

MACROINVERTEBRATE ASSEMBLAGES IN GORGONA ISLAND STREAMS: SPATIAL PATTERNS DURING TWO CONTRASTING HYDROLOGIC PERIODS

ENSAMBLAJE DE MACROINVERTEBRADOS DE LAS QUEBRADAS DE LA ISLA GORGONA: PATRONES ESPACIALES DURANTE DOS PERIODOS HIDROLÓGICOS CONTRASTANTES

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Abstract

Studies comparing various streams are scarce in tropical insular systems and inexistent in Colombia. In order to understand the spatial patterns of macroinvertebrates in tropical insular streams, and the environmental drivers of such patterns, we tested for patterns among streams but using a nested sampling design from streams to microhabitats in Gorgona Island (Colombia, Tropical Eastern Pacific) during two seasons (low and high precipitation). We found that benthic macroinvertebrate assemblages showed clear differences among streams despite of the variability within nested levels. Hydrologic disturbance tended to homogenize spatial patterns in most of the streams. Although ordinations of sampling units using either macroinvertebrate composition or environmental variables were not fully consistent, it was evident that water physicochemistry influenced by underlying geology was a pervasive driver of macroinvertebrate distribution. We highlight the importance of incorporating multiscale sampling designs for studying distributions of macroinvertebrates in tropical islands, and for biomonitoring.

Key words: Gorgona Island, hydrologic disturbance, macroinvertebrate assemblages, multiscale patterns, tropical insular streams, water physicochemistry

Resumen

Los estudios que comparan varias quebradas son aun escasos en los ambientes insulares tropicales e inexistentes en Colombia. Se sometió a prueba la hipótesis de que los ensamblajes de macroinvertebrados son diferentes entre quebradas utilizando un diseño de muestreo completamente anidado desde el nivel de quebrada hasta el nivel del microhábitat en la Isla Gorgona (Pacífico Oriental Tropical Colombiano) durante dos periodos hidrológicos contrastantes (época seca y época lluviosa). Se encontró que los ensamblajes de macroinvertebrados son diferentes entre quebradas a pesar de las diferencias observadas en niveles inferiores anidados. El disturbio hidrológico tendió a homogenizar los patrones espaciales. Aunque las ordenaciones basadas en la composición de macroinvertebrados de los ensamblajes y las variables ambientales no fueron completamente consistentes, fue evidente que las características físico-químicas del agua, influenciadas por la geología, explicaban la distribución de los macroinvertebrados. Resaltamos la importancia de incorporar diseños de muestreo multinivel para estudiar los ensamblajes de macroinvertebrados insulares tropicales y para el biomonitoreo.

Palabras clave: disturbio hidrológico, ensamblajes de macroinvertebrados, físico-química del agua, Isla Gorgona, patrones multi-espaciales, quebradas tropicales insulares

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INTRODUCTION

Understanding ecological patterns and their drivers is a main challenge in science and it is cornerstone for developing management principles (Levin 1992). Because these patterns and processes are linked to multiple scales (Boyero 2003, Levin 1992), their detection depends on appropriate selection of observation scales (Levin 1992, Parsons et al. 2004, Poff 1997). For this reason, the problem of scale must be considered a primary objective of ecological investigation (Wiens 1989). This problem is particularly critical in streams that show extreme heterogeneity in their environmental conditions and biotic assemblages at multiple spatial scales, from microhabitats to landscapes and complete ecoregions (Heino et al. 2004). Streams are hierarchically organized (Frissell et al. 1986) and thus their physical and biotic properties are highly variable in time and space (Cooper et al. 1998, Hildrew and Giller 1994, Poff 1997). For this reason, the emergence of scale as an important ecological concept (Levin 1992, Wiens 1989) has stimulated multi-scale-research in streams (Parsons et al. 2004). In streams, as in any ecosystem, it is critical to make an appropriate selection of the scales of observation within the context of the hierarchical theory (Wiens 1989). Then, the selection could be derived from a parallel physical hierarchy such as the fluvial geomorphic hierarchy proposed by Frissell et al. (1986).

Despite of the current progress on multiscale research in streams, there are still few studies incorporating this hierarchical context (e.g., Parsons et al. 2003 and Thomson et al. 2004). According to the review by Parsons et al. (2004), studies examining the distribution of lotic macroinvertebrate assemblages have focused on either end of the spatial hierarchy and have used a stratified design (macroscale: Corkum

1991, 1992, Li et al. 2001, Rabeni et al. 1999, Sheldon and Walter 1998, Townsend et al. 1997; microscale: Boyero and Bailey 2001, Downes et al. 1993, 1995, Downes et al. 2000). In addition, Robson et al. (2005) cautioned on the high universal variation at the scale of the sampling unit in riffles at perennial cobble-bed streams in Australia, and highlighted that few studies had been conducted to examine the change of this source of variation along time or if the results apply to other habitats (such as pools) or other stream type (e.g., intermittent).

These investigations have been conducted in continental-temperate zones, and they are scarce in the Tropics (Boyero 2000, Jacobsen et al. 2008). Additionally, these have been conducted mainly in disturbed systems, despite the importance of searching for patterns at pristine or protected systems to understanding the structure of natural communities and to develop management plans, especially at insular tropical systems (Dudgeon 1994, Smith et al. 2003). For this reason, we aimed to understand the spatial patterns of macroinvertebrates and their environmental drivers at a protected natural insular area off the Pacific Coast of Colombia (Gorgona Island). Past research in this small island has reported that the numerous streams are heterogeneous in terms of macroinvertebrate assemblages, despite their homogeneous geology and water chemistry (Cala 1990, Vásquez et al. 1996, Zamora et al. 1996, Zapata et al. 1991). However, the generality of this statement needs to be tested because those studies: a) did not use fully-nested sampling designs, and b) did not employ enough sampling effort. Similar limitations in sampling designs are observed in most studies on stream macroinvertebrates in Colombia (JF Blanco in preparation), as bio-monitoring has been the main theme over the past thirty years (Roldán and Ruíz 2001). Therefore, the current understanding of ecological patterns

and processes at insular and continental streams in Colombia, as elsewhere in the Tropics (Smith et al. 2003), is still incomplete. In addition, it is not clear if the concepts, paradigms and management plans derived from high latitudes could be applied in these systems (Boulton et al. 2008). For this reason, tropical stream ecologists are developing approximations to understand, to manage and to conserve these environments (Ramírez et al. 2008). The results show that studies with comparative focus are necessary, because insular systems differ of continentals in a huge range of geologic, climatic, biogeographic and anthropocentric characteristics. We expect to provide the baseline information

for including Gorgona Island in future global comparisons.

