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Understanding fishing-induced extinctions in the Amazon

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ABSTRACT

1. Science and policy worldwide are influenced by predictions from bioeconomic theory that fishing cannot lead fish populations to extinction because fishing effort inevitably moves away from depleted resources. Yet such predictions contradict evidence of fishing-induced extinctions and in particular a model, called 'fishing-down', that explains historical reductions in mean size of harvested species in tropical multispecies fisheries through the gradual depletion and extinction of large-bodied species.
2. This study analysed data on fisheries for *Arapaima* spp., the most historically important and overexploited fishes of the Amazon Basin, to evaluate whether they supported bioeconomic or fishing-down predictions. The evaluation was based on census data on arapaima populations and interview data from 182 fishers with respect to fishing practices and management regulations, which were collected in 81 fishing communities covering 1040 km^2 of Amazonian floodplains.
3. Arapaima populations were found to be 'depleted' in 76% of the fishing communities, 'overexploited' in 17%, 'well-managed' in 5%, and 'unfished' in only 2%. Population densities were zero (i.e. locally extinct) in 19% of the communities. Twenty-three per cent of the fishers in each community harvested arapaima regardless of population status. Similarly, the percentage of the catch in compliance with the size regulation did not vary with population status, but compliance with the season regulation in communities with 'overexploited' or 'depleted' populations (72%) was lower than in communities with 'well-managed' or 'unfished' populations (97%).
4. These results support fishing-down predictions that fishing pressure continues to occur even when fish populations are depleted. The fishing-down process appeared to occur because of low gear selectivity and larger body-size of target species as well as high species value and low fishing costs. These results and available data elsewhere suggest that fishing-induced extinctions are more common than previously thought, endangering biodiversity and ecosystem functioning. Such extinctions are probably going unnoticed because high levels of illegal fishing, geographic heterogeneity, and data scarcity make their identification difficult.

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KEY WORDS: *Arapaima* spp; biodiversity; conservation; food security; floodplains; Osteoglossidae; overfishing

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INTRODUCTION

The notion that fishing cannot lead a species to extinction has influenced science and policy for many decades. This notion was founded on the old idea that marine species are highly resilient to fishing (Roberts and Hawkins, 1999). It was founded also on predictions from bioeconomic theory that fishing can overexploit and even deplete fish populations but cannot lead them to extinction because the high costs of fishing-depleted populations inevitably move effort away from them (Gordon, 1954). Such optimistic predictions have profound implications for tropical fisheries. Not only are tropical fisheries embedded in the most biodiverse ecosystems, playing key roles in the maintenance of global biodiversity (Roberts *et al.,* 2002), they also produce one-third of global capture fish yields (Castello *et al.,* 2007), sustaining key income- and food-security services for the world's poorest populations (Allison and Ellis, 2001; Pauly *et al.*, 2005). Bioeconomic predictions that fishing does not cause extinction thus imply that tropical fisheries do not threaten biodiversity, food web structure and functioning, and income- and food-security services.

Evidence has been emerging, however, that fishing causes extinctions. A literature review found that fishing induced 55% of 133 documented local, regional, and global extinctions of marine populations (Dulvy *et al.,* 2003). The highly fecund *Bahaba taipingensis* (Scienidae) was found to be facing fishing-induced near extinction (Sadovy and Cheung, 2003). In another example, 22 of 163 species of groupers may soon be at risk of fishing-induced extinctions (de Mitcheson *et al.,* 2013). Such evidence has been changing perceptions, although slowly. Whereas the resilience of marine species is no longer thought to protect them from extinction (Dulvy *et al.,* 2003), the notion that economic extinctions prevent species extinctions remains prevalent in many policy and scientific arenas. For example, it was recently stated that 'where management is weak or nonexistent, multiple fishers compete to catch fish from a given population… An equilibrium… is reached only when… catch rates are barely sufficient to cover the costs of fishing. The population is then maintained at this level through biological processes of natural growth and reproduction' (Beddington *et al.,* 2007). Belief in this economic prediction is probably due to a lack of studies assessing its validity, although it already has been argued that effort rarely can be directed fully onto or away from any single species because most fisheries are multispecies, even in temperate regions (Dulvy *et al.,* 2003). It has been argued also that the prices of some fishes are inversely proportional to their abundance (Pinnegar *et al.,* 2002) such that the higher values of overexploited species can promote extinction (Dulvy *et al.,* 2003).

Few are aware that there is an alternative model, called the 'fishing-down' process, which explains the depletion and extinction of species caused by fishing in tropical multispecies fisheries (Welcomme, 1999). The fishing-down process differs from the 'fishing down marine food webs' concept (Pauly *et al.,* 1998), which predicts declines in trophic levels. The fishing-down process stems from the notion that body size largely determines extinction risk (Reynolds *et al.,* 2001). Large-bodied animals tend to be more sought-after and possess life-history traits associated with vulnerability, including late maturity, low intrinsic rates of population increase, behaviour that increases catchability, and dependence on vulnerable habitats (Reynolds *et al.,* 2002). The fishing-down process predicts that historical increases in fishing effort in tropical multispecies fish communities reduce the mean body size of harvested species through the gradual replacement of depleted large-bodied species with small-bodied ones (Castello *et al.*, 2013a). Bioeconomic and fishing-down predictions thus differ mainly with respect to whether fishing continues once fish populations become depleted.

