Natural history study of an understudied sea catfish species from Panama (Siluriformes: Ariidae)

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The semi-anadromous sea catfish species *Cathorops tuyra* (Ariidae, Besudo sea catfish) from the Tropical Eastern Pacific has been found reproductively active in the freshwater rivers and lakes of the Panama Canal. Despite growing concerns for biodiversity, reports on natural history are lacking for many Neotropical sea catfishes. We aimed to provide data on the diet and seasonal timing of spawning of *C. tuyra* for an autochthonous, semi-anadromous, brackish water population from Rio Santa Maria and an allochthonous freshwater non-migrating population from Rio Chagres, an affluent to the Panama Canal, to understand how changing from semi-anadromous to residential lifestyle affects the natural history of a species. Fish from both sampling sites were dissected and information on stomach content, size, weight, parasitic load, sex, maturity, and number of eggs were recorded. In Rio Chagres, there was a female bias and individuals were larger and in pre-spawning mode compared to Rio Santa Maria. Parasite prevalence was low in Rio Chagres and zero in Rio Santa Maria. The diets were very similar between populations: gastropods, bivalves, and insects were the most important prey items in both rivers representing a diverse omnivorous diet that is similar to that of other catfishes.

Keywords: Cathorops, Diet, Freshwater invasion, Natural history, Panama Canal.

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El bagre de mar semi-anádromo *Cathorops tuyra* (Ariidae, Bagre besudo) del Pacífico Oriental Tropical se encuentra reproductivamente activa en los ríos y lagos del Canal de Panamá. A pesar de la creciente preocupación por la biodiversidad, faltan informes sobre la historia natural de muchos de los bagres Neotropicales. Nuestro objetivo es proporcionar datos básicos sobre la dieta y el momento del desove estacional de *C. tuyra* para una población autóctona semi-anádroma de agua salobre de Río Santa María y una población alóctona residente de agua dulce de Río Chagres para comprender cómo el cambio de un estilo de vida semi-anádromo a residencial afecta la historia natural de una especie. Se disecaron peces de ambos sitios de muestreo y se registró la información de contenido del estómago, tamaño, peso, carga parasitaria, sexo, madurez y número de huevos. En Río Chagres hubo un sesgo femenino y los individuos eran más grandes y estaban en modo pre-desove que en Río Santa María. La prevalencia de parásitos fue baja en el Río Chagres y cero en Río Santa María. Las dietas fueron muy similares entre poblaciones: gasterópodos, bivalvos e insectos fueron las presas más importantes en ambos ríos, lo que representa una dieta omnívora diversa, que es similar a la de otros bagres.

Palabras clave: Canal de Panamá, *Cathorops*, Dieta, Historia natural, Invasión de agua dulce.

INTRODUCTION

A few decades after the finalization of the construction of the Panama Canal in 1914, researchers discovered that marine and brackish species dispersed into the freshwater rivers and lakes of Panama and even have crossed the oceanic divide (McCosker, Dawson, 1975; Smith *et al*., 2004). One of the species that dispersed into the freshwater rivers that feed the Panama Canal is the anadromous or semi-anadromous *Cathorops tuyra* (Meek & Hildebrand, 1923), which was known to occur in Eastern Pacific estuaries and lower reaches of rivers (Fischer *et al*., 1995; McDowall, 1988; Lucas, Baras, 2001). The species has been observed in the artificial lakes of the Panama Canal — Lake Gatùn and Lake Alajuela (Fig. 1) (Stange *et al*., 2016; Sharpe *et al*., 2017), as well as in Gatùn River, west of Panama City (A. Vega, 2015, pers. comm.). The *Cathorops tuyra* populations in Lake Alajuela (D. Sharpe, 2015, pers. comm.) and in Chagres River (M. Stange, June 2018, pers. obs.) are reproductively active. However, it remains unknown what impact these fish may have on other species as they spread farther into the Panama Canal ecosystem or possibly cross over to the Atlantic drainage of the Canal where they could potentially hybridize with other *Cathorops* species from which they have been separated since the final closure of the Panama Canal 2.8 million years ago (Stange *et al*., 2018). *Cathorops tuyra* are also of commercial relevance as they are an important food source for the Indigenous people of South and Central America (Cooke, Jimenez, 2004). Despite their importance, much is unknown about the species with the IUCN listing the species as Data Deficient (DD) (Cooke *et al*., 2010) and it is difficult to assess what impact their invasion may have with little natural history information available. Feeding studies can provide significant insights that are vital for elucidating the biology of a single species as well as understanding how entire ecosystems function (Slobodkin, 1994). These insights include information on habitat preferences, prey selection, ecosystem structure, and energy transfers within food webs (Hyslop, 1980). An understanding of the diet of a species can also be valuable in assessing ecosystem integrity and decision-making with regards to natural resources (Winemiller, Polis, 1996). All of this information could greatly assist in the understanding of how a *Cathorops tuyra* invasion could impact the ecosystem. For many ariid species, a thorough investigation of their migration mode, seasonal timing of migration and spawning, and their diet is lacking from the current literature. Most work in this respect has been done in Brazil and in species of commercial value (Lucas, Baras, 2002; Denadai *et al*., 2012, 2013; Avigliano *et al*., 2017). Stomach content analysis is the most convenient and often the only way available of researching the feeding habits of a particular species given limited resources (Hynes, 1950; Buckland *et al*., 2017).

The goal of this work was to collect fundamental natural history data by comparing feeding items (*e.g*., plants, crustaceans) and reproductive activity (*e.g*., resting, developing eggs) from *Cathorops tuyra* populations in two habitats, one native brackish and one allochthonous freshwater population. We applied stomach content analysis, visual inspection and measurements to assess parasite prevalence, size distributions, and reproductive activity in these two populations. A closely related ariid species of the same genus is known to be omnivore that feeds on fish, invertebrates, plant material, and plankton (Denadai *et al*., 2013). We expect to find both populations to be omnivorous with the brackish population to be feeding mostly on mangrove species whereas the freshwater population has the potential to scavenge human organic waste that gets disposed into the Rio Chagres by nearby settlements.

