

A survey of freshwater fishes and their macroparasites in the Guanacaste Conservation Area (ACG), Costa Rica

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Norwegian Institute for Nature Research

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The cichlid *Astatotheros alfari*, Rio Sapoa, ACG.

Photo: O.T. Sandlund

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Abstract

Sandlund, O.T., Daverdin, R.H., Choudhury, A., Brooks, D.R. & Diserud, O.H. 2010. A survey of freshwater fishes and their macroparasites in the Guanacaste Conservation Area (ACG), Costa Rica. - NINA Report 635. 45 pp.

Freshwater fish were collected mainly by electrofishing in 27 localities in rivers and streams within the Area de Conservacion Guanacaste in northwestern Costa Rica, in June 1998 (rainy season), February 1999 and March 2001 (dry season). The fish were identified and analyzed for macroparasites. Fourteen localities were in rivers draining to the Atlantic, and 13 draining to the Pacific. On the Pacific slope, three localities were seasonal streams with small catchment areas. Five localities lacked fish, probably due to effluents from volcanic areas. A total of 36 fish species were recorded, including one new to science; *Poecilopsis santaelenae*. The most commonly occurring species were the catfish *Rhamdia rogersi* (11 sites), the cichlid *Astatheros alfari* (10 sites), and the guppy *Poecilia gillii* (9 sites). A total of 25 fish species were recorded on the Pacific slope, and 26 species on the Atlantic slope. On the Pacific slope, sampling sites were at altitudes from 8 to 880 m a.s.l.; on the Atlantic slope from 205 to 675 m a.s.l. On both slopes the number of species per site decreased with increasing altitude. Fish communities at lower altitudes included species feeding on detritus and plant material as well as species feeding on invertebrates and fish. At higher altitudes, species feeding on invertebrates became increasingly dominant. At the uppermost sites, the only recorded fish species were invertebrate feeders.

A total of 50 parasite taxa were recorded by necropsy and visual inspection of the fish material. Both prevalence and abundance of parasites were generally quite low. So far two species have been described as new to science; *Wallinia chavarria* and *Paracreptotrema blancoi*. During the rainy season (June 1998), 29 parasite taxa were identified from 369 dissected fish hosts. In the two dry season samples, 25 parasite taxa were identified from 277 hosts in 1999, while 26 taxa were found in 450 hosts in 2001. Twelve parasite taxa were found only in the wet season, 21 taxa were found only in the dry season, while 17 taxa were found in both seasons.

The parasite data were analysed with regard to how host diversity, host sample size and sampling season (dry or wet) affects parasite diversity, providing the following conclusions. Within each season, the number of host species analysed is the most important factor determining the recorded number of parasite taxa. Within each host species, it appears that increasing the number of analysed individual hosts from one site and season is as important for the number of recorded parasite taxa as adding hosts from different sampling sites or seasons. Our data also show that the number of parasite taxa recorded in fish (all host species) sampled in the rainy season is lower than in samples from the dry season. Finally, there is a large turnover of parasite taxa between seasons.

The macroparasite fauna of fishes in Guanacaste rivers generally follows the biogeographical patterns and history of their hosts. The parasite fauna of the cichlids resemble the fauna reported from southern Mexico, while the parasites recorded in the characid fish species show the connection to the parasites of characids in South America. The parasites recorded in the Cyprinodontiformes fishes (families Poeciliidae, Rivulidae, etc) in this study are consistent with the distribution of these parasites in middle America (Mexico to Panama).

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Resumen

Sandlund, O.T., Daverdin, R.H., Choudhury, A., Brooks, D.R. & Diserud, O.H. 2010. Muestreo de peces de agua dulce y de sus macroparásitos en el Área de Conservación Guanacaste (ACG), Costa Rica. - NINA Report 635. 45 pp.

Se capturaron peces de agua dulce principalmente por medio de electrofishing, en 27 localidades en ríos y quebradas ubicadas en el Área de Conservación Guanacaste, en el noroeste de Costa Rica. Las capturas se condujeron en junio de 1998 (época lluviosa), y en febrero de 1999 y en marzo del 2001 (época seca). En cada individuo se identificó la especie y luego se analizó la infección de macroparásitos. Los cursos de agua de 14 localidades drenaban al Atlántico, y 13 al Pacífico. En la vertiente del Pacífico, 3 localidades estaban ubicadas en quebradas estacionales de cuencas pequeñas. En 5 localidades no se encontraron peces, probablemente debido al efecto de afluentes de zonas volcánicas. En total, se registraron 36 especies de peces, incluyendo una especie nueva para la ciencia: *Poecilopsis santaelenae*. Las especies más comunes fueron el bagre *Rhamdia rogersi* (11 localidades), el cíclido *Astatheos alfari* (10 localidades), y el guppy *Poecilia gillii* (9 localidades). Veinticinco especies fueron registradas en la vertiente del Pacífico, y 26 en la del Atlántico. En la vertiente Pacífica, las localidades de muestreo se encontraron a alturas entre 8 y 880 m s.n.m, y en la vertiente Atlántica entre 205 y 675 m s.n.m. En ambas vertientes, el número de especies por localidad disminuyó con la altura. Las comunidades de peces a alturas bajas incluyeron especies que se alimentan de detritos y de material vegetal, así como también especies depredadoras de invertebrados y de peces. La dominancia de especies depredadoras de invertebrados aumentó con la altura y en las localidades más altas, sólo se registraron especies de este grupo.

En las muestras de peces, se registraron 50 taxa de parásitos en total. Tanto la prevalencia como la abundancia de parásitos fueron en general relativamente bajas. Hasta el momento, se han identificado 2 especies nuevas para la ciencia; *Wallinia chavarría* y *Paracreptotrema blancoi*. Durante la época lluviosa (junio de 1998), se encontraron 29 taxa de parásitos en 369 huéspedes disecados. En los dos muestreos en la época seca se registraron 25 taxa de parásitos en 277 individuos huésped en 1999 y 26 taxa en 450 huéspedes en el 2001. Doce taxa de parásitos fueron encontrados solamente en la estación lluviosa, 21 taxa, sólo en la época seca y 17 se registraron en ambas estaciones.

Los datos de parásitos fueron analizados con respecto a cómo la diversidad y el tamaño de muestra de los huéspedes, y la estación (seca o lluviosa) afectan su diversidad. Los resultados indican que dentro de cada estación, el número de especies huésped es el factor más importante que determina el número de taxa de parásitos. Para cada especie huésped, hay indicaciones de que aumentar el número peces en una localidad y en una estación es tan importante para determinar el número de parásitos registrados como agregar peces de distintas localidades y estaciones de muestreo. Nuestros datos también señalan que el número de taxa de parásitos (todas las especies huésped) muestreados en la época lluviosa es más bajo que en las muestras de la época seca. Finalmente, hay un alto grado de recambio de taxa de parásitos entre estaciones.

La fauna de macroparásitos de peces en los ríos de Guanacaste generalmente sigue los patrones biogeográficos de distribución de sus huéspedes. La asociada a los cíclidos se asemeja a la fauna reportada para el sur de México, mientras que los parásitos asociados a los Characidae están relacionados con los parásitos de Characidae de América del Sur. Los parásitos de los peces Cyprinodontiformes (familias de los Poeciliidae, Rivulidae, etc.) de este estudio tienen una distribución semejante a la de estos parásitos en Centro América (México y Panamá)

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Foreword

This survey of freshwater fishes and their parasites in Guanacaste Conservation Area (Area Conservacion de Guanacaste, ACG) was initiated as part of a larger survey of vertebrate parasites in this area (see <http://www.parasitesrus.com/content/?ps=1>). ACG was intended as the geographic site for the planned All Taxa Biodiversity Inventory (ATBI) (Janzen & Hallwachs 1994). When this mega biodiversity exercise had to be abandoned in its full scale format, some groups of scientists involved in the planning of the ATBI decided to continue the effort to inventory "their" respective taxonomic groups in ACG to the extent that funding could be obtained. The parasites of vertebrates were one of the groups where work on an inventory was initiated, coordinated by professor Dan Brooks. The NINA staff joined the field work and analysis of results. With funding from the Natural Sciences and Engineering Research Council of Canada (NSERC) and Norwegian Institute for Nature Research (NINA), we were able to collect freshwater fish and analyse their parasite fauna during three field periods, in June 1998 (at the beginning of the rainy season), and February 1999 and March 2001 (during the dry season). This somewhat delayed report describes the results of the surveys of 1998, 1999 and 2001, in order to provide an overview of the collected biodiversity data, as a possible baseline for future aquatic research activities in the ACG.

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Trondheim, November 2010

Odd Terje Sandlund

1 Introduction

The aim of the survey was to start mapping the occurrence and distribution of freshwater fish species and their macroparasites in the rivers of ACG. This report describes the results of field surveys performed during the rainy season of 1998 and the dry seasons of 1999 and 2001.

The species composition and distribution of the fresh water fish fauna in Costa Rica is fairly well known in general terms, in particular through the work of Professor W.A. Bussing, University of Costa Rica (Bussing 1985, 1987, 1998). The ACG is situated in a part of the country where the freshwater fish fauna has received little attention. One reason may be that the fauna is expected to contain relatively few species, due to the biogeography and immigration history of this fauna element in this particular area (Bussing et al. 1996, Smith & Bermingham 2005).

Important factors expected to influence the occurrence of fish species in this area are e.g. the position of rivers in relation to the major Pacific-Atlantic watershed divide (Smith & Bermingham 2005), altitude, and dry season water volume of the rivers. A survey aiming to establish the role of these biogeographical and physical factors on the observed distribution of fish will need to include collection on many sites (Bell 2003). Over three field periods, during the rainy season in 1998, and the dry season in 1999 and 2001, a total of 27 localities were sampled.

The fish material has been deposited at the Museum of Zoology, University of Costa Rica, San José, and at the Tropical Dry Forest Research Station, Santa Rosa, ACG.

In contrast to the fish fauna, the parasites of fishes in the fresh waters of Central America remain poorly known (Watson 1976; Choudhury et al. 2002; Rodríguez-Ortiz et al. 2004a, b; Choudhury et al. 2006; Scholz et al. 2004; Salgado-Maldonado 2008). This study is the first comprehensive and concerted study on the parasites of a diverse assemblage of fishes from a variety of drainages of differing hydrological and geographical characteristics in a particular region of Central America.

The parasite material is currently in the possession of one of us (AC) and will be deposited at the U.S. National Parasite Collection and the National Parasite Collection in Costa Rica as and when the taxonomic work is complete. Specimens of two described species, *Wallinia chavarriae* and *Paracreptotrema blancoi* have already been deposited at the U.S. National Parasite Collection.



Quebrada Aserradero (locality 4; 155 m a.s.l.).

2 Study area

In 2001 ACG included an area of 1100 km² on land and 430 km² marine areas (**Figure 1**). The land area straddles the watershed between the Pacific and the Atlantic. All rivers on the Atlantic slope of ACG drain to Lake Nicaragua. Consequently they belong to the Rio San Juan watershed, and also the San Juan biogeographical province (Smith & Bermingham 2005). On the Pacific slope, however, there are a number of separate and smaller watersheds in addition to major parts of the conservation area draining to the Rio Tempisque watershed, but they all belong to the Chiapas-Nicaragua biogeographical province (Smith & Bermingham 2005). The majority of the smaller lowland rivers on the Pacific side are seasonal, but some receive sufficient groundwater to maintain some permanent pools through the dry season. ACG straddles the watershed divide between the Pacific and the Atlantic, but while the conservation area reaches all the way to the Pacific Ocean, it is restricted to relatively high altitudes on the Atlantic side. Thus, our sampling sites on the Atlantic slope were at altitudes from 205 to 675 m above sea level, whereas on the Pacific side we were able to collect fish from practically sea level (8 m a.s.l.) to 570 m a.s.l. (**Table 1**). One investigated Pacific slope locality was situated at 880 m a.s.l., but it was devoid of fish, probably due to poor water quality.

