REVIEWS IN FISHERIES SCIENCE
2018, VOL. 0, NO. 0, 1–21
https://doi.org/10.1080/23308249.2018.1463511

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Review of Fisheries Resource Use and Status in the Madeira River Basin (Brazil, Bolivia, and Peru) Before Hydroelectric Dam Completion

Carolina R. C. Doria[a,b], Fabrice Duponchelle[b,c], Maria Alice L. Lima[a], Aurea Garcia[b,d], Fernando M. Carvajal-Vallejos[f], Claudia Coca Méndez[e], Michael Fabiano Catarino[g], Carlos Edwar de Carvalho Freitas[c,g], Blanca Vega[e], Guido Miranda-Chumacero[h], and Paul A. Van Damme[e,i]

[a]Laboratory of Ichthyology and Fisheries – Department of Biology, Federal University of Rondônia, Porto Velho, Brazil; [b]Laboratoire Mixte International – Evolution et Domestication de l'Ichtyofaune Amazonienne (LMI – EDIA), Iquitos (Peru), Santa Cruz (Bolivia); [c]Institut de Recherche pour le Développement (IRD), UMR BOREA (IRD-207, MNHN, CNRS-7208, Sorbonne Université, Université Caen Normandie, Université des Antilles), Montpellier, France; [d]IIAP, AQUAREC, Iquitos, Peru; [e]FAUNAGUA, Institute for Applied Research on Aquatic Resources, Sacaba-Cochabamba, Plurinational State of Bolivia; [f]Alcide d'Orbigny Natural History Museum, ECOSINTEGRALES SRL (Ecological Studies for Integral Development and Nature Conservation), Cochabamba, Plurinational State of Bolivia; [g]Department of Fisheries Science, Federal University of Amazonas, Manaus, Brazil; [h]Wildlife Conservation Society, Greater Madidi Tambopata Landscape Conservation Program, La Paz, Bolivia; [i]Unit of Limnology and Aquatic Resources (ULTRA), University of San Simón, Cochabamba, Bolivia

ABSTRACT
The Madeira River, which drains one of the major tributary river basins of the upper Amazon, contributes to small-scale fisheries in Peru, Bolivia, and Brazil. This paper provides a base-line of fisheries resources and their status in six sub-basins of the Madeira River: upper Madre de Dios River basin (Peru), Beni and Mamoré River basins (Bolivia), Iténez or Guaporé River basin (Bolivia and Brazil), middle Madeira, and (two sections of the) lower Madeira River (Brazil). Data were collected between 2009 and 2011, before the completion of two hydroelectric dams in the Brazilian portion of the basin. Biophysical, social, and biological indicators were used to characterize the fisheries. The results show an overall small-scale multispecies fisheries pattern but with notorious differences between the Madeira sub-basins. The Beni and Mamoré sub-basin shows the largest flooded area, with associated higher total fisheries yields. Trophic level of the catch, diversity, and mean weight of fish caught were shown to be very sensitive to exploitation level, river water type (white or clear water), flooded area, and the introduction of *Arapaima gigas* in Bolivia. The Bolivian fisheries are characterized by less exploited stocks, whereas stocks in Peru and Brazil show signs of intensive exploitation, resulting in fisheries of smaller bodied, lower trophic-level species. Landing data in the upper basin show a predominant reliance on migrating fish resources, which might be vulnerable to the construction of dams. These data serve as a baseline to evaluate anthropogenic impacts on the Madeira River basin fisheries in the future.

KEYWORDS
Amazon; freshwater ecosystem; trophic level; diversity; fish catch

Introduction

The Madeira River is one of the principal upper tributaries of the Amazon River. It is traditionally subdivided into a lower stretch, characterized by a steep-walled channel and a very narrow floodplain, and an upper basin, delineated by rapids and waterfalls just upstream of Porto Velho, Brazil. This upper basin contributes around 60% of the discharge of the Madeira River basin as a whole (Vauchel, 2008), which itself accounts for approximately 15% of the total output of the Amazon River (Latrubesse et al., 2005). The vast inundation area of the upper basin includes a high number of floodplain lakes (Crespo and Van Damme, 2011).

Carvajal-Vallejos et al. (2014) registered 814 fish species in the Bolivian Amazon, whereas 1,008 species have been registered for the Brazilian sections of the Madeira River basin, including the border rivers with Bolivia (Ohara et al., 2015). Considering that many have a basin-wide occurrence, the total number of species in the Madeira basin is approximately 1,373 (www.amazon-fish.com). This high aquatic biodiversity supports important small-scale commercial and subsistence fisheries, which contribute to rural and peri-urban livelihoods and to food security. Fish is an important commercial product in urban markets (Doria et al., 2012), where income generated by the different

CONTACT Carolina R. C. Doria carolinarcdoria@unir.br Laboratory of Ichthyology and Fisheries – Department of Biology, Federal University of Rondônia, Campus - BR 364, Km 9, 5. CEP: 76801-059, Porto Velho- RO Brazil.

nodes in the fish value chain is re-invested in goods and food (Coca Méndez et al., 2012). Fish is also the main protein source in most riverine communities. Overall, annual per capita Amazon fish consumption in the Madeira basin varies between 0 and 169 kg/year (Isaac and Almeida, 2011; Pérez et al., 2014; Issac et al., 2015).

So far, all published information on fisheries activities in the Madeira has treated the three countries sharing the Madeira basin separately, with none taking account of the Madeira basin as a whole. The amount of available information is also unequally distributed among the three countries, with Brazil having generated the most and Peru the least. In the Brazilian portion of the basin, the first important study, carried out in the seventies, qualitatively and quantitatively analyzed fisheries activities in the main markets, detailing fishing effort, fishing grounds, and gears for Siluriformes and Characiformes in particular (Goulding, 1979). During the eighties and nineties, a few authors published information on the fisheries landings and specific composition in the main regional markets (Santos, 1986), on the dietary and migratory habits of commercially important species (Boischio, 1992) and on the fisheries of the main markets in Rondônia for socioeconomic and ecological zonation (ZSEE, Doria et al., 1998). The number of publications increased from the year 2000 onwards (Cardoso and Freitas, 2007), particularly when the Laboratory of Ichthyology and Fisheries of the Federal University of Rondonia (LIP-UNIR) started a systematized monitoring of the fisheries in the Brazilian portion of the Madeira (Doria and Queiroz, 2008; Doria and Lima, 2008, 2015; Doria et al., 2012, 2016; Doria and Brasil de Souza, 2012; Lima et al., 2012, 2016; Sant'anna et al., 2014). Using official maximum landing values from the main landing ports of the Brazilian portion of the Madeira, during the period 1978–1998, Barthem and Goulding (2007) provided a way to estimate the maximum total annual landings for the Brazilian portion of the Madeira (3,460 tons = 2% of 173,000 tons for the whole Amazon basin). All these studies were restricted to specific parts of the basin or the study of specific species and none provided an estimate of maximum potential catches for the Brazilian portion of the basin.

In the Bolivian portion of the Madeira basin, the first important published study was based on experimental fisheries (1983–1987) and a bibliographic review of existing grey literature on Bolivian Amazon fisheries (Lauzanne et al., 1990). These authors concluded that in the eighties, Amazonian fisheries in Bolivia were by far underexploited, with a total annual production of ~1,500 tons (mainly for the Béni and Mamoré sub-basins). Later, a few authors documented the local population status of some commercial fish species (Loubens and Panfili, 1992, 1995, 1997, 2000, 2001; Reinert and Winter, 2002; Loubens 2003, Van Damme et al., 2005; Duponchelle et al., 2007; Córdova et al., 2012). Recently, Van Damme et al. (2011) reviewed available information on commercial fisheries based on official statistics and interviews with stakeholders. In recent years, the focus was given to the description of the fisheries of *Arapaima gigas*, an introduced species in the northern Bolivian Amazon (Miranda-Chumacero et al., 2012b; Van Damme et al., 2015; Carvajal-Vallejos et al., 2017).

In the Peruvian portion of the Madeira, the Madre de Dios sub-basin, there are only three significant studies, two of them in grey literature. These, carried out in the eighties (Montreuil and Campos, 1988) and nineties (Chang, 1996), described fishing activities, gear, localities, and the main landed species. They also emphasized that fisheries activities in the Madre de Dios were less developed than in the other Peruvian rivers. Chang (1996) reported 40 main landed species and total catches of ~ 49 tons during 1995–1996 in Puerto Maldonado, the main city of the Madre de Dios region. The most recent study, based on scientific surveys of the main landing sites of Puerto Maldonado, reported maximum annual landings of 56.8 tons during the period of 1995–1998, and 50 exploited species (Cañas, 2000).

Amazon fisheries are increasingly threatened by overexploitation, climate change, dams, and other human-related impacts (Allan et al., 2005; Ficke et al., 2007; Castello et al., 2013). The integrated ecosystem approach to fisheries has been proposed as one of the appropriate ways to understand and mitigate these threats (Garcia et al., 2003; Jennings, 2005), but this requires a good understanding of the social, economic and ecological factors that control the fish productivity. A recommended first step within the ecosystem approach is to determine key indicators that provide information on the: state of the ecosystem, fishing pressure or other threats and response to management actions (Jennings, 2005).

The overall geomorphological, geological, and climatic characteristics of the Amazon aquatic systems determine primary and secondary productivity, and thus also fish production and fish landings (Junk and Wantzen, 2004; Junk, 2007). However, commercial fisheries landings may also be influenced by the socioeconomic and political context in which they take place (Barthem and Fabré, 2004). Demand for fish in the markets, for example, may greatly influence the behavior of fishers and their fisheries. Commercial fisheries may be considered as indicators of both the aquatic environment and the socioeconomic context in which they develop. In the same way, population and community metrics (size-based, species-based, and tropho-dynamic indicators) are potentially useful indicators of ecosystem structure and functioning over time as well as of anthropogenic impacts and socioeconomic factors (Blanchard et al., 2005). The paucity of baseline data does not allow a real understanding of the status of the fishery resources and is a threat to its longer-term effective management and assessment of the real impacts of construction in the Madeira basin (such as hydroelectric dams).

