BIODIVERSITY OF FRESHWATER FISHES OF TRINIDAD AND TOBAGO, WEST INDIES

Dawn Arlene Teresa Phillip

A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews

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BIODIVERSITY OF FRESHWATER FISHES OF TRINIDAD AND TOBAGO, WEST INDIES

Abstract

The proximity of the speciose South American continent to Trinidad and Tobago ensures that these islands have a rich and dynamic fauna. According to the equilibrium theory of island biogeography (MacArthur & Wilson 1967), these islands should be subjected to frequent immigrations from the nearby continent, and these additions will, in response, fuel local extinctions to maintain a balance of species richness. The aquatic habitat is further impacted by man's activities, (Government of Trinidad and Tobago 1962; (Government of Trinidad and Tobago 1976b) which have the potential to amplify the natural rates of immigration and extinction. Despite the possible consequences, the effects of this disturbance on the fish fauna have not been studied. A survey of the islands' freshwater fishes was therefore carried out to investigate the natural spatial and temporal dynamics of local fish communities, and the effects of anthropogenic perturbations, on these. These baseline data can be used as a benchmark to address some of the problems that are threatening the fish diversity of Trinidad and Tobago.

The fish fauna of Trinidad and Tobago is diverse. Total species richness was estimated at between 37 and 40. Four zoogeographic zones were recognised. A zone of Antillean fishes included Tobago and the north coast of Trinidad. A zone of recent colonising South American fauna existed along the south coast of Trinidad. The rest of Trinidad contained a relict South American fauna dating back to the time when Trinidad was still part of the mainland. Included here was a centrally located zone of unstable fauna at risk of local extinction.

The fish fauna was temporally dynamic due to frequent colonisation and extinction events. Examination of the historic record showed that observed species richness varied from 38 to 43 between the mid 1950s and the present. During this time there were 15 introductions and 12 local extinctions. A conservative estimate was that a new species was recorded for Trinidad almost every three years. The geographic distribution of species also showed temporal changes which indicated a natural tendency of the fauna to vary over time.

Human interference, particularly the introduction of exotic fish species and long-term habitat alteration, has affected species diversity. Forty seven percent of the new introductions and 43% of the extinctions were human-introduced exotics. About four fifths of sites in Trinidad, and almost one fifth of the sites in Tobago, were either perturbed or polluted. Polluted rivers coincided with areas of high urbanisation and industrial development in the west and southwest of Trinidad.

Several effects of human interference on the fauna were recorded. Almost 8% of the sites examined contained one of the three exotic species still extant on the island. At each of these sites, the exotic species accounted for between 1.3% and 80.4%, by number, of the fish caught. Some of the effects of habitat disturbance on individual sites were increased frequency of diseases, extirpation of species, changes in species richness and other diversity measures, and the eventual regression of the fish community to opportunistic species (*r*-strategists).

The potential of two fishes, *Poecilia reticulata* and *Astyanax bimaculatus,* as indicator species was examined. *Astyanax* showed better potential as an indicator of habitat quality as it was not found in depauperate communities, typical of severely disturbed habitats, and its proportional abundance and biomass were negatively affected by pollution. *Poecilia* populations, on the other hand, were found to be insensitive to habitat quality when the above-mentioned criteria were used. They did, however, have a high frequency of diseased individuals at polluted sites.

One of the aims of conservation is to protect that portion of biodiversity most at risk of extinction, the rare species (Rabinowitz 1986). Over 70% of freshwater fish species found in Trinidad and Tobago were classified as rare in these islands. This fact, in addition to the loss of diversity recorded for some sites indicates that the implementation of a management strategy for the conservation of the freshwater fish fauna of Trinidad and Tobago is imperative. The management strategy should focus on the amelioration and protection of aquatic habitats since at least 80% of the rare species had either a restricted geographic distribution or narrow habitat specificity. Additionally, protection from overexploitation should be offered to commercially important species with only small populations. Finally, a minimum sample size of 35 sites, spread over different zoogeographic areas, is recommended for estimating species richness for monitoring, an intrinsic part of any management strategy.

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CONTENTS CONT'D

CHAPTER 1. Introduction

In recent years there has been increasing interest in environmental issues growing out of the realisation that the state of the environment is of fundamental importance to the quality of human existence. We depend on our environment (physical and biological) for ecosystem services (United Nations Environment Programme 1995) water, food, clothing, shelter, medicine, in short, for life. Furthermore, one of the major doctrines of biocentric thinking is that each species has its own intrinsic value (Ehrlich et al. 1995; Freedman 1995). Because all aspects of the environment are interrelated, our own existence will have impacts on the very environment on which we depend. These impacts can have either positive or negative effects on the organisms with which we co-exist. It is the latter case which causes most concern at present.

There has been a growing perception that human activity can, and has, resulted in the loss of genetic variation of species, and the loss of populations of plants and animals, whole communities and even the extinction of species (Soule 1983; Freedman 1995; Primack 1998). These losses have been brought about either directly through overutilisation of resources or indirectly through habitat alteration or destruction (United Nations Environment Programme 1995). The consequence has been a reduction in the number of species, or biodiversity, either on a local scale or on a global scale (Freedman 1995; Pimm et al. 1995).

Biodiversity, as defined by the United Nations Environment Programme (1995), is the total variability of life on earth. It encompasses the concepts of genetic diversity and ecological diversity. Genetic diversity is concerned with genetic variation within and between populations of the same species. It is crucial for adaptability to environmental change (Freedman 1995; Primack 1998). Lack of genetic variability can lead to extinction due to increased vulnerability of populations to disease and pests (Ehrlich et al. 1981; Roberds et al. 1990), pollution (Primack 1998) and climate shifts (Pollard 1985; Singh & Wheaton 1991). Genetic variability is lower for small populations, such as threatened and endangered species, than for large populations (Primack 1998). But even for some large populations, genetic variation can be severely reduced by anthropogenic factors. For instance, current agricultural practices, such as selective breeding, can result in the loss of genetic variation in domesticated species (Primack 1998).

Ecological diversity describes the number of species and their relative abundances in given areas. It also attempts to relate trends in community structure to biotic interactions within the community and interactions between the biotic and abiotic components of the environment. Much of this diversity has been threatened by man through overexploitation, introduction of exotic species, or habitat alteration (Freedman 1995). These factors operate by fragmenting populations into smaller groups that may succumb to dilemmas associated with low genetic variability of small populations. Examples of extinctions caused by these three factors are the Dodo (*Raphus cuculatus*) which was over-hunted, certain endemic haplochromine cichlids now extinct from lake Victoria after the introduction of Nile perch, and the North American black-footed ferret (*Mustela nigripes*) which succumbed because of habitat alteration.

It is difficult to predict the impacts of man's activities on biodiversity without prior knowledge of what species are present and a proper understanding of the factors that affect biodiversity. There is a paucity of the necessary information, particularly in the tropics. The Amazonian forest is an excellent example of this situation and ecological surveys there are still uncovering numerous new species at an amazing rate.

The status of freshwater fish in most of the rivers in the world is poorly known (Moyle & Leidy 1992). Moyle and Leidy estimated that about 20% of freshwater fish species worldwide are in serious decline or extinct. This is especially likely to be important in tropical areas. Despite the pioneering work of biologists such as Lowe-McConnell (1975) it is well known that there have been fewer ecological studies carried out in the tropics than in temperate regions. However findings from temperate studies may be relevant to tropical systems.

The present study is concerned with the biodiversity of freshwater fishes of the neighbouring Caribbean islands of Trinidad and Tobago, situated on the South American continental shelf (Figure 1.1). The climate is tropical, with two seasons annually, a wet season and a dry season. As one would expect from their location, the fauna of these two islands is influenced by the Caribbean islands to the north, and South America to the south. The aquatic habitat of these islands is predominantly riverine. Lake-type habitats are restricted to small pools and man-made reservoirs.

Background

The deteriorating conditions of the inland waters and fish fauna of Trinidad have attracted attention for some time. In the early 1950s, concern about the effects of a well developed export aquarium trade, based on locally captured species, on community structure or habitats prompted Price (1955) to conduct a survey of the freshwater fishes of Trinidad. In 1958 a committee was appointed to "examine the problem of the pollution of rivers (in Trinidad)...by oil, sewage and effluent from factories and mills..." (Government of Trinidad and Tobago 1962, p. 1). Despite the early cautions and recommendations of the committee, factory effluent is still discharged directly into streams and rivers (Moore & Karasek 1984). Biologists who have been working in Trinidad since the 1970s reported the degeneration of

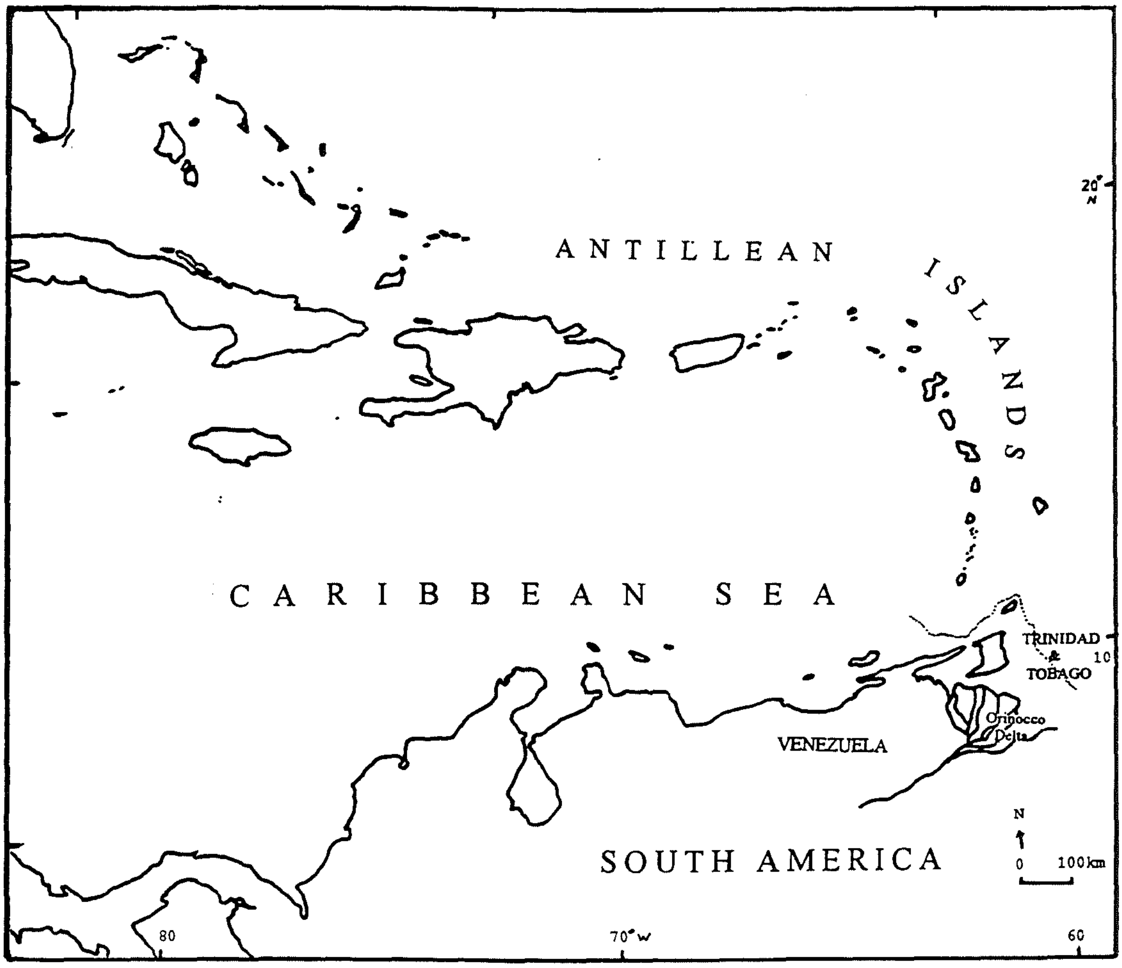


Figure 1.1. Map of the Caribbean region showing the location of Trinidad and Tobago on the South American continental shelf opposite the Orinoco Delta in northeastern Venezuela. The Antillean islands are to the north.

streams, rivers, and associated fish communities in the Northern Range, (Endler 1986; Reznick & Baxter 1994). They associated these changes with increased human settlement and activity along the upper portions of the affected streams.

Several studies have been carried out on inland water quality of Trinidad and Tobago; however most have been on the Caroni River drainage basin. This is because it is the largest and most important river system in the country, providing 40% of the surface water, and supplying about 50% of the potable water used in Trinidad (Siung-Chang 1990). Most of the population and manufacturing industries in Trinidad are located within the catchment area of this river system. From these surveys, the major types of pollution were found to be domestic, agricultural and industrial wastes (Government of Trinidad and Tobago 1976a). An overview of the main sources of threat to the freshwater fishes will now be given.

Deforestation

Forestry management practice in Trinidad and Tobago allows felling of selected tree species and conversion of naturally forested areas to plantation forestry. However, illegal agricultural practices, such as squatting, marijuana cultivation, tree felling and shifting cultivation with associated deforestation, continue to be a problem (Kenny 1995). According to the National Physical Development Plan of Trinidad and Tobago (Government of Trinidad and Tobago 1978), 58% of the land area is still under natural and secondary forest types. There was an increased incidence of squatting on marginal lands on the southern slopes of the Northern Range. Kenny (1995), estimated the percentage of forested land to be closer to 15%. Endler (1986) gave several examples of the effects of deforestation on fish communities in the Northern Range. For example, forest cutting in the catchment area of the Arima River in 1983 resulted in the loss of all fish from a tributary of the river. Two years later, only *Rivulus hartii* had successfully recolonised affected parts of the river.

Domestic waste

It is common practice in Trinidad and Tobago for domestic wastewater to be discharged into open drains, from whence it eventually enters river systems (Government of Trinidad and Tobago 1976b). Derelict vehicles, discarded household appliances and furniture, as well as other household garbage are dumped into streams (Plate 1.1a). These can trap leaves and branches flowing downstream, causing the river to stagnate, and resulting in anaerobic conditions in the dry season (Government of Trinidad and Tobago 1976a). The effects of domestic effluent and other wastes on fish can be detrimental. For example, declining fish densities in the Aripo River near the Aripo Village was blamed on extensive development taking place in the village since in 1983 (Endler 1986).

Overfishing

Endler (1986) gave several examples of the effects of overfishing on fish communities in the Northern Range. Endler reported that increased settlement on the El Cedro River, for instance, resulted in increased fishing pressure so that there were very few fish seen after 1981. By 1983, only guppies, *Poecilia reticulata*, were present.

Pesticides

Information on the effects of pesticide use on water quality in Trinidad is limited. Most studies have been concentrated on the Caroni drainage basin. Pesticides were found in almost all samples of water, soil, detritus and algae collected from the Caroni swamp, and there was evidence of bioaccumulation of these toxins in fish (Deonarine 1980). One of the major sources of pesticides here is thought to be the Aranguez vegetable farming area (Siung-Chang 1990). There have also been periodic fish kills in rivers due to the improper utilisation of pesticides by domestic users or farmers (Siung-Chang 1990). Two major spills of insecticides resulted in major fish kills in the Arima River between 1981 and 1982 (Endler 1986).

a.

b.

c.

Plate 1.1 Some of the main types of pollution found in Trinidadian rivers: a. domestic waste, Couva River; b. oil pollution, Erin River and c. the effects of industrial waste, Tacarigua River (note grey moss covering river bed).

Agricultural wastes

Thirty five percent of land area in Trinidad is cultivated by plantation crops, secondary tree crops and lastro (Government of Trinidad and Tobago 1978; Kenny 1995). In the early 1970s there were over 70 livestock farms in the Caroni River catchment area alone (Government of Trinidad and Tobago 1976a). Agricultural wastes from these areas contribute pollution in the form of high suspended solids, organic matter, pesticides, nutrients and pathogens (Government of Trinidad and Tobago 1976b).

Earthworks

It is estimated that about 8% of the land area of Trinidad is developed or under mining (Government of Trinidad and Tobago 1978). Illegal quarrying occurs, as well as sanctioned quarrying in reserves (eg. the Long Stretch Reserve) (Kenny 1995). The primary source of suspended solids in the Caroni River comes from gravel washing and quarrying activities along the Arima, Maturita and Aripo rivers in the Wallerfield and Arima area (Endler 1986). It was estimated that a substantial portion of suspended solids in mountainous streams in Trinidad comes from logging and roadworks (Lackhan 1980). Quarrying activities in the Arima River have left sections of the river devoid of fish for years (Endler 1986; Kenny 1995).

Oil production

Oil from oil fields, refineries and shipping, was recognised as a major source of pollution in Trinidad since the 1950s (Government of Trinidad and Tobago 1962). This pollution occurred in rivers such as the Guaracara, and more recently the Erin (Plate 1.1b), but the attitude at the time is best described by the following quote from the (Government of Trinidad and Tobago 1962, p. 5):

> "The Guaracara suffers from surface oil pollution and heavy oil pollution on the sides and bottom. There was no evidence that these conditions caused any particular hardship...some small streams in

the area of the oilfields are polluted and cannot support fish life, but at best they could only hold small fish and nothing in the nature of a fish industry had been established."

Industrial wastes

Pollution from industrial sources had been recognised as a major problem in Trinidad since the 1950s, when it was recommended that "no effluent whatever...be discharged into watercourses" (Government of Trinidad and Tobago 1962, p. 12). At this time, the Caroni River had already been seriously affected, with some portions of it "devoid of fish" (Government of Trinidad and Tobago 1962, p. 6). Fish kills reported just downstream of the Nestlé factory in the dry season (Government of Trinidad and Tobago 1976a) are probably caused by the factory's effluent which pours into the St. Joseph River. Since 1958, there have been complaints concerning the effluent from the Caroni Ltd. distillery (Government of Trinidad and Tobago 1962). This effluent sometimes resulted in fish kills in the dry season (Government of Trinidad and Tobago 1976a). Known industrial pollutants, believed to have originated from industrial estates on the Caroni River, have been found in river water by Moore & Karasek (1984). The effects of industrial pollution on some rivers such as the Tacarigua (Plate 1.1c) are obvious.

Given the deteriorating conditions of rivers in Trinidad, increasing population size with attendant urbanisation, and the government-sanctioned drive toward accelerated industrialisation and developments in the agricultural sector, it is necessary to take steps to protect the aquatic habitat and aquatic life. The present study will focus on freshwater fishes.

Objectives

The overall objective of the current study is to gain a better understanding of freshwater fish communities of Trinidad and Tobago in order to provide quantitative baseline data which can be used as a benchmark to address some of the problems threatening fish diversity. The total species richness of freshwater fishes in Trinidad and Tobago will be estimated and the spatial and temporal patterns of this diversity described. Aspects of community structure, such as whether certain species tend to be found together, and whether community structure changes along streams, will also be examined. Water quality will be measured, and some of the impacts of pollution on biodiversity will be assessed.

The chapters of this thesis are organised by separate topics, and each chapter can stand alone. Where necessary, however, there is cross referencing of information shared between chapters. The first chapter gives the background information on the importance of studying biodiversity in general, focusing on issues concerning Trinidad and Tobago and the present study. Several factors contributing to the threat to the biodiversity of freshwater fishes are described. Finally, the objectives of the present study are stated.

Chapter 2 describes the study area, Trinidad and Tobago, and several features relevant to the study. The location of the islands, and descriptions of the climate, geology, topography and freshwater drainage systems are included here. The rationale behind the selection of sample sites, and an account of field and laboratory methods are given.

The importance of total species richness is discussed and methods for its estimation are outlined in Chapter 3. Ten of these estimators are applied to the data to obtain estimates for Trinidad and Tobago's fresh water fish fauna. The performance of the estimators is assessed for the present data set, and a minimum sample size for future estimates of fish species richness of Trinidad and Tobago is recommended.

Zoogeographic and other spatial patterns in the distribution of the fishes are discussed in Chapter 4. The existing theory of the zoogeography of the fish is described, and another suggested. The two theories are tested using several analytical methods. Longitudinal trends in fish diversity along rivers are also considered here.

Chapter 5 looks at changes in the fish fauna since the early 19th century, but more specifically during the last 45 years. Trends in species richness, extinctions, colonisations and introductions are discussed. Changes in the distribution of species on the island are also discussed in the context of natural and anthropogenic factors.

Changes in diversity caused by pollution are examined in Chapter 6. Three measures of diversity are used: species richness, and Shannon-Weiner and Berger-Parker diversity indices. Some of the widely distributed species are assessed as possible indicator species.

A summary of results is presented in Chapter 7. Based on these, recommendations for conservation of the freshwater fish fauna and suggestions for future research are made.

CHAPTER 2. Methodology

Study area

Trinidad and Tobago, the most southerly of the Caribbean chain of islands, are situated between 10° 2′ and 11° 2′ N Latitude and 60° 30′ and 61° 50′ W Longitude. They are located on the South American continental shelf near the Orinoco Delta off northeastern Venezuela (Figure 1.1). Trinidad is 11.3 km from Venezuela at the nearest point while Tobago is 30.6 km off the northeastern coast of Trinidad.

Trinidad was once part of the South American mainland from which it separated as recently as the last Ice Age. This historical link is reflected in the geology and natural history of the island. The total land area of Trinidad is about 4,820 km^2. The island is divided into five main topographical regions: the Northern, Central and Southern Ranges with two intervening low-lying areas, the Northern or Caroni Lowlands and the Southern Lowlands (Figure 2.1). The geological make-up of Trinidad is complex, in terms of the variety of rock types and the structural complexity in which these are associated (Barr 1981).

The Northern Range is a series of strongly up-folded formations representing part of the eastern extremity of the Andean Mountain Range in South America which originates in Columbia and extends through Venezuela to Trinidad and Tobago. It is separated from the Northern or Coastal Range of Venezuela by four drowned valleys (Barr 1981). The Northern Range is the oldest and highest mountain range in Trinidad. It is composed of metamorphic rocks (170 million years old) from the Jurassic and Cretaceous. It is about 16 km wide, and rises steeply to over 914 m. The north coast slopes are steep and precipitous. The southern slopes are more gentle and are cut through by south-flowing rivers which have wide interior basins (Hardy 1981). Next in age is the

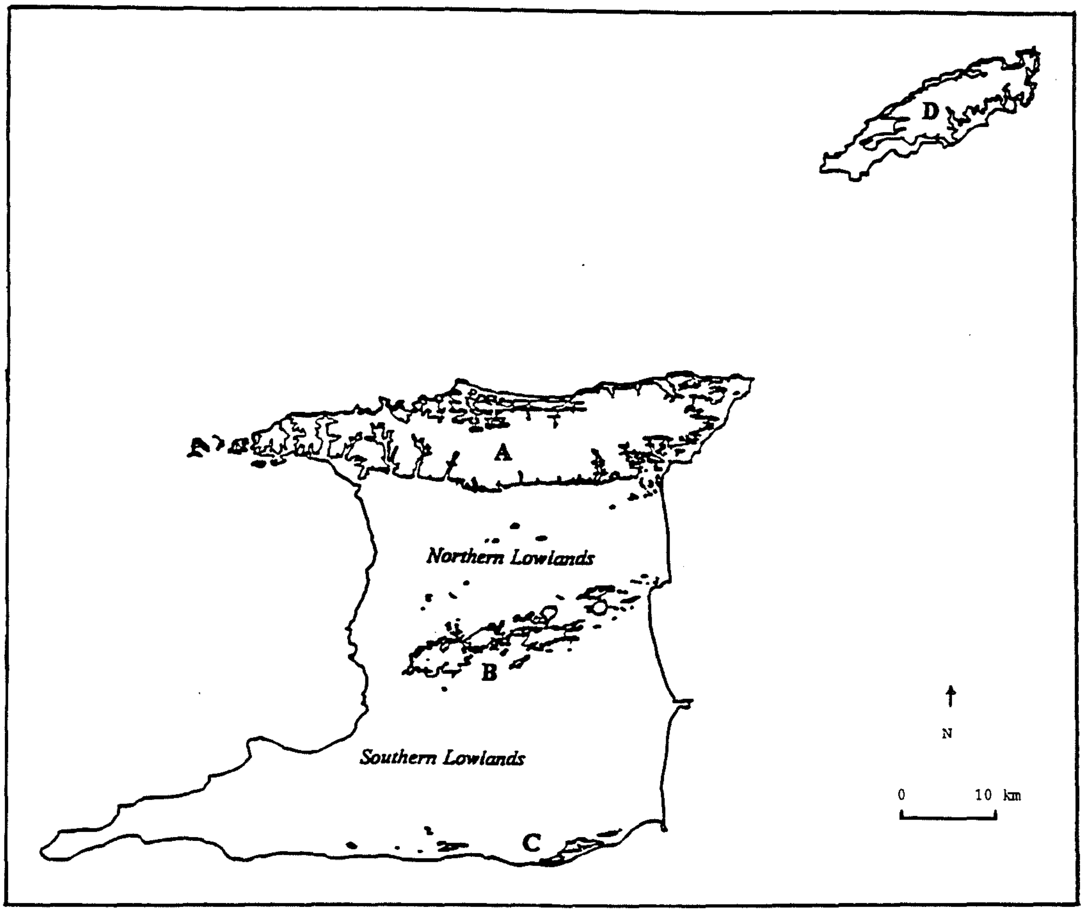


Figure 2.1. Map of Trinidad and Tobago showing the main topographic regions: the mountain ranges (A. Northern Range; B. Central Range; C. Southern Range and D. Main Ridge) and the intervening plains (Northern and Southern Lowlands). Distance between Trinidad and Tobago not to scale.

Central Range with formations dating back from the Cretaceous, and Eocene with Miocene formations along the southern, eastern and western borders. It is an anticlinal uplift with strong folding along its central and southern borders (Barr 1981). The youngest of the three, the Southern Range, has formations dating from the Miocene. It is a series of smaller anticlinal folds, maximum height less than 244 m, that are separated by a complicated fault system. This leads to a diverse topography that includes low, rolling hills, rugged, deeply dissected hills and a scattering of mud volcanoes (Barr 1981).

For the most part the rest of the island is made up of the lowlands composed of sandy, silty and clayey formations from the Miocene, Pliocene, Pleistocene and recent (5 to 25 million years) (Hardy 1981). It is believed that the Northern Lowlands have been a low-lying area for a relatively long time since the whole area is characterised by several river terraces at varying levels above the present alluvial flats (Hardy 1981). These have resulted in the formation of the extensive plains and the higher level benches and bevelled platforms on the foot-hills of the Northern and Central Ranges. The terrain of the Southern Lowlands is gently undulating. The Northern Lowlands are composed of soft sands and clays, with superficial gravel terraces as well as river and swamp alluvium (Hardy 1981). The Southern Lowlands are composed predominantly of soft sands and clays (Hardy 1981).

The land area of Tobago is 308 km^2. A single mountain range, the Main Ridge, runs almost the entire length of the island (Figure 2.1). The terrain in the southwestern portion of the island is gently undulating. The geology of Tobago is not nearly as well known as that of Trinidad.

Drainage systems

The main river systems in Trinidad drain the southern slopes of the Northern and Central Ranges (Figure 2.2). These are the Caroni and (north) Oropuche rivers to the north, and the Ortoire and (south) Oropuche rivers to the south. Several smaller river systems drain the coastal sides of the Northern and Southern Ranges and the remaining areas. The Caroni and (north) Oropuche drainage areas are characterised by mature river systems with broad alluvial-filled valleys and meander belts in the lower reaches. The drainage systems of the south are similar, but lack the extensive terrace and flood plain topography of the north (Barr 1981). The Caroni, Nariva, northern and southern Oropuche rivers all have extensive swamps at their mouths. The major drainage systems of Tobago are the Courland, Hillsborough, Goldsborough and Richmond rivers.

Rivers are reflections of the terrestrial systems that make up their watersheds (Sioli 1975). As rain water percolates through the soil, it picks up soluble mineral ions as well as mobilisable solids including soil fractions. It can be seen that the chemical composition of the water and physical composition of the bottom substrate will depend on the geology and geochemistry of the catchment area. Streams in the Northern Range and most of Tobago are characterised by clear, fast-flowing water with a firm substrate composed of a range of material from boulders to gravel (Plate 2.1a). Stream characteristics change as one progresses southward through the island to younger, less statuesque mountains. The substrates become increasingly composed of sand and mud, and water velocity decreases while turbidity increases (Plate 2.1b). On the plains, streams tend to have turbid, sluggish water flowing over muddy substrates. Some natural drainage systems have been modified to relieve flood-prone areas on the plains in the wet season, as well as to provide irrigation during the dry season. The modifications include

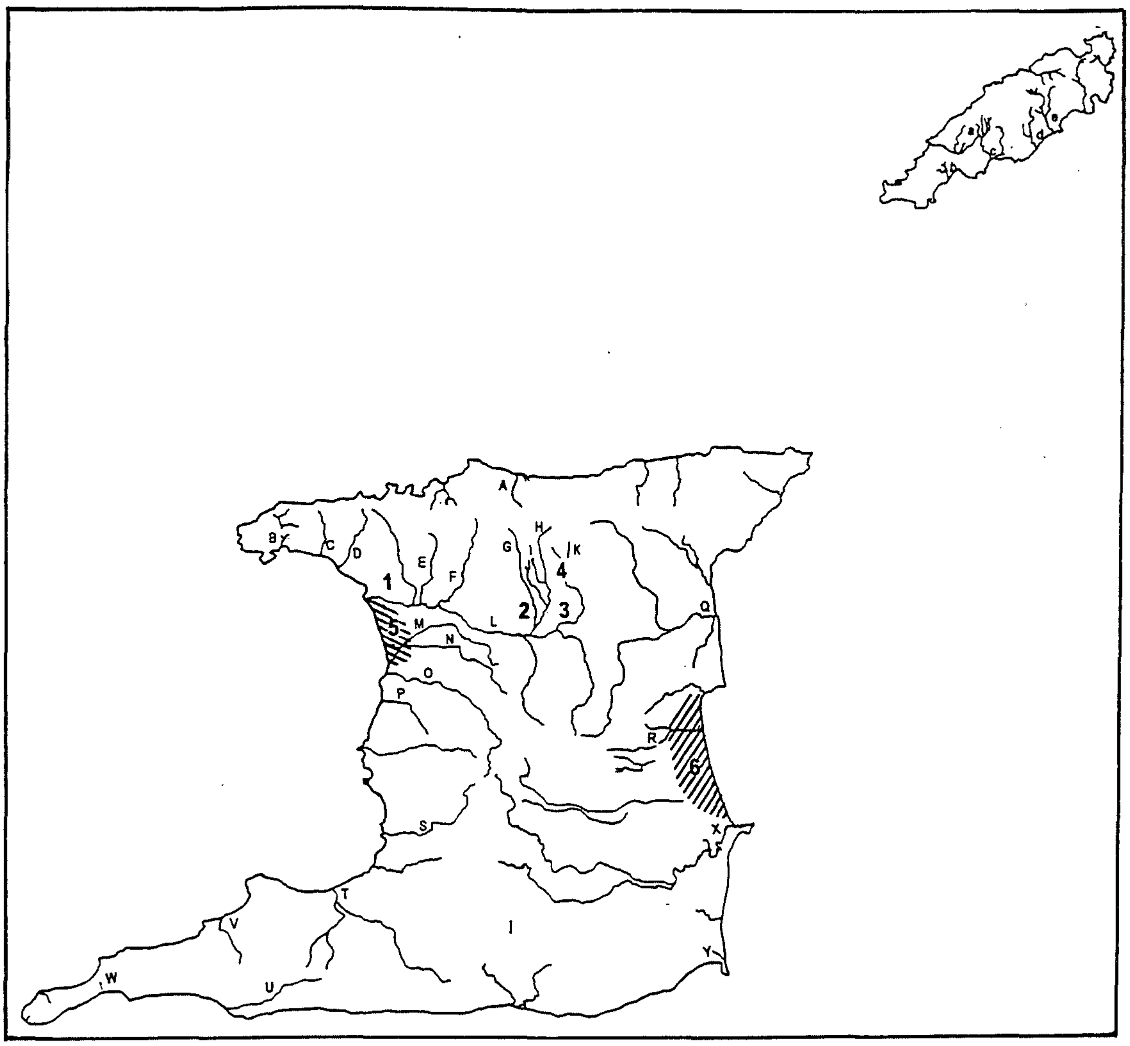


Figure 2.2. Map of Trinidad and Tobago showing major river systems, rivers and places mentioned in the text. Map not to scale.

A. Curaguate R.	M. Guayamare R.	1. Aranguez
B. Cuesa R.	N. Cunupia R.	2. Arima
C. Diego Martin R.	O. Caparo R.	3. Wallerfield
D. Maraval R.	P. La Cuesa R.	4. Aripo V'ge
E. St Joseph R.	Q. North Oropuche R.	5. Caroni swamp
F. Tacarigua R.	S. Guaracara R.	6. Nariva swamp
G. Arima R.	T. South Oropuche R.	a. Courland R
H. Guanapo R.	U. Erin R.	b. Lambeau R.
I. El Cedro R.	V. Guapo R.	c. Hillsborough R.
J. Maturita R.	W. B1/71	d. Goldsborough R.
K. Aripo R.	X. Ortoire R.	e. Richmond R.
L. Caroni R.	Y. Guayaguayare R.	

a.

b.

Plate 2.1 Mountain streams typical of: a. Tobago and Northern Range, Trinidad; b. Central Range.

the straightening, deepening and widening of the natural water courses as well as the dredging of river mouths.

Climate

Trinidad and Tobago experience two seasons which differ mainly in precipitation. There is a dry season from January to May and a wet season from June to December, with a brief dry spell, the petite carême, in September. Average annual rainfall of Trinidad and Tobago is 1830 mm with 92% of the rain falling in the wet season (Berridge 1981). The driest month is usually March (with an average monthly rainfall of 33.6 mm) and the wettest months are from June to August and November (with average monthly rainfall of over 50 mm). Rainfall varies spatially as well. The northeastern portion of Trinidad receives the heaviest rainfall in the island (Berridge 1981). Here, mean seasonal rainfall is 1016 mm and 2032 mm for the dry and wet seasons respectively (1939 - 1968) as compared to 254 mm and 635 mm respectively for the same seasons in the western peninsulas. The pattern of rainfall is similar in Tobago (Berridge 1981). Rainfall is highest in the mountains in the northern part of the island and decreases in all directions from this area. Total annual rainfall in 1972 ranged from 3050 mm in the north to 1270 mm in the southwest. Of this rainfall, 2290 mm fell in the north and 1020 mm in the southwest during the wet season (Berridge 1981).

Between 1946 and 1975, air temperatures varied between 33.3 and 17.6°C (Berridge 1981). More recently, however, day-time temperatures of over 35°C have been recorded. Mean seasonal variation in air temperature is only in the order of two to three degrees Celsius with cooler temperatures generally in the dry season. Diurnal variations are greater; up to 10 - 15°C differences between night and day (Berridge 1981).

Selection of sampling sites

The present project was carried out to provide information that could be used in the management and conservation of the freshwater fishes of Trinidad and Tobago (see Chapter 1 for further details). Ninety one sites representing all the major drainages, biogeographic regions and river types were sampled (Figure 2.3). Each stream or river was examined at one to three locations depending on its length. It was the intention that sampling sites would be selected to allow comparison of species diversity along rivers and streams as well as between clean and polluted sites in otherwise similar rivers or streams. Efforts were also made to revisit sites used in a previous survey by Kenny (1995). For ease of access, sites were located where streams and rivers were crossed by roads following the tradition set by Price (1955) and Kenny (1995). Price admitted a shortcoming in using these intersections for site selection; it left areas with few roads, such as the north coast and the oil fields of the southeast, under sampled.

Frequency of sampling

Field sampling was carried out over a 2-year period. During this time twenty two sampling sites were visited twice to establish differences in water quality and species diversity between the wet and dry seasons.

Field techniques

Biological

Fish were collected from known lengths of streams. The length chosen was short enough to be fished thoroughly, yet long enough for all species present to be represented in the catch. The sampling site also had to include the major habitat types (e.g. pool and riffle) present in the river at

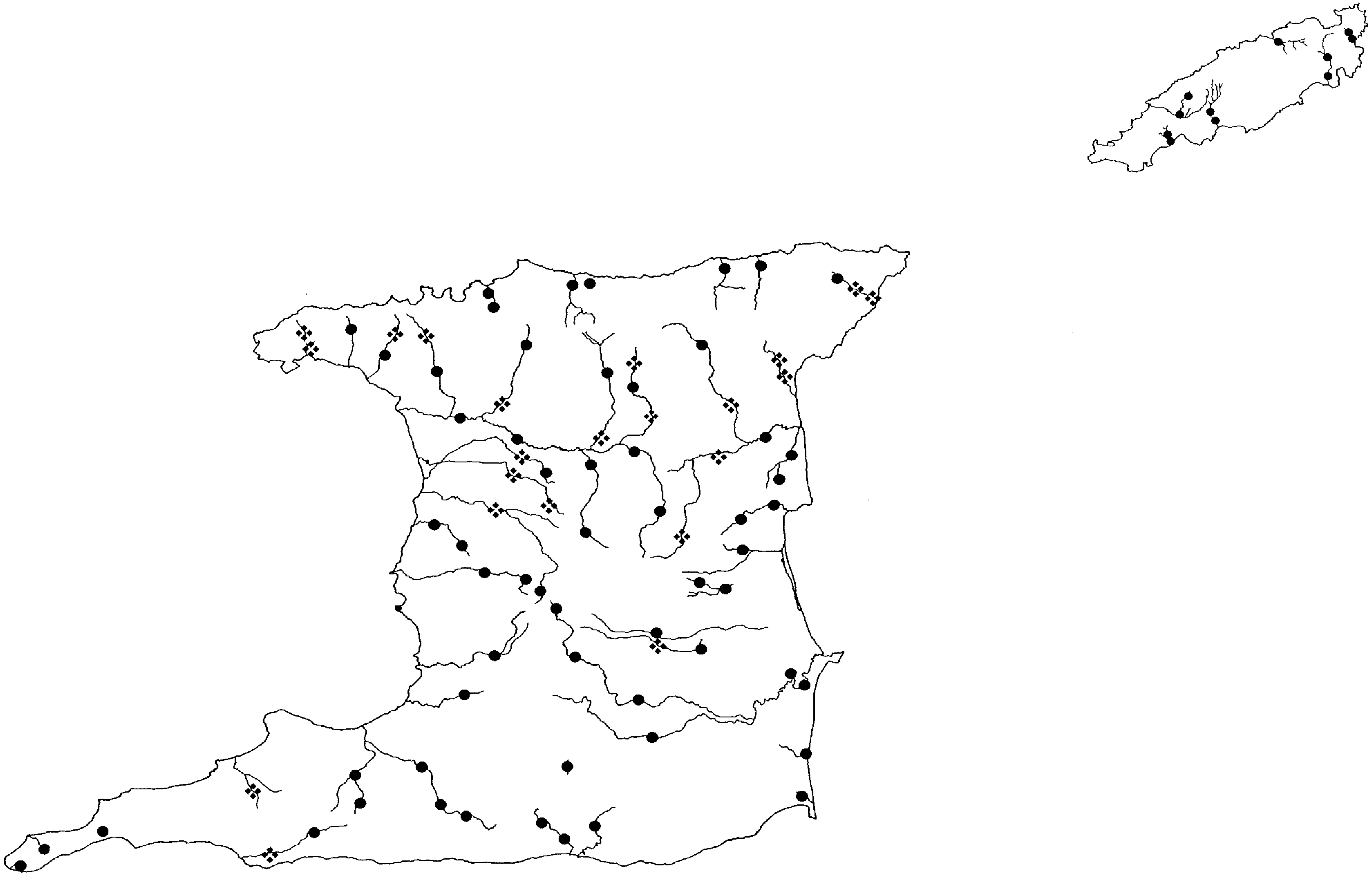


Figure 2.3. Sample sites in Trinidad and Tobago. Sites that were sampled once are indicated by ● and those sampled twice by ❖. Maps not to scale.

that point. An average length of 50m was used. Longer stretches were sampled for the larger rivers since it was felt that the diversity of fish in these would be more patchy and widely dispersed to match the distribution of habitat types found therein.

