

Variation at multiple trophic levels mediates a novel seagrass–grazer interaction

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ABSTRACT: Herbivores can have highly variable effects across their ranges, sometimes with unanticipated effects on trophic dynamics that in turn affect management and conservation programs. In seagrass beds, small invertebrate grazers (mesograzers) are expected to benefit the habitat-forming plants by removing competing algae; however, harm by mesograzers has been documented increasingly in a number of regions. In San Francisco Bay, California, USA, a gammaridean amphipod (*Ampithoe valida*), native to the US East Coast and putatively introduced to Pacific coastlines, reaches outbreak densities and consumes large quantities of eelgrass *Zostera marina*, while it is not known to do so elsewhere in its range. Using a series of mesocosm experiments, we manipulated predator (fish) identity and density, herbivore assemblage, and habitat complexity to test how variation at multiple trophic levels influences the abundance and role of *A. valida*. Reductions in *A. valida* abundance by native San Francisco Bay shiner surfperch and bay pipefish were less pronounced than by a pinfish brought in from North Carolina, USA; however, the former 2 predators enhanced eelgrass biomass, while consumption of both amphipods and eelgrass by pinfish netted limited benefits to eelgrass. Increasing density of the surfperch in a separate experiment did not further reduce *A. valida* abundance but nonetheless strengthened positive effects on eelgrass, presumably through behavioral response to increased threat. The presence of a second (introduced) grazer reduced predation pressure on *A. valida*, weakening the trophic cascade to the detriment of eelgrass. Increasing habitat complexity by substituting flowering shoots reduced predation success, leading to higher *A. valida* abundances. Our results point to the importance of predator control of *A. valida* to reduce eelgrass damage; however, the strength of the trophic cascade across this grazer's range is likely to be modulated by composition of predator and grazer assemblages as well as flowering rates and phenology.

KEY WORDS: Amphipod · Trophic interaction · Eelgrass · Predator · Trophic cascade

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INTRODUCTION

Herbivores occupy a central position in food webs; therefore, their functional roles and densities depend in part on the abundance, traits, and behavior of the particular species surrounding them at one or more trophic levels. For example, a failure of either predators or plant defenses to control herbivore densities and grazing rates can result in severe plant defoliation (Wallner 1987, Liebhold et al. 2000). Such damage is especially worrisome when affecting founda-

tional plant species at the core of restoration and conservation programs (e.g. Coomes et al. 2003). For example, seagrasses (rooted marine angiosperms) provide highly valued habitat and ecosystem services (Short & Wyllie-Echeverria 1996, Fourqurean et al. 2012) but are declining worldwide at unprecedented rates (Orth et al. 2006, Waycott et al. 2009). Efforts to develop restoration techniques (e.g. Meehan & West 2002, Marion & Orth 2010) and identify barriers to successful restoration and conservation programs (e.g. Orth et al. 2010, Cunha et al. 2012)

must be grounded in an understanding of the trophic interactions that contribute to seagrass performance.

Mesograzers (small invertebrate grazers such as amphipods, isopods, and gastropods) are often thought to be important, if not critical, to the health and persistence of seagrass meadows (Hay et al. 2004, Whalen et al. 2013). These small invertebrates are considered an important conduit in the transfer of energy from primary producers to higher-order consumers (Kikuchi 1974). Additionally, by grazing epiphytic algae that outcompete seagrasses for light, mesograzers can increase seagrass growth by up to 200% (Duffy et al. 2001). Generally, invertebrate consumption of the plants themselves is thought to be minimal (see review in Valentine & Duffy 2006), but there are documented exceptions in field and mesocosm experiments (Nienhuis & Groenendijk 1986, Short et al. 1995, Zimmerman et al. 1996, Duffy et al. 2001, 2003, Bostrom & Mattila 2005, Douglass et al. 2007, Best & Stachowicz 2012). Further, evidence from kelp forests demonstrates that microcarnivorous fish can prevent outbreaks of mesograzers and, ultimately, increase kelp performance (Davenport & Anderson 2007). Yet in seagrass systems, there is little empirical evidence for strong cascading effects of predators on plant biomass (Heck et al. 2000, Duffy et al. 2005, Douglass et al. 2007, Jorgensen et al. 2007, Moksnes et al. 2008, Poore et al. 2009, but see Lewis & Anderson 2012). When this phenomenon does occur, it seems to depend on whether mesograzers directly harm the seagrass (Best & Stachowicz 2012, Lewis & Anderson 2012) and on the trophic level of predators removed (i.e. 3rd, or microcarnivore, versus 4th, or piscivore, level will have opposite effects). Potentially complicating these interactions, differences in the physical complexity of vegetative versus flowering shoots might differentially affect availability of refuge as well as food resources available to higher trophic levels. Morphologically simple vegetative shoots and highly branched structurally complex flowering shoots can develop different invertebrate community assemblages (Nakaoka et al. 2008) or abundances (Carr et al. 2011); thus, timing and rates of flowering could contribute to trophic interactions. For example, complexity that enhances invertebrate abundances could reduce predator control of invertebrates, promoting their effects, whether beneficial or detrimental, on the habitat-forming plants.

The gammaridean amphipod *Ampithoe valida* has been observed to reach outbreak densities and consume large quantities of the seagrass *Zostera marina* (eelgrass) in San Francisco Bay, CA, USA (Boyer &

Wyllie-Echeverria 2010, Reynolds et al. 2012), although it is not known to do so in other parts of its range, e.g. Chesapeake Bay, VA, USA (Douglass et al. 2011); Beaufort, NC, USA (E. Sotka pers. comm.); Bodega Bay, CA, USA (Best & Stachowicz 2012, 2013); Willapa Bay, WA, USA (J. Ruesink pers. comm.); NE Japan (M. Nakaoka pers. comm.). *A. valida* has long been presumed introduced to San Francisco Bay from the US Atlantic Coast (Cohen & Carlton 1995, Chapman 2007), a contention supported by some recent genetic data but undergoing further evaluation (Pilgrim & Darling 2010, E. Sotka, L. Scheinberg, & K. Boyer unpubl. data). Regardless of its introduction history, the very high densities and damaging effects of this amphipod in San Francisco Bay eelgrass beds have led to much recent interest, in part due to its interference with restoration programs (Boyer & Wyllie-Echeverria 2010, Reynolds et al. 2012).