Support for the fishing-down process comes from multispecies stock-production models, which are like those for single species fisheries, showing increasing yields with increasing effort up to a maximum, at which point they differ in showing constant, not declining, yields with increasing effort (Lae, 1997; Lorenzen *et al.,* 2006). Such constancy in yields is maintained by the successive depletion and replacement of target species. As larger-bodied species become depleted, they can become extinct because the harvest of smaller-bodied species normally involves nets that often also select juveniles of the larger-bodied ones. The fishing-down process shrunk the mean total length of harvested species in the Oueme River in West Africa from 78 cm in the 1950s to 57 cm in the 1970s and then to 22 cm in the 1990s, leading to the disappearance of four species from catches by 1965 (Welcomme, 1999). In the Amazon River in South America, fishing-down shrunk the mean maximum length of harvested species from 206 cm in the early 1900s to 79 cm today, leaving several species under varying degrees of extinction risk, including manatees (*Trichechus inunguis*), three turtle species (*Podocnemis* spp.), two crocodilian species (*Crocodilus crocodilus, Melanosuchus niger*), and one or more species of arapaima fishes (*Arapaima* spp.; Da Silveira and Thorbjarnarson, 1999; Castello *et al.,* 2013a).

Fishing-down and bioeconomic predictions are two competing hypotheses on the potential of fishing to cause extinction. To improve understanding of fishing impacts in tropical fish communities, this study evaluated whether the dynamics of fisheries for arapaima supported bioeconomic or fishing-down predictions. The evaluation was based on data collected on the abundance, levels of fishing pressure, and sustainability of fishing practices for arapaima in floodplain communities of the Amazon river mainstem, near the municipality of Santarém, State of Pará, Brazil (Figure 1). The fishing-down prediction should be observable through locally extinct populations or continued fishing of depleted populations. The bioeconomic prediction should be observable through absence of local extinctions or presence of sustainable fishing practices if fishing continued after initial depletions.

ARAPAIMA FISHERIES IN THE AMAZON

Biology, ecology, and population status of arapaima

The taxonomy of arapaima is poorly studied, so the geographical distribution is known only for the

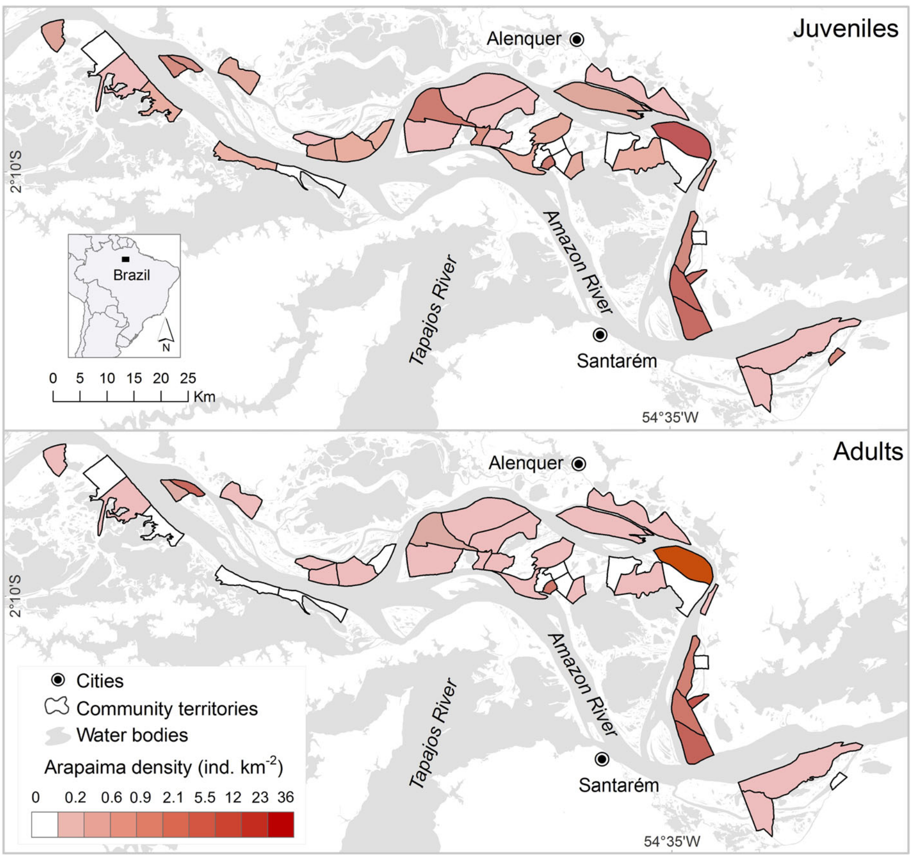

Figure 1. The study area in the lower Amazon region, showing censused arapaima densities in 41 communities. Population densities are measured as ind km^{-2} of juveniles (1–1.5 m TL) and adults (>1.5 m TL). Inset shows location of study area in Brazil (black rectangle).

genus and undescribed species may exist (Stewart, 2013a, b; Castello *et al.*, 2014). The genus was wrongly considered to be monotypic for 140 years (Günther, 1868) despite previous description of four species by Schinz (in Cuvier, 1822; *A. gigas*) and Valenciennes (in Cuvier and Valenciennes, 1847; *Arapaima agasizzii, Arapaima mapae,* and *Arapaima arapaima*). *Arapaima gigas*, whose type specimen came from the study area, has not been seen in the field since the original specimen, which was obtained in about 1787 (Stewart, 2013a, b). Because of this taxonomic uncertainty, we refer to arapaima only at the genus level.

Historical overexploitation has led *Arapaima gigas* to be listed in Appendix II of the Convention on International Trade of Endangered Species of Wild Fauna and Flora (Castello and Stewart, 2010). This species is now listed also in the IUCN Red List of Threatened Species as 'Data Deficient', which means: 'there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status' (World Conservation Monitoring Centre, 1996). In Brazil, arapaima were not included in the national list of endangered species owing to lack of data.

The largest arapaima populations occur in whitewater floodplains, a complex mosaic of seasonally inundated forests, lakes, and channels that are completely flooded annually (Irion *et al.,* 1997). Arapaima are fished in floodplain lakes when low water levels (September–January) force all fish to seek refuge in remaining aquatic habitats (Castello, 2008a). These fishes are vulnerable to fishing and highly sought-after. Each individual is valuable, as they grow up to 3 m in length and 200 kg in weight and attain high market prices (Arantes *et al.,* 2010). They are obligate air-breathers that are exposed to harpoon-specialist fishers every 5–15 min when they surface to breathe (Castello, 2004). They are particularly vulnerable when they spawn in nests built on the margins of floodplain forests surrounding lakes and channels. Males engaged in parental care are defenceless against fishers who use such habitats as daily transport routes (Castello, 2008b).

