

The Effects of Introduced Water Hyacinth on Habitat Structure, Invertebrate Assemblages, and Fish Diets

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ABSTRACT: The South American floating aquatic plant water hyacinth (*Eichhornia crassipes*) has a history of worldwide invasions, including a 1904 introduction into the Sacramento-San Joaquin Delta, California. The native pennywort (*Hydrocotyle umbellata*) occupies similar habitats in the Delta and is extensively used by resident invertebrates and fish. We sought to discover if an invader would be functionally equivalent to the native plant, by asking whether the encroaching hyacinth modified the invertebrate assemblage structure and fish-invertebrate food web relative to pennywort. We sampled epiphytic, epibenthic, and benthic invertebrates, and plant canopy insects in patches of hyacinth and pennywort, and analyzed fish diets at three sites in the Delta during 1998. We also measured habitat structure (leaf density, root biomass, and surface area). In 1999, following control and absence of hyacinth, we again measured epiphytic invertebrates in pennywort. We found differences between hyacinth and pennywort in structure, associated invertebrates, and fish diets. Most measurements inferred functional non-equivalency between hyacinth and pennywort, although some functional equivalency and natural variation existed. Leaf and insect densities were significantly higher in pennywort and there were also significant differences in insect assemblage compositions. Hyacinth roots in the water column had significantly more surface area. Densities of epibenthic and benthic aquatic invertebrates were typically greater in pennywort and taxonomic compositions of aquatic invertebrate assemblages showed significant differences. Amphipods and isopods living epiphytically in the root masses were particularly abundant, including several newly discovered introduced species: the amphipod *Crangonyx floridanus* and the isopods *Caecidotea racovitzai* and *Asellus hilgendorfi*. The native amphipod *Hyaella azteca* was more abundant in pennywort and heavily preyed upon by fish, while the non-indigenous *C. floridanus* was more abundant in hyacinth and not prevalent in fish diets. The introduction of hyacinth to the Delta has caused significant ecological alterations in the surrounding community, due to hyacinth being functionally different from native patches of pennywort.

Introduction

Ecological theory predicts that non-indigenous species that will have the most impact are those that represent something fundamentally new to a given system (Simberloff 1991; Ruesink et al. 1995; Parker et al. 1999). Although this appears to be most often the case, we sought to illuminate whether an invader that was similar in appearance to a common native could be non-equivalent in its function. Floating aquatic vegetation (FAV) canopies of the non-indigenous water hyacinth (*Eichhornia crassipes*) in the Sacramento-San Joaquin Delta of California are fundamentally similar to those of the native pennywort (*Hydrocotyle umbellata*), as both form canopies of floating vegetation. Although hyacinth and pennywort form similar patches of floating vegetation, it is a question whether or not they are functional equivalents—providing similar functions to the surrounding biotic community. We compared the habitat struc-

ture, invertebrate assemblages, and diets of fish associated with hyacinth and pennywort in order to determine whether or not they were functional equivalents.

Comparative studies of functional equivalency are often used to test how human-altered systems compare to natural states, such as in restored wetlands (Simenstad and Thom 1996) or transplanted seagrass beds (Williams and Davis 1996). Specific tests of the functional role of non-indigenous species relative to natives are rare. One such test in a terrestrial system (Stromberg 1998) has shown that there can be some functional redundancy (Westman 1990), while other tests show significant alterations (Vitousek 1986). Filling such gaps in our knowledge is important, as invasive species are often difficult if not impossible to keep under control (Drake and Mooney 1989), and the congruent ecological impacts of specific invaders are not well known (Parker et al. 1999). If we can uncover such ecological effects, we can better manage and predict the fates of current and future biological invasions.

Hyacinth is native to Brazil and has become

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widespread on a global scale, first being introduced to the Sacramento River in California by ornamental pond enthusiasts in 1904 (Finlayson 1983; Gopal 1987). Once the plants are introduced they rapidly increase in coverage, as hyacinth has the highest growth rate of any saltwater, freshwater, or terrestrial vascular macrophyte (Wolverton and McDonald 1978). In the Delta, hyacinth covered 506 ha or 22% of the waterways by 1981 (Finlayson 1983). Such prevalence sparked an extensive chemical control program headed by the California Department of Boating and Waterways (CDBW 1998), which actively controls coverage of hyacinth by spraying the chemical 2,4-D. As a result of these efforts, the extensive mats found especially in tropical climates (Gopal 1987) were controlled during the course of our study, and patches of hyacinth and pennywort were similar in coverage.

In many systems hyacinth is an ecosystem engineer (Jones et al. 1997; Crooks and Khim 1999), modifying the surrounding habitat by providing a structurally complex canopy. In addition to forming a dense floating mat, roots hanging in the water column and leaves projecting above the water surface provide complex structures that can be inhabited by other species. Organic deposition from the canopy can cover the underlying benthic zone, leading to low dissolved oxygen levels (Gopal 1987). Effects of these characteristics on community dynamics when hyacinth coexists with native FAV counterparts are unknown, and are often a subject of curiosity among investigators (Gopal 1987; Masifwa et al. 2001).

FAV can be beneficial as a nursery habitat for juvenile fishes and invertebrates (Werner and Hall 1979; Gopal 1987; Schramm and Jirka 1989; Dibble et al. 1996). Roots hanging down into the water column are important as habitat for epiphytic invertebrates, especially amphipods (Schramm et al. 1987). Epiphytic invertebrates are typically much more abundant than benthic and epibenthic invertebrates, and their densities are positively correlated to the amount of FAV surface area available for colonization (Crowder and Cooper 1982; Schramm et al. 1987). Fish such as bluegills (*Lepomis macrochirus*) selectively feed on epiphytic invertebrates over other sources of prey (Werner and Hall 1979; Schramm and Jirka 1989). The effects of hyacinth on the fish-invertebrate food web in the Delta could be pervasive due to the prominence of hyacinth in shallow water areas.

Pennywort is the predominant native FAV in the Delta. Although pennywort and hyacinth both form floating canopies and tend to occupy similar habitats, we hypothesize that a hyacinth invasion could alter key habitat structure components, leading to surrounding community alterations. Such

effects may not be as readily apparent compared to invaders that either occupy vacant niches and substantially modify the existing environment, such as introductions of fish predators when native piscivores are absent (Brown and Moyle 1991), or mussel invasions into mudflats previously uninhabited with mussel mats (Crooks and Khim 1999). Our research sought to illuminate any community alterations caused by the hyacinth invasion.

