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Published in:
Earth Systems and Environmental Sciences

DOI:
10.1016/B978-0-12-821139-7.00121-5

Conservation of Coral-Associated Fauna

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Glossary

Bleaching Disruption of the endosymbiotic relationship between coral polyps and the zooxanthellae algae that live inside their tissue, resulting in the ejection of the symbionts and a consequent whitening of a coral colony. Sign of environmental stress.
Functional role The role of a species in an ecosystem based on its traits.
Functional redundancy Species performing the same functional role in an ecosystem are called redundant. Functional redundancy is ensured when two or more species perform the same function(s).
Global warming Gradual and continuous temperature increase in the earth's atmosphere mainly due to human activities.
Generalist A species that can live in many different habitats and/or feed on many different organisms. Generalist symbiont fauna associates with multiple, often unrelated, hosts. Less susceptible to disturbances in their environment.
Gleaning Collection of marine organisms for food, particularly at low tide from shallow coastal areas.
Host specificity Identity and number of host species used by a symbiont. A high degree of host specificity means a small number of host species, and vice-versa.
IUCN Red List The most comprehensive inventory of the global conservation status of biological species. It uses a set of criteria (e.g., rate of decline, population size, area of geographic distribution) to allocate species into one of nine categories: Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD), and Not Evaluated (NE).
Ocean acidification A progressive reduction in the pH of ocean water due to the increase in the concentration of dissolved carbon dioxide from emissions by human activities.
Specialist A species that has a very narrow range in terms of habitat and/or food requirements. Specialist symbiont taxa associate with one, or a few closely related, host(s). More susceptible to disturbances in their environment.
Stony corals Also known as scleractinian or hard corals. The coral skeletons are mainly made from calcium carbonate.
Symbiont (obligate/facultative) Species living in symbiosis with a host organism. Obligate symbionts are unable to live without their host(s), whereas facultative symbionts can survive without their host(s).
Symbiosis Biological interaction between two or more dissimilar species. Can take one of three main forms: mutualistic, commensalistic or parasitic. In a mutualistic relationship both organisms benefit from the association, whereas in a commensalistic relationship one species benefits and the other species neither benefits nor gets harmed. In a parasitic relationship one species benefits at the expense of the other.

Abstract

Coral reefs are some of the most biodiverse ecosystems harboring thousands of species, many of them symbionts that play important roles in the survival of their hosts. These associated taxa, mostly invertebrates, remain largely unstudied and the conservation status of the majority of these species is not assessed. With coral reefs under severe global and local threats, effective conservation measures based on a whole ecosystem approach are needed. The IUCN Red List is the most up to date inventory of species' conservation status, yet does not include symbiont fauna of important host organisms. Here we suggest including associated taxa in future endangerment assessments, especially those living in obligate symbiosis.

Importance of coral reefs

Coral reefs are some of the most diverse ecosystems in the world. The high species diversity and productivity level observed in these ecosystems translates into a wide range of ecological functions, such as provision of food and habitat for many marine organisms, protection of the coastline from erosion by tidal storms and promotion and maintenance of the global calcium balance and carbon cycle (Moberg and Folke, 1999). In addition to its ecological role, a healthy coral reef ecosystem also has important social, economic and cultural value. Approximately 500 million people worldwide depend to some extent on coral reefs, for food, income, coastal protection and other resources with at least 30 million depending almost entirely on coral reefs as a source of livelihood (Wilkinson and Souter, 2008).

Coral reefs harbor hundreds of thousands of species while occupying not more than 0.1–0.5% of the total ocean floor (Moberg and Folke, 1999). They are thought to be home to over 30% of all known marine species, making them some of the most diverse ecosystems on the planet (Costello, 2015; Fisher et al., 2015). Different coral species provide different functional roles, mostly through the type of habitat they offer (e.g., branching vs massive) but also through the species associating with these corals (Stella et al., 2011). A shift in coral species assemblages is, for example, known to alter the community of reef fishes, and hence the functional role offered in a reef ecosystem. These shifts can result from bleaching events or diseases, significantly altering the functional composition of a reef and homogenizing the species assemblage (Hughes et al., 2018b; Richardson et al., 2018). Estimates suggest that the total number of known species (both described and undescribed) is far removed from the actual number of species, with certain taxa remaining almost unexplored (e.g., mollusks, copepods, nematodes; Fisher et al., 2015). A large proportion of this biodiversity is overlooked because of a lack of commercial interest, charisma, diminutive size and/or taxonomic expertise.

