Corrections

ECOLOGY

Correction for "Recovery of a top predator mediates negative eutrophic effects on seagrass," by Brent B. Hughes, Ron Eby, Eric Van Dyke, M. Tim Tinker, Corina I. Marks, Kenneth S. Johnson, and Kerstin Wasson, which appeared in issue 38, September 17, 2013, of *Proc Natl Acad Sci USA* (110:15313–15318; first published August 27, 2013; 10.1073/pnas.1302805110).

The authors note that Fig. 2 appeared incorrectly. The authors note that they "unintentionally labeled Fig. 2*C* 'Grazer biomass (g DW) *shoot (cm)$^{-1}$' instead of 'Grazer biomass (mg DW) *shoot (cm)$^{-1}$.' " The corrected figure and its legend appear below. This error does not affect the conclusions of the article.

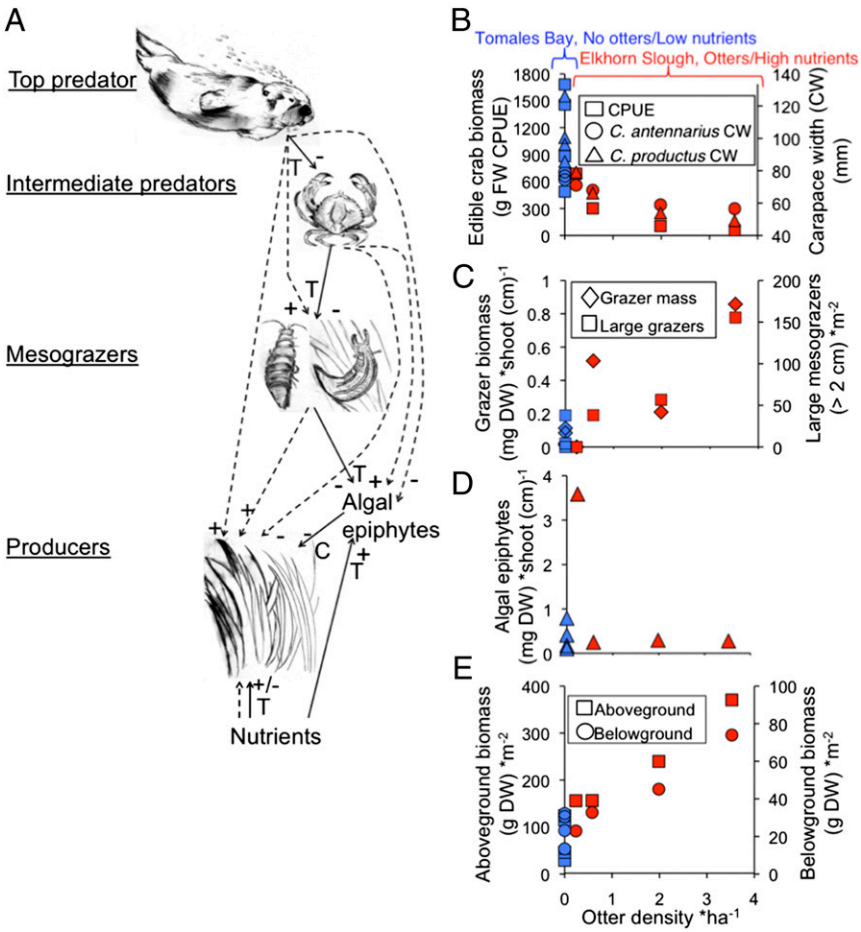

Fig. 2. (*A*) Interaction web of top-down and bottom-up effects in the eelgrass study system. The top predator is the sea otter (*E. lutris*), the mesopredators are crabs (*Cancer* spp. and *Pugettia producta*), the epiphyte mesograzers are primarily an isopod (*I. resecata*) and a sea slug (*P. taylori*), and algal epiphyte competitors of eelgrass primarily consist of chain-forming diatoms, and the red alga *Smithora naiadum*. Solid arrows indicate direct effects, dashed arrows indicate indirect effects, and the plus and minus symbols indicate positive and/or negative effects on trophic guilds and eelgrass condition. C, competitive interaction; T, trophic interaction. (Original artwork by A. C. Hughes.) (*B*–*E*) Survey results testing for the effects of sea otter density on eelgrass bed community properties (Tables S2 and S3). Elkhorn Slough (sea otters present and high nutrients) eelgrass beds (n = 4) are coded in red, and the Tomales Bay reference site (no sea otters, low nutrients) beds (n = 4) are coded in blue. (*B*) Crab biomass and size structure of two species of *Cancer* crabs; (*C*) grazer biomass per shoot and large grazer density; (*D*) algal epiphyte loading; and (*E*) aboveground and belowground eelgrass biomass. DW, dry weight; FW, fresh weight.

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MICROBIOLOGY

Correction for "Programmed Allee effect in bacteria causes a tradeoff between population spread and survival," by Robert Smith, Cheemeng Tan, Jaydeep K. Srimani, Anand Pai, Katherine A. Riccione, Hao Song, and Lingchong You, which appeared in issue 5, February 4, 2014, of *Proc Natl Acad Sci USA* (111:1969–1974; first published January 21, 2014; 10.1073/pnas.1315954111).

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SYSTEMS BIOLOGY

Correction for "Analysis of proteome dynamics in the mouse brain," by John C. Price, Shenheng Guan, Alma Burlingame, Stanley B. Prusiner, and Sina Ghaemmaghami, which appeared in issue 32, August 10, 2010, of *Proc Natl Acad Sci USA* (107:14508–14513; first published August 10, 2010; 10.1073/pnas.1006551107).

