

Trophic cascades in seagrass meadows depend on mesograzer variation in feeding rates, predation susceptibility, and abundance

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ABSTRACT: Seagrasses provide important habitat for fishes and invertebrates but are declining around the globe, often due to overgrowth by algae. One hypothesis for this overgrowth is that overfishing of top consumers has led to greater numbers of small predatory fishes that reduce the abundance of mesograzers. This trophic cascade hypothesis requires that the same species that control algal biomass are also susceptible to fish predation. While mesograzers are known to vary in their feeding rates on algae and seagrasses, much less is known about variation in predation susceptibility and how this is related to grazing abilities. For 6 common mesograzers from Bodega Harbor, California, USA, we assessed feeding rates on macroalgae (*Ulva* spp.), epiphytic microalgae, and eelgrass. We then assessed predation susceptibility using juvenile cabezon *Scorpaenichthys marmoratus* in tanks of eelgrass habitat with and without *Ulva*. We found that the fastest consumers of all 3 primary producers were the least susceptible to predation. This appeared to be due to predator avoidance strategies; fish consumed visible caprellids at a higher rate than the larger consumers, which were either better camouflaged or able to avoid predation by building tubes within the macroalgae. Using our feeding and predation rates, along with relative abundances from field surveys, we calculated the expected trophic cascade effect with and without grazer species differences. Because fish predation was skewed towards the most abundant but least important (per capita) grazers, incorporating trait variation led to a 50 to 80% reduction in expected trophic cascade effects. Examining other seagrass communities for either similar grazer species or a similar mismatch between feeding rates and predation susceptibility may improve our understanding of the variation in trophic cascade effects across systems.

KEY WORDS: Epiphytes · Overgrowth · Amphipod · Eelgrass

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INTRODUCTION

Globally, seagrass ecosystems provide habitat for a diversity of fish and crustaceans as well as a number of ecosystem services, including sediment stabilization and nutrient cycling (Hemminga & Duarte 2000, Orth et al. 2006, Valentine & Duffy 2006). They are also declining at an accelerating rate (Waycott et al. 2009), often in association with overgrowth by micro- and macroalgae, which grow rapidly and prevent adequate light from reaching seagrass blades (Va-

liela et al. 1997, McGlathery 2001). Such blooms of algae may be increasing due to eutrophication of coastal waters or to food web alterations that reduce the numbers of the invertebrate grazers that regulate algal abundance (Hughes et al. 2004, Heck & Valentine 2007). This hypothesis that trophic cascades are partly responsible for global seagrass declines is based on evidence that grazers such as crustaceans and gastropods can have substantial impacts on algal abundance and on the idea that overfishing of top predators could increase the abundance of the fish

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that eat these grazers (Heck & Valentine 2007). In support of this hypothesis, recent field experiments have shown that in regions of Scandinavia with high densities of invertivorous fish, fish exclusion can lead to increases in grazer density and decreases in algae (Moksnes et al. 2008, Eriksson et al. 2009, Baden et al. 2010, Sieben et al. 2011). This parallels evidence for similar fish-invertebrate-periphyton trophic cascades in freshwater benthic systems (Power 1990, Bronmark et al. 1992, Martin et al. 1992, Vonesh et al. 2009).

Over a wide range of seagrass systems, however, the effect of predators on algal growth and seagrass production appears to be variable. Pinfish, an important consumer of mesograzers in Florida seagrass systems (Nelson 1979, Stoner 1979), will also consume epiphytic algae (Gacia et al. 1999, Heck et al. 2000), and (under nutrient enrichment) seagrass itself (Heck et al. 2006). Such omnivory has been widely documented as preventing trophic cascades (Persson 1999, Bruno & O'Connor 2005, Finke & Denno 2005, Eriksson et al. 2010). Along with this vertical heterogeneity in trophic structure, differences among species within a trophic level can also affect the potential for trophic cascades (Persson 1999). For example, in a large Caribbean food web, tri-trophic linkages between a producer, consumer, and predator species were less likely to contain 2 strong interactions than if assembled by chance (Bascompte et al. 2005). Instead, some consumers had strong interactions with predators, while others had strong interactions with prey. In cases in which a single consumer taxon was strongly linked to both a producer and a predator, omnivory was more likely (Bascompte et al. 2005). This mismatch between the most effective consumers and those most susceptible to predation may be an important mechanism for food web stability.

In seagrass systems, invertebrate grazers vary in their feeding rates on microalgae, macroalgae, and seagrasses themselves (Duffy & Hay 1991, Duffy et al. 2001, Raberg & Kautsky 2007, Jaschinski & Sommer 2008, Hughes et al. 2010). Although much less is known about species-specific predation susceptibility, species do vary in ways that may affect their visibility and escape success, such as size, coloring, and behavior. For example, caprellid amphipods cling to seagrass blades and are very slow swimmers, whereas amphipod amphipods hide in tubes between seagrass blades or in folds of macroalgae. In this study, we assessed for the first time both variation in feeding rates and variation in predation susceptibility for the same grazer species. We also mea-

sured the abundance of these species in field surveys. We then used these data to show how variation in these traits alters the potential for trophic cascades to increase overgrowth of the seagrass *Zostera marina* by macroalgae or epiphytic microalgae. We argue that predicting the effect of trophic cascades on algal abundance and seagrass photosynthesis depends on the extent to which the most important consumers of algae are also the most susceptible to fish predation.

MATERIALS AND METHODS

Study system

We conducted our study in Bodega Harbor, California, USA (38° 19.110' N, 123° 04.294' W). Bodega Harbor contains several large intertidal and sub-tidal beds of *Zostera marina* (hereafter eelgrass), as well as extensive mud flats. Eelgrass beds reach maximum density in summer and fall, with 100 to 250 shoots m⁻² and average shoot length ranging from 80 to 130 cm. Water temperature ranges from 6°C in the winter to 24°C in shallow beds during low tides in summer and fall (nearby ocean temperatures reach only 17°C). The warm temperatures and increased light influx between May and October correlate with increased growth of epiphytic microalgae and *Ulva* spp. macroalgae (hereafter *Ulva*), both of which compete with eelgrass for light and reduce eelgrass growth (Olyarnik 2008, Hughes et al. 2010).

