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# Diet shift of Red Belly Pacu *Piaractus brachypomus* (Cuvier, 1818) (Characiformes: Serrasalmidae), a Neotropical fish, in the Sepik-Ramu River Basin, Papua New Guinea

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Introduction of fish species is a globally widespread practice that causes losses of native species and homogenization of diversity within and across continents. Diet assessments are important tools to depict the ecological function of species introduced into novel ecosystem and possible direct and indirect ecological effects. In this study, we compare the diet of *Piaractus brachypomus*, a mainly frugivorous Neotropical fish, introduced into the Sepik-Ramu River Basin (Papua New Guinea) nearly two decades ago, to that of similar size individuals from Neotropical populations in the Amazon and Orinoco River basins (South America). In contrast to native populations that feed mainly on terrestrial plants and invertebrates, the diet of introduced *P. brachypomus* is mainly composed of fish remains and aquatic plants, while terrestrial plants are frequently consumed but in relatively smaller amounts. These findings show that *P. brachypomus* has an inherently plastic diet that can be adjusted when displaced to a novel geographic area. While trophic plasticity increases the likelihood of a species to establish breeding populations after its introduction, it also reduces our ability to predict negative effects on native species.

La introducción de peces es una práctica que se extiende globalmente y que causa perdida de especies nativas y homogenización de la diversidad dentro y entre continentes. Los estudios de dieta son herramientas útiles para definir la función ecológica de una especie introducida en un ecosistema nuevo y los posibles efectos directos e indirectos. En este estudio describimos la dieta de *Piaractus brachypomus*, una especie de pez Neotropical principalmente frugívora, que fue introducida en el río Sepik (Papua Nueva Guinea) hace casi dos décadas; y la comparamos con aquella de individuos de tamaño corporal similar de poblaciones nativas en las cuencas de los ríos Amazonas y Orinoco (América del Sur). En contraste con las poblaciones nativas que se alimentan principalmente de frutas y semillas, plantas e invertebrados terrestres, la dieta de individuos de *P. brachypomus* introducidos se compone principalmente de restos de peces y plantas acuáticas, mientras que plantas terrestres son consumidas frecuentemente pero en pequeñas cantidades. Estos resultados indican que *P. brachypomus* tiene una dieta plástica que puede adaptarse cuando la especie se desplaza a un área geográfica nueva. A pesar de que la plasticidad trófica aumenta la probabilidad de que una especie establezca poblaciones reproductivas después de la introducción, también reduce nuestra habilidad de predecir los efectos negativos sobre especies nativas.

**Key words:** Exotic fish, Fruit-eating fish, Species introduction, Red Belly Pacu, Stocking.

## Introduction

Introduced species can have effects at multiple levels, from species, to food webs, to ecosystem function (Chapin III *et al.*, 1998; Grosholz, 2002; Ehrenfeld, 2010). The ecological effects of introduced species are difficult to forecast and quantify (Lodge, 1993; Ricciardi *et al.*, 2013) and can derive enormous economic and social costs (Pimentel *et al.*, 2000; 2005). Although highly context dependent and species-specific, diet and trophic position are important predictors of the ecological impacts that non-native species have on novel ecosystems (Ricciardi *et al.*, 2013). As non-native species become integrated into new ecosystems, food consumption enhances their likelihood of successful establishment while at the same time reduces food availability for native consumers and increases mortality of native prey. Quantitative dietary analyses are, therefore, useful tools to assess direct and indirect ecological impacts of non-native species as it allows defining the functional ecology of the introduced species (Ricciardi *et al.*, 2013).

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Fish are some of the most commonly introduced organism worldwide (Gozlan *et al*., 2010). Introduction of fish species threatens biodiversity by extinction or displacement of native species (Moyle & Leidy, 1992); reduction of spatial distinctiveness; or biotic homogenization within and across regions (Rahel, 2002; Olden *et al*., 2008). The main reasons for intentional fish introductions are aquaculture, pet trade, and stocking for recreation or food (Gozlan *et al*., 2010). *Piaractus brachypomus* (Cuvier) (Characiformes, Serrasalmidae), or Red Belly Pacu, is native to South America where it is widely distributed in floodplain rivers of the Amazon and Orinoco Basins. It is a large, long-lived species (up to 72 cm SL and 28 years in age; Loubens & Panfili, 2001), highly adapted to exploit floodplain resources where fruits and seeds are dominant items in the diet of both juveniles and adults (Knab-Vispo *et al*., 2003; Lucas, 2008).