Given the importance of coral reefs for the preservation of ecosystem services and biodiversity, their conservation is of paramount importance, particularly with the threats coral reefs currently face. It has been suggested that the loss of biodiversity is occurring at a greater rate than our increase in knowledge, and this is particularly true for marine systems and for the lesser-studied species - the small majority - within those systems (Powderham and Van der Meij, 2021). Hence in this review we will turn our focus to the conservation status of marine (in)vertebrates associated with stony corals, and lack thereof, and provide suggestions for further conservation measures and endangerment assessments of these species.

Coral reefs under pressure

Coral reefs as ecosystems have long been subjected to environmental pressures, resulting in fluctuating species numbers, abundance and overall density. Coral reefs have shown to be resilient and able to adjust under challenging conditions but the accelerated pace of global climate change, and its various effects - such as coral bleaching - are impacting slow-growing corals on an unprecedented scale. Threats to coral reefs, linked to global stressors, but also to regional and local anthropogenic pressures (destructive fishing methods, tourism and pollution) have been subjecting coral reefs to an alarming rate of disappearance in recent years (Carpenter et al., 2008).

At a global scale, global warming and overfishing are some of the main factors contributing to the disappearance and decline of coral reefs (Dietzel et al., 2021, Fig. 1A). Bleaching events, resulting from a rise in ocean temperatures, have been increasing in frequency since at least 1980 and the time between bleaching events is also shortening, not providing enough time for the corals to recover which often leads to increased coral die-off (Hughes et al., 2018a). Climate change is also linked to a decline in pH called ocean acidification due to increased carbon dioxide absorption by the oceans, which can lead to an impaired ability of corals to grow. Another major threat is overfishing, as mainly apex and mesopredators are targeted for food consumption, disrupting the balance in coral reef ecosystems. Intensive fishing practices can lead to the disappearance and/or decline of key functional groups of species from reefs, which will also put the corals at risk (Harborne et al., 2017).

At regional and local scales, destructive fishing practices and low water quality (coastal development, land run-off, pollution, tourism) are the two main drivers of coral loss (Fig. 1A). Destructive fishing methods - such as blast fishing - have direct impacts on local coral cover, but even less invasive methods like reef gleaning can degrade shallow reefs. Low water quality results from a local concentration of nutrients and sediments which have also been shown to result in, for example, a reduction of calcification rates, reproduction, growth, coral cover, species richness and increased coral mortality (Harborne et al., 2017).

Combined, these threats have had a detrimental impact on coral reefs around the world and this is reflected in a 2008 assessment on the conservation status of all known coral reef-building species (stony corals, reef-building octocorals, hydrocorals). Over 80% of the species were assigned a status according to the International Union for Conservation of Nature (IUCN) Red List Criteria (Fig. 1C) and one third of the species were assigned to a high extinction risk category, mostly due to climate change (Carpenter et al., 2008). A more recent analysis of population sizes and global extinction risk of reef-building corals revealed that two-thirds of the examined coral species have population sizes exceeding 100 million colonies. While local depletion has been shown to threaten coral reefs, with potentially ecologically devastating impacts, the global extinction risk of most species is suggested to be lower than previously estimated (Dietzel et al., 2021).

