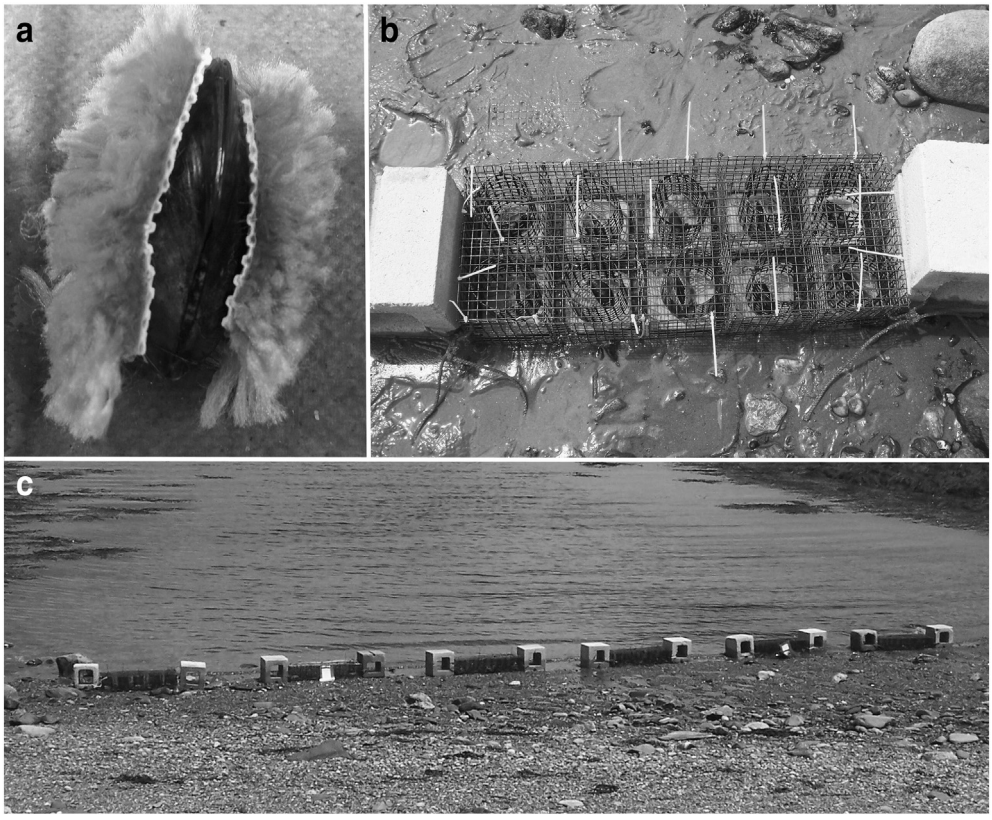

Fig. 1. (a) Mussel with artificial epibionts attached to each valve, (b) wire mesh cage showing individual mussel compartments, and (c) mussel cages at the beginning of 24-hour deployment during low tide at Fort Stark, New Castle, NH.

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cylinders were placed into the center of each compartment to prevent mussel clumping (Fig. 1b).

Three exposed (high wave exposure) sites, Rye Harbor State Park (43.00091° N, 70.74337° W), Odiorne Point State Park (43.04201° N, 70.71478° W) and Fort Stark (43.05836° N, 70.71160° W) and three sheltered (low wave exposure) sites, Rye Harbor State Park (43.00054° N, 70.74388° W), the UNH Coastal Marine Lab (43.07162° N, 70.71236° W) and Sander's Point (43.05639° N, 70.73139° W) were chosen for deployment. At each field site, 6 cages containing 10 mussels each were attached in the mussel zone by securing two ropes through the cages and onto cement blocks (Fig. 1c). Thirty artificially-fouled mussels and 30 non-fouled mussels were placed in alternating compartments of cages and placed concurrently at low tide. The cages remained in the field for 24 h, after which time byssal thread production was determined by counting individual threads. The same process was carried out with fresh mussels at all sites beginning at low tide for the following 5 days. The experiment was repeated in June, 2009, June, 2010, January, 2012 and June, 2012.

