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. The extirpation of large parts of the native freshwater fish fauna by this predator persists until now. 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, 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, and Lake Gatun inside the Panama Canal is a special example of this in the tropics. The introduction of Cichlid fishes from Africa , the Amazon (Peacock 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. 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 time31,32), 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 freshwater fauna.
Interestingly, we document a net increase in taxonomic richness in the post-expansion fish community of Lake Gatun. This trend is driven mainly by the addition of new marine fish species to the community that represents a high level of ecological novelty (sensu33), as the resident freshwater species have little or no eco-evolutionary experience (sensu34,35) 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 Bell39). 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. 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. 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.

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). 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. 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. 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.

Shipping in inland and maritime waters has had well-recognized adverse effects on biodiversity, particularly via the introduction of invasive species. 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, 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. 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 and to plan targeted mitigation and prevention strategies, such as the design and implementation of fish deterrents to canal entry. 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. 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.