COMMUNITY ECOLOGY

Katharyn E. Boyer · Peggy Fong

Co-occurrence of habitat-modifying invertebrates: effects on structural and functional properties of a created salt marsh

Abstract The roles of co-occurring herbivores that modify habitat structure and ecosystem processes have seldom been examined in manipulative experiments or explored in early successional communities. In a created marsh in southern California (USA), we tested the individual and combined effects of two epibenthic invertebrates on nutrient and biomass pools, community structure, and physical habitat features. We manipulated snail (*Cerithidea californica*) and crab (*Pachygrapsus crassipes*) presence in field enclosures planted with pickleweed (*Salicornia virginica*) at elevations matching the plant's lower extent in an adjacent natural marsh. In the 4-month experiment, *C. californica* altered habitat structure by reducing sediment surface heterogeneity and shear strength (a measure of sediment stability) markedly throughout the enclosures. Both invertebrates had strong negative effects on a group of correlated sediment physicochemical characteristics, including nitrogen and organic matter concentrations and soil moisture. In addition, both invertebrates greatly reduced benthic chlorophyll *a*, a proxy for biomass of microphytobenthos. Compared to controls, macroalgal cover was up to sixfold lower with crabs present, while snails increased cover at low elevations of enclosures. Unexpectedly, macroalgal cover was eliminated with both species present, perhaps through *P. crassipes* consumption of larger thalli and *C. californica* reduction in cover of recruits. Neither species influenced the *S. virginica*

canopy (quantified with an index of branch length and number); however, at the lower elevation of enclosures, the two species together negatively impacted the plant canopy. The two invertebrates' modifications to our experimental marshes led to distinct suites of biotic and physicochemical features depending on their presence or co-occurrence, with the latter producing several unexpected results. We propose that the roles and interactions of habitat-modifying fauna deserve further attention, particularly in the context of efforts to conserve and restore the processes found in natural systems.

Keywords Habitat modifier · Invertebrate · Restoration · *Salicornia* · Sediments

K. E. Boyer (✉) · P. Fong
Department of Ecology and Evolutionary Biology,
University of California, 621 Charles E. Young Drive,
Los Angeles, CA 90095-1606, USA

Present address: K. E. Boyer
Romberg Tiburon Center for Environmental Studies and
Department of Biology, San Francisco State University,
3152 Paradise Drive, Tiburon, CA 94920, USA
E-mail: katboyer@sfsu.edu
Tel.: +1-415-3383751
Fax: +1-415-4357120

Introduction

Organisms that modify habitats through alterations in physical structure or the cycling or state of materials can have strong direct or indirect effects on community structure (Jones et al. 1994, 1997, Bruno and Bertness 2001). Appreciation of the roles of habitat-modifying species has advanced with increased experimentation in a wide variety of systems (e.g., Flecker 1996; Fournier et al. 2003; Lill and Marquis 2003; Bakker et al. 2004) and with recognition that such species can be integral to conservation concerns such as overfishing, invasion of exotic species, and persistence of threatened habitats (Coleman and Williams 2002; Crooks 2002). Studies of biota that strongly influence the functioning of ecosystems, with feedbacks to community properties, help to link the often-separate subdisciplines of community and ecosystem ecology (Jones and Lawton 1995; Chapin et al. 1997; Ernest and Brown 2001).

Animals modify habitats through a variety of mechanisms including disturbance of soils, removal of plant tissues, and deposition of waste materials, which, in turn, can regulate ecosystem processes such as nutrient cycling and productivity (Peterson and Heck 1999;

Wilby et al. 2001). Consumption of live and dead organic matter can lead to changes in the size, state, or location of materials important to other species (Flecker 1996; Crowl et al. 2001). In some cases, alteration of habitats results from trophic activity (e.g., earthworm burrowing; Thompson et al. 1993), while in others it occurs independent of feeding (e.g., prairie dog burrowing; Whicker and Detling 1988).

While it is recognized that fauna can have important effects on the structure and functioning of ecosystems, manipulative experiments have rarely been conducted on the relative contributions of different consumers or consumer assemblages that occur in a given habitat (Pringle et al. 1999; Schläpfer and Schmid 1999). This is certainly true for marine systems (Duffy 2002; Emmerson and Huxham 2002), even though the coastal zone has produced many examples of strong control by individual consumer species over physicochemical habitat features that can feed back to other biota (e.g., Bertness 1985; Gerdol and Hughes 1994; Crooks 1998; Widdicombe and Austen 1998). For example, fiddler crabs aerate reduced sediments through burrowing, stimulating production of cordgrass, which in turn stabilizes the sediments, thus facilitating burrowing (Bertness 1985). As marine soft sediments are commonly burrowed, ingested, and transported by marine fauna, these systems may frequently harbor multiple species that strongly influence habitat structure and/or ecosystem processes. For example, both a polychaete and a gastropod significantly affect ammonium release from sediments at one mudflat in Scotland, while at another, both an amphipod and another polychaete substantially influence this process (Emmerson et al. 2001). Nutrient flux is one of many physicochemical and biological features that could be altered by bioturbating species and species combinations in soft-sediment systems.

Habitats constructed for restoration purposes present a unique opportunity to test the relative effects of different species combinations on habitat structure and ecosystem processes in a relatively controlled setting. However, restoration sites have only rarely been used for such purposes (Zedler et al. 2001), and to our knowledge have not addressed the relative influence of different faunal species on ecosystem properties. In this study, we tested the individual and combined effects of two common epibenthic macroinvertebrates, a snail and a crab, on nutrient and biomass pools and the physical structure of a newly created salt marsh in southern California.