Mesograzers in this system also peak in summer and fall, and include 11 common amphipod species, 2 isopods, and 4 mollusks. While one of the mollusks, the sea hare *Phyllaplysia taylorii*, is an important grazer of epiphytic microalgae (Hughes et al. 2010), it is more patchily distributed and lower in abundance than the crustacean grazers in this system. After measuring feeding rates on eelgrass, *Ulva*, and microalgae for each of the amphipod and isopod species in our system, we selected 6 species for further study. These species vary in their taxonomic group, origin, size, and behavior (Table 1), as well as their abundance and feeding rates, but include the most widely distributed mesograzers in Bodega Harbor eelgrass beds and the species with the fastest consumption rates on all 3 potential primary producers (R. Best unpubl. data). Subsets of all of these mesograzer species have also been reported from several other northeastern Pacific estuaries, including Boundary Bay in British Columbia, Willapa Bay in Washington, Coos Bay in Oregon, and

Table 1. Description of the grazer species studied

Species	Order	Family	Origin	Max. length (mm)	Max. width (mm)	Behavior
<i>Idotea resicata</i>	Isopoda	Valvifera	Native	45	8	Swimming/clinging
<i>Caprella californica</i>	Amphipoda	Caprellidae	Native	30	1	Clinging
<i>Caprella mutica</i>	Amphipoda	Caprellidae	Introduced	35	1.5	Clinging
<i>Ampithoe lacertosa</i>	Amphipoda	Ampithoidae	Native	25	7	Tube building
<i>Ampithoe sectimanus</i>	Amphipoda	Ampithoidae	Native	12	4	Tube building
<i>Ampithoe valida</i>	Amphipoda	Ampithoidae	Introduced	13	4	Tube building

Humboldt Bay, Tomales Bay, and San Francisco Bay in California.

The most abundant fish predators in Bodega Harbor include juvenile cabezon *Scorpaenichthys marmoratus*, juvenile perch (Embiotocidae; adults are much less abundant), rockfish *Sebastes* spp., sanddab *Citharichthys sordidus*, 3-spined stickleback *Gasterosteus aculeatus*, and in some years pipefish *Syngnathus* spp. and staghorn sculpin *Leptocottus armatus* (Bozdech 2004, Dowd 2006, Yip 2006). We chose to study juvenile cabezon because they are relatively abundant in Bodega Harbor from early spring to late fall, when they migrate to rocky reef habitat for adulthood, and have previously been shown to consume amphipods and isopods (as well as larger prey) in our system (Lewis 2002, Yip 2006, J. Hobbs pers. comm.). They are also found in other northeastern Pacific estuaries, and show annual variation in density that is thought to be driven by oceanographic conditions and variability in recruitment success (Wilson et al. 2008). This is in contrast to systems in which changes in the density of invertivorous fish may be driven by harvesting of top predators; we are investigating only the 3-level trophic relationship between small fish, mesograzers, and primary producers.

Juvenile cabezon grow larger than other abundant fish in the system, and have an especially large gape for their length, which should make them most able to consume our largest grazers. Gut-content analysis from Bodega Harbor is consistent with this: only cabezon had *Idotea* and a substantial fraction of amphipods in their guts, whereas stickleback, perch, sculpin, and sanddab consumed mostly *Heptacarpus* shrimp and/or polychaetes (Yip 2006). Given that adult mesograzers have a larger effect on algal biomass than juveniles (Moksnes et al. 2008), and that adults of the most important grazers in our system are large relative to gape size for most of these fish species, juvenile cabezon appear to be the most likely to consume these individuals.

Feeding trials

We measured species-specific feeding rates using 48 h no-choice feeding trials. We placed 2 ind. of a single grazer species in 250 ml plastic cups filled with seawater, and after 24 h starvation, added a single food source of either eelgrass, *Ulva*, or microalgae. Because we were gathering feeding rate data as part of a larger study including several other species of grazers, we used a total of 4 separate trials, 2 in the summer of 2009 and 2 in the summer of 2010, with the replicates for each combination of species with food type split between at least 2 trials. This also served to ensure that our results reflect true differences between species that hold over temporal variation in food quality. We used a total of 10 replicate cups per food type per grazer species, as well as 10 no-grazer controls for each food in each trial to account for growth or decay. These trials were conducted in an indoor wet lab on a 12 h light:12 h dark cycle.

For the eelgrass and *Ulva* replicates we used approximately 2 cm² of food, and measured consumption as change in wet weight, after adjusting the starting weight by the average percent change in control cups for that food in that trial. This amount of food was never completely depleted by the grazers. For the microalgae replicates we used 9 cm² pieces of window screen covered with microalgae and measured consumption as the reduction in chlorophyll relative to no-grazer controls for that trial. We obtained the microalgae by anchoring sheets of window screen (1 mm mesh size) on a horizontal frame within an eelgrass bed in Bodega Harbor for 2 wk prior to the feeding trials, cutting the sheets into 9 cm² pieces with even coverage of algae, and then randomly assigning these pieces to treatment and control cups.

To measure chlorophyll concentrations we froze the window screen in individual vials and extracted and calculated chlorophyll *a*, *b*, and *c* according to Parsons et al. (1984), using 10 ml of methanol/acetone/de-ionized water (45:45:10) as the extraction reagent

(Duffy & Harvilicz 2001), and a Beckman Coulter Spectrophotometer. Because change in chlorophyll *a* (hereafter chl *a*) was highly correlated with change in total chlorophyll, and represented most of the total, we simply used the decrease in the chl *a* concentration as our relative measure of grazing rate on epiphytic algae. Because we could not measure chlorophyll for individual replicates before and after feeding, we also measured chlorophyll abundance on 10 randomly selected pieces at the trial outset (the pre-trial control). We found that average chlorophyll was significantly higher in the control cups at the end of the trial than in this pre-trial control group, and therefore used only the final control measurement as a representation of average initial chlorophyll level plus growth.

Predation trials

We measured species-specific susceptibility to fish predation in 38 l (50 cm long × 25 cm wide × 30 cm tall), flow-through, outdoor aquaria planted with 15 shoots of eelgrass collected from Bodega Harbor, cleaned of all epiphytes and epifauna, cut to 30 cm in length, and anchored in clean sand. This density of shoots (120 m⁻²) is within the range of observed field densities but was low enough to facilitate recovery of all grazers at the end of the experiment. Because some of the grazer species are known to build tubes in *Ulva* to reduce vulnerability to fish predation (Olyarnik 2008), we assessed predation (1) with eelgrass only, and (2) with eelgrass plus 18 g wet weight of *Ulva*, added in 3 separate pieces anchored into the sand. We surrounded each tank with a double layer of shade cloth to reduce light to natural levels.

