Invertebrate Biology

Invertebrate Biology x(x): 1–7.

DOI: 10.1111/ivb.12144

Effects of artificial epibionts on byssogenesis, attachment strength, and movement in two size classes of the blue mussel, *Mytilus edulis*

Yvette L. Garner,[a,b] and Marian K. Litvaitis

Department of Natural Resources and the Environment, University of New Hampshire, Durham, New Hampshire 03824, USA

Abstract. Blue mussels (*Mytilus edulis*) can alter the strength of byssal attachment and move between and within mussel aggregations on wave-swept shores, but this movement ability may be limited by epibiont fouling. We quantified the effects of artificial epibiont fouling on the production of byssal threads, attachment strength, and movement in two size classes of blue mussels. In a factorial experiment, large epibiont-covered mussels produced more functional byssal threads (i.e., those continuous from animal to substrate) after 24 h than large unfouled and small fouled mussels, but not more than small unfouled mussels. Small unfouled mussels formed and released more byssus bundles compared to any other treatment group, which indicates increased movement. Conversely, epibiont fouling resulted in decreased numbers of byssus bundles shed, and therefore reduced movement in small mussels. Epibiont-covered mussels started producing byssal threads sooner than unfouled mussels, while small mussels began producing byssal threads earlier compared to large mussels. Mean attachment strength from both size classes increased by 9.5% when mussels were artificially fouled, and large mussels had a 34% stronger attachment compared to small mussels. On the other hand, a 2.3% decrease in attachment strength was found with increasing byssus bundles shed. Our results suggest that fouling by artificial epibionts influences byssal thread production and attachment strength in large mussels, whereas epibionts on small mussels impact their ability to move. Mussels are able to respond rapidly to fouling, which carries implications for the dynamics of mussel beds in their intertidal and subtidal habitats, especially in relation to movement of mussels within and among aggregations.

Additional key words: Epibiosis, byssal thread, mussel, *Mytilus*, bivalve

As ecosystem engineers, blue mussels (*Mytilus edulis* Linnaeus 1758) increase the heterogeneity and diversity of their intertidal and subtidal habitats (Borthagaray & Carranza 2007). For example, dense mussel beds modify the complexity of the substrate and offer additional attachment sites for sessile organisms on hard and soft substrates worldwide (Buschbaum et al. 2009). However, plant and animal epibionts that attach directly onto mussel shells negatively affect the growth and survival of the mussels (Dittman & Robles 1991; Buschbaum & Saier 2001; Thieltges 2005; Thieltges & Buschbaum 2007) and increase the chance of dislodgement of the basibiont (Witman & Suchanek 1984). In the Gulf of Maine, USA, naturally occurring epibionts associated with *M. edulis* include barnacles, colonial and solitary tunicates, bryozoans, the slipper limpet (*Crepidula fornicata* Linnaeus 1758), sea lettuce (*Ulva* spp. Linnaeus 1753), and kelp, although coverage varies between seasons and with site.

Three-dimensional (3-D) epibionts (e.g., kelp, barnacles, slipper limpets) increase the height of the mussel, and thus increase the probability it will be dislodged, compared to epibionts that form thin layers (e.g., encrusting bryozoans, colonial tunicates, and sheet-like sponges) (Witman & Suchanek 1984). The increased chance of dislodgement of mussels covered with 3-D epibionts is due to increased hydrodynamic forces exerted on the mussel, specifically faster flow velocities that lead to higher drag-induced loading (Witman & Suchanek 1984; Dittman & Robles 1991; Thieltges 2005; O'Connor et al. 2006; Thieltges & Buschbaum 2007). In

[a]Address for correspondence.
E-mail: ygarner@westga.edu
[b]Present address: Department of Biology, University of West Georgia, Carrollton, Georgia 30118, USA

addition, kelp epibionts also heighten the risk of dislodgement by increasing the size of the structure that the byssus must anchor to the substrate (Witman & Suchanek 1984). To remain tethered to the substrate, mussels deploy collagenous byssal threads, which are rapidly secreted by a groove in the foot and are cured in seawater (Waite 2002). Byssal threads can be modified under various biotic and abiotic conditions, including epibiont fouling, water flow, and predation (Thieltges & Buschbaum 2007; Garner & Litvaitis 2013).

