

**Benthic Invertebrate Communities in the Peripheral Wetlands of Elkhorn Slough
Ranging from Very Restricted to Well Flushed by Tides**

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Abstract

The peripheral wetlands of Elkhorn Slough had radically different benthic invertebrate communities that were divided into two habitat types, those with minimal or very restricted tidal exchange and those better flushed by the tide. The very restricted wetlands had more frequent extreme water quality events, hypoxia, hypersalinity, and hyposalinity. They were decompositional systems full of decaying green algal mats, which probably have very high microbial diversity. The number of species and abundances were low, and dominance was high. By late summer and fall of 2007, hypersalinity, algal decay, and hypoxia were widespread and intensive. Animal die offs were common. After the winter rains, animals recolonized these highly disturbed wetlands. The presence of dead tube mats in summer 2007 samples suggests that the cycle repeats each year. Only one wetland was a perennial estuary without late-season hypersalinity, Porter Marsh. It had the highest species diversity and the best-developed benthic communities within the very restricted wetland group. The little estuary was maintained by drainage from farm irrigation. Fresh water is the most important natural resource missing from the wetlands. Elkhorn Slough itself was once an extensive estuary dominated by fresh water inputs from vast areas of wet landscape. It is now a marine embayment: the surrounding landscape is dry. The better-flushed wetlands were divided into those with and without large culverts restricting tidal exchange. There was little difference between the two groups, which were thus considered together. Cluster analysis separated the benthic communities into those with very restricted tidal exchange and those with better flushing. Species diversity and abundance were higher in the better-flushed systems, and dominance by one or a few species was lower. The most extreme very restricted wetlands dried up by late summer. So, there was a hydrographic and disturbance gradient ranging from seasonally dry to very restricted to better flushed. Certain species were consistent indicators of the three parts of the gradient. In general, two insects characterized the seasonally dry systems. The same insects, the brackish water snail, and certain oligochaetes and polychaetes were indicators of the other very restricted wetlands. Seven species were consistent indicators for the better-flushed wetlands. All were present in every better-flushed system, and none were present in the very restricted systems. We recommend an experiment to improve habitat conditions in West Bennett Slough, with the prediction that the ecosystem will become more like Whistlestop Lagoon.

Introduction

Several decades ago some of us helped initiate water quality monitoring in the peripheral wetlands of Elkhorn Slough. We did this so we could sample the benthic invertebrate communities and relate their structure to the extreme habitat variations, including fluctuations in tidal exchange and fresh water inflow linked to hypoxia, hypersalinity, and hyposalinity. Decades later, this is the objective of the present study.

The management of the peripheral wetlands has become a significant concern for local resource managers, especially how they could be changed to improve wetland ecosystems. There are also potential models for evaluating how future landscape experiments might improve wetland habitats, rather than continue to degrade them as we have done by reducing fresh water inputs, limiting tidal exchange, and creating odd habitats behind roads and culverts (Ritter et al. 2008). So our objective is relevant to important wetland management, but driven by longstanding curiosity.

Methods

Eighteen peripheral wetlands of Elkhorn Slough (Figure 1) were divided into three hydrographic regimes: 1) those well flushed by tidal movement of water from the main slough; 2) those with restricted tidal flushing; and 3) those with very restricted tidal flow. The Well Flushed wetlands had no culverts constraining tidal flow, and were peripheral to the main Elkhorn Slough. They were South Marsh, Rookery Lagoon, Parsons Slough, Five Fingers, and Pick-n-Pull Marsh. The mouth of West Bennett Slough was Well Flushed by six large culverts, but the back part of this system was designated Restricted. This was the only wetland where we assigned different flow regimes to the back and mouth areas, because of the high flow at the mouth. The Restricted wetlands were separated from Elkhorn Slough by large, open culverts (North Azevedo Pond, Whistlestop Lagoon). The Very Restricted systems fell into one of three groups; some were separated from the tide by small culverts with minimal flow (Mid Azevedo Pond, East Bennett Slough); some by large culverts with gates to prevent saltwater inflow (although these leaked; Lower Moro Cojo Slough, Porter Marsh); one system with gates set for low inflow (North Marsh); and the final group was further back in one of the previously mentioned wetlands (Struve Pond, Estrada Marsh, North Strawberry Marsh, Upper Moro Cojo).

We collected benthic invertebrate samples during 2 survey periods, to capture the late summer/early fall community and the spring community – before and after the winter season rains. Samples were collected within a 2-3 week period to minimize temporal variability. Our sampling periods were from August 14 to September 4, 2007 and from April 4 to April 24, 2008, during which we visited 1-3 systems per day. Two of the very restricted sites, Mid Azevedo Pond and Struve Pond, were dry in the summer and were therefore not sampled in 2007. All other sites were sampled during both survey periods.

Before quantitative sampling, we explored each system via small motor boat, canoe, and/or kayak to assess variability of habitats and select sampling strata. We scuba dived, snorkeled, and waded in some. Our general sampling strategy was to avoid higher intertidal regions, where the sediment is exposed to the air frequently and invertebrate communities are known to be poorly

developed (few species live here). In systems with little tidal amplitude, we avoided deeper channels and concentrated at the shallower edge of the system, where communities are also better developed (e.g., Karr and Chu 1999). Four quantitative infaunal samples were collected in each system during each sampling period. If benthic macroalgae were present, we sampled from algae-clear areas if possible. In addition, during our 2007 exploration we collected supplementary infaunal samples, both qualitative and quantitative, when system variability or our particular interests were high. All sample locations were recorded using differential GPS so that we could reoccupy the same location in the second sampling period. Infauna samples were collected by hand-held cores (0.0078 m², 0.1 m diam x 0.01 m depth), and washed over a 0.5 mm screen. Animals were relaxed by treatment with magnesium chloride and samples were subsequently fixed in 4% buffered formaldehyde for 48 h and then transferred to 80% ethanol for storage and/or archiving. All seasonal samples and a subset of supplementary samples were sorted, while the remaining supplementary samples were archived for future processing. Prior to sorting, samples were stained with rose Bengal. Organisms were sorted and identified to the lowest possible taxon. We sorted and identified organisms from 85 quantitative infaunal samples and 35 qualitative samples. In addition we archived 27 quantitative infaunal samples for potential future work.

In the first year of sampling, grain size samples were collected immediately adjacent to each infaunal core (0.0007 m², 0.03 m diam x 0.01 m depth) and stored upright during transport to prevent mixing. Grain size cores were refrigerated at the laboratory. We selected a single grain size core per system for processing and resampled the same location during the next survey period. Ultimately we were able to analyze all cores collected during the 2007 survey period. Particle size analyses were carried out with a Beckman-Coulter LS 13 320 laser particle size analyzer. For the relatively coarse, silt to sand size beach samples, the analyses were done with an attached dry module and conventional (Fraunhofer), laser beam diffraction (from 0.4 µm to 2 mm). For very fine sediments, particle size analyses were done with an aqueous module equipped with a pump and a built-in ultrasound unit. This module analyzes very small (~1 g) amounts of sediments and the measured size distributions ranges from 0.04 µm to 2 mm. Measurements of such a wide particle size range are possible because the particle sizer equipped with the aqueous module combines conventional laser beam diffraction with polarized intensity differential scatter (PIDS), which measures particles between 0.4 and 0.04 µm (Beckman Coulter Inc., 2003). A total of 110 grain size samples were processed.

Means and standard errors of various community parameters were plotted by system. All analyses were conducted using Primer 6. Bray-Curtis similarity matrices of fourth root transformed infaunal sample data were examined by cluster analysis to look for community patterns within each date (Summer 2007, Spring 2008) and a SIMPROF test determined where clustering was significant at the 5 % level. Individual species contributions to the separation of the different tidal regimes (Very Restricted, Restricted, Well Flushed) within each sampling period was examined using the SIMPER procedure. Two way ANOSIM was conducted with date and tidal regime as main effects and pairwise comparisons were completed within dates. To explore how peripheral wetland communities differed from those in the main channel of Elkhorn Slough, we merged the data presented here with those from a previous study of main channel stations (Oliver et al. in prep.) and conducted some preliminary cluster analyses.

Results

General Community Patterns and Tidal Flow Regimes

The Very Restricted systems had a higher percentage of observations of extreme water quality, including hypersalinity, hyposalinity, and hypoxia (Table 1). The Very Restricted and Restricted wetlands usually had a larger sediment grain size than the Well Flushed systems (Figure 2). The four peaks in grain size in the Very Restricted systems (Figure 2) were not caused by sand, but by large organic particles. These deposits were poorly consolidated mud with high water and organic content. Often these mucky muds were underlain with a much firmer and cleaner mud, which was an old marsh deposit. One primary source of organic material was decomposing green macroalgae, *Ulva intestinalis* (formerly *Enteromorpha intestinalis*), which was the dominant macroalgae in all the peripheral wetlands. The larger grain size in North Azevedo Pond was caused by sand, not organic particles (Figure 2). This was the only sampling site with high sand content, and also had the highest standard deviation for grain size distribution (Figure 3).

The cluster analysis generally separated benthic invertebrate communities into the three flow regimes (Figures 4 and 5), with little overlap in community similarity between systems with Very Restricted flow and those with better tidal flushing (Well Flushed and Restricted). Struve Pond and Mid Azevedo Pond were dry in summer of 2007, but were sampled in spring 2008. These two wetlands had the most extreme restricted tidal flow: they dried up by late summer. Because of these two additional sites in spring 2008, there was a more distinct separation of wetlands with Very Restricted flow from those with better tidal flushing in the 2008 cluster dendrogram (Figure 5). The number of species and individuals were usually lower in wetlands with Very Restricted flow compared to Well Flushed and Restricted systems (Figures 6 and 7). There was almost no overlap in species number (species diversity) between the Very Restricted and more flushed systems (Figure 6). In the Very Restricted wetlands, species diversity and total abundance were usually highest in spring 2008. In the more flushed systems, species diversity was often highest in summer 2007, while abundance showed no consistent seasonal trend (Figures 6 and 7). Community dominance was highest in the Very Restricted wetlands (Figure 8), where species diversity and total number of individuals were usually lowest (Figures 6 and 7). There was no consistent seasonal pattern in dominance for the three hydrographic regimes (Figure 8).

Insects were one of the best indicator taxa for the Very Restricted wetlands (Figure 9, Table 2). These included the water boatman (*Trichocorixa reticulata*), which is exclusive to brackish or saline water (Usinger 1956), and midge fly larvae (Chironomidae). The latter was the dominant insect in the two seasonally dry wetlands, and water boatmen were the most abundant insects in the other Very Restricted wetlands. Oligochaete worms and anemones occurred in a wide range of hydrographic conditions, however, there were no anemones in the two systems that dried out in late summer and also none in East Bennett Slough (Figures 10 and 11, Table 2). Polychaete worms were also absent in the seasonally dry wetlands, and common in most of the other systems regardless of tidal regime (Figure 12, Table 2). In contrast, molluscs and crustaceans were usually much more abundant in the more flushed systems (Figures 13 and 14, Table 2). Almost all of the molluscs in the Very Restricted systems were the rare brackish water snail, *Tryonia imitator*. Only one of these very small snails was found in a more flushed wetland, Parsons Slough (Table 3). On the other hand, the larger, introduced snail, *Batillaria*

atramentaria, occurred in a wider variety of flow regimes (Table 3). While nemertean worms were never abundant, none occurred in the wetlands with Very Restricted flow (with the exception of two individuals in North Marsh), but they were present in all of the more flushed systems. We collected a total of 124 species from all quantitative samples processed.

Cluster analysis revealed significant differences in community structure across sites (shown by red lines in each dendrogram (Figures 2 and 3). Two way ANOSIM results confirmed that main effects of date and tidal regime were highly significant (p-values of 0.002 and 0.001, respectively). Additional one way ANOSIM analyses were conducted on each sampling period separately to tease out differences in tidal regime. For both years, all Pairwise comparisons of tidal regime were significantly different, with p-values ranging from 0.001 to 0.014. SIMPER analysis demonstrated a rate of high dissimilarity in community composition of different tidal regimes. Very Restricted sites were > 80 % dissimilar to both Restricted and Well Flushed sites, which were about 69% dissimilar to each other (Appendix 1).

In the following sections, we consider the benthic invertebrate communities and habitats in each peripheral wetland in more detail. Our naming convention was to label stations A-D, with A stations positioned closest to the source of tidal exchange and D stations positioned furthest away from the source of tidal exchange.

Very Restricted Tidal Flow Mid Azevedo Pond (Seasonally Dry)

Mid Azevedo Pond (Figure 15) was one of the two wetlands with the most restricted tidal flow. It dried out each summer, and filled with winter rains. There was very limited tidal flow at extreme high tides through a small culvert under the railroad dike. The pond was 40 cm deep at station D (Figure 15). The highest salinity was recorded in this system (89 ‰), as well as the lowest during the April sampling (Table 1). The system commonly became hypoxic in summer (Table 1). Beck and Bruland (2000) also documented extreme water quality in Mid Azevedo, especially hypoxia. The sediment was a fine mud (Figure 2), which was so hard because of the extreme drying that we were able to take samples by walking rather than by boats. The variation in sediment grain size (standard deviation) was similar to the other wetlands (Figure 3). The pond was surrounded by pickleweed (*Salicornia virginica*) and inside this was a fringe of green macroalgae (*Ulva intestinalis*), which also occurred in patches throughout the pond becoming thicker and more continuous around the mouth. There was a sparse cover of widgeon grass (*Ruppia maritima*) in patches throughout the pond. The pond water was opaque and a dull orange color, presumably caused by a bloom of phytoplankton or another microbial community.

There were very few species and individuals of benthic invertebrates in Mid Azevedo (Figures 6 and 7). Oligochaete worms accounted for 80% of the individuals (Tables 2 and 4). *Paranais littoralis* was the most abundant; it occurred in all of the wetlands with Very Restricted tidal flow except Struve Pond; and occurred in only one of the Restricted flow wetlands (North Azevedo Pond). *Paranais* sp. was in Struve Pond (Table 5), and this may be the same species. *Paranais littoralis* is characteristic of polluted sediments (Persoone and de Pauw 1968, Gray et al. 1979). Fly larvae (Chironomidae) accounted for most of the remaining fauna, and are also characteristic of highly disturbed sediments (Karr and Chu 1999). The fly larvae and oligochaetes formed

patches of dense tube mats. Water boatmen (*Trichocorixa reticulata*) were common in the core samples (Table 4), and were observed swimming throughout the pond. The only crustaceans present were small cylindroleberidid ostracods that are known to colonize disturbed habitats, and one tanaid (*Zeuxo normani*) which lives in chemically contaminated sediments and colonizes disturbed habitats (Ferraro and Cole 1997, Guerra-García and García-Gómez 2006.) Therefore, the entire community was composed of highly opportunistic taxa that occur in disturbed aquatic habitats and during early succession. The sample collected the furthest from the mouth (station D) had the least number of species and individuals (Table 4).

Struve Pond (Seasonally Dry)

The habitat conditions in Struve Pond (Figure 16) were very similar to Mid Azevedo Pond (Table 1, Figures 2 and 3), including the water depth, relatively firm fine sediment, and aquatic plant patterns: *Ruppia* was present. Mixing between Struve Pond and East Bennett Slough was severely limited by a barrier in the connecting channel (Figure 15), and may only occur during peak runoff and perhaps coincident peak tides. The pond water depth was 30-50 cm. The pond filled with winter rain and became severely hypoxic and hypersaline as it evaporated (Table 1). The water was also very opaque, but the color was a dull green. We took a water sample to Sara Tanner at Moss Landing Marine Labs, who found the dominant phytoplankton was a group of primitive green flagellates (Micromonadophyceae) that may be the earliest ancestors of the green algae (Mattox and Stewart 1984). The group produces dormant cysts that could recolonize the pond after seasonal drying.

Like Mid Azevedo, there were very few species and individuals of benthic invertebrates in Struve (Figures 6 and 7). Almost 74% of the individuals were chironomid fly larvae (Tables 2 and 5), which were only abundant in these two seasonally dry ponds. The chironomids also formed a dense tube mat in Struve. The three oligochaete taxa that were identified to species (Table 5) only occurred in Struve Pond. As we indicated earlier, the genus *Paranais* occurred almost exclusively in wetlands with Very Restricted tidal flow. We collected one of the special status brackish water snails, which could easily recolonize the pond from East Bennett Slough (Table 3, Figure 15). The cluster analysis showed a strong similarity between samples from Struve and Mid Azevedo Pond (Figure 5), both seasonally dry systems. Like Mid Azevedo, the sample collected the furthest from the mouth (station D) had the least number of species and individuals (Table 5), and the entire benthic community was composed of the same species with highly opportunistic life histories.

East Bennett Slough

Tidal flow was higher in East Bennett Slough (Figure 16) than both of the seasonally dry systems. The 1989 earthquake damaged the small culvert under Highway One, permitting tidal exchange that had been largely prevented for decades with a control structure. In addition, there was local subsidence caused by the earthquake that may have permitted greater inflow. Prior to the earthquake, Struve Pond and East Bennett were dominated by freshwater and harbored the endangered Santa Cruz Long-toed Salamander (Talent and Talent 1980). During Summer 2007, we sampled during an ebbing tide and observed tidal mixing above station D (Figure 16). The sampling water depths were 20-50 cm, but the depth was almost 1 m in parts of the central

channel. Again, the system was surrounded by pickleweed, and contained green algal mats (*Ulva intestinalis*) and *Ruppia*. Periods of hypersalinity, hyposalinity, and hypoxia were common (Table 1). In summer 2007, the salinity was 60 ‰. The sediment grain size was relatively coarse (Figure 2), and was likely caused by large organic particles rather than sand. The bottom was a very unconsolidated mud with high organic content. At station C, there was a firm mud below a 20 cm layer of this mucky deposit. We observed several dead carp (*Cyprinus carpio*) at the edge of the water, and a school of at least a dozen breaking the water surface while swimming. The dead and live fish were about 30 cm long.

The number of species and especially individuals was very low in East Bennett (Figures 6 and 7). The species composition was similar to the two seasonally dry ponds, except for the presence of a spionid polychaete worm, *Polydora nuchalis*, another *Polydora* that may be the same species, *Capitella*, and two amphipod crustaceans (Table 6). Only the *Polydora* were abundant, forming dense tube mats along the edge of the water. Once again, the back of the system (Station D) had the fewest species and individuals, but also the second largest local population of brackish water snail (Tables 6 and 3). Spatial variations could account for any seasonal differences observed (Table 6). The polychaetes in this system are also highly opportunistic species (Blake and Ruff 2007: *Polydora*). *Capitella capitata* is the most well know marine and estuarine indicator of disturbed sediments (Grassle and Grassle 1974, Pearson and Rosenberg 1978, Weisberg et al. 2008). The sediment often contains dead shells of the non-native bivalve, *Gemma gemma*, and dead shells of the non-native snail, *Batillaria attramentaria*.

North Marsh Complex Estrada Marsh

Tidal flows entered Estrada Marsh through a few breaks in the dike separating it from North Marsh, which is separated from the main slough by large culverts with tide gates that are partially open (Figure 17). We sampled at the southern end of the marsh because of very stagnant conditions and extensive green algal growth further north. No regular water quality data were collected from the site. In summer 2007, the salinity was 47 ‰. The water was only 30 cm deep, but strongly stratified with warmer water on the bottom. There were extensive patches of decaying green algal mats (*Ulva intestinalis*) in a mosaic of pickleweed, which fringed the entire marsh. Some *Ruppia* was present, but heavily overgrown with green algae. The bottom was covered with a layer of organic rich mud that was only a few centimeters to 10 cm thick on top of a firm peat-rich mud, which was the old marsh sediment. The coarse grain size (Figure 2) was probably large organic particles in the mucky surface deposit.

Estrada had very low species diversity (Figure 6) and total numbers of individuals (Figure 7), with a large increase in both parameters by spring 2008. Polychaete worms accounted for 89 % of the individuals in summer 2007, and 73 % in spring 2008 (Table 3, Figure 12). In summer 2007, we observed patches of *Capitella* tubes with no living animals; in some places the tubes were overgrown with green algae (*Ulva intestinalis*). Occasionally the algal mats floated to the surface, were flipped over by the wind, and the smothered *Capitella* tubes were on the top. No tubes contained live animals. By spring, large numbers of *Capitella* recolonized the sediment and were the numerical dominants (Table 7). Polydorida polychaetes also increased dramatically (Table 7). Tube-dwelling, non-native amphipods (*Monocorophium insidiosum*) were also

abundant in spring (Table 7, Figure 14). There were a large number of small burrowing anemones in one core, probably juveniles of *Edwardsia handi* (Figure 11, Table 7). So, there was clearly a spring recruitment following the winter rains after a period of hypersaline, warm water. We also collected another anemone for the first time in the Very Restricted wetlands, the non-native *Drillactis* sp. (Table 7). Water boatmen were present in many patches throughout the sampling area in both seasons, but only a few were captured in cores. As usual, the fauna was dominated by many of the same opportunistic species described previously.

