Sediment resuspension and boundary layer flow dramatically increase the growth rates of interface-feeding spionid polychaetes

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Abstract

Most spionid polychaetes switch from surface deposit feeding to suspension feeding as current velocity and the flux of suspended food particles increase in the benthic boundary layer. This hydrodynamically mediated feeding behavior has been well studied, but the impact of flow on the growth rates of juvenile spionids has not been tested extensively. I performed two experiments in counter-rotating annular flumes to measure the growth of Polydora cornuta and Streblospio benedicti in a range of flow conditions. Experiment 1 tested the effects of sediment resuspension. The body volumes of individual worms were measured before and after a 7-day exposure to steady, unidirectional flow velocities ranging from 0.5 to 18 cm s⁻¹ (Uₕ₅mm = velocity measured 5 mm above bottom). Sediment collected from the worms’ field site was added to each flume as the only food resource. The sediment’s critical erosion velocity was ~13 cm s⁻¹ (Uₜₙ₉₉ = 0.9 cm s⁻¹). When flumes were set to Uₕ₅mm ≤ 12 cm s⁻¹, the relative growth rate (RGR) of small Polydora (initial body length = 1–4 mm) equaled 0.19 day⁻¹ on average, and the RGR of a larger class of juvenile Polydora (6–9 mm) equaled 0.06 day⁻¹. When Uₕ₅mm = 15 or 18 cm s⁻¹ and some sediment became resuspended, the RGR of small and large Polydora equaled 0.37 and 0.22 day⁻¹, respectively. Streblospio grew more slowly than Polydora, but showed a similar relative increase in RGR when flow exceeded the erosion velocity. To better test the effects of non-erosive flows, a second experiment was performed with phytoplankton added to the flumes. Experiment 2 tested four velocities (Uₕ₅mm = 3, 6, 9, or 12 cm s⁻¹), and each flow treatment was replicated four times. Increases in velocity and the flux of microalgae significantly increased the RGR of Streblospio and Polydora, with an average RGR of 0.53 day⁻¹ for small Polydora exposed to Uₕ₅mm = 12 cm s⁻¹. The growth rates of Polydora and Streblospio in the flume experiments are much greater than those reported for similar polychaetes in still water, demonstrating that studies of spionid nutrition and population dynamics must consider realistic flow regimes.

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1. Introduction

Invertebrates that forage on deposited sediments or suspended particles dominate most soft-sediment ben-

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geophysical processes, especially due to their tube-building and feeding activities (e.g., Aller, 1982; Aller and Yingst, 1985; Luckenbach et al., 1988; Thrush et al., 1993). Although identification of the food resources assimilated by these microphages has been troublesome and controversial, progress toward predicting effects of food resources on the abundance of individuals, the distribution of populations, and the structure of communities has been steady (e.g., Fauvachard and Jumars, 1979; Lopez and Levinton, 1987; Jumars et al., 1990; Wilson, 1991; Miller et al., 1992; Jumars, 1993; Mayer et al., 1993, 1995).

Some benthic microphages can facultatively switch between feeding on surficial sediment or suspended particles depending on hydrodynamic conditions (e.g., Brafield and Newell, 1961; Taghon et al., 1980; Dauer et al., 1981; Olafsson, 1986; Levinton, 1991; Miller et al., 1992; Taghon, 1992; Taghon and Greene, 1992; Bock and Miller, 1996, 1997). The nutrition of these facultative “interface feeders” (Dauer et al., 1981) will be influenced both by the quality and quantity of food near the sediment–water interface and the hydrodynamic conditions in the benthic boundary layer. Furthermore, any ecological or geochemical effects that result from the feeding activities of interface-feeding microphages will be influenced by flow conditions. In particular, flows that favor the growth, reproduction, and high population density of interface-feeding benthos are likely to have far-reaching ecological and geochemical implications.

Although the effects of flow on the feeding behavior of interface-feeding benthos have been well documented, the nutritional significance of hydrodynamic conditions has not been widely tested. Several hypotheses and limited data do, however, provide hints to the likely effects of flow on the nutrition of interface feeders. For example, surface deposit feeders probably benefit from the transport and local deposition of food particles (Lopez and Levinton, 1987; Taghon and Greene, 1992; Bock and Miller, 1995, 1996). Passive suspension feeders generally benefit from an increased flux of particulate food as flow increases (Jumars and Nowell, 1984; Muschenheim, 1987; Frechette et al., 1989), but a quantitative understanding of the nutrition of suspension feeders will require an understanding of the mechanisms of particle capture and retention (e.g., Shimeta and Koehl, 1997) because faster flows can reduce the ingestion rates of some species (Okamura, 1985; Braimah, 1987; Wildish et al., 1987; Wildish and Miyares, 1990; Taghon and Greene, 1992). In addition, flow alters the quantity and quality of particles in suspension (e.g., Muschenheim, 1987; Mayer et al., 1993; Bock and Miller, 1995, 1996).

Perhaps the most integrative assessment of an animal’s nutrition is its growth rate, especially for pre-reproductive juveniles. Few data exist on the growth rates of facultative, interface feeders. In particular, the relative contributions of deposit-feeding activity and suspension-feeding activity to juvenile growth have received limited attention.