We are interested in exploring how environmental context influences the abundance and impact of *A. valida* on eelgrass, to better understand why we see extensive damages in only a portion of the range in which *A. valida* and *Z. marina* co-occur. We conducted a series of mesocosm experiments to determine if (1) predator identity (including a predator that co-occurs with *A. valida* on the US East Coast) is important to eelgrass biomass due to differential effects on *A. valida* herbivory, (2) effects of predator identity interact with the herbivore assemblage to influence eelgrass, and (3) predator density and increased habitat complexity (complex flowering versus simple vegetative shoots) alter predation success and, thus, the strength of cascading trophic effects. We show that direct damage to eelgrass by *A. valida* in San Francisco Bay, a novel impact for this amphipod anywhere in its range, can be countered by cascading effects of fish predation but that the composition of predator and grazer assemblages as well as flowering rates and phenology are all likely to influence the strength of these effects.

MATERIALS AND METHODS

We addressed 3 questions with the experimental design outlined in Fig. 1. All experiments were run between August 2007 and September 2008 at San Francisco State University's Romberg Tiburon Center in translucent, 45 l plastic mesocosm tanks (50 × 35 × 35 cm, 1 × w × h). Tanks were placed in water tables to maintain temperatures comparable to field conditions and individually supplied with aeration and sand-filtered flowing water from San Francisco

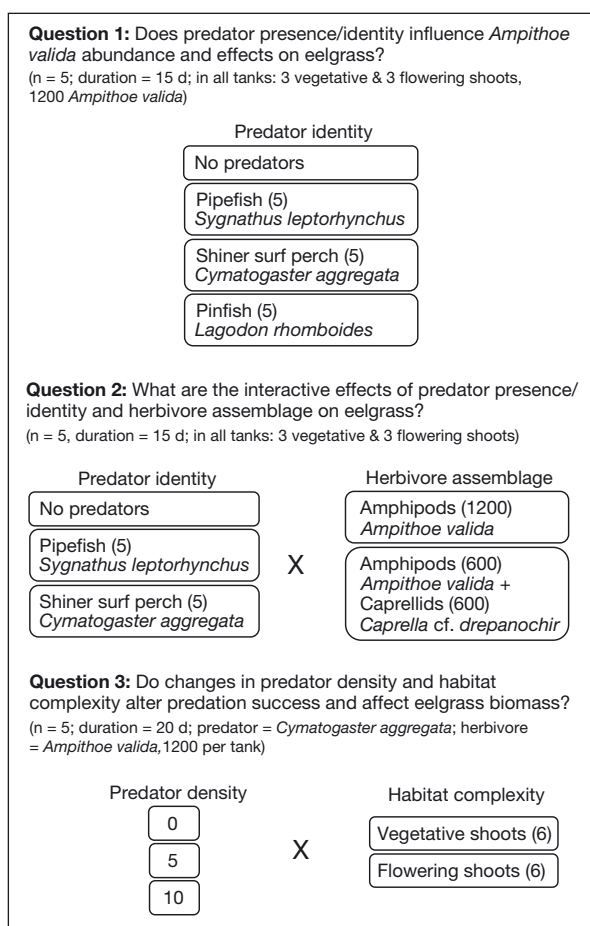


Fig. 1. Design of mesocosm experiments addressing the study's 3 questions. n: number of mesocosms

Bay. Fiberglass window screening over tanks simulated reduced light conditions of the bay, and each outflow pipe was also covered with this screening to prevent escape of invertebrates or fish. Water tables were enclosed by chicken wire fence to deter predation by birds and other wildlife. All experiments included eelgrass *Zostera marina*, a cosmopolitan seagrass species native to San Francisco Bay and temperate estuaries throughout the world (Green & Short 2003), and *Ampithoe valida*, a tube-building gammaridean amphipod. This amphipod was first recorded in San Francisco Bay in 1941 and presumed introduced (Cohen & Carlton 1995, Chapman 2007). Preliminary DNA sequence data from the mitochondrial gene (COI) supports the introduction of an Atlantic lineage (Pilgrim & Darling 2010) but also reveals a cryptic lineage that appears to be native to the Bay (E. Sotka, L. Scheinberg, & K. Boyer unpubl. data), suggesting that the cosmopolitan *A. valida* is a cryptic species complex.

Expt 1: Influence of predator presence/identity on *Ampithoe valida* abundance and effects on eelgrass

This experiment included 3 predatory fish: *Cymatogaster aggregata* (shiner surfperch), *Syngnathus leptorhynchus* (bay pipefish), and *Lagodon rhomboides* (pinfish). *C. aggregata* and *S. leptorhynchus* are both native to San Francisco Bay. They are 2 of the most abundant fish species in local eelgrass beds (Carr 2008, Boyer unpubl. data) and are known to prey on gammaridean amphipods as well as other small invertebrates (Emmett et al. 1991). *L. rhomboides* is common in temperate and subtropical seagrass meadows along the Atlantic and Gulf coasts of North America (Huh 1986) and known to feed on seagrass (*Thalassia testudinum*, *Syringodium filiforme*, and *Zostera marina*) (Adams 1976, Stoner 1980, Stoner & Livingston 1984) and small invertebrates, including *A. valida* (Duffy & Hay 1994). This fish species does not occur locally but was included to permit comparison of effects of a predator from *A. valida*'s range on the US East Coast (where *A. valida* is not known to damage eelgrass, perhaps in part due to effective predators) to those of native predators in the amphipod's presumed introduced range in San Francisco Bay (where predators may be less effective).

