Biodiversity Impacts Across Time and Space: The Case of the Introduced Piscivore, *Cichla monoculus,* in Panama

Meagan Deviaene[1] and Karling Roberts[2]

[1]McGill University Department of Microbiology 3775 University St., Room 511 Montreal, QC H3A 2B4
[2]McGill University School of Environment 3534 University St., Montreal, Quebec H3A 2A7

Report for Smithsonian Tropical Research Institute:

Diana Sharpe
Smithsonian Tropical Research Institute Fellow
NAOS Laboratories
Panama City, Panamá
Phone: +507.212.8840
E-mail: sharped@si.edu

Number of Days Spent of Project: 38
Number of Days Spent in the Field: 15

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For: Diana Sharpe, *STRI Fellow, NAOS Laboratories, Panama City, Panamá*

Context. Freshwater ecosystems, especially reservoirs, provide excellent habitats in which to study anthropogenic effects. Humans dictate the physical environment of these milieus with their construction, and their biotic composition with introductions of a nonindigenous species purposely translocated for economic, social, or other gains. Introductions often set the course to invasion where the introduced species "cause(s) economic or environmental harm or harm to human health". Panama is especially susceptible to this threat, as 3 of its largest lakes are man-made reservoirs and two of which are components of the Panama Canal, allowing a wider distribution of the introduced and invasive species.

Peacock bass (*Cichla monoculus*) is a piscivorous predator that is native to the amazon river basin but has been frequently introduced to other regions with the goal of improving artisanal and recreational fishing. Peacock bass were introduced in Panama in 1967. By 1970 they were identified in lake Gatún, and by 1973 had invaded all parts of the lake except for the Trinidad arm (the southwest arm). These early stages of the introduction were monitored by Zaret and Paine who found that in the area of Lake Gatún invaded by peacock bass, 7 of 11 previously abundant species had been eliminated, and 3 more were reduced. Only one native species increased in abundance, likely due to the demise of its natural predators. Since this occurrence, introductions of piscivores including those of the *Cichla* genera have been shown to reduced richness, diversity and abundance of the native fish community.

Goals. In this study, we repeat Zaret and Paine's sampling techniques in the same locations in order to determine the long-term effects of peacock bass invasion on fish communities. Additionally, we compare the fish communities in two invaded lakes, Lake Gatún and Lake Alajuela, and one non-invaded lake, Lake Bayano, in Panama. We intend to establish an understanding of the effects of the introduction of this species in Panama, both through time and space.

Methods. Fish communities from three large reservoirs were sampled repeatedly through the wet and dry seasons. Two methods were used in order to obtain a representative sample of different sizes of fish making up the communities at each site, as well as to properly reproduce the historic methods to which we have compared our data. Beach seining was replicated, consistent with the methods of Zaret and Paine, and in the same sampling sites. Gill nets were used, consistent with the method of Gutiérrez *et al.* (1995) in order to compare to this historic data. In addition, the specimens collected with both beach seine and gill nets were used to make comparisons between study lakes. Four biodiversity indices, Species Richness, Shannon's Index, Simpson's Index, and the Berger-Parker Dominance Index were calculated for each method at each lake, as well as a catch per unit effort to deduce abundances. This was repeated considering only the native species.

Results. The long-term impacts of *C. monoculus* showed that since 1972 there has been a severe reduction in the diversity and abundance of the species that inhabited the littoral zone before the introduction of *C. monoculus,* as well as a reduction of *C. monoculus* populations. When the fish community samples acquired with gill nets in Lake Gatún and Lake Alajuela were compared to samples collected in 1994, disappearances and appearances and species were found to have occurred, with appearances occurring for both native and non-native species. The appearances of native species in 2014 samples may have been caused by increased sampling effort and slight differences in gill net mesh size, while the appearances of non-native species are hypothesized to be caused by intentional and unintentional introductions. It is also hypothesized that the disappearances represent actual extirpations or severe reductions in the abundances of those species.

When samples of the littoral zone-associated fish community were sampled in lakes Gatún, Alajuela, and Bayano, we found that the abundance, evenness and species richness of fish captured was much lower in lakes Alajuela and Gatún than in lake Bayano. However, when the fish community was sampled with gill nets, a different trend was found. Results acquired with gill nets still showed drastic reduction in fish abundance in Lake Gatún and Lake Alajuela compared to Lake Bayano, however both Lake Gatún and Lake Alajuela showed greater species diversity and evenness than Lake Bayano. The analysis was repeated considering only the native species and yielded the same results.

Conclusions. The long-term impacts of *C. monoculus* suggest that it extirpates or greatly reduces the abundance of diurnal species that inhabit the littoral zone. As such, we recommend that *C. monoculus* should not be introduced into ecosystems outside of its range which have species assemblages in this area that are desirable to keep. As for how *C. monoculus* impacts the nocturnally active, nearshore species community, it is clear that their abundance may be negatively impacted, however more of these species may be able to co-exist with *C. monoculus* facilitated by differential habitat use, either in space or in time. Further investigation into the sizes of these surviving populations, as well as the characteristics that allow them to co-exist with *C. monoculus* in Lake Gatún and Lake Alajuela are valuable in determining which communities might or might not be amenable to the introduction of Peacock bass.

Many introductions which have led to harmful invasions have been unintentional, making them very hard to avoid. In light of this and the likelihood that such accidents will continue into the future to the detriment of regional and global biodiversity, it is the responsibility of everyone to utilize the information regarding the potential harm caused by introduction of species leading to invasion, and further which cases prove disastrous, or beneficial. We hope that the current study can assist in building the knowledge base necessary to make responsible decisions about species introductions especially within highly threatened systems such as freshwater ecosystems.

HOST INSTITUTION

The Smithsonian Tropical Research Institute is a bureau of the Smithsonian Institute outside of the United States that was established in 1923 with the goal of documenting and understanding biodiversity in the neotropical environment of Panama. At the time of its founding, it consisted only of a small field station on Barro Colorado Island, a landmass of 15.2 square kilometers created when the Chagres River was dammed, flooding the surrounding area in the creation of the Panama Canal.

Since then, the organization has expanded now encompassing a network of 11 principal research facilities in the Republic of Panama, including 3 main marine research stations on the Atlantic and Pacific coasts, and a canopy crane. Making use of these services are 900 visiting scientists a year and 38 permanent staff scientists. Training of future leaders in the field is emphasized, and a range of university field courses have been hosted through STRI, from universities such as Princeton, McGill, University of Florida, Michigan State, Florida Atlantic, University of Panama, Organization for Tropical Studies, and Union College.

A strong relationship with the Republic of Panama, STRI's host nation, was formalized in the Panama Canal Treaties of 1977. This relationship was renewed and extended in 1985 when Panama granted STRI the status of International Mission, and again in 1997 when the country offered custodianship of STRI facilities beyond the termination of the Panama Canal Treaties. STRI's relationship with the Republic of Panama continues to be of central importance.

Long term ecological terrestrial and oceanic monitoring studies are a focus of the work done at STRI. For example, permanent forest plots have been established in 15 tropical countries to document tree demography, and monitor the consequences of landscape transformation on forest integrity in the central Amazon region. On the marine end, scientists are conducting a global survey of levels of genetic isolation in coral reef organisms.

The overarching goal behind all research done at the Smithsonian Tropical Research Institute is described by its mission statement: "To increase understanding of the past, present and future of tropical biodiversity and it's relevance to human welfare."

INTRODUCTION

Globally, the rate of biotic exchange has increased due to improvements in transport systems and globalization of economic activities (Mack *et al*. 2000). These exchanges, which may be intentional or unintentional, often set the course for invasion, where invasion is defined as 'a non-indigenous species whose introduction does or is likely to cause economic or environmental harm or harm to human health' (National Invasive Species Council 2003b). Although The term ''invasive'' has been used to describe (1) any introduced non-indigenous species; (2) introduced species that spread rapidly in a new region; and (3) introduced species that have harmful environmental impacts, particularly on native species (Ricciardi and Cohen, 2007), for the purposes of this report the aforementioned National Invasive Species Council (2003b) definition will be used. In addition, for the remainder of the paper the term 'introduced species' will refer to a non-indigenous species purposely translocated into an area for the purpose of economic, social, or other gains.

