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A hitchhiker's guide to manta rays – Patterns of association between *Mobula alfredi* and *M. birostris* and their symbionts in the Maldives

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A hitchhiker's guide to manta rays - Patterns of association between *Mobula alfredi* and *M. birostris* and their symbionts in the Maldives.

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By

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Word Count: 4000

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Abstract

Despite comprising some of the largest species in the marine environment, manta rays (*Mobula alfredi, M. birostris*) remain among the most enigmatic. Considerable knowledge gaps remain, particularly regarding their behavioural ecology. Manta rays are often sighted with an array of smaller hitchhiker species, which utilise their hosts as a sanctuary for the shelter, protection, and sustenance they provide. Research into the well-known remora hitchhiking species within the Echeneidae family and their diverse host species has revealed insights into manta ray behavioural and spatial ecology. However, the underlying patterns between manta rays and all of their hitchhiker species remain elusive. This study aims to explore these patterns of association between manta rays with all of their associated hitchhiker species in the Maldives. Utilising long-term photographic data, collected by the Manta Trust's Maldivian Manta Ray Project, the factors influencing the presence of hitchhiker species such as manta ray sex and behaviour, as well as spatiotemporal factors, were analysed. Here for the first time, associations between *M. alfredi* and *M. birostris* with hitchhiker species other than those belonging to the family Echeneidae are described. A variation in the species of hitchhiker associated with *M. alfredi* and *M. birostris* was identified, with the sharksucker remora (*Echeneis naucrates*) and giant remora (*Remora remora*) being the most common respectively. The odds for hitchhiker species presence varied with the different explanatory variables. The presence of sharksucker remoras exhibited a marked seasonal variation, possibly influenced by the behavioural activity and spatiotemporal variation of *M. alfredi*. Biological associations are often one of the first components of biodiversity to be altered by

abiotic change. Given the widespread effects that anthropogenic activities are having on the world's oceans, a greater understanding of the symbiotic interactions of manta rays is essential.

Key words used in this report include:

Manta ray

Symbiosis

Maldives

Hitchhiker

Remora

Introduction

Life in the ocean is bountiful; reflected not only by the sheer number of species but also the diversity of biotic interactions in which different species can engage [1,2]. Symbiosis, when considered in its most broad sense, describes different species living together [3]. Symbiotic interactions are numerable in marine ecosystems and are fundamental in regulating the distribution, abundance and diversity of species [4,5]. Algae-coral and cleaner-client mutualisms provide traditional textbook examples [6]. However, the competitive life as a marine species may also encourage long-term or temporary associations in order to gain food or protection [2,7]. Nevertheless, our understanding of such in marine megafauna remains limited due to the logistical challenges associated with studying complex associations in mobile organisms over large spatial scales [8].

Manta rays (*Mobula alfredi, M. birostris*) are large, filter-feeding batoid rays, with a pelagic existence and circumglobal distribution in tropical and subtropical waters [9-11]. They are characteristically slow to mature, have low fecundity, and exhibit migratory and aggregatory behaviours, rendering them significantly vulnerable to exploitation [9,11]. Consequently, both species are classified as vulnerable on the IUCN Red List of Endangered Species [12,13] - in large part due to targeted fisheries and bycatch [14-16]. Their successful conservation depends upon bridging knowledge gaps regarding their biology and ecology [17,18].

The Maldives is home to a globally significant subpopulation of both species of manta ray [11]. Here, previous research has identified associations between *M. alfredi* and the sharksucker remora (*Echeneis naucrates*) [19,20]. The sharksucker is a neritic species and is physiologically unable to remain attached to their host when they dive at depth to forage on zooplankton. Consequently, sharksucker remoras spend periods of time free-swimming in suitably warm and shallow reef environments and will re-associate with a manta ray upon their return [21-23]. Large female and heavily pregnant manta rays have been shown to host a greater number of sharksucker remoras [20,23]. Drapella [20], hypothesised that this was most likely due to particular species of elasmobranchs residing in shallower depths at near-term pregnancy, where the warmer water temperature aids thermoregulation and reduces the gestation period [24]. Therefore, there is an increasing likelihood that sharksuckers will associate with individuals spending more time in a shallow reef habitat [20,23].

Symbionts associated with a given host should be reflective of the characteristic assemblage of species that occupy the environment where the host spends time [8]. Thus, the study of symbiosis provides an opportunity to unveil population-wide and long-term patterns into the spatial and behavioural ecology of marine fauna [5,8]. Manta rays are often observed with a following of other species such as the golden trevally (*Gnathanodon speciosus*), which also utilise these hosts for protection and sustenance [23]. However, information regarding manta ray interactions, the presence of hitchhikers and patterns relating to the time of year, sex or other explanatory variables remains scarce [25].

The links between interspecific interactions are sensitive to the abiotic environment in which they occur [5]. Considering the widespread effects that anthropogenic activities are already having on marine habitats, a concerted effort to increase our understanding of symbiosis is essential [26,27]. The current study aimed to explore the patterns of association between manta rays and all of their associated hitchhiker species in the Maldives and thereby suggest potential factors that make manta rays more likely to acquire hitchhikers. The presence of a hitchhiker was analysed as a function of manta ray species, sex, maturity status, pregnancy status, behavioural activity, as well as spatiotemporal factors (the ‘explanatory variables’). Such analysis could highlight how these symbiotic interactions are structured, their underlying generative processes, and provide valuable ecological insight [2].

It was hypothesised that (i) there would be a difference in the hitchhiker species associated most commonly with each of the two manta ray species; (ii) there would be a difference between the explanatory variables tested and the presence of hitchhikers; (iii) the presence of a hitchhiker species would stay relatively constant throughout the study period; and (iv) the presence of hitchhikers would exhibit some degree of variation between the time of year (i.e. seasonal variation).

Materials and methods

Data acquisition

Since 2005, the Maldivian Manta Ray Project (MMRP), the founding project of the Manta Trust, has contributed significantly to advances in mobulid research and has developed an extensive sighting database for *M. alfredi* and *M. birostris* [28]. The current study utilised photographic data ranging from 1993 to 2018, including over 120,000 images of over 64,000 sightings of 4662 individual *M. alfredi* and 388 sightings of 378 individual *M. birostris.*

Study area

The Maldives archipelago is a nation consisting of 26 coral atolls and 1,992 islands situated in the northern Indian Ocean (Fig 1) [29].

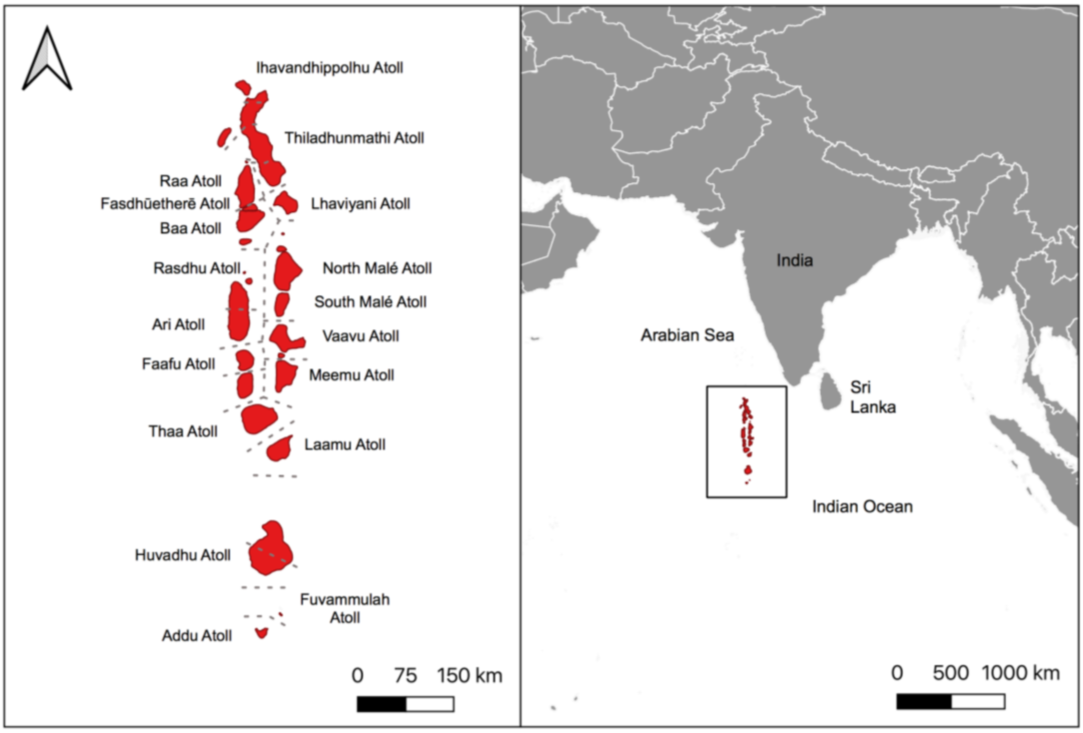

Fig 1. A map of the Maldives archipelago located to the south west of India. Diagram includes atolls to indicate locations of manta ray sightings (created using QGIS 3.8.2).

Due to the geographic location of the Maldives, the archipelago experiences distinct seasons in its oceanographic environment [29]. The biannual reversal of winds and accompanying ocean currents result in an SW monsoon season (May-October) and a NE monsoon (December-March). November and April are considered months of seasonal transition [30]. Evidence has shown that in the Maldives *M. alfredi* exhibit a biannual migration, travelling east-west during the NE monsoon and west-east during the SW monsoon. Such a marked variation determines changes in the aggregation sites, as well as the predominant behavioural activity exhibited by *M. alfredi* (Fig 2) [30,31].