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NEUROSCIENCE

Correction for "Mapping the receptor site for α-scorpion toxins on a Na^+ channel voltage sensor," by Jinti Wang, Vladimir Yarov-Yarovoy, Roy Kahn, Dalia Gordon, Michael Gurevitz, Todd Scheuer, and William A. Catterall, which appeared in issue 37, September 13, 2011, of *Proc Natl Acad Sci USA* (108:15426–15431; first published August 29, 2011; 10.1073/pnas.1112320108).

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Recovery of a top predator mediates negative eutrophic effects on seagrass

Brent B. Hughes[a,1], Ron Eby[b], Eric Van Dyke[b], M. Tim Tinker[a,c], Corina I. Marks[d], Kenneth S. Johnson[e], and Kerstin Wasson[a,b]

[a]Department of Ecology and Evolutionary Biology, Long Marine Laboratory, University of California, Santa Cruz, CA 95060; [b]Elkhorn Slough National Estuarine Research Reserve, Watsonville, CA 95076; [c]US Geological Survey, Western Ecological Research Center, Santa Cruz, CA 95060; [d]Seafloor Mapping Lab, Division of Science and Environmental Policy, California State University, Monterey Bay, Seaside, CA 93955; and [e]Monterey Bay Aquarium Research Institute, Moss Landing, CA 95039

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A fundamental goal of the study of ecology is to determine the drivers of habitat-forming vegetation, with much emphasis given to the relative importance to vegetation of "bottom-up" forces such as the role of nutrients and "top-down" forces such as the influence of herbivores and their predators. For coastal vegetation (e.g., kelp, seagrass, marsh, and mangroves) it has been well demonstrated that alterations to bottom-up forcing can cause major disturbances leading to loss of dominant vegetation. One such process is anthropogenic nutrient loading, which can lead to major changes in the abundance and species composition of primary producers, ultimately affecting important ecosystem services. In contrast, much less is known about the relative importance of apex predators on coastal vegetated ecosystems because most top predator populations have been depleted or lost completely. Here we provide evidence that an unusual four-level trophic cascade applies in one such system, whereby a top predator mitigates the bottom-up influences of nutrient loading. In a study of seagrass beds in an estuarine ecosystem exposed to extreme nutrient loading, we use a combination of a 50-y time series analysis, spatial comparisons, and mesocosm and field experiments to demonstrate that sea otters (*Enhydra lutris*) promote the growth and expansion of eelgrass (*Zostera marina*) through a trophic cascade, counteracting the negative effects of agriculturally induced nutrient loading. Our results add to a small but growing body of literature illustrating that significant interactions between bottom-up and top-down forces occur, in this case with consequences for the conservation of valued ecosystem services provided by seagrass.

eutrophication | food web | estuary | resilience

Understanding the relative influence of "bottom-up" vs. "top-down" forces on vegetated assemblages has long been an important conceptual goal of the study of ecology (1–4). As many vegetated habitats have declined globally in past decades (5–8), with concurrent losses of valued ecosystem services, investigations of drivers of vegetation sustainability have also taken on applied significance and urgency in conservation science (9, 10). Human activities have altered bottom-up forces, for instance by increasing nutrient availability (11, 12), and top-down forces, by hunting and fishing of top predators (5, 13). Detecting the relative role of such alterations and interactions between them is critical for supporting key vegetated habitats and their ecosystem services.

Investigations of bottom-up and top-down forces in a single system can be challenging. Changes at the top of food webs have been demonstrated to affect vegetation in a diversity of ecosystems (5, 13–15). However, apex predators have been depleted or lost entirely across most of the natural world (5, 13), including many near-shore marine systems (5, 16). It is difficult to understand ecosystem-level effects of an apex predator if it is extremely rare or absent (17). Nearshore systems lacking apex predators have often undergone conspicuous changes in bottom-up forces resulting from human activities, so attention has focused on these latter changes, rather than on a potential role for apex predators or for interactions between top-down and bottom-up changes to the ecosystems. The few studies that have successfully investigated the relative importance of bottom-up and top-down factors on dominant vegetation over ecosystem scales have determined that strong interactions can occur (3, 18, 19).

Seagrasses are a globally distributed group of marine angiosperms that provide valued ecosystem services, such as fueling secondary production, creation of habitat for many other species (9), shoreline protection, and carbon sequestration from the surrounding seawater and overlying atmosphere (8, 10). Seagrass beds have declined in many regions of the world, often because of the smothering effects of algal epiphytes that are enhanced by nutrient loading (8, 20, 21). Furthermore, top-down consumer control, via mesograzers and small predators, has also been established as an important factor in regulating the interaction between seagrass and their algal competitors, especially in elevated nutrient loading and eutrophic conditions (16, 22–27). Mediation of competitive interactions between primary producers is directly controlled by herbivores, which have consistently demonstrated preferential consumption of algal epiphytes vs. seagrasses (27–30), thus benefitting rather than harming the dominant primary producer. Additionally, there is strong evidence from cage experiments that intermediate predators (such as fish and crabs) are capable of regulating grazer assemblages in seagrass beds (22, 23, 25, 26), leading to a trophic cascade that mediates the competition between seagrass and their epiphytes. Seagrass ecosystems thus provide an opportunity to examine bottom-up and top-down forces, and the interaction between them.

Significance

Many coastal vegetated ecosystems have declined, affected by human alterations to "bottom-up" forces such as nutrient loading from agriculture and by "top-down" forces such as overfishing of predators. Examining the interactions between such bottom-up and top-down changes is challenging, because top predators have disappeared from many of these ecosystems. A highly nutrient-loaded estuary in California recently colonized by a recovering sea otter population provided an unusual opportunity to examine these interactions. We demonstrate that top-down effects of sea otters mitigate negative effects of nutrient loading, enhancing growth of seagrass. Grazers that remove algae from seagrass are favored by decreased crabs resulting from otter predation. Recovery of top predators can thus support resilience of coastal vegetated ecosystems.

