Spatial Variations in the Distribution of Benthic Macroinvertebrate Functional Feeding Groups in Tropical Rivers

Marielle Kristine T. Doong[a], Jonathan A. Anticamara[a,b*], Francis S. Magbanua[a,]**

[a] Institute of Biology, University of the Philippines Diliman, Quezon City 1101, Philippines,
*Email: jaanticamara@up.edu.ph, **Email: fsmagbanua@up.edu.ph

[b] UP Diliman Invertebrate Museum, Institute of Biology, University of the Philippines Diliman,
Quezon City 1101, Philippines

Received 26 May 2021 Accepted 21 June 2021 Published 30 June 2021
DOI: https://doi.org/10.51264/inajl.v2i1.11

Abstract

Functional feeding group (FFG) is an approach that classifies macroinvertebrates based on their utilization of organic matter food resources. Across streams and rivers, variations in the distribution of FFGs reflect the unequal distribution of food resources, which are affected by varying environmental conditions and disturbances to the ecosystem. In the tropics, the distribution of FFGs does not follow the pattern observed in temperate streams. This study aims to (1) determine the FFGs present in selected Philippine tropical streams, (2) assess the variations in FFG distributions and how the distributions vary across space, and (3) evaluate how FFG distributions are affected by certain environmental factors and habitat structure. Benthic macroinvertebrates were collected in 2010 from five sites and assigned to their primary FFG based on published literature. Across study sites, the macroinvertebrates collected were classified into gathering collectors (total $n = 4{,}640$), scrapers ($n = 1{,}670$), filtering collectors ($n = 1{,}545$), predators ($n = 632$), and shredders ($n = 270$). Within and between sites, these FFGs varied significantly. Variations explained the upstream-downstream and north-south variations in the mean of FFG abundance in width and depth of the stream, discharge, temperature, pH, riparian vegetation, and habitat stability and variability. This study reveals that the FFG approach is a useful bioassessment tool in tropical aquatic systems. However, there is still a need for verification of the findings in other streams and seasons.

Keywords: Biomonitoring, habitat quality assessment, rapid bioassessment protocols, water quality.

INTRODUCTION

Bioassessment (or Biomonitoring) is a method of evaluating the current status of biological systems and their responses to certain environmental conditions (Reece & Richardson, 2000). In aquatic systems, bioassessment involves surveying and directly measuring the relative densities of the organisms living in a defined study area (Barbour *et al.*, 1999). Often, bioassessment requires selecting a specific group of organisms that play key roles in the study area. For instance, plankton (e.g., Wachnicka *et al.*, 2011; Lavoie *et al.*, 2011), fish (e.g., Hitt & Angermeier, 2011; Frimpong & Angermeier, 2010), and invertebrates (e.g., Harper *et al.*, 2012; Fu *et al.*, 2008) are among the bioindicator organisms that are commonly monitored in bioassessment.

However, some scientists prefer to use benthic macroinvertebrates in bioassessment (Reece & Richardson, 2000). Benthic macroinvertebrates continuously respond to short- and long-term disturbances of their habitat (Park *et al.*, 2008), such as flooding, siltation brought about by deforestation (Stanford, 2006), agriculture effluents, and urban pollution (Compin & Céréghino, 2007). In addition, their sedentary foraging, short life cycles, and preference for habitats around toxic sediments make benthic macroinvertebrates ideal candidates for bioassessment indicators (Reece & Richardson, 2000). Moreover, benthic macroinvertebrates are generally intermediate trophic level consumers and are indispensable in channeling trophic flow from the bottom-up and top-down directions (Wallace & Webster, 1996).

More recent bioassessment practices involve measuring an ecosystem's structural and functional attributes (Riipinen *et al*., 2008). In bioassessments that aim to evaluate the structural attributes of ecosystems, such as physical habitat and composition of biotic communities (Elosegi *et al*., 2006), species diversity, presence of indicator species (Riipinen *et al*., 2008), and species biomass (Barbour *et al.*, 1999) are measured. On the other hand, bioassessments that focus on the functional attributes of the ecosystem indirectly gather information on the functions performed by species within a system (Elosegi *et al*., 2006).

In general, species develop traits adapted to their environment (Townsend & Hildrew, 1994). Those traits enable them to perform specific functions, such as biomass production (De Groot *et al*., 2002), decomposition (Hooper *et al*., 2005), nutrient cycling, food production (Altieri, 1999), and resource gathering or utilization (Townsend & Hildrew, 1994). Therefore, species traits or functions within ecosystems define how organisms utilize, affect, and alter the biotic and abiotic components of the ecosystem (Marcot & Heyden, 2001). Moreover, species' functions are tightly integrated into the structure and condition of the habitat (Srivastava, 2006). They are greatly affected by the disturbance and alteration in their structure and components. By monitoring the densities or behavior of species performing similar functions in a system, modifications to their habitat could be detected (Fonesca & Ganade, 2001).

An aggregation of taxonomically distinct species that perform similar functions within an ecosystem is known as a functional group (Fonesca & Ganade, 2001). Functional groups represent an ecological structure of a suite of species within a community. They can be helpful for making generalized predictions on the community's responses to disturbances and alterations (Wilson, 1999). In classifying organisms into specific functional groups, the criteria for species inclusion, the type of function, and the set of traits are considered (Fonesca & Ganade, 2001). Among the functional groups used in published literature are guilds (based on the similarity in resource exploitation), trophic levels (based on the organisms' position in the food chain), and ecosystem engineers (based on how organisms form or alter their habitat) (Gerino *et al*., 2003).

The use of different functional group classifications aids researchers in the comparative study of communities while focusing on specific functional relationships within a study system (Simberloff & Dayan, 1991). For instance, groups classified according to feeding functions are useful when dealing with studies regarding food dynamics, trophic relationships, and system alteration brought about by fluctuating environmental conditions (Gerino *et al*., 2003). On the other hand, groups classified according to habitat formation and alteration functions are useful for exploring issues on population dynamics when modification of the environment is necessary for survival and issues on interactions within communities impacted by environmental changes (Berke, 2010). For these reasons, functional groups are widely used in ecosystem biological assessment (Merritt *et al*., 2002). Among the commonly employed functional approaches in bioassessment are the trophic level and the feeding group approaches (Gerino *et al.*, 2003; Rawer-Jost *et al*., 2000).

The Functional Feeding Group (FFG) (Cummins, 1973; Cummins, 1974) – i.e., filtering collectors, gathering collectors, predators, scrapers, and shredders is an approach that classifies macroinvertebrates according to their mode of food acquisition (Cummins & Klug, 1979) and organic resource utilization (Simberloff & Dayan, 1991). The FFG to which a macroinvertebrate belongs is primarily determined by mouthpart morphology (Cummins, 1973). The distribution and proportion of FFG within a stream are influenced by the availability and amount of specific food resources (Vannote *et al.*, 1980). Changes in the distribution of FFGs in spatial scale denote variations in the food base's environmental conditions (Park *et al*., 2008).

