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Flow variation and substrate type affect dislodgement of the freshwater polychaete, *Manayunkia speciosa*

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Abstract. We quantified microscale flow forces and their ability to entrain the freshwater polychaete, *Manayunkia speciosa*, the intermediate host for 2 myxozoan parasites (*Ceratomyxa shasta* and *Parvicapsula minibicornis*) that cause substantial mortalities in salmonid fishes in the Pacific Northwest. In a laboratory flume, we measured the shear stress associated with 2 mean flow velocities and 3 substrates and quantified associated dislodgement of polychaetes, evaluated survivorship of dislodged polychaetes, and observed behavioral responses of the polychaetes in response to increased flow. We used a generalized linear mixed model to estimate the probability of polychaete dislodgement for treatment combinations of velocity (mean flow velocity = 55 cm/s with a shear velocity = 3 cm/s, mean flow velocity = 140 cm/s with a shear velocity = 5 cm/s) and substrate type (depositional sediments and analogs of rock faces and the filamentous alga, *Cladophora*). Few polychaetes were dislodged at shear velocities <3 cm/s on any substrate. Above this level of shear, probability of dislodgement was strongly affected by both substrate type and velocity. After accounting for substrate, odds of dislodgement were 8× greater at the higher flow. After accounting for velocity, probability of dislodgement was greatest from fine sediments, intermediate from rock faces, and negligible from *Cladophora*. Survivorship of dislodged polychaetes was high. Polychaetes exhibited a variety of behaviors for avoiding increases in flow, including extrusion of mucus, burrowing into sediments, and movement to lower-flow microhabitats. Our findings suggest that polychaete populations probably exhibit high resilience to flow-mediated disturbances.

Key words: *Ceratomyxa*, *Parvicapsula*, shear, invertebrate drift, flow, Klamath River.

The dynamics of flow strongly influence the lives of lotic aquatic organisms (Craig 1990, Hart et al. 1996) and their community structure (Resh et al. 1988, Lake 1990, Giller et al. 1991, Nelson and Lieberman 2002). Flows affect larval and adult dispersal; movement of gametes, nutrients, and food particles; and waste removal (Wotton 1988, Rudek et al. 1991, Gaylord and Gaines 2000), and flow variation greatly influences the morphology, physiology, and behavior of lotic organisms (Statzner 1988, Craig 1990, Lancaster et al. 2006). High flows, such as spates and floods, or fluctuating

flows in the context of managed rivers may lead to reorganization of river substrates and the associated benthos because of increased, and often variable, velocities and hydraulic forces (Troelstrup and Hergenrader 1990, Lake 2000). Resultant scour and fill patterns may redistribute organisms or may reduce populations (Giller et al. 1991, Cobb et al. 1992, Death 1996, Matthaei et al. 1997, Mosisch and Bunn 1997).

Invertebrates use a number of methods to cope with flow-mediated disturbance, including movements to low-flow microhabitats (Lancaster 1999) where hydraulic forces are less severe and lower levels of disturbance are experienced. Examples of this behavior include seeking refuge in the hyporheic zone (Dole-Olivier et al. 1997) and entering the drift and swimming down toward the substrate in areas with reduced flow (Lancaster 1999). Selection of habitats

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with stable substrates or macrophytes may be used as a long-term strategy to reduce exposure to the effects of high flows (Richardson and Mackay 1991). Some invertebrates have specific morphological and behavioral adaptations including a streamlined body shape, physical attachment mechanisms (e.g., claws, suckers, hooks, and mucus), formation of drag-minimizing colonies, use of ballast materials (e.g., mineral cases of some Trichoptera), and rheotaxis (Schnauder et al. 2010).

Most investigators of invertebrate response to flow have quantified large-scale flow and habitat descriptors, such as mean velocity and mean depth (Davis and Barmuta 1989), substrate particle size, and general ecological classifications of the preferences of species (Schnauder et al. 2010). These large-scale measurements have proven useful in habitat models used for purposes like river restoration (Gore et al. 1998, Parasiewicz 2001), but they offer limited insight into the near-bed flow microhabitat in which benthic invertebrates are found. Microhabitat flows usually differ significantly from macrohabitat flows. For example, flows near the substrate typically are slower as a result of interactions with substrate roughness or the presence of a boundary layer (Muschenheim et al. 1986, Vogel 1994). Assessing microhabitat flows necessitates fine-scale measurements that can be difficult to obtain in the field. An alternative approach is to use a laboratory flume, which provides a controlled environment in which to quantify flow effects on substrates and biota (Muschenheim et al. 1986).

One way in which flows may affect invertebrate distributions is by dislodging animals from the substrate. Relatively few investigators have sought to quantify microscale flow forces and their ability to dislodge invertebrates from substrates (Dorier and Vaillant 1953/1954, Dussart 1987, Schnauder et al. 2010). Thus, a large body of data concerning species-specific behaviors of benthic invertebrates related to changes in near-bed hydraulics is lacking (Lancaster 1999, Palmer et al. 1996). Investigators who have sought to quantify these forces typically have concentrated on relatively large, common taxa such as *Ecdyonurus* (Dorier and Vaillant 1953/1954) and *Calopteryx* (Schnauder et al. 2010), but only coarse-flow measures have been related to less-studied organisms, such as Bryozoa (Mason et al. 1970), Oligochaeta (Marchese 1987), and Polychaeta (Stocking and Bartholomew 2007), which can be abundant in aquatic systems.

