ECOLOGY OF *MANAYUNKIA SPECIOSA*

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ABSTRACT

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Manayunkia speciosa Leidy is a freshwater polychaete that is widely distributed in coastal areas of the United States and Canada. Relatively little is known about the ecology of this species. However, the discovery that *M. speciosa* plays an obligate role in the life cycle of two parasites (*Ceratomyxa shasta* Noble and *Parvicapsula minibicornis* Kent) that can cause substantial mortalities in juvenile Pacific salmon (*Oncorhynchus* spp.) has sparked an interest in the ecology of this polychaete. Salmon of the Klamath River basin, California-Oregon, have experienced particularly high mortalities due to the parasites and management agencies in the region are actively seeking strategies to reduce loss of salmon due to the parasites. One strategy that has been developed is the use of flow manipulations to dislodge the polychaete from areas in which it is found in the Klamath River. The purpose of this study was: 1) to characterize invertebrate assemblages associated with *M. speciosa* to look for drivers of polychaete distribution, 2) to experimentally determine flow forces (shear stress) required to dislodge polychaetes from substrates on which they are found in the Klamath River, and 3) to compare experimentally determined shear stresses with those found in typical macrohabitats containing *M. speciosa*. Results from the invertebrate study showed that *M. speciosa* occurs on stable substrates in areas of high invertebrate diversity, including invertebrates that are marine relicts. Polychaete tenacity was dependent on both flow velocity and substrate type, with polychaetes most likely to be dislodged from depositional sediments, and dislodged worms

suffered few mortalities. River measurements in macrohabitats exceeded shear stresses needed to dislodge worms from substrates in some areas. Taken together, it is unlikely that *M. speciosa* populations will face substantial mortalities as a direct result of flow manipulations. However, definitive statements cannot be made without further study.

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CHAPTER 1

BACKGROUND AND SIGNIFICANCE OF *MANAYUNKIA SPECIOSA* IN THE KLAMATH RIVER SYSTEM, OREGON AND CALIFORNIA

The Klamath River once the supported the third largest run of Pacific salmon in the continental United States, provided for robust commercial and recreational fisheries, and provided for food and cultural needs of native tribes. Today, however, runs are in serious decline due to land use changes and competition for limited water resources (NMFS 2007). It is therefore important for management agencies to address the multiple causes of declining salmon runs, including such issues as reduced flows, alterations of habitat, and disease agents. *Manayunkia speciosa* Leidy plays an important role in the health of salmon stocks from the Pacific Northwest, particularly in the Klamath River Basin. While historically overlooked in aquatic samples due to its small size and irregular distribution (Holmquist 1973, Light 1969, Mackie and Qadri 1971, Pettibone 1953), it is now known that this polychaete plays an obligate role in the life cycle of two myxozoan pathogens of salmon, *Ceratomyxa shasta* and *Parvicapsula minibicornis* (Bartholomew et al. 1997, 2006). In the Klamath River, located in southern Oregon and northern California, these parasites have a significant impact on outmigrant survivorship of salmon smolts. In 2004, for example, an estimated 45% of juvenile salmon were infected with *C. shasta*, while estimates of greater than 90% of juvenile salmon were infected with *P. minibicornis* (Nichols and Foott 2006). Polychaete densities have been found to be greatest below Iron Gate Dam, and in particular in the section of the river between the tributaries of the Scott and Shasta Rivers. Presumably, due to the high abundance of worms, this section of the Klamath has also been found to be a major area of infection for juvenile salmon (Bartholomew et al. 2007, Hallet and Bartholomew 2006). As a result, it has been suggested by management agencies that populations of *M. speciosa* be targeted for control, with manipulations of river flow being the primary method.

Manayunkia speciosa (Sabellidae) is a freshwater polychaete with a wide-ranging distribution throughout the United States and Canada (Brehm 1978, Carlton 1979, Croskery 1978, Hiltunen 1965, Holmquist 1973, Mackie and Qadri 1971, Rolan 1974, Pettibone 1953, Spencer 1976; Fig. 1.1). This worm reproduces sexually, with embryos brooding within the maternal tube, for a period of 6 to 8 weeks. Once juvenile worms reach a total length of 1 mm, they leave the maternal tube and are capable of independent survival. In the Klamath River, mature *M. speciosa* individuals dominate the populations in spring, with immature individuals being more prevalent by mid-summer (Willson et al. 2010), which may in part be an adaptation to dynamic river flows. *M. speciosa* is found in both lakes and streams in slower moving waters of typically less than 0.45 m/s flow (Mackie and Qadri 1971, Stocking and Bartholomew 2007). These worms tend to be associated with fine sediments covered with fine benthic organic matter (FBOM), which is necessary for the construction of a tube-shaped living structure (Holmquist 1973, Leidy 1883). Populations of *M. speciosa* are typically distributed in a patchy manner (Holmquist 1973, Stocking and Bartholomew 2007), with highest recorded densities being about 45,000 individuals per m^2 (Hiltunen 1965), though densities are usually much lower. Although polychaetes are known to be abundant in certain sections of the Klamath River, much remains unknown about the specific drivers of polychaete presence and abundance within the river. Ecological requirements of other more commonly studied benthic invertebrates are well known, and information on the composition and structure of invertebrate assemblages which co-occur with *M. speciosa* may help to clarify habitat requirements of *M. speciosa*. However, large-scale studies of the invertebrate communities in the Klamath River are lacking.

The Klamath River is a 423 km river originating in southern Oregon, and flowing through northern California, eventually emptying into the Pacific Ocean (Fig. 1.2). The river contains seven dams, including power generation facilities that affect flows. Additionally, competing interests including municipal power, agriculture, and water quality also influence how flow regimes are managed (KHSA 2010, NMFS 2007). Due to high demands for the water from the Klamath River and its tributaries, current flows are much reduced from historic levels, and are often managed with little regard to approximation of natural, historic river flux (KBRA 2010). Studies have shown that managed flows can have significant impacts on the benthos of a river system and its inhabitants, and can alter natural patterns in flow, mobilization of substrates, stream channel complexity, and invertebrate drift (e.g., Freeman et al. 2001, Magilligan and Nislow 2005, Palmer et al. 1992, Troelstrup and Hergenrader 1990, Ziser 1985). Periods of high flows lead to sediment transport including scouring of the fine benthic sediments and as well as removal or relocation of macrophytes and larger substrates (e.g., Jakob et al. 2003, Patten et al. 2001, Poff et al. 1997, Power et al. 1996). Increased flows due to flooding or increased reservoir discharge are known to reorganize substrates through changing scour and fill patterns (e.g., Bond and Downes 2003, Lake 2000, Matthaei et al. 1999), and have been shown to increase drift of benthic invertebrates (e.g., Andrews and Minshall 1979, Imbert and Perry 2000, Matthaei et al. 1999). Further, increased floods have been shown to markedly decrease benthic invertebrate populations in some systems (Jowett 2003). It is likely that flow regimes can play a crucial role in *M. speciosa* survival and distribution by removal of sediment necessary for tube construction, removal of macrophyte refugia, and reorganization of the stream benthos through scour and redeposition of mobile substrates which may stress or dislodge the polychaetes or cause variation in habitat.

Moderated flows have reduced maximum shear throughout the river and have likely caused an increase in polychaete populations due to the increase in habitat that the worms find favorable. It is therefore hypothesized that as reduced flows have led to the expansion of polychaete habitat, increasing flows and subsequent shear within worm habitat will decrease polychaete populations in the river by disrupting habitats that are necessary for worm survival. Because the myxozoan parasites responsible for salmon mortalities depend on *Manayunkia* for completion of their life cycle, reducing polychaete populations will also reduce salmonid pathogens in the river, thereby reducing mortalities of salmon.

In order to determine feasibility of using flows to decrease *Manayunkia* populations in the Klamath River, it is necessary to determine what shear forces are required to dislodge the worms from their habitat, as well as resultant mortalities. Laboratory flume experiments were set up to measure the shear forces required to scour *M. speciosa* from multiple substrates, and subsequent mortalities were quantified. Additionally, micro-scale flows in which the polychaete is found were characterized through use of field measurements of polychaete habitats. Flow characteristics of the river at locations of high worm densities were also characterized in the field under differing flow regimes to quantify flow velocity and shear extremes experienced by typical *Manayunkia* populations, and to compare “real world” shear forces experienced by the worms to critical shear values determined in the lab.

In addition, in order to clarify environmental drivers that work in conjunction with hydrologic constraints to limit polychaete populations, taxonomy and functional feeding groups of invertebrate assemblages throughout the lower Klamath River were described. This provides insight into ecosystem parameters such as food availability, which likely work in conjunction with hydrology and geology to determine suitable polychaete habitat.

The major objective of this research was to better understand the environmental drivers of *M. speciosa* distribution. The specific objectives of this study were divided into the following chapters: 1) Invertebrate assemblages in the lower Klamath River, with respect to *M. speciosa*, 2) Impact of flows and substrate type on dislodgement of *M*. *speciosa*, and 3) Prediction of near-bed flows by macrohabitat types.

APPENDIX I

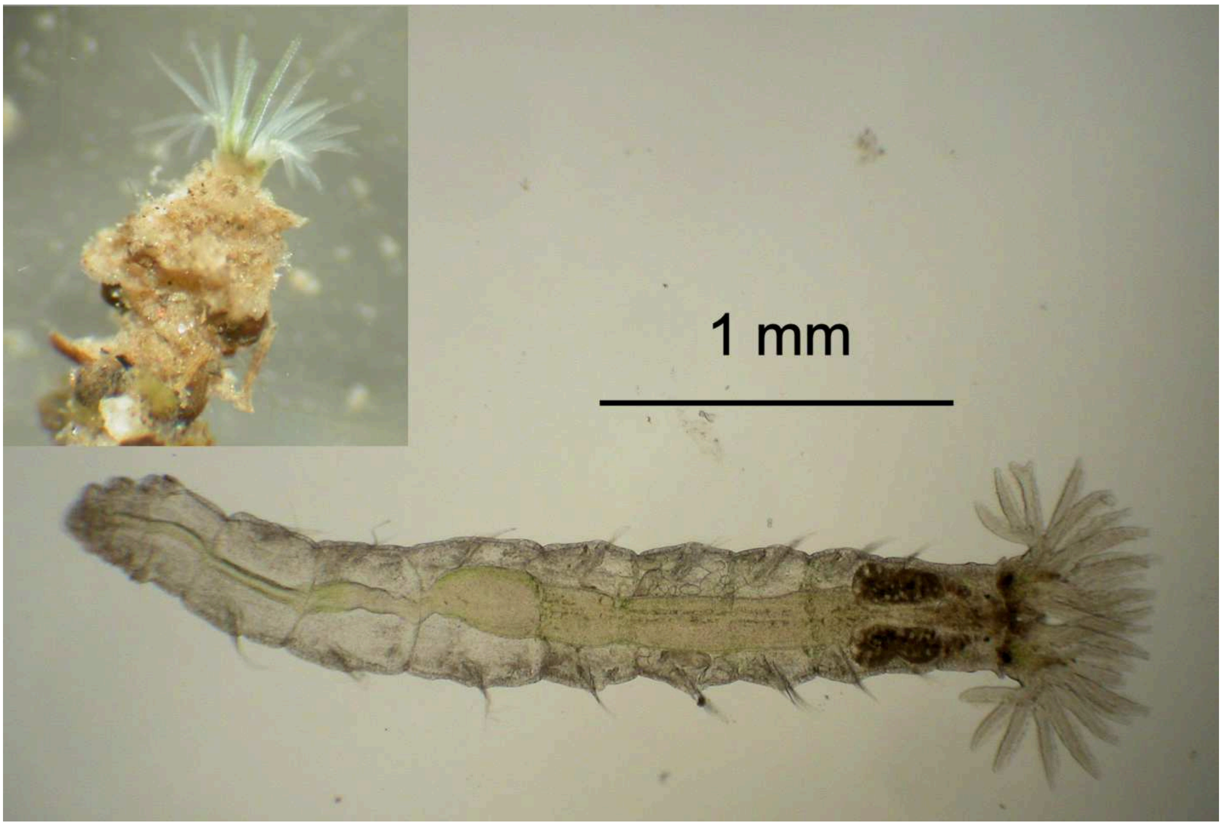

Figure 1.1. *Manayunkia speciosa*. This widely distributed freshwater polychaete acts as an intermediate host for two parasites that have significant effects on mortality of juvenile salmon in the Klamath River Basin. Photo provided by Sarah Willson (2007). For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this dissertation.

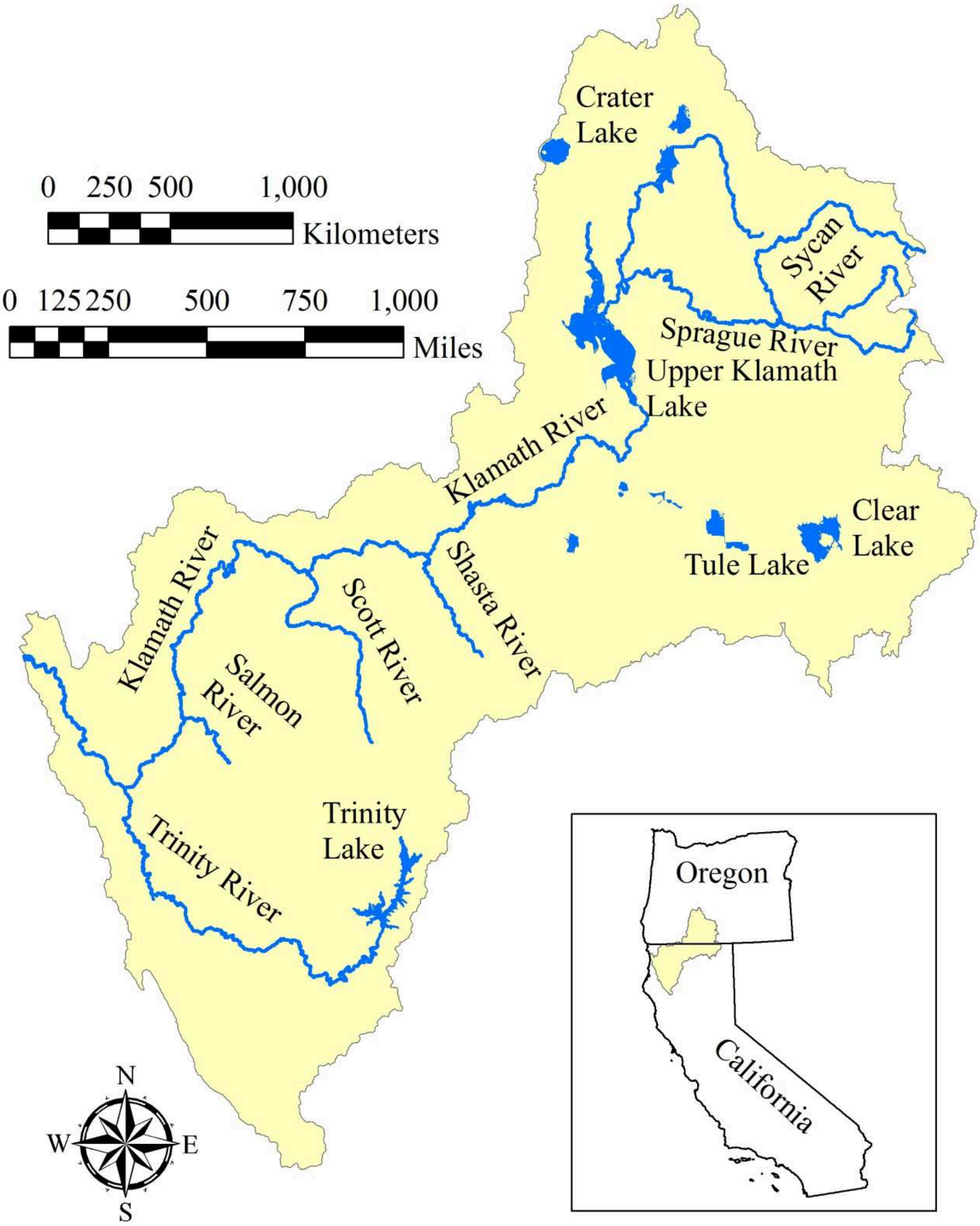

Figure 1.2. The Klamath River Basin. The Klamath River hosts populations of *M. speciosa*, an intermediate host of two myxozoan pathogens that are responsible for substantial mortalities of juvenile salmon in the river.

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CHAPTER 2

INVERTEBRATE ASSEMBLAGES IN THE LOWER KLAMATH RIVER, WITH REFERENCE TO *MANAYUNKIA SPECIOSA*

INTRODUCTION

Manayunkia speciosa Leidy (Canalipalpata: Sabellidae) is a freshwater polychaete distributed within the Great Lakes and along coastal areas of North America (Pettibone 1953, Hiltunen 1965, Mackie and Qadri 1971, Holmquist 1973, Rolan 1974, Spencer 1976, Brehm 1978, Croskery 1978, Carlton 1979). This small filtering collector is usually an inconspicuous member of the total benthic invertebrate community, and little is known about its ecology and life history. This polychaete has been identified as the intermediate host for two myxozoan parasites (*Ceratomyxa shasta* Noble and *Parvicapsula minibicornis* Kent) of salmonid fishes in the Pacific Northwest (Bartholomew et al. 1997, 2006). These parasites have caused substantial mortality of juvenile salmonids, particularly in the mainstem of the lower Klamath River basin below Iron Gate Dam (Foott et al. 1999, 2004).

A desire to reduce disease incidence in Klamath River salmon has sparked interest in the distribution and basic life history information of *M. speciosa*. This information may help management agencies target populations of this polychaete and offer a means to disrupt the disease cycle of the parasite and reduce fish mortality in the Klamath River and elsewhere. Previous studies from other locations have reported that *M. speciosa* is a habitat generalist, which tolerates a wide range of environmental conditions in water chemistry (e.g., pH, dissolved oxygen), temperature, and water flow (Hiltunen 1965, Holmquist 1973, Poe and Stefan 1974, Rolan 1974). In the Klamath River, polychaetes have also been found to occupy a variety of substrate types, such as macrophyte beds, fine sediments, cobbles, and boulders (Stocking and Bartholomew 2007, Willson et al. 2010).

Although polychaetes have been examined in the Klamath River, the composition and structure of invertebrate assemblages in the Klamath River have not been previously described (Stocking and Bartholomew 2007). Because the ecology and environmental requirements of many benthic taxa are more well-known than those of polychaetes, information on other benthic taxa commonly found with polychaetes may help define habitat parameters where polychaetes occur. Information on invertebrate assemblages will also become important for assessment of non-target impacts of management strategies that may be used for salmon disease control.

