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Research Note

Three-way symbiotic relationships in whale sharks

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Abstract. Symbiotic relationships between fishes and other organisms are not always easily defined, and three-way symbiotic relationships are rarely reported. Here we examine the relationship between the endangered whale shark, echeneids (remoras and sharksuckers) and a symbiotic copepod. Through their symbiosis with whale sharks, sharksuckers gain one food source from the host's parasites and energetically-free transportation to foraging areas, where they are also able to feed on the prey targeted by their hosts. The relationship between whale sharks and sharksuckers is complex, and most accurately described as mutualism. Likewise, the whale shark and copepod relationship is also complex, and could be described as a parasitic relationship with commensal or even mutualistic characteristics. Although echeneids are not considered to form host-specific relationships and can be free-ranging, the whale shark copepod occurs only on whale sharks; its survival inextricably linked to that of its host.

Keywords: commensalism, copepods, Echeneidae, mutualism, parasitism, sharksuckers.

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Introduction

Symbiosis – whereby two species live together – is common in fishes, and can include parasitism, mutualism, and commensalism (Helfman *et al.* 2009). In a form of commensalism, various species of teleost fish are known to seek refuge around the huge frame of the whale shark (*Rhincodon typus* (Smith 1828)) (Rowat and Brooks 2012). These commensal species benefit by increased protection from predators while the host (the whale shark) is purportedly unharmed by their presence. However, symbiotic relationships between fishes and other organisms are not always easily defined.

There is a general consensus that members of the Echeneidae (remoras and suckerfishes), which are recognised by having a spinous dorsal fin uniquely modified into a large anteriorly-placed oral adhesive disc (Britz and Johnson 2012), have a mutualistic relationship with their hosts, including whale sharks (Fig. 1). Members of this family have been found to have a high proportion of parasitic (or commensal) copepods in their diet which they remove from the bodies of their hosts (Cressey and Lachner 1970). Although this benefits the host (elasmobranch), as well as protection, the teleost gains the advantages of 'hitchhiking' a ride and remaining in close proximity to this food source. Planktonic dietary sources may also be important for echeneids, however it is thought that this can be derived from a coprophagous life-style (Williams *et al.* 2003), or that some species, such as the sharksucker (*Echeneis naucrates* Linnaeus 1758) may be free-ranging for extensive periods (Cressey and Lachner 1970). Their degree of mutualism has been shown to vary ontogenetically, with the likelihood of sharksuckers picking parasitic copepods off their host being dependent on the size of the individual (Cressey and Lachner 1970). For example, a study of the diet of 95 sharksuckers ranging in length from 57 to 630 mm standard length (SL), found that the largest individual to have ingested parasitic copepods was only 311 mm SL (Cressey and Lachner 1970). Larger individuals must therefore source alternative dietary items.

Three-way symbiosis in whale sharks

The whale shark copepod (*Pandarus rhincodonicus* Norman, Newbound and Knott 2000) (Fig. 1) has been found on whale sharks throughout the Pacific and Indian Oceans (Norman *et al.* 2000; Meekan *et al.* 2017). Believed to be a commensal species that feeds off microorganisms from the skin of the whale shark (Norman *et al.* 2000), a recent study extracted whale shark DNA from these copepods (Meekan *et al.* 2017). This suggests that they may also be parasitic, possibly consuming epidermal fragments and mucous from their hosts. At 11 cm thick, the whale shark's skin is the thickest of all known sharks (Stead 1963), whereas at <1 cm, the copepods oral cone is unlikely to perforate the skin and the mandibles are thought to be better suited to scraping surface microbiota from the host's skin (Norman *et al.* 2000).

Fig. 1. Anterior view of a whale shark (*Rhincodon typus*) mouth, including whale shark copepods (*Pandarus rhincodonicus*) attached to the top and bottom lips and the sharksuckers (*Echeneis naucrates*) feeding on euphausiids (Photograph: Brad Norman).