The methods and gear used to sample fish depended on several factors: width and depth of stream; substrate type (e.g. sand or rock); organic substrate type (e.g. algae or branches); turbidity, water current speed. Records were made of fish seen but not caught.

Electrofishing was found to provide a better representation of fish assemblage structure than other methods such as seining (Dauble 1980). In addition, it could be used in areas poorly sampled by other gears (e.g. areas with dense vegetation or branches). It was therefore employed wherever conditions were suitable, particularly in the clear, stony-bottomed streams of the Northern Range and Tobago (Plate 2.2a). In the deep pools of these streams, electrofishing was supplemented by visual census techniques. Seining was used for most of the survey since the majority of the rivers are turbid and not suitable for electrofishing (Plate 2.2b). Large deep rivers were sampled with gillnets and a trammel net described in Table 2.1.

Except for the large rivers, fishing was carried out during the day. Where possible, block nets were deployed at the upstream and downstream ends of the sampling station before sampling. Where currents were too strong, the river too wide or too deep, it was not possible to block the river and catch per unit of effort was used instead of total catch.

In the large rivers, fishing was carried out at night when the use of the gill and trammel nets would be most effective. The nets were set at or just before nightfall, and retrieved 3 to 4 hours later. They were then reset and retrieved at dawn.

a.

b.

Plate 2.2 The main fishing methods used in my study
a. electrofishing- clear mountain streams
b. seining- turbid lowland streams.

Table 2.1. Description of nets used in overnight sampling of large rivers.

Net	Mesh size (cm)	Length (m)	Depth (m)
Trammel	-	35	3
Inner	3		
Outer	15		
Gill (1)	2.5	14	4.5
Gill (2)	0.8	25	3.5

The total catch from each site was sorted by species. The total biomass and number of individuals in each species in the catch was recorded. Weights (to the nearest 0.1g) were obtained from a top loading field balance (See Appendix I for data recording sheet).

Physical measurements

Several habitat variables were measured at three points for each sampling site. If the site contained more than one habitat type, the measuring points were placed to include up to three of these. Otherwise, the points were positioned at the upper, middle and lower ends of the sampling station. Measurements were made approximately midway between the banks of the river. Water depth (m) was measured with a meter rule. Stream width and sampling station length (m) were measured with a fibreglass tape measure. Water current was measured initially with a Pygmy current meter that gave readings in revolutions per minute. Several problems were encountered with the functioning of the current meter and eventually water current was measured by timing the movement of a heavy rubber ball. Both sets of measurements were standardised to m/s. Stream bank height was estimated to the nearest 0.25m. Primary and secondary stream substratum were characterised as either bedrock, boulder, rock, gravel, sand or mud. Algae and other periphyton were estimated as percentage of substrate covered. Presence of emergent vegetation along the banks was noted. Forest closure over the stream was estimated to the nearest 5% (See Appendix I for data recording sheet).

Chemical parameters

Water chemistry parameters were either measured in situ or in the laboratory. In situ measurements were made at the same points at which physical measurements were taken. Where measurements were to be made in the laboratory, duplicate or triplicate samples were collected at the upstream end of the sampling site. Each collection was made midway between the river banks, and at mid-depth in the water column. Water for oil and grease determination was collected at the water surface. Samples were stored on ice and, in most cases, analysed the same day. Samples collected for determining heavy metals and oil and grease were preserved with nitric and hydrochloric acids respectively for later analysis (See Appendix I for data recording sheet).

The water quality parameters measured and justifications are given in the ensuing list:

- oil and grease - pollution by petroleum hydrocarbons is a problem in rivers in the oil producing Southern Basin. Certain constituents of petroleum hydrocarbons cause surface films that impede the diffusion of oxygen into the water;

- suspended solids - quarrying and deforestation in the Northern Range, and earthworks throughout the islands lead to elevated levels of suspended inorganic matter. Its significance relates to physical effects particularly on light penetration and bottom sediment. Suspended solids can have a major effect on primary productivity and clogs fish gills. Concentrations less than 25 mg/L appear to have little effect on most fish (Alabaster 1980). It is unlikely that concentrations of inert sediments that do not exceed 80 mg/L will do serious damage to a fish population although they may reduce growth rate and abundance (Hynes 1973). Levels of suspended solids therefore need to remain high (over 100 mg/L) for several weeks to have a significant impact on fish populations;

- ammonia (NH_3) - in high concentrations, it is very toxic to aquatic life. In the absence of dissolved oxygen, free ammonia may occur as a result of protein breakdown;

- total phosphorous - in waste waters it occurs almost solely as phosphates (American Public Health Association 1985). Sources of phosphorous in water are detergents, water treatment plant effluent, fertilisers, body wastes and food residues. It is essential to the growth of living organisms and can be the nutrient that limits the primary productivity of a stream (American Public Health Association 1985). Phosphorous enters water bodies in many forms, only some of which are immediately available for plant growth, but others may become so through microbial activity in the water. Total phosphorous may therefore be a reasonable measure of the fertility of a body of water. The effect of forest removal is to increase phosphorous in the water (American Public Health Association 1985);

- conductivity - used to distinguish freshwater sites from estuarine;

- dissolved oxygen - essential to fish life. Low DO increases ammonia toxicity (Lloyd 1992);

- biochemical oxygen demand - the oxygen requirement of a body of water for biochemical degradation of organic material, oxidation of reduced forms of nitrogen and inorganic ions (American Public Health Association 1985). Fish kills may result if the BOD of a body of water exceeds its DO;

- pH - indicates the intensity of acidity or basicity of water. In natural waters, it usually ranges from 4 to 9 although most waters are usually slightly basic because of the presence of carbonates and bicarbonates (American Public Health Association 1985). As the pH of water decreases below 5.5 the harmful effects on fish increase (Lloyd 1992);

- alkalinity - acid-neutralising capacity of a body of water;

- hardness - sum of the calcium and magnesium concentrations both expressed as mg calcium carbonate/L. Calcium concentration reduces the toxicity of some heavy metals (Lloyd 1992);

- zinc - toxic to fish at very high levels. Sub-lethal levels have been shown to reduce growth and fecundity of some fish species (Lloyd 1992);

- copper - toxicity similar to that of zinc (Lloyd 1992).

Laboratory methods

Measurements were made with a HACH water quality test kit. In some cases, water colour and/or turbidity affected the reliability of the results obtained, hence other methods were substituted where necessary, and where possible. When feasible, chemical parameters were measured using USEPA accepted Standard Methods (American Public Health Association 1989, 1995).

Conductivity and salinity: Conductivity and salinity were measured in situ with a conductivity meter, Standard methods

2510 B and 2520 B respectively (American Public Health Association 1995). The conductivity meter used was a CO150 HACH conductivity/TDS meter with platinum electrode that gives a direct readout.

Total dissolved solids: Total dissolved solids (TDS) was measured by the Potentiometric method, HACH method 8006 (HACH 1994) with a CO150 HACH conductivity/TDS meter with platinum electrode which gives a direct readout.

Dissolved oxygen and temperature: Dissolved oxygen and temperature were measured in situ by the Membrane electrode method, Standard method 4500-O G (American Public Health Association 1995), using either a Jenway 9200 or a YSI dissolved oxygen meter.

pH: pH was measured by the Electrometric method, Standard method 4500-H+ B (American Public Health Association 1995), either in situ with an EC10 portable HACH pH/mV/temperature meter, or in the laboratory with a pH orp test kit. Laboratory measurements were taken only when the field meter was not available.

Oil and grease: Oil and grease were determined by the Partition-gravimetric method with n-hexane as the solvent, Standard Method 5520 B (American Public Health Association 1995). The solvent of choice is trichlorotrifluoroethane that extracts more thoroughly than n-hexane. However because of environmental concerns, there is a tendency to revert to n-hexane as the extracting solvent. Its extracting capabilities are improved by the addition of small amounts of (methyl-tert-butyl ether) MTBE. Oil and grease is such a broad measure (American Public Health Association 1995) that it was felt that any improved accuracy inherited with the addition of MTBE was not warranted in the present study.

Suspended solids: Suspended solids were determined by the Photometric method, HACH Method 8006 (HACH 1994), using a HACH spectrophotometer.

Biochemical oxygen demand (BOD): BOD was determined by a 5-day BOD test Standard Method 5210 B (American Public Health Association 1995).

Nitrogen-Ammonia: Ammonia was determined by two methods, Nesselerization, Standard Method 417 B (American Public Health Association 1985) and the Ammonia-selective electrode method, Standard Method 4500-NH3 D (American Public Health Association 1995). At the beginning of the study, when sampling was taking place in the clear-water streams of the Northern Range, ammonia was determined by the Nesslerization method using an HACH spectrophotometer. This colourimetric method was not suitable for most of the rivers of the rest of the island, as turbidity and water colour were interferences. The ammonia-selective electrode method was then adopted and used for the remainder of the study.

Total phosphorus: Total phosphorus was determined by the Vanadomolydophoshporic acid colourimetric method, Standard Method 4500-P C (American Public Health Association 1995), following Persulphate digestion, Standard Method 4500-P B5 (Association American Public Health 1995).

Total alkalinity: Total alkalinity, expressed as $CaCO_3$, was determined by the Titration method, Standard Method 2320 B (American Public Health Association 1995).

Calcium hardness (HACH): Calcium hardness was determined by the EDTA titrimetric method, Standard Method 2340 C (American Public Health Association 1995).

Zinc: Zinc concentration was determined by Direct air-acetylene flame atomic absorption spectroscopy, Standard Method 3500-Zn B (American Public Health Association 1995).

Copper: Copper concentration was determined by Direct air-acetylene flame atomic absorption spectroscopy, Standard method 3500-Cu B (American Public Health Association 1995).

CHAPTER 3. Estimation of species richness

Introduction

The threat of widespread extinctions due to global climate changes and extensive habitat modifications has made the estimation of diversity a priority (Coddington *et al.* 1996). Rates of species extinctions are believed to be already alarmingly rapid in the tropics (Coddington *et al.* 1991) making the need for conservation in these areas a crucial issue. Total species richness is the iconic measure of diversity (Peet 1974; United Nations Environment Programme 1995). There are a variety of other interpretations of diversity, but species richness remains the simplest, most intuitive and useful measure (Magurran 1988). Despite its simplicity, it has been used successfully as an indicator of diversity (Abbot 1974; Connor 1978; Harris 1984), and it remains a valuable tool for conservation, management (Coddington *et al.* 1991; Coddington *et al.* 1996) and environmental monitoring (Magurran 1988).

Estimation of local species richness is of fundamental importance for extrapolation to larger geographic scales (Coddington *et al.* 1996). Regional diversity is a function of the species richness of communities (alpha diversity) as well as the variability in species composition along ecological gradients (beta diversity). The estimation of species richness becomes doubly important because alpha diversity is an intrinsic part of beta diversity (Coddington *et al.* 1996).

Although most information on species richness has traditionally come from community ecologists and systematists, both groups have undoubtedly underestimated total species richness (Coddington *et al.* 1991). While it might be possible to obtain accurate estimates of species richness of groups such as large sessile organisms by simply counting all individuals, even then total enumeration is usually not a practical option (Silva & Coddington 1996; Chazdon *et al.* in press). A more practical approach would be to obtain estimates by extrapolation from sample data (Silva & Coddington 1996; Chazdon *et al.* in press). Although Preston (1948) and Williams (1964) showed that total species richness could be estimated, substantial interest only developed with current concerns over the loss of global biodiversity.

Methods of estimating species richness

Three classes of methods for estimating species richness have been suggested (Chazdon *et al.* in press).

Fitting parametric distributions of species richness
If relative abundance data from a single sample fits a species abundance distribution, a parameter of this distribution can be used to estimate the total species richness (S), or the number of species in larger samples (Chazdon *et al.* in press). The most widely used distributions are the log series, log normal and the Poisson log-normal (Preston 1948; Pielou 1975; Miller & Wiegert 1989). Cohen's (1959, 1961) method, for instance, is based on a log-normal distribution.

Extrapolation from species-accumulation curves
Another group of methods extrapolates species richness from species-accumulation or species-area curves. These curves are plots of the cumulative number of species for some cumulative measure of effort (e.g. samples or area). The curve is extrapolated to give species richness for larger sample sizes, larger area sampled, or to the asymptote to give total species richness (Clench 1979; Palmer 1990; Soberón & Llorente 1993; Colwell & Coddington 1994). Examples of this class of estimator are maximum likelihood estimators, MMRuns and MMMean (Raaijmakers 1987) based on

the rectangular hyperbolic Michaelis-Menten model (Michaelis & Menten 1913),

$$S_{MM} = \left(\frac{Sn}{B+n} \right)$$

and Coleman's (1981, 1982) random placement approach.

$$S_{Cole} = S\left(1 - e^{-Kn}\right)$$

where

S = no. of species in the pool

n = no. of units of sampling

B = sampling effort needed to detect 50% of the species

K = a fitted constant that controls the shape to the curve

Non-parametric estimators of species richness

The final type of estimator is the non-parametric estimator. This type of estimator uses either species presence/absence (incidence) or species relative abundance data. These methods are reviewed by Colwell & Coddington (1994) and Chazdon *et al.* (in press), and include a series of jackknife estimators for estimation of population size from mark-recapture data (Burnham & Overton 1978, 1979). Burnham & Overton (1978, 1979) suggested that the methods could also be used for estimation of S. Jackknifing reduces the bias of estimates (Miller 1964), however when applied to estimation of S, it reduces the underestimation of the true number of species based on the number present in the sample (Colwell & Coddington 1994). Two orders of Jackknife estimators are used to estimate S from incidence data: Jack1 is a first-order jackknife estimator of species richness (Burnham & Overton 1978; (Burnham & Overton 1979; Heltshe & Forresort 1983), and Jack2, a second-order jackknife estimator of species richness (Smith & van Belle 1984):

$$S_{Jack1} = S_{Obs} + Q_1\left(\frac{m-1}{m}\right)$$

$$S_{Jack2} = S_{Obs} + \left[\frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)}\right]$$

where

S_{obs} = total number of species observed in all samples pooled

Q_i = number of species that occur in exactly i samples

m = total number of samples

Smith & van Belle (1984) developed a bootstrap estimator of S based on the proportion of quadrats containing each species. This method, therefore requires only incidence data.

$$S_{Boot} = S_{Obs} + \sum_{k=1}^{S_{Obs}} (1-p_k)^m$$

where

$p_{k=}$ = proportion of samples that contain species k

Chao (1984) developed an estimator of S (Chao1) based on the number of rare species in the sample. Rare species were defined as the number of species represented by only a single individual (singleton) or two individuals (doubletons). This estimator therefore relies on species abundance data.

$$S_{Chao1} = S_{Obs} + \frac{F_1^2}{2F_2}$$

The variance estimator that computes the standard deviation for Chao1 is

$$\text{var}(S_{Chao1}) = F_2\left(\frac{G^4}{4} + G^3 + \frac{G^2}{2}\right)$$

where

$$G = \frac{F_1}{F_2}$$

F_i = number of species that have exactly i individuals when all samples are pooled

A few years later, Chao developed an analogous estimator (Chao2) for use with incidence data (Chao 1987). In this instance, rare species were those that occurred in either one sample (uniques) or two samples (duplicates).

$$S_{Chao2} = S_{Obs} + \frac{Q_1^2}{2Q_2}$$

The variance estimator used to compute the standard deviation for Chao2 is the same as that for Chao1, but with

$$G = \frac{Q_1}{Q_2}$$

The newest set of estimators are based on the statistical concept of sample coverage. Sample coverage is the proportion of total species richness that is actually sampled (see Chazdon *et al.* in press). The two estimators are ACE (Abundance-based Coverage Estimator) and ICE (Incidence-based Coverage Estimator) (Chao *et al.* 1993; Lee & Chao 1994). They are designed to overcome problems of overestimation of S that occur when sample numbers are low, or when some species are very common in the sample and others very rare (Colwell 1997).

First note that for abundance data

$$S_{Obs} = S_{rare} + S_{abund}$$

The sample coverage estimate based on abundance data is then

$$C_{Ace} = 1 - {F_1}/{N_{Rare}}$$

where

$$N_{Rare} = \sum_{i=1}^{10} iF_i$$

and

S_{rare} = number of rare species (each with $\leq$ 10 individuals) when all samples are pooled

S_{abund} = number of abundant species (each with > 10 individuals when all samples are pooled

N_{rare} = total number of individuals in rare species

This sample coverage estimate is therefore the proportion of all individuals in rare species that are not singletons. The ACE estimator of species richness is

$$S_{Ace} = S_{abund} + \frac{S_{rare}}{C_{Ace}} + \frac{F_1}{C_{Ace}}\gamma^2_{Ace}$$

where γ^2_{Ace}, which estimates the coefficient of variation of the F_i's, is

$$\gamma^2_{Ace} = \max\left\{\frac{S_{rare}}{C_{Ace}}\frac{\sum_{I=1}^{10} i(i-1)F_i}{(N_{rare})(N_{rare}-1)} - 1, 0\right\}$$

For the sample coverage estimate based on incidence data, first note that

$$S_{Obs} = S_{\inf r} + S_{freq}$$

The sample coverage estimator is then

$$C_{Ice} = 1 - Q_1 / N_{\inf r}$$

where

$$N_{\inf r} = \sum_{j=1}^{10} jQ_j$$

and

S_{infr} = number of infrequent species (each found in $\leq$ 10 samples)

S_{freq} = number of frequent species (each found in > 10 samples)

N_{infr} = total number of incidences (occurrences) of infrequent species

Thus, the sample coverage estimate is the proportion of all individuals in infrequent species that are not uniques. Then the ICE estimator of species richness is

$$S_{Ice} = S_{freq} + \frac{S_{\inf r}}{C_{Ice}} + \frac{Q_1}{C_{Ice}} \gamma_{Ice}^2$$

where γ_{Ice}^2, which estimates the coefficient of variation of the Qj's, is

$$\gamma_{Ice}^2 = \max\left\{ \frac{S_{\inf r}}{C_{Ice}} \frac{m_{\inf r}}{(m_{\inf r} - 1)} \frac{\sum_{j=1}^{10} j(j-1)Q_j}{(N_{\inf r})^2} - 1, 0 \right\}$$

Like the Chao estimators, ACE and ICE are based on rare species in the sample. ACE is based on species with 10 or less individuals in the sample (Chao *et al.* 1993), and ICE on species found in 10 or less sampling units (Lee & Chao 1994).

The performance of some of the species richness estimators, in terms of reliability/accuracy and precision, have been tested and reported in the literature. Baltanás (1992) evaluated the performance of estimators of species accumulation curves, the Cohen (1959, 1961) method and the jack knife procedure (Heltshe & Forresort 1983). The performances of the latter two estimators were similar. The accuracy of the estimators was found to be influenced by the representativeness of the samples used. The jackknife procedure was more influenced by sample representativeness than the Cohen's method which produced more precise results. Both methods tended to underestimate true species richness. Despite this, (Palmer 1990) suggested that these methods can be used for comparing communities once they were of similar structure. Finally, Baltanás (1992) found that the jackknife procedure did not provide good results when unique species are not present, whereas the Cohen method does.

Colwell & Coddington (1994) reviewed the seven non-parametric methods and found that the Chao2 and Jackknife2, followed by the jackknife1 and Michaelis-Menten estimators gave the least biased results for small samples. They found the Chao2, which requires only incidence data, to be remarkably accurate even when based on a few samples. Since the sampling carried out in my study was by no means exhaustive, these methods were used to obtain more accurate estimates of the total species richness of the freshwater fauna of Trinidad and Tobago.

Methods

The freeware program, EstimateS (Colwell 1997) was used to estimate S for the freshwater fishes of Trinidad and Tobago. The program computes a species accumulation curve as well as 10 species richness estimators, and standard deviations of the estimates where possible. The estimators are Coleman, MMRuns, MMMeans, Bootstrap, Jack1, Jack2, Chao1, Chao2, ACE and ICE. These methods were all used, because, as stated in Coddington *et al.* (1991), the convergence of estimates obtained by several methods is evidence that they are all estimating the same quantum.

The analyses were run with abundance and incidence matrices. Each row in the matrix represented a single sample, and each column the abundance data for a single species.

The analysis begins by calculating estimates of S from a single sample, selected at random. Other samples are added at random and the estimates are re-calculated for the pooled samples after each sample has been added. Each sample is added once until all the samples have been used. The more samples used, the more accurate the estimates of S. The species accumulation curve is constructed as samples are added to the analysis.

Species richness is known to vary between samples. The shape of the species accumulation curve will thus be affected by the order in which samples are added. To improve the shape of the species accumulation curve, therefore, EstimateS allows the order in which the samples are added to be randomised several times, and an average curve obtained. If multiple randomisations are specified, the entire process is repeated the designated number of times. The estimates are then averaged over all the randomisations thereby reducing any possible effects of sample order on estimation.

Some investigation was required to determine a suitable minimum number of randomisations for the dataset. Values of 50, 100 and 150 randomisations were tried. There was not much change in performance in most of the estimators between 50 and 150 randomisations, with the exception of the Michaelis-Menten estimators. The value of 100 was finally accepted as a compromise between the smoothness of the curves and the time it takes the program to perform the estimations.

The performance of the estimators was assessed based on two criteria: the speed with which the final estimate is reached, and stability of the estimate once this value is attained. One possible factor affecting the performance of the estimators was the spatial distribution or patchiness of the species. Patchiness can vary from zero to unity, where zero represents an even distribution (Colwell 1997). Three levels of patchiness, 0.2, 0.5 and 0.8, were considered using abundance data, and the level of patchiness giving the optimal result (0.2) was applied to the incidence data. The best results were displayed as plots of estimates and species accumulation curve against the cumulative number of species. These plots were used to visually assess the performance of each estimator.

Results

Maximum observed species richness was 38 (Table 3.1). Estimates of S varied from 37.2 (Michaelis-Menten), to 40 (Jack1&2). The estimates agreed closely with each other (Mean=37.8; S.D.=1). Varying patchiness had no effect on the final value of S given by any of the estimators.

The species accumulation curve showed that it was approaching an asymptotic value, but was still increasing slightly (Figure 3.1; Table 3.2). The mean standard deviations (MSDs) of the estimators were decreasing indicating that they, too, were approaching asymptotic values. Lowest MSDs were obtained for the Cole, ACE and Chao1 estimators. MMMean and MMRuns had the steepest approach to the asymptote. Both however underestimated S. ICE and MMRuns showed a tendency to produce a spike in the estimate at very low sample numbers. Chao2 also showed a steep approach to the asymptote, however its curve was the most unstable as indicated by its having the highest MSD shown in Table 3.2. MSDs were generally low, however. Bootstrap and Cole, MMMeans and MMRuns, Jack1 and Jack2, and ACE and ICE formed pairs of curves that were similar to each other (Figure 3.1).

Table 3.1. Observed and estimated species richness of freshwater fishes of Trinidad and Tobago.

Estimator	Species richness
Observed	38.0
ACE	38.8
ICE	39.3
Chao1	38.3
Chao2	39.0
Jack1	40.0
Jack2	40.0
Bootstrap	39.1
MMRuns	37.2
MMMeans	37.3
Cole	38.0
Mean	38.7
S.D.	1.0

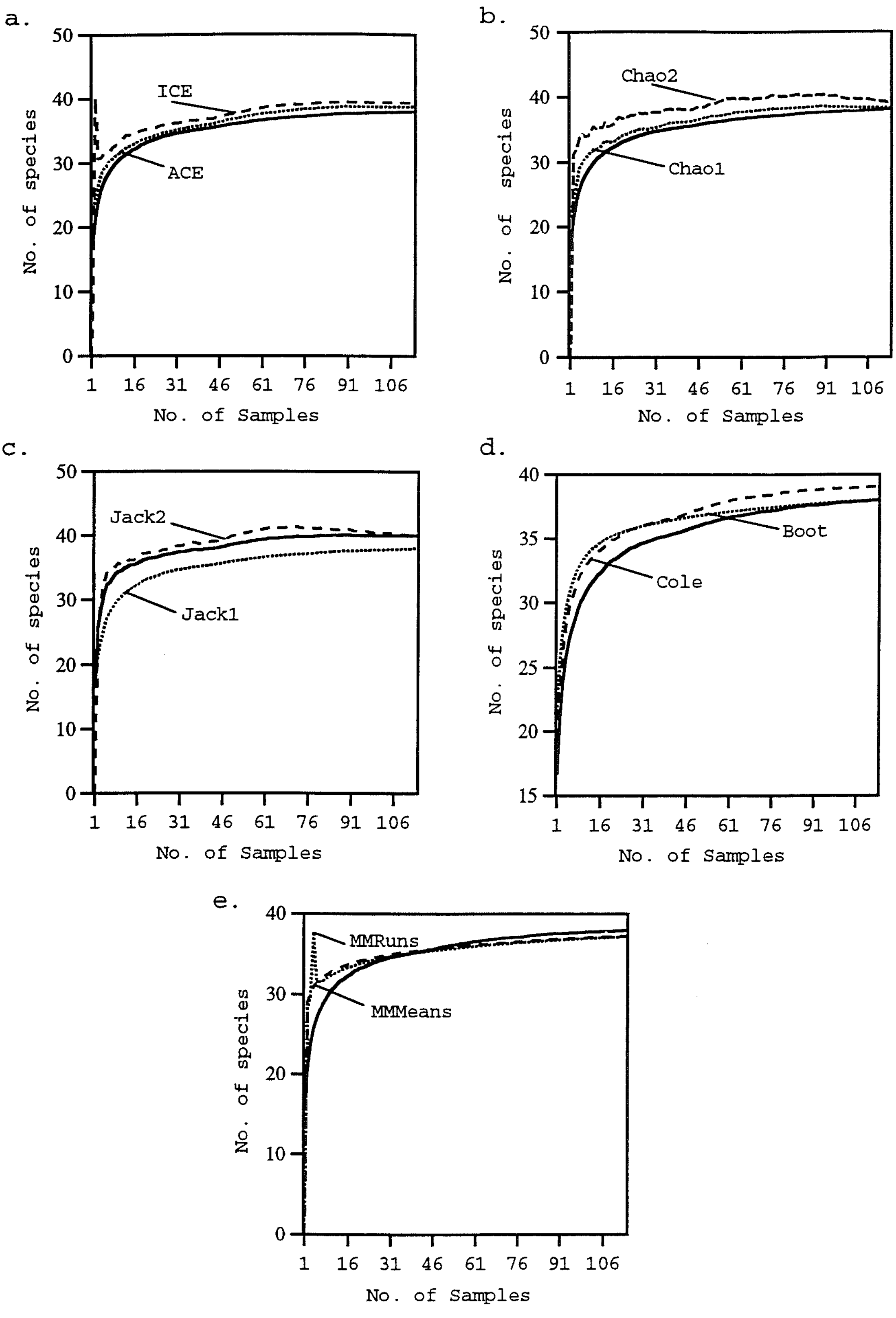


Figure 3.1. Species richness estimates for Trinidad and Tobago freshwater fishes: a. ACE and ICE; b. Chao1 and Chao2; c. Jack1 and Jack2; d. Cole and Bootstrap; e. MMMean and MMRuns. The solid line in each panel is the species accumulation curve

Table 3.2. Observed and estimated species richness of freshwater fishes of Trinidad and Tobago at six sample sizes (mean standard deviations are given in brackets).

Richness Estimator	Number of samples					
	20	40	60	80	100	114
Sobs	33.3	35.28	36.6	37.36	37.78	38
	(1.2)	*(1.12)*	*(0.89)*	*(0.72)*	*(0.42)*	*(0)*
ACE	33.89	35.86	37.55	38.47	38.71	38.76
	(1.42)	*(1.52)*	*(1.49)*	*(1.4)*	*(0.92)*	
ICE	35.22	36.71	38.49	39.26	39.34	39.3
	(2.14)	*(1.89)*	*(1.95)*	*(1.58)*	*(1.03)*	*(0)*
Chao1	34.21	36.02	37.68	38.31	38.34	38.25
	(1.69)	*(1.31)*	*(1.86)*	*(1.75)*	*(1.27)*	*(0.73)*
Chao2	36.91	38.03	39.7	40.4	39.68	39
	(5)	*(4.25)*	*(4.84)*	*(4.69)*	*(3.17)*	*(1.87)*
Jack1	36.45	37.83	39.44	40.06	40.04	39.98
	(1.66)	*(1.49)*	*(1.6)*	*(1.58)*	*(1.46)*	*(1.4)*
Jack2	37.34	38.89	41.01	41.22	40.43	40
Bootstrap	34.90	36.53	37.89	38.61	38.91	39.05
MMRuns	33.86	35.24	35.99	36.56	36.98	37.2
MMMeans	34.21	35.46	36.16	36.70	37.09	37.30
Cole	35.19	36.41	37.07	37.52	37.85	38
	(1.04)	*(0.9)*	*(0.78)*	*(0.61)*	*(0.37)*	*(0)*

Discussion

The estimates of total species richness (S) were very similar to each other, and indicated that the total number of freshwater fish in Trinidad and Tobago was about 39. The close agreement suggests strongly that the results are accurate (Coddington *et al.* 1991) and that these methods are well suited for use with this dataset.

Non-parametric methods, for example Jack1&2, gave slightly higher estimates than the Michaelis-Menten methods. In general, the results were similar to the observed species richness recorded in Trinidad from surveys carried out since the 1950s (see Chapter 5).

MMRuns and MMMean both underestimated S. Chazdon *et al.* (in press) also reported a similar negative bias in the estimation of S by a Michaelis-Menton estimator in an older version of EstimateS, however they did not offer any explanation for this observation. Keating & Quinn (1998) showed that the Michaelis-Menton model was not robust to differences in community structure and suggested that their results indicated that the model assumed a highly even community structure. They further concluded that the model would usually yield poor estimates of S and recommended caution in its use.

The methods were very similar in performance in that they had all reached over 87 percent of the final estimate after only 20 samples, and variances in the estimates declined sharply thereafter. In fact, the performance, in terms of the rapid approach to the asymptote, is better than reported in some studies (for example Colwell & Coddington (1994); Chazdon *et al.* (in press)). Colwell & Coddington (1994) give some insight into the reason for the rapid climb of some of the estimates. According to Colwell and Coddington, Jack1&2 and Chao2 estimators should correlate closely with sample size until half, or the square root of twice, the total fauna is reached. It can be seen from the species accumulation curve (Figure 3.1) that these values are attained by the addition of the second sample. The steep climb of the species accumulation curve may also indicate that a large proportion of the species are widely distributed throughout the islands. After about 35 samples had been added to the analyses, most estimators had arrived at within 95% of the final estimate of species richness. This value could be used as a minimum for smaller-scaled studies requiring estimates of S.

Although the performances of the estimators were very similar, it was possible to select Chao2 and Jack2 as the better ones based on my study. Colwell & Coddington (1994) also recommended these two estimators, but suggested that they were best suited for small numbers of samples. Other estimators have been recommended as well. Chazdon *et al.* (in press), for example, recommended ICE for sites with high species richness. Incidence-based methods gave slightly higher estimates of total species richness than their abundance-based counterparts (ICE vs ACE, and Chao2 vs Chao1, respectively). This implies that fishes have a very patchy distribution and few species are found in extremely low numbers. Comparison of the numbers of singletons and doubletons, as well as uniques and duplicates support this. There were 3.5 and 3.16 singletons and doubletons, as compared to 16.77 and 11.9 uniques and duplicates. Distribution patterns of the fish will be further discussed in Chapter 4.

In conclusion, the models provided by EstimateS seem to be good estimators of S for my data. The close agreement between total observed species richness and the estimates of S implies a good coverage of the freshwater fishes by my study. The results also indicate that a minimum of about 35 samples are required for a good estimate of species richness. The suitability of these methods for estimating tropical fish diversity has implications for use on a wider scale, for instance, future estimation of diversity in the Amazon.

CHAPTER 4. Spatial patterns

INTRODUCTION

Evidence gained over the years has led to a single conclusion concerning the zoogeography of freshwater fishes in Trinidad and Tobago. The theory was first stated by Price (1955) and Boeseman (1960), but was later refined by Kenny (1995). All three authors, (Price 1955; Boeseman 1960 and Kenny 1995), believed freshwater fish colonised the islands from two sources: the Antillean island chain to the north, and the South American mainland to the south (Figure 1.1). It is estimated that during the last glaciation, some 12,000 years ago, the sea surface was 100 to 150m below its current level (Barlett & Barghoorn 1973; Campbell 1982). At that time, Trinidad was part of the South American continent. Kenny (1995) provides evidence that the separation of Trinidad from the mainland occurred as recently as 1600 years ago. Before the separation, a land bridge located at the extreme end of the southwestern peninsula of Trinidad (Figure 4.1), facilitated the movement of fish from South America. Price (1955), Boeseman (1960) and Kenny (1995) believed that most of the South American fauna colonised Trinidad during the pre-separation period.

Essentially, the two groups of fish remain geographically separated on the islands. Antillean fishes are found in streams draining the northern side, and eastern and western extremities of the Northern Range, and in Tobago. South American fishes occupy the rest of Trinidad. Both Price (1955) and Boeseman (1960) noted the restricted distributions of some fishes either just south of the Northern Range, or on the southwestern peninsula. Price (1955) surmised that the former could have been either a relict distribution pattern that had existed while Trinidad was still part of the mainland, or due to chance

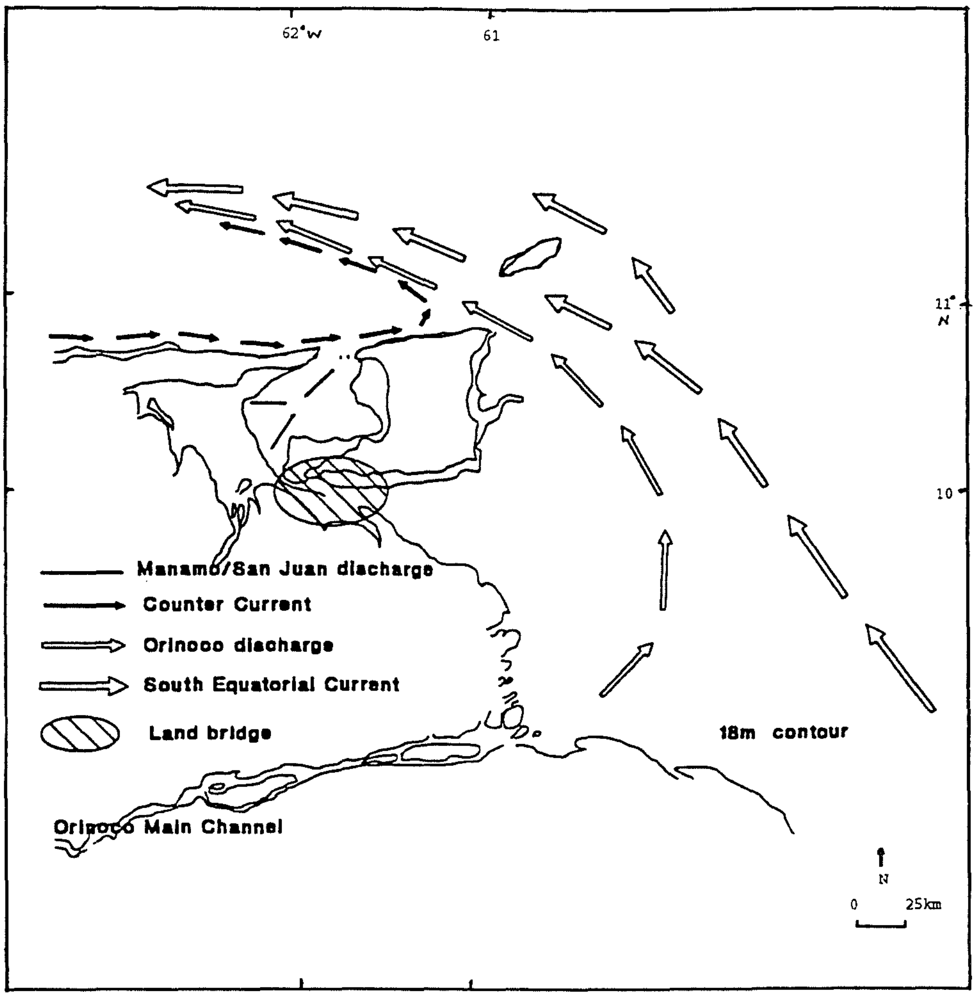


Figure 4.1. Map of Trinidad and the northeastern coast of Venezuela showing the presumed land bridge evident at the 18m contour. Source: Kenny (1995).

colonisation of only these streams. Kenny (1995) believed that these fishes belonged to the relict South American fauna, and that their distributions on the island have been receding because of habitat degradation or competition from exotic species. They therefore represented unstable populations at risk of local extinction. The fish distributed only on the southwestern peninsula were believed to be recent colonists from South America (Price 1955; Boeseman 1960 and Kenny 1995). Kenny (1995) divided the South American fishes into three zoogeographic groups: Stable and Unstable Relict, and Colonising. The Stable Relict group represented the bulk of the South American fauna that existed in the island before it was separated from the mainland. This group was distributed through most of Trinidad, south of the Northern Range. The Unstable Relict group was the name given to the Relict South American fauna whose distribution was diminishing. This group was found in a limited area just south of the Northern Range. The four zoogeographic zones are shown in Figure 4.2a.

