

Invertebrate assemblages in the lower Klamath River, with reference to *Manayunkia speciosa*

DAVID M. MALAKAUSKAS AND MARGARET A. WILZBACH*

Department of Entomology, Michigan State University, East Lansing, MI 48824 USA (DMM)

U. S. Geological Survey, California Cooperative Fish Research Unit, Humboldt State University, Arcata, CA 95521 USA (MAW)

*Correspondent: wilzbach@humboldt.edu

The freshwater polychaete, *Manayunkia speciosa* Leidy (Canalipalpata: Sabellidae), is the intermediate host for two myxozoan pathogens (*Ceratomyxa shasta* and *Parvicapsula minibicornis*) that cause substantial mortalities of juvenile salmon in the Pacific Northwest, particularly in the Klamath River below Iron Gate Dam in California. Information on the distribution of *M. speciosa* in the Klamath River may facilitate targeted control of polychaete populations to disrupt the parasites that affect fish populations. We sampled invertebrate assemblages in the lower Klamath River in the summer and fall of 2005 and 2006 to estimate distribution patterns of *M. speciosa* and to characterize assemblage structure of invertebrates in reaches where the polychaete was both collected and not collected. The polychaete was most often found in a reach of river extending 100 km downstream from the Shasta River (river km 185–287). The reach in which it was found supported high taxonomic richness of invertebrates and a high abundance of filtering collectors including marine relicts such as sponges, unionid mussels, and bryozoans. We suggest that the large, stable substrate on which these were found represents primary, optimal habitat for the polychaete, also a marine relict. Reaches above and below the zone where we collected polychaetes showed a general trend of reduced taxonomic richness as distance away from the polychaete zone increased, and also showed differing relative abundances of non-insect taxa and functional feeding groups. Differences in invertebrate assemblages between years were coincident with large differences in water flows. We suggest flows and food resources may play important roles in invertebrate distribution patterns.

Key words: *Ceratomyxa shasta*, filtering collector, FPOM, functional feeding groups, Iron Gate Dam, Klamath River, *Manayunkia speciosa*, marine relict, polychaete, salmon disease

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 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 structure 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 km² 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 (*O. tshawytscha*), coho salmon (*O. kisutch*), steelhead (*O. mykiss*), and cutthroat trout (*O. clarkii*).

Collections.—Twenty-two sites were sampled for benthic assemblages throughout the Klamath River between Iron Gate Dam to below Klamath Glen (Figure 1; Appendix II). 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.