Mytilid mussels are known to have several antifouling mechanisms such as the texture and chemical composition of the shell periostracum, although these defenses are reduced as the antifouling layer erodes with age (Wahl et al. 1998; Bers et al. 2006a,b). Additional methods to reduce fouling include active swiping movements of the foot against the outside of the shell; however, this behavior is only possible in individuals <3 cm in length (Theisen 1972). As a result, young mussels and those within aggregations exhibit less fouling than older or solitary mussels. However, studies suggest that smaller mussels may also become heavily fouled in intertidal and subtidal zones (Wahl et al. 1998; Buschbaum & Saier 2001).

Juvenile and adult mussels are capable of movement by crawling, although adult movement occurs on a micro-geographic scale compared to that of their younger counterparts (Anthony & Svane 1995a,b; Hunt & Scheibling 1998; Schneider et al. 2005; Liu et al. 2011). As a consequence, mussel beds are spatially and temporally dynamic entities, with continual movement within and between aggregations. Hunt & Scheibling (1998) suggest that the dispersal of large mussels increases the rate of recovery of disturbed mussel beds and influences the dynamics of existing mussel aggregations. In addition, predation alters movement patterns in mussels, as evidenced by rapid clumping behavior upon exposure to lobster effluent (Côté & Jelnikar 1999). To relocate, mussels must break their existing byssal attachment (Wiegemann 2005). Hence, the number of bundles of byssal threads left behind can be used as a proxy for quantifying mussel movement (Ishida & Iwasaki 2003). Furthermore, the ability to move appears to be size dependent, with smaller mussels able to move more often than larger individuals (Wiegemann 2005).

Epibionts can affect the movement of the basibiont. Periwinkles, *Littorina littorea* Linnaeus 1758, fouled with acorn barnacles (*Balanus crenatus* Bruguière 1789) or Pacific oysters (*Crassostrea gigas* Thunberg 1793) show reduced mobility (Buschbaum & Reise 1999; Eschweiler & Buschbaum 2011). Similarly, sea scallops (*Placopecten magellanicus* Gmelin 1791) covered with the colonial tunicate *Didemnum vexillum* Kott 2002 decrease both vertical and horizontal swimming distances (Dijkstra & Nolan 2011), and individuals of the spiny scallop (*Chlamys hastata* Sowerby 1842) fouled by barnacles experience increased drag and energy requirements (Donovan et al. 2003). Although Thieltges (2005) suggests that epibionts may also hinder mobility in mussels, that hypothesis has not been tested. Hence, our objective was to determine the effects of epibiont fouling on byssal thread production and on movement for two size classes of mussels. Byssogenesis was quantified by the number and strength of byssal threads produced, while numbers of abandoned byssus bundles were used to compare mussel movement.

Methods

Mussels of small (20–45 mm) and large (45–70 mm) size classes (96 individuals per size class) were collected from the University of New Hampshire Coastal Marine Laboratory Pier, New Castle, New Hampshire, USA (43.071971°N, 70.711465°W). All epibionts and byssal threads were removed, mussels were measured using digital calipers (General Tools and Instruments, New York, NY, USA), labeled with queen bee tags (The Bee Works, Orillia, ON, Canada), and epibiont growth was simulated on half of the mussels of both size classes. Simulation of epibionts was standardized by attaching small pieces of high-pile carpet (~7.3 cm^2, 3.0 g wet weight per small mussel; ~20.2 cm^2, 8.1 g wet weight per large mussel) to both mussel valves with cyanoacrylate glue (Fig. 1A). Using artificial epibionts, the biotic or abiotic variation of natural epibionts was eliminated and uniformity of cover was established.

