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INVASIVE CORDGRASS MODIFIES WETLAND TROPHIC FUNCTION

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Abstract. Vascular plants strongly control belowground environments in most ecosystems. Invasion by vascular plants in coastal wetlands, and by cordgrasses (*Spartina* spp.) in particular, are increasing in incidence globally, with dramatic ecosystem-level consequences. We examined the trophic consequences of invasion by a *Spartina* hybrid (*S. alterniflora* × *S. foliosa*) in San Francisco Bay (USA) by documenting differences in biomass and trophic structure of benthic communities between sediments invaded by *Spartina* and uninvaded sediments. We found the invaded system shifted from an algae-based to a detritus-based food web. We then tested for a relationship between diet and tolerance to invasion, hypothesizing that species that consume *Spartina* detritus are more likely to inhabit invaded sediments than those that consume surface algae. Infaunal diets were initially examined with natural abundance stable isotope analyses and application of mixing models, but these yielded an ambiguous picture of food sources. Therefore, we conducted isotopic enrichment experiments by providing ^{15}N-labeled *Spartina* detritus both on and below the sediment surface in areas that either contained *Spartina* or were unvegetated. Capitellid and nereid polychaetes, and oligochaetes, groups shown to persist following *Spartina* invasion of San Francisco Bay tidal flats, took up ^{15}N from labeled native and invasive *Spartina* detritus. In contrast, we found that amphipods, bivalves, and other taxa less tolerant to invasion consumed primarily surficial algae, based on ^{13}C enrichment experiments. Habitat (*Spartina* vs. unvegetated patches) and location of detritus (on or within sediments) did not affect ^{15}N uptake from detritus. Our investigations support a ''trophic shift'' model for ecosystem response to wetland plant invasion and preview loss of key trophic support for fishes and migratory birds by shifting dominance to species not widely consumed by species at higher trophic levels.

Key words: deposit feeder; detritus; ecosystem modification; food chain; infauna; isotope enrichment; plant invasion; salt marsh; San Francisco Bay; Spartina foliosa; Spartina *hybrid; stable isotope analysis.*

INTRODUCTION

Vascular plants have been shown to strongly influence belowground animal communities in a wide range of ecosystems (Palmer et al. 2000, Snelgrove et al. 2000, Wardle et al. 2004). Plants can alter the abundance (Griffiths et al. 1992), community composition, and diversity (DeDeyn et al. 2004) of soil or sediment microbe and animal communities, and therefore, the flow of organic matter, energy, and nutrients (Wardle et al. 2004).

While mechanisms of influence may involve structural, physical, or chemical changes to the environment, the importance of plant detritus is often overlooked (Moore et al. 2004). Detritus is a widespread feature of most ecosystems and the majority of primary production is returned to the environment via detrital pathways (Polis and Strong 1996, Moore et al. 2004). The presence of large quantities of detritus can affect trophic dynamics by changing biochemical conditions, providing food resources, and lengthening food chains (Hairston and Hairston 1993). Despite its importance, detritus has featured only rarely in development of ecological theory.

The lack of focus on detritus is particularly evident for the developing field of invasion biology. Plant invasions are widespread and are recognized as a major force for global change (Vitousek et al. 1997). They can modify community structure and ecosystem function by changing resource availability, disturbance frequency, microclimate, elemental cycling, and trophic interactions (Chapin et al. 1997, 2000). However, few studies that document changes in community structure due to plant invasions address the mechanisms involved (Levine et al. 2002). Understanding the mechanisms by which introduced plants modify ecosystems will help conservation ecologists and invasion biologists predict future changes.

Plant invasions in coastal wetlands

Algal and vascular plant invasions of the coastal zone are widespread and have caused local extinctions, genetic modifications, species displacement, and hab-

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itat degradation (Grosholz 2002). Cordgrasses (plants in the genus *Spartina* Schreb.) are unusually successful invaders in coastal wetlands and have spread across the globe (Ayers et al. 2004, and references therein). A number of *Spartina* species (*S. alterniflora*, *S. densiflora*, *S. patens*) and hybrids including *S. anglica* C. E. Hubbard, *S. townsendii* H & J. Groves, and a hybrid of *S. alterniflora* × *S. foliosa* (hereafter referred to as ''hybrid *Spartina*''; Ayers et al. 2004) have expanded to cover previously unvegetated mudflat habitat during invasion. Researchers studying invasive *Spartina* have reported altered faunal composition and abundance (e.g., Hedge and Kriwoken 2000) and predicted possible food web changes (Simenstad and Thom 1995), but have not conducted detailed trophic studies.

Spartina alterniflora (Atlantic cordgrass), introduced into San Francisco Bay in the 1970s, rapidly spread into tidal flat habitat where the native *S. foliosa* (Pacific cordgrass) does not grow (Callaway and Josselyn 1992). Hybridization of *S. alterniflora* and *S. foliosa* during the 1980s led to vigorous hybrids that have spread widely in south San Francisco Bay (Ayres et al. 1999, 2003) and now cover more than 793 ha (Zaremba and McGowan 2004). The hybrid *Spartina* has outcompeted native *S. foliosa* and *Salicornia virginica* in marsh settings and also covers large areas that were previously unvegetated tidal flat (Ayers et al. 2003, 2004). An initial investigation at the Elsie Roemer Bird Sanctuary, San Francisco Bay, California, USA, where the hybrid *Spartina* has expanded over muddy sand flats for ~30 years (Ayers et al. 2003), documented 75% lower macrofaunal density and significant changes in species composition in the invaded (vegetated) sediments relative to adjacent uninvaded tidal flat (Neira et al. 2005).

Trophic roles of invasive plants

Within salt marsh ecosystems, natural abundance isotopic analyses have provided a valuable means of identifying consumer diet items, and in particular the trophic roles of *Spartina* (e.g., Haines 1976, Peterson et al. 1985). For trophic pathways of invasive plants to be detected with isotope analysis it is necessary for the invaders to have isotopic signatures distinctive from native food sources. This can be problematic if different potential food sources have overlapping signatures, or if there are congeneric native species present. One alternative is to enrich the invasive plants with ^{13}C or ^{15}N and track the labeled C or N into consumer tissues. Here we apply both natural abundance and enrichment approaches to identify consumption of hybrid *Spartina* detritus and test this as a possible cause of faunal change following hybrid *Spartina* invasion in San Francisco Bay.

We consider the role of an invasive hybrid *Spartina* and its detritus as an agent of community reorganization in coastal wetland ecosystems. Here we evaluate evidence for a shift in trophic structure and test the hypothesis that observed changes in belowground invertebrate communities may be a bottom-up response to altered food availability. We used natural abundance and isotopic enrichment experiments to address two general questions: (1) Which species and trophic groups consume *Spartina* detritus and which consume algae? and (2) Are specific feeding groups more or less resistant to invasion? To better understand the dynamics of *Spartina* influence on belowground animal diets we tested the null hypotheses that (a) the same taxa consume native and invasive *Spartina*, and (b) invasive *Spartina* consumption is independent of habitat (tidal flat vs. invaded sediments), location of the detritus (surface vs. subsurface), and exposure time.

Methods And Materials

Benthic community structure

Sampling was conducted on a sand flat at the Elsie Roemer Bird Sanctuary in central San Francisco Bay (37°45′35″ N, 122°28′48″ W). The area is covered by 10.8 ha of invasive hybrid *Spartina*, and native *S. foliosa* is no longer present at this site. Sediments here were coarse, ~90% sand on the tidal flat and ~60% sand in vegetated patches, with organic contents of 1–1.5% and 1.7–3.5%, respectively (Neira et al. 2005). Elevations were 0.98 ± 0.05 m (mean ± SE) above mean low water in the invaded vegetated area and 0.64 ± 0.06 m on the adjacent tidal flat within 3 m of the vegetation border.

