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Biogeography and Ecology of Santa Cruz Island Streams

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UNIVERSITY OF CALIFORNIA
Santa Barbara

Biogeography and Ecology of Santa Cruz Island Streams

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Ecology, Evolution, and Marine Biology

by

Laura Jane Furlong

Committee in charge:

Professor Adrian M. Wenner, Chairperson

Professor Scott D. Cooper

Professor Armand M. Kuris

June 1999

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This process has been an incredible source of growth for me as an individual and a scientist. The benefits have far outweighed the costs. I am grateful that I have had the opportunity to work on such an interesting project in such a wonderful environment. I am also thankful that I have had the chance to work with so many talented and interesting individuals.

I would like to express my appreciation to my mentor and friend, Adrian Wenner. From my first visit to Santa Cruz Island, I knew that Adrian was a truly unique individual. I will always value Adrian's special insights into the philosophy and process of science. I am grateful that Adrian conceived this project and then supported me through this process. His encouragement and help were invaluable.

I also thank my committee members, Scott Cooper and Armand Kuris, for contributing their insight and expertise to this process. I would like to give Scott Cooper a special word of thanks for taking the time to read and comment on my entire dissertation several times. My dissertation was improved in both quality and depth as a result of his comments.

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Studies of Entomology and Biogeography.
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ABSTRACT

Biogeography and Ecology of Santa Cruz Island Streams

by

Laura Jane Furlong

Records indicate that entomologists have collected insects from the California Channel Islands since the late 1800s. Despite over 100 years of entomological collection on the islands, several aquatic insect groups remain poorly described. This study represents the first intensive collection of California Channel Island aquatic insects. Samples taken from seven Santa Cruz Island streams from 1990 to 1997 yielded 41 taxa previously undescribed from the California Channel Islands and 47 new records for Santa Cruz Island. Compared to the nearby mainland, Santa Cruz Island streams support a depauperate fauna. Of the 161 total taxa (generic level) listed for Santa Cruz Island and the nearby mainland, only 97 occur on the island. The assemblage of taxa on Santa Cruz Island does not represent a random subset of the total. Aquatic flies (Diptera) and beetles (Coleoptera) are over-represented on the island, while caddisflies (Trichoptera) and stoneflies (Plecoptera) are under-represented. This disharmonic island assemblage may result from differences in the dispersal and colonization abilities of aquatic insect taxa. In addition, the depauperate nature of riparian vegetation on Santa Cruz Island might exclude aquatic groups relying heavily upon allochthonous stream input.

The aquatic insect assemblages of Santa Cruz Island vary among streams, habitats within streams, and seasons. Contrary to theoretical expectations, streams with larger catchments do not support greater numbers of total taxa or taxa within individual orders. The stream with the smallest catchment, Black Point, supports the greatest number of taxa. In contrast to streams with larger catchments, Black Point rarely experiences winter scour. Therefore, differences in disturbance regime may contribute to the observed variation in richness among island streams. A disturbance experiment did not support the hypothesis that disturbance frequency results in decreased taxonomic richness. However, this experiment did illustrate that the effects of experimental disturbance vary with substratum type and taxonomic group.

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DISSERTATION INTRODUCTION

The California Channel Islands consist of a diverse group of eight "fringing islands" (Carlquist 1974) located off the southern California coast (Figure i.1). Separated from the mainland by distances ranging from 20 to 98 km, the islands vary greatly in size (2.6 to 249 km^2), topography, vegetation, and land use history. The islands form two distinct groups, the Southern and Northern Channel Islands. The Southern Channel Islands (Santa Barbara, San Clemente, Santa Catalina and San Nicholas) are widely separated and have relatively independent origins and geological histories. In contrast, the Northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz, and Anacapa) are geographically close and geologically linked.

The California Channel Islands are emergent topographic units in a complex assortment of seafloor basins and ridges known as the California Continental Borderland (Vedder and Howell 1980). Due to past eustatic sea level fluctuations and crustal deformations, the degree of island emergence from the sea has varied. Over the last 500,000 years, high elevation portions of Santa Rosa, Santa Cruz and Santa Catalina Islands (and possibly San Miguel and San Clemente) were constantly above water (Figure i.2, Vedder and Howell 1980). During the last glacial maximum (approximately 18,000 years ago) low sea levels united the four Northern Channel Islands, forming a "super-island," Santarosae (Figure i.3, Vedder and Howell 1980). In spite of sea level fluctuations during the Pleistocene, no evidence of a land bridge linking the Northern Channel Islands to the southern California mainland exists (Vedder and Howell 1980, Wenner and Johnson 1980).