With a goal of better understanding factors affecting the distribution of *M. speciosa*, our objectives were to sample and describe the assemblage of invertebrates occurring in the presence and absence of the polychaete within the lower Klamath River. Using data from two sampling years, we described invertebrate structure both taxonomically and by functional feeding group. The latter approach provided insight into the nutritional base which supports invertebrate assemblages, and can provide insights into such ecosystem parameters as the relative degree of autotrophic compared to heterotrophic production (Cummins et al. 2005). Although *M. speciosa* also occurs above Iron Gate Dam in the upper Klamath Basin, we restricted this study to the lower river as salmon are not affected by the myxozoan parasites above the dam, which is presently a barrier to anadromy.

MATERIALS AND METHODS

Study Area

The Klamath River runs approximately 425 km from its origins in southern Oregon and northeastern California to its mouth at the Pacific Ocean, in northern California and drains a 40,632 km^2 basin. The river is divided by Iron Gate Dam (river km 306) and geological changes into upper and lower basins (NMFS 2007). The upper basin is largely managed by the Klamath Reclamation Project that regulates four lakes and reservoirs through a series of seven dams that provide water for agriculture and generation of power; land in the lower basin is largely managed by the U.S. Forest Service. Four of the major tributaries of the Klamath River enter below Iron Gate dam, and all but the Salmon River are impacted by water diversion for agriculture (CRS 2005). The lower basin supports commercial, tribal, and recreational fisheries, which were historically much larger. However, salmonid populations in the river have declined substantially from historic levels due to land, water, and fish management practices (NOAA 2009). Anadromous salmonids within the lower basin include spring and fall-run Chinook salmon (*Oncorhynchus twshawytscha*), coho salmon (*O. kisutch*), steelhead (*O. mykiss*), and cutthroat trout (*O. clarkii*).

Collection

Twenty-two sites were sampled for benthic assemblages throughout the Klamath River between Iron Gate Dam to below Klamath Glen (Figure 1, Table 2.1). Sites were selected based on accessibility and water depth (i.e., wadeability), and a desire to space sites evenly throughout the study area. Sites were sampled in fall (September and October) 2005 and in late summer-fall (July through October) 2006. All sites were sampled one time in each individual year.

Invertebrates were sampled using a D-frame net (250 µm mesh) for 30 second intervals from dominant habitats at each site. Habitat types included coarse and fine sediments as well as beds of rooted vascular macrophytes and *Cladophora*. At each site, the specific habitats that were sampled were those that were most representative of that site. Plant beds, for example, were not sampled if not present at a site; only coarse sediments were sampled from shallow erosional habitats if fine sediments and plant beds were not present. Three composite samples were collected at each site by agitating the substrate or macrophytes by foot or by hand (Plafkin et al. 1989, Gerth and Herlihy 2006). In the lower, deeper stretches of the river, a Petite Ponar® was used to collect invertebrates when necessary. All invertebrates were preserved in 70% ethanol and taken to the lab to be processed and identified.

Samples were sorted under a dissection microscope with adjustable power (maximum magnification of 60×). A hybrid volume-count method was used, with the goal of identifying at least 200 invertebrates (Walsh 1997), which has been shown to be an effective way to estimate relative taxonomic richness (Vinson and Hawkins 1996, Growns et al. 1997). To facilitate handling, large samples were split into two or four subsamples using a plankton splitter prior to sorting. A random split was then chosen and invertebrates were completely removed and identified to the lowest taxonomic resolution possible. A large proportion of invertebrates, as well as insects were immature (early instars), which often prevented reliable identification past the family level. Therefore, we used family level classifications of insects or lower resolution of non-insects in data analyses. Family-level identifications have widely been accepted for use in evaluating gross impacts (e.g., Kingston and Riddle 1989, Lenat and Resh 2001, Waite et al. 2004). Mature specimens were identified to the highest possible resolution to construct a comprehensive list of the taxa present in our samples.

Data Analyses

Data obtained from composite samples from a single sampling site, for a single year, were combined for analysis purposes, which yielded 22 site samples for 2005 and 22 site samples for 2006. Oligochaeta were eliminated from calculations, as accurate counts were difficult to obtain due to the damaged and fragmented condition of specimens.

We analyzed data on a river-reach basis for several reasons. The semi-quantitative sampling over heterogeneous areas included multiple habitat types, and did not allow for the determination of polychaete-inverterbrate associations at a fine scale. The inability to identify a large percentage of invertebrates past coarse taxonomic resolution also limited the information that could be inferred due to the loss of information associated with higher resolution identifications. Finally, because polychaetes were mostly found in a restricted length of river, and we sought to elucidate general patterns in polychaete-invertebrate assemblages (river km 185–287), we used presence and absence of polychaetes in samples to define river reaches. Reach one (*n*=10; *n* represents a sampling site) extended upstream from river km 8 at Klamath Glen to river km 185 at Independence Creek. Reach two (*n*=9), where polychaetes were present, extended from river km 185 to river km 287, at the Interstate 5 rest area. Reach three (*n*=3) extended from river km 287 to river km 306 at Iron Gate Dam.

Bray-Curtis dissimilarity matrices (Bray and Curtis 1957) were constructed for invertebrate assemblages based on fourth-root transformed data to reduce weighting of the most abundant taxa and to preserve relative abundances (Clarke 1993). Rare taxa were considered to be those that occurred in fewer than two samples in either year, and these were eliminated from analyses. Nonmetric multidimensional scaling (NMDS) ordinations were performed on resultant matrices, with river reach used as a grouping variable and proxy for *Manayunkia* presence to graphically represent differences in assemblage structure. Additional visualization of assemblage structure was accomplished with diversity (taxonomic richness) curve plots with end point corrections (Hammer and Harper 2006). A difference in overall taxonomic richness between years was tested using a Wilcoxon signed-rank test. A two-way Analysis of Similarity (ANOSIM; Clarke 1993) was performed on data from both years and on all three reaches using 9,999 permutations. Subsequent one-way ANOSIMs were performed on each year with individual reach as a categorical variable using 9,999 permutations. Similarity Percentage Analyses (SIMPER; Clarke 1993) were also conducted with Bray-Curtis dissimilarity measures on fourth-root transformed data to determine contributions of individual taxa to overall dissimilarity among reaches and to overall dissimilarity between years. ANOSIMs, NMDS ordination plots, SIMPER analyses, and diversity plots were performed using PAST 2.16 software (Hammer et al. 2001). The Wilcoxon signed-rank test was performed using R 2.15.1 (R development Core Team 2012).

Invertebrate taxa were assigned to functional feeding groups (Cummins and Klug 1979) based on Thorpe and Covich (2001) and Merritt et al. (2008), and relative abundance of each feeding group was calculated for samples from each sampling site in 2005 and 2006. Functional feeding group classifications included filterers, gatherers, predators, scrapers, and shredders. Relative abundance data of filterers, scrapers, and predators were square-root or log transformed to meet assumptions of normality. Shredder abundance did not meet assumptions of normality even after transformation due to absences of this group from samples at multiple sites. Therefore, analyses were performed without shredder data. Effects of year and reach on relative abundance of each functional group were analyzed with a two-way ANOVA. Pairwise differences among reaches were evaluated with a Tukey-Kramer test. Differences between years in the number of sites in which *Manayunkia* were found was analyzed with a chi-squared test. ANOVAs and chi-squared tests were performed using NCSS (Hintze 2004).

RESULTS

Polychaetes were found at five of the 22 sites in 2005 and at nine of the 22 sites in 2006. Five individuals were found in reach one in 2006; four at Dolan Bar (river km 95) and one at Big Bar (river km 81). No polychaetes were found in reach three. Polychaete abundance was low in samples and comprised an average of 4.3% (*SD*=8.3) and 0.59% (*SD*=0.71) of the total number of invertebrates in 2005 and 2006, respectively. The greatest number of polychaetes was found at the mouth of Horse Creek where it accounted for 90% of the total polychaetes found in 2005. Removal of Horse Creek polychaetes from the dataset yielded more similar results between years, with an average relative abundance in 2005 of 0.45% (*SD*=0.47) and an average abundance in 2006 of 0.54% (*SD*=0.75). Horse Creek polychaetes were only removed from the dataset used for the previous calculation of polychaete abundance. The five most abundant taxonomic groups in samples from each of the reaches in 2005 and 2006 are shown in Table 2.2.

Taxonomic structure of invertebrate assemblages differed both between river reaches and years (two-way ANOSIM; R=0.46, P<0.001 for reaches; R=0.90, P<0.001 for years; Figure 2.2). Subsequent pairwise comparisons between reaches within years were all significant at (P≤0.05) (one-way ANOSIM; Table 2.3, Figure 2.3). The overall difference in the distribution of taxonomic richness between years was also significant (W=51, P=0.025). Differences in reach-specific invertebrate assemblages reflected primarily proportional differences in abundance rather than presence or absence of specific taxa. In 2005, Cladocera, Amphipoda, Copepoda, Leptohyphidae, and Gastropoda were the top five taxa contributing to dissimilarity between reaches, with a cumulative contribution of 22%. A greater percentage of dissimilarity was attributable to the top taxa contributing to dissimilarity in 2006 than in 2005. In 2006, differences in the top five taxa, including Gastopoda, Hydracarina, Baetidae, Leptohyphidae, and Cladocera, cumulatively contributed 37% of the dissimilarity among reaches. Comparing between years, the top five taxa responsible for dissimilarity between 2005 and 2006 were all non-insect groups, and included Copepoda, Cladocera, Ostracoda, Gastropoda, and Hydracarina, with a cumulative contribution of 32%. The average overall percentage of dissimilarity between reaches was 44.35 and 51.46 in 2005 and 2006 respectively. Overall percentage of dissimilarity between sampling years was 48.63.

A total of 145 invertebrate taxa were identified, of which 115 taxa were insects (Tables 2.4 and 2.5). The 2005 analyses included 42 taxa and the 2006 analyses included 48 taxa. Taxonomic richness increased gradually in an upstream direction, and dropped precipitously near Iron Gate Dam. Generally, lowest taxonomic richness was seen in reaches one and three, and highest taxonomic richness occurred in reach two where polychaetes were most abundant (Figure 2.4).

Composition of some functional feeding groups differed between years and river reaches, but there were no significant interaction effects between year and reach for any functional feeding group. Relative abundances of scrapers ($F_{1,\,38}$=13, P<0.001), filterers, including *M. speciosa* ($F_{1,\,38}$=24, P=0.000), and gatherers ($F_{1,\,38}$=37, P=0.000) differed between 2005 and 2006 (two-way ANOVA; Figure 2.5). Relative abundance of filterers ($F_{2,\,38}$=11, P<0.001) differed among reaches in both years, with the lowest relative abundance found in the most downstream reach (Figure 2.6). However, relative filterer abundances remained proportionately higher in the upper reaches in both years. Overall, the relative abundance of gatherers was highest in all reaches, and the relative abundance of shredders was lowest. While shredder abundance was not analyzed due to prevalent absences in reach one, we observed a pattern of greater relative abundance of shredders in upper reaches (reaches two and three). In 2005, 22% of reach one sites contained shredders, while 100% of reach two and reach three sites contained shredders. In 2006, 22% of reach one sites contained shredders, while 89% of reach two sites and 67% of reach three sites contained shredders, suggesting a greater relative abundance of shredders in both years in samples taken in higher reaches.

Differences in assemblage structure between the two sampling years were coincident with pronounced differences in flows between the two years. Flows in the Klamath River during the 2005 water year were about average for the ten year period from 2001 to 2010, with flows in water year 2006 being about twice the average for the same ten year period (Figure 2.7). Both overall taxonomic richness and the relative abundance of invertebrates within functional feeding groups differed between years. A greater proportion of taxa in 2006 were gatherers. This increase reflected a drop in relative abundance of filterers and scrapers, rather than increased abundance of gatherers themselves. The number of sites in which *Manayunkia* were found did not differ between years (X^2_1=1.7, P>0.19), but small numbers of polychaetes were found further downstream than they had been collected the year before.

DISCUSSION

The prevalence of *M. speciosa* within a restricted section (reach two) of the lower Klamath River was similar to the distribution pattern of other filter-feeding invertebrate taxa, though filterers were relatively abundant in reach three in 2006, and also associated with a general plateau of taxonomic richness. The distribution of *M. speciosa* within a 100 km section of the 300 km lower river suggests that environmental conditions within reach two were particularly favorable to the polychaete.

The high abundance of other filtering collectors within the same reach suggests that at least part of the explanation for the distribution of polycheates lies with its food supply. Wallace and Merrit (1980) reported abundance of filter-feeders in lotic waters is strongly influenced by both quality and quantity of the seston on which they feed, and Richardson and Mackay (1991) reported that food availability is often the dominant factor in the filter-feeder abundance. Taxon-specific morphological traits restrict the size range of particles ingested by filter-feeders, but most filter-feeders are unable to select particles based on food quality (Cummins and Klug 1979). Their highest growth rates and population sizes are achieved where food quality as well as quantity is greatest. For example, high abundances of filter-feeding invertebrates such as larval black flies and hydropsychid caddisflies are often observed in lake outlets and dam tailwaters of impoundments, where they respond to an abundant input of high-quality plankton and bacterially-rich detritus; precipitous declines downstream have been attributed to declining seston quality (Wallace and Merritt 1980). The fine particulate organic matter (FPOM, 0.45 µm to <1 mm), which not only constitutes the food supply of *M. speciosa*, but also provides the materials used in constructing the tube in which it lives, is likely rich in both quantity and quality within reach two. FPOM includes both living (e.g., bacteria, algae, protozoans) and non-living material, and originates from many sources. Breakdown of coarse particulate organic matter (e.g., from decomposition of macrophytes), and planktonic or sloughed algae are among the sources considered to be richest in nutritive quality (Richardson and Mackay 1991, Allan and Castillo 2007). Macrophyte beds line the streambanks in reach two. Consistent with the high nutrient levels found in this reach, high algal concentrations are predicted from models of algal biomass (Deas and Orlob 1999). Another source of FPOM derives from flocculation of dissolved organic matter, and we commonly observed flocculent foam in eddies and backwaters throughout reach two.

A second factor potentially driving the distribution and abundance of *Manayunkia* in the lower Klamath River is suggested from taxa commonly occurring on or around rocks on which the polychaetes were found. *M. speciosa* is one of the few freshwater representatives of the predominantly marine Polychaeta, and is believed to be a marine relict (Rolan 1974, Croskery

1978, Glasby and Timm 2008)—that is, an animal whose presently extinct ancestors lived in salt water but became adapted to life in fresh water when an area formerly covered by the sea slowly transitioned to fresh water. While our study concentrated on broad-scale, reach-wide influences on *M. speciosa* distribution rather than small-scale drivers of its habitat, we observed several other marine relicts to be common associates of the polychaete within this reach, particularly on the large, stable substrates that other members of the filtering functional group preferentially inhabit (Paillex et al. 2007). Relicts included *Hydra*, freshwater sponges (phylum Porifera), the byrozoan family Plumatellidae, the lymnaeid snail *Lanx*, and unionid mussels. We suggest that the stable substrates these taxa inhabit represent a primary, optimal habitat for *M. speciosa*, as these substrates are resistant to scour. However, stable substrates that lack sufficient texture, such as smooth cobbles, allow for less firm attachment for invertebrates and less FPOM accumulation (Didley et al. 1991, Quinn et al. 1996, Lau and Martinez 2003), and are not likely utilized by *M. speciosa*. Although dense colonies of polychaetes have also been found on organically enriched sand grains (Stocking and Bartholomew 2007), this substrate does not allow for secure attachment in the presence of high flows (Malakauskas, unpublished data). These colonies are therefore likely to be displaced during high flows, unless channel morphology or rock outcroppings reduce flow exposure, and may be only seasonally persistent. The polychaete population we sampled at the mouth of Horse Creek, for example, was largely eliminated by the flows and subsequent rearrangement of the substrate during the high flow event in the winter of 2005-2006. In large river systems, substrate availability at suitable current velocities has been found to be a limiting factor for other populations of filter-feeding invertebrates (Wallace and Merritt 1980).

While substrate availability may be limiting to *M. speciosa*, broad-scale geomorphologic parameters did not appear to explain either the distribution of the polychaete or other invertebrates. A shift from a geomorphically stable channel with a plant assemblage dominated by aquatic macrophytes, including the filamentous green alga *Cladophora*, to an active alluvial channel dominated by periphyton, occurred below the Scott River in the middle of river reach two (Pacificorp 2005); this was the reach with the greatest invertebrate taxonomic richness. Habitat heterogeneity often promotes increased taxonomic richness (e.g. MacArthur and MacArthur 1961, MacArthur and Wilson 1967) but this did not appear to drive invertebrate distributions, as samples throughout the reach maintained a fairly consistent taxonomic richness irrespective of channel morphology.

Water flow may be a third major factor affecting the distribution of polychaetes and other invertebrates in the Klamath River. A sample size of two years does not permit strong confidence, but considerable differences in annual flows between the years was also coincident with differences in taxonomic structure of invertebrate assemblages among reaches, differences in functional feeding group composition, and differences in the spatial extent of *M. speciosa* distribution. Differences between years in taxonomic structure were most apparent for non-insect taxa. The five groups contributing most to dissimilarity between years were all reduced in abundance in 2006. These groups are all wide-ranging, but are often found in association with littoral macrophytes and in organically enriched sediments (Mastrantuono 1991, Thorpe and Covich 2001), which are commonly scoured during high flows (Power et al. 1996, Poff et al. 1997, Patten et al. 2001, Jakob et al. 2003).

Decreased relative abundances of filter-feeders and scrapers in the year of higher flows is consistent with other findings of reduced filterer and scraper abundance after flooding, and is attributed to a decrease in the habitat stability on which these feeding groups rely (Paillex et al. 2007). As previously noted, a large decrease in polychaete numbers at the Horse Creek sampling site, where they were most abundant in 2005 was associated with a dramatic physical reorganization of habitat. Although the number of sites in which polychaetes were found did not differ between the two years, polychaetes were distributed further downstream following high flows in 2006. This result suggests the possibility of flow-mediated dispersal via catastrophic drift, as has been shown in other invertebrate taxa (e.g., Andrews and Minshall 1979, Matthaei et al. 1999, Imbert and Perry 2000), though sampling error cannot be ruled out. High, pulsed flows may not be effective in reducing polychaete populations, as they may be merely distributed further downstream. Stocking and Bartholomew (2007) found polychaetes more widely distributed in the lower river (reach one) than we did, but also found that polychaete densities were lower below the Trinity River, which could explain why they were absent in our samples.

The paucity of polychaetes found in reach one, however, suggests that the lowermost section of river does not provide ideal habitat for *M. speciosa*. The higher discharge, increase in water depth, and increased turbidity of the reach inhibit macrophyte development and probably reduce benthic algal production (PacifiCorp 2005, Hudon et al. 2000). Asarian et al. (2010) reported that diatom assemblages in reach 1 shift from non-nitrogen fixing species which use environmentally available nitrogen, to nitrogen fixing forms, which suggests that the reach is nitrogen limited (Cuffney et al. 1997). Declines in the quality of FPOM as a food resource for filter-feeders is suggested by the reduced abundance of filtering collectors and increased abundance of gathering collectors. Benthic-feeding, gathering collectors dominate when FPOM becomes a food resource of suitable quality only after accumulating and conditioning in the sediments (Cummins et al. 2005).

