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REVIEWS

Atlantic Tarpon in the Tropical Eastern Pacific 80 years after it first crossed the Panama Canal

Gustavo A. Castellanos-Galindo · D. Ross Robertson · Bernald Pacheco-Chaves · Arturo Angulo · Carolina Chong-Montenegro

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Abstract The opening of the Panama Canal ~ 100 years ago created a migration pathway between the Caribbean Sea and the Pacific Ocean for euryhaline marine organisms that can cope with passage through 65 km of freshwater. The Atlantic Tarpon, *Megalops atlanticus*, a prized recreational-fishery species in its native geographic range, where it is considered "Vulnerable" by the IUCN Red List, is one species that has swum through the canal to the Tropical Eastern Pacific (TEP). Since Tarpon were first seen in the Pacific locks of the Panama Canal in the late 1930′s, ~ 25 y after the opening of the canal, and large adults were subsequently observed in Panama Bay over many years, it has remained unclear whether this species has become established and is reproducing in the TEP. Here we review evidence showing that the Tarpon's TEP geographic range now extends along ~ 2600 km of the coastline (Guatemala to the Colombia/Ecuador border), and that adults are moderately common in the southern parts of that area. General ichthyoplankton surveys in the TEP over the last 50 year have not detected any Tarpon larvae. Small juveniles have been

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G. A. Castellanos-Galindo (✉)
Leibniz Centre for Tropical Marine Research (ZMT), Fahrenheitstr. 6, 28359 Bremen, Germany
e-mail: gustavoa80@yahoo.com

D. R. Robertson
Smithsonian Tropical Research Institute, Balboa, Panama
e-mail: drr@stri.org
URL: https://stri.si.edu/scientist/d-ross-robertson

B. Pacheco-Chaves
Departamento de Investigación y Desarrollo, Instituto Costarricense de Pesca y Acuicultura, Puntarenas 333-5400, Costa Rica

A. Angulo
Museo de Zoología and Centro de Investigación en Ciencias del Mar y Limnologia (CIMAR), Universidad de Costa Rica, San Pedro de Montes de Oca, 11501–2060 San José, Costa Rica

A. Angulo
Laboratório de Ictiologia, Departamento de Zoologia e Botânica, UNESP, Universidade Estadual Paulista "Júlio de Mesquita Filho", Rua Cristóvão Colombo, 2265, São José do Rio Preto, SP CEP 15054–000, Brazil

C. Chong-Montenegro
School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY 11794, USA

found throughout the main part of its TEP range, up to 700 km from the Panama Canal. As such fish typically are sedentary and have never been seen inside the Panama Canal, they most likely were spawned in the TEP. At present, nothing is known about the basic ecology of Tarpon in the TEP and possible effects it might have on native ecosystems there.

Keywords Ecological effects · Invasive species · Maritime canals · *Megalops atlanticus* · Reproduction

Introduction

While maritime canals provide significant savings to seaborne trade by shortening routes, they also serve as invasion corridors for non-native species (Gollasch et al. 2006). Since their openings in the late 19th and early 20th centuries the three main existing canals in the world (Kiel, Suez and Panama) have been differentially involved in the introduction of alien aquatic biota in the world's oceans (Gollasch et al. 2006). While some of these introduced species have had deleterious effects on native ecosystems in areas to which they have spread, in most cases the ecological consequences are poorly known and difficult to assess. However, not all introductions lead to large populations that have adverse impacts on ecosystems into which they are introduced (Davis et al. 2011; Parker et al. 2013).

The Panama Canal, the most important shipping passage in the Western Hemisphere, is an aquatic invasion hotspot (Ruiz et al. 2009; Seebens et al. 2013). To some extent the permeability of this waterway to alien species is reduced by its freshwater nature, in the form of the Gatun and Miraflores lakes, which prevent successful transit of species not able to tolerate such conditions (McCosker and Dawson 1975). However, since its opening in 1914, the Panama Canal has allowed the transit, either ship-mediated or unaided, of various aquatic organisms in both directions between the Caribbean Sea and the Tropical Eastern Pacific Ocean (TEP). About 90 species, including both plants and animals, have been documented in or passing through the Panama Canal (reviewed in Cohen 2006), and this number is likely to increase due to the recent expansion of the canal's lock systems as well as a general increase in traffic through the canal (Muirhead et al. 2015).

The first reference to a successful species transfer in the Panama Canal was that of Hildebrand (1937, 1939), who documented the presence of adult Atlantic Tarpon, *Megalops atlanticus* Valenciennes 1847 (hereafter referred to as Tarpon), in the seaside locks at the Pacific entrance to the canal in the mid 1930s, and stated that this species had transited to the Pacific end of the canal. Ten years later Swanson (1946) observed Tarpon immediately outside the Pacific entrance of the Panama Canal, but found no indications of their presence further afield in Panama Bay. Since then the range over which sightings of Tarpon have occurred has gradually expanded, from various points in Panama Bay, to western as well as eastern Panama (Diaz and Tribaldos 1991), and to Costa Rica and Colombia (Cohen 2006), with more recent reports in Costa Rica and southern Colombia (e.g., Castellanos-Galindo and Zapata 2013; Robertson and Allen 2015; Neira and Acero P 2016).

Given a recent increase in the number of sightings of adult and juvenile Atlantic tarpon in the TEP, this review summarizes what currently is known about the presence of this species in this region. Here we address three main questions: (1) What is the current geographic range of Tarpon in the TEP and is that range expanding? (2) Is successful reproduction of Tarpon occurring in the TEP; i.e. are older juveniles being produced from eggs spawned in that region. (3) What is the potential for Tarpon to become invasive (i.e. to have detrimental effects on native ecosystems) in the TEP. Finally we suggest some research topics that need to be addressed to better understand the population biology of TEP Tarpon and the ecological consequences of its presence there.

Methods

The Panama Canal

The canal consists mainly of a large, topographically complex freshwater lake, 425 km^2 Gatun Lake, which is 26 m above sea-level and is connected to the sea by sets of locks at either end. Prior to 2016 there were three locks at each end of the canal, a single set of three at Gatun on the Caribbean end, and two sets at the Pacific end: one lock at Pedro Miguel, and two locks at Miraflores, the lower one of which connects to the sea. Pedro Miguel and Miraflores locks are separated by

2 km wide freshwater Miraflores Lake. There is a 13 km long, narrow cut (Gaillard Cut) through the continental divide connecting the western edge of Gatun Lake at Gamboa to the Pedro Miguel locks. The level of Gatun Lake is maintained by inflow from the Chagres River, which enters the lake at Gamboa. The shipping route through the canal is ~ 65 km long. There is a spillway dam at Gatun that drains overflow from Gatun Lake into the final reaches of the Chagres river, which enters the sea ~ 20 km from Gatun locks, and another draining overflow from Miraflores Lake, at Miraflores adjacent to the Miraflores locks. In 2016 new, larger locks were added at each end of the canal to accommodate larger ships. Each of those is a single set of three locks and the Pacific set bypasses Miraflores Lake entirely.