To provide support for his proposed recent colonising fauna, Kenny (1995) examined the barriers to post-separation colonisations and concluded that they were transgressable. Trinidad is very close to South America (Figure 4.1). The intervening sea posed two problems, the physical feat of swimming the distance between the two land masses, and the ability of freshwater fishes to survive in saline water. Prevailing currents around Trinidad facilitate the movement of colonising fishes from South America to Trinidad. The major current, the south equatorial, flows along the east coast of South America in a west northwesterly direction (Figure 4.3). When it reaches the southeastern tip of Trinidad, it divides into two. One branch passes in a westerly direction through the Columbus Channel, and the other in a northerly direction along the east coast. The flow through the Columbus Channel is very strong reaching speeds of up to 7.41km/hr

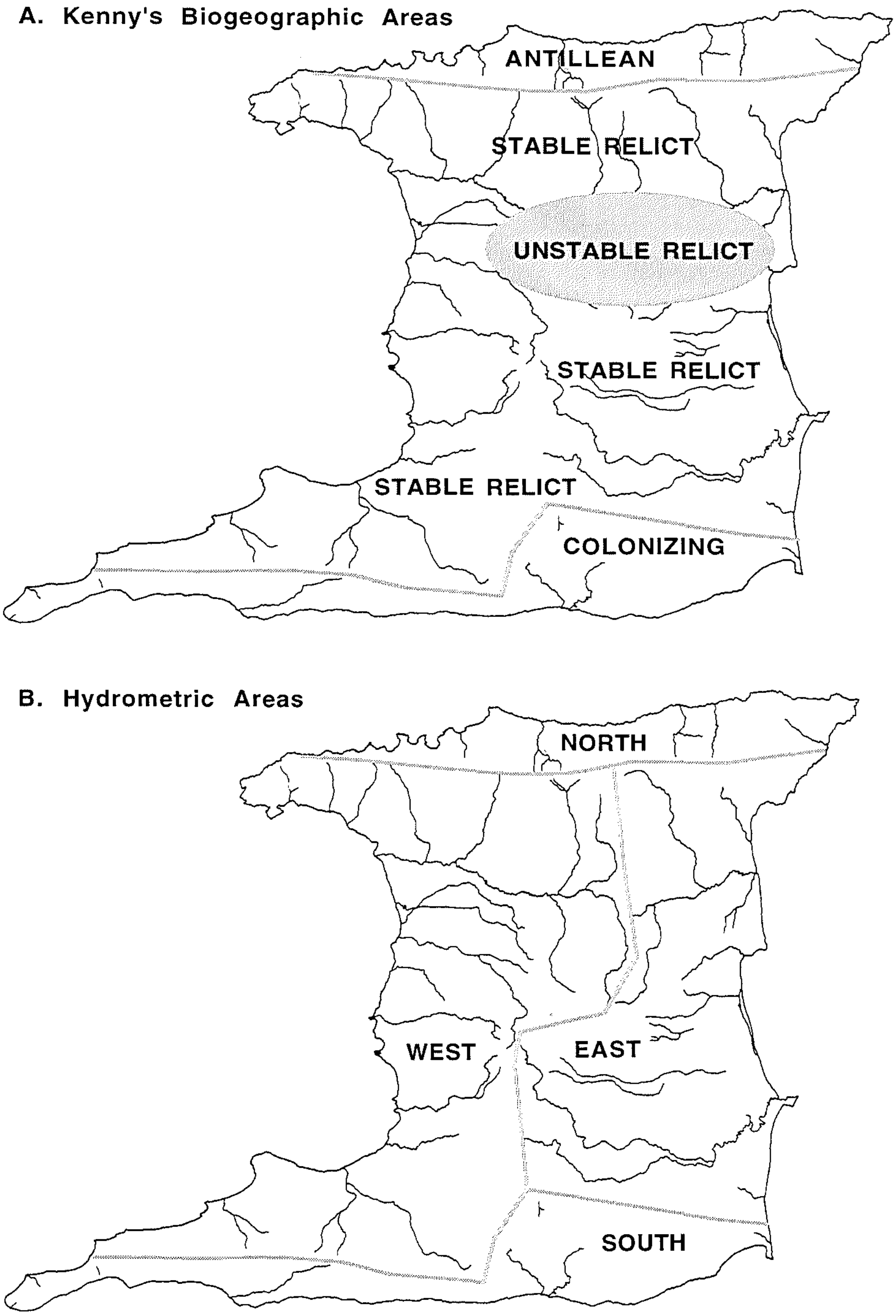


Figure 4.2 Proposed zoogeographic regions for Trinidadian freshwater fish

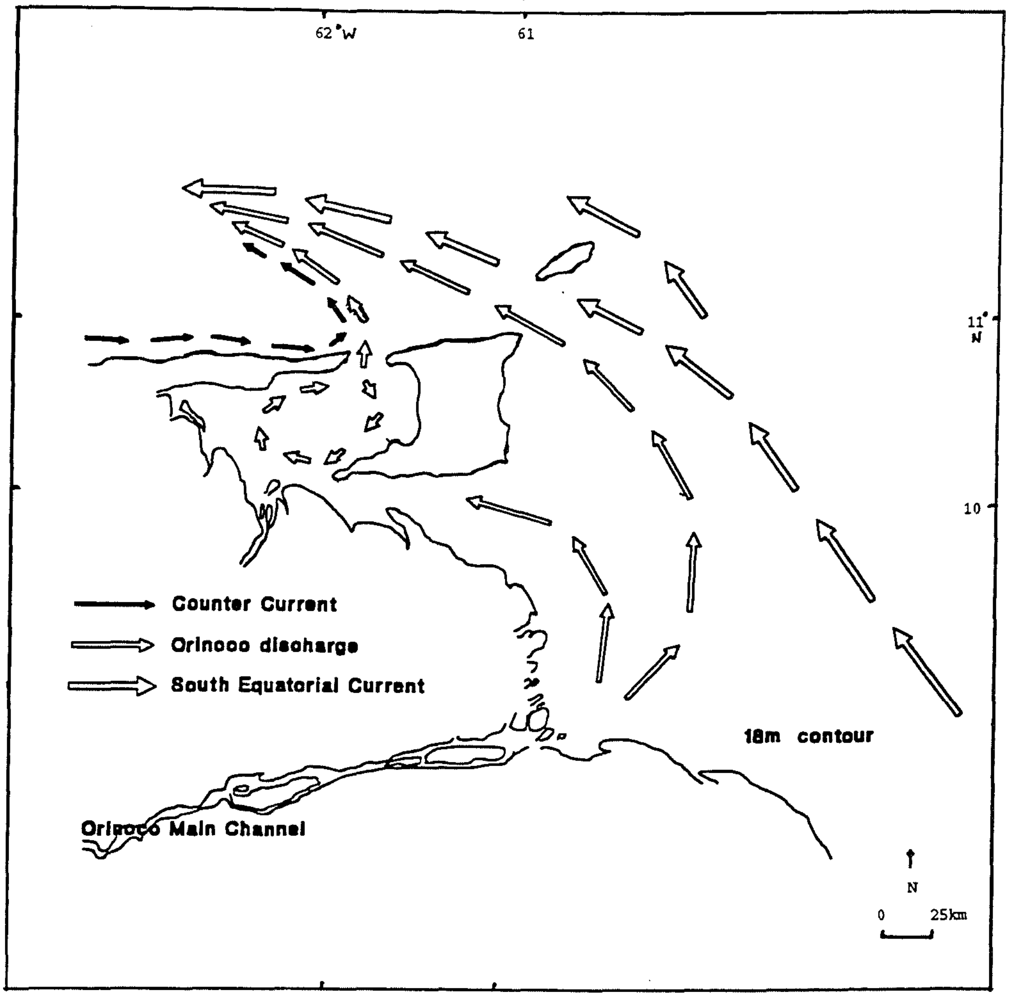


Figure 4.3. Map of Trinidad and the northeastern coast of Venezuela showing the main sea currents around Trinidad. Source: Adapted from Kenny (1995).

at times. In addition, the distance the fish need to travel is relatively short. Trinidad is only 11.3 km from Venezuela. When distance, current speed and direction are considered, it can be expected that colonisation events will occur more frequently along the south coast rather than the East Coast. If the location on the mainland of the Rio Macareo to the east is also considered, then there is an increased chance that the colonists will make landfall on the southwestern peninsula.

The other barrier is the physiological ability of freshwater fishes to survive in the sea. During the rainy season, when freshwater discharges are highest, salinities of surface waters drop to between five and 15 parts per thousand (ppt) in the Columbus Channel to the south of Trinidad (Gade 1961) (Figure 4.4). The lower end of this range is realised on the southwestern peninsula, which is close to the points of discharge of two river systems, the Rio Macareo and the Rio Pedernales. On the east coast, surface salinity is less affected by freshwater discharge. Here, salinity may fall to below 20 ppt. Preliminary evidence suggests that some of the recent colonising caracoids have salinity tolerances of up to 12 ppt (Clarke unpubl. data). These fish would therefore be able to survive the low salinities experienced in the Columbus Channel and on the east coast during the rainy season.

Apart from zoogeographic spatial patterns, fish also show patterns of distribution within individual streams. Species diversity of freshwater fish communities is believed to be related to habitat diversity (Gorman & Karr 1978; Guégan *et al.* 1998), or environmental factors (Sheldon 1968; Tonn & Magnuson 1982; Pont *et al.* 1995). However as a general rule, species diversity in rivers increases with distance from the headwaters, usually as a result of the addition of species downstream rather than the replacement of already existing ones (Sheldon 1968).

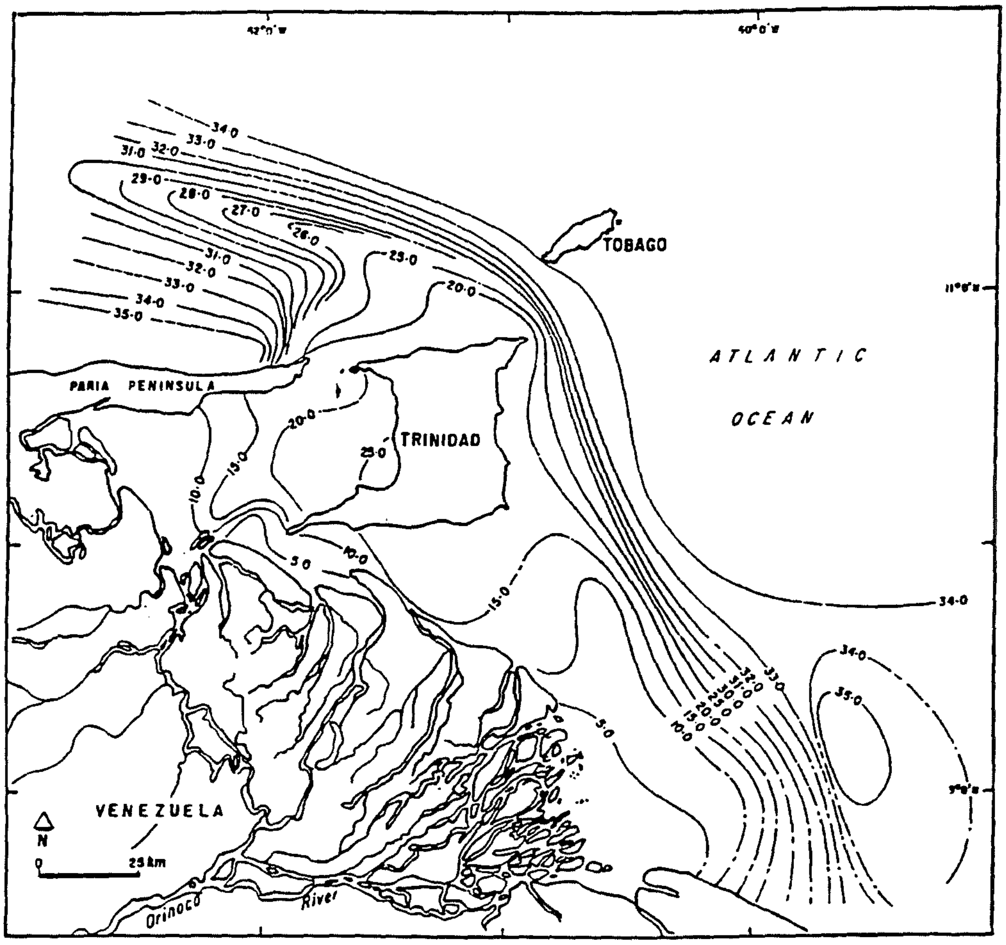


Figure 4.4. Map of Trinidad and the northeastern coast of Venezuela showing wet season coastal surface water salinities (ppt). Source Kenny (1995) redrawn from Gade (1961).

Even though anecdotal evidence has been provided to support Kenny's theory, it has never been formally tested. The aim of this chapter, therefore, is to examine the geographic distribution of fishes in Trinidad. Longitudinal trends in diversity in streams will also be examined

METHODS

Kenny's zoogeographic theory was tested against another plausible theory based on hydrometric regions. If the preceding arguments for the ability of fish to overcome possible barriers in reaching Trinidad are considered, it will be seen that an alternate zoogeographic pattern of fish distributions could be possible for Trinidad. It has already been stated that it is very likely that fish have colonised the streams along the north coast of Trinidad from the Antillean islands to the north. In addition, recent colonisations are very possible along the south and east coasts. Since the chance of colonisation is greater along the south than along the east coast, it is possible that the species colonising either coast will differ. Rivers in Trinidad can therefore be grouped into four hydrometric areas that coincide with the four coasts of the island (as used by Kenny 1995) in his species distribution maps) (Figure 4.2b). If movement of fish between hydrometric areas is limited, they can act as zoogeographic areas.

When the zoogeographic areas of the two theories are compared, it will be seen that the north and south coast areas are the same. The difference between the theories therefore lies in the manner of division of the central region into two zoogeographic areas. According to Kenny's theory, this region is divided into the Stable and Unstable Relict Faunal areas. In contrast, in the Hydrometric Area theory, the same region is divided into East and West Coast faunal areas.

The two theories on the zoogeography of Trinidad will be tested using several statistical methods to analyse distributional data collected in the present survey. Additionally, longitudinal trends in diversity along stream lengths will also be examined. It is predicted that the data will show that the zoogeographic zones described by Kenny (1995) are valid, and that species richness increases downstream.

The data

The analyses required information on the distribution of all the freshwater fishes found in Trinidad and Tobago. For this purpose, incidence, rather than abundance, data were used. Unusual sites that may have introduced biases were omitted from the analyses. These were estuarine, polluted or inadequately sampled sites. In addition, for sites that had been visited more than once (Figure 2.3), the data were combined so that there was only one entry per site in the database. Upstream and downstream sites were analysed separately because the downstream increase in species richness within a single stream may bias the results.

Two versions of the database were created, one for each of the two hypotheses to be tested. For each of these databases, the sites were grouped by zoogeographic area, for example, north, south, east and west coast hydrometric areas. In addition, mountainous sites were separated from lowland sites for those areas with a sufficiently large numbers of sites.

The boundary of the Unstable Relict area was determined by using the distribution of five species of fish with geographic ranges restricted to the area just south of the Northern Range. Some of these were fishes whose restricted distributions had drawn the attention of Price (1955) and Boeseman (1960), and that prompted Kenny (1995) to put forward the theory of the Unstable Relict fauna. Others were fish whose ranges were reduced since the 1980s survey (Kenny 1995) indicating a decline on the island. The five species were *Gymnotus carapo, Steindachnerina argentea, Hemibrycon taeniurus, Odontostilbe pulcher* and *Hemigrammus unilineatus.* The boundary of the area was placed so that all sites with at least three of these species were included as part of the Unstable Relict fauna.

A river water quality index (WQI) was developed using parameters measured in the field (see Chapter 6 for details). The WQI was used to distinguish between polluted and non-polluted sites. Eight water quality parameters that could affect fish survival, and that gave the best indications of polluted water quality were used: biochemical oxygen demand (BOD), ammonia (NH3), total phosphorus (P), pH, copper (Cu), zinc (Zn) and oil & grease. A 3-tiered rating system (see Chapter 6, Table 1) was used to assign points to each site for these criteria. The product of the points was used as the water quality index (WQI). Sites with a WQI of greater than 108 were considered to be polluted and were omitted from the analyses.

<u>Data analysis</u>- *Is Kenny's zoogeographic theory a better description of the zoogeography of Trinidad's freshwater fishes than the hydrometric area theory?*
Three methods were used to test this.

Complementarity

The first analytical method chosen was based on the assumption that the fauna at sites within a single zoogeographic area should be similar to each other. Complementarity between all possible pairs of sites within each zoogeographic area was calculated. The complementarity of two biotas has been defined as the "proportion of all species in the two sites that occurs in only one or the other of them" (Colwell & Coddington 1994,

p. 112). The complementarity (C) of two sites, j and k, can be calculated from the following equation

$C_{jk} = (U_{jk})/(S_{jk})$

Where U_{jk} is the number of species not shared by the two sites, and S_{jk}, the total species richness of the two sites.

$U_{jk} = S_j+S_k-2V_{jk}$,
$S_{jk} = S_j+S_k-V_{jk}$,

where S_j and S_k are the species richness of the two sites, and V_{jk} is the number of species in common between them. C therefore varies from zero when the species composition of the two sites are exactly alike, to unity when they are completely dissimilar. C is also known as the Marczewski-Steinhaus (M-S) distance (Holgate 1969; Pielou 1984). It is the complement of the widely used Jaccard Index (Colwell & Coddington 1994).

The incidence matrix for each zoogeographic region was imported into the EstimateS freeware package (Colwell 1997) and analysed using the shared species option. The output matrix included the values of V and S for all possible pairs of sites within each region. These values were used to calculate C. The distribution of C values was plotted in histograms for each region separately. It was expected that if Kenny's theory was correct, complementarity for the Unstable Relict Area would be closer to zero than that for the Stable Relict area. If the Hydrometric Area theory was correct, the complementarity for the Stable Relict Area would be skewed towards unity.

Venn diagrams

Venn diagrams were then used to look at the distribution of species among the zoogeographic areas proposed by the two theories. It was anticipated that the diagrams would show that the major separation of the fauna of Trinidad was between the Antillean and South American groups. Also, that the central region of Trinidad can be divided into two zones described by one of the two zoogeographic theories. A larger overlap of species between streams of the east and west coast areas than those of the Stable and Unstable areas, would indicate that the Kenny hypothesis better describes the fauna than the hydrometric area hypothesis.

Cluster Analysis

Finally, Ward's Cluster analysis was performed on the incidence matrix, alternately using the sites and species as the cases. The data should cluster by zoogeographic regions and faunal groups in the two analyses respectively. Both results were displayed in the form of dendrograms.

Within-stream trends in diversity

Longitudinal trends in species diversity were examined using abundance data for selected streams. Streams chosen were those with two sites along the main river. Those streams with polluted or undersampled sites were omitted from the analyses. Shannon-Weiner (Shannon & Weiner 1949) and Berger-Parker (Berger & Parker 1970) diversity indices were chosen based on recommendations by Magurran (1988). They were calculated using the Alpha Diversity software (Pisces Conservation Ltd. 1997). The two indices are described by the following equations:

Berger Parker Index: $d = N_{max}/N$

Shannon index: $H = -\sum[(n_i/N)\ln(n_i/N)]$

where

N_{max} = the number of individuals in the most abundant species

N = total number of individuals of all species combined

n_i = number of individuals in the i^{th} species

Differences between the diversity of paired sites in a stream was tested using paired t-tests. The null hypothesis for these tests was that there was no difference in these measures between upstream and downstream sites.

RESULTS

Complementarity - predict greater similarity of fauna in Unstable Relict area than Stable Relict area.

Complementarity was generally similar for the various zoogeographic areas proposed by both theories (Figure 4.5). There was a wide spread of values from about 25% to about 95%, with modes of either 55 to 65%. The histogram for the Unstable Relict fauna showed lower complementarity values (zero to 65%) as compared to the other zoogeographic areas. Complementarity for this area was also lower than that for the Stable Relict area (modes at 35 and 55% respectively). This indicates that the Unstable Relict area has a more homogenous fauna than the other zoogeographic areas. The Unstable Relict area can therefore be regarded as a distinct zoogeographic area as predicted by Kenny (1995).

Venn diagrams - predict a major division of the fauna into South American and Antillean groups; overlap between east and west coast faunas greater than between those of the Stable and Unstable Relict areas.

Two Venn diagrams were presented for each zoogeographic theory. This was to allow comparisons between zoogeographic areas that appeared opposite each other in one diagram. The Venn diagrams for the two theories showed that the greatest division in the fauna was between the fauna of the northern slopes of the Northern Range and the rest of Trinidad. There were only four species shared between these two areas (Figure 4.6). These four species, *Poecilia reticulata, Rivulus hartii, Aequidens pulcher* and *Astyanax bimaculatus,* were all South American in origin.

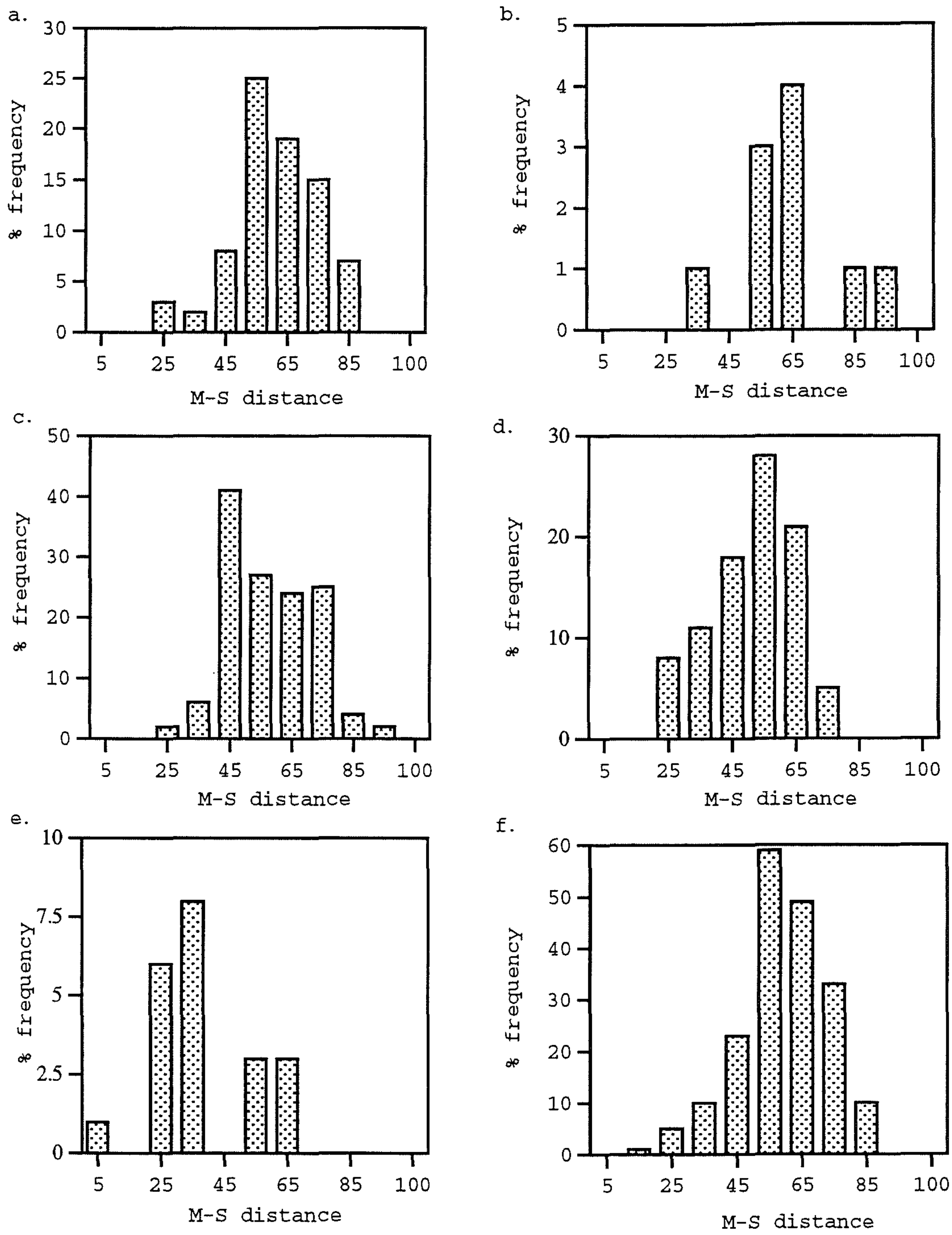


Figure 4.5. Complementarity of riverine fish faunas among two stream types and four zoogeographic areas in Trinidad: a. western mountainous, b. eastern mountainous, c. western lowland, d. eastern lowland, d. Unstable relict, and e. Stable relict.

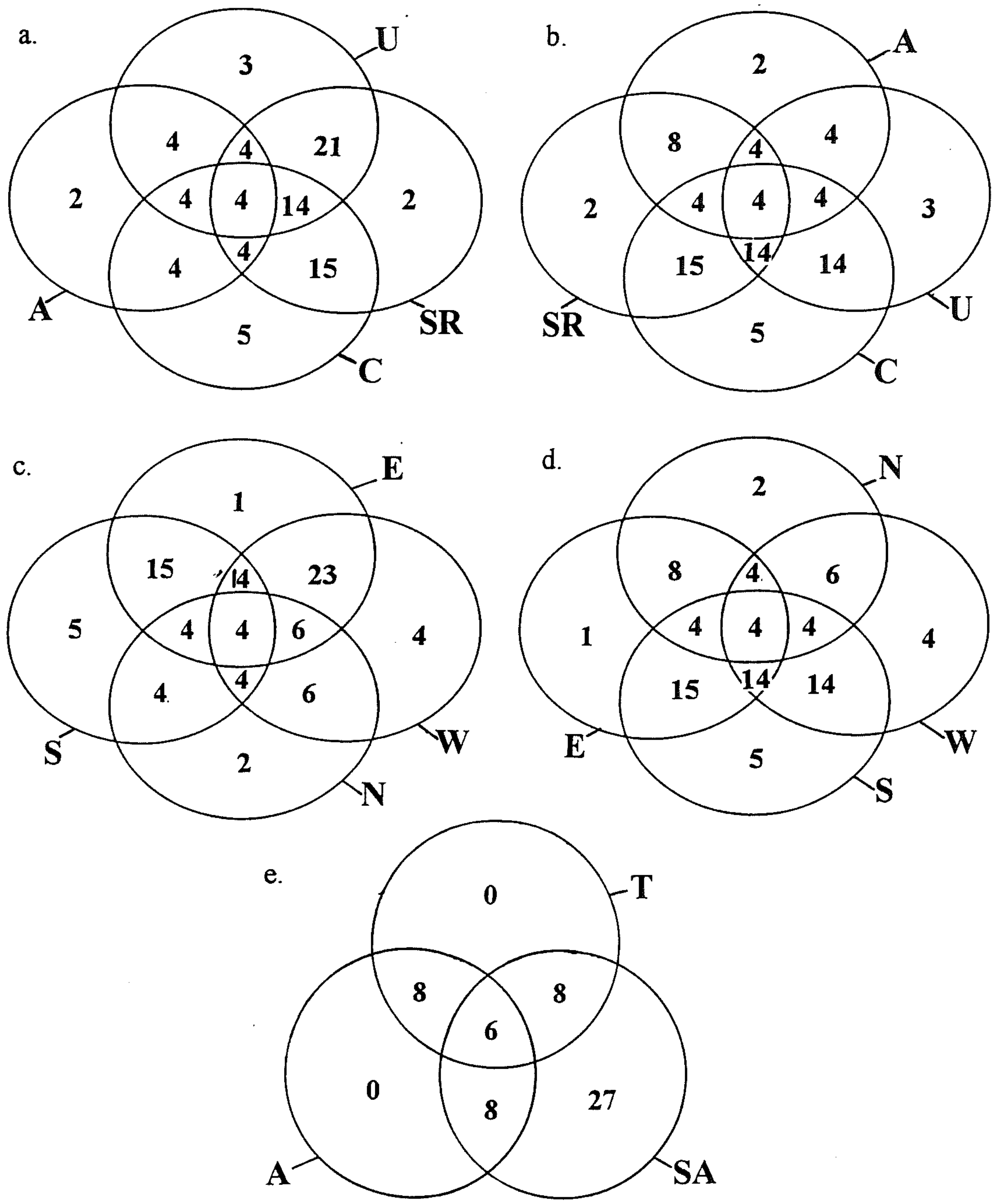


Figure 4.6 Venn diagrams showing the distribution of fish species between zoogeographic areas of Trinidad and Tobago: a,b. Kenny's hypothesis; c,d. the Hydrometric area hypothesis; and e. between Trinidad and Tobago. Zoogeographic areas are: Antillean (A); Stable Relict (RS); Unstable Relict (U); Colonising (C); north (N); south (S); east (E); west (W) and Tobago (T).

There was also considerable overlap between east and western coast faunas with 23 of a total of 32 species (72%) shared between them, and four and five species, respectively, unique to either area. There was a slightly smaller overlap of species between the Unstable and Stable Relict areas with 21 species shared of the total of 32 (66%), and three and eight species respectively unique to either area. The south coast or colonising area and the west coast at five each, had the highest number of unique species of all the areas. The east coast, with only one unique species, had the lowest number. There are two South American and one introduced fishes in Tobago: *Poecilia reticulata, Rivulus hartii* and *Oreochromis mossambicus* respectively.

Cluster analysis - predict that sites and species belonging to the Unstable Relict area will form distinct clusters.
The Euclidean distances for the sites clustered by their species composition are shown in the dendrogram in Figure 4.7. When these clusters are plotted on a distribution map of Trinidad and Tobago (Figure 4.8) it can be seen that the Antillean fauna forms a separate group located on the north coast of Trinidad as well as in Tobago. This group can be further subdivided into sites with only Antillean fauna, and those with Antillean and South American or introduced species. This second group occurs in southwest Tobago and northeast Trinidad. Another important group of sites that separate out as a cluster coincides with the location of the Unstable Relict fauna. Along the south coast, the sites in the southwest form a separate cluster, with the rest of the south coast, clustering with the Stable Relict fauna.

Clustering of species by distribution showed a similar pattern (Figure 4.9). The Antillean fauna, gobiids, eleotrids, *Anguilla* and *Agonostomus*, formed a distinct group. Additionally, three of the five species with distributions limited to the region of the Unstable Relict

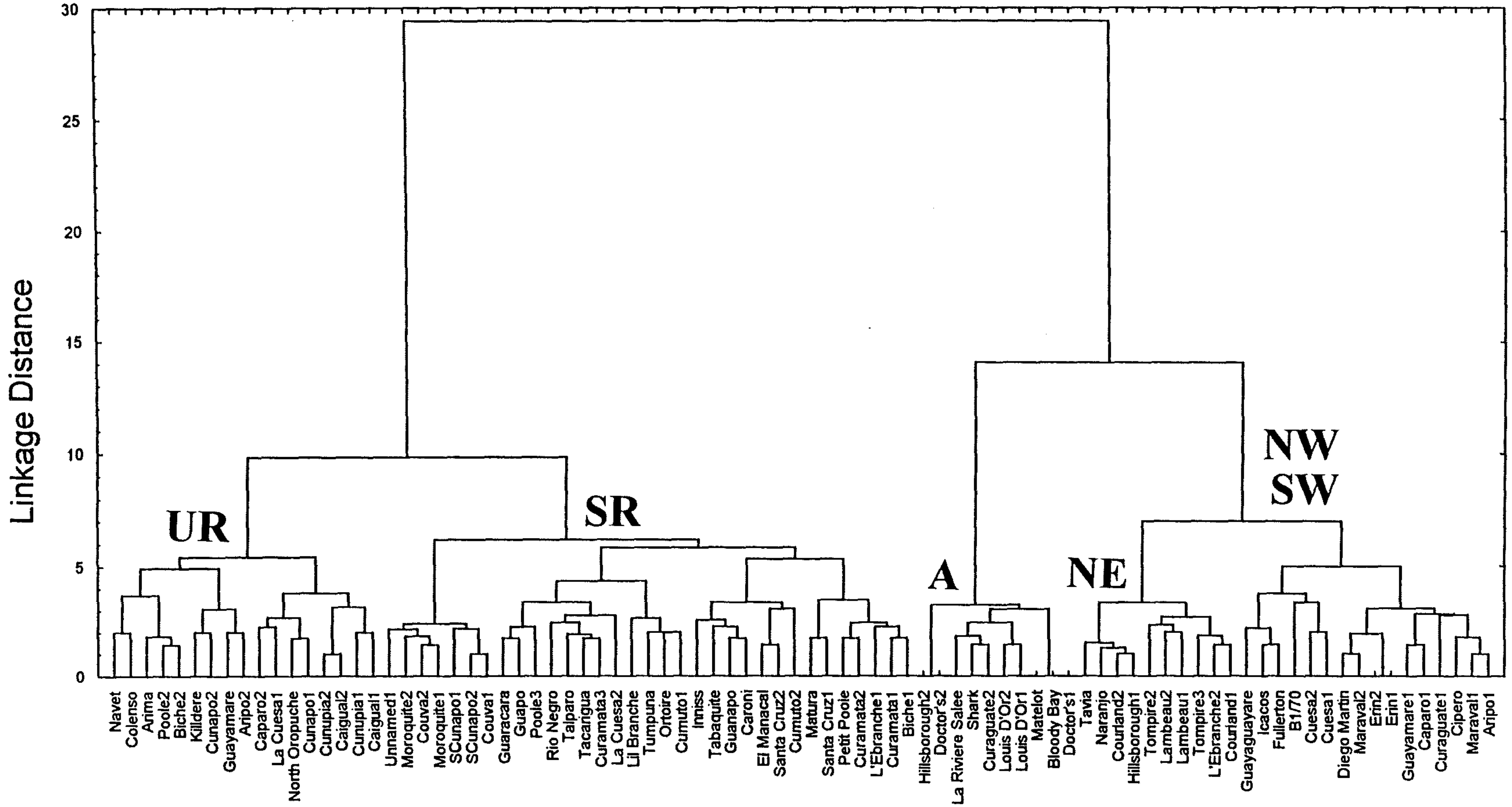


Figure 4.7 Ward's cluster analysis of sampling site similarity based on species assemblage: Stable Relict (**SR**); Unstable Relict (**UR**); Antillean (**A**); northeastern peninsula (**NE**); southwestern peninsula(**SW**) and northwestern peninsula(**NW**).

