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Patterns of selectiveness in the Amazonian freshwater fisheries: implications for management

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Tropical fisheries, which are considered multi-species, may show selectiveness. We analyzed the degree of selectivity of fish catches in 46 sites along the Amazon basin through the percentage of biomass corresponding to the most caught fish species. Amazonian fisheries were considered moderately selective, as 54% of the sites directed more than a quarter of fishing effort to one fish species and in 87% of the sites more than half the fishing effort was directed to five fish species. Commercial fisheries were more selective than subsistence fisheries. Eleven fish species (nine of them migratory) have received more fishing pressure in the studied Amazonian regions and the catch composition differed among regions. We thus recommend that fisheries management in the Amazon basin should distribute fishing effort among more fish species; incorporate the particularities of commercial and subsistence fisheries; evaluate fishing effects on ecosystem services; and consider the biological characteristics of preferred fish.

Keywords: fish conservation; fisheries management; freshwater fishes; overfishing; migratory fishes

1. Introduction

Tropical aquatic ecosystems support great environmental heterogeneity and high diversity of fish species (Pauly 1979; Welcomme 1985). Tropical fisheries are considered to be multi-specific, because of the variety of fishing gear used, habitats exploited, and several fishes and invertebrate species exploited simultaneously, seasonally or sequentially (Welcomme 1985; Bayley and Petrere 1989; Vass *et al.* 2010). The temporal variation of catch per unit effort (CPUE) and fishing yields in inland multi-species fisheries differ from single-species fisheries, as fishing yields may be maintained in the former through the fishing down process of replacement of larger and over-exploited fish species by smaller fish (Welcomme 1999; van Oostenbrugge *et al.* 2002; Welcomme *et al*. 2010). Tropical fisheries have been usually assumed to be multi-species (Pauly *et al.* 2002; van Oostenbrugge *et al.* 2002), but some of these fisheries may be selective, directing most of the fishing pressure to one or a few valued fish (Bayley and Petrere 1989; Aswani and Hamilton 2004; Vass *et al.* 2010). Selective fisheries can affect the biodiversity, by altering the composition of fish communities and trophic structure (Garcia *et al.* 2012). Therefore, it is important to evaluate the degree of selectivity among alleged multi-species fisheries (van Oostenbrugge *et al.* 2002).

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The Amazon basin is the largest freshwater ecosystem in the world (Welcomme 1985) and has one of the world's richest freshwater fish fauna (Junk, Soares, and Bayley 2007). Fishing activity has an important role in the economy and subsistence in the Amazon basin, where fish is one of the most important sources of animal protein (Bayley and Petrere 1989; Batista *et al.* 1998; Isaac and Almeida 2011). Albeit the biggest fish market of the Brazilian Amazon (Manaus city) commercializes around 100 fish species (Batista and Petrere 2003; Santos, Ferreira, and Zuanon 2006), few fish species may account for most of the biomass landed in the Amazon basin (Bayley and Petrere 1989; Cerdeira, Ruffino, and Isaac 2000; Cetra and Petrere 2001). South American fisheries, including Amazon fisheries, in general are not considered to be overfished, as large fish are still regularly caught and sold and fish production in some regions is lower than the maximum sustainable yield (Bayley and Petrere 1989; Welcomme *et al.* 2010). Nonetheless, there is evidence of overexploitation of some large commercial fish species in the Amazon fisheries, such as pirarucu (*Arapaima gigas*), tambaqui (*Colossoma macropomum*), dourada (*Brachyplatystoma rousseauxii*) and filhote (*B. filamentosum*) (Smith 1985; Petrere *et al.* 2004; Isaac, Silva, and Ruffino 2008; Garcia *et al.* 2009). Furthermore, fish landed in the Brazilian Amazon had been recorded by popular names, which may correspond to more than one biological species with different life histories (Santos, Ferreira, and Zuanon 2006). Therefore, the degree of selectivity should be evaluated to inform policy and management actions for Amazon inland fisheries.

We made a broad meta-analysis of the spatial and temporal patterns of fish catches from 46 sites in the Amazon basin to assess the fishing selectivity and provide suggestions to improve the fisheries management. To our knowledge, this is one of the first studies to perform such meta-analysis of selectiveness for tropical fisheries. This approach can be applied in other regions, where fisheries need to be managed but data is scarce, according to the data-less management approach (Johannes 1998). We addressed the following research questions and hypotheses about multi-species Amazonian fisheries:

(1) Which is the degree of selectivity of these fisheries? Based on previous studies (Bayley and Petrere 1989; Cerdeira, Ruffino, and Isaac 2000; Batista and Petrere 2003; MacCord *et al.* 2007; Hallwass *et al.* 2011), we expect that most of these fisheries would concentrate fishing effort in one or a few fish species;

(2) Which variables influence fishing selectiveness? We expect that fishing selectiveness would be positively related to CPUE and total annual production, and inversely related to the number of species and year when the study was conducted. According to the fishing down process in inland multi-species fisheries, a replacement of large preferred fish species by smaller ones over time can result in an increase in the number of species caught and in the fishing effort to maintain the total production, but with a potential decrease in CPUE, as large fish become scarce (Welcomme 1985, 1999). Furthermore, according to the ecological theories of niche and optimal diet, fishers from less productive sites (lower CPUE and total production) would expand their niche (lower selectiveness) by catching less preferred fishes, the inverse occurring in more productive sites (Begossi and Richerson 1992, 1993). We also expect that fishing selectiveness would differ among major Amazonian regions, because ecological constraints (water properties, nutrient load) may influence the availability of target fish species (Welcomme 1985; Junk, Soares, and Bayley 2007). The relationship between fishing selectiveness and population size is less predictable;

Although an increasing demand for preferred fish may increase the selectivity, at some point such demand could reduce the selectivity to supply the needs of the population for fish and by overexploitation of preferred fish. We also expected that commercially oriented fisheries aiming to supply larger markets would be more selective, as middlemen may select preferred fish (Bayley and Petrere 1989; Hallwass *et al.* 2011);

(3) Which are the most caught fish species and did they differ among the studied Amazonian regions? We expect that the composition of the five most caught species would differ among regions, due to the high heterogeneity of tropical environments (Welcomme 1985; Junk, Soares, and Bayley 2007) or market preferences.

2. Materials and methods

2.1. Study area

We gathered fish landings data from 15 studies conducted all over the Amazon basin (Table 1). We grouped the 46 studied sites (usually cities or small fishing villages) in four geographic regions of the Amazon basin: central ($n = 14$ sites), south-west ($n = 8$), lower ($n = 11$) and eastern ($n = 13$) (Figure 1). Some of the studied sites may include a wider area; for example, Manaus is located in central Amazon (Table 1) and it is the biggest fish market analyzed, receiving fishes from several Amazonian rivers (Purus, Middle and Low Solimões, Madeira, Upper Amazonas and Juruá) (Batista and Petrere 2003; Fernandes, Vicentini, and Batista 2009).

