A Three-Stage Symbiosis Forms the Foundation of Seagrass Ecosystems

Tjisse van der Heide,[1]* Laura L. Govers,[2] Jimmy de Fouw,[3] Han Olff,[1] Matthijs van der Geest,[3] Marieke M. van Katwijk,[2] Theunis Piersma,[3,4] Johan van de Koppel,[5] Brian R. Silliman,[6] Alfons J. P. Smolders,[7] Jan A. van Gils[3]

Seagrasses evolved from terrestrial plants into marine foundation species around 100 million years ago. Their ecological success, however, remains a mystery because natural organic matter accumulation within the beds should result in toxic sediment sulfide levels. Using a meta-analysis, a field study, and a laboratory experiment, we reveal how an ancient three-stage symbiosis between seagrass, lucinid bivalves, and their sulfide-oxidizing gill bacteria reduces sulfide stress for seagrasses. We found that the bivalve–sulfide-oxidizer symbiosis reduced sulfide levels and enhanced seagrass production as measured in biomass. In turn, the bivalves and their endosymbionts profit from organic matter accumulation and radial oxygen release from the seagrass roots. These findings elucidate the long-term success of seagrasses in warm waters and offer new prospects for seagrass ecosystem conservation.

Seagrass meadows are important ecological and thus economic components of coastal zones worldwide (*1*, *2*). In many areas, coral reefs and seagrass meadows are tightly linked habitats that form the basis for marine biodiversity (*3*). Seagrasses serve as a keystone habitat for migrating coral reef species as well as thousands of other animals, including waterbirds, fish, dugongs, manatees, and turtles; are important carbon and nutrient sinks; and are important to fisheries and coastline protection (*1*–*3*). Dense seagrass meadows attenuate currents and waves and trap pelagic and benthic organic matter in the sediment (*2*, *4*, *5*). Owing to a lack of oxygen in many coastal marine sediments, an important fraction of organic matter is decomposed by bacteria that use the abundant sulfate in seawater as an electron acceptor instead of oxygen and produce toxic sulfide as a metabolic end product (*6*). Although seagrasses transport oxygen into their roots and the surrounding rhizosphere (radial oxygen release) (*2*, *7*), sulfide production outpaces oxygen release under warmer conditions, resulting in sulfide accumulation and seagrass mortality (*2*, *7*, *8*). Seagrass beds tend to accumulate organic matter, and so it is expected that seagrass beds would build up toxic sulfides and hence have a limited productivity and diversity (*2*). But this is not the observed case, and the underlying reason for the long-term persistence of seagrass ecosystems is an enigma (fig. S1A).

We tested the hypothesis that a three-stage symbiosis between seagrasses, associated burrowing lucinid bivalves, and their symbiotic gill bacteria contribute to reducing the cyclic build-up of sulfide (fig. S1, B to D). Paleo records suggest that the Lucinidae and their endosymbiotic relation date back to the Silurian (*9*–*11*), but that they increasingly diversified since the evolutionary emergence of seagrasses in the late Cretaceous (*2*, *12*, *13*). Seagrass communities later became widespread in the Eocene, and lucinid remains frequently occur in association with their deposits since (*13*, *14*). Lucinids and their gill-inhabiting bacteria have a symbiosis in which the bivalves transport sulfide and oxygen to their gills (fig. S1D), where the bacteria oxidize sulfide for synthesizing sugars that fuel growth of both organisms (*15*–*19*). We hypothesized that seagrass meadows may provide an optimal habitat for these bivalves and their symbionts by indirectly stimulating sulfide production through high organic matter input and by providing oxygen through radial oxygen release from the roots. In turn, lucinids remove sulfide, which could relieve any stress caused to seagrass growth by sulfide accumulation as organic matter is degraded (fig. S1, A and B).

Indirect support for our hypothesis was provided by a worldwide meta-analysis of 84 studies describing the fauna of seagrass beds in 83 sites covering the entire climatic distribution of seagrasses, combined with a 110-point field survey

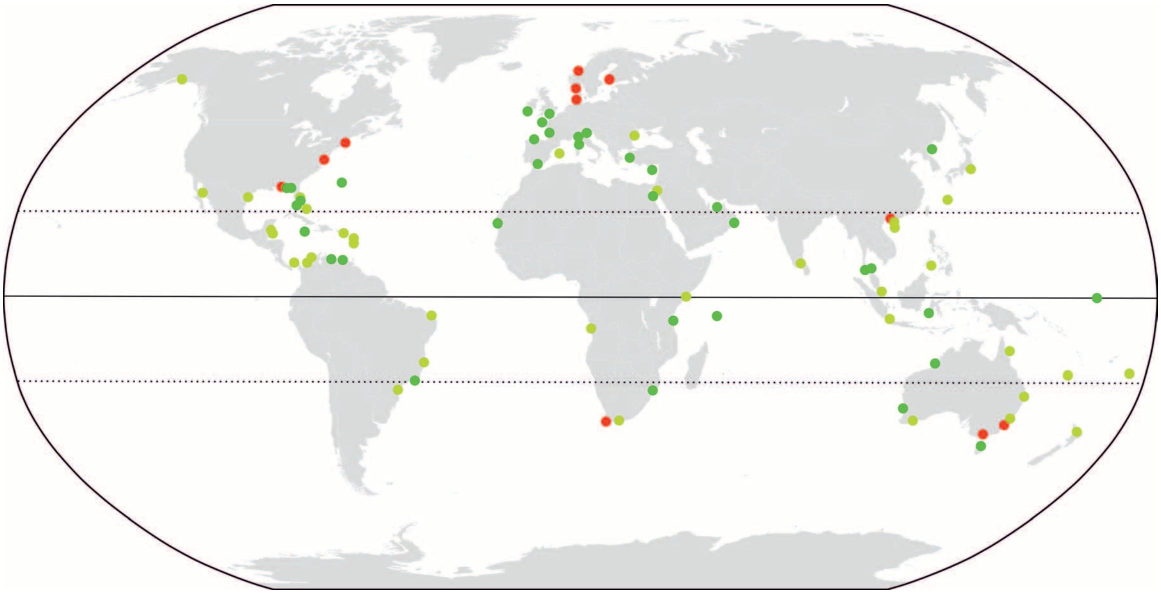

Fig. 1. Presence (green; dark points are quantitative, light points are qualitative) and absence (red) of lucinids in seagrass ecosystems based on our meta-analysis. The bivalves were present in 97% (93% of the quantitative sites) of all tropical seagrass beds, 90% (83% of the quantitative sites) of the subtropical beds, and 56% (50% of the quantitative sites) of the temperate seagrass meadows. The seagrass-lucinid association spans six out of seven continents, at least 18 genera of lucinids, and 11 out of 12 seagrass genera (and *Ruppia* spp.). Only meadows of *Phyllospadix* spp., a seagrass genus that grows on bare rock, did not contain Lucinidae. The analyzed ecosystems generally contained high (~100 individuals per square meter) to extremely high densities (>1000 individuals per square meter) of lucinids (table S1).

---

[1] Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, Post Office Box 11103, 9700 CC Groningen, Netherlands. [2] Department of Environmental Science, Institute for Water and Wetland Research, Radboud University Nijmegen, Faculty of Science, Heyendaalseweg 135, 6525 AJ Nijmegen, Netherlands. [3] Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, Post Office Box 59, 1790 AB Den Burg, Texel, Netherlands. [4] Animal Ecology Group, CEES, University of Groningen, Post Office Box 11103, 9700 CC Groningen, Netherlands. [5] Centre for Estuarine and Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, Post Office Box 140, 4400 AC Yerseke, Netherlands. [6] Department of Biology, University of Florida, Gainesville, FL 32611, USA. [7] Department of Aquatic Ecology and Environmental Biology, Institute for Water and Wetland Research, Radboud University Nijmegen, Faculty of Science, Heyendaalseweg 135, 6525 AJ Nijmegen, Netherlands.

*To whom correspondence should be addressed. E-mail: t.van.der.heide@rug.nl

that we conducted at Banc d'Arguin, Mauritania (*20*). The meta-analysis reveals a relationship that covers 11 out of 12 seagrass genera (and *Ruppia* spp.) and at least 18 genera of Lucinidae (Fig. 1 and table S1). Only meadows of *Phyllospadix* spp., a seagrass genus that grows on bare rock, do not associate with Lucinidae. The association spans six out of seven continents, with bivalve densities ranging from 10 to over 1000 individuals per square meter. The bivalves were present in 97% of the tropical seagrass sites, 90% of the subtropical meadows, and 56% of the temperate seagrass beds surveyed, indicating that the association may be dependent on temperature-related sulfide production (*8*). Furthermore, results from our field study showed a positive correlation between seagrasses and lucinids that explained 42% of their respective variation [Pearson's correlation coefficient (r) = 0.65] (fig. S2).

To experimentally test our hypothesis (fig. S1B), we investigated the effects of sulfide oxidation by the lucinid bivalve *Loripes lacteus* on the production of the seagrass species *Zostera noltii* and the potential reciprocal benefits for *Loripes* in a full factorial experiment under controlled conditions (*20*). We set up *Zostera*, *Loripes*, *Zostera-Loripes*, and bare sediment treatments in the top sections of 40 two-compartment columns (fig. S3), which were placed in a large seawater basin. The lower compartment of each column contained anaerobic seawater and an injection tube through which sulfide was added twice a week in half of the columns. The injected sulfide was allowed to diffuse into the top section through a porous membrane.

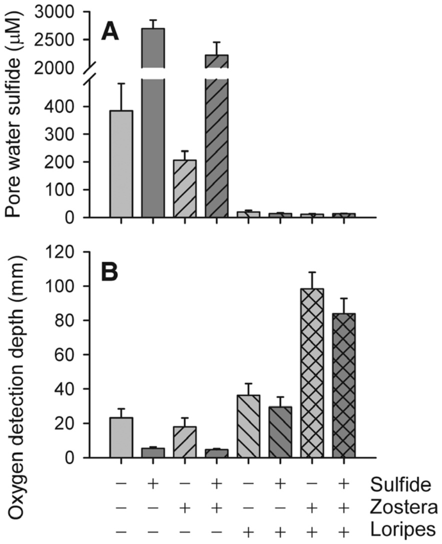

Fig. 2. (**A**) Pore water sulfide concentrations and (**B**) oxygen detection depth after 5 weeks; error bars represent SEM ($n = 5$ replicates). Oxygen detection depth decreased as sulfide was added [analysis of variance (ANOVA) $F_{1,32} = 8.9$, $P < 0.006$]. The presence of *Loripes* reduced sulfide levels (repeated measures ANOVA: $F_{1,32} = 268.8$, $P < 0.001$) and increased oxygen detection depth ($F_{1,32} = 125.0$, $P < 0.001$). Reduction of the sulfide concentration by *Zostera* alone was less, but still significant ($F_{1,32} = 6.8$, $P = 0.014$). That interactions occurred between *Zostera* and *Loripes* was apparent in the oxygen measurements ($F_{1,32} = 48.3$, $P < 0.001$) but was also significant in the sulfide data ($F_{1,32} = 7.8$, $P = 0.009$). The interaction between *Loripes* and sulfide was significant for the sulfide measurements ($F_{1,32} = 102.7$, $P < 0.001$) but not for the oxygen data ($F_{1,32} = 0.3$, $P = 0.578$).