A total of 27 localities were sampled, 14 on the Atlantic slope and 13 on the Pacific slope (**Table 1**). At two localities on the Atlantic slope and three on the Pacific slope, we were not able to catch any fish. These are all localities with permanent water. However, being situated close to and draining the active volcanic area at Rincón de la Vieja, it seems likely that the water quality renders them unfit for fish. A closer description of the fished localities is given in **Annex 1**.

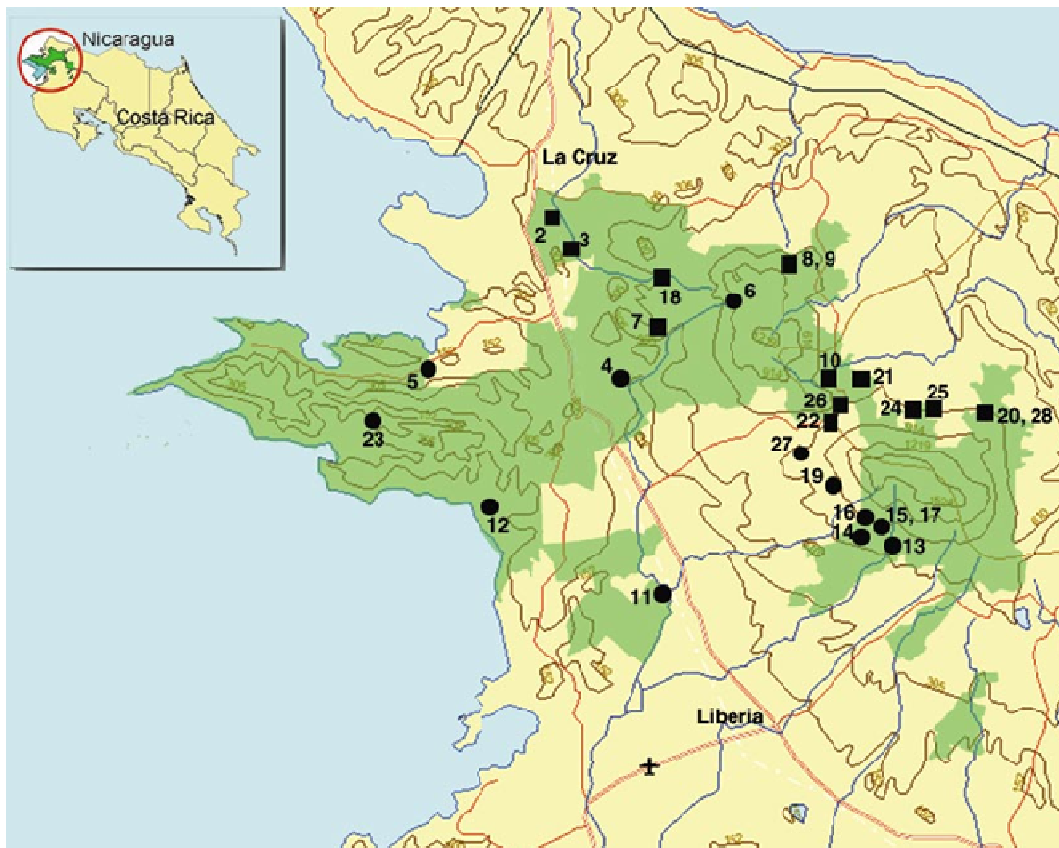


Figure 1 Guanacaste Conservation Area (ACG; green colour) with the position of sampled localities indicated (numbers refer to **Table 1**). Filled circles: Pacific drainage, filled squares: Atlantic drainage. Detailed descriptions of the localities are given in **Annex 1**.

Table 1 Localities sampled during the fish survey, June 1998, February 1999, and March 2001. For locality positions, see **Figure 1**. All river systems on the Atlantic slope are tributaries to the Rio San Juan/Lake Nicaragua, while river systems on the Pacific side are separate catchments. Asterisk (*) indicates that we caught no fish at the site. Detailed descriptions of the localities are given in **Annex 1**.

Locality no	Name	River system	UTM position	Altitude, m a.s.l.
Atlantic slope				
2	Rio Sapoa	Sapoa	3608 3339	205
3	Rio Sapoa	Sapoa	3617 3308	240
7	Quebrada Limonal	Sapoa	3676 3263	310
8	Rio Orosi	Orosi	3804 3300	675
9	Arroyo Lagunas	Orosi	3807 3299	675
10	Rio Pizote	Pizote	3843 3254	465
18	Quebrada Jorco (Rio El Hacha)	Sapoa	3675 3286	295
20	Quebrada Buenos Aires	Pizote	3937 3212	355
21	Rio Blanco	Pizote	3856 3191	540
22	Rio Cucaracho	Pizote	3839 3170	625
24*	Rio Azul	Pizote	3905 3203	420
25*	Rio Pénjamo	Pizote	3926 3201	370
26	Lagunita San Gerardo	Pizote	3844 3180	570
28	Rio Negro	Pizote	3938 3213	350
Pacific slope				
4	Quebrada Aserradero	Tempisque	3652 3200	155
5	Rio Murcielago	Murcielago	3472 3204	40
6	Rio Tempisquito	Tempisque	3730 3266	570
11	Rio Tempisquito	Tempisque	3693 3018	60
12	Rio Poza Salada	Nisperal	3559 3089	8
13*	Rio Colorado	Tempisque	3889 3062	880
14*	Rio Blanco	Tempisque	3855 3043	560
15*	Quebrada Agria	Tempisque	3863 3048	570
16	Arroyo sin nombre	Tempisque	3856 3052	570
17	Quebrada Zanja Tapata	Tempisque	3849 3055	590
19	Quebrada Tibio (Góngora)	Tempisque	3813 3040	400
27	Quebrada Tibio (Hca. Perla)	Tempisque	3794 3056	300
23	Rio Potrero Grande	Potrero Grande	3446 3164	80

3 Material and methods

3.1 Fishing methods

Fish was sampled by means of electro-shocker, gill nets, traps, and dip nets. The usefulness of the portable electro-shocker (produced by S. Paulsen, Trondheim, Norway) is restricted to shallow waters (less than 0.5 m). As most rivers and streams in ACG are quite small, it was possible to use the shocker at most localities. However, even in the smallest streams, the deeper pools could not be sampled with this gear. In pools and deeper localities, two types of gillnets, survey nets and "troll nets" were used. The survey nets (1.5 m x 24 m) are made from monofilament nylon, and contain 12 panels of mesh sizes between 6 and 55 mm (knot-to-knot) (Appelberg et al. 1995). These nets were used in all pools deeper than approx. 1 m. The "troll nets" are constructed of three layers of spun nylon mesh. The mesh size of the middle one is 50 mm (knot-to-knot), whereas the outer layers have larger mesh sizes, 135 mm. This construction provides efficient nets for a variety of fish sizes larger than the minimum size caught

by the 50 mm mesh. The troll-nets were used in larger and deeper pools (> 1.5 m). Dip-nets and fish funnel traps were used on a few occasions.

These fishing methods are relatively non-destructive, generally killing only the fishes that are caught. They are, however, selective and do probably not catch all fish species. For a complete inventory of the fish fauna, more destructive methods, e.g. rotenone, will have to be applied (Bussing et al. 1996). Even with a variety of sampling methods, however, the sample size has to be large to ensure that also rare fish species are present in the samples. This obviously constitutes a dilemma particularly in a protected area, where the number of organisms killed during research should be kept at a minimum.

The fish were kept alive in water tanks, or dead on cool storage until brought back to the laboratory at Estación Santa Rosa for identification and dissection. Some of the material had to be kept frozen until it could be dissected. Some of the live material was photographed in an aquarium prior to dissection and analysis for parasites.

3.2 Fish material

A total of 3,212 fish have been caught during three sampling periods, in June 1998 (1,230 fish), February 1999 (1,112 fish), and March 2001 (870 fish) (cf. **Annexes 2, 3, 4**, and **Table 2**). A total of 1,523 fish were caught in the rivers draining to the Pacific, whereas 1,689 fish were caught in rivers draining to the Atlantic.

All fish were identified to species according to Bussing (1998) and the body length measured (to the nearest mm). Most of the sampled fish were also weighed (0.1 g). Sex and maturity stage was recorded for dissected fish. For adult individuals in some of the species, sex may be determined from external characters. This was done in particular for species of the Poeciliidae family (guppies). A total of 1096 fish were dissected in order to collect and identify macroparasites.

A sample of guppies from Rio Potrero Grande, which we were unable to identify, was sent to Prof. William Bussing for identification. These were subsequently described as *Poeciloipsis santaelena* n. sp. (Bussing 2008).



Electrofishing in Arroyo Sin Nombre (locality 16; 570 m a.s.l.) Photo: R.H. Daverdin

3.3 Parasite methods

Parasites were located by sight under stereo microscopes in fish tissues (skin, eyes, gills, muscles, inner organs) and body cavity. Parasites were fixed and preserved following methods in Van Cleave & Mueller (1932) and Pritchard & Kruse (1982). Parasites were killed and simultaneously fixed in heated or unheated fixatives (10% buffered or nonbuffered formalin for all parasites, also 70% ethanol for nematodes). Fixation in heated (steaming) formalin was accompanied by brief vigorous shaking of the capped vial; this aided in relaxing the fixed worms, especially helminths. Platyhelminths, copepods, and leeches were stained in acetocarmine or Ehrlich's hematoxylin and processed for permanent slide mounts. Nematodes were cleared in a solution of 5% glycerin in 70% ethanol, and temporarily mounted in glycerine on slides with a coverslip. Parasites were examined using Olympus BX-41 and BX-51 compound microscopes with Nomarski DIC (differential interference contrast) optics. Drawings were made using a drawing tube attached to the microscope and measurements were made using an ocular graticule calibrated with a 1mm 1/100 objective micrometer. Parasites were identified using reviews and summaries of regional fauna as well as primary literature. In many cases, the morphology and/or morphometrics of the parasites differed to a lesser or greater extent from published descriptions of similar species. Consequently, the parasites were identified to genus and differentiated on the data tables (**Annexes 6, 7, 8**) either by the hosts they were specific to (in parentheses) or by providing species names in parentheses followed by a question mark (?). Species names in parentheses indicate known species the parasite in question was most similar to.



A pool in Rio Potrero Grande in the dry season (locality 23; 80 m a.s.l.). Poecilopsis santaelenae, n.sp., was recorded at this site.

