ECOLOGICAL ROLES OF EXPLOITED SEA CUCUMBERS

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Abstract   Sea cucumbers (Echinodermata: Holothuroidea) are large and abundant members of marine benthic communities. Over-exploitation worldwide has raised concern because they have important functions within ecosystems. The ecological roles of commercially-exploited sea cucumbers (Aspidochirotida and Dendrochirotida) are reviewed here, focussing on recent literature. Of the 70+ species commercially exploited, at least 12 regularly bury into sand and mud, playing major roles in bioturbation. Most aspidochirotids are deposit feeders, reducing the organic load and redistributing surface sediments, making them bioremediators for coastal mariculture. Sea cucumbers excrete inorganic nitrogen and phosphorus, enhancing the productivity of benthic biota. This form of nutrient recycling is crucial in ecosystems in oligotrophic waters such as coral reefs. Feeding and excretion by sea cucumbers also act to increase seawater alkalinity and dissolved inorganic carbon of surrounding waters, which contributes to local buffering of ocean acidification. Sea cucumbers host more than 200 species of parasitic and commensal symbionts from seven phyla, thereby enhancing ecosystem biodiversity. They are preyed upon by many taxa, thereby transferring animal tissue and nutrients (derived from detritus and microalgae) to higher trophic levels. Over-exploitation of sea cucumbers is likely to decrease sediment health, reduce nutrient recycling and the capacity of ecosystems to buffer against ocean acidification, diminish biodiversity of associated symbionts and reduce the transfer of organic matter from detritus to higher trophic levels. Ecosystem-Based Fisheries Management needs to consider the importance of sea cucumbers in marine ecosystems and implement regulatory measures to safeguard their ecological roles.

Introduction

Sea cucumbers (Echinodermata: Holothuroidea) are significant members of benthic invertebrate communities, occurring in all of the major oceans and seas of the world. They contribute greatly to community biomass (Birkeland 1988, Billett 1991) and their behaviours and biology have important effects on physico-chemical processes of soft-bottom and reef ecosystems.

Commercially-exploited sea cucumbers, all from the Orders Aspidochirotida and Dendrochirotida, provide a source of income to millions of coastal fishers worldwide (Purcell

et al. 2013) and a source of nutrition to perhaps more than 1 billion Asian consumers. Presently, around 10,000 tonnes of dried sea cucumber is traded internationally per annum (Purcell et al. 2013), corresponding to roughly 200 million animals extracted from marine ecosystems each year. The commercial species are often the largest of all holothuroids and can occur in high abundance in unfished habitats (Conand 1989, 1990, Purcell et al. 2009, Eriksson et al. 2010). The ecology of exploited species is of special interest because their natural abundance can be altered greatly by fishing (Hasan 2005, Price et al. 2010, Friedman et al. 2011). Thus, the effects on ecosystem processes and other biota are concomitantly impacted by fishing.

Understanding the ecological roles of exploited species is essential for Ecosystem-Based Fisheries Management (EBFM), which aims to sustain healthy marine ecosystems and the fisheries they support (FAO 2003, Pikitch et al. 2004). EBFM has become a popular management paradigm owing to a realisation that over-exploitation of certain species can trigger cascading effects on ecosystems that might diminish their ability to withstand other broad-scale stressors. Fisheries management must take into account the likely effects of fishing on other species in the ecosystem and on ecological processes (Link 2002, Pikitch et al. 2004). An EBFM approach requires an understanding of how exploited species are linked to other components of the ecosystem and the influence they have on ecosystem processes. Such an understanding helps to devise specific regulations for key species and inform policy for responsible fisheries management. Conservation measures are also needed for more than a dozen species that have been listed as Vulnerable or Endangered with extinction (Purcell et al. 2014).

Aspidochirotid and dendrochirotid sea cucumbers occur in a vast array of habitats, from wave-exposed zones on coral reefs to deep soft-bottom cold-temperate habitats (Purcell et al. 2012). They are exploited in the Pacific, Atlantic and Indian Oceans, and in the major seas such as the Mediterranean, Caribbean, Bay of Bengal, Arabian Sea, Gulf of Mexico and North Sea (Toral-Granda et al. 2008, Purcell et al. 2013).

Ecology and behaviours differ greatly among species. For example, some routinely bury in sediments, others hide in reef crevices or are relatively sedentary (Purcell et al. 2012). Most of the exploited species are deposit-feeders, gathering organic detritus and sediments from the sediment surface (e.g. most of the aspidochirotids), and some are suspension-feeders that hold their tentacles in the water current and trap passing phytoplankton and micro-organisms (e.g. dendrochirotids). As a consequence of their ecological diversity, the roles that sea cucumbers play in marine ecosystems are also varied among species.

Here we provide a contemporary review of the ecological roles of aspidochirotid and dendrochirotid sea cucumbers that are exploited worldwide. We discuss the roles that the exploited holothuroids play in five main ecological arenas: contributing to sediment health; recycling nutrients; influencing seawater chemistry; bolstering high biodiversity through symbiotic associations; and forming pathways of energy transfer in food chains. The review concludes with policy implications for resource managers needing to balance these positive effects on the productivity and diversity of the ecosystems with socio-economic pressures for fishers to exploit this resource.

Maintaining and improving sediment health
Bioturbation

Bioturbation (from Latin *turbatio*, meaning to stir up or disturb) refers to a reworking, stirring or mixing, of sediment layers by organisms. Bioturbation of sediments on reefs, lagoons and seagrass meadows has numerous physico-chemical effects on sediment permeability and water content, chemical gradients in pore water, sediment particle composition of upper sediments, and rates of remineralisation and inorganic nutrient efflux (Reise 2002, Lohrer et al. 2004). Sediment oxygen concentrations increase through improved sediment permeability

and when bioturbation pushes lower sediments to the surface where they interact with oxygen in the water column (Solan et al. 2004). The biological consequences include enhancement of primary production, infaunal biodiversity and infaunal biomass (Solan et al. 2004).

A relatively small proportion of exploited sea cucumbers bury in sediments to bioturbate sub-surface layers (Table 1). Many of the commercially-exploited sea cucumbers inhabit soft-bottom habitats such as coral reef lagoons, inshore seagrass meadows, mangrove systems, and deeper continental shelf habitats (Purcell et al. 2013). Some of these species bury partly or totally under the sediment surface, sometimes on a daily cycle (Yamanouti 1939, Yamanouchi 1956, Clouse 1997, Mercier et al. 1999). Sand and silt are pushed aside by this activity, thereby mixing surface and sub-surface sediment layers.