Taghon and Greene (1992) measured rates of egestion (~ feeding) and growth of two spionids (Boccardia pugettensis and Pseudopolydora kempi japonica) in conditions that restricted worms to deposit feeding only, suspension feeding only, or a combination of deposit feeding and suspension feeding. When conditions allowed Boccardia to suspension feed, growth rates were faster than when worms were restricted to deposit feeding. Estimates of worms’ gross growth efficiencies suggest that suspension feeding is the more profitable of the two feeding modes for Boccardia. Results differed, however, for Pseudopolydora. Generally, growth rates were either unaffected or declined as flow increased, and the gross growth efficiencies of Pseudopolydora did not differ between deposit-feeding and suspension-feeding treatments. Taghon and Greene (1992) noted that the availability of suspended food particles in their Pseudopolydora experiments might have been limiting (the experiments used unfiltered water from a flow-through seawater system without any enrichment of suspended particles in the flume). Furthermore, similar experiments designed to test the effects of population density on rates of feeding and growth found that, irrespective of density, both Boccardia and Pseudopolydora responded similarly to a pulsed, bedload supply of deposited food vs. a continuous flux of suspended food (Taghon, 1992). Data from these initial experiments do not facilitate general conclusions about the growth of interface-feeding spionids in a wide range of hydrodynamic conditions. What seems most clear is that general conclusions cannot be made across species.

In this paper, I expand on the seminal tests of flow’s influence on the growth rates of interface-feeding spionids (Taghon, 1992; Taghon and Greene,
by measuring the growth rates of two other species *Polydora cornuta* and *Streblospio benedicti* in a range of hydrodynamic conditions. In contrast to the experiments of Taghon (1992) and Taghon and Greene (1992) in which the availability of suspended particles might have been limiting, the flume experiments described in this paper include controlled additions of suspended algae. Furthermore, the experiments include field-collected sediment as a natural source of deposited food. Most importantly, the experiments described here included independent replicates of each flow treatment (i.e., multiple flumes) to allow rigorous statistical comparisons among the various hydrodynamic treatments.

2. Methods

2.1. Description of the flumes

All experiments were conducted in counter-rotating annular flumes at Rutgers University’s Institute of Marine and Coastal Sciences. The flumes’ design is based on that of a flume at the Delft University of Technology in The Netherlands (Visser et al., 1992). Four identical counter-rotating annular flumes exist at Rutgers University, allowing multiple flumes to be run simultaneously. The flumes have an outside diameter of 400 cm. The channel is 30 cm wide. The maximum water-column depth is 42 cm. At a depth of 20 cm, the flume’s volume is 700 l. To create a current, the flume’s top is lowered to the water surface and rotated to create a shear. The top is constructed of PVC and a titanium plate, which is the portion that contacts the water surface. In addition to driving the flow, the titanium plate also serves as a heat exchanger to control temperature by circulating controlled amounts of chilled water within the flume’s top. To reduce secondary, cross-channel flow that results from water moving in a continuous circle, the entire flume channel can be rotated in the opposite direction of the top plate’s rotation (Visser et al., 1992).

2.2. Field collections and preliminary set-up of flume experiments

The spionid polychaetes *P. cornuta* and *S. benedicti* were collected alive from an intertidal sandflat at Shark River Island, NJ, USA. The collection site was ~25 m seaward of a *Spartina* saltmarsh, at an elevation ~0.1 m above mean low water. Larger members of each species were collected by sieving the surficial 3–5 cm of sediment through a 1-mm mesh. Smaller members of each species were collected by removing the surface 1 cm of sediment from an area ~0.5 m², adding that sediment to a 2-l bucket of seawater, and gently stirring the contents to create a slurry. The slurry was poured through a 0.5-mm sieve to concentrate small polychaete tubes. Collected tubes were transferred to a 2-l bucket of seawater for transport to the laboratory.

All worm tubes collected in the field were transported to Rutgers University for sorting to species and size class within a species. Sorting was completed within 2 days of collection from the field. Sorted worms were maintained in glass bowls of 5 µm filtered seawater at 15 °C. To allow sorted worms to construct sediment tubes, a few drops of silty seawater that had been frozen and thawed were added to each bowl containing 25–50 worms. Sorted worms were either used in experiments or discarded no longer than 4 days after they had been collected from the field.

Prior to each experimental run, sorted worms were anesthetized in 3% MgCl₂ and divided into two length classes for each species. The body-length classes for *P. cornuta* were 1–4 and 6–9 mm. This species typically becomes sexually mature at a body length of ~1 cm (Hentschel, 1998a), although, occasionally, I observed gametes in individuals from the Shark River Island population as small as 8 mm. The classes for *S. benedicti* were 0.5–3.0 and 4–5 mm. This species begins producing gametes at a body length of ~5 mm (personal observation). Length measurements were made by video microscopy using a Wild stereomicroscope, a Sony CCD video camera, and NIH Image software. In addition to measuring each individual’s total body length, I made measurements of its body width at five locations between the anterior and posterior end. At the magnifications used, measurements had a precision of 0.01 mm. Length and width measurements were used to calculate each individual’s body volume at the start of an experimental run, modeling the worm as a series of four
conical frustums. The volume of each frustum is calculated as

$$V = \frac{\pi}{3}L \left[ \left( \frac{W_1}{2} \right)^2 + \left( \frac{W_1}{2} \frac{W_2}{2} \right)^2 + \left( \frac{W_2}{2} \right)^2 \right]$$  \hspace{1cm} (1)

where \(V\) is the volume of the frustum, \(L\) is the length of the frustum, and \(W_1\) and \(W_2\) are the two width measurements at each end of the frustum. The entire body volume of a worm is calculated by summing the volumes of the four conical frustums.

