

Community Effects of the Non-Indigenous Aquatic Plant
Water Hyacinth (*Eichhornia crassipes*) in the
Sacramento/San Joaquin Delta, California

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Abstract

Community Effects of the Non-Indigenous Aquatic Plant
Water Hyacinth (*Eichhornia crassipes*) in the
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Biological invaders are widespread and can alter population dynamics and community structure of native ecosystems. Substantial habitat alteration by non-indigenous species can additionally affect the surrounding community. Aquatic plants are particularly invasive, especially in areas that are modified by humans. Water hyacinth (*Eichhornia crassipes*) is a floating aquatic plant that is non-indigenous to the Sacramento/San Joaquin Delta, California. Hyacinth is native to Brazil, and has a history of worldwide invasions. A common native that functionally occupies similar habitats as hyacinth is pennywort (*Hydrocotyle umbellata*). Based on the utilization of such habitats by invertebrates and fish, my main scientific question was: Has hyacinth modified the invertebrate assemblage structure and fish-invertebrate food web as compared to pennywort? To assess this, I sampled invertebrates in hyacinth and pennywort and analyzed fish diets in the surrounding area at three sites in the Delta during 1998 and 1999. I also took measurements of leaf density, root structure, dissolved oxygen and temperature.

Ecological differences between hyacinth and pennywort were linked to habitat architecture. Insects had higher densities in pennywort, and there were significant differences in the composition of insect assemblages. Leaf density was higher in pennywort, although hyacinth formed taller canopies. Taxa richness and diversity of invertebrates were usually higher in pennywort early in the summer, but were higher in hyacinth during later months. Hyacinth roots had more surface area and biomass, and dissolved oxygen levels were lower. Overall densities of epibenthic and benthic macroinvertebrates were usually greater in pennywort, and taxonomic compositions of aquatic invertebrate assemblages did show significant differences. Amphipods and isopods were particularly abundant living epiphytically in the root masses, including several new introduced species: the amphipod *Crangonyx floridanus*, and the isopods *Caecidotea racovitzai* and *Asellus hilgendorffii*. In general, *C. floridanus* was significantly more abundant in hyacinth and was not prevalent in fish diets, presumably due to the greater refuge value of hyacinth roots. The native amphipod *Hyaella azteca* was often significantly more abundant in pennywort, and was heavily preyed upon by fish. Coupled with the management challenges of hyacinth, such ecological modifications make it an even more influential invader.

TABLE OF CONTENTS

	Page
List of Figures.....	iii
List of Tables.....	v
Introduction.....	1
Materials and Methods.....	8
Study Area.....	8
Physical Sampling.....	9
Biological Sampling.....	11
Epiphytic Macroinvertebrates.....	11
Epibenthic/Benthic Macroinvertebrates.....	12
Insects.....	12
Fish.....	13
Data Interpretation and Statistical Tests.....	16
Results.....	18
General Characteristics.....	18
Physical Sampling.....	18
Biological Sampling.....	19
Epiphytic Macroinvertebrates.....	19
Epibenthic/Benthic Macroinvertebrates.....	21
Insects.....	23
Fish.....	24

Discussion.....	50
Biological and Physical Differences.....	50
New Discoveries of Amphipods and Isopods.....	54
Introduced Species Theory.....	55
List of References.....	60
Appendix A: Descriptions of Introduced Amphipods and Isopods.....	74

LIST OF FIGURES

Number	Page
Figure 1. Map of study sites.....	17
Figure 2. Leaf density of hyacinth and pennywort.....	28
Figure 3. Regression of weight differences for known surface areas.....	28
Figure 4. Surface area of roots.....	29
Figure 5. Biomass of roots.....	29
Figure 6. Dissolved oxygen levels.....	30
Figure 7. Water temperatures.....	30
Figure 8. Overall density and standing stock of epiphytic macroinvertebrates.....	31
Figure 9. Density of common epiphytic macroinvertebrates.....	32
Figure 10. Standing stock of common epiphytic macroinvertebrates.....	33
Figure 11. Cumulative numerical percent of dominant epiphytic macroinvertebrates	34
Figure 12. Overall density of epibenthic/benthic macroinvertebrates.....	34
Figure 13. Density of common epibenthic/benthic macroinvertebrates.....	35
Figure 14. Cumulative numerical percent of dominant epibenthic/benthic macroinvertebrates.....	36
Figure 15. Overall density of insects.....	36
Figure 16. Density of common insects.....	37
Figure 16 (continued). Density of common insects.....	38
Figure 17. Cumulative numerical percent of dominant insects.....	39
Figure 18. IRI graphs of fish diets for bluegills caught adjacent to FAV at Site A.....	40

Figure 19. IRI graphs of diets for fish caught directly underneath hyacinth at Site C.....	41
Figure 20. Top five prey items of common nearshore juvenile fish.....	42
Figure 21. Descriptive diagrams of amphipods and isopods.....	85

LIST OF TABLES

Number	Page
Table 1. Average densities of epiphytic macroinvertebrates for all sites.....	43
Table 2. Average standing stock of epiphytic macroinvertebrates for all sites.....	44
Table 3. Taxa richness and the Shannon-Weiner diversity index.....	45
Table 4. Average densities of epibenthic/benthic macroinvertebrates at all sites.....	46
Table 5. Average densities of terrestrial insects at all sites.....	47
Table 6. Fish caught adjacent to patches of hyacinth and pennywort at Site A.....	48
Table 7. Values for the Ivlev Electivity Index between <i>C. floridanus</i> and <i>H. azteca</i>	49
Table 8. Fish caught directly underneath patches of hyacinth at Site C.....	49
Table 9. Native range and non-indigenous populations of the amphipod <i>Crangonyx floridanus</i> and the isopods <i>Caecidotea racovitzai</i> and <i>Asellus hilgendorfi</i>	59
Table 10. Samples, sites, and dates of occurrences of the amphipod <i>Crangonyx floridanus</i> and the isopods <i>Caecidotea racovitzai</i> and <i>Asellus hilgendorfi</i>	86
Table 11. Summary of the criteria for introduced species.....	86

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Introduction

Biological invaders such as water hyacinth (*Eichhornia crassipes*) have become widespread on a global level (Drake and Mooney 1989). Although policy to control the spread of invasive species is becoming more common, the congruent ecological impacts of specific organisms are less well known. Exotic species can alter the population dynamics and community structure of native ecosystems (Elton 1958, Mooney and Drake 1986, Luken and Thieret 1997). They tend to be most successful in disturbed habitats (Drake and Mooney 1989), consistent with the intermediate-disturbance hypothesis (Connell 1978, Moyle and Light 1996). Ecological concern over non-indigenous species is especially applicable to the Sacramento/San Joaquin Delta, CA, as this estuary is considered one of the most modified by human activity in the United States (Nichols et al. 1986), and may be the most invaded estuary in the world (Cohen and Carlton 1998).

Aquatic plant invasions are a nuisance worldwide, especially in environments that have been extensively modified by humans (Barret 1989). Invasive plant theory predicts that a release from environmental constraints due to altered hydrology can often lead to a successful invasion (Galatowitsch et al. 1999). As a result, disruptions of wetland ecosystems involving irrigation canals, hydroelectric projects and construction of artificial lakes make such areas particularly susceptible to invasions (Barret 1989). The rapidly colonizing nature of many aquatic plants coupled with modified hydrological regimes often produces conditions for successful invasions (Crawley 1987, Ashton and Mitchell 1989, Rejmanek and Richardson 1996). Such a combination is exemplified to

the extreme for worldwide invasions of hyacinth, as hyacinth is often termed a 'perfect invader' (Ashton and Mitchell 1989).

Non-indigenous species such as hyacinth can be particularly influential in the surrounding community due to habitat alteration. Studies on habitat-modifying organisms, or 'ecosystem engineers', have increased in recent years (Jones et al. 1994, 1997, Bertness et al. 1999) and are beginning to be applied more to non-indigenous species (Bertness 1984, Posey 1988, Vitousek 1990, Richardson et al. 1995, Ricciardi et al. 1997, Schmitz et al. 1997, Woods 1997, Crooks 1998, Crooks and Khim 1999). Crooks and Khim (1999) provide detailed examples of biogenic structures in many different aquatic habitats. Hyacinth can be labeled as such an invasive habitat modifier, as it provides a structurally complex canopy. In addition to the effects of forming a dense vegetative mat, the physical structure of the roots hanging in the water column and the leaves above water provide habitat for other species. Furthermore, organic fallout from the canopy can influence the benthic zone.

Introduced populations of hyacinth are the focus of controversy over issues of control and management all over the world (Gopal 1987). The plants are valued by ornamental pond enthusiasts for their beautiful flowers, which is how most introductions of hyacinth are initiated (Gopal 1987). It is remarkably easy to order hyacinth, even in locations where non-indigenous wild populations are established. Once the plants are introduced into the natural environment they rapidly increase in coverage, as hyacinth has the highest growth rate of any saltwater, freshwater or terrestrial vascular macrophyte (Wolverton and McDonald 1979). Doubling times range between 6-18 days (Gopal

1987, Schmitz et al. 1993). For these reasons, hyacinth has earned such nicknames as 'the weed from hell' and 'the beautiful devil' (Gopal 1987).

Hyacinth is native to Brazil and was first introduced to North America at the Cotton Centennial Exposition in New Orleans in 1884 (Gopal 1987). Thereafter, it rapidly became established in Florida by 1890. The first record in California is from 1904 when it was found in Yolo County around Clarksburg (Bock 1966, USCOE 1985, Gopal 1987). By 1947 it started to become a problem in the Sacramento/San Joaquin Delta, and by 1972 there were requests to control its abundance (USCOE 1985). Its early distribution in California was documented in detail by Bock (1966). In the 1980's, its prevalence in the Delta reached high enough levels that it became a hindrance to boat traffic. There are several reasons why hyacinth may have taken so long to prosper in the Delta, including: (1) An increase in stable freshwater flows in the area due to dams, reducing the severity of floods and high flows in the winter that can flush hyacinth out of the system. Such an abiotic factor associated with the altered hydrologic regime has also been attributed to the success of invasive fish in the Delta (Moyle and Light 1996); and (2) Hyacinth is a tropical plant, so it may have taken awhile for it to adapt to the temperate climate of central California (Finlayson 1983). In any case, 506 hectares of hyacinth covered the Delta in 1981, or 241 of the 1094 kilometers of waterways (Finlayson 1983). This was the spark to initiate an extensive biological and chemical control program headed by the California Department of Boating and Waterways (DBW), which actively controls coverage of hyacinth with spraying of the chemical 2,4-D. 202 hectares of hyacinth were treated with 2,4-D in 1983 with an annual budget of \$200,000.

Although the abundance of hyacinth has drastically decreased in the Delta, control efforts have steadily increased, as 985 hectares of hyacinth were chemically treated during 1998-99 with an annual budget of approximately \$1,000,000 (CDBW 1998, Pat Thalken, pers. com.). The weevils *Neochetina bruchi* and *N. eichhorniae* and the moth *Samaodes albiguttalis* were released as biological control agents in 1982 and 1983, without much success (USCOE 1985). Further control with biological agents has not been pursued.

Despite all the focus by society and management on the problems and control of hyacinth, the ecological processes associated with hyacinth have not been researched adequately in the Delta. Effects of hyacinth on community dynamics as compared to its native functional counterparts are particularly unknown. Pennywort (*Hydrocotyle umbellata*) is the predominant native floating aquatic vegetation (FAV) in the Delta. Pennywort tends to occupy similar habitats as hyacinth, but again, research has not been done to see how fish and invertebrates use these habitat types. One would expect a modification in community dynamics in response to changes in: spatial complexity of the vegetative structure, shading effects of dense canopies, amount and location of plant biomass, densities of vegetation patches, plant detritus deposition rate, growth rates, dissolved oxygen levels, and rates of evapotranspiration (Penfound and Earle 1948, McVea and Boyd 1975, Wolverton and McDonald 1978, Center and Spencer 1981, Crowder and Cooper 1982, Reddy 1984, Gopal 1987, Jantrarotai 1990, Schmitz et al. 1993, Madsen 1997). Research specific to hyacinth and pennywort in Florida has shown that overall dry biomass of hyacinth is 259% greater than pennywort (Reddy 1984). Other research in Florida on hyacinth and a different species of pennywort (*Hydrocotyle*

ranunculoides) has shown that overall dry biomass of hyacinth is 161% greater, and the maximum root length of hyacinth is 164% greater (Jantrarotai 1990).

The roots of hyacinth can be important habitat for epiphytic macroinvertebrates (aquatic invertebrates living on macrophytes; Hutchinson 1967, Schramm et al. 1987), especially amphipods (Schramm et al. 1987, Bailey et al. 1993, Bryan 1993). Epiphytic invertebrates can be much more abundant than benthic invertebrates and are positively correlated to the amount of colonizable surface area available (Marcheck 1966, Crowder and Cooper 1982, Dvorak and Best 1982, Schramm et al. 1987). Furthermore, fish such as bluegills (*Lepomis macrochirus*) selectively feed on epiphytic invertebrates over other sources of prey (Werner and Hall 1976, 1979, Keast 1978, Mittelbach 1984, Schramm and Jirka 1989). FAV can also be beneficial as a nursery habitat for juvenile fishes and many invertebrates (Sazima 1985, Gopal 1987, Werner and Hall 1988, Schramm and Jirka 1989, Dibble 1996). Effects of hyacinth on the fish-invertebrate food web in the Delta are unknown, and could be important due to the prominence of hyacinth as a major habitat zone in shallow water areas. This is all dependent on patch size, as large patches of hyacinth can cause low dissolved oxygen levels, high input of plant detritus, and senescence of submerged vegetation (Lynch et al. 1947, Gopal 1987). However, with the onslaught of chemical control against hyacinth in the Delta, canopies of hyacinth usually remain constrained to small patches fringing the marsh edge. Back channels in the marsh can also become overrun with hyacinth due to limited access by chemical control methods.

A comprehensive ecosystem study in the Sacramento/San Joaquin Delta provided the opportunity to address gaps in the knowledge of hyacinth (BREACH; Simenstad et al. 1999). BREACH focused on predicting the rates and patterns of restoration of breached-levee wetlands. Research on hyacinth fit into the overall BREACH study objectives, as hyacinth canopies form on the marsh fringe and may be influential in the development of the adjacent marsh community. In warmer climates where hyacinth grows throughout the year, permanent floating islands are created, which deposit large amounts of organic matter. These floating islands can greatly accelerate pathways of succession, allowing emergent and eventually riparian vegetation to colonize (Penfound and Earle 1948, Trivedy et al. 1978, Gopal 1987, Woods 1997). Although such patterns of succession have been reported in Louisiana (Penfound and Earle 1948), this pathway is abbreviated in central California, as low winter temperatures inhibit growth of hyacinth, usually preventing formation of such permanent floating islands.

Based on the previous statements involving the utilization of FAV by invertebrates and fish, the main scientific question for my research is: Has hyacinth modified the invertebrate assemblage structure and the associated fish-invertebrate food web as compared to its native functional counterpart pennywort? Within this broad question, my research has five main objectives:

- (1) Determine whether there are significant differences between hyacinth and pennywort in the physical parameters of leaf density, surface area and biomass of roots, dissolved oxygen and water temperature.

- (2) Determine whether there are significant differences in epiphytic macroinvertebrate assemblage composition and abundance between hyacinth and pennywort.
- (3) Determine whether there are significant differences in epibenthic and benthic macroinvertebrate assemblage composition and abundance between hyacinth and pennywort.
- (4) Determine whether there are significant differences in insect assemblage composition and abundance between hyacinth and pennywort.
- (5) Determine whether the diets of resident fishes are different surrounding patches of hyacinth and pennywort.

Materials and Methods

Study Area

All study sites were located in the Sacramento/San Joaquin Delta, California, USA (~38.0° N, 121.5° W). Three study sites were utilized in this project, hereafter referred to as Site A (Mandeville Tip), Site B (Brown's Island), and Site C (Mildred island) (Fig. 1). These three sites were a subset of the study sites used for the BREACH research program (Simenstad et al. 1999). This area has a mild temperate climate, and represents one of the most northern established populations of hyacinth in the world (Bock 1966, Finlayson 1983, Gopal 1987). The Delta is heavily influenced by human activity, including agricultural, recreational and industrial activities (Nichols 1986). Historically, the Delta was almost all wetlands characterized by the tule grass (*Scirpus* spp., hereafter referred to as 'tule') with some natural levees and riparian habitat (woody vegetation, mostly *Salix* spp.; Atwater et al. 1979, TBI 1998). Approximately 97% of these wetlands have been leveed and drained predominantly for agricultural purposes (Atwater and Belknap 1980, Herbold and Moyle 1989, SFEP 1991). Consequently, the majority of channels are now rip-rapped and constrained and deep water ship channels are regularly dredged. Although salinity wedges have historically entered the Delta, current water management has prevented this from happening, mainly due to controlled water flows that increase freshwater inflow during summer months (Kelley 1966, Nichols et al. 1986, CDWR 1993). Such water management maintains freshwater available for irrigation and drinking purposes. Due to freshwater usage, the overall flow into San Francisco Bay is less than 40 percent of historic levels (Nichols et al. 1986). Benthic

sediments in the Delta are soft-bottom, consisting of a mixture of sand, silt and clay (Hazel 1966, Siegfried et al. 1980, Hymanson et al. 1994). Tidal range is approximately one to two meters (Kelley 1966, CDWR 1993).

Sampled FAV patches were located on the marsh fringe. FAV patches were not utilized if they did not look healthy, since this could indicate recent chemical control with 2,4-D. Five patches of both hyacinth and pennywort were randomly sampled at each site. These patches occupied indentations in the marsh fringe and were separated by clumps of tule. The exception to this was the pennywort patches at Site A where patches were not clearly delineated by tule separation. For this reason, a transect line was deployed through this site and five random points along the transect were sampled.

Site A was studied in the months of April, June and July 1998, and June 1999. Chemical control at Site A exterminated all patches of hyacinth in August 1998. Therefore, sampling was conducted at Sites B and C in the months of August 1998 and June 1999.

Physical Sampling

Intensive sampling of the physical structure of the FAV canopies was done in June 1998 at Site A, and August 1998 at Sites B and C. This was congruent with epiphytic invertebrate sampling described below. Leaf density was determined by counting the number of leaves in a 0.5-m² quadrat. Surface area of the canopies was roughly determined by measuring the length and width of each patch. The roots from the epiphytic invertebrate sampling were analyzed for biomass and surface area. Biomass

was determined by measuring preserved wet weight of the roots. The roots were blotted dry with a towel, allowed to air dry for 10 minutes, and weighed to nearest milligram. Surface area of the roots was measured using a surfactant technique (Harrod and Hall 1962, Hicks 1977). A soapy solution was mixed in a bucket, containing 60 ml of Liquinox soap in 6 liters of water. This soapy solution was left overnight so that the bubbles dispersed. For each root sample, five 1 gram dried samples (as above) were taken and dipped in the soapy solution. The excess soap was shaken off, so that a monolayer of soapy solution was retained around the root surface. Each sample was then reweighed. The difference in weight can be standardized to the weight difference from known surface areas, allowing calculations of surface area for the root samples. Known surface areas of 25, 100, 225, 400, 625, and 900 cm² for tinfoil were utilized to calculate these weight differences as above, five samples for each surface area. A regression was fit to this data and the model was used to calculate surface area of the root samples from their weight differences. All weight differences from the root samples fell within those of the known surface areas.

Measurements of dissolved oxygen and temperature were taken at each FAV patch congruent with sampling of epiphytic invertebrates in August of 1998 at Sites B and C. These measurements were taken with a YSI model handheld meter, with the probe directly underneath the FAV canopies.

Biological Sampling

Epiphytic Macroinvertebrates

Epiphytic macroinvertebrates living in association with the root masses of the vegetation were sampled by manually collecting plant samples (Schramm et al. 1987, 1989). Amount of canopy surface area sampled was determined by correlating the number of leaves in each plant sample to the number of leaves in a 0.5-m² quadrat. Samples were taken in the middle of the FAV canopies, with five replications for each month of sampling. All macroinvertebrates were then separated from the collected root mass by vigorously shaking each root sample in a bucket containing 10% isopropyl alcohol, causing the macroinvertebrates to detach from the roots. The alcohol-solution was then sieved at 0.5 mm to collect only the macroinvertebrates and fixed in 5% buffered formaldehyde solution. These samples were later preserved in 70% isopropanol in the laboratory. Roots from each sample were retained separately in 70% isopropanol and brought to the laboratory, in order to take measurements of surface area and biomass (as above). Any additional macroinvertebrates that were not detached from the roots in the alcohol-solution were later separated in the laboratory. Invertebrates were counted and identified to the lowest practical taxonomic level with light microscopy. Standing stock was estimated by measuring the preserved wet weight of each taxon. Excess liquid was towed-off, and each taxonomic group weighed to nearest 0.1 mg. Numbers and standing stock of invertebrates were standardized to 1 m² surface area of the canopy, allowing for comparisons between strata and with other invertebrate sampling as density (number/m²) and standing stock (g/m²), respectively.

