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# Disturbance facilitates the coexistence of antagonistic ecosystem engineers in California estuaries

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**Abstract.** Ecological theory predicts that interactions between antagonistic ecosystem engineers can lead to local competitive exclusion, but disturbance can facilitate broader coexistence. However, few empirical studies have tested the potential for disturbance to mediate competition between engineers. We examined the capacity for disturbance and habitat modification to explain the disjunct distributions of two benthic ecosystem engineers, eelgrass *Zostera marina* and the burrowing ghost shrimp *Neotrypaea californiensis*, in two California estuaries. Sediment sampling in eelgrass and ghost shrimp patches revealed that ghost shrimp change benthic biogeochemistry over small scales (centimeters) but not patch scales (meters to tens of meters), suggesting a limited capacity for sediment modification to explain species distributions. To determine the relative competitive abilities of engineers, we conducted reciprocal transplantations of ghost shrimp and eelgrass. Local ghost shrimp densities declined rapidly following the addition of eelgrass, and transplanted eelgrass expanded laterally into the surrounding ghost shrimp-dominated areas. When transplanted into eelgrass patches, ghost shrimp failed to persist. Ghost shrimp were also displaced from plots with structural mimics of eelgrass rhizomes and roots, suggesting that autogenic habitat modification by eelgrass is an important mechanism determining ghost shrimp distributions. However, ghost shrimp were able to rapidly colonize experimental disturbances to eelgrass patch edges, which are common in shallow estuaries. We conclude that coexistence in this system is maintained by spatiotemporally asynchronous disturbances and a competition–colonization trade-off: eelgrass is a competitively superior ecosystem engineer, but benthic disturbances permit the coexistence of ghost shrimp at the landscape scale by modulating the availability of space.

**Key words:** antagonism; bioturbation; competition; disturbance; ecosystem engineering; eelgrass; estuary; ghost shrimp; habitat modification; *Neotrypaea californiensis*; sediment biogeochemistry; *Zostera marina*.

## INTRODUCTION

A fundamental challenge in ecology is to explain the coexistence of species competing for limited resources (Gause 1932, Hutchinson 1961). Diverse assemblages of primary producers and consumers may coexist despite intense competition for space (Paine 1966, Connell 1978), even when strong competitors are organisms that create or modify habitat (ecosystem engineers [Jones et al. 1994]). For ecosystem engineers that modify the same abiotic resource in contrasting ways, ecological theory predicts that antagonism can arise and result in local exclusion of inferior competitors (Hastings et al. 2007). However, general competition models show that inferior competitors may persist at the landscape scale when disturbances remove competitively dominant species or

change the availability of limiting resources (Sousa 1979, Roxburgh et al. 2004). Disturbances that are asynchronous in space and time, or disproportionately affect certain species (Chesson and Huntly 1997), should have a particular capacity for facilitating coexistence, such as in competition–colonization trade-off models (e.g., Levin and Paine 1974). Despite these theoretical advances, few studies have examined the causes and consequences of antagonism between ecosystem engineers or tested the potential for disturbance to mediate such competition (Jones et al. 2010).

Estuaries are ideal systems for testing how disturbance influences competition between ecosystem engineers because they are home to many different types of habitat-modifying species living within or emerging from the sediment, such as rooted plants, sessile invertebrates, and burrowing infauna (Jones et al. 1994). Shallow estuaries are also characterized by numerous natural (e.g., waves, erosion, sedimentation) and anthropogenic (e.g., dredging, vessel impacts, fishing, aquaculture) benthic disturbances that vary

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greatly in their frequency, spatial extent, and magnitude of impact (Walker et al. 2006).

We explored the potential for antagonistic ecosystem engineering and disturbance to explain disjunct distributions of two benthic species, eelgrass *Zostera marina* L. and the ghost shrimp *Neotrypaea californiensis* Dana 1854 (see Plate 1 and Appendix A: Fig. A1), which are conspicuous soft-sediment engineers that co-occur in estuaries along the west coast of North America from southern Alaska, USA, to Baja California Sur, Mexico (MacGinitie 1934, McRoy 1968). Eelgrass produces a dense canopy of leaves and a thick mat of rhizomes and roots within surface sediments. These biogenic structures alter hydrodynamics (Abdelrhman 2003), sediment accretion (Bos et al. 2007), belowground architecture (Marbà and Duarte 1998), and biogeochemical fluxes (Marbà et al. 2006). Ghost shrimp are highly mobile burrowers, constructing complex networks of tunnels and chambers up to 90 cm deep (Dumbauld et al. 1996), and living in dense aggregations up to 500 individuals/m<sup>2</sup> (Posey 1986a). Continuous bioturbation by burrowing shrimps changes sediment resuspension (Siebert and Branch 2006), granulometry (Ziebis et al. 1996), and biogeochemistry (Webb and Eyre 2004). Many seagrasses are sensitive to sediment burial (Cabaço et al. 2008), and eelgrass growth can depend on sediment nitrogen (Williams and Ruckelshaus 1993). However, it is also possible that seagrass rhizomes and roots inhibit burrowing infauna (Orth et al. 1984). Thus, antagonistic modification of the benthic environment by eelgrass and ghost shrimp may result in competition for space, but disturbance may foster their apparent landscape-scale coexistence within California estuaries.

We empirically assessed the potential for disturbance to mediate the coexistence of antagonistic ecosystem engineers by addressing three sequential questions in this system: (1) Are eelgrass and ghost shrimp antagonistic ecosystem engineers? (2) What mechanisms explain their inverse spatial relationship? (3) Does disturbance facilitate coexistence? We first quantified observations of species distributions and measured habitat modification. Next, we assessed relative competitive abilities through reciprocal transplantation experiments. Lastly, we evaluated the capacity for benthic perturbations to mediate landscape-scale coexistence by conducting two disturbance experiments.

## METHODS

### *Study regions*

Our study took place from June 2010 to June 2012 at Tomales Bay (38°10' N, 122°54' W) and Mission Bay (32°46' N, 117°14' W), located in northern and southern California, USA, respectively (Fig. 1A, B). Although separated by ~800 km, both estuaries exhibit typical mediterranean seasonality in temperature and salinity, with winter freshwater inflow and hypersalinity during long, dry summers (Largier et al. 1997). Eelgrass and ghost shrimp are abundant throughout both bays in

intertidal and shallow-subtidal areas where sandy beaches or mudflats are present.

