

Evidence of infaunal effects on porewater advection and biogeochemistry in permeable sediments: A proposed infaunal functional group framework

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ABSTRACT

Bioturbating infauna significantly modify reaction and transport processes in permeable sediments, though most studies to date are limited in the scope of species examined. We conducted a comparative field study measuring density-dependent effects of six common bioturbating species on porewater advection and biogeochemistry, across three intertidal permeable sediment habitats. The species in this study are; head-down like deposit feeders (*Abarenicola pacifica* and *Balanoglossus aurantiacus*), surface deposit feeders (*Diopatra cuprea* and *Onuphis jenneri*) and gallery diffusers (*Upogebia pugettensis* and *Neotrypaea californiensis*). Tracer loss from gel diffusers was used to assess relative differences in porewater advection among sites, and porewater peepers were used to measure solute concentrations of carbon, nitrogen, phosphate, and silicate in experimental plots. Characteristic surface features of different infauna were counted and used as a proxy for infaunal density. Density of surface features was then used in regression analyses as an explanatory variable affecting porewater transport and chemistry. Significant infaunal density effects on porewater transport or biogeochemistry were found in all but one species, *D. cuprea*. The species-specific attributes and mechanisms by which these infauna affect permeable sediment processes are explored. A process based functional group framework is presented for permeable sediments. Bulk granulometric properties also were assessed. There were little to no within-site effects of porosity, hydraulic conductivity, or organic matter on porewater transport and biogeochemistry. However, significant across-site differences in granulometry and site properties were found and these are addressed in relation to infaunal effects on porewater transport and chemistry.

1. Introduction

Intertidal and shallow subtidal coastal sediments host diverse communities of infauna, including many that alter sediment biogeochemistry in complex ways. Many infaunal-permeable sediment studies have focused on arenicolid polychaete species (e.g. Huettel, 1990; Timmerman *et al.*, 2002; Meysman *et al.*, 2006; Volkenborn and Reise, 2007),

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although other studies include freshwater oligochaetes and crustaceans (Jones and Jago, 1993, D'Andrea *et al.*, 2002, 2004; Nogaro *et al.*, 2006; Mermillod-Blondin and Rosenberg, 2006; Waldbusser and Marinelli, 2006). Recent modeling (Meysman *et al.*, 2005; Timmerman *et al.*, 2006), laboratory (Wethey and Woodin 2005; Na *et al.*, 2008), and field studies (Volkenborn and Reise, 2007) of arenicolids have provided valuable insights into permeable sediment bioirrigation and emphasized the importance of specific behaviors (Wethey *et al.*, 2008). However, permeable sediment habitats are diverse and other infauna and behaviors are potentially significant. Coastal ecosystems are sensitive to changes in benthic processes (Torgersen *et al.*, 1997; Meile and Van Cappellen, 2003; Tyler *et al.*, 2003; Lucea *et al.*, 2005) and changes to the infaunal community population structure and activity have the potential to significantly affect benthic biogeochemistry (Waldbusser *et al.*, 2004). Therefore, important goals for coastal ecosystems research should be: (1) determination of the range of infaunal effects on sedimentary processes and (2) identification of common traits among infauna affecting these processes that may be used to simplify diverse communities. Assigning infauna to functional groups based on their impact on porewater advection and biogeochemistry may improve our understanding of benthic processes and dynamics in coastal ecosystems.

Functional groups have been traditionally developed and used to understand the interactions of various environmental parameters with infaunal community composition; for example, the loss of larger deeper dwelling infauna in response to organic enrichment of sediments (Pearson and Rosenberg, 1978). By collapsing species into groups with similar functions, this approach has been, and continues to be, useful in identifying general patterns of species shifts in relation to natural and anthropogenic events (Fauchald and Jumars, 1979; Hutchings, 1998; Pearson, 2001). While sediment properties may determine large-scale distributions of infauna (and often functional groups), benthic infauna in turn affect rates of nutrient cycling or particle mixing (Kristensen, 2000). The cyclical nature of animal-sediment interactions poses heuristic and theoretical challenges to investigators and we suggest that the functional group approach may prove useful in simplifying the role of infauna on sediment processes.

Several studies have shown that traditional functional groupings have had moderate success in predicting the effects of different infauna on biogeochemical fluxes (Michaud *et al.*, 2006) or particle mixing (D'Andrea *et al.*, 1996, 2002). Traditional functional groupings in diffusion-dominated marine sediments have used feeding modes or guilds (Fauchald and Jumars, 1979; Hutchings, 1998) or particle mixing effects (Pearson, 2001; Biles *et al.*, 2002; Gerino *et al.*, 2003). Mermillod-Blondin and Rosenberg (2006) illustrated that functional groups may have differential effects on sediment processes depending on whether sediments were diffusion-dominated or permeable. Given the discrepancies in applying traditional functional groups to infaunal effects on sediment processes, we develop a different approach as suggested by Gerino *et al.* (2003). Rather than define groups first based on behavior, we measure the effects of several different infauna on porewater advection and biogeochemistry and group them based on their

measured impacts on biogeochemical processes. Although this approach of measuring effects first then grouping organisms afterwards may require considerably more empirical data to determine its efficacy, it provides an alternative functional group framework that directly links infaunal effects to sediment porewater processes. We, however, recognize that our proposed framework below is only one of several components to understanding the general patterns of infaunal effects on sediment processes, and other environmental variables will alter porewater advection.

Porewater advection within permeable sediments exchanges reactive particulates, rapidly removes metabolites, stimulates biogeochemical processes, and increases organic matter remineralization rates, relative to diffusive sediments (e.g. Huettel *et al.*, 1996, 1998). There are several physical processes that promote porewater advection in permeable sediments. Currents and surface gravity waves create flow interactions with sediment surface topography that result in oscillating or constant pressure gradients capable of inducing porewater advection (Reimers *et al.*, 2004). Larger scale pressure gradients may also drive porewater advection through tidal flats (Le Hir *et al.*, 2000; Billerbeck *et al.*, 2006), submarine groundwater aquifers (Burnett *et al.*, 2003), or beneath tidal marshes (Jahnke *et al.*, 2003).

Infauna have diverse life history strategies that include myriad behaviors and biogenic sediment structures, many of which may alter porewater advection by: (1) altering sediment granulometry (e.g. Rhoads and Young, 1970), (2) modifying the topography of the sediment surface interacting with overlying water flows (Huettel and Gust, 1992; D'Andrea *et al.*, 2002; Wild *et al.*, 2005) or (3) pumping water into sediments (Wetthey and Woodin, 2005; Wetthey *et al.*, 2008). These effects are not mutually exclusive. The spatial scale of individual infaunal effects is localized to areas immediately surrounding a burrow, feeding funnel, or other structure created through infauna activity. Many of these localized effects increase permeability and counter normal sediment compaction processes (Craig *et al.*, 1998), although others increase compaction (Waldbusser and Marinelli, 2006); however, data are generally lacking to generalize these effects. Infauna may have broad scale impacts on the seafloor when their individual activities and effects are integrated over larger spatial scales. For example, Volkenborn and Reise (2007) have shown that populations of arenicolids increase the permeability of intertidal sediments relative to areas where the arenicolids have been excluded. Abundant smaller organisms can also have substantial effects on permeable sediments; D'Andrea *et al.* (2004) found that dense populations of amphipods were responsible for enhancing diffusive sediment mixing and creating void spaces in the presence of several larger, less abundant species. A combination of organism density, infaunal behavior, and sediment properties should ultimately determine whether infaunal communities will affect permeable sediment processes over broader scales. Grouping infauna that have measurable effects on porewater advection and biogeochemistry then identifying common behavioral attributes such as feeding mode or activity will provide a conceptual framework that may be expanded, modified, or dismissed as more empirical data are collected.

A field-based investigation of infaunal density on porewater advection and biogeochemistry in permeable sediments was carried out. The primary objectives were: (1) measure the effects of a few large bioturbating infauna on permeable sediment processes at their natural densities, (2) determine relationships among density, sediment biogeochemical processes, and functional traits, (3) develop a functional group framework that may be used, expanded and modified for future studies of infauna in permeable sediments. We measured plot-scale effects of six infaunal species on porewater advection and biogeochemistry within permeable sediment sites. Natural variability of infaunal density across small spatial scales was used to avoid disrupting the sediment habitat, while maintaining similarities in sediment properties. Sediment granulometry was measured within and across sites to ensure plots within sites were similar to each other and effects were most likely due to differences in infaunal density. Differences across sites in granulometry were evaluated and broader scale environmental variables were related to among-site variability.

2. Methods

a. Sites and organisms

This study was conducted at three tidal flats in the USA: False Bay located on San Juan Island, Washington (lat = 48.489, lon = -123.066), Cara's Flat located in the coastal bays area of Virginia (lat = 37.591, lon = -75.616), and Debidue Flat located east of Georgetown, South Carolina (lat = 33.335, lon = -79.167). All three sites are well flushed with coastal waters over daily tide cycles, consist of fine sands, and contain relatively low organic matter (described further below). Resident bioturbating benthic infauna create distinct surface features visible at low tide when each of the flats are exposed that were used as a proxy for local abundances. Although this method precludes exact measurement of abundance, it provides an estimate of abundance as evidenced by creation of features associated with individual organisms. General effects of the study organisms are summarized in Figure 1 and detailed below.

i. False Bay, WA, USA. False Bay is an embayment that drains fully during the lower of the mixed semi-diurnal tides. The average daily tidal range is ~2.3 m. The exposed tidal flats comprise a series of sand bars, pools, and creeks creating greater topographic relief over shorter distances than the other two sites described below. Sediment ripples were generally parallel and had a wavelength of roughly 8 cm during the time of this study. The sample area is located near the head of the bay on a shallow sand bar subject to exposure times ranging from 4 to 12 hrs.