Table 1 Commercially-exploited sea cucumber species known to bury and have a significant bioturbation role.

Species	Habitat	References
Actinopyga miliaris	Sandy reef flats	Purcell et al. (2012)
Actinopyga spinea	Sandy reef flats, seagrass beds and coral reef lagoons	Purcell et al. (2012) (Fig. 1)
Anthyonidium chilensis	Sandy or rocky intertidal habitats	Guisado et al. (2012)
Bohadschia argus	Soft sediments of reef lagoons near hard reef	Personal observations (Fig. 1)
Bohadschia marmorata	Silty sand in seagrass beds	Yamanouti (1939), Yamanouchi (1956), Clouse (1997)
Bohadschia vitiensis	Coral reef lagoons	Yamanouti (1939), Yamanouchi (1956), Conand et al. (2010)
Holothuria arenicola	Coral reef lagoons	Pawson & Caycedo (1980), Hammond (1982)
Holothuria isuga	Coral reef lagoons	Personal Observations
Holothuria lessoni	Sandy reef flats, seagrass beds and coral reef lagoons	Conand (1990), Personal observations (Fig. 1)
Holothuria scabra	Sandy reef flats and seagrass beds	Yamanouti (1939), Yamanouchi (1956), Conand (1990), Mercier et al. (1999), Mercier et al. (2000), Skewes et al. (2000), Purcell (2004), Purcell (2010), Wolkenhauer et al. (2010)
Holothuria spinifera	Coastal sandy habitats	Purcell et al. (2012)
Parastichopus regalis	Sandy and rubble bottoms	M. González-Wangüemert personal communication

Burying by certain species appears to mix sediments tens of centimetres deep, and a cavity is sometimes left by the animals (Fig. 1). The bioturbation action displaces at least their own body volume in sediments (Purcell 2004). Considering that the burying species are between a few hundred grams and several kilograms in weight, and potentially burying once per day, the bioturbation effect over long time scales is likely to be substantial where they are relatively abundant. Second to thalassinidean shrimps (Reise 2002), it appears that burying holothuroids are likely to be major bioturbators of sediments on tropical reefs.

Deposit-feeding aspidochirotids that remain on the sediment surface disturb the upper sediment layer through ingestion and release of faecal casts and by their locomotion across the surface. This bioturbation activity can play an important role in redistribution of surface sediments and influences biotic interactions and the water-sediment interface (e.g. Uthicke 1999).
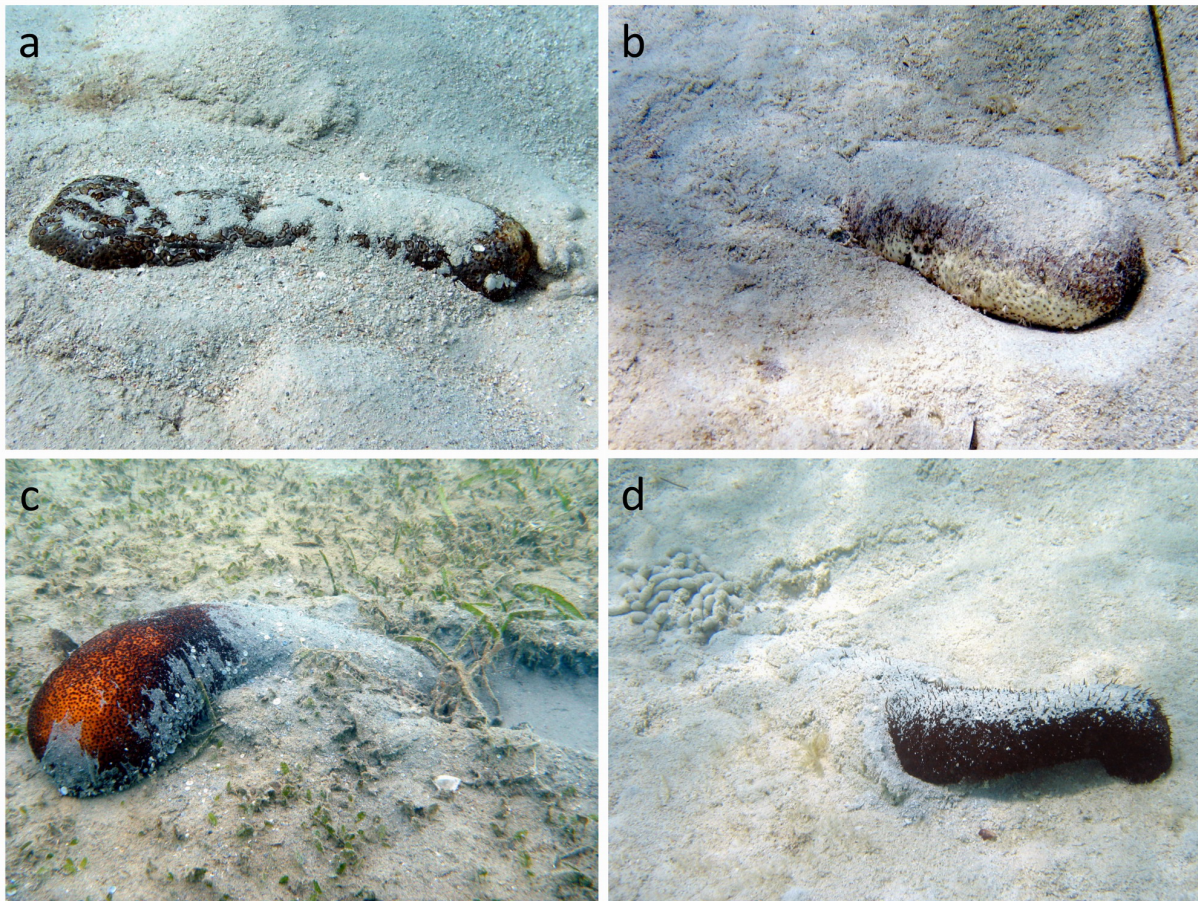
Figure 1. Bioturbation of sediments by sea cucumbers. a) *Bohadschia argus* (length: 40 cm) half-buried in sediments in a coral reef lagoon (Lizard Island, Australia). b) *Holothuria lessoni* (approx. length: 40 cm) partly emerged from sediments on a coral reef flat (New Caledonia). c) *Bohadschia vitiensis* (approx. length: 35 cm) coming out of sediments in a sheltered bay (New Caledonia). Notice the large excavated area of sediments left by the burying activity. d) *Actinopyga spinea* (approx. length: 30 cm) coming out of soft sediments on a shallow reef flat (New Caledonia). Photos: SW Purcell.

