A SURVEY OF THE FISH ECTOPARASITES
OF THE ESSEQUIBO RIVER
IN THE IWOKRAMA FOREST, GUYANA

A Thesis

Presented to the

Faculty of the College of Graduate Studies and Research

Angelo State University

In Partial Fulfillment of the

Requirements for the Degree

MASTER OF SCIENCE

by

CARL BRYCE HUBBELL

December 2018

Major: Biology

A SURVEY OF THE FISH ECTOPARASITES

OF THE ESSEQUIBO RIVER

IN THE IWOKRAMA FOREST, GUYANA

by

CARL BRYCE HUBBELL

APPROVED:

Dr. Nicholas J. Negovetich

Dr. Ned E. Strenth

Dr. Robert C. Dowler

Dr. Herman O. Howard

December 31st, 2018

APPROVED:

Dr. Susan E. Keith
Dean, College of Graduate Studies and Research

ACKNOWLEDGMENTS

I am grateful to Operation Wallacea for inviting me on the expedition, covering international traveling expenses, and for providing in-country resources (lodging, transportation, food). I would like to thank the expedition's volunteers, local Amerindian guides, medics, and scientists for their help fishing, processing specimens, and collecting data. Thank you for your friendship and expert guidance on picking fishing locations, the Guyanese wilderness, Iwokrama's fish fauna, and productive fishing techniques. I would like to thank Raquel Gibson for all of her help both in Georgetown and Iwokrama. I would like to thank Thomas Horsley for his photograph of a *Braga* sp. specimen. Additionally, a special thanks to the Guyanese EPA for issuing collecting permits and allowing this research to take place in their amazing country.

I would like to thank Angelo State University for providing access to useful resources, facilities, and staff. I am grateful to the ASU Library for the use of interlibrary loans and access to literature search engines; both were essential in finding sources. I would like to thank the members of my thesis committee for editing this document. I am particularly grateful to my professors, Dr. Negovetich and Dr. Strenth, for their friendship, advice, and mentorship. I would like to thank both of them for letting me use their laboratories and equipment (dissecting scope, preservatives, collecting vials, and forceps) for this study. Dr. Strenth, thank you for honing my interest in arthropods early in my academic career and for your good sense of humor. Dr. Negovetich, thank you for sparking my interest in parasites and for getting me to academic meetings such as SWAP. I thank both of you for the patience and understanding you each showed me during my time at ASU. Finally, I would like to thank my family for their endless support throughout this project from start to finish.

ABSTRACT

Very few surveys on ectoparasites have been done in Guyana. To address this deficit, a collecting expedition for fish and their ectoparasites was conducted on the Essequibo River within the Iwokrama Forest. During the 2014 wet season, 210 fish of 26 species were captured and analyzed for ectoparasites. Approximately 12% of fish had ectoparasites. Infected fish included 10 species from 2 orders (Characiformes and Siluriformes). Thirteen species of ectoparasites were found including 9 branchiurans, 2 isopods, 1 parasitic catfish (Stegophilinae), and 1 leech (Hirudinea). Characiformes hosted the majority of parasitic isopods where they occurred primarily on the body of the host, but some were found on the fins. Siluriformes hosted the majority of branchiurans. These ectoparasites were predominately found on the body of the host, with several attached to the head of the fish. Siluriformes also hosted most of the parasitic catfish that attached primarily to the fins with some parasites attaching to the body. Hirudinea was found exclusively on the fins of Siluriformes. Newly reported parasite species for Guyana include *Argulus multicolor*, *Argulus juparanaensis*, *Argulus spinulosus*, *Argulus silvestrii*, *Dolops discoidalis*, *Dolops bidentata*, *Dolops nana*, *Dolops geayi*, and *Braga* sp. This is the second reported *Vanamea symmetrica* encounter in Guyana since 1925, and the first report for the Essequibo River. Several new records of parasite-host interactions are also reported in this study.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

During the summer of 2014, an expedition to survey, collect, and report fish species and their macro-ectoparasites was led on the Essequibo River in Iwokrama. This study was part of a larger expedition, the fourth annual Operation Wallacea Guyana expedition. This expedition surveyed the biodiversity of the birds, mammals, reptiles, amphibians, fish, and invertebrates of Iwokrama. This report was generated from the findings of the fish surveys.

Guyana, Iwokrama, and the Essequibo River

Guyana is a country in northeastern South America bordered by Brazil, Venezuela, Suriname, and the Atlantic Ocean. The Iwokrama Reserve is located in central Guyana, is primarily composed of lowland rainforest, and is approximately 371,000 ha in size (Fig. 1). Three rivers are within Iwokrama: the Essequibo, the Siparuni, and the Burro Burro (Watkins et al., 2004). The Essequibo is South America's third longest river and Iwokrama's largest river. Its main channels span 250-500 m wide on average, and its widest points can be upwards of 1 km (Hawkes and Wall, 1993). At its deepest during the wet season, the river reaches a depth of 40 m (Hawkes and Wall, 1993). The Essequibo flows northward into the Atlantic Ocean from its headwaters in the Acarai Mountains of southern Guyana.

Comparative Parasitology

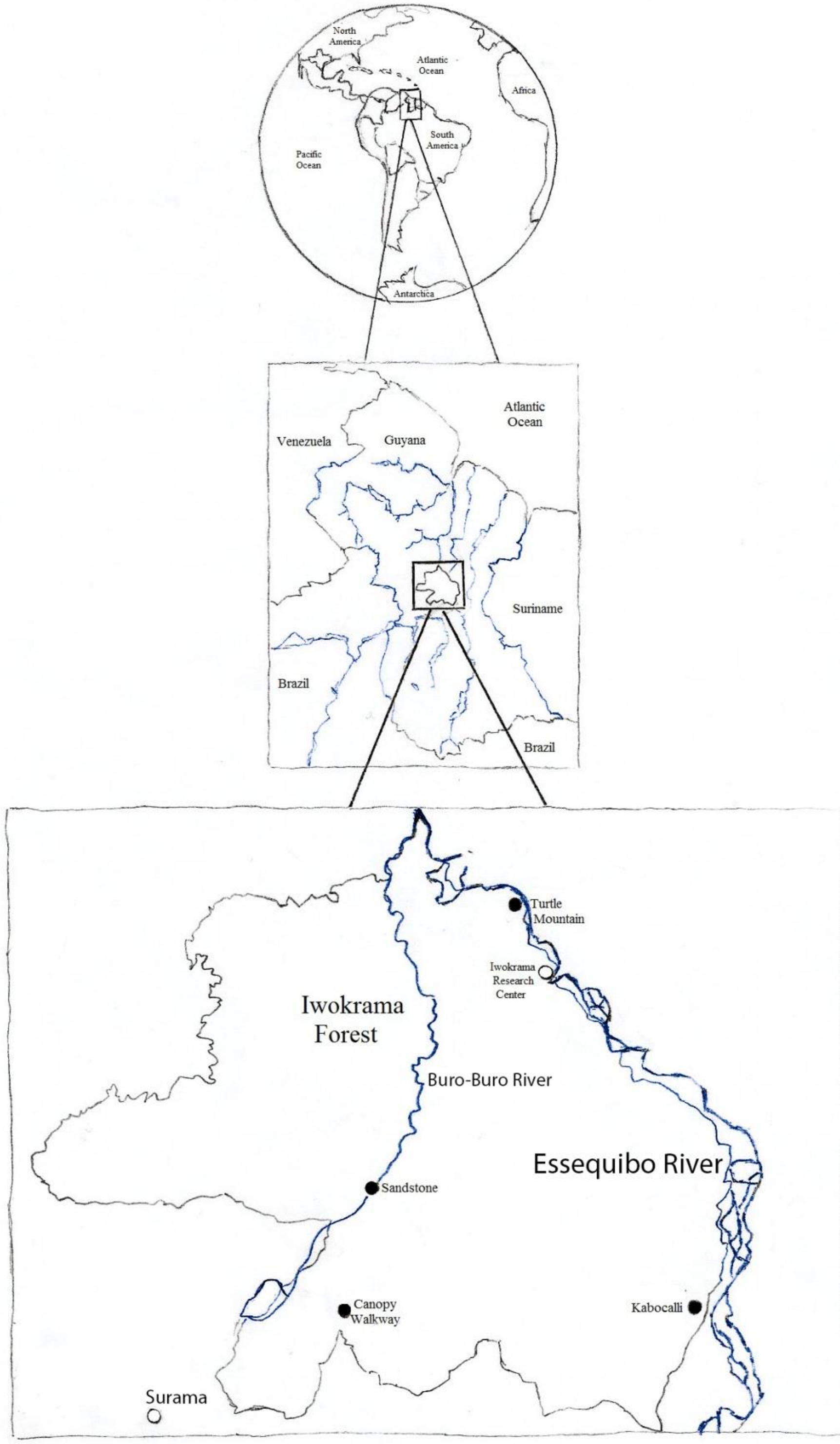

Figure 1. A map of the Iwokrama and Surama forests. Important features include the two surveyed rivers (the Burro Burro and the Essequibo) and the survey sites used by the Opwall expedition (as indicated by the black and white circles).

Past Surveys and Potential Fish Parasite Diversity in Iwokrama and Guyana

Few surveys investigating fish parasites have occurred in Guyana (Boone, 1918; Van Name, 1925). Most of the known surveys reported on parasitic isopods (Tables 1-3). Van Name (1925) reported on both aquatic and terrestrial isopods collected from the forests and rivers near the Kartabo field station. The field station was positioned near the confluence of the Mazaruni and Cuyuni rivers in the Bartica district of northern Guyana (Beebe et al., 1917). The report covered mostly free-living isopods, but it did include some insight on the parasitic forms of the region. For instance, Van Name (1925) described two new species of isopod fish parasites (*Vanamea symmetrica* and *Livoneca guianensis*) from the family Cymothoidae. He also reported on the presence of two previously described isopod fish parasites (*Telotha henselii* and *Excorallana berbicensis*). A few years earlier Boone (1918) described *E. berbicensis* (Excorallanidae) from two specimens collected by a missionary in 1913 on the Berbice River, also in northern Guyana.

Isopod Species	Countries Reported	Fish Host Orders	Fish Host Families	Fish Host List
Vanamea symmetrica	Guyana	Characiformes	**Triportheidae***	***Triportheus rotundatus****
	Brazil		Characidae	*Myleus (Myloplus) rubripennis*
	Venezuela			*Serrasalmus elongatus*
				Serrasalmus rhombeus
		Perciformes		*Serrasalmus spilopleura*
			Gasteropelecidae	*Carnegiella strigata*
		Siluriformes	Cichlidae	*Cichla monoculus*
				Cichla ocellaris
			Doradidae	*Hemidoras carinatus*
			Pimelodidae	*Brachyplatystoma* sp.
			Trichomycteridae	*Vandellia cirrhosa*
Braga **species**	**Guyana***	Siluriformes	**Auchenipteridae***	***Centromochlus romani****
		Characiformes	Characidae	***Tetragonopterus chalceus****
Braga amapaensis	Brazil	Characiformes	Acestrorhynchidae	*Acestrorhynchus guyanensis*
Braga cichlae	Brazil	Characiformes	Characidae	*Cynopotamus humeralis*
		Perciformes	Cichlidae	*Cichla ocellaris*
				Cichla temensis
Braga nasuta	Brazil	Siluriformes	Loricariidae	*Hypostomus* sp.
Braga fluviatilis	Brazil	Characiformes	Characidae	*Salminus* sp.
	Surinam	Perciformes	Cichlidae	*Cichlasoma* sp.
			Sciaenidae	*Pogonias cromis*
		Siluriformes	Pimelodidae	*Pseudoplatystoma* sp.
			Loricariidae	*Hypostomus* sp.
				Loricaria anus
Braga patagonica	Brazil	Atheriniformes	Atherinopsidae	*Odontesthes (Atherinichthes)* sp.
	Surinam	Characiformes	Characidae	*Salminus hilarii*
				Serrasalmus sp.
			Erythrinidae	*Hoplias malabaricus*
		Perciformes	Sciaenidae	*Pogonias* sp.

Bold* = Newly recorded parasite from this survey.

Table 1. Country records of Isopoda (*Vanamea* and *Braga*). Reports are from Guyana and neighboring countries. Table generated using Salgado-Maldonado et al. (2000) and Thatcher (2006).

	Countries Where Species Reported	**Fish Host Orders**	**Fish Host Families**	**Fish Host List**
Cymothoidae				
***Anphira* species**				
A. branchialis	Brazil	Characiformes	Characidae	*Pygocentrus nattereri* *Serrasalmus spilopleura*
A. junki	Brazil	Characiformes	Triportheidae	*Triportheus albus* *Triportheus flavus*
A. xinguensis	Brazil	Characiformes	Characidae	*Ossubtus xinguensis*
***Artystone* species**				
A. trysibia	Brazil	Perciformes	Cichlidae	*Crenicichla lacustris* *Geophagus brasiliensis*
A. minima	Brazil	Characiformes	Lebiasinidae	*Nannostomus beckfordi*
***Asotana* species**				
A. magnifica	Brazil	Characiformes	Characidae	*Serrasalmus* sp.
***Livoneca/Lironeca* Species**				
L. guianensis	Guyana	Characiformes Siluriformes	Anostomidae Pimelodidae	*Leparinus fasciatus* *Pimelodus clarias* *Brachyplatystoma* sp.
L. Orinoco	Venezuela	Perciformes	Cichlidae	Various Cichlid species
***Nerocila* species**				
N. armata	Guyana Brazil	Characiformes Perciformes Siluriformes	Anostomidae Cichlidae Auchenipteridae	*Leporinus fasciatus* *Crenicichla saxatilis* *Cichla ocellaris* *Pseudauchenepteris nodosus*
***Paracymothoa* species**				
P. astyanactis	Brazil	Characiformes	Characidae	*Astyanax bimaculatus*
P. tholoceps	Venezuela	Characiformes	Erythrinidae	*Hoplias macropthalmus*

Table 2. Country records of 6 genera of Isopoda (Cymothoidae). Reports are from Guyana and neighboring countries. Table generated using Salgado-Maldonado et al. (2000) and Thatcher (2006).