In addition to counting threads after 24 h, strength of byssal attachment was also evaluated using a Vernier Dual-Range Force Sensor (Vernier Software and Technology, Beaverton, OR, USA). A piece of monofilament line was secured around each mussel and hooked onto the force sensor, applying a steady force normal to the substrate until failure of byssal threads occurred. The point of maximum force required (N) to break the threads was noted.

To evaluate the effects of temperature on mussel growth, mussel cages were placed in the intertidal zone at the same wave exposed and sheltered sites for 11 weeks as described above. Mussel length, width, height, and wet weight were recorded and water temperature readings were obtained from the UNH Coastal Marine Laboratory Monitoring Station, New Castle, NH (43.072284° N, 70.710328° W), which takes temperature readings twice per hour. Temperatures were averaged for the duration of the study.

An Onset HOBO water level data logger (Onset Computer Corporation, Bourne, MA) was used to measure changes in water pressure at the exposed and sheltered field sites. The water level logger was deployed in the intertidal zone for 6 h of the tidal cycle on 23 May 2012, 29 May 2012 and 1 June 2012 for exposed sites and on 22 May 2012, 24 May 2012 and 31 May 2012 for sheltered sites. The logger takes temperature and pressure measurements every second.

2.3. Data analysis

A three-way factorial ANOVA was used to test the effects of wave exposure (fixed; wave exposed versus sheltered site), epibiont presence (fixed; fouled versus unfouled mussels), and temperature (fixed; summer versus winter) on byssal thread counts and change in mussel length (SYSTAT, Richmond, CA, USA). Significant differences between treatments were evaluated with Tukey's honest significant difference post hoc analysis of variance in SYSTAT. After byssal thread strength data were log transformed, a multiple linear regression was utilized (Microsoft Excel 2007). The assumptions of normality and homoscedasticity were visually assessed via a log (strength) histogram, residual plots, and Q–Q plots, yielding no apparent deviations from these assumptions. Significant wave heights for each field site were determined from pressure data using MATLAB (The MathWorks, Inc., Natick, MA, USA) and wave heights for field sites were compared using a Kruskal–Wallis test in SYSTAT.

3. Results

3.1. Twenty-four hour byssal thread production

Wave exposed and sheltered field sites differed in terms of significant wave height, with average wave heights of 1.36 m at exposed sites, and of 0.22 m at sheltered sites ($n = 3$, $p = 0.05$). More byssal threads were produced at low wave exposure sites (average number 5.97 ± 0.24 S.E.) compared to mussels at high wave exposure sites (average number 4.81 ± 0.25 S.E.) (Fig. 2a; $n = 699–718$, $p = 0.001$; Table 1). More byssal threads were produced during summer (average number 7.85 ± 0.17 S.E.) compared to winter (average number 2.92 ± 0.30 S.E.) (Fig. 2b; $n = 340–1077$, $p < 0.001$; Table 1). Mussels fouled with artificial epibionts produced more byssal threads (average number 5.97 ± 0.24 S.E.) than mussels left unfouled (average number 4.80 ± 0.24 S.E.) (Fig. 2c; $n = 708–709$, $p = 0.001$; Table 1). Using multiple regression, a relative increase of 3.8% in total attachment strength to the substrate was found with every additional byssal thread that the mussel produced ($p < 0.001$, $n = 516$; Table 2). An increase in strength of 6.7% was observed in the presence of an epibiont ($p < 0.001$; Table 2), and an increase in strength of 17.1% was observed in winter (average water temperature 4.9 °C) compared to summer (average water temperature 13.3 °C) ($p < 0.001$; Table 2). Conversely, a relative