Invasive species are now considered one of the most significant threats to global biodiversity, second to habitat loss (Simberloff 2003). In the United States, invasive species are partly or fully responsible for the extinction or imperiled status of 49% of species that fall under these descriptions (Wilcove *et al.* 1998). When discussing freshwater ecosystems, invasive species threaten their diversity and function, and magnify the impacts of other anthropogenic assaults (Wilcove *et al.* 1998; Simon and Townsend 2003). It has been found that for freshwater ecosystems, biotic exchange is the most important driver of biodiversity change (Sala *et al.* 2000) and invasive species the most important cause of extinction (Lodge 2001). This is significant, given than over 20% of freshwater fishes may be threatened or endangered (Kaufman 1989; Williams and Nowak 1986).

Freshwater biodiversity is particularly vulnerable to the impacts of non-indigenous species because of the high occurrence of endemic species, and because of the role freshwater ecosystems play in global trade and transit routes, food production, and commercial and recreational fishing. Many non-indigenous freshwater species have been introduced intentionally. The majority of these introductions have been for or because of aquaculture, but a large number have also been for recreational and commercial fishing (De Silva *et al.* 2006; Gozlan 2008). Introductions of species desired for recreational and commercial fishing have been known to have detrimental impacts on the host ecosystem, as these species are often top predators. Many studies have shown the catastrophic consequences that non-native predators can have on native biota (Zaret and Paine 1973; Kaufman 1992; Witte *et al.* 199; Moyle and Light 1996; Macchi *et al.* 1999; Gratwicke and Marshall 2001; Townsend 2003; Eby *et al.* 2006), including dramatic losses of biodiversity and increased top-down effects, at times impacting the entire ecosystem. In terms of the composition of the reservoir biota, the establishment of exotic predators typically leads to one of two outcomes: replacement of native predators or an increase in predator species richness (Eby *et al.* 2006). Changes in the food web often comprise increased top-down control, novel food-web linkages, modified food-web linkages, as well as potential for either increased or decreased coupling of habitats and ecosystems. High stocking rates of predatory sports fishes have often resulted in an elevated abundance of top predators, leading to a potential imbalance between predator consumption and prey abundance (*abid.*).

Although invasive species can result in extremely harmful consequences for global biodiversity, Gozlan (2008) points out that on the global scale, the majority of freshwater fish introductions are not identified as having an ecological impact while having great societal benefits. Introductions of new species for aquaculture, for example, are responsible for a large number of these overall beneficial introductions. However, given the dramatic and harmful impacts that invasive species have, a current need is the ability to discern the harmful, invasive, species from those introductions which deliver beneficial outcomes for society without harming biodiversity.

Peacock bass, the common name of a group of species of the genus *Cichla,* are a highly sought after game species. They are piscivorous predators, lacustrine-adapted, and highly productive in man made reservoirs (Fernando 1991). Species of the genus *Cichla* are native to the amazon but have been frequently introduced to ponds, lakes, and reservoirs with the goal of improving artisanal and recreational fishing (Agostinho *et al.* 2004). However, these introductions of peacock bass have often resulted in large declines in native fish diversity and abundance (Zaret and Paine 1973; Menezes *et al.* 2012). The short-term impacts of introduced peacock bass on their host ecosystems and fish communities have been well studied, and are reviewed below.

Pelicice and Agostinho (2009) found reduced richness and diversity of the native fish community due to introduction *Cichla kelberi* into the Parana River basin, Brazil. A 95% decrease in mean fish density and an 80% reduction in mean fish species richness was observed. In addition, they predicted complete assemblage extinction by the summer of 2010.

Menezes *et al.* (2012) found the similar impacts to Pelicice and Agostinho (2009) on fish species richness in Brazilian lakes, but no significant differences were noted in total fish catch per unit of effort. This study also investigated impacts on the zooplankton and phytoplankton biomass, plankton diversity and the zooplankton:phytoplankton biomass ratio, but found no significant differences between lakes with and without peacock bass.

Interestingly, Latini and Petrere (2004) found that when many species, namely *Cichla cf. monoculus* & *Astronotus ocellatus* and *Pygocentrus nattereri* , are introduced alongside one another there are no significant differences in overall community diversity between reservoirs with the introduced species and reservoirs without them. However, when they compared only the composition of the native fish community, all the lakes with alien fish species had lower native species richness than lakes without alien species.

Another interesting finding is the apparent lack of a refugia function as a means of evading peacock bass by prey species. That is, vegetated habitats provide very little protection from predation by the peacock bass (Kovalenko *et al.* 2010; Latini and Petrere 2004). This is in contradiction to other findings that suggest that machrophytes create habitat complexity, which in turn creates refugia for prey species from predation (Sih 1987; Dibble *et al.* 1996; Stuart-Smith *et al.* 2007). It is believed the refugia function does not apply to peacock bass due to its utilization of these areas, in particular for reproduction (Latini and Petrere 2004).

Vieira *et al.* (2009) found that environmental variables did not directly influence the reproduction of *Cichla piquiti.* This species seemed to be well reproductively adapted to its non-native Neotropical reservoir environment, which displays significantly different climate conditions from its original habitat. The fish showed no statistically significant sexual dimorphism in size, and no interference from the annual hydrology cycle on health condition. The species presented plasticity in reproduction and in allocation of resources, enhanced by the aseasonality of the reservoir and its exploitation of native species.

Another documented effect of peacock bass introductions are impacts on the diets of the previous dominant predator of the ecosystem. Fugi *et al.* (2008) investigated the trophic interaction between *Cichla kelberi* (Peacock bass) and *Galeocharax knerii* (Dogfish) in the Corumba reservoir in Goias State, Brazil between 1997 and 2000. Niche breadth and overlap were assessed during periods of absence or low abundance of peacock bass (I) and periods of high abundance of peacock bass (II and III). Dogfish displayed greater niche breadth during periods of low peacock bass abundance (Period I), and the lowest niche breadth was observed during Period II. Within the same period, the peacock bass demonstrated a broad foraging niche. During Period III, the dogfish showed an increase of its niche breadth, while the peacock bass showed a simultaneous decrease in niche breadth, due to an increase in cannibalism. Taken together, this indicates that pressure from the peacock bass has induced the dogfish to assume changes in their diet, most likely due to a deficiency in their previous food source.

Cichla monoculus, a species of peacock bass, was introduced to the Chagres River in Panama in 1967 (Panama Canal Review 1971). By 1970 the predators were identified in lake Gatún, and by 1973 had invaded all parts of the lake except for the Trinidad arm (the southwest arm) (Zaret and Paine 1973). The immediate effects of these peacock bass invasions on native fish communities was well documented. Zaret and Paine (1973) reported that in the area of Lake Gatún invaded by peacock bass, 7 of 11 species that were abundant before the arrival of *C. monoculus* had been eliminated, and 3 more were reduced. Only one native species increased in abundance, likely due to the demise of its natural predators. They additionally reported many second and third- order changes at other trophic levels of the ecosystem, for example a decrease in the bird community feeding on small fish, and changes in the zooplankton community.

Zaret and Paine (1973) were able to document the immediate effects of *C. monoculus* on lake Gatún's ecosystem, however this, and most other studies on the impacts of peacock bass on their host ecosystems and fish communities, do not describe the long term impacts of this invasive piscivore. The current study aims to describe quantitatively the long-term impacts of *C. monoculus* on its host fish community in lake Gatún, through comparisons of the current fish community with that reported by Zaret and Paine in 1973 and before the invasion. A similar sampling technique will be used in the same sampling locations in order to make these comparisons. Studies in which long-term impacts of invasive species can be quantified are rare, since data of the ecosystem before it was invaded is often lacking. Therefore, studies such as the current one are extremely valuable, especially in freshwater ecosystems which are highly threatened by invasive species (Sala *et al.* 2000).

A survey of the fish communities in Lake Gatún and Lake Alajuela was performed in 1994. Comparisons of our data with this data set were performed in order to asses changes taking place in the fish communities of these lakes. Although this comparison does not demonstrate the effects of *C. monoculus* on fish communities, it aids in understanding the history of the fish communities in these lakes and how they are changing through time.

Finally, we will be comparing the fish communities in two invaded lakes, Lake Gatún and Lake Alajuela, and one uninvaded lake, Lake Bayano, in Panama. This will offer quantitative data on how these fish communities differ in Panama, and will add to the previous work showing how peacock bass impact fish communities outside of their native range.