	Countries Where Species Reported	Fish Host Orders	Fish Host Families	Fish Host List
Cymothoidae				
***Philosomella* species**				
P. cigarra	Brazil	Characiformes	Characidae	*Cynopotamus humeralis*
***Riggia* species**				
R. acuticauda	Brazil	Siluriformes	Loricariidae	*Ancistrus* sp.
R. brasiliensis	Brazil	Characiformes	Anostomidae	*Leporinus copelandi*
				Leporinus octofasciatus
				Leporellus vitattus
				Schizodon nasutus
R. cryptocularis	Brazil	Characiformes	Characidae	*Odontostilbe* sp.
		Siluriformes	Loricariidae	*Ancistrus* sp.
R. nana	Brazil	Characiformes	Anostomidae	*Leporinus striatus*
R. paranensis	Brazil	Characiformes	Curimatidae	*Curimata platana*
				Cyphocarax gilberti
***Telotha* species**				
T. henselii	Guyana	Characiformes	Erythrinidae	*Hoplias malabaricus*
	Brazil	Perciformes	Cichlidae	*Geophagus* sp.
	Surinam	Siluriformes	Pimelodidae	*Brachyplatystoma* sp.
				Pimelodus clarias
T. lunaris	Brazil	Gymnotiformes	Apteronotidae	*Sternarchus brasiliensis*
T. silurii	Brazil	Siluriformes	Pimelodidae	*Iheringichthyes labrosus*
Excorallanidae				
***Excorallana* species**				
E. berbicensis	Guyana	Clupeiformes	Engraulidae	*Lycengraulis grossidens*
Excorallana sp.	Brazil	Siluriformes	Auchenipteridae	*Ageneiosus brevifilis*

Table 3. Country records of Isopoda (Cymothoidae and Excorallanidae). Reports are from Guyana and neighboring countries. Table generated using Salgado-Maldonado et al. (2000) and Thatcher (2006).

Aside from Isopoda being documented in Guyana, it is likely that a great diversity of other major fish parasite groups, i.e., Branchiura, is present in the country (Tables 4-5). This is likely considering these parasite groups are documented in numerous fish host species in nations bordering Guyana (Thatcher, 2006). Many of these same host species are native to Guyana (Eigenmann, 1912; Watkins et al., 2004). Furthermore, Guyana has several drainage areas that connect Venezuelan, Surinamese, and Brazilian waterways (Rosales, 2003). These interconnected waterways permit the sharing of fish species between the countries. Bicknell (2005) attributed the high fish diversity of Guyana's Rupununi savannahs to interconnectedness of Brazilian and Guyanese rivers that flood during the rainy seasons. The Rupununi and Rewa rivers of these savannahs flow into the Essequibo River just south of Iwokrama, and thus connect the reserve to this exchange zone. Watkins et al. (2004) suggested that this interconnectedness of waterways along with Iwokrama's geographic position between three different icthyo-faunal regions (the Orinoco, the Eastern Guiana Shield, and the Amazon) is what promotes the reserve's high fish diversity of 400 reported species. It is likely that, in addition to exchanging fish species, parasite species on the fish are also being shared between waterways. Several studies have suggested parasite diversity is positively associated with host diversity (Wisniewski, 1958; Gardner and Campbell, 1992; Hechinger and Lafferty, 2005; Hechinger et al., 2007). With Iwokrama's high fish diversity it is likely the region also possesses high parasite diversity. The two largest fish orders in Iwokrama reported by Watkins et al. (2004) are Siluriformes and Characiformes. These orders have numerous species listed as hosts for branchiurans and isopods throughout South America (Salgado-Maldonado et al., 2000; Thatcher, 2006; Luque et al., 2013).

Argulus Species	Nations Found	Host Orders	Host Families	Host Species
A. multicolor	**Guyana***	**Siluriformes***	**Pimelodidae***	***Phractocephalus hemiliopterus****
	Brazil		**Auchenipteridae***	***Ageneiosus inermis****
	Venezuela	Characiformes	Characidae	*Colossoma macropomum*
				Pygocentrus nattereri
			Cynodontidae	*Hydrolycus scomberoides*
				Rhaphiodon vulpinus
			Triportheidae*	***Triportheus rotundatus****
		Perciformes	Cichilidae	*Cichla temensis*
				Geophagus jurupari
				Oreochromis niloticus
A. juparanaensis	**Guyana***	**Siluriformes***	Doradidae	*Megalodoras* sp.
	Brazil		**Pimelodidae***	***Pseudoplatystoma fasciatum****
				Astyanax bimaculatus
		Characiformes	Characidae	*Pygocentrus nattereri*
				Serrasalmus marginatus
				Serrasalmus spilopleura
		Perciformes	Sciaenidae	*Pachyurus bonariensis*
				Pachyurus squamipennis
		Myliobatiformes	Potamotrygonidae	*Potamotrygon motoro*
A. spinulosus	**Guyana***	Characiformes	**Cynodontidae***	***Hydrolycus scomberoides****
	Brazil		Erythrinidae	*Hoplias malabaricus*
		Perciformes	Cichilidae	*Oreochromis niloticus*
A. silvestrii	**Guyana***	Siluriformes	Pimelodidae	***Leiarius marmoratus****
	Argentina			*Pseudoplatystoma corruscans*

Bold* = Newly recorded parasite from this survey.

Table 4. Country records of Branchiura (*Argulus*). Reports are from Guyana and neighboring countries. Table generated using Thatcher (2006).

Branchiuran Species	**Countries Reported**	**Host Orders**	**Host Families**	**Host Species**
Dolops bidentata	**Guyana***	**Siluriformes***	**Pimelodidae***	***Pseudoplatystoma fasciatum****
	Brazil	Characiformes	Anostomidae	*Schizodon fasciatum*
	Suriname			*Rhytiodus microlepis*
			Characidae	*Colossoma bidens*
				Pygocentrus nattereri
			Cynodontidae	*Raphiodon vulpinus*
			Prochilodontidae	*Prochilodus nigricans*
		Perciformes	Cichlidae	*Astronotus ocellatus*
		Synbranchiformes	Synbranchidae	*Synbranchus marmoratus*
Dolops geayi	**Guyana***	Siluriformes	**Auchenipteridae***	***Trachycoryestes trachycoryestes****
	Brazil		Doradidae	*Megalodoras* sp.
	Venezuela	Characiformes	Characidae	*Salminus maxillosus*
	Argentina		Prochilodontidae	*Prochilocus lineatus*
	Paraguay	Perciformes	Erythrinidae	*Hoplias malabaricus*
			Cichlidae	*Aequidens pulcher*
				Astronotus ocellatus
				Crenicichia geayi
				Crenicichia sp.
Dolops nana	**Guyana***	**Siluriformes***	**Auchenipteridae***	***Trachycoryestes trachycoryestes****
	Brazil	Characiformes	Anostomidae	*Leporinus elongatus*
				Leporinus fasciatus
				Leporinus friderici
				Leporinus obtusidens
				Leporinus sp.
			Characidae	*Salminus* sp.
Dolops discoidalis	**Guyana***	**Siluriformes***	**Pimelodidae***	***Phractocephalus hemiliopterus****
	French Guyana			***Pseudoplatystoma fasciatum****
		Characiformes	Erythrinidae	*Hoplias malabaricus*
Dipteropeltus hirundo	Brazil	Characiformes	Characidae	*Serrasalmus piraya*
	Venezuela			*Salminus maxillosus*
				Salminus brevidens
		Siluriformes	Pimelodidae	*Luciopimelodus pati*

Bold* = Newly recorded parasite from this survey.

Table 5. Country records of Branchiura (*Dolops* and *Dipteropeltus*). Reports are from Guyana and neighboring countries. Table generated using Thatcher (2006) and Luque et al. (2013).

Major Iwokrama Fish Host Taxa

Siluriformes: Commonly known as catfish, Siluriformes is a massive order of fishes with nearly 2,900 species (Nelson, 2006). Over half of catfish species are found in the Americas, with the rest being distributed across every continent except Antarctica. They are perhaps the most ecologically diverse group of fishes in the world, with representatives including top predators, armored herbivores, and tiny parasites. In Iwokrama, catfish were the second most speciose fish order listed by Watkins et al. (2004) with 130 species. Important catfish families for this study include Auchenipteridae and Pimelodidae. Auchenipteridae, or driftwood catfish, get their name because many of its members routinely hide in submerged logs and driftwood. The family includes tiny insectivorous wood catfish to larger piscivorous bottlenose catfish. Auchenipterids are an unarmored group with smooth, slimy skin. Pimelodidae are commonly referred to as long-whiskered or naked catfish due to representatives having unarmored, smooth-skinned "naked" bodies and lengthy barbels. This commercially important family includes some of South America's largest predatory fish species.

Characiformes: Like catfish, Characiformes are an extraordinarily diverse group of fishes that occupy numerous ecological niches. This exclusively freshwater order has almost 1,700 species dwelling in Africa and the New World (Nelson, 2006). Characins are best represented in the Greater Amazonia region of South America (van der Sleen and Albert, 2018). Characins come in a multitude of different shapes, sizes, and colors. A trait found in most species is a small adipose fin directly in front of the caudal fin. In Iwokrama, characins are the most speciose fish order with 190 species listed by Watkins et al. (2004). Some important families to mention for this study include the Characidae, Triportheidae, and Cynodontidae. Characidae is the largest family of Characiformes and historically includes tetras, pacus, and piranhas. Characids hold numerous niches and serve important roles in flooded forest ecosystems as predators, prey, and seed dispersers (Goulding 1983). Triportheidae, or elongate hatchetfish, are so named due to the hatchet-like body shape of species within its largest genus, *Triportheus*. Triportheids are small fish that prefer to dwell near the river's surface. Cynodontidae includes vampire tetras, baiaras, and payaras. Cynodontids are long-bodied, swift predators that are characterized by well-defined canine teeth, lengthy lower jaws, and large pectoral fins.

Ectoparasites of South American Freshwater Fishes

Isopoda: Two families of isopods parasitize freshwater fish in South America: Cymothoidae and Excorallanidae (Salgado-Maldonado et al., 2000; Thatcher, 2006). South America has the most diversity of freshwater Cymothoidae with 32 species (Thatcher, 2006; Wilson, 2008). A wide variety of hosts are infected by isopods including cichlids, characids, catfish, knifefish, anchovies, and rays (Salgado-Maldonado et al., 2000; Thatcher, 2006; Luque et al., 2013). Isopod parasitism strategies range from ectoparasitism of fish gills, skin, and fins, to replacing the host's tongue, or in some species, even burrowing into the host's body cavity (Thatcher, 2006; Smit et al., 2014). According to Thatcher (2006) and Smit et al. (2014), cymothoid life cycles begin with an adult male and female mating on a fish host. After mating, the gravid female forms a marsupium pouch on her ventral side and lays eggs. The eggs are kept in the marsupium where they hatch as pullus. The pullus molt once before they are born by exiting the marsupium through a posterior slit. After birth the young isopods are called manca.

Manca look like tiny adults with some exceptions. Unlike adults, manca have enlarged eyes, six pairs of legs, are heavily pigmented, and actively swim (Smit et al., 2014). Manca hunt by swimming toward the surface, where they then go motionless and slowly sink back down. During the descent, they either find a fish or swim back up to repeat the process. If a fish is found, the manca clings to it and feeds on soft tissues until it is brushed off by the fish. Manca have been known to kill smaller, more fragile fish (Thatcher, 2006). Because of this, manca often feed on several fish until they molt into adults, at which time they gain a seventh pair of legs, lose the ability to swim, and dwell permanently on a final host. Cymothoids are protandrous hermaphrodites and the first near-adult manca to arrive on a host will go from male to female. Any arriving after a female is present will remain male and the cycle begins anew (Thatcher, 2006; Smit et al. 2014).

Branchiura: After the African Tropics, the Neotropics have the second highest global diversity of freshwater Branchiura with 33 species (Poly, 2008). In South America, there are 26 species of freshwater branchiurans in 3 genera: *Argulus*, *Dolops*, and *Dipteropeltus* (Thatcher, 2006). Branchiurans infect numerous host fish, including cichlids, characids, catfish, and bony tongue fishes (Thatcher, 2006; Luque et al., 2013). Branchiurans feed on blood and live on the bodies, fins, and gills of fish (Thatcher, 2006). The life cycle of Branchiura is as follows: male and female adults mate while unattached to fish host. The female lays strings of eggs on aquatic structures (plants, logs, rocks, and others). The eggs hatch into young branchiurans which then attach and feed on fish hosts where they mature into adults (Thatcher, 2006).

Hirudinea: The Neotropics have roughly 107 leech species, making it second only to Eurasia in global freshwater leech diversity (Sket and Trontelj, 2008). Two families are reported to parasitize South American freshwater fish: Glossiphoniidae and Piscicolidae (Thatcher, 2006; Sket and Trontelj, 2008). Leeches cling to fish with adhesive suckers and feed on blood. Thatcher (2006) states a typical leech life cycle (including Piscicolidae & Glossiphoniidae) begins with two monoecious adults mating, exchanging sperm, and fertilizing each other. After fertilization, eggs are released from the genital pore and are encapsulated in a protective cocoon that is secreted from the clitellum. The cocoons are shed into the environment where the eggs hatch into young leeches. Glossiphoniids differ from this life cycle with their exhibition of parental care. After the eggs are laid, they are relocated to the ventral surface of the adult leech body where they are bound in membranous capsules. After hatching, young leeches remain attached to the parent until they grow sufficiently large, at which time they detach and swim away.

Parasitic Fishes: The only known vertebrates to parasitize South American freshwater fish are other fish, commonly known as candirus. Candirus are specialized catfish adapted to a life of parasitism. All candirus are within two subfamilies of Trichomycteridae: Vandellinae and Stegophilinae (Fernandez and Schaefer, 2009). Vandellines are sanguivores that feed by bleeding gill filaments (Kelley and Atz, 1964). Stegophilines feed on mucus, scales, skin, and bits of flesh (Baskin et al., 1980). Little is known about candiru reproduction. Guyana has six known species of parasitic catfish (Eigenmann, 1912; Schmidt, 1987).

Purpose of this Study

Despite the potentially high diversity of fish ectoparasite species in Iwokrama, no such surveys have been done to the author's knowledge. It is the purpose of this study to add to the current knowledge of Guyana's fish parasite diversity. This research represents the first ever general survey that reports on the macro-ectoparasites present in the region and on the fish hosts they infect.

MATERIALS AND METHODS

Survey Sites

Specimens were collected from three sites within the Iwokrama forest. The locations were selected by Operation Wallacea, a British conservation organization, as part of a fish diversity survey. Within the Iwokrama forest, surveys took place on the Essequibo River at Turtle Mountain, Kabocalli, and the Iwokrama River Lodge during the month of July in 2014 (Fig. 1).

Three habitat types were surveyed within the individual sites: flooded forest, open water, and creeks. Flooded forest is defined as any section of river that has encroached on and submerged a section of forest where water is normally absent during the dry season. There is a heavy presence of both trees and other submerged terrestrial plant life in the flooded forest habitat, and these sections of river are typically of shallower water depth (less than 3 meters). Open water habitat is any section of river that is notably absent of flooded terrestrial vegetation. It includes sections of "natural" river that are constantly submerged in both wet and dry seasons. The shoreline beaches that become flooded during the wet season are also considered part of this habitat. The depth of open water varies and includes the deepest portions of the river as well as the shallower waters of the flooded beaches bordering the flooded forest. Creek habitats include any small streams or brooks that are fed from within the forest and flow down to the main river. Creeks will constantly have water during both the dry and wet seasons. Like open water, little to no terrestrial vegetation is present in the creek habitat. Similar to the main river, creeks flood and expand during the wet season and contract some during the dry season. The depth of creek habitat ranges somewhat with proximity to the river. The closer a part of a creek is to the main river the deeper it generally is. Thus, the mouth of the creek (where it meets the river) is usually the deepest.

