Beta diversity of pelagic assemblages at fish aggregating devices in the open ocean

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Owing to difficulties in accessing the vast open ocean, the beta (β) diversity of pelagic fish assemblages remains poorly studied. We investigated the relationship between assemblage similarity and geographical distance between anchored fish aggregating devices (FADs), sampled by standardised underwater visual censuses in three anchored FAD arrays in the Indian Ocean—at the Maldives, the Seychelles and Mauritius. The use of two complementary indices of β-diversity, based on presence/absence data (Jaccard similarity coefficient) and abundance data (Bray–Curtis index), revealed that geographical distance between sampling sites (from 4 to 257 km) appeared to have no effect on the similarity of fish assemblages associated with FADs within each array. The results of this preliminary study question the generalisation of the paradigm of an increase in β-diversity with geographic distance to the open-ocean fish community. Large-scale studies using a variety of datasets should be conducted to further investigate patterns of β-diversity in the open ocean.

Keywords: FADs, Indian Ocean, Maldives, Mauritius, pelagic fish diversity, Seychelles, species composition, underwater visual census

Introduction

Characterising how diversity changes according to different spatial and temporal scales is a fundamental goal in community ecology (e.g. Legendre and Fortin 1989). However, the study of patterns in fish diversity in the open ocean, the largest ecosystem on the earth (Angel 1993), is still in its infancy. This situation is largely due to the logistical and financial constraints associated with collecting relevant data for the analysis of biodiversity in such a difficult-to-access environment (Gaertner et al. 2008). As a consequence, the first attempts to infer worldwide patterns of species richness were restricted to both large predatory fishes and fisheries-dependent datasets (Worm et al. 2003; Trebilco et al. 2011). Although fisheries data remain an important data source, they have several shortcomings, and fisheries-independent methods are needed to complement the general picture of the diversity in pelagic ecosystems (Murphy and Jenkins 2010). In the last decade, several non-destructive and reproducible fisheries-independent methods have been developed to study pelagic fish assemblages, such as midwater baited camera surveys (Letessier et al. 2013; Santana-Garcon et al. 2014) or underwater visual censuses (UVCs) at fish aggregating devices (FADs) (Gaertner et al. 2008). Anchored or drifting FADs are artificial floating devices built by fishers to facilitate the capture of targeted pelagic species, usually tunas (Hunter and Mitchell 1967; Fonteneau et al. 2000). Several studies have investigated pelagic fish assemblages at FADs (Castro et al. 1999; Dempster 2005; Addis et al. 2006; Andaloro et al. 2007; Taquet et al. 2007). Gaertner et al. (2008) advocated that sampling at FADs allows the study of a well-delimited and reproducible part of the pelagic fish community, which then can help the monitoring of open-ocean fish diversity.

Beta (β) diversity involves investigations of species changes in space and/or time, as well as ecological connectivity (Anderson et al. 2011). As such it allows the identification of heterogeneous communities and is thus regarded as a valuable tool for conservation and ecosystem-based fisheries management (Anderson et al. 2013). Generally, β-diversity has been found to increase with respect to geographical distance in both terrestrial and marine environments (Soininen et al. 2007; Shackell et al. 2012). We tested this hypothesis for open-ocean pelagic fish diversity. We assessed changes in β-diversity between pairs of FADs along a spatial gradient within anchored FAD arrays in three areas of the Indian Ocean, considered as three different case studies.

Materials and methods

In each of the anchored FAD arrays (at the Maldives, the Seychelles and Mauritius) (Appendix 1), UVCs were conducted by SCUBA divers on four specific anchored FADs which were sampled on the same day. These UVCs were repeated (conditions permitting) five times in the Maldives, four times in the Seychelles, and three times in Mauritius, between May 2008 and January 2011 (Table 1). All the surveyed FADs were anchored at depths greater than 300 m and were thus considered to be offshore deep-water FADs. The FAD design within each country was identical but could differ between countries. In the Maldives, the floating structure of the FAD consisted of a single large fibreglass buoy (1.5 m in diameter), whereas in Mauritius and the Seychelles a chain of rigid buoys (0.2 m in diameter) was used. The dives were conducted between 08:00 and 15:00, at 15 m depth and for a 30-minute duration, following a standardised UVC protocol (Gaertner et al. 2008). The horizontal visibility during the UVCs varied between 15 and 20 m, and thus we considered that the volumes sampled during all the UVCs were comparable. Owing to safety concerns, the UVCs were performed only in calm to moderate sea conditions (i.e. wind speed <30 km h^{-1}, wave height <1.5 m, and surface current speed ≤1.9 km h^{-1}). Tuna species were not included in the censuses as they often occurred outside the visual range of the scientific divers, making estimations of these species particularly inaccurate (Gaertner et al. 2008).