After an individual worm was measured, it was briefly transferred from 3% MgCl\(_2\) to filtered seawater and then placed in a small, numbered vial containing sediment. The vials (2 cm high \(\times\) 1.4 cm diameter) were constructed from 5-ml pipet tips with Hot Melt Glue sealing one open end. The sediment had been collected from the field site, frozen and thawed, sieved in seawater to remove particles greater than 0.3 mm, and frozen and thawed again prior to being added to vials. A worm typically built a sediment tube inside its vial within 1 h. Vials containing worms were placed in holes drilled within 1.3-cm-thick PVC slabs (\(\sim 15 \times 30\) cm, \(W \times L\)). Each PVC slab contained 20–30 vials that were separated horizontally by at least 2 cm. Locations of individual vials within and among slabs were random. Slabs containing vials were then placed in a seawater table (15 °C, salinity = 30). All 80–110 worms for a single experimental run were measured, implanted in vials, and placed in the seawater table during a single 12-h period. Worms acclimated to vials overnight in the seawater table for an additional 15–18 h prior to being implanted in the flumes.

The day following measurement and acclimation to vials, PVC slabs containing vials were implanted into a 2-cm-deep layer of silica sand (\(\sim 0.75\) mm diameter) that had been spread evenly throughout a flume. PVC slabs were planted in a single section of the flume, roughly one-eighth of the channel’s total circumference. Vials occupied the center 10 cm of the channel. The sand layer in the entire flume was smoothed to a height of 2 cm so the top edges of the vials were flush with the sand–water interface. I ensured an evenly smooth sand–water interface by using a bulldozer device that clamped to the flume’s top and was slowly rotated to smooth the sand. The bulldozer’s blade spanned the entire width of the flume channel and could be adjusted in vertical increments as small as 0.5 mm. The height of the sand–water interface was controlled precisely by adjusting the bulldozer and adding or deleting small amounts of sand.

After vials were implanted in the sand layer, the flume was filled with 5-\(\mu\)m filtered seawater to achieve a 28-cm deep water column above the sand. A thin layer (\(\sim 2\) mm thick) of field-collected sediment was then deposited above the sand layer and the vials within it. This was accomplished by sieving (1-mm mesh) a 2-l bucket of field-collected sediment, which had been frozen and thawed, into the flume’s water column. To ensure that the thin layer of field-collected sediment was evenly dispersed throughout the flume, the sieving occurred during a 15-min period while the flume rotated slowly (\(\sim 0.3\) rpm). The resulting slurry was allowed to settle overnight, forming the smooth \(\sim 2\)-mm layer above the sand and vials within it. Flow treatments began the following morning, 15–18 h after the field-collected sediment was added.

The thin layer of field-collected sediment ensured that worms ingesting deposited or re-suspended sediment in the flume were feeding on material that was similar in nutritional value to natural sedimentary food. Analysis of enzymatically hydrolyzable amino acids (EHAA: Mayer et al., 1995) revealed that the frozen–thawed sediment added to the flumes was slightly less nutritious (EHAA= 0.6 mg g\(^{-1}\)) than unfrozen surficial sediment from the Shark River Island site (EHAA= 0.8 mg g\(^{-1}\)). Mayer et al. (1995) report similar decreases in EHAA due to freezing.

The total time period for preliminary, set-up activities (measurements of worms’ initial body sizes, acclimation to vials, and acclimation to the flumes) was \(\sim 48\) h. To establish the amount of growth that occurred during the \(\sim 48\) h after worms were initially measured and before the flow treatments were established, I exposed a group of worms to the preliminary 48-h protocol and then removed the PVC slabs (and vials) from the flume without exposing the worms to flume flow.

To remove the PVC slabs, the flume’s water column was drained and sediment near the location of PVC slabs was cleared until the edges of the PVC slabs were exposed. I then gently lifted each PVC
slab out of the flume. The vials within each slab remained buried below the smooth, 2-mm layer of field-collected sediment even after the PVC slabs had been removed from the flumes. To remove numbered vials from the PVC slabs, the vials were gently pushed upward through the holes that contained them. Once the upper edge of each vial extended 1–2 mm above the sediment layer, vials could be removed individually from each PVC slab without disturbing the worms inside each vial. I then sieved (0.3-mm mesh) the contents of each numbered vial into a glass bowl to recover individual worms that had been measured 2 days earlier. Each recovered individual was re-measured to calculate its body volume at the end of the preliminary, acclimation period. Relative growth rates (RGR) were calculated according to Fisher (1920) as

$$RGR = \frac{\ln(V_f) - \ln(V_i)}{\text{time}}$$

(2)

where $V_i$ and $V_f$ are measurements of each individual’s final and initial body volume, respectively.