### *Spatial relationship and sediment modification*

To quantify the spatial relationship between eelgrass and ghost shrimp, we conducted intertidal surveys (wading at low tide) at Tomales Bay in summer 2010 and intertidal/subtidal surveys (scuba diving at high tide) at Mission Bay in summer 2012 (subtidal areas at Tomales Bay could not be accessed due to logistical constraints). At Tomales Bay, we surveyed three sites along the eastern shore: Hamlet, MacDonald, and Cypress Grove (Fig. 1A); at Mission Bay, we surveyed one site: Mariner's Cove (Fig. 1B). At each site, we haphazardly chose three alongshore locations and conducted 50-m transects from the first co-occurrence of eelgrass and ghost shrimp along a depth gradient towards deeper water. Every 3 m along the transect line, we counted eelgrass shoots and ghost shrimp burrow mounds (i.e., burrow surface openings) in a 625-cm<sup>2</sup> quadrat. Using burrow surface openings as a proxy for ghost shrimp abundance is a rapid and nondestructive method that has been experimentally validated (Posey 1986b, Dumbauld and Wyllie-Echeverria 2003, Butler and Bird 2007). Burrow mounds scale linearly with ghost shrimp abundance because each ghost shrimp excavates a separate Y-shaped burrow, with two surface openings converging to a vertical network of tunnels and chambers (MacGinitie 1934, Griffis and Chavez 1988). If abandoned, burrows and their surface openings soon collapse (Swinbanks and Luternauer 1987, Dumbauld et al. 1996).

To characterize how eelgrass and ghost shrimp modify the sediments they occupy, we measured biogeochemical parameters over both small and large spatial scales (i.e., centimeters vs. meters to tens of meters; see Appendix B: Fig. B1) at Hamlet during summer 2010. To determine small-scale impacts of bioturbation, we collected sediment cores (1.5 cm diameter × 5 cm deep) from paired burrow mounds and adjacent non-mound areas (i.e., coring 0–1.5 cm and 3–4.5 cm from the burrow entrance, respectively;  $n = 12$  pairs). To determine larger, patch-scale effects, we also collected sediment samples from within 12 haphazardly selected (unpaired) eelgrass and ghost shrimp patches (defined here as discrete areas dominated by eelgrass or ghost shrimp, generally on the range of 400 cm<sup>2</sup> to >100 m<sup>2</sup> [see Plate 1]). Sediments were frozen and later analyzed for the percentage of fine sediments (wet-sieving at 63 μm), organic matter (loss-on-ignition at 550°C for 24 h), and sediment ammonium (porewater + adsorbed) concentration (spectrophotometrically following extraction in KCl [Koroleff 1976]).

We tested for differences in sediment parameters over small scales using paired-samples *t* tests and over patch scales using independent-samples *t* tests. Prior to performing *t* tests, as well as all statistical analyses used in other experiments (see following experiments), we

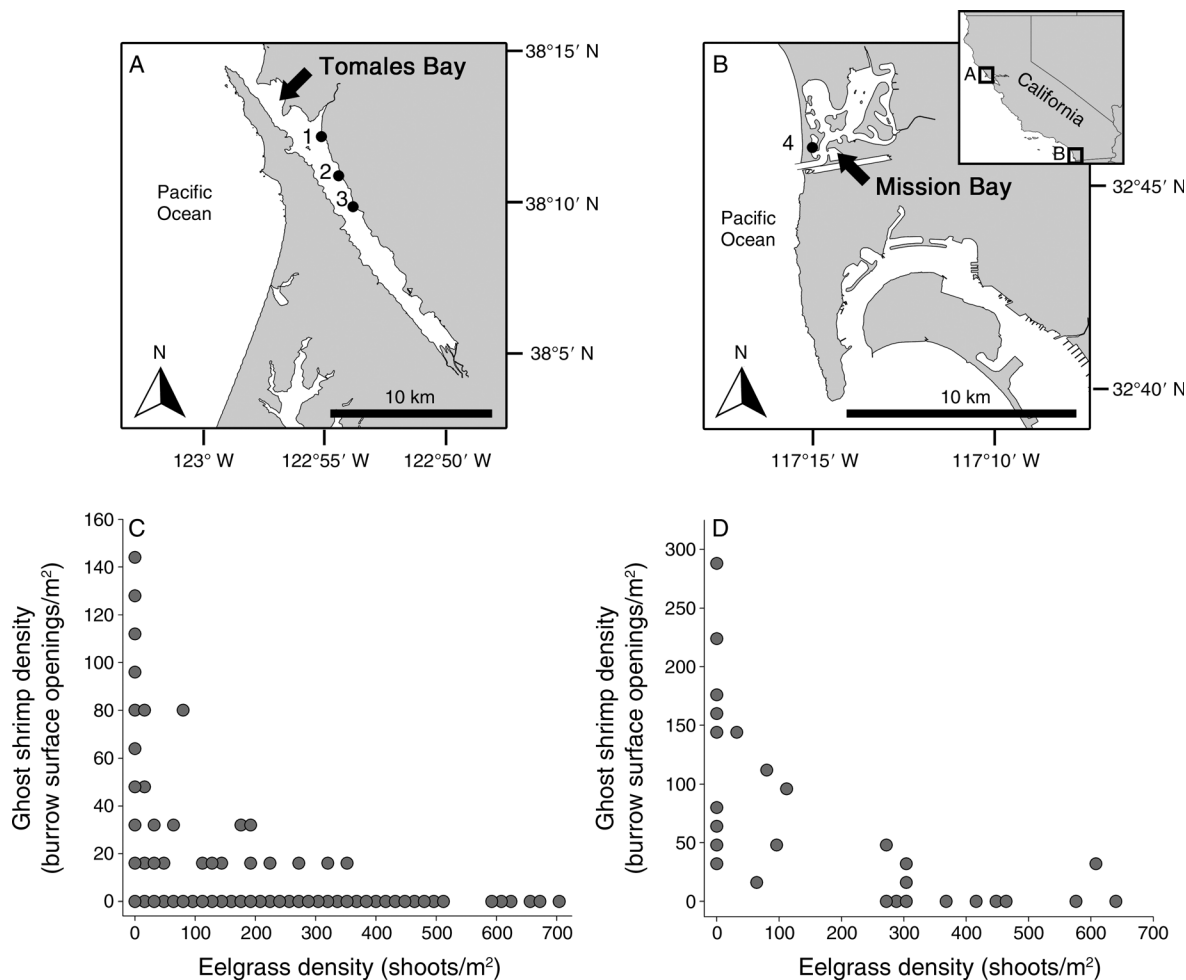


FIG. 1. Study sites at (A) Tomales Bay and (B) Mission Bay. Numbers indicate sites: (1) Hamlet, (2) MacDonald, (3) Cypress Grove, and (4) Mariner's Cove. (C) and (D) Relationship between densities of eelgrass and ghost shrimp at (C) Tomales Bay and (D) Mission Bay. Surveys were conducted at all sites; measurements of sediment modification and all experiments took place at Hamlet.