Perhaps a more interesting question is why polychaetes were not found in the reach of river immediately below Iron Gate Dam (reach 3). Sampling in subsequent years by co-authors and others substantiate that *M. speciosa* does not maintain dense populations in reach 3 (Malakauskas, personal observation), in contrast to the dense populations of other filter-feeders often observed below other impoundments (Richardson and Mackay 1991). An explanation is not immediately apparent, but it does not appear to be food-based. Releases from Iron Gate Dam are rich in inorganic phosphorus and nitrogen, resulting in high primary productivity including high algal biomass immediately downstream to the Interstate 5 rest area (river km 287) (Deas and Orlob 1999, Asarian et al. 2010). Although this reach has fewer deposits of fine sediments than further downstream (Holmquist-Johnson and Milhouse 2010), macrophyte beds are present which provide both food and habitat in this reach, as in reach two. Other filter-feeding invertebrates, including larval black flies and some chironomid midges, were present in reach three, but not in great enough numbers that they were likely to competitively displace the polychaete. Additionally, our field observations suggest that *M. speciosa* and larval black flies do not often overlap spatially, on a fine scale, which is perhaps due to the preference for faster waters that many black fly species exhibit (Merritt et al. 2008).

Penstock withdrawals for water releases from Iron Gate Dam often contain low dissolved oxygen (DO) levels in the summer and fall, which is often exacerbated by high primary productivity. These low DO levels have been observed for about 10 to 15 miles below the dam, until the confluence of the Shasta River (Deas and Orlob 1999). However, the invertebrate assemblage in reach three, although reduced in taxonomic richness relative to reach two, did not harbor taxa noted for tolerance to low DO (as is the polychaete). Temperature related impacts from the dam are another possibility. Water releases from the dam in late spring, summer, and early fall are typically below equilibrium temperature by 2 to 4°C, with temperature effects diminishing with distance downstream (Basdekas and Deas 2007). However, seasonal temperature effects are a greater source of variation than longitudinal differences in water temperature between Iron Gate Dam and the river mouth, and *M. speciosa* appears to be thermally tolerant. It has been observed in water temperatures ranging from 2.8 to 28.3°C in a Pennsylvania river (Poe and Stefan 1974), and in locations as thermally divergent as Alaska and the Gulf Coast of the United States (Holmquist 1973, Brehm 1978).

One final explanation for the reduced polychaete abundance and an overall reduction of taxonomic richness immediately below Iron Gate Dam may be the serial discontinuity concept. This theory states that large tributaries and high dams, such as Iron Gate, cause downstream aquatic biota to “reset” toward an ecosystem more representative of a lower order stream (Ward and Sanford 1983). More specifically, Iron Gate Dam and its associated reservoir may be a barrier to downstream migration of polychaetes and other invertebrates. Subsequently, only lotic invertebrates with winged adult stages would be able to recolonize the river immediately below the dam if they get displaced by a disturbance event. However, a definitive explanation for the paucity of polychaetes immediately below Iron Gate Dam awaits further research.

APPENDIX II

Table 2.1. Location and reach number of invertebrate sampling sites in the lower Klamath River, California.

Site No.	Reach	Site Name	GPS Coordinates
1	1	Klamath Glen	41° 30’ 42.7” N, 124° 00’ 06.5” W
2	1	Lower River 2	41° 30’ 30.2” N, 124° 00’ 30.2” W
3	1	Lower River 3	41° 28’ 28.4” N, 123° 56’ 40.2” W
4	1	Lower River 4	41° 23’ 27.5” N, 123° 55’ 29.0” W
5	1	Lower River 5	41° 20’ 51.3” N, 123° 51’ 57.9” W
6	1	Big Bar	41° 15’ 16.0” N, 123° 38’ 04.6” W
7	1	Dolan Bar	41° 18’ 54.0” N, 123° 31’ 36.7” W
8	1	Salmon River	41° 22’ 44.4” N, 123° 28’ 18.5” W
9	1	Green Riffle	41° 25’ 58.9” N, 123° 30’ 25.4” W
10	1	Dillon Creek	41° 34’ 30.6” N, 123° 32’ 22.4” W
11	2	Independence Creek	41° 39’ 34.6” N, 123° 26’ 59.5” W
12	2	Indian Creek	41° 47’ 24.5” N, 123° 22’ 44.2” W
13	2	Klamath River Resort	41° 48’ 22.4” N, 123° 20’ 54.4” W
14	2	New 49ers Camp	41° 51’ 45.9” N, 123° 16’ 10.2” W
15	2	Scott River	41° 46’ 42.6” N, 123° 02’ 12.7” W
16	2	Horse Creek	41° 49’ 24.4” N, 123° 00’ 17.1” W
17	2	Beaver Creek	41° 51’ 51.5” N, 122° 49’ 08.9” W
18	2	Shasta River	41° 49’ 16.4” N, 122° 35’ 30.1” W
19	2	I5 Rest Area	41° 50’ 57.3” N, 122° 34’ 16.2” W
20	3	Copco Agar Bridge	41° 53’ 57.3” N, 122° 30’ 30.4” W
21	3	Private Fishing Area	41° 55’ 33.1” N, 122° 26’ 50.2” W
22	3	Iron Gate Dam	41° 55’ 52.4” N, 122° 28’ 30.9” W

Table 2.2. The five most abundant invertebrate groups collected in benthic samples from each of three reaches of the lower Klamath River (below Iron Gate Dam) in 2005 and 2006.

Year	Reach 1		Reach 2		Reach 3	
	Taxon	% Mean Abund.	Taxon	% Mean Abund.	Taxon	% Mean Abund.
2005	Chironomidae	19	Copepoda	41	Cladocera	46
	Cladocera	16	Cladocera	17	Copepoda	14
	Copepoda	15	Chironomidae	10	Chironomidae	9.3
	Ostracoda	11	Gastropoda	9.1	Gastropoda	7.6
	Hydracarina	10	Ostracoda	4.9	Nematomorpha	4.5
2006	Chironomidae	75	Chironomidae	60	Chironomidae	66
	Baetidae	9.1	Gastropoda	7.3	Simuliidae	15
	Leptohyphidae	3.8	Baetidae	6.4	Nemertea	3.6
	Hydracarina	3.8	Copepoda	4.9	Ostracoda	3.5
	Ceratopogonidae	2.0	Cladocera	4.6	Gastropoda	3.3

Table 2.3. ANOSIM pairwise comparisons between invertebrate communities in three reaches of the Klamath River below Iron Gate Dam. R-values are in the top right triangles and p-values are in the bottom left triangles. All p-values were significant (*P*<0.05).

	2005 Samples			2006 Samples		
	Reach 1	Reach 2	Reach 3	Reach 1	Reach 2	Reach 3
Reach 1		0.386	0.4777		0.4631	0.9236
Reach2	0.001		0.4667	0.0002		0.3314
Reach 3	0.0219	0.0283		0.0038	0.0427	

Table 2.4. Insect taxa found in the lower Klamath River, CA, below Iron Gate Dam. Reference specimens can be found at the California Cooperative Fish and Wildlife Research Unit at Humboldt State University, Arcata, CA.

Taxon, Column 1	Taxon, Column 2
COLEOPTERA	**LEPIDOPTERA**
DYTISCIDAE	CRAMBIDAE
Hygrotus	*Petrophila*
ELMIDAE	
Microcylloepus similis	**MEGALOPTERA**
Dubiraphia giulianii	SIALIDAE
Lara avara	*Sialis*
Optioservus	
HALIPLIDAE	**NEUROPTERA**
Haliplus robertsi	SISYRIDAE
Peltodytes	*Climacia californica*
HYDROPHILIDAE	
Tropisternus	**ODONATA**
PSEPHENIDAE	ANISOPTERA
Eubrianax edwardsii	AESHNIDAE
Psephenus falli	*Aeshna walkeri*
	CORDULIIDAE
DIPTERA	*Epitheca canis*
ATHERICIDAE	*Macromia magnifica*
Atherix pachypus	GOMPHIDAE
BLEPHARICERIDAE	*Gomphus kurilis*
CERATOPOGONIDAE	*Octogomphus specularis*
Atrichopogon	*Ophiogomphus morrisoni*
Probezzia	*Ophiogomphus occidentis*
CHIRONOMIDAE	LIBELLULIDAE
Chironominae	*Libellula saturata*
Chironomini	ZYGOPTERA
Tanytarsini	CALOPTERYGIDAE
Rheotanytarsus	*Calopteryx aequabilis*
Diamesinae	*Hetaerina americana*
Tanypodinae	COENAGRIONIDAE
Orthocladiinae	*Argia agriodes*
DIXIDAE	*Argia emma*
EMPIDIDAE	*Enallagma*
Hemerodromia	*Ischnura*
EPHYDRIDAE	
PHORIDAE	**PLECOPTERA**
PSYCHODIDAE	CAPNIIDAE
SIMULIIDAE	*Capnia*

Table 2.4 (cont'd).

- *Metacnephia*
- *Prosimulium*
- *Simulium*

STRATIOMYIDAE
- *Odontomyia*

TABANIDAE
- TIPULIDAE
- *Antocha*
- *Hexatoma*

EPHEMEROPTERA

AMELETIDAE
- *Ameletus*

BAETIDAE
- *Acentrella insignificans*
- *Baetis bicaudatus*
- *Beatis tricaudatus*
- *Callibaetis fluctuans*
- *Callibaetis pictus*
- *Camelobaetidius maidu*
- *Centroptilum*
- *Procloeon*

CAENIDAE
- *Caenis latipennis*

EPHEMERELLIDAE
- *Caudatella heterocaudata*
- *Drunella doddsii*
- *Drunella flavilinea*
- *Drunella grandis*
- *Drunella spinifera*
- *Ephemerella*
- *Serratella tibialis*
- *Timpanoga hecuba*

HEPTAGENIIDAE
- *Cinygmula*
- *Epeorus*
- *Heptagenia elegantula*
- *Ironodes*
- *Rhithrogena*

ISONYCHIIDAE
- *Isonychia velma*

CHLOROPERLIDAE
- *Sweltsa*

LEUCTRIDAE
- *Despaxia augusta*

NEMOURIDAE
- *Zapada*

PERLIDAE
- *Callineuria californica*
- *Claassenia sabulosa*
- *Hesperoperla pacifica*

PERLODIDAE
- *Isoperla*

PTERONARCYIDAE
- *Pteronarcys californica*

TRICHOPTERA

BRACHYCENTRIDAE
- *Amiocentrus aspilus*
- *Brachycentrus americanus*

CALAMOCERATIDAE
- *Heteroplectron californicum*

GLOSSOSOMATIDAE
- *Glossosoma*

HELICOPSYCHIDAE
- *Helicopsyche borealis*

HYDROPSYCHIDAE
- *Hydropsyche*

LEPTOCERIDAE
- *Ceraclea*
- *Ylodes frontalis*
- *Mystacides alafimbriata*
- *Mystacides sepulchralis*
- *Nectopsyche gracilis*
- *Oecetis disjuncta*

LIMNEPHILIDAE
- *Dicosmoecus gilvipes*
- *Hydatophylax hesperus*
- *Onocosmoecus unicolor*

PHILOPOTAMIDAE
- *Wormaldia*

PHYRGANEIDAE

Table 2.4 (cont'd)

LEPTOHYPHIDAE
Tricorythodes minutus
LEPTOPHLEBIIDAE
Paraleptophlebia
SIPHLONURIDAE
Parameletus columbiae
Siphlonurus occidentalis

HEMIPTERA
CORIXIDAE
Hesperocorixa laevigata
Sigara mckinstryi
GELASTOCORIDAE
Gelastocoris oculatus
GERRIDAE
Aquarius remigis
Metrobates trux
NAUCORIDAE
Ambrysus mormon
SALDIDAE
Salda buenoi
VELIIDAE
Rhagovelia distincta

Phyrganea cinerea
POLYCENTROPODIDAE
Polycentropus
PSYCHOMYIIDAE
Psychomyia
SERICOSTOMATIDAE
Gumaga
UENOIDAE
Neophylax splendens
Neothremma

Table 2.5. Non-insect taxa found in the lower Klamath River, CA, below Iron Gate Dam. Reference specimens can be found at the California Cooperative Fish and Wildlife Research Unit at Humboldt State University, Arcata, CA.

Taxon, Column 1	Taxon, Column 2
ANNELIDA	**MOLLUSCA**
SABELLIDAE	SPHAERIIDAE
Manayunkia speciosa	*Pisidium*
HIRUDINEA	*Sphaerium*
NAIDIDAE	UNIONIDAE
Chaetogaster	ANCYLIDAE
TUBIFICIDAE	*Ferrissia*
Branchiura sowerbyi	LYNAEIDAE
	Lanx alta
ARTHROPODA	PLANORBIDAE
ACARI	*Helisoma*
ASELLIDAE	PHYSIDAE
Caecidotea	*Physa*
ASTACIDAE	PLEUROCERIDAE
Pacifastacus leniusculus	*Juga*
ENTOMOBRYIDAE	
CYCLOPOIDA	**NEMATA**
HARPACTICOIDA	
OSTRACODA	**NEMERTEA**
AMPHIPODA	TETRASTEMMATIDAE
CLADOCERA	*Prostoma*
CNIDARIA	**PLATYHELMINTHES**
HYDRIDAE	PLANARIIDAE
Hydra	*Dugesia*
OLINDIIDAE	MACROSTOMIDA
Craspedacusta sowerbyi	
	PORIFERA
ECTOPROCTA	
PLUMATELLIDAE	**TARDIGRADA**
Plumatella	HYPSIBIIDAE

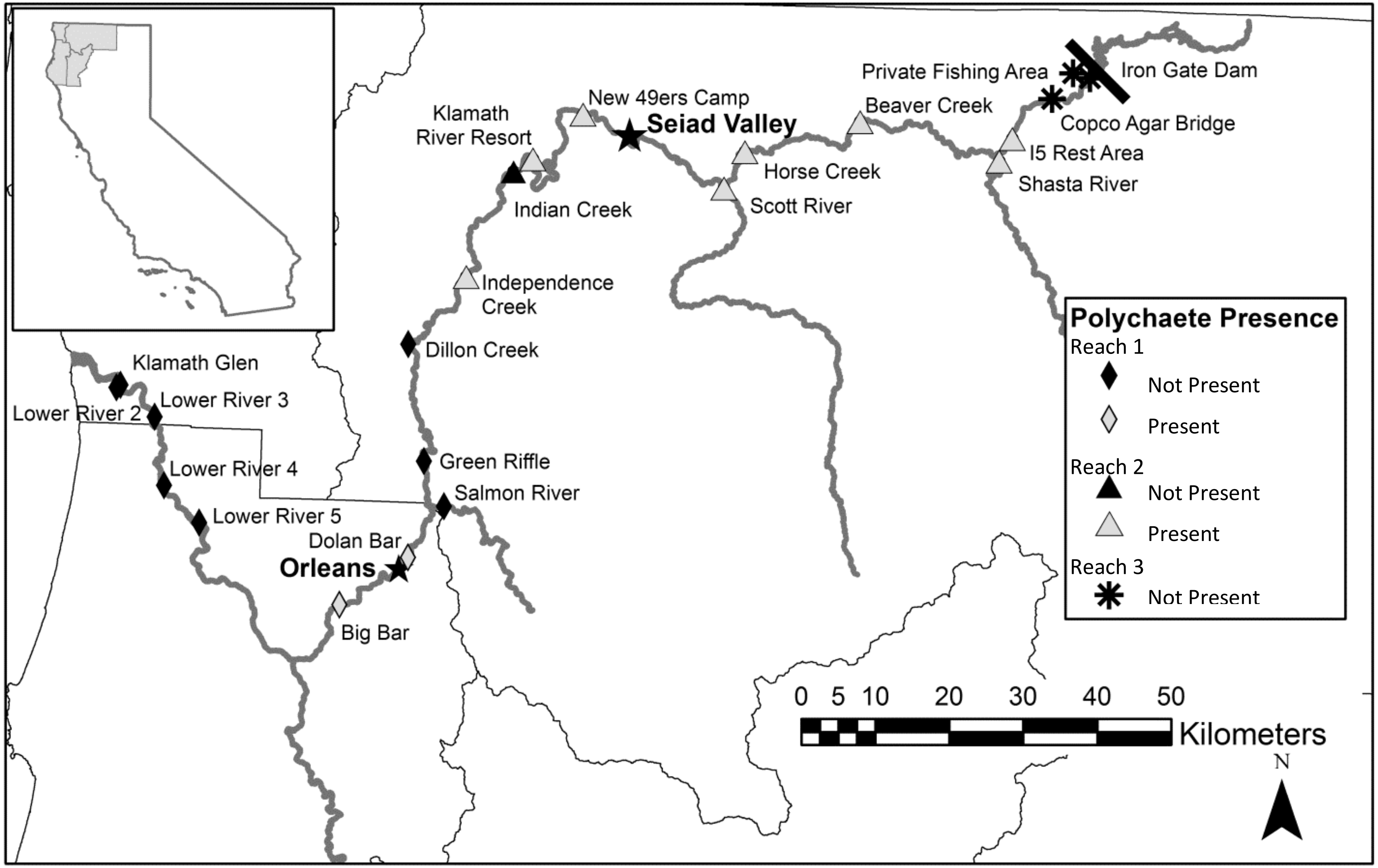


Figure 2.1. Map of sampling sites from the Klamath River, below Iron Gate Dam, Siskiyou, Del Norte, and Humboldt counties, California, USA, 2005-2006.