Biology of *Megalops atlanticus* in its native range

The Atlantic Tarpon is one of two members of the family Megalopidae, in the order Elopiformes (Nelson et al. 2016). The native geographic range of the only other member of the family, the Indo-Pacific Tarpon (*Megalops cyprinoides*) does not overlap with that of the Atlantic Tarpon and *M. cyprinoides* is not known east of the Society Islands, 5500 km west of the TEP (see https://www.iucnredlist.org/species/166868/46642796).

The native range of *M. atlanticus* includes warm temperate, subtropical and tropical waters of both the Eastern and Western sides of the Atlantic Ocean. In the Western Atlantic its range extends from Nova Scotia to Argentina, whereas in the Eastern Atlantic the species is distributed from Senegal to Angola (Tropical West Africa), with exceptional records on the coasts of Ireland, France, Spain and Portugal (Crabtree et al. 1995; Adams et al. 2012, Ferraris 2016). Virtually all published information about the biology of this species relates to the Northwest Atlantic population. The Tarpon is a large [to 2.5 m total length (TL) and 161 kg], highly migratory, predatory pelagic fish with a long life span (up to 43–78 years). It matures at a large size and considerable age: minimum ~ 95 cm fork length (FL) for males and ~ 130 cm FL for females, and 7–10 years respectively, in the US, but matures at a smaller size in Costa Rica and Brazil (Crabtree et al. 1997). For simplicity here we will refer to Tarpon of 100 cm TL (equivalent to ~ 90 cm FL) or greater as adults, and those less than that size as juveniles, although some individuals in the TEP may mature at greater than 100 cm. The species has a wide tolerance to different temperatures (~ 15–40 °C), salinities (fresh to hypersaline water) and oxygen levels in the waters it inhabits (Crabtree et al. 1997; Ault 2008).

Tarpon reproduce by migrating, en masse, from near-shore waters to the edge of the continental shelf to spawn (Crabtree et al. 1992; Baldwin and Snodgrass 2008). Eggs are pelagic and leptocephalus larvae develop in offshore waters for 20-50 days, before recruiting to coastal lagoons and estuaries, where they spend the next 0.5–2 years, perhaps longer. Between that stage and when they mature Tarpon inhabit coastal and brackish waters before eventually also using freshwater environments (Rohtla and Vetemaa 2016). In the native range small juveniles mostly live in brackish habitats, but a few spend time in freshwater or hypersaline water (Rohtla and Vetemaa 2016; Seeley and Walther 2018). They often inhabit stagnant, hypoxic lagoonal and mangrove habitats that have an abundance of organic matter, and can readily survive in such habitat due to possessing an enlarged, air-breathing swim bladder, which is retained by adults. A need of these obligatorily air-breathing fishes to periodically replenish air in the swim bladder by "rolling" at the surface and their tendency to leap from the water facilitates detection of large and small Tarpon by observers. In marine habitats of Florida and the Gulf of Mexico adult Tarpon are known to roll or leap from the water, which they do day and night, an average of nine times a day (Luo and Ault 2012). Rolling occurs more frequently in hypoxic waters and at higher water temperatures. The use of hypoxic habitat by juveniles is thought to be important for their survival by providing protection from other predatory fishes that are physiologically unable to cope with low-oxygen conditions (Geiger et al. 2000). Adults are primarily coastal fishes, but readily enter rivers, including those on the Pacific coast of Panama, and commonly ascend 200 km up the Rio San Juan from the Caribbean Sea to Lake Nicaragua (Brown and Severin 2007).

Atlantic Tarpon is a highly prized species in recreational fisheries throughout its native range, particularly in the Gulf of Mexico and Caribbean Sea, where many local fisheries are thought to have collapsed due to overfishing, lack of regulation and habitat degradation (Adams et al. 2014). Currently this species is listed as Vulnerable to extinction due to these adverse conditions by the International Union for the Conservation of Nature (IUCN) in its original distribution range (Adams et al. 2012, 2014).

Data collection

For information on the location and size of Tarpon in the TEP we relied on published scientific sources, news reports that included photographs that acted as vouchers (and from which TLs could be estimated in some cases), and formal interviews of fishers. Tarpon are easy to recognize as there are no fishes in the TEP that resemble them, and they achieve a large size. Hence fishers we interviewed invariably were well aware of this species and were able to make confident assertions about their experiences relating to occurrences and sizes of individuals, and referred to it by the same Spanish common name as used in the Caribbean: Sábalo Real.

Information on the potential occurrence of Tarpon larvae in TEP waters was obtained from several published studies of regional icthyoplankton surveys. In addition we examined a set of plankton samples collected over a year in Panama Bay for the occurrence of Tarpon larvae, which are readily identifiable (Chacón Chaverri and McLarney 1992). We also obtained information on the occurrence of Tarpon larvae in plankton samples collected over an 8 year period (1991–1996) during oceanographic cruises in the Pacific coast of Colombia (Beltrán-León and Ríos 2000).

Between 2016 and 2018, we made field trips to seven sites on the Pacific coasts of Costa Rica (two sites within the Gulf of Nicoya, Tárcoles, Golfito, Térraba-Sierpe and Golfo Dulce and Osa Peninsula), 13 sites scattered along the coast of Panama and three sites in northern Colombia (Bahía Solano, El Valle and Gulf of Tribugá) (Fig. 1). During these field trips we interviewed fishers about their catches of Tarpon and whether they had caught or seen small juveniles. This information was complemented with data published in the scientific and grey literature, some of it supported by museum specimens. Confirmed records of occurrence of Tarpon at locations we sampled or conducted interviews at and those of Diaz and Tribaldos (1991) and Neira and Acero P (2016) are presented in Fig. 3 (see also Supplement Tables S1 and S2).