The variations in the distribution of FFGs in several studies conducted in temperate streams (e.g., Hawkins & Sedell, 1981; Minshall *et al.*, 1985; Grubaugh *et al*., 1996; RosiMarshall & Wallace, 2002) did not exactly match the findings of studies conducted in tropical streams. In temperate streams, the FFG distribution follows the pattern predicted by the River Continuum Concept (RCC) by Vannote *et al.* (1980) based on a pristine stream system in North America. The RCC describes how high densities of shredders and collectors in headwaters reflect high rates of leaf litter processing in these areas.

In large rivers, collectors' densities increase as particulate organic matter processed upstream is transported downstream. Scrapers' densities are higher in mid-sized streams due to sufficient light penetrating through the water that enhances periphyton photosynthesis. This condition is the favored resource of scrapers (Dudgeon, 1999). In contrast, the results of similar studies conducted in tropical streams (e.g., Tomanova *et al*., 2007; Jiang *et al.,* 2011) did not exactly match the patterns predicted by the RCC for temperate streams. One potential explanation for the discrepancy of RCC results in temperate versus tropical streams is the complexity of the tropical freshwater systems in terms of physicochemical parameters and habitat quality, which could potentially mask the effect suggested by the RCC (Tomanova *et al.*, 2007; Li & Dudgeon, 2009).

Given this background, this study aims to (1) determine the various FFGs present in tropical streams in the Philippines, (2) assess how the distributions of these FFGs vary within sites from upstream to downstream and between sites from north to south, and (3) evaluate how environmental factors and habitat quality affect such variations.

METHODS

Study Sites

The study was conducted in the Philippines ($13^0$00' N, $122^0$00' E) – a tropical country with distinct wet (June to October) and dry (November to May) seasons. The study included five river systems (sites) located across the Philippine archipelago (Figure 1): (1) Bacman streams in Pocdol Mountains, Albay-Sorsogon, (2) Leyte streams in TongonanKananga, (3) Bacolod streams in Mt. Kanla-on, Northern Negros, (4) Dumaguete streams in Mt. Talinis, Southern Negros and (5) Apo streams in Mt. Apo, North Cotabato. All sites were located close to the geothermal production fields managed by the Energy Development Corporation (EDC).

Field macroinvertebrate sampling and sample processing

Macroinvertebrate samples were collected in the rainy season from June to September 2010. Sampling was carried out in seven sampling locations in Bacman, nine in Leyte, seven in Bacolod, 11 in Dumaguete, and 10 in Apo (Figure 1). The distribution of upstream and downstream areas is presented in Table 1.

Three replicate macroinvertebrate samples were collected at each sampling point using a Surber sampler (area 30 x 30 cm^2; 500 µm mesh), disturbing the substrate with a metal rod for two minutes. The upper 10 cm of the stream substratum within the sampler was disturbed to dislodge attached macroinvertebrates (Magbanua *et al.*, 2010). Large debris present within the 30 x 30 cm^2 area was rinsed and inspected for attached organisms before being removed. The macroinvertebrate samples collected were preserved in 95% ethanol, stored in plastic bottles, and transported to the laboratory at the University of the Philippines Diliman.

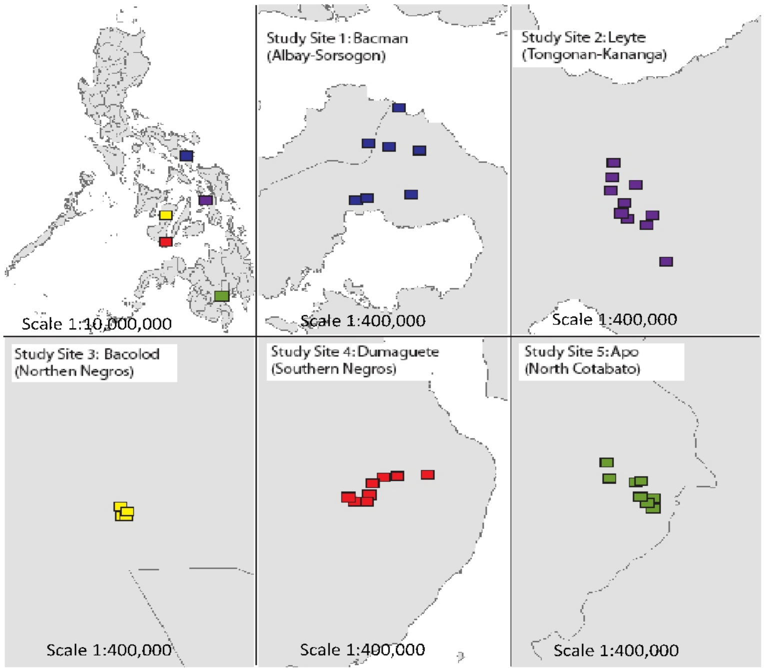

Figure 1. Location of the study sites on the map. The locations within each sampling site are also shown.

Table 1. Study sites and the number of upstream and downstream areas.

Study site	No. upstream	No. downstream
Bacman	3	4
Leyte	5	4
Bacolod	4	3
Dumaguete	6	5
Apo	5	5

The samples were washed and elutriated (i.e., all organic materials were separated from inorganic materials such as sediments and stones). All individuals were sorted under a stereoscopic microscope and identified to the lowest possible taxonomic level (family, subfamily, and mostly genus) using the available dichotomous keys of Blakely *et al*. (2010), Dudgeon (1999), Mekong River Commission (2006), Yule & Yong (2004), Pennak (1978), Bouchard (2004), Pescador & Richard (2004) for Ephemeroptera, Epler (2010) for Coleoptera, Polhemus & Polhemus (1988) for Aphelocheirinae, and Zettel *et al.* (1996) for Naucoridae. Not all individuals were identified down to the genus level due to limitations in the current taxonomic knowledge of tropical taxa. However, the consulted literature provided the classification of most taxa into specific FFGs on the family level. For the families that were not readily classifiable, the identification was made at the genus level. In this study, the lowest taxonomic level identified for most individuals was the genus level. Genus level was sufficient in dealing with studies using a functional approach, as Doledec *et al*., (2000) and Gayraud *et al.* (2003) showed.

The allocation of the individuals to their primary FFGs was based on Cummins *et al.* (2004), Dudgeon (1999), Yule (1996), Bouchard (2004), Barbour *et al.* (1999), Mekong River Commission (2006), Merritt *et al.* (1996), Mishra & Nautiyal (2011), Polhemus and Polhemus (1988) for *Aphelocheirus*, Henriques-Oliveira *et al.*, (2003) for Chironominae and Orthocladiinae, Oscoz *et al.* (2011) for Apataniidae, Angradi (1996), Buckingham & Bennett (2001) for *Parapoynx*, Giller & Malmqvist (1998) for Tipulinae, Spanhoff *et al.* (2003) for Psychomyiidae, Tomanova *et al.* (2006) for Dixidae, Kocarek *et al.* (2008) for Orthoptera, Maros *et al.* (2005) for Gryllotalpidae, Merritt *et al.* (1996) for *Potamanthellus* spp., Price *et al.* (2011) for Blattodea, Shepard *et al.* (2011) for *Eulichas*, and CSIRO (2021) for Thaumaleidae.