MATERIAL AND METHODS

Sample Collection and Processing. We bought fish from local fishermen in Paris, Herrera, Panama, and Gamboa, Colon, Panama which did not require a collection permit. Specimens were caught approximately 13 km upstream the estuary in the freshwater part of Rio Santa Maria (08°07'04.4"N 80°33'01.7"W) and in the freshwater Rio Chagres, Puente del Rio Chagres, Colon (09°11'34.66"N 79°39'9.42"W) (Fig. 1) using hook and line (size 7 hooks), as netting is prohibited during spawning season. All specimens were caught between February 6th and 12th, 2019. We kept fish on ice at all times to slow down digestive action and transferred them to the laboratory for immediate processing following Manko (2016). We investigated a total of 101 individuals, 50 from Rio Chagres and 51 from Rio Santa Maria. A voucher specimen for *Cathorops tuyra* from Panama can be found in the fish collection of the Smithsonian Tropical Research Institute, Panama under catalog number STRI–5724.

During processing, we weighed and photographed each fish. We measured the standard (SL) and total length (TL) and carried out an external visual examination to note any special features such as injuries or ectoparasites that may impact findings. Next, we made an abdominal-ventro-sagittal incision from the anal aperture to behind the isthmus of the gills. Once the abdominal cavity was opened, we examined it and the organs for any remarkable features and determined sex by investigating the gonads for egg or semen production. Any visible endoparasites were noted and preserved in 70% ethanol for further identification. Then we removed, uncoiled, measured (DTL), and weighed the entire digestive tract before splitting it lengthwise to remove the contents, which were stored in 70% ethanol for further examination. If a digestive tract was empty, we recorded this. The emptied digestive tract was then weighed again. Next, we removed and weighed gonads. If the individual was producing eggs, we counted the eggs. To carry out prey identification, we emptied stomach contents per individual into a petri dish and identified prey to lowest possible taxonomic group under a dissecting scope. Prey were then sorted into major taxonomic prey item groups of fish, bivalves, crustaceans, gastropods, insects, plants, and other invertebrates that could not specified (including eggs and larvae). At this time, we also further analyzed preserved parasites under the dissecting scope to obtain an identification when possible.

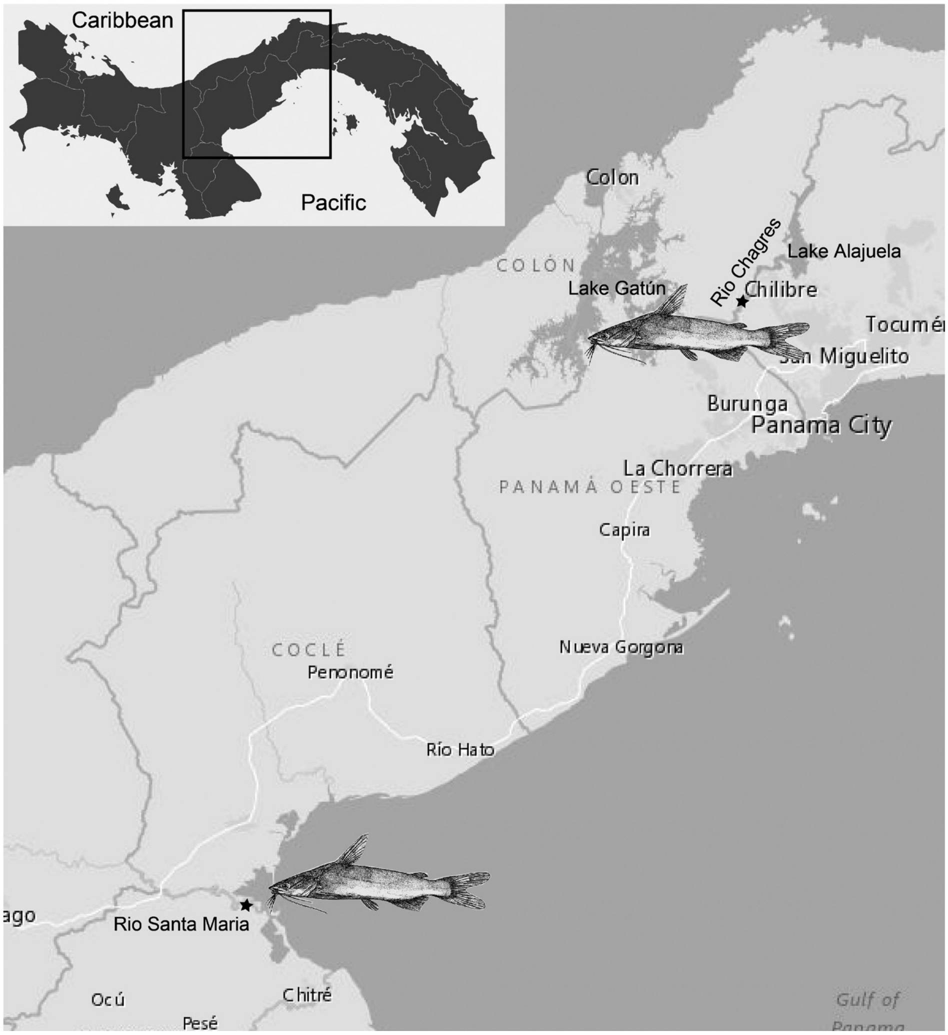

FIGURE 1 | Map of Panama and the two sampling locations indicated with stars: in Rio Santa Maria near Paris, Herrera (08°07'04.4"N 80°33'01.7"W) and in Rio Chagres, Puente del Rio Chagres, near Gamboa, Colon (09°11'34.66"N 79°39'9.42"W). We collected 50 fish from the Rio Chagres and 51 fish from the Rio Santa Maria.