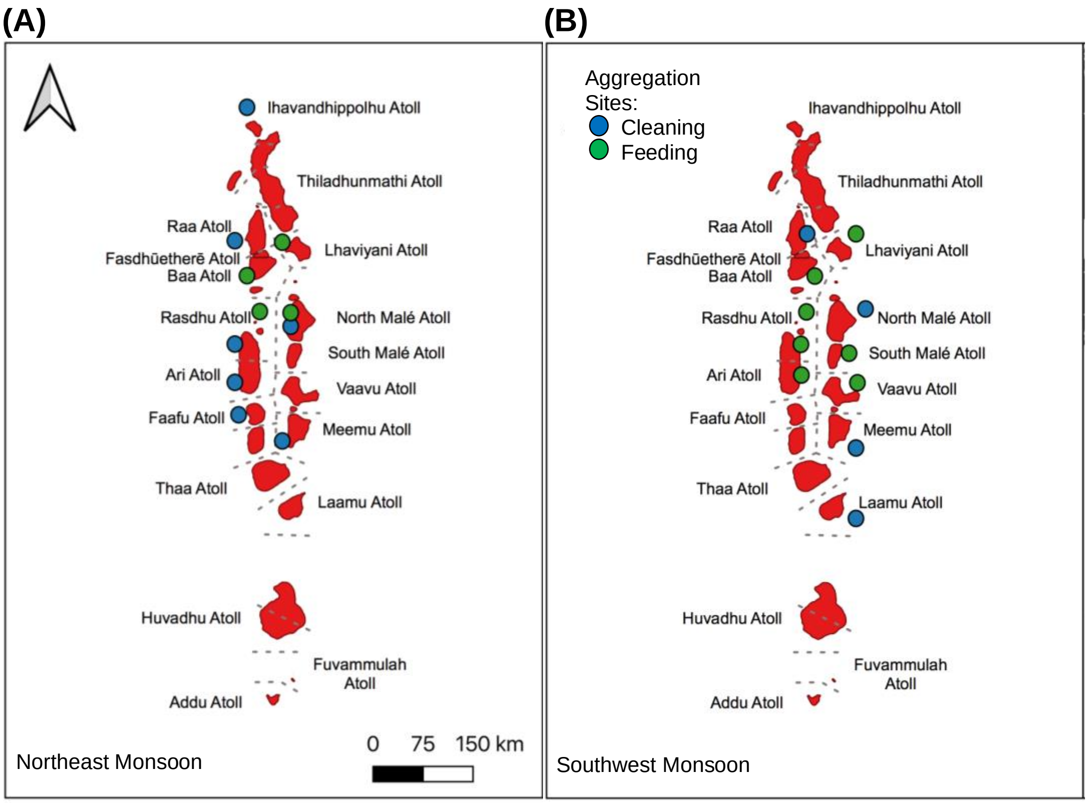

Fig 2. A map of the Maldives archipelago with seasonal *M. alfredi* cleaning and feeding aggregation sites. The atolls are categorised into the predominant behavioural activity exhibited by *M. alfredi* in the NE and SW monsoon season. Cleaning sites provide areas of several benefits such as parasite removal, social and reproductive interactions. Feeding sites provide locations of concentrated food source [11,32].

Manta rays

Manta ray sightings (images of manta ventral surfaces, date, time and location) are logged year-round by trained observers and citizen science contributors to a photo-ID database. The variation in their unique ventral body pigmentation enables individuals to be distinguished from an existing ID catalogue. Species were identified as either *Mobula alfredi* (reef manta ray) or *M. birostris* (oceanic manta ray). Further information recorded for each sighting included gender, maturity status (adult, subadult, juvenile), pregnancy status (heavily pregnant, pregnant, not pregnant), behavioural activity (cleaning, feeding, courtship, cruising (just swimming), breaching, deceased) and any external injuries. This methodology is consistent with Stevens [10] and Marshall and Bennet [33]. Individual mantas whose gender was unknown were removed from the analysis.

Identification of hitchhiker species

The images were visually analysed for the presence of hitchhiker species. Identification was determined using existing photographs (Fig 3) and fish identification books [33]. For each sighting, a hitchhiker species was recorded as either present (1) if one or more individuals were observed in the image/images or absent (0) if none were observed (S1 Appendix, Table 1 and 2). The quality, angle and distance of images varied, which sometimes made hitchhikers unidentifiable - these were not included in the data. Echeneid species that were too small to be identified confidently were classified as juvenile remoras.

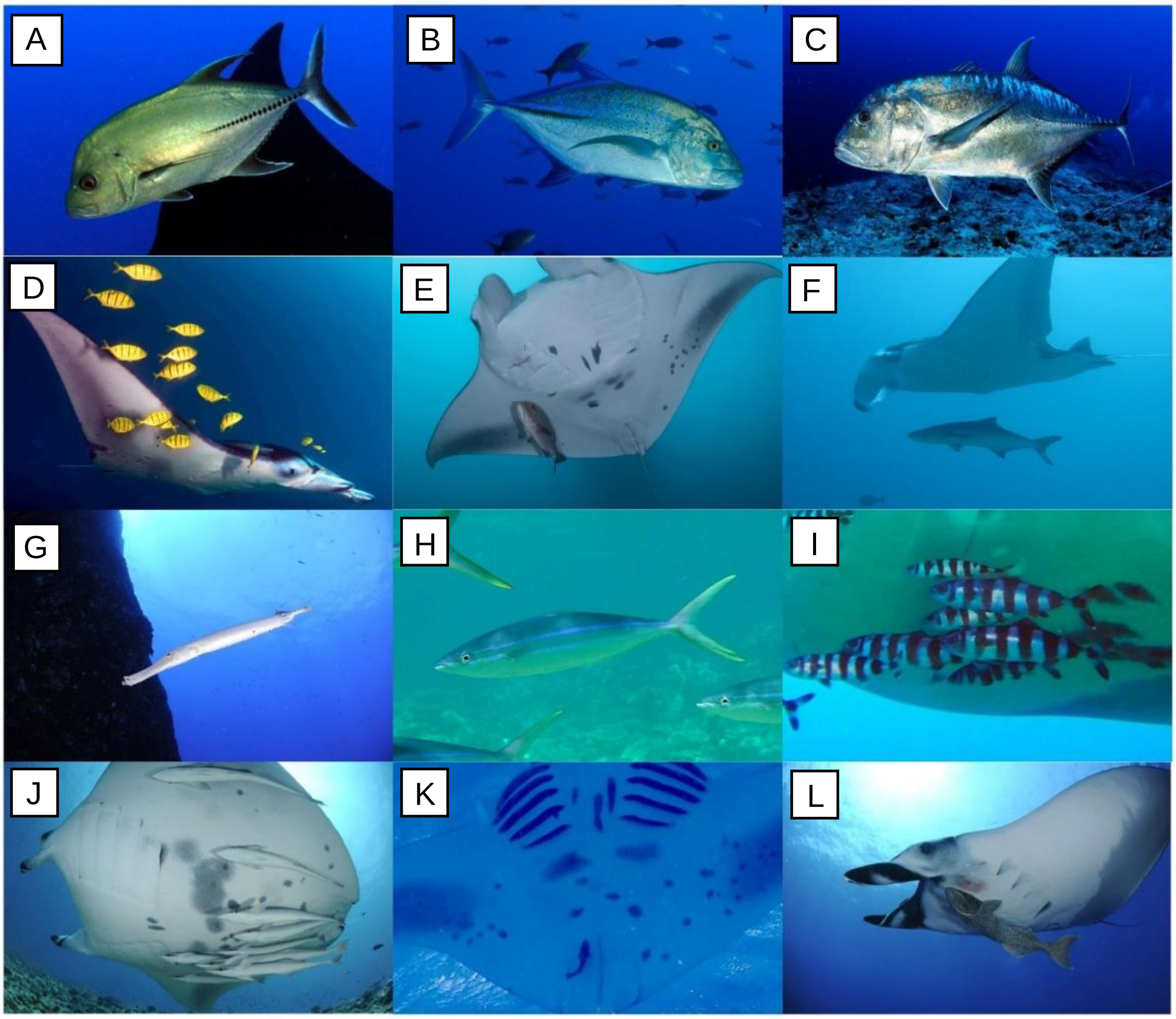

Fig 3. Example images of hitchhiker species used for identification. (A) Black Trevally *Caranx lugubris,* (B) Bluefin Trevally *Caranx melampygus*, (C) Giant Trevally *Caranx ignobilis,* (D) Golden Trevally *Gnathanodon speciousus,* (E) Red Snapper *Lutjanus bohar,* (F) Cobia *Rachycentrol canadum,* (G) Chinese Trumpetfish *Aulostomus chinessis,* (H) Rainbow Runner *Elagatis bipinnulata,* (I) Pilot Fish *Naucrates doctor,* (J) Sharksucker Remora *Echeneis naucrates,* (K) Little Remora *Remora albescens,* and (L) Giant Remora *Remora remora.* (The Manta Trust).

Data Analysis

Including the temporal variable (date) as a fixed effect in the modelling procedure would have created a highly complex model. Thus, the temporal variation in hitchhiker presence between 2014-2018 was investigated separately as an observed time series for exploratory analysis. 2014-2018 represented the time period with the greatest number of sightings, as well as providing a suitable period from which to visualise trends (i.e. seasonality).

