



REPORT

Did the historic overharvesting of sea cucumbers make coral more susceptible to pathogens?

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Abstract Detritivore sea cucumbers appear to have been abundant on historic tropical reefs, but (1) have been heavily exploited since at least the mid-1800s, (2) often show minimal recovery post-harvest, and (3) are relatively depleted from modern marine communities. Because they were more abundant, fed on bacteria, microalgae, and other organics, and processed tremendous masses of sediments, removing these detritivores from tropical seas may have suppressed removal of sedimentary pathogens, and impacted co-occurring species in ways that are not documented. We conducted enclosure and exclosure experiments of the sea cucumber *Holothuria atra* in a back reef lagoon in Moorea, French Polynesia and found that excluding this sea cucumber increased a measure of sediment surface pigmentation by about 10 × but also decreased the potency of extracts from a co-occurring coral (*Acropora cytherea*) against the heat-activated coral pathogen *Vibrio coralliilyticus* by a significant 52%. This suggests that the large-scale removal of detritivores from shallow tropical seas may make some co-occurring foundation species more susceptible to pathogens during periods of elevated temperatures or other stresses.

Keywords Coral pathogen · Detritivore · *Holothuria atra* · Sea cucumber · *Vibrio coralliilyticus*

Introduction

Humans have selectively removed large top-consumers from many of Earth's ecosystems (Estes et al. 2011). The loss of these major consumers commonly produces strong trophic cascades that alter community composition and ecosystem function, with effects being well documented across a range of marine, terrestrial, and freshwater ecosystems (Power et al. 1996; Jackson et al. 2001; Myers et al. 2007; Ripple et al. 2014). Human harvesting has also strongly impacted lower trophic levels in some ecosystems, but, with the exception of the well-documented effects of herbivore removals in marine systems (Steneck et al. 2017), the effects of removing lower trophic levels are inadequately understood. Because detritivores consume microbes and suppress the accumulation of organics, on which microbes feed (Purcell et al. 2016; Lee et al. 2018), it is possible that overharvesting detritivores may allow pathogens to increase and may enhance the exposure or susceptibility of co-occurring organisms to pathogens. This type of interaction appears to occur when the absence of seagrass beds (which normally help remove microbes) allows a buildup of pathogens that enhance the frequency of disease in co-occurring organisms like corals (Lamb et al. 2017). Here, we investigated potential indirect effects of the widespread removal of detritivores (holothurians, or sea cucumbers) from shallow tropical reefs on the potency of coral defenses against a common microbial pathogen.

Sea cucumbers have been a desired food in Asia for centuries. Many of the more accessible areas in the tropical Indo-Pacific were harvested by the early- to mid-1800s

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(Conand 1990; Kinch et al. 2008). As time progressed and harvests continued, the geographic area searched expanded dramatically and especially since the 1960s; this resulted in severe overfishing world-wide, with declining sizes, a shift from harvesting desirable to less-desirable species, and from harvesting in near-shore to off-shore areas (Kinch et al. 2008; Anderson et al. 2011). Because sea cucumbers are valuable, can be easily harvested, and commonly fail to recover following extensive harvest, the fisheries have been characterized as “mining of lootable resources” (Conand 1990; Eriksson et al. 2017). As examples, (1) 50 yr after large-scale harvest of sea cucumbers from the Federated States of Micronesia during the 1930s, Richmond (1997) was able to find only two individuals of one of the edible species and (2) Uthicke et al. (2004) found no recovery of populations on the Great Barrier Reef 4 yr after closing the fishery and suggested that recovery intervals were likely 40–50 yr. Lack of density records from early harvests make it impossible to adequately assess virgin densities of sea cucumbers, but early publications reported densities of up to $> 50/\text{m}^2$ in some remote locations (Seale 1911; Bakus 1968; Lawrence 1979). The lack of rigor in reporting methods of these early studies, makes it difficult to determine the spatial extent of such densities or whether such high densities were common. Because sea cucumbers feed on bacteria, microalgae, and other organics in sediments, and process 9–82 kg/individual/yr of sediment through their gut (Purcell et al. 2016), local productivity at such high-density sites would have to have been unusually high to maintain these densities. The worldwide removal of sea cucumbers from most shallow tropical seas represents a dramatic loss of “waste management” from these systems. The loss of this ecosystem service could result in sediments serving as reservoirs for marine pathogens, blooms of sediment-associated cyanobacteria or other microalgae, disruption of nutrient cycling and storage (Uthicke 2001; Allgeier et al. 2017), and other complex effects that might impact corals, the foundation species of tropical reefs.