Mussels were maintained in unfiltered continuously flowing seawater at the UNH Coastal Marine Laboratory. Tanks were exposed to an ambient light regime, although mussels were never in direct sunlight. After byssal threads emanating from between the shells were trimmed, mussels were placed individually into sixty-four 177-mL glass bowls (16 bowls with small fouled mussels, 16 bowls with small unfouled mussels, 16 bowls with large fouled, 16 bowls with large unfouled mussels) filled with unfiltered seawater and were randomly arranged in a seawater table supplied with flowing ambient seawater (Fig. 1B). The experiment was repeated three times. To keep temperatures consistent in all bowls,

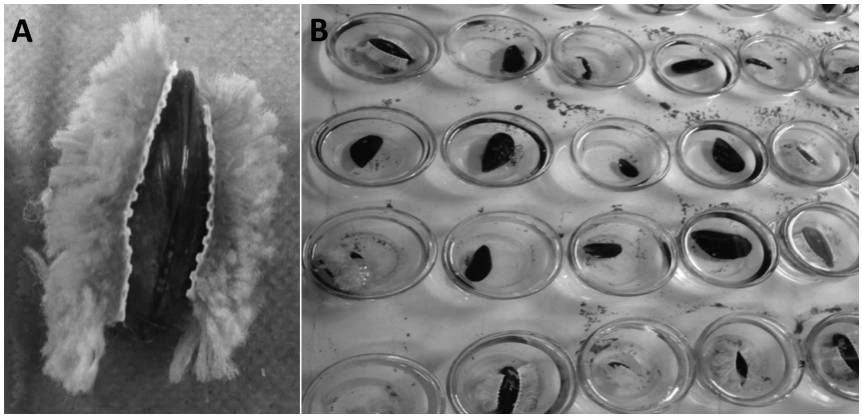

Fig. 1. A. Mussel with artificial epibionts attached to each valve, and **B.** large and small fouled and unfouled mussels in glass bowls randomly arranged in a seawater table.

the waterline of the seawater table was maintained 1 cm below the top edge of the bowls. Treatment bowls were maintained as static systems after the experiment started to avoid the introduction of confounding factors including water velocity and agitation, which have been shown to alter byssal thread production (Young 1985; Moeser et al. 2006).

Numbers of byssal threads attached to the glass bowls (i.e., functional threads continuous between mussel and substrate) were counted after 1.5, 3, 4.5, 6, 9, and 24 h for all mussels. In addition, after 24 h, numbers of abandoned byssus bundles were noted, and byssal thread attachment strength was measured using a Vernier Dual-Range Force Sensor (Vernier Software and Technology, Beaverton, OR, USA). A small piece of monofilament fishing line was attached around each mussel and secured onto the force sensor. A steady force was applied normal to the substrate until byssal thread failure occurred, at which point the maximum force (N) necessary to break the threads was recorded.

A two-way randomized complete block ANOVA, with trial as the blocking factor, was used to test the effects of mussel size and epibiont fouling on byssal thread counts, number of abandoned byssus bundles, and time to thread production start (SYSTAT, Richmond, CA, USA). Mussel size was a fixed factor with two levels (small vs. large mussels), epibiont fouling was a fixed factor with two levels (fouled vs. unfouled), and trial was a random factor with three levels. Significant differences between treatments were evaluated with Tukey's honest significant difference post hoc analysis of variance in SYSTAT. After the data for byssal thread strength were log-transformed, a multiple linear regression was used (Microsoft Excel 2007) to evaluate relationships between thread strength and treatments. The assumptions of normality and homoskedasticity were visually assessed via a log (strength) histogram, residual plots, and Q-Q plots, yielding no apparent deviations from these assumptions.