The influence of fishing on arapaima population dynamics appears to be strong. When Brazil's minimum size limit of 1.5 m in total length (TL) is followed, arapaima grow fast, to 88 cm TL in one year, reaching maturity at 3–4 years of age when they measure 157–164 cm TL (Arantes *et al.,* 2010). When the size limit is not followed, selective removal of the faster-growing, under-sized individuals not only removes potential spawners but also lowers overall mean body growth rates. In such conditions, arapaima length at age is on average 27 cm shorter, and they reach maturity at 5 years of age, which results in significantly lower intrinsic rates of population increase (Arantes *et al.,* 2010; Castello *et al.,* 2011a).

Arapaima fisheries in the study area

In the study area, arapaima are exploited by floodplain fishers living in geographically dispersed communities. For them, fish is the most economically and nutritiously important resource. Some 40 different fish species are exploited over the course of the year through daily fishing trips of a few hours in wooden canoes (McGrath *et al.,* 1998; Castello *et al.,* 2013b). Gillnets dominate the catch, but castnets, long-lines, fishing poles, and harpoons are also used. Arapaima are harvested mostly using harpoons and gillnets, but many young arapaima are caught as bycatch in gillnets directed to other smaller-bodied species (Batista and Freitas, 2003).

Pressure over natural resources has been increasing in the study area because of new techniques, human population growth, and economic development (Figure 1; McGrath *et al.,* 1993; Isaac *et al.,* 2008). Expansions of cattle ranching and agriculture have led to deforestation of 56% of floodplain forests (Renó *et al.,* 2011). Five of the nine most exploited species in the study area, including arapaima, are thought to be overexploited, although there are few formal stock assessments (Isaac and Ruffino, 1996; Ruffino and Isaac, 1999; Castello *et al.,* 2011b). Fisheries management in Brazil has relied on minimum size and closed season regulations, but compliance has been dismal owing to lack of government resources and large geographical areas (Crampton *et al.*, 2004; Castello *et al.,* 2013b). Also, fisheries in Brazil are managed as open access resources, which means that all citizens have equal rights of use (McGrath *et al.,* 2008). Consequently, fishing for arapaima is banned in the Brazilian states of Acre and Amazonas where exception is made for community-based management (CBM) schemes, but it is open in Pará State based on size and season limits. Many floodplain fishers have sought to curb overfishing by establishing CBM schemes via implementation of gear, season, and area regulations that are developed locally by each community (Castro and McGrath, 2003). The non-migratory behaviour of arapaima make them suitable for, and hence a target of, CBM (Arantes *et al.,* 2006; Castello *et al.,* 2009, 2011c).

METHODS

Field data were collected based on censusing arapaima populations and through interviews with local fishers on levels of fishing pressure and the sustainability of fishing practices. To evaluate whether the data supported bioeconomic or fishing-down predictions, the data were analysed for each community to assess population status per community and to evaluate how levels of fishing pressure and the sustainability of fishing practices varied with population status.

Data collection

Between July and September 2011, structured interviews were conducted with 182 fishers from 81 communities, resulting in an average of 2.2 fishers being interviewed per community, with a minimum of two and a maximum of three fishers per community. The fishers interviewed were selected following best-available methods for researching local knowledge (Berkes *et al.*, 2000; Davis and Wagner, 2003). Interviewed fishers were selected by peers of their own communities as being 'experts' on fisheries matters. The fishers were interviewed with respect to arapaima populations, management, and fishing practices in the interviewees' own communities. To assess arapaima populations, interviewees were asked to classify arapaima abundance (zero, low, medium, and high) and its trend in recent years (decreasing, stable, or increasing). To assess fishing pressure, interviewees were asked to estimate total number of fishers, and fishers targeting arapaima. To assess the sustainability of fishing practices, interviewees were asked to identify months of the year arapaima harvests occurred, if any, and typical TL of harvested individuals (in 20 cm size-classes). Interviewees also were asked if there were CBM rules for arapaima that were followed by the fishers. Field notes and interview results were transcribed and coded for quantitative analyses.

Arapaima populations were censused during November and December 2011, in 41 of the 81 communities included in the interviews, using the method of Castello (2004) that allows expert fishers to count the arapaima at the moment of aerial breathing, in two size classes: juvenile (1–1.5 m TL) or adult (>1.5 m TL). The counting method can be accurate and precise if properly applied. Arapaima were censused by eight trained fishers whose individual counts possessed errors $<$ 30%, as shown by the method of Arantes *et al.* (2007), which compares fishers' counts of arapaima with seine catches of the individuals in the same closed lakes. The eight fishers who were trained in the arapaima censusing method were selected for this work first on the basis of their interest in learning the method, and later based on an informal assessment of their knowledge and skills on arapaima fishing, following guidelines for identifying expert fishers provided in Castello (2004) and Castello *et al.* (2009). The same group of eight fishers censused arapaima populations in lakes of all 41 surveyed communities. In each community, a minimum of one and a maximum of four lakes were censused. Arapaima density in the territory of each censused community was quantified per floodplain area (ind km^{-2}), excluding river channels, because such territories comprise different sets of lakes that together host local arapaima populations (Castello *et al.,* 2009, 2011b).