The aim of this paper was to test if streams on Gorgona Island were homogeneous in terms of macroinvertebrate assemblages, biotic (e.g., leaf litter standing stocks, riparian forest classification) and abiotic (e.g., geology, geomorphology, hydraulics, water physico-chemistry) properties. Patterns were compared between two seasons (low and high precipitation).

MATERIALS AND METHODS

Study area. Gorgona Island is a continental volcanic massif (Kerr 2005), (9 x 2.5 km)

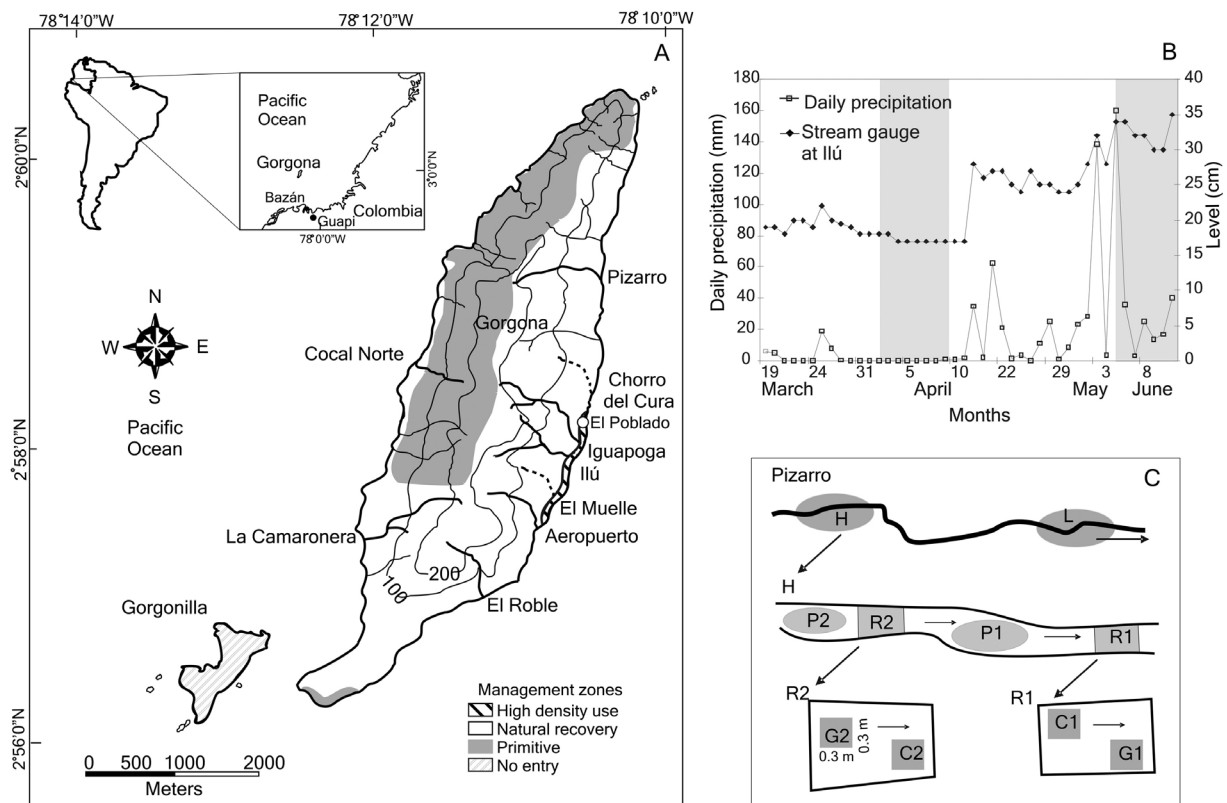


Figure 1. A. Location of Gorgona Island and sampling streams of the Gorgona Island (Tropical Eastern Pacific, Colombia) (Modify of Díaz et al. 2001). Zonation based in management plan 1998-2003 (UAESPNN 2005). B. Hydrologic conditions during sampling periods. Shaded areas correspond to sampling days during 2008. C. Nested sampling design to each stream. Reaches H: higher-elevation and L: low-elevation. Habitats P: pools and R: riffles. Microhabitats G: gravel and C: cobble. 1 and 2: sampled units

in the Colombian Tropical Eastern Pacific (figure 1; 2° 47' - 3° 06' N, 78° 06' - 78° 18' W), 54 km off Guapi. Elevation ranges from 0 to 330 masl. Nearly 90% of the island is steep gradient (50-75%) surrounded by smooth gradient (< 12%) lowlands. Average air temperature, relative humidity and annual rainfall are 26 °C, 90%, and 6.778 mm, respectively. Two climatic seasons are differentiated in Gorgona: rainy (May-November) and low precipitation (December-April), (Díaz et al. 2001, UAESPNN 2005). High annual precipitation feeds nearly 100 streams, 25 of which are permanent. Nine of these were selected to this study (Appendix 1). A detailed account of hydrology and stream physico-chemistry is found in Blanco (2009a, b, this issue).

Gorgona was a penitentiary island between 1960 and 1982, but it was declared National Natural Park (NNP) in 1983. Because of intervention during the penitentiary period, natural and disturbed forests occur on the island. Accordingly, the management plan (UAESPNN 2005) establishes three zones: **1)** primitive, **2)** natural recovery, and **3)** high-density use (figure 1A). A detailed account of landuse history is found in Valencia-G. et al. (2009, this issue).

Sampling. It was conducted during two seasons in 2008: low (2-9 April) and high (4-10 June) precipitation (figure 1B). In both seasons, we applied the “underlying hierarchy” approach (Parsons et al. 2004). Sampling units (0.3 x 0.3 m plots) were distributed across the fluvial spatial hierarchy (i.e. from subregions to microhabitats) as shown in figure 1C. We sampled 9 streams (2 within the Western Slope, and 7 at the Eastern Slope). However during the rainy season, El Roble stream was not sampled due to a flashflood. Benthic organisms were collected

using a Surber net (0.09 m², 0.5 mm mesh), preserved in 70% alcohol and transported to the laboratory to be identified to the lowest possible taxonomic level (genus or family morphotype, and subfamily to Chironomidae) using the available literature and expert knowledge. Biotic and abiotic descriptors were qualitatively and quantitatively measured at each hierarchical level (Appendices 2 and 3). Thirty four descriptors and twenty five were respectively measured during low and high precipitation periods.