Model system and hypotheses

The lower salt marsh edge adjacent to creeks and mudflats harbors a number of deposit-feeding and burrowing macro-invertebrates in estuaries worldwide (e.g., Lee et al. 1981; Richardson et al. 1998; Riera et al. 1999). This study focused on the horn snail *Cerithidea californica* Haldeman, which occurs in lower salt marsh and mudflat habitats from Tomales Bay (Marin County),

California (USA), to Laguna San Ignacio in Baja California, Mexico (Morris et al. 1980), and the shore crab *Pachygrapsus crassipes* Randall, which occurs both in the rocky intertidal and lower elevation salt marshes from northern Oregon to the Gulf of California (Jensen 1995). In southern California estuaries, these species commonly co-occur among *Salicornia virginica* L. (pickleweed), the dominant vascular plant along channel edges (Zedler et al. 1999). Through ingestion of surficial sediments, *C. californica* consumes microphytobenthos and detritus from vascular plants and macroalgae (Whitlach and Obrebski 1980), and is thought to play an important role in N cycling (Fong et al. 1997). *C. californica* is an abundant native epibenthic invertebrate, with densities up to 2,000 /m^2 (K. Boyer and P. Fong unpublished data, McCloy 1979). *P. crassipes* is omnivorous, consuming macroalgae, microphytobenthos, detritus, and small invertebrates (Hiatt 1948; Quammen 1984) and occupies burrows along creeks and mudflats near and among vegetation (Sousa 1993) reaching densities of 64 /m^2 (Willason 1981). *P. crassipes* creates burrows by enlarging depressions that form by other means; e.g., sediment scouring adjacent to plant roots or rocks (Hiatt 1948) or takes over burrows excavated by co-occurring crab species (*Hemigrapsus oregonensis*; Willason 1981), although *P. crassipes* is the only abundant crab at our study site.

We hypothesized that both *C. californica* and *P. crassipes* have substantive effects on the structure and functioning of lower *S. virginica* marshes, but that different ecosystem attributes result from their largely distinct diets and modes of physical disturbance, with species co-occurrence resulting in a complimentary assortment of ecosystem properties. However, we also suspected that overlapping resource use and interference between species could lead to complex and unexpected patterns in habitat structure and/or processes.

Materials and methods

In a 2 × 2 factorial experiment, we varied the presence of *C. californica* and *P. crassipes* in enclosures at a marsh created for restoration purposes at Mugu Lagoon, on the Naval Base Ventura County, CA, USA (34°06′N, 119°07′W). Treatments included addition of *C. californica* (snails), *P. crassipes* (crabs), both invertebrates (both), or neither (control) in a randomized complete block design ($n = 5$), with blocks to account for a potential gradient with distance from an adjacent natural marsh.

The restoration site was graded (from dredged material, 96% sand) 6 months prior and remained unvegetated. We positioned 20 2 × 2-m plots separated by 1-m spaces along the graded slope. Plot elevations, surveyed to match the lower *S. virginica* in the adjacent natural marsh, were ∼0.44 (lower edge) to 0.56 m (upper edge) above mean sea level relative to the National Geodetic Vertical Datum. In early April 1998, small *S.*

virginica (20.6 ± .8 [SE] cm maximum height, $n = 50$ randomly selected individuals) started the previous fall from cuttings were planted in each plot in a 5×5 array, after removing plants that had recruited from seed (*S. virginica* only, range = 3–136 seedlings; mean among plots = 23 ± 7). During the experiment, ~2 *S. virginica* recruits per plot were removed; no other vascular plants recruited.

In mid-June, enclosures were installed around each plot. PVC pipe supported a 60-cm tall plastic mesh (6.4-mm openings) inserted 15 cm into sediments (to reduce crab burrowing in or out of enclosures). Lids of fiberglass window screen reduced light by 38% (SE = 0.04; five measures over a 2-h mid-day period; LI-COR-1000 meter, Lincoln, NE, USA).

To begin the experiment, invertebrates were added to enclosures on June 24–25, 1998. Live *C. californica* of the most common length (2–3 cm, K. Boyer unpublished data) were collected from the adjacent marsh; these were too broad to escape through the enclosure mesh and too large for *P. crassipes* to handle (Sousa 1993). The density added (275 /m^2) was comparable to that of the adjacent *S. virginica* marsh at this time (330 ± 142 (SE) per m^2). While snails attempting to escape enclosures can indicate crowding (Byers 2000), densities on the inside walls of enclosures were consistently low compared to outside surfaces (grand mean of biweekly counts = 6 ± 2 snails/enclosure vs. 57 ± 8 snails/enclosure , respectively).

Pachygrapsus crassipes was collected with minnow traps and the most abundant size (2–4 cm carapace width) added to enclosures in a 1:1 sex ratio. Twenty crabs were added to each enclosure (= 5 /m^2), a conservative density considering the ~8 burrows/m^2 in the adjacent natural marsh in June 1998 (A. Armitage unpublished data) and that these crabs are often observed sharing burrows. As *P. crassipes* reportedly only enlarges burrows begun by other means, we added holes to assist burrowing by driving a 1.27-cm diameter pipe 8 cm into the 16 spaces between plants in all enclosures.

The macroalga *Enteromorpha intestinalis* was added every 2 weeks beginning June 25, as enclosures eliminated rafting algae common in adjacent areas. Algae were collected, cleaned of debris, gently squeezed to remove excess water, measured volumetrically (500 ml/enclosure, ~350-g wet mass), and distributed throughout each plot. The quantity added each time reflected densities on mudflats outside the enclosures at the start of the experiment.

Sampling was conducted at low tide in late August and October 1998, in addition to biweekly assessments. As enclosures were along a slope, we sampled both the upper and lower portions to account for differences in inundation. To avoid edge effects, we did not sample within 20 cm of the enclosure walls.

In August and October, chlorophyll *a* concentration was measured in the top 1 cm of sediment as a proxy for biomass of microphytobenthos. Three 1.5-cm diameter cores were taken from random locations 30 cm from the upper and lower edges of each plot, combined, placed on ice in the dark, and frozen at −15°C. Pigment extraction and measurement employed standard spectrophotometric methods and equations (Parsons and Strickland 1963; Lorenzen 1967). In October only, percent cover of macroalgae was estimated with a point intercept frame in both the upper and lower zones (macroalgae were rare in August and not sampled). Algae were collected from throughout plots and analyzed for total N and P at the Division of Agriculture and Natural Resources (DANR) lab (Davis, CA, USA) using standard methods. In August and October, we recorded the number and lengths of all branches (including the main stem, from the sediment surface) on two plants (at the same position in each plot) in each enclosure zone. These measures were combined into a canopy index ([total length/maximum total length] + [number of branches/maximum number of branches]), which permitted a non-destructive comparison incorporating both plant size and architecture.