It is hypothesized that the long-term impacts of *C. monoculus* on the fish community in Lake Gatún will be a decrease in abundance and species richness. The hypothesized difference between the short-term impacts and long term-impacts are that further decreases in fish abundance and diversity will occur, and that the abundance of *C. monoculus* will also decline. We expect these results because as *C. monoculus* removes species from the community through predation, its feeding will be more highly concentrated on the smaller number of species that remain, placing even higher extinction pressure upon them. In addition, *C. monoculus* may have indirect effects on some fish species through competition or the spread of disease, which may not be noticeable in the short term data but could be revealed in the long term data. Finally we expect a decrease in the abundance of *C. monoculus* because as it erodes its potential food sources, fewer individuals of *C. monoculus* will be able to be supported. Since *C. monoculus* is still present in Lake Gatún we expect to find that some prey species have been able to co-exist with the introduced predator.

When investigating the differences between the fish communities in Lake Alajuela and lake Gatún, between 1994 and 2014, we expect to find only small differences between the two sampling periods. The impacts of a specific perturbation are not being investigated in this analysis. Instead, the goal of this exercise is to compare how the current fish communities in Lake Gatún and Lake Alajuela have changed through time, and data from 1994 is what is available to us. Changes that are observed between the two time periods could be allocated to a number of changes which have occurred over the past 20 years, which will be discussed.

Finally, it is hypothesized that the fish communities in Lake Alajuela and Lake Gatún will show less abundance and less diversity that the fish community in lake Bayano, as observed in the aforementioned studies. This is because lake Bayano does not have *C. monoculus,* and therefore its small fish species and the young of larger fish species are relieved from the intense predatory pressure that we assume *C. monoculus* is placing on these fish in Lake Gatún and Lake Alajuela.

METHODS

Study sites

Fish communities from three large reservoirs in Panama were sampled (Table 1). Two reservoirs, Lake Gatún and Lake Alajuela, have had *C. monoculus* introduced while one reservoir, Lake Bayano, does not have *C. monoculus.* One to four locations in each lake were selected as sample sites which were repeatedly sampled throughout the wet and dry seasons (Table 2). Sites were chosen based on accessibility and correspondence with sites that were sampled historically by Zaret and Pain (1973) and Gutiérrez *et al.* (1995).

Sampling

Two methods of sampling were used in order to obtain fish community data comparable to the two historical sources, and to make cross-lake comparisons. In order to make comparisons with data collected by Zaret and Paine (1973) around Barro Colorado Island (BCI) and Cuipo, and to make comparisons between the littoral zone-associated fish communities of the study lakes, a 10 X 2.5m beach seine with 1.27cm diameter mesh was used to sample shallow waters around the shores of the lakes during the dry season (January - April). Sampling was performed with the beach seine by securing one end to the shore while the other end was extended perpendicular to the shoreline to its full length or until water became too deep to walk. The net was then dragged in an arc back to the shore, creating a quarter-circle shaped area that was swept by the net. Catch was identified to species on site and then put on ice to be preserved for further processing or photographed and released.

In order to make comparisons with data collected by Gutiérrez *et al.* (1995) and to make cross-lake comparisons of the fish communities active in the evening, night and morning in areas near the shore, gill nets were used during the wet (June - December) and dry (January - April) seasons to sample near shore waters, 2 - 6 m deep. Gill nets were 50m long with 6 panels of mesh ranging in size from 1.27-7.62cm. Three gill nets were set at each sampling site and allowed to soak overnight for 15-18 hours. Each sampling site was sampled during both the wet and the dry season, and this data was combined for our analyses.

Temporal Data Analysis

Two historical studies exist with which modern data on fish communities in Panama impacted by *C. monoculus* can be compared. The first is Zaret and Paine (1973), which described the immediate impacts of invasion by *C.monoculus* on the fish community around BCI. In addition, they described the differences in community structure between a part of the lake near the town of Cuipo, which was not yet invaded, and locations around BCI, which had recently been invaded. Fish community data collected by beach seining was used to calculate comparable catch per unit effort (CPUE) and Species Richness indices for the two sampling sites, and comparisons were made through time. Comparisons of CPUE revealed how the fish community at each site differs and has changed through time. Finally, comparisons of how the fish communities in Cuipo and BCI have changed from prior to invasion to currently were conducted. Changes recorded during the period of invasion (1966-1972) documented by Zaret and Paine were compared to the changes observed in the fish community measured currently in order to illustrate the differences and similarities between the short and long term impacts of *C. monoculus* on fish communities.

The second historical study was done by Gutiérrez *et al.* (1995) at sites in Lake Gatún, Lake Alajuela. Fish community data collected with gill nets was used to calculate comparable Species Richness indices for Lake Gatún and Lake Alajuela. In addition presence-absence data from 1994 and 2013-2014 were compared in order to analyze if changes in species composition have taken place over the last 20 years.

Spatial Data Analysis

Fish community data collected with both beach seine and gill nets was used to make comparisons between study lakes. Rarefraction curves were calculated using the Bootstrap method in order to ensure that the sampling performed at each lake was adequate. Four biodiversity indices, Species Richness, Shannon's Index, Simpson's Index, and Berger and Parker's Dominance Index were calculated for each lake. Calculations were made separating the fish community data obtained using gill nets, from the data collected with the beach seine. Calculations were also made with all species captured, as well as for only native species captured, in order to understand how *C. monoculus* impacts the different parts of the fish community targeted by each gear and the entire fish community as well as the native fish community. Multiple biodiversity indices were appropriate for the current study in order to gain a more comprehensive understanding of how the introduced piscivore, *C. monoculus,* impacts the various aspects of fish community biodiversity. In addition, CPUE for both beach seine and gill net catch was calculated for each lake.

RESULTS

***Long term impacts of* C. monoculus**

Comparisons between the fish communities detected by Zaret and Paine (1973) in 1972 and those detected by the current data, show differences in species richness, abundance, and community structure. CPUE near BCI in 1972 was much lower than CPUE near Cuipo in 1972, and CPUE at both BCI and Cuipo in 2014 are two orders of magnitude lower than in the same locations in 1972 (Figure 1). In addition to an overall decrease in CPUE, CPUE for most species decreased between 1972 and 2014, with CPUE for many species going to 0 (Table 3). The only species whose CPUE increased in 2014 were species that were not captured in 1994.

In Zaret and Paine (1973), *C. monoculus* was found to have eliminated 4 of 7 previously abundant fish species around BCI and to have severely reduced the abundance of 2 other species over a time span of 6 years (Table 4). When a similar analysis is done for the fish species in Cuipo, comparing data from 1972, before *C. monoculus* invaded, to data collected in 2014, up to 40 years after *C. monoculus* invaded, similar drastic decreases in species abundances occurred. 10 of 11 species captured in Cuipo in 1972 were not caught in 2014 samples. The one species that did reappear in 2014 samples, *Astyanax reberrimus,* was drastically reduced (Table 5). Of the three other species captured in 2014 samples, *Hoplias microlepsis* is a native species, *Oreochromis niloticus* is an introduced species, and *Athrinella sp.* is a marine sardine, a species which likely entered Lake Gatún through the Panama Canal's locks. It should be noted that although not captured in our beach seine samples, *Roeboides guatemalensis* and *Gobiomorus dormitor* still persist in the area as they were captured by gill net in 2014.

When comparing the samples taken at BCI in 1972, after *C. monoculus* had invaded, to those taken in 2014, further reductions in species richness and abundance appear to have occurred. Four of the six species that remained in the area in 1972 after the introduction of *C. monoculus,* were not caught in 2014 samples. The two species that were recaptured, *C. monoculus* and *Poecilia mexicana,* were drastically reduced (Table 6). The two other species captured at BCI in 2014, *O. niloticus,* and *Mesonautus festivus*, are both introduced species. Similar to in Cuipo, *R. guatemalensis* and *A. ruberrimus* were not captured in our beach seines but were captured in gill nets set around BCI in 2014.