Fish Collection Techniques

During this survey, most non-protected fish encountered were analyzed for ectoparasites. Fish were captured using both active and inactive fishing methods. Active fishing methods included hook and line fishing (rod-and-reel or hand line), dip nets, and cast nets. Inactive fishing methods utilized stationary fishing devices (SFDs), such as trotlines, set lines, and fish traps. About a week was spent at each of the sites, and typically two collecting trips were made each day. Trips occurred once in the early morning, from 04:30 to 10:00 hours, and once in the evening, from 15:30 to 19:00 hours.

During trips, hook and line fishing accounted for most of the active fishing methods used to capture small to large-sized fish species. Dip nets were used mostly on evening trips to catch small fish seen swimming at the river surface. Cast nets were used to catch small to mid-sized fish on occasion, and were only used in areas devoid of heavy shoreline vegetation and underwater snags. SFDs were set out at dusk during the majority of evening fishing trips and were checked at dawn the following morning. Fish traps were used near boat landings to catch small fish, such as *Corydoras* catfish and tetras. Setlines and trotlines were used to catch mid- to large-sized fish, such as wolf fish and giant river catfish. Notably, trip times would sometimes vary depending on the weather and/or productivity of the fishing.

Parasite Collection Techniques

Upon capture, fish were identified to the most specific taxonomic level possible and were quickly examined for ectoparasites. All easily visible portions of the fish's external anatomy where ectoparasites may reside were searched. The surveyed anatomical regions included the fins (dorsal, pectoral, pelvic, anal, and caudal), the head (mouth, gills, operculum, and upper head), and the body (dorsal skin and ventral skin). The skin of the body region was divided in half, with any section above the lateral line being considered "dorsal" and any section below the lateral line termed "ventral." If ectoparasites were found, they were enumerated by type, and their anatomic location on the fish was noted.

Discovered parasites were then removed delicately from the fish with padded forceps (Carvalho et al., 2003; Carvalho et al., 2004). Immediately after removal, collected ectoparasites (with the exception of leeches and copepods) were preserved in 70% ethanol. For leeches, specimens were first placed in near-boiling water to properly narcotize them (Bush, 2009). Narcotized leeches were then preserved in 70% ethanol. Copepods were preserved in 10% formalin after removal from the host. Fish length was recorded after the fish was thoroughly scanned and all ectoparasites were collected. Fish were measured from the tip of the lower jaw to the end of the tail to the nearest 0.1 cm. Most fish were released following data collection, but some were retained and preserved as a reference collection. All collected fish were either preserved in 70% ethanol or 10% formalin. Fish and parasite specimens are currently deposited at Angelo State University.

Data Analysis

Parasites and fish were identified to the most specific taxonomic level possible using all available resources. For collected ectoparasites, identifications were made with the use of Thatcher (2006), Van Name (1925), and Salgado-Maldonado et al. (2000). Fishes that were difficult to identify were identified with the aid of local Amerindian guides, van der Sleen and Albert (2018), and fish survey reports made available by the Guyanese EPA

(Armbruster, 2002; Watkins et al., 2004; De Souza, 2005; Vari et al., 2009; De Souza et al., 2012).

Analysis of collected data followed standard techniques in community ecology and parasitology. Specifically, Spearman's rho was calculated to examine correlations between host characteristics and the presence and intensity of each parasite. Statistical Significance was set at 0.05 for use in these tests. Prevalence and intensity followed the definitions of Bush et al. (1997). Prevalence was calculated by dividing the number of infected host fish by the total number of host fish surveyed then multiplied by 100. Mean Intensity was calculated by dividing the total number of ectoparasites by the total number of hosts that were infected with them.

RESULTS

Collection Results

During the expedition, a total of 210 individual fish were captured and analyzed for ectoparasites. Among the fish surveyed, there were 26 different species reported from 11 families and 4 orders (Table 6). Twenty-six out of the 210 surveyed fish were infected with ectoparasites. These infected fish included 10 species from the orders Characiformes and Siluriformes (Table 7). Within Characiformes, 4 species among the following families were found to host ectoparasites: Characidae (2 species), Triportheidae (1 species), and Cynodontidae (1 species). For Siluriformes, 6 species from two families yielded ectoparasites: Auchenipteridae (3 species) and Pimelodidae (3 species). In total, there were at least 13 distinct species of ectoparasites found during the survey. The ectoparasites comprised 9 species of branchiurans, 2 species of isopods, 1 species of parasitic catfish (Vandellinae), and 1 species of leech (Hirudinea; Table 8). Across all individual parasites collected, 44.7% were Branchiura, 34.8% were Isopoda, 18.9% were Stegophilinae, and 1.5% were Hirudinea. Overall, there was a correlation between parasite intensity and fish length when looking at the entire population of surveyed fishes (Fig. 2).

FISH ORDER	FISH FAMILY	FISH SPECIES	IRL	TM	KC	Totals
Characiformes	**Anostomidae**	*Leporinus friderici*	-	-	1	1
	Characidae	*Brycon* sp.	-	1	-	1
		Myloplus cf. planquettei	-	1	-	1
		Pygocentrus nattereri	-	13	-	13
		Serrasalmus rhombeus	5	25	10	40
		Serrasalmus serrulatus	-	2	-	2
		Tetragonopterus chalceus	-	39	16	55
	Cynodontidae	*Hydrolycus scomberoides*	-	-	1	1
	Erythrinidae	*Hoplias malabaricus*	-	2	-	2
	Gasteropelecidae	*Carnegiella sternicla*	-	1	-	1
	Triportheidae	*Agoniates halecinus*	-	7	-	7
		Triportheus rotundatus	1	25	5	31
Siluriformes	**Auchenipteridae**	*Ageneiosus inermis*	-	3	1	4
		Ageneiosus sp.	-	1	-	1
		Centromochlus romani	-	-	1	1
		Tatia musaica	-	1	2	3
		Trachycorystes trachycorystes	-	23	4	27
		Trachyelopterus galeatus	-	1	-	1
	Doradidae	*Pterodoras granulosus*	-	1	-	1
	Pimelodidae	*Leiarius marmoratus*	-	-	1	1
		Phractocephalus hemiliopterus	-	1	2	3
		Pimelodus ornatus	-	1	6	7
		Pinirampus pinirampu	-	1	-	1
		Pseudoplatystoma fasciatum	2	1	-	3
Perciformes	**Sciaenidae**	*Plagioscion squamosissimus*	-	1	-	1
Myliobatiformes	**Potamotrygonidae**	*Potamotrygon orbignyi*	-	1	-	1
		Totals	8	152	50	210

Table 6. Number of fish collected at each site.
IRL=Iwokrama River Lodge, TM=Turtle Mountain, KC=Kabocalli.

FISH SPECIES	*Serrasalmus rhombeus*	*Tetragonopterus chalceus*	*Hydrolycus scomberoides*	*Triportheus rotundatus*	*Ageneiosus inermis*	*Centromochlus romani*	*Trachycorystes trachycorystes*	*Leiarius marmoratus*	*Phractocephalus hemiliopterus*	*Pseudoplatystoma fasciatum*
Braga sp.	------	50	------	------	------	50	------	------	------	------
Vanamea symmetrica	95.5	------	------	4.5	------	------	------	------	------	------
Glossiphoniidae species	------	------	------	------	------	------	100	------	------	------
Stegophilus sp.	8	------	------	------	------	------	------	------	92	------
Argulus juparanaensis	------	------	------	------	------	------	------	------	------	100
Argulus multicolor	------	------	------	33.3	33.3	------	------	------	33.3	------
Argulus silvestrii	------	------	------	------	------	------	------	100	------	------
Argulus spinulosus	------	------	100	------	------	------	------	------	------	------
Argulus sp.	------	------	------	------	------	------	------	------	100	------
Dolops bidentata	------	------	------	------	------	------	------	------	------	100
Dolops geayi	------	------	------	------	------	------	100	------	------	------
Dolops nana	------	------	------	------	------	------	100	------	------	------
Dolops discoidalis	------	------	------	------	------	------	------	------	51.2	48.8

Table 7. Composition (%) of parasite species found attached to fish.

TAXA	FAMILY	SPECIES	IRL	TM	KC	TOTALS	CR	FF	OW
Isopoda									
	Cymothoidae	*Braga* sp.	-	-	2	2	2	-	-
		Vanamea symmetrica	5	11	28	44	1	5	38
Hirudinea									
	Glossiphonidae	*Glossiphonid* sp.	-	-	2	2	2	-	-
Trichomycteridae									
	Stegophilinae	*Stegophilus* sp.	2	-	23	25	23	-	2
Branchiura									
	Argulus	*Argulus juparanaensis*	-	2	-	2	2	-	-
		Argulus multicolor	-	1	2	3	1	1	1
		Argulus silvestri	-	-	2	2	-	-	2
		Argulus spinulosus	-	-	1	1	1	-	-
		Argulus sp.*1*	-	-	4	4	4	-	-
	Dolops	*Dolops bidentata*	1	-	-	1	-	-	1
		Dolops geayi	-	1	1	2	1	1	-
		Dolops nana	-	1	-	1	1	-	-
		Dolops discoidalis	4	22	17	43	39	-	4
		Totals	12	38	82	132	77	7	48

Table 8. Number of parasites collected at each site and for each habitat. IRL=Iwokrama River Lodge, TM=Turtle Mountain, KC=Kabocalli.

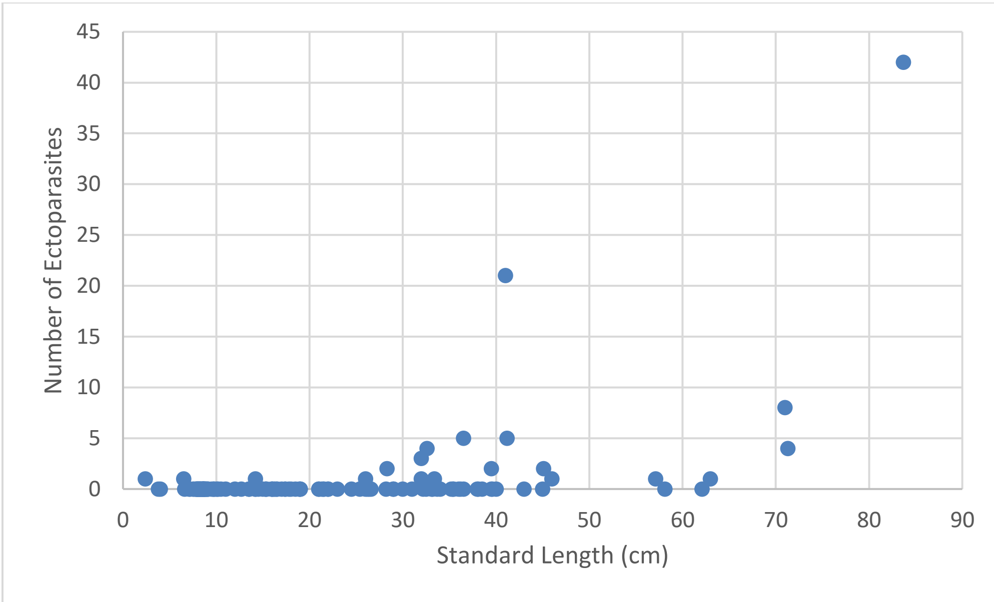

Figure 2. Scatterplot of all fish lengths and parasite intensities. This graph shows a correlation between the standard length of all surveyed fish and the number of ectoparasites (Spearman's rho=0.36, P<0.0001).

Fish Survey

Characiformes: Characiformes represented nearly three-quarters of the captured fish (Fig. 3). In total, 12 species across 6 families were captured: Anostomidae (1 species), Erythrinidae (1 species), Gasteropelecidae (1 species), Characidae (6 species), Triportheidae (2 species), and Cynodontidae (1 species). This order was almost exclusively caught using rod and reel; very few fish were caught by another fishing method. Characiformes made up over half (57.7%) of all the infected fish. Most of the characiformids were captured in flooded forest habitats (65.16%), followed by open water (32.26%), and then creek habitats (2.58%).

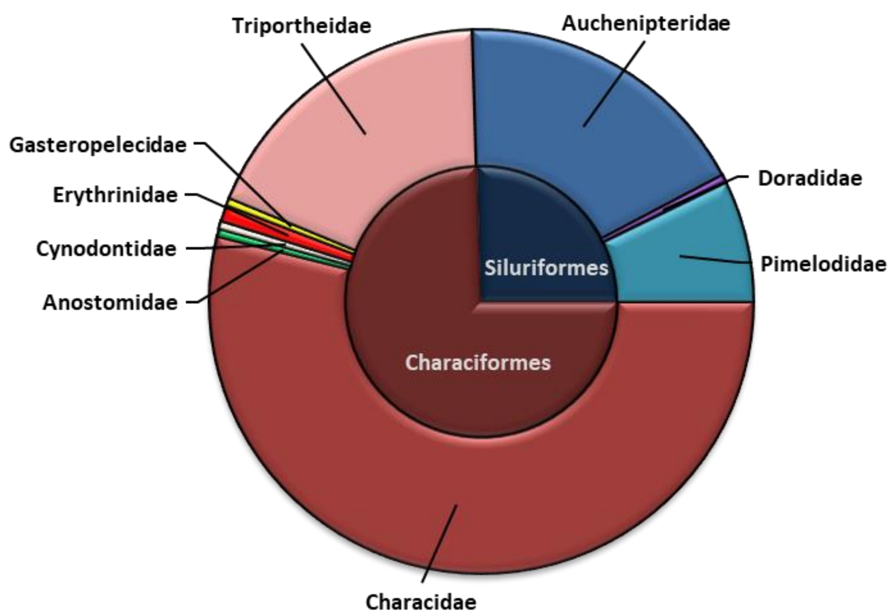

Figure 3. The relative frequencies of the two major fish orders represented. These frequencies are shown from among all captured fish—Characiformes and Siluriformes—as well as the represented families within each order. Due to low capture rates, Perciformes and Myliobatiformes were not included.

Characidae had the most individual fish surveyed of any Characiformes family. In fact, this family alone accounted for over half of all the individual fish surveyed during the study (53.33%). The two most commonly encountered species of characids were *Tetragonopterus chalceus* and *Serrasalmus rhombeus*. Ten percent of the Characidae caught were infected with ectoparasites. Three species of parasites were found in this group: 2 isopods (*V. symmetrica* and *Braga* sp.) and 1 species of parasitic catfish (*Stegophilus* sp.). The most prevalent parasite species seen in Characidae was *V. symmetrica*, with almost all individuals of this species (over 95%) seen on black piranhas (*S. rhombeus*). Of the black piranhas captured, 25% were infected with *V. symmetrica*. Interestingly, for all black piranhas hosting *V. symmetrica*, it was the only ectoparasite present on these fish, with a range of 1 to 21 and a mean intensity of 4.2 ± 1.9 SE. The black piranhas surveyed ranged in length from 12.0 cm to 41.2 cm and averaged 24.80 cm ±1.47 SE. Using Spearman's correlation coefficient, there was a positive correlation between fish length and parasite intensity for black piranhas (Spearman's rho=0.48, $P<0.002$; Fig. 4). On average, black piranhas harboring *V. symmetrica* were longer (30.95 cm ± 2.51 SE) than their non-infected counterparts (22.17 cm ± 1.63 SE; t-Test: $t_{38}=3.24$, $P<0.003$). The parasitic catfish, *Stegophilus* sp., were found on only one black piranha that was 39.5 cm long and was caught in open water at the Iwokrama River Lodge.