In October 1998, we assessed *C. californica* density, shell length, mortality, and number of recruits. Dead snails and recruits each composed < 2% of enclosure populations. For *P. crassipes*, we noted the absence of chelae as an assessment of aggressive behavior. There were no patterns by treatment for any of these measures (data are not presented). We observed bubble snail (*Acteocina inculta*) recruitment in some plots and in August collected and pooled three cores (2.5-cm diameter, 4 cm deep) per high or low elevation and quantified densities. In October, using the same coring methods, densities of the major taxonomic groups (family or genus) of all infauna > 0.5 mm were estimated. At the end of the experiment, we counted crab-initiated burrows (i.e., those not at the locations of our experimental holes).
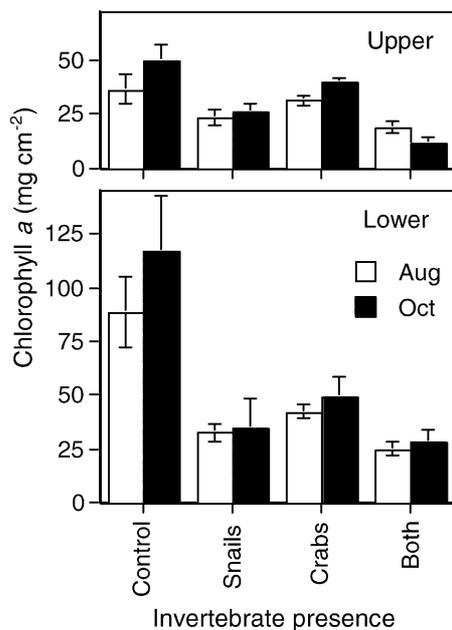
We measured a number of sediment physicochemical characteristics that could be important to marsh development. Changes in topography were tracked by recording biweekly the number of depressions visible from our experimental hole additions. In October, at four random locations each at the high and low elevations, we evaluated the relative stability or erodibility of the sediment surface by measuring shear strength; i.e., the force needed to penetrate the sediment surface with a torsional vane shear tester. In August and October, three soil cores (2.5-cm diameter, 4 cm deep) were collected and pooled for each elevation. Soil moisture was determined as mass lost upon drying (55°C), bulk density as dry mass per soil volume, and organic content as loss on ignition (400°C for 10 h). Saturated soil pastes prepared from dried soils were used to make relative estimates of pH (Accumet pH meter) and salinity (soil water expressed through filter paper onto a Leica refractometer). Soils were analyzed at DANR for total Kjeldahl N (TKN), ammonium and nitrate, and total P.

Data analyses employed a blocked 3-factor ANOVA (± snails, ± crabs, high/low elevation) for data from a single date, or blocked 4-factor ANOVA (with the addition of date = August or October). We used principal components analysis (PCA) to reduce the large

number (9) of soil variables from cored sediments. The PCA resulted in extraction of three factors with eigenvalues >1, and we conducted a blocked 4-factor ANOVA on the three sets of variables derived from the factor scores. A repeated measures ANOVA was used to examine data on the persistence of experimental holes over five dates. In addition, we compared algal N and P among the snail and control plots (see results) with t-tests. A Bonferroni-adjusted $\alpha = 0.005$ insured that reports of statistical significance were very conservative. Interactions of the snail and crab treatments with the block could not be tested, as each block included only one replicate of each treatment. All other interactions were tested and not significant unless noted. Logarithmic transformations were performed as necessary to improve the homogeneity of variances. $n = 5$, except in the "both" treatment, in which one replicate was dropped due to problems with an enclosure.

Results

Biomass of benthic chlorophyll a was greatly reduced relative to control levels with either snails ($F_{1,44} = 176.54$, $P = 0.0001$) or crabs ($F_{1,44} = 48.12$, $P = 0.0001$) present, with similar effects found in both August and October (Fig. 1). With both species present, reductions in chlorophyll a were additive. The biomass of chlorophyll a was significantly greater in the lower zone of enclosures than in the upper zone ($F_{1,44} = 56.03$, $P = 0.0001$), with control plot biomass 100% greater at the lower elevation (Fig. 1).
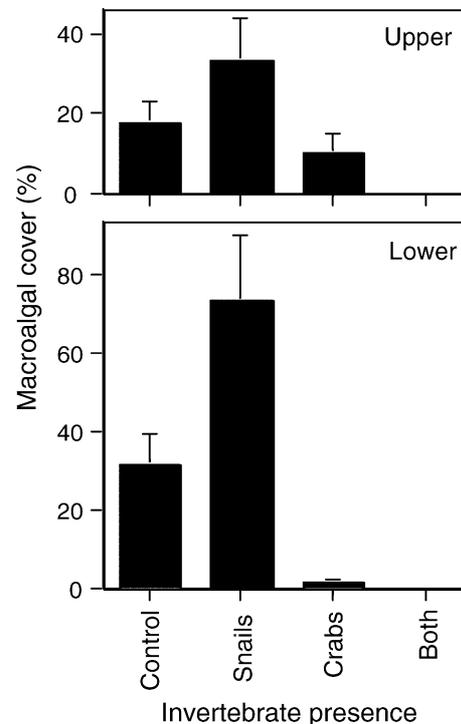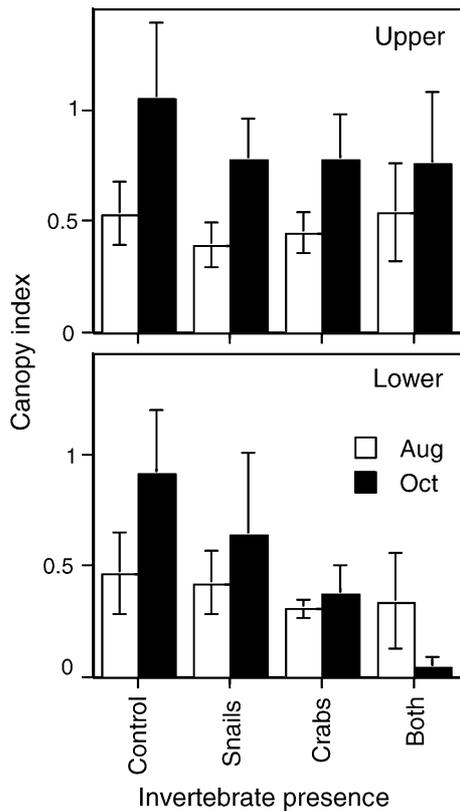
Macroalgal cover in October was twofold greater with snails present than in controls in the lower zone of enclosures (Fig. 2), but was not statistically greater in the snail treatment overall ($P = 0.1282$). Macroalgal cover was significantly lower where crabs were present than in controls ($F_{1,22} = 176.26$, $P = 0.0001$), six times lower at the low elevation (Fig. 2). With both snails and crabs present, all macroalgae were eliminated, resulting in an interaction between the snail and crab treatment ($F_{1,22} = 23.16$, $P = 0.0001$).