Methods

STUDY AREA

Our three study sites were located in the central and western Sacramento-San Joaquin Delta of California: Site A (Mandeville Tip, 38.0°4'N, 121°32'W), Site B (Brown's Island, 38.0°2'N, 121°52'W), and Site C (Mildred Island, 37.0°59'N, 121°31'W). These sites were chosen because they contained discrete patches of both hyacinth and pennywort. The Delta is heavily influenced by human activity, including agricultural, recreational, and industrial activities (Nichols et al. 1986). Historically, the Delta was almost all wetlands characterized by tule vegetation (*Scirpus* spp.) with some natural levees and riparian habitat (woody vegetation, mostly *Salix* spp.; TBI 1998). Approximately 95% of these wetlands have been leveed and drained predominantly for agricultural purposes, and the majority of the Delta's remaining historic channels are rip-rapped and constrained (TBI 1998). Although salt water historically entered the Delta, current water management attempts to prevent this, mainly through controlled water flows that increase freshwater inflow during summer months to maintain freshwater available for irrigation and drinking purposes (Nichols et al. 1986). Benthic sediments in the Delta are an unconsolidated mixture of sand, silt, and clay (Hymanson et al. 1994). Tidal influence ranges between 1 to 2 m (CDWR 1993).

STUDY DESIGN

Healthy FAV patches not chemically controlled with 2,4-D were sampled in areas that bordered a marsh. Habitat structure measurements and invertebrate samples were collected in 5 patches of both hyacinth and pennywort at each site. Patches were chosen by a random number generator corresponding to the patch number along a transect drawn parallel to shore (Fig. 1). These patches occupied indentations in the marsh and were generally separated by clumps of tule vegetation. Patches were fairly small and discrete (30.96 m² average surface area, 3.92 SE) and were used only if they formed a fringe along the marsh, not if they occupied an entire channel. Since the overall size and shape of the patches could not be controlled

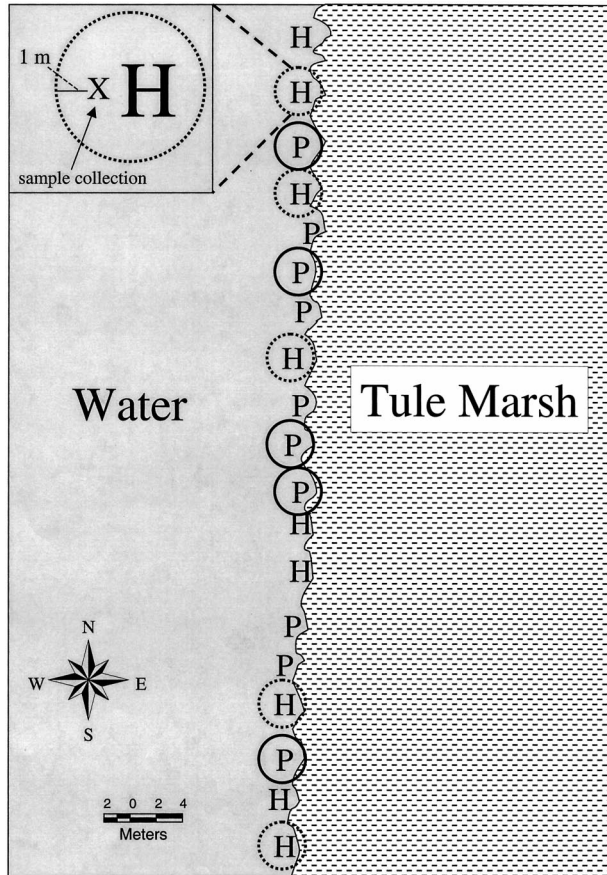


Fig. 1. Illustration of a typical sampling design at a study site. Shallow water is light gray, tule marsh (*Scirpus* spp.) is hatched, H = hyacinth patches, and P = pennywort patches. Circled patches are those randomly selected for sampling along a transect south to north (patches 1, 3, 6, 7, 8 for hyacinth; 1, 4, 5, 8, 10 for pennywort). Inset is the specific location of sample collection, 1 m in from the water's edge at the center of each patch.

due to the study design of sampling natural patches, we minimized the natural variation by designating sampling to the center of each patch, 1 m in from the water's edge (Fig. 1). We focused on the outer edge as other studies have documented changes in invertebrate communities between the edge and interior of patches (Bailey and Litterick 1993; Masifwa et al. 2001). Patch edges also offered higher association with surrounding fish and ease of access for sampling by boat. Patches of hyacinth and pennywort were not intermixed, but occasionally bordered each other. All patches were sampled in approximately 1 m of water, with the roots hanging freely halfway into the water column.

Description of the habitat structure and invertebrate sampling frequency is summarized in Table 1. In 1998, habitat structure and epiphytic invertebrates were sampled in June at Site A, and in

August at Sites B and C. Epibenthic-benthic invertebrates and terrestrial canopy insects were sampled in April, June, and July at Site A and August at Site B. Sampling was not conducted at Site A after July as hyacinth patches were exterminated with chemical control by CDBW.

Hyacinth was absent at all three study sites in 1999, although residual patches remained in interior marsh channels and boat marinas in the surrounding area. The lack of hyacinth in 1999 was attributed to intensive chemical spraying by CDBW during fall and winter 1998 and spring 1999, several cold freezes during the winter that caused high mortality of overwintering plant material, and high winter outflows that flushed clumps of hyacinth out of the Delta into San Francisco Bay. We took advantage of this unforeseen hyacinth removal experiment by sampling epiphytic invertebrates in pennywort at all three sites in June 1999. Such a plan allowed us to measure interannual variation and to determine if the invertebrate community changed with the absence of hyacinth. Although this was an originally unplanned segment of our research, the issue of the effect of the removal of non-indigenous species is a vital question in both research and management (Westman 1990).

PHYSICAL SAMPLING

Intensive sampling of hyacinth and pennywort habitat structure was conducted in June 1998 at Site A and in August 1998 at Sites B and C, congruent with epiphytic invertebrate sampling (Table 1). Entire patch surface area was estimated by measuring the maximum length and width of each patch. Leaf density was measured at the location of sampling by counting the number of leaves in a 0.5 m² quadrat ($n = 5 \text{ site}^{-1}$). Roots collected for epiphytic invertebrate sampling (described below) were measured for biomass and surface area. Root wet biomass was measured by blotting the roots dry with a towel, allowing to air dry for 10 min, and weighing to the nearest milligram. Root surface area was measured using the surfactant technique originally developed by Harrod and Hall (1962). A soapy solution consisting of 60 ml of Liquinox soap in 6 l of water was mixed in a bucket and left overnight so that the bubbles dispersed. For each root sample, five 1-g subsamples were 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 subsample was then reweighed. The surface area of the root samples was determined by regressing the differences in weight to those measured from the same process for known surface areas of tinfoil (25, 100, 225, 400, 625, and 900 cm²; $n = 5$).