3.4 Statistical methods

When comparing samples to evaluate differences in e.g. abundance distributions for the parasite taxa between locations, we must first consider the randomness induced by the sampling process. Even samples from exactly the same location and time may show considerable differences. If the sampling effort varies, expected differences will increase even more. We have applied a simulation test method that corrects for sampling in general, as well as for varying sampling sizes, under the null hypothesis of no difference between populations (or locations, seasons, etc.). If there is no difference between the two communities, the two samples can be pooled to provide an improved estimate of the abundance distribution. In each simulation, we draw, from the pooled sample and without replacement, two new samples of the same sizes as the two original ones. Each observation is thereby assigned to one of the samples, with probability equal to the sample size over the sum of the two sample sizes. For each pair of simulated samples we calculate an appropriate test statistic, e.g. the difference in number of parasite taxa. The observed difference in the number of parasite taxa (i.e. from the original samples) is then compared to the distribution of simulated differences under the null hypothesis and we may calculate a p-value for the simulation test (e.g. Good 1994).

Table 2 Recorded fish species, the number of localities where they occurred, and the total number of fish in the samples from ACG rivers. The five investigated localities without fish are excluded from the number of fished localities.

	Atlantic slope	Pacific slope	Total
No. of fished locs.	12	10	22
Name			
Characidae			
<i>Astyanax aeneus</i>	6	4	10
<i>Brycon guatemalensis</i>	2		2
<i>Bryconamericanus scleroparius</i>	5	2	7
<i>Roeboides bouchellei</i>	2	2	4
Poeciliidae			
<i>Alfaro cultratus</i>	4		4
<i>Brachyrhaphis olomina</i>	1	5	6
<i>Phallichthys amates</i>	2		2
<i>Poecilia gillii</i>	5	4	9
<i>Poecilopsis</i> spp.		1	1
<i>Priapichthys annectens</i>	6		6
Poeciliidae indet.	1		1
Ariidae			
<i>Arius guatemalensis</i>		1	1
<i>A. seemanni</i>		1	1
Cichlidae			
<i>Amphilophus citrinellus</i>	1		1
<i>Archocentrus nigrofasciatus</i>	3	4	7
<i>Astatheros alfari</i>	9	2	11
<i>Astatheros longimanus</i>		2	2
<i>Hypsophrys nicaraguensis</i>	2		2
<i>Neetroplus nematopus</i>	3	1	4
<i>Parachromis dovii</i>	5	3	8
<i>Theraps underwoodi</i>	2		2
<i>Tilapia</i> sp..		1	1
Pimelodidae			
<i>Rhamdia guatemalensis</i>	4	2	6
<i>R. rogersi</i>	7	4	11
<i>R. nicaraguensis</i>	3	3	6
Rivulidae			
<i>Rivulus isthmensis</i>	4	2	6
Gobiesocidae			
<i>Gobiesox nudus</i>	2		2
Gobiidae			
<i>Awaous transandeanous</i>		2	2
<i>Sicydium salvini</i>		2	2
Gymnotidae			
<i>Gymnotus maculosus</i>	6		6
Mugilidae			
<i>Agonostomus monticola</i>		3	3
Eleotridae			
<i>Dormitator latifrons</i>		1	1
<i>Eleotris picta</i>		3	3
<i>Gobiomorus dormitor</i>	1	2	3
<i>G. maculatus</i>	1	3	4
Synbranchidae			
<i>Synbranchus marmoratus</i>	1		1
Number of species	26	25	36
Number of fish	1689	1523	3212

We have also used a resampling procedure to illustrate the relationship between host sample size and the number of parasite taxa recorded in the sample. For any sample (e.g. the number of fish hosts, n_s , dissected one year at a given location) we draw, at random without replacement, a sub-sample of n fish ($n=1, 2, \dots, n_s$) and count the number of parasite taxa belonging to this sub-sample. This is repeated 1000 times for each value of n . We thereby obtain a curve describing the relationship between host sample size and number of parasite taxa (average of the 1000 simulations), which is similar to a rarefaction curve (Sanders 1968). In addition, the simulations provide an indication of the uncertainty in the sample size – parasite taxa relationship.

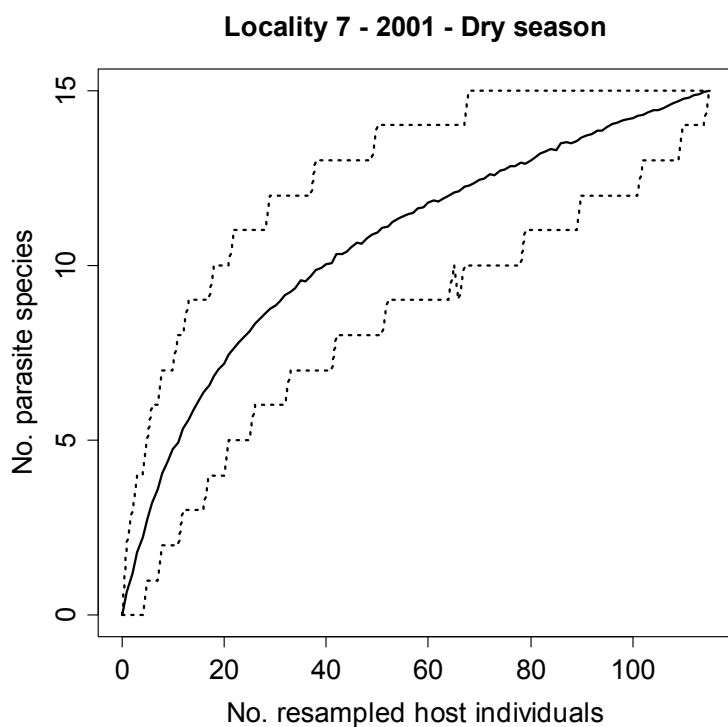


Figure 2 Example of the relationship between host number and parasite species number based on the resampling procedure described in the text. The dotted lines give approximate 95% confidence limits, but the upper limit from ca. 70 resampled hosts is restricted to the total number of observed parasite species (15) and should therefore not be applied.



Rio Sapoá (locality 2; 205 m a.s.l.).

4 Results

4.1 Occurrence and distribution of freshwater fish species

A total of 36 species of fish were recorded in our samples from the rivers of ACG (Table 2), 25 species in the Pacific drainages and 26 species in the Atlantic drainages. As the sampling stations on the Atlantic slope all were above 200 m altitude, a comparison of fish fauna richness should only include localities above this altitude. On the Pacific side this would include only five sites (localities 6, 16, 17, 19, and 27), where only 7 fish species were recorded.

The highest number of species recorded at any one locality was 17 species at the lower locality in Rio Sapoa (locality 2) (see **Annex 2**). At two localities (no. 17 and 22), both at relatively high altitudes, only one species was recorded. Five localities were devoid of fish (no., 13, 14 and 15, and 24 and 25; **Figure 1** and **Table 1**). These localities were at relatively high altitude in rivers draining directly from the active area of Volcan Rincón de la Vieja, implying that poor water quality may be the reason for the absence of fish (cf. Pringle & Triska 1991).

The 36 fish species represent 12 families (Table 2). Our samples include nine species of the family Cichlidae. The most commonly occurring cichlid was *Astatheros alfari* (mojarra), occurring in 50% of the localities with fish. The predatory *Parachromis dovii* (guapote) was also quite common, occurring in the catches at 8 out of 22 localities. One of the cichlids, a *Tilapia* species, has quite recently been introduced into the Tempisque system, probably by escaping or having been released from aquaculture operations.

The Poeciliidae family (guppies) is represented by six species in our samples. (The single individual listed as Poecilidae indet. from Lagunita San Gerardo is not counted as a separate species here.) The most common guppy in ACG is *Poecilia gillii*, which occurs in samples from nine out of 22 localities. At two localities only one species was recorded, and in both cases, this was a poecilid. In Rio Cucaracho on the Atlantic slope the sole species was *Priapichthys annectens*, whereas in Rio Zanja Tapata on the Pacific slope it was *Brachyrhaphis olomina*. In Rio Potrero Grande, we collected an unidentified poeciliid which was subsequently described by Prof. William Bussing as *Poecilopsis santaelena* nov. sp. (Bussing 2008).

The Characidae family is represented by four species in our samples. The most frequently occurring species is *Astyanax aeneus* (sardina), which was found at ten out of 22 localities.

The Eleotridae family is represented by five species, including three *Rhamdia* species and two *Gobiomorus* species. *R. rogersi* was recorded at 50% of the localities, whereas the other species were recorded at six localities each. The Eleotridae species are typical of the lower stretches of the Pacific rivers, but *Gobiomorus* spp. was also recorded on the Atlantic side.



Rivulidae, *Rivulus isthmensis*, 62 mm body length, Arroyo Lagunas (locality 9; 675 m a.s.l.)

4.2 Fish communities

4.2.1 Species diversity vs. altitude

Although the altitudinal distribution of our sampling sites differ between the Pacific and the Atlantic slopes, in both cases there are clear negative correlations between the altitude of localities and the number of fish species present (**Figure 3**). All localities where our samples contained four species or less were more than 400 m above sea level. On the Atlantic slope, four localities with more than ten species were at 350 m a.s.l. or less. On the Pacific slope, two of our low-lying localities (< 200 m a.s.l.) had more than 10 species of fish. Three Pacific slope rivers (Rio Murcielago, Rio Potrero Grande, and Rio Poza Salada) had comparatively few species of fish. These are all more or less seasonal rivers with small catchment areas, containing only small pools of water in the dry season. It may be noted that the gradients of the two regression models (excluding the seasonal rivers) are not significantly different, that is, the effect of change in altitude on the number of fish species is of the same magnitude along both slopes. The different intercepts (“number of species at sea level”) is in accordance with the fact that the fauna on the Pacific side of the watershed is poorer in species (cf. Smith & Bermingham 2005). The common gradient for the two slopes (again excluding the seasonal rivers) is -0.024 ($N=18$; $R^2=0.74$), so we would expect to “lose” one species for every 42 meters increase in altitude.

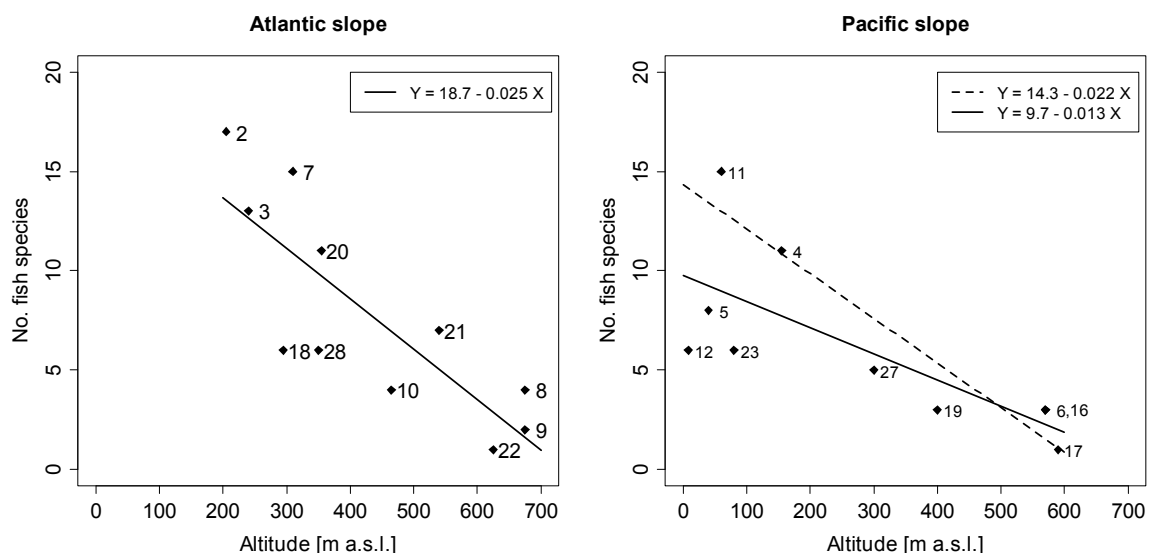


Figure 3 Recorded number of fish species versus altitude in ACG rivers draining to the Atlantic (left) and to the Pacific (right). Numbers on data points refer to locality number in Table 1 and Figure 1. For localities on the Atlantic slope, we have $R^2 = 0.67$. For the Pacific slope, the dotted regression line concerns localities with permanent water ($N = 7$; $R^2 = 0.87$), whereas the bold line represents all localities ($N = 10$; $R^2 = 0.54$), including the low-lying small watersheds with seasonal water (locs. 5, 12 and 23). All regressions are significant ($p < 0.05$).