Macroalgal N and P concentration could only be measured in enclosures with sufficient tissue available. Grand means for *Enteromorpha* spp. tissues were $2.05 \pm 0.16\%$ N and $0.14 \pm 0.01\%$ P ($n = 10$; 5 snail, 4 control, and 1 crab enclosure) and for *Ulva* spp. were $2.96 \pm 0.60\%$ N and $0.25 \pm 0.04\%$ P ($n = 4$; 2 snail, 1 control, and 1 crab enclosure). *T*-tests on *Enteromorpha* N and P concentration in the snail versus control treatments revealed no significant differences.

A fourfold increase in *S. virginica* branching occurred between August (24.1 ± 3.1 branches/two plants, grand mean) and October (91.7 ± 15.4 branches), although plant canopies were not significantly more robust overall in October (plant canopy index, Fig. 3; $F_{1,44} = 6.55$, $P = 0.0140$ [$\alpha = 0.005$]). Plant canopies were not significantly affected by snail or crab presence, nor were there interactions among these treatments. However, at the lower elevation, additions of both invertebrates led to declines of 95% in the plant canopy index relative to

Fig. 1 Biomass of chlorophyll a in surface sediments (August and October) in the *upper* and *lower* elevation of enclosures, with invertebrates absent (*control*) or present (*snails, crabs,* or *both*). *Bars* represent means $\pm$ 1 SE. Some *error bars* are too small to be visible

Fig. 2 Percent cover of macroalgae in October, in the *upper* and *lower* elevation of enclosures, with invertebrates absent (*control*) or present (*snails, crabs,* or *both*). *Bars* represent means $\pm$ 1 SE. Some *error bars* are too small to be visible

Fig. 3 Canopy index values of *Salicornia virginica* (incorporating branch lengths and numbers of branches as described in Materials and methods) in October, in the *upper* and *lower* elevation of enclosures, with invertebrates absent (*control*) or present (*snails, crabs,* or *both*). *Bars* represent means ± 1 SE

controls (Fig. 3). Canopy index values were significantly greater at the high than low elevation ($F_{1,44}=10.80$, $P=0.0020$), primarily due to the "both" treatment reducing the overall mean at the lower elevation.
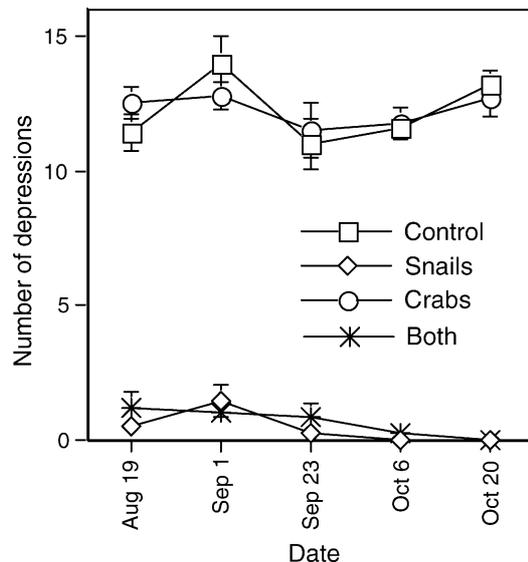
The presence of *P. crassipes* tended to reduce *A. inculta* densities on the sediment surface in August ($2,853\pm1,750$ and 407 ± 407 individuals/m² in the control and crab treatments, respectively), but the effect was not significant ($F_{1,44}=6.07$, $P=0.0177$ [$\alpha=0.005$]). *C. californica* alone had no effect on *A. inculta* densities, but the bubble snail was completely absent in the "both" treatment.

In October, the density of infaunal invertebrates was highly variable and it was apparent without conducting statistical analyses that there were no significant differences among treatment means. In the upper zone of plots, oligochaetes were most abundant ($16,667\pm2,377$ individuals/m²; 91% of total counts) and all other taxa (insect larvae, polychaetes, nematodes) comparatively less frequent ($\leq2\%$, or ≤366 individuals/m²), while the lower zone included oligochaetes ($13,120\pm2,972$ /m², 40%), polychaetes (*Capitella* spp., $9,184\pm5,073$ /m², 28%; *Polydora* spp., $2,270\pm928$ /m², 8%), amphipods (*Corophium* spp., $3,294\pm1,529$ /m², 10%), and nematodes ($3,115\pm1,041$ /m², 10%).

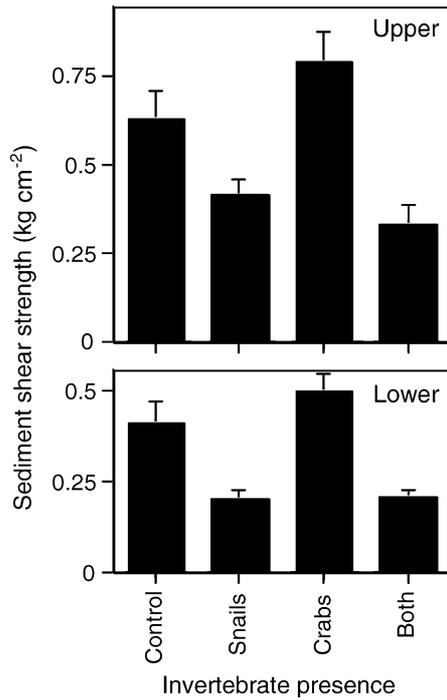*Cerithidea californica* smoothed the sediment surface, dramatically reducing the number of added holes persisting over time (Fig. 4, $F_{1,50}=1,441.89$, $P=0.0001$). Where *C. californica* was present, only 5% of the holes remained in August and none were visible by October. In the controls, ~80% of the holes remained through October; a similar result in the crab treatment suggests that *P. crassipes* was not maintaining the holes as burrows. The crab initiated burrows elsewhere in the plots (mean#/enclosure in October = 3 ± 0.9, range 1–9) but at low tide were often seen in shallow depressions in the lower zone of enclosures.