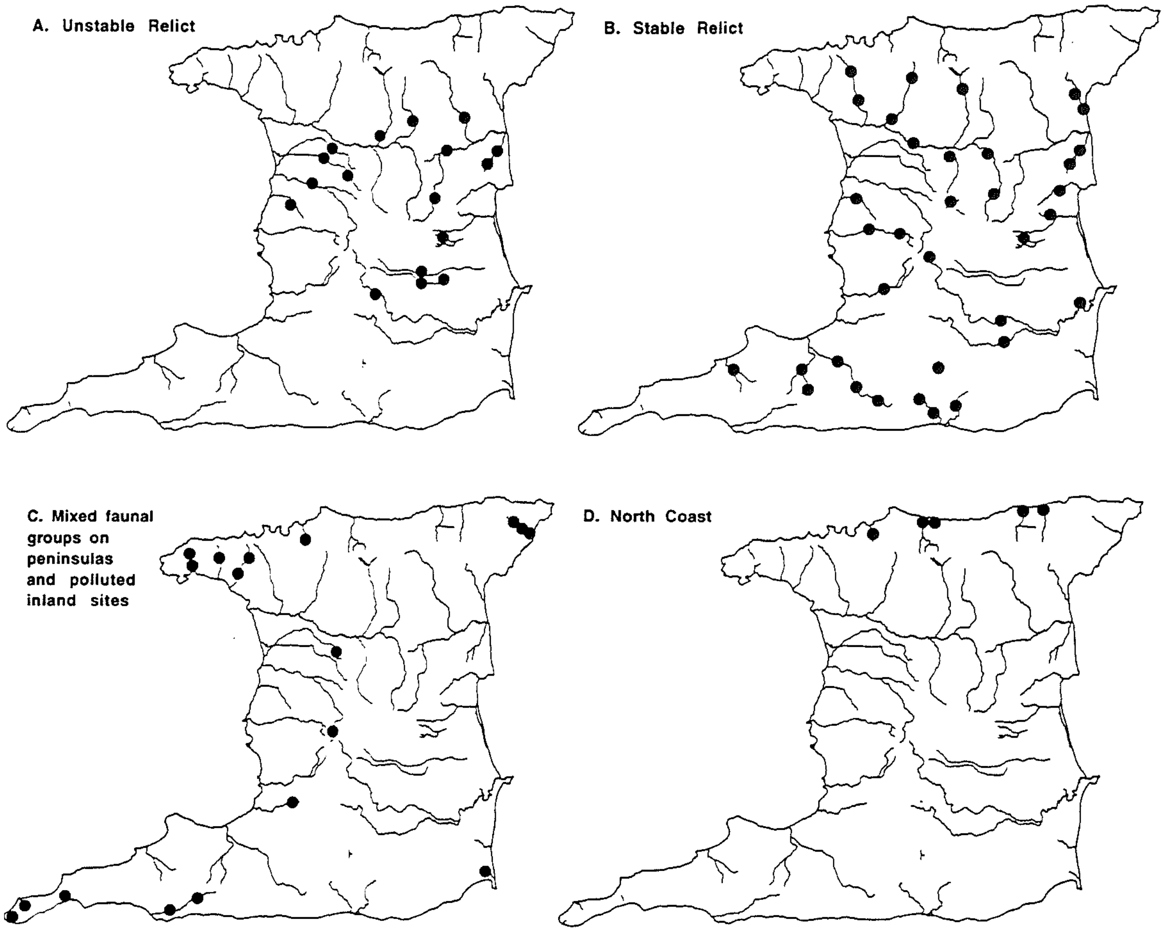


Figure 4.8 Geographic distribution of faunal groupings as indicated by cluster analysis: a. Unstable Relict; b. Stable Relict; c. Mixed Antillean and South American Faunas (peninsulas) and polluted inland sites; and d. Antillean

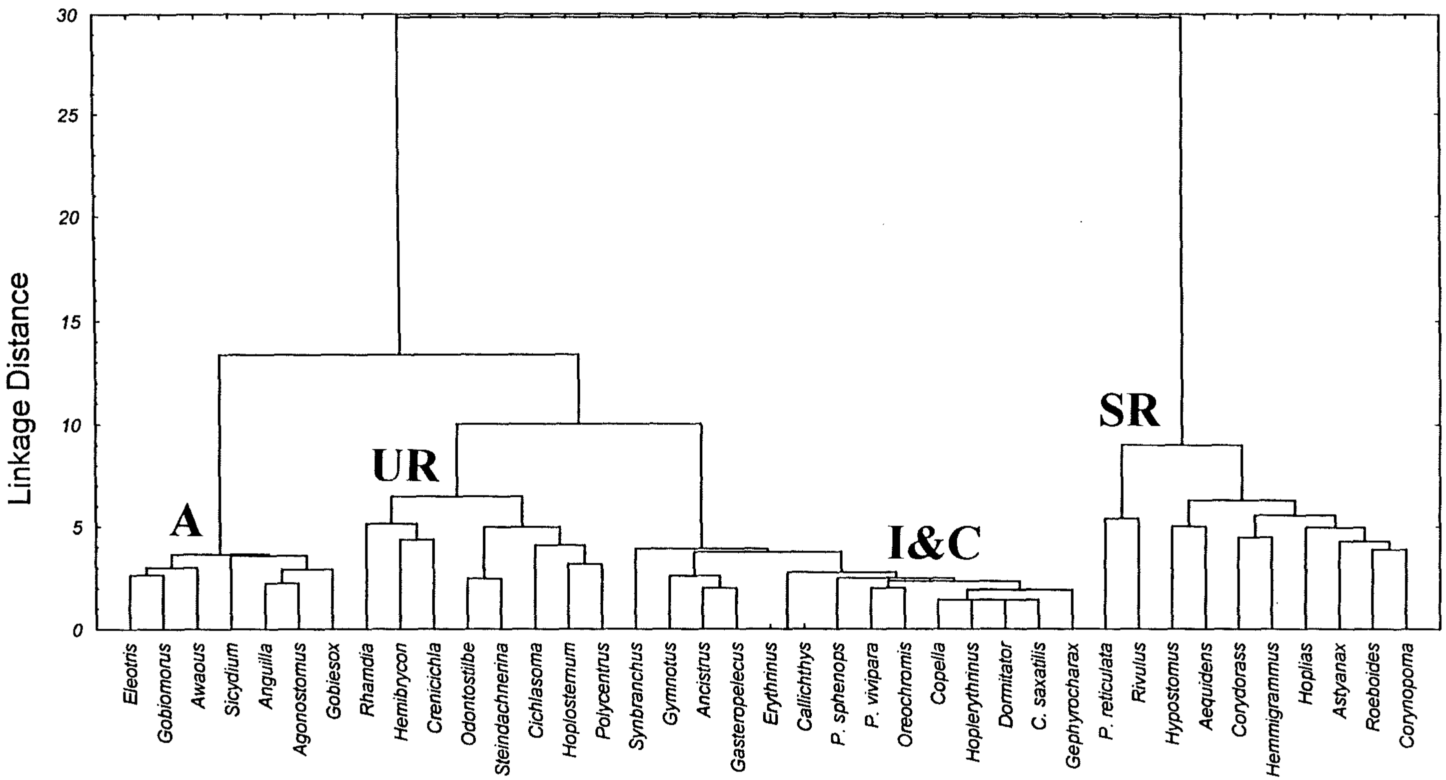


Figure 4.9 Ward's cluster analysis of species based on their distributions: Antillean (**A**); Stable Relict (**SR**); Unstable Relict (**UR**); introduced and colonising (**I&C**).

fauna, *Odontostilbe pulcher, Hemibrycon taeniurus,* and *Steindachnerina argentea,* also clustered closely together, as did widely distributed species such as *Poecilia reticulata.*

Within-stream trends in diversity - predict species diversity increases with distance from headwaters

Mean species richness and Shannon-Weiner index increased, whereas mean Berger-Parker index decreased downstream. However, these differences were not statistically significant (Table 4.1). If their distributions are examined, Trinidadian fishes can be divided into two groups. Most species, for example *Poecilia reticulata, Rivulus hartii, Hypostomus robinii* and *Rhamdia quelen,* were found in both upper and lower reaches of streams throughout their range. A few however, like *Ancistrus cirrhosus* and *Polycentrus schomburgkii* were found mainly in the lower parts of streams (see maps in Appendix II).

Table 4.1: Results of paired t-tests comparing species diversity measures between upstream and downstream sites (df=16).

Diversity measure	Mean upstream	Mean downstream	T	p
Species richness	6	7.24	1.358	0.193
Shannon-Weiner	1.122	1.263	0.826	0.421
Berger-Parker	0.563	0.52	0.514	0.614

DISCUSSION

One of the aims of zoogeography is to identify patterns in the distribution of organisms, and to relate these distributions to historical and/or evolutionary events. In the tropics where biodiversity is high, and the barriers to dispersal may be variously effective across the spectrum of existing species, zoogeography becomes even more challenging for scientists. Human interferences, such as the transplantation of species within and between geographic areas, across natural barriers to movement, can confuse otherwise obvious patterns of distribution.

The fish fauna of Trinidad and Tobago is diverse and has a heterogeneous distribution, even within a single zoogeographic area. Nevertheless, it was possible to discern patterns in the distribution of species or groups of species. The results given above provide convincing evidence for a major separation of the fauna into two zoogeographic regions on either side of the Northern Range. This division was evident in every analysis carried out on the data. Judging from the scarcity of northern movement of fish across these mountains, the Northern Range was almost as efficient a barrier as the intervening sea separating the Trinidad from Tobago. A few species have been able to move southward around the edges of the Northern Range barrier. Cluster analysis of sites shows this clearly with streams on the northwestern and northeastern peninsulas of Trinidad separating out as clusters distinct from other north, west or east coast sites (Figures 4.7, 4.8). The Venn diagram (Figure 4.6) also shows a clear overlap between the species found on the north coast and those in the streams of the east and west coasts, with a greater overlap on the east coast (8 vs. 6 species).

The species that have managed to move south are *Agonostomus monticola, Eleotris pisonis* and *Sicydium punctatum* to the east, as well as *Eleotris pisonis, Awaous taiasica* and *Gobiomorus dormitor* to the west. It is not surprising that these fish have been able to move south as they are all peripheral fishes and can tolerate saline conditions. The discrepancies between the numbers of species listed here and those indicated in the Venn diagram can be accounted for by the occurrence of three South American species on the north coast.

Kenny (1995) believed that some of the northward movement of fish was probably natural. He cited the easterly flowing nearshore current flowing along the north coast, from the tip of the northwestern peninsular to Blanchisseuse, as a possible aid to this movement. Much of the northward movement across the Northern Range barrier, though, is believed to have been with human assistance. Upper Curaguate River, for instance, has a population of fish species typical of streams on the other side of the Northern Range. Species found at this site included *Astyanax bimaculatus, Poecilia reticulata, Aequidens pulcher, Rivulus hartii,* and according to local villagers, red hybrid tilapia and a loricariid. The villagers claim that an aquaculture facility nearby is responsible for some of these introductions. Human intervention was also responsible for the northward movement of tilapia, *Oreochromis mossambicus*. This fish was introduced into Trinidad in the 1960s and was recently collected in Lambeau River near Scarborough, Tobago. It had been introduced to Tobago for aquaculture by the Fisheries Division in the early 1990s.

The next major division of the data appears to be within the South American fauna, between the streams of the south coast, the so-called Colonising fauna (Kenny 1995) and the streams to the north. There are five species whose distributions in Trinidad are restricted to this area.

They are *Erythrinus erythrinus, Callichthys callichthys, Oreochromis, Dormitator maculatus* and *Gephyrocharax valencia*. *Oreochromis* is a recent human introduction that, therefore, should not be allowed to confound discussions on issues of zoogeography. The limited distribution of *Dormitator maculatus* and *Callichthys callichthys* may be due to choice of sample sites and sampling error respectively. Both species have been known to have wider distributions in Trinidad for some decades. *Dormitator maculatus* generally occurs in the lower reaches of rivers, a habitat that was avoided in the present survey. It was found in the southwestern peninsula which is a low-lying area with lotic habitats not unlike lower courses of streams. *Callichthys callichthys* on the other hand requires a special technique, cast netting (Plate 4.1), for its capture, especially where it occurs in low densities. It was reported to occur at several other sites throughout Trinidad by local villagers. This leaves two species on which to base any discussion on the uniqueness of the southern fauna, *Erythrinus erythrinus* and *Gephyrocharax valencia*. Neither of these had previously been recorded or reported from any other locality in either Trinidad or Tobago. These two species may have colonised Trinidad recently and have not yet spread very far. Thus far, the data supports both theories on the zoogeography of Trinidad and Tobago. Both theories have in common separate geographic areas along the north and south coasts.

Results of complementarity and cluster analyses indicate that there is a distinct faunal group within the central region of Trinidad. Cluster analysis of sites located this fauna just south of the Northern Range (Figure 4.8). The Unstable Relict area proposed for the complementarity analysis falls entirely within this region.

Some of the differences observed in the Venn diagrams between the Stable and Unstable faunas are caused by migration of Antillean fishes and human introductions of

Plate 4.1 Throwing a cast net is considered the most efficient means of capturing armoured catfishes.

exotic species into the Stable zoogeographic area. Five of the eight species of fish found in the Stable, but not in the Unstable zoogeographic area, are Antillean species, and one, *Poecilia sphenops,* is an introduced species. *P. vivipara*, is restricted to the lower reaches of rivers, a habitat that does not occur in the Unstable Relict zoogeographic area. The remaining species, *Hoplerythrinus unitaeniatus*, was found at a single site just outside the border proposed for the Unstable Relict area for the complementarity analyses, but within the border for the same area suggested by cluster analysis. It can therefore be argued that this species should be included with the Unstable Relict fauna.

The Venn diagrams indicate a difference between the faunas of the east and west coast drainages. However, these differences can also be explained in terms of the southward movement of Antillean fish into these areas. *Sicydium punctatum* and *Agonostomus monticola* are found only in the northeast, and *Awaous taiasica* is found only in the northwest. Introductions of exotic species have added to the differences between the two coastal faunas. Two introduced species, *Poecilia sphenops* and *Copella arnoldi* are only found in west coast drainages. That leaves two South American species, *Hoplerythrinus* and *Gasteropelecus,* that are not found in both the east and west coast drainages. They are, however, both found in the Unstable zoogeographic area.

Many studies have shown that species diversity increases downstream in rivers (Larimore et al. 1952; Sheldon 1968; Hughes & Gammon 1987). Gilliam *et al.* (1993) found a similar trend for the Guanapo River in the Northern Range. The results of the present study, however, did not show any significant longitudinal trends in species diversity in streams in Trinidad and Tobago. There are several reasons why this may be so. Hugueny & Paugy (1995) similarly found no significant relationship between species richness and distance from source in some African rivers. Hugueny and Paugy suggested that this was because their samples were obtained at the end of the upstream-downstream gradient in species richness. Alternately, if species richness fluctuates along the length of a river, then samples taken at points too close together, or at an insufficient number of points, may fail to show the overall longitudinal trend in species richness. Hughes & Gammon (1987) found this to be the case in the Willamette River in Oregon.

Another possibility is that disturbance has affected species richness in downstream sites. Most of the streams examined in the present survey were perturbed (see Chapter 6). Eleven of the 17 sites used for this test had perturbed lower reaches. Practices such as dredging of downstream portions of streams for flood control are common in Trinidad. Such physical alterations can result in losses in biodiversity (Gorman & Karr 1978; Moyle & Leidy 1992), a theme that is revisited in Chapter 6.

In conclusion, the data show that there is a major division of the fauna into two groups divided geographically by the Northern Range. The larger faunal group is further subdivided into three. One group was found in the central part of the island in an area extending from the foot hills of the Northern Range to the foothills of the southern slopes of the Central Range. Another group was located on the southwestern peninsula. The final group occupied the rest of the area to the south of the Northern Range. This distribution of zoogeographic areas is similar to that predicted by Kenny (1995) (Figure 4.2), indicating that this hypothesis is a valid interpretation of the zoogeography of freshwater fishes of Trinidad.

CHAPTER 5. Temporal patterns in species richness

Introduction

Two factors, Trinidad's proximity to the South American mainland, and the propensity of humans to alter their environment, suggest that the freshwater fish fauna of Trinidad will be a temporally dynamic one. According to MacArthur & Wilson's (1967) theory of island biogeography, the number of species present on an island is a balance between immigration from nearby land masses, and extinction from the island. Immigration is directly proportional to the distance between the island and the mainland whereas extinction is proportional to the number of species already existing on the island. As species richness approaches saturation, local extinction should equal immigration. Since Trinidad is only 13 km from South America, a high rate of immigration can be expected. Local extinction rates should indicate the degree of saturation of the island. It has been shown in Chapter 4 that the zoogeography of the island, with its Colonising and the Unstable zoogeographic zones, reflects this. Zoogeography, however, only gives a snapshot of the average distribution trends without any indication of time scale. To superimpose a time factor on these events, the historical records for the island need to be consulted.

Published historical records of fish surveys are fairly recent. The first, a report by Bennett (1831a, 1831b) of *Cichlasoma taenia* (erroneously called *Chromis taenia*), dates back only to the early part of the last century. Since then, a number of reports of varying depth and coverage have been published. The first survey of fishes was published by Leotaud (1858), however only generic names and the numbers of species contained therein were listed in most cases. In the same year, Gill (1858) published descriptions of 23 species of freshwater fishes from the "Western Portion" of Trinidad. Lutken (1874, 1875a, 1875b) next published his work on the catfishes and characins of Trinidad.

The next comprehensive paper, published by Regan (1906), brought the number of fish recorded from fresh and brackish water to 41. Ten years later, Fowler (1915) listed about 35 species of fish from fresh and brackish water. In the 1950s, Price (1955) published an annotated inventory of about 39 freshwater fishes. His collections were the basis of major papers on the freshwater fishes by Boeseman (1960, 1964). Boeseman's papers included, for 40 species of freshwater fish, identification keys, taxonomic notes and some distribution data. Boeseman's paper remained the major contemporary work on Trinidad's fish fauna for the next 35 years, until Kenny (1995) published his memoirs on the freshwater fishes of Trinidad. Kenny (1995) updated the species list giving critical reviews of earlier catalogues by Boeseman (1960) and Price (1955). He included distribution maps for individual species, and, for the first time, photographs of some of the fish.

The detail given in the last three surveys make it possible for comparisons to be made between the fauna of Trinidad over time. This chapter will, therefore, look at the rate of immigration and extinction of freshwater fishes in Trinidad. In addition, changes in the distribution of the fauna since the mid 1950s will be examined.

Methods

The species present in Trinidad over time were determined from the literature. A chronicle of all the species recorded for the island, dating back from the first published record by Bennett (1831a), was produced. It showed, for each species, the duration of its existence in Trinidad. Unless explicitly stated otherwise, it was assumed that a species' presence on the island was continuous between the dates of its first and last published records. Of the surveys reported in the literature, only the more recent ones (Price 1955; Boeseman 1960; Kenny 1995; the present study) were of sufficient geographic coverage to adequately indicate total species richness. In his report, Price (1955) pointed out recent colonists and introductions. It was therefore possible to look at species introductions to Trinidad from his survey onwards. Local extinctions occurring prior to this period, are implied by the disappearance from the historical record of species already noted on the island.

Determining changes in distribution patterns, required information on the geographic ranges of fish in Trinidad. This type of detail was available from three surveys, Price (1955), Kenny (1995) and the present study. For each species, Price (1955) either listed the drainages in which it was found, or gave the boundaries of its distribution. Site-specific incidence data were available for the surveys by Kenny (1995) and the present study. It was therefore possible to determine changes in the geographic ranges of species in Trinidad since the 1950s.

Twenty seven of the sites visited by Kenny (1995) could be paired with the same or nearby sites in the present survey. For each pair of sites, the change in species composition between the two surveys was calculated. The equation used for calculating species change was similar to that for calculating complementarity using the M-S distance as described in Chapter 4.

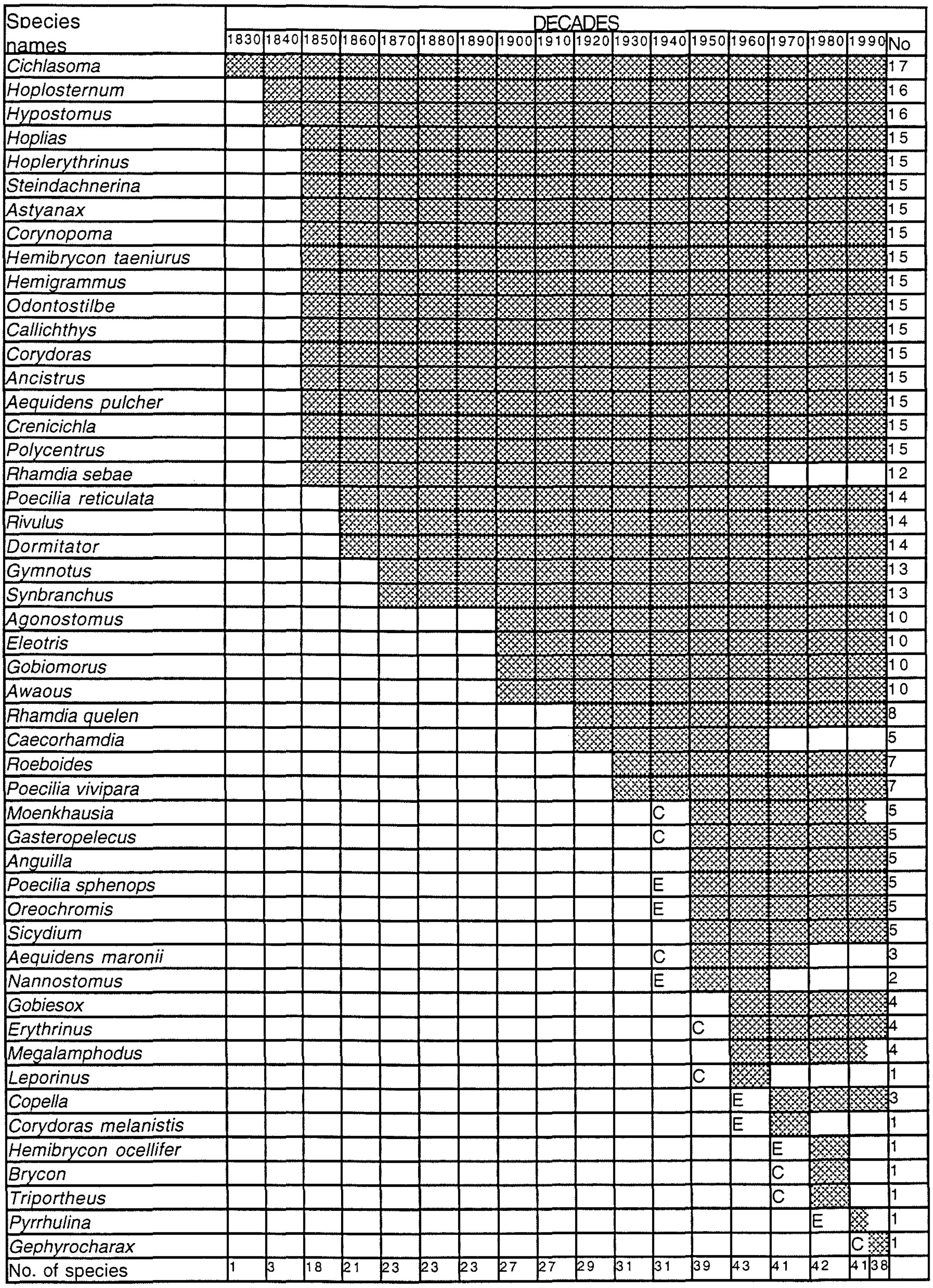
It was possible to divide the paired sites almost equally into northern and southern groups separated by the Caroni and North Oropuche drainages. Changes in species richness and composition of sites in the north and south of Trinidad, between the two surveys were compared using a 2-sample t-test and a Wilcoxon-Mann-Whitney test respectively.

RESULTS

The fish fauna of Trinidad is a dynamic one having undergone several changes in species composition during its recorded history. The Antillean fauna (see Chapter 4) appeared to be very stable in species composition, with no new colonisations occurring since Price's (1955) survey, and no known extinctions in its recorded history (Figure 5.1). The South American fauna, on the other hand, showed considerable temporal dynamism. By the turn of the century, a total of 22 mainland fishes, one of which had already gone locally extinct, had been identified in Trinidad. Another five species were added by the 1940s, without further extinctions. Over the next 40 years or so, there were 15 new additions, and 12 extinctions. Total species richness varied between 38 and 43, with the changes occurring only among the South American fauna.

A substantial portion (47%) of the new species recorded for Trinidad since the beginning of the 1950s have been exotics introduced by man. Of the seven exotic species introduced to the island since then, only three, *Poecilia sphenops, Oreochromis mossambicus,* and *Copella arnoldi*, were still

Figure 5.1. Record of fish present in Trinidad since the 1830s.



where: C = natural colonist, E = introduced exotic,

No. = no. of decades

found during the current survey. Similarly, of the eight natural colonists, only three, *Gasteropelecus sternicla, Erythrinus erythrinus* and *Gephyrocharax valencia* are still found in Trinidad.

Although the ranges of most species have remained the same since Price's (1955) survey, some had changed. Six species, *Roeboides dayi, Hemibrycon taeniurus, Ancistrus cirrhosus, Crenicichla alta, Aequidens pulcher* and *Poecilia sphenops* had range extensions (Figure 5.2). *Roeboides'* distribution had changed little between the 1950s (Price 1955), and the early 1980s (Kenny 1995), however by the present survey, it had spread from eastern drainages to the Caroni, and as far south as La Cuesa and South Oropuche Rivers. The spread of *Hemibrycon* involved a change in habitat. In Price's and Kenny's surveys, it was restricted to clear streams of the Northern Range whereas in the present study it was also found in muddy lowland streams as far south as Caparo and Ortoire Rivers. *Poecilia sphenops,* a recent introduction (Price 1955), had spread from Diego Martin River to the neighbouring Maraval River by the time of Kenny's survey. Since then, its distribution has remained unchanged.

Some species distributions, for example *Hemigrammmus unilineatus, Hoplerythrinus unitaeniatus* and *Copella arnoldi*, have become more restricted (Figure 5.3). In some cases, the species may have already had a narrow distribution. For instance, Price (1995) found *Hoplerythrinus unitaeniatus* only in the Oropuche and Nariva drainages, and Kenny (1995) only in streams along the east coast from the North Oroupuche drainage in the north to the Ortoire drainage in the south. In the present study, *Hoplerythrinus* was found in a single stream, Aripo River, the easternmost stream draining into the Caroni River. Others, *Hemigrammus unilineatus* for instance, had been widely distributed throughout the area of Trinidad south of

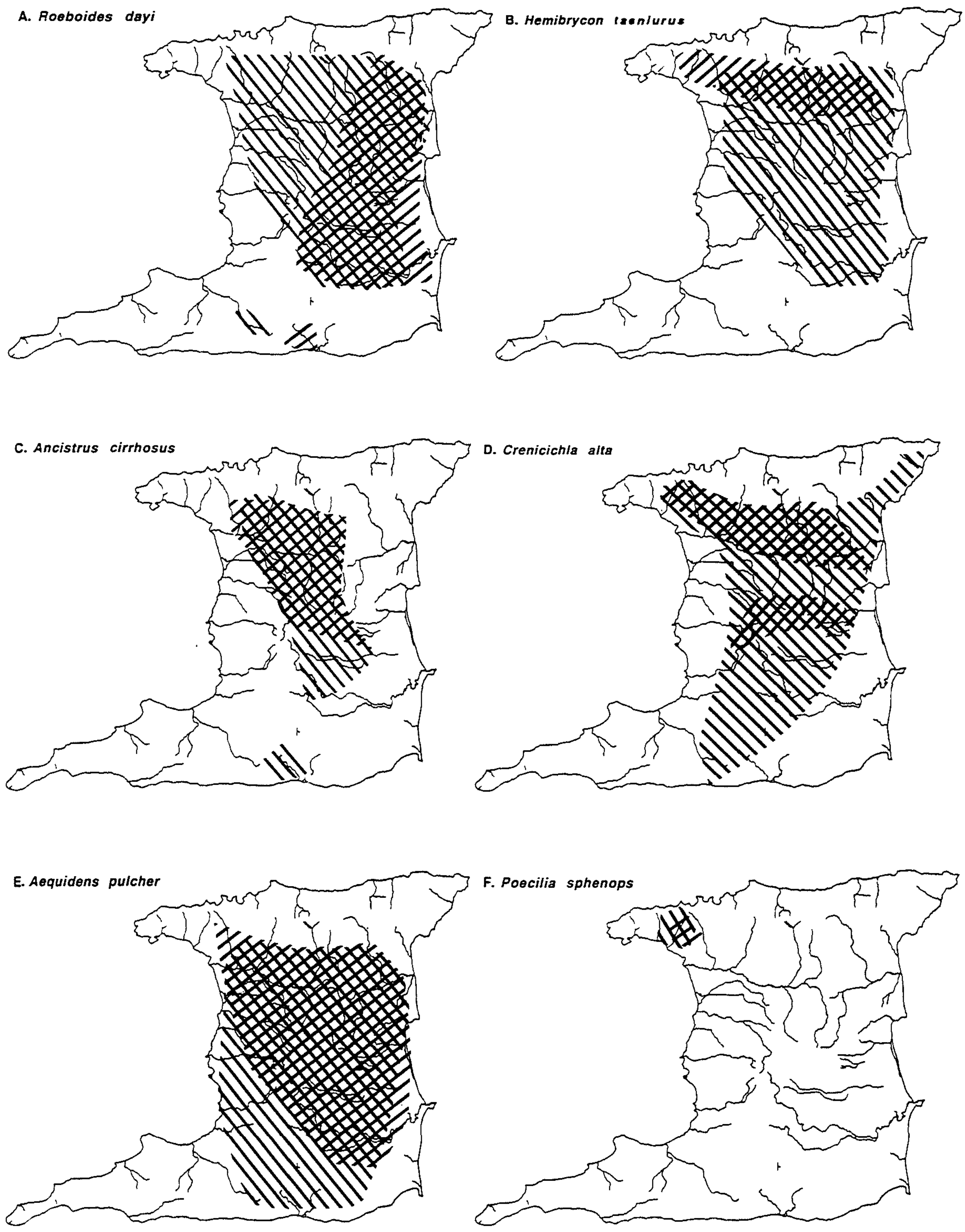


Figure 5.2 Distribution of six species of freshwater fishes in Trinidad during the 1950s (////) and 1990s (\\\\)
a. *Roeboides dayi*; b. *Hemibrycon* taeniurus;
b. *Ancistrus cirrhosus*; d. *Crenicichla alta*;
e. *Aequidens pulcher*; f. *Poecilia sphenops*

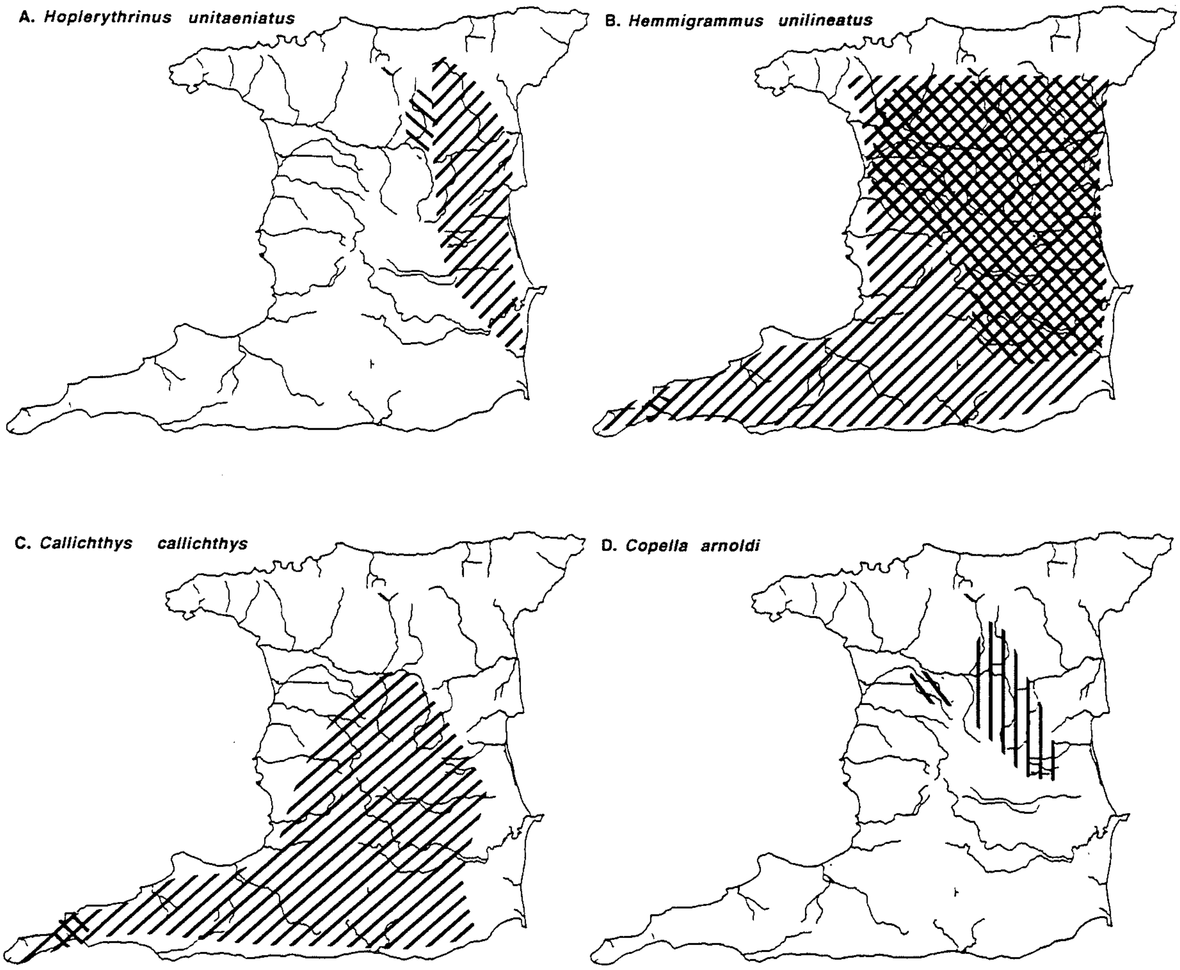


Figure 5.3 Distribution of four species of freshwater fishes in Trinidad showing range contractions between the 1950s (////), 1980s (||||) and mid-1990s (\\\\)

a. *Hoplerythrinus unitaeniatus*;
b. *Hemigrammus unilineatus*;
c. *Callichthys callichthys*;
d. *Copella arnoldi*

the Northern Range in the 1950s (Price 1955) and 1980s (Kenny 1995). In the present survey, it was confined to eastern drainages, the easternmost streams of the Caroni drainage as well as the Cunupia and Guayamare rivers and had been lost from streams draining the southwestern peninsula, south coast and some streams draining the west coast. *Copella* was found in the easternmost lowland streams of the Caroni drainage and streams draining into the Nariva swamp by Kenny (1995). In the present survey, it was found in only a single location on the Guayamare River. Specimens have been collected from the Nariva swamp however (pers. obs.) indicating that it has shifted from a riverine existence to the swamp.

Yet other species showed a shift in the boundaries of their distributions between 1980 and 1998. The most dramatic movement was made by *Gasteropelecus sternicla* whose distribution progressed from a single locality in the southwestern peninsula to two streams on the east coast (Figure 5.4). Other range displacements were less marked. *Steindachnerina argentea,* and *Odontostilbe pulcher* shifted slightly southward from the Northern Range into streams on the plains.

Species richness of twenty seven sites throughout north and south Trinidad (N=14 and 13 respectively) were compared between 1980 and 1998. Changes in species richness of these sites, compared between 1980 and 1998, varied from a decrease of two to a gain of up to eight species. Mean change in species richness was significantly greater in the south (mean change=1.93 and 4.62; $T=2.83$; $p=0.0095$; $df=23$). This change was most pronounced in the eastern part of south Trinidad, where five of the seven sites examined showed an increase in species richness of six to eight species.

Species composition had changed for all sites, including those for which species richness had remained the same.

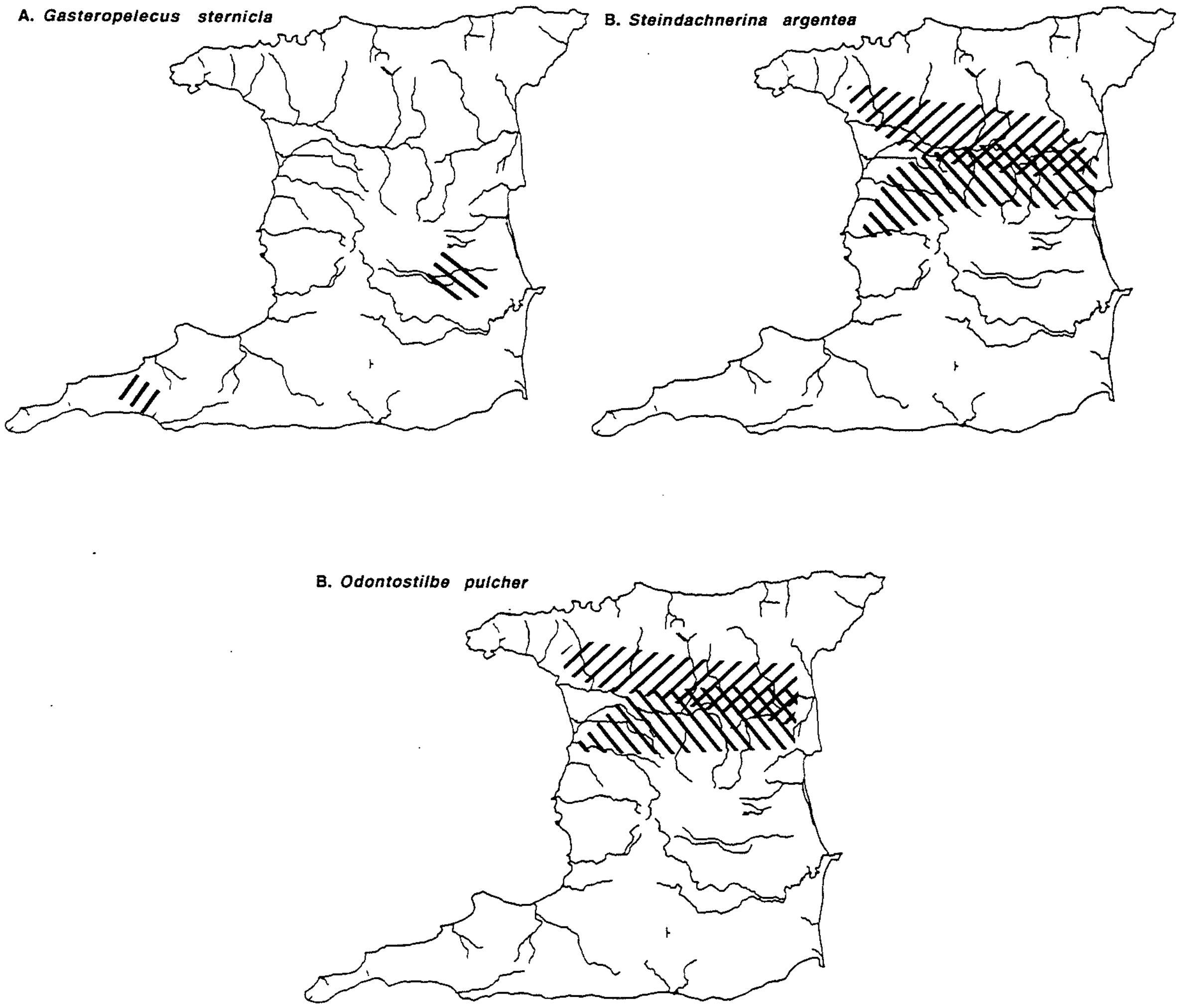


Figure 5.4 Distribution of three species of freshwater fishes in Trinidad showing range shifts between the 1980s (\\\\\\) and 1990s (///)
a. *Gasteropelecus sternicla*;
b. *Steindachnerina argentea*;
c. *Odontostilbe pulcher*

Percentage change varied in magnitude from 25% to 100%. Sites in the north changed between 33 and 89%, whereas sites in the south changed between 60 and 100%, with the exception of one site that changed by 25% (Figure 5.5). Five of the sites in the south had demonstrated a complete turnover of species. When percentage change for sites in the north and south of the island was compared, it was seen that the shifts in species composition were significantly greater in the south (Median change=64.6% and 85.7%; W=145.5; p=0.0153). Four sites had shown a complete change in species composition. All of these sites were located in the southern part of the island.