Global, regional and local threats, albeit quite distinct and acting at different intensities, have been predicted to threaten 90% of all coral reef species by 2030, with this number being expected to reach nearly 100% by 2050 (Burke et al., 2011). Combined, these

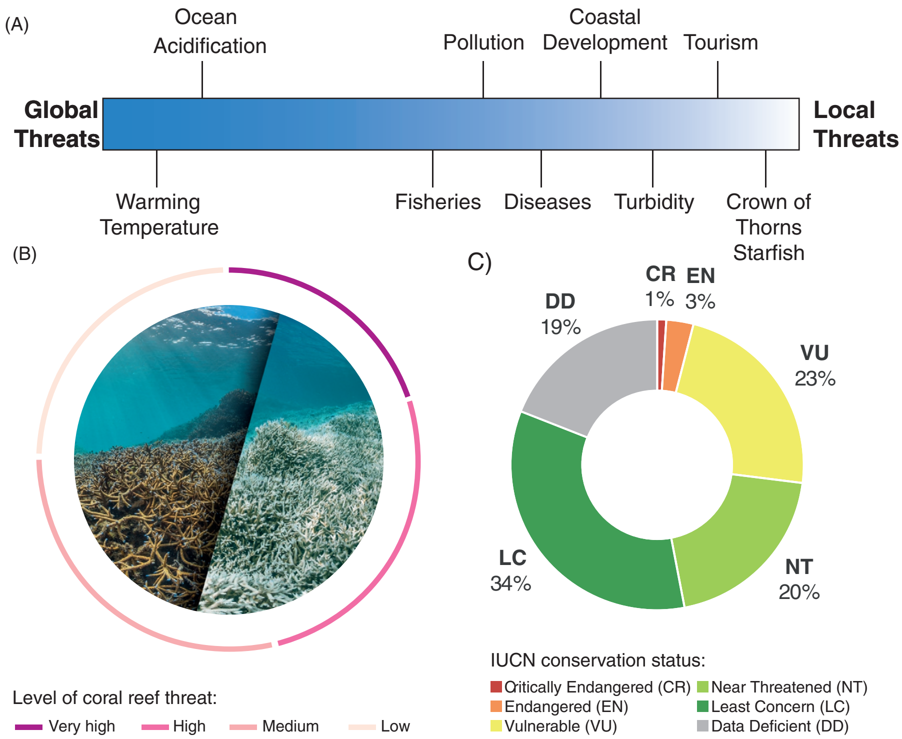

Fig. 1 Threats to coral reefs and their overall decline. (A) Global and local threats are outlined on a spectrum depending on their perceived level of impact; (B) Percentage of coral reefs threatened by global and local threats combined, ranging from low to very high; photograph highlights the transition from living to dying coral due to coral bleaching in American Samoa between 2014 and 2015; (C) IUCN conservation status of coral reef species. (B) Adapted from Burke L, Reytar K, Spalding MD, and Perry A (2011) *Reefs at Risk*. Revisited. World Resources Institute; (© Photo credit: Underwater Earth | XL Catlin Seaview Survey); (C) adapted from Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortés J, Delbeek JC, DeVantier L, Edgar GJ, Edwards AJ, Fenner D, Guzmán HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR et al. (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science*, 321(5888): 560–563, doi:10.1126/science.1159196.

events currently threaten 75% of coral species (Fig. 1B) and have been responsible for an increased die-off of corals and a subsequent disappearance of associated reef species. Moreover, a sharp decline in these host-symbiont systems has consequences at ecosystem level due to restructuring of species assemblages and loss of functionality (Harborne et al., 2017; Hughes et al., 2018a).

Diversity of coral-associated fauna

Invertebrate and small vertebrate species living in symbiosis with a host coral make up the vast majority of the diversity on coral reefs. For small-sized symbionts there are many benefits to having scleractinians as hosts. The corals provide them with refuge from predators, food sources (coral tissue, mucus or detritus), settlement cues and a hard exoskeleton that can be used by burrowing and gall-forming species (Castro, 1988). Branching corals in particular support large epifaunal communities (Stella et al., 2011; Pisapia et al., 2020).