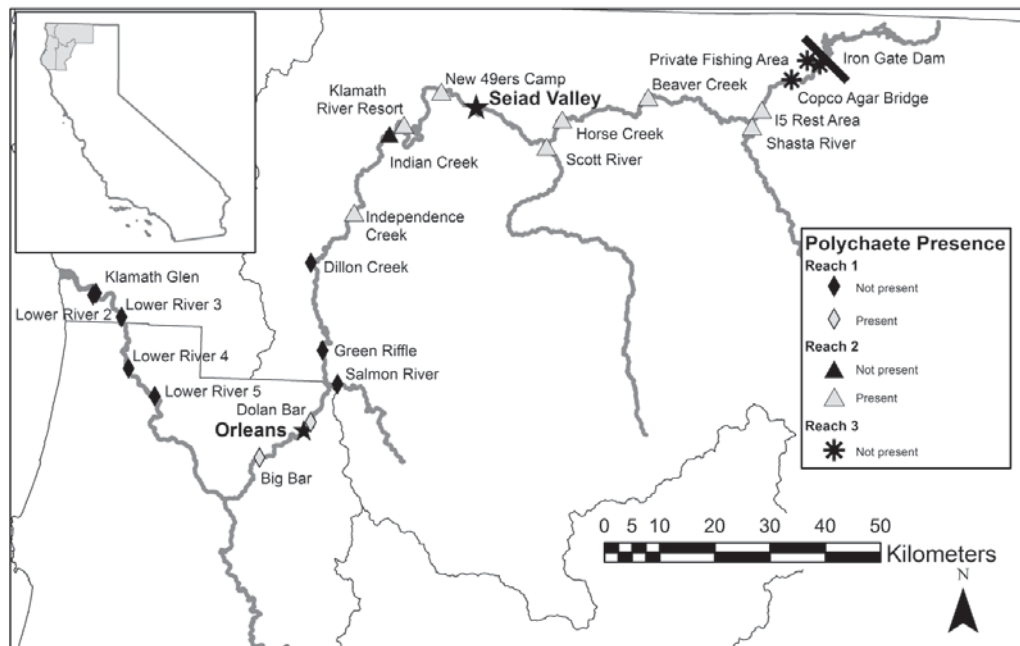


Figure 1.—Map of the sampling sites from the Klamath River, below Iron Gate Dam, Siskiyou, Del Norte, and Humboldt counties, California, USA, 2005-2006.

Invertebrates were sampled using a 250- μ m D-frame net for 30 second intervals from 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 the 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, Grown 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 non-insects and insects were immature (early instars), which often prevented reliable identification beyond family. Therefore, we used family-level classifications of insects, or lower resolution of non-insects, in data analyses. Family-level identifications have been widely 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, 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-invertebrate 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 or non-detection of polychaetes in samples to define river reaches. Reach one ($n=10$ sites) extended upstream from river-km 8 at Klamath Glen to river-km 185 at Independence Creek. Reach two ($n=9$ sites), where polychaetes were present, extended from river-km 185 to river-km 287, at the Interstate 5 rest area. Reach three ($n=3$ sites) 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 throughout the entire river 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 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 retained in other data analyses. The five most abundant taxonomic groups in samples from each of the reaches in 2005 and 2006 are shown in Table 1.

Year	Reach 1		Reach 2		Reach 3	
	Taxon	% Mean Abundance	Taxon	% Mean Abundance	Taxon	% Mean Abundance
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 1.— 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.

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). Subsequent pairwise comparisons between reaches within years all were

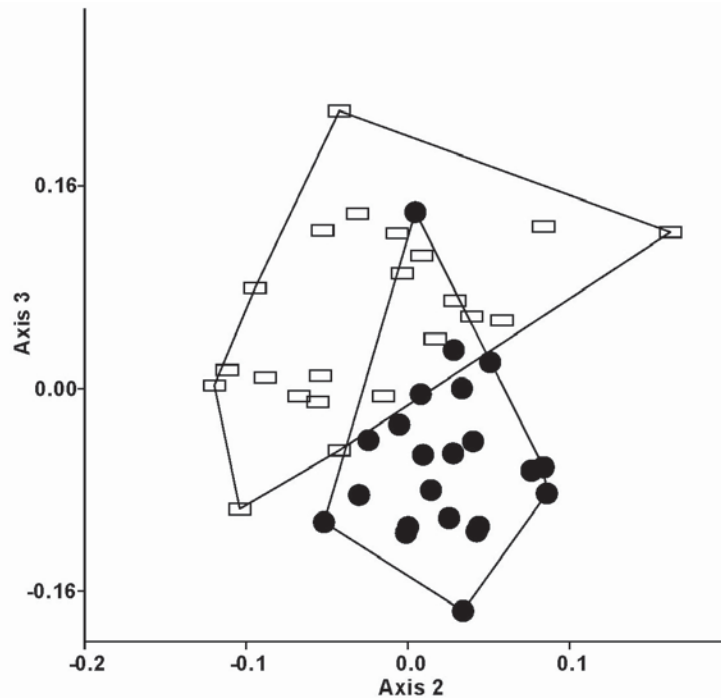


FIGURE 2.—Non-metric multidimensional scaling ordinations with convex hulls showing community structure differences between the 2005 and 2006 sampling years. The 2005 sampling year experienced average flows, while 2006 experienced elevated flows. Rectangles represent sites from 2005, and circles represent sites from 2006. Results show a three dimensional solution (Stress = 0.1726).

significant (one-way ANOSIM; $P\leq 0.05$; Table 2, Figure 3). The overall difference in the distribution of taxonomic richness between years also was 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, Leptohiphidae, 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 Gastropoda, Hydracarina, Baetidae, Leptohiphidae, 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.