Within each FAD array, we investigated the effects of the geographical distance between each pair of FADs i and j on the composition of their fish assemblage. Here, low values of similarity indices indicated high β-diversity. We used two complementary similarity indices: Jaccard's coefficient of similarity (S_{ij}) and the Bray–Curtis similarity index (1–BC_{ij}); S_{ij} is based on presence/absence data and takes into account the proportion of unshared species between two FADs, whereas 1–BC_{ij} is based on abundance data (Anderson et al. 2011). A log transformation, log(n+1), was applied to the abundance data n to minimise the effect of highly abundant species (e.g. schooling fish), prior to calculating the Bray–Curtis index. The pairwise comparisons were computed independently within each FAD array and on the same sampling dates only. This was done to exclude possible seasonal effects as reported in other studies (Dempster 2005). Furthermore, linear mixed-effects models were used to test the effect of the geographical distance on each index (Y_{ij}) for each FAD array. Each pair of UVCs was classified according to the date on which they were carried out. The sampling-date effect (μo_i) was thus treated as random variations around a population mean, and the distance between anchored FADs ($\beta_1 \text{dist}_{ij}$) was assessed as a fixed continuous covariate, as follows:

$$Y_{ij} = \beta_0 + \beta_1 \text{dist}_{ij} \times \mu o_i + \varepsilon_{ij}$$

Results

A total of 19 species (12 families), 14 species (9 families) and 21 species (10 families) were observed in the Maldives, the Seychelles and Mauritius, respectively (Figure 1). Carangidae (such as *Elagatis bipinnulata*, *Caranx sexfasciatus* and *Decapterus macarellus*) were the most frequent recorded species in each FAD array (Figure 1a). Figure 1b displays the distribution of fish species richness for each FAD array. The Maldives had a higher mean species richness per UVC (mean 7.3 [SD 2.4]; Kruskal–Wallis test: χ^2 = 20.8, df = 2, p < 0.05) than both Mauritius (mean 4.7 [SD 1.7]) and the Seychelles (mean 3.8 [SD 1.2]). β-diversity expressed through both the S_{ij} and 1–BC_{ij} similarity indices generally exhibited no trend with an increase in geographical distance between FADs in each FAD array (i.e. the geographical distance between

Table 1: Summary of the sampling by underwater visual census (UVC) conducted at anchored fish aggregating devices (FADs) in three countries in the western Indian Ocean, between May 2008 and January 2011

Area	Sampling date (no. UVCs)	Total no. of UVCs	No. of FAD pairs compared	Distance between FADs (km)
Maldives	Nov 2009 (4)	19	27	39–257
	Feb 2010 (3)			
	Apr 2010 (4)			
	Oct 2010 (4)			
	Jan 2011 (4)			
Seychelles	Jan 2010 (4)	15	21	4–34
	Apr 2010 (4)			
	Oct 2010 (4)			
	Dec 2010 (3)			
Mauritius	May 2008 (3)	11	15	11–31
	Oct 2010 (4)			
	Dec 2010(4)			