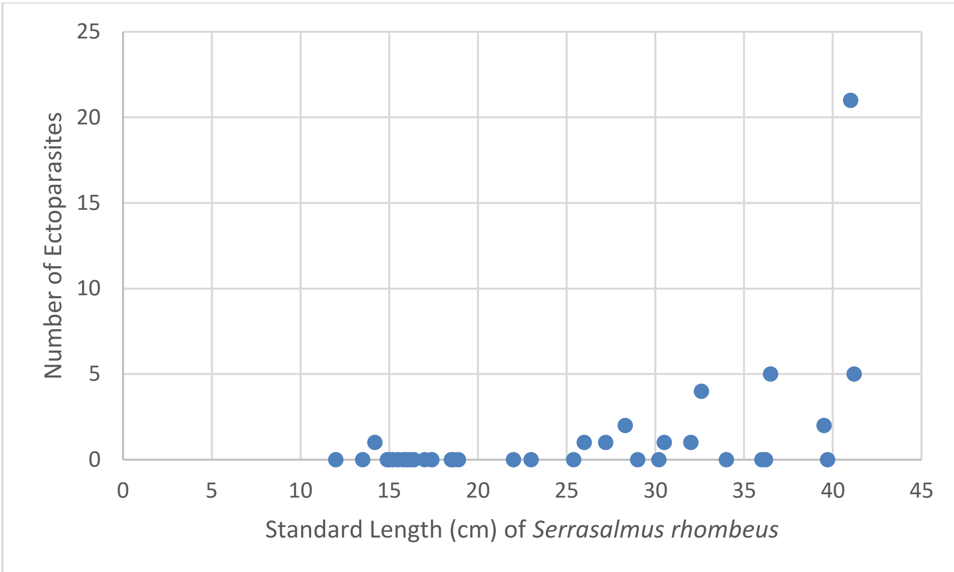

Figure 4. Scatterplot of all *Serrasalmus rhombeus* lengths and parasite intensities. This graph shows a correlation between the standard length of *Serrasalmus rhombeus* and the number of ectoparasites (Spearman's rho=0.48, *P*<0.002)

On 1 individual black spot tetra, *T. chalceus,* a single *Braga* sp. isopod was discovered attached to its upper head. This lone *Braga* sp. was the only type of ectoparasite found on the surveyed black spot tetras. Despite being the most commonly seen characid fish, only 1.8% of *T. chalceus* were infected. Individuals of *T. chalceus* ranged in length from 6.5 cm to 11.0 cm and had an average length of 8.59 cm ±0.12 SE. The single infected tetra was also the smallest one observed in the study at 6.5 cm length; it was caught in a creek at Kabocalli.

Triportheidae was the next most commonly encountered family of Characiformes. Of the two species observed—*Triportheus rotundatus* and *Agoniates halecinus*—*T. rotundatus* had the most individuals surveyed and was the only Triportheid species hosting ectoparasites. *Triportheus rotundatus* lengths ranged from 12.7 cm to 21.5 cm and had an average length of 15.98 cm ± 0.40 SE. Two species of ectoparasites were found on *T. rotundatus*: the isopod

V. symmetrica and the branchiuran *Argulus multicolor*. Ectoparasites infected 6.45% of surveyed *T. rotundatus*. Of the infected fish, there was one fish hosting 2 *V. symmetrica* and one fish hosting 1 *A. mulitcolor*.

Cynodontidae was one of the least frequently encountered Characiformes fish families during the study. Only one individual—*Hydrolycus scomberoides*—was captured in a creek at Kabocalli. This fish was 46.0 cm in length and had one branchiuran, *Argulus spinulosus,* found in its mouth.

Siluriformes: Siluriformes made up a little over a quarter of all surveyed fish (25.23%). Twelve species were observed across three families: Auchenipteridae (6 species), Doradidae (1 species), and Pimelodidae (5 species). The majority of catfish were captured with the trotline method (52.83%), followed by rod (39.62%) then by hand net (7.54%). Most catfish were captured in creeks (41.50%) with the remainder of catches being split almost in half between open water (28.30%) and flooded forest (30.18%) habitats. About one-fifth of encountered catfish were infected with ectoparasites (20.75%), and Siluriformes made up 42.3% of all infected fish observed. The parasite fauna of Siluriformes was composed of 8 species of branchiurans, 1 isopod species, 1 parasitic catfish species, and 1 species of leech.

The driftwood catfish, Auchenipteridae, were the most encountered catfish family during the study and accounted for 69.81% of all Siluriformes captured. Ectoparasites infected 13.51% of all encountered driftwood catfish. Of the 6 species of fish encountered, 3 were infected by parasites: *Trachycoryestes trachycoryestes, Ageneiosis inermis,* and *Centromochlus romani*. The 3 uninfected species were *Ageneiosis* sp., *Trachyelopterus* *galeatus,* and *Tatia musaica*. The most abundant species encountered were *T. trachycoryestes* and *A. inermis*.

The black driftwood catfish, *T. trachycoryestes,* made up 72.97% of the auchenepterid captures. Specimens ranged in length from 24.5 to 43.0 cm and averaged 32.87 cm ± 0.97 SE. Ectoparasites infected 11.11% of *T. trachycoryestes*. The number of ectoparasites per fish ranged from 1 to 3, with a mean intensity of 1.7 ± 0.7 SE. Three parasite species were found on the black driftwood catfish: 1 species of glossophonid leech and 2 branchiurans, *Dolops geayi* and *Dolops nana*. The average length of infected fish (34.97 cm ± 2.30 SE) was longer than that of non-infected fish (32.61 cm ± 1.05 SE). Black driftwood catfish infected with *D. geayi* averaged 32.70 cm ± 0.70 SE in length.

The bottlenose catfish, *Ageneiosis inermis*, made up 10.81% of driftwood catfish catches. Individuals of *A. inermis* averaged 51.38 cm ±6.75 SE long and ranged in length from 35.4 to 63.0cm. The largest specimen caught (63.0 cm) was also the only individual harboring any ectoparasites. This specimen was caught with a rod in open water at Kabocalli and had the branchiuran *A. multicolor* residing in its gills. The only other infected Auchenepterid was a tiny *C. romani* measuring 2.4 cm in length. This fish was captured with a hand net at the surface of a creek in the evening. A *Braga* sp. isopod was found clinging to the operculum of the small fish.

The naked catfish, Pimelodidae, were the second most encountered family of catfish and made up 28.30% of total captured Siluriformes. Ectoparasites were found on 40.00% of the pimelodids. Out of the 5 encountered species, 3 species hosted ectoparasites: *Phractocephalus hemiliopterus*, *Pseudoplatystoma fasciatum,* and *Leiarius marmoratus*. The uninfected species were *Pimelodus ornatus* and *Pinirampus pinirampu*. Although the uninfected *P. ornatus* was the most commonly encountered species during the study, *P. hemiliopterus* and *P. fasciatum* tied for the second most commonly encountered species.

The red tail catfish, *P. hemiliopterus*, was the largest species of fish captured during the study. Individuals ranged in size from 71.0 to 90.5 cm with an average length of 81.73 cm ± 5.71 SE. Red tail catfish made up 20% of total pimelodid captures. There were 4 species of ectoparasites found on these fish: 3 branchiurans (*Argulus* sp., *A. multicolor, Dolops discoidalis*) and 1 parasitic catfish (*Stegophilus* sp.). There were 2 infected fish found during the study. The parasite loads of these fish were 8 and 42, and multiple species of ectoparasites were found on each infected fish. The red tail with the smallest parasite load (8 ectoparasites) was also the smallest surveyed *P. hemiliopterus* at 71.0 cm long. It hosted both *D. discoidalis* and *A. multicolor*. The red tail with the heaviest parasite load (42 ectoparasites) hosted the most ectoparasites of any fish surveyed in the entire study. This individual was the third largest fish in this study at 83.7 cm long and hosted 15 *D. discoidalis*, 4 *Argulus* sp., and 23 *Stegophilus* sp. (Fig. 5A).

Captured *P. fasciatum* ranged in size from 57.1 to 99.0 cm with an average length of 75.80 cm ± 12.30 SE. All 3 individuals captured during the survey were infected with ectoparasites, with 3 branchiurans recorded: *Argulus juparanaensis*, *Dolops bidentata*, and *D. discoidalis* (Fig. 5B). The range of ectoparasites was 1 to 19 individuals per fish with a mean intensity of 8.0 ± 5.6 SE individuals per fish.

Only 1 *L. marmoratus* was captured during the survey. This individual was 45.1 cm long and was captured in open water at Kabocalli. There were 2 *Argulus silvestrii* branchiurans found on the ventral skin of this fish.

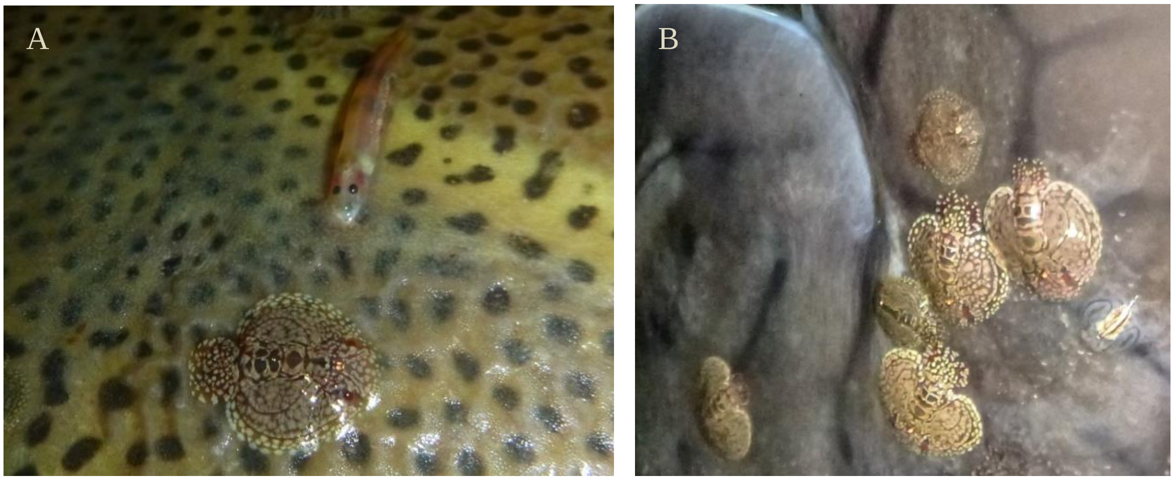

Figure 5. In-situ photos of candiru and Branchiura at attachment sites prior to collection. **A.** *Dolops discoidalis* and *Stegophilus* sp. on the skin of *Phractocephalus hemiliopterus*. Note the well camouflaged coloration of *Dolops discoidalis* blending in with the skin color of its host. **B.** *Dolops discoidalis* and *Argulus juparanaensis* on the head and gill plate of *Pseudoplatystoma fasciatum*.

Perciformes and Myelobatiformes: A single species of Perciformes was found, *Plagioscion squamosissimus*. This individual was 58.1 cm in length and was caught on rod at Turtle Mountain. A single species Myelobatiformes was found, *Potamotrygon orbignyi*. This individual was 33.2 cm in length and was caught on rod at Turtle Mountain. Neither of these fish hosted any ectoparasites.

Parasite Survey

Branchiurans: Branchiurans accounted for almost half of all encountered parasites (44.7%). Aside from being the most numerous group, they were also the most speciose. They were primarily found on catfish, with only a few individuals found on characiformids. Branchiurans were most often discovered on fish captured in creeks, then open water, and finally flooded forests. These were found on every section of the fish hosts except the pelvic fins. Infection sites for branchiurans were ranked in order from most to least common and include ventral skin (28.07%), dorsal skin (24.56%), upper head (15.79%), operculum (14.04%), gills (8.77%), caudal fin (3.51%), and for the least common sites—each less than 2%—the dorsal, pectoral, and anal fins (Fig. 6). Among captured branchiurans, 72.88% were *D. discoidalis*, 6.78% were *Argulus* sp., 5.08% were *A. multicolor*, 3.39% were *A. juparanaensis*, 3.39% were *A. silvestrii*, 3.39% were *D. geayi*, 1.69% were *A. spinulosus*, 1.69% were *D. bidentata,* and 1.69% were *D. nana*. Branchiurans were found on both large fish and small fish (length range: 21.0 to 99.0 cm; average length: 55.18 cm ± 6.70 SE. They were rarely found on fish infected with other parasite taxa.

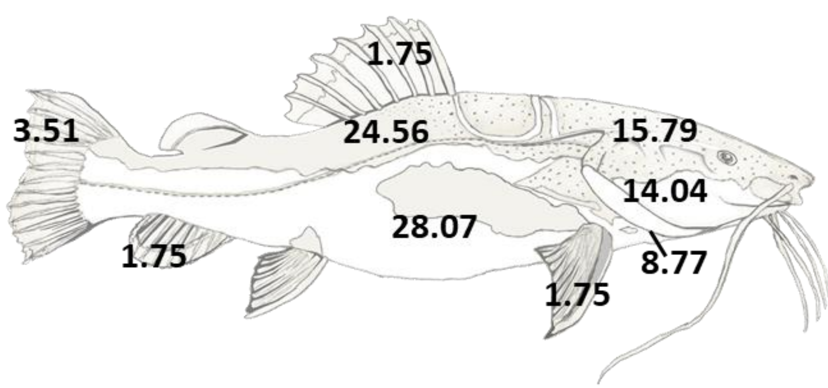

Figure 6. Preferred infection sites of branchiurans on Siluriformes fish. Note the number at each site is a percentage of the total number of branchiurans encountered.

Isopods: Isopods were the second most frequently encountered parasite taxa and represented 34.8% of all encountered parasites. The predominant hosts for isopods were characiformids; there was just one catfish host. Isopods were more often on fish captured in open water compared to flooded forest and creeks. They were found on every section of the fish except the gills. Preferred infection sites for isopods ranked from highest to lowest included the dorsal fin (35.56 %), dorsal skin (24.44%), ventral skin (22.22%), and the least common sites—each 2.22%—the upper head, operculum, pectoral fins, pelvic fins, anal fin, and caudal fin (Fig. 7). Among captured isopods, 95.65% were *V. symmetrica*, and 4.35% were *Braga* sp. Notably, *V. symmetrica* and *Braga* sp. were not found to co-occur on the same fish host. In addition, neither was found to share the fish host with any other ectoparasite.

