# A Comparison of Freshwater Macroinvertebrate Communities on Small Caribbean Islands

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*An ongoing survey of macroinvertebrates inhabiting the relatively unstudied freshwater habitats on 14 small Caribbean islands was initiated in 1991. These collections have yielded almost 200 species; when these species are combined with collections previously made by other researchers, a total of at least 328 freshwater macroinvertebrates are now known from these islands. The dominant taxa on the islands include several species of snails, shrimps, mayflies, dragonflies, damselflies, beetles, and other insects. Many of these species have fairly widespread distributions across the islands. Most stream species are associated with leaf packs, and most pond species are associated with aquatic macrophytes. As is typical of tropical island systems, the macroinvertebrate faunas of these islands are sparse, most likely because of their oceanic origin, their small size, and the frequent disturbances to their freshwater environments.*

*Keywords: biodiversity, freshwater, macroinvertebrates, streams, Caribbean islands*

**Much still remains unknown about the freshwater** invertebrates of the Lesser Antilles and other small Caribbean islands. While some groups have been studied, such as shrimps and crabs (Chace and Hobbs 1969), dragonflies and damselflies (Donnelly 1970), and caddisflies (Flint 1968, 1996, Flint and Sykora 1993), many others have yet to be surveyed. Where data from previous investigations exist, they are often limited in scope (Hynes 1971, Harrison and Rankin 1976, Stark 1994) or may be outdated (Hinton 1971, Peters 1971, Peck 1981, Bennett and Alam 1985). Furthermore, additional collections may extend ranges of known species or uncover new species (Bass and Volkmer-Ribeiro 1998, Bass 2000, 2003).

Often differences between the kinds of macroinvertebrates present in temperate portions of North America and South America and those of the tropical Caribbean islands are seen at the species level. Most of the insect orders found in temperate freshwater environments are also present in the tropics. However, stoneflies are greatly underrepresented on small Neotropical islands, with only the genus *Anacroneuria* being reported from Trinidad and Tobago (Hynes 1971, Stark 1994). Decapod crustaceans, such as prawns, crayfish, and crabs, are much more diverse and widespread in tropical streams than in temperate flowing waters (Chace and Hobbs 1969, Covich 1988). Some of those crustaceans may fill the roles of amphipods and isopods, which are almost absent in tropical streams (Fryer 1977).

Tropical stream communities appear to be composed of the same trophic guilds as temperate ones, but they have relatively lower densities of shredders in the headwaters. Therefore, it has been suggested that the breakdown of leaf litter, which is facilitated by shredders in temperate streams, must be brought about largely by microbes in tropical streams (Ramirez and Pringle 1998, Dudgeon and Wu 1999, Bass 2003, Turner 2003). Irons and colleagues (1994) determined that the constant high temperatures of the tropics encouraged leaf litter decay through increased and continuous microbial activity in the streams.

## Biodiversity survey

An ongoing survey of macroinvertebrates inhabiting freshwater habitats on small Caribbean islands was initiated in 1991. The islands studied in this investigation include Barbados, Tobago, Grenada, St. Lucia, Dominica, Montserrat, Nevis, St. Kitts, Saba, Antigua, Cayman Brac, Little Cayman, Grand Cayman, and Guanaja. Objectives of this research included (a) determining the species of macroinvertebrates inhabiting freshwater habitats of small Caribbean islands, (b) noting microhabitat preferences for species, (c) determining the relative abundance of each species, and (d) comparing the macroinvertebrate fauna known from each island to that of other small Caribbean islands. Governmental bodies and nongovernmental organizations on the selected islands were also interested in obtaining information from a biodiversity survey of freshwater macroinvertebrates.