The objective of this article is, therefore, to provide an integrative review of the status of fisheries in the three countries sharing the Madeira River basin and sub-basins (Bolivia, Brazil, Peru) before the construction of dams, using a set of indicators to understand which factors and pressures affect the fisheries. This synthesis is also expected to create a dialogue on the data gaps and measures which are needed to provide sustainable fisheries management, as well as predict and mitigate impacts of human activities in the basin.

Material and methods

Study area

The Madeira River is probably the most geographically complex tributary basin of the Amazon River. With approximately 1,370,000 km^2 of total area, its drainage area represents more than 20% of the entire Amazon basin, extending to three countries, with 51% of its area in Brazil, 42% in Bolivia, and 7% in Peru (Barthem and Goulding, 2007). It receives the discharge from the Mamoré and Beni rivers, which drain the Bolivian Andes and, through the Madre de Dios River, the southern part of the Peruvian Andes (Venticinque et al., 2016). Using ecological and geomorphological information, the Madeira River basin was subdivided into four study areas: (a) white water rivers of the upper Madeira River basin (MRB); (b) clear water rivers of the upper MRB; (c) middle MRB; and (d) lower MRB. These study areas largely coincide with the aquatic ecoregions distinguished by Abell et al. (2008; Table 1), and with the "major tributary basins" of Venticinque et al. (2016). The four study areas were subdivided in six sub-basins (Table 1).

The "white water rivers of the upper MRB" (study area A) drain the Andes mountains in the southwestern part of the basin. These white waters are heavily loaded with Andean suspended sediments and transport huge quantities of organic matter, such as limbs, stems, and trees (Barthem and Goulding, 2007). They are characterized by their meandering courses, bordered by oxbow lakes with varying degrees of connectivity. Approximately 30% of this Bolivian Amazon basin can be considered as a periodically inundated wetland, mostly located in the lowlands (Crespo and Van Damme, 2011). The area was divided into two subsections by country: the (upper) Madre de Dios river basin in Peru (sub-basin A1), and the Mamoré, Beni and (lower) Madre de Dios rivers in Bolivia (sub-basin A2; Table 1).

The "clear water rivers of the upper MRB" (study area B) drain the Brazilian Precambrian shield towards the east (Abell et al., 2008). This section corresponds to the Iténez (or Guaporé) River, which drains eroded soils and therefore has low mineral and suspended material content (Figure 1). The river channel is stable, and low sedimentation rates do not allow the isolation of oxbow lakes.

The "Middle MRB" (study area C) extends between Guajara-Mirím and the now flooded waterfall of Teotônio. In this section, after the confluence of white and clear waters at the border of Bolivia and Brazil, the Madeira River changes abruptly. The edge of the Central Brazilian Shield created a series of 19 rapids, the most important of which were Salto Jirau, Teotônio, and Santo Antônio waterfalls (Molina Carpio, 2011), since 2012 flooded by the Jirau and Santo Antônio hydropower dam reservoirs. The Madeira River channel in this sec-

Table 1. Sub-basins of the Madeira River basin and corresponding Aquatic Ecoregions (based on Abell et al., 2008).

Study áreas	Corresponding Aquatic Ecoregions[a]	Sub-basins	Landing sites surveyed
A. Upper Madeira (white water river basins)	"Mamoré-Madre de Dios Piedmont" (N°318)	A1. Upper Madre de Dios basin (Peru)	*Puerto Maldonado
		A2. Beni, Mamoré and (lower) Madre de Dios river basins (Bolivia)	*TCO Tacana *Riberalta *Puerto Villarroel
B. Upper Madeira (clear water river basins)	"Guaporé-Iténez" (N° 319)	B. Iténez or Guaporé River basin (shared by Bolivia and Brazil)	*Costa Marques / Surpresa[b]
C. Middle Madeira (white water river)	"Madeira Brazilian Shield" (N° 321)	C. Middle Madeira river basin between Guajará-Mirim and Vila de Teotônio (Brazil), including the Abuná River.	*Guajará-Mirim / Nova Mamoré / Iata / Fortaleza do Abunã / Abunã / Jaci-Paraná / Vila do Teotônio[b]
D. Lower Madeira (white water river)	"Amazon Lowlands" (N° 316)	D1. Lower Madeira River basin between Porto Velho and Humaitá (Brazil)	*Porto Velho / São Sebastião / São Carlos / Cuniã / Nazaré / Calama / Humaitá[b]
		D2. Lower Madeira River basin between Manicoré and Nova Olinda	*Manicoré/ Borba / Novo Aripuanã e Nova Olinda[b]

For each sub-basin the fisheries landing sites surveyed are listed.
[a] Codes according to Abell et al. (2008).
[b] Landing data for these points were pooled.

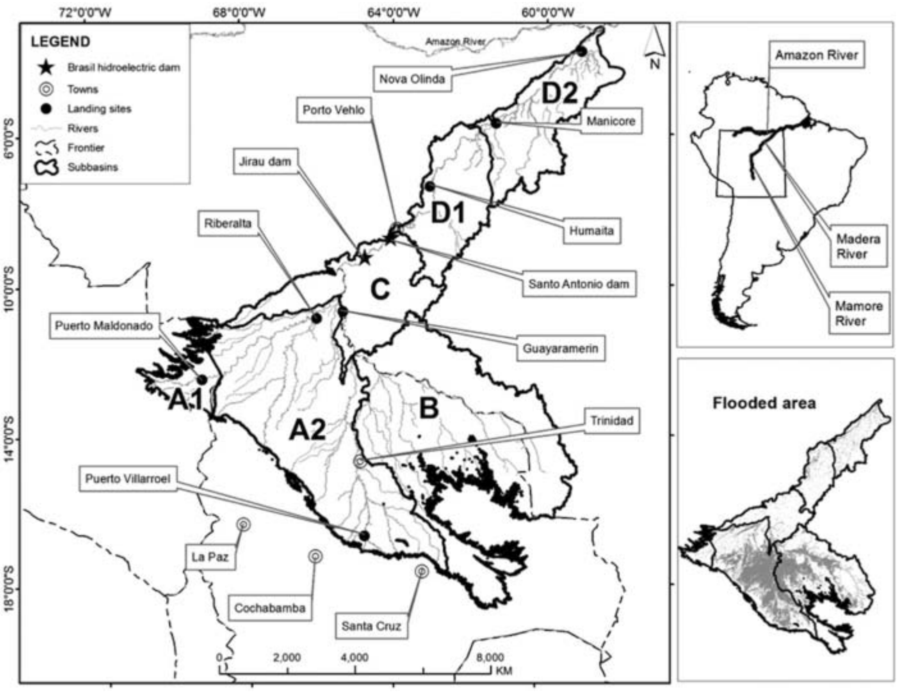

Figure 1. Sub-basins of the Madeira River. For a detailed description of the sub-basins see Table 1. The flood-plain map is adapted from Melack and Hess (2008).

tion is narrow and deep, with banks of up to 30 m high in the dry season (Torrente-Vilara et al., 2011).

At the transition between the Brazilian Shield and the Amazon Lowlands, the lower part of the MRB (study area D) keeps on flowing in a narrow channel, but no longer interrupted by waterfalls. In this section, the river receives sediments from the central Amazon floodplain. This area was also divided into two sections (D1 and D2; Table 1).

Characterization of the ecosystems

We used the flooded area to characterize the sub-basins, considering the surface area of floodplain rivers (A), the surface area of permanent floodplain lakes (B), the surface area of temporally flooded area (C), and the Total flooded area (A+B+C). This estimation was calculated based on a map elaborated by Melack and Hess (2008) using JERS-1 radar mosaics. In sub-basin D1, three polygons that coincided with upland savannas and with a reservoir were therefore excluded from the calculations. Missing information for the section south of 61°L was complemented with data from Crespo and Van Damme (2011), who mapped inundation patterns based on vegetation data provided by Navarro and Ferreira (2007).

Characterization of fisheries in sub-basins

Socioeconomic indicators and landing data

We collected information on socioeconomic indicators for which data were available in the literature or which could be calculated from primary or secondary data. For each sub-basin, data on the number of commercial fishers and overall fish landings were researched, based on a variety of sources. Annual landing volumes were then used to calculate the number of fishers per unit of flooded area and catch per unit of flooded area. Although this does not represent a true index of fishing effort, it allowed exploration of differences in the level of fishery pressure.

The primary and secondary data used from specific landing sites situated along the Madeira River and its headwaters, in Brazil, Bolivia, and Peru were as follows.

In Peru (sub-basin A1), the data were provided by the Dirección Regional de la Producción de Madre de Dios (DIREPRO, 2012) for the period of 2009–2011. These fish landing data (number of landed species, total landed weight for each species, and fishing area) were obtained on a daily basis at the different sites of the Madre de Dios basin. The total number of fishers registered in the three provinces (Tambopata, Manu, Tahuamanu) in 2011 was obtained from DIREPRO (2012). Mean total annual catch data were calculated averaging the data available for the three consecutive years. Some species names were corrected using the list published by Ortega et al. (2012). Unfortunately, fish length and weight data, and fishing effort were not available for these catch data.

In Bolivia, the socioeconomic information (sub-basins A2 and part of B1) is based on population data from the National Institute of Statistics (INE, 2001), which provided the number of persons that auto-identified as fishers for 121 landing points during the national population census conducted in 2001. We assume that the number of fishers did not change significantly between 2001 and 2007, the year of fisheries yield estimation by Van Damme et al. (2011), considering that no major investment in the fisheries sector was done during this period. Approximate landing data for 2007 were obtained by the above-mentioned authors, who estimated total yield based on interviews with key informants (salesmen, officials, local leaders, and fishers) and fisheries statistics in 12 landing points, where approximately 45% of the total number of fishers were concentrated. In two localities (Puerto Villarroel, Trinidad), the data were based partly on official fisheries statistics provided by the Servicio Departamental Agropecuario y Ganadería (SEDAG), complemented with interviews and secondary data. Estimated annual yields for Guayaramerín, Cachuela Esperanza, Villa Bella, El Sena, Puerto Rico, Porvenir, Santa Ana de Yacuma, Exaltación, and Rurrenabaque, where no official statistics are available, were based on unpublished market data and structured interviews that allowed for an estimation of total catch volume. Data for Riberalta were obtained from a year of catch records (Coca Méndez et al., 2012), where data for Bella Vista and six communities within the indigenous territory TIOC (Territorio Indígena Originario Campesino) Tacana were extracted from Córdova et al. (2012) and Miranda-Chumacero et al. (2012a). The total estimated annual landings for the 12 localities were used to calculate the mean annual catch per fisher, which was then used to estimate the annual catch in the remaining (109) localities. This assumes that there is no significant relationship between the catch per unit effort of a fisher and the number of fishers present in a landing site, as argued by Van Damme et al. (2011).