Therefore the long-term impacts of *C. monoculus* on the littoral zone-associated fish community in Lake Gatún were similar to the short-term impacts in that in both cases fish abundance and species diversity decreases. The long-term impacts were different in that some species that persisted through the first few years after introduction were lost in the long term, and the reductions in fish abundance were much greater. In addition, a decrease in *C. monoculus* also occurred whereas the short-term impacts are an increase in the abundance of *C. monoculus.*

Fish community changes over 20 years

When fish community data collected using gill nets in 1994 is compared to fish community data collected with gill nets in 2014, differences in the species composition and species richness of the communities are revealed (Table 7). In Lake Gatún, Species Richness increased from 9 to 19 between the two sampling periods. In Cuipo, Species Richness increased from 5 to 9. Finally in Lake Alajuela, species richness remained the same (Figure 2). In Lake Gatún 3 of the 9 species caught in 1994 appeared in 2014 samples. In Lake Alajuela, 4 of the 10 species caught in 1994 appeared in 2014 sampled. Therefore, in Lake Gatún 14 species not previously detected occurred in 2014 samples and in Lake Alajuela 6 previously undetected species occurred in 2014 samples. Of these previously undetected species, 5 in Lake Gatún and 3 species in Lake Alajuela are either introduced species or marine fish species which have entered Lake Gatún through the canal's lock system.

Impacts of* C. monoculus *across space

Sampling Adequacy

A species rarefaction curve was used to deduce sampling adequacy at each sample lake. Rarefraction curves for each lake reached an asymptote (Figure 1), and we therefore assumed the sampling effort in all three lakes was adequate.

S*pecies Richness*

1,577 Individuals were captured across the 3 study lakes, encompassing 28 different native and introduced species. Species Richness was greatest in Lake Gatún with 21 different fish species observed, followed by Lake Bayano, with 13 species and Lake Alajuela with 12 species (Figure 3). Eight of the species encompassing the richness in Lake Gatún are non-indigenous, four in Lake Alajuela and only one in Lake Bayano. Therefore the Species Richness of the native fish community is 13, 8, and 11, for Lake Gatún, Lake Alajuela, and Lake Bayano, respectively.

CPUE

The CPUE was the lowest in the lakes where the peacock bass was introduced (Table 8), for both the gill net and beach seine gears, with an increase of 1500% in the catch per unit effort in lake Bayano compared to lake Gatún. This indicates a greater abundance of fish in lake Bayano when compared to affected lakes (Figure 4).

Biodiversity

When Shannon's Index is calculated for all species captured using data collected by gill nets, the results suggest that Lake Gatún has the highest diversity and evenness, followed by Lake Alajuela then Lake Bayano (Figure 5). The same trend is observed when Simpson's Index is calculated using gill net data (Figure5). When the Berger-Parker Dominance index is calculated using gill net data, we see the Lake Bayano has the least even community, followed by Lake Alajuela then Lake Gatún. When the indices are calculated for species captured using beach seine data, Shannon's index is highest for Lake Bayano, followed by Lake Gatún then Lake Alajuela. When Simpson's index is calculated using this data, Lake Bayano has the highest index followed by Lake Alajuela then Lake Gatún.

Shannon's Index and Simpson's Index for the native species community captured with gill nets were highest for Lake Gatún, followed by Lake Alajuela then Lake Bayano. The Berger-Parker index suggested the same results as the Shannon's and Simpson's indices, with Lake Bayano having the lease even community and Lake Gatún have the most even community. When these indices were calculated for the native species community captured by beach seine, biodiversity was found to be highest in Gatún, followed by Bayano and then Alajuela.

DISCUSSION

Long-term impacts of **C. monoculus**

The findings of the current study suggest that the long term impacts of *C. monoculus* on the littoral zone-associated fish community is an extreme decrease in abundance and a decrease in biodiversity. These impacts are deducted from a decrease in CPUE of 2 and 3 orders of magnitude and the complete or near complete loss of 8 and 10 species around BCI and Cuipo, respectively, compared to their pre-*Cichla* state from over 40 years ago. These findings were expected, as *C. monoculus* is a voracious predator with a wide diet breadth, known to be cannibalistic (Novaes *et al.* 2004).

In addition to the changes to the fish community likely caused by interactions between *C. monoculus* and other species, our data show that other, anthropogenic, perturbations have been impacting the littoral zone fish communities in Lake Gatún. One such perturbation is additional introductions of non-indigenous species by humans as well as the entrance of marine species into the lake through the Panama canal's lock system. One such introduction was of *O. niloticus,* the nile tilapia, which now comprises the largest portion of the fish biomass currently inhabiting the littoral zone around BCI and Cuipo. Another introduced species, *Mesonautus festivus*, is a common ornamental fish for freshwater fish tanks, and was described in Lake Gatún for the first time as recently as 2006 (Rigoberto Gonzalez, *personal communication*). Finally the individual fish from the genus *Athrinella* which was captured in Cuipo is a marine sardine, likely having entered the lake through the canal's locks. Therefore lake Gatún's fish community is a continuously changing system, to which introduced species can be added to supplement lost biodiversity and abundance. However, so far, no new species have been able to reach densities similar to those of the species present before *C. monoculus* invaded Lake Gatún. Furthermore, what biodiversity has been replaced within Lake Gatún by non-indigenous species cannot make up for the losses of biodiversity that occur at the regional or global scales when native populations are lost.

Although many species appear to have been extirpated from lake Gatún, some have been able to persist and co-exist at low densities with *C. monoculus.* Such species include *R. guatemalensis, G. dormitor,* and *A. reberrius.* A similar situation was the case in Lake Victoria, where *Lates niloticus,* the nile perch, was introduced, to the detriment of hundreds of endemic haplochromine cichlid species (Witte *et al.* 1992). In Lake Victoria, although an estimated 200 species of cichlids went extinct, some species were able to persist alongside the nile perch. An important factor associated with which species were extirpated and which could co-exist with the nile perch was the amount of habitat overlap species had with the introduced predator. Species whose preferred habitat was similar to that of the nile perch were those that were extirpated. This was demonstrated by the near complete loss of demersal fish biomass after the introduction. Contrastingly, species that were able to persist have a preferred habitat that does not overlap with the nile perch, such as the littoral zone (Witte *et al.* 2000). A similar phenomenon may be taking place in Lake Gatún, with the habitat use of species that have been able to persist having little spatial or temporal overlap with *C. monoculus.* For example, based on observations made during the current sampling period, it is believed that *R. guatemalensis* is mainly active in the night, whereas *C. monoculus,* as a visual predator, prefers to hunt during the day.

Alternatively, species who have persisted in Lake Gatún along with *C. monoculus* may have adapted to the novel predators through changes in life history traits. The ability of a native species to adapt to fishing pressure and the nile perch through changes in life history traits was observed in Lake Victoria basin (Sharpe *et al.* 2012). That *A. reberrimus, R. guatemalensis,* and *G. dormitor* have all been detected in either BCI or Cuipo in 2014 with gill nets but not with beach seine suggests that perhaps these species have changed their habitat use, either temporally or spatially, in response to pressure from *C. monoculus.* Investigations of habitat use by species that have persisted and of other life history characteristics that may have adapted in order to increase survival and fecundity in light of the predatory pressures placed on them by *C. monoculus* could shed light on how these species, and not others, are able to co-exist with the introduced predator.

Although the invasion by *C. monoculus* likely played a major role in the extirpation of a number of species in Lake Gatún and in the large decrease in overall fish abundance, other factors may also be playing a role in these changes. Lake Gatún is a reservoir formed to provide the majority of the water needed for the Panama Canal, and as such is a highly perturbed system. A major trade route passes through Lake Gatún, therefore large cargo ships as well as other boat traffic are constantly passing through the lake. Past experience with canals such as the Erie, Welland, and Suez canals has shown that major biological changes occur to the freshwater ecosystems connected to them over long time spans, and the impacts might not be felt or noticed for many decades (Aron and Smith 1971). Furthermore, construction in and around the canal, such as the lock expansion currently underway, have had drastic effects on the turbidity of the water in much of the lake, and may be having other environmental impacts that are less noticeable. How these environmental perturbations directly and indirectly impact Lake Gatún's ecosystem and its fish community are not well understood and cannot be excluded when thinking about what may be impacting the ecosystem. Finally, fishing pressure, either recreational or for consumption, has increased throughout Lake Gatún's history. Although *C. monoculus* and *O. niloticus* are the main species targeted, little is known about how often untargeted species are captured and how this impacts their survival and abundance. Nonetheless, it is likely that high fishing pressure has at least played a role in the apparent decrease in *C. monoculus* abundance.

