Fishing and drought effects on fish assemblages of the central Amazon Basin

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\section*{ABSTRACT}

One method with considerable potential for understanding fishing and environmental impacts on fish assemblages is size spectra (SS) and diversity size spectra (DSS) analysis—a regression of Ln abundance or Shannon diversity against the natural logarithm of body size of fish assemblages. But the usefulness of this method for application to tropical freshwater fish assemblages is uncertain. Here, we assessed the extent to which SS and DSS analyses explained changes in the exploited fish assemblage related to fishing effort and river droughts. To do this, we used correlation analyses on historical datasets of river water level, fishing effort, and fish length measurements for 56 fish species in three of the largest rivers of the Amazon Basin. In calculating the SS and DSS analysis statistics, we found that linear regressions adjusted well to the diversity and Ln(abundance) data plotted against Ln(fork length). In analysing SS and DSS statistics in relation to fishing and environmental impacts, we found that the slope of SS was negatively correlated to drought intensity with a lag of zero years in all rivers. The slope of SS also was negatively correlated to fishing effort with a lag of three years in two rivers and a lag of two years in one year. The slope of DSS was not correlated to drought intensity and fishing effort in any of the rivers. Our results provide support for the use of SS analysis to investigate fishing and environmental effects on exploited fish assemblages in tropical freshwater environments.

\section*{1. Introduction}

There is an increasing need to understand and mitigate the impacts of fishing on marine and freshwater ecosystems (Fogarty and Murawski, 1998; Jackson et al., 2001; Pauly et al., 2002). A promising approach to the current fisheries crisis is ecosystem-based fisheries management (Pikitch et al., 2004), which is inspired by recognition that maintaining healthy marine ecosystems is fundamental to the fisheries they support. Although of relatively recent origin, ecosystem approaches are becoming a routine part of fisheries assessment and management (Garcia and Cochrane, 2003; Tegner and Dayton, 1999). New methods to identify anthropogenic effects on exploited fish assemblages and ecosystems are being tested and developed.

Body size influences many ecological processes, from individual rates up to the structure of food webs and the provision of ecosystem services such as food (Blanchard, 2011). Given the importance of body size of individuals, one approach with considerable potential for understanding fishing impacts on fish assemblages is size spectra (SS) analysis: a regression of logarithmic abundance against the logarithmic body size of fish assemblages. SS analysis is based on the idea that the biomass and numbers of individuals of all species in a system decrease log-linearly with increasing body (Blackburn and Gaston, 1994, 1997, 1999; Pope and Knights, 1982). The slope and intercept of SS can be compared over time or across different conditions. Differences in slopes have been interpreted in terms of differential mortality rates and trophic transfer efficiencies. For example, an increase in the slope of SS can be attributed to an increase in the abundance of small-sized individuals relative to larger individuals (Dulvy et al., 2004). Interpretations that changes in fishing mortality cause changes in the slope and intercept of SS are supported by fisheries simulations (Gislason and Rice, 1998), data from the North Sea (Gislason and Rice, 1998) and a number of regions globally (Bianchi et al., 2000).
Another related but less tested method is Diversity Size Spectra (DSS) Analysis, which computes species diversity across different body sizes (Hutchinson and MacArthur, 1959). As in SSA, DSS analysis is based on the idea that typically there are few large individuals within species and few large-bodied species (Rice and Gislason, 1996). DSS analysis can be used to assess changes on the overall composition of sizes encompassed by different species in a system.

The SS and DSS of fish assemblages can be expected to respond to fishing and environmental changes in direct and indirect ways (Daan et al., 2005; Piet and Jennings 2005). For example, the proportionally greater removal of larger individuals, which is a common effect of fishing, is expected to lead to increases in the slope of SS while also causing compensatory effects on small fish, which in turn may lead to further increases in the slope of SS. The time scales and mechanisms behind these responses remain unclear due to the difficulty of understanding whole assemblage dynamics. For instance, lags of six to 12 years between fishing effort and the slope of SS have been documented in the North Sea (Daan et al., 2005). One factor that can explain the lag of assemblage responses to fishing or environmental changes is age of recruitment to the fishery. Environmental conditions during larval and juvenile stages typically have profound effects on the biomass and abundance of the resulting cohorts growing to adult stages or recruiting to the fishery (Fuiman and Werner, 2002).

Despite its promise, the reliability and usefulness of SS and DSS analyses in freshwater ecosystems have not been tested, as to date all SS and DSS analyses have focused on marine ecosystems (Murry and Farrell, 2014). It is not clear if SS analysis works in tropical fish assemblages, particularly in regions where data are scarce (Bianchi et al., 2000; Murry and Farrell, 2014). An analysis of SS of tropical demersal fish assemblages across different latitudes showed consistent responses to differences in ecosystem productivity and exploitation levels (Bianchi et al., 2000). But that study found non-conclusive results as to the extent to which the slope of SS reflects changes in exploitation levels of tropical fish assemblages facing environmental noise.

