

A new wave of marine fish invasions through the Panama and Suez canals

Recent engineered expansions of the Panama and Suez canals have accelerated the introduction of non-native marine fishes and other organisms between their adjacent waters. Measures to prevent further invasions through canals should be incorporated into global shipping policies, as well as through local efforts.

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The world is inexorably connected by shipping corridors that are expected to be increasingly used in coming years^{1,2} as world maritime trade grows by an estimated 3.5% per year³. Canals have transformed shipping routes since at least the sixth century BC. Alongside their role in global economies, they have established connections between ocean basins and marine biotas that were separated for millions of years⁴. Two of these, the Panama and Suez canals, are major shipping corridors that are considered hotspots for biological invasions⁵.

The Suez Canal (opened in 1869) is a marine, sea-level canal and the Panama Canal (opened in 1914) is a freshwater canal approximately 29 m above sea level and accessed by locks at each end. Previously, both canals incorporated constraints to biotic exchange between the marine biogeographic regions that they connect. The Bitter Lakes of the Suez Canal historically served as hypersaline barriers that limited movement of marine species, but the progressive enlargement of the canal has diluted these lakes. This enhanced habitability of the canal has facilitated the establishment in the Mediterranean Sea of over 400 marine non-native species (NNS), including more than 100 species of marine fishes, from the Red Sea⁶ (called Lessepsian migration⁷). Within the Panama Canal, Lake Gatun, a large artificial freshwater lake enclosed by the locks, has formed a barrier preventing most marine species in the Caribbean Sea and Eastern Pacific from moving to the opposite ocean because they do not tolerate freshwater. However, the Panama Canal has also recently been expanded, allowing more movement of marine fishes into Lake Gatun.

Recent expansions of the Panama and Suez canals

Activity through the Panama and Suez canals account for 10% of the gross domestic product (GDP) of Panama and Egypt,

respectively. Canal expansion projects have been fundamental to the economies and competitiveness of both countries. Recent expansion of the Suez Canal, which finished in 2015, included the construction of an additional, 35-km long channel. Expansion of the Panama Canal, completed in 2016, included the construction of new larger locks that allow the transit of large NeoPanamax vessels.

Previous predictions^{8–10} that these expansions would lead to an increase in NNS introductions are proving correct. Eight new Lessepsian fish species have passed through the Suez Canal into the Mediterranean since 2015 (Supplementary Table 1), representing an 8% increase in species number and a twofold increase in the average annual detection rate¹¹ compared to the period 1869–2015. In Panama, we have documented an increase in marine species just four years after the expansion. Over the century prior to the 2016 expansion, 18 marine fish species were recorded inside Lake Gatun. Between 2019 and 2020, using the same standardized gillnet sampling methods at the same sites as in ref.¹², we recorded 11 previously unreported marine fishes contributing to a total of 29 now known to occur in the lake (Fig. 1, Supplementary Table 2). Further, the abundance of some marine species (jacks, snooks, marine mojarras and ladyfish) has greatly increased in parts of the lake, almost entirely replacing the freshwater fish present shortly before 2016¹² (Supplementary Tables 3 and 4).

Higher abundances of marine fish in Lake Gatun increase the risk of such species invading in both directions to the opposite ocean. Proxies such as salinity-tolerant diatom species in lake sediments reveal a long-term increase in salinity of the lake¹³. However, the recent changes in the lake fish community may be due to more recent increases in salinity¹⁴, as observed from comparison of data collected before and after the canal expansion (Supplementary

Tables 5 and 6), and to more ship traffic and lock usage. The new locks have a different design to the original locks and may serve as more effective fish ladders. They include large water-saving basins designed to retain and recirculate some of the lockage water. They also bypass Miraflores Lake, which separates two sets of original locks on the Pacific side and restricts organisms from moving into Lake Gatun (Fig. 1).