4.2.2 Fish community structure

The diet of the fish species indicates the trophic position of the species (i.e. the position of the species in the aquatic food web at the locality). It may also indicate the potential load of parasite species transmitted through the food chain. We did not, however, detect any indication that parasite fauna of the host species reflecting the trophic ecology of the host.

The diet types of the fish species recorded in the localities of ACG are listed in **Table 3**. The diet classes are: detritus (dead organic material), fresh plant material, invertebrates, and fish. The classification of species according to diet is based on information in the literature and our own observations. The majority of species (29 spp.) include invertebrates and/or fish in their

diets, whereas only five species appear to be vegetarian, eating only detritus and fresh plant material. There are few diet specialists among the fish species in this material. One species (the cichlid *Amphilophus citrinellus*) is reported to be eating only detritus whereas six species are believed to eat only invertebrates (Bussing 1998). Four species eat detritus and fresh plant material. Ten species eat invertebrates and fish. It may be expected that most of the invertebrate eaters would also take fish if there is fish prey of a suitable size available. Five species add fresh plant material (often seeds) to their otherwise carnivorous habits. Six species eat mainly detritus and fresh plant material (often algae growing on the substratum), but with some invertebrates, whereas one species (the characid *Astyanax aeneus*) is reported to eat all types of food.

This diet classification of fish species reveals a common trend. In the species rich communities, species with a vegetarian or mixed diet are prominent in the catches. As the number of fish species decreases, species with a carnivorous diet become relatively more important. In the high altitude localities with 1-3 fish species, all species are carnivores (see **Annex 9**). Rio Zanja Tapata on the Pacific side and Rio Cucaracho on the Atlantic side have one poeciliid species each. Although these are different species (*Brachyrhaphis olomina* in R. Zanja Tapata, and *Priapichthys amates* in R. Cucaracho), they are both invertebrate eaters, feeding mainly on insect larvae and adults (Bussing 1998). The length distributions in our samples from these two localities were also similar. *B. olomina* in R. Zanja Tapata was between 20 – 55 mm, with a modal length of 35 mm. *P. annectens* in R. Cucaracho was between 15 - 75 mm, with a modal length of 25 mm.



Rio Pénjamo
(locality 25; 370
m a.s.l.), one of
the fishless
sites.



Poeciliidae, *Phallichthys amates*,
female: 55 mm; male: 43 mm, *Que-
brada Limonal* (locality 7; 310 m
a.s.l.).

Table 3 General feeding habits (diet classes) according to literature, of the fish species recorded in ACG (Bussing 1987, 1994, 1998; Winemiller 1990; Winemiller et al. 1995).

Fish family / Species	Detritus	Plant material	Invertebrates	Fish
Characidae				
<i>Astyanax aeneus</i>	X	X	X	X
<i>Brycon guatemalensis</i>		X	X	X
<i>Bryconamericanus scleroparius</i>		X	X	
<i>Roeboides bouchellei</i>			X	X
Gymnotidae				
<i>Gymnotus maculosus</i>			X	
Ariidae				
<i>Arius guatemalensis</i>			X	X
<i>A. seemanni</i>			X	X
Pimelodidae				
<i>Rhamdia guatemalensis</i>			X	X
<i>R. nicaraguensis</i>		X	X	X
<i>R. rogersi</i>			X	X
Rivulidae				
<i>Rivulus isthmensis</i>			X	
Poeciliidae				
<i>Alfaro cultratus</i>			X	
<i>Brachyrhaphis olomina</i>			X	
<i>Phallichthys amates</i>	X	X	X	
<i>Poecilia gillii</i>	X	X		
<i>Poecilopsis sp.</i>	X	X		
<i>Priapichthys annectens</i>			X	
Gobiesocidae				
<i>Gobiesox nudus</i>			X	X
Synbranchidae				
<i>Synbranchus marmoratus</i>			X	X
Cichlidae				
<i>Amphilopus citrinellus</i>	X			
<i>Archocentrus nigrofasciatus</i>	X	X	X	
<i>Astatheros alfari</i>	X	X	X	
<i>Astatheros longimanus</i>			X	
<i>Hypsophrys nicaraguensis</i>	X	X	X	
<i>Neetroplus nematopus</i>	X	X		
<i>Parachromis dovii</i>			X	X
<i>Theraps underwoodi</i>		X	X	
Mugilidae				
<i>Agonostomus monticola</i>		X	X	
Gobiidae				
<i>Awaous transandeanus</i>	X	X	X	
<i>Sicydium salvini</i>	X	X		
Eleotridae				
<i>Dormitator latifrons</i>	X	X	X	
<i>Eleotris picta</i>			X	X
<i>Gobiomorus dormitor</i>			X	X
<i>G. maculatus</i>			X	X

Most freshwater localities within the borders of ACG are small streams and rivers. This is reflected in the fact that the fish communities consist of small species, or relatively small individuals of potentially large species. At all localities, a major proportion of fish in the samples were smaller than 10 cm in length, and very few fish were larger than 25 cm. One exception is the lowland locality in Rio Tempisquito, where the *Arius* species is a relatively large sized element of the fauna (up to 35 cm body length). This is also the only surveyed locality where crocodiles (*Crocodilus aculeatus*) were present.

4.3 Macroparasites

4.3.1 Parasite diversity

A total of 50 parasite taxa were recorded in the analyzed fish (Table 4; Annexes 5, 6, 7, 8). During the rainy season in 1998, 29 parasite taxa were identified from a total of 369 dissected fish hosts. During the dry season in 1999, 25 parasite taxa were identified from 277 hosts, while in 2001, a total of 26 taxa were identified from 450 hosts. Twelve parasite taxa were found only in the wet season, 21 taxa were found only in the dry season, while 17 taxa were found in both seasons. Nine taxa have been identified to species. Two species new to science have been described from the material (the trematodes *Wallinia chavarria*; Choudhury et al. 2002, and *Paracreptotrema blancoi*; Choudhury et al. 2006), but it appears reasonable to expect that more previously undescribed species will be identified from our sample.

Table 4 Parasite taxa identified in freshwater fish from ACG during the three sampling periods in 1998 (rainy season), and 1999 and 2001 (dry season).

Taxon	1998	1999	2001	Taxon	1998	1999	2001
Acanthocephala		X	X	<i>Procamallanus</i> sp.	x	X	X
<i>Acanthostomum minimum</i>	X	X	X	<i>Procamallanus rebecca</i>	X	X	X
Ascaridoidea gen. sp.	X			<i>Prosthenhystera (obesa)</i>	X		
Capillaridae gen. sp.	X	X	X	Proteocephalidae gen.sp.	X		X
Cestoda gen. sp.			X	<i>Rhabdochona (neocaballeroi)</i>	X	X	X
Clinostomatidae gen. sp.		X	X	<i>Rhabdochona kidderi</i>	X	X	
<i>Contracecum</i> sp.		X	X	<i>Rhabdochona</i> sp.(ex. <i>Eleotris</i>)	X		X
<i>Crassicutis cichlasomae</i>	X	X	X	<i>Rhabdochona</i> sp. (ex. <i>Rhamdia</i>)	X		X
<i>Cucullanus</i> n.sp.		X		<i>Rhabdochona</i> sp. (<i>cubensis</i>)		X	
<i>Cucullanus pimelodellae</i>		X		<i>Rhabdochona kidderi</i>		X	
Digenea gen. sp.		X	X	Rhabdochonidae			X
Digenea gen. sp. (metacercaria)	X		X	<i>Rondonia (rondoni)</i>	X		
Ergasilidae	X			<i>Saccocoelioides</i> sp. 1	X	X	X
<i>Genarchella</i> sp.	X		X	<i>Saccocoelioides</i> sp. 2	X		
<i>Hysterothylacium</i> sp. (larvae)		X		<i>Saccocoelioides sogandaresi</i>	X		X
<i>Mesostephanus</i> sp.?(metacercaria)			X	<i>Saccocoelioides</i> sp. 3	X	X	
Monogenea gen. sp.	X	X		<i>Saccocoelioides</i> sp. 4	X		
Nematoda gen. sp.		X	X	<i>Spinitectus (mexicanus)</i>		X	X
<i>Neocucullanus</i> sp.	X			<i>Spinitectus agonostomi</i>			X
<i>Neoechinorhynchus golvani</i>		X		<i>Spinitectus</i> sp.	X	X	X
<i>Oligogonotylus manteri</i>	X	X		<i>Spiroxys</i> sp. (immature)		X	
<i>Paracreptotrema mendezi</i>		X		Spirurida (ex. <i>Rivulus</i> sp.)	X		
<i>Paracreptotrema blancoi</i>	X		X	Spirurida gen.sp.	X		X
<i>Pseudocaecincola</i> sp.	X			Strigeidae gen. sp.		X	
				<i>Wallinia chavarria</i>	X	X	X



Pimelodidae, *Rhamdia rogersi*, 125 mm, Rio Sapoá (locality 2; 205 m a.s.l.).

4.3.2 Effects of host diversity and sample size on the number of parasite taxa

The resampling procedure provides some understanding on how sampling season influences the diversity of recorded parasite taxa. **Figure 4** shows that within one host species, locality and year (here; the 29 individuals of the most abundant host species *Astyanax aeneus* from Rio Sapoa, locality 2, in 1998), we seem to reach a limit at around 5 parasite taxa. Increasing the number of *A. aeneus* from Rio Sapoa in 1998 would probably not have yielded more parasite taxa (green curve). We would probably gain more by increasing the number of host species in the sample to be dissected from Rio Sapoa in 1998, since the curve for the pooled sample for all host species (red line; 119 fish, 11 host species) seems not to approach the asymptote. If all localities in 1998 are pooled, we obtain the black curve (369 fish, 21 species, 8 localities). Some additional parasite taxa seems to be gained by resampling at random from all localities instead of within Rio Sapoa, but the effect of locality does not seem to be that strong. Thus, within the season, the number of host species sampled seems to be the most important factor determining the recorded number of parasite taxa.