Manayunkia speciosa Leidy (Canalipalpata: Sabelliidae) is a small freshwater polychaete that occurs in the Great Lakes and coastal areas of North America (Pettibone 1953, Hazel 1966, Holmquist 1973) (Fig. 1).

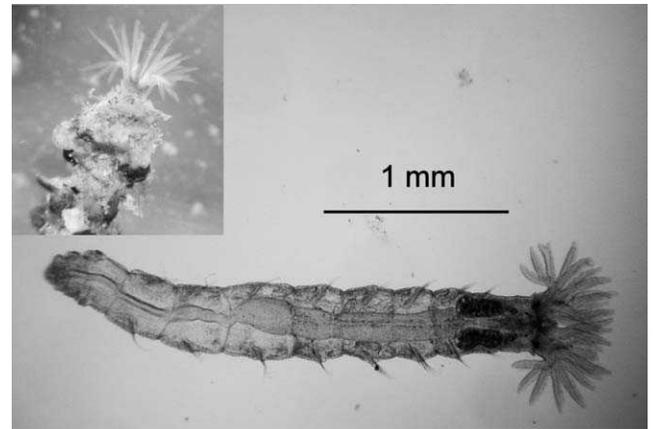


FIG. 1. *Manayunkia speciosa* is the intermediate host for myxozoan parasites *Ceratomyxa shasta* and *Parvicapsula minibicornis* which are responsible for substantial mortalities among juvenile Pacific salmon in the Pacific Northwest, especially in the Klamath River basin. Pictured is an adult worm without its tube. Inset: an adult worm inside of its tube in a feeding posture.

It is a habitat generalist that tolerates a broad range of water chemistry (pH, dissolved O₂), temperature, depth, and mean velocity (Hiltunen 1965, Holmquist 1973, Poe and Stefan 1974, Rolan 1974). *Manayunkia speciosa* is a suspension feeder, but its specific food requirements remain unknown. It reproduces sexually and appears to have an annual life cycle. Juvenile polychaetes are brooded in the maternal tube until capable of independent survival (Willson et al. 2010).

In the Klamath River, the polychaete occupies a variety of substrates including depositional sediments, bedrock, woody debris, and macrophyte beds (Stocking and Bartholomew 2007, Willson et al. 2010). This benthic polychaete usually occupies a tube (Leidy 1883), except in cases of physical disturbance (Willson et al. 2010), and can be locally abundant with reported densities >40,000 individuals/m² (Pettibone 1953, Stocking and Bartholomew 2007). It has become an organism of increasing interest because it is an intermediate host for 2 myxozoan parasites, *Ceratomyxa shasta* Noble and *Parvicapsula minibicornis* Kent, which have recently caused mortalities in wild and stocked juvenile salmonids in the Pacific Northwest, including Alaska (Follett et al. 1994), the Fraser River (British Columbia, Canada) (Ching and Munday 1984), the Columbia River basin (British Columbia, Washington, Oregon, Idaho, USA) (Hoffmaster et al. 1988), the Klamath River basin (California, Oregon, USA) (Hazel 1966), and the Pit (Noble 1950), Sacramento, and San Joaquin river systems in California (Hendrickson et al. 1989). Mortalities among salmonids have been particularly substantial

in the lower Klamath River basin (Foott et al. 1999, 2004).

We quantified shear stresses needed to dislodge *M. speciosa* in a laboratory flume from substrates similar to those on which the polychaete is found in the Klamath River basin to facilitate future predictions of polychaete response to altered flows and to gain a greater understanding of the basic biology of this species, which may potentially offer insights to guide management strategies. We quantified *M. speciosa* substrate tenacity with an approach similar to that used by Schnauder et al. (2010) to facilitate comparisons with values obtained for other freshwater lotic taxa. We modeled probability of dislodging the polychaete as a function of velocity and substrate type, and described the behavioral responses of *M. speciosa* to varying flows and substrate types.

Methods

Collection and culture of the polychaete

We collected polychaetes attached to rocks from the Klamath River, California, upstream of the Interstate 5 rest area (lat 41°51'35.8"N, long 122°34'00.1"W) in late June and late October 2011. We placed the rocks in coolers with ice and river water and transported them to the Humboldt State University fish hatchery. We maintained the polychaetes in culture facilities described by Willson et al. (2010). Before beginning a trial, we brought the rocks to the laboratory and scanned them visually with the aid of a dissection microscope to find and remove individual polychaetes. We put the polychaetes in small crystallizing dishes in an aerated 20-L aquarium until they were needed. We maintained the aquarium at an ambient temperature of 20°C, and changed the water weekly with fresh water from the fish hatchery.