Sediment cleaning

Almost all aspidochirotid sea cucumbers are deposit-feeders on organic detritus mixed with sand and silt in the upper few millimetres of sediments, and they defaecate sand that is generally less organic-rich than that which they consumed (Mercier et al. 1999). The ecological contribution of deposit-feeding is important as a pathway for regeneration and mineralisation of surface sediments.

Many aspidochirotid holothuroids choose organic-rich sediments and detritus from those available to them in their habitat (Hauksson 1979, Moriarty 1982, Hammond 1983, Amon & Herndl 1991, Uthicke & Karez 1999, Slater et al. 2011), although some species appear to be rather non-selective (Uthicke 1999, Uthicke & Karez 1999). They mostly digest bacteria, cyanobacteria, decaying plant (e.g. seagrass and algae) matter, some diatoms, foraminiferans, fungi, and other organic matter that constitute detritus (Yingst 1976, Moriarty 1982, Uthicke 1999, MacTavish et al. 2012). In particular, bacteria have been a commonly-reported component of holothuroid diets (Moriarty 1982, Moriarty et al. 1985, Amon & Herndl 1991). Sea cucumbers consume infauna associated with the sediment (Moriarty 1982, Hammond 1983, Uthicke 1999), but more data are needed to determine what they actually consume and digest. Sea cucumbers appear unable to utilise macroalgae or seagrass (Yingst 1976), so they

do not compete with macroherbivores. Stable isotope analysis of trophic transfer would be useful to provide insights into the diet of deposit-feeding species.

Sediments defaecated by holothuroids are often lower in organic matter content than the sediments ingested, inferring that they act to 'clean' sediments (Amon & Herndl 1991, Mercier et al. 1999, Uthicke 1999, Michio et al. 2003, Paltzat et al. 2008, MacTavish et al. 2012, Yuan et al. 2015). In effect, the role of sea cucumbers can be likened to that of earthworms. Gut transit of sediments by aspidochirotid holothuroids also appears to facilitate bacterial decomposition of remaining (refractory) organic matter in sediments (MacTavish et al. 2012). Importantly, the volume of sediments ingested and defaecated per year is often remarkable (9-82 kg ind^{-1} y^{-1}) (e.g., Yamanouti 1939, Bonham & Held 1963, Hammond 1982, Coulon & Jangoux 1993, Uthicke 1999, Mangion et al. 2004), so their role in cleaning sediments can be considered extensive.

We have heard of anecdotal accounts from fishers in Papua New Guinea and Fiji that establishment of cyanobacterial mats on reef sediments followed the extraction of sea cucumbers. This effect has been found experimentally in tanks (Moriarty et al. 1985, Uthicke 1999, Michio et al. 2003). Part of this effect may be attributed to disturbance of the upper sediments by the movement of the sea cucumbers, which prevent the establishment of the cyanobacteria. As sea cucumbers have been found to consume cyanobacterial mats (Uthicke 1994), this effect may be a direct consequence of feeding.

Nutrient recycling

Recycling of organic matter has been suggested to be one of the main ecosystem functions of holothuroids, especially in coral reef environments where inorganic nutrients are sparse (Massin 1982, Birkeland 1988). Digestion of nitrogen-rich compounds (e.g. proteins) by holothuroids leads to conversion of organic nitrogen into inorganic forms, which in turn can be taken up by primary producers as nutrient sources (Fig. 2). Similar to most marine invertebrates, aspidochirotid holothuroids excrete inorganic nitrogen as ammonium (Webb et al. 1977, Mukai et al. 1989, Uthicke 2001a). Small amounts of phosphate are also released (Uthicke 2001a). Although individual-based rates of ammonium excretion are small, elevated values can be measured directly behind feeding holothuroids. Based on high densities of sea cucumber populations, daily area-specific fluxes of these nutrients are high, and in the range of other nutrient flux rates on coral reefs such as nitrogen fixation, or phosphate and ammonium flux rates into the sediments (Wilkinson et al. 1984, Hansen et al. 1987, Capone et al. 1992, Uthicke 2001a).

In coral reef environments, it has been demonstrated that nutrients released by commercially-exploited holothuroids can increase productivity of primary producers. In aquaria and field experiments, benthic microalgal communities (microphytobenthos) had increased productivity when in close proximity to holothuroids by receiving their waste products (Uthicke & Klumpp 1997, 1998). Interestingly, these microalgal communities are also one of the main food sources of the holothuroids. Therefore, on one hand, deposit feeding reduces the microalgae and, on the other, nutrient release by sea cucumbers increases productivity. Uthicke (2001b) calculated that at natural holothuroid densities for two species studied on the Great Barrier Reef, the overall effect on the microalgae was positive. Thus, one can refer to the holothuroid-algae interaction as a form of gardening, as was also suggested for lugworms (Hylleberg 1975). However, it is unclear to how many holothuroid species this applies. In polyculture conditions, deposit feeding of the temperate aspidochirotid *Apostichopus japonicus* also converts nitrogen in particulate wastes to inorganic nitrogen, which can be absorbed by commercially valuable macroalgae (Yuan et al. 2015). A study on another temperate species (*Australostichopus mollis*) confirmed that nutrient release from holothuroids can increase benthic productivity, although the study focussed on nutrients released from interstitial water (MacTavish et al. 2012). In that study, losses of microalgae

from consumption by sea cucumbers outweighed the increased productivity of microalgae from nutrients they excreted.
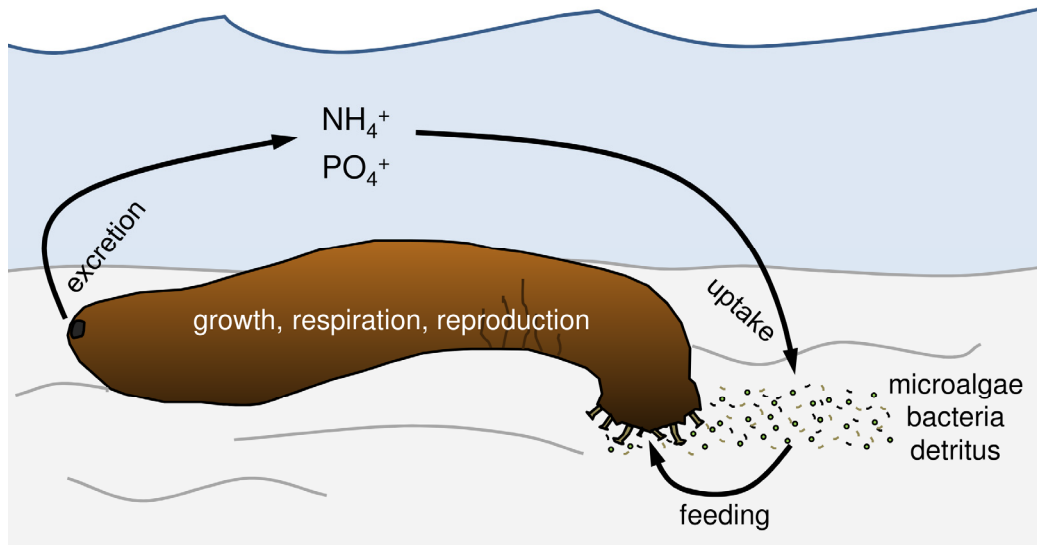