TABLE 2.—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
Reach 2	0.001		0.4667	0.0002		0.3314
Reach 3	0.0219	0.0283		0.0038	0.0427	

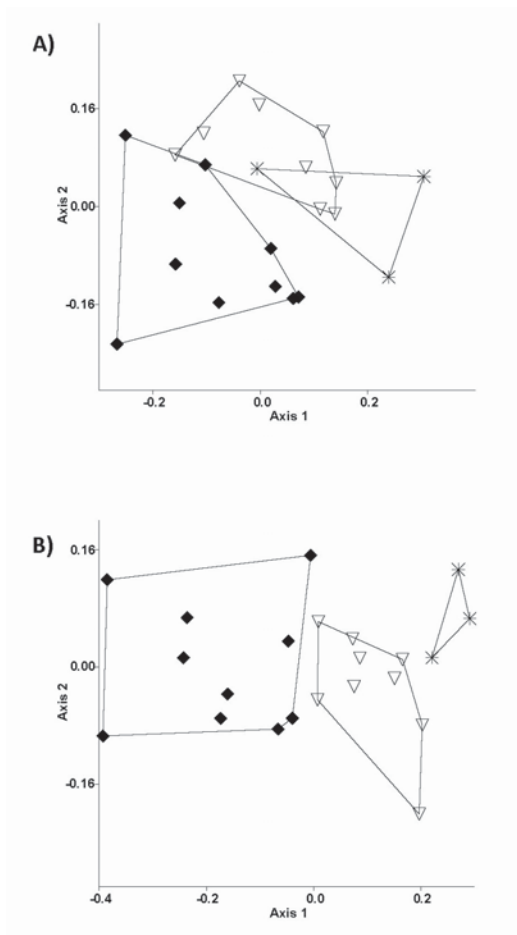


FIGURE 3.—Non-metric multidimensional scaling ordinations with convex hulls showing community structure of three reaches of the Klamath River below Iron Gate Dam. Diamonds represent sampling sites in the lowest reach (reach one) of the river, triangles represent sites in the middle reach (reach two) 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).

A total of 145 invertebrate taxa were identified, of which 115 taxa were insects (Appendices III and IV). 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 4).