To each tank we added 30 grazers: a mix of 5 ind. of each of our 6 grazer species (Table 1). This density (240 ind. m⁻²) is well within the middle 50% of field observations of the combined density of these 6 species, based on the July and September field sampling we describe below. After allowing the grazers 24 h to acclimate and choose their microhabitat, we added a single juvenile cabezon *Scorpaenichthys marmoratus* (hereafter cabezon) of recorded length (range: 8 to 11 cm) and allowed it to feed for 12 h of daylight. Cabezon field density ranges from 0 to 0.2 m⁻² of eelgrass bed (Yip 2006), so only a single fish was used per tank. Prior to the predation trials, we held all cabezon in tanks of equal densities, with natural habitat, and fed them a standardized diet of frozen squid each day, except for a 24 h starvation period preceding the trial. Because cabezon are diurnal, we

measured their predation rates during 12 h of daylight to represent a daily rate.

Over 3 consecutive trial periods during September 2010, we conducted 10 treatment replicates (with fish) and 5 control replicates (without fish) for each habitat type. An independent but identically maintained group of fish was used in each trial. At the end of each trial we sieved all water, vegetation, and sand to recover and identify remaining grazers. We adjusted for species differences in probability of recovery independent of predation by subtracting the average number of each species missing from controls from the number eaten in each treatment replicate for that habitat type. The number missing from controls was never more than 1, with an average of 0.4 ind. for the treatment without *Ulva* and 0.3 with *Ulva*.

We chose to assess species-specific predation rates using a mixed community of grazers because we wanted to measure the choices fish might make in the mixed communities they encounter in the field. However, we also conducted single species trials for 5 of the 6 grazer species (all but *Ampithoe sectimanus*) using methods identical to those described above, but with 10 grazers of a single species and 3 replicates per species per habitat treatment. These trials were conducted in August 2010, using fish maintained in the same way as those in the mixed grazer trials. To test the extent to which relative predation rates depend on community composition, we regressed the relative feeding rates from these single species trials on the feeding rates in the mixed species trials. If the order of increasing predation susceptibility between species is consistent between the 2 types of trials, we should see a strong positive relationship. If, however, predation susceptibility depends on the other choices that cabezon have available, i.e. the composition of the grazer community, then we might see no relationship or a negative relationship.

Field sampling

In addition to variation in feeding rates and predation susceptibility, grazer species vary in their relative abundance. This further constrains both the potential of individual species to control primary producers and the probability they will be consumed by fish predators. To account for this, we measured abundance of all grazer species at 5 Bodega Harbor eelgrass beds in July and September (both within the period of maximum fish abundance) of 2009 and

2010. At each site, 5 replicate samples were taken 10 m apart along a transect, in approximately 0.6 m of water. To sample we collected a vertical core of the water column using a fine mesh bag (<500 μm) affixed to a flexible 30 cm diameter hoop, capturing all vegetation and animals and transporting the sample bags to the lab. We then cleaned each blade of eelgrass and algae of grazers, collected the grazers on a 1 mm sieve, identified and counted adults of each species, and converted this to number per m^2 .

To characterize the distribution of algae in our system we cleaned, dried, and weighed all pieces of *Ulva* in our samples, and converted this to weight per m^2 . We also determined the density of microalgae by randomly selecting 4 full leaves from each sample, scraping, filtering, drying, and weighing all epiphytes from these leaves, and dividing the dried weight by the leaf surface area.

Analysis

Our first objective was to determine if the most important consumers were also the most susceptible to fish predation. To identify differences between grazers in feeding rates and predation susceptibility we used mixed effects models. For the feeding rate data, we used 1 model for each primary producer (*Ulva*, eelgrass, and microalgae), with amount eaten per ind. per 24 h as the response variable, grazer species as the fixed effect, and trial as the random effect. For the predation data, we used 1 model for each habitat type (with or without *Ulva*), with number of individuals eaten as the response variable, grazer species as the fixed effect, and both tank and trial as random effects. We also included fish length as a covariate to account for variation in predation intensity or preferences associated with fish size.

We conducted these analyses in SAS (SAS Institute 2008) using the MIXED procedure with the Kenward Rogers method for estimating denominator degrees of freedom (Littell et al. 1996). To identify significant differences between multiple grazer species while maintaining an experiment-wise α of 0.05 we used a Tukey-Kramer adjustment, and to test the significance of random effects we used likelihood ratio tests. All residuals were checked for adherence to assumptions of normality and equal variance and no transformations were necessary.

Using a mixed model framework to analyze the predation data allowed us to calculate species-specific predation rates while factoring out variation due to multiple trials and to individual fish, which is

essential for the further analyses described below. It also provided one way to test for significant differences between predation rates by using tank as a random effect to account for non-independence between the multiple species in each tank. However, multiple-choice feeding trials can carry an additional problem of negative correlations among observations within a single experimental unit (Lockwood 1998), which can arise when the time spent consuming individuals of one species translates directly into fewer consumed of another species. We therefore also conducted a rank transformation to remove these correlations. We ranked all observations in the analysis regardless of block, and then analyzed the ranks in a randomized complete block ANOVA (Conover & Iman 1981, Iman et al. 1984). This method has far greater power than other rank-based methods when data are normally distributed (Iman et al. 1984) and has recently been used in similar studies of diet selection in seagrass systems (Prado & Heck 2011). We conducted this analysis for each habitat type in SAS (SAS Institute 2008) using the RANK and GLM procedures, with tank as the block, grazer species as the effect, and again with a Tukey-Kramer adjustment for multiple comparisons (Conover & Iman 1981).

Our second objective was to compare the expected trophic cascade effect of fish predation on primary producers with or without information on grazer trait variability (feeding rate, predation susceptibility, and abundance). To do this, we used the least-squares mean estimates of feeding and predation rates, as well as average field abundance. To calculate average abundance in field samples for each species we again used a mixed effects model, with abundance as the response variable, grazer species as the fixed effect, and sampling period and eelgrass bed as the random effects. To meet assumptions, we log-transformed abundance and then back-transformed least squares means for presentation.

Under each of 4 scenarios, we calculated the amount of each primary producer (eelgrass, *Ulva*, and microalgae) that would no longer be removed due to consumption of grazers by a single cabezon. In each case, we first determined how many individuals of each of the 6 grazer species would be eaten per day in that scenario. We then multiplied the number eaten by that grazer species' daily per capita feeding rate. Finally, we summed these products across all 6 species. Our objective here was to compare the *relative* trophic cascade effect that would be expected with or without accounting for grazer trait differences. We did not attempt to calculate *absolute* algal biomass remaining in the field because this would

require additional data on predator abundance and primary producer abundance and growth rates. Important assumptions underlying these calculations (i.e. that feeding on each primary producer is independent of the other primary producers, and that both species-specific predation rates and total number of grazers eaten are independent of grazer community composition) are evaluated in the 'Results'. The scenarios are described in order of increasing incorporation of variability among grazer species. Sample calculations from each scenario are given in Table A2 in Appendix 1. The scenarios are as follows:

(1) All grazer species are equal. The number of each grazer species eaten is the average total number of grazers eaten divided by the 6 species. The feeding rate for each species is the average of all 6 grazer species' feeding rates.