Flume description

We constructed an experimental flume modified from Vogel and LaBarbera (1978) (2.6 m long × 1.35 m high × 0.44 m wide) in-house at Humboldt State University for use in experimental trials (Fig. 2). The flume was a closed-circuit, recirculating system, with a channel that was 43 cm wide × 26 cm high × 175 cm long internally. Water was returned through a loop of 20.3-cm polyvinyl chloride (PVC) pipe ~5.3 m in length. The water was moved by 2 propellers on a shaft powered by a 2-HP, 3-phase inverter-duty AC induction motor. To decrease large-scale turbulence, we placed a 35-mm-long collimator made of parallel sheets of 1.3-cm egg crate light diffuser upstream of the center of the flume. We filled the flume with

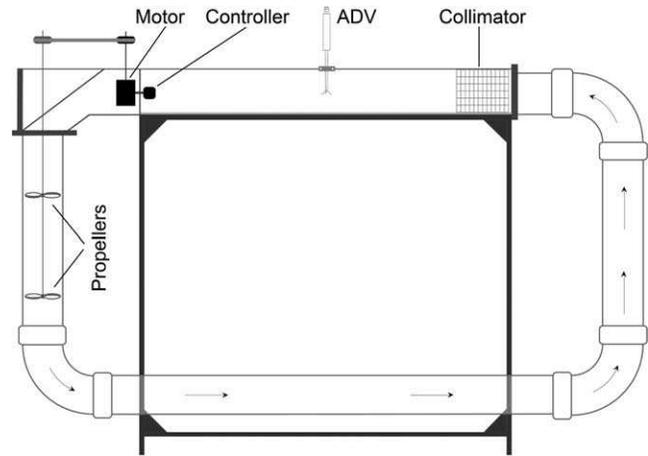


FIG. 2. Diagram of the experimental flume. The flume was 2.6 m long × 1.35 m high × 0.44 m wide. Water was moved by 2 propellers on a shaft, powered by a 2-HP AC induction motor. Velocity readings were measured with an Acoustic Doppler Velocimeter (ADV) placed in the center of the channel, directly above the polychaetes.

dechlorinated tap water and kept it at ambient indoor temperatures (18°C) for all trials.

Experimental trials

We evaluated polychaete dislodgement and behavioral responses to combinations of 2 mean flow velocities and 3 different substrates. We placed polychaetes on a substrate that was then placed in standing water in the flume, and we gradually increased the flow to mean velocities equal to 55 or 140 cm/s. We tested 3 substrate types: fine sediments, and analogs of rock faces and the filamentous green alga *Cladophora*. We ran 5 treatment trials and 5 control trials for each velocity/substrate combination. In control trials, we left polychaetes in standing water for the duration of the experiment. All controls were paired with a treatment and carried out simultaneously. Previous investigators (Willson et al. 2010) and pilot trials showed that polychaetes can experience substantial mortality from handling and that they may wander prior to construction of their fixed retreat, even on substrates where they are commonly found (sensu Lewis 1968). We also observed that senescent polychaetes were less able to affix to the substrates. We ran trials over several months, so controls helped us ensure that dislodgement was independent of age. *Manayunkia speciosa* is susceptible to mortality in tap water that is not properly conditioned, and controls allowed us to eliminate tap water as a cause of mortality. Thus, controls allowed assessment of true dislodgement of living, affixed polychaetes.

We used 20 polychaetes, ranging in length from 2 to 3 mm, per trial, and we used each animal only once. A trial included a 30-min period during which the open-channel velocity was increased to its terminal level followed by a 45-min period of polychaete exposure to the test velocity. We ran trials during daylight hours with overhead fluorescent lighting. We measured dislodgement as % individuals remaining on the substrate at the end of a trial. We observed polychaete behaviors, including tube-building, feeding, movements on or off substrates, direction of movements, and response to collisions with entrained sediments throughout each trial.

We chose test velocities and substrate types to simulate polychaete habitats in the Klamath River. Our choices also were influenced by results of pilot trials. We set the low-flow level to 55 cm/s after observing that polychaetes were not dislodged from any substrate type in the flume at mean velocities <55 cm/s. We chose the maximum working mean velocity that we could produce in the channel as the high-flow velocity. Both velocities would be likely to occur only in swift runs or riffles. Three of the most common substrates from which polychaetes have been collected in the Klamath River are beds of *Cladophora* or vascular macrophytes, organically enriched fine sediments, and large stable substrates, such as boulders or large woody debris (Stocking and Bartholomew 2007, Willson et al. 2010, Malakauskas and Wilzbach 2012). Establishing live plants in the flumes would have been difficult and the flumes were not large enough to accommodate boulders, so we developed analogs of these substrates for use in the trials. We also experimented with aquarium gravel (median particle size = 4.5 mm) as a substrate in preliminary trials, but we discarded this treatment after finding that the polychaetes abandoned it immediately.

We mimicked rock faces with 15 × 15-cm unglazed ceramic tiles and *Cladophora* with square finishing pads of synthetic fibers (3M, St. Paul, Minnesota), hereafter referred to as pseudophora (Fig. 3). We cut pseudophora squares to be 254 × 254 × 2-mm high and affixed each square to the center of a tile with Defthane polyurethane (Deft, Inc., Irvine, California). We obtained depositional sediments and fine benthic organic matter (FBOM) from Fern Lake (lat 40°52'29.4"N, long 124°04'25.9"W) on the Humboldt State University campus. We filtered sediments through a 500-μm screen and stored them dry in 34 × 32 × 14-cm-high plastic tubs until use (Willson et al. 2010).

