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Holding On to a Shifting Substrate: Plasticity of Egg Mass Tethers and Tethering Forces in Soft Sediment for an Intertidal Gastropod

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Abstract. Staying attached at a favorable site can be a major challenge for organisms in flow. Meeting this challenge depends on properties of the attachment structure and substrate, the nature of fluid flow, and the ability to adjust attachment force in response to hydrodynamic conditions. A broad taxonomic range of adult stages use adhesion or suction to attach to hard substrates in intertidal habitats, which experience flow from waves and tidal currents. We address the unique challenges of attachment to soft sediment in reproductive structures deposited on tidal flats. Egg masses of the opisthobranch mollusc *Melanochlamys diomedea* are anchored to the sediment by a buried tether composed of gel and sediment. In the field, populations differed in absolute tethering force and tethering force per unit size (= tenacity). Population differences in tenacity persisted for egg masses oviposited under common conditions in the laboratory. Adults exposed to greater flow produced tethers with greater tenacity but without an increase in tether size. Tethers tended to fail by slippage rather than breakage, indicating that tethering force depends more on frictional interaction with sediment than on strength of the tether axis. These results suggest that adults respond to variation in risks of embryo dislodgment by adjusting the tethering properties of egg masses, and that these adjustments involve more than simple changes in tether length or mass.

Introduction

A major challenge for many organisms is to resist the forces of fluid motion that could remove them from advantageous sites. Meeting this challenge is especially critical for sessile or sedentary organisms that select settlement or deposition sites on the basis of their favorable characteristics (Spight, 1977; Highsmith, 1982; Larsson and Jonsson, 2006). Organisms that suffer removal from such sites can face transport to less favorable physical environments, increased predation, reduced feeding and mating opportunities, and physical damage (Carrington, 1990; Acuna and Zamponi, 1996; Cadee, 1999; Gray and Hodgson, 2004; Silva *et al.*, 2004; Schneider *et al.*, 2005; Lopez-Rocha and Naegel, 2007; Morritt *et al.*, 2007; Gaylord *et al.*, 2008; Zardi *et al.*, 2008; but see Miller *et al.*, 2007). As a result, many organisms rely on structures that use adhesives or suction to hold to a substrate with enough attachment and material strength to avoid dislodgment (Bell and Gosline, 1996; Wahl, 1996; Kitzes and Denny, 2005; Fowler-Walker *et al.*, 2006).

Resisting the force of water motion is a particular challenge in intertidal habitats, where waves, swash, and tidal currents can contribute to dynamic and unpredictable changes in biomechanical stress and risk of dislodgment (Denny, 1994; Trussell, 1997; Rilov *et al.*, 2004; D'Amours and Scheibling, 2007). Moreover, among intertidal habitats, soft-sediment tidal flats create a special challenge for attachment because the stability of the physical substrate is poor and highly variable (Chapman *et al.*, 2010). While many adults on tidal flats can burrow during periods of significant water motion, several of these organisms deposit reproductive structures—egg ribbons, strings, globes, or capsules (Hurst, 1967)—that lack a behavioral means of

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Abbreviations: AL, Argyle Lagoon; FB, False Bay; GB, Garrison Bay; MB, Mitchell Bay.

regulating exposure. Several species of gastropod mollusc and polychaete annelid, for example, anchor gelatinous masses to soft or hard surfaces on tidal flats (Hurst, 1967; Strathmann, 1987). Despite the potential for increased exposure to risks from other physical stresses (*e.g.,* temperature, desiccation, ultraviolet light; Moran, 1999; Strathmann and Hess, 1999; Podolsky, 2003), the consistent use of attachment devices by such species suggests that retention at the site of oviposition is typically beneficial (Spight, 1977; Woods and Desilets, 1997; Przeslawski and Davis, 2007).

Many intertidal organisms show adaptive patterns of variation in body features in response to variation in physical conditions, particularly when these features entail significant investment or tradeoffs (Carrington, 2002). Comparisons among related species in different environments, for example, reflect widespread correspondence between properties of attachment structures and flow regime (Dudgeon and Johnson, 1992; Denny and Gaylord, 1996; Bell and Gosline, 1997; Rilov *et al.*, 2004). Similarly, a diverse set of sessile marine organisms exhibits plasticity of morphology or behavior in response to variability in the risk of dislodgment from water motion, including algae (Kawamata, 2001; Stewart, 2004; Kitzes and Denny, 2005), plants (Sultan, 2000; Fowler-Walker *et al.*, 2006; Puijalon *et al.*, 2007), colonial cnidarians (Harvell and LaBarbera, 1985; Bell, 2002; Chang *et al.*, 2007), bivalves (Bell and Gosline, 1997), and gastropods (Wahl, 1996; Trussell, 1997; Wright and Nybakken, 2007). These studies suggest that traits influencing the probability of dislodgment can be a major target of selection.

In contrast to evidence for plasticity in adult attachment structures, the plasticity of attachment at early life-history stages is rarely examined. A response in the construction of attachment structures to variation in flow could be adaptive if detachment had consequences for the development or survival of embryos. For example, untethered egg masses of the squid *Sepioteuthis australis* showed higher mortality than those that remained tethered (Steer and Moltschaniwskyj, 2007). For intertidal egg masses, removal from deposition sites in tide pools could lead to stranding on higher ground or transport to subtidal habitats where embryos could be at greater risk of predation or delayed development (Fernandez *et al.*, 2007; Brante *et al.*, 2008). Thus, investment in egg mass tethers could enhance adult fitness by helping to retain embryos at favorable sites. Although several forms of extraembryonic investment can enhance adult fitness through effects on offspring survival (*e.g.,* Rawlings, 1996, 1999; Chaparro *et al.*, 1999; Podolsky, 2004), the adaptive plasticity of such forms of investment is not well understood (Gibson and Gibson, 2004).

