Report

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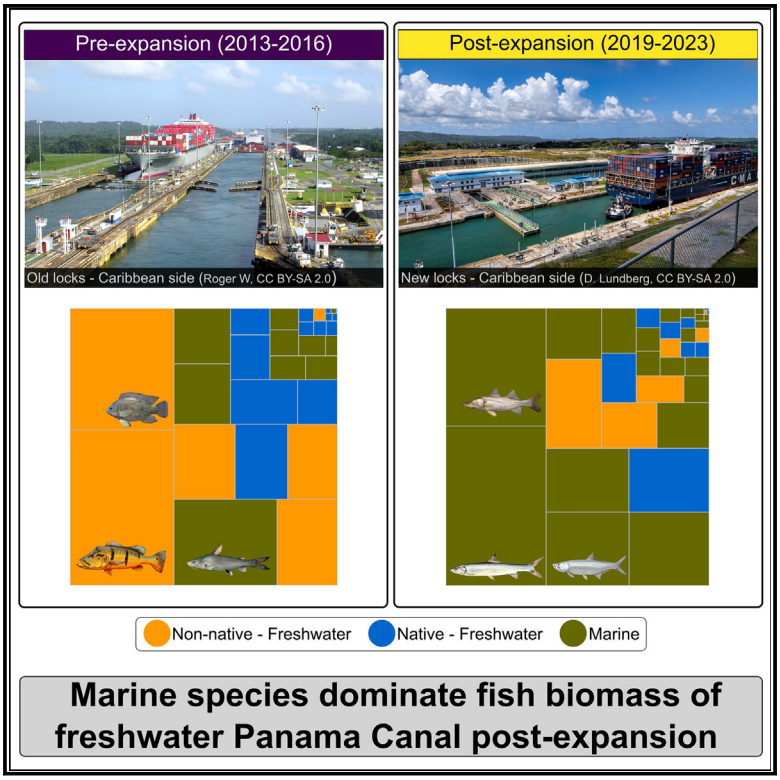
# New fish migrations into the Panama Canal increase likelihood of interoceanic invasions in the Americas

## Graphical abstract




## Highlights

- The expanded Panama Canal is currently experiencing a major biotic reconfiguration
- The former freshwater fish community is now replaced by a marine one
- Large marine fish predators are changing the food web of this tropical system
- The exceptional changes increase chances of interoceanic migrations in the Americas

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## In brief

Castellanos-Galindo et al. compare the fish communities of the freshwater section of the Panama Canal before and after its recent expansion. The fish community has shifted to one dominated by marine species, altering the functional structure of this system and increasing the probability of marine fish invasions between Atlantic and Pacific oceans.

Castellanos-Galindo et al., 2025, Current Biology *35*, 1364–1372
March 24, 2025 
https://doi.org/10.1016/j.cub.2025.01.049

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Report

# New fish migrations into the Panama Canal increase likelihood of interoceanic invasions in the Americas

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https://doi.org/10.1016/j.cub.2025.01.049

## SUMMARY

Maritime shipping is vital for commercial trade and well recognized as a main pathway for the spread of non-native species.[1] For over a century, the Panama Canal in Central America has played a major role in global trade, connecting the Atlantic and Pacific oceans. Historically, the introduction of species through the Panama Canal has been relatively low, largely due to the existence of a soft barrier—the freshwater Lake Gatun—inside the canal.[2–4] However, the 2016 expansion of the Panama Canal involved major structural changes to the canal's lock system, which may have increased the likelihood that more marine fish species and greater numbers of them enter the lake and eventually cross the canal. To test this prediction, we used standardized quantitative comparisons of the fish communities of Lake Gatun, a system with a rich record of biological introductions,[5,6] before (2013–2016) and after (2019–2023) the canal expansion. We observed a shift from a freshwater-dominated to a marine-dominated fish community in several areas inside the lake after 2016. The increase in marine organisms in this aquatic corridor may represent a potential invasion in progress, with a greater likelihood of some species eventually passing through the canal and colonizing the opposite ocean. The ecological and evolutionary consequences of these changes are difficult to predict. However, as most of these marine fishes are top predators with wide niche breadths, their colonization of Atlantic and Pacific oceans will likely alter ecological interactions and potentially lead to ecosystem-level changes.

## RESULTS

Biological invasions are a major cause of ongoing global environmental change.[7] They have the capacity to alter ecosystems, often leading to detrimental effects on society.[8,9] An increasingly interconnected world via (maritime) commercial trade will increase invasions around the world.[1,10–13] Canals are primary receivers of non-native (marine) species,[4,14,15] acting as sources for their secondary spread in nearby regions.[16,17] A known example of this phenomenon is the Suez Canal, responsible for the introduction of more than 400 marine species into the Mediterranean Sea via the Red Sea.[18,19] Rivaling the Suez Canal in size and importance for regional and global transportation,[20] the Panama Canal has also the potential to facilitate marine species introductions between the Atlantic and the Pacific oceans in the Americas.[21–23]

Unlike Suez, the Panama Canal is not a sea-level canal and, instead, a series of locks at both ends provide access to a large freshwater reservoir called Lake Gatun, 26 m above sea level (Figure 1). The old lock system that opened in 1914 and the presence of Lake Gatun has limited the exchange of marine species through the canal since its construction.[3,23–25] New larger locks that were added during the recent expansion of the Panama Canal between 2007–2016 now allow the transit of mega-vessels (Neo-Panamax) through this waterway, leading to increased water demand on the canal's watershed, including Lake Gatun, after this expansion.[26] However, the permeability of the new canal's configuration to the incursion of marine species is not well understood.