For the Bolivian points where SEDAG do not provide reliable catch compositions, other data sources were used to characterize landings: (1) data for the TIOC Tacana, a territory with five commercial fisheries communities, were obtained from Miranda-Chumacero et al. (2012a); (2) data from Riberalta were collected by daily fishing port monitoring between August 2008 and July 2009 (Coca Méndez et al., 2012); and (3) data from Puerto Villarroel, on the upper Ichilo River, are based on monitoring of daily catches by fishermen of the local fisher organization ASPECO in 2011 (Van Damme et al., 2011).

For the Brazilian portion of sub-basin B1 (Iténez River basin) information was based on Doria and Brasil de Souza (2012). In sub-basins C and D1 in Brazil, primary data were collected in 2009, 2010, and 2011 by the Laboratory of Ichthyology and Fisheries (Federal University of Rondônia) from the Fisheries Monitoring Program of the Santo Antônio Energia and Energia Sustentável do Brasil Dams. In these programs, the annual fisheries landings were calculated based on daily data collected at sixteen sites, in fisheries markets in cities (CFM) or in riverine communities (RC; 15 in the state of Rondônia and one in the state of Amazonas). Monitoring was carried out by interviews of fishers at the landing sites, recording their name, total landings, landings per species, type of boats, equipment, effort (number of days/ expedition and number of fishers per boat), and the total lengths of fish in a subsample.

Data for the Lower Madeira (sub-basin D2) section were provided by the fishing colonies of Manacapuru, Novo Aripuanã, Borba, and Nova Olinda do Norte, all within the state of Amazonas. The Federal University of Amazonas (UFAM), based on averaged data for 2010 and 2011, provided information on annual fish production. In all municipalities, there were gaps in the data collected in 2011. Thus, the monthly averages were calculated on the landing data available for each location and extrapolated for the months where such data did not exist. The sum of the amounts available and extrapolated in 2011 to all municipalities was used as the total landings in the Lower Madeira region. The number of fishers for the Middle and Lower Madeira was obtained from unpublished fisheries statistics from the authors' database.

There is heterogeneity in species identification amongst the data sets, some species being identified differentially at species, genus, or at family level. To allow comparisons, some of the species were thus grouped in higher taxa.

Biological indicators

Species identifications were checked against the most recent nomenclature (www.amazon-fish.com). Because of the common use of local names in the fisheries literature, a compilation based on Brazilian, Peruvian, and Bolivian sources (Carvajal-Vallejos et al., 2011; Ortega et al., 2012; Queiroz et al., 2013) was constructed for interpretation of the data (Appendix 1).

Seven biological and catch-related indicators were calculated:

1. The number of species in the landings was calculated, including species that were reported at least twice (equivalent to Hill's index N0; Hill, 1973).
2. The species were classified on the basis of their migration patterns as long-distance migrator (>1500 km), middle-distance migrator (100–1,500 km) or resident fish (<100 km), according to the literature (Barthem and Goulding, 2007; Van Damme et al., 2011; Queiroz et al., 2013; Appendix 1).
3. The trophic level of each species (TL_i) was based on records in Fishbase (Froese and Pauly, 2015).

(4) The trophic level of the landings (TL_t) measures the weighted mean trophic level of species exploited by the fishery, representing the trophic position of the whole catch. Thus, it is an indicator of the species composition of the catch in terms of trophic positioning (Shin et al., 2010). TL_t was calculated as follows:

$$TL_t = \left(\sum_{i=1}^{s} (p_i * \ TL_i) \right) \ / \ P$$

with p_i is the proportion of each species within the catch

(5) A weight index (W) was calculated based on the mean weight reported in landings (Appendix 1). The weight index of fish landed is calculated as:

$$W = \frac{P}{N}$$

with P is the total weight of catch (all species); N is the total number of fish landed (all species).

(6) Diversity of the catches was estimated by adapting Hill's diversity indices N1 and N2 (Hill, 1973), replacing the number of fish by their total weight in the landings:

$$\mathrm{N1} = e^H = e \sum_{i=1}^{s} (p_i)^2$$

$$\mathrm{N2} = \frac{1}{D} = \frac{1}{\left(- \sum_{i=1}^{s} (p_i * \ log_2 \ p_i) \right)}$$

with H is the Simpson index; D is the Shannon–Wiever index.

The unit of both indices is the "number of species," N1 representing the "number of abundant species" and N2 the "number of very abundant species" (with the total number of species > N1 > N2; Hill, 1973).

(7) The relative frequency of each taxonomical order was calculated, as well as the frequency of introduced species in the landings (species that has been translocated from one basin or sub-basin to another, extralimital introductions according to Vitule et al., 2014).

Dissimilarity (Euclidean Distances) between landing sites was calculated using unweighted pair-group average (UPGA) clustering on log-transformed data at the genus level (statistical package STATISTICA/CSS).

Results

Characterization of the ecosystem

The Madeira River sub-basins have very distinct geomorphologies. The most distinct characteristic of the upper Madeira is the presence of extensive floodplains in Bolivia, the largest occurring in the Mamoré and Beni river basins, occupying more than 47% of the total surface area below 300 m above sea level (Table 1). The second largest floodplain in the study area is located in the Iténez sub-basin, covering 28.1% of the total basin surface.

Another distinct characteristic is the series of waterfalls in the middle Madeira between Cachuela Esperanza, on the Beni River, Guayaramerín on the Mamoré River, and Santo Antônio upstream of the town of Porto Velho (Figure 1). Several of these waterfalls have now been flooded by the Jirau and Santo Antônio hydroelectric impoundments upstream of Porto Velho, but were intact during the time of data collection. Further downstream, the river flows through a deep channel bordered by narrow floodplains occupying less than 16% of the total surface area (Table 2).

The surface area of floodplain lakes is relatively well correlated with the surface of flooded area. These lakes occupy 0.2% of the total surface of flooded area in the Beni and Mamoré river basins (upper Maderia) and 0.5–0.6% in the lower Madeira River (Table 2). Floodplain lakes have very distinct geomorphologies in the different sub-basins. In the Upper Madre de Dios (A1) and Beni and Mamoré river basins (A2), the floodplain lakes are oxbow lakes, old river meanders isolated from the main river stem; in the Iténez (or Guaporé) basin (B) most of the lakes remain permanently connected with the main river stem, whereas in the Madeira basin (C, D1, D2) the lakes are formed temporally or permanently in depressions along the river stem.

Social indicators influencing catch and effort

Notwithstanding the very different methods used in the three countries to estimate fisher numbers, some general patterns can be deduced. The number of commercial fishers increases downstream along the Madeira River (Table 3). The middle and lower Madeira host the highest numbers of fishers, including many boats from other municipalities operating in this region (mainly from Manaus, the largest urban center in the state of Amazonas), suggesting a higher fishing effort in these sections of the Madeira basin. The lowest density of fishers is found in the Iténez or Guaporé basin, shared by Brazil and Bolivia (Table 3).

The highest overall catch was recorded in the Beni, Mamoré, and lower Madre de Dios sub-basins (A2) with 2,980 t/year, a large portion of which was captured in the

Table 2. Physical characterization of sub-basins of the Madeira river basin.

Basins Country	Upper Madre de Dios(A1) Peru	Beni, Mamoré and LMD (A2) Bolivia	Iténez or Guaporé (B) Bolivia-Brazil	Middle Madeira (C) Brazil	Lower Madeira (D1) Brazil	Lower Madeira (D2) Brazil
Surface area (< 300 masl) (km^2)	24,353	248,482	265,559	98,481	75,838	84,658
Surface area of floodplain rivers (A) (km^2)	496	2,770	787	675	1,053	2,695
Surface area of floodplain rivers (% of total sub-basin surface)	2.0	1.1	0.3	0.7	1.4	3.2
Surface area of permanent floodplain lakes (B) (km^2)[a]	22	559	54	77	346	489
Surface area of permanent floodplain lakes (% of total surface)	0.1	0.2	0.0	0.1	0.5	0.6
Surface of seasonally flooded area (C) (km^2)	1,347	115,280	73,655	5,293	6,041	10,107
Surface of seasonally flooded area (% of total sub-basin surface)	5.5	46.4	27.7	5.4	7.9	11.9
Surface of total flooded area (A+B+C) (km^2)	1,865	118,609	74,495	6,045	11,010	13,290
Surface of total flooded area (% of total sub-basin surface)	7.7	47.7	28.1	6.1	9.8	15.7

LMD, Lower Madre de Dios; Masl, meters above sea level.

[a] Estimates based on LANDSAT images of august 2010 (excluding tectonic lakes).

floodplain lakes and flooded areas. However, total fish landings per surface of flooded area in these sub-basins are lower than in the Madeira River downstream (C and D1) and much lower than in the Peruvian section of the basin (A1). However, when only permanent water bodies (rivers and lakes) are considered, the Beni, Mamoré, and lower Madre de Dios sub-basins have the highest landings per 100 km^2. The Iténez/Guaporé sub-basin (B) does not fit this pattern, showing a lower landing rate than all the other sub-basins, even after combining Bolivian and Brazilian landing data (Table 3). The annual landings per fisher range between 0.8 and 3.0 t/year in the upper sub-basins of the Madeira (Madre de Dios, Beni, and Mamoré sub-basins in Peru and Bolivia) and between 0.1 and 0.6 t/year in the Iténez/Guaporé and middle and lower Madeira sub-basins (Table 3).

Biological indicators of landings

All fisheries in the sub-basins are multispecies, exploiting at least 10 species (Table 4). The total number of species and/or species groups recorded in the commercial

Table 3. Fisheries characteristics in sub-basins of the Madeira River basin.