Size classes. Due to lack of developmental information past the juvenile stage, division of specimens into ontogenetically informed size classes was not possible. Instead, we chose to use a size binning approach, which can take into account gape size, a major influencer on feeding (Schael *et al*., 1991; Bremigan, Stein, 1994). To facilitate comparisons of prey preference per given size class, we divided our samples in three size bins based on standard deviations from the average standard length (SL) of all fish: size class I — one standard deviation below average or smaller (20.73 cm and lower); size class II — between one standard deviation below and one standard deviation above average (20.73–27.62 cm); size class III — one standard deviation above average and larger (27.63 cm and above) (Fig. 2A).

Stomach content analysis. We recorded the presence or absence of each prey type across all individuals to express the relative importance of each prey item and to broadly assess the diet of a population (Manko, 2016). From this data the number of occurrences is summed and represented as a percentage basis using frequency of occurrence. Frequency of occurrence for each prey category was calculated as:

$$\%F_i = \frac{N_i}{N} \times 100$$

where $\%F_i$ is the frequency of occurrence of a given item *i*, N_i is the number of stomachs that contain item ***i***, and ***N*** is the total number of stomachs examined that were not empty (Hynes, 1950; Hyslop, 1980).

We did this for each size class within a river and for the totals from each river as well. This metric was used instead of a metric that includes the abundance of each prey item as this would be difficult to assess given *C. tuyra* habit of crushing prey during feeding and the severity of digestion in our samples (Cooke, Jiménez, 2008; Denadai *et al*., 2012). To easily compare the occurrence of each prey item across size classes and rivers, we made a heat map using the calculated $\%F_i$'s.

Testing for differences between Rio Chagres and Santa Maria populations. We performed analyses of co-variance (ANCOVAs) using R v.4.0.2 (R Development Core Team, 2020) and the package rstatix v.0.7.0 (Kassambara, 2021) to test for differences between populations. Residuals were verified to ensure assumptions were met for each test. We tested for (i) a difference in weight within each sex and across all sexes between populations from Rio Chagres and Rio Santa Maria while controlling for SL; for (ii) a difference in DTL between rivers while controlling for SL; and (iii) for a difference in stomach content weights while controlling for SL between rivers and between size classes within rivers. We also tested for a difference in the length-weight relationship between rivers by log transforming total length and weight values and then fitting a regression model with river as an interactor variable (Bolger, Connolly, 1989) (Fig. 2B). Additionally, we fit regressions to each river separately and tested for allometric or isometric growth by running a t-test to determine if the slopes significantly differed from three. If the slope is equal to three then the population is said to be growing isometrically, if the slope differs from three then the population is growing allometrically (Blackwell *et al*., 2000).