Here, we use fish abundance and distribution data that we collected in Lake Gatun in a quantitative, standardized way before (2013–2016) and after (2019–2023) the canal expansion to investigate (1) the contemporary community changes experienced by aquatic communities inside this canal and (2) the risks that these changes pose for potential interoceanic species introductions. This dataset provides a unique opportunity to

 

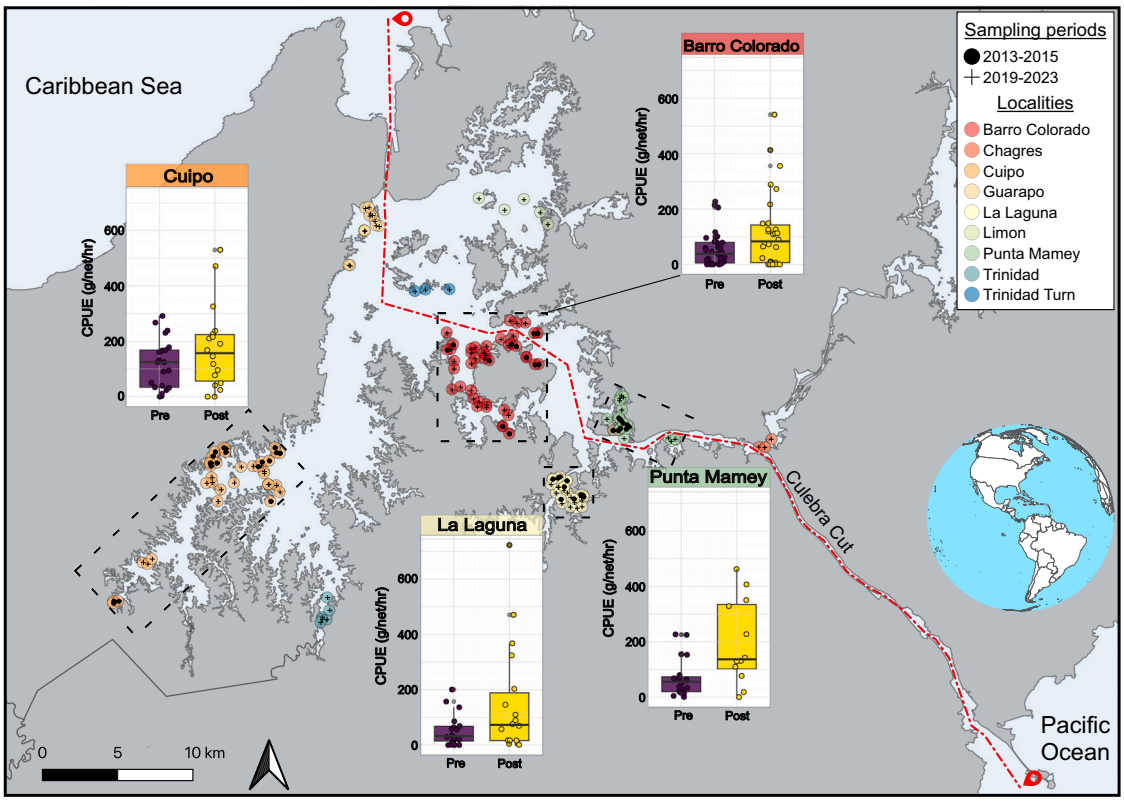


**Figure 1. Changes in CPUE pre- vs. post-Panama Canal expansion**

Panama Canal in Central America (transit route in red dashed line) with Lake Gatun in the middle and Caribbean Sea and Pacific Ocean on the left upper corner and the right bottom corner, respectively. The map shows all gillnet fish sampling localities between 2013 and 2023. Boxplots (with median and interquartile ranges) showing differences (Table S3) in CPUE (biomass) pre vs. post expansion are shown for the four localities that were repeatedly sampled in 2013–2015 and 2019–2023 (see also Figure S2 and Tables S3 and S4).

understand the changes that the biotic communities within the Panama Canal are experiencing after expansion. It also provides insight to evaluate potential invasions in progress, enabling management strategies to prevent adverse interoceanic marine fish invasions.

## Lake Gatun's fish biomass is now higher and dominated by marine fishes

Fish catch-per-unit-effort (CPUE) in terms of both biomass and abundance was higher post expansion (Figures 1 and S2; Tables S3 and S4). At the two localities closest to the Pacific canal entrance (La Laguna and Punta Mamey; Figure 1), our overnight gillnet sets usually contained more (Table S4) and larger fishes in the post-expansion dataset.

