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Seed dispersal by fishes in tropical and temperate fresh waters: The growing evidence

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ABSTRACT

Fruit-eating by fishes represents an ancient (perhaps Paleozoic) interaction increasingly regarded as important for seed dispersal (ichthyochory) in tropical and temperate ecosystems. Most of the more than 275 known frugivorous species belong to the mainly Neotropical Characiformes (pacus, piranhas) and Siluriformes (catfishes), but cypriniforms (carps, minnows) are more important in the Holarctic and Indomalayan regions. Frugivores are among the most abundant fishes in Neotropical floodplains where they eat the fruits of a wide variety of trees and shrubs. By consuming fruits, fishes gain access to rich sources of carbohydrates, lipids and proteins and act as either seed predators or seed dispersers. With their often high mobility, large size, and great longevity, fruit-eating fishes can play important roles as seed dispersers and exert strong influences on local plant-recruitment dynamics and regional biodiversity. Recent feeding experiments focused on seed traits after gut passage support the idea that fishes are major seed dispersers in floodplain and riparian forests. Overfishing, damming, deforestation and logging potentially diminish ichthyochory and require immediate attention to ameliorate their effects. Much exciting work remains in terms of fish and plant adaptations to ichthyochory, dispersal regimes involving fishes in different ecosystems, and increased use of nondestructive methods such as stomach lavage, stable isotopes, genetic analyses and radio transmitters to determine fish diets and movements.

1. Introduction

1.1. Importance of seed dispersal by animals

Animals are major dispersers of fruits and seeds with 30% of angiosperm families biotically dispersed and another 22% with both biotic and abiotic dispersal (Tiffney and Mazer, 1995; Tiffney, 2004). Moreover, nearly two-thirds (64%) of gymnosperm families are biotically dispersed (Herrera, 1989). This plant–animal interaction is an integral part of the biology of the individual species involved and the intact functioning of ecosystems (Howe and Smallwood, 1982; Nathan and Muller-Landau, 2000; Herrera, 2002; Tiffney, 2004; Bolmgren and Eriksson, 2010). In the tropics, where contemporary biotic dispersal is most diversified, birds and mammals, especially bats and monkeys, are principal dispersers of tree seeds in rain forests (Fleming et al., 1987; Howe and Westly, 1988). Half to over 90% of tropical trees and shrubs depend on fruit-eating vertebrates to disperse their seeds (Howe and Smallwood, 1982), and frugivorous species can compose 80% of the bird and mammal biomass in tropical moist forests (Terborgh, 1986). Only in recent decades have fishes been considered to be important seed dispersers, even though early fishes might have been the first vertebrate seed dispersers, perhaps 300 million years ago (Tiffney, 2004).

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1.2. Context of fishes among other vertebrate seed dispersers

Seed dispersal by fishes, or ichthyochory, is an ancient (possibly Paleozoic) ecological interaction that is beginning to receive more attention as new evidence demonstrates that the consumption of fruits by fishes is not a rare process concerning just a few fish and plant species in a particular area (Correa et al., 2007; Galetti et al., 2008; Lucas, 2008; Anderson et al., 2009). Rather, fruit consumption by fishes is a widespread phenomenon that has been documented in all biogeographic regions and involves more than 275 fish (Table 1; Appendix A) and numerous plant species. Fishes are likely to be the earliest vertebrate seed dispersers, a hypothesis derived from the distribution patterns of diverse cordaitalean trees (extinct coniferophytes) in wetlands, lowland rivers, and estuarine channels during the late Carboniferous (Tiffney, 1984, 1986). Increasing fossil evidence demonstrates that diverse assemblages of angiosperms were already established in the early Cretaceous (Eriksson et al., 2000; Friis et al., 2010). These assemblages were composed of shrubs and herbaceous species, including aquatic forms associated with wetlands and characterized by fleshy fruits with small seeds (Friis et al., 2010). Thus, fishes could have had an important role in seed dispersal of early angiosperms before the radiation of small terrestrial vertebrates (i.e. multituberculates, primates and rodents), which occurred nearly 80 million years (late Cretaceous and early Tertiary, Eriksson, 2008) after the first angiosperms evolved. Reluctance to consider fishes among potential seed dispersers in recent paleontological studies of the evolution of angiosperms and seed dispersal systems (e.g., Tiffney, 2004; Eriksson, 2008; Friis et al., 2010) largely results from the failure of ichthyologists to recognize and describe fishes as seed dispersers even though nineteenth-century naturalists such as Richard Spruce (1908) had mentioned such fishes.

Ichthyochory can be considered a generalized dispersal system, in which fruit-eating fishes consume fruits of plants that are visited by other frugivores and supplement their diet with alternative food resources when fruits are scarce (Correa et al., 2007) or when the fishes feed opportunistically on fruits or seeds. Even though a generalized dispersal system yields large overlap among frugivores, the collective effect on seed dispersal has significant effects for plant recruitment and distribution patterns (Howe, 1993) because different dispersers usually have different deposition patterns (e.g., Medellín and Gaona, 1999; Banack et al., 2002; Clark et al., 2004, 2005).

Because fruit-eating fishes could overlap with other dispersers and consume fruits of multiple plants that are available at the same time, most fish species likely are not exerting directional selective pressures on particular fruit traits, as occur in some specialized seed dispersal systems (e.g., elaiosome in ant-dispersed fruits, Manzaneda and Rey, 2009; and fruit color in species dispersed by birds and primates, Lomáscolo and Schaefer, 2010). Selective pressures, however, are likely to have influenced the evolution of particular morphological and behavioral adaptations in fishes that consume large quantities of fruits. Among Neotropical serrasalmid (Characiformes) fishes, for instance, fruit consumption is important for species of two clades with conspicuous morphological traits in dentition and gut morphology that can be correlated to a more efficient use of fruit resources (Correa et al., 2007). By contrast, species in a third, carnivorous, clade display different traits. This difference suggests that seasonal, highly abundant fruit types in Amazonian floodplain forests constitute an additional niche dimension that could have driven adaptive radiation of serrasalmid frugivorous fishes, similar to that for the radiation of frugivorous mammals during the Eocene (Eriksson, 2008).

Table 1
Number of species with number of genera and families represented of the fruit-eating (+ African grain-eating) fishes in six biogeographic regions. See Appendix A for identifications.

Region	Species	Genera	Families
Palearctic	9	8	2
Nearctic	4	2	2
African			
Frugivores	12	7	4
Granivores	41	19	11
Indomalayan	55	25	9
Australasian	6	5	4
Neotropical	149–151	75	17
Total species	276–278		

Whether fruit-eating fishes are opportunistic or selective consumers remains an open question. In a meta-analysis of fruits types consumed by Neotropical fishes, Correa et al. (2007) found that drupes, palm fruits, capsules and berries were the most common types, accounting for 76% of 431 cases of fruit consumption. Several studies report fishes consuming fruits of many plant species, but, in the majority of cases, the fruits of only one or two species account for most of the total volume of consumed items in the main, 2–3 month feeding period during high water (e.g., Goulding, 1980; Lucas, 2008; Anderson et al., 2009). The relative dominance of one or few fruits in the diet can be a result of foraging specialization or an opportunistic strategy where fishes consume the most abundant fruit species. Anderson et al. (2009) conducted a three-year study on feeding patterns of two large species of fruit-eating fishes in the Peruvian Amazon (*Colossoma macropomum* and *Piaractus brachypomus*, Serrasalmidae, Characiformes) and found no evidence of selective feeding at the site investigated. This study was the first to try to determine how fruit availability influenced consumption. Interestingly, however, these two fish taxa consumed only 35% of the fruit species available to fishes at the study site.

As mostly generalized feeders, frugivorous fishes overlap the diets of other vertebrate seed dispersers and in some cases consume fruits only on a seasonal basis. A question arises about how ichthyochory compares to hydrochory (i.e. seed dispersal by water) or seed dispersal by other vertebrates. Fruit-eating fishes can be highly diverse in some systems (e.g., Amazonian floodplains), and locally abundant, even in systems where only one or few fish species consume fruits. Some of these species attain large body sizes (Correa et al., 2007) and are characterized by high mobility (Horn, 1997; Anderson et al., 2011). Fruit-eating fishes can ingest large volumes of fruits (Banack et al., 2002), have positive effects on seed germination (Kubitzki and Ziburski, 1994; Chick et al., 2003; Lopes de Souza, 2005; Anderson et al., 2009), reduce seed dormancy (Horn, 1997; Pollux et al., 2006; Maia et al., 2007), and have long gut-retention times (Agami and Waisel, 1988; Horn, 1997; Pollux et al., 2006; Anderson et al., 2011). All of these attributes positively influence the effectiveness of vertebrate seed dispersers (e.g., Schupp, 1993). Even though we recognize that studies evaluating the effectiveness of ichthyochory are still limited (Correa et al., 2007), we have learned enough to predict that fruit-eating fishes are important to the process of seed dispersal in several ways: (1) enhance seedling establishment (Anderson et al., 2009); (2) influence upstream distribution patterns (Horn, 1997); (3) disperse large-sized seeds (Kubitzki and Ziburski, 1994; Correa et al., 2007); (4) disperse non-buoyant seeds (Piedade, 1985; Kubitzki and Ziburski, 1994; Galetti et al., 2008); (5) disperse seeds of aquatic plants (Agami and Waisel, 1988; Pollux et al., 2006); and (6) generate long-distance dispersal kernels (Anderson et al., 2011).

1.3. Importance of floodplain forests and riparian zones

Floodplains are wetlands that oscillate between terrestrial and aquatic phases (Junk et al., 1997), and they are clearly seasonal environments. The regularly recurring flooded period has been defined as a “flood pulse” (Junk et al., 1989); thus, it is closely associated with the evolution of interactions between plants and animals. Unlike in permanent swamps and lakes, interactions in seasonal floodplains are limited in time because of the flooding periodicity. Flooding amplitudes can range from a few centimeters up to 15 m every year but average 5–12 m for the Amazon River, with the higher values farther upstream; flood durations can vary between a few days and eight months (Goulding et al., 2003). Vegetation can be composed of both herbaceous and woody species, but monodominant stands also occur in highly diverse floodplain forests. Floodplain forests and riparian zones represent environments where typical terrestrial and typical aquatic characteristics are combined. Most scientific research, however, has been focused on well-defined ecosystems that are easier to quantify without the influence of flooding water. Many features of these integrated, terrestrial-aquatic systems are poorly known compared to the understanding we have of purely terrestrial or purely aquatic ecosystems. This lack of knowledge is of particular concern given that vast areas worldwide are covered by floodplain forests and riparian zones and are important for the ecology and economy of entire regions.