The arenicolid polychaete *Abarenicola pacifica* and two species of thalassinid shrimp, *Upogebia pugettensis* and *Neotrypaea californiensis*, are found in high densities in this portion of the flat. These two taxonomic groups will be referred to as arenicolids and thalassinids, respectively. The thalassinids are treated as one taxonomic unit, given their functional similarities in the creation of large galleries and the inability to determine

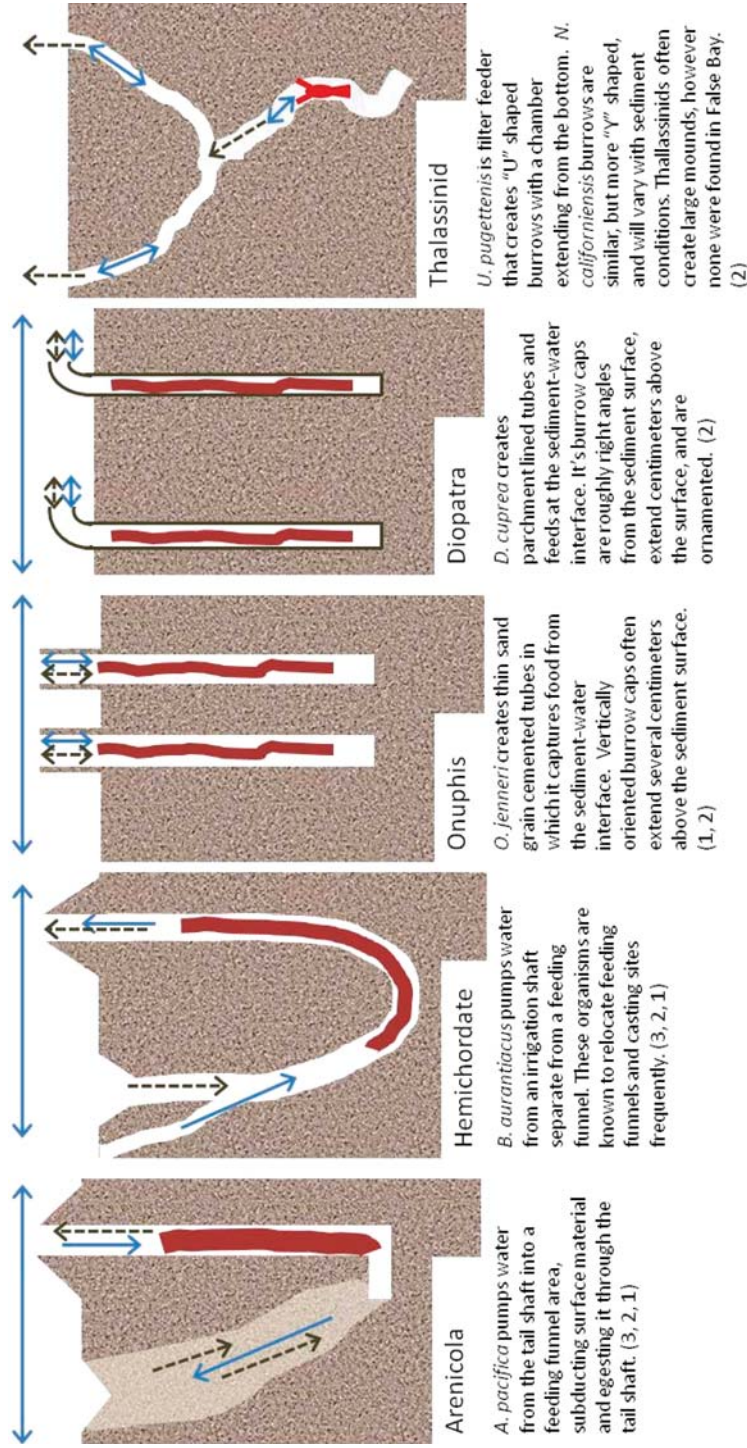


Figure 1. Illustration of general water and particle movement due to activities of the study organisms. Solid arrows represent water flows, dashed arrows represent particle movement. These are general patterns known for these species, and we acknowledge more complex secondary flows occur. The porewater advection due to tidal draining is not included on the current schematics, because the flow interactions between infauna and porewater advection is poorly characterized. Following the functional group scheme presented, infauna may affect porewater advection by: 1) topography, 2) permeability, and 3) irrigation. These numbers are listed and ordered in each panel to indicate the effects of each species.

species identity without digging up the flat. It is likely that the dominant thalassinid at this site is *U. pugettensis*, given the burrows that were retrieved were clay lined in relation to the unlined burrows of *N. californiensis* (Miller and Curran, 2001; Griffen *et al.*, 2004). Thalassinids may filter or deposit feed (Posey *et al.*, 1991; Ziebis *et al.*, 1996; Pinn *et al.*, 1998; Atkinson and Taylor, 2005). We recognize the highly diverse nature of the thalassinids in burrow structure (e.g. Griffis and Chavez, 1988), behavior and life history (e.g. Dumbauld *et al.*, 1996), but group these here as they are more similar to each other in general burrow architecture than the arenicolid. In contrast to the thalassinids, the arenicolid is a head-down deposit feeder that creates a J-shaped, mucus-lined burrow. *A. pacifica* pumps overlying water through its tail shaft fluidizing sediment in the J-portion of the burrow (Huettel, 1990; Riisgard and Banta, 1998; Meysman *et al.*, 2006). This irrigation activity allows the arenicolids to subduct and feed on fresh organic matter, resulting in localized areas of increased permeability (Jones and Jago, 1993).

ii. *Cara's Flat, VA, USA*. The flat is adjacent to a tidal salt marsh that has been slowly encroaching across the flat from south to north (M. Luckenbach, pers. comm.). A gradient in sediment characteristics exists from finer grained muddy sediments adjacent to the marsh, to sandy sediments adjacent to the small creek connected to the ocean. Along this gradient is also a gentle slope from the higher muddy/marsh areas to the sandy sediment closer to the creek. The sediment surface is relatively flat over the plot scales of 0.25 m². During this study, ripples were small (1 cm wavelength) or absent. The semi-diurnal spring tidal range at this location is roughly 1.5 m, with exposure maximum exposure times of four hours during the sampling period.

In the fine-sands area of *Cara's Flat* (closer to the creek than marsh), the dominant infauna are the hemichordate *Balanoglossus aurantiacus* (referred to as hemichordate) and onuphid polychaete *Diopatra cuprea* (referred to as *Diopatra*). *B. aurantiacus* is a large deep-dwelling deposit feeder that inhabits a u-shaped tube. It uses multiple feeding funnels to subduct surface material in the anterior end of the burrow to depth, and creates new feeding funnels over time periods of hours to days (Duncan, 1987). This feeding behavior is similar, though not identical to the arenicolids, as it subducts surface sediment into the base of the burrow. Therefore, *B. aurantiacus* is considered a head-down deposit feeder for the purposes of this study. Unconsolidated fecal mounds are evident at their tail shaft (Fig. 1). *Diopatra cuprea*, the onuphid polychaete commonly known as the junk worm, is a surface-feeding omnivore (Myers, 1972; Brenchley and Tidball, 1980). It lives in a leathery parchment tube with various shell fragments, algae, and other materials glued to its burrow. The top of the tube (tube cap) extends several centimeters from the sediment surface into the overlying water. *Diopatra* will orient its tube cap perpendicular to water flows at lower organism densities to maximize passive burrow flushing (Brenchley and Tidball, 1980). The burrow linings of *diopatra* are relatively impermeable compared to other infauna (Aller, 1983).

iii. *Debidue Flat, SC, USA*. This is a well-studied intertidal flat located in a shallow tidal creek network on North Island, adjacent to North Inlet (Grant, 1981; D'Andrea *et al.*, 2002). The tidal range of 1.7 m is heavily moderated by local winds. Most of the area has fringing tidal marshes, situated between a barrier island and North Island. The upper 2–3 cm of sediment on the flat regularly migrates over a few days with the changing tides (Grant, 1981). Ripples and changes to surface topography were noted during experiments, as movement of ripples is observed in consecutive daily sediment surface photographs. The surface ripples were not as parallel as False Bay, indicating that the flow direction is probably more variable. Wavelengths in sediment features were approximately 20 cm in length. Maximum exposure times of roughly six hours occurred during the sampling period.

Debidue Flat has a lower muddier area with a diverse infaunal community and a sandier higher section dominated by the onuphid polychaete *Onuphis jeneri* (referred to as onuphis). Studies were focused on the sandier upper and mid-level portions of the flat where both onuphid polychaetes, *O. jeneri* and *Diopatra cuprea*, co-occur. *O. jeneri* is a surface deposit feeder, smaller in size than diopatra. It builds tubes that extend several centimeters from the sediment surface; onuphis burrows are thin, flimsy, and made from sand grains embedded in a polysaccharide matrix. The diffusional characteristics of these burrows have been characterized (Aller, 1983; Hannides *et al.*, 2005) and found to be more permeable to diffusive exchange than *D. cuprea* burrows (Aller, 1983).

b. *Study design*

The goals of this study were to measure infaunal effects on porewater advection and biogeochemistry. We used the natural variability of large infauna within sites and established replicate experimental plots across these faunal density gradients at each study site. Therefore, we are using a density-dependent approach to quantify infaunal effects on permeable sediment processes within sites and then comparing across the three sites. We assumed that any density-dependent effects were linear in nature and used linear regression to examine these relationships. The sampling design at each site varied slightly according to site characteristics and previous measurements made, although the general methodology and comparisons within sites are similar. In all investigations, the experimental plots were 50 × 50 cm quadrats marked by wooden dowels.