2.2. Data collection

We searched for publications about Amazonian fisheries in the scientific platforms Thomson Reuters Web of Knowledge (ISI) and Scientific Electronic Library Online (SciELO), as well as in gray literature (theses and reports). We used the terms “fisheries” and “Amazon” (in English and Portuguese) in the research in the ISI and SciELO platforms, which resulted, respectively, in 169 and 29 studies, but some of these studies deal with fish ecology or ecotoxicology. This number of studies was similar to that found by Alves and Minte-Vera (2013), who record 103 studies in the Amazon basin, plus nine in the Araguaia-Tocantins Basin that we included here as part of the Amazon basin (eastern Amazon). We selected those studies that informed the biomass of at least the five fish species that were most caught, because five species usually account for most of the catches (Bayley and Petrere 1989; Batista and Petrere 2003; Hallwass *et al.* 2011), and several studies do not show the complete list of species caught. We also included in our research Brazilian scientific journals and books that are not on international data bases. We thus selected and analyzed 15 published studies that report the needed data on fish landings from 46 sites of the Amazon basin (Table 1). We selected, for our meta-analysis, those studies that describe a clear methodology to record fish landings in well-defined landing sites or ports, that include a reasonable time span (months or years) recording fish landings in at least two hydrological seasons (low and high water), and that show data on the number of species caught, total annual fish production, and, when possible, CPUE. We considered fish landing sites as sampling units for analyses. These sites included from small fishing villages with hundreds of people to big Amazonian cities, such as Manaus, which has more than one million inhabitants. We separated the fisheries

Table 1. Characteristics, data sources and fish landings' data for the 46 fisheries surveys analyzed in four geographic regions of the Amazon basin. Codes for the studied fisheries (sites and years) are the same that as those shown in Figure 3.

Region	Site	Codes	Year	Number of fish species caught [a]	Annual production (t)	CPUE ($kg \times fisher^{-1} \times day^{-1}$)	Population size[b]	Fishing scale	Frequency of gill nets use	Source
Central Brazilian Amazon	Manaus	Ma_70	1970	36	10,859	–	Large	Commercial	>75%	Honda *et al.* (1975)
		Ma_71	1971	36	11,130	–	Large	Commercial	>75%	
		Ma_72	1972	36	11,144	–	Large	Commercial	>75%	
		Ma_73	1973	36	9,538	–	Large	Commercial	>75%	
		Ma_74	1974	36	14,746	–	Large	Commercial	>75%	
		Ma_94	1994	39	25,084	–	Large	Commercial	NI[c]	Batista and Petrere (2003)
		Ma_95	1995	39	22,322	–	Large	Commercial	NI[c]	
		Ma_96	1996	39	23,589	–	Large	Commercial	NI[c]	
		Ma_99	1999[d]	–	–	–	Large	Commercial	100%	Fernandes, Vicentini, and Batista (2009)[d]
	Manacapuru	Mu_03	2003[e]	–	592[f]	–	Large	Commercial	100%	
		Mu_01	2001	34	2,104.2	100	Large	Commercial	NI[c]	Gonçalves and Batista (2008)
		Mu_02	2002	32	2,065.6	100	Large	Commercial	NI[c]	
	Jarauá	Ja_03	2003	26	199.3[g]	46.3	Small	Commercial	24%	MacCord *et al.* (2007)
	Ebenezer	Eb_03	2003	45	61.6[g]	50.4	Small	Commercial	70%	
South-west Amazon	Manicoré	Me_02	2002	32	225.4	–	Medium	Commercial	NI[c]	Cardoso and Freitas (2008)
	Porto Velho	PV_04	2004	56	310.1[h]	35.2	Large	Commercial	>50%	Doria *et al.* (2012)
	Guajará-Mirim	GM_04	2004	53	107.4[h]	65	Medium	Commercial	>50%	
	Teotônio	Te_04	2004	47	4.6	26.6	Small	Commercial	>50%	
	Jacy Paraná	JP_04	2004	52	14.3	11.1	Small	Commercial	>50%	
	Nova Mamoré	NM_04	2004	54	18	22.2	Medium	Commercial	>50%	
	Abunã	Ab_04	2004	52	5.4	11.1	Small	Commercial	>50%	
	Loreto region	Lo_95	1995[e]	65	12,368[f]	–	Large	Commercial	NI[c]	Garcia *et al.* (2009)
Lower Amazon	Santarém	Sa_92	1992	–	3,713	–	Large	Commercial	>50%	Ruffino and Isaac (1994)
		Sa_93	1993	63	4,280	14.0	Large	Commercial	>70%	Isaac, Milstein, and Ruffino (1996)
	Monte Alegre	MA_94	1994	70	8,320	22	Large	Commercial	>50%	Cerdeira, Ruffino, and Isaac (2000)
	Aracampina	Ar_05	2005[e]	40	111	8[i]	Small	Subsistence	65%	Castello *et al.* (2013)

(*continued*)

Table 1. (*Continued*)

Region	Site	Codes	Year	Number of fish species caught [a]	Annual production (*t*)	CPUE (kg×fisher^{-1} ×day^{-1})	Population size[b]	Fishing scale	Frequency of gill nets use	Source
	Pixuna	Px_05	2005[e]	40	89	10.6[i]	Small	Subsistence	55%	
	Santa Maria	SM_05	2005[e]	40	128	9.4[i]	Small	Subsistence	65%	
	Santana	Sn_04	2004[e]	40	395	11[i]	Small	Subsistence	58%	
	São Benedito	SB_96	1996[e]	40	38	8[i]	Small	Subsistence	24%	
	São José	SJ_96	1996[e]	40	93	4.8[i]	Small	Subsistence	66%	
	São Miguel	Si_04	2004[e]	40	48	13.8[i]	Small	Subsistence	0%	
	São Raimundo	SR_96	1996[e]	40	63	5.4[i]	Small	Subsistence	57%	
Eastern Brazilian Amazon[j]	Cametá	Ca_81	1981	46	596.1	–	Medium	Commercial	>50%	de Mérona *et al.* (2010)
	Mocajuba	Mo_81	1981	50	251.7	–	Small	Commercial	>50%	
	Ituquara	It_81	1981	50	34.5	–	Small	Subsistence	75%	
	Tucuruí	Tu_81	1981	60	414.6	–	Large	Commercial	>50%	
	Marabá	Mr_81	1981	50	315.4	–	Medium	Commercial	>50%	
	Imperatriz	Im_88	1988	64	857.5	5.3	Large	Commercial	>50%	Cetra and Petrere (2001)
	Imperatriz	Im_98	1998	69	7,452.4	–	Large	Commercial	>50%	
	Baião	Ba_07	2007	18	58.2	30.2	Medium	Commercial	>90%	Hallwass *et al.* (2011)
	Açaizal	Ac_07	2007	39	36.8	7.1	Small	Subsistence	94%	
	Calados	Cl_07	2007	39	16.2	4.4	Small	Subsistence	>50%	
	Ituquara	It_07	2007	57	41.6	5.7	Small	Subsistence	55%	
	Joana Peres	JP_07	2007	42	30.2	8	Small	Subsistence	70%	
	Umarizal	Um_07	2007	40	16.4	5.1	Small	Subsistence	54%	

[a] Fish species here refers to popular names of fish caught, which may sometimes correspond to groups of species.
[b] Population size was categorized on the basis of the number of inhabitants in each studied site: small (1−10,000 people), medium (10,001−50,000) and large ($\geq$ 50,001).
[c] NI means not informed: the study did not mention the frequency of gear used in the fish landings sampled.
[d] This survey includes only fish landings on which fishers used gillnets.
[e] This value corresponds to the median range of sampled years.
[f] This value corresponds to the mean production of sampled years.
[g] We estimated the annual production for these sites, considering six fishing days each week during 52 weeks per year, or 312 fishing days per year (156 days on each season), which was then multiplied by the average daily catches (kg) on each season (high and low water).
[h] This production was obtained for one landing point only, and did not represent the total production of this city.
[i] CPUE was originally calculated as kg/fisher/hr, but here we multiply this value by 8 hr, which is the average time per fishing trip found by Cerdeira, Ruffino, and Isaac (2000) in the Lower Amazon.
[j] Studies conducted in the Tocantins River, Brazilian Amazon.