2.3. Experiment 1: effects of sediment resuspension

Individuals of *P. cornuta* and *S. benedicti* that had been measured and acclimated to flumes (see above) were exposed to one of several constant, unidirectional flow velocities. For each experimental run, two annular flumes were run simultaneously for 7 days. PVC slabs containing vials of individual worms were randomly assigned to each flume. The entire experiment included seven constant, unidirectional flows and an eighth treatment consisting of a still-water flume that received a 30-min pulse of the fastest flow each day (Table 1). For simplicity, I refer to each flow treatment by the horizontal velocity measured 0.5 cm above the sediment–water interface ($U_{5mm}$). Because resuspension of some components of the 2-mm layer of field-collected sediment began at $U_{5mm} = 13$ cm s$^{-1}$, I replicated the 12 and 15 cm s$^{-1}$ flumes three times. In total, therefore, 12 flumes were run during the entire 3-month experimental period. Flow treatments were assigned to each of the two flumes of a single run in a completely randomized design, with the added constraint that any two flumes in a single run would not be assigned the same flow treatment.

<table>
<thead>
<tr>
<th>$U_{5mm}$ (cm s$^{-1}$)</th>
<th>$U_*$ (cm s$^{-1}$)</th>
<th>Top rotation* (rpm)</th>
<th>Bottom rotation* (rpm)</th>
</tr>
</thead>
<tbody>
<tr>
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<td>NA</td>
<td>0.14</td>
<td>0.1</td>
</tr>
<tr>
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<td>0.7</td>
<td>1.27</td>
<td>0.91</td>
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<tr>
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<td>0.8</td>
<td>1.63</td>
<td>1.17</td>
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<tr>
<td>18</td>
<td>0.9</td>
<td>2.00</td>
<td>1.42</td>
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</table>

Velocity profiles were measured with a Dantec laser-Doppler velocimeter. $U_{5mm}$ is the unidirectional velocity measured 5 mm above the sediment. $U_*$ is the shear velocity determined from the semi-logarithmic vertical velocity profile (Gross and Nowell, 1983). To achieve minimal secondary, cross-stream flow, the top and bottom of the flume are rotated in opposite directions at the indicated rotations per minute (rpm).

* The top and bottom rotation rates are mean values in a range of that extended ± 0.005.

Initially, each flume included 15–18 small *P. cornuta*, 12 large *P. cornuta*, 10–13 small *S. benedicti*, and 12 large *S. benedicti*. Generally, 90% or more of the pre-measured worms implanted into a flume were recovered at the end of each 7-day run. Temperature was controlled at 20 °C, ranging between 19.2 and 20.5 °C.

To avoid pseudoreplication (Hurlbert, 1984), statistical comparisons involving the effects of flow treatment used the mean RGR within each flume. I tested the null hypothesis that the RGR of each species-size class did not vary due to flow velocity by performing a Spearman rank correlation and Hoteling–Pabst test (Conover, 1980) on the mean RGR of worms from each flume and the flow velocity (the still-water flume pulsed to $U_{5mm} = 18$ cm s$^{-1}$ for 30 min each day was excluded from this analysis). I then focused on the effect of sediment resuspension by (1) performing a Mann–Whitney $U$ test comparing the RGR of the three replicate flumes at 12 cm s$^{-1}$ and the three replicate flumes at 15 cm s$^{-1}$ and (2) performing a Mann–Whitney $U$ test comparing the RGRs from all seven flumes in which sediment was not resuspended (i.e., $U_{5mm} \leq 12$ cm s$^{-1}$) to the RGRs of the four flumes in which sediment was resuspended during the 7-day period (i.e., $U_{5mm} \geq 15$ cm s$^{-1}$). All statistical tests were planned a priori. Nonparametric tests based on ranks were chosen due to small sample size.
sizes and unreplicated treatments at $U_{5\text{mm}}$ $<$ 12 cm s$^{-1}$.

The concentration of suspended food particles was not quantified in the flumes run during Experiment 1. After completion of the experiment, however, each flume was modified to include a syringe-needle port (16 gauge) in its inside wall (8 cm above the sediment) to facilitate the filtering of water samples. To estimate the concentrations of particulate C and N resuspended during Experiment 1, I set up a single flume with layers of sand and field-collected sediment (as above) and initially set $U_{5\text{mm}}$ = 12 cm s$^{-1}$. Shortly after initiating flow, three samples of the flume’s water were collected by draining through the needle port. The triplicate samples were filtered onto pre-combusted GF/C filters for measurement of particulate C and N concentrations on a Carlo-Erba CHNS Analyzer. The velocity was then increased to 15 cm s$^{-1}$, and three additional water samples were filtered 5 h later. The velocity was maintained at 15 cm s$^{-1}$ for 7 days, and triplicate water samples were filtered 1, 2, 4, and 7 days after flow was initiated. The flume was then cleaned and set up again for a 7-day flow treatment that remained constant at $U_{5\text{mm}}$ = 12 cm s$^{-1}$.