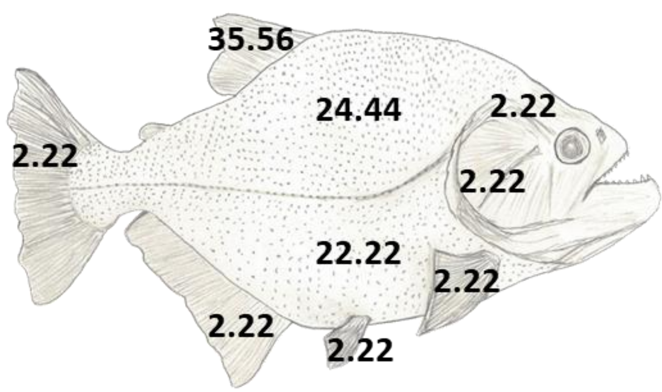

Figure 7. Preferred infection sites of isopods on Characiformes fish. Note the number at each site is a percentage of the total number of isopods encountered.

Parasitic Catfish and Leeches: Parasitic catfish (candiru) were the third most encountered parasite taxa, representing 18.9% of all encountered parasites. The only species of candiru encountered during the study was *Stegophilus* sp. (Fig. 8). They were noted on most sections of the fish host except the gills, anal fin, and caudal fin. Preferred infection sites for *Stegophilus* sp. on the siluriform host, *P. hemiliopterus*, ranked from highest to lowest included the caudal fin (30.43%), dorsal skin (26.09%), ventral skin (13.04%), dorsal fin (8.70%), pectoral fin (8.70%), and the least common sites—each 4.35%—the upper head, operculum, and pelvic fin (Fig. 9). On the characiform host, *Stegophilus* sp. was found only on the ventral skin. The siluriform host (83.7 cm) was captured in a creek, and the characiform host (39.5 cm) was captured in open water. No other species of ectoparasite were present on the characiform host. On the siluriform host, both *D. discoidalis* and *Argulus* sp. were also present, but *Stegophilus* sp. made up over half of the ectoparasite population (Fig. 5A).

Leeches were the least encountered parasite. Only 2 individual Glossiphoniidae leeches of the same species were found on the fins of a single *T. trachycorystes* host.

Figure 8. *Stegophilus* sp. on the skin of *Phractocephalus hemiliopterus*.

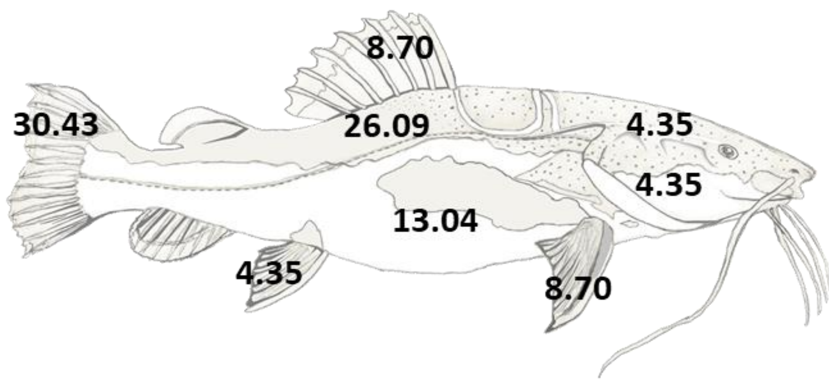

Figure 9. Preferred infection sites of parasitic catfish. These candiru (Stegophilinae) infections are reported from Siluriformes fish. Note the number at each site is a percentage of the total number of parasitic catfish encountered.

DISCUSSION

For Guyana, newly reported parasite species are *A. multicolor*, *A. juparanaensis*, *A. spinulosus*, *A. silvestrii*, *D. discoidalis*, *D. bidentata*, *D. nana*, *D. geayi*, and *Braga* sp. (Fig. 10 A-D, F-I and Fig. 11A). An unidentified *Argulus* sp. was also encountered during the survey, but it is unknown whether this is a new country record or not (Fig. 10E). Since its discovery by Van Name in 1925, this is the second reported *V. symmetrica* encounter in Guyana and likely the first for the Essequibo River (Fig. 11B). In addition to reporting the parasite and host species represented in Iwokrama, this survey has other new findings. Several new parasite-host interactions for branchiurans and isopods are reported along with some general observations on correlations between study variables, such as fish length and parasite intensity.

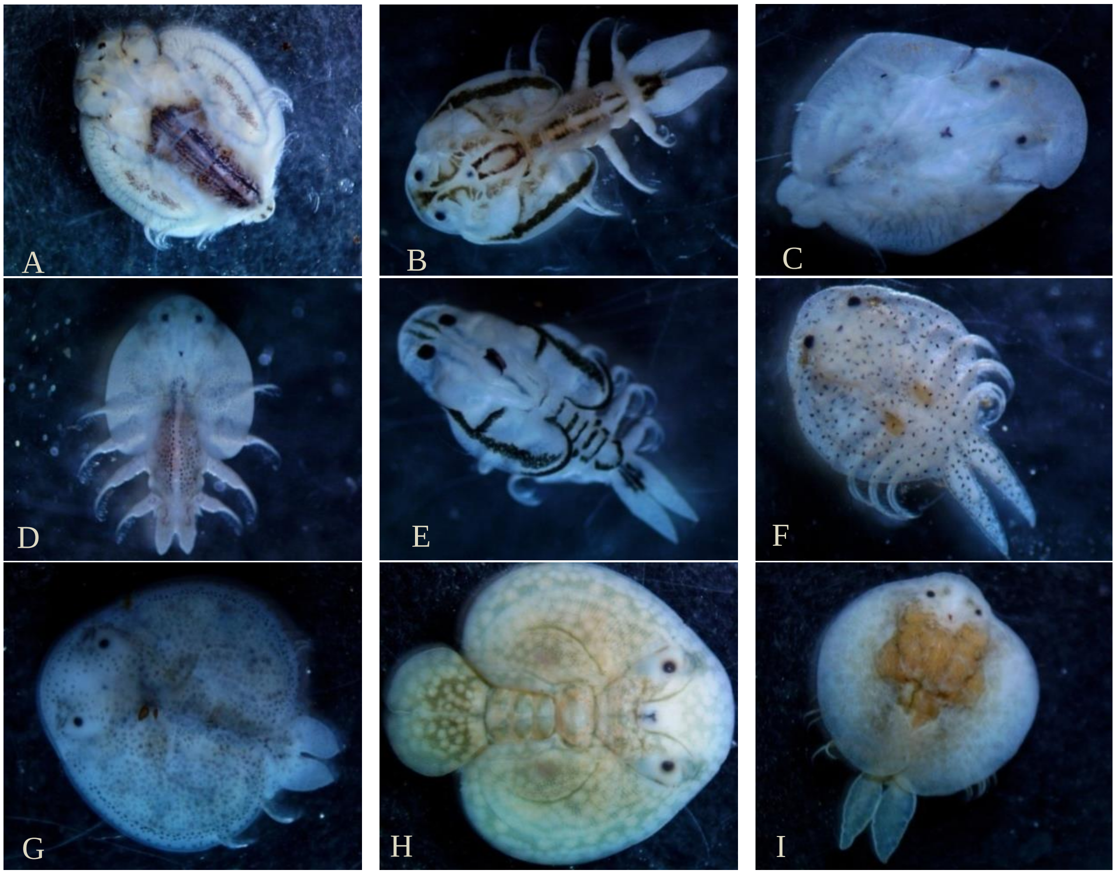

Figure 10. Photographs of the branchiuran species encountered during the survey. **A.** *Argulus juparanaensis*. **B.** *Argulus multicolor*. **C.** *Argulus silvestrii*. **D.** *Argulus spinulosus*. **E.** *Argulus* sp. **F.** *Dolops geayi*. **G.** *Dolops bidentata*. **H.** *Dolops discoidalis*. **I.** *Dolops nana*.

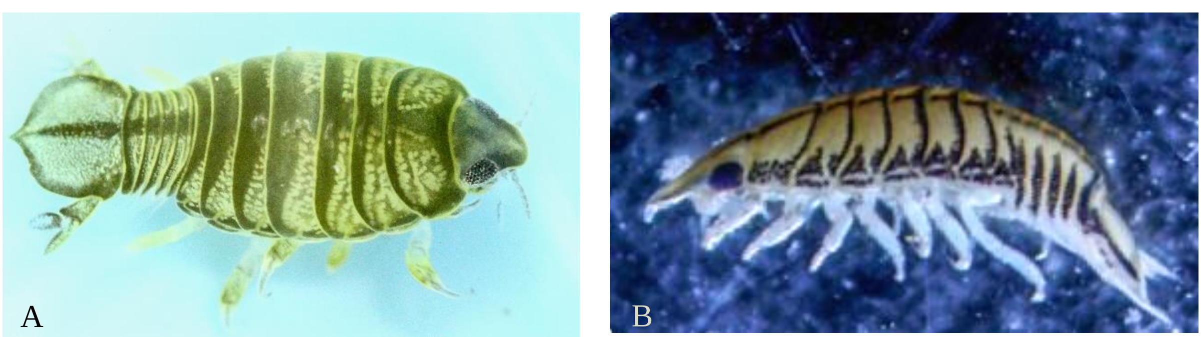

Figure 11. Photographs of the isopod species encountered during the survey. **A.** *Braga* sp. **B.** *Vanamea symmetrica*.

Host-Parasite Interactions

This study demonstrated a statistically significant correlation between fish length and ectoparasite intensity across all surveyed infected fish (26 individuals from 10 species; Fig. 2). This correlation was particularly true when limiting analysis to only *S. rhombeus*, the species with the most infected individual fish in the study (Fig. 4). For instance, of the 40 surveyed piranhas, 23 piranhas were shorter than 25 cm in length. Out of this group just 1 specimen contained a parasite. In contrast, among the 17 fish longer than 25 cm 10 specimens had parasites.

The correlation between parasite intensity and host size has been found in many studies (Carvalho et al., 2004; Cloutman and Becker 1977; Hamann, 1998; Zelmer and Arai, 1998). There are several reasons why parasites might exhibit higher prevalences and intensities on larger hosts. With the increase in host body size, there is an increase in the quantity of resources available for a greater number of ectoparasites to exploit. Specifically, larger hosts provide greater quantities of food for parasites, such as blood, skin, fins, and mucus. They also physically have more space on which an increased number of ectoparasites can live. Moreover, larger fish are potentially an easier target for free swimming parasites such as, branchiurans and manca isopods to successfully find and attach to the host. Cloutman and Becker (1977) suggested this phenomenon might occur between the parasitic copepod *Ergasilus centrarchidaerum* and largemouth and spotted bass when they observed greater rates of infections in larger fish. They suggested that larger fish likely have an increased probability of coming into contact with more copepods due to their greater size. Within species, larger fish are generally older than smaller fish. Zelmer and Arai (1998) observed that it is often difficult to isolate the two variables of size and age when analyzing their effects on parasite populations. Age affects both parasite intensity and fish size. Older fish have been in the environment longer and thus have had more time to accumulate more parasites. However, not all studies support the correlation between length and intensity. For example, Carvalho et al. (2003), while investigating host-parasite interactions between branchiurans and piranhas, found no correlation between fish length and parasite intensity. Aside from length and age, other factors may affect parasite prevalence and intensity on hosts. These factors may include environmental conditions, host population factors, fish species, and host behavioral traits.

Environmental conditions can affect parasite prevalence and intensity by increasing or decreasing stress factors on fish. The level of these stress factors in turn make fish more or less susceptible to parasite infestations. Fish living in more stressful environmental conditions are likely more vulnerable to parasites and vice versa. Stress can reduce healthy body functions that help fish defend themselves against pathogens and parasites. These body functions can range from immune responses to respiratory function.

As aquatic animals, one important factor affected by environmental conditions is water quality. Conditions that affect water quality can sometimes have human origins, as seen with pollution and human-caused habitat alterations (Lafferty and Kuris, 1999). Other times these conditions result purely from natural phenomenon, as is the case with hydrological seasons greatly changing aquatic habitats. A good example of this can be seen in the dequadas of Brazil's Pantanal wetlands.

"Dequada" is a local name for periodic fish die-offs that occur during the region's dry season. At this time, water quality greatly deteriorates and puts huge environmental stressors on fish populations (Macedo et al., 2015). As water levels are lowered, dissolved oxygen levels are reduced, and dissolved carbon dioxide levels are increased. These three factors together create a stressful environment for fishes trapped in drying river beds, making normal respiratory functions more difficult. While these fish are stressed, their defenses against pathogens and parasites are diminished. Parasites can take advantage of decreased fish immunity and thus can increase in both prevalence and intensity in fish populations. In the Pantanal, Carvalho et al. (2004) observed that *Pygocentrus nattereri* (red bellied piranha) during the dequada had higher intensity and prevalence of branchiuran infestations.

These harsh dry season conditions also alter other host factors, such as density, population size, and host behavioral traits. Host population factors and host behavioral traits affect prevalence and intensity by either increasing or decreasing parasite transmission rates between hosts. For example, the more dense a host population is in an environment, the easier it is for hosts to exchange parasites. This is seen with crowded fish in shallower, dry season pools. Fish that would typically be spread throughout a large river are instead trapped in closer proximity to each other in these smaller volume pools.

Host population size, when tied to high host density, gives parasites access to more hosts they can infect. This in turn can increase the prevalence of a parasite in that host population. Lafferty and Kuris (1999) reported that density and population size affected parasite transmissibility when they discussed withered foot syndrome in black abalone. In this case, a previously uncommon pathogen grew to enormous prevalence following both increased density and population size in black abalone (Lafferty and Kuris, 1999). If these factors are also tied to environmental conditions adverse to the host, such as poor water quality, then parasite intensity can also increase among infected individuals.

Host behavioral traits also play a role in how parasites are transferred between hosts. If a host species is solitary, it may be harder for these lone hosts to exchange parasites. Conversely, if a host species is social, it may be easier for parasites to infect new hosts. Carvalho et al. (2004) reported more branchiurans infecting a social species of piranha (*P. nattereri*) than a solitary species (*Serrasalmus marginatus*). If tied together with environmental conditions and population density, solitary hosts could be forced into unusually close proximity to infected fish. This could allow for higher rates of parasite transmission to solitary species.

In this study, it is difficult to determine statistically if there are any individual parasite preferences for different fish host species because of the small sample size of individual fish species. Despite small sample sizes, some casual observations can be made. Of the 26 infected fish, only 5 hosted more than 1 species of parasite. Of these 5 fish, 4 are among the top 5 longest of the surveyed fishes (71.0 cm in length or greater). Of the 5 host fish with multiple species of ectoparasites, only 2 exhibited more than one parasitic species in the same anatomical site on the body. The shared site was dorsal skin on the first specimen (fish of length 99.0 cm). On the second specimen (length 83.7 cm), shared sites were caudal fin, dorsal skin, operculum, upper head, and ventral skin.