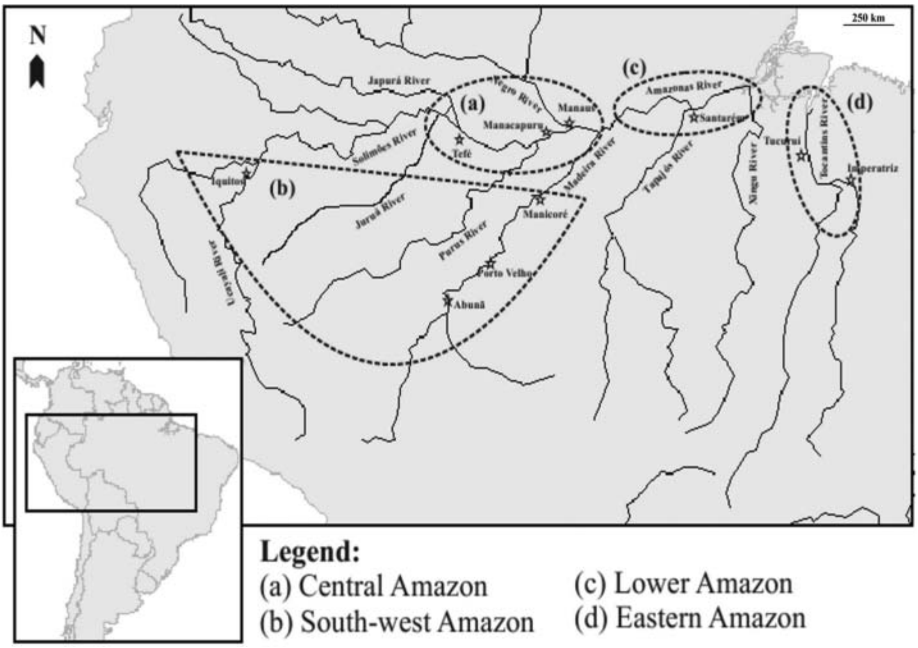

Figure 1. The Amazon basin with its major rivers: the studied regions are identified by dashed contours and lower case letters.

analyzed into two types: commercial and subsistence, according to Bayley and Petrere (1989). Commercial fisheries land fish in urban markets, using mainly motor boats or powered canoes and with capacity to store fish and ice. Subsistence fisheries land fish in small communities, using mainly paddled canoes or small powered canoes, sometimes with small iceboxes (low storage capacity). We adopted these criteria because the size of boats may influence the range of fishing grounds explored by fishers, and boat size and storage capacity have been shown to be positively related to the amount of fish caught by Amazonian commercial fishers (Almeida, Lorenzen, and McGrath 2003; Isaac, Silva, and Ruffino 2008). We could not differentiate commercial fisheries in more refined categories, because of the lack of detailed information about these fisheries, such as fleet size and capacity, engine power and amount of ice used.

The population size was categorized as small (1−10,000 inhabitants), medium (10,001−50,000) and large (above 50,001). If not provided in the studies analyzed, we obtained population data from the Brazilian Institute of Geography and Statistics (IBGE). We considered the year when the study was conducted, or the median of sampled years when the study included data from more than one year.

Studies of fish landings in the Amazon usually record fish by their popular or local names, but we only included in our meta-analysis those studies that inform both popular and scientific names of fish caught. We also checked the correspondence between popular and scientific names of the main fish species caught in fish landings through the FishBase electronic database (Froese and Pauly 2012) to verify how many scientific species corresponded to each popular name. We also consulted published inventories of the Amazonian fish species that mention both popular and scientific names of fishes (Santos *et al.* 2004; Santos, Ferreira, and Zuanon 2006). Therefore, when a popular name included more than one fish species, we divided the amount of biomass reported for this fish among the reported species for the region. For example, we divided the reported biomass of the fish *jaraqui* between two species (*Semaprochilodus insignis* and *S. taeniurus*), because this local name usually corresponds to these two species in most Amazonian regions, except for eastern Amazon, where only one species occurs (*S. brama*) (Santos *et al.* 2004).

We did not include the fishing gear used in our analysis because, in most of the studied sites, fishers use mainly gillnets (used in more than 50% of fish landings). In only three of the 39 sites, where we found information on fishing gear, fishers use gillnets in less than 50% of fish landings (Table 1).

2.3. *Data analysis*

We provided a quantitative approach to analyze fishing selectiveness through categories based on the biomass of the main fish species caught. We could not find, in the literature, a clear indicator of the degree of selectivity for multi-species fisheries. We thus arbitrarily organized our data in four categories of selectiveness, according to the proportion of biomass corresponding to the first most caught fish species; (a) >50% of total biomass: high selectiveness; (b) 25%−50% of total biomass: moderate selectiveness; (c) 10%−24% of total biomass: low selectiveness; and (d) <10% of total biomass: multi-specific, as effort would be more distributed among several species. We seek to be more conservative regarding the proposed categories because tropical and Amazon fisheries are considered multi-species and around 100 species are sold in markets in the Amazon (Batista and Petrere 2003; Santos, Ferreira, and Zuanon 2006). This contrasts sharply to the situation of temperate selective fisheries, where all the catch may correspond to five or six species. Therefore, even if one species comprises 40% of the catch, more than 40 species usually make the rest of the catch, such as, for example, in fisheries in the Tocantins, Upper Madeira and Solimões Rivers (Cetra and Petrere 2001; MacCord *et al.* 2007; Hallwass *et al.* 2011; Doria *et al.* 2012). This is why we opted for the benchmark of 50%, as this corresponds to more than half the total catch. However, the criteria for selectiveness could be adjusted for other fisheries, as appropriate.

We measured selectiveness on the basis of the first, the first three and the first five fish species that were most caught in each site. We then did exploratory analyses to check the possible influence of the following variables on the observed selectiveness in each site: region of the Amazon basin, year when the study was conducted, total number of fish species caught, CPUE, population size, total annual fish production and fishing type (commercial or subsistence). We undertook regression analysis to verify the influence of four independent continuous variables (year, total number of species caught, total annual production and CPUE) on the three dependent variables related to fish selectiveness (proportions of the first, three and five fish species that were most caught on each site) separately, considering the 46 landing sites as replicates (Table 1). The analysis of the CPUE (kg $\times$ fisher^{-1} $\times$ day^{-1}) was based on 27 sites, due to the lack of these data for the other 19 sites. In regression analyzes, we checked the homoscedasticity of residuals and then we ran different curve adjustments (linear, exponential, logarithmic and geometric) to verify possible non-linear relationships. In order to check the influence of independent categorical variables on the fish selectiveness, we made non-parametric analyses (median comparisons): (a) Mann−Whitney (U) test to verify the differences on selectiveness between commercial and subsistence fisheries and (b) Kruskal−Wallis analyses, with an a posteriori Dunn test, to verify the influence of two independent categorical variables (region and population size) on fish selectiveness. We used these non-parametric analyses because variances were not homogeneous. We made all these statistical analyses using the R software (R Development Core Team 2009).

