Title

Does the River Continuum Concept Work in Small Island Streams? Functional Feeding Group Variation Along a Longitudinal Gradient

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DOES THE RIVER CONTINUUM CONCEPT WORK IN SMALL ISLAND STREAMS? FUNCTIONAL FEEDING GROUP VARIATION ALONG A LONGITUDINAL GRADIENT

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Abstract. The River Continuum Concept (RCC) predicts that as the form of particulate organic matter available in streams and rivers varies longitudinally, so will the functional feeding groups (FFGs) of benthic macroinvertebrates. The RCC was developed based on data from continental streams; therefore, its applicability to the unique ecology of island streams is virtually untested. The purpose of this study was to discover if the RCC works in the small streams of Moorea, French Polynesia. Three sites along an elevational gradient were sampled for benthic macroinvertebrates in five streams of similar catchment size. Each sample was sorted and all taxa were assigned to a FFG. Species richness and FFG variation along a longitudinal gradient were compared to RCC predictions. Patterns in the longitudinal variation of crustacean/mollusc species richness and shredder, grazer, and predator percent composition were found to match RCC predictions. However, total species richness, insect species richness, and the percent composition of collecting organisms did not. Therefore, an alternative theoretical framework is needed to accurately describe FFG variation in tropical streams.

Key words: River Continuum Concept, benthic macroinvertebrates, functional feeding groups, species richness, island streams, Moorea

INTRODUCTION

The River Continuum Concept (RCC) was proposed to explain the longitudinal variation of benthic macroinvertebrate communities in freshwater catchments (Vannote et. al. 1980). The RCC postulates that as stream size increases and the composition of available organic matter changes, the functional feeding groups (FFGs) will also change to reflect the increase in habitat diversity and the shift in food availability (Vannote et. al. 1980). The RCC assumes an abundance of macroinvertebrate taxa, especially insects, and a substantial catchment size.

Because the RCC was developed using data collected from large continental streams in North America, its usefulness to the unique biology of small island streams is largely untested. Island streams have many particular features that may affect the application of the RCC. First, their watersheds are generally small, so streams meet the ocean no larger than mid-sized, fifth-order streams. Second, the banks of island streams are often heavily vegetated, providing a continuous supply of organic matter, but frequent flooding washes away the accumulated plant material (Resh 1995). This is different from continental streams, where riparian vegetation is often reduced as stream order increases. Third, the majority of organisms found within island streams are not insects but diadromous crustaceans and molluscs (Greathouse 2006).

As with most other islands, it is unknown whether the RCC applies in the streams on Moorea, French Polynesia, an island located 18 kilometers west of Tahiti (Resh 1990). Most streams on Moorea are small, reaching only third order before reaching the Pacific. The Opunohu River to the north has the largest catchment on the island, reaching only fifth order as it enters Opunohu Bay.

The objectives of this study were to: (1) describe the macroinvertebrate fauna of the small streams of Moorea; (2) determine how the functional feeding groups of macroinvertebrates change along a longitudinal gradient in these streams; and (3) determine if the River Continuum Concept applies to the streams on Moorea. I postulate that the RCC will not apply on Moorea because of its low aquatic insect diversity and the diadromous nature of the majority of its in-stream fauna.

METHODS

Study sites

Five streams with similar catchment sizes were selected from different regions of the island (Fig. 1). Each stream was divided into three different sites: (1) a low-gradient, 50-meter reach starting at the first riffle from the mouth; (2) a high-gradient, 25-meter mid-reach; and (3) a high-gradient, 12.5-meter reach at the headwaters, the highest reach possible to sample with a D-frame net. Each site was partitioned into three subsites based on stream morphology (riffle, run, pool, and step). The physical parameters describing each site are found in Table 1.

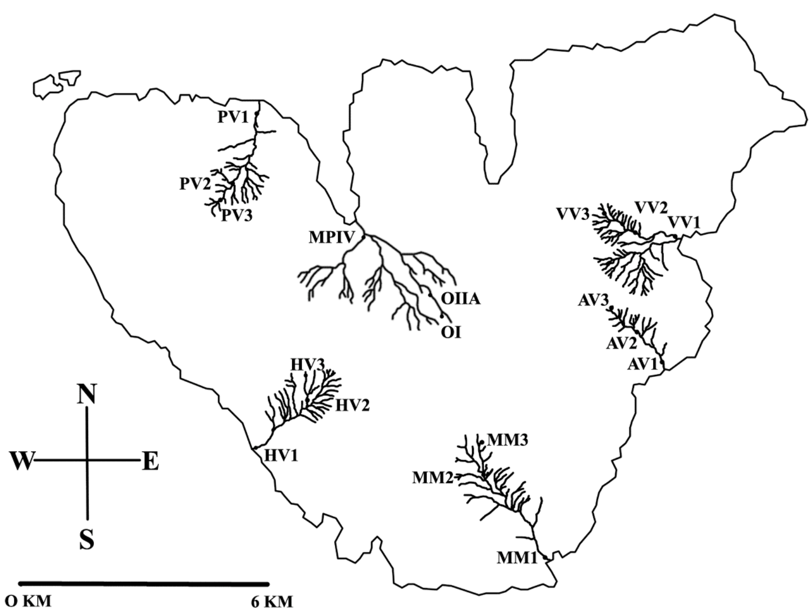

Fig. 1: Map of Moorea and 15 study sites

Maatea-Mahaerua (MM)

The town of Maatea is located on the east side of Moorea, just above the southernmost point of the island (Fig. 1). The Mahaerua River follows the Toto Valley, starting from the south-facing slope of Mount Tohiea, and meets the Pacific as a third-order stream at the southwest end of Maatea. Site MM1 is located approximately 109 meters upstream from the circum-island road. The furthest downstream reach is bisected by an artificial riffle and both banks are leveed. The morphology is primarily composed of runs (78%) and a large shallow pool (20%) created by the riffle (Table 1). Flow is highly influenced by the tide, causing the depth to fluctuate approximately 20 cm every few minutes, but the salinity is unaffected (Table 1).

Sites MM2 and MM3 were both accessed by the road approximately 150 meters from the left bank of the Mahaerua; a tall brick wall is to the south, a convenience store with a large Hinano sign is to the north. Site MM2 is located 1.5 kilometers from the mouth. It is reached by following the road past a farm to a large dip in the road before a steep hill. A small tributary stream bisects the road at this point. The sampled reach extends 25 meters upstream from the confluence. Site MM3 is 2.2 kilometers from the mouth of the Mahaerua. It is accessed by hiking upstream from the end of the road for approximately 15 minutes. The right branch is followed at each confluence. A small island splits the channel in the upper eight meters of the 12.5-meter reach.

Papetoai-Vaihana (PV)

The town of Papetoai is located on the north side of Moorea, immediately west of the entrance to Opunohu Bay (Fig. 1). The Vaihana River flows from the northern face of Mount Tautuapae down the northwest facing Terahimaua Valley. The mouth of the Vaihana River outlets into the Pacific Ocean as a fourth-order stream just east of “Chez Kiri” in Papetoai. Site PV1 is approximately 30 meters upstream from the circum-island road. A road approximately 50 meters west of the mouth of the Vaihana leads to site PV2; it intersects the main road between a residence surrounded by tall hedges and a low grey-brick wall. It is one of two paved roads in Papetoai. Site PV2 is located 10m upstream from the end of this road. Site PV3 is reached by hiking approximately 2.5 hours upstream from site PV2. Site PV3 is unique from the other headwater sites sampled because the channel was restricted within a narrow bedrock canyon.

