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Assessing the multicomponent aspect of coral fish diversity: The impact of sampling unit dimensions

Nicolas Loiseau[a,*], J.-C. Gaertner[b], M. Kulbicki[c], B. Mérigot[d], G. Legras[a], M. Taquet[b], N. Gaertner-Mazouni[a]

[a] University of French Polynesia, UMR-241 EIO (UPF, IRD, Ifremer, ILM) Papeete, Labex Corail, French Polynesia
[b] Institut de Recherche pour le Développement (IRD), UMR-241 EIO (UPF, IRD, Ifremer, ILM), Labex Corail, Centre IRD de Tahiti, BP, 98713 Papeete, French Polynesia
[c] UR 227 "Coreus", Labex Corail, IRD, Laboratoire Arago, BP 44, 66651 Banyuls/mer, France
[d] Université Montpellier 2, UMR MARBEC, CRH, Av. Jean Monnet, BP 171, 34203 Sète, France

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A B S T R A C T

The influence of variations in sampling unit dimensions on the assessment of fish species structuring has been widely documented. However, this issue has been restricted to a very limited range of community and population indices (mainly species richness and density). Here, we have investigated this issue through the analysis of 13 diversity indices related to 3 diversity components (number of species, evenness and functional diversity). We analyzed a large set of 257 standardized underwater visual census (UVC) transects dealing with 254 coral fish species. The sensitivity of the indices to the variation in sampling unit dimensions was studied by comparing a range of 55 couples of transect length and width representing 34 sampling surfaces. We found that the extent and profile of the sensitivity to changes in transect dimensions strongly varied both from one index to another and from one dimension to another (length and width). The most sensitive indices were more strongly impacted by variation in length than width. We also showed that for a fixed transect surface, the couple of chosen length and width may alter the assessment of indices related to each of the three main diversity components studied. Some widely used diversity indices, such as species richness and Shannon index, appeared to be very sensitive to changes in transect length and width. In contrast, while still very little used in coral fish studies, two functional diversity indices (FDiv, FEve), and to a lesser extent an evenness index (Berger–Parker), remained robust in the face of change in sampling dimensions. By showing that the variation in sampling dimensions (length, width and surface) may impact diversity indices in a contrasting manner, we stress the need to take into account the sensitivity of the indices to this criterion in the process of selection of the indices to be analyzed in diversity studies. Finally, we found that 30 m long*5 m wide transects might be a suitable compromise size for assessing the patterns of each of the three major complementary components of coral fish diversity.

1. Introduction

Underwater visual censuses (UVC) can provide rapid estimates of relative diversity, abundance, biomass, and length frequency distributions of marine macro-species. For this reason, it is by far the most widely used method for coral reef ecosystems in studies dealing with the population and community dynamics, ecology and management of numerous taxa, such as coral (Nadon and Stirling, 2006; Osborne et al., 2011), echinoderms (Dalleau et al., 2010; Johansson et al., 2013), and fishes (Chabanet et al., 1997; McClanahan et al., 2007; D'agata et al., 2014). At the scale of the tropical belt, and in particular in the Pacific Ocean, UVC focusing on fishes are mainly based on transects (Bozec et al., 2005; Berumen and Pratchett, 2006).

Despite their success, UVCs – like any other field sampling methods – suffer from several drawbacks. For instance, previous fish studies showed that the presence and movements of the diver

Abbreviations: UVC, underwater visual census; MAE, Mean Absolute Error equation; SD, standard deviation; S, species richness; D_{mg}, Margalef index; H', Shannon index; 1-D, Simpson index; J, Pielou index; H_{eip}, Heip index; $1/d$, Berger–Parker index; Q, Rao index; FD, FD index; FRic, functional richness; FEve, functional evenness; FDis, functional dispersion; FDiv, functional divergence.

* Corresponding author. Tel.: +689 40866443.
E-mail address: nicolas.loiseau@upf.pf (N. Loiseau).

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(Dickens et al., 2011), as well as the observer's experience and training level (Williams et al., 2006), may affect the accuracy of estimates. Other factors affecting fish count accuracy include species characteristics (e.g. crypticity, mean size), the type of substrata and the sampling conditions (see review in suppl. material Kulbicki et al., 2010; Bozec et al., 2011). Numerous authors also noted that the detection of species and density estimates respond differently to transect dimensions (Sale and Sharp, 1983; Mapstone and Ayling, 1998; Kulbicki and Sarramégna, 1999; Kulbicki et al., 2010). A non-exhaustive analysis of the literature shows that studies dealing with coral fish diversity were based on a wide range of transect lengths (from 10 m, Bejarano et al., 2013 to 250 m, Westera et al., 2003) and width (from 1 m, Heinlein et al., 2010 to open width, Kulbicki et al., 2010). In this context, reef ecologists are faced with the problem of defining the most suitable width and length of sample units for properly assessing and monitoring coral fishes in time and space (Kulbicki et al., 2010). This issue is of particular importance in the current context where monitoring coral fish diversity patterns is increasingly in demand at large scale (Bellwood and Hughes, 2001; Stuart-Smith et al., 2013) but is often based on the compilation of preexisting local data bases with non- or poorly-standardized sampling protocols (Bellwood and Hughes, 2001; Mora et al., 2011; Mouillot et al., 2014). To date, investigations of the impact of variation in sampling unit dimensions on coral fish assessment has been restricted to a very limited range of community descriptors, mainly species richness and species density/abundance (Samoilys and Carlos, 2000; Stewart and Beukers, 2000; Kulbicki et al., 2010). In contrast, little consideration has been paid to the response of the other facets (or components) of coral fish diversity to the variability of these sampling criteria. For instance, the direction and extent to which variation in spatial unit sampling dimensions may alter our perception of patterns in evenness or functional diversity has still not been assessed. This gap is particularly striking in a context where diversity is now considered as a complex and multi-component concept that cannot be reduced to a single index (Purvis and Hector, 2000; Villéger et al., 2008). Along these lines, we have tested the influence of transect dimensions (length and width) on the assessment of multiple indices related to three major complementary diversity components (number of species, evenness and functional diversity).