We made a non-metric multi-dimensional scaling (NMDS) ordination based on the Bray–Curtis similarity index and randomization test (10,000 permutations) to check differences on catch composition among the 46 sites sampled in the four studied regions (Figure 1). The data matrix included the biomass proportion of the five fish species that were most caught in each site (36 species in all the sites). We then made the analysis of similarities (ANOSIM) to compare the composition of the most caught fish species among the four studied regions, followed by similarity percentage analysis (SIMPER) to check which species most explained the dissimilarity among the four regions. We performed the NMDS, ANOSIM and SIMPER analyses using the PRIMER 6 software program (Clarke and Gorley 2006).

3. Results

3.1. Selectivity of the Amazonian multi-species fisheries

When the first main exploited fish species was considered, 54% of the studied sites showed a trend to be moderately selective (25%–50% of total biomass), 44% were low selective (10%–24% of total biomass) and a few sites were either highly (>50% of total biomass) or not selective (<10% of total biomass), (4% and 2%, respectively). The three most caught species accounted for more than half the total biomass in 52% of the sites, and for more than 25% of total biomass in all sites, while the five most caught species accounted for more than half the total biomass in 87% of the studied sites (Figure 2).

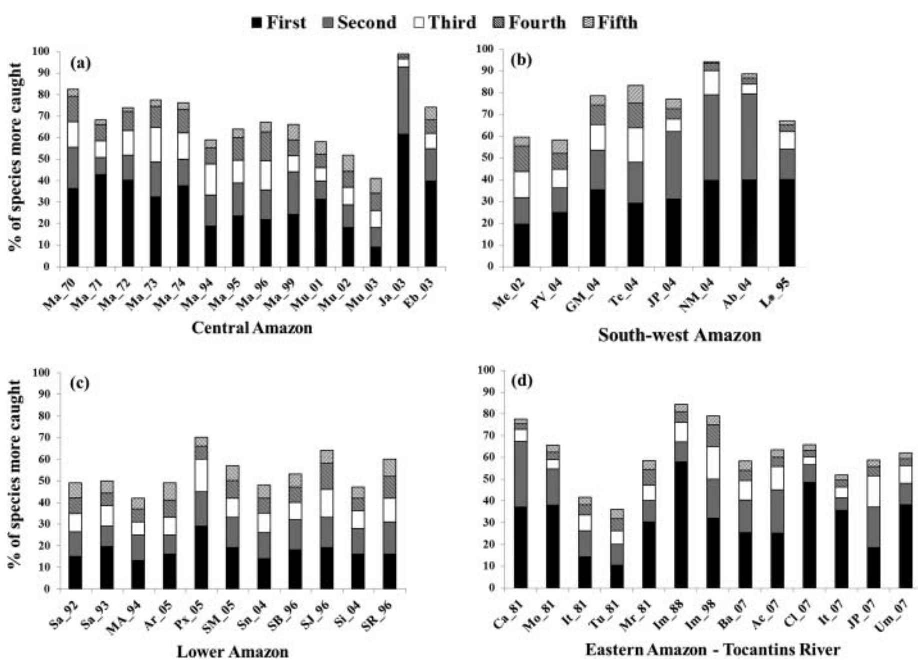

Figure 2. The percentage of total biomass that corresponded to the five most caught fishes in 46 sites sampled in four regions of the Amazon basin. Details and codes for the sites are provided in Table 1.

Therefore, relatively few Amazonian fisheries showed a high selectiveness (exploiting mainly one species), but most of the studied fisheries concentrated fishing effort in up to five species (Figure 2).

3.2. Variables influencing fish selectiveness in the Amazon

Fishing selectiveness was influenced by fishing type and region. The commercial fisheries were more selective, considering the proportion of biomass of the first ($U = 141.5$, $p = 0.02$) (Figure 3(a)), three ($U = 146.5$, $p = 0.03$) (Figure 3(b)) and five ($U = 154$, $p = 0.05$) (Figure 3(c)) most caught species. The lower Amazon region showed a lower selectiveness than the other regions, considering the proportion of biomass of the main fish species caught ($H = 14.8$, $p = 0.002$) (Figure 4(a)). When considering the proportion of biomass of the three most caught species, the lower Amazon region showed a lower selectiveness than the central and southwest regions ($H = 12.7$, $p = 0.005$, Figure 4(b)), and the lower Amazon showed a lower selectiveness than the southwest region, when considering the five most caught species ($H = 9.4$, $p = 0.02$) (Figure 4(c)). The outlier points indicated that selectiveness varied among sites within regions (Figure 4). None of the other independent variables (year, total number of species caught, total annual production, CPUE and population size) were related to fish selectiveness ($p > 0.15$ in all curve adjustments).

3.3. Comparison of the most caught fish species among the Amazonian regions

The ANOSIM analysis (global $R = 0.59$, $p = 0.001$) indicated differences among the four regions sampled regarding the five fish species that were most caught (Figure 5). The SIMPER analysis indicated a low average similarity among sites within regions (central Amazon = 49.6%; lower Amazon = 58.7%; southwest Amazon = 26.5%; eastern Amazon = 42.3%), whereas the average dissimilarity was high among regions (all > 66%).

The fish species that most influenced the observed differences among regions were: the tambaqui (*Colossoma macropomum*) and two species of the jaraqui (*Semaprochilodus* spp.), which were more abundant in the central Amazon and differentiated this region from the others. The more abundant fishes in the lower Amazon region were the surubim (*Pseudoplatystoma fasciatum*) and acari (*Pterygoplichthys pardalis*), which differentiated this region from the others. The dourada (*Brachyplatystoma rousseauxii*) differentiated the lower Amazon from central and eastern Amazon and the tambaqui differentiated the lower Amazon from the southwest and eastern Amazon. Two species of the matrinchã (*Brycon cephalus* and *B. amazonicus*) were more abundant in the south-west Amazon, distinguishing this region from all others. Finally, the pescada (*Plagioscion squamosissimus*) and the mapará (*Hypophthalmus marginatus*) were more abundant in the eastern Amazon. The curimatá (*Prochilodus nigricans*) was among the most caught fish in the four studied regions (Table 2).

4. Discussion

4.1. Selectivity of the Amazonian fisheries

Our meta-analysis of fisheries surveys in 46 sites in four major regions of the Amazon basin indicated that most of these fisheries were moderately selective (first main fish species corresponded to 25%−50% of total biomass caught). Although some of the