North Strawberry Pond

There was very restricted tidal flow into Strawberry Pond via a small culvert under Elkhorn Road (Figure 17). Extreme hypersalinity, hyposalinity, and hypoxia were common here (Table 1). In summer 2007, the salinity in the middle of the pond was 55 ‰. The water depth was around 20 cm and always less than 30 cm. The sediment was an organic-rich muck, which probably contained large organic particles making grain size coarse here (Figure 2). Large bottom areas were covered with a slimy orange-yellow sponge in sheets as much as 1 cm thick. The sponge made the water appear the same dull orange. Green algal patches occurred primarily around the edges, and *Ruppia* was found throughout the wetland, often fouled by the sponge. Pickleweed surrounded the entire water area. We observed *Capitella* overgrown by the sponge in the same manner as the green algal mats overgrew the polychaete tubes in Estrada Marsh. Under the sponge in Strawberry Pond, we found tubes with dead *Capitella* that apparently had been preserved by the hypersaline water.

Strawberry also had very low species diversity (Figure 6) and total number of individuals (Figure 7), with higher numbers in spring. Polydorid polychaetes and water boatmen (Figure 9) were abundant in both seasons (Table 8). No other wetland contained so many water boatmen (Figure 9: the peak in Struve were fly larvae). The oligochaete *Paranais littoralis* was only captured in spring, when it accounted for the second highest animal density observed in a single core (1400) (Figure 10). This core was taken from the back of the system (Table 8: Station D), where we often observed a large decrease in animal numbers in other wetlands (Tables 4-6), highlighting the large spatial variation in community structure within the peripheral wetlands. We also encountered a few non-native anemones (*Drillactis* sp.) in Strawberry. The species composition here was similar to Estrada Marsh and the other Very Restricted systems described thus far with opportunistic species dominating.

North Marsh

Salt water from Elkhorn Slough enters North Marsh through large culverts with control gates that were partially opened. The gates were kept low enough to prevent tidal flooding of Elkhorn Road between North Marsh and Strawberry Pond (Figure 17). A relatively deep (1-2 m) but small hole was eroded in the marsh by the culvert inflow (Figure 17). Station A was located at the edge of the eroded pond in 40 cm of water. The pond and the channel with the sweeping bend were covered with large sheets of another green algae (*Ulva lobata* or *expansa*). The dominant algal cover in the rest of the wetland was *Ulva intestinalis*, which formed dense mats in all the peripheral wetlands. Periods of extreme water quality were less frequent at the station near the culverts, because of strong tidal inflows (Table 1). The water quality in most of North Marsh was

somewhere in between conditions in the front of Strawberry Pond (Figure 17) and the pond next to the culverts. In summer 2007, the salinity in most of the marsh was 45 ‰. We sampled during an incoming tide and observed the marine water spread over the surface of this hypersaline water. Many top smelt entered the marsh with the slough water, and appeared to be feeding on water boatmen. The water depth in most of the rest of the marsh was 30-40 cm. Large patches of *Ruppia* were common, and there were fist-sized and slightly larger balls of another green algae here and there (*Cladophora sericea*). The wetland was fringed by pickleweed. The sediment was a mucky, black, organic-rich deposit (20 cm thick or more) on top of a firm, peat deposit. The unconsolidated mud apparently contained large organic particles accounting for the coarse grain size (Figure 2). The prevailing winds transported floating green algae (*Ulva intestinalis*) toward the landward edge of the marsh, where it accumulated in a continuous decomposing band (a light brown color in Figure 17). This decomposing interface was present year round, and contained patches of white bacterial mats and small, shallow patches of open water that were full of water boatmen (Figure 18). Phalaropes commonly roosted on the mat and fed on water boatmen here and throughout the marsh.

The species diversity of benthic invertebrates was higher in North Marsh than for all the other wetlands discussed thus far, but was still lower than the trend for the better-flushed systems (Figure 6). One third of the species occurred only at Station A (next to the inflowing slough water: Figure 17), and were more characteristic of the better-flushed systems, i.e., they clustered closer to these stations (Figures 2 and 3). If Station A is removed, the diversity in North Marsh is similar to the Very Restricted wetlands discussed previously (Figure 6). This wetland had the greatest number of polychaete species among the Very Restricted systems: 14 compared to 7 for Porter Marsh, which had the second highest number. Total numbers of individuals was low in the marsh (Figure 7). In summer 2007, crustaceans accounted for 57 % of the individuals, and were mostly *Monocorophium* at Station A (Table 9). Polychaetes accounted for 19 %, distributed among several species. They accounted for 71 % of the individuals in spring 2008, and were mostly *Capitella* (Table 9). The most abundant oligochaete was *Limnodriloides monotheucus*, which was only common in two Very Restricted wetlands, North Marsh and Porter Marsh. Three small anemone species occurred here (Figure 11): the non-native *Drillactis* was the most abundant (Table 9). In the pond at Station A, qualitative observations revealed *Nebalia gerkenae*, *Allorchestes angusta*, and the non-native *Ampithoe valida* on the green algae. We also found several living brackish water snails, and more dead shells. The large, non-native snail *Batillaria attramentaria* was common throughout the wetland, especially in the open water areas around Stations B and C (Figure 17). A single serpulid worm or an anemone fouled some individuals since this was a subtidal population. Water boatmen were common in the marsh, and very abundant at the edges around dense green algal mats in various stages of decay.

Moro Cojo Slough Upper Habitat

The water quality station in upper Moro Cojo is adjacent to a large cement culvert under Highway One, and does not represent eastern back-slough areas (Figure 19). Nevertheless, extreme events of hyposalinity and hypoxia were common (Table 1). The highest salinity recorded at the station during the study period was almost 53 ‰ (Table 1). During the summer 2007 survey, the salinity was 35 ‰ at Station A with a layer of warmer water near the bottom

with a salinity of 42 ‰. We observed this distinct stratification at several places further up the slough as well. The water depth was 60 cm at Station A, which was in a central channel and depression around the culvert. It was 30-40 cm deep at Stations B and C, and 20 cm at Station D. Sparse stands of *Ruppia* occurred throughout the system. There were very dense, wide bands of green algae with smaller areas of open water in the middle. Again, pickleweed fringed the entire system. At Station C and above, there was a distinct vertical decomposition sequence in the thick algal mats: green plants near the water surface grading to white decomposing stands on the sediment surface. Upper Moro Cojo had the most extensive cover of microbial communities that were visually distinct. These formed large white mats (similar to *Beggiatoa*) in association with decomposing green algae, and even more extensive regions of purple cyanobacteria (Figure 20). The surface sediments were thick mucky muds with strong sulfur emissions, on top of firm mud from the old marsh. Despite an organic-rich mud, the sediment grain size did not show the coarse particle peak observed in some of the other systems (Figure 2). The sediment at all stations contained dead shells of the tiny brackish water snail, and around Station A there were also many dead shells of *Gemma gemma*. We found a few dead shells of the larger non-native snail *Battillaria*.

Small fish were common in Moro Cojo and easy to see because of the relatively clear water in summer 2007. They included sticklebacks, tidewater gobies, sculpin, and long-jawed mudsuckers (from high to lowest abundance). During March 2006, Gage Dayton captured a large steelhead in Castroville Slough less than 700 m up-slough from Station D (Figure 21). It was swimming upstream in an historical creek that is now a dead-end ditch.

The benthic invertebrate communities in the Upper Moro Cojo had a low species diversity (Figure 6) and total number of individuals (Figure 7) with high dominance (Figure 8). Molluscs accounted for 46 % of the fauna, because of the largest regional population of the brackish water snail (Tables 3 and 10). As a result, this was the only Very Restricted system with a fairly large number of molluscs (Figure 13). Polychaetes were 43 % and 51 % of the fauna for the two sample periods (Table 3); and oligochaetes were 44 % in spring when there were no brackish water snails in the samples, although they were still observed (Tables 3 and 10). *Capitella* was the dominant polychaete worm. There were two relatively abundant oligochaete worms. *Paranais littoralis* only occurred in the spring (Table 10), which was true at all the Very Restricted sites, except the Lower Moro Cojo (Table 11) and a few animals in North Marsh (Table 9). *Tubificoides brownae* was encountered for the first time in a Very Restricted site. Like the wetlands in the North Marsh complex, we found a few non-native *Drillactis* sp. in the Upper Moro Cojo. The non-native amphipod *Monocorophium insidiosum* was abundant in spring (Table 10). In summer 2007, the brackish water snails were found from the surface down to the top of the hypersaline bottom water, where dense concentrations of snails abruptly decreased to none. Although not captured in the core samples, we observed many dense aggregations of water boatmen, brine flies (*Ephydra gracilis*) at the water edge, and a few large estuarine amphipods, *Eogammarus confervicolous*, near Station A (Figure 19). Again, species composition was similar to the other Very Restricted wetlands, with mostly highly opportunistic species that live in disturbed habitats.

Lower Moro Cojo Slough

Salt water enters Lower Moro Cojo through leaking tide gates on large culverts under Moss Landing Road, where the water quality station is located (Figure 19). The control structures were erected to exclude salt water. The watershed of the Moro Cojo Slough is the second largest among the study wetlands. Porter is the largest. These two are much larger than any watersheds draining into the rest of the peripheral wetlands. As a result, in rainy years the entire slough can fill with freshwater and it can take 1-2 weeks for the freshwater to drain through the flap gates at Moss Landing Road. The frequency of extreme hypersalinity, hyposalinity, and hypoxia was similar to the water quality station in Upper Moro Cojo (Table 1). In summer 2007, the salinity in the lower slough was 34 ‰. There was also a warmer layer of water near the bottom. This system had the most extensive cover of green algae of all the peripheral wetlands (*Ulva intestinalis*). The upper slough was second. It was common to smell hydrogen sulfide from Moss Landing Road. A strip of open water was often present along the west side because the tide gates were on this side (Figure 19). The water depth was 40 cm at Station A, shoaling to the east and heading up slough.

The sediment grain size and texture in the lower region was similar to the upper slough (Figures 2 and 3). Near the back, the sediment contained dead shells of the small non-native clam *Gemma gemma* and dead shells of the small brackish water snail were common with some very dense patches. This was the only Very Restricted system where we found dead shells of larger clams (*Macoma nasuta*). Near the mouth, we also observed one siphon from a much larger butter clam (*Saxidomus nuttallii*), and a small burrow mound from a ghost shrimp (*Neotrypaea californiensis*). These animals were living! Sticklebacks were the most common fish, and tidewater gobies were less abundant than we observed in the upper slough.

The species diversity (Figure 6) and total number of individuals were relatively low in Lower Moro Cojo (Figure 7), clearly below the higher trend in the better-flushed wetlands. Polychaete worms accounted for 55 % and 60 % of the individuals, and oligochaetes 30 % and 37 % (Table 2). The brackish water snail was present (Table 11), sometimes in very abundant patches, but not as nearly as abundant and widespread as it was in the upper slough (Table 2). *Capitella* was the dominant polychaete, and *Streblospio* was also abundant (Table 11). The same two oligochaete species were abundant in both the upper and lower slough (Tables 10 and 11). These four annelid worms have highly opportunistic life histories, colonized disturbed habitats, and live in polluted sediments. The non-native *Monocorophium* was the only abundant crustacean in the lower slough. About a third of the species in Table 11 were more characteristic and abundant in the better-flushed peripheral wetlands and the main Elkhorn Slough. Qualitative observations revealed the leptostracan crustacean, *Nebalia gerkenae*, another extremely opportunistic species, abundant in regions of the slough within the green algae, which also harbored dense patches of copepods near the water surface. The eastern side and shallower side of the slough had a more depauperate fauna, characterized by many water boatmen at the surface and near the bottom below the algae, and the larvae (pupae) of brine flies on the algal surface. The west side had more *Nebalia*, *Monocorophium*, and small anemones (*Drillactis*). Near the mouth, we found a 30 cm polychaete, *Nereis brandti*, on the bottom, and an *Eogammarus* on the tide gate. So, in general, the lower slough had many species that were more common in better-flushed wetlands, but mostly along the western side nearer to the mouth. This pattern was similar to the mouth of North Marsh at Station A (Table 9).

Porter Marsh

Porter Marsh is separated from Elkhorn Slough by four large culverts with flap gates to prevent saltwater intrusion and freshwater outflow. The gates leak saltwater. Porter Marsh has the largest watershed of all the peripheral wetlands. Upstream of Station D, there is a Y in the channel, where Watsonville Creek and Carneros Creek meet (Figure 22). Watsonville Creek heads north at the fork in Figure 22 and contains fresh water. In summer 2007, there was fresh water at the creek (ditch) juncture. The fresh water was from agricultural drainage in the Pajaro Valley. There were hyposaline extremes (<5 ‰) in 56% of the measurements taken by the ES volunteer water quality monitoring program (1999-2008) at the Carneros Creek water quality station upstream from Porter Marsh. The salinity near the culverts was 27 ‰. The surface salinity was 20 ‰ between Stations C and D (Figure 22), and 30 ‰ near the bottom at 40 cm, where it was warmer as well. The highest frequency of extreme hyposalinity occurred at Porter Marsh (Table 1). There were no extreme hypersalinity events and a relatively low frequency of hypoxia events (Table 1). Porter Marsh has the only estuary persisting into the summer in Elkhorn Slough. It is less than 1000 m long. The main marsh channel is surrounded by a large pickleweed marsh (Figure 22). Mats of *Ulva intestinalis* were common throughout the system, especially along the water edge. We did not locate any *Ruppia*. The sediment was an unconsolidated mud throughout (Figure 2).

Among the Very Restricted wetlands, species diversity was highest in Porter Marsh (Figure 6); and the number of oligochaete species was almost twice as high (7 spp.) compared to the next highest in North Marsh and Lower Moro Cojo (Tables 12, 9, 11). Polychaete worms accounted for 52% and 65% of the individuals. Oligochaete worms accounted for 33% and 28% (Table 2). *Capitella* dominated in summer 2007, and *Streblospio* in spring 2008 (Table 3). Among the oligochaetes, *Tubificoides brownae* was most abundant, and like *Limnodriloides monotheucus* only occurred in the better-flushed systems, except for Porter Marsh and one other Very Restricted system (Moro Cojo). *Paranais littoralis* occurred in all of the Very Restricted systems and only one of the better flushed. However, the four remaining oligochaete species occurred only in Porter (Table 12). The non-native anemone, *Drillactis* sp., was most abundant here and in North Marsh among the Very Restricted systems (Tables 12 and 9, Figure 11). In addition to the live brackish water snails (Tables 12 and 2), we found dead shells of *Tryonia* in the sediment. Qualitative observations revealed many shrimp, *Palaemon macrondactylus*, throughout the system and mysid crustaceans, *Neomysis mercedis*, swimming next to floating algae between stations C and D. The archived sample taken just beyond D (Figure 22) appeared to have many oligochaetes, probably *Tubificoides*. We also observed a steelhead (at least 30 cm long) leap in front of our boat.

Restricted Wetlands North Azevedo Pond

Tidal inflow to North Azevedo is limited by a large cement culvert under the railway dike near Station A (Figure 15), and by the relatively high elevation of the marsh. Most of the marsh is drained by intermediate tides, but depressions and channels retain some water at low tide. The high mudflats were once vegetated marsh. They are now fringed by pickleweed, and harbored a very large and extensive population of the introduced mud snail, *Batillaria attramentaria*. We often use these intertidal snail populations to define the higher intertidal, where we avoided

taking samples because infaunal invertebrate communities are usually better developed lower on the shore. Our qualitative samples suggested lower numbers as well, so the seasonal stations were established in and near a shallow ponded region near the culvert. This made the survey results more comparable to the other peripheral wetland samples. However, we did archive a number of quantitative core samples taken throughout the higher marsh (Figure 15). Periods of extreme water quality were not frequent here (Table 1). During our sampling in summer 2007, the salinity was 32 ‰. The sediment was medium sand (Figure 2) mixed with mud and thus had a large variation in grain size (Figure 3). A peat deposit was below the sand. Station D was outside the sandy pool along a very shallow channel that drained at low tide. There was a 2 cm layer of black sandy mud above a muddy peat layer with small patches of white bacterial mats here and there on the sediment surface.

Patches of green algal mats (*Ulva intestinalis*) covered parts of the higher tide flat, but much of the area was free of macroalgae. The station region (Figure 15: A-C) had small patches of the low growing, non-native red algae, *Caulacanthus* and *Chaetomorpha* along the edges, and isolated growths of *Bryopsis pennatula* and a non-native *Gracilariopsis* in the pool. The orange sponge, *Hymeniacidon ?sinapium*, was the dominant animal cover inside and around both ends of the culvert. Arrow gobies were common and there were a few small top smelt in the station pool.

Species diversity increased dramatically in the systems with better tidal flushing compared to the Very Restricted wetlands, starting with North Azevedo Pond (Figure 6). The crustaceans (28 %), polychaetes (28 %), and oligochaetes (20 %) accounted for 76 % of the species- a total of 35. Total numbers of individuals also generally increased (Figure 7), while dominance decreased (Figure 8) as high abundance was spread among several species (Table 13). In summer 2007, the small non-native clam, *Gemma gemma*, accounted for 55 % of the individuals and all the molluscs (Tables 2 and 13), which caused the highest peak in molluscs during the study (Figure 13). Polychaetes accounted for 20 %, and oligochaetes 19 % (Table 2). In spring 2008, crustaceans accounted for 74 % of the individuals (Table 2), mostly two small tube builders, *Monocorophium* and *Zeuxo*, and a third, the non-native *Grandidierella japonica* (Table 13). There was a dramatic difference between the fauna at Stations A-C and D, where the two former crustaceans were most abundant and *Gemma* was least (Table 13). North Azevedo was the only better-flushed wetland (Restricted and Well Flushed) with the oligochaete *Paranais littoralis*, which was only present in the spring (Table 13). The small non-native anemone *Diadumene* sp. was conspicuous on the bottom, and most abundant in North Azevedo as was the nemertean worm, *Lineus rubescens* (Table 13). We also observed lined shore crabs (*Pachygrapsus crassipes*) in burrows at the edge of the pickleweed, and the non-native green grab (*Carcinus maenas*) in the pool and culvert area. *Nebalia gerkenae* and the non-native amphipod *Melita nitida* were present in algal patches we examined in the pool.

Whistlestop Lagoon

Whistlestop Lagoon was a unique subtidal pond with very little intertidal area and a large open culvert where we took an archived sample (Figure 23). In summer 2007, the water was clear and the salinity was 34 ‰. There were few extreme water quality events during the study period (Table 1). It was a dramatic contrast to the perennial subtidal marine ponds or lagoons in the

Very Restricted wetland group (East Bennett, North Marsh Complex, and Moro Cojo), where *Ulva intestinalis* mats dominated, extreme water quality was frequent, and algal decomposition was the norm. Although the water was clear in the North Marsh complex and Moro Cojo during the summer 2007 surveys, we could see little plant and animal diversity. Whistlestop was full of arrow gobies and many invertebrates. There was gravel along the edge by the road and other intertidal edges around the mouth. Here there were patches of *Gracilariopsis* and dead shells of *Protothaca staminea* and European flat oysters, *Ostrea edulis*, as well as small patches of live native oysters, *Ostrea conchaphila*. The rest of the intertidal habitat and extensive subtidal region near the mouth to Station A (Figure 23) was covered with large sheets of green algae (*Ulva lobata* or *expansa*), that had a light cover of sediment and looked generally decrepit. There was a deeper hole around the culvert (over 2 m) that rose rapidly to about a meter throughout the mouth of the lagoon to at least Station A (Figure 23), where the depth gradually shoaled and we snorkled in 30-40 cm of water throughout most of the remaining system. We saw a starry flounder in the culvert depression (over 30 cm in length), and there were huge gooseneck barnacles, crabs, and mussels in the culvert.

The extensive, shallower pond was covered with the green algae *Chaetomorpha*, where mud crabs were commonly hiding (*Hemigrapsus oregonensis*). The tentacles of a small brown anemone were common, probably *Diadumene* sp. (Table 14). Small nodule-like sponges and a tubular sponge were attached to algal fronds as well as many hydroids and an occasional tunicate. The area of open mud increased in the back part of the lagoon and was about 10 % of the bottom beyond Station D (Figure 23). The abundant mud crabs may maintain the open-sediment regions. Hydroids and the cover of two larger sponges (red and orange) increased towards the back lagoon, where there were some 1 m patches of *Chaetomorpha*. There were many dead razor clam shells, but we found no live animals. *Batillaria* was common, and there were fresh dead shells of another mollusc, *Tagelus subteres*, which had apparently been preyed on. There were also occasional patches of white bacterial mats. The extreme back end contained mats of *Ulva intestinalis*, which had a light cover of sediment, and the deposit was a deeper soft mud. Throughout most of the pond there was a mud bottom (Figure 2), sometime with hard clay underneath.