Model Selection

A logistic mixed effects model was used to investigate potential relationships between a binary outcome variable, i.e. the presence of a hitchhiker species with a group of explanatory variables such as manta ray gender. The model contained a random intercept to account for the correlation arising from individual mantas being repeatedly observed. To compare the goodness-of-fit, a GLMM model without random effects was tested. To ensure sufficient credibility to reliably estimate the parameters, categories of variables with cell counts below five were combined or removed such as injury type and breaching behaviour. The category ‘fresh mating wound’ from the pregnancy status variable was not included, since it was not possible to determine pregnancy status. The full model included the explanatory variables: manta ray gender, maturity status, pregnancy status, behavioural activity and sub-region (location of sighting).

The Akaike information criterion (AIC) was used for the model selection procedure to determine the most important variables to include in the model. A lower AIC between two candidate models implies an improved fit to the data. The model was run separately for each of the hitchhiker species, and all of the variable combinations were tested (S2 Appendix, Tables 1-5). Next, the parameters (explanatory variables) with the lowest AIC were interpreted on the log odds scale (exp(parameter)) to obtain odds ratio values. The significance of each parameter was determined by whether the 95% confidence interval (CI) crossed one (non-significant). A narrow CI indicated that the estimate was known more precisely, in comparison to a wider CI which had a greater uncertainty.

The analysis was performed using RStudio version 1.3.1056 [35].

Results

Eleven different species of hitchhiker were identified with *M. alfredi* and five species with *M. birostris* (Fig 4). The results showed very few counts of certain species. Therefore, the analysis was conducted on the those with sufficient data, which included the golden trevally, red snapper, sharksucker remora, and juvenile remora for *M. alfredi,* as well as the giant remora for *M. birostris.*

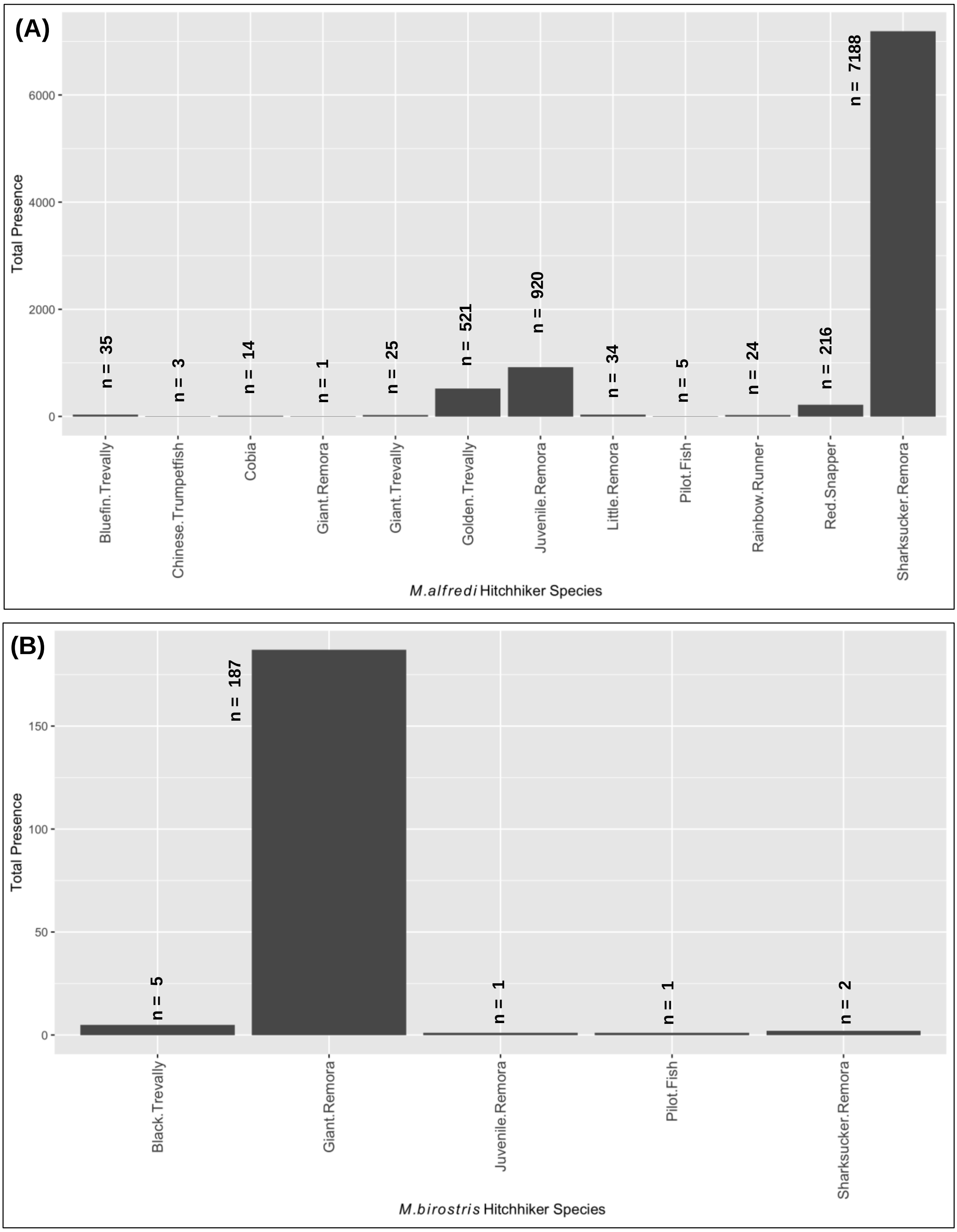

Fig 4. The total presence of the identified hitchhiker species. (A) *M. alfredi* and (B) *M. birostris* hitchhiker species. n = the total number (presence) recorded.

Temporal variation in the presence of hitchhikers

The proportion of *M. alfredi* encounters with a sharksucker remora present was higher than those with a golden trevally, red snapper and juvenile remora throughout 2014-2018 (Fig 5). Golden trevally, red snapper and juvenile remora made up a more comparable proportion of *M. alfredi* sightings, with a small degree of volatility.

The distinct monsoonal seasons result in a variation in survey effort (number of manta excursions/interactions) [11], which is depicted in Fig 5C. In 2018, the year with the greatest overall number of *M. alfredi* sightings (n=9209), 27.2% (n=2504) of the sightings occurred in the NE monsoon season and 72.8% (n=6705) in the SW monsoon. Despite this variation, the proportion of sharksucker remora presence is greatest within the beginning months (January-April) of the year. In 2018, sharksucker remoras were present 1224 times, with 58.7% (n=719) observed in the NE monsoon and 41.3% (n=505) in the SW monsoon.

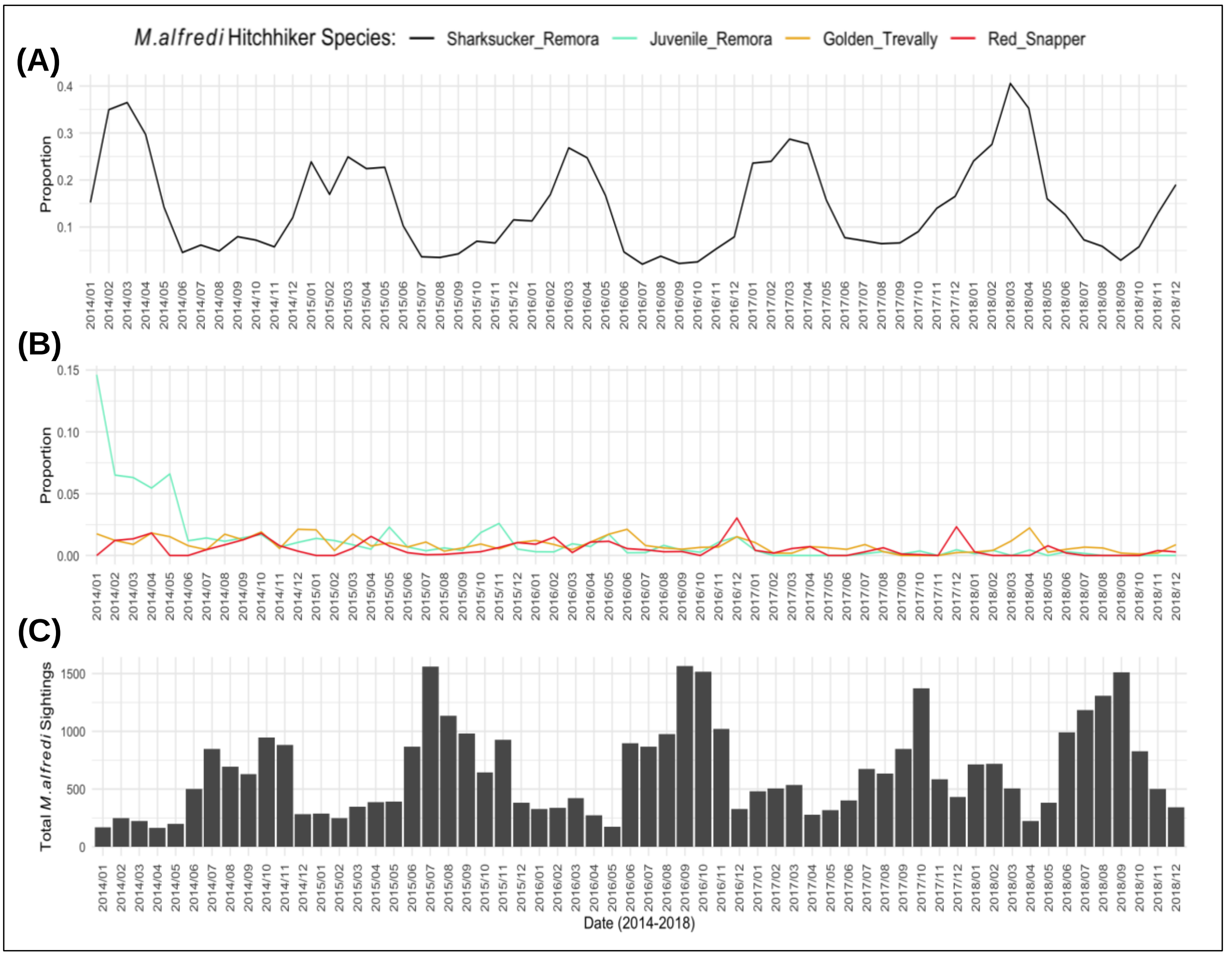

Fig 5. Observed time series plot for *M. alfredi* hitchhiker species and sightings per-month from 2014-2018. (A) sharksucker remora and (B) golden trevally, red snapper and juvenile remora, shown as a proportion of (C) the total number of *M. alfredi* sightings.