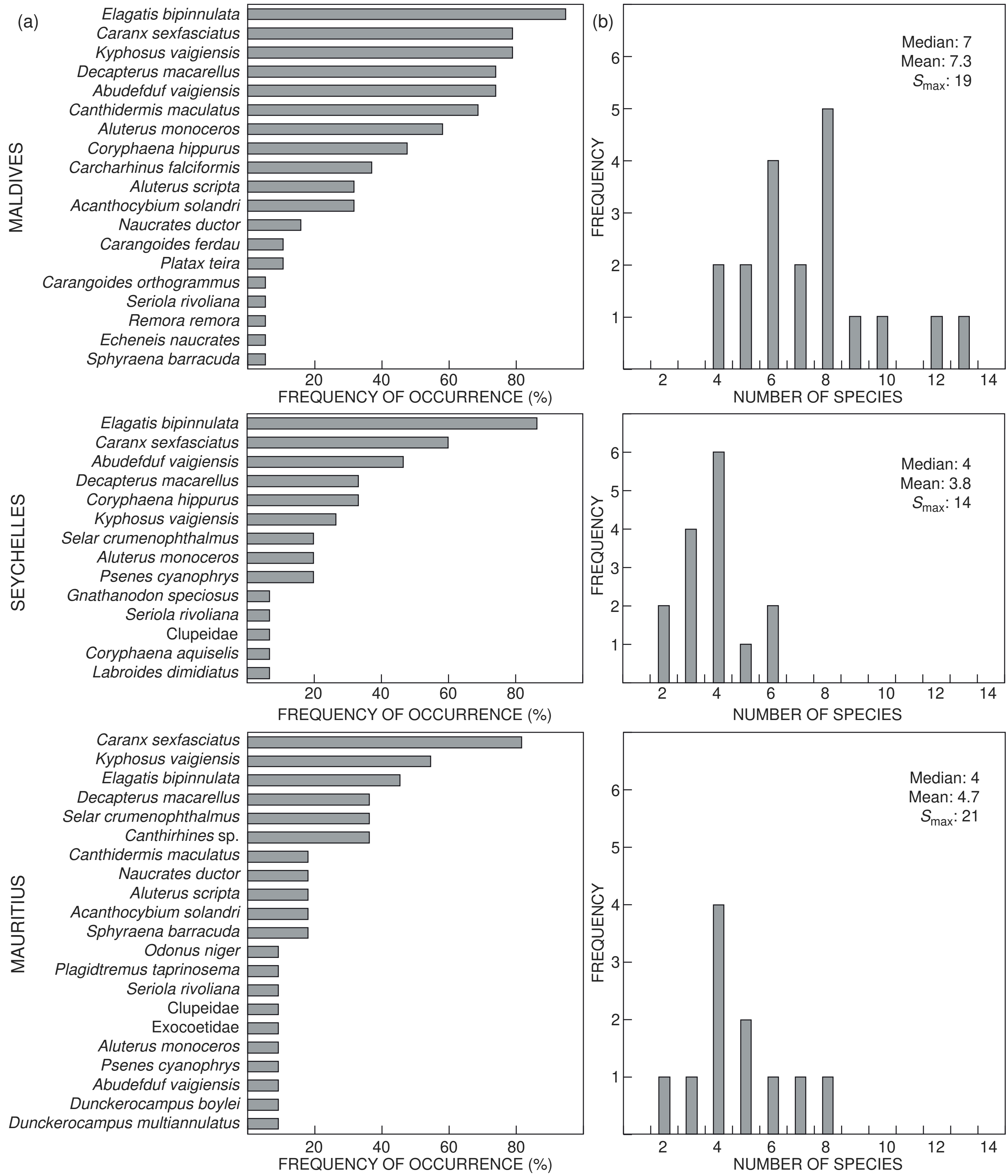

Figure 1: (a) Overall frequency of occurrence and (b) frequency of species richness observed per underwater visual census at anchored fish aggregating devices in the three study areas (Maldives, Seychelles and Mauritius) between May 2008 and January 2011. S_{max} = maximum species richness

FADs was generally not a significant fixed-effect in the mixed models) (Figure 2; Appendix 2). The only significant test result occurred with 1–BC_{ij} (p = 0.04) for the Maldives, and is clearly explained by index values computed for the two distances in this array (39 and 158 km). Finally, both S_{ij} and 1–BC_{ij} similarity values indicate that there is an overall low similarity (mean S_{ij} 0.33 [SD 0.12]; mean 1–BC_{ij} 0.33 [SD 0.14]) of fish assemblages between two pairs of FADs (Figure 2).

Discussion

Standardised UVC observations allowed us to investigate fish assemblage patterns among a delimited component of the epipelagic diversity, and species richness measured here is comparable to that of previous studies measuring pelagic fish diversity using baited remote underwater video systems (BRUVS) (Bouchet and Meeuwig 2015; Rees et al. 2015; Santana-Garcon 2015), UVCs (Addis et al. 2006; Gaertner et al. 2008), and fisheries data at FADs (Lezama-Ochoa et al. 2015; Ruiz et al. 2018). Among the wide variety of available methods to assess β-diversity, Anderson et al. (2011) outlined two different conceptual types of β-diversity: (i) a non-directional variation in species' identities or community structure among sample units within a given area or region at a given spatial (or temporal) scale; and (ii) a directional turnover in community structure or species' identities along a spatial, temporal or environmental gradient. We used indices from the second category as we investigated the effect of geographical distance between each pair of FADs on the fish assemblage composition. Surprisingly, in each FAD