2. Geographic distributions and major lineages of frugivorous fishes

2.1. Holarctic: Palearctic + Nearctic regions

Little information is available on seed dispersal by fishes in the Holarctic region, particularly when compared to tropical regions, which contain a much higher diversity of frugivorous fish species (Table 1; Appendix A). This scarcity of knowledge may result from real differences in fruit type between tropical and temperate regions (Pollux et al., 2006). In tropical regions, the production of fleshy fruits is prevalent among aquatic and riparian plants (Figuerola et al., 2002), and, here, a wide variety of fishes are known to consume fruits and seeds. Most temperate aquatic and riparian plants, on the other hand, produce hard, grain-like fruits with a very small proportion of edible pulp material (Figuerola et al., 2002). Consequently, fishes that specialize in consuming fruits (frugivores) and seeds (granivores) are notably absent. Instead, in temperate regions, seeds are thought to be primarily dispersed by zoobenthivores, omnivores and herbivores that ingest seeds accidentally (unintentionally), while feeding on aquatic plants, or while foraging in detritus layers in search of invertebrate prey (Pollux et al., 2006; Pollux, 2011).

Evidence for ichthyochory in the temperate zone stemming from stomach-content analyses is generally sparse and largely anecdotal. Presumably, this lack of information is a direct corollary of the unintentional nature of seed ingestion by temperate consumers. Incidental seed ingestion commonly results in low seed quantities in the digestive tract of fishes. As a result, dietary studies rarely mention the presence of seeds in the stomachs of these fishes and, instead, categorize the seeds as ‘plant item’, ‘unidentifiable debris’ or ‘rest of material’. Yet, even if these fishes were to ingest small quantities of seeds, and infrequently, they might still contribute significantly to plant dispersal in temperate regions (Pollux et al., 2006; Pollux, 2011). Thus, the importance of temperate fishes as seed dispersers is still poorly understood and most likely being underestimated. Carps and minnows (Cyprinidae, Cypriniformes) appear to form the most important group of seed dispersers in temperate regions, although a few other species also are known to ingest seeds (Appendix A).

2.2. African region

Ichthyochory in Africa has not yet been evaluated, although fruit and seed consumption has been documented in natural history studies on multiple species across the continent (Table 1; Appendix A). Reports on fruit-eating fishes are limited, despite the considerable expanse of forested floodplains throughout western Africa (i.e. coastal portions of Liberia, Cote d’Ivoire, Ghana, Nigeria and Cameroon) and the Congo Basin. It is in these areas where the largest potential for ichthyochory would be expected. The extensive swamp forests in the lower Niger basin and the seasonally flooded forests in the Congo River basin, which hold the largest fish diversity on the continent (Lévêque, 1997), are similar to the *varzea* and oligotrophic *igapó* forests of the Amazon basin (Morley, 2000). The forests of this region, however, suffered major episodes of contraction and expansion during the last glacial maximum in the Quaternary, resulting in four isolated refuges during the Pleistocene ($\leq$1.6 Ma) that together represented only 10% of the forest cover in the Holocene, just slightly larger than the present distribution (Morley, 2000). Although the forests expanded again during the Holocene, this increase occurred only about 12,000 years ago (Morley, 2000). Whether this period was sufficiently long to allow a Holocene radiation of fish species adapted to using fruit resources from the flooded forests efficiently remains to be investigated.

Both frugivory and granivory are represented in the African region (Table 1; Appendix A). Most of the fruit-eating species are omnivores with frugivorous tendencies. All of these species are medium- to large-sized fishes (15–60 cm total length) that could potentially consume and disperse large quantities of seeds. Given the highly diverse fish fauna of Africa, other species not reported here likely also feed on fruits. Granivory appears to be fairly common among African freshwater fishes (Table 1; Appendix A), perhaps influenced by the extensive savannas and grasslands that cover the floodplains of some of the major rivers (e.g., Niger, Zambezi and Orange rivers). The specialized oral dentition of certain members of the Alestidae (Characiformes), the pharyngeal teeth of some Cyprinidae and the muscular gizzard of *Heterotus niloticus* (Osteoglossidae, Osteoglossiformes) suggest that these species are mainly seed predators, although they could still disperse certain seeds effectively (Norconk et al., 1998). The potential for effective seed dispersal by catfishes (Siluriformes) is higher than for some of the other species mentioned because they swallow entire seeds and have benthic habits; however, too little information is available to assess the relative importance of ichthyochory by African fishes. Future research efforts should focus on all aspects of the biology of fruit eating, grain eating and ichthyochory by African fishes, especially in the Congo basin.

2.3. Indomalayan region

Our understanding of ichthyochory in the Indomalayan region is still rudimentary, despite numerous but mostly anecdotal reports (Corlett, 1998). Primary production within many river systems is low, so that numerous fish species depend heavily on allochthonous plant matter, including fruits (Inger and Chin, 1962; Lowe-McConnell, 1987). The importance of floodplain and riparian forests for local fish communities and fisheries in the region is well known in this respect, although few quantitative studies exist (Chevey and Le Poulain, 1940; Dick and Martin-Smith, 2004). Consumption of fruits by fishes seems to be genuinely rarer than in the Neotropics (Table 1; Appendix A), although more frugivorous taxa very likely will be identified in the future. Whereas the Amazon Basin remained relatively stable in the recent geological past, areas of comparable lowland river systems in the Indomalayan region, particularly on the Sunda Shelf, expanded and contracted repeatedly as a result of Pleistocene sea-level changes. Although sea levels remained low for extended periods of time, therefore exposing large floodplains, these intervals were frequently interrupted by substantial rises of sea level during interglacial periods (Voris, 2000). Larger floodplains comparable to those of the Amazon basin therefore possibly did not last long enough to allow for the evolution of tighter interactions between plants and fishes.

At least 55 species of primary and secondary freshwater fishes in nine families within the Indomalayan Region are known to consume fruits regularly or occasionally (Table 1; Appendix A). Cyprinids represent the most diverse fish family in the large river systems of mainland tropical Asia and the Sunda Shelf. Frugivorous cyprinids usually belong to the larger-bodied representatives within their respective lineages, and the 16 frugivorous cyprinid species that co-occur in the Kapuas floodplains of Danau Sentarum in West Kalimantan include small surface dwellers, medium- to large-bodied midwater species, and mostly large, benthopelagic species.

Besides cyprinids, a variety of other fish lineages are represented among the fruit-eating species in the region (Appendix A). At least four families of catfishes (Siluriformes) contain frugivorous species, including large benthopelagic members of the Pangasiidae and Bagridae that are able to swallow large seeds. Giant gouramies (Osphronemidae, Perciformes) are known to depend heavily on fruits seasonally in the lower Mekong and the upper Kapuas rivers. A number of pufferfishes (Tetraodontidae, Tetraodontiformes) have adapted to freshwater, where plants make up a large part of their diets (Inger and Chin, 1962).

A number of frugivorous fish species have been introduced into the region because of their use in aquaculture, and some have established feral populations. These exotic taxa include the cyprinids *Cyprinus carpio* and *Leptobarbus hoevenii*, the catfishes *Clarias* spp. and the giant gourami *Osphronemus goramy* (Inger and Chin, 1962; Kottelat et al., 1993; Atack, 2006). Naturalized populations of the cyprinids *Barbonymus gonionotus*, *Osteochilus hasseltii* and *C. carpio* have been found in northern Sulawesi (Haryono and Tjakrawidjaja, 2004), an area from where no native frugivorous fishes are known. Local extinctions of indigenous cyprinids have been associated with the introduction of *C. carpio* in India (Kottelat and Whitten, 1996). Frugivorous characiforms (*Mylossoma* spp., *Piaractus* spp., Serrasalmidae) have been introduced from the Neotropics as aquarium or aquaculture fish, but whether they exist as feral populations in the region is unknown to us.

2.4. Australasian region

Fruit-eating fishes in the Australasian region thus far are known to be low in diversity (Table 1) and to occur exclusively in the tropical areas of northern Australia and New Guinea (Appendix A). The available information on frugivory by native fish species of New Guinea originates in the larger southern river systems. The Neotropical serrasalmid *Piaractus brachypomus* was introduced into the Sepik River, New Guinea, where it supports an established fishery (Correa et al., 2007). Effects of this exotic frugivore on native fish assemblages or floodplain vegetation, however, are unknown.

2.5. Neotropical region

Neotropical frugivorous fishes are distributed from Central America to southern Brazil, with the largest diversity concentrated in the Amazon River basin. The Amazon holds the largest diversity of freshwater fishes in the world (Reis et al., 2003), and so it is not surprising that the vast majority of records of fruit-eating fishes come from this river basin alone. Based on published analyses of gut contents, 149–151 fish species belonging to 75 genera have been reported to consume fruits and seeds in the Neotropics (Table 1; Appendix A). Lack of taxonomic resolution increases the difficulty of obtaining accurate estimates of the number of fruit-eating fish species. Goulding (1980), for instance, argued that at least 200 fish species in the Amazon basin are likely to feed on seasonally available fruits and seeds. Neotropical fruit-eating fishes range from small- and medium-sized characids and cichlids (Cichlidae, Perciformes) that mainly feed on aquatic and terrestrial invertebrates and occasionally consume fruits and seeds, to large omnivorous catfishes (Doradidae, Pimelodidae) and herbivorous serrasalmids that consume considerable amounts of fruits. Numerous small fish species also are known to feed on the seeds of herbaceous plants, such as native floodplain rice (*Oryza* spp., Poaceae), but remain poorly studied.