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[1]To whom correspondence should be addressed. E-mail: bbhughes@ucsc.edu.

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Recovery of top predator populations has the potential to restore trophic structure and ecosystem function to degraded ecosystems. We found an ideal study system to examine the potential role of recovering apex predators in mediating bottom-up effects, a nutrient-loaded and eutrophic estuarine ecosystem supporting eelgrass (*Zostera marina*) and recovering sea otters (*Enhydra lutris*). Sea otters are keystone species capable of structuring nearshore communities (kelp forests and soft-bottom) through their high predation pressure (31–33). We used a 50-y time series tracking ecosystem degradation and recolonization by sea otters, spatial comparisons between sites with varying sea otter predation and nutrient loading, and manipulative mesocosm and field experiments to investigate the interaction between bottom-up forces and a recovering top predator population.

Results and Discussion

Study System and Historical Trends. Elkhorn Slough is a highly nutrient-loaded (Fig. 1 *A* and *B*) and eutrophic (34) estuary on the central coast of California. The adjacent watershed is dominated by an agricultural landscape. Annual fertilizer sales in the watershed region increased from 200 tons nitrogen in the 1930s to 30,000 tons in 2005, which has resulted in an exponential increase in nutrient concentrations in Elkhorn Slough through time ($P < 0.0005$, $R^2 = 0.90$; Fig. 1*A* and Table S1*A*). We calculate that the current nutrient load to the Elkhorn Slough estuary is 407 kg $N{\cdot}ha^{-1}{\cdot}y^{-1}$ (Table S1*B*), a load surpassing that of most global coastal waters considered highly eutrophic (20, 21, 35).

Our time-series analyses revealed remarkable expansion displayed by eelgrass in face of extreme nutrient loading (Fig. 1*A*) and concurrent loss of the adjacent salt marsh (36), which has been demonstrated to buffer the harmful effects of nutrient loading and eutrophication (20). Increases in nutrient concentrations as early as the 1970s (mean NO_3, 16.2 μM) began to exceed baseline levels reported from the 1920s (mean NO_3, 0.5 μM) (37) and concentrations from adjacent ocean sources (mean NO_3, 5.0 μM) (38). Nutrient concentrations more than doubled from 1971 (mean NO_3, 13.1 μM) to 1977 (mean NO_3, 29.6 μM). This increase in nutrients coincided with declines in eelgrass bed extent from 1965 to 1984 (Fig. 1*A*). However, the expected decline in eelgrass has reversed twice during the past three decades, in the first instance following initial recolonization of Elkhorn Slough by sea otters, and in the second instance following a sharp increase in otter abundance after a period of lower numbers. Before sea otters first colonized in 1984, eelgrass was at an all time low (2 ha), and nutrient concentrations, although still high, were an order of magnitude lower than the most recent period of eelgrass recovery (Fig. 1*A*). The otter density following the initial colonization was lower than the more recent period, yet their effect was probably sufficient to promote expansion of eelgrass in lower nutrient conditions, as sea otters are capable of greatly reducing their prey populations (i.e., crabs) in short time periods (<3 y) (39). Sea otter densities were significantly correlated with extent of eelgrass ($P < 0.019$, $R^2 = 0.52$; Table S1*C*), and since the initial sea otter recolonization in 1984, eelgrass bed extent increased by 600% (Fig. 1*A*). In a global context (Fig. 1*B*), this expansion of eelgrass in the setting of severe nutrient loading is anomalous; empirical evidence from other estuaries as well as modeling (20, 21, 35) predicts that Elkhorn Slough should have undergone dramatic seagrass loss, not expansion. However, following the most recent period of sea otter decline (2000–2004; Fig. 1*A*), the relationship between nutrient loading and seagrass loss was much closer to the model prediction from estuaries worldwide (Fig. 1*B*).

If a sea otter-driven trophic cascade was contributing to the expansion of eelgrass beds, we hypothesized that the most likely trophic link between otters and mesograzers would be crabs, which are a common prey item for sea otters (40), and are the primary intermediate predator in sea otter diets. We examined otter foraging data from the past decade and determined that crabs of all species comprised 52% of the total diet of sea otters foraging on or near eelgrass beds in Elkhorn Slough, with crabs