2.4. Experiment 2: effects of phytoplankton flux

In Experiment 1, the concentration of food particles available to suspension feeders was extremely low unless the flow velocity exceeded the critical erosion velocity of the field-collected sediment (i.e., $U_{5\text{mm}}$ $\geq$ 13 cm s$^{-1}$). A more general test of the effects of flow on worms’ growth rates requires that suspended food particles be present in the water column at slower flows; measurable concentrations of suspended particles always occur in nature. Therefore, I followed Experiment 1 with a subsequent experiment in which suspended microalgae were added to the flumes each day.

This experiment was limited to four constant flow treatments ($U_{5\text{mm}}$ = 3, 6, 9, or 12 cm s$^{-1}$), and each treatment was replicated four times (i.e., four flumes were set to each flow velocity). As in Experiment 1, two flumes were run simultaneously and temperature was controlled at 20 °C. Because of the unexpectedly rapid growth rates observed in Experiment 1 (see Results), the duration of the runs in Experiment 2 was reduced from 7 to 3 days. Each of the 16 flumes in the full experiment was assigned a flow velocity in a completely randomized design, with the added constraint that the same velocity would not be assigned to both flumes within a single 3-day run.

A nonliving algal slurry (C-5 Slurry, Coast Seafoods, Quilcene, WA) was added to each flume. This slurry is composed of several phytoplankton genera, including *Thalassiosira*, *Skeletonema*, *Chaetoceros*, and *Isochrysis*. The slurry has a cell concentration on the order of $10^9$ cells ml$^{-1}$, a particulate C concentration of 35 g l$^{-1}$, and a particulate N concentration of 7 g l$^{-1}$ (Carlo-Erba analysis of diluted slurry samples filtered onto pre-combusted GF/C filters). A pulse of the algal slurry was added each day during a 3-day experimental run. At the beginning of the first day, 15 ml of the slurry was added to each flume. To replenish some of the algal particles that deposited over time, additional 5-ml pulses were added 24 and 48 h after the initial 15-ml of algal slurry had been added. During the 5-min period in which the algal slurry was added to a flume, the velocity of each flume was increased to 12 cm s$^{-1}$ to ensure adequate mixing of the algae. Although I refer to each flow treatment as one of four constant velocities, readers should be aware of this brief 5-min deviation that occurred each day. The water in each flume was sampled 30 min before and 30 min after each addition of algae by draining through the syringe-needle port in the flume’s inside wall and filtering onto pre-combusted GF/C filters for measurement of particulate C and N concentrations. In addition, a water sample was taken when the experiment ended after 72 h of controlled flow. Similar analysis was performed on water samples collected from the Shark River Island field site 1–2 h after low tide on several dates during summer and fall months.

Initially, each flume in Experiment 2 included 11–15 small *P. cornuta* and 10–12 large *P. cornuta*. Flumes in six of the eight paired-flume runs also included 8–12 small *S. benedicti*, and 8–12 large *S. benedicti*. *S. benedicti* was omitted from two of the runs (i.e., 4 of 16 total flumes in the experiment) due to limited numbers available in field collections. Consequently, the data for *P. cornuta* include four replicate flumes for each of the four flow velocities, while data for *S. benedicti* include three replicate flumes for each flow velocity. As in Experiment 1, ~ 90% of the pre-measured worms implanted into a flume were recovered at the end of each 3-day run.
Data were analyzed in two ways. First, the RGRs of each species-size class were compared among the four flow velocities by 1-way ANOVA ($n = 4$ replicate flumes per flow velocity for *P. cornuta* and $n = 3$ for *S. benedicti*). Second, the RGR of each flume was compared across the average flux of particulate nitrogen in each flume. This second comparison was planned a priori to account for the fact that the concentration of suspended microalgae varied among the four replicate flumes in a given flow velocity. The average particulate-nitrogen concentration of each flume was computed by averaging each flume’s seven measurements of particulate nitrogen concentration that occurred during the 3-day experimental run. The average near-bottom flux of particulate nitrogen for each flume was estimated by multiplying a flume’s average particulate nitrogen concentration by $U_{5\text{mm}}$ for each flume.

3. Results

3.1. Growth during the 2-day acclimation period

Small *P. cornuta* subjected to the 48-h acclimation period but removed from a flume and re-measured without exposure to flow had an average RGR of 0.04 day$^{-1}$. This growth rate is much less than those measured following exposure to flow (below) and, therefore, represents a small source of error when computing RGR based only on the time period when flumes were running (7 days in Experiment 1 or 3 days in Experiment 2).

3.2. Experiment 1: effects of sediment resuspension

Sediment resuspension was visibly evident when $U_{5\text{mm}}$ exceeded 13 cm s$^{-1}$. Although suspended food particles were not quantified in the flumes run during Experiment 1, analysis of suspended particulate nitrogen in two additional flumes was performed (Fig. 1). Particulate nitrogen concentration quickly increased after $U_{5\text{mm}}$ was increased from 12 to 15 cm s$^{-1}$ and remained higher than that of the flume maintained at $U_{5\text{mm}} = 12$ cm s$^{-1}$ for at least 4 days (Fig. 1).