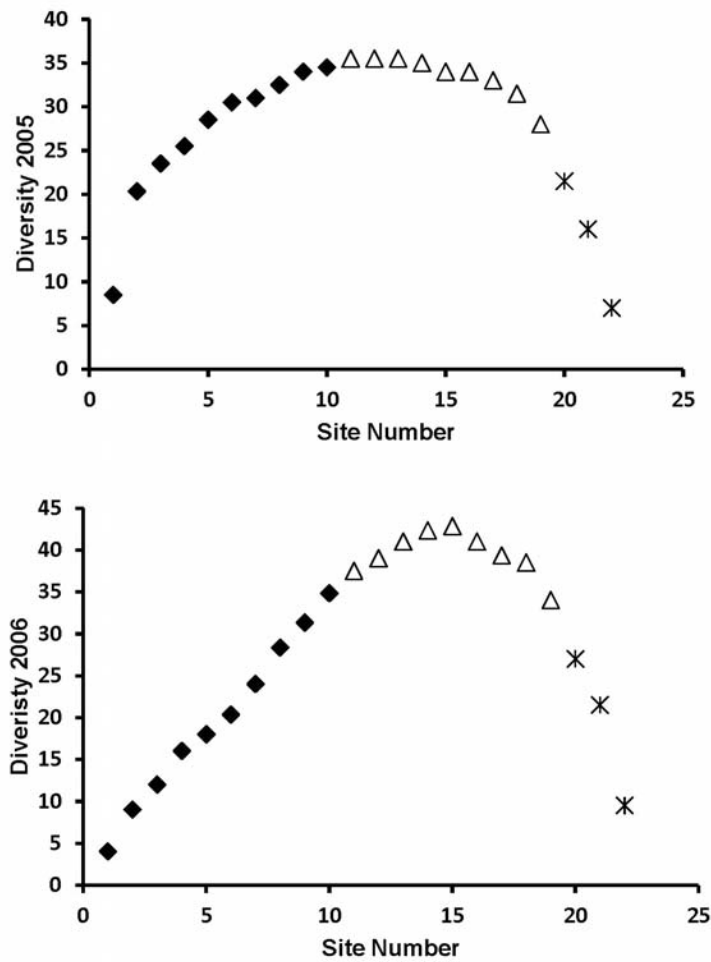


FIGURE 4.—Taxonomic richness curves of invertebrate assemblages in the Klamath River below Iron Gate Dam. Site number increases with distance upriver. Diamonds represent sampling sites in the lowest reach (reach one) of the river, triangles represent sites in the middle reach (reach two) where *Manayunkia 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.

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 ($F_{1,38}=24, P<0.001$), and gatherers ($F_{1,38}=37, P<0.001$) differed between 2005 and 2006 (two-way ANOVA; Figure 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 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.

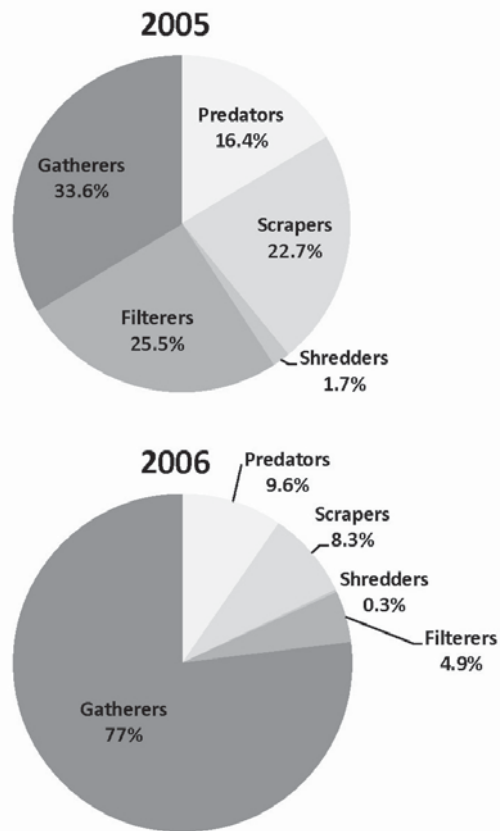


FIGURE 5.—Relative abundance of functional feeding groups by year. ANOVA indicated significant differences ($P<0.05$) between years in mean abundances of scrapers, filterers, and gatherers. Percentages represent means.