Vaiare-Vaipohe (VV)

The town of Vaiare is located on the east side of Moorea at the base of Vaiare Bay, near the Gare Maritime. The Vaipohe River flows from the ridge between Mount Tearai to the north and Mount Mouaputa to the south. Approximately twenty meters from the mouth

Table 1: Abiotic characteristics of study sites. Measurements were made from mid-October to mid-November 2006. Ru=run, Ri=riffle, P=pool, S=step. Opunohu data was collected by Resh et al. (1990)

Site	MM1	MM2	MM3	PV1	PV2	PV3
Reach length	50	25	12.5	50	25	12.5
pH	6	6	6	6	6	6
Conductivity (uS/cm)	122.9-132.6	89.7	95.6	123.5	95.5	93.2
Salinity (ppt)	0.1	0	0	0.1	0	0
Turbidity (NTU)	5.7	2.25	8.64	1.6	3.62	1.62
Width (m)	7.1	2.2	2.5	5	7.6	2
Depth (m)	.27-.62	.12-.45	.02-.18	.05-.15	.07-.76	0.25
Temperature in air/water (°C)	33/26.2	27/23.2	26/21.8	22/22	23/22	22/22.3
Elevation (m)	5	73	141	13	80	268
Distance from mouth (km)	0.109	1.5	2.19	0.03	0.94	2.29
Stream order	3	3	1	4	3	2
Morphology (%)	78Ru, 2Ri, 20P	30Ri, 25P, 45S	60Ri, 40S	35Ru, 65Ri	30Ri, 30P, 40S	45Ru, 25Ri, 30P
Site	VV1	VV2	VV3	AV1	AV2	AV3
Reach length	50	25	12.5	50	25	12.5
pH	6	6	6	5-6	6	7
Conductivity (uS/cm)	148	134.9	114.6	94.5	78.7	66.1
Salinity (ppt)	0.1	0.1	0.1	0	0	0
Turbidity (NTU)	3.94	2.43	2.4	2.8	7.8	3
Width (m)	2.5	3.5	2	3.6	3	2.7
Depth (m)	0.01	0.25	0.07	.07-.17	.08-.73	.1-.43
Temperature in air/water (°C)	33/25.5	29/24.1	27/23.5	26/24.4	25/23.7	25-22.9
Elevation (m)	11	75	190	1	50	311
Distance from mouth (km)	0.2	0.9	1.6	0.075	0.73	1.26
Stream order	4	4	2	2	2	1
Morphology (%)	45Ru, 55Ri	40Ru, 20Ri, 20P	80Ri, 20P	40Ru, 60Ri	20Ru, 60Ri, 20P	30P, 70S
Site	HV1	HV2	HV3	MPIV	OIIA	OI
Reach length	50	25	12.5	--	--	--
pH	6	6	6	7.6	7.6	9.2
Conductivity (uS/cm)	128.1	119.4	115.1	120	120	113
Salinity (ppt)	0.1	0.1	0.1	--	--	--
Turbidity (NTU)	3.6	1.5	4.5	--	--	--
Width (m)	6.5	2.4	1.2	12	2	5
Depth (m)	0.01	.09-.25	.05-.17	0.5-1.0	0.2-0.3	0.001-0.3
Temperature in air/water (°C)	28/25.1	25/24.2	24/23	25/23	27/23	26/26
Elevation (m)	16	118	225	2	122	335
Distance from mouth (km)	0.02	1	2	0.4	3.1	4.0
Stream order	3	2	1	4	2	1
Morphology (%)	40Ru, 60Ri	50Ru, 20Ri, 30P	40Ru, 20Ri, 40 P	--	--	--

it intersects the Nuuati, entering the Pacific Ocean as a fifth-order stream. Site VV2 is approximately 200 meters from the mouth. The reach extends 50 meters from the upstream side of the bridge on the road immediately to the right of the mouth. Site VV2 is reached by following the road to the head of the Vaiare-Paopao cross-island trail. It is to the right of the end of the road through the stand of coconut palms. Site VV3 is reached by following the main channel upstream about 45 minutes from site VV2. The reach extends from the base of a four-meter waterfall 12.5 meters downstream.

Afareiaitu-Vaioro (AV)

The town of Afareiatu is on the eastern side of Moorea. The Vaioro River flows from the southeast face of Mount Mouaputa and meets the Pacific Ocean as a second-order stream at the north end of Afareiatu. Site AV1 is 75 meters upstream from the mouth. There was significantly more garbage within the reach than observed at other low-gradient sites. Site AV2 is approximately 750 meters from the mouth of the Vaioro River and extends 25 meters upstream from the base of the trail to the top of Mouaputa. The head of the Mouaputa trail branches off to the left across the stream from the trail to the Vaioro waterfall. Site AV3 is reached by hiking for approximately two hours up the Mouaputa trail. The trail follows the stream for most of its length. The sampling site is located just downstream of the confluence where the trail leaves the stream and extends up a steep hill with a coconut palm at the top. The trail crosses just upstream of the site, but causes minimum impact.

Haapiti-Vairemu (HV)

The town of Haapiti is located on the western side of Moorea. The Vairemu River runs from the southwest face of Mount Mouapu and enters the Pacific Ocean as a third order stream. The mouth is located in the middle of town to the north of a soccer field. Site PV1 is 20 meters upstream from the mouth and there is a road along the unvegetated right bank. Sites PV2 and PV3 are reached by following the road on the right bank. Approximately one kilometer up, there is a fork in the road. Site PV2 is reached by taking the fork to the right until the main channel is reached. The reach extends 25 meters upstream from the road. Site PV3 is reached by taking the left fork for another kilometer until it can no longer be traveled by car. The site is past the length of road covered by herbaceous vegetation. A dry streambed crosses the road at the top of the hill. The dry bed is followed until running water is reached. The right bank is mostly sediment and highly susceptible to erosion.

The OpunohuRiver catchment

The Opunohu river catchment is the largest on Moorea. The Opunohu is located on the north side of the island. It flows from the northern slope of Mt. Tohiea and meets the Opunohu Bay as a fifth-order stream. Resh et al. (1990) surveyed this stream, and it is used as a comparison to the five streams that I sampled. Comparable sites are: site MPIV, which is located 0.4 km upstream from the mouth of the Opunohu on a fourth-order tributary that flows down the Mouapu valley; Site OIIA, which is a second-order site near Marae de Titiroa; and site OI, which is a first-order stream reached by following a south-bound trail from the Belvedere (Resh et al. 1990).

Functional feeding groups

Benthic macroinvertebrates are assigned to FFGs based on feeding mode and food preference (Vannote et al. 1980). Shredders feed on living and dead plant material, breaking down the coarse particulate organic matter (CPOM) into fine particulate organic matter (FPOM). Collectors gather or filter the FPOM. Grazers scrape off the algae attached to available surfaces within the stream. Predators feed on living organisms (Merritt and Cummins 1996).

Benthic macroinvertebrate sampling

Benthic macroinvertebrates were collected at each site using a D-frame net and a small aquarium net. Each of 15 sites was divided into three subsites. Each subsite was sampled with three one-minute kicks of the D-net across the width of the stream. If the stream was too narrow, the three kicks were done longitudinally starting downstream. In addition, a five-minute search was performed in each sub-site. Instream rocks were inspected for gastropods and an aquarium net was used to catch shrimp. Organisms were sorted and identified in the laboratory using a 10x microscope. Each specimen was identified to the species level if possible. Others were identified to family.

Data analysis

The total number of individuals and biomass estimates were calculated for each sample. The latter was determined by assigning each species identified a biomass equivalence (BME) number, with one Chironomid (Diptera) as the basic unit (Appendices A–E). The BME was a rough estimate; gastropods and shrimp were divided into size classes in five-millimeter increments. Crabs were assigned a BME based on the size of their carapace.