Epibenthic/Benthic Macroinvertebrates

Benthic cores were used to sample epibenthic and benthic macroinvertebrates beneath FAV canopies at sites A and B. Cores were taken to 10 cm depth beneath the sediment surface with a core area of 0.0024 m². The core was made of metal pipe with sharp edges so that it was able to cut through the organic material underneath the canopies. Samples were taken in the middle of the FAV canopies, with five replications for each month of sampling. The core was inserted into a hole in each patch, sampling both epibenthic macroinvertebrates in the water column (approximately 1 m depth) and benthic macroinvertebrates in the sediment. Samples were immediately fixed in 5% buffered formaldehyde solution containing rose bengal dye. The samples were sieved at 0.5 mm in the laboratory in order to clean the samples of sediment and retain only macroinvertebrates. The samples were then transferred and preserved in 70% isopropanol. Invertebrates were counted and identified to the lowest practical taxonomic level with light microscopy. As with the epiphytic invertebrate sampling, numbers of invertebrates were standardized to 1 m² surface area of the canopy, allowing for comparisons between strata and with other invertebrate sampling as density (number/m²).

Insects

Passive insect fallout traps were used to sample insects living in association with the FAV canopies at sites A and B. These traps consisted of a rectangular tray (0.0782 m²) partly filled with soapy water. The soap disrupts the surface tension of the water, trapping insects that come into contact with the water (Sutherland 1996). Samples were

taken in the middle of the FAV canopies, with five replications for each month of sampling. The trays were nestled into the canopy, so that they floated on the water surface with the leaves of the canopy surrounding the tray. These traps were tethered with PVC poles to the specific site, allowing vertical movement with the tides. The trays were deployed for 24 hours after which the soapy water was sieved at 0.106 mm and the insects preserved in 70% isopropanol. Invertebrates were counted and identified to the lowest practical taxonomic level with light microscopy. As with the other invertebrate sampling, numbers of insects were standardized to 1 m² surface area of the canopy, allowing for comparisons between strata and with other invertebrate sampling as density (number/m²).

Fish

At Site A, fish were sampled in nearshore habitat adjacent to FAV during June and July 1998. The California Department of Water Resources (DWR) directed this sampling as part of the BREACH study (Simenstad et al. 1999). Depletion beach seine sampling (7.6 m x 1.2 m, 3.2 mm mesh) inside block-net enclosures (range 30-48 m²) under 1.5 meters water depth was used to capture fish along the marsh edge. FAV patches were located on the same marsh edge. Perimeter stakes were set at least 24 hours in advance to minimize disturbance in the area. The following day the area was surrounded with block nets (25 m x 1.2 m, 3.2 mm mesh). The enclosure was repeatedly swept with a beach seine to remove fish. At least four hauls in alternating directions were conducted until juvenile fish catch decreased for two consecutive hauls. Fish

species were counted and the first twenty of each species measured in fork length (mm). A subset of bluegills (*Lepomis macrochirus*) were preserved in 5% buffered formaldehyde solution and saved for fish diet analysis. Bluegills were chosen for diet analysis because they are omnivorous fish that have been shown to feed on macroinvertebrates in FAV habitats (Werner and Hall 1979, McGinnis 1984, Schramm and Jirka 1989), are opportunistic feeders, and were present in substantial abundance to guarantee sufficient sample size. Bluegills are also non-indigenous to the Delta.

DWR did not conduct fish sampling directly adjacent to FAV at Sites B and C. However, they did sample fish in many areas surrounding sites A, B, and C using the same methodology as above. Representative fish of common species from these areas were saved for diet analysis.

The density of the FAV canopies and steep incline of the channels made it near impossible to use seine nets to sample fish directly underneath FAV. Seining (7.6 m x 1.2 m, 3.2 mm mesh) was only successful in directly sampling five patches of hyacinth at Site C. The net was pulled underneath the canopy, during which the entire patch of hyacinth was thrown behind the net allowing the net to be hauled onto the shore. Because this method is destructive, it was not used on the native pennywort patches. All fish sampled from the hyacinth patches were preserved in 5% buffered formaldehyde solution and saved for fish diet analysis. This enabled comparisons with DWR sampling adjacent to FAV to ensure that fish diets between adjacent habitat and underneath FAV were comparable, and that bluegills actively utilize FAV habitat. Various other techniques of sampling fish directly underneath FAV were attempted without much

success. Other techniques were found either not to be cost effective (pop-nets), and/or not to have sufficient sample size (minnow traps).

Fish saved for diet analysis were measured (fork length in mm, preserved wet weight in g). The stomachs were then dissected from the fish and the gut contents removed. Overall gut contents were blotted dry and weighed. Taxa were then separated and identified to the lowest possible taxonomic level with light microscopy. Each taxonomic group was then counted, blotted dry and weighed. Levels of stomach content digestion and stomach fullness were estimated. Prey items were then ranked based on modified Index of Relative Importance values (IRI; Pinkas 1971, Cailliet 1977, Simenstad et al. 1991, Shreffler et al. 1992):

$$\text{IRI} = \frac{\% \text{ frequency}}{\% \text{ of occurrence}} \times \left[\frac{\% \text{ numerical}}{\% \text{ composition}} + \frac{\% \text{ gravimetric}}{\% \text{ composition}} \right]$$

Diet overlap with sampled aquatic prey resources was calculated using a modified Percent Similarity Index (PSI; Hulbert 1978):

$$\text{PSI} = \sum_{i=1}^n \text{minimum} (p_{xi}, p_{yi})$$

where p_{xi} = percentage of prey i in predator x , and p_{yi} = percentage of prey i in sampled aquatic prey resources. Ivlev's electivity index was used to compare differences in fish selectivity of the major amphipod taxa present in the sampled invertebrates (Ivlev 1961):

$$E_i = (r_i - p_i)/(r_i + p_i)$$

where E_i is the index of electivity, r_i is the percent of a prey item in the fish diet, and p_i is the percent of a prey item in the environment. Values fall between a range of -1 to 1, with positive values indicating positive selectivity, negative values indicating negative selectivity, and values around 0 indicating neutral selectivity. The Ivlev electivity index was chosen as it is easy to interpret, and gives similar results to other indices (Lechowicz 1982, Kline 1996).

Data Interpretation and Statistical Tests

Measurements of density (number/m²), taxa richness, and the Shannon-Weiner diversity index were calculated for all invertebrate sampling. Similar measurements of standing stock (g preserved wet/m²) were calculated only for epiphytic macroinvertebrates. Mean numbers and standard errors for each taxon were calculated. Parametric two sample t-tests were used to statistically compare means for biological and physical sampling between hyacinth and pennywort at each study site ($\alpha = 0.05$). Therefore, for all measurements between hyacinth and pennywort, $H_0: u_1 = u_2$ and $H_a: u_1 \neq u_2$. The parametric t-test is a robust statistic, meaning it can withstand considerable departures from its underlying assumptions of normality and homogeneity of variance, especially if $n_1 = n_2$ and the test is two-tailed, as is the case with our study design (Simenstad et al. 1991, Zar 1996).

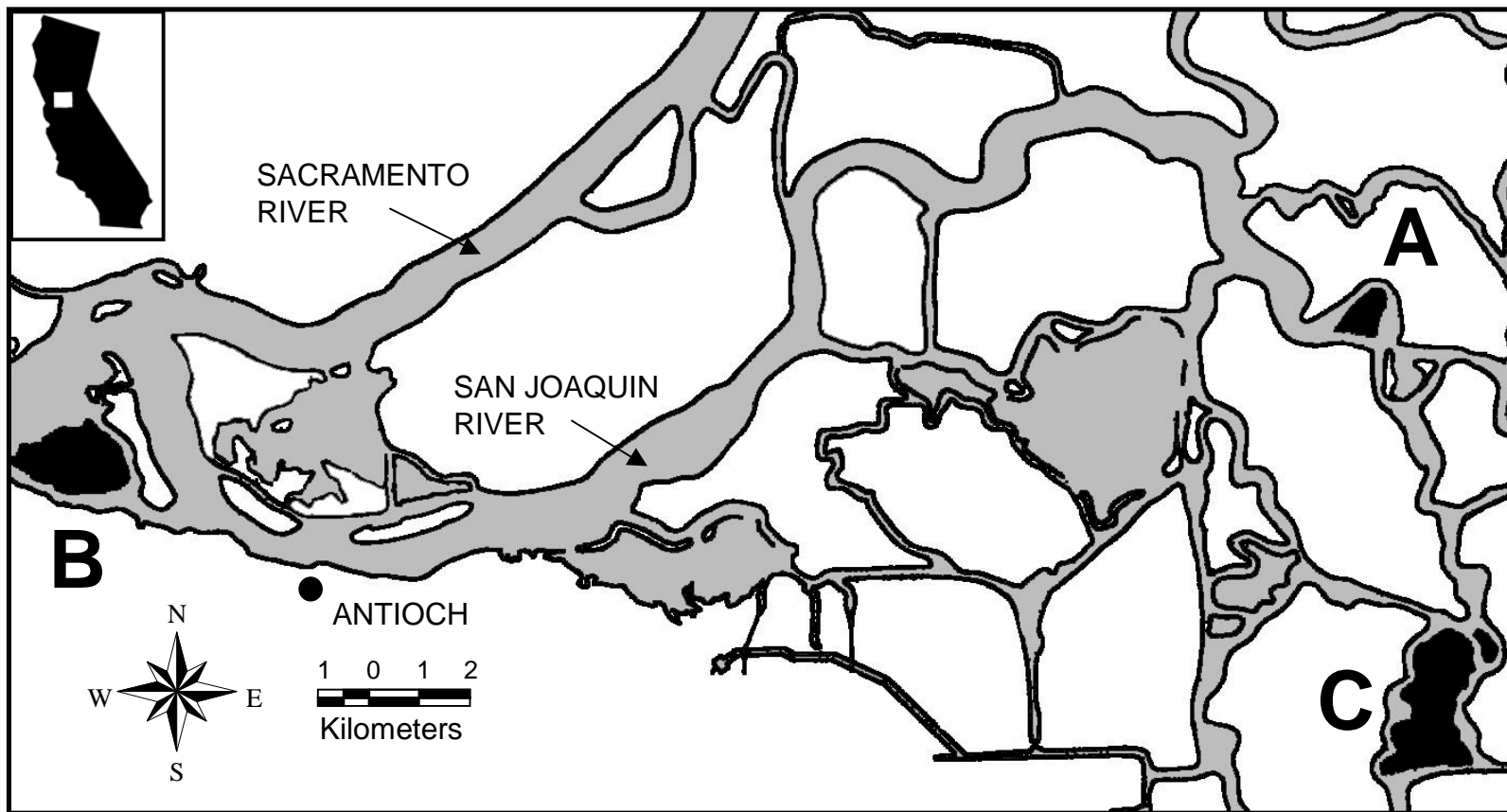


Figure 1. Map of Study Sites. Water is shaded grey, land is white, and study sites are black. Inset is the state of California. Site A = Mandeville Tip, Site B = Brown's Island, Site C = Mildred island.

Results

General Characteristics

Pennywort and hyacinth occurred in separate patches, sometimes directly bordering each other. Small amounts of the semi-aquatic plant *Ludwigia* spp. were found to grow occasionally with both hyacinth and pennywort. Hyacinth was absent at our study sites in June 1999, although residual patches remained in back channels of wetlands and marinas in the surrounding area. The lack of hyacinth in 1999 was due to the following: (1) DBW intensively sprayed 2,4-D throughout the summer months and into mid-December; (2) There were several heavy freezes during the winter, which caused high mortality of carry-over plant material; (3) It was a wet winter, which created a high flow flushing plant material out of the Delta into San Francisco Bay; and (4) DBW started 2,4-D spraying early in spring 1999 with more crews than ever before (Pat Thalken, pers. com.). Pennywort was still sampled in June 1999 so that interannual variation could be measured, as well as to determine if the invertebrate community changed with the absence of hyacinth.

Physical Sampling

All patches were of the same magnitude in size, and occupied similar habitats fringing the marsh edge. The average canopy surface area was 30.96 m², ranging from 8.69-50.90 m². Water depth was approximately 1 m for all invertebrate sampling. Pennywort always had a higher density of leaves than hyacinth, significantly higher at Sites A and C (Fig. 2).

Weight differences of known surface areas produced an extremely tight regression model for calculating the surface area of roots ($R^2=0.99$; Fig. 3). Hyacinth always had a greater root surface area than pennywort, significantly higher at Site B (Fig. 4). Similarly, hyacinth tended to have a greater root biomass than pennywort (Fig. 5), although no significant differences were detected.

Dissolved oxygen levels directly underneath the FAV canopies were significantly lower in hyacinth than pennywort at Site C, and slightly lower at Site B (Fig. 6). These spot values were taken during the same time period, and indicate that hyacinth can have significantly lower dissolved oxygen levels than pennywort. Concurrent water temperatures showed no significant differences (Fig. 7).

Biological Sampling

Epiphytic Macroinvertebrates

There were no consistent trends in total overall density and standing stock of epiphytic macroinvertebrates at any of the sites (Fig. 8). However, there were taxonomic differences between hyacinth and pennywort specific to each study site (Tables 1, 2). At Site A in June 1998, there was a dramatic contrast in assemblage composition, with the amphipod *Crangonyx floridanus* being the most abundant taxon in hyacinth in terms of both density and standing stock, and the amphipod *Hyalella azteca* being most abundant in pennywort (Figs. 9, 10). *C. floridanus* had not been previously reported in the Delta. These amphipods had different contributions numerically and gravimetrically, as *C. floridanus* density in hyacinth was 187% that of *H. azteca* in pennywort, but only 62.5%

in terms of standing stock. The amphipods *C. floridanus* and *Corophium spinicorne* were significantly more abundant in terms of density and standing stock in hyacinth. The amphipod *H. azteca*, the isopod *Caecidotea racovitzai*, and the oligochaete *Stylaria lacustris* were significantly more abundant in terms of density and standing stock in pennywort, and turbellarians were more abundant in terms of standing stock. *C. racovitzai* had also not been previously reported in the Delta. Pennywort was slightly higher than hyacinth in taxa richness, and much higher in diversity (Table 3).

Sites B and C in August 1998 did not show the same dramatic contrasts in epiphytic macroinvertebrate assemblages as in Site A. At Site B, the amphipod *Gammarus daiberi* was the most abundant species in both hyacinth and pennywort (Figs. 9, 10). *G. daiberi* is a large amphipod, which accounts for the high levels of standing stock at Site B. The only significant difference was that the standing stock of the oligochaete *S. lacustris* was higher in pennywort. At Site C, the amphipod *H. azteca* was the most abundant species in patches of both hyacinth and pennywort. The only significant difference was that the density of chironomid larvae was higher in pennywort. Hyacinth was higher than pennywort in taxa richness and diversity at both sites (Table 3).

Results of the June 1999 sampling indicated that there was minimal interannual variation in invertebrate assemblages, as the most abundant taxon present at each site was the same between 1998 and 1999 (Fig. 11). In patches of pennywort at Site A, *H. azteca* was 50% of the overall density in June 1998 and 65% in June 1999. At Site B, *G. daiberi* was 84% of the overall density in August 1998 and 61% in June 1999. At Site C, *H. azteca* was 86% of the overall density in August 1998 and 57% in June 1999.

C. floridanus almost completely vanished in June 1999 when hyacinth was absent from the study sites (Fig. 11). At all sites during 1998, *C. floridanus* was denser in hyacinth than pennywort. When the sites were devoid of hyacinth patches in June 1999, *C. floridanus* was completely absent from pennywort patches at Sites A and B, and was only 0.23% of overall invertebrate density at Site C.

Epibenthic/Benthic Macroinvertebrates

Overall densities of epibenthic and benthic macroinvertebrates were greater underneath patches of pennywort than hyacinth at Site A during all months of sampling, but were significantly more abundant in pennywort only during June (Fig. 12). Oligochaetes were the predominant benthic invertebrate under both hyacinth and pennywort. Species-specific trends in the epibenthic macroinvertebrates were similar to those in the epiphytic macroinvertebrates (Fig. 13, Table 4). *C. floridanus* was the predominant epibenthic taxon under hyacinth, and *H. azteca* was the predominant epibenthic taxon under pennywort. *C. racovitzai* was also always more dense under pennywort. *H. azteca* was significantly more dense under pennywort during June and July, and *C. racovitzai* and turbellarians were significantly more dense under pennywort during June. Pennywort was higher in taxa richness and diversity in April, while hyacinth was higher in June and July (Table 3).

Overall densities were almost equal in hyacinth and pennywort at Site B during August 1998 (Fig. 12). Oligochaetes were once again the most abundant benthic invertebrate (Fig. 13). The most striking difference was that there were no amphipods or

isopods underneath hyacinth patches at all, therefore overall densities of amphipods and isopods were significantly higher under pennywort ($p < 0.015$; Table 4). *G. daiberi* was the major epibenthic taxon under pennywort, as was the case with the epiphytic macroinvertebrates. Pennywort was much higher in taxa richness and diversity (Table 3) because hyacinth was almost devoid of epibenthic invertebrates.

As was the case with the epiphytic macroinvertebrates, there was minimal interannual variation in invertebrate assemblages, as the most abundant taxon present at each site was the same between 1998 and 1999 (Fig. 14). Under patches of pennywort at Site A, *H. azteca* was 76% of the overall epibenthic density in June 1998, and 53% in June 1999. At Site B, *G. daiberi* was 50% of the overall epibenthic density in August 1998, and 83% in June 1999.

When hyacinth was absent in June 1999, *C. floridanus* almost completely vanished from the epibenthic community, as it did in the epiphytic community (Fig. 14). *C. floridanus* was more abundant in hyacinth than pennywort at Site A during all months in 1998. When the sites were devoid of hyacinth patches in June 1999, *C. floridanus* in turn was completely absent from epibenthic samples in pennywort at Site A. *C. floridanus* was not found in the epibenthos at either hyacinth or pennywort at Site B in 1998, but it must be remembered that no epibenthic amphipods were found at all in these hyacinth patches. At Site B, *C. floridanus* only accounted for 0.63% of the overall density in June 1999.

Insects

Overall densities of terrestrial insects were significantly greater in pennywort than hyacinth at Site A during all months of sampling (Fig. 15). FAV differences and seasonal differences were apparent (Fig. 16; Table 5). In April, Ephydriidae were significantly more abundant in hyacinth, and Psychodidae were significantly more abundant in pennywort. Ephydriidae and Psychodidae both decreased in June and July, with Collembola becoming significantly more abundant in hyacinth by July, and Cicadellidae significantly more abundant in pennywort in both June and July. Chironomidae were significantly more abundant in hyacinth during April, but were significantly more abundant in pennywort during June and July. Other significant findings were higher values in pennywort of Aphididae and Sphaeroceridae in April, Dolichopodidae, Sphaeroceridae, and Staphylinidae in June, and Araneae, Delphacidae, Hymenoptera, and Mymaridae in July. Aphididae and Hemiptera were significantly greater in hyacinth in July. Pennywort was higher in taxa richness, while hyacinth was higher in diversity throughout all months (Table 3).

Overall densities were also greater in pennywort than hyacinth at Site B in August 1998, but differences were not statistically significant (Fig. 15). Pennywort did have significantly greater densities of Chironomidae and Araneae (Fig. 16; Table 5). Cicadellidae were very abundant, more so in pennywort, although the differences were not significant. These trends were similar to those found at Site A in July 1998. Hyacinth was higher in both taxa richness and diversity (Table 3).

There was minimal interannual variation, the main difference being more Collembolans in pennywort during June 1999 (Figs. 17). However, specific taxonomic differences could not be determined, as Collembolans were only identified to Order.

Fish

Most of the fish captured adjacent to patches of hyacinth and pennywort at Site A during June and July of 1998 were juveniles (Table 6). The majority of these fish were non-indigenous to the Delta. The native species splittail (*Pogonichthys macrolepidotus*), tule perch (*Hysterocarpus traski*) and prickly sculpin (*Cottus asper*) accounted for only 24% of the numerical catch in June and 3% in July.

Diet analysis of bluegills indicated differences among the major prey items between fish caught adjacent to hyacinth and pennywort (Fig. 18). Based on IRI values, the predominant prey item for bluegills adjacent to pennywort in both June and July was *H. azteca*, which was also the most common epiphytic and epibenthic macroinvertebrate found in those pennywort patches. Adjacent to hyacinth patches, the major prey items of bluegills in June were the amphipod *G. daiberi*, the isopod *Asellus hilgendorffii*, and insects of the family Aphididae. *A. hilgendorffii* had not been previously reported in the Delta. In July, the major prey items were chironomid larvae, gastropods, *G. daiberi*, and the copepod *Pseudodiaptomus forbesi*. These prey items did not directly coincide with the major aquatic macroinvertebrates found in hyacinth. *C. floridanus* was the major epiphytic and epibenthic macroinvertebrate found in hyacinth, which was the ninth ranked prey item in June, and was not found in the prey items at all in July. Ivlev

Electivity Index values between *C. floridanus* in hyacinth and *H. azteca* in pennywort also suggest differences in preference for these two major prey resources, as *C. floridanus* always had lower values (Table 7).