We examined inter-population variation and plasticity of attachment devices for egg masses of an opisthobranch gastropod, *Melanochlamys diomedea* Bergh, that reproduces on soft-substrate tidal flats. Egg masses of *M. diomedea* are attached to the substrate by a buried tether, and the strength of hydrodynamic forces that could lead to dislodgment varies at different spatial and temporal scales. Intensive daily censuses of egg masses on transects at our main study site (False Bay, San Juan Island, Washington) indicate that disappearance rates are highly variable and occur in a pattern that reflects variation in tidal flows and turbulent weather, with up to 24% of masses removed on a given day (R. D. Podolsky, unpubl.), suggesting that tethering structures can play a critical role in resisting dislodgment from water movement. We combine field observations of egg mass properties and laboratory manipulations of flow to answer three questions: (1) Do natural populations living under different hydrodynamic conditions vary in the size of egg masses, tethers, and tethering forces? (2) Do properties of the egg mass tether and of local sediment help to explain variation in tethering force in the field? (3) Do adults in the laboratory respond to manipulation of water flow by altering basic properties of egg masses or tethers and by adjusting the force needed to dislodge an egg mass from the substrate?

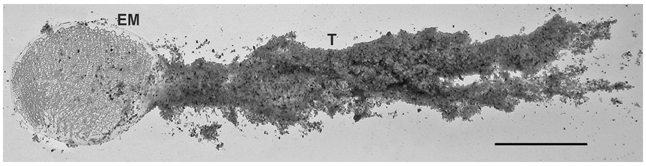

Figure 1. Egg mass of *Melanochlamys diomedea* from False Bay, pulled from sediment with the tether intact. Embryos can be seen in coiled strings throughout the mass. EM = egg mass, T = Tether. Scale bar = 1 cm.

Materials and Methods

Study system

Melanochlamys diomedea Bergh is a small cephalaspidean opisthobranch mollusc found on soft-substrate tidal flats from central California to southern Alaska (Behrens, 1991). In the study area, its balloon-shaped gelatinous egg masses, containing thousands of encapsulated embryos, are deposited in relatively calm bays in tidal channels or shallow pools that retain water at low tide. The egg mass is anchored to the substrate by a tether constructed by incorporating sediment particles into a long gelatinous axial extension of the terminal end of the mass (Fig. 1). The tether, which is composed of numerous strands and sheets that create contact with the surrounding sediment, is buried firmly in the substrate by the adult as the final act of oviposition. Adults (length 1 to 2 cm) produce egg masses (length 0.5 to 2.5 cm) with tethers (length 1 to 10 cm) that vary in size depending on the population and season. Masses remain tethered to the substrate for 7 to 10 days before embryos hatch and spend more than a month in the plankton as feeding larvae (Strathmann, 1987).

Parts of this study involved four intertidal sites on San Juan Island, Washington, where *M. diomedea* reproduces during late spring and summer. Tidal flats are exposed by low tides in the late morning or early afternoon. These habitats experience tidal currents and wave action, the magnitude of which varies among sites, as reflected by the rate of dissolution of gypsum clods (Jokiel and Morrissey, 1993). False Bay (FB) is a relatively exposed site with strong tidal forces and occasional wave action—owing to local topography and exposure to swells originating in the Strait of Juan de Fuca (Dent and Uhen, 1993)—and fast clod dissolution (3.6 times faster than in still water; R. D. Podolsky, unpubl.); Mitchell Bay (MB) experiences both moderate tidal currents and moderate wave action (clod dissolution = 2.5 times faster than in still water [2.5x]); Argyle Lagoon (AL) experiences moderate tidal currents in the area surveyed but no wave action, and moderate clod dissolution (2.1x); and Garrison Bay (GB) nearby to Mitchell Bay experiences mild tidal flow, no wave action, and slow clod dissolution (1.3x). Because the timing of reproduction varies across sites, egg masses were not available in sufficient numbers at GB during the time of field studies, and adults were not available in sufficient numbers at MB or AL at the time of laboratory studies. These field sites are near the Friday Harbor Laboratories, University of Washington, on San Juan Island, where laboratory measurements and experiments were carried out.

Field comparisons

To measure the relative force necessary to remove an egg mass from sediment *in situ*, egg masses were pulled from their substrates at three field locations (False Bay, Argyle Lagoon, and Mitchell Bay) during a series of low tides in June and July 2010. Measurements were done in shallow water (depth 3–14 cm), where egg masses are typically deposited, so that masses were always submerged. All masses found at each visit to the site were pulled. To pull the mass it was gently cradled by a plastic collar cut from the bulb of a plastic transfer pipette with a hole punched in its center to allow the tether to pass through undisturbed. The collar was connected to a digital force gauge (Model DS2-0.4, Imada, Inc.) by a thinly peeled strand of dental tape, chosen for its light weight and low elasticity. The force gauge recorded peak force during a slow and steady pull (approximately 0.5 cm s^{-1}) perpendicular to the substrate. Although the directionality of forces experienced by egg masses in flow is likely complex, we chose to standardize measurements using perpendicular pulls because (1) tethering force could depend on the angle of pulling relative to the main axis of the tether, (2) any undetected angling of tethers below sediment would have added too much noise to measurements for any pulling direction other than vertical, and (3) although the force gauge provides an extremely sensitive measure at this scale ($<$ 100 mN), it recorded accurately only when vertical. Because the peak force before the tether slipped from the sediment was always greater than the mass of the egg mass and its tether out of water, we were confident of recording the peak holding force even when measured in shallow water. A few centimeters from where each egg mass was pulled, we also measured the resistance of the sediment to compaction using a force penetrometer (Geotest Instrument Corp, Model E280) with a customized adapter foot (5-cm diameter) that was scaled appropriately for measuring these relatively compactable sediments.

Each egg mass was then transferred intact in a numbered vial to the Friday Harbor Laboratories where it was kept cool in a sea table before processing. Egg masses were examined under a dissecting microscope and assigned to one of three stages: Early (cleavage to tri-lobed gastrulation), Mid (post-gastrulation to early velar bud), and Late (veliger). Tethers were separated from egg masses with a razor blade at the point where sediment was first incorporated into the gel. Masses and tethers were then blotted using a standard technique to prevent sticking (separated from paper towel by 300-μm plastic mesh) and placed into individual aluminum weigh boats. We recorded the mass of each egg mass and its tether when wet, then after oven-drying at 75 °C for 12 h, then after ashing at 400 °C for 6 h. Results for dry mass and ash-free dry mass were qualitatively similar to those for wet mass and are not presented here, since wet mass better reflects forces experienced *in situ*.