In June 2001, paired sediment cores (18.1 cm^2 surface area and 6 cm depth) were collected in patches invaded by hybrid *Spartina* (HY) and in adjacent tidal flat (TF) sediments for quantitative analyses of macrofaunal density and biomass (animals >0.3 mm) and belowground plant detrital biomass (dry mass). Ten blocks containing HY and TF habitat were sampled to obtain a total of 20 cores (10 pairs). Samples were sieved through a 0.3 mm mesh and retained material was sorted under a dissecting microscope. Macrofauna and plant detritus were removed and weighed on an analytical balance. Additional cores were collected for analysis of the natural abundance stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of infauna, microalgae, and sediments. Benthic microalgal biomass was estimated by measuring the chl *a* content of surface sediments (0–0.5 cm) according to Plante-Cuny (1973).

Natural abundance isotope sampling and processing

During 24–27 June 2001 the ten blocks were sampled for hybrid *Spartina*, macroalgae (*Ulva* sp. and *Enteromorpha* sp.), microalgae, suspended particulate organic matter (POM), and sediment organic matter (SOM) to determine natural abundance isotopic signatures of consumer food sources in TF and HY habitat. Collection and processing methods were similar to those described in Moseman et al. (2004). POM was sampled by collecting 2 L of local tidal creek water

that was filtered onto a Whatman GFF. SOM was sampled by collecting surface sediment in an 18.1-cm^2 core (2 cm deep), washing, drying, and homogenizing sediments. Where feasible, diatom mats and cyanobacteria mats were sampled separately. Both types of microalgae were separated from sediments using centrifugation with Ludox (Blanchard et al. 1988), filtered, cleaned, and dried. Infauna were collected with a plastic core (18.1 cm^2 × 6 cm depth) and transferred to the laboratory where they were sieved through a 300-μm mesh sieve and sorted live under a dissecting microscope. They were then identified (usually to species) and rinsed with Milli Q water. One to 10 individuals were placed in preweighed tin cups, oven dried at 60°C to constant mass (range 0.1–2 mg), and acidified with 10% platinum chloride.

Isotope enrichment experiments

Two enrichment experiments were conducted. The first examined the ability of infauna to consume *Spartina foliosa*, a native cordgrass species endemic to Alta and Baja California that is being displaced by hybrid *Spartina* (Ayers et al. 2003). This was a single isotope enrichment experiment in which *S. foliosa* was labeled with ^{15}N ammonium sulfate. The second experiment was designed to identify consumers of the invasive *Spartina* and algae. This involved a dual labeling experiment in which ^{13}C bicarbonate was used to label macroalgae and microalgae on the sediment surface and ^{15}N ammonium sulfate was used to label hybrid *Spartina*.

Isotopic labeling

Experiment 1.—*Spartina foliosa* (in Mission Bay, California) was labeled with ^{15}N by enclosing plants in situ in groups of 4–6 in plastic pots (26 cm diameter × 28 cm depth; 6 pots total) with the bottoms cut out. Sediments surrounding the *S. foliosa* plants were injected daily with 50 mL of 6 mmol/L ammonium sulfate (98 atom % $^{15}NH_4$) per pot for a 3-d period (methods modified from White and Howes 1994). Plants were harvested 13–14 weeks after injection and frozen.

Prior to use in Experiment 1, the ^{15}N-labeled *S. foliosa* plants were thawed, the roots, culms, standing live and dead blades were separated, and the plant material was chopped into pieces ~5 mm long. In April 2002 at the Elsie Roemer site, nylon litter bags (15 × 17 cm, with 4.5 mm mesh) filled with either 9–15 g of roots, 15–18 g of culms, or 2–5 g of live or dead blades, were deployed ~1–2 cm below the sediment surface along a 3-m transect in HY and TF habitats. We buried seven bags of detritus (two replicates of culms, roots, and live blades, and one bag of dead blades) in each habitat, holding them in place with wooden dowels. We collected bags 50 days later and sorted associated living macrofaunal invertebrates within 24 hours.

Experiment 2.—In August 2002 a dual labeling experiment was conducted in six 0.25-m^2 quadrats (three TF and three HY) about 70 m from Experiment 1. Hybrid *Spartina* was labeled at Elsie Roemer using tracer injections (5 × 10 mL of 12 mmol/L $^{15}NH_4SO_3$ per day) made around hybrid *Spartina* roots on four consecutive days. Plants were harvested 93 days after the first injection. Hybrid *Spartina* detritus (5.7 g of culms and blades) was introduced in two modes in each quadrat: either buried in litter bags (with four bags per quadrat) or spread uniformly onto the sediment surface (in three circular 90 cm^2 plots per quadrat), pressed 1 mm into the sediment with forceps, and marked at the center with a thin red wire. Once *Spartina* treatments were in place, we sprayed 250 mL of 12 mM $NaH^{13}CO_3$ (99 atom %; ISOTEC, Sigma-Aldrich, St. Louis, Missouri, USA) prepared in filtered seawater on the sediment surface of each quadrat to label macroalgae (*Ulva* spp. and *Enteromorpha* spp.) and microalgae that were present on the sediment (as in Middelburg et al. 2000).

Immediately after tracer application (time 0), samples of infauna, macroalgae, microalgae, POM, and SOM were collected for analysis of $\delta^{13}C$ and $\delta^{15}N$ signatures to check for labeling artifacts. Microalgae were collected for isotopic analyses subsequently on days 1 and 4 using methods identical to those for natural abundance studies. Sediments with surface-deployed *Spartina* (half of one circular plot) were sampled to 4 cm depth after ~1 h (= time 0), and then 4, 17, and 74 days after the start of the experiment. One detritus litterbag per quadrat was collected at 17, 74, and 215 days after initiation of the experiment. Litterbag and surface samples were preserved in 8% buffered formalin. Within one week samples were sieved onto a 0.3-mm mesh and infauna were sorted and processed for isotopic analyses.

Stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) were measured by a PDZ Europa (Crewe, UK) 20–20 mass spectrometer connected to an elemental analyzer at the University of California, Davis, Stable Isotope Facility. Stable isotope abundance is expressed in parts per thousand (‰), a deviation from international standards. Working standards, sucrose and ammonium sulfate, were $\delta^{13}C = -23.83‰$ vs. VPDB or $\delta^{15}N = +1.33‰$ vs. air N_2, as defined by the following equation:

$$\delta X = (R_{\text{samp}}/R_{\text{std}} - 1) \times 1000 \quad (1)$$

where $X = {}^{13}C$ or ^{15}N, and R = ratio of heavy to light isotope content (^{13}C:^{12}C or ^{15}N:^{14}N). Values are expressed as the mean ± SE.

To test for effects of formalin preservation on isotope signatures, we cut in half 48 macrofaunal animals (15 marsh taxa) and froze one half and preserved the other for one week. Comparing preserved and frozen animals, we found $\delta^{15}N$ values were 0.14‰ heavier after preservation (paired t test, $P = 0.683$). By contrast, $\delta^{13}C$ values were, on average, 0.5‰ lighter after preservation (paired t test; $P = 0.0004$). Because these effects were nonsignificant ($\delta^{15}N$) or very small ($\delta^{13}C$), and in the latter case in a direction opposite to the effect

expected from ingestion of ^{13}C-labeled algae, we concluded that short-term preservation would not bias interpretation of our isotope enrichment experiments.