Overlap between prey items and potential macroinvertebrate prey was also higher in pennywort (Fig. 18). PSI with the prey resources in pennywort was 23.7% for epiphytic and 23.4% for epibenthic macroinvertebrates during June, and 69.5% for epibenthic macroinvertebrates in July. Overlap with prey resources in hyacinth was 4.9% for epiphytic and 11.1% for epibenthic macroinvertebrates during June, and 10.7% for epibenthic macroinvertebrates in July. Most of the overlap between macroinvertebrate prey items and resources was due to amphipods, isopods, gastropods, and chironomid larvae. Discrepancies were due to either differences in species of amphipods and isopods, as was the case with hyacinth, or due to the presence of planktonic organisms such as cladocerans, ostracods, and copepods in the diet.

Most of the fish captured directly underneath 5 patches of hyacinth at Site C during August 1998 were juveniles (Table 8). The majority of these fish were non-indigenous to the Delta, the only native fish caught was one prickly sculpin accounting for 2% of the numerical catch. Other common captured organisms included the non-indigenous crayfish *Procambarus clarkii* and the giant water bug (family Belostomatidae).

Diet analysis of the fish living directly underneath the hyacinth canopy indicated that they were utilizing the prey resources in the canopy (Fig. 19). The most abundant amphipod in the prey was *H. azteca*, which was also the most abundant epiphytic and

epibenthic macroinvertebrate. *H. azteca* was the predominant prey item for larger bluegills (size 2) and juvenile largemouth bass (*Micropterus salmoides*). Other common prey items for these fish were zygoptera nymphs and chironomid larvae, which were also found as prey resources in hyacinth. *H. azteca* was still in the top three or four prey items of smaller fish such as bluegills (size 1) and rainwater killifish (*Luciana parva*). The diets of these smaller fish were composed mainly of planktonic organisms, such as the copepod *P. forbesi* and the cladoceran *Ceriodaphnia* spp. For this reason, PSI with epiphytic and epibenthic macroinvertebrates for larger bluegills and juvenile largemouth bass was approximately 40%, and approximately 10% for smaller bluegills and rainwater killifish.

Ivlev Electivity Index values between *C. floridanus* and *H. azteca* in hyacinth further demonstrated the differences in preference for these two potential prey items (Table 7). Both amphipods were found in the diets of larger bluegills and juvenile largemouth bass, and *C. floridanus* always had lower Ivlev Electivity Indices than *H. azteca*.

The top five prey items based on IRI values of common nearshore juvenile fish in the area surrounding the study sites are illustrated in Fig. 20. Bluegills and largemouth bass are established non-indigenous species, while chinook salmon (*Oncorhynchus tshawytscha*), splittail, tule perch and prickly sculpin are natives. It is apparent that the amphipods *H. azteca* and *G. daiberi* were major prey items in almost all of these species. *C. floridanus* was absent from the major prey items, which was the amphipod found to be prevalent in hyacinth canopies. Other common prey items included chironomids,

copepods, cladocera, the isopod *Caecidotea racovitzai*, and the amphipod *Corophium spinicorne*.

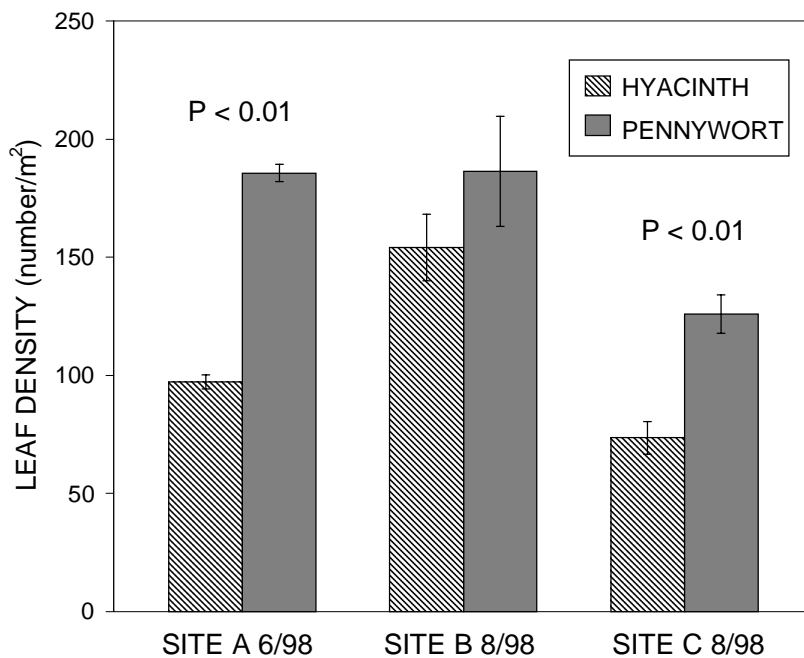


Figure 2. Leaf density of hyacinth and pennywort. P-values show significant results from two sample t-tests, error bars are \pm standard error, $n = 5$ for each bar.

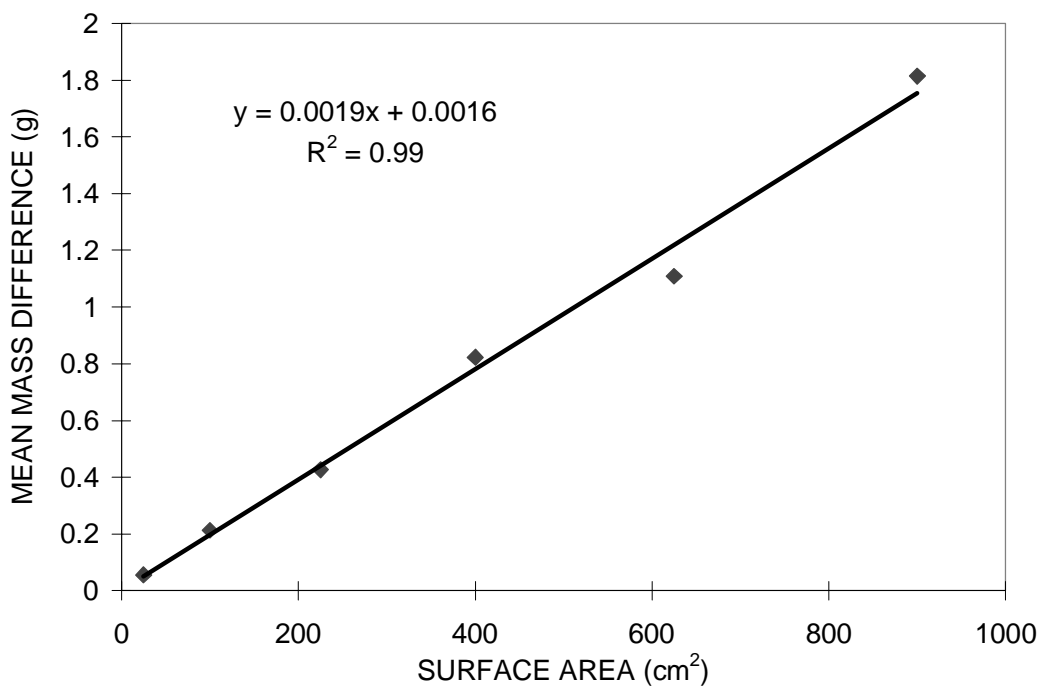


Figure 3. Regression of mass differences for known surface areas used for calculating the surface area of roots. Each point represents 5 samples.

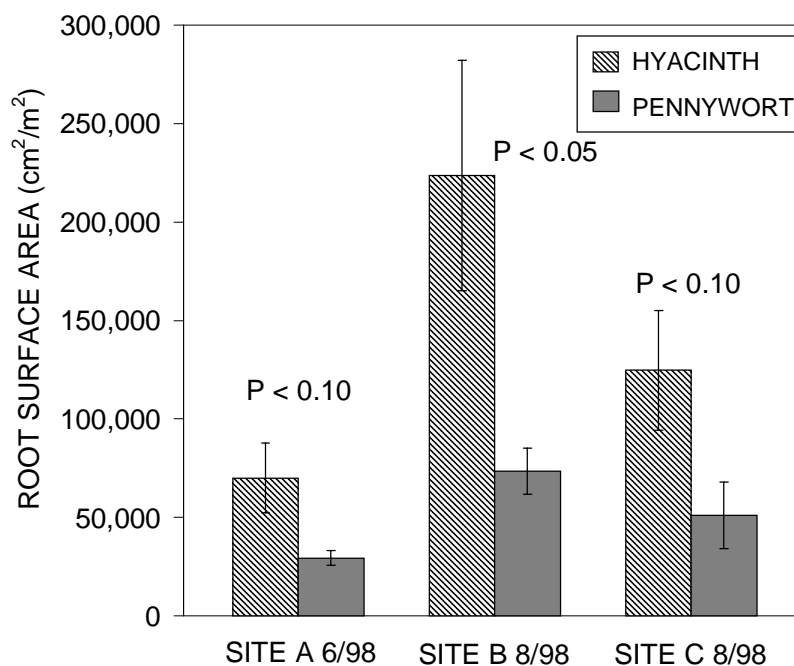


Figure 4. Surface area of roots (cm²/m² of canopy). P-values show results from two sample t-tests, error bars are ± standard error, n = 5 for each bar.

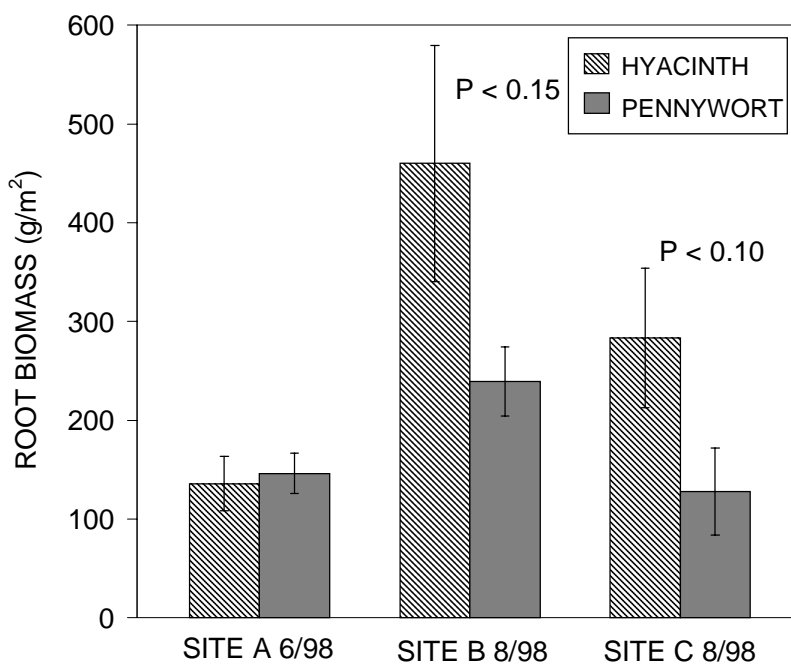


Figure 5. Biomass of roots (g wet/m² of canopy). P-values show results from two sample t-tests, error bars are ± standard error, n = 5 for each bar.

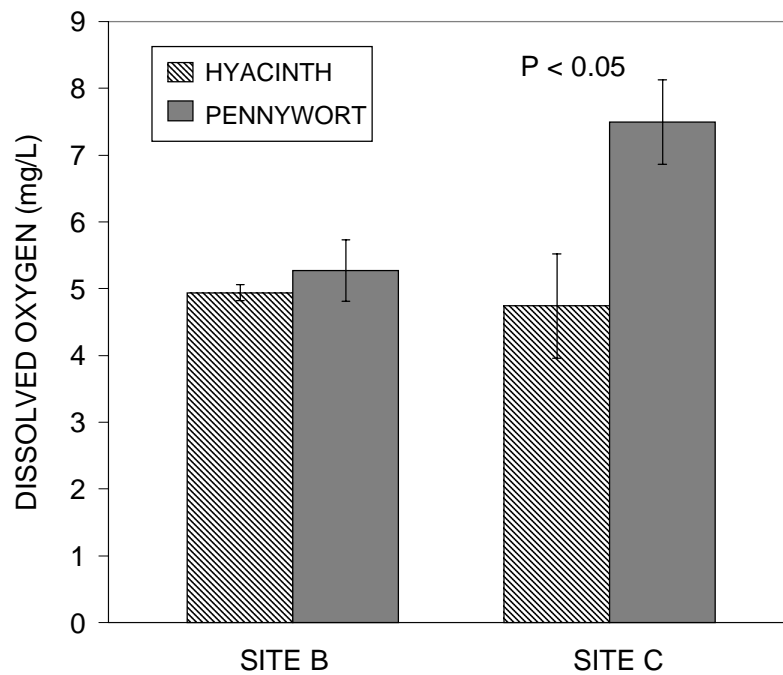


Figure 6. Dissolved oxygen levels (mg/L) from 8/98. P-values show results from two sample t-tests, error bars are \pm standard error, $n = 5$ for each bar.

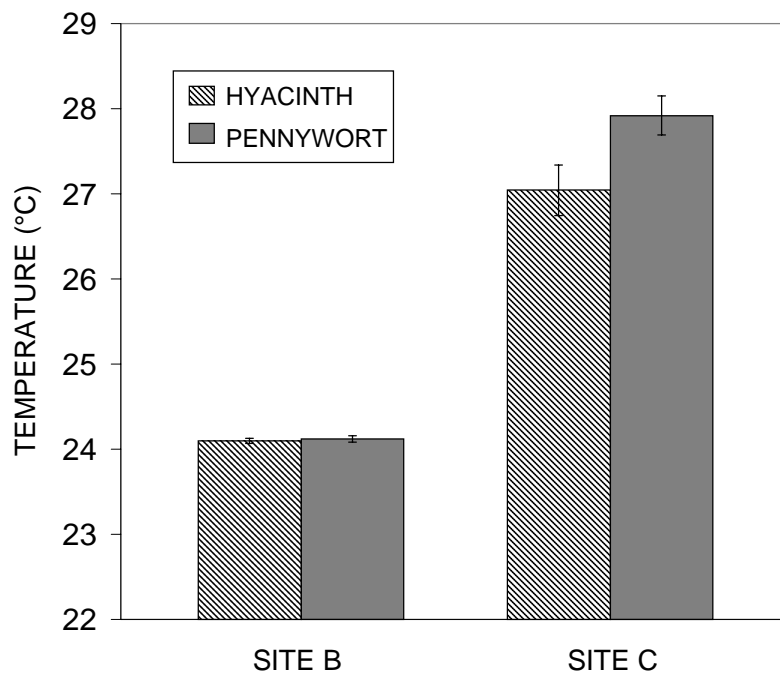


Figure 7. Water temperature in $^{\circ}\text{C}$ from 8/98. Error bars are \pm standard error, $n = 5$ for each bar.

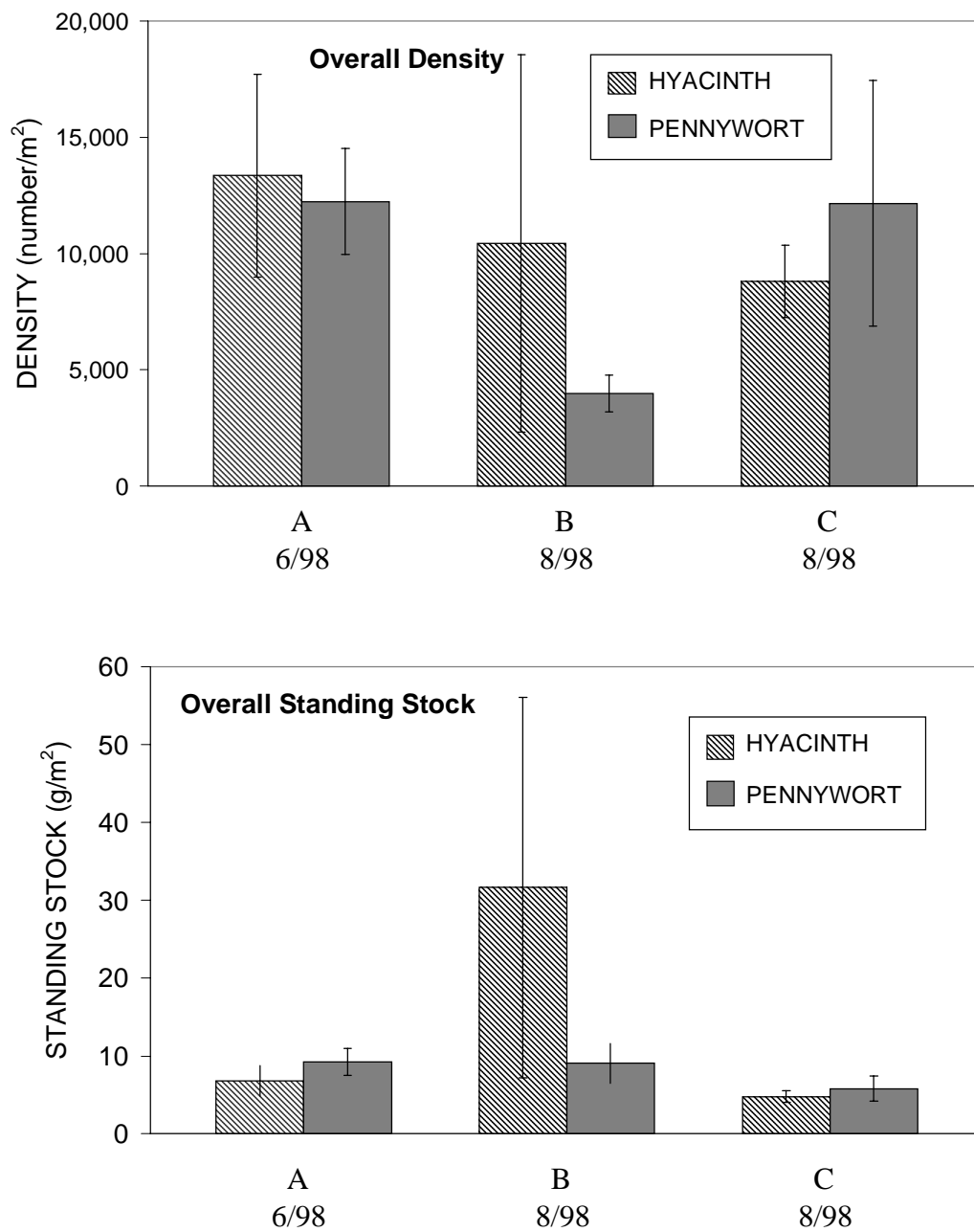


Figure 8. Overall density and standing stock of epiphytic macroinvertebrates per m² of canopy at Sites A, B, and C. Error bars are \pm standard error, $n = 5$ for each bar.