In this investigation, we evaluated the effects of the sea cucumber *Holothuria atra* on (1) surficial sediments in a tropical lagoon and (2) the potency of a co-occurring coral's (*Acropora cytherea*) defense against the coral bleaching pathogen *Vibrio coralliilyticus*.

Materials and methods

Site, focal coral, and impacts of sea cucumber presence

We studied the effects of the locally abundant sea cucumber *Holothuria atra* on the coral *Acropora cytherea* in a shallow back reef lagoon on the north shore of

Mo'orea, French Polynesia (17.4894° S, 149.8825° W). During a preliminary haphazard swim around our study area, we counted the first 3,000 sea cucumbers encountered. All but one were *H. atra*, so we focused on only this species. Density of *H. atra* was determined across 30 haphazardly selected sandy patches in the shallow back reef lagoon. In each patch, we used Under Armor's Map My Run app, walked around the perimeter of each patch to trace its outline, and used Google Earth to calculate the area in each of these 30 patches (ranging from 2.48 to 17.26 m²), counted all *H. atra*, and calculated *H. atra*/m² in each patch.

Outplants of the coral *A. cytherea* were caged with four *H. atra* ($n = 15$) or with zero *H. atra* ($n = 15$) and these cage treatments were used to assess how sea cucumbers affected sediments and the coral outplants. *H. atra* enclosed in cages ranged from about 9–14 cm in length, as is typical for individuals at our site. The 30 coral outplants used in the experiment had been fragmented from numerous *A. cytherea* colonies in the shallow backreef lagoon near our outplant site, epoxied into the cut off neck of a plastic soda bottle, screwed into an upturned plastic cap imbedded in a small paddy of cement (see Clements and Hay 2019), and allowed to recover for 2 months on a rack in the shallow back reef lagoon adjacent to our experimental patch before deployment in our experiment. We nestled the concrete bases holding our corals into the sediment so that the 1.5 cm high bottleneck containing the coral was the only barrier between the fragment and the sediment below. Each 50 cm × 50 cm × 10 cm tall cage (1 cm² mesh, see Fig. 1) was placed ≥ 60 cm away from any adjacent cage and a coral was planted near the center of each cage. This produced a 3 × 10 grid of cages each containing a single coral transplant.

Cages holding or excluding sea cucumbers were assigned at random, and all sea cucumbers were removed from within about 10 m of the 2 m deep area on which the cages were located. All replicates were monitored daily for 30 d (29 May through 28 June 2019), with notes made daily regarding visual estimates of any tissue death occurring on corals. Any sea cucumbers that escaped enclosures (three incidents) or that invaded control cages (one incident) were replaced or excluded within 24 h. The outer sides of all cages were brushed every other day to prevent fouling.

The area holding the cages was bordered by bommies of dead coral and by large colonies of the corals *Porites lobata* and *Porites rus*. Nearby, large colonies of *Acropora pulchra*, other species of *Acropora*, and species of *Pocillopora*, *Porites*, *Stylophora*, and *Pavona* were also common.

This density of *H. atra* in our enclosure cages (16/m²) represented 128% more than the mean density of *H. atra* at

Fig. 1 An enclosure cage containing four *H. atra* and an outplanted coral



our study site, but it was only 70% of the maximal density ($23/\text{m}^2$) in the patches we measured and is within the range of historic densities reported decades ago from some remote sites (Seale 1911; Bakus 1968), presumably sites from which harvests had not previously occurred. Historic densities on undisturbed reefs are not well documented, but the above reports indicate that historic densities in some locations were as high or higher than those used in our experiment.

