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ABSTRACT

A survey of macroinvertebrates inhabiting the freshwater environments of Tobago was made during April, May, and June of 1996. This collection yielded 61 species, bringing the total number of freshwater macroinvertebrate taxa known from Tobago to 112. Dominant taxa included a few species of gastropods, decapod crustaceans, ephemeropterans, odonates, hemipterans, and coleopterans. Species richness was usually greatest in streams having cobble substrates and flowing through undisturbed forested land. Generally this macroinvertebrate fauna is sparse when compared to that of continents, most likely due to the relatively small size of Tobago and to a much lesser extent, human disturbance of freshwater environments in some areas of the island. Further studies are likely to find additional species that were previously unknown to occur on Tobago, some of which may be endemic to the island.

INTRODUCTION

Tobago is a small island lying on the northeastern edge of the South American continental shelf in the southeastern Caribbean basin. This oval-shaped island is approximately 43 km long and 14 km wide. It has a central spine of mountains rising 567 m above sea level and comprises approximately 302 km². Tobago is separated by about 33 kilometers of sea from its sister island of Trinidad. Although rocks present on Tobago are assumed to be of Cretaceous age (Maxwell 1948) and Comeau (1991) speculates Tobago was continuous with Trinidad as recently as 14,000 y.b.p., it is unknown exactly when Tobago separated from Trinidad or the South American continent (Hardy 1975). The central mountain range shows no signs of having ever been submerged (Flint 1996).

Several types of aquatic environments are present in Tobago. Steeply flowing streams and rivers drain toward the southeast or northwest from the central mountainous spine. Many of the smaller streams exhibit periods of intermittent flow. Near the coast, some rivers flow slowly across a narrow lowland, forming a marsh prior to entering the sea. Two larger marshes are present on the low, flat southwestern portion of Tobago.

Very little is known about the freshwater invertebrates of the Lesser Antilles and other nearby small islands. Some investigations were made on nearby islands including Trinidad (Hynes 1971; Alkins *et al.* 1981; Alkins-Koo 1990) and St. Vincent (Harrison and Rankin 1975, 1976a, 1976b; McKillop and Harrison 1980), but similar published efforts are generally lacking for Tobago. While some invertebrate groups have been studied, such as decapod crustaceans (Chace and Hobbs 1969; Hart 1980), odonates (Donnelly 1970), and trichopterans (Flint 1968, 1996), many others have yet to be surveyed. In cases where previous investigations exist, they are often limited in scope to a few sites or taxa (Hynes 1948; Hinton 1971; Nieser and Alkins-Koo 1991; Botosaneanu and Alkins-Koo 1993; Stark 1994). Furthermore, additional collections can yield previously unknown populations or species (Flint 1996; Bass and Volkmer-Ribeiro 1998).

The objectives of this investigation include: 1) determine the species of aquatic macroinvertebrates inhabiting freshwaters of Tobago; 2) note microhabitat preferences of each species; 3) determine the relative abundance of each species; and 4) compare the Tobago macroinvertebrate fauna to that on other small Caribbean Islands.

METHODS

Seventeen sampling sites were established in various freshwater habitats across Tobago (Fig.1). Macroinvertebrate collections were made during April, May, and June 1996. Water temperature was also recorded from each site at the time of collection.

Several methods of collecting were used to ensure as many species as possible were captured. Submerged debris, such as stones, leaves, and wood, were carefully examined by eye and inhabitants were picked from the substrate using forceps. A dip net was swept through aquatic vegetation and the water column to capture macroinvertebrates occupying those microhabitats. The microhabitat of each specimen was noted. A drift net was used at two sites to collect additional samples during the night. Specimens were preserved in 70% ethanol and returned to the laboratory for further identification. The list of taxa known from Tobago was compared to those of other small Caribbean Islands by applying Sorenson's index of similarity (1948).



Fig. 1. Map indicating location of collecting sites in Tobago. Specific locations and dates of collections are listed below Table 1.