The presence of *Loripes*, and to a lesser extent of *Zostera*, decreased sediment sulfide levels. After 5 weeks, pore water sulfide concentrations in the top sections of the sediment controls reached about 400 µM, whereas the semiweekly addition of sulfide caused levels to increase to nearly 2700 µM (Fig. 2A). The presence of *Zostera* decreased sulfide levels to ~200 µM in the controls and 2200 µM in the sulfide addition treatments. In contrast, sulfide levels remained low when *Loripes* was present (~15 µM), even in the sulfide addition treatments. As expected, the oxygen detection depth was reduced when sulfide was added but increased when only *Loripes*, but not *Zostera*, was present because of sulfide-oxidation and intake of surface water (Fig. 2B). *Zostera* alone did not significantly affect sediment oxygen conditions. The joint presence of *Zostera* and *Loripes* enhanced oxygen detection depth beyond that of their separate effects.

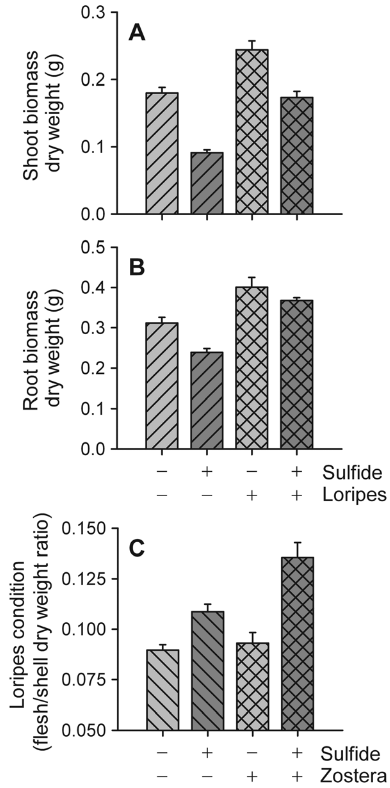

Fig. 3. (**A**) *Zostera* shoot and (**B**) root dry weight biomass per column and (**C**) *Loripes* condition expressed as the dry weight flesh/shell ratio after 5 weeks; error bars represent SEM ($n = 5$ replicates). *Zostera* biomass was reduced by means of sulfide addition (ANOVA: shoots $F_{1,16} = 72.6$, $P < 0.001$; roots $F_{1,16} = 12.0$, $P = 0.003$), whereas the presence of *Loripes* had a positive effect on both shoot ($F_{1,16} = 61.3$, $P < 0.001$) and root biomass ($F_{1,16} = 50.2$, $P < 0.001$). We found no significant effects on rhizome biomass. *Loripes* condition was positively affected by both sulfide addition (ANOVA: $F_{1,16} = 37.3$, $P < 0.001$) and *Zostera* presence ($F_{1,16} = 9.0$, $P = 0.008$). We also found a significant positive combined effect of the presence of *Zostera* and sulfide on *Loripes* condition ($F_{1,16} = 5.4$, $P = 0.034$).

Our experiment showed that *Zostera* production is facilitated by *Loripes*, both in the control and in the sulfide-addition treatments. In the treatments without *Loripes*, sulfide addition reduced *Zostera* shoot biomass to 50% of the controls (Fig. 3A). Reduced shoot biomass was accompanied by decreased root biomass (Fig. 3B) and impaired phosphate uptake (*20*). In contrast, the addition of *Loripes* increased *Zostera* shoot biomass 1.9-fold and root weight 1.5-fold, as seen in the sulfide-addition treatments. In the treatments without additional sulfide, the presence of *Loripes* increased both shoot and root weight by 1.4-fold and 1.3-fold, respectively.

Loripes condition, expressed as the flesh/shell dry weight ratio, was positively affected by sulfide addition (Fig. 3C). Furthermore, the addition of *Zostera* did not affect *Loripes* in the units to which no sulfide was added but improved the bivalve's condition in the sulfide treatments. As hypothesized, the positive effect of *Zostera* on *Loripes* seems to result from radial oxygen release from the seagrass roots (fig. S1B). Although sulfide was almost completely removed in all *Loripes* treatments (Fig. 2A), the bivalve was less able to profit from the addition of sulfide in the absence of *Zostera* (Fig. 3C). This indicates that at least in the *Loripes* units without seagrass, sulfide was not completely oxidized by the symbiotic bacteria because of oxygen limitation.

Overall, our results confirm our hypothesis that a three-stage symbiosis between seagrass, lucinids, and sulfide-oxidizing bacteria reduces sulfide stress in seagrass meadows. Even though radial oxygen release by *Zostera noltii* and of seagrasses in general is limited (*21*, *22*), *Loripes* in our experiment clearly benefitted from the increased oxygen input in the sediment. In the field, the positive effects of seagrasses on lucinids are not confined to sediment oxygenation alone but also by indirectly stimulating sulfide production and releasing dissolved organic molecules (*2*, *18*). The positive effects of *Loripes* on *Zostera* in our experiment could not be explained by differences in nutrient availability (*20*). Plants were not nutrient-limited, but both *Zostera* and *Loripes* significantly lowered dissolved ammonium and phosphorus in the sediment pore water, whereas sulfide addition increased nutrient availability (fig. S4). We found that in our experiment, the negative effects of sulfide addition on *Zostera* biomass could not fully be prevented by *Loripes* addition (Fig. 3A), despite the removal of almost all sulfide by *Loripes* after 3 days. As the observed experimental effects could not be attributed to differences in nutrient availability, this is most likely caused by the pulsed nature of our sulfide supply. This may have led to short periods of exposure of *Zostera* to toxic sulfide levels.

Coastal ecosystems, and seagrass meadows in particular, are currently declining at an alarming and increasing rate worldwide, leading to loss of biodiversity (*1*). Extensive restoration efforts have had little success so far (<30%), despite their extremely high costs (±$100,000 per hectare) (*23*). Similar to the function of mycorrhizae, pollinators, or seed dispersers in terrestrial systems (*24*–*26*), our findings indicate that restoration efforts should not only focus on environmental stressors such as eutrophication, sediment runoff, or high salinity as a cause of decline but should also consider internal ecological interactions, such as the presence and vigor of symbiotic or mutualistic relations. Breakdown of symbiotic interactions can affect ecosystem functioning, with bleaching events in coral reefs as a clear example (*27*). Similar to the well-known symbiosis between corals and their unicellular algal endosymbionts (*28*), we conclude that symbioses, rather than one defining species, forms the foundation of seagrass ecosystems.

References and Notes

1. M. Waycott *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 12377 (2009).
2. A. W. D. Larkum, R. J. Orth, C. M. Duarte, *Seagrasses: Biology, Ecology, and Conservation* (Springer, Berlin, 2006).
3. I. Nagelkerken, *Ecological Connectivity Among Tropical Coastal Ecosystems* (Springer Science and Business Media, Dordrecht, 2009).
4. T. van der Heide *et al.*, *Ecosystems (N. Y.)* **10**, 1311 (2007).
5. T. van der Heide, E. H. van Nes, M. M. van Katwijk, H. Olff, A. J. P. Smolders, *PLoS ONE* **6**, e16504 (2011).
6. B. B. Jørgensen, *Nature* **296**, 643 (1982).
7. M. L. Calleja, N. Marba, C. M. Duarte, *Estuar. Coast. Shelf Sci.* **73**, 583 (2007).
8. M. S. Koch, S. Schopmeyer, C. Kyhn-Hansen, C. J. Madden, *J. Exp. Mar. Biol. Ecol.* **341**, 91 (2007).
9. J. D. Taylor, E. A. Glover, in *The Evolutionary Biology of the Bivalvia*, E. M. Harper, J. D. Taylor, J. A. Crame, Eds. (Geological Society of London, London, 2000), pp. 207–225.
10. L. Liljedahl, *Palaeontology* **34**, 219 (1991).
11. D. L. Distel, *Bioscience* **48**, 277 (1998).
12. S. M. Stanley, in *Patterns of Evolution as Illustrated by the Fossil Record*, A. Hallam, Ed. (Elsevier, Amsterdam, Netherlands, 1977), pp. 209–250.
13. J. D. Taylor, E. A. Glover, L. Smith, P. Dyal, S. T. Williams, *Zool. J. Linn. Soc.* **163**, 15 (2011).
14. G. J. Vermeij, *Proc. R. Soc. B Biol. Sci.* **278**, 2362 (2011).
15. C. M. Cavanaugh, *Nature* **302**, 58 (1983).
16. J. J. Childress, P. R. Girguis, *J. Exp. Biol.* **214**, 312 (2011).
17. M. Johnson, M. Diouris, M. Lepennec, *Symbiosis* **17**, 1 (1994).
18. L. K. Reynolds, P. Berg, J. C. Zieman, *Estuaries Coasts* **30**, 482 (2007).
19. A. E. Anderson, *Am. Zool.* **35**, 121 (1995).
20. Materials and methods are available as supplementary materials on *Science* Online.
21. K. Sand-Jensen, O. Pedersen, T. Binzer, J. Borum, *Ann. Bot. (Lond.)* **96**, 613 (2005).
22. J. M. Caffrey, W. M. Kemp, *Aquat. Bot.* **40**, 109 (1991).
23. M. S. Fonseca, W. J. Kenworthy, B. E. Julius, S. Shutler, S. Fluke, in *Handbook of Ecological Restoration*, M. R. Perrow, Ed. (Cambridge Univ. Press, Cambridge, 2002), pp. 149–170.
24. M. G. A. van der Heijden *et al.*, *Nature* **396**, 69 (1998).
25. J. Bascompte, P. Jordano, *Annu. Rev. Ecol. Evol. Syst.* **38**, 567 (2007).
26. U. Bastolla *et al.*, *Nature* **458**, 1018 (2009).
27. K. E. Carpenter *et al.*, *Science* **321**, 560 (2008).
28. A. C. Baker, *Annu. Rev. Ecol. Evol. Syst.* **34**, 661 (2003).

Acknowledgments: We thank G. Quaintenne and H. Blanchet for their help with the collection of *Loripes*; J. Eygensteyn and E. Pierson for technical assistance; and G. J. Vermeij, H. de Kroon, T. J. Bouma, E. J. Weerman, and C. Smit for their comments on the manuscript. T.v.d.H. was financially supported by the "Waddenfonds" program; M.v.d.G. and T.P. by the Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO)–WOTRO Integrated Programme grant W.01.65.221.00 awarded to T.P.; and J.d.F. and J.v.G. by the NWO–VIDI grant 864.09.002 awarded to J.v.G. B.S. was supported by an NSF CAREER award, the Andrew Mellon Foundation, and the Royal Netherlands Academy Visiting Professorship. The authors declare no conflicts of interest. A detailed description of all materials and methods, sources, as well as supplementary information are available as supplementary materials. The data are deposited in DRYAD at http://dx.doi.org/10.5061/dryad.210mp.