Environmental parameters sampling

Along with the macroinvertebrate samples collection, the stream's physical and chemical properties within each sampling point at each site were assessed. For water quality, the following parameters were measured: discharge (m^3/s), water temperature (^0C), dissolved oxygen (mg/L), conductivity (µS/cm), pH, and total dissolved solids (g/L). The instruments used for measuring were YSI EcoSense DO 200 (Yellow Spring, OH, USA) for dissolved oxygen (DO) and temperature measurements, YSI EcoSense EC 300 (Yellow Spring, OH, USA) for conductivity, total dissolved solids (TDS), salinity, and also for temperature, and Electric Current Meter (Ogawa Seiki Co., Ltd., Japan) for discharge. Wetted stream width was measured as the average of three equidistant transects, and water depth (m) was measured as the average of three evenly spaced points along transects (Magbanua *et al.*, 2010).

Habitat quality assessment

For habitat quality, the United States Environmental Protection Agency's Rapid Bioassessment Protocols (RBP) (Barbour *et al*., 1999) was used in assessing the following parameters: bottom substrate/instream cover, embeddedness, streamflow/velocity, canopy cover, channel alteration, and pool/riffle ratio, bank stability, bank vegetative protection, streamside cover, and riparian vegetative zone width. Each parameter was given a score between 0 and 20, following the description given in the form, i.e., a 0 score as the poorest quality and a 20 as the optimal quality.

Data analysis

Significant variations in the mean abundances of functional feeding groups, mean values for physicochemical parameters, and scores for habitat quality assessment within and between sites were tested using ANOVA in SPSS 17.0. To test for significant trends in the differences in the mean abundance of each FFG, the mean values for the physicochemical parameters and habitat quality scores within sites from upstream-to-downstream, and between sites from north-to-south, Pearson's correlation test was used. Significant correlations between FFG abundances and environmental parameters were also tested using Pearson's correlation test.

RESULTS AND DISCUSSION

Results

Identified FFGs in representative Philippine tropical streams

The macroinvertebrates collected from the five river systems were classified into the following functional feeding groups: gathering collectors (total *n* = 4,640 in all study sites), scrapers (*n* = 1,670), filtering collectors (*n* = 1,545), predators (*n* = 632), and shredders (*n* = 270). Below is the list of macroinvertebrate taxa collected and their corresponding functional feeding group classification (Table 2).

Table 2. Macroinvertebrate taxa and their functional feeding group (FFG) based on published literature.

Taxon	FFG	Reference
Acari	Predator	Bouchard, 2009
Amphipoda	Gathering Collector	Barbour *et al.*, 1999
Architaenioglossa	Scraper	Cummins *et al.*, 2004
Blattodea	Shredder	Price *et al.*, 2011
Coleoptera		
Curculionidae	Shredder	Bouchard, 2009
Dryopidae	Shredder	Cummins *et al.*, 2004
Dytiscidae	Predator	Dudgeon, 1999
Hoperius	Predator	Dudgeon, 1999
Elmidae (larva)	Gathering Collector	Cummins *et al.*, 2004
Elmidae (adult)	Scraper	Bouchard, 2009
Eulichadidae	Shredder	Shepard, 2011
Eulichas		
Gyrinidae	Predator	Dudgeon, 1999
Haliplidae	Scraper	Dudgeon, 1999
Hydrophilidae	Predator	Cummins *et al.*, 2004
Lampyridae	Predator	Cummins *et al.*, 2004
Psephenidae	Scraper	Dudgeon, 1999
Scirtidae	Filtering Collector	Dudgeon, 1999
Cyphon	Scraper	Barbour *et al.*, 1999
Sacodes	Filtering Collector	Dudgeon, 1999
Staphylinidae	Predator	Cummins *et al.*, 2004
Collembola	Shredder	Mekong River Commission, 2006
Sminthurdidae		
Sphaeridia	Gathering Collector	Barbour *et al.*, 1999
Decapoda		
Atyidae	Shredder	Barbour *et al.*, 1999
Gecarcinucidae		
Perithelphusa	Shredder	Barbour *et al.*, 1999
Sesarmidae		
Geosesarma	Shredder	Fratini *et al.*, 2005
Sesarmoides	Shredder	Fratini *et al.*, 2005
Caridina	Shredder	Barbour *et al.*, 1999
Diptera		
Athericidae	Predator	Cummins *et al.*, 2004
Blephariceridae	Scraper	Cummins *et al.*, 2004
Ceratopogonidae	Predator	Dudgeon, 1999
Atrichopogon	Gathering	Cummins *et al.*,

Taxon	FFG	Reference
	Collector	2004
Bezzia	Predator	Dudgeon, 1999
Ceratopogoninae	Predator	Dudgeon, 1999
Leptoconopinae	Predator	Dudgeon, 1999
Chironomidae		
Chironominae	Filtering Collector	Henriques-Oliveira *et al.*, 2003
Orthocladiinae	Filtering Collector	Henriques-Oliveira *et al.*, 2003
Tanypodinae	Predator	Dudgeon, 1999
Culicidae	Gathering Collector	Barbour *et al.*, 1999
Dixidae	Filtering Collector	Tomanova *et al.*, 2006
Ecnomidae	Predator	Dudgeon, 1999
Empididae	Predator	Dudgeon, 1999
Ephydridae	Gathering Collector	Barbour *et al.*, 1999
Limoniidae	Gathering Collector	Barbour *et al.*, 1999
Antocha		
Psychodidae	Gathering Collector	Cummins *et al.*, 2004
Simuliidae	Filtering Collector	Dudgeon, 1999
Stratiomyidae	Gathering Collector	Bouchard, 2009
Syrphidae	Gathering Collector	Barbour *et al.*, 1999
Tabanidae	Predator	Barbour *et al.*, 1999
Thaumaleidae	Scraper	CSIRO, 2012
Tipulidae		
Limoniinae	Predator	Dudgeon, 1999
Tipulinae	Shredder	Giller & Malmqvist, 1998
Ephemeroptera		
Baetidae	Gathering Collector	Cummins *et al.*, 2004
Caenidae	Gathering Collector	Dudgeon, 1999
Ephemerellidae	Gathering Collector	Barbour *et al.*, 1999
Heptageniidae	Scraper	Bouchard, 2009
Leptophlebiidae	Gathering Collector	Cummins *et al.*, 2004
Neoephemeridae	Scraper	Mishra & Nautiyal, 2011
Neoephemeropsis		
Potamanthellus	Gathering Collector	Merritt *et al.*, 1996
Prosopistomatidae	Scraper	Dudgeon, 1999
Tricorythidae	Gathering Collector	Barbour *et al.*, 1999
Gastropoda	Scraper	Cummins *et al.*, 2004
Neritidae	Scraper	Cummins *et al.*, 2004
Hemiptera		
Gerridae	Predator	Dudgeon, 1999
Naucoridae	Predator	Dudgeon, 1999
Veliidae	Predator	Dudgeon, 1999
Lepidoptera		
Crambidae		
Elophila	Shredder	Bouchard, 2009
Eoophyla	Scraper	Mekong River Commission, 2006
Parapoynx	Scraper	Buckingham & Bennett, 2001
Potamomusa	Shredder	Mekong River