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## The physical environment of the islands

Most of the small islands in the Caribbean basin were formed as a result of volcanic activity or sediment uplift (see Craig [2003] for more discussion on island formation). On volcanic islands, the gradient is fairly steep, resulting in many fast-flowing streams that have bottom substrates composed mostly of rocks. Leaf debris is abundant in pools and other places where flow is reduced. The islands are primarily forested, and rainfall is abundant, especially at higher elevations. Grenada, St. Lucia, Dominica, Montserrat, Nevis, St. Kitts, Saba, Guanaja, and Tobago are volcanic in origin. However, Tobago is a continental island that was once connected to the South American continent. There is little relief and less elevational gradient on islands formed by sediment uplift. Their forests are less developed and mostly absent, as rainfall is not as abundant. This has resulted in few permanent streams being present, and many ponds have been constructed to provide water supplies. The sediments of these ponds are generally soft, composed mostly of mud and silt. Islands formed by sediment uplift include Barbados, Antigua, Grand Cayman, Little Cayman, and Cayman Brac.

A total of 205 sites were sampled in various freshwater habitats across the Lesser Antilles and other small Caribbean islands (figure 1). All islands included in this investigation are less than 800 square kilometers ($km^2$) in surface area. The number of sites varied on each island, depending on island size—one site was selected for every 5 to 10 $km^2$ of island area. Each site has been visited at least once, and many sites were sampled more frequently as opportunities arose to return to those sites. Water temperature was recorded at each site.

Several methods of collecting were used to ensure that as many species as possible were captured. Submerged debris, such as stones, leaves, and wood, was carefully examined in the field, and inhabitants were removed from the substrate with forceps. In addition, a dip net was swept through aquatic vegetation and the water column to capture macroinvertebrates occupying those microhabitats. The microhabitat from which each specimen was taken was noted. A drift net was also used at several sites to collect samples of macroinvertebrates drifting downstream with the current. Specimens were preserved in 70% ethanol and returned to the laboratory for further taxonomic study.

In addition to the field collections, the published literature was also examined and previous records were included in this article. Finally, Sorenson's Index of Similarity (1948) was used to calculate faunal similarity between the islands investigated and determine whether the aquatic macroinvertebrate populations on each island were composed of the same species or different species.

## A near-doubling of the known species

Freshwater macroinvertebrates had never been collected on several of the islands studied. A total of at least 328 species are now known from these 14 islands. Of these, 191 species were