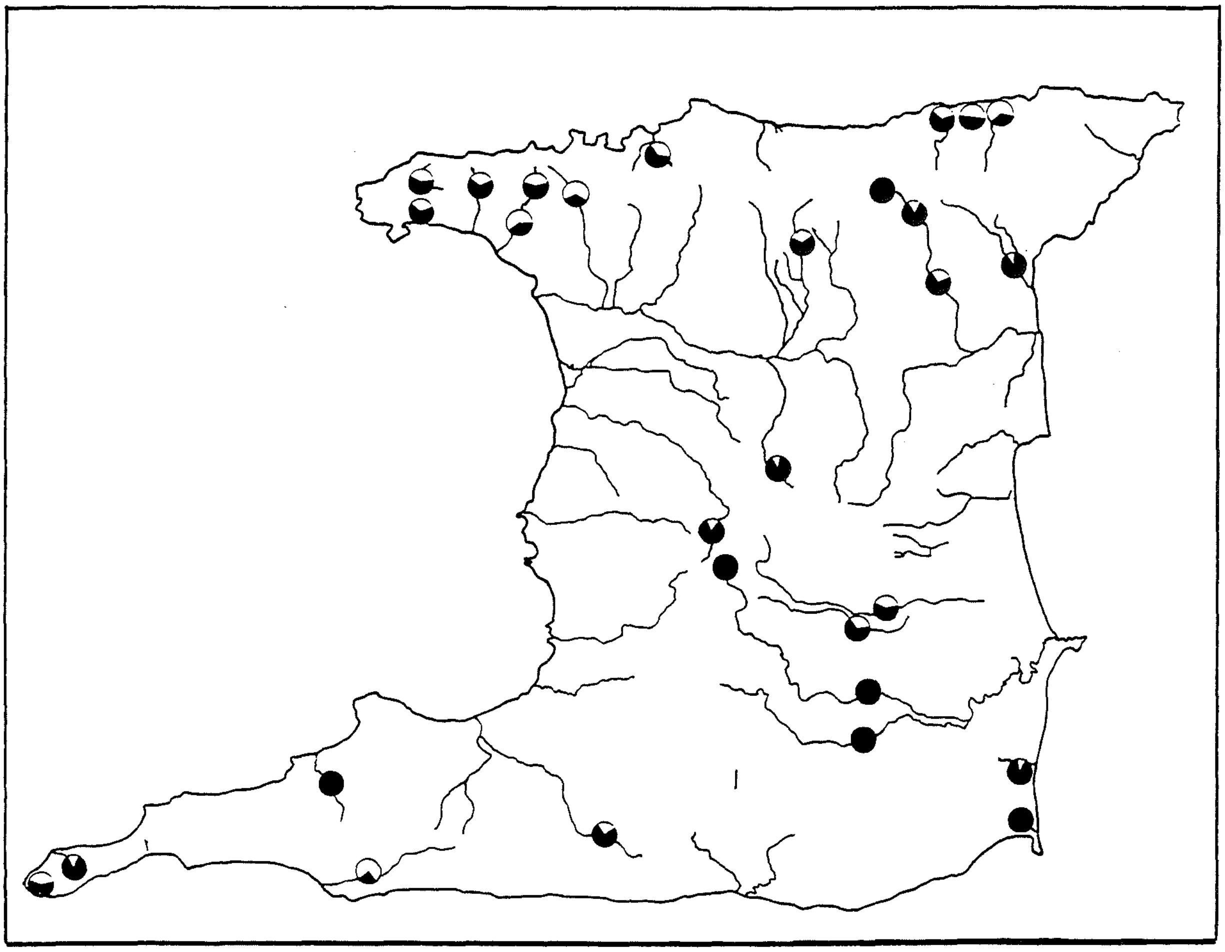


Figure 5.5 Changes in species composition of individual sites between 1980-81 and 1996-1998. Shaded portions of pie charts represent percentage change.

Discussion

The results showed that the fresh water fish fauna of Trinidad had been in a state of flux between the 1950s and the present. During this period, there was a relatively large number of new introductions (15) balanced by an almost equal number of local extinctions (12) (Figure 5.1). These figures indicated that a new species was recorded for Trinidad about every three years. This was a conservative estimate of the rate of introductions, since not all new colonists or accidental releases would have survived long enough to be discovered. In addition, some of the introductions may have been of species already extant on the island.

There was an almost equal number of newly introduced exotic species recorded as there were new natural colonists during the last 50 years. Local extinctions from both groups were also equal indicating that neither group was more capable of establishing permanent populations on the island.

Given such high rates of colonisations and introductions, the total species richness was found to be unexpectedly constant. This was achieved by a rate of extinction that was almost equal to the rate of introductions. It may be that fish communities here are saturated (see Ricklefs (1990)). In such a case, new species can only be added by causing the extinction of another (Ricklefs 1987). Alternatively, the new species may be preyed into local extinction by species such as *Hoplias malabaricus*.

Changes in species composition of individual sites over time should confirm whether or not these communities are saturated. Of the 27 sites for which this was possible, 24 showed an increase in the number of species present between Kenny's survey and the current one. This implies that these communities were unsaturated. On the other hand, the differences may have been due to variation in sampling effort between the two surveys. Kenny's survey was a qualitative one, and was therefore more likely to miss some species of fish at each site. The current survey, however, was a quantitative one that attempted to entirely fish out most sample sites. This survey was therefore likely to collect species missed by Kenny.

The geographic distribution of species also showed temporal changes since Price's survey. What was not clear was the relative roles of natural events and human intervention in such spatio-temporal trends. Some of the changes in the distribution of fishes and in the species composition of fish communities indicated that there may have been a natural tendency of the fauna to change over time. This may have been the case where changes were easily explained in terms of human intervention or even natural environmental changes in the habitat (Kenny 1995). The movement of Antillean fauna into the Stable Relict zoogeographic zone, and the spread of *Poecilia sphenops* into a neighbouring stream were such examples. Natural seasonal events resulting in short term habitat alterations could have also lead to changes in the fauna. Kenny (1995) cited several examples of the effect of dry season dry-out on the fauna of small intermittent streams along the south coast.

In other instances, human interference was implicated. Kenny (1995) commented on the role of human interference on the freshwater fish fauna, citing long term habitat alteration and introduction of exotic fish species through the aquarium trade as two major factors. Indeed, habitat disturbances in the Northern Range may have been instrumental in the removal of *Odontostilbe* and *Steindachnerina* from these streams unto the plains. Endler (1986) and Reznick (1994) gave descriptive accounts of some of the anthropogenic disturbances taking place in the Northern Range, and the effects of these activities, on the fish fauna of specific streams. There was a complete disappearance of fish in parts of some of the streams. Endler (1986) reported that siltation from quarrying activities, and spills of pesticides in the upstream portions of Northern Range streams had resulted in temporary defaunation of these areas. Re-faunation from unaffected areas occurred when improved conditions were restored. On the plains, the loss of *Hemigrammus* from the more populated and/or industrialised parts of its range may be another example.

Changes in species composition and species richness throughout the island may have been an interplay between natural and anthropogenic factors, as even sites in remote areas were affected. Rates of turnover, however, were greater in the south where much of the land area was impacted by activities associated with oil production. The changes in the fauna between the 1980s and 1990s may have been due to differences in sampling effort, as already discussed. However, this cannot completely explain some observations such as the higher degree of changes noted on the Ortoire, Guayaguayare and Guapo rivers. These rivers all pass through oilfields and are subjected to disturbance from oil spills. It may be that disturbance experienced by these had increased from low levels in 1980, to intermediate levels in 1998, and in response, diversity increased in accordance with Connell's intermediate disturbance hypothesis (Connell 1975).

Further indirect evidence to support the theory that human activities have affected the distribution of fishes in Trinidad comes from Endler's (1986) report. He added a time factor by mentioning, for several streams, that human settlement and activities increased in the early 1980s. This was around the time that most of the field work for Kenny's survey was carried out. If it is assumed that similar patterns of development were taking place elsewhere in the island, it can help explain why distribution patterns that had remained the same between the 1950s and 1980s, had changed so much by the mid 1990s. The effects of pollution on diversity will be examined further in Chapter 6.

In summary, the fish fauna of Trinidad is temporally dynamic. Total species richness changed with each new survey carried out since 1955. Some species have been added, by both natural colonisations and human introductions, and others have gone locally extinct. The dynamic nature of the fauna was also reflected in changes in species distributions between the mid 1950s and the present. Accelerated distributional changes since the early 1980s, a time of increased human settlement and activity, hints at anthropogenic influences behind these changes.

CHAPTER 6. Pollution

Introduction

Inland water bodies have traditionally been important to mankind. Our use of rivers and streams has imposed physical, and more recently, chemical changes on them. These activities have potentially deleterious effects on the diversity of aquatic life. With a population of over 1.6 million, it is not surprising to find that Trinidad's inland watercourses have been affected by urbanisation. Streams have been redirected, dredged and canalised to prevent or reduce flooding in areas of human settlement. Rivers here have traditionally been used as a garbage disposal system for domestic refuse, from food waste, household chemicals, and food containers, to large household appliances and cars.

Trinidad and Tobago also has a well-established agricultural industry. Kenny (1995) estimated that a little less than 35% of the land area in Trinidad may be used for agriculture. Intensive culture of sugar cane in the western parts of the Northern and Southern Lowlands involves the heavy application of pesticides, herbicides and fertilisers. The use of these chemicals is not regulated, and there is evidence that they have leached into the Caroni River Basin (Government of Trinidad and Tobago 1976a; Siung-Chang 1990).

Animal husbandry is also an important part of the agricultural industry. Recently there has been anxiety about the practice of dumping of animal wastes, particularly from large processing plants, into rivers. Of particular concern was that this practice was carried out in the Caroni River which is a major source of potable water. For aquatic organisms like fish however, the use of smaller streams for such purposes is more critical.

Finally, Trinidad is also highly industrialised. The main component of the industrial sector is the petroleum and petrochemical industry. Oil is produced on shore in the Southern part of the island in an area referred to as the Southern Basin. There is an oil refinery on the western coast of southern Trinidad, and several manufacturing plants for petrochemicals, cement, nitrogenous fertilisers, urea and methanol along the western coast. In addition to the petroleum-based industry, there is a manufacturing industry based primarily along the foothills of the Northern Range, and along the western coast of Trinidad. (http://www.tcol.co.uk.trinidad/trin2.htm). The effects of these activities on the aquatic environment need to be known.

Fish are thought to be good indicators of trends in aquatic biodiversity because their variety can reflect a range of environmental conditions (Moyle & Cech 1988). Most studies on the effects of pollution on aquatic life have been carried out in temperate regions. In the tropics, there has been little work on the effects of pollution on freshwater fish communities and the topic remains poorly understood.

Methods

The first step in determining the effects of pollution on fish was to identify the polluted sites. For this purpose, criteria had to be developed for deciding water quality. Several water quality guidelines and criteria exist for streams and rivers in the literature; however the vast majority of these are for temperate regions. Indeed, even the focus of most of these was not strictly relevant for the purpose of the present study. They were usually concerned with water for human and agricultural uses, rather than with water quality suitable for the preservation of aquatic life.

It was decided to use a simple system of three categories of water quality: clean, perturbed and polluted. Eight water quality parameters were used for this classification: dissolved oxygen (DO), biochemical oxygen demand (BOD), zinc (Zn), copper (Cu), ammonia (NH_3), oil and grease (O&G), pH and phosphorus (P). Points were assigned for each parameter according to whether readings indicated the site was clean (1 point), perturbed (3 points) or polluted (4 points), and the product of the scores gave the water quality index (WQI) for the site.

Water quality guidelines from Brazil (Government of Brazil 1986), Canada (Ministry of Supply and Services Canada. 1995) and the European Economic Community (Lloyd 1992), as well as water quality measurements reported for other tropical rivers, streams (Haripersad-Makhanlal & Ouboter 1993) and aquaculture ponds (Boyd 1982) were used as rough benchmarks for delimiting the categories of water quality for the present study. The categories were compared with the range of values obtained in the present study to verify that they were suitable for Trinidadian rivers and streams. As a test of reliability, the WQI was calculated for the full complement of sites. Any obvious inconsistencies between the WQI and the observed conditions were taken as an indication that the WQI was not a robust index of water quality and needed refinement.

Cluster analysis of sites was carried out using the eight parameters used for the WQI. It was expected that polluted sites would either cluster together, or be put in unexpected positions given their locations. A matrix of sites by mean values of the eight water quality parameters was used for this analysis. Mean values for each water quality parameter were calculated from replicate tests done for each visit. For sites visited more than once, the means were averaged over the visits to provide a single entry per site.

Cluster analysis was carried out using Ward's method in the Statistica statistical software programme. The results were presented as dendrograms. Sites with similar water types should cluster together, hence, polluted sites should form separate clusters from clean sites.

To observe the effect of pollution on species richness, species richness frequency histograms were composed for non-polluted (ie. clean and perturbed) and polluted sites separately. This was carried out for sites located on the plains within the western drainages of the Stable Relict zoogeographic area (see Chapter 4) only. Other sites were not included because they may have introduced a bias in the analysis. This was because it had already been shown that the faunas of the other zoogeographic areas were different, and that species richness increased downstream. There was also a difference between the faunas of the eastern and western parts of the island.

As far as possible, each polluted site was paired with a similar non-polluted, reference site. Pairs were chosen that were similar in physical characteristics, stream order and zoogeography. The main difference between pairs, therefore, was assumed to be water quality. Shannon-Weiner and Berger-Parker diversity indices were calculated for the sites (see Chapter 4 for equations). The indices were calculated using the Alpha Species Diversity & Richness software package (Pisces Conservation Ltd. 1997). The diversity indices for upstream and downstream sites of different water quality, polluted and non-polluted, were compared using a 2-way ANOVA. The merits and limitations of using indices of species richness and diversity to assess the effects of environmental degradation on fish communities are discussed by Fausch et al. (1990).

Finally, the potential of two widely distributed fishes, *Poecilia reticulata* and *Astyanax bimaculatus*, as indicator species was examined using their incidence functions. Incidence functions (J) were employed by Diamond (1975) to determine the survival prospects of species on islands as a function of island size. J gives the probability of finding a particular species on an island as a function of its species richness (S), and hence size. For most species, J=0 below some value of S. This means that, in the long term, the species will not survive on islands below a certain size or species richness (Diamond & May 1981).

Since pollution affects the species richness of a community (Pearson & Rosenberg 1978), J could be used to investigate the potential of indicator species by looking at their survival prospects as S decreases. J was calculated by placing rivers into groups of similar species richness. J for a particular species was the fraction of rivers, in a given group, in which that species was found.

Pollution stress results in changes in the dominance of the component species of communities (Gray 1989). The proportional contributions of *Poecilia* and *Astyanax* were abundance and biomass were therefore compared for paired polluted and non-polluted sites using one-way ANOVAs.

Results

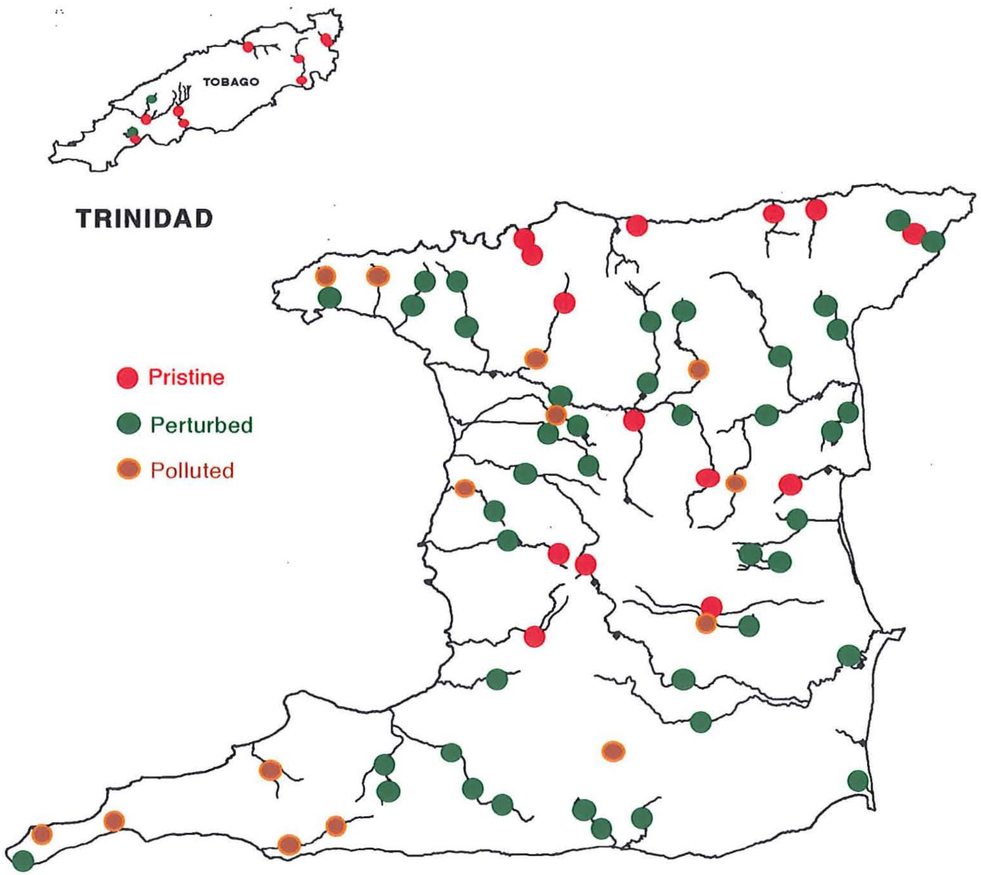
The criteria for assessing water quality in the present study are shown in Table 6.1. WQIs in the range of one to 2304 were obtained. A WQI of one indicated that the water was pristine, between three and 48 that the water was perturbed, and above 108 that it was polluted. All polluted sites (N=13) were found in Trinidad (Figure 6.1). These were mainly in the western and southwestern part of the island, with an apparent concentration of very polluted sites in the southwest. Ten of the polluted sites were located on the plains. None of the sites visited along the north coast of Trinidad were polluted. There were only fourteen pristine sites in Trinidad. Of these, twelve were mountainous and two lowland. Nine of the sites in Tobago were pristine, the other 2 were perturbed, and none were polluted.

Table 6.1. Criteria for the assessment of water quality of rivers in Trinidad and Tobago.

Parameter (value)	Clean (1)	Perturbed (3)	Very polluted (4)
DO (mg/l)	05-10	2-5	<2
BOD (mg/l)	0-4	4-6	>6
pH	6-9	5-6	<5
NH3 (mg/l)	0-1	1-3	>3
P (mg/l)	0.00-0.12	0.12-0.50	>0.5
Cu (mg/l)	0.001-0.019	0.019-0.050	>0.05
Zn (mg/l)	0.001-0.100	0.1-0.2	>0.2
Oil (mg/l)	00-10	10-80	>80

The WQI was successful in distinguishing sites that were obviously polluted, for example Erin and Tacarigua Rivers (Plate 1.1). However, it classified as polluted some sites that may be more correctly considered perturbed. 'Polluted' sites such as B1/71, were located in isolated

Figure 6.1 Distribution of pristine, polluted and perturbed sites in Trinidad and Tobago. See text for details of site classifications. Maps are not to scale.



areas where the likelihood of pollution seemed remote. The weakness in the WQI probably rested in its inability to distinguish natural environmental variation such as exists between the streams of the Northern Range and those of the rest of the island.

The results of the cluster analysis of sites using mean water quality measurements for the eight parameters used to determine water quality are shown in Figure 6.2. Polluted sites, ie. those with a high WQI, formed three small clusters. One cluster contained sites on the Erin and Guapo rivers that are severely affected by oil pollution, another cluster contained sites, like Diego Martin and Cuesa, with high BOD, and phosphorus, and low DO. The third cluster contained three sites with high WQIs, but which had not appeared to be polluted at the time of sampling. Of all the combinations of water parameters tried, clustering by BOD and phosphorus gave the closest agreement with the WQI (Figure 6.3). Eleven of the 13 polluted sites formed a single cluster.

Species richness ranged from three to 17 species per site for the sites included in the analysis. Non-polluted sites contained from four to 16 species whereas very polluted sites had one to five species (Figure 6.4). There was one exception of a very polluted site with 13 species of fish. This is one of the sites that may have been incorrectly classified by the WQI.

Berger-Parker indices ranged from 0.214 to 1.0, with higher values for the polluted sites. The difference in this index between polluted and non-polluted sites was significant ($F_{1,24}=4.25$, $p=0.05$). Shannon-Weiner indices for the fourteen paired polluted/non-polluted sites ranged from zero to 2.02. Although the measure was usually less for the polluted sites, the difference between the Shannon-Weiner index for polluted and non-polluted sites was not significant ($F_{1,24}=2.45$, $p=0.13$).

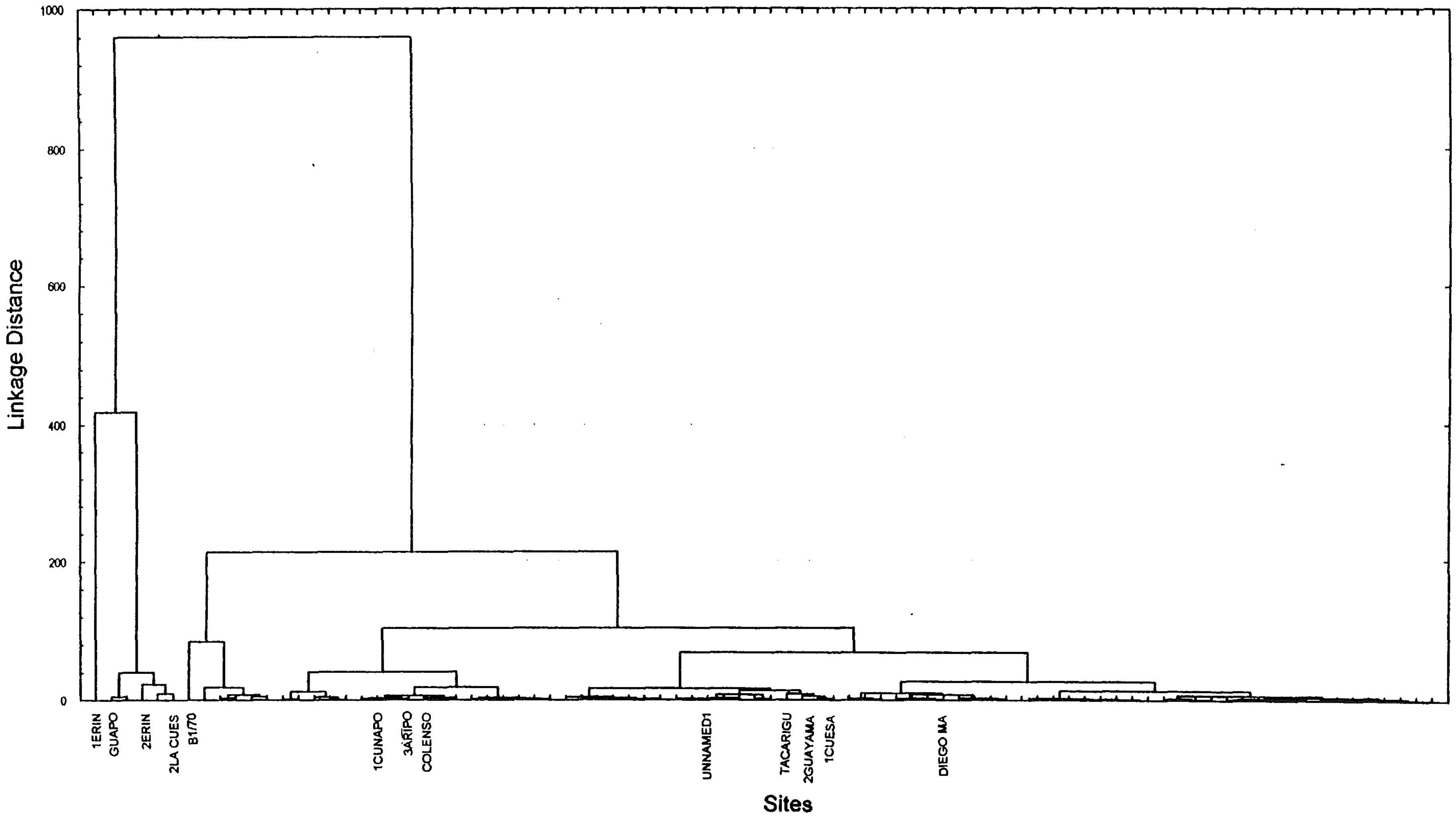


Figure 6.2. Ward's cluster analysis of sampling site similarity, based on eight water quality parameters: DO, BOD, pH, NH_3, P, Cu, Zn, and oil & grease. Only polluted sites are indicated.

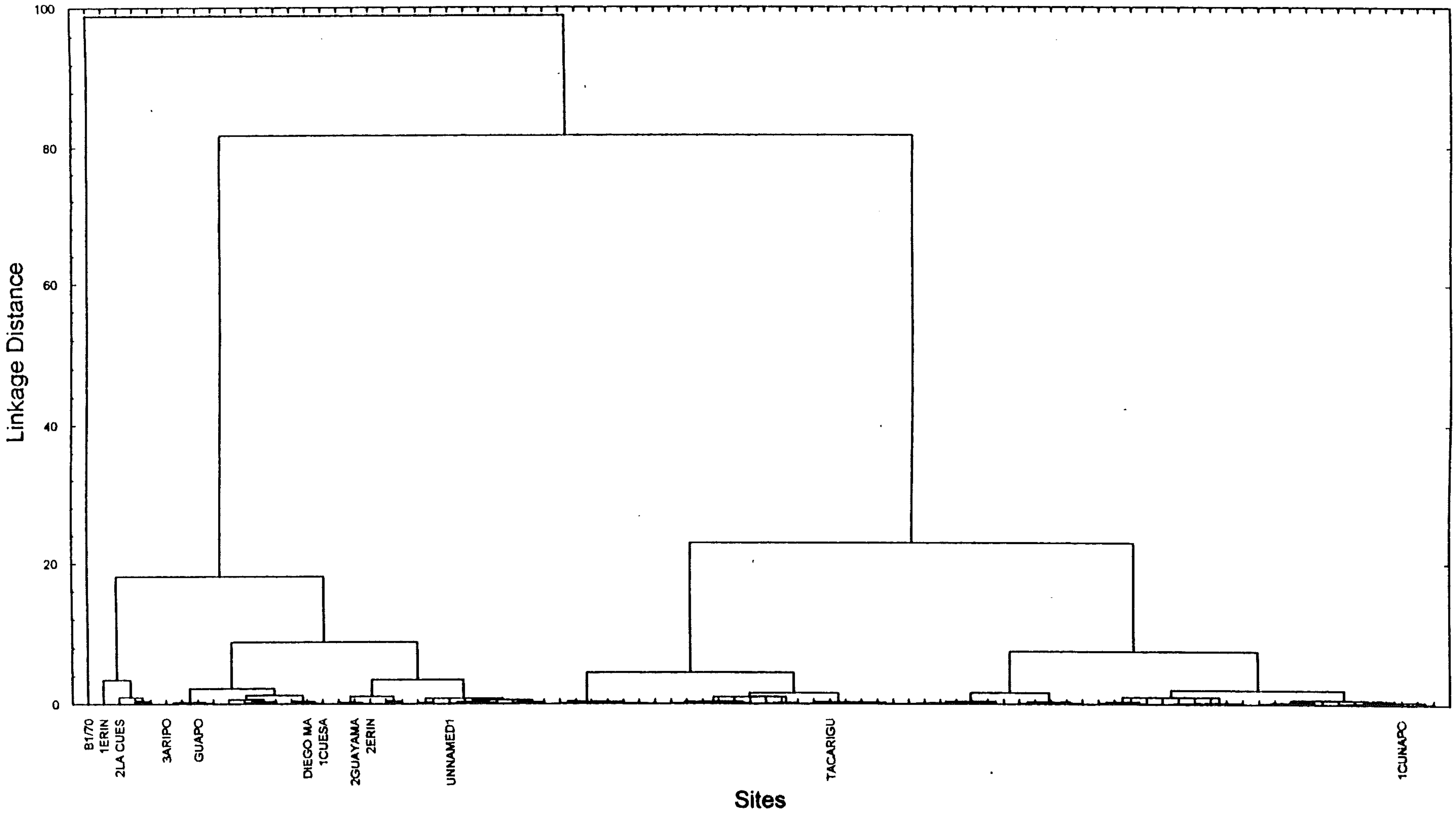


Figure 6.3. Ward's cluster analysis of sampling site similarity, based on two water quality parameters: BOD and P. Only polluted sites are indicated.

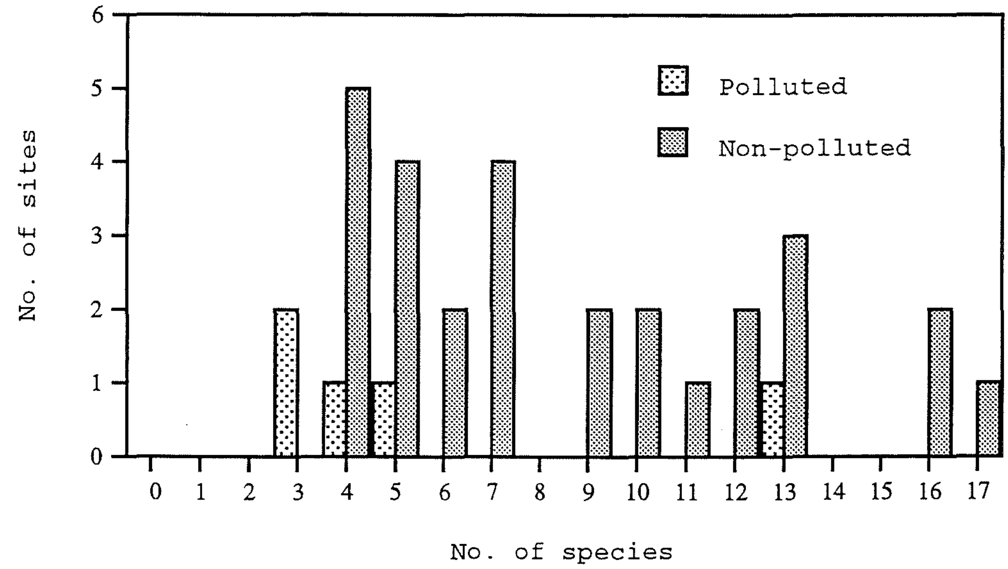


Figure 6.4. Number of species of fresh water fishes found in polluted and non-polluted low-land sites in the western hydrometric area of Trinidad.

The incidence patterns for the two fishes chosen showed quite different trends (Figure 6.5). *Poecilia reticulata* were found in streams with all levels of species richness (S). However, the likelihood of finding *Astyanax bimaculatus* increased with S, from zero, in streams with only one or two species, to unity, in streams where S was greater than 11.

When differences in proportional abundance and biomass between polluted and non-polluted sites were considered for these two species, two different trends were also found. There was no significant difference, for *Poecilia reticulata*, in abundance ($F_{1,24}$=1.2, p=0.283) or biomass ($F_{1,24}$=1.92, p=0.178) between the two classes of sites. For *Astyanax bimaculatus*, however, there were significant differences in abundance ($F_{1,24}$=6.58, p=0.017) and biomass ($F_{1,24}$=4.76, p=0.039) between the two classes of sites. *Astyanax* tended to be less abundant and contribute less to the total biomass of fish in polluted sites than in non-polluted sites.

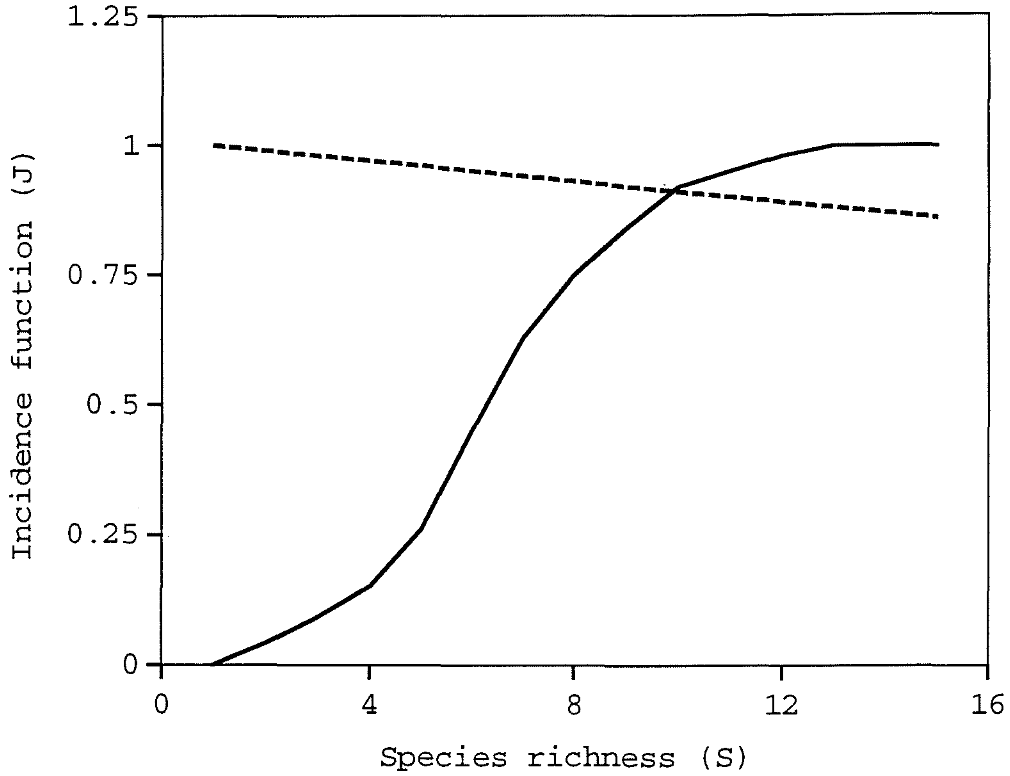


Figure 6.5. Incidence functions for *Poecilia reticulata* (----) and *Astyanax bimaculatus* (——) in Trinidadian rivers. the incidence, J, represents the fraction of riverine sites with a fixed number of species, S, in which the species occurs.

Discussion

Worldwide, the majority of human settlement is located along inland and coastal water bodies. The most perturbed rivers are in these areas due to the effects of urbanisation, agriculture and industrial development (Moyle & Leidy 1992). The situation is similar in Trinidad. The western part of the island is the most densely populated and industrialised part of the country. Along the west coast are located the major towns, an industrial estate and an oil refinery. Densely populated towns, two industrial estates and several factories are also found along the foot hills of the Northern Range; however, they are mostly located in the catchment of the Caroni River which empties along the west coast. Tobago differs from Trinidad in having smaller pockets of urbanisation and less developed agricultural and industrial sectors. Tourism is important, but is concentrated in the southwest, an area almost devoid of rivers.

The WQI showed that most streams in Trinidad, and a few in Tobago were perturbed. The most severely disturbed rivers were those located in the west and southwestern peninsula of Trinidad, near sources of urban and industrial pollution. Polluted sites in the southwestern peninsula were, with one exception, found within oilfields, and showed visible signs of oil pollution (eg. Plate 1.1b).

The possible effects of pollution that may have been detected at these sites were increased frequency of disease, reduced diversity, regression to opportunistic species (*r*-strategists) and reduction in the mean size of organisms (Gray 1989). Casual observations of diseased and deformed fishes in the field confirm the increased frequency of diseased fish with increasing levels of pollution. Thirty eight percent of the polluted sites were found to have fish with diseases or deformities visible to the naked eye, as opposed to 14% of the perturbed and zero percent of the pristine sites (pers. obs.).

Species richness and the Shannon-Weiner and Berger-Parker diversity indices indicated that fish diversity was indeed lower for polluted sites than for non-polluted sites, although not significantly so in the latter case. Polluted western streams contained fewer fish species (3 to 5), as compared to similar non-polluted streams, (4 to 17). These indicators of diversity were, in fact, lowest for the most polluted sites. The lowest value of the Shannon-Weiner index (H), for example, was 0.372 for the heavily polluted Erin River. For non-polluted rivers, by comparison, $H>1$. The higher Berger-Parker index of polluted streams implied an increase in dominance of a few species. The noticeable reduction in diversity observed here, suggested that disturbance levels were either high, or that pollution had been ongoing for some time, since reduction in diversity is a late response to environmental stress (Gray 1989).

The effects of stress on communities, as predicted by Pearson (1978), are an initial increase in species richness and biomass, followed by a decrease in both (Figure 6.6). There is also an increase in abundance, associated with dominance of a few 'opportunistic' species, when species richness begins to fall. Peak abundance is accompanied by a rise in biomass, and followed by a decline in all measures in diversity. It has already been discussed (see Chapter 5) that many of the sites examined may have been at intermediate levels of disturbance as indicated by increased species richness since the early 1980s. Kenny (1995) mentioned elevated biomasses of fish in streams receiving agricultural and biological wastes. He however alluded to the possibility of fish kills during periods of low stream flow. There were sites where the fish communities had progressed to the last two stages in their disturbance-induced regression.

Two sites visited on the Erin River had communities at the penultimate stage of decline. This river is located within an oil-producing area in southern Trinidad. At the times

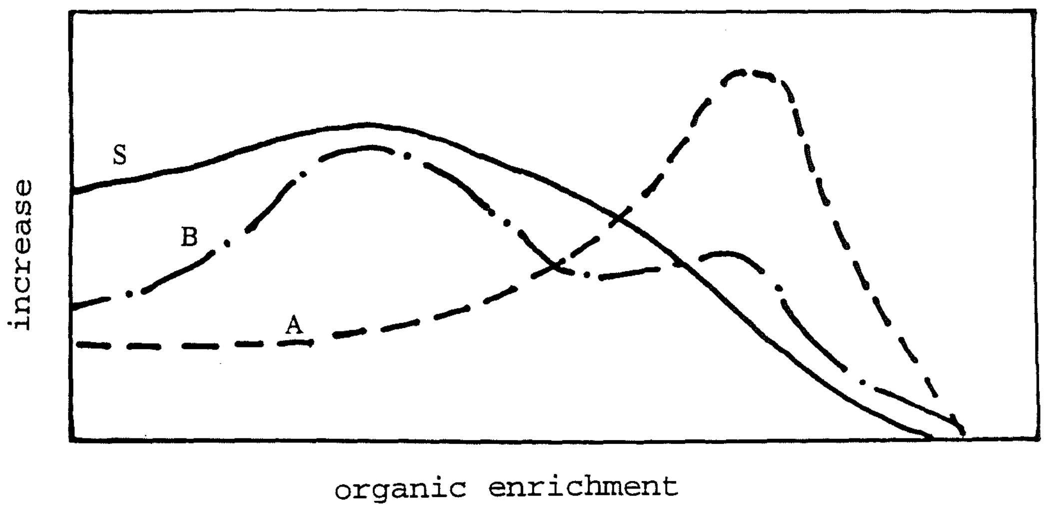


Figure 6.6 Generalised model of effects of organic enrichment on species (S), abundance (A) and biomass (B). Source: Pearson & Rosenberg (1978).

of visit, the river showed clearly visible signs of oil pollution. The water surface, river banks and vegetation were covered by oil (Plate 1.1b). The water here contained as much as 350 mg/L of oil. BOD and DO were recorded at 0.3 and 13.5 mg/L respectively. The community was comprised of only two species, *Poecilia reticulata* and *Rivulus hartii*. Abundance and biomass of fish in this river were very high for such small species, 3.08 to 7.18 individuals/m^2 and 1.79 to 4.15 g/m^2 respectively.