Naturalists have worked on the California Channel Islands since the late 1800's (Miller 1985). Early work primarily focused on plant and animal collections (Junak et al. 1995, Miller 1985), whereas recent endeavors range from biotic surveys and biogeographical studies to conservation and management efforts (Philbrick 1967, Power 1980, Hochberg 1993, Halvorson and Maender 1994). Past taxonomic surveys on the islands addressed many groups of organisms, providing information essential to thoughtful conservation planning (Table i.1); however, the largest and most diverse group of island fauna, the insects, has received little attention.

Records indicate that entomological collections for the islands began in the 1890s, and efforts to collect and catalogue California Channel Island insects continue (Miller 1985). With notable exceptions (Table i.2), most collections were cursory; as a result, the distributions of several insect groups remain poorly known. My primary goal was to add to existing entomological information by collecting and cataloguing aquatic taxa from the largest of the California Channel Islands, Santa Cruz. My work provides a foundation for future Santa Cruz Island studies of stream ecology and baseline information for watershed management plans. In addition, my study addresses biogeographical and ecological aspects of Santa Cruz Island stream insects.

The first chapter of my dissertation addresses a fundamental and important question: Which aquatic insect taxa inhabit Santa Cruz Island? To answer this question, I reviewed previous island records and examined existing collections at the Santa Barbara Museum of Natural History, Natural History Museum of Los Angeles County, and the Santa Cruz Island Field Station. I relied most heavily, however, on my collections taken over a span of seven years. Employing cumulative taxa per collection effort curves, I addressed the adequacy of my collection efforts.

The second chapter compares the taxonomic compositions of Santa Cruz Island streams with those of the nearby mainland. To obtain a mainland species list, I used previously published taxa lists, examined the collections housed at the Santa Barbara Museum of Natural History, and took supplemental samples from local coastal streams. This section considers the results of these comparisons in light of biogeographical expectations. I also compare the results of my study with observations from other islands.

The third and fourth chapters examine "within island" variation in taxonomic richness at various spatial and temporal scales. The third chapter describes variations in taxonomic richness between streams, between habitat types (pools and riffles), and between seasons. Viewing each stream as a habitat island, chapter four explores the hypothesis that large streams support greater taxonomic richness than small streams. In addition, I offer alternative explanations for between-stream differences in richness, the most important being disturbance regime.

Chapter five describes an experimental approach to one of the factors determining insect taxonomic richness in Santa Cruz Island streams. I conducted a disturbance experiment to determine the effect of different disturbance intervals on taxonomic richness. I hypothesized that different levels of disturbance between streams may contribute to observed differences in taxonomic richness. Streams or reaches with high taxonomic richness may support taxa that do **and** do not persist through disturbance events, such as scour associated with floods. In contrast, streams or reaches with low taxonomic richness may support **only** taxa persisting through such disturbance events. To test this hypothesis, I designed a disturbance experiment that varied disturbance frequency, comparing the effect(s) of this manipulation in a reach typically experiencing winter scour to a reach that does not. I used the information resulting from this experiment to explain the effects of disturbance regime on taxonomic richness-area relationships.

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Table I.1: Important taxonomic surveys of California Channel Island land organisms, excluding invertebrates.

Group	Island(s)*	References and Notes
Plants	SCL	Raven 1963
	SNI	Foreman 1967
	SCT	Thorne 1967
	SBI	Philbrick 1972
	SCI	Junak et al. 1995
Land Vertebrates	All	Wenner and Johnson 1980 (Fossil and Historical)
Herptofauna	All+	Savage 1967
	All	Wilcox 1980
Birds	All	Power 1972
	All	Diamond and Jones 1980
Mammals	All	van Bloeker 1967

*Island abbreviations:

All - All Califoria Channel Islands
SBI - Santa Barbara Island
SCI - Santa Cruz Island
SCL - San Clemente Island
SCT - Santa Catalina Island
SNI - San Nicolas Island
\+ Survey includes Pacific islands off Baja California

Table i.2: Taxonomic surveys of California Channel Island insects.

Taxon	Island*	References
Orthoptera	All	Rentz and Weissman 1982
	All	Weissman 1985
Homoptera		
Pseudococidae	All	Rust et al. 1985
Lepidoptera	All	Miller 1984
	All	Powell 1994
Microlepidoptera	All	Powell and Wagner 1993
Coleoptera	SBI	Miller and Miller 1985
Cicindelidae	All	Nagano 1985
Hymenoptera	SCI	Thorpe et al. 1994
Apoidea, Specidae	All	Rust et al. 1985
Apoidea	ANA	Rust 1985

* See Table I

ANA - Anacapa

Figure i.1. The location of the California Channel Islands. (from Valentine and Lipps 1967).