Sub-basins Country	Upper Madre de Dios (A1) Perú	Beni, Mamoré and LMD (A2) Bolivia	Iténez / Guaporé (B) Bolivia-Brazil	Middle Madeira (C) Brazil	Lower Madeira (D1) Brazil	Lower Madeira (D2) Brazil
Number of commercial fishers	341[a]	1010[b]	128 (Br)[c] 57 (Bo)[b]	565[c]	1 095[c]	1 557
Number of fishers per 100 km^2 of total flooded area[e]	18.3	0.9	0.2	9.3	14.8	11.7
Number of fishers per 100 km^2 of permanent water bodies (rivers+lakes)	65.8	30.3	22.0	75.1	78.3	48.9
Mean total annual fish landings (t/year)	290[d]	2 980[c]	40 (Br)[c] 100 (Bo)[c]	318[c]	492[c]	132[c]
Mean total annual fish landings/surface of total flooded area (t/year/100 km^2)[e]	15.5	2.5	0.2	5.3	6.6	1.0
Mean total annual fish landings / surface of permanent water bodies (rivers+lakes)	56.0	89.5	16.6	42.3	35.2	4.1
Mean annual landings/fisher (t)	0.9	3.0	0.8	0.6	0.4	0.1

LMD, Lower Madre de Dios.

[a] Source DIREPRO (2012) for the year 2011.

[b] Based on population census data (INE, 2001), interpreted by Van Damme et al. (2011), extrapolated using estimated population growth between 2001 and 2007, and assuming that 25% of fishermen from Guayaramerín fish in the Iténez or Guaporé River basin (B1) and the remaining 75% in the Mamoré River basin (A2).

[c] Data provided by fishermen using interview methodology described in the main text.

[d] Mean total annual catches between 2009 and 2011 (DIREPRO 2012).

Table 4. Relative abundance (%) of fish species in landing regions (Bolivia, Brazil, Peru). Scientific name and its descriptors source: http://www.fishbase.org.

Country Basin Landing sites	Peru Upper Madre de Dios (A1) Puerto Maldonado	 TCO Tacana	Bolivia Beni and Mamoré (A2) Riberalta	 Puerto Villarroel	Bolivia/Brazil Iténez or Guaporé (B) Various	 Middle Madeira (C) Various	Brazil Lower Madeira (D1) Various	 Lower Madeira (D2) Various
Sampling years	2009-2011	2002-2009	2010-2011	2006-2008	2009-2011	2009-2011	2009-2011	2010-2011
Mean annual capture (t)	290	41	198	60	80	636	984	264
OSTEOGLOSSIFORMES								
Arapaima gigas (Cuvier, 1829)	0.4	—	79.0	—	0.2	1.1	1.0	<0.1
Osteoglossum bicirrhosum (Cuvier, 1829)	—	—	—	—	—	<0.1	0.7	<0.1
CLUPEIFORMES								
Pellona castelnaeana (Valenciennes, 1847)	—	—	—	3.1	0.3	<0.1	0.3	—
Pellona flavipinnis (Valenciennes, 1837)	—	—	—	—	<0.1	<0.1	—	—
CHARACIFORMES								
Leporinus spp.	—	—	—	—	0.2	<0.1	0.4	<0.1
Schizodon fasciatus (Spix & Agassiz, 1829)	—	—	—	—	0.9	1.4	1.7	—
Brycon amazonicus (Spix & Agassiz, 1829)	—	—	<0.1	—	0.6	9.6	9.4	12.3
Brycon melanopterus; B. cephalus (Cope, 1872; Günther, 1869)	1.4	0.8	—	—	1.1	<0.1	0.6	<0.1
Triportheus angulatus (Spix & Agassiz, 1829)	—	—	0.1	—	—	<0.1	0.8	—
Triportheus auritus (Valenciennes, 1850)	—	—	—	—	<0.1	<0.1	3.9	—
Triportheus spp.	—	—	—	—	—	—	—	3.1
Colossoma macropomum (Cuvier, 1816)	1.2	3.0	11.5	3.2	10.1	5.3	0.9	<0.1
Metynnis hypsauchen (Müller & Troschel, 1844)	—	0.5	—	—	—	—	—	—
Myleus or *Mylossoma* sp 1	—	—	—	—	—	<0.1	—	—
Myleus or *Mylossoma* sp. *2*	—	—	—		—	—	<0.1	—
Myleus or *Mylossoma* sp. *3*	—	—	—	—	—	<0.1	<0.1	—
Mylossoma duriventre (Cuvier, 1818)	0.4	0.3	0.1	—	2.9	1.4	20.5	11.7
Piaractus brachypomus (Cuvier, 1818)	2.6	10.1	0.5	6.2	1.0	0.5	0.8	<0.1
Pygocentrus nattereri (Kner, 1858)	—	1.1	0.4	—	4.6	1.2	0.7	—
Serrasalmus rhombeus (Linnaeus, 1766)	—	—	—	—	<0.1	<0.1	<0.1	<0.1
Serrasalmus spilopleura (Kner, 1858)	—	—	—	—	<0.1	<0.1	<0.1	—
Serrasalmus sp.	—	0.2	—	—	—	<0.1	<0.1	<0.1
Potamorhina altamazonica (Cope, 1878)	—	—	<0.1	—	—	<0.1	0.3	—
Potamorhina latior (Spix & Agassiz, 1829)	12.8	—	—	—	—	1.9	4.0	5.5
Psectrogaster amazonica (Eigenmann & Eigenmann, 1889)	—	—	<0.1	—	—	<0.1	1.0	—
Psectrogaster rutiloides (Kner, 1858)	1.4	—	—	—	—	—	—	—
Cynodon gibbus (Agassiz, 1829); *Hydrolicus scomberoides* (Cuvier, 1819); *H. armatus* ((Jardine, 1841); *Raphiodon vulpinus* (Spix & Agassiz, 1829)	1.9	1.5	<0.1	1.4	—	<0.1	<0.1	—
Hoplerythrinus sp.	—	0.4	<0.1	—	—	<0.1	<0.1	<0.1
Hoplias malabaricus (Bloch, 1794)	<0.1	0.3	0.2	—	0.3	0.7	0.7	<0.1
Anodus spp.; *Hemiodus* spp.	4.7	—	—	—	—	1.3	—	—
Prochilodus nigricans (Spix & Agassiz, 1829)	8.0	3.0	0.2	3.2	6.5	22.2	13.6	8.4
Semaprochilodus insignis (Jardine, 1841)	—	—	—	—	0.2	0.6	7.1	—
Semaprochilodus taeniurus (Valenciennes, 1821)	—	—	—	—	1.3	0.2	2.6	—
Semaprochilodus spp.	—	—	—	—	—	—	—	46.4

SILURIFORMES							
Ageneiosus inermis (Linnaeus, 1766); *A. ucayalensis* (Castelnau, 1855)	—	0.4	0.1	—	<0.1	<0.1	<0.1	—
Trachyelyopterus galeatus (Linnaeus, 1766)	—	—	—	—	—	<0.1	—	—
Hoplosternum littorale (Hancock, 1828)	—	0.8	0.5	—	<0.1	<0.1	4.2	—
Oxydoras niger (Valenciennes, 1821)	—	—	—	0.3	0.3	0.3	0.1	<0.1
Pterodoras granulosus (Valenciennes, 1821)	—	11.6	<0.1	—	—	—	—	<0.1
Hypostomus spp.	—	—	—	—	—	<0.1	<0.1	<0.1
Pterygoplichthys lituratus (Kner, 1854); *P. pardalis* (Castelnau, 1855)	—	—	—	—	<0.1	2.3	0.6	—
Pterygoplichthys disjunctivus (Weber, 1991)	1.0	0.3	0.1	—	—	—	—	—
Brachyplatystoma filamentosum (Lichtenstein, 1819)	0.5	6.1	0.3	8.5	0.5	3.5	2.5	<0.1
Brachyplatystoma platynemum (Boulenger, 1898)	3.8	—	—	—	<0.1	2.6	1.1	—
Brachyplatystoma rousseauxii (Castelnau, 1855)	1.8	9.7	0.2	2.2	0.5	1.5	4.8	<0.1
Brachyplatystoma vaillantii (Valenciennes, 1840)	—	—	—	—	—	2.3	0.2	—
Brachyplatystoma tigrinum (Britski, 1981)	0.3	—	—	—	—	—	—	—
Calophysus macropterus (Lichtenstein, 1819)	—	1.0	—	—	<0.1	0.2	3.0	—
Hypophthalmus edentatus (Spix & Agassiz, 1829); *H. marginatus* (Valenciennes, 1840)	1.8	—	—	—	—	0.2	0.2	—
Leiarius marmoratus (Gill, 1870)	1.7	1.8	0.6	—	<0.1	<0.1	<0.1	—
Perrunichthys perruno (Schultz, 1944)	—	1.4	—	—	—	—	—	—
Phractocephalus hemioliopterus (Bloch & Schneider, 1801)	—	3.0	0.1	5.2	6.9	1.3	2.1	1.1
Pimelodina flavipinnis (Steindachner, 1876)	25.1	—	—	—	—	—	—	—
Pimelodus aff. *Blochii* (Valenciennes, 1840)	1.8	—	—	—	—	<0.1	0.4	—
Pinirampus pirinampu (Spix & Agassiz, 1829)	3.4	0.3	<0.1	0.9	0.7	20.4	1.3	<0.1
Platynematichthys notatus (Jardine, 1841)	—	—	—	—	<0.1	0.2	<0.1	—
Platystomatichthys sturio (Kner, 1858)	0.1	—	—	<0.1	—	—	—	—
Pseudoplatystoma punctifer (Castelnau, 1855)	6.9	—	0.2	33.6	4.2	3.5	1.4	—
Pseudoplatystoma tigrinum (Valenciennes, 1840)	3.7	—	3.6	20.7	18.0	1.1	0.7	3.1
Pseudoplatystoma sp.	—	14.5	—	—	—	<0.1	<0.1	—
Sorubim lima (Bloch & Schneider, 1801); *S. elongates* (Littmann, Burr, Schmidt & Isern, 2001); *S. maniradii* (Littmann, Burr & Buitrago-Suarez, 2001)	—	0.6	—	—	—	<0.1	<0.1	—
Sorubimichthys planiceps (Spix & Agassiz, 1829)	—	5.1	0.2	3.2	—	0.2	0.2	—
Zungaro zungaro (Humboldt, 1821)	10.1	21.4	1.7	6.7	0.3	5.6	0.5	<0.1
PERCIFORMES								
Astronotus crassipinnis (Heckel, 1840)	—	—	—	—	3.8	0.5	1.7	<0.1
Cichla pleiozona (Kullander & Ferreira, 2006)	—	—	—	—	7.9	3.0	2.4	1.6
Cichla temensis (Humboldt, 1821)	—	—	—	—	—	0.5	0.1	—
Cichla sp. 1	—	—	—	—	—	<0.1	<0.1	—
Cichla sp. 2	—	—	—	—	23.0	<0.1	—	—
Geophagus proximus (Castelnau, 1855)	—	—	—	—	—	<0.1	0.1	—
Heros efasciatus (Heckel, 1840)	—	—	—	—	—	<0.1	<0.1	—
Satanoperca jurupari (Heckel, 1840)	—	—	<0.1	—	—	—	—	—
Plagioscion squamosissimus (Heckel, 1840)	1.6	1.0	0.3	0.8	3.5	0.7	0.7	0.6
Others	1.3[a]	—	1.7	—	<0.1	2.0	0.8	1.1

Fish species were ordered according to annex 1. See methods section for a list of landing sites in the Iténez (or Guaporé) and Madeira basins.