Like North Azevedo, Whistlestop had high species diversity (Figure 6), but a lower total number of individuals (Figure 7) and an even lower dominance (Figure 8). While the species composition broadly overlapped, the dominants were quite different in the summer and less so by spring (Table 14). We collected the same total number of species (35), but the crustaceans accounted for 31 %, and the polychaetes and oligochaetes each were 20 %. Polychaetes accounted for 52 % of the individuals in summer and only 8 % in spring. Crustaceans were 34 % in summer and 63 % in spring (Table 2). The dominant polychaetes were *Capitella* and *Streblospio* (Table 14), which were not abundant in North Azevedo (Table 13). The dominant crustaceans included the same three tube dwellers, *Monocorophium*, *Zeuxo*, and *Grandidierella*. The dominant oligochaetes were similar too. However, there was no *Gemma* in Whistlestop (Table 14, Figure 13). Whistlestop samples clustered together in the spring (Figure 3), and in the summer, except for Station D (Figure 2). They also were clustered relatively close to the North Azevedo samples.

West Bennett Slough

The tide enters West Bennett Slough through six large, open culverts (Figure 24). The deep hole at the mouth was much larger and deeper (3-4 m) than the erosion depressions at Whistlestop and North Marsh. There were also much smaller, shallow eroded depressions adjacent to the culverts at Porter and North Azevedo. The deep area graded to about a meter behind Station D at the mouth (Green points in Figure 24) and broad sheets of green algae (*Ulva lobata* or *expansa*) covered much of the sediment from Station B to about half way to Station A in the upper slough (Yellow points in Figure 24). The six culverts were installed after the 1989 earthquake, which caused Jetty Road to collapse. Since 1946, tidewater entered the wetland through a single culvert that gradually flattened over time, causing a 1/3 reduction in the pipe area. The deep hole was scoured out after the six new culverts were installed in 1991. Unlike Whistlestop, the upper slough was a very large intertidal flat with shallow channels around the marsh periphery (Figure 24). The sediment was muddy sand around the edges and on the large, light-brown, high-intertidal islands (Figure 24). The shallow channels were a soft mud (Figure 2) grading into sandier sediments beneath. Green algal mats (*Ulva intestinalis*) covered much of the upper marsh. During the summer 2007 survey, the sun baked the algal mats and the ebbing tidewater was milky white and then black, meeting clear water in the long channel between the upper Stations A and B (Yellow points in Figure 24). The upper marsh channels smelled of hydrogen sulfide. Periods of extreme water quality were more frequent here compared to Whistlestop and any of the Well Flushed wetlands (Table 1). Before the installation of the six new culverts, the marsh was more like Whistlestop, primarily a large subtidal system, but there were few observations of water quality and even fewer of the benthos from that time. Two species characterize much of the marsh, *Batillaria* and *Nebalia*. *Batillaria* were even on the large sheets of *Ulva* in the channels and on the upper flats, with tremendous spatial variation in their abundance. *Nebalia* nestled in all the macroalgae, and occurred in very abundant patches. We observed about 300 Phalaropes eating *Nebalia* in the upper slough.

Upper West Bennett Slough

The species diversity (Figure 6) and total number of individuals were relatively high in the upper slough (Figure 7); dominance was low (Figure 8). There were a total of 33 species: 33 % polychaetes, 20 % crustaceans, and 20 % oligochaetes. Crustaceans accounted for 85 % of the individuals in summer and 65 % in spring (Table 2). The dominants were *Monocorophium*, *Nebalia*, and *Allorchestes* (Table 15). There was high spatial variation in the samples from summer 2007 (Table 15). Station B clustered with the Well Flushed wetlands, and the other three stations clustered with the Very Restricted systems, but Station C was unique (Figure 2). Station C was in a mat of green algae, *Chaetomorpha*, where we suspected high numbers of *Allorchestes*, which was the case in both seasons (Table 15). This habitat was not widespread in the slough, so this amphipod was over-represented for the system. In spring 2008, Station A, instead of B, harbored a fauna that clustered with the Well Flushed systems (Figure 3). *Leptochelia*, *Exogone*, and *Nutricola* may be the best indicators of the Well Flushed wetlands, but also *Cumella*, *Eteone*, *Sphaerosyllis*, and *Monocorophium acherusicum*. All these species were at Station B in summer and Station A in spring, except *Cumella*, which was only at Station A in spring (Table 15). The large number of *Capitella* in the spring was probably not related to spatial variation: *Capitella* increased in a number of the peripheral wetlands in spring 2008.

West Bennett Slough Mouth

Species diversity (Figure 6) and number of individuals were higher at the mouth compared to the upper slough (Figure 7), and dominance was lower (Table 8). Of the 37 species present, 35% were polychaetes and 27% were crustaceans. Crustaceans accounted for 85% of the individuals in summer, and 84% in spring (Table 2). The numerically dominant crustaceans were *Nebalia*, *Monocorophium insidiosum*, *Leptocheilia*, *Cumella*, and *Allorchestes* (Table 16). *Exogone*, *Streblospio*, and *Capitella* were the most abundant polychaetes. Although only one mollusk was numerous in the quantitative samples, the small clam *Nutricola*, large *Batillaria* were still common around the slough mouth. The seven species that were present in the upper slough and appear to indicate the better-flushed systems (Restricted but especially Well Flushed) were all present at the slough mouth. Unlike the upper slough, the mouth stations clustered closely together in the summer (Figure 2), and relatively closely in the spring (Figure 3). Of course the mouth stations covered a much smaller geographic area, and were all strongly influenced by tidal exchange through the culvert system (Figure 24).

Well Flushed Wetlands

South Marsh-Parsons Slough Complex

None of the Well Flushed wetlands were constrained by culverts. Tidewater enters the large South Marsh-Parsons Slough complex under a large opening under the railway trestle (Figures 1 and 25). Prior to the mid 1980's, the entire region was diked to exclude tidewater, and was used for a variety of other land uses from freshwater hunting ponds to cattle pasture. The marsh subsided almost a meter while it was diked. The main channel and linear features in South Marsh (Figure 23) were excavated by the California Department of Fish and Game in hopes of improving wildlife habitat before the South Marsh dike was cut open in 1984. The dike isolating Parsons Slough was eroded open by tidal action soon after this. Prior to dike breaching, the opening under the railway trestle was about a meter deep. The opening is now over 8 m deep and about 50 m wide. Extensive tidal erosion has occurred and continues at accelerating rates throughout the marsh complex. Periods of extreme water quality were the least frequent in the Well Flushed wetlands (Table 1). However, since there were no water quality monitoring stations in Parsons Slough, Five Fingers, and Pick-n-Pull, the data in Table 1 were taken from a station in the main channel of Elkhorn Slough near Mid Azevedo Marsh (Figure 1). This site was used because it was located in an upper slough water mass where the tidal exchange takes about 10 days, and therefore might be more similar to the South Marsh-Parsons Complex where tidal exchange was constrained by the railway opening. Figures 1, 23 and 24 show the complex at a low tide. All of the wetlands were fringed by pickleweed marshes.

South Marsh

In summer 2007, species diversity was high (Figure 6) and total number of individuals was relatively high at least when compared to the Very Restricted wetlands (Figure 7). However, both diversity and abundance were extremely low by spring compared to all the Restricted and Well Flushed systems (Figures 6 and 7). Spring species diversity fell into the range of the Very Restricted wetlands for the only time. Polychaetes accounted for 45 % of the 31 species,

crustaceans 25 %, and oligochaetes 19 %. Polychaetes and crustaceans each accounted for 39 % of the individuals in the summer (Table 2). Polychaetes were 40 % and oligochaetes 37 % of the individuals in spring (Table 2), but this was an extremely sparse fauna (Table 17). *Streblospio* and an oligochaete were abundant in one sample, and *Allorchestes* in another. In contrast, during the summer many animals were abundant (Table 17). The extreme seasonal variation was reflected in the cluster analysis. In the summer, three South Marsh stations clustered together, and Station D clustered in the middle of the Well Flushed group (Figure 2). In spring, the stations covered a much wider range in the clustering. Station A had only three species, and since Station C had the same species the two stations clustered together (Figure 3). The sparse spring fauna may be related to the heavy cover of *Ulva intestinalis*. Our normal sample protocol was to sample in bare sediment without an algal mat, but none was available around the stations in spring. Algal mats can harbor rich faunas, but they can also smother an underlying community. Clearly there was a dramatic seasonal event, and the fauna had not recovered yet.

We also surveyed and sampled in the deep central channel in South Marsh, which was about 3 m deep at D2, 4 m at C2 (Figure 23), and 5-9 m near the railway opening (Figure 25). The channel at D-2 contained a thin layer of soft mud and near the edge we found dense patches of small dead *Gemma* shells that had apparently been concentrated by eroding sediment. There were many crab burrows and some exposed clay, but no clam siphons. There was lots of exposed clay along the channel sides. At C2, there were similar erosional features, but more exposed clay on the channel bottom and many large burrowing clam siphons of the pholad *Zirfaea pilsbryi*. Near the railway opening, the channel bottom was littered with dead shells from larger clam species (*Macoma*, *Protothaca*, *Tresus*, *Zirfaea*), and the number of large burrowing clam siphons was greatest. A few large shells of *Saxidomus nuttallii* had been broken by feeding sea otters and discarded on the channel bottom. Core samples from stations C2 and D2 are shown in Appendix 1. The 7 species that characterized the Well Flushed wetlands were all present in these channel samples and the intertidal samples (Table 17).

Rookery Lagoon

Rookery Lagoon could be named Stinging Lagoon for the annoying nematocyst stings of *Edwardsia californica*, a burrowing anemone that lives in a mud burrow, extends the tentacles like a daisy, and stings when handled, especially in washing cored sediment through a 0.5 mm screen. An Antarctic *Edwardsia* has a similar morphology, feeding habitats, and size (Oliver and Slattery 1985). The opening to Rookery Lagoon is a dike break under the reserve bridge (Figure 23). The species diversity was very high (Figure 6): there were 39 species in the seasonal samples (Table 18). Abundance of benthic invertebrates was high (Figure 7), and dominance was near the lowest for the study (Figure 8). Polychaetes accounted for 31 % of the species, oligochaetes and cnidarians were each 21 %, and crustaceans were 18 %. In summer, crustaceans were 59 % of the individuals, and polychaetes were 28 % (Table 2). In spring, 80 % of the individuals were crustaceans; polychaetes and molluscs were each 8 %. Rookery stations clustered in the Well Flushed community data (Figures 2 and 3). All seven species of the Well Flushed indicators were present (Table 18).

Rookery had the largest number of anemone species in the study (Table 19). It was the only wetland with large numbers of edwardsiids. We were stung in a related study from only one

other location: mud from the main channel of the upper slough. An edwardsiid was the only abundant anemone here, so *Anemonactis* was apparently not the stinger.

Much of the lagoon bottom was covered with mats of green algal sheets (*Ulva lobata* or *expansa*), with *Ulva intestinalis* common around the marsh edge. Large *Batillaria* and *Macoma nasuta* (1 cm) were common. The most extreme habitat sampled in Rookery Lagoon was around Station C2. It had 304 of the non-native amphipod, *Grandidierella japonica*, and 443 non-native *Gemma* clams (more than 38,000 per square meter): two indicators of disturbance (Appendix 2).

Parsons Slough

Species diversity was high in Parsons (Figure 6): it had the highest number of species (46). Polychaetes were 35 %, crustaceans were 24%, and oligochaetes were 22 % of the species. Number of individuals was high and dropped slightly in the spring (Figure 7), as did diversity (Figure 6). In contrast, dominance increased (Figure 8). Dominance and diversity were inversely related in the study data (Figures 6 and 8). Crustaceans accounted for 35 % of the individuals, 33 % were polychaetes, and 24 % were oligochaetes in summer (Table 2). Crustaceans were 46%, molluscs were 26 %, polychaetes were 17 %, and oligochaetes were 14 % in spring (Table 2). The 7 species of Well Flushed indicators were all present both seasons, except *Cumella* in summer 2007 (Table 20). The Parsons stations clustered within the Well Flushed group, except for Station A each year (Figures 2 and 3). This was one of the highest tide flats sampled, and only an oligochaete was abundant each year (Table 20). Only two of the seven species of Well Flushed indicators were present. Station A clustered by itself each year (Figures 2 and 3). We sampled two other Parsons sites in summer 2007 (Figure 25). Station A2 had a rich, normal fauna: all seven of the Well Flushed indicator species were present. C2 was also very high in the intertidal, like Station A, and only three of the seven indicators were present (Appendix 1). We surveyed the channel habitats as well. There was a gradient from the mouth to the back similar to the channel in South Marsh. The upper channel had crab burrows and a thin unconsolidated muddy clay on a hard clay, with clam shell debris, exposed hard clay substrate, and many large boring pholad clams at the mouth. We encountered large leopard sharks and bat rays in the channel, especially near steep channel walls. *Batillaria* and patches of *Chaetomorpha* were common, and *Ulva intestinalis* was the main algal cover, especially higher on the tide flats.

Five Fingers

The species diversity (Figure 6), number of individuals (Figure 7), and dominance were similar to Parsons (Figure 8). There were 30 species: 30 % were polychaetes and 27 % crustaceans. The number of individuals was spread among several groups (Tables 2 and 21). The seven Well Flushed indicator species were all present (Table 21). There also was a slight drop in both diversity and abundance in the spring (Figures 6 and 7), but dominance decreased rather than increased as it did in Parsons (Figure 8). The Five Fingers stations clustered in a similar pattern each year within the Well Flushed group (Figures 2 and 3). *Ulva* spp. were the dominant macroalgal cover, and *Batillaria* was common.

Pick-n-Pull Marsh

The mudflats around the central drainage channel were an old pickleweed marsh, so the elevations were high. The flats were covered with green algal mats (many bleached patches) and *Batellaria*. We located all station in the center of the channel (Figure 26). Species diversity and abundance were high (Figures 6 and 7) and dominance was low (Figure 8). When the diversity and abundance dropped in the spring, dominance increased. There were 41 species: 32 % polychaetes, 20 % crustaceans, and 20 % oligochaetes. There were six cnidarian species. Most of the individuals were polychaetes and crustaceans (Table 2). The seven Well Flushed indicator species were all present (Table 22). In both years, the stations clustered closely together at the Well Flushed end of the tidal flow gradient (Figures 2 and 3). The system was closest to the ocean and had the least impeded tidal exchange (Figure 26). The channel habitat features changed in a manner similar to that observed in the South Marsh and Parsons Slough channels. The upper channel (Figure 26: D) had crab burrows and a thin deposit of fine sediment (not organic-rich). The lower channel (A) had bivalve shell debris, exposed hard clay, large siphons of the boring pholad clams, broken *Saxidomus* shells from otter predation, and excavation pits from sea otters or rays.

Discussion

Variation

Variation is the music of the spheres to ecologists, a wise one claimed. In our study, there were sometimes extreme variations between two samples. Station A was established too high on the tide flat in Parsons Slough where there were only two abundant animals, both oligochaete worms. The samples here were radically different from all of the other samples taken (Figures 2 and 3). Our sampling protocol was to avoid the higher marsh and sample where the benthic invertebrate communities were more diverse and abundant along the lower intertidal flats. So, while we hoped to stratify sampling to concentrate in the low tidal elevations, we made a mistake with Parsons Station A. One core in Strawberry Marsh had 1400 *Paranais*, an extremely opportunistic oligochaete. There was also variation within each wetland from the mouth to the backwaters. Station A was at the mouth, and D in the upper wetland habitats. For the wetlands with very restricted tidal exchange, station D often had the lowest species diversity and abundance, with an occasional odd ball like the 1400 *Paranais* (Table 8). There was also temporal variation captured by sampling at two times: summer 2007 and spring 2008. *Capitella* often increased dramatically in the spring, after being smothered by green algal mats and a sponge and living in hypersaline waters in summer and fall throughout the North Marsh Complex (North Marsh, Estrada, and Strawberry). Species diversity increased from summer to spring in wetlands with very restricted tidal exchange, and increased in the best-flushed wetlands (Figure 6). A diverse and abundant community was at Station C during summer and shifted to Station B during spring in upper Moro Cojo Slough (Table 15). In spring, there was a radical decline in the intertidal benthic community in South Marsh (Table 17, Figures 6 and 7). There were also large-scale geographic variations. The intertidal and subtidal benthic communities along the main slough channel were similar to benthos in peripheral wetlands that were well flushed by tides. We did a summer and spring cluster analysis that included the data from the main slough (Appendix 2). These show better clustering of slough stations from the mouth to the

inland end, and no distinct clustering patterns for the peripheral systems, because they were more variable. There was variation related to watershed size. Among wetlands with very restricted tidal exchange, Porter Marsh was the most diverse, had high abundance, and low dominance (Figures 6, 7, and 8). It was the only perennial estuary surviving in Elkhorn Slough, because of water drainage from the largest watershed.

Hydrographic or Disturbance Gradients

Despite variations between samples, variations along wetland exchange gradients (A-D), variations related to other geographic processes, and variations over time, there were distinct and consistent community patterns related to tidal regime. The restricted and well-flushed wetlands clustered together, and the very restricted and the seasonally dry wetlands clustered together (Figures 2 and 3). These two wetland groups, very restricted and better flushed, differed for many community patterns. Species diversity and abundance were higher in better-flushed systems (Figures 6 and 7), and dominance was lower (Figure 8). Species diversity (species/sample area) was negatively correlated with dominance in 14 of 16 seasonal changes (Figures 6 and 8). Insects were more abundant in the very restricted wetlands (Figure 9). Molluscs and crustaceans were more abundant in the better-flushed systems (Figures 13 and 14).

Different species were consistently common in each type of tidal regime (Table 23). They were system indicators. Fly larvae and water boatmen indicated seasonally dry wetlands and some of the very restricted systems that do not dry out. *Paranais* indicated any of the very restricted wetlands (dry and not). *Polydora* and *Tryonia* indicated only very restricted systems that did not dry out. *Capitella* and *Monocorophium insidiosum* indicated very restricted systems that did not dry, and the better-flushed systems. *Tubificoides*, *Limnodriloides*, *Drillactis*, *Streblospio*, and *Grandidierella* indicate better-flushed wetlands, and only Porter, Moro Cojo, and North Marsh in the very restricted group. Seven species were consistent indicators of better-flushed wetlands: *Leptochelia*, *Exogone*, *Nutricola*, *Monocorophium acherusicum*, *Cumella*, *Eteone*, and *Sphaerosyllis*. The Restricted wetlands had all seven of the indicator species for the Well Flushed. These two hydrographic regimes had many similarities, including similar patterns in cluster analyses, species diversity, total and group abundances, and dominance (relative abundance). So, we consider them a large group of better-flushed peripheral wetlands.

Indicator species like those in Table 23 are important metrics for a number of quantitative disturbance indices (Weisberg et al. 1997, Karr and Chu 1999, Hunter et al. 2001). In addition to the abundance of an indicator species, the total number of species, the number of crustacean and mollusc species, and other summary parameters are useful metrics (Karr and Chu 1999, Ranasinghe et al. 2009). Community data can be used to rank habitats from disturbed to less disturbed. The ranks obtained from quantitative indices have been compared to ranks developed from best professional judgment (Weisberg et al. 2008), showing high agreement (Ranasinghe et al. 2009). This disturbance natural history is so robust that rankings by professional benthic ecologists agree at 92 %, and five quantitative disturbance indices all compared well with this gold standard (experienced benthic ecologists) (Weisberg et al. 2008, Ranasinghe et al. 2009).

Whistlestop Lagoon, West Bennett Slough, and Sheet Holes

Porter Marsh is the only surviving perennial estuary in Elkhorn Slough, and has the best developed benthic community among all of the Very Restricted wetlands. This little estuary is maintained by summer runoff from farm irrigation. The most positive impact we could have on the peripheral wetlands is to restore the estuary and in particular the freshwater ends of the peripheral wetlands. They dried up decades ago, leaving hypersaline ponds full of decaying green algae.