Fish community changes over 20 years

Comparisons of current data with data collected in 1994 with gill nets suggest that the fish communities of lakes Gatún and Alajuela have changed considerably over the past 20 years. For example, in Lake Gatún in 2013-2014, 19 species of fish were captured using gill nets, whereas only 9 species were captured in 1994. Similarly, when looking at samples collected near Cuipo specifically, the number of species caught increased from 5 in 1994 to 9 in 2014. In lake Alajuela there was no increase in the number of species caught, with 10 species being detected in each time period.

In all locations analyzed, substantial change in the species compositions of the samples occurred with only 3 and 4 species appearing in both 1994 and 2014 samples in Lake Gatún and Lake Alajuela, respectively. Of the species which occurred in only 2014 samples, some are known to be native and others non-native in both Lake Gatún and Lake Alajuela. A possible reasons for why species considered to be native to Lake Alajuela and Lake Gatún were caught in 2014 but not in 1994 is differences in sampling effort and gear type. In both sampling periods, gill nets with multiple panels of varying mesh size were used for sampling. However, in 2014 gill nets featured an additional panel whose mesh size was smaller than the smallest mesh size used in 1994. This may account for why some small sized species occur in 2014 samples and not 1994 samples, such as *R. guatemelensis.* In addition, in 2013-2014, an effort of 993.69, 226.42, and 190.25 gill net hours were used in Lake Gatún, Cuipo, and Lake Alajuela, respectively whereas in 1994 150, 30, and 90 gill net hours were used in Lake Gatún, Cuipo, and Lake Alajuela, respectively. This difference suggests that it is more likely for rare species to be detected in 2014 samples than in 1994 samples and may explain why some species captured in 2014 were not captured in 1994. However, neither of these differences in sampling method explain why some species captured in 1994 were not captured in 2014. That the current, more intensive sampling did not capture these species suggests that they have substantially decreased in abundance or have been extirpated.

Why these recent changes in the fish communities have occurred may be explained by a variety of factors, only a few of which will be discussed here. As previously mentioned, a number of non-native species are thought to have recently entered lake Gatún and lake Alajuela, either by intentional introduction or through the canal's lock system. In addition to explaining the appearance of new species, these nonnative species may have attributed to the apparent decline or loss of other species. The main mechanisms through which these nonnative species may have impacted other species is through competition, predation, or the spread of diseases (Simberloff 2000). Another factor that may be impacting the fish communities is changes to their environment. For example, it has been noted that as reservoirs age, fish species diversity decreases (Agostinho *et al.* 2008). In addition, landscape and land use change surrounding the reservoirs and the watersheds feeding into the reservoirs can impact the reservoirs ecosystem. Changes in land use and landscape play a large role in determining what and how much nutrients enter the ecosystem, as well as erosion and sedimentation rates. All of these inputs to the reservoirs may impact the fish community, either directly or indirectly (Schindler *et al.* 2000).

Comparisons Between Panamanian Reservoirs

When fish communities were compared between two reservoirs with *C.monoculus* and one without, differences in CPUE, biodiversity, and species composition were evident. Overall, CPUE was substantially higher in Lake Bayano than in Lake Alajuela or Lake Gatún, for both gear types used. However, overall species richness was highest for lake Gatún, followed by Alajuela then Bayano. When Shannon's index and Simpson's Index were calculated based on data collected with each gear separately, the different gears suggest different trends. When data was collected with gill nets, both Shannon's and Simpson's diversity are highest in Lake Gatún, followed by lake Alajuela then lake Bayano, suggesting that diversity and evenness are highest in Lake Gatún and lowest in Lake Bayano. Berger-Parker's dominance index suggests the same trend. However, when the indices are calculated from data collected with beach seine, different trends appear. Based on beach seine data, Bayano has the highest Shannon diversity, followed by Gatún then Alajuela, whereas for Simpson's index Bayano has the highest followed by Alajuela then Gatún.

The CPUE results very clearly suggests that the highest numerical abundance of fish occurs in Lake Bayano, far exceeding that of Lake Alajuela and Lake Gatún. This finding is similar to that of Gratwicke and Marshall (2001), who found that stream communities with the introduced predators *Micropterus salmoides* and *Serranochromis robustus* had 50% lower total abundance of fish compared to communities without the introduced predators.

The community in Lake Bayano is composed of mainly small sardines, with *Roeboides occidentalis* dominating in abundance. Nonetheless, the abundances of larger species and species at relatively high trophic levels are still higher or similar to those in lakes Gatún and Alajuela. CPUE with beach seine further exemplifies the difference in abundance of small and young fishes in lakes Gatún and Alajuela compared to Lake Bayano, with CPUE being 3 and 2 orders of magnitude lower in lakes Gatún and Alajuela, respectively, than in Lake Bayano. This finding was expected and is in line with our hypotheses. Our findings agree with those of Pelicice and Agostinho (2009), who found that in the Rosana Reservoir in Brazil, 2 years after the introduction of a peacock bass species there was a 95% decline in macrophyte-associated native fish density.

That species richness was higher in both Lake Gatún and Lake Alajuela than in Lake Bayano was an unexpected finding. This is very different from what other research on *Cichla* introduction,s and piscivore introductions in general, have found. For example, Moyle and Cech (1996) found that the most harmful types of introductions for freshwater biodiversity were piscivorous. The truth of this finding is illustrated by the findings of Pelicice and Agostinho (2009) where in a Brazilian reservoir an 80% decline in species richness had occurred within 2 years after the introduction of *Cichla*. Similarly, in Africa, upon the introduction of the nile perch, an enormous decline in native fish biodiversity occurred (Witte *et al.* 1992). Finally, Menezes *et al.* (2012) also found that fish diversity was significantly lower in Brazilian lakes with introduced peacock bass than in those without.

When the biodiversity indices were calculated for only the native fish communities from each lake, the trends were similar to those observed for the entire fish community. When the indices were calculated with gill net data, Lake Gatún was found to have the most diverse and even native species community based on calculations of Shannon's, Simpson's, and Berger-Parker's indices. Shannon's index suggested that Lake Bayano had the intermediate biodiversity, while Simpson's index suggests the Lake Alajuela has the intermediate biodiversity. Again these results were unexpected, as all other studies have found that lakes with *C. monoculus* have lower biodiversity. For example, an analysis similar to the current one as done by Latini and Petrere (2004), who found that native fish diversity was lower in Brazilian lakes with exotic species than in those without.

When the biodiversity indices were calculated for the native, diurnal, littoral zone species community, Lake Gatun was found to have the highest biodiversity followed by Lake Bayano then Lake Alajuela. These results, again, are not in line with our hypotheses and the findings of other studies.

That all other studies regarding fish biodiversity in relation to the introduction of *Cichla* species disagree with our data collected by gill net suggests that other factors may be impacting that fish biodiversity in our study lakes. However, this is only true necessarily for the fish community outside of that which occupies the littoral zone during the day.

One such factor could be Lake Gatún's unique role as a major part of the Panama Canal. This makes Lake Gatún available to marine species which can the lake enter through the canal's locks. In addition, recent introductions of exotic fish species have been made to lakes Gatún and Alajuela. These potentially very recent perturbation to the fish communities in our study lakes may mean that these communities are not at an equilibrium, allowing a higher biodiversity to persist than would otherwise be expected.

Furthermore, studying introductions in freshwater lakes in Panama is an interesting practice in itself, as the three largest lakes in the country are manmade reservoirs. In transitioning from a river to a reservoir, some fish poorly adapt to the changes such as from lotic to lentic water (Agostinho *et al.* 2008) and fail to utilize the differing physical qualities, notably the pelagic and deep waters, (Fernando and Holcik 1999) instead remaining close to the shore in the mouth of tributaries and in shallows. This can lead to a change in the fish community structure, in that fish displaying generalist behavior can become more successful in this habitat (Fernando and Holcik 1982). This illustrates the importance of sampling multiple different habitat types within the same lake in order to obtain a holistic picture of its fish community.