Supplementary Materials

www.sciencemag.org/cgi/content/full/336/6087/1432/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S4
Tables S1 and S2
References (*29*–*119*)

2 February 2012; accepted 27 April 2012
10.1126/science.1219973

Fear of Predation Slows Plant-Litter Decomposition

Dror Hawlena,[1,2]* Michael S. Strickland,[1,3] Mark A. Bradford,[1] Oswald J. Schmitz[1]

Aboveground consumers are believed to affect ecosystem functioning by regulating the quantity and quality of plant litter entering the soil. We uncovered a pathway whereby terrestrial predators regulate ecosystem processes via indirect control over soil community function. Grasshopper herbivores stressed by spider predators have a higher body carbon-to-nitrogen ratio than do grasshoppers raised without spiders. This change in elemental content does not slow grasshopper decomposition but perturbs belowground community function, decelerating the subsequent decomposition of plant litter. This legacy effect of predation on soil community function appears to be regulated by the amount of herbivore protein entering the soil.

The quantity and quality of detrital inputs to soil regulate the rate at which microbial communities perform ecosystem processes such as decomposition, nitrogen (N) mineralization, and carbon (C) sequestration (*1*, *2*). Because uneaten plant litter makes up the majority of detritus (*3*), it is assumed that these belowground ecosystem processes are only marginally influenced by biomass inputs from higher trophic levels in aboveground food webs, such as herbivores themselves (*4*). We provide evidence here, however, that predators may influence the decomposition of plant litter via a legacy effect of predation risk. Specifically, a physiological stress response to the risk of predation changes the elemental content of herbivore biomass. In turn, the decomposition of these stressed herbivores alters the function of belowground communities, leading to an overall decrease in the decomposition of plant litter.

Our work addresses whether food web structure (especially the existence of predators) influences ecosystem functioning via changes in the nutritional contents of prey (*5*, *6*). The prevailing view is that food web structure does not influence prey body C-to-N (C:N) contents, because to survive and reproduce, prey must maintian relatively constant body C:N ratios (*7*). However, this view assumes that predator effects on prey are entirely consumptive (*5*). Instead the presence of predators generates fear, leading to physiological stress responses in prey, such as elevated metabolism and the synthesis of heat shock proteins (*8*). Together, these stress responses increase basal energy demands (*9*–*12*) that, in nutrient-limited systems, reduce the energy available for the competing demands of production (that is, reproduction and growth) (*13*). Thus, to meet heightened maintenance-energy demands, stressed herbivores divert energy from production, as well as increase their consumption of energy-rich carbohydrates (*12*). Given that the amount of energy used for production correlates positively with N demand, and that herbivores have limited ability to store excess nutrients, stressed herbivores should also excrete more N (*8*, *14*). N excretion is further enhanced because chronically heightened stress hormone levels increase the breakdown of body proteins to produce glucose (*15*). Ultimately, prey stressed by predation risk should increase their body C:N ratio (*8*), and this is observed in field and laboratory experiments (*12*, *16*).

In this study we asked whether predators can regulate plant-litter decomposition through

---

[1]School of Forestry and Environmental Studies, Yale University, 370 Prospect Street, New Haven, CT 06511, USA. [2]Department of Ecology, Evolution and Behavior, The Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Givat-Ram, Jerusalem 91904, Israel. [3]Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA.

*To whom correspondence should be addressed. E-mail: dror.hawlena@mail.huji.ac.il

www.sciencemag.org/cgi/content/full/336/6087/1432/DC1

Supplementary Material for

A Three-Stage Symbiosis Forms the Foundation of Seagrass Ecosystems

Tjisse van der Heide,* Laura L. Govers, Jimmy de Fouw, Han Olff,
Matthijs van der Geest, Marieke M. van Katwijk, Theunis Piersma, Johan van de Koppel,
Brian R. Silliman, Alfons J. P. Smolders, Jan A. van Gils

*To whom correspondence should be addressed. E-mail: t.van.der.heide@rug.nl

Published 15 June 2012, *Science* **336**, 1432 (2012)
DOI: 10.1126/science.1219973

This PDF file includes:

Materials and Methods

Supplementary Text

Figs. S1 to S4

Tables S1 and S2

References (*29*–*119*)

Materials and Methods.

Meta-analysis.

To test the seagrass-lucinid association, we performed an extensive, worldwide meta-analysis that covered the entire climatic distribution of seagrasses. Criteria for including a study were: (1) seagrasses were present at the site, and (2) when Lucinidae were present, they were found inside the seagrass bed. In total, we analyzed 84 studies that sampled the fauna of seagrass beds in a total of 83 areas (temperature range = 1 to 33 ºC, mean = 22 ºC). Overall, 36 sites were from tropical areas, 31 from subtropical and 16 from temperate areas; quantitative data were available for 46 out of 83 sites. Apart from the geographical location of each site, and the seagrass and lucinid families found, we also report the annual seawater temperature range. These were obtained from freely available satellite imagery of the long-term monthly means (1971 – 2000) of the sea surface temperature (*29*).

Field study.

We conducted a field survey at Banc d'Arguin (Mauritania) to test the strength of the relation between seagrass biomass and lucinid density. Banc d'Arguin consists of about 500 km^2 of intertidal flat dominated by mixed meadows of *Zostera noltii*, *Halodule wrightii* and *Cymodocea nodosa* that are inhabited by the lucinid bivalve *Loripes lacteus* (*30*). In total, we sampled 110 stations across seven intertidal flats. *Loripes* was sampled up to a depth of 20 cm using a cylindrical 15-cm diameter PVC core sampler and seagrass was sampled with a 7-cm diameter corer. Each sample was sieved over a 1-mm mesh sieve. Next, *Loripes* was counted and seagrass biomass was determined after drying for 24-h at 70 ºC. Prior to linear regression analysis, *Loripes* counts and seagrass dry weight from the cores were transformed with the Box-Cox procedure to achieve normality and homoscedasticity (*31*).

Laboratory experiment.

Organisms and sediment for the experiment were collected in Arcachon Bay (southwest France) and transported at 15 ºC to the laboratory, where both species were separately acclimatized for three weeks in 100-L polyethylene tanks. *Zostera* units contained 15 cm of sediment and 20 cm of surface water; *Loripes* tanks contained 30 cm of sediment and 5 cm of surface water. We used artificial seawater (33-35 PSU Tropic Marin at 20 ºC) throughout the acclimatization period and during the experiment; pH was kept at 8.1 to 8.3 by CO_2 aeration. Light period was 16 h day^{-1}; intensity at the leaf surface was 300 µmol m^{-2} s^{-1}, similar to growing season conditions in the field (*32*). During this three-week period, we did not observe any bivalve mortality, and seagrasses exhibited healthy vegetative growth.

Experimental setup. The lower 6-cm tall sections of 40 two-compartment PVC columns (diameter 8.4 cm) were filled with anaerobic seawater (Fig. S3). These 330-ml sections contained an injection tube and were separated from their upper compartments through a porous 0.1-mm membrane. Sediment was passed through a 1-mm sieve and transferred to the upper 12-cm tall sections (surface area: 0.0055 m^2). Depending on the treatment, each unit then received either 1) *Loripes*, 2) *Zostera*, 3) both *Zostera* and *Loripes*, or 4) no further treatment. Nine *Loripes* specimens were added to each *Loripes* treatment (~1600 ind. m^{-2}; mean shell length ~9 mm) and 5 seagrass ramets with 2 or 3 shoots (12 shoots in total) were planted in each unit containing *Zostera* (~2200 sh. m^{-2}; ~0.12 g shoot, ~0.06 g rhizome and ~0.03 g DW root biomass per column). Each ramet contained one apical shoot to allow vegetative growth. Pilot experiments showed that this approach ensured consistent colonization of the units within the two-week adjustment period, with no detectable mortality of the plants. Densities of both species were well within reported ranges of densities in the field (up to 23000 sh. m^{-2} for *Zostera* and 3700 ind. m^{-2} for *Loripes*) (*33-35*).

A full factorial experiment was designed with eight treatments and five replicates per treatment. The columns were randomly placed in a 40-cm high 250-L polyethylene basin where water flow and oxygen saturation (measured with a 556 Multi Parameter Sampler, Yellow Springs Instruments) were maintained by two aquarium water pumps, and pH was kept constant (8.1-8.3) by CO_2 aeration. After setup, the units were allowed to adjust for two weeks. During this period, sulfide levels in the treatments containing *Loripes* stabilized at ~7 μM, while sulfide in treatments without *Loripes* increased to ~233 μM. Following the adjustment period, the experiment was performed for five weeks. Sulfide levels in the lower compartments of the sulfide addition treatments were increased twice a week by 3.3-ml injections of 100 mM Na_2S solution with pH adjusted to sediment conditions (pH 7.5) with HCl, while control treatments were injected with anaerobic water. Before each injection, we used 5 cm Rhizon samplers to extract 3 ml of pore water from the main root zone (top 6 cm) of each upper compartment into vacuumized 30 ml flasks containing 3 ml Sulfide Anti-Oxidation Buffer (SAOB). After each sampling, columns were re-randomized in the basin to minimize possible differences in light levels and water flow velocities between units. Sulfide concentrations were determined immediately with an ion selective silver/sulfide electrode (Thermo Scientific (USA), Orion 9416 BN; reference electrode: Orion 900200). Oxygen detection depth was measured after five weeks with an oxygen-sensitive microelectrode (Microscale Measurements, 1-mm tip). Ammonium, nitrate and total dissolved phosphorus in the sediment pore water were also measured after five weeks. We used 5 cm Rhizon samplers to extract 10 ml of pore water from the main root zone (top 6 cm) of each upper compartment into vacuumized 30 ml flasks. Ammonium and nitrate concentrations were determined colorimetrically. Ammonium was measured with salicylate (*36*) and nitrate was determined by sulfanilamide after reduction of nitrate to nitrite in a cadmium column (*37*). Dissolved phosphorus was measured on an Inductively Coupled Plasma emission spectrophotometer (ICP; Spectroflame, Spectro). Total nitrogen concentration in *Zostera* leaves was measured in freeze-dried tissues by a CNS analyzer (type NA1500; Carlo Erba Instruments, Milan, Italy) (*36*). Total phosphorus was measured by ICP after digestion with nitric acid (*36*). *Zostera* shoot, root and rhizome biomass and *Loripes* flesh were measured as dry weight after 24 h of freeze-drying. *Loripes* shell weight was measured after drying for 24 h at 70 ºC. *Loripes* condition was expressed as flesh/shell dry weight ratio, which is a commonly used size-and-age independent measure of fitness in bivalves (*38*). Sulfur contents in the *Loripes* tissues were measured on ICP, following nitric acid digestion.

Statistical analyses. Data were tested for normality prior to analysis. Sulfide data were analyzed with Repeated-Measures three-factor ANOVA. All other variables were analyzed by two- or three-factor ANOVA. All relevant and/or significant effects and interactions are mentioned in the figure legends or supporting text. A complete overview of the statistical output for Figures 2, 3 and S4 is provided in Table S2.