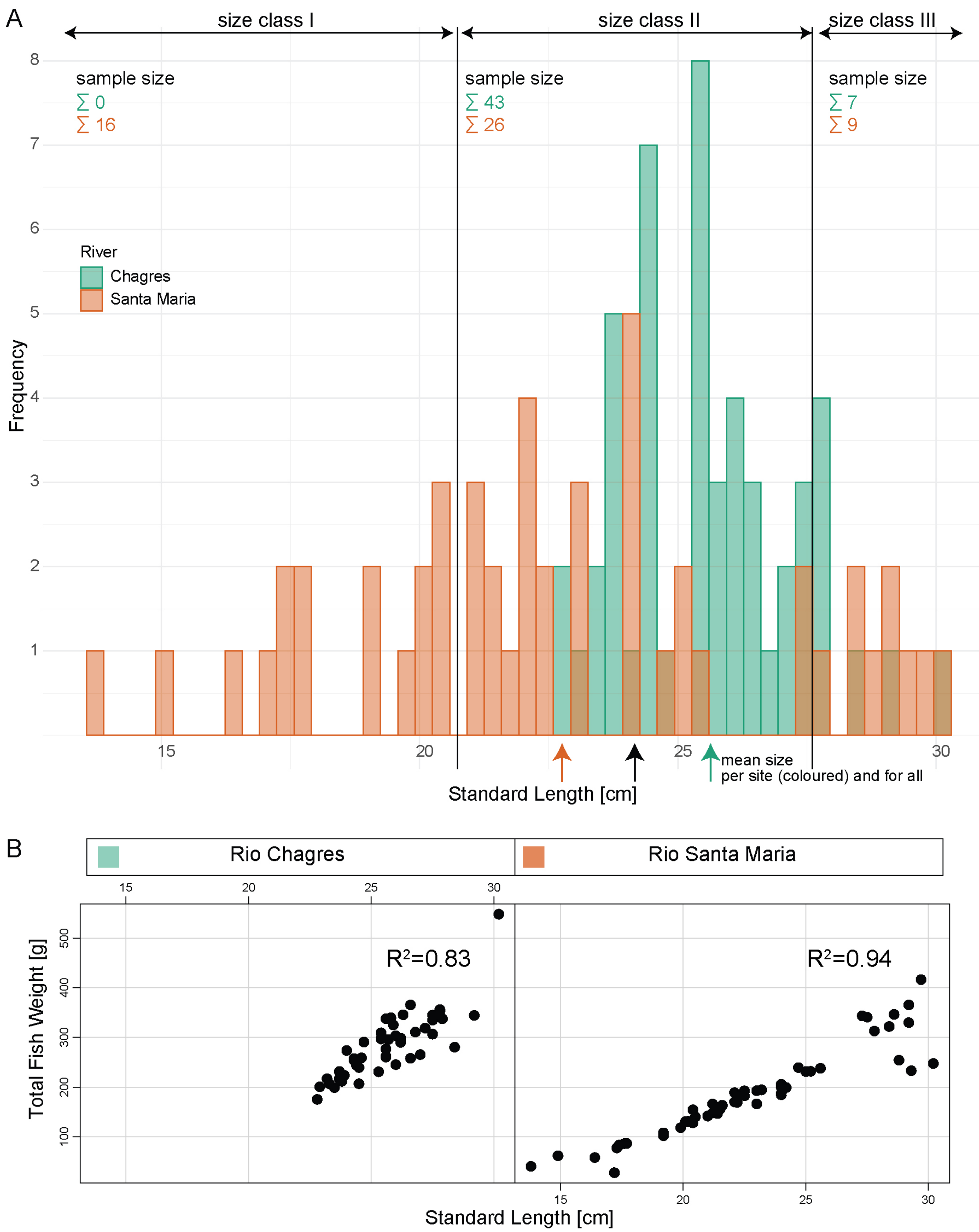

FIGURE 2 | Size distribution of *Cathorops tuyra* (February 2019) from Rio Santa Maria and Rio Chagres, Panama. **A.** Size histogram and size bins. Rio Chagres (freshwater population) in green, Rio Santa Maria (estuarine population) in orange. Size classes were defined by determining the mean standard length for all individuals (indicated by black arrow) and then going one standard deviation below and above to make the cut offs (indicated by the solid black lines) such that size class one was individuals up to one standard deviation below the average while size class three was made up of individuals above one standard deviation above average and size class two was all the individuals between those two standard deviations. The colored arrows indicate the mean standard lengths of each river. **B.** Weight-size relationship of 50 Rio Chagres and 51 Rio Santa Maria specimens.

Reproductive analysis. We calculated the average weight per egg and average gonad to body weight ratio for each size class and each river along. We then plotted the number of eggs *vs.* total gonad weight, standard length, and fish weight. We quantitatively compared the state of maturity in females of both populations by calculating the gonadosomatic index for each population (GSI [gonad weight x body weight^{-1}] x 100) (Shafi, 2012; Flores *et al*., 2015).

RESULTS

Size and weight distribution in Rio Chagres and Rio Santa Maria specimens. In Rio Santa Maria, the total length of individuals sampled ranged from 17 to 35.5 cm while the standard length ranged from 13.8 to 30.2 cm. In Rio Chagres, the total length ranged from 26.6 to 35.7 cm and the standard length ranged from 22.8 to 30.2 cm. Rio Santa Maria had 16 individuals in size class I, 26 in size class II, and 9 in size class III. Rio Chagres had 43 individuals in size class II, and 7 individuals from size class III (Fig. 2A). Notably, smaller individuals (< 26 cm) were absent from our catch in Rio Chagres, despite multiple collecting efforts. Rio Chagres sample counted 36 females, eight males, and six unassigned individuals; the Rio Santa Maria sample counted 29 females, no males, and 22 unassigned individuals.

The average (AVG) weight across all sexes, was significantly larger in individuals from Rio Chagres (uncorrected AVG = 283.5 g, size-corrected AVG = 251 g +/-5.22 g) than in individuals from Rio Santa Maria (uncorrected AVG = 186.6 g, size-corrected AVG = 218 g +/- 5.16 g) when controlling for standard length (DFn/DFd [Degrees of Freedom in the numerator/Degrees of Freedom in the denominator] = 1/98, F = 18.69, P = 0. 00004). When looking just within each sex, the difference was still significant within females (DFn/DFd = 1/62, F = 8.24, P = 0.006) and within individuals whose sex could not be identified (DFn/DFd = 1/25, F = 25.66, P = 0.00003). There were too few males in Santa Maria to test for differences between males. The length-weight relationship was not significantly different between rivers (P = 0.69). The slope of the regression was not significantly different from three in both rivers meaning that both populations are growing isometrically (Chagres: t = -0.77; DF = 48; P = 0.45 and Santa Maria: t= -0.74, DF = 49, P = 0.46).

Parasites. No external parasites were found on fish from either location. In the Rio Chagres two fish had endoparasites near the gonads and stomach and three fish had parasites near the stomach only (Fig. 3A). The parasites were a type of nematode, possibly belonging to the family Anisakidae, but could not be identified further. None of the fish from Rio Santa Maria had parasites, however, eight individuals had clear, blister-like lesions on the outside of their intestines (Fig. 3B). It is possible that these blisters may be of parasitic origin, but we could not make further identification without histology. We concluded that the few parasites found would not have any significant effect on the feeding ability of the investigated specimens since they had similar stomach content weights to unaffected individuals.

Stomach content analysis. The average DTL was not significantly different between rivers when controlling for SL (DFn/DFd = 1/98, F = 0.03, P = 0.86). Of the 50 specimens sampled at Rio Chagres, 41 (or 81%) did not have empty stomachs. A similar rate was observed in the Rio Santa Maria population since 45 out of 51 (or 88%) samples did not have empty stomachs. The average stomach content weight was significantly larger in Rio Santa Maria (uncorrected AVG = 4.86 g, size-corrected AVG = 5.42 g +/- 0.444 g) than in Rio Chagres (uncorrected AVG = 3.48 g, size-corrected AVG = 2.87 g +/- 0.422 g) when controlling for standard length (DFn/DFd = 1/83, F = 15.89, P = 0.0001, R2 = 0.23). There were no significant differences between size classes in stomach content weight (Chagres: DFn/DFd = 1/38, F = 0.1, P = 0.75; Santa Maria: DFn/DFd = 2/41, F = 0.55, P = 0.58).

We recorded a broad spectrum of ingested prey items, ranging from plant matter, fish, crustaceans, bivalves, and detritus (Fig. 4). Due to high levels of digestion, it was difficult to identify many prey items to lower taxonomic levels such as genus or species. However, *Polymesoda* sp. clam was identified in the stomach contents of many fish from Rio Santa Maria and in none of the individuals from Rio Chagres. Additionally, there were pieces of shell that were likely *Corbicula* sp. clam in stomach contents of individuals from Rio Chagres. In both rivers there were remains of snail shells (Figs. 4E–G) and in Rio Chagres some of these shells could be identified as red-rimmed melania (*Melanoides tuberculata*). There were also crab and shrimp legs identified in Rio Santa Maria but they could not be further identified. Many insects, whole or in pieces, were identified in the stomach contents. There were remains of fly wings, beetle shells and legs, and some possible ant heads (Figs. 4I and J). Insect eggs and larvae were also present in many stomachs. Although difficult to identify, there were remains of beetle larvae, dragonfly larvae, midge larvae and eggs, and chironomidae larvae (Figs. 4H, K, and L).