Statistical analyses and mixing models

All tests were conducted with JMP 4.0 statistical software (SAS Institute, Cary, North Carolina, USA). Comparisons of density and biomass in TF vs. HY settings were made for individual species with paired *t* tests ($n = 10$ pairs). Because comparisons among trophic groups involved multiple species in each group, we used species mean isotopic signatures as replicates for tracer uptake comparisons of surface vs. subsurface vs. carnivore feeding groups, employing one-way ANOVA with a posteriori Tukey's HSD tests. We tested differences among feeding group uptake of label separately for each time point and habitat (TF or HY). Effects of *Spartina* species (*foliosa* vs. hybrid), habitat (TF vs. HY), and location (surface vs. subsurface) on community ^{15}N uptake were each examined independently with paired *t* tests, using species mean $\delta^{15}N$ signatures as replicates. The mean $\delta^{15}N$ signature of each species in each treatment was determined by averaging mean signatures from each of three quadrats. All time points were tested separately. A paired approach was required because of the inherent initial differences in species values due to different trophic position and because multivariate analysis (e.g., MANOVA) was complicated by the presence of different species among samples (missing cells). Effects of habitat and location on ^{15}N label uptake at the species level were also tested with one-way ANOVA for each species present on each date (17 species total; $n = 3$ per treatment). All data were tested for normality and homoscedasticity and square root transformed as needed prior to analysis.

Mixing models were applied to estimate the fraction of *Spartina* and other food sources in the diets of infauna. For TF natural abundance data, we applied a single isotope, two-source model for $\delta^{13}C$ (Fry and Sherr 1984) in which we grouped food sources with similar signatures (i.e., POM/SOM/diatoms and *Spartina*/*Ulva*):

$$(\delta^{13}C_{anim} - \delta^{13}C_{mix})/(\delta^{13}C_{S/U} - \delta^{13}C_{mix}) \qquad (2)$$

where animal refers to each infaunal species, mix refers to POM/SOM/diatoms, and S/U refers to *Spartina*/*Ulva*.

To separate *Spartina* and *Ulva* at HY sites (where they had distinctive signatures) we then applied a concentration dependent, three-source, two-isotope mixing model (Phillips and Koch 2002). The three food sources were (1) POM/SOM/diatoms, (2) hybrid *Spartina*, and (3) *Ulva*/cyanobacteria. Concentrations of C and N were determined for each food source by CHN analysis. A trophic shift of +1‰ was applied to $\delta^{13}C$ values (Fry and Sherr 1984) and a trophic shift of +3.5‰ was applied to $\delta^{15}N$ for each trophic level (Minagawa and Wada 1984, Post 2002). We applied a single trophic level shift to deposit feeding or grazing animals; known carnivores were analyzed with a two trophic level shift. While the actual trophic shift may vary (McCutchan et al. 2003), estimates of source contributions appear to be robust (i.e., similar with different trophic shifts).

To analyze consumer uptake of ^{15}N from labeled *Spartina* (lbl *Sp.*), a single isotope, two-source, N-based mixing model was applied. We treated labeled detritus as one food source and unlabeled (background) food sources as a second using the formula

$$(\delta^{15}N_{anim} - \delta^{15}N_{back})/(\delta^{15}N_{lbl\ Sp.} - \delta^{15}N_{back}). \qquad (3)$$

Using this approach we calculated the percentage of N in animal tissues derived from the labeled *Spartina*, with upper estimates based on use of the lightest natural N sources in the system (diatoms, POM) and lower estimates based on use of the heaviest natural N in the system (*Ulva* or *Spartina*). A trophic level shift was applied.

For the dual isotope experiment, we also calculated change in animal $\delta^{13}C$ ($\Delta\delta^{13}C$) and $\delta^{15}N$ ($\Delta\delta^{15}N$) by subtracting the values for background animals in unenriched sediments from the values for animals exposed to ^{15}N-labeled *Spartina* or ^{13}C-labeled algae. Separate background values were applied to animals from HY and TF plots. Where background values were not available, we used tracer-free time 0 isotopic signatures.

Results

Benthic community patterns

Macrofaunal densities were 75% lower in *Spartina*-invaded sediments (108 674 ± 45 100 individuals/m^2 [mean ± SE]) than on adjacent, uninvaded tidal flats (412 541 ± 54 807 individuals/m^2; paired *t* test, $P = 0.0008$). Corresponding biomass values were 57% lower in invaded sediments (99.1 ± 43.58 g/m^2) than in tidal flat sediments (230.1 ± 40.70 g/m^2; paired *t* test, $P = 0.033$). We observed a significantly lower biomass of surface-feeding infauna (mainly bivalves and amphipods) in *Spartina*-invaded sediments (76.4 ± 35.8 g/m^2) than in uninvaded tidal flat sediments (209.3 ± 37.0 g/m^2; paired *t* test, $P = 0.034$), but no difference in biomass of subsurface deposit feeders (capitellid polychaetes and oligochaetes; 16.4 ± 4.5 vs. 12.7 ± 2.5 g/m^2, respectively; $P = 0.360$), or of carnivores and omnivores (nereid and phyllodocid polychaetes; 6.21 ± 2.8 vs. 8.2 ± 1.2 g/m^2, respectively; $P = 0.609$). Results for densities were similar to biomass for surface feeders ($P = 0.0003$), subsurface deposit feeders, ($P = 0.167$), and carnivore/omnivores ($P = 0.250$). Defining intolerance to invasion as a significant density drop, we found that most surface-feeding taxa declined in sediments invaded by *Spartina*, but most subsurface feeders and carnivores did not (Table 1).

The standing stock of belowground plant detritus (0–6 cm; determined by weighing plant material >300

TABLE 1. Mean densities and feeding modes of major macrofaunal species in sediments invaded by hybrid *Spartina* and in unvegetated sediments at the Elsie Roemer Bird Sanctuary, San Francisco Bay, California, USA, in April 2001.

Species	Classification	Tidal flat (no./m²)	Percentage of total	*Spartina* (no./m²)	Percentage of total	Change (%)	Invasion tolerant? Yes/no	Invasion tolerant? *P*
Carnivores/herbivores								
Eteone californica	Polychaeta	4033	1.0	3923	3.6	−2.7	yes	0.97
Eteone dilatae	Polychaeta	4972	1.2	718	0.7	−85.6	no	<0.001
Sphaerosyllis californiensis	Polychaeta	3702	0.9	1989	1.8	−46.3	yes	0.31
Tanaidacea	Crustacea	2983	0.7	55	0.1	−98.1	yes	0.17
Cumacea	Crustacea	221	0.1	55	0.1	−75.0	yes	0.28
Nematostella vectensis	Anthozoa	276	0.1	166	0.2	−40.0	yes	0.44
Nereis succinea	Polychaeta	276	0.1	221	0.2	−20.0	yes	0.73
Traskorchestia traskiana	Crustacea	0	0.0	110	0.1	>100.0	yes	0.17
Total		16 464	4.0	7127	6.6			
Surface feeders								
Pseudopolydora kempi	Polychaeta	4475	1.1	2155	2.0	−51.9	yes	0.22
Polydora cornuta	Polychaeta	2155	0.5	276	0.4	−87.2	no	0.10
Streblospio benedicti	Polychaeta	18 840	4.6	5249	4.8	−72.1	no?	0.11
Pygospio elegans	Polychaeta	64 641	15.7	2762	2.5	−95.7	no	0.03
Tharyx sp.	Polychaeta	22 486	5.5	663	0.6	−97.1	no	0.007
Gemma gemma	Bivalvia	88 122	21.4	276	0.3	−99.7	no	0.006
Venerupis philippinarum	Bivalvia	829	0.2	884	0.8	+6.7	yes	0.90
Corophiidae	Crustacea	97 514	23.6	15 138	13.9	−84.5	no	0.002
Grandidierella japonica	Crustacea	20 387	4.9	2873	2.6	−85.9	no	0.05
Total		319 448	77.4	30 276	28.0			
Subsurface deposit feeders								
Tubificoides brownae	Oligochaeta	40 110	9.7	37 901	34.9	−5.5	yes	0.92
Tubificoides fraseri	Oligochaeta	6354	1.5	387	0.4	−93.9	yes	0.24
Tectidrilus diversus	Oligochaeta	23 204	5.6	0	0.0	−100.0	no	0.02
Enchytraeidae	Oligochaeta	0	0.0	3923	3.6	>100.0	yes	0.19
Heteromastus filiformis	Polychaeta	1934	0.5	3039	2.8	+57.1	yes	0.40
Capitella spp.	Polychaeta	3149	0.8	4199	3.9	+33.3	yes	0.49
Total		74 751	18.1	49 448	45.5			
Other		1878	0.5	21 713	20.0			