The proportion of *M. birostris* sightings with a giant remora present was highly volatile throughout the study period, with no *M. birostris* sightings occurring in a number of months (Fig 6). The greatest number of *M. birostris* sightings occurred in March-April 2014 and 2018.

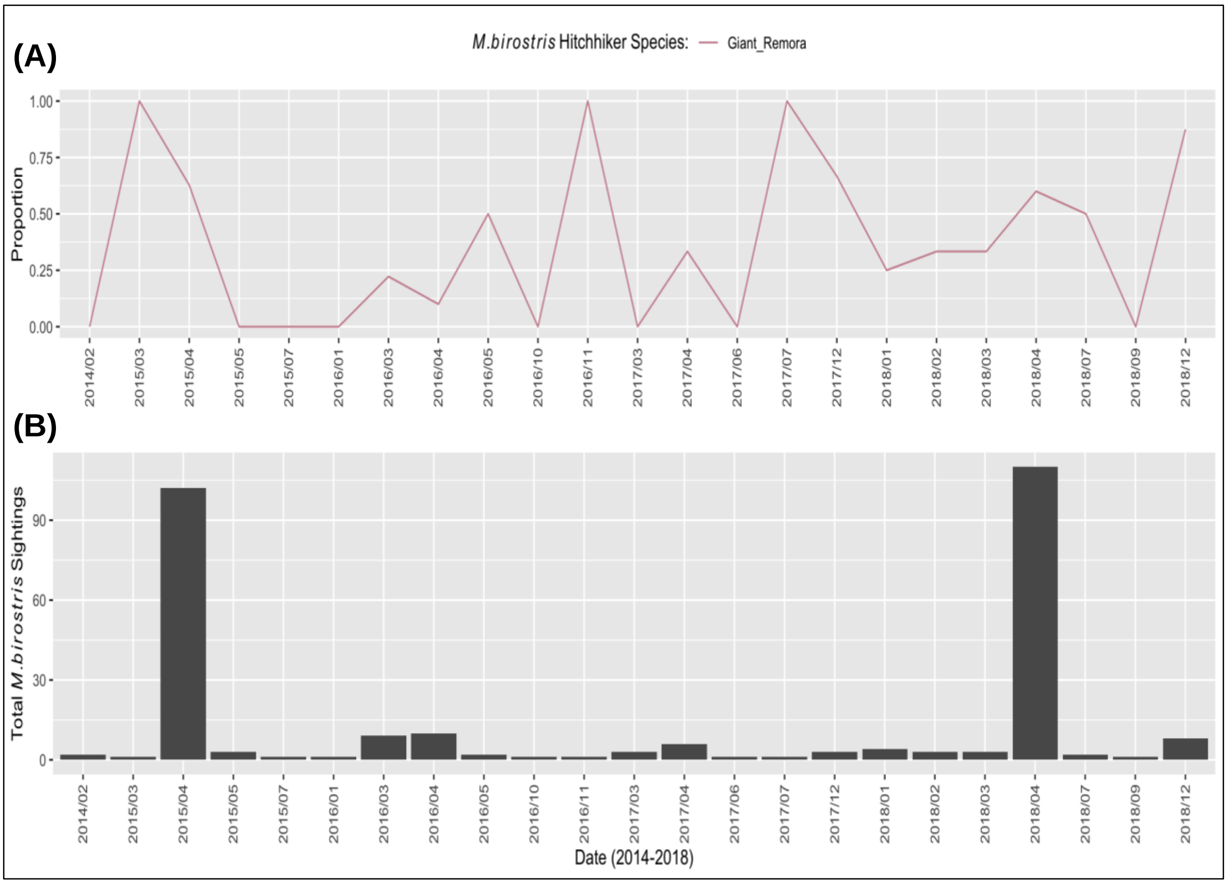

Fig 6. Observed time series plot for *M. birostris* hitchhiker species and sightings per-month from 2014-2018. (A) the giant remora shown as a proportion of (B) the total number of *M. birostris* sightings.

Patterns hitchhiker presence and explanatory variables

The odds ratio values obtained for the each of the explanatory variables and hitchhiker species are presented in Table 1. Only the results that were statistically significant at the 5% significance level are discussed.

Table 1. The parameter estimates (odds ratios, 95% CI, p-value) representing the associations between the presence of a hitchhiker species and the explanatory variables. Variables correspond to each chosen model. Empty cells represent the baseline category. The statistically significant results are shaded.

Explanatory Variable	Total hitchhiker count (n)	Estimate (exp)	Lower 95% CI	Upper 95% CI	p-value
Mobula alfredi					
Golden trevally					
Maturity Status - Adult	329				
Maturity Status - Juvenile	184	1.57	1.23	2.00	<0.001
Maturity Status - Subadult	6	0.76	0.31	1.83	>0.05
Behavioural Activity - Feeding	261				
Behavioural Activity - Cleaning	230	1.38	1.12	1.70	<0.001
Behavioural Activity - Courtship	7	1.09	0.50	2.36	>0.05
Behavioural Activity - Cruising	21	1.53	0.95	2.46	>0.05
Red Snapper					
Behavioural Activity - Cleaning	193				
Behavioural Activity - Courtship	5	0.42	0.15	1.18	>0.05
Behavioural Activity - Cruising	17	1.16	0.68	1.97	>0.05
Sharksucker Remora					
Gender - Female	5035				
Gender - Male	2112	0.59	0.51	0.67	<0.001
Maturity Status - Adult	5580				
Maturity Status - Juvenile	1438	0.72	0.62	0.84	<0.001

Explanatory Variable	Total hitchhiker count (n)	Estimate (exp)	Lower 95% CI	Upper 95% CI	p-value
Maturity Status - Subadult	129	1.02	0.70	1.49	>0.05
Pregnancy - Pregnant	283				
Pregnancy - Heavily Pregnant	332	1.75	1.35	2.26	<0.001
Pregnancy - No	6532	0.55	0.46	0.66	<0.001
Behavioural Activity - Cleaning	4398				
Behavioural Activity - Courtship	250	2.04	1.69	2.46	<0.05
Behavioural Activity - Cruising	222	1.21	1.02	1.43	<0.001
Behavioural Activity - Feeding	2276	0.63	0.58	0.68	<0.001
Sub-Region - North Malé Atoll	2300				
Sub-Region - Addu Atoll	120	0.76	0.59	0.96	<0.05
Sub-Region - Ari Atoll	1797	0.70	0.64	0.77	<0.001
Sub-Region - Baa Atoll	1720	0.32	0.29	0.35	<0.001
Sub-Region - Faafu Atoll	26	0.78	0.46	1.30	>0.05
Sub-Region - Fasdhūtherē Atoll	61	0.55	0.40	0.76	<0.001
Sub-Region - Ivandhippolhu	12	0.82	0.39	1.72	>0.05
Sub-Region - Laamu Atoll	399	0.55	0.48	0.63	<0.001
Sub-Region - Lhaviyani Atoll	259	0.63	0.53	0.75	<0.001
Sub-Region - Meemu Atoll	85	0.78	0.58	1.04	>0.05
Sub-Region - Raa Atoll	151	0.57	0.46	0.70	<0.001
Sub-Region - Rasdhu Atoll	106	0.78	0.60	1.01	>0.05
Sub-Region - South Malé Atoll	31	0.49	0.32	0.76	<0.001

Explanatory Variable	Total hitchhiker count (n)	Estimate (exp)	Lower 95% CI	Upper 95% CI	p-value
Sub-Region - Thiladhunmathi Atoll	54	0.51	0.37	0.71	<0.001
Sub-Region - Vaavu Atoll	13	0.36	0.20	0.66	<0.001
Juvenile Remora					
Gender - Female	528				
Gender - Male	389	1.34	1.02	1.72	<0.05
Maturity Status - Adult	550				
Maturity Status - Juvenile	341	1.95	1.47	2.59	<0.001
Maturity Status - Subadult	26	1.71	0.92	3.19	>0.05
Behavioural Activity - Cleaning	206				
Behavioural Activity - Courtship	10	1.35	0.70	2.61	>0.05
Behavioural Activity - Cruising	28	2.04	1.31	3.18	<0.001
Behavioural Activity - Feeding	673	2.32	1.86	2.90	<0.001
Sub-Region - Addu Atoll	19				
Sub-Region - Ari Atoll	160	0.48	0.29	0.81	0.01
Sub-Region - Baa Atoll	399	0.33	0.20	0.54	<0.001
Sub-Region - Fasdhūtherē Atoll	33	0.76	0.39	1.50	>0.05
Sub-Region - Laamu Atoll	30	0.29	0.16	0.54	<0.001
Sub-Region - Lhaviyani Atoll	77	1.22	0.70	2.12	>0.05
Sub-Region - Meemu Atoll	7	0.67	0.28	1.64	>0.05
Sub-Region - North Malé Atoll	162	0.72	0.43	1.21	>0.05
Sub-Region - Raa Atoll	6	0.25	0.10	0.62	<0.001