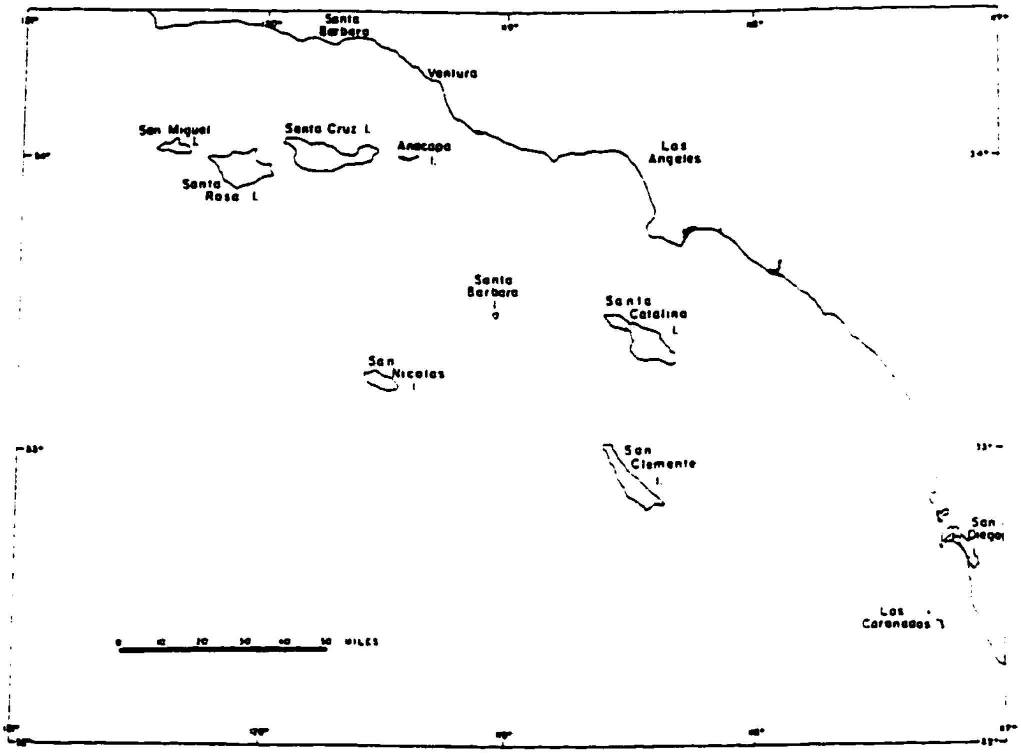

Santa Barbara
Ventura
San Miguel I.
Santa Cruz I.
Anacapa I.
Santa Rosa I.
Los Angeles
Santa Barbara I.
Santa Catalina I.
San Nicolas I.
San Clemente I.
San Diego
Los Coronados I.
34°
33°
0 10 20 30 40 50 MILES

Figure i.2. Estimated shorelines for Southern California and the California Channel Islands during a period of maximum sea levels (within the last 500,000 years; from Vedder and Howell 1980).