In Rio Chagres gastropods were the most common prey ($\%F_i = 0.659$) followed closely by bivalves ($\%F_i = 0.61$) and then insects ($\%F_i = 0.561$) (Fig. 5). Plants and crustaceans were predated on in low occurrence and there was no other invertebrate prey. When looking at size class differences in prey, there were large discrepancies between sample

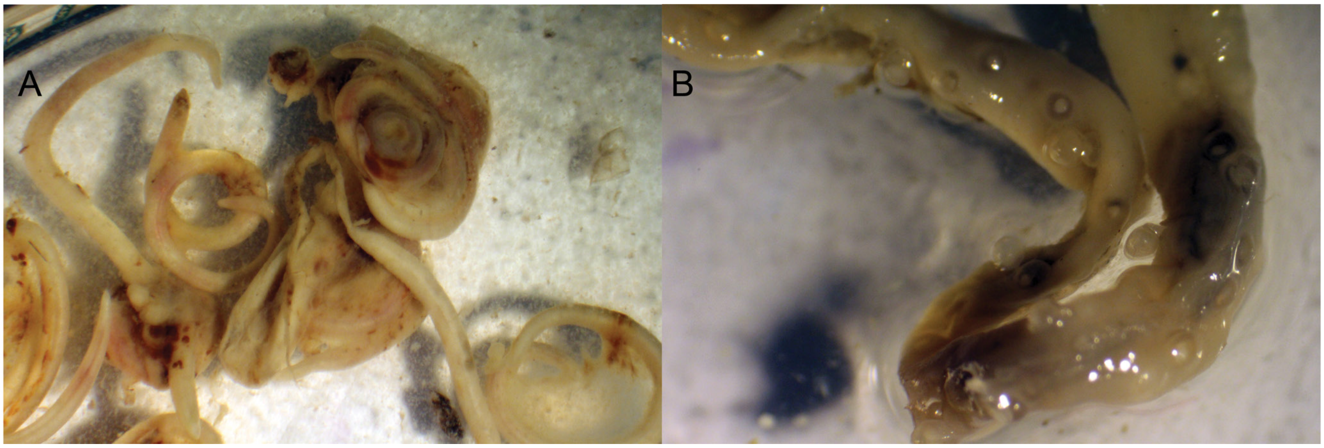

FIGURE 3 | Examples of parasites and lesions found in dissected *Cathorops tuyra* individuals. **A.** An example of parasites found in individuals from Rio Chagres, possibly belonging to the family Anisakidae. **B.** An example of the blister-like lesions on the outer wall of the intestines found in individuals from Rio Santa Maria.

sizes for each size class, with size class II having much more individuals than size class III and size class I being absent, making it difficult to draw conclusions. However, the main difference between these two size classes was that size class II predated on bivalves at a much higher rate.

In Rio Santa Maria, gastropods (%F_i = 0.489) and insects (%F_i = 0.489) were tied for the most common prey, with bivalves (%F_i = 0.467) right behind. Crustaceans were also in a fairly high occurrence (%F_i = 0.4), followed by plants and other invertebrate in lower occurrence (Fig. 5). There were very few differences in prey between size classes (Fig. 5).

FIGURE 4 | Examples of prey items identified in each category. Fish were caught in each river and taken back to the lab to be dissected. Stomach contents were removed and prey items were identified under a dissection microscope. **A** and **B** are examples of bivalves, likely belonging to Polymesoda. **C** was a fish, could not be identified any further than that. **D** is a leg from a crustacean, likely a shrimp. **E**, **F** and **G** are all examples of gastropods. **H**, **I**, and **J** are from the insect category. **K** and **L** are from the category invert others while **M** is an example of plant material. **N** is an example of unidentifiable matter which is also possibly consumed detritus.

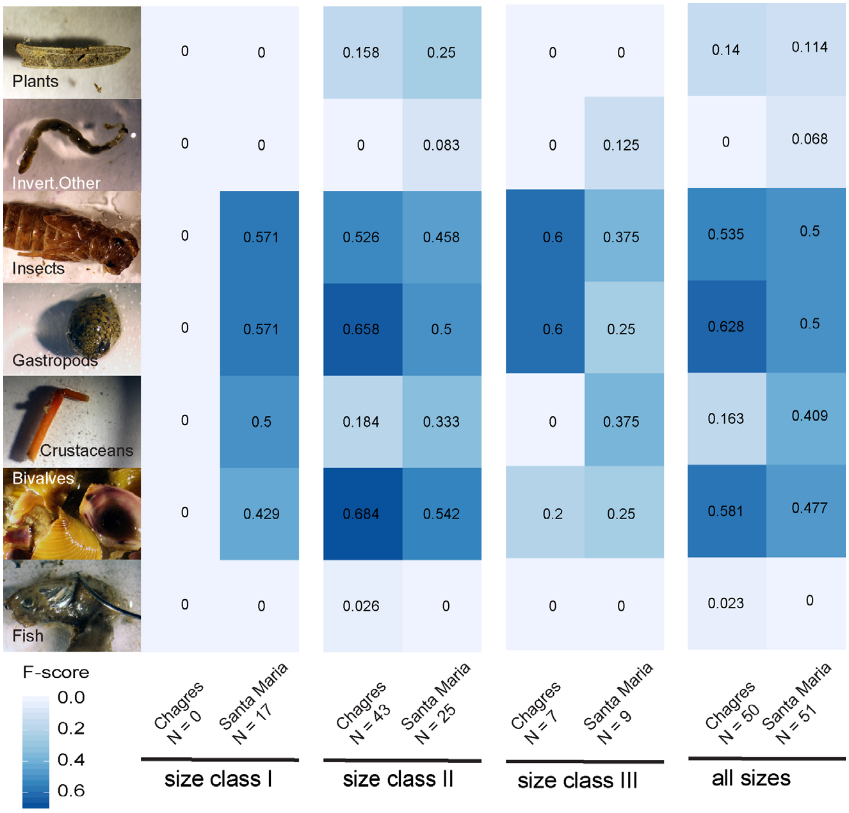

FIGURE 5 | Comparison of frequency occurrence (F-score) for seven prey categories in stomach contents of *Cathorops tuyra* broken down by size class for Chagres River (freshwater) and Santa Maria River (brackish) populations. Color intensity in the heat map represents frequency of occurrence with darker areas implying higher frequency of a given prey item recorded and vice versa. N: sample size.