To assess the capacity for Tarpon to become invasive in the TEP, we used a decision-support tool developed for screening the invasiveness potential of aquatic non-native species. The Aquatic Species Invasiveness Screening Kit (AS-ISK) contains a list of 55 questions that are answered by experts to make an assessment about the potential invasibility of a species. The first 49 questions (Basic Risk Assessment—BRA) are divided in two sections: (1) biogeographical and historical traits of the evaluated taxon—13 questions, and (2) biological and ecological interactions—36 questions. Six additional questions comprise the Climate Change Assessment (CCA) module and are intended to evaluate risks associated to predicted changes in climate (see Table S1 in Copp et al. 2016). Each of the 55 questions, is required to have a level of confidence (1 = low; 2 = medium; 3 = high; 4 = very high) that is used to assign an overall confidence-level to the assessment (Copp et al. 2016).

Results and discussion

History of information on the occurrence of Tarpon in the TEP

Hildebrand (1939) documented, for the first time, the presence of Tarpon 1–2 m long in the Miraflores and Gatun lakes of the Panama Canal. In 1937 he observed four individuals of this size range at the Miraflores locks when these were de-watered, and stated that Tarpon had passed through the canal. A few years later Swanson (1946) made visits to the Pacora River, 20 miles east of the Panama Canal, over several years and questioned fishers about Tarpon in other rivers. He concluded that at that time Tarpon were not found in those rivers. McCosker and Dawson (1975) reported catches of adult specimens (1–1.5 m TL) in the Miraflores locks in the early 1970s, and that sport-fishers in the Bay of Panama often recorded catching Tarpon, although they did not observe the species at Panama City fish markets. Averza (1984) noted the capture of Tarpon at Coiba Island, in the Gulf of Chiriquí and Averza (2005) included a photograph of a 5.7 kg ($\sim$ 1 m TL) Tarpon caught in a river draining into the eastern side of Panama Bay 300 km from the Panama Canal in 1984. In the late 1980s Diaz and Tribaldos (1991) interviewed fishers at sites along the

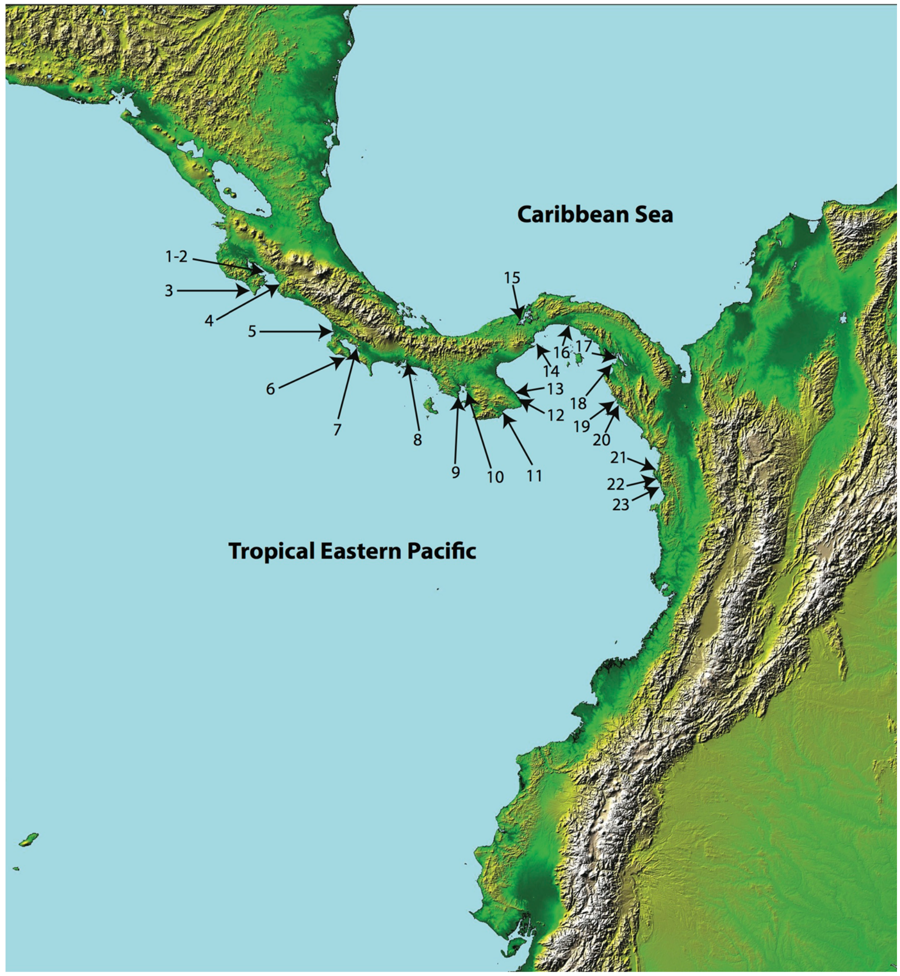

Fig. 1 Localities visited in 2016-2018 in the Tropical Eastern Pacific where field surveys and formal interviews of resident artisanal fishers where conducted during 2016-18. Name of localities and description of interviews are given in Supplemental Table S1

Pacific coast Panama, and noted Tarpon reports from 26 sites between the central Gulf of Chiriquí in western Panama and Jaque near the Panama/Colombia border on eastern side of the Gulf of Panama. They also recorded juveniles as small as ~ 0.9 kg (~ 50 cm TL) in a permanent lagoon at Punta Chame. Cohen (2006) reviewed information available on Tarpon in the TEP in the early 2000s and extended its range to southern Costa Rica and northern Colombia. Since then there have been several media reports documenting both juvenile and adult Tarpon in southern Costa Rica and Panama (e.g., http://www.ticotimes.net/2011/07/06/tarpon-on-the-pacific-coast-you-betcha.; http://www.ticotimes.net/2017/05/14/tarpon-pacific). One of us (B-PC) has recently (2016) documented the presence of Tarpon at several localities in the Gulf of Nicoya, further north in Costa Rica, and the information included here constitutes the first report of this species in that area.

Most of these "newer" records were included in a map of the distribution of Tarpon records in Robertson and Allen (2015) (https://biogeodb.stri.si.edu/sftep/en/thefishes/species/2522, accessed on 16/10/2018), which shows georeferenced records of Tarpon between the Gulf of Chiriquí and near the Panama/Colombia border. On the northern Colombian Pacific coast, Castellanos-Galindo and Zapata (2013) reported the presence of Tarpon since at least 2007, based on interview-results and photographs made available by artisanal fishers. In 2013–14 Neira and Acero P (2016) conducted interviews of fishers at 12 locations scattered along the northern part of the Pacific coast of Colombia. Those fishers reported catching Tarpon at all sites, with ~ 18% comprising small juveniles up to 50 cm TL, another 14% of large juveniles between

50 and 100 cm TL, and the remainder adults up to 250 cm TL (see Fig. 2).