Supplementary Text

Both *Zostera* and *Loripes* significantly lowered dissolved ammonium and phosphorus in the sediment pore water, while sulfide addition increased their availability (Fig. S4). Nitrate concentrations were 0.8 ±0.9 μM (mean ±SD) on average with no significant differences between treatments. Mean leaf nitrogen and phosphorus content were 1.78 ±0.26 and 0.15 ±0.02 % dry weight respectively, which is around reported median values from the field for both (1.8 and 0.2 % DW respectively) (*39*). None of the treatments had any significant effect on leaf nitrogen. Leaf phosphorus content was unaffected by *Loripes*, but decreased significantly in the sulfide addition and sulfide addition with *Loripes* treatments (from 0.17 ±0.01 to 0.13 ±0.01 % DW; ANOVA: $F_{1,16}=29.0$, $p<0.001$). Apparently, high sulfide levels impaired phosphorus uptake by *Zostera* in the sulfide addition treatment, leading to decreased leaf phosphorus content, despite high dissolved phosphorus availability in the pore water (Fig. S4). Our pulsed sulfide addition also seemed to impair phosphorus uptake in the sulfide addition with *Loripes* treatment, which, by interacting with the reduced dissolved phosphorus pool may have limited growth of *Zostera* under our conditions (Fig. 3).

Sulfide addition resulted in a significant increase in the relative (ANOVA: $F_{1,16}=13.8$, $p=0.002$) and absolute sulfur content (ANOVA: $F_{1,16}=24.1$, $p<0.001$) in the flesh of the bivalves. Relative sulfur content was 2.0 ±0.2 % (g:g) in the control treatments and 3.0 ±0.9 % in the sulfide addition treatments. The total amount of sulfur stored in *Loripes* tissues per unit was 1.3 ±0.2 mg in the control treatments and 3.0 ±1.1 mg in the sulfide addition treatments. These results suggest that the increased sulfide availability led to increased storage of sulfur in the tissues of the bivalves, for instance as sulfur granules in the gills (*19*). We found no significant effects of *Zostera* on *Loripes* sulfur content.

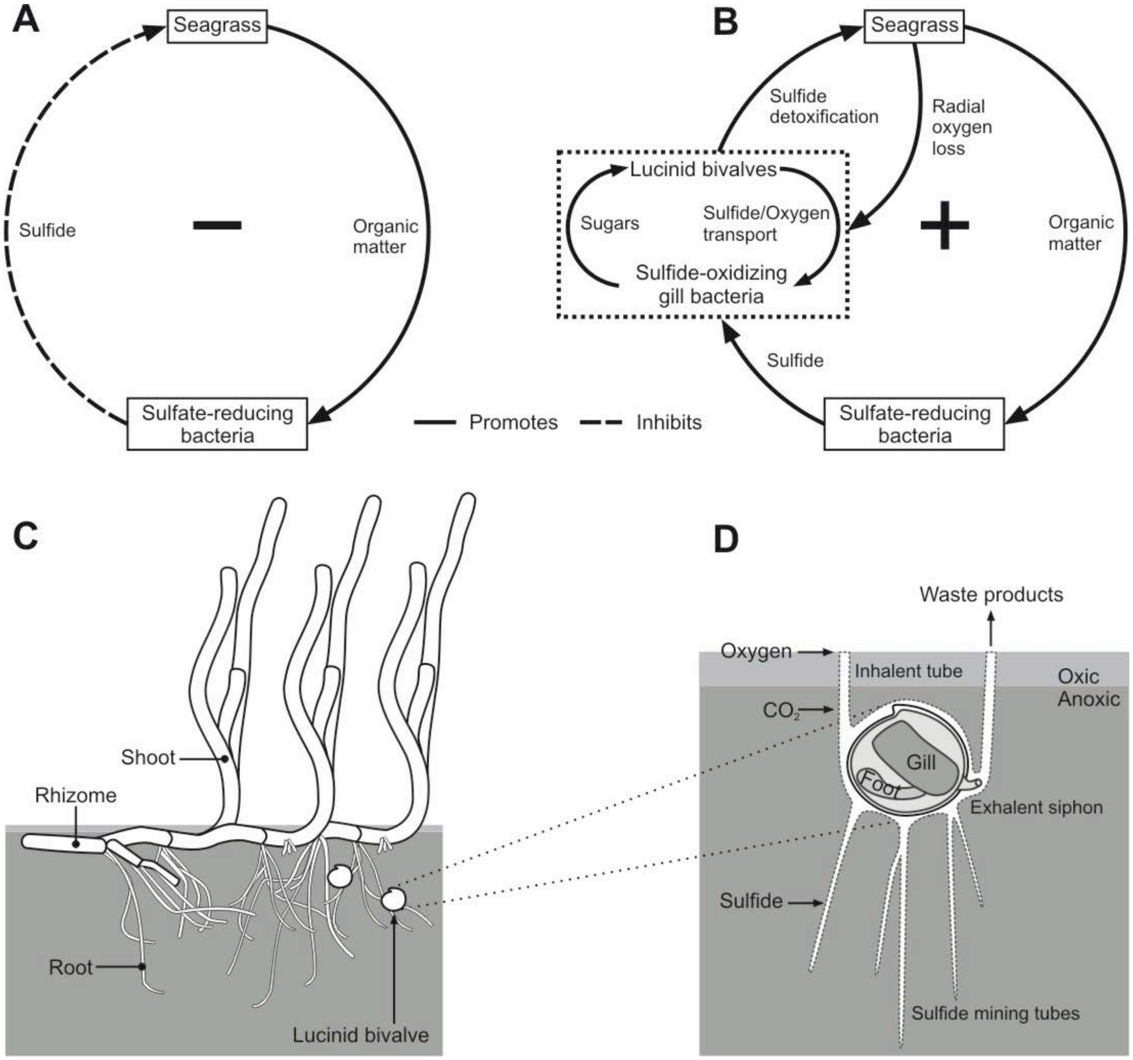

Figure S1. (**A**) Seagrasses generally create a negative feedback on their own growth through organic matter accumulation, which stimulates production of toxic sulfide by heterotrophic sulfate-reducing bacteria. (**B**) We propose in this study that the presence of lucinid bivalves and their sulfide-oxidizing gill-symbionts breaks the negative feedback, resulting in a network of positive interactions. (**C**) The bivalves are found in high abundances in the root zones of seagrass meadows in warmer, mild temperate to tropical regions where sulfide production rates are high. (**D**) They occur in the anoxic zone of the sediment and use their highly extensile foot to create tubes for sulfide mining, export of waste products and import of oxygen and CO_2 from the sediment pore water and surface water (*18, 19*). Both sulfide and oxygen are transported to the gills where chemoautotrophic bacteria oxidize sulfide for synthesizing sugars that fuel growth of both the bacteria and the bivalve (*16-19*).

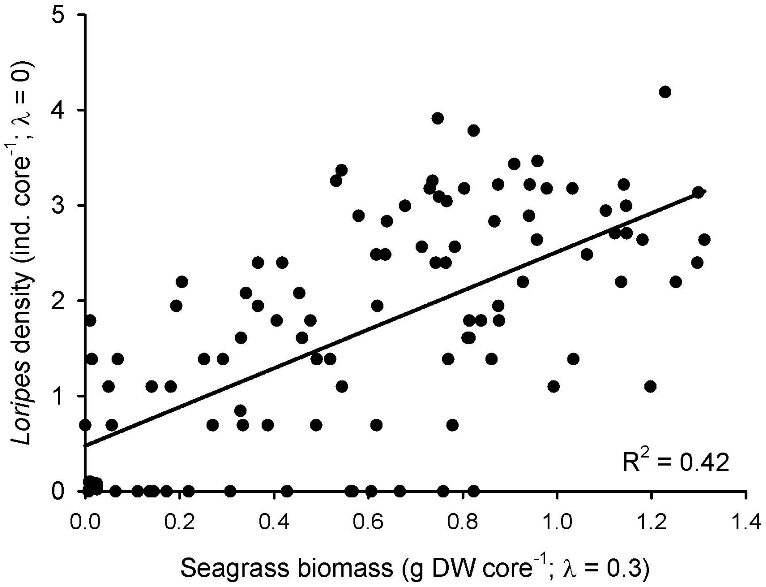

Fig. S2. Positive correlation (Pearson's r = 0.65) between seagrass biomass and *Loripes* density on Banc d'Arguin. *Loripes* counts and seagrass dry weight from the cores were transformed using the Box-Cox procedure prior to plotting and the regression analysis (see Materials and Methods).

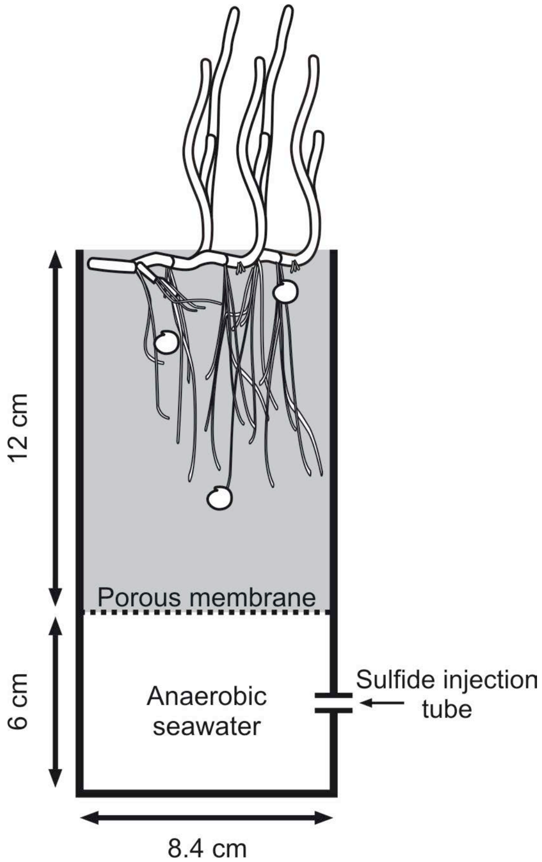

Fig. S3. Schematic drawing of the setup of an experimental unit. The dimensions of the top section were chosen to fit the organisms and to resemble field conditions. The lower section was kept large enough to allow rapid mixing and upward diffusion. Sulfide was injected twice a week in the sulfide addition treatments and allowed to diffuse from the lower compartment into the upper section through a 0.1-mm porous membrane.