Each taxon was assigned to a FFG. All sub-samples from each site were combined, and the percentage of each FFG in each site was calculated based on the number of individual organisms and the BME estimate.

Statistical analyses of species richness and FFG percent composition were performed using JMP 5.1 (SAS Institute 2003). Normally distributed data were analyzed using ANOVA and the student's t-test. All other data were analyzed using the Wilcoxin and Tukey tests.

RESULTS

Species richness

A total of 52 taxa were found in the 15 sites sampled (Appendices A–E). Species richness ranged from 14 to 23 in the headwaters, 14-19 in the mid-reaches, and 15 to 29 near the mouth (Appendices A–E). Highest species richness was found at the mid-elevation sites in the Vairemu and Vaioro Rivers (HV2 and AV2) and the site with the least lowest species richness was the mid-elevation site on the Vaihana River (PV2, Fig. 2). The number of taxa was relatively constant in the Vaipohe River (VV).

The highest insect taxa richness was found at downstream site PV1, the lowest at downstream site AV1 (Fig. 3). The highest species richness of crustaceans and molluscs occurred at downstream sites MM1, PV1, and AV1, while the lowest occurred at upstream sites MM1 and AV3 (Fig. 4). Fifteen taxa occurred exclusively at one site. Overall, the number of individual species did not change much from headwaters to mouth, but the species richness of insects was highest in high-elevation sites and the species richness of crustaceans and molluscs was highest in the lowest-elevation sites (Fig. 2-4). Statistical analysis found a significant difference only in mollusc and crustacean richness between low, mid, and high elevations.

Functional feeding group longitudinal variation

Macroinvertebrate FFG composition showed variation from headwaters to mouth. The percentage of grazers increased in three of the five streams sampled (i.e. PV, VV, and AV) based on number of individual organisms (Fig. 5) and the BME estimate (Fig. 6). The percentage of shredding organisms decreased from upstream to downstream along the continuum both by number and BME. The percentage of predators remained constant in three of five streams (MM, AV, HV), ranging from approximately five to ten percent of each sample. The BME estimate of predators showed no similar trends between the different catchments sampled. The percentage of collectors decreased in three of the five streams sampled (PV, VV, and AV) by individual numbers. Like the predators, the BME composition of collectors showed no distinctive trend. Statistical analysis found no significant difference between the elevational variations observed in FFGs.

The Opunohu River catchment

In the Opunohu, total species richness increased from 19 in the high-gradient site to 28 in the low-gradient site (Fig. 7). Crustacean and mollusc taxa increased from 3 in the headwaters (OI) to 13 near the mouth (MPIV). The number of insect taxa varied; the highest species richness (12) was found in the high-gradient site, while the lowest (6) was found in the mid-reach site (OIIA). The percentage of shredding organisms stayed constant across the continuum (Fig. 7). The percentage of grazers increased from headwaters to mouth. Both predators and collectors showed drastic variability between the three sites. The percentage of predators decreased from 86% in site OI to 5% in site OIIA. The collectors increased from 13% in site OI to 85% in site OIIA. Collector and grazer proportions did not vary much between sites OIIA and MPIV (Fig. 8).

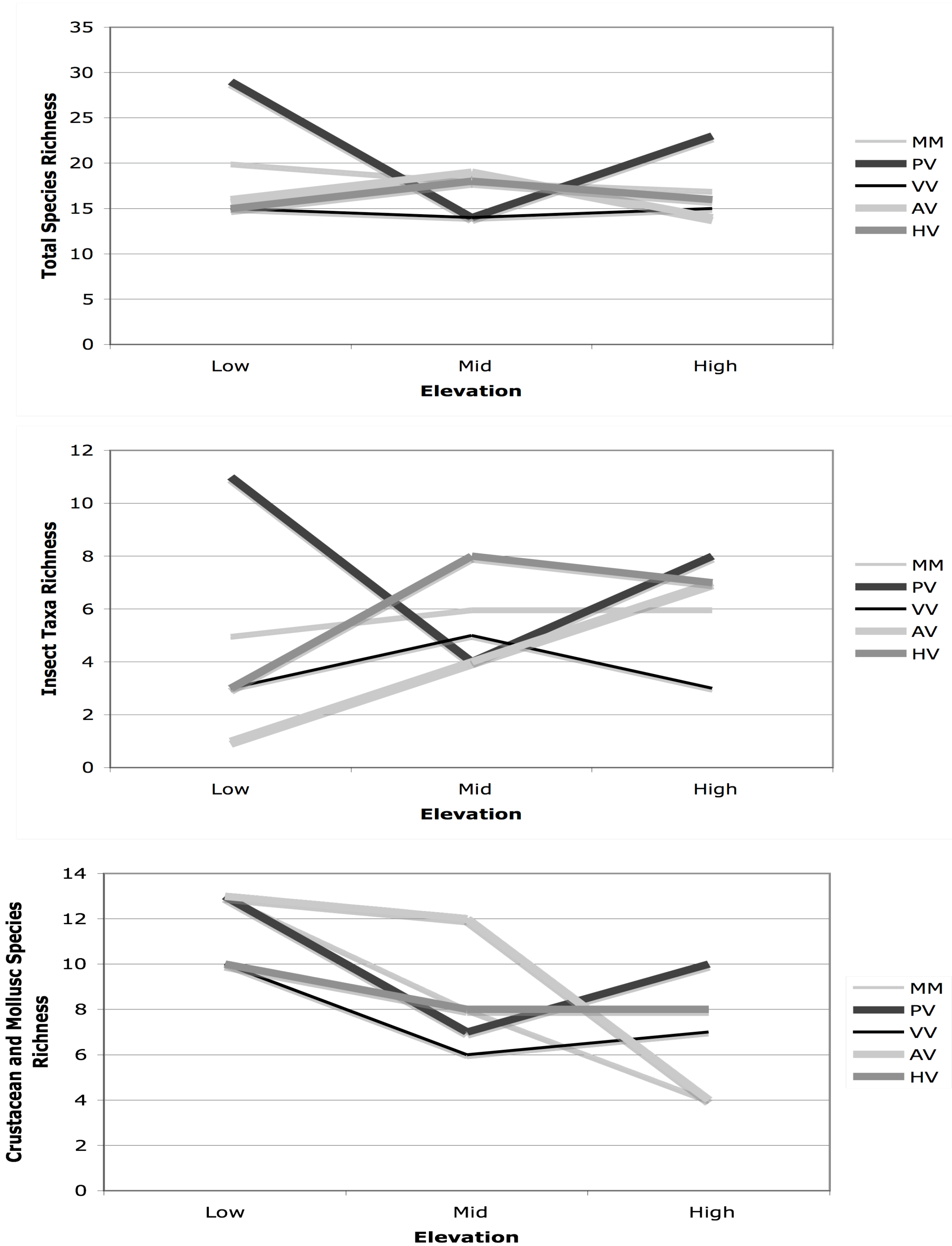

Fig. 2: Species richness at fifteen study sites. Richness was calculated using the total number of taxa found, the number of insect taxa and the number of mollusc and crustacean taxa.