tested for homogeneity of variances using Cochran's test and used normal probability plots to test for normality. When necessary, we log-transformed ( $\ln[x + 1]$ ) data to meet the assumptions of parametric analyses.

#### *Reciprocal transplantation experiments*

In June 2010, we transplanted eelgrass into ghost shrimp patches to determine (1) if eelgrass could persist in ghost shrimp patches, (2) whether the introduction of eelgrass affected the abundance of ghost shrimp, and (3) how sediment biogeochemistry changed following the introduction of eelgrass. This experiment and all others (see following experiments) were conducted at one site, Hamlet, in Tomales Bay. We transplanted eelgrass as intact rhizomes into square plots of 354 leaf shoots/m<sup>2</sup> (the mean density at Tomales Bay) and ~100% cover. To prevent dislodgment by hydrodynamic forces, we anchored each rhizome using V-shaped bamboo staples (Davis and Short 1997). To determine whether the effect

of eelgrass on ghost shrimp and sediment biogeochemistry depends on patch size, we conducted transplantations at four spatial scales: 0.02 m<sup>2</sup>, 0.09 m<sup>2</sup>, 0.25 m<sup>2</sup>, and 1 m<sup>2</sup> ( $n = 5$ , except for the loss of one 0.09-m<sup>2</sup> plot). Small eelgrass patches such as these are common at the areas in which we worked, and although eelgrass exists in larger patches as well, these were not feasible to create. We also designated eelgrass and ghost shrimp control plots (1 m<sup>2</sup>;  $n = 5$ ), which were unmanipulated except for the addition of bamboo staples. Plots were located in haphazardly selected ghost shrimp patches 25–30 m from shore (about 0.3 m below mean lower low water), spaced 2–3 m apart, and randomly assigned treatments.

We quantified eelgrass and ghost shrimp persistence through time by sampling plots during low tides over the course of seven months (3, 7, and 30 weeks after transplantation). Eelgrass abundance was visually estimated as percentage of cover (to the nearest 100 cm<sup>2</sup>).

At 30 weeks, we also quantified lateral eelgrass expansion into the surrounding ghost shrimp patches by measuring the maximum distance of rhizome growth from the original transplantation edge. Ghost shrimp density was estimated by counting surface burrow openings within a haphazardly placed 400-cm<sup>2</sup> quadrat (all burrows were counted in 0.02-m<sup>2</sup> plots). To determine if sediment biogeochemistry was affected by transplantation, we collected five sediment cores from haphazard locations in each plot after 3 and 30 weeks, and processed sediment samples as described previously. We tested for differences in response variables using separate analyses of variance (ANOVAs; one per sampling period). For this experiment and others where ANOVAs revealed strong evidence of a treatment effect on dependent variables ( $P < 0.05$ ), we made post-hoc pairwise comparisons using Tukey's honestly significant difference test and adjusted post-hoc comparisons for unbalanced data using the Tukey-Kramer method (Kramer 1956).

For our second transplantation experiment, we tested (1) whether adult ghost shrimp could establish burrows in eelgrass patches, penetrating past rhizomes and roots, and if so (2) how they persisted over time in eelgrass patches relative to unvegetated sediments. Therefore, in April 2012, we haphazardly chose eight separate eelgrass patches with adjacent unvegetated sediment that lacked burrows (all patches located ~20 m from shore and separated by >10 m). At each separate patch ecotone, we established two plots (25 cm diameter): one on the eelgrass side and one on the unvegetated side, with all plots >1 m from the edge. Then, elsewhere at the site, we extracted 16 ghost shrimp from their burrows using a hand pump and transplanted 2 ghost shrimp to each plot ( $n = 8$  pairs of plots). To allow ghost shrimp to burrow in the absence of predation (e.g., from shorebirds), we protected each pair of ghost shrimp for 24 h with a galvanized-wire cage (25 cm diameter  $\times$  30 cm high; mesh size = 1.3 cm), buried to 15 cm depth. All ghost shrimp began burrowing immediately upon release. We assessed ghost shrimp persistence by counting surface burrow openings within each plot 24 hours and 1 month after transplantation. We tested for differences in surface burrow mound density using separate paired-samples  $t$  tests (one per sampling period).

#### *Rhizome–root structural mimic experiment*

Findings from reciprocal transplantation experiments suggested that eelgrass has strong and rapid negative effects on local ghost shrimp abundance. We hypothesized that eelgrass rhizomes and roots exclude ghost shrimp by impeding the formation or maintenance of surface openings or other burrow structures (Brenchley 1982), or otherwise interfering with shrimp behavior. To evaluate this possibility, it was necessary to isolate the effects of belowground biogenic structure from other potential eelgrass impacts, such as changes to hydrodynamics (Abdelrhman 2003). To accomplish this, we

created structural mimics of eelgrass rhizomes (see Appendix C: Fig. C1) collected from high- and low-density areas (0.25 m<sup>2</sup> with 884 and 294 shoots/m<sup>2</sup>, respectively) by tracing rhizomes on plywood and carving these out using a palm router with 3.175-mm hemispherical bit. We created castings within the separate high-density and low-density molds using marine-grade polyurethane adhesive (3M Marine Fast Cure Adhesive Sealant 5200, 3M Company, St. Paul, Minnesota, USA), which dries to a durable, flexible, negatively buoyant solid. We simulated roots using nylon fibers (2–5 cm long) attached to rhizome castings with water-resistant spray adhesive (3M Hi-Strength 90 Spray Adhesive). We allowed generous curing times and soaked mimics in flowing seawater for 72 hours prior to field deployment.