[a] For Peru, others include piraña (*Pygocentrus nattereri* and *Serrasalmus* spp.), leguía (*Auchenipterus nuchalis* / spp.), piro (*Megalodoras irwini*), sardina (*Triportheus elongatus* / *T. angulatus*), turushuqui (*Oxydoras niger*), shiruy (*Hoplosternus littorale* / *H. thoracatum*), lisa (*Schizodon fasciatus* / *Leporinus trifasciatus*).

catches in the Madeira basin is at least 83, but is more likely over 100, taking into account that within some genuses (e.g., *Hypostomus* and *Leporinus*) more than one unidentified species was recorded and that the category "others" could represent at least 12 species. The number of commonly captured species (defined as the ones representing more than 0.1% of total annual volume) varied between 10 (lower Madeira, D) and 40 (middle Madeira, C), with the upper sub-basins showing intermediate values (Table 4).

Species composition and relative abundance were very different among the landings, although some species occurred in almost all sub-basins, including the migratory *Colossoma macropomum, Piaractus brachypomus, Prochilodus nigricans* (Characiformes), *Brachyplatystoma filamentosum, B. rousseauxii, Phractocephalus hemioliopterus, Pinirampus pirinampu, Pseudoplatystoma punctifer, Zungaro zungaro* (Siluriformes), and the resident *Plagioscion squamosissimus* (Perciformes) (Appendix 1).

Fish species of the orders Characiformes and Siluriformes were dominant in the landings of almost all sub-basins: Characiformes dominated in downstream areas in Brazil (C, D), whereas Siluriformes prevailed in the landings of the upper basins (A1, A2) in Bolivia and Peru (Table 5). Yet, looking more closely, important differences were observed between Bolivia and Peru (Table 4). In Bolivia, most captured Siluriformes were the large and highly valued *Brachyplatystoma* and *Pseudoplatystoma* species. These large-bodied species occurred in lower proportion in Peruvian landings, where they were replaced by smaller catfish species feeding lower in the food web (Appendix 1), such as *P. pirinampu, Pimelodina flavipinnis, Leiarius marmoratus, Hypophthalmus* spp., and small Characiformes. This tendency was even more pronounced when comparing Bolivia with Brazil. Similarly, the two largest and most valued Characiformes, *C. macropomum* and *P. brachypomus*, were much more abundant in Bolivian landings than in the Peruvian or the Brazilian, where smaller species (such as *P. nigricans, Brycon amazonicus, Mylossoma duriventre*, etc.) dominated the catches (Table 4). Two exceptions were observed to this overall dominance of Characiformes and Siluriformes: the introduced species *Arapaima gigas* (Osteoglossiformes) dominated the landings of Riberalta in the lower Beni, and Perciformes (Cichlidae) represented close to 30% of overall catches in the clear waters of the Iténez/Guaporé River basin (compared to less than 11% of the catches in the other, mainly white water, sub-basins; Tables 4 and 5).

Fish production was based primarily on middle-distance migratory species, except in the Lower Beni where the resident *A. gigas* dominated the landings (Table 5). Long-distance migratory species occupied less than 10% of total catch in all study areas, with a prominent presence of *B. rousseauxii* in the TIOC Tacana – Beni River (Bolivia) and in the lower Madeira (D1, Brazil), where the species represented respectively 9.7 and 4.8% of the catches (Table 4).

Only two introduced species occurred in the landings (Appendix 1). *Arapaima gigas* occupied the larger portion of the catches in Riberalta and was rare both in the upper Madre de Dios basin (A1) and in the middle Madeira (C), where floodplain lakes are scarce. It has not yet appeared in the catches of the upper Beni and upper

Table 5. Taxonomic classification, migratory and feeding habits and origin of the species in landings in the Madeira sub-basins.

Basins	A1		A2		B	C	D1	D2
Landing sites	PM	TCO	Riberalta	PV	Var.	Var.	Var.	Var.
Taxonomic classification								
% Osteoglossiformes	0.0	0.0	**79.0**	0.0	0.0	0.0	0.0	0.0
% Clupeiformes	0.0	0.0	0.0	3.1	2.1	0.4	0.6	0.0
% Characiformes	36.9	21,1	13.0	14.0	34.7	**62,2**	**65.5**	**89.5**
% Siluriformes	**61.2**	**77,9**	7.7	**82.0**	33.8	27.0	27.4	6.6
% Perciformes	1.8	1.0	0.3	0.8	**29.3**	10.4	6.6	4.0
Migratory habits								
% Long-distance migratory species	6.3	9.7	0.2	2.2	9.1	1.8	2.1	0.2
% Middle-distance migratory species	91.4	86.5	19.4	97.0	51.0	61.6	80.3	94.9
% Resident species	2.3	3.8	**80.5**	0.8	**39.9**	**36.6**	17.6	5.0
Origen								
% Introduced species	0.5	0.0	**79.0**	0.0	4.6	2.9	1.7	0.0
% Native species	99.5	100.0	**21.0**	100.0	95.4	97.1	98,3	100.0
Feeding habits								
% Carnivorous species	29.8	66.9	**86.5**	**82.2**	56.0	54.4	24.8	9.9
% Detritivorous species	24.9	3.0	0.3	3.2	16.6	14.9	**51.9**	**75.1**
% Herbivorous species	2.1	0.0	0.0	0.0	0.0	1.0	1.4	0.1
% Omnivorous species	33.9	3.0	1.2	2.0	20.1	9.3	16.4	1.4
% Frugivorous species	6.3	14.7	12.1	9.4	**20.6**	6,6	14.2	9.8

Underlined bold data deserve special attention and are discussed in the text. (PM = Puerto Maldonado; TCO = TCO Tacana; RIB. = Riberalta; PV = Puerto Villarroel; Var. = various landing sites). See Table 4 for names of basins and see Material and Methods for a list of landing sites in the Iténez or Guaporé and Madeira river basins.

Table 6. Metric and trophic index values in the Madeira sub-basin landings (PM = Puerto Maldonado; TCO = TCO Tacana; RIB. = Riberalta; PV = Puerto Villarroel; Var. = various landing sites.

River basin	Upper Madre de Dios (A1)		Beni and Mamoré (A2)		Iténez or Guaporé (B)	Middle Madeira (C)	Madeira downstream (D1)	Madeira downstream (D2)
Landing sites	PM	TCO	RIB.	PV	Var.	Var.	Var.	Var.
Richness (total number of recorded species)	26+	43	28+	16	37+	60+	56+	28+
Richness (number of species representing > 0.1% of total weight)	25	27	20	15	26	32	40	10
Hill diversity index H1	13.9	12.8	2.4	8.4	27.1	26.9	39.0	7.0
Hill diversity index H2	9.1	9.1	1.6	5.6	23.0	13.3	35.0	3.9
Weight index of fish landed	—	8.7	41.0	10.8	11.1	11.6	7.0	—
Trophic level of landings	3.32	2.96	4.18	4.14	3.66	2.70	2.50	2.20

See Table 5 for names of subbasins and see the Material and Methods section for a list of landing sites in the Iténez and Madeira River basins.

Ichilo rivers (Table 5). It is caught in low percentages in the lower Madeira basin, where it is native. The second is *Semaprochilodus insignis*, which was introduced in the Iténez/Guaporé basin more than a decade ago (Carvajal-Vallejos et al., 2011), representing 3% of the annual catches.

Large carnivorous species occupied the larger portion of the catches in the Bolivian Amazon and the upper Madeira basin (C), whereas their contribution was much lower (< 30%) in Peru and in the lower sections of the Madeira River in Brazil, where smaller detritivorous and omnivorous species were more abundant. Frugivorous species, such as *C. macropomum, Mylossoma* spp., and *Brycon falcatus*, were particularly important in the Iténez/Guaporé basin, where they occupied more than 20% of total annual catch (Table 5).

Species diversity of the landings was highest in Brazil, intermediate in Peru and lowest in Bolivia. The average weight index of fish varied between 7.0 and 11.6 (Table 6). The lower Beni area was an exception to this, where the average capture weight of 41 kg was due to large individuals of *A. gigas*, which dominanted the landings. The trophic level of landings was highest in Bolivia, intermediate in Peru, and lowest in Brazil (Table 6).

Similarity analyses clustered the landing sites in the upper white water sub-basins (A1, A2) of the Madeira River on one side and the landing sites of the middle (B, C) and lower (D1, D2) sub-basins on the other side (Figure 2). The landing site of Riberalta, where the introduced *Arapaima gigas* makes up most of the catches, occupied the most isolated position.