Data analyses. Total densities of taxa were calculated for each microhabitat (individual observation unit) pooling all individual sampling units, then we obtained 43 total density values during low precipitation season and 39 during high precipitation. Since the organisms were identified at different taxonomic levels (family, genus or morph) we call them “operational taxonomic units” (OTUs) for convenience. Total densities, biotic and abiotic variables were square-root transformed (Costa and Melo 2008, McCune and Mefford 1999, Von Ellenrieder 2007). Richness (number of OTUs), Shannon’s diversity index, and Pielou’s diversity index were computed for describing assemblage structure at each stream.

Among-stream patterns. The similarities among streams were tested by firstly ordinating sampling units with a Non-Metric Multidimensional Scaling (NMDS) based on macroinvertebrate OTU composition (Ilmonen and Paasivirta 2005, Legendre and Legendre 1998, McCune and Mefford 1999). Mean NMDS coordinates and standard deviations were computed by pooling all sampling units within a single stream and plotted using PAST (Palaeontological statistics, version 1.82b, Hammer et al. 2001). Differences among streams were then tested using the Multiple Response Permutation Procedure

(MRPP) using Sorensen (Bray-Curtis) measure of distance (Dinger et al. 2006, Heino et al. 2005, McCune and Mefford 1999, Soldner et al. 2004, Von Ellenrieder 2007). The above procedure was repeated using a matrix of abiotic and biotic descriptors (qualitative and quantitative) to test for differences among streams based in the "parallel hierarchy". Seasonal consistency of spatial patterns was tested by separately running the analyses for both low and high precipitation periods. NMDS and MRPP analyses were performed with PCORD (version 4.25, McCune and Mefford 1999, MjM Software, Gleneden Beach, Oregon).

RESULTS

Assemblage structure. Number of OTUs, Shannon's diversity index, Pielou's evenness index and mean density changed across streams and between sampling periods (table 1). Pizarro and Ilú showed the largest number of OTUs and diversity values. El Chorro

del Cura, El Roble, El Muelle showed low richness, particularly during the rainy season. These streams also exhibited low diversity. Regarding temporal patterns, richness was reduced at all streams (except Ilú) during the rainy period. Diversity did not show a clear temporal pattern because it was reduced at some streams and increased at some others. In addition the degree of reduction of diversity during the rainy season was highly variable among streams, as high as > 20% at Pizarro, Cocal Norte and El Muelle. Evenness was relatively high (> 70%) in all streams. Percent of change between sampling periods was variable among streams. Mean density was reduced at all streams (except Ilú and Pizarro) during the rainy period.

Taxonomic composition. We found 10 arthropod orders (9 Insecta and 1 Crustacea), and 31 families (table 2). Trichoptera was the richest order, followed by Ephemeroptera,

Table 1. Descriptors of macroinvertebrate assemblage structure at nine streams in Gorgona Natural Nacional Park (**SP** = *Sampling periods*: **L** = low precipitation; **H** = high precipitation. **%**: Percent change between periods. *Stream codes*: **AP** = Aeropuerto, **CC** = Chorro del Cura, **CN** = Cocal Norte, **CR** = La Camaronera, **IG** = Iguapoga, **IL** = Ilú, **M** = El Muelle, **PZ** = Pizarro, **RB** = El Roble. El Roble was not sampled during the high precipitation period)

Index	Sam- pling period	Stream								
		IL	IG	PZ	CC	AP	M	CN	CR	RB
Richness (# OTUs)	L	25	26	29	20	25	19	23	26	15
	H	33	22	22	12	21	11	17	18	-
	%	32	-15	-24	-40	-16	-42	-26	-31	-
Shannon's Diversity	L	2,71	2,61	2,72	2,43	2,61	2,67	2,69	2,24	2,48
	H	2,63	2,65	2,09	2,26	2,40	2,18	2,11	2,43	-
	%	-3	2	23	-7	-8	-18	-22	8	-
Pielou's Evenness	L	0,84	0,80	0,81	0,81	0,81	0,91	0,86	0,69	0,91
	H	0,75	0,86	0,68	0,91	0,79	0,91	0,74	0,84	-
	%	-11	7	-16	-12	-2	0	-14	22	-
Mean Density (ind.m ²)	L	74,5	130,1	90,5	122,2	236,1	313,9	238,9	270,8	50,9
	H	126,8	120,8	140,5	75,0	130,6	61,1	144,1	61,1	-
	%	70,2	-7,1	55,2	-38,6	-44,7	-80,5	-39,7	-77,4	-

Table 2. Relative densities and frequencies of families collected by season in streams sampled in Gorgona Natural Nacional Park (Tropical Eastern Pacific, Colombia)

Order	Family	Relative density (%)		Relative frequency (%)	
		Low	High	Low	High
Ephemeroptera	Leptophlebiidae	33.8	43.9	88.4	100.0
	Leptohyphidae	1.2	2.9	27.9	30.8
	Baetidae	1.1	5.7	9.3	53.8
	Nesameletidae ?	3.9	3.3	32.6	38.5
Trichoptera	Hydropsychidae	8.2	3.3	74.4	33.3
	Glossosomatidae	0.2	0.3	7.0	7.7
	Philopotamidae	0.1	0.2	4.7	5.1
	Calamoceratidae	-	0.1	-	2.6
	Leptoceridae	0.8	0.7	16.3	12.8
	Xiphocentronidae	0.2	0.1	4.7	2.6
	Polycentropodidae	0.3	0.5	7.0	5.1
	Hidroptilidae	0.1	-	2.3	-
	Perlidae	2.5	3.0	39.5	38.5
Plecoptera	Corydalidae	0.2	0.4	9.3	10.3
Megaloptera	Coenagrionidae	5.6	3.0	69.8	41.0
	Gomphidae	1.0	0.8	20.9	12.8
Odonata	Platystictidae	0.6	2.2	16.3	15.4
	Megapodagrionidae	0.1	0.5	2.3	10.3
	Psephenidae	5.3	7.0	44.2	53.8
	Ptilodactylidae	4.1	4.1	62.8	41.0
Coleoptera	Elmidae	7.7	6.9	76.7	66.7
	Staphylinidae	0.1	0.2	2.3	5.1
	Veliidae	2.3	1.1	34.9	23.1
	Gerridae	0.5	-	14.0	-
Lepidoptera	Pyralidae	0.4	0.1	9.3	2.6
Diptera	Tipulidae	2.3	1.1	46.5	23.1
	Simuliidae	0.6	0.6	9.3	12.8
	Chironomidae	12.8	2.7	79.1	35.9
	Ceratopogonidae	0.1	-	4.7	-
	Atyidae	3.1	5.0	32.6	43.6
Decapoda	Palaemonidae	0.6	0.1	14.0	2.6

