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Associated Data

Data supplied by the author:

Zooplankton data is available at the UQ eSpace public repository: <https://doi.org/10.14264/98ddbde>

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Reef manta rays forage on tidally driven, high density zooplankton patches in Hanifaru Bay, Maldives

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Manta rays forage for zooplankton in tropical and subtropical marine environments, which are generally nutrient-poor. Feeding often occurs at predictable locations where these large, mobile cartilaginous fishes congregate to exploit ephemeral productivity hotspots. Investigating the zooplankton dynamics that lead to such feeding aggregations remains a key question for understanding their movement ecology. The aim of this study is to investigate the feeding environment at the largest known aggregation for reef manta rays *Mobula alfredi* in the world. We sampled zooplankton throughout the tidal cycle, and recorded *M. alfredi* activity and behaviour, alongside environmental variables at Hanifaru Bay, Maldives. We constructed generalised linear models to investigate possible relationships between zooplankton dynamics, environmental parameters, and how they influenced *M. alfredi* abundance, behaviour, and foraging strategies. Zooplankton biomass changed rapidly throughout the tidal cycle, and *M. alfredi* feeding events were a significant predictor of high zooplankton biomass. *Mobula alfredi* switched from non-feeding to feeding behaviour at a prey density threshold of 53.7 mg m^{-3} ; more than double the calculated density estimates needed to theoretically meet their metabolic requirements. The highest numbers of *M. alfredi* observed in Hanifaru Bay corresponded to when they were engaged in feeding behaviour. The community composition of zooplankton was different when *M. alfredi* were feeding (dominated by copepods and crustaceans) compared to when they were present but not feeding (more gelatinous species present than in feeding samples). The dominant zooplankton species recorded was *Undinula vulgaris*, a large-bodied calanoid copepod species which blooms in oceanic waters, suggesting offshore influences at the site. Here, we have characterised aspects of the

feeding environment for *M. alfredi* in Hanifaru Bay and identified some of the conditions that may result in large aggregations of these threatened planktivores, and this information can help inform management of this economically important marine protected area.

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24

25 Abstract

26 Manta rays forage for zooplankton in tropical and subtropical marine environments, which are
27 generally nutrient-poor. Feeding often occurs at predictable locations where these large, mobile
28 cartilaginous fishes congregate to exploit ephemeral productivity hotspots. Investigating the
29 zooplankton dynamics that lead to such feeding aggregations remains a key question for
30 understanding their movement ecology. The aim of this study is to investigate the feeding
31 environment at the largest known aggregation for reef manta rays *Mobula alfredi* in the world.
32 We sampled zooplankton throughout the tidal cycle, and recorded *M. alfredi* activity and
33 behaviour, alongside environmental variables at Hanifaru Bay, Maldives. We constructed
34 generalised linear models to investigate possible relationships between zooplankton dynamics,
35 environmental parameters, and how they influenced *M. alfredi* abundance, behaviour, and
36 foraging strategies. Zooplankton biomass changed rapidly throughout the tidal cycle, and *M.*
37 *alfredi* feeding events were a significant predictor of high zooplankton biomass. *Mobula alfredi*
38 switched from non-feeding to feeding behaviour at a prey density threshold of 53.7 mg m⁻³; more
39 than double the calculated density estimates needed to theoretically meet their metabolic

40 requirements. The highest numbers of *M. alfredi* observed in Hanifaru Bay corresponded to
41 when they were engaged in feeding behaviour. The community composition of zooplankton was
42 different when *M. alfredi* were feeding (dominated by copepods and crustaceans) compared to
43 when they were present but not feeding (more gelatinous species present than in feeding
44 samples). The dominant zooplankton species recorded was *Undinula vulgaris*, a large-bodied
45 calanoid copepod species which blooms in oceanic waters, suggesting offshore influences at the
46 site. Here, we have characterised aspects of the feeding environment for *M. alfredi* in Hanifaru
47 Bay and identified some of the conditions that may result in large aggregations of these
48 threatened planktivores, and this information can help inform management of this economically
49 important marine protected area.

50

51

52 Introduction

53 Manta rays are large planktivores that inhabit tropical and subtropical waters globally, which are
54 generally oligotrophic ([Marshall et al. 2009](#)). Therefore, to meet their metabolic needs, manta
55 rays need to locate pulses of zooplankton productivity. Similar to other tropical planktivores,
56 such as leatherback turtles *Dermochelys coriacea* ([Hays et al. 2006](#)) and whale sharks *Rhincodon*
57 *typus* ([Rohner et al. 2015](#)), manta rays aggregate where and when conditions result in elevated
58 local productivity ([Dewar et al. 2008](#), [Anderson et al. 2011](#), [Jaine et al. 2012](#)). However, these
59 productivity ‘hotspots’ are ephemeral in nature and often difficult to locate and characterise
60 ([Harris et al. 2020](#), [Harris et al. 2021](#)), which makes the direct study of planktivore feeding
61 ecology challenging.

62 There are a variety of approaches used to study a species’ diet, including stomach contents
63 analysis, biochemical analyses, and direct observation. Two studies have recently explored the
64 diet of manta ray species based on stomach contents: one on oceanic manta rays *Mobula*
65 *birostris* taken in a fishery in the Philippines ([Rohner et al. 2017](#)), and one on a historic stomach
66 sample from a reef manta ray *M. alfredi* collected from eastern Australia ([Bennett et al. 2017](#)).
67 Traditionally, lethal approaches for dietary analysis, such as stomach contents analysis, are
68 inappropriate for vulnerable marine fishes ([Cortés 1997](#)), and only offer a ‘snapshot’ of a
69 species’ diet ([Rohner et al. 2013](#)). Instead, biochemical approaches, including stable isotope and
70 fatty acid analysis, are non-lethal methods that provide an integrated signal that represents the
71 long-term diet and trophic position of species. Biochemical analysis has inferred that *M. birostris*
72 off Ecuador derive much of their calorific intake by feeding at depth ([Burgess et al. 2016](#)), as do
73 *M. alfredi* off eastern Australia ([Couturier et al. 2013](#)), and *M. alfredi* in the Seychelles target
74 pelagic zooplankton sources ([Peel et al. 2019](#)). Nevertheless, biochemical analyses lack
75 resolution, such as identifying and quantifying preferred prey species, whereas direct observation
76 of animal feeding allows simultaneous sampling of the feeding environment.

77

78 Currently, the only detailed direct observation of the diet in manta rays is from an aggregation
79 site off eastern Australia, where *M. alfredi* was observed feeding near the surface ([Armstrong et](#)

80 [al. 2016](#)). The study found *M. alfredi* feeding events were significantly associated with greater
81 zooplankton biomass, but were not influenced by zooplankton size or species composition.
82 Further, feeding activity and zooplankton density was tidally driven at this site. Similarly, the
83 occurrence of *M. alfredi* in Komodo National Park in Indonesia was heavily influenced by tide,
84 and was considered likely to be related to feeding activity ([Dewar et al. 2008](#)). An *in situ* prey
85 density threshold of 11.2 mg m⁻³ was determined for *M. alfredi* foraging in eastern Australia
86 ([Armstrong et al. 2016](#)). However, a theoretical estimate of the density threshold to meet their
87 metabolic requirements (25.2 mg m⁻³) suggests they require additional energy from alternate
88 food sources, such as foraging at depth ([Armstrong et al. 2016](#)).