Future scenarios for shipping and fish invasions at both canals

The Panama and Suez canals are important corridors for world trade; their use shortens shipping distances and reduces CO₂ and sulfur emissions. When they were originally built, little was known or thought about the environmental consequences of their construction. However, the considerable body of knowledge now available on the risk of NNS introductions can inform future environmental risk assessments. Changes in shipping routes due to ongoing shifts in trade and climate change may alter usage patterns of both canals¹⁵. Tariffs, transit times and capacity are all factors that influence competition between the two canals and contribute to the rationale for canal expansions. Climate change may also alter the pace of NNS introductions through the canals: the ‘tropicalization’ of the Mediterranean is expected to provide conditions more suitable for establishment of Lessepsian migrants from the Red Sea¹⁶. Similarly, recurring drought in Panama is expected to reduce freshwater input to Lake Gatun and potentially increase salinity and the risk of marine NNS transiting the canal. There are hundreds of native species of marine fishes on the Pacific and Atlantic coasts of Panama that are known to tolerate brackish water (Supplementary Note 1), and even a slightly brackish canal could allow some to cross to the opposite ocean.

Now is the time to incorporate these economic, social and environmental scenarios with scientific knowledge about

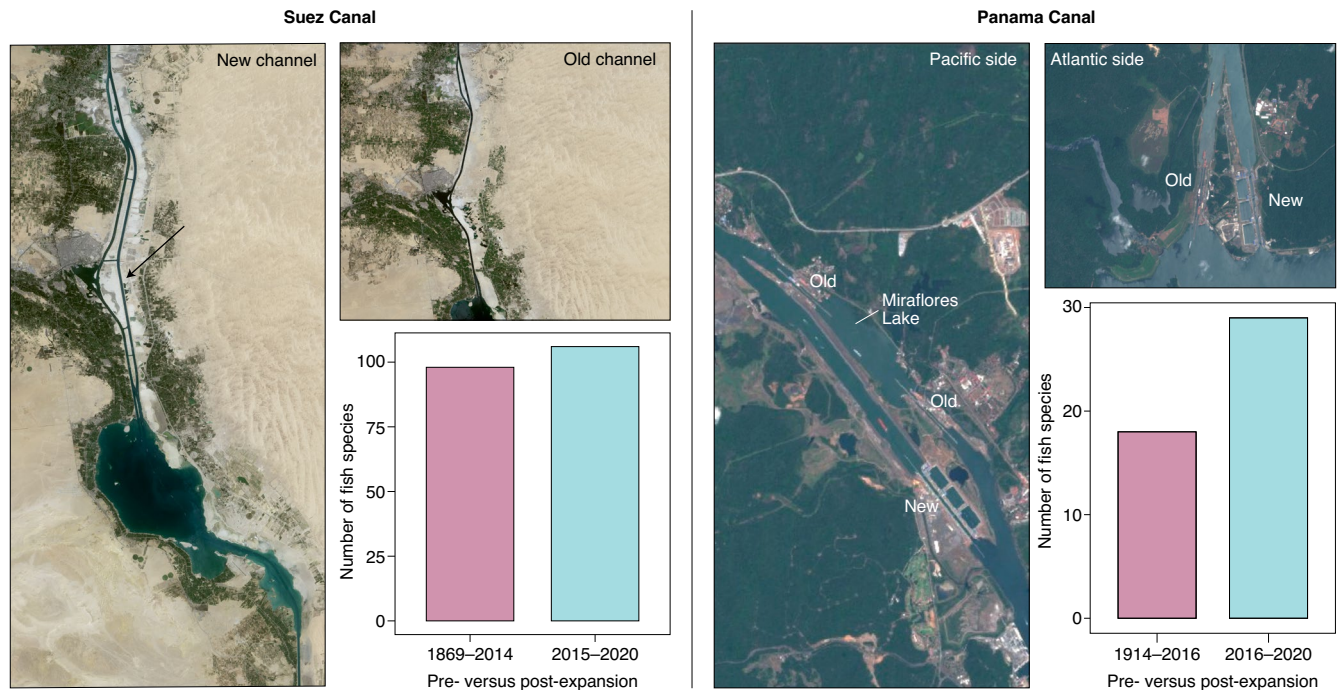


Fig. 1 | Major, recent expansion works in the Suez and Panama canals, and the increase in non-native marine fish species in the Mediterranean Sea (Suez) and Lake Gatun (Panama). Note the dual channels of the Suez Canal, large recirculation (water-saving) basins beside the new Panama locks, and old Pacific locks with Miraflores Lake in between. For fish data, see Supplementary Tables 1 and 2. Credit: Suez Canal images adapted from NASA Earth Observatory images by Jesse Allen, using Landsat data from the US Geological Survey (USGS) Global Visualization Viewer (GloVis); Panama Canal images contain modified Copernicus data (2018) processed by Sentinel Hub.

the risk posed by NNS. The introduction of the Indo-Pacific lionfish into the Greater Caribbean¹⁷ serves as an example of possible ecosystem consequences of the introduction of NNS through the two canals. The lionfish became a Lessepsian migrant invading the Mediterranean in around 2012, and enhanced access to that sea may have facilitated its ongoing rapid population expansion there¹⁸. The lionfish, which has severely impacted Caribbean reefs through its consumption of native fishes and crustaceans¹⁷, is an ecologically resilient species that can tolerate low salinity conditions. Its presence near the Atlantic entrance to the Panama Canal poses a risk for it invading the Eastern Pacific if increased salinification of Lake Gatun continues.