Odonata, Coleoptera, and Diptera. Leptophlebiidae (Ephemeroptera) was the most abundant and frequent family islandwide, particularly during the rainy period. The Chironomidae were also abundant and frequent but mainly during the low precipitation period. Hydropsychidae (Trichoptera) and Coenagrionidae (Odonata) were also frequent,

but not abundant, during the low precipitation. The Psephenidae, Ptilodactylidae, and Elmidae (Coleoptera) were frequent during both periods but not abundant. Decapod shrimps (Atyidae: *Potimirim*, Palaemonidae: *Macrobrachium*) were observed but not abundant in our collections. The gastropod *Neritina latissima* was also observed, but it was not collected in our

samplings because it was restricted to the first hundred meters upstream from the confluence with the ocean and it was not abundant.

Patterns among streams. *Macroinvertebrate assemblages.* The NMDS and MRPP showed separation of sampling units among stream assemblages during both seasons (figure 2). During the low precipitation season (table 3), the streams at the Western Slope

(Cocal Norte and La Camaronera) exhibited distinctive macroinvertebrate assemblages. In contrast, Cocal Norte showed more similarities with several streams at the central part of the Eastern Slope. Macroinvertebrate assemblages at the two most isolated streams at the Eastern Slope (El Roble and Pizarro) were similar to neighbouring streams but not between them. During the high precipitation period, the differences between the two streams at the Western Slope were maintained.

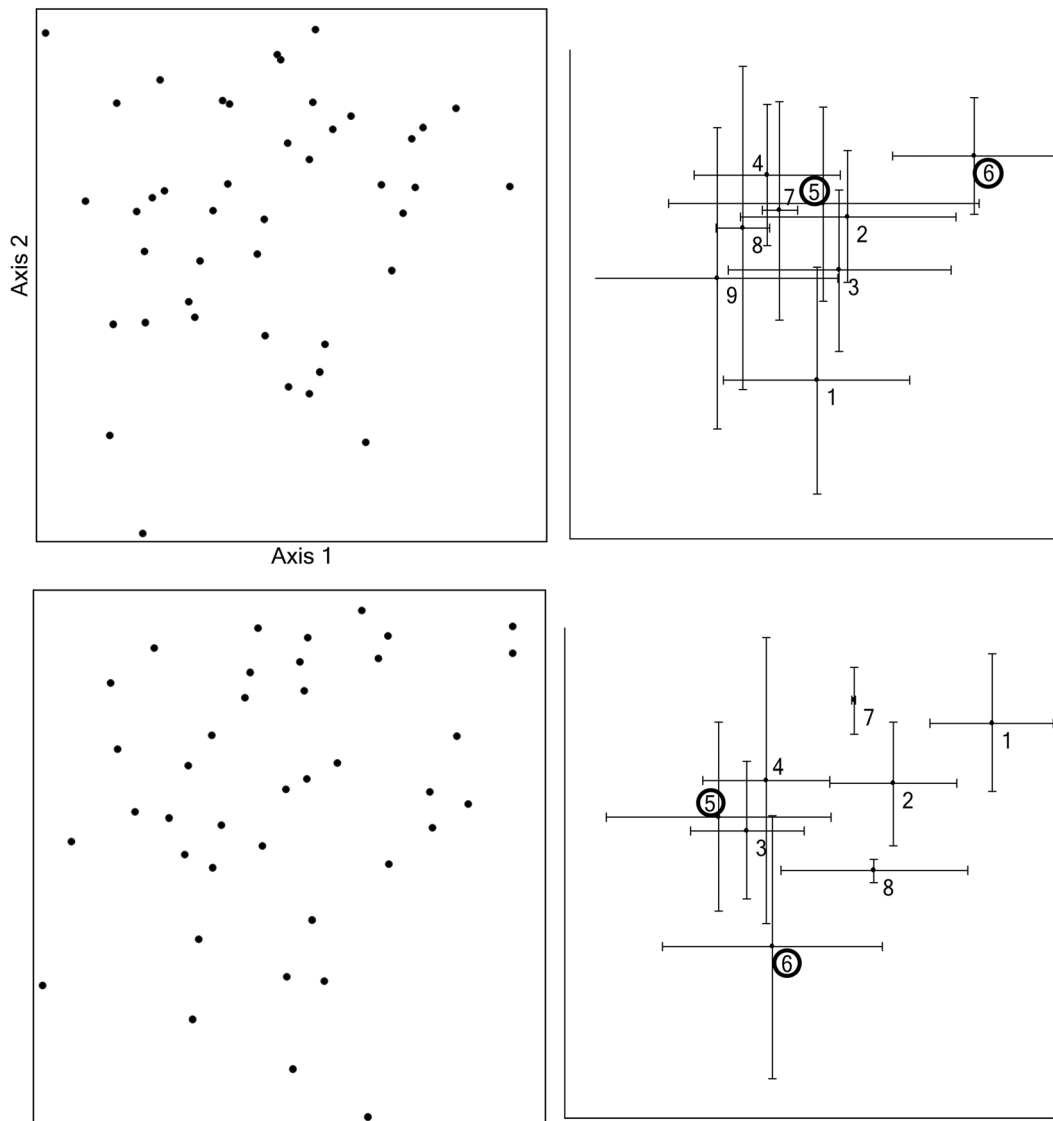


Figure 2. NMDS ordination based on macroinvertebrate OTU composition for low precipitation (top, stress 16.25) and high precipitation (bottom, stress 16.53). Mean NMDS coordinates and standard deviations at side showed separation between streams of the Gorgona Island (Tropical Eastern Pacific, Colombia) (1= Ilú, 2= Iguapoga, 3= Pizarro, 4= Aeropuerto, 5= Cocal Norte, 6= La Camaronera, 7= El Muelle, 8= Chorro del Cura, 9= El Roble. Numbers inside circles correspond to western streams)

However, both streams showed similarities with the smallest streams at the opposite slope. Contrary to the previous season, they showed similarities with Pizarro, but not with Ilú and Iguapoga. During this season, Pizarro was more similar to most streams at the Eastern Slope.