The shear strength of surface sediments was >60% higher in the upper than in the lower zone of plots in the controls when measured in October (Fig. 5; $F_{1,22}=31.75$, $P=0.0001$). Relative to controls, *C. californica* reduced shear strength by ~40% ($F_{1,22}=57.51$, $P=0.0001$). *P. crassipes* had no effect on sediment shear strength.
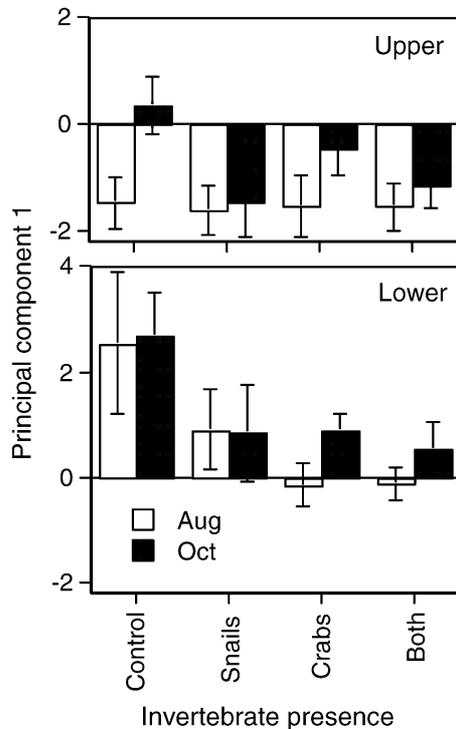
Of the three factors that resulted from principal components analysis of the nine cored sediment variables, the first factor (PC1) was highly positively correlated with TKN ($R^2=0.83$, $P=0.0001$), ammonium ($R^2=0.81$, $P=0.0001$), organic matter ($R^2=0.78$, $P=0.0001$), and soil moisture ($R^2=0.90$, $P=0.0001$), less so with salinity ($R^2=0.47$, $P=0.0001$), and negatively with bulk density ($R^2=0.78$, $P=0.0001$). The new variable derived from the PC1 factor scores was greater in magnitude at lower than upper elevations (Fig. 6; $F_{1,41}=46.23$, $P=0.0001$). In addition, it was negatively affected by snail presence ($F_{1,41}=10.65$, $P=0.0022$) as well as crab presence ($F_{1,41}=10.54$, $P=0.0023$) (Fig. 6). The second factor (PC2) was positively correlated with total P ($R^2=0.67$, $P=0.0001$) and pH ($R^2=0.72$, $P=0.0001$). The resulting PC2 variable was greater in

Fig. 4 Number of experimental depressions persisting over time with invertebrates absent (*control*) or present (*snails, crabs,* or *both*). Data are means ± 1 SE

Fig. 5 Shear strength of sediments in October, in the *upper* and *lower* elevation of enclosures, with invertebrates absent (*control*) or present (*snails*, *crabs*, or *both*). *Bars* represent means ± 1 SE

Fig. 6 Factor scores for first principal component (PC1) in August and October, in the *upper* and *lower* elevation of enclosures, with invertebrates absent (*control*) or present (*snails*, *crabs*, or *both*). PC1 was highly positively correlated with sediment total nitrogen, ammonium, organic matter, and moisture, and negatively correlated with bulk density. *Bars* represent means ± 1 SE

magnitude at high than low elevations ($F_{1,41} = 14.70$, $P = 0.0004$) and greater in October than August ($F_{1,41} = 44.02$, $P = 0.0001$), but was not affected by invertebrate treatment. There were no significant differences in the variable from a third PC factor that was positively correlated with nitrate ($R^2 = 0.94$, $P = 0.0001$).

Discussion

In general, the importance of consumer species identity and composition in structuring habitats and altering ecosystem processes is probably underappreciated (Duffy 2002). The ecological literature increasingly presents experimental studies and observational accounts of fauna shaping their environments in dramatic ways; e.g., through alterations to nutrient cycling (Frank et al. 2002, Wilby et al. 2001) and transport and/or redistribution of the substratum (Flecker 1996; Statzner et al. 2000). However, manipulations to examine the relative effects of multiple habitat-modifying consumer species in the same system are less common (Thompson et al. 1993; Duffy et al. 2003; Machicote et al. 2004) and few studies have explored interactive effects of consumer species with strong functional roles (Emmerson et al. 2001; Bakker et al. 2004; Hunt-Joshi et al. 2004). Such studies help to elucidate which features might be lost from natural ecosystems with extinction of one or more functionally important consumer species, and what might be gained through restoration activities that include these species or assemblages.

Habitat-modifying fauna in southern California marshes

In our study, two dominant epibenthic invertebrates modified a wide variety of structural and functional features of a created *Salicornia* marsh. In addition, invertebrate co-occurrence altered several outcomes measurably, either through additivity of single species effects or unexpected interactive effects.

Both *C. californica* and *P. crassipes* strongly influenced primary producers, thus affecting habitat structure and potentially altering trophic structure. Strong negative effects of both invertebrates on benthic chlorophyll *a* were likely due to a combination of consumption of microphytobenthos and disturbance to the sediments. For *C. californica*, trophic effects and disturbance are closely linked, as the snail ingests sediments while grazing. Similarly, *P. crassipes* ingests microalgae (Page 1997), disturbing surfaces with its chelae (Hiatt 1948).

Snails and crabs had contrasting effects on macroalgae. Snails may facilitate the growth of macroalgae through release of microalgal-derived nitrogenous waste to the water column (Fong et al. 1997). Our finding of no increased algal tissue N in the snail treatment may have resulted from dilution of N during algal growth.