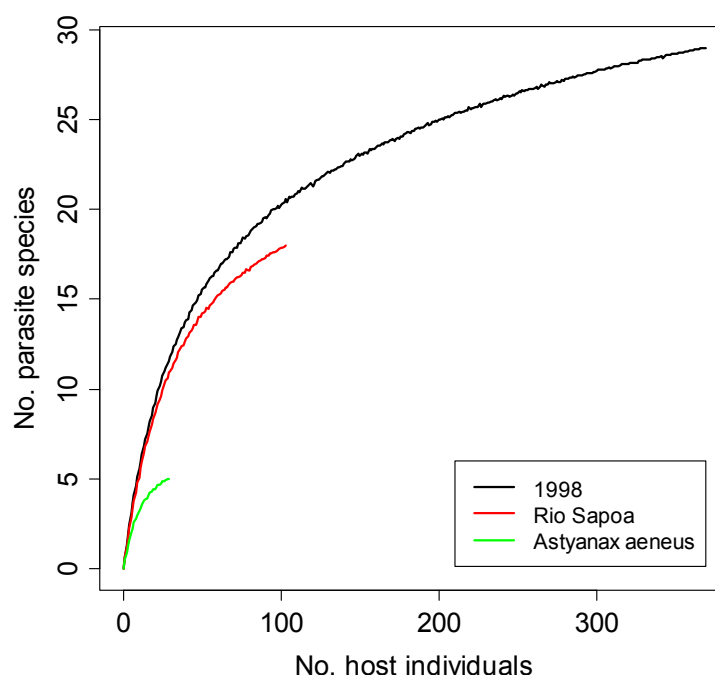


Figure 4 Relation between the number of fish hosts examined and the number of parasite species identified in the samples from 1998. Green curve: all *Astyanax aeneus* from Rio Sapoa (locality 2), red curve: all individuals of all fish species at this locality, and black curve: all fish from all localities surveyed in 1998. The method is described in section 3.4 on p. 12.

Similarly, we can study how the number of fish of one host species (within locality and year) affects the number of parasite taxa, how sampling this host species at several localities (in the same year) affects the number of parasite taxa, and how sampling this host species at several localities over several years affects the number of parasite taxa. This is illustrated for *Astyanax aeneus* in **Figure 5**. At location 2 (Rio Sapoa) in 1998 we have a sample of 29 individuals of *A. aeneus*, but only eight are parasite hosts. When we pool all *A. aeneus* from all sampled locations in 1998 together, we find 51 host individuals, but only three more parasite hosts, i.e. a total of 11 hosts. If we further pool all the three years together, we have dissected 127 individuals of *A. aeneus* and found that 31 of them are parasite hosts. **Figure 5** shows that the majority of *A. aeneus* individuals collected in 1998 were caught on the Rio Sapoa location, and that the additional individuals from other locations only contributed one more parasite taxon. The rate of increase in the number of parasite taxa is also reduced when we pool the locations together, probably due to the high number of fish without parasites. Pooling all three years did

not change the relationship, indicating that the parasite load of *Astyanax aeneus* is the same in all years, both dry and wet seasons.

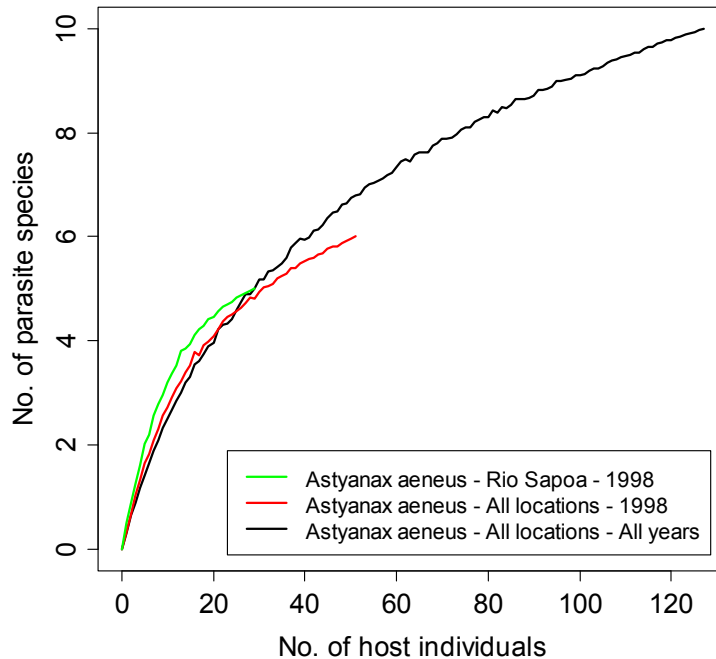


Figure 5 Relation between the number of hosts of one particular fish species examined and the number of parasite taxa identified. Green curve: all *Astyanax aeneus* collected from Rio Sapoá (locality 2) in 1998, red curve: all *Astyanax aeneus* from all localities surveyed in 1998, and black curve: all *Astyanax aeneus* from all localities from all three years. The method is described in section 3.4 on p. 12.



Poeciliidae, *Poecilia gillii*, male (left): 105 mm, female (right): 64 mm, Rio Sapoá (locality 2; 205 m a.s.l.).

4.3.3 Seasonal variation

The number of parasite taxa occurring only in the rainy (12) or dry (21) seasons, respectively, versus the number of taxa occurring in both seasons (17), seems to indicate a shift in the composition of the parasite compound community between seasons (cf. **Table 4**).

In order to test if the difference between samples (i.e. seasons) is larger than what we can expect from sampling effects alone, we perform the simulation test described in paragraph 3.4. The null hypothesis in the test is that the two samples are from the same (statistical) population, i.e. the observed differences in the number of parasite taxa between samples can be explained by random sampling and varying sample sizes. The alternative hypothesis is that the

observed difference between the two samples is larger than expected, that is, the populations we sample from are different (in terms of the parasite taxa present).

This approach is first applied to the samples from location 7 (Q. Limonal), which was sampled all three years with a relatively good number of hosts. If we start by comparing the two samples from the dry season (1999 and 2001), we can pool the two samples and simulate 10.000 new pairs of samples of the same sizes as the original ones. **Figure 6**, top panel, shows the distribution for the number of parasite taxa in the simulated “1999-samples” (43 fish hosts drawn at random from the 158 fish hosts in the pooled sample) with the red point indicating the number of parasite taxa in the original sample ($s_{99}=10$). The middle panel of **Figure 6** shows the distribution from the simulated “2001-samples” (the remaining 115 fish hosts in each simulation; $s_{01}=15$). Finally, the lower panel of **Figure 6** shows the distribution of simulated differences in the number of parasite taxa. The observed difference ($s_{99} - s_{01} = -5$) is well within the 95% confidence interval (blue vertical lines) with $p = 0.44$. Thus, we have no reason to believe that the actual numbers of parasite taxa in the fish communities are different in the dry seasons of 1999 and 2001, the observed difference can be explained by differing sample sizes, and we may pool the dry season samples from the two years.

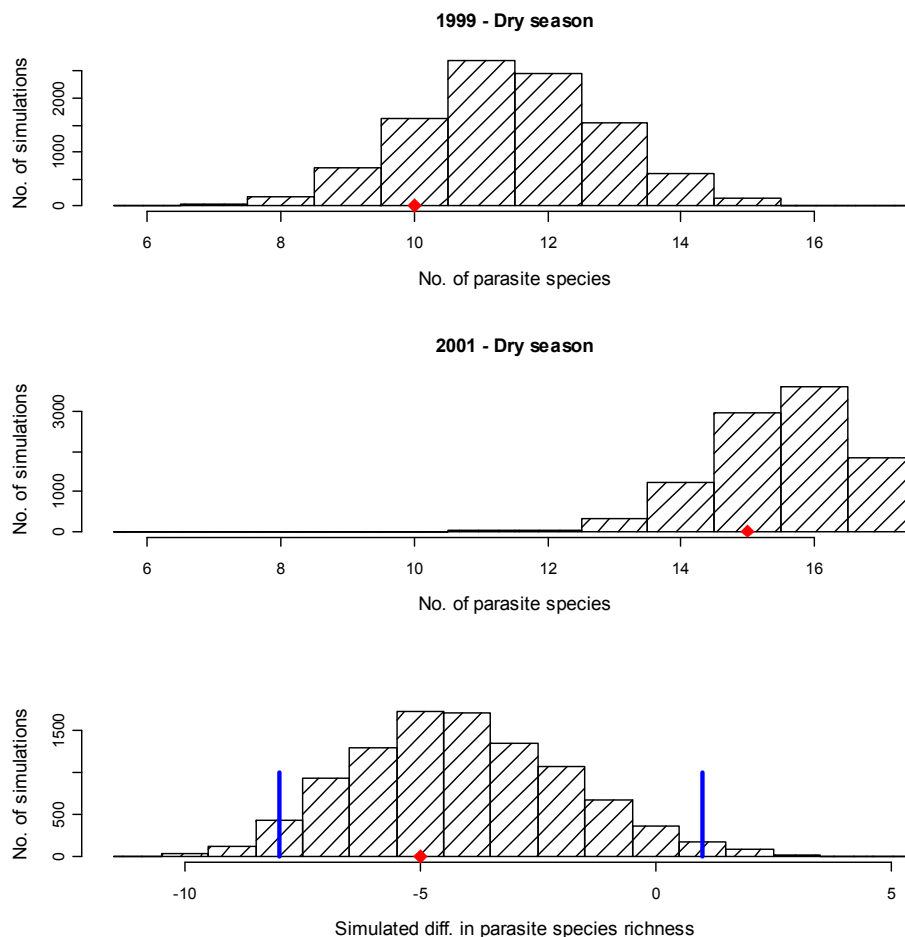


Figure 6 Simulated distributions of number of parasite taxa at location 7, for the two dry seasons (top and middle panels), and the null distribution for the expected difference in number of parasite taxa between the two samples (lower panel). The red diamond at the baseline of all histograms shows the values observed in the original data set and the blue vertical lines in the lower panel gives the 95% confidence limits of the null distribution.

We then proceed to compare the location 7 sample from the wet season (1998) with the pooled dry season samples (1999 and 2001). **Figure 7** indicates that we observe fewer parasite taxa in the wet season than what we should expect if there were no difference in parasite fauna between seasons ($p=0.008$).

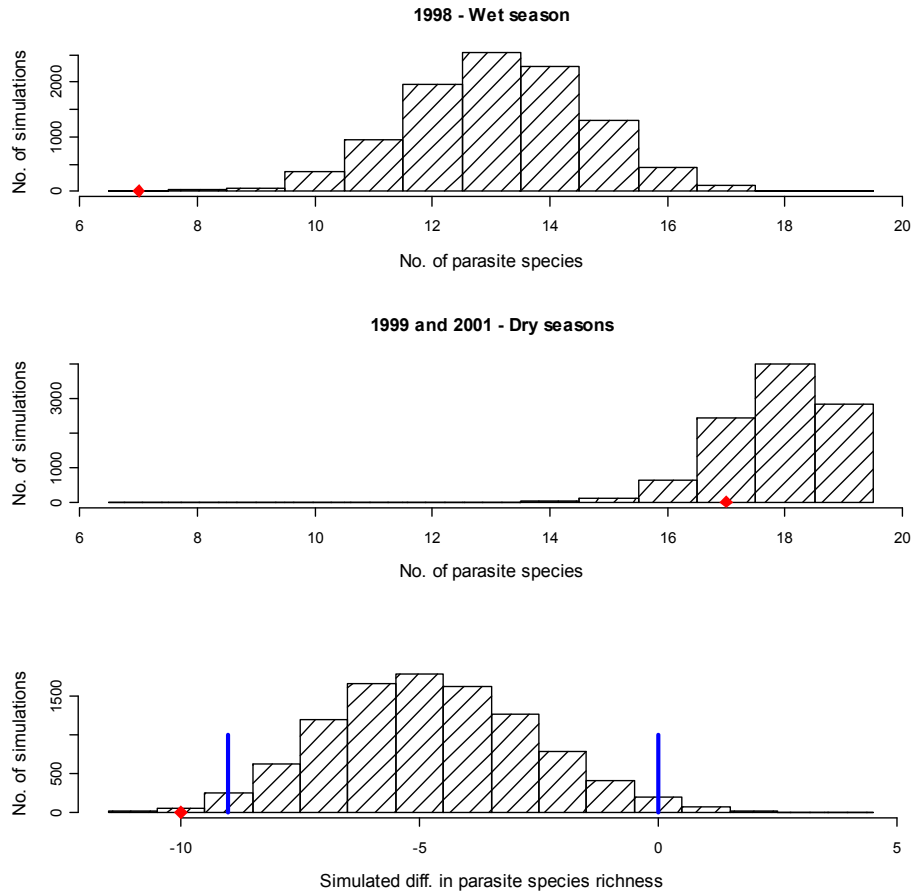


Figure 7 Simulated distributions of number of parasite taxa at location 7, for the wet season (top panel), the dry seasons (middle panel), and the null distribution for the expected difference in number of parasite taxa between the two seasons (lower panel). The red diamond at the baseline of all histograms shows the values observed in the original data set and the blue vertical lines in the lower panel gives the 95% confidence limits of the null distribution.