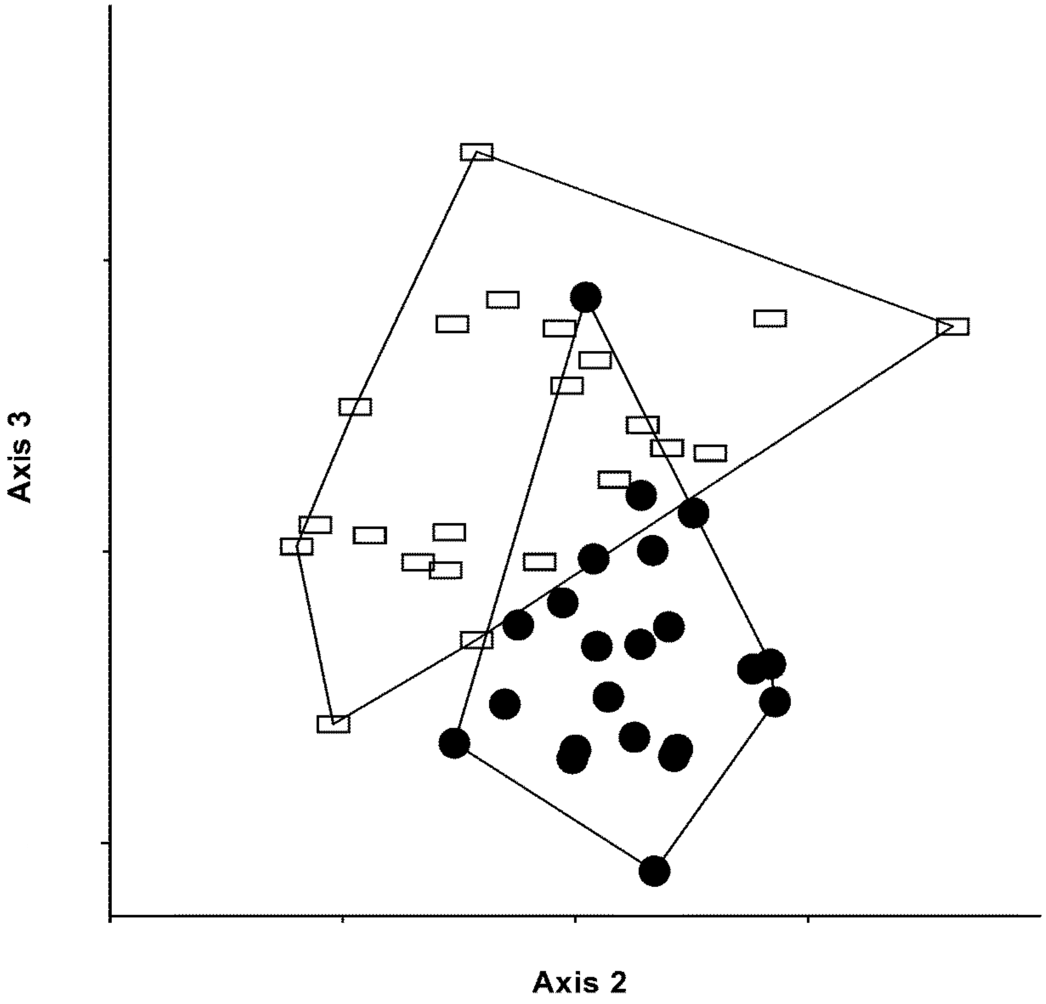
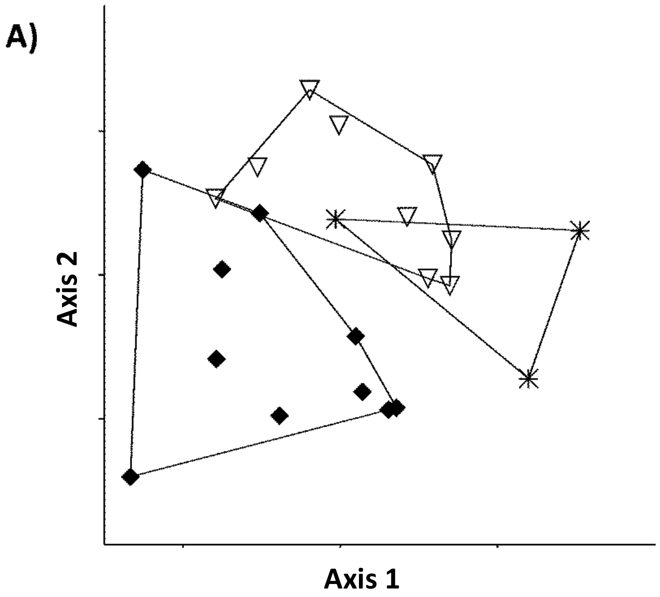


Figure 2.2. Non-metric multidimensional scaling ordinations with convex hulls showing community structure differences between the 2005 and 2006 sampling years. The 2005 sampling year experienced average flows, while 2006 experienced elevated flows. Rectangles represent sites from 2005, and circles represent sites from 2006. Results show a three dimensional solution (Stress = 0.1726). Samples in 2006 exhibited greater taxonomic richness and a greater proportion of Chironomidae.



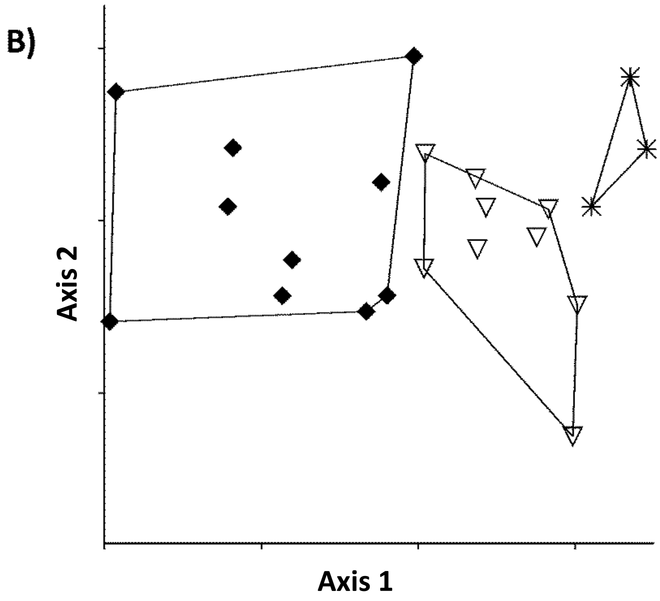


Figure 2.3. Non-metric multidimensional scaling ordinations with convex hulls showing community structure of three reaches of the Klamath River below Iron Gate Dam. Diamonds represent sampling sites in the lowest reach (reach one) of the river, triangles represent sites in the middle reach (reach two) where *Manayunkia speciosa* were found, and stars represent sampling sites (reach three) closest to Iron Gate Dam. (A) Results from the 2005 sampling year represent a three dimensional solution (Stress = 0.1941). (B) Results from the 2006 sampling year show a two dimensional solution (Stress = 0.1339).

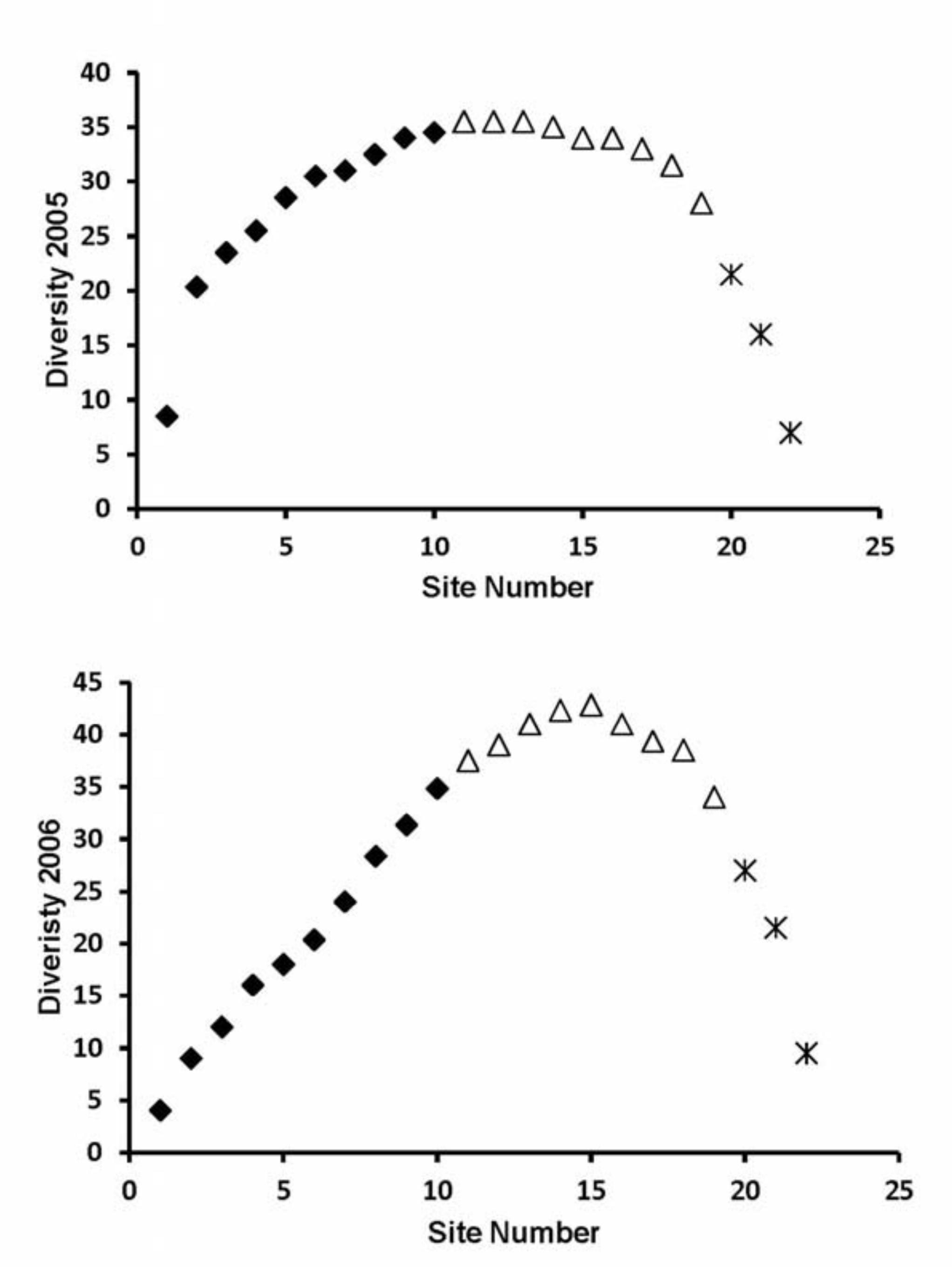


Figure 2.4. Curves of invertebrate community diversity (taxonomic richness) in the Klamath River below Iron Gate Dam. Site number increases with distance upriver. Diamonds represent sampling sites in the lowest reach (reach one) of the river, triangles represent sites in the middle reach (reach two) where *Manayunkia speciosa* were found, and stars represent sampling sites (reach three) closest to Iron Gate Dam. The river experienced flood conditions in December of 2005 and January of 2006.

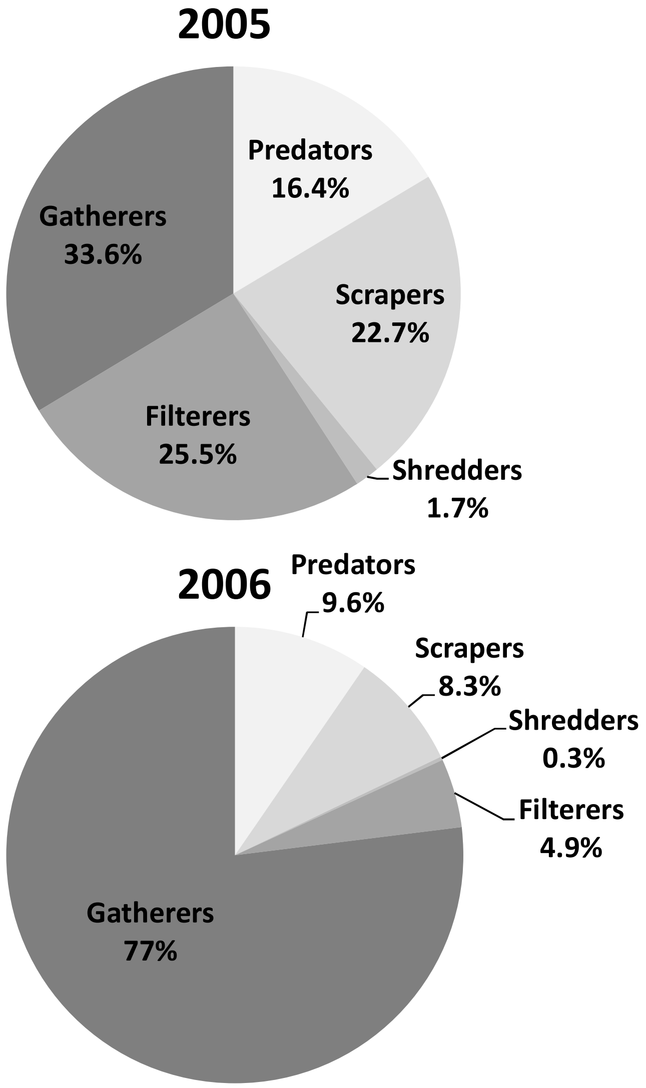


Figure 2.5**.** Relative abundance of functional feeding groups by year. ANOVA indicated significant differences (*P*<0.05) between years in mean abundances of scrapers, filterers, and gatherers. Percentages represent means.

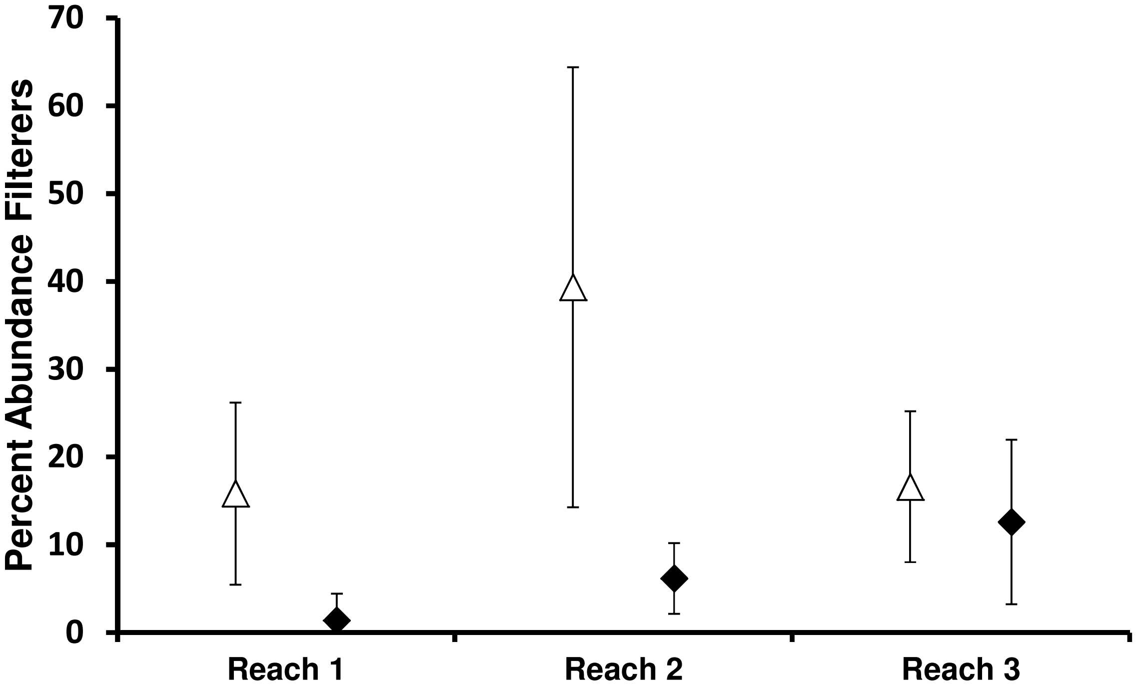


Figure 2.6. Mean percent abundance of filterers in three reaches of the Klamath River below Iron Gate Dam. Reach one exhibited lower relative abundance of filterers consistently for both years. Mean percent abundance is represented by triangles in 2005 and diamonds in 2006. Error bars represent one standard deviation.

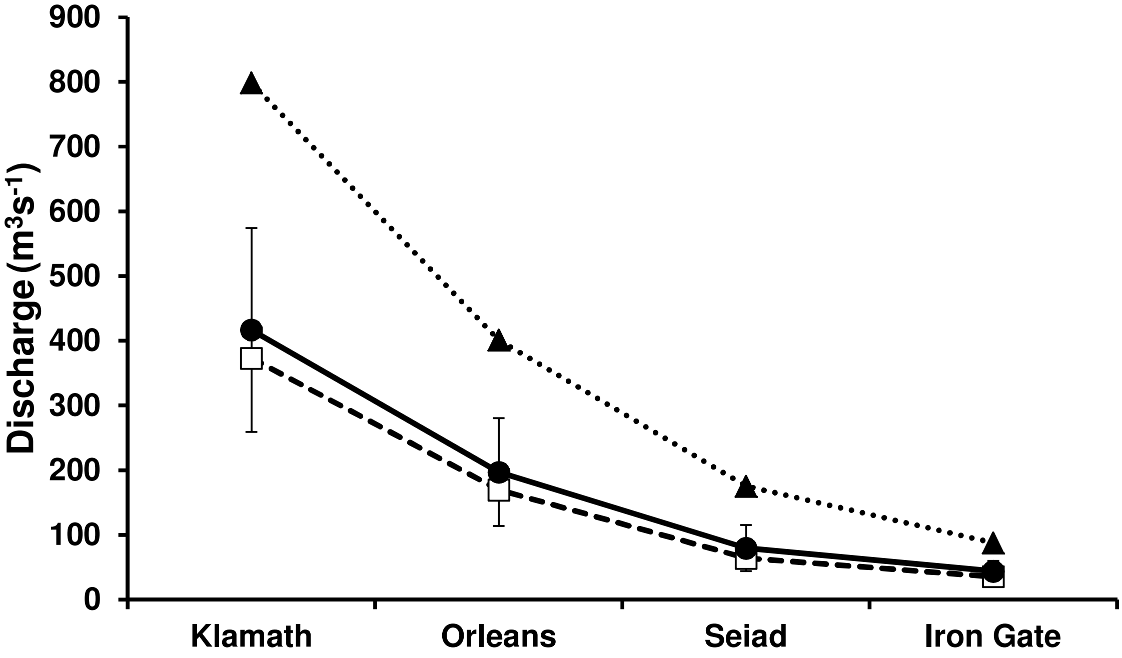


Figure 2.7. Mean annual discharge in the Klamath River for the 2005 and 2006 water years. The graph is oriented with the site nearest the mouth of the river on the left. Triangles represent 2006, squares represent 2005, and circles represent the mean annual flow for the years 2001 to 2010. Error bars represent one standard deviation. Data were obtained from http://waterdata.usgs.gov/nwis/sw.

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CHAPTER 3

FLOWS AND SUBSTRATE TYPE AFFECT DISLODGEMENT OF THE FRESHWATER POLYCHAETE, *MANAYUNKIA SPECIOSA*

INTRODUCTION

The dynamics of flow play an important role in the lives of lotic aquatic organisms (e.g., Craig 1990, Hart et al. 1996) and their community structure (e.g., Lake 1990, Giller 1991, Resh et al. 1988, Nelson and Lieberman 2002). Flows affect larval and adult dispersal, as well as movement of gametes, nutrients, food particles, and waste removal (Wotton 1988, Rudek et al. 1991, Gaylord and Gaines 2000), and flow variation greatly influences the morphology, physiology and behavior of lotic organisms (e.g., Statzner 1988, Craig 1990, Lancaster et al. 2006). High flows such as spates and floods, or fluctuating flows in the context of managed rivers, may lead to reorganization of river substrates and the associated benthos due to increased, and often variable, velocities and hydraulic forces (Troelstrup and Hergenrader 1990, Lake 2000). Resultant scour and fill patterns may redistribute organisms or may reduce populations (e.g., Giller et al. 1991, Cobb et al. 1992, Death 1996, Matthaei et al. 1997, Mosisch and Bunn 1997). As flow is a defining feature of riverine environments, invertebrates utilize a number of methods to cope with flow-mediated disturbance, including movements to low flow microhabitats (Lancaster 1999), where hydraulic forces are less severe and lower levels of disturbance are experienced. Examples of this behavior include seeking refuge in the hyporheic zone (Dole-Olivier et al. 1997), and entering the drift and swimming down toward the substrate in areas with reduced flow (Lancaster 1999). Selection of habitats with stable substrates or macrophytes may also be used as long-term strategies to reduce exposure to the effects of high flows (Richardson and Mackay 1991). Invertebrates have also developed specific morphological and behavioral adaptations including a streamlined body shape, physical attachment mechanisms (e.g., claws, suckers, hooks and mucus), formation of drag-minimizing colonies, the addition of ballast materials (e.g., mineral cases of some Trichoptera), and rheotaxis (Schnauder et al. 2010).