Is the Tarpon's range in the Tropical Eastern Pacific increasing?

Since the reports of Swanson (1946) and McCosker and Dawson (1975) ~ 80 and ~ 45 years ago, respectively, of adult Tarpon in Panama Bay, it is evident this species has been gradually expanding its range both northwards and southwards in the TEP (Figs. 3, 4). The most recent published compilation of information on the range of Tarpon in the TEP was by Cohen (2006), who noted records between "Costa Rica and Colombia" without specifying where the sightings in those countries occurred. In September 2017 and March 2018, two small adult Tarpons, each ~ 1 m TL were captured at Acajutla, El Salvador, ~ 1700 km along the coastline from Panama Bay and ~ 350 km from the northern border of Costa Rica (Barraza 2018).

In 2018 Enrique Barraza, who reported the 2018 captures in El Salvador, provided two more pieces of information about Tarpon in that area: (1) divers reported seeing Tarpon at Los Cobanos reef, near Acajutla in about 2015; (2) a fisher provided a photograph of a Tarpon about 1.5 m long caught at Puerto San Jose, Guatemala on August 9, 2013. In the south, adult Tarpon have been found at the Colombia/Ecuador border, ca 800 km from Panama Bay. From these reports the current distribution range of Tarpons in the TEP is ~ 2600 km along the coast of six countries between Guatemala and the Colombia/Ecuador border, and has apparently expanded over the past 20 year (see Fig. 4). However, we recognize that, rather than just an expansion, this apparent increase in the Tarpon's range could reflect a combination of increased research by ichthyologists (e.g. Neira and Acero P 2016) and the greater availability of electronic media (e.g. internet and social media) to fishers, who now are able to report the catch of rare or unexpected and charismatic fish species.

Information available on movements of adult Tarpon in the Atlantic on the other hand indicates that it is quite possible that some of the adult Tarpon found in the TEP far from the entrance to the Panama Canal migrated there after passing through the canal. Data pop-up archival transmitting (PAT) tags in the Greater Caribbean used by Luo et al. (2008), for example, indicated that adult Atlantic Tarpon moved an average of 12.6 km day^{-1} (range 0–52.6 km day^{-1}). At that average rate of movement adults found in Guatemala and the Colombia/Ecuador border would have needed to travel four and 2.4 months, respectively, to get from the Pacific entrance of the Panama Canal to those sites. The smallest Tarpon that Luo et al. (2008) tagged was a fish 27 kg, which, based on lengths of fish about this weight given by Kurth (2016), likely was ~ 1.4 m TL. That fish moved 1160 km in 5–6 months. Given Tarpon's large size and migratory habits it seems a mystery why this species has not spread throughout the TEP. Limitations on suitable habitat for adults do not appear to be an issue. Aquamaps (Kaschner et al. 2016) constructs global maps of the distribution of suitable habitat for different species based on envelopes of the depth range of a species and variation in sea temperature, salinity and primary productivity throughout its native range. The Aquamap for Tarpon indicates that this species presently occupies < 50% of the suitable habitat in the TEP, which extends from the US/Mexico border, through the Gulf of California and south to central Peru (see Fig. 5).

Overfishing may be involved in restricting an expansion of Tarpon throughout the TEP. Tarpon is overfished in its native range due to artisanal fisheries and recreational fisheries that have been active for many years and are still ongoing, even though it is of no commercial interest as a food-fish, due to low palatability and an abundance of small bones scattered throughout its musculature. In Pacific Colombia a variety of uses have been found for Tarpon by artisanal fishers (Neira and Acero P 2016). The ten countries (Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador and Peru) that have coastlines bordering the TEP all have problems with overfishing (Polidoro et al. 2012), and large coastal populations of subsistence, artisanal and commercial fishers. These may have sufficient impact to inhibit the geographical and population expansion of a late-maturing, long-lived fish like Tarpon, even if it is not highly desirable as a food-fish. Finally, due to its late maturity, the small number of generations possible (~ 6–7, Adams et al. 2012, 2014) during the 80 year since Tarpon was first confirmed in the Pacific in 1946 could have limited the rate of a population expansion during the initial stages of any increase due to breeding in the TEP.

Fig. 2 Tarpon captured in different localities in the Tropical Eastern Pacific. **a** Large adult landed in Bahía Solano (6.236°N. − 77.409°W), Colombia, **b** large adult captured by sport fishers between Bahía Solano and Cabo Marzo (6.677°N, − 77.540°W) in Colombia, **c** small adult captured at the mouth of Térraba-Sierpe River (8.982°N, − 83.660°W) Costa Rica; **d** Juvenile Tarpon (∼ 50 cm TL) captured in Carate, Osa Peninsula, Costa Rica (8.430°N, − 83.436°W), **e** 1 m TL Tarpon captured at Yuca, near of Chira Island, Gulf of Nicoya, Costa Rica (10.137°N, − 85.134°W) and **f** 21 cm TL juvenile Tarpon captured at mouth of Térraba-Sierpe River, Costa Rica (8.954°N, − 83.699°W)

Is the Tarpon reproducing in the TEP?

Are small juvenile Tarpon in the Panama Canal?

Small (20–50 cm TL) juvenile Tarpon have been repeatedly caught, in small numbers, along the Pacific coast between Costa Rica and Colombia. Whether such individuals were spawned in the TEP, indicating the existence of a self-reproducing population there, or were spawned in the Caribbean and swam through the canal before being collected in the Pacific is unclear. Although small juvenile Tarpon prefer brackish water they are found in freshwater, and have been caught in the upper reaches of rivers in Belize (A Adams pers com, March 2019). Breder (1925) observed numerous Tarpon of varying sizes on the seaward side of the Gatun dam spillway that discharges from Lake Gatun, and recorded catches of fish at that point as small as 26 cm Standard Length, indicating that small juveniles do occur near the Atlantic entrance to the canal. Further, Tarpon leptocephali do enter rivers, so should be able to enter Gatun Lake by accompanying ships through the locks. To date no ichthyoplankton sampling has been done in that lake that might have detected Tarpon larvae, if present. Hence the possibility that juveniles caught in the TEP were spawned in the Caribbean cannot simply be dismissed (Cohen 2006). The presence of small juveniles in the Gatun or