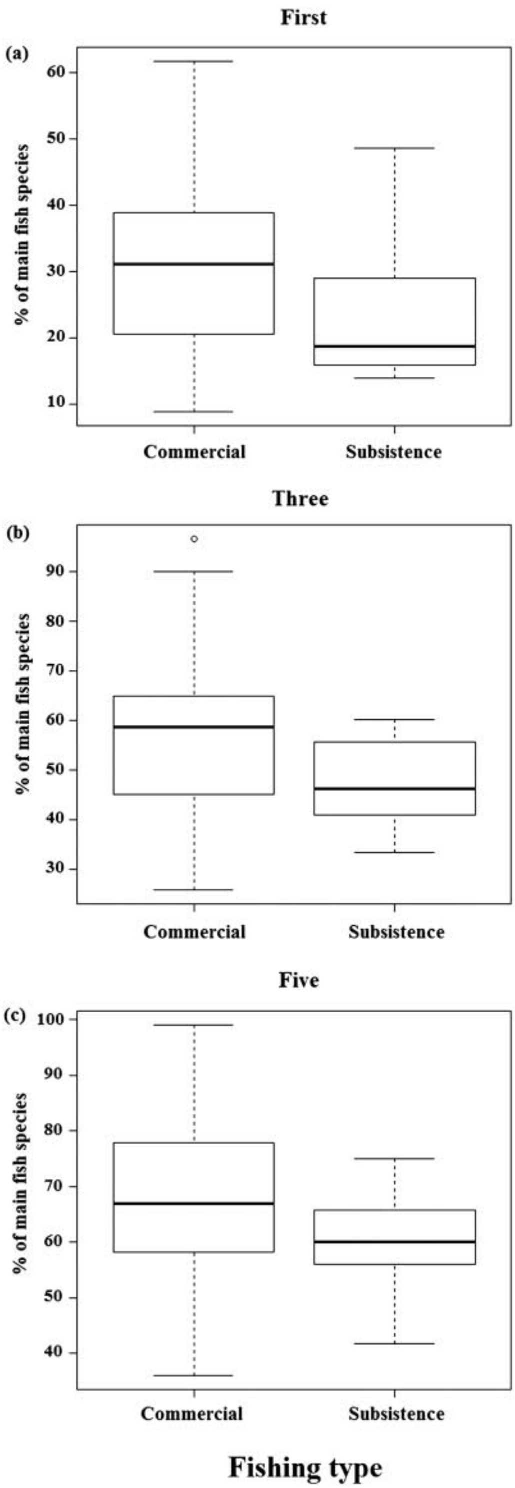

Figure 3. Comparison between the selectivity of commercial and subsistence fisheries in the Amazon basin ($N = 46$) based on the proportions of the (a) first; (b) three; and (c) five fish species that were most caught on each site. Median (darker line in the box plot), minimum and maximum values (vertical lines) and outer lines of the box plots showing the quartiles (25% and 75%). Circles are outliers.

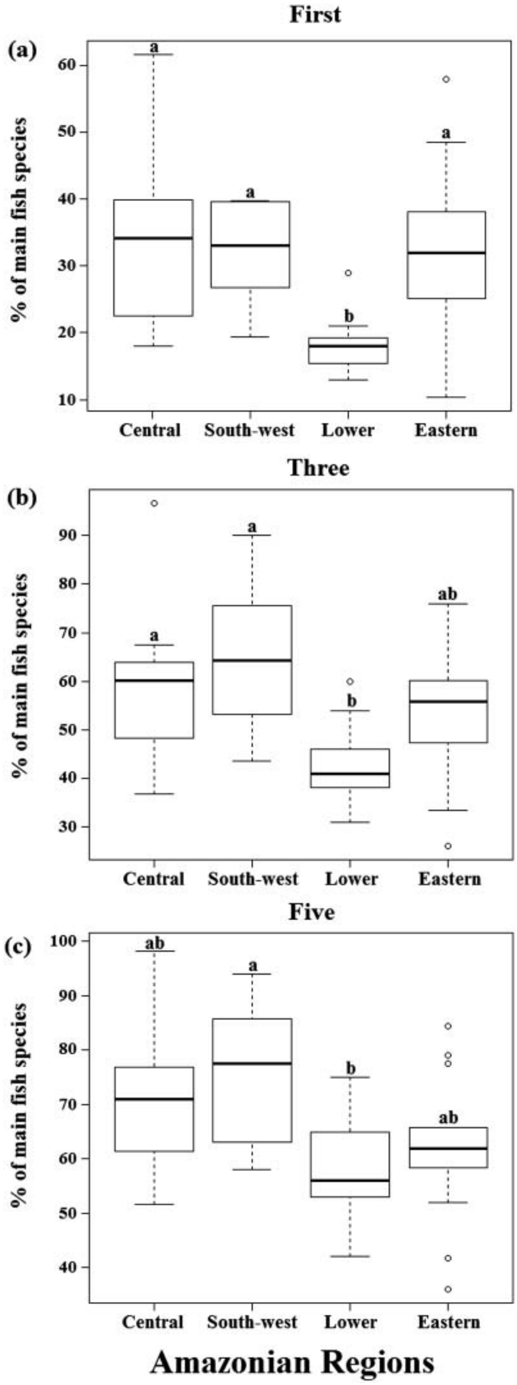

Figure 4. Comparison among the four studied regions of the Amazon basin ($N = 46$) and the fish selectiveness of the proportions of the (a) first; (b) three; and (c) five fish species that were most caught on each site. Median (darker line in the box plot), minimum and maximum values (vertical lines) and outer lines of the box plots showing the quartiles (25% and 75%), Dunn test: $a > b$, $p < 0.05$. Circles are outliers.

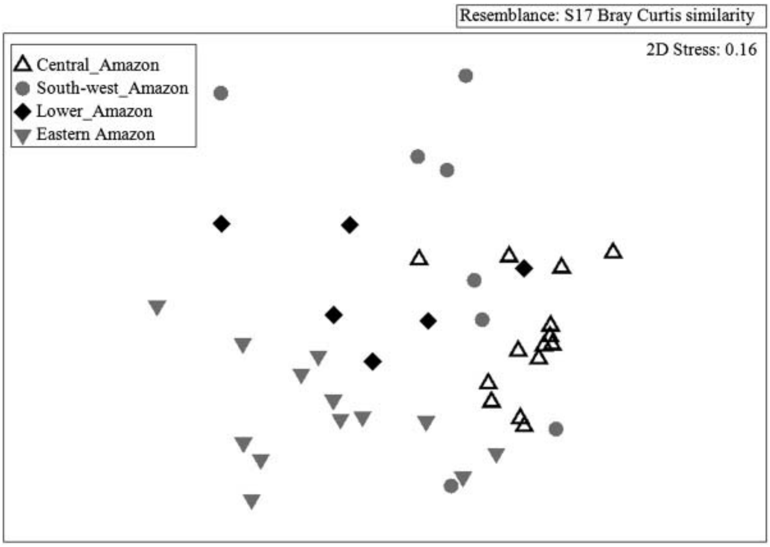

Figure 5. NMDS ordination (stress = 0.16) plot based on the composition (% of biomass) of the five most caught fish species in 46 sites in four regions of the Amazon basin.

studied fisheries showed a high selectivity as previously observed (Bayley and Petrere 1989; Cetra and Petrere 2001; Batista and Petrere 2003; MacCord *et al.* 2007), some fisheries were less selective. We observed that in two of the studied sites more than half of the fishing effort was concentrated in a single species, but in the majority of the sites fishing effort was directed to five fish species. Our results thus indicated that selectiveness varies among Amazonian fisheries, being important to report the composition of the catch in these tropical fisheries, because some species may receive a greater share of fishing effort. Overfishing of these preferred fish could be masked in landing statistics by sequential overexploitation through species replacement (Welcomme 1999; van Oostenbrugge *et al.* 2002).

Contrary to our hypotheses, fish selectiveness was not positively related to fishing productivity (total amount of fish caught and CPUE), as it would be expected according to the niche and optimal diet theories applied to fishers' behavior (Begossi and Richerson 1992, 1993; Begossi *et al.* 2012). This may be due to the influence of other factors that we could not include in our analyses, such as other economic activities performed by the studied fishers and market influence (Oliveira and Begossi 2011). Indeed, we observed a higher selectiveness for commercial fisheries. In these commercially oriented fisheries in major Amazonian cities (Batista and Petrere 2003; Fernandes, Vicentini, and Batista 2009; Doria *et al.* 2012), market demand may keep fishing effort concentrated in one or a few more valuable fish species, even if fishing productivity declines. Some commercial fishers may also act as middlemen, buying the most valuable fish from subsistence fishers to resell these fish on the markets, which would increase the selectiveness of commercial fisheries (Bayley and Petrere 1989; Hallwass *et al.* 2011). Fishing selectiveness can be overestimated due to bycatch, as some of the fish species caught could be discarded before landing. We found only two punctual studies from commercial fisheries in the central Amazon indicating that bycatch is influenced by production of fish and market demand, water level of rivers and gear used (Batista and Freitas 2003; Batista and Barbosa 2008). On the other hand, subsistence fishers, who were less selective, have a

Table 2. Contribution of the most caught fish species for the observed dissimilarity (SIMPER analysis) among the four studied regions in the Amazon basin: central Amazon (Ce), southwest Amazon (SW), lower Amazon (Lo) and eastern Amazon (Ea). We show only the fish species that contributed to more than 5% of the overall dissimilarity.