Explanatory Variable	Total hitchhiker count (n)	Estimate (exp)	Lower 95% CI	Upper 95% CI	p-value
Sub-Region - South Malé Atoll	9	0.68	0.27	1.71	>0.05
Mobula birostris					
Giant Remora					
Gender - Female	114				
Gender - Male	64	0.47	0.28	0.81	<0.01
Maturity Status - Adult	126				
Maturity Status - Juvenile	34	0.79	0.40	1.54	>0.05
Maturity Status - Subadult	18	0.42	0.19	0.91	<0.01
Behavioural Activity - Cruising	169				
Behavioural Activity - Courtship	9	0.62	0.22	1.71	>0.05
Sub-Region - Fuvahmulah	172				
Sub-Region - Addu Atoll	6	0.21	0.07	0.65	<0.001

Golden Trevally

The odds of a golden trevally being present when a juvenile manta ray is observed is 1.57 times that of an adult manta ray (95% CI 1.23 and 2.00). The odds of a golden trevally being present when a manta ray exhibiting cleaning behaviour is observed is 1.38 times that of a feeding manta ray (95% CL 1.12 and 1.70) (Table 1).

Sharksucker Remora

The odds of a sharksucker remora being present when a male manta ray is observed is 0.59 times that of a female, and the odds of a juvenile manta ray having a sharksucker remora present is 0.72 times that of an adult. The odds of a sharksucker remora being present when a non-pregnant manta is observed is 0.55 times the case where a pregnant manta is observed. Moreover, the odds of observing a sharksucker remora with a heavily pregnant manta has estimated odds of 1.75 that of a pregnant manta. The odds of a manta ray exhibiting feeding behaviour is 0.63 times lower than that of cleaning behaviour, whereas courtship behaviour had 2.04 times higher odds for sharksucker remora presence than that of cleaning behaviour. North Malé Atoll, Ari Atoll and Baa Atoll had the greatest total counts (n) for sharksucker remora presence. The estimated odds of a sharksucker remora being present when a manta is observed at North Malé Atoll was greater than the other sub-regions.

Juvenile Remora

In contrast to the sharksucker remora, the odds of a juvenile remora being present when a male manta ray is observed is 1.34 times that of a female. The odds of a juvenile manta ray having a juvenile remora present is 1.95 that of an adult manta ray. The odds of a juvenile remora being present when a manta ray is observed exhibiting cruising and feeding behaviour is 2.04 and 2.32 times that of a manta ray cleaning respectively. The estimated odds of a juvenile remora being present when a manta is observed at Addu Atoll was greater than the other sub-regions.

Giant Remora

The odds of a giant remora being present when a male *M. birostris* is observed is 0.47 times that of a female. The majority of the oceanic manta ray sightings were recorded at Fuvahmulah Atoll (n=172) and were exhibiting cruising behaviour (n=169).

Discussion

Here for the first time, associations between *M. alfredi* and *M. birostris* with hitchhiker species other than those belonging to the family Echeneidae were described. In line with the original hypotheses (i) a difference in the hitchhiker species associated most commonly with each of the two manta ray species was identified; (ii) the explanatory variables had varying impacts on the presence of different hitchhiker species; (iii) the presence of hitchhiker species stayed relatively constant throughout the analysed time period (2014-2018) with some degree of volatility; and (iv) the presence of sharksucker remoras exhibited a clear seasonal variation.

Mobula alfredi

The range of hitchhiker species identified in association with *M. alfredi* and *M. birostris* illustrate how the company you keep can act as an important life-history strategy. By associating with larger-bodied species, certain symbionts engage in a relationship evident of commensalism, gaining protection from predation and enhanced foraging opportunities [2,25,36]. Species of the family Carangidae have been observed to associate with scalloped hammerheads (*Sphyrna lewini*) to get closer to prey items. When following cownose rays, the cobia (*Rachycentron canadum*) has been observed to occupy a position above the ray to forage on rejected prey [37]. Thus, follower-feeding associations may be at the root of certain interactions observed within this study. Additionally, Stevens *et al.* [23] described the golden trevally to utilise the shelter of a manta ray host until they are mature enough to survive by themselves and seek the protection of shoals.

Relatively few works in the literature have explored the hitchhikers identified, particularly the non-echeneid species. Still, little is known regarding the ecology of echeneids, particularly in the Maldives. Generally, obligate symbiosis of juvenile echeneids is known to become a facultative relationship for adult remoras [21]. Juvenile manta rays are known to spend the majority of their time in shallow water such as protected lagoons and spend less time visiting cleaning stations [23,38]. The more time spent within a shallower habitat, the greater chance there is of associating with reef-dwelling hitchhikers [20]. Thus, juvenile manta rays may provide a more suitable host for the juvenile remora, as well as the golden trevally [39] that require continued protection in comparison to adult manta rays who may dive at depth more frequently [22].

The patterns of association identified for the golden trevally and juvenile remora could have been influenced by their relatively low sample size. No significant pattern for red snapper presence was identified, which is likely due to a lack of data. It was noted that the sightings images were focused on the ventral surface (in order to get a suitable ID shot), but species such as the golden trevally often reside in the mouth or on the dorsal surface. Therefore, it is likely that the total number of hitchhikers was underestimated. Further research in different manta populations where the presence of these species is greater is necessary to understand these associations more completely. Additionally, further research of the hitchhiker species that were initially identified in the study (Fig 4) but did not have sufficient data for the analysis warrant investigation.

As of yet, no seasonal trends in sharksucker remora presence have been documented at any other geographic location. The higher proportion of sharksucker remoras in the NE monsoon suggests that occurrences within this period are influential on the hitchhikers observed. The alternating currents of the seasonal monsoons subsequently fluctuate the promotion of nutrient-rich upwellings (increased chlorophyll-α), supporting zooplankton biomass, and providing a food source for planktivores [23,30]. The longer duration of the SW monsoon provides a period of enhanced primary productivity. In contrast, the NE monsoon can experience suppressed primary productivity as a result of low-salinity surface water inflow from the eastern Indian Ocean. These fluctuations result in a predictably rhythmic environment, which manta rays exploit adaptively (Fig 2) [30,31].

Ari Atoll is situated on the west side of the archipelago. It is known for its cleaning aggregation sites, as well as higher abundances of *M. alfredi* throughout the NE monsoon (Fig 2). Despite seasonal survey effort, Ari Atoll had the second-highest total count of manta ray sightings with a sharksucker remora present. In the Maldives, cleaning sites are predominantly located within shallow coral reefs and have been suggested to also act as locations for behavioural thermoregulation, as well as predator avoidance [23]. Greater abundances of not only manta rays but also large skipjack and yellow tuna have been observed in the less productive NE monsoon [30]. This led Anderson *et al.* [30] to suggest that there may be an increase in primary productivity associated with a deep chlorophyll maximum (DCM) that is not visible to satellite technology (SeaWiFS). Manta rays are poikilothermic with an optimal thermal temperature of 20-26℃ but are able to endure colder temperatures for short periods due to a counter-current heat-exchange mechanism. This physiological adaption enables manta rays to forage on zooplankton blooms within the deep scattering layer at depths of over 672 metres and temperatures of 7.6℃ [40]. Thus, basking in warmer shallow waters such as cleaning stations prior to and post deep forays enables manta rays to physiologically prepare for and recover from the large metabolic costs incurred from deep foraging bouts [23,40]. Behavioural thermoregulation has also been used to explain why the spine-tail devil ray (*Mobula japanica*), the whale shark (*Rhincodon typus*) and various tuna species return to shallow habitats after deep dives [41-43]. To support this hypothesis, more data on the depth profiles of manta ray dives utilising satellite tracking technologies specifically at locations in the Maldives is required, along with chlorophyll-α measurements.

It should be noted that there was a bias in sighting seasonality and survey effort at specific sites. Baa atoll is known for its feeding aggregation sites such as the Hanifaru Bay Marine Protected Area (MPA). In the SW season, Hanifaru Bay is surveyed most frequently [23]. Despite this, the atoll had significantly lower odds for sharksucker remora presence in comparison to North Malé Atoll. North Malé Atoll is situated on the east side of the archipelago. It is also known for its cleaning aggregation sites, as well as higher abundances of *M. alfredi* throughout the SW monsoon (Fig 2). However, the longer duration of the SW monsoon could have been influential in the result.

Furthermore, studies have demonstrated that female manta rays are significantly more likely to be sighted at cleaning stations than males [10]. Sex-specific site selection is reflected in the result that female manta rays have greater odds for an association with sharksucker remoras than males. Cleaning sites are utilised as locations for social interactions (i.e. courtship displays), which could explain the result that *M. alfredi* exhibiting courtship behaviour had greater odds for sharksucker remora presence than cleaning behaviour [23].