Taxon	FFG	Reference
		Commission, 2006
Nematoda	Scraper	Mekong River Commission, 2006
Neuroptera		
Nevrorthidae	Predator	Cummins *et al.*, 2004
Odonata		
Amphiterygidae	Predator	Dudgeon, 1999
Cordulegastridae	Predator	Dudgeon, 1999
Corduliidae	Scraper	Dudgeon, 1999
Gomphidae	Predator	Barbour *et al.*, 1999
Libellulidae	Predator	Bouchard, 2009
Platycnemididae	Predator	Dudgeon, 1999
Zygoptera	Predator	Barbour *et al.*, 1999
Oligochaeta	Gathering Collector	Dudgeon, 1999
Orthoptera		
Gryllotalpidae	Predator	Maros *et al.*, 2005
Tetrigidae	Scraper	Kocarek *et al.*, 2008
Plecoptera		
Leuctridae	Shredder	Bouchard, 2009
Nemouridae		
Nemoura	Shredder	Barbour *et al.*, 1999
Perlidae	Predator	Dudgeon, 1999
Trichoptera		
Apataniidae	Scraper	Oscoz *et al.*, 2011
Brachycentridae	Scraper	Bouchard, 2009
Calamoceratidae	Shredder	Cummins *et al.*, 2004
Dipseudopsidae	Gathering Collector	Dudgeon, 1999
Ecnomidae	Predator	Dudgeon, 1999
Glossosomatidae		
Agapetus	Scraper	Barbour *et al.*, 1999
Glossosoma	Scraper	Barbour *et al.*, 1999
Hydropsychidae	Filtering Collector	Dudgeon, 1999
Hydroptilidae	Scraper	Bouchard, 2009
Leptoceridae		
Leptocerus	Filtering Collector	Cummins *et al.*, 2004
Setodes	Gathering Collector	Merritt *et al.*, 1996
Limnephilidae	Shredder	Cummins *et al.*, 2004
Odontoceridae	Scraper	Dudgeon, 1999
Philopotamidae	Filtering Collector	Dudgeon, 1999
Phryganeidae	Shredder	Barbour *et al.*, 1999
Polycentropodidae	Predator	Dudgeon, 1999
Psychomyiidae	Scraper	Spanhoff *et al.*, 2003
Rhyacophilidae	Predator	Dudgeon, 1999

Figure 2 shows the mean abundances of the FFGs across the five study sites. The mean abundance of gathering collectors was highest in Dumaguete and Apo, and lowest in Bacolod. The mean abundance of scrapers was higher in Leyte and Apo, and was similar in the other three sites. Filtering collector mean abundance was almost similar across all five sites. The mean abundance of predators was highest in Apo, and similar in the other sites. Shredder mean abundance was highest in Leyte and similar in the other four sites.

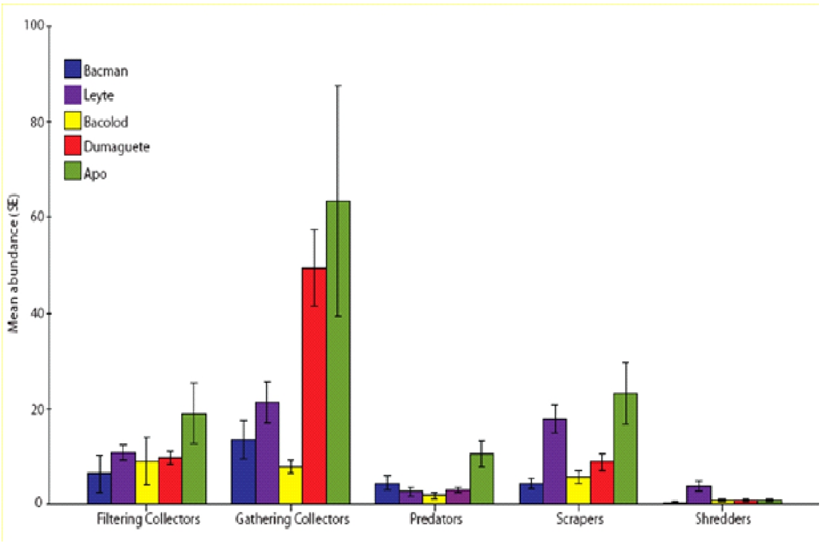

Figure 2. Mean of the mean abundances (± Standard Errors SE) of FFGs from the sampling locations within the study sites. Sites are arranged from north to south orientation of the Philippines – see Figure 1.

Figure 3 shows the mean abundances of FFGs within each study site**.** Generally, collectors were dominant, while shredders were the least dominant within sites. In Bacman, filtering collectors dominated in the three upstream locations, while gathering collectors dominated the four downstream areas. Generally, shredders were the scarcest FFG within site.

Leyte was functionally diverse because not all locations are dominated by only one FFG. The areas were dominated either by filtering collectors, gathering collectors, or scrapers. In this site, however, predators and shredders were poorly represented, with predators having the fewest individuals.

Bacolod was also functionally diverse. The domination in the locations was distributed among the filtering collectors, gathering collectors, and scrapers. Predators and shredders were represented by few individuals.

In Dumaguete, gathering collectors dominated. All other four FFGs were poorly represented, especially the shredders.

In Apo, all FFGs were more abundant in the downstream locations than in the upstream locations. Gathering collectors dominated the downstream areas in the site.

Spatial variations in FFG diversity: within and between study sites

Spatial variations in the mean abundances of FFGs within some of the study sites were observed, with an apparent increase or decrease going downstream in certain FFGs ($P<0.05$) in some sites. In terms of upstream-downstream gradient, all FFGs significantly varied ($P<0.05$) within Apo and Leyte, while no upstream-downstream gradients in FFGs were observed ($P>0.05$) within Bacman and Bacolod. In Dumaguete, gathering collectors and scrapers significantly varied ($P<0.05$) but with no upstream-downstream trend ($P>0.05$), while filtering collectors, predators, and shredders mean abundances had no differences ($P>0.05$) across all the sampling points.