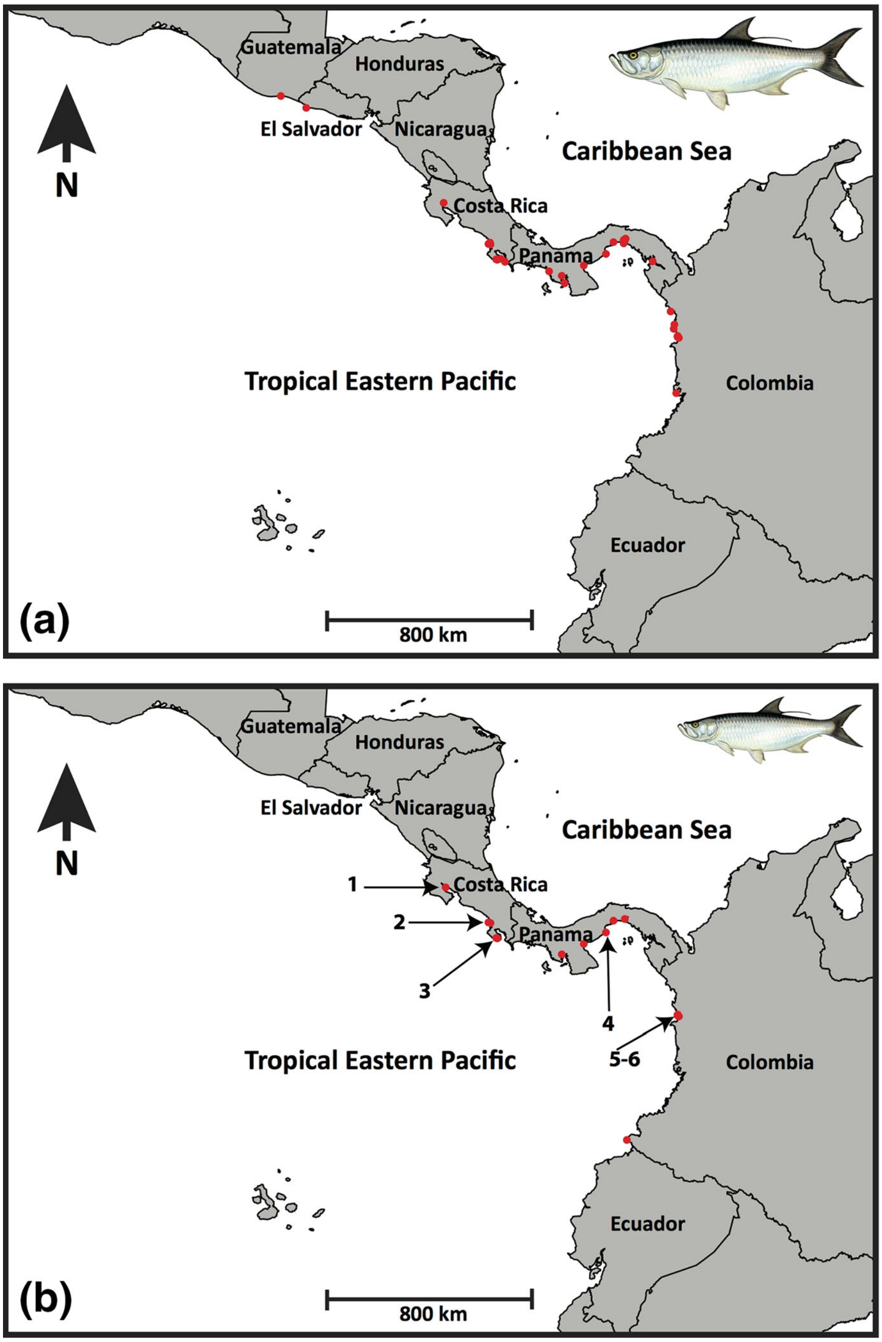

Fig. 3 Location of collected Tarpon (*Megalops atlanticus*) records in the Tropical Eastern Pacific. **a** Adult (> 1 m) specimens; **b** small (< 50 cm TL) and large juvenile (50–< 100 cm TL). Reports based on Diaz and Tribaldo (1991), Neira and Acero P (2016), and the information recently collected by the authors. Arrows in (**b**) indicate sites where small juveniles (< 50 cm TL) have been reported: (1) Bebedero River, Gulf of Nicoya, (2) mouth of Terraba-Sierpe River, and (3) Osa Peninsula in Costa Rica; (4) Punta Chame in Panama; and (5) Nuquí and (6) Coquí in Colombia. Details about localities, georeferencing coordinates, and Tarpon sizes are in Supplemental Table S2

Miraflores lakes would mean it is possible that small juveniles found along the Pacific coast originated in the Caribbean and swam through to canal to the TEP.

Reports of Tarpon by Hildebrand (1937, 1939) in the canal lakes refer only to fish of ~ 1 m TL and larger. Hildebrand (1937) specifically investigated the possibility that juvenile Tarpon were inside those lakes and concluded that they were not, that local fishers confused them with atherinids because they used the same generic common Spanish name (Sábalo vs Sábalo Real for Tarpon), and that no reproduction was occurring inside the canal. No Tarpon smaller than ~ 1 m TL have been collected inside the canal during any scientific study (Zaret and Rand 1971;