Next, in April 2012, we established circular plots (0.25 m<sup>2</sup>; located 15–20 m from shore and spaced >2 m apart) within haphazardly selected ghost shrimp patches and randomly applied one of four treatments: true (unmanipulated) control, procedural control, low-density mimic, and high-density mimic ( $n = 6$ , except for the loss of two high-density mimics). We planted rhizome–root mimics 1–3 cm deep and secured them to the sediment with five metal garden stakes. For procedural control plots, we planted a high-density mimic, removed it, and added five stakes. To determine treatment impacts on ghost shrimp abundance, we counted surface burrow openings within plots before the manipulation, and one and two months post-manipulation. We tested for differences in ghost shrimp density using separate ANOVAs (one per sampling period).

#### *Eelgrass disturbance experiments*

To determine the effect of benthic perturbations on the coexistence of eelgrass and ghost shrimp, we conducted two eelgrass disturbance experiments. Ghost shrimp migrate laterally into new habitat by burrowing or by crawling along the sediment surface (Posey 1986b, Harrison 1987). Additionally, ghost shrimp colonization can occur through the recruitment of planktonic postlarvae (Feldman et al. 1997). In an attempt to distinguish among these mechanisms and test the importance of the spatial pattern of disturbance, we undertook (1) an eelgrass patch-interior disturbance experiment to test for ghost shrimp colonization via postlarval settlement, and (2) an eelgrass patch-edge disturbance experiment to test for lateral ghost shrimp colonization.

For the patch-interior disturbance experiment, we removed eelgrass from the center of moderately sized patches ( $\geq 5.25$  m diameter, i.e., with at least 3 m of eelgrass surrounding disturbances). We excavated all vegetation (shoots, rhizomes, and roots) by hand and were careful not to remove sediments or modify sediment elevation. We created patch-interior disturbances in July 2010 to provide the greatest potential for recruitment of postlarvae, because ghost shrimp settle-



PLATE 1. Intertidal and shallow subtidal areas in several California estuaries are characterized by patchy distributions (left) of eelgrass (*Zostera marina*) and burrowing ghost shrimp (*Neotrypaea californiensis*; indicated by burrow surface openings) with abrupt ecotone transitions (right). Photo taken at Mariner's Cove in Mission Bay (San Diego, California, USA). See Appendix A: Fig. A1 for color version. Photo credit: K. A. Hovel.

ment peaks in late summer through early fall (Dumbauld et al. 1996). We hypothesized ghost shrimp would be more likely to colonize larger disturbances than smaller ones because of the greater area of unoccupied substrate and longer duration for which that area was unvegetated (Petraitis and Latham 1999). Therefore, we also included the spatial scale of disturbance as a factor, producing square removals of 0.02 m<sup>2</sup>, 0.09 m<sup>2</sup>, 0.25 m<sup>2</sup>, 1 m<sup>2</sup>, and 2.25 m<sup>2</sup> ( $n = 5$ , except for the loss of one 2.25-m<sup>2</sup> plot due to damage from drifting oyster aquaculture bags), which correspond to the size of common eelgrass disturbances (Walker et al. 2006). We selected eelgrass patches haphazardly (20–30 m from shore and separated by >3 m at their nearest point) and assigned treatments randomly, including undisturbed eelgrass and ghost shrimp control plots (1 m<sup>2</sup>;  $n = 5$ ). We assessed eelgrass recovery and ghost shrimp colonization through time by sampling plots during low tides over the course of nine months (3, 7, 30, and 43 weeks after disturbance), measuring eelgrass abundance, ghost shrimp density, and sediment biogeochemistry as described previously. We tested for differences in all response variables using separate ANOVAs (one per sampling period).

For the eelgrass patch-edge disturbance experiment (April–June 2012) we utilized a randomized complete block design. We haphazardly chose 12 eelgrass patches (all located 20–30 m from shore and >10 m apart) and established a block at each patch ( $n = 12$ ). Each block (1 × 1 m) straddled the ecotone and contained four square plots (0.25 m<sup>2</sup>), each with a separate treatment (see diagram in Appendix D). On the eelgrass side of the block, we randomly designated one plot as an eelgrass control and the other plot as an eelgrass disturbance, removing eelgrass as just described. On the ghost shrimp side of the block, both plots served as controls: one adjacent to the eelgrass control plot (“ghost shrimp

control 1”) and the other bordering the eelgrass disturbance plot (“ghost shrimp control 2”). To evaluate ghost shrimp colonization, we measured burrow surface openings within each plot before the disturbance, and four and eight weeks post-disturbance. We tested for differences in ghost shrimp density using separate two-way ANOVAs (treatment and blocking factors as main effects) for each sampling period.

## RESULTS

### *Spatial relationship and sediment modification*

Confirming our early observations (see Plate 1), surveys at Tomales Bay and Mission Bay revealed a strong inverse relationship between ghost shrimp and eelgrass densities (Fig. 1C, D). Ghost shrimp density declined precipitously between about 50 to 100 shoots/m<sup>2</sup> and few ghost shrimp burrows were present beyond ~300 shoots/m<sup>2</sup>.

Sediment biogeochemical parameters displayed consistent differences over small spatial scales but not patch scales (Appendix B). Sediments collected from burrow mounds contained less fine sediment ( $t_{10} = 2.413$ ,  $P = 0.036$ ), organic matter ( $t_9 = 3.131$ ,  $P = 0.012$ ), and ammonium ( $t_{11} = 8.616$ ,  $P < 0.001$ ) than adjacent non-burrow mound sediments. In contrast, there were no differences for any of these parameters in sediments collected from haphazardly selected ghost shrimp and eelgrass patches (Appendix E).