Treatments were the addition of *C. aggregata*, *S. leptorhynchus*, *L. rhomboides* or no predators, in tanks with eelgrass and *A. valida* (Fig. 1). Predator treatments were stocked with 5 fish per tank based on 2008 field counts (for *C. aggregata* and *S. leptorhynchus*) and results from another experiment which demonstrated that 5 *C. aggregata* caused significant effects on mesograzer mortality and shoot condition (Carr 2008, see Question 3 in Fig. 1). *C. aggregata* were purchased from a local bait shop. *S. leptorhynchus* were collected from an eelgrass bed north of Point San Pablo, in Richmond, CA. *L. rhomboides* were collected from a marina in Beaufort, NC, by colleagues and shipped to us for this experiment. Fish species were kept in separate, round 378 l tanks with flow-through bay water and aeration for at least 3 d before the experiment and offered live gammarid and caprellid amphipods (collected from nearby eelgrass beds) twice a day, until 1 d before the experiment. Fish ranged from 8 to 17 cm standard length (SL), and the range of sizes was standardized across mesocosms in *C. aggregata* and *L. rhomboides* treatments (mean \pm SE, 9.6 ± 2.3 cm SL). *L. rhomboides* has several distinctive feeding stages (Stoner & Livingston 1984, Heck et al. 2006), and our experiment included mature pinfish that consume both inverte-

brates and eelgrass tissue. Due to the differences in shape between *S. leptorhynchus* and the other 2 species, *S. leptorhynchus* were longer (mean \pm SE, 15.4 \pm 1.9 cm SL) but similar in mass. Fish were examined daily, and dead fish were replaced throughout the experiment. Final fish densities were slightly lower than the initial densities in the *C. aggregata* and *S. leptorhynchus* treatments (mean \pm SE per mesocosm: 4.5 \pm 0.6, 4 \pm 0.8, respectively), while the final density of *L. rhomboides* was the same as the initial density (5 \pm 0). An Emperor Aquatics, Inc[®] Smart Ultraviolet Water Sterilizer (Model 0205, 120 VAC, 60 Hz), capable of treating 50 l of water min⁻¹, was placed at the end of the flow-through system to kill any bacteria and/or larvae associated with *L. rhomboides* before water was returned to the bay. Upon termination of the experiment, all *L. rhomboides* were sacrificed.

Three vegetative and 3 flowering shoots were twist-tied to bamboo stakes, which were glued into the tanks with non-toxic aquarium sealant. Eelgrass shoot densities used in the experiment (30 m⁻²) reflected moderate field densities (ranging from 1.3 to 64.6 m⁻² in 2007, Carr et al. 2011). The top portion of shoots floated at the surface as is typical in shallow field conditions during a part of the tidal cycle. Eelgrass was collected from a bed near Point Richmond, CA. Shoots were dipped in freshwater 3 times for 1 min each to remove fauna (Holmlund et al. 1990 for algae), resulting in removal of 92% of individuals from shoots (L. A. Carr unpubl. data). Before and after the experiment, all shoots were blotted dry with 3 paper towels and weighed, and change in the weight per vegetative or flowering shoot in each tank was used in the statistical analyses. Using an additional set of mesocosms with eelgrass only (n = 5), change in shoot wet weight was calculated and averaged among tanks, then used to correct values from treatment tanks to account for changes in plants not attributable to fauna.

We added 1200 *A. valida* to each treatment tank, to represent the mean field density per shoot measured during peak abundance (Carr et al. 2011, Reynolds et al. 2012; ~100 per vegetative shoot and 300 per flowering shoot = 1200 *A. valida* total across 3 shoots of each type). *A. valida* were collected from an eelgrass bed north of Point San Pablo, in Richmond, CA, and held in tanks with flow-through bay water and aeration before the experiment. Only *A. valida* individuals >4 mm and <10 mm were used in the experiments.

The experiment was terminated when amphipod density was substantially reduced but not fully

depleted where fish were present. Fish were removed with nets and counted. Tank contents were run through a 500 μ m sieve, separating leaf litter and any remaining amphipods. Remaining amphipods were preserved in 70% ethanol and counted.

We conducted 2-factor ANOVA on the percent change from initial amphipod abundance and change in shoot wet weights, using predator presence/species as a fixed factor. For all experiments we conducted 2-factor ANCOVA on final shoot wet weights with initial wet weight as a covariate and shoot type and fish density/presence/identity as fixed factors. As there was no significant effect of covariate, all subsequent analyses were run as ANOVA. Analysis was followed with Tukey's HSD post-hoc tests. R (v. 2.10.1, R Development Core Team 2009) was used for all analyses.

Expt 2: Interactive effects of predator presence/identity and herbivore assemblage on eelgrass

The experimental set-up was similar to that in Question 1, but pinfish were not included, and predator identity was crossed with 2 herbivore treatments: *A. valida* only (1200 ind.) and *A. valida* + *Caprella* cf. *drepanochir* (600 of each species). *C. cf. drepanochir* is native to the Japanese coast (Chapman 2007) and assumed to be a filter-feeder as it spends most of its time in an upright position and does not appear to cause eelgrass damage (Takeuchi & Hirano 1995, Lewis 2013). In 2007, approximately quarterly sampling of mesograzers community composition at 5 different eelgrass beds across San Francisco Bay showed *C. cf. drepanochir* peak abundance averaged ~250 per vegetative shoot and >700 per flowering shoot, with up to 4500 additional juvenile caprellids also likely to be *C. cf. drepanochir* (Carr et al. 2011). This caprellid was present at 4 of the 5 sites at every sampling period and was the most abundant mesograzers species at each of these sites on both flowering and vegetative shoots (Carr et al. 2011). *C. cf. drepanochir* were collected from the same eelgrass bed as *A. valida*. Mesocosms with plants only (n = 5) were used to correct for changes to biomass not attributable to fauna, as for Question 1. All other methods used were the same as for Question 1.