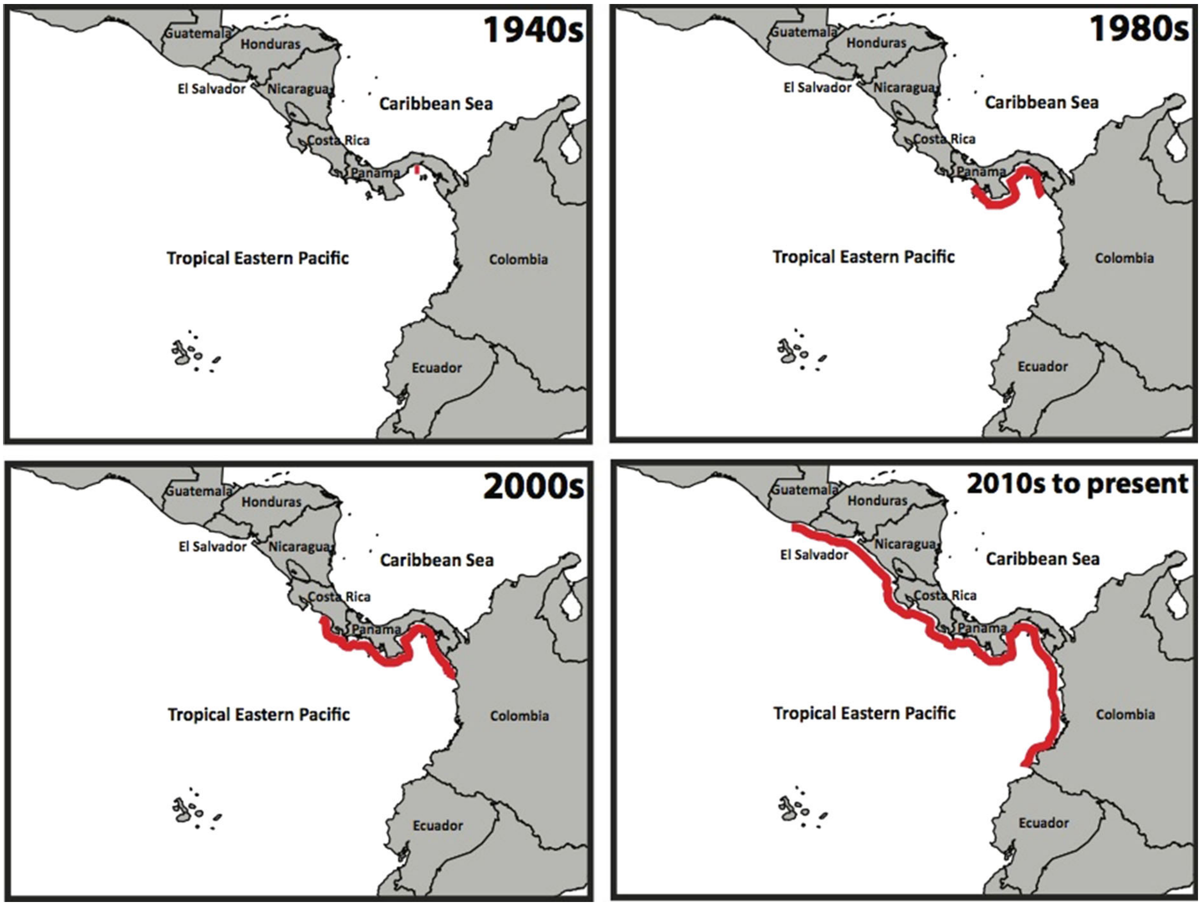

Fig. 4 Range expansion of Tarpon (*Megalops atlanticus*) in the Tropical Eastern Pacific since the 1940s

Fig. 5 Aquamap of occupied habitat in the native range of Tarpon (*Megalops atlanticus*), and environmentally equivalent habitat in the TEP

Gutiérrez et al. 1995; Smith et al. 2004; Sharpe et al. 2017). Rigoberto Gonzalez, who currently is the manager of the freshwater fish collection at STRI, previously was employed by the Aquaculture Department of the Panama Government (*Dirección Nacional de Acuicultura de Panamá*). There are more than ten thousand people living in shoreline communities scattered around Gatun Lake, and throughout 1980–1992 he worked intensively with artisanal fishers in that Lake at points scattered all around its shores to assess what they were catching (e.g. González 1993). Over the course of that work the only Tarpon he observed or obtained information about were > ~ 1 m TL (pers. comm. to DRR, 2018). Diana Sharpe spent several years (2013–2016) studying effects of invasive species on the fish fauna of Gatun Lake (Sharpe et al. 2017). Her work included gillnetting small fishes. The only Tarpon she observed in the Lake were fish on the order of 1 m TL, and she saw no smaller fish being caught during several recreational fishing tournaments she observed (pers. comm. to DRR, 2018). During May 2018 one of us (GC-G) made a two-day visit to Cuipo, a village on the northern shore of Gatun Lake with a population of 2500 people where many artisanal fishers live who fish in that lake. He made gillnet samplings at four sites along the shores of that lake near Cuipo but did not catch any Tarpon. Three active artisanal fishers resident at Cuipo whom he interviewed indicated that large Tarpon were relatively common in the lake, but they had never seen small fish.

In conclusion, an abundance of research activity in a broad range of lake habitats at various times over the past 80 year has failed to detect Tarpon smaller than ~ 1 m TL in Gatun Lake, a finding confirmed by artisanal fishers living on the edges of the lake and by recreational fishers who visit the lake. Although, in the Atlantic, small juvenile Tarpon often occur in low-accessibility habitats, the habit of regularly rolling and leaping from the surface, particularly in hypoxic and warm waters, should have made them detectable if present in Gatun Lake. We conclude that, although an absence of evidence of juveniles in that lake does not represent indisputable evidence of their absence there, all existing information indicates that only adult Tarpon occur in Gatun and Miraflores lakes. Thus only adults seem likely to have migrated through the canal from the Caribbean to the TEP, although some of the adults in those lakes may include fish that have reentered the canal from the Pacific, after initially crossing from the Caribbean.

Tarpon larvae in the TEP?

We obtained data on the possible occurrence of Tarpon larvae in the TEP from four sources: (1) Between 1967 and 1968, EASTROPAC II cruises involving four different vessels made extensive plankton samplings in the TEP. Three hundred and fifty-five plankton-sampling stations between 20°N and 5°S and from 77°W to 120°W were made during those cruises. Most stations were oceanic, but coastal areas also were included (see Fig. 1 in Ahlstrom 1971). About 26 stations were sampled in the coastal and oceanic areas of Costa Rica, Panama and Colombia. No Elopiform larvae were collected during those sampling campaigns. (2) Ramírez-Coghi (1986), Molina-Ureña (1996) and Beltrán-León and Ríos (2000) collected coastal and oceanic ichthyoplankton from the Pacific coast of Costa Rica and Colombia between 1985 and 1998 during 18 different oceanographic cruises and an 8-month survey of an estuarine system in the Gulf of Nicoya, Costa Rica. No Tarpon larvae were recorded by those authors. (3) More recent (since 2008) ichthyoplankton sampling in the Costa Rican and Colombian Pacific has not recorded Tarpon leptocephali (A.R. Ramírez-Coghi and B. Beltrán-León, pers. comm. to AA and GC-G, 2017). Off the Pacific coast of Colombia, B. Beltrán-León has collected coastal ichthyoplankton samples during the past 20 years as part of different monitoring schemes. Yearly ERFEN (*Estudio Regional del Fenómeno El Niño*) cruises have been made to monitor ENSO effects, at 25 stations distributed throughout the Colombian Exclusive Economic Zone in the Pacific Ocean. B. Beltrán-León has analyzed samples from these cruises since 2000. Other research cruises along the mangrove-dominated coast of the southern Colombian Pacific, with monthly ichthyoplankton monitoring at 24 stations, were made between 2008 and 2010 (see details in Zapata et al. 2013). No Tarpon leptocephali were collected during any of those cruises (B. Beltrán-León, pers. comm. to GC-G, 2017) (4) In July 2017, plankton samples collected at the Naos Island Laboratory near the Pacific entrance to the Panama Canal were examined with a stereoscope by G C-G to evaluate the presence of Tarpon larvae. These samples were obtained by Rachel Collin of the Smithsonian Tropical Research Institute between March 2015 and June 2016, using a pump that collected water at high tides during both day and night at c.a. 1 m depth. Each sample consisted of 100 gallons of pumped water that was filtered with a 100 µm mesh size net. No Tarpon larvae were found in any of the 315 plankton samples collected in that program.