Benthic community and coral responses

On the final day of the experiment (day 30), we visually assessed the condition of the sediments in each cage and collected sediment samples to assess organic content of near surface sediments. For the visual assessments, we removed and replaced each cage with a 50 cm × 50 cm quadrat holding a white piece of paper in the corner to allow white balancing in image analyses, and photographed the sediment with a GoPro Hero 7 black camera. Images were analyzed with coral point count software to assess the color intensity of the sediment. The software generated 5 randomized points that were each ranked visually on a scale of 0 to 5, with 0 being no pigmentation and 5 indicating a dark coloration (green or rusty brown) associated with algal/cyanobacterial cover.

Organic content of sediments in each replicate was assessed by scraping 30–40 mL of surficial sediments from the top ~ 5 mm of each caged area into a 50 ml plastic tube. Samples were immediately placed on ice and stored

in a – 80 °C freezer upon return to shore. Organic content was later assessed by thawing, stirring the contents, drying a sub-sample from each replicate to a constant weight at 60 °C, ashing these for 3 h at 450 °C, and calculating organic content as ash-free-dry mass.

Previous research indicated that a different *Acropora* spp. (*A. millepora*) contained defenses against the coral pathogen *Vibrio coralliilyticus* (BAA-450), but that the defense was compromised by the coral's association with competing seaweeds (Beatty et al. 2019). Following the methods of Beatty et al. (2019), we assessed whether sea cucumber presence affected the potency of “coral water” (sensu Beatty et al. 2019) from *A. cytherea* against this same coral pathogen. This “coral water” was acquired by collecting 2 ml displacement volumes of chips from each outplanted coral ($n = 15/\text{treatment}$), separately agitating chips from each coral in 2 ml of unfiltered reef water for 20 s, and transferring the liquid from this sample into a sterile Eppendorf tube. These samples were then placed on ice in the field and frozen at – 20 °C upon return to the lab. Thus, “coral water” contained reef water and coral mucus or compounds liberated due to chipping and agitation. Each sample of coral water was collected with a paired sample of seawater from the water column adjacent to the coral that was sampled. This served as a control for anything that might be in the seawater used to agitate each coral sample.

We used 100 µl of these coral water samples (paired with a control = the adjacent reef seawater) to test the anti-*Vibrio* activity of coral from the treatments with versus

without sea cucumbers. Each coral water and paired sea-water sample was aliquoted into sterile 96-well round-bottom plates, lyophilized on a freeze dryer, and UV-C-irradiated (TUV30W G30T8, Philips Amsterdam, The Netherlands) for 90 s to kill any microbial cells that may have survived lyophilization. To the dried material in the bottom of each well, we then added 100 μ l of *V. coralliilyticus* bacterial cell suspension at 100 cells/ml in marine broth (Difco 2216, Becton Dickinson, Franklin Lakes, NJ).

Inoculum cultures were added to the wells during log growth phase and were incubated at 28 °C without shaking for 24 h. This temperature is near the seasonal mean in Mo'orea and represents a temperature at which *V. coralliilyticus* is virulent. Prior to starting the 24 h incubation, 2,3,5-Triphenyl tetrazolium chloride (TTC; TCI America Portland, Oregon) was added (0.05 μ g/ μ l final concentration) to each well. Addition of TTC allows a direct measurement of *V. coralliilyticus* metabolic activity because *Vibrio* metabolism reduces TTC to the red compound triphenylformazan, assessed by change in coloration as quantified by absorbance at 490 nm via a BioTek ELx800 absorbance reader (BioTek, Winooski, VT; see Beatty et al. 2019). We used this method rather than conducting direct cell counts or measuring turbidity associated with cell density because density assesses both live and dead and healthy and unhealthy cells; this method assesses only those cells that are metabolically active. Background absorbance was measured in blanks containing lyophilized and UV-C-irradiated coral water or reef water reconstituted in marine broth with TTC but without bacteria. Blank-corrected measurements allowed determination of relative *V. coralliilyticus* metabolism. This was expressed as a ratio of metabolism in the coral water compared to the control (reef seawater collected adjacent to the coral).