Figure 2. Nutrient recycling by sea cucumbers. Soluble nitrates and phosphates excreted by sea cucumbers into surrounding seawater can be absorbed by nearby corals, macroalgae, microalgae and bacteria. In turn, the nutrient composition of the microalgae and bacteria is enriched and they can be eaten by the sea cucumber or other deposit feeders, thus forming a recycling loop in the ecosystem.

Few other studies of holothuroid-plant interactions have been reported. One exception is a detailed field study investigating how overfishing of a commercially-important species, *Holothuria scabra* (called 'sandfish'), would affect productivity and growth of seagrass (Wolkenhauer et al. 2010). This study indicated that, in some cases, seagrass grew more slowly and biomass decreased where *H. scabra* was excluded. It was assumed that, similar to the case with microalgae, seagrasses can rapidly take up recycled ammonium and phosphate, thereby increasing productivity. Seagrasses may also have benefited from re-mineralised nutrients from sea cucumber feeding and/or nutrients released from the pore water in sediments because *H. scabra* routinely buries into sediments.

In addition to 'full' digestion and nutrient release, as part of the sediment 'cleaning' (discussed above) deposit-feeding holothuroids may partially digest organic matter making it more amenable to degradation by bacteria or biota on other trophic levels. For example, a Mediterranean species (*Holothuria tubulosa*) feeding on seagrass detritus can facilitate increased uptake of the detritus into the sediment (Costa et al. 2014).

Whereas most commercially-exploited holothuroids are deposit-feeders, dendrochirotids such as *Cucumaria frondosa* are suspension-feeders, trapping mainly phytoplankton with their tentacles (Hamel & Mercier 1998). Little is known about nutrient recycling by these animals but it can be assumed that these also release ammonium as a metabolic by-product. However, high levels of urea in body fluids of a congeneric species (*C. miniata*) suggest that this may also be an important excretion product (Jackson & Fontaine 1984).

Influence on local water chemistry

Coral reef ecosystems are dominated by sandy habitats composed mostly of calcium carbonate ($CaCO_3$) sediments from skeletons of calcifying organisms. Recent studies indicate that several aspidochirotid sea cucumber species can increase local seawater alkalinity (AT) and dissolved inorganic carbon (DIC) through their digestive processes and release of ammonia, thereby facilitating calcification by associated organisms such as corals and

calcareous algae (Schneider et al. 2011, 2013) (Fig. 3). Dissolution of carbonate sand in the sea cucumber digestive tract due to the low pH of gut fluids results in production of faecal casts higher in pH than the surrounding water (Hammond 1981, Schneider et al. 2011, 2013). This, along with the release of ammonia from the sea cucumber body (Uthicke & Klumpp 1997, Uthicke 2001a), increases the buffering capacity of surrounding seawater (Fig. 3). Thus, at a local scale, the increase in AT/DIC due to the presence of sea cucumbers is likely to contribute to reef resilience by enhancing the capacity of reef organisms to calcify (Schneider et al. 2011, 2013). The release of ammonia provides nutrients to the zooxanthellae symbionts of corals which increases their productivity which would also promotes calcification.
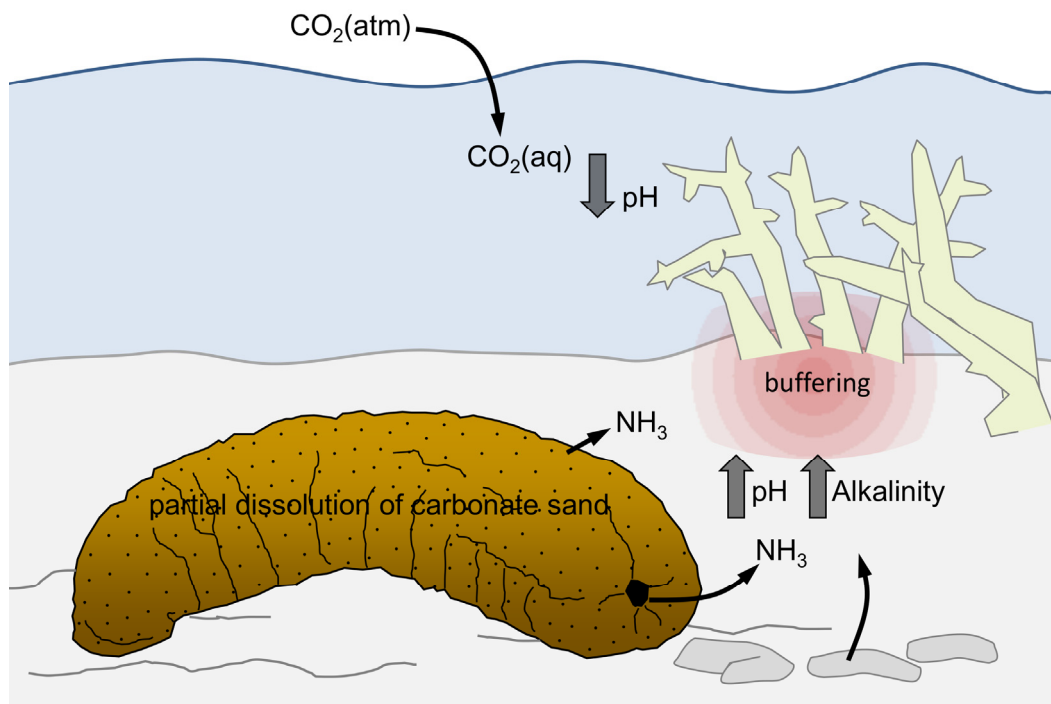

Figure 3. Influence of sea cucumbers on local water chemistry. Atmospheric CO_2 dissolves in seawater lowering pH, a process called ocean acidification which also lowers the saturation stage of carbonate minerals (Kleypas et al. 1999, Branch et al. 2013). Carbonate sands ingested by sea cucumbers are partially dissolved in the gut and the animals also release ammonia, resulting in an increase in pH and total alkalinity of surrounding water (Schneider et al. 2011, 2013). Thus, the metabolic activity of sea cucumbers may help buffer the effects of acidification at local scales and along with providing nutrients to promote photosynthesis of zooxanthellate (*Symbiodinium*) symbionts are likely to facilitate coral calcification.