### *Reciprocal transplantation experiments*

Within the first three weeks, transplanted eelgrass declined slightly from 100% cover (likely due to transplantation shock [Zimmerman et al. 1995]), but nearly all transplantations persisted in ghost shrimp patches throughout the experiment except for the smallest size (0.02 m<sup>2</sup>), which died out between 7 and

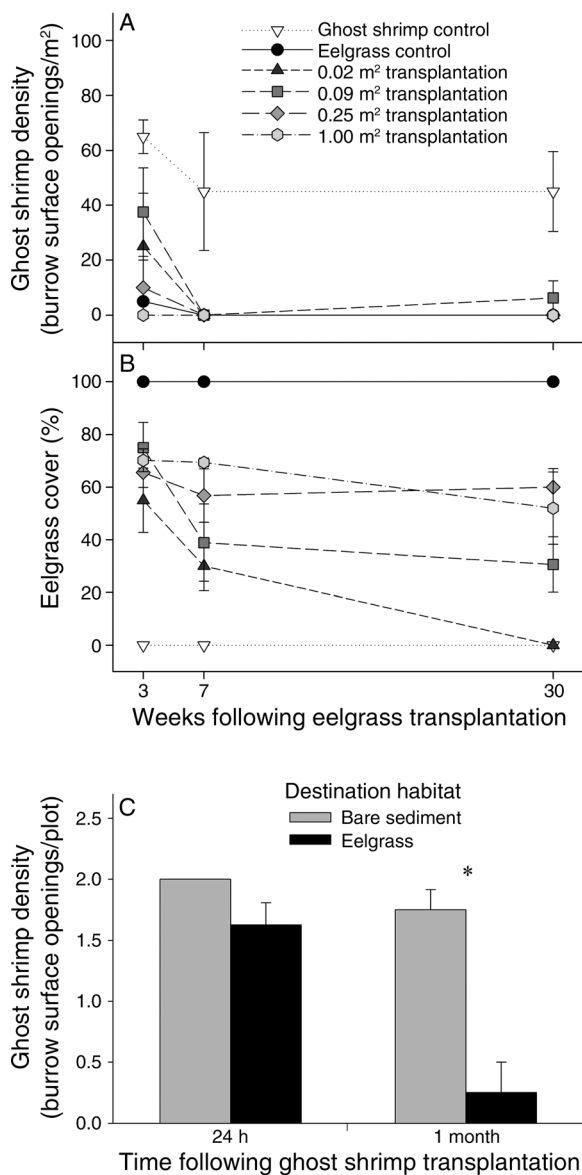


FIG. 2. Results from the reciprocal transplantation experiments. Time courses are shown as (A) ghost shrimp density (mean  $\pm$  SE), measured as burrow surface openings/m<sup>2</sup>, and (B) eelgrass cover (%) following transplantation of eelgrass into ghost shrimp patches. (C) Bars show ghost shrimp density (mean  $\pm$  SE), measured as burrow surface openings/plot, following transplantation of ghost shrimp into bare sediment or adjacent eelgrass patches after 24 hours and one month. In (C), the asterisk indicates a significant difference ( $P < 0.05$ ) between treatments within the sampling period.

30 weeks (Fig. 2B, Table 1; Appendix F). Eelgrass cover in transplantations was generally less than eelgrass control plots but more than ghost shrimp control plots. At the end of the experiment, surviving eelgrass transplantations had expanded into the surrounding ghost shrimp patches at a rate of  $39.3 \pm 25.6$  cm/yr (mean  $\pm$  SD).

Transplanted eelgrass had rapid negative impacts on local ghost shrimp abundances (Fig. 2A, Table 1; Appendix F). Prior to manipulation, ghost shrimp density was apparently uniform among all eelgrass transplantation plots. Three weeks following transplantation, ghost shrimp density in smaller transplantations (0.09 m<sup>2</sup> and 0.02 m<sup>2</sup>) was no different than in ghost shrimp control plots ( $P = 0.794$  and  $P = 0.108$ , respectively), but ghost shrimp density in larger transplantations (1.00 m<sup>2</sup> and 0.25 m<sup>2</sup>) was lower than that of ghost shrimp control plots ( $P = 0.003$  and  $P = 0.019$ , respectively). However, after seven weeks all transplantation plots, regardless of size, had lower ghost shrimp densities than ghost shrimp control plots ( $P < 0.001$ ). This pattern persisted through 30 weeks. In contrast, sediment parameters did not differ among treatments at 3 or 30 weeks (Appendix F), suggesting that temporal patterns of ghost shrimp density were not caused by changes to sediment biogeochemistry.

In the ghost shrimp transplantation experiment, nearly all transplanted ghost shrimp successfully burrowed within 24 hours (Fig. 2C), and there was no difference in the density of burrow surface openings between plots in eelgrass and bare-sediment patches ( $t_7 = 2.049$ ,  $P = 0.080$ ). However, after one month eelgrass plots had fewer burrow mounds than bare-sediment plots ( $t_7 = 3.969$ ,  $P = 0.005$ ).

#### Rhizome-root structural mimic experiment

Rhizome-root structural mimics caused decreases in ghost shrimp density over time (Fig. 3, Table 1; Appendix G). Ghost shrimp density did not vary among treatments before manipulation ( $P = 0.546$ ). However, after four weeks ghost shrimp density was lower in high-density rhizome-root mimic plots than either true control or procedural control plots ( $P = 0.025$  and  $P = 0.006$ , respectively). After eight weeks, both high-density and low-density rhizome-root mimic plots had lower ghost shrimp density than true control and procedural control plots ( $P < 0.001$ ), but they did not differ from one another ( $P = 0.664$ ). Ghost shrimp density did not differ between true control and procedural control plots after four or eight weeks ( $P = 0.859$  and  $P = 0.843$ , respectively), indicating no effect of the planting procedure.

#### Eelgrass disturbance experiments

In the eelgrass patch-interior disturbance experiment, ghost shrimp generally failed to colonize disturbances of any size (Fig. 4A, Table 1; Appendix H). For all time periods, ghost shrimp density was higher in ghost shrimp control plots than in all other treatments. Eelgrass largely recovered from patch-interior disturbances within 43 weeks (Fig. 4B, Table 1; Appendix H). During the majority of the experiment, eelgrass recovery was uniform: there was no difference in eelgrass cover among different-sized disturbance plots at 3, 7, and 30 weeks following disturbance ( $P \geq 0.092$ ). By 43 weeks,

TABLE 1. Results of ANOVAs testing for effects of the eelgrass transplantation experiment, rhizome–root structural mimic experiment, and eelgrass disturbance experiments on the density of ghost shrimp (burrow surface openings/m<sup>2</sup>) and eelgrass cover (%).