Laboratory experiment

To measure tether production in a common garden and to manipulate hydrodynamic conditions, adults were collected from False Bay and Garrison Bay and placed in mesh-sided plastic containers in a flow-through seawater table until they were introduced into the experiment. (We did not use adults from nearby Mitchell Bay or from Argyle Lagoon because they could not be located in sufficient numbers at that time.) The experiment involved placing 14 randomly selected adults of one population into each of 18 "mini-flumes," 9 for each population.The mini-flumes were arrayed linearly in a sea table, with treatment-population-replicate combinations assigned at random.

The mini-flumes (Fig. 2) were constructed from plastic trays (38.1 × 7.6 × 5.1 cm, Rubbermaid) filled uniformly to a depth of about 2.5 cm with sediment collected from the surface of False Bay and submerged in 3.5 cm of seawater in a sea table. Small submersible fountain pumps (Model DP-70, Dolphin) submerged in the same sea table were used to recirculate table water back into flumes to produce flow through them. Water was delivered by the pumps through

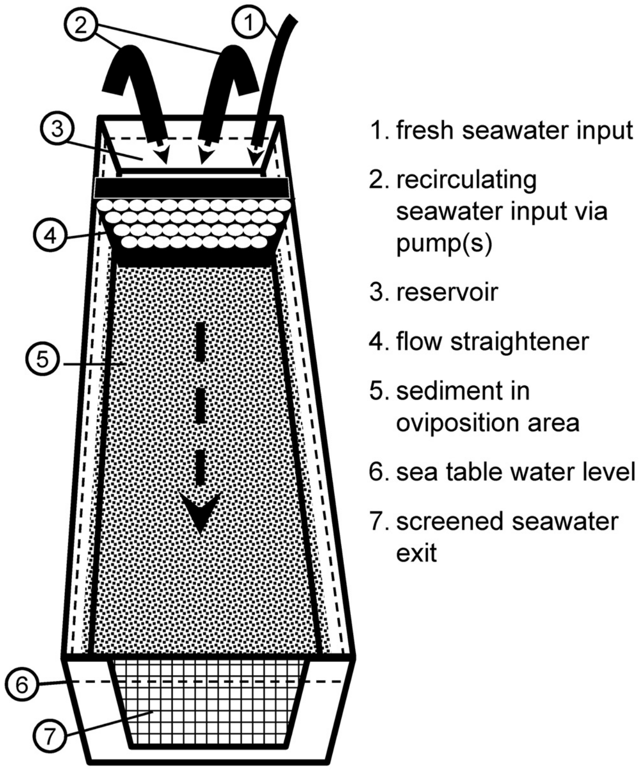

Figure 2. Schematic of mini-flume. Seawater was recirculated from the surrounding sea table into the reservoir by 0 (low-), 1 (medium-), or 2 (high-) flow submersible pumps. It then flowed through a straightener and across sediment in the oviposition area, exiting *via* a screened wall that retained adults. Flumes in all treatments had a small input of fresh seawater.

tubing to a small reservoir on one end of the tray and allowed to flow passively through a 1-cm-thick flow straightener and then across the sediment before exiting through a screen wall at the other end of the flume. The "High" flow treatment was fed by two pumps and the "Medium" flow treatment by one; no pumps were used for the "Low" flow treatment. Each flume also had a small trickle of fresh seawater from the seawater system at Friday Harbor Laboratories, which was distributed to the 18 flumes using three 6-valve irrigation manifolds (0.2 l/min; Agrifim, Fresno, CA) attached to the seawater input. As a result of these water inputs, average rates of flow through the tray in the three treatments were 8.4 (High), 4.3 (Medium), and 0.3 cm s^{-1} (Low). Pumps were cycled between on and off for 6-h periods, resulting in two 6-h "tidal" flows every 24 h. Each flow treatment included three replicate flumes, set with timers to start 8 h apart; the staggering was done to balance the design so that we could distinguish the effects of time-of-day from tidal cycles on deposition times (results not reported here). Thus, the final design involved 2 adult SOURCE populations (False Bay, Garrison Bay) × 3 FLOW rates (Low, Medium, High) × 3 REPLICATE flumes for a total of 18 flumes.

Before being introduced into the mini-flume, blotted wet masses for the 126 adults per population were measured (FB: 0.521 ± 0.15 g; GB: 0.405 ± 0.019 g). During the experiment, masses were pulled from sediment with a force gauge and measured using the same techniques as described for the field study.

Statistical analysis and presentation

Factors associated with variation in egg mass size, tether size, and tethering force were analyzed using ANOVA and ANCOVA. Egg mass size was used as a covariate for tether size, and tether size was used as a covariate for tethering force. In laboratory experiments, because egg mass qualities could have changed over time in captivity, we also used time since the start of the experiment as a covariate. Where a covariate was used in any analysis, homogeneity of slopes was confirmed before its interactions with other fixed effects were excluded from the analysis. Instances where variables were transformed to meet assumptions about normality, homogeneity of variances, or homogeneity of slopes are indicated in the text. In analyses of laboratory data, the random variable REPLICATE always produced poorer information criterion scores (Akaike information criterion and Bayesian information criterion) when included in a mixed-model analysis, and so was removed from each analysis (Burnham and Anderson, 2002). In the field, about 12% of tethers broke before slipping from sediment; these records were excluded from analyses other than the relationship between breakage and egg mass age.

For clarity, several factors are represented as uppercase letter codes: adult SOURCE (FB or GB), tethering FORCE (N), flume FLOW (Low, Medium, High), developmental STAGE (Early, Middle, Late), and DAY (day of egg mass deposition since adults were placed in flumes at the start of the experiment). Egg mass and tether properties, however, are described in words. Source populations are abbreviated as AL (Argyle Lagoon), FB (False Bay), GB (Garrison Bay), and MB (Mitchell Bay). Statistical analyses were performed using PASW Statistics (ver. 18, SPSS Inc.). Unless noted, reported values are mean ± 1 SEM.