Considering the ecology of both the host and the symbiont, the results illustrate that the pattern of association between sharksucker remoras and *M. alfredi* is, in part, determined by behavioural activity, which is in turn driven by the spatiotemporal variation in manta ray presence. Therefore, the overlap in habitat-use of cleaning sites provides a potential explanation for why female, cleaning, courting and pregnant manta rays have a greater association with sharksucker remoras. Based upon the current findings, and to rule out any bias that may result from seasonal survey effort, the presence of hitchhiker species in the NE and SW monsoon need to be investigated separately. In particular, the focus should be within specific sub-regions (more specifically at site level) to tease apart the associations.

Mobula birostris

Unlike the relationship between *M. alfredi* and the sharksucker remora, the association between *M. birostris* and the giant remora is highly specific, with the remora rarely leaving the protection of its host [25]. The majority of sightings are restricted to Fuvahmulah Atoll between March-April, with individuals primarily cruising through this site. Here, most of the individuals are only observed once, suggesting that the population is transient rather than utilising it for a particular behavioural activity [44]. This creates challenges in identifying a pattern of association between the giant remora and the behaviour of *M. birostris.* However, the distinct variation in sex ratio with a greater population of females suggests that their movements may be linked to reproduction or differences in foraging strategies between the sexes. Nothing is known about where *M. birostris* travel to when they leave these atolls, but future findings could reveal valuable insights into the observed presence of the giant remora [44]. Becerril-García *et al.* [25] used photographs of *M. birostris* in the Gulf of Mexico to investigate the association with the total number of giant remoras. No significant difference was identified between the number of remoras and manta ray sex, morphotype and month. As this study investigated the total number of remoras and was conducted for only one year, it is difficult to draw comparisons between the results. However, the author did infer that the presence of remoras could be influenced by the level of ectoparasites, host population size, diving behaviour and surrounding environmental conditions. Therefore, investigations into these factors could identify patterns of association, and ultimately reveal further insight into the ecology and activities of these animals.

Despite biological associations often being one of the first components of biodiversity to be altered by abiotic change, the associations between interacting species are often overlooked in regard to our changing world [5,45,46]. Disconcertingly, climatic change in the Maldives is becoming increasingly apparent, with weakening SW monsoon winds, rising sea surface temperatures and a 20% phytoplankton decrease in the past 60 years [10,47]. This is an important consideration since the presence and abundance of *M. alfredi* is driven by the availability of phytoplankton, and that the fitness benefits and degree of dependency between hitchhikers and manta rays remain unknown [10,30]. Research has already identified the potential for a reduction in the stability and pervasiveness of cleaner-client interactions under environmental change [48]. Thus, it begs the question of how stable hitchhiker associations will be under fluctuating environmental conditions [49]. Hitchhiker species may potentially act as an indicator species, reflecting the health of the manta ray population and providing warning signals of potential ecological shifts [50]. Therefore, an enhanced effort to document and understand these symbiotic interactions is critical.

Conclusion

Manta rays provide a midwater habitat for a broad range of species that require the protection and sustenance these hosts afford [20,23,25]. Until now, these interactions have remained undocumented or briefly addressed in the literature. The exact mechanisms driving the patterns of associations observed are beyond the scope of this study. However, the findings could serve as a basis for a deeper understanding of the symbiotic relationships of manta rays and ultimately impact the ecological knowledge of both the host and the symbiont.

The periodic changes in the environment, which determine the rhythmic movements and behaviours of manta rays in the Maldives, potentially affect crucial symbiotic interactions [49]. Given the rapid pace at which anthropogenic activities are altering oceans worldwide, significant effort should be aimed at understanding these interactions [5,45,46]. Further research of hitchhikers in different manta ray populations is warranted to evaluate whether the associations and structures found within the Maldives apply to other geographic locations, as well as understanding their generative processes more holistically. While it could be said that these hitchhikers are just along for the ride, they could also play a valuable role in the ecological understanding and conservation of such a valuable and vulnerable species.

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Supporting Information

S1 Appendix

Table 1. A summary of the total *M. alfredi* sightings and the presence of associated hitchhiker species categorised by the explanatory variables.

			Hitchhiker Species							
		Total *M. alfredi* Sightings	Sharksucker Remora		Juvenile Remora		Little Remora		Giant Remora	
Variable	Category		Present	%	Present	%	Present	%	Present	%
	Total	**63977**	**7188**	**11.2**	**920**	**1.4**	**34**	**0.1**	**1**	**0.0**
Gender	Female	38567	5076	13.2	531	1.4	23	0.1	1	0.0
	Male	25410	2112	8.3	389	1.5	11	0.0	0	0.0
Maturity Status	Adult	46040	5621	12.2	553	1.2	21	0.0	1	0.0
	Juvenile	16674	1438	8.6	341	2.0	13	0.1	0	0.0
	Subadult	1263	129	10.2	26	2.1	0	0.0	0	0.0
Pregnancy	Pregnant	1417	283	20.0	3	0.2	2	0.1	0	0.0
	Heavily Pregnant	929	332	35.7	10	1.1	0	0.0	1	0.1
	Fresh Mating Wound	266	41	15.4	3	1.1	0	0.0	0	0.0
	Not Pregnant	61365	6532	10.6	904	1.5	32	0.1	0	0.0
Behavioural Activity	Cleaning	22072	4426	20.1	208	0.9	5	0.0	0	0.0
	Cruising	1510	222	14.7	28	1.9	0	0.0	0	0.0
	Courtship	909	254	27.9	10	1.1	0	0.0	1	0.1
	Feeding	39484	2285	5.8	674	1.7	29	0.1	0	0.0
	Breaching	1	0	0.0	0	0.0	0	0.0	0	0.0
	Deceased	1	1	100.0	0	0.0	0	0.0	0	0.0
Sub-Region	Addu Atoll	655	120	18.3	19	2.9	0	0.0	0	0.0
	Ari Atoll	9570	1813	18.9	161	1.7	7	0.1	0	0.0
	Baa Atoll	36786	1730	4.7	400	1.1	19	0.1	1	0.0
	Dhaalu Atoll	7	0	0.0	0	0.0	0	0.0	0	0.0
	Faafu Atoll	115	26	22.6	4	3.5	0	0.0	0	0.0
	Fasdhūetherē Atoll	798	61	7.6	33	4.1	1	0.1	0	0.0
	Gaafu Atoll	5	1	20.0	0	0.0	0	0.0	0	0.0
	Goidhu Atoll	22	3	13.6	1	4.5	0	0.0	0	0.0
	Ihavandhippolhu Atoll	67	12	17.9	0	0.0	0	0.0	0	0.0
	Laamu Atoll	3403	402	11.8	30	0.9	1	0.0	0	0.0
	Lhaviyani Atoll	1674	261	15.6	77	4.6	1	0.1	0	0.0
	Meemu Atoll	426	86	20.2	7	1.6	0	0.0	0	0.0
	North Malé Atoll	7835	2306	29.4	162	2.1	2	0.0	0	0.0
	Raa Atoll	1133	153	13.5	7	0.6	0	0.0	0	0.0
	Rasdhu Atoll	533	106	19.9	3	0.6	1	0.2	0	0.0
	South Malé Atoll	262	32	12.2	9	3.4	1	0.4	0	0.0
	Thaa Atoll	13	1	7.7	0	0.0	0	0.0	0	0.0

		Thiladhunmathi Atoll	406	54	13.3	2	0.5	1	0.2	0	0.0
		Thoddu Atoll	24	0	0.0	0	0.0	0	0.0	0	0.0
		Vaavu Atoll	210	13	6.2	3	1.4	0	0.0	0	0.0
		Vattaru Atoll	21	4	19.0	2	9.5	0	0.0	0	0.0
		Unkown	12	4	33.3	0	0.0	0	0.0	0	0.0
Injury Type		Boat Strike	24	5	20.8	0	0.0	0	0.0	0	0.0
		Fishing Line/Hook	140	24	17.1	3	2.1	0	0.0	0	0.0
		Net Entanglement	4	0	0.0	0	0.0	0	0.0	0	0.0
		Rope Entanglement	1	0	0.0	0	0.0	0	0.0	0	0.0
		Infection/Disease	6	2	33.3	0	0.0	0	0.0	0	0.0
		Predatory Bite	168	40	23.8	2	1.2	1	0.6	0	0.0
		No Injury	63612	7112	11.2	915	1.4	33	0.1	1	0.0
		Unkown	22	5	22.7	0	0.0	0	0.0	0	0.0