Given its importance in the aquarium, aquaculture and sport fishing industries, *P. brachypomus* has been introduced in 14 countries of Asia, Europe, North and Central America, and Oceania (Cáleta *et al*., 2011; Froese & Pauly, 2013). A major introduction of 'Pacu' (along with seven other fish species) took place in the lower and middle Sepik-Ramu River Basin, northern Papua New Guinea (Oceania), between 1995 and 1997, as part of a fish stock enhancement project coordinated and sponsored by the United Nations (Coates, 1997). *Piaractus brachypomus* was selected for the stocking program because, in addition to the high quality of its meat, it was assumed that given its frugivorous habits it would fill empty niches with little impact on the ecology of the Sepik-Ramu indigenous fishes (Coates, 1993a, 1993b). Although this introduction was extensively planned, and the benefit for the local people heavily weighted (Coates, 1997), the evaluation of environmental risks is largely controversial (*e.g.*, Paxton, 1989; Coates, 1993a, 1993b). To date, there are no follow-up studies looking at the fate of *P. brachypomus* after its introduction in the Sepik-Ramu River (Dudgeon & Smith, 2006; Gehrke *et al*., 2011). The frequency with which *P. brachypomus* has been introduced worldwide gives broad relevance to ecological data from populations that are established outside their native range.

Here, we test the hypothesis that non-native *P. brachypomus* exploit allochthonous floodplain food resources in the Sepik River in the same way native populations do in their range (Coates, 1993a). First we describe the diet of introduced *P. brachypomus* from the Sepik River and then use a comparative approach to access potential diet shifts of the introduced population with respect to that of natural populations. This study provides much needed information on food resource use of introduced *P. brachypomus* that will help guide efforts to further evaluate ecological impacts on the Sepik's native floodplain fish fauna.

## Material and Methods

**Study area.** The Sepik is the longest river in Papua New Guinea (PNG, 1100 km long, 78000 km$^2$ catchment) and its lower reaches are interconnected with the lower Ramu River through channels and a shared floodplain (Dudgeon & Smith, 2006). The Sepik-Ramu River Basin is a near-pristine system containing 78 species of diadromous and primary freshwater fishes, most of which are derived from marine lineages (Dudgeon & Smith, 2006). This relatively low fish diversity, nearly half of that of the Fly River in southern PNG, is likely the result of a recent geological history and the lack of estuarine areas that are important as nursery grounds (Coates, 1993b; Dudgeon & Smith, 2006). Despite having an extensive floodplain (35000 km$^2$, Coates, 1997) covered with diverse aquatic macrophytes (Osborne, 1993) and swamp grasses and forests (Paijmans, 1975; Mitchell *et al*., 1980), few native fish species in the basin have adapted to exploit floodplain resources, another potential cause for markedly low fish yields (Coates, 1993b; Gehrke *et al*., 2011).

**Data collection.** Thirty specimens of *P. brachypomus* were sourced from the fish market at Angoram, East Sepik Province, located 60 km above the mouth of the Sepik River, in October 2007 (rising water season, Fig. 1). The market is located by the river shore and fish are sold directly by fishermen. Specimens were randomly selected from multiple fishermen to represent the range of sizes observed at the market. Based on interviews to fishermen, we were able to establish that fish were captured with gillnets in a nearby oxbow lake and in the Sepik River around Angoram. Whole fish (abdominal cavity injected with 40% formaldehyde) or excised stomachs were fixed in 10% formaldehyde after determining standard length (SL in mm). Specimens were deposited in the Auburn University Museum (USA) fish collection (AUM 47475).