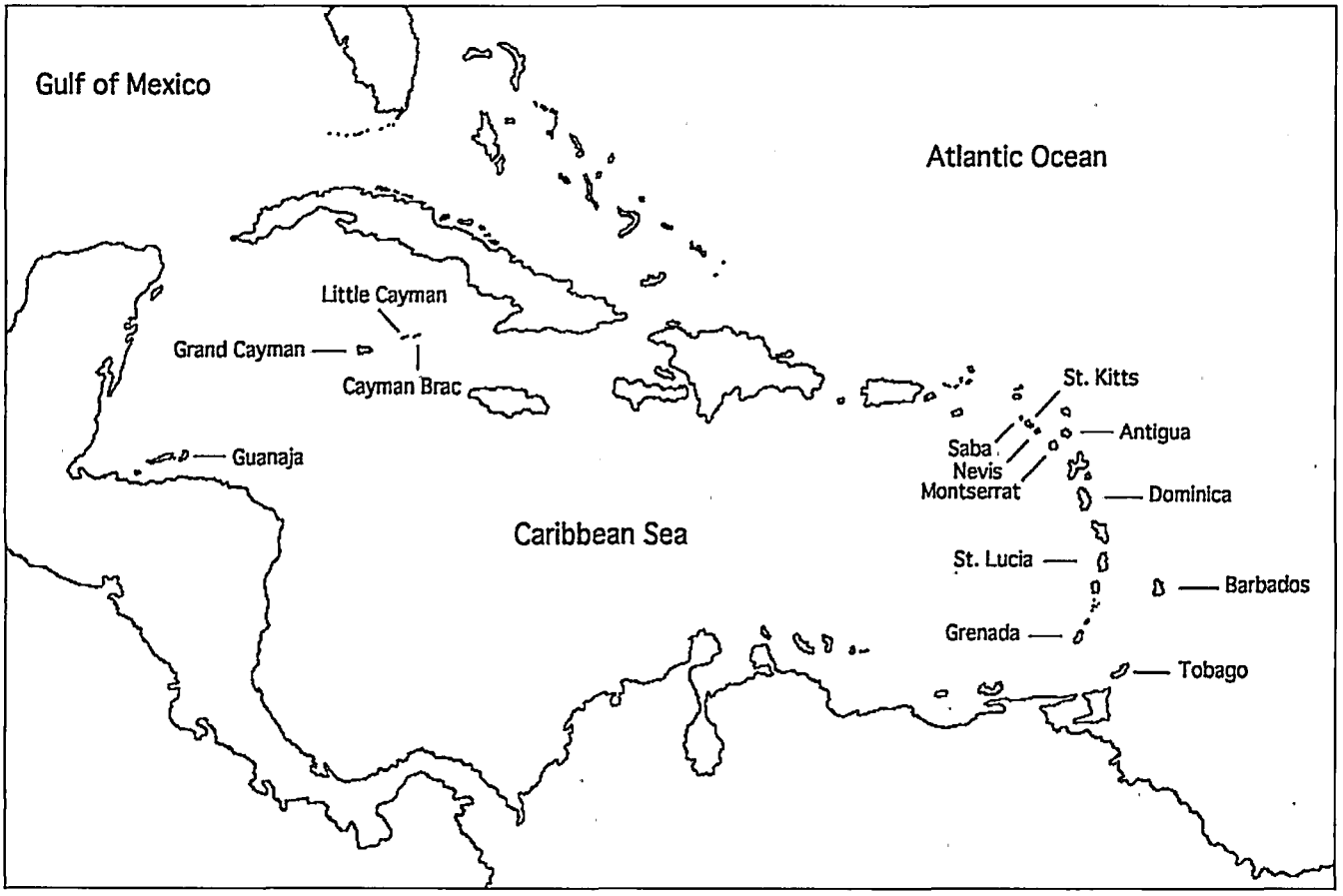


*Figure 1. Map of the Caribbean basin, indicating islands sampled in this investigation.*

collected during this investigation, while 186 species had been previously reported in the literature. As a result of this collecting effort, 147 species were reported for the first time from these Caribbean islands. It should be noted that it is possible several of these taxa may actually represent more than one species. This is due to the poor state of taxonomy in some groups and the presence of life cycle stages in which diagnostic features have yet to develop.

Of the major taxa investigated, the Trichoptera (caddisflies) included the most species (table 1). A total of 84 species of caddisflies have been identified from the Caribbean islands in this study. This relatively high number of species is a reflection of intensive collecting in the region by Oliver S. Flint Jr. (Flint 1968, 1996, Flint and Sykora 1993). It is quite possible there are additional species belonging to other invertebrate groups that will be discovered when collecting efforts equal to those of the trichopterists have been realized. Many species of dipterans (two-winged flies), coleopterans (beetles), odonates (dragonflies and damselflies), hemipterans (semiaquatic and aquatic bugs), and gastropods (snails) have already been noted on these small islands. Decapods (shrimps and crabs), ostracods (seed shrimps), and ephemeropterans (mayflies) are common as well.

*Table 1. Species richness within selected taxa.*

| Taxonomic group | Number of species |
|---|---|
| Porifera | 1 |
| Platyhelminthes | 1 |
| Oligochaeta | 5 |
| Hirudinea | 2 |
| Gastropoda | 27 |
| Pelecypoda | 1 |
| Cladocera | 1 |
| Ostracoda | 19 |
| Amphipoda | 3 |
| Decapoda | 19 |
| Hydrocarina | 1 |
| Ephemeroptera | 14 |
| Odonata | 39 |
| Plecoptera | 1 |
| Hemiptera | 33 |
| Megaloptera | 2 |
| Trichoptera | 84 |
| Lepidoptera | 2 |
| Coleoptera | 40 |
| Diptera | 19 |