Here, we applied SS and DSS analyses to a comprehensive dataset on the fish assemblage exploited by fisheries in the Amazon Basin in order to address the following research questions: Do river droughts (i.e. low water levels) and fishing effort influence the SS of the fish assemblage? Do river droughts and fishing effort influence the DSS of the fish assemblage? And, what is the lag of possible drought and fishing effort effects on the SS and DSS of the fish assemblage?

2. Methods

We applied SS and DSS analyses to an 11-year dataset of multi-gear, multispecies fish catches in three of the largest rivers of the Amazon Basin. The data were based on landings recorded in Manaus, Brazil, totalling 58,047 fishing trips and 299,857 length measurements of 56 different fish species or taxonomic groups. The slopes of annual SS and DSS were assessed by means of correlation analyses in relation to annual indices of fishing effort and river drought conditions.

2.1. Study area, fishes, and fisheries

The study area comprised the Madeira, Purus, and Amazon (which here includes the Solimões) Rivers (Fig. 1). The ecosystem in these rivers is the várzea river-floodplain – a complex mosaic of seasonally inundated rain forests, lakes, and winding channels formed by the seasonal and predictable flooding of river waters stemming from the Andes Mountains (Irion et al., 1997). On average, river water levels begin to rise around December, reaching their maximum level around June, at which time they begin to drop, reaching their lowest level in October. Average seasonal water level variation in the study area during the study period was 12 m.

Many Amazonian fishes have evolved seasonal migratory strategies to exploit resources in the floodplains that are not available to them in river channels (Fernandes, 1997; Hermann et al., 2016; Winemiller and Jepsen, 1998). Many fish species migrate to the floodplains when water levels overflow river channels and flood adjacent floodplains, where they feed on abundant plant-based food resources and find protection from predators (Castello, 2008; Goulding, 1980). The decline of water levels forces fishes to migrate out of the floodplains back to river channels and floodplain lakes, where fishes are more vulnerable to natural predators and fishing gear (Nolan et al., 2009; Welcomme, 1985). Natural mortality in floodplain lakes during low water levels (i.e. dry season) is gener-
ally high and mainly attributable to decreased water quality (e.g. anoxia) an increased predation (Welcomme, 1979).

Fish assemblages in the Central Amazon region comprise three main groups: 1) resident species, such as Colossoma macropomum, that spend their entire life-cycles in floodplain habitats; 2) migratory characiforms, in particular Semaprochilodus insignis, Prochilodus nigricans, S. taeniurus, Mylibdae, that seasonally migrate to the floodplains during high water levels, but which also conduct longitudinal migrations along river channels, and; 3) migratory Siluriforms, including Brachyplatystoma spp., that exclusively migrate along river channels, though their juveniles often inhabit floodplain lakes (Barthem and Fabré, 2004).

The fish assemblage analysed here was exploited by the Manaus fishing fleet, which is composed of about 2500 boats (Batista et al., 2004). Median (1st–3rd quartile) boat length is 14.0 m (12.0–16.0). They are typically operated by 8–12 fishers in fishing trips to a wide range of locations lasting between 10 and 28 days (Batista and Petere, 2007). The main gears used are seines and gill nets, although other gears also are used, including line and long-line (Batista et al., 2004). The catch was dominated by characiform taxa (Appendix A).

2.2. Data sources and processing

Data on fish length and fishing effort were derived from the systematic sampling of fishing trips that arrived in Manaus between 1994 and 2004. Fishing effort was standardized in terms of number of fishers and days spent fishing (not including travel time) for each year (fisher*days). Fish fork length in millimetres was taken on measurements of a minimum of 30 individuals of each species a day. The resulting number of fishing trips and fish length measurements was 122,572 for the Amazon River, 140,185 for the Purus River, and 37,100 for the Madeira. A total of 56 fish species was included, though 28 species comprised 99% of the measured specimens.

The reliability of the foregoing SS and DSS analyses of fisheries data depends on the constancy over time of the proportional contribution of different gears. The log likelihood ratio statistic (G) indicated that no effect was observed in the proportional contribution of different gears over time (p > 0.05). Also, the reliability of the foregoing analyses depends on the assumption that fish catches landed in Manaus accurately represent fish catches. Previous studies indicated that discards negligible in the study area (Batista and Barbosa, 2008; Batista and Freitas, 2003), allowing us to consider the landing data as representative fish catches.