We conducted 2-factor ANOVA on the percent change in mesograzers abundance and change in eelgrass wet weight per vegetative or flowering shoot, using predator species and mesograzers assemblage as fixed factors. Analysis was followed by Tukey's HSD post-hoc tests.

Expt 3: Effects of changes in predator density and habitat complexity on predation success and eelgrass biomass

The experimental set-up was similar to the 2 described above but focused on density-dependent effects of *C. aggregata* and the role of habitat complexity (vegetative vs. flowering shoots) in mediating responses. Fish densities (0, 5, or 10 per mesocosm) were chosen to represent a realistic range based on 2007 field counts (Carr 2008, W. Norden & L. Martin unpubl. data). Fish ranged from 3 to 10 cm SL, and the range of sizes was standardized across mesocosms (mean \pm SE, 5.7 ± 1.8 cm SL). Final fish densities were slightly lower than the initial densities of 0, 5 and 10 per tank (mean \pm SE: 0 ± 0 , 4.66 ± 0.41 and 8 ± 0.33 , respectively). Six vegetative or 6 flowering shoots were used in each tank, and we added 1200 *A. valida* to each tank to be consistent with the previous experiments; all methods were as described above. The experiment was terminated when amphipods were visually reduced but not fully depleted (20 d).

We assessed algae growing on the sides of mesocosms to quantify differences in primary producer composition across treatments. Photographs of one wall with the same orientation in each tank were overlaid with a 15×15 cm quadrat with 100 pre-marked points. Each point was scored as brown microalgal film, green filamentous algae, bare substrate or an amphipod nest, and percent cover for each category was calculated.

We conducted 2-factor ANOVA on final shoot wet weights and percent change in *A. valida* abundance using shoot type and fish density as fixed factors. We also fitted a generalized linear model (GLM) to

Table 1. Results from the predator presence/identity experiment (Question 1): 1-factor ANOVAs on the percent change in *Ampithoe valida* abundance and on change in eelgrass vegetative or flowering wet weight

Factor	SS	df	F	p
Percent change in <i>A. valida</i> abundance (square root transformed)				
Predator presence/identity	2.23	3	14.03	0.0002
Error	0.74	16		
Change in vegetative shoot wet weight				
Predator presence/identity	27.68	3	9.64	0.0061
Error	51.72	16		
Change in flowering shoot wet weight (power transformed)				
Predator presence/identity	2032.99	3	7.09	0.0030
Error	1529.70	16		

examine differences in shoot biomass with increasing fish density.

RESULTS

Predator presence/identity

A. valida abundance was strongly influenced by predator identity (Table 1, Fig. 2A, Tukey's HSD post hoc results). Pinfish brought from *A. valida*'s US East Coast range (North Carolina) were the most effective predators (nearly 100% removal), followed by the San Francisco Bay natives: shiner surfperch (80% removal) and pipefish (45% removal) (Fig. 2A). In

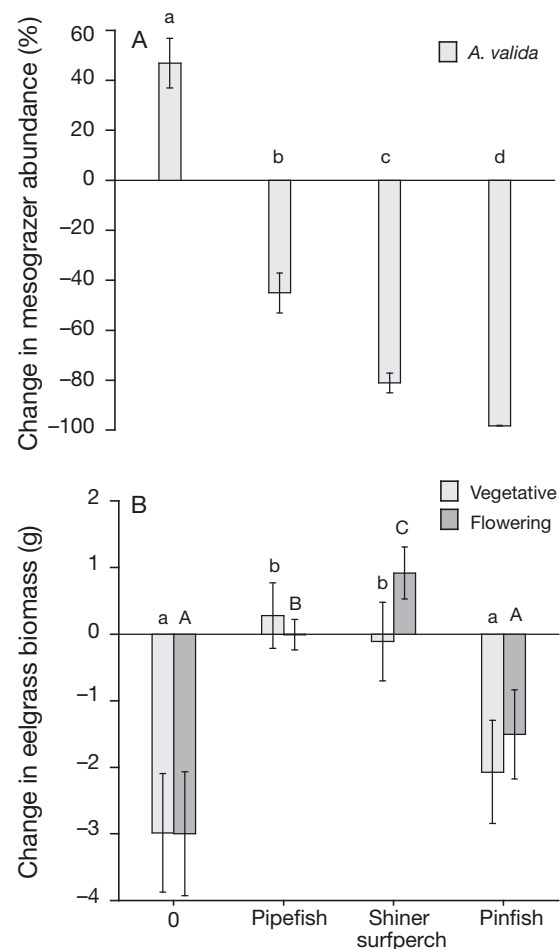


Fig. 2. Effects of predator presence/identity (Question 1) on (A) percent change in *Ampithoe valida* abundance (Tukey's HSD results presented with lower case letters) and (B) change in eelgrass wet weight per vegetative or flowering shoot where Tukey's HSD results are presented with either lower case (vegetative) or upper case (flowering) letters. Error bars represent ± 1 SE; $n = 5$. Mean initial shoot biomass was 14.36 ± 0.51 g (vegetative) and 15.08 ± 0.59 g (flowering)

mesocosms without predators, *A. valida* abundances increased by ~50 % (Fig. 2A).