Experiment and source of variation	Ghost shrimp density (burrow surface openings/m <sup>2</sup> )			Eelgrass cover (%)		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Eelgrass transplantation experiment						
Week 3	5, 23	5.30	<b>0.002</b>	5, 23	24.90	<b>&lt;0.001</b>
Week 7	5, 23	13.32	<b>&lt;0.001</b>	5, 23	21.08	<b>&lt;0.001</b>
Week 30	5, 23	8.71	<b>&lt;0.001</b>	5, 23	28.00	<b>&lt;0.001</b>
Rhizome–root structural mimic experiment						
Week 0	3, 18	0.73	0.546			
Week 4	3, 18	6.30	<b>0.004</b>			
Week 8	3, 18	23.76	<b>&lt;0.001</b>			
Eelgrass patch-interior disturbance experiment						
Week 3	6, 27	6.92	<b>&lt;0.001</b>	6, 27	284.75	<b>&lt;0.001</b>
Week 7	6, 27	4.75	<b>0.002</b>	6, 27	125.31	<b>&lt;0.001</b>
Week 30	6, 27	6.09	<b>&lt;0.001</b>	6, 27	18.59	<b>&lt;0.001</b>
Week 43	6, 27	7.57	<b>&lt;0.001</b>	6, 27	282.53	<b>&lt;0.001</b>
Eelgrass patch-edge disturbance experiment						
Week 0						
Treatments	3, 33	26.49	<b>&lt;0.001</b>			
Block	11, 33	2.41	<b>0.025</b>			
Week 4						
Treatments	3, 33	37.18	<b>&lt;0.001</b>			
Block	11, 33	7.51	<b>&lt;0.001</b>			
Week 8						
Treatments	3, 33	27.93	<b>&lt;0.001</b>			
Block	11, 33	2.25	<b>0.036</b>			

Note: *P* values <0.05 are shown in boldface type.

however, eelgrass cover in smaller disturbances (0.02 m<sup>2</sup>, 0.09 m<sup>2</sup>, and 0.25 m<sup>2</sup>) was equivalent to that in eelgrass control plots ( $P \geq 0.552$ ), while larger disturbance plots (1.00 m<sup>2</sup> and 2.25 m<sup>2</sup>) showed slightly less recovery ( $P < 0.001$ ). Sediment parameters in the eelgrass patch-interior disturbance experiment did not differ among treatments at 3, 30, or 43 weeks (Appendix H), agreeing with results from the eelgrass transplantation experiment and from eelgrass and ghost shrimp patch-scale sediment sampling.

In contrast to the patch-interior disturbance experiment, ghost shrimp rapidly colonized disturbances to eelgrass in the patch-edge disturbance experiment (Fig. 4C, Table 1; Appendix I). Before we created disturbances, eelgrass control plots and eelgrass disturbance plots had lower ghost shrimp densities than both adjacent ghost shrimp control plots ( $P < 0.001$ ). Four weeks following disturbance, ghost shrimp density in disturbance plots was higher than eelgrass control plots but lower than both ghost shrimp control plots ( $P \leq 0.002$ ). Eight weeks following disturbance, ghost shrimp density in disturbance plots was still higher than in eelgrass control plots ( $P < 0.001$ ), but no different than either of the ghost shrimp control plots ( $P = 0.299$  and  $P = 0.660$ , for ghost shrimp control 1 and ghost shrimp control 2 plots, respectively).

## DISCUSSION

We found that disturbance and a competition–colonization trade-off facilitate the landscape-scale coexistence of two antagonistic ecosystem engineers in California estuaries. Eelgrass and ghost shrimp modify their surroundings in contrasting ways, resulting in indirect interspecific competition. In the absence of disturbance, eelgrass outcompetes ghost shrimp for

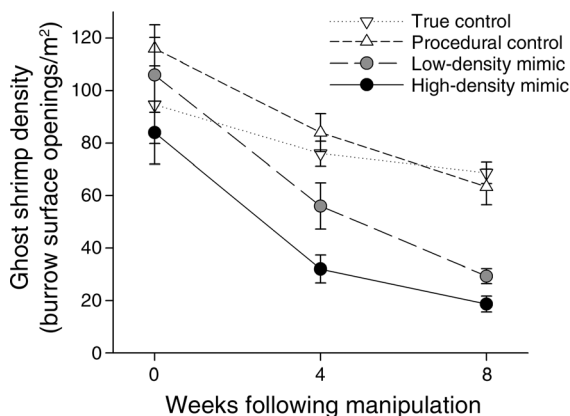


FIG. 3. Results from the rhizome–root structural mimic experiment. Time courses are shown for ghost shrimp density (mean  $\pm$  SE) following manipulation.



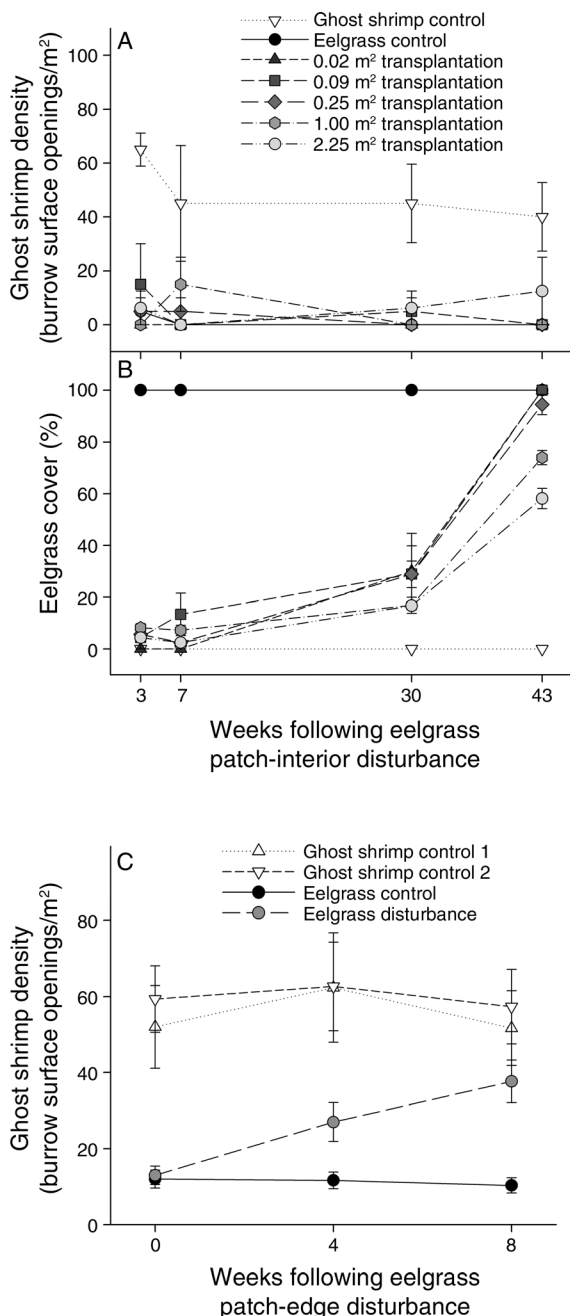


FIG. 4. Results from the eelgrass disturbance experiments. Time courses for (A) ghost shrimp density (mean  $\pm$  SE) and (B) eelgrass cover (%) following removal of eelgrass from patch interiors. (C) Time courses for ghost shrimp density following removal of eelgrass from patch edges. See *Methods: Eelgrass disturbance experiments*.