Local names (scientific name)[a]	Maximum length (cm)[b]	Size of first maturation (cm)[b]	Age of first maturation (years)[b]	Migratory behavior[c]	Abundance per region[d]				Comparison (% dissimilarity)	Mean dissimilarity (± SD)[e]	Contribution (%)[f]
					Ce	SW	Lo	Ea			
Tambaqui (*Colossoma macropomum*)	100	62	3.5	Migratory	24.2	6.1	11.8	0.02	Ce X SW	11.7 ± 1.6	15.7
									Ce X Lo	9.5 ± 1.6	14.3
									SW X Lo	5.9 ± 1.9	7.6
									Ce X Ea	14.0 ± 1.7	17.8
									Lo X Ea	6.9 ± 2.4	9.5
Matrinchã1 (*Brycon cephalus*)	45	32	–	Migratory	2.5	14.7	0	0.5	Ce X SW	8.1 ± 0.9	10.9
									SW X Lo	8.2 ± 0.8	10.6
									SW X Ea	8.3 ± 0.8	10.0
Matrinchã2 (*Brycon amazonicus*)	45	32	–	Migratory	0.7	14.6	0	0.4	Ce X SW	8.0 ± 0.8	10.8
									SW X Lo	8.2 ± 0.8	10.6
									SW X Ea	8.3 ± 0.8	10.0
Surubim (*Pseudoplatystoma fasciatum*)	110	60	–	Migratory	0.8	1.8	11.2	0.6	Ce X Lo	6.0 ± 2.8	9.0
									Lo X Ea	6.2 ± 3.1	8.6
									SW X Lo	5.3 ± 2.6	6.9
Dourada (*Brachyplatystoma rousseauxii*)	180	85.1[g]	3.5	Migratory	0.8	6.2	6.1	2.0	Ce X Lo	3.5 ± 0.9	5.3
									SW X Lo	4.5 ± 0.9	5.7
Acari (*Pterygoplichthys pardalis*)	50	–	1.4	Sedentary	0.1	0.2	10.5	0.8	Ce X Lo	5.9 ± 1.4	9.0
									SW X Lo	5.8 ± 1.4	7.5
									Lo X Ea	5.7 ± 1.3	7.9
Jaraqui1 (*Semaprochilodus* spp.)	36	25	2	Migratory	8.1	2.4	1.7	2.5	Ce X Lo	4.2 ± 1.5	6.3
									Ce X SW	4.2 ± 1.4	5.6
									Ce X Ea	4.2 ± 1.4	5.4

(*continued*)

Table 2. (*Continued*)

Local names (scientific name)[a]	Maximum length (cm)[b]	Size of first maturation (cm)[b]	Age of first maturation (years)[b]	Migratory behavior[c]	Abundance per region[d]				Comparison (% dissimilarity)	Mean dissimilarity (± SD)[e]	Contribution (%)[f]
					Ce	SW	Lo	Ea			
Jaraqui2 (*Semaprochilodus* spp.)	36	25	2	Migratory	8.1	2.4	0.4	-	Ce X Lo	4.5 ± 1.5	6.8
									Ce X SW	4.2 ± 1.4	5.6
									Ce X Ea	4.7 ± 1.5	6.0
Pescada (*Plagioscion squamosissimus*)	50	19	3	Sedentary	0.6	0.2	5.3	17.3	Ce X Ea	10 ± 1.1	12.8
									SW X Ea	10.1 ± 1.1	12.2
									Lo X Ea	8.4 ± 1	11.6
Mapará1 (*Hypophthalmus marginatus*)	50	32	1.7	Migratory	0.8	0.2	3.3	13	Ce X Ea	7.3 ± 1.2	9.3
									Lo X Ea	6.5 ± 1.1	9.0
									SW X Ea	7.4 ± 1.2	8.9
Curimatá (*Prochilodus nigricans*)	50	26	1.9	Migratory	13.1	13.9	7.5	14.1	Ce X SW	7.3 ± 1.3	9.8
									Ce X Lo	4.6 ± 1.2	6.9
									SW X Lo	6.3 ± 1.0	8.2
									Ce X Ea	7.2 ± 1.1	9.2
									SW X Ea	8.8 ± 1.1	10.6
									Lo X Ea	6.3 ± 0.9	8.7

[a] Biological species corresponding to popular names of fishes caught can vary among regions, and even within regions, but we considered in this analysis only the most common fish species that correspond to a given popular name, or the unique fish species corresponding to a popular name in the studied region: for example, in the eastern Amazon we found only one species of pescada (*Plagioscion squamosissimus*) and one species of mapará (*Hypophthalmus marginatus*) (Santos *et al.* 2004).
[b] Based on Santos *et al.* 2004; Santos, Ferreira, and Zuanon 2006; Batista and Isaac 2012; Córdoba *et al.* 2013.
[c] Based on Fernandes 1997; Petrere *et al.* 2004; Santos, Ferreira, and Zuanon 2006.
[d] Simple mean abundance of the percentage of biomass landed in each region. The absence of values for some fish species in some regions does not necessarily mean that those fishes are not caught in that region, but that those fishes accounted for less than 5% of the overall dissimilarity.
[e] Mean dissimilarity and standard deviation between the pair of regions being compared.
[f] Contribution of each fish species to the dissimilarity between the pair of regions being compared.
[g] Average of males and females.

limited fishing effort, as they use paddled canoes or low-powered engines, few fishing gear, shorter fishing trips and they do not always carry ice to store the fish caught (Batista *et al.* 1998; Cerdeira, Ruffino, and Isaac 2000; Hallwass *et al.* 2011). Therefore, subsistence fishers may explore a more limited area compared to commercial fishers, and the former can thus expand their food niche by diversifying their fish catches. Moreover, subsistence fishers tend to sell the most valuable fishes and consume less valuable fish, thus reducing bycatch (Begossi and Richerson 1992; Batista *et al.* 1998). Subsistence fishers may also distribute fishing effort among more species to reduce the risk of zero catches in seasons of reduced fish availability (Silvano and Begossi 2001).

The lack of a temporal pattern on fishing selectiveness did not conform to our hypothesis derived from the fishing down process (Welcomme 1999), as we did not observe a lower selectiveness in more recent fisheries. This may be because fish stocks in the Amazon basin may still support the selective fishing pressure needed to attend the current market demand, and preferred fishes, such as tambaqui and large catfish are still being caught (Batista and Petrere 2003; Petrere *et al.* 2004; Fabré and Barthem 2005; MacCord *et al.* 2007; Doria *et al.* 2012). Another factor that was not analyzed, but that could influence the temporal pattern of fish selectiveness, is the flood pulse (Junk, Bayley, and Sparks 1989). The intensity and strength of flood pulse during high water influences fish abundance in subsequent years, due to increased recruitment, survival and growth (Welcomme 1985, 1999; de Mérona and Gascuel 1993). These natural changes in fish abundance between years may have influenced fishing selectiveness.