Predator identity had a significant effect on eelgrass wet weight of both shoot types (Table 1, Fig. 2B, Tukey's HSD post-hoc results). Both pipefish and shiner surfperch tended to have positive effects on eelgrass biomass. Pipefish presence led to significant increases in vegetative shoot mass, while shiner surfperch significantly increased flowering shoot mass, relative to no-predator treatments (Fig. 2B, Tukey's HSD post-hoc tests). Despite strong control of *A. valida* by pinfish, this predator tended to have negative effects on eelgrass.

Predator presence/identity × herbivore assemblage

Predator presence/identity and herbivore assemblage both significantly affected *A. valida* abundance (Table 2, Fig. 3A,B, Tukey's HSD post-hoc results). Both pipefish and shiner surfperch significantly reduced *A. valida* abundance, with the effect much stronger for surfperch, a pattern that held whether or not caprellids were also present (Fig. 3A,B). In the presence of *C. cf. drepanochir*, compared to *A. valida* only treatments, *A. valida* abundance was much

Table 2. Results from the predator presence/identity × herbivore assemblage experiment (Question 2): One- or 2-factor ANOVAs on percent change in *Ampithoe valida* abundance, percent change in *Caprella cf. drepanochir* abundance, and change in eelgrass vegetative or flowering wet weight

Factor	SS	df	F	p
Percent change in <i>A. valida</i> abundance (square root transformed)				
Predator identity (P)	1.13	2	52.63	<0.0001
Herbivore assemblage (H)	2.65	1	246.76	<0.0001
P × H	0.06	2	25.85	<0.0001
Error	0.26	24		
Percent change in <i>C. cf. drepanochir</i> abundance				
Predator identity	0.0004	2	0.01	0.9900
Error	0.1712	12		
Change in vegetative shoot wet weight (power transformed)				
Predator identity (P)	4982.01	2	9.87	0.0008
Herbivore assemblage (H)	2029.14	1	8.03	0.0092
P × H	2100.72	2	4.16	0.0280
Error	6065.68	24		
Change in flowering shoot wet weight (power transformed)				
Predator identity (P)	6578.12	2	28.02	<0.0001
Herbivore assemblage (H)	12.33	1	0.11	0.7500
P × H	1406.46	2	5.99	0.0078
Error	2816.85	24		

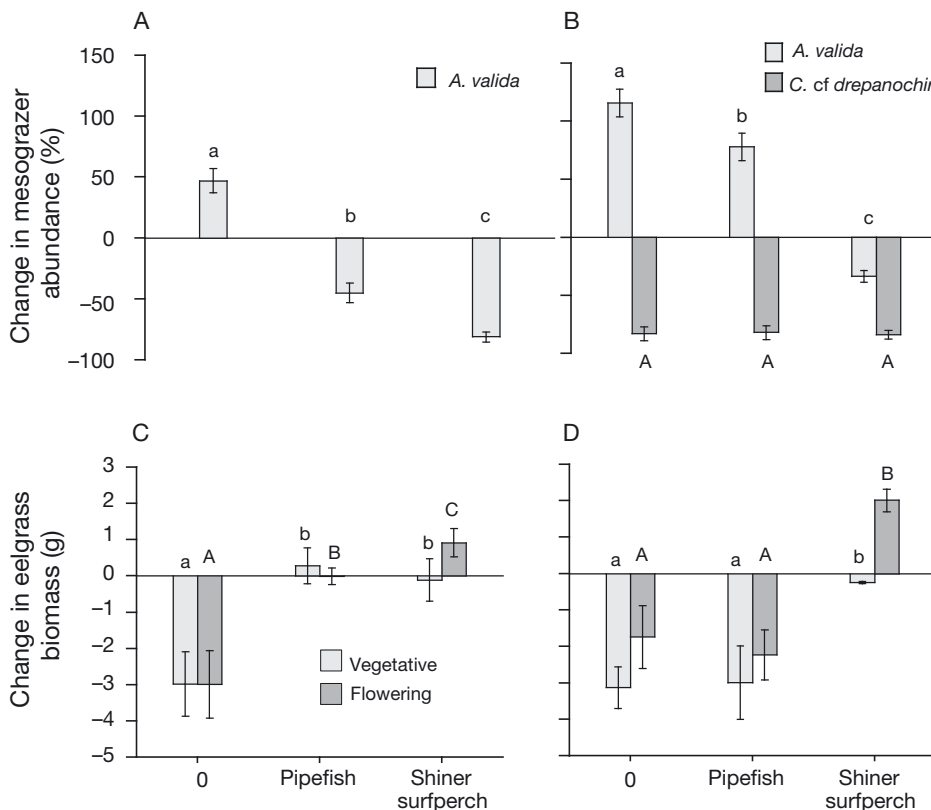


Fig. 3. Results from predator presence/identity × herbivore assemblage experiment (Question 2). Effects of predator presence/identity on percent change in abundance of (A) *Ampithoe valida* alone and (B) *A. valida* and *Caprella cf. drepanochir* together. Tukey's HSD post-hoc results are presented with either lower case (*A. valida*) or upper case (*C. cf. drepanochir*) letters. Change in eelgrass wet weight per vegetative or flowering shoot with presence of (C) *A. valida* only and (D) both mesograzers. Tukey's HSD post-hoc results are presented with either lower case (vegetative) or upper case (flowering) letters. Error bars represent ±1 SE; n = 5. Mean initial shoot biomass was 14.45 ± 0.53 g (vegetative) and 14.41 ± 0.58 g (flowering)

greater across predator identity or presence treatments (Table 2, significant predator \times herbivore assemblage interaction, Fig. 3A,B). In the no-predator treatment with *C. cf. drepanochir* present, final *A. valida* abundances increased by over 100% but only by ~40% when alone (Fig. 3A,B). In the pipefish treatments, final *A. valida* abundances decreased by ~50% in the *A. valida* only tanks and increased by ~70% in the presence of *C. cf. drepanochir*. *A. valida* abundance decreased in shiner surfperch treatments but less so when *C. cf. drepanochir* was present (~30%) than when it was not (~80%) (Fig. 3A,B). In contrast to *A. valida*, *C. cf. drepanochir* numbers declined similarly (by about 80%) among predator presence/identity treatments (Table 2, Fig. 3B).