Poeciliidae, *Brachyrhapis olomina*, male: 47 mm, female: 50 mm, Rio Tempisquito (locality 6; 570 m a.s.l.).

The indication that the parasite load is different between wet and dry seasons is supported by the results from the resampling procedure (**Figure 8**). Even if the sample size (number of fish hosts) is increased in the wet season (extrapolating the red curve) it does not indicate that we will find many more parasite taxa. Thus, the difference in number of parasite taxa in the wet and dry seasons cannot be explained by difference in sample sizes alone.

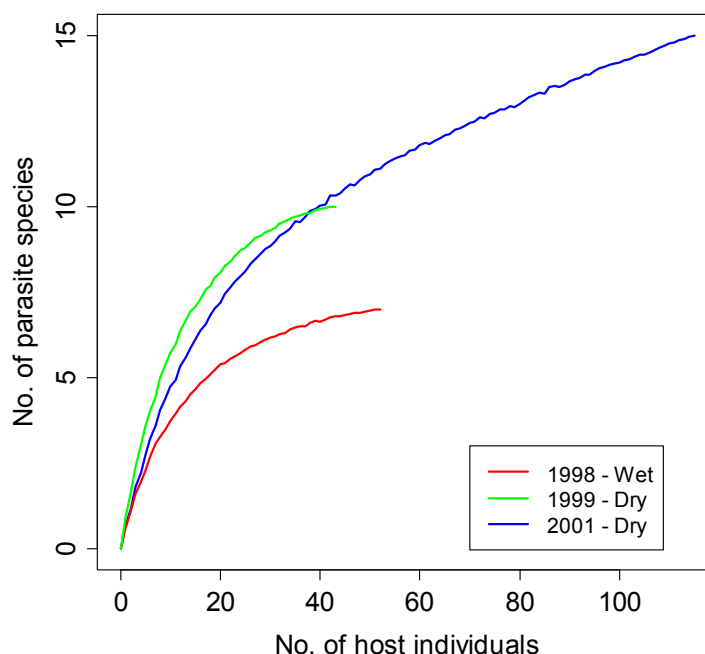


Figure 8 Relation between the number of fish hosts examined (all species and all localities) and the number of parasite species identified, in the wet season of 1998 (red curve), and the dry seasons of 1999 and 2001 (green and blue curve, respectively).

However, although we do not find any significant difference in the number of parasite taxa between the wet season and the dry seasons when all the locations are pooled ($p=0.24$), there is a large turnover of parasite taxa represented in the samples (cf. **Table 4**). Our sample sizes are too small to test this species turnover in a proper way. An indication is provided by comparing the list of parasite taxa present in the samples from the same fish species and locality, in the dry and wet seasons, respectively. Our material allows this comparison for three localities (loc. 2+3, Rio Sapoá upper and lower; loc. 4, Q. Aserradero; and loc. 5, Rio Murcielago, see **Table 5**). In this material, only between 0 and 21% of the total number of recorded parasite taxa were found both in the wet and dry season.

Table 5 Parasite taxon turnover between the wet and dry seasons. Loc. number refers to **Table 1**. N host species indicates the number of fish species sampled in both seasons.

Locality name	Loc. number	N host species	N parasite taxa			
			total	wet season	dry season	both seasons
Rio Sapoá	2+3	7	19	16	7	4
Q. Aserradero	4	5	12	5	9	2
Rio Murcielago	5	4	6	2	4	0

5 Discussion

5.1 Fish diversity and distribution

During our surveys we have identified 36 fish species in the rivers of the Guanacaste Conservation Area. Apparently, the number of species caught on the Pacific and the Atlantic slopes are similar (25 vs. 26 species). If we exclude the low-altitude sites (below 200 m) on the Pacific side, only seven species were recorded on this side of the continental divide. This result accords with fact that the fish fauna of the Pacific side of northern Costa Rica (which is within the Chiapas-Nicaragua biogeographical province) contain fewer species than the Atlantic side (San Juan province) (Bussing et al. 1996; Smith & Bermingham 2005). The background for this lies mainly in the immigration history of fishes to this region, with the drier Pacific side of the watershed being less accessible for fish species unable to migrate in saline waters along the coast from the source region in north-western South America (Miller 1966; Myers 1966; Bussing 1985). However, sea level regression during the interglacial periods may mean that saltwater tolerance is of less importance during dispersal of these fish species than the general geological mechanisms causing rivers to change course and be connected to a neighbouring watershed or river channel (Smith & Bermingham 2005). Concerning the occurrence of species in the two adjacent San Juan and Chiapas-Nicaragua biogeographical provinces, we have observed some minor discrepancies compared to the information in Smith & Bermingham (2005). We recorded both the characid *Bryconamericanus scleroparius* and the cichlid *Neetroplus nematopus* on the Pacific slope (i.e. the Chiapas-Nicaragua biogeographical province), whereas Smith & Bermingham (2005) report them to be restricted to the San Juan province. The reason for this is probably that our survey was more detailed than previous surveys at the local level in ACG. Local conditions in the area where the catchment areas of Rio Sapoa and Rio Tempisquito border on each other (cf. **Figure 1**, localities 4 and 6, and 7 and 18), seem to be well suited for river catchment processes, possibly leading to migration of species between the biogeographical provinces.



Gobiidae, *Sicydium salvini*, 54 mm, Rio Murcielago (locality 5; 40 m a.s.l.).



Characidae, *Bryconamericanus scleroparius*, 97 mm, Quebrada Limonal (locality 7; 310 m a.s.l.).

Even in our quite restricted data set, we see the generally observed trend that the number of species decreases with altitude. The rate of decrease is similar on both sides of the divide, but the intercept (“number of species at sea level”) reflects the richer fauna on the Atlantic side (Smith & Bermingham 2005). In this case, the main reason for a decreasing number of species with altitude is probably the steep river gradients. At high altitudes, minimum water temperatures might also restrict some species. All our investigated sites are in forest, implying that the supply of organic material of a terrestrial origin (allocthonous material) is quite abundant.

5.2 Parasite diversity

The parasite faunal composition, in general, follows the biogeographical patterns and history of the hosts. The freshwater fishes of central America are largely neotropical in origin (e.g., Cichlidae, Characidae, Heptapteridae). The most widely cited scenario involves the colonization of this area by cichlids, characids and freshwater catfishes from South America once the isthmian landbridge was established in the Miocene or in the case of some salinity tolerant migrants (some cichlids) as components of the land-bridge were being assembled (Smith & Bermingham 2005). It is also hypothesized that some families such as Cichlidae and Poeciliidae underwent significant adaptive radiation in the lower central American region (Smith & Bermingham 2005).

The parasite fauna of cichlids reported in this study resembles closely the fauna reported from southern Mexican cichlids (Vidal-Martinez et al. 2001; Pérez-Ponce de León & Choudhury 2005). The finding of trematodes such as *Wallinia chavarriae*, *Prosthenhystera obesa* and *Paracreptotremtina* (likely *aguierrepequeno*) in the small bodied characids (*Astyanax* and *Bryconamericus*) connects it to the South American characid parasite fauna. The presence of nematodes such as *Neocucullanus* sp. in *Brycon guatemalensis* and *Cucullanellus pimelodelae* in the catfish *Rhamdia nicaraguense* further reinforces this neotropical/South American connection, as these parasite taxa also are associated with the South American fauna..



Poeciliidae, *Alfaro cultratus*, 56 mm, Rio Sapoa (locality 3; 240 m a.s.l.).



Characidae, *Astyanax aeneus*, 79 mm, Rio Sapoa (locality 2; 205 m a.s.l.).

In general, members of the Cyprinodontiformes (Poeciliidae, Rivulidae etc.) are abundant in Central American freshwaters but their continental affinities are equivocal and the origin of the order may be traced back to a basal marine atherinomorph ancestry. The parasites reported from cyprinodontiform hosts in this study include *Saccocoelioides* (resembling closely *S. sogandaresi*) from *Poecilia gilli*, a 'new' trematode genus and species, *Paracreptotrema blancoi*, the nematode *Spinitectus mexicanus* (or a species very similar to it) from *Priapichthys annectens* (Choudhury et al. 2006), and the trematode *Paracreptotrema mendezi* in *Brachyrhaphis olomina*. All of these records are consistent with the distribution of these parasites from middle America (Mexico extending to Panama).

The number of parasite species recorded within one season in our study appears mainly to depend on the number of host (i.e. fish) species analyzed, perhaps reflecting a certain host specificity. Increasing the number of individuals of one host species, or adding more individuals of the same host species from more localities have less impact on recorded parasite diversity. The general picture is also that the parasite load is quite moderate, both in terms of prevalence (proportion of fish infected) and mean abundance. This is in accordance with the observations of Choudhury & Dick (2000) and Poulin (2001). Our observation in this respect may be due to the small body size and short life span of many of the host species (cf. Poulin 1995). It is, however, surprising that we found few parasite taxa also in the largest individual fishes investigated (*Arius* spp. from location 11).

Our data strongly indicate a high turnover rate of parasite taxa between seasons. On the three localities which were sampled both in the wet and dry seasons, only 0 – 21% of all parasite taxa recorded were found in both seasons. On the other hand, we found no significant difference between the species richness of parasite communities in two dry seasons. This indicates that there might be a stable seasonal pattern. It is generally claimed that fish parasite communities are non-equilibrium systems, and that replicable patterns are hard to find (Poulin & Valtonen 2002, Kennedy 2009, but see Hartvigsen 1995). A longer time series than what is represented by our data would be required to confirm a seasonal pattern in the parasite fauna of ACG freshwater fishes.

6 Summary

Fish were collected in rivers within the Guanacaste Conservation Area (ACG) at 14 localities (205-675 m a.s.l.) on the Atlantic side, and 13 localities (8-880 m a.s.l.) on the Pacific side. The freshwater fish fauna of this area is relatively species poor, with only 36 species recorded during our survey; 25 on the Pacific and 26 on the Atlantic side of the continental divide. Excluding the low-altitude (<200 m a.s.l.) localities on the Pacific side, only seven fish species were recorded. In both catchments, the number of fish species decreased with altitude. One species new to science was collected and later described by Bussing (2008) as *Poecilopsis santele-nae*.