In preliminary trials, *M. speciosa* would not affix to any substrate unless some fine particulate organic

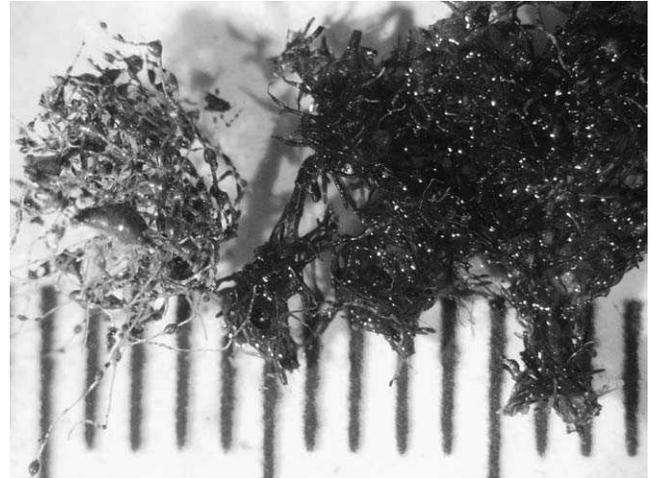


FIG. 3. Comparison of *Cladophora* (right) and an experimental analog (pseudophora) (left). Pseudophora was used as a substitute for *Cladophora* in flume trials. Vertical lines at bottom are 1 mm apart.

matter was present, so we added ~0.5 cm³ of FBOM to the center of each substrate type. After preparation, each substrate (unglazed tiles, tiles with pseudophora squares, and acrylic trays with fine sediments) was placed in separate 25 × 20 × 8-cm-high plastic containers filled with hatchery water. We removed polychaetes from their tubes (preliminary trials showed that doing so facilitated attachment to substrates) and placed 20 of them on the center of each substrate. After 1 h, we added an air bubbler to each container and allowed polychaetes to acclimate for 24 h prior to the start of a trial. During this time, the polychaetes reconstructed their tubes. Before we placed substrates in the flume, we counted the polychaetes again to ensure that all 20 individuals were present.

For trials with tile and pseudophora, we removed the substrates from their containers and placed them in a 15 × 15-cm trench cut into a 1-cm-thick sheet of foam that was placed on the bottom of the flume. This step prevented separation of flow around an isolated tile. For sediment trials, we placed 2 pieces of foam, painted with polyurethane and coated with sediment, flat on the bottom of the channel in series, with a 15-cm gap between them. We placed a 15 × 15 × 1-cm-high acrylic tray of sediment in the space between the foam sheets and added aquarium gravel and sediment to fill the spaces between the tray and the channel walls. We used this approach to reduce the amount of sediment and gravel entrained in the flow.

After each trial, we removed the substrate from the flume and returned it to a plastic container with air bubblers for 48 h at 20°C, after which we counted

polychaetes on the substrates and assessed mortalities. We also collected sediment that was scoured during the course of the sediment trials from the flume with a turkey baster and plastic spoon. We examined the sediment for polychaetes and set these individuals aside for 48 h before mortalities were evaluated. Our previous work showed that polychaete death from physical injury occurred within this time frame (Willson et al. 2010).

We measured velocity during each trial to characterize open-channel and near-bed flows at the test velocities. We waited for 10 min after reaching the terminal velocity for flows to stabilize before making measurements. We made all velocity measurements with a SonTek (SP-AV10M01) Acoustic Doppler Velocimeter (ADV) (SonTek/YSI, San Diego, California) mounted above the center of the flume, directly over the polychaetes. For each trial, we made 17 measurements, starting at a height of 10 mm above the bed (Finelli et al. 1999) at 5-mm intervals (sampling volume height and diameter = 9 mm and 6 mm, respectively) to obtain a velocity profile and Reynolds stress ($-\overline{u'w'}$; where u' and w' are temporally averaged velocity fluctuations in the streamwise and vertical directions, respectively) profile for use in calculations, such as to obtain shear velocity. At each height, we sampled 3-dimensional flow-velocity measurements at a rate of 10 Hz over a period of 45 s. The high-flow setting resulted in a surface wave and flow separation around the probe, leading to encapsulation of the probe head by air. As a result, we were unable to obtain measurements above a height of ~4.5 cm. However, we obtained enough data points to run a regression and to make calculations with respect to flows experienced by *M. speciosa*.

We obtained a Reynolds stress profile from u' and w' at 9 heights (5 runs at each velocity–substrate combination) above the bed. We used a regression to estimate Reynolds stress at the bed and calculated the shear velocity (U_*) as:

$$U_* = \sqrt{-\overline{u'w'}}$$

Researchers have used many methods to express velocities experienced by invertebrates, including measurements at a height of 5 mm above the bed. Therefore, to facilitate comparison with other published values, we used a least squares regression of $\ln(z)$ vs U , where z is height above the bed and U is its associated mean velocity, to calculate velocities 5 mm above the bed.

We used the Reynolds number (Re) to characterize the mean flow. This dimensionless value is a ratio of inertial to viscous forces (Vogel 1994) and is calculated as:

$$Re = \frac{UR_h}{\nu}$$

where R_h is the hydraulic radius of the flume, and ν is the kinematic viscosity of water. Re values >2000 indicate turbulent flows, whereas values <500 indicate laminar flows. We used a least squares regression of z vs velocity with data from velocity profiles obtained at 9 mean velocities (ranging from 14–125 cm/s) to estimate U for calculating Re at the high-flow setting.