The large diversity of trees, shrubs and vines distributed in seasonally flooded savannas and forests of the Orinoco, Amazon and Paraguay river basins provide a rich source of fruits and seeds for fishes. Numerous plant species in these wetlands have their fruiting phenology tightly synchronized with the annual flood pulse, releasing large amounts of fruits and seeds that fall into the water and become available to fish (Kubitzki and Ziburski, 1994). Waldhoff and Maia (2002), for instance, listed 79 plant species whose fruits are consumed by Amazonian fishes, and Da Silva et al. (2003) compiled a list of 133 plant species whose fruits and seeds are consumed by the large serrasalmid *Colossoma macropomum*. Effectiveness of fishes as seed dispersers (e.g., effects of passage through the fish digestive system on seed viability and germination rates), however, has been evaluated for only a few species (Kubitzki and Ziburski, 1994; Horn, 1997; Mannheimer et al., 2003; Lopes de Souza, 2005; Maia et al., 2007; Anderson et al., 2009, 2011).

The high diversity of frugivorous fishes in the South American tropics also is probably related in part to the extensive lowland watersheds that have existed in the western portion of the present-day Amazon and Orinoco river basins since the beginning of the Cenozoic era, about 67 Ma (Lundberg et al., 1998; Hoorn et al., 2010). The associated rain forests appear to have persisted through the global cooling events of the terminal Eocene and, unlike in tropical Africa, no conclusive evidence exists for Pleistocene reductions of tropical South American forests into refuges (Nelson et al., 1990). Instead, the moist conditions that continued through the Quaternary facilitated the maintenance of highly diverse rain forests (Morley, 2000).

Fossil serrasalmid fishes from the late Cretaceous and the entire Cenozoic, however, suggest an earlier origin of the family, with generic-level diversification by 13.5 Ma in the middle Miocene (Lundberg et al., 1986; Lundberg, 1998). Moreover, fossil teeth of the herbivorous serrasalmids *Mylossoma* spp. and *Colossoma macropomum* have been recovered from the Lower Miocene (approximately 20-15 Ma), providing evidence of morphological stasis in these taxa with highly specialized dentition for fruit and seed consumption (Dahdul, 2004).

A scenario of large drainages with old forested wetlands and old fishes adapted to fruit and seed consumption suggest an ancient and tight interaction between fishes and fruits in South America. Given this long and parallel evolutionary history, South American floodplain savannas and forests, in particular those in the Amazon and Orinoco river basins, perhaps have been the primary areas for the development of ichthyochorous species. Thus, South America stands as a prime location where more comprehensive studies can be focused to understand better the evolutionary history and ecological implications of ichthyochory.

3. Ecology of frugivorous fishes with evidence for their role as major seed dispersers

3.1. Floodplain forests and seasonal environments

Floodplain forests and riparian zones are often highly productive despite growth reductions during the aquatic period (Worbes, 1992; Parolin, 2000). The resulting formation of annual growth rings found in many tree species of seasonally flooded environments allows calculations of biomass production and growth responses to environmental stresses even though it is in the tropics. Although few data are available, annual fruit production in nutrient-rich, white-water floodplains of the Amazon River is estimated at 16–53 million tons; the Amazonian tree *Myrciaria dubia* (Myrtaceae), for example, produces up to 12.7 tons of fruit per hectare per year (Maia, 2001).

Fruits often mature during the high-water period, and, not surprisingly, hydrochory and ichthyochory are among the primary means of diaspore dispersal. The timing of fruit maturity and the presence of dispersal agents are tightly linked. The close relationship frequently encountered between fish and tree species presumably has evolved from the reciprocal benefit. In these environments where hydrology is the major driving factor, flowering plants and mobile fish meet at periodic intervals. For the fishes, the flooded forests offer shelter, space for reproduction and a major food resource. The fishes ensure upstream seed dispersal (Horn, 1997) in an environment in which diaspores otherwise are carried mainly downstream, although other dispersers such as bats and monkeys provide multidirectional transport.

The mutualistic-type relationships between plants and fishes, however, do not appear to be strict, and we recognize the existence of alternative means of dispersal for the plant diaspores and other food resources for the fishes. The plants and fishes probably do not depend entirely on each other, but they substantially enhance each other's survival and vitality. Fish also feed on young leaves, fruits, seeds, and insects that fall from the trees. Thus, the maintenance of fishery stocks that are used extensively by humans living along waterways largely depends on the continued existence of functioning riparian forests.

3.2. Size, longevity and migratory behavior

The frugivorous fish species inhabiting Neotropical ecosystems vary in size from <20 cm to >1 m in length. Even within a species, the quantity of seeds dispersed increases with fish size, and the species composition of seeds changes with individual fish size (Kubitzki and Ziburski, 1994; Galetti et al., 2008; Anderson et al., 2009). Few studies have quantified the longevity of fruit-eating fishes, although some of these species apparently can have extended life spans. For example, *Colossoma macropomum* has been estimated to live up to 65 years (Reinert and Winter, 2002). Otoliths obtained from individuals captured for sale at fish markets, or for local consumption, could be used to determine the average age of adults in contemporary populations. Many species of large-bodied frugivorous fishes, however, are heavily exploited, which decreases both the average age and size of individuals. Larger individuals of *Piaractus mesopotamicus*, *P. brachypomus* and *C. macropomum* (all Serrasalmidae), have been shown to be more effective dispersers than smaller individuals (Kubitzki and Ziburski, 1994; Galetti et al., 2008; Anderson et al., 2009; Fig. 1); therefore, pressure from the fisheries likely alters not only the age and size structure of natural populations but the quality of seed dispersal.

The majority of Neotropical fruit-eating fishes are characiforms (Anostomidae, Characidae and Serrasalmidae) and siluriforms (especially Auchenipteridae, Doradidae and Pimelodidae) (Araujo-Lima and Goulding, 1997; Mannheimer et al., 2003; this article). These groups likely differ in their effectiveness as seed dispersers. Members of the Characidae masticate and destroy many of the seeds they consume because of their crushing, molariform teeth; in contrast, catfish primarily digest fruit pulp and defecate or regurgitate intact seeds. Most of the medium to large, heavily fruit- and seed-eating species in South America migrate seasonally. For example, in a tagging and mark-recapture experiment performed on *Piaractus mesopotamicus* in the Paraná River, the fish moved 16.4–32.6 km/day upstream (Makrakis et al., 2007). Although exact migratory distances have not been determined successfully by tagging experiments in the Amazon River, migrations are well known to fishers who accompany and exploit fish schools during fish movements for spawning (high water) and dispersal (end of high-water and low-water seasons).

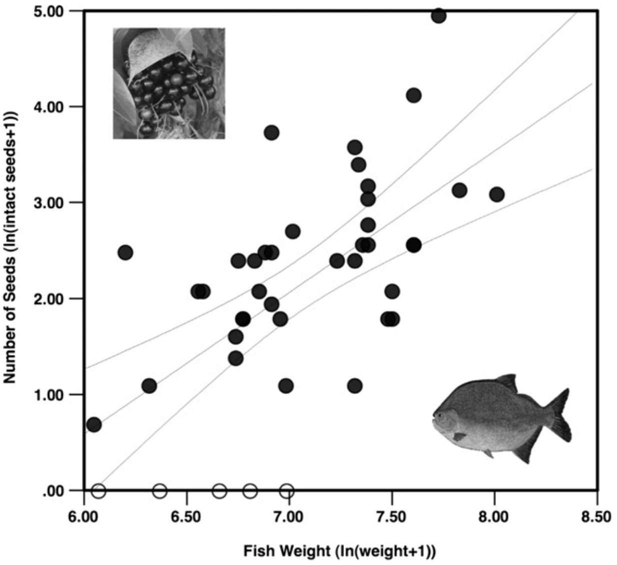


Fig. 1. Larger compared to smaller individuals of *Piaractus mesopotamicus* disperse more intact seeds of the palm *Bactris glaucescens*. (from Galetti et al., 2008, with permission.)

For fruit-eating fishes, annual migrations act to disperse subadult populations from nutrient-rich, white-water nursery habitats to the often extensive flooded forest of the nutrient-poor, clear-water and black-water rivers where subadults and adults feed heavily (M. Goulding, pers. observ.). Adults from these same tributaries (e.g., Negro and right-bank tributaries of the Madeira in Brazil) undertake annual downstream dispersal migrations, but always upriver in the main stem (e.g., Madeira and Amazon), which in effect leads to colonization of tributaries farther upstream. Fish-fruit interactions in the lower courses of black-water and clear-water tributaries, then, are tied directly to the relative quantities of frugivorous fish that migrate into and out of an individual tributary in any given year. As the fisheries data indicate, these numbers can vary greatly from year to year for an individual tributary. Resident populations of different migratory frugivorous species (e.g., *Myleus* and *Metynnis*, Serrasalmidae) apparently never leave the clear-water and black-water tributaries where they live because schools are not encountered by fishers, which they would if the fishes migrated downstream to white-water rivers.

Many migratory species may enter flooded forest soon after entering a black-water or clear-water tributary subsequent to spawning in a white-water river channel at the beginning of the floods and then slowly work their way upstream while feeding in the inundated forests (M. Goulding, pers. observ.). If this scenario is correct, then we could logically predict that massive, net upstream seed-dispersal occurs. Importantly, however, interbasin migratory species are largely confined to the lower 200–300 km of the black-water and clear-water rivers; thus, any large upstream dispersal would be restricted to the lower courses only of the tributaries. Tagging or quantitative experimental fishing is needed to determine exactly how migratory species disperse themselves along the lower courses of the black-water and clear-water tributaries subsequent to spawning.