89
90 Manta rays exhibit behavioural plasticity in relation to their feeding environment. In eastern
91 Australia ([Jaine et al. 2012](#)), Indonesia ([Dewar et al. 2008](#)), and the Chagos Archipelago ([Harris](#)
92 [et al. 2021](#)), surface feeding by manta rays is frequently observed during daylight hours, and
93 other large planktivores, such as basking sharks *Cetorhinus maximus* ([Sims and Merrett 1997](#))
94 and *R. typus* ([Prebble et al. 2016](#)) also employ this strategy. In the Red Sea, *M. alfredi* swim in
95 various circular patterns when feeding on zooplankton in shallow water ([Gadig and Neto 2014](#)).
96 At Ningaloo Reef in Western Australia, *M. alfredi* is frequently observed to use a combination of
97 feeding modes, including surface feeding, somersaulting, and bottom feeding (AOA *pers. obs.*).
98 A unique strategy of “cyclone” feeding has been described at Hanifaru Bay in the Maldives,
99 where multiple individuals manipulate the water column to create a vortex that concentrates
100 zooplankton on which they then feed ([Stevens 2016](#)). Eight different feeding strategies have been
101 described at this site, and have been related to prey density using a subjective visual assessment
102 of the water column ([Stevens et al. 2018](#)). However, zooplankton density or composition has yet
103 to be quantified in relation to these strategies. Upwards of 250 individual manta rays aggregate in
104 Hanifaru Bay during peak feeding events, making it the largest known *M. alfredi* aggregation site
105 in the world ([Harris et al. 2020](#)). This is therefore an ideal location to test hypotheses regarding
106 habitat use, aggregative behaviour, feeding strategies, and zooplankton dynamics for this species.

107
108 Here, we investigate the food environment for *M. alfredi* at Hanifaru Bay. Manta rays are of
109 economic importance to both ecotourism and fisheries industries and have a conservative life
110 history, and so identifying the foraging requirements and habitat preferences of these threatened
111 rays should aid future conservation efforts ([Stewart et al. 2018](#)). We analyse the zooplankton
112 dynamics (biomass, size structure, and community composition) in relation to *M. alfredi*
113 presence, behaviour and feeding strategies, to improve our understanding of the feeding
114 dynamics of this large planktivorous species. This study aims to relate changes in zooplankton
115 biomass to *M. alfredi* behaviour; to establish a critical prey density threshold for feeding at this
116 site, and to determine whether prey density influences the type of feeding strategy *M. alfredi*
117 employ to exploit their prey. Further, we aim to investigate whether *M. alfredi* foraging
118 behaviour is influenced by changes in the zooplankton community composition, or size structure.

119

120

121 **Materials & Methods**

122 *Study Site*

123 The Maldives has a large resident population of *M. alfredi* which undertake biannual migrations
124 linked to the changing monsoons (seasons) within the archipelago ([Anderson et al. 2011](#); Fig
125 1A). During the Southwest Monsoon, or *Hulhangu* (April – November), *M. alfredi* frequent
126 foraging aggregation sites on the eastern side of the nation's atolls ([Harris et al. 2020](#)). One site,
127 Hanifaru Bay, is situated on the eastern edge of Baa Atoll, and attracts large feeding
128 aggregations of this species annually ([Stevens 2016](#), [Harris et al. 2020](#)). Hanifaru Bay is a small
129 reef inlet (700 m long by 200 m wide) which forms part of a core marine protected area within
130 the Baa Atoll UNESCO Biosphere Reserve (5°17'N, 73°15'E; Fig 1B). The shallow (maximum
131 depth 22 m) inlet is periodically inundated with zooplankton-rich water. Motorised boat activity
132 and SCUBA diving are prohibited in Hanifaru Bay due to the high numbers of manta rays and
133 other megafauna that access the inlet ([Murray et al. 2020](#)).

134

135 *Data collection*

136 Fieldwork was conducted in the lead up to the new moon in August 2017, under Ministry of
137 Fisheries Permit No. (OTHR)30-D/PRIV/2017/280, and Ministry of Environment Permit No's.
138 EPA/2017/RP-01 & EPA/2016/PSR-M02. At this time of year, lunar and monsoonal currents
139 combine to transport zooplankton from outside the atoll edge into Hanifaru Bay ([Stevens 2016](#)).
140 The currents form a back eddy, trapping and concentrating plankton in this shallow reef inlet,
141 resulting in *M. alfredi* foraging opportunities which peak during spring and high tides ([Stevens](#)
142 [2016](#)). Sampling was conducted during daylight hours and across the tidal cycle from 13 – 21
143 August 2017. Zooplankton was collected by two people using a 200 µm-mesh net towed by hand
144 at the surface for a ~50 m transect between two coral features at the eastern end of Hanifaru Bay
145 (Fig 2A). A flowmeter was fitted to the plankton net to allow calculation of the volume of water
146 sampled. Flowmeter calibration was performed prior to the field trip in a swimming pool of
147 known length to establish an accurate measurement of distance per flowmeter revolution.
148 Samples were kept on ice and fixed with 10% buffered formalin solution at the end of each day.

149

150 Each net tow was accompanied by an in-water observer recording manta ray activity in vicinity
151 of the tow. This included: (1) manta ray abundance; (2) behaviour (Feeding, Non-feeding – when
152 manta rays were present but not feeding, and Absent – when manta rays were not present); and
153 (3) most common feeding strategy employed (as described in Stevens 2016; Fig 2B).

154

155 Temperature and salinity data were collected at 1 s intervals from a CTD unit deployed at the site
156 for the study duration (except for ~24 hrs from 17 – 18 August for battery exchange).

157 Temperature and salinity ranges were relatively small throughout the study (28.6 – 29.2°C and
158 34.3 – 35.0 ppt respectively). These variables were excluded from the models as their inclusion
159 resulted in missing values. Tide data were obtained from a local government representative.

160

161 *Sample processing*

162 Zooplankton samples were processed in the CSIRO Plankton Ecology Laboratory in Brisbane,
163 Australia. Flowmeter readings and the area of the net mouth were used to estimate the volume of
164 water filtered.

165

166 *Zooplankton biomass*

167 Zooplankton samples were split into two halves using a Folsom splitter ([Harris et al. 2000](#)). The
168 first half was used to determine dry mass, with each sample oven-dried at 70°C for 24 hrs prior
169 to weighing. Zooplankton dry mass (hereafter referred to as biomass) per unit volume of filter-
170 seawater for each tow was calculated by dividing the dry mass of the sample (mg) by the volume
171 of filtered water (m³):

172

$$173 \text{Biomass (mg m}^{-3}\text{)} = \text{Dry mass (mg)} / \text{Volume of water filtered (m}^3\text{)}$$

174

175 *Zooplankton identification*

176 The second half of the sample was used to examine size structure and community composition
177 via a 2400 dpi ZooScan system and microscopy. The Hydroptic v3 ZooScan (EPSON Perfection
178 V700 Flatbed) is a high resolution, waterproof scanner that digitises particles for size and
179 biovolume measurements ([Gorsky et al. 2010](#)). An aliquot of each sample was prepared using a
180 Stemple pipette of known volume and placed on the scanning tray. To avoid overlap, particles
181 were manually separated using a cactus spine. Once separated, the sample was scanned and
182 particles were extracted into vignettes for categorisation into broad taxonomic groups (24
183 groups) using Plankton ID software (Version 1.2.6) and manual validation ([Gorsky et al. 2010](#)).
184 Objects classified as sand, fibre, detritus, bubbles and shadows were excluded from further
185 analysis (as per [Rohner et al. 2015](#)). For visualisation, taxa that comprised <5% of the total
186 abundance were grouped as “other”, and these included cnidaria, polychaetes, echinoderm
187 larvae, bryozoan larvae, fish larvae, salps, and various classes of arthropods.