The risks of transporting NNS are being addressed as part of a more sustainable agenda for the shipping industry. The United Nations Convention on the Law of the Sea (UNCLOS) and the Convention on Biological Diversity (CBD) incorporate mandates for member states to prevent and manage NNS introductions¹⁹. These conventions, to which both Egypt and Panama are signatories, are suitable instruments to develop practices based on science for environmental impact

assessments. Further, through the 2017 Ballast Water Management Convention, the International Maritime Organization (IMO; the UN agency responsible for sustainable shipping) has implemented guidelines and obligations to reduce the spread of NNS via ship ballast water, sediment and hull biofouling^{20,21}. We suggest that canals should be explicitly included in these legal agendas. Considering the slow pace of international policy making, an additional way to manage NNS in canals could be to engage key actors of the shipping industry that are willing to address this issue in the quest for a more sustainable ocean economy²². The UN Decade of Ocean Science for Sustainable Development (2021–2030) provides the ideal framework to accelerate the science and management needed to control NNS in canals and more broadly in the shipping industry.

In addition, several measures could be considered now to decrease and mitigate the risk of ongoing and future invasions through these canals. Re-salinizing the Bitter Lakes using brine from desalinization plants at the Suez Canal²³ has been proposed, although careful consideration of possible unintended consequences would be needed. At the Panama Canal, the freshwater nature of Lake Gatun has been an effective barrier

for most marine species, and that can be restored. Past actions to limit NNS in the Great Lakes of North America could provide alternative approaches. For example, environmental DNA²⁴ and sonar detection²⁵ could be used for studying movements of NNS in the canals, and acoustic, electric and hydrological fish deterrents^{26,27} could be tested. Combined with the appropriate decision-support tools²⁸, these measures could enable effective management of NNS. Finally, the socio-ecological consequences of NNS introduced via the two canals are poorly understood. In the Mediterranean, NNS have replaced native species in several fisheries and blooms of unwanted NNS, such as jellyfish, impact tourism^{6,29}. Any measure to manage NNS in canals should include all stakeholders and acknowledge all potential socio-ecological and economic effects. □

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Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41559-020-01301-2>.

Supplementary information

A new wave of marine fish invasions through the Panama and Suez canals

In the format provided by the
authors and unedited

Supplementary Materials for

A new wave of marine fish invasions through the Panama and Suez Canals

Supplementary Table 1. Lessepsian fish introductions into the Mediterranean Sea from the Red Sea before the Suez Canal expansion (pre-2015) and after (post-2015). Source: Mediterranean EASIN (<http://alien.jrc.ec.europa.eu/SpeciesMapper/>).