(2) Grazer species vary in their feeding rates and susceptibility to predation. The number of each grazer species eaten is the species-specific mean predation rate determined in this study. The feeding rates for this and the 2 following scenarios are the species-specific mean feeding rates determined in this study.

(3) Grazer species vary in abundance and feeding rates. The number of each grazer species eaten is the average total number of grazers eaten multiplied by the proportional abundance of that grazer (where proportional abundance is the average field abundance of the 6 grazer species scaled to sum to 1). This assumes grazers are eaten as they are encountered, and predation susceptibility depends only on relative abundance. Predation susceptibility on an individual basis is equal across species.

(4) Grazer species vary in abundance, feeding rate, and susceptibility to predation. The number of each grazer species eaten is the species-specific mean predation rate multiplied by its relative abundance, and scaled so that the rates sum to the average total number of grazers eaten. Predation susceptibility in this scenario is thus jointly determined by the relative abundance and the relative predation rates determined in this study.

RESULTS

Variation in feeding and predation rates

For all 3 foods, feeding rates were significantly different across the 6 grazer species, and were not affected by variation among trials (Table 2). The order of the grazers' feeding rates also varied among the 3 foods (Fig. 1A–C). *Ampithoe lacertosa* was by far the fastest consumer of macroalgae (*Ulva*), but only an average grazer of eelgrass and the second fastest consumer of microalgae. *Idotea ressecata* was the fastest consumer of eelgrass and microalgae. The introduced species *A. valida* was a relatively important consumer of eelgrass but not algae. On the low end of the spectrum, *Caprella californica* and the introduced *C. mutica* were the slowest consumers of all 3 foods, and consumed only microalgae at a rate significantly greater than zero.

Grazer species also showed significant variation in predation susceptibility, both with and without *Ulva*

Table 2. Statistical significance of grazer variation in feeding rates, predation susceptibility, and abundance. GLMM: general linear mixed model on number eaten per day for each species. Significant p-values ($p < 0.05$) are in **bold**

Response variable	Fixed effect	df	F	p	Random effect	p
Feeding rate						
<i>Ulva</i> (mg ind. ⁻¹ d ⁻¹)	Grazer species	5,54	105.52	<0.0001	Trial	1
Eelgrass (mg ind. ⁻¹ d ⁻¹)	Grazer species	5,54	16.48	<0.0001	Trial	1
Microalgae (µg chl a ind. ⁻¹ d ⁻¹)	Grazer species	5,54	107.82	<0.0001	Trial	0.8
Predation rate with <i>Ulva</i> (no. fish⁻¹ d⁻¹)						
GLMM	Grazer species	5,51	3.85	0.005	Trial	0.04
GLMM	Fish length	1,53	3.65	0.06	Tank	0.2
Rank-transformation test	Grazer species	5,45	3.45	0.01		
Predation rate without <i>Ulva</i> (no. fish⁻¹ d⁻¹)						
GLMM	Grazer species	5,53	6.17	<0.0001	Trial	0.5
GLMM	Fish length	1,53	0.21	0.6	Tank	0.8
Rank-transformation test	Grazer species	5,45	6.76	<0.0001		
Abundance (no. m ⁻²) ^a	Grazer species	5,552	187.12	<0.0001	Sampling period Site	0.01 <0.0001