In False Bay, a block design was used to locate plots of different densities of arenicolids and thalassinids within close (< 5 m) proximity of each other. Plots were chosen that were dominated by arenicolids, thalassinids, or a mixture of both, and these three treatments were applied once within each of three blocks, resulting in nine total plots. The porewater advection measurements were conducted 19 July 2004 to 21 July 2004, and porewater solutes were measured from 4 August 2004 to 10 August 2004, within the same experimental plots.

Experimental plots at Cara's Flat also consisted of three blocks and three plots within each block. All the plots within a block at Cara's Flat were within several meters of each

other, and plots were selected on the basis of the abundance of either hemichordates or diopatra. The same plots were used for both the porewater advection and chemistry measurements. Advection measurements were made 22 July 2005 to 24 July 2005, and porewater solutes were measured 17 August 2005 to 22 August 2005.

Experimental plots at Debidue Flat were arranged in transects across the flat, with each experimental plot roughly within a meter of the next plot. The advection measurements were arranged in two different transects, one across the sandy area and one across a slightly less sandy area higher in diopatra density. Both transects had eight experimental plots. Porewater solutes were only measured in the sandy area, with one transect of nine plots. The porewater solute and advection measurement sites were different due to the fact that the porewater solutes were measured one year after the advection measurements and the site markers would not last the winter. Porewater advection measurements were made 16 October 2005 to 18 October 2005, and porewater solutes were measured 10 July 2006 to 16 July 2006. Granulometry was measured during the 2005 sampling period and not during the 2006 period. We, therefore, assume that there were no significant changes in granulometry between the two sampling periods.

c. Organism density

The densities of infauna within each experimental plot were estimated by daily replicate photographs of each plot and enumeration of surface features (tubes, fecal coils, burrow openings) associated with different infauna (Fig. 1) (Kraeger and Woodin, 1993; Widdicombe *et al.*, 2003; Waldbusser and Marinelli, 2006) during the period when advection and biogeochemistry measurements were made. In all field investigations, at least three sets of daily photographs were taken. Each surface photograph was then inspected and distinct digital markers were placed on each type of feature. The software package Image-J was used to produce scaled maps of the burrow features, as well as count, and record the spatial coordinates, of each feature. The counts were then averaged over the days that photographs were taken to determine average densities of each organism within each plot. More than a year after the initial image processing, several images from each site were reviewed and counts redone manually for quality control.

d. Advection measurements

The rates of porewater advection within each experimental plot were inferred by quantifying loss of a tracer from replicate gel diffusers inserted into the sediment. This method is described in Waldbusser and Marinelli (2006) and reviewed briefly here. Acrylamide gel plugs made following Browne and Zimmer (2001) containing 1 mg ml^{-1} of fluorescein were cast in $1.1 \times 9 \text{ cm}$ cylinders. Tracer is released to the surrounding sediment from a gel via diffusion. As advection occurs next to and around the gel, it removes the tracer that was diffused out of the gel, creating a steeper concentration gradient; and, therefore, larger loss of tracer from the gel. In this respect, tracer loss is proportional to advective flow. Gels were inserted vertically into the sediment via core

replacement and buried approximately 1–2 cm below the sediment surface. Within each plot, five replicate gels were aligned perpendicular to the slope of the sediment surface. The spatial coordinates of the gels within the plot were recorded so that they could be retrieved with minimal sediment disruption at the end of the experimental period.

The acrylamide gels were deployed during the low tide portion of spring tides at Cara's Flat and Debidue Flat or the exceptionally good semi-diurnal tide at False Bay for 48 hrs. After the 48-hr deployment, the gels were retrieved from the experimental plots at low tide. Any sediment attached to the gel was gently wiped from the gel surface. A 5-mm subsection was taken 1 cm from both the near surface and deep ends of the gel to evaluate differences in porewater flow with depth. These subsections were placed into pre-weighed 5-ml sample vials, weighed again, and diluted with 2.5 ml of deionized water. Any gels that were exposed on the sediment surface or had been damaged while they were deployed in the sediment were noted. During the back equilibration, all samples were kept dark in a 4°C refrigerator. After the back equilibration period, the fluorescein concentration in the deionized water was determined on either a Turner Designs fluorometer, or an Agilent high performance liquid chromatographer (HPLC) equipped with a fluorescence detector and calibrated to at least 5 standard solutions of fluorescein. The concentration of the fluorescein in the gels ($Fluor_{gel}$) was then determined from the dilution factor of the gel volume and diluent by:

$$Fluor_{gel} = \left(\frac{Gel_V + Dil_V}{Gel_V} \right) * Fluor_{sample} \quad (1)$$

where Gel_V is the volume of the gel section, Dil_V is the volume of diluent, and $Fluor_{sample}$ is the fluorescein measured in the back equilibrated sample.

e. Porewater solutes

Porewater peepers (Hesslein, 1976) were used to determine time averaged porewater concentrations of ammonium (by Koroleff, 1976), nitrate (by EPA 353.3), phosphate (by Eaton *et al.*, 1995), silicate (by Strickland and Parsons, 1972), alkalinity (by EPA 310.2), pH (standard potentiometric electrode), dissolved inorganic carbon (DIC), and calcite saturation state. The calculation of DIC and saturation state from alkalinity and pH was conducted using the co2sys.exe program (Lewis and Wallace, 1998). All chemical analyses were run on a Smartchem discrete chemical analyzer (Westco Scientific). The porewater peepers were constructed of PVC plastic and have a sampling depth range of roughly 10 cm. Each peeper had ten wells and each well was roughly 0.75 cm deep, 3.2 cm wide, and 0.8 cm high, encompassing a volume of roughly 2 ml. The wells of the peeper were filled with 15% acrylamide gel polymerized with potassium persulfate, rather than ammonium persulfate to prevent ammonium contamination of samples (Engstrom and Marinelli, 2005). The acrylamide gels within the peeper wells were allowed to polymerize overnight and were then placed in a sodium chloride solution of 30 ppt in order to prevent

conductive haline circulation on the face of the peeper due to ionic imbalance between porewater and the hydrated acrylamide (Grigg *et al.*, 1999).

The peepers were hydrated for five days prior to deployment in the field. Before deployment, peepers were affixed with 0.45 μm Magna Nylon filter paper in a shallow water bath to prevent trapped air bubbles behind the filter paper. Three replicate peepers were deployed in each experimental plot and oriented such that the narrow edge of the peeper was perpendicular to the relief of the flat. Peepers were deployed for five to six days, and daily photographs of each plot were taken during the deployment. Upon retrieval, peepers were extracted from the sediment, wiped clean of sediment, quickly placed in zip-lock bags in a cooler until returned to the laboratory. Once in the lab, peepers were kept in a 4°C refrigerator while the gels from each peeper were extracted and placed into individual pre-weighed sample vials. All gels were extracted from the peepers within 24 hrs of retrieval. Gels and sample vials were weighed again, and 8 ml of deionized water was added to each sample to back equilibrate solutes within the gels for 48–72 hrs. Spot checks of salinity were conducted on the back equilibrated water to ensure that peepers had not evapo-concentrated solutes.

f. Granulometry

Sediment granulometry was measured in order to identify larger scale controls on porewater transport and possible mechanisms by which infauna may affect porewater transport and biogeochemistry. All plots within sites were sampled for granulometry, but the methods differed slightly. Three 3-cm diameter cores were taken and combined for each experimental plot in False Bay and Debidue Flat, while separate triplicate cores for each plot were taken for Cara's Flat, with surface and deep subsections of each core. Cores were taken to a depth of roughly 10–15 cm. Sediment samples were placed in sealed containers, in the dark and frozen within 12 hrs of collection. Porosity was measured by loss of mass by drying at 60°C. Samples were weighed, dried for 24 hrs, re-weighed, then dried for subsequent 24-hr periods until there was no change in mass. After a stable mass measurement was attained, the sample was placed on a sieve shaker for 15 min. with a distribution of five sieves from 0 to 3.5 phi on the Krumbein phi scale and a pan. Percent fine content is defined as material passing the 3.5 phi sieve. The mass of sediment remaining on each sieve was weighed and granulometric properties were determined by the methods of Folk and Ward (1957). Representative sediment subsamples from the mixed sediment cores were taken for organic carbon and nitrogen after drying by high temperature combustion and elemental analysis (EPA #440.0 1997) to determine background quantities of organic matter. Hydraulic conductivity was measured by the constant-head permeameter method on collected sediment, and permeability calculated from the dynamic viscosity of the fluid used in the permeameter measurements following Boudreau (1997).

g. Statistical analyses

In order to determine organism effects and the role of sediment properties, organism density and sediment granulometric variables at each site were treated as independent variables in multiple step-wise regression analyses. The response or dependent variables in the regression analyses were the fluorescein remaining in the gels (a proxy for porewater advection), or depth-integrated porewater solute concentrations at each site. Analyses of the original block design for False Bay and Cara's Flat found that there were no differences in sediment properties among blocks, nor was the variance component due to blocking found to be statistically significant. Therefore, these data were analyzed using a regression analysis. The step-wise regression technique can be used to eliminate correlated variables and identify multiple statistically significant independent variables acting on one dependent variable. All data were averaged within each experimental plot, and these within-plot averages were used for all regression analyses at a given site. Differences in the grand means within sites of near surface versus deep sections of the fluorescein gels were determined by analysis of variance (ANOVA). If a significant difference was found, separate regressions for the surface and deep sections of the gels were conducted.