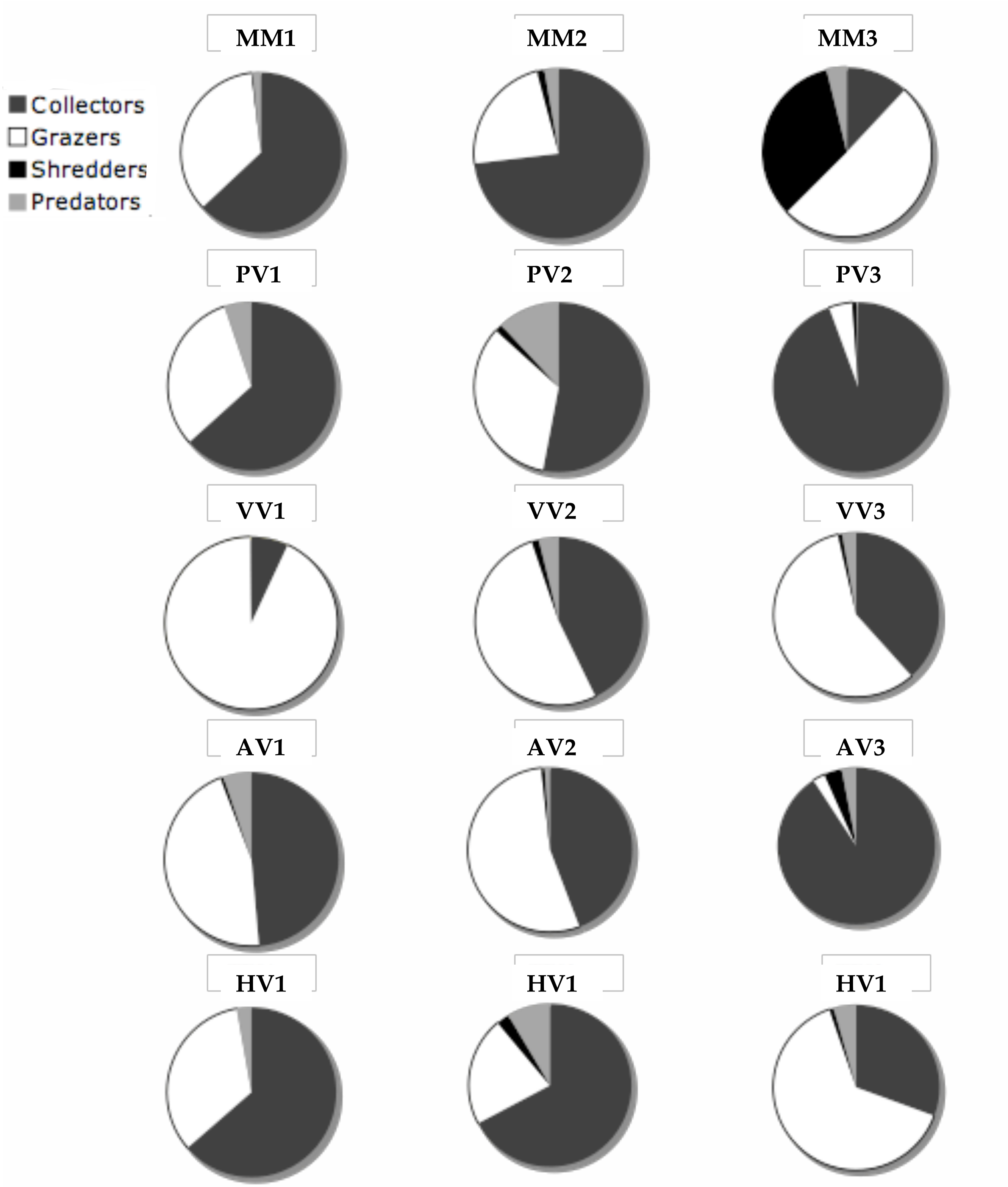

Fig. 3: Functional feeding group composition by abundance of individuals.

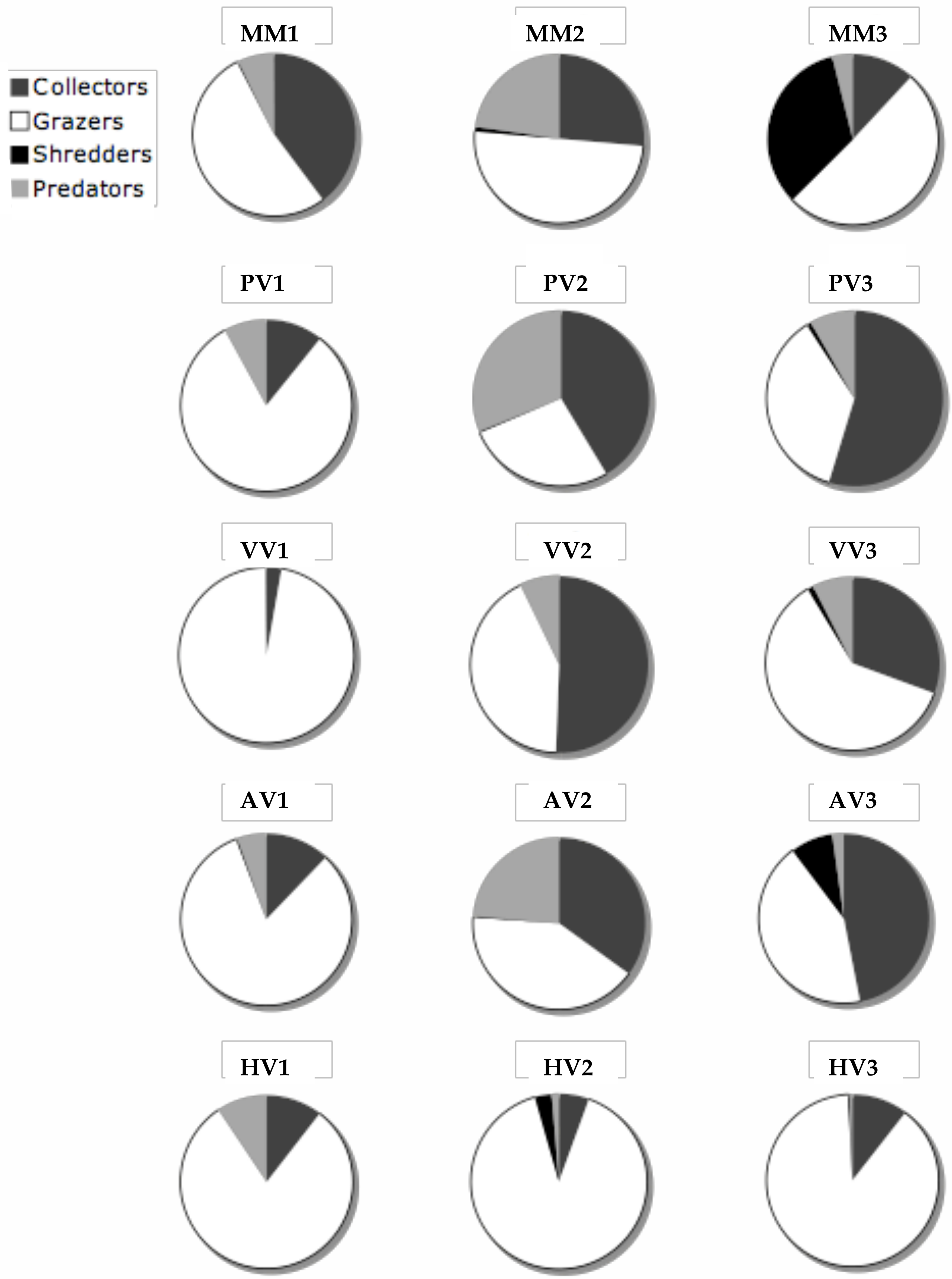

Fig. 4: Functional feeding group composition by biomass equivalence.