Environmental characteristics. The ordinations based on environmental variables were not consistent with those based on macroinvertebrate assemblages (figure 3, table 4). During the low precipitation period, despite the differences in geology between Cocal Norte and La Camaronera (volcanic and sedimentary, respectively), they were similar in terms of the descriptors used. In addition, La Camaronera was similar to several streams at the Eastern Slope (Aeropuerto, El Muelle, and El Chorro del Cura). Cocal Norte was not similar to El Muelle, Ilú, and Iguapoga as observed using

macroinvertebrate assemblages. Ilú and El Roble (1 and 9, respectively in figure 3) were different from all streams. During the rainy period, Cocal Norte and La Camaronera (5 and 6, respectively in figure 3) differed among them and among the streams at the Eastern Slope. In addition, while Iguapoga (2 in figure 3) differed from all streams at the Eastern Slope, Ilú was similar to all streams. During the low precipitation period, hydraulic (mean water velocity, Reynolds and Froude numbers), and geomorphic (channel slope) variables correlated with Axis 1, while water physicochemistry (pH, conductivity, alkalinity, and CO₂ concentration) and leaf litter richness and biomass correlated with Axis 2 (table 5). During the rainy period, management zones correlated with Axis 1, while water physicochemistry (conductivity and alkalinity), geology and geomorphology (channel slope), and leaf litter biomass correlated with Axis 2.

Table 3. Values of the A statistic for Multiple Response Permutation Procedure (MRPP). Pairwise comparisons between streams of the Gorgona Island (Tropical Eastern Pacific, Colombia), for each season based on macroinvertebrate OTUs matrix [IL = Ilú, IG = Iguapoga, PZ = Pizarro, AP = Aeropuerto, CN = Cocal Norte, CR = La Camaronera, M = El Muelle, CC = Chorro del Cura, RB = El Roble (x = insufficient data for conducting the analysis, ** $p < 0.01$, * $p < 0.05$)]

Season	Streams								
		IL	IG	PZ	AP	CN	CR	M	CC
Low precipitation	IG	0.033							
	PZ	0.067	0.035						
	AP	0.180**	0.051	0.209*					
	CN	0.053	0.019	0.154*	0.148				
	CR	0.214**	0.160**	0.289**	0.221**	0.089*			
	M	0.096	0.138	0.240*	-0.085	0.063	0.206*		
	CC	-0.035	0.074	0.039	-0.032	0.042	0.073	x	
	RB	0.013	0.111	0.098*	0.167*	0.111	0.212**	0.148	-0.084
High precipitation	IG	0.088							
	PZ	0.287**	0.064						
	AP	0.233**	-0.09	-0.026					
	CN	0.28**	0.255**	0.078	0.079				
	CR	0.345**	0.141*	0.073	0.1	0.208**			
	M	0.044	-0.063	-0.009	0.021	0.042	0.067		
	CC	0.140*	-0.042	0.014	0.042	0.233	0.059	x	

Table 4. Values of the A statistic for Multiple Response Permutation Procedure (MRPP). Pairwise comparisons between streams of the Gorgona Island (Tropical Eastern Pacific, Colombia), for each season based on a matrix of physical, chemical, geomorphologic, and riparian forest features, and management zoning [**IL** = Ilú, **IG** = Iguapoga, **PZ** = Pizarro, **AP** = Aeropuerto, **CN** = Cocal Norte, **CR** = La Camaronera, **M** = El Muelle, **CC** = Chorro del Cura, **RB** = El Roble (x = insufficient data for conducting the analysis, ** $p < 0.01$, * $p < 0.05$)]

Season	Streams								
		IL	IG	PZ	AP	CN	CR	M	CC
Low precipitation	IG	0.258**							
	PZ	0.296**	0.114						
	AP	0.372**	0.153	0.208*					
	CN	0.415**	0.269*	0.343**	0.139				
	CR	0.444**	0.187*	0.248**	0.115	0.107			
	M	0.241**	0.063	0.129	0.106	0.339*	0.106		
	CC	0.224**	0.106*	0.132	0.063	0.095	0.053	x	
	RB	0.327**	0.241*	0.410**	0.444**	0.444**	0.394**	0.360*	0.317*
High precipitation	IG	0.146*							
	PZ	0.090	0.162*						
	AP	0.132	0.306**	0.360**					
	CN	0.233*	0.444**	0.340**	0.444**				
	CR	0.203**	0.154*	0.237**	0.219**	0.248**			
	M	0.073	0.254*	0.207*	0.339*	0.317*	0.192*		
	CC	0.130	0.317*	0.315**	0.402*	0.317*	0.229*	x	

DISCUSSION

Taxonomic composition. In Gorgona Island's streams, insects dominated over gastropods and decapods, groups otherwise dominant in insular tropical streams (Bass 2003). Such dominance in species richness and abundance may result from the continental origin of the island, as observed elsewhere (Bass 2003, March et al. 2003, Smith et al. 2003). The short distance between Gorgona Island and the continent (< 54 km) may explain the presence of all insect orders commonly found in tropical islands (Bass 2003). The most abundant insect orders were Ephemeroptera, Diptera, Coleoptera and Trichoptera, especially the families Leptophlebiidae, Chironomidae, Elmidae and Hydropsychidae, respectively. This pattern has been reported, in general, for tropical stream assemblages (Jacobsen et al. 2008) and is similar to the reported by Boyero and Bailey

(2001) at Juncal stream (Coiba Island, Panamá). The authors indicated that the above-mentioned families (except Hydropsychidae, and including Psephenidae) were the most abundant and common.