Results

After 24 h, large fouled mussels deposited more functional byssal threads (average number 12.71±0.96 SE) compared to the large unfouled (average number 7.60±0.96 SE) and small fouled treatments (average number 7.15±0.96 SE), but not compared to any other treatment type (Fig. 2; n=48, $p<0.001$; Table 1). Small unfouled mussels (average number 1.85±0.21 SE) formed and released more byssus bundles compared to any other treatment group (Fig. 3; n=48, p=0.01; Table 2). Epibiont fouling resulted in fewer byssus bundles deposited by

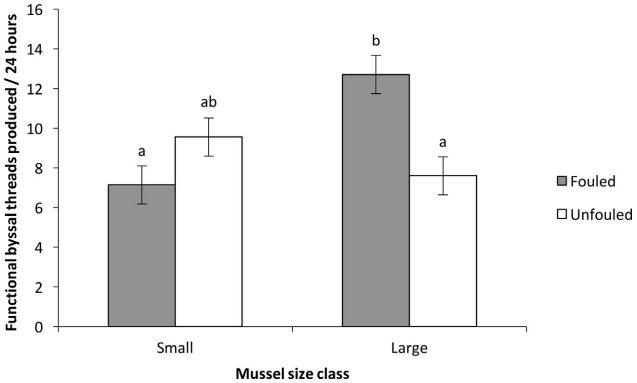

Fig. 2. Mean (±SE) number of functional byssal threads produced after 24 h for small versus large mussels with and without epibiont fouling; $p<0.001$. The characters above the error bars denote significant differences between the treatment means based on Tukey's honest significant difference post hoc analysis of variance.

Table 1. Results of two-way randomized complete block ANOVA for functional byssal threads produced after 24 h, with trial as a blocking factor and mussel size and epibiont fouling as fixed factors (df, degrees of freedom; MS, mean square; F, value of the F-statistic; p, p-value).

Source of variation	df	MS	F	p
Trial	2	2.38	0.05	0.95
Mussel size	1	155.88	3.54	0.06
Epibiont	1	86.67	1.97	0.16
Epibiont x mussel size	1	678.76	15.40	<0.001
Error	186	44.08		

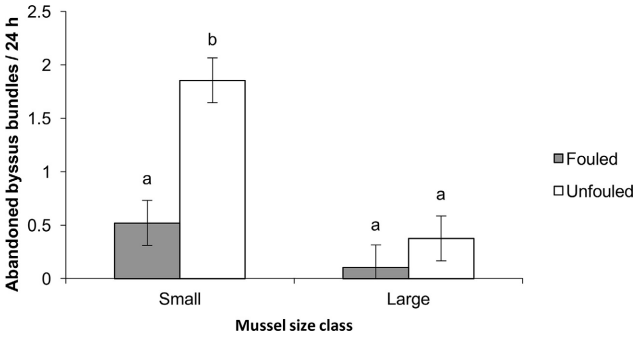

Fig. 3. Mean (±SE) number of byssus bundles formed and detached by small versus large mussels in relation to epibiont fouling; p=0.01. The characters above the error bars denote significant differences between the treatment means based on Tukey's honest significant difference post hoc analysis of variance.

Table 2. Results of two-way randomized complete block ANOVA for number of abandoned byssus bundles after 24 h, with trial as a blocking factor and mussel size and epibiont fouling as fixed factors (df, degrees of freedom; MS, mean square; F, value of the F-statistic; p, p-value).

Source of variation	df	MS	F	p
Trial	2	1.63	0.77	0.46
Mussel size	1	43.13	20.44	<0.001
Epibiont	1	30.88	14.64	<0.001
Epibiont x Mussel size	1	13.55	6.42	0.01
Error	186	2.11		

small mussels (average number 0.521±0.21 SE) (Fig. 3; n=48, p=0.01; Table 2). Both small and large fouled mussels (average time 12.15 h±1.06 SE) started producing byssal threads sooner than unfouled mussels (average time 16.70 h±1.07 SE) (sample size per treatment combination was n=87–88, p=0.003; Table 3). Fouled and unfouled small mussels (average time 12.77 h±1.09 SE) began producing byssal threads earlier compared to large mussels

Table 3. Results of two-way randomized complete block ANOVA for time to start byssal thread production, with trial as a blocking factor and mussel size and epibiont fouling as fixed factors (df, degrees of freedom; MS, mean square; F, value of the F-statistic; p, p-value).