RESULTS & DISCUSSION

Water temperatures, measured during the collection period, ranged from 23°C in tributaries of the Argyle and Bloody Bay Rivers to 32°C in Courland and Bloody Bay Rivers. Generally cooler temperatures were measured in small streams at higher elevations of the mountain forests while warmer temperatures occurred in lowland rivers. This 9°C difference in temperature was much greater than the 2.2°C reported in the Arima River system in Trinidad through a similar elevation gradient (Hynes 1971).

to 112 taxa (Table 1). The major findings are summarized below. **Gastropoda**

Prior to this collection, 71 species of freshwater macroinvertebrates had been reported from Tobago, and most of these were caddisflies (Botosaneanu and Alkins-Koo 1993; Flint 1996) and shrimps (Hart 1980). Sixty-one taxa were collected during this study. Of these, only 20 had been previously reported, bringing the total number of freshwater macroinvertebrates known from Tobago Ten species of aquatic snails were collected on Tobago. The introduced *Melanoides tuberculata* was abundant in several habitats across the island. Three species of nerites were present, grazing on algae growing on submerged rocks. The left-handed pond snail, *Physella*, was uncommon on Tobago, but is usually abundant on other nearby islands of the Lesser Antilles.

Table 1. List of freshwater macroinvertebrates, including collecting sites, life cycle stages present, relative occurrance, microhabitats,and proposed trophic relationships in Tobago during April, May, and June 1996. Life cycle: A, adult; J, juvenile; L, larva; N, nymph.Occurrence: +++ abundant, ++ common, + uncommon.

Таха	Collections	Life Cycle	Occurrence	Microhabitat	Trophic Relationship*
Gastropoda Hebetancylus excentricus Marisa cornuarietis Melanoides tuberculata Neritina clenchi Neritina virginea Neritina usnea Physella cubensis cubensis Pomacea sp.** Pyrgophorus parvulus Tropicorbis pallidus	4 5, 6, 7 4 - 9, 12, 15, 16, 18 1, 3, 9, 13, 15, 17 9 9, 17 6 ** 4 - 6, 13, 15 13	A A A A A A A A A A A A A A A A A A A	+ +++ ++ + + + + + + + +	Detritus Detritus Detritus Rock Rock Rock Detritus Detritus Detritus	Algivore Algivore Algivore Algivore Detritivore
Bivalvia Eupera cubensis	6	А	+	Sediment	Bacterial feeder
Amphipoda Grandidierella sp.	1	А	+	Detritus	Detritivore
Decapoda Atya innocous Atya scabra Atya sp. Eudaniela garmani***	8, 14, 15, 20 20 2, 8 - 11, 14, 16, 18 11, 18	J, A J, A J, A	+ ++ +	Detritus Detritus Stream bottom	Omnivore, Collector Omnivore, Collector Omnivore, Collector
Jonga serrei Macrobrachium acanthurus Macrobrachium carcinus Macrobrachium crenulatum Macrobrachium sp. Palaemon pandaliformis Potimirim sp. Sesarma rectum Xiphocaris elongata	13, 15, 17, 20 13, 20 20 7, 20 2, 4, 5, 7 - 10, 12, 14 - 16, 18, 20 1, 3 20 2, 4, 8 - 12, 14, 16, 18 20 15, 20	J, A J, A J, A J, A J, A A	+ + ++++ + +	Detritus Detritus Detritus Detritus Detritus Detritus	Omnivore, Predator Omnivore, Predator Omnivore, Predator Omnivore, Predator
Ephemeroptera Americabaetis sp. Baetodes sp. Caenis sp. Farrodes sp. 1 Leptohyphes zalope Leptohyphes sp. 1 Tricorythodes sp. Odonata Argia sp. Dythemis sp. Erythemis vesicula? Ischnura ramburii	12, 14 - 16, 18 18 14 7 - 10, 14 - 16, 18 14 9, 16, 18 9 2, 8, 9, 11, 12, 14 - 16, 18 7 1, 13 1, 3 - 6, 13		++ + + + + + + + + + + + + +	Detritus Detritus Detritus Detritus Detritus Detritus Detritus Detritus Detritus Detritus Detritus Detritus Detritus	Collector Collector Collector Collector Predator Predator Predator Predator
Micratnyria sp. Plecoptera Anacroneuri isleta	20	A	+	Detritus	Predator
Hemiptera Belostoma subspinosum Brachymetra albinervis Brachymetra unca Buenoa antigone Gelastocoris flavus Limnogonus franciscanus Mesovelia amoena Mesovelia mulsanti Microvelia hinei	6 2 - 4, 7, 8, 10 - 12, 15, 18, 20 10, 20 4, 20 20 2, 4, 20 20 1, 2, 4, 6, 20 20	A N, A A A A A A A A	+ ++++ + + ++	Detritus Neuston Detritus Neuston Neuston	Predator Predator Predator Predator Predator Predator Predator Predator Predator