Data analyses

To identify arapaima population status, census data were classified based on the following density range classes: depleted (0–2.2 ind km^{-2}), overexploited (2.3–17.7 ind km^{-2}), well-managed (17.8–32.4 ind km^{-2}), and unfished (>32.5 ind km^{-2}). These classes were derived by interpolating point density estimates for different arapaima population statuses in equivalent várzea floodplains from the Mamirauá Reserve in the Solimões River: 4.4 ind km^{-2} is overexploited, 31.1 ind km^{-2} is well-managed, and 33.8 ind km^{-2} is (close to) unfished conditions (Castello *et al.*, 2011b). To assess historical trends in arapaima abundance, the accuracy of interview responses on arapaima abundance (low, medium, or high) was assessed by comparing them with censused data for communities for which such data were available. Then, interview responses on historical trends in arapaima abundance (decreasing, stable, or increasing) were quantified. To determine whether fishing pressure for arapaima has ceased or continued, the percentage of fishers targeting arapaima was calculated based on the total number of fishers for each community, and this percentage was compared across communities possessing different arapaima population statuses (i.e. depleted, overexploited, well-managed, and unfished). To quantify the sustainability of fishing practices, response data on months of the year when arapaima harvests occurred, if any, and typical TL of harvested individuals (in 20 cm size-classes) were used to calculate the percentage of the catch that was in compliance with size (>1.5 m TL) and season (May–November) regulations. Such percentages of compliance with size and season regulations were compared across communities possessing different arapaima population statuses. Finally, interview responses on existence of CBM rules were quantified, and the effectiveness of these rules was assessed by comparison with population census data in the same communities.

RESULTS

Population status

The censusing surveys indicated that arapaima populations were ‘depleted’ in 76% of the fishing communities, ‘overexploited’ in 17%, ‘well-managed’ in 5%, and ‘unfished’ in only 2%. Population densities were zero (i.e. locally extinct or extirpated) in 19% of the communities. In total, 1825 juveniles and 1630 adults were censused in 1040 km^2 of floodplain area, resulting in extremely low median arapaima population densities around 0.55 ind km^{-2} for all size classes, with 0.34 ind km^{-2} for juveniles and 0.11 ind km^{-2} for adults (Figures 1 and 2).

The foregoing assessment is supported by fishers’ perceptions: 55% of the fishers classified arapaima abundance as being ‘low’ in communities where median censused arapaima abundance was 0.15 ind km^{-2}, 27% classified it as ‘medium’ where it was 0.74 ind km^{-2}, and 2% classified it as ‘high’ where it was 2.39 ind km^{-2} (Mann–Whitney U-tests, $P < 0.01$ for each pair-wise comparison). Such congruence between census and fishers’ perception data supports the following inference of declining abundance: 76% of the fishers said that arapaima abundance in recent years has decreased, 20% of them said it has increased, and 4% said it has remained the same.

Fishing pressure

On average, 23% of the fishers per community harvested the arapaima, and this level of fishing pressure was maintained regardless of population status. Although the mean percentage of fishers at each community targeting the arapaima was lower in communities where arapaima populations were ‘depleted’ or ‘overexploited’ (mean = 15%) than in communities where they were ‘well-managed’ or ‘unfished’ (mean = 33%), that difference was not statistically significant (Kruskal–Wallis test, $P = 0.5$).

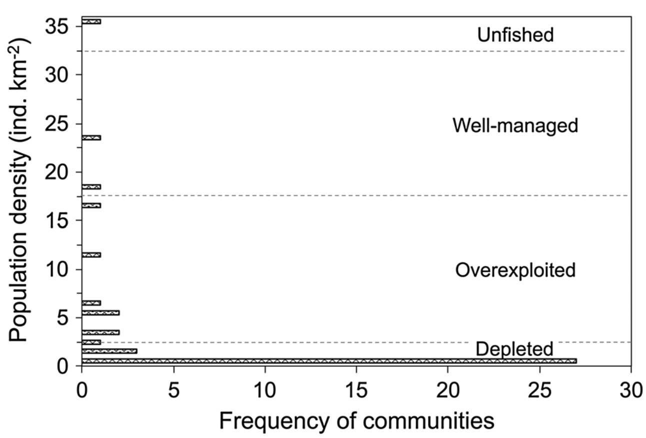

Figure 2. Censused arapaima population densities in 41 communities of the lower Amazon region and associated population statuses classified based on Castello *et al.* (2011a).

Sustainability of fishing practices

Compliance with season regulations varied with population status, but compliance with size regulations did not. The percentage of the catch that was in compliance with the season regulation (mean = 97%) was significantly higher in communities where arapaima populations were 'well-managed' or 'unfished' than in communities where they were 'depleted' or 'overexploited' (mean = 72%; Mann–Whitney U-tests, $P < 0.05$). The percentage of the catch in compliance with the size regulation did not vary with population status (Kruskal–Wallis test, $P = 0.5$), and it was extremely low on average, only 19%.

Only 27% of communities had management rules for arapaima harvests that were followed by the fishers, but those were effective at conserving arapaima and explained the high degree of spatial heterogeneity in arapaima density (Figure 1). Median arapaima density in communities with CBM rules (10.02 ind km^{-2}) was two orders of magnitude higher than in communities without (0.55 ind km^{-2}; Mann–Whitney U-test, $P < 0.05$). CBM areas contained 2506 individuals (or 75%) of the total censused.

DISCUSSION

Fishing-induced extinctions of arapaima

These results support fishing-down predictions that fishing pressure continues to occur even when fish populations are depleted. Contrary to bioeconomic predictions, arapaima populations were found to be 'depleted' in 76% of the communities and locally extinct in 19% of them (Figure 1), yet fishers continued to harvest arapaima regardless of population depletion, as indicated by lack of variation in the percentage of fishers targeting arapaima (23%) across communities with different population status. The sustainability of such harvesting practices also contradicted bioeconomic predictions. Compliance with the closed season regulation in communities with 'overexploited' or 'depleted' populations (72%) was lower than in communities with 'well-managed' or 'unfished' populations (97%). Such continued unsustainable fishing practices that exploit depleted populations is probably the reason why 76% of the fishers believe that arapaima abundance in recent years has decreased.