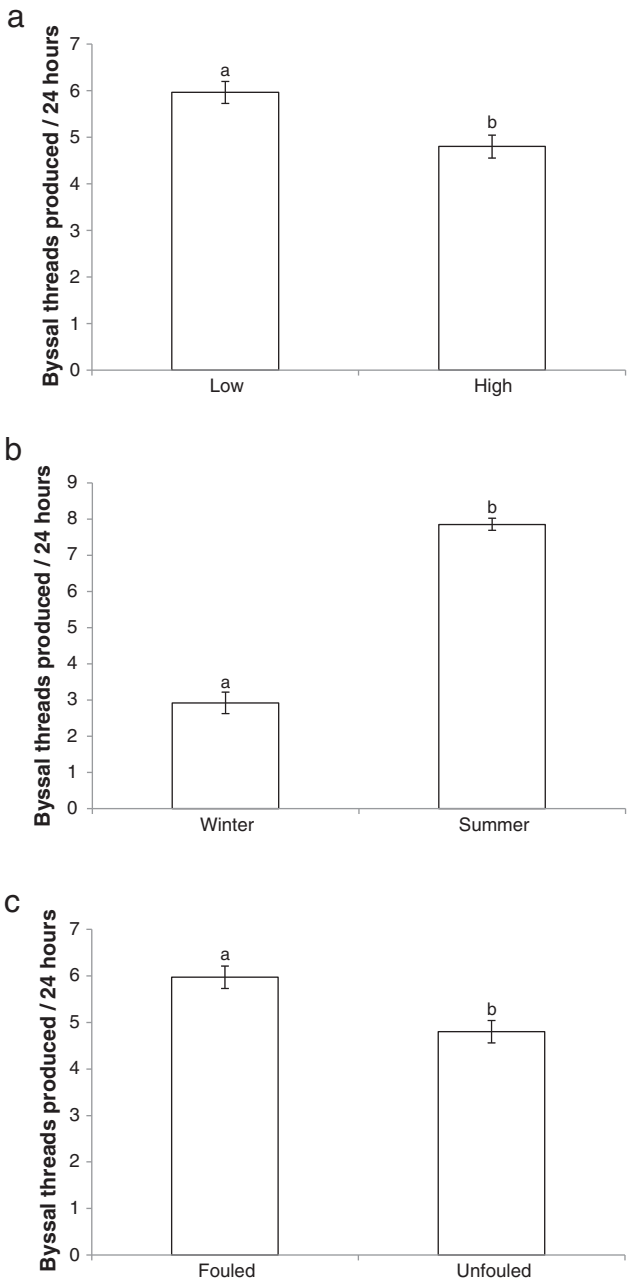

Fig. 2. Mean number (±S.E.) of byssal threads produced in response to (a) wave exposure, (b) temperature, and (c) epibiont fouling; $p \leq 0.001$.

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Table 1
Results of 3-way ANOVA for byssal thread production after 24 h with wave exposure, epibiont fouling and temperature as fixed factors (df = degrees of freedom, MS = mean square, F = value of the F-statistics, p = p-value).

Source of variation	df	MS	F	p
Wave exposure	1	347.79	11.61	0.001
Epibiont	1	354.60	11.83	0.001
Temperature	1	6271.90	209.31	<0.001
Wave exposure × epibiont	1	4.76	0.16	0.69
Wave exposure × temperature	1	94.79	3.16	0.08
Epibiont × temperature	1	2.42	0.08	0.78
Wave exposure × epibiont × temperature	1	1.42	0.05	0.83
Error	1409	29.97		

decrease of 3.1% in byssal thread strength was found with wave exposure (n.s., p = 0.07; Table 2).

3.2. Eleven-week mussel growth

Mussels at high wave exposure sites (average growth 1.86 mm ± 0.12 S.E.) grew more than those at low wave exposure sites during summer (average growth 1.00 mm ± 0.12 S.E.) (Fig. 3; n = 146–176, p = 0.001; Table 3). Epibiont fouling did not have a significant effect on mussel growth (n = 315–329, p = 0.361; Table 3).