Notes: Species with no significant density reduction in invaded sediments are considered invasion tolerant. ''Other'' represents species <1.5% of total and includes *Pseudopolydora paucibranchiata*, *Boccardia proboscidea*, *Fabricia* sp., *Dorvillea* sp., Goniadidade, *Musculista senhousia*, *Mya arenaria*, *Tellina* sp., *Hyale* sp., *Amphitoe valida*, Caprellidae, *Exosphaeroma inornata*, *Gnorimosphaeroma* sp., Poduridae, Halacaroidea, Nemertina, and Turbellaria. A paired *t* test ($\alpha = 0.05$) was used to determine whether there was a significant reduction in density within invaded sediments. Where $P < 0.10$, the species is designated as invasion intolerant.

μm in infaunal cores) was 4.3 times higher in *Spartina*-invaded patches (453 ± 149 g/m²) than in the open tidal flat (105 ± 48 g/m²; $P = 0.044$). In 2001, there was no significant difference in microalgal biomass (based on chl *a*) in the invaded vs. uninvaded sediments in our study ($P = 0.170$; chl *a* = 7.05 ± 2.00 μg/g biomass and 4.18 ± 0.45 μg/g biomass, respectively). However, microalgal productivity, measured with CO_2 flux measurements in the light and dark, was about 50% lower, and microalgal biomass (determined from chl *a*) was lower in *Spartina*-invaded sediments than in the adjacent open tidal flat at Elsie Roemer in 2003 and 2004 (A. C. Tyler and E. D. Grosholz, *unpublished manuscript*).

Natural abundance isotopic signatures and trophic inferences

Dual isotope plots illustrate mean natural abundance $\delta^{13}C$ and $\delta^{15}N$ signatures of key primary producers and consumers in sediments invaded by hybrid *Spartina* (HY) and tidal flat (TF) sediments (Fig. 1). It was impossible to distinguish the particulate organic matter (POM), sediment organic matter (SOM), and diatom samples from one another based on $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 1A, B; Appendix A), suggesting that resuspension and deposition processes may mix these entities. On average, *Ulva* and mixed microalgae (cyanobacteria + diatom mat) $\delta^{13}C$ signatures were heavier than the POM, SOM, and diatoms, and were similar to one another in the HY habitat, although *Ulva* $\delta^{13}C$ values were highly variable (from −13.95‰ to −19.44‰). *Spartina* $\delta^{13}C$ signatures were distinctive from other food sources in HY patches, but on the tidal flat they could not be distinguished from *Ulva* $\delta^{13}C$ signatures (Fig. 1B; Appendix A).

Based on a two-source mixing model (using POM/SOM/diatoms as one source and *Spartina*/*Ulva* as another), we estimated high *Spartina* and/or *Ulva* consumption (>80% of diet) for the tidal flat genera *Traskorchestia*, *Capitella*, *Eteone* (two species), *Nereis*, *Tharyx*, and *Polydora*. Given the greater prevalence of *Ulva*, this is the most likely food source for these taxa

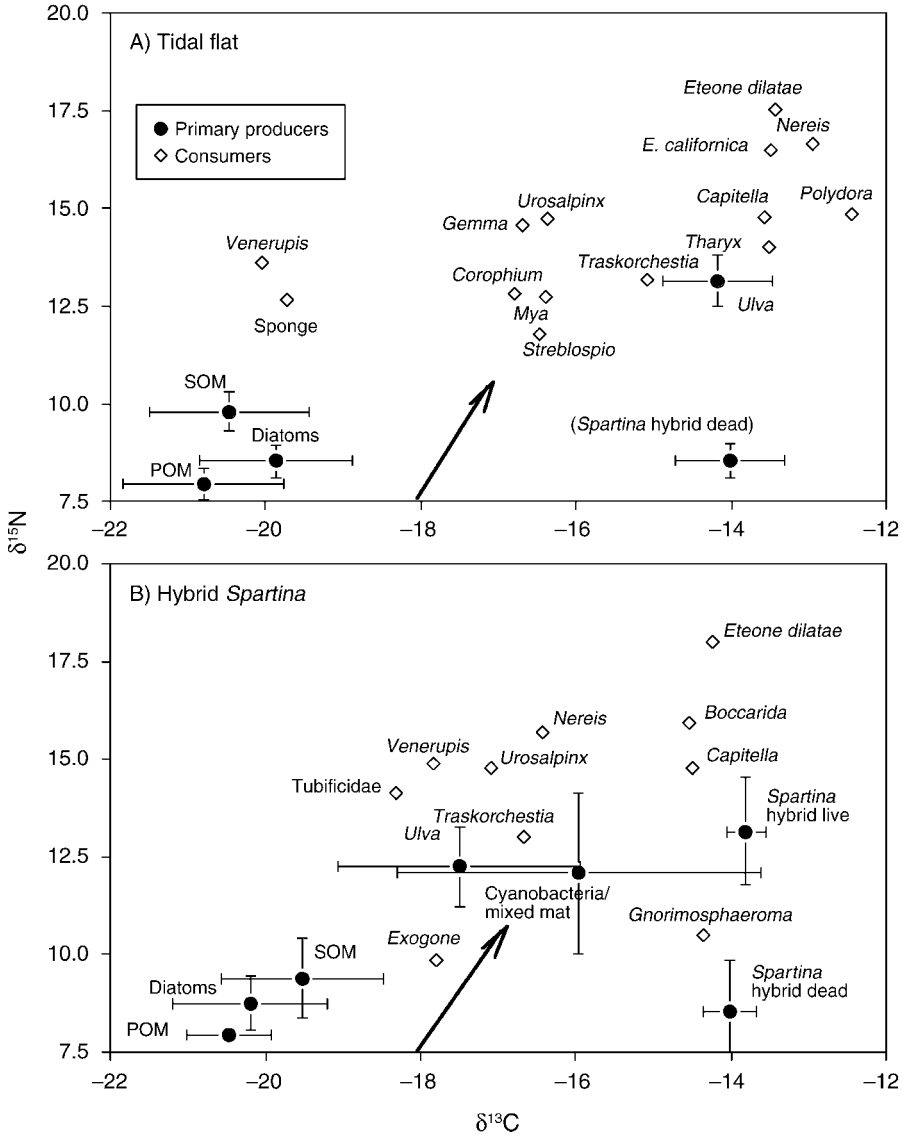

FIG. 1. Dual isotope plot of natural abundance $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± SE) of major primary producers and infaunal consumers in (A) tidal flat sediments and (B) sediments invaded by hybrid *Spartina*. The arrow represents one trophic level shift. Abbreviations are: SOM, sediment organic matter; POM, particulate organic matter. Parentheses enclosing ''*Spartina* hybrid dead'' indicate measurement for detritus.

on the tidal flat. Use of three-source mixing models, which separate *Spartina* from *Ulva* (with cyanobacteria) and from SOM/POM/diatoms in the HY system (where *Ulva* and *Spartina* have different signatures) suggests that *Spartina* formed >20% of the diet in *Traskorchestia*, *Capitella*, *Eteone dilatae*, *Nereis succinea*, and *Gnorimosphaeroma* sp. Predators *Urosalpinx cinerea* and *Carcinus maenas* consume prey species with at least 20% *Spartina* in their diet (Appendix B). The combined sources of SOM/POM/diatoms (or their consumers) form >75% of the diet of *Nereis succinea*, an unidentified sponge, *Geukensia demissa*, *Venerupis philippinarum* and *Urosalpinx cinerea* (Appendix B). These analyses suggest, but do not reveal definitively, which taxa consume hybrid *Spartina*. Thus, an isotopic tracer approach was adopted to answer these questions.