^aLog transformed for analysis

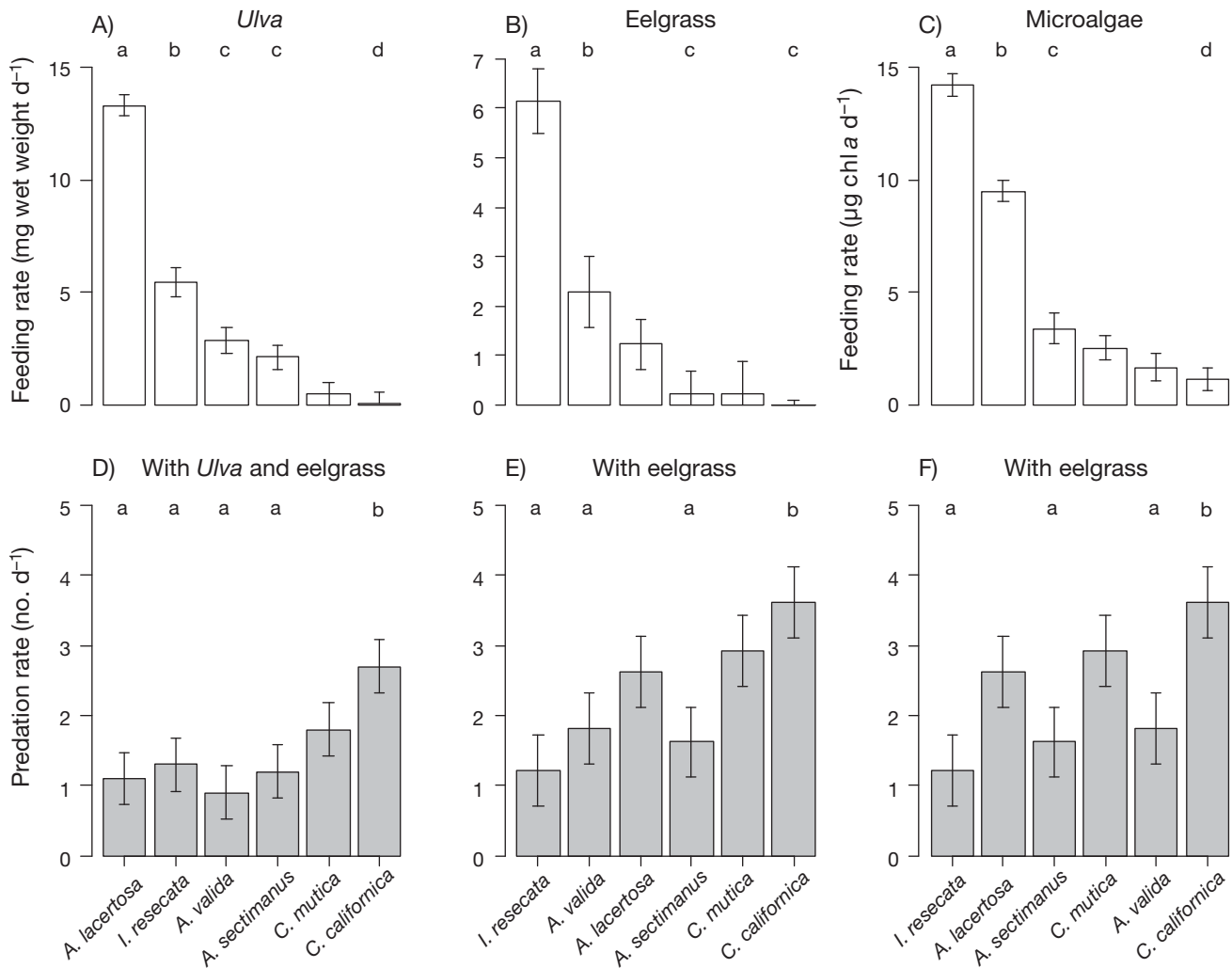


Fig. 1. Species-specific feeding and predation rates of the 6 mesograzer species studied. Top: (A, B, C) show feeding rates on *Ulva*, eelgrass, and microalgae in decreasing order for that food. Below: (D, E, F) show predation rates in the same order (D: predation rates with *Ulva* present; E, F: predation rates with *Ulva* absent). Letters indicate significant differences between species (which for panels (D, E, F) are supported by multiple comparison tests on both the untransformed and rank-transformed data); species without a letter are intermediate. Error bars are ± 1 SE from the untransformed mixed model analyses. For full species names and characteristics see Table 1

(Table 2). To identify the correspondence between feeding rate and predation susceptibility, we show the grazer species ordered according to feeding rate for each food (Fig. 1A–C), and present the predation rates for the same species in that order below (Fig. 1D–F). For this comparison, we show the predation rates with *Ulva* present for comparison to feeding rates on *Ulva*, and the predation rates without *Ulva* for comparison to feeding rates on eelgrass and microalgae.

With *Ulva* present, all 3 *Ampithoe* species and *Idotea reseccata* experienced less predation than *Caprella californica*, with *C. mutica* showing an intermediate predation rate (Fig. 1D). This means that in

cases where *Ulva* is the dominant competitor of eelgrass, the species most able to control *Ulva* should be the least susceptible to predation (Fig. 1A,D).

When *Ulva* was absent, predation susceptibility was lowest for the most important consumers of both eelgrass and epiphytic microalgae. The species with the fastest consumption of eelgrass (*Idotea reseccata* and *Ampithoe valida*, Fig. 1B) showed significantly lower predation susceptibility than the 2 *Caprella* species, which did not consume eelgrass at a significant rate (Fig. 1E). Similarly for microalgae, the species with the highest consumption rates had somewhat lower predation rates (Fig. 1C,F). Overall, this trend appears to hold across the 3 columns of Fig. 1;

the most important consumers were the least susceptible to fish predation.

Finally, we found that the relative predation rates measured in our mixed species trials followed the same pattern in our single species predation trials (Fig. 2). The presence of *Ulva* did not affect the slope of this relationship ($p = 0.7$) but did marginally affect the intercept ($p = 0.06$) by reducing total predation for both single and mixed trials. Overall, there was a strong positive relationship between the predation rates on each species alone and in mixture ($F_{1,6} = 25.21$, $p = 0.002$, $R^2 = 0.81$).

Field abundance

In addition to variation in feeding and predation rates, the 6 grazer species in our study also showed substantial differences in abundance (Fig. 3). The native caprellid *Caprella californica* was by far the most abundant, followed by *Ampithoe lacertosa* and *Idotea resecata*, which were both significantly more abundant than the remaining 3 species. Grazer species differences in abundance were highly significant ($p < 0.0001$) despite the significant random effects of both time and site on abundance (Table 2). We used the mean species abundances over all samples, but using the abundances from any particular time period yields similar results.

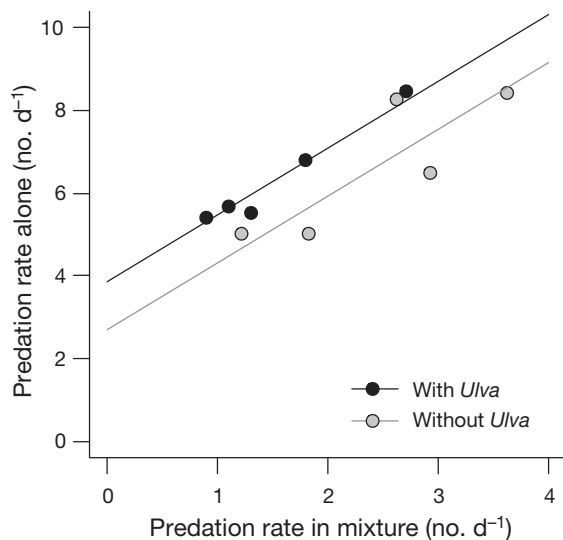


Fig. 2. Predation rate on each of 5 grazer species measured in both grazer mixtures and alone (the 6th species, *Ampithoe sectimanus*, was not included in the single species trials). For each species, predation is either unaffected by habitat or higher in the absence of *Ulva*. Points with the same x-value are not the same species, so the higher intercept for the *Ulva* treatment reflects an effect of species rather than an effect of habitat

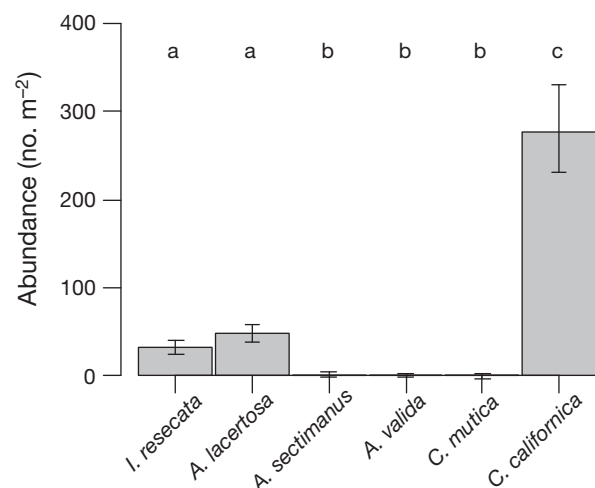


Fig. 3. Average abundance of each species. Abundance was log-transformed for analysis and least squares means were back-transformed. Different letters indicate significant differences between species. Error bars are ± 1 SE. For full species names see Table 1

Expected trophic cascade effects

The relative magnitude of trophic cascade effects predicted in this system was substantially decreased by accounting for species-specific grazer variation. Assuming all grazers were equivalent in their feeding preferences and susceptibility to predators, we calculated that predation by 1 additional juvenile cabezon should result in approximately 35 mg more *Ulva*, 20 mg more eelgrass, or 70 μg more microalgal chl a per day (Fig. 4). Accounting for the variation in feeding and predation rates reported here reduced these estimates, as did accounting for differences among species in field abundance. In combination, the expected size of the trophic cascade effect was reduced by 71% for *Ulva*, 80% for eelgrass, and 54% for microalgae (Fig. 4).