3.3. Influence on local plant-recruitment dynamics and regional biodiversity

Flooded forests and riparian vegetation are important if not critical sources of food for fishes in Neotropical wetlands. Given that fruiting tends to occur during annual inundations (e.g., Parolin et al., 2004; Haugaasen and Peres, 2007), fish have access to the majority of fruits produced in Amazonian floodplain habitats. Fruit-eating fishes may play vital roles in plant recruitment, gene flow between plant populations, and the maintenance of plant diversity. Neotropical fishes consume and disperse massive quantities of seeds from a large number of tree and liana species in proportion to their local abundance. Depending on the size of the seed, a large fruit-eating fish could contain from one to many thousands of seeds in its digestive tract (Goulding, 1980, 1993; Kubitzki and Ziburski, 1994; Horn, 1997; Mannheimer et al., 2003; Galetti et al., 2008; Lucas, 2008; Anderson et al., 2009, 2011). In addition, the migratory behavior and extensive mobility of fish could translate into extremely long-distance seed dispersal, as has been shown recently for *Colossoma macropomum* (Anderson et al., 2011). Seed dispersal effectiveness, however, depends not only on the quantity of seeds dispersed, but also on the quality of dispersal (Schupp, 1993). Seeds collected from the digestive tracts and fecal matter of fishes are capable of successful germination, and, indeed, the seeds of some plant species show enhanced germination rates or rapid seedling growth after passing through the gut of fish (Kubitzki and Ziburski, 1994; Horn, 1997; Anderson et al., 2009).

Beyond these statements, however, we know little about the post-dispersal fates of seeds. A large percentage of floodplain species are seemingly adapted to dispersal by fish because of when they produce fleshy fruits. Unfortunately, more questions than answers remain regarding the seed-to-seedling transition. For example: Do fish disperse seeds to microsites that are suitable for germination and seedling establishment? Do fish enable seeds to escape host-specific pests or pathogens by dispersing them far enough away from adult conspecifics? Does seed dispersal by fish result in clumped patterns of seed distributions, or are seeds scattered? Does dispersal by fish promote rapid germination and seedling growth, so that plants can survive subsequent long-term submersion? These questions will require detailed investigations of fish movement patterns and observational and experimental studies of seedling recruitment, which will elucidate the roles of various fish species in structuring floodplain plant communities. Moreover, very few studies have compared the quantities of seeds dispersed and the quality of seed dispersal among frugivores (but see Wenny, 2000); thus, we know little about how seed dispersal by fish differs from dispersal by other vectors (but see Banack et al., 2002; Anderson et al., 2011). Further studies of functional redundancy among seed dispersers are needed to understand the relative importance of frugivorous fishes in the regeneration biology of floodplain forest plants.

3.4. Evidence from feeding experiments

Seed-feeding trials refer to experiments in which known numbers of seeds are fed to individual fish under controlled conditions, after which the feces are collected at regular intervals and checked for the presence of non-digested seeds. Commonly, feeding trials are followed by germination trials in which the retrieved seeds are planted to germinate under climate-controlled conditions (Pollux, 2011).

Feeding trials provide a powerful tool to study key questions in the dispersal ecology of plant species, such as: Can fish disperse seeds? What is the probability of germination after fish-mediated dispersal? What is the potential dispersal distance? Two experimental studies in the Neotropics help to provide some answers to these questions. Horn (1997) in a series of feeding trials showed that the seeds of the riparian fig tree *Ficus insipida* (=*F. glabrata*) require approximately 18–36 h to pass through the digestive tract of the characid fish *Brycon guatemalensis*. Potential dispersal distances can be inferred by combining information on seed retention times in the fish's gut with the fish's migratory behavior. Using radiotelemetry, Horn (1997) found that *B. guatemalensis* exhibited migratory behavior, ranging from 0.1 to 1.0 km upstream over a period of 7–14 days. Germination trials showed that the fig seeds retained their viability after passing through the fish's gut. Taken together, these data suggest that *B. guatemalensis* can indeed contribute to the dispersal of *F. insipida*. More recently, Anderson et al. (2011) combined seed-retention experiments with fine-scale radiotracking of wild *Colossoma macropomum* to show that the fish disperses seeds extremely long distances (up to >5 km), among the longest reported, and that the dispersal distances increase with fish size.

In an experimental study with a Palearctic fish species, Pollux et al. (2007) showed that the majority of seeds of the riparian helophyte *Sparganium emersum* pass through the digestive tract of the common carp (*Cyprinus carpio*) within 4–10 h while retaining their capacity to germinate. Maximum seed dispersal distances were subsequently modeled by combining seed retention times with the optimum swimming speed (U_{opt}) of carp. Assuming a U_{opt} of 1–2 body lengths per second (bl s^{-1}; Jobling, 1995) and non-stop linear migratory movements, the maximum potential seed dispersal distances by the carp (body length *c.* 25 cm) range from 13.5 to 27 km (Pollux et al., 2007).

Feeding trials also can provide deeper insight into the functional aspects of plant–fish interactions. Comparative studies, using plants or fishes from different populations or species, allow the investigation of how trait variation within and among species may affect the probability of fish-mediated dispersal (Pollux, 2011). For instance, plant species that produce smaller seeds are more likely to be ingested by fishes, yet, at the same time, have a lower probability of survival compared to larger and harder seeds (Agami and Waisel, 1988; Smits et al., 1989; Pollux et al., 2006, 2007). Furthermore, seeds that lack a hard protective coat are more likely to sustain damage to their seed embryo during gut passage, resulting in a decline of viability. By contrast, pulp removal and scarification of the seed coat during gut passage is more likely to enhance germination of seeds that have a hard (scleridial) protective coat (Agami and Waisel, 1988; Smits et al., 1989; Pollux et al., 2006, 2007; Anderson et al., 2009). Other studies have examined inter- and intra-specific variation among fishes. Survival of the seeds of the submerged macrophytes *Najas marina* (Najadaceae) and *Ruppia maritima* (Ruppiaceae) depends on the fish species that consume them, with probabilities ranging from 5% survival in the common carp (*Cyprinus carpio*), 35% in grass carp (*Ctenopharyngodon idella*), to 60% in tilapia (*Oreochromis* sp., Cichlidae) (Agami and Waisel, 1988). It is not clear whether this difference among fish species was related to interspecific variation in digestive physiology or, perhaps, to size variation of the fishes used in the experiment.

Fish size, as discussed earlier, has been shown to affect the probability of dispersal in a number of different ways. For example, ingestion of fruits *of Forestiera acuminata* (Oleaceae) by channel catfish (*Ictalurus punctatus*) varies intraspecifically depending on fish size, with smaller fish (<20 cm) feeding on the fruits by scraping off the pulp and then spitting out the seeds with only the larger individuals (40–60 cm) being able to swallow, and, hence disperse, the fruits (Adams et al., 2007). Seeds produced in the floodplain forests of Pacaya-Samiria (northeastern Peru) also have a higher chance of being dispersed when consumed by large, adult individuals of the fish species *Colossoma macropomum* compared to smaller juveniles, but here it is because juveniles are more likely to crush the seeds with their molariform teeth than the big adults that can swallow the seeds whole (Anderson et al., 2009).

4. Environmental and anthropogenic impacts on frugivorous fishes

4.1. Overfishing

Frugivorous fishes are among the most sought-after species in the Amazon because of their highly regarded flavor (M. Goulding, pers. observ.). The largest characiforms, *Colossoma macropomum* and *Piaractus brachypomus*, both have been overfished in much of the Amazon basin. Because of the easy detection of their migratory schools, populations of *P. brachypomus* were greatly reduced beginning in the late 1960s and early 1970s. Today, large schools of this species are rare, and most individuals seen in markets are juveniles or fish less than about two years of age. Young *P. brachypomus* can still be relatively common in floodplain lakes of the Amazon River, and recruitment probably comes from the upper Amazon River and perhaps the Purus River, as adults are now rarely encountered in the lower courses of black-water and clear-water tributaries where they were once abundant. *Colossoma macropomum* also has been seriously overfished in most of the Amazon where it is found, and young fish are being heavily exploited in white-water floodplain lakes in the absence of large juveniles and adults (Isaac and Ruffino, 1996; Reinert and Winter, 2002). The smaller frugivorous characiforms, especially the serrasalmids, can be heavily exploited locally, but none currently appears threatened with commercial extinction. Species of *Brycon*, especially the largest species, *B. amazonicus*, are extensively fished during the seasonal migrations; all exploitation of these taxa during spawning runs probably should be prohibited. Based on fisheries statistics (Barthem and Goulding, 2007), total catches of frugivorous fishes have fallen by a minimum of 50% since the 1970s; thus, total biomass of and seed dispersal and seed predation by fish presumably also have decreased by similar amounts.

Aquaculture production now accounts for a large part of the *Colossoma macropomum* sold in Manaus, Brazil, and, with increased production and falling prices, fishing effort toward wild fish could decrease (M. Goulding, pers. observ.) Some discussion has occurred about an expanded aquaculture for the species to stock natural habitats, but, before any such experiments are undertaken, comparative genetic studies of farmed and wild fish should be completed to ensure that that the wild populations have a gene pool equally as diverse as that of the farmed fish.

4.2. Dams and impoundments

Several studies in Brazil have shown that the construction of dams causes marked changes in the fish communities with the decline of long-distance migratory species as the most conspicuous change (Agostinho et al., 2008). The Itaipu Reservoir on the Upper Paraná River in southern Brazil is associated with the disproportionate loss of the larger migratory species after the dam was completed (Agostinho et al., 2003). These large, economically-important species included the frugivorous *Piaractus mesopotamicus* and the piscivorous *Salminus brasiliensis* (Characidae). In a study of the impacts of the Serra da Mesa dam on the Tocantins River, Albrecht et al. (2009) reported that two members of the omnivore guild, *Brycon falcatus* and *B. gouldingi*, and the diverse herbivore guild increased in abundance when the reservoir filled, but then declined or disappeared in the reservoir when the inundated riparian vegetation died out from the flooding. To date, seven large dams exist on the Amazon, two are under construction on the Madeira River, and at least 12 are planned to be built within the next decade in Brazil alone. Because no dams thus far constructed in the Amazon basin have been investigated at an ecosystem level, it is difficult to know how they might impact frugivorous fishes.