Thus, over the last 50 years, extensive general ichthyoplankton sampling programs in the general area of the TEP where adult Tarpon occur have not produced any Tarpon larvae. This may be due to the lack of a directed sampling (cf Crabtree et al. 1992) aimed at detecting larval Tarpon in offshore areas of the TEP or intercepting them when they enter coastal habitats at the end of their larval lives. Alternatively, current systems in the TEP may not be conducive to retention of sufficient Tarpon larvae to achieve measureable levels of abundance in non-directed plankton surveys. Finally, due to the long generation time of Tarpon ($\sim$ 12 year; Adams et al. 2012) the population of spawners simply may not have built up to the level where they produce quantities of leptocephali that are detectable in general plankton surveys. Low densities of larvae in the sea or entering coastal habitats at particular places and times (both unknown for the TEP) would be much harder to detect than 50 cm juveniles in coastal environments. Hence in the case of Tarpon larvae in the TEP we do not regard absence of evidence as evidence of absence.

Juvenile Tarpon in the TEP

Previous publications on Tarpon in the TEP and the results of fisher interviews (see Table S1) show that juvenile Tarpon have been found at various sites in central and southern Costa Rica, the Gulf of Panama, and Colombia (Fig. 3b). During the late 1980s Diaz and Tribaldos (1991) found small juveniles in a brackish lagoon of Punta Chame (8.61°N, − 79.74°W), 40 km from the Pacific entrance to the Panama Canal. That lagoon disappeared in 2009 as a result of storm erosion (http://www.panamaamerica.com.pa/content/punta-chame-pierde-su-atractivo-lago-salado.). In 2017, four fishers of Punta Chame had memories of catching juvenile Tarpon in that lagoon prior to its disappearance.

Small juvenile Tarpon ($\sim$ 17 cm TL) have been captured using block nets in mangrove creeks of northern Brazil (Barletta et al. 2003). The macrotidal regime and mangrove seascapes found in North Brazil resemble those found on the Pacific coasts of Colombia and Panama, although the tide range at the Brazil site is only about half that in the Gulf of Panama (see Figure S1). However, over the last 10 years, block-net sampling at several localities of the Pacific coast of Colombia, and more recently in Panama, has not produced any juvenile Tarpon (Castellanos-Galindo and Krumme 2013; GC-G unpublished information). Small juvenile Tarpon, 20 cm and $\sim$ 30 cm TL, recently have been captured at southern Costa Rica, and juveniles $<$ 50 cm TL have been reported in Colombia and Panama (Figs. 2d and f; 3b). However, these individuals have been few and far between in time and space. In the Atlantic, small juvenile Tarpon tagged mostly in Florida have shown strong site-fidelity, with 50% of them captured at the same site and almost 90% recaptured within 5 km of the initial capture over periods of $\sim$ 8–9 months (Kurth 2016). This immobility supports the notion that small juveniles caught in the Pacific distant from the Panama Canal were spawned in the Pacific.

Whereas adult Tarpon may be sufficiently mobile to be able to cover the entire TEP range currently occupied by this species, small juveniles captured recently in southern Costa Rica are unlikely to have migrated $\sim$ 700 km from the Panama Canal to where they were caught. The same applies to small juvenile Tarpon reported from Pacific Colombia $\sim$ 400 km from the Panama Canal. Unlike the situation with highly mobile adults, for which capture location per se provides no information about where they originated, the locations of small juveniles in the Pacific far from the Panama Canal entrance do provide an indication of which ocean they were spawned in.

Suitability of coastal habitat in the TEP for juvenile Tarpon after their larval stage?

In the West Atlantic small juvenile Tarpon entering coastal habitats at the end of their larval lives rely, in large part, on hypoxic brackish coastal lagoons that are thought to provide "safe-harbor" from predators unable to cope with such conditions (Chacón Chaverri and Mclarney 1992; Mace et al. 2018; Wilson et al. 2019). For example, Lewis et al. (1983) showed that in the fish community in upper mangrove zones of the Indian River Lagoon in Florida Tarpon was the only top carnivore present. In the northwest Atlantic such "safe-harbor" habitat is abundant, due to the existence of extensive coastal lagoon systems and a small tidal range (< 1 m throughout the Caribbean and Gulf of Mexico; see Figure S1) that produces very little change in the areal extent of such habitat over the course of the tidal cycle, as well as minimizing tidal flushing that, by enhancing oxygenation of such habitat, would provide greater access to predators. However, in the southern half of the TEP, centered on the Gulf of Panama, the tidal range is much greater; up to 6 m (Figure S1). In consequence of this large tidal range the amount of potential juvenile habitat would change drastically over the tidal cycle because large areas of mangroves and other intertidal habitats are completely drained at low tide (our observations). In addition the large tidal range likely increases tidal flushing of intertidal habitats that enhances oxygenation and reduces the availability of hypoxic, low-predation habitat. There is some evidence that such is the case: in macrotidal mangrove areas in the Gulf of Montijo, Pacific coast of Panama (7.75°N, − 81.20°W), oxygen concentrations are generally high (5.72 mg/l; GC-G, unpublished data) and rates of fish predation in mangroves on the Pacific coast of Panama and Colombia may be higher than in mangroves on the northwest Atlantic (Pülmanns et al. 2018; G. Castellanos-Galindo, unpublished data). This leads us to suggest that successful reproduction of Tarpon in the part of the TEP centered on the Gulf of Panama may be limited in part by a general lack of hypoxic, "safe-harbor", coastal lagoon habitats of the type apparently preferred by small juvenile Tarpon in the Atlantic (Geiger et al. 2000).