space through physical alteration of the benthic environment. Ghost shrimp densities declined rapidly following the addition of eelgrass (Fig. 2A) and transplanted eelgrass expanded laterally into the surrounding ghost shrimp-dominated areas. Ghost shrimp

transplanted to eelgrass patches failed to persist (Fig. 2C), and rhizome–root mimics quickly displaced ghost shrimp (Fig. 3). Although eelgrass outcompetes ghost shrimp for space via the production of belowground structure, disturbances to eelgrass patch edges are rapidly colonized by ghost shrimp living in adjacent habitat (Fig. 4C) and provide a spatiotemporal refuge for this inferior competitor.

#### *Ecosystem engineering*

Few studies have attempted to tease apart multiple mechanisms of habitat modification by ecosystem engineers. Our findings support the view that community-level impacts in coastal and estuarine sediments are often stronger for autogenic than allogenic mechanisms (Wilson 1990). For example, structural mimics of polychaete tubes have equivalent impacts on faunal abundance and diversity as live animals (Woodin 1978, Zühlke et al. 1998). Similarly, invasive mussels change native infaunal communities primarily by creating dense mats of byssal threads, not through allogenic changes (Crooks and Khim 1999). These patterns may be partly explained by the greater physical complexity and superior durability of autogenic constructs in unstructured soft-sediment habitats (Jones et al. 1994).

In our study, we found eelgrass to be an effective autogenic ecosystem engineer. The structure of macrophyte rhizomes and roots has been suggested as a major control on benthic marine and estuarine assemblages (Ringold 1979, Orth et al. 1984), but to our knowledge this study represents the first rigorous experimental test of this mechanism free from potentially confounding factors. We posit that the eelgrass rhizome–root matrix, or concomitant changes to sediment structure, interferes with the ability of ghost shrimp to form or maintain burrow surface openings or other burrow structures (e.g., turnaround chambers). In the laboratory, ghost shrimp burial time increases sixfold in the presence of eelgrass rhizomes and roots (Brenchley 1982). In our field study, transplanted ghost shrimp succeeded in forming burrows within eelgrass patches, but they did not maintain them (Fig. 2C). Furthermore, rhizome–root mimics were equally effective in displacing ghost shrimp as live eelgrass (Figs. 2A and 3), offering strong evidence for this mechanism. Because ghost shrimp burrows are vertically oriented and relatively narrow ( $11.9 \pm 4.6$  cm [mean  $\pm$  SD] in horizontal extent [Griffis and Chavez 1988]), we speculate that ghost shrimp displaced in our experiments migrated laterally, away from eelgrass, and established burrows in unvegetated habitat free of biogenic obstacles. Our findings support early observations of an inverse spatial relationship between these species (Harrison 1987, Swinbanks and Luternauer 1987) and echo patterns from South African estuaries, where sediment stabilization by seagrass reduces penetrability by burrowing shrimp (Siebert and Branch 2006, 2007).

Burrowing shrimps and other marine bioturbators have been described as archetypes of allogenic ecosystem engineering (Levinton 1995). Ghost shrimp in our study modified sediments over small scales, excavating coarse, organically poor, low-nutrient sands and depositing them at the surface (Appendix B). However, they failed to have detectable engineering effects at the patch scale. These results are consistent with findings from other regions, which show no correlation between grain size and ghost shrimp abundance (Harrison 1987, Swinbanks and Luternauer 1987).

We conclude that eelgrass is, in general, resistant to habitat modification by ghost shrimp. This finding is in contrast to benthic species that are sensitive to ghost shrimp bioturbation, such as clams (Peterson 1977), oysters (Dumbauld et al. 1997), and several deposit-feeding invertebrates (Posey 1986a). Small-scale habitat modification by ghost shrimp may have had stronger impacts if eelgrass sexual reproduction played a larger role in our study system. In the State of Washington, USA, ghost shrimp burial reduces the survival and growth of seeds in the congener *Zostera japonica* (Dumbauld and Wyllie-Echeverria 2003). In our study, however, eelgrass spread was dominated by asexual growth in both the patch-interior disturbance experiment and the eelgrass transplantation experiment; only rarely did we observe seedlings.

The outcome of competition between autogenic and allogenic engineers may be mediated by differences in the relative rates of habitat construction and decay. For example, sediment excavation by an invasive isopod outpaces lateral spread and sediment accretion by saltmarsh plants, leading to bank erosion (Davidson and de Rivera 2010). In our system, ghost shrimp exhibit low rates of sediment turnover relative to some tropical and subtropical burrowing shrimps, which are able to smother or shade adjacent seagrass (Suchanek 1983, Siebert and Branch 2006, 2007). In Indonesia, several burrowing shrimp species harvest seagrass leaves (Kneer et al. 2008), creating circular gaps in otherwise contiguous meadows (S. L. Williams, *personal observation*). In other systems, such as New Zealand estuaries, co-occurring seagrass and burrowing shrimp have no measurable effects on each other (Berkenbusch et al. 2007). Thus the sign and strength of interactions between seagrasses and burrowing shrimps appear to vary by region and species.

#### *Disturbance and coexistence*

At equilibrium, interspecific competition is expected to lead to deterministic local extinction of the inferior competitor (Connell 1961). However, disturbance can increase the potential for coexistence by creating spatial and temporal variation in niche availability (Connell 1978, Sousa 1979). Based on ecological theory, we identify three processes to increase the potential for landscape-scale coexistence in our system: (1) environmental heterogeneity caused by spatiotemporally asyn-

chronous disturbances (Pacala and Tilman 1994), (2) differential resistance to certain disturbances (Hastings 1980), and (3) a trade-off between competitiveness and colonization ability (Levin and Paine 1974).