Reproductive analysis and sex bias. In Rio Chagres, there appeared to be a bias towards catching reproductively active females (producing eggs). 37 unambiguous females were caught and 29 carried maturing eggs (Fig. 6A). The smallest mature female in the Rio Chagres had a standard length of 22.9 cm (Fig. 6B) and a weight of 200.5 g. In Rio Santa Maria, there were 29 unambiguous females caught and 5 carried maturing eggs (Figs. 6A–CC). There was a high incident of undetermined sex (N = 22) and individuals in size class I (N = 16) indicating a high proportion of immature individuals. The smallest mature female in Rio Santa Maria had a standard length of 24.7 cm and a weight of 239 g.

The females from the Rio Chagres had a higher average gonad weight-body weight ratio than Rio Santa Maria, whereas the average weight per egg was higher at Rio Santa Maria (Chagres: 0.398 g/egg ± 0.237 s.d., Santa Maria: 0.701 g/egg ± 0.401 s.d.). Gonad weight increased with number of eggs (Fig. 6C). As we were not able to distinguish males from females that were not reproductively active without histological analyses, the SL and weight at maturity could not be calculated for males. Additionally, the Rio Chagres population had a mean GSI of 5.33 (± 3.45 s.d.; median 5.85) and the Rio Santa Maria population a mean GSI of 2.17 (± 3.53 s.d.; median 0.76), indicating that the two populations do not breed at the same time.

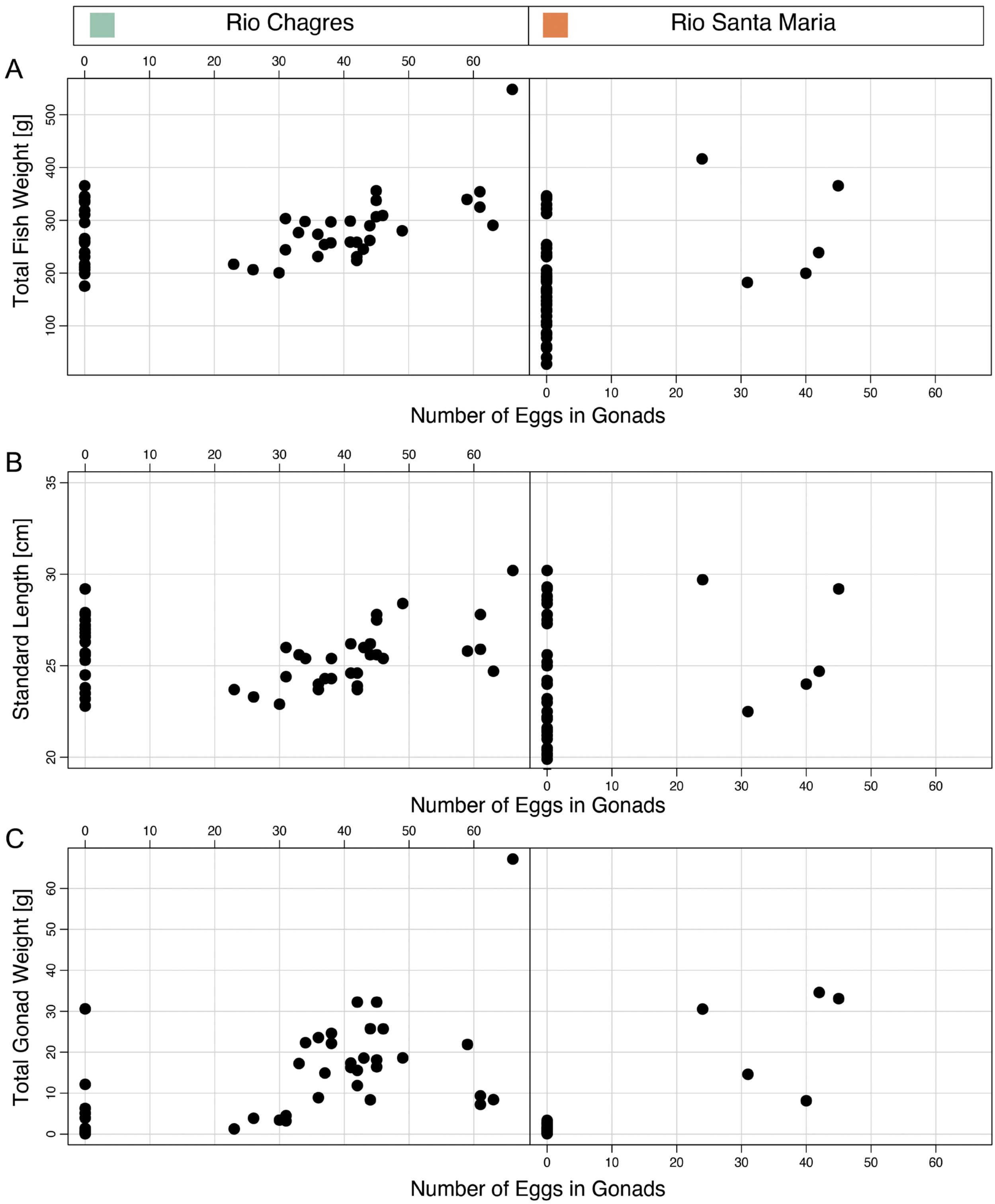

FIGURE 6 | Number of eggs of freshwater and brackish *Cathorops tuyra* females from Rio Chagres and Rio Santa Maria, Panama, respectively, plotted against total weight (**A**), standard length (**B**), and gonad weight (**C**). Specimens were caught February 2019 during mid dry season. From 50 specimens caught in Rio Chagres 37 specimens were identified as females of which 29 carried mature eggs. The Rio Santa Maria sample, contained individuals from all three size classes, 29 out of 51 specimens were identified as females, only 5 of which were in pre-spawning phase.