In Bacman, the mean abundances of filtering collectors did not exhibit an upstream-downstream trend ($P>0.05$). In Leyte, only the mean abundance of gathering collectors increased downstream ($R=0.404$, $P=0.024$), while all other FFGs did not show the upstream-downstream difference ($\mathrm{R}\leq 0.148$, $P\geq 427$). In Dumaguete, none of the FFG showed an upstream-downstream pattern ($\mathrm{R}\leq 0.093$, $P\geq 0.438$). In Apo, the mean abundances of filtering collectors ($R=0.433$, $P=0.017$), gathering collectors ($R=0.494$, $P=0.006$), predators ($R=0.577$, $P=0.001$), and scrapers ($R=0.665$, $P<0.0001$) significantly increased downstream, while shredders ($R=0.300$, $P=0.108$) did not exhibit an upstream-downstream trend.

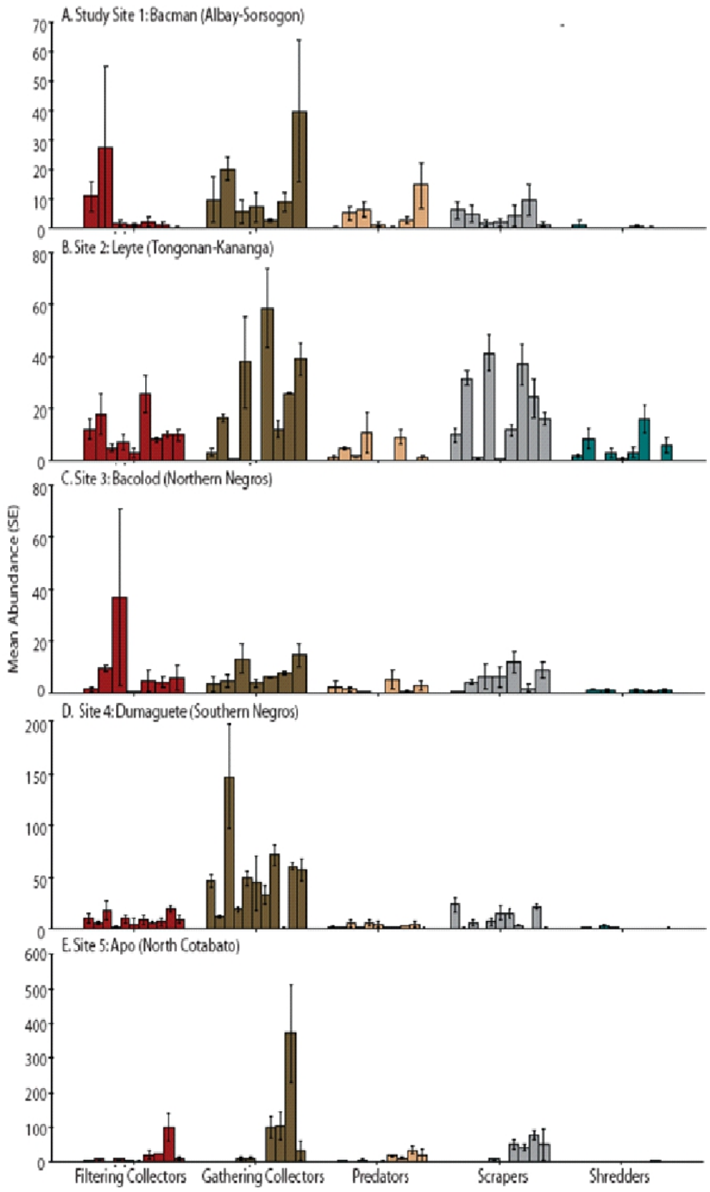

Figure 3. Mean abundances (± SE) of the FFGs from sampling locations (arranged upstream-to-downstream) within study sites.

Comparing the mean abundances of the FFGs between study sites, only the filtering collectors did not exhibit significant variation (*P*=0.228). Gathering collectors (*R*=0.266, *P*=0.002), predators (*R*=0.230, *P*=0.007) and scrapers (*R*=0.180, *P*=0.036) significantly increased from north-to-south indicating variation across three Pleistocene aggregated island complexes (i.e., Greater Luzon for Bacman site, Greater Negros-Panay for Bacolod and Dumaguete sites, and Greater Mindanao for Leyte and Apo sites) in the Philippines. Although shredder abundances were significantly variable between sites (*P*<0.001), they did not exhibit a north-south trend (*R*=-0.126, *P*=0.145).

Spatial variations in environmental conditions: within and between sites

Within each study site, the mean values for temperature, DO, conductivity, TDS, and pH varied significantly (*P*<0.001). In Bacman, mean discharge (*R*=0.664, *P*<0.001), and conductivity (*R*=0.626, *P*<0.001) increased downstream, while temperature (*R*=-0.401, *P*<0.001) decreased. In Leyte, discharge significantly increased downstream (*R*=0.316, *P*=0.001). Discharge (*R*=0.485, *P*<0.001), temperature (*R*=0.603, *P*<0.001), conductivity (*R*=0.837, *P*<0.001) and TDS (*R*=0.836, *P*<0.001) increased, while DO (*R*=-0.373, *P*<0.001) decreased downstream in Bacolod. In Dumaguete, discharge (*R*=0.289, *P*<0.001), temperature (*R*=0.610, *P*<0.001) and conductivity (*R*=0.384, *P*<0.001) increased, while DO (*R*=-0.322,

$P<0.001$) decreased. Discharge ($R=0.725$, $P<0.001$), temperature ($R=0.544$, $P<0.001$) and pH ($R=0.799$, $P<0.001$) increased downstream in Apo, while TDS ($R=-0.395$, $P<0.001$) decreased (Figure 4a and 4b).

Between sites, the mean values for discharge, temperature, DO, TDS, conductivity, and pH varied significantly ($P<0.05$). Mean values for discharge ($R=0.218$, $P=0.000$), pH ($R=0.351$, $P<0.001$) and TDS ($R=0.140$, $P=0.000$) increased downstream, while temperature ($R=-0.514$, $P<0.001$) decreased. DO ($R=0.037$, $P=0.356$), and conductivity ($R=0.070$, $P=0.081$) did not exhibit a north-to-south trend (Figure 5).

Mean values for wetted width and depth were significantly different ($P<0.05$) within all study sites. Wetted width increased downstream in Bacman ($R=0.610$, $P<0.001$), Leyte ($R=0.380$, $P<0.001$), Dumaguete ($R=0.416$, $P<0.001$) and Apo ($R=0.380$, $P<0.001$), and decreased downstream in Bacolod ($R=-0.605$, $P<0.001$). Depth increased downstream in Bacman ($R=0.431$, $P<0.001$), Dumaguete ($R=0.265$, $P=0.001$), and Apo ($R=0.842$, $P=0.000$), and did not exhibit a trend in Leyte and Bacolod ($P>0.05$). Between sites, wetted width ($P<0.001$) and depth ($P<0.001$) were significantly different. Wetted width increased from north to south ($R=0.249$, $P<0.001$), while depth did not exhibit a trend ($R=0.053$, $P=0.187$).