In each of these shared anatomical sites, it is unclear if there is competition between parasites of different species or between individual parasites of the same species. Competition might be for host surface area as well as for food (blood, mucus, or scales). For example, on the first specimen, the 99.0 cm length *P. fasciatum*, the dorsal skin hosted 2 *A. juparanaensis* and 5 *D. discoidalis,* each of which were observed to move freely about the skin surface of the host (Hubbell, 2014, personal observation). Thus, the shared site may have been coincidence on this single host individual.

On the second specimen, the 83.7 cm long *P. hemiliopterus*, there were many sites shared by more than one species of parasite. The upper head supported 5 *D. discoidalis* and 1 *Stegophilus* sp. The operculum hosted 3 *D. discoidalis* and 1 *Stegophilus* sp. The caudal fin hosted 2 *D. discoidalis* and 7 *Stegophilus* sp. Three *D. discoidalis* and 6 *Stegophilus* sp. shared the dorsal skin. The last shared site, the ventral skin, hosted 1 *Argulus* sp., 2 *D. discoidalis*, and 3 *Stegophilus* sp. At each of these sites, *D. discoidalis* and *Stegophilus* sp. coexisted, with the former eating blood and the latter eating mucus and skin, effectively occupying separate dietary niches. Despite the dietary differences among these parasites, there still may be competition for surface area on the host. In addition to this, it is possible that *Argulus* sp., also a sanguinivore, may occasionally compete with *D. discoidalis* for blood while on the ventral skin of a shared host.

Remarks on New Host Records

Dolops species Host Records: This is the first report of *D. bidentata* on a Siluriformes host species, specifically, *P. fasciatum* (Table 5). *Dolops bidentata* has been reported mostly on Characiformes fish with a few infections recorded on other hosts such as cichlids and swamp eels (Thatcher, 2006; Luque et al., 2013).

This is the first instance of *D. nana* infecting a Siluriformes host, being found on the auchenipterid, *T. trachycoryestes* (Table 5). *Dolops nana* has mostly been reported on Characiformes fish in Brazil with one report of the parasite on a cichlid fish (Thatcher, 2006; Luque et al., 2013; Neves, et al., 2013).

The presence of *D. geayi* on *T. trachycoryestes* is a new host record for both this species and the family Auchenipteridae (Table 5). A multitude of fish hosts are reported for *D. geayi*, including catfish, characins, and cichlids (Thatcher, 2006; Luque et al., 2013). Of the encountered *Dolops* species, *D. geayi* has the widest geographical range and is found in 5 South American countries, 2 of which border Guyana (Thatcher, 2006).

The presence of *D. discoidalis* on *P. hemiliopterus* and *P. fasciatum* in this study are not new host records for this parasite (Table 5). Aside from *D. discoidalis* being previously found on these hosts, it has been reported on other catfish, cichlids, characins, and arapaima. This parasite has been found in several countries prior to this study including Argentina, Bolivia, Brazil, French Guiana, Paraguay, and Venezuela (Thatcher, 2006).

Argulus species Host Records: This is the first report of *A. multicolor* on the species *P. hemiliopterus* and *A. inermis*, the families Pimelodidae and Auchenipteridae, and the order Siluriformes (Table 4). The characin, *T. rotundatus*, is the first Triportheidae host reported for *A. multicolor* (Table 4).

Hydrolycus scomberoides is a newly reported host species for *A. spinulosus* and is the first Cynodontidae host found to be infected with this parasite (Table 4). *Argulus multicolor* and *A. spinulosus* have been found almost evenly divided between characin and cichlid hosts in Brazil and Venezuela for *A. multicolor* and Brazil for *A. spinulosus* (Thatcher, 2006; Luque et al., 2013).

Argulus silvestrii was formerly listed on one pimelodid catfish, *Pseudoplatystoma corruscans,* in Argentina (Thatcher, 2006). Thus, *L. marmoratus* is a newly reported host for *A. silvestrii* and is the second pimelodid host reported for this parasite (Table 4).

Prior to this study, *A. juparanaensis* was exclusively reported in Brazil infesting characins, freshwater drum, stingrays, and catfish (Thatcher, 2006; Luque et al., 2013). This study found *A. juparanaensis* on the catfish, *P. fasciatum*, a host on which it has previously been reported (Table 4).

Braga species Host Records: Two individual isopods of likely the same species (genus *Braga*) were encountered during the study (Fig. 17). The infection of the family Auchenipteridae was new for *Braga* sp., and likewise new for the two infected species of fish, *C. romani* and *T. chalceus* (Table 1). Members of the genus *Braga* have been reported in Argentina, Brazil, and Surinam and found on characins, cichlids, catfish, drum, and silversides (Salgado-Maldonado et al., 2000; Thatcher, 2006).

Vanamea symmetrica Host Records: The presence of *V. symmetrica* on *T. rotundatus* is a new host record for both Triportheidae and the species *T. rotundatus* (Table 1). Aside from this new host, the black piranha (*S. rhombeus*) was the only other fish species infected by *V. symmetrica* during the study. Finding *V. symmetrica* on these characins is reasonable given that the parasite is reported on mostly Characiformes fish, all of which are closely related to *T. rotundatus* and *S. rhombeus* (Table 1). Thatcher (1993b), in his re-description of *V. symmetrica*, reported the isopod infesting two piranhas of the same genus (*Serrasalmus*) as the black piranha in Brazil. Trilles (1973) reported *V. symmetrica* infesting the Characiformes fish, *Carnegiella strigata*, which is a member of Gasteropelecidae, a family of fishes closely related to Triportheidae (Mariguela et al. 2015). In Guyana, Van Name (1925) reported *V. symmetrica* on two characins: (1) *Myleus rubripinnis*, a pacu-like fish closely related to piranhas, and (2) *S. rhombeus*, the same black piranha this study found the parasite infesting. Aside from characins, Van Name (1925) also reported *V. symmetrica* on catfish and cichlids.

Remarks on Encountered Parasites

Dolops species Infection Sites: Branchiurans in the Brazilian Amazon have shown some discrimination in the types of fish hosts they parasitize, as well as which host body regions (skin, gills, and etc.) they prefer to infect (Malta, 1982a; Malta, 1982b; Malta, 1983; Malta and Varella, 1983). With regard to the genus *Dolops*, infections have mainly been reported on the skin of the host fish, but some species have been found clinging to the gills of infected fish (Luque et al. 2013). Our expedition had many similar findings when examining the preferred infection sites of *Dolops* branchiurans with minor exceptions. We exclusively found these parasites on the skin and the fins, but not the gills, of infected host fish. For instance, our survey found *D. discoidalis* solely on host fish skin, which agrees with past reports (Yamaguti, 1963; Malta, 1982b; Lemos de Castro and Silva, 1985; Malta, 1998; Thatcher, 2006; Eiras et al., 2010; Luque et al., 2013). *Dolops bidentata*, a species similar to *D. discoidalis,* was found on the skin of the host fish during the study. This agrees with Silva-Souza et al. (2011) and Malta (1982b), but conflicts with Luque et al. (2013), who reported *D. bidentata* not only infesting fish host skin but also the gills. This seems curious because this species, just like *D. discoidalis*, is relatively large in size when compared to other smaller, typically gill-dwelling branchiurans, such as many *Argulus* species or *D. geayi*.

Interestingly, despite being solely reported from fish gills, our study found *D. geayi* infesting the skin and fins of host fish. Branchiurans reproduce off-host and swim well (Thatcher, 2006). It could be that these *D. geayi* were encountered while en route to or from their host fish gill chamber. *Dolops nana* was found infesting host fins in this study. In the past, *D. nana* has been found on both the gills and body surfaces of infected hosts, which is consistent with our observations (Lemos de Castro, 1950; Yamaguti, 1963; Lemos de Castro and Silva, 1985; Malta, 1998; Guidelli et al., 2006; Takemoto et al., 2009; Eiras et al., 2010).

Dolops adaptations as Skin Parasites: *Dolops discoidalis* and *D. bidentata* are both well adapted to dwelling on the body surface of fish with their streamlined, flattened, disc-shaped bodies and heavily pigmented carapaces (Fig. 10G and 10H). The disc-shaped body allows these parasites to "skate" quickly across the surface of a fish's body from one feeding location to another. The disc shape greatly reduces the amount of drag exerted on these parasites as the fish swims around. This body shape also likely provides the parasites with a "suction-like" ability which allows these *Dolops* to better cling to fish skin, in conjunction with their hook-shaped first maxillae.

Pigment may help camouflage these parasites (Fig. 5B). Sazima et al. (1990) observed *S. marginatus* "clean" branchiurans off larger red bellied piranhas (*P. nattereri*). These smaller piranhas swam up to receptive *P. nattereri* that allowed them to get close enough to feed on the ectoparasites. Perhaps this cryptic coloration helps *D. discoidalis* and *D. bidentata* blend in better with the fish skin color and reduces the likelihood of being picked off by "cleaner" fish (Fig. 5B).

Larger size may also be advantageous for skin parasites, such as *D. discoidalis.* In combination with a disc-shaped body, larger size may result in greater attachment strength via suction. The increased carapace diameter would yield a larger surface area in contact with the fish body. Underneath the carapace, there is likely lower pressure between the attached parasite and the fish compared to the external pressure along the parasite's exposed dorsal surface. Suction force equals surface area multiplied by external pressure, thus larger

Dolops may have the advantage of greater force of attachment related to suction. Also, when the parasite is not moving, the sides of the carapace can fold downward, decreasing the water flow under the parasite and making it less likely to be swept away by water currents.

Gill Parasite Adaptations: All of these traits serve well for life as a skin parasite but would likely detract from life as a gill parasite. With lack of predators, gill parasites have little benefit from camouflage, as is evident in the reduced pigment seen in adult mouth-dwelling cymothoids. Gill parasites also do not necessarily need to be as large as skin parasites. Larger body sizes can be cumbersome and disadvantageous in the less open and smaller confines of a fish's gill chamber. Luque et al. (2013) and Malta (1982a) reported *D. geayi* solely on the gills of fish hosts. *Dolops geayi* is tiny in comparison with skin parasites like *D. discoidalis*. For example, *D. geayi* is reported to attain standard lengths of 2.5-4.0 mm versus 9.9-11.9 mm for *D. discoidalis* (Thatcher, 2006), a quarter to a third of the size of *D. discoidalis*.

Argulus species Infection Sites: Amazonian species of freshwater *Argulus* in general are reported mostly infecting fish gills, with a few reports of *Argulus* infecting the skin, bodies, and mouths of fish (Luque et al. 2013). Several of the species encountered in this study, specifically *A. multicolor, A. juparanaensis,* and *A. spinulosus,* are well documented fish gill parasites (Lemos de Castro, 1949; Lemos de Castro, 1950; Yamaguti, 1963; Silva, 1980; Malta, 1982a; Malta, 1983; Lemos de Castro and Silva, 1985; Malta, 1998; Peralta et al., 1998; Malta and Varella, 2000; Carvalho et al., 2003; Thatcher, 2006; Eiras et al., 2010). This study's *Argulus* collections matched up well with these reports. Most *Argulus* were encountered either directly on host fish gills or in relatively close proximity to the gills, with a few exceptions found on the ventral skin.

Of the 4 encountered *Argulus* sp., 3 were found on fish gills with 1 individual found on the host's skin. The *A. juparanaensis* of this study were found on the skin just outside the operculum, very close to the gills. The 1 encountered *A. spinulosus* was found in the mouth of a *H. scomberoides*, a region also very near the gills. *Argulus multicolor* were mostly found clinging to gills. An exception to this was that 1 *A. multicolor* was found at the base of a *T. rotundatus* pectoral fin, a body region not far from the entrance to this fish's gill chamber (Fig. 12A).Given the close proximity of these *Argulus* branchiurans to the host fish gills, it is possible that these typical gill parasites were encountered while they were en route to their preferred infection site.

Argulus silvestrii was the exception to our *Argulus* being found near the gills. It was found the farthest from the fish host gills, on the ventral belly skin of a single catfish. Despite this, it is still possible that these *A. silvestrii* were collected while they were en route to or from their host fish gill chamber, as was suspected with the other encountered *Argulus*. Branchiurans have a decent swimming ability when outside the host and are perfectly capable of leaving and returning to hosts (Thatcher, 2006).

Braga species Infection Sites: Both *Braga* sp. were found on the head regions of these fish (Fig. 12B). According to numerous interviews with Amerindians local to the survey sites, this parasite is commonly found on the heads of small fish.

Figure 12. In-situ photographs of *Argulus multicolor* and *Braga* sp. attachment sites. Photographs were taken immediately before these parasites were collected from hosts and preserved. **A.** *Argulus multicolor* just after sliding off the pectoral fin of *Triportheus rotundatus*. **B.** *Braga* sp. on the operculum of *Centromochlus romani*.

Vanamea symmetrica Infection Sites and Encountered Life Stages: Exclusively manca and juvenile *V. symmetrica* were encountered during the study (Figs. 13A-C). This is expected, as all encountered *V. symmetrica* were found clinging to the skin or fins of examined fish (Fig. 14). Juvenile and manca cymothoids are typically reported on the outer bodies and fins of intermediate fish hosts (Brusca, 1978; Brusca, 1981; Salgado-Maldonado et al., 2000; Thatcher, 2006). Van Name (1925) specifically reported young *V. symmetrica* attaching to the skin of fish. Sexually mature adults of this species (both male and female) are said to inhabit the mouth cavities of the fish they infect (Thatcher, 1993b; Fig. 15A-D).

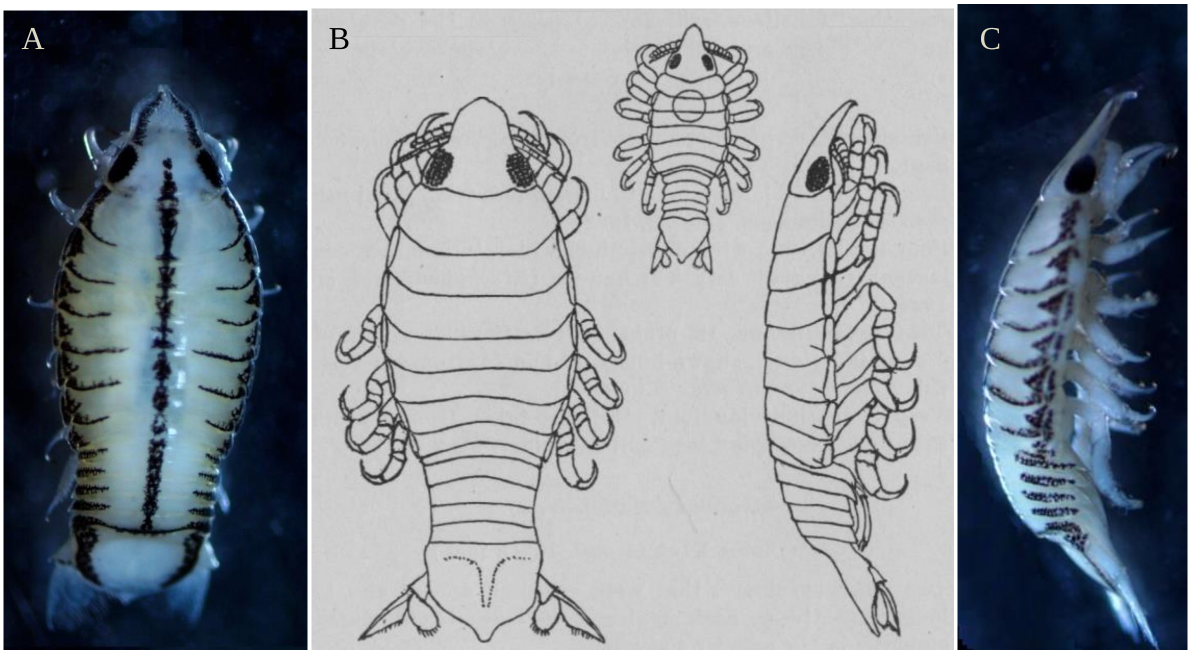

Figure 13. Photos of *Vanamea symmetrica* from Guyanese expeditions. Juvenile *Vanamea symmetrica* collected during this expedition compared to drawings from the original Van Name (1925) publication first describing the species. *Vanamea symmetrica* was the only parasite previously reported from Guyana collected during this expedition.
A. Dorsal view of juvenile *Vanamea symmetrica* collected on this survey. **B.** Plate X from Van Name (1925) showing the dorsal and lateral views of juvenile *Vanamea symmetrica* as well a manca stage *V. symmetrica* in the middle. Note the 6 pairs of legs on the smaller manca vs. the 7 pairs of legs on the two larger juveniles. **C.** Lateral view of juvenile *Vanamea symmetrica* collected on this survey.