Results

Population comparison of egg mass size, tether size, and tethering force

Egg mass size and tether size (both measured as log-transformed wet mass) were both significantly larger at FB than at MB and at MB than at AL (ANOVA, Fig. 3A, B). However, ANCOVA involving SOURCE as a factor found no significant relationship between tether size and the covariate egg mass size ($F_{1,138} = 0.295$, $P = 0.59$; Fig. 4). Thus, egg mass and tether sizes were positively related across but not within populations.

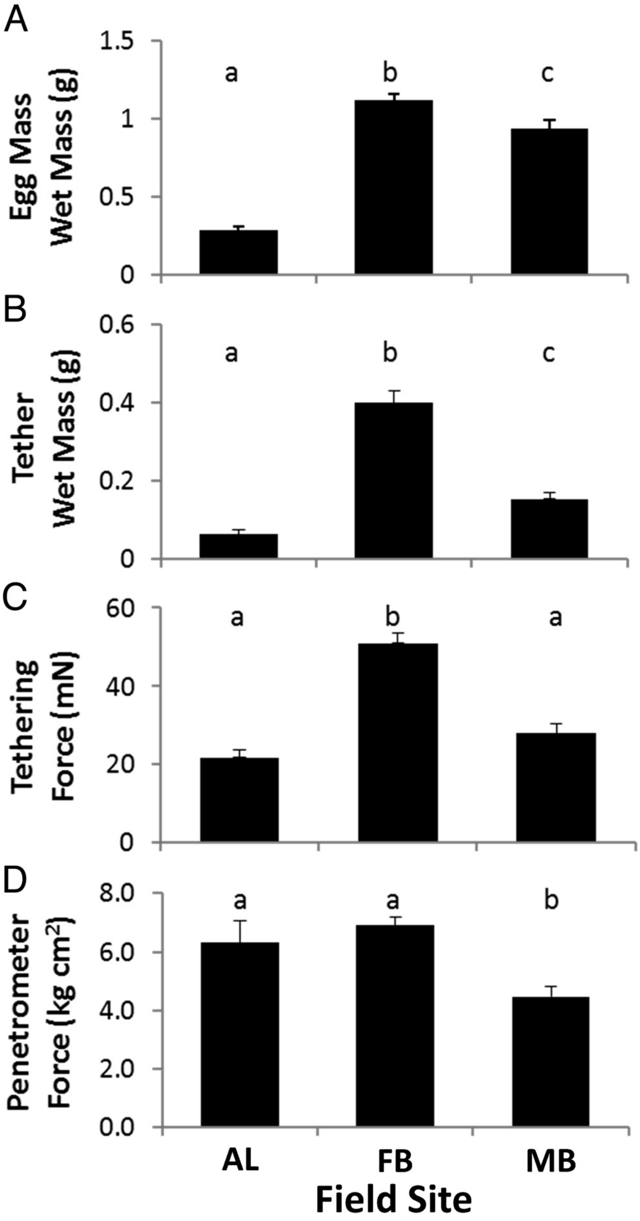

Figure 3. Comparisons among field sites in (A) egg mass size, (B) tether size, (C) tethering force, and (D) sediment resistance as measured with a penetrometer. Each bar shows mean + 1 SE for untransformed values. Data were transformed as described in the text to meet assumptions before analysis. Sample sizes are given in the text. Bars in each graph with different lowercase letters were significantly different at $\alpha = 0.05$ (sequential Bonferroni adjustment).

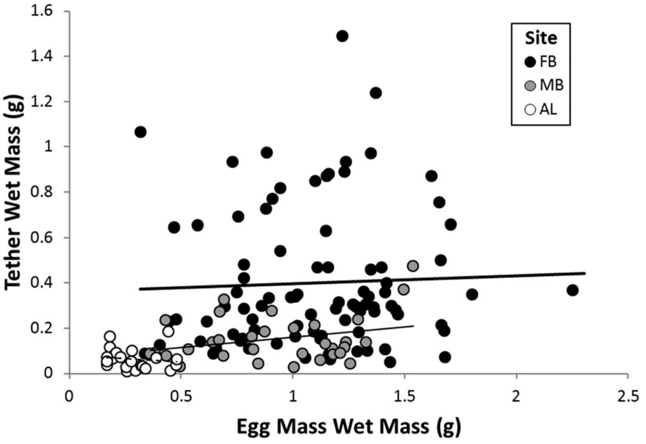

Figure 4. Tether size as a function of egg mass size for egg masses deposited at three field sites. Ordinary least-squares regression lines are for False Bay (FB, bold; $n = 96$), Mitchell Bay (MB, fine; $n = 35$), or Argyle Lagoon (AL, dashed; $n= 23$).

Tethering force (N) was positively related to tether size. ANCOVA found that log-transformed tether wet mass was a significant covariate for log-transformed FORCE ($F_{1,138} = 9.05$, $P = 0.003$; Fig. 5), and that SOURCE had a significant effect on log-transformed FORCE ($F_{2,138} = 9.06$, $P < 0.001$). The estimated marginal means for log-transformed FORCE were significantly greater at FB (0.618 ± 0.026) than at MB (0.431 ± 0.039) or at AL (0.387 ± 0.056); the latter two did not differ. Given the combined effects of differences in absolute tether size and in tethering force per unit tether size, the average tethering force of masses was significantly greater at FB than at the other two sites, which did not differ (Fig. 3C). When added to the model, egg mass STAGE did not have a significant effect on log-transformed FORCE for unbroken tethers ($F_{2,128} = 0.055$, $P = 0.95$). However, a greater percentage of late-stage masses (21.3%, $n = 61$) broke before slipping from sediment than did mid-stage (7.1%, $n = 56$) or early-stage masses (7.5%, $n = 53$; $\chi^2 = 7.06$, df = 2, $P < 0.03$).