Analysis of stomach contents was conducted on 29 specimens from the Angoram fish market. Stomach contents were observed under a dissecting microscope. Individual food items were separated, identified to the lowest feasible taxon, and quantified using volumetric and occurrence methods described by Hyslop (1980) and Winemiller (1989). The relative importance of different foods to the diet of *P. brachypomus* in the lower Sepik was assessed by calculating proportional volumetric contribution (%Vol) and frequency of occurrence (%FO) of each food type.

The diet of *P. brachypomus* from the Sepik River (160 - 340 mm SL) was then compared against that of 82 *P. brachypomus* from the Amazon (data sets 1 to 5) and Orinoco river basins (data sets 6 and 7; Fig. 1): 1) Tarapoto Lake, Colombia (rising waters, n = 8, 115 - 175 mm SL, S. B. Correa, unpublished data); 2) Caquetá River, Colombia (falling waters, n = 8, 310 - 380 mm SL, S. B. Correa, unpublished data); 3) Caquetá River, Colombia (low waters, n = 11, 290 - 340 mm SL, S. B. Correa, unpublished data);

4) Tocantins River, Brazil (downstream from Tucuruí Reservoir, n = 7, 120 - 270 mm SL, de Mérona *et al.*, 2001); 5) Tocantins River, Brazil (Tucuruí Reservoir, n = 32, 110 - 335 mm SL, de Mérona *et al.*, 2001); 6) Caura River, Venezuela (falling waters: n = 9, 130 - 320 mm SL, Knab-Vispo *et al.*, 2003); and 7) Caura River, Venezuela (low waters, n = 7, 130 - 320 mm SL, Knab-Vispo *et al.*, 2003). Fish from the Tarapoto Lake were collected between January to April 2007 and those from the Caquetá River between August to December 2009. Fishing was conducted during the day using gill nets. Fish were measured and dissected within an hour after capture. Stomachs were preserved in 70% ethanol.