All statistical evaluations of the effects of sea cucumbers on traits of the benthos and of corals were evaluated by Fisher–Pitman permutation tests.

Results

Density of *H. atra* at our study site was $7.1 \pm 4.7/\text{m}^2$ (mean $\pm$ 1SE), with densities ranging from 1.7 to $23.0/\text{m}^2$ across the 30 patches we assessed. The sediment pigmentation ranking differed between cages with versus without sea cucumbers, with mean value being $\sim 10 \times$ greater in cages excluding sea cucumbers (Fig. 2a, $p < 0.001$, Fisher–Pitman permutation test, $n = 15$). Despite this difference in surface pigmentation, % organics of sediments (as measured by % ash-free-dry-mass) did not differ significantly as a function of enclosure or exclusion of sea cucumbers (Fig. 2b, $p = 0.150$, Fisher–Pitman permutation test, $n = 15$).

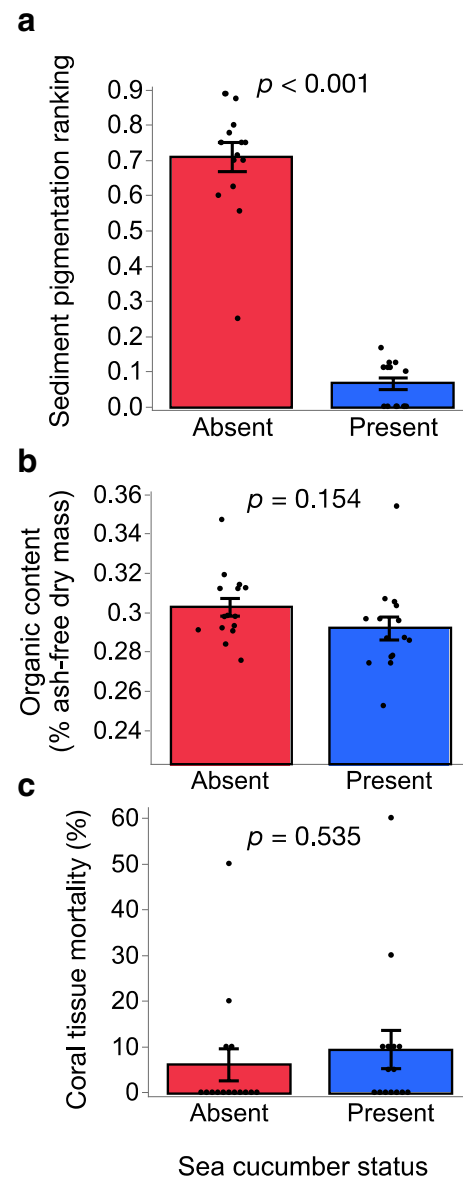


Fig. 2 **a** Sediment pigmentation ranking (a combination of percent cover and intensity of pigmentation on the sediment surface—a proxy for the abundance of cyanobacteria, diatoms, or other surface algae) when sea cucumbers were absent versus present in experimental cages on the lagoonal back reef. **b** Sediment organic content (% ash-free-dry-mass) as a function of sea cucumber absence/presence, and **c** percentage of coral tissue death as a function of sea cucumber absence/presence. $n = 15$ for each treatment, all values are mean $\pm$ SE, and all p values are from Fisher–Pitman permutation tests

Mean percent tissue death of *A. cytherea* was low ($< 10\%$) in both treatments and did not differ as a function of sea cucumber inclusion or exclusion over the 30 d of our experiment (Fig. 2c, $p = 0.535$, Fisher–Pitman permutation test, $n = 15$).

Coral water from *A. cytherea* suppressed the growth of the coral pathogen *Vibrio coralliilyticus*, but the potency of this suppression varied as a function of sea cucumber

presence (Fig. 3). Coral water from treatments with sea cucumbers suppressed pathogen metabolism by 35% while coral water from treatments without sea cucumbers suppressed the pathogen by only 23% (Fig. 3; $p < 0.024$, Fisher–Pitman permutation test, $n = 15$). The presence of sea cucumbers therefore enhanced the coral’s suppression of the pathogen by $\sim 52\%$.