Species	Common name	Family	pre-2015	post-2015
<i>Ablennes hians</i>	Flat needlefish	Belonidae		X
<i>Abudefduf vaigiensis</i>	Indo-Pacific sergeant	Pomacentridae	X	
<i>Acanthopagrus bifasciatus</i>	Twobar seabream	Sparidae	X	
<i>Alepes djedaba</i>	Shrimp scad	Carangidae	X	
<i>Apogonichthyoides pharaonis</i>	Pharaoh cardinalfish	Apogonidae	X	
<i>Argyrops filamentosus</i>	Soldierbream	Sparidae		X
<i>Atherinomorus forskalii</i>	Red Sea hardyhead silverside	Atherinidae	X	
<i>Callionymus filamentosus</i>	Blotchfin dragonet	Callionymidae	X	
<i>Chaetodon austriacus</i>	Blacktail butterflyfish	Chaetodontidae	X	
<i>Chaetodon larvatus</i>	Hooded butterflyfish	Chaetodontidae	X	
<i>Champsodon capensis</i>	Gaper	Champsodontidae	X	
<i>Champsodon nudivittis</i>	Nakedband Gaper	Champsodontidae	X	
<i>Cheilodipterus novemstriatus</i>	Indian Ocean twospot cardinalfish	Apogonidae	X	
<i>Coryogalops ocheticus</i>		Gobiidae	X	
<i>Crenidens crenidens</i>	Karanteen seabream	Sparidae	X	
<i>Cryptocentrus caeruleopunctatus</i>	Harlequin prawn-goby	Gobiidae	X	
<i>Cyclichthys spilostylus</i>	Spotbase burrfish	Diodontidae	X	
<i>Cynoglossus sinusarabici</i>		Cynoglossidae	X	
<i>Decapterus russelli</i>	Indian scad	Carangidae	X	
<i>Diplogrammus randalli</i>	Randall's fold dragonet	Callionymidae		X
<i>Dussumieria elopoides</i>	Slender rainbow sardine	Clupeidae	X	
<i>Encrasicholina gloria</i>	Red Sea anchovy	Engraulidae	X	
<i>Epinephelus areolatus</i>	Areolate grouper	Serranidae		X
<i>Epinephelus coioides</i>	Orange-spotted grouper	Serranidae	X	
<i>Epinephelus fasciatus</i>	Blacktip grouper	Serranidae	X	
<i>Epinephelus geoffroyi</i>		Serranidae		X
<i>Epinephelus malabaricus</i>	Malabar grouper	Serranidae	X	
<i>Equulites elongatus</i>	Elongate ponyfish	Leiognathidae	X	
<i>Equulites klunzingeri</i>		Leiognathidae	X	
<i>Etrumeus golanii</i>		Clupeidae	X	
<i>Fistularia commersonii</i>	Bluespotted cornetfish	Fistulariidae	X	
<i>Glaucostegus halavi</i>	Halavi ray	Glaucostegidae	X	