The greater tethering force per unit wet mass for tethers at FB relative to other sites could have involved either other properties of tethers or properties of the sediment with which tethers interact. To evaluate a second property of

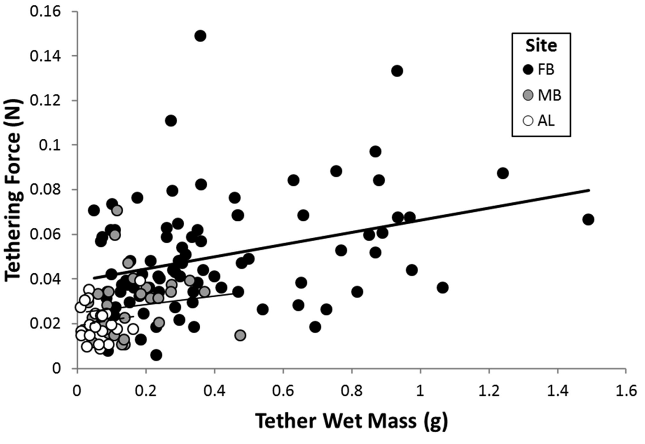

Figure 5. Tethering force as a function of tether size for egg masses deposited at three field sites. Ordinary least-squares regression lines are for False Bay (FB, bold; $n = 92$), Mitchell Bay (MB, fine; $n = 30$), or Argyle Lagoon (AL, dashed; $n = 23$).

tethers, we measured the lengths of fully extended tethers from digitized images for a subset of the egg masses from FB and MB. Controlling for tether wet mass, we found no significant partial correlation between tether length and tethering force (all values log-transformed) at either FB (df = 25, $r = 0.072$, $P = 0.72$) or MB (df = 28, $r = 0.13$, $P = 0.49$). As a comparison of sediment properties, penetrometer readings were significantly higher (*i.e.*, sediment was less compactible) at FB than at MB (Fig. 3D), which could help to explain why MB masses were more easily dislodged. However, controlling for log-transformed tether wet mass, we found no significant partial correlation between penetrometer reading near the egg mass and log-transformed tethering force at either field site (FB: df = 84, $r = 0.147$, $P = 0.18$; MB: df = 29, $r = 0.228$, $P = 0.218$). Thus, neither tether length nor sediment compaction appear to explain the mass-specific differences in tethering force we measured between sites. We did not attempt to compare other aspects of shape because it is difficult to standardize how the intricate three-dimensional folds of tethers are laid out for two-dimensional images.

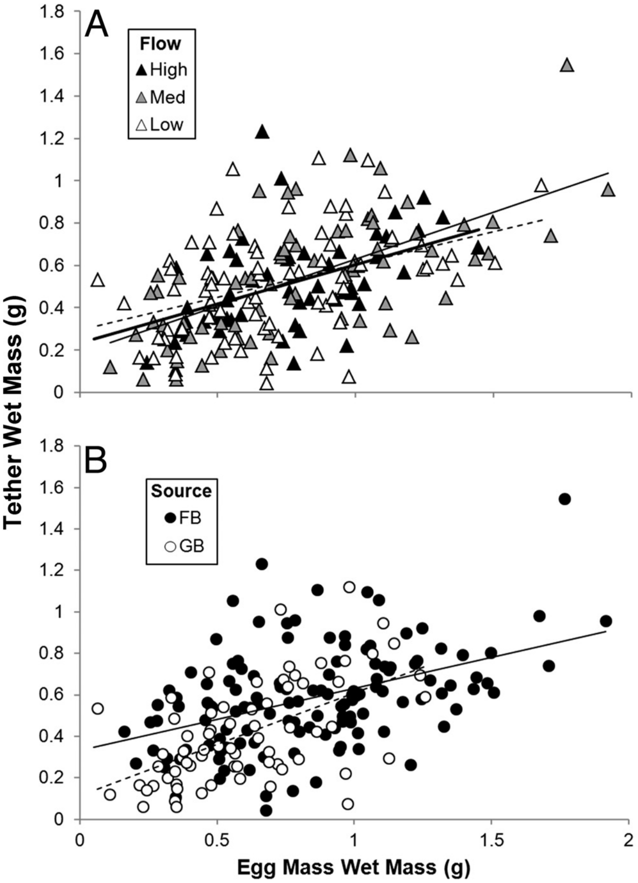

Figure 6. Tether size as a function of egg mass size in laboratory flumes (A) at three flow rates and (B) for individuals from two source populations. Ordinary least-squares regression lines in graph A are for High (bold), Medium (fine), or Low (dashed) flow, and in graph B are for False Bay (FB, solid) and Garrison Bay (GB, dashed).

Experimental comparison of egg mass and tether properties in response to water flow

Flow rate did not influence the size of egg masses produced by adults in the experimental flumes. ANOVA found no effect of FLOW ($F_{2,202} = 0.465$, $P = 0.63$), but a significant effect of adult SOURCE ($F_{1,201} = 12.64$, $P < 0.001$), on the wet mass of egg masses. FB adults produced significantly larger egg masses (0.806 ± 0.026 g) than those from GB (0.645 ± 0.037 g; estimated marginal means). The interaction between FLOW and SOURCE was not significant ($F_{2,202} = 1.30$, $P = 0.28$).

Similarly, flow rate did not influence relative or absolute tether size (Fig. 6A). ANCOVA found a significant effect of SOURCE ($F_{1,191} = 7.5$, $P = 0.007$), but no effect of FLOW ($F_{2,191} = 0.065$, $P = 0.94$) on tether wet mass using egg mass wet mass as a covariate; the interaction of SOURCE and FLOW was not significant ($F_{2,191} = 0.65$, $P = 0.55$). However, the interaction between SOURCE and the covariate was significant ($F_{1,191} = 7.5$, $P = 0.007$), requiring graphical inspection to understand the effect of SOURCE: FB adults produced substantially larger tethers at small egg mass sizes than did GB adults, but tether size converged at larger egg mass sizes (Fig. 6B). As expected (though unlike for egg masses from the field), egg mass size was strongly positively predictive of tether size ($F_{1,191} = 52.88$, $P < 0.001$).