Spatial variations in habitat quality: within and between sites

The RBP scores for bottom substrate, embeddedness, streamflow, canopy cover, channel alteration, pool to riffle ratio, bank stability, bank vegetative protection, streamside cover, and riparian vegetative zone width within sites were variable (scores ranged from 5 to 20) (Figure 5). From upstream-to-downstream, scores for embeddedness ($R=0.447$, $P<0.001$), streamflow ($R=0.866$, $P<0.001$), channel alteration ($R=0.309$, $P=0.001$), pool to riffle ratio ($R=0.612$, $P<0.001$), and riparian vegetative zone width ($R=0.401$, $P<0.001$) increased in Bacman. In contrast, bank vegetative protection decreased ($R=-0.224$, $P=0.022$).

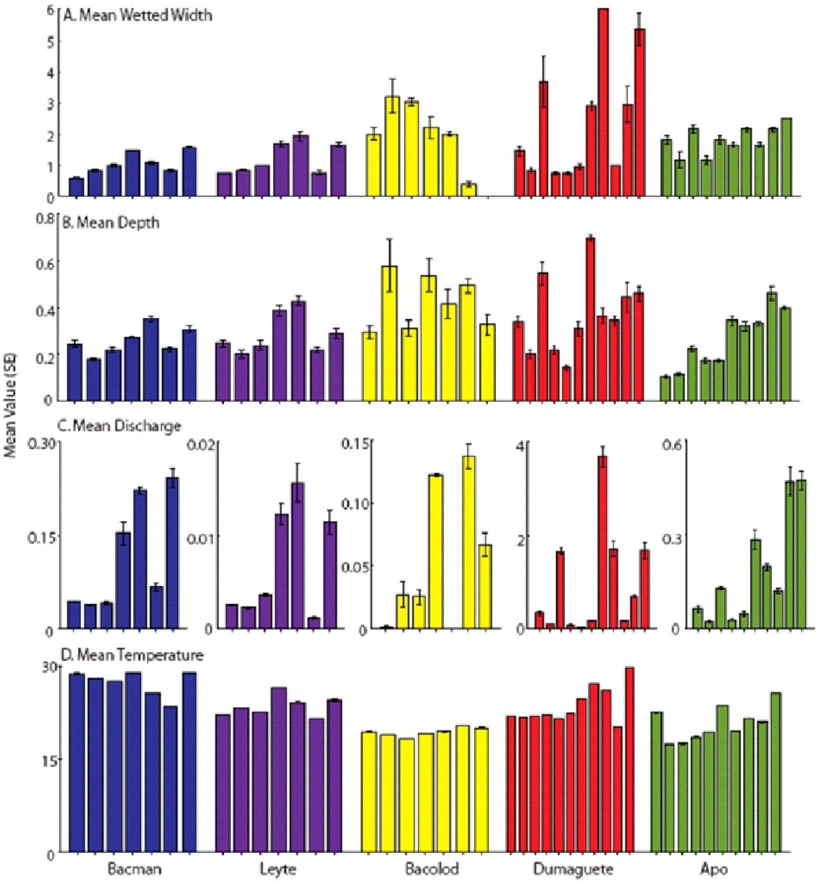

Figure 4a. Mean values (± SE) for environmental parameters in each sampling site (arranged upstream-to-downstream) within study sites. Wetted width (m), depth (m), discharge (m^3/sec), and temperature (^{0}C).

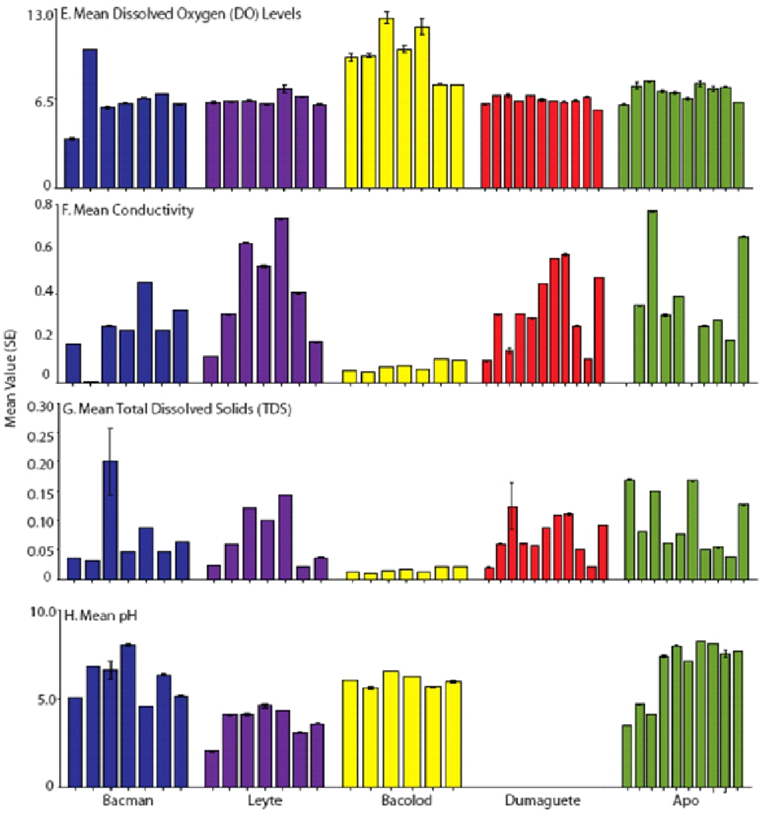

Figure 4b. Mean values (± SE) for environmental parameters in each sampling site (arranged upstream-to-downstream) within study sites. DO (mg/L), conductivity (μS/cm), TDS (g/L), and pH.

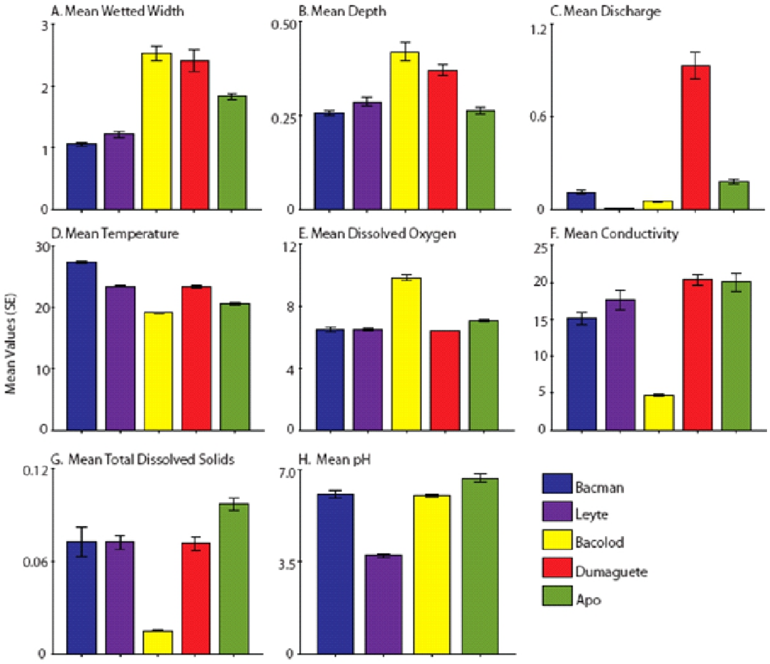

Figure 5. Mean values (± SE) for environmental parameters from sampling locations within the study sites (arranged northernmost-to-southernmost). Wetted width (m), depth (m), discharge (m^3/sec), temperature (^{0}C), DO (mg/L), conductivity (μS/cm), TDs (g/L), and pH.