TABLE 1. Invertebrate and habitat structure sampling design. Numbers are sample size, blanks indicate no sampling conducted. H = hyacinth, P = pennywort. Patches of hyacinth were exterminated with chemical control at Site A (Mandeville Tip) in August 1998, after which sampling was shifted to Sites B and C (Brown's Island and Mildred Island, respectively). Patches of hyacinth were absent at all study sites in 1999 (see text).

	1998								1999	
	April		June		July		August		June	
	H	P	H	P	H	P	H	P	H	P
Site A, Mandeville Tip										
Epiphytic			5	5						5
Epibenthic-Benthic	5	5	5	5	5	5				
Insect	5	5	5	5	5	5				
Habitat Structure			5	5						
Site B, Brown's Island										
Epiphytic							5	5		5
Epibenthic-Benthic							5	5		
Insect							5	5		
Habitat Structure							5	5		
Site C, Mildred Island										
Epiphytic							5	5		5
Habitat Structure							5	5		

BIOLOGICAL SAMPLING

Epiphytic Invertebrates

Epiphytic invertebrates living in association with the root masses of hyacinth and pennywort were collected in June 1998 at Site A and in August 1998 at Sites B and C, and in pennywort at all three sites in June 1999 ($n = 5 \text{ site}^{-1}$; Table 1). Epiphytic invertebrates were sampled by manually collecting 1–2 plants ($\leq 0.5 \text{ m}^2$ quadrat described above) and immediately placing them in a bucket (Schramm et al. 1987; Schramm and Jirka 1989). The bucket contained a 10% isopropyl alcohol solution, causing the invertebrates to detach from the root masses by vigorously shaking each sample. This was then sieved at 0.5 mm to collect only the macro-invertebrates and fixed in a 10% buffered formaldehyde solution. These samples were later transferred to 70% isopropanol in the laboratory. The roots from each sample were retained separately in 70% isopropanol and brought to the laboratory for measurements of surface area and biomass (described above). Any additional invertebrates that did not detach from the roots in the alcohol solution were later separated in the laboratory. This technique effectively sampled invertebrates living in direct association with the roots, as Schramm and Jirka (1989) found that most invertebrates remained on the roots when disturbed.

We calculated densities of epiphytic invertebrates (number above m^2 bottom; Schramm and Jirka 1989) by correlating the number of leaves in each epiphytic plant sample ($\leq 0.5 \text{ m}^2$) to the leaves in a 0.5 m^2 quadrat (described above). Invertebrates were counted and identified to the lowest practical taxonomic level with light microscopy.

Standing stock of invertebrates was estimated by measuring preserved wet biomass. Each taxonomic group was blotted dry and weighed to the nearest 0.1 mg. Numbers and standing stock of invertebrates were standardized to number above 1 m^2 bottom, allowing for comparisons between strata and with epibenthic-benthic and insect sampling as density (number m^{-2} bottom) and standing stock (g m^{-2} bottom; Schramm and Jirka 1989). All estimates are based on the same unit definition of area. Taxa richness (number of taxa) and the Shannon-Wiener diversity index were also calculated:

$$H' = -\sum_{i=1}^n p_i \log p_i$$

where p_i = the proportion of species i in the community (the # of individuals of species i /the total # of individuals in the community; Zar 1996).

Epibenthic-Benthic Invertebrates

A 1-m long corer was used to sample epibenthic and benthic invertebrates beneath hyacinth and pennywort canopies at Site A in April, June, and July 1998 and at Site B in August 1998 ($n = 5 \text{ site}^{-1}$; Table 1). Cores with an internal core area of 0.0024 m^2 were taken to a 10 cm depth beneath the sediment surface. The core was inserted into each patch at approximately 1 m water depth, sampling both epibenthic invertebrates at the water-sediment interface and benthic invertebrates in the sediment. Samples were immediately fixed in 10% buffered formaldehyde solution containing rose bengal dye, and later transferred to 70% isopropanol in the laboratory. Invertebrates were

counted and identified to the lowest practical taxonomic level with light microscopy. Numbers of invertebrates were standardized to number m^{-2} bottom, and taxa richness and the Shannon-Wiener diversity index calculated (as above for epiphytic invertebrates).

Insects

Insect fallout traps (Sutherland 1996) were used to sample insects living in association with hyacinth and pennywort canopies at Site A in April, June, and July 1998 and at Site B in August 1998 ($n = 5 \text{ site}^{-1}$; Table 1). These traps consisted of a rectangular tray (0.0782 m^2) filled with approximately 3 cm of soapy water. The trays were nestled into each canopy, so that they floated on the water surface with the leaves of the canopy surrounding the tray. Trays were tethered to PVC poles at each specific site, allowing vertical movement with the tides. The trays were deployed for 24 h, after which the contents were sieved at 0.106 mm and the insects preserved in 70% isopropanol. Insects were counted and identified to the lowest practical taxonomic level with light microscopy. Numbers of insects were standardized to number m^{-2} bottom, and taxa richness and the Shannon-Wiener diversity index were calculated (as above for epiphytic and epibenthic-benthic invertebrates).

Fish

Fish were sampled directly adjacent to hyacinth and pennywort patches at Site A during June and July 1998 in order to see if fish surrounding FAV incorporate FAV prey into their diet. Rectangular block-net enclosures (range 30–49 m^2) were used to collect fishes within intertidal and nearshore subtidal areas less than 1.3 m wading depth. Enclosure methods are recommended for collecting small and juvenile fishes because they have high catch efficiencies and provide quantitative data useful for comparing fish densities between habitats and sites (Rozas and Minello 1997). Sample areas were delineated with 4 perimeter stakes at least 24 h in advance to minimize disturbance of the area at the time of sampling. The following day the sampling area was quickly enclosed with block-nets secured to the perimeter stakes. A minimum of 4 passes with a beach seine ($7.6 \times 1.2 \text{ m}$, 3.2 mm mesh) was taken within each enclosure to collect the fish.