Flow rate significantly influenced the force required to dislodge tethers of a given size (Fig. 7). ANCOVA found a significant effect of both SOURCE ($F_{1,192} = 18.3$, $P < 0.001$) and FLOW ($F_{2,191} = 3.91$, $P = 0.022$) on FORCE, using tether wet mass as a covariate; the interaction between FLOW and SOURCE was not significant ($F_{2,191} = 1.15$, $P = 0.32$). Pairwise comparisons at $\alpha = 0.05$ with a sequential Bonferroni correction (Rice 1989) found that tethering force was significantly greater at FLOW levels 2 (3.82 ± 0.19 g) and 1 (3.73 ± 0.16 g) than at flow level 0 (3.22 ± 0.16 g; estimated marginal means; Fig. 7A). Tethering forces at the higher flow rates were not significantly different. Also, mean tethering force for egg masses produced by adults from FB (4.02 ± 0.12 g) was significantly greater than for those from GB (3.16 ± 0.16 g; Fig. 7B).

Because all flumes had sediment from a single source, the effect of adult SOURCE on tethering force when controlling for tether mass must have resulted from some other property of the tether. As with the field data, we tested whether tether length relative to mass (as a measure of shape) could help to explain this effect. For neither source population, however, did we find a significant effect of FLOW on tether length with tether wet mass as a covariate (FB adults: $F_{2,125} = 2.8$, $P = 0.064$; GB adults: $F_{2,65} = 0.43$, $P = 0.66$). Similarly, for neither population did we find a significant partial cor-

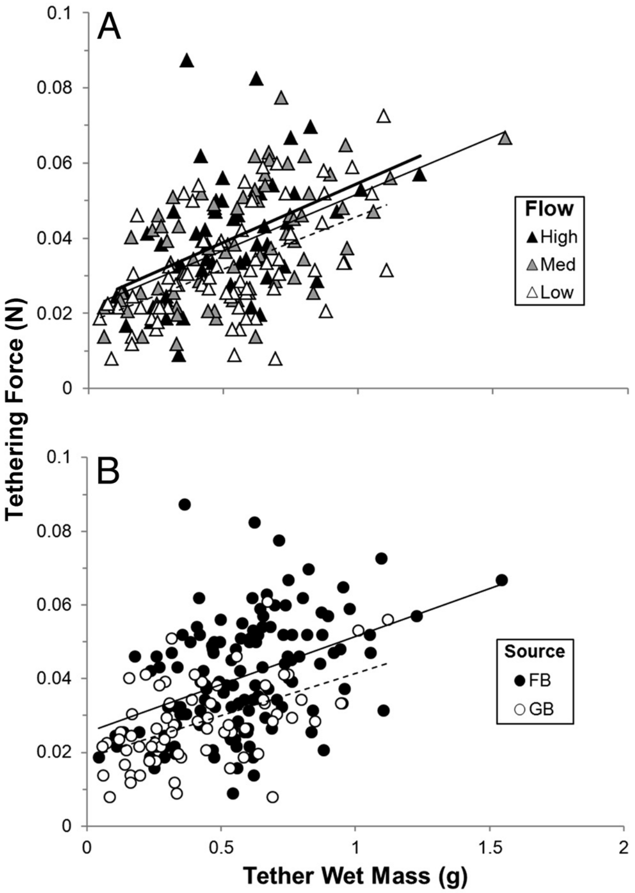

Figure 7. Tethering force as a function of tether size for egg masses deposited in laboratory flumes (A) at three flow rates and (B) for individuals from two source populations. Ordinary least-squares regression lines as in Fig. 5.

relation between tether length and FORCE, controlling for tether wet mass (FB adults: $r = 0.148$, $P = 0.096$; GB adults: $r = 0.082$, $P = 0.51$).

Discussion

Like other intertidal organisms (Denny, 1994; Gaylord, 1999), the sessile embryo clutches of *Melanochlamys diomedea* must withstand forces from waves and tidal currents. Two main features distinguish this system from most others in which this challenge has been addressed: egg masses must remain connected to an unstable substrate that is itself strongly influenced by flow, and the traits involved in resisting dislodgment must be maternally transmitted to an external structure. Because hydrodynamic forces in the intertidal are highly variable in space and time, adults might therefore use predictive information to adjust the properties of egg mass tethers in anticipation of conditions that embryos are likely to experience (see Kingsolver and Huey, 1998; Menu *et al.*, 2000). Our results from field observations and laboratory experiments support this hypothesis but suggest that, contrary to expectations, these adjustments involve more than simple changes in tether size.

In the field, adults from populations that produced larger egg masses also endowed them with larger tethers. The largest were from False Bay, which is the most exposed site and has the greatest tidal currents, owing to the way that flow is concentrated into the tidal channels where egg masses are deposited. Assuming that larger egg masses experience higher hydrodynamic loading and increased dislodgment force (Denny *et al.*, 1985; Trussell *et al.*, 1993; Bell and Gosline, 1997; Thomsen and Wernberg, 2005; D'Amours and Scheibling, 2007; Wolcott, 2007), these population differences are consistent with studies of other organisms—including algae, mussels, snails, and echinoderms—that show a general relationship between attachment strength and the force of water motion (Branch and Marsh, 1978; Denny and Gaylord, 1996; Carrington, 2002; Riis and Biggs, 2003; Rilov *et al.*, 2004; Thomsen *et al.*, 2004; Santos and Flammang, 2007; but see D'Amours and Scheibling, 2007). While our experimental data also showed a positive correlation between egg mass size and tether size, the two variables were uncorrelated in the field within each population. This lack of correlation suggests that other sources of variation unaccounted for by the variables we measured—egg mass age, tether length, and local sediment compaction—could be obscuring the relationship between egg mass size and tether size in the field.