The Very Restricted wetlands are decompositional systems, with short, simple food chains. Water boatmen eat decaying green algae and associated microbial communities, which are likely to be extremely diverse. Phalaropes and shore birds eat water boatmen; top smelt eat water boatmen; egrets eat top smelt and sticklebacks; and pelicans eat top smelt, stickleback, and water boatmen: very limited food webs. The large subtidal ponds of the North Marsh complex, East Bennett Slough, and Moro Cojo Slough have very limited tidal exchange, and poorly developed benthic communities. In contrast, Whistlestop Lagoon has one big culvert, almost no intertidal habitat, and the benthic communities are difficult to distinguish from the Well Flushed wetlands with open tidal exchange, and large intertidal habitats. Although there are six large culverts in West Bennett Slough, this system is disturbed by algal die off and hypoxia not observed in the shallow, subtidal lagoon at Whistlestop. By capping culverts in West Bennett, we may convert much of the highly disturbed upper intertidal areas into less disturbed subtidal lagoon like Whistlestop. This would also reduce marsh erosion in West Bennett. The historical installation of culverts and widespread drying of regional watersheds produced many habitat experiments that were sampled in the present study. These are the peripheral wetlands. These historical experiments were by-products of land use changes that were not meant to test useful hypotheses about wetland ecosystems. It is past time to start experiments that are designed to learn how to recover and conserve the regional wetlands. We recommend capping 4 of the 6 culverts as early as possible to see if we can develop a richer subtidal more like Whistlestop.

This brings us to our final comments about sheet holes. A number of wetlands with larger culverts have relatively deep erosional holes around the culverts. The mouth regions are dominated by green algae with fronds that are large sheets (*Ulva lobata* or *expansa*). The sheets cover the sediment and greatly limit the development of benthic invertebrate communities. If there were a way to limit sheet growth (herbivores?), the underlying bottoms would be much more diverse with higher abundance and more complex food webs. Obviously we need more experiments - the ones aimed at useful hypotheses instead of those continuing to expand the human disturbance landscape.

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Table 1. Salinity and dissolved oxygen in the peripheral wetlands of Elkhorn Slough. All data are collected monthly in the Elkhorn Slough volunteer water quality monitoring program, with the exception of North and South Marsh data, collected as part of the NERR system-wide monitoring program, and the Parsons, Five Fingers, and Pick-n-Pull data, which are taken from the MBARI LOBO buoy at Kirby Park. The hypoxia values in parentheses are from daily averages, all other averages are monthly.

Station	Extreme Conditions			Salinity (ppt)			Dissolved Oxygen (mg/L)		
	Hyper-salinity (> 50 ppt)	Hypo-salinity (< 5 ppt)	Hypoxia (≤ 2 mg/L)	April Average	August Average	Yearly Range	April Average	August Average	Yearly Range
Seasonally Dry/Very Restricted									
M Azevedo	10.48%	12.10%	6.14%	14.80	59.40	0.01-89.4	9.10	6.50	0.6-21.8
Struve	5.52%	7.73%	6.88%	15.20	42.20	0.08-74.1	10.70	5.90	0.1-19.5
Very Restricted									
E Bennett	3.14%	4.40%	1.37%	23.80	40.20	0.14-65.7	10.10	5.60	1.7-18.9
Estrada									
Strawberry	12.94%	4.71%	8.00%	25.10	44.60	0.13-72.1	9.50	8.80	0.3-17.8
N Marsh	0.00%	0.23%	2.97% (4.88%)	31.50	35.00	18.4-38.2	7.70	3.70	1.0-14.7
Moro Cojo	0.55%	9.29%	3.64%	19.00	32.80	0.12-52.6	11.10	8.20	0.1-21.9
L Moro Cojo	0.60%	11.45%	1.32%	17.90	30.50	0.13-64.0	10.10	7.40	0.9-18.8
Porter	0.00%	17.58%	0.62%	14.90	31.60	0.36-49.5	11.50	9.40	1.9-27.6
Restricted									
N Azevedo	0.65%	1.31%	1.47%	29.90	33.80	3.9-60.1	9.80	7.10	0.5-19.3
Whistlestop	0.00%	0.56%	0.60%	30.00	31.50	0.1-39.5	9.50	7.30	1.3-16.6
W Bennett	0.56%	3.91%	0.00%	25.40	31.40	0.2-63.9	10.10	8.30	2.4-20.5
Well Flushed									
W Ben Mouth	0.54%	1.09%	1.80%	26.20	32.20	0.3-63.5	9.50	7.50	0.2-19.1
S Marsh	0.00%	0.00%	0% (0.57%)	30.67	31.73	28.4-32.7	6.72	5.78	5.1-8.5
Rookery	0.00%	1.12%	0.58%	29.60	31.20	0.1-44.0	8.50	7.00	0.5-16.5
Parsons	0.00%	0.00%	0.00%	29.60	34.90	21.3-35.5	6.90	6.10	4.6-10.5
Five Fingers	0.00%	0.00%	0.00%	29.60	34.90	21.3-35.5	6.90	6.10	4.6-10.5
Pick-n-Pull	0.00%	0.00%	0.00%	29.60	34.90	21.3-35.5	6.90	6.10	4.6-10.5

Table 2. Percent abundance of the major taxonomic groups in the peripheral wetlands of Elkhorn Slough.

System	Summer 2007						Spring 2008					
	% Insect	% Oli	% Poly	% Moll	% Crust	Tot Ind	% Insect	% Oli	% Poly	% Moll	% Crust	Tot Ind
Seasonally Dry/Very Restricted												
M Azevedo							19.3	79.9	0.0	0.0	0.8	124.5
Struve	Dry season -- no samples collected						74.0	13.3	0.0	0.1	12.6	210.3
Very Restricted												
E Bennett	47.7	0.0	36.1	15.5	0.7	38.8	26.4	0.7	71.3	0.9	0.7	110.8
Estrada	0.0	1.9	88.7	9.4	0.0	13.3	0.4	12.2	73.4	0.0	6.8	216.0
Strawberry	43.0	0.0	56.7	0.0	0.2	165.8	10.3	63.5	26.1	0.0	0.0	628.5
North Marsh	0.0	19.0	19.6	0.0	56.9	88.3	0.0	8.5	71.5	0.0	13.4	273.5
Moro Cojo	0.0	11.0	42.6	45.7	0.2	147.8	0.7	44.1	51.2	0.0	3.8	287.5
L Moro Cojo	0.1	29.1	54.8	3.6	11.9	235.5	0.1	37.5	60.4	0.0	1.5	584.5
Porter	1.6	32.7	51.9	0.2	5.5	113.3	1.0	27.7	65.4	0.4	3.4	409.3
Restricted												
N Azevedo	0.0	20.3	2.2	55.3	19.1	502.8	0.04	12.8	6.6	5.1	73.7	574.0
Whistlestop	0.2	12.6	51.6	0.7	34.3	149.3	0.0	27.9	8.2	0.3	63.0	312.8
W Bennett	0.0	1.1	7.4	5.1	85.4	874.5	0.0	2.7	33.2	0.2	63.9	450.0
Well Flushed												
W Ben Mouth	0.0	0.3	11.8	2.5	85.4	1141.8	0.0	0.5	9.9	5.7	83.8	1380.5
South Marsh	0.0	15.1	39.2	3.4	39.1	460.0	0.0	37.5	39.8	1.2	20.1	64.8
Rookery	0.0	5.3	28.0	4.5	59.0	595.3	0.0	2.6	8.4	8.0	80.5	541.8
Parsons	0.0	24.0	32.9	5.4	35.5	844.5	0.0	14.5	17.6	21.9	45.6	527.5
Five Fingers	0.0	18.0	28.1	19.8	31.0	889.8	0.0	7.6	34.7	8.7	48.6	366.8
Pick-n-Pull	0.0	4.7	24.4	8.3	60.5	960.0	0.0	1.1	40.1	2.5	56.2	1835.3

Table 3. The number of brackish water snails, *Tryonia imitator*, and the much larger non-native snails, *Batillaria attramentaria*, in the peripheral wetlands.

<i>Tryonia imitator</i>			<i>Batillaria attramentaria</i>		
System	Tidal Regime	Total	System	Tidal Regime	Total
Struve	Very Restricted	1	N Marsh	Very Restricted	18
E Bennett	Very Restricted	28	L Moro Cojo	Very Restricted	18
Estrada	Very Restricted	5	N Azevedo	Restricted	33
Moro Cojo	Very Restricted	270	Whistlestop	Restricted	3
L Moro Cojo	Very Restricted	16	W Bennett	Restricted	83
Porter	Very Restricted	7	W Ben Mouth	Well Flushed	5
Parsons	Well Flushed	1	S Marsh	Well Flushed	9
			Parsons	Well Flushed	37
			Five Fingers	Well Flushed	14

Table 4. Benthic invertebrates per 0.0078 m² in Mid Azevedo Pond.

Mid Azevedo Pond

Species	Group	Spring 2008			
		A	B	C	D
<i>Paranais littoralis</i> cf	Oligochaeta	200	140		
Chironomidae	Insecta	52	7	10	2
<i>Trichocorixa reticulata</i>	Insecta	13	2	1	9
Cylindroleberididae	Crustacea	1	2		
Oligochaeta	Oligochaeta		1	1	
<i>Zeuxo normani</i>	Crustacea		1		
<i>Tectidrilis</i> spp.	Oligochaeta			55	
<i>Tubificoides brownae</i>	Oligochaeta			1	

Table 5. Benthic invertebrates per 0.0078 m² in Struve Pond.

Struve Pond		Spring 2008			
Species	Group	A	B	C	D
Chironomidae	Insecta	216	178	164	62
<i>Paranais</i> n. sp.	Oligochaeta	25			
Cylindroleberididae	Crustacea	24	12	59	11
<i>Trichocorixa reticulata</i>	Insecta	1			
cf <i>Amphichaeta raptisae</i>	Oligochaeta		16	30	
Oligochaeta	Oligochaeta		9	30	
<i>Monopylephorus rubroniveus</i>	Oligochaeta		2		
<i>Trichocorixa reticulata</i>	Insecta			1	
<i>Tryonia imitator</i>	Mollusca				1

Table 8. Benthic invertebrates per 0.0078 m² in North Strawberry Pond.

North Strawberry Pond

Species	Group	Summer 2007				Spring 2008			
		A	B	C	D	A	B	C	D
<i>Polydora nuchalis</i>	Polychaeta	226	102	48		46	11	239	178
<i>Trichocorixa reticulata</i>	Insecta	108	83	71	23	86	90	39	43
<i>Drillactis</i> sp.	Cnidaria	1				4			
<i>Monocorophium insidiosum</i>	Crustacea		1						
<i>Paranais littoralis</i> cf	Oligochaeta					160	34		1400
Spionidae	Polychaeta					108	8		
<i>Capitella capitata</i>	Polychaeta					60	2		3
Oligochaeta	Oligochaeta					1		2	

Table 10. Benthic invertebrates per 0.0078 m² in upper Moro Cojo Slough.

Moro Cojo

Species	Group	Summer 2007				Spring 2008			
		A	B	C	D	A	B	C	D
<i>Capitella capitata</i>	Polychaeta	148	88	8	4	234	127	223	
<i>Tubificoides brownae</i>	Oligochaeta	27	38			14			
<i>Tryonia imitator</i>	Mollusca	7	192	19	52				
<i>Polydora nuchalis</i>	Polychaeta	1	1		1			2	
<i>Streblospio benedicti</i>	Polychaeta	1				1			
<i>Monocorophium insidiosum</i>	Crustacea		1			19	8	10	
<i>Drillactis</i> sp.	Cnidaria			3		2			
<i>Paranais littoralis</i> cf	Oligochaeta					80	400		
<i>Allorchestes angusta</i>	Crustacea					2	1		
Chironomidae	Insecta						1		

Table 14. Benthic invertebrates per 0.0078 m² in West Bennett Slough.

West Bennett Slough

Species	Group	Summer 2007				Spring 2008			
		A	B	C	D	A	B	C	D
<i>Batillaria attramentaria</i>	Mollusca	14			69				
<i>Limnodriloides monotheucus</i>	Oligochaeta	10							
Oligochaeta	Oligochaeta	10							
<i>Tubificoides</i> spp.	Oligochaeta	7							
<i>Monocorophium insidiosum</i>	Crustacea	3	506	15	2	405	76	17	21
<i>Nebalia gerkenae</i>	Crustacea	2	2	226		1	101	35	9
<i>Eteone californica</i>	Polychaeta	1	22			3	1	1	
<i>Grandidierella japonica</i>	Crustacea	1	82	3		7			
<i>Platynereis bicanaliculata</i>	Polychaeta	1							
<i>Leptochelia dubia</i>	Crustacea		260			14	1		
<i>Streblospio benedicti</i>	Polychaeta		109		1	7	9	6	1
<i>Nutricula tantilla</i>	Mollusca		89	4	1	2		1	
<i>Exogone lourei</i>	Polychaeta		74			17	7	2	
<i>Allorchestes angusta</i>	Crustacea		34	1849	1	10	7	206	15
<i>Anemonactis</i> sp.	Cnidaria		28						
<i>Tharyx parvus</i>	Polychaeta		13		7				
<i>Pseudopolydora kempfi</i>	Polychaeta		11						
<i>Sphaerosyllis bilineata</i>	Polychaeta		11						
<i>Monocorophium acherusicum</i>	Crustacea		2			3			
<i>Pseudopolydora paucibranchiata</i>	Polychaeta		2						
<i>Lineus rubescens</i>	Nemertea		1	3	1				
Palaeonemertea	Nemertea		1						
<i>Tectidrilis</i> spp.	Oligochaeta				12				
<i>Capitella capitata</i>	Polychaeta				3	8	192	157	187
<i>Polydora cornuta</i>	Polychaeta				1				
<i>Cerebratulus</i> sp.	Nemertea			1					
Cnidaria	Cnidaria			1					
<i>Drillactis</i> sp.	Cnidaria			1					
<i>Syllides minutus</i>	Polychaeta			1					
<i>Cumella vulgaris</i>	Crustacea					219	4		
cf <i>Tenedrilus</i> cf <i>calvus</i>	Oligochaeta						46		
Oligochaeta	Oligochaeta						1		
<i>Tubificoides brownae</i>	Oligochaeta						1		

Table 19. Anemones in peripheral wetlands. All stations and both seasons.

Species	W Ben Mouth	S Marsh	Parsons	Five Fingers	Pick n Pull	Rookery
<i>Edwardsia californica</i>						44
<i>Anemonactis</i> sp.					3	16
<i>Edwardsia handi</i>						8
<i>Diadumene</i> sp.	1		2	1		3
<i>Drillactis</i> sp.	1	53	113	117	66	3
<i>Edwardsia</i> sp.						1
Edwardsiidae					2	1
Actiniaria					1	
<i>Flosmaris grandis</i>					3	
TOTAL	2	53	115	118	75	76

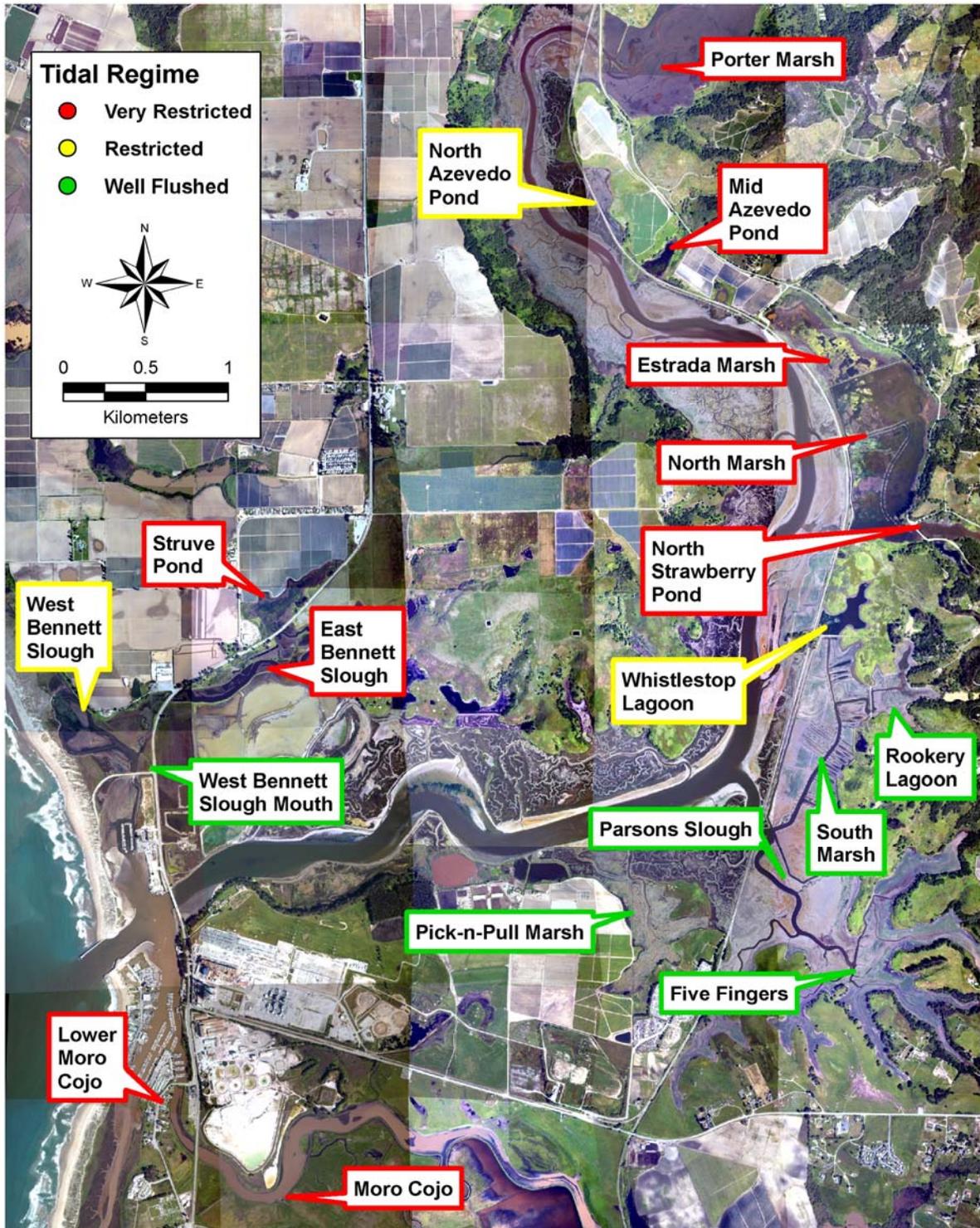


Figure 1. The location of the peripheral wetlands of Elkhorn Slough where benthic invertebrate communities were sampled.