<i>Gymnothorax reticularis</i>		Muraenidae	X	
<i>Hemiramphus far</i>	Black-barred halfbeak	Hemiramphidae	X	
<i>Herklotsichthys punctatus</i>	Spotback herring	Clupeidae	X	
<i>Himantura leoparda</i>	Leopard whipray	Dasyatidae		X
<i>Himantura uarnak</i>	Honeycomb stingray	Dasyatidae	X	
<i>Hippocampus fuscus</i>	Sea pony	Syngnathidae	X	
<i>Hyporhamphus affinis</i>	Tropical halfbeak	Hemiramphidae	X	
<i>Jaydia queketti</i>	Spotfin cardinal	Apogonidae	X	
<i>Jaydia smithi</i>	Smith's cardinalfish	Apogonidae	X	
<i>Lagocephalus guentheri</i>	Diamondback puffer	Tetraodontidae	X	
<i>Lagocephalus sceleratus</i>	Silver-cheeked toadfish	Tetraodontidae	X	
<i>Lagocephalus suezensis</i>		Tetraodontidae	X	
<i>Leiognathus berbis</i>	Berber ponyfish	Leiognathidae		X
<i>Liza carinata</i>	Keeled mullet	Mugilidae	X	
<i>Lutjanus argentimaculatus</i>	Mangrove red snapper	Lutjanidae	X	
<i>Monotaxis grandoculis</i>	Humpnose big-eye bream	Lethrinidae	X	
<i>Muraenesox cinereus</i>	Daggertooth pike conger	Muraenesocidae	X	
<i>Nemipterus randalli</i>	Randall's threadfin bream	Nemipteridae	X	
<i>Ostorhinchus fasciatus</i>	Broadbanded cardinalfish	Apogonidae	X	
<i>Ostracion cubicus</i>	Yellow boxfish	Ostraciidae	X	
<i>Oxyurichthys petersi</i>		Gobiidae	X	
<i>Papillojuliceps longiceps</i>	Tentacled flathead	Platycephalidae	X	
<i>Parablennius thysanias</i>	Tasseled blenny	Blenniidae	X	
<i>Parexocoetus mento</i>	African sailfin flyingfish	Exocoetidae	X	
<i>Parupeneus forsskali</i>	Red Sea goatfish	Mullidae	X	
<i>Pelates quadrilineatus</i>	Fourlined terapon	Terapontidae	X	
<i>Pempheris rhomboidea</i>		Pempheridae	X	
<i>Petroscirtes ancylodon</i>	Arabian fangblenny	Blenniidae	X	
<i>Platycephalus indicus</i>	Bartail flathead	Platycephalidae	X	
<i>Plotosus lineatus</i>	Striped eel catfish	Plotosidae	X	
<i>Pomacanthus imperator</i>	Emperor angelfish	Pomacanthidae	X	
<i>Pomacanthus maculosus</i>	Yellowbar angelfish	Pomacanthidae	X	
<i>Pomadasys stridens</i>	Striped piggy	Haemulidae	X	
<i>Priacanthus hamrur</i>	Moontail bullseye	Priacanthidae	X	
<i>Priacanthus sagittarius</i>	Arrow bulleye	Priacanthidae	X	
<i>Pteragogus trispilus</i>		Labridae	X	
<i>Pterois miles</i>	Devil firefish	Scorpaenidae	X	
<i>Rachycentron canadum</i>	Cobia	Rachycentridae	X	
<i>Rastrelliger kanagurta</i>	Indian mackerel	Scombridae	X	
<i>Rhabdosargus haffara</i>	Haffara seabream	Sparidae	X	
<i>Rhynchoconger trewavasae</i>		Congridae	X	
<i>Sardinella gibbosa</i>	Goldstripe sardinella	Clupeidae	X	
<i>Sargocentron rubrum</i>	Redcoat	Holocentridae	X	