A subsample of collected fishes were preserved in 10% buffered formaldehyde solution and transferred to the laboratory for diet analysis. We focused on non-indigenous bluegills (*L. macrochirus*) as an indicator species for examining potential effects of hyacinth on food web dynamics because they are omnivorous fish that have been shown to

feed opportunistically on invertebrates in FAV habitats (Werner and Hall 1979; Schramm and Jirka 1989), and they accounted for 55% of the numerical fish catch in preliminary sampling directly underneath hyacinth ($n = 5$ patches sampled) and were one of the most abundant fish collected in all fish sampling.

Fish were also sampled in many areas surrounding the study sites using the same methods as above. Additional fish species from these areas were saved for diet analysis to see if prey items found in FAV habitats were incorporated at a larger scale into the Delta food web.

Fish saved for diet analysis were measured (fork length) and weighed (preserved wet weight). The stomachs were then dissected 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 ranked using a standardized system (Terry 1977). Prey items were then ranked based on modified Index of Relative Importance values (IRI; Pinkas et al. 1971; Simenstad et al. 1991):

$$\begin{aligned} \text{IRI} = & \% \text{ frequency of occurrence} \\ & \times [\% \text{ numerical composition} \\ & + \% \text{ gravimetric composition}] \end{aligned}$$

Diet overlap with sampled aquatic prey resources was calculated using a modified Percent Similarity Index (PSI; Hurlbert 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 the sampled aquatic prey resources y . Ivlev's electivity index was used to compare differences in fish selectivity on the major amphipod taxa present in the sampled prey resources (Ivlev 1961). The Ivlev electivity index was chosen as it is easy to interpret and gives similar results to other indices (Lechowicz 1982; Kline and Wood 1996).

DATA INTERPRETATION AND STATISTICAL TESTS

Parametric two-sample t -tests were used to statistically compare means for biological and physical sampling between hyacinth and pennywort at each study site ($\alpha = 0.05$). For all measurements between hyacinth and pennywort $H_0: \mu_1 = \mu_2$ and $H_a: \mu_1 \neq \mu_2$. The parametric t -test is a robust statistic, meaning it can withstand considerable departures from its underlying assumptions of normality and

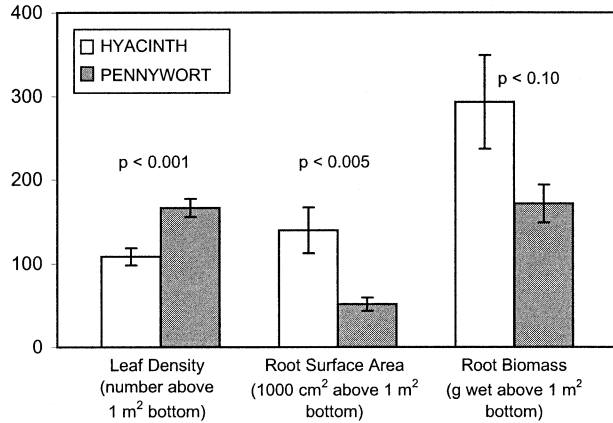


Fig. 2. Mean leaf density (number above 1 m² bottom), surface area of roots (1,000 cm² above 1 m² bottom), and biomass of roots (g wet above 1 m² bottom) combined for all sites and dates (n = 15). Error bars show ± 1 SE.

homogeneity of variance. This is especially the case 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).

Results

PHYSICAL SAMPLING

The physical structure of the hyacinth canopy was significantly different from that of pennywort. Patches of pennywort had significantly higher leaf densities than hyacinth ($p < 0.001$; Fig. 2). Hyacinth had almost 3 times greater root surface areas than pennywort ($p < 0.005$), based on the regression model of weight differences of known surface areas ($y = 0.0019x + 0.0016$, $R^2 = 0.99$). No significant differences at $p < 0.05$ in root biomass were detected, although values tended to be greater for hyacinth ($p < 0.10$).

BIOLOGICAL SAMPLING

Epiphytic Invertebrates

Taxonomic composition of epiphytic root invertebrates was strikingly different depending on the site and month (Fig. 3a), with total densities showing no significant difference (Fig. 4a). At Site A in June 1998 there was a dramatic contrast in assemblage composition, with the non-indigenous amphipod *Crangonyx floridanus* significantly more abundant in hyacinth in terms of both density and standing stock ($p < 0.05$) and the native amphipod *Hyaella azteca* more abundant in pennywort ($p < 0.01$). These amphipods differed in numeric and gravimetric contributions, as *C. floridanus*' density in hyacinth was 187% that of *H. azteca* in pennywort, but conversely only 62.5% in terms of standing stock. Density and standing stock of the amphipod *Corophium spinicorne* was significantly more

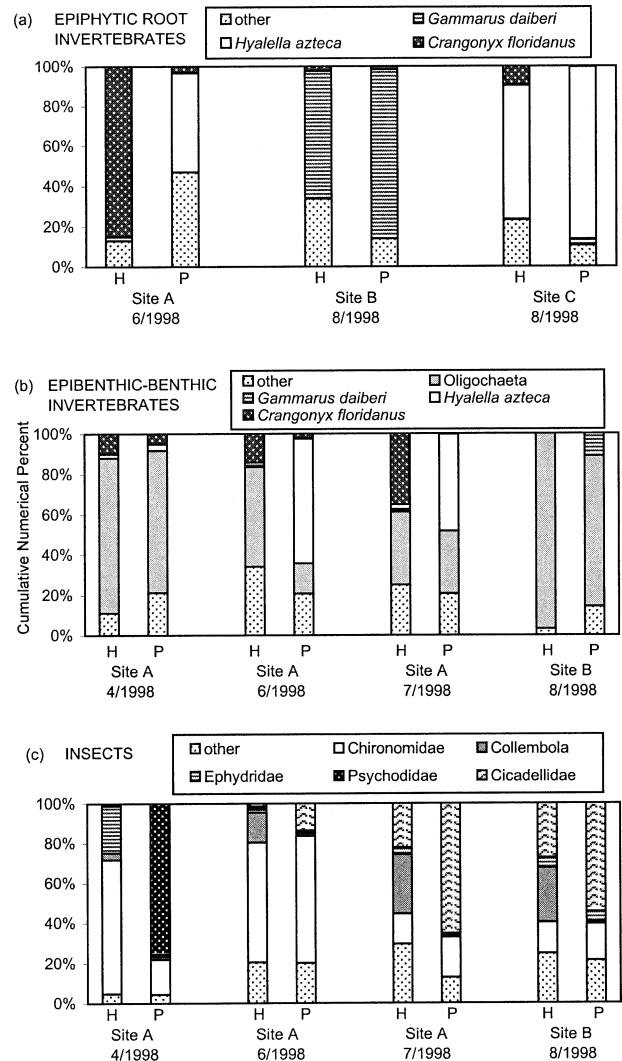


Fig. 3. Cumulative numerical percent of dominant taxa for epiphytic invertebrates (a), epibenthic-benthic invertebrates (b), and terrestrial insects (c). H = hyacinth, P = pennywort.

abundant in hyacinth ($p < 0.05$), while the isopod *Caecidotea racovitzai* ($p < 0.05$) and the oligochaete *Stylaria lacustris* ($p < 0.001$) were significantly more abundant in pennywort. *C. floridanus* and *C. racovitzai* have not been previously reported in the Delta. All of these significant taxon differences accounted for 87.7% of the total invertebrate density (Table 2). Taxa richness of epiphytic invertebrates in pennywort was slightly higher than hyacinth, and diversity was much higher in June (Fig. 4d).