Another site was at the final stage of regression. The Tacarigua River site (WQI=144), located below an industrial estate, was very polluted. There was the smell of H_2S in the air, the gravel stream bed was completely covered by thick grey moss (Plate 1.1c), and, but for some *Poecilia reticulata*, the stream was devoid of fish. At the first visit, species richness, abundance and biomass were low (1.46 individuals/m^2 and 0.21 g/m^2 respectively). By the second visit, a further decline was recorded. Species richness had declined to a single species, and abundance and biomass to 0.12 individuals/m^2 and 0.01 g/m^2 respectively.

Mean size of organism should decrease along a gradient of increasing organic pollution (Pearson & Rosenberg 1978) as a result of a shift towards the dominance of small-sized species (Gray 1989). This, too, was found to be so since *Poecilia reticulata* and *Rivulus hartii* were the smallest species of fish found in Trinidad and Tobago.

The WQI used for assessing water quality in the present study was generalised in that the same criteria were used for the whole country. However, the complex intrinsic geologic and topographic make up of the country (see Chapter 2) points to a heterogeneous natural water quality throughout the island. The system therefore failed to distinguish between variation that is natural, and that due to anthropogenic disturbance. The WQI therefore needs to be revised to reflect the variation existing in Trinidad and Tobago.

The WQI should have classified sites in order of increasing pollution. However, some of the most polluted sites had lower WQI than others that did not appear to be polluted. Tacarigua River and B1/71 are good examples of this. The Tacarigua River site (WQI=144) was very polluted (see above). B1/71 had the highest WQI (2304) recorded, and a rich and diverse fauna. The conditions at B1/71 were probably quite natural for streams in the area. The site was located in thick secondary forest in a very flat, low-lying area near the tip of the southwestern peninsula. Flow of the naturally sluggish water was blocked by a fallen tree downstream, creating stagnant conditions. This combined with the degradation of a large input of allochthonous organic material from overhanging vegetation would lead to the anoxic conditions found at the time of sampling. One site classified as polluted with a high WQI had a speciose fish fauna and did not appear to be polluted at the time of sampling, suggesting that the WQI may not be a robust indicator of pollution. The WQI was however largely successful.

The use of species to indicate water quality was developed by Ruth Patrick in the 1940s (Lewis 1996). Since then, there has been much criticism of the assumptions underlying the approach, its methodologies and incorrect applications (Landres & Thomas 1988; Noss 1990). However, it still remains a useful tool in environmental monitoring. Several criteria for the assessment of indicator species are given by the United Nations Environment Programme (1995), modified from Brown (1991). Most are beyond the scope of the present study:

1. "high taxonomic and ecological diversity (many species in each locale or system);
2. close association with and identification of the conditions and responses of other species;

3. high ecological fidelity;
4. relatively high abundance and damped fluctuations (ie. they are always present and are easy to locate in the field);
5. narrow endemism or, if widespread, well differentiated (either locally or regionally);
6. well known taxonomy and easy identification;
7. good background information (eg. on genetics, behaviour, biochemistry, ecology, biogeography);
8. large random samples encompassing all species variation;
9. functional importance within the ecosystem is understood;
10. predictable, rapid, sensitive, analysable and linear response to disturbance".

My study examined the potential of two common fishes, one 'opportunistic' (*Poecilia reticulata*) and the other, 'non-opportunistic' (*Astyanax bimaculatus*) as potential indicator species. Both species are among the four most widely distributed fishes throughout the country. Good background information is available on both species. *Poecilia* has been used as a model by behavioural ecologists for decades, and *Astyanax* was the subject of a research project (Alkins 1987), and is cultured commercially for the bait fishery in Suriname (I. Ramnarine, pers. com.). The data presented here showed that the incidence, proportional abundance and biomass of *Poecilia* populations were insensitive to habitat quality. *Astyanax*, on the other hand, seemed to be a more suitable indicator of habitat quality. It was not found in depauperate communities such as are typical of severely disturbed habitats, and its proportional abundance and biomass were negatively affected by pollution. Unfortunately it was not found in Tobago, thus another fish will need to be examined as an indicator species there. One possibility there is the ubiquitous *Sicydium punctatum*.

Pollution of streams has become a problem in Trinidad, and may be becoming so in Tobago. The most affected streams were those draining the more populous and industrialised areas of the west and southwest of Trinidad. Here the situation had advanced to such a level that fish species had been extirpated from affected stretches of some rivers, and possibly from most of the Erin River. One possible indicator species had been identified as a tentative step toward a solution to this loss in fish biodiversity.

Chapter 7. Summary and future research

The overall objective of my research was to provide quantitative baseline data which can be used as a benchmark to address some of the problems threatening fish diversity of Trinidad and Tobago. It is believed that deforestation, pesticides from agricultural sources, overfishing, earthworks (Endler 1986; Reznick 1994) and oil pollution (Government of Trinidad and Tobago. 1962) are the main anthropogenic factors adversely affecting the fish fauna. Given the continued deterioration of rivers in Trinidad, the increasing population size with attendant urbanisation, and the government-sanctioned drive toward accelerated industrialisation and developments in the agricultural sector, it is urgent that steps are taken to protect aquatic habitat and aquatic life.

One of the initial steps in the conservation process was to quantify this diversity. Next it was necessary to understand the biological organisation of this diversity and how it changed in space and time. Aspects of the biological organisation considered were community structure, whether certain species tended to be found together, and what type of communities were found in different geographic areas. Once features of the fish fauna were understood, the question of anthropogenic impacts on the fauna were addressed.

Quantification of fish biodiversity

Total species richness (S) was used as the measure of diversity. Estimates of S were between 37 and 41 species, which is similar to observed values of S obtained from surveys carried out since the mid 1950s.

Organisation of fish biodiversity

The fish fauna of Trinidad and Tobago is diverse and has a heterogeneous distribution. Both historical events and current ecological conditions are relevant to the distribution of species within Trinidad and Tobago. The overall conclusion is that Trinidad's freshwater fish can be divided into four zoogeographic zones according to Price (1955) and Kenny (1995) (Figure 4.2a). The zones are based on the distribution of the fishes from the two main historic sources for the island, the Antillean island chain, and South America. The first of these zones contains Antillean fishes and is comprised of streams draining the northern slopes of the Northern Range and Tobago. The remaining three zones contain South American fishes. One of these zones, representing recent colonists, is located along the southern coast, while another, representing unstable populations, is centered in the middle of the island. The rest of the land area is occupied by an old, stable South American fauna. There has been movement of fish around the island, including across zoogeographic borders. Movement of Antillean fishes into streams draining the east and west coasts is believed to be due to natural dispersal.

The results showed that the fresh water fish fauna of Trinidad has been in a state of flux, at least since the mid 1950s. During this period there has been a relatively large number of new additions, balanced by an almost equal number of local extinctions. A conservative estimate was that a new species is recorded for Trinidad almost every three years. The balance between additions and extinctions suggests that Trinidad, as a whole, is 'saturated' (see Ricklefs (1990)), although changes in species composition of individual sites implied that these communities may be unsaturated. Alternatively, the differences between surveys may be due to variation in sampling effort.

The geographic distribution of species also showed temporal changes. Some of the changes in the distribution and species composition of the fish fauna indicated a natural tendency of the fauna to change over time. The movement of

Antillean fauna into the Stable Relict zoogeographic zone, is one example of this.

The composition of freshwater fish communities may generally be explained on the basis of two criteria: zoogeographic zone, and position along the stream length. As shown by cluster analysis, the probability of finding a particular species differs from one zoogeoraphic area to the next. To take an extreme example, the probability of finding *Erythrinus erythrinus* or *Gephyrocharax sternicla* outside of the Colonising Area is zero. Position along the length of the stream has a weak influence on the size of the fish community, and, as shown in Chapter 6 using incidence functions, some species of fish are found preferentially in communities of a specific size.

Human impacts on biodiversity

Human interference, particularly as a result of long term habitat alteration and the introduction of exotic fish species, has had significant effects on the freshwater fish fauna (Kenny 1995). On a large scale, these activities have affected species composition, total species richness, and the distribution of fish species in the islands, especially Trinidad.

Approximately 47% of the new species and 33% of local extinctions recorded for Trinidad since the mid 1950s have been exotic species introduced by man. Although the consequences of these unnatural introductions on the local fauna have not been examined, a few observations indicate their disruptive potential. Almost 8% of the sites examined contained one of the three exotic species still extant on the island. At each of these sites, the exotic species accounted for between 1.3% and 80.4%, by number, of the fish caught.

Apart from the introduction of exotics, human intervention is documented, or has been implicated, in the extension of fish distributions locally. One documented example was the introduction of *Oreochromis mossambicus* to Tobago by the Fisheries Division in the early 1990s.

The effects of disturbance of the habitat by man are more widespread. Pollution of streams is a serious problem in Trinidad. Tobago seems to be following a similar fate. The Water Quality Index showed that about four fifths of the sites visited in Trinidad, and almost one fifth of the sites in Tobago, were either perturbed or polluted. Polluted rivers occurred in the west and southwest of Trinidad, in areas of high urbanisation, agriculture and industrial development. Comparison of fish communities between polluted and non-polluted sites indicated that habitat perturbation has had several impacts on the fauna. Some of the effects at individual sites were increased frequency of diseases (such as fungal infections and gut parasites), extirpation of species, changes in species richness and other diversity measures, and the eventual regression of the community to opportunistic species (*r*-strategists). In the worst cases, for example Erin River, the fish communities had been reduced to diseased *Poecilia reticulata* and *Rivulus hartii*.

The utility of two common fishes, one 'opportunistic' (*Poecilia reticulata*) and the other, 'non-opportunistic' (*Astyanax bimaculatus*) as indicator species was examined. *Astyanax* showed potential as an indicator of habitat quality as it was not found in depauperate communities such as are typical of severely disturbed habitats, and its proportional abundance and biomass were negatively affected by pollution. *Poecilia* populations, on the other hand, were found to be insensitive to habitat quality when the above-mentioned criteria were used. However, the frequency of diseases in *Poecilia* may be a useful indicator of pollution. Unfortunately *Astyanax* is not found in Tobago, and *Poecilia* has a very restricted distribution there. Another indicator species, such as the widespread *Sicydium punctatum* may have to be sought for Tobago.

Conservation

Monitoring is an intrinsic part of any conservation or management strategy. Results of species estimation analyses indicated that sampling a minimum of about 35 sites should be adequate for estimating S for the freshwater fishes of Trinidad and Tobago. A major concern of conservation is to protect that portion of the biodiversity most at risk of extinction, the rare species (Rabinowitz & Dillon 1986). A species can be classified as rare if it exists over a narrow geographic range, is highly habitat-specific, or is only found in small populations (Rabinowitz & Dillon 1986). Table 7.1 shows that over 70% of freshwater fishes in Trinidad and Tobago can be classified as locally rare according to these criteria. This fact, in addition to the loss of diversity recorded for some sites, indicates that the implementation of a management strategy for the conservation of the freshwater fish fauna of Trinidad and Tobago is imperative. Information on rarity given in Table 7.1 can be used to set priorities for the conservation of some of these species. For instance, priority may be given to the five species that fit all the criteria for rarity. Twenty one (70% of rare) species have restricted distributions, indicating that simply by preserving these habitats a substantial portion of the biodiversity of fish would be conserved. Protection of individual species can be given to those occurring in only small populations. Suggestions for future research are given in the next section.

Table 7.1. Frequency of freshwater fishes of Trinidad and Tobago assigned to each category of rarity.

	Geographic distribution	Wide		Narrow	
	Habitat specificity	Broad	Restricted	Broad	Restricted
population size	Somewhere large	11	5	1	6
	Everywhere small	5	5	0	5

Future research

- Investigate more closely the euryhaline fishes found the lower courses of streams in Trinidad & Tobago;

- Trans-drainage movement of fish in Trinidad (e.g. movement across flooded forests and savannahs, or along the coast in the rainy season) could be examined to help clarify questions about whether some changes in the distribution of fishes could possibly be natural;

- Tacarigua River has shown a marked difference in species composition during the two visits made in the present study. The site used was downstream of an industrial complex. It would be interesting to look at water chemistry and faunal composition along this stream to determine (a) "normal" composition, (b) how far downstream does the depauperation effect reache (c) rate of depauperation (d) rate of rehabilitation (e) possible long term trends;

- As recently as the early 1980s (Kenny 1995), the Erin River had a species composition similar to unpolluted streams in the south. However by 1997, the number of species had dwindled to only two, *Rivulus* and *P. reticulata*. It would be informative to (a) carry out a monitoring study to look at the degradation of species composition with time in streams near production wells/facilities (b) try to rehabilitate Erin River and examine changes in water quality and species richness/composition (c) develop methods of rehabilitating water/habitat quality;

- Re-examine changes in *P. reticulata* abundance/biomass with water quality. Although significant trends were not found in my study, it is common knowledge among Trinidadians that *P. reticulata* are particularly abundant in the most polluted canals. *P. reticulata* may still be a good indicator species;

- Examine more closely the effects of exotics on biodiversity. Some evidence implying negative impacts have been presented here and the question deserves further consideration especially in light of government's contribution to the problem;

- Identify potential keystone species and understand their function. It is important to identify such species because of their crucial role in maintaining the biodiversity of ecological communities. Predatory species may occupy these key roles.

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APPENDIX I

Data sheets used in the field and laboratory.

[1]SITE INFORMATION

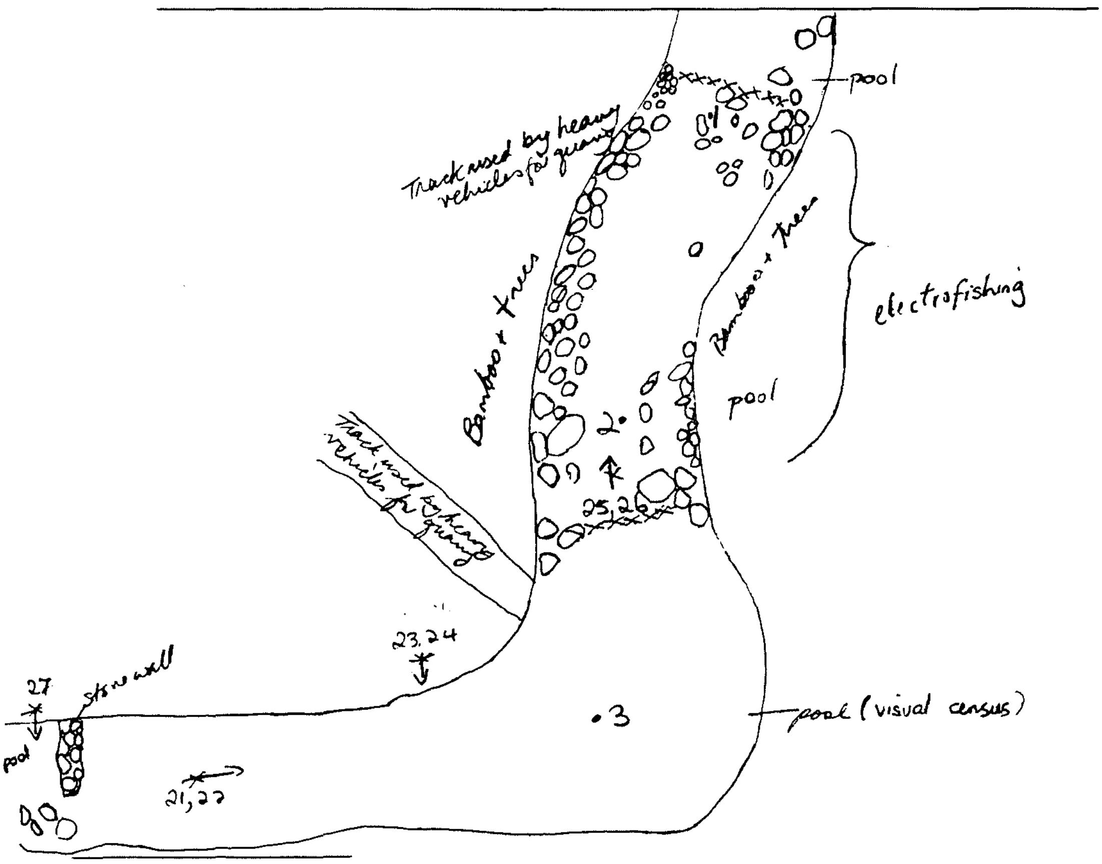
Drainage basin Louis D'Or Date: 97/12/07
River: Louis D'Or Arrival time: 9:10
Station no.: 00.03.01 Departure time: 12:00
Reference location: 1-2 Km up turn off between Delaford + Roxborough

Slope(°) 1.0 Station length (m): 35 + 26(+) * electrofishing (+) visual survey
Weather: Sunny c̄ cloud Stream type: Upper
Topography: Mountainous Land use: 2° forest
Film roll no.: 17 8778 Exposure no./view taken: 21-22 = from downstream to pool
23-24 = from bank to pool; 25-26 = from downstream to run/riffle upstream
27 = relaxing in pool downstream

Checklist of possible anthropogenic activities

Swimming ___
Fishing ___
Cooking ___
Drinking ___
Camping ___
Hiking ___
Domestic waste ___
Appliance dump ___
Chemical dump ___
Offal ___
Car washing ___
Other quarrying

SITE SKETCH



[1] Please return to Dawn Phillip, Dept. of Zoology, The University of the West Indies, St. Augustine, Trinidad.

[2]PHYSICO-CHEMICAL MEASUREMENTS

Drainage basin: Louis D'Or River: Louis D'Or

Station no.: 00.03.01 Date: 97.12.07

PARAMETER	STATION 1	STATION 2	STATION 3
habitat type	riffle	run / ?	pool
width (m)	4.4	6.4	10.4
depth (m)	0.26	0.35	1.13
current speed (counts/m) ~~cts~~ s/m	1.19, 1.5	1.41, 1.4	39.91, 26.91
dominant substrate	small boulders	small stones	sand
other substrate	small stones	boulders	~~st~~ rocks
organic matter	leaf	leaf	leaf
forest closure (%)	98	90	20
left bank height (m)	1.25	1.25	<1
right bank height (m)	5	4	>10
bank stable (left)	Y	Y	Y
bank stable (right)	Y	n (undercut)	N
periphyton	20	10	0
macrophyton	n	n	0
temperature (°C)	25	25	25.5
dissolved oxygen (mg/l)	8.5	8.5	8.1
dissolved solids (mg/l)	190	190	
conductivity (μs)	367 382	367 382	
salinity ($^0/_{00}$)	0.173	0.173	
pH	8.15	8.28	
suspended solids (mg/l)	0	0	
alkalinity (mg/l $CaCO_3$)	157	155	
hardness, calcium (mg/l $CaCO_3$)	72	75	
copper (mg/l)	0	0	
ammonia (mg/l)	0.16	0.17	
phosphorus (mg/l)	0.07	0.06	
zinc (mg/l)	0	0	
oil and grease (mg/l)			
B.O.D. (mg/l)	1.8	1.8	1.8

Notes Clear, fast-flowing. Large / deep artificial pools have been formed by the excavation of materials for the construction industry. The visual Census was carried out in one such pool (station 3)

[2] Please return to Dawn Phillip, Dept. of Zoology, The University of the West Indies, St. Augustine, Trinidad.

[3]BIOLOGICAL DATA

Drainage basin: Louis D'Or River: Louis D'Or

Station no.: 00.03.01 Date: 97.12.07

Fishing methods used: Electrofishing + visual census

Effort: One pass

SPECIES (* indicates species seen but not caught)	BIOMASS (G)	NO. OF FISH	NO. INFECTED	NO. DEFORMED
Agonostomus monticola	160	4		
Sicydium punctatum	14	7		
Anguilla rostrata	227	1		
Gobiomorus dormitor	151	1		
Gobiesox nudus	22	1		
Prawns	47	12		
Crabs	46	1		
VISUAL CENSUS OF	DREDGED	POOL (2	6 m)	
Gobiomorus dormitor	906	6		
Agonostomus monticola	1353	33		
Sicydium punctatum	>400	>200		

NOTES:

[3] Please return to Dawn Phillip, Dept. of Zoology, The University of the West Indies, St. Augustine, Trinidad.

APPENDIX II

Distribution maps of the freshwater fishes of Trinidad and Tobago are given in the following pages. Large dots indicate sites at which individual species are found. Small dots indicate sample sites. Below is a recent list of all the species expected to be found in Trinidad. The freshwater fishes collected in my study are shown in bold. The numbers correspond to codes used to identify individual species in the database.

Family: Erythrinidae
1. ***Erythrinus erythrinus***
2. ***Hoplerythrinus unitaeniatus***
3. ***Hoplias malabaricus***

Family: Curimatidae
4. ***Steindachnerina argentea***

Family: Gasteropelecidae
5. ***Gasteropelecus sternicla***

Family : Anostomidae
Leporinus frederici

Family: Characidae
6. ***Astyanax bimaculatus***
8. *Brycon siebenthalae*
9. ***Corynopoma riisei***
54. ***Gephyrocharax valencia***
10. ***Hemibrycon taeniurus***
11. *Hemibrcon ocellifer*
12. *Megalamphodus axelrodi*
13. *Moenkhausia bondi*
14. ***Odontostilbe pulcher***
15. ***Roeboides dayi***
16. *Triportheus elongatus*
50. ***Hemigrammus unilineatus***

Family: Lebiasinidae
17. ***Copella arnoldi***
18. *Nannostomus unifasciatus*
19. *Pyrrhulina laeta*

Family: Gymnotidae
20. ***Gymnotus carapo***

Family: Callichthyidae
21. ***Callichthys callidhthys***
22. ***Corydoras aeneus***
23. ***Hoplosternum littorale***

Family: Loricariidae
24. ***Ancistrus cirrhosus***
25. ***Hypostomus robinii***

Family: Pimelodidae
26. ***Rhamdia quelen***

Familly: Auchenipteridae
27. *Pseudauchenipterus nodosus*

Family: Anguillidae
28. ***Anguilla rostrata***

Family: Synbranchidae
29. ***Synbranchus marmoratus***

Family: Poeciliidae
30. *Poecilia picta*
31. ***Poecilia reticulata***
32. ***Poecilia sphenops***
33. ***Poecilia vivipara***

Family: Rivulidae
34. ***Rivulus hartii***

Family: Mugilidae
35. ***Agonostomus monticola***

Family: Cichlidae
36. *Aequidens maronii*
37. ***Aequidens pulcher***
38. ***Cichlasoma taenia***
39. ***Crenicichla alta***
40. ***Oreochromis mossambicus***

Family: Eleotridae
41. ***Dormitator maculatus***
42. ***Eleotris pisonis***
43. ***Gobiomorus dormitor***

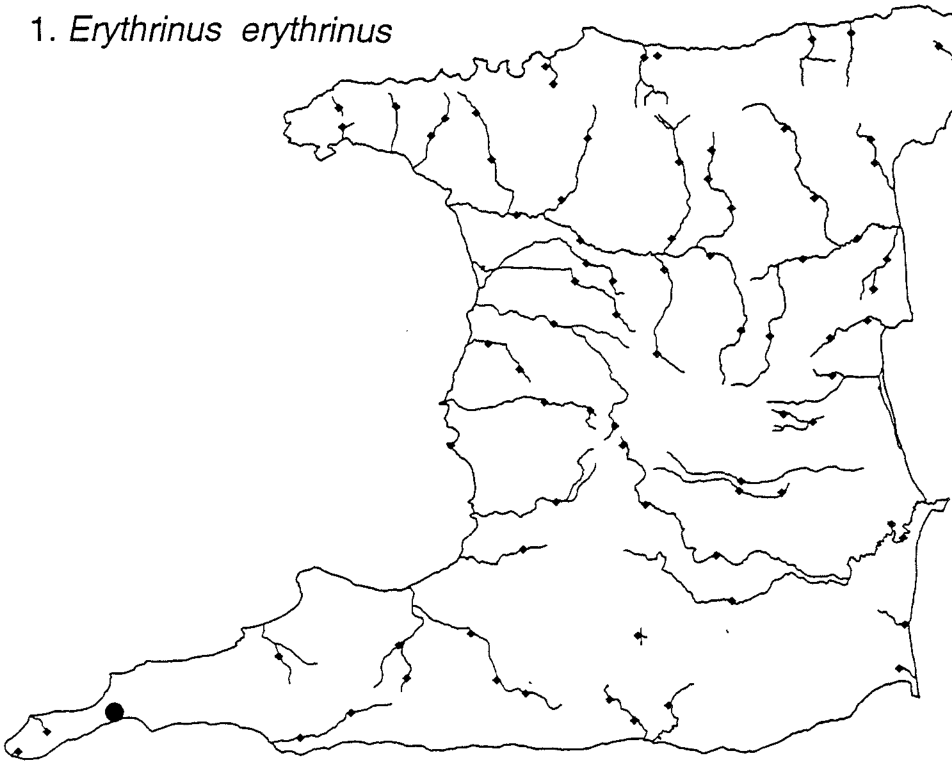
Family: Gobiidae
44. ***Awaous taiasica***
45. ***Sicydium punctatum***

Family: Nandidae
46. ***Polycentrus schomburgkii***

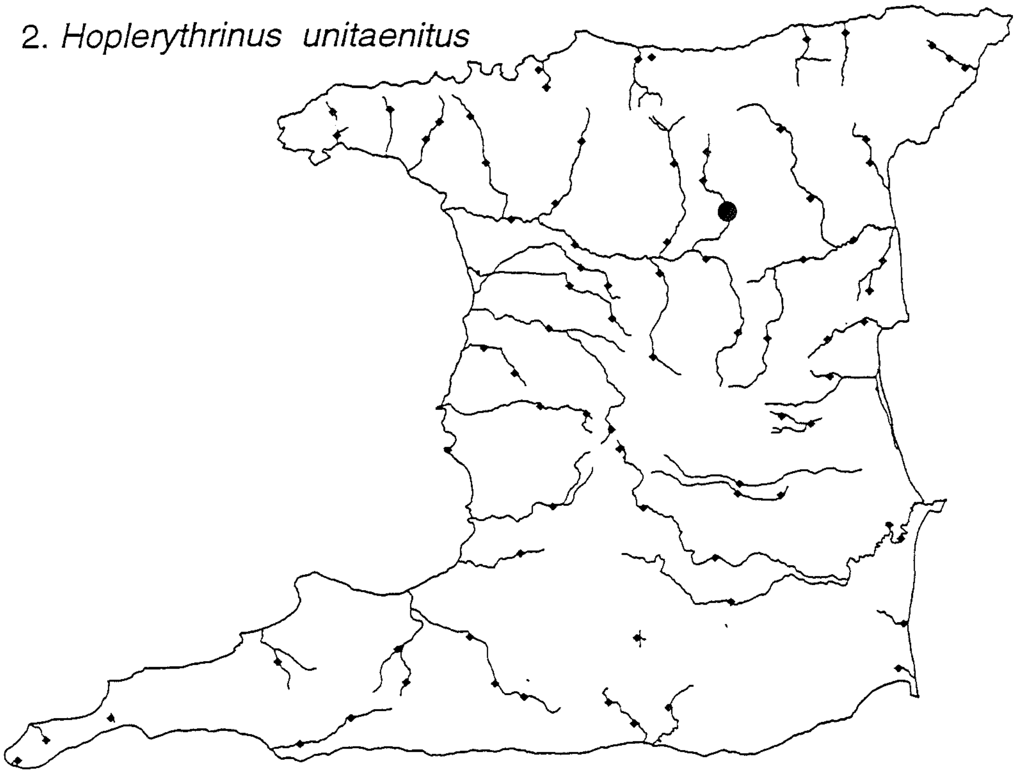
Family: Gobiesocidae
47. ***Gobiesox nudus***