Both whale shark copepods and echeneids have developed uniquely different morphologies and mechanisms to cope with the substantial drag forces associated with living in a symbiosis with the world's largest fish (see Norman *et al.* 2000; Britz and Johnson 2012). The attachment of both copepods and echeneids has previously been shown to be a hydrodynamic burden to their host, creating a parasitic relationship, where the host no longer benefits from the relationship and indeed is negatively impacted (e.g. Helfman *et al.* 2009). Some hosts actively try to dislodge echeneids and copepods (e.g. Ritter 2002; Brunnschweiler 2006; Misganaw and Getu 2016), although we are not aware of reports of whale sharks actively trying to dislodge these organisms. Understandably, the impact of ectoparasites is likely to be far more pronounced in smaller fishes; the large size of the whale shark may render such relationships innocuous. These relationships may therefore be more accurately described as commensal (or perhaps even mutualistic), and in the case of the whale shark copepod's relationship with the whale shark, perhaps a combination of parasitism (as inferred by the presence of whale shark DNA in the copepods), commensalism and mutualism (the copepod hitches a ride and removes microbiota from the host).

Whale sharks at Ningaloo Reef, Western Australia, are routinely sighted accompanied by symbiotic echeneids and other commensal teleosts, and an estimated 26% of whale sharks there host the whale shark copepod (Norman *et al.* 2000). Copepods are frequently found surrounding the oral cavity of whale sharks (Figs 1, 2), facing anteriorly on the shark to reduce drag and possibly selecting this area because of its thin boundary layer (Norman *et al.* 2000). The concentration of copepods in this specific location on the shark may also be a consequence of the copepods selecting a location where they are less susceptible to predation by the echeneids, or mean that these fish are able to prey more heavily on those copepods that attach to other parts of the body of the shark. In this manuscript we discuss the endangered nature of the whale shark and what this may mean for any symbiont species that may be host-specific and therefore also be in need of conservation protection.

Methods

Feeding by large oceanic fish such as the whale shark is often difficult to observe and record, particularly as they are wide ranging and highly mobile. Whale sharks typically feed at night when their phototrophic planktonic prey ascend to the surface and aggregate (Gleiss *et al.* 2013), whereas most human observations of individuals occur during the day (Norman *et al.* 2017). The study of feeding by commensal or mutualistic species without performing large numbers of dietary dissections is also difficult.

Whale sharks in the Maldives have been observed feeding on euphausiids (krill) that are attracted to the lights of tuna fishing boats as commercial fishers collect bait fish at night. A tourism resort in Thaa Atoll in the Maldives, COMO Maalifushi, has developed a similar methodology to facilitate whale shark ecotourism for its guests. A light mounted on a moored vessel is used to attract a high concentration of euphausiids at night, which in turn attracts whale sharks with their symbiotic echeneids (Figs 1, 2). This method was used in this study and the photographic images were captured using a GoPro HERO5 video camera (GoPro Inc., San Mateo, CA, USA) over a 2-h period during one evening in 2018 while snorkeling with feeding whale sharks (Figs 1, 2). Similar observations were collected over four additional nights in 2018, providing further evidence of active foraging of symbiotic echeneids and the whale shark.

Results and Discussion

Both sharksuckers (*E. naucrates*) and remoras (*Remora remora* (Linnaeus 1758)) were observed feeding on the euphausiid swarm that had attracted their whale shark host (Figs 1, 2;