The stepwise regression provides best-fit combinations of independent variables for one to the total number of variables in the regression. For these analyses a maximum of five variables were put into the model for the selection process. Adjusted r-squared, mean square error (MSE), and Mallows' cp index were used to identify the best possible model with fewest possible variables by maximizing adjusted r-squared and minimizing MSE and Mallows cp. Collinearity of independent variables was checked by the condition index of the independent variables (calculated by Eigen values), using 5 as a value that requires further investigation. With a condition index below 5, the variables in the model are not artificially lowering MSE because of correlated variables.

Once the best fitting independent variables were determined with stepwise regression, the regression (simple or multiple—depending on result of selection process) with only these parameters was run, and statistical significance was evaluated for each variable in the model. If a variable chosen with the stepwise regression was not significant in the multiple regression model, then the variable was removed from the model, and the model was re-run. Natural log transformations were made on variables as needed in order to meet assumptions of normality and homoscedascity. Once a suitable model was determined for each regression, overly influential data points were evaluated by studentized residuals (> 2) and Cook's distance (> 1). If overly influential data points were found, these were examined, removed, and the regression was re-run without these points. If no change in the results was found due to removal of the point, it was left in the regression because the presence or absence of the point did little to change the inference of the analysis. In some cases removing one data point created a second overly influential data point; these were not removed from subsequent analyses. No more than one data point was removed from any regression analysis run. All statistical analyses were conducted using SAS software version 8.

Table 1. Grand site means (μ) and standard deviations (σ) of sediment characteristics among experimental sites.

	False Bay, WA (9)		Cara's Flat, VA (54)		Debidue Flat, SC (16)	
	μ	$\pm\sigma$	μ	$\pm\sigma$	μ	$\pm\sigma$
Grain (phi)	2.92	0.12	2.35	0.10	2.44	0.03
Grain (um)	133.08	11.05	197.50	13.34	185.29	4.10
% Fines	17.44	4.03	1.12	0.51	0.17	0.04
Porosity	0.43	0.01	0.39	0.02	0.44	0.01
HydraulicCond.	3.62	2.25	9.09	4.09	9.29	1.09
Permeability	3.55	2.20	8.92	5.15	9.12	1.07
Sorting	1.82	0.05	1.39	0.04	1.38	0.02
Skewness	0.00	0.01	0.00	0.01	-0.01	0.02
Kurtosis	1.08	0.02	1.10	0.01	1.09	0.01
Organic C	0.19	0.02	0.11	0.04	*0.04	n/a
Organic N	0.02	0.01	0.01	0.01	n/a	n/a

Organic C and N are in units of percent by weight, permeability values are 10^{-12} m^2 , and hydraulic conductivity values are 10^{-5} m s^{-1} . Numbers in parentheses indicate the number of samples from each site.

*From D'Andrea *et al.* (2002).

3. Results

a. Differences among sites

Sediment granulometry, organic inputs, and physical forces are potentially important covariates with infaunal community composition in these muddy-sand intertidal habitats. Not surprisingly, differences in granulometry, porewater solute concentrations, and porewater advection were evident among the three sites (Tables 1 and 2). The primary differences among sites in sediment characteristics were in grain size and percent fines, and no significant difference in sediment permeability among sites was found, though a general inverse relationship with percent fines content was found (Table 1). Within-site variability in sediment permeability was relatively large; however, the range of permeability among sites was less than an order of magnitude from $3.55\text{--}9.12 \times 10^{-12} \text{ m}^2$ (Table 1). Percent fine sediment decreased by roughly an order of magnitude across each site from False Bay to Cara's Flat to Debidue Flat (Table 1). The larger fine sediment content in False Bay was likely due to clay particles associated with the clay lens found roughly 30 cm beneath the surface sediment layer (Waldbusser and Marinelli, 2006). No significant relationship between percent fine sediment and organic carbon was found at False Bay as was found at Cara's Flat (Fig. 2). Organic carbon at Debidue was taken from previous studies (D'Andrea *et al.*, 2002), and therefore we did not evaluate this relationship at Debidue Flat.

Fluorescein remaining in the gels is the inverse of porewater advection, i.e. less fluorescein indicates higher rates of porewater advection. The grand means of fluorescein in the tracer gels indicate False Bay is subject to the highest integrated rate of porewater

Table 2. Grand site means (μ) and standard deviations (σ) of porewater solute concentrations, averaged across all peepers and depths within each site.

	False Bay, WA		Cara's Flat, VA		Debidue Flat, SC	
	μ	$\pm\sigma$	μ	$\pm\sigma$	μ	$\pm\sigma$
Ammonium	313.14	195.95	120.00	35.50	168.67	29.19
Nitrate	n/a	n/a	6.13	5.54	1.92	1.66
DIN	n/a	n/a	126.13	36.60	170.58	28.82
Phosphate	5.52	7.51	11.05	9.08	0.93	1.52
Silicate	101.73	86.03	280.78	72.88	204.24	110.75
Ph	6.92	0.19	6.78	0.14	6.19	0.11
Alkalinity	2513.73	823.21	1677.36	301.47	1445.04	506.13
DIC	2759.97	844.58	1854.17	330.15	2197.17	728.47
Calcite Sat.	0.44	0.29	0.28	0.11	0.05	0.03
Aragonite Sat.	0.28	0.19	0.19	0.07	0.03	0.02

All values are in $\mu\text{mol L}^{-1}$ except for alkalinity in $\mu\text{eq L}^{-1}$, and saturation state and pH are dimensionless.

advection, followed by Debidue Flat, then Cara's Flat (Fig. 3). The mean values among sites of fluorescein remaining in the gels was inversely related to tidal range, strongly suggesting that differences in tidal draining during low tide (due to differences in hydrostatic head) were driving the among-site variability in porewater advection (Fig. 3). Interestingly, percent fine sediment content of the sediment does not follow this trend in porewater advection (or tidal range), nor does it appear that increased percent fine sediment inhibits porewater advection as may be expected.

Differences in porewater solute concentrations among sites suggest that tidal range and associated tidally driven porewater advection impacts solute concentrations, while other solutes were positively related to percent fine sediment. The grand site means of porewater silicate, DIC, and ammonium within each site were consistent with tidal range (Fig. 4). Increased tidal range increased DIC ($r^2 = 0.73$) and ammonium ($r^2 = 0.99$) concentrations, and decreased silicate concentrations ($r^2 = 0.96$). Alternatively, saturation state ($r^2 = 0.70$), alkalinity ($r^2 = 0.97$), and pH ($r^2 = 0.47$) were correlated with percent fine sediment content of sediment across sites (Fig. 5).

b. Within-site infaunal effects

Density-dependent effects of infauna on porewater advection (in all three sites, Table 3) and porewater solute concentrations (in two sites, Table 4) were found. Behaviorally similar deep-dwelling deposit feeders at False Bay and Cara's Flat significantly decreased solute concentrations; whereas the thalassinids at False Bay significantly increased solute concentrations (Table 4). The onuphid polychaete *Onuphis jenneri* at Debidue Flat significantly increased porewater advection (lower fluorescein concentration in gels), yet this increase in porewater advection was not accompanied by changes to porewater solute

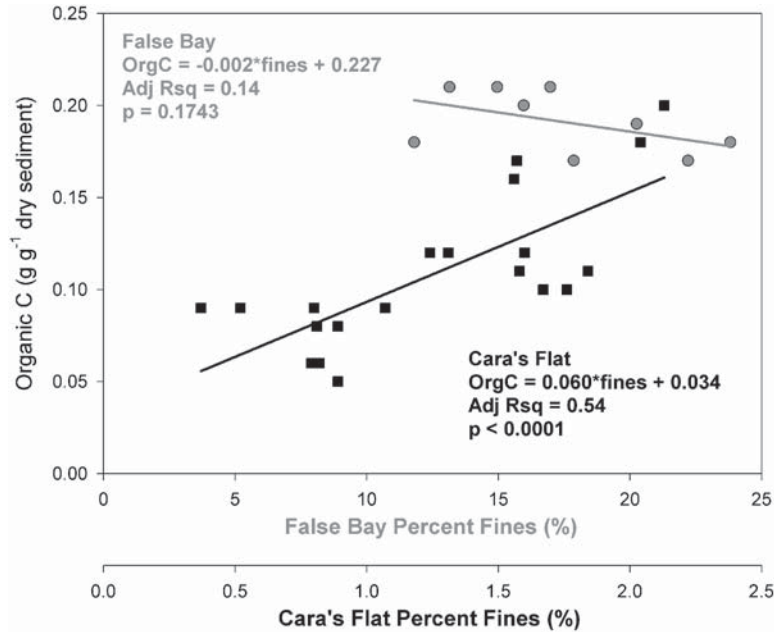


Figure 2. Percent sediment organic carbon content versus percent fine sediment at False Bay (grey) and Cara's Flat (black). Note the order of magnitude difference on the x-axis between False Bay and Cara's Flat. There was no significant relationship between organic C and fines at False Bay, whereas the relationship was highly significant at Cara's Flat. Plot specific samples were not taken at Debidue Flat.