DISCUSSION

Populations do not differ in overall health. The prevalence of parasites was low in Rio Chagres and there were no macroscopic parasites in the Rio Santa Maria sample. This result is unexpected as during introductions, invaders are often assumed to leave behind their parasites (Torchin *et al*., 2003) or lose parasites that are brought over due to a number of pressures (Torchin *et al*., 2002). It is possible that the individuals in Rio Chagres are experiencing some new parasites for the first time as the species spreads into the area. Parasites may be present in prey items; especially since Rio Chagres is known to be increasingly polluted with human waste and garbage (Weekes *et al*., 2013; Carse, 2016). Another possibility is that the stress of habitat change is making individuals more susceptible to parasite infection in Rio Chagres as compared with Rio Santa Maria (Alpert, 2006). However, due to the low abundance and overall good appearance of individuals, the parasites present in the Rio Chagres individuals are likely not significantly detrimental to their health. The observed lack of parasites in the Rio Santa Maria population suggests that individuals moving into Rio Chagres are potentially not bringing in any new parasites with them which would have contributed to their possible impact on the ecosystem (Dunn *et al*., 2012; Chalkowski *et al*., 2018).

It is unknown what the blister like lesions on the intestines of eight individuals from Rio Santa Maria were (Fig. 3), but they indicate that the Rio Santa Maria specimens are not of better health. Rio Santa Maria is the site of more agricultural development than the Rio Chagres and it is possible that the blisters may be due to exposure to agricultural by-products as it is known that agricultural run-off can have negative impacts on fish health (Cuffney *et al*., 2000; Allan, 2004; Linde-Arias *et al*., 2008). It is also possible that these lesions were due to a parasite of some sort that is not present in the Rio Chagres but this could not be determined without further histology.

The larger mean SL in the allochthonous Rio Chagres sample compared to the brackish Rio Santa Maria may indicate that predation or mortality rate might be lower allowing individuals to grow larger (Fig. 2). It is unlikely that the size difference is due to diet change with little difference found in composition of diets between the two populations (Fig. 5). This is further corroborated by the findings of larger size-corrected average stomach content weight in the generally smaller Rio Santa Maria individuals ($P < 0.01$). The failure to capture individuals of size class I in Rio Chagres could be due to different habitat use of these individuals within the river, such as shallower waters, or a fishing spot preference by the fisher. Interestingly, the maximum TL of individuals recorded at both sites (35.5 and 35.7 cm) was larger than the previously considered maximum TL of 29 cm (Kailola, Bussing, 1995).

Desynchronised breeding season in Rio Santa Maria and Rio Chagres *Cathorops tuyra* populations. We observed desynchronized breeding behaviour in February 2019, during high dry season, between the semi-anadromous euryhaline population from Rio Santa Maria, and by the dams locked freshwater population of Rio Chagres. In a previous sampling effort in Rio Chagres in early June 2018 (onset of rainy season), we found yolk-sac fry of about 6 cm in size, which notably is double the size of yolk-sac fry in the related *Cathorops spixii* (Agassiz, 1829) from Brazil (Lima *et al*., 2012), indicating that the breeding season in this population lasts at least from February to May/June.

The Rio Santa Maria sample contained only few individuals that were in maturing phase and most were in resting phase. Since we lack seasonal information on the Santa Maria population, we tried to quantitatively compare the state of maturity in females of both populations using the gonadosomatic index (GSI), which indicated that the two populations do not breed at the same time. *Cathorops tuyra* is a semi-anadromous species that is likely to breed in the estuaries, so we had expected to find more mature individuals in the freshwater stretch of the Rio Santa Maria. It remains unclear when and where the native population breeds. Alternatively, it is possible that instead we observed differential reproductive investment as opposed to desynchronized breeding, however, several pieces of evidence suggest otherwise. We found that, although individuals from Rio Santa Maria were on average smaller, they were feeding more, as determined by size-corrected stomach content weight, and reproductive analysis (GSI) suggested they were in a resting state. Conversely, individuals from Rio Chagres were larger, had larger investment in eggs, as they were reproductively active, but were feeding less.

Rio Chagres and Rio Santa Maria specimens do not differ in diet. *Cathorops tuyra* is assumed to be a specialized feeder of the mangrove clam *Polymesoda* sp. (R. Cooke, 2018, pers. comm.) due to its specialised teeth morphology with large molariform teeth that can be used to crush hard shells (Cooke, Jiménez, 2008). A clam species similar in shape but invasive to the Panama Canal, *Corbicula* spp. (Lee *et al*., 2005), could potentially serve as a substitute. As expected, the *Polymesoda* clam was identified in the stomach contents of many fish from Rio Santa Maria (Figs. 4A,B). Similar remnants were identified in the stomach contents of individuals from Rio Chagres, and it is likely that these belonged to *Corbicula* as *Polymesoda* is not known to reside in this river. This possibly represents a dietary shift to this newly available species.

Unexpectedly, bivalves were not the most important prey category across all size classes but were instead of high importance for small, immature individuals (size class I) in Rio Santa Maria and of the most importance for average-sized individuals (size class III, immature and mature individuals) in both rivers but of lower importance for larger-sized individuals (size class III, all mature) in both rivers (Fig. 5). The *Polymesoda* clam is small in size, sexually mature at 30 mm (Baker, 1930), and so this discrepancy in prey importance may be due to size class III having a larger mouth and therefore a larger availability of alternative prey types (Scharf *et al*., 2000). It is also possible that larger individuals exhibit differing foraging behaviour which may lead to differences in diet diversity (Schmitt, Coyer, 1982). This is supported by the diversity of the diet of Rio Santa Maria size class III but not by the decreased diversity of diet in Rio Chagres size class III. It is possible that although *Corbicula* is able to serve as a substitute for the *Polymesoda* clam, it is not in high enough abundance to support the larger individuals in Rio Chagres. Additionally, the individuals from Rio Chagres have the opportunity to feed on waste from the surrounding human settlements which would also lead to a decrease in diet diversity (Weekes *et al*., 2013; Carse, 2016). Processed foods digest faster and would be difficult to identify so our study would be unable to track this food preference.