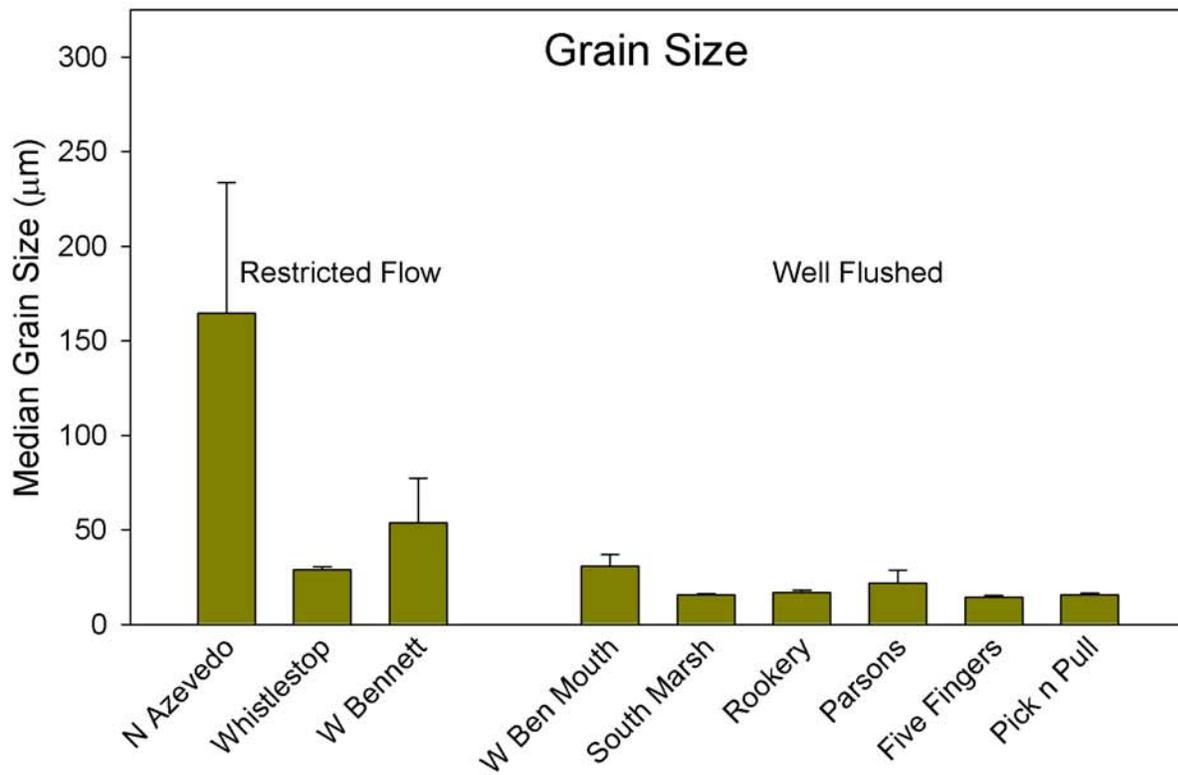
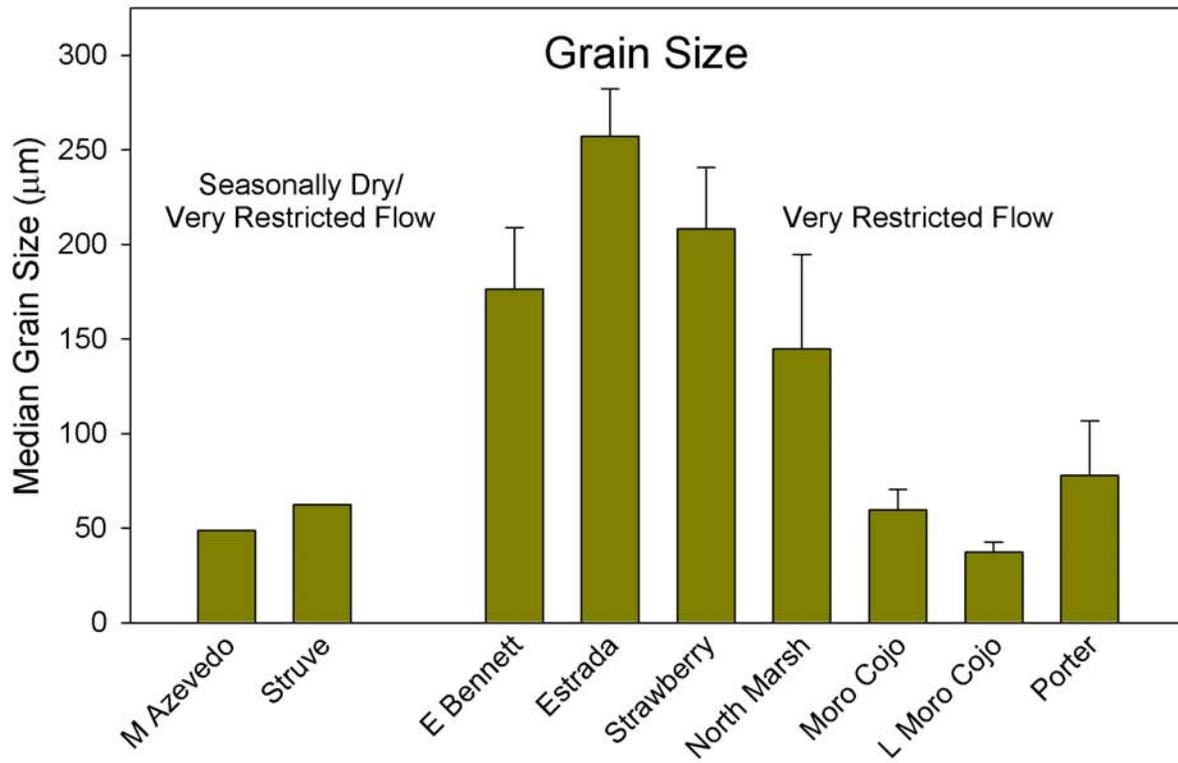


Figure 2. Median grain size of sediment in the peripheral wetlands. Means and standard errors.

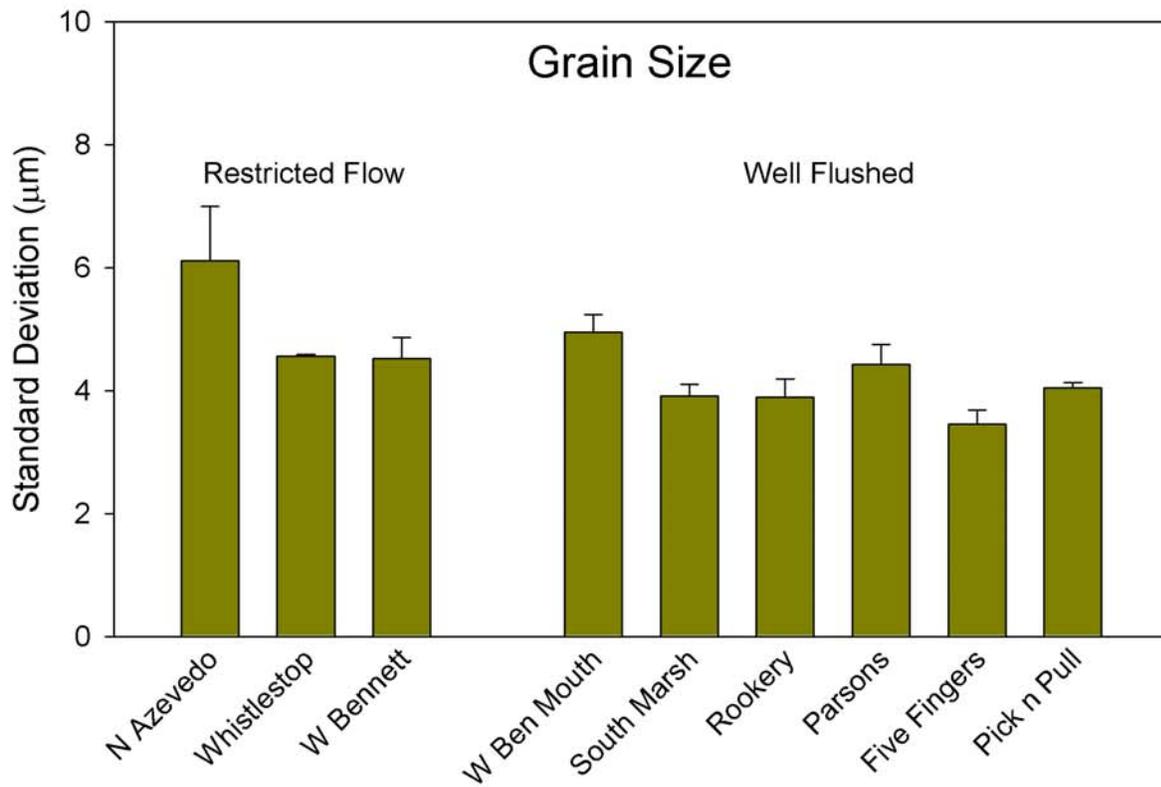
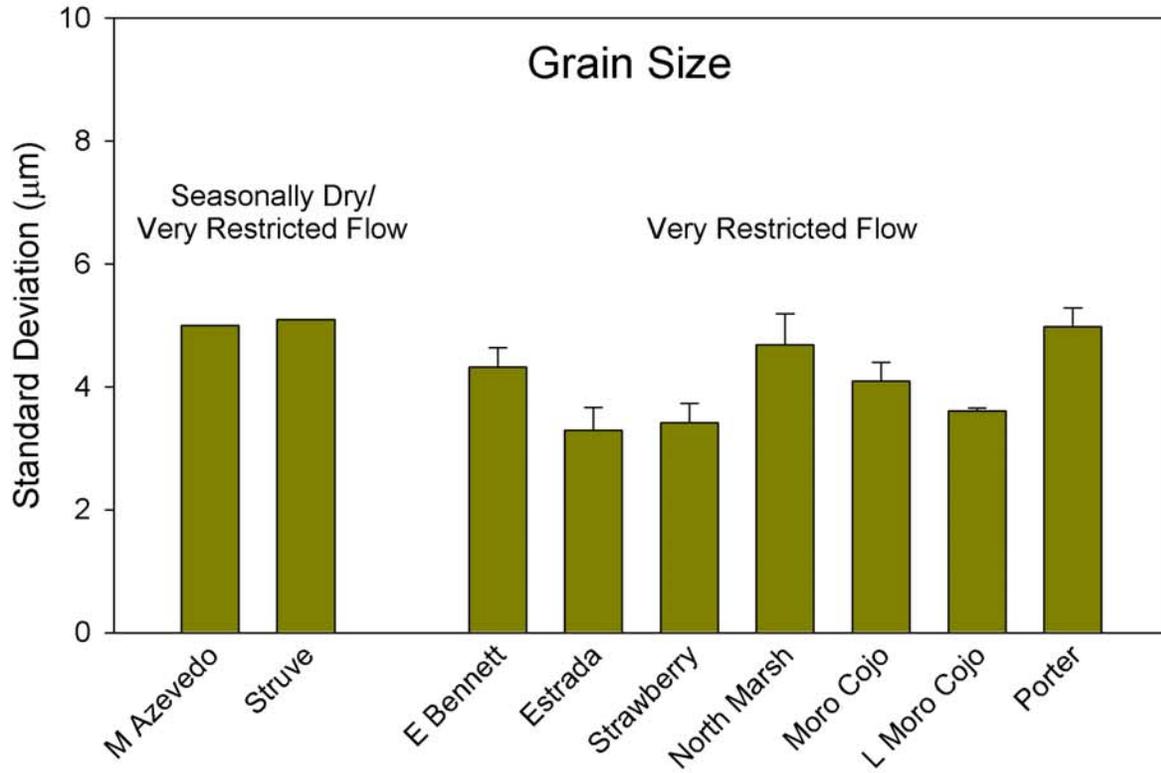


Figure 3. Standard deviation of sediment grain size in the peripheral wetlands. Means and standard errors.

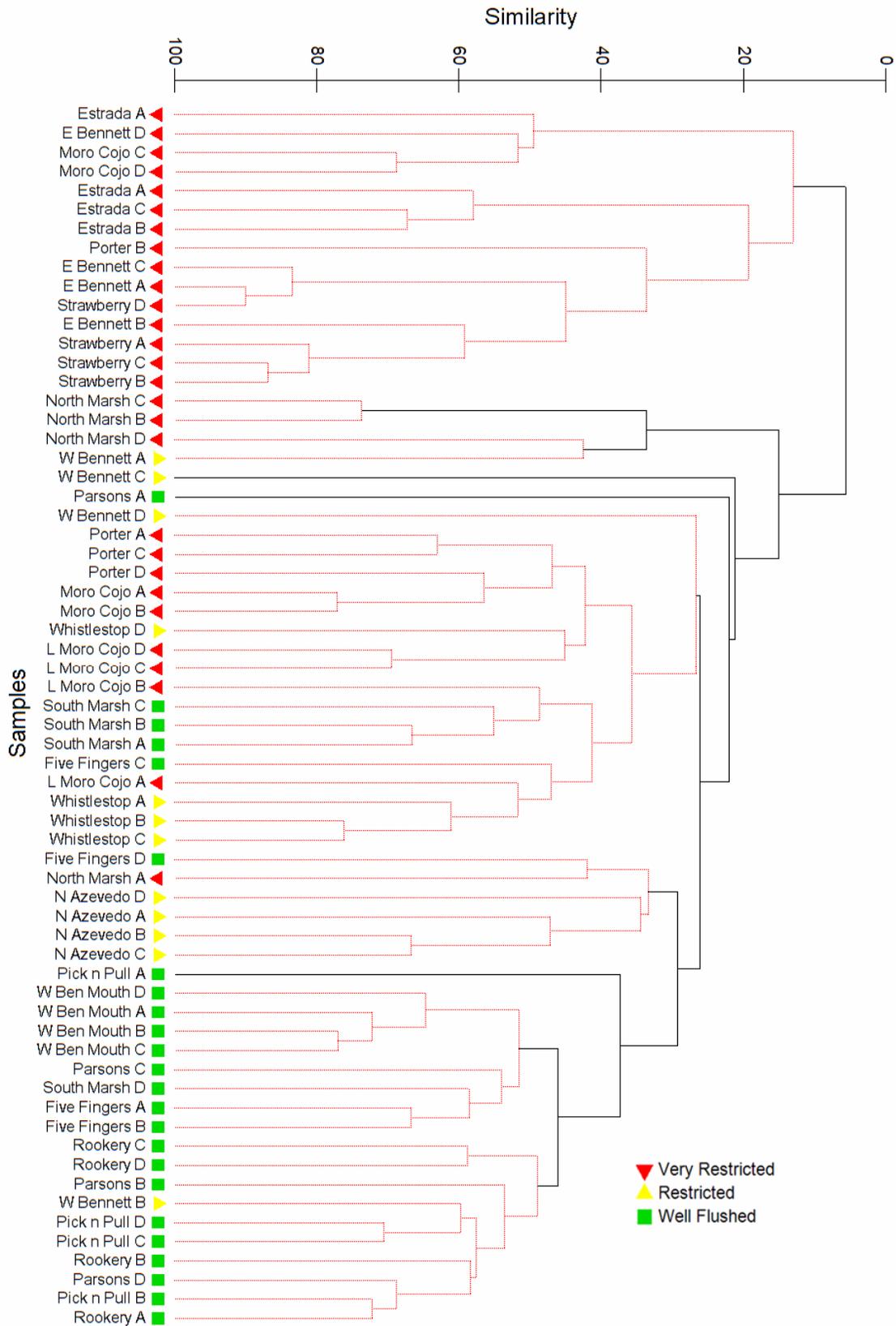


Figure 4. Separation of benthic invertebrate communities sampled in the peripheral wetlands using a cluster analysis. Samples were collected in August 2007.

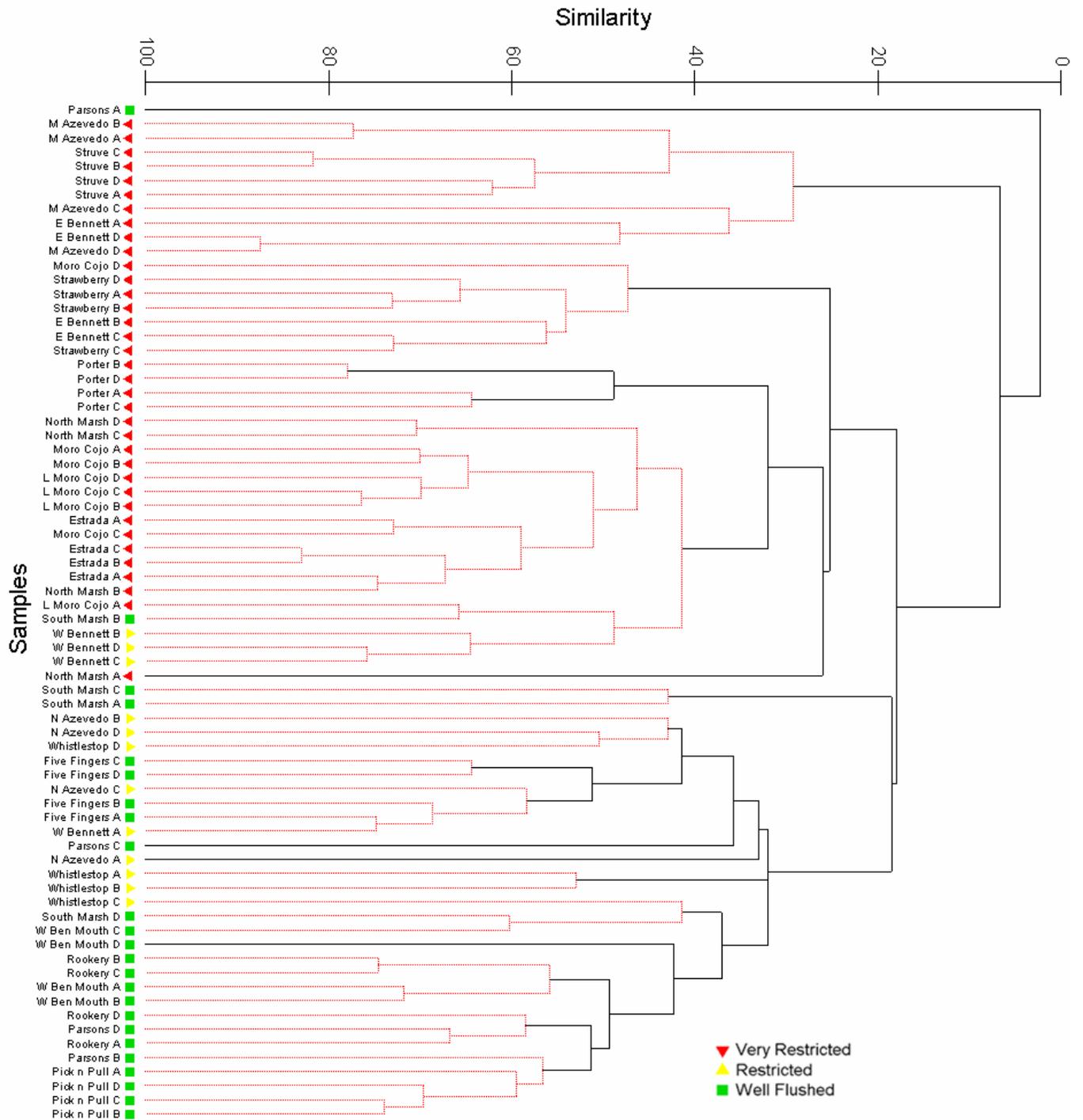


Figure 5. Separation of benthic invertebrate communities sampled in April 2008 using a cluster analysis, with the addition of two more peripheral wetlands (Struve Pond and Mid Azevedo Pond).

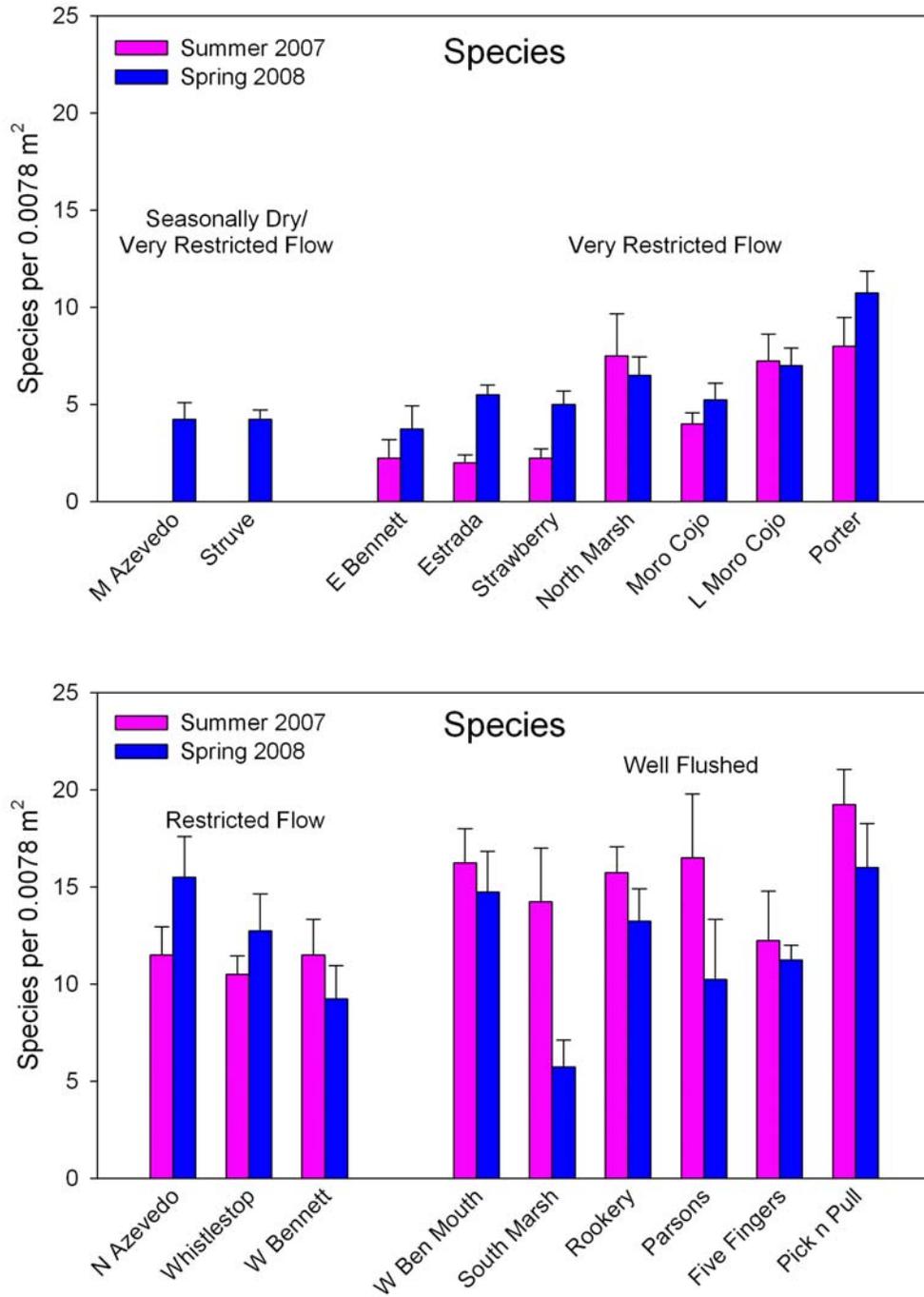


Figure 6. Number of species of benthic invertebrates in the peripheral wetlands. Means and standard errors (N=4 per datum).