				Hitchhiker Species							
			Total *M. alfredi* Sightings	Golden Trevally		Bluefin Trevally		Red Snapper		Cobia	
Variable				Present	%	Present	%	Present	%	Present	%
		Total	**63977**	**521**	**0.8**	**35**	**0.1**	**216**	**0.3**	**14**	**0.0**
Gender	Category	Female	38567	337	0.9	23	0.1	138	0.4	11	0.0
		Male	25410	184	0.7	12	0.0	78	0.3	3	0.0
Maturity Status		Adult	46040	331	0.7	24	0.1	165	0.4	8	0.0
		Juvenile	16674	184	1.1	11	0.1	47	0.3	6	0.0
		Subadult	1263	6	0.5	0	0.0	4	0.3	0	0.0
Pregnancy		Pregnant	1417	11	0.8	1	0.1	9	0.6	0	0.0
		Heavily Pregnant	929	5	0.5	2	0.2	8	0.9	1	0.1
		Fresh Mating Wound	266	2	0.8	0	0.0	1	0.4	1	0.4
		Not Pregnant	61365	503	0.8	32	0.1	198	0.3	12	0.0
Behavioural Activity		Cleaning	22072	230	1.0	32	0.1	194	0.9	5	0.0
		Cruising	1510	21	1.4	2	0.1	17	1.1	0	0.0
		Courtship	909	7	0.8	0	0.0	5	0.6	0	0.0
		Feeding	39484	263	0.7	1	0.0	0	0.0	9	0.0
		Breaching	1	0	0.0	0	0.0	0	0.0	0	0.0
		Deceased	1	0	0.0	0	0.0	0	0.0	0	0.0
Sub-Region		Addu Atoll	655	2	0.3	2	0.3	6	0.9	0	0.0
		Ari Atoll	9570	88	0.9	17	0.2	43	0.4	4	0.0
		Baa Atoll	36786	285	0.8	4	0.0	78	0.2	7	0.0
		Dhaalu Atoll	7	0	0.0	0	0.0	0	0.0	0	0.0
		Faafu Atoll	115	1	0.9	0	0.0	0	0.0	0	0.0
		Fasdhūetherē Atoll	798	10	1.3	0	0.0	0	0.0	0	0.0
		Gaafu Atoll	5	0	0.0	0	0.0	0	0.0	0	0.0
		Goidhu Atoll	22	0	0.0	0	0.0	1	4.5	0	0.0
		Ihavandhippolhu Atoll	67	1	1.5	0	0.0	0	0.0	0	0.0
		Laamu Atoll	3403	35	1.0	1	0.0	23	0.7	0	0.0

		Lhaviyani Atoll	1674	12	0.7	5	0.3	4	0.2	0	0.0
		Meemu Atoll	426	4	0.9	0	0.0	0	0.0	0	0.0
		North Malé Atoll	7835	59	0.8	5	0.1	51	0.7	2	0.0
		Raa Atoll	1133	8	0.7	0	0.0	7	0.6	0	0.0
		Rasdhu Atoll	533	2	0.4	1	0.2	2	0.4	1	0.2
		South Malé Atoll	262	1	0.4	0	0.0	1	0.4	0	0.0
		Thaa Atoll	13	1	7.7	0	0.0	0	0.0	0	0.0
		Thiladhunmathi Atoll	406	7	1.7	0	0.0	0	0.0	0	0.0
		Thoddu Atoll	24	0	0.0	0	0.0	0	0.0	0	0.0
		Vaavu Atoll	210	5	2.4	0	0.0	0	0.0	0	0.0
		Vattaru Atoll	21	0	0.0	0	0.0	0	0.0	0	0.0
		Unkown	12	0	0.0	0	0.0	0	0.0	0	0.0
Injury Type		Boat Strike	24	0	0.0	0	0.0	0	0.0	0	0.0
		Fishing Line/Hook	140	1	0.7	0	0.0	0	0.0	0	0.0
		Net Entanglement	4	1	25.0	0	0.0	0	0.0	0	0.0
		Rope Entanglement	1	0	0.0	0	0.0	0	0.0	0	0.0
		Infection/Disease	6	0	0.0	0	0.0	0	0.0	0	0.0
		Predatory Bite	168	2	1.2	0	0.0	0	0.0	0	0.0
		No Injury	63612	517	0.8	35	0.1	216	0.3	14	0.0
		Unkown	22	0	0.0	0	0.0	0	0.0	0	0.0

Variable	Category		Total *M. alfredi* Sightings	Hitchhiker Species: Chinese Trumpetfish		Rainbow Runner		Pilot Fish	
				Present	%	Present	%	Present	%
		Total	**63977**	**3**	**0.0**	**24**	**0.0**	**5**	**0.0**
Gender		Female	38567	2	0.0	13	0.0	2	0.0
		Male	25410	1	0.0	11	0.0	3	0.0
Maturity Status		Adult	46040	2	0.0	17	0.0	4	0.0
		Juvenile	16674	1	0.0	7	0.0	1	0.0
		Subadult	1263	0	0.0	0	0.0	0	0.0
Pregnancy		Pregnant	1417	0	0.0	0	0.0	0	0.0
		Heavily Pregnant	929	0	0.0	0	0.0	0	0.0
		Fresh Mating Wound	266	0	0.0	0	0.0	0	0.0
		Not Pregnant	61365	3	0.0	24	0.0	5	0.0
Behavioural Activity		Cleaning	22072	2	0.0	6	0.0	3	0.0
		Cruising	1510	1	0.1	1	0.1	0	0.0
		Courtship	909	0	0.0	1	0.1	0	0.0
		Feeding	39484	0	0.0	16	0.0	2	0.0
		Breaching	1	0	0.0	0	0.0	0	0.0
		Deceased	1	0	0.0	0	0.0	0	0.0
Sub-Region		Addu Atoll	655	0	0.0	0	0.0	0	0.0
		Ari Atoll	9570	1	0.0	4	0.0	1	0.0

		Baa Atoll	36786	0	0.0	14	0.0	3	0.0
		Dhaalu Atoll	7	0	0.0	0	0.0	0	0.0
		Faafu Atoll	115	0	0.0	0	0.0	0	0.0
		Fasdhūetherē Atoll	798	0	0.0	1	0.1	0	0.0
		Gaafu Atoll	5	0	0.0	1	20.0	0	0.0
		Goidhu Atoll	22	0	0.0	0	0.0	0	0.0
		Ihavandhippolhu Atoll	67	0	0.0	0	0.0	0	0.0
		Laamu Atoll	3403	0	0.0	0	0.0	0	0.0
		Lhaviyani Atoll	1674	0	0.0	0	0.0	0	0.0
		Meemu Atoll	426	0	0.0	0	0.0	1	0.2
		North Malé Atoll	7835	2	0.0	3	0.0	0	0.0
		Raa Atoll	1133	0	0.0	1	0.1	0	0.0
		Rasdhu Atoll	533	0	0.0	0	0.0	0	0.0
		South Malé Atoll	262	0	0.0	0	0.0	0	0.0
		Thaa Atoll	13	0	0.0	0	0.0	0	0.0
		Thiladhunmathi Atoll	406	0	0.0	0	0.0	0	0.0
		Thoddu Atoll	24	0	0.0	0	0.0	0	0.0
		Vaavu Atoll	210	0	0.0	0	0.0	0	0.0
		Vattaru Atoll	21	0	0.0	0	0.0	0	0.0
		Unkown	12	0	0.0	0	0.0	0	0.0
Injury Type		Boat Strike	24	0	0.0	0	0.0	1	4.2
		Fishing Line/Hook	140	0	0.0	0	0.0	1	0.7
		Net Entanglement	4	0	0.0	0	0.0	0	0.0
		Rope Entanglement	1	0	0.0	0	0.0	0	0.0
		Infection/Disease	6	0	0.0	0	0.0	0	0.0
		Predatory Bite	168	0	0.0	0	0.0	0	0.0
		No Injury	63612	3	0.0	24	0.0	3	0.0
		Unkown	22	0	0.0	0	0.0	0	0.0

Table 2. A summary of the total *M. birostris* sightings and the presence of associated hitchhiker species categorised by the explanatory variables.

			Hitchhiker Species									
		Total *M. birostris* Sightings	Sharksucker Remora		Juvenile Remora		Giant Remora		Black Trevally		Pilot Fish	
Variable	Category		Present	%	Present	%	Present	%	Present	%	Present	%
	Total	**196**	**2**	**1.0**	**1**	**0.5**	**187**	**95.4**	**5**	**2.6**	**1**	**0.5**
Gender	Female	124	1	0.8	1	0.8	120	96.8	2	1.6	0	0.0
	Male	72	1	1.4	0	0.0	67	93.1	3	4.2	1	1.4
Maturity Status	Adult	137	2	1.5	0	0.0	130	94.9	4	2.9	1	0.7
	Juvenile	36	0	0.0	1	2.8	35	97.2	0	0.0	0	0.0
	Subadult	18	0	0.0	0	0.0	18	100.0	0	0.0	0	0.0
	Unkown	5	0	0.0	0	0.0	4	80.0	1	20.0	0	0.0
Pregnancy	Pregnant	1	0	0.0	0	0.0	1	100.0	0	0.0	0	0.0
	Heavily Pregnant	0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
	Fresh Mating Wound	0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
	Not Pregnant	0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
	Unkown	195	2	1.0	1	0.5	186	95.4	5	2.6	1	0.5
Behavioural Activity	Cleaning	2	0	0.0	0	0.0	2	100.0	0	0.0	0	0.0
	Cruising	9	2	22.2	1	11.1	9	100.0	5	55.6	1	11.1
	Courtship	184	0	0.0	0	0.0	175	95.1	0	0.0	0	0.0
	Feeding	1	0	0.0	0	0.0	1	100.0	0	0.0	0	0.0
Sub-Region	Addu Atoll	9	0	0.0	0	0.0	8	88.9	0	0.0	1	11.1
	Ari Atoll	1	1	100.0	0	0.0	0	0.0	0	0.0	0	0.0
	Baa Atoll	0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
	Faafu Atoll	1	1	100.0	0	0.0	0	0.0	0	0.0	0	0.0
	Fuvahmulah Atoll	180	0	0.0	1	0.6	174	96.7	5	2.8	0	0.0
	Gaafu Atoll	0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
	Laamu Atoll	1	0	0.0	0	0.0	1	100.0	0	0.0	0	0.0
	Lhaviyani Atoll	2	0	0.0	0	0.0	2	100.0	0	0.0	0	0.0
	Meemu Atoll	0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
	North Malé Atoll	0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
	Raa Atoll	0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
	Rasdhu Atoll	2	0	0.0	0	0.0	2	100.0	0	0.0	0	0.0
Injury Type	Deformity	0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
	Fishing Line	5	0	0.0	0	0.0	4	80.0	0	0.0	1	20.0
	Predatory Bite	13	0	0.0	0	0.0	12	92.3	1	7.7	0	0.0
	No Injury	162	2	1.2	1	0.6	155	95.7	4	2.5	0	0.0
	Unkown	16	0	0.0	0	0.0	16	100.0	0	0.0	0	0.0

S2 Appendix

Table 1. The AIC values obtained from the logistic mixed effects modelling procedure for golden trevally presence. Includes all of the explanatory variable combinations organised from lowest to highest.