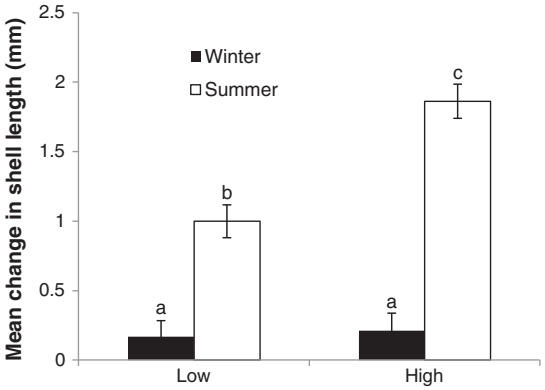

Fig. 3. Mean change in shell length (mm) (±S.E.) for mussels at low vs. high wave exposure sites for summer and winter deployments; p = 0.001. The characters above the error bars denote significant differences between the treatment means based on Tukey's honest significant difference post hoc analysis of variance.

4. Discussion

Our results showed that high wave action not only failed to increase byssal thread production, but even restricted byssogenesis and resulted in an overall weaker byssal attachment. At low wave exposure, mussels produced more threads which had a collectively stronger attachment. This is in contrast to studies which suggest a positive linear relationship between byssal thread production and water flow (Bell and Gosline, 1997; Carrington, 2002). Successful byssogenesis is dependent on sustained contact between the foot and substrate (Moeser et al., 2006). Upon exposure to high flow velocities, the mussel foot is dislodged from the substrate and thread secretion is interrupted, resulting in the production of fewer threads (Moeser et al., 2006). At protected sites, mussels were able to secrete numerous high quality byssal threads presumably due to low disturbance by wave activity. Our study supports findings by Moeser et al. (2006) and Carrington et al. (2008) which also showed that mussels experience limitation to byssal thread production at high flow regimes. Even though byssal thread production is restricted by high flow, the ability of mussels to form dense aggregations is an adaptive behavior which modulates water flow and enables the weak foot to mold and attach new threads to the substrate (Carrington et al., 2008).

Temperature also influenced byssal thread production with more threads produced during summer, a time of increased average temperature. However, despite the increased number of threads, overall tensile strength was weaker during summer. The ability of *M. edulis* to produce stronger threads during the winter has been attributed to periods of increased wave action brought about by winter storms in Rhode Island, USA (Carrington, 2002). Low attachment strength during summer despite high numbers of threads, has been shown in Rhode Island to coincide with poor quality threads, specifically weaker individual threads that are more prone to decay (Moeser et al., 2006). While increased attachment strength of mussels in winter was thought to result from increased thread number (Bell and Gosline, 1997; Carrington, 2002), our results again confirm the findings of Moeser et al. (2006) that stronger individual threads are responsible for the stronger attachment. Of course, additional environmental and physiological factors may contribute to increased number of threads and their attachment strengths. For example, changes to salinity (Young, 1985), nutrient levels (Carrington, 2002) and predator presence could affect byssogenesis. Specifically, Leonard et al. (1999) showed that blue mussels in hydrodynamically protected environments in the Gulf of Maine were under greater predation pressure than individuals in wave exposed areas, and produced an increased number of byssal threads as a result. Hence, it is conceivable that the presence of environmental cues from crabs or damaged conspecifics could have influenced byssogenesis at our field sites. Furthermore, energetic requirements of reproduction may also limit byssal thread production (Carrington, 2002).

Fouling with artificial epibionts resulted in the production of more threads of higher attachment strength. Previous studies, which used biological epibionts, were equivocal. Specifically, fouling by the slipper limpet *C. fornicata*, results in increased byssal thread production (Thieltges and Buschbaum, 2007), whereas O'Connor et al. (2006) found that mussels do not alter attachment strength and thread production in response to algal epibionts. By standardizing epibiont cover, we were able to demonstrate that epibionts alter byssogenesis not only with regards to number of threads produced but also attachment strength.