SS statistics were calculated for each river and year by plotting the natural logarithm of the numbers of individuals (in 10-cm fork classes) against the natural logarithm of the mid-length in the same group. The smaller fish sizes, which were not fully recruited to the fishery, i.e., fork length <20 cm, were excluded to avoid a curvature bias in the spectrum size (Shin et al., 2005). DSS statistics were calculated by plotting an index of species diversity against the mid-length of each 10-cm class. Diversity was measured by the Shannon-Wiener index (Magurran, 1988), which combines data on species richness and numbers of individuals per taxon. For each SS and DSS analysis, the slopes of the linear regressions were estimated based on the least squares method. The homogeneity of variances was evaluated by inspection of the distribution of the residuals versus predicted values and by computing the residuals normality using Shapiro-Wilk test.

Daily data on river water levels were obtained from publicly available historical records (www.ana.gov.br). River water level data at Manaus was used to calculate an index of drought intensity for all rivers. Manaus provides the most representative water level estimates for our study area given that most fishing sites were

<table>
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<tr>
<th>River</th>
<th>Year</th>
<th>b</th>
<th>s.e.b.</th>
<th>a</th>
<th>s.e.a.</th>
<th>F</th>
<th>p-value</th>
<th>R²</th>
</tr>
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</tr>
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<td>0.88</td>
</tr>
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near Manaus and other available water level data for the Purus and Madeira Rivers are from locations far upstream. An index of drought intensity was calculated for every year as the difference between the historical average and the minimum water level observed in a given year.

2.3. Data analysis

We addressed our research questions using two-tailed correlation analyses in each of the three rivers to test for possible correlations between the slope of SS and DSS in a given year and fishing effort and drought intensity zero, one, two, and three years...
Table 2
Correlation analyses among size spectra (SS), diversity size spectra (DSS), drought intensity, and fishing effort in the Amazon, Madeira and Purus rivers.

<table>
<thead>
<tr>
<th>Variables</th>
<th>River</th>
<th>Lag (year)</th>
<th>r</th>
<th>t</th>
<th>df</th>
<th>p-value</th>
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before. These zero to three year lags were chosen based on previous studies in the Amazon showing that the average age-at-catch of dominant taxa is between two and three years, and that hydrological effects on fish catches take about two and years to take place (Castello et al., 2015; Isaac et al., 2016). All analyses were performed using R (R Core Team, 2013).

### 3. Results

Linear regressions adjusted well to the diversity and Ln(abundance) data plotted against Ln(fork length). In all cases, coefficients of determination were high ($r^2 > 0.7$), the intercept and slope parameters for both SS and DSS were statistically different from zero ($p < 0.01$; Table 1), and residuals were normally distributed.

Drought intensity was negatively correlated to the slope of SS with a lag of zero years in all rivers (Fig. 2). In the Amazon River, there was also a mildly significant ($p = 0.056$) negative correlation between the slope of SS and drought intensity with a lag of two years (Table 2). Such drought effects appeared to occur via decreases in the abundance of larger individuals (i.e. fork length > 80 cm) and proportional increases in the abundance of smaller individuals (i.e. fork length ~ 20–30 cm; Fig. 3). The larger species included *Pseudoplatystoma tigrinum* and *Serrasalmus planiceps*, and the smaller species included *Prochilodus nigricans*, *Bycon amazonicus*, *Plagioscion spp.*, and *Hypophtalmus* spp. (Fig. 4).

Fishing effort was correlated to the slope of SS in all rivers, but the lag and direction of correlations varied depending on the river (Table 2). The slope of SS was negatively correlated to fishing effort in the Madeira and Amazon rivers with a lag of three years, but in the Purus River it was negatively correlated with a lag of two years (Table 2). Because effort in any given year could potentially vary in relation to drought conditions (e.g., extreme drought preventing fishing) or fish abundance (e.g., fishers increasing effort in "good" years), we assessed possible correlations between effort and drought intensity. Fishing effort and drought intensity were not correlated in any of the rivers regardless of the lag ($p > 0.1$). Drought
assemblages may not be suitable for SS analysis because of their high diversity of species and fast body growth (Bianchi et al., 2000), our results suggest that SS analysis can be applied to fishing data to detect population changes in tropical freshwater ecosystems.