Both size classes of *P. cornuta* revealed a significant correlation between RGR and flow velocity (Fig. 2; Spearman’s rank correlation $= 0.852$ and 0.898 for the small and large size class, respectively; $P < 0.001$ for each size class). Members of the smaller size class grew noticeably faster than did larger worms (Fig. 2). By the end of the 7-day period in the flumes, small *P. cornuta* that had grown 30–40% per day (Fig. 2) had increased their body volume by an order of magnitude and achieved sizes that correspond to those of sexual maturity (a body length of $\approx 1$ cm). In fact, several of the *P. cornuta* that were implanted in high-flow flumes as juveniles had brooded eggs within their tubes at the end of the 7-day period.

The data show a stepwise increase in RGR between $U_{5\text{mm}} = 12$ cm s$^{-1}$ and $U_{5\text{mm}} = 15$ cm s$^{-1}$ that coincides with the onset and maintenance of sediment resuspension (Fig. 2). Comparing the RGRs of the three replicate flumes at $U_{5\text{mm}} = 12$
cm s⁻¹ and the three replicate flumes at $U_{5\text{mm}}=15$ cm s⁻¹ reveals a significant difference for both size classes of \textit{P. cornuta} (Fig. 2; Mann–Whitney \textit{U} test, $P=0.050$). Furthermore, a comparison between all seven flumes in which prolonged sediment resuspension did not occur ($U_{5\text{mm}}\leq12$ cm s⁻¹) and all four flumes in which prolonged sediment resuspension did occur ($U_{5\text{mm}}\geq15$ cm s⁻¹) also revealed significant differences in RGR for both size classes of \textit{P. cornuta} (Fig. 2; Mann–Whitney \textit{U} test, $P=0.008$). Data from the single flume that was set to a still-water treatment but received a brief 30-min pulse to $U_{5\text{mm}}=18$ cm s⁻¹ each day did not suggest that RGR was affected by brief pulses of fast flow (Fig. 2).

Similarly, both size classes of \textit{S. benedicti} revealed a significant correlation between RGR and flow velocity (Fig. 3; Spearman’s rank correlation = 0.667 and 0.704 for the small and large size class, respectively; $P=0.019$ and 0.009 for the small and large size class, respectively). The data also show a stepwise increase in RGR between $U_{5\text{mm}}=12$ cm s⁻¹ and $U_{5\text{mm}}=15$ cm s⁻¹ that coincides with the onset and maintenance of sediment resuspension (Fig. 3). Comparing the RGRs of the three replicate flumes at $U_{5\text{mm}}=12$ cm s⁻¹ and the three replicate flumes at $U_{5\text{mm}}=15$ cm s⁻¹ revealed a significant difference for the small size classes of \textit{S. benedicti} (Fig. 3; Mann–Whitney \textit{U} test, $P=0.014$ for both size classes). As seen with \textit{P. cornuta}, data from the single flume that was set to a still-water treatment but received a 30-min pulse to $U_{5\text{mm}}=18$ cm s⁻¹ each day did not suggest that RGR was affected by brief pulses of fast flow (Fig. 3).

### 3.3. Experiment 2: effects of phytoplankton flux

Daily additions of nonliving algal slurry provided a continuous source of suspended food particles at all flow velocities between $U_{5\text{mm}}=3$–12 cm s⁻¹ during the 3-day experimental runs (Fig. 4). Al-
though water samples were not collected isokinetically, the fact that the initial concentrations of particulate nitrogen did not vary among the four velocity treatments (Fig. 4) suggests that there was little or no sampling bias correlated with velocity. There did, however, appear to be more deposition of suspended algae over time at faster flows (Fig. 4). This is especially evident when comparing the average particulate nitrogen concentrations among the four velocities (Fig. 5) and probably results from more frequent contacts with the bed and with other suspended particles (i.e., aggregation) at faster flows. At the end of the 3-day runs, increased
water clarity and algal aggregates (\( \sim 1 \) mm diameter) were commonly observed in the flumes running at \( U_{5\text{mm}} = 12 \) cm s\(^{-1}\). Measurements of water samples collected from the Shark River Island field

Fig. 6. Relative growth rates vs. flow velocity in Experiment 2. (A) A small size class of *P. cornuta* (initial length = 1 – 4 mm) and (B) a large size class of *P. cornuta* juveniles (initial length = 6 – 9 mm). Each plotted symbol represents the mean relative growth rate of approximately 10 – 15 individual worms from a single flume (the S.D. of any mean from a single flume was \( \sim 0.10 \)), and a different symbol shape is used for each velocity treatment. Current velocities were measured 5 mm above the sediment–water interface (\( U_{5\text{mm}} \)).

Fig. 7. Relative growth rates vs. the calculated average flux of particulate nitrogen 5 mm above the sediment–water interface. (A) A small size class of *P. cornuta* (initial length = 1 – 4 mm) and (B) a large size class of *P. cornuta* juveniles (initial length = 6 – 9 mm). Each plotted symbol represents the mean relative growth rate of approximately 10 – 15 individual worms from a single flume. Symbol shapes correspond to those of flow velocities indicated in Fig. 6 (i.e., squares indicate \( U_{5\text{mm}} = 3 \) cm s\(^{-1}\)).
site revealed particulate nitrogen concentrations ranging between 0.1 and 0.6 mg N l\(^{-1}\) with a mean of 0.34. The achieved average concentrations of particulate nitrogen suspended in the water of the flumes is, therefore, similar to field conditions (Fig. 5).