Could the trend of low and declining population be attributed to floodplain deforestation? The available evidence suggests not. The 'well-managed' or better (>17.8 ind km^{-2}) arapaima densities observed in three communities engaged in CBM (Figures 1 and 2) suggest that overfishing, not deforestation (Renó *et al.,* 2011), explains the observed population patterns. These high arapaima densities also endorse the reference data used here to determine population status (e.g. 'depleted'; Castello *et al.,* 2011a).

The zero arapaima densities observed in eight community territories reflect local extinctions (Figures 1 and 2), because the censused floodplain lakes in each territory were expected to host local arapaima populations (or at least, offer suitable habitat) in the absence of fishing. Such lakes were devoid of arapaima 2 years old and older, which are the ages at which they are included in the counts (i.e. > 1 m TL; Arantes *et al.,* 2010). If there were young of the year individuals (i.e. < 1 m) in those lakes, the absence of adults (Figure 1) would indicate that they immigrated from surrounding lakes during the previous high water. Such lakes without adult arapaima may be population sinks, with no individuals surviving to reproduce.

The observed persistence of unsustainable fishing practices over extremely low and declining populations appears to have caused local extinctions of arapaima, and it will probably continue to do so. Few communities (27%) have implemented rules for arapaima, and the widespread use of gillnets targeting smaller-bodied species causes bycatch of juvenile arapaima, further undermining their populations (Castello *et al.,* 2011a). Such widespread lack of management and incidental bycatch is expected to cause additional local extinctions of arapaima (Figure 1). Local extinctions usually signal the potential for regional extinctions, which are the first steps towards global extinctions (Pitcher, 2001).

Fishing-down may be exerting impacts on one or more arapaima species, depending on their life-history traits. For example, it has been estimated that if a slower-growing arapaima species with maturity at

6–7 years ever existed, it would have been eliminated by fishing mortality rates that are today considered to be sustainable for arapaima, even if current size and season regulations were followed (Castello *et al.,* 2011a). Similar fishing effects on sympatric skate species have been observed in the North Atlantic, where fishing pressure on skates nearly caused the extinction of a skate species that was unrecognized taxonomically, primarily because of its larger body size and later age of reproduction (Dulvy and Reynolds, 2009).

Fishing-induced extinctions

These findings indicate that fishing causes more impact on tropical fish communities than previously recognized (Dulvy *et al.*, 2003). Fishing-induced extinctions affect tropical aquatic ecosystems and biodiversity. Tropical fisheries based on the use of gillnets generally lead to an increase in diversity of target species, because of the progressive elimination of larger-bodied species and the naturally higher abundances of smaller-bodied species (Welcomme, 1999). In the study area, the diversity of target species in communities where arapaima have become locally extinct is higher than in communities where arapaima are 'well-managed' or better (Castello *et al.*, 2013b). However, tropical multigear fisheries generally decrease the diversity of target species by targeting, and hence progressively depleting, the entire fish assemblage (Jennings *et al.*, 1995; Welcomme, 1999). Species extinctions undermine diversity in functional groups and can produce cascading effects. In the Amazon, ecological extinction of manatees, turtles, and capybaras (*Hydrochaerus hydrochaerus*) have been linked to historical growth of aquatic and semi-aquatic macrophyte beds (Junk, 2000). Losses of apex predatory species and primary consumers alter whole ecosystems through modification of energy flows with severe consequences for biodiversity (Estes *et al.*, 2011).

Do fishing-induced extinctions undermine fishery yields and associated income- and food-security services? Two meta-analyses based on datasets covering a diversity of tropical fisheries worldwide found that multispecies catch–effort responses followed a negative parabolic curve, indicating that yields increase with effort up to a maximum and then decrease with increasing effort (Bayley, 1988; Halls *et al.*, 2006). However, two other comprehensive meta-analyses found that multispecies catch–effort responses conformed to the asymptotic model in which catch levels increase up to a maximum and remain stable indefinitely with increasing effort (Laë, 1997; Lorenzen *et al.*, 2006). Thus, it remains uncertain whether fishing-induced extinctions undermine tropical multispecies fisheries yields. However, loss of target species adversely affects the livelihoods of fishers by making gillnet-based fisheries dependent on the natural productive cycles of fewer species (Jennings and Polunin, 1996). Fishers may be forced also to adapt to new species and gears and to find new fishing grounds. In addition, differences between species availability and market preferences may affect fishers' economy (Hoeinghaus *et al.*, 2009), at least until people adjust to the less desirable species.

Lessons from the Amazon

Examination of the conditions in which arapaima extinctions occurred suggests that many fishing-induced extinctions in the tropics are going unnoticed because three characteristics of the fishing-down process make it difficult to identify:

1. *Lack of data*: Most tropical countries possess limited human and financial resources to study the biology, taxonomy, and ecological interactions of fishery species as well as to monitor and assess fisheries statuses (Mahon, 1997; Johannes, 1998). Such data scarcity precludes identification of population declines.
2. *Illegal fishing*: Where fishery regulations exist in the tropics, compliance is low owing to poor enforcement. Not only does illegal fishing targeting intensely exploited resources occur at the margins of limited fishery monitoring systems, it also limits the usefulness of catch statistics and undermines the sustainability of such resources. Lack of compliance with size and season regulations degrades the capacity of fish populations to sustain fishing pressure and recover from overexploitation (Myers and Mertz, 1998).

3. *Geographic heterogeneity*: The tropics possess large numbers of small-scale fishery stocks because of high species diversity (Stevens, 1989). Inter-community differences in fishing practices, ecological conditions, and economic activities, which also are high in the tropics (Castello *et al.,* 2013b), create heterogeneous mosaics of resource abundance that are not captured by deficient monitoring schemes based in a few cities (Figure 1).