Fish community composition at Lake Gatun before and after the canal expansion was different (likelihood ratio test = 228.1, $p < 0.001$, Table S5). The biomass of the lake's fish community prior to the Panama Canal expansion was dominated (57%) by non-native freshwater species (particularly the Peacock Bass, *Cichla ocellaris* var. *monoculus* and the Nile Tilapia, *Oreochromis niloticus*), whereas marine species constituted only 26% and native freshwater fishes 17% of total community biomass (Figure 2). A few years after the canal expansion, in the same areas sampled pre-expansion, the fish community was dominated (76%) by marine species (particularly the Southern Ladyfish, *Elops smithi*). Introduced and native freshwater fish species now compose only 13% and 11%, respectively, of the total fish community biomass (Figure 2).

Considering all localities sampled in 2019–2023 (i.e., including the five localities exclusively sampled in 2019–2023), we found a higher biomass of marine fish species (74%), indicating that most of Lake Gatun is now dominated by marine, euryhaline fish species (Figure 2). Of these marine species, 18 have entered the canal from the Atlantic, whereas five species have entered from the Pacific Ocean (see Table S2). Non-native and native freshwater fish species constitute 13% each of the remaining fish community biomass. The main difference in our complete 2019–2023 dataset is the presence of a native freshwater species (*Brycon chagrensis*)—which is particularly abundant in areas close to the main tributary of Lake Gatun, the Chagres River—in the top-3-ranked species (Figures 1 and 2).

## Higher functional diversity and top predator dominance in Lake Gatun's fish communities post expansion

We found 15 new functional groups (or functional entities [FEs] *sensu*,[27] see STAR Methods) in the fish community of Lake Gatun after the canal expansion. The most representative (by weight) are those composed of macro-carnivore and pelagic species with large sizes and weights (e.g., the marine *E. smithi*, *Megalops atlanticus*, and *Strongylura marina*). Conversely, eight

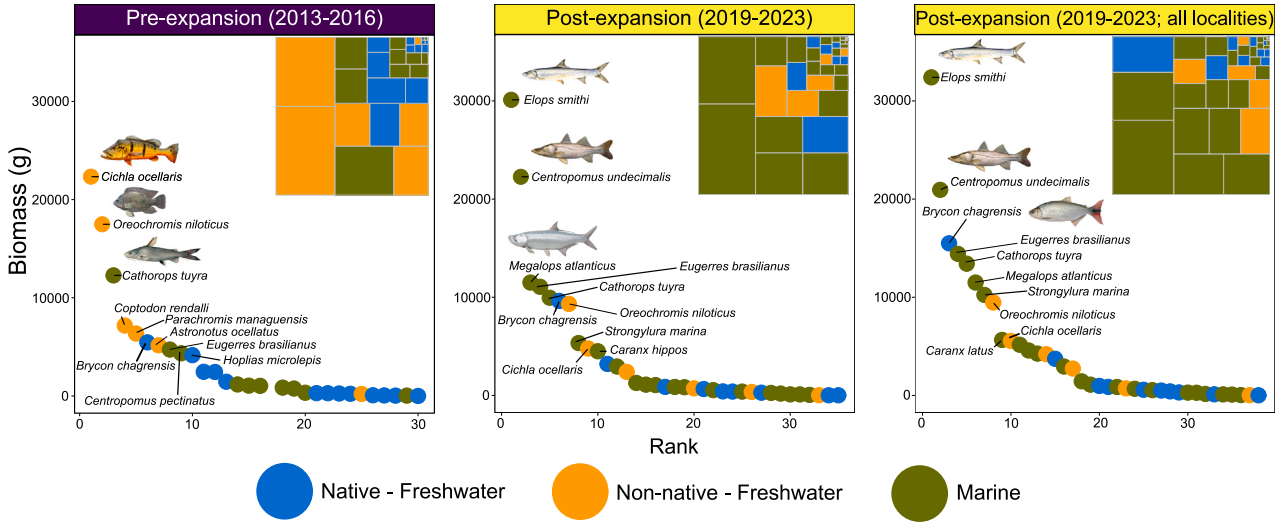


**Figure 2. Changes in fish community composition pre- vs. post-Panama Canal expansion**

Rank biomass plots of fish communities pre- (2013–2016) vs. post- (2019–2023) Panama Canal expansion at the same four localities, and post expansion (2019–2023), covering five additional localities within Lake Gatun. Treemaps at the top right of each plot show the respective fish composition using the three categories shown on the bottom of the figure: native freshwater fishes, non-native freshwater fishes, and marine fishes, with the latter representing the highest level of ecological novelty. Each square in a treemap represents a fish species, and the size of the square represents the proportional biomass of this species in the community (see also Figure S3 and Table S2).

pre-expansion FEs are absent in the post-expansion Lake Gatun fish fauna: those corresponding predominantly to native freshwater fish species of generally small sizes with detritivorous and omnivorous feeding habitats (e.g., *Cyphocharax magdalenae*, *Isthmoheros tuyrensis*, *Andinoacara coeruleopunctatus*, and *Brycon petrosus*; Figure 2). Both functional richness (FRic) and divergence (FDiv) were higher for the post-expansion vs. pre-expansion fish community (0.809 vs. 0.66 and 0.829 vs. 0.771, respectively), indicating a richer fish community after the canal expansion in terms of functional traits.

Mean body size of individuals in the Lake Gatun fish community remained similar before and after the canal expansion (~20 cm standard length [SL]). However, the interquartile range of the post-expansion fish community is now broader, with more fish greater than 30 cm SL compared with the pre-canal community. This is largely due to the presence of large marine fish species such as needlefish and ladyfish. However, small marine pelagic species (sardines and anchovies) also were relatively abundant in the post-expansion fish community, as reflected in the lower interquartile range for marine fishes (see Figure 3B, right).