				-		-	
Таха	Collections	Life Cycle	Occurrence	Microhabitat	Trophic Relationship*	Collections: 1. Bacolet River, Baco Tobago 24 April 1	olet, 996
Microvelia longipes Microvelia mimula Microvelia pseudomarginata Microvelia pulchella Microvelia sp. near tumida Microvelia sp. Ochterus perbosci Paravelia brachialis Rhagovelia insularis Rhagovelia tenuipes Trenobates tavlori	20 20 20 20 20 2, 9 20 20 10 - 12, 14, 15, 16, 18, 20 20	A A A A A A A A A A A A A A A A A A A	+	Neuston	Predator Predator Predator Predator Predator Predator Predator Predator Predator Predator Predator	 Bon Accord Spring Bon Accord Tobage April 1996 Courland River, Courland, Tobago, 26 April 96 Hillsborough West River, Mesopotami Tobago, 26 April 1 	; ; 2, 26 <u>a</u> , 996
Trochopus plumbea Trichoptera Amphoropsyche sp. Austrotinodes adamsae Cerasmatrichia argylensis Cernotina mandeba	20 20 20 20 20 20 20	A A A A A A			Predator	 Hillsborough East River, Hillsborougi Tobago, 26 April 1 Buccoo Marsh, Buccoo, Tobago, 2 April 1996 Arnos Vale Creek. 	h, 996 7
Chimarra bidens Chimarra caribea tobaga Chimarra flinti Chimarra sp. Chimarrhodella tobagoensis	20 20 20 15, 16, 18, 19 20	A A A L A	+	Detritus	Collector	Arnos Vale, Tobago April 1996 8. Little Englishmen's Creek, East of Cas), 27 s Bay tara,
Helicopsyche margaritensis Hydroptila grenadensis Hydroptila tobaga	9, 15, 20 20 20	L, A A A	+	Rock	Scraper	Tobago, 27 April 1 9. Bloody Bay River, Bloody Bay Tobag	996 m 27
Leptonema albovirens Leucotrichia botosaneanui Leucotrichia tritoven Neotrichia armata Neotrichia tauricornis Neotrichia unamas Ochrotrichia geminata	14 - 17, 20 20 20 20 20 20 20 20	L, A A A A A A A	++	Detritus	Collector	April 1996 10. Argyle River Tribu, 4 ¹ /4 mile marker, Main Ridge Forest Reserve, Tobago, 2 Argil 1006	tary, 28
Ochrotrichia oblonaata Ochrotrichia platygona Oxyethira azteca Polycentropus altmani Polyplectropus pugiunculatus Protoptila ignera	20 20 20 11, 20 20	A A A L, A A	+	Detritus		11. Bloody Bay River Tributary, Gilpin T Main Ridge Forest Reserve, Tobago, 2 April 1996	race, 28
Khyacopsyche duplicispina Smicridea anomala Smicridea bivittata Smicridea tobada Wormaldia plana Xiphocentridae sp.	20 20 20 20 20 20 20	A A A A A A				12. Argyle River Tribu Bridge 1961, Main Ridge Forest Reser Tobago, 28 April 1 13. Roxborough River.	tary, ve, 996
Xipnocentron piscicaudum Xiphocentron stenotum Zumatrichia anomaloptera	20 20 20	A A L, A				Roxborough, Tobay 29 April 1996 14. Drift Sample-Argy	зо, le
Petrophila sp.	9	L	+	Rock	Scraper	River Tributary, 4 mile marker, Main I Forest Reserve, Tol	!/4 Ridge bago.
Cyphon sp. Elsianus clypeatus Enochrus psuedochraceus Heterelmis simplex codrus Hexaculloepus smithi	15 20 6 20 20	A	+ +	Detritus Detritus	Predator, Herbivore	28 April 1996 15. Tyrrel's Bay Creek Speyside, Tobago, . May 1996	; 31
Hydrocanthus sp. Limnichorus moratus Microcylloepus carinatus Neoelmis pusio	6 16 20 20	A	+ +	Hydrophyte Detritus	Predator	16. Delaford Creek, La d'Or Nurseries, Delaford, Tobago, May 1996	nuis 31
Phanocerus congener Phanocerus congener Psephenops smithi Tropisternus setiger	20 16, 18 5, 6	A A A	+ + +	Rock Detritus	Scraper Collector	17. King's Bay River, K Bay, Tobago, 31 M 1996 18. Argyle River, Argyl	'ing's 'ay le
Diptera Ablabesmyia sp. Anopheles sp. Chironomidae sp. Chironomus sp. Euparyphus sp. Fittkauimyia sp. Pseudochironomus sp.	13 3, 4 13 4, 6, 13 15 5 9		+ + + + + +	Sediment Detritus Sediment Sediment Detritus Sediment Sediment	Predator Collector Collector Collector Collector Collector	Falls, Tobago, 1 Ju 1996 19. Drift Sample-Tyrre Bay Creek, Speysia Tobago, 1-2 June 1 20. Reported by other researchers.	ne l's le, 1996