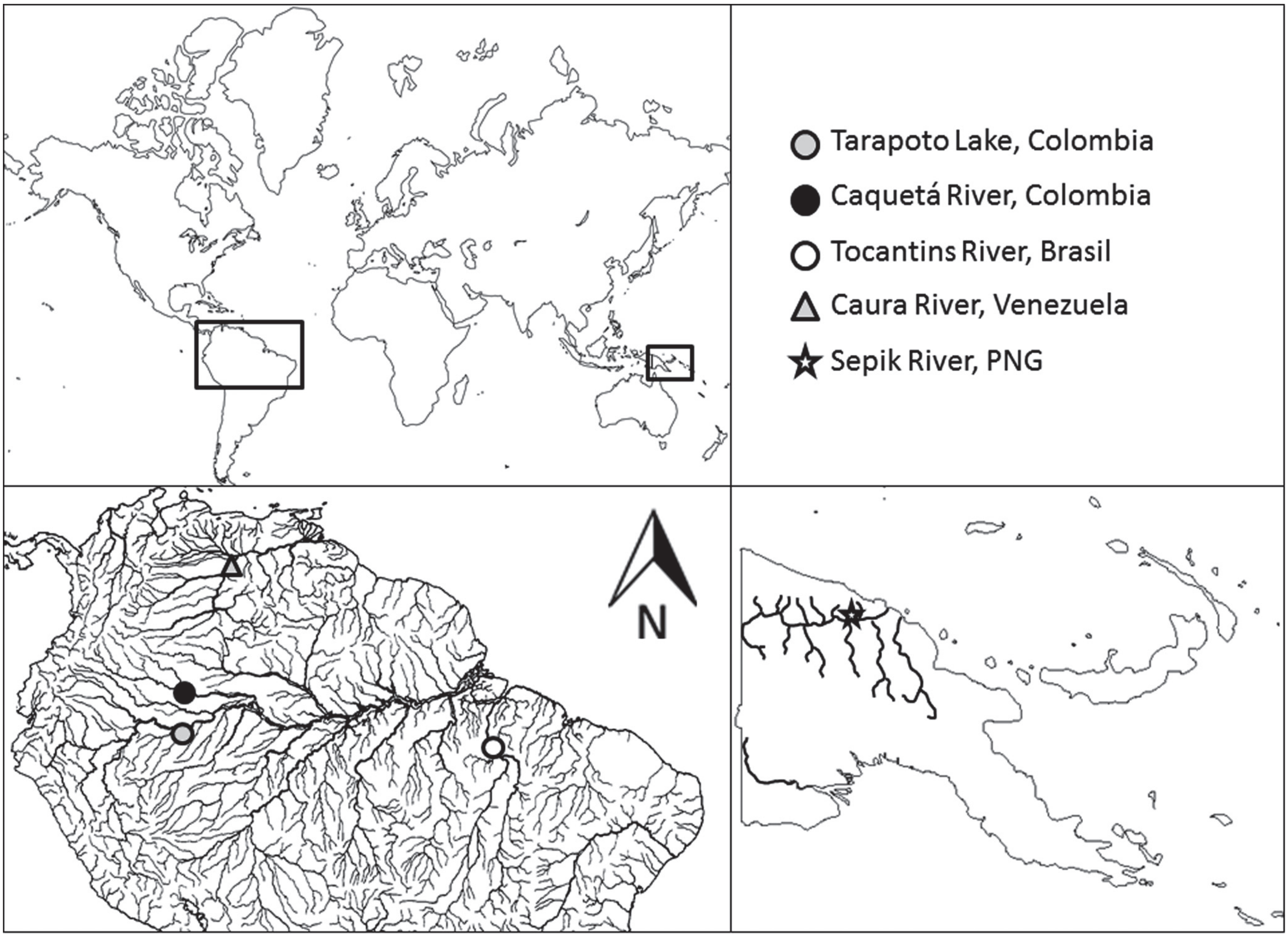


**Fig. 1.** Map of sampling site and locations of comparative studies. Circles represent sites in the Amazon Basin (Colombia: Tarapoto Lake and Caquetá River; Brazil: Tocantins River). The triangle represents a site in the Orinoco Basin (Venezuela: Caura River). The star represents the sampling site at the lower Sepik River, Papua New Guinea (PNG).

**Data analysis.** To facilitate comparison with other data sets, we combined several food categories observed in the diet of 'Pacu' from the Sepik (Table 1) into broader functional categories shared by all data sets (Fig. 2). Differences in the diet among the introduced and native populations were analyzed via Bray-Curtis (Polar) ordination of arcsine-square root transformed volumetric proportions of six broad food categories. Bray-Curtis ordination is particularly recommended over other ordination methods when the aim is to compare multiple groups with respect to reference points (McCune & Grace, 2002). Sepik and Tarapoto were selected as the reference points representing introduced and natural populations, respectively, as they were both sampled in the same hydrological season (rising-waters). The correlation between each food category and ordination axes was calculated using Pearson Correlation. The ordination and correlations were performed with PC-ORD ver. 6.0 (McCune & Mefford, 2011).

## Results

Sepik River specimens of *P. brachypomus* ranged from 160 to 340 mm SL (mean 229.7 ± SD 55.5, n = 30). This sample represents the range of sizes observed at the market and corresponds to first- and second-year juveniles, and third-year sub adults (Loubens & Panfili, 2001). The diet of juvenile *P. brachypomus* in the Sepik was composed of 28 different food resources, which comprise 11 broad food categories (Table 1). Fish remains and aquatic plant material can be considered main dietary categories based on their relative high volume and frequency of occurrence, while terrestrial plant material and fruits and seeds also were frequently consumed but in smaller amounts.

The large abundance of fish remains and aquatic plant material in the diet of introduced *P. brachypomus* contrasted with the diet of *P. brachypomus* in natural populations in which terrestrial plant material (mainly fruits and seeds) was the dominant food in all cases (mean ± SD: 80.2 ± 16.1 % volume) (Fig. 2). Other food resources consumed by natural populations included fish remains (8.9 ± 8.5 % volume), aquatic invertebrates (7.8 ± 9.5 % volume), and terrestrial invertebrates (1.7 ± 3.0 % volume) (Fig. 2).