We also characterized the effective drift velocity ($U_{\perp,d}$) and the body-length Re (Re_l) at the low- and high-velocity settings. $U_{\perp,d}$ represents the average flow experienced by invertebrates (Schnauder et al. 2010) and has a direct relationship with drag forces acting upon the body of the organisms:

$$U_{\perp,d} = \frac{\int_0^h U(z) dz}{h}$$

where h is the average height of the invertebrate. We used $U_{\perp,d}$ to calculate Re_l :

$$Re_l = \frac{U_{\perp,d} l}{\nu}$$

where l is the length of the invertebrate. Here, l represents the average tube width of an individual polychaete. Some polychaetes formed aggregates of tubes, so we also used the length of the mass of tubes as a length. Re_l values are typically <10 for lotic invertebrate larvae and >1000 for adult forms (Statzner 1988). As Re_l decreases, drag forces become proportionately greater than lift forces (Vogel 1994), and drag forces typically are more important than lift forces for benthic, lotic invertebrates (Statzner 1988).

Statistical analyses

We modeled worm dislodgement as a binary random variable, $y_i \sim Bin(1, \pi_i)$, where y_i is 1 if worm_{*i*} is dislodged, and 0 if not, and π_i is the probability of dislodgement. To assess the effects of treatments on dislodgement probability, while additionally accounting for correlation among responses from the same experimental trials, we used a binomial generalized linear mixed model with a logit link function, and a random effect for trials where

$$E[Y|\delta] = g^{-1}(X\beta + Z\delta)$$

and X is a design matrix of treatment levels, β is a vector of regression coefficients, Z is a design matrix specifying the trial for each observation, δ is a vector of random effects parameters, and $g()$ represents the logit link function. We assessed the significance of

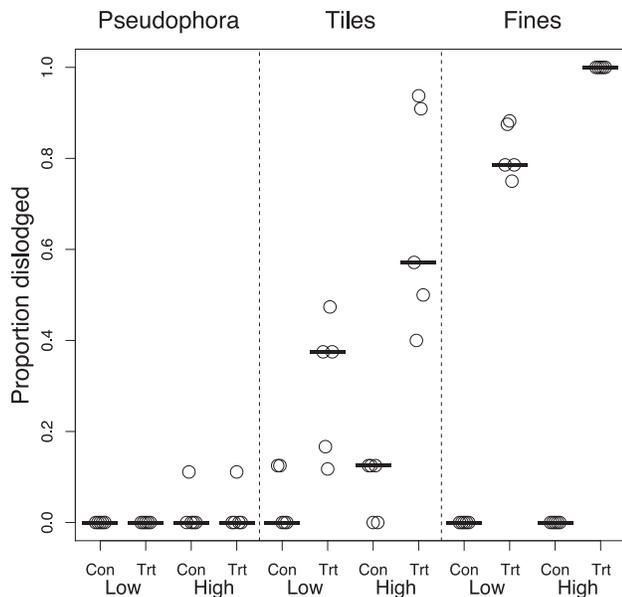


FIG. 4. Observed proportions of dislodgement of individuals among the 5 trials with each combination of control (Con = 0 flow), velocity (Trt = 55 cm/s or 140 cm/s), and substrate type (pseudophora, tiles, and fine sediments). Pseudophora and tiles were analogs of *Cladophora* and rock faces, respectively. All controls were paired with a treatment and carried out simultaneously. Observed proportions are jittered. Bars represent medians.

treatment effects via likelihood ratio tests. Model parameters were estimated with SAS software's GLIMMIX procedure using adaptive Gauss–Hermite quadrature to approximate the log-likelihood (SAS Institute, Cary, North Carolina).

Results

Probability of dislodgement

There was strong evidence that variation in polychaete dislodgement, within combinations of the velocity treatment levels with the tile and sediment substrates, could not be attributed to random polychaete behavior or laboratory conditions. The odds of dislodgement for tile and sediment substrates for noncontrol trials was estimated to be 374× higher (95% CI: 124–1126) than control trials, after accounting for velocity and substrate effects. On pseudophora substrates, observed polychaete dislodgement probabilities among the control and noncontrol trials were nearly identical at each velocity level (Fig. 4). Though this condition precluded the separation of observed dislodgement on the pseudophora substrates from random chance or laboratory conditions in the strictest sense, the low levels of dislodgement on pseudophora substrates overall warranted their inclusion in a

TABLE 1. Estimated probabilities (95% CI) of dislodgement for combinations of velocity and substrate analogs of *Cladophora* (pseudophora), bare rockface (tile), and fine sediments. The trials took place at mean velocities of 55 cm/s and 140 cm/s for low and high velocity trials, respectively.

Velocity	Substrate		
	Pseudophora	Tile	Fine sediment
Low	0.002 (0.001, 0.015)	0.25 (0.14, 0.40)	0.86 (0.74, 0.93)
High	0.012 (0.002, 0.088)	0.73 (0.56, 0.85)	0.980 (0.94, 0.99)

broader analysis of substrate and velocity effects on the probability of dislodgement.

Considering the noncontrol trials only, the odds of dislodgement was associated with substrate type ($p < 0.001$) and velocity ($p < 0.001$). After accounting for substrate, the odds of dislodgement at high velocity was estimated to be 8× higher than at low velocity (95% CI: 3–21.6). Relative to pseudophora substrates, the odds of dislodgement on tile and sediment substrates were estimated to be 214× higher (95% CI: 24–1879) and 3990× higher (95% CI: 373–>40,000), respectively, after accounting for velocity effects. These stark odds differences reflect the gradient in observed proportions of dislodgement (Fig. 4), and estimated probabilities of dislodgement for each combination of velocity and substrate (Table 1).