Family: Centropomidae
51. *Centropomus sp.*

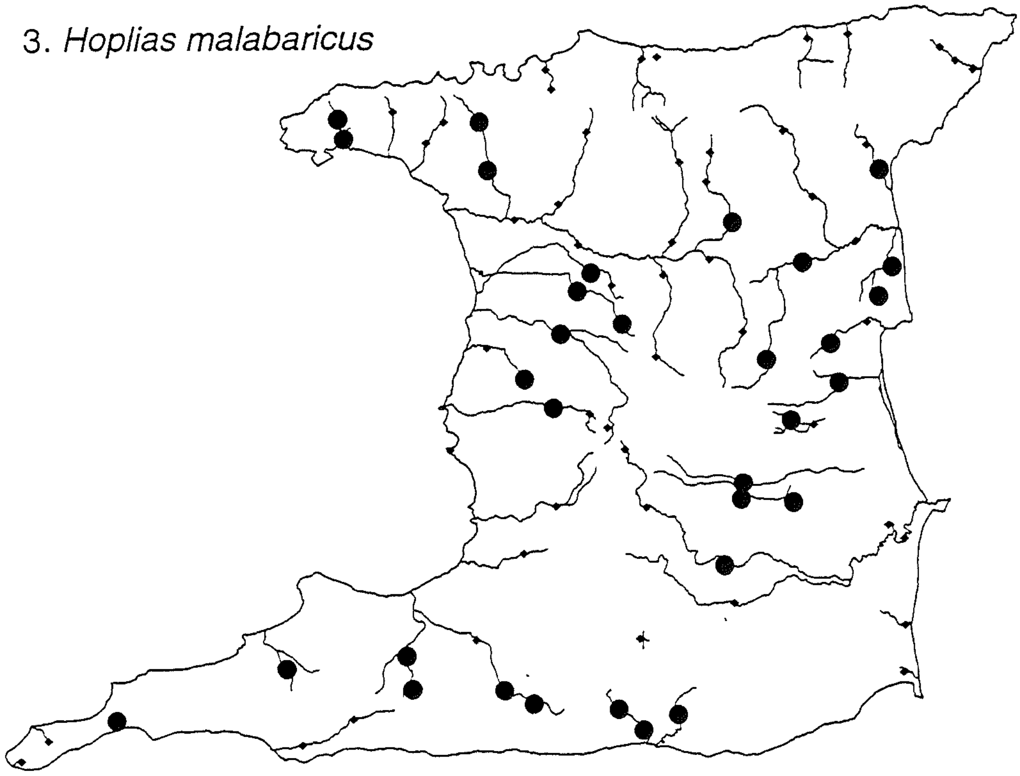
1. *Erythrinus erythrinus*



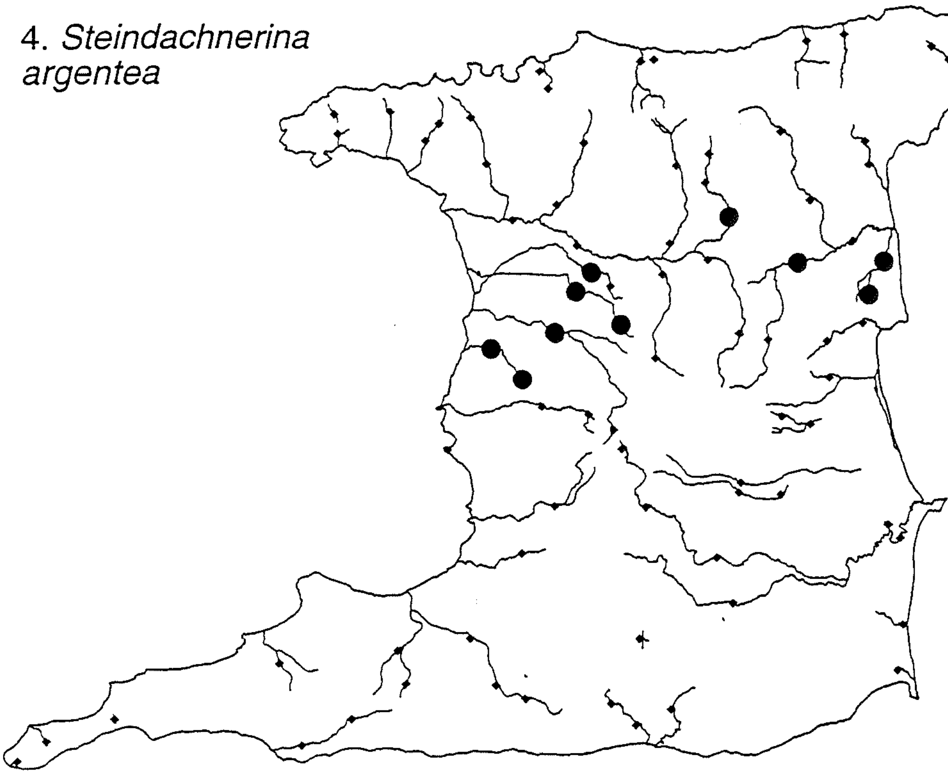
2. *Hoplerythrinus unitaenitus*



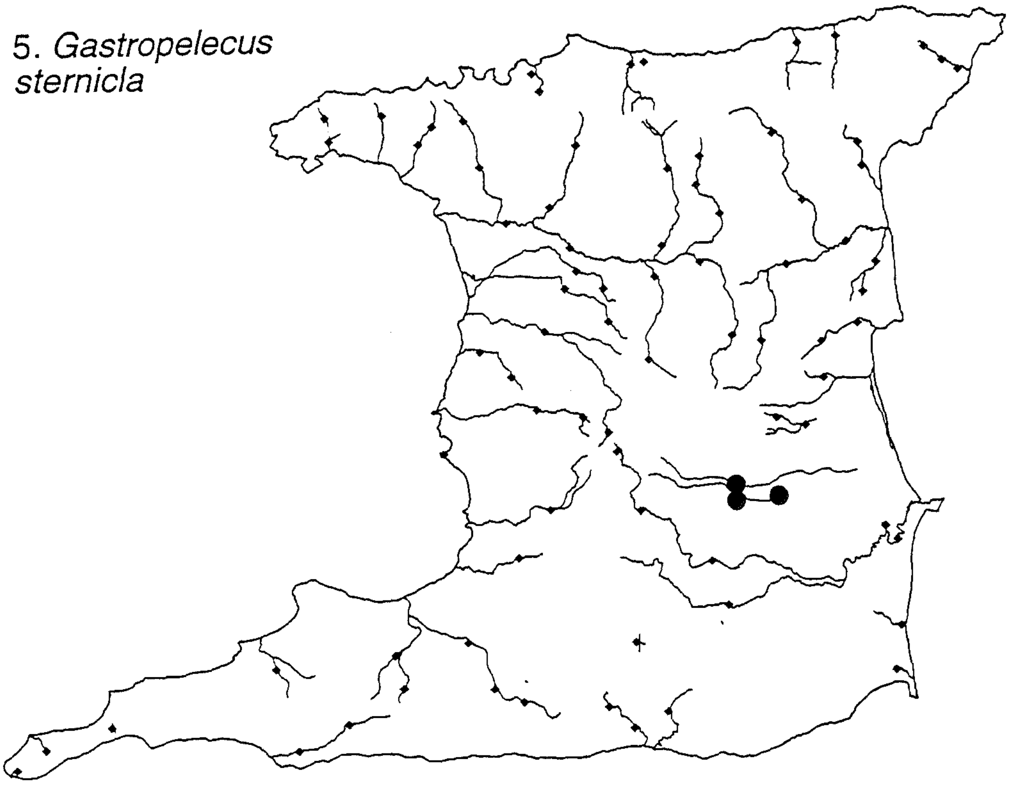
3. *Hoplias malabaricus*



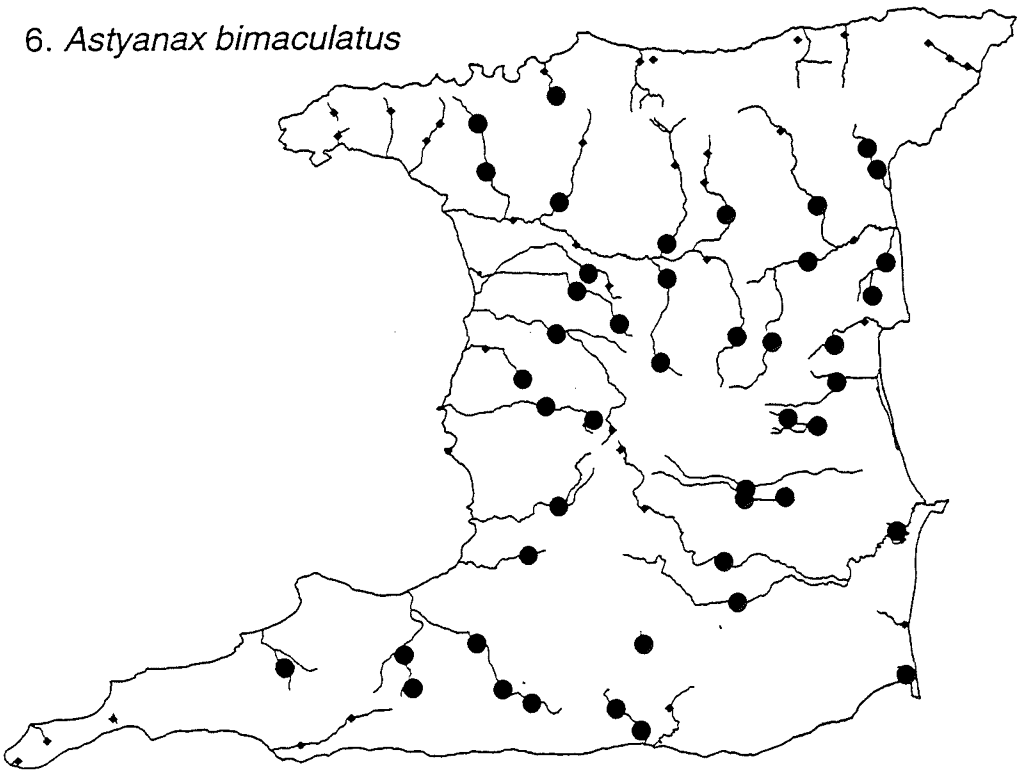
4. *Steindachnerina argentea*



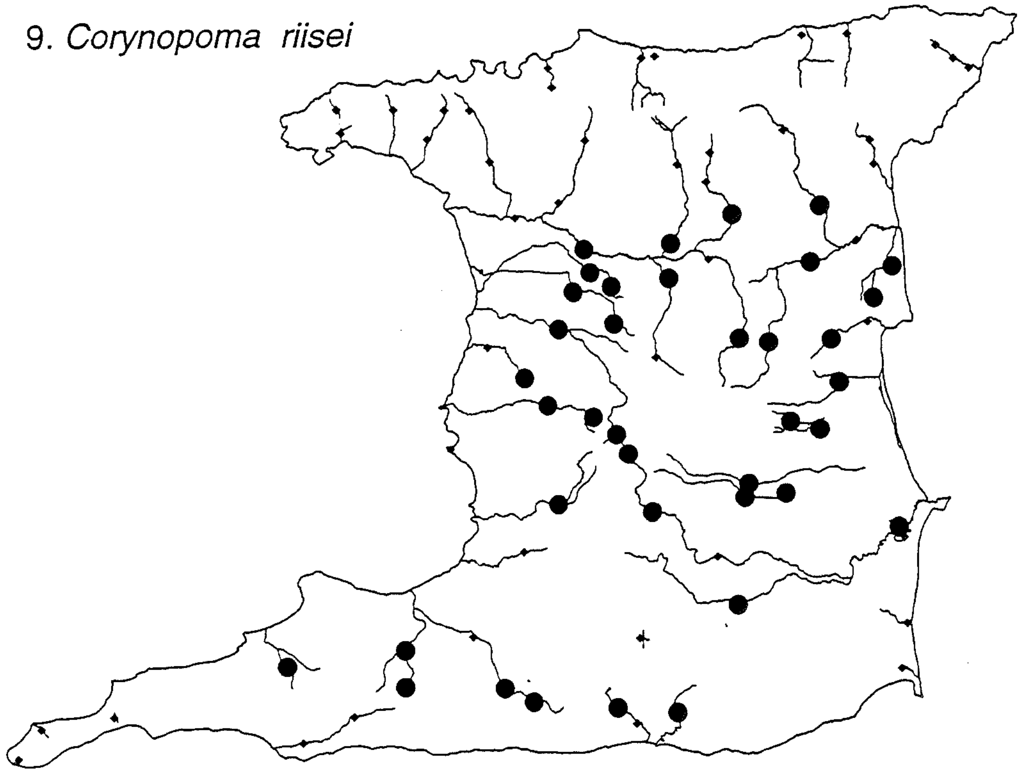
5. *Gastropelecus sternicla*



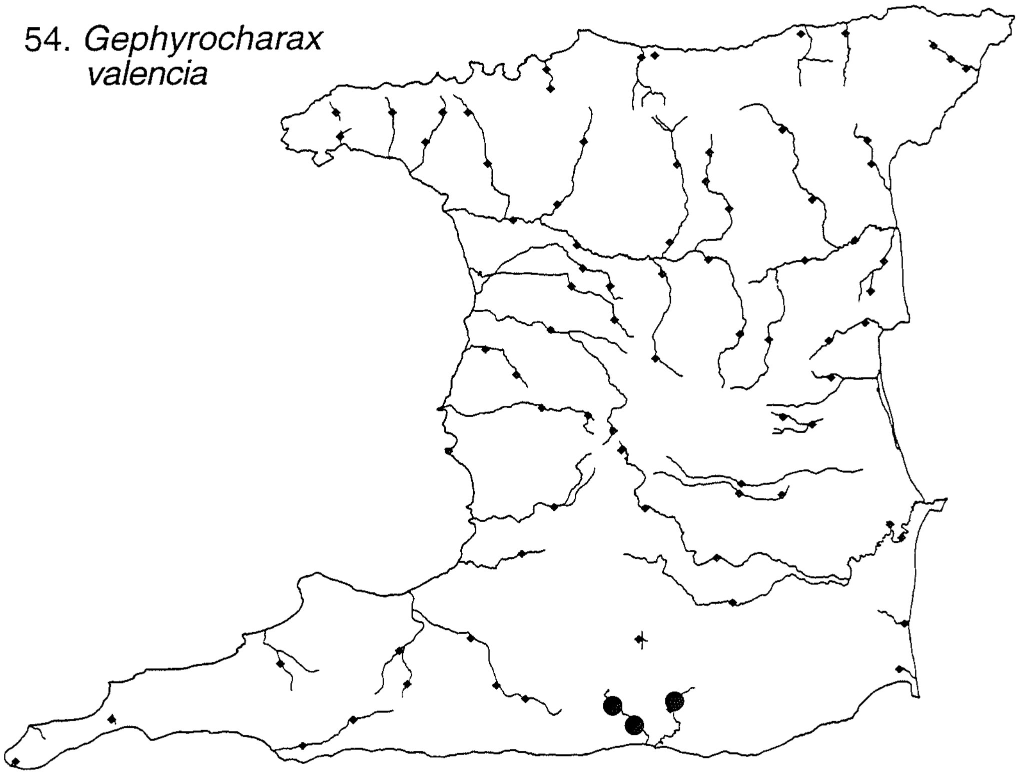
6. *Astyanax bimaculatus*



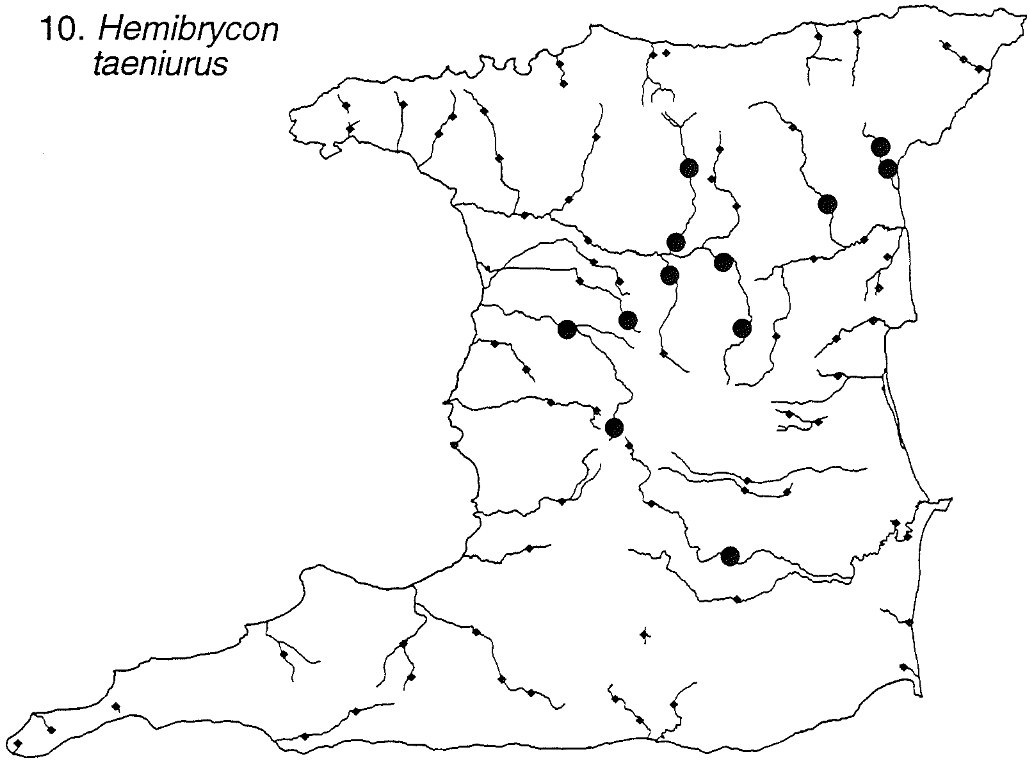
9. *Corynopoma riisei*



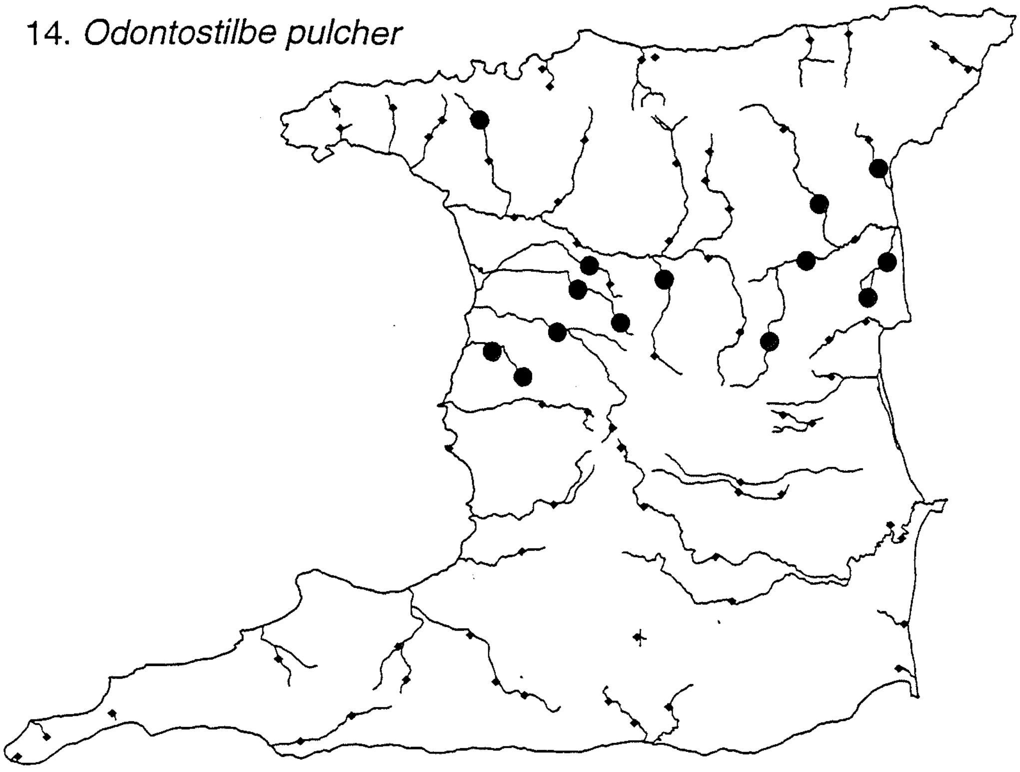
54. *Gephyrocharax valencia*



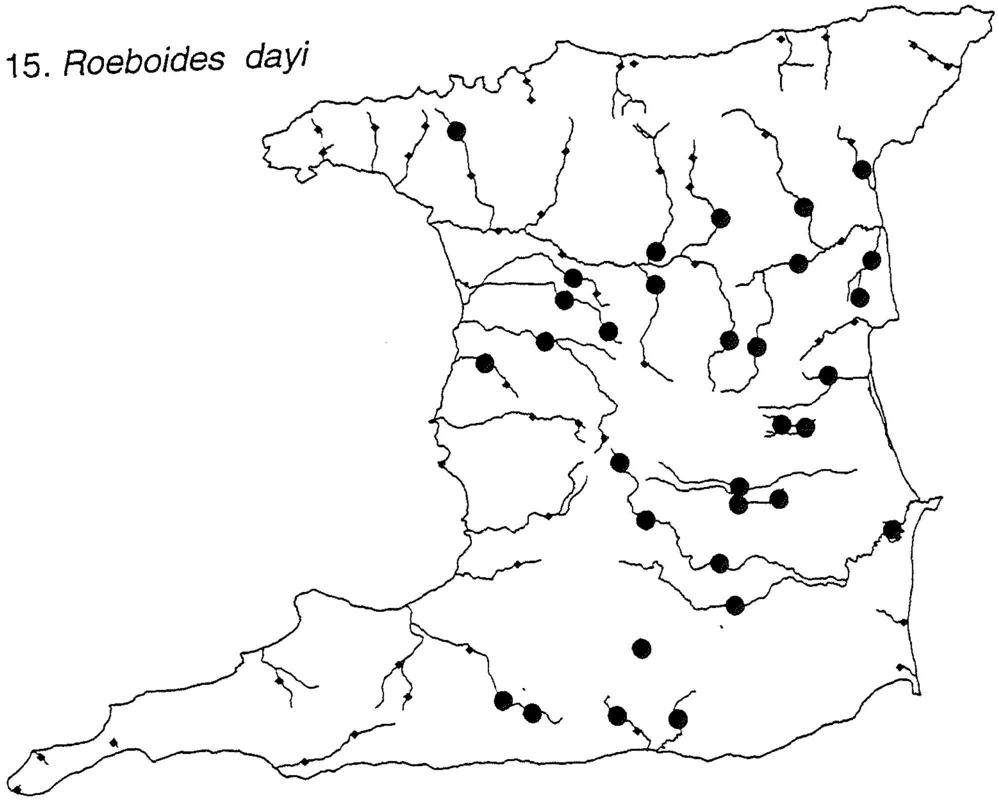
10. *Hemibrycon taeniurus*



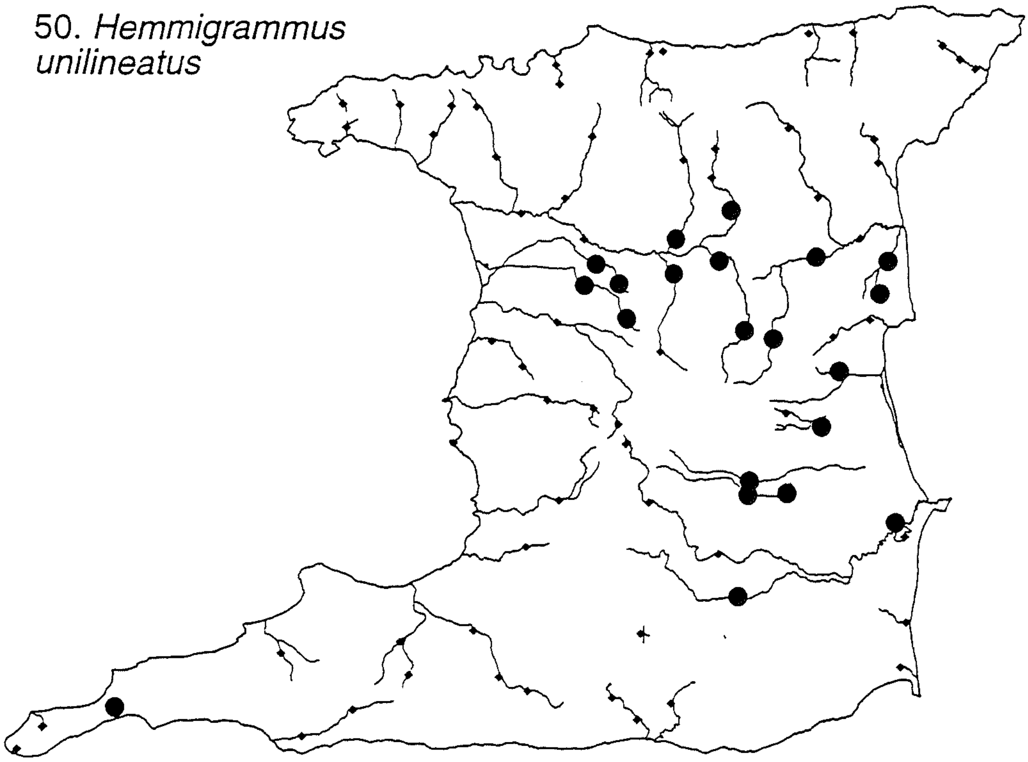
14. *Odontostilbe pulcher*



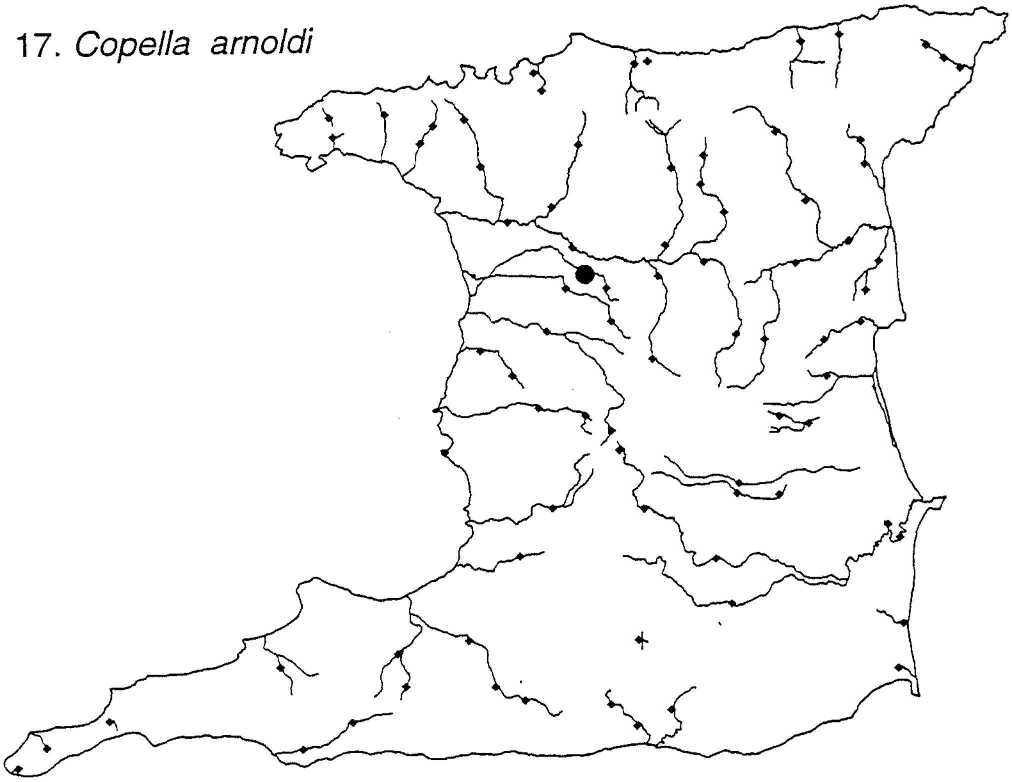
15. *Roeboides dayi*



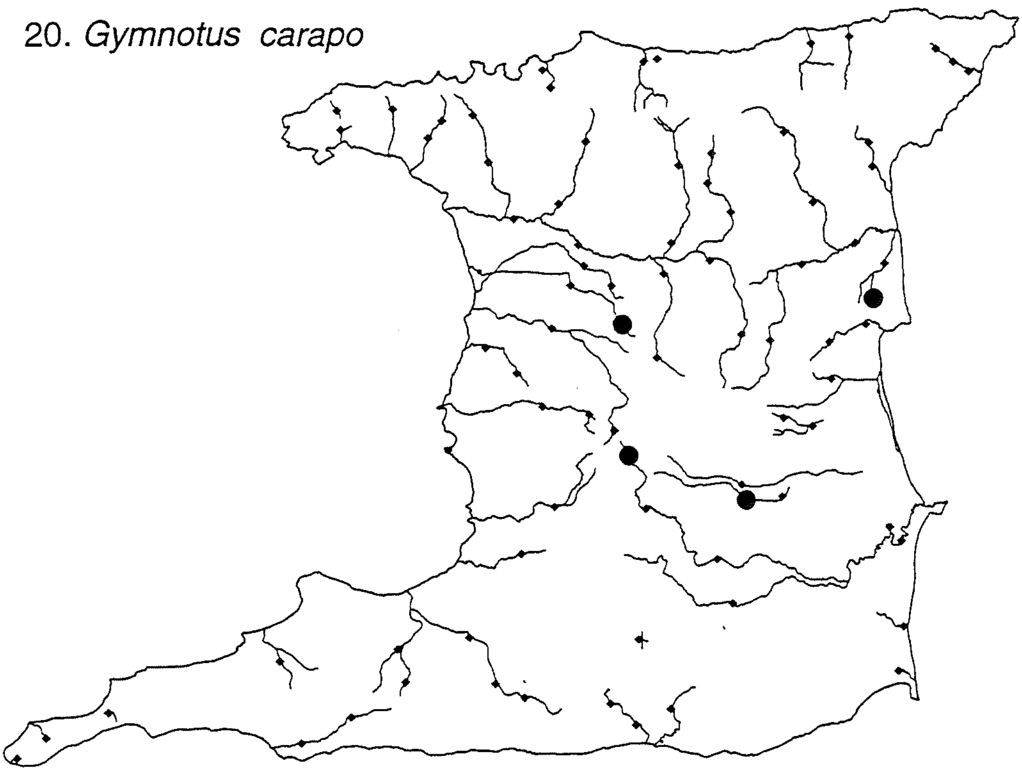
50. *Hemmigrammus unilineatus*



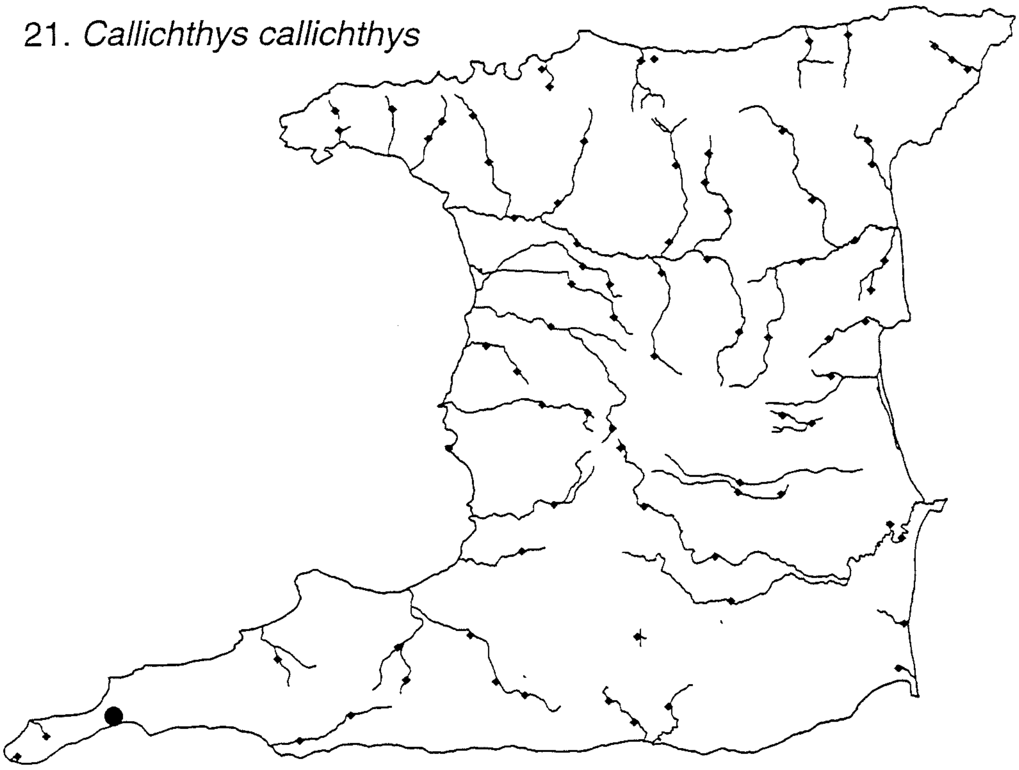
17. *Copella arnoldi*



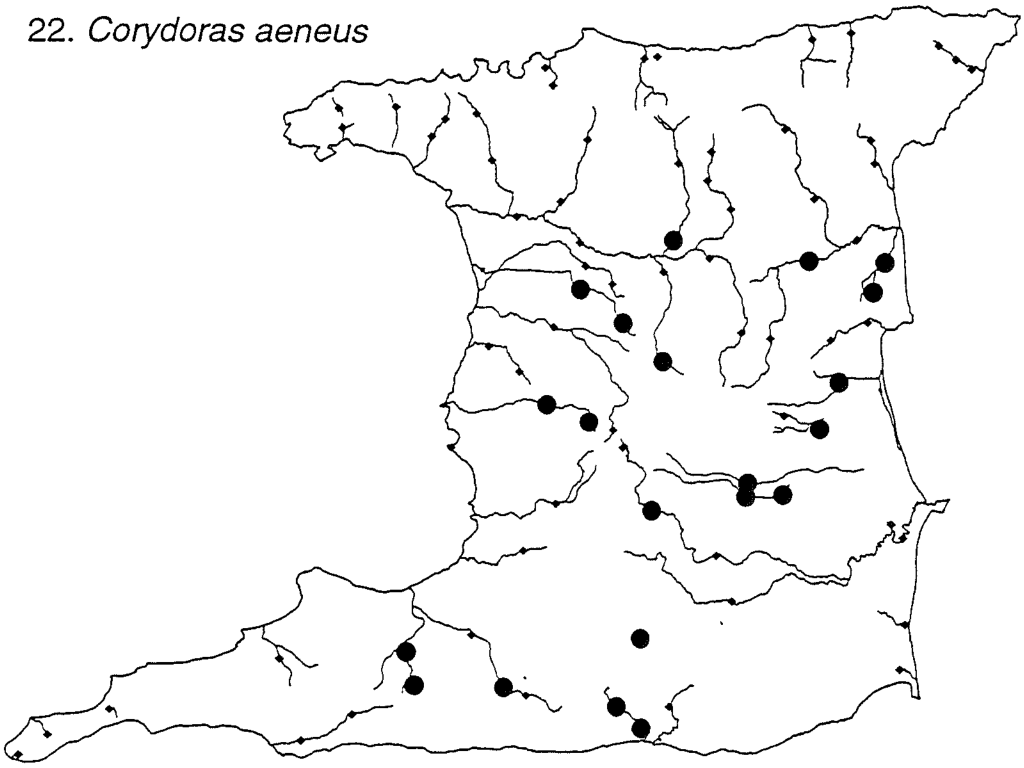
20. *Gymnotus carapo*



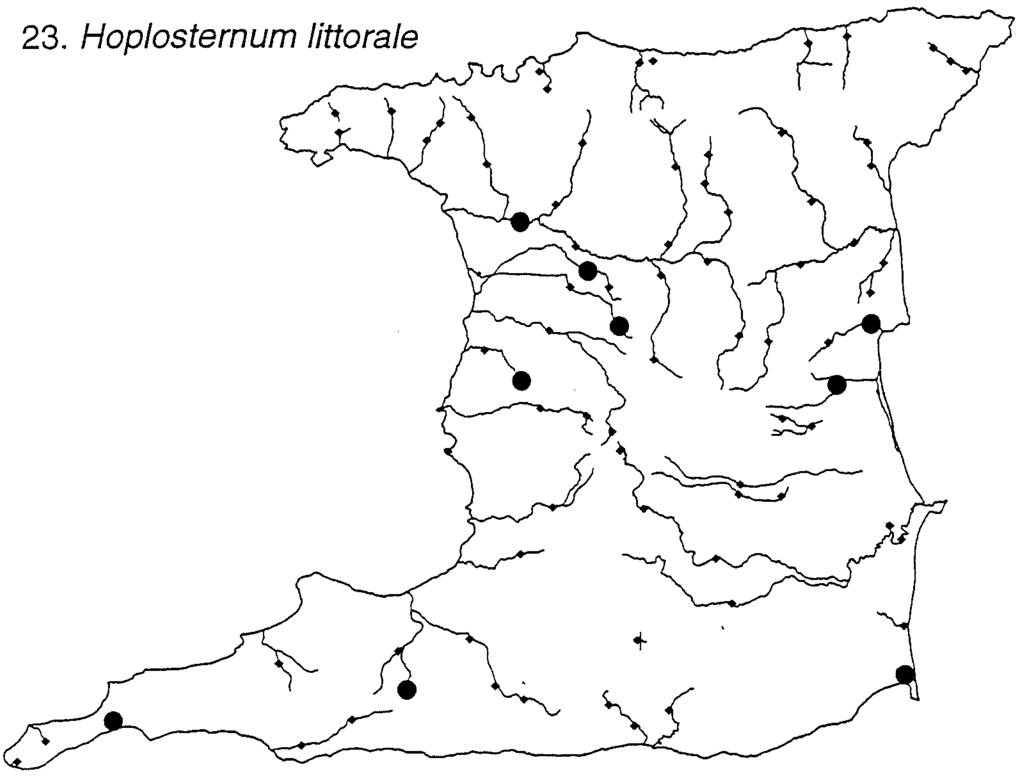
21. *Callichthys callichthys*



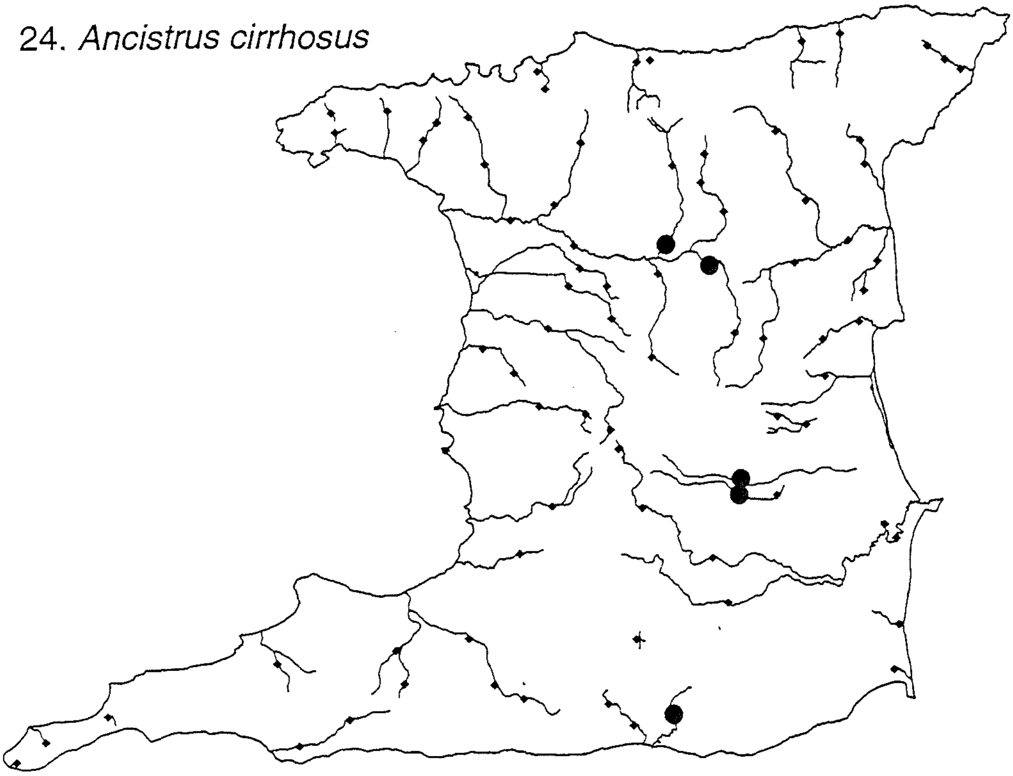
22. *Corydoras aeneus*



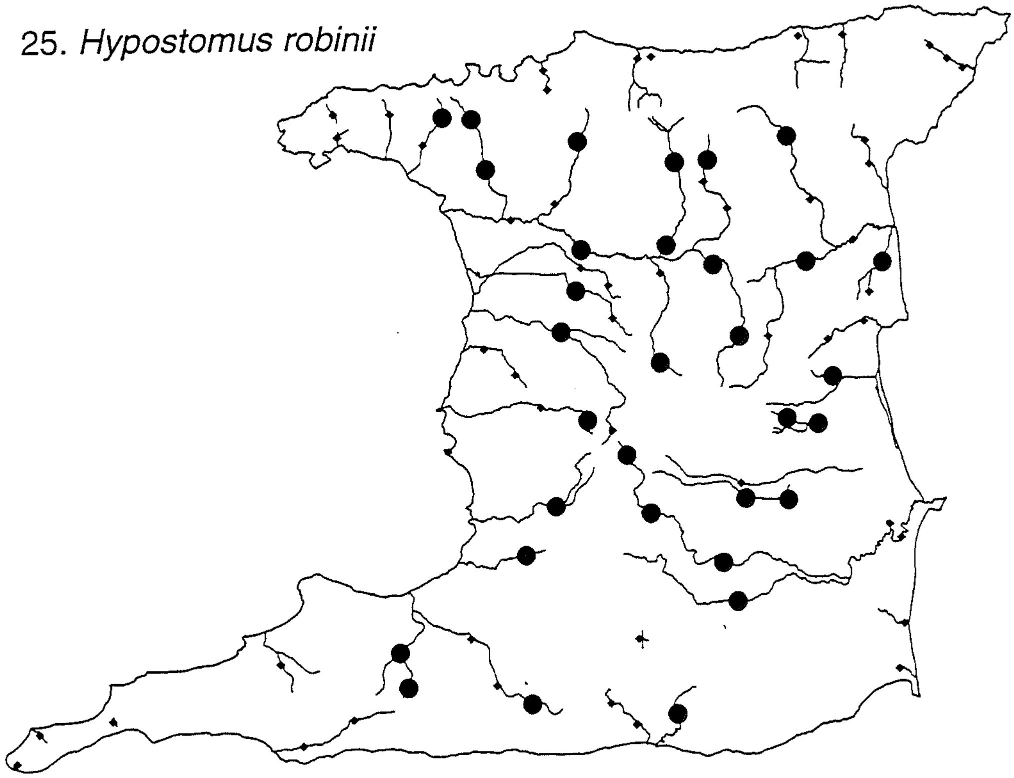
23. *Hoplosternum littorale*