concentrations. The taxonomically similar onuphid polychaete *Diopatra cuprea* did not significantly impact porewater advection or solute concentrations at Debidue Flat or Cara's Flat (Table 3). Individual site and organism effects are examined in greater detail below.

i. False Bay, WA. Density-dependent effects of arenicolids and thalassinids were evaluated by stepwise regression analyses of organism density, porosity, percent fine sediment, grain size, and organic C on fluorescein or porewater solutes. There was no significant difference in fluorescein concentrations between the surface and deep sections of the tracer gels (ANOVA $p = 0.6780$, $F_{1,16} = 0.18$), therefore, these values were averaged for each gel. Due to significant correlation between arenicolid and thalassinid density in False Bay, separate stepwise regressions were run with arenicolid and thalassinid density in two different models inclusive of sediment variables listed above. No statistically significant models of thalassinid density effects (alone and in combination with sediment variables) on fluorescein were found. The arenicolid stepwise regression found a two-parameter model with arenicolid density and grain size to be the best linear model explaining variability in fluorescein gel concentrations ($p = 0.0043$, $F_{2,8} = 15.51$, $\text{adj } R^2 = 0.78$). The results from the two-parameter model indicate that increasing arenicolid density decreases fluorescein

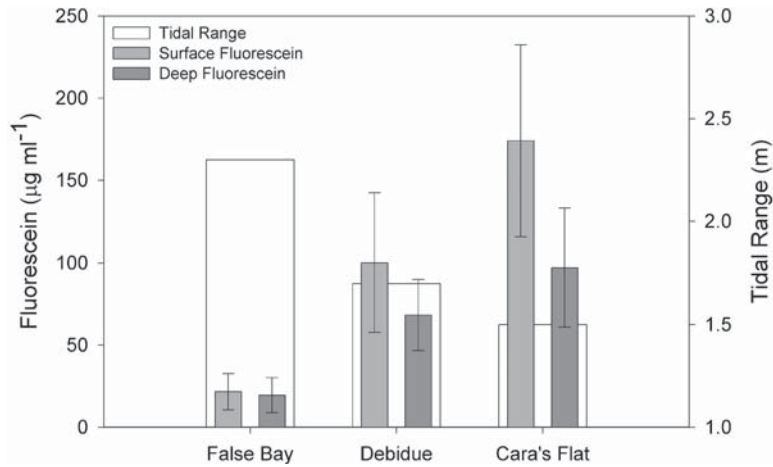


Figure 3. The grand means by site of fluorescein remaining in gels relative to tidal range at each experimental site. Surface and deep fluorescein refers to the near surface and deep subsections of the gels. Error bars are standard deviations. Fluorescein remaining in the gel is the inverse of porewater advection, i.e. less fluorescein indicates higher rates of porewater advection.

concentrations (increasing advection) (Table 3, Fig. 6) and increasing grain size increases fluorescein concentrations (decreasing advection). The range in grain size values was roughly 30 μm , resulting in a coefficient of variance (CV) of 0.04%.

Statistically significant effects of both arenicolid and thalassinid density on porewater solute concentrations were detected with simple linear regression. No significant differences were detected in sediment parameters in the original analyses of this data set (Waldbusser and Marinelli, 2006), and variances in sediment parameters were very small (Table 1). Therefore, simple linear regressions were run for each organism density separately on each solute, resulting in separate analyses of arenicolid and thalassinid densities on porewater solute concentrations. For both groups of regressions, concentration data were natural log transformed. Higher arenicolid densities were associated with significantly reduced porewater concentrations of: ammonium ($p = 0.0179$, $t_{1,8} = 3.08$, $\text{adj } R^2 = 0.51$), phosphate ($p = 0.0078$, $t_{1,8} = 3.69$, $\text{adj } R^2 = 0.61$), silicate ($p = 0.0095$, $t_{1,8} = 3.54$, $\text{adj } R^2 = 0.59$), alkalinity ($p = 0.0475$, $t_{1,8} = 2.49$, $\text{adj } R^2 = 0.37$), and DIC ($p = 0.0222$, $t_{1,8} = 2.92$, $\text{adj } R^2 = 0.49$). Higher thalassinid densities were associated with significantly increased porewater concentrations of: ammonium ($p = 0.0284$, $t_{1,8} = 2.75$, $\text{adj } R^2 = 0.45$), phosphate ($p = 0.0013$, $t_{1,7} = 5.68$, $\text{adj } R^2 = 0.82$), silicate ($p = 0.0116$, $t_{1,7} = 3.58$, $\text{adj } R^2 = 0.63$), alkalinity ($p = 0.0004$, $t_{1,7} = 7.21$, $\text{adj } R^2 = 0.88$), DIC ($p = 0.0001$, $t_{1,7} = 2.92$, $\text{adj } R^2 = 0.92$), Ω aragonite ($p = 0.0290$, $t_{1,7} = 2.86$, $\text{adj } R^2 = 0.51$), and Ω calcite ($p = 0.0290$, $t_{1,7} = 2.86$, $\text{adj } R^2 = 0.51$). The denominator degrees of freedom are lower in several of the thalassinid regressions because an overly influential data point was found and removed. As noted previously (Waldbusser and Marinelli, 2006), the densities of arenicolids and thalassinids in False Bay are negatively

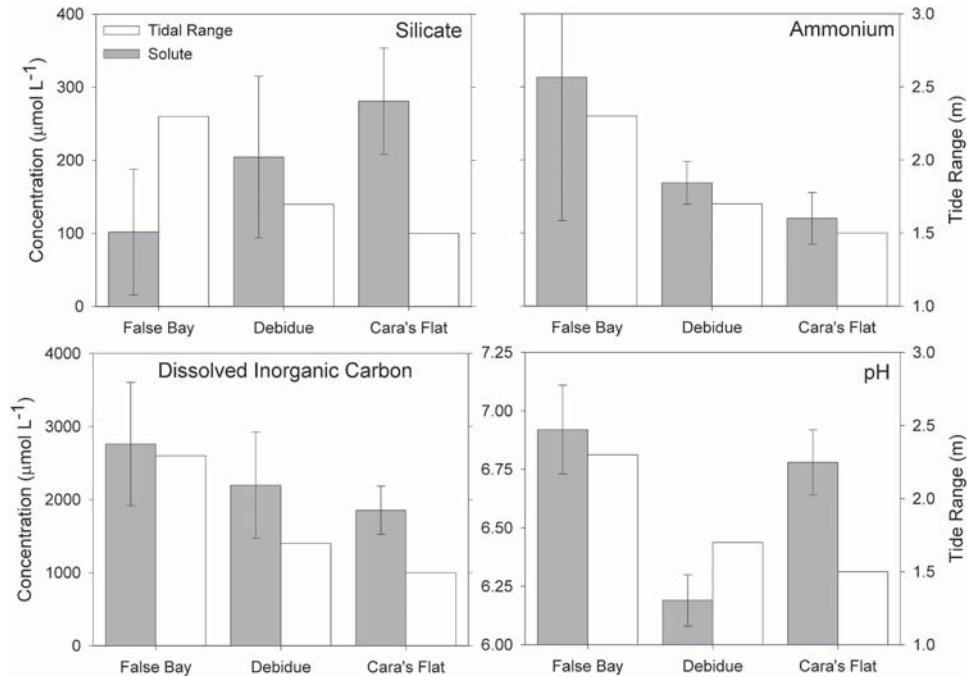


Figure 4. Grand site means of porewater silicate, ammonium, DIC, and pH concentrations versus tidal range for each experimental site. Left y-axis is concentration (grey) and right y-axis is tidal range (white), and error bars are standard deviations.

correlated, so differential organism effects on porewater chemistry are suggestive. Overall, the results show taxon-specific influence on solutes that are subject to different formation and uptake processes in permeable sediments.

ii. *Cara's Flat, VA*. Fluorescein concentrations were significantly lower in deep sections of the gels relative to surface gel sections (ANOVA $p = 0.0002$, $F_{1,17} = 23.56$), indicating increased rates of porewater advection ~ 10 cm deep in the flat relative to near the sediment surface. Accordingly, separate regression analyses were run for organism and sediment effects on surface and deep gel fluorescein concentrations. Diffusional properties of the gels (Browne and Zimmer, 2001) would prevent significant axial transfer of fluorescein between the surface and deep sections of the gels (~ 8 cm) over the two-day deployment. The stepwise regression for near-surface fluorescein concentrations best fit a model with percent fine sediment and hemichordate density; however, it was not significant. A simple linear regression of hemichordate density on near-surface fluorescein concentrations also was not significant ($p = 0.2528$, $F_{1,8} = 1.55$, $\text{Adj. } R^2 = 0.06$). The stepwise regression for fluorescein remaining in the deep gel sections indicated a three parameter model including percent fine sediment, hemichordate and diopatra densities was the best fit to explain