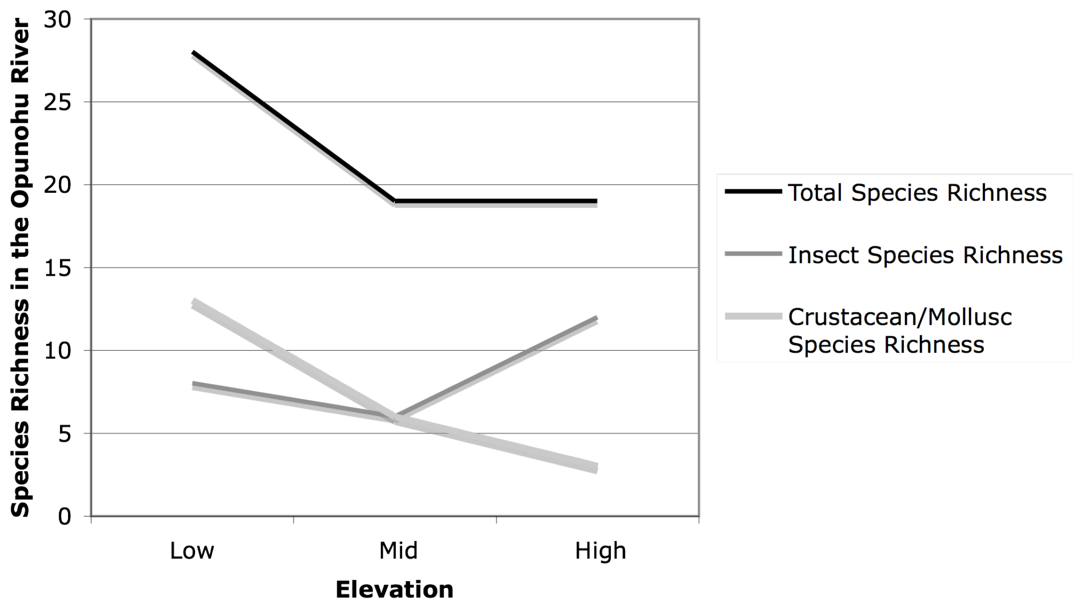

Fig. 5: Species richness in the Opunohu River catchment

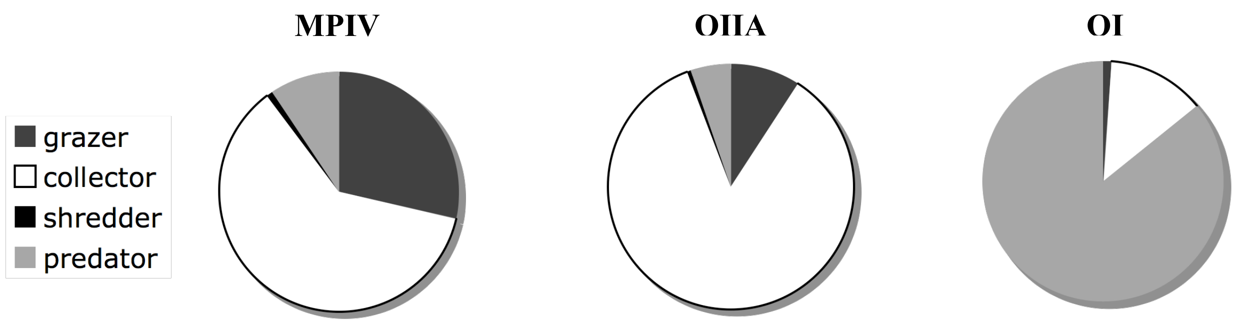

Fig. 6: Functional feeding group composition by abundance of individuals in the Opunohu River catchment.

Discussion

Does species richness match RCC predictions?

The RCC predicts that species richness increases from upstream to downstream as the size of the stream increases. In the small streams sampled on Moorea, the total species richness did not vary significantly between high-gradient, mid-reach, and low-gradient sites. The highest variation was seen in the PV catchment, where species richness ranged from 14 to 29 (Fig. 2), but the lowest richness was found in the mid-elevation site. The pattern of insect species richness also did not match RCC predictions. Although ANOVA found no significant difference between elevations, the number of insect species increased from mouth to headwaters in HV and AV and remained constant in the Mahaerua River (MM) and VV. This trend could be attributed to the small size of many insect species in these rivers and the susceptibility of insect larvae to the frequent disturbances caused by flooding observed in island streams.

The pattern of species richness for gastropod molluscs and crustaceans did match RCC predictions, increasing from headwaters to mouth down the continuum. The aquatic gastropods and decapods of Moorea are all marine in origin and their larvae must still return to the sea to mature (Greathouse 2006). This is a possible explanation for why the highest concentration of species was found closer to the mouth. The streams were also large at lower elevations, providing more habitat and allowing resource partitioning between more species of grazing gastropods.

In the Opunohu River catchment, patterns of total species richness did follow RCC predictions, increasing from 19 in the headwaters to 28 at the mouth (Fig. 7). The number of mollusc and crustacean species increased down the continuum while the number of insect species decreased.

Do FFGs match RCC predictions?

Shredders

The pattern of shredders found along an elevational gradient in Moorean streams matched RCC predictions. The percentage of shredding individuals decreased from upstream to downstream in all streams sampled, with the exception of HV. According to the RCC, shredding organisms should compose one-third of the functional community in high elevation sites, but shredder biomass was depauperate in all headwaters sites sampled except MM3 (Fig. 6). Shredding organisms were 18% of individuals found and 34% of the biomass (Figs 5-6).

Shredding insects were mostly absent on Moorea. Only one family of shredders was present, Pyralidae (Lepidoptera). Only two individuals of Pyralidae were found, one in a headwaters site, one in a site near the mouth (Appendices A-B). The major shredders found in this study were Taltrids (Amphipoda) and two species of millipede, *Oxidus gracilis* Koch (Paradoxosomatidae) and *Glyphiulus grnulatus* Gervais (Cambalopsidae).

Grazers

The pattern of grazers along the streams sampled also matched RCC predictions, increasing down the continuum in three of five streams. In MM and HV the number of individuals decreased but the rough estimate of BME remained relatively constant from headwaters to mouth. It's not an issue of canopy cover because all headwaters sites had similar coverage. Grazers were the only FFG that matched the predictions made by the RCC in the Opunohu.

Predators and collectors

The RCC predicts that the proportions of predators and collectors should remain constant for streams smaller than fifth order. The prediction for predators applied in all but one stream, PV. Predators should compose about ten percent of all samples, but they only appeared in that abundance in two samples, HV2 and PV2. The low percentage of predatory species may result from competition with fish for food (Greathouse and Pringle 2006), an aspect not considered in this study.

The functional composition of collectors should either stay the same or increase down the continuum. In all streams sampled, the proportion of collectors varied greatly and did not show a trend in abundance or BME. Atyid shrimp were classified as collectors 2/3 of the time and *Macrobrachium* shrimp and crabs were classified as spending 1/2 of their time collecting (Greathouse and Pringle 2006).

A potential problem with the results of this study is that the exact role of many of the macroinvertebrates found in the functional communities of Moorea is not known. Crustaceans, such as shrimp and crabs, are generally omnivores and it is not known how much of their time is divided between each feeding mode or how life history affects feeding preference. The role of crustaceans in the continuum can only be estimated. The large crustaceans composed a high proportion of the biomass in the system, resulting in a higher percentage of collectors (Fig. 5).

Some aspects of the RCC applied to the small streams of Moorea, but others did not. Longitudinal patterns of crustacean/mollusc species richness and shredder, grazer, and predator percent composition matched RCC predictions. Total species richness, insect species richness, and the percent compostion of collecting organisms did not. Although statistical analysis found no significance between the longitudinal variations observed in FFGs, the RCC was developed only to show trends, some of which were observed in the streams on Moorea. A more comprehensive study by Greathouse and Pringle (2006) in Puerto Rico found similar results even though the island of Puerto Rico is much larger than Moorea, much closer to a major land mass, and contains higher-order streams. The Puerto Rico study also found a greater diversity of insects, including beetles (Coleoptera), mayflies (Ephemeroptera), and caddisflies (Trichoptera) (Greathouse and

Pringle 2006); these insect orders were not found in Moorean streams.