Additionally, characteristics of our study design may be in part responsible for our dramatically different results compared to those of other studies. For example, much more sampling effort was exerted in Lake Gatún across a higher number of sampling sites, than in the other lakes. In Lake Alajuela, an intermediate number of sampling sites and an intermediate amount of sampling effort was used. Finally, in Lake Bayano, sampling was restricted to one area of the lake comparable to one sampling site in either Gatún or Alajuela, and much less effort was dedicated to to this lake. Although the species rarefraction curve for lake Bayano suggests that enough sampling effort was exerted in this lake, this in fact only applies to the lake's one sampling site. A different sampling site with a different habitat may have revealed new species since, as mentioned above, riverine species that find themselves in a reservoir may adapt differentially to their new conditions, leading to discriminatory use of different lake habitats.

Finally, despite the relatively high diversity of fish species present in Lake Gatún, it is important to consider the abundance of each species, and the effort that was required to catch these species. Our data suggests that populations of almost all species in Lake Gatún are very low. Understanding whether this is a viable equilibrium or whether the densities of the populations of fishes in Lake Gatún will continue to change is important when making statements about the health or viability of the ecosystem. The lack of small and juvenile fish in our sampling may suggest that little reproduction of the fish species is occurring, which can be a side-effect of low population densities (Courchamp *et al.* 1999). If this were to be the case, the fish populations in Lake Gatún may not be viable and what we may be seeing is an even distribution of a large number of non-viable fish populations.

PROJECT LIMITATIONS AND RECOMMENDATIONS

The results of our project were limited by a few factors which may have introduced confounding variables into our results. These limitations have been discussed above, but will be listed again here, for clarity. Likely the most important limitation of the project to date was the inability to sample an equal number of different sites at all sample lakes. Since only one site was sampled at Bayano while four were sampled throughout Lake Gatún and three throughout Lake Alajuela, it cannot be said with certainty that the differences in diversity we are seeing between the locations are real, or if they are due to species-area relationships, in which larger areas include more habitat types and more speices. In addition to this, a limitation of our project is the lack of replications. Since Bayano is the only reservoir in Panama comparable to Alajuela and Gatún without peacock bass, there is way to determine if the observations made of the fish communities are applicable to other systems without peacock bass, or if its community is being impacted by confounding variables. Also, the lack to replicates means that it is difficult to perform statistical analyses of the results, increasing the difficulty of assessing the significance of results. Yet another limitation of the current analyses was an inability in some cases to identify species past the genus level, requiring lumping of species into genera rather than species. Being able to identify species to the species level is very important, especially for a study on biodiversity. Doing so allows the full diversity of a community to be better understood and allows for interesting analyses to be done the phylogenetic and genetic diversity of the system as well. More importantly, some a few individuals collected in Bayano were not able to be identified at all due to time constraints and were subsequently removed from the analysis. However these individual may represent an important and significant amount of the species richness in Bayano, and should be identified and included in future analyses. Finally, given the time constraints of the project we were unable to perform analyses comparing fish biomass between lakes. These analyses could reveal further interesting trends as the dominant species assemblages in each lake are rather different in their attainable sizes, and species caught across lakes were often very different sizes depending on which lake they were caught in.

As the project continues on past the current point, some recommendations can be made in order to cope with the aforementioned limitations. Firstly we recommend that additional sample sites be explored in Bayano is order to ensure the the trends in species richness observed amongst the study lakes are real, and not due to species-area relationships. In addition we recommend that the current analyses be re-run after all specimens have been identified to species. Finally we recommend that analyses be run once all specimens have been weighed in order to understand how actual biomass within each ecosystem differs.

CONCLUSION

The long-term impacts of *C. monoculus* that were able to be quantified in the current study were those impacts on the littoral zone-associated fish fauna of Lake Gatún. The analysis showed that the long-term impacts have been a severe reduction in the diversity and abundance of the species that inhabited this zone before the introduction of *C. monoculus.* In addition this analysis suggested a reduction in the population of *C. monoculus* has also occurred. These finding were in line with our hypotheses and agree with the findings of many other studies of the impacts of *C. monoculus* on the native fish communities to which they are introduced and the general consensus about the impacts of introduced piscivorous predators.

When samples of the littoral zone-associated fish community were sampled in lakes Gatún, Alajuela, and Bayano, results similar to those of other studies were obtained, with the abundance, evenness and species richness of fish captured in samples being much lower in lakes Alajuela and Gatún than in lake Bayano. However, when the fish community was sampled with gill nets, a different trend was found. Results acquired with gill nets still showed drastic reduction in fish abundance in Lake Gatún and Lake Alajuela compared to Lake Bayano, however both Lake Gatún and Lake Alajuela showed greater species diversity and evenness than Lake Bayano.

In addition, when the fish community samples acquired with gill nets in Lake Gatún and Lake Alajuela were compared to samples collected in 1994, it became clear that many changes have occurred to the fish communities in these two reservoirs over the past 20 years. Both disappearances and appearances and species were found to have occurred, with appearances occurring for both native and non-native species. The appearances of native species in 2014 samples may have been caused by increased sampling effort and slight differences in gill net mesh size while the appearances of non-native species are hypothesized to be caused by intentional and unintentional introductions. It is also hypothesized that the disappearances represent actual extirpations or severe reductions in the abundances of those species.

In conclusion the long-term impacts of *C. monoculus* of littoral-zone associated, diurnal fish species suggest that *C. monoculus* should not be introduced into ecosystems outside of its range which have species assemblages in these areas that are desirable to keep. Whether it be economically important species that use the habitat, a high number of endemics, a unique genetic strain, etc., *C. monoculus* will extirpate or greatly reduce the abundance of species that inhabit this area. As for how *C. monoculus* impacts the community of species targeted by gill nets, namely nocturnally active, nearshore species, it is clear that their abundance may be negatively impacted, however more of these species may be able to co-exist with *C. monoculus.* It is hypothesized that this co-existed is facilitated by differential habitat use, either in space or in time. Further investigation into whether the sizes of the populations of the species co-existing with *C. monoculus* in Lake Gatún and Lake Alajuela are viable will reveal which species can be considered as able to co-exist with *C. monoculus.* In addition, analysis of the characteristics of species which are able to co-exist with *C. monoculus* will be important in determining which communities, if any, peacock bass can safely be introduced into and which communities they should not be introduced into.

Similar analyses could be done for other highly sought after piscivorous species in order to maintain freshwater biodiversity as well as quality fisheries. Many introductions which have led to harmful invasions have been unintentional, making them very hard to avoid. In light of this and the likelihood that such accidents will continue into the future to the detriment of regional and global biodiversity, it is the responsibility of everyone to help conserve biodiversity in the ways that we can, by stopping irresponsible, intentional species introductions. Enough information exists on the potential harm caused by introduced species that turn invasive, what is now necessary is a better understanding of in which cases introduction turn disastrous and in what situations they are beneficial. We hope that the current study is a step in the right direction towards building the knowledge base necessary to make responsible decisions about introduced species, especially when considering making introductions to highly threatened systems such as freshwater ecosystems.

Acknowledgements

We we would like to thank our internship supervisor, Diana Sharpe, for her constant support, input, and helpful discussion throughout our time working along side her.

Diana Sharpe

We would also like to thank all those who helped us with our field work, without whom this project would not have been possible: Celestino Martinez, Luis Fernando De Leon, Victor Frankel, Rigoberto Gonsalez, Señor Felix and his family, Señor Bernardo and his family, and Señor Norberto.

Finally we would like to thank Dr. Mark Torchin and all the members of his lab for providing us with equipment and lab space, and Señor Carlitos and the staff at NAOS laboratories.

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Appendix 1 - Figures and Tables

Table 1. Summary of time spent on internship

Dates	**Activity**	**Description**
January 9	Meeting with Diana	Discuss project background, potential internship projects, and schedule.
January 10	Background research	Literature search for background information on invasive species and peacock bass
January 16-18	Background research	Literature search for background information on invasive species and peacock bass, and biodiversity indices
January 30-February 1	Trip to BCI	Learn sample collection and processing methods and collect first set of samples
February 1-3	Work plan and progress report	Finalized project schedule, finished literature review, finalized reviewed how sampling and project in general was progressing.
February 3-4	Background research	Research on biodiversity indices and catch-per-unit-effort calculations
February 5-7	Trip to Cuipo	Collected samples from Cuipo sampling sites.
February 8-11	Work on informal presentation	Evaluation of how project has been going so far. Reflection on difficulties and things to change in the future.
February 17-19	Trip to Alajuela	Collected samples from Lake Alajuela.
March 20-21	Data compiling	Entering data to a digital format and perform preliminary analyses.
March 31-April 1	Trip to BCI	Collected samples at other Lake Gatun Sampling sites
April 4-6	Trip to Bayano	Collected samples from Lake Bayano
April 6-11, 17-25	Data analysis, product production, final report, and presentation	Compilation of final data collection trips, analysis of data, creation of product for Diana, writing of final report and preparation of final presentation.