Enrichment experiments

Experiment 1.—At the start of the experiment, labeled *Spartina foliosa* detritus had mean $\delta^{15}N$ values of 2278‰, 1752‰, 1744‰, and 1998‰ (equivalent to 320%, 270%, 269%, and 294% ^{15}N enrichment) for roots, culms, green leaves, and dead leaves, respectively. $\delta^{15}N$ analysis of macrofaunal tissues revealed three distinct suites of species label-uptake patterns. Three taxa (*Nereis succinea*, *Capitella* sp., and tubificid oligochaetes) incorporated significant amounts of $\delta^{15}N$

label after 50 d, such that >1% of their N was estimated to have been derived from labeled *Spartina* detritus (Appendix C). Five taxa (the surface feeding polychaetes *Streblospio benedicti* and *Polydora* spp., the allegedly carnivorous polychaete *Eteone dilatae*, the bivalve *Macoma petalum*, and an anemone) exhibited minor uptake of ^{15}N label (0.4–1.0%). *Gemma gemma*, tanaids, ostracods, cumaceans, *Musculista senhousia*, *Venerupis philippinarum*, *Tharyx* sp., *Urosalpinx cinerea*, and *Traskorchestia traskiana* had less (<0.3%) or no uptake of ^{15}N derived from *S. foliosa* detritus (Appendix C). Culms and living blades yielded higher macrofaunal labeling for some taxa (e.g., *Nereis succinea* and tubificid oligochaetes), possibly suggesting greater palatability or higher nitrogen leach rate. Only *Capitella* appeared capable of acquiring substantial quantities of ^{15}N equally from roots and blades (Appendix C). However, due to variable ^{15}N signals, there was no significant difference in mean isotopic signatures (or percentage uptake) among different plant part treatments for *Capitella* ($P = 0.417$), *Nereis* ($P = 0.278$), or across species (ANOVA with species as replicates, $P = 0.500$). Standing live blades yielded higher ^{15}N uptake than standing dead blades in six or seven species (paired *t* test, $P = 0.052$). Highest uptake from dead blades was seen in *Nereis* and *Capitella* (Appendix C).

Experiment 2.—The hybrid *Spartina* detritus deployed in this experiment had a mean δ^{15}N signature of 1264 ± 134‰, equivalent to 222% ^{15}N enrichment. Elevated ^{15}N (up to +49‰) was observed in microalgal primary producers within 24 h, (possibly reflecting N leaching from hybrid *Spartina* detritus) but the signals were an order of magnitude lower than that of hybrid *Spartina* detritus (Appendix D). Uptake of ^{13}C tracer by microalgae (–9.77‰) and macroalgae (*Ulva* sp. −1.85‰ and *Enteromorpha* sp. +2.30‰) was rapid (within 24 h) but modest (Appendix D).

Isotope signatures reveal that different taxa consume hybrid *Spartina* detritus and algae (Figs. 2, 3). The greatest *Spartina*-derived ingestion, as indicated by elevation of δ^{15}N signatures above background ($\Delta\delta^{15}$N) at 4 d and 17 d was by species normally considered to be subsurface deposit feeders (i.e., the tubificid oligochaete genera *Tectidrilus* and *Tubificoides* and capitellid polychaete *Heteromastus filiformis*; Fig. 2). ^{15}N-labeled hybrid *Spartina* contributed from 1.5% to 8% of the N in these animals (Appendix E). Lesser uptake of ^{15}N label from hybrid *Spartina* detritus (1–1.5%) was observed in several other taxa, including the annelids *Capitella* sp., *Nereis succinea*, and *Polydora* spp., and the amphipod *Grandidierella japonica*. (Fig. 2; Appendix E).

Many of these label uptake patterns for Experiment 2 using hybrid *Spartina* mirror those observed in Experiment 1 with labeled *S. foliosa* (Appendix C). We found no significant difference in percentage of ^{15}N label derived by litterbag infauna from *S. foliosa* detritus (50-d exposure) vs. hybrid *Spartina* detritus (17-d and 74-d exposure; paired *t* tests using species as replicates, 17 d, $P = 0.276$; 74 d, $P = 0.816$).

In Experiment 2, oligochaetes and capitellid polychaetes remained heavily labeled with hybrid *Spartina*-derived ^{15}N tracer 215 days after the labeled detritus was introduced (Fig. 2; Appendix E). *Tharyx* sp. and *Tectidrilus diversus* were heavily labeled only at 215 days (Fig. 2). Throughout the experimental period there was little ingestion of *Spartina*-derived N (<1% of tissue N from labeled detritus) by the bivalves *Macoma petalum*, the amphipod *Corophium* sp., the surface-feeding polychaetes *Polydora nuchalis* and *Streblospio benedicti*, and by carnivores *Eteone californica*, *E. dilatae* and *Harmothoe imbricata* (Fig. 2; Appendix E).

Species uptake of *Spartina*-derived ^{15}N was similar when detritus was deployed on the surface or in subsurface litterbags (Appendix F; paired *t* test with species as replicates, all $P \geq 0.28$ for 17-d and 74-d treatments in the hybrid and mudflat). Label uptake was also similar in animals exposed to detritus on the mudflat vs. in *Spartina*-invaded plots (Appendix G; paired *t* test with species as replicates, all $P \geq 0.21$ for surface (4, 17, 74 d) and subsurface (17, 74, 215 d) treatments). Individual, species-level tests (ANOVA) yielded no effect of habitat or position within sediment on label uptake except for *Nereis succinea*, which had higher label ingestion in HY than TF deployed at the surface for 4 days ($P = 0.081$) and in litterbags for 215 days ($P = 0.081$).

A comparison of δ^{15}N signatures among invertebrate feeding types revealed significant ^{15}N enrichment (with δ^{15}N greater by a factor of two) for TF subsurface deposit feeders relative to surface feeders or carnivores/omnivores. This was true for assemblages exposed to surficial ^{15}N-labeled *Spartina* detritus for 4, 17, and 74 days (ANOVA, 4 d, $P = 0.038$; 17 d, $P = 0.044$, 74 d, $P = 0.0014$) but there were no significant differences among feeding groups at time 0 ($P > 0.05$; Fig. 4). Similar patterns were observed in the TF litterbag and HY experiments (Fig. 4).

Ingestion of ^{13}C-labeled algae was most evident in TF consumers, mainly among the bivalves *Gemma gemma* and *Macoma petalum*, the polychaetes *Tharyx* sp., and the amphipod *Grandidierella japonica* (Fig. 3). High ^{13}C label in *Eteone californica* may have been derived from predation on the aforementioned species. Of these, only *G. japonica* ingested significant amounts of both the ^{15}N and ^{13}C tracers (Figs. 2, 3). For species ingesting labeled food sources, δ^{15}N and δ^{13}C signatures were often higher at day 4 than day 17 (Figs. 2, 3).