The observed difference in fishing selectiveness among the four studied regions may be related to environmental heterogeneity of Amazonian fisheries regarding the kind of water (black, white or clear), habitats (lakes, rivers, channels, tributaries, flooded forest), gears (hook and line, harpoon, gillnet, cast net) and seasons (Bayley and Petrere 1989; Junk, Soares, and Bayley 2007). The lower Amazon region, which showed a lower selectivity, has extensive floodplain areas that are very fertile and productive, besides high environmental heterogeneity (a mosaic of tributaries, lakes, river channels and seasonally flooded forests). These ecological characteristics help to support a high diversity and abundance of large commercial fishes, such as surubim, dourada and tambaqui (Isaac, Milstein, and Ruffino 1996; Cerdeira, Ruffino, and Isaac 2000; Isaac, Silva, and Ruffino 2008; Castello *et al.* 2013). Furthermore, fish landed in Santarém, which is the main port of lower Amazon, is directed to two different markets (Isaac, Milstein, and Ruffino 1996; Fabré and Barthem 2005): (a) exportation of catfish to other Brazilian regions; and (b) scale fishes to local market, since catfishes are usually not eaten by Amazonian people (Begossi, Hanazaki, and Ramos 2004). This heterogeneity in commercialization may further explain the lower selectivity observed in this region. Yet another factor that may have contributed to increase or maintain the availability of large fish and the distribution of fishing effort among preferred fish species could be the several co-management initiatives (fishing accords) in the lower Amazon that regulate fishing and exclude outsiders (Castro and McGrath 2003; Almeida, Lorenzen, and McGrath 2009; Lopes, Silvano, and Begossi 2011).

In most of the sites (36 of 39) analyzed that have available data on fishing gear, gillnets were the main fishing gear used by fishers (Table 1). Gillnets are less selective fishing gear, which usually select fish according to size not species, but the decision of how, when and where to catch fish with gillnets are choices that fishers make according to their local knowledge about the environment and fish ecology (Johannes, Freeman, and Hamilton 2000; Salas and Gaertner 2004; Silvano *et al.* 2008). In this sense, fishers' knowledge, behavior and skills could influence more the fishing selectiveness in Amazon fisheries than the fishing gear used. Therefore, individual choices of fishers can contribute to understanding fishing selectiveness (Begossi, Hanazaki, and Ramos 2004; Begossi *et al.* 2012). Indeed, studies on fisheries management have been increasingly considering fishers' behavior and decisions (Salas and Gaertner 2004; Hallwass *et al.* 2013a).

4.2. Main fish species caught

Our results indicated that some preferred fish species have received more fishing pressure and these fishes should thus receive priority focus in management. As expected, the composition of the main fish species caught differed among the four studied regions (Figure 5). Therefore, the local and regional environmental heterogeneity is an important factor that management plans should consider, since the average similarity on catch composition was low, even among sites within regions.

We considered the total amount of fish caught during all seasons in our analyses, but some fisheries may show seasonal variation in catch composition (Isaac, Milstein, and Ruffino 1996; Batista *et al.* 1998; Batista and Petrere 2003; MacCord *et al.* 2007). The Amazon basin has a well-marked seasonality, as water levels may vary around 10 meters on average between the low and high water seasons (de Mérona and Gascuel 1993; Junk 2001). This high variation between hydrological seasons influences the life histories and behavior of fish, as well as fishers' behavior, and consequently the fish species caught (Welcomme 1985; Santos, Ferreira, and Zuanon 2006; Hallwass *et al.* 2011, 2013a). Therefore, even some fish species that are not among the most caught ones may have strategic importance to fishers in some seasons (Hallwass *et al.* 2011, 2013a). In general, Amazonian fishes show two main migratory patterns related to spawning and feeding, and associated with hydrological seasons: (1) short lateral migrations between river and floodplains; and (2) long longitudinal migrations in the main river channel, either upstream or downstream (Welcomme 1985; Fernandes 1997; Batista and Isaac 2012). Fishers usually have knowledge about fish migrations (Valbo-Jorgensen and Poulsen 2000; Silvano *et al.* 2006), and they may thus use their knowledge to direct fishing effort to catch schools of migratory fish. This could at least partially account for the observed moderate selectivity of Amazonian fisheries, since 9 from 11 of the more caught fishes show some kind of migratory behavior (Table 2). Catfishes that migrate long distances are usually caught in the main channel of white water rivers, while characiformes (scale fish) that make short lateral migrations are usually caught in the floodplain lakes and in the river margins (Barthem, Ribeiro, and Petrere 1991; Barthem and Goulding 1997; Fernandes 1997; Petrere *et al.* 2004; Fabré and Barthem 2005; Batista and Isaac 2012).

The ordination analysis was limited by the lack of replicates to account for temporal and spatial variation in all sites. Furthermore, some of the studied sites include also a temporal variation in the composition of the main fish species caught, which increased the variability (dissimilarity) among sites within regions. For example, we got data from five years in the 1970s and four years in the 1990s from the biggest market in the central Amazon (Manaus city, Table 1). Although it was the main fish landed in this region, the tambaqui was not among the five most caught species in the two studies made in the 1990s, because the landings of this fish declined over time in Manaus market (Batista and Petrere 2003). Similarly, Garcia *et al.* (2009) show a significant decline and replacement of large fish species by small and fast growing fish species, in a temporal series of 22 years in the Loreto region (Peru), southwest Amazon. There is growing evidence that some preferred target fish species, such as tambaqui, pirarucu and large catfishes, have been heavily exploited and show a risk of overfishing in the Amazon basin (Batista and

Petrere 2003; Petrere *et al.* 2004; Garcia *et al.* 2009). These species share some biological traits, such as large size, long lifespan, late reproduction and make long migrations (Table 2). Historical data in the Amazon indicate the overexploitation of some fishing resources showing these biological traits, such as manatees (*Trichechus inunguis*), the giant river turtle (*Podocnemis expansa*) (Smith 1985) and more recently, the pirarucu (Isaac, Silva, and Ruffino 2008; Garcia *et al.* 2009).

The lower Amazon region showed a relatively high abundance of three important commercial migratory fish species (tambaqui, surubim and dourada), as well as the acari, which is a sedentary fish with low commercial value that is usually caught in lakes near the fishing communities (Castello *et al.* 2013; Silvano *et al.* 2014). Therefore, this Amazonian region may have more commercial fish species available, besides showing a great diversity of fishing gear, habitats and fishing purposes (either for subsistence or market oriented) (Isaac, Milstein, and Ruffino 1996; Cerdeira, Ruffino, and Isaac 2000; Fabré and Barthem 2005). The southwest Amazon region showed the lowest similarity in catch composition among the sites sampled. Only in this region, the matrinchã, a migratory fish, was among the main fish species caught (Table 2). This fish accounted for 60% to 80% of the total biomass landed in three sites sampled in the upper Madeira River (Doria *et al.* 2012). The pescada (sedentary) and mapará (migratory) were among the main fish caught in the eastern Amazon, especially in those sites sampled in the lower Tocantins River, which has clear water and a large dam upstream (Hallwass *et al.* 2011, 2013b). While other migratory fish species differed in their importance among regions, the curimatá was among the five most caught species in the majority (76%) of the 46 sites analyzed, and it was among the five main fish species caught in all regions, varying between 7.5% and 14% of total biomass landed (Table 2). The curimatá has medium size and shows relative lower size at first reproduction among the main fish species caught (Table 2). This indicates that the curimatá may be currently one of the most widely exploited species in Amazonian fisheries. This fish may be thus more resilient to the fishing pressure and environmental changes, such as dams (Hallwass *et al.* 2011, 2013b).