There are hundreds of species (crustaceans, mollusks, worms, fishes) that depend exclusively on one or a few, often closely related, host corals (Fig. 2). Close to 900 invertebrate species are known to associate with stony corals and over half of them are in an obligate symbiotic relationship with their hosts. A review of the coral family Fungiidae showed that it hosts a myriad of symbionts; the long-tentacled mushroom coral *Heliofungia actiniformis* Quoy and Gaimard, 1833 hosts at least 23 different associates (Fig. 2B). On the other hand, certain mushroom corals host none or just a few symbionts, hypothesized to be the result of the evolutionary history of the coral or the type of habitat they offer (e.g., coral dimensions such as diameter or thickness; Hoeksema et al., 2012). A study on small obligate coral-dwelling gobies revealed a high degree of specialization, with each goby species associating only with a small number of acroporid coral hosts (Duchene et al., 2013). Careful observations from either the host's or the symbiont's perspective will often result in new host-symbiont records, even in relatively well-studied reef systems (Van der Meij, 2014, 2015a).

Understanding the nature of the relationship (obligate/facultative) between host and symbiont is of particular importance to predict the consequences of global coral cover decline on coral-associated taxa. However, even this basic information is often unknown or difficult to determine. The nature of obligate symbiosis, for example, suggests that symbionts are, by default, endangered when their hosts are not able to adapt and switch to another host in time (Sotka, 2005; Stella et al., 2011). Facultative symbionts display a higher degree of host flexibility with many species being defined as generalists, meaning that they can associate with multiple and not necessarily closely related hosts. These symbionts have a higher chance of survival should one, or some, of their hosts become endangered.

Fig. 2 Examples of host-symbiont relationships on coral reefs. (A) The guard crab *Trapezia rufopunctata* on *Pocillopora* sp.; (B) The pipefish *Siokunichthys nigrolineatus* on *Heliofungia actiniformis*; (C) The feather duster worm Sabellidae sp. in *Dipsastraea* sp.; (D) The shrimp *Vir colemani* on *Plerogyra lichtensteini;* (E) The hermit crab *Paguritta* sp. in *Montipora* sp.; (F) The acoel cf. *Waminoa* sp. on *Acropora* sp.; (G) The tube-building fan worm *Spirobranchus* sp. in *Porites* sp. (H) The corallivorous nudibranch *Phestilla viei* on *Pavona explanulata;* (I) The gall crab *Lithoscaptus semperi* in *Trachyphyllia geoffroyi.* As the ID's are assessed from photographs, they are consequently indicative. *© Photo A-G by AJ Powderham and H-I by SET van der Meij/BT Reijnen.*—Fig. (I) was previously published in Van der Meij (2015: Fig. 3F), under a CC BY 4.0 license. van der Meij SET (2015) A new gall crab species (Brachyura, Cryptochiridae) associated with the free-living coral Trachyphyllia geoffroyi (Scleractinia, Merulinidae). *ZooKeys*, 72(500): 61–72, doi: 10.3897/zookeys.500.9244.

Functional role of coral-associated fauna

The ecological role of stony corals has three main functions: (1) as foundation species by contributing to carbon production for reef-based food webs; (2) provision of habitat for coral-dwelling species; and (3) establishment of a structural framework by limestone deposition thus contributing to habitat complexity and therefore increasing biodiversity (Stella et al., 2011 and references therein). The study of functional roles in coral reef environments is almost exclusively dedicated to stony corals and fish (but see Castro, 1988, 2015, for other examples). The latter are known to play an important role in ecosystem functioning through nutrient cycling, bioerosion, sediment removal, or trophic control. Despite the apparent high abundance of reef fish species and the assumed high levels of functional redundancy in some reefs, this does not confer insurance for all functional roles. It has been suggested that over one third of all functional roles of fishes are assured by a single species, hence many functional roles are at risk of disappearing (Mouillot et al., 2014).