Among consumers, there was a negative relationship between invasion tolerance (percentage change in density between TF and HY sediments) and surface algae ingestion ($\Delta\delta^{13}$C; Fig. 5). With one exception, animals that ingested the most labeled algae were least tolerant of *Spartina* invasion. A positive relationship between

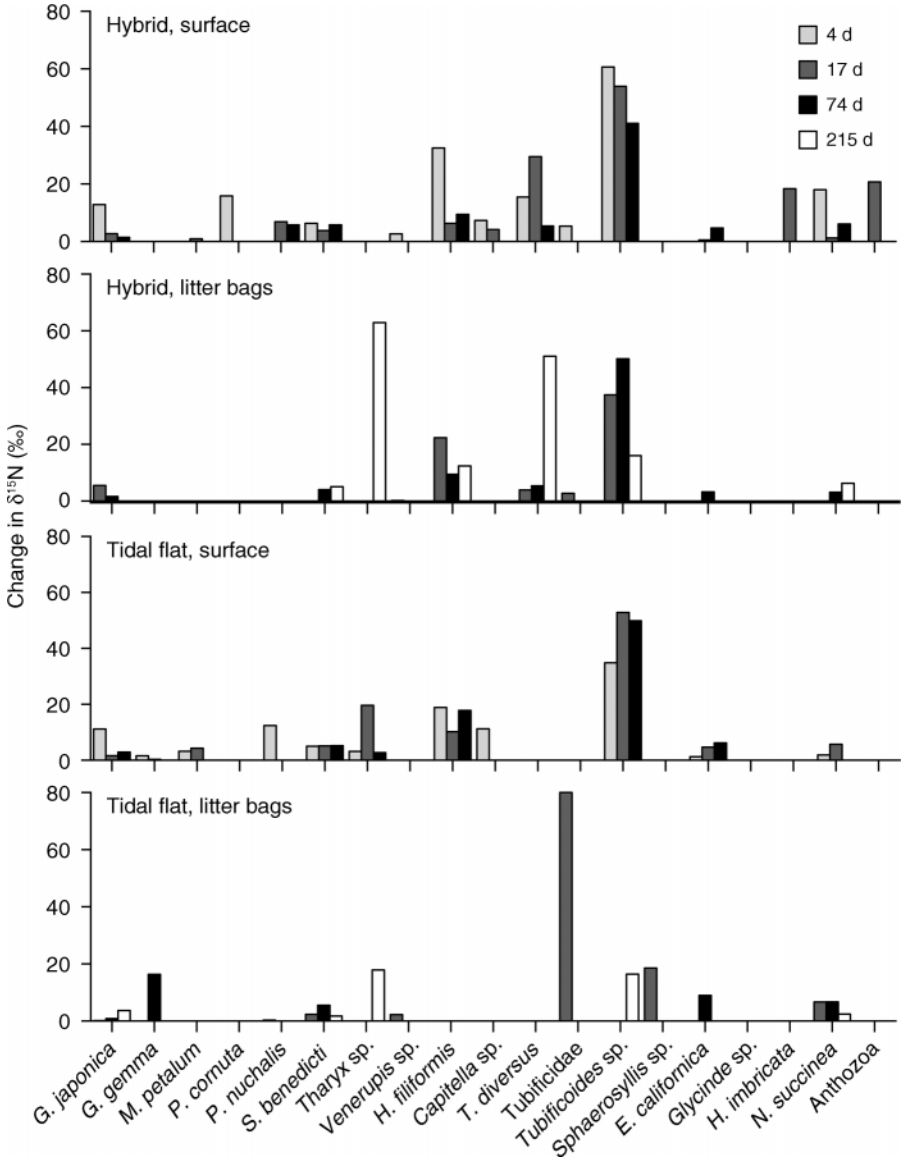

FIG. 2. Change in mean $\delta^{15}N$ values ($\Delta\delta^{15}N$) of macrofauna exposed to ^{15}N-labeled *Spartina foliosa* detritus placed in *Spartina*-invaded (hybrid) and tidal flat sediments. Data are shown for 4-d, 17-d, and 74-d exposure in surface experiments and 17-d, 74-d, and 215-d exposure for litter bag experiments. Data are calculated as mean $\delta^{15}N$ of the labeled specimen minus mean $\delta^{15}N$ of the background specimens ($\Delta\delta^{15}N$).

invasion tolerance and ^{15}N label ingestion was not observed, despite the fact that many species with the least density decline (Table 1) obtained the most ^{15}N label from hybrid *Spartina* detritus (Fig. 2).

DISCUSSION

Invader influence on food webs

Simenstad and Thom (1995) predicted that *Spartina* invasion would be capable of altering community trophic structure. The present study is the first to document a bottom-up mechanism underlying such an effect through a shift from an algae-based system to a primarily detrital-based system. While there are numerous cases where invasive species have broad impacts that alter food chains in a way that affects ecosystem organization (Spencer et al. 1991, Vitousek et al. 1996, O'Dowd et al. 2003, Roemer et al. 2003), most of the aquatic examples involve invasive animals such as introduced predatory fish (Hurlbert et al. 1972) or zooplankters (e.g., Spencer et al. 1999). Often these effects cascade up the food chain, influencing mammals and birds through effects on fish (Spencer et al. 1991, 1999). Trophic shifts can result from single species introductions, for example, when filter-feeding bivalves reduce the availability of phytoplankton and alter light regimes, thereby modifying entire food webs

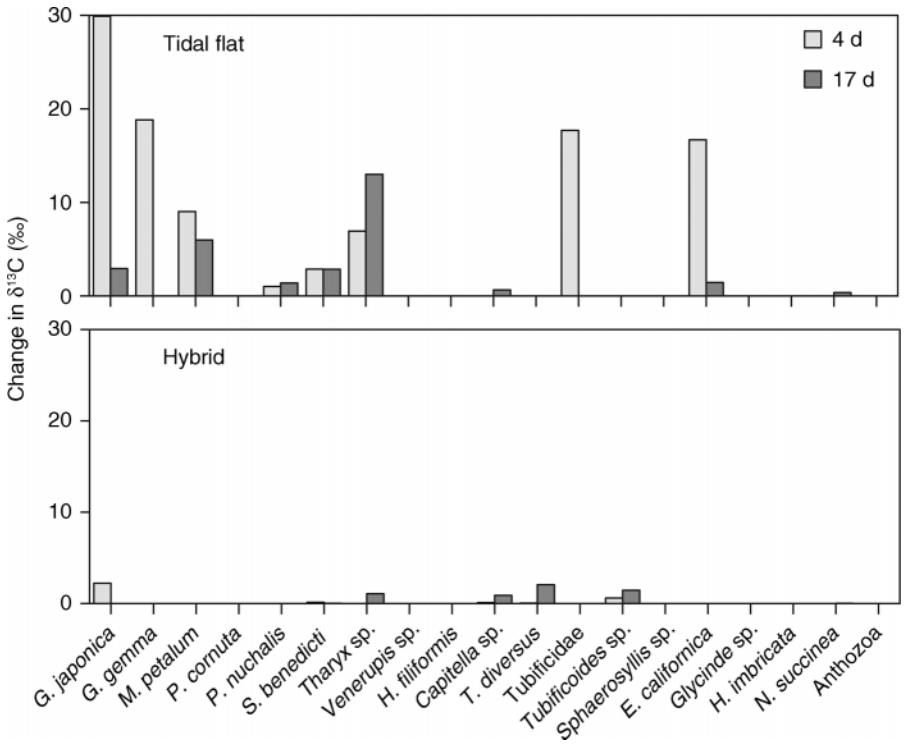

FIG. 3. Change in mean $\delta^{13}C$ values ($\Delta\delta^{13}C$) of macrofauna exposed to ^{13}C-labeled surface algae in *Spartina*-invaded (hybrid) and tidal flat sediments. Data are shown for samples collected 4 and 17 days after spraying the surface with ^{13}C bicarbonate. Data are calculated as mean $\delta^{13}C$ of the labeled specimen minus mean $\delta^{13}C$ of the background specimens ($\Delta\delta^{13}C$).

(Alpine and Cloern 1992, Fanslow et al. 1995). Change in the cover of wetland plant species by invasion or other processes (e.g., land reclamation, restoration efforts, storms, or other disturbances) is common. Where trophic consequences of these changes have been examined, the focus has typically been on diets of one consumer species (e.g., Wainright et al. 2003), rather than on the entire community.