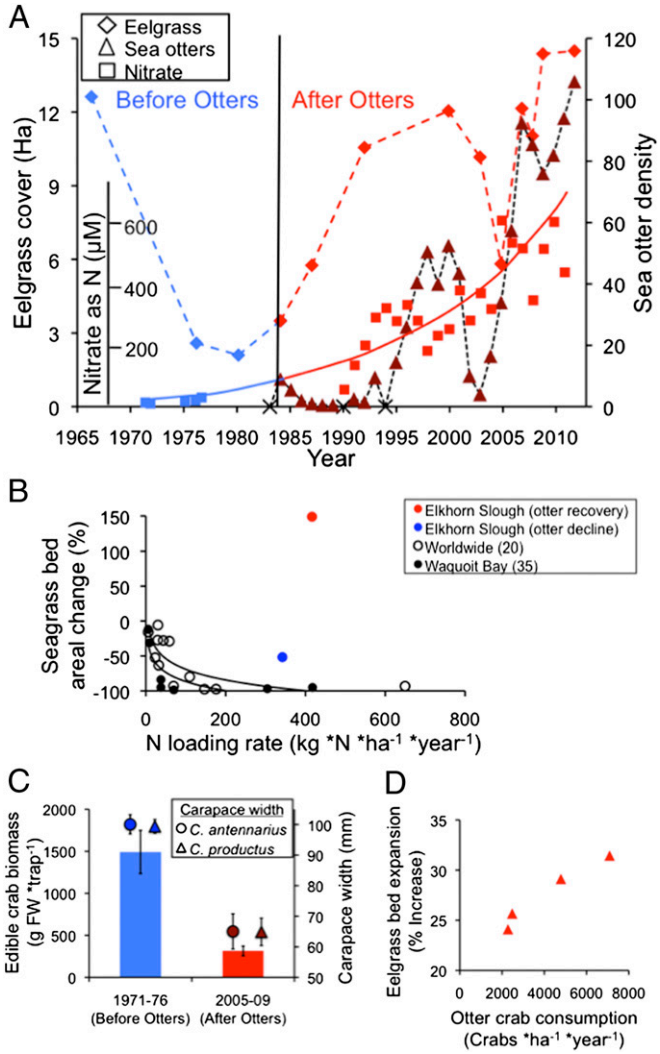

Fig. 1. Historical analysis of nutrients, eelgrass, sea otters, and crabs in Elkhorn Slough. (*A*) Fifty years of eelgrass declines and expansion driven by bottom-up nutrient loading and top-down sea otter-driven trophic cascade effects. Nitrate data ($N = 28$) represent the annual mean, and the solid line is a an exponentially modeled linear function of the entire data series (1971–2011; Table S1*A*). Sea otter ($N = 30$) and eelgrass ($N = 13$) data are represented by dotted lines to visually show trends. (*B*) Metaanalysis showing the relationship between land-derived nitrogen loads entering estuaries and percent change of seagrass estimated from areal surveys. Worldwide and Waquoit Bay, MA (an estuary with varying nutrient loading), data are redrawn from Burkholder et al. (21) (with permission from the publisher). Elkhorn Slough data (Table S1*B*) are not included in the log-linear relationship (solid lines), but are plotted for periods following sea-otter decline (2000–2004), and sea-otter recovery (2005–2010) to demonstrate departure from the model. (*C*) Results from crab surveys a decade before sea otter colonization (1971–1976) and two decades after sea otter colonization (2005–2009; Table S1*D*; *Methods* provides a sample size description). (*D*) Eelgrass bed expansion (2006–2012) at eelgrass beds ($n = 4$) in Elkhorn Slough (calculated as the percent increase in cover of eelgrass as a function of available eelgrass habitat, measured in hectares; Fig. S3) correlated with estimated sea otter predation on crabs in standardized 1-ha plots (Fig. S2) in each bed (Table S1*E*).

from the genus *Cancer* making up 43% of the sea otter diet (Fig. S1). Sea otters are well known to limit populations of their macroinvertebrate prey, including crabs (41), and thus we predicted that the expansion of otter populations in the estuary should have resulted in negative impacts on crabs. Indeed, we detected a significant decline in the biomass ($P < 0.0005$) and

size of crabs in the estuary (*Cancer antennarius*, $P < 0.0005$; and *Cancer productus*, $P < 0.0005$; Fig. 1*C*). Sea otters were most likely to cause declines in crab populations because sea otters were expanding during a period when other crab predators, namely sharks and rays, were in a state of decline, in part as a result of overfishing from four decades (1951–1995) of annual "shark derbies" (42). Additionally, leopard sharks (*Triakis semifasciata*), one of the most abundant top predators in the estuary, experienced a diet shift from crabs before otter colonization to fat innkeeper worms (*Urechis caupo*) after sea otter colonization, indicating an overall decline in crab availability (43). Furthermore, crab harvesting in Elkhorn Slough has declined in the past two decades compared with the 1970s when crab harvesting was common (44), and, in 2007, most of the estuary was declared a Marine Protected Area, thus eliminating all crab harvesting in and around the eelgrass beds. The offshore "rock crab" fishery, which includes both *C. antennarius* and *C. productus*, is a relatively small fishery compared with the much larger Dungeness crab (*Cancer magister*) fishery, and yielded only an average of 3,000 kg annually from 1960 to 2010 (45) and peaked in 1989 when eelgrass was in a period of recovery (Fig. 1*A*). The decrease in populations of other top predators and the lack of overharvesting of crabs in and around the estuary all suggest that the observed decline in *Cancer* crab biomass and size in Elkhorn Slough was a a result of sea otter predation.

To more closely examine the potential relationship among otters, crabs, and eelgrass, we quantified otter predation on crabs in each eelgrass bed in Elkhorn Slough from 2006 to 2012 (*SI Methods*) and correlated it with eelgrass bed expansion (i.e., percent increase in eelgrass cover) after recovery from the most recent decline (2000–2004) in which >50% of eelgrass was lost. Eelgrass expansion during the ensuing 6-y period was positively correlated with sea otter predation on crabs ($P = 0.021$, $R^2 = 0.96$; Fig. 1*D* and Figs. S2 and S3).

Combining results from historical analyses on the relationship among otters, crabs, and seagrass with previous published results on the control of algal epiphytes on seagrass by mesograzers (22–30) generated a hypothesized mechanism by which sea otters mediate bottom-up effects on seagrass. In our conceptual model, a four-level trophic cascade modulates negative algal epiphyte effects on eelgrass, with sea otters controlling intermediate predator crab populations, thereby releasing mesograzers from predation and enhancing their grazing effects on algal epiphytes (Fig. 2*A*).