A total of 50 parasite taxa were recorded from 1096 dissected hosts of all collected fish species. The parasite faunal composition in general follows the biogeographical patterns and history of the hosts. Two species new to science have so far been described from the material; the trematodes *Wallinia chavarria* (Choudhury et al. 2002), and *Paracreptotrema blancoi*; (Choudhury et al. 2006). The recorded number of parasite taxa increased with the number of fish host species analyzed and by repeated sampling over seasons.

There was a substantial turnover of parasite taxa over time. Comparing the same host species from the wet and dry season from three localities, only between 0 and 21% of the parasite taxa were recorded in both seasons. Our analyses also indicate that the number of parasite taxa present in the fish communities were lower in wet season than in the dry season samples. To establish the stability of this pattern would require repeated sampling over several years.

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Annex 1

Description of fish sampling localities, Guanacaste 1998-2001

Atlantic drainage			
River/stream	Loc. no.	UTM	Description
Rio Sapoa	2	3608 3339	205 m a.s.l. 100 m stretch of riffle below a pool with depths up to more than 3 m. The river width was 5-20 m. Riffle substrate: stones up to 50 cm diameter, and coarse gravel. Pool substrate: sand and fine silt, with some large stones and dead wood. Pool banks partly overhanging soil. Riparian vegetation: large overhanging trees, but large areas of water were open to the sky. No significant aquatic macrovegetation. Kingfishers, herons and caimans were observed. Locality sampled in June 1998 and February 1999.
Rio Sapoa	3	3617 3308	240 m a.s.l. Shallow pool/riffle stretch, substratum: large stones and boulders (<100 cm diameter) with some gravel and smaller stones. River 2-15 m wide, riparian trees almost totally shadowing the water. Much coarse detritus (leaves and woody material) present on the substratum. Very little macrophyte vegetation. Locality sampled in June 1998 and February 1999.
Quebrada Limonal	7	3676 3263	310 m a.s.l. Small (1-4 m wide) slow-flowing stream with small riffles and deeper (up to 1 m) pools. Substratum: sand and gravel in the riffles and fine silt in the pools. Pool banks overhanging and the riparian vegetation creates shaded habitats in most of the fished stretch of approx. 300 m. No macrophyte vegetation. Locality sampled in June 1998, February 1999 and March 2001.
Quebrada Jorco	18	3675 3286	295 m a.s.l. Small (1-4 m wide) swift-flowing stream over stones and boulders, only small pools. Drains via Rio El Hacha into Rio Sapoa. Locality sampled in February 1999.
Rio Orosi	8	3804 3300	675 m a.s.l. Stream approx. 5 m wide, with a stony substratum and mixed riffles and small pools. Adjacent to Estacion Pitilla. Overhanging riparian forest. Locality sampled in February 1999.
Arroyo Lagunas	9	3807 3299	675 m a.s.l. Very small (1-2 m wide) slow flowing tributary to Rio Orosi, at Estacion Pitilla. Substratum of sand and silt, overhanging dense riparian vegetation.
Rio Pizote	10	3843 3254	465 m a.s.l. Slow flowing river (5-10 m wide) over silt and stones. Locality sampled in June 1998.
Rio Negro	28	3938 3213	350 m a.s.l. Swift flowing river (approx. 10 m wide) over stones and boulders. Riparian forest shades only the edge of the river. Locality sampled in March 2001. Rio Negro is a tributary to Rio Pizote.
Quebrada Buenos Aires	20	3937 3212	355 m a.s.l. Small (1-3 m wide) tributary to Rio Negro. Sampled section is swift flowing over large boulders, forming small pools among the stones. The channel is completely shaded by the riparian forest. Locality sampled in March 2001.
Rio Penjamo	25	3926 3201	370 m a.s.l. Heavily influenced by effluents from the section of Volcan Rincon's slope which is most heavily influenced by volcanic activity. No fish recorded.
Rio Azul	24	3905 3203	420 m a.s.l. Heavily influenced by effluents from the section of Volcan Rincon's slope which is most heavily influenced by volcanic activity. No fish recorded.
Rio Blanco	21	3856 3191	540 m a.s.l. Similar to Rio Negro (locality number 28).
Rio Cucaracho	22	3839 3170	625 m a.s.l. Small swift flowing stream (pools up to 4 m wide) over large stones and boulders at the bottom of a deep ravine. The riparian vegetation and the deep ravine cause the stream habitat to be very dark even during daytime. Close to Puesto San Christobal
Lagunita San Gerardo	26	3844 3180	570 m a.s.l. Pond (approx. 60 by 150 m) created by damming a small creek by Puesto San Gerardo. Some macrophyte vegetation.

Annex 1, continued

Pacific drainage			
River	Loc. no.	UTM	Description
Rio Tempisque watershed			
Rio Tempisquito close to Estacion Maritza	6	3730 3266	570 m a.s.l. Relatively small stream (3-10 m wide), fast-flowing over boulders and stones, with small pools. No higher aquatic vegetation. The high cloud forest along the banks shades the stream in its entire width, and provides large quantities of coarse terrestrial detritus. Locality sampled in June 1998.
Rio Tempisquito	11	3693 3018	60 m a.s.l. River channel 50 – 100 m wide with a sequence of whitewater and slowflowing sections. Locality sampled in February 1999.
Quebrada Aserradero	4	3652 3200	155 m a.s.l. Tributary to Rio Tempisquito from the north. River consists mainly of large and deep pools, connected by short riffles among boulders. The pools were 20-40 m wide, providing good light conditions in spite of the high gallery forest along the banks. Substratum in the pools consisted of boulders and silt, covered by extensive submerged vegetation. Locality sampled in June 1998 and March 2001.
Quebrada Tibio by Cerro Góngora	19	3813 3040	400 m a.s.l. Small stream (1-4 m wide), fast flowing over large stones and boulders. Locality sampled in February 1999.
Quebrada Tibio by Hca. Perla	27	3813 3040	300 m a.s.l. Wider stream (4-10 m), with gravel and stones, and some pools. Locality sampled in February 1999.
Quebrada Zanja Tapata	17	3849 3055	590 m a.s.l. Small stream (3-5 m wide) with a strong current over large stones and boulders. Q. Zanja Tapata is a tributary to Rio Blanco. Locality sampled in February 1999.
Rio Blanco	14	3855 3043	560 m a.s.l. Fast flowing stream (5-10 m) over stones and boulders. No fish recorded. Locality sampled in February 1999.
Quebrada Agria	15	3863 3048	570 m a.s.l. Small fast flowing stream (2-5 m) over stones and boulders. Locality sampled in February 1999. No fish recorded. Tributary to Rio Blanco.
Arroyo sin nombre		3856 3052	570 m a.s.l. Very small tributary entering Rio Blanco from the north. The creek has a very small catchment area. As it was not marked on the map, we have named it for the purpose of this report. Locality sampled in February 1999.
Rio Colorado close to Puesto Las Pailas	13	3889 3062	880 m a.s.l. Major tributary to Rio Blanco from the south. The stream (5-10 m wide) is fast flowing over gravel, stones and boulders. No fish recorded. Locality sampled in February 1999.
Small (seasonal) watersheds			
Rio Murcielago	5	3472 3204	40 m a.s.l. close to Puesto Murcielago. River bed is dry over large sections during the dry season, but groundwater flow maintains some sections of permanent surface water. Stream channel approx 10 m wide with riffles and small pools, which are well shaded by the high riparian forest. The river drains the northern side of Cerro Santa Elena and ends in the Pacific in the Bahia Tomas of Golfo de Santa Elena. Abundant allochthonous organic material (leaves and dead wood) Locality sampled in June 1998, February 1999, and March 2001.
Rio Potrero Grande	23	3446 3164	80 m a.s.l. River channel is of the same size as Rio Murcielago, but has less surface water towards the end of the dry season, with only the occasional pool of water. Below the sampled section, the river is completely dry over several kms before it enters the estuary at Playa Potrero Grande. Locality sampled in March 2001.
Rio Poza Salada	12	3559 3089	8 m a.s.l. Habitat similar to Rio Murcielago and Potrero Grande, but only very small pools of water left in the late dry season. A tributary to Rio Nisperal, which enters the Pacific at Playa Naranjo.

Annex 2 Fish catches in ACG rivers in June 1998.

Locality no.	Pacific slope						Atlantic slope											
	4		5		6		2		3		7		8		9		10	
Name	Q. Aserradero		Rio Murcielago		Rio Tempisquito (upper)		Rio Sapoa (lower)		Rio Sapoa (upper)		Q. Limonal		Rio Orosi		A. Lagunas		Rio Pizote	
Fish species	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Characidae																		
<i>Astyanax aeneus</i>	110	44,35	8	29,63			102	28,65	10	9,71	5	2,20						
<i>Brycon guatemalensis</i>							2	0,56	1	0,97								
<i>Bryconamericanus scleroparius</i>									18	17,48	22	9,69					4	26,67
<i>Roeboides bouchellei</i>	3	1,21					2	0,56			5	2,20						
Gymnotidae																		
<i>Gymnotus maculosus</i>													1	0,97				
Pimelodidae																		
<i>Rhamdia guatemalensis</i>	1	0,40					1	0,28	4	3,88								
<i>Rhamdia rogersi</i>					24	33,80	18	5,06	10	9,71	5	2,20	11	9,57				
Poeciliidae																		
<i>Alfaro cultratus</i>							4	1,12	3	2,91	46	20,26						
<i>Brachyrhaphis olomina</i>					42	59,15					1	0,44						
<i>Phallichthys amates</i>											70	30,84					1	6,67
<i>Poecilia gillii</i>	75	30,24	3	11,11			63	17,70	9	8,74	6	2,64						
<i>Priapichthys annectens</i>													93	80,87	1	1,47		
Rivulidae																		
<i>Rivulus isthmensis</i>					5	7,04					4	1,76			67	98,53		
Cichlidae																		
<i>Amphilophus citrinellus</i>							2	0,56										
<i>Archocentrus nigrofasciatus</i>	39	15,73					28	7,87	5	4,85	22	9,69						
<i>Astatheros longimanus</i>	9	3,63																
<i>Astatheros alfari</i>	4	1,61					6	1,69	4	3,88	41	18,06	10	8,70			8	53,33
<i>Hypsophrys nicaraguensis</i>							45	12,64	1	0,97								
<i>Neetroplus nematopus</i>							64	17,98	22	21,36								
<i>Parachromis dovii</i>	7	2,82					17	4,78	15	14,56								
<i>Theraps underwoodi</i>							1	0,28										
Mugilidae																		
<i>Agonostomus monticola</i>			1	3,70														
Gobidae																		
<i>Awaous transandeanus</i>			1	3,70														
<i>Sicydium salvini</i>			2	7,41														
Eleotridae																		
<i>Eleotris picta</i>			5	18,52														
<i>Gobiomorus dormitor</i>			2	7,41			1	0,28										
<i>Gobiomorus maculatus</i>			5	18,52													2	13,33
Sum	248	100	27	100	71	100	356	100	103	100	227	100	115	100	68	100	15	100

Annex 3 Fish catches in ACG rivers in February 1999. Three additional localities (cf. # 13, 14, and 15 in Table 1) were investigated, but did not contain fish.