In Leyte, bottom substrate (R=0.362, *P*<0.001), embeddedness (R=0.482, *P*<0.001), pool to riffle ratio (R=0321, *P*<0.001), and bank stability (R=0.201, *P*=0.017) scores increased significantly, while streamflow (R=-0.362, *P*<0.001), channel alteration (R=-0.240, *P*=0.004), bank vegetative protection (R=-0.487, *P*<0.001), streamside cover (R=-0.196, *P*=0.021), and riparian vegetative zone width (R=-0.328, *P*<0.001) scores decreased. Scores for streamflow (R=0.663, *P*<0.001), bank stability (R=0.429, *P*<0.001), and streamside cover (R=0.577, *P*<0.001) significantly increased downstream in Bacolod, while bottom substrate (R=-0.294, *P*=0.002), embeddedness (R=-0.289, *P*=0.003), and bank vegetative protection (R=-0.588, *P*<0.001) scores significantly decreased. In Dumaguete, scores for embeddedness (R=0.520, *P*<0.001) and streamflow (R=0.219, *P*=0.005) increased, while scores for canopy cover (R=-0.419, *P*<0.001), pool to riffle ratio (R=-0.294, *P*<0.001), bank stability (R=-0.482, *P*<0.001), bank vegetative protection (R=-0.508, *P*<0.001), and riparian vegetative zone width (R=-0.276, *P*<0.001) decreased. In Apo, bottom substrate (R=0.472, *P*<0.001), streamflow (R=0.203 , *P*=0.013), canopy cover (R=0.719, *P*<0.001), channel alteration (R=0.472, *P*<0.001), pool to riffle ratio (R=0.513, *P*<0.001), bank stability (R=0.406, *P*<0.001), and bank vegetative protection (R=0.266, *P*=0.001) significantly increased downstream.

The scores also varied among sites. From north-to-south, mean scores for bottom substrate (*R*=0.164, *P*<0.001), pool to riffle ratio (*R*=0.221, *P*<0.001) and bank vegetative protection (*R*=0.217, *P*<0.001) significantly increased, while embeddedness (R= -0.125, *P*=0.001), streamflow (*R*=-0.214, *P*<0.000) and streamside cover (*R*=-0.133, *P*=0.001) significantly decreased. On the other hand, canopy cover, channel alteration, bank stability, and riparian vegetative zone width mean scores did not exhibit a trend (R≤0.065, P≥0.093 in all cases).

Correlations between FFG diversity, environmental conditions, and habitat quality

Within the study sites, the variations in the mean abundances of all FFGs, which did not exhibit clear upstream-downstream trends, appeared to be significantly influenced by the variations in the physicochemical and habitat quality parameters.

In Bacman, the mean abundance of scrapers increased with decreasing wetted width (R=-0.455, *P*=0.038). With increasing mean scores for channel alteration (R=-0.436, *P*=0.048) and pool to riffle ratio (R=-0.433, *P*=0.050), the mean abundance of shredders decreased. Moreover, a decrease in bank vegetative protection score (R=-0.468, *P*=0.032) was significantly correlated with the increase in the mean abundance of gathering collectors.

In Leyte, the mean abundance of gathering collectors was positively correlated with mean temperature (R=0.608, *P*=0.003) and negatively correlated with riparian vegetative zone width and bank vegetative protection (R≥-0.4660, *P*≤0.013 in both cases). Increasing mean values for conductivity, and increasing scores for bank stability, pool to riffle ratio, and embeddedness significantly correlated (R≥-0.495, *P*≤0.023 in all cases) with decreasing mean abundance of filtering collectors. Predators increased with increasing substrate cover score (R=0.389, *P*=0.041)and decrease with increasing streamflow (R=-0.389, *P*=0.041). Scrapers increased with an increase in substrate cover (R=0.390, *P*=0.040) and decreased with an increase in TDS, streamflow, and streamside cover scores (R≥-0.390, *P*≤0.040 in all cases). Shredders decreased with increasing streamflow score (R=-0.701, *P*<0.001) and increased with increasing substrate cover (R=0.701, *P*<0.001), canopy cover (R=0.388, *P*=0.041), and riparian vegetative zone width scores (R=0.387, *P*=0.040).

Except for pH and streamside cover, all the other environmental parameters did not significantly correlate with the mean abundance of all FFGs (data not shown) in Bacolod. Predators decreased with increasing pH (R=-0.539, *P*=0.021), and gathering collectors increased with increasing streamside cover scores (R=0.590, *P*=0.005).

In Dumaguete, gathering collectors increased with increasing wetted width, TDS, and streamflow score (R≥0.372, *P*≤0.033 in all cases) and decreased with an increasing score for substrate cover (R=-0.672, *P*<0.001). Filtering collectors also decreased with increasing substrate cover (R=-0.396, *P*=0.023). As dissolved oxygen levels and canopy cover scores increased, predators also significantly increased (R≥0.350, *P*≤0.046 in both cases). Increasing temperature correlated with decreasing scrapers (R=-0.490, *P*=0.018). Shredders increased with increasing scores for streamside cover, riparian vegetative zone width, and substrate cover (R≥0.406, *P*≤0.019 in all cases).

In Apo, all FFGs increased with increasing depth (R≥0.372, *P*≤0.043 in all cases) and decreased with increasing TDS (R≥-0.383, *P*≤0.037 in all cases). Filtering and gathering collectors, predators, and scrapers increased with increasing discharge (R≥0.453, *P*≤0.012 in all cases). Except for shredders, the other four FFGs significantly increased with increasing canopy cover (R≥0.386, *P*≤0.035 in all cases). Scrapers increased with an increase in pH, pool to riffle ratio, channel alteration, bank vegetative protection, and substrate cover (R≥0.366, *P*≤0.046 in all cases). Predators increased with increasing pool to riffle ratio, bottom substrate, and canopy cover (R≥0.368, *P*≤0.046 in all cases). The increasing bank vegetative protection and pool to riffle ratio correlated with increasing mean shredder abundance (R≥0.369, *P*≤0.045 in both cases).