Spatial Comparisons. To examine the importance of sea otters in estuarine eelgrass beds, we compared properties of eelgrass beds between Tomales Bay and Elkhorn Slough, CA, which are similar in many physical (46) and biological attributes but differ in the presence of sea otters and nutrient loading. Nitrate concentrations are lower in Tomales Bay (0–23 μM) (47) than they are in the eutrophic (34, 48) Elkhorn Slough (10–600 μM). Elkhorn Slough presently supports as many as 120 otters, but sea otters have yet to recolonize Tomales Bay. The reason for this difference is historical accident: southern sea otters recovered from a remnant population in central California after near extermination from the maritime fur trade industry. The current northern range extent is at Pigeon Point, ~185 km south of Tomales Bay as the otter swims (49), thus precluding the use of Tomales Bay by sea otters in the present day. However, prehistoric midden site records indicate that sea otters were once common in estuaries along the entire central California coast, including the Tomales Bay region (50).

We systematically sampled both estuaries for eelgrass aboveground and belowground biomass, algal epiphyte load, grazer biomass and density, and crab biomass and size. Eelgrass beds in Elkhorn Slough had significantly lower crab biomass ($P = 0.034$) and size [for both of the common large crab species, *C. antennarius* ($P = 0.034$) and *C. productus* ($P = 0.009$); Fig. 2*B*] and greater aboveground eelgrass biomass ($P = 0.035$) than Tomales Bay (Fig. 2*E*), as predicted for the estuary with otters present

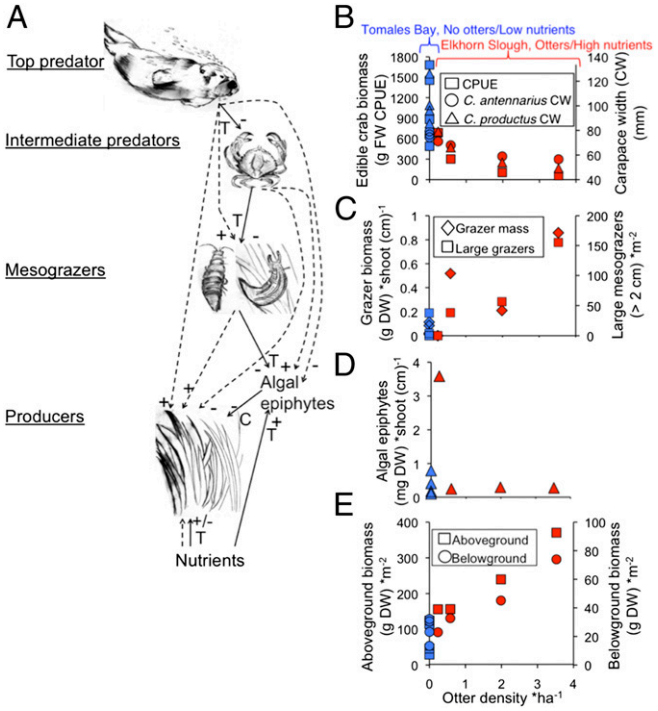

Fig. 2. (*A*) Interaction web of top-down and bottom-up effects in the eelgrass study system. The top predator is the sea otter (*E. lutris*), the mesopredators are crabs (*Cancer* spp. and *Pugettia producta*), the epiphyte mesograzers are primarily an isopod (*I. resecata*) and a sea slug (*P. taylori*), and algal epiphyte competitors of eelgrass primarily consist of chain-forming diatoms, and the red alga *Smithora naiadum*. Solid arrows indicate direct effects, dashed arrows indicate indirect effects, and the plus and minus symbols indicate positive and/or negative effects on trophic guilds and eelgrass condition. C, competitive interaction; T, trophic interaction. (Original artwork by A.C. Hughes.) (*B–E*) Survey results testing for the effects of sea otter density on eelgrass bed community properties (Tables S2 and S3). Elkhorn Slough (sea otters present and high nutrients) eelgrass beds ($n = 4$) are coded in red, and the Tomales Bay reference site (no sea otters, low nutrients) beds ($n = 4$) are coded in blue. (*B*) Crab biomass and size structure of two species of *Cancer* crabs; (*C*) grazer biomass per shoot and large grazer density; (*D*) algal epiphyte loading; and (*E*) aboveground and belowground eelgrass biomass. DW, dry weight; FW, fresh weight.

(Table S2). Crab biomass and sizes for Tomales Bay (Fig. 2*B*) were similar to those for Elkhorn Slough before the otter recolonization (Fig. 1*C*), further indicating that otters are controlling crab populations in Elkhorn Slough. Eelgrass belowground biomass, epiphyte loading, grazer biomass, and large mesograzer density (*Phyllaplysia taylori* and *Idotea resecata* >2 cm, the size class most likely to be consumed by crabs; Fig. 2 *C–E*) did not significantly differ between estuaries between Tomales Bay and Elkhorn Slough, but varied in the direction predicted by our model (Fig. 2*A*).

Remarkably, comparisons between Tomales Bay and Elkhorn Slough indicated that eelgrass can perform equally, if not better, in nutrient-loaded and eutrophic conditions (34) (Movie S1). High spatial variation of crabs, grazers, epiphytes, and eelgrass abundance characterize Elkhorn Slough, indicating the potential for a gradient in the key forcing processes (Fig. 2 *B–E*). Our analyses indicate that sea otters are a key driver of this variation (Table S3). Otter density across eelgrass beds within Elkhorn Slough was negatively correlated with crab biomass ($P = 0.043$, $R^2 = 0.92$) and size (*C. antennarius*, $P = 0.040$; $R^2 = 0.92$; and *C. productus*, $P = 0.061$, $R^2 = 0.88$; Fig. 2*B*). Large mesograzer density varied positively and significantly ($P = 0.041$, $R^2 = 0.92$; Fig. 2*C*) with increased sea otter density. Although the sea otter density gradient was not significantly correlated with grazer

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biomass (Fig. 2*C*), the covarying trend was in the predicted direction (Fig. 2*A*). Algal epiphyte loads on seagrass significantly decreased with increased sea otter density ($P = 0.025$, $R^2 = 0.77$; Fig. 2*D*). Finally, eelgrass shoot density ($P = 0.003$, $R^2 = 0.99$), aboveground biomass ($P = 0.012$, $R^2 = 0.98$), and belowground biomass ($P = 0.013$, $R^2 = 0.97$; Fig. 2*E*) significantly increased with higher sea otter density.