Sites B and C in August 1998 did not show the same dramatic contrasts in epiphytic invertebrate assemblages as in Site A (Fig. 3a). At Site B, the amphipod *Gammarus daiberi* was the most abundant species in both hyacinth and pennywort. The only significant difference was higher densities and

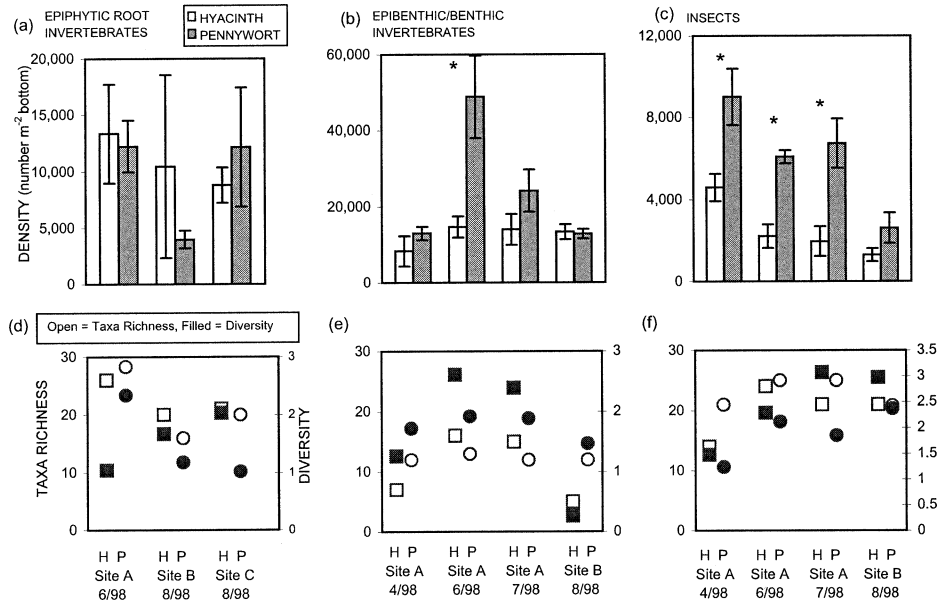


Fig. 4. Mean overall densities, taxa richness, and Shannon-Weiner diversity for epiphytic invertebrates (a and d), epibenthic-benthic invertebrates (b and e), and terrestrial insects (c and f). * $p < 0.05$, error bars show ± 1 SE. H and squares = hyacinth, P and circles = pennywort.

standing stock of the oligochaete *S. lacustris* in pennywort ($p < 0.05$; other details are available from the authors). At Site C, the amphipod *H. azteca* was the most abundant species in both hyacinth and pennywort. The only significant difference was higher densities of chironomid larvae in pennywort ($p < 0.05$). Taxa richness and diversity were higher in hyacinth at both sites (Fig. 4d).

Hyacinth Removal Experiment

Results of the June 1999 sampling indicated that there was minimal interannual variation in overall epiphytic invertebrate assemblages at pennywort patches, as the most abundant taxon present at each site was the same between 1998 and 1999 (Fig. 5). However, the amphipod *C. floridanus* that was so prevalent in hyacinth in 1998 did not colonize pennywort when hyacinth was not present in 1999. *C. floridanus* was not found in pennywort patches at Sites A and B in June 1999 and was only 0.23% of the overall invertebrate density at Site C.

Epibenthic-Benthic Invertebrates

At Site A, overall densities of epibenthic and benthic invertebrates were significantly greater underneath patches of pennywort than hyacinth during June ($p < 0.05$; Fig. 4b). Oligochaetes were the most abundant benthic invertebrate in the sediment under both hyacinth and pennywort (Fig. 3b). Species-specific trends in the epibenthic invertebrates at the water-sediment interface were similar to those in the epiphytic root invertebrates (Fig. 3b and data available from authors). *H. azteca* was significantly more dense under pennywort compared to hyacinth during June and July ($p < 0.05$), and *C. racovitzai* ($p < 0.01$) and turbellarians ($p < 0.05$) were significantly more dense under pennywort during June. All of these significant taxon differences between hyacinth and pennywort accounted for 0% to 60.1% of the total invertebrate densities depending on the month (Table 2). Taxa richness and diversity were higher in penny-

TABLE 2. Percent of invertebrate densities accounted for by taxon determined to be significantly different ($p < 0.05$) between hyacinth and pennywort. Blanks indicate no sampling conducted.

	Site A Mandeville Tip			Site B Brown's Island	Site C Mildred Island
	April 1998	June 1998	July 1998	August 1998	August 1998
Epiphytic		87.7%		0.4%	1.9%
Epibenthic-Benthic	0%	60.1%	30.3%	6.7%	
Insect	94.8%	80.0%	88.8%	17.9%	

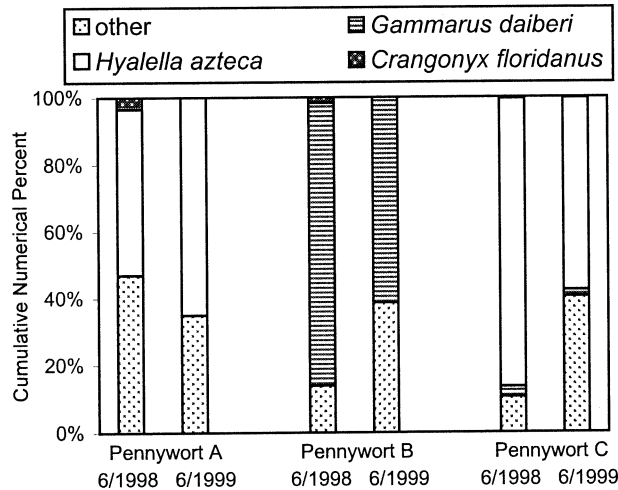


Fig. 5. Cumulative numerical percent of dominant epiphytic invertebrates at pennywort in 1998 and 1999.

wort in April, but higher in hyacinth in June and July (Fig. 4e).