Synthesizing the results from our disturbance experiments, we found that loss of eelgrass creates spatio-temporal refugia for competitively inferior ghost shrimp, but that the spatial pattern of disturbance matters tremendously (Sousa 1984). In our study, ghost shrimp rapidly colonized disturbances to eelgrass patch edges (Fig. 4C). All burrows found in this experiment were relatively large, indicating they belonged to adult ghost shrimp and strongly suggesting colonization was the result of lateral movement from adjacent ghost shrimp patches. By contrast, ghost shrimp failed to colonize disturbances to eelgrass patch interiors, even after 43 weeks (Fig. 4A). We suspect that adult ghost shrimp are unlikely to migrate past the eelgrass ecotone and thus they never encountered these areas of unvegetated habitat. Our results also indicate a failure of planktonic recruitment to the experimental disturbances over the 10 months during which we observed these plots. Recruitment of ghost shrimp postlarvae is highly variable, both within and among years (Dumbauld et al. 1996), and it is possible that our experiment was conducted during a low-recruitment period.

Asynchronous benthic disturbances are common at both Tomales Bay and Mission Bay. Disturbances to eelgrass that we have observed at our study sites include swell, storm surge, desiccation, and grazing by migratory geese. Additional disturbances at our sites that primarily harm eelgrass but have the potential to affect ghost shrimp include boating impacts, trampling from foot traffic, and blooms of macroalgae (*Ulva* sp. and *Gracilaria* sp.) that shade the benthos and induce anoxia (Olyarnik and Stachowicz 2012). Differential resistance of eelgrass and ghost shrimp to this variety of disturbance agents provides an additional mechanism for coexistence (Hastings 1980).

Although an inferior competitor, ghost shrimp have a colonization advantage relative to eelgrass due to both a faster rate of lateral spread and a greater potential for long-distance dispersal. Our transplanted eelgrass expanded at a rate typical for this species (~26 cm/yr [Marbà and Duarte 1998]). Eelgrass took about 10 months to completely recover from 0.25-m<sup>2</sup> disturbances to patch interiors. By contrast, migrating ghost shrimp fully colonized disturbances of this size to eelgrass patch edges in no more than two months. In addition to rapid proximate colonization by adults, ghost shrimp can colonize distant habitats by the recruitment of planktonic postlarvae (Dumbauld et al. 1996). The large dispersal potential of ghost shrimp is evident from the high population connectivity measured for several estuaries distributed over 300 km of coastline in the U.S. Pacific Northwest (Kozuka 2008). Eelgrass also is capable of sexual reproduction, but the vast majority of seeds disperse only a few meters from parent plants

(Orth et al. 1994). Thus, although both species have the capacity for local and distant dispersal, ghost shrimp have a greater potential for dispersal to new habitats both within and among estuaries.

Minor differences in tidal distributions for eelgrass and ghost shrimp also seem important to the competition–colonization trade-off. In the California estuaries we studied, ghost shrimp achieve high densities ( $>100$  burrow surface openings/m<sup>2</sup>) slightly above (several vertical centimeters) and below (1–2 vertical meters) eelgrass tidal limits (M. C. N. Castorani, *unpublished data*). Eelgrass is likely restricted by temperature (Marsh et al. 1986) or desiccation stress (Boese et al. 2005) in the upper-intertidal and light limitation at depth (Dennison 1987). These limited high-intertidal and low-subtidal zones, which appear marginal for eelgrass but suitable for ghost shrimp, may promote ghost shrimp persistence at the landscape scale by providing a spatial refuge from competition and a source of colonizers to nearby eelgrass disturbances.

### Conclusions

Operating in isolation, neither disturbance nor a competition–colonization trade-off necessarily fosters coexistence (Chesson and Huntly 1997). The California estuaries we studied are characterized by (1) spatially asynchronous benthic disturbances that modulate the availability of unoccupied space and predominantly impact eelgrass, and (2) clear differences in competitiveness and colonization abilities between two ecosystem engineers. Together, these result in a mosaic landscape with discrete patches dominated by eelgrass or ghost shrimp. Although eelgrass is sensitive to disturbance and slow to recover, once established it physically excludes and inhibits ghost shrimp through autogenic habitat modification. In spite of their inability to coexist with or outcompete eelgrass, ghost shrimp persist at the landscape scale by rapidly colonizing disturbances to the edges of eelgrass patches and maintaining source populations above and below the eelgrass depth range. Theory demonstrates that antagonistic habitat modification can lead to local competitive exclusion, yet disturbance can facilitate broader coexistence. Our findings lend empirical support to these predictions and highlight the key role disturbance can play in structuring ecological communities.

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#### SUPPLEMENTAL MATERIAL

##### Appendix A

A color version of Plate 1: photographs of a shallow subtidal area at Mission Bay (San Diego, California, USA) showing eelgrass and ghost shrimp are patchily distributed with abrupt ecotone transitions ([Ecological Archives E095-202-A1](#)).

##### Appendix B

Graph of sediment biogeochemical parameters sampled over small spatial scales and patch scales ([Ecological Archives E095-202-A2](#)).

##### Appendix C

Photograph of rhizome–root structural mimics ([Ecological Archives E095-202-A3](#)).

##### Appendix D

Conceptual diagram of the randomized complete block design used in the eelgrass patch-edge disturbance experiment ([Ecological Archives E095-202-A4](#)).

##### Appendix E

Table of independent-samples *t* test results for sediment parameters surveyed over patch scales ([Ecological Archives E095-202-A5](#)).

##### Appendix F

ANOVA table for results from the eelgrass transplantation experiment ([Ecological Archives E095-202-A6](#)).

##### Appendix G

ANOVA table for results from the rhizome–root structural mimic experiment ([Ecological Archives E095-202-A7](#)).

##### Appendix H

ANOVA table for results from the eelgrass patch-interior disturbance experiment ([Ecological Archives E095-202-A8](#)).

##### Appendix I

ANOVA table for results from the eelgrass patch-edge disturbance experiment ([Ecological Archives E095-202-A9](#)).