Scientists interested in documenting fishing-induced extinctions should consider alternative data and analytical approaches to overcome the inadequacy of conventional approaches. Sophisticated analysis of comprehensive fisheries statistics, as is done in Europe and North America for example, is seldom an option in the tropics. Rather, scientists in these regions will benefit from historical records (Hardt, 2009) as well as fishers' knowledge to document past and current fishery patterns, among other data sources (Berkes *et al.,* 2000; Johannes *et al.,* 2000; Sadovy and Cheung, 2003). In the present study, fishers' ecological knowledge was used as the primary basis for assessing arapaima populations and document fishing practices and trends. The usefulness of local ecological knowledge to overcome data scarcity and promote user participation in management and conservation schemes has been the topic of increased interest in recent years (Berkes *et al.*, 2000), but little has been done to apply it (Castello *et al.*, 2011c). The time has come to apply local ecological knowledge for problem solving. Combining alternative research methods with conventional methods such as those based on catch statistics, even if limited in availability, can foster aquatic conservation research in regions of the world that need it the most.

The findings of this study suggest that fishing-down is caused not only by the impacts of low gear selectivity on the larger-bodied species, as originally proposed (Welcomme, 1999), but also by the economics of the small-scale fisheries that dominate fish yields in the tropics (McManus *et al.,* 1992; Mahon, 1997). Because most small-scale fisheries are low-cost, fishers can exploit high-value, large-bodied resources even at very low abundances. In this study, fishers continued to target the arapaima despite depletion, because they use home-made canoes and harpoons and can locate and harvest even a single arapaima when it surfaces to breathe. Even if fishers were to try to move effort away from large-bodied overexploited species, as bioeconomic theory predicts, incidental harvest of juveniles caused by gillnets would further undermine the survival of the large-bodied species. This inability of tropical small-scale fishers to curb overfishing in the face of declining fish populations is partly explained by the literature on poverty traps, which suggests that lack of economic alternatives makes fishers unable to overcome market- or environment-related shocks such as declining resources (Allison and Ellis, 2001). In small-scale fisheries in Kenya, fishers from poorer households were less likely to stop fishing than fishers from wealthier households (Cinner *et al.*, 2009).

Curbing the fishing-down process requires management policies that are multi-pronged to address issues related not only to size and season of target species but also to gear and poverty. The studied community of Ilha de São Miguel offers a lesson in this regard: it banned the use of gillnets and seines two decades ago and today it possesses the highest arapaima densities in the region (35 ind km^{-2}; Figures 1 and 2). Although banning gillnets can be expected to disrupt food and income security because of their disproportionate contribution to catches, multispecies catch per unit effort in Ilha de São Miguel is the highest in the study area (Castello *et al.*, 2011a; 2013b). Castnets are allowed, however, and they yield abundant fishes for local consumption, so food security is not compromised. Similarly, in Papua New Guinea, selective restrictions on the use of gillnets, line fishing, and spearguns improved the conservation of fish communities associated with coral reefs (McClanahan and Cinner, 2008). Addressing the poverty of the fishers is more difficult, however, but it can be done by providing targeted assistance in the form of education, insurance, and institutional support (Costanza, 1987) as well as alternative-livelihood opportunities (McClanahan *et al.*, 2005). Although historically many such assistance programmes have failed (Allison and Ellis, 2001), the need to address the socioeconomic context of tropical fisheries for their conservation demands further work on the topic. This is particularly important in river conservation schemes where biodiversity protection often conflicts with maintaining ecosystem services (e.g. food security) to an extent much greater than in other ecosystems. The conservation of species exploited by tropical small-scale fisheries in river ecosystems thus requires integrative approaches to fostering environmental conservation and human wellbeing (Castello *et al.*, 2013a; Ormerod, 2014).

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REFERENCES

Allison EH, Ellis F. 2001. The livelihoods approach and management of small-scale fisheries. *Marine Policy* **25:** 377–388.

Arantes C, Garcez DS, Castello L. 2006. Densidades de pirarucu (*Arapaima gigas*, Teleostei, Osteoglossidae) em lagos das Reservas de Desenvolvimento Sustentável Mamirauá e Amanã, Amazonas, Brasil. *Uakari* **2:** 37–43.

Arantes CC, Castello L, Garcez DS. 2007. Variações entre contagens de *Arapaima gigas* (Schinz) (Osteoglossomorpha, Osteoglossidae) feitas por pescadores individualmente em Mamirauá, Brasil. *Pan-American Journal of Aquatic Sciences* **2:** 263–269.

Arantes CC, Castello L, Stewart DJ, Cetra M, Queiroz HL. 2010. Population density, growth and reproduction of arapaima in an Amazonian river-floodplain. *Ecology of Freshwater Fish* **19:** 455–465.

Batista VS, Freitas VS. 2003. O descarte de pescado na pesca com rede de cerco no baixo rio Solimões, Amazônia Central. *Acta Amazonica* **33:** 127–143.

Bayley PB. 1988. Accounting for effort when comparing tropical fisheries in lakes, river-floodplains, and lagoons. *Limnology and Oceanography* **33**: 963–972.

Beddington JR, Agnew DJ, Clark CW. 2007. Current problems in the management of marine fisheries. *Science* **316:** 1713–1716.

Berkes F, Colding J, Folke C. 2000. Rediscovery of traditional ecological knowledge as adaptive management. *Ecological Applications* **10:** 251–262.

Castello L. 2004. A method to count pirarucu *Arapaima gigas*: fishers, assessment and management. *North American Journal of Fisheries Management* **24:** 379–389.

Castello L. 2008a. Lateral migration of *Arapaima gigas* in floodplains of the Amazon. *Ecology of Freshwater Fish* **17:** 38–46.

Castello L. 2008b. Nesting habitat of pirarucu *Arapaima gigas* in floodplains of the Amazon. *Journal of Fish Biology* **72:** 1520–1528.

Castello L, Stewart DJ. 2010. Assessing CITES non-detriment findings procedures for *Arapaima* in Brazil. *Journal of Applied Ichthyology* **26:** 49–56.