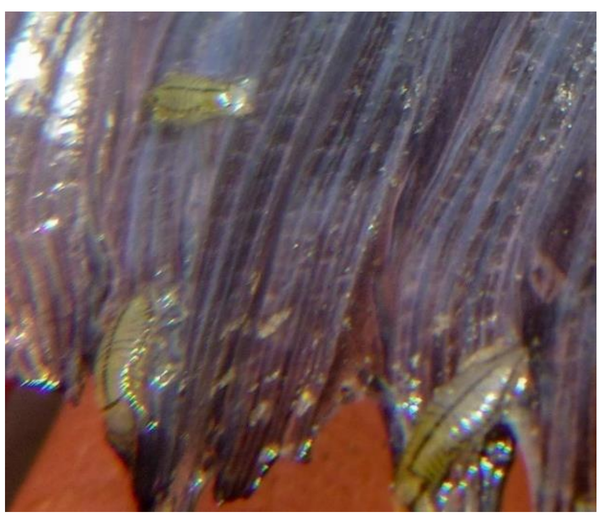

Figure 14. *Vanamea symmetrica* on the anal fin of a black piranha.

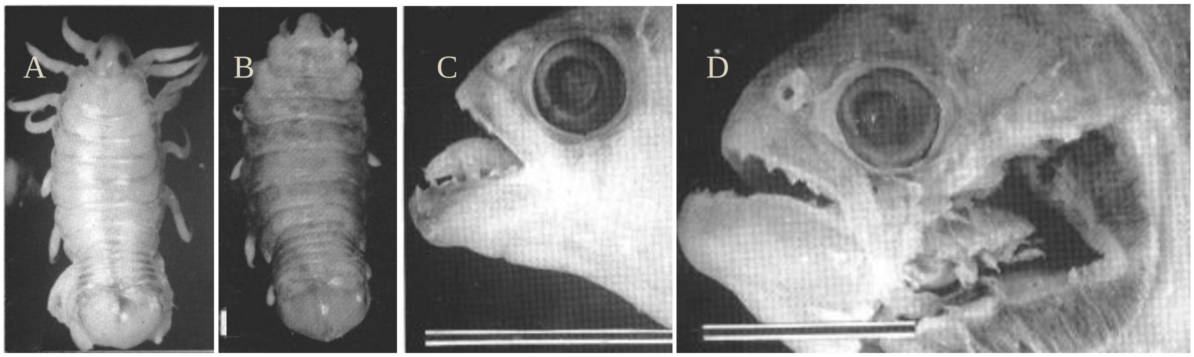

Figure 15. Photos of adult *Vanamea symmetrica* from Thatcher (1993). **A.** Adult male. **B.** Adult female. **C.** Adult male in mouth. **D.** Adult female in gill chamber.

No adult *V. symmetrica* were encountered on the expedition. This is despite surveying many fish closely related to those previously reported to host adult *V. symmetrica* (Van Name, 1925; Thatcher, 1993b). Additionally, adult specimens have been collected in northern Guyana during the same month (July) as the *V. symmetrica* collected in this study (Van Name, 1925). Several variables individually or combined could help explain why we encountered the juvenile isopods instead of adults.

Perhaps juveniles make up a larger percentage of total isopod populations than adults. Unfortunately, few studies have investigated the life stage distributions (juvenile-versus-adult) of cymothoids and, as far as the author knows, no studies have investigated these distributions regarding *V. symmetrica*. Aside from juveniles just being more prevalent than adults, two key variables may have made adult cymothoids hard to find during this study: (1) the seasonality of the region potentially causing fluctuations in the prevalence of certain ectoparasites on fish, and/or (2) the study's small sample sizes. Both of these topics are covered in more depth in the next section, "Limitations of the Survey".

LIMITATIONS OF THE SURVEY

Seasonality is a limitation of this survey. This expedition took place during the summer wet season so it is limited to observations on the fish parasite communities for this time of year. Seasonality is an important factor to consider when studying parasites from regions that undergo seasonal changes. This is especially true when considering parasite prevalence. Some studies have shown ectoparasitic crustaceans infesting fish to exhibit seasonal patterns in prevalence (Schram, et al., 1998; Morales-Serna, et al., 2011; Aneesh et al., 2013). Thus, a parasite maybe more or less prevalent on hosts at certain times of the year (or seasons). Because of this, it would be more likely to encounter this parasite during the time period they are most prevalent.

With regard to Branchiura, numerous studies have investigated the seasonal prevalence of these parasites on fish in the Brazilian Amazon (Malta, 1982a; Malta, 1982b; Malta, 1983; Malta and Varella, 1983; Neves et al., 2013). In these studies, the prevalence of branchiuran species varied some in response to the wet and dry seasons. For instance, 7 species including several from this survey (*D. bidentata, D. discoidalis, D. geayi, A. juparanaensis,* and *A. multicolor*) increased in prevalence during the wet season in June and July (Malta, 1982a; Malta, 1982b; Malta, 1983; Malta and Varella, 1983). Inversely, Malta (1983) found *Argulus pestifer* to be more prevalent in November and December, which is the dry season. Unlike these other branchiurans, Neves et al. (2013) found the prevalence of *Dolops nana* (also found in this study) not to differ between the wet and dry seasons.

Like branchiurans, some cymothoids have shown seasonal fluctuations in prevalence on fish hosts (Bragoni et al., 1984; Aneesh et al., 2013). In a tropical region of India, the prevalence of several cymothoids was highest in the “dry” pre-monsoon season and was relatively low in the "wet" monsoon season (Aneesh et al., 2013). These agree with observations stated by Amerindians about the Iwokrama's cymothoids. According to numerous interviews, Amerindians said they generally saw more, large cymothoids infesting the mouths of fish they capture during the dry season than those captured in the wet season (when this survey was done). The large size of these isopods as well as their preferred infection site matches well with the description of adult stage cymothoids.

Perhaps this survey was conducted when adult mouth-dwelling isopods, like *V. symmetrica* and *Braga* sp., are less prevalent on host fish and are therefore more difficult to encounter. Similarly, maybe this same season is a good time of year to encounter certain branchiurans. Given the seasonal fluctuations of ectoparasites in other rivers (Malta, 1982a; Malta, 1982b; Malta, 1983; Malta and Varella, 1983), it is likely seasonal changes also occur within Iwokrama's fish parasite communities between the wet and dry seasons. These changes likely correlate with changing environmental and biotic conditions such as water level, water flow, salinity, and host population density. To assess this topic further, surveys in the dry season would need to be conducted.

The other major limitation of this expedition was its sample size. This study was a general survey that examined a broad number of different fish species. The total sample size was 210 individual fish across 26 surveyed species. Despite the large quantity of fish species surveyed, many individual fish species had sample sizes that were smaller than was optimal. Poulin (1999) made statistically significant observations on ectoparasite-fish host interactions from sample sizes of at least 20 fish of the same species. In our survey, all but 4 fish species had sample sizes less than 20. The top 4 most numerous fish species harboring parasites were *T. chalceus* (55 individuals), *S. rhombeus* (40 individuals), *T. rotundatus* (31 individuals), and *T. trachycoryestes* (27 individuals). Statistically significant observations can be made with these sample sizes. For instance, we noted a correlation between parasite intensity and fish length in the black piranha (*S. rhombeus*) population. In spite of this observation though, larger sample sizes for most surveyed fish species would still have been desirable.

Research by Aneesh et al. (2013) was similar to this study in that a broad number of different host fish species were surveyed (56 in total) for multiple parasite species (4 cymothoids). Unlike this study, Aneesh et al. (2013) had an enormous aggregate sample size of 13,829 total individual fish. In regard to individual fish species, sample sizes ranged from as few as 18 to as many as 1,329. One fourth of individual sample sizes in the Aneesh study were 42 or less, sizes comparable to those in our study. With such large sample sizes Aneesh et al. (2013) could easily make strong statistical observations on host-parasite interactions with many of its surveyed fish species.

Other similar studies surveyed fewer fish species for multiple parasite species (branchiurans and isopods). Those studies also typically sampled more fish per species. Both Carvalho et al. (2003) and Carvalho et al. (2004) surveyed a small number of piranha species. For instance, Carvalho et al. (2004) examined 252 piranhas of a single species (*P. nattereri*) for branchiurans and cymothoids. Carvalho et al. (2003) had a slightly broader survey investigating branchiurans from 3 piranha species: *P. nattereri* (237 individuals), *Serrasalmus spilopleura* (273 individuals), and *S. marginatus* (35 individuals). Aside from *S. marginatus*, both Carvalho studies had much larger sample sizes per fish species than our study and thus were better equipped for evaluating correlations between parasites and individual fish species.

In contrast to sample sizes of individual host species, the total sample size (210) was sufficient to analyze certain host-parasite interactions. This was especially true when examining correlations with variables that were measureable across all fish species and parasite taxa, i.e. fish length and parasite intensity. However, when analyzing the smaller sample sizes of lone fish species, finding correlations between these variables remained difficult to impossible in most cases. As such, out of 26 observed species, correlations could only be generated in one of the most prevalent species surveyed, the black piranha, *S. rhombeus* (40 individuals surveyed).

Small sample sizes of surveyed fish may have made it hard to find certain "rarer" parasites and/or parasite life stages (adult isopods) that are less abundant in fish populations. In Aneesh et al. (2013), no species with a sample size of less than 280 was found to host ectoparasites. Most species sample sizes in the Carvalho et al. (2003, 2004) were close in size to 280 per fish species (237, 252, and 273). In both studies, about 30% of all piranha species surveyed were infected with ectoparasites. In Carvalho et al. (2004), about half of the ectoparasites were adult isopods giving a prevalence of infection of 15.5%. Based on Naing et al. (2006), which described a formula from Daniel (1999) to approximate an adequate sample size to survey the less prevalent portions of the population, 196 fish are required to detect with 95% confidence a parasite with a prevalence of 15 %. To detect a parasite that infects 1% of the population, I would need to sample of 1,522 individuals.

Given my small sample sizes for individual fish species, it is likely that I did not sample enough ectoparasite-bearing fish, and therefore missed surveying certain fish infected with somewhat rare parasites and/or life cycle stages. For example, the black piranha, the fish species with the most encountered *V. symmetrica*, had a sample size of 40 individuals. This is roughly five times smaller than the predicted sample size expected to successfully detect individual fish infected with adult isopods. This may in part explain why only juvenile *V. symmetrica* were detected in my study and not adults.

In addition to small sample sizes and seasonality, the diversity of fishing methods may have impacted the capture rates of certain fish species over others. These multiple methods were employed to catch a wide range of different fish species (26 species in total). The overall goal of the project was a broad survey of the fish and their ectoparasites. To that end, despite the limitations of this study, the project is deemed more than adequate.

CONCLUSION

Just as reports of past expeditions aided this study, the information presented here can help future expeditions in Guyana. These 13 newly reported ectoparasites did shed some light on what fish parasites are present in the Essequibo River of the Iwokrama Reserve, Guyana. There is still much to learn about Guyana's fish ectoparasites including several questions that could serve as the basis for future studies in Guyana or surrounding regions: Do fish ectoparasite communities differ between Guyana's rivers and eco-regions? How do changes in the wet and dry seasons affect fish parasite communities in Guyana? Is host selection for these parasites based more on host ecological niche or host taxa? How genetically related are these parasites to those in other regions of South America? Are there consistent differences in parasite fauna and their infection rates in different kinds of fish? Finally, do patterns in the ectoparasite community match those of the endoparasite community? These questions, as well as the data reported in this study, could provide a good starting point for future expeditions to this understudied part of the world.

LITERATURE CITED

Aneesh, P. T., K. Sudha, K. Arshad, G. Anilkumar, and J. P. Trilles. 2013. Seasonal fluctuation of the prevalence of cymothoids representing the genus *Nerocila* (Crustacea, Isopoda), parasitizing commercially exploited marine fishes from the Malabar coast, India. Acta Parasitologica 58: 80–90.

Armbruster, J. W. 2002. Report to the Guyana EPA 2002 AUM/ANSP/UG/Iwokrama expedition to the Rupununi. Report: Guyana EPA, Georgetown, Guyana.

Baskin, J. N., T. M. Zaret, and F. Mago-Leccia. 1980. Feeding of reportedly parasitic catfishes (Trichomycteridae and Cetopsidae) in the Río Portuguesa basin, Venezuela. Biotropica 12: 182–186.

Beebe, W., G. I. Hartley, and P. G. Howes. 1917. Tropical Wildlife in British Guiana. The New York Zoological Society, New York City, New York, U.S.A. 504 pp.

Bicknell, J. 2005. Patterns of fish diversity in the Rupununi Savannahs, Guiana Shield. Bachelors of Science Thesis, University of Kent, Canterbury, United Kingdom. 13 pp.

Boone, P. L. 1918. Description of ten new isopods. Proceedings of the United States National Museum 54: 591–604.

Bragoni, G., B. Romestand, and J. P. Trilles. 1984. Parasitoses a cymothoadien chez le loup, *Dicentrarchus labrax* (Linnaeus, 1758) en elevage I. ecologie parasitaire dans le cas de L'etang de Diana (haute-corse) (Isopoda, Cymothoidae). Crustaceana 47: 44–51.

Brusca, R. C. 1978. Studies on the cymothoid fish symbionts of the eastern Pacific (Isopoda, Cymothoidae) I. Biology of *Nerocila californica*. Crustaceana 34: 141–154.

Brusca, R. C. 1981. A monograph on the Isopoda Cymothoidae (Crustacea) of the eastern Pacific. Zoological Journal of the Linnean Society 73: 117–199.