4.3. Deforestation and logging

Deforestation has heavily impacted the Amazon River floodplain, especially the lower course below the Negro River (M. Goulding, pers. observ.). Almost no natural floodplain forest is left on the lower Amazon River, but the Amazon estuary is in relatively better condition. Fruit-eating fishes are still common in this region primarily because the lower Amazon River with its vast floodplain lakes is a major nursery for many migratory species. Recruits come from populations spawning upstream. Local fish markets on the lower Amazon River region display few adult frugivorous species, but young fish are commonly for sale. Floodplains originally were deforested for jute farming, but, since the 1970s, cattle and water-buffalo ranching have been more important. These grazing ungulates trample forest seedlings. Even where satellite imagery may show a standing forest, the understory is usually missing because of this livestock activity, and so the forest is functionally dead. Livestock also destroy floating meadows on which many frugivorous and other species depend for protection from predators. Floodplain deforestation historically has been moving upriver and now is prevalent on the Solimões River (Amazon River in Brazil upriver of the confluence with the Negro River). Thus far, floodplains of the white-water tributaries, such as the Madeira and Purus, have not been heavily deforested, but this condition could change with the rebuilding of the interfluvial highway (Br-319) between the Purus and Madeira rivers, a road built in the 1970s but largely abandoned until recently. Other roads along the edge of the Amazon River floodplain also are leading to greater deforestation, especially near large urban centers such as Manaus.

4.4. Climate change

Climate change may play a long-term role in fish seed dispersal. The frequency of extreme events associated with climate change (e.g., flooding and drought, Parry et al., 2007) could have drastic effects on some fish populations and their habitats (Marengo et al., 2008; FAO, 2009), as well as fish-forest interactions. Extreme droughts can cause large reductions in populations of fishes (Merron et al., 1993) and increased mortality of less drought-resistant plants (Parolin et al., 2010). Severe flooding and drought also can exacerbate the impacts of human-caused disturbances (Sparks et al., 1990). Given that flood level mediates fish access to fruits in floodplain zones, extreme drought and flooding events could strongly curtail seed dispersal. The diets of frugivorous fishes change in diversity and composition with changes in flood level (even as little as 25 cm) in seasonally flooded systems (Lucas, 2008). Exceptionally low floods limit fish access to potentially large areas of floodplain vegetation, thus restricting diets to fewer, lower-elevation species. The expected increase in the frequency of extreme events such as flooding and drought could severely alter fish seed dispersal even though fish seed consumption and dispersal have evolved during climate changes on a geological time scale (Hoorn, 2006; Hoorn et al., 2010). Present-day climate change, however, combined with anthropogenic impacts on fish populations and their habitats, could impart negative, synergistic effects on fish seed dispersal.

5. Future studies

5.1. Evolution and adaptation in seasonal environments

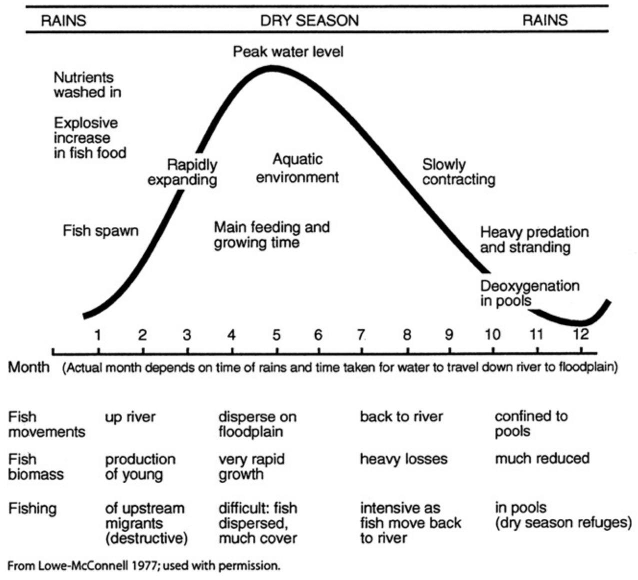
Even though fruit consumption by fishes has been reported in all six of the world’s biogeographic regions, our knowledge of this fish–plant interaction varies so greatly among regions that we cannot generalize about morphological, physiological or behavioral adaptations associated with fruit consumption and seed dispersal by fishes. A major challenge associated with sorting out adaptations to frugivory in a comparative, phylogenetic manner is that the fishes, especially in tropical regions, live in a highly seasonal, floodplain environment. These fluctuations create a seasonal progression of events for many species living in large, tropical rivers (Lowe-McConnell, 1975; Fig. 2). Thus, any study of the evolution of adaptive traits in lineages with fruit-eating species needs to consider, and expect, phenotypic plasticity and ontogenetic shifts in diet and associated features. Multiple traits ought to be assessed in several species within a monophyletic assemblage using comparative methods (e.g., Pagel, 1994).

5.2. *Dispersal regimes in different ecosystems*

Despite the vast areas covered by floodplain forests and riparian zones and their huge ecological and economical importance, little is known about dispersal regimes in these ecosystems anywhere in the world. We need to differentiate between large flood-pulsed rivers and small ones dominated by unpredictable flash floods. Wetland classifications are only rudimentary for most flooded ecosystems, especially in tropical regions, and inventories of the resident plant and animal biotas are highly fragmentary. We can only postulate that dispersal linked to fish species is probably important in floodplain forests in all regions of the world, as long as the ecosystems are old enough to allow for co-evolution and adaptation.

5.3. *Increased use of nondestructive methods*

The high plant diversity in the diets of frugivorous fishes increases the need for obtaining large sample sizes to allow well-supported conclusions to be made about ichthyochory. Nondestructive methods as alternatives to killing fishes and dissecting them to study their diets should be used whenever possible to minimize the impact on local fish populations, especially in protected areas, or when conducting long-term studies of fruit resources or frugivore assemblages.



Fish movements	up river	disperse on floodplain	back to river	confined to pools
Fish biomass	production of young	very rapid growth	heavy losses	much reduced
Fishing	of upstream migrants (destructive)	difficult: fish dispersed, much cover	intensive as fish move back to river	in pools (dry season refuges)

From Lowe-McConnell 1977; used with permission.

Fig. 2. Seasonal progression of events for many fish species in tropical floodplain rivers. (modified from Lowe-McConnell, 1975, by Helfman et al., 1997, with permission from latter.)

Several nondestructive methods can be applied more broadly to expand our knowledge of ichthyochory: (1) Stomach lavage on live fishes can be used instead of gut dissection, but possible physical damage to the digestive tract needs to be assessed in preliminary trials (Giles, 1980). The effectiveness of the dissection and lavage methods is influenced by factors such as fish size, the morphology of the stomach and the type of diet (Waters et al., 2004). (2) Stable isotopes can be used to quantify local movements and migratory patterns of fish, assess seasonal habitat usage and dietary shifts, and determine trophic position (Kennedy et al., 2002; Oliveira et al., 2006; Durbec et al., 2010), all of which can influence the quantity of seeds dispersed and the quality of the process. (3) Population genetic analyses using highly polymorphic molecular markers (e.g., AFLPs or microsatellites) may provide information about fish-mediated dispersal in the field. Molecular analysis has shown that the large serrasalmid frugivore *Colossoma macropomum* forms one panmictic population along a 2,200-km section of the Amazon River (Santos et al., 2007), indicating frequent and large-scale migratory movements by this fish species. The question remains as to what extent migratory behaviors translate into long-distance seed dispersal. Genetic analyses of plants may help to provide further insights into the distance, direction or frequency of seed dispersal by fishes. Direct measures require the genotyping of seeds or seedlings and all of their potential maternal plants; parentage analyses can be conducted to link each seed or seedling to the maternal parent. Certain fruits (e.g., drupes) contain endocarps composed of maternal tissue, which can help to map dispersed seeds in relation to the maternal plant (Godoy and Jordano, 2001). If this direct method is too costly or time-consuming, indirect genetic measures can be used in which genotypes are obtained from a representative sample of individuals in different populations. (4) Radio transmitters can be used to quantify short-term movement patterns during the flood season when fish have access to fruit (Horn, 1997). Seed retention in the digestive tract combined with radiotracking of fish movements can be used to model the probability that a seed moves a given distance from the maternal plant and could reveal long-distance seed dispersal. As mentioned above, Anderson et al. (2011) reported just such results, showing that *Colossoma macropomum* has long gut-retention times and disperses seeds to favorable habitats over hundreds and thousands of meters, among the longest distances yet recorded for a frugivore.

6. Conclusions

In this review, we provide information showing that fruit-eating fishes:

A. Occur in all six biogeographic regions and comprise at least 276 species, with the large majority in tropical latitudes.
B. Belong to a broad array of fish lineages, but mostly are cypriniforms (minnows and carps), characiforms (tetras, pacus and piranhas), and siluriforms (catfishes).
C. Have been most studied in the Neotropical region, but those in the Indomalayan region, especially, have gained in recognition.
D. Eat the fruits of a wide variety of trees and shrubs in floodplains and riparian zones and act as seed dipersers, seed predators, or both.
E. Tend to be large-bodied, highly mobile and long-lived, all of which enhance seed dispersal.

F. Can be major seed dispersers in floodplain and riparian habitats based on seed-feeding experiments and estimates of numbers of seeds transported.

G. Have been diminished ecologically by overfishing, damming, deforestation and logging, all of which result in smaller fish, reduced populations, altered diets and broken migrations.

H. Have led to exciting research questions – on fish and plant adaptations to ichthyochory, dispersal regimes in different ecosystems and increased use of nondestructive methods.

7. Recommended future studies

Based on the information supplied in this review, the following studies ought to be undertaken on fruit-eating fishes:

A. Close the loop from the fruit ingested by the fish to the seed deposited to the seedling germinated, by using genetic markers and other approaches.

B. Test for phenotypic plasticity vs. genetic adaptation in the evolution of frugivory in seasonal environments, through feeding experiments, comparative methods and phlyogenetic analyses.

C. Evaluate the roles of fishes and other dispersal agents in different ecosystems, by using detailed biodiversity surveys of fruit-eating species and plant-animal interactions, genetic markers, microarray analysis, stomach lavage, stable isotopes and radio transmitters.