Natural abundance stable isotope approaches have proved useful in documenting changes in food web structure involving multiple species. For example, they reveal El Niño-induced variation in the relative importance of marine and terrestrial food sources on islands (e.g., Stapp et al. 1999), and changes in trophic structure following species invasions (Vander Zanden et al. 1999, Wainright et al. 2003). However, mixing of food sources and many ambiguities in nitrogen trophic shifts indicate that natural abundance isotope data should be interpreted with independent evidence (Hart and Lovvorn 2002). Isotope enrichment experiments can provide this evidence.

We have shown that pulsed isotope enrichment of wetland plants (in this case *Spartina*) can demonstrate clearly which community members consume this plant (or C and N derived from that plant) as a food resource, but will not necessarily define its nutritional significance. Natural abundance and enrichment isotope data combined reflect consumption of *Spartina*-derived (either *foliosa* or hybrid) N by *Nereis succinea*, *Capitella* sp., *Eteone dilatae*, and *Polydora cornuta*. Enhanced uptake of labeled detritus in tubificid oligochaetes may have resulted from accelerated leaching of N due to freezing or other experimentation artifacts. *Eteone californica*, and *Traskorchestia* sp. had natural abundance signatures indicative of *Spartina*/*Ulva* contribution but minimal ^{15}N uptake in enrichment experiments. This suggests that *Ulva* rather than *Spartina* is their primary food source. However, as a predator, *Eteone* may have experienced a lag in uptake of ^{15}N derived from labeled detritus. Alternatively, high mobility of both *E. californica* and *Traskorchestia* sp. might have led us to sample recent immigrants with limited exposure to ^{15}N-labeled *Spartina* hybrid.

Role of Spartina *nitrogen: direct and indirect transfer*

Experimental methods could have biased *Spartina* detritus palatability results. Palatability of *Spartina* could have been enhanced by fungal degradation on standing dead blades in Experiment 1 (Newell and Bärlocher 1993, Graça et al. 2001) but we did not observe this in ^{15}N uptake (Appendix C), and fungal standing crop was not measured. Possibly fungal colonization occurred on all forms of detritus during the 50-d experiment.

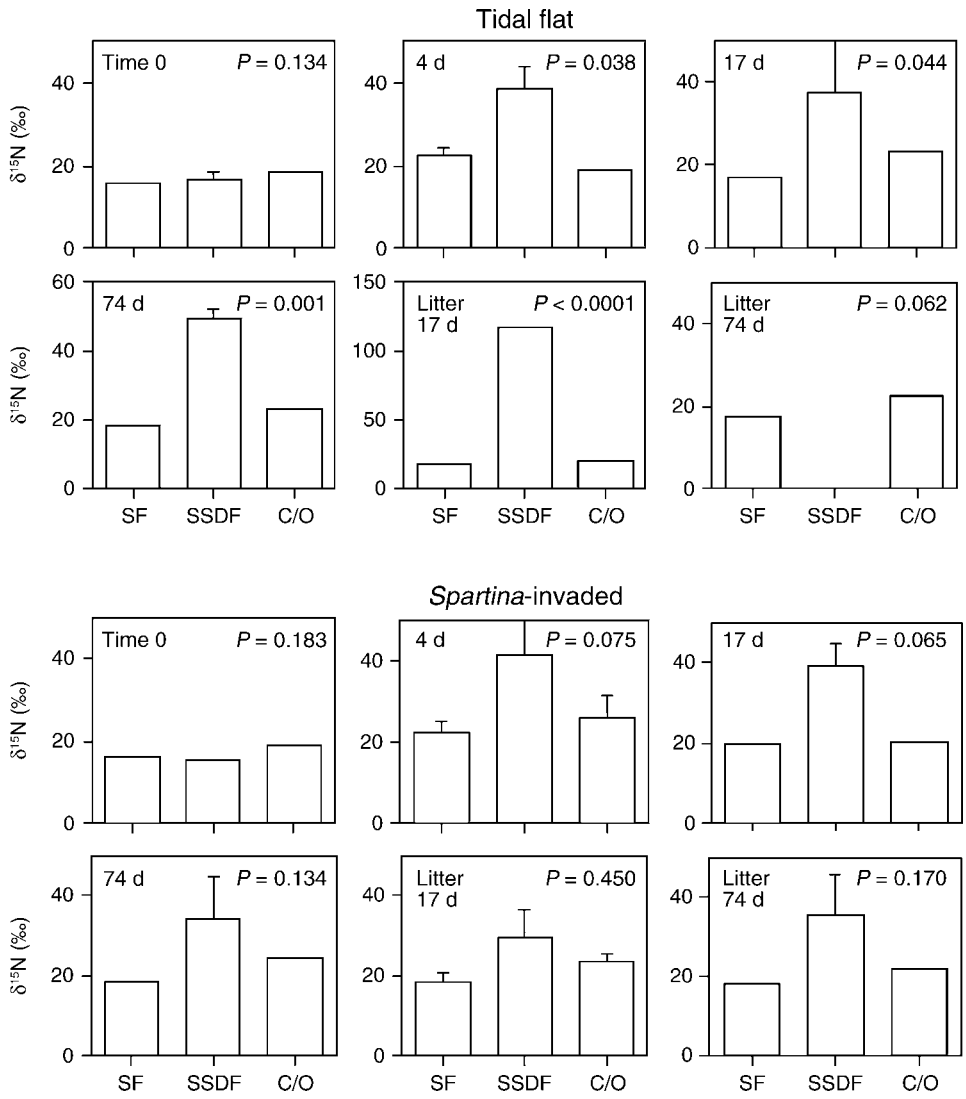

FIG. 4. Mean (± SE) $\delta^{15}N$ signatures of infaunal feeding groups following varying periods of exposure to ^{15}N-labeled hybrid *Spartina* detritus at the sediment surface (upper few millimeters) or in litter bags (buried 2 cm) in open tidal flats or in sites invaded by *Spartina* hybrid. Feeding group values were obtained by averaging species means. The apparent absence of error bars typically reflects very small error terms (not visible) or in some cases where $n = 1$, there is no error term. *P* values reflect results of a one-way ANOVA comparing surface feeders (SF), subsurface deposit feeders (SSDF), and carnivore/omnivores (C/O).

Although this experiment was intended to examine the direct ingestion of invasive *Spartina* by wetland consumers, it is possible that the labeled N made its way into consumer tissues by leaching or remineralization of N and subsequent uptake by bacteria or algae. *Spartina*-derived N could have been ingested in several forms, particularly in longer term experiments. However, of the animals that were ^{15}N labeled after 215 days, only *Tharyx* sp. and *Tectidrilus diversus* failed to show uptake early in the experiment. The possibility that *Spartina* fuels microbial production in marsh sediments by providing energy through sulfur compounds, without contributing carbon, has been suggested by Peterson et al. (1985). The observed ^{15}N enrichment of microalgae in Experiment 2 (up to 64‰ at 4 days; Appendix D) suggests that there may also be transfer of N, a limiting nutrient in most wetland systems, to benthic algae. The freezing of detritus prior to experimentation could have accelerated the leaching of N, and accessibility via bacterial remineralization.