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

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

Manayunkia speciosa Leidy (Canalipalpita: Sabellidae) is a small freshwater polychaete that occurs in the Great Lakes and coastal areas of North America (e.g., Pettibone 1953, Hazel 1966, Holmquist 1973). It is a habitat generalist, tolerating a broad range of environmental conditions in water chemistry (e.g., pH, dissolved oxygen), temperature, depth and mean velocity (Hiltunen 1965, Holmquist 1973, Poe and Stefan 1974, Rolan 1974). *M.* s*peciosa* is a suspension feeder, though its specific food requirements remain unknown. It has an annual life cycle, and sexual reproduction. Juvenile worms are brooded in the maternal tube until capable of independent survival (Willson et al. 2010).

Within the Klamath River, the worm has been found to occupy a variety of substrates including depositional sediments, bedrock, woody debris, and macrophyte beds (Stocking and Bartholomew 2007, Willson et al. 2010). This benthic polychaete usually occupies a tube (Leidy 1883) except in cases of physical disturbance (Willson et al. 2010), and can be locally abundant with reported densities of over 40,000 individuals per m^2 (Pettibone 1953, Stocking and Bartholomew 2007). It has become an organism of increasing interest because it is an intermediate host for two parasites of Salmonidae, *Ceratomyxa shasta* Noble and *Parvicapsula* *minibicornis* Kent, which have recently caused mortalities in wild and stocked juvenile salmonids within the Pacific Northwest, including salmonids in Alaska (Follett et al. 1994), the Fraser River (British Columbia; Ching and Munday 1984), the Columbia River basin (British Columbia, Washington, Oregon, Idaho; Hoffmaster et al. 1988), the Klamath River basin (California, Oregon; Hazel 1966), and the Pit (Noble 1950), Sacramento, and San Joaquin river systems (California; Hendrickson et al. 1989). Mortalities among salmonids due to *C. shasta* and *P. minibicornis* have been particularly substantial within the lower Klamath River basin (Foott et al. 1999, 2004).

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

METHODS

Collection and culture of the polychaete

Polychaetes attached to rocks from a location where *Manayunkia speciosa* had been found in previous years were collected from the Klamath River, CA, just upstream of the

Interstate 5 Rest Area (41° 51′ 35.8″ N, 122° 34′ 00.1″ W). Rocks were placed in coolers with ice and river water and transported back to the Humboldt State University fish hatchery. The polychaetes were maintained in culture facilities described in Willson et al. (2010). Collections occurred in late June and late October of 2011. Prior to the start of a trial, rocks were brought into the lab and visually scanned under a dissection microscope to locate and remove individual polychaetes. The polychaetes were then placed in small crystallizing dishes in an aerated 5 gallon aquarium until they were needed for use. The aquarium was kept at 20 °C, and weekly water changes were made using water from the fish hatchery.

Flume description

An experimental flume modified from Vogel and LaBarbera (1978), measuring 2.6 m in length, 1.35 m in height and 0.44 m in width, was constructed in-house at Humboldt State University for use in experimental trials (Fig. 3.1). The flume was a closed-circuit, recirculating system, with the channel measuring 43 cm wide, by 26 cm high, by 175 cm long internally. Water was returned though a loop of 20.3 cm PVC pipe of approximately 5.3 m in length. The water was moved by 2 propellers on a shaft that was powered by a 2 HP, 3 phase inverter duty AC induction motor. In order to decrease large-scale turbulence, a collimator 35 mm in length was made from parallel sheets of 1.3 cm egg crate light diffuser and placed upstream of the center of the flume. The flume was filled with dechlorinated tap water and kept at 18 °C for all trials.

Experimental trials

Polychaete dislodgement and behavioral responses to increases in two mean flow velocities were evaluated in separate trials using three different substrates. For trials, worms were placed on a substrate which was then placed in standing water in the flume and water was gradually increased to a mean velocity of 55 cm/s or 140 cm/s. Three substrate types were tested: fine sediments, analogues of rock faces and the filamentous green alga *Cladophora*. Five trials were conducted for each of the 6 combinations of substrate and velocity level. We also conducted 5 control trials for each velocity—substrate combination. In control trials, polychaetes were left in standing water for the entire duration of the experiment. All controls were paired with a treatment and carried out simultaneously. Previous work (Willson et al. 2010) and pilot trials showed that polychaetes were susceptible to potentially substantial mortality from handling and that polychaetes may wander prior to construction of their fixed retreat, even on substrates in which they are commonly found (*sensu* Lewis 1968). Additionally, we observed that senescent worms were less able to affix to the substrates. Trials took place over several months, so controls throughout ensured that dislodgement was independent of age. Finally, *M. speciosa* is susceptible to mortality in tap water that is not properly conditioned, and controls allowed us to eliminate tap water as a cause of mortality. Therefore controls ensured that we were assessing true dislodgment of living, affixed polychaetes.

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

Test velocities and substrate types were chosen to simulate polychaete habitats in the Klamath River, and were also influenced by results of pilot trials. The low flow level was set to 55 cm/s after observing that polychaetes were not dislodged from any substrate type in the flume at mean velocities below this point. The high flow level was the maximum working mean velocity that we were able to produce in the channel. Both velocities would likely only be able to occur in swift runs or riffles. Three of the most common substrates in which polychaetes have been collected in the Klamath River include beds of *Cladophora* or vascular macrophytes, organically enriched fine sediments, and large, stable substrates such as boulders or large woody debris (Stocking and Bartholomew 2007, Willson et al. 2010, Malakauskas and Wilzbach 2012, Chapter 2). Establishing live plants in the flumes would have been difficult and the flumes were not large enough to accommodate boulders, thus we developed analogues of these to use for the trials. In preliminary trials we also experimented with the use of aquarium gravel (D50 = 4.5 mm) as a substrate, and discarded this as a treatment choice after finding that the polychaetes immediately abandoned it.

Rock faces were mimicked with unglazed ceramic tiles measuring 15 cm × 15 cm. *Cladophora* was mimicked with square finishing pads of synthetic fibers (3M, St. Paul, Minnesota), hereafter referred to as “pseudophora” (Fig. 3.2). Pseudophora squares were cut to be 6.25 cm^2 and 2 mm high and were affixed to the center of a tile with Defthane polyurethane (Deft, Inc., Irvine, California). Depositional sediments and fine benthic organic matter (FBOM) used in the trials were obtained from Fern Lake (40° 52′ 29.4″ N, 124° 04′ 25.9″ W), on the Humboldt State University campus. Sediments were filtered through a 500 µm screen and stored dry until use (Willson et al. 2010).

Preliminary trials established that *M*. *speciosa* would not affix to any substrate if some fine particulate organic matter was not also present, and we thus added approximately 0.5 cm^3 of FBOM to the center of each of the substrate types. After preparation, all substrates were placed in plastic containers measuring 25 cm × 20 cm and 8 cm in height filled with hatchery water. Worms were removed from their tubes, as preliminary trials showed that this facilitated attachment to substrates, and then placed on the center of each substrate. After 1 h had elapsed, an air bubbler was added to each container. Polychaetes then acclimated for 24 h prior to the start of a trial, during which time all tubes were reconstructed. Before substrates were placed in the flume, worms were again counted to ensure that all 20 individuals were present.

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

Following an experimental trial, the substrate was removed from the flume and returned to a plastic container with air bubblers for 48 h at 20 °C, after which worms on the substrates were counted and mortalities were assessed. Additionally, sediment that was scoured during the course of the sediment trials was collected from the flume using a turkey baster and plastic spoon. Sediment was examined to locate worms, and these polychaetes were set aside for 48 h before mortalities were evaluated, as previous work has shown that injured worms can take a day or two to die (Willson et al. 2010).

Velocity measurements were made during a trial to characterize and compare open channel and near-bed flows at the test velocities. Following the gradual increase in channel velocity over 30 min to the terminal velocity, we waited 10 min for flows to stabilize before taking velocity readings. All velocity measurements were made using a SonTek (SP-AV10M01) Acoustic Doppler Velocimeter (ADV) (SonTek/YSI, San Diego, California) which was mounted above the center of the flume, directly over the polychaetes. Seventeen measurements, starting at a height of 10 mm (Finelli et al. 1999), were taken at 5 mm intervals above the bed (sampling volume height and diameter 9mm and 6 mm, respectively) for each trial to obtain a velocity profile and Reynolds stress ($-\overline{u'w'}$), an internal measure of molecular forces, for use in calculations such as determining shear velocity. At each height, 3-dimensional flow velocity measurements were sampled at a rate of 10 Hz over a period of 45 s. The high flow setting resulted in a surface wave and flow separation around the probe, leading to encapsulation of the probe head by air. As a result, measurements could not be obtained above a height of about 4.5 cm. However, sufficient data points were obtained to perform a regression and to make calculations with respect to flows experienced by *M. speciosa*.

A Reynolds stress profile was obtained using temporally averaged velocity fluctuations in the streamwise (u') and vertical directions (w') at 9 heights (5 runs at each velocity-substrate combination) above the bed. A regression analysis was then used to estimate Reynolds stress at the bed, and the shear velocity (U_*) was calculated as

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

Authors have used multiple methods to express velocities experienced by invertebrates, including measurements at a height of 5 mm above the bed. Therefore, we also calculated velocities at 5 mm above the bed to allow comparison with other published values. Least squares regression of $\ln z$ (where z is the height above the bed) against U was used to calculate U at a height of 5 mm.

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

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

where U is the mean velocity, R_h is the hydraulic radius of the flume, and ν is the kinematic viscosity of water. Reynolds numbers greater than 2000 indicate turbulent flows while values of less than 500 indicate laminar flows. A regression of velocity against height, using data from velocity profiles obtained at nine mean velocities (ranging from 14 cm/s to 125 cm/s) was used to estimate a mean velocity for calculation of a Reynolds number at the high flow setting.

In addition, we also characterized the effective drift velocity and the body length Reynolds numbers at the low and high velocity settings. Effective drift velocity represents the average flow experienced by invertebrates (Schnauder et al. 2010) and has a direct relationship with drag forces acting upon the body of the organisms:

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

where h is the average height of the invertebrate. The effective drift velocity in turn was used to calculate the body length Reynolds number:

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

where l is the length of the invertebrate. Here, l represented the average tube width of an individual worm. As some worms formed aggregates of tubes, the length of the tube mass was also used as a length. Body length Reynolds numbers are typically below 10 for lotic invertebrate larvae and over 1000 for adult forms (Statzner 1988). As Re_l decreases, drag forces become proportionately greater than lift forces (Vogel 1994), with drag forces being typically more important for benthic, lotic invertebrates (Statzner 1988).

Statistical analyses

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

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

and **X** is a design matrix of treatment levels, $\boldsymbol{\beta}$ is a vector of regression coefficients, **Z** is a design matrix specifying the trial for each observation, **δ** is a vector of random effects parameters, and *g()* represents the logit link function. We assessed the significance of treatment effects via likelihood ratio tests. Model parameters were estimated with SAS software's GLIMMIX procedure using adaptive Guass-Hermite quadrature to approximate the log-likelihood (SAS Institute Inc., 2008).

RESULTS

Probability of dislodgement

There is strong evidence that variation in polychaete dislodgement, within combinations of the velocity treatment levels with the tile and sediment substrates, could not be attributed to random polychaete behavior or laboratory conditions. The odds of dislodgement for tile and sediment substrates for non-control trials was estimated to be 374 times higher (95% CI: 124 to 1126) than control trials, after accounting for velocity and substrate effects. On pseudophora substrates, observed polychaete dislodgement probabilities among the control and non-control trials were nearly identical at each velocity level (Fig. 3.3). Though this condition precluded the separation of observed dislodgement on the pseudophora substrates from random chance or laboratory conditions in the strictest sense, the low levels of dislodgement on pseudophora substrates overall warranted their inclusion in a broader analysis of substrate and velocity effects on the probability of dislodgement.

Considering the non-control trials only, the odds of dislodgement was associated with substrate type ($P < 0.001$) and velocity ($P < 0.001$). After accounting for substrate, the odds of dislodgement at high velocity was estimated to be 8 times higher than low velocity (95% CI: 3 to 21.6). Relative to pseudophora substrates, the odds of dislodgement on tile and sediment substrates were estimated to be 214 times higher (95%CI: 24 to 1879) and 3990 times higher (95% CI: 373 to over 40,000), respectively, after accounting for velocity effects. These differences reflect the gradient in observed proportions of dislodgement (Fig. 3.3), and estimated probabilities of dislodgement for each combination of velocity and substrate (Table 3.1).

Flows and polychaete response

Shear velocities averaged 2.3 cm/s at the low flow level and 4.7 cm/s at the high flow level. Flows at both velocities exceeded the threshold value of 2000, and were turbulent, with Reynolds numbers of 6×10^5 and 1.6×10^6 for low and high velocities, respectively. Shear velocities were higher for trials conducted on fine sediments compared to other substrates which may reflect the influence of the gravel sublayer (Table 3.2). Actual shear stress for a homogeneous layer of sand would likely be similar to those found for the other substrates at the low velocity trials. Average velocity of the flow field around the polychaetes (i.e., the effective drift velocity) was 38.3 cm/s at the low flow level and 103.7 cm/s at the high flow level. Body-length Reynolds numbers were all greater than 100, which combined with high mean flow Reynolds numbers, indicated that the worms were affected to a greater extent by pressure drag than by lift forces.

Isolated worms were observed to experience the least dislodgement within tile trials, while worms that were in ball-shaped masses experienced the greatest dislodgement as would be expected due to increased drag. Additionally, some worms were lost immediately after velocity increases despite efforts to slowly increase velocities. Worms within the pseudophora remained affixed to the substrate even when fine sand and FBOM was scoured out from around them. Polychaetes from the sediment trials were typically scoured as a group of worms as the mucus trails that they made while burrowing formed a matrix that stabilized the substrate around the colony. This stabilization was evident as sediment was scoured from around the upstream and lateral sides of the mucus matrix before the actual worm colony was dislodged. Worms that were not scoured from the sediment at the low velocity were often affixed to the heavier gravel under the sediment.

Survivorship of dislodged polychaetes

No mortalities occurred among worms that remained on substrates after velocity trials (total n = 198). Forty-nine percent (n = 56) of worms were recovered from scoured sediments and 98% survived. Most worms recovered were no longer in tubes, though it could not be determined if this was a direct result of dislodgement, or a result of handling. Additionally, 3 tubes without worms were recovered from scratches in the acrylic channel sides at the end of trials.

General behavioral observations

Polychaetes in the lab constructed tubes that were visually similar to those constructed by worms found in depositional areas in the Klamath River. Materials used in tube construction were most coarse near the proximal end (the base), and often had particles of reduced or very fine size diameters in the distal section. Three distinct sections were thus observed in polychaete tubes: a loose base of mucus and relatively more coarse organic and inorganic particles (generally <500 µm), a middle section with relatively intermediate organic particles (<250 µm), and a distal section with very fine (<5 µm), regular particles. Individual particles from the very fine, distal section were individually distinguishable only under 400× magnification.

M. speciosa did not colonize any substrate that lacked FBOM. Polychaetes that were deposited on the tile without FBOM generally responded by rolling on the tile for a short time, after which the worms either elevated their posterior ends away from the substrate, while moving them in a circular or back and forth direction, or immediately began to move away from the center of the tile. Those that moved away from the center of the tile often ended up off of the tile or underneath it. This basic set of behaviors was observed on other substrates as well, including gravel in preliminary trials that lacked FBOM. When deposited on a tile containing a thin layer of FBOM, worms rolled through it, coating their bodies. If too little FBOM was available, worms generally rolled into each other and formed a ball-shaped mass. If sufficient FBOM was present, worms built individual tubes. Worms added to pseudophora substrates without FBOM burrowed down into the substrate until they reached the tile, and then moved away from the center of the tile. Worms that were added to the sediment substrate immediately burrowed into the substrate, and often immediately made a tube. A portion of the worms also moved through the sediment leaving tracks of mucus before constructing a tube.

Extension of tentacles into the water column was not observed to be directly affected by flow at the low velocity. However, when worm tubes were subject to collision from inorganic or organic particles in the water, or buffeted sufficiently by the flow at the high velocity, worms retreated into their tubes. If collisions ceased, worms once again extended their tentacles into the water column after a lapse of several minutes. In trials on tiles, worms exhibited a variety of behaviors in response to increasing flows. These included retreat into their tubes, tube evacuation, and movement away from the center of the tile, and eventually underneath it. This movement was either in a direction perpendicular to the mean direction of flow or in the downstream direction. Worms were never observed moving upstream in response to flow. A small number (estimated at 10 to 20%) of worms that evacuated their tubes were also observed to move downstream on extruded strands of mucus, the length of which increased over time. The extrusion of mucus allowed some individuals to move in suspension to the end of the tile where they reaffixed themselves and then moved underneath it. In some cases, worms reaffixed themselves to the tile multiple times as they proceeded downstream. A few worms were lost to the current while hanging from mucus strands.

DISCUSSION

Our findings suggest that the high flows in this study influence *M. speciosa* distribution directly by restricting habitable substrates to those with greater stability and texture and by preventing attachment of the polychaete to substrates in extreme flow environments. However, the worm exhibits attachment abilities comparable to taxa found in higher gradient lotic reaches, and are therefore likely to tolerate a wide range of velocities, provided sufficiently stable substrates for attachment. This polychaete also exhibits behaviors in response to changes in flow including movement to areas of lower velocity which may minimize effects on individuals during times of higher flows. As polychaetes on highly mobile substrates are more likely to be displaced than polychaetes on stable substrates, predictions of *M. speciosa* response to altered flows must therefore consider the relative proportions of the population which occupy each type of habitat, which may differ among systems depending upon such potential factors as food availability, competition, predation, and patterns of dispersal.