At Site B overall densities were almost equal in hyacinth and pennywort during August 1998 (Fig. 4b). Oligochaetes were once again the most abundant benthic invertebrate in the sediment (Fig. 3b). The most striking difference was that there were no amphipods or isopods underneath hyacinth patches at all, so overall densities of amphipods and isopods were significantly higher under pennywort ($p < 0.015$; Fig. 3b). As with the epiphytic invertebrates, *G. daiberi* was the major epibenthic taxon under pennywort. Taxa richness and diversity was much higher in pennywort due to hyacinth being devoid of amphipods and isopods (Fig. 4e).

Insects

Overall densities of canopy insects were significantly greater in pennywort than hyacinth at Site A in April ($p < 0.05$), June ($p < 0.0005$), and July ($p < 0.05$; Fig. 4c). Taxonomic composition was markedly different as well (Fig. 3c and data available from authors). In April, Ephydriidae were significantly more abundant in hyacinth than pennywort ($p < 0.05$), and Psychodidae were significantly more abundant in pennywort ($p < 0.005$). These insects both decreased in later months, when Collembola became significantly more abundant in hyacinth in July ($p < 0.05$) and Cicadellidae significantly more abundant in pennywort in June ($p < 0.001$) and July ($p < 0.0005$). Chironomidae were significantly more abundant in hyacinth in April ($p < 0.01$), but were significantly more abundant in pennywort in June ($p < 0.001$) and July ($p < 0.0005$). Eleven less abundant taxa

also had significant density differences between hyacinth and pennywort (data available from authors). The combined significant taxa differences between hyacinth and pennywort accounted for 80% to 94.8% of the total insect densities depending on the month (Table 2). Taxa richness was higher in pennywort, while diversity was higher in hyacinth throughout all months (Fig. 4f).

At Site B, overall insect densities were not statistically greater in pennywort than hyacinth in August 1998 ($p < 0.15$; Fig. 4c). Taxonomic assemblages were similar to those found at Site A in July 1998 (Fig. 3c), although the only significant differences were greater densities of Chironomidae ($p < 0.05$) and Araneae ($p < 0.05$) in pennywort than hyacinth (data available from authors). Taxa richness and diversity were both higher in hyacinth (Fig. 4f).

Fish Assemblages and Diet Analysis

Most of the fish captured adjacent to patches of hyacinth and pennywort at Site A in June and July 1998 were juveniles and non-indigenous to the Delta (Table 3). The native splittail (*Pogonichthys macrolepidotus*), tule perch (*Hysterothorax traski*), and prickly sculpin (*Cottus asper*) accounted for only 8.2% of the numerical catch. Also captured in low abundance was the non-indigenous mitten crab (*Eriocheir sinensis*).

Bluegill feeding differed between fish caught adjacent to hyacinth and pennywort (Table 4). Based on percent total importance (IRI), the predominant prey item for bluegills adjacent to pennywort in both June and July was the native amphipod *H. azteca*, which was also the most common epiphytic and epibenthic invertebrate found in those pennywort patches. This was not the case in hyacinth, where the dominant fish prey items were not the same as the most abundant aquatic invertebrates. In hyacinth, the non-indigenous amphipod *C. floridanus* was the major epiphytic and epibenthic invertebrate, but was only the ninth ranked prey item in June and was not in the prey items at all in July (Table 4). Lower Ivlev electivity index values for *C. floridanus* in hyacinth compared to *H. azteca* in pennywort also reflect differences in preference for these two major prey resources (Table 4).

Similarity (PSI) between fish prey items and sampled invertebrates was also higher in pennywort (Table 4). Similarity in pennywort was 23.7% for epiphytic and 24.3% for epibenthic invertebrates during June, and 69.5% for epibenthic invertebrates in July. Similarity in hyacinth was 4.9% for epiphytic and 11.1% for epibenthic invertebrates during June, and 10.7% for epibenthic invertebrates in July. Most of the overlap between invertebrate prey items and resources was due to am-

TABLE 3. Species, number, and lengths of fish and crabs caught adjacent to patches of hyacinth and pennywort at Site A (Mandeville Tip) during June and July 1998 (n = 14 enclosure seine samples). * indicates native species. na = measurements not available.

Common Name	Scientific Name	#	Forklength (mm)	
			Mean	Range
Bigscale Logperch	<i>Percina macrolepida</i>	1	93	93
Black Crappie	<i>Pomoxis nigromaculatus</i>	5	127	34–212
Bluegill	<i>Lepomis macrochirus</i>	96	98	43–171
Brown Bullhead	<i>Ictalurus nebulosus</i>	2	266	241–291
Common Carp	<i>Cyprinus carpio</i>	1	201	201
Golden Shiner	<i>Notemigonus crysoleucas</i>	58	47	26–114
Inland Silverside	<i>Menidia beryllina</i>	59	29	21–40
Largemouth Bass	<i>Micropterus salmoides</i>	472	45	21–502
Mitten Crab	<i>Eriocheir sinensis</i>	23	38	6–55
Prickly Sculpin*	<i>Cottus asper</i>	29	36	22–65
Redear Sunfish	<i>Lepomis microlophus</i>	127	116	36–247
Splittail*	<i>Pogonichthys macrolepidotus</i>	6	56	41–80
Spotted Bass	<i>Micropterus punctulatus</i>	3	100	98–102
Tule Perch*	<i>Hysterocarpus traski</i>	46	66	38–190
Shad	<i>Dorosoma</i> spp.	4	na	na
Yellowfin Goby	<i>Acanthogobius flavimanus</i>	56	42	26–85

phipods, isopods, gastropods, and chironomid larvae. Discrepancies were due to either differences in species of amphipods and isopods, as was the case in hyacinth patches, or due to the presence of planktonic organisms such as cladocerans, ostracods, and copepods in the diet.

Similar trends were found in the diet analysis of other common nearshore juvenile fish in the area surrounding the study sites (Table 5). Bluegills and largemouth bass (*Micropterus salmoides*) are established non-indigenous species, while chinook salmon (*Oncorhynchus tshawytscha*), splittail, tule perch, and prickly sculpin are natives. The native amphipod *H. azteca* was found to be a major prey item in almost all of these species (Table 5), signifying its importance in the larger Delta fish-invertebrate food web. The non-indigenous *C. floridanus* was absent from the major prey items in all species, again illustrating its restricted habitat to patches of hyacinth.