Predator presence/identity had significant effects on eelgrass biomass (Table 2, Fig. 3C,D). In the absence of predators, all eelgrass shoots lost substantial biomass (Fig. 3C,D). In the pipefish treatments with *A. valida* as the only invertebrate present, eelgrass biomass was unchanged from initial levels, but it declined dramatically when both *A. valida* and *C. cf. drepanochir* were included (Fig. 3D, Table 2, significant predator \times herbivore assemblage interaction). Eelgrass shoots in the shiner surfperch treatments had similar biomass (3- to 4-fold greater than with no predators present) regardless of herbivore assemblage (Fig. 3C,D). Often, flowering shoots had somewhat greater biomass compared to vegetative shoots (Fig. 3C,D).

Predator density \times habitat complexity

A. valida abundances were affected by both fish (shiner surfperch) presence and shoot type (Table 3, Fig. 4). The no-predator treatments had ~4 \times more amphipods, with *A. valida* numbers doubling (from initial 1200 to ~2750) on both the flowering and vegetative shoots (Table 3, Fig. 4A). Increasing fish density from 5 to 10 did not further reduce *A. valida* abundance (Fig. 4A). Flowering shoot tanks ended the experiment with significantly greater *A. valida* abundances, an effect consistent across fish density treatments (no shoot type \times fish density interaction, Table 3, Fig. 4A).

Shiner surfperch presence led to a significant increase in eelgrass wet weight (Table 3, Fig. 4B). A greater density of surfperch strengthened the benefit to eelgrass for both vegetative and flowering shoots (Fig. 4B; vegetative: $R^2 = 0.41$, $p = 0.00158$; flowering: $R^2 = 0.28$, $p = 0.00296$), even though more fish did not increase amphipod removal (Fig. 4A). Flowering

Table 3. Results from the predator (fish) density \times habitat complexity (shoot type) experiment (Question 3): 2-factor ANOVAs on percent change in *Ampithoe valida* abundance and change in eelgrass wet weight

Factor	SS	df	F	p
Percent change in <i>A. valida</i> abundance				
Fish density (F)	6.02	2	84.99	<0.0001
Shoot type (S)	0.55	1	15.44	0.0006
F \times S	0.14	2	2.03	0.1534
Error	0.85	24		
Change in eelgrass wet weight				
Fish density (F)	68.90	2	9.40	0.0010
Shoot type (S)	40.27	1	10.99	0.0030
F \times S	26.19	2	3.58	0.0540
Error	84.26	24		

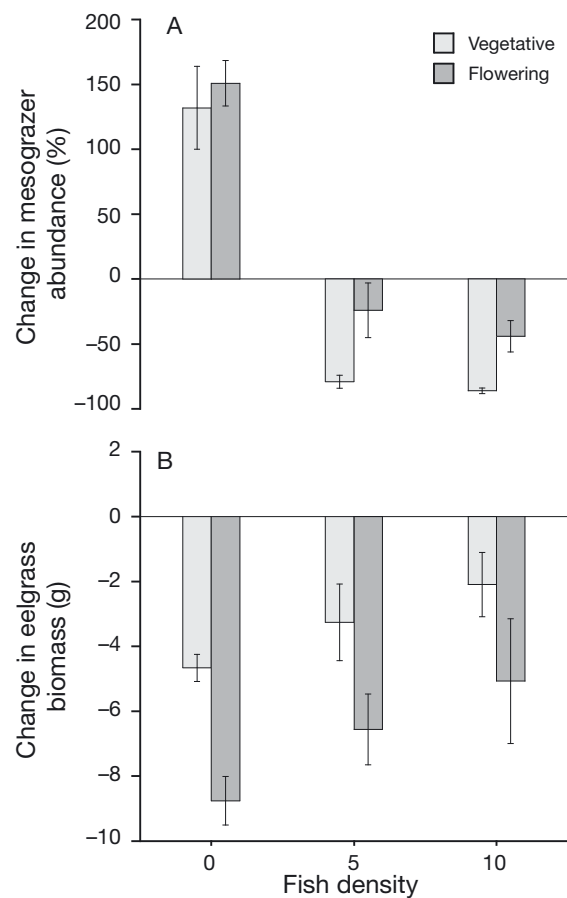


Fig. 4. Results from predator density \times habitat complexity experiment (Question 3). Effects of shiner surfperch (fish) density and shoot type (vegetative or flowering) on (A) percent change in *Ampithoe valida* abundance in vegetative and flowering shoot treatments, and (B) change in eelgrass wet weight per vegetative or flowering shoot with *A. valida* present. Error bars represent ± 1 SE; $n = 5$. Mean initial shoot biomass was 10.04 ± 0.47 g (vegetative) and 22.62 ± 0.65 g (flowering)