Flows and polychaete response

U_* averaged 2.3 cm/s at the low-flow level and 4.7 cm/s at the high-flow level. Flows at both velocities exceeded the threshold value of 2000 and were turbulent, with $Re = 6 \times 10^5$ and 1.6×10^6 for low and high velocities, respectively. U_* was higher for trials on fine sediments than on other substrates, a result that may reflect the influence of the gravel sublayer (Table 2). Actual U_* for a homogeneous layer of sand would probably be similar to values for the other substrates in the low-velocity trials. Mean velocity of the flow field around the polychaetes ($U_{\perp,d}$) was 38.3 cm/s at the low-flow level and 103.7 cm/s at the high-flow level. Re_l values were all >100, which combined with high mean flow Re indicated that the polychaetes were affected to a greater extent by drag than by lift forces.

Isolated polychaetes experienced the least dislodgement in tile trials, whereas polychaetes that were in ball-shaped masses experienced the greatest dislodgement, as would be expected because of increased drag. Moreover, some polychaetes were lost immediately after velocity increases despite efforts to increase

TABLE 2. Mean (95% confidence intervals) values for hydraulic variables and body measurements of polychaete exposed to experimental velocity/substrate treatments. U_s is shear velocity, $U_{\perp,d}$ is the effective drift velocity, $U_{z=5}$ is the velocity at a reference height of 5 mm above the bed, l is the average length of a polychaete tube, h is the height of a polychaete tube above the bed, and Re_l is the body-length Reynolds number. $l > 0.5$ mm represents aggregates of clumped individuals.

Velocity	Laboratory substrate	Substrate represented	U_s (cm/s)	$U_{\perp,d}$ (cm/s)	$U_{z=5}$ (cm/s)	l (mm)	h (mm)	$Re_l \times 10^2$
Low	Tile	Rock face	1.9 (1.6, 2.1)	40 (37, 43)	51 (49, 53)	0.5–3	1–3	1.9–13
High	Tile	Rock face	4.0 (3.7, 4.2)	110 (108, 112)	116 (113, 119)	0.5–3	1–3	5.4–34
Low	Pseudophora	<i>Cladophora</i>	1.9 (1.8, 2.1)	40 (33, 47)	52 (46, 58)	0.5	1–3	1.7–2.3
High	Pseudophora	<i>Cladophora</i>	4.3 (4.0, 4.7)	108 (103, 113)	122 (117, 127)	0.5	1–3	5.3–5.8
Low	Fines	Fines	3.2 (3.1, 3.3)	35 (33, 37)	50 (48, 52)	0.5	1–3	1.6–1.8
High	Fines	Fines	5.7 (5.5, 6.0)	93 (91, 95)	125 (122, 128)	0.5	1–3	4.6–4.7

velocities slowly. Polychaetes in the pseudophora remained affixed to the substrate even when fine sand and FBOM was scoured from around them. Polychaetes in the sediment trials typically were scoured as a group because the mucus trails that they made while burrowing formed a matrix that stabilized the substrate around the colony. This stabilization was evident because sediment was scoured from the upstream and lateral sides of the mucus matrix before the polychaete colony was dislodged. Polychaetes that were not scoured from the sediment at low velocity were often affixed to the heavier gravel under the sediment.

Survival of dislodged polychaetes

No mortalities occurred among polychaetes that remained on substrates after velocity trials (total $n = 198$). Forty-nine percent ($n = 56$) of polychaetes were recovered from scoured sediments and 98% survived. Most polychaetes recovered were no longer in tubes, but we were unable to determine whether this situation was a direct result of dislodgement or a result of handling. Three tubes without polychaetes were recovered from scratches in the acrylic channel sides at the end of trials.

General behavioral observations

Polychaetes in the laboratory constructed tubes similar to those constructed by polychaetes in depositional areas in the Klamath River. Polychaete tubes had 3 distinct sections: a loose base of mucus and relatively coarse organic and inorganic particles (generally $<500 \mu\text{m}$), a middle section with intermediate-sized organic particles ($<250 \mu\text{m}$), and a distal section with very fine ($<5 \mu\text{m}$), regular particles. Individual particles from the distal section were distinguishable only under $400\times$ magnification.

Manayunkia speciosa did not colonize any substrate that lacked FBOM. Polychaetes that were deposited

on a tile without FBOM generally responded by rolling on the tile for a short time, after which the polychaetes either elevated their posterior ends away from the substrate while moving them in a circular or back-and-forth direction or immediately began to move away from the center of the tile. Those that moved away from the center of the tile often ended up off the tile or under it. This basic set of behaviors also was observed on other substrates, including gravel in preliminary trials that lacked FBOM. When deposited on a tile with a thin layer of FBOM, polychaetes rolled through it, coating their bodies. If too little FBOM was available, polychaetes generally rolled into each other and formed a ball-shaped mass. If sufficient FBOM was present, polychaetes built individual tubes. Polychaetes added to pseudophora without FBOM burrowed into the substrate until they reached the tile, and then moved away from the center of the tile. Polychaetes that were added to the sediment substrate immediately burrowed into the substrate, and often immediately made a tube. Some polychaetes also moved through the sediment leaving tracks of mucus before constructing a tube.