In conclusion, the overall findings of tropical island stream studies demonstrate that the RCC generally applies to tropical island streams, but that it functions through top-down control, a process not included in the current RCC (Greathouse 2006). Therefore an alternative theoretical framework is needed to accurately describe FFG variation in tropical streams.

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APPENDIX A: Benthic macroinvertebrate species found in the Mahaerua River. Samples were collected 17 October and 18 October 2006. BME= Biomass Equivalence.

SPECIES	FUNCTIONAL FEEDING GROUP	SITE MM1	SITE MM2	SITE MM3
MOLLUSCA				
Family Neritidae				
Neritina auriculata Lamarck	grazer	N (58) BME (4800)		
Septaria porcellana Linnaeus	grazer	N (1) BME (15)		
Clithon spinosa Budgin	grazer	N (7) BME (2370)		
Neritina canalis Lamarck	grazer	N (12) BME (780)	N (2) BME (2880)	N (1) BME (15)
Neritina turrita Gmelin	grazer	N (2) BME (6)	N (3) BME (750)	
Neritilia rubida Pease	grazer	N (10) BME (150)	N (47) BME (715)	N (68) BME (1020)
Family Thiaridae				
Thiara granifera Lamarck	grazer	N (36) BME (660)	N (1) BME (15)	N (1) BME (15)
Melanoides tuberculata Müller	grazer	N (2) BME (50)		
Family Planorbidae	grazer			
Family Limnaeidae				
Species A	grazer			
Species B	grazer			
CRUSTACEA				
Family Atyidae				
Atyoida pilipes Newport	1/3 grazer, 2/3 collector	N (484) BME (11000)	N (1) BME (150)	N (1) BME (50)
Caridina weberi De Man	1/3 grazer, 2/3 collector		N (1) BME (60)	
Family Palaemonidae				
Macrobrachium lar Fabricius	1/2 collector, 1/2 predator	N (3) BME (320)	N (1) BME (4000)	
Macrobrachium australe Guérin-Méneville	1/2 collector, 1/2 predator	N (5) BME (650)		
Macrobrachium latimanus von Martens	1/2 collector, 1/2 predator			
Famiy Grapsidae				
Geosesarma angustifrons larva Milne-Edwards	collector	N (4) BME (12)		
Geosesarma angustifrons Milne-Edwards	1/2 collector, 1/2 predator	N (20) BME (2500)		
Labuanium trapesoideum Milne-Edwards	1/2 collector, 1/2 predator			
Order Isopoda	shredder	N (1) BME (10)		
Order Copepoda	collector			
Order Ostracoda	grazer			
Family Talitridae	shredder		N (1) BME (15)	N (29) BME (435)
INSECTA				
Order Odonata				
Family Libellulidae	predator		N (1) BME (4)	N (2) BME (8)
Family Coenegrionidae	predator		N (4) BME (24)	N (11) BME (66)
Order Hemiptera				

SPECIES	FUNCTIONAL FEEDING GROUP	SITE MM1	SITE MM2	SITE MM3
Family Saldidae				
Saldula tahitiensis Cobben	predator			
Order Diptera				
Family Chironomidae				
Chironomini sp. A	collector	N (27) BME (27)	N (151) BME (151)	N (27) BME (27)
Chironomini sp. B	collector	N (32) BME (32)	N (5) BME (5)	N (14) BME (14)
Orthocladinae	collector	N (1) BME (1)		
Family Tabanidae	predator			
Family Ephydridae				
Apuvillus cheesemanae Edwards	grazer		N (2) BME (4)	N (1) BME (2)
Family Psychodidae	collector			
Family Stratiomyiidae	collector			
Family Dolichopodidae	predator			
Family Ceratapogonidae	collector			
Family Simuliidae				
Simulium dussertorum Craig	collector			
Simulium sp.	collector			
Simulium exasperans Craig	collector			
Simulium malardei Craig	collector			
Simulium lotii Craig	collector		N (6) BME (18)	N (48) BME (144)
Order Lepidoptera				
Family Pyralidae				
Species A	shredder	N (1) BME (2)		
Species B	shredder			
Order Collembola	collector	N(1) BME (2)		
NEMATODA	collector			
OLIGOCHAETA				
Species A	collector	N (118) BME (300)	N (14) BME (35)	N (12) BME (30)
Species B	collector			
Worm with many spines	collector		N (1) BME (4)	
ACARINA				
Species A	predator		N (1) BME (0.5)	N (3) BME (1.5)
Species B	predator			N (3) BME (1.5)
Species C	predator			
Species D	predator			N (1) BME (0.5)
DIPLOPODA				
Family Cambalopsidae				
Glyphiulus grnulatus Gervais	shredder		N (2) BME (40)	N (12) BME (240)
Family Paradoxosomatidae				
Oxidus gracilis Koch	shredder			N (1) BME (40)
TOTAL NUMBER OF TAXA		20	18	17

APPENDIX B: Benthic macroinvertebrate species found in the Vaihana River. Samples were collected 27 October 2006. BME= Biomass Equivalence.

SPECIES	FUNCTIONAL FEEDING GROUP	SITES PV1	PV2	PV3
MOLLUSCA				
Family Neritidae				
Neritina auriculata Lamarck	grazer			
Septaria porcellana Linnaeus	grazer	N (28) BME (14885)		
Clithon spinosa Budgin	grazer	N (17) BME (12280)		
Neritina canalis Lamarck	grazer	N (15) BME (5820)	N (1) BME (2000)	N (2) BME (2880)
Neritina turrita Gmelin	grazer			
Neritilia rubida Pease	grazer	N (51) BME (765)	N (15) BME (295)	N (17) BME (255)
Family Thiaridae				
Thiara granifera Lamarck	grazer	N (246) BME (5200)	N (19) BME (430)	N (11) BME (375)
Melanoides tuberculata Müller	grazer	N (1) BME (300)	N (12) BME (1130)	N (4) BME (460)
Family Planorbidae	grazer	N (1) BME (2)		
Family Limnaeidae				
Species A	grazer	N(1) BME (2)		
Species B	grazer			N (1) BME (3)
CRUSTACEA				
Family Atyidae				
Atyoida pilipes Newport	1/3 grazer, 2/3 collector	N (59) BME (1270)	N (11) BME (2720)	N (23) BME (6090)
Caridina weberi De Man	1/3 grazer, 2/3 collector			N (5) BME (620)
Family Palaemonidae				
Macrobrachium lar Fabricius	1/2 collector, 1/2 predator	N (1) BME (60)	N (3) BME (4300)	N (3) BME (2850)
Macrobrachium australe Guérin-Méneville	1/2 collector, 1/2 predator	N (13) BME (7250)	N (7) BME (6400)	
Macrobrachium latimanus von Martens	1/2 collector, 1/2 predator			
Famiy Grapsidae				
Geosesarma angustifrons larva Milne-Edwards	collector			
Geosesarma angustifrons Milne-Edwards	1/2 collector, 1/2 predator			
Labuanium trapesoideum Milne-Edwards	1/2 collector, 1/2 predator	N (1) BME (50)		
Order Isopoda	shredder			N (1) BME (10)
Order Copepoda	collector			
Order Ostracoda	grazer	N (1) BME (1)		
Family Talitridae	shredder			N (3) BME (45)
INSECTA				
Order Odonata				
Family Libellulidae	predator	N (1) BME (4)		
Family Coenegrionidae	predator	N (36) BME (216)	N (12) BME (72)	N (1) BME (6)
Order Hemiptera				