Discussion

BIOLOGICAL AND PHYSICAL DIFFERENCES

Patterns between the habitat structure and associated biological communities of the non-indig-

enous hyacinth and the native pennywort illustrate how a shift in the dominant FAV in the Delta has affected both the aquatic and vegetative canopy communities. Key findings show physical differences in aquatic root and canopy leaf structure, as hyacinth has greater root surface area and pennywort has higher leaf density. Significant differences in invertebrate assemblages between hyacinth and pennywort account for up to 88% of epiphytic invertebrates, 60% of epibenthic-benthic invertebrates, and 95% of insect assemblages (Table 2). Invertebrates associated with hyacinth occur less in the diets of adjacent fish than do invertebrates associated with pennywort.

The aquatic root mass of hyacinth has a more structurally complex surface area than pennywort. Such contrasts in root mass architecture may explain differences in invertebrates that live around the roots of the two plants. Low dissolved oxygen levels could also be influencing the invertebrate community. In Texas, Madsen (1997) found that hyacinth had the lowest dissolved oxygen levels as compared to milfoil, hydrilla, pondweed, and a native mix of submersed plants, and was the only plant to have averages below 5 mg⁻¹. This 5 mg⁻¹

TABLE 4. Diet analysis of bluegills caught adjacent to hyacinth and pennywort at Site A (Mandeville Tip) in June and July 1998 (n = 5 per sample event). Diet rank, % Index of Relative Importance (IRI), and Ivlev Electivity Index are given for the most abundant sampled prey resource from each strata: *Crangonyx floridanus* in hyacinth and *Hyaella azteca* in pennywort. Percent Similarity Index (PSI) is given for all epiphytic and epibenthic sampled prey resources.

	Date	Diet Rank	Diet % IRI	Ivlev Electivity Index	Epiphytic PSI	Epibenthic PSI	Forklength Mean (mm)
Hyacinth	June 1998	9	0.11%	-0.989	4.9%	11.1%	108.6
	July 1998	—	—	-1.0	na	10.7%	61.6
Pennywort	June 1998	1	26.58%	-0.487	23.7%	24.3%	83.0
	July 1989	1	97.20%	0.1393	na	69.5%	88.2

TABLE 5. Percent Index of Relative Importance (IRI) of *Hyalella azteca* and *Crangonyx floridanus* in diets of common near-shore juvenile fish in the area surrounding the study sites.

Species	% IRI of <i>H. azteca</i>	% IRI of <i>C. floridanus</i>	Sample Size	Forklength Mean (mm)
Bluegill	27.85	0.015	90	78.6
Chinook Salmon	15.04	—	29	46.1
Largemouth Bass	19.38	0.024	50	96.3
Prickly Sculpin	67.13	—	16	40.2
Splittail	5.60	—	21	51.9
Tule Perch	22.47	—	30	60.2

separation is notable because it represents the level at which many fish start to experience oxygen stress (Madsen 1997). Lower levels of dissolved oxygen were likely the reason that we found no epibenthic amphipods and isopods beneath the hyacinth canopy at Site B in August 1998. These hyacinth patches did have an abundance of amphipods and isopods living epiphytically amongst the roots that suggests that these invertebrates could potentially be taking refuge in the root mass from underlying hypoxia (Gopal 1987). Pennywort at the same site did have amphipods and isopods living both epibenthically underneath the canopies and epiphytically among the roots. Overall densities of epibenthic and benthic invertebrates were generally greater in pennywort than hyacinth throughout all sampling.

Patterns of taxa richness and diversity for all aquatic invertebrates tended to follow a seasonal trend. 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 subsequent months (August for epiphytic, June and July for epibenthic-benthic; Fig. 4d,e). The exception was higher richness and diversity for epibenthic-benthic invertebrates in pennywort at Site B in August, but as discussed above this is likely due to hyacinth being almost devoid of epibenthic invertebrates, presumably caused by low dissolved oxygen levels. Higher richness and diversity in hyacinth later in the season could be related to its extensive growth rate, providing more colonizable substrate later in the year (Gopal 1987). In Florida, Jantrarotai (1990) found that overall dry biomass of hyacinth was 161% greater than pennywort (*Hydrocotyle ranunculoides*), and maximum root length 164% greater, maximized in late summer.

Pennywort patches have more leaves per unit area than hyacinth. The structurally dense canopy may explain the greater overall density of insects in pennywort as well as taxonomic differences of the insect assemblages. Pennywort was also richest

in taxa throughout all sampling except for August at Site B, and was lower in diversity throughout all months (Fig. 4f).

Amphipods clearly dominate aquatic invertebrate assemblages in FAV and are important fish prey. Numerous studies have shown that amphipods such as *H. azteca* are vulnerable to bluegill predation (Crowder and Cooper 1982; Schramm and Jirka 1989). Amphipods were found to be proportionally more abundant in the FAV canopies than in the fish diets, presumably due to the refuge provided by the root mass structure. This agrees with results from Florida lakes, where amphipods were most abundant epiphytically and less abundant benthically and in fish diets (Schramm and Jirka 1989). The same study also found that hyacinth roots provided a refuge from fish predation for *H. azteca*, with *H. azteca* accounting for 69% to 86% of invertebrate densities (Schramm et al. 1987).

The major difference in amphipods between hyacinth and pennywort was the prevalence of the non-indigenous *C. floridanus* in hyacinth. *C. floridanus* was reduced to barely detectable levels with the absence of hyacinth in 1999, lending even more credence that *C. floridanus* is preferentially associated with hyacinth. This also suggests that once an invader is removed from a system, aspects of the community can return to a more natural pre-invasion state (Westman 1990).

IRI and Ivlev electivity index values indicate that *C. floridanus* is not abundant in fish diets (Tables 3 and 4). This is in contrast to the native *H. azteca*, which was significantly more abundant in pennywort at Site A and a common prey in fish diets. *C. floridanus* may not be abundant in fish diets for a variety of reasons, including refuge function of hyacinth roots from fish predation, low caloric value and small size of *C. floridanus*, and poor taste of *C. floridanus*. Refuge function is the most likely contribution to its low abundance in fish diets, given research in Florida showing that hyacinth roots can provide a refuge for invertebrates from fish predation (Schramm and Jirka 1989). We consider low caloric value to also be influential, as the standing stock of one *C. floridanus* is 0.343 mg, and that of one *H. azteca* is 1.056 mg (calculated from values in authors' data). *C. floridanus* has 33.43% less gravimetric value than *H. azteca*. We consider poor taste not to be much of an influence, as 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 in British Columbia (Levings et al. 1995).