Extension of tentacles into the water column did not appear to be directly affected by flow at the low velocity. However, polychaetes retreated into their tubes when tubes were struck by inorganic or organic particles in the water or were buffeted sufficiently by flow at the high velocity. If collisions ceased, polychaetes extended their tentacles into the water column after a lapse of several minutes. In trials on tiles, polychaetes exhibited a variety of behaviors in response to increasing flows. These behaviors included retreat into their tubes, tube evacuation, and movement away from the center of the tile and eventually under it. This movement was either in a direction perpendicular to the mean direction of flow or downstream. Polychaetes were never observed moving upstream in response to flow. A small number (estimated at 10 to 20%) of polychaetes that evacuated their tubes moved downstream on extrud-

ed strands of mucus, the length of which increased over time. Extrusion of mucus allowed some individuals to move in suspension to the end of the tile where they reattached themselves and moved under the tile. In some cases, polychaetes reattached themselves to the tile several times as they proceeded downstream. A few polychaetes were lost to the current while hanging from mucus strands.

Discussion

Our findings suggest that high flows influence *M. speciosa* distribution directly by restricting habitable substrates to those with greater stability and texture and by preventing attachment of the polychaete to substrates in extreme flow environments. However, *M. speciosa* exhibits attachment abilities comparable to those of taxa found in higher-gradient reaches. Therefore, they are likely to tolerate a wide range of velocities if they have sufficiently stable substrates for attachment. *Manayunkia speciosa* behaviors in response to changes in flow include movement to areas of lower velocity, which may minimize effects on individuals during times of higher flows. Polychaetes on highly mobile substrates are more likely to be displaced than polychaetes on stable substrates, so predictions of *M. speciosa* response to altered flows must consider the proportions of the population that occupy each type of habitat. These proportions may differ among systems depending on factors, such as food availability, competition, predation, and patterns of dispersal. Jordan (2012) found that *M. speciosa* densities did not differ among channel units classified as runs, eddies, and pools over a 2-y study in the Klamath River. This result suggests that a management policy based on attempts to displace polychaetes from fine sediments in depositional habitats in an effort to reduce ceratomyxosis in salmon probably would remove only part of the population. Polychaetes persisting on more stable substrate would be available to recolonize vacated sediments even if displaced polychaetes died.

U_* faced by the benthic polychaetes under test velocities was comparable to other near-bed values reported in the literature. Our low-flow trials produced U_* values comparable to the higher U_* values recorded by Schnauder et al. (2010), who tested tenacity of a collection of invertebrates from a regulated, lowland river with a sandy bed in an experimental flume. Specifically, *M. speciosa* dislodged at the lower flow had a tenacity similar to that of *Gomphus vulgatissimus* (Odonata:Gomphidae) and *Bithynia tentacula* (Neotaenioglossa:Bithyniidae), both of which typically are found in slower waters

with depositional substrates. *Manayunkia speciosa* that remained affixed in the higher-flow trials had tenacity comparable to the Tricladida and *Goera pilosa* (Trichoptera:Goeridae), and a greater tenacity than many snails and dragonflies collected from streams with relatively steep grades and coarse substrates (Statzner et al. 1988). These findings are in accord with observations that *M. speciosa* tolerates a range of flow conditions (Hiltunen 1965, Poe and Stefan 1974). The low Re_l values for *M. speciosa* individuals fell within the typical range of small, larval invertebrates (Statzner 1988) and reflect its tube morphology. Re_l values indicated that drag forces acting on the polychaete dominate over lift forces and may explain why polychaete tubes appear to be long and conspicuous only later in the season in the Klamath River when flows are lower. Tube length also is probably related to size of the polychaetes, with larger polychaetes building larger tubes. However, variation in tube size was less pronounced among individuals of different size classes than was variation throughout the year (DMM, personal observation). The shape of this polychaete's tube also may be an adaptation to its low mobility while in its tube and to the multidirectional, swirling flows in which it often is found. A cylindrical shape offers a consistent profile to flow regardless of direction within the transverse flow plane.

The proportion of polychaetes dislodged was a function of the interaction between flow and substrate type. The greatest detachment occurred in fine sediments at both flow levels, whereas little detachment occurred in pseudophora at either flow. These results support the hypothesis that stable substrates are likely to form the primary habitat of *M. speciosa* (Stocking and Bartholomew 2007, Malakauskas and Wilzbach 2012). *Manayunkia speciosa* can reach densities $>50,000/m^2$ on fine sediments during periods of low and stable flows in the Klamath River (Jordan 2012), but these populations probably are transient. Preference of the polychaete for stable substrate would also be consistent with habitat preferences of suspension-feeding lotic invertebrates in general (Richardson and Mackay 1991). Filter-feeders must live in flows sufficiently high to deliver food items, but must avoid being detached from the substrate. Macrophytes and *Cladophora* probably buffer the polychaetes against dislodgement during catastrophic flooding because of the reduced current velocities within the structure of these plants (sensu Nikora et al. 1998). Macrophytes and *Cladophora* also trap FBOM (Madsen et al. 2001), which polychaetes feed on and use for construction of their tubes. Moreover, polychaete colonies themselves may alter local near-bed

flows resulting in increased stabilization of substrates and deposition of sediments, including fine particulate organic matter (FPOM) (e.g., Daro and Polk 1973, Jumars and Nowell 1984, Frithsen and Doering 1986). Aggregates of closely spaced tubes can lead to skimming flows (Friedrichs et al. 2000), a condition in which the maximum turbulent kinetic energy and shear stress occurs above the bed (Nowell and Church 1979). This possibility together with the mucus-related sediment stabilization we observed suggests that polychaete resistance to dislodgement may be higher in the river, when polychaetes occur in higher numbers, than in flume trials. Flow alteration by polychaete colonies probably also leads to increased deposition of sediments, bringing additional FPOM to the polychaetes.