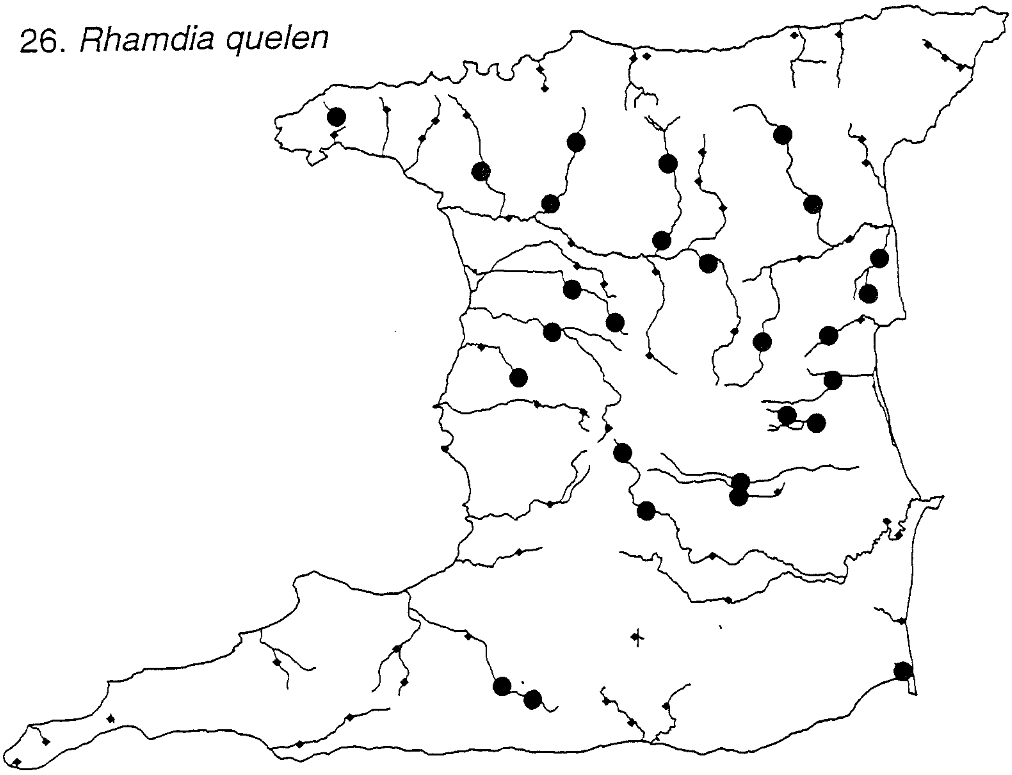
24. *Ancistrus cirrhosus*



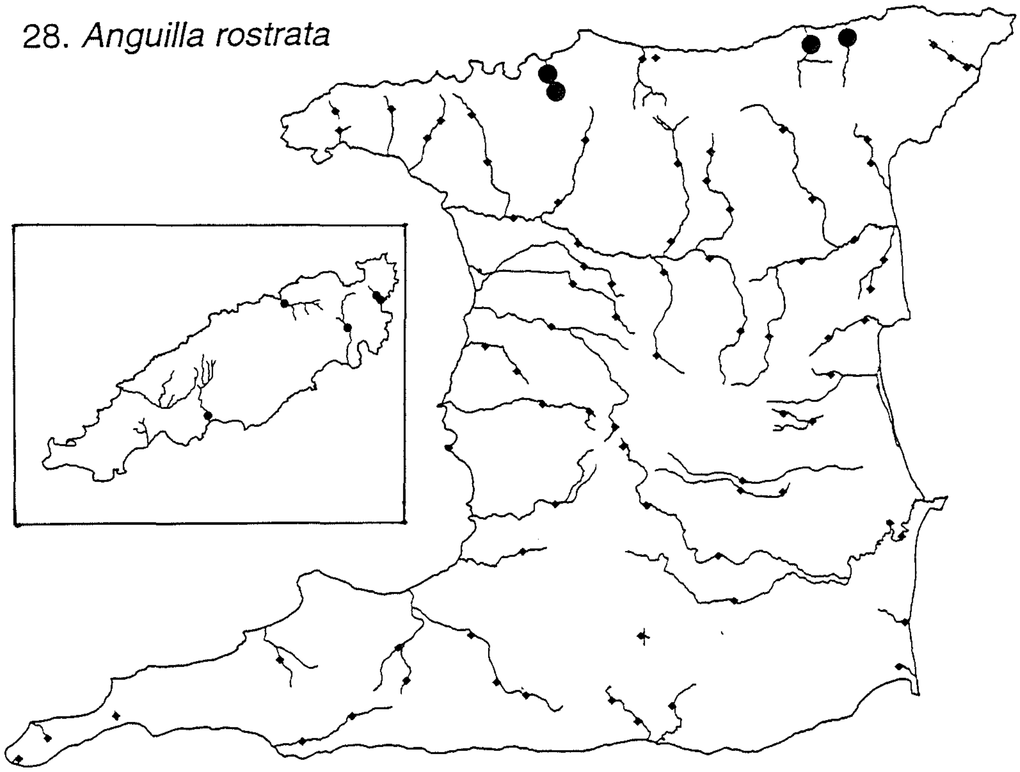
25. *Hypostomus robinii*



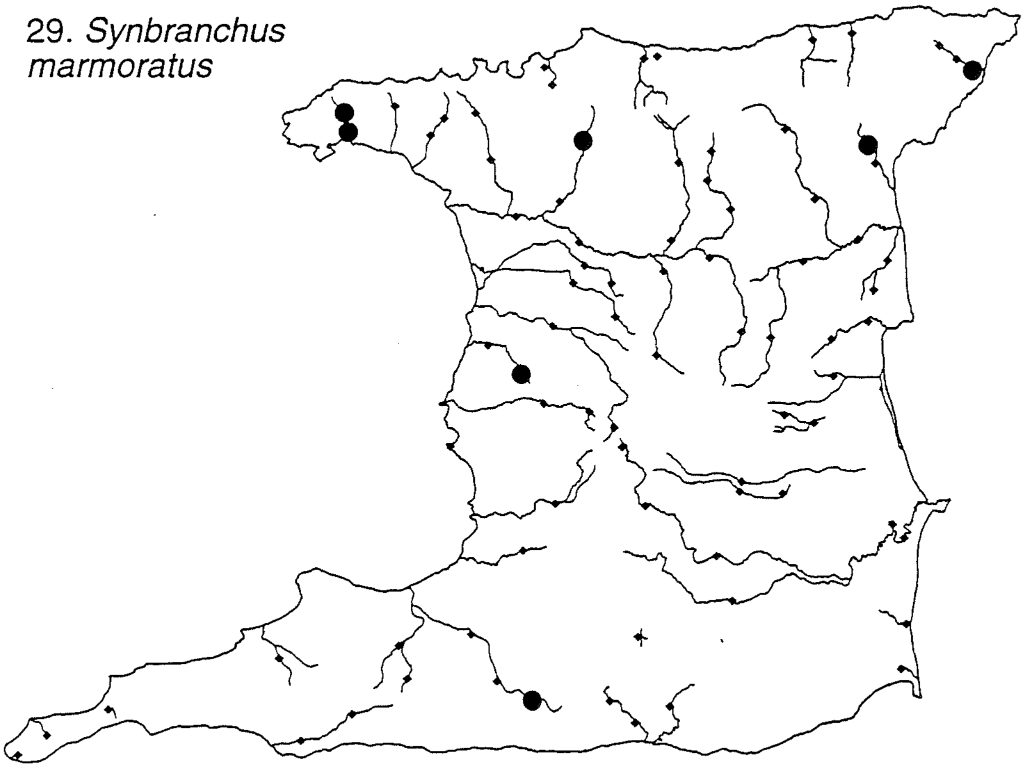
26. *Rhamdia quelen*



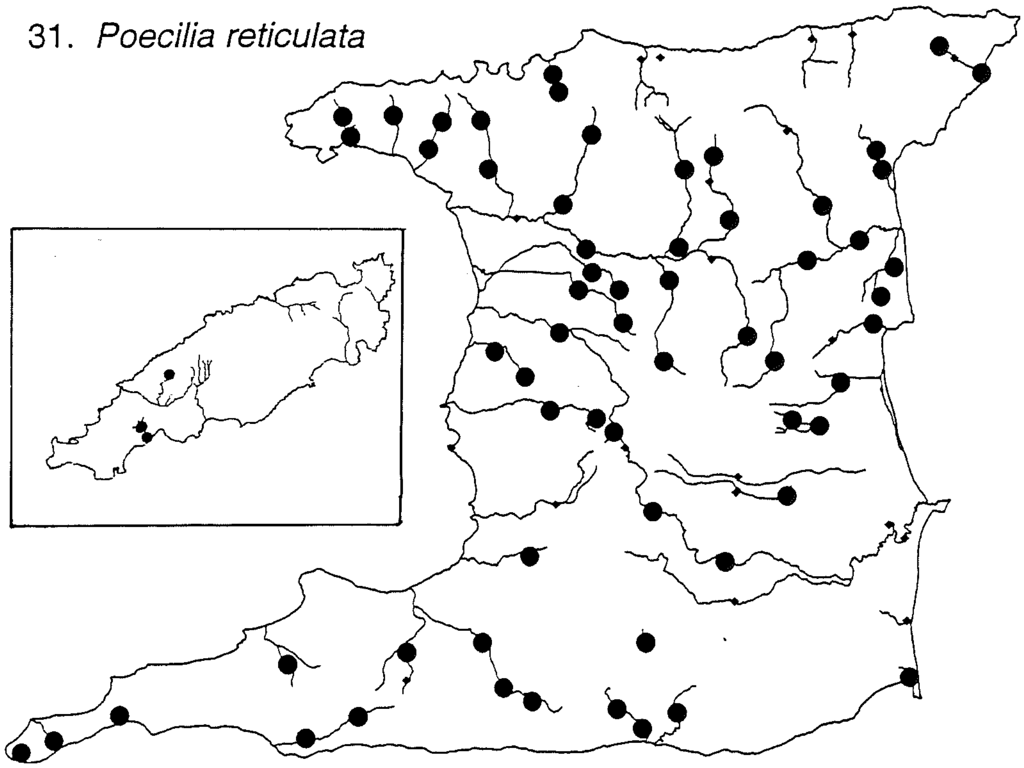
28. *Anguilla rostrata*



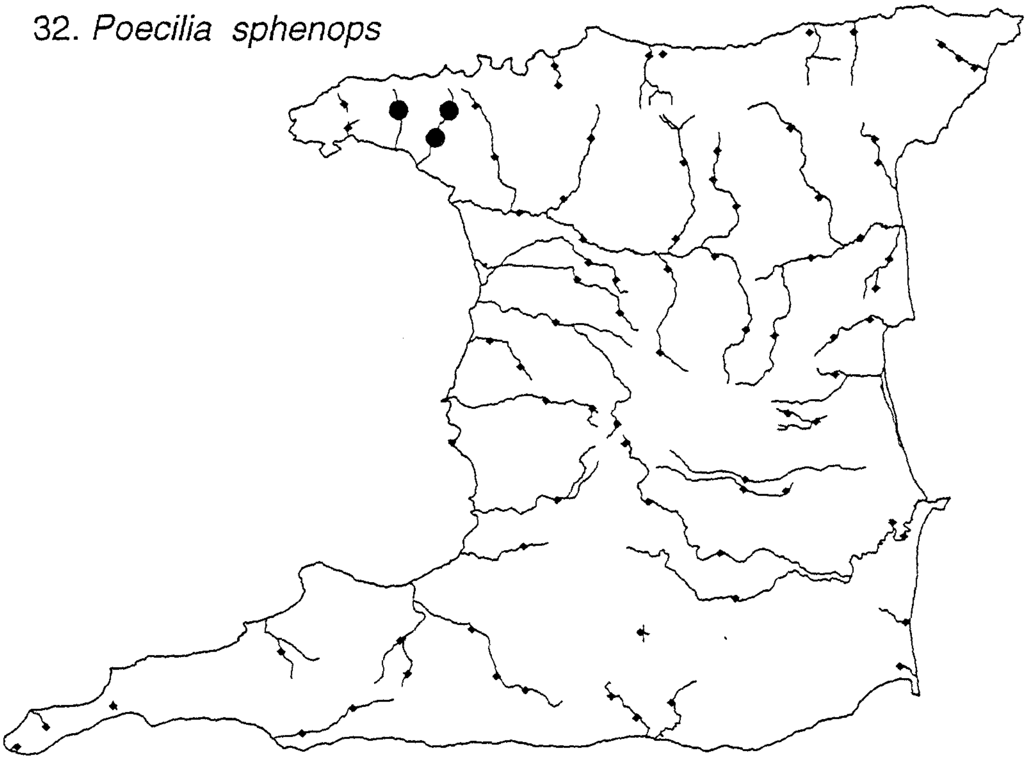
29. *Synbranchus marmoratus*



31. *Poecilia reticulata*

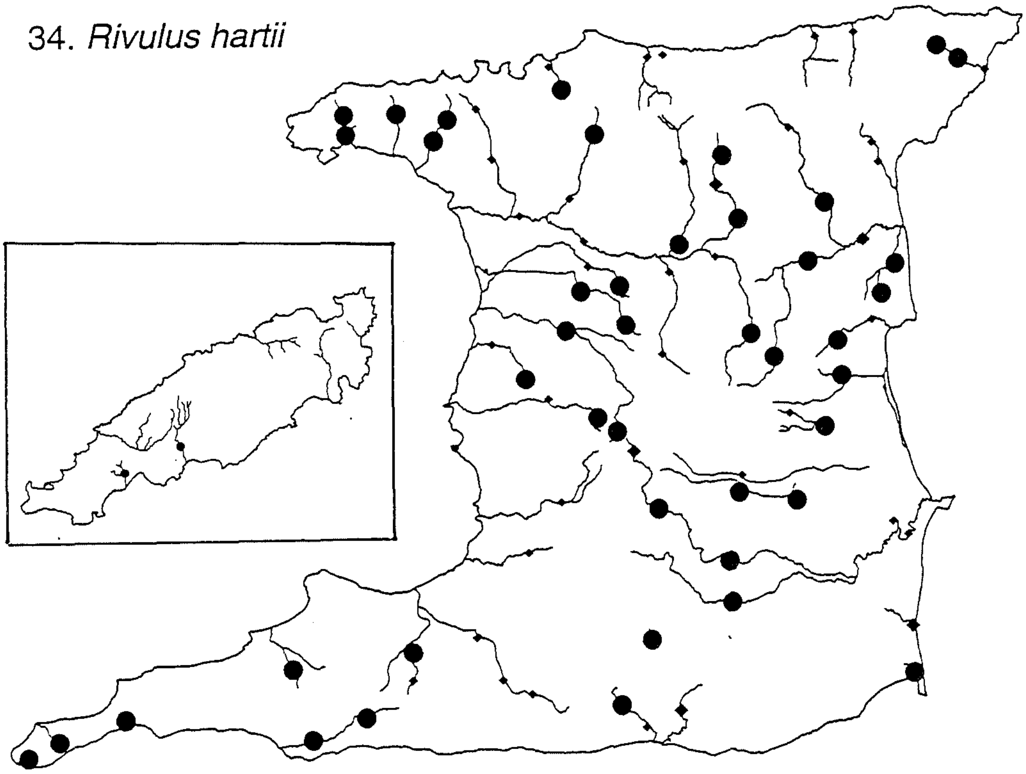


32. *Poecilia sphenops*

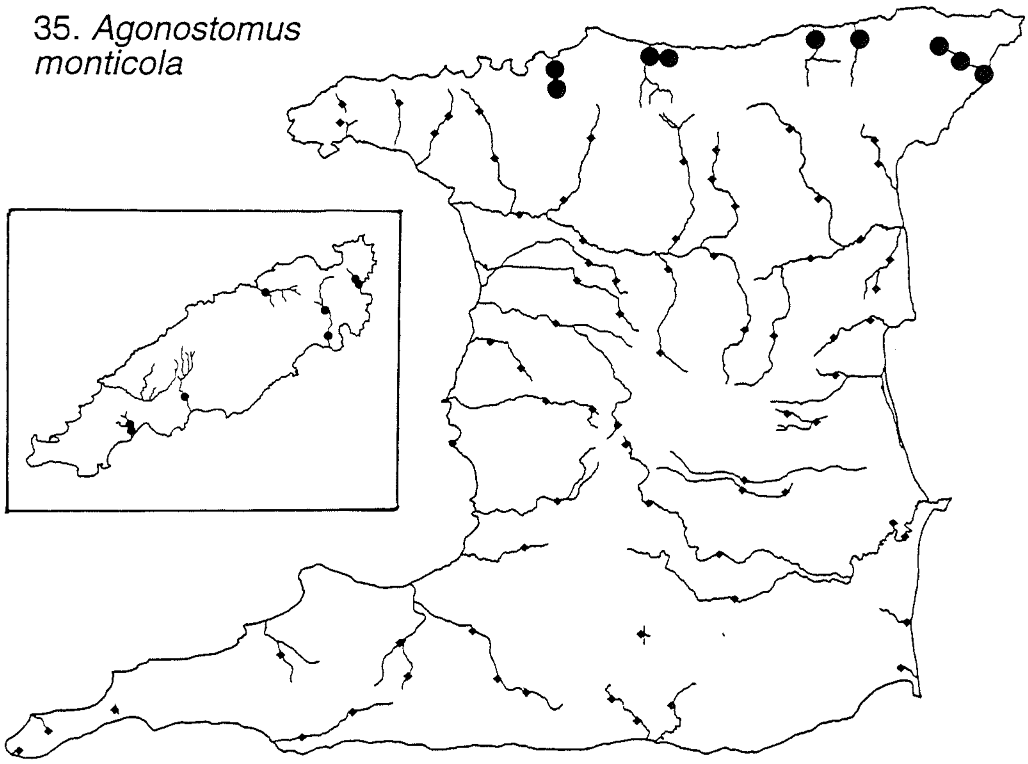


33. *Poecilia vivipara*

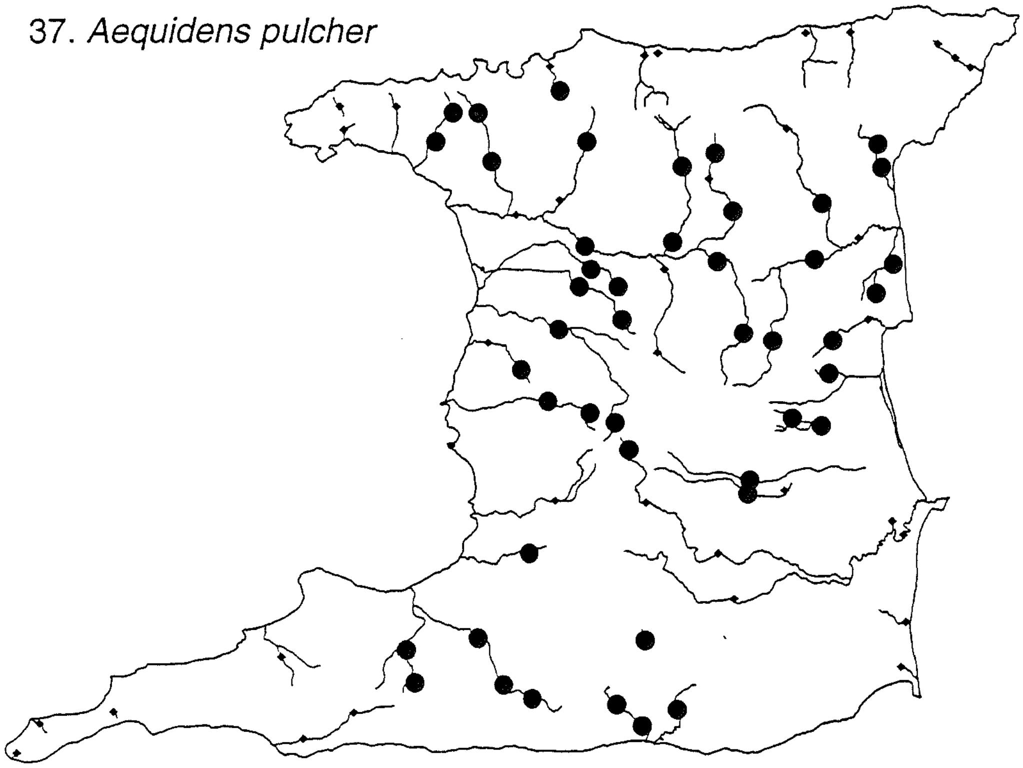
34. *Rivulus hartii*



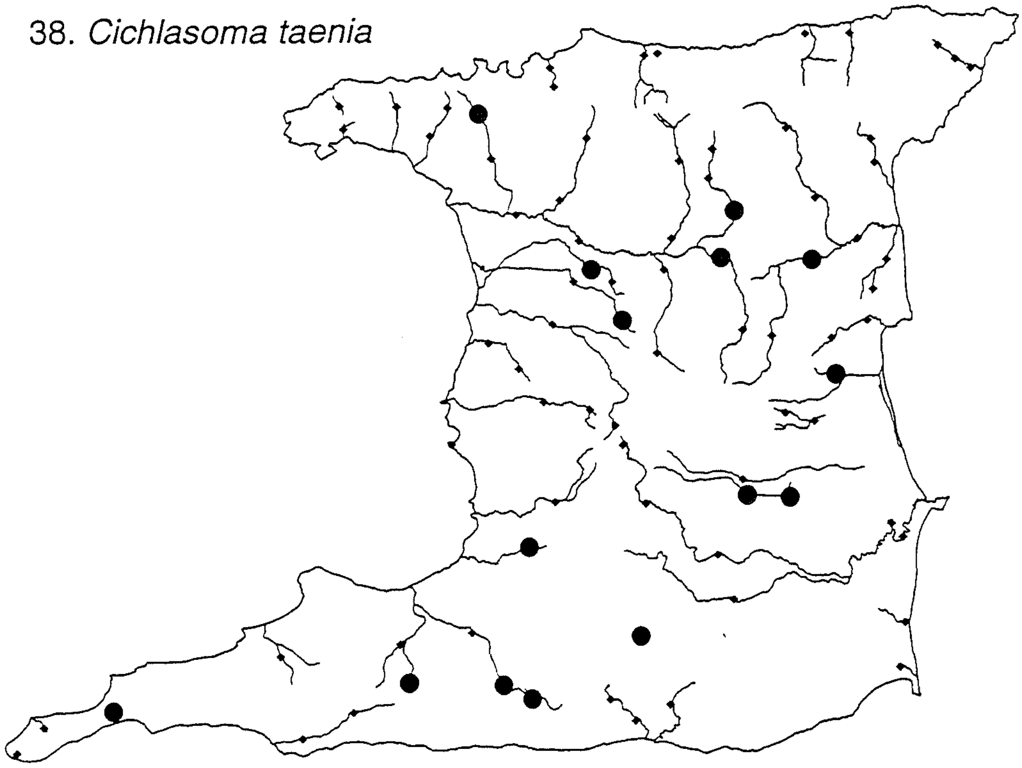
35. *Agonostomus monticola*



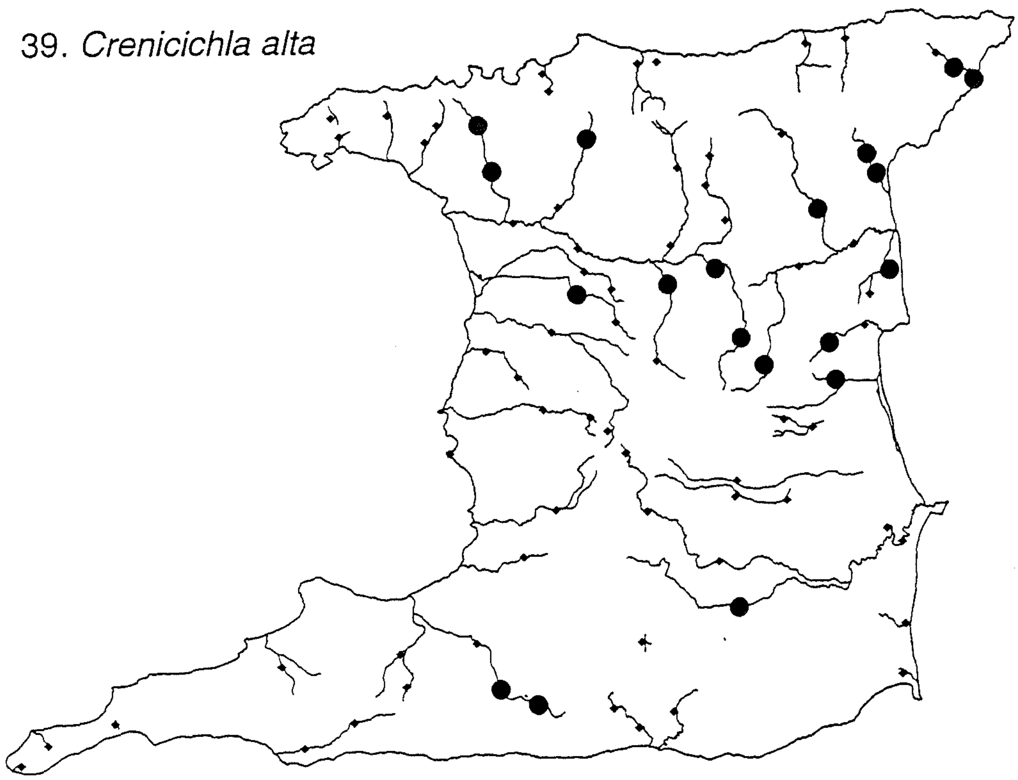
37. *Aequidens pulcher*



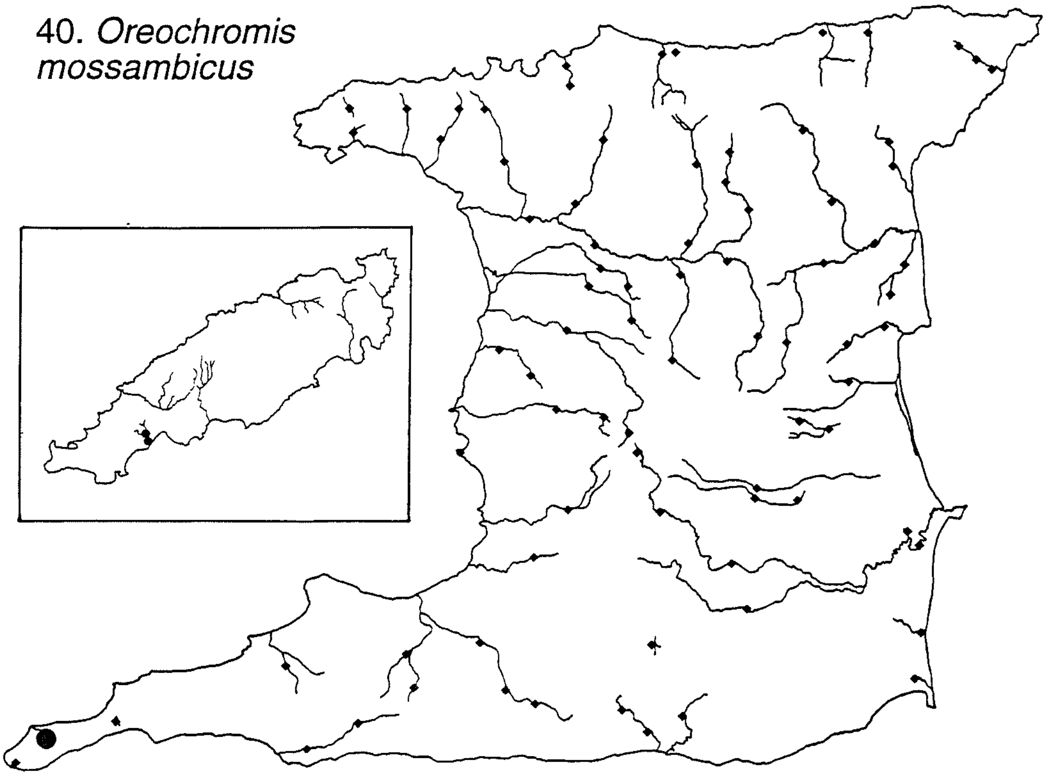
38. *Cichlasoma taenia*



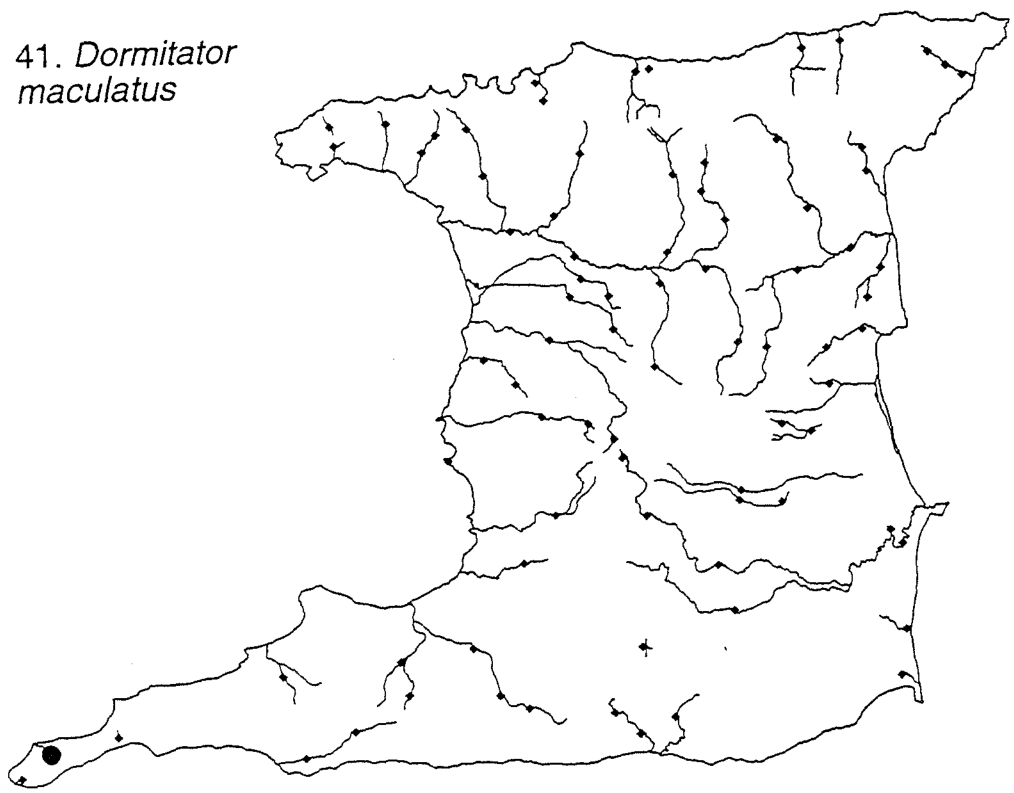
39. *Crenicichla alta*



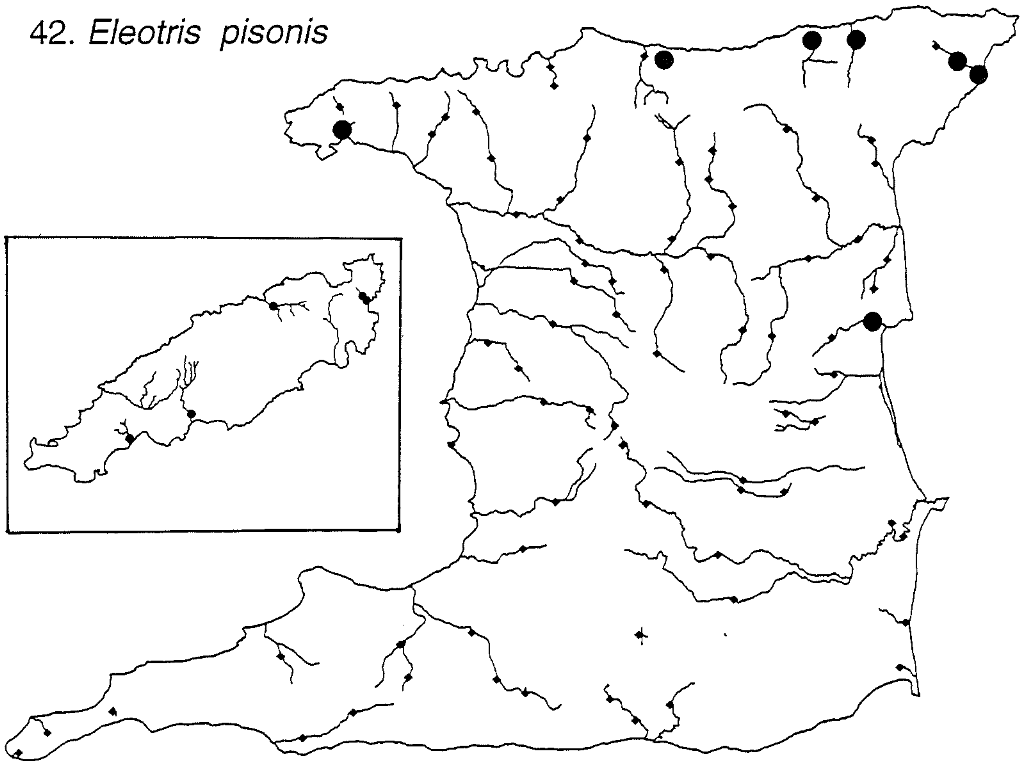
40. *Oreochromis mossambicus*



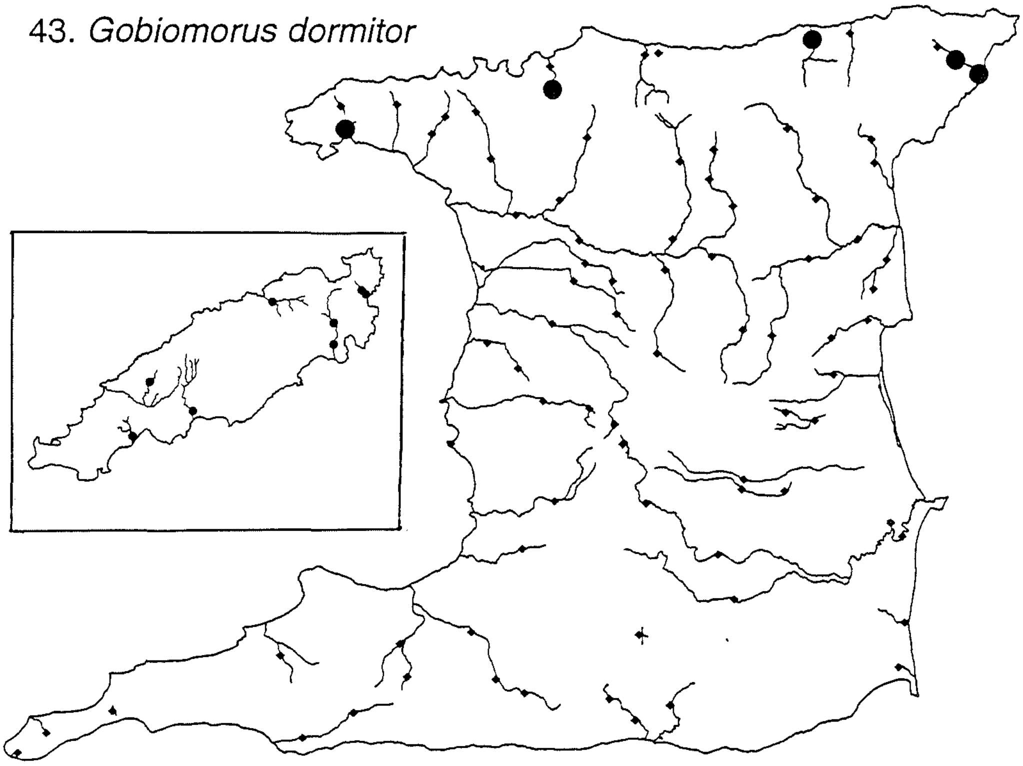
41. *Dormitator maculatus*



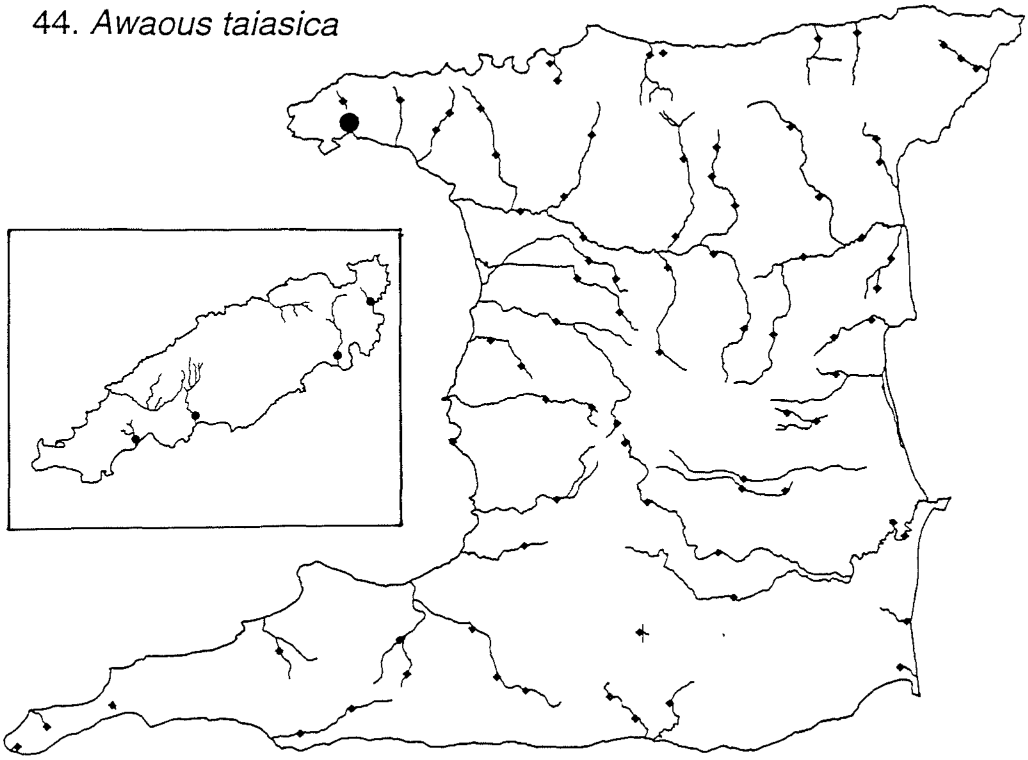
42. *Eleotris pisonis*



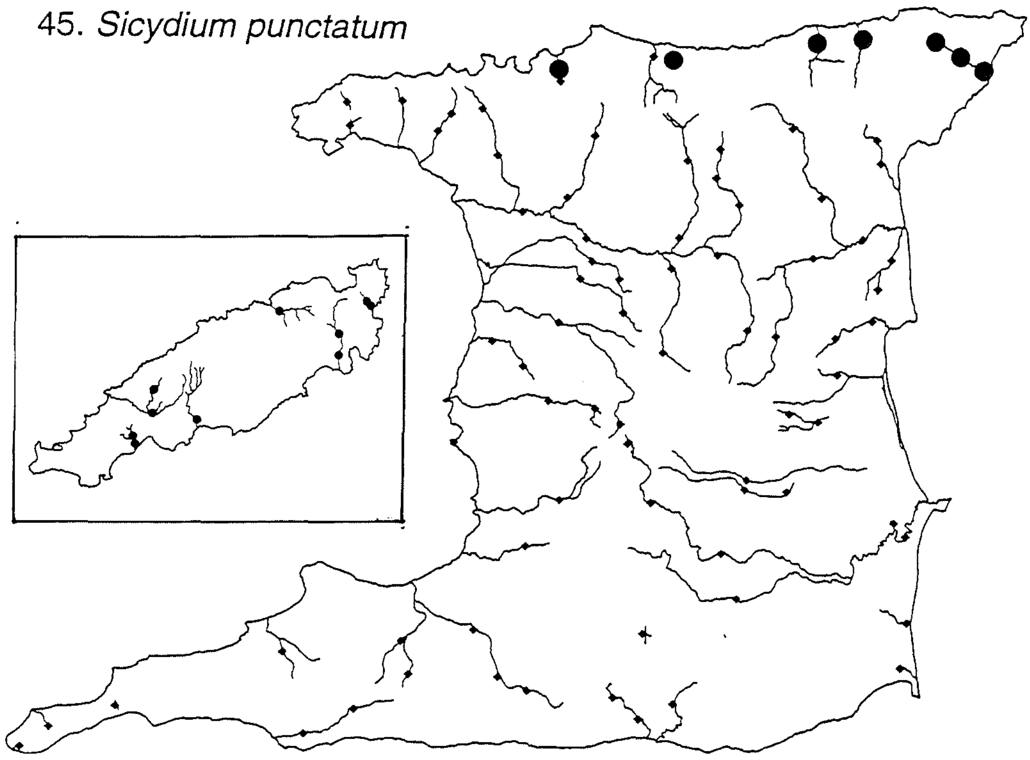
43. *Gobiomorus dormitor*



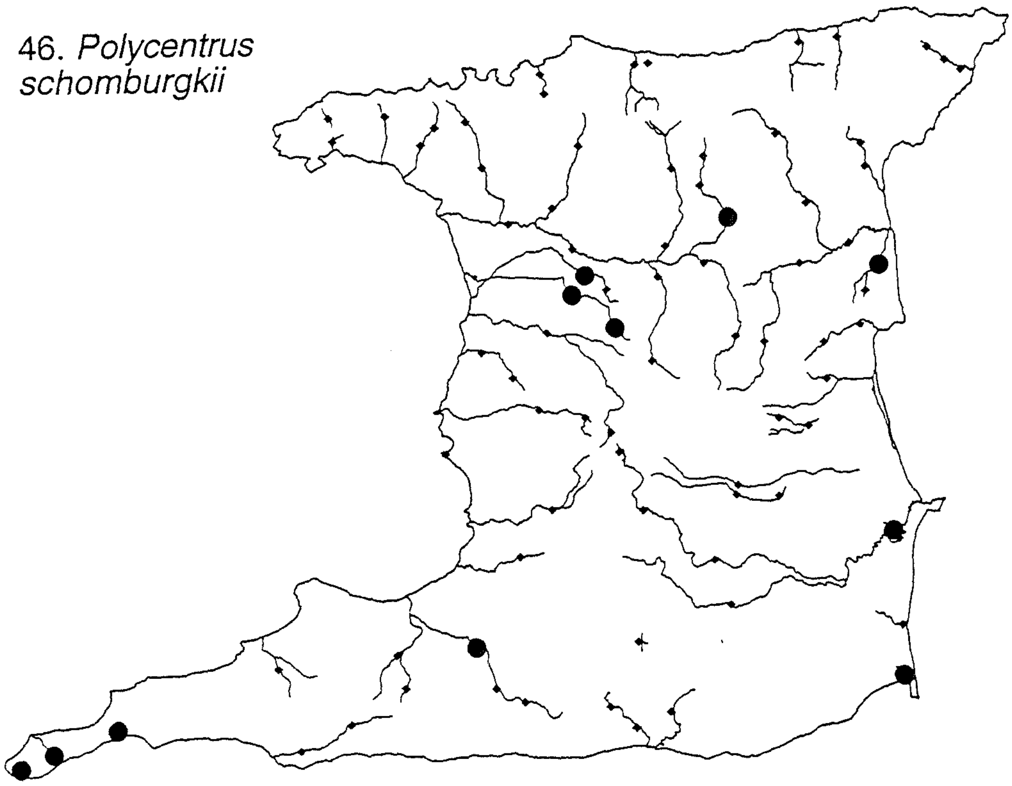
44. *Awaous taiasica*



45. *Sicydium punctatum*



46. *Polycentrus schomburgkii*



47. *Gobiesox nudus*