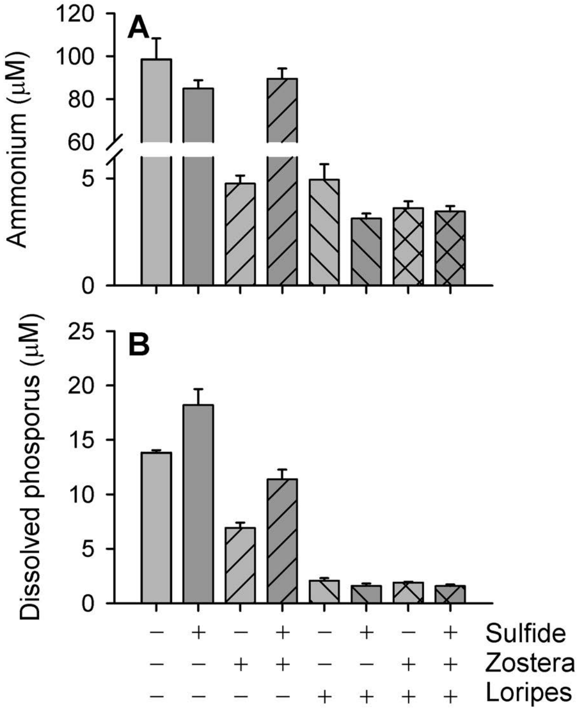

Fig. S4. Pore water ammonium and dissolved phosphorus contents after five weeks; error bars represent SEM (n=5). Ammonium (**A**) was lowered significantly by *Zostera* (ANOVA: $F_{1,32}$=59.7, p<0.001) and *Loripes* ($F_{1,32}$=505.9, p<0.001), while sulfide addition caused an increase ($F_{1,32}$=35.2, p<0.001). We found significant interactions between all treatments (*Z*L*: $F_{1,32}$=57.1, p<0.001; *Z*S*: $F_{1,32}$=73.3, p<0.001; *L*S*: $F_{1,32}$=39.3, p<0.001; *Z*L*S*: $F_{1,32}$=68.5, p<0.001). The treatment effects on dissolved phosphorus (**B**) were similar to ammonium, with significant effects of *Zostera* ($F_{1,32}$=58.2, p<0.001), *Loripes* ($F_{1,32}$=562.1, p<0.001) and sulfide addition ($F_{1,32}$=19.6, p<0.001). We found significant interactions of *Zostera* and *Loripes* ($F_{1,32}$=55.1, p<0.001), and *Loripes* and sulfide addition ($F_{1,32}$=28.2, p<0.001).

Table S1. Lucinid bivalve densities found in seagrass beds. These data provide a basic indication of the association between seagrasses and lucinids worldwide.

Area (source)	**Temp.**	**Clim.**	**Seagrass genus**	**Lucinid genus**	**Density**
North America					
Alaska (*40, 41*)	5 – 13	Temp.	*Zostera*	Lucinidae	p
Boston Harbor (*42*)	3 – 18	Temp.	*Zostera*		0
Chesapeake Bay (*43*)	1 – 23	Temp.	*Zostera*		0
Apalachee Bay, Florida (*44*)	18 – 29	Subtr.	*Syringodium, Thalassia*	*Codakia*	+
Biscayne Bay, Florida (*45*)	24 – 30	Subtr.	*Halodule, Syringodium, Thalassia*	*Anodontia, Codakia, Lucina*	++/+++
Florida Bay, Florida (*18*)	24 – 30	Subtr.	*Halodule, Syringodium, Thalassia*	*Anodontia, Codakia, Lucinesca*	++/+++
Indian River lag., Florida (*46*)	23 – 29	Subtr.	*Thalassia*	*Lucina*	p
St. Joseph's Bay, Florida (*47*)	18 – 29	Subtr.	*Thalassia*	*Lucina*	++/+++
Pensacola Bay, Florida (*48*)	18 – 29	Subtr.	*Halodule*		0
Redfish Bay, Texas (*49*)	19 – 29	Subtr.	*Halodule, Thalassia*	*Anodontia, Lucina, Phacoides*	p
Gulf of California, Mexico (*50*)	19 – 30	Subtr.	*Zostera, Halodule, Ruppia*	*Codakia, Divalinga*	p
Bahia de Chetumal, Mexico (*51*)	27 – 29	Trop.	*Syringodium, Thalassia*	*Codakia, Lucina*	p
Turneffe Islands, Belize, Mexico (*52*)	27 – 29	Trop.	*Thalassia*	*Codakia, Parvilucina*	p
Bocas del Toro, Panama (*53*)	27 – 29	Trop.	*Halodule, Syringodium, Thalassia*	*Codakia, Diplodonta Lucina, Phacoides*	p
Bahama's (*54*)	24 – 29	Trop.	*Thalassia*	*Codakia*	p
Jamaica (*55, 56*)	27 – 29	Trop.	*Thalassia*	*Anodontia, Codakia, Ctena, Divaricella, Lucina, Parvilucina*	+++/++++
St Croix, Virgin Islands (*57*)	26 – 29	Trop.	*Halodule, Syringodium, Thalassia*	*Codakia, Divalinga, Lucina, Parvilucina*	p
Guadeloupe (*58*)	26 – 29	Trop.	*Thalassia*	*Anodontia, Codakia*	p
Martinique (*54*)	26 – 29	Trop.	*Thalassia*	*Lucina*	p
Bermuda (*59, 60*)	19 – 28	Subtr.	*Thalassia*	*Codakia, Ctena*	++/+++
South America					
Bahia de Neguange, Columbia (*61*)	26 – 29	Trop.	*Thalassia, Syringodium*	*Codakia, Lucina, Anodontia*	p
Santiago de Tolú, Columbia (*62*)	27 – 29	Trop.	*Thalassia*	*Lucina*	p
Morrocoy, Venezuela (*63*)	26 – 28	Trop.	*Thalassia*	*Codakia*	+
Mochima Bay, Venezuela (*64*)	25 – 28	Trop.	*Thalassia*	*Codakia*	+++
Parracho de Maracajaú, Brazil (*65*)	26 – 28	Trop.	*Halophila, Halodule*	*Codakia, Divaricella*	p
Abrolhos Bank, Bahia Brazil (*66*)	25 – 28	Trop.	*Halodule, Halophila*	*Codakia, Ctena, Parvilucina*	p
Ilha do Japonês, Brazil (*67, 68*)	23 – 27	Trop.	*Halodule*	*Codakia, Divaricella*	++++

Table S1 (continued)

Ilha do Mel, Paranaguá, Brazil (*69*)	18 – 26	Trop.	*Halodule*	*Lucina*	p
Europe					
Western Atlantic, Norway (*70*)	6 – 13	Temp.	*Zostera*		0
Skagerrak, Atlantic, Norway (*70*)	4 – 17	Temp.	*Zostera*		0
Baltic, Finland (*71*)	1 – 16	Temp.	*Zostera*		0
Sylt, Wadden Sea (*72*)	4 – 18	Temp.	*Zostera*		0
South England (*73*)	8 – 17	Temp.	*Zostera*	*Lucinoma*	+
South Ireland (*74*)	9 – 17	Temp.	*Zostera*	*Lucinoma*	+++
Brittany, France (*75, 76*)	10 – 17	Temp.	*Zostera*	*Loripes, Lucinoma, Lucinella*	+++/++++
Arcachon, France (*77*)	12 – 21	Temp.	*Zostera*	*Loripes*	++
Eo estuary, Atlantic coast, Spain (*78*)	13 – 19	Temp.	*Zostera*	*Loripes*	++/+++
Mediterranean, Spain (*79*)	15 – 23	Subtr.	*Zostera*	*Lucinella*	+++
Mallorca, Spain (*80*)	14 – 25	Subtr.	*Posidonia*	*Ctena, Loripes, Lucinella*	p
Corsica, France (*34*)	13 – 24	Subtr.	*Cymodocea*	*Loripes*	+++/++++
Prelo Bay, Ligurian Sea (*81*)	13 – 23	Subtr.	*Posidonia*	*Lucinella*	++/+++
Venice lag., Italy (*82, 83*)	10 – 26	Subtr.	*Cymodocea, Zostera*	*Loripes*	+++/++++
Izmir Bay, Turkey (*84*)	15 – 23	Subtr.	*Zostera*	*Loripes*	++
Cyprus (*85*)	17 – 28	Subtr.	*Posidonia*	*Loripes, Myrtea*	+
Black Sea, Romania (*86*)	6 – 24	Temp.	*Zostera*	*Loripes, Lucinella*	p
Africa					
Banc d’Arguin, Mauritania (*35*)	18 – 26	Subtr.	*Cymodocea, Halodule, Zostera*	*Loripes*	+++/++++
Baia da Corimba, Angola (*87*)	22 – 29	Trop.	*Halodule*	*Loripes*	p
Kismayo, Somalia (*88*)	25 - 29	Trop.	*Halodule, Thalassia*	*Codakia, Lucina*	p
Zanzibar, Tanzania (*89*)	25 – 29	Trop.	*Cymodocea, Thalassia, Enhalus, Thalassodendron*	Lucinidae	++/++++
Mahé, Seychelles (*90*)	26 – 30	Trop.	*Thalassia*	*Anodontia, Codakia, Ctena,*	++
Inhaca, Mozambique (*91*)	23 – 27	Trop.	*Cymodocea, Halodule, Zostera*	*Anodontia, Cardiolucina, Loripes, Lucina, Pillucina*	++
Langebaan lag., South-Africa (*92*)	15 – 19	Subtr.	*Zostera*		0
Swartvlei estuary, South-Africa (*93*)	17– 22	Subtr.	*Zostera*	*Loripes*	p

Table S1 (continued)

Asia/Pacific					
Jordan, Red Sea (*94*)	21 – 28	Subtr.	*Halodule, Halophila*	*Rasta*	p
Egypt, Red Sea (*95*)	22 – 29	Subtr.	*Cymodocea, Halodule, Halophila*	*Cardiolucina, Divaricella, Pillucina, Wallucina*	++++
United Arab Emirates (*96*)	21 – 33	Subtr.	*Halodule, Halophila*	*Anodontia, Pillucina*	++++
Oman (this study)	25 – 28	Trop.	*Halodule, Halophila*	*Pillucina*	++++
Palk Bay, India (*97*)	27 – 30	Trop.	*Cymodocea, Halodule, Syringodium, Thalassodendron*	*Codakia, Lucina*	p
Posyet Bay, Sea of Japan (*98*)	2 – 21	Temp.	*Zostera*	*Pillucina*	+++
Tokyo, Bay of Japan (*99*)	16 – 26	Subtr.	*Zostera*	Lucinidae	p
Okinawa, Japan (*100*)	22 – 29	Subtr.	*Cymodocea, Enhalus, Halodule, Halophila, Thalassia*	*Codakia, Epicodakia*	p
Guangxi, China (*101*)	20 – 29	Trop.	*Halodule, Halophila, Zostera*		0
Guangdong, China (*101*)	21 – 29	Trop.	*Halodule, Halophila*	*Pillucina*	p
Hainan, China (*101*)	22 – 29	Trop.	*Cymodocea, Enhalus, Halodule, Thalassia*	*Pillucina*	p
Tubbataha Reefs, Philipines (*100*)	27 – 30	Trop.	*Halodule, Halophila, Thalassia*	*Epicodakia*	p
Kungkrabaen Bay, Thailand (*102*)	28 – 30	Trop.	*Halodule*	*Anodontia, Indoaustriella, Pillucina*	++++
Had Chao Mai, Thailand (*103*)	28 – 30	Trop.	*Cymodocea, Enhalus, Halodule, Halophila, Thalassia*	*Pillucina*	++++
Pulau Semakau, Singapore (*104*)	28 – 29	Trop.	*Cymodocea, Enhalus, Halodule, Halophila, Syringodium, Thalassia*	*Anodontia*	p
Bone Batang, Indonesia (*105*)	28 – 30	Trop.	*Cymodocea, Enhalus, Halodule, Halophila, Thalassia,*	Lucinidae	+++
Banten Bay, Indonesia (*106*)	28 – 30	Trop.	*Cymodocea, Enhalus, Halodule, Halophila, Syringodium, Thalassia*	*Anodontia, Codakia*	p
Tongapatu, Tonga (*100*)	23 – 27	Trop.	*Halodule*	*Codakia, Epicodakia*	p
Tarawa Atoll (*107*)	28 – 29	Trop.	*Thalassia*	*Codakia, Wallucina*	++/+++