188

189 To investigate which species were responsible for the majority of the biomass at the site when
190 overall biomass values in the water were high, samples were analysed taxonomically via
191 microscopy. A subsample was prepared using a Stempel pipette, and organisms were identified
192 and counted in a Bogorov tray using a microscope. Dominant members were identified to genus
193 or species with assistance from trained plankton taxonomists at the CSIRO Plankton Ecology
194 Laboratory ([Eriksen et al. 2019](#)).

195

196 *Zooplankton size structure*

197 A size distribution of the sample particles, known as a Normalised Biomass Size Spectra, was
198 produced to analyse the size structure of the zooplankton community ([Vandromme et al. 2012](#)).
199 Spherical biovolume was calculated from the size measurements obtained from ZooScan. Each

200 particle was assigned to one of 50 logarithmic size categories based on its spherical biovolume.
201 The sum of the spherical biovolume of the particles in each size class (mm^3) was standardised by
202 the fraction of sample scanned and the volume of water filtered (m^3), and normalised by dividing
203 this value by the width of the size class measured in biovolume (mm^3). Both axes of the
204 Normalised Biomass Size Spectra use a logarithmic scale.

205

206 *Drivers of zooplankton biomass and manta numbers*

207 To investigate potential drivers of zooplankton abundance and *M. alfredi* visits to Hanifaru Bay,
208 we constructed generalised linear models (GLMs) using R ([R Core Team 2019](#)). Separate
209 analyses were conducted for two response variables: (i) Zooplankton biomass (mg m^{-3}), with a
210 Gamma error structure and log-link function; and (ii) Manta ray abundance (number of *M.*
211 *alfredi* observed during zooplankton sampling), with a negative binomial error structure and log-
212 link function (Poisson error structure was overdispersed). We visually inspected diagnostic plots
213 to assess assumptions of homogeneity of variance and normality. Predictors in both models were
214 Tide (hours from high tide) and Behaviour (Feeding, Non-feeding and Absent). To account for
215 the circular nature of Tide (~12-hr cycle), the variable was transformed using a truncated Fourier
216 series (a harmonic function of sines and cosines). This ensures that the cyclical nature of this
217 predictor is captured, while guaranteeing that the response values predicted at the extremes of the
218 predictor range are the same (i.e., the same prediction for Zooplankton biomass or Count at times
219 of 0 and 24 hours). For the Manta ray abundance model, the Behaviour predictor was reduced to
220 two categories – namely Feeding and Non-feeding, and Zooplankton biomass (mg m^{-3}) was
221 included as a predictor. Models were plotted on the response scale using the package “visreg” in
222 R ([Breheny and Burchett 2017](#)).

223

224 *Critical thresholds for feeding behaviour and strategy*

225 We assessed whether there might be a critical threshold for *M. alfredi* feeding – i.e., a level
226 above which the likelihood of feeding increases dramatically. We thus used a GLM with a
227 binomial error structure to analyse manta ray behavioural response (Non-Feeding = 0, Feeding =
228 1) in relation to zooplankton biomass (mg m^{-3}) as a predictor. The critical density threshold was
229 taken as the zooplankton biomass at which the proportion of feeding was 0.5.

230

231 Feeding samples were categorised into either Solo feeding (Straight, Surface and Somersault) or
232 Group feeding (Piggy-back and Chain) based on the most common strategy observed in the
233 manta rays ([Stevens 2016](#)). A GLM with a binomial error structure was used to analyse manta
234 ray feeding strategy response (Solo = 0, Group = 1) in relation to zooplankton biomass (mg m^{-3})
235 as a predictor. The critical density threshold was taken as the zooplankton biomass at which the
236 proportion of Group feeding was 0.5.

237

238 *Zooplankton community analysis*

239 To determine how different the zooplankton communities were for the *M. alfredi* behaviours
240 (Feeding or Non-Feeding), non-metric multidimensional scaling was used based on abundance
241 counts of the different taxonomic groups from the Zooscan analysis. The Bray Curtis distance
242 measure was used because it is unaffected by joint absences of taxonomic groups in samples. To
243 account for abundance of certain taxa, data were transformed using a root transformation. To test
244 for differences in community composition between *M. alfredi* behaviours (Feeding and Non-
245 Feeding), we performed an adonis analysis, a multivariate analysis of variance. Both the adonis
246 and non-metric multidimensional scaling were conducted using the “vegan” package in R
247 ([Oksanen et al. 2007](#)).

248

249

250 Results

251 A total of 77 zooplankton samples were collected (Feeding = 33, Non-feeding = 22, and Absent
252 = 22) over a period of nine days. Zooplankton biomass ranged between 0.7- and 643.1 mg m⁻³
253 (mean = 90.7, SD = 130.9).

254

255 GLM analyses showed that Zooplankton biomass in Hanifaru Bay was significantly related to
256 Tide and Behaviour (Fig 3). Zooplankton biomass was greatest just following high tide ($t = -$
257 3.83, $p = 0.0003$, Fig 3A), and *M. alfredi* were more commonly observed feeding when
258 zooplankton biomass was higher ($t = -2.83$, $p = 0.006$, Fig 3B).

259

260 Manta ray behaviour was significantly related to zooplankton biomass ($z = 3.08$, $p = 0.002$), with
261 a prey density threshold of 53.7 mg m⁻³ calculated for feeding *M. alfredi* (Fig 4).

262

263 Manta ray abundance was significantly predicted by Behaviour ($z = -5.55$, $p = 0.000000003$; Fig
264 5), with more *M. alfredi* present when they were feeding in Hanifaru Bay. Tide and Biomass did
265 not predict manta ray abundance.

266

267 There was no significant difference in zooplankton biomass among different feeding strategies
268 during the study (ANOVA: $F = 1.02$, $df = 4,28$, $p = 0.41$). In addition, there was no significant
269 difference in zooplankton biomass, when samples were pooled into Solo feeding strategies and
270 Group feeding strategies ($z = 0.98$, $p = 0.33$). However, only groups were observed feeding when
271 biomass concentrations exceeded 200 mg m⁻³.

272

273 *Zooplankton community composition*

274 There were differences in the zooplankton community composition between Feeding and Non-
275 feeding samples when analysed using non-metric multidimensional scaling on the Zooscan
276 taxonomic counts (Fig 6A). The 95% confidence ellipses for Feeding and Non-feeding were not
277 overlapping, implying that they were significantly different zooplankton community
278 compositions, and this was confirmed by the adonis analysis ($F = 9.42$, $df = 1,53$, $p = 0.001$).