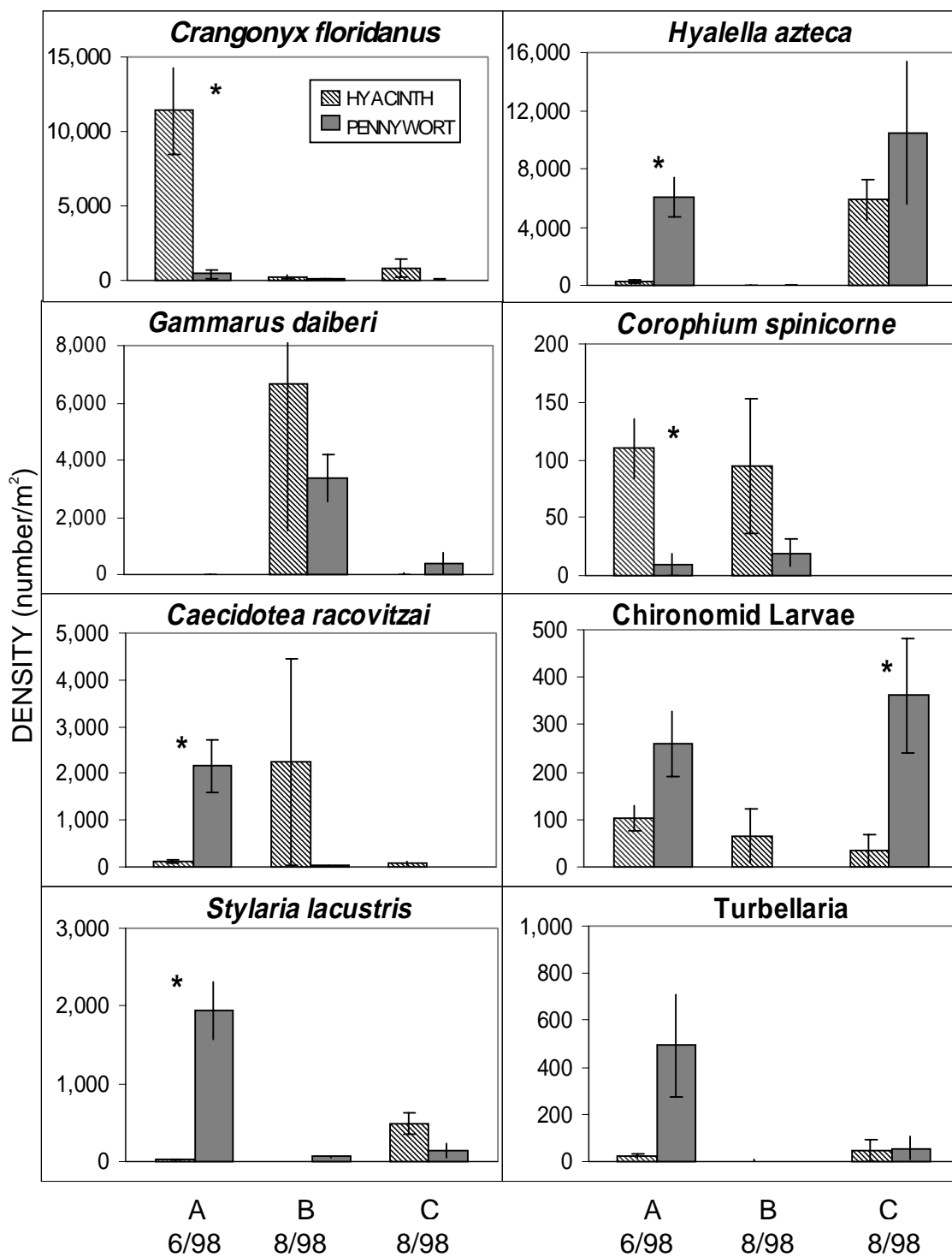


Figure 9. Density of common epiphytic macroinvertebrates per m² of canopy at Sites A, B, and C. * P < 0.05, error bars are ± standard error.

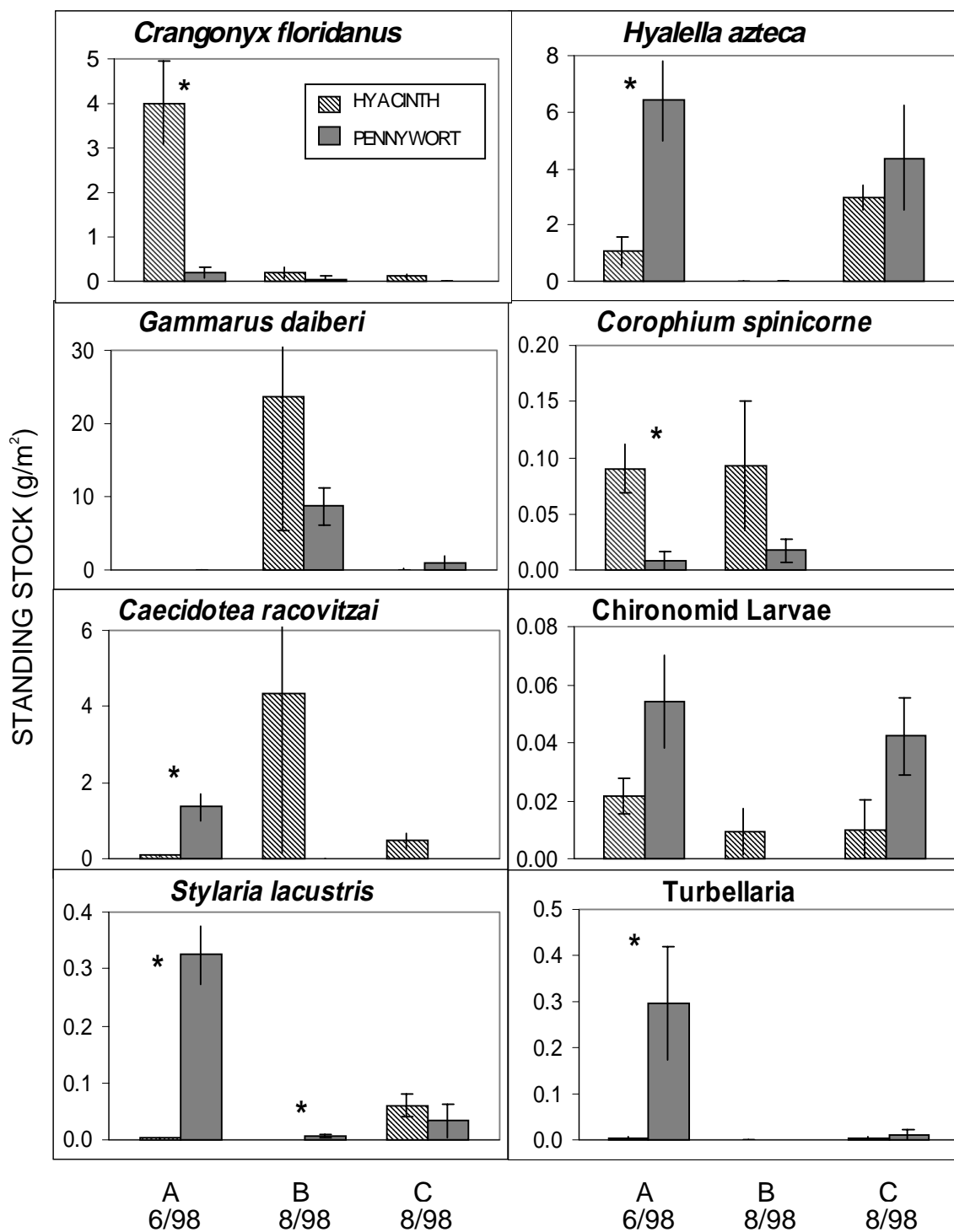


Figure 10. Standing stock of common epiphytic macroinvertebrates per m² of canopy at Sites A, B, and C. * P < 0.05, error bars are ± standard error.

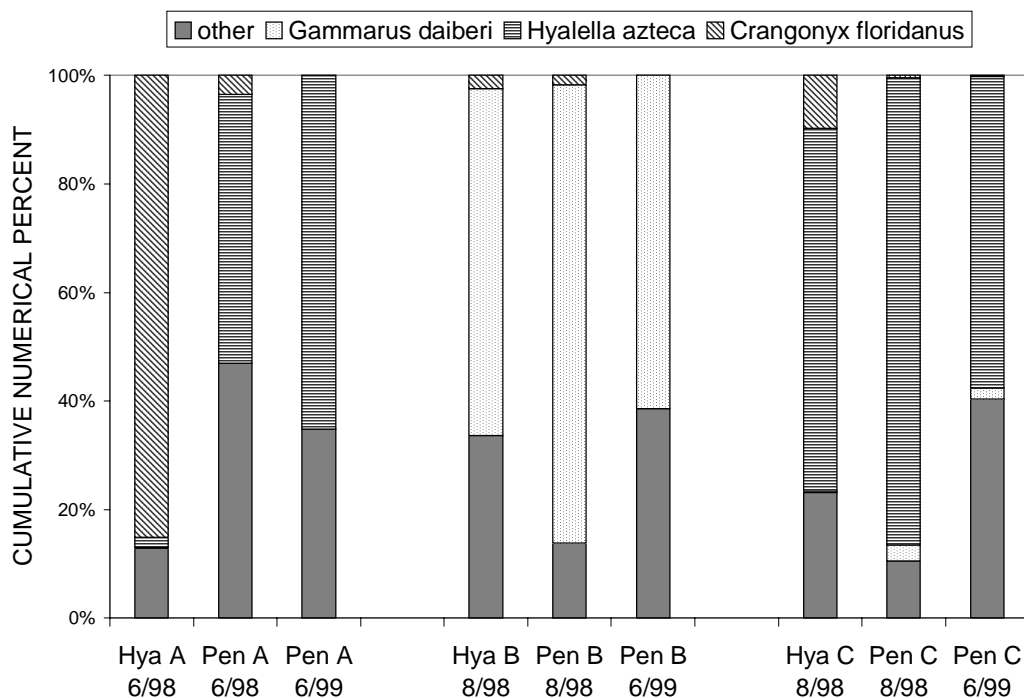


Figure 11. Cumulative numerical percent of dominant epiphytic macroinvertebrates in 1998 and 1999 at Sites A, B, and C. Hya = Hyacinth, Pen = Pennywort.

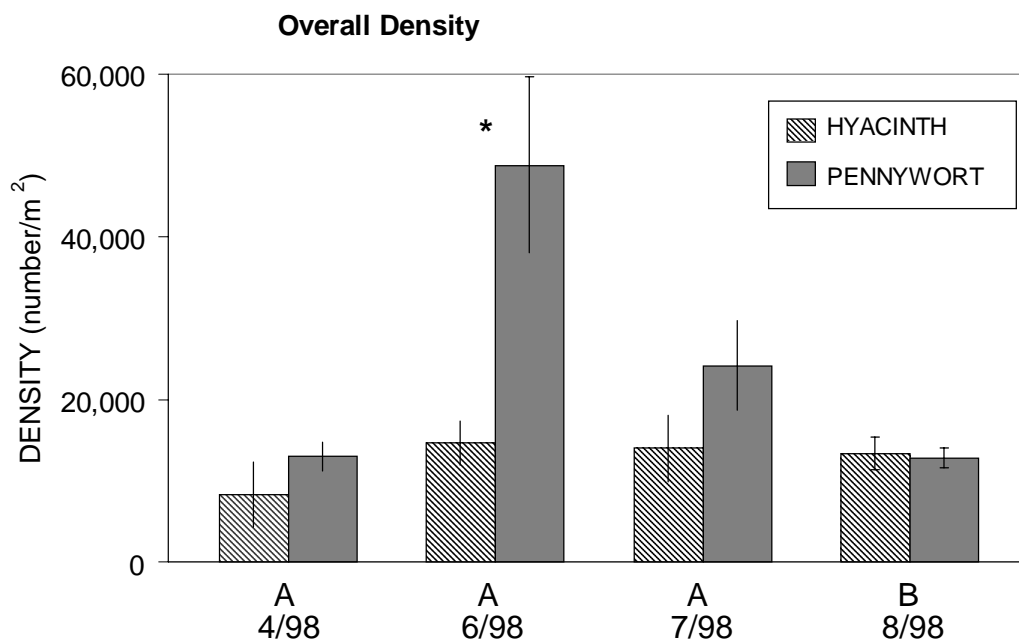


Figure 12. Overall density of epibenthic/benthic macroinvertebrates per m^2 of canopy at Sites A and B. * $P < 0.05$, error bars are \pm standard error.

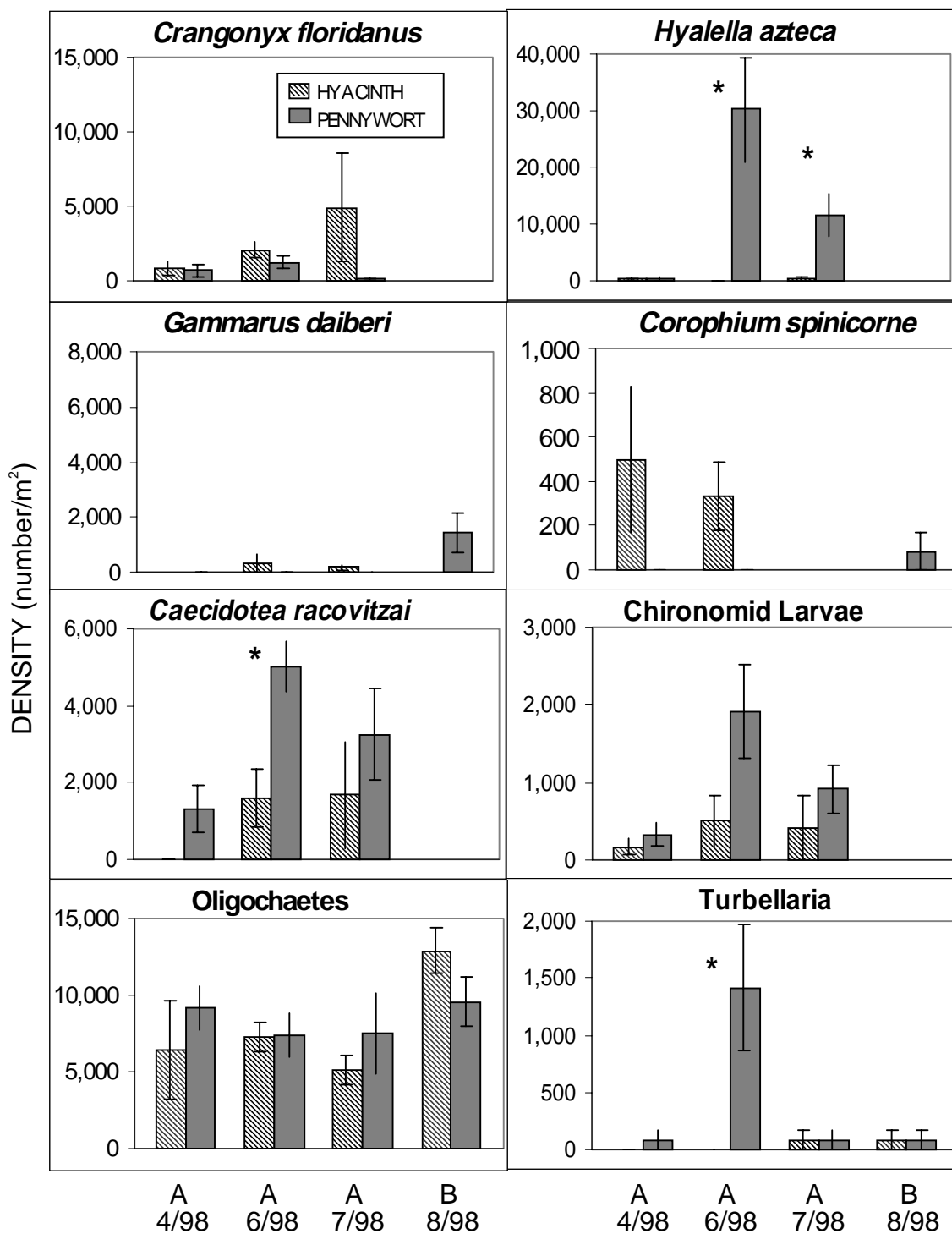


Figure 13. Density of common epibenthic/benthic macroinvertebrates per m² of canopy at Sites A and B. * P < 0.05, error bars are ± standard error.

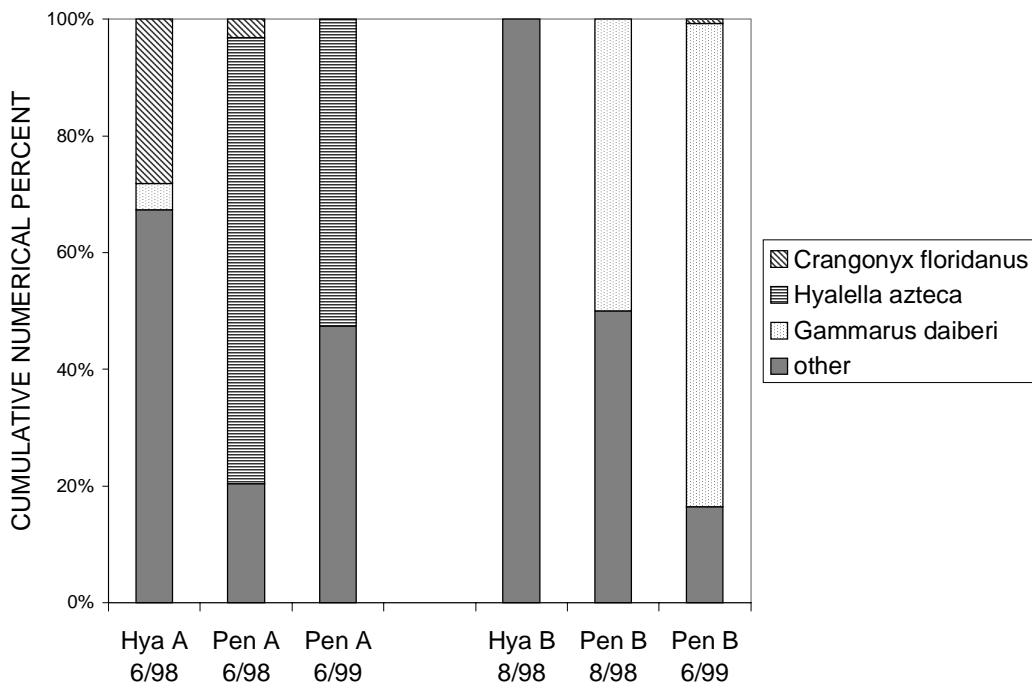


Figure 14. Cumulative numerical percent of dominant epibenthic/benthic macroinvertebrates 1998-99 at Sites A and B. Hya = Hyacinth, Pen = Pennywort.

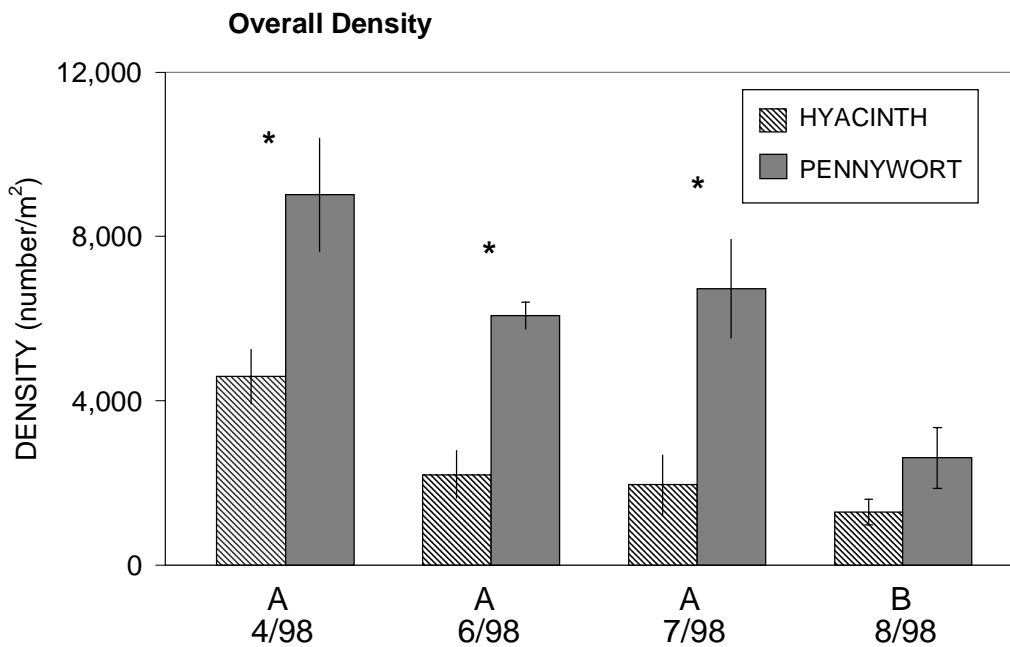


Figure 15. Overall density of insects per m² of canopy at Sites A and B. * P < 0.05, error bars are ± standard error.