Table S1 (continued)

Oceania					
Roebuck Bay, Australia (*108*, this study)	25 – 30	Trop.	*Halodule, Halophila*	*Anodontia, Ctena, Divaricella*	+++
Lizard Island, Australia (*109*)	25 – 29	Trop.	*Halophila*	*Anodontia, Chaviana, Wallucina*	p
Moreton Bay, Australia (*109*)	21 – 26	Subtr.	*Cymodocea, Halodule, Halophila, Zostera*	*Anodontia, Pillucina*	p
Rottnest Island, Australia (*110*)	19 – 23	Subtr.	*Posidonia*	*Wallucina*	+++/++++
South-West Australia (*111*)	16 – 20	Subtr.	*Amphibolis, Posidonia,*	*Anodontia*	p
New South-Wales, Australia (*112*)	19 – 24	Subtr.	*Halophila*	*Wallucina*	p
New South-Wales, Australia (*113*)	17 – 23	Subtr.	*Halophila, Zostera*		0
Western Port, Victoria, Australia (*114, 115*)	13 – 18	Temp.	*Halophila, Zostera*		0
Tasmania (*116, 117*)	12 – 16	Temp.	*Heterozostera. Ruppia, Zostera*	*Wallucina*	++/+++
New Caledonia (*118*)	24 – 28	Subtr.	*Cymodocea, Halodule, Thalassia*	*Anodontia, Codakia, Ctena*	p
Slipper Island, New Zealand (*119*)	15 – 21	Subtr.	*Zostera*	*Divaricella*	p

Temp. depicts the mean annual temperature range based on the sea surface temperature (ºC);
Clim. indicates type of climate (tropical, subtropical or temperate);
Lucinid density (spatial average): + = 1-10; ++ = 11-100; +++ = 101-1000; ++++ = >1000 ind/m^2
p = present (no abundance data); u = uncertain; 0 = absent.

Table S2. Overview of the statistical output from the analyses of the data presented in Figures 2, 3, and S4.

Treatment	**df**	**F**	**p**
Sulfide measurements (Fig. 2A; repeated measures ANOVA)			
Zostera	1	6.8	0.014
Loripes	1	268.8	<0.001
Sulfide	1	109.7	<0.001
Zostera * Loripes	1	7.8	0.009
Zostera * Sulfide	1	2.2	0.150
Loripes * Sulfide	1	102.7	<0.001
Zostera * Loripes * Sulfide	1	2.4	0.127
Error	32		
Oxygen measurements (Fig. 2B; ANOVA)			
Zostera	1	39.3	<0.001
Loripes	1	125.0	<0.001
Sulfide	1	8.9	0.006
Zostera * Loripes	1	48.3	<0.001
Zostera * Sulfide	1	0.0	0.862
Loripes * Sulfide	1	0.3	0.578
Zostera * Loripes * Sulfide	1	0.5	0.505
Error	32		
Zostera shoot biomass (Fig. 3A; ANOVA)			
Loripes	1	61.3	<0.001
Sulfide	1	72.6	<0.001
Loripes * Sulfide	1	0.9	0.348
Error	16		
Zostera root biomass (Fig. 3B; ANOVA)			
Loripes	1	50.2	<0.001
Sulfide	1	12.0	0.003
Loripes * Sulfide	1	1.7	0.211
Error	16		
Loripes fitness (Fig. 3C; ANOVA)			
Sulfide	1	37.3	<0.001
Zostera	1	9.0	0.008
Sulfide * Zostera	1	5.4	0.034
Error	16		
Ammonium (Fig. S4A; ANOVA)			
Zostera	1	59.7	<0.001
Loripes	1	505.9	<0.001
Sulfide	1	35.2	<0.001
Zostera * Loripes	1	57.1	<0.001
Zostera * Sulfide	1	73.3	<0.001
Loripes * Sulfide	1	39.3	<0.001
Zostera * Loripes * Sulfide	1	68.5	<0.001
Error	32		
Phosphorus (Fig. S4B; ANOVA)			
Zostera	1	58.2	<0.001
Loripes	1	562.1	<0.001
Sulfide	1	19.6	<0.001
Zostera * Loripes	1	55.1	<0.001
Zostera * Sulfide	1	0.0	0.888
Loripes * Sulfide	1	28.2	0.000
Zostera * Loripes * Sulfide	1	0.0	0.965
Error	32		

References and Notes

1. M. Waycott *et al.*, Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 12377 (2009). doi:10.1073/pnas.0905620106 Medline

2. A. W. D. Larkum, R. J. Orth, C. M. Duarte, *Seagrasses: Biology, Ecology, and Conservation* (Springer, Berlin, 2006).

3. I. Nagelkerken, *Ecological Connectivity Among Tropical Coastal Ecosystems* (Springer Science and Business Media, Dordrecht, 2009).

4. T. van der Heide *et al.*, Positive feedbacks in seagrass ecosystems—Implications for success in conservation and restoration. *Ecosystems (N. Y.)* **10**, 1311 (2007). doi:10.1007/s10021-007-9099-7

5. T. van der Heide, E. H. van Nes, M. M. van Katwijk, H. Olff, A. J. P. Smolders, Positive feedbacks in seagrass ecosystems—evidence from large-scale empirical data. *PLoS ONE* **6**, e16504 (2011). doi:10.1371/journal.pone.0016504 Medline

6. B. B. Jørgensen, Mineralization of organic matter in the sea bed—The role of sulphate reduction. *Nature* **296**, 643 (1982). doi:10.1038/296643a0

7. M. L. Calleja, N. Marba, C. M. Duarte, The relationship between seagrass (*Posidonia oceanica*) decline and sulfide porewater concentration in carbonate sediments. *Estuar. Coast. Shelf Sci.* **73**, 583 (2007). doi:10.1016/j.ecss.2007.02.016

8. M. S. Koch, S. Schopmeyer, C. Kyhn-Hansen, C. J. Madden, Synergistic effects of high temperature and sulfide on tropical seagrass. *J. Exp. Mar. Biol. Ecol.* **341**, 91 (2007). doi:10.1016/j.jembe.2006.10.004

9. J. D. Taylor, E. A. Glover, in *The Evolutionary Biology of the Bivalvia*, E. M. Harper, J. D. Taylor, J. A. Crame, Eds. (Geological Society of London, London, 2000), pp. 207–225.

10. L. Liljedahl, Contrasting feeding strategies in bivalves from the Silurian of Gotland. *Palaeontology* **34**, 219 (1991).

11. D. L. Distel, Evolution of chemoautotrophic endosymbioses in bivalves—Bivalve-bacteria chemosymbioses are phylogenetically diverse but morphologically similar. *Bioscience* **48**, 277 (1998). doi:10.2307/1313354

12. S. M. Stanley, in *Patterns of Evolution as Illustrated by the Fossil Record*, A. Hallam, Ed. (Elsevier, Amsterdam, The Netherlands, 1977), pp. 209–250.

13. J. D. Taylor, E. A. Glover, L. Smith, P. Dyal, S. T. Williams, Molecular phylogeny and classification of the chemosymbiotic bivalve family Lucinidae (Mollusca: Bivalvia). *Zool. J. Linn. Soc.* **163**, 15 (2011).

14. G. J. Vermeij, Shifting sources of productivity in the coastal marine tropics during the Cenozoic era. *Proc. R. Soc. B Biol. Sci.* **278**, 2362 (2011). doi:10.1098/rspb.2010.2362 Medline

15. C. M. Cavanaugh, Symbiotic chemoautotrophic bacteria in marine invertebrates from sulphide-rich habitats. *Nature* **302**, 58 (1983). doi:10.1038/302058a0

16. J. J. Childress, P. R. Girguis, The metabolic demands of endosymbiotic chemoautotrophic metabolism on host physiological capacities. *J. Exp. Biol.* **214**, 312 (2011). doi:10.1242/jeb.049023 Medline

17. M. Johnson, M. Diouris, M. Lepennec, Endosymbiotic bacterial contribution in the carbon nutrition of *Loripes lucinalis* (Mollusca: Bivalvia). *Symbiosis* **17**, 1 (1994).

18. L. K. Reynolds, P. Berg, J. C. Zieman, Lucinid clam influence on the biogeochemistry of the seagrass *Thalassia testudinum* sediments. *Estuaries Coasts* **30**, 482 (2007). doi:10.1007/BF02819394

19. A. E. Anderson, Metabolic responses to sulfur in lucinid bivalves. *Am. Zool.* **35**, 121 (1995).

20. Materials and methods are available as supplementary materials on *Science* Online.

21. K. Sand-Jensen, O. Pedersen, T. Binzer, J. Borum, Contrasting oxygen dynamics in the freshwater isoetid *Lobelia dortmanna* and the marine seagrass *Zostera marina*. *Ann. Bot. (Lond.)* **96**, 613 (2005). doi:10.1093/aob/mci214 Medline

22. J. M. Caffrey, W. M. Kemp, Seasonal and spatial patterns of oxygen production, respiration and root rhizome release in *Potamogeton perfoliatus* L. and *Zostera marina* L. *Aquat. Bot.* **40**, 109 (1991). doi:10.1016/0304-3770(91)90090-R

23. M. S. Fonseca, W. J. Kenworthy, B. E. Julius, S. Shutler, S. Fluke, in *Handbook of Ecological Restoration*, M. R. Perrow, Ed. (Cambridge Univ. Press, Cambridge, 2002), pp. 149–170.