279 Crustaceans (such as copepods) were more associated with Feeding samples, compared to
280 gelatinous taxa (such as chaetognaths and eggs), which were more associated with Non-feeding
281 samples.

282

283 Calanoid copepods comprised 66.3% of Feeding samples compared to 46.7% of Non-feeding
284 samples (Fig 6C and 6D respectively). Chaetognaths were 5.3% of Feeding samples, and 11.9%
285 of Non-feeding samples. Fish eggs were less than 2% of Feeding samples, and 13.0% of Non-
286 feeding samples. Based on microscopy, juvenile and adult *Undinula vulgaris* were the dominant
287 calanoid copepod species in both Feeding and Non-feeding samples (25.0% and 30.7%
288 respectively, Fig 6B).

289

290 *Zooplankton size structure*

291 Analysis of the size structure of zooplankton from Hanifaru Bay revealed that the biovolume of
292 zooplankton increased in the majority of size categories when *M. alfredi* were feeding (Fig 7).
293 The biovolume of zooplankton was significantly higher across particle size categories during *M.*
294 *alfredi* Feeding events than Non-feeding events (Mean total standardised biovolume: Feeding =
295 288.4 and Non-feeding = 172.1; $t = -2.66$, $df = 51.38$, $p = 0.01$). Feeding and Non-feeding
296 samples had similar biovolumes of small and large particles, but Feeding had significantly more
297 moderate-sized particles (from $10^{-1.2}$ to $10^{0.5}$ mm^3).

298

299

300 **Discussion**

301 *Summary*

302 Zooplankton concentrations influence the number of *M. alfredi* present and their observed
303 behaviour in Hanifaru Bay. Rapid changes in zooplankton are observed across the tidal cycle,
304 and *M. alfredi* feed when biomass reaches a critical density which is higher than predicted to
305 meet their theoretical metabolic requirements. *Mobula alfredi* forage when the zooplankton
306 community is dominated by calanoid copepods, and are less likely to feed when there are greater
307 numbers of gelatinous taxa (such as chaetognaths or eggs). Taxonomic analysis reveals large-
308 bodied copepods, *Undinula vulgaris*, dominate the zooplankton environment at Hanifaru Bay,
309 suggesting oceanic incursions may play an important role in bringing zooplankton to this small
310 reef inlet.

311

312 *Tidal influence on zooplankton density and manta ray foraging*

313 Manta rays feed when zooplankton biomass is high, which is typically observed on the high to
314 ebbing tide at Hanifaru Bay. Oceanographic investigations in Hanifaru Bay suggest tidal currents
315 draw zooplankton into the shallow reef systems of the atoll, where they become trapped inside
316 due to a back-eddy mechanism created by the unique shape of the reef system and the
317 combination of the lunar and monsoon currents (Hosegood *pers comms*). Tides are known to
318 influence the distribution and abundance of zooplankton around island inlets in the Great Barrier

319 Reef ([Alldredge and Hamner 1980](#)), and have been shown to influence manta ray feeding
320 behaviour at aggregation sites in Indonesia ([Dewar et al. 2008](#)), eastern Australia ([Armstrong et
321 al. 2016](#)), and the Chagos Archipelago ([Harris et al. 2021](#)). Therefore, short-term *in situ*
322 observations of zooplankton concentrations in relation to tidal cycles and manta ray behaviour
323 can help inform when *M. alfredi* are likely to be observed in Hanifaru Bay.

324

325 *Animal movements and productivity hotspots*

326 Large planktivores seeking to exploit ephemeral food sources in surface waters are likely to
327 respond to currents and water movements that concentrate zooplankton. *Cetorhinus maximus*
328 forages along thermal fronts ([Sims and Quayle 1998](#)), *R. typus* targets regions of upwelling
329 ([Ryan et al. 2017](#)), and surface foraging in *M. alfredi* is often tidally driven ([Dewar et al. 2008](#),
330 [Armstrong et al. 2016](#)). In conjunction with responding to physical oceanographic cues, animals
331 that seek patchily distributed prey sources are also likely to congregate in areas where they have
332 previously encountered energetically rewarding prey abundances, resulting in larger numbers of
333 animals in reliable foraging regions. For example, *M. alfredi* predictably switch to the down-
334 current side of the atolls in the Maldives in response to monsoonal winds and primary
335 productivity ([Harris et al. 2020](#)). Area-restricted search theory predicts that animals will remain
336 localised in areas where they have a higher probability of encountering prey ([Bailey et al. 2019](#)),
337 and this perhaps explains why some *M. alfredi* individuals remain in Hanifaru Bay when not
338 feeding. This location also has two cleaning stations used by *M. alfredi* ([Stevens 2016](#)), and it is
339 hypothesised manta rays will frequent cleaning stations in close proximity to foraging
340 opportunities ([Armstrong et al. 2021](#)). Manta rays in Palmyra Atoll used area-restricted searching
341 when adjacent to ledges or channels with high plankton concentrations, but their movements
342 were more random at larger spatial scales ([Papastamatiou et al. 2012](#)). Area-restricted searching
343 has also been observed in two dolphin species (*Tursiops truncatus* and *Delphinus delphis*) in
344 areas of high prey availability, and where they have had previous successful foraging experience,
345 suggesting memory plays a role in their movement ecology ([Bailey et al. 2019](#)). For *M. alfredi*,
346 their apparent preference for returning to the same cleaning stations over time ([Armstrong et al.
347 2021](#)), suggests they may form a cognitive map of shallow reef environments, and this is likely
348 the case for known productivity hotspots as well.

349

350 *High critical feeding threshold for manta rays at Hanifaru Bay*

351 The critical prey density threshold for *M. alfredi* feeding in Hanifaru Bay (53.7 mg m^{-3}) is more
352 than four times higher than that in east Australia where *M. alfredi* feeds (11.2 mg m^{-3} ; [Armstrong
353 et al. 2016](#)), and in east Africa where *R. typus* feeds (12.4 mg m^{-3} ; [Rohner et al. 2015](#)). It is also
354 double the theoretical prey density threshold calculated to meet the metabolic requirements for
355 *M. alfredi* (25.2 mg m^{-3} ; [Armstrong et al. 2016](#)), which may explain why this site hosts such a
356 large feeding aggregation of this species. However, these large planktivorous elasmobranchs are
357 assumed to feed in the mesopelagic layer ([Couturier et al. 2013](#), [Burgess et al. 2016](#)), so an
358 understanding of the prey densities available at these depths is required to gauge the relative

359 importance of aggregations sites such as Hanifaru Bay in meeting these species' energetic
360 requirements. Sampling zooplankton at depth remains a logistical challenge for researchers, but
361 with technological advances, such as satellite tags equipped with accelerometer data loggers, and
362 unmanned video submersibles ([Stewart et al. 2018](#)), these inferences can be better investigated.