D. Investigate granivorous fishes, largely understudied, in Africa especially, and other regions.

E. Integrate all of the above, with an emphasis on nondestructive methods.

Acknowledgments

We thank Pierre-Michel Forget for giving us the opportunity to present a review of seed dispersal by fishes at the 5th International Symposium-Workshop on Frugivores and Seed Dispersal convened in Montpellier, France, and to submit this manuscript on the topic.

Appendix A. Fish species, by biogeographic region, that consume fruits and seeds.

Order and family	Species	River basin	Country	Source
Holarctic: Palearctic + Nearctic regions				
Cypriniformes				
Cyprinidae	*Abramis brama*	Wloclawek reservoir lake, Rhine River	Poland, the Netherlands	Wielgosz, 1989; Bergers, 1991
	Blicca bjoerkna	Wloclawek reservoir lake, Rhine River	Poland, the Netherlands	Wielgosz, 1989; Bergers, 1991
	Ctenopharyngodon idella	Reservoir lake	Israel	Agami and Waisel, 1988
	Cyprinus carpio	Carmargue, Lake Banyoles, Meuse River	France, Spain, the Netherlands	Crivelli, 1981; Garcia and Adelman, 1985; García-Berthou, 2001; Pollux et al., 2006, 2007
	Notropis baileyi	Halawakee Creek	USA	Mathur and Ramsey, 1974
	Notropis girardi	Canadian River	USA	Wilde et al., 2001
	Notropis potteri	Brazos River	USA	Perkin et al., 2009
	Phoxinus phoxinus	River Brathay, Lake Windemeer	UK	Frost, 1943
	Rutilus rutilus	Wloclawek reservoir, Rhine River Lakes	Poland, the Netherlands	Szczyglinska, 1987; Wielgosz, 1989; Bergers 1991
	Scardinius acarnanicus	Lysimachia and Trichonis	Greece	Iliadou, 1991
	Scardinius erythrophthalmus	Lake Hiidenvesi	Finland	Nurminen et al., 2003
Perciformes				
Centrarchidae	*Lepomis gibbosus*	Lake Banyoles	Spain	García-Berthou and Moreno-Amich, 2000
Siluriformes				
Ictaluridae	*Ictalurus punctatus*	Mississippi River	USA	Chick et al., 2003; Adams et al., 2007
African Region				
Frugivory				
Characiformes				
Alestidae	*Alestes liebrechtsii*	Congo	Dem. Repub. Congo	Matthes, 1964
	Brycinus grandisquamis	Congo	Dem. Repub. Congo	Matthes, 1964; Lauzanne, 1998
	Brycinus longipinnis	Bia River	Ivory Coast	Dietoa et al., 2007
	Brycinus poptae	Congo	Dem. Repub. Congo	Matthes, 1964
	Bryconaethiops microstoma	Congo	Dem. Repub. Congo	Matthes, 1964
Citharinidae	*Distichodus atroventralis*	Congo	Dem. Repub. Congo	Matthes, 1964
	Distichodus sexfasciatus	Congo	Dem. Repub. Congo	Matthes, 1964
	Xenocharax spilurus	Congo	Dem. Repub. Congo	Matthes, 1964
Siluriformes				
Clariidae	*Clarias ebriensis*	Niger	Nigeria	Ezenwaji, 2002
	Clarias gariepinus	Nile to Orange	Widely distributed through Africa	Skelton, 2003
Schilbeidae	*Schilbe intermedius*	Cucune, Okavango, Zambezi, Phongono Nile, Senegal	Zimbawe, Mozambique, Uganda, Senegal	Skelton, 2003

(*continued on next page*)

Appendix A (*continued*)

Order and family	Species	River basin	Country	Source
	Schilbe tumbanus	Congo	Dem. Repub. Congo	Matthes, 1964
Granivory				
Characiformes				
Alestidae	*Alestes baremoze*	Niger	Mali	Matthes, 1977
	Alestes dentex	Niger, Nile, Sénegal, Chad, Mayo Kebbi	Mali, Sudan, Sénegal, Chad	Blache, 1964; Bishai, 1977; Matthes, 1977; Bailey, 1994; Moreau et al., 1995
	Alestes sp.	n/a	East Africa	Cooper, 1996
	Brycinus batesii	n/a	Cameroon	Lauzanne, 1998
	Brycinus brevis	Bénué	Ghana, Nigeria	Lauzanne, 1998
	Brycinus imberi	Phongolo Rufigi, Zaire	Zambia, Zimbawe, Mozambique	Skelton, 2003
	Brycinus leuciscus	Niger	Mali	Matthes, 1977; Moreau et al., 1995
	Brycinus macrolepidotus	Chad	Chad	Blache, 1964; Lauzanne, 1998
	Brycinus nurse	Chad, Niger	Chad, Mali	Blache, 1964; Matthes, 1977
	Micralestes acutidens	Niger	Mali	Matthes, 1977
Cypriniformes				
Cyprinidae	*Barbus altianalis*	n/a	East Africa	Lauzanne, 1998
	Barbus anoplus	Limpopo, Orange	South Africa	Skelton, 2003
	Barbus bifrenatus	Cunene, Okavango, Upper Zambezi, Kafue, Zambian Zaire, Limpopo	Zimbawe, Botswana, South Africa	Skelton, 2003
	Barbus bynni occidentalis	Chad, Niger, Senegal, Volta, Ouémé, Ogun	Chad, Nigeria, Senegal, Ghana, Benin	Lauzanne, 1998
	Barbus mattozi	Zambezi	Zimbawe, Angola	Skelton, 2003
	Barbus neumayeri	Mpanga River	Uganda	Schaack and Chapman, 2004
	Barbus trevelyani	Keiskamma & Buffalo	South Africa	Skelton, 2003
	Barbus unitaeniatus	Zambian Zaire, Cunene, Okavango, Zambezi Phongolo	Zambia, Zimbawe, Mozambique	Skelton, 2003
	Chelaethiops bibie	Nile	Sudan	Bailey, 1994
	Labeo senegalensis	Cross River	Nigeria	Offem et al., 2009
	Labeobarbus kimberleyensis	Orange-Vaal River System	n/a	Lauzanne, 1998
Siluriformes				
Clariidae	*Clarias gariepinus*	Chad, Nile to Orange	Chad, Widely distributed through Africa	Blache, 1964; Skelton, 2003
	Clarias sp.	n/a	East Africa	Cooper, 1996
	Heterobranchus sp.	n/a	East Africa	Cooper, 1996
Claroteidae	*Chrysichthys auratus*	Cross River	Nigeria	Offem et al., 2009
Mochokidae	*Synodontis leopardina*	Zambezi	Zambia	Winemiller and Kelso-Winemiller, 1996
	Synodontis macrostigma	Zambezi	Zambia	Winemiller and Kelso-Winemiller, 1996
	Synodontis membranacea	Niger	n/a	Owolabi, 2008
	Synodontis nigromaculata	Zambezi	Zambia	Winemiller and Kelso-Winemiller, 1996
	Synodontis obesus	Cross River	Nigeria	Offem et al., 2009
	Synodontis zambezensis	Zambezi to Phongolo	Zambia, Zimbawe, Mozambique	Skelton, 2003
	Synodontis sp.	n/a	East Africa	Cooper, 1996
Schilbeidae	*Schilbe intermedius*	Cucune, Okavango, Zambezi, Phongono, Nile, Senegal	Angola, Zambia, Zimbawe, Mozambique, Uganda, Senegal	Skelton, 2003
	Schilbe sp.	n/a	East Africa	Cooper, 1996; Lauzanne, 1998
Perciformes				
Cichlidae	*Sargochromis codringtonii*	Okavango, Zambezi	Zambia	Skelton, 2003; Winemiller, 1991
	Tilapia zillii	Chad	Chad	Blache, 1964
Osteoglossiformes				
Mormyridae	*Hyperopisus bebe*	n/a	n/a	Lauzanne, 1998
	Mormyrus tapirus	Cross River	Nigeria	Offem et al., 2009
Osteoglossidae	*Heterotis niloticus*	Sô, Nile, Omo, Lake Turkana, Niger, Chad	Widely distributed through north and east Africa	D'Aubenton, 1955; Blache, 1964; Cooper, 1996; Lauzanne, 1998; Adite et al., 2005
Polypteriformes				
Polypteridae	*Polypterus senegalus senegalus*	Nile	Sudan	Bailey, 1994
Lepidosireniformes				
Protopteridae	*Protopterus annectens annectens*	Cross River	Nigeria	Offem et al., 2009
Indomalayan Region				
Cypriniformes				

Appendix A (*continued*)