<i>Saurida lessepsianus</i>		Synodontidae	X	
<i>Scarus ghobban</i>	Blue-barred parrotfish	Scaridae	X	
<i>Scomberomorus commerson</i>	Narrow-barred Spanish mackerel	Scombridae	X	
<i>Sebastapistes nuchalis</i>		Scorpaenidae	X	
<i>Siganus javus</i>	Streaked spinefoot	Siganidae	X	
<i>Siganus luridus</i>	Dusky spinefoot	Siganidae	X	
<i>Siganus rivulatus</i>	Marbled spinefoot	Siganidae	X	
<i>Silhouettea aegyptia</i>	Red Sea goby	Gobiidae	X	
<i>Sillago suezensis</i>		Sillaginidae	X	
<i>Sorsogona prionota</i>	Halfspined flathead	Platycephalidae	X	
<i>Sphyraena chrysotaenia</i>	Yellowstripe barracuda	Sphyraenidae	X	
<i>Sphyraena flavicauda</i>	Yellowtail barracuda	Sphyraenidae	X	
<i>Spratelloides delicatulus</i>	Delicate round herring	Clupeidae	X	
<i>Stephanolepis diaspros</i>	Reticulated leatherjacket	Monacanthidae	X	
<i>Stolephorus indicus</i>	Indian anchovy	Engraulidae		X
<i>Synanceia verrucosa</i>	Stonefish	Synanceiidae	X	
<i>Synchiropus sechellensis</i>	Seychelles dragonet	Callionymidae	X	
<i>Terapon jarbua</i>	Jarbua terapon	Terapontidae	X	
<i>Terapon puta</i>	Small-scaled terapon	Terapontidae	X	
<i>Tetrosomus gibbosus</i>	Humpback turretfish	Ostraciidae	X	
<i>Torpedo sinuspersici</i>	Variable torpedo ray	Torpedinidae	X	
<i>Torquigener flavimaculosus</i>	Yellowspotted puffer	Tetraodontidae	X	
<i>Trachurus indicus</i>	Arabian scad	Carangidae	X	
<i>Tridentiger trigonocephalus</i>	Chameleon goby	Gobiidae	X	
<i>Trypauchen vagina</i>		Gobiidae	X	
<i>Tylerius spinosissimus</i>	Spiny blaasop	Tetraodontidae	X	
<i>Tylosurus choram</i>	Red Sea houndfish	Belonidae	X	
<i>Tylosurus crocodilus crocodilus</i>	Hound needlefish	Belonidae	X	
<i>Upeneus moluccensis</i>	Goldband goatfish	Mullidae	X	
<i>Upeneus pori</i>	Por's goatfish	Mullidae	X	
<i>Vanderhorstia mertensi</i>	Mertens' prawn-goby	Gobiidae	X	

Supplementary Table 2. Marine fish species recorded in the Lake Gatun at the Panama Canal pre-2016 and post-2016. The Origin column indicates whether the species is native to the Pacific or the Atlantic oceans.

Species	Common name	Family	Origin	Pre-2016 ¹	Post-2016 ²
<i>Achirus mazatlanus</i>	Mazatlan sole	Achiridae	Pacific	X	
<i>Cathorops tuya</i>	Besudo sea catfish	Ariidae	Pacific	X ⁵	X
<i>Strongylura marina</i>	Atlantic needlefish	Belonidae	Atlantic		X
<i>Caranx bartholomaei</i>	Yellow jack	Carangidae	Atlantic	X ⁵	
<i>Caranx hippos</i>	Crevalle jack	Carangidae	Atlantic		X ³
<i>Caranx latus</i>	Horse-eye jack	Carangidae	Atlantic		X ³
<i>Centropomus ensiferus</i>	Swordspine snook	Centropomidae	Atlantic	X ⁵	
<i>Centropomus parallelus</i>	Fat snook	Centropomidae	Atlantic	X ⁵	X ³
<i>Centropomus pectinatus</i>	Tarpon snook	Centropomidae	Atlantic	X ⁵	
<i>Centropomus undecimalis</i>	Common snook	Centropomidae	Atlantic	X ⁵	X ³
<i>Centropomus viridis</i>	White snook	Centropomidae	Pacific	X	
<i>Elops affinis</i>	Machete	Elopidae	Pacific	X	
<i>Elops smithi</i>	Malacho	Elopidae	Atlantic		X
<i>Anchoa parva</i>	Little anchovy	Engraulidae	Atlantic	X ⁵	X
<i>Lycengraulis grossidens</i>	Atlantic sabretooth anchovy	Engraulidae	Atlantic		X
<i>Diapterus auratus</i>	Irish mojarra	Gerreidae	Atlantic		X
<i>Diapterus peruvianus</i>	Peruvian mojarra	Gerreidae	Pacific	X	
<i>Diapterus rhombeus</i>	Caitipa mojarra	Gerreidae	Atlantic		X
<i>Eucinostomus jonesii</i>	Slender mojarra	Gerreidae	Atlantic		X
<i>Eugerres brasiliensis</i>	Brazilian mojarra	Gerreidae	Atlantic	X ⁵	X
<i>Eugerres lineatus</i>	Streaked mojarra	Gerreidae	Pacific	X	
<i>Eugerres plumieri</i>	Striped mojarra	Gerreidae	Atlantic	X ⁵	
<i>Gerres cinereus</i>	Yellow fin mojarra	Gerreidae	Atlantic	X	
<i>Lutjanus colorado</i>	Colorado snapper	Lutjanidae	Pacific		X ^{3,4}
<i>Dajaus monticola</i>	Mountain mullet	Mugilidae	Both	X	
<i>Mugil curema</i>	White mullet	Mugilidae	Both	X ⁵	X
<i>Megalops atlanticus</i>	Atlantic Tarpon	Megalopidae	Atlantic	X	X
<i>Micropogonias furnieri</i>	Whitemouth croaker	Sciaenidae	Atlantic		X
<i>Cynoscion albus</i>	Whitefin weakfish	Sciaenidae	Pacific		X ³