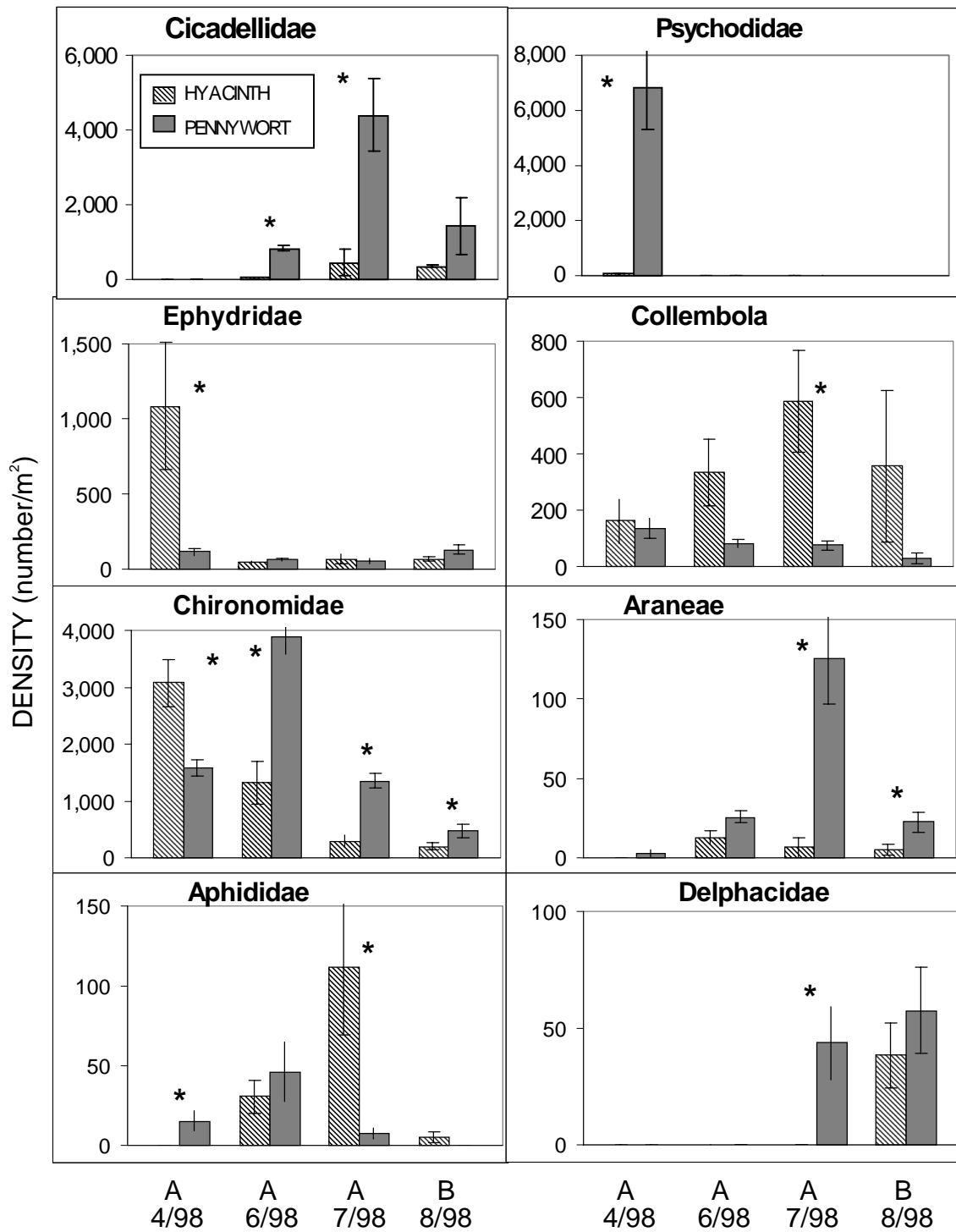


Figure 16. Density of common insects per m² of canopy at Sites A and B. * P < 0.05, error bars are \pm standard error.

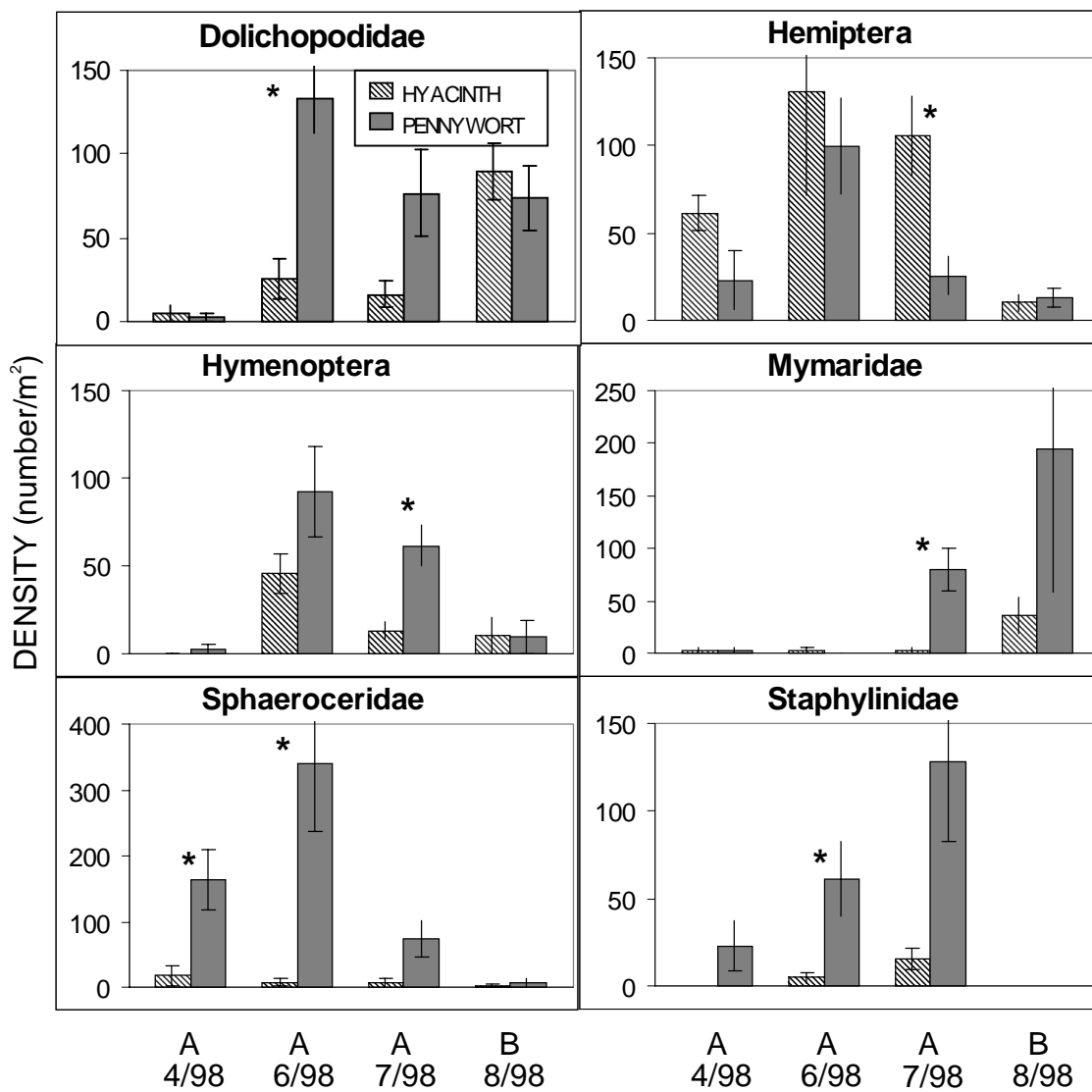


Figure 16 (continued). Density of common insects per m² of canopy at Sites A and B. * P < 0.05, error bars are \pm standard error.

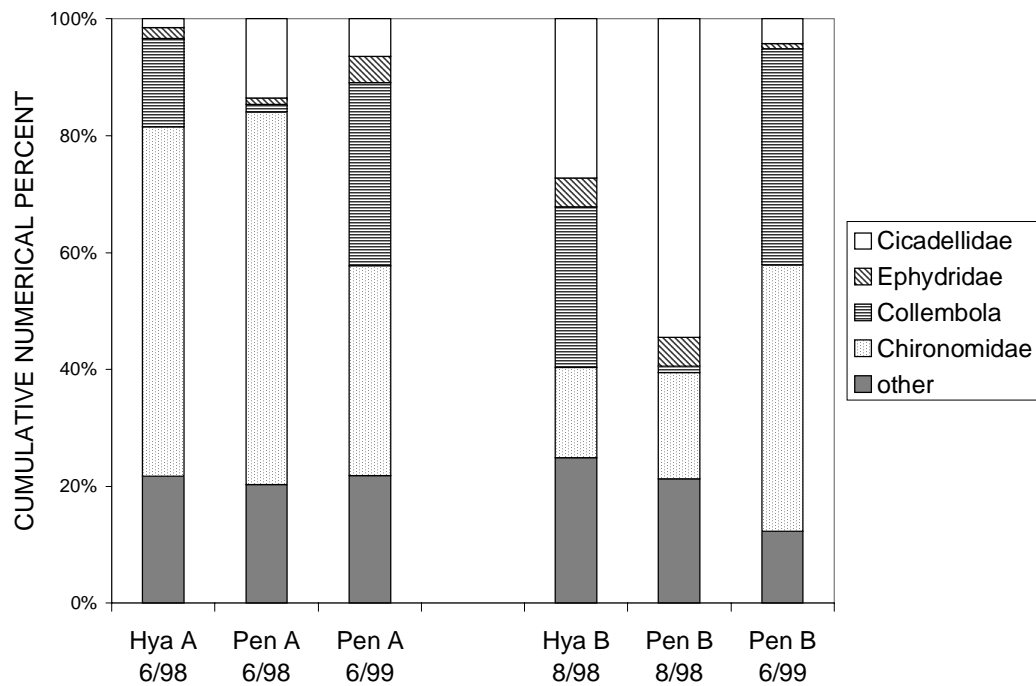


Figure 17. Cumulative numerical percent of dominant insects in 1998 and 1999 at Sites A and B.

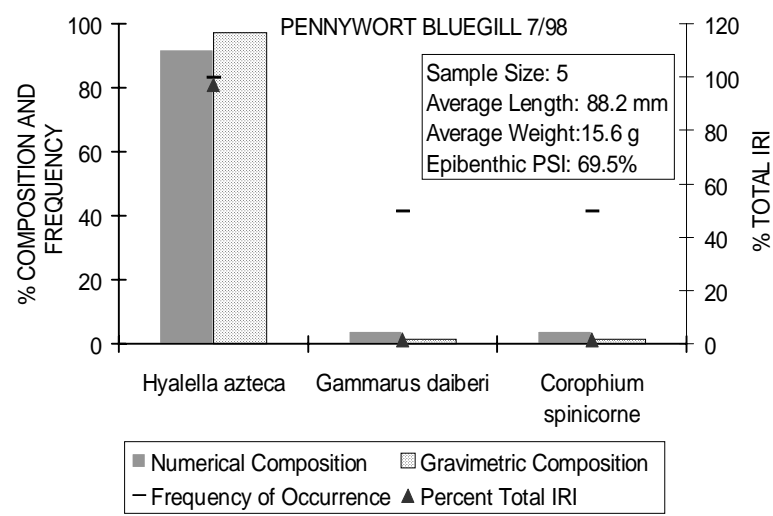
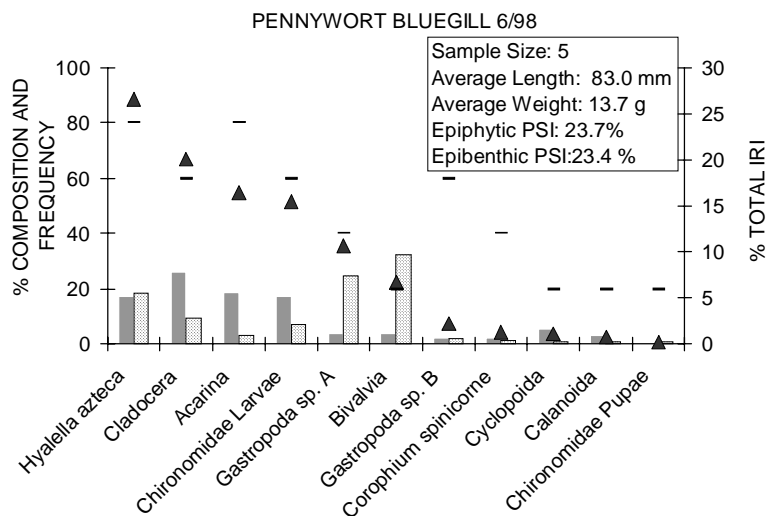
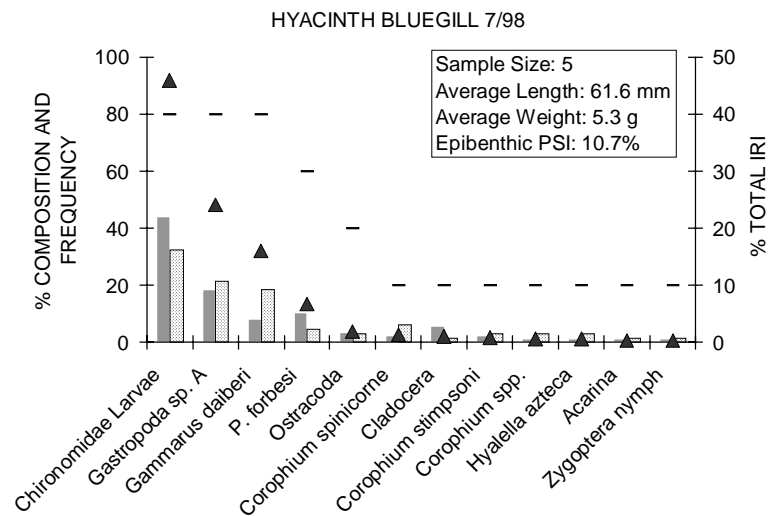
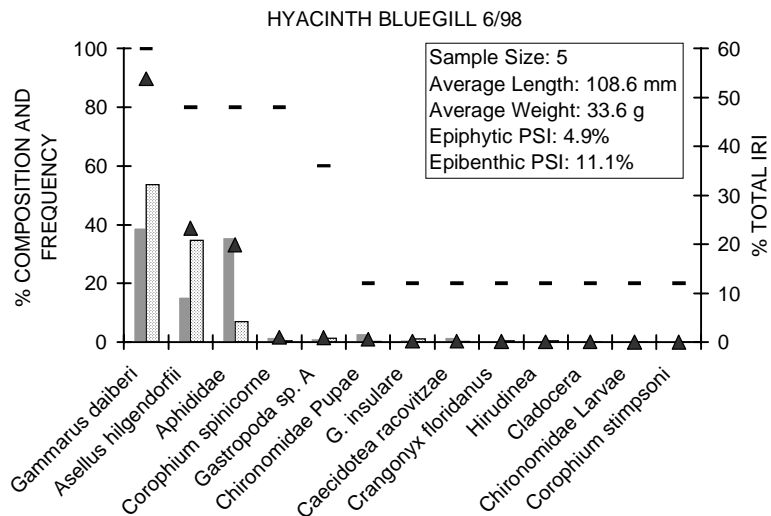


Figure 18. Fish diets for bluegills caught adjacent to hyacinth and pennywort at Site A in June and July 1998. Prey are ranked in declining values of percent total IRI.

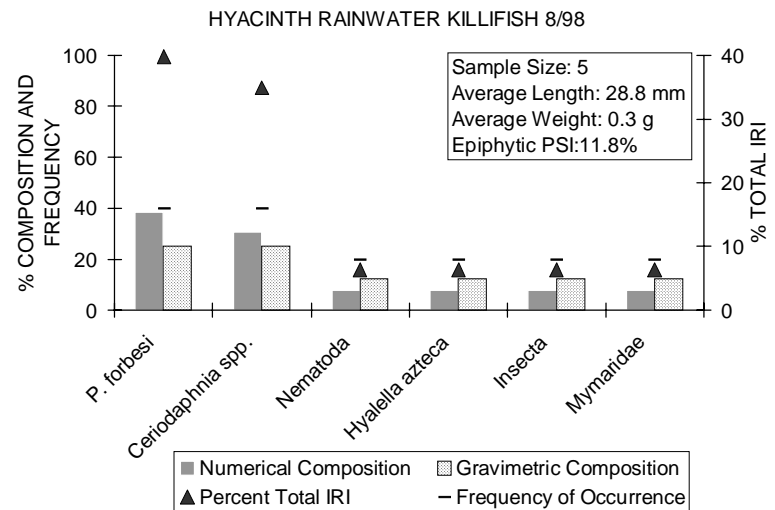
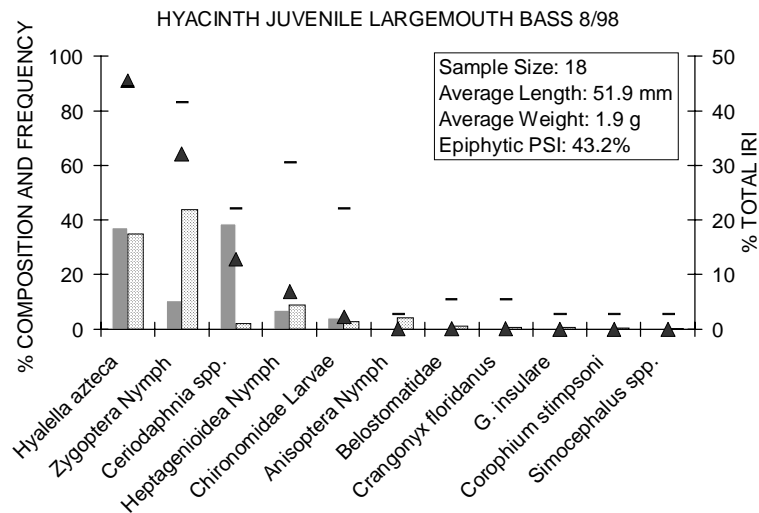
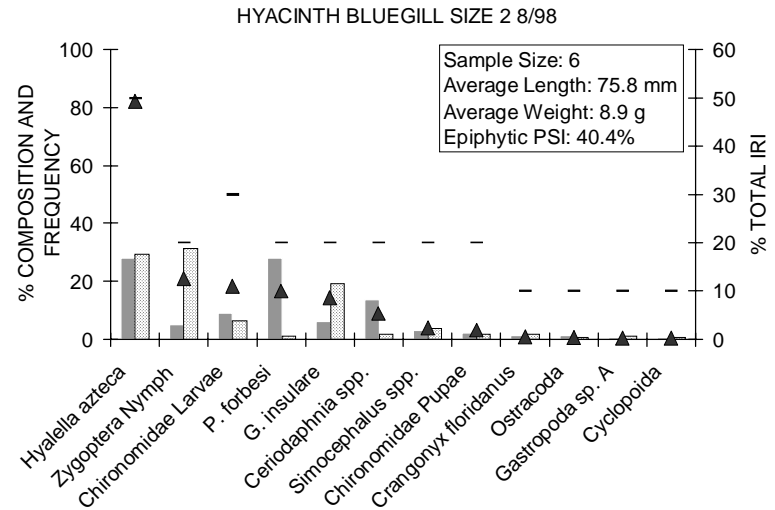
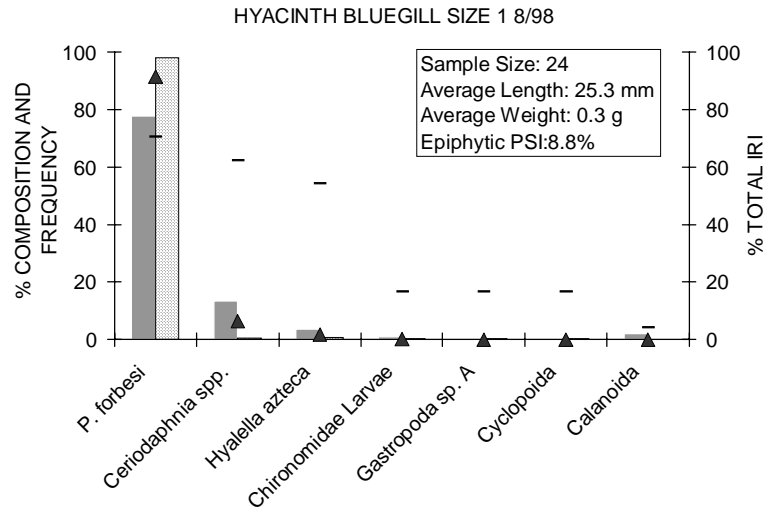


Figure 19. IRI graphs of diets of fish caught directly underneath hyacinth at Site C during August 1998. Prey are ranked in declining values of percent total IRI.