24. M. G. A. van der Heijden *et al.*, Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**, 69 (1998). doi:10.1038/23932

25. J. Bascompte, P. Jordano, Plant-animal mutualistic networks: The architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **38**, 567 (2007). doi:10.1146/annurev.ecolsys.38.091206.095818

26. U. Bastolla *et al.*, The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* **458**, 1018 (2009). doi:10.1038/nature07950 Medline

27. K. E. Carpenter *et al.*, One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* **321**, 560 (2008). doi:10.1126/science.1159196 Medline

28. A. C. Baker, Flexibility and specificity in coral-algal symbiosis: Diversity, ecology, and biogeography of Symbiodinium. *Annu. Rev. Ecol. Evol. Syst.* **34**, 661 (2003). doi:10.1146/annurev.ecolsys.34.011802.132417

29. NOAA/OAR/ESRL/PSD, (NOAA/OAR/ESRL/PSD, Boulder, Colorado, USA, 2011).

30. W. J. Wolff *et al.*, Biomass of macrobenthic tidal flat fauna of the Banc d’Arguin, Mauritania. *Hydrobiologia* **258**, 151 (1993). doi:10.1007/BF00006193

31. G. E. P. Box, D. R. Cox, An analysis of transformations. *J. R. Stat. Soc., B* **26**, 211 (1964).

32. M. F. Isaksen, K. Finster, Sulphate reduction in the root zone of the seagrass *Zostera noltii* on the intertidal flats of a coastal lagoon (Arcachon, France). *Mar. Ecol. Prog. Ser.* **137**, 187 (1996). doi:10.3354/meps137187

33. J. E. Vermaat, F. C. A. Verhagen, Seasonal variation in the intertidal seagrass *Zostera noltii* Hornem: Coupling demographic and physiological patterns. *Aquat. Bot.* **52**, 259 (1996). doi:10.1016/0304-3770(95)00510-2

34. M. A. Johnson, C. Fernandez, G. Pergent, The ecological importance of an invertebrate chemoautotrophic symbiosis to phanerogam seagrass beds. *Bull. Mar. Sci.* **71**, 1343 (2002).

35. M. van der Geest, J. A. van Gils, J. van der Meer, H. Olff, T. Piersma, Suitability of calcein as an in situ growth marker in burrowing bivalves. *J. Exp. Mar. Biol. Ecol.* **399**, 1 (2011). doi:10.1016/j.jembe.2011.01.003

36. L. P. M. Lamers, H. B. M. Tomassen, J. G. M. Roelofs, Sulfate-induced entrophication and phytotoxicity in freshwater wetlands. *Environ. Sci. Technol.* **32**, 199 (1998). doi:10.1021/es970362f

37. E. D. Wood, F. J. A. Armstrong, F. A. Richards, Determination of nitrate in sea water by cadmium-copper reduction to nitrite. *J. Mar. Biol. Assoc. U. K.* **47**, 23 (1967). doi:10.1017/S002531540003352X

38. A. Lucas, P. G. Beninger, The use of physiological condition indices in marine bivalve aquaculture. *Aquaculture* **44**, 187 (1985). doi:10.1016/0044-8486(85)90243-1

39. C. M. Duarte, Seagrass Nutrient Content. *Mar. Ecol. Prog. Ser.* **67**, 201 (1990). doi:10.3354/meps067201

40. S. C. Jewett, T. A. Dean, R. O. Smith, A. Blanchard, ‘Exxon Valdez’ oil spill: Impacts and recovery in the soft-bottom benthic community in and adjacent to eelgrass beds. *Mar. Ecol. Prog. Ser.* **185**, 59 (1999). doi:10.3354/meps185059

41. T. A. Dean, S. C. Jewett, Habitat-specific recovery of shallow subtidal communities following the Exxon Valdez oil spill. *Ecol. Appl.* **11**, 1456 (2001). doi:10.1890/1051-0761(2001)011[1456:HSROSS]2.0.CO;2

42. A. S. Leschen, R. K. Kessler, B. T. Estrella, *Eelgrass Restoration Used as Construction Impact Mitigation in Boston Harbor, Massachusetts* (Massachusetts Division of Marine Fisheries, New Bedford, 2009).

43. R. J. Orth, Benthic infauna of eelgrass, *Zostera marina*, beds. *Chesap. Sci.* **14**, 258 (1973). doi:10.2307/1350754

44. F. G. Lewis, A. W. Stoner, An examintation of methods for sampling macrobenthos in seagrass meadows. *Bull. Mar. Sci.* **31**, 116 (1981).

45. H. B. Moore, L. T. Davies, T. H. Fraser, R. H. Gore, N. R. Lopez, Some biomass figures from a tidal flat in Biscayne bay, Florida. *Bull. Mar. Sci.* **18**, 261 (1968).

46. P. M. Mikkelsen, P. S. Mikkelsen, D. J. Karlen, Molluscan biodiversity in the Indian river lagoon, Florida. *Bull. Mar. Sci.* **57**, 94 (1995).

47. M. R. Fisher, S. C. Hand, Chemoautotrophic symbionts in the bivalve *Lucina floridana* from seagrass beds. *Biol. Bull.* **167**, 445 (1984). doi:10.2307/1541289

48. A. W. Stoner, H. S. Greening, J. D. Ryan, R. J. Livingston, Comparison of macrobenthos collected with cores and suction sampler in vegetated and unvegetated marine habitats. *Estuaries* **6**, 76 (1983). doi:10.2307/1351809

49. Center for Coastal Studies, *Current Status and Historical Trends of the Estuarine Living Resources Within the CCBNEP Study Area* (Center for Coastal Studies, Texas A&M University, Corpus Christi, 1996).

50. J. Torra Cosio, L. Bourillón, "Inventario y monitoreo del canal del infiernillo para el comanejo de los recursos marinos en el territorio" (SNIB- CONABIO Mexico City, 2000).

51. V. F. Quesada *et al*., "Programa de manejo parque nacional Arrecifes de Xcalak" (Mexico National Protected Areas Commission, Mexico City, Mexico, 2004).

52. I. Hauser, W. Oschmann, E. Gischler, Modern bivalve shell assemblages on three atolls offshore Belize (Central America, Caribbean Sea). *Facies* **53**, 451 (2007). doi:10.1007/s10347-007-0111-7

53. Continental Shelf Associates, *Synthesis of Available Biological, Geological, Chemical, Socioeconomic, and Cultural Resource Information for the South Florida Area. Supplemental Report: A Comparison of Seagrass Beds in Panama and South Florida* (U.S. Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, 1995).

54. M. T. Brissac, "Nature, diversité et spécificité de l'association Lucinidae/bactéries sulfo-oxydantes" (Universite Pierre et Marie Curie Paris, 2009).

55. M. Greenway, Trophic relationship of macrofauna within a Jamaican seagrass meadow and the role of the echinoid *Lytechinus varriegatus* (Lamarck). *Bull. Mar. Sci.* **56**, 719 (1995).

56. J. B. C. Jackson, The ecology of the molluscs of *Thalassia* communities, Jamaica, West Indies. II. Molluscan population variability along an environmental stress gradient. *Mar. Biol.* **14**, 304 (1972). doi:10.1007/BF00348180

57. C. A. Ferguson, A. I. Miller, A sea change in Smuggler's Cove? Detection of decadal-scale compositional transitions in the subfossil record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **254**, 418 (2007). doi:10.1016/j.palaeo.2007.06.021

58. O. Gros, M. Liberge, H. Felbeck, Interspecific infection of aposymbiotic juveniles of *Codakia orbicularis* by various tropical lucinid gill-endosymbionts. *Mar. Biol.* **142**, 57 (2003).

59. M. Aurelia, paper presented at the Seminar on organism-sediment interelationship, Bermuda, 1969.

60. M. Schweimanns, H. Felbeck, Significance of the occurrence of chemoautotrophic bacterial endosymbionts in lucinid clams from Bermuda. *Mar. Ecol. Prog. Ser.* **24**, 113 (1985). doi:10.3354/meps024113

61. J. M. Diaz, in *Las Praderas de Pastos Marinos en Colombia Estructura y Distribución de un Ecosistema Estratégico*, J. M. Díaz Merlano, L. M. Barrios Suárez, D. I. Gómez-LópezDiaz, Eds. (Instituto de Investigaciones Marinas y Costeras "José Benito Vives De Andréis" Santa Marta, Columbia, 2003), vol. 10, pp. 159.

62. A. Otero-Otero, J. Romani Lobo, “Macroinvertebrados asociados a pastos marinos (*Thalassia testudinum*) en el golfo de Morrosquillo (Zone de Berrugas) Departamento de Sucre” (Universidad de Sucre, Sincelejo, Columbia, 2009).

63. R. Bitter-Soto, Benthic communities associated to *Thalassia testudinum* (Hydrocharitaceae) at three localities of Morrocoy National Park, Venezuela. *Rev. Biol. Trop.* **47**, 443 (1999).

64. O. D. Díaz, I. Liñero-Arana, [Mollusks community associated to *Thalassia testudinum* (Bank et Köning 1805), in Mochima Bay, Venezuela]. *Acta Cient. Venez.* **55**, 44 (2004). Medline

65. A. S. Martinez, “Distribuiç ao e abundância da malacofauna epibentônica no parracho de Maracajaú, RN, Brasil” (Universidade federal do Rio Grande do norte centro de biociêcias, Natal, RN Brazil, 2008).

66. G. F. Dutra, G. R. Allen, T. Werner, S. A. McKenna, *A Rapid Marine Biodiversity Assessment of the Abrolhos Bank, Bahia, Brazil*; Rapid Assesment Program, Bulletin of Biological Assesment (Washington, USA, 2005), vol. 38, pp. 160.

67. L. V. Marques, J. C. Creed, Biologia e ecologia das Fanérogamas marinhas do Brazil. *Oecol. Bras.* **12**, 315 (2000).

68. J. C. Creed, M. Kinupp, Small-scale change in mollusk diversity along a depth gradient in a seagrass bed off Cabo Frio (Southeast Brazil). *Brazilian J. Oceanogr.* **59**, 267 (2011). doi:10.1590/S1679-87592011000300007

69. E. C. G. Couto, M. Savian, Caracterização sedimentológica da planície intertidal da parte sul do saco do limoeiro (Ilha do Mel - Paraná - Brasil). I. implicações ecológicas. *Braz. Arch. Biol. Technol.* **41**, 0 (1998). doi:10.1590/S1516-89131998000200011

70. S. Fredriksen, A. De Backer, C. Bostrom, H. Christie, Infauna from *Zostera marina* L. meadows in Norway. Differences in vegetated and unvegetated areas. *Mar. Biol. Res.* **6**, 189 (2010). doi:10.1080/17451000903042461

71. C. Boström, E. Bonsdorff, Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L) beds in the northern Baltic Sea. *J. Sea Res.* **37**, 153 (1997). doi:10.1016/S1385-1101(96)00007-X

72. K. Reise, *Tidal Flat Ecology: An Experimental Approach to Species Interactions* (Springer-Verlag, New York, 1985), pp. 191.

73. P. R. Dando, A. J. Southward, E. C. Southward, Chemoautotrophic symbionts in the gills of the bivalve mollusc *Lucinoma borealis* and the sediment chemistry of its habitat. *Proc. R. Soc. Lond. B Biol. Sci.* **227**, 227 (1986). doi:10.1098/rspb.1986.0021

74. A. L. Dale, R. McAllen, P. Whelan, *Management Considerations for Subtidal Zostera marina Beds in Ireland* (Department of Zoology, Ecology & Plant Science University College Cork, Dublin, Ireland, 2007).