Table 2
Results of multiple regression assessing relative changes in byssus attachment strength in relation to epibiont presence, wave exposure, the addition of individual byssal threads, and temperature, $p < 0.001$, $r^2 = 0.65$. Equation: log (attachment strength) = $B_o + B_1 * \text{epibiont} + B_2 * \text{wave exposure} + B_3 * \text{byssal thread} + B_4 * \text{temperature}$.

	Coefficients	Standard error	P-value	Exponentiated coefficients
Intercept	−0.13574	0.01938	<0.001	0.87307
Epibiont	0.06500	0.01800	<0.001	1.06716
Wave exposure	−0.03174	0.01757	0.071	0.96876
Byssal thread	0.03736	0.00170	<0.001	1.03806
Temperature	0.15816	0.02012	<0.001	1.17136

Table 3
Results of 3-way ANOVA for change in mussel length (mm) after 11 weeks with wave exposure, epibiont fouling and temperature as fixed factors (df = degrees of freedom, MS = mean square, F = value of the F-statistics, p = p-value).

Source of variation	df	MS	F	p
Wave exposure	1	32.84	14.19	<0.001
Epibiont	1	1.93	0.84	0.36
Temperature	1	245.87	106.20	<0.001
Wave exposure × epibiont	1	0.00	0.00	0.99
Wave exposure × temperature	1	26.88	11.61	0.001
Epibiont × temperature	1	0.39	0.17	0.68
Wave exposure × epibiont × temperature	1	0.01	0.01	0.94
Error	636	2.32		

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Byssus production constitutes a substantial cost for *M. edulis*, requiring 44% of total carbon and 21% of total nitrogen produced (Hawkins and Bayne, 1985). Griffiths and King (1979) show a direct trade-off between byssus production and growth for the ribbed mussel, *Aulacomya ater* (Molina, 1782). Our findings indirectly support the notion that such a trade-off in energy allocation also occurs in blue mussels. Mussels at high wave exposure sites produced fewer threads (because of their inability to maintain contact between the foot and substrate), allowing for the reallocation of energy resources into increased growth. Food availability and immersion time are known to influence the growth rate of mussels, with increased growth for individuals positioned lower in the intertidal zone (Buschbaum and Saier, 2001). Hence, our observed increased growth during summer may also be attributed to increased food availability at wave exposed field sites, where presumably larger volumes of water are circulated to the mussels. Similar results have been reported for *Perna perna* (Linnaeus, 1758) and have been linked to an increase in nutrients due to increased water volumes (McQuaid and Lindsay, 2000).

Plant and animal epibionts can reduce mussel growth by altering hydrodynamic conditions and to a lesser extent, by filtering out food particles or by creating a stagnant boundary layer which limits the amount of food available (Buschbaum and Saier, 2001; Dittman and Robles, 1991; Thieltges, 2005; Thieltges and Buschbaum, 2007). The changes to hydrodynamic conditions surrounding the mussel caused by epibionts could exacerbate effects of low food availability in sheltered wave environments. Thieltges (2005) showed that slipper limpet epibionts protrude into the water column, causing stronger hydrodynamic forces around the mussels. As a consequence, mussels expend more energy towards byssal thread production than growth. We were able to demonstrate that artificial epibiont presence did not affect mussel growth independently, however we can infer that epibionts indirectly brought about reduced growth to mussels strongly attached to the substratum which supports previous work (Thieltges, 2005; Thieltges and Buschbaum, 2007). In addition to a drag-induced trade-off between byssal thread production and growth resulting from epibiont presence, food availability and wave exposure are also likely to control mussel growth. As evident from this study, mussels living in the intertidal zone are faced with many factors, both biotic and abiotic, which influence their byssogenesis and growth. Using artificial epibionts, we were able to limit the biological mussel–epibiont interactions and focus primarily on the effects of physical factors. Thus, we were able to show that byssogenesis is influenced by temperature, wave action, and epibiont presence, whereas growth is affected by wave action and temperature.

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