SPECIES	FUNCTIONAL FEEDING GROUP	SITE PV1	PV2	PV3
Family Saldidae				
Saldula tahitiensis Cobben	predator	N (2) BME (8)		
Order Diptera				
Family Chironomidae				
Chironomini sp. A	collector	N (236) BME (236)	N (58) BME (58)	N (13) BME (13)
Chironomini sp. B	collector	N (465) BME (465)	N (3) BME (3)	N (1) BME (1)
Orthocladinae	collector			
Family Tabanidae	predator	N (1) BME (1)		
Family Ephydridae				
Apuvillus cheesemanae Edwards	grazer	N (2) BME (4)		
Family Psychodidae	collector	N (2) BME (3)		
Family Stratiomyiidae	collector	N (1) BME (2)		
Family Dolichopodidae	predator	N (1) BME (1)		
Family Ceratapogonidae	collector			
Family Simuliidae				
Simulium dussertorum Craig	collector			N (1) BME (3)
Simulium sp.	collector			N (6) BME (18)
Simulium exasperans Craig	collector			N (827) BME (3305)
Simulium malardei Craig	collector			N (1) BME (3)
Simulium lotii Craig	collector		N (5) BME (15)	N (26) BME (78)
Order Lepidoptera				
Family Pyralidae				
Species A	shredder			
Species B	shredder			
Order Collembola	collector	N (3) BME (6)		
NEMATODA	collector			
OLIGOCHAETA				
Species A	collector	N (19) BME (47.5)	N (2) BME (5)	N (14) BME (35)
Species B	collector			N (1) BME (40)
Worm with many spines	collector			N (1) BME (4)
ACARINA				
Species A	predator	N (4) BME (2)	N (1) BME (0.5)	
Species B	predator	N (2) BME (1)		
Species C	predator	N (5) BME (2.5)		
Species D	predator	N (5) BME (2.5)		
DIPLOPODA				
Family Cambalopsidae				
Glyphiulus grnulatus Gervais	shredder		N (2) BME (40)	N (3) BME (60)
Family Paradoxosomatidae				
Oxidus gracilis Koch	shredder			N (1) BME (40)
TOTAL NUMBER OF TAXA		29	14	23

APPENDIX C: Benthic macroinvertebrate species found in the Vaipohe River. Samples were collected 2 November 2006. BME= Biomass Equivalence.

SPECIES	FUNCTIONAL FEEDING GROUP	SITES VV1	VV2	VV3
MOLLUSCA				
Family Neritidae				
Neritina auriculata Lamarck	grazer			
Septaria porcellana Linnaeus	grazer			
Clithon spinosa Budgin	grazer	N (4) BME (4480)		
Neritina canalis Lamarck	grazer	N (53) BME (37150)	N (8) BME (6020)	N (2) BME (1080)
Neritina turrita Gmelin	grazer	N (8) BME (22200)		
Neritilia rubida Pease	grazer	N (1003) BME (15045)	N (55) BME (825)	N (110) BME (1650)
Family Thiaridae				
Thiara granifera Lamarck	grazer	N (372) BME (7575)	N (13) BME (275)	N (4) BME (185)
Melanoides tuberculata Müller	grazer	N (1) BME (100)	N (3) BME (130)	N (6) BME (715)
Family Planorbidae	grazer			
Family Limnaeidae				
Species A	grazer			
Species B	grazer			
CRUSTACEA				
Family Atyidae				
Atyoida pilipes Newport	1/3 grazer, 2/3 collector	N (110) BME (3300)		
Caridina weberi De Man	1/3 grazer, 2/3 collector		N (2) BME (180)	N (30) BME (2400)
Family Palaemonidae				
Macrobrachium lar Fabricius	1/2 collector, 1/2 predator	N (3) BME (300)		N (1) BME (600)
Macrobrachium australe Guérin-Méneville	1/2 collector, 1/2 predator	N (4) BME (360)	N (7) BME (2430)	N (3) BME (460)
Macrobrachium latimanus von Martens	1/2 collector, 1/2 predator			
Famiy Grapsidae				
Geosesarma angustifrons larva Milne-Edwards	collector			
Geosesarma angustifrons Milne-Edwards	1/2 collector, 1/2 predator			
Labuanium trapesoideum Milne-Edwards	1/2 collector, 1/2 predator			
Order Isopoda	shredder			
Order Copepoda	collector			
Order Ostracoda	grazer			
Family Talitridae	shredder	N (1) BME (15)		
INSECTA				
Order Odonata				
Family Libellulidae	predator		N (1) BME (4)	
Family Coenegrionidae	predator		N (1) BME (6)	N (2) BME (12)
Order Hemiptera				

SPECIES	FUNCTIONAL FEEDING GROUP	SITE VV1	VV2	VV3
Family Saldidae				
Saldula tahitiensis Cobben	predator			
Order Diptera				
Family Chironomidae				
Chironomini sp. A	collector	N (7) BME (7)	N (35) BME (35)	N (51) BME (51)
Chironomini sp. B	collector	N (6) BME (6)	N (10) BME (10)	N (2) BME (2)
Orthocladinae	collector			
Family Tabanidae	predator			
Family Ephydridae				
Apuvillus cheesemanae Edwards	grazer			
Family Psychodidae	collector			
Family Stratiomyiidae	collector			
Family Dolichopodidae	predator			
Family Ceratapogonidae	collector			
Family Simuliidae				
Simulium dussertorum Craig	collector			
Simulium sp.	collector			
Simulium exasperans Craig	collector			
Simulium malardei Craig	collector			
Simulium lotii Craig	collector		N (1) BME (3)	
Order Lepidoptera				
Family Pyralidae				
Species A	shredder			
Species B	shredder			
Order Collembola	collector	N (3) BME (6)		
NEMATODA	collector		N (1) BME (1)	N (1) BME (1)
OLIGOCHAETA				
Species A	collector	N (18) BME (45)	N (14) BME (35)	N (11) BME (27.5)
Species B	collector			
Worm with many spines	collector	N (1) BME (4)		
ACARINA				
Species A	predator			N (1) BME (0.5)
Species B	predator			
Species C	predator			N (1) BME (0.5)
Species D	predator			
DIPLOPODA				
Family Cambalopsidae				
Glyphiulus grnulatus Gervais	shredder		N (2) BME (40)	
Family Paradoxosomatidae				
Oxidus gracilis Koch	shredder			N (2) BME (80)
TOTAL NUMBER OF TAXA		15	14	15

APPENDIX D: Benthic macroinvertebrate species found in the Vaioro River. Samples were collected 7 November and 11 November 2006. BME= Biomass Equivalence.