Source of variation	df	MS	F	p
Trial	2	341.44	3.45	0.03
Mussel size	1	472.10	4.77	0.03
Epibiont	1	902.63	9.12	0.003
Epibiont x Mussel size	1	113.11	1.14	0.29
Error	169	99.00		

Table 4. Results of multiple regression evaluating relative changes in byssus attachment strength in relation to mussel size, the addition of individual byssal threads, number of abandoned byssus bundles, and epibiont fouling; p<0.001, r^2=0.71. Exponentiated coefficients represent relative effect of a one unit increase. Equation: log (Attachment Strength)=B_o+B_1(mussel size)+B_2(byssal thread)+B_3(byssus bundle)+B_4(epibiont fouling).

	Coefficients (B_x)	Standard error	p-value	Exponentiated coefficients
Intercept	−0.55906	0.03578	<0.001	0.57175
Mussel size	0.29227	0.03058	<0.001	1.33947
Byssal thread	0.03294	0.00220	<0.001	1.03349
Byssus bundle	−0.02283	0.01014	0.03	0.97742
Epibiont fouling	0.09105	0.02993	0.003	1.09533

(average time 16.06 h±1.04 SE) (n=83–92, p=0.03; Table 3). Byssal thread production started later in the first trial (average time 17.17 h±1.34 SE) compared to the third (average time 12.43 h±1.30 SE) (n=55–61, p=0.03; Table 3).

Using multiple regression, a 9.5% relative increase in total attachment strength was found for fouled mussels (p=0.003, n=173; Table 4), and an increase of 3.4% in total attachment strength to the substrate was found with each additional byssal thread that the mussel produced (p<0.001; Table 4). Large mussels exhibited a 34% stronger attachment than small mussels (p<0.001; Table 4). A 2.3% relative decrease in strength was recorded with increased byssus bundles released (p=0.03; Table 4).

Discussion

Despite possessing antifouling properties, young mussels have the potential to become fouled

(Theisen 1972; Wahl et al. 1998; Buschbaum & Saier 2001; Bers et al. 2006a,b). Small unfouled mussels are known to travel greater distances and to change their attachment site more often than large or fouled mussels (Uryu et al. 1996; Wiegemann 2005); however, we observed a decrease in movement frequency in small fouled mussels as indicated by decreased numbers of abandoned byssus bundles. Without epibiont fouling, small mussels formed and released more byssal bundles, were quick to initiate the deposition of byssal threads, and overall produced threads with weaker attachments. Small mussels free of epibiont fouling might invest more energy into the continued deposition and release of byssal threads and movement rather than the formation of strong threads in one location. Our study also supports findings by Witman & Suchanek (1984) that attachment strength is size dependent in *Mytilus edulis*, with more force required to remove larger mussels from the substrate.

Our findings also have implications for understanding the ability of smaller mussels to move within and between mussel beds, ultimately affecting the dynamics of mussel aggregates. Although all size classes of mytilids are capable of extensive crawling, the phenomenon is especially prevalent in small individuals, which continue movement long after their initial settlement, presumably in search of a suitable microhabitat (Seed 1976; Seed & Suchanek 1992; Wiegemann 2005). Mussel beds are dynamic entities and their size structure has been shown to change drastically over time (Khaitov 2013). However, smaller mussels have been found to dominate mussel beds throughout the year, likely due to reduced growth rates brought about by intraspecific competition for food and space. Additionally, small mussels in natural mussel aggregations have been shown to suffer from limited mobility due to entanglement in byssal threads of larger mussels (Seed 1969; Kautsky 1982; Seed & Suchanek 1992). Despite the negative impacts caused by epibiont fouling, studies by O'Connor et al. (2006) reveal that fouling by algal epibionts specifically does not affect mussel recruitment.