363

364 *Manta ray feeding strategies*

365 In the current study, plasticity in *M. alfredi* feeding strategies in response to changes in prey
366 biomass in Hanifaru Bay is not supported. This contrasts with work previously conducted in
367 Hanifaru Bay that found manta rays were significantly more likely to employ group feeding
368 strategies as prey density increased ([Stevens 2016](#)). The previous work was based on a
369 qualitative visual index for prey density, with data obtained over a long time period (> 5 years)
370 and included aggregations upwards of 150 animals. However, we did see that when zooplankton
371 biomass values were very high, over 200 mg m⁻³, that only Group feeding strategies were used,
372 and no Solo feeding was seen. But in either scenario, it is uncertain whether the observations are
373 due to true cooperative feeding strategies, or simply that coordinate movements reduce collisions
374 with other manta rays ([Stevens 2016](#)). It is likely our relatively short sampling duration failed to
375 detect this phenomenon, and our results suffer from small sample size. More work needs to be
376 done to quantitatively assess whether the presence of higher zooplankton biomass is positively
377 correlated with group feeding events.

378

379 *Zooplankton composition and size*

380 Differences in the composition of the zooplankton community were observed between *M. alfredi*
381 feeding and non-feeding events, and *M. alfredi* was observed feeding when the overall
382 biovolume of zooplankton was greater. Calanoid copepods dominate the zooplankton community
383 for manta rays at Hanifaru Bay, with *U. vulgaris* the most prominent species. *Undinula vulgaris*
384 is a key species in tropical areas due to its large size and tendency to swarm in high numbers,
385 making it a good food resource for planktivorous fishes ([Alvarez-Cadena et al. 1998](#)). This
386 species has been observed at numerous large planktivore feeding aggregation sites, including
387 those visited by *M. alfredi* in eastern Australia ([Couturier et al. 2013](#), [Armstrong et al. 2016](#)), *R.*
388 *typus* in the Gulf of Tadjoura, Djibouti ([Boldrocchi et al. 2018](#)), both *M. birostris* and *R. typus* in
389 the Gulf of California ([Notarbartolo-di-Sciara 1988](#), [Lavaniegos et al. 2012](#)), and both *M. alfredi*
390 and *R. typus* in the Philippines ([Canencia and Metillo 2013](#), [Yap-Dejeto et al. 2018](#)). *Undinula*
391 *vulgaris* is considered an indicator of the influence of neritic-oceanic waters in reef
392 environments, and its local distribution can suggest oceanic water sources ([Alvarez-Cadena et al.](#)
393 [1998](#)). Further investigation into the ecology of *U. vulgaris* in tropical environments may aid our
394 understanding of how vital swarms of this species are for supporting large tropical planktivores,
395 and whether their distribution and abundance is likely to be impacted by a rapidly changing
396 climate.

397

398

399 **Conclusions**

400 Identifying important foraging opportunities for vulnerable species such as manta rays remains a
401 goal for implementing effective conservation strategies for the species. Here, we conducted the
402 first analysis of the food environment for *M. alfredi* at Hanifaru Bay, and highlighted the
403 importance of tidal regimes and high zooplankton density in driving *M. alfredi* aggregations at
404 this site. Conducting high resolution investigations into the dietary basis of aggregations can help
405 inform drivers of species movements and habitat preferences. This can be challenging in remote
406 locations where resources are sparse, and where fieldwork is logistically difficult (i.e., hand-
407 towing for zooplankton is seldom recorded in methods), which may provide an explanation as to
408 why most feeding studies for marine megafauna have only superficially investigated zooplankton
409 dynamics. This study failed to record the zooplankton dynamics during a mass feeding
410 aggregation at this site, and so our findings are suggestive of what can be observed at this
411 location, but they may not provide the whole picture. Longer term sampling, and more targeted
412 methodologies that allow for sampling of zooplankton throughout the water column, will help
413 elucidate what leads to mass feeding aggregations and the role of different feeding strategies for
414 *M. alfredi* at this site. Here, we have determined the importance of zooplankton dynamics in
415 driving the aggregative behaviour of *M. alfredi* at their largest aggregation site at Hanifaru Bay,
416 and this information can help inform management of this ecologically and economically
417 important marine protected area and core zone within a UNESCO Biosphere Reserve.

418

419

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425

426

427

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551

Figure 1

Figure 1. Study site in Hanifaru Bay in Baa Atoll, The Maldives.

A) Map of The Maldives, black star indicates location of Hanifaru Bay in Baa Atoll; and B) Satellite image of Hanifaru Island and Lagoon, with key study site of Hanifaru Bay (Credit: Copernicus Sentinel data 2020, accessed via USGS EarthExplorer and processed by AJA).

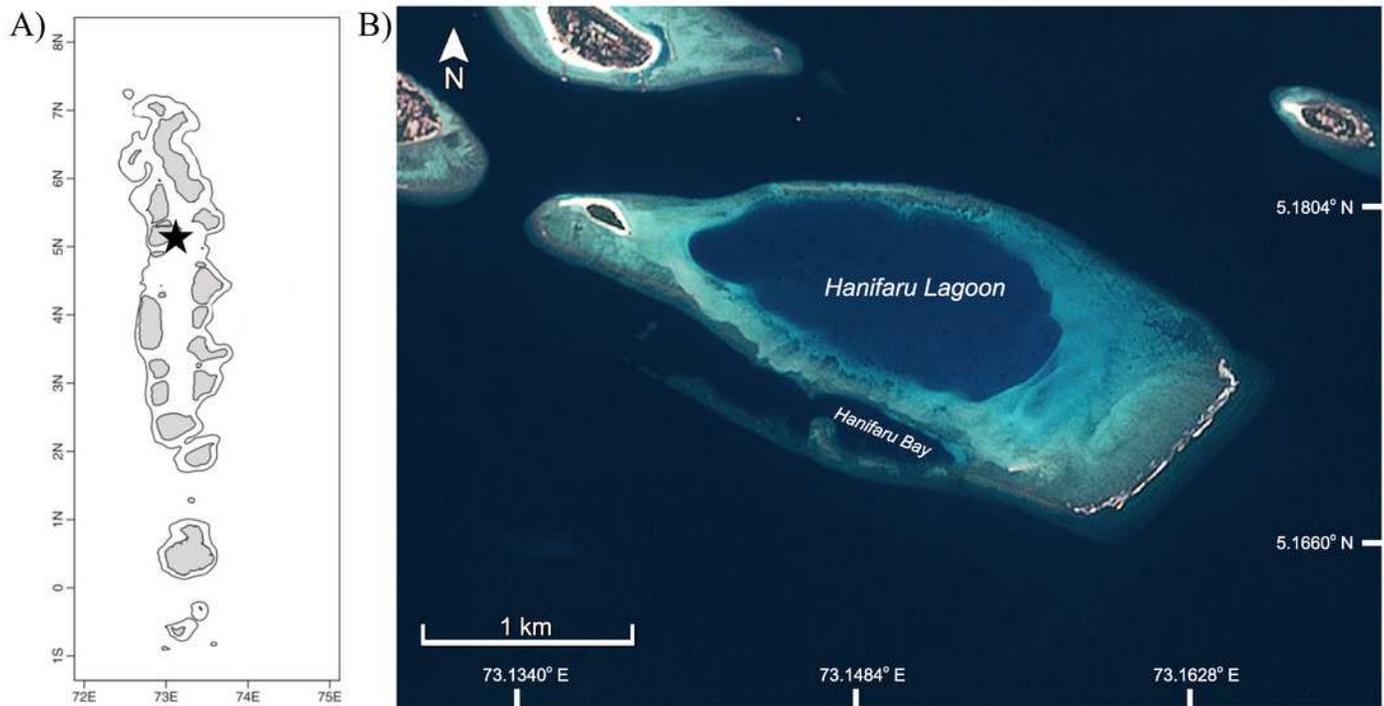


Figure 2

Figure 2. Zooplankton sampling and reef manta ray *Mobula alfredi* feeding strategies.