Fig. 8. Relative growth rates vs. flow velocity in Experiment 2. (A) A small size class of *S. benedicti* (initial length = 0.5 – 3 mm) and (B) a large size class of *S. benedicti* (initial length = 4 – 5 mm). Each plotted symbol represents the mean relative growth rate of approximately 8 – 12 individual worms from a single flume (the S.D. of any mean from a single flume was ~ 0.07), and a different symbol shape is used for each velocity treatment. Current velocities were measured 5 mm above the sediment–water interface ($U_{5\text{mm}}$).
Both size classes of *P. cornuta* had significantly faster RGR as flow velocity increased (Fig. 6; $F_{3,12} = 3.708, P = 0.043$ and $F_{3,12} = 5.881, P = 0.010$ for small and large worms, respectively). Plotting RGR vs. the calculated average flux of particulate nitrogen 5 mm above the bottom also shows that RGR increased as the flux of suspended microalgae increased (Fig. 7; $F_{1,14} = 8.069, P = 0.013$ and $F_{1,14} = 7.018, P = 0.019$ for small and large worms, respectively). Both approaches to analyzing the data suggested that RGR reached an asymptote at $RGR \sim 0.5 \text{ day}^{-1}$ for small *P. cornuta* and $RGR \sim 0.35 \text{ day}^{-1}$ for large *P. cornuta* (Figs. 6 and 7).

Similarly, both size classes of *S. benedicti* revealed significantly faster RGR as flow velocity increased (Fig. 8; $F_{3,8} = 12.21, P = 0.002$ and $F_{3,8} = 5.972, P = 0.019$ for small and large worms, respectively). Plotting RGR vs. the calculated average flux of particulate nitrogen 5 mm above the bottom also showed that RGR increased as the flux of suspended algae increased (Fig. 9; $F_{1,10} = 5.826, P = 0.036$ and $F_{1,10} = 9.404, P = 0.011$ for small and large worms, respectively). Both analyses of the data suggested that RGR reached an asymptote at $RGR \sim 0.25 \text{ day}^{-1}$ for both size classes (Figs. 8 and 9).

4. Discussion

Results of Experiments 1 and 2 demonstrate the importance of flow and the flux of suspended food particles in promoting the growth of juvenile spionids. Both of the laboratory flume experiments were designed to control food and flow conditions in ways that are not possible in situ. In addition, the experimental designs included multiple flumes as independent replicates, avoiding “pseudoreplication” of flow treatments (Hurlbert, 1984).

Experiment 1 tested the effect of resuspending sediment; neither the quality nor quantity of food was manipulated in any way other than by the sediment transport that occurred when $U_{5mm}$ exceeded $13 \text{ cm s}^{-1}$. Both species tested, *P. cornuta* and *S. benedicti*, grew significantly faster when sediment transport occurred. Sediment transport could enhance the growth rate of interface-feeding spionids by supplying the feeding ambit of deposit feeders with new food particles (Levinton and Lopez, 1977; Kihslinger...
and Woodin, 2000) or by transporting lighter components of the sediment into the benthic boundary layer where suspension feeders can capture particles. The flow treatment in which flumes were set to a still-water condition except for a daily 30-min pulse to briefly resuspend sediments provides some evidence that a daily resupply of food for deposit-feeding spionids is insufficient to affect the worms’ growth rate noticeably. The results demonstrate that periods of prolonged flow that favor suspension-feeding activity are required to significantly enhance the growth rates of juvenile spionids. The lack of a correlation between growth rate and flow velocity at \( U_{50 mm} \leq 12 \ cm \ s^{-1} \) can be explained by the fact that, at flows slower than the critical erosion velocity, the filtered water in the laboratory flumes contained few suspended food particles.

Experiment 2 was designed to test this conclusion by adding a controlled concentration of phytoplankton to the flumes. When microalgae were present as food for suspension-feeding spionids, growth rate correlated positively with velocity from \( U_{50 mm} = 3 \ to \ 12 \ cm \ s^{-1} \). This probably resulted because flow increased the horizontal flux of suspended food particles encountered by suspension-feeding worms. Direct observations of feeding behavior were not possible during the annular-flume experiments, but several studies have demonstrated that \( P. \ cornuta \), \( S. \ benedicti \), and many other spionids increase their suspension-feeding activity at faster flows and higher particle fluxes (Taghon et al., 1980; Dauer et al., 1981; Miller et al., 1992; Taghon, 1992; Taghon and Greene, 1992; Bock and Miller, 1996, 1997). In addition to increasing the flux of suspended food, faster velocities also enhanced the deposition of microalgae slightly (Figs. 4 and 5). Deposit feeding worms might have benefited from a slightly higher supply of particles to the sediment, but the magnitude of this effect on worms’ growth relative to that of suspension feeding is probably small because, in total, all of the \( \sim 50 \) worms in a flume could sample at most 1% of the sediment surface (1.8 m\(^2\)) by deposit feeding (i.e., most of the microalgae that deposited passively would become incorporated into sediment that was beyond the feeding radius of any sedentary worm with palps shorter than 1 cm). In nature, however, the combination of enhanced deposition and the transport of sediment in bedload or suspension as flow increases will probably supplement the growth of all microphagous benthos, including obligate deposit feeders.