Mesocosm and Field Experiments. To test the proposed mechanisms underlying the individual links in our ecological model (Fig. 2*A*), we conducted a series of mesocosm and field experiments. The mesocosm experiment supported the postulated food web links among crabs, mesograzers, epiphytes, and eelgrass. Mesocosms simulating low otter predation had decreased overall sea slug biomass and increased large (*P. taylori* >2 cm) sea slug mortality through observed predation by crabs (Fig. 3*A*), which led to increased algal epiphyte loads (Fig. 3*B*) and a net loss in eelgrass biomass and reduced rhizome elongation (Fig. 3*C* and Table S4). The reduced mortality rate of large sea slugs in the treatment mimicking high sea otter predation suggested that smaller crabs are inefficient predators, thereby releasing mesograzers from predation and increasing grazing efficiency.

We verified the underlying mechanism of the sea otter-driven trophic cascade effects on eelgrass by using a field cage experiment that tested for (*i*) no sea otter predation (crab inclusion), (*ii*) simulated sea otter predation (crab and otter exclusion), and (*iii*) actual sea otter predation (crabs and otters included). After 1 mo, grazer biomass and large grazer density (*P. taylori* and *I. resecata* >2 cm, the size class most likely to be consumed by crabs) were significantly greater (Fig. 3*D*) in the cages with simulated and actual sea otter predation (Table S5). As predicted, algal epiphyte loads were significantly lower (Fig. 3*E*), and aboveground and belowground eelgrass biomass (Fig. 3*F*) as well as shoot density (Table S5) was significantly greater in treatments with actual and simulated sea otter predation.

Conclusion

Taken together, these lines of evidence strongly indicate that complex top-down effects of sea otter predation have resulted in positive benefits to eelgrass beds, mitigating the effects of continuing and increasing nutrient loading in Elkhorn Slough. Our findings add to a growing body of literature in seagrass ecology (22–30) that highlights the importance of consumer controls in regulating the conflict between seagrasses and their algal epiphytes. In this case, the addition of an apex predator mediates species interactions at the base of the food web and counteracts the negative effects of anthropogenic nutrient loading. Our findings depart from a view of nature built largely around bottom-up control, which has been the dominant predictor in explaining seagrass loss for more than three decades (12, 20, 21, 35, 51, 52).

Here we have demonstrated that sea otters initiate a trophic cascade in estuarine ecosystems superficially similar to that in the more familiar kelp forest model (31, 33): in both cases, increases in sea otters result in increases in the dominant, habitat-forming coastal vegetation. However, the mechanism by which sea otter predation supports vegetated habitat differs fundamentally between kelp forests and estuaries: the estuarine trophic cascade involves four trophic levels, not three. The explanation for this apparent anomaly lies in two details of the natural history of the estuarine autotrophs and their herbivores: the herbivores preferentially feed on epiphytic algae vs. eelgrass, and the epiphytic algae can harm eelgrass through shading effects in the absence of herbivory (Fig. 2*A*). These indirect effects may be particularly pronounced in nutrient-loaded systems, which foster ephemeral algal growth. More broadly, multilevel trophic cascades involving indirect effects may be particularly important in systems with strong alteration of bottom-up controls (3, 16). Our findings highlight the importance of unraveling the potentially interactive nature of these key ecological processes when assessing the drivers of vegetated ecosystems.

Methods

Historical Trends. To detect correlations between eelgrass cover and bottom-up and top-down forces, we synthesized data from a variety of sources. We determined trends in the bottom-up influences on the Elkhorn Slough eelgrass beds by constructing a time series of nutrient concentrations in Elkhorn Slough. All samples were collected in the lower part of the estuary adjacent to the historical and present day distribution of eelgrass and sea otters. Surface