Contrary to our findings, previous studies at the island (Cala 1990, Zamora et al. 1996, Zapata et al. 1991) reported the presence of gastropods and a broad distribution and dominance of stream shrimps. Such differences may reflect the different sampling nets used in those studies and our study. The Surber method used in our study is more efficient for collecting insects than shrimps. This method sub-estimates shrimp abundance because they are highly mobile as postlarvae and adults, and they drift as larvae (Ramírez and Pringle 1998a, b). Field observations and leaf litter samples for studies in progress in Gorgona Island (Longo, data not published)

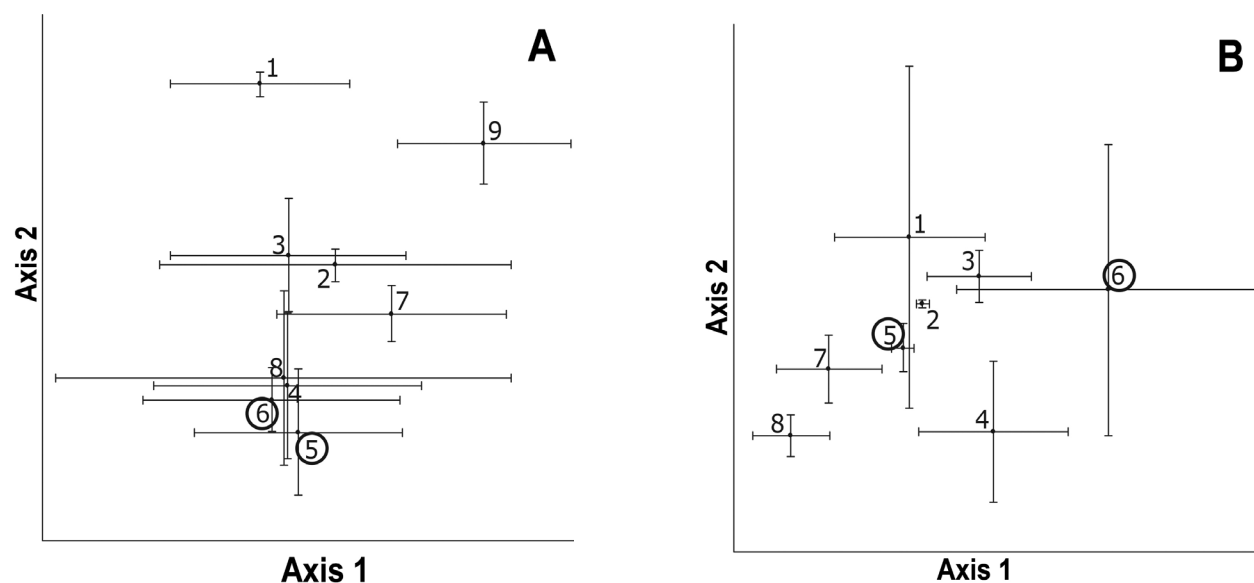


Figure 3. NMDS ordination based on environmental variables obtained for low precipitation (A., stress 11.37) and high precipitation (B., stress 8.15). Mean NMDS coordinates and standard deviations at side showed separation between streams of the Gorgona Island (Tropical Eastern Pacific, Colombia) (1 = Ilú, 2 = Iguapoga, 3 = Pizarro, 4 = Aeropuerto, 5 = Cocal Norte, 6 = La Camaronera, 7 = El Muelle, 8 = Chorro del Cura, 9 = El Roble)

indicate, higher shrimps abundances than the reported by our study. The inclusion of other sampling methods and variables would have let us obtaining higher abundances and testing for marked distribution patterns as reported for shrimps in other tropical islands (Fièvet et al. 2001, Fossati et al. 2002, Pyron et al. 1999).

Gastropods were not found in this study. However, *Neritina latissima* was observed at the lowest elevations in some streams (not included in sampling) and with low abundances. According to Blanco and Scatena (2006) this

limited distribution of neritid gastropods could be related to barriers (cascades and dams), steep slopes, absence of connectivity with ocean (thus restricting upstream migration) and water chemistry (high conductivity and concentrations of dissolved ions).

Temporal variation. In addition to the observed reduction in macroinvertebrate abundances in Gorgona Island (Gómez-Aguirre 2009), we here reported a reduction in richness and an homogenization of taxonomic composition of the assemblage during the rainy period

Table 5. Correlation index of environmental variables with ordination axes shown in figure 3

Low precipitation		High precipitation	
Axis 1	Axis 2	Axis 1	Axis 2
Mean velocity (0,94)	pH (-0,87)	Irradiance (0,64)	Conductivity (-0,93)
Reynolds number (0,95)	Conductivity (-0,93)	Manag. zone (-0,58)	Alkalinity (-0,56)
Froude number (0,95)	Alkalinity (-0,82)		Geology (-0,51)
Channel slope (-0,83)	Carbon dioxide (0,82)		Channel slope (-0,69)
	Litter richness (-0,57)		Litter biomass (0,59)
	Litter biomass (-0,71)		

(although differences among several streams were still evident). It is well known that flash flooding is an important disturbance in temperate and tropical streams, temporally reducing benthic invertebrate abundances because of the catastrophic drift and the alteration of potential flow refugia (Flecker and Feifarek 1994, Hildrew and Giller 1994, Matthaei et al. 2000, Ramírez and Pringle 1998b, Ramírez et al. 2006). In Gorgona Island assemblage homogenization occurred at intermediate spatial scales (reach and habitat) during the rainy season, but differences were observed between cobble and gravel patches (Gómez-Aguirre 2009).

Spatial patterns. The differences observed among macroinvertebrate assemblages in Gorgona Island streams may partially reflect physical, chemical and biological properties. The assemblages at El Roble may reflect the highly turbulent nature of the streamflow, and the steep slope. These properties also correlated with leaf litter poverty and scarcity. Assemblages at Cocal Norte, although located on the Western Slope, were more similar to streams at the central part of the Eastern Slope probably because the watershed divide is not high enough to isolate them. On the contrary, El Roble and Pizarro located at opposite ends of the Eastern Slope are very far from each other and therefore their assemblages are very distinct. Therefore, adult insect migration is a seemingly important homogenizing process in Gorgona Island. It is, however, surprising that marked spatial differences occurred along the main axis of the island given that it is only 9 km long. During the rainy period, although macroinvertebrate assemblages were homogenized across streams, water physico-chemical properties and litter standing stocks were significantly different among streams and slopes.