Carbon and nitrogen stable isotope analysis revealed a food web in Lake Gatun dominated by abundant, high-trophic-level marine predators after the canal expansion (12 of 16 marine species in the post-expansion food web). Despite having a few high-trophic-level marine fishes (six from 10 relatively rare marine species), the pre-expansion food web had a larger representation of mid- and high-trophic-level native freshwater species compared with the post-expansion food web (Figure 4). Introduced freshwater fish species continued to be represented by low-trophic-level species (mainly Tilapias) and the middle- to high-trophic-level Peacock Bass in both pre- and post-expansion food webs.

## DISCUSSION

50 years ago, Zaret and Paine published a pioneering, now classic example of the stark ecosystem consequences that the introduction of a non-native apex predator (the Amazonian Peacock Bass) could have in the tropical Lake Gatun in Panama.[5] The extirpation of large parts of the native freshwater fish fauna by this predator persists until now.[29] In the present study, we found that this same lake, a critical section of the Panama Canal, is experiencing another major ecological re-shuffling following the canal expansion completed in 2016. Localized changes were observed a few years ago,[25] and our comprehensive pre- and post-expansion dataset reveals that this tropical lake is now dominated in most parts by predatory marine fish species that have entered from both the Atlantic (78%) and Pacific (22%) oceans.

The biological changes taking place inside the large, central reservoir section of the Panama Canal have two major implications: (1) a major modification of the lake's food web (see Figure 4), altering its ecology and impacting the people depending on it (e.g., small-scale artisanal and recreational fishers), and, ultimately, (2) an increased likelihood of successful interoceanic fish invasions between the Pacific and Atlantic oceans through the canal due to the higher number of marine fish species distributed throughout Lake Gatun that are able to persist in the system.

### Shift to a novel, marine-dominated fish community in Lake Gatun

Reservoirs are a well-recognized facilitator of species introductions,[30] and Lake Gatun inside the Panama Canal is a special example of this in the tropics. The introduction of Cichlid fishes from Africa (Nile Tilapia, *O. niloticus*), the Amazon (Peacock