The presence of high density sea cucumber populations, as characteristic of unfished reefs (Purcell et al. 2009, Muthiga & Conand 2014, Eriksson & Byrne 2015), may be particularly important for the integrity of reefs due to the potential of sea cucumbers to buffer changes in local carbonate chemistry caused by ocean acidification. The increase in ocean acidification due to anthropogenic CO_2 emissions (Kleypas et al. 1999) impairs the ability of calcifiers to produce $CaCO_3$ and has resulted in a marked reduction in reef calcification (Hoegh-Guldberg et al. 2007, De'ath et al. 2009, Silverman et al. 2009, Veron et al. 2009, Fabricius et al. 2014). This is a major threat to the integrity of coral reefs and the vast diversity of species and local human communities that depend on these ecosystems (Bellwood et al. 2004, Hoegh-Guldberg et al. 2007, Dove et al. 2013).

Further research is required on the contribution of other species in tropical carbonate sandy ecosystems (e.g. other deposit-feeding invertebrates, bioeroding endolithic organisms and microbes) to sediment dissolution and the influence of the release of respiratory CO_2 by

the sea cucumbers. Such research will enable us to fully understand the contribution of sea cucumbers to community metabolism and their potential role in increasing local alkalinity to support reef calcification.

Symbiotic relationships

The Holothuroidea have long been recognised as having many biotic associates. Both aspidochirotid and dendrochirotid commercial species tend to be relatively large as adults, with thick body wall and their populations can often occur at high density, yet most of the symbiosis studies have been on aspidochirotids.

Symbionts of sea cucumbers are commensals and parasites from at least nine phyla (Jangoux 1990, Eeckhaut et al. 2004) (Table 2). Parmentier and Michel (2013) recently outlined the different symbiosis categories (parasitism, mutualism, commensalism) and the sometimes ambiguous boundaries between them. This review therefore uses the classical definitions following Combes (1995): *parasites* are linked to organisms by "trophic, interspecific and durable relationships"; *mutualism* involves a reciprocal benefit, with symbiotic mutualism implying a long-term exchange; *commensalism* refers to symbionts benefiting by living on or inside their host with no reciprocal benefit to the host, and includes the benefit of transport (phoretism) or shelter (inquilinism) to the symbiont.

Further to the previous syntheses by Jangoux (1990) and Eeckhaut et al. (2004), the present review incorporates new studies published during the last decade, including some involving large collections of holothuroids (Table 2). In addition to the direct benefits to the lives of the symbionts, these relationships act to increase total ecosystem biodiversity – especially in the case of obligate relationships, where the symbiont would struggle to exist in the ecosystem without the sea cucumber host.

Hosts to ectocommensals

Many ectocommensal species are known to live on commercial holothuroids, namely those in the Aspidochrotida. The ectocommensals belong to several phyla and the species have generally been only listed taxonomically in the literature. The most commonly reported are the Plathyhelminthes, the Polychaeta, the Arthropoda (copepods, crabs and a few shrimps) and the Gastropoda (Eeckhaut et al. 2004). 'Piggybacking' on the host allows the ectocommensal a refuge against predators and they can often feed on external food sources.

Recent studies have reported that the common Indo-Pacific *Holothuria atra* acts as a critical host to discoid diatoms (Bacillariophyta) (Riaux-Gobin & Witkowski 2012) and the opisthobranch gastropod *Plakobranchus ocellatus* (Mercier & Hamel 2005). In the latter case, the sea cucumber host provides the commensal with a protected spawning site, and thus can be seen as crucial for its population biology.

Both crabs and shrimps can be ectocommensals and can display intraspecific antagonism (Lyskin & Britaev 2005), suggesting a territorial behaviour on their host sea cucumbers. The shrimp *Periclimenes imperator* shows a very wide variety of hosts including 11 holothuroids (Fransen & Hoeksema in press). One large commercially-exploited holothuroid, *Stichopus herrmanni*, hosts many different epibiont species, including some echinoderms, such as synaptid sea cucumbers and ophiuroid seastars (Fig. 4e, f), which do not affect the diurnal movement nor the feeding rates of the host (Purcell & Eriksson 2015).

Table 2   Organisms known to form symbiotic relationships with commercially-exploited holothuroids, by major taxon, with the approximate number of symbiont species. n/i = not identified.