Differences in the diet of *P. brachypomus* from the Sepik River in comparison with those from natural populations were reflected in the ordination, as the Sepik population was widely separated from all other populations (Fig. 3). The first two ordination axes accounted for 81.46% of the variance in the distance between populations. Axis one was positively correlated with the proportion of terrestrial plant material in the diet (r = 0.95, $P < 0.01$) and negatively correlated with the proportion of fish remains (r = -0.95, $P < 0.01$) and aquatic plant material (r = -0.88, $P < 0.01$). Distance between the Sepik and each of the other populations was consistently higher than the distance among all populations excluding that from the Sepik (average distance = 0.56 and 0.26, respectively, where larger values indicate a higher dissimilarity in the diet).

**Table 1.** Percentage frequency of occurrence (%FO) and volume (%Vol) contributed by 11 food categories to the diet of Pacu (*Piaractus brachypomus*) in the lower Sepik River, PNG.

| Food Item | % F | % Vol |
|---|---|---|
| *Autochthonous* | | |
| Aquatic plant material [leaves (including monocots), stems, and roots] | 65.52 | 26.89 |
| Fish remains (bones, scales, fin rays and guts) | 62.07 | 49.94 |
| Aquatic insects (Diptera: Chironomidae, Physicodidae) | 13.79 | 0.03 |
| Aquatic invertebrates (Decapoda) | 3.45 | 0.07 |
| *Allochthonous* | | |
| Terrestrial plant material (leaves, stems, and wood) | 93.10 | 8.17 |
| Fruit and seeds (9 taxa, plus unidentified fragments) | 37.93 | 9.89 |
| Terrestrial insects | 17.24 | 0.03 |
| Mammal remains (teeth and hair) | 6.90 | 0.18 |
| *Unknown origin* | | |
| Plant fibers and partially digested unidentified plant matter | 51.72 | 4.46 |
| Arthropod parts | 10.34 | 0.22 |
| Other (debris) | 6.90 | 0.11 |

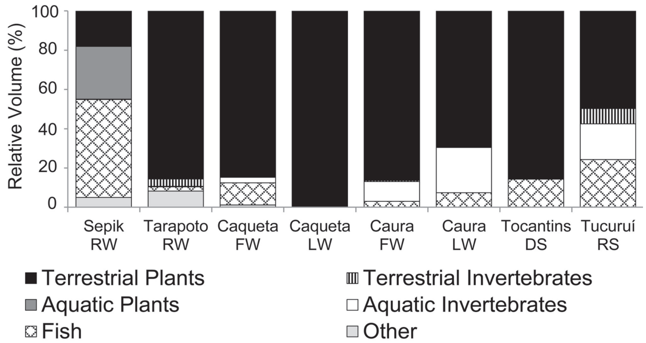


**Fig. 2.** Comparison of the relative contribution of food categories to the diet (% volume) of *Piaractus brachypomus* of introduced (Sepik River) and natural populations (Colombia: Tarapoto Lake and Caquetá River; Brazil: Tocantins River and Tucuruí Reservoir; Venezuela: Caura River). Food items included in each category are listed in Table 1. Category "Other" includes: mammals, arthropods, plant material of unknown origin, and debris (Sepik); detritus (Tarapoto); gravel (Caquetá FW). Abbreviations: FW, falling water season, LW, low water season; RW, rising water season; DS, downstream from reservoir; RS, reservoir.

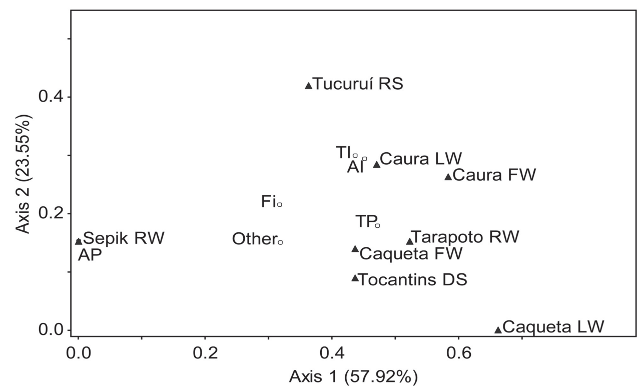


**Fig. 3.** Bray Curtis (Polar) ordination of arcsine-square root transformed volumetric proportions of food categories. Abbreviations: AP, aquatic plants; AI, aquatic invertebrates; Fi, fish remains; TP, terrestrial plants; TI, terrestrial invertebrates. Other includes: mammals, arthropods, plant material of unknown origin, and debris (Sepik); detritus (Tarapoto); gravel (Caquetá FW). Site abbreviations follow those in Fig. 2.