A) Zooplankton samples were collected by two snorkellers surface swimming a 200 μm -mesh net with flowmeter for ~ 50 m; and B) Ethogram of feeding strategies: i) Straight, ii) Surface, iii) Chain, iv) Piggy-back, v) Somersault, vi) Cyclone, vii) Sideways, and viii) Bottom (Illustration credit: Marc Dando).

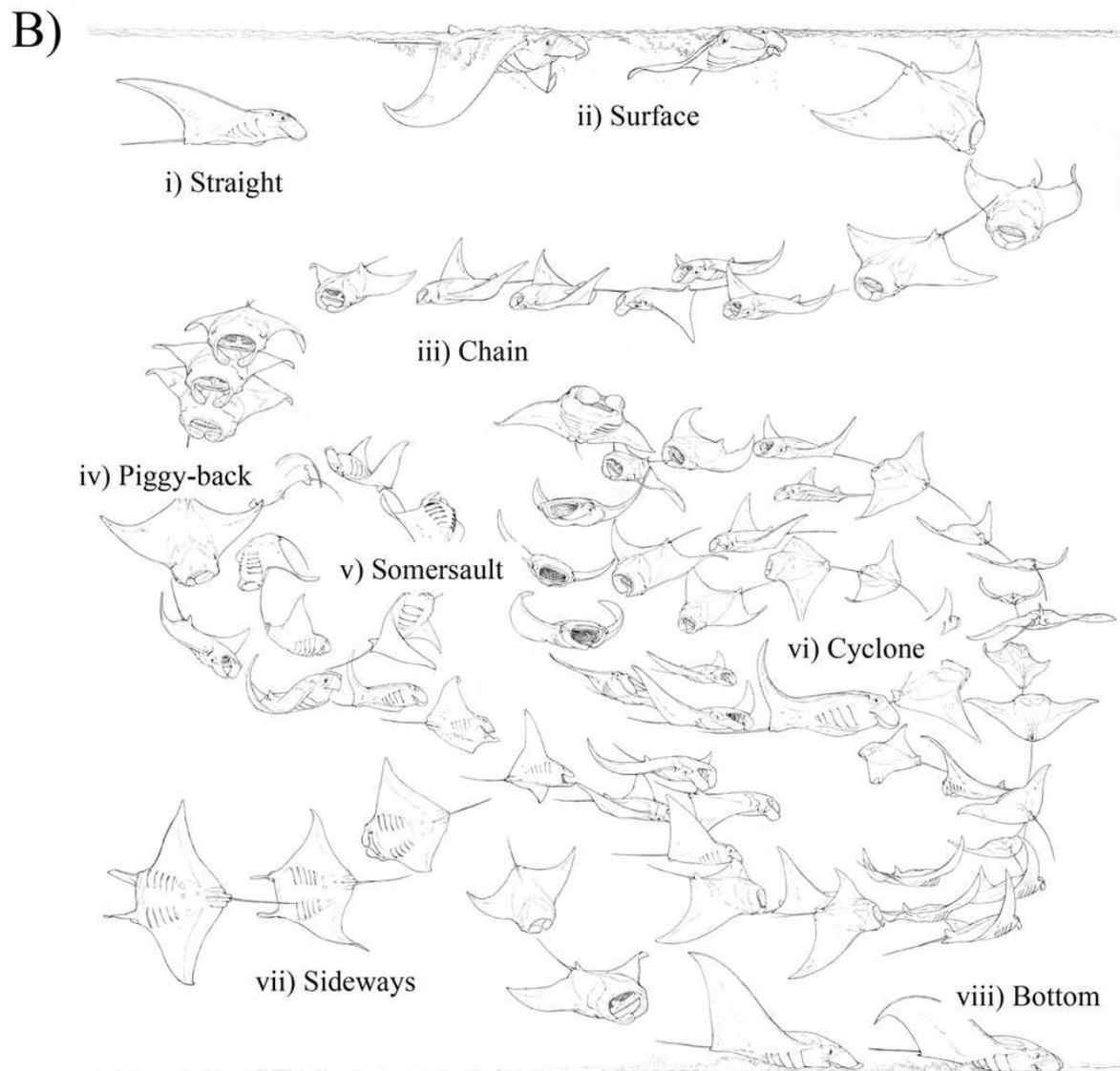


Figure 3

Figure 3. Predictors of Zooplankton biomass in Hanifaru Bay, Maldives.

Significant predictors of Zooplankton biomass included A) Tide (hours from high tide), and B) Manta ray behaviour (Feeding, Non-feeding and Absent). Biomass is on the response scale, with 95% confidence intervals.