| Symbiont major taxon	Symbiont Genera	Host holothuroid species	References
Chromista: Bacillariophyceae	*Cocconeiopsis*	*Holothuria atra*	Riaux-Gobin & Witkowski (2012)
Protozoa			
Ciliophora	*Boveria, Licnophora*	*Parastichopus californicus*	Eeckhaut et al. (2004)
Gregarinasina	*Cystobia, Diplodina, Goniospora, Lithocystis, Urospora*	*Cucumaria frondosa, Holothuria tubulosa*	Eeckhaut et al. (2004)
Acoelomorpha: Acoela	*Aechmalotus, Aphanostoma, Meara, Octocoelis*	*Parastichopus tremulus*	Jangoux (1990)
Platyhelminthes: Rhabdocoela	*Anoplodium, Paranotothrix, Wahlia,* others	*Actinopyga miliaris, Australostichopus mollis, Holothuria arenicola, H. impatiens, H. forskali, Stichopus herrmanni*	Jangoux (1990), Eeckhaut et al. (2004)
Annelida: Polychaeta			
Polynoidae	*Arctonoe, Gastrolepidia*	*Apostichopus japonicus, A. parvimensis, Australostichopus mollis, Actinopyga echinites, A. mauritana, Bohadschia argus, H. atra, H. edulis, H. leucospilota, H. scabra, H. nobilis, Parastichopus californicus, Pearsonothuria graeffei, Stichopus chloronotus, S. herrmanni, S. horrens, Thelenota ananas, T. anax*	Cameron & Fankboner (1989), Martin & Britayev (1998), Britaev & Lyskin (2002), Lyskin & Britaev (2005), Purcell & Eriksson (2015)
Ctenodrilidae	*Ctenodrilus*	*Holothuria tubulosa*	Martin & Britayev (1998)
Mollusca			
Bivalvia	n/i	n/i	Eeckhaut et al. (2004)
Gastropoda: Opisthobranchia	*Plakobranchus*	*Holothuria atra, H. leucospilota, Thelenota anax*	Mercier & Hamel (2005)
Gastropoda: Eulimidae	*Melanella, Megadenus, Enteroxenos*	*Actinopyga mauritiana, Bohadschia argus, Holothuria arenicola, H. atra, H. cinerascens, H. edulis, H. grisea, H. mexicana, H. pervicax, Isostichopus badionotus, Parastichopus californicus, Stichopus chloronotus, S. herrmanni*	Jangoux (1990), Cameron & Fankboner (1989), Queiroz et al. (2013), Eeckhaut et al. (2004), Purcell & Eriksson (2015)
Crustacea			
Decapoda	*Periclimenes, Lissocarcinus, Hapalonotus, Pinnotheres, Chlorodiella*	*Bohadschia subrubra, B. vitiensis, H. atra, H. fuscogilva, H. lessoni, Holothuria scabra, Stichopus chloronotus, S. herrmanni, Thelenota ananas*	Jangoux (1990), Hamel et al. (1999), Eeckhaut et al. 2004, Caulier et al. (2013), Caulier et al. (2014), Lyskin & Britaev (2005), Purcell & Eriksson (2015)
Copepoda	*Allantogynus, Synaptiphilus*	*Actinopyga* spp*., Holothuria poli, H. tubulosa*	Jangoux (1990), Eeckhaut et al. (2004)
Echinodermata			
Ophiuroidea	*Ophiothela*	*Stichopus chloronotus, S. herrmanni*	Purcell & Eriksson (2015)
Holothuroidea	*Synaptula*	*S. herrmanni*	Purcell & Eriksson (2015)
Osteichthyes: Carapidae	*Carapus, Encheliophis*	*Bohadschia argus, Holothuria fuscopunctata, H. tubulosa, Isostichopus fuscus, Parastichopus regalis, Thelenota ananas, T. anax*	Markle & Olney (1990), Parmentier & Das (2004), Parmentier & Vandewalle (2005), Parmentier et al. (2006), Parmentier et al. (2010), González-Wangüemert et al. (2014)
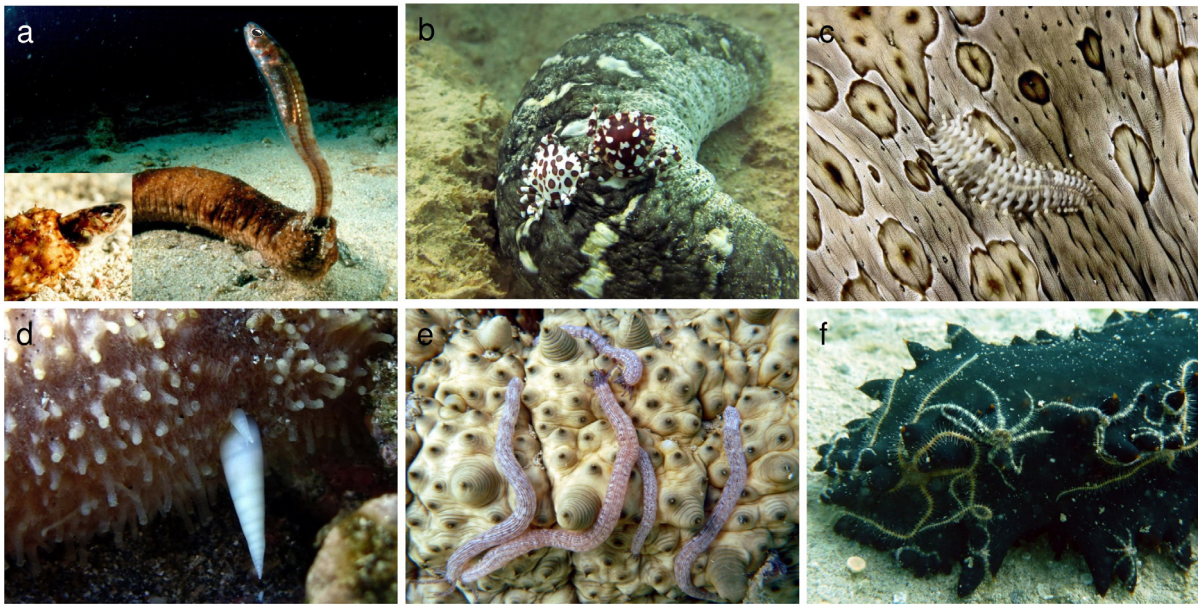
Figure 4. Commensals and parasites of commercially-exploited sea cucumbers. a) Endocommensalism by the pearlfish *Carapus acus* (Family Carapidae) partly emerged from the anus of *Holothuria tubulosa* (Mediterranean Sea), with inset of head of the pearlfish (photos: D. Bay and E. Parmentier); b) Two Harlequin crabs *Lissocarcinus orbicularis* on the body wall of *Holothuria scabra* (Madagascar) (photo: G. Caulier and I. Eeckhaut); c) An ectocommensal scaleworm *Gastrolepidia clavigera* on the body wall of *Bohadschia argus* (Indonesia) (photo: B. Jones and M. Shimlock, Secret Sea Visions); d) A parasitic snail (Family Eulimidae) on *Holothuria verrucosa* (La Réunion) (photo: P. Bourjon); e) Five ectocommensal sea cucumbers *Synaptula media* on the outer body wall of *Stichopus herrmanni* (New Caledonia) (photo: S. Purcell); f) Numerous ectocommensal brittle stars *Ophiothela* cf. *danae* on the body wall of *Stichopus chloronotus* (New Caledonia) (photo: S. Purcell).

Twelve species of pinnotherid crabs are often associated with several holothuroids, with the Harlequin crab *Lissocarcinus orbicularis* (Fig. 4b) being a frequent symbiont (Eeckhaut et al. 2004). Caulier et al. (2014) found that sea cucumbers (eight species) are obligate hosts to these crabs on reefs of south-western Madagascar. The crabs benefit from the predator-deterrence properties of the saponin chemicals produced by the host, which also attracts them to find the host sea cucumbers (Caulier et al. 2013). Research on the crabs' diet shows that the host tissues contribute a food source, but not an exclusive diet (Caulier et al. 2014).

Hosts to endocommensals

Endocommensals live freely in various organs and body spaces of holothuroids, but mostly in the digestive tract where they can exit the hosts. In a similar way to the ectocommensals, they find effective refuge against predators. Endocommensals of sea cucumbers include species from many different phyla, including Protozoa (gregarines, coccidias), Platyhelminthes (Acoeles, numerous Turbellaria, Rhabdocoela and Trematoda), and nine species of fishes (Table 2).