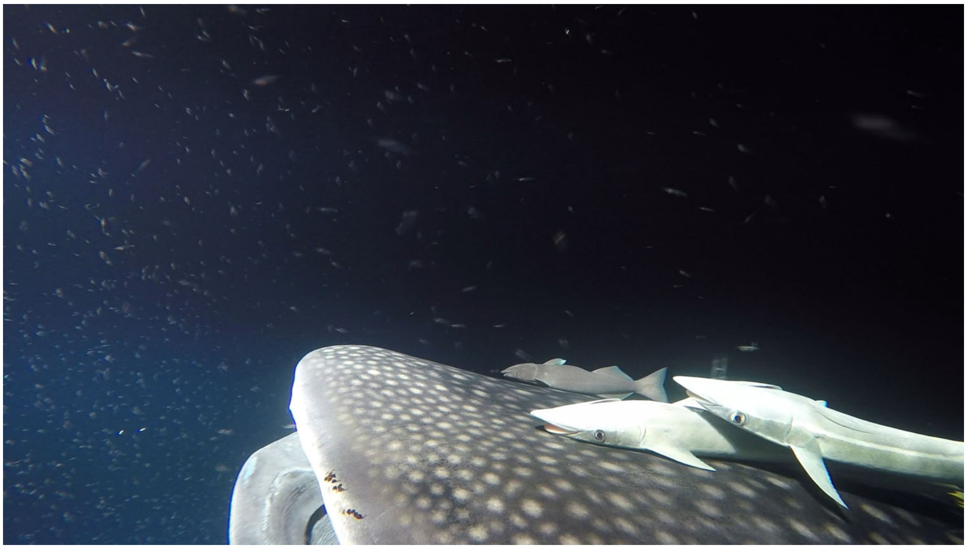

Fig. 2. A whale shark (*Rhincodon typus*), sharksuckers (*Echeneis naucrates*) and a remora (*Remora remora*) nocturnally feeding on euphausiids; with whale shark copepods (*Pandarus rhincodonicus*) visible on the shark's top lip (Photograph: Brad Norman).

Supplementary Material Video S1). The whale shark had commensal copepods concentrated around its oral cavity and these may not have been an accessible prey option for the sharksuckers or remoras. The sharksuckers observed were all >400 mm SL and as Cressey and Lachner (1970) failed to find commensal or parasitic copepods in the diet of sharksuckers >311 mm SL, it seems that the sharksuckers are benefitting from being passively transported to an area of high prey abundance and are likely to be feeding on the same prey as their hosts. A similar feeding event was previously reported for a species of echeneid by Clark and Nelson (1997), where the commensal teleosts were observed to detach themselves from the feeding host to prey on planktonic copepods in the Gulf of California. Without field observations such as these, an analysis of the sharksucker stomach contents (through dissections) may have led to the conclusion that these fish contained a high proportion of euphausiids as a result of a coprophagous diet or free-ranging life-style. Additionally, overly frequent provisioning of whale sharks, by attracting euphasiids could affect their normal behaviours and alter the diet of their associated shark suckers. Although the ramifications of overly intense feeding have been studied (Thomson *et al.* 2017), the effects on associated sharksuckers and remoras is unknown.

Echeneids are not considered to form host-specific relationships and can be free-ranging, to our knowledge, but the whale shark copepod (*P. rhincodonicus*) occurs only on whale sharks. Therefore, their survival is likely to be inextricably linked to that of their hosts. A study of the critically endangered largetooth sawfish (*Pristis pristis* (Linnaeus 1758)), suggested a decline in this elasmobranch species may lead to a concomitant decline in a similarly host-specific parasitic copepod (Morgan *et al.* 2010). Parasites are poorly represented on the IUCN Red List of Threatened Species despite many being threatened or co-threatened with their hosts (see Morgan *et al.* 2010; Kwak *et al.* 2020). Considering that whale sharks are globally listed as endangered (Pierce and Norman 2016), it may be prudent to similarly recognise the whale shark copepod as endangered. This highlights the need for symbiotic relationships to be considered in conservation planning to ensure the maintenance of healthy ecosystems (Lymbery *et al.* 2020).

Conclusion

Through their symbiosis with whale sharks, echeneids gain one food source from the host's parasites and energetically-free transportation to areas where they can forage on another food source (Video S1). These findings suggest that while the whale shark copepod may be considered a commensal, mutualistic or parasitic species, the relationship between whale sharks and echeneids is most accurately described as mutualism. The symbiotic relationships and host-specificity of animals must be considered to ensure the conservation of all members in symbiotic relationships, rather than just the host species.

These observations present new perspectives about a three-way symbiosis revolving around whale-sharks, although the data are limited to a specific site and a small number of observations. The lack of data on these interactions is because opportunities to observe whale sharks feeding at night are limited. Nevertheless, more data are needed to determine how widespread and frequent these occurrences may be, and we encourage those observing such interactions to record and document them.

Conflict of interest

The authors declare no conflicts of interest.

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