The relationship between growth rate and the flux of particulate nitrogen appeared to reach a plateau for each species and size class within a species. I suggest that these asymptotes (e.g., RGR \( \sim 0.5 \ day^{-1} \) for the small size class of \( P. \ cornuta \)) reflect the maximum possible growth rate at the temperature of the experiment (20 \( ^\circ \)C). Alternatively, the data could be explained by either a reduction in feeding activity at faster flows or by a possible reduction of particle-retention efficiency at faster flows (Shimeta and Koehl, 1997).

The hypothesis that worms in the \( U_{50 mm} = 12 \ cm \ s^{-1} \) flumes of Experiment 2 were growing at maximal rates is supported indirectly by comparing the growth rates measured in this study to the published growth rates of these and other microphagous polychaete species. In general, the growth rates measured in Experiment 2 are much faster than those measured in previous studies of polychaete growth (e.g., Marsh et al., 1989; Taghon, 1992; Taghon and Greene, 1992; Bridges et al., 1994). In particular, the growth rates in Experiment 2 are nearly double the growth rate of 0.14 \( \text{day}^{-1} \) measured by Bridges et al. (1994) for still-water \( S. \ benedicti \) cultures fed saltmarsh mud. The growth rates in Experiment 2 are also three to five times faster than the rates of \( \sim 0.01-0.08 \ \text{day}^{-1} \) measured by Taghon (1992) and Taghon and Greene (1992) for juvenile spionids in a laboratory flume. Taghon (1992) and Taghon and Greene (1992) used unfiltered seawater without any supplement of algae or other nutritious particles, and they note that the concentration of suspended particles might have been limiting in at least some of their experiments. The addition of microalgae to the annular flumes and the daily measurement of particulate nitrogen concentrations ensured that the concentration of suspended particles in Experiment 2 was similar to that of water at the site where worms were collected.

One way to test the alternative explanation that worms feed less or have lower retention efficiencies in faster flows would be to manipulate the flux of suspended food particles by altering both the flow velocity and the concentration of food particles independently. By manipulating both variables, one could create the same flux of suspended food at two different flow velocities. Alternatively, direct observations
of particle-contact rates and retention efficiencies (e.g., Shimeta and Koehl, 1997) could clarify how spionids’ feeding mechanics vary with flow.

The results and conclusions of Experiments 1 and 2 have several implications for the dynamics of spionid populations and the communities in which they often are abundant and important members (e.g., Noji and Noji, 1991; Cummings et al., 1996; Stehlik and Meise, 2000; Bolam and Fernandes, 2002). Several authors have developed demographic models of spionid populations that point to juvenile growth rate as a central parameter (e.g., Levin and Huggett, 1990; Zajac, 1991a,b; Levin et al., 1996). Because these studies were based, in part, on rates of juvenile growth and development measured in still-water laboratory experiments, the number of individuals in a spionid population is likely to increase much more rapidly in nature, where some flow always occurs. Given the strong influence that flow has on the growth rates of juveniles, it seems likely that egg production by adults will also vary with hydrodynamic conditions. Furthermore, the significant growth that was measured over time intervals as small as 3 days suggests that variability of flow over short time scales (e.g., due to storms or the lunar tidal cycle) is likely to have consequences for the growth of juvenile spionids. For example, spionid larvae that recruit to the benthos a few days before the maximal tidal exchange during a spring tide will probably grow more rapidly than will juveniles that recruit during neap tides. Several recent studies have pointed to the early juvenile period as a possible bottleneck in the dynamics of benthic populations (e.g., Hentschel and Jumars, 1994; Olafsson et al., 1994; Gosselin and Qian, 1997; Hunt and Scheibling, 1997; Hentschel, 1998a,b); even a few days of favorable flow might ease the transition from pelagic larva to benthic juvenile. Similarly, flow varies spatially on a range of scales. Efforts to understand the causes of spatial patchiness in soft-sediment communities will benefit from characterization of the hydrodynamic conditions inside and outside of dense spionid patches. Of course, quantitative predictions about in situ growth rates are difficult to extraplate from the laboratory flume experiments because flow is never constant for 3 or 7 days anywhere in nature. More elaborate flume experiments, such as simulating tidal currents, and field observations will be required to predict the effects of small scale variability of flow in time and space. In general, however, the data identify flow and the flux of suspended food particles as major determinants of spionid growth.

If growth to a larger size confers increased survival, the importance of flow’s effects on spionid nutrition and growth will be even broader. In particular, the secondary production of spionids is likely to be much higher when flow conditions favor suspension feeding. A major food resource for many bottom-feeding fishes will, therefore, be enhanced greatly in places where or at times when hydrodynamic conditions favor the feeding and growth of spionids.

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References