Order and family	Species	River basin	Country	Source
Cyprinidae	*Barbodes strigatus*	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Barbonymus collingwoodii	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Barbonymus gonionotus	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Barbonymus schwanenfeldii	Kapuas	Indonesia	Giesen, 1987; P. Widmann & A. Tjiu (Unpubl. results)
	Catlocarpio siamensis	Mekong	Cambodia	Rainboth, 1996
	Hypsibarbus wetmorei	Tembeling, Perak, Pahang	Malaysia	Khoo et al., 1987; Tan, 1980
	Leptobarbus sp.	Kapuas	Indonesia	Vaas, 1952
	Leptobarbus melanopterus	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Leptobarbus melanotaenia	Kapuas	Indonesia	Giesen, 1987; P. Widmann & A. Tjiu (Unpubl. results)
	Leptobarbus hoevenii	Kuching River, Tembeling, Kapuas, Mekong, Chao Phrya	Malaysia, Indonesia, Cambodia, Laos, Thailand	Atack, 2006; Giesen, 1987; Rainboth, 1996; Roberts, 1993; Tan, 1980
	Luciosoma setigerum	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Neolissochilus hexagonolepis	Tembeling, Perak, Pahang	Malaysia	Khoo et al., 1987; Tan, 1980
	Neolissochilus stracheyi	Mekong	Cambodia	Rainboth, 1996
	Osteochilus sp.	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Osteochilus kappenii	Kapuas	Indonesia	Giesen, 1987
	Osteochilus kelabau	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Osteochilus melanopleurus	Kapuas	Indonesia	Giesen, 1987; P. Widmann & A. Tjiu (Unpubl. results)
	Osteochilus schlegelii	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Osteochilus waandersii	Kapuas	Indonesia	Giesen, 1987; P. Widmann & A. Tjiu (Unpubl. results)
	Paralaubuca typus	Mekong	Laos	Bardach, 1959
	Puntioplites bulu	Segama, Kinabatangan, Tembeling	Malaysia	Inger and Chin, 1962; Tan, 1980
	Puntioplites waandersi	Kapuas	Indonesia	Giesen, 1987; P. Widmann & A. Tjiu (Unpubl. results)
	Puntioplites sp.	Mekong	Laos	Roberts, 1993
	Puntius binotatus	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Puntius sp.	Kapuas	Indonesia	Vaas, 1952
	Rasbora caudimaculata	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Tor douronensis	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Tor sinensis	Mekong	Cambodia	Rainboth, 1996
	Tor cf. *tambra*	Mekong	Laos	Roberts, 1993; Roberts and Baird, 1995
	Tor tambroides	Tembeling, Perak, Pahang Mekong	Cambodia	Khoo et al., 1987; Tan, 1980; Rainboth, 1996
Osteoglossiformes				
Osteoglossidae	*Notopterus notopterus*	Mekong	Laos	Bardach, 1959
Perciformes				
Nandidae	*Pristolepis fasciata*	Kapuas, Mekong	Indonesia, Cambodia	Giesen, 1987; Rainboth, 1996
Osphronemidae	*Osphronemus exodon*	Mekong	Cambodia	Rainboth, 1996
	Osphronemus goramy	Kapuas, Mekong	Indonesia, Cambodia, Laos	Giesen, 1987; Rainboth, 1996; Roberts, 1993; P. Widmann & A. Tjiu (Unpubl. results)
	Osphronemus septemfasciatus	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
Silurifomes				
Bagridae	*Hemibagrus nemurus*	Mekong	Laos	Roberts, 1993
Clariidae	*Clarias batrachus*	Mekong	Laos, Singapore	Bardach, 1959; Ridley, 1930
	Clarias cf. *meladerma*	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Clarias teijsmanni	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
Pangasiidae	*Helicophagus waandersii*	Mekong	Laos	Roberts, 1993
	Pangasius bocourti	Mekong	Laos	Roberts, 1993; Roberts and Baird, 1995
	Pangasius conchophilus	Mekong	Laos	Roberts and Baird, 1995
	Pangasius djambal	Mekong	Cambodia	Rainboth, 1996
	Pangasius krempfi	Mekong	Laos	Roberts and Baird, 1995
	Pangasius larnaudiii	Mekong	Cambodia, Laos	Rainboth, 1996; Roberts, 1993; Roberts and Baird, 1995
	Pangasius mahakamensis	Mahakam	Indonesia	Pouyaud et al., 2002
	Pangasius nasutus	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Pangasius niuewenhuisii	Mahakam	Indonesia	Roberts and Vidthayanon, 1991
	Pangasius polyuranodon	Mekong	Cambodia, Laos	Rainboth, 1996; Roberts and Baird, 1995
	Pangasius rheophilus	Unspec.	Indonesia	Pouyaud and Teugels, 2000
Siluridae	*Kryptopterus* sp.	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
	Ompok hypophthalmus	Kapuas	Indonesia	P. Widmann & A. Tjiu (Unpubl. results)
Tetraodontiformes				
Tetraodontidae	*Auriglobus* sp.	Unspec. Kalimantan	Indonesia	MacKinnon et al., 1996

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Appendix A (*continued*)

Order and family	Species	River basin	Country	Source
	Auriglobus modestus	Kapuas	Indonesia	Roberts, 1989
	Tetraodon sp.	Unspec. Kalimantan	Indonesia	MacKinnon et al., 1996
Australasian Region				
Elopiformes				
Megalopidae	*Megalops cyprinoides*	Unspec. tropics	Australia	Pusey and Arthington, 2003
Perciformes				
Kuhliidae	*Kuhlia rupestris*	Coastal drainages of Queensland	Australia	Allen et al., 2002; Merrick and Schmida, 1984; Pusey and Arthington, 2003
Terapontidae	*Hephaestus fuliginosus*	Coastal drainages of Northern Territory and Queensland	Australia	Allen et al., 2002; Merrick and Schmida, 1984; Pusey and Arthington, 2003
	Hephaestus tulliensis	Unspec. tropics	Australia	Pusey and Arthington, 2003
Siluriformes				
Ariidae	*Arius macrorhynchus*	Digul, Lorentz, Fly	Indonesia, Papua New Guinea	Allen, 1991; Roberts, 1978
	Neoarius taylori	Fly	Papua New Guinea	Allen, 1991; Roberts, 1978; van der Pijl, 1982
Neotropical Region				
Characiformes				
Anostomidae	*Abramites hypselonotus*	Amazon	Brazil	M. Goulding (Pers. observ.)
	Anostomoides laticeps	Amazon	Brazil	M. Goulding (Pers. observ.)
	Laemolyta taeniata	Amazon	Brazil	M. Goulding (Pers. observ.)
	Laemolyta varia	Amazon	Brazil	M. Goulding (Pers. observ.)
	Leporellus vittatus	Amazon	Brazil	M. Goulding (Pers. observ.)
	Leporinus agassizii	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006
	Leporinus brunneus	Amazon	Brazil, Colombia	Goulding et al., 1988; Blanco-Parra and Bejarano-Rodriguez, 2006
	Leporinus desmotes	Amazon	Brazil	M. Goulding (Pers. observ.)
	Leporinus elongatus	Paraná	Brazil	Duraes et al., 2001
	Leporinus fasciatus	Amazon	Brazil, Colombia	Goulding et al., 1988; Blanco-Parra and Bejarano-Rodriguez, 2006
	Leporinus friderici	Amazon, Paraná, Approuague, Sinnamary	Brazil, French Guiana	Gottsberger, 1978; Goulding, 1980; Boujard et al., 1990; Duraes et al., 2001, Melo et al., 2004
	Leporinus klausewitzi	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006
	Leporinus maculatus	Amazon	Brazil	M. Goulding (Pers. observ.)
	Leporinus trifasciatus	Amazon	Brazil	M. Goulding (Pers. observ.)
	Leporinus yophorus	Amazon	Brazil	M. Goulding (Pers. observ.)
	Schizodon fasciatus	Amazon	Brazil	M. Goulding (Pers. observ.)
	Schizodon vittatum	Amazon	Brazil	M. Goulding (Pers. observ.)
Characidae	*Acnodon normani*	Amazon	Brazil	Leite and Jegu, 1990
	Acnodon senai	Amazon	Brazil	Leite and Jegu, 1990
	Aphyocharax sp.	Amazon	Brazil	Melo et al., 2004
	Astyanax altiparanae	Paraná, Piracicaba	Brazil	Gomiero et al., 2003
	Astyanax bimaculatus	Amazon	Brazil	Melo et al., 2004
	Astyanax cf. *guianensis*	Amazon	Brazil	Goulding et al., 1988
	Astyanax fasciatus	Amazon, Claro, Sirena	Brazil, Costa Rica	Winemiller, 1983; Winemiller and Morales, 1989; Melo et al., 2004
	Astyanax sp.	Orinoco	Venezuela	Prejs and Prejs, 1987
	Brycon amazonicus	Amazon	Brazil	Lopes de Souza, 2005
	Brycon cephalus	Amazon	Brazil, Colombia	Goulding, 1980; S.B. Correa (Unpubl. results)
	Brycon chagrensis	Chagres	Panama	Menezes, 1969
	Brycon falcatus	Amazon	Brazil, Colombia	Melo et al., 2004; Blanco-Parra and Bejarano-Rodriguez, 2006
	Brycon ferox	Mucuri River	Brazil	Lima and Castro, 2000
	Brycon gouldingi	Rio Tocantins	Brazil	Albrecht et al., 2009
	Brycon guatemalensis	Sarapiqui	Costa Rica	Horn, 1997; Banack et al., 2002
	Brycon hilarii	Amazon, Paraná	Brazil	Gottsberger, 1978; Sabino and Sazima, 1999; Reys et al., 2009
	Brycon melanopterus	Amazon	Brazil, Colombia	Goulding, 1980; Lopes de Souza, 2005; Blanco-Parra and Bejarano-Rodriguez, 2006; S.B. Correa (Unpubl. results)
	Brycon opalinus	Paraiba do SulRiver	Brazil	Gomiero et al., 2008
	Brycon petrosus	n/a	Panama, Honduras	Menezes, 1969
	Brycon vermelha	Mucuri River	Brazil	Lima and Castro, 2000
	Bryconamericus sp.	Amazon	Brazil	Melo et al., 2004
	Chalceus spp. (2–3 species)	Amazon	Brazil	M. Goulding (Pers. observ.)
	Creagrutus cf. *caucanus*	Amazon	Brazil	Goulding et al., 1988
	Creagrutus hildebrandi	Catatumbo	Colombia	Galvis et al., 1997

Appendix A (*continued*)