Note: Ten other species collected in the lake prior to 2016 [*Atherinella chagresi* (Atherinopsidae), *Eleotris picta*, *E. pisonis*, *Gobiomorus dormitor*, *G. maculatus*, *Leptophilypnus fluviatilis* (Eleotridae); *Awaous banana*, *Parrella lucretiae* (Gobiidae); *Microphis lineatus*, *Pseudophallus elcapitanensis* (Syngnathidae)] are small fishes, in which adults live in freshwater and brackish habitats, rather than marine habitats, and in many cases likely were in streams in areas now occupied by the canal before it was constructed.

1. Species reported by Hildebrand (1939), Breder (1944), Zaret & Paine (1973), Averza et al. (2004), and Sharpe et al. (2017) between 2013 and 2016 (prior to opening of the new locks).
2. Sampling conducted with the same methods as Sharpe et al (2017) at four localities (Cuipo, Escobal, Nueva Providencia and Arenosa) in Lake Gatun between November 2019 and March 2020.
3. Species increasingly captured by recreational fishers (voucher photographs) in Lake Gatun in 2018-2020.
4. Species registered by Panama Canal Authority (2017).
5. Species reported by Sharpe et al. (2017) in Lake Gatun between 2013-2015

Supplementary Table 3. Changes in fish species composition at Cuipo, Lake Gatun using standardized gillnet sampling (see details in Sharpe et al. 2017) in 2013-2016 (n = 22) vs 2019-2020 (n=6). Marine species in bold.

Cuipo (2013-2015)	Cuipo (2019-2020)
<i>Astronotus ocellatus</i>	<i>Eugerres brasiliensis</i>
<i>Cichla monoculus</i>	<i>Caranx latus</i>
<i>Cyphocharax magdalenae</i>	<i>Micropogonias furnieri</i>
<i>Eugerres brasiliensis</i>	<i>Centropomus parallelus</i>
<i>Hemiancistrus aspidolepis</i>	<i>Centropomus undecimalis</i>
<i>Hoplias microlepis</i>	<i>Diapterus auratus</i>
<i>Isthmoheros tuyrense</i>	<i>Roeboides guatemalensis</i>
<i>Mesonauta festivus</i>	
<i>Oreochromis niloticus</i>	
<i>Parachromis managuensis</i>	
<i>Roeboides guatemalensis</i>	
<i>Tilapia rendalli</i>	

Supplementary Table 4. Other sampling stations in November 2019 (with approximate coordinates in parenthesis) dominated by marine fishes with no standardized fish sampling prior to 2016. Sample size at each location = 3.

Escobal (9° 14.6197' N, 79° 56.0848' W)	Nueva Providencia (9° 15.1862' N, 79° 51.5155' W)
<i>Elops smithi</i>	<i>Diapterus rhombeus</i>
<i>Caranx latus</i>	<i>Diapterus auratus</i>
<i>Eugerres brasiliensis</i>	<i>Eucinostomus jonesii</i>

Supplementary Table 5. Surface salinity measurements at different station in the Lake Gatun between 2019-2020. Coordinates correspond to locations for gillnet sampling of fishes