The correlations found here between the slope of SS and minimum water levels with a lag of zero years indicate that drought conditions in a given year influence the size structure of Amazonian freshwater fish assemblages in the same year. This finding is consistent with theoretical expectations that extreme low water events cause high mortality rates among aquatic fauna in streams, rivers, and other types of freshwater ecosystems (Matthews and Marsh-Matthews, 2003). Habitat shrinkages increase fish densities, thereby intensifying biotic interactions such as predation and competition for resources (Matthews, 1998; Schlosser et al., 2000; Zaret and Rand, 1971). Habitat shrinkages, together with high temperatures, usually decreases water quality in terms of oxygen, pH, and nutrient content, causing fish to enter torpor or even die (Magoullick and Kobza, 2003; et al., 2003Matthews and Marsh-Matthews, 2003; Tramer, 1977). This occurs in tropical freshwater environments even though many tropical fish possess physiological adaptations to tolerate poor water quality (Lowe-McConnell, 1987). Drought intensity was also found to exert the strongest hydrological influence on multispecies fisheries yields in the Central (e.g. Freitas et al., 2012; Mersona and Gascuel 1993) and Lower Amazon regions (Castello et al., 2011a,b; Isaac et al., n.d.). Such documented impacts were also consistent with estimates of natural mortality caused by (normal) seasonal low waters as recorded in the Kafue River, in Zambia, where high water fish biomass decreased by 40% during the subsequent low water season (Lagler et al., 1971). Highly seasonal environments favouring increased proportions of small sized species and individuals were also found to occur elsewhere (Welcomme and Merona, 1988), Oceania (Chessman, 2013) and Asia (Hogan, 2011).

The negative correlation between the slope of SS and drought intensity with a lag of two years that was mildly significant in the Amazon River (Table 2) also is consistent with previous studies. Two and year lags have been found between high and low river waters and fish catches in the Lower Amazon region (Castello et al., 2015; Isaac et al., 2016). Such lags have been shown to correspond to the average age-at-catch of the dominant taxa (Isaac et al., 2016). Because the taxa in our study area is expected to have the same age-at-catch, the negative correlation found here in the Amazon River could potentially be explained by the adverse effects of low water levels on the survival of fish during their juvenile stages.

The negative correlation between the slope of SS and fishing effort with two and year lags could be due to the birth-recruitment delay caused by fishing mortality over fish populations (Bence and Nisbet, 1989; Caley et al., 1996). An effect of fishing effort in terms of reducing the proportion of larger-sized fishes could be expected to have delayed effects on the fish assemblage after the time it takes for the offspring to be recruited to the fishery (Bianchi et al., 2000; Cislassen and Lassen, 1977; Law et al., 2012). As mentioned above, previous studies have found two and year lags between high and low waters and fish catches in the Lower Amazon region. High slopes of SS could denote fishing effects over large (60–90 cm FL) fishes such as Pimelodidae and the Osteoglossum bicirrhosum, which generally possess low rates of population growth (Barthem and Fabrè, 2004).

The general lack of correlations between the slope DSS and drought intensity or fishing effort is difficult to explain. On one hand, it could indicate that DSS may not be reliable to assess environmental effects on species diversity across different body sizes in tropical multispecies fisheries. One the other hand, environments with high fish diversity generate highly diverse multispecies landings (Welcomme et al., 2010) as is the Amazon case (Batista and Petrere, 2003; Batista et al., 2014; Castello et al., 2013a, 2013b). In

4. Discussion

Fish assemblage data derived from Amazonian fishing activities fitted well to linear regressions of size and diversity data, and the slopes of SS were sensitive to an index of drought intensity. This was so even though the fishery data analysed here is multispecies and multigear, including 56 fish species or taxonomic groups and a range of gears. Contrary to previous suggestions that tropical fish intensity and fishing effort were not correlated to the slope DSS in any of the rivers (Table 2).
our data, many taxa are referred to only via common names that, in fact, often encompass several species. So, taxonomic uncertainty of recorded taxa, even large sized fishes (e.g. Pseudoplatystoma; Buitrago-Suarez and Burr, 2007), could explain the lack of correlations between the slope DSS and droughts or fishing effort. Though not encouraging, these results are in line with a previous study (Gislason and Rice, 1998) that also did not find correlations between the slope of DSS and fishing effort.

These findings imply that future expected increases in the frequency and intensity of droughts in the Amazon (Castello and Macedo, 2016) will adversely affect Amazonian fish assemblages and associated fisheries. The results herein indicate that such stronger and more frequent drought events will influence not only fish biomass as indicated by previous studies (Castello et al., 2015; Isaac et al., 2016), but also the relative fisheries yield of fish species of different sizes. Such relative changes in the body sizes of various taxa may have the potential to affect trophic dynamics and associated ecosystem functions. Given that Amazonians possess high rates of per capita fish consumption, there is a need to prevent further river hydrological alterations and develop adaptation strategies to minimize associated impacts on income and food security.

Acknowledgements

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Appendix A.

Table A1
Table A1
Species or taxonomic groups recognized in fishery landings at Manaus city with their common names, number of fish fork lengths (FL) measured, average FL, and standard deviation (s.d.) of FL.

<table>
<thead>
<tr>
<th>Specie or taxonomic groups</th>
<th>Common name</th>
<th>n</th>
<th>FL (cm)</th>
<th>s.d.</th>
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<td>curimatá</td>
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