Discussion

Removal of upper-level consumers commonly produces cascading impacts on community structure and function (Jackson et al. 2001; Estes et al. 2011; Ripple et al. 2014), but the effects of large-scale removal of detritivores from marine systems is poorly understood. In our experiment, exclusion of sea cucumbers not only increased surface associated pigmentation indicative of increased microbes and microalgae (see also Purcell et al. 2016; Lee et al. 2018; Wolfe et al. 2018), but also reduced the potency of a coral’s defense against a common heat-activated bleaching pathogen. Removal of a critical detritivore species, or a decrease in detritivore diversity, also can produce significant impacts in freshwater ecosystems (Taylor et al. 2006; Boyero et al. 2021). Our manipulation of a single species might therefore underestimate the “missing effects” of the numerous species of sea cucumbers that have been harvested from most shallow tropical seas.

Sea cucumbers, including *H. atra*, feed on surface associated bacteria, cyanobacteria, meiofauna, fungi, decaying seagrasses and macroalgae, and sediment-associated organics in general (Moriarty 1982; Moriarty et al. 1985; Uthicke 1999; Purcell et al. 2016; Wolfe et al. 2018). They process and clean tremendous masses of sediments in

areas where they occur in high abundance, and cyanobacterial and microalgal mats sometimes appear following extensive harvesting of sea cucumbers (Purcell et al. 2016). There is minimal information on among-species variance in feeding effects or on how impacts vary with sea cucumber density or diversity in nature, but it is estimated that sea cucumbers process sediments at rates of 9–82 kg/individual/yr making them of great importance as cleaners of organics, bacteria, and microalgae from sediments in marine environments (Purcell et al. 2016; Lee et al. 2018). Uthicke (1999) documented *H. atra* processing 67 kg dry mass of sediment/day/individual. Scaling this to a year and the mean density of *H. atra* we observed yields an estimate of these sea cucumbers processing > 170 kg dry mass of sediment/m²/yr at our study site. This feeding could considerably suppress the abundance of microbial pathogens in reef sediments, and these previous studies on feeding are consistent with the large changes in surface pigmentation that we noted following exclusion of *H. atra* in our experiment.

Curiously, despite the dramatic effects of sea cucumber presence on surface pigmentation, we did not detect a significant effect on percent organics in surface sediments. This may indicate that (1) the algal/cyanobacterial pigmentation we were assessing visually was only surficial and that we diluted and mixed this too much when sampling sediments up to 5 mm deep or (2) the sea cucumber was consuming only a modest, and specific, portion of the organics in the sediments. Close observation of *H. atra* feeding suggests that they are feeding only on the upper partial mm of the sediment surface; our sampling included sediments beyond this depth.

Our short-term field assay indicated that the absence of sea cucumbers made washes from the coral *A. cytherea* less potent against the common coral pathogen *Vibrio coralliilyticus*. This coral bleaching pathogen becomes more virulent at elevated temperatures, like other heat activated pathogens that affect numerous species of echinoderms (Harvell et al. 2019) or fishes (Genin et al. 2020). Thus, global-scale depletion of sea cucumbers (Purcell et al. 2013, 2016; Eriksson et al. 2017) may have elevated the exposure to, and susceptibility of, corals, and possibly other species, to disease when temperatures rise.

In previous experiments with a different *Acropora*, the anti-*Vibrio* potency of washes from *A. millepora* declined significantly when the coral occurred in areas with elevated abundance of macroalgae (Beatty et al. 2019). This mirrors the decline in anti-*Vibrio* activity of *A. cytherea* that we document here when bacteria and microalgae on nearby sediment surfaces increase following the exclusion of *H. atra*. It is possible that holothurians and other detritivores represent “essential cleaning services” that have been suppressed in coral reefs, seagrass beds, and other shallow