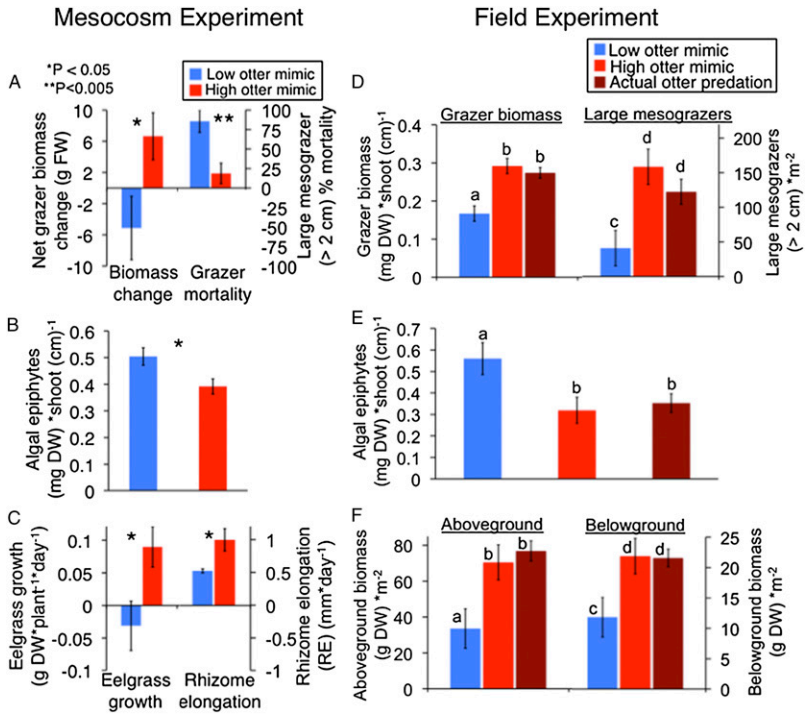

Fig. 3. Results from a 30-d mesocosm experiment (*A*–*C*) comparing the effects of simulated low (large crab treatment; $n = 8$) and high (small crab treatment; $n = 7$) sea otter predation on (*A*) net change in grazer biomass and grazer mortality, (*B*) algal epiphyte load, and (*C*) eelgrass growth and rhizome elongation (Table S4). (*D*–*F*) Results from a 30-d field cage experiment (Fig. S5) testing for the effects of simulated low sea otter predation (i.e., cages including crabs and excluding sea otters; $n = 6$), simulated high sea otter predation (i.e., cages excluding crabs and sea otters; $n = 8$), and actual high sea otter predation (which included (*i*) partial cage control that allowed access to both sea otters and crabs yet included the top of the cage to test for shading effects on the seagrass and (*ii*) cage-free plots; $n = 16$) on (*D*) grazer biomass and large grazer density, (*E*) algal epiphyte load, and (*F*) aboveground and belowground eelgrass biomass. Differences in lettering indicates significant differences based on randomized blocked ANOVA and Tukey HSD tests (Table S5). DW, dry weight; FW, fresh weight. Error bars are ±1 SEM.

water samples were collected monthly by hand and analyzed for nitrate as nitrogen (in micromolars; *SI Methods*). We modeled the increase in nitrate concentrations by correlating the year to the mean annual nitrate concentration ($N = 28$) by using regression analysis.

We mapped eelgrass cover in the estuary and quantified change through time by interpreting low altitude vertical aerial imagery acquired between 1966 and 2012. We only used years ($N = 13$) through which eelgrass cover could be determined with high confidence based on historical descriptions and recent ground surveys of distribution (*SI Methods*). To determine the long-term trends in sea otter densities in Elkhorn Slough, we used the standardized biannual census counts from the US Geological Survey (USGS) (www.werc.usgs.gov). This database has summarized sea otter abundance in Elkhorn Slough from 1-d surveys in the spring and fall from 1985 to 2012. Sea otters first entered Elkhorn Slough in 1984, so, for this year, we used a study by Kvitek et al. (32) to estimate the number of otter arrivals in the estuary. To determine the relationship between sea otter abundance and eelgrass cover, we used regression analysis by correlating eelgrass cover for all available years during the sea otter expansion period (1984–2012) with the mean annual sea otter density ($N = 10$).

We summarized land-derived nutrient loads from 2004 to 2012 and percent change in eelgrass during the most recent period of sea otter decline (2000–2004) and otter recovery (2005–2012). The nitrate load to Elkhorn Slough was determined from hourly measurements of nitrate concentration and water depth at the Land/Ocean Biogeochemical Observatory L01 mooring near the mouth of Elkhorn Slough (53). The volume flux past the mooring each hour was determined from the change in water depth and the observed bathymetry of the system above the mooring. The accuracy of these volume fluxes was independently assessed by comparison with a long-term set of Acoustic Doppler Current Profiler data collected at the L01 mooring (54). The total nitrate flux was then determined from the volume flux times the observed nitrate. The nitrate load from terrestrial sources was estimated as the volume flux times the fraction of any observed nitrate concentration greater than 30 μM. The 30-μM threshold was chosen because nitrate in surface waters of Monterey Bay never exceeds this value (55). The nitrate load from terrestrial sources is a minimum estimate because it ignores any nitrate from terrestrial sources when nitrate concentrations are less than 30 μM. However, the load estimated for terrestrial sources is 66% of the total load and cannot be seriously in error because there is also a nonnegligible load from ocean sources. The final annual load values were calculated by dividing nitrogen load (in kilograms) by the total wetland area (in hectares) for Elkhorn Slough (36). Finally, we used the mean nitrogen load from 2004 to represent the most recent period of eelgrass and sea otter decline, and the mean from 2006 to 2012 to represent the most recent period of eelgrass and otter recovery for a global comparison with other estuaries (20, 21, 35).

We tested for the effects of long-term otter predation on the Elkhorn Slough crab population by comparing two time periods: 1971 to 1976 (a decade before otter immigration) and 2005 to 2009 (two decades after otter immigration). Data were collected from a similar region in the lower part of the estuary directly adjacent to the present-day and historical distributions of eelgrass and sea otters (*SI Methods*). We calculated crab biomass caught in standardized crab traps by converting the carapace width values of each crab to an edible biomass by using a power function (56), and summed up the total biomass for each trap. To ensure independence among samples, we used the mean crab mass per trap per day [$n = 17$ (1971–1976), $n = 26$ (2005–2009)] and mean daily carapace width for the two most abundant crab species, *C. antennarius* [$n = 14$ (1971–1976), $n = 12$ (2005–2009)] and *C. productus* [$n = 14$ (1971–1976), $n = 11$ (2005–2009)]. We compared crab biomass and size among the two time periods by using an independent-samples t test.