## Species richness related to island size and elevation

"Species richness" refers to the number of species present in an area. It was interesting to examine the relationship between the species richness of freshwater macroinvertebrates present on an island and the area of that island (table 2). Darlington (1957) stated that as the island area of some West Indian islands increased by a factor of 10, the number of species in these islands' herptofauna doubled. In the current study involving freshwater macroinvertebrates, the trend of smaller islands containing fewer species and larger islands containing more species appears to apply in general terms. However, on closer examination, the patterns of macroinvertebrate species richness are not exactly like those observed by Darlington in herptofauna. It seems that island elevation may also be an important factor influencing the number of macroinvertebrate species present, because islands with higher elevations tend to experience greater rainfall, creating more freshwater environments. When these two factors are considered together, with island area multiplied by island maximum elevation, Darlington's hypothesis fits better, but the outcome is still not entirely as predicted.

There is probably no simple explanation describing why Darlington's hypothesis does not conform entirely to observations of freshwater macroinvertebrates on the islands studied. The discrepancy is probably attributable to several factors, including periodic disturbances, environmental differences among the islands, and collector bias. Disturbance on small Caribbean islands may be both natural and anthropogenic. Possibly the greatest natural disturbance to the fauna in streams on these islands is heavy rainfall from tropical storms. The historical record illustrates that tropical storms frequently track across these islands, and the intensity varies at different locations with different storms. The rising water levels and increased flow scour the substrate and destroy many individuals. I visited St. Kitts approximately 5 weeks after the passage of Hurricane Lenny in 1999, which produced more than 12 inches of rainfall in a 48-hour period. Sampling of streams, especially at lower elevations, yielded relatively few individuals compared with previous visits. Johnson and colleagues (1998) described how populations of atyid shrimp recover and become reestablished following such events in Puerto Rico. Furthermore, these storms may occur frequently enough to prevent the aquatic community composition from stabilizing and reaching equilibrium. Field observations of population sizes indicate that many freshwater habitats on these islands are undersaturated. In addition, there are considerable environmental differences between islands of volcanic origin and those formed by sediment uplift, as described earlier. While studying bat distributions, Koopman (1958) showed how differences in ecology among southern Caribbean islands can distort the area–diversity curve. Human populations are also increasing on these islands, and this has led to changes in macroinvertebrate populations at some of the collecting sites. As discussed earlier, some groups of macroinvertebrates and certain islands have received more attention by scientists; for that reason, the available data may be somewhat skewed.

## Dispersal ability and notable distributions

To become abundant on an island, a species must first successfully disperse to that island. Most of the invertebrates inhabiting freshwater environments on the Caribbean islands have some mechanism for dispersal that allows them to traverse ocean waters. Structures such as the wings of

*Table 2. Species richness in relation to island area and maximum elevation.*

| Island | Number of species | Area (square kilometers) | Maximum elevation (meters) | Area x elevation |
|---|---|---|---|---|
| Cayman Brac | 6 | 37 | 43 | 1591 |
| Saba | 9 | 13 | 887 | 11,531 |
| Grand Cayman | 13 | 197 | 18 | 3546 |
| Guanaja | 18 | 69 | 415 | 28,635 |
| Little Cayman | 19 | 26 | 13 | 338 |
| Montserrat | 25 | 83 | 915 | 75,945 |
| Antigua | 46 | 402 | 280 | 112,560 |
| St. Kitts | 59 | 176 | 1156 | 203,456 |
| St. Lucia | 63 | 616 | 950 | 585,200 |
| Nevis | 64 | 93 | 985 | 91,605 |
| Barbados | 83 | 430 | 340 | 146,200 |
| Grenada | 101 | 344 | 840 | 288,960 |
| Tobago | 103 | 300 | 549 | 164,700 |
| Dominica | 125 | 751 | 1447 | 1,086,697 |

adult insects could be used to fly from one island to another. Larval stages of some other invertebrates, such as freshwater nerite snails and some decapod crustaceans, tolerate marine water and may be able to drift between islands as zooplankton. All new arrivals must locate suitable areas for colonization within a given period of time. This and other studies from locations around the world indicate that certain groups of organisms are frequently present in streams of small tropical islands (Harrison and Rankin 1976, Kinzie and Ford 1977, Resh et al. 1990, Yule 1996, Bass 2000, 2003).