Another interesting prey item that was identified in high frequency was the red-rimmed melania gastropod (*Melanoides tuberculata*) that is invasive to Panama (Garcés, Garcia, 2004). This gastropod was identified in the stomachs of individuals from Rio

Chagres but not in individuals from Rio Santa Maria despite the species being known to have spread to this river (Vega *et al*., 2006). It is possible that the gastropod is in lower numbers in Rio Santa Maria than in Rio Chagres as information regarding abundances is lacking.

In general, the diet of *Cathorops tuyra*, both freshwater and brackish water, is a fairly diverse, omnivorous diet (Fig. 4) as opposed to the specialized clam diet hypothesized earlier. This generalist omnivore diet is similar to the diet of other sea catfishes (Denadai *et al*., 2012, 2013; Dantas *et al*., 2013) and indicates that the allochthonous *C. tuyra* have the potential to compete with a variety of other species within Rio Chagres. While naturally sympatric species will likely consume slightly different prey in order to minimize niche overlap (Schoener, 1974; Blaber *et al*., 1994; Darnaude *et al*., 2001), allochthonous and invasive species may disrupt this (Vander Zanden *et al*., 1999; Britton *et al*., 2010). It is possible that over time, increased competition for food resources as a result of various species' invasions through the Panama Canal will lead to dietary shifts in both native and introduced species, however, currently we did not see a major shift in diet of *C. tuyra*. Even still, it is difficult to predict how species' invasions will impact ecosystems as new species interactions and other factors at play can completely alter existing food webs in unpredictable ways (Mack *et al*., 2000; Kornis *et al*., 2014).

Distribution throughout the Panama Canal. The invasion and crossing of marine fish species via the transisthmian connection of the Panama Canal has gained recent attention as more marine species are sighted in the Canal (Castellanos-Galindo *et al*., 2020). For future studies, it would be recommended to study the distribution of the *Cathorops tuyra* freshwater population across Gatun Lake to infer the probability of trans-isthmian crossing of that species. Fishers and the Barro Colorado Islands game wardens (guardabosque) report the presence of *C. tuyra* throughout the lake, but no study has confirmed its distribution (D. Sharpe, 2015, pers. comm.). Here, we report the presence of *C. tuyra* at Barro Colorado Island at the Smithsonian Tropical Research Institute dock. The species generally prefers slowly running waters, like small streams entering larger streams over muddy bottoms.

Study limitations. Male-mouth brooding in this species and the sampling restriction for the use of nets during the spawning season might have caused the female bias in the Chagres population, which was obviously spawning in the time, whereas the Rio Santa Maria population was not yet spawning, but still males evaded our sampling effort here.

It is likely that, as in other closely related species, *Cathorops tuyra* can consume larger amounts of one or another prey item depending on availability and this may change seasonally so it is important to note that our study only represents the feeding habits of *C. tuyra* in February (Dantas *et al*., 2013). Additionally, while it was assumed that the masses of unidentified material present in stomach contents were too digested to identify, it is also possible that this is actually detritus (Fig. 4N). Previous studies have found that *Cathorops* spp. feed on detritus in significant amounts either by accident during bottom feeding or on purpose (Denadai *et al*., 2013), but in the present study there was no way to easily distinguish between detritus and digested prey.

It is also important to keep in mind that this stomach content analysis has limitations, the main one being that the metric used, frequency of occurrence, fails to take into account the abundance of each prey item within the samples (Hynes, 1950; Hyslop, 1980). For this reason, we cannot draw conclusions regarding the amounts of each prey consumed or the relative importance of prey types within the diet composition (Lima-Junior, Goitein, 2001). However, as in this study, other studies have found that it is frequently impossible to separate prey items for quantification (counting, weighing, etc.) and as such frequency of occurrence is a good metric to use when this is not possible (Hynes, 1950; Hyslop, 1980; Lima-Junior, Goitein, 2001). If resources permit, a better method of quantifying the relative amounts of each prey item would need to be used to determine the relative importance of each prey item which could provide important information regarding diet preferences. A stable isotope analysis could help to ascertain whether the Rio Chagres population does feed more on human organic waste and position the species within the food web with a greater degree of certainty (Wada *et al*., 1991; Iken *et al*., 2001).

Additionally, due to a lack of information regarding ontogenetic shifts in our study species, we based our size classes on length alone, hoping to take into account gape size differences that likely impact feeding capabilities (Schael *et al*., 1991; Bremigan, Stein, 1994). Because of this and due to our lack of size class I individuals from Rio Chagres, we may have not captured differences in habitat use between immature and mature adults. Our study also did not include any juveniles which in other closely related species are known to use different habitats and resources (Dantas *et al*., 2012, 2013). Still, given the lack of currently available literature this study represents a good starting point for further feeding ecology and life history information.

In conclusion, stomach content analysis revealed that *Cathorops tuyra* has a generalist, omnivorous diet centered around bivalves, gastropods, crustaceans, and insects with plants and fish also being infrequently preyed on. The evidence presented in this study suggests that the Rio Chagres *C. tuyra* population has successfully transitioned from a semi-anadromous to a resident life cycle and is breeding from February to May/June. It remains to be determined when and where the semi-anadromous population breeds.

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AUTHORS' CONTRIBUTION

Janay Fox: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing-original draft, Writing-review and editing.

Máximo Jiménez A.: Investigation, Resources, Validation, Writing-review and editing.

Madlen Stange: Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing-original draft, Writing-review and editing.

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The authors declare no competing interests.

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