Few studies have been dedicated to the functional roles of the invertebrate fauna of coral reefs, but they likely influence coral health and serve as an important trophic link between corals and other reef organisms. Pocilloporid corals for example, when in possession of obligate decapod crustacean symbionts (*Trapezia* spp., *Alpheus lottini* Guérin, 1829), demonstrate higher survival rates than corals divested of their symbionts (Glynn, 1983). Crabs of the genus *Trapezia* are also known to increase survival of their *Pocillopora* hosts and reduce consumption rates of their hosts by predatory sea stars and vermetid snails, which is something that has been observed not only with adult crabs but also with juveniles (Stier et al., 2010; Rouzé et al., 2014). The presence of *Trapezia* appears to be stimulated by the coral hosts themselves through the production of lipid rich fat bodies by the coral polyps. Removal of crabs has shown an abrupt reduction in the production of these fat bodies, suggesting that the corals produce them in order to attract their symbiotic crustaceans (Stimson, 1990).

Moreover, symbiotic crabs can also be active in the protection of their stony coral hosts through other mechanisms such as feeding on overgrowing algae as well as fighting off predators. The removal of seaweed and other invertebrates by crabs of the genus *Mithrax* has shown to be beneficial for corals that harbor these crabs. These coral hosts would otherwise experience dense covers of epibionts that would result in reduced growth and increased mortality (Stachowicz and Hay, 1999).

The active protection of hosts is not the only defense mechanism employed by symbionts. The presence of hydrozoans on coral hosts has shown to significantly reduce coral mortality from predation and diseases. It has even been suggested that hydrozoans may help corals to resist environmental stress (Montano et al., 2017). Many host-symbiont relationships remain largely unstudied so the mechanisms employed in safeguarding each other are still a mystery for many of these relationships.

The relationships between species on coral reefs are intricate and involve many more species than initially thought, with the disappearance of one of the links in this complex ecosystem potentially having cascading effects. A shift in species composition at an ecosystem level could have irreparable consequences, where the disappearance of some species could lead to a loss in key functional roles, for example. In the best case scenario, a shift in species can still be enough to ensure the maintenance of key functional roles by continuing to provide sustenance and refuge for many species. The disappearance of many symbiotic species that depend directly and exclusively on specific coral species is, however, unavoidable, even if key functional roles are still assured.

Conservation status of coral-associated species

While assessments on the population trends and conservation status of coral species are more frequent than other marine taxa (with the exception of megafauna and species of commercial value), little to nothing is known about the population size or trends of marine invertebrates, including coral-dwelling species. With nearly 900 known invertebrates depending to some extent on corals for habitat, shelter or settlement cues, there are very few assessments of conservation statuses for the different reef taxa, despite their functional role in the coral reef ecosystem.

For species associated with reefs - but not necessarily as associates of corals - some conservation assessments have been conducted, particularly for species of commercial interest. A few examples include lobsters, sea cucumbers and cone snails, but despite thorough assessments, a high number of species in these groups are Data Deficient according to the IUCN Red List criteria (Kemp et al., 2012; Peters et al., 2013; Purcell et al., 2014). Unregulated fishing, alongside habitat destruction, is the main threat to all these species, particularly when they are known to inhabit impacted habitats. Cone snails, for example, are reduced in numbers in areas where coral cover has been extensively damaged (Peters et al., 2013).

Apart from the aforementioned IUCN Red List assessments that have been done for groups of species that are either charismatic or have a high economic value, there are also national assessments compiled by individual countries, which result in more thorough conservation assessments. However, these lists can classify a species as 'nationally critical,' while not being threatened at a global level. There has been an increase in the number of species assessed over the years, particularly in places where environmental monitoring has been implemented for many years (e.g., Australia, Singapore, USA) but the conservation status of the vast majority of species remains unknown. At least 90% of all marine species are invertebrates, however, less than 1% of them have had their status evaluated. Around 25% of the invertebrates that had their status assessed are threatened with extinction. If this trend is extrapolated to the remainder of marine invertebrates, many more species are likely to be at risk with estimates ranging from 20% to 40% of all marine invertebrates being threatened (Kemp et al., 2012).