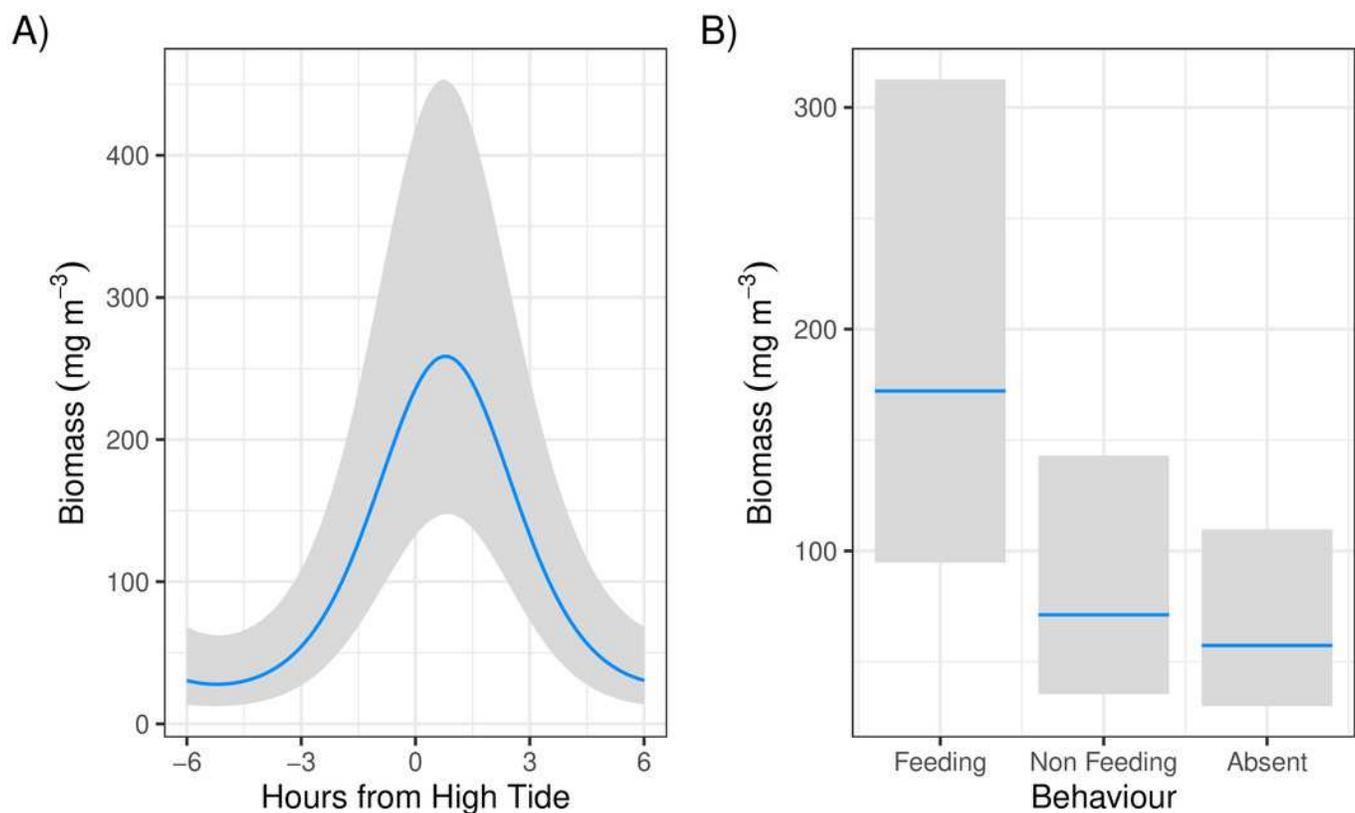


Figure 4

Figure 4. Critical prey density foraging threshold.

Logistic regression of reef manta ray *Mobula alfredi* behaviour (Feeding = 1, Non-feeding = 0) in relation to zooplankton biomass (mg m^{-3}). The black dashed line represents the critical prey density threshold of zooplankton biomass required to trigger manta ray feeding from *in situ* sampling (53.7 mg m^{-3}), and the red dashed line represents the theoretical prey density threshold calculated to meet the metabolic requirements of foraging *M. alfredi* (25.2 mg m^{-3} ; Armstrong et al. 2016).

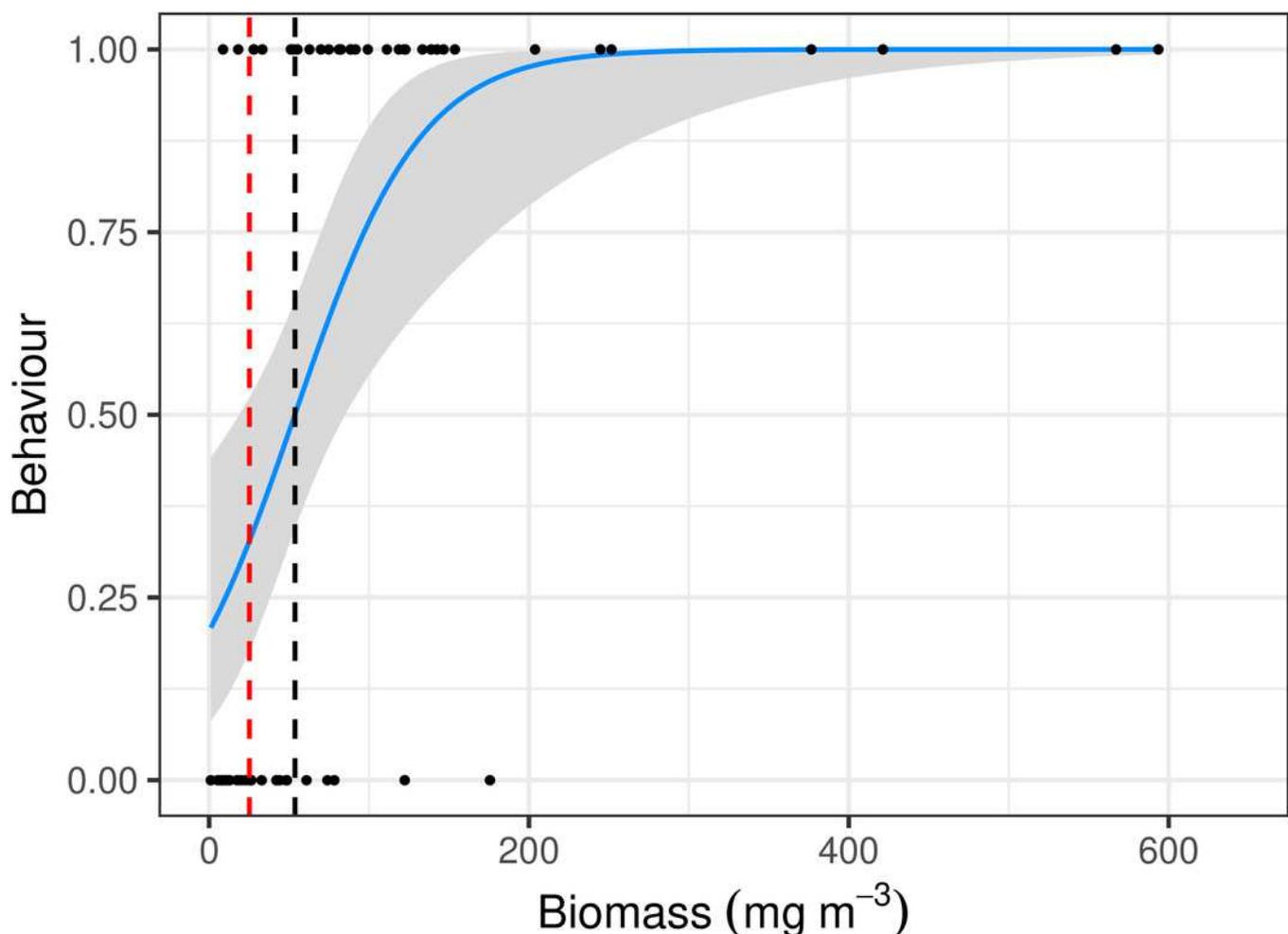


Figure 5

Figure 5. Predictors of reef manta ray *Mobula alfredi* abundance in Hanifaru Bay, Maldives.

Feeding Behaviour was a significant predictor of greater manta ray numbers in Hanifaru Bay. Manta ray abundance is on the response scale, with 95% confidence intervals.