SPECIES	FUNCTIONAL FEEDING GROUP	SITES		
		AV1	AV2	AV3
MOLLUSCA				
Family Neritidae				
Neritina auriculata Lamarck	grazer	N (38) BME (3915)		
Septaria porcellana Linnaeus	grazer	N (1) BME (260)	N (1) BME (260)	
Clithon spinosa Budgin	grazer	N (22) BME (1665)		
Neritina canalis Lamarck	grazer	N (28) BME (10600)	N (3) BME (1280)	N (1) BME (880)
Neritina turrita Gmelin	grazer	N (11) BME (610)	N (7) BME (2760)	
Neritilia rubida Pease	grazer	N (7) BME (105)	N (80) BME (1200)	
Family Thiaridae				
Thiara granifera Lamarck	grazer	N (11) BME (165)	N (1) BME (35)	
Melanoides tuberculata Müller	grazer		N (2) BME (135)	
Family Planorbidae	grazer			
Family Limnaeidae				
Species A	grazer			
Species B	grazer		N (1) BME (3)	
CRUSTACEA				
Family Atyidae				
Atyoida pilipes Newport	1/3 grazer, 2/3 collector	N (63) BME (1860)	N (9) BME (1280)	N (5) BME (1040
Caridina weberi De Man	1/3 grazer, 2/3 collector	N (7) BME (180)	N (12) BME (1250)	N (6) BME (680)
Family Palaemonidae				
Macrobrachium lar Fabricius	1/2 collector, 1/2 predator		N (1) BME (1500)	
Macrobrachium australe Guérin-Méneville	1/2 collector, 1/2 predator	N (1) BME (120)		
Macrobrachium latimanus von Martens	1/2 collector, 1/2 predator		N (1) BME (6000)	
Famiy Grapsidae				
Geosesarma angustifrons larva Milne-Edwards	collector	N (1) BME (3)		
Geosesarma angustifrons Milne-Edwards	1/2 collector, 1/2 predator	N (30) BME (2270)		
Labuanium trapesoideum Milne-Edwards	1/2 collector, 1/2 predator	N (1) BME (50)		
Order Isopoda	shredder			
Order Copepoda	collector		N (1) BME (1)	
Order Ostracoda	grazer			
Family Talitridae	shredder	N (2) BME (30)		N (6) BME (90)
INSECTA				
Order Odonata				
Family Libellulidae	predator			
Family Coenegrionidae	predator			N (13) BME (78)
Order Hemiptera				

SPECIES	FUNCTIONAL FEEDING GROUP	SITE		
		AV1	AV2	AV3
Family Saldidae				
Saldula tahitiensis Cobben	predator			
Order Diptera				
Family Chironomidae				
Chironomini sp. A	collector	N (71) BME (71)	N (25) BME (25)	N (353) BME (353
Chironomini sp. B	collector		N (1) BME (1)	N (14) BME (14)
Orthocladinae	collector			
Family Tabanidae	predator			
Family Ephydridae				
Apuvillus cheesemanae Edwards	grazer		N (1) BME (2)	N (6) BME (12)
Family Psychodidae	collector			
Family Stratiomyiidae	collector			
Family Dolichopodidae	predator			
Family Ceratapogonidae	collector			N (1) BME (1)
Family Simuliidae				
Simulium dussertorum Craig	collector			
Simulium sp.	collector			
Simulium exasperans Craig	collector			
Simulium malardei Craig	collector			
Simulium lotii Craig	collector		N (1) BME (3)	N (30) BME (90)
Order Lepidoptera				
Family Pyralidae				
Species A	shredder			
Species B	shredder			N (1) BME (4)
Order Collembola	collector			
NEMATODA	collector			
OLIGOCHAETA				
Species A	collector	N (16) BME (40)	N (41) BME (102.5)	N (2) BME (5)
Species B	collector			
Worm with many spines	collector			
ACARINA				
Species A	predator		N (1) BME (0.5)	
Species B	predator			
Species C	predator			N (1) BME (0.5)
Species D	predator			
DIPLOPODA				
Family Cambalopsidae				
Glyphiulus grnulatus Gervais	shredder		N (1) BME (20)	N (9) BME (180)
Family Paradoxosomatidae				
Oxidus gracilis Koch	shredder			
TOTAL NUMBER OF TAXA		16	19	14

APPENDIX E: Benthic macroinvertebrate species found in the Vairemu River. Samples were collected 10 November and 14 November 2006. BME= Biomass Equivalence.

SPECIES	FUNCTIONAL FEEDING GROUP	SITES		
		HV1	HV2	HV3
MOLLUSCA				
Family Neritidae				
Neritina auriculata Lamarck	grazer	N (2) BME (860)		
Septaria porcellana Linnaeus	grazer		N (1) BME (120)	
Clithon spinosa Budgin	grazer	N (17) BME (2180)		
Neritina canalis Lamarck	grazer	N (38) BME (17560)	N (11) BME (5420)	N (3) BME (1620)
Neritina turrita Gmelin	grazer	N (10) BME (6225)	N (12) BME (2010)	N (2) BME (2700)
Neritilia rubida Pease	grazer	N (3) BME (45)	N (28) BME (420)	N (55) BME (825)
Family Thiaridae				
Thiara granifera Lamarck	grazer	N (22) BME (290)	N (1) BME (15)	N (2) BME (30)
Melanoides tuberculata Müller	grazer	N (1) BME (100)	N (2) BME (200)	N (5) BME (370)
Family Planorbidae	grazer			
Family Limnaeidae				
Species A	grazer			
Species B	grazer			
CRUSTACEA				
Family Atyidae				
Atyoida pilipes Newport	1/3 grazer, 2/3 collector	N (7) BME (210)	N (3) BME (290)	
Caridina weberi De Man	1/3 grazer, 2/3 collector		N (2) BME (170)	N (10) BME (980)
Family Palaemonidae				
Macrobrachium lar Fabricius	1/2 collector, 1/2 predator	N (1) BME (5000)		
Macrobrachium australe Guérin-Méneville	1/2 collector, 1/2 predator	N (5) BME (1400)		
Macrobrachium latimanus von Martens	1/2 collector, 1/2 predator			
Famiy Grapsidae				
Geosesarma angustifrons larva Milne-Edwards	collector			
Geosesarma angustifrons Milne-Edwards	1/2 collector, 1/2 predator			
Labuanium trapesoideum Milne-Edwards	1/2 collector, 1/2 predator			
Order Isopoda	shredder			N (1) BME (10)
Order Copepoda	collector			N (1) BME (1)
Order Ostracoda	grazer			
Family Talitridae	shredder			
INSECTA				
Order Odonata				
Family Libellulidae	predator			
Family Coenegrionidae	predator	N (5) BME (30)	N (23) BME (138)	N (5) BME (30)
Order Hemiptera				

SPECIES	FUNCTIONAL FEEDING GROUP	SITE		
		HV1	**HV2**	**HV3**
Family Saldidae				
Saldula tahitiensis Cobben	predator			
Order Diptera				
Family Chironomidae				
Chironomini sp. A	collector	N (62) BME (62)	N (140) BME (140)	N (6) BME (6)
Chironomini sp. B	collector	N (38) BME (38)	N (18) BME (18)	N (6) BME (6)
Orthocladinae	collector			
Family Tabanidae	predator			
Family Ephydridae				
Apuvillus cheesemanae Edwards	grazer		N (1) BME (2)	N (1) BME (2)
Family Psychodidae	collector			
Family Stratiomyiidae	collector			
Family Dolichopodidae	predator			
Family Ceratapogonidae	collector			
Family Simuliidae				
Simulium dussertorum Craig	collector			
Simulium sp.	collector			
Simulium exasperans Craig	collector			
Simulium malardei Craig	collector			
Simulium lotii Craig	collector	N (4) BME (12)	N (10) BME (30)	N (2) BME (6)
Order Lepidoptera				
Family Pyralidae				
Species A	shredder			
Species B	shredder			
Order Collembola	collector		N (1) BME (2)	
NEMATODA	collector			
OLIGOCHAETA				
Species A	collector	N (69) BME (172.5)	N (7) BME (17.5)	N (7) BME (17.5)
Species B	collector			
Worm with many spines	collector		N (1) BME (4)	N (5) BME (20)
ACARINA				
Species A	predator			
Species B	predator			
Species C	predator			
Species D	predator			
DIPLOPODA				
Family Cambalopsidae				
Glyphiulus grnulatus Gervais	shredder		N (1) BME (20)	N (1) BME (20)
Family Paradoxosomatidae				
Oxidus gracilis Koch	shredder		N (6) BME (240)	
TOTAL NUMBER OF TAXA		15	18	16