We also found evidence that some major assumptions underlying this analysis are reasonable. First, we evaluated the potential for a trophic cascade for each primary producer separately, which assumes that grazing rates on each food in the field are independent of the availability of other foods. Several lines of evidence support this assumption for at least the most abundant species in this system. *Caprella californica* fed exclusively on epiphytic microalgae (Fig. 1A–C), so its feeding rate should not depend on eelgrass or *Ulva* abundance. For *Idotea resecata* and *Ampithoe lacertosa*, we found previously that feeding rates for both species on eelgrass and *Ulva* does not depend on whether or not the grazers have only a

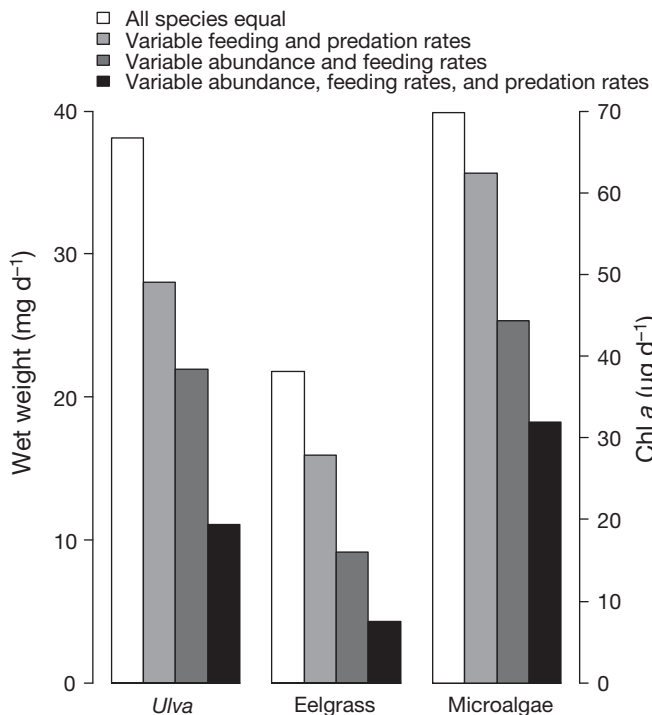


Fig. 4. Expected additional amount of each primary producer resulting from predation by 1 additional fish per day under 4 scenarios of grazer trait variation. Amounts are measured in wet weight for *Ulva* and eelgrass and in chl *a* for microalgae. For details of the 4 scenarios see 'Materials and methods: Analysis'

single food or a choice of both (R. Best unpubl. data). In addition, the spatial distributions of the 2 major algal primary producers in our system (*Ulva* and microalgae) are largely non-overlapping (Fig. 5), such that grazers will rarely have a choice between these 2 foods at any particular place and time.

Second, we assumed that the species-specific predation rates would not depend on the composition of the grazer community which fish would encounter in the field. Whereas our experimental communities consisted of 30 ind. evenly distributed between 6 species, the abundance of these species in the field is not even (Fig. 3). However, predation rates on single grazer species were positively correlated with their predation rates in the mixed-grazer trials (Fig. 2), meaning that relative predation susceptibility may be robust to variation in grazer composition in the field.

Third, we used the average total consumption from the mixed-grazer predation trials (9.4 total individuals consumed with *Ulva* and 12.9 without *Ulva*) across all scenarios in this analysis, varying only the proportional contribution of each grazer species to that total according to predation susceptibility and/or

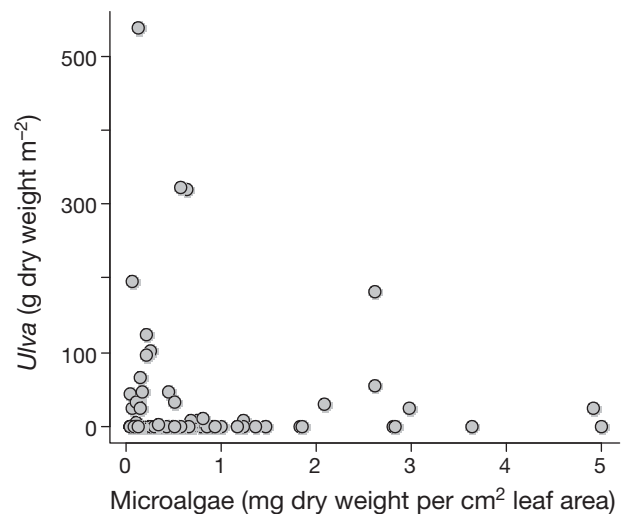


Fig. 5. Abundance of *Ulva* and microalgae in field samples

relative abundance. This assumes that the total number of grazers consumed per fish per day does not depend on the composition of the grazer community which fish encounter in the field. It is possible, however, that total consumption is actually higher in communities with higher relative abundances of *Caprella californica*, which might be common in the field (Fig. 3). Higher predation on *C. californica* should not affect our calculations for *Ulva* or eelgrass because this species does not consume macrophytes (Fig. 1A,B). For epiphytic microalgae, however, this could lead to a somewhat greater trophic cascade effect than we predict. Further studies of how grazer community composition drives total consumption rates would be helpful in evaluating this assumption.

DISCUSSION

We found significant variation among grazer species in feeding rates, predation susceptibility, and abundance, with predation pressure skewed towards the least important (per capita) and most abundant consumer (*Caprella californica*). Thus, the impact of trophic cascades on primary producer abundance in our system should be less than would have been expected without knowledge of grazer variation in feeding rates and predation susceptibility. The high abundance of grazers and invertivorous fishes that consume grazers in seagrass beds makes it logical to conclude that a strong trophic cascade is likely. However, evidence for trophic cascades and top-down control of the grazer trophic level in seagrass systems has so far been mixed (Douglass et al. 2010). If the

negative correlation between predation susceptibility and grazer impact that we observe occurs in some systems and not others, this may partly explain the variation in results.