Watershed geology and water properties (particularly conductivity) explained spatial

patterns among streams in Gorgona Island (see Blanco 2009a in this issue). In addition, habitat and microhabitat-scale hydraulics were coupled with channel geomorphology, particularly with slope. Leaf litter standing stock may reflect both channel and riparian processes. For instance, the reduced leaf litter biomass observed at El Roble may result from the high gradient and the flashy hydrograph. On the other hand, reduced leaf litter richness and biomass in several streams may reflect past deforestation (Ilú, Iguapoga, El Muelle, El Chorro del Cura, Aeropuerto) or tree falling and landsliding disturbances (La Camaronera, Pizarro) (see Valencia-G. et al. 2009 in this volume for detailed analysis). Therefore, future studies should look for impacts of land conversion during the penitentiary period (1960-1982) on macroinvertebrate assemblages, because legacies of past land uses have been reported elsewhere (Harding et al. 1998, Iwata et al. 2003).

The lack of complete agreement between stream classifications based either on macroinvertebrate assemblages or independent variables suggest that assemblages could have occurred by chance and that the populations not necessarily were in equilibrium, thus controlled by particular environmental factors (Crowl and Schnell 1990, Evans and Norris 1997). Nonetheless, the sedimentary geology at La Camaronera seems to be a pervasive feature separating macroinvertebrate assemblages from those in volcanic streams elsewhere in the island (Gómez-Aguirre 2009). Overall, pH, conductivity, and alkalinity exerted a stronger influence on macroinvertebrates. The influence of geology on physicochemical factors such as conductivity and pH, which are positively related with the densities of benthic insects, has been previously reported by Ramírez and Pringle (1998b) and Ramírez et al. (2006) at volcanic landscapes in Costa Rica. In addition to geology, stream physicochemistry

is affected by atmospheric inputs such as sea salt aerosols (Blanco 2009a in this issue).

In conclusion, Gorgona Island showed a rich macroinvertebrate assemblage typical of continental insular streams, where non-diadromous insects coexist with several species of diadromous decapods and a gastropod. Macroinvertebrate assemblages differed among study streams but spatial patterns were inconsistent with differences in environmental differences other than pH and conductivity seemingly influenced by watershed geology. We are confident that differences in macroinvertebrate assemblages and environmental factors among streams are robust because our hierarchical sampling design covered several reaches, habitats and microhabitats. Therefore among stream patterns were unbiased due to variability at finer scales. We recommend that future studies explore additional biotic and abiotic variables for explaining differences of macroinvertebrate assemblages among streams.

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Appendix 1. Study streams at Gorgona Island NNP (Tropical Eastern Pacific, Colombia). In parenthesis other names found in previous literature and cartography. Coordinates at the confluence with the ocean, and altitude of sampled reaches. A general description is given.

Slope	Stream	Observations
Eastern	Pizarro 2° 58.570' N, 78° 10.215' W 20 and 50 masl	Stream of meandering course. Basaltic rock with thick layer of clay. At higher-elevation reach there is a dam used for a hydroelectric power microstation since 2005. The sampled reaches are 10m up-stream (higher-reach) of dam and 10m up-stream (lower-reach). Abundant small-medium rocks, rounded cobbles, pebbles and leaf litter. The higher reach presents a native species forest, fallen logs and glides that produce sequences of pools and riffles. In this zone was wood exploitation of <i>Campnosperma panamensis</i> , <i>Brosimum utile</i> and <i>Carapa guianensis</i> during penal period. The lower reach presents sequences of riffles-pools, step-pool and waterfalls.
	Chorro del Cura (La Piscina, Impisú) 2° 58.018' N, 78° 10.333' W 20 masl	The reach is straight, confined and stepped. Basaltic rocks and clay banks. Abundant small and big rocks and leaf litter. In riffles, the dominant substrates are blocks and gravel. Sequences of waterfalls and pools limited by blocks. The final reaches of this stream present a strong human intervention because of maintenance of tourist cabins. Up-stream of “El Chorro del Cura” tank, the riparian vegetation is in succession (short shrubland) and alternating ferns (<i>Pteridium aquilinum</i>) with emergent pioneers as <i>Cecropia garciae</i> and <i>Miconia</i> spp.
	Iguapoga (El Poblado) 2° 57.957' N, 78° 10.342' W 25 masl	Meandering course. Abundant small-medium rocks. Riffles-pools series. Basaltic rocks. Seasonally a sand bar develops in the mouth. The reach is dominated by secondary forest. In this zone was fruit plantations of <i>Persea americana</i> , <i>Citrus sinensis</i> , <i>Mammea americana</i> , <i>Artocarpus altilis</i> and <i>Ficus citrifolia</i> .
	Ilú (Trinidad, La Planta, La Microcentral, Acueducto, Abad, La Marranera) 2° 57.812' N, 78° 10.401' W 10 and 35 masl	Stream with first order tributaries. Tributary at higher reach is called “El Acueducto”. Since penal period this stream is source of water to the aqueduct and the hydroelectric power microstation. The higher reach is dominated by native forest. At there are sequences of pools-waterfalls and step-pools. The lower reach is dominated by secondary forest. Straight course. Abundant small-medium rocks. This reach is a riffle (large of 30 m) with some pools.
	El Muelle (Zanjón, Zanja del Muelle) 2° 57.491' N, 78° 10.544' W 20 masl	This stream runs parallel to the port and the cemetery. Meandering course. Volcanic rocks. Abundant small rocks and leaf litter. The sampled reach corresponds to a tributary with pools-riffles series. At the riparian zone there are introduced species (fruit trees and coconuts plants), ferns <i>Pteridium aquilinum</i> and emergent <i>Cespedesia macrophylla</i> are dominants.
	Aeropuerto (El Peinemono, Tunechanque, La Azufrada) 2° 57.289' N, 78° 10.677' W 10 masl	Meandering course. Basaltic rocks. Abundant small rocks and leaf litter. The reach presents pools-riffles series, bars and islands at active channel, and abandoned channels at inundation plain. Riparian zone with vegetation of secondary growth vegetation (medium-small shrubland) and introduced species. Ferns and emergent trees of pioneer species, <i>Cyathea</i> sp., and coconuts.
	El Roble (Ipiri) 2° 56.832' N, 78° 11.050' W 25 and 50 masl	Stream in front of “Playa Blanca” reef. Confined and stepped bed. Substrates are principally vitreous basalts and arcillite. Pebbles, blocks and megablocks are abundant. Riparian forest is dominated by <i>Buchenavia</i> sp. trees. Frequent slides and fallen trees at bank. Both reaches are stepped with pools-waterfalls series.