Shear velocities faced by the benthic polychaetes under test velocities were comparable to other near-bed values reported in the literature. Our low flow trials produced shear velocities that were comparable to the higher shear velocities recorded by Schnauder et al. (2010), who tested tenacity of a collection of invertebrates from a regulated, lowland river with a sandy bed in an experimental flume. Specifically, *M. speciosa* that were dislodged at the lower flow had a similar tenacity to that of *Gomphus vulgatissimus* (Odonata: Gomphidae) and *Bithynia tentacula* (Neotaenioglossa: Bithyniidae), which are both typically found in slower waters with depositional substrates. *M. speciosa* that remained affixed in the higher flow trials had a comparable tenacity to the Tricladida and *Goera pilosa* (Trichoptera: Goeridae), and a greater tenacity than many snails and dragonflies collected from streams with relatively steep grades and course substrates (Statzner et al. 1988). These findings suggest that this polychaete species is able to tolerate some habitats in lotic waters, and is well-suited to tolerate managed flow conditions found in the Klamath River. A low body-length Reynolds number for *M. speciosa* individuals fell within the typical range of small, larval invertebrates (Statzner 1988) due to its tube morphology. This indicates drag forces acting on the polychaete dominate over lift forces, and may explain why polychaete tubes appear to be longer and more conspicuous only later in the season in the Klamath River, when flows are lower. Tube length may also be related to size of the polychaetes, with larger worms building larger tubes, however we observed that variation in tube sizes among individuals of different size classes was less pronounced than variation throughout the year. The tube shape of this polychaete may also be an adaptation to the worm's low mobility while in its tube and to the multidirectional, swirling flows in which it is often found. A cylindrical shape offers a consistent profile to flow regardless of direction within the transverse flow plane.

The proportion of polychaetes dislodged was a function of flows and substrate type. The greatest detachment occurred in the sediment at both flow levels while little detachment occurred in the pseudophora substrate at either flow level. This supports the hypothesis that stable substrates form the primary habitat of *M. speciosa* (Stocking and Bartholomew 2007, Malakauskas and Wilzbach 2012, Chapter 2). This is also consistent with findings of habitat preferences for suspension feeding lotic invertebrates in general (Richardson and Mackay 1991), which must live in flows sufficiently high to deliver food items, but which must avoid being detached from the substrate. Macrophytes and *Cladophora* housing polychaetes likely serve to buffer the worms against catastrophic flooding due to the reduced current velocities contained within (*sensu* Nikora et al. 1998). Macrophytes and *Cladophora* also trap fine benthic organic matter (FBOM) (Madsen et al. 2001) which worms feed on and use for construction of their tubes. Polychaete colonies themselves may also serve to alter local near-bed flows resulting in increased stabilization of substrates and deposition of sediments, including fine particulate organic matter (FPOM) (e.g., Daro and Polk 1973, Jumars and Nowell 1984, Frithsen and Doering 1986). Aggregates of closely-spaced tubes have been observed to lead to skimming flows (Friedrichs et al. 2000), a condition in which the maximum turbulent kinetic energy and shear stress occurs above the bed (Nowell and Church 1979). Taken together with the mucus-related sediment stabilization we observed, this may suggest that polychaete resistance to dislodgement may be higher in the river than our laboratory findings when polychaetes occur in higher numbers. This flow alteration also likely leads to increased deposition of sediments, bringing additional FPOM to the polychaetes.

Estimated probablility of dislodgement of polychaetes from the tile substrate was 25% and 73% under low and high velocities, respectively, and was intermediate to associated probabilities of detachment from the sediment and pseudophora substrates. Tiles probably most accurately tested actual tenacity of individual worms without the influence of the highly moveable sediments and flow buffering of the pseudophora. However, the tile substrate proved to be the most challenging when attempting to induce polychaete attachment and some worms were likely unable to fully attach before our trials. Aggregates of polychaetes exhibited greater surface area, and higher body-length Reynolds numbers, and therefore experienced greater drag and lift forces. When considering an unglazed tile as a representation of a rock substrate, it must also be considered that the tile has less roughness than many natural rocks on which *M. speciosa* is found, and therefore provides less surface area for mucus attachment. Surfaces of greater roughness have been shown to allow for greater invertebrate tenacity (Richardson and Mackay 1991, Lau and Martinez 2003). The lack of a biofilm on the tiles may have also been a factor since some invertebrates have enhanced attachment abilities in the presence of a biofilm (Zardus et al. 2008). In addition to potentially greater attachment abilities on natural rocks, *M. speciosa* were commonly observed to occur within rock crevices or interstices in the river. Flow over these depressions can be classified as skimming when individual roughness elements are of sufficient height and density (Morris 1955). We commonly observed polychaetes to be locally distributed around boulders in the river. Boulders experience significantly different hydraulic forces over the entirety of their surfaces based on boulder morphology, and orientation, and this effect has been shown to influence invertebrate community structure (Bouckaert and Davis 1998). Combined, these factors suggest the dislodgement we observed on this substrate may underestimate polychaete tenacity in a natural setting.

Polychaetes exhibited unexpected behavioral plasticity in response to increased flows as tube-dwelling polychaetes are typically considered to be sessile; invertebrates which have that have a greater ability to resist dislodgement often do so at the expense of mobility (Martinez 2001). In addition to retreating deeper into their tubes and burrowing into sediments in response to flow-mediated disturbance, *M. speciosa* exhibited more active flow-avoidance behaviors. Worms were observed to evacuate their tubes at higher flows while on the tile substrate, and relocated under the tile. The burrowing into sediments and retreat under the tiles suggests that these worms may actively seek out low flow microhabitats during periods of high flows in nature, similarly to other lotic invertebrates (e.g., Marmonier and Cruezé des Châtelliers 1991, Dole-Olivier et al. 1997, Lancaster 1999). However, it is unlikely that relocation would be frequent during the low flow season as females brood young in their tubes, and worms experience increased predation when outside of their tubes (Willson et al. 2010). Polychaetes were also able to cope with flows by trailing downstream on extruded strands of mucus. A number of lotic invertebrate larvae, including hydropsychid and polycentropid caddisflies, and simuliid blackflies, trail downstream on silk threads in a similar manner in order to enhance their settling abilities (Rader 1997).

Mortalities among recovered worms that had experienced high flows or had been dislodged from substrates were extremely limited, though half of the dislodged worms were not recovered, and their survivorship is unknown. This suggests the hypothesis that *M. speciosa* may not suffer significant mortalities as a direct result of dislodgement in a natural system. In a natural river, higher discharge events persist for much longer than the experimental flume flows, so it is possible that worms may experience higher mortality rates during catastrophic drift than were observed in our study. Survivors from flume trials passed through collimators and propellers suggesting that worms may be able to withstand harsh flow conditions, though these characteristics are not representative of a natural riverine environment. Further study is warranted before definitive statements about worm survivorship with respect to flows can be made. It is likely that potential flow-mediated mortalities would result from settlement in suboptimal habitats as has been observed in other polychaetes (Zamorano et al. 1995). Worms that were collected after being scoured from the sediment substrate were often found outside of their tubes making them more susceptible to predation. Willson et al. (2010) observed that predaceous Tubificidae and Macrostomida prey upon polychaetes when outside of their tubes. In the current study, we also observed protists apparently preying on injured polychaetes. *M. speciosa* in the Klamath River have not been found in anoxic substrates (Stocking and Bartholomew 2007) and it is likely that worms settling in these habitats would also experience greater mortalities. Conversely, it is also possible that flow-mediated dislodgement may offer a means of dispersal, as we observed several polycheate tubes stuck to scratches in the acrylic walls of our flume channel after high flow trials, although none of these tubes contained worms.

M. speciosa exhibits a substrate tenacity and behavioral plasticity that makes it well-adapted to life in lotic systems. Management strategies that seek to induce polychaete mortality directly through flow-mediated dislodgement will likely be unsuccessful, though it is not possible to predict likelihood of worm survival associated with resettlement without further study. Though worms in fine sediments may be relatively easy to displace, such strategies should also consider both the macro-habitat (geomorphic channel unit) and the microhabitat distribution of the worm, as many worms are found in sheltered areas, such as behind rock outcroppings or in rock crevices (Malakauskas and Wilzbach 2012, Chapter 2). Impacts to non-target species, which play important roles in stream ecosystem metabolism and in providing prey for juvenile salmon, should also be considered in the development of any management plans involving flow manipulation. The plausibility of reducing the salmonid parasites *C*. *shasta* and *P*. *minibicornis* though flow-mediated reduction of *M*. *speciosa* populations seems low based on the current study, but awaits further elucidation through additional study.

APPENDIX III

Table 3.1. Estimated probabilities (95% Confidence Intervals) of dislodgement of polychaetes for combinations of velocity and substrate analogues of *Cladophora* (“pseudophora”), bare rockface, and fine sediments. The trials took place at mean velocities of 55 cm/s and 140 cm/s for low and high velocity trials respectively.

	Substrate		
Velocity	*Cladophora*	Rockface	Fines
Low	0.002 (0.001, 0.015)	0.25 (0.14, 0.40)	0.86 (0.74, 0.93)
High	0.012 (0.002, 0.088)	0.73 (0.56, 0.85)	0.98 (0.94, 0.99)

Table 3.2. Hydraulic parameters (95% Confidence Intervals) and polychaete body measurements exposed to experimental conditions of velocity and substrate type. U_* is shear velocity, $U_{\perp,d}$ is the effective drift velocity, $U_{z=5}$ is the velocity at a reference height of 5 mm above the bed, l is the average length of a polychaete tube, h is the height of a polychaete tube above the bed, and Re_l is the body-length Reynolds number.

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

[a] Lengths over 0.5 mm represent aggregates of clumped individuals

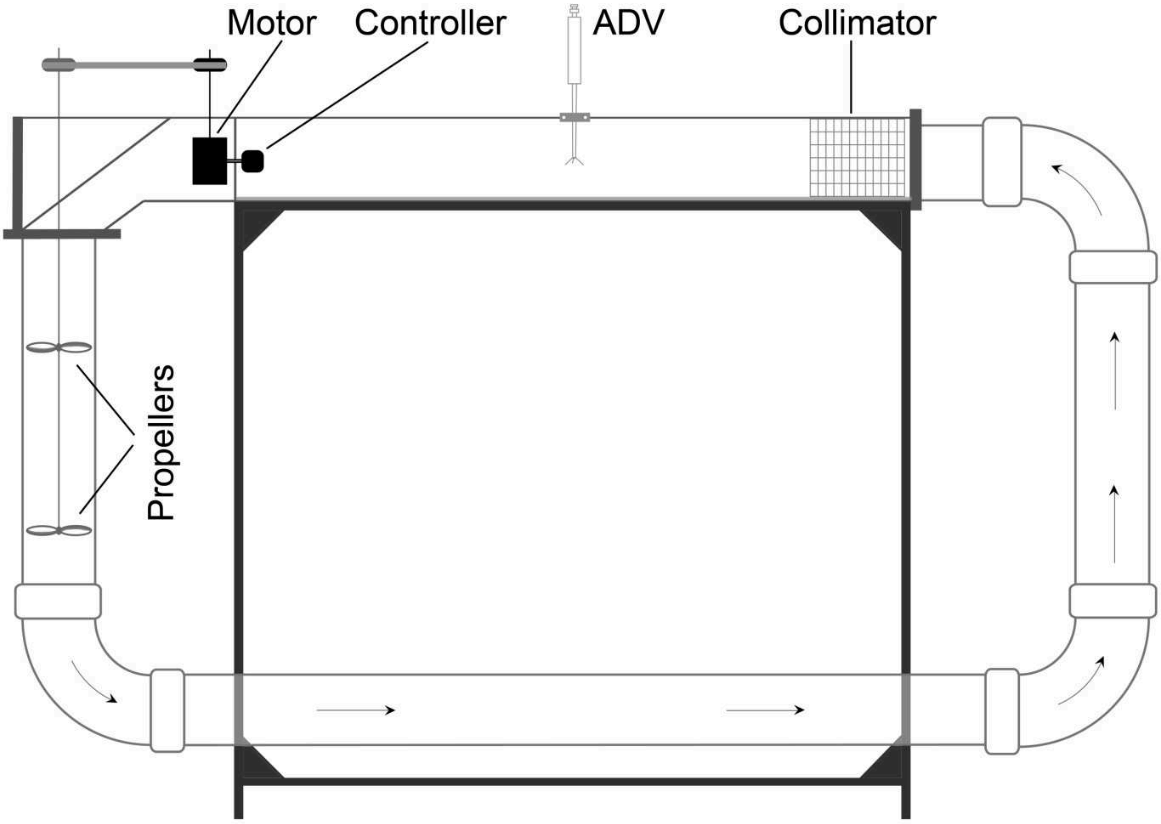

Figure 3.1. Experimental flume setup. The flume measured 2.6 m in length, 1.35 m in height and 0.44 m in width. The water was moved with two propellers on a shaft, powered by a 2 HP AC induction motor. Velocity readings were taken using an acoustic Doppler velocimeter (ADV) in the center of the flume channel, and directly over the polychaetes.

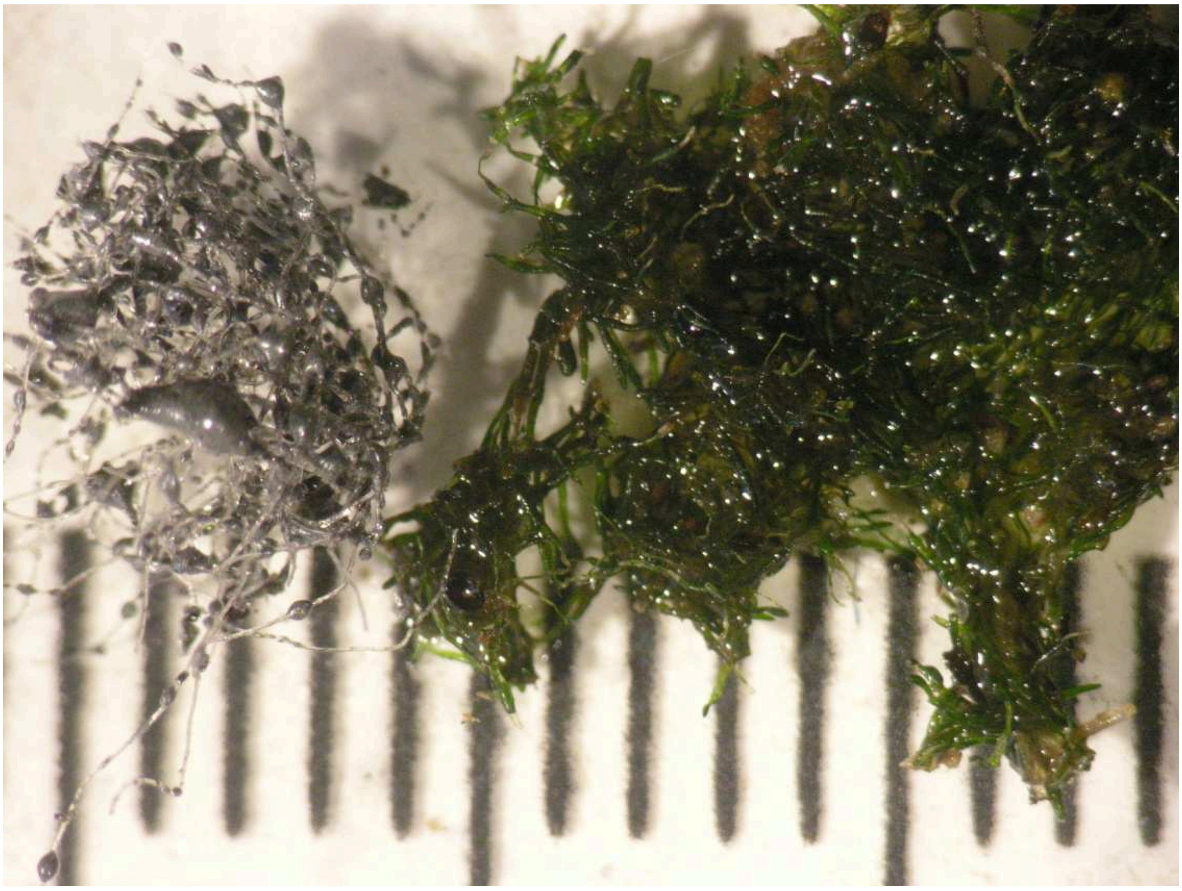

Figure 3.2. Comparison of *Cladophora* and an experimental analogue. A “pseudophora” analogue (left) was used as a substitute for actual *Cladophora* (right) as a substrate in a flume for *Manayunkia speciosa*. Vertical lines at bottom are 1 mm apart.

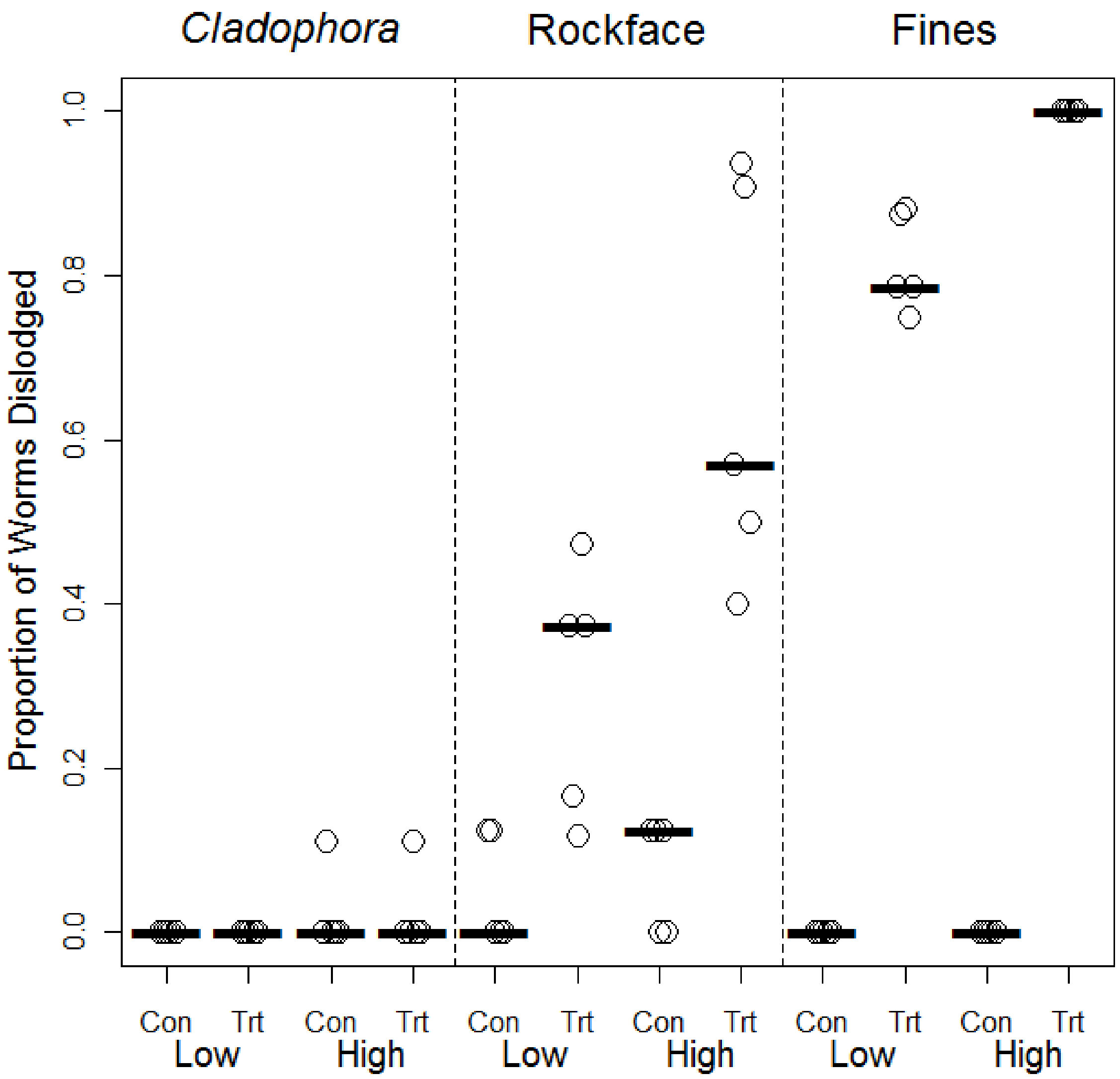

Figure 3.3. Observed proportions of dislodgement among the 5 trials at each combination of control, velocity, and substrate. Trials occurred at mean velocities of 55 cm/s and 140 cm/s for low and high trials respectively. Paired controls accompanied all treatment trials. Substrates were analogues of *Cladophora*, rockface, and fine sediments. Observed proportions are jittered to allow visualization of overlapping points. Bars represent median values.