Differences in feeding niche among grazers have been demonstrated in several other seagrass and algae systems (Duffy & Hay 1991, Duffy et al. 2001, Raberg & Kautsky 2007, Jaschinski & Sommer 2008), and there are several reasons to think that similar patterns of predation susceptibility may not be unique to our system. Below, we consider the generality of our predictions by examining patterns in grazer population growth, size, and habitat use that may be relevant to other seagrass systems.

Generality of the negative relationship between grazing rates and predation susceptibility

Of the grazer species in our community, caprellids were the most susceptible to predation. Caprellids are long but very thin (Table 1), cling to eelgrass high in the canopy, sometimes wave back and forth in search of food, and are slow to escape. This behavior appears to make them highly vulnerable to predation. Caine (1991) found that shiner perch *Cymatogaster aggregata* strike in response to caprellid movement and feed on them almost exclusively, when they are available. Two studies in other habitats used fish gut-content analysis in comparison with surveys of grazer abundance (Page et al. 2007, Vazquez-Luis et al. 2010) and also found that caprellids were selectively consumed to a greater extent than gammarid amphipods. A similar approach in a Florida seagrass system showed that selective feeding on caprellids increased with seagrass density, presumably because other more cryptic species had greater opportunities to hide (Stoner 1979). If caprellids also have weak per capita effects on epiphytic algae in these systems, then predation pressure may be focused on the least important grazers (per capita) wherever caprellids form a substantial fraction of the grazer community. This does not necessarily mean that caprellids as a group are unimportant in controlling seagrass epiphytes; they graze epiphytic algae without damaging eelgrass, and large numbers of individually inefficient grazers can have large effects (Silliman & Bortolus 2003). It means only that, in comparison to other species, many individual caprellids can be lost to predation before there is a major impact on microalgal abundance.

The persistence of abundant summer caprellid populations in Bodega Bay and other northeastern

Pacific estuaries, despite their predation susceptibility, may be due to a tradeoff between rapid growth rate and predator avoidance, as previously demonstrated with fish predation on dragonflies (McPeck 1998). In our system, caprellids increase more rapidly than other mesograzers at the start of the summer season in Bodega Harbor, while the larger, slower growing, and better camouflaged isopods reach peak abundance a full 2 mo later. This suggests there might be different strategies to deal with predation, with some species having fewer, slower growing, larger individuals with higher feeding rates and lower predation susceptibility, and other species producing greater numbers of individuals that are less efficient grazers per capita and more susceptible to predation but able to grow and reproduce quickly.

While this tradeoff contradicts the notion that larger grazers are more apparent and thus more susceptible to predation (Nelson 1980), previous work reports both positive (Moksnes et al. 2008) and negative (Eriksson et al. 2009) correlations between mesograzer size and predation. In our study, the largest (by length) grazers (Table 1) were found on opposite ends of the predation susceptibility spectrum. This suggests that cryptic morphology or behavior may overwhelm the effects of size on predation susceptibility. In this study and in previous work in this system (Olyarnik 2008, our Fig. 1D,E), tube building in *Ulva* substantially reduced predation susceptibility for *Ampithoe lacertosa*, which is by far the largest amphithoid in this system and the fastest consumer of *Ulva* (Fig. 1A).

In our study, we considered only the effect that fish predation may have on grazer abundance, but predator presence can also change the habitat choices (Wellborn et al. 1996, Resetarits 2001, Vonesh et al. 2009) and consumption rates (Schmitz et al. 1997, Duffy et al. 2005) of existing grazers. For tube-building amphipods that use the macroalgae they consume as a refuge (e.g. *Ampithoe lacertosa*), there should be little tradeoff between feeding and protection from predators, and predator avoidance might actually serve to concentrate grazers in areas with abundant macroalgae. This should help buffer the system against macroalgal trophic cascades. In habitats with scarcer protection, however, feeding and refuge use may not occur simultaneously, and grazing rates on microalgae could be lower in the presence of fish. If species such as *Idotea resicata*, the fastest consumer of microalgae, are successful at avoiding predation because they are camouflaged while feeding along eelgrass blades, then behavioral responses to fish presence should be consistent with the abundance-based effects we found. If, on the

other hand, the grazers that are least susceptible to fish predation only accomplish this via greatly reduced activity that includes reduced feeding rates, this could counteract the effects we found.

The extent to which fish presence changes the relative feeding rates of different grazer species on different primary producers would be an excellent avenue for further research, as would the relative effects of different fish species. Because cabezon consumed the thinner but more visible of the mesograzers in our system, we expect that smaller-gaped fish species may have similar if not more extreme feeding preferences for caprellids and small amphipods. However, other fish species may have additional behavior-induced effects on grazer feeding rates that warrant investigation.

Effects of grazer trait variation on eelgrass itself

In our system, both *Ulva* and microalgae compete with eelgrass for light, with *Ulva* reaching high abundance in shallow areas (over 500 g dry weight m^{-2}) but epiphytic algae present in a greater number of samples (Fig. 5). We have observed both microalgal accumulation and shading from *Ulva* to reduce eelgrass growth in mesocosms (Hughes et al. 2010; R. Best unpubl. data), and have seen *Ulva* decrease eelgrass biomass and shoot density in the field (Olyarnik 2008). We found a larger reduction in predicted trophic cascade effect due to grazer trait variation for *Ulva* (71%) than for microalgae (54%). This is because microalgae was consumed by all of the grazer species in our study, including the predation-susceptible caprellids. This does not mean that overgrowth by microalgae is more likely than overgrowth by macroalgae in our system, only that there is less variation among species in their consumption of microalgae. Because of this, in systems where the only threat to seagrass is overgrowth by epiphytic microalgae, accounting for grazer trait variation may have a smaller effect.

The hypothesis that seagrass decline may be due to trophic cascades assumes that small invertebrate grazers feed exclusively on algae, rather than directly on eelgrass, which is true for most but not all grazer species in both our system and others (Heck & Valentine 2006). The skew in predation pressure towards the slowest consumers of algae should have a positive effect on eelgrass, since predation by fish should not lead to as much additional algae growth as would occur if predation focused on grazers with high per capita grazing rates. However, we also

found relatively low vulnerability to predation for the few species that do consume eelgrass, including *Idotea ressecata* and the introduced species *Ampithoe valida* (Fig. 1E). This means there is also lower potential for cabezon predation to reduce direct consumption of eelgrass than we would expect using average mesograzer grazing and predation rates (Fig. 4). Thus, the skew in predation susceptibility has both positive and negative implications for eelgrass. Eelgrass should face not only a smaller than expected increase in its competitors but also a smaller than expected escape from its own grazers.