Order and family	Species	River basin	Country	Source
	Creagrutus sp.	Amazon	Brazil	Melo et al., 2004
	Ctenobrycon hauxwellianus	Amazon	Brazil	Marlier, 1967
	Hemigrammus levis	Amazon	Brazil	Goulding et al., 1988
	Hemigrammus sp.	Amazon	Brazil	Melo et al., 2004
	Hyphessobrycon sp.	Amazon	Brazil	Goulding et al., 1988
	Hyphessobrycon eques	Amazon	Brazil	Marlier, 1967
	Hyphessobrycon savagei	Claro, Sirena	Costa Rica	Winemiller, 1983; Winemiller and Morales, 1989
	Jupiaba zonata	Amazon	Brazil	Goulding et al., 1988
	Moenkhausia collettii	Amazon	Brazil	Goulding et al., 1988
	Moenkhausia grandisquamis	Amazon	Brazil	Goulding et al., 1988
	Moenkhausia lepidura	Amazon	Brazil	Goulding et al., 1988
	Moenkhausia oligolepis	Amazon	Brazil	Goulding et al., 1988
	Moenkhausia sanctaefilomenae	Amazon	Brazil	Melo et al., 2004
	Oligosarcus hepsetus	Amazon, Paraná	Brazil, Argentina	Menezes, 1969
	Roeboides dayi	Orinoco	Venezuela	Prejs and Prejs, 1987
	Tetragonopterus argenteus	Amazon, Orinoco	Brazil, Venezuela	Prejs and Prejs, 1987; Melo et al., 2004
	Tetragonopterus chalceus	Amazon	Brazil	Goulding et al., 1988
	Triportheus albus	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006; S.B. Correa (Unpubl. results)
	Triportheus angulatus	Amazon	Brazil, Colombia	Goulding, 1980; Almeida, 1984; Melo et al., 2004; Yamamoto et al., 2004; Blanco-Parra and Bejarano-Rodriguez, 2006; Maia et al., 2007; S.B. Correa (Unpubl. results)
	Triportheus auritus	Amazon	Colombia	S.B. Correa (Unpubl. results)
	Triportheus elongatus	Amazon	Brazil, Colombia	Goulding, 1980; Almeida, 1984; Claro et al., 2004; Lopes de Souza, 2005; Blanco-Parra and Bejarano-Rodriguez, 2006
	Triportheus sp.	Amazon	Brazil	Gottsberger, 1978; Goulding, 1980; Goulding et al., 1988
Hemiodontidae	*Argonectes longiceps*	Amazon	Brazil	Goulding et al., 1988
	Hemiodus immaculatus	Amazon	Brazil	Lopes de Souza, 2005
	Hemiodus unimaculatus	Amazon	Brazil, Colombia	Goulding et al., 1988; Blanco-Parra and Bejarano-Rodriguez, 2006
Serrasalmidae	*Colossoma macropomum*	Amazon	Brazil	Gottsberger, 1978; Goulding, 1980; Goulding and Carvalho, 1982; Kubitzki and Ziburski, 1994; Da Silva et al., 2003; Lopes de Souza, 2005
	Metynnis argenteus	Amazon	Brazil	M. Goulding (Pers. observ.)
	Metynnis hypsauchen	Amazon	Brazil, Colombia	Lopes de Souza, 2005; S.B. Correa (Unpubl. results)
	Metynnis sp.	Amazon	Brazil	Goulding et al., 1988
	Myleus asterias	Amazon	Colombia	S.B. Correa (Unpubl. results)
	Myleus pacu	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006
	Myleus rhomboidalis	Approuague, Sinnamary	French Guiana	Boujard et al., 1990; Planquette et al., 1996
	Myleus setiger	Amazon	Brazil	M. Goulding (Pers. observ.)
	Myleus schomburgkii	Amazon	Brazil, Colombia	Goulding et al., 1988; S.B. Correa (Unpubl. results)
	Myleus torquatus	Amazon	Brazil, Colombia	Goulding et al., 1988; S.B. Correa (Unpubl. results)
	Myleus sp.	Amazon	Brazil	Melo et al., 2004
	Myloplus rubripinnis	Amazon	Brazil, Colombia	Lopes de Souza, 2005; Blanco-Parra and Bejarano-Rodriguez, 2006; S.B. Correa (Unpubl. results)
	Mylossoma acanthogaster	Catatumbo	Colombia	Galvis et al., 1997
	Mylossoma aureum	Amazon	Brazil, Colombia	Gottsberger, 1978; Goulding, 1980; S.B. Correa (Unpubl. results)
	Mylossoma duriventre	Amazon	Brazil, Colombia	Gottsberger, 1978; Goulding, 1980; Claro et al., 2004; Lopes de Souza, 2005; S.B. Correa (Unpubl. results)
	Mylossoma sp.	Amazon	Brazil	Goulding, 1980
	Piaractus brachypomus	Amazon, Orinoco	Brazil, Colombia, Venezuela	Marlier, 1967; Canestri, 1970; Honda, 1974; Gottsberger, 1978; Goulding, 1980, Knab-Vispo et al., 2003; S.B. Correa (Unpubl. results).
	Piaractus mesopotamicus	Paraná	Brazil	Galetti et al., 2008
	Pristobrycon aureus	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006

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Appendix A (*continued*)

Order and family	Species	River basin	Country	Source
	Pristobrycon calmoni	Amazon	Colombia	Blanco-Parra and Bejarano-Rodriguez, 2006
	Pristobrycon striolatus	Amazon	Colombia, French Guiana	Planquette et al., 1996; Blanco-Parra and Bejarano-Rodriguez, 2006
	Pygopristis denticulata	Amazon	Brazil	M. Goulding (Pers. observ.)
	Serrasalmus altuvei	Amazon	Brazil	M. Goulding (Pers. observ.)
	Serrasalmus gouldingi	Amazon	Brazil	M. Goulding (Pers. observ.)
	Serrasalmus hastatus	Amazon	Brazil	M. Goulding (Pers. observ.)
	Serrasalmus manueli	Amazon	Brazil	M. Goulding (Pers. observ.)
	Serrasalmus spilopleura	Amazon	Brazil, Colombia	M. Goulding (Pers. observ.); S.B. Correa (Unpubl. results)
	Serrasalmus rhombeus	Amazon	Brazil	Goulding, 1980
	Serrasalmus sp.	Amazon	Brazil	Goulding, 1980
	Tometes makue	Amazon	Brazil	M. Goulding (Pers. observ.)
Cypriniformes				
Anablepidae	*Oxyzygonectes dovii*	Claro	Costa Rica	Winemiller and Morales, 1989
Poeciilidae	*Brachyrhaphis rhabdophora*	Claro	Costa Rica	Winemiller and Morales, 1989
Gymnotiformes				
Electrophoridae	*Electrophorus electricus*	Amazon	Brazil	Goulding, 1980
Sternopygidae	*Sternopygus macrurus*	Amazon	Brazil	Goulding et al., 1988; Melo et al., 2004
Osteoglossiformes				
Osteoglossidae	*Osteoglossum bicirrhosum*	Amazon	Brazil	De Arango, 1947 (cited in: van der Pijl, 1972)
Perciformes				
Cichlidae	*Acarichthys heckelii*	Amazon	Brazil	Marlier, 1967
	Amphilophus diquis	Claro	Costa Rica	Winemiller and Morales, 1989
	Apistogramma ramirezi	Orinoco	Venezuela	Prejs and Prejs, 1987
	Archocentrus sajica	Claro	Costa Rica	Winemiller and Morales, 1989
	Astronotus ocellatus	Amazon	Brazil	Goulding et al., 1988
	Biotodoma wavrini	Amazon	Brazil	Goulding et al., 1988
	Dicrossus filamentosus	Amazon	Brazil	Goulding et al., 1988
	Geophagus altifrons	Amazon	Brazil	Goulding et al., 1988
	Geophagus surinamensis	Amazon	Brazil	Melo et al., 2004
	Heros severus	Amazon	Brazil	Goulding et al., 1988
	Satanoperca jurupari	Amazon	Brazil, French Guiana	Goulding et al., 1988; Le Bail et al., 2000
	Retroculus lapidifer	Amazon	Brazil	Melo et al., 2004
	Uaru amphiacanthoides	Amazon	Brazil	Goulding et al., 1988
Eleotridae	*Dormitator latifrons*	Claro	Costa Rica	Winemiller and Morales, 1989
	Eleotris picta	Claro, Sirena	Costa Rica	Winemiller, 1983
Siluriformes				
Ageneiosidae	*Ageneiosus* sp.	Amazon	Brazil	Goulding et al., 1988
Aspredinidae	*Buconocephalus* sp.	Amazon	Brazil	Melo et al., 2004
Auchenipteride	*Auchenipterichthys* sp.	Amazon	Brazil	Goulding et al., 1988
	Auchenipterus longimanus	Amazon	Brazil	Mannheimer et al., 2003
	Tocantinsia piresi	Amazon	Brazil	Carvalho and Kawakami-Resende, 1984
	Trachelyopterus galeatus	Amazon	Brazil, French Guiana	Le Bail et al., 2000; Claro-Jr et al., 2004
	Trachycorystes (4+ species)	Amazon	Brazil	Goulding, 1980; Goulding et al., 1988; M. Goulding (Pers. observ.)
Doradidae	*Astrodoras asterifrons*	Amazon	Brazil	M. Goulding (Pers. observ.)
	Lithodoras dorsalis	Amazon	Brazil	Goulding, 1980; Goulding, 1993; Kubitzki and Ziburski, 1994
	Megalodoras uranoscopus	Amazon	Brazil	Goulding, 1980; Goulding et al., 1988
	Platydoras armatulus	Amazon	Brazil	M. Goulding (Pers. observ.)
	Platydoras costatus	Amazon	Brazil	Goulding et al., 1988
	Pterodoras granulosus	Amazon, Paraná	Brazil	Goulding, 1980; de Souza-Stevaux et al., 1994
	Scorpiodoras heckelii	Amazon	Brazil	M. Goulding (Pers. observ.)
Loricaridae	*Loricaria sp.*	Amazon	Brazil	Armbruster, 2004; Melo et al., 2004
	Crossoloricaria sp.			Armbruster, 2004
	Spatuloricaria sp.	Amazon	Brazil	Melo et al., 2004
Pimelodidae	*Calophysus macropterus*	Amazon	Brazil	Goulding, 1980
	Phractocephalus hemioliopterus	Amazon	Brazil	Goulding, 1980; Kubitzki, 1985; Goulding et al., 1988
	Pimelodella cristata	Amazon	Brazil	Melo et al., 2004
	Pimelodella sp.	Amazon	Brazil	Gottsberger, 1978
	Pimelodus blochii	Amazon	Brazil	Goulding, 1980; Melo et al., 2004; Blanco-Parra and Bejarano-Rodriguez, 2006
	Pimelodus (4–5 species)	Amazon	Brazil	M. Goulding (Pers. observ.)
	Platynematichthis notatus	Amazon	Brazil	Blanco-Parra and Bejarano-Rodriguez, 2006
	Rhamdia schomburgkii	Amazon	Brazil	Gottsberger, 1978
	Sorubim lima	Amazon	Brazil	Gottsberger, 1978

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