Several taxa are very common and have been collected from many sites across the islands investigated. *Melanoides tuberculata* is a common and widespread species of prosobranch snail that was introduced into Lesser Antillean streams, where it thrives today. Several species of another snail, *Physella,* are also abundant on these islands. Since this genus is a pulmonate—it has a lung—it is not limited by low dissolved oxygen levels in the water and therefore may occur in a variety of freshwater environments. As on many other tropical oceanic islands, shrimps, including several species of Atyidae and *Macrobrachium,* are common in streams. These shrimps replace temperate isopod and amphipod crustaceans, filling their functional roles in tropical streams (Fryer 1977). Often several species of shrimps can be found at a single site, because they usually occupy different niches—the atyids are primarily collectors, whereas *Macrobrachium* species are mostly predators. Large shrimps are important food resources for many people living in rural villages. Several groups of insects are also common in freshwater habitats of small Caribbean islands. These include the dragonfly *Orthemis ferruginea;* the damselfly *Ischnura ramburii;* several species of back swimmers, *Buenoa* spp.; the water treader, *Mesovelia* spp.; the broad-shouldered water strider, *Microvelia* spp.; and several species of water striders in the genera *Limnogonus* and *Trepobates.*

Several noteworthy observations have been made regarding the taxonomy and biogeography of certain species. Bass and Volkmer-Ribeiro (1998) reported a sponge, *Radiospongilla crateriformis,* from temporary ponds in Barbados and Nevis. Although this sponge had been previously reported from the eastern United States, southeastern Canada, China, Japan, southeastern Asia, and Australia, it was the first discovery of a freshwater sponge from a Caribbean island. Since that finding was published, another site on Nevis has produced this species, but despite considerable effort, no specimens have been collected on any other islands. Because sponges lack the ability to actively move about, they must disperse passively, which means it is quite unlikely they would be transported to a suitable habitat. Furthermore, these freshwater species do not tolerate the marine waters that must be crossed to reach these oceanic islands. Bass and Volkmer-Ribeiro (1998) speculated that *R. crateriformis* is transported while the sponge is in the drought-resistant gemmule stage, possibly carried in the feathers of migrating birds or on the wind.

A possible new species of nerite snail was collected on Montserrat, but there has been disagreement among taxonomic authorities regarding its exact status, and additional specimens are necessary. However, volcanic activity on the island completely destroyed the only stream valley from which this population was collected. If this is indeed an undescribed species whose only population existed in this valley, then this would be a documented case of a species extinction caused by a natural disturbance.

Several undescribed species of mayflies may exist in collections from Dominica, but adult specimens possessing fully developed genitalia are needed to confirm this suspicion. An undescribed species of midge larva (Tanypodinae) was collected from a small spring in Saba, but, for this species as for the mayflies, adult specimens with fully developed genitalia are required for confirmation. As additional collections of freshwater macroinvertebrates on small Caribbean islands continue, it is quite likely that more new species will be discovered.