* Determined for non-insects from Thorp & Covich (2001) and for insects from Merritt & Cummins (1996).

** A single dead specimen (shell) was found in Kilgwyn Marsh on 27 April, 1997.

*** Several individuals were observed but not collected.

Bivalvia

Only a single species of freshwater clam was collected. The fingernail clam, Eupera cubensis, was found in the sediments of Buccoo Marsh where it filters and feeds on bacteria suspended in the water. This clam has a widespread distribution throughout the Holarctic, including islands of the Lesser Antilles, such as Nevis (Bass 2000).

Amphipoda

Grandidierella was collected from submerged detritus along the edge of the Bacolet River. Amphipods are usually detritivores and scavengers.

Decapoda

Decapods are one of the best known groups of freshwater invertebrates in Tobago (Chace and Hobbs 1969; Hart 1980). A total of 11 freshwater decapods have been reported from the island. These include 10 species of shrimp and one species of crab. Here, the shrimp, Potimirim, is reported for the first time from Tobago. The Atya sp. and Macrobrachium sp. listed in Table 1 probably belong to species that were previously reported. Whereas both Atya and Macrobrachium are omnivorous as juveniles, Atya develops into a collector and Macrobrachium becomes more predacious as it matures (A. Covich, pers. com.). All shrimps were usually found in streams among submerged detritus and plant roots.

Ephemeroptera

At least seven species of mayflies are known from Tobago. This number may be higher since some genera listed may contain more than one species. Accurate species determinations of mayflies often require the adult stage and the collections contained only the aquatic nymphs. Farrodes grenadensis was previously reported from nearby Grenada by Edmunds et al. (1976). However, based on differences in color and maculation of the abdomen, another species, Farrodes sp. 1, was determined to be present in this collection (M. Pescador, pers. com.). Leptohyphes zapode was recently found in Tobago (Baumgardner, D.E., Burian, S.K. and Bass, D., unpublished observations). It is possible some of the specimen designated Leptohyphes sp. 1 collected in this investigation may actually be Leptohyphes zapode, but the definitive characteristics had not yet developed in the specimen.

Odonata

Five species of odonates have been collected in Tobago. Of these, three are dragonflies and two are damselflies. The most common taxa observed include Argia sp. and Ischnura ramburii. All are predators and nymphs live among submerged leaf debris. Since the adults are strong fliers, odonates have a fairly widespread distribution in the West Indies, with only a few species being endemic to a single island (Flint 1978). No endemic species of this group are known to exist on Tobago.

Plecoptera

Stark (1994) described a new species of stonefly, Anacroneuria isleta, from forested areas of eastern Tobago. This is the only known species of stonefly on the island and it appears to be endemic to Tobago. The immature stage, presumably aquatic, is unknown and I did not encounter this species in my collections.

Hemiptera

Hemipterans were a common group encountered during this investigation, being collected from most sites. Of the 20 species listed in Table 1, 19 were already known to occur on Tobago (Nieser and Alkins-Koo 1991). Most water bugs collected in the present study were various species of water striders, with Brachymetra albinervis, Mesovelia mulsanti, and Rhagovelia isularis being the most common taxa found. All are predators of smaller insects. The phenomena of wing polymorphism and flightlessness were observed in several populations. The loss of wings is a widespread phenomenon that has been well documented in water striders (Schuh and Shlater 1995; Thorp and Covich 2001) and among island populations (Darwin 1859). This loss of wings is beneficial since the energy cost to maintain them may be high (Roff 1986) and they may be of little value on a small island (Darwin 1859), especially if the aquatic habitats are persistent so flight is not necessary (Roff 1990). Although wings may be a useful mechanism as a means for dispersal, they may also be considered deleterious if an insect flies away from an island because its chance for survival is greatly reduced once it journeys over the sea (Darwin 1859). However, it is unlikely flying insects would leave an island in large numbers (Roff 1990).