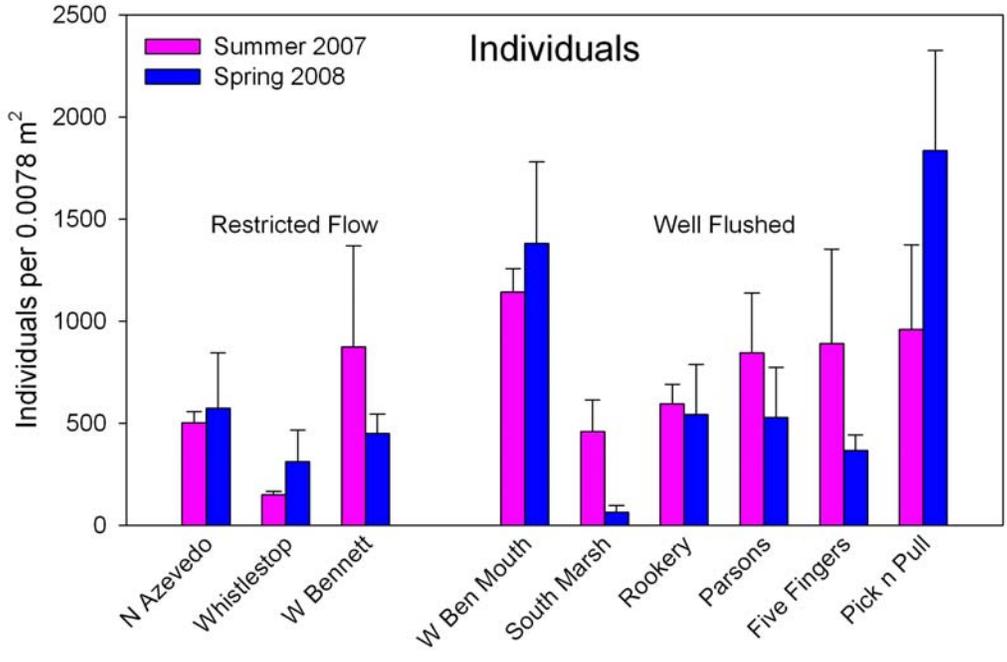
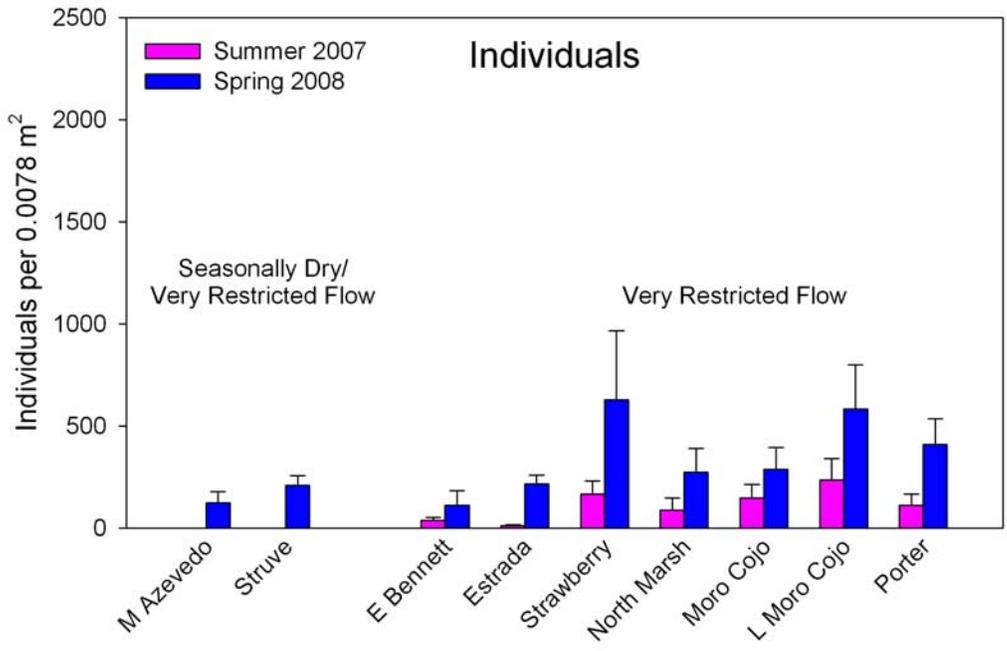


Figure 7. Number of individuals of benthic invertebrates in the peripheral wetlands. Means and standard errors (N=4 per datum).

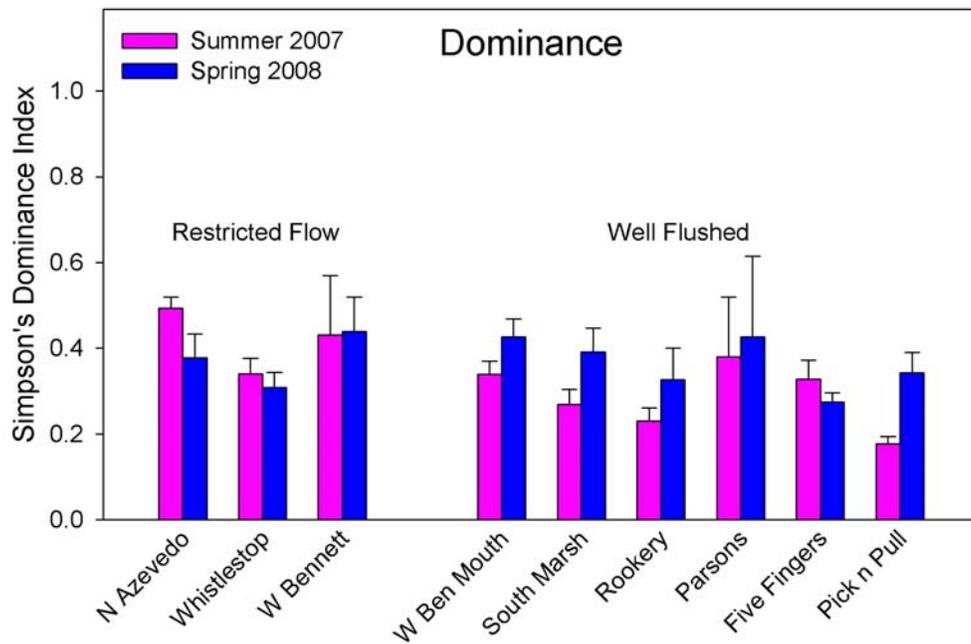
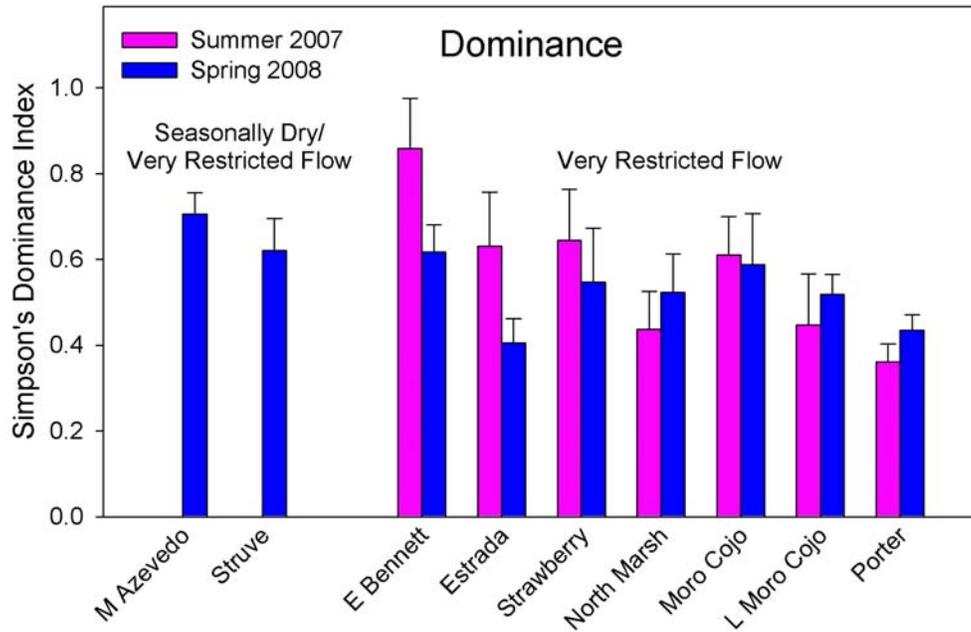


Figure 8. Simpson's dominance index for benthic invertebrate communities in the peripheral wetlands. Means and standard errors (N=4 per datum). One equals greatest dominance.

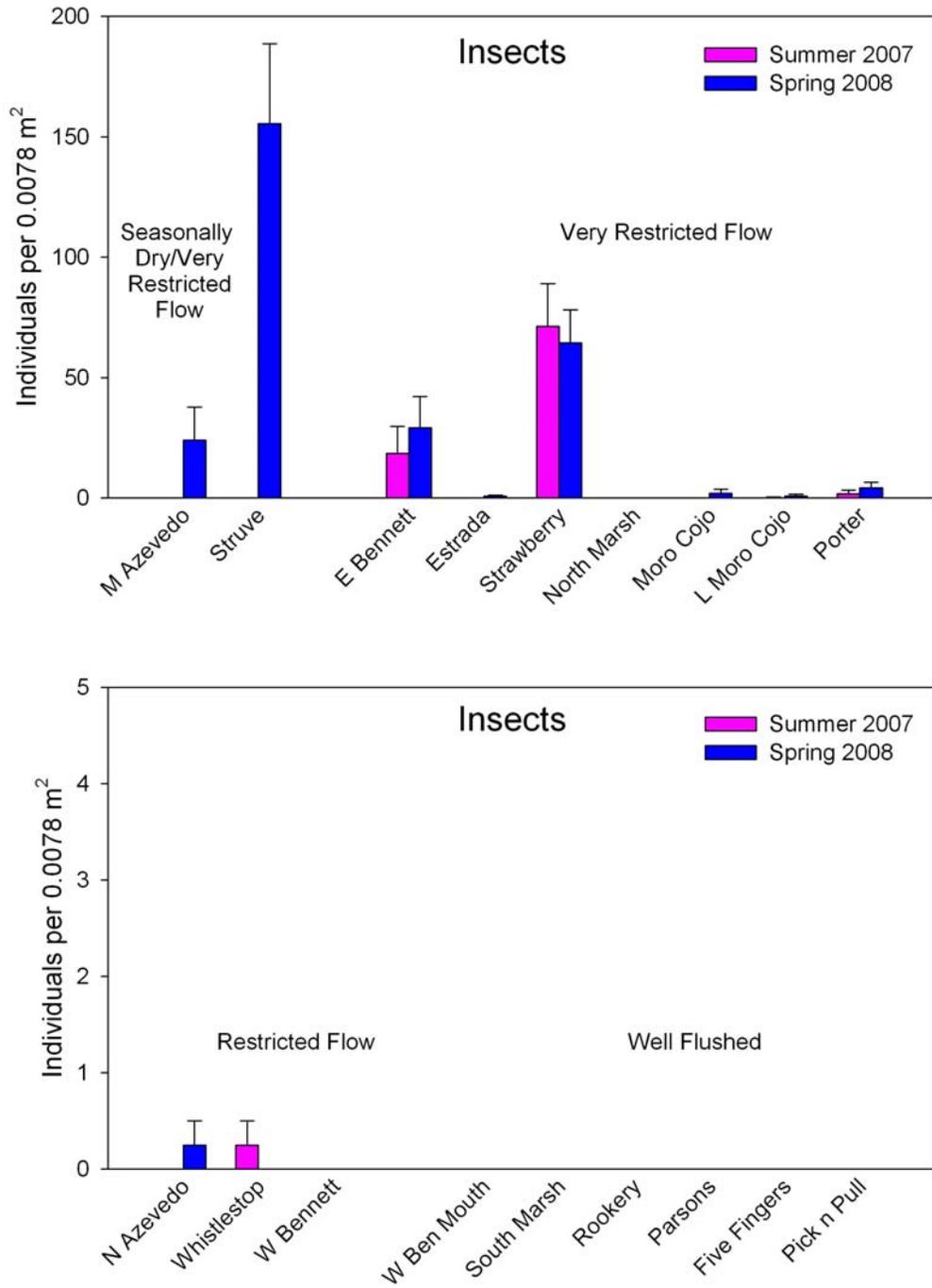


Figure 9. Abundance of insects in the peripheral wetlands. Means and standard errors (N=4 per datum).

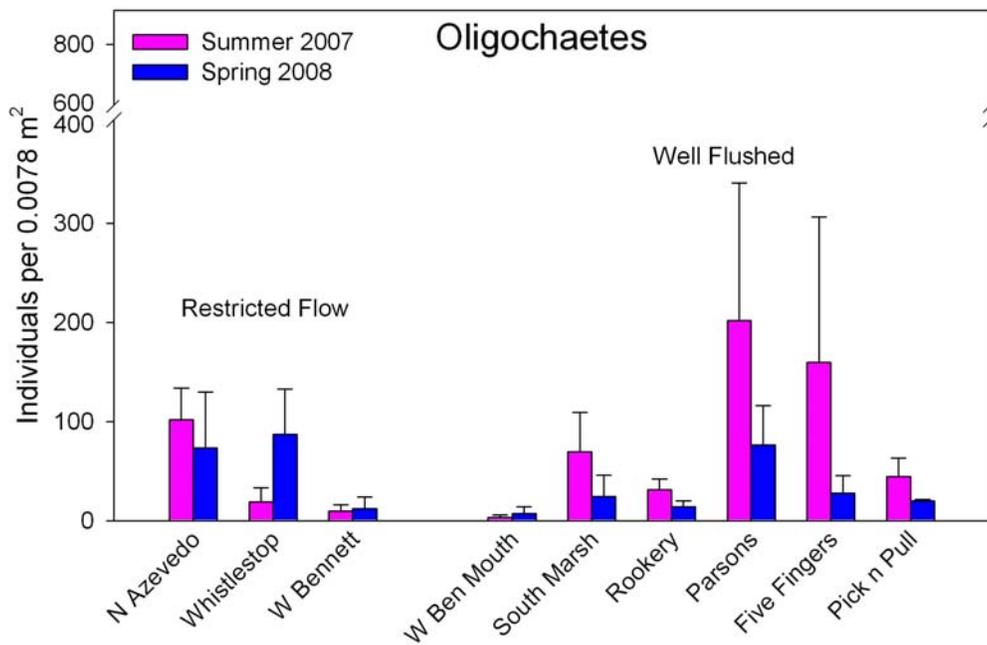
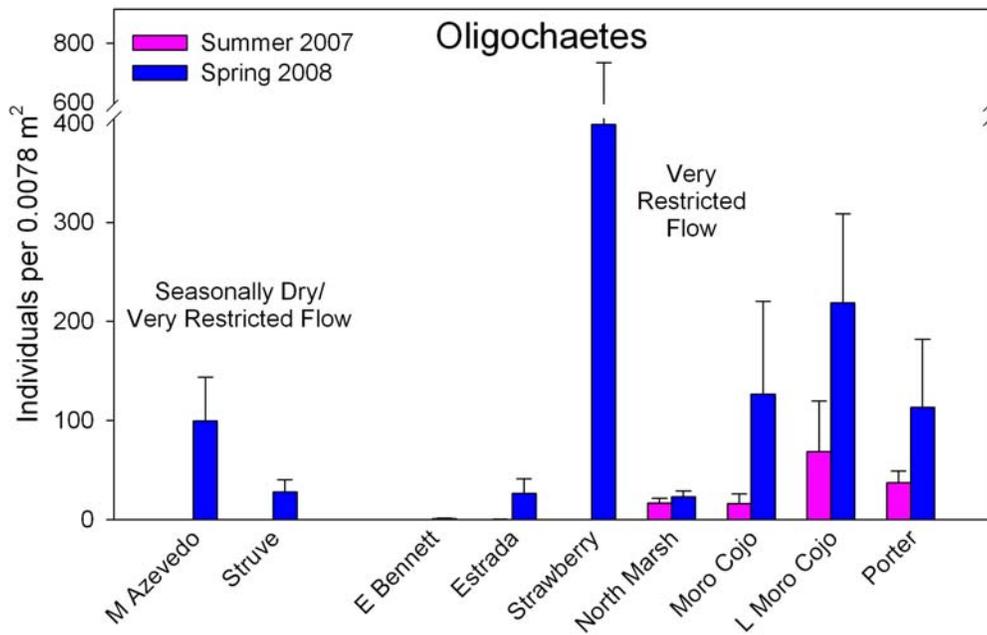


Figure 10. Abundance of oligochaetes worms in the peripheral wetlands. Means and standard errors (N=4 per datum).

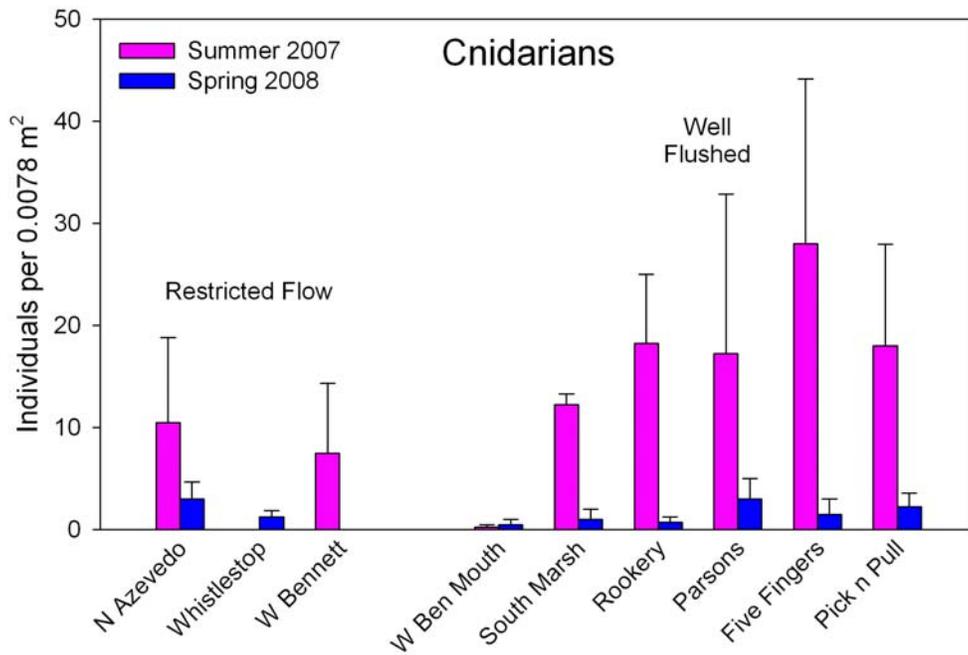
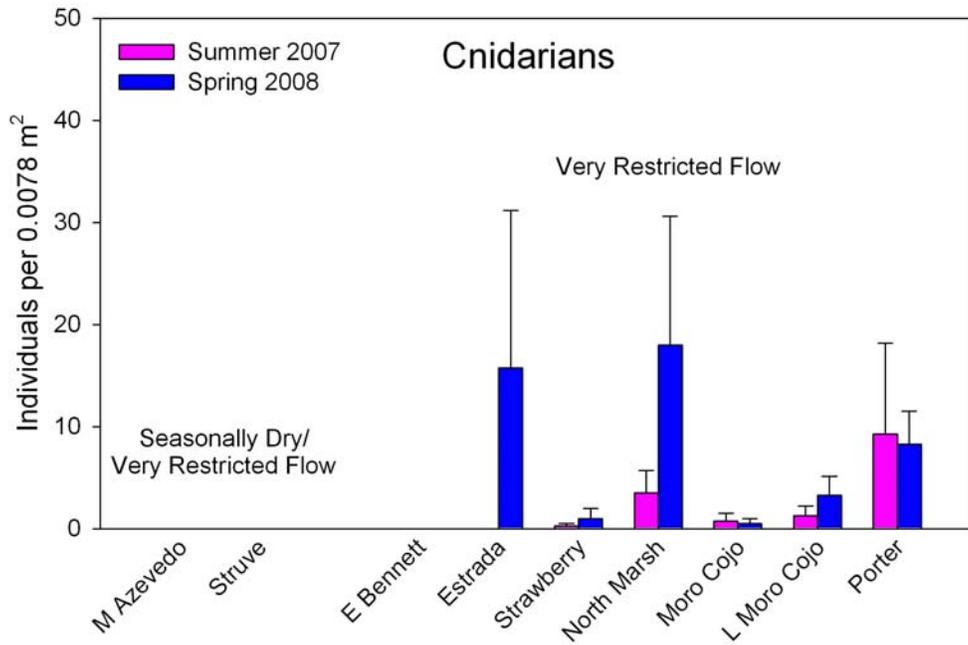


Figure 11. Abundance of cnidarians (primarily anemones) in the peripheral wetlands. Means and standard errors (N=4 per datum).