Nevertheless, there are a few, possibly suitable, coastal lagoons with permanent water in the southern Pacific of Costa Rica (Fig. 6), and Punta Chame (Panama) prior to 2009, in which juvenile Tarpon have been collected. Such habitat may also be much more available in the extensive coastal lagoonal systems along the Pacific coast of El Salvador, and, particularly, southern Mexico, where the tidal range is much smaller than in the southern half of the TEP (Figure S1).

Is *Megalops atlanticus* likely to become invasive in the TEP?

The results of the AS-ISK assessment indicate that Tarpon has a relatively high risk of becoming invasive in the TEP. The BRA score obtained for this species (27; see Table 1) is a little higher than that obtained in a recent assessment carried out for Cobia (*Rachycentron canadum*) in the TEP (BRA = 20, which indicates a moderately high risk of becoming invasive; Castellanos-Galindo et al. 2018). Indications that Tarpon may be already reproducing in the TEP and its high tolerance to environmental stress (e.g. wide range of salinity and aquatic oxygen values) are primarily responsible for the higher BRA value for Tarpon than for Cobia. However, nothing currently is known about the trophic ecology of Tarpon in the TEP, a first step towards assessing what impact it might have. The only biological information available on Tarpon in the TEP that bears on the question of its

Fig. 6 Permanent coastal lagoons in Costa Rica (Golfo Dulce) that could represent suitable habitat for juvenile Tarpon in the TEP: **a** Pejeperro (8.42°N, − 83.40°W) and **b** Pejeperrito (8.44°N, − 83.44°W) in the Osa Peninsula. Juvenile Tarpon have been collected at Carate beach on the seaward side of these two lagoons (see Fig. 2d)

Table 1 Summary of AS-ISK scores for Tarpon (*Megalops atlanticus*) in the TEP (see Supplemental Table S3 for details). For details about the scoring system see Table S1 of Copp et al. (2016)

Statistics	Score
Basic Risk Assessment (BRA)	27.0
BRA + Climate Change Assessment (CCA)	33.0
A. Biogeography/Historical	**3.0**
1. Domestication/Cultivation	0.0
2. Climate, distribution and introduction risk	1.0
3. Invasive elsewhere	2.0
B. Biology/Ecology	**24.0**
4. Undesirable (or persistence) traits	6.0
5. Resource exploitation	7.0
6. Reproduction	0.0
7. Dispersal mechanisms	4.0
8. Tolerance attributes	7.0
C. Climate change	**6.0**
9. Climate change	6.0
Confidence	0.73

actual impact is that relating to its restricted geographic range, the low abundance of juveniles, and apparent low abundance of adults. That combination points to a low current impact.

Eighty years after it first entered the TEP, and with the continued ability to do so since that event, Tarpon does not appear to have a substantial population in that region. Non-native organisms, including marine fishes, often exhibit substantial lags before their populations expand to the point that they have significant impacts in their new environment (Crooks 2005, Azzurro et al. 2016). While 80 years may seem a long time, that represents only 6–7 generations for Tarpon (see Adams et al. 2012). Low current abundance of Tarpon may in part reflect a long lag-period of expansion for a slow-growing, late-maturing, long-lived organism like Tarpon.

While Tarpon may have the potential to become invasive by having adverse impacts in the TEP its demography and population status in its native range indicates that is not particularly likely. Fishing and habitat degradation in its native range represent major threats for this long-lived, slow maturing species that have put its population at risk there. A population in the TEP will face the same threats and there is no reason to think it will be more successful at coping with them than the population in the Atlantic.

Conclusions and some directions for future research

Although it is clear that Tarpon can survive in and, almost certainly, is breeding to some extent in the TEP its ecological impact there is unknown. Research on the trophic ecology, growth and reproductive status (gonadal activity) of this species in the TEP would help clarify what impact it might be having and how successful it is at exploiting local food resources.

If we are correct in suggesting that reproduction of Tarpon in the TEP could be limited by the lack of suitable habitat (hypoxic, "safe-harbor" tidal lagoons; see Wilson et al. 2019) for young juveniles after settlement at the end of the pelagic larval stage—then its population may never expand much beyond its present level. Assessment of the availability of such habitats, of physical conditions (O_2, salinity, pH) in them and of their predatory fish faunas in both microtidal (Mexico, see Figure S1) and macrotidal parts of the TEP, would be useful in that context.

Recent advances in the use of salinity proxies (Sr/Ca ratios and $\delta^{13}C$) deposited in the scales of Tarpon and in the otoliths of other fishes have allowed quantification of variation in the dependency of individuals over the course of their life histories on fresh-, brackish- and marine habitats in their native ranges (Rohtla and Vetemaa 2016, Seeley and Walther 2018, Shirai et al. 2018). Confirmation of successful Tarpon reproduction in the TEP would be provided by the demonstration, using such salinity proxies, that some individuals in the TEP never entered freshwater during the juvenile stage, and thus must have completed early development in the TEP rather than passing through the Panama Canal as juveniles.

There is as yet little information on the comparative genetics of the TEP and West Atlantic populations of Tarpon. Studies based on both mtDNA (Blandon et al. 2002) and microsatellites (A. Adams pers comm to G C-G, 2017) that compared TEP Tarpon to those from the native range have involved too few TEP individuals to be very informative. Comparative studies of genetic variation and genetic assessment of the possibility of adaptation through natural selection in TEP Tarpon (cf. Bernardi et al. 2016) and data on use of habitats of different salinities (as indicated by isotope analyses) by that species in TEP and West Atlantic could also provide a basis for understanding how a non-native species such as Tarpon copes with a very different new environment.

The recent expansion of the Panama Canal seems likely to have effects on the transfer of alien species between TEP and Western Atlantic (Muirhead et al. 2015; MacIsaac et al. 2016). The additional, larger lock systems, which began functioning in 2016, incorporate a recirculating system that involves inflow of seawater, and are expected to increase Gatun Lake salinity (Wijsman 2013). Hence this likely will enhance the exchange of euryhaline marine species between both sides of the Isthmus. More and larger locks and increased shipping movements through the canal inevitably will facilitate the transit of more Tarpon. Monitoring of Tarpon catches on the Pacific coast of Panama could indicate the extent to which that is occurring.

An increasing recreational fishing sector in Colombia, Panama, Costa Rica and potentially, elsewhere in the TEP, can benefit from the existence of Tarpon in the region (e.g. Tarpon fishing in the Bayano River of Pacific Panama: http://www.panamacanalfishing.com/). Much of the information presented here has come from local sport fishing operators in those countries. Future research on this species should involve partnerships with this sector in order to understand more comprehensively the implications of the presence of a population of Tarpon that is slowly expanding in the TEP.

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