Discussion

Characteristics and limitations of the collection system

Few of the Amazon countries sharing the Madeira basin possess reliable fisheries data collection systems (Batista and Petrere Jr, 2007; García Vásquez et al., 2009; Batista et al., 2012), making basin-wide comparisons a challenge. Because of these limitations, this study is based on data collected in very different ways, ranging from governmental initiatives to participative monitoring and private-sponsored scientific data collection. Peru at present is the only country with a governmental fisheries statistics system, although it only records total volumes of the most common species. In Bolivia, the official fisheries data collection system by Centro de Desarrollo Pesquero (CDP) was dismantled in 1995. Since then, only isolated data are available, collected by nongovernmental initiatives (Van Damme et al., 2011), with the most reliable being those collected through various forms of participatory monitoring. These systems provide more detailed data than the state-sponsored ones, but they are generally localized and time-limited. However, Brazil designed and implemented a very detailed governmental data collection system that collapsed in 2010, due to changes in state priorities (Batista et al., 2012). This system was complemented with private initiatives of base-line

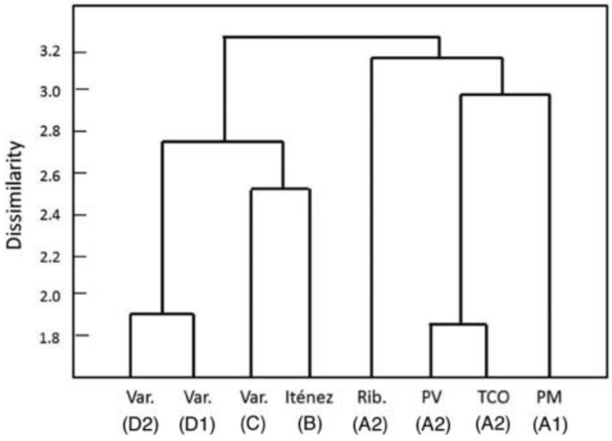

Figure 2. Dendrogram showing the dissimilarity between landing sites, using unweighted pair- group average clustering on log-transformed data at genus level. (PM, Puerto Maldonado; TCO, Tacana; Rib., Riberalta; PV, Puerto Villarroel; Var., various landing sites). See Table 4 for names of sub-basins and Material & Methods for a list of landing sites in the Iténez and Madeira river basins.

fisheries data collection of environmental impact studies, such as the one used in this study for the upper and middle Madeira. Because of its scientific nature, this data collection system provides relatively detailed daily fisheries data (Doria et al., 2012).

Standardized basin-wide estimation of the number of fishers is also deficient. In Bolivia, the only data source is the National Institute of Statistics (INE), based on auto-identification as a fisher with no distinction made between different types of commercial fishers (Paz and Van Damme, 2008). Data on the number of fishers affiliated to associations does not reflect the real number of active fishers (Van Damme et al., 2011), so they were not used in this study. Similarly, the total number of fishers registered in Brazilian fisheries Colonias and associations is greater than the number of active fishers, although these numbers were considered in this study. This may explain why the annual catches per fisher in the middle and lower Madeira sub-basins (C1, D1, D2) are unexpectedly low (Table 3). Notwithstanding the very different characteristics of these fisheries data collection systems, we believe that the present data compilation is sufficiently robust to detect overall patterns and provide a baseline for future comparisons. Characteristics and limitations of each collection system, however, should be taken into account during interpretation.

Biophysical factors influencing the fish volume and catch composition

Barthem and Fabré (2004) determined that fish volumes and catch composition are influenced by the physical habitat and its environmental seasonality, as well as by the characteristics of the fisheries resources and the capacity of the fleet, which might explain some of the observed regional differences in the Madeira basin.

Regional differences in frequency and extension of flooding events may greatly affect fisheries production (Castello et al., 2015; Pinaya et al., 2016), with larger floodplains providing higher fish production (Bayley and Petrere Jr., 1989; Isaac et al., 2004). The extensive floodplains in the Mamoré and Beni sub-basins, from where a high proportion of fish landings originate (Van Damme et al., 2011; Coca Méndez et al., 2012), likely account for part of the observed high catches per unit area of permanent water bodies compared to other areas. The Itenez or Guaporé sub-basin, however, which hosts the second largest flooded area of the Madeira basin, has the lowest fish landings of all sub-basins. The low number of fishermen in this sub-basin accounts for a large part of these low overall landings, as attested by the relatively high landings/fisher (Table 3).

Geochemical factors may also be involved. The clear-water rivers of the Iténez/Guaporé basin drain eroded pre-cambrian soils, which results in overall lower productivity than white-waters originating from the Andes (Junk et al., 1989; Junk, 1997; Saint-Paul et al., 2000) and catch composition patterns (Saint-Paul et al., 2000). The low sedimentation rates of clear waters do not allow lake isolation in the sub-basin (Van Damme et al., 2014), which influences habitat structure. The high water transparency resulting from low sediment suspended transport favors visual predators such as *Cichla pleiozona*, an abundant species in the catches of this basin.

Specific local characteristics of fishery fleets are influenced by the heterogeneous geomorphology of the river and floodplain habitats. The middle portion of the Madeira presents limitations for navigation due to rapids and occasional drought periods, determining the types of fishing and boats that can be used. However, the lower portions have greater navigability, which allows the use of larger boats and more efficient fishing equipment.

Fisheries historic data, social factors, and demand

During our study period, the observed total landings were five to six times greater than those reported 15 years ago by Chang (1999) and Cañas (2000) for the Peruvian portion of the Madre de Dios, about twice as much as those reported 30 years ago for Bolivia (Lauzanne et al., 1990), but approximately three times lower than those estimated by Barthem and Goulding (2007) for Brazil in the period of 1978–1998.

For Peru, previous studies used scientific surveys whereas we used official statistics, which are difficult to compare directly. Although official statistics can have several flaws (see discussion below) and might be overestimated, it is logical that, as observed in the other Peruvian regions over the last 20 years (García Vásquez et al., 2009), total landings also have increased in the Madre de Dios to face the demand of the rapidly growing population in the main Amazonian cities in Peru. The population of Puerto Maldonado increased by 387% between 1981 and 2017, in particular owing to mining activities along the river (Gobierno Regional de Madre de Dios, 2017).

In the case of Bolivia, although the estimation methods used between the two periods were very different, the fact that total landings have doubled over 30 years in the Bolivian Amazon, where fisheries were notoriously poorly developed (Lauzanne et al., 1990), is not unexpected.

More surprising are the apparently decreasing landings in the Brazilian portion of the Madeira, where human populations have also steadily increased and where demand for fish has not abated. These differences could come from the method used by Barthem and Goulding (2007), who pooled the maximum observed landings of 66 principal landing sites in the Amazon basin to obtain a basin-wide estimate of 173,000 tons. Using only official peak values is likely to give much higher estimates than mean observed values by scientific surveys. It is unlikely, however, that fisheries landings in the Brazilian portion of the Madeira have decreased since the late nineties. As an example, mean total annual landings remained stable over the last twenty years before the dams in the city of Porto Velho (Doria et al., 2012; Doria and Lima, 2015) and in the state of Rondônia (Ruffino, 2014), which represent the Brazilian portion of the Madeira, as well as other sub-basins not considered in this study.

Socioeconomic market factors may also influence observed inter-basin differences (Barthem and Fabré, 2004). The downstream portion of the river has higher proximity to major markets, which facilitates marketing and enables fisheries of small-sized cheaper species. The upstream area, mainly in the Bolivian Amazon, is far away from the major markets and is characterized by high fuel costs (Coca Méndez et al., 2012), which increases transportation and ice costs and reduces profitability of fisheries of smaller-sized low-value fish species. In the Peruvian portion of the upper Madre de Dios sub-basin, most fishing activities occur relatively close to the main market of Puerto Maldonado, the major city of the region, though much smaller than the market cities of the Brazilian portion of the Madeira basin.

The culturally-determined diets of the different human populations living in the basin are another factor that should be taken into account when comparing the trends between sub-basins. Bolivia has one of the lowest overall fish consumption rates in the area, between two and five kg per year (FAO, 2014). By comparison, per capita fish consumption in Brazil is 5–10 kg/yr and 20–30 kg/yr in Peru (amongst the highest in the South-American continent; FAO, 2014).

Fish consumption associated with subsistence fisheries by riverine communities or relying on local markets can be substantially higher. For example, Isaac and Almeida (2011) estimated a consumption of 31 kg/yr per capita for the Brazilian Amazon, whereas DIREPRO (2012), Isaac et al. (2015), and Pérez et al. (2014) reinforced the role of fish as the main source of cheap protein for Amazon River communities. Doria et al. (2016) report the equivalent of 160 kg/yr per capita in a community of the lower Madeira. Although cultural preferences may influence locally the fish species and amount being consumed (Barthem and Fabré, 2004; Cordova et al., 2012), the overall pattern is that fish are essential to food security in the Amazon and Madeira basin.

State of the fish caught

Overall, Madeira basin fisheries can be characterized as small-scale artisanal multispecies, using simple fishing gear, and fishing boats traveling short to middle-long distances (max. 400 km) with ice blocks to cool the catch (Coca Méndez et al., 2012; Doria et al., 2012). With at least 87 species (and probably over 100) in the overall landings of the three countries, commercial fisheries exploit less than 10% of the total species richness of the Madeira basin (Doria et al., 2012). A greater number of species is occasionally present in the landings, but these may remain under-reported, especially in the governmental landing data, and each probably represents less than 0.1% of the annual catch (Carvajal-Vallejos et al., 2011). For example, for the Upper Madre de Dios area (A1, Peru), the number of exploited species recorded during this study was lower than that observed between 1995 and 1998 in the same region in scientific surveys (Cañas, 2000). This is likely the result of a better distinction of individual species in Cañas (2000) compared to the pooled species in the official statistics used in the present study. Indeed, the tendency in fisheries of the Peruvian Amazon is reported to be towards diversification, with an increasing number of exploited species (García Vásquez et al., 2009). Of the species recorded in the overall basin, only 56 occurred in more than 1% of any catch. In all fisheries examined in this study, 80% of the landings were accounted for by less than 20 species, emphasizing the high dependence on a relatively small number of highly valued taxa (see also Cañas, 2000; Carvajal-Vallejos et al., 2011; Doria et al., 2012).

Alternatively, the differences in the catch composition in the different countries may reflect a historical “fishing down of the food web” (Pauly et al., 2000) in some sub-basins. Larger, highly-valued species (*Brachyplatystoma* spp. *Pseudoplatystoma* spp., *C. macropomum*, and *P. brachypomus*) made up most of the landings in Bolivia, where fisheries are the least intense, whereas small or mid-sized characids dominate the catch in the Brazilian part of the Madeira, where fishing has been the most intense, Peru representing an intermediate situation. This interpretation has also been reported for the Peruvian Amazon fisheries of the Loreto and Ucayali regions (García Vásquez et al., 2009; Vela et al., 2013). Moreover, these results also reflect the realities of human population densities along the rivers between the three countries, with Brazil the most populated and Bolivia the least.