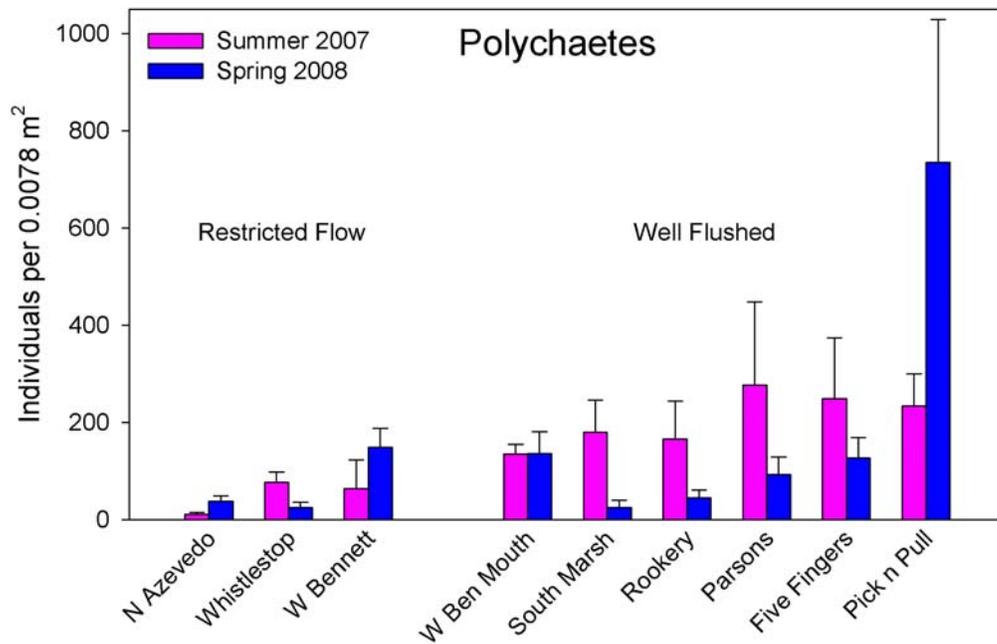
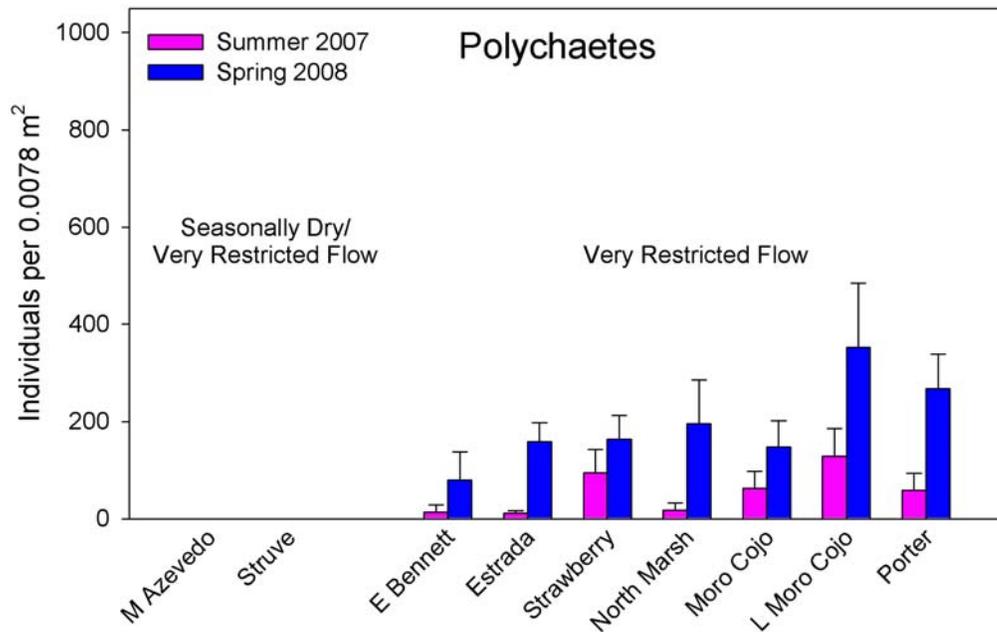


Figure 12. Abundance of polychaete worms in the peripheral wetlands. Means and standard errors (N=4 per datum).

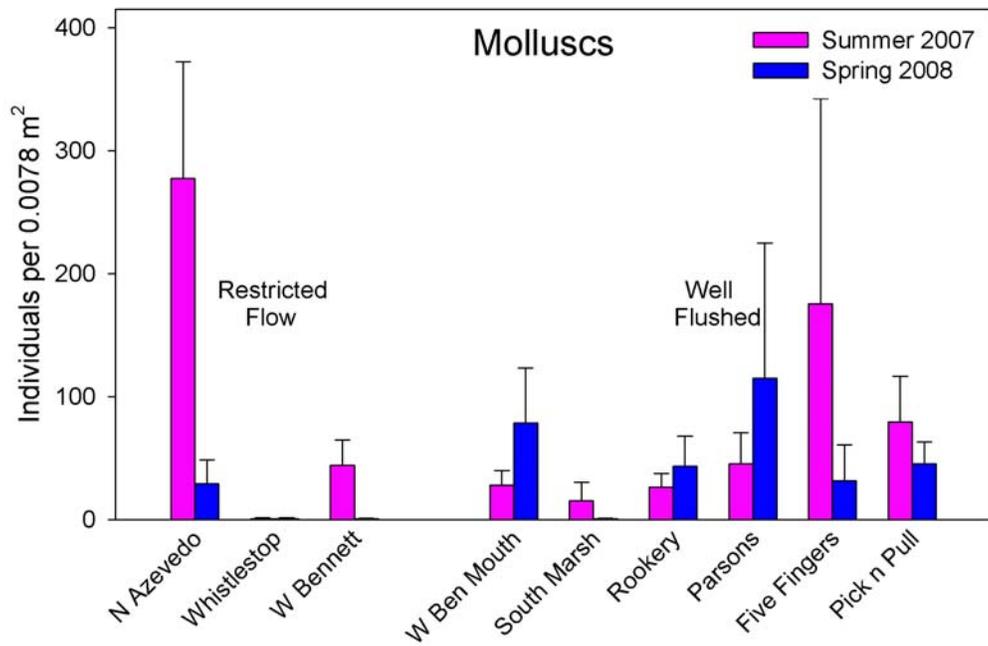
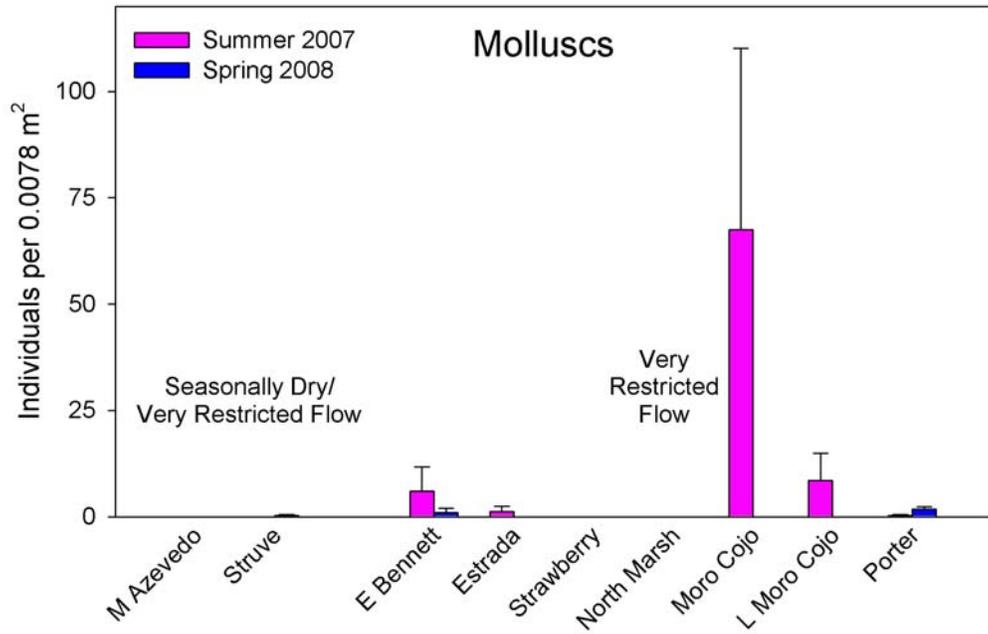


Figure 13. Abundance of molluscs in the peripheral wetlands. Means and standard errors (N=4 per datum).

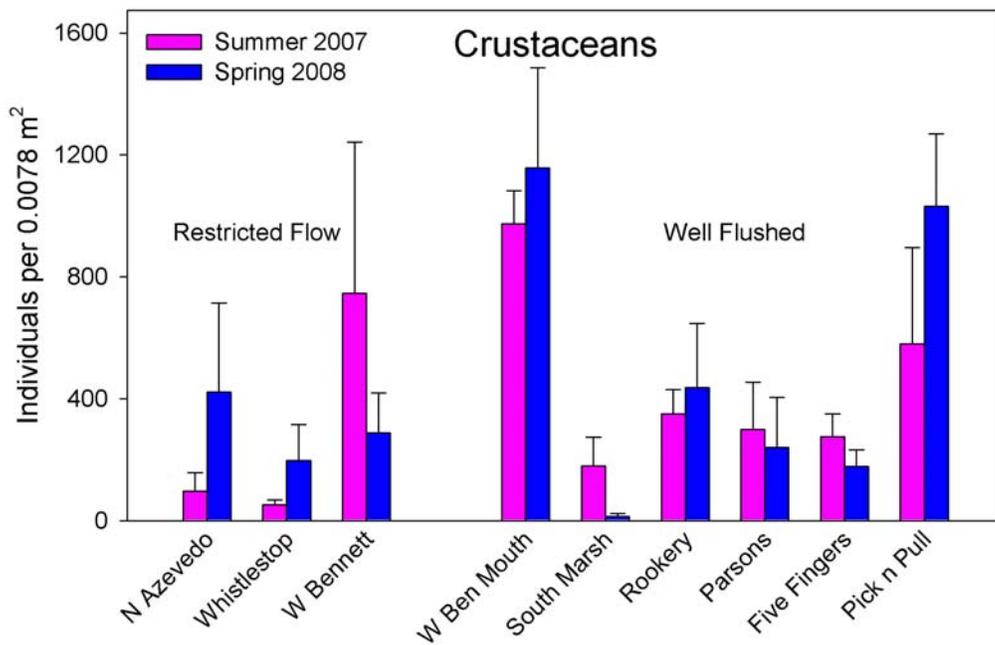
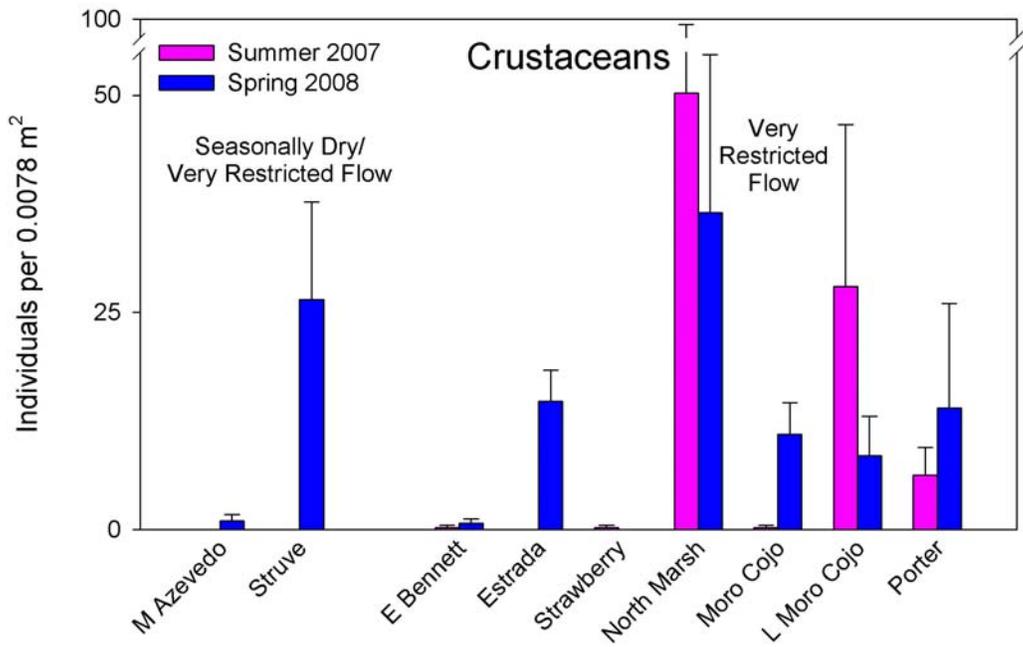


Figure 14. Abundance of crustaceans in the peripheral wetlands. Means and standard errors (N=4 per datum).

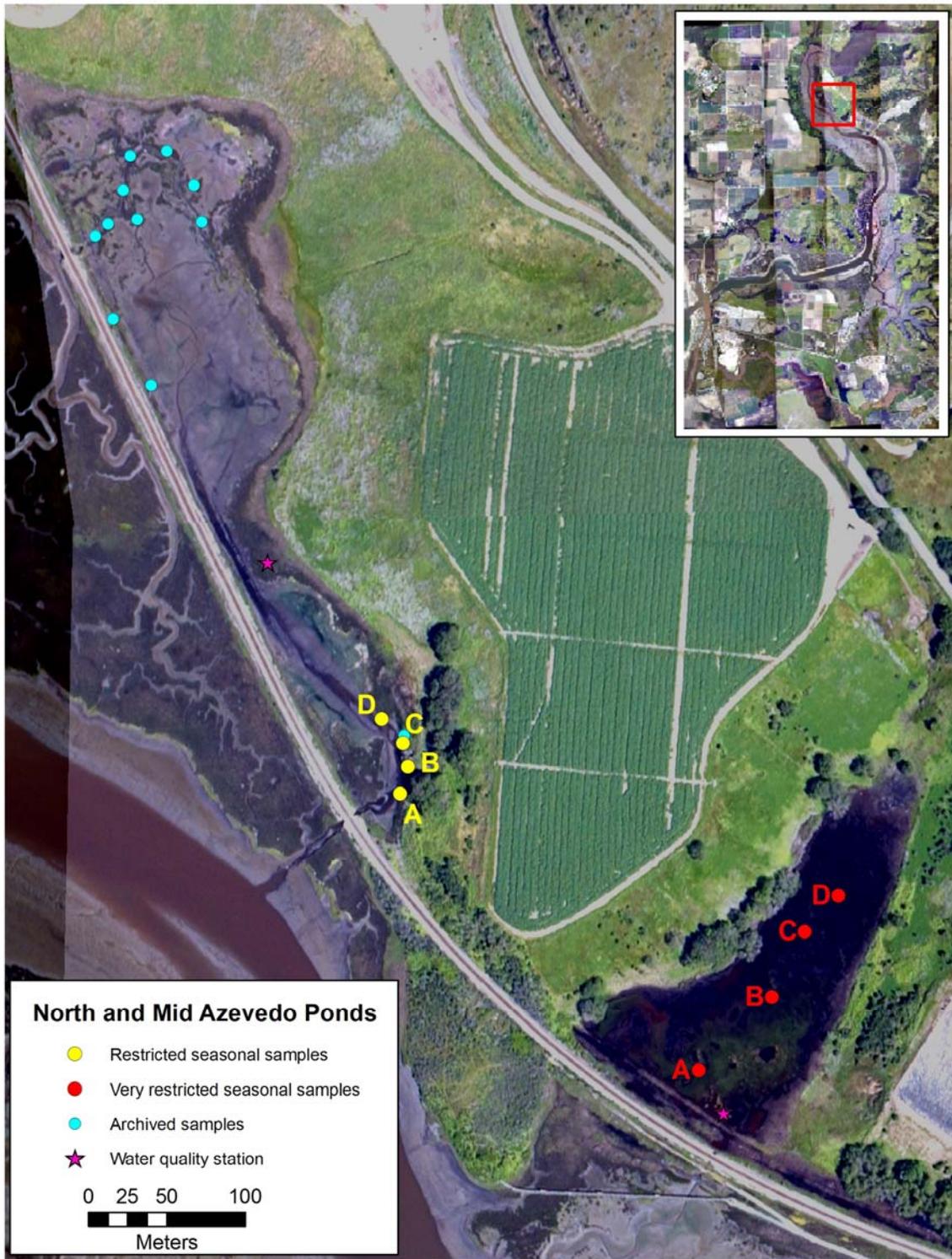


Figure 15. North (above) and Mid (below) Azevedo Ponds.



Figure 16. Struve Pond and East Bennett Slough.

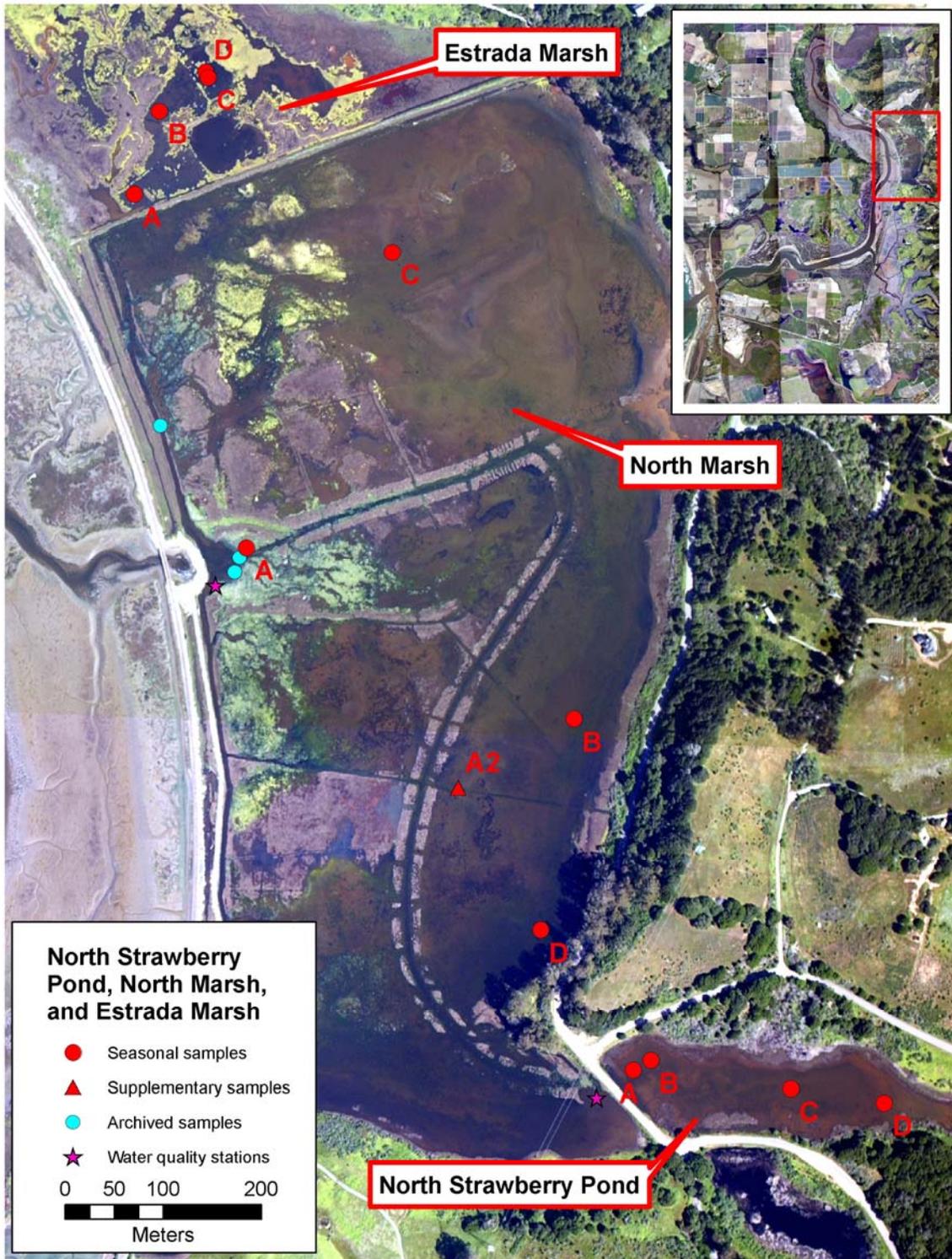


Figure 17. Estrada Marsh, North Marsh, and North Strawberry Pond.