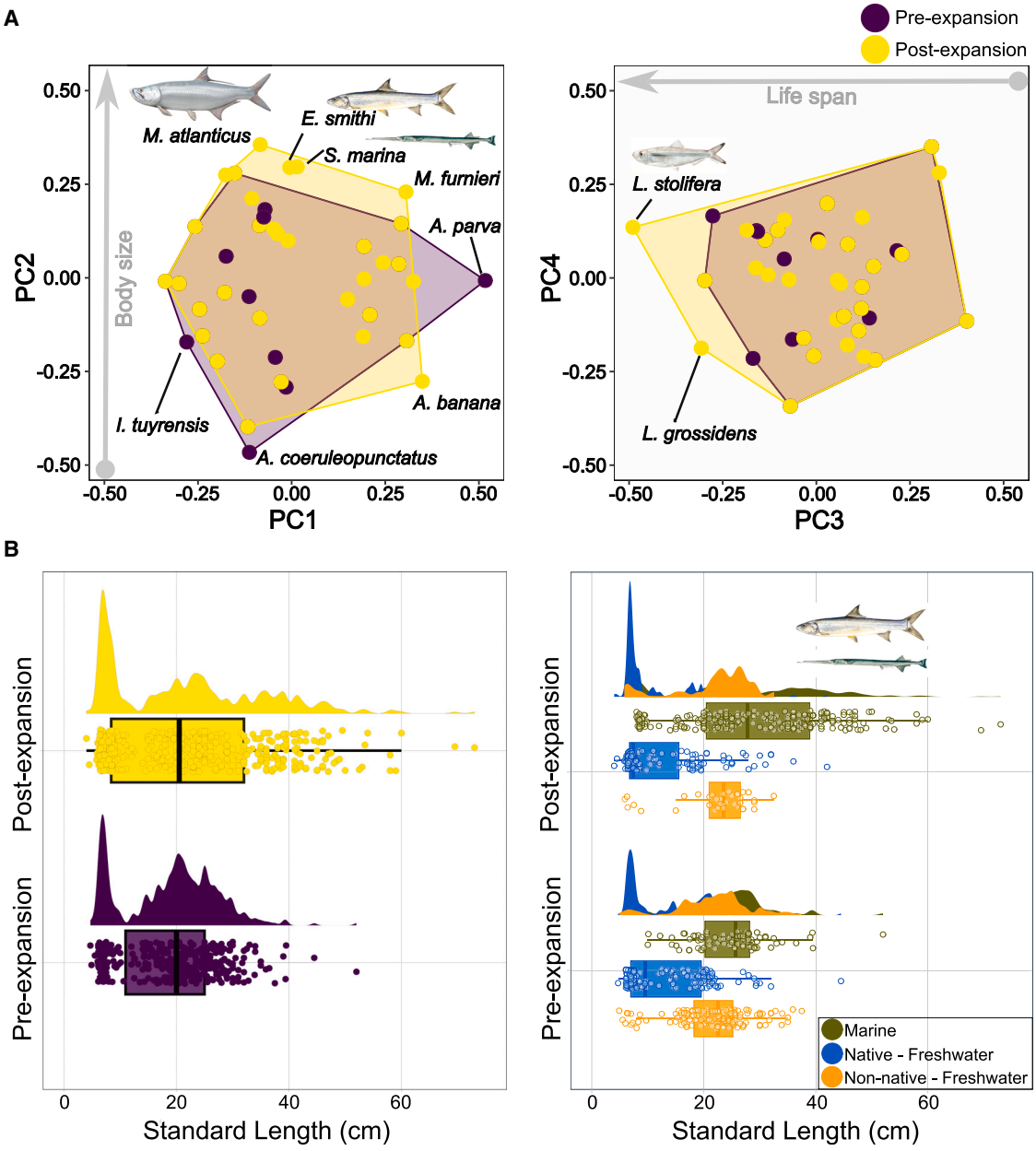


**Figure 3. Functional changes in Lake Gatun's fish communities pre- vs. post-Panama Canal expansion**

(A) Principal coordinate analysis (PCoA) of functional fish diversity pre- vs. post-Panama Canal expansion. The PCoA shows the distribution of functional entities (FEs) in functional spaces where axes represent PC1-PC2 and PC3-PC4 from a PCoA on functional traits (see also Figures S4 and S5 and Table S6). The overall convex hull includes all 45 fish species found at Lake Gatun between 2013 and 2023, grouped in 41 FEs. The color-filled areas show the functional volume filled by each fish community pre- and post-canal expansion. Colored circles represent FEs present in the fish fauna. Gray arrows indicate the main functional trait associated with PC2 and PC3.

(B) Length distribution of the fish community at Lake Gatun before (2013–2015) and after (2019–2023) the Panama Canal expansion (left plot, see also Figure S6). Fish length distributions pre and post expansion are disaggregated by fish categorization (see bottom legend in right plot). Fish illustrations on the right plot exemplify that marine species in the post-expansion length distribution are mostly large-sized fishes.

All boxplots show median and interquartile ranges.

Bass, *C. ocellaris* var. *monoculus*), and Central America (Jaguar Cichlid, *Parachromis managuensis*), among others, has caused severe declines in native freshwater fish populations in this reservoir.[28] These introductions are also responsible for the homogenization of biotic communities (the process by which species invasions and extirpations cause the loss of taxonomic, functional, or genetic distinctiveness over time[31,32]), if one considers that the lake has been dominated for a few decades by the widely introduced freshwater Peacock Bass and Nile Tilapia, at the expense of the decline or disappearance of the native