Most islands have several species of hemipterans represented by both winged and nonwinged forms of adults. The loss of wings is a widespread phenomenon that has been well

*Table 3. Similarity values for the islands of Tobago (Tob), Grenada (Gre), Barbados (Bar), St. Lucia (StL), Dominica (Dom), Montserrat (Mon), Nevis (Nev), St. Kitts (StK), Saba (Sab), Antigua (Ant), Cayman Brac (CBr), Little Cayman (LCa), Grand Cayman (GCa), and Guanaja (Gua).*

| | Tob | Gre | Bar | StL | Dom | Mon | Nev | StK | Sab | Ant | CBr | LCa | GCa | Gua |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tob | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Gre | 0.22 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Bar | 0.12 | 0.16 | — | — | — | — | — | — | — | — | — | — | — | — |
| StL | 0.17 | 0.22 | 0.13 | — | — | — | — | — | — | — | — | — | — | — |
| Dom | 0.13 | 0.17 | 0.13 | 0.22 | — | — | — | — | — | — | — | — | — | — |
| Mon | 0.08 | 0.08 | 0.08 | 0.13 | 0.11 | — | — | — | — | — | — | — | — | — |
| Nev | 0.10 | 0.09 | 0.18 | 0.10 | 0.11 | 0.11 | — | — | — | — | — | — | — | — |
| StK | 0.12 | 0.10 | 0.17 | 0.10 | 0.13 | 0.20 | 0.24 | — | — | — | — | — | — | — |
| Sab | 0.02 | 0.03 | 0.02 | 0.01 | 0.02 | 0.00 | 0.03 | 0.02 | — | — | — | — | — | — |
| Ant | 0.08 | 0.08 | 0.15 | 0.09 | 0.08 | 0.11 | 0.25 | 0.18 | 0.04 | — | — | — | — | — |
| CBr | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.01 | 0.00 | 0.07 | 0.04 | — | — | — | — |
| LCa | 0.03 | 0.01 | 0.06 | 0.04 | 0.01 | 0.05 | 0.11 | 0.07 | 0.04 | 0.12 | 0.32 | — | — | — |
| GCa | 0.00 | 0.00 | 0.00 | 0.01 | 0.01 | 0.00 | 0.01 | 0.01 | 0.05 | 0.05 | 0.46 | 0.33 | — | — |
| Gua | 0.05 | 0.03 | 0.04 | 0.02 | 0.03 | 0.02 | 0.05 | 0.03 | 0.00 | 0.05 | 0.00 | 0.03 | 0.00 | — |

documented in water striders (Schuh and Slater 1995, Thorp and Covich 2001) and among island populations (Darwin 1876). 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 1876), especially if the aquatic habitats are persistent and flight is consequently 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 1876). However, it is unlikely that flying insects would leave an island in large numbers (Roff 1990).

As noted earlier, a large proportion of the species known from these small Caribbean islands are caddisflies (Flint 1968, 1996, Botosaneanu and Alkins-Koo 1993, Flint and Sykora 1993). Although caddisflies were collected at low elevations and on some of the islands that had little relief, their diversity was greater on mountainous islands, particularly in forested streams. This is expected, since, as a group, caddisflies tend to be more rheophilic (Wiggins 1996). Caddisfly adults are not very strong fliers, so they are not capable of traveling great distances. Because many of these species are restricted to one or a few nearby Caribbean islands, it appears that the Lesser Antilles may serve as a theater for caddisfly evolution, causing a greater number of species to develop by limiting them to separate islands, much as it does for anolis lizards (Roughgarden 1995). Flint (1978) reported that 79% of the trichopterans known from the Antilles are restricted to a single island. Similar patterns have been observed in dipterans and odonates in the Hawaiian islands (Brasher 2003).

An unexpected observation regarding the aquatic beetle fauna in Dominica developed as this survey was conducted. There are many suitable habitats on Dominica to support aquatic beetles, yet only a few species have been collected. Islands considerably smaller than Dominica have records of more beetle species. The question of why the diversity of aquatic beetles in Dominica is so low requires further investigation.

Tobago, the sixth largest island studied, has the second highest number of macroinvertebrate species. This is probably for two reasons: (1) It is the island closest to a continent, and therefore the easiest island to colonize; and (2) it is a continental island, once having been a part of South America, and its diversity probably results from its continental derivation (McArthur and Wilson 1967). Grenada is the island nearest Tobago, but farther from the mainland; it has slightly fewer species, although Grenada has a greater land area and considerably higher elevation (table 2).