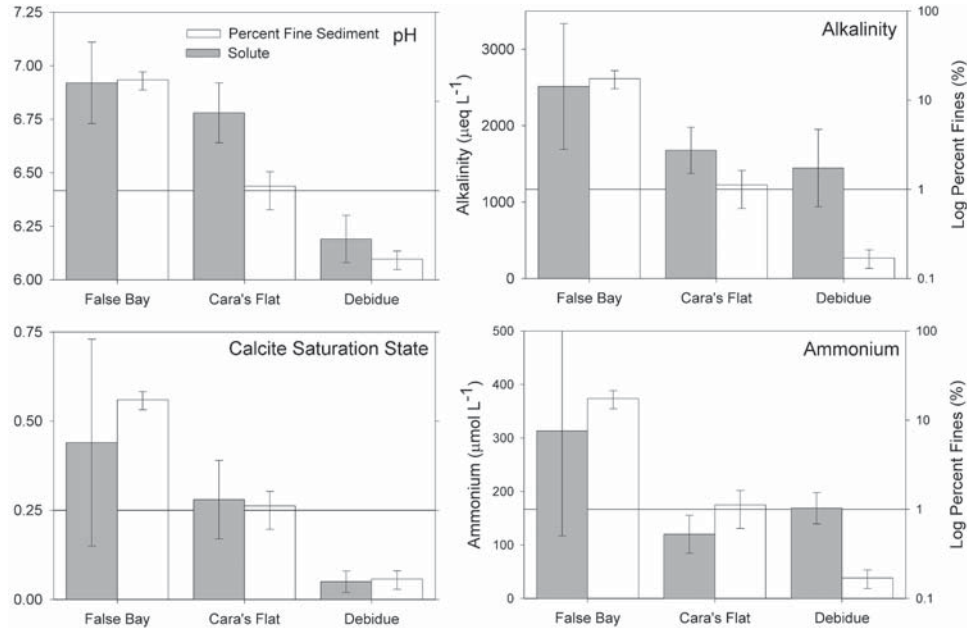


Figure 5. Grand site means of porewater pH, alkalinity, saturation state, and ammonium concentrations versus percent fine sediment for each experimental site. Solute concentrations are plotted on the right y-axis, percent fine sediment is plotted on the left y-axis and on a log scale. Percent fine sediment is plotted in white and mean solute concentration in grey.

variance in deep gel fluorescein concentrations. When running the three parameter model for the deep section of the gels, only hemichordate density was significant in explaining variance in the fluorescein remaining in the gels. A simple linear regression was run with hemichordate density on deep fluorescein gel concentrations and was significant ($p = 0.0099$, $F_{1,8} = 12.31$, $\text{Adj. } R^2 = 0.59$) (Fig. 6). These results indicate that hemichordates had a significant effect on increasing porewater advection at depth, no effect on near sediment surface advection, and these effects were independent of sediment characteristics. No significant effects of diopatra density on fluorescein gel concentrations in deep or near-surface gel sections were found. It should also be noted that maximum densities of hemichordate and diopatra in Cara's Flat (~ 15 and 16 per m^2 , respectively) were much lower than arenicolid and thalassinid (~ 75 and 60 per m^2 , respectively) densities in False Bay.

The stepwise regressions for porewater solutes identified a two-parameter model with hemichordate and percent fine sediment as the best fit model to explain variance in solute concentrations. Solute concentrations of nitrate ($p = 0.0462$, $F_{2,7} = 6.05$, $\text{Adj. } R^2 = 0.59$), phosphate ($p = 0.0010$, $F_{1,7} = 35.86$, $\text{Adj. } R^2 = 0.83$), and silicate ($p = 0.0072$, $F_{1,7} = 15.97$, $\text{Adj. } R^2 = 0.68$) were significantly affected by hemichordate density and percent fine sediment. Percent fine sediment was not significant in the two-parameter

Table 3. Results of best-fit regression analyses of fluorescein concentrations remaining in gels, for the three sites.

Site/Model	Parameter	p-value	Adj. R ²	p-value model
False Bay “Best Fit”	Arenicolid Density (▼ 2–70 m ⁻²)	0.0025	0.78	0.0043
	Grain Size (▲ 117–153 μm)	0.0084		
False Bay Thalassinid	Thalassinid Density	0.0819	0.28	0.0819
Cara’s Flat Surface	Hemichordate Density	0.2528	0.06	0.2528
Cara’s Flat Deep	Hemichordate Density (▼ 0–15 m ⁻²)	0.0099	0.59	0.0099
Debidue Surface	Onuphis Density (▼ 8–79 m ⁻²)	0.0096	0.71	0.0001
Debidue Deep	Porosity (▲ 0.42–0.45)	0.0051		
	Porosity (▲ 0.42–0.45)	0.0005	0.59	0.0005

Arrows indicate significant decrease (▼) or increase (▲) in gel fluorescein concentration ($\alpha = 0.05$) indicating an increase or decrease in porewater advection, respectively. Numbers in parentheses below parameters indicate range of measured values for the parameter. The first p-value (t-test) is the probability for the given variable, and the “p-value model” is the probability for the full model (F-test). Surface and deep at Cara’s Flat and Debidue Flat refer to different models run on the surface and deep subsections of the gels, as both sites showed significant difference between gel sections.

Table 4. Results of regression analysis of organism density on depth integrated porewater concentrations.

	False Bay		Cara’s Flat		Debidue Flat
	Arenicolid Density	Thalassinid Density	Hemichordate Density	Diopatra Density	Onuphis Density
Ammonium	▼(0.51, 0.0179)	▲(0.45, 0.0284)	n/s	n/s	n/s
Nitrate	n/a	n/a	▼(0.59, 0.0462)	n/s	n/s
DIN	n/a	n/a	n/s	n/s	n/s
Phosphate	▼(0.61, 0.0078)	▲(0.81, 0.0013)	▼(0.83, 0.0010)	n/s	n/s
Silicate	▼(0.59, 0.0095)	▲(0.62, 0.0116)	▼(0.68, 0.0072)	n/s	n/s
pH	n/s	n/s	n/s	n/s	n/s
Alkalinity	▼(0.37, 0.0475)	▲(0.87, 0.0004)	n/s	n/s	n/s
DIC	▼(0.48, 0.0222)	▲(0.91, 0.0001)	n/s	n/s	n/s
Ω Aragonite	n/s	▲(0.50, 0.0290)	n/s	n/s	n/s
Ω Calcite	n/s	▲(0.50, 0.0290)	n/s	n/s	n/s

Direction of triangles indicate the direction of a significant effect of organism density on specific solute ($\alpha = 0.05$), n/s = not significant, and n/a = measurements of solute not available. Numbers in the parentheses are the adjusted R² for the model and p-value for the variable. Some of the models included sediment parameters in addition to the organism densities based on model selection criteria, see text for full explanation.

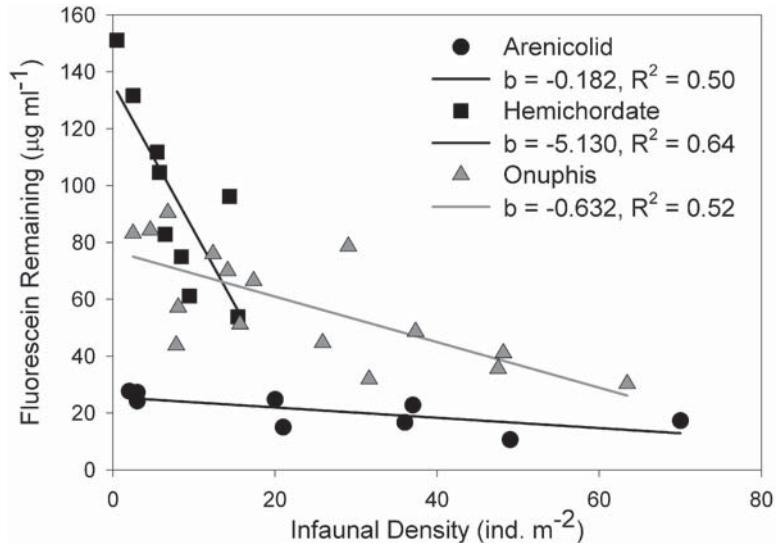


Figure 6. Fluorescein remaining in gels versus density of the three flow enhancers in this experiment (arenicolid, hemichordate, and onuphis). The fluorescein concentrations in the arenicolid versus fluorescein plot (circles) are average of deep and surface gel sections. The fluorescein concentrations in the hemichordate regression (squares) are for the deep gels only, and surface gels for the onuphis (grey triangles). Note the slope and fit from each significant regression analyses. The slopes are the per organism effects on fluorescein remaining in the gels for each species and site.

model explaining variance in phosphate and silicate concentrations. Therefore percent fine sediment was dropped for subsequent analyses, and a simple linear regression was run for hemichordate density effects on phosphate and silicate porewater concentrations. Higher hemichordate density was associated with significantly decreased phosphate and silicate concentrations (Fig. 7). In the significant two-parameter model explaining variability in nitrate, nitrate concentrations decreased with increasing hemichordate density ($p = 0.0183$, $t_{1,7} = 3.45$) and increased with increasing percent fine sediment ($p = 0.0494$, $t_{1,7} = 2.58$). In the significant models for phosphate, silicate, and nitrate, there was an overly influential data point as determined by studentized residuals and Cook's distance. This data point was therefore removed.

iii. *Debidue Flat, SC*. Fluorescein concentrations were significantly greater in the near-surface sections of the gels than the deep sections by one-way ANOVA ($p = 0.0045$, $F_{1,31} = 9.43$), as was seen in Cara's Flat. Therefore, separate stepwise regressions were run for the surface and deep subsection fluorescein concentrations of the gels. The stepwise regression determined that a two-parameter model with *O. jenneri* density and porosity was the best for explaining variance in the amount of fluorescein remaining the gels. A significant model was fit for both the near-surface gels ($p = 0.0001$, $F_{2,15} = 19.00$, adj $R^2 = 0.71$) and the deep gels ($p = 0.0090$, $F_{2,15} = 6.92$, adj $R^2 = 0.44$), though only