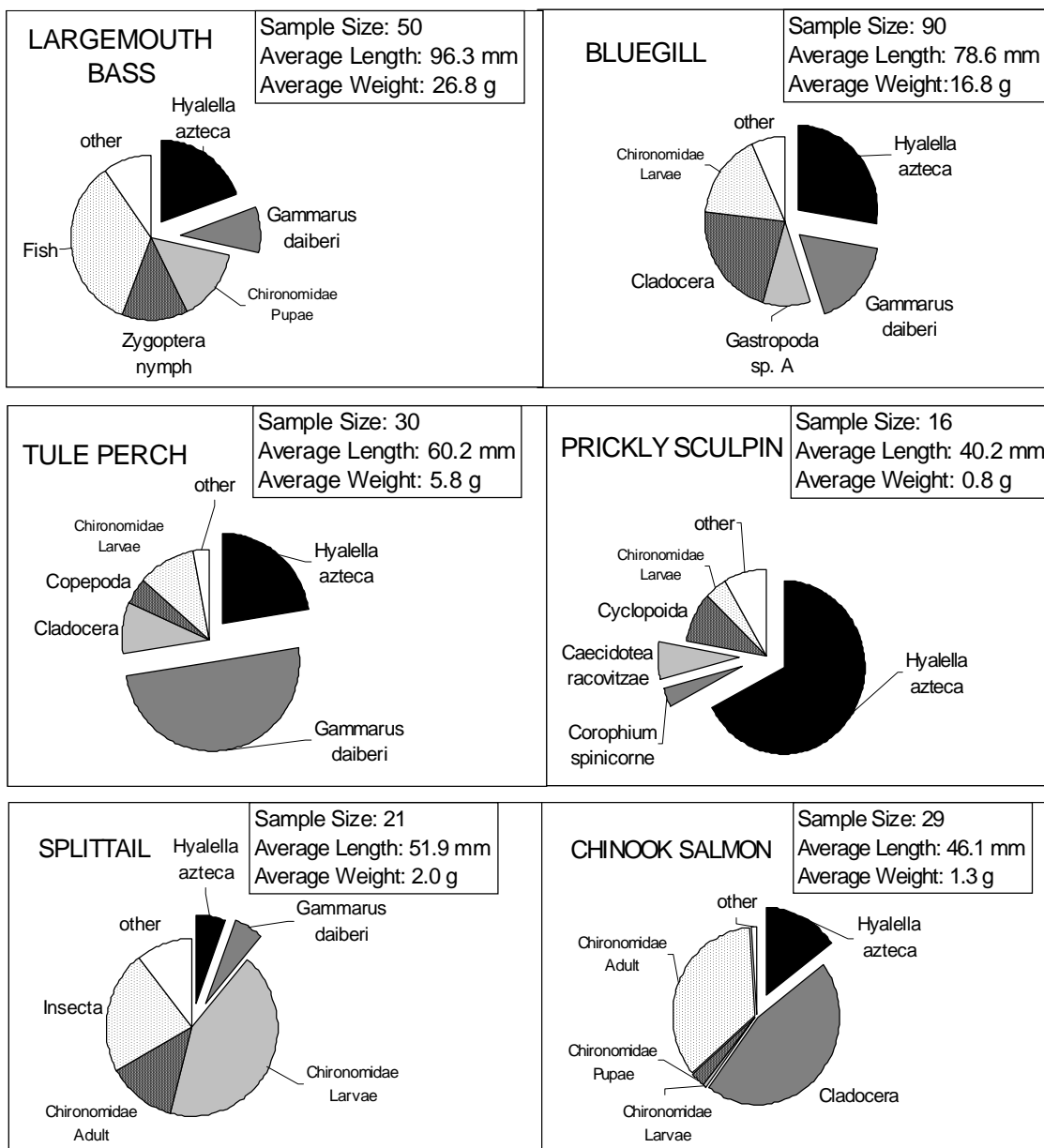


Figure 20. Top five prey items based on IRI values of common nearshore juvenile fish in the area surrounding the study sites. Separated pie slices represent amphipods and isopods.

Table 1. Average densities (number/m² of canopy) of all epiphytic macroinvertebrates at Sites A, B, and C (n=5). Significant differences from two sample t-tests are highlighted. H = Hyacinth, P = Pennywort.

taxa	Site A			Site B			Site C		
	6/98 H	6/98 P	6/99 P	8/98 H	8/98 P	6/99 P	8/98 H	8/98 P	6/99 P
Hydrozoa	-	28.9	-	-	-	6.2	11.6	-	-
Turbellaria	22.2	494.1	-	2.4	-	-	49.2	55.2	-
Polychaeta	-	-	-	-	-	8.5	-	-	-
Oligochaeta	-	-	-	15.1	-	-	-	-	-
Oligochaete bud	2.3	65.8	-	-	-	-	-	-	-
<i>Stylaria lacustris</i>	13.0	1938	6.3	-	58.1	106.8	485.9	128.8	75.3
Hirudinea	-	-	-	2.4	-	-	-	-	-
<i>Helobdella fusca</i>	6.8	13.8	8.1	-	-	-	13.0	6.1	-
Gastropod sp. A	186.9	322.8	341.5	60.4	48.4	126.9	95.4	21.5	1260
Gastropod sp. B	824.1	135.7	16.3	66.5	-	30.9	-	3.1	58.9
Ancylidae (limpet)	14.7	25.4	-	-	-	11.2	-	6.1	-
Araneae	7.0	3.7	5.4	4.4	9.7	-	1.4	24.5	-
Acarina	4.6	9.1	-	-	-	-	1.4	-	-
Ostracoda	-	-	-	7.3	-	-	57.8	30.7	-
Cladocera- <i>Eurycercus lamellatus</i>	150.9	58.4	-	69.1	19.4	-	312.4	98.1	13.1
Copepoda	3.4	6.4	-	16.5	58.1	-	360.1	15.3	-
Cyclopoida	-	-	-	-	-	6.2	-	-	-
Isopoda- <i>Caecidotea racovitzai</i>	115.2	2153	20.9	2246	29.0	11.2	72.3	-	196.1
<i>Gnorimosphaeroma insulare</i>	106.6	32.1	85.3	797.5	222.6	1025	-	3.1	5.5
<i>Munna</i> spp.	-	-	-	-	19.4	-	-	-	-
Amphipoda- <i>Corophium spinicorne</i>	109.8	9.1	-	94.5	19.4	254.9	-	-	5.5
<i>Crangonyx floridanus</i>	11371	422	-	259.9	67.8	-	856.1	49.1	9.8
<i>Gammarus daiberi</i>	6.8	-	-	6676	3359	2576	23.1	368.0	82.5
<i>Hyalella azteca</i>	252	6072	1033	-	-	-	5889	10463	2417
Astacidae (crayfish)	-	-	-	3.7	-	-	-	-	-
<i>Procambarus clarki</i>	-	-	-	-	-	-	4.3	-	-
Insecta larvae-unknown	-	-	-	2.0	-	-	92.6	3.1	-
Collembola-Isotomidae	20.7	7.4	17.6	-	-	-	-	-	-
Sminthuridae	4.6	7.4	6.8	2.4	-	-	-	-	-
Anisoptera nymph	-	-	-	-	-	-	-	3.1	-
Zygoptera nymph	-	-	-	53.3	19.4	8.5	428.1	490.7	81.7
Thysanoptera	-	-	-	-	19.4	-	-	-	-
Hemiptera	1.6	-	-	-	-	-	-	-	-
Hydrometra	3.3	7.4	-	-	-	-	-	-	-
Homoptera-Aphididae	-	-	12.2	-	-	14.1	2.9	-	-
Cicadellidae larvae	-	-	6.3	-	19.4	-	1.4	24.5	-
Coleoptera larvae-unknown	0.4	12.9	-	1.9	9.7	-	-	-	-
Dytiscidae	-	-	-	1.9	-	-	-	-	-
Staphylinidae	-	-	-	-	-	-	-	3.1	-
Diptera adult-unknown	-	-	5.9	-	-	-	-	-	-
Chironomid larvae	102.2	259.6	12.7	65.0	-	11.2	34.7	361.9	6.6
Chironomid pupae	2.7	-	-	-	-	-	11.6	-	-
Chironomid adult	1.0	22.0	8.1	3.9	-	-	-	-	-
Sciaridae	1.0	-	-	-	-	-	-	-	-
Tipulidae larvae	16.2	-	-	-	-	-	-	-	-
Tipulidae pupae	0.4	-	-	-	-	-	-	-	-
Hymenoptera	2.3	-	-	-	-	-	-	-	-
Fish eggs	-	129.3	-	-	-	-	-	-	-
Overall	13354	12237	1587	10452	3978	4198	8804	12159	4212

Table 2. Average standing stock (g/m² of canopy) of all epiphytic macroinvertebrates at Sites A, B, and C (n=5). Significant differences from two sample t-tests are highlighted. H = Hyacinth, P = Pennywort.

taxa	Site A			Site B			Site C		
	6/98		6/99	8/98		6/99	8/98		6/99
	H	P	P	H	P	P	H	P	P
Hydrozoa	-	0.0054	-	-	-	0.0012	0.0020	-	-
Turbellaria	0.0046	0.2959	-	0.0005	-	-	0.0045	0.0119	-
Polychaeta	-	-	-	-	-	0.0017	-	-	-
Oligochaeta	-	-	-	0.0023	-	-	-	-	-
Oligochaete bud	0.0005	0.0045	-	-	-	-	-	-	-
<i>Stylaria lacustris</i>	0.0017	0.3248	0.0013	-	0.0068	0.0096	0.0601	0.0339	0.0111
Hirudinea	-	-	-	0.0034	-	-	-	-	-
<i>Helobdella fusca</i>	0.0745	0.1449	0.0675	-	-	-	0.1755	0.0976	-
Gastropod sp. A	0.0935	0.1906	1.5672	0.0178	0.0072	1.0813	0.0191	0.0099	0.5900
Gastropod sp. B	0.3108	0.0358	0.0049	0.0180	-	0.0051	-	0.0014	0.0262
Ancylidae (limpet)	0.0040	0.0038	-	-	-	0.0034	-	0.0022	-
Araneae	0.0188	0.0089	0.0076	0.0134	0.0375	-	0.0030	0.0640	-
Acarina	0.0008	0.0018	-	-	-	-	0.0004	-	-
Ostracoda	-	-	-	0.0005	-	-	0.0107	0.0033	-
Cladocera- <i>Eurycercus lamellatus</i>	0.0184	0.0080	-	0.0087	0.0013	-	0.0338	0.0071	0.0026
Copepoda	0.0002	0.0006	-	0.0014	0.0066	-	0.0719	0.0025	-
Cyclopoida	-	-	-	-	-	0.0006	-	-	-
Isopoda- <i>Caecidotea racovitzai</i>	0.2695	1.3657	0.0181	4.3298	0.0069	0.0045	0.4544	-	0.1150
<i>Gnorimosphaeroma insulare</i>	0.7523	0.0823	0.0717	3.2376	0.1143	1.5196	-	0.0052	0.0017
<i>Munna</i> spp.	-	-	-	-	0.0087	-	-	-	-
Amphipoda- <i>Corophium spinicorne</i>	0.0902	0.0082	-	0.0932	0.0169	0.2328	-	-	0.0039
<i>Crangonyx floridanus</i>	4.0133	0.1961	-	0.2060	0.0513	-	0.1016	0.0066	0.0029
<i>Gammarus daiberi</i>	0.0341	-	-	23.5620	8.7466	7.3128	0.0895	1.0108	0.3146
<i>Hyalella azteca</i>	1.0446	6.4105	1.6821	-	-	-	2.9652	4.3685	3.7087
Astacidae (crayfish)	-	-	-	0.0730	-	-	-	-	-
<i>Procambarus clarki</i>	-	-	-	-	-	-	0.6917	-	-
Insecta larvae-unknown	-	-	-	0.0016	-	-	0.0137	0.0024	-
Collembola-Isotomidae	0.0031	0.0011	0.0036	-	-	-	-	-	-
Sminthuridae	0.0010	0.0019	0.0034	0.0007	-	-	-	-	-
Anisoptera nymph	-	-	-	-	-	-	-	0.0012	-
Zygoptera nymph	-	-	-	0.0236	0.0119	0.0051	0.0581	0.1084	0.0294
Thysanoptera	-	-	-	-	0.0059	-	-	-	-
Hemiptera	0.0022	-	-	-	-	-	-	-	-
Hydrometra	0.0007	0.0015	-	-	-	-	-	-	-
Homoptera-Aphididae	-	-	0.0043	-	-	0.0042	0.0007	-	-
Cicadellidae larvae	-	-	0.0038	-	0.0099	-	0.0008	0.0052	-
Coleoptera larvae-unknown	0.0019	0.0660	-	0.0080	0.0378	-	-	-	-
Dytiscidae	-	-	-	0.0026	-	-	-	-	-
Staphylinidae	-	-	-	-	-	-	-	0.0028	-
Diptera adult-unknown	-	-	0.0071	-	-	-	-	-	-
Chironomid larvae	0.0215	0.0541	0.0025	0.0093	-	0.0034	0.0101	0.0422	0.0013
Chironomid pupae	0.0010	-	-	-	-	-	0.0078	-	-
Chironomid adult	0.0005	0.0092	0.0065	0.0023	-	-	-	-	-
Sciaridae	0.0003	-	-	-	-	-	-	-	-
Tipulidae larvae	0.0162	-	-	-	-	-	-	-	-
Tipulidae pupae	0.0014	-	-	-	-	-	-	-	-
Hymenoptera	0.0006	-	-	-	-	-	-	-	-
Fish eggs	-	0.0142	-	-	-	-	-	-	-
Overall	6.7823	9.2358	3.4516	31.6156	9.0696	10.1851	4.7746	5.7873	4.8074

Table 3. Measurements of taxa richness and the Shannon-Weiner diversity index for epiphytic macroinvertebrates, terrestrial insects, and epibenthic/benthic macroinvertebrates at Sites A, B, and C. Hyacinth samples are shaded.

EPIPHYTIC MACROINVERTEBRATES	TAXA RICHNESS	SHANNON-WEINER DIVERSITY INDEX
HYACINTH A 6/98	26	1.04
PENNYWORT A 6/98	28	2.34
HYACINTH B 8/98	20	1.65
PENNYWORT B 8/98	16	1.18
HYACINTH C 8/98	21	2.00
PENNYWORT C 8/98	20	1.02
INSECTS		
HYACINTH A 4/98	14	1.45
PENNYWORT A 4/98	21	1.24
HYACINTH A 6/98	24	2.29
PENNYWORT A 6/98	25	2.12
HYACINTH A 7/98	21	3.07
PENNYWORT A 7/98	25	1.85
HYACINTH B 8/98	21	2.97
PENNYWORT B 8/98	20	2.32
EPIBENTHIC/BENTHIC MACROINVERTEBRATES		
HYACINTH A 4/98	7	1.26
PENNYWORT A 4/98	12	1.72
HYACINTH A 6/98	16	2.61
PENNYWORT A 6/98	13	1.92
HYACINTH A 7/98	15	2.39
PENNYWORT A 7/98	12	1.89
HYACINTH B 8/98	5	0.26
PENNYWORT B 8/98	12	1.47

Table 4. Average densities (number/m² of canopy) of all epibenthic/benthic macroinvertebrates at Sites A and B (n=5). Significant differences from two sample t-tests are highlighted. Significant differences at Site B represent a combination of all amphipods and isopods. H = Hyacinth, P = Pennywort.

taxa	Site A							Site B		
	4/98		6/98		7/98		6/99	8/98		6/99
	H	P	H	P	H	P	P	H	P	P
Hydrozoa	-	-	-	83.3	-	-	-	-	-	416.7
Turbellaria	-	83.3	-	1417	83.3	83.3	-	83.3	83.3	83.3
Nematoda	-	166.7	83.3	-	166.7	-	-	83.3	333.3	166.7
Polychaeta- <i>Neanthes</i> spp.	-	-	-	-	-	-	-	83.3	-	-
<i>Manayunkia speciosa</i>	-	83.3	-	-	-	-	-	-	-	-
<i>Fabriciola berkeleyi</i>	-	-	-	-	-	-	-	-	83.3	-
Oligochaeta	6417	9167	7250	5917	5083	7500	8833	12917	9583	1917
<i>Stylaria lacustris</i>	-	-	-	1417	-	-	-	-	-	-
Hirudinea	-	-	-	-	-	-	83.3	-	-	-
<i>Dina microstoma</i>	-	250.0	83.3	-	-	83.3	-	-	83.3	83.3
Gastropod sp. A	-	333.3	166.7	416.7	83.3	-	250.0	-	-	166.7
Gastropod sp. B	-	-	250.0	-	-	-	-	-	-	-
Ancylidae (limpet)	83.3	-	-	-	-	-	-	-	-	-
Juvenile Bivalve	-	83.3	-	-	-	-	166.7	-	-	666.7
<i>Corbicula fluminea</i>	-	-	-	-	-	-	-	-	83.3	-
Acarina	-	-	-	-	-	83.3	-	-	-	-
Ostracoda	-	-	416.7	583.3	83.3	166.7	-	166.7	666.7	-
Cladocera	-	-	583.3	416.7	-	-	83.3	-	-	-
Calanoid Copepod	-	-	83.3	-	-	-	-	-	-	-
<i>Pseudodiaptomus forbesi</i>	-	-	-	-	-	-	83.3	-	83.3	-
Cyclopoid Copepod	-	-	750.0	-	83.3	-	-	-	83.3	-
Isopoda- <i>Caecidotea racovitzai</i>	-	1333	1583	5000	1667	3250	83.3	-	-	416.7
<i>Gnorimosphaeroma insulare</i>	83.3	83.3	83.3	-	-	83.3	83.3	-	250.0	250.0
Amphipoda- <i>Corophium spinicorne</i>	500.0	-	333.3	-	-	-	-	-	83.3	500.0
<i>Crangonyx floridanus</i>	833.3	666.7	2083	1250	4917	83.3	-	-	-	83.3
<i>Gammarus daiberi</i>	-	-	333.3	-	166.7	-	-	-	1417	10500
<i>Hyalella azteca</i>	166.7	416.7	-	30167	333.3	11583	833.3	-	-	-
Insect larvae-unknown	-	-	-	83.3	-	-	-	-	-	-
Collembola-Isotomidae	-	-	-	-	166.7	-	-	-	-	83.3
Onychiuridae	-	-	-	-	83.3	-	-	-	-	-
Hemiptera	-	-	-	83.3	-	-	-	-	-	-
Homoptera	-	-	-	-	83.3	-	-	-	-	-
Aphididae	-	-	-	-	500.0	-	-	-	-	-
Cicadellidae larvae	-	-	-	-	-	166.7	-	-	-	-
Diptera-Chironomid larvae	166.7	333.3	500.0	1917	416.7	916.7	-	-	-	83.3
Chironomid pupae	83.3	-	-	-	-	-	-	-	-	-
Chironomid adult	-	-	83.3	-	83.3	-	83.3	-	-	-
Hymenoptera	-	-	-	-	-	166.7	-	-	-	-
Mymaridae	-	-	-	83.3	-	-	-	-	-	-
Overall	8333	13000	14667	48833	14000	24167	10583	13333	12833	15417

Table 5. Average densities (number/m² of canopy) of all terrestrial insects at Sites A and B (sample size in parentheses at head of each column). Significant differences from two sample t-tests are highlighted. H = Hyacinth, P = Pennywort.

taxa	Site A							Site B		
	4/98		6/98		7/98		6/99	8/98		6/99
	H	P	H	P	H	P	P	H	P	P
	(5)	(5)	(5)	(5)	(4)	(5)	(5)	(5)	(4)	(5)
Araneae	-	2.6	12.8	25.6	6.4	125.3	15.3	5.1	22.4	12.8
Acarina	71.6	58.8	2.6	5.1	6.4	-	-	-	-	17.9
Aphididae	-	15.3	30.7	46.0	111.9	7.7	43.5	5.1	-	7.7
Collembola	161.1	135.5	332.5	79.3	585.0	74.2	337.6	355.5	28.8	555.0
Zygoptera	-	-	10.2	15.3	54.3	84.4	-	12.8	16.0	2.6
Terebrantia	5.1	2.6	5.1	7.7	-	5.1	12.8	-	3.2	2.6
Hemiptera	61.4	23.0	130.4	99.7	105.5	25.6	10.2	10.2	12.8	2.6
Hydrometra	-	-	-	5.1	-	2.6	-	-	-	-
Homoptera	-	-	-	-	-	2.6	5.1	5.1	-	2.6
Cicadellidae	-	-	33.2	826.1	434.8	4396	69.1	352.9	1423	63.9
Delphacidae	-	-	-	-	-	43.5	2.6	38.4	57.5	5.1
Coleoptera	2.6	10.2	2.6	10.2	12.8	33.2	5.1	2.6	-	2.6
Staphylinidae	-	23.0	5.1	61.4	16.0	127.9	2.6	-	-	-
Trichoptera	-	2.6	2.6	12.8	25.6	10.2	10.2	2.6	3.2	-
Diptera-unknown	23.0	5.1	23.0	143.2	121.5	46.0	15.3	51.2	95.9	7.7
Cecidomyiidae	-	-	20.5	2.6	-	5.1	-	-	-	-
Ceratopogonidae	12.8	28.1	12.8	15.3	-	17.9	-	25.6	28.8	17.9
Chironomidae	3074	1568	1322	3875	294	1353	386.2	199.5	473.1	685.4
Dolichopodidae	5.1	2.6	25.6	133.0	16.0	76.7	15.3	89.5	73.5	23.0
Ephydriidae	1084.4	112.5	40.9	66.5	63.9	56.3	48.6	63.9	127.9	12.8
Phoridae	-	5.1	2.6	15.3	6.4	12.8	-	-	16.0	-
Psychodidae	56.3	6798	28.1	17.9	6.4	-	7.7	2.6	3.2	-
Sciaridae	-	28.1	35.8	143.2	19.2	12.8	-	-	3.2	2.6
Sphaeroceridae	17.9	163.7	7.7	340.2	6.4	74.2	23.0	2.6	6.4	12.8
Syrphidae	-	-	-	5.1	-	-	2.6	5.1	-	-
Tipulidae	12.8	20.5	71.6	38.4	51.2	2.6	2.6	-	-	10.2
Hymenoptera	-	2.6	46.0	92.1	12.8	61.4	12.8	10.2	9.6	40.9
Chalcidoidea	-	-	-	-	-	-	-	17.9	9.6	-
Mymaridae	2.6	2.6	2.6	-	3.2	79.3	48.6	35.8	195.0	12.8
Overall	4591	9010	2207	6082	1960	6737	1077	1294	2609	1501

Table 6. Species, number, and lengths of all fish caught adjacent to patches of hyacinth and pennywort at Site A during June and July 1998. Native species are in bold, sample size is at the head of each column. Hya = Hyacinth, Pen = Pennywort.