Reduced movement of small fouled mussels likely results in increased susceptibility to predation due to a decrease in the escape response of the mussels. For example, Côté & Jelnikar (1999) documented an increased clumping behavior when mussels were exposed to lobster effluent. Thus, if epibiont presence interferes with aggregate formation, then higher mortality is likely. However, such conclusions may not be generalized across epibiont or predator species. Laudien & Wahl (1999) found that epibionts provide protection from predators such as the sea star *Asterias rubens* Linnaeus 1758. Wahl et al. (1997), on the other hand, showed that epibiontic bay barnacles (*Balanus improvisus* Darwin 1854) increased the susceptibility of mussels to predation by the shore crab *Carcinus maenas* Linnaeus 1758, whereas fouling by the hydrozoan *Laomedea flexuosa* Alder 1857 decreased predation risk. Further illustrating the complexity of interactions with epibionts, Calderwood et al. (2015) found that barnacle fouling does not necessarily protect mussels from predation by the sea star *A. rubens*.

Epibionts increase drag forces, causing increased dislodgement, especially during high wave activity (Witman & Suchanek 1984). However, the effects of fouling by epibionts on the number and attachment strength of byssal threads are equivocal. We found that epibiont cover on large mussels did not affect mobility, but instead resulted in an increase in the number and strength of byssal threads. Similarly, mussels fouled by a natural epibiont (*Crepidula fornicata*) have been shown to produce more byssal threads compared to unfouled mussels (Thieltges & Buschbaum 2007). On the other hand, O'Connor et al. (2006) showed that algal epibionts do not influence the attachment strength and thread production in blue mussels; however, a subsequent study revealed that mussel survival was negatively influenced by algal epibionts on sheltered shores (O'Connor 2010).

By standardizing epibiont fouling, we were able to demonstrate that epibiont presence not only influenced the production of byssal threads and attachment strength in large individuals of *M. edulis*, but also reduced the movement in small mussels. In addition, the mussels in this study were not exposed to hydrodynamic forces caused by water flow, but instead encountered conditions similar to those found in a tide pool (Martinez 2007). Hence, hydrodynamic forces appear not to be responsible for the changes we observed in byssal thread production in larger fouled mussels and movement in smaller mussels. Instead, we attribute the respective increased byssogenesis and reduced movement to added weight due to epibiont fouling, which has been shown to negatively impact the valve functioning and filter feeding abilities of individuals of *M. edulis* (Carman et al. 2016). Possible costs of reduced movement ability for small mussels include the inability to relocate to better positions within the mussel aggregation for feeding, increased likelihood of burial in soft sediment beneath mussel beds, and vulnerability to predation due to the added stress of epibiosis (Thieltges 2005; Calderwood et al. 2014).

Fouling by artificial epibionts elicits different responses in small and large *M. edulis* in a controlled lab setting. Although larger mussels demonstrated changes in byssal thread production and attachment strength, small mussels experienced decreased mobility as a result of epibiont presence. This reaction to epibiont fouling suggests that mussels are capable of changing their physiological and behavioral processes in the presence of a newly settled epibiont. In addition, factors other than altered hydrodynamic forces due to epibiont fouling influence byssal thread production and movement in *M. edulis*. Biological factors that affect movement patterns and byssal thread production, such as differences in species interactions and epibiont biomass, require further study. Mussels are abundant competitors on rocky and sedimentary intertidal and subtidal shores, and hence, any changes to their spatial dynamics could impact the community structure of the surrounding intertidal environment and affect their ability to move between and within aggregations.

Acknowledgments. We are grateful for the assistance of Louise Garner, Blaine Garner, and Nate Rennels in laboratory studies. Thanks to Dan Maynard for his help with statistics. This work was supported by the UNH Marine Program, the Ruth E. Farrington Fund of the Department of Natural Resources and the Environment at UNH, the UNH Graduate School, and the College of Science and Mathematics at the University of West Georgia. Partial funding was provided by the New Hampshire Agricultural Experiment Station. This is Scientific Contribution Number 2653. This work was supported by the USDA National Institute of Food and Agriculture Hatch Project 222760.

References

Anthony KR & Svane I 1995a. Effects of substratum instability on locomotion and pedal laceration in *Metridium senile* (Anthozoa: Actiniaria). Mar. Ecol. Prog. Ser. 124(1): 171–180.