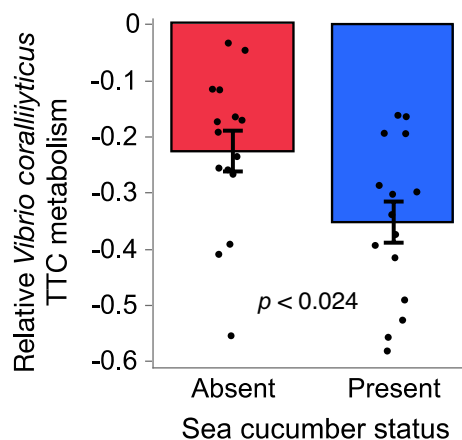


Fig. 3 Mean percentage ($\pm$ SE) by which coral water from *A. cytherea* suppressed the metabolism of the coral pathogen *Vibrio coralliilyticus*. $n = 15$ for each treatment. The p value is from a Fisher–Pitman permutation test

tropical systems for decades to centuries. The large-scale removal of these detritivores could be exacerbating the coral bleaching and disease outbreaks that have occurred worldwide (Harvell et al. 2002; Hughes et al. 2018).

For most present-day reefs, the density of sea cucumbers at our study site is high, but it seems possible that densities at our site could be similar to historic densities at productive sites prior to global-scale harvests. Sea cucumbers have been harvested for human consumption for centuries (Anderson et al. 2011), are still being harvested at rapid rates, their populations recover slowly, or not at all, following harvest (Uthicke et al. 2004; Kinch et al. 2008), and very high densities of holothurians were reported in some remote areas prior to large-scale harvesting (summarized by Purcell et al. 2016). The historic “natural” densities of sea cucumbers in shallow tropical systems are unclear due to the persistent and broad-scale harvesting of sea cucumbers for centuries before quantitative population studies were conducted. Despite the paucity of sea cucumbers on modern reefs, there are still approximately 200,000,000 individuals harvested each year (Purcell et al. 2016), and both historic accounts of harvesting in the 1800s and densities of > 50 individuals/m² reported on areas of some remote reefs in the 1960s suggest that densities of sea cucumbers on some pristine reefs may have been considerable (Seale 1911; Bakus 1968; Lawrence 1979; Purcell et al. 2016).

In French Polynesia, the first reported export of sea cucumbers occurred in 1810 (Kinch et al. 2008) and continued throughout the 1800s, but records of harvest quantities were not reported until the 1930s when about 60,000 kg were exported (Stein 2018). After this, records are available for only certain years and reports often pooled sea cucumbers with fishes; it appears that exports were uncommon between 1940 and 2008, but harvest increased dramatically between 2008 and 2011 when exports rose from 3 to 125 tones/yr (Stein 2018)—falling dramatically in 2012 when regulations were imposed. The species we studied, *H. atra*, is a relatively low value species but is still exported or used locally for food in 23 of the 26 countries or regions surveyed across Polynesia, Micronesia, Melanesia, Australia, and New Zealand (Kinch et al. 2008). In some areas of modern reefs that are remote and protected, like Tetiaroa, French Polynesia, *H. atra* occur in densities similar to those at our study site (M Hay and C Clements, personal observation) and 50 and 60 yr old Tahitians on Moorea report that when they were young, sea cucumbers were common to dense in areas on Moorea that are now largely devoid of sea cucumbers (Teurumereariki Hinano Murphy and Teihotu Brando, personal communication).

The top-down and cascading ecological effects of removing large consumers are well documented and

dramatic (Jackson et al. 2001; Estes et al. 2011; Ripple et al. 2014). It is possible that there is a less appreciated, but also important, bottom-up cascade caused by the removal of these critical “waste-management experts” from coral reefs and similar systems where holothurians were once abundant. Lack of investigations into the broader impacts of holothurian removal makes it impossible to assess whether the effects of *H. atra* are unique or common to other holothurians and whether the reduced suppression of a common coral pathogen will have long-term impacts on coral mortality in the field—especially during periods of elevated temperatures or other stresses. However, our findings suggest that the effects of removing detritivores from natural communities deserves additional investigation. Because *H. atra* is of low value for commercial beche-de-mer but plays a positive ecosystem function by cleaning sediments and enhancing coral traits that suppress pathogens, it may be wise policy to forgo the minor financial benefit of commercial harvest for the ecosystem benefits that these sea cucumbers provide, as suggested recently by Purcell et al. (2016).

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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