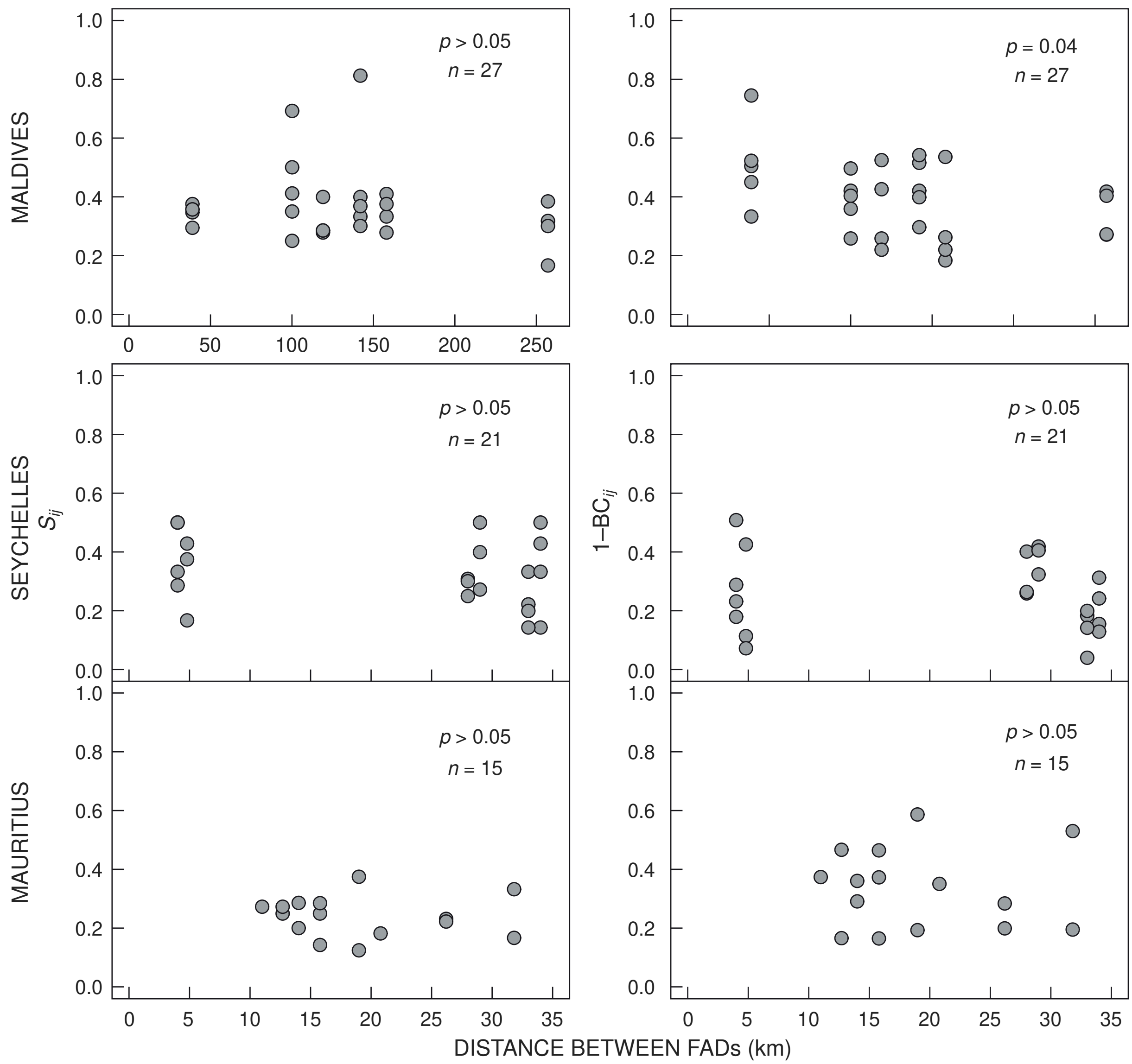

Figure 2: Jaccard (S_{ij}) and Bray–Curtis (1–BC_{ij}) similarity indices compared at different distances between the anchored fish aggregating devices within each study area (Maldives, Seychelles and Mauritius). The p-values refer to the linear mixed-effects models, and n denotes the number of pairwise comparisons on the same sampling day

array, the geographical distance between sampling sites (from 4 to 257 km) generally had no effect on the similarity of assemblages for both indices. Patterns in β-diversity are sensitive to variation in the number of species measured at alpha (α) diversity between two assemblages when sampling effort differs (Chase et al. 2011). Thus, comparing assemblages when this effort differs automatically induces changes in β-diversity. In such a case, the β-diversity Raup–Crick index, based on presence/absence data, accounts for the effect of differential α-diversity on measuring β-diversity (Chase et al. 2011). However, sampling effort was standardised in our study, and the Raup–Crick values (not shown) confirmed results from the Jaccard indices.