Most recently, the introduction of *A. gigas* in the Peruvian and Bolivian sections of the Madeira basin (Carvajal-Vallejos et al., 2011; Miranda-Chumacero et al., 2012b; Van Damme et al., 2014) has changed fisheries catches drastically in the upper Madeira basin. Van Damme et al. (2011) and Van Damme and Carvajal-Vallejos (2013) reported a rapid change in Bolivia from catches dominated by migrating Siluriform and Characiform fish species before 2008, to catches dominated by lake-dwelling *Arapaima* after 2011. This change in catch composition is mostly explained by the large size and increasing attractiveness of *Arapaima* in urban markets, as well as by the relatively easy access to this resource, and has triggered an ongoing boom in fisheries development.

Management strategies influencing the fish catch

Finally, fish catch and composition are also influenced by fisheries regulations. In the Bolivian Amazon, fisheries are banned during the high water season (November to March), and during migratory periods in Brazil, whereas no such restriction exists in the Peruvian Amazon. In the Brazilian portion of the Iténez or Guaporé basin, fishing was additionally heavily restricted for five years (2011–2016) which resulted in a significant decrease in the number of fishers and fish landings (see Table 3) in comparison with previous years. Doria and Brasil de Souza (2012) reported a mean total catch between 400 and 500 t/year in the period 2009–2011, whereas only 128 t were reported in 2012 when fisheries restrictions were already in place. Certain fisheries resources, mostly in lakes, can also be protected under formal or informal community fishery management agreements or access restrictions, which is common in Bolivia (Coca Méndez et al., 2012; Macnaughton et al., 2015), Peru (García Vásquez et al., 2009), and Brazil (Vidal, 2010).

Concluding remarks

In spite of the overall similar small-scale multispecies fisheries pattern, this study revealed significant differences between the Madeira sub-basins, determined by the physical, social, and ecological factors that characterize each area. The total productive flooded area is a key factor influencing fishing in the Bolivian sub-basin, whereas higher social demand in Brazil and Peru reflects in greater exploitation in these countries, that is not so closely tied to physical productivity factors. The invasion of Bolivian waters by *A. gigas*, and its rapidly developing fisheries, is also providing socioeconomic novelty to fisheries development in this country. Despite the overall great diversity and richness of the catch composition in the upper basin, there still is a high dependence on only a relatively small number of migratory fish species (that are potentially affected by dams).

The diversity of the catch appears to reflect the cultural dietary habits in the different countries. Nevertheless, the relative trophic level of landings suggests possible historical over-exploitation in Brazil and Peru of high trophic level and larger bodied fish, resulting in the currently more diversified focus on smaller-bodied fish at lower trophic levels.

Ecosystem services provided by the rivers and their floodplains are threatened by human interventions, many of which exert transboundary impacts, which should stimulate the coordination of tri-national dialogue, planning, and mitigation efforts (Peru–Bolivia–Brazil). Dam development, habitat destruction, species introductions, and overexploitation represent the main threats to Amazon fisheries (Barletta et al., 2010; Castello and Macedo, 2015; Winemiller et al., 2016; He et al., 2017). Landscape alterations, especially deforestation of riverbanks, inundated floodplains, and headwater basins can also affect fish populations and communities and consequently the fisheries (Martelo et al., 2008).

As the socioeconomic indicators introduced in the present document are expected to react rapidly, this study will serve as a baseline against which the impacts of these threats, and of recent dam construction, could be measured in the near future.

This study shows that major international cooperation is necessary to: (1) adopt a shared comparable monitoring scheme to better understand the Madeira fisheries and their trends, (2) unified management practices for sustainable fishing, particularly of migratory fish whose migration routes span more than one country, and (3) diminish and mitigate migratory barriers and other threats that will influence crucial subsistence and commercial fisheries and related food security.

Acknowledgments

Fisheries data in Brazil were collected through the Monitoring Program financed by the Jirau and Santo Antonio Hydroelectric power plants. Fisheries data in Peru were kindly provided by Euzebio Carpio Chavez (Director of fisheries) and Rosaluz Milagros Velarde Retamozo from DIREPRO (Dirección Regional de Pesquería del Madre de Dios), Madre de Dios. Fisheries data in Riberalta were collected thanks to support by the CIFSRF (Canadian International Food Security Research Fund), a program of the International Development Research Centre (IDRC), through the project "Amazon Fish for Life". Data collection in Puerto Villarroel was supported by WWF-Bolivia. The writing of the manuscript was made possible thanks to a WWF-grant to the latter author enabling data systematization and to a CIFSRF project ("Amazon Fish for Food"), with financial support by the Government of Canada, provided through Global Affairs Canada (GAC). In Brazil this article was supported by Foundation of Support to Research of the Amazon (PAREV/FAPEAM 019/2010); CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior), through the PRÓ_AMAZÔNIA/CAPES (Project No.: 021/2012) and by scholarship support provided to graduate students and post-doctoral researchers involved in this study (MALL 7487-14-2). The authors are grateful to Joachim Carolsfeld for the revision of the text.

ORCID

Carolina R. C. Doria http://orcid.org/0000-0003-1638-0063

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Appendix 1. Fish species caught, local names, mean weight at capture and ecological characteristics (trophic level, migratory habits, native status). Within each order, fish families and species are ordered alphabetically. * = not recorded; Br = Brazil; Bo = Bolivia; Pe = Peru; LD = Long-distance migration; MD = medium distance migration; R = resident; N = native species; I = introduced species. Mean weights at capture in Brazil were obtained from measurements taken at random during the surveys; mean weights at capture in Bolivia were obtained from Puerto Villarroel fisheries in 2008, except for the mean weight of *Arapaima gigas*, which was obtained from 67 individuals captured by indigenous fishermen in Trinida, close to Riberalta.

Order/family/ scientific name	Local names			Mean weight at capture (kg)		Trophic level	Food habits	Migratory habits	Native or introduced
	Peru	Brazil	Bolivia	Brazil	Bolivia				
OSTEOGLOSSIFORMES									
Arapaimatidae									
Arapaima gigas	Paiche	Pirarucu	Paiche	48.8 ± 15.7 (*N* = 5)	48.8 ± 43.0 (*N* = 67)	4.50	C	R	N (Br) I (Bo, Pe)
Osteoglossidae									
Osteoglossum bicirrhosum	*	Aruanã	*	1.9 ± 1.5 (*N* = 237)	*	3.39^{a}	C	R	N
CLUPEIFORMES									
Pristigasteridae									
Pellona castelnaeana	*	Apapá-Amarelo	Sardinón/Belea/Dorado de escama	3.1 ± 1.4 (*N* = 425)	4.2. ± 1.4 (*N* = 17)	3.71^{a}	C	MD	N
Pellona flavipinnis	*	Apapá-Branco	Sardinón/Belea/Dorado de escama	*	*	4.50^{c}	C	MD	N
CHARACIFORMES									
Anostomidae									
Leporinus spp.	*	Aracú-Cabeça gorda	Lisa/Piau/Boga	0.4 ± 0.04 (*N* = 13)	*	2.00^{d}	D	MD	N
Schizodon fasciatus	*	Aracú-Comum	Lisa/Piau/Uruchila	0.25 ± 0.04 (*N* = 182)	*	2.04^{e}	D	MD	N
Characidae									
Brycon amazonicus	*	Jatuarana	Yatorana	1.5 ± 0.8 (*N* = 1571)	1.5	2.00^{a}	F	MD	N
Brycon melanopterus	Sábalo	Matrinxã	*	0.7 ± 0.1 (*N* = 64)	*	2.50^{a}	F	MD	N
Brycon cephalus	*	*	Mamuri/Yatorana	0.7^{7}	0.7	2.00^{d}	F	MD	N
Brycon falcatus	—*	Matrinxã	Matrinchan	0.7^{7}	*	2.60^{e}	F	MD	N
Triportheus angulatus	*	Sardinha papuda	Sardina/Pechuga	0.1 ± 0.01 (*N* = 20)	0.2	2.76^{e}	D	MD	N
Triportheus auritus	*	Sardinha comprida	*	0.1 ± 0.02 (*N* = 860)	*	2.76^{e}	D	MD	N
Curimatidae									
Potamorhina altamazonica	*	Branquinha-cabeça-lisa	Branquiña/Llorona/Sabalina	0.2 ± 0.001 (*N* = 4)	0.5	2.06^{e}	D	MD	N
Potamorhina latior	Yahuarachi	Branquinha-comum	Llorona/Sabalina	0.8 ± 1.08 (*N* = 440)	*	2.06^{e}	D	MD	N
Psectrogaster amazônica	*	Branquinha cascuda	Llorona/Sabalina	0.1 ± 0.1 (*N* = 25)	0.5	2.06^{e}	D	MD	N
Psectrogaster rutiloides	Chio chio	*	Llorona/Sabalina	*	*	2.06^{e}	D	MD	N
Cynodontidae									
Cynodon gibbus;	Chambira	Peixe cachorro/Pirandará	Cachorro	1.9 ± 0.06 (*N* = 6)	1.5	4.50^{c}	C	MD	N
Hydrolicus scomberoides;	Chambira	Peixe cachorro/Pirandará	Cachorro	1.9^{g}	1.5^{g}	4.5^{c}	C	MD	N
Hydrolicus armatus;	Chambira	Peixe cachorro/Pirandará	Cachorro	1.9^{g}	1.5^{g}	4.4^{e}	C	MD	N
Raphiodon vulpinis	Chambira	Peixe cachorro/Pirandará	Cachorro	1.9^{g}	1.5^{g}	4.5^{c}	C	MD	N