In the 1996 IUCN Red List, only two crustaceans that rely on marine ecosystems to some or all extent were included: the coconut crab (*Birgus latro* (Linnaeus, 1767)) and the California Bay pea crab (*Parapinnixa affinis* Holmes, 1900). The first one had already been included in the list of 1981, but the pea crab was a new addition. Despite it being a minute percentage of species represented in the global assessment of endangered species at the time, there have been some great improvements in recent years with many new additions to the list currently consisting of just over 200 species of marine crustaceans that have had an assessment. Unfortunately, we are still far from having an encompassing knowledge of the current status of marine invertebrates in general and coral-associated species in particular (Fig. 2), but efforts are being made in the right direction with lists being produced for entire groups of species.

IUCN Red listing does not involve extensive surveys in order to assess the conservation status of all marine invertebrates. Rather, it is based on collating (published) information on species in order to do an assessment. In the case of obligate symbionts that only associate with a single or a reduced number of hosts that share the same level of threat, a partial solution could be to use the host as a proxy for the level of endangerment of the symbiont. For facultative symbionts it is harder to predict what the outcome of a host going extinct would be given the adaptive potential of the symbionts. However, for obligate symbiotic species associating with endangered host species, their conservation status should be the same as that of their (least threatened) host(s), and not independently assessed. Given the paucity of information on the natural history of many symbiont taxa, this approach would also potentially allow to classify certain symbiont species and help raise awareness of their current endangerment status (Fig. 3).

Coral-dwelling gall crabs

Gall crabs (Cryptochiridae) live in obligate symbiosis with stony corals and are uniquely adapted to living with a host by creating a dwelling in the coral skeleton (Fig. 2I). The nature of the symbiosis with their coral hosts is under debate, and subject of ongoing research. They are most common on tropical shallow-water reefs, but have been recorded from >500 m depth. These diminutive crabs are associated with most coral families, with Acroporidae, Euphylliidae and Poritidae as notable exceptions. The diversity of

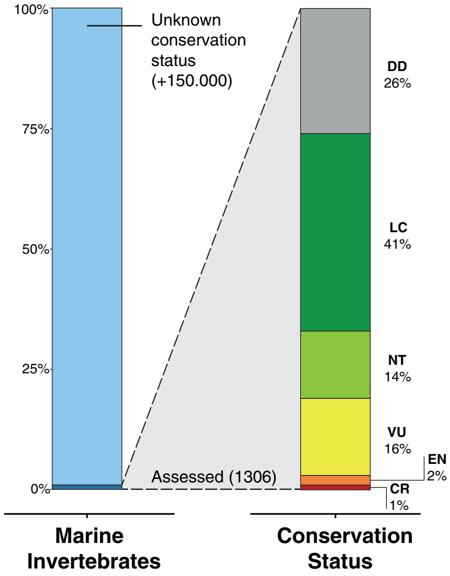

Fig. 3 Less than 1% of the described marine invertebrate fauna (~150.000 species (left bar), based on Kemp et al. (2012) and Fisher et al. (2015)) had their conservation status assessed. The assessed invertebrates (1306 species, right bar) are categorized according to the IUCN conservation status in the right column. Categories of the IUCN Red List conservation status correspond with Fig. 1.

gall crabs is intrinsically related with the diversity of their hosts; the majority of species can be found in the Coral Triangle with the Red Sea as a secondary center of diversity. Cryptochirid crabs are host specific and mostly inhabit a single or several closely related coral species (Castro, 2015). Recent studies by the authors have revealed high levels of (cryptic) diversification, e.g., in the genera *Fungicola* and *Opecarcinus*, revealing even stricter levels of host specificity than previously assumed (Van der Meij, 2015a; Xu et al., in press). Interestingly, there is one exception to this rule. The generalist species *Troglocarcinus corallicola* Verrill, 1908 associates with at least 25 different host species across eight coral families in the Atlantic Ocean (van der Meij, 2014). Given their strict host specificity, many gall crab species are as much at risk of extinction as their coral hosts.