Our findings contrast with the general pattern in β-diversity usually observed for many communities in marine ecosystems, in which the similarity in species assemblage decreases with distance between sites; this is known as the distance-decay relationship (Soininen et al. 2007; Shackell et al. 2012). Generally, environmental factors play a central role in this relationship that is observed in other ecosystems. However, few studies have investigated the influence of environmental factors at small-scale (~1–20 km) or meso-scale (~20–200 km) on pelagic fish. Sub-mesoscale frontal dynamics (1–10 km) in the Mozambique Channel were observed to shape the distribution of marine top predators (Tew Kai et al. 2009), and in the Humboldt Current System fine-scale ocean dynamics (1–4 km) were found to affect the seascape from zooplankton to predators (Bertrand et al. 2014). However, no studies have investigated the effect of oceanographic conditions on the composition of species assemblages at FADs.

In conclusion, our results question the current perception of fish diversity in pelagic ecosystems, suggesting heterogeneity in assemblages among FADs even at close distances and in a seemingly featureless environment. Pelagic fishes are considered to be highly mobile organisms, with the standard order of magnitude of the horizontal scale in the distribution of communities considered to be large (~10^3 km: Angel 1993). These features are peculiar to the pelagic realm, and could explain why the distance-decay relationship, which is observed in most marine and terrestrial ecosystems, was not observed here in a pelagic ecosystem. Equipping FADs with oceanographic probes would allow the collection of *in situ* data and the investigation of whether or not environmental changes can occur at small spatial scales.

Additionally, investigation of the behavioural dynamics driving multispecies aggregations could help to interpret our results. One hypothesis is that fish assemblages from FADs that are close to each other (e.g. a few kilometres apart) could have interactions that could shape their composition. For instance, complex behavioural processes within species (e.g. social behaviour) or between species (e.g. agonistic behaviour) could affect species occurrence and abundance at such FADs. Hence, there is a need to collect additional simultaneous *in situ* data (particularly behavioural data) on fish assemblages to develop a better understanding of the processes that forge pelagic diversity patterns in the open ocean at spatial scales over which such processes take effect. Finally, a meta-analysis using a variety of available datasets should be conducted to further investigate patterns of β-diversity in the open ocean.