Trichoptera

Four species of immature trichopterans were collected from freshwater environments in Tobago during this study. However, only one of these, Leptonema albovirens, was common. Most caddisfly larvae were found among submerged leaf debris and rocks. In previous studies, Botosaneanu and Alkins-Koo (1993) reported at least 19 species of caddisflies were collected from six sites in Tobago. Flint (1996) listed 33 species of caddisflies from Tobago, of which seven are endemic to Tobago while another six are limited to only Tobago and Trinidad. As additional collections are made on nearby islands and the South American mainland, it is suspected some of the species currently thought to be endemic may be discovered to have greater ranges than are currently known. Lepidoptera

Petrophila was the only aquatic lepidopteran found on Tobago. Larvae were collected from their small, self-spun silken retreats covering the indentations of rocks in shallow stream environments. These larvae scrape algae and other organic material from the surface of submerged rocks, probably during hours of darkness. Coleoptera

Hinton (1971) reported six species of elmids (riffle beetles) existing in Tobago. Although 13 species of freshwater beetles are known from Tobago today, none appear to be common or occur in large numbers. It is interesting to note that no more than one species was collected from any site.

Diptera

Seven species of dipteran larvae were encountered during this investigation, including five midges. Because midge larvae are often very small and primarily inhabit the sediments, a more extensive sampling effort of the sediments would probably yield additional species.

Species richness varied between the sites sampled. Sites having greatest diversities generally were those of streams having cobble substrates and flowing through forested land where human impact appeared minimal. Species richness was greatest at a site in the Argyle River near Argyle Falls and lowest in an isolated pool of a non-flowing section of King's Bay River.

Hynes (1971) concluded the zonation of stream macroinvertebrates in the Arima River system of Trinidad was based largely on elevational differences. For this study of Tobago macroinvertebrates, it is difficult to conclude which, if any, of the

parameters of elevation, water temperature, suitable microhabitat, or some other environmental factor was more important in determining whether a species could exist at a site. Most species of molluscs, odonates, coleopterans, and dipterans seemed restricted to lower elevations. Only the crab, *Eudaniela garmani*, and the trichopteran, *Polyplectropus pugiunculatus*, were found exclusively at higher elevations. Many taxa, including shrimps, ephemeropterans, hemipterans, and trichopterans were collected at several elevations.

Table 2: Sorensen's index of similarity values comparing the freshwater macroinvertebrate fauna of Tobago to that of other small Caribbean Islands, including distances to those islands from Tobago. 0.00 = 0% common taxa and 1.00 = 100% common taxa.

Island	Distance (km)	Similarity Value	
Grenada	125	0.22	
Barbados	215	0.12	
St. Lucia	260	0.17	
Dominica	450	0.13	
Montserrat	620	0.08	
Antigua	645	0.08	
Nevis	685	0.10	
St. Kitts	700	0.12	
Saba	760	0.02	
Cayman Brac	2240	0.00	
Little Cayman	2280	0.03	
Grand Cayman	2360	0.00	
Guanaja	2775	0.05	

Of the 13 islands listed in Table 2 for which similar collections were made by the author, Tobago shares the greatest faunal similarity with Grenada. This is a reasonable result as Grenada is near Tobago and possesses a similar terrain. Tobago showed no species in common with Cayman Brac and Grand Cayman. Both of these are small, low-lying distant islands that possessed fewer and very different freshwater habitats. It appears that distance between these small islands is the most critical factor determining faunal similarity, but other factors such as island area, island elevation, and habitat similarity should also be considered.

The macroinvertebrates inhabiting freshwater environments of Tobago today may have been present before Tobago became separated from the mainland or colonized the island after it drifted away from the continent. Species that colonized the island may have done so by either actively flying (e.g. winged insect adults) or being passively carried by wind or water currents (e.g. larvae of nerites and shrimps). Those species that were carried by water currents must also be tolerant of seawater during the period of dispersal. Due to its close proximity to South America and its recent connection to that continent, it seems likely that much of the fauna of Tobago would be dominated by species tracing their ancestral populations to the freshwaters on the South American mainland as suggested by the distributions of shrimps (Hart 1980) and trichopterans (Flint 1996). Further studies of macroinvertebrates in freshwaters of Tobago are likely to find additional species that were previously unknown to occur here, some of which may be endemic.

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