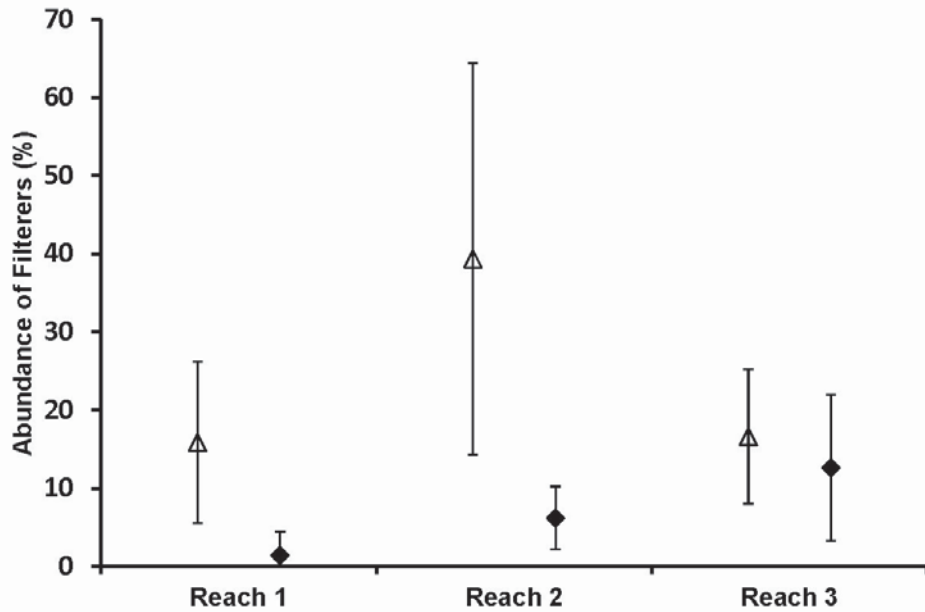


FIGURE 6.—Mean percent abundance of filterers in three reaches of the Klamath River below Iron Gate Dam. Reach one exhibited lower relative abundance of filterers consistently for both years. Mean percent abundance is represented by triangles in 2005 and diamonds in 2006. Error bars represent one standard deviation.

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 7). Both overall taxonomic richness and the relative abundance of invertebrates

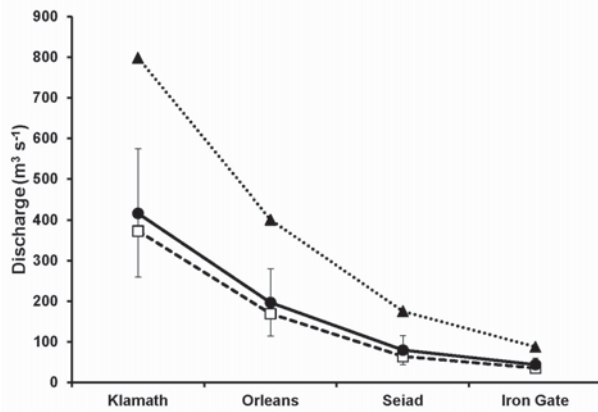


FIGURE 7.—Mean annual discharge in the Klamath River for the 2005 and 2006 water years. The graph is oriented with the site nearest the mouth of the river on the left. Triangles represent 2006, squares represent 2005, and circles represent the mean annual flow for the years 2001 to 2010. Error bars represent one standard deviation. Data were obtained from <http://waterdata.usgs.gov/nwis/sw>.

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 ($\chi^2_1=1.7$, $P>0.19$), 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, and also associated with a general plateau of taxonomic richness. The distribution of *M. speciosa* within a 100-rkm section of the 300-rkm 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 polychaetes lies with its food supply. Wallace and Merritt (1980) documented evidence that 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) concluded that food availability is often the dominant factor in 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 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 both constitutes the food supply of *M. speciosa*, and 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 byozoan 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 (Dudley et al. 1991, Quinn et al. 1996, Lau and Martinez 2003), and are not likely heavily 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 (D. M. Malakauskas, unpublished data). These colonies are therefore likely to be displaced during high flows and may be only seasonally persistent unless channel morphology or rock outcroppings reduce flow exposure. 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 inference, 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). 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); sampling error, however, 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 also undetected 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 the animal. 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). Nutrient concentrations are reduced, and a shift in diatom assemblages that Asarian et al. (2010) observed from predominantly non-nitrogen fixing species which use environmentally available nitrogen to predominantly nitrogen-fixing forms suggests that the reach may be nitrogen limited or that the N:P ratio is reduced (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. Sampling in subsequent years by co-authors and others substantiate that *M. speciosa* does not maintain dense populations there (D. M. Malakauskas, personal observation), in contrast to the dense populations of other filter-feeders often observed below other impoundments. 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 that 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 16-24 km below the dam, to 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 to explain reduced polychaete abundance in reach three. 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 the dam may have a basis in the serial discontinuity concept (Ward and Stanford 1983). This theory posits 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. 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 larval stages become displaced downstream during a disturbance event. However, a definitive explanation for the paucity of polychaetes immediately below Iron Gate Dam awaits further research.

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APPENDIX I.—UNPUBLISHED DOCUMENTS CITED IN THE TEXT.