Locality no. Name	Pacific slope												Atlantic slope									
	5 Rio Murcielago		11 Rio Tempisquito (lower)		12 Rio Poza Salada		16 Arroyo sin Nombre		17 Q. Zanja Tapata		19 Rio Tibio (upper)		27 Rio Tibio (lower)		2 Rio Sapoa (lower)		3 Rio Sapoa (upper)		7 Q. Limonal		18 Rio El Hacha	
Fish species	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Characidae																						
<i>Astyanax aeneus</i>	27	54,0	368	78,1	6	7,8									3	5,2	2	4,9	48	25,1	1	4,0
<i>Bryconamericanus scleroparius</i>			4	0,8											5	8,6	10	24,4	22	11,5		
<i>Roeboeides bouchellei</i>			7	1,5											1	1,7						
Gymnotidae																						
<i>Gymnotus maculosus</i>			1	0,2											1	1,7						
Ariidae																						
<i>Arius guatemalensis</i>			11	2,3																		
<i>Arius seemanni</i>			27	5,7																		
Pimelodidae																						
<i>Rhamdia guatemalensis</i>			4	0,8															1	0,5	3	12,0
<i>Rhamdia nicaraguensis</i>											8	27,6	2	8,7								
<i>Rhamdia rogersi</i>			4	0,8							1	3,4			4	6,9	3	7,3	6	3,1		
Poeciliidae																						
<i>Alfaro cultratus</i>																	3	7,3	26	13,6	1	4,0
<i>Brachyrhaphis olomina</i>							74	77,9	56	100,0	20	69,0	2	8,7					7	3,7		
<i>Phallichthys amates</i>																			23	12,0		
<i>Poecilia gilli</i>	5	10,0	18	3,8	33	42,9									21	36,2	6	14,6	2	1,0	8	32,0
Rivulidae																						
<i>Rivulus isthmensis</i>							18	18,9											3	1,6		
Cichlidae																						
<i>Archocentrus nigrofasciatus</i>			3	0,6			3	3,2					8	34,8	18	31,0	7	17,1	15	7,9		
<i>Astatheros alfari</i>													2	8,7			1	2,4	38	19,9	9	36,0
<i>Astatheros longimanus</i>			15	3,2																		
<i>Neetroplus nematopus</i>			2	0,4											2	3,4	3	7,3				
<i>Parachromis dovii</i>			3	0,6									9	39,1	3	5,2	6	14,6			3	12,0
<i>Tilapia sp.</i>			3	0,6																		
Mugilidae																						
<i>Agonostomus monticola</i>	6	12,0			2	2,6																
Gobidae																						
<i>Sicydium salvini</i>	3	6,0																				
Eleotridae																						
<i>Dormitator latifrons</i>					2	2,6																
<i>Eleotris picta</i>	2	4,0			2	2,6																
<i>Gobiomorus dormitor</i>			1	0,2																		
<i>Gobiomorus maculatus</i>	7	14,0			32	41,6																

Annex 4 Fish catches in ACG rivers in March 2001. Two additional localities were investigated (cf. # 24 and 25 in Table 1), but did not contain fish.

Locality no.	Pacific slope						Atlantic slope												
	4		5		23		7		28		20		21		22		26		
	Q. Aserradero		Rio Murcielago		R. Potrero Grande		Q. Limonal		Rio Negro		Q. Buenos Aires		Rio Blanco		Rio Cucaracho		Lag. San Gerardo		
Fish species	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	
Characidae																			
<i>Astyanax aeneus</i>	71	47,7	7	10,4			1	0,4	2	7,4	1	1,7							
<i>Bryconamericanus scleroparius</i>	1	0,7					33	12,1					1	2,9					
<i>Roeboeides bouchellei</i>	7	4,7																	
Gymnotidae																			
<i>Gymnotus maculosus</i>							1	0,4	2	7,4	1	1,7							
Pimelodidae																			
<i>Rhamdia nicaraguensis</i>	4	2,7					1	0,4			6	10,3	2	5,9					
<i>Rhamdia rogersi</i>	1	0,7					2	0,7	3	11,1	7	12,1	10	29,4					
Poeciliidae																			
<i>Alfaro cultratus</i>							43	15,8											
<i>Brachyrhaphis olomina</i>							6	2,2											
<i>Phallichthys amates</i>							123	45,1											
<i>Poecilia gillii</i>	41	27,5	38	56,7			25	9,2			1	1,7							
<i>Poeciliidae indet.</i>																	1	2,9	
<i>Poecilopsis sp</i>					110	68,8													
<i>Priapichthys annectens</i>									17	63,0	17	29,3	15	44,1	67	100,0			
Rivulidae																			
<i>Rivulus isthmensis</i>							9	3,3			11	19,0	3	8,8					
Gobiesocidae																			
<i>Gobiesox nudus</i>									2	7,4	1	1,7							
Synbranchidae																			
<i>Synbranchus marmoratus</i>							1	0,4											
Cichlidae																			
<i>Archocentrus nigrofasciatus</i>	15	10,1					15	5,5											
<i>Astatheros alfari</i>	7	4,7					13	4,8			9	15,5	2	5,9			34	97,1	
<i>Neetroplus nematopus</i>											2	3,4							
<i>Parachromis dovii</i>	2	1,3							1	3,7	2	3,4							
<i>Theraps underwoodi</i>													1	2,9					
Mugilidae																			
<i>Agonostomus monticola</i>			9	13,4	21	13,1													
Gobiidae																			
<i>Awaous transandeanus</i>			2	3,0	2	1,3													
<i>Sicydium salvini</i>					5	3,1													
Eleotridae																			
<i>Eleotris picta</i>			7	10,4	16	10,0													
<i>Gobiomorus maculatus</i>			4	6,0	6	3,8													
Sum	149	100,0	67	100,0	160	100,0	273	100,0	27	100,0	58	100,0	34	100,0	67	100,0	35	100,0	

Annex 5 Host-Parasite List – Guanacaste, Costa Rica 1998-2001.***Agonostomus monticola*** (n=28)

Clinostomatidae gen. sp. (L)
Contraceacum sp. (L)
 Mesostephanus sp. (L)
 Monogenea gen. sp.
 Nematoda gen. sp.
Procamallanus sp.
Spinitectus agonostomi
 Cestoda (Proteocephalidea) gen. sp.

Alfaro cultratus (n=26)

Nematoda gen. sp.
 Rhabdochoniidae gen. sp.
Spinitectus sp.
 Spirurida gen. sp.

Archocentrus nigrofasciatus (n=82)

Clinostomatidae gen. sp. (L)
Crassicutis cichlasomae
 Digenea gen. sp. (L.)
Saccocoelioides sp. 3
Procamallanus (rebecca)
Rhabdochona kidderi
 Rhabdochoniidae gen. sp.
Rondonia (rondoni).
 Nematoda gen. sp.

Arius guatemalensis (n=11)

Digenea gen. sp.

Arius seemani (n=27)

Digenea gen. sp. (L)
Contraceacum sp. (L)
 Cucullanidae gen. sp.

Astatheros alfari (n=113)

Clinostomatidae gen. sp. (L)
Contraceacum sp. (L)
Crassicutis cichlasomae
Hysterothylacium sp. (L)
Procamallanus sp.
Procamallanus (rebecca)
 Proteocephalidea gen. sp.
Rhabdochona sp.
Rhabdochona kidderi
Spiroxys sp. (L)

Astatheros longimanus (n=19)

Contraceacum sp. (L)
Crassicutis cichlasomae
 Nematoda gen. sp. (L)
Rhabdochona (kidderi)

Astyanax aeneus (n=128)

Contraceacum sp. (L)
 Ergasilidae gen. sp.
 Monogenea gen. sp.
 Digenea gen. sp. (L)
Prosthenhystera obesa
Saccocoelioides sp.
Wallinia chavarriae
Procamallanus (neocaballeroi).

Awaous transandeanus (n=2)

Procamallanus sp.
 Proteocephalidea gen. sp.

Brachyrhaphis olomina (n=37)

Digenea gen. sp.
 Monogenea gen. sp.
Paracreptotrema mendezii
Procamallanus sp.

Brycon guatemalensis (n=2)

Saccocoelioides sp.
Neocucullanus sp.

Bryconamericus scleroparius (n=92)

Digenea gen. sp. (L.)
 Ergasilidae gen. sp.
 Monogenea gen. sp.
 Nematoda gen. sp.
Wallinia chavarriae
Saccocoelioides sp. 1
Rhabdochona (neocaballeroi/acuminata)

Dormitator latifrons (n=2)

No parasites recorded

Eleotris picta (n=25)

Acanthocephala gen. sp.
 Digenea gen. sp. (L)
 Nematoda gen. sp.
 Proteocephalidae gen. sp.
 Rhabdochoniidae gen. sp.

Gobiesox nudus (n=1)

No parasites recorded

Gobiomorus dormitor (n=5)

Digenea gen. sp.
 Capillariidae gen. sp.
Contraceacum sp. (L)

Gobiomorus maculatus (n=30)

Rhabdochoniidae gen. sp.

Annex 5, continued

Gymnotus cylindricus (n=4)
Clinostomatidae gen. sp. (L)

Gymnotus maculosus (n=3)
No parasites recorded

Hypsophrys nicaraguensis (n=15)
Crassicutis cichlasomae
Saccocoelioides sp.

Neetroplus nematopus (n=32)
Digenea gen. sp.
Ergasilidae gen. sp.
Saccocoelioides sp. 3
Rondonia (*rondoni*).
Procamallanus (*rebecca*)
Rhabdochona (*kidderi*)

Parachromis dovii (n=42)
Crassicutis cichlasomae
Genarchella sp.
Monogenea gen. sp.
Oligogonotylus manteri
Procamallanus rebecca sp.
Proteocephalidae gen. sp.
Pseudocaecincola sp.
Rhabdochona sp.
Rhabdochona kidderi

Parachromis managuense (n=1)
Contracaecum sp. (L)
Monogenea gen. sp.
Nematoda gen. sp.
Neoechinorhynchus golvani

Phallichthys amates (n=23)
Contracaecum sp. (L)

***Poeciliopsis* sp.** (n=33)
No parasites recorded

Poecilia gilli (n=91)
Ergasilidae
Monogenea gen. sp.
Digenea gen.sp. (L)
Saccocoelioides sogandaresi

Priapichthys annectens (n=56)
Digenea gen. sp.
Paracreptotrema blancoi
Rhabdochonidae gen. sp.
Spinitectus mexicanus
Spirurida gen. sp.

Rhamdia guatemalensis (n=9)
Cucllanus pimelodellae
Procamallanus sp.

Rhamdia nicaraguense (n=22)
Acanthostomum minimum
Capillariidae gen. sp.
Contracaecum sp. (L)
Crassicutis cichlasomae
Cucllanus pimelodellae
Digenea gen. sp.(L)
Procamallanus sp.

Rhamdia rogersi (n=90)
Digenea gen. sp.
Monogenea gen. sp.
Acanthostomum minimum
Clinostomatidae gen. sp.
Capillariidae gen. sp.
Contracaecum sp.
Rhabdochona sp.
Spirurida gen. sp.
Strigeidae gen. sp. (L)

Rivulus isthmensis (n=28)
Digenea gen. sp.
Contracaecum sp.
Rhabdochona (*cubensis*)
Spinitectus sp.

Roebooides bouchellei (n=1)
Nematoda gen. sp.

Sicydium salvini (n=7)
Clinostomatidae gen. sp.

Synbranchus marmoratus (n=1)
Contracaecum sp. (L)
Proteocephalidae gen. sp.

Theraps underwoodi (n=1)
No parasites recorded

***Tilapia* sp.** (2)
No parasites recorded

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