Pearlfishes (Family Carapidae) (Markle & Olney 1990) are often cited as parasites (Jangoux 1990, Eeckhaut et al. 2004) as they can provoke small injuries or reduce gonad tissues of the holothuroid hosts (Parmentier et al. 2006), but the nature of the relationship is contentious. At least nine species are known to live in sea cucumbers in many geographical areas (Eeckhaut et al. 2004). Pearlfishes are of special interest owing to their various adaptations and the obligate nature of the commensalisms. Sexual pairs of pearlfish can be found in sea cucumbers, which are believed to also serve as breeding sites (González-Wangüemert et al. 2014). Using isotope analyses, Parmentier and Das (2004) found that *Carapus* species probably leave their hosts to feed on external sources (Fig. 4a), while *Encheliophis* species eat organs of their holothuroid hosts. Large commercially-exploited sea

cucumbers are the preferred hosts for certain *Carapus* species and it seems that the pearlfish are often relatively uncommon among individuals in sea cucumber host populations (Conand and Olney unpublished data, Markle & Olney 1990, Parmentier et al. 2006, González-Wangüemert et al. 2014).

Hosts to parasites

Likewise for the commensals, parasites can be ectobiotic or endobiotic. Endoparasites most often occur in the digestive tract and the coelomic or hemal systems of the host sea cucumbers (Jangoux 1990, Eeckhaut et al. 2004). Some umagilid flatworm species (Platyhelminthes) are reported to compete with their host for nutrients and swim in the gut or coelomic fluid where they breed, so their life history stages rely on the sea cucumber hosts (Shinn 1983).

Numerous species of gastropods in the Family Eulimidae (33 species cited by Jangoux 1990) are ectoparasites using their proboscis to penetrate the body wall (Fig. 4d) and feed on the coelomic fluid, nevertheless without serious consequences to the host. The most abundant symbiont collected by Lyskin & Britaev (2005) was the polychaete *Gastrolepidia clavigera* (Fig. 4c) which, similar to melanellid gastropods, feeds almost exclusively on the host tissues.

As discussed, several *Encheliophis* pearlfishes (Carapidae) feed on holothuroid tissues and are considered parasites. They have several morphological adaptations in the jaws and teeth, supporting their parasitic lifestyle, in which they differ from *Carapus* species (Parmentier et al. 2010). Similarly, sea cucumbers are an obligate host to the pea crab, *Pinnotheres halingi*, which lives in the respiratory tree of *Holothuria scabra* and can be considered parasitic because it induces atrophy of the respiratory tree (Hamel et al. 1999). *Holothuria atra* is a host for parasitic entochonchid gastropods (M. Byrne, pers. obs.). These bizarre parasites enter the sea cucumber as a larva, attach to the digestive tract and then grow into a spiral vermiform structure that forms a brood chamber for the developing young, which leave the holothuroid host through the anus (Byrne 1985b).

Value to food chains

A sacrificial role played by sea cucumbers is to act as prey to predator species, thereby acting as a conduit for transferring energy from microalgae and organic detritus to consumers at higher trophic levels. Many of the predators themselves are fished by humans. Although sea cucumbers have chemical defences (e.g. saponins, terpenes) and sticky Cuvierian tubules to deter predators (Stonik et al. 1999, Hamel & Mercier 2000, Van Dyck et al. 2009, 2011), they are known to be consumed by a diversity of predators from at least seven phyla (Table 3) (also see Francour 1997). Sea cucumbers are known to be eaten by at least 19 species of sea star, 17 species of crustaceans, several gastropods and around 30 species of fishes (Francour 1997, Dance et al. 2003).

In temperate regions, certain species of sea stars are major predators of aspidochirotid and dendrochirotid sea cucumbers (Jangoux 1982, Yu et al. 2015). Some sea stars in the genus *Solaster* appear to specialise their feeding on non-commercial sea cucumber species and can induce evisceration and consume the released organs (Byrne 1985a). *Solaster endeca* is the main predator of the dendrochirotid *Cucumaria frondosa* (So et al. 2010). Temperate sea cucumbers are also eaten by marine mammals of high trophic levels, such as sea otters (*Enhydra lutris*). Although the sea otters typically eat other prey such as sea urchins and bivalves, the aspidochirotid *Parastichopus californicus* are easy prey and their populations declined dramatically some decades after the introduction of sea otters in south-eastern Alaska (Larson et al. 2013). Therefore, sea cucumbers can be significant food sources for multiple trophic levels.

In tropical regions, a wide range of benthic invertebrates and fishes avidly consume sea cucumbers (Table 3). For example, large gastropods such as *Tonna perdix* prey on sea cucumbers, engulfing them with their large flexible siphon (Life in the Coral Reef of Réunion

2015). Sea cucumbers are also eaten by Triton snails (Conand 1994, Kyoung & Jae 2004), which themselves have been threatened by shell collectors. Predation by fishes is considered to be minor (Francour 1997) but fishes can swallow juvenile sea cucumbers whole (Dance et al. 2003), so their predation impact might be significant in some areas.

Table 3 Predators of commercially-exploited sea cucumber species.