Shifts in trophic pathways

There was concordance between diet preferences and abundance patterns in our comparison of uninvaded tidal flat and adjacent *Spartina*-invaded marsh. The most abundant species in the hybrid patches (*Tubificoides brownae*) and several species whose densities showed no change in invaded patches (*Capitella* sp.,

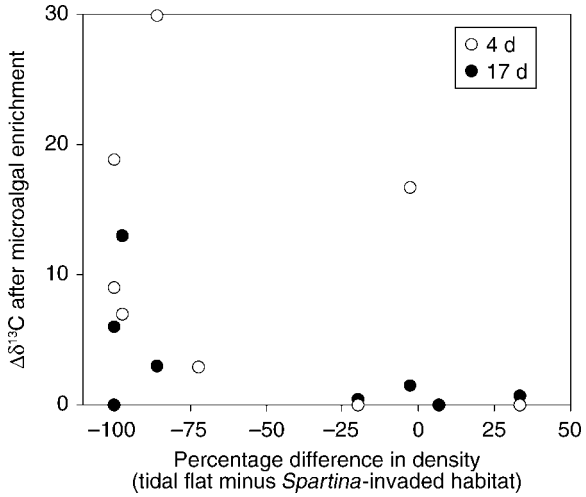

FIG. 5. Uptake of ^{13}C-labeled algae ($\Delta\ \delta^{13}C$) by individual species plotted as a function of their tolerance to invasion (percentage difference in density between uninvaded tidal flat and marsh invaded by *Spartina*). For a given symbol, each point represents a different species. Data are presented for species collected 4 days and 17 days after placement of the tracer.

Heteromastus filiformis, *Nereis succinea*; Table 1) were major consumers of ^{15}N-labeled native and hybrid *Spartina* detritus (Fig. 2). In contrast, bivalves and amphipods that consumed primarily algae exhibited much reduced densities in invaded sediments (Fig. 5). These observations support the hypothesis that changes in composition following plant invasion were driven at least in part by bottom-up processes related to the decreased availability of algae and increase in detritus.

Trophic succession, in which community patterns are driven by changes in food supply (and accompanying physical conditions), is recognized along pollution gradients (Pearson and Rosenberg 1978) but has received limited attention in other marine situations. Bottom-up processes, including those mediated by sediment properties, are recognized as significant influences on soft sediment communities (Lenihan and Micheli 2002), so we expected that large scale, invader-mediated changes in food availability would alter trophic structure. Similar trophic shifts, from primarily surface feeding to detritivore communities, have been observed in newly restored salt marsh ecosystems as plant cover develops over initially unvegetated sediment (Levin and Talley 2002, Moseman et al. 2004).

While the focus of this study has been on documenting food web alteration, other factors, including habitat-flow interactions, physiological tolerance, and top-down control of the community structure of benthos, may also structure this ecosystem (Neira et al. 2006). In addition to direct changes in availability of detritus and algae, indirect changes in food supply for benthos may be mediated by hybrid *Spartina* reduction of flow speed affecting flux of suspended particulates. For instance, recent studies have documented reduced growth of bivalves in hybrid *Spartina* meadows at nearby sites in San Francisco Bay, presumably due in part to reduced flow and food flux (Brusati 2004). At the Elsie Roemer site hybrid *Spartina* presence reduces mean flow on the tidal flat by 25% or more, entraining suspended fauna, increasing sedimentation rates, reducing particle grain size, and increasing organic matter content of sediments (Neira et al. 2006). These effects, combined with plant detritus accumulation, lead to high rates of sulfate reduction and sulfide buildup within vegetated sediments (C. Neira, *unpublished data*). An inability to tolerate more sulfidic marsh sediments, and greater susceptibility to marsh-associated predators such as green crabs could have reduced the densities of surface-feeding taxa in a manner disproportionate to the other feeding groups. These factors have been explored experimentally in the Elsie Roemer system (Neira et al. 2006).

Implications for San Francisco Bay and other ecosystems

The spread of hybrid *Spartina* throughout central and south San Francisco Bay (Ayers et al. 2004) is likely to force a shift from taxa feeding largely on surface algae to detritivores, with accompanying declines in animal biomass and density. Detritivore enhancement may have positive feedbacks on growth of the invasive *Spartina*, through greater regeneration of nutrients by detritus breakdown within the sediments (Bengstton et al. 1996). Loss of key secondary producers, in this case the surface feeders most preferred by foraging birds and fishes, may have cascading effects upward with negative implications for threatened and endangered species (Simenstad and Thom 1995).

Tidal wetlands, which provide critical trophic and habitat support for fishes, shellfish, and migratory birds, appear particularly susceptible to change through plant invasion (e.g., Posey 1988, Chambers et al. 1999). The preponderance of evidence from natural abundance stable isotopes and tracers suggests that hybrid *Spartina* is not consumed by the surface feeders and various carnivores that are key diet items for tidal flat fish and birds. Recent isotopic studies of epifauna at multiple sites in San Francisco Bay and adjacent estuaries suggest that native and hybrid *Spartina* are not contributing significantly to the nutrition of larger crustaceans and mollusks, although *S. foliosa* may contribute more at some sites (Brusati and Grosholz, *in press*). In Atlantic ecosystems, *Spartina alterniflora* is a key nutritional element in wetlands, with invertebrate intermediaries (e.g., annelids, gastropods, crabs) transferring *Spartina*-derived carbon to fish and shellfish (Currin et al. 1995, Wainright et al. 2003). In contrast, the hybrid *Spartina* in San Francisco Bay may do little to support higher trophic levels. The grass shrimp and killifish characteristic of Atlantic and Gulf coast marsh-

es are absent in San Francisco Bay, where the top predators (birds, flatfish) mainly consume tidal flat infauna.

Observed shifts in faunal community composition are compounded with altered habitat structure to produce massive state changes from open tidal flat to vegetated marsh systems. Such transformations caused by *Spartina* invasion are occurring in Willapa Bay (Simenstad and Thom 1995) and elsewhere in the Pacific Northwest (Daehler and Strong 1996). The open habitats represent dwindling resupply stations for birds migrating north–south along the Pacific Flyway (Page et al. 1999). Over time, climate change, and especially rising sea level, will interact with the invasive cordgrass to exacerbate food supply and habitat loss in San Francisco Bay. As the world's most invaded estuary (Cohen and Carlton 1995) this region offers a preview of the complex responses of coastal ecosystems to human transformations (Vitousek at al. 1997). Given the rapidly accelerating rate of plant species introduction and expansion globally (Vitousek et al. 1996), especially for *Spartina*, we might expect to observe similar trophic transformation and altered ecosystem support functions worldwide.

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APPENDIX A

Background (natural abundance) $\delta^{13}C$ and $\delta^{15}N$ signatures of primary producers, sediment organic matter (SOM), and marsh suspended particulate organic matter (POM) (*Ecological Archives* E087-023-A1).

APPENDIX B

Estimated proportion of *Spartina* hybrid and other food sources in macrofaunal diets based on natural abundance stable isotope data (*Ecological Archives* E087-023-A2).

APPENDIX C

The $\delta^{15}N$ signatures of macrofauna exposed to different parts of ^{15}N-labeled *Spartina foliosa* in litter bags for 50 days (*Ecological Archives* E087-023-A3).

APPENDIX D

Isotopic signatures of primary producers in a dual isotope labeling experiment shown as a function of time and habitat (*Ecological Archives* E087-023-A4).

APPENDIX E

Percentage of ^{15}N derived from labeled hybrid *Spartina* detritus in experiments conducted in hybrid-*Spartina* invaded and tidal flat sediments (*Ecological Archives* E087-023-A5).

APPENDIX F

Mean $\delta^{15}N$ signatures of macrofauna exposed to ^{15}N-labeled hybrid *Spartina* detritus on the surface vs. subsurface in litter bags (*Ecological Archives* E087-023-A6).

APPENDIX G

Mean $\delta^{15}N$ signatures of macrofauna exposed to ^{15}N-labeled hybrid *Spartina* detritus in tidal flat vs. hybrid sediments for 17-d exposure, surface; 17-d exposure, litter bags; 74-d exposure, surface; and 74-d exposure, litter bags (*Ecological Archives* E087-023-A7).

APPENDIX H

Mean $\delta^{15}N$ signatures of macrofauna given as a function of time that they are exposed to ^{15}N-labeled hybrid *Spartina* detritus at the sediment surface in tidal flat and hybrid-invaded sites and in subsurface in litterbags at tidal flat and hybrid-invaded sites (*Ecological Archives* E087-023-A8).