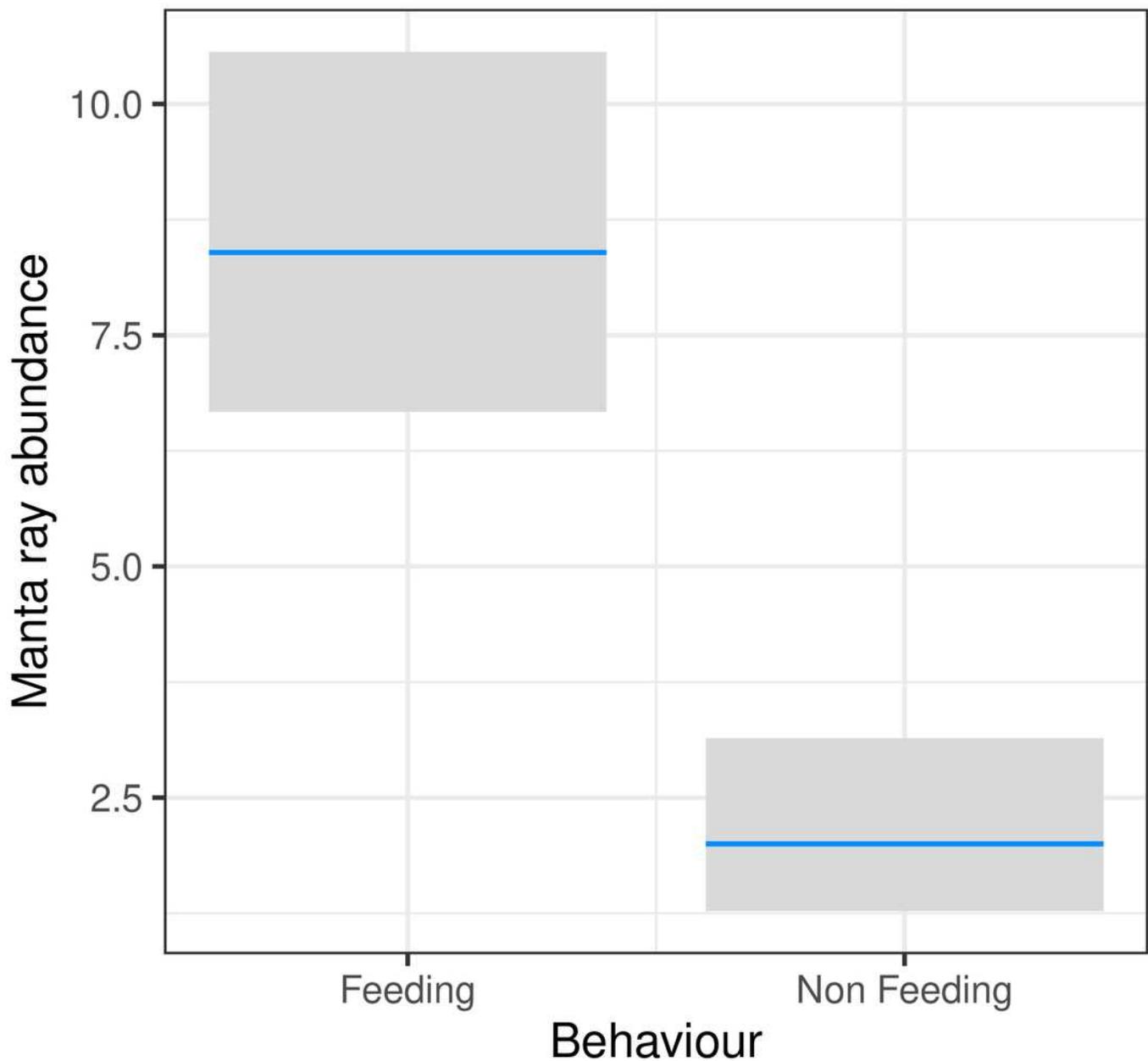


Figure 6

Figure 6. Zooplankton composition and reef manta ray *Mobula alfredi* behaviour.

A) Non-metric multidimensional scaling analysis of zooplankton community composition. Ellipses represent 95% confidence intervals and broad taxonomic groups are labelled as per their association with manta ray behaviours. B) *Undinula vulgaris* specimens (Credit: Julian Uribe-Palomino). Percentages of zooplankton community composition in Hanifaru Bay in relation to manta ray behaviour: C) Feeding; and D) Non-feeding. 'Other' comprises taxonomic groups that contributed less than 5% to the total community composition.

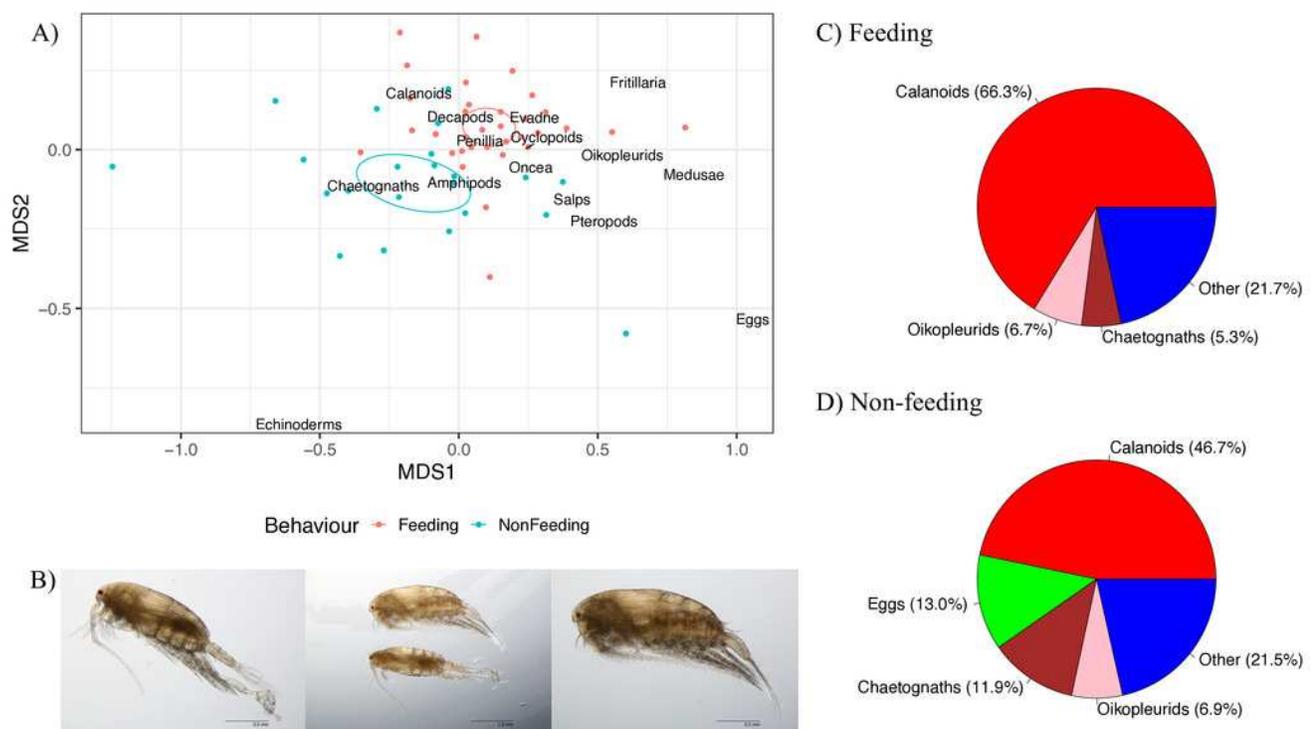


Figure 7

Figure 7. Zooplankton size structure analysis.

Normalised Biovolume Size Spectra of the zooplankton community when reef manta rays *Mobula alfredi* are Feeding ($n = 33$) and Non-feeding ($n = 22$). Dashed lines represent standard error.