——— 1995b. Effects of substratum instability on locomotion and pedal laceration in *Metridium senile* (Anthozoa: Actiniaria). Mar. Ecol. Prog. Ser. 124(1): 171–180.

Bers AV, D'Souza F, Klijnstra JW, Willemsen PR, & Wahl M 2006a. Chemical defense in mussels: antifouling effects of crude extracts of the periostracum of the blue mussel *Mytilus edulis*. Biofouling 22(4): 251–259.

Bers AV, Prendergast GS, Zurn CM, Hansson L, Head RM, & Thomason JC 2006b. A comparative study of the anti-settlement properties of mytilid shells. Biol. Lett. 2: 88–91.

Borthagaray AI & Carranza A 2007. Mussels as ecosystem engineers: their contribution to species richness in a rocky littoral community. Acta Oecol. 31(3): 243–250.

Buschbaum C & Reise K 1999. Effects of barnacle epibionts on the periwinkle *Littorina littorea* (L.). Helgol. Mar. Res. 53(1): 56–61.

Buschbaum C & Saier B 2001. Growth of the mussel *Mytilus edulis* L. in the Wadden Sea affected by tidal emergence and barnacle epibionts. J. Sea Res. 45: 27–36.

Buschbaum C, Dittmann S, Hong J, Hwang I, Strasser M, Thiel M, Valdivia N, Yoon S, & Reise K 2009. Mytilid mussels: global habitat engineers in coastal sediments. Helgol. Mar. Res. 63: 47–58.

Calderwood J, O'Connor NE, Sigwart JD, & Roberts D 2014. Determining optimal duration of seed translocation period for benthic mussel (*Mytilus edulis*) cultivation using physiological and behavioural measures of stress. Aquaculture 434: 288–295.

Calderwood J, O'Connor NE, & Roberts D 2015. The effects of transportation stress and barnacle fouling on predation rates of starfish (*Asterias rubens*) on mussels (*Mytilus edulis*). Aquaculture 444: 108–113.

Carman MR, Lindell S, Green-Beach E, & Starczak VR 2016. Treatments to eradicate invasive tunicate fouling from blue mussel seed and aquaculture socks. Manage. Biol. Invasion. 7(1): 101–110.

Côté IM & Jelnikar E 1999. Predator-induced clumping behaviour in mussels (*Mytilus edulis* Linnaeus). J. Exp. Mar. Biol. Ecol. 235(2): 201–211.

Dijkstra JA & Nolan R 2011. Potential of the invasive colonial ascidian, *Didemnum vexillum*, to limit escape response of the sea scallop, *Placopecten magellanicus*. Aquat. Invasions 6(4): 451–456.

Dittman D & Robles C 1991. Effect of algal epiphytes on the mussel *Mytilus californianus*. Ecology 72(1): 286–296.

Donovan DA, Bingham BL, From M, Fleisch AF, & Loomis ES 2003. Effects of barnacle encrustation on the swimming behaviour, energetics, morphometry, and drag coefficient of the scallop *Chlamys hastata*. J. Mar. Biol. Assoc. U.K. 83(4230): 1–7.

Eschweiler N & Buschbaum C 2011. Alien epibiont (*Crassostrea gigas*) impacts on native periwinkles (*Littorina littorea*). Aquat. Invasions 6(3): 281–290.

Garner YL & Litvaitis MK 2013. 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. J. Exp. Mar. Biol. Ecol. 446: 52–56.

Hunt HL & Scheibling RE 1998. Spatial and temporal variability of patterns of colonization by mussels (*Mytilus trossulus*, *M. edulis*) on a wave-exposed rocky shore. Mar. Ecol. Prog. Ser. 167: 155–169.

Ishida S & Iwasaki K 2003. Reduced byssal thread production and movement by the intertidal mussel *Hormomya mutabilis* in response to effluent from predators. J. Ethol. 21(2): 117–122.