75. C. Hily, M. Bouteille, Modifications of the specific diversity and feeding guilds in an intertidal sediment colonized by an eelgrass meadow (*Zostera marina*) (Brittany, France). *Life Sci.* **322**, 1121 (1999).

76. J. Y. Monnat, “Introduction á l’étude de la reproduction chez *Lucinoma borealis* (Linné), Bivalvia, Lucinacea” (Faculté de Science, Brest, 1970).

77. H. Blanchet, X. de Montaudouin, A. Lucas, P. Chardy, Heterogeneity of macrozoobenthic assemblages within a *Zostera noltii* seagrass bed: Diversity, abundance, biomass and structuring factors. *Estuar. Coast. Shelf Sci.* **61**, 111 (2004). doi:10.1016/j.ecss.2004.04.008

78. L. de Paz, J. M. Neto, J. C. Marques, A. J. Laborda, Response of intertidal macrobenthic communities to long term human induced changes in the Eo estuary (Asturias, Spain): implications for environmental management. *Mar. Environ. Res.* **66**, 288 (2008). doi:10.1016/j.marenvres.2008.04.004 Medline

79. J. L. Rueda, C. Salas, Molluscs associated with a subtidal *Zostera marina* L. bed in southern Spain: Linking seasonal changes of fauna and environmental variables. *Estuar. Coast. Shelf Sci.* **79**, 157 (2008). doi:10.1016/j.ecss.2008.03.018

80. A. B. Centeno, “Ecología de Caulerpales: Fauna y Biomarcadores” (Mallorca, Spain, 2008).

81. A. C. Harriague, C. N. Bianchi, G. Albertelli, Soft-bottom macrobenthic community composition and biomass in a *Posidonia oceanica* meadow in the Ligurian Sea (NW Mediterranean). *Estuar. Coast. Shelf Sci.* **70**, 251 (2006). doi:10.1016/j.ecss.2005.10.017

82. A. Sfriso, T. Birkemeyer, P. F. Ghetti, Benthic macrofauna changes in areas of Venice lagoon populated by seagrasses or seaweeds. *Mar. Environ. Res.* **52**, 323 (2001). doi:10.1016/S0141-1136(01)00089-7 Medline

83. F. Pranovi, D. Curiel, A. Rismondo, M. Marzocchi, M. Scattolin, Variations of the macrobenthic community in a seagrass transplanted area of the Lagoon of Venice. *Sci. Mar.* **64**, 303 (2000).

84. M. E. Cinar, Z. Ergen, B. Ozturk, F. Kirkim, Seasonal analysis of zoobenthos associated with a *Zostera marina* L. bed in Gulbahce Bay (Aegean Sea, Turkey). *Mar. Ecol. Pubbl. Stn. Zool. Napoli* **19**, 147 (1998).

85. M. Argyrou, A. Demetropoulos, M. Hadjichristophorou, Expansion of the macroalga *Caulerpa racemosa* and changes in softbottom macrofaunal assemblages in Moni Bay, Cyprus. *Oceanol. Acta* **22**, 517 (1999). doi:10.1016/S0399-1784(00)87684-7

86. S. Nicolaev, T. Zaharia, “Report on the state of the marine and coastal environment in 2010” (NIMRD, Constanta, Romania, 2011).

87. C. I. Van-Dunem do Sacramento Neto dos Santos, “Comunidades de macroninvertebrados e peixes associades à pradaria marinha de *Hadule wrightii* (Ascherson, 1868) na Laguno do Mussulo, Angola” (Universidade de Lisboa, Lisboa, 2007).

88. G. Chelazzi, M. Vannini, Zonation of intertidal molluscs on rocky shores of southern Somalia. *Estuar. Coast. Mar. Sci.* **10**, 569 (1980). doi:10.1016/S0302-3524(80)80076-4

89. J. S. Eklöf, M. de la Torre-Castro, L. Adelskold, N. S. Jiddawi, N. Kautsky, Differences in macrofaunal and seagrass assemblages in seagrass beds with and without seaweed farms. *Estuar. Coast. Shelf Sci.* **63**, 385 (2005). doi:10.1016/j.ecss.2004.11.014

90. J. D. Taylor, M. S. Lewis, The flora, fauna and sediments of the marine grass beds of Mahé, Seychelles. *J. Nat. Hist.* **4**, 199 (1970). doi:10.1080/00222937000770201

91. W. F. de Boer, H. H. T. Prins, Human exploitation and benthic community structure on a tropical intertidal flat. *J. Sea Res.* **48**, 225 (2002). doi:10.1016/S1385-1101(02)00160-0

92. T. Siebert, G. M. Branch, Interactions between *Zostera capensis* and *Callianassa kraussi*: influences on community composition of eelgrass beds and sandflats. *Afr. J. Mar. Sci.* **27**, 357 (2005). doi:10.2989/18142320509504095

93. A. K. Whitfield, The benthic community of the Southern Cape estuary - Structure and possible food sources. *Trans. R. Soc. S. Afr.* **47**, 159 (1989). doi:10.1080/00359198909520160

94. J. D. Taylor, E. A. Glover, M. Zuschin, P. C. Dworschak, W. Waitzbauer, Another bivalve with dreadlocks: Living Rasta lamyi from Aqaba, Red Sea (Bivalvia: Lucinidae). *J. Conchol.* **38**, 489 (2005).

95. M. Zuschin, J. Hohenegger, Subtropical coral-reef associated sedimentary facies characterized by molluscs (Northern bay of Safaga, Red Sea, Egypt). *Facies* **38**, 229 (1998). doi:10.1007/BF02537367

96. G. R. Feulner, R. J. Hornby, Intertidal molluscs in UAE lagoons. *Tribulus (Abu Dhabi)* **16**, 17 (2006).

97. C. S. Gophinadha-Pillai, K. K. Appukuttan, Distribution of molluscs in and around the coral reefs of the southeastern coast in India. *J. Bombay Nat. Hist. Soc.* **77**, 26 (1980).

98. V. I. Kharlamenko, S. I. Kiyashko, A. B. Imbs, D. I. Vyshkvartzev, Identification of food sources of invertebrates from the seagrass *Zostera marina* community using carbon and sulfur stable isotope ratio and fatty acid analyses. *Mar. Ecol. Prog. Ser.* **220**, 103 (2001). doi:10.3354/meps220103

99. N. Whanpetch, “Variability and consequences of seagrass vegetation effect on macrobenthic invertebrate communities” (Chiba University, Chiba, Japan, 2011).

100. M. Yamaguchi, in *Asian Marine Biology*, M. B., Ed. (University Press, Hong Kong 1999), vol. 15, pp. 217.

101. X. Huang, “National report on seagrass in the South China Sea–China” (South China Sea Institute of Oceanology, Chinese Academy of Sciences, Guangzhou, China, 2008).

102. E. Meyer, B. Nilkerd, E. A. Glover, J. D. Taylor, Ecological importance of chemoautotrophic lucinid bivalves in a peri-mangrove commnity in eastern Thailand. *Raffles Bull. Zool.* **18**, 41 (2008).

103. M. Nakaoka, H. Mukai, S. Chunhabundit, Impacts of dugong foraging on benthic animal communities in a Thailand seagrass bed. *Ecol. Res.* **17**, 625 (2002). doi:10.1046/j.1440-1703.2002.00520.x

104. S. K. Tan, R. K. H. Yeo, The intertidal molluscs of Pulau Semakau: Preliminary results of “project Semakau”. *Nat. Singapore* **3**, 287 (2010).

105. J. A. Vonk, M. J. A. Christianen, J. Stapel, Redefining the trophic importance of seagrasses for fauna in tropical Indo-Pacific meadows. *Estuar. Coast. Shelf Sci.* **79**, 653 (2008). doi:10.1016/j.ecss.2008.06.002

106. T. E. Kuriandewa, “National report on seagrass in the South China Sea–Indonesia” (Puslit Oseanografi, Lipi, Jakarta, Indonesia, 2008).

107. G. Paulay, Benthic ecology and biota of Tarawa Atoll lagoon: Influence of equatorial upwelling, circulation and human harvest. *Atoll Res. Bull.* **487**, 1 (2000).

108. T. Piersma *et al*., "Roebuck Bay invertebrate and bird mapping 2006" (Royal Netherlands Institute for Sea Research Texel, The Netherlands, 2006).

109. J. D. Taylor, E. A. Glover, in *Proceedings of the 13th international marine biological workshop—The Marine Fauna and Flora of Moreton Bay, Queensland*, D. P. J. F., J. A. Phillips, Eds. (Queensland Museum, South Brisbane, Australia, 2008), vol. 54, pp. 75–104.

110. P. A. G. Barnes, C. S. Hickman, in *The seagrass Flora and Fauna of Rottnest Island, Western Australia*, D. I. Walker, F. E. Wells, Eds. (Western Australian Museum, Perth, 1999), pp. 215–238.

111. P. A. Hutchings, F. E. Wells, W. D. I., G. A. Kendrick, in *The Flora and Fauna of the Albany Area, Western Australia*, W. F. E., W. D. I., H. Kirkman, R. Lethbridge, Eds. (Western Australian Museum, Perth, 1991), pp. 611–633.

112. P. J. Gibbs, G. B. Maguire, L. C. Collett, The macrobenthic fauna of *Halophila* seagrass meadows in New South Wales. *Wetlands* **4**, 23 (1984).

113. J. G. McKinnon, P. E. Gribben, A. R. Davis, D. F. Jolley, J. T. Wright, Differences in soft-sediment macrobenthic assemblages invaded by *Caulerpa taxifolia* compared to uninvaded habitats. *Mar. Ecol. Prog. Ser.* **380**, 59 (2009). doi:10.3354/meps07926

114. G. J. Edgar, C. Shaw, G. F. Watson, L. S. Hammond, Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Fort, Victoria. *J. Exp. Mar. Biol. Ecol.* **176**, 201 (1994). doi:10.1016/0022-0981(94)90185-6

115. G. F. Watson, A. I. Robertson, M. J. Littlejohn, Invertebrate macrobenthos of the seagrass communities in Western Port, Victoria. *Aquat. Bot.* **18**, 175 (1984). doi:10.1016/0304-3770(84)90086-X

116. G. J. Edgar, N. S. Barrett, D. J. Gradon, "A classification of Tasmanian estuaries and assessment of their conservation significance using ecological and physical attributes, population and land use" (Published by the Marine Research Laboratories, University of Tasmania Tasmania, 1999).

117. G. J. Edgar, N. S. Barrett, P. R. Last, The distribution of macroinvertebrates and fishes in Tasmanian estuaries. *J. Biogeogr*. **26**, 1169 (1999). doi:10.1046/j.1365-2699.1999.00365.x

118. E. A. Glover, J. D. Taylor, Diversity of chemosymbiotic bivalves on coral reefs: Lucinidae (Mollusca, Bivalvia) of New Caledonia and Lifou. *Zoosystema* **29**, 109 (2007).

119. A. M. Schwarz, M. Morrison, I. Hawes, J. Halladay, Physical and biological characteristics of a rare marine habitat: sub-tidal seagrass beds of offshore islands. *Sci. Conserv.* **269**, 5 (2006).