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CHAPTER 4

MACROHABITAT TYPES DO NOT PREDICT NEAR-BED FLOWS EXPERIENCED BY THE FRESHWATER POLYCHAETE *MANAYUNKIA SPECIOSA*

INTRODUCTION

Benthic invertebrates in aquatic systems must often contend with dynamic environments resulting from complex interactions between substrates and flow, however many ecological studies report only general habitat classifications based on macrohabitat types, such as runs, pools, or riffles (Arend 1999), which largely fail to consider substrate-flow interactions. Underlying the use of this classification scheme are the assumptions that variability in the benthic assemblages of interest will be lower within a macrohabitat type than in the river at large, and that flow and other physical factors to which macroinvertebrates are known to be differentially responsive will be comparable among habitats with the same classification (Jowett 1993). One limitation of macrohabitat-based sampling is the subjective manner in which habitat units are classified. A standardized methodology for classifying macrohabitats has not yet been widely accepted (Arend 1999), and observer bias as well as inconsistent protocols may compromise repeatability, precision, and transferability of the classification among studies or streams (Roper and Scarnecchia 1995, Poole et al. 1997). Distinction among habitat units may be particularly difficult in large streams where transitions tend to be more gradual (Arend 1999). However, understanding flows at a scale that is relevant to aquatic organisms is crucial for predicting their abundance, distribution, and response to disturbance. Moreover, using a subjective habitat classification method makes comparison between studies and systems difficult.

In order to reduce the subjective nature of macrohabitat classifications, some authors have attempted to describe run, riffle, and pool macrohabitats using such hydraulic parameters as Froude number (Wolman 1955), ratios of velocity to depth (Allen 1951, Jowett 1993), and water surface slope (Yang 1971). However, these parameters, by themselves, are still unable to describe the near-bed flows (Davis and Barmuta 1989, Jowett 1993) which are directly experienced by benthic organisms. For example, Horne et al. (1992) found that congeneric black fly species occupied different flow velocities even within the same macrohabitat type. Hart et al. (1996) found that the spatial distribution of suspension-feeding larval blackflies was better predicted by velocities measured at 2mm above the streambed than at 10 mm, and that current speed at 10 mm above the bed poorly predicted current speed at 2 mm.

In order to obtain ecologically useful flow classifications, Davis and Barmuta (1989) proposed the use of standard hydraulic parameters combined with the reporting of the four near-bed flow types: isolated roughness flow, wake interference flow, skimming flow (Morris 1955), and chaotic flow (Smith 1975). All of these flow types occur over rough substrates, and are defined based on the longitudinal spacing between substrate roughness elements, and the wakes that develop behind these roughness elements. Isolated roughness flow occurs when there is sufficient space between roughness elements for developed wakes to fully dissipate before interacting with a downstream roughness element; wake interference flow occurs when the distance between roughness elements is approximately equal to the length of the wake; skimming flow is present when roughness elements are spaced closely together, so that the bulk flow moves over the substrate with semi-stable eddies remaining between roughness elements (Morris 1955). The final flow type, chaotic flow, occurs when the substrate roughness height is similar to the water depth, and is characterized by complex, three-dimensional flows (Smith 1975, Nowell and Jumars 1984).

Some lotic invertebrate taxa have been associated with hydraulic parameters such as roughness height, Froude number, Reynolds number, stream slope, and shear stress (e.g., Statzner et al. 1988, Growns and Davis 1994, Rempel et al. 2000). Additionally, Quinn et al. (1996) found that the presence of upstream roughness elements decreased general invertebrate abundance and diversity, with filter feeders most strongly affected. It was also shown that small-scale differences in velocity, depth and substrate roughness influence distribution of invertebrates within riffles (Brooks et al. 2005). Jaag and Ambuhl (1964) predicted that the stable eddies within skimming flows may provide shelter for lotic invertebrates within high-velocity environments, which may help to explain patchy distributions of invertebrates in some macrohabitats. Despite these observations, to our knowledge, no one has investigated the relationship between near-bed and macrohabitat classifications, though it has been predicted that pool habitats most commonly contain skimming near-bed flows (Young 1993).

We sampled multiple macrohabitat types to determine if they show a positive correlation with near-bed flows. The sites are part of an ongoing habitat study for *Manayukia speciosa*, an important intermediate host for two parasites of Pacific salmon (Bartholomew et al. 1997; 2006) in the Pacific Northwest (Foott et al. 1999; 2004, Bradford 2010). Previous studies have attempted to relate *M. speciosa* distribution to macrohabitat types (Stocking and Bartholomew 2007) with limited success. *M. speciosa* was used as a model organism as its size gives a point of reference for micro-scale flows experienced by many freshwater invertebrates.

MATERIALS AND METHODS

Study Area

The Klamath River runs approximately 425 km from its origins in southern Oregon to its mouth at the Pacific Ocean in northern California. The river drains an area of approximately 47,000 km^2 which produces approximately 18% of all of the discharge in California (Benke and Cushing 2005), with the annual mean discharge near the mouth from 1963 to 2004 being 495 m^{3}s^{-1} (Webster et al. 2004). The river is divided into upper and lower basins (NMFS 2007) by Iron Gate Dam (river km 306). There is relatively constant gradient of 0.25% through most of the lower basin. The river exhibits a geomorphically stable channel and vegetative community which is dominated by submersed aquatic macrophytes, including abundant populations of the filamentous green alga, *Cladophora*, from Iron Gate Dam down to the Scott River confluence (rkm 230). Water releases from the dam, which are often used for power generation, are typically cooler than equilibrium temperature by 2 to 4°C in spring and early summer, and temperature effects diminish with distance downstream. Effects on temperature in the fall and winter are comparably moderate. The highest temperatures below the dam are found between the Scott and Shasta Rivers (Basdekas and Deas 2007) which is also the area of highest infectivity for *Ceratomyxa shasta* and *Parvicapsula minibicornis* (Stocking and Bartholomew 2007). This warm region is found within an area of high nutrient concentration (Asarian et al. 2010) and macroinverterbrate diversity (Malakauskas and Wilzbach 2012, Chapter 2) within the lower river.

Sample sites

Sample sites (Figure 4.1, Table 4.1) were chosen to complement ongoing studies by collaborators. The sites were all located in the stretch of river between the Scott and Shasta rivers. Nine sampling sites were chosen within this area based on known polychaete distributions and sentinel fish study records: 1) Tree of Heaven campground, 2) the Klamath Community Center, and 3) the Klamath River near Beaver Creek. Each reach contained three sampling sites which were initially chosen so that each reach contained a sampling site which included a pool, eddy, and run (Stocking and Bartholomew (2007), following criteria in Arend (1999). The pool at the Klamath Community Center, however, was washed out during the 2010 winter, so no pool measurements were taken.

Near-bed flow measurements

Mean flow descriptors, near-bed flow descriptors, and near-bed flow classification were determined using a number of field measurements, including the mean velocity (U), water depth (D), and substrate characteristics. Near-bed flows result from an interaction between water flow and the substrate, including the size and arrangement of the substrate elements. Accordingly, roughness height (k), distance between roughness elements (λ), and the length of the space between roughness elements (j) were also estimated.

A bed profiler was fabricated in-house at Humboldt State University for use in field measurements following the design of Young (1993). The profiler consisted of a 1 m length of square aluminum tubing, with 1 m length (5 mm thickness) welding rods inserted through holes drilled every 25 mm. Tygon (Saint-Gobain Corp., Valley Forge, PA) tubing was used to make sleeves for each welding rod, and served to hold the tubes in place for accurate measurements. Field measurements were taken by placing the profiler over the substrate, parallel to the mean flow direction, and adjusting individual rods to rest on the bed. Profiles were then recorded on poster board, using indelible markers and later measured. A minimum of three profiles were taken at each sampling site and were spaced approximately 20 cm apart (Young 1993). Ten random depth measurements were taken at each sample site and averaged to determine mean depth. Bankfull depth was also estimated using evidence such as the presence of silt or organics deposited by floods, changes in bed and bank materials, and vegetation patterns (Gordon et al. 1992). Velocities were measured at low flows using an electromagnetic flow meter (Flo-Mate 2000, Hach, Loveland, CO). Measurements were taken at 0.6 depth from the surface, at ten random locations at each sample site. Twenty-five rocks were chosen randomly and measurements of the diameters of rocks along the x-axis were taken, with the x-axis being parallel to the mean direction of flow. The median of the lengths along the x-axis of the individual rocks was then used to calculate a d_{50} (Young 1992).

Flow description

Mean flow was described using Reynolds (Re) and Froude (Fr) numbers. The Reynolds number is a ratio of inertial to viscous forces (Reynolds 1883). Reynolds numbers below 500 are laminar and over 2000 are turbulent. Intermediate values represent transitional flow. The Reynolds number was calculated as:

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

where U is the mean velocity, D is the mean depth, and ν is the kinematic viscosity of water, which varies with water temperature.

The Froude number is a ratio of inertial to gravitational forces (Belanger 1828). Froude numbers less than one are subcritical or tranquil flow, a number of one is critical, and numbers over one are supercritical, which are characterized by broken, white water (Davis and Barmuta 1989). The Froude number was calculated as:

$$Fr = \frac{U}{\sqrt{gD}}$$

where g is the acceleration due to gravity (9.8 m/s^2), U is the mean velocity, and D is the mean depth.

Flow microenvironment parameters included shear velocity (friction velocity) and Reynolds roughness. Shear velocity (U_*) is a measure of shear stress acting on the bed (Davis 1986) expressed in units of velocity. Shear velocity can be estimated in a river using the following equation:

$$U_* = \frac{U}{5.75 \log\left(12\frac{D}{k}\right)}$$

where U is the mean velocity, D is the mean depth, and k is the roughness height (Smith 1975).

Reynolds roughness (Re_*) can be used to describe if flow is hydraulically rough or smooth. Numbers <5 are hydraulically smooth, numbers >70 are hydraulically rough, and intermediate numbers are transitional (Schlichting 1960). As Reynolds roughness increases in value, the flow at upstream and downstream sides of roughness elements increases in asymmetry (Nowell and Jumars 1984). For example, organisms at the upstream side of a rock experience greater relative velocities than organisms at the downstream side (Davis and Barmuta 1989). Therefore, locations with greater Reynolds roughness numbers will experience more complex microflows (Bouckaert and Davis 1998). Reynolds roughness is calculated:

$$Re_* = \frac{U_* k}{\nu}$$

where U_* is shear velocity, k is the roughness height, and ν is the kinematic viscosity of water.

Roughness height (k) was calculated as two times the standard deviation of all individual roughness elements in a profile (Young 1993, McCormick 1994). Average streamwise spacing of roughness elements (λ) was found by measuring the distance between crests of consecutive roughness elements and streamwise groove width (j) was found by subtracting the d_{50} from the streamwise spacing of roughness elements. The critical roughness element spacing (j_{crit}) was used to differentiate between wake interference flow and isolated roughness flow, and was found using the following equation (Young 1992):

$$j_{crit} = \left[2.46k\left(\frac{D-k}{k}\right)^{0.42}\right] - d_{50}$$

where D is depth and k is the roughness height.

Near-bed flow classification followed the methods Young (1992), and was obtained using the variables of depth (D), spacing of roughness elements (λ), groove width (j), critical roughness element spacing (j_{crit}), and roughness height (k). Flows were designated as chaotic if D was less than $3k$, which excluded other flow types. For flows where j was greater thanj_{crit}, flow was isolated roughness flow. If j was not greater thanj_{crit}, then flow was wake interference flow or skimming flow. Flow in which k was greater than j was wake interference flow, and skimming flow was present when j was greater than k.

Statistical analyses

A principal components analysis (PCA) ordination was performed to determine the relationship between macrohabitat type and a subset of hydraulic variables, as PCA is typically effective in analyzing environmental factors (Clarke 1993). As there were more variables than sites, five variables were chosen a priori. The Reynolds number and Froude number were chosen as they are mean flow descriptors, and depth, d50, and shear velocity were chosen as they are commonly measured hydraulic variables. Variables were square root or fourth root transformed to meet assumptions of normality. The analysis was carried out using a correlation matrix as variables were measured on a different scale. PCA was performed in PAST 2.16 (Hammer et al. 2001). A MANOVA was performed on the five variables using run and eddy-pool as grouping variables, and subsequent ANOVAs were used to determine significance of individual variables. These analyses were performed using NCSS (Hintze 2004).

RESULTS

Flow conditions

Reynolds and Froude numbers for all sample sites indicated mean flows in all macrohabitat types were turbulent and subcritical, with highest Froude numbers being observed in the runs (Table 4.2). Reynolds roughness numbers indicated flows were hydraulically rough, a condition in which flow microhabitats exhibit heterogeneity and one in which sediment entrainment is more likely. These high Reynolds roughness numbers also indicated that the boundary layer was fully turbulent. Shear velocities were highest in runs and lower in pools and eddies (Table 4.2). Polychaete habitats exhibited three of the four near-bed flow types: wake interference, skimming, and chaotic flow, with only isolated roughness flow being absent (Table 4.3). All sites exhibited the same flow at low and bankfull conditions except for the eddy at Tree of Heaven, which was dominated by chaotic flows at low summer depths and skimming flows at bankfull depths.

Statistical analyses

The first two principal components accounted for 93% of the total variance between sample sites. The first principle component accounted for 76% of the variance (Eigenvalue=3.8) and the second component accounted for 17% of the variance (Eigenvalue=0.89). Generally, run habitats were grouped separately from pool and eddy habitats and pools and eddies grouped together (Figure 4.3). Reynolds number, Froude number and shear velocity were strongly associated with component 1, while depth was the variables that showed the greatest inverse association. Substrate diameter and depth were most strongly associated with component 2, while Froude number and shear velocity showed weak inverse associations (Table 4.54). The PCA biplot suggested that runs contained greater shear velocities and Froude numbers than eddy-pools, but were less deep. The MANOVA indicated a significant difference between eddy-pools and runs with respect to the five hydraulic variables (Wilks' lambda= 0.004, $F_{5,2}$=110, P=0.009). Subsequent univariate analyses showed that depth ($F_{1,6}$=16, P=0.007), shear velocity ($F_{1,6}$=8, P=0.030), and Froude number ($F_{1,6}$=11, P=0.016) were significantly different in the sites tested. A Fisher's Exact Test comparing near-bed flow types with macrohabitat types showed no evidence that that near-bed flow type was dependent on macrohabitat (P=1).

DISCUSSION

While use of a classification which distinguishes among channel geomorphic units is relevant for organisms that occupy the water column, it is less useful in understanding the flow microenvironment experienced by benthic organisms (Davis and Barmuta 1989), especially organisms of reduced size such as *Manayunkia speciosa*. Our results indicated that Froude number, shear velocity, and depth, were different in eddy-pools than in runs. Conversely, near-bed flow classifications, which better explain conditions experienced by benthic invertebrates, like *M. speciosa*, did not show an association with the macrohabitat classification scheme. Further, use of the macrohabitat classification scheme only allows for qualitative descriptions of such potentially important habitat parameters such as bed shear stress, while use of parameters affecting near-bed flows allows for quantitative estimates. Taken together, this suggests that invertebrate studies using macrohabitat classifications fail to consider near-bed flows, and may offer, in part, an explanation as to why some organisms, such as *M. speciosa*, exhibit an irregular distribution within similar macrohabitats.

The Froude number showed the greatest ability to differentiate between the run, pool, and eddy ecological habitat types when pools and eddies were considered as a single category. This suggests that pools and eddies are hydraulically similar, and may not warrant separate classification when used in the Klamath River (Stocking and Bartholomew 2007). Jowett (1993) found that the Froude number and the ratio of velocity to depth were the parameters that were most closely associated with ecological habitat classifications, which generally agreed with our findings. However, we did not evaluate the velocity to depth ratio separately as it is inherent in the Froude number. While, Jowett (1993) found that Froude numbers below 0.18 could often accurately classify a habitat as a pool, all of our sample sites, including runs, yielded Froude numbers of <0.05. This suggests that classifications using hydraulic parameters may be system specific, or may be related to stream order. Suspension feeding invertebrates have been reported to be most common in locations with Froude numbers near one (Statzner et al. 1988, Wetmore et al. 1990), which would indicate suspension feeders prefer swifter waters (Quinn and Hickey 1994) that transport abundant food particles. Further, Quinn et al. (1996) found a significant decrease in suspension feeder abundance in the slower water downstream of roughness elements. The fact that *M. speciosa* is found in areas with low Froude numbers and areas with large roughness elements (e.g., eddy at Tree of Heaven Campground) supports an hypothesis that food may not be limiting in sections of the lower Klamath River where polychaetes are most dense (Malakauskas and Wilzbach 2012, Chapter 2). As low Froude numbers can indicate depositional areas, the persistence of *M. speciosa* in pools and other slow-water habitats may also be reflective of their ability to facultatively feed from the substrate. This ability has been observed in multiple species of Sabellidae (Fauchald and Jumars 1979) and may also be the case for *M. speciosa*. Stocking and Bartholomew (2007) reported that *M. speciosa* may leave their tubes to graze on the substrate, but in many hours of observation during laboratory culture (Willson et al. 2011, Malakauskas and Wilzbach 2012, Chapter 2) we have only observed case-abandonment in response to physical disturbance.