Alternative mechanisms for snail-enhanced macroalgal cover include grazing on epiphytes that may intercept light or nutrients otherwise available to the macroalgae (Heck et al. 2000), and snail reductions of microphytobenthos releasing the macroalgae from competition for nutrients. In contrast, *P. crassipes* consumed large quantities of macroalgae, which are known to be an important food for the crab (Hiatt 1948). Bubble snails may have supplemented the crab's diet; however, other known prey that were available and even relatively common in October (e.g., polychaetes and oligochaetes; Quammen 1984; Talley and Levin 1999) were not consumed measurably, suggesting that availability of macroalgae may limit consumption of other prey.

While *C. californica* and *P. crassipes* had opposing effects on macroalgal cover, together they unexpectedly eliminated macroalgae. We propose that both invertebrates consume macroalgae but at different life stages: crabs on the large thalli and snails on the small recruits. While previous studies suggest that macroalgae are not an important food for *C. californica* (Whitlach and Obrebski 1980; Fong et al. 1997), the snail may have dramatic effects on early life stages, as suggested by a recent microcosm study (reduction of cover of *E. intestinalis* recruits by >60%; K. Boyer and P. Fong unpublished data). Hence, the snail may enhance the growth of larger thalli while simultaneously removing small recruits. Another possibility is that *P. crassipes* herbivory on macroalgae produces detritus that is small enough for grazing by *C. californica*, increasing removal of algae when the two invertebrates co-occur.

Vascular vegetation was affected by crabs and snails only when they co-occurred, and only in the lower portion of the enclosures. On several occasions, we observed *P. crassipes* grazing the *S. virginica* branches at lower, moister elevations where the crabs tended to congregate at low tide. Invertebrate reductions in sediment N and organic matter could also have negatively influenced *S. virginica* growth, as could have sediment disturbance. While the exact mechanism is not certain, these two species may together play a role in setting the lower elevational limit for *S. virginica*.

Cerithidea californica produced striking changes in the marsh surface through decreases in substratum complexity and shear strength. Diatoms excrete mucopolysaccharides for use in attachment and locomotion, resulting in films that trap and bind sediments and increase the critical erosion threshold (Grant et al. 1986; Sullivan 1999) and cyanobacteria also physically bind particles with secretions (Paterson 1994). Our data suggest that *C. californica* disturbs these biofilms, as has been found with other grazers on marsh and mudflat surfaces (Gerdol and Hughes 1994; Cadée 2001). In contrast, the crab did not reduce sediment shear strength although it significantly reduced sediment chlorophyll *a*, suggesting that it removes microalgae without disturbing sediment-binding biofilms. As diatoms congregate in the top few millimeters of sediment during the day, they are more susceptible to disturbance than their mucus films

(Grant et al. 1986), while diatom migration (and thus mucus films) can reach a centimeter or more in depth (Underwood 1997). Disturbance of surface sediments by snails and the formation of burrows and shallow depressions by crabs may have augmented sediment moisture evaporation and drainage, as suggested by decreased moisture levels and increased bulk density with either invertebrate present.

Implications for conservation and restoration

Rather than advocating a particular outcome from our treatments, we emphasize the broader lesson that multiple fauna can alter a wide range of structural and/or functional features of an ecosystem, and that their combined effects are not necessarily predictable from those of the individual species. These results have implications for conservation in any system where more than one consumer is likely to perform strong functional roles. For instance, assemblages of tilefish and grouper that burrow in continental shelf edge and slope sediments, thus providing habitat for other species and probably altering sediment biogeochemistry, are at risk from increased fishing pressure as well as disturbance from oil and gas exploration (Coleman and Williams 2002). Experimental comparisons of species effects within such an assemblage of habitat modifiers would help to predict the effects of local extinctions due to fishing and other human activities, the threats of which may vary in intensity for different species.

Such experiments are relevant in places where invasions by non-native species are likely to cause reduced densities or losses of native fauna that shape structure or function. For example, *C. californica* has been largely extirpated from several central California estuaries through competition with an introduced snail (Byers 2000), can be restricted to higher marsh habitats through competition with another (Race 1982), and may lose marsh-edge habitat through erosion by an exotic isopod (Talley et al. 2001). Similarly, a predaceous flatworm introduced to the British Isles could have a major impact on soil ecosystems by reducing densities of earthworms (Boag and Yeates 2001), which are well known for redistributing soil and organic material, enhancing microbial activity and nutrient release, and increasing soil aeration and root penetration (Edwards 2004). Further study is also needed of the habitat-modifying effects of introduced fauna (Crooks 2002). For example, a number of non-native earthworms, which vary in their consumption and mixing of surface and deeper soils, are invading northern temperate forests that lack native earthworms (Bohlen et al. 2004). Experiments revealing the interactive effects of different earthworm invaders, and of the earthworms in combination with deer grazing and defecating in the system (Augustine et al. 1998) would allow predictions of habitat changes under different scenarios of invasion and context.

The roles of consumers in altering structural and functional properties of ecosystems are also an important consideration in restoration. A plant focus is typical in restoration practice, partly due to the assumption that once plants are established, animals will follow (Palmer et al. 1997). However, not all fauna will arrive on their own to newly available habitat. For instance, salt marsh invertebrates with planktonic larvae (e.g., *P. crassipes*) need a hydrological connection to an existing population in order to establish at a restoration site; species whose larvae do not disperse as plankton (e.g., *C. californica*) are even less likely to recruit (Talley and Levin 1999). Grassland plants that rely for pollination on the many bee fauna with small foraging areas may not have sufficient seed set to persist at restoration sites to which the bees do not disperse (Reed 1995; Buchmann and Nabhan 1996), leading to communities with different plant species composition than intended. Managers of restoration projects should consider species roles and recruitment limitations to help determine if introductions of key fauna are desirable.