Bush, A. O., Lafferty, K. D., Lotz, J. M., and A. W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology. 83: 575-583.

Bush, S. E. 2009. Field Guide to Collecting Parasites. Natural History Museum and Biodiversity Research Center. University of Kansas, Lawrence, Kansas, U.S.A. 16 pp.

Carvalho, L. N., K. Del-Claro, and R. M. Takemoto. 2003. Host-parasite interaction between branchiurans (Crustacea: Argulidae) and piranhas (Osteichthyes: Serrasalminae) in Pantanal wetland of Brazil. Environmental Biology of Fishes 67: 289–296.

Carvalho, L. N., R. Arruda, and K. Del-Claro. 2004. Host-Parasite interactions between the piranha *Pygocentrus nattereri* (Characiformes, Characidae) and isopods and branchiurans (Crustacea) in the Rio Araguaia basin, Brazil. Neotropical Ichthyology 2: 93–98.

Cloutman, D. G., and D. A. Becker. 1977. Some ecological aspects of *Ergasilus centrarchidarum* Wright (Crustacea: Copepoda) on largemouth and spotted bass in Lake Fort Smith, Arkansas. Journal of Parasitology 63: 372–376.

Daniel, W.W. 1999. Biostatistics: A Foundation for Analysis in the Health Sciences, 7th edition. John Wiley & Sons, New York, New York. 755 pp.

De Souza, L. 2005. Report to the Guyana EPA 2005. Expedition to the Rupununi "The Biogeography of Freshwater Fishes around the Guyana Shield and the movement of fishes through Portals in the Rupununi Savanna." Report: Guyana EPA, Georgetown, Guyana.

De Souza, L. S., J. W. Armbruster, and D. C. Werneke. 2012. The influence of the Rupununi Portal on distribution of freshwater fish in the Rupununi district, Guyana. Cybium 36: 31–43.

Eigenmann, C. H. 1912.The fresh-water fishes of British Guiana, including a study of the ecological grouping of species, and the relation of the fauna of the plateau to that of the lowlands. Memoirs of the Carnegie Museum 5: 1–578.

Eiras, J. C., R. M. Takemoto, and G. C. Pavanelli. 2010. Diversidade dos Parasitos de Peixes de Água Doce do Brasil. Editora Clichetec, Maringá, Paraná, Brazil. 333 pp.

Fernandez, L., and S. A. Schaefer. 2009. Relationships among the Neotropical candirus (Trichomycteridae, Siluriformes) and the evolution of parasitism based on analysis of mitochondrial and nuclear gene sequences. Molecular Phylogenetics and Evolution 52: 416–423.

Gardner, S. L., and M. L. Campbell. 1992. Parasites as probes for biodiversity. Journal of Parasitology 78: 596–600.

Goulding, M. 1983. The role of fishes in seed dispersal and plant distribution in Amazonian floodplain ecosystem. Sonderbd. Naturwiss. Ver. Hamburg 7: 271–283.

Guidelli, G. M., W. S. G. Tavechio, R. M. Takemoto, and G. C. Pavanelli. 2006. Parasite fauna of *Leporinus lacustris* and *Leporinus friderici* (Characiformes, Anastomidae) from the Upper Paraná River floodplain, Brazil. Acta Scientiarum, Biological Sciences 28: 281–290.

Hamann, M. I. 1998. Aspectos ecológicos de la relácion parasitaria entre juveniles de *Braga fluviatilis* Richardson,1911 (Crustacea, Cymothoidae) y *Serrasalmus spilopleura* Kner, 1860 (Pisces, Characidae) en poblaciones naturales del Nordeste Argentino. Physis 55: 15–22.

Hawkes, M. D., and J. R. D. Wall. 1993. The Commonwealth and Government of Guyana Rain Forest Programme, Phase I, Site Resource Survey, Main Report. Report: Natural Resources Institute (NRI)/University of Greenwich, Chatham, United Kingdom.

Hechinger, R. F., and K. D. Lafferty. 2005. Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. Procedings of the Royal Society B: Biological Sciences 272: 1059–1066.

Hechinger, R. F., K. D. Lafferty, T. C. Huspeni, A. J. Brooks, and A. M. Kuris. 2007. Can parasites be indicators of free-living diversity? Relationships between species richness and the abundance of larval trematodes and of local benthos and fishes. Oecologia 151: 82–92.

Kelley, W. E., and J. Atz. 1964. A pygidiid catfish that can suck blood from goldfish. Copeia 1964: 702–704.

Lafferty, K. D., and A. M. Kuris. 1999. How environmental stress affects the impacts of parasites. Limnolology Oceanograpy 44(3, part 2): 925-931.

Lemos de Castro, A. 1949. Contribuição ao conhecimento dos crustáceos argulídeos do Brasil (Branchiura: Argulidae), com descrição de uma nova espécie. Boletim do Museu Nacional 93: 1–8.

Lemos de Castro, A. 1950. Contribuição ao conhecimento dos crustáceos argulídeos do Brasil. II. Descrição de duas espécies novas. Anais da Academia Brasileira de Ciências 22: 245–252.

Lemos de Castro, A and J. Loyola E Silva. 1985. Branchiura. Pages 1-23 *in* R. Schaden, ed. Manual de Identificação de Invertebrados Límnicos do Brasil. National Council for Scientific and Technological Development (CNPq) from the Brazilian Ministry of Science and Technology, Brasília, Federal District, Brazil.

Luque, J. L., F. M. Vieira, R. M. Takemoto, G. C. Pavanelli, and J. C. Eiras. 2013. Checklist of Crustacea parasitizing fishes from Brazil. Check List 9: 1449–1470.

Macedo, H. A., J. C. Stevaux, A. Silva, E. R. Merino, F. N. Pupim, and I. Bergier. 2015. Methodology for analysis of distribution and classification of the intensity of dequada fish kill events in the Pantanal wetland. Geografia 40: 163-176.

Malta, J. C. O. 1982a. Os argulideos (Crustacea, Branchiura) da Amazonia Brasileira. Aspectos da ecologia de *Dolops discoidalis* Bouvier, 1899, e *Dolops bidentata* Bouvier, 1899. Acta Amazonica 12: 521–528.

Malta, J. C. O. 1982b. Os argulideos (Crustacea, Branchiura) da Amazonia Brasileira. Aspectos da ecologia de *Dolops geayi* Bouvier, 1897, e *Argulus juparanaensis* Castro, 1950. Acta Amazonica 12: 701–705.

Malta, J. C. O. 1983. Os argulideos (Crustacea, Branchiura) da Amazonia Brasileira. 4. Aspectos da ecologia de *Argulus multicolor* Stekhoven, 1937, e *Argulus pestifer* Ringuelet, 1948. Acta Amazonica 13: 489–495.

Malta, J. C. O. 1998. Maxillopoda. Branchiura. Pages 67-74 *in* P.S. Young, ed. Catalogue of Crustacea of Brazil. Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brazil.

Malta, J. C. O., and A. Varella. 1983. Os argulideos (Crustacea, Branchiura) da Amazonia Brasileira. 3. Aspectos da ecologia de *Dolops striata* Bouvier, 1899, e *Dolops carvalhoi* Castro, 1949. Acta Amazonica 13: 299–306.

Malta, J. C. O., and A. Varella. 2000. *Argulus chicomendesi* sp. n. (Crustacea: Argulidae) parasita de peixes da Amazônia brasileira. Acta Amazonica 30: 481–489.

Mariguela, T. C., F. F. Roxo, F. Foresti, and C. Oliveira. 2015. Phylogeny and biogeography of Triportheidae (Teleostei: Characiformes) based on molecular data. Molecular Phylogenetics and Evolution 96: 130–139.

Morales-Serna, F. N., M. Rubio-Godoy, and S. Gomez. 2011. Seasonality of parasitic copepods on bullseye puffer, *Sphoeroides annulatus* (Pisces: Tetraodontidae),from the northwestern coast of mexico. Journal of Parasitology 97: 565–573.

Naing, L., T. Winn, and B.N. Rusli. 2006. Practical issues in calculating the sample size for prevalence studies. Archives of Orofacial Sciences 1: 9-14.

Nelson, J. S. 2006. Fishes of the World, 4th ed. John Wiley and Sons, Inc., Hoboken, New Jersey, U.S.A. 622 pp.

Neves, L. R., F. B. Pereira, M. Tavares-Dias, and J. L. Luque. 2013. Seasonal influence on the parasite fauna of a wild population of *Astronotus ocellatus* (Perciformes: Cichlidae) from the Brazilian Amazon. Journal of Parasitology 99: 718–721.

Peralta, A. S. L., J. L. Carvalho Jr., E. Matos, and N. M. S. Freire. 1998. Ocorrência de *Argulus juparanaensis* Lemos de Castro, 1950 (Branchiura: Argulidae) em arraia de fogo *Potamotrygon motoro* (Miller and Henle, 1841) (Rajiforme: Potamotrygonidae) no igarapé do salito, município de Cachoeira do Arari, Marajó, Estado do Pará. Entomologia e Vectores 5: 49–54.

Poly, W. J. 2008. Global diversity of fish lice (Crustacea; Branchiura; Argulidae) in freshwater. Hydrobiologia 595: 209–212.

Poulin, R. 1999. Body size vs abundance among parasite species: positive relationships? Ecography 22: 246–250.

Rosales, J. 2003. Hydrology in the Guiana Shield and possibilities for payment schemes. Report: Guiana Shield Initiative (GSI) of the Netherlands Committee for IUCN, Amsterdam, North Holland, The Netherlands.

Salgado-Maldonado, G., A. N. Garcia Aldrete, and V. M. Vidal-Martinez. 2000. Metazoan parasites in the neotropics: a systematic and ecological perspective. Instituto de Biologia, Universidad Nacional Autonoma de Mexico, Mexico City, State of Mexico, Mexico. 310 pp.

Sazima, I. and F. A. Manchado. 1990. Underwater observations of piranhas in western Brazil. Environmental Biology of Fishes 28: 17-31.

Schmidt, R. E. 1987. Redescription of *Vandellia beccarii* (Siluriformes: Trichomycteridae) from Guyana. Copeia 1987: 234–237.

Schram, T. A., J. A. Knutsen, P. A. Heuch, and T. A. Mo. 1998. Seasonal occurrence of *Lepeophtheirus salmonis* and *Caligus elongates* (Copepoda: Caligidae) on sea trout (*Salmo trutta*), off southern Norway. Journal of Marine Science 55: 163–175.

Silva, N. M. M. 1980. *Argulus spinulosus* sp. n. (Branchiura: Argulidae), em peixes de água doce do Rio Grande do Sul, Brasil. Iheringia Série Zoologia 56: 15–23.

Silva-Souza, A. T., V. D. Abdallah, R. K. Azevedo, and J. L. Luque. 2011. Expanded description of *Dolops bidentata* (Bouvier, 1899) (Branchiura: Argulidae) based on specimens collected on *Pygocentrus nattereri* Kner, 1858 (Characiformes) from Poconé Wetland, MT, Brazil. Brazilian Journal of Biology 71: 145–149.

Sket, B., and P. Trontelj. 2008. Global diversity of leeches (Hirudinea) in freshwater. Hydrobiologia 595: 129–137.

Smit, N. J., N. L. Bruce, and K. Hadfield. 2014. Global diversity of parasitic isopod crustaceans of the family Cymothoidae. International Journal for Parasitology: Parasites and Wildlife 3: 188-197.

Takemoto, R. M., G. C. Pavanelli, M. A. P. Lizama, A. C. F. Lacerda, F. H. Yamada, L. H. A. Moreira, T. L. Ceschini, and S. Bellay. 2009. Diversity of parasites of fish from the Upper Paraná River floodplain, Brazil. Brazilian Journal of Biology 69: 691–705.

Thatcher, V. E. 1993b. *Vanamea* gen. nov. for *Lironeca symmetrica* Van Name, 1925, (Crustacea, Isopoda, Cymothoidae) and a redescription of the species based on specimens from Brazilian piranhas. Acta Amazonica 23: 287–296.

Thatcher, V. E. 2006. Amazon Fish Parasites, 2nd ed. Pensoft Publishers, Sofia, Bulgaria. 508 pp.

Trilles, J. P. 1973. Notes documentaries sur les Isopodes Cymothoadiens parasites de poisons d’eau douce del’ Amerique du Sud. Bulletin du Muséum National D’Histoire Naturelle, Zoologie 88: 239–272.

Van der Sleen, P, and Albert, J. S. 2018. Field Guide to the Fishes of the Amazon, Orinoco, and Guianas. Princeton University Press, Princeton, New Jersey, U.S.A. 763 pp.

Van Name, W. G. 1925. The isopods of Kartabo, Bartica District, British Guiana. Zoologica 6: 461–503.

Vari, R. P., C. J. Ferraris Jr., A. Radosavljevic, and V. A. Funk. 2009. Checklist of the freshwater fishes of the Guiana Shield. Bulletin of the Biological Society of Washington 17: 1–94 .

Watkins, G., W. Saul, E. Holm, C. Watson, D. Arjoon, and J. Bicknell. 2004. The fish fauna of the Iwokrama Forest. Proceedings of the Academy of Natural Sciences of Philadelphia 154: 39–53.

Wilson, G. D. F. 2008. Global diversity of isopod crustaceans (Crustacea: Isopoda) in freshwater. Hydrobiologia 595: 231–240.

Wisniewski, W. L. 1958. Characterization of the parasitofauna of a eutrophic lake. Acta Parasitologica Polonica 6: 1–64.

Yamaguti, S. 1963. Parasitic Copepoda and Branchiura of Fishes. Interscience Publishers, New York City, New York, U.S.A. 1104 pp.

Zelmer, D. A., and H. P. Arai. 1998. The contributions of host age and size to the aggregated distribution of parasites in yellow perch, *Perca flavescens*, from Garner Lake, Alberta, Canada. Journal of Parasitology 84: 24–28.

BIOGRAPHY

Carl Bryce Hubbell was born on January 20, 1989 in Fort Worth, Texas. He is the fourth child and first son of two physicians, Dr. Carl Hubbell and Dr. Sheila Horsley. Bryce grew up in a large family with 3 brothers and 4 sisters in addition to numerous pets. He originally gained an interest in nature from following his older sisters around on outdoor adventures to various neighborhood creeks and forests where they would catch snakes and turtles.

This interest grew into a full blown fascination with natural history in general. Bryce has travelled extensively throughout Canada and the United States, including Alaska. He has a particular fondness for the Neotropics and has been to several countries in both Central and South America as well as the Caribbean. Bryce caught his interest in ichthyology from his love of fishing. He did his undergraduate studies at Angelo State University and obtained a bachelors of science in 2012, majoring in Evolutionary Ecology. His interest in inverts (invertebrates) and parasites truly took off while at ASU when introduced to professors such as Dr. Strenth and Dr. Negovetich. This current project came about by combining his interests in fish as well as inverts. He didn't quite get his fill of academic pursuits, and thus here he is once again working hard at Angelo State, pursuing a Masters in Biology.