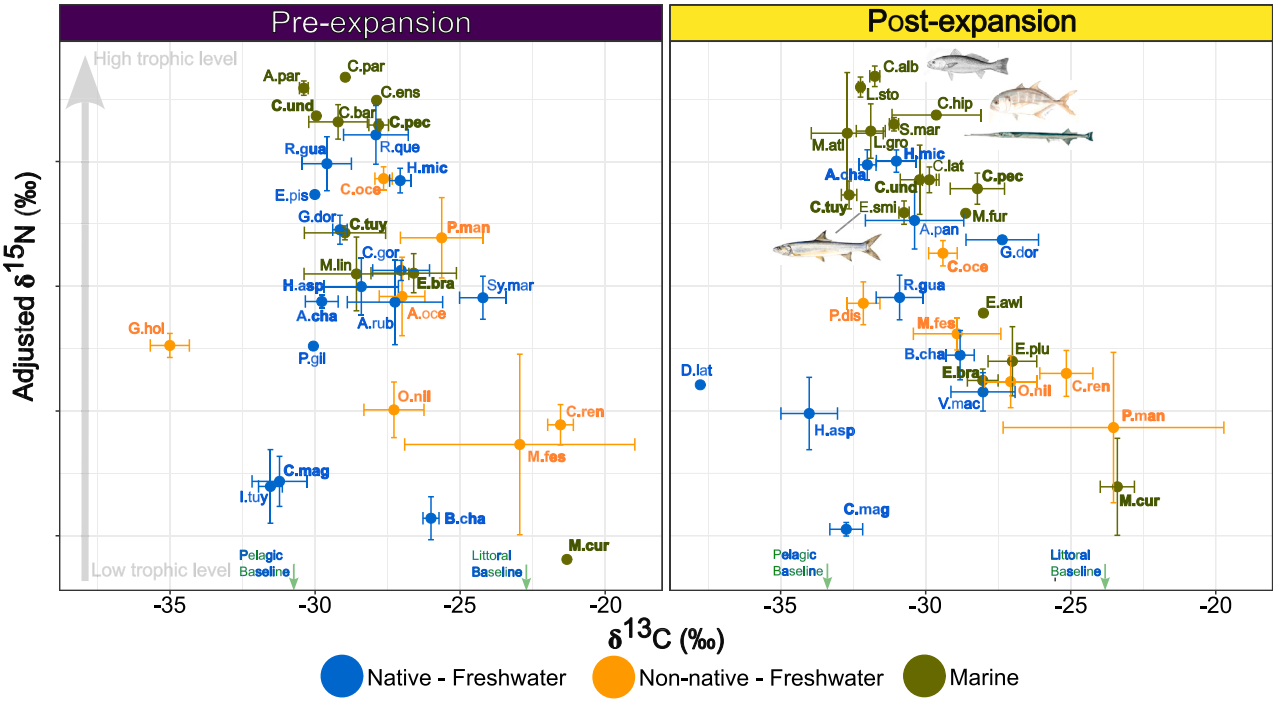


**Figure 4. Food web changes in Lake Gatun's fish communities**

Carbon ($\delta^{13}C$) and nitrogen (adjusted $\delta^{15}N$, see STAR Methods) stable isotope biplots of fish communities at Lake Gatun pre- vs. post-Panama Canal expansion. The pre-expansion food web is based on Sharpe et al.[28] Mean (±SE) stable isotope values are shown for each species (see species codes in Table S7). Species codes in bold are those found in both time periods. Note that most of the marine species in the post-expansion plot were not present in the pre-expansion time. See STAR Methods and Table S7 for details about the stable isotope analysis.

freshwater fauna.[5,29] Interestingly, we document a net increase in taxonomic richness in the post-expansion fish community of Lake Gatun (see Table S2). This trend is driven mainly by the addition of new marine fish species to the community that represents a high level of ecological novelty (*sensu*[33]), as the resident freshwater species have little or no eco-evolutionary experience (*sensu*[34,35]) in interacting with the marine fish species that have different functional traits. Consequently, the addition of these marine species results in an increase in the FRic of the community; both large, demersal species and short-lived small pelagic fish entering the lake through the canal have increased the functional volume occupied by the post-expansion fish community (Figure 3A). The introduction of large predators into aquatic ecosystems has been linked to the reduction of fish, benthic invertebrates, and zooplankton populations and an increase in phytoplankton, resulting in trophic cascades.[8,36,37] In a highly invaded and environmentally variable aquatic system like Lake Gatun, little is known about the ecosystem processes (biological, physical, and chemical) taking place (but see Salgado et al.[6]). The addition of large predatory fishes to this system will certainly modify the flows of energy and nutrients,[38] deserving careful investigation in the future.

The setting of Lake Gatun in the middle of an interoceanic canal makes this freshwater reservoir unique. In the last 200 years, only a few cases of freshwater invasions by marine or estuarine species have been documented in the world (reviewed in Lee and Bell[39]). From an evolutionary perspective, freshwater systems experiencing invasions by marine organisms can be ideal systems for observing adaptations in progress that can occur in very short timescales.[40] In this context, Lake Gatun also provides an ideal natural experiment to observe potential rapid evolutionary adaptations to a new freshwater environment from species coming from the Pacific or Atlantic oceans.

The Panama Canal, and especially the Lake Gatun, has a history of interest to anglers.[41–43] The long-term presence of marine gamefish like Tarpon and marketable non-native freshwater fishes like Peacock Bass and Nile Tilapia makes this location attractive to local artisanal fishers as well as national and international recreational fishers. More apex predators of marine origin in this system may represent an opportunity for the recreational fishing sector but might challenge artisanal fishers targeting introduced freshwater fishes. Changing fishing gear to target unfamiliar fishes that behave very differently could represent an economic obstacle for artisanal fishers.[44]

## The current potential for interoceanic fish invasions through the Panama Canal

Compared with the other large interoceanic canal in the world (i.e., the Suez Canal), the number of documented fish interoceanic transits through the Panama Canal has been historically low (<10 species).[3,25] With the exception of the large, highly mobile Atlantic Tarpon (*M. atlanticus*),[41,42] most documented transits have been by small cryptic species like gobies and

blennies.[3,4] More recently, eDNA water sampling at both entrances of the canal has revealed some other species potentially crossing the canal,[23] but caution is needed with this method because some species from the Pacific and the Atlantic are closely related and barcode reference libraries do have reliability issues.[45] Our standardized dataset over the last 10 years indicates that the majority of marine fish species currently inside Lake Gatun have an Atlantic origin (Table S2). Interestingly, four of the five Pacific species have only been recorded post expansion, indicating that the permeability of the Pacific side of the canal for the passage of species may have increased. The fifth Pacific species (the sea catfish *Cathorops tuyra*) was recorded in the pre-expansion sampling; however, we have recently recorded this species very close to the Caribbean side of the lake near the locks, suggesting that this species is now widespread in the lake and has high potential to invade the Atlantic Ocean through the canal. Similarly, most of the new Atlantic species recorded in our post-expansion dataset were found close to the Chagres River (La Laguna and Punta Mamey localities), the last section of the canal before the Culebra Cut that leads to the locks at the Pacific side of the canal (Figure 1). This indicates that the potential for these species to migrate to the Pacific is also high. It is worth noting that our sampling methodology (experimental, large-mesh gillnets) very likely missed small and cryptic benthic marine fishes such as gobies and blennies, some of which are known to have transited the canal in the past.[3]