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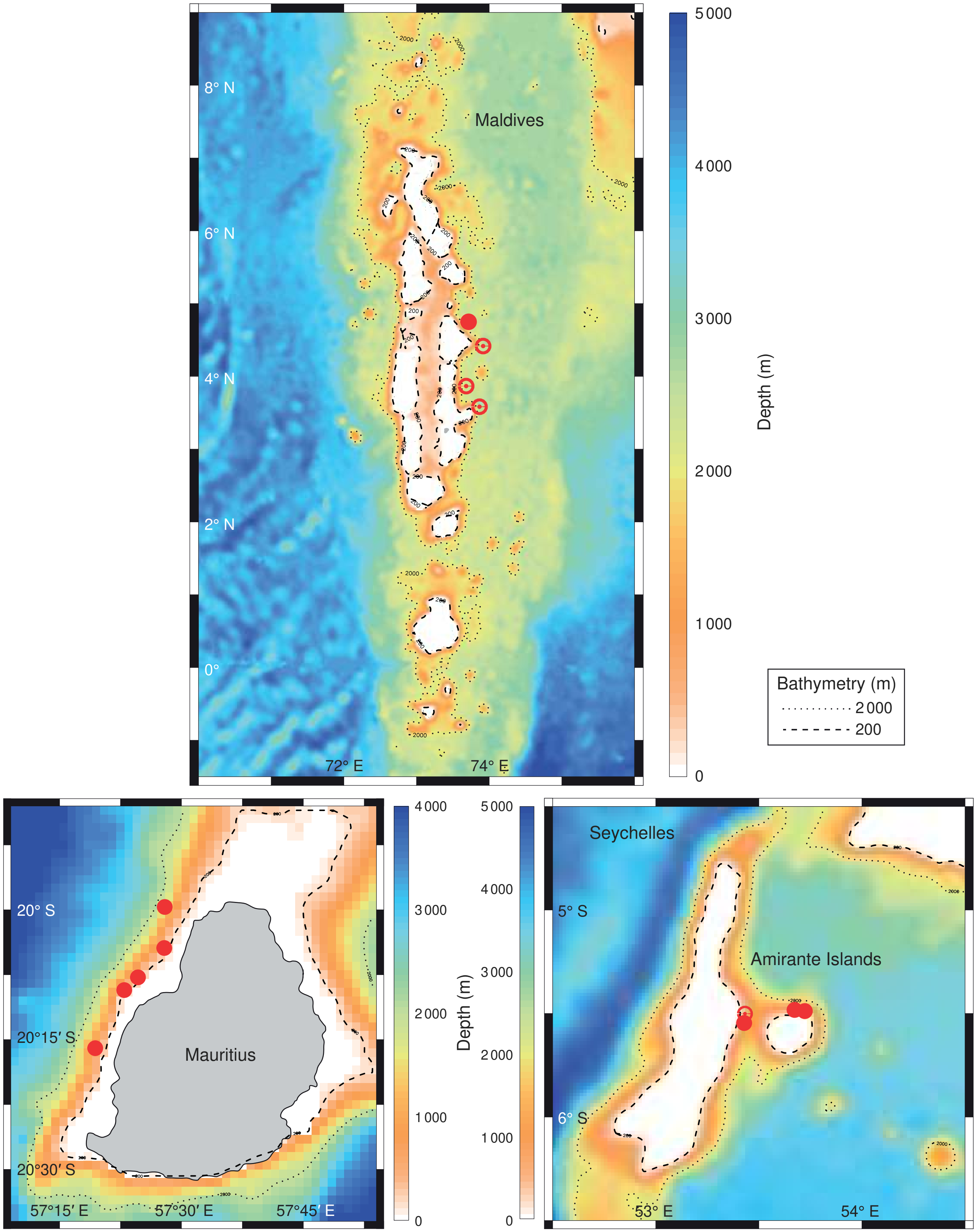

Appendix 1: Maps of the Maldives, the Seychelles and Mauritius, with red dots denoting the positions of the experimental anchored fish aggregating devices

Appendix 2a: Summary results of the linear mixed-effects model for the Bray–Curtis similarity index (1–BC_{ij}). Bold values are significant

Predictors	Maldives			Mauritius			Seychelles		
	Estimates	CI	*p*-value	Estimates	CI	*p*-value	Estimates	CI	*p*-value
(Intercept)	0.49	0.38–0.60	**<0.001**	0.35	0.13–0.57	0.002	0.28	0.16–0.39	**<0.001**
Distance	−0.00	−0.00–0.00	**0.043**	−0.00	−0.01–0.01	0.871	−0.00	−0.01–0.00	0.565
Random effects									
σ^2	0.01			0.02			0.01		
τ_{00}	0.00_{Season}			0.00_{Season}			0.00_{Season}		
ICC	0.27						0.13		
N	5_{Season}			3_{Season}			4_{Season}		
Observations	27			15			21		
Marginal R^2/ Conditional R^2	0.118/0.356			0.002/NA			0.014/0.145		

Appendix 2b: Summary results of the linear mixed-effects model for the Jaccard similarity index (S_{ij}). Bold values are significant

Predictors	Maldives			Mauritius			Seychelles		
	Estimates	CI	*p*-value	Estimates	CI	*p*-value	Estimates	CI	*p*-value
(Intercept)	0.41	0.30–0.52	**<0.001**	0.25	0.15–0.36	**<0.001**	0.38	0.28–0.48	**<0.001**
Distance	−0.00	−0.00–0.00	0.424	−0.00	−0.01–0.00	0.707	−0.00	−0.01–0.00	0.221
Random effects									
σ^2	0.02			0.00			0.01		
τ_{00}	0.00_{Season}			0.00_{Season}			0.00_{Season}		
ICC	0.02			0.45			0.09		
N	5_{Season}			3_{Season}			4_{Season}		
Observations	27			15			21		
Marginal R^2/ Conditional R^2	0.024/0.047			0.006/0.454			0.064/0.145		