Estimated π_i of polychaetes from the tile substrate was 25 and 73% under low and high velocities, respectively, and was intermediate to associated π_i from sediment and pseudophora. Tiles probably tested actual tenacity of individual polychaetes most accurately because they lacked the influence of the highly moveable sediments or flow buffering by pseudophora. However, inducing attachment of polychaetes to the tile substrate was challenging, and some polychaetes probably were unable to attach fully before our trials. Thus, bare rock may not be a primary habitat, even when covered with modest amounts of FBOM. Aggregates of polychaetes had greater surface area and higher Re_i and, therefore, experienced greater drag and lift forces than individuals. An unglazed tile has less roughness or texture than many natural rocks on which *M. speciosa* is found and, therefore, provides less surface area for mucus attachment. Greater surface roughness allows greater invertebrate tenacity (Richardson and Mackay 1991, Lau and Martinez 2003). The lack of a biofilm on the tiles also could have been a factor because biofilms can enhance the ability of some invertebrates to attach to a surface (Zardus et al. 2008). *Manayunkia speciosa* were commonly observed in rock crevices or interstices in the river (DMM, personal observation). Flow over these depressions can be classified as skimming when individual roughness elements are of sufficient height and density (Morris 1955). We frequently found polychaetes clustered around boulders in the river (Malakauskas and Wilzbach 2012). Hydraulic forces can differ significantly across the surfaces of boulders depending on boulder morphology and orientation, and this effect can influence invertebrate community structure (Bouckaert and Davis 1998). Combined, these factors suggest that our results from unglazed tiles may underestimate polychaete tenacity in a natural setting.

Manayunkia speciosa exhibited unexpected behavioral plasticity in response to increased flows because tube-dwelling polychaetes are considered to be sessile. Invertebrates with ability to resist dislodgement often do so at the expense of mobility (Martinez 2001). However, *M. speciosa* exhibited active flow-avoidance behaviors in addition to retreating deeper into their tubes and burrowing into sediments in response to flow-mediated disturbance. Some individuals on tiles evacuated their tubes at higher flows and relocated under the tile. These behaviors suggest that, like other lotic invertebrates (e.g., Marmonier and Cruézé des Châtelliers 1991, Dole-Olivier et al. 1997, Lancaster 1999), *M. speciosa* may actively seek low-flow microhabitats during periods of high flows. *Manayunkia speciosa* also may actively choose appropriate microflow habitats in which to build tubes for initial settlement during more stable conditions. However, relocation may be uncommon during the low-flow season because females brood young in their tubes, and polychaetes experience increased predation when outside of their tubes (Willson et al. 2010). Polychaetes also were able to cope with flows by trailing downstream on extruded strands of mucus. A number of lotic invertebrate larvae, including hydroptychid and polycentropid caddisflies and simuliid blackflies, trail downstream on silk threads in a similar manner to enhance their settling abilities (Rader 1997).

Mortalities among recovered polychaetes that had experienced high flows or had been dislodged from substrates were extremely limited, suggesting that *M. speciosa* is unlikely to suffer significant mortalities as a direct result of dislodgement in a natural system. Polychaetes may experience mortality during catastrophic drift, but survivors from flume trials endured passage through collimators and propellers, suggesting that polychaetes may be able to withstand harsh flow conditions, though these characteristics are not representative of a natural riverine environment. However, further study is warranted before definitive statements about polychaete survivorship with respect to flows and sediment scour can be made. Potential flow-mediated mortalities probably would result from settlement in suboptimal habitats, as has been observed in other polychaetes (Zamorano et al. 1995). Polychaetes collected after being scoured from the sediment substrate were often outside their tubes, a condition that would make them susceptible to predation in a natural setting. Predaceous Tubificidae and Macrostromida prey upon polychaetes that are out of their tubes (Willson et al. 2010). We observed protists apparently preying on injured polychaetes in our study. *Manayunkia speciosa* have not been found in

anoxic substrates in the Klamath River (Stocking and Bartholomew 2007), and polychaetes settling in these habitats probably would experience mortalities. Conversely, flow-mediated dislodgement may offer a means of dispersal. We observed several polychaete tubes embedded in scratches in the acrylic walls of our flume channel after high-flow trials, although none of these tubes contained polychaetes.

Manayunkia speciosa exhibits a substrate tenacity and behavioral plasticity that suits it well to lotic systems. Management strategies that seek to induce polychaete mortality directly via flow-mediated dislodgement probably will be unsuccessful, but we cannot predict the likelihood of polychaete survival associated with resettlement without further study. Polychaetes in fine sediments may be relatively easy to displace, but managers should consider both macrohabitat (geomorphic channel unit) and microhabitat distribution of the polychaete. Many polychaetes are found in sheltered areas, such as behind rock outcroppings or in rock crevices (Malakauskas and Wilzbach 2012), where they are likely to persist even in high flows. Negative effects of high flows on nontarget species, which play important roles in stream ecosystem metabolism and provide prey for juvenile salmon, should be considered when developing any management plan involving flow manipulation. The plausibility of reducing the parasites *C. shasta* and *P. minibicornis* though flow-mediated reduction of *M. speciosa* populations seems low based on our results, but awaits further elucidation through additional study.

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