Erythrinidae									
Hoplerythrinus sp. 1	*	Jejú	Yeyú	0.1 ± 0.01 (*N* = 10)	0.7	3.41^{a}	C	R	N
Hoplias malabaricus	Huasaco	Traira	Bentón	1.8 ± 0.9 (*N* = 326)	1.5	4.50^{f} (3.80^{a})	C	R	N
Hemiodontidae									
Anodus spp. (A. elongatus?)	Yulilla	Charuto	Saona/Salmon	0.5	*	3.4^{c}	O	MD	N
Hemiodus spp. (H. amazonum?)	Yulilla	Charuto	Saona/Salmon	0.5	*	2.7^{e}	D	MD	N
Prochilodontidae								3.90	
Prochilodus nigricans	Boquichico	Curimatã	Sábalo	0.8 ± 0.7 (*N* = 1272)	1.0	2.33^{f}	D	MD	N
Semaprochilodus insignis	*	Jaraqui-escama-grossa	Sabalina	0.2 ± 0.1 (*N* = 525)	*	2.00^{f}	D	MD	N (I: Bo)
Semaprochilodus taeniurus	*	Jaraqui-escama-fina	*	0.2 ± 0.06 (*N* = 54)	*	2.00^{f}	D	MD	N
Serrasalmidae									
Colossoma macropomum	Gamitana	Tambaqui	Pacú	6.3 ± 3.4 (*N* = 80)	13.3 ± 6.5 (*N* = 85)	2.00^{e}	F	MD	N
Metynnis hypsaucheri	*	*	*	*	0.5	2.90^{e}	F	MD	N
Myleus spp.	*	Pacu-Jumento; Pacu-Marreca; Pacu-Olhudo	*	0.3^{7}	*	2.00^{e}	F	MD	N
Mylossoma spp	*	Pacu-Jumento; Pacu-Marreca; Pacu-Olhudo	*	0.3^{7}	*	2.52^{a}	F	MD	N
Mylossoma duriventre	Palometa	Pacu-comum	Pacupeba/Plato	0.3 ± 0.3 (*N* = 1024)	0.7	2.00^{e}	F	MD	N
Piaractus brachypomus	Paco	Pirapitinga	Tambaqui/Pirapitinga	1.3 ± 1.7 (*N* = 62)	5.3 ±1.4 (*N* = 68)	2.00^{e}	F	MD	N
Pygocentrus nattereri	*	Piranha-caju	Piraña roja/ Palometa	0.2 ± 0.05 (*N* = 120)	0.7	3.72^{a}	C	R	N
Serrasalmus rhombeus	*	Piranha-preta	Piraña/Piraña blanca	0.5 ± 0.4 (*N* = 24)	*	4.15^{b} (3.57^{a})	C	R	N
Serrasalmus spilopleura	*	Piranha-amarela	*	0.1 ± 0.1 (*N* = 3)	*	3.16^{a}	C	R	N
Serrasalmus sp. 1	*	Piranha-Mafurá	Piraña	*	0.6	4.15^{e}	C	R	N
SILURIFORMESleft									
Auchenipteridae									
Ageneiosus inermis	*	Mandubé	Manduvé/Seferino/Boca de sapo	0.7 ± 0.4 (*N* = 7)	0.7	3.98^{a}	O	MD	N
Ageneiosus ucayalensis	*	Mandubé	Manduvé/Seferino/Boca de sapo	0.7^{7}	0.7	3.70^{a}	O	MD	N
Trachyelyopterus galeatus	*	Cangati	*	*	*	3.14^{a}	O	MD	N
Callichthyidae									
Hoplosternum littorale	*	Tamoatá	Buchere	0.1 ± 0.05 (*N* = 407)	0.4	2.68^{b}	D	R	N
Doradidae									
Oxydoras niger	*	Cuiu-cuiu	Tachacá/Cuyucuyú/Boni	2.6 ± 1.8 (*N* = 6)	6.6 ± 1.7 (*N* = 4)	2.76^{a}	O	MD	N
Pterodoras granulosus	*	*	Tachacá	*	5.0	2.55^{a}	O	MD	N

(*Continued on next page*)

Appendix 1. *(continued)*

Order/family/ scientific name	Local names			Mean weight at capture (kg)		Trophic level	Food habits	Migratory habits	Native or introduced
	Peru	Brazil	Bolivia	Brazil	Bolivia				
Loricariidae									
Hypostomus spp.	*	Bodó	Carancho	0.5 ± 0.2 (*N* = 63)	*	2.10[e]	D	R	N
Pterygoplichthys lituratus	*	Acari-Bodo	Carancho/Zapato	0.3 ± 0.08 (*N* = 12)	*	2.00[e]	D	MD	N
Pterygoplichthys pardalis	*	Acari-Bodo	Carancho/Zapato	0.3[7]		2.00[a]	D	MD	N
Pterygoplichthys disjunctivus	Carachama	*	*	*	0.5	2.00[a]	D	MD	N
Pimelodidae									
Brachyplatystoma filamentosum	Salton	Filhote/Piraiba	Dorado/Pirahiba/Bacalao	12.7 ± 7.4 (*N* = 419)	16.3 ± 6.2 (*N* = 147)	3.55[f]	C	MD	N
Brachyplatystoma platynemum	Mota flemosa	Babão	Blanquillo/Baboso	5.6 ± 3.4 (*N* = 1401)	*	3.41[f]	C	LD	N
Brachyplatystoma rousseauxii	Dorado	Dourada	Dorado/Plateado/Saltador	11.9 ± 4.7 (*N* = 3194)	11.1 ± 4.4 (*N* = 14)	3.24[f]	C	LD	N
Brachyplatystoma tigrinum	Cebra	*	*	*	*	4.20[e]	C	MD	N
Brachyplatystoma vaillantii	*	Piramutaba	*	1.9 ± 1.6 (*N* = 87)	*	3.10[f]	C	MD	N
Calophysus macropterus	*	Pintadinho	Blanquillo	1.1 ± 0.08 (*N* = 4)	1.8	2.64[f]	C	MD	N
Hypophthalmus edentatus/	Maparate	Mapará	Mapara	0.2 ± 0.03 (*N* = 19)	*	2.91[a]	C	MD	N
Hypophthalmus marginatus	Maparate	Mapará	Mapara	0.2[7]	*	3.40[c]	C	MD	N
Leiarius marmoratus	Ashara	Jandiá	Tujuno/Pira	1.7 ± 0.8 (*N* = 15)	1.7	4.50[c]	C	MD	N
Perrunichthys perruno	*	*	Tujuno	*	1.5	4.50[c]	C	MD	N
Phractocephalus hemioliopterus	*	Pirarara	General/Pirarara	14.7 ± 4.9 (*N* = 774)	12.3 ± 7.2 (*N* = 161)	3.47[f]	C	MD	N
Pimelodina flavipinnis	Mota punteada	*	Blanquillo	*	*	3.20[c]	O	MD	N
Pimelodus aff. *Blochii*	Bagre	Mandi	Mandin/Chupa	0.9 ± 5.7 (*N* = 6)	*	3.11[a]	O	MD	N
Pinirampus pirinampu	Mota fina	Barbachata	Blanquillo/Piranambú/ Barba chata	2.4 ± 1.2 (*N* = 1117)	4.3 ± 1.1 (*N* = 167)	3.09[f]	C	MD	N
Platynematichthys notatus	*	Coroatá	*	1.8 ± 1.0 (*N* = 84)	*	4.30[e]	C	MD	N
Platystomatichthys sturio	Pico de pato		Chicotillo	*	1.0	4.00[e]	C	MD	N
Pseudoplatystoma fasciatum	Doncella	Surubim	Surubi/Pintado	5.0 ± 2.1 (*N* = 372)	10.5 ±4.0 (*N* = 187)	3.25[f]	C	MD	N
Pseudoplatystoma tigrinum	Puma zungaro	Surubim caparari	Semicuyo/Carapari/Chuncuina	4.3 ± 2.0 (*N* = 79)	13.6 ± 4.7 (*N* = 191)	4.50[b]	C	MD	N
Pseudoplatystoma sp. 1	*	Surubim-pintado	*	5.4 ± 2.4 (*N* = 323)	?	4.44	C	MD	N
Pseudoplatystoma sp. 2	*	Surubim-tigre	*	*	*	4.44	C	MD	N
Sorubim lima	*	Bico-de-pato	Pico de pato/Paleta/Tawalla	*	0.7	4.10[a/]	C	MD	N
Sorubim elongatus	*	Bico-de-pato	Pico de pato/Paleta/Tawalla	*	0.7 7	4.00[e]	C	MD	N
Sorubim maniradii	*	Bico-de-pato	Pico de pato/Paleta/Tawalla	*	0.7[7]	3.90[e]	C	MD	N
Sorubimichthys planiceps	*	Surubim-lenha	Paleta	3.3 ± 0.7 (*N* = 20)	5.8 ± 1.7 (*N* = 147)	4.50[c]	C	MD	N
Zungaro zungaro	Zúngaro	Jaú	Chanana/Muturo/Jaú	16.04 ± 6.8 (*N* = 221)	14.8 ± 8.1 (*N* = 191)	3.49[f]	C	MD	N
PERCIFORMES									

Cichlidae									
Astronotus crassipinnis	*	Acará-açú	Palometa real	0.9 ± 0.8 ($N = 212$)	*	3.00[e]	O	R	N
Cichla pleiozona	*	Tucunaré-açú	Tucunaré/Yacundá	1.6 ± 1.4 ($N = 448$)	1.6	4.20[e]	C	R	N
Cichla temensis	*	Tucunaré-pinima	*	1.0 ± 1.1 ($N = 37$)	*	4.49[c]	C	R	N
Cichla sp. 1	*	Tucunaré-Tatu	*	*	*	4.20[e]	C	R	N
Cichla sp. 2	*	Tucunaré	*	*	*	4.20[e]	C	R	N
Geophagus proximus	*	Acaratinga	*	0.2 ± 0.05 ($N = 13$)	*	2.20[e]	O	R	N
Heros efasciatus	*	Acará-roxo	*	*	*	2.67[a]	O	R	N
Satanoperca jurupari	*	*	Serepapa	*	0.3	3.10[e]	O	R	N
Sciaenidae									
Plagioscion squamosissimus	Corvina	Pescada	Corvina	1.7 ± 1.5 ($N = 245$)	4.3 ± 1.1 ($N = 8$)	4.35[b](3.97 a)	C	R	N

[a] Trophic level estimated from a number of food items using a randomized resampling routine (reviewed by Froeser & Pauly, 2015).

[b] Based on diet studies reviewed by Froeser and Pauly (2015).

[c] Tentative trophic level derived from 1 + troph of a single food item (Froeser & Pauly, 2015).

[d] Trophic level inferred from exclusive plant/detritus food items.

[e] Based on size and trophic level of closest relative (based on criteria used by Froeser & Pauly, 2015).

[f] Based on diet studies conducted on individuals from the Madeira river.

[g] Weight assumed to be the same as species of the same family within the catch.