Shipping in inland and maritime waters has had well-recognized adverse effects on biodiversity, particularly via the introduction of invasive species.[46] The Panama Canal, as a major artery in the global maritime transportation network, will surely continue to play a vital role in global shipping in the coming decades. Despite severe El Niño-related droughts that have intermittently limited canal operations and ship transits in the last decade,[47] this passageway remains fundamental, particularly during geo-political situations like the current one that affect the other existing large maritime canal (Suez Canal). Various nature-based solutions (e.g., changing pasture to agroforestry) and large infrastructure modifications (e.g., new dams and reservoirs) have been and are being considered to mitigate effects of current and future environmental changes affecting canal operations.[48,49] These discussions revolve around water use by the canal itself and for the Panamanian population but rarely address the biotic communities living in those fresh and adjacent marine coastal waters. Our work reveals that these communities are rapidly changing and that these changes point to a higher likelihood of interoceanic exchanges and invasion of marine biota between the Atlantic and Pacific oceans. Our results also point out which species and specific functional traits are more likely to invade new ocean basins. This is critical to understand the potential impact of future invasions[50] and to plan targeted mitigation and prevention strategies, such as the design and implementation of fish deterrents to canal entry.[51,52] Ultimately, keeping the inner section of the Panama Canal as a freshwater "barrier" should prevent a wider range of marine fishes with distinct functional traits from completing interoceanic migrations.

The ecological implications of a more "permeable" Panama Canal were subject to debate more than 50 years ago when the proposal of a sea-level canal was discussed.[53] An expanded Panama Canal once again requires debate on what is needed to design appropriate experiments that improve our capacity to predict the potential ecological and evolutionary consequences of and mitigation efforts for marine invasions between ocean basins. Any engineered or nature-based solution designed to solve the current operational problems of the canal should consider its implications for control of the marine fish communities that now dominate and continue to enter this system.

## RESOURCE AVAILABILITY

### Lead contact

Questions or comments about data, results, and conclusions should be made to the lead contact, Gustavo A. Castellanos-Galindo (gustavoa80@yahoo.com).

### Materials availability

This study did not generate new unique reagents.

### Data and code availability

- Fish community and stable isotope data from 2013–2016 are available from Sharpe et al.[28,29] The DOIs are provided in the key resources table.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

## ACKNOWLEDGMENTS

G.A.C.-G. was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation; CA 2261/3-1, project number 471823073) and a STRI Fellowship. Additional funding for field work was provided by the National Geographic Society (grant #3221-4 to D.M.T.S.). The Panama Canal Authority (ACP) has facilitated our research activities at the canal throughout these years by granting access to the study sites and providing timely feedback and field support when it has been requested. We thank all the small-scale and recreational fishers (particularly Richard Cahill) across Lake Gatun who shared their fishing experience with us. L. Aponte, M. Deveaine, L.F. De Leon, V. Frankel, I. Geladi, C. Martínez, L. Ortíz, K. Roberts, R. Ryan, C. Schlöder, T. Stewart, and M. Valverde provided valuable field and lab assistance. We thank Rigoberto Gonzalez for all the support he has given to our investigations. We also thank O. Sanjur, L. Dutari, and C. de Leon at STRI for providing feedback on the manuscript and assistance with administration. We thank the three anonymous reviewers that provided critical comments to improve the manuscript.

## AUTHOR CONTRIBUTIONS

G.A.C.-G., M.E.T., D.R.R., J.M.J., and D.M.T.S. conceptualized the study. D.M.T.S. collected and processed the 2013–2016 dataset. G.A.C.-G. and V.B. collected and processed the 2019–2023 dataset. G.A.C.-G. analyzed the whole dataset, produced the graphs, performed the statistical analyses, and wrote the first original draft. All authors contributed to reviewing and editing the manuscript.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
  - Study site

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2025.01.049.

Received: October 25, 2024
Revised: December 13, 2024
Accepted: January 23, 2025
Published: February 20, 2025

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## STAR★METHODS

### KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Deposited data | | |
| Fish community composition data (pre Panama Canal expansion) | Sharpe et al.[29] | https://doi.org/10.1002/ecy.1648 |
| Fish and invertebrate's Carbon and Nitrogen Stable Isotope data (pre Panama Canal expansion) | Sharpe et al.[28] | https://doi.org/10.1002/ecy.4173 |

### EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

#### Study site

The Panama Canal is an 82 km waterway located in Central America. It connects the Atlantic (Caribbean Sea) and the Pacific (eastern) oceans by "cutting" the Isthmus of Panama. Built between 1881 and 1914, it has been for a long time considered as an engineering marvel. Probably the most salient feature of this canal is the artificial Lake Gatun.[54] This lake (known locally as *Embalse Gatún*) is fundamental for canal operations, as it allows: (a) ship navigation for ca. 50% of the waterway and (b) the use of water for lockages each time a ship enters or leaves the canal. Lake Gatun is a ~425 $km^2$ reservoir located in the Chagres River valley. The Chagres was dammed in 1910, inundating a vast area of tropical rainforest well-known for its high biodiversity.[49] This inundated rainforest, then converted into Lake Gatun, has since its creation undergone a variety of anthropogenic transformations at different times, including land-use changes and non-native species introductions.[6]

With a freshwater fish fauna composed of both Pacific and Atlantic slope riverine native species,[55] Lake Gatun has experienced repeated introductions of non-native freshwater fishes. The best documented case is that of the Peacock Bass (*Cichla ocellaris* var. *monoculus*),[56] a predatory cichlid from the Amazon that has reduced populations of native freshwater fish species.[5,29] Additionally, a few species of marine origin have survived the freshwater conditions of Lake Gatun, eventually crossing the Canal.[3,41] A rich record of community and food-web changes,[2,3,5,28,29] makes Lake Gatun a rare example of a tropical system where the long-term effects of biological introductions can be traced.[29] This is especially relevant, as most of our understanding about the development of biological invasions comes from examples in temperate regions.[57–59]