## Discussion

Our results do not support the hypothesis that *P. brachypomus* introduced into the Sepik River exploit allochthonous floodplain food resources as populations do in their native ranges. The diet of juvenile *P. brachypomus* from the Sepik River, principally composed of fish remains and aquatic plants, greatly differs from that of individuals in natural populations which prefer allochthonous resources, mainly fruits, seeds and other plant material (Knab-Vispo *et al.*, 2003; Lucas, 2008; Anderson *et al.*, 2009). The small volume accounted by fruits and seeds in the diet of 'Pacu' from the Sepik River may be influenced by low availability of these food items for a species that is highly adapted to feed on them. Unlike highly diverse South American floodplains forests, the lower Sepik River floodplain is characterized by swamp forests of variable canopy density that, although rich in species, are commonly dominated by few species (*e.g.*, *Campnosperma brevipetiolatum* Volkens, *C. auriculatum* Hook. f. (Anacardiaceae), *Melaleuca cajuputi* Powell (Myrtaceae) (Paijmans, 1975)). Hence, the Sepik floodplain may not produce as many fruits, or fruiting phenology may not be synchronized with the floods as occur in Neotropical floodplains (Parolin *et al.*, 2004). 'Pacu' from native populations rarely feed on aquatic plants (Goulding, 1980; Knab-Vispo *et al.*, 2003), but leaves and stems of such plants represented a large proportion of the diet of 'Pacu' from the Sepik. These findings support local people's claims that *P. brachypomus* are consuming aquatic vegetation causing declines in native floodplain fish populations (Gehrke *et al.*, 2011). Although the mechanism is unclear, it is possible that consumption of aquatic macrophytes reduces habitat for aquatic invertebrates resulting in lower food availability for native floodplain fishes. This possible indirect effect of the introduction of *P. brachypomus* is worrisome as most native floodplain fish species in the Sepik-Ramu system feed on aquatic insects and their larvae (Coates, 1993b).

Fish appear as a main food resource for the introduced population. Fish remains found among stomach and intestinal contents of *P. brachypomus* from the Sepik River included scales, fin rays, bones, and in few instances, visceral organs of other fishes. Scales were numerous and of different types and sizes, many of which were decaying (*i.e.*, brown and brittle), suggesting that 'Pacu' could have pick them up from the river bottom. Bones of various types and sizes included large vertebrae, mandibular and opercular elements, and teeth. Pieces of liver, stomach, and intestines of other fishes were also found among stomach contents of few specimens. The nature of these fish remains suggests carrion feeding instead of predation of other fishes. Protein-rich fish remains may have become an important part of the diet when other preferred foods are not available. In addition to nuts and seeds, other hard-shelled food resources such as snails, mussels, crabs, and crayfish, are important in the diet of *Piaractus mesopotamicus*, a sister species from the Cuiaba River (Paraná-Paraguay River Basin, Brazil) (Correa *et al. in prep.*). The ability of *Piaractus* species to crush hard foods is facilitated by strong jaws and a dentition composed of two rows of molar-like teeth. Far from hydrodynamic, the laterally compressed oval-shaped body of *Piaractus* species allows them to easily rotate up and down to pick foods from the water surface or the bottom, but it is not designed for speed to enable catching fast moving fishes. Such design constraints may help explaining why introduced *P. brachypomus* has opted for carrion feeding and not predation of other fishes. Interestingly, *P. brachypomus* is now called "ball cutter" among the local villagers purportedly due to few reported cases in which fishermen have been bitten in their testicles while wading in the water. Such cases have brought worldwide attention to the introduction of *P. brachypomus* into the Sepik River, including an episode of the popular television series "River Monsters" by Jeremy Wade and several news articles. We hope that such interest can be channelized into research to further investigate the biology of introduced *P. brachypomus*, its interactions with other species, and possible effects on floodplain ecosystem functioning in the Sepik-Ramu River Basin.