We estimated eelgrass bed expansion within Elkhorn Slough as the percent change in eelgrass cover (in hectares) from 2006 to 2012 as a function of otter predation over the same survey period. Georeferenced aerial imagery from May 24, 2006, and May 5, 2012, was used to conduct object-based classification of the surface area extent of eelgrass beds (Fig. S3). Areas of suitable habitat for eelgrass were spatially delineated by using high-resolution (2 m) multibeam bathymetry from 2005 and 2011 and aerial Light Detection and Ranging (2 m) from 2004 and 2011 to create continuous digital elevation models in ArcMap version 10.1 (Environmental Systems Research Institute, Redlands, CA). To measure crab predation by sea otters, we used observational data on sea otter foraging collected between 1999 and 2012 by field staff of the Monterey Bay Aquarium and USGS. This data set comprised >10,000 observed feeding dives recorded from tagged and untagged sea otters feeding in the main channel of Elkhorn Slough. We analyzed these data by using a previously described Monte Carlo simulation algorithm for estimating prey-specific consumption rates from observational data while accounting for sampling uncertainty (57). By multiplying the mean estimated consumption rate by the average density of otters in each eelgrass bed (Fig. S2), we calculated the rate of crab predation (in crabs per hectare per year) in each of the four eelgrass beds (*SI Methods*). Eelgrass bed expansion was calculated by subtracting the percent coverage of eelgrass within the available habitat in 2006 by the percent coverage of eelgrass within the available habitat in 2012 for each of the four eelgrass beds (Fig. S3). We used linear regression to determine the relationship between eelgrass bed expansion as a function of sea otter predation ($n = 4$).

Spatial Comparisons. To determine eelgrass condition and community structure at eelgrass beds with varying sea otter densities, we sampled across 100-m transects at the only four large beds in Elkhorn Slough (36° 48′ 45″ N, 121° 46′ 10″ W; Fig. S2) and four Tomales Bay beds (38° 11′ 53″ N, 122° 56′ 30″ W). All transects bisected the central portion of each bed as well as the standardized 1-ha sea otter foraging/crab survey area (as detailed later; although Tomales Bay had no sea otter surveys, as none were present). Elkhorn Slough eelgrass beds were sampled in July and August 2012, and Tomales Bay beds were sampled in August 2012. At each bed, we systematically sampled eelgrass every 10 to 12 m by using 0.50 × 0.50-m quadrats. Within each quadrat ($N = 8$), we counted all eelgrass shoots and collected five shoots along with >7 cm of their rhizome and root material. All shoots were scraped free of algal epiphytes and all grazers were removed and counted. All grazers, epiphytes, and eelgrass were dried at 60 °C for 24 h and weighed.

We quantified crab densities, biomass, and sizes at Elkhorn Slough and Tomales Bay. At Elkhorn Slough, a single crab trap was placed in each of the four eelgrass beds during the month of July 2012. The same method was used to sample crabs at the four eelgrass beds in Tomales Bay for 1 wk in August 2012. We calculated the catch per unit effort (CPUE) for each daily trapping effort by converting the carapace width values of each crab to an edible biomass using a power function (56), and summed up the total biomass for each CPUE. CPUE was standardized to the total soak time (in hours) for each daily sampling effort. The mean CPUE and mean daily carapace width for the two most abundant crab species, *C. antennarius* and *C. productus*, were used in the final regression analysis ($N = 4$; *SI Methods*).

To determine variation in sea otters among the four beds in Elkhorn Slough, we surveyed otter densities in the eelgrass survey beds during summer 2012. We counted all otters within each bed at the start of observations and at 15-min intervals. Observation periods were 1 to 2 h and were performed weekly to twice weekly at each bed during the study period (May 15 to July 29, 2012).

Eelgrass community-dependent variables [CPUE and *C. antennarius* and *C. productus* carapace width (in millimeters), grazer biomass (in milligrams per centimeter of shoot), large grazer density (in number per square meter), algal epiphytes (in milligrams per centimeter of shoot), shoot density (in shoots per square meter), and eelgrass aboveground and belowground biomass (in grams per square meter)] from beds at Tomales Bay were compared with Elkhorn Slough ($n = 4$) by using an independent-samples t test. We used regression analysis to determine the relationship between otter density and the dependent variables among beds in Elkhorn Slough ($n = 4$).

Mesocosm and Field Experiments. To test whether the predicted top-down mechanisms were valid, we conducted a mesocosm experiment. The mesocosms consisted of transplanted eelgrass and mesograzers with standardized sizes, densities, and biomass. Mesocosms were subjected to two treatments: small crabs (mimicking crab populations under heavy otter predation) and large crabs (mimicking low otter predation; Fig. 1*C*). We measured response parameters after 30 d at the various trophic levels, including mesograzer (sea slug) biomass and mortality, epiphyte biomass, and eelgrass biomass and rhizome elongation, which are important indicators of condition and growth rates in seagrass (58) (*SI Methods*). All shoots were scraped free of algal epiphytes, and all grazers were removed and counted. All grazers, epiphytes, and eelgrass were dried at 60 °C for 24 h and weighed. We used an independent-samples t test to determine differences among small ($n = 8$) and large ($n = 7$) crab treatments.

We next conducted a field experiment to validate results from the mesocosm experiment in a nutrient-loaded estuarine environment (Fig. S4), and to include an actual sea otter predation treatment. By using a randomized block design, we placed enclosures (cages) on an eelgrass bed in Elkhorn Slough with high sea otter densities, in four different treatments: (*i*) simulated low otter predation (closed cage containing two large crabs), (*ii*) simulated high otter predation (closed cage without crabs), (*iii*) actual sea otter predation in the enclosure (cage open to otter and crab predation),

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and (*iv*) actual sea otter predation without an enclosure (to serve as control for cage effects; *SI Methods* and Fig. S5). Eelgrass shoot lengths were standardized and each cage was seeded with 20 large mesograzers. We used ANOVA to test for treatment effects ($N = 8$) on grazer mass, algal epiphyte mass, shoot density, and aboveground and belowground eelgrass biomass, as well as density of large (>2 cm) mesograzers. Finally, we tested for differences among individual treatments by using a Tukey honestly significant difference (HSD) test (*SI Methods*).

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