4.3. Management suggestions and ecological implications

The moderate selectiveness observed in several of the studied sites in the Amazon basin suggests that these fisheries could be managed according to the conventional single species management approach. This approach may help to prevent the fishing down process in tropical inland fisheries that show high fishing pressure on a few preferred species (Welcomme 1999). The main rules applied to single species management worldwide refer to gear, size limits and seasonal fishing restrictions (Garcia *et al.* 2012). Some of these rules have been applied in the Brazilian Amazon (Batista and Isaac 2012; Hallwass *et al.* 2013a), but some of them have not been effective, such as closed fishing seasons (Corrêa, Kahn, and Freitas 2014).

Although fishers still rely on several fish species in at least some of the studied sites, conservation priorities for maintaining fish biodiversity may not necessarily improve fisheries, if they did not contemplate the most important fish species (Table 2), or important fish habitats, such as floodplain lakes (Silvano, Ramires, and Zuanon 2009; Silvano *et al.* 2014). These preferred fishes are usually large migratory species that have a long lifespan, late reproduction and a widespread geographic distribution (Barthem and Goulding 1997; Fernandes 1997; Batista and Isaac 2012). We propose five management recommendations, based on our results.

First, as already mentioned in a previous study (Bayley and Petrere 1989), it would be desirable that Amazonian fishers diversify their catches, distributing fishing effort among more fish species. However, the observed pattern of concentration of fishing effort may be partially influenced by cultural preferences (Begossi, Hanazaki, and Ramos 2004; Begossi *et al.* 2012), which are hard to change. Thus, fishing quotas associated with value adding through fish processing (e.g. cleaning and filleting) by local cooperatives run by fishers may be a promising way to diversify fishers' work, aiming to reduce the fishing effort (as fishers would spend part of their time processing fish) and improve fishers' profits (Hallwass, Lopes, and Silvano 2014).

Second, the observed differences on selectiveness between commercial and subsistence fisheries could drive distinct management plans. For example, the more selective commercial fisheries usually exploit a wide area, but land in fixed major ports located in the main Amazonian cities, such as Manaus, Belém, Santarém or Porto Velho. Therefore, management of these fisheries could focus on the most caught species, with intensive monitoring performed by Brazilian environmental agencies (top-down management). Subsistence fisheries are less selective, explore a more limited area and land in scattered ports. For these fisheries, co-management should be more appropriate, as it involves the participation of fishers in the elaboration of management rules (bottom-up management) (Lopes, Silvano, and Begossi 2011). Co-management has potential to increase fish abundance, fishing productivity and to avoid overexploitation of preferred fish in small-scale fisheries in the Amazon by protecting important fish habitats, such as floodplain lakes (Almeida, Lorenzen, and McGrath 2009; Silvano, Ramires, and Zuanon 2009; Silvano *et al.* 2014). However, co-management arrangements aimed to conserve stocks of highly migratory fishes, such as large catfishes (Barthem and Goulding 1997), should include a wider geographical scale, being thus more challenging.

Third, some of the most exploited fish species have ecological roles and may provide relevant ecosystem services, which could be considered in a holistic ecosystem-based fisheries management (EBFM) framework. For example, overfishing of large fishes in marine ecosystems may affect important ecological processes, such as algal dominance in coral reefs (Bellwood, Hoey, and Choat 2003), and predator−prey relationships (Graham, Evans, and Russ 2003), and mutualistic relationships (Silvano, Tibbetts, and Grutter 2012). However, few studies have addressed the potential cascading ecological effects from fishing in tropical freshwater ecosystems. The tambaqui and matrinchã are large migratory and frugivorous fish, which are important seed dispersers and seed predators in the Amazonian flooded forests (Goulding 1980). The curimatá is a large detritivorous and migratory fish, which influences nutrient recycling in tropical rivers (Flecker 1996). Therefore, it would be important to investigate potential fishing effects on the ecological services provided by those fishes, such as seed dispersion (Anderson *et al.* 2011). Conversely, deforestation of tropical floodplain forests may adversely affect fish production, as observed in a Venezuelan stream (Wright and Flecker 2004) and suggested in the Negro River, Brazilian Amazon (Silvano *et al.* 2008).

Fourth, most of the main fish species caught in Amazon fisheries are migratory, including both large catfishes and characins (Table 2). Although the kind of migratory movements may vary among these species, management plans should incorporate the main migratory routes and seasons in an integrated way through an EBFM approach. Therefore, fishes that make lateral migration need protection of floodplain lakes to ensure their reproduction (Silvano, Ramires, and Zuanon 2009; Silvano *et al.* 2014), while fishes that make longitudinal migrations need identification and protection of bottlenecks in their migratory routes (Barthem and Goulding 1997). Besides migratory behavior, it is also important to consider, in management plans, the fishes' biological characteristics, such as maximum length, size and age of the first sexual maturation, through rules related to quotas or minimum size of catch, aimed to secure reproduction and to reduce the risk of overexploitation of preferred fish species (Magnuson-Ford *et al.* 2009). Fishers' knowledge may be useful to indicate some of these biological characteristics, such as main migratory routes and size of first reproduction of commercial fishes (Valbo-Jorgensen and Poulsen 2000; Silvano *et al.* 2006; Hallwass 2015).

Fifth, major environmental changes under course in the Amazon basin may negatively affect some of these preferred commercial fish species, disproportionately affecting fisheries and food security in fishing villages and even in major cities. For example, interviews with fishers and fish landing data indicate that the migratory fish jaraqui disappeared from the lower Tocantins River (eastern Amazon), 20 years after the Tucuruí reservoir was built (Hallwass *et al.* 2013b). Moreover, fish ladders built to guarantee fish migration in impounded rivers may not work in the Amazon (Agostinho *et al.* 2007). There are currently three large dams being built in the Brazilian Amazon basin, one in the Xingu River (Belo Monte Dam), and two in the Madeira River (Santo Antônio and Jirau Dams). These dams have been contentious, and the two dams in the Madeira River will possibly affect the studied fisheries that rely heavily on migratory fishes, such as matrinchã and dourada (Barthem and Goulding 1997; Barthem, Ribeiro, and Petrere 1991; Doria *et al.* 2012). Therefore, the consequences of large dams to local fisheries in tropical rivers should be considered, both in fisheries management and regional development plans (Barthem, Ribeiro, and Petrere 1991; Petrere 1996; Zhong and Power 1996; Fearnside 2001, 2006, 2014; Dugan *et al.* 2010).

5. Conclusions

Most of the studied Amazonian fisheries were considered as moderately selective, directing most of the fishing effort to catch five fish species. Eleven preferred fish species, nine of which are migratory, have received more fishing pressure throughout the Amazon basin. Selectiveness differs according to the purpose of the fishery (commercial fisheries are more selective) and among major Amazonian regions (lower Amazon is less selective). According to these results, fisheries management and policy in the Amazon basin should aim to: (a) distribute fishing effort among more fish species; (b) elaborate distinct management plans according to fishing type (commercial or subsistence); (c) conduct assessments of the potential fishing effects on the ecological services provided by those most caught fishes; (d) incorporate the main biological characteristics of these preferred fish; and (e) implement broad and long-term fisheries monitoring in the Amazon basin.

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