Although our sampling is limited (*i.e.*, one area during one season), our results suggest that juvenile and subadult 'Pacu' from the Sepik have shifted to a more generalized diet in comparison to individuals in native populations. Niche shifts are not uncommon following the natural expansion of a species distribution range, the colonization of new habitats, or habitat alterations (*e.g.*, Koch *et al.*, 1995; Wanink & Witte, 2000; Tobler, 2008). Despite the preference by both juvenile and adult *P. brachypomus* for foods derived from terrestrial plants (Knab-Vispo *et al.*, 2003; Lucas, 2008), the species is naturally adapted to live in a variable environment where annual hydrological fluctuation causes major shifts in the availability of food and other resources. Flexible foraging behavior may allow *P. brachypomus* to exploit novel resources in novel environments. This phenomenon has previously been observed in a reservoir population isolated by construction of a dam on the Tocantins River, Amazon River Basin. Within a year of dam construction, *P. brachypomus* in the Tucuruí Reservoir shifted to a more generalist diet relative to that of individuals caught downstream from the reservoir (See Fig. 2 and de Mérona *et al.*, 2001). De Mérona *et al.* (2001) argued that this dietary shift was influenced by changes in food availability. Similar diet shifts occurred among two omnivorous *Brycon* species in the Serra da Mesa hydroelectric dam, also on the Tocantins River (Albrecht *et al.*, 2009).

A plastic diet, large body size and longevity (up to 70 cm SL and 28 years; Loubens & Panfili, 2001), and the capacity to achieve large local abundances and wide distributions, are characteristics that, according to invasive species theory (Ruesink *et al.*, 1995; Moyle & Marchetti, 2006), may have contributed to successful establishment of *P. brachypomus* in the lower Sepik. One remarkable aspect of this establishment is that despite the complex long-distance migratory reproductive behavior of the species in its natural distribution (Barthem & Goulding 2007), *P. brachypomus* are successfully reproducing in this system. The extensive floodplain of the Sepik/Ramu River Basin likely provides conditions comparable to those in lowland South American rivers where migration and spawning occurs in the main river channel and floodplain habitats are important feeding and nursery grounds (Agostinho *et al.*, 2003, Araujo-Lima & Ruffino, 2003). Whether introduced *P. brachypomus* perform an annual reproductive migration in the Sepik/Ramu River Basin remains to be evaluated. In addition to increasing the chance of a species establishing itself in a foreign environment, trophic plasticity decreases our ability to predict negative effects on native species. Given that *P. brachypomus* are highly vagile and masticate and disperse intact seeds (Correa *et al*., 2007; Anderson *et al*., 2009), effects of *P. brachypomus* introductions can extend beyond native fishes to floodplain-vegetation recruitment dynamics and to other vertebrate frugivores. Species interactions across taxonomic groups are rarely accounted for when predicting and evaluating the effects of species introductions (Herbold & Moyle, 1986; Spencer *et al*., 1991). The absence of follow up studies after the introduction of *P. brachypomus* in the Sepik-Ramu system (Dudgeon & Smith, 2006; Gehrke *et al*., 2011) precludes our understanding of how the species became established in this new environment. We do not know if the diet shift occurred gradually or abruptly, however it is likely that trophic plasticity has played a pivotal role in allowing the species to use available food resources and obtain energy necessary to survive, reproduce and become established. To further evaluate the ecological impacts of *P. brachypomus* upon native fish, future studies should focus on characterizing the feeding ecology of juveniles and adult *P. brachypomus* and co-occurring species in multiple habitats through the annual hydrologic cycle. Given the recent introductions of fishes that have occurred in the Sepik-Ramu River, which is known for its unique geological history and evolutionary and ecological features, this system provides an opportunity for studying direct and indirect effects of species introductions on complex interactions in geographically isolated, minimally impacted systems.

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