Discussion

Spatial patterns in functional feeding groups

All functional feeding groups proposed by Cummins (1973, 1974) were represented in the tropical streams in this study. The occurrence of each group was varied and was found to depend on interacting environmental conditions and habitat quality, which ultimately influence the availability of their food resources (Cummins, 1975). Collectors were the most represented group and may imply the importance of seston (floating organisms and non-living matter) transport in the water column (Uwadiae, 2010). Scrapers occur less frequently than collectors do, reflecting the less importance of periphyton primary production (Dudgeon, 1999). Shredders were the least represented, as was observed in other studies in tropical streams (e.g., Li & Dudgeon, 2008; Li & Dudgeon, 2009). The low predator abundance implies a balanced trophic structure as physiochemical perturbation results in an extreme imbalance in predator proportions (Park *et al.*, 2008).

Gathering collectors and filtering collectors, which dominate all the five river systems, are generalist feeders (Barbour *et al.*, 1999). Generalist feeders can utilize more diverse food materials than specialized feeders (scrapers and shredders) do (Park *et al.*, 2008). Even in urban streams, gathering collectors can utilize available food sources sufficiently (Suren & McMutrue, 2005). The domination of generalist feeding in tropical streams denotes an adaptation of the macroinvertebrates to fluctuations in food resources. Furthermore, when particular food items are limited, the generalist strategy could reduce competition by exploiting other readily available food resources (Tomanova *et al.*, (2006). Hence, despite perturbations in their habitat, generalist feeders can survive (Uwadiae, 2010).

The higher abundance of collectors in the downstream sites than in the upstream sites in the mountainous streams corresponds with the RCC prediction. The downstream sites of the streams received fine particulate organic matter (FPOM) that was processed upstream. Furthermore, with the increase in width from upstream to downstream, the general reduction in detrital particle size increases as the detritus are transported (Dudgeon, 1999). Jiang *et al.* (2011) also found a positive correlation between gathering collectors and stream width and related it to the preponderance of human activities, such as agriculture, along wide-channeled portions of rivers.

The absence of the upstream-downstream trend predicted by RCC in the mean abundance of collectors in the other streams could be attributed to other environmental factors. For instance, high discharge (also reflected by high RBP scores for streamflow) enhances the transport of particulate organic matter (Uwadiae, 2010). In deep pools, leaves are deposited and processed by shredders to form FPOM pools as the velocity of particles exceeds the current velocity (Cummins, 1974; Speaker *et al.*, 1984; Wallace & Webster, 1996). From these FPOM pools, collectors derive their food sources. Another factor, high temperature, increases the rate of organic matter decomposition (Burke *et al.*, 2003; Friberg *et al.*, 2009), hence enhances the availability of FPOM.

Functional feeding groups and correlates

In this study, Pearson correlation tests revealed a negative correlation between TDS and filtering collectors and a positive correlation between TDS and gathering collectors. Uwadiae (2010), on the contrary, found a significant positive relationship between TDS and filtering collector density (Uwadiae, 2010). High TDS could reflect high amounts of organic matter transported or retained in the water column – but not always. The proportion of organic matter in TDS may not always be greater than the other dissolved components. Furthermore, the rate at which organic matter is suspended in the water column exceeds that of transport. Hence, TDS values alone are not enough to determine correlations with filtering and gathering collectors' abundances.

The scarcity of shredders in the tropics, in general, could be attributed to a limitation in palatable leaf litter inputs. Most of the tropical forest tree species have unpalatable leaves due to the production of secondary compounds as defense mechanisms against herbivory animals (Li & Dudgeon, 2009).

Pearson correlation test revealed a significant increase in shredder abundance and a significant decrease in scraper abundance in slightly acidic waters. In acidic waters (pH 3.5-3.7) with relatively lower DO levels, partly decomposed leaf litters build up layers of peat. In this build-up, leaf species that lack defensive compounds (which is typical of tropical species) will rapidly break down (Dudgeon, 1999), thereby providing shredders with palatable leaf litter to utilize. On the contrary, scrapers are intolerant to acidity. In a stream that suffered an accidental acid spill in California, the perturbation was detected only by the functional measure of the percentage of scrapers (Resh & Jackson, 1993; Resh, 1994).

Bottom substrate, bank stability, channel alteration, bank vegetative protection, embeddedness, and pool to riffle ratio are the habitat quality parameters that may characterize the stability and variability of the habitat. Stable habitats are characterized by a high mixture of gravel, submerged logs, undercut banks, and less gravel and deposits of fine materials (Barbour *et al.*, 1999). High habitat stability favored predators, scrapers and shredders, but reduced filtering and gathering collectors. Stable habitat provides attachment for scrapers and filtering collectors (Cummins *et al.*, 2005). However, filtering collectors did not increase significantly due to the lack of fine material deposits in these habitats. Habitat variability favored predators, scrapers, and shredder but did not significantly affect the abundance of gathering and filtering collectors, probably because they can quickly adapt to any type of habitat (Tomanova *et al.*, 2006). High variability provides a wider range of food resources that the FFGs could utilize. The amount of leaf litter inputs into the stream could be characterized by canopy cover, riparian vegetative zone width, and streamside cover. High leaf litter input provides shredders with sufficient food sources (Compin and Céréghino, 2007; Li & Dudgeon, 2008, 2009). As shredders process more coarse particulate organic matter (CPOM) into FPOM, more food resources are available for the collectors and the predators that prey on them. On the contrary, scrapers decreased along with increasing streamside cover. Shading that inhibited sunlight from penetrating the streams, thereby inhibiting periphyton photosynthesis (Sabater *et al.*, 1998; Jiang *et al.*, 2011).

Clear trends and correlations that were found in several study sites were not detected in other study sites. For example, RCC prediction for collectors' abundance was exhibited in Apo but not in the four other study sites. Another positive correlation between shredders and riparian vegetation was detected in Bacman, Leyte, Dumaguete, and Apo, but not in Bacolod. Increasing the number of sampling points within study sites may provide a better picture of aquatic ecosystem functioning. Furthermore, the classification of each taxon into a particular guild undermines the possibility of alternative food resource utilization employed by some organisms. The fuzzy coding technique used by Tomanova *et al.* (2006), which characterizes the affinity of an organism to each FFG, could be applied.

CONCLUSION

Functional Feeding Group measurements could be used to assess short and long-term impacts in aquatic habitats that may not be detected using physicochemical parameters. The lack of trend in the distribution of FFGs along the upstream-downstream gradient indicates high variability in the stream's environmental conditions and habitat quality.

The FFG method also reduces the risk of erroneous assessments brought about by uncalibrated physicochemical measurement tools. The functional feeding group approach can be an effective tool in assessing the physical and chemical condition and the habitat quality of tropical streams. However, there is still a great need to verify how the patterns observed in the current research will vary with time, season, and other streams in the Philippines.

ACKNOWLEDGEMENTS

We thank the Energy Development Corporation, Diliman Science Research Foundation, and the Institute of Biology of the University of the Philippines Diliman for financial and logistical support. Special thanks to Dino Angelo E. Ramos, Gizelle A. Batomalaque, and colleagues from the Energy Development Corporation and the Institute of Biology for their help in the field. We acknowledge the Philippine Department of Environment and Natural Resources for the permits to collect specimens for scientific studies.

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