Recognizing consumers with strong effects as habitat modifiers is not always straightforward. For some species assemblages, such as stream invertebrates, the state of taxonomic knowledge does not allow for detailed study of species effects (Richardson and Jackson 2002). In other cases, important habitat modifiers may be inconspicuous beside larger or more obvious species. An exclosure study in a floodplain grassland found voles to exceed cattle in their effects on annual mineralization of nitrogen, partly because voles distributed feces at a much finer scale across the landscape (Bakker et al. 2004). Many other systems may harbor multiple habitat modifiers that are dissimilar in size; e.g., rabbits and harvester ants in oak communities (Dhillion 1999), and phytophagous insects and deer in grasslands (Ritchie et al. 1998). Our experiment explored the effects of two obvious (abundant, relatively large, highly visible) epibenthic invertebrates, but a number of less apparent (small, buried) sediment infauna have the potential to control features such as sediment stability, oxygenation, and nutrient dynamics (Emmerson et al. 2001). We cannot assume a priori that large or obvious species are more influential than small or cryptic ones in controlling structure and processes in these or other systems.

In summary, our manipulative experiment showed that both *Pachygrapsus crassipes* and *Cerithidea californica* strongly influenced the physical structure, community structure, and nutrient and biomass pools of a transplanted *S. virginica* marsh, with additive, complimentary, and opposing effects all contributing to the resulting suite of ecosystem characteristics depending on species presence or co-occurrence. Several unexpected effects with both species present (e.g., complete removal of macroalgae, negative effects on pickleweed canopies at low elevations) support the use of manipulative experiments to reveal the complex results of species co-occurrence. We suggest that there is a need for greater experimental inquiry into the role of fauna and faunal assemblages on structural and functional features of both restored and natural habitats.

References

Augustine DJ, Frelich LE, Jordon PA (1998) Evidence for two alternate stable states in an ungulate grazing system. Ecol Appl 8:1260–1269

Bakker ES, Olff H, Boekhoff M, Gleichman JM, Berendse F (2004) Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. Oecologia 138:91–101

Bertness MD (1985) Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. Ecology 66:1042–1055

Boag G, Yeates GW (2001) The potential impact of the New Zealand flatworm, a predator of earthworms, in Western Europe. Ecol Appl 11:1276–1286

Bohlen PJ, Groffman PM, Fahey TJ, Fisk MC, Suarez E, Pelletier DM, Fahey RT (2004) Ecosystem consequences of exotic earthworm invasion of north temperate forests. Ecosystems 7:1–12

Bruno JF, Bertness MD (2001) Habitat modification and facilitation in benthic marine communities. In: Bertness MD, Gaines SD, Hay ME (eds) Marine community ecology. Sinauer, Sunderland, pp 201–218

Buchmann SL, Nabhan GP (1996) The forgotten pollinators. Island Press, Washington

Byers JE (2000) Effects of body size and resource availability on dispersal in a native and a non-native estuarine snail. J Exp Mar Biol Ecol 248:133–150

Cadée GC (2001) Sediment dynamics by bioturbating organisms. In: Reise K (ed) Ecological comparisons of sedimentary shores. Ecological studies 151. Springer, Berlin Heidelberg New York, pp 127–148

Chapin FS, Walker BH, Hobbs RJ, Hooper JU, Lawton JH, Sala OE, Tilman D (1997) Biotic controls on the functioning of ecosystems. Science 277:500–503

Coleman FC, Williams SL (2002) Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends Ecol Evol 17:40–44

Crooks JA (1998) Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. Mar Ecol Prog Ser 162:137–152

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166

Crowl TA, McDowell WH, Covich AP, Johnson SL (2001) Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. Ecology 82:775–783

Dhillion S (1999) Environmental heterogeneity, animal disturbances, microsite characteristics, and seedling establishment in a *Quercus havardii* community. Rest Ecol 7:399–406

Duffy JE (2002) Biodiversity and ecosystem function: the consumer connection. Oikos 99:201–219

Duffy JE, Richardson JP, Canuel EA (2003) Grazer diversity effects on ecosystem functioning in seagrass beds. Ecol Lett 6:637–645

Edwards CA (2004) Earthworm ecology, 2nd edn. CRC, Boca Raton

Emmerson M, Huxham M (2002) How can marine ecology contribute to the biodiversity-ecosystem functioning debate? In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and ecosystem functioning. Oxford, New York, pp 139–146

Emmerson MC, Solan M, Emes C, Paterson DM, Raffaelli D (2001) Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. Nature 411:73–77

Ernest SKM, Brown JH (2001) Homeostasis and compensation: the role of species and resources in ecosystem stability. Ecology 82:2118–2132

Flecker AS (1996) Ecosystem engineering by a dominant detritivore in a diverse tropical stream. Ecology 77:1845–1854

Fong P, Desmond JS, Zedler JB (1997) The effect of a horn snail on *Ulva expansa* (Chlorophyta): consumer or facilitator of growth? J Phycol 33:353–359

Fournier C, Rosenheim JA, Brodeur J, Laney LO, Johnson MW (2003) Herbivorous mites as ecological engineers: indirect effects on arthropods inhabiting papaya foliage. Oecologia 135:442–450

Frank DA, Juns MM, Guido DR (2002) Consumer control of grassland plant production. Ecology 83:602–606

Gerdol V, Hughes RG (1994) Effect of *Corophium volutator* on the abundance of benthic diatoms, bacteria and sediment stability in two estuaries in southeastern England. Mar Ecol Prog Ser 114:109–115

Grant J, Bathmann UV, Mills EL (1986) The interaction between diatom films and sediment transport. Estuar Coast Shelf Sci 23:225–238

Heck KL Jr, Pennock JR, Valentine JF, Coen LD, Sklenar SA (2000) Effects of nutrient enrichment and small predator density on seagrass ecosystems: an experimental assessment. Limnol Oceanogr 45:1041–1057

Hiatt RW (1948) Biology of the lined shore crab, *Pachygrapsus crassipes* Randall. Pac Sci 2:134–213

Hunt-Joshi TR, Blossey B, Root RB (2004) Root and leaf herbivory on *Lythrum salicaria*: implications for plant performance and communities. Ecol Appl 14:1574–1589

Jensen GC (1995) Pacific coast crabs and shrimps, 2nd edn. Sea Challengers, Petaluma

Jones CG, Lawton JH (1995) Linking species and ecosystems. Chapman and Hall, New York

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957

Lee RF, Dornselif B, Gonsoulin F, Tenore K, Hanson R (1981) Fate and effects of a heavy fuel oil spill on a Georgia salt marsh. Mar Environ Res 5:125–143