The ecological role of gall crabs is not well understood, but they are omnipresent with about 20% of host corals inhabited on any reef. However, their prevalence differs between species and across environmental gradients, potentially making them suitable indicators for reef health (van Tienderen and van der Meij, 2016). Their abundance and visibility on the reef surface makes them an ideal model taxon for surveys. Moreover, gall crabs have recently been observed to fluoresce (Bähr and van der Meij, 2019), which greatly aids their discovery on reefs and provides the option to compare techniques for biodiversity estimates of small taxa.

Given that attempts by researchers since the 1960s to cultivate gall crabs in aquaria have been unsuccessful, any report on gall crabs in seawater aquaria is also an indication that the corals were collected and not cultivated. Popular corals in the aquarium trade include the 'open brain coral' *Trachyphyllia geoffroyi* Audouin, 1826, classified by the IUCN as Near Threatened. Global climate change, habitat reduction and local anthropogenic pressures are among the stressors for this species. This coral is targeted in high numbers for the aquarium trade, hence adding overharvesting to the list of stressors. The cryptochirid *Lithoscaptus semperi* van der Meij, 2015 (Fig. 2I) is strictly associated with *T. geoffroyi*, meaning it is as much at risk as its host.

Conservation measures

Most species on reefs are invertebrates, many of them undiscovered and unnamed, particularly nematodes, crustaceans and mollusks (Costello, 2015; Fisher et al., 2015). Currently, over half of the described coral-associated invertebrates have an obligate relationship with their hosts, meaning that their survival is fully dependent on that of their hosts. Obligate symbionts can also have multiple host species, in which case the level of survival is intrinsically related to the level of host specificity and the conservation status of its least threatened host. Generalist symbionts, for example, have a better chance of surviving a potential decline in coral cover because they have multiple hosts, other than specialist symbionts which associate with one or a few closely related coral species. In addition, one third of all known associated invertebrates (~300 species) have their relationship status with their host(s) classified as unknown (Stella et al., 2011), highlighting how little is known about these species.

Successful conservation of coral-associated fauna depends on the conservation of their coral hosts. This is an example of where conservation measures will need a holobiont approach, ideally extended to the whole ecosystem, rather than being targeted at an individual species level. It is also pivotal to understand the nature of the relationship (obligate or facultative) between the coral host and the symbionts in question, in order to estimate the level of endangerment for the symbionts. A more complete overview of host-symbiont relationships, as well as the diversity, distribution, and functional roles of associated fauna is urgently needed. Inclusion of species in the IUCN's Red List of Threatened Species will hopefully bring them into the spotlight and help raise awareness to the dangers many coral-associated species face and how imperiled they are by association.

Concluding remarks

Despite the important role of symbiosis on coral reefs, very little is known about the various symbiont taxa, let alone the best practice to protect them. The number of known species (formally described and undescribed) is likely to be a gross underestimation of the actual number of species present on reefs and yet, less than 1% of the currently known marine invertebrates had their conservation status assessed. There are few studies focusing on marine invertebrate conservation (see Carlton (2013) for a review on the difficulties in assessing marine invertebrates), highlighting the need for more research on this topic.

Certain coral-associated taxa can be used as environmental indicators (see section on coral-dwelling gall crabs). However, the suitability of associated taxa as indicators of overall reef health by monitoring the numbers and population trends requires further work, since little is known about (natural) fluctuations in population numbers and how that relates to seasonality and/or external factors such as pollution, temperature, host mortality, etc.

The functional roles symbionts confer onto their hosts is also shrouded in mystery. We highlighted some examples where symbionts are responsible for warding off predators and algae from smothering the coral and thus may increase survival rates of the hosts. However, the intricacies of most of these host-symbiont relationships still elude us. Unfortunately, our level of understanding is being outpaced by the decline in coral reefs, which consequently impacts these valuable host-symbiont systems.

Acknowledgments

We are grateful to Alan Powderham for providing the photographs highlighting the diversity of species on coral reefs, and to Underwater Earth | XL Catlin Seaview Survey for the use of their photograph that highlights coral bleaching in a beautiful yet devastating way. Sammy DeGrave and Mark Costello provided constructive comments on an earlier version of the text.

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