June		n=6	n=4	n=10		
Common Name	Scientific Name	Hya	Pen	sum	Mean Forklength (mm)	Forklength Range
Bigscale Logperch	<i>Percina macrolepida</i>	1	0	1	93	93
Black Crappie	<i>Pomoxis negromaculatus</i>	3	0	3	188	162-212
Bluegill	<i>Lepomis macrochirus</i>	24	39	63	100	43-171
Brown Bullhead	<i>Ictalurus nebulosus</i>	1	1	2	266	241-291
Golden Shiner	<i>Notemigonus crysoleucas</i>	3	34	37	51	26-114
Inland Silverside	<i>Menidia beryllina</i>	2	1	3	30	27-32
Largemouth Bass	<i>Micropterus salmoides</i>	5	6	11	110	25-290
Mitten Crab	<i>Eriocheir sinensis</i>	5	4	9	44	35-55
Prickly Sculpin	<i>Cottus asper</i>	15	8	23	33	22-65
Redear Sunfish	<i>Lepomis microlophus</i>	28	66	94	123	36-247
Splittail	<i>Pogonichthys macrolepidotus</i>	4	1	5	52	41-59
Spotted Bass	<i>Micropterus punctulatus</i>	2	1	3	100	98-102
Tule Perch	<i>Hysterochirus traski</i>	11	24	35	64	38-190
Yellowfin Goby	<i>Acanthogobius flavimanus</i>	20	22	42	39	26-68
July						
Common Name	Scientific Name	Hya	Pen	sum	Mean Forklength (mm)	Forklength Range
Black Crappie	<i>Pomoxis negromaculatus</i>	1	1	2	35	34-35
Bluegill	<i>Lepomis macrochirus</i>	9	24	33	95	45-164
Common Carp	<i>Cyprinus carpio</i>	0	1	1	201	201
Golden Shiner	<i>Notemigonus crysoleucas</i>	1	20	21	39	30-86
Inland Silverside	<i>Menidia beryllina</i>	13	43	56	29	21-40
Largemouth Bass	<i>Micropterus salmoides</i>	9	452	461	43	21-502
Mitten Crab	<i>Eriocheir sinensis</i>	1	13	14	34	18780
Prickly Sculpin	<i>Cottus asper</i>	0	6	6	47	35-62
Redear Sunfish	<i>Lepomis microlophus</i>	2	31	33	96	49-192
Splittail	<i>Pogonichthys macrolepidotus</i>	0	1	1	80	80
Tule Perch	<i>Hysterochirus traski</i>	2	9	11	75	66-86
Shad	<i>Dorosoma spp.</i>	4	0	4	-	-
Yellowfin Goby	<i>Acanthogobius flavimanus</i>	8	6	14	49	30-85

Table 7. Values for the Ivlev Electivity Index between *Crangonyx floridanus* and *Hyalella azteca*. Values are for bluegills adjacent to patches of hyacinth and pennywort at Site A during June and July 1998, and for bluegills and largemouth bass in patches of hyacinth at Site C during August 1998.

Site A Bluegills		
	Hyacinth	Pennywort
	<i>Crangonyx floridanus</i>	<i>Hyalella azteca</i>
June	-0.989	-0.487
July	-1.0	0.1393

Site C August		
	<i>Crangonyx floridanus</i>	<i>Hyalella azteca</i>
Bluegills	-0.730	-0.409
Largemouth Bass	-0.895	-0.284

Table 8. Species, number, and lengths of all fish caught directly underneath patches of hyacinth at Site C during August 1998. Native species are in bold, sample size is at the head of the column.

August		n=5		
Common Name	Scientific Name	#	Mean Forklength (mm)	Forklength Range
Bluegill size 1	<i>Lepomis macrochirus</i>	24	25.3	19-34
Bluegill size 2	<i>Lepomis macrochirus</i>	6	75.8	66-91
Largemouth Bass	<i>Micropterus salmoides</i>	19	51.9	39-66
Rainwater Killifish	<i>Luciana parva</i>	5	28.8	24-33
Brown Bullhead	<i>Ictalurus nebulosus</i>	3	35.0	34-37
Prickly Sculpin	<i>Cottus asper</i>	1	95	95

Discussion

Biological and Physical Differences

There are notable, significant differences between the FAV communities of the non-indigenous hyacinth and the native pennywort in the Sacramento/San Joaquin Delta. These differences range from physical structure to associated biological communities. Links between the physical structure and biological organisms of hyacinth and pennywort illustrate how a shift in the dominant FAV in the Delta has affected both the aquatic and terrestrial communities. The aquatic root mass of hyacinth has a more structurally complex surface area and more biomass than pennywort. Such a difference in root structure can explain the difference in macroinvertebrates that live in and around the roots of the two plants, as well as the lower levels of dissolved oxygen underneath the hyacinth canopy. Average spot measurements of dissolved oxygen were below 5 mg/L for hyacinth, and above 5 mg/L for pennywort. Other research has shown similar results. Hyacinth has the lowest dissolved oxygen levels as compared to milfoil, hydrilla, pondweed, and a native mix of submersed plants in Texas, and was the only plant to have averages below 5 mg/L (Madsen 1997). 5 mg/L represents the level at which fishes start to experience oxygen stress (Madsen 1997). Research specific to the Delta has shown that dissolved oxygen levels reached 0 mg/L three days out of a week in June, when measurements were taken every fifteen minutes underneath a large mat of hyacinth that completely covered a 15 meter wide slough (David Spencer, pers. com.). Lower levels of dissolved oxygen were likely the reason that hyacinth at Site B in August 1998 was completely devoid of epibenthic amphipods and isopods beneath the canopy. These

hyacinth patches did have an abundance of amphipods and isopods living epiphytically amongst the roots, which suggests that these macroinvertebrates could potentially be taking refuge in the root mass from underlying hypoxia (Bryan 1993). Pennywort at the same site did have amphipods and isopods living both epibenthically and epiphytically. Overall densities of epibenthic and benthic macroinvertebrates were greater in pennywort than hyacinth during all sampling, except at Site B during August 1998 when values were approximately equal.

Patterns of taxa richness and diversity for all aquatic macroinvertebrates tend to fall along a seasonal gradient. Both taxa richness and Shannon-Weiner diversity indices were higher in pennywort during the first month of sampling (June for epiphytic, April for epibenthic/benthic), but were higher in hyacinth for all subsequent months (August for epiphytic, June and July for benthic/epibenthic; Table 3). The exception to this is pennywort having higher measurements for epibenthic/benthic macroinvertebrates at Site B in August. As discussed above, this is due to hyacinth being almost devoid of epibenthic invertebrates, presumably because of low dissolved oxygen levels. Such a pattern of values being higher in hyacinth in later months can be related to hyacinth reaching its maximum root growth later in the season (Figs. 4,5), thus providing more colonizable substrate. Similar data has been collected for hyacinth and a different species of pennywort (*Hydrocotyle ranunculoides*) in Florida, which shows that overall dry biomass of hyacinth is 161% greater, and that the difference in biomass is maximized in late summer (Jantrarotai 1990). The maximum root length of hyacinth in the same study was 164% greater than *H. ranunculoides* (Jantrarotai 1990).

The leaf structure of pennywort is denser than hyacinth, which may explain the greater overall density of insects in pennywort, as well as the taxonomic differences of the insects living in the two canopies. Pennywort was higher in taxa richness for all months and sites, except for August at Site B. However, the high leaf density of pennywort did not correspond to all indicators, since hyacinth had greater diversity throughout all months (Table 3). Hyacinth can grow a taller canopy, which may effect biological patterns of the insect assemblages as well.

Although there were site differences in aquatic invertebrate assemblages, these were consistent across years, as the most abundant taxon present at each site was the same between 1998 and 1999. There was also only minor interannual variation in insect assemblages, the main difference being more Collembolans in pennywort during June 1999. Collembolans were more abundant in hyacinth in 1998, so it is possible that with the absence of hyacinth in June 1999 Collembolans adequately relocated to living in pennywort.

It is clear that amphipods are the predominant aquatic macroinvertebrate in FAV communities as well as important fish prey. Numerous studies have shown that amphipods such as *H. azteca* are vulnerable to bluegill predation (Keast 1978, Crowder and Cooper 1982, Mittelbach 1984, Schramm and Jirka 1989). However, based on PSI values, amphipods were found to be proportionally more abundant in the FAV canopies than in the fish diets, presumably due to the refuge function of the root mass structure. This agrees with research conducted at lakes in Florida, USA, where Schramm and Jirka (1989) found that amphipods were most abundant epiphytically, and were less abundant

both benthically and in fish diets. They also found that hyacinth roots provided a refuge for *H. azteca* from fish predation. *H. azteca* in hyacinth accounted between 69-86% of invertebrates in this system (Schramm et al. 1987), and was the most abundant taxon in south Florida canals (O'Hara 1968).

The major difference in amphipods between hyacinth and pennywort is the prevalence of *Crangonyx floridanus* in hyacinth. *C. floridanus* nearly vanished with the absence of hyacinth in 1999, lending even more credence that *C. floridanus* is preferably associated with hyacinth. *C. floridanus* is the smallest amphipod in this system, so it is possible that it prefers the branching network and larger surface area of the hyacinth roots. Furthermore, *C. floridanus* is not abundant in fish diets, as supported by both IRI and Ivlev Electivity Index values (Figs. 18-20; Table 7). This is in contrast to the amphipod *H. azteca* that was common in fish diets, and significantly more abundant in pennywort at Site A. There are a number of factors why *C. floridanus* may not be abundant in the fish diet, including: (1) Refuge function of hyacinth roots from fish predation; (2) Low caloric value and small size of *C. floridanus*; and (3) Poor taste of *C. floridanus*. The first scenario is the most likely, as research in Florida has shown that hyacinth roots can provide a refuge for invertebrates from fish predation (Schramm and Jirka 1989). Scenario two is also possible, as the standing stock of one *C. floridanus* is 0.000343 g, and one *H. azteca* 0.001056 g (Tables 1, 2). Therefore, *C. floridanus* is 33.43% smaller gravimetrically than *H. azteca*. With regards to the third scenario, it is not likely that *C. floridanus* is unpalatable to fish. Work has not been done specific to *C. floridanus*, but research has shown that a close congener, *Crangonyx richmondensis*, is

eaten by chum, chinook, and sockeye salmon fry in freshwater tidal creeks of the lower Fraser River, British Columbia (Levings et al. 1995).

New Discoveries of Amphipods and Isopods

The results from the biological sampling and fish diet analysis illustrate both the prominence and trophic importance of amphipods and isopods in this system. Of even further importance is the fact that three of these species, the amphipod *Crangonyx floridanus* and the isopods *Caecidotea racovitzai* and *Asellus hilgendorffii*, are first records for the Delta. *A. hilgendorffii* was distinct from the other two species, as it was not found in FAV. All three species occurred to some degree in a variety of fish diets, and thus are being incorporated in the Delta food web. Other amphipods and isopods sampled in this study include the native amphipods *Hyaella azteca*, *Corophium spinicorne* and *Corophium stimpsoni*, the previously known introduced amphipod *Gammarus daiberi*, and the native isopod *Gnorimosphaeroma insulare*. Conspicuously absent were the native isopods *Caecidotea tomalensis* and *Caecidotea occidentalis*.

Current knowledge suggests that *C. floridanus*, *C. racovitzai* and *A. hilgendorffii* are non-indigenous to the Delta, as all of these species are native elsewhere and have never before been documented in the Delta (Table 9). Specific criteria have been developed to assign the newfound presence of species in locations outside of their described range into categories of non-indigenous, cryptogenic, or native (Carlton 1996). The application of these criteria to *C. floridanus*, *C. racovitzai* and *A. hilgendorffii* are presented in Appendix A, and support their status of non-indigenous to the Delta.

The newfound presence of these crustaceans could have significant ramifications apart from just adding their names to the already lengthy list of non-indigenous species in the Delta. Amphipods and isopods are known to be intermediate hosts of a number of parasites, including acanthocephalan parasites of fish (Nagasawa et al. 1983, Yasumoto and Nagasawa 1996). *Asellus hilgendorfii* has specifically been shown to serve as an intermediate host for numerous species of acanthocephalans that parasitize salmonids and other fish in waters of Japan (Nagasawa and Egusa 1981, Nagasawa et al. 1983, Mayama 1989). Infection occurs when fish prey upon *A. hilgendorfii* that contain acanthocephalan larvae. Adult acanthocephalans parasitize the intestinal tract of the definitive host fish (Nagasawa et al. 1983). Studies have shown that salmonids can have infection levels of 83-100% depending on the season, when *A. hilgendorfii* is only 2.1 % of the total wet weight of food items in the fish diet (Nagasawa et al. 1983). Thus, even though *A. hilgendorfii* occurs in low abundance in the diets of fish in the Sacramento/San Joaquin Delta, it could still potentially infect the entire population of salmonids with acanthocephalan parasites. It remains to be seen whether or not non-indigenous acanthocephalans were introduced along with *A. hilgendorfii* into the Delta, and if this is in turn infecting endangered native salmonids and other fish.

Introduced Species Theory

Despite the onslaught of non-indigenous species worldwide, it is often difficult to determine what the congruent ecological effects are of such invasions (Drake and Mooney 1989, Luken and Thieret 1997). Oftentimes, sufficient monitoring is not

available to document changes caused by a specific invading organism. By comparing the community dominated by an exotic organism to that of an available native functional counterpart, it is possible to illuminate changes that may have arisen due to the establishment of that exotic organism. My research has shown that hyacinth can be characterized by a distinctly different invertebrate assemblage and associated fish-invertebrate food web as compared to its native functional counterpart, pennywort. The presence of hyacinth is associated with minor to major shifts in invertebrate assemblages depending on the site, and can alter the Delta fish-invertebrate food web. Such community-level effects can be typical of habitat-altering invaders such as hyacinth (Bertness 1984, Posey 1988, Vitousek 1990, Richardson et al. 1995, Ricciardi et al. 1997, Schmitz et al. 1997, Woods 1997, Crooks 1998, Crooks and Khim 1999) as hyacinth is not only widely abundant, but also provides structurally complex substrate to other organisms in both the aquatic and terrestrial zones.

The habitat-altering characteristic of hyacinth may also affect restoring wetlands in the area, as canopies of both hyacinth and pennywort form on the marsh fringe and may be influential in the development of the adjacent marsh community. There is vast interest in the Delta on predicting the rates and patterns of restoration of breached-levee wetlands, as exemplified by the BREACH research program (Simenstad et al. 1999). Succession in Louisiana follows a pathway of submerged aquatic vegetation, floating aquatic vegetation, emergent marsh vegetation, and willow forest (Penfound and Earle 1948). This pathway of succession is also supported in other warm climates where hyacinth grows throughout the year, as permanent floating islands are created which

deposit large amounts of organic matter (Trivedy et al. 1978, Gopal 1987, Woods 1997). Although this pathway is abbreviated in central California due to low winter temperatures that inhibit continuous growth of FAV canopies, rates of wetland restoration could still be accelerated due to increased deposition of organic material. Growth of semi-aquatic plants such as *Ludwigia* spp. on canopies of both hyacinth and pennywort could also stabilize the canopies, allowing emergent marsh vegetation to obtain a foothold in colonization. Such pathways warrant more research in the Delta, as the current study focused primarily on ecological issues.

Hyacinth in the Delta has followed a predictable pathway of plant invasion theory, as once natural environmental constraints in the area were lifted due to an altered hydrological regime, its invasive nature was allowed to flourish (Finlayson 1983, Barret 1989, Galatowitsch et al. 1999). Such a combination of appropriate abiotic and biotic factors often turn hyacinth into a 'perfect invader' (Ashton and Mitchell 1989). Hyacinth is one of the most influential invaders in the current Delta, with an annual chemical control budget of approximately \$1,000,000 (CDBW 1998, Pat Thalken, pers. com.). Its detrimental effects are comparable to other aquatic invaders in the area, such as the submerged aquatic plant *Egeria densa* (Obrebski et al. 1999), the clam *Corbicula fluminea* (Hymanson et al. 1994, Cohen and Carlton 1995), the Chinese mitten crab *Eriocheir sinensis* (Cohen and Carlton 1995), the Asian copepod *Pseudodiaptomus forbesi* (Cohen and Carlton 1995), and numerous species of non-indigenous fish (McGinnis 1984, Moyle and Light 1996).

It is noteworthy that in the process of studying one non-indigenous species, three more have been discovered. The amphipod *Crangonyx floridanus* and the isopods *Caecidotea racovitzai* and *Asellus hilgendorffii* are first records for the Delta, and have proven to be recent invaders into the system. This is not overly surprising, as the Delta is a highly human-modified system (Nichols et al. 1986), and may be the most invaded area in the world (Cohen and Carlton 1998). It is possible that hyacinth may have facilitated the invasions of these macroinvertebrates, as a function of its habitat-altering characteristics. Hyacinth does seem like a viable vector of introduction especially for *C. floridanus*, due to the prevalence of *C. floridanus* in the hyacinth community. The discovery of these three new species adds to the already lengthy list of 84 documented non-indigenous species in the Delta (Cohen and Carlton 1998). This keeps pace with the calculations of Cohen and Carlton (1998), as they determined that one new invasive species is currently established every 14 weeks in this system. No doubt future research will uncover still more invaders and their congruent ecological impacts, as has proven to be the case with hyacinth.

Table 9. Native range and non-indigenous populations of the amphipod *Crangonyx floridanus* and the isopods *Caecidotea racovitzai* and *Asellus hilgendorffii*, all first records for the Delta.

Species	Described Native Range	Non-Indigenous Populations
<i>Crangonyx floridanus</i>	Eastern and east-central United States (Holsinger 1972, Zhang 1997)	Colorado and Oregon USA, and Japan (Zhang 1997), California (this study)
<i>Caecidotea racovitzai</i>	Northeastern United States and southeastern Canada, Florida and Georgia USA (Williams 1970)	Washington and Utah USA (Bowman 1974, 1975, Williams 1970), California (this study)
<i>Asellus hilgendorffii</i>	Eastern Siberia, China, and Japan (Henry and Magniez 1995)	California (this study)

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Appendix A: Descriptions of Introduced Amphipods and Isopods

The amphipod *Crangonyx floridanus* and the isopods *Caecidotea racovitzai* and *Asellus hilgendorffii* are first records for the Delta. Samples, sites, and dates where the species occurred are summarized in Table 10. Additional sampling in habitats besides hyacinth and pennywort took place as part of the BREACH study (Simenstad et al. 1999). Brief descriptions of the species are outlined below, and in Figure 21.

Crangonyx floridanus Bousfield, 1963

Although species of the genus *Crangonyx* are often difficult to separate, it is relatively easy to distinguish *Crangonyx floridanus* from other amphipods in freshwater areas of the Delta. Two species that may be confused with *C. floridanus* are the native *Hyalella azteca*, and the non-indigenous *Gammarus daiberi* (Figure 21A-C). Adults of these species can be separated by differences in the lengths of antenna 1 and 2. *C. floridanus* has antenna 1 longer than antenna 2 (Figure 21A), *G. daiberi* has antenna 1 and 2 approximately the same length (Figure 21B), and *H. azteca* has antenna 1 shorter than antenna 2 (Figure 21C). Other distinguishing characteristics of *G. daiberi* include the presence of an accessory flagellum with 4-5 segments on antenna 1, as well as long setae specifically on the antennae and the extended uropod 3 (Figure 21B). *H. azteca* can be further identified by its large gnathopod 2 (Figure 21C). The three species can also be separated somewhat by size differences of adults, as relative sizes agree with published accounts documenting *C. floridanus* as the smallest (length 3.4-6.5 mm; Bousfield 1963), *G. daiberi* as the largest (8-12.5 mm; Bousfield 1969), and *H. azteca* as intermediate (4-8 mm; Pennak 1989). The taxonomic guides presented in Zhang (1997) or others

(Bousfield 1963, Holsinger 1972, Pennak 1989) should be used to key *C. floridanus* to species, as it is entirely possible that more than one species of the genus *Crangonyx* exists in the Delta.

Dr. John Holsinger identified *C. floridanus*, stating, "...we have a record of an introduction of *floridanus* in Japan...Presumably, the population you've sampled is also the result of an introduction." (pers. com.). Further details and definition of terms can be found in Pennak (1989) for *C. floridanus* and *H. azteca*, Bousfield (1963), Holsinger (1972), and Zhang (1997) for *C. floridanus*, and Bousfield (1969) for *G. daiberi*. *G. daiberi* is endemic to the Atlantic coast of North America, and was first detected in the Delta in 1983 (Hymanson et al. 1994, Cohen and Carlton 1995).