Figure 18. Decomposing green macroalgae (*Ulva* spp.) at the border of North Marsh along Elkhorn Road. White microbial mats are common in the large bands of thick black organic debris (December 2008).

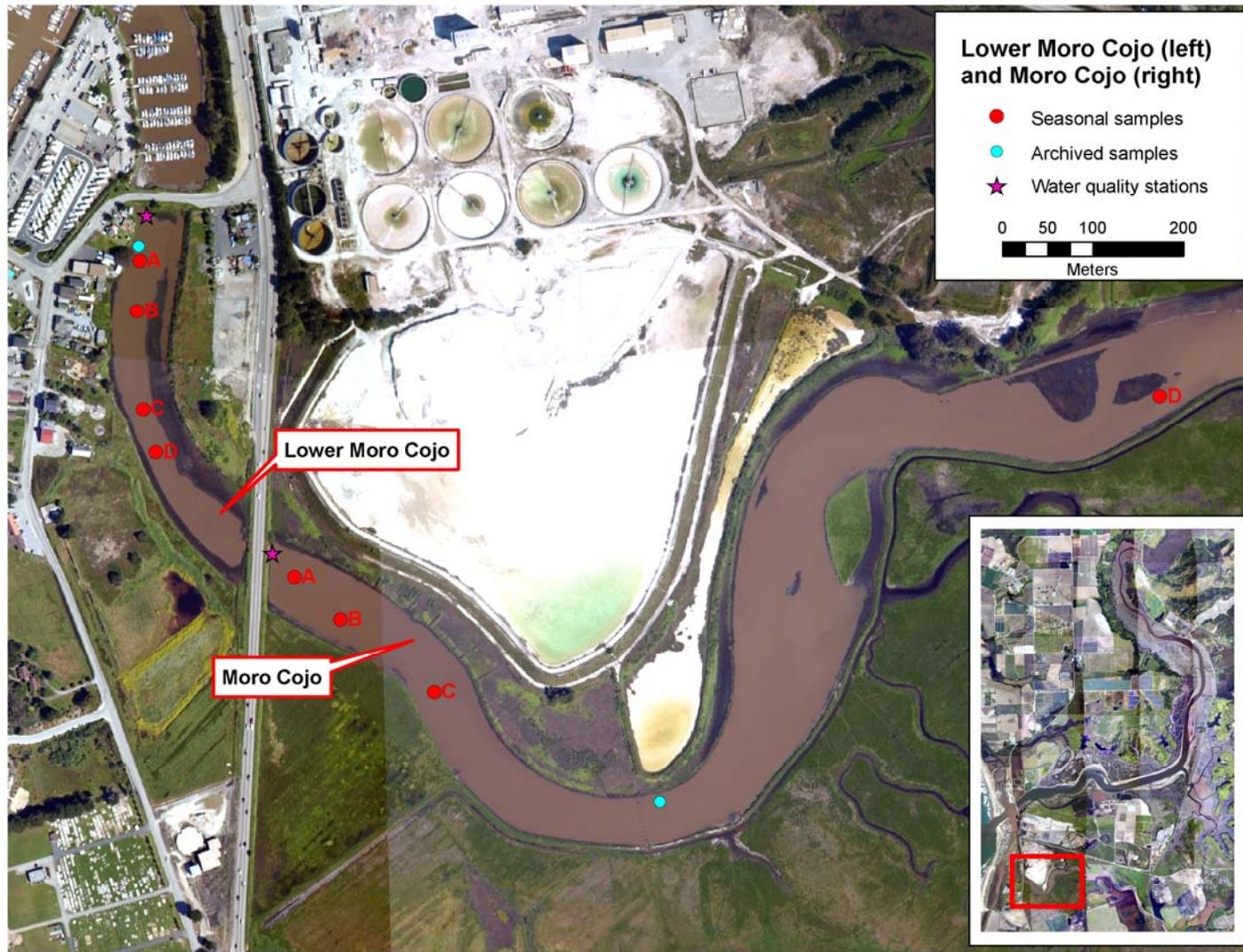


Figure 19. Moro Cojo Slough.



Figure 20. A white *Beggiatoa*-like microbial mat and purple cyanobacteria around Moro Cojo Slough.



Figure 21. A large, dying steelhead captured by Gage Dayton in March 2006 in Castroville Slough near the juncture with the main channel of Moro Cojo Slough. This is horrible steelhead habitat.

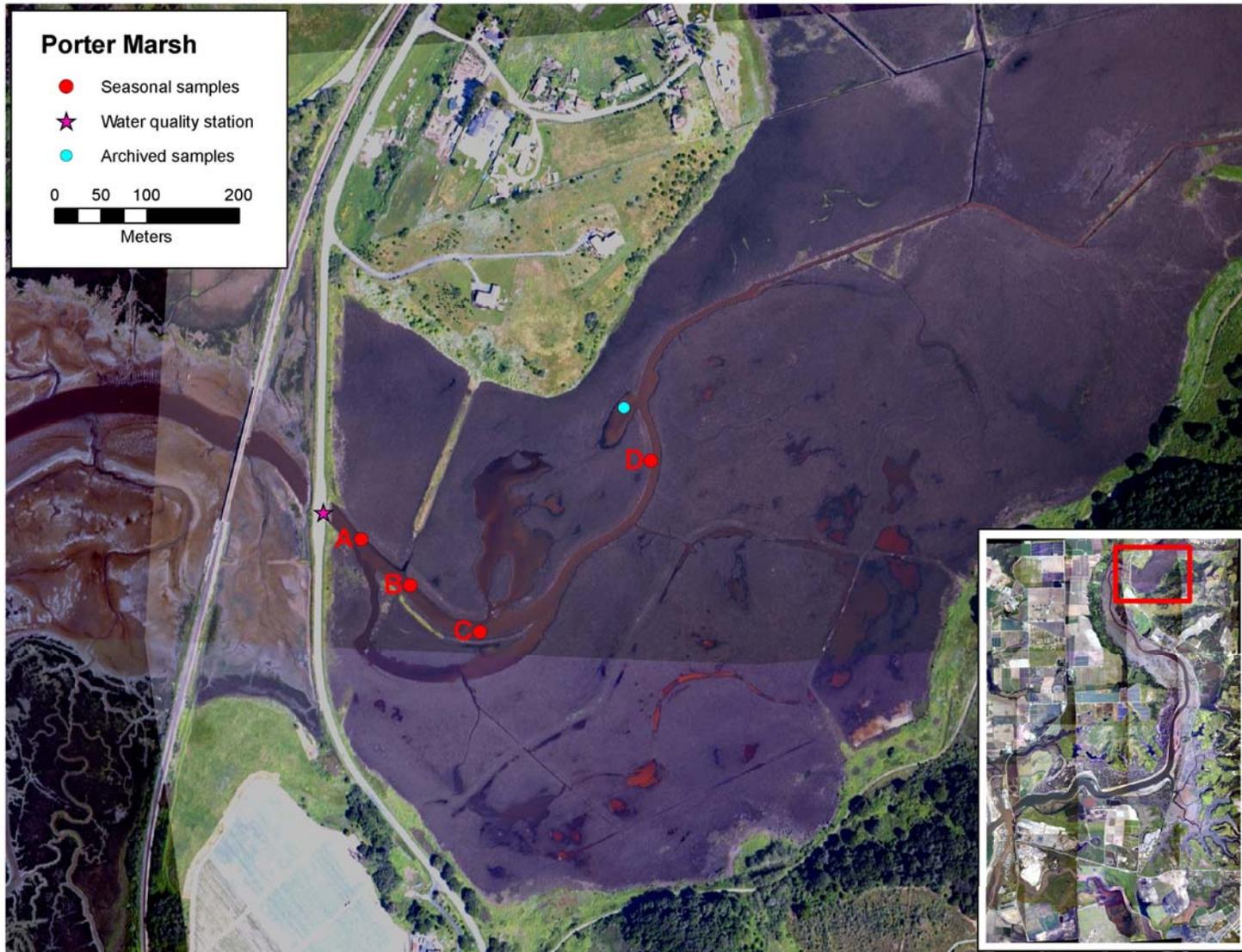


Figure 22. Porter Marsh.

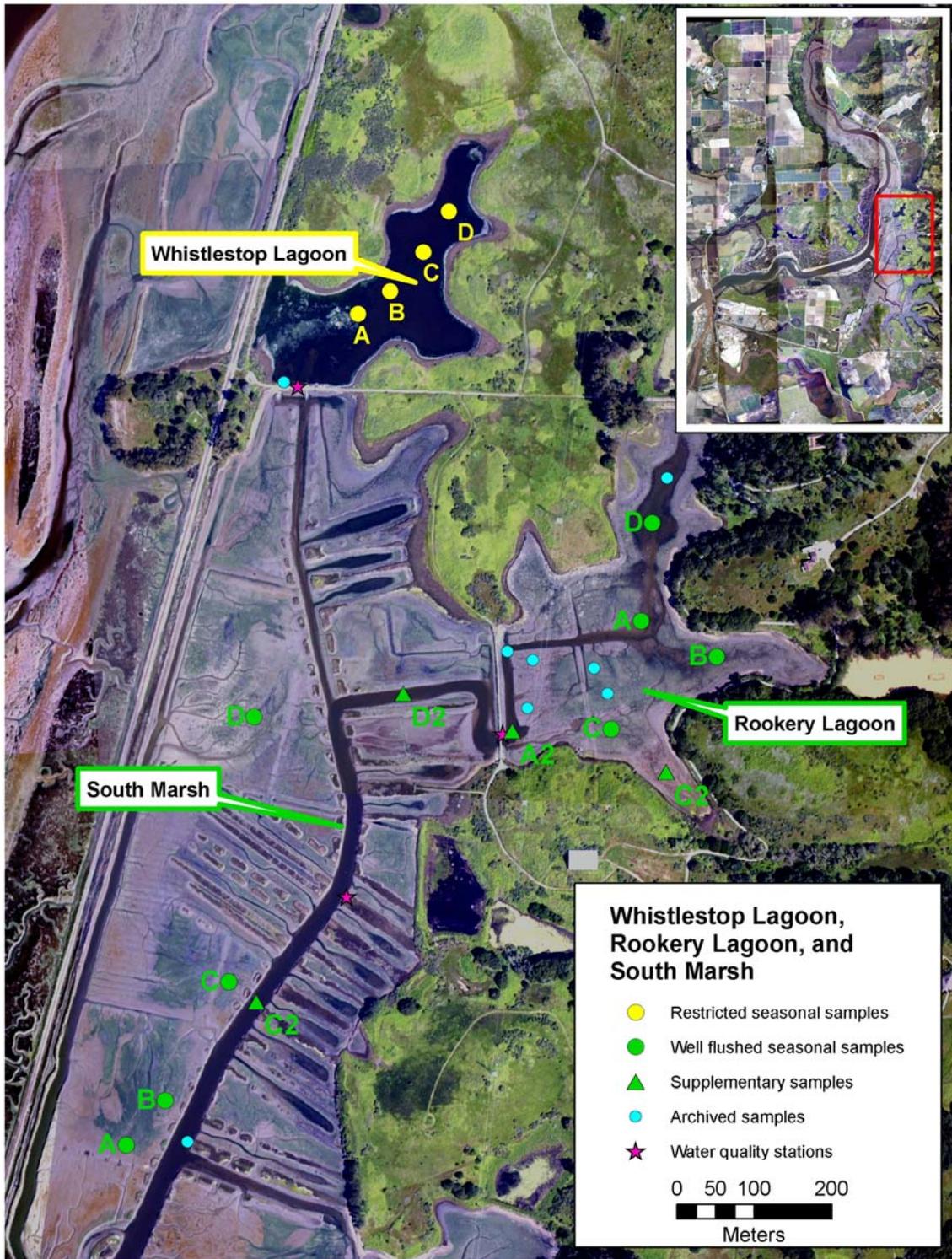


Figure 23. Whistlestop Lagoon, Rookery Lagoon, and South Marsh.



Figure 24. West Bennett Slough.

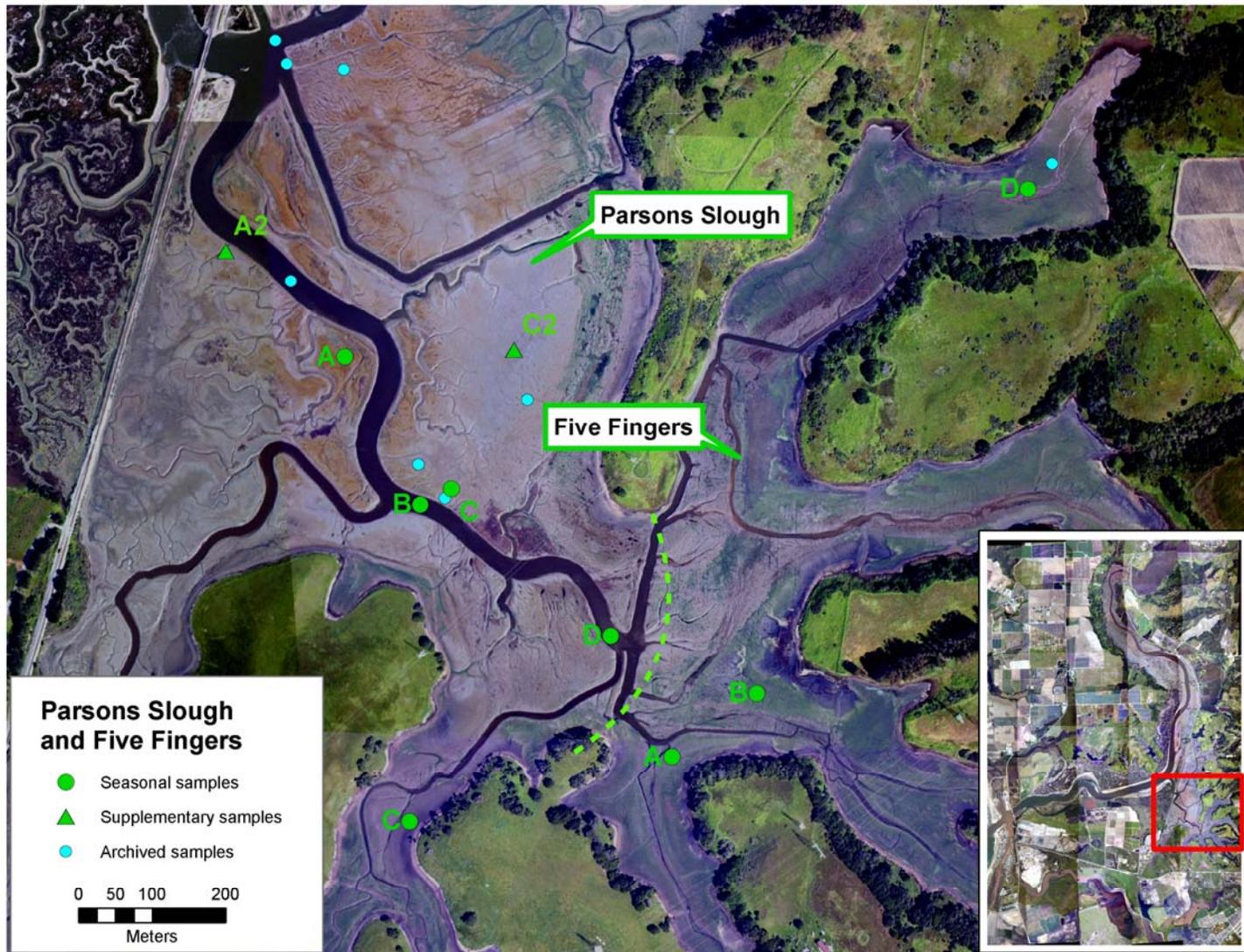


Figure 25. Parsons Slough and Five Fingers Marsh.

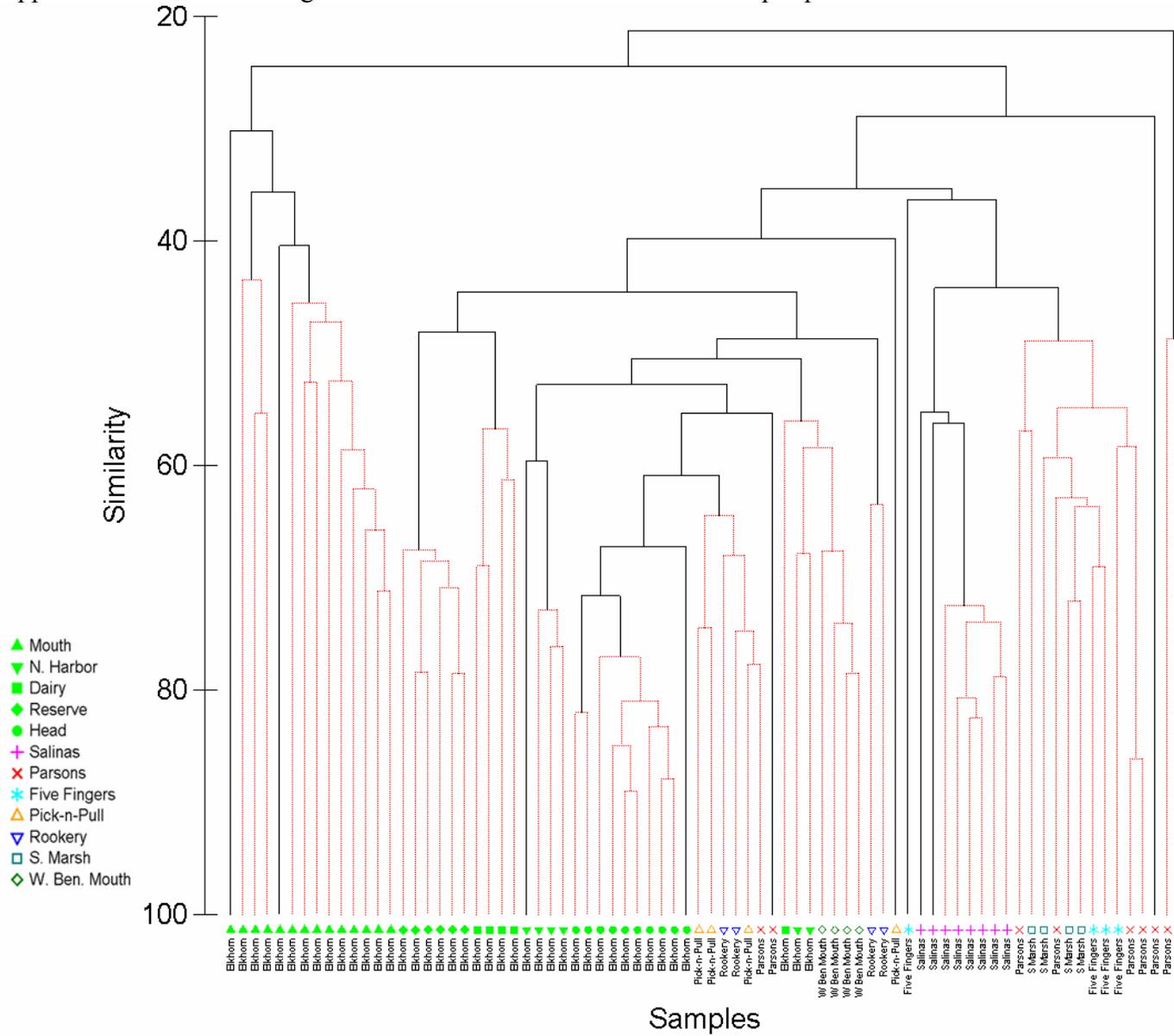


Figure 26. Pick-n-Pull Marsh.

Appendix 1. Results of ANOSIM and SIMPER analyses on seasonal peripheral wetland data.

Main Effects	Global R		P-value			
Year	0.099		0.002			
Tidal Group	0.436		0.001			
					SIMPER	
	R Statistic		P-value		(% dissimilarity)	
Within Year Pairwise Comparisons	2007	2008	2007	2008	2007	2008
Very Restricted v. Restricted	0.168	0.339	0.004	0.003	86.77	82.87
Restricted v. Well Flushed	0.364	0.169	0.001	0.014	69.26	69.67
Very Restricted v. Well Flushed	0.649	0.545	0.001	0.001	88.27	88.84

Appendix 3. Cluster dendrogram of main channel intertidal and 2007 peripheral wetlands data.



Appendix 3, continued. Cluster dendrogram of main channel intertidal and 2008 peripheral wetlands data.