Predator major taxon	Prey holothuroid species	References
Annelida: Polychaeta	*Cucumaria frondosa*	Medeiros-Bergen & Miles (1997)
Crustacea		
Copepoda	*Apostichopus japonicus* (larvae)	Yu et al. (2015)
Decapoda	*Cucumaria miniata*	Francour (1997)
	Psolus chitonoides	Francour (1997)
	Holothuria scabra	Purcell & Simutoga (2008), Lavitra et al. (2009), Robinson & Pascal (2012),
	Apostichopus japonicus	Yu et al. (2014), Yu et al. 2015)
	Holothuria scabra (in captivity)	Pitt et al. (2004), Bell et al. (2007)
	Stichopus tremulus	Francour (1997)
	Parastichopus californicus	Francour (1997)
Gastropoda		
Tonnidae	various species	Francour (1997)
Columbellidae	*Psolus chitonoides*	Francour (1997)
Ranellidae	*Apostichopus japonicus, Bohadschia argus*	Conand (1994), Kyoung & Jae (2004))
Asteroidea	various species	Francour (1997)
	Holothuria scabra	Purcell & Simutoga (2008)
	Cucumaria frondosa	So et al. (2010)
	Apostichopus japonicus	Hatanaka et al. (1994), Yu et al. (2014), Yu et al. (2015)
	Australostichopus mollis	Slater & Jeffs (2010)
	Parastichopus californicus	Cameron & Fankboner (1989)
Pisces		
Elasmobranchii	*Stichopus chloronotus*	Francour (1997)
Actinopterygii		
Balistidae	*Holothuria scabra*	Dance et al. (2003)
Labridae	*Holothuria scabra*	Dance et al. (2003), Francour (1997)
Lethrinidae	*Holothuria scabra*	Dance et al. (2003)
Nemipteridae	*Holothuria scabra*	Dance et al. (2003)
Sparidae	*Cucumaria* sp.	Francour (1997)
Gadidae	*Stichopus tremulus, Parastichopus californicus*	Francour (1997)
Hexagrammidae	*Cucumaria* spp.	Francour (1997)
Pinguipedidae	*Australostichopus mollis*	Francour (1997)
Sebastidae	*Apostichopus japonicus*	Yu et al. (2014)
Testudines: Cheloniidae	*Holothuria scabra*	reports from fishers, S.W. Purcell pers. comm.
Mammalia: Carnivora		
Phocidae	*Thyonidium* sp.	Francour (1997)
Mustelidae	*Parastichopus californicus*	Larson et al. (2013)
Odobenidae	several species	Francour (1997)

In some instances, sea cucumbers offer their internal organs to the predator, through voluntary evisceration, in place of being killed. *Stichopus* species can also shed parts of their body wall in an effort to distract a predator (Kropp 1982). Hence, sea cucumbers may infrequently pass on parts of their body tissue to higher trophic levels.

The literature shows that sea cucumbers and their tissues transfer energy to a high number of both benthic (e.g. crabs, gastropods and sea stars) and benthopelagic predator species (e.g. mammals and fishes), and it is difficult to gauge which groups are most significant in sea cucumber predation globally. Dendrochirotid sea cucumbers use suspension-feeding, thereby contributing to pelagic-benthic coupling by taking phytoplankton and occasional zooplankton from the water column and transforming the matter into benthic

animal tissue (Hamel & Mercier 1998). Clearly, sea cucumbers present a significant pathway by which energy and nutrients from detritus and plankton can be transferred to benthic and benthopelagic food webs.

Policy implications

The broad roles that exploited sea cucumbers play in ecosystems are promoting habitat health, amplifying biodiversity and supporting productive food chains. In more specific terms, the services they provide are: improving sediment quality, water chemistry and nutrient recycling, which benefit ecosystem health and productivity; increasing species richness through symbioses with smaller parasitic and commensal organisms; and forming a substantive link in the transfer of energy in deposited detritus and microalgae to higher trophic levels in marine food webs.

The accumulation of waste products from uneaten food, faeces and pseudofaeces on the sea bed in coastal mariculture operations is an environmental concern (Paltzat et al. 2008). Sediment bioremediation is valued because commercially-exploited sea cucumbers have the potential to reduce waste loading and offer additional, high-value, harvestable seafood. Waste organic matter in sediments underlying farmed shellfish can be reduced by the aspidochirotes *Australostichopus mollis* (Slater & Carton 2009, MacTavish et al. 2012, Zamora & Jeffs 2012), *Parastichopus californicus* (Paltzat et al. 2008), and *Apostichopus japonicus* (Zhou et al. 2006, Yuan et al. 2015). Hence, there is opportunity to take advantage of the sediment-cleaning role of sea cucumbers in modified coastal habitats.

For predators that rely heavily on sea cucumbers as a major food source, depletion of sea cucumber populations through fishing is likely to have a negative impact. For example, the sea star *Solaster endeca* is known to be more abundant where their prey sea cucumber *Cucumaria frondosa* is also abundant (So et al. 2010). Thus, over-exploitation of sea cucumbers may result in a loss of biodiversity or abundance of these predator species or cause them to switch to other prey species, potentially resulting in cascading effects in the ecosystem.

Sustainable exploitation of dense sea cucumber populations may be possible if investments are made to determine commercially-viable stocks and manage fishing to within modest and sustainable limits. Unfortunately, history shows that such prudent management is rarely applied (Purcell et al. 2013). Populations of exploitable species are often fished to critically low levels at which they struggle to repopulate naturally (Bell et al. 2008, Friedman et al. 2011) and probably cease to make significant contributions to ecosystems. Population declines over broad geographic ranges were sufficiently serious to result in the listing of 13 holothuroid species as vulnerable or endangered with extinction (Purcell et al. 2014). Exploitation by fishing may have a cascading impact on biodiversity because depletions in host sea cucumber populations will also deplete symbiont populations (see Table 2).

This review suggests that large-scale depletions through excessive fishing are likely to have indirect effects on the productivity and diversity of soft-bottom habitats such as seagrass beds and coral reef lagoons. Fishery management should be especially conservative on coral reefs because it is in these carbonate-rich habitats that sea cucumbers can most affect ocean chemistry. Coral reefs are in decline globally from the impacts of a range of broadscale stressors (Hoegh-Guldberg 1999, Pandolfi et al. 2003, Bellwood et al. 2004, Hoegh-Guldberg et al. 2007). The changes to local water chemistry and nutrient availability by the feeding activities of sea cucumbers offer tangible contributions to coral reef resilience. However, the potential enhancement of reef calcification through the influence of sea cucumbers on water chemistry is only likely to be effective in areas which are not highly flushed, where the sea cucumbers are in high densities and where they live in close association with coral, as is the case for *Stichopus herrmanni* (Fig. 3) in the unfished lagoon system investigated by Schneider et al. (2011, 2013).

Fishery management espousing EBFM principles must take into account the ecosystem services provided by sea cucumbers. For example, species-specific bans or catch limits could be imposed to limit fishing of some of the burying species (Table 1), as these are most important in bioturbation of sediments. Many finfish fisheries target species that feed on soft-bottom invertebrates, so it is conceivable that fisheries productivity could decline as a consequence of depletions in sea cucumber populations. Some sea cucumber species may warrant specific protection if they are especially important in coastal and offshore food chains. Research to further understand their predators, and the importance of sea cucumbers to their diets, would help resource managers to better evaluate the potential ecosystem benefits from stricter regulatory measures on fishing sea cucumbers. Some exploited species, such as *Holothuria atra,* have a low commercial value to fishers and can occur in high densities and process great quantities of sand and detritus (Uthicke 1999). Another ecosystem-based policy could be to exclude low-value species from the lists of permissible species to be harvested because the financial return for fishers and exporters is relatively low but they still have an important value to the ecosystem.

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