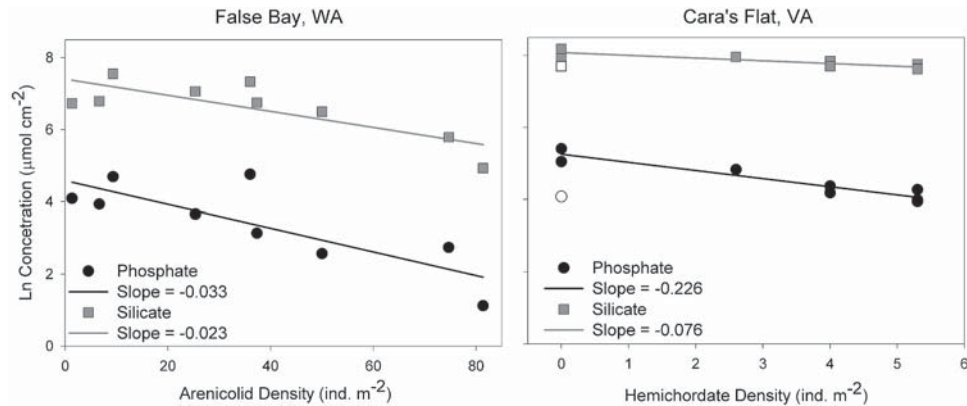


Figure 7. Depth integrated concentration of porewater phosphate (black circles) and silicate (grey squares) plotted against arenicolid and hemichordate density (left and right panels, respectively). The concentrations are natural log transformed, and note the order of magnitude difference in the x-axes scales. The slopes for each significant regression are noted in the figure legend. The slopes are the per individual effect of each species on solute concentrations. The unfilled symbols in the Cara's Flat panel are the statistical outliers removed per methods.

porosity was statistically significant in the deep gel section model. In the near-surface fluorescein gels model, both onuphis density and porosity were highly significant, but it is important to note that the variance in porosity was quite small, with a range of 0.42 to 0.45. This would indicate that although the porosity is statistically significant, it probably is not environmentally relevant. The porosity term was left in the model due to the statistical findings. More interesting was that the onuphis density had a significant effect on fluorescein remaining in the near-surface gels (or porewater transport).

The porewater chemistry study at Debidue Flat was restricted to the sandier upper section of the flat (dominated by *O. jenneri*) due to the significant effect of *O. jenneri* on porewater advection determined by the fluorescein gels. The porewater chemistry study was conducted the season after the fluorescein study, and therefore, the same sites could not be maintained throughout the winter. No sediment granulometry samples were taken during the porewater study because the samples from the previous season indicated very little variability in any of the values (Table 1). A simple linear regression of *O. jenneri* density on porewater solute concentrations found no significant effects of density on any of the solutes measured (ammonium, nitrate, phosphate, silicate, DIC, pH, alkalinity, or saturation state).

4. Discussion

The results from this multi-species, multi-site investigation indicate that different infaunal species have specific identifiable impacts on permeable sediment processes and that differences in site characteristics (such as tidal range) are important covariates (Fig. 3). Thus, broad scale across-site variability in porewater advection may be driven by

site-specific characteristics, but porewater advection across smaller spatial scales is significantly modified by the type and abundance of bioturbating infauna. The total number of species examined in this study was small, but nevertheless provides a comparative context. In spite of potential variability in sediment properties over small spatial scales, statistically significant effects of infauna on porewater advection were measured at all three sites (Table 3), and porewater chemistry at two sites (Table 4). In most cases the within-site variability in sediment parameters was very small or did not co-vary with organism density or porewater advection and solute concentrations (Table 1, 3, 4). These results suggest that not all infauna affect porewater processes the same way, though similarities among some infauna exist. Therefore, it may be possible to begin defining functional groups that link infaunal, porewater advection, and solute dynamics in permeable sediments.

We utilized natural variability of infaunal surface features within undisturbed natural habitats; this provides a powerful approach in that organisms were not handled, nor were sediments modified by sieving, therefore retaining the natural depth gradients of organic matter. Two possible shortcomings of this approach are: uncertainty in the relationship between surface features and actual abundance, and the possibility of additional unidentified covariates confounding abundance and porewater advection. We validated that given features were associated with a given species, but did not develop statistical relationships between surface features and abundance. The deep-dwelling nature and rapid burrowing of these species prevents this kind of estimate without significant disruption to these habitats by extensive digging. Rather we relied on our significant experience of working with these species and understanding their activity rates and residence times in specific habitats. Secondly, we assume that infaunal density over the small within-site spatial scales is not reflective of changes in sediment properties, and additionally that these potentially confounding sediment properties are not influencing porewater advection. It is well documented that distributions of infauna over larger spatial scales are controlled by variables such as depth, exposure time, organic content, and grain properties. However, within-site variability of exposure times and sediment properties was negligible.

a. Functional groups and porewater processes

Functional groups have been used to find similarities among benthic infauna (e.g. Fauchald and Jumars, 1979; Hutchings, 1998; Pearson, 2001; Mermillod-Blondin and Rosenberg, 2006) that help explain interactions (Woodin, 1976) as well as effects on sediment processes. The utility in applying the functional group approach is to allow one to group common characteristics of infauna, thereby simplifying the complexity found in benthic sediment systems. However, the applicability of any one functional group scheme to all questions and scales of interest in the benthos is likely limited. With that caveat, we do believe there is a utility in taking a functional group approach, especially for research examining the links between the structure of benthic infaunal communities and their effects on sediment reaction and transport processes. A functional group approach must be applied within a broader context of environmental variables, and other metrics of community

structure such as density, biomass, and individual size. Without inclusion of these potentially confounding variables, any broader applicability of functional group schemes and comparison across studies will be limited.

Several studies have found links between functional groups and biogeochemical processes in muddy sediments (Widdicombe and Austen, 1998; Biles *et al.*, 2002; Gerino *et al.*, 2003; Michaud *et al.*, 2006; Caliman *et al.*, 2007; Norling *et al.*, 2007). Permeable sediments, however, are subject to porewater advection which significantly changes the reaction-transport dynamics within these habitats (Huettel *et al.*, 1996). Therefore, we propose a functional group scheme for permeable sediments that groups infauna by positive, negative, or no effects on porewater advection. These effects are further decomposed to what specific mechanisms the given infauna has on porewater advection (Fig. 1): (1) changes to sediment permeability, (2) changes to surface topography, and (3) direct pumping of overlying water into the sediment. The infauna in the current study may be grouped as porewater advection enhancers (arenicolid, hemichordate, and onuphis), porewater advection inhibitor (thalassinid), and non-affecter (diopatra), based on their effects on gel-diffusers and porewater peepers. Interestingly, similar effects on porewater advection may be caused by very different mechanisms. For example, among the advection enhancers, the arenicolid, and to a lesser degree the hemichordate, pump water into the sediment to ingest sediment; whereas onuphis changes sediment topography from the extended burrow cap and all three likely alter the movement of water through the tidal flat by the creation of microscale structures such as burrows and feeding pockets (Fig. 1). The effects of the different infauna are discussed in more detail below.

We suggest that most infaunal organisms will alter sediment permeability through the creation of void spaces and more or less permeable structures/interfaces as in burrow linings. From our measurements, we cannot discern how the different infaunal structures actually interact with porewater advection; this remains a formidable challenge to future work in this field. However, our data does illustrate that various infaunal life history strategies affect advection differently, and these effects were not related to bulk sediment properties (Tables 3, 4). It is important to note that larger across-site variability in porewater advection and chemistry is driven by site specific characteristics (Figs. 3, 4, 5), and discussed further below.

We use the gel diffusers to primarily identify significant variability in porewater advection, and present chemistry data to highlight that these differences in advection appear to affect concentrations of several porewater constituents. However, both phosphate and silicate concentrations in the porewater are sensitive to flushing with overlying water, and therefore provide further evidence of porewater advection within sites where reactive material did not vary across plots. Active ventilation of burrows can maintain silicate porewater concentrations below equilibrium values (Marinelli, 1992, 1994), and within permeable sediments silicate is typically at a higher degree of undersaturation relative to diffusion dominated sediments (Ehrenhauss and Huettel, 2004). Phosphate is also sensitive to irrigation, due to oxygen-enhanced adsorption and should respond similarly to infaunal

modification of porewater advection. The advective flow enhancers (with the exception of *onuphis*) lowered porewater silicate concentrations, while the flow inhibitor thalassinid increased porewater silicate (Table 4, Fig. 7). The difference between the *onuphis* and other flow enhancers is probably in part due to differences among sites in reactive organic material and fines content (Table 1), and differences between the head-down and surface deposit-feeding modes. Similar to silicate, the advection-enhancing organisms decreased porewater phosphate (except *onuphis*) and the advection inhibitor (thalassinid) increased porewater phosphate (Table 4, Fig. 7). The mechanisms by which the different infauna affect porewater advection and chemistry are discussed below in more detail and infauna are grouped by general differences in behavior.