Tether holding force, on the other hand, was consistently correlated with tether size, within and between populations in the field and laboratory. Not surprisingly, a correspondence between resistive force and size is found across diverse types of attachment structures, including bivalve byssal threads (Bell and Gosline, 1997; Caro *et al.*, 2008), the algal stipe/holdfast (Kitzes and Denny, 2005; Thomsen and Wernberg, 2005), the gastropod foot (Rilov *et al.*, 2004; Silva *et al.*, 2008), and echinoderm tube feet (Santos and Flammang, 2008). Larger tethering forces in False Bay might have been a simple scaling consequence of larger adult size; our experimental results, for example, showed that the larger adults from False Bay produced larger egg masses and tethers than did the smaller adults from Garrison Bay. However, both laboratory and field data showed an effect of adult population source on tethering force beyond the effect of tether size. In the field, tethering force per unit tether size (size-specific force, or "tenacity") was greater in False Bay than at the other two sites. In turn, this difference could have resulted from properties of tethers or of the sediment with which tethers interact. When housed in common sediment in the laboratory, however, the tethers of False Bay adults still showed greater tenacity. (It is possible that familiarity with the False Bay sediment used in laboratory experiments led to greater tenacity for masses from False Bay adults; however, an earlier experiment found no significant statistical interaction between the effects of adult source and sediment source on tether properties.) Furthermore, adults exposed to greater flow in the laboratory produced tethers with greater tethering force but without a significant change in tether size. Together, these results indicate that (1) populations differ in absolute holding force as a consequence of differences in tether size, (2) populations also differ in some aspect of tether construction that changes holding force independent of tether size, (3) adults can respond to flow by plastically adjusting the holding force of tethers, and that (4) they do so by some means other than increasing tether mass or length relative to mass.

The results of laboratory culture indicate that larvae of *M. diomedea* spend at least 40 days in the plankton after hatching from egg masses (Strathmann, 1987; Mach and Podolsky, 2005). The long planktonic larval phase and broad geographic range of *M. diomedea* along the northeast Pacific coast (Behrens, 1991) suggest that settlers are likely to arrive from different sources and, in turn, could encounter a range of hydrodynamic conditions. Nevertheless, adults from populations separated by just a few kilometers on San Juan Island differed in their construction of tethers in the field and in a common garden in the laboratory. If these nearby intertidal populations are genetically mixed, as seems likely given the fine geographic scale (Todd *et al.*, 1998) and simulations of larval dispersal trajectories in the region (Engie and Klinger, 2007), then local selection is unlikely to be responsible for population differences in attachment force, because the consequences of selection would not be manifest until settlement and reproduction of the dispersed generation. This life-history constraint distinguishes this system from others in which the importance of local selection in determining attachment forces of adults has been addressed (*e.g.,* Trussell, 1997; Kemppainen *et al.*, 2005; Prowse and Pile, 2005). Instead, our data are consistent with phenotypic plasticity of tether construction, which appears to be operating at two scales: a coarse component that leads to population differentiation—involving differences in tether size per unit mass size, and perhaps the differential development of anatomy or behaviors that influence tether construction—as well as a fine component in response to immediate flow conditions, involving adjustment of properties other than tether size. This fine-tuning of tether properties could be important for responding to changes in hydrodynamic forces at different parts of a tidal cycle or reproductive season, as seen in the number and material properties of mussel byssal threads (Carrington, 2002; Carrington *et al.*, 2009).

While relationships among hydrodynamic stress, attachment force, and structure size are widespread across diverse attachment structures, the tendency to plastically adjust attachment force without a change in structure size is atypical. In snails, for example, holding force of the foot is largely determined by size rather than by changes in tenacity (Trussell, 1997; Rilov *et al.*, 2004). Similarly, both detachment and drag forces of macroalgae are more often determined by thallus size than by shape (Milligan and DeWreede, 2004; Thomsen and Wernberg, 2005), although in the intertidal alga *Hormosira banksii*, failure occurred predominantly at the holdfast-substrate interface rather than through breakage of the stipe (McKenzie and Bellgrove, 2009). In mussels, holding force can be increased by changing the effective size of the byssal attachment complex, involving increases in byssal thread number or thickness (Bell and Gosline, 1997). On the other hand, Moeser and Carrington (2006) found that seasonal differences in attachment force were at least partly explained by changes in material properties of byssal threads, and Kitzes and Denny (2005) found that algae along a gradient of wave force showed changes in not only the diameter but also the material strength of stipes. On a much shorter time scale, limpets can switch between two modes of foot attachment with different holding forces—glue-like adhesion and suction—in response to hydrodynamic conditions experienced over a tidal cycle (Smith, 1992), and the tensile strength of a sea star tube foot can be rapidly altered by changes in mutable collagenous tissue (Hennebert *et al.*, 2010). These examples highlight that the effectiveness of different attachment devices may be governed by the particular properties of the structure and by the relative importance of material strength *versus* attachment strength.

In *M. diomedea*, what changes in tether construction could account for population differences in tethering force, or for the ability of adults to plastically adjust tethering force, independent of a change in tether size? Because tethers generally slipped rather than broke under the forces we imposed, the force of resistance likely depends on how the tether interacts with sediment. We are focusing on three hypotheses for future analysis. (1) Adults could change the shape of tethers in a way that we did not detect using the coarse measure of length relative to mass. The three-dimensional structure of tethers involves thick stems, thin strands, and flat sheets, the proportions of which could be altered to change the surface area in contact with sediment. (2) Adults could shift the size or shape distribution of sediment particles that are incorporated into the tether and thereby influence its surface properties. Several tube-dwelling polychaetes, for example, select larger particles for tube building and smaller particles for deposit feeding relative to the available distribution of sizes (Grémare, 1988; Noffke *et al.*, 2009), whereas caddisfly larvae can select particles with relatively smooth surfaces for construction of a smooth inner tube wall (Okano *et al.*, 2010). (3) An adult could alter the orientation of a tether relative to the sediment surface. To standardize measurements, we pulled tethers orthogonal to the substrate, but the magnitude of resistive forces is likely to depend on the angle of the pulling force applied relative to the long axis of the tether.