Table 2. Study lakes Summary of pertinent statistics regarding the lakes from which fish specimens were collected

Lake	Surface Area	Year formed	Cichla monoculus present?
Lake Gatun	425 km²	1914	Yes
Lake Alajuela	50.2 km2		Yes
Lake Bayano	353 km²	1976	No

Table 3. Sampling sites

Lake	Site Name	GPS coordinates	Historical studies done at site
Lake Gatun	BCI		Zaret and Paine (1973)
	La Laguna		Gutiérrez et al. (1995)
	Punta Mamay		Gutiérrez et al. (1995)
	Cuipo		Zaret and Paine (1973); Gutiérrez et al. (1995)
Lake Alajuela	Rio Pequení		Gutiérrez et al. (1995)
	Peña Blanca		Gutiérrez et al. (1995)
	Quebrada Tranqilla		N/A
Lake Bayano	Isla Maje		N/A

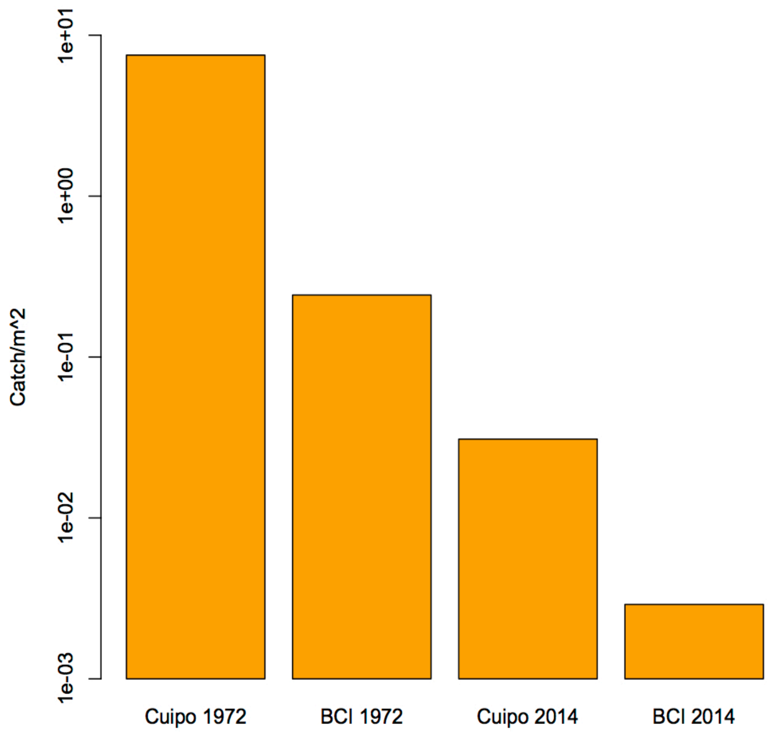

Figure 1. Number of fish caught per area of lake swept by a beach seine at Cuipo and BCI in 1972 by Zaret and Paine (no Cichla in Cuipo yet) and in 2014

Table 4. Catch per unit effort of each specie detected at around BCI and Cuipo. Data from 1972 taken from Zaret and Paine (1973), when Cichla had not yet invaded Cuipo.

Family	Species	Fish caught /m^2			
		1972		2014	
		Cuipo	BCI	Cuipo	BCI
Characinidae	*Astyanax ruberrimus*	2.04	0	0.0073	0
	Compsura gorgonae	1.5	0	0	0
	Hoplias microlepsis	0	0	0.0018	0
	Pseudocheirodon affinis	0.089	0	0	0
	Roeboides guatemalensis	2.5	0.028	0	0
Cichlidae	*Aequidens coeruleopunctatus*	0.13	0	0	0
	Cichla monoclus	0	0.019	0	0.0004
	Cichlasoma (Parotocinclus??) maculicuada	0.089	0.048	0	0
	Cryptoheros panamensis	0.051	0	0	0
	Oreochromis niloticus	0	0	0.02	0.0017
	Mesonautus festivus	0	0	0	0.0004
Eleotridae	*Eleotris pisonis*	0.051	0.132	0	0
	Gobiomorus dormitor	0.57	0.013	0	0
Poeciliidae	*Gambusia nicaraguagensis*	0.28	0	0	0
	Poecilia mexicana	0.22	0.0027	0	0.0004
	Atherinella sp.	0	0	0.0018	0
Total CPUE		7.52	0.2427	0.0311	0.0029
Species Richness		11	6	4	4

Table 5. Fate of species sampled at BCI between 1972 and 2014.

Family	Species	Increase (%)	Decrease (%)
Characinidae	*Roeboides guatemalensis*		100
Cichlidae	*Cichla monoculus*		80
	Oreochromis niloticus	100	
	Mesonautus festivus	100	
	Cichlasoma (Parotocinclus??) maculicuada		100
Eleotridae	*Gobiomorus dormitor*		90
	Eleotris pisonis		100
Poeciliidae	*Poecilia mexicana*		85

Table 6. (Zaret and Paine 1973) Diurnal Barro Colorado Island fish species with percentage change following Cichla appearance. Data collected over 6 years.

Family	Species	Increase (%)	Decrease (%)
Characinidae	*Astyanax ruberrimus*		100
	Roeboides guatemalensis		90
Cichlidae	*Aequidens coeruleopunctatus*		100
	Cichla ocellaris	100	
	Cichlasoma maculicuada	50	
Eleotridae	*Gobiomorus dormitor*		90
Poeciliidae	*Gambusia nicaraguagensis*		100
	Poecilia mexicana		100

Table 7. Percent change in abundance of fish species in Cuipo since 1972, with *C. monoculus* appearing in the area within a few years after initial data collection. Comparison of Zaret and Paine's 1972 data to 2014 data.

Family	Species	Increase (%)	Decrease (%)
Characinidae	*Astyanax ruberrimus*		95
	Roeboides guatemalensis		100
	Compsura gorgonae		100
	Hoplias microlepsis	100?	
	Pseudocheirodon affinis		100
Cichlidae	*Aequidens coeruleopunctatus*		100
	Cichlasoma maculicuada		100
	Oreochromis niloticus	100	
	Neetroplus panamensis		100
Eleotridae	*Gobiomorus dormitor*		100
	Eleotris pisonis		100
Poeciliidae	*Gambusia nicaraguagensis*		100
	Poecilia mexicana		100
	Atherinella sp.	100	

Table 8. Species caught and species richness detected in years 1994 and 2014 in three sampling sites: Lake Gatun, Lake Alajuela, and Cuipo. 1994 data collected by (Gutiérrez *et al*. 1994).