Lill JT, Marquis RJ (2003) Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. Ecology 84:682–690

Lorenzen CJ (1967) Determination of chlorophyll and pheo-pigments: spectrophotometric equations. Limnol Oceanogr 12:343–346

Machicote M, Branch LC, Villarreal D (2004) Burrowing owls and burrowing mammals: are ecosystem engineers interchangeable as facilitators? Oikos 106:527–535

Mahall BE, Park RB (1976) The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay III Soil aeration and tidal immersion. J Ecol 64:811–820

McCloy MJ (1979) Population regulation in the deposit-feeding mesogastropod *Cerithidea californica* as it occurs in a San Diego salt marsh. MS Thesis, San Diego State University, San Diego

Morris RJ, Abbott DP, Haderlie EC (1980) Intertidal invertebrates of California. Stanford University Press, Stanford

Page HM (1997) Importance of vascular plant and algal production to macro-invertebrate consumers in a southern California salt marsh. Estuar Coast Shelf Sci 45:823–834

Palmer MA, Ambrose RF, Poff NL (1997) Ecological theory and community restoration ecology. Rest Ecol 5:291–300

Parsons TR, Strickland JDH (1963) Discussion of spectrophotometric determination of marine plant pigments with revised equations for ascertaining chlorophylls and carotenoids. J Mar Res 21:155–163

Paterson DM (1994) Microbiological mediation of sediment structure and behaviour. In: Stal LJ, Caumette P (eds) Microbial Mats. Nato ASI Series, vol G35. Springer, Berlin Heidelberg New York

Pennings SC, Callaway RM (2000) The advantages of clonal integration under different ecological conditions: a community-wide test. Ecology 81:709–716

Peterson BJ, Heck KL (1999) The potential for suspension feeding bivalves to increase seagrass productivity. J Exp Mar Biol Ecol 240:37–52

Pringle CM, Hemphill N, McDowell WH, Bednarek A, March JG (1999) Linking species and ecosystems: different biotic assemblages cause interstream differences in organic matter. Ecology 80:1860–1872

Quammen ML (1984) Predation by shorebirds, fish, and crabs on invertebrates in intertidal mudflats: an experimental test. Ecology 65:529–537

Race MS (1982) Competitive displacement and predation between introduced and native mud snails. Oecologia 54:337–347

Raffaelli D, Emmerson M, Solan M, Biles C, Paterson D (2003) Biodiversity and ecosystem processes in shallow coastal waters: an experimental approach. J Sea Res 49:133–141

Reed CC (1995) Insects surveyed on flowers in native and reconstructed prairies (Minnesota). Restorat Manag Notes 13:210–213

Richardson JS, Jackson MJ (2002) Aquatic invertebrates. In: Perrow MR, Davey AJ (eds) Handbook of ecological restoration. Cambridge University Press, Cambridge, pp 300–323

Richardson AMM, Swain R, Wong V (1998) Relationship between the crustacean and molluscan assemblages of Tasmanian saltmarshes and the vegetation and soil conditions. Mar Freshwater Res 49:785–799

Riera P, Stal LJ, Nieuwenhuize J, Richard P, Blanchard G, Gentil F (1999) Determination of food sources for benthic invertebrates in a salt marsh (Aiguillon Bay, France) by carbon and nitrogen stable isotopes: importance of locally produced sources. Mar Ecol Prog Ser 187:301–307

Ritchie ME, Tilman D, Knops JMH (1998) Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology 79:165–177

Schläpfer F, Schmid B (1999) Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. Ecol Appl 9:893–912

Sousa WP (1993) Size-dependent predation on the salt-marsh snail *Cerithidea californica* Haldeman. J Exp Mar Biol Ecol 166:19–37

Statzner B, Fievet E, Champagne JY, Morel R, Herouin E (2000) Crayfish as geomorhpic agents and ecosystem engineers: biological behavior affects sand and gravel erosion in experimental streams. Limnol Oceanogr 45:1030–1040

Sullivan MJ (1999) Applied diatom studies in estuaries and shallow coastal environments. In: Stoermer EF, Smol JP (eds) The diatoms: applications for the environmental and earth sciences. Cambridge University Press, Cambridge, pp 334–351

Talley TS, Levin LA (1999) Macrofaunal succession and community structure in *Salicornia* marshes of southern California. Estuar Coast Shelf Sci 49:713–731

Talley TS, Crooks JA, Levin LA (2001) Habitat utilization and alteration by the invasive burrowing isopod, *Sphaeroma quoyanum*, in California salt marshes. Mar Biol 138:561–573

Thompson L, Thomas CD, Radley JMA, Williamson S, Lawton JH (1993) The effect of earthworms and snails in a simple plant community. Oecologia 95:171–178

Underwood GJC (1997) Microalgal colonization in a saltmarsh restoration scheme. Estuar Coast Shelf Sci 44:471–481

Whicker AD, Detling JK (1988) Ecological consequences of prairie dog disturbances. BioScience 38:778–785

Whitlach RB, Obrebski S (1980) Feeding selectivity and coexistence in two deposit-feeding gastropods. Mar Biol 58:219–225

Widdecombe D, Austen MC (1998) Experimental evidence for the role of *Brissopsis lyrifera* as a critical species in the maintenance of benthic diversity and the modification of sediment chemistry. J Exp Mar Biol Ecol 228:241–255

Wilby A, Shachak M, Boeken B (2001) Integration of ecosystem engineering and trophic effects of herbivores. Oikos 92:436–444

Willason SW (1981) Factors influencing the distribution and coexistence of *Pachygrapsus crassipes* and *Hemigrapsus oregonensis* (Decapoda:Grapsidae) in a California salt marsh. Mar Biol 64:125–133

Zedler JB, Callaway JC, Desmond JS, Vivian-Smith G, Williams G, Sullivan G, Brewster AE, Bradshaw BK (1999) Californian salt-marsh vegetation: an improved model of spatial pattern. Ecosystems 2:19–35

Zedler JB, Callaway JC, Sullivan GD (2001) Declining biodiversity: why species matter and how their functions might be restored in Californian tidal marshes. Bioscience 51:1005–1017