In an analogous system, for example, Stokes *et al.* (1996) demonstrated that particular angles of plant root growth are optimal to resist uprooting from the force of wind.

It is also unclear what tradeoffs or constraints in tether construction lead organisms to plastically adjust rather than simply overbuild tethering capacity, as seen in several rocky intertidal systems (Denny, 2006). Although tethers are built from seemingly low-cost materials—sediment particles in a gel matrix that is >98% water—gel accounted for a surprisingly high percentage (30% to 58%) of the total organic investment in egg masses of three related opisthobranch species (Lee and Strathmann, 1998), and similar values have been reported for material that makes up egg capsules and attachment stalks of some prosobranchs (Stickle, 1973; Perron, 1981). Thus, material costs could help to constrain investment in the tether as a proportion of total investment in the egg mass, particularly if dislodgment risk increases with egg mass size. It is also possible that more effective tethering—involving, for example, greater particle selectivity, more precise particle placement, or finer infiltration of gel into sediment—requires greater investment of energy or time. We plan to test the latter hypothesis by analyzing time-lapse video from the flume experiments to measure the time needed for tether construction under different flow conditions.

The assumption that tethers generally slip rather than break could depend on whether they respond similarly to natural forces and to those we imposed in this study. In some intertidal environments, for example, selection on features that resist dislodgment may be imposed more by accelerating forces of breaking waves than by sustained forces of currents (Denny and Gaylord, 1996). Given the relative protection of habitats in which *M. diomedea* reproduces, however, egg masses likely encounter tidal currents more regularly than breaking waves, which are more characteristic of higher energy, rocky habitats. Anecdotally, we have found that even when masses are pulled with greater acceleration from sediment, they still tend to dislodge by tether slippage rather than breakage, except for those in more advanced developmental stages when gel has begun to thin as embryos approach hatching. Our field measurements in this study supported this impression, in that only 7% of early-to-mid stage tethers broke, while three times that percentage broke at advanced stages. It is also possible that the standardized pulling direction we used could bias in favor of slippage, as pulling angle has been shown to change the magnitude of force needed to dislodge algae (McKenzie and Bellgrove, 2009) though not crabs (Lau and Martinez, 2003). However, in a separate study that followed marked egg masses on transects, we found that only 7% of 741 egg masses that disappeared between daily censuses left behind an intact tether, and 81% of those were late-stage masses close to hatching (R. D. Podolsky, unpubl.), numbers that are similar to our pulling records. Together, these observations support the hypothesis that tether failure generally occurs as a result of frictional interaction with sediment rather than from failure of the main tether axis.

In relying mostly on friction, egg mass tethers are distinctive from attachment structures that have been a focus of research on resistance to dislodgment from hard intertidal substrates. In turn, their structural features, which involve a highly flexible gelatinous core with imbedded hard particles, reflect both a common theme in the design of flexible but reinforced biological materials (Koehl, 1982) and the unique challenges of maintaining contact with a shifting substrate. Attachment structures more typically use adhesives (barnacles, anemones, algae, bivalves; MacDonald *et al.*, 2010; Stewart *et al.*, 2010) or a combination of suction and adhesion (prosobranchs, chitons, echinoderms; Smith, 1992; Santos and Flammang, 2006; Kim *et al.*, 2010) to connect to firm substrate, and detachment typically results from breakage of a structure or seal rather than from slippage. Even typically hard-bottom forms that are found in soft-sediment habitats—such as algae, anemones, and mussels—often attach to a hard substrate at or below the sediment surface (Peterson and Heck, 2001; Mouritsen and Poulin, 2003; Thomsen, 2004). Some semi-infaunal bivalves can anchor strictly by attachment to sediment particles, though particle sizes tested in these studies were larger than those in the tidal flats where egg masses of *M. diomedea* are tethered, and each byssal thread was attached to just one or a few particles (Meadows and Shand, 1989; Pelc and Alexander, 1999). In one of the only other uses of friction to resist dislodgment in the intertidal, attachment forces exerted by crab legs were about two orders of magnitude greater on rock than on mud (Lau and Martinez, 2003). Strength of attachment to mud was also at least an order of magnitude lower than the holding forces of tethers in our study—that is, crab legs are far poorer at using friction to hold to soft substrate. Still, the holding force of an entire tether in sediment at False Bay (on average only about 50 mN) is well below the attachment force of just a single sea star tube foot on hard substrate (Hennebert *et al.*, 2010). Given this low capacity, tethering force might therefore set an upper limit on egg mass size or on the range of habitats where attachment force is strong enough to overcome dislodgment force (Gray and Hodgson, 2004; Jonsson *et al.*, 2006). In fact, given the ability of adults to avoid periods of strong water motion by burrowing, it seems likely that biomechanical limits on reproductive structures rather than adult ecological requirements (Spight, 1977) could be what restricts this species to low-energy habitats (see Siddon and Witman, 2003).

Our findings help to establish a new dimension in understanding risks to encapsulated development (Przeslawski, 2004) and the role of maternal effects in egg mass design and embryo protection. If favorable sites are chosen for egg mass deposition (Spight, 1977; Demartini, 1991; Biermann *et al.*, 1992; von Dassow and Strathmann, 2005) and if retention at those sites has important consequences for embryo development or survival (Steer and Moltschaniwskyj, 2007), then maternal investment in the reliability of attachment structures should be as important as site selection. Given the material cost of gel and the energetic and time costs of sediment incorporation and burial, tethers represent a form of extraembryonic material investment that benefits development but is lost at hatching, analogous to the use of gel in egg masses to space embryos for reducing hypoxia (Strathmann and Strathmann, 1995; Lee and Strathmann, 1998), the use of gel or capsules to protect embryos from predators or physical stresses (Rawlings, 1999; Przeslawski, 2004), and the use of jelly coats surrounding eggs to improve fertilization success (Podolsky, 2004). In addition to determining which features of tethers are manipulated to alter tethering forces, future work should establish experimentally whether adults protect embryos from risks of intertidal water motion by controlling the timing of reproduction, as they appear to do in response to thermal risks (Podolsky, 2003).

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