i. Arenicolid and Hemichordate. Feeding by subducting surface material in a feeding funnel requires significant pumping of overlying water into the sediment (Timmerman *et al.*, 2002, 2006; Meysman *et al.*, 2005, 2006), resulting in nonlocal transport through the sediment column. Subduction and mixing of sediment decreases sediment compaction and increases the permeability of sediment on localized spatial scales in the burrow/feeding funnel/fecal mound (Jones and Jago, 1993; Craig *et al.*, 1998; Wild *et al.*, 2005), though results from these studies are suggestive and more work is needed on the small-scale dynamics. Localized increases in permeability would, however, result in localized increases in porewater advection under the same pressure gradient compared to other nonmixed sediments. Additionally, dense populations of arenicolids have been shown to strip organic-rich fine material (Wild *et al.*, 2005; Volkenborn and Reise, 2007) and create an “open bed” for advective exchange. The maximum population sediment ingestion rates for the organisms in this study were roughly 0.35 L sediment per m² per day for the arenicolids in False Bay (estimated from Linton and Taghon, 2000), and almost 2.0 L of sediment per m² per day for the hemichordates in Cara’s Flat (estimated from Duncan, 1987; Thayer, 1983). These calculations suggest that irrigation and mixing of sediment due to feeding are important mechanisms by which the head-down deposit feeders fluidize the sediment column bed and alter associated transport/reaction processes (Tables 3 and 4, Figs. 6 and 7). Furthermore, an attribute such as sediment ingestion rate may be extremely useful to simplify effects of mixed infaunal communities on permeable sediment processes.

ii. Onuphis & Diopatra. The surface deposit feeder *O. jenniferi* enhanced porewater advection but *D. cuprea* did not. *O. jenniferi* and *D. cuprea* do cause nonlocal particle transport by ingesting sediment at the sediment surface and defecating at depth, but given the lack of fluidization and sedentary nature, their overall particle mixing and irrigation effects are small (Swift, 1993). Additionally both *D. cuprea* and *O. jenniferi* tube caps extend several centimeters above the sediment surface. Projecting tube caps into the overlying water may interact with strong tidal flows, creating pressure gradients that drive porewater advection within the upper sediment layers (Huettel and Gust, 1992). *O. jenniferi* burrows are thin and made of mucus-bound sand grains which are more permeable than the

leathery tubes of diopatra based on porosity of burrow walls (Aller, 1983; Hannides *et al.*, 2005). Tube cap orientation also varies between the two species; *O. jeneri* tube caps are oriented vertically whereas *D. cuprea* tube caps are usually curved over and down towards the sediment surface (Fig. 1).

The only measurable effect of the surface deposit feeders was the increased porewater advection due to *O. jeneri* in Debidue Flat (Table 3). Lack of a concomitant porewater solute effect may be due to the lower concentration of organic matter at Debidue Flat (Table 1). The onuphis-enhanced porewater advection may be due to active irrigation of their burrows, their higher density (than diopatra), and more permeable burrow walls. It is also possible that passive irrigation (Ray and Aller, 1985; Libelo *et al.*, 1994; Munksby *et al.*, 2002) of these burrows is responsible for increased porewater advection. While winnowing of fines from the surface sediments by selective particle ingestion during feeding would be a possible mechanism for increased sediment permeability and porewater advection, the small variability in sediment parameters across the *O. jeneri* density gradient indicates this is likely not a dominant mechanism (Table 1, 3).

iii. Thalassinids. Given that the burrows retrieved in False Bay were clay lined, it is likely that the majority of thalassinids at the site were *U. pugettensis*. Our findings indicate that thalassinids are advection inhibitors due to their effects of increasing porewater silicate and phosphate (Table 4), though no significant effects on the gels were found (Table 3). Both silicate and phosphate concentrations in porewater are sensitive to mixing with overlying water, and therefore serve as proxies for irrigation/advection. The presence of relatively impermeable burrows (likely *U. pugettensis*) within the sediment column should act to decrease porewater advection by relatively impermeable burrows that impede flow while limiting exchange between porewater and overlying water (Waldbusser and Marinelli, 2006). Therefore, thalassinid species that create impermeable tubes, and other permeability lowering species such as suspension feeders (through biodeposition) represent a third group or mechanism by which infauna may affect permeable sediment processes; through decreasing sediment permeability. Little evidence of porewater flow inhibitors in permeable sediments has been found experimentally or otherwise (e.g., D'Andrea *et al.*, 2002), and this relatively unexplored theme is potentially an important aspect of biogenic sediment modification.

b. Within-site effects of granulometry

Bulk sediment measurements of parameters such as porosity, percent fine sediment, or grain size provide valuable information about the physical environment at a given site and the context in which animal-sediment interactions manifest. The fine-scale modification of sediment properties by infauna, such as sediment fluidization in arenicolid feeding funnels (e.g. Jones and Jago, 1993, Craig *et al.*, 1998), is often not captured in typical bulk grain analyses. Sediment structures created by infauna are usually destroyed and incorporated in the typical coring and sieving measurements for granulometry. For example, a burrow

represents a highly porous section of the sediment column on mm to cm scales, but once that burrow is cored and sieved it no longer is accurately accounted for in the overall sediment properties. Therefore, bulk sediment properties, as usually measured, do capture important general properties, but may often miss the fine-scale structural effects by which infauna modify sediment structure and porewater transport.

Bulk sediment properties within some sites co-vary with infaunal density, though the variability in bulk grain parameters was small (Table 1) and probably not sufficient to drive changes in transport and chemistry. Within False Bay, the arenicolid effect of increasing porewater advection was confounded by a statistically significant negative effect of increasing grain size on porewater advection (Table 3). The range of values in False Bay grain size was 30 μm . Additionally, the statistical grain size effect was negative with respect to advection, opposite of what would be expected; i.e., advection increasing with increased grain size. Within Cara's Flat, the decrease in porewater nitrate with increasing hemichordate density was statistically confounded by a barely significant effect of nitrate increase with increasing fines ($p = 0.0494$, $t_{1,7} = 2.58$). Percent fine sediment content in the flat ranged from 0.64 to 1.49%. The positive relationship between fines and nitrate may be related to increased reactive substrate (Fig. 2). However, the exact mechanisms by which hemichordates and fines content are affecting nitrate in the porewater cannot be determined from the current study. Lastly, increases in porosity at Debidue Flat were found to decrease porewater advection (Table 3) but the range of porosity measured was only 0.42 to 0.45 and again likely not relevant. Although there were some statistical effects of granulometry, the relative changes within sites in these values were very small and probably not environmentally relevant.

c. Across-site effects of granulometry

The functional group effects suggested by this data are embedded within general across-site differences, and therefore, the environmental effects cannot be fully disengaged from the differential effects of functional groups. In fact, previous studies have noted that differences in sediment properties can vastly alter the effects of similar organisms on sediment properties. For example, Jones and Jago (1993) noted corophium amphipods increased permeability in sandy sediments, while Meadows and Tait (1989) found that corophium amphipods decreased permeability in muddy sediments. Mermillod-Blondin and Rosenberg (2006) also highlight the differential species effects based on sediment type. The primary difference among sites in this study is the two order of magnitude change in fines content from False Bay to Cara's Flat to Debidue Flat (Table 1). The lowest percent fine sediment at Debidue Flat corresponds with the smallest organism effects on porewater solute concentrations (Tables 3 and 4). However, the order of magnitude decrease in fines content at Cara's Flat does not translate into significantly lower effects of hemichordates relative to arenicolids on porewater chemistry (Fig. 6). Unfortunately only one species was located at two different sites making comparative statistical analyses across sites impossible.

It is clear that different functional groups of organisms follow large-scale distributional patterns related to sediment/physical properties (e.g. Pearson and Rosenberg, 1978). This relationship may be used to focus efforts on habitats where certain functional groups will be found. For example, within the study area of Debidue Flat, no head-down deposit feeders were found, likely due to the lower of fines content and organic matter (Table 1). Permeability was also highest at Debidue Flat, and measured maximum hydraulic conductivities approached the limits of efficient bio-pumping, 10^{-4} m s^{-1} (Meysman *et al.*, 2005). However, some measured hydraulic conductivities just exceeded this limit in Cara's Flat where the hemichordate was found, with values as high as $1.8 \times 10^{-4} \text{ m s}^{-1}$. It should be noted that the values determined by Meysman *et al.* (2005) were for arenicola. The minor differences in burrow architecture and behavior between the arenicola and hemichordate require more empirical and modeling work to determine the broader applicability of these values across different species. This comparison does highlight that the effects of head-down deposit feeders on permeable sediment processes are likely limited to a range of permeable sediment habitats having higher fines and lower hydraulic conductivity. Qualitative in nature, this result suggests that infaunal effects in physically dynamic environments are context dependent, and limits the possible organism-habitat combinations that need to be quantified.

5. Conclusions

Infauna affect permeable sediments and specifically porewater advection by modifying sediment permeability, creating topography that interacts with overlying water flows, and bioirrigation. Traditional functional groups related to feeding mode or guild may not be adequate to fully capture relevant mechanisms by which infauna modify permeable sediment processes. Grouping organisms based on their effects on permeable sediment processes, in particular porewater advection, simplifies complex infaunal behavior and provides a framework for predictive models. An alternative functional classification scheme for infauna in permeable sediments would therefore be a two tier system of classifying first porewater enhancers and inhibitors and then identifying mechanisms. This classification scheme is presented to help refine functional groups in permeable sediments, identify potentially important groups of infauna, and provide a framework for future modeling work.

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