Grazer trait variation may help explain weak evidence for trophic cascades in some seagrass systems

In this study, mesograzer variation in feeding niche, predation susceptibility, abundance, and distribution all contributed to a decrease in the expected strength of the trophic cascade. Furthermore, there are reasons to expect that the same pattern could be important in some other seagrass systems. The same grazer community is found in several estuaries along the west coast of North America, and caprellids in particular may play a similar role. They appear to be important fish food in many systems (Stoner 1979, Caine 1991, Page et al. 2007, Vazquez-Luis et al. 2010), generally do not consume macrophytes (Caine 1977, Guerra-García & Tierno de Figueroa 2009), and have slow feeding rates on epiphytes. They may therefore absorb a substantial fraction of predation pressure with little effect on lower trophic levels. At the other end of our grazer spectrum, the amphipods represent a large and diverse family of grazers that are common components of seagrass systems globally (Poore et al. 2008) and may be widely protected from predation by their behavior of building tubes within their food plants (Duffy & Hay 1994).

Previous studies have explained the lower than expected strength of trophic cascades as a consequence of omnivory (Persson 1999) or the broad taxonomic class (e.g. vertebrate vs. invertebrate) of predator and herbivore (Borer et al. 2005), but much more attention may need to be paid to variation in traits among species within a trophic level. As others have noted, this requires that we collect data on the relative abundance of herbivores by size and species rather than gross trophic level biomass (Persson 1999, Moksnes et al. 2008). In combination, we also need further research on the potential tradeoffs between life history, morphology, and behavior that determine the ecolog-

ical roles played by particular widespread taxonomic groups. Given these data, we can better predict the proportion of grazer species in seagrass systems globally that are both important consumers and highly susceptible to predation, the dual criteria necessary for strong trophic cascades to occur.

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Appendix 1. Sample calculation of expected trophic cascade effects

Calculations used for comparing the trophic cascade effect on *Ulva* abundance under different scenarios of grazer trait variation. In each case, we calculate the additional amount of *Ulva* expected to remain in the system due to removal of herbivores by predation by 1 juvenile cabezon in 1 d. These calculations produce the 4 bars in the first column of Fig. 4. Table A1 shows species-specific and average rates, with each column labeled with a letter. These letters are then used to indicate the data used in calculations for each scenario (Table A2). The calculations involved the following steps: (1) Determine how many of each of the 6 grazer species would be eaten per day. (2) Multiply the number eaten by that species' daily per-capita feeding rate. This gives the total amount of *Ulva* no longer eaten by that species. (3) Sum these products across all 6 species.

Thus, under a scenario without grazer trait variation (Scenario 1), we predict that 1 cabezon would increase the amount of *Ulva* present in our system by 38.2 mg per day. In contrast, including all sources of trait variation we predict the increase in algae to be only 11.1 mg, a 71% decrease from 38.2

Table A1. Data

Grazer species	Predation rate (no. d ⁻¹)	Feeding rate on <i>Ulva</i> (mg d ⁻¹)	Abundance (no. m ⁻²)	Proportional abundance (sums to 1)
	A	C	E	F
<i>Idotea resecata</i>	1.3	5.5	31.8	0.1
<i>Caprella californica</i>	2.7	0.1	276.6	0.8
<i>Caprella mutica</i>	1.8	0.5	0.0	0.0
<i>Ampithoe lacertosa</i>	1.1	13.3	47.4	0.1
<i>Ampithoe sectimanus</i>	1.2	2.1	1.0	0.0
<i>Ampithoe valida</i>	0.9	2.9	0.0	0.0
Total	9.4			1.0
	B	D		
Average	1.6	4.1		

Table A2. Calculations

Scenario 1: All species equal	No. eaten B	Feeding rate D	No. eaten × feeding rate	Scenario 3: Variable abundance and feeding rates	No. eaten F × 9.4 ^a	Feeding rate C	No. eaten × feeding rate
<i>Idotea resecata</i>	1.6	4.1	6.4	<i>Idotea resecata</i>	0.8	5.5	4.6
<i>Caprella californica</i>	1.6	4.1	6.4	<i>Caprella californica</i>	7.3	0.1	0.7
<i>Caprella mutica</i>	1.6	4.1	6.4	<i>Caprella mutica</i>	0.0	0.5	0.0
<i>Ampithoe lacertosa</i>	1.6	4.1	6.4	<i>Ampithoe lacertosa</i>	1.2	13.3	16.6
<i>Ampithoe sectimanus</i>	1.6	4.1	6.4	<i>Ampithoe sectimanus</i>	0.0	2.1	0.1
<i>Ampithoe valida</i>	1.6	4.1	6.4	<i>Ampithoe valida</i>	0.0	2.9	0.0
Total	9.4		38.2 mg d⁻¹	Total	9.4		22.0 mg d⁻¹
Scenario 2: Variable feeding and predation rates	No. eaten A	Feeding rate C	No. eaten × feeding rate	Scenario 4: Variable abundance, feeding rates, and predation rates	No. eaten (A × F) × [9.4/Σ(A × F)] ^b	Feeding rate C	No. eaten × feeding rate
<i>Idotea resecata</i>	1.3	5.5	7.1	<i>Idotea resecata</i>	0.5	5.5	2.5
<i>Caprella californica</i>	2.7	0.1	0.3	<i>Caprella californica</i>	8.3	0.1	0.8
<i>Caprella mutica</i>	1.8	0.5	0.9	<i>Caprella mutica</i>	0.0	0.5	0.0
<i>Ampithoe lacertosa</i>	1.1	13.3	14.7	<i>Ampithoe lacertosa</i>	0.6	13.3	7.8
<i>Ampithoe sectimanus</i>	1.2	2.1	2.5	<i>Ampithoe sectimanus</i>	0.0	2.1	0.0
<i>Ampithoe valida</i>	0.9	2.9	2.6	<i>Ampithoe valida</i>	0.0	2.9	0.0
Total	9.4		28.0 mg d⁻¹	Total	9.4		11.1 mg d⁻¹

^aPredation rate is now determined only by relative abundance, which is scaled to the same total predation as in previous scenarios

^bPredation rate is now determined by both relative abundance and relative predation, and scaled to the same total predation as in previous scenarios