Station: georeferenced coordinates	Date	Salinity (ppt)
Escobal area		
9° 14.8155' N, 79° 55.6805' W	2019-11-15	0.48
9° 14.6197' N, 79° 56.0848' W	2019-11-15	0.48
9° 13.3620' N, 79° 56.6162' W	2019-11-15	0.43
9° 12.5160' N, 79° 56.4166' W	2020-03-13	0.43
9° 14.7918' N, 79° 55.5699' W	2020-03-13	0.47
9° 15.2458' N, 79° 55.8861' W	2020-03-13	0.49
9° 15.4575' N, 79° 56.0682' W	2020-03-13	0.49
9° 08.7780' N, 79° 57.4491' W	2019-11-27	0.29
9° 11.5215' N, 79° 57.0840' W	2019-11-16	0.40
Cuipo area		
9° 06.1152' N, 79° 59.8462' W	2019-11-26	0.19
9° 06.0668' N, 80° 00.5677' W	2019-11-26	0.18
9° 05.4358' N, 79° 59.5715' W	2019-11-26	0.19
9° 06.0972' N, 80° 00.1371' W	2020-02-27	0.21
9° 05.8362' N, 79° 59.7343' W	2020-02-27	0.19
9° 05.1454' N, 79° 59.1630' W	2020-02-27	0.20

Supplementary Table 6. Historical surface salinity measurements (ppt) at two stations near the Gatun Locks (Escobal and Bateria 35) by the Panama Canal Authority (<https://micanaldepanama.com/nosotros/cuenca-hidrografica/>) (accessed on 01.05.2020). Station abbreviation and UTM coordinates are given in parenthesis.

Year	Escobal (ESC; 613957, 1010765)		Bateria 35 (BAT; 614566, 1014757)	
	Mean	Max	Mean	Max
2003	0.03	0.04	0.03	0.04
2004	0.03	0.04	0.04	0.04
2005	0.04	0.04	0.04	0.04
2008	<0.10	0.10	<0.10	<0.10
2009	<0.10	<0.10	<0.10	<0.10
2010	0.04	0.05	0.04	0.05
2012	<0.10	<0.10	<0.10	<0.10
2013	<0.10	<0.10	<0.10	<0.10
2014	<0.10	<0.10	<0.10	<0.10
2015	<0.10	<0.10	<0.10	<0.10
2016	0.12 ¹	0.18	0.13 ¹	0.22
2017	0.20	0.25	0.23	0.27
2018	0.21	0.26	0.22	0.25

¹ Some values in the reports appeared as <0.10. To calculate means a value of 0.1 was given to those cells.

Supplementary Note 1. Marine fish species tolerant to fresh- and brackish waters in the Pacific and Caribbean coasts of Panama

To determine the number of marine fish species that could tolerate fresh- or brackish water in the Caribbean Sea and the Eastern Pacific Ocean and thus potentially cross the Panama Canal we consulted two comprehensive sources: (1) the International Union for the Conservation of Nature (IUCN) Red list marine fish assessments for both regions (Information provided by Christi Linardich to DR Robertson) and (2) Smithsonian online marine fish information systems from both regions [Robertson & Allen (2015), Robertson and Robertson & van Tassell (2019)].

1. IUCN Red list source (Polidoro et al. 2012; Linardich et al. 2019)

Total number of marine fish species assessed from both coasts: 1302

Marine fish species able to tolerate freshwater: 127

Marine fish species able to tolerate brackish water: 437

2. Smithsonian online information systems (available at <https://bioeodb.stri.si.edu/sftep/en/pages> and <https://bioeodb.stri.si.edu/caribbean/en/pages>).

By using the Research Engine function and filtering the number of marine fish by functional group and salinity tolerance (freshwater or brackish) present in the Panamanian Exclusive Economic zone the following results are obtained:

Eastern Pacific

Marine fish species able to tolerate freshwater: 122

Marine fish species able to tolerate brackish water: 266

Caribbean Sea

Marine fish species able to tolerate freshwater: 87

Marine fish species able to tolerate brackish water: 214

Both databases indicate that > 100 species of marine fish able to tolerate freshwater in these two regions, and that if brackish water tolerant species are considered, the numbers increase to ~400 species.

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