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**APPENDIX II.—SITE NUMBER, REACH NUMBER, SITE NAME AND GEOGRAPHIC
COORDINATES OF INVERTEBRATE SAMPLES COLLECTED IN THE LOWER
KLAMATH RIVER, SISKIYOU, DEL NORTE, AND HUMBOLDT COUNTIES,
CALIFORNIA, IN 2005 AND 2006.**

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

**APPENDIX III.—INSECTA FROM THE KLAMATH RIVER BELOW IRON GATE DAM,
SISKIYOU COUNTY, CALIFORNIA.**

Taxon, Column 1

Taxon, Column 2

COLEOPTERA

DYTISCIDAE

Hygrotus

ELMIDAE

*Microcylloepus similis**Dubiraphia giulianii**Lara avara**Optioservus*

HALIPLIDAE

*Haliphys robertsi**Peltodytes*

HYDROPHILIDAE

Tropisternus

PSEPHENIDAE

*Eubrianax edwardsii**Psephenus falli***DIPTERA**

ATHERICIDAE

Atherix pachypus

BLEPHARICERIDAE

CERATOPOGONIDAE

*Atrichopogon**Probezzia*

CHIRONOMIDAE

Chironominae

Chironomini

Tanytarsini

Rheotanytarsus

Diamesinae

Tanypodinae

Orthoclaidiinae

DIXIDAE

EMPIDIDAE

Hemerodromia

EPHYDRIDAE

PHORIDAE

PSYCHODIDAE

SIMULIIDAE

LEPIDOPTERA

CRAMBIDAE

*Petrophila***MEGALOPTERA**

SIALIDAE

*Sialis***NEUROPTERA**

SISYRIDAE

*Climacia californica***ODONATA**

ANISOPTERA

AESHNIDAE

Aeshna walkeri

CORDULIIDAE

*Epithea canis**Macromia magnifica*

GOMPHIDAE

*Gomphus kurilis**Octogomphus specularis**Ophiogomphus morrisoni**Ophiogomphus occidentis*

LIBELLULIDAE

Libellula saturata

ZYGOPTERA

CALOPTERYGIDAE

*Calopteryx aequabilis**Hetaerina americana*

COENAGRIONIDAE

*Argia agriodes**Argia emma**Enallagma**Ischnura***PLECOPTERA**

CAPNIIDAE

Capnia

APPENDIX III.—CONTINUED.

Metacnephia
Prosimulium
Simulium

STRATIOMYIDAE

Odontomyia

TABANIDAE

TIPULIDAE

Antocha
Hexatoma

EPHEMEROPTERA

AMELETIDAE

Ameletus

BAETIDAE

Acentrella insignificans
Baetis bicaudatus
Baetis tricaudatus
Callibaetis fluctuans
Callibaetis pictus
Camelobaetidius maidu
Centroptilum
Proclaeon

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

LEPTOHYPHIDAE

Tricorythodes minutus

LEPTOPHLEBIIDAE

Paraleptophlebia

SIPHONURIDAE

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

Phyrganea cinerea

POLYCENTROPODIDAE

Polycentropus

PSYCHOMYIIDAE

Psychomyia

APPENDIX III.— CONTINUED.

<i>Parameletus columbiae</i>	SERICOSTOMATIDAE
<i>Siphonurus occidentalis</i>	<i>Gumaga</i>
HEMIPTERA	UENOIDAE
CORIXIDAE	<i>Neophylax splendens</i>
<i>Hesperocorixa laevigata</i>	<i>Neothremma</i>
<i>Sigara mckinstriyi</i>	
GELASTOCORIDAE	
<i>Gelastocoris oculatus</i>	
GERRIDAE	
<i>Aquarius remigis</i>	
<i>Metrobates trux</i>	
NAUCORIDAE	
<i>Ambrysus mormon</i>	
SALDIDAE	
<i>Salda buenoi</i>	
VELIIDAE	
<i>Rhagovelia distincta</i>	

APPENDIX IV.—NON-INSECT INVERTEBRATE TAXA FROM THE KLAMATH RIVER
BELOW IRON GATE DAM, SISKIYOU COUNTY, CALIFORNIA.

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