	1994			**2014**		
Species	**Lago Gatun**	**Lago Alajuela**	**Cuipo**	**Lago Gatun**	**Lago Alajuela**	**Cuipo**
Brycon charensis	x	x	x	x	x	
Astyanax ruberrimus		x		x	x	
Colossoma macropomum		x				
Cyprinus carpio		x				
Rhamdia guatamalensis (Rhamdia quelen?)	x	x	x			
Hypostomus panamensis	x	x				x
Eugerres sp.			x	x		
Parotocinclus maculicauda	x	x		x		
Cichla monoculus	x	x	x	x	x	x
Oreochromis niloticus	x			x	x	x
Gambusia nicaraguensis	x	x				
Hoplias microlepsis	x	x	x	x	x	x
Hoplias malabracius				x		
Gobiomorus dormitor	x			x		
Astronotus ocellatus				x	x	x
Mesonauta festivus				x		x
Parachromis managuensis				x	x	x
Cyphocharax magadalenae				x	x	x
Roeboides guatemalensis				x	x	x
Rhamdia quelen				x		
Cathotrops tuyra				x	x	
Centropomus sp.				x		
Cichlasoma tuyrense				x		
Riqueza de especies:	9	10	5	19	10	9

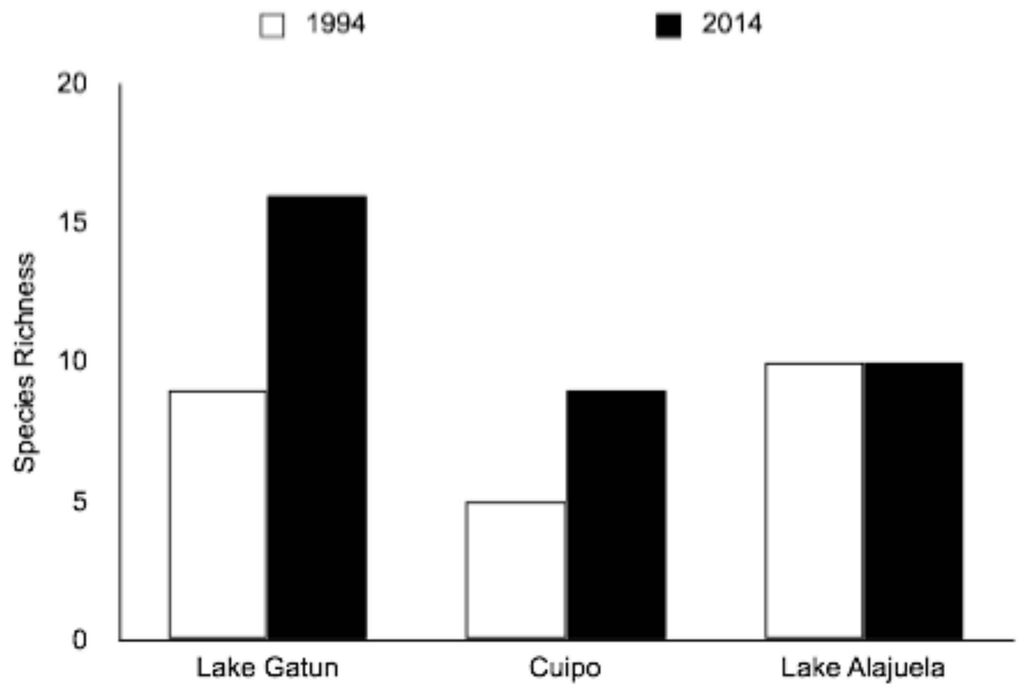

Figure 2. Species richness in Lake Gatun, Cuipo, and Lake Alajuela based on samples collected in 1994 and 2014.

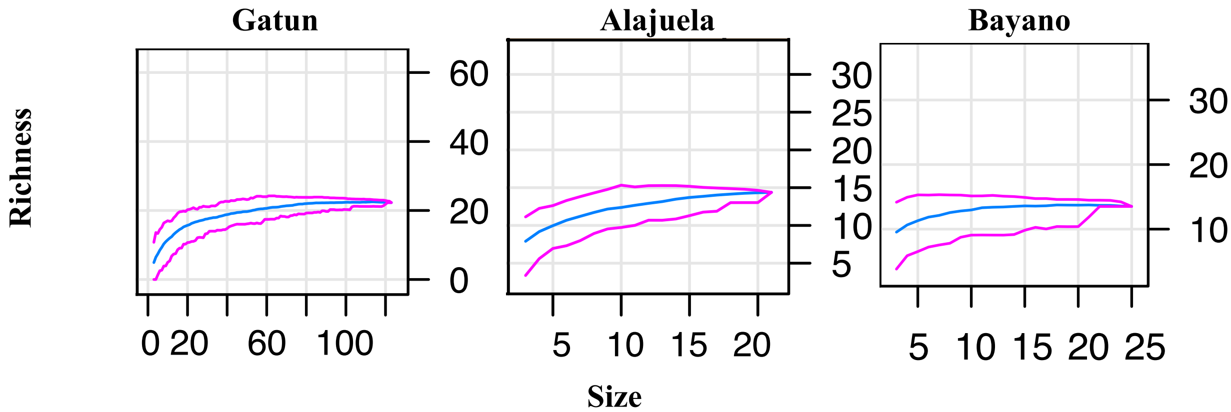

Figure 3. Species Rarefaction Curves. The bootstrap method was used to compute species rarefaction curves for collection at each sample lake

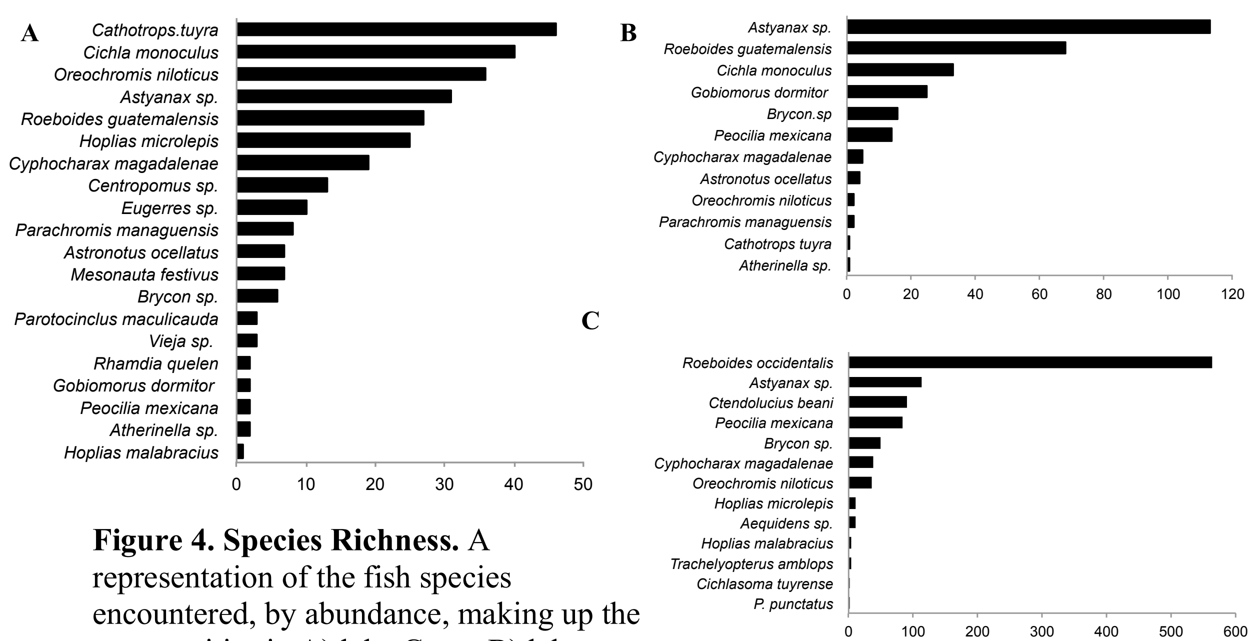

Figure 4. Species Richness. A representation of the fish species encountered, by abundance, making up the communities in A) lake Gatun B) lake Alajuela and C) lake Bayano, respectively

Table 9. Community Biodiversity Comparisons. Catch per unit effort**,** Shannon's, Simpson's and Berger-Parker's dominance indices were calculated for the communities sampled with gill nets (GN) and the community collected by beach seine (BS). Catch per unit effort is expressed in catch/hour for the gill net data, and catch/m^2 for the beach seine data.

	Gatun		**Alajuela**		**Bayano**	
	GN	**BS**	**GN**	**BS**	**GN**	**BS**
Catch per unit effort	0.284	0.008021	1.121	0.03397	4.652	2.521
Shannon's	0.8525	0.6911	0.6889	0.4219	0.5384	0.7401
Simpson's	0.5298	0.3680	0.3770	0.4310	0.1965	0.5786
Berger-Parker	0.1749	-	0.4154	-	0.6307	-

Appendix 2

Products for Host Institution

Appendix 3
Ethical Certificates

PANEL ON RESEARCH ETHICS
Navigating the ethics of human research

TCPS 2: CORE

Certificate of Completion

This document certifies that

Karling Roberts

has completed the Tri-Council Policy Statement:
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Date of Issue: **27 March, 2014**

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Date of Issue: **9 April, 2014**