Specifically, we have addressed the following questions: How sensitive are the indices of the main diversity components to variations in transect dimensions? Are there thresholds in transect length and/or width beyond which our perception of the diversity of an assemblage tends to stabilize? For a fixed surface unit, may the variation in the shape of the transect (i.e. length vs. width) impact our assessment of diversity indices?

2. Material and methods

2.1. Indices considered

The diversity indices considered in the present study were selected in such a way as to enable us to cover a wide range of data types in terms of nature (availability or not of functional information) and accuracy (e.g. presence absence vs. abundance per species). The extent of their use in coral fish studies and their ability to describe complementary aspects of species diversity were 2 additional criteria used for the selection of the set of diversity indices considered. The complementarity of the diversity indices was estimated on the basis of both their conceptual and statistical properties and their empirical relationships. Regarding the latter point, indices showing complementary diversity patterns as well as those offering redundant information were identified through a principal component analysis (PCA) and Spearman rank correlation coefficients (see Mérigot et al., 2007). On this basis, we selected 13 diversity indices related to three major complementary diversity components: number of species, evenness and functional diversity. The number of species component is still, by far, the most widely used component of diversity in both marine and terrestrial ecosystems (Chiarucci et al., 2011). Here we investigated this component through two indices: the number of species per transect (species density S) and Margalef's index (D_{mg}) (Margalef, 1958), which adjusts the number of species according to the total number of individuals sampled in each census. The evenness component is thought to play a major role in terms of both ecosystem response and ecosystem functioning (Hillebrand et al., 2008; Wittebolle et al., 2009). Because evenness indices may highlight different aspects of the variability in abundance distribution among species, we computed three complementary indices: Heip (H_{eip}, Heip, 1974), Berger–Parker ($1/d$, Berger and Parker, 1970) and Pielou (J, Pielou, 1969) indices that exhibit different sensitivity to dominant or rare species (see Beisel et al., 2003). We also computed two heterogeneous indices: Shannon-Wiener index H' (Shannon and Weaver, 1949) and the Simpson diversity index 1-D (Simpson, 1949). This widely used family of indices combines both the number of species and evenness components in a single value.

All the indices mentioned above assume that each species contributes to diversity in the same manner and they do not explicitly take into account functional differences between species. However, functional diversity is assumed to be a major driver of ecosystems functioning (Tilman et al., 2001). In particular, functional diversity has been found to be more sensitive to human pressure than species richness of coral fishes (D'agata et al., 2014). Consequently, we additionally computed six indices that quantify different aspects of functional diversity of a faunal assemblage (hereafter referred to as functional diversity indices). Because collecting presence–absence data can be easier and less costly than collecting abundance data, we investigated the FD index (Petchey and Gaston, 2006). This index is the sum of distances between species on a functional tree. We also computed Rao's quadratic entropy (Rao, 1982; Botta-Dukát, 2005), one of the most popular functional indices in ecology (Pavoine, 2012). This index measures the average distance between two randomly selected individuals in the community and takes into account both functional traits and the distribution (abundance) of these traits within the assemblage. Finally, we computed FRic, FEve, FDiv (Villéger et al., 2008) and FDis (Laliberté and Legendre, 2010) on the basis of the functional space theory (Cornwell et al., 2006). Indices not ranged between 0 and 1 were standardized between 0 and 1 (dividing by the maximum) in order to facilitate their comparison.

2.2. Data set

We analyzed data issued from the TYPATOLL program (Dufour and Harmelin-Vivien, 1997; Kulbicki et al., 2010). Sampling was conducted from November to December, in 1995 and 1996, in the central Tuamotu Archipelago on 10 atolls (Kulbicki et al., 2010). At each station, four 50 m long transects were set 100–300 m apart (4 m depth on average). Each transect was cut into five 10 m long sectors. Along each transect, divers recorded the species name of each fish encountered, the number of fish and distance of the fish to the transect (open width). In order to minimize observer bias, data analyzed in this study were restricted to UVC carried out by two experienced coral fish divers (Kulbicki M. and Moutham G.). These two divers had been previously trained together to identify fish species, fish distance to the transect and the number of individuals within schools. Data related to eight functional traits were available and used in this study for computing the functional