Castello L, Castello JP, Hall CAS. 2007. Problemas en el manejo de las pesquerias tropicales. *Gaceta Ecológica* **18**: 65–73.

Castello L, Viana JP, Watkins G, Pinedo-Vasquez M, Luzadis VA. 2009. Lessons from integrating fishers of arapaima in small-scale fisheries management at the Mamirauá Reserve, Amazon. *Environmental Management* **43:** 197–209.

Castello L, McGrath DG, Beck PSA. 2011a. Resource sustainability in small-scale fisheries in the Lower Amazon floodplains. *Fisheries Research* **110:** 356–364.

Castello L, Stewart DJ, Arantes CC. 2011b. Modeling population dynamics and conservation of arapaima in the Amazon. *Reviews in Fish Biology and Fisheries* **21:** 623–640.

Castello L, Viana JP, Pinedo-Vasquez M. 2011c. Participatory conservation and local knowledge in the Amazon várzea: the pirarucu management scheme in Mamirauá. In *The Amazon Várzea: The Past Decade and the Decade Ahead*, Pinedo-Vasquez M, Ruffino M, Padoch CJ, Brondízio ES (eds). Springer: New York; 259–273.

Castello L, McGrath DG, Hess LL, Coe MT, Lefebvre PA, Petry P, Macedo MN, Reno V, Arantes CC. 2013a. The vulnerability of Amazon freshwater ecosystems. *Conservation Letters* **6:** 217–229.

Castello L, McGrath DG, Arantes CC, Almeida OT. 2013b. Accounting for heterogeneity in small-scale fisheries management: the Amazon case. *Marine Policy* **38:** 557–565.

Castello L, Stewart DJ, Arantes CC. 2014. O que sabemos e precisamos fazer a respeito da conservação do pirarucu (*Arapaima* spp.) na Amazônia. In *Biologia, Conservação e Manejo Participativo de Pirarucus na Pan-Amazônia,* Amaral E (ed.). Instituto de Desenvolvimento Sustentável Mamirauá: Tefé, Brasil; 17–31.

Castro F, McGrath DG. 2003. Moving toward sustainability in the local management of floodplain lake fisheries in the Brazilian Amazon. *Human Organization* **62:** 123–133.

Cinner JE, Daw T, McClanahan TR. 2009. Socioeconomic factors that affect artisanal fishers' readiness to exit a declining fishery. *Conservation Biology* **23**: 124–130.

Costanza R. 1987. Social traps and environmental policy. *BioScience* **37**: 407–412.

Crampton WGR, Castello L, Viana JP. 2004. Fisheries in the Amazon várzea: historical trends, current status, and factors affecting sustainability. In *People in Nature: Wildlife Conservation in South and Central America*, Silvius K, Bodmer R, Fragoso JMV (eds). Columbia University Press: New York; 76–95.

Cuvier G. 1822. *Das Thierreich eingetheilt nach dem bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie. Mit vielen Zusätzenversehen von H.R. Schinz. Vol.* **2**. Cotta: Stuttgart and Tübingen.

Cuvier G, Valenciennes A. 1847. *Histoire naturelle des poissons. Tome dix-neuvième. Suite du livre dix-neuvième. Brochets ou*

Lucioïdes. Livre vingtième. De quelques familles de Malacoptérygiens, intermédiaires entre les Brochets et les Clupes. Libraire de la Société Géologique de France: Paris.

Da Silveira R., Thorbjarnarson JB. 1999. Conservation implications of commercial hunting of black and spectacled caiman in the Mamirauá Sustainable Development Reserve, Brazil. *Biological Conservation* **88**: 103–109.

Davis A, Wagner JR. 2003. Who knows? On the importance of identifying "experts" when researching local ecological knowledge. *Human Ecology* **31**: 463–489.

de Mitcheson YS, Craig MT, Bertoncini AA, Carpenter AA, Cheung WWL, Choat JH, Cornish AS, Fennessy ST, Ferreira BP, Heemstra PC, *et al*. 2013. Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. *Fish and Fisheries* **14:** 119–136.

Dulvy NK, Reynolds JD. 2009. Biodiversity: skates on thin ice. *Nature* **462:** 417.

Dulvy NK, Sadovy Y, Reynolds JD. 2003. Extinction vulnerability in marine populations. *Fish and Fisheries* **4:** 25–64.

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, *et al*. 2011. Trophic downgrading of planet Earth. *Science* **333**: 301–306.

Gordon HS. 1954. The economic theory of a common property resource: the fishery. *Journal of Political Economy* **62:** 124–142.

Günther A. 1868. *Catalogue of the Physostomi, containing the Families Heteroptygii, Cyprinidae, Gonorynchidae, Hyodontidae, Osteoglossidae, Clupeidae, Chirocentridae, Alepocephalidae, Notopteridae, Halosauridae, in the Collection of the British Museum. Catalogue of the Fishes in the British Museum, Vol.* **7**. British Museum Trustees: London.

Halls AS, Welcomme RL, Burn, RW. 2006. The relationship between multi-species catch and effort: among fishery comparisons. *Fisheries Research* **77**: 78–83.

Hardt MJ. 2009. Lessons from the past: the collapse of Jamaican coral reefs. *Fish and Fisheries* **10:** 143–158.

Hoeinghaus DJ, Agostinho AA, Gomes LC, Okada EK, Pelicice FM, Kashiwaqui EAL, Latini JD, Winemiller KO. 2009. Effects of river impoundment on ecosystem services of large tropical rivers: embodied energy and market value of artisanal fisheries. *Conservation Biology* **23**: 1222–1231.

Irion G, Junk WJ, Mello JASN. 1997. The large central Amazonian river floodplains near Manaus: geological, climatological, hydrological and geomorphological aspects. In *The Central Amazon Floodplain: Ecology of a Pulsing System*, Junk WJ (ed.), Springer Verlag: Berlin; 23–46.