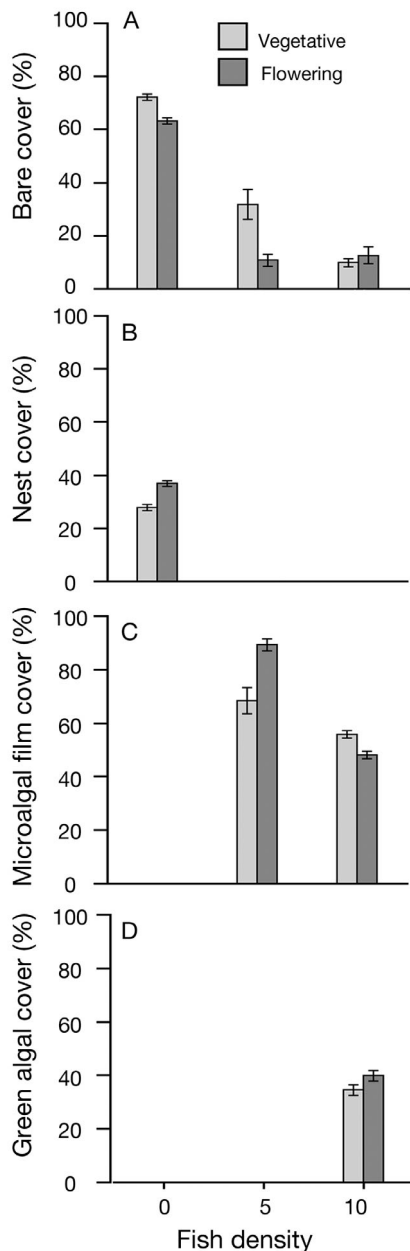


Fig. 5. Results from predator (fish) density \times habitat complexity experiment (Question 3). Percent cover of (A) bare substrate, (B) amphipod nests, (C) brown microalgal film, and (D) filamentous green algae on tank walls at the end of the experiment. Error bars represent ± 1 SE; $n = 5$

shoots lost significantly more tissue than vegetative shoots in all treatments (Table 3, Fig. 4B).

Fish density affected the final algal community composition in the mesocosms. With no fish present, sides of the tanks were devoid of algae (diatoms or green macroalgae) but had $\sim 40\%$ cover of amphipod nests (Fig. 5). When fish were present at either density, no nests were seen and brown microalgal film

was present at $\sim 50\text{--}80\%$ cover. When fish were present at high density, green macroalgae became evident ($\sim 35\%$ cover) in addition to microalgal film.

DISCUSSION

We investigated how variation at multiple trophic levels influences the abundance and role of the mesograzers *Ampithoe valida* in the trophic dynamics of a temperate seagrass system in San Francisco Bay. Even though some amphipod species do consume seagrass tissue (Best & Stachowicz 2013), none are documented to defoliate seagrasses like *A. valida* does in San Francisco Bay (Reynolds et al. 2012). Our experiments showed that the effect on seagrass biomass differs depending on a variety of factors, including predator presence, identity and density, the presence of another (introduced) invertebrate, and the degree of seagrass structural complexity (flowering vs. vegetative shoots).

Predator identity influenced the presence and strength of cascading trophic dynamics, due to differences in feeding strategy and efficiency. We found strong evidence of carnivorous fish indirectly benefiting eelgrass in a classic trophic cascade, as both vegetative and flowering shoots had greater biomass in treatments with the native shiner surfperch or pipefish. Although pinfish shipped to us from *A. valida*'s range on the US East Coast were the most successful consumers of amphipods, they have an omnivorous foraging strategy (Stoner 1980, Darcy 1985) and also ate eelgrass. In fact, their indirect positive effect on eelgrass biomass through consumption of amphipods was almost entirely offset by direct eelgrass damage, with final biomass comparable to that of the no-predator treatments. Notably, pinfish were a novel predator to the San Francisco Bay amphipods, and we assume prey naïveté increased predation vulnerability; hence, we would expect negative effects of pinfish grazing on eelgrass to exceed positive effects of amphipod removal (rather than nearly matching in magnitude) where amphipods were not naïve to these predators. As predicted by theory, the inclusion of an omnivorous predator dampened the potential trophic cascade (Bruno & O'Connor 2005). In contrast, a shortage of omnivorous predators in San Francisco Bay eelgrass beds (Carr 2008, K. Boyer unpubl. data) is likely to promote indirect predation benefits to eelgrass.

Foraging success of predators on *A. valida*, as well as cascading trophic effects, were influenced by the presence of another common mesograzers in San

San Francisco Bay, the introduced caprellid *Caprella* cf. *drepanochir*. Final *A. valida* abundances were higher in the presence of *C. cf. drepanochir*, suggesting that this caprellid facilitates *A. valida* survivorship, possibly because shiner surfperch prefer caprellids to gammarid amphipods, and will feed on them almost exclusively (Caine 1991, Page et al. 2007, Vazquez-Luis et al. 2010, Best & Stachowicz 2012). Notably, effects of this facilitation on the trophic cascade depended on which predator was present. Positive effects of shiner surfperch on eelgrass were consistent whether or not caprellids were present along with *A. valida*. In contrast, caprellid presence apparently altered pipefish foraging in a way that negated positive effects on eelgrass found when *A. valida* was the only mesograzer present. Although the mechanism limiting *A. valida* consumption by pipefish when the caprellid was present is unclear, this finding contributes to a growing body of literature documenting the importance of non-consumptive predator–mesograzer interactions in foundational marine plant systems (e.g. Molis et al. 2011, Reynolds & Sotka 2011).

Final *A. valida* abundances in the predator (shiner surfperch only) density experiment provide support for both direct (predation) and indirect (behavior modification in the presence of a predator) interactions. While increasing shiner surfperch density from 5 to 10 did not further decrease amphipod abundance, it strengthened positive effects on eelgrass. This suggests that the amphipods may alter their behavior in the presence of higher fish densities. In support of this hypothesis, tanks with the highest density of fish (10) had extensive coverage of green filamentous algae and brown diatom film, while low fish-density (5) tanks were exclusively covered in brown diatom film, suggesting amphipods were emerging from hiding places to consume the green algae when fewer predators were present. In contrast, epiphytes were absent from the no-fish tanks and amphipod nests littered the walls. When there were no predators present, the amphipods increased in abundance, exhausted all epiphytic material and consumed live eelgrass tissue.