Explanatory Variable	AIC Value (Low to High)
Maturity Status + Behavioural Activity	5737.822
Gender + Maturity Status + Behavioural Activity	5739.616
Maturity Status	5742.099
Maturity Status + Behavioural Activity + Pregnancy	5742.104
Maturity Status + Behavioural Activity + Sub-Region	5742.386
Gender + Maturity Status	5743.595
Gender + Maturity Status + Behavioural Activity + Sub-Region	5744.032
Gender + Maturity Status + Behavioural Activity + Pregnancy	5744.25
Gender + Behaviour	5744.476
Maturity Status + Pregnancy	5745.559
Maturity Status + Behavioural Activity + Pregnancy + Sub-Region	5746.28
Gender	5746.526
Behavioural Activity	5746.917
Gender + Maturity Status + Pregnancy	5747.008
Gender + Behavioural Activity + Pregnancy	5747.353
Gender + Behavioural Activity + Sub-Region	5748.649

Gender + Pregnancy	5749.586
Maturity Status + Sub-Region	5749.727
Gender + Maturity Status + Pregnancy + Behavioural Activity + Sub-Region	5750.04
Behavioural Activity + Pregnancy	5750.102
Gender + Maturity Status + Sub-Region	5750.26
Behavioural Activity + Sub-Region	5751.234
Gender + Behavioural Activity + Pregnancy + Sub-Region	5751.81
Gender + Sub-Region	5752.727
Pregnancy	5752.737
Gender + Maturity Status + Pregnancy + Sub-Region	5754.136
Sub-Region	5755.9
Behavioural Activity + Pregnancy + Sub-Region	5755.904
Gender + Pregnancy + Sub-Region	5756.063
Maturity Status + Pregnancy + Sub-Region	5756.54
Pregnancy + Sub-Region	5759.208

Table 2. The AIC values obtained from the logistic mixed effects modelling procedure for red snapper presence. Includes all of the explanatory variable combinations organised from lowest to highest.

Explanatory Variable	AIC Value (Low to High)
Behavioural Activity	2212.654
Gender	2213.011
Gender + Behaviour	2213.547
Pregnancy	2213.92
Behavioural Activity + Pregnancy	2214.315
Maturity Status	2214.526
Maturity Status + Behavioural Activity	2214.643
Gender + Maturity Status	2214.681
Gender + Pregnancy	2214.694
Gender + Maturity Status + Behavioural Activity	2215.189
Gender + Behavioural Activity + Pregnancy	2215.336
Sub-Region	2215.838
Maturity Status + Pregnancy	2215.933
Maturity Status + Behavioural Activity + Pregnancy	2216.319
Gender + Sub-Region	2216.556
Gender + Maturity Status + Pregnancy	2216.568
Gender + Maturity Status + Behavioural Activity + Pregnancy	2217.148
Maturity Status + Sub-Region	2217.835
Gender + Pregnancy + Sub-Region	2218.706

Gender + Behavioural Activity + Sub-Region	2219.022
Maturity Status + Behavioural Activity + Sub-Region	2220.082
Gender + Behavioural Activity + Pregnancy + Sub-Region	2220.302
Gender + Maturity Status + Behavioural Activity + Sub-Region	2221.04
Behavioural Activity + Sub-Region	2222.769
Gender + Maturity Status + Pregnancy + Behavioural Activity + Sub-Region	2223.002
Gender + Maturity Status + Pregnancy + Sub-Region	2223.638
Maturity Status + Behavioural Activity + Pregnancy + Sub-Region	2224.5
Maturity Status + Pregnancy + Sub-Region	2224.586
Gender + Maturity Status + Sub-Region	2224.999
Behavioural Activity + Pregnancy + Sub-Region	2225.843
Pregnancy + Sub-Region	2230.616

Table 3. The AIC values obtained from the logistic mixed effects modelling procedure for sharksucker remora presence. Includes all of the explanatory variable combinations organised from lowest to highest.

Explanatory Variable	AIC Value (Low to High)
Gender + Maturity Status + Pregnancy + Behavioural Activity + Sub-Region	34470.2
Gender + Behavioural Activity + Pregnancy + Sub-Region	34486.82
Behavioural Activity + Pregnancy + Sub-Region	34526.53
Maturity Status + Behavioural Activity + Pregnancy + Sub-Region	34528.15
Gender + Maturity Status + Behavioural Activity + Sub-Region	34618.73
Gender + Behavioural Activity + Sub-Region	34645.91
Gender + Maturity Status + Pregnancy + Sub-Region	34663.13
Gender + Pregnancy + Sub-Region	34692.53
Maturity Status + Behavioural Activity + Sub-Region	34697.84
Maturity Status + Pregnancy + Sub-Region	34725.81
Pregnancy + Sub-Region	34729.84
Gender + Maturity Status + Sub-Region	34821.61
Gender + Sub-Region	34864.85
Maturity Status + Sub-Region	34905.87
Sub-Region	34914.15
Gender + Maturity Status + Behaviour al Activity + Pregnancy	35108.17
Gender + Behavioural Activity + Pregnancy	35121.4
Behaviour al Activity + Pregnancy	35149.88
Behavioural Activity + Sub-Region	35149.88

Maturity Status + Behavioural Activity + Pregnancy	35151.11
Gender + Maturity + Behavioural Activity	35266.98
Gender + Behaviour	35290.39
Maturity Status + Behavioural Activity	35328.14
Behavioural Activity	35329.11
Gender + Maturity Status + Pregnancy	35461.65
Gender + Pregnancy	35492.54
Maturity Status + Pregnancy	35510.24
Pregnancy	35518.15
Gender + Maturity Status	35636.55
Gender	35680.73
Maturity Status	35703.26

Table 4. The AIC values obtained from the logistic mixed effects modelling procedure for juvenile remora presence. Includes all of the explanatory variable combinations organised from lowest to highest.

Explanatory Variable	AIC Value (Low to High)
Gender + Maturity Status + Behavioural Activity + Sub-Region	8452.132
Maturity Status + Behavioural Activity + Sub-Region	8454.411
Gender + Maturity Status + Pregnancy + Behavioural Activity + Sub-Region	8455.853
Maturity Status + Behavioural Activity + Pregnancy + Sub-Region	8457.536
Behavioural Activity + Sub-Region	8470.045
Behavioural Activity + Pregnancy + Sub-Region	8472.238
Gender + Behavioural Activity + Sub-Region	8473.603
Gender + Behavioural Activity + Pregnancy + Sub-Region	8474.416
Gender + Maturity Status + Sub-Region	8515.838
Gender + Maturity Status + Pregnancy + Sub-Region	8516.06
Maturity Status + Pregnancy + Sub-Region	8522.075
Maturity Status + Sub-Region	8522.457
Sub-Region	8546.271
Gender + Maturity Status + Behavioural Activity	8546.947
Gender + Sub-Region	8548.092
Gender + Maturity Status + Behavioural Activity + Pregnancy	8549.538
Gender + Pregnancy + Sub-Region	8549.968
Maturity Status + Behavioural Activity	8550.835
Maturity Status + Behavioural Activity + Pregnancy	8552.834

Behavioural Activity	8566.772
Gender + Behaviour	8568.714
Behavioural Activity + Pregnancy	8568.758
Gender + Behavioural Activity + Pregnancy	8570.702
Gender + Maturity Status	8588.82
Gender + Maturity Status + Pregnancy	8590.808
Maturity Status	8595.945
Maturity Status + Pregnancy	8597.927
Gender	8621.348
Pregnancy	8621.45
Gender + Pregnancy	8623.248
Pregnancy + Sub-Region	8548.262

Table 5. The AIC values obtained from the logistic mixed effects modelling procedure for giant remora presence. Includes all of the explanatory variable combinations organised from lowest to highest.

Explanatory Variable	AIC VALUE (lowest to highest)
Gender + Maturity Status + Sub-Region	381.9904
Gender + Maturity Status + Behavioural Activity + Sub-Region	383.1385
Gender + Sub-Region	384.1423
Gender + Behavioural Activity + Sub-Region	384.4502
Maturity Status + Sub-Region	388.497
Gender + Maturity Status	388.5637
Maturity Status + Behavioural Activity + Sub-Region	389.3258
Behavioural Activity + Sub-Region	389.3807
Sub-Region	389.4454
Gender	389.5124
Gender + Maturity Status + Behavioural Activity	390.0152
Gender + Behavioural Activity	390.2948
Maturity Status	394.547
Behavioural Activity	395.0878
Maturity Status + Behavioural Activity	395.7452