Shear velocity has been shown to shape benthic communities (Statzner et al. 1988, Jowett et al. 1991), and we found greater shear velocities in runs versus eddy-pools. For example, riffles have been shown to harbor lower densities of invertebrates than transitional areas and pools, due to the increased shear stresses present in these habitats (Blettler et al. 2010), and areas of lower shear stress within riffles exhibit greater invertebrate diversity and density (Brooks et al. 2005). *M. speciosa* has also been shown to be constrained by shear stress within an experimental flume (Malakauskas and Wilzbach 2012, Chapter 2). Increased shear stress also has non-direct effects on invertebrates, such as increased scour of sediments. As *M. speciosa* requires fine particulate organic matter (FPOM) to construct its tube (Leidy 1883), habitats with shear stresses high enough to remove FPOM and minimize deposition of fine sediments likely prove inaccessible to the polychaete. Mean shear stress in a given habitat, however, may be too general to be able to predict polychaete abundance as we found that even at low, summer flows, some habitats already exceed the dislodgement threshold found for *M. speciosa* in laboratory flume experiments. For example, we estimated mean shear velocity in the run at the Klamath Community Center, where *M. speciosa* is present, to be over 9 cm/s, while shear velocities of 4 cm/s were shown to dislodge 70% of polychaetes from a rock substrate (Malakauskas and Wilzbach 2012, Chapter 2). Therefore, while mean shear stress may predict relative habitat suitability, mean shear stress cannot predict absolute presence or absence of *M. speciosa* and small scale substrate characteristics must also be considered. Colonization of substrates by periphyton and invertebrates has been shown be more successful when colonizing surfaces with rough rather than smooth textures (Quinn et al. 1996). This is likely due to the reduced shear stresses within the grooves that these rough surfaces provide as well as the greater attachment abilities they afford (Lau and Martinez 2003).

Persistence of *M. speciosa* in high shear sites suggests the importance of microflow habitats. Roughness Reynolds numbers for all sample sites were above 70, which indicated a heterogeneous flow habitat, and indicated asymmetric flow around individual roughness elements (Nowell and Jumars 1984). Asymmetric flow can shape invertebrate communities, with many taxa showing a preference for wakes (Bouckaert and Davis 1998). Brooks et al. (2005) found that Reynolds roughness numbers explained more spatial, taxonomic and density variation among invertebrate assemblages in riffles than other hydraulic variables, and that microhabitats were therefore important in determining the character of invertebrate assemblages. Additionally, the microdistributions of larval midges and blackflies have been linked with substrate heterogeneity and velocity (Ruse 1994, Hart 1996). Moreover, isolated upstream roughness (resulting in isolated roughness flow) elements have been shown to decrease invertebrate abundance, including filter feeders (Quinn et al. 1996). It is therefore likely that *M. speciosa* exhibits greatest densities where microflows are most suitable, and it is also likely that these favored conditions are highly localized, which may describe the observed patchiness of its distribution (*sensu* Jowett 2003, Stocking and Bartholomew 2007). While it is possible that even near-bed flows of the type measured in the present study may be too coarse to adequately describe highly localized polychaete populations, the use of near-bed flow classifications still warrant further research, as they may potentially offer a more fine-scale resolution of habitat than is currently known.

Parameters in near-bed classification did not show associations with ecological macrohabitat classifications. Three of the four near-bed flow types were found in our sample sites with both skimming and wake interference flows being most common, and these two flow types were found in both runs and pools. Therefore, use of the ecological classification scheme was shown to be unable to describe near-bed flows which are likely more relevant for benthic invertebrate distributions (Young et al. 2002), which may explain why previous attempts to predict *M. speciosa* abundance and distribution using an ecological classification have been unsuccessful (Stocking and Bartholomew 2007). Skimming flows offer shelter from mean flows while providing moving water that circulates food (Jaag and Ambuhl 1964), and may therefore provide optimal habitat for polychaetes.

APPENDIX IV

Table 4.1. GPS coordinates for sample sites representing ecological habitats in which *Manayunkia speciosa* are found.

Site	Habitat	Coordinates
Community Center	Eddy	41° 50’ 24.58” N, 122° 50’ 14.77” W
Community Center	Run	41° 50’ 23.55” N, 122° 50’ 13.10” W
Near Beaver Creek	Pool	41° 52’ 03.09” N, 122° 48’ 40.89” W
Near Beaver Creek	Eddy	41° 52’ 04.22” N, 122° 48’ 27.71” W
Near Beaver Creek	Run	41° 52’ 01.95” N, 122° 48’ 34.93” W
Tree of Heaven	Pool	41° 49’ 34.83” N, 122° 39’ 37.75” W
Tree of Heaven	Eddy	41° 49’ 35.59” N, 122° 39’ 39.21” W
Tree of Heaven	Run	41° 49’ 37.59” N, 122° 39’ 38.85” W

Table 4.2. Reynolds (Re), Froude (Fr) numbers, and mean velocities (U) as well as shear velocity (U_*) and Reynolds roughness (Re_*) of near-bed flows in eddy, run, and pool habitats in three reaches of the lower Klamath River during low, summer flows of 2011.

Reach	Macrohabitat	Re ($\times 10^3$)	Fr ($\times 10^{-4}$)	U (cm/s)	U_* (cm/s)	Re_*
Community Center	Eddy	156	20.8	8.70	0.547	200
Community Center	Run	602	481	111	9.61	6170
Near Beaver Creek	Pool	288	52.1	19.7	1.43	1030
Near Beaver Creek	Eddy	278	62.5	22.0	1.36	2930
Near Beaver Creek	Run	251	107	30.4	2.11	656
Tree of Heaven	Pool	142	16.7	7.30	0.440	134
Tree of Heaven	Eddy	112	36.3	11.3	1.35	5670
Tree of Heaven	Run	173	124	29.7	3.17	5190

Table 4.3. Near-bed flow type and parameters (measured in meters) used in their determination for baseline summer and bankfull flows in eddies, runs, and pools in three reaches of the lower Klamath River. Measurements include mean height of roughness elements (k), streamwise spacing of roughness elements (j), streamwise groove width between roughness elements, critical groove width, and mean depth (D). Flow types represent wake interference flow (WIF), skimming flow (SKF) and chaotic flow (CTF).

									Bankfull		
Reach	Habitat	k	λ	j	j_{crit}	k/D	k/j	Type	j_{crit}	k/D	Type
CC	Eddy	0.037	0.093	0.071	0.435	0.020	0.517	WIF	0.536	0.013	WIF
CC	Run	0.064	0.109	0.040	0.298	0.118	1.62	SKF	0.531	0.040	SKF
NB	Pool	0.072	0.116	0.049	0.545	0.049	1.47	SKF	0.711	0.028	SKF
NB	Eddy	0.216	0.250	0.128	0.910	0.171	1.69	SKF	1.26	0.093	SKF
NB	Run	0.031	0.118	0.100	0.281	0.038	0.311	WIF	0.409	0.016	WIF
TH	Pool	0.030	0.167	0.117	0.377	0.016	0.261	WIF	0.464	0.010	WIF
TH	Eddy	0.419	0.724	0.124	0.574	0.423	3.38	CTF	1.23	0.204	SKF
TH	Run	0.164	0.138	0.055	0.514	0.281	2.97	SKF	0.934	0.099	SKF

Table 4.4. Principle component variable loadings.

Variables	Component 1	Component 2
Froude Number (Fr)	0.5072	-0.1466
Shear Velocity (U_*)	0.4976	-0.1928
Reynolds Number (Re)	0.4564	0.3299
Depth (D)	-0.4156	0.5464
Substrate Diameter (d_{50})	0.3378	0.7307

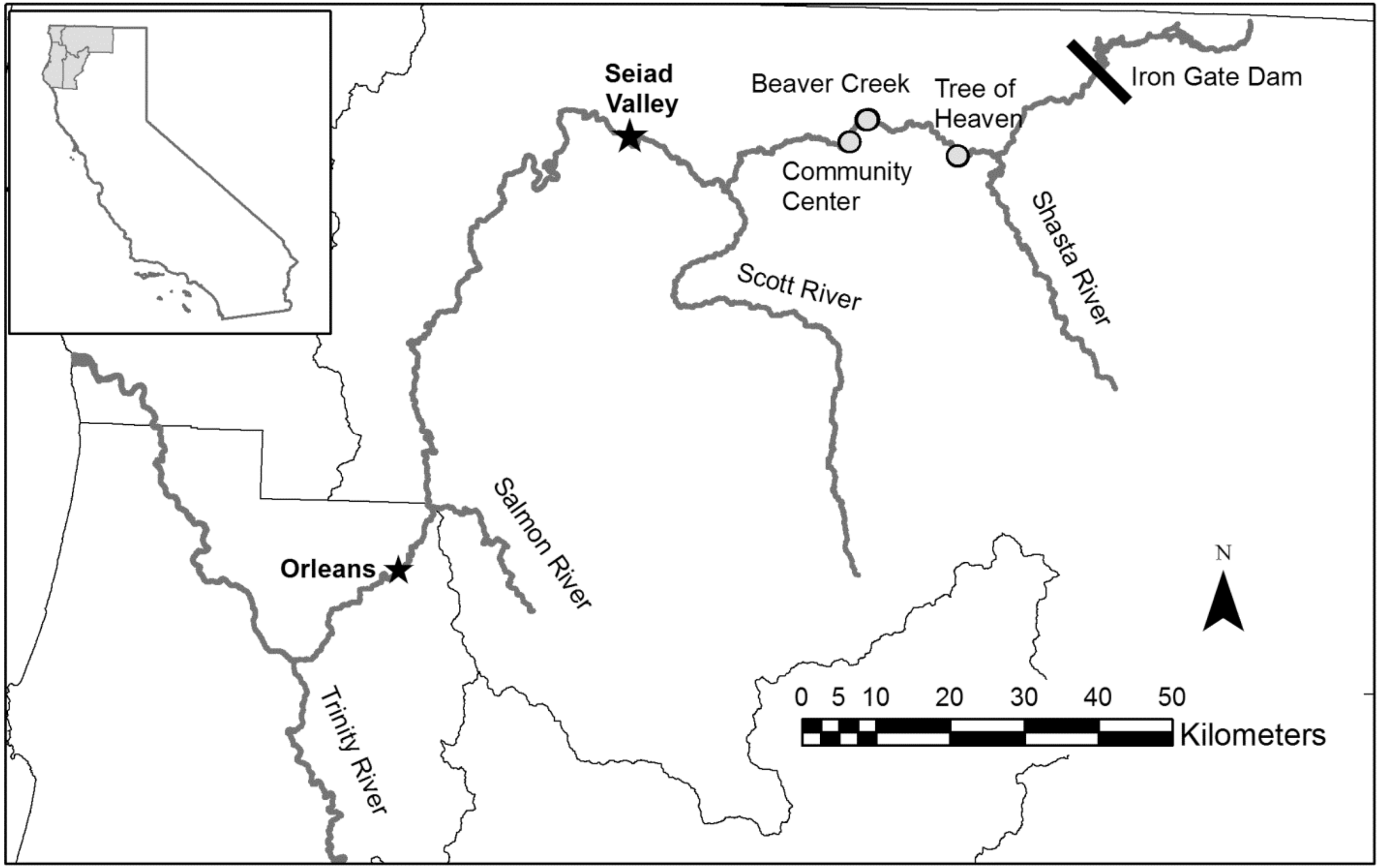

Figure 4.1. Sampling locations. Hydraulic parameters, including those needed to predict near-bed flows, were measured at eight sites spread out over three sampling locations to classify *Manayunkia speciosa* habitat type.

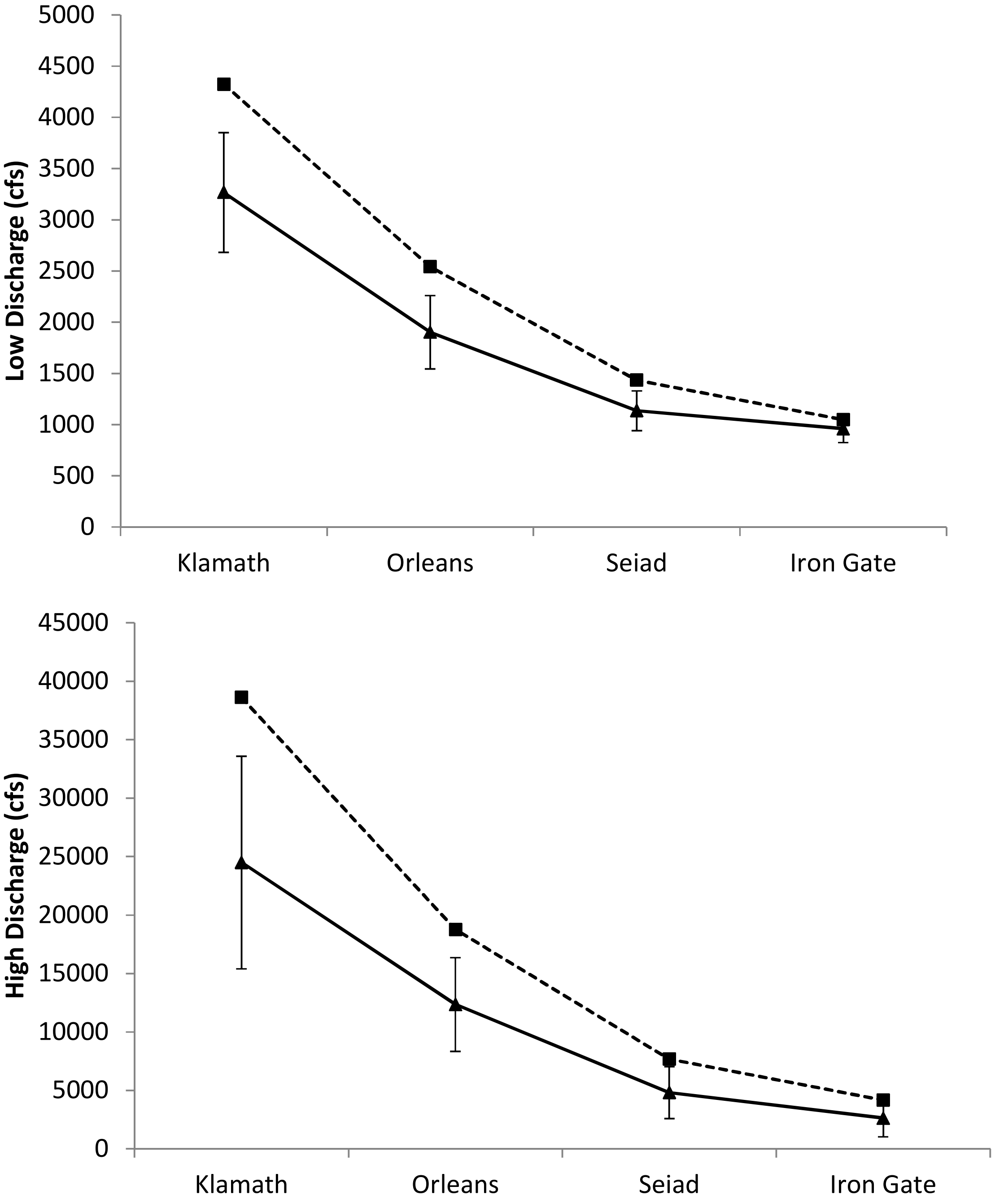

Figure 4.2. Mean discharges in the Klamath River during typical low (August) and high flow (April) months. Dotted lines represent discharges for the 2011 calendar year, and solid lines indicate mean discharges for the decade ending in 2011. Error bars represent one standard deviation.

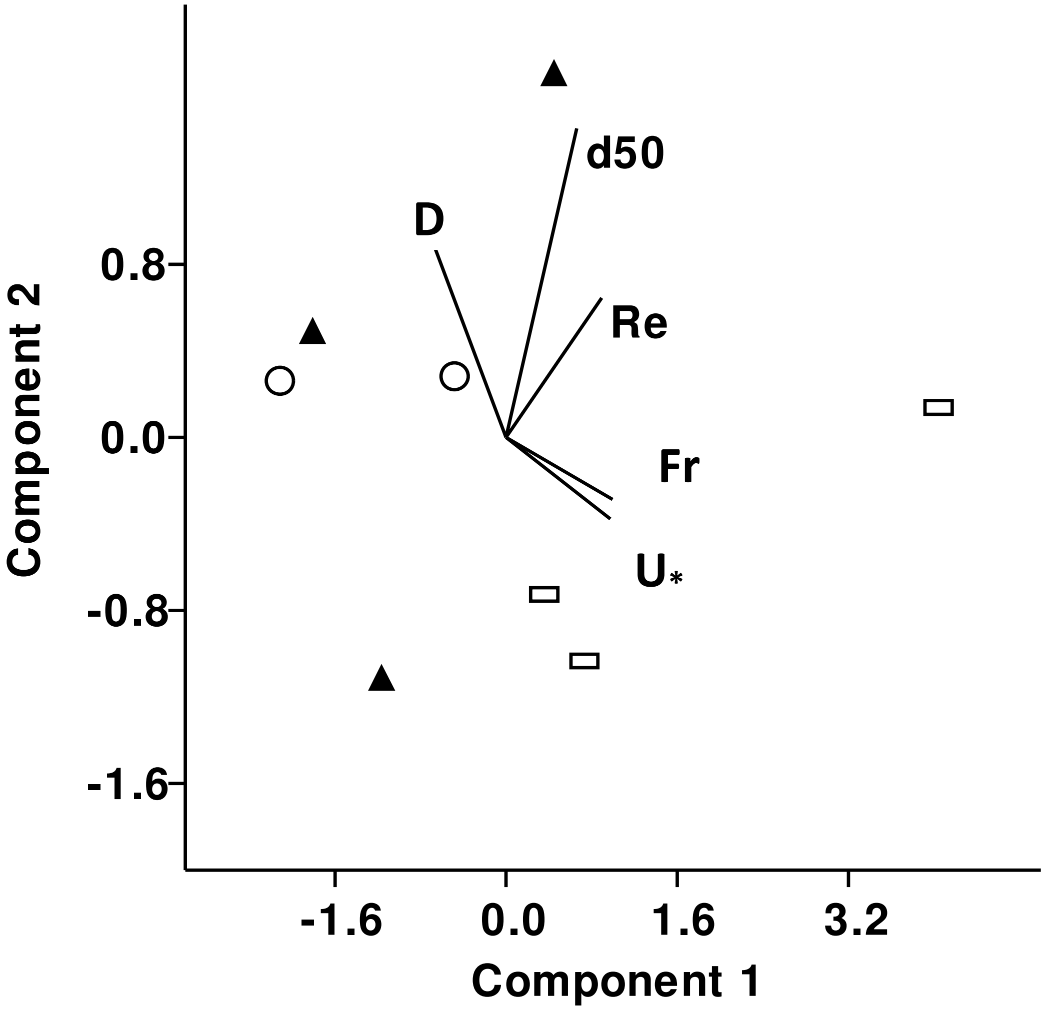

Figure 4.3. Principle components analysis (PCA) ordination biplot for physical variables recorded in eight study sites, including convex hulls. The variables were Reynolds number (Re), Froude number (Fr), depth (D), substrate diameter (d_{50}), and shear velocity (U_*). The biplot axes show the direct relationships between sites and parameters.

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