Isaac V, Ruffino M. 1996. Population dynamics of tambaqui, *Colossoma macropomum* Cuvier, in the Lower Amazon, Brazil. *Fisheries Management and Ecology* **3**: 315–333.

Isaac VJ, Da Silva CO, Ruffino ML. 2008. The artisanal fishery fleet of the lower Amazon. *Fisheries Management and Ecology* **15:** 179–187.

Jennings S, Polunin N, 1996. Impacts of fishing on tropical reef ecosystems. *Ambio* **25**: 44–49.

Jennings S, Grandcourt SMl, Polunin NVC. 1995. The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs* **14:** 225–235.

Johannes RE. 1998. The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends in Ecology & Evolution* **13:** 243–246.

Johannes RE, Freeman MMR, Hamilton RJ. 2000. Ignore fishers' knowledge and miss the boat. *Fish and Fisheries* **1:** 257–271.

Junk WJ. 2000. The central Amazon river floodplain: concepts for the sustainable use of its resources. In *The Central Amazon Floodplain: Actual Use and Options for a Sustainable Management*, Junk WJ, Ohly JJ, Piedade MTF, Soares MGM (eds). Backhuys Publishers: Lieben; 75–94.

Lae R. 1997. Does overfishing lead to a decrease in catches and yields? An example of two West African coastal lagoons. *Fisheries Management and Ecology* **4:** 149–164.

Lorenzen K, Almeida O, Arthur R, Garaway C, Khoa SN. 2006. Aggregated yield and fishing effort in multispecies fisheries: an empirical analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **63:** 1334–1343.

Mahon R. 1997. Does fisheries science serve the needs of managers of small stocks in developing countries? *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 2207–2213.

McClanahan TR, Cinner JE. 2008. A framework for adaptive gear and ecosystem-based management in the artisanal coral reef fishery of Papua New Guinea. *Aquatic Conservation: Marine and Freshwater Ecosystems* **18**: 493–507.

McClanahan, TR, Maina J, Davies J. 2005. Perceptions of resource users and managers towards fisheries management options in Kenyan coral reefs. *Fisheries Management and Ecology* **12**: 105–112.

McGrath DG, Castro F, Futemma C, Amaral BD, Calabria J. 1993. Fisheries and evolution of resource management on the Lower Amazon floodplain. *Human Ecology* **21:** 167–195.

McGrath DG, Silva UL, Martinelli MC. 1998. A traditional floodplain fishery of the lower Amazon River, Brazil. *Naga, the ICLARM Quarterly* **1:** 4–11.

McGrath DG, Cardoso A, Almeida OT, Pezzuti J. 2008. Constructing a policy and institutional framework for an ecosystem-based approach to managing the Lower Amazon floodplain. *Environment, Development and Sustainability* **10**: 677–695.

McManus JW, Nañola JCL, Reyes RB, Kesner KN. 1992. *Resource Ecology of the Bolinao Coral Reef System*, ICLARM Studies and Reviews, ICLARM: Manila.

Myers RA, Mertz G. 1998. The limits of exploitation: a precautionary approach. *Ecological Applications* **8:** 165–169.

Ormerod, SJ. 2014. Rebalancing the philosophy of river conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* **24**: 147–152.

Pauly D, Christensen V, Dalsgaard J, Froese R, Francisco T. 1998. Fishing down marine food webs. *Science* **279:** 860–863.

Pauly D, Watson R, Alder J. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. *Philosophical Transactions of the Royal Society B – Biological Sciences* **360:** 5–12.

Pinnegar JK, Jennings S, O'Brien C, Polunin NVC. 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Applied Ecology* **39:** 377–390.

Pitcher TJ. 2001. Fisheries managed to rebuild ecosystems? Reconstructing the past to salvage the future. *Ecological Applications* **11:** 601–617.

Renó VF, Novo EMLM, Suemitsu C, Rennó CD, Silva TSF. 2011. Assessment of deforestation in the Lower Amazon floodplain using historical Landsat MSS/TM imagery. *Remote Sensing of Environment* **115:** 3446–3456.

Reynolds JD, Jennings S, Dulvy NK. 2001. Life histories of fishes and population responses to exploitation. In *Conservation of Exploited Species*, Reynolds JD, Mace GM, Redford KH, Robinson JG (eds). Cambridge University Press: Cambridge; 147–168.

Reynolds JD, Dulvy NK, Roberts CM. 2002. Exploitation and other threats to fish conservation. In *Handbook of Fish Biology and Fisheries*, Hart PJ, Reynolds JD (eds). Blackwell: Cornwall; 319–341.

Roberts CM, Hawkins JP. 1999. Extinction risk in the sea. *Trends in Ecology & Evolution* **14:** 241–246.

Roberts CM, McClean CJ, Veron JEN, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, *et al*. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* **295:** 1280–1284.

Ruffino ML, Isaac VJ. 1999. Dinâmica populacional do surubim-tigre, *Pseudoplatystoma tigrinum* (Valenciennes, 1840) no médio Amazonas (Siluriformes, Pimelodidae). *Acta Amazonica* **29:** 463–476.

Sadovy Y, Cheung WL. 2003. Near extinction of a highly fecund fish: the one that nearly got away. *Fish and Fisheries* **4:** 86–99.

Stevens GC. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* **33:** 240–256.

Stewart DJ. 2013a. A new species of *Arapaima* (Osteoglossomorpha: Osteoglossidae) from the Solimões River, Amazonas State, Brazil. *Copeia* **2013:** 470–476.

Stewart DJ. 2013b. Re-description of *Arapaima agassizii* (Valenciennes), a rare fish from Brazil (Osteoglossomorpha: Osteoglossidae). *Copeia* **2013:** 38–51.

Welcomme RL. 1999. A review of a model for qualitative evaluation of exploitation levels in multi-species fisheries. *Fisheries Management and Ecology* **6:** 1–19.

World Conservation Monitoring Centre. 1996. *Arapaima gigas*. In IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>. Downloaded on 11 November 2013.