#### Data collection

We have sampled fish communities at Lake Gatun in the last ~10 years using multi-panel experimental gill nets (mono-filament, 45 m long, 3 m deep, six panels with stretched meshes ranging from 2.54 cm to 15.24 cm). Sampling in 2013-2016 took place at four main localities (see details in Sharpe et al.[29] and Figure 1). In 2019-2023, sampling took place at the same four localities of[29] (see Table S1), but an additional four localities were also examined (Figure 1). In both time periods, sampling was conducted during both wet and dry seasons. Gillnets were set in the evening (~ 18:00h) and retrieved in the following morning (~ 06:00h). Almost all fish collected were identified to the lowest taxonomic level, measured (standard and total length in cm) and weighed (in g). To derive weights for some fishes in our 2013-2016 dataset, we used length-weight relationship formulas available in Froese and Pauly.[60] Fish species were categorized as freshwater native, freshwater non-native or marine based on Sharpe et al.[29] and Myers.[61]

All samples were collected with permission from Panama's Ministry of Environment (MiAmbiente Permit #s: SE/AP-21-13, SC/A-29-13, SE/AP-11-15, SE/AP-40-15, SE/A-30-2019, SE/A-36-19 and ARBG-0130-2022), and all handling of live vertebrates was done in compliance with the Smithsonian Tropical Research Institute's (STRI) Institutional Animal Care Committee (IACUC Protocol #s: 2013-0507-2016, 2016-0224-2019, 2018-0415-2021, SI-21041).

### METHOD DETAILS

#### Stable Isotope analyses

To reconstruct the food webs of the fish communities at Lake Gatun pre- and post-expansion, we collected fishes and invertebrates between 2013-2018 (pre-expansion) and between 2019-2024 (post-expansion) and analysed them using stable isotope analysis (SIA) of carbon and nitrogen. These collections included primarily those from our gillnet sampling but also include opportunistic collections with hand nets, beach seines, cast nets, minnow traps, baited bottle traps, and angling. Invertebrate samples were composed of snails (*Pomacea* sp. and *Melanoides tuberculata*) and filter-feeding bivalves (*Anodonta luteola*, *Corbicula fluminea*) that represent the base of Lake Gatun's littoral and pelagic food webs, respectively.[62,63] The complete list of fishes and invertebrates analyzed with SIA and their body size ranges can be found in Table S7.

Details about SIA procedures of samples collected between 2013-2018 can be found in Sharpe et al.[28] Samples collected between 2019-2024 were analysed at the biogeochemistry laboratory of the Smithsonian Tropical Research Institute. For bulk nitrogen and carbon, samples were analysed on a Thermo Flash 1112 Elemental Analyzer following AOAC Official Method 972.43. Isotopes

were analysed using Flash 1112 Elemental Analyzer coupled to a Thermo Delta V Advantage Isotope Ratio Mass Spectrometer (IRMS). Isotope data were normalized using standard reference materials USGS40 ($\delta^{15}$N= -4.52, $\delta^{13}$C= -26.39) and USGS41a ($\delta^{15}$N= +47.55, $\delta^{13}$C= +36.55).

## QUANTIFICATION AND STATISTICAL ANALYSIS

To assess the sample completeness of our datasets, we used rarefaction and extrapolation sampling curves of Hill numbers using the R package *iNEXT*.[64] (See Figure S1) To assess the effect of time and location on the catch per unit effort data (biomass and abundance), we used a hurdle (zero-inflated) log-link Gamma model using the glmmTMB R package.[65] To evaluate differences in fish community structure between the 2013-2016 and the 2019-2023 datasets, we used the R package *mvabund*,[66] which provides a model-based approach to the analysis of multivariate (abundance) data (see Table S5). The input data for these analyses were catch-per-unit-effort (CPUE) of our gillnet samplings expressed as fish abundance (number of fish × net$^{-1}$ × h$^{-1}$) or biomass (grams × net$^{-1}$ × h$^{-1}$). To understand potential changes in the fish community's functional diversity between the 2013-2016 and 2019-2023 datasets, we also used the R package *mFD*.[67] For this, we chose eight ordinal and categorical traits (position in the water level, Maximum body mass, Maximum size class, Body shape, Mouth position, Diet, Spawning, Life span) to characterize each species (See Table S6). Species were then grouped into functional entities (FEs), which are groups of species that share similar traits. Functional trait-based distances between FEs were calculated using the Gower distance metric to build a functional space in which indices could be computed (see details in Figures S4 and S5 and in Mouillot et al.[68]). These distances between FEs were then used to generate a multidimensional space through a Principal Coordinate Analysis (PCoA). For both pre- and post-expansion food webs, $\delta^{15}$N values of all fishes were adjusted according to their respective $\delta^{15}$N baselines to facilitate comparisons (see details in Sharpe et al.[28] and in Table S7). After that, both food webs were visually compared using standard $\delta^{13}$C vs $\delta^{15}$N biplots.