INTRODUCED SPECIES THEORY: FUNCTIONAL EQUIVALENCY

For a variety of reasons, it is often difficult to determine ecological effects of non-indigenous species on native ecosystems (Drake and Mooney 1989; Parker et al. 1999). Sufficient monitoring is usually not available to document changes caused by an invading organism. By comparing the community dominated by an exotic organism to that of a native counterpart, it is possible to illuminate changes that may have arisen due to the establishment of that exotic organism. This is especially useful in many cases such as ours when pre-invasion data are not available.

Our research has shown that hyacinth can be characterized by a distinctly different invertebrate assemblage and fish-invertebrate food web as compared to its native counterpart pennywort. Although floating canopies of hyacinth do not represent a fundamentally new habitat type in the Delta, they have proven on most counts not to be functionally equivalent to native floating canopies of pennywort. Some functional redundancy in the invertebrate assemblages does exist (Westman 1990; Stromberg 1998), notably in the epiphytic invertebrates at Sites B and C (Table 2). The 87.7% significant taxon difference in epiphytic assemblages at Site A was also reflected into the surrounding fish-invertebrate food web (Tables 3 and 4). Differences in insect assemblages were consistent throughout monthly sampling, ranging between 80.0–94.8% in the April, June, and July samplings at Site A, while epibenthic-benthic assemblages were more variable, ranging between 0.4–60.1% (Table 2). Although most measurements signify non-functional equivalency between hyacinth and pennywort, some redundancy and natural variation does exist as there is some overlap in measured values.

Detrimental impacts are much more obvious when an invader either occupies a vacant niche, such as introduced pikeminnow (*Ptychocheilus grandis*) filling a top fish predator role when native piscivores are absent (Brown and Moyle 1991), or in some way modifies the existing habitat, such as *Musculista senhousia* converting mudflats to mussel beds (Simberloff 1991; Ruesink et al. 1995; Crooks and Khim 1999; Parker et al. 1999). Our research has shown that invaders can have significant ecological impacts even when there are similar pre-existing native species. In the case of hyacinth, certain structural elements and associated invertebrates and fish-feeding proved to be different from the native pennywort. It remains to be seen whether this holds true only for invaders such as hya-

cinth that provide structurally complex substrate on which other organisms can inhabit.

It is important that patches of the native pennywort were abundant enough to provide a suitable comparison, although it is unknown whether or not pennywort has decreased in abundance via competitive exclusion since the invasion of hyacinth. Since hyacinth remains firmly established in the Delta despite an extensive chemical control program, it will be critical to monitor abundance of hyacinth and pennywort and their associated communities in future years. Community dynamics would undoubtedly change if hyacinth once again developed extensive mats, as it does more often in tropical climates (Gopal 1987).

Hyacinth in the Delta has followed a predictable pathway of plant invasion theory—once natural environmental constraints in the area were lifted due to an altered hydrological regime caused by dams and channelization, the invasive hyacinth flourished (Finlayson 1983; Barret 1989; Galatowitsch et al. 1999). Although disturbance is not required for a successful hyacinth invasion, 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 Delta in terms of recent control efforts, due to its extensive blocking of waterways. During 1998–1999, 985 ha of hyacinth were chemically treated with an annual budget of approximately \$1,000,000 (CDBW 1998). The weevils *Neochetina bruchi* and *N. eichhorniae* and the moth *Samaodes alboguttalis* were also imported and released as biological control agents in 1982 and 1983, but without much success (USCOE 1985). Combined with our ecological findings, the detrimental effects of hyacinth add to those of other prominent aquatic invaders in the Delta, such as the submerged aquatic plant *Egeria densa*, the clam *Corbicula fluminea*, the Chinese mitten crab *Eriocheir sinensis*, the Asian copepod *Pseudodiaptomus forbesi*, and numerous species of non-indigenous fish (Hymanson et al. 1994; Cohen and Carlton 1995).

It is noteworthy that in the process of studying one non-indigenous species, three more were discovered—the amphipod *C. floridanus* and the isopods *C. racovitzai* and *Asellus hilgendorffii* (Table 6; Magniez and Toft 2000; Toft et al. 2002). Such new discoveries of non-indigenous species are not overly surprising, given the extent that the San Francisco Bay-Delta ecosystem has been anthropogenically modified and colonized by invasive species (Nichols et al. 1986; Cohen and Carlton 1998). This sheds light on the need for more diligent research—for example, *A. hilgendorffii* has specifically been shown to serve as an intermediate host for numerous species of acanthocephalans that para-

TABLE 6. Native range and non-indigenous populations of the amphipod *Crangonyx floridanus* and the isopods *Caecidotea racovitzai* and *Asellus hilgendorfi*. See Toft et al. (2002) for a more detailed discussion of non-indigenous status.

Species	Described Native Range	Non-Indigenous Populations
<i>C. floridanus</i>	Eastern and east-central U.S. (Holsinger 1972; Zhang 1997)	Colorado and Oregon, U.S., and Japan (Zhang 1997), California (this study)
<i>C. racovitzai</i>	Northeastern U.S. and southeastern Canada, Florida, and Georgia, U.S. (Williams 1970)	Washington and Utah, U.S. (Williams 1970, Bowman 1974), California (this study)
<i>A. hilgendorfi</i>	Eastern Siberia, China, and Japan (Henry and Magniez 1995)	California (this study; Magniez and Toft 2000)

sitize salmonids and other fish in its native waters of Japan (Nagasawa et al. 1983). It is possible that hyacinth may have been the vector of introduction for these crustaceans, and facilitated their invasions as a function of its habitat-providing characteristics. As a general test of this vector, we ordered 4 hyacinth plants from an ornamental pond supply company, and they arrived teeming with live invertebrates including many amphipods (*Hyalella* spp.). Hyacinth does seem like a viable vector of introduction especially for *C. floridanus* due to its prevalence in the hyacinth community, although other methods of introduction are certainly available (Cohen and Carlton 1998). The discovery of these three new species adds to the already lengthy list of 84 documented non-indigenous species in the Delta, and keeps pace with calculations that one new invasive species is currently established every 14 wk in this system (Cohen and Carlton 1998). Given that many of these species may already be well established by the time they are discovered, future research should focus not only on documenting their occurrence but also on assessing their ecological roles in the surrounding community.

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