Kautsky N 1982. Quantitative studies on gonad cycle, fecundity, reproductive output and recruitment in the

Baltic *Mytilus edulis* population. Mar. Biol. 68: 143–160.

Khaitov V 2013. Life in an unstable house: community dynamics in changing mussel beds. Hydrobiologia 706: 139–158.

Laudien J & Wahl M 1999. Indirect effects of epibiosis on host mortality: seastar predation on differently fouled mussels. Mar. Ecol. 20(1): 35–47.

Liu G, Stapleton E, Innes D, & Thompson R 2011. Aggregational behavior of the blue mussels *Mytilus edulis* and *Mytilus trossulus*: a potential prezygotic reproductive isolation mechanism. Mar. Ecol. 32(4): 480–487.

Martinez MM 2007. Locomotion: intertidal challenges. In: Encyclopedia of Tidepools and Rocky Shores. Denny MW & Gaines SD, eds., pp. 335–338. University of California Press, Berkeley and Los Angeles, CA.

Moeser GM, Leba H, & Carrington E 2006. Seasonal influence of wave action on thread production in *Mytilus edulis*. J. Exp. Biol. 209: 881–890.

O'Connor NE 2010. Shore exposure affects mussel population structure and mediates the effect of epibiotic algae on mussel survival in SW Ireland. Estuar. Coast. Mar. Sci. 87: 83–91.

O'Connor NE, Crowe TP, & McGrath D 2006. Effects of epibiotic algae on the survival, biomass and recruitment of mussels, Mytilus L. (Bivalvia: Mollusca). J. Exp. Mar. Biol. Ecol. 328(2): 265–276.

Schneider K, Wethey D, Helmuth B, & Hilbish T 2005. Implications of movement behavior on mussel dislodgement: exogenous selection in a *Mytilus* spp. hybrid zone. Mar. Biol. 146(2): 333–343.

Seed R 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. 1. Breeding and settlement. Oecologia 3: 277–316.

——— 1976. Ecology of marine mussels. In: Marine Mussels: Their Ecology and Physiology, Bayne BL. ed., pp. 13–65. Cambridge University Press, London, England.

Seed R & Suchanek TH 1992. Population and community ecology of *Mytilus*. In: The Mussel Mytilus: Ecology, Physiology, Genetics and Culture. Gosling E, ed., pp. 87–157. Elsevier, Amsterdam.

Theisen BF 1972. Shell cleaning and deposit feeding in *Mytilus edulis* L. (Bivalvia). Ophelia 10: 49–55.

Thieltges DW 2005. Impact of an invader: epizootic American slipper limpet *Crepidula fornicata* reduces survival and growth in European mussels. Mar. Ecol. Prog. Ser. 286: 13–19.

Thieltges DW & Buschbaum C 2007. Mechanism of an epibiont burden: *Crepidula fornicata* increases byssus thread production by *Mytilus edulis*. J. Molluscan Stud. 73(1): 75–77.

Uryu Y, Iwasaki K, & Hinoue M 1996. Laboratory experiments on behaviour and movement of a freshwater mussel, *Limnoperna fortunei* (Dunker). J. Molluscan Stud. 62(3): 327–341.

Wahl M, Hay M, & Enderlein P 1997. Effects of epibiosis on consumer–prey interactions. Hydrobiologia 355(1–3): 49–59.

Wahl M, Kroger K, & Lenz M 1998. Non-toxic protection against epibiosis. Biofouling 12: 205–226.

Waite JH 2002. Adhesion à la moule. Integr. Comp. Biol. 42(6): 1172–1180.

Wiegemann M 2005. Adhesion in blue mussels (*Mytilus edulis*) and barnacles (genus *Balanus*): mechanisms and technical applications. Aquat. Sci. 67(2): 166–176.

Witman JD & Suchanek TH 1984. Mussels in flow: drag and dislodgement by epizoans. Mar. Ecol. Prog. Ser. 16(3): 259–268.

Young GA 1985. Byssus-thread formation by the mussel, *Mytilus edulis*: effects of environmental factors. Mar. Ecol. Prog. Ser. 24: 261–271.