## Island-specific habitats and species preference

Covich (1988) reported that many tropical species of gastropods and decapods colonize freshwater streams in the Caribbean from nearshore marine habitats, especially at lower elevations. However, these species typically decline and tend to be replaced by insects in upstream waters at higher elevations on many Caribbean islands, possibly because of differences in leaf detritus inputs (Hynes 1971, Harrison and Rankin 1976). Studies of small oceanic islands in the Pacific basin, including Hawaii (Kinzie and Ford 1977), Fiji (Haynes 1987), and Moorea (Resh et al. 1990), have yielded similar findings. The same general patterns, although somewhat less distinct, were observed in streams on all the islands studied in this investigation.

Since most of the collections were made through visual observation of microhabitats, it is possible to describe the microhabitat preferences shown by different species. Leaf debris, especially leaf packs where currents are present, is the preferred microhabitat for most stream macroinvertebrates. Very few species were observed on bare rocks. A notable exception is the larvae of the lepidopteran *Petrophila* spp., which occupy indentations of rocks and enclose themselves in a silken retreat. Most macro-

invertebrate species in ponds are associated with aquatic macrophytes, since the muddy bottoms are very low in dissolved oxygen concentration.

### Island proximity and shared species

Ninety-one pairwise comparisons of the number of species present on each island were made, and low similarity values were generally observed (table 3). The highest value, 0.46, occurs between Grand Cayman and Cayman Brac. In fact, the three highest similarity values are among the three Cayman islands. This is not surprising, considering the close proximity of these islands to each other and their isolation from all the others involved in this study. Six pairs of islands have similarity values ranging from 0.20 to 0.25. In all of those cases, the pairs of islands lie adjacent to each other, and in most cases they have similar environments. All the other island pairs compared have similarity values lower than 0.20, indicating that the macroinvertebrate species composition is not very similar among these small islands.

### Conclusion

At least 328 species of freshwater macroinvertebrates have been identified from 14 small Caribbean islands. It is quite likely that the discovery of new species will continue as other researchers continue to collect distribution records and survey the islands. Most stream species prefer leaf debris as a microhabitat, while pond species are associated with aquatic macrophytes. The most common and widespread species have strong dispersal capabilities, usually related to flight or tolerance of saltwater. Although species richness is related to island size, elevation, and location, other factors are also involved in determining the number of species found on an island. The macroinvertebrate faunas on these islands are generally sparse compared with those of the continents, most likely because of their oceanic origin, their small size, and the frequent disturbances to their freshwater environments.

Natural disturbances such as tropical storms and heavy rainfall have probably decimated stream populations in the past, and these events will continue to affect that fauna. Human populations on these islands have certainly grown in recent years, and the detrimental effects of their activities on aquatic habitats are growing. Numerous studies documenting the effects of human activities on stream macroinvertebrates have been conducted in temperate continental streams (Hynes 1960, Mackie 2001), but few such investigations have been reported for streams on small tropical islands. A recent PhD dissertation (Turner 2003) addressed this concern, but much work on this topic is still needed.

Conservation efforts on many small Caribbean islands in recent years have mostly been associated with economics—protecting reefs and beaches to attract tourists. However, people who live on the islands have long recognized the importance of the freshwater environments as sources of water for consumption and bathing as well as habitats for food resources. Major threats to these freshwater environments include siltation from upstream land development and pollution from agrochemical applications. Some island governments, such as that of St. Kitts, now restrict access to certain mountain streams at higher elevations to protect water quality. Others, such as the government of Dominica, have included many freshwater habitats in their national park system to protect these habitats and to encourage ecotourism. Biodiversity surveys, such as the one presented here, play an important role in providing information that may be used for protecting aquatic environments and the species they support. We must know what species are present and understand their ecological roles in order to better conserve and manage these natural resources for the future.

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