(Continuation **Appendix 1**)

Western	La Camaronera (Piabí) 2° 57.177' N, 78° 11.879' W 15 and 35 masl	Stream in front of “La Camaronera” reef. Meandering course. Mixed geology: basaltic rocks, intrusive, sedimentary and metamorphic. Native forest and mature secondary with clearing produced by slides and fallen trees. Bars, medium rocks and leaf litter are abundant. Both reaches presents pools-riffles series.
	Cocal Norte (La Máncora) 2° 58.418' N, 78° 11.501' W 10 masl	Stream located at primitive zone (primary forest). Meandering course. Basaltic rocks. Clearings are product of slides and fallen trees. Dense understory is dominated by shrubs, lianas and herbs. Medium rocks and leaf litter are abundant. The reach corresponds to short zone of step pools and riffles.

Appendix 2. Qualitative variables included in this study.

Hierarchical level	Variable	Category	Description
Stream	Vegetation management zone (UAESPNN 2005)	Primitive	Unaltered zone or with minimum human intervention in its natural structures.
		Natural recuperation	Zone that has experienced changes in their natural environment. This area is destined to natural recovery or restoration mechanisms for obtaining a desired state of ecological evolution cycle.
Reach	Vegetation successional state	Native species forest	Zones with mature secondary forest, where human intervention was low. Continuous canopy. Tall and thick trees as <i>Carapa guianensis</i> and <i>Buchenavia</i> sp.
		Secondary forest	Previously, tree logging of <i>Carapa guianensis</i> and <i>Buchenavia</i> sp. Discontinuous canopy. Differentiated stratification dominated by <i>Vismia baccifera</i> , <i>Cespedesia macrophylla</i> , <i>Cecropia garciae</i> , <i>Triolena spicata</i> , <i>Tara</i> sp., <i>Tetrorchidium gorgonae</i> , and <i>Wedelia brasiliensis</i> .
		Introduced species forest	Discontinuous canopy, continuous coverage of mixed-wood types without distinct stratification. Previously, zones with fruit trees plantations including <i>Cocos nucifera</i> , <i>Crescentia cujete</i> , <i>Artocarpus altilis</i> , <i>Ficus citrifolia</i> .
		Shrubland	Continuous shrub canopy, emergent trees scattered. Previously, crops and tree plantations and logging areas. Dominance of ferns (<i>Pteridium aquilinum</i>).
	Geology	Sedimentary rocks	Clays with shales and silts and thin layers of sandstone. Thin-media conglomerates, banded, with inserted layers of sand (Gansser 1950).
		Basaltic igneous rocks	Calc-alkaline basalts of fractured afanitic texture with high content of glass. Associated with komatiitic basalts and komatiites, microcrystals of olivine and pyroxene enclosed in glass, numerous fractures filled with chlorite, epidote, carbonate and zeolite. The glass is brown (palagonite), this indicates a high iron content and low proportion of silica (Llinás et al. 1990).

Appendix 3. Qualitative and quantitative variables measured at each hierarchical level and the range of variation within each season of the Gorgona Island (Tropical Eastern Pacific, Colombia) (*variables included only for analyses of low precipitation season. **only for high precipitation period)

Hierarchical level	Variable and measured method	Range	
		Low precipitation	High precipitation
	Vegetation management zone (Appendix 2) <i>Zonation map of Management Plan 1998-2003 (Appendix 2, (UAESPNN 2005)</i> Elements (mg/l)*	Primitive vs Natural recovery	
Stream	Total phosphorus - <i>Photometry</i>	0,148-0,957	0,560-5,320
	Sulphate - <i>Capillary electrophoresis</i>	0,652-4,802	
	Chloride - <i>Capillary electrophoresis</i>	1,8-6,5	1,998-7,195
	Total organic carbón - <i>Oxidation</i>	14,9-89,6	11,9-45,5
	Vegetation successional stage	Native species forest.	Secondary forest.
	<i>According to field descriptions (Appendix 1)</i>	Introduced species forest	Shrubland
	Geology - <i>According to lithologic units (Kerr 2005) and field descriptions (Appendix 1)</i>	Sedimentary rocks Basaltic igneous rocks	
Reach	Flow (m ³ /s) - <i>Velocity-area method</i>	0,0007-0,7584	0,0123-0,0780
	Altitude (masl) - <i>Altimeter</i>	10-50	10-50
	Slope - <i>Clinometer</i>	0,25-4,00	0,25-4,00
	Active channel mean width (m) - <i>Meter</i>	3,05-9,60	3,05-9,60
	Leaf litter biomass (g)	8,68-169,42	17,09-94,62
	Leaf litter morphotypes (#)	3-17	2-42
	Mean wet channel width (m) - <i>Meter</i>	0,717-3,175	1,263-4,844
	Alkalinity (mmol CaCO ₃ /l) - <i>Titration with H₂SO₄</i>	0,578-2,800	0,167-0,400
	Conductivity (µMhos/cm) - <i>Potentiometric method - Conductimeter</i>	131-2400	55-1400
	Dissolved oxygen concentration (mg/L) - <i>Potentiometric method - Oximeter</i>	6,86-8,49	6,17-8,38
Habitat	Dissolved CO ₂ concentration (mg/L) - <i>Titration with NaOH</i>	0-4,286	0-6,857
	Water temperature (°C) - <i>Potentiometric method - Oximeter</i>	24,9-27,3	22,8-23,7
	Oxygen saturation (%) - <i>Potentiometric method - Oximeter</i>	81,1-98,4	72,2-98,5
	pH - <i>Potentiometric method - pH meter</i>	7,52-8,52	7,25-8,36
	Light intensity (µmol/m ² s) - <i>Luxometer</i>	2,81-1557,70	13,89-131,82
	Canopy openness (%)** - <i>Densimeter</i>		8,1-37,8
	Mean water velocity (m/s)* - <i>Flowmeter</i>	0,00-0,43	
	Mean water depth (cm) - <i>Ruler</i>		
Microhabitat		4,733-21,233	7,883-25,811
	Bottom roughness coefficient		
	$K_v = (5C_1 + 3C_2 + C_3)/9$, C_i = value for the more abundant substrate in the i th category 4 = boulder, 3 = cobbles, 2 = pebble, 1 = gravel, sand, silt	0,556-2,852	0,556-3,000
	Reynolds number*	0,0-3994,8	
	$Re = \frac{Uz}{\nu}$		
	U = bottom velocity, z = depth, ν = Kinematic viscosity		
	$Fr = \frac{U}{\sqrt{gz}}$	0,0-0,2	
	Froude number*		