Caecidotea racovitzai Williams, 1970 and *Asellus (Asellus) hilgendorffii* Bovallius, 1886

The body shapes of these two species are extremely difficult to distinguish upon casual observation (Figure 21D), and will thus be treated together. Keys are currently only developed for adult males of the species. Two key distinguishing structures are located on gnathopod 1 and pleopod 2 (Figures 21E-H). *A. hilgendorffii* has 2 teeth-like spines located on the palm of the propodus of gnathopod 1 (Figure 21E), while *C. racovitzai* has a triangular process near the midpoint (Figure 21F). Also, *A. hilgendorffii* has a basal spur on the endopod of pleopod 2 (Figure 21G), which is not present on *C. racovitzai* (Figure 21H) or any other species in the genus *Caecidotea*. Size cannot be used to distinguish the two species, as published lengths for adults of *C. racovitzai* (4-15 mm; Williams 1972) and *A. hilgendorffii* (7-15 mm; Birstein 1964) overlap. The sizes of

our specimens also fall into this range. The two recorded native isopods *Caecidotea occidentalis* and *Caecidotea tomalensis* were not found in this study, and are described in Bowman (1974).

Identification of *A. hilgendorfii* was confirmed by Dr. Guy Magniez, who has provisionally assigned the specimen as, “*Asellus (Asellus) hilgendorfii* forme de Californie...a species without doubt of human-mediated origin into the Delta” (Magniez and Toft, in prep). Dr. Noboru Nunomura has also examined samples of *A. hilgendorfii*, stating that the specimens are, “different from Japanese species of *A. hilgendorfii*” (pers. com.). Dr. Doug Smith confirmed the identification of *C. racovitzai*, saying, “Regarding the *Caecidotea*, they are certainly *racovitzai*. They may all be introduced, but I am not sure.” (pers. com.). Dr. Julian J. Lewis has also confirmed the identification of *C. racovitzai* (pers. com.). Further details and definition of terms for *C. racovitzai* can be found in Pennak (1989) and Williams (1972), and for *A. hilgendorfii* in Henry and Magniez (1995) and Birstein (1964).

Criteria for introduced species

Current knowledge suggests that *C. floridanus*, *C. racovitzai* and *A. hilgendorfii* are non-indigenous to the Delta. Although this may be taken for granted based on the fact that they are native elsewhere and are new to the Delta, I used specific criteria that have been developed to assign the newfound presence of species in locations outside of their described range into categories of non-indigenous, cryptogenic, or native (Carlton 1996). Lindroth (1957) initially proposed five general criteria for the recognition of

introduced terrestrial species. Carlton (1979) expanded these criteria into six sets, divided into thirteen categories. Chapman (1988) and Chapman and Carlton (1991, 1994) have further developed these criteria, applying them to temperate amphipods and isopods.

The following nine criteria presented by Chapman and Carlton (1994) were used to assess the likely invasions of *C. floridanus*, *C. racovitzai* and *A. hilgendorffii*: (1) Appearance in local regions where not found previously; (2) Expansion of local range subsequent to first appearance; (3) Access to human mechanisms of dispersal; (4) Association with known introductions; (5) Prevalence in or restriction to artificial or altered environments; (6) Discontinuous or restricted regional distribution; (7) Disjunct global distribution; (8) Insufficient life history adaptations for global dispersal; and (9) Exotic evolutionary origin. The degree to which each species met these nine attributes are summarized in Table 11 and as follows:

Attribute 1: Appearance in local regions where not found previously. All three species meet this criterion. A recent extensive review of the biological invasions of the San Francisco Bay and Delta did not document their presence (Cohen and Carlton 1995). Numerous studies have been conducted on the benthos of the Delta utilizing Ponar and Peterson dredges in channels, and none of these studies have reported their presence (Hazel 1966, Siegfried 1980, Herbold and Moyle 1989, Hymanson et al. 1994). These same studies have documented the native isopods *Asellus occidentalis*, *Asellus tomalensis*, *Gnorimosphaeroma insulare*, and *Asellus* spp., as well as the amphipods *Hyaella azteca*, *Corophium* spp., *Gammarus* spp., and the recent introduction of

Gammarus daiberi. However, a review of some of the isopods documented as *A. occidentalis* in Hymanson et al. (1994) has shown that these were actually *A. hilgendorffii*, the first specimen of which was collected in 1978 (Wayne Fields, pers. com.). Such initial misidentifications are common when exotic species first appear in a system. None of these reports have documented *Crangonyx* spp., although recent monitoring continual with that reported in Hymanson et al. (1994) has captured a few specimens starting in 1995, as well as a specimen of *Caecidotea racovitzai* in January 1999 (Wayne Fields, pers. com.). Other recent monitoring in submerged aquatic vegetation of the non-indigenous *Egeria densa* has documented only the amphipods *Hyaella azteca* and *Corophium* spp. (Obrebski et al. 1999). Historic reports on fish diets in the Delta have only documented *Corophium* spp. and *Gammarus* spp., as well as some isopods (Turner 1966).

Although the available data does support this criterion, it should be noted that most previous studies were conducted in deeper channels, not in shallow-water areas with dense aquatic vegetation. Such habitats have typically been undersampled in the Delta. However, as mentioned above, the sudden appearance of these three species in the ponar sampling continuous with that described in Hymanson et al. (1994) shows that these species can be found in such habitats. Coarse taxonomic resolution may also have obscured their initial discovery.

Attribute 2: Expansion of local range subsequent to first appearance. This criterion is not known for any of the species, as this is the first report of these three species in the

Delta and surrounding area. Only future monitoring will be able to adequately assess any such range expansions.

Attribute 3: Access to human mechanisms of dispersal. All three species meet this criterion. The San Francisco Bay estuary is considered one of the most modified by human activity in the United States (Nichols 1986), and may be the most invaded estuary in the world (Cohen and Carlton 1998). Such high levels of human modification and invasion rate make it clear that there are substantial human mechanisms for dispersal of organisms.

There are currently 84 established non-indigenous species in the freshwater Delta (Cohen and Carlton 1998). Ballast water and shipfouling have been associated with many of these species, including the invasion of the amphipod *Gammarus daiberi* (Cohen and Carlton 1995). Additionally, the introduction of *C. floridanus* into Japan and Oregon has been blamed on ballast water (Zhang 1997). Such a mechanism could also account for the presence of the three new species in the Delta, as a large port area encompassed the sampling locations. The Delta supports two major inland ports, Sacramento at the northern edge of the Delta and Stockton on the southeastern edge. These two ports account for the transport of 5 million tons of cargo annually (CDWR 1993). Most vessels are bulk carriers that arrive to port empty of cargo, subsequently loading grain and wood products (Carlton et al. 1990). Therefore, the majority of the vessels arrive with thousands of tons of ballast water taken up from their home port, which they release either in the ship channels upon approach or entirely at dockside (Carlton et al. 1990). Source regions for these species also have an abundance of shipping activity, as the

described ranges of *C. racovitzai* and *C. floridanus* encompass numerous shipping centers in eastern North America (Williams 1970, Zhang 1997), as does *A. hilgendorffii* around the Sea of Japan (Henry and Magniez 1995).

Another viable human mechanism of dispersal is the transport of non-indigenous aquatic plants. As documented in this report, *C. floridanus* and *C. racovitzai* cling to the roots of the non-indigenous plant hyacinth, as well as parrot's feather (*Myriophyllum aquaticum*). Such attachment to pond plants on their removal from water has been attributed to the distribution of the non-indigenous *Crangonyx pseudogracilis* in Ireland (Costello 1993). Zhang (1997) has also attributed the presence of *C. floridanus* in Colorado and *C. pseudogracilis* in Arizona and Nevada as transported along with aquarium vegetation or fish containers from eastern localities. In addition, the described distributions of *C. floridanus* in Florida and Louisiana (Holsinger 1972) and *C. racovitzai* in Florida (Williams 1970) overlap with the distribution of hyacinth in those states. Although the exact vector of introduction of hyacinth into the Delta is unknown, it is extremely likely that it was transported as an ornamental pond plant shortly after its introduction into Louisiana and Florida (Bock 1966, Gopal 1987).

Other potential mechanisms of human dispersal that are of less prevalence include: (1) Fisheries stocking; (2) Releases or escapes from breeding and rearing facilities, and aquariums; (3) Introductions for biological control; (4) Plantings of exotic vegetation for marsh restoration and erosion control; and (5) Importation with shipments of live seafood and bait (Cohen and Carlton 1995, 1998). Cohen and Carlton (1995) give several examples of species released through these vectors.

Attribute 4: Association with known introductions. All three species meet this criterion. As previously mentioned, the San Francisco Bay and Delta is possibly the most invaded estuary in the world, and there are currently 84 established non-indigenous species in the freshwater Delta (Cohen and Carlton 1998). *C. floridanus* and *C. racovitzai* were found to live in association with the non-indigenous aquatic plants hyacinth and parrot's feather. Other abundant exotic organisms found to live in the same community as the three species include the amphipod *G. daiberi* and the clam *Corbicula fluminea*. All three species were also found with *G. daiberi* and the non-indigenous copepod *Pseudodiaptomus forbesi* in fish diets. Although the three new species are associated with known introductions in the Delta, species associations in their native described ranges are lacking.

Attribute 5: Prevalence in or restriction to artificial or altered environments. All three species meet this criterion. As mentioned earlier, the Delta is an extremely anthropogenically modified environment (Nichols 1986). Approximately 97% of the historic wetlands in the Delta have been leveed for agricultural purposes (Atwater and Belknap 1980, SFEP 1991). Of the eight sites where the species were found (Table 10; see Simenstad et al. 1999 for more information on sites), five of these are breached-levee restored wetlands (DO, LI, MI, SH, and VE). Two of these sites also have large depositions of dredged material (DO and VE). All sites are adjacent to rip-rapped levees, with the exception of one (BR). In addition, six of the sites directly border ship channels to Stockton and Sacramento (BR,DO,LI,SH,UM,VE), with the other two (MI and SM) being a few miles from the ship channel. There is also an abundance of recreational boat

use and fishing in the area. As shown earlier, *C. floridanus* and *C. racovitzai* are found in the non-indigenous hyacinth community. Although the three new species are prevalent in artificial environments, current natural habitats are rare and undersampled in this area.

Attribute 6: Discontinuous or restricted regional distribution. All three species meet this criterion. *A. hilgendorffii* has never before been found in North America (Henry and Magniez 1995). The only report of *C. racovitzai* in western North America is from Washington and Utah (Williams 1970, Bowman 1975), but these populations are both probable introductions (Bowman 1974, 1975). The only reports of *C. floridanus* in western North America are from Colorado and Oregon, but as with *C. racovitzai* these populations are probable introductions (Zhang 1997). It should again be noted that habitats in which these species occur are generally poorly sampled on the West coast of North America, and coarse taxonomic resolution could have additionally obscured their presence.

Attribute 7: Disjunct global distribution. All three species meet this criterion. *C. floridanus* is widely distributed in the eastern and east-central United States (Zhang 1997), its native described range (Holsinger 1972). In addition to the new discovery of its presence in California, populations in Colorado and Oregon are likely to be introduced, and it has also been introduced into Japan (Zhang 1997). *C. racovitzai* has a fairly continuous distribution in the northeastern United States and southeastern Canada, and a subspecies occurs in Florida and Georgia (Williams 1970). As previously mentioned, there are populations in Washington and Utah (Williams 1970, Bowman 1975) which are probably introduced (Bowman 1974), in addition to its presence in

California. *A. hilgendorffii* has never before been documented in North America. The described native range of this species surrounds the Sea of Japan, in eastern Siberia, China, and the entire Japanese archipelago (Henry and Magniez 1995).

Attribute 8: Insufficient life history adaptations for global dispersal. All three species meet this criterion. Amphipods and isopods are brooders (Pennak 1989), and therefore do not have larval stages that are conducive for natural oceanic or intercontinental dispersal. This is especially significant because these species all occur in isolated freshwater systems as opposed to continuous marine coastlines.

Attribute 9: Exotic evolutionary origin. *A. hilgendorffii* fully meets this criterion, but it can not be completely satisfied for *C. floridanus* and *C. racovizai*. *A. hilgendorffii* definitely has exotic origins, as the genus *Asellus* consists solely of far-eastern species (Birstein 1964, Henry 1993, Henry and Magniez 1995). The only North American species of *Asellus* is *A. alaskensis*, which occurs north of the Arctic Circle in Alaska and has clear Asian affinities (Bowman 1975). There have also been reports of *A. aquaticus* from Greenland, although populations are not presently found and past populations have been attributed to temporary invasions via ballast water (Williams 1970).

Almost all species of the genus *Crangonyx* occur in eastern North America, east of the Rocky Mountains (Holsinger 1972, Zhang 1997). The ancestor of the genus *Crangonyx* might have evolved in the middle-western region of North America (Zhang 1997). Documented Pacific coast epigeal species include: *C. richmondensis* in Oregon, Washington, British Columbia, and Alaska; probable introductions of *C. pseudogracilis*

in Oregon, Arizona, and Nevada; and *C. floridanus* in Colorado and Oregon (Zhang 1997).

The genus *Caecidotea* also consists mostly of species in eastern North America (Williams 1970). Only two native species on the Pacific coast are known, *C. occidentalis* and *C. tomalensis* (Williams 1970, Bowman 1974). *C. communis* and *C. racovitzai* have both been documented in Washington, but these populations are probably introduced, as are populations of *C. communis* in Colorado and *C. racovitzai* in Utah (Bowman 1975).

Even though *C. floridanus* and *C. racovitzai* appear not to have originated on the Pacific coast of North America, the genera *Crangonyx* and *Caecidotea* are both common throughout North America, and therefore attribute 9 cannot be completely satisfied for these two species.

Summary of nine attributes. The three species satisfy almost all of the attributes of non-indigenous species for the Delta (Table 11). *C. floridanus* and *C. racovitzai* satisfy 7 of the 9 criteria, and *A. hilgendorfi* satisfies 8 of the criteria, with the remaining criteria not having enough evidence to either confirm or negate.

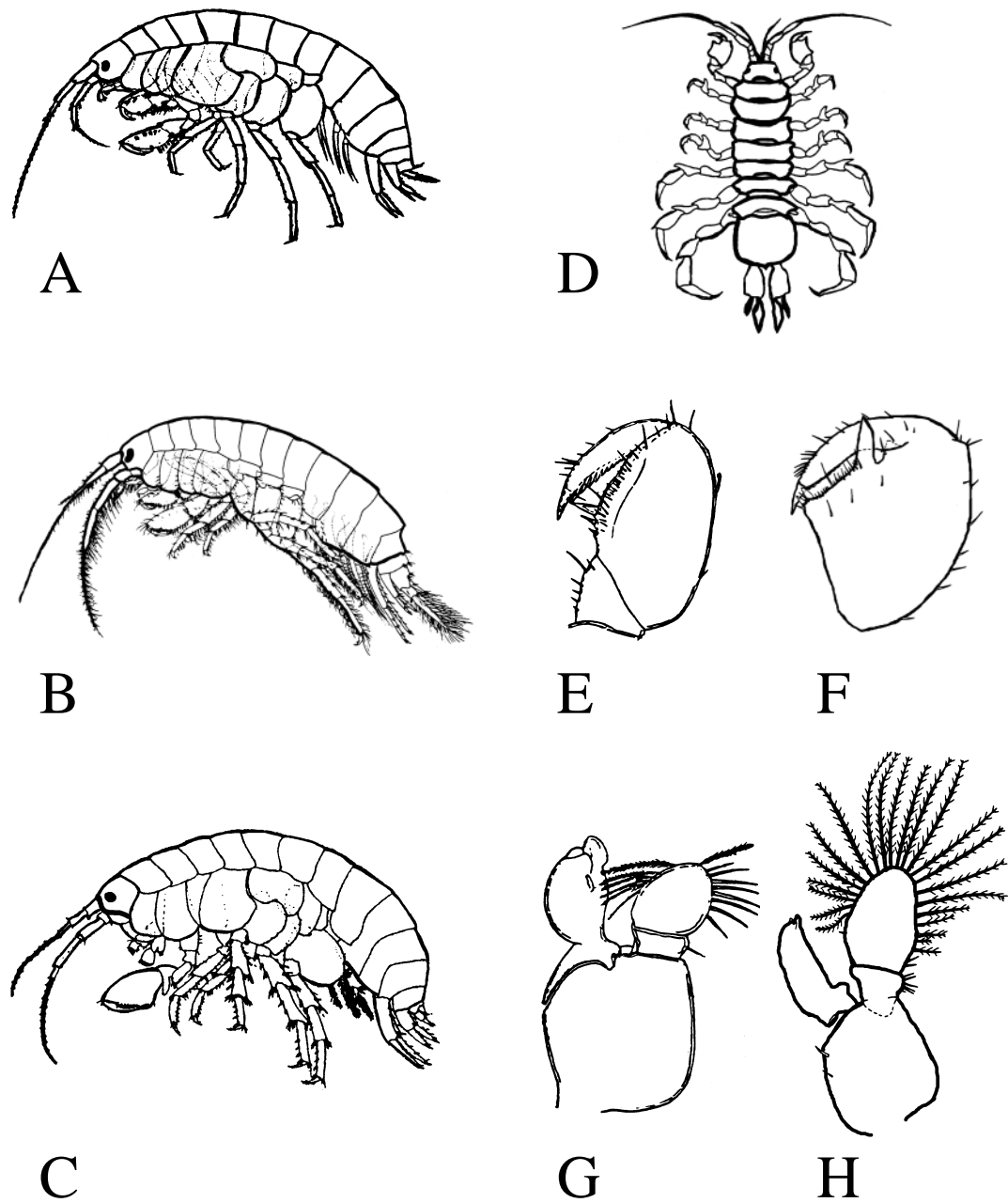


Figure 21. Descriptive diagrams of amphipods and isopods (A) *Crangonyx floridanus* (from Barnard and Barnard 1983). (B) *Gammarus daiberi* (from Bousfield 1969). (C) *Hyaella azteca* (from Pennak 1989). (D) Body morphology of *Caecidotea racovitzai* and *Asellus hilgendorffii* (from Pennak 1989). (E) Propodus of gnathopod 1 of *Asellus hilgendorffii* (from Birstein 1964). (F) Propodus of gnathopod 1 of *Caecidotea racovitzai* (from Williams 1972). (G) Pleopod 2 of *Asellus hilgendorffii* (from Birstein 1964). (H) Pleopod 2 of *Caecidotea racovitzai* (from Williams 1972).

Table 10. Samples, sites, and dates of occurrences of the amphipod *Crangonyx floridanus* and the isopods *Caecidotea racovitzai* and *Asellus hilgendorffii*. Sample codes: E = Emergent vegetation (*Scirpus* spp.), R = Riparian vegetation, H = Hyacinth, P = Pennywort, F = Parrot's Feather, B = Bluegill, L = Largemouth Bass, S = Sacramento Squawfish, T = Tule Perch. Site codes: BR = Brown's Island, DO = Donlon Island, LI = Lindsey Slough, LM = Lower Mandeville Tip, MI = Mildred island, SH = Sherman Island, SM = Sand Mound Slough, UM = Upper Mandeville Tip, VE = Venice Cut. Additional sampling in habitat besides hyacinth and pennywort was part of the BREACH study.

Species	Method	Samples	Sites	Dates
<i>Crangonyx floridanus</i>	Benthic Cores	E,R,H,P,F	BR,DO,LI,SH,SM,UM,VE	4/98, 6-7/98, 4/99, 6/99
	Floating Vegetation Roots	H,P,F	BR,LI,MI,UM	6/98, 8/98, 6/99
	Fish Diet	B,L	LM,VE	4/98, 9/98
<i>Caecidotea racovitzai</i>	Benthic Cores	E,R,H,P,F	BR,LI,MI,SH,SM,UM,VE	4/98, 6-8/98, 3-4/99, 6/99
	Floating Vegetation Roots	H,P,F	BR,LI,MI,UM	6/98, 8/98, 6/99
	Fish Diet	B	LM,VE	4/98, 6-7/98
<i>Asellus hilgendorffii</i>	Benthic Cores	E,R	UM,VE	6-7/98
	Fish Diet	B,L,S,T	LM,MI	5/98, 7-8/98

Table 11. Summary of the criteria for introduced species. Y = Yes, satisfies the attribute. ? = not enough evidence to confirm or negate the attribute.

Species	Attributes								
	1	2	3	4	5	6	7	8	9
<i>Crangonyx floridanus</i>	Y	?	Y	Y	Y	Y	Y	Y	?
<i>Caecidotea racovitzai</i>	Y	?	Y	Y	Y	Y	Y	Y	?
<i>Asellus hilgendorffii</i>	Y	?	Y	Y	Y	Y	Y	Y	Y