In a number of other locations, mesograzers have been documented consuming live eelgrass tissue in mesocosm experiments but not in the field (see references in Valentine & Duffy 2006). It may be that predators typically prevent mesograzer densities from reaching abundances at which herbivory on eelgrass tissue is noticeable or exceeds positive effects of epiphyte removal (Douglass et al. 2007). Nelson (1979) found 0–750 amphipods m^{-2} (of any species) in a survey of seagrasses from MA to FL,

USA, and the *Zostera* Experimental Network recently found <1 *A. valida* per shoot in locations where the amphipods were identified to species (Japan, and WA, NC, and VA, USA; E. Duffy and P. Reynolds pers. comm.). *A. valida* can also be sparse at some sites and seasons in San Francisco Bay (none to a few individuals; Carr et al. 2011), but peak abundances of ~300 individuals per flowering shoot and 100 per vegetative shoot (densities up to 3200 m^{-2}) lead to extensive grazing directly on eelgrass tissue, as shown in mesocosm experiments and observed in the field (Boyer & Wyllie-Echeverria 2010, Carr et al. 2011, Reynolds et al. 2012). In the current study, 300 *A. valida* per shoot (final average per vegetative or flowering shoot) in the no-predator treatment led to loss of 3–4 g wet weight per shoot (20–30% reduction) relative to the treatments with predators (final counts of 40–100 *A. valida* per shoot) in the 2 wk experiment. Very high final counts of *A. valida* were within the measured range of field abundances (maximum 588 per shoot; Reynolds et al. 2012); however, we caution that absolute values of eelgrass consumption from these experiments should not be used to estimate effects on eelgrass in the field.

High field densities of *A. valida* in San Francisco Bay could be partly due to the lower predation susceptibility of *A. valida*; caprellids and other gammarid amphipods have higher susceptibility and are readily and preferentially consumed by fish, including shiner surfperch (Caine 1991, Best & Stachowicz 2012). Hence, these findings suggest a possible important ecosystem role for caprellids, a mesograzer species often overlooked in seagrass–mesograzer interaction studies. As caprellids seem to be preferentially consumed by fish, this could limit predation on mesograzers (e.g. *A. valida*) that have stronger top-down effects on eelgrass or epiphytes, resulting in possible changes to seagrass ecosystem functioning.

The morphologies of flowering and vegetative seagrass shoots differ from each other in several ways that could influence higher order trophic dynamics. Perhaps most importantly, fruits develop on the spathes of flowering seagrass shoots, creating crevices and divots in which grazers can hide. These spaces appear to be quite important as refugia (Nakaoka et al. 2008, Carr et al. 2011). While artificial seagrass mimics have been used to determine how habitat complexity affects predation rates (e.g. Hovel & Lipcius 2001), we used live eelgrass shoots to understand how the plant tissues themselves affect and are affected by trophic interactions at higher levels.

Several studies have found that habitat complexity significantly decreases the foraging success of predators (Nelson 1979, Grabowski 2004). Our study corroborates these results: fish presence led to significantly lower *A. valida* abundance on structurally simple vegetative shoots compared to complex flowering shoots. However, other studies have found contrasting results; structurally complex elements do not universally offer better refuge from predation (e.g. Holmlund et al. 1990, Byers et al. 2010). Predator behavior may account for differential foraging success in structurally complex habitats (Almany 2004). Increased complexity could benefit sit-and-wait predators by providing more sites for predators to attack and shielding predators from prey (Coen 1981). In contrast, visual predators that actively pursue prey are less efficient in structurally complex habitats, as increased complexity hinders their ability to maneuver and see prey (Flynn & Ritz 1999). Shiner surfperch visually seek out and pursue prey; therefore, this study provides support for predator behavior as a major determinant of the effect of habitat complexity on foraging success.

In San Francisco Bay, fish community composition and abundance differ among eelgrass beds (Carr 2008, K. Boyer unpubl. data), and as beds are known to differ in their flowering rates and phenology (Boyer & Wyllie-Echeverria 2010), the top-down effects of predators are likely to vary over both space and time. It is worth mentioning that predation rates in San Francisco Bay eelgrass systems may differ from what was observed in mesocosms, due to constrained prey with a fixed density of predators. Nonetheless, our results are consistent with recent findings from other studies in the field in both seagrass (Lewis & Anderson 2012) and kelp forest (Davenport & Anderson 2007) systems that microcarnivorous fish can negatively affect mesograzers grazing rates and increase kelp and seagrass performance.

In conclusion, ecologists have long been interested in herbivore regulation of primary producers (e.g. Hairston et al. 1960, Mattson & Addy 1975, Simberloff et al. 1978, Dial & Roughgarden 1995), and grazers that have highly variable abundances and effects across their ranges remain an important focus of inquiry and management interest (e.g. Berg et al. 2006, Edburg et al. 2012). As herbivores are now frequently found in or relocated to novel habitats with new suites of species at one or more trophic levels, the ability to predict their functional roles and effects on ecosystem properties will become increasingly important for effective conservation and restoration (Hobbs et al. 2009). In this study, we showed that out-

breaks and direct damage to eelgrass by *A. valida* in San Francisco Bay, not observed elsewhere in this mesograzers' range, may be supported by insufficient predation (low numbers or efficiency), the presence of another mesograzers with greater predation susceptibility (and that also interfered via some non-consumptive mechanism in the case of one predator), as well as the presence of flowering shoots, which enhanced predation refuge. Our results are consistent with other recent mesocosm (Bodega Bay, CA; Best & Stachowicz 2012) and field studies (San Diego Bay, CA; Lewis & Anderson 2012) finding evidence of trophic cascades in which predators ultimately benefit seagrasses by controlling grazers. These studies support a growing awareness that protection or enhancement of predator populations in places where mesograzers harm seagrasses could be key in conservation efforts for these habitat-forming plants.

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