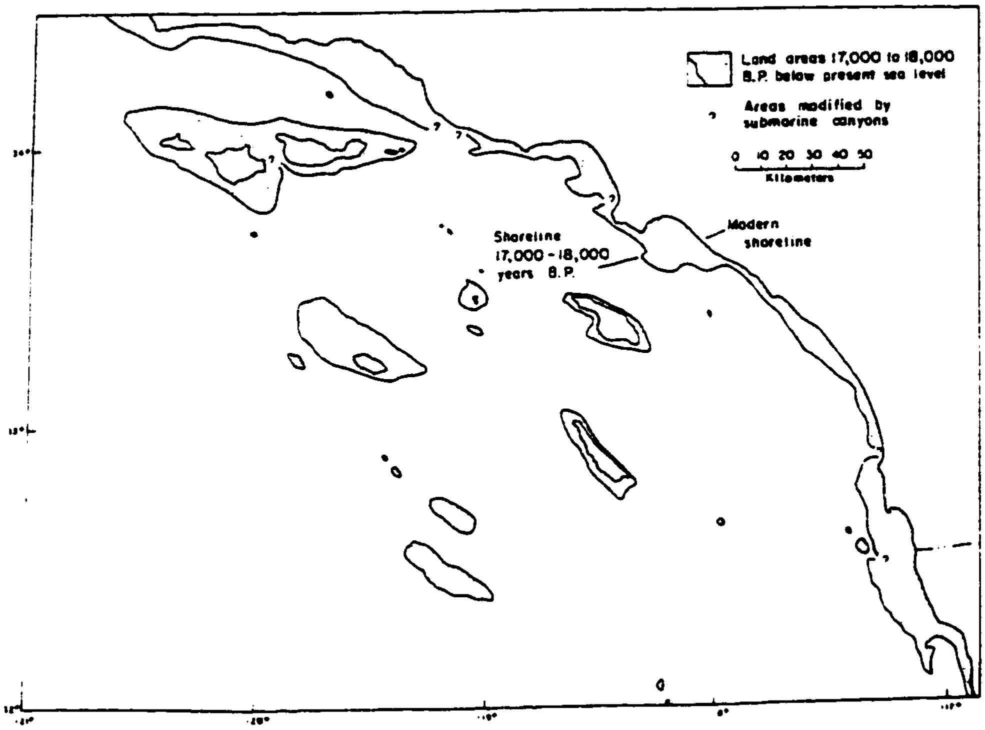
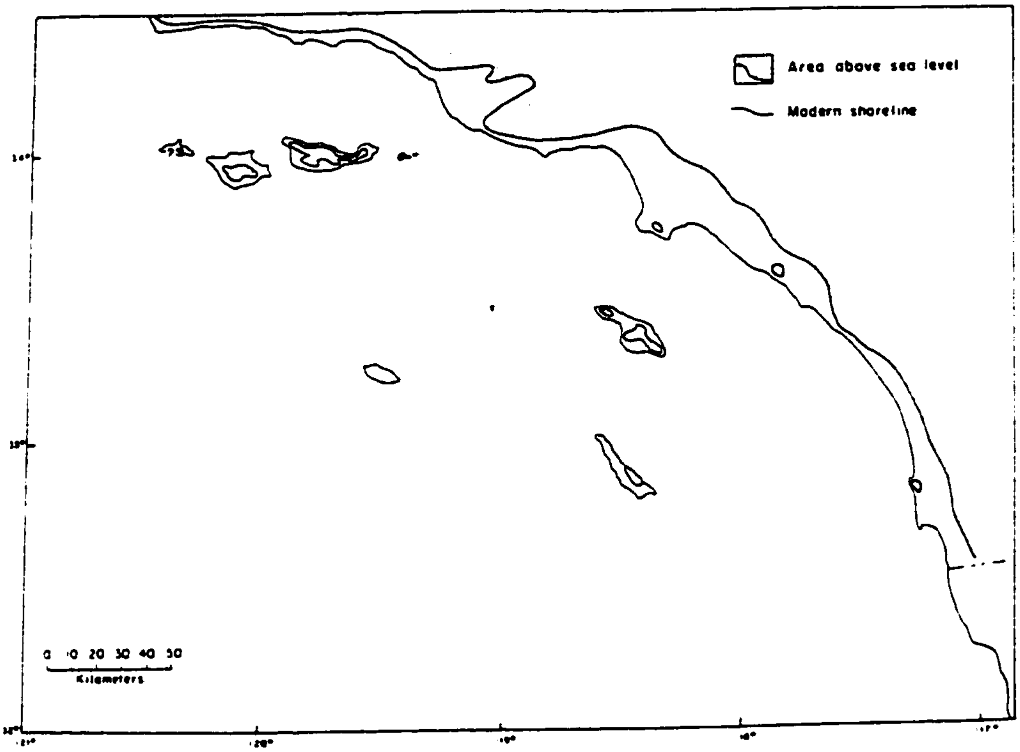

Land areas 17,000 to 18,000 B.P. below present sea level
Areas modified by submarine canyons
0 10 20 30 40 50
Kilometers
Modern shoreline
Shoreline 17,000 - 18,000 years B.P.
?

Figure i.3. Estimated shorelines of Southern California and the California Channel Islands during the glacial maximum approximately18,000 years ago (modified from Vedder and Howell 1980).


Area above sea level
Modern shoreline
0 10 20 30 40 50
Kilometers

CHAPTER I

INSECT SPECIES COMPOSITION OF SANTA CRUZ ISLAND STREAMS

INTRODUCTION

A basic knowledge of the system under consideration is an essential component to any ecological, evolutionary, or biogeographical study. Although largely descriptive, natural history studies which address the presence, absence, and distribution of species allow initial observations of patterns in ecological systems. These observations often lead to interesting questions and provide the foundation for subsequent experimental investigation(s). In addition, descriptive studies provide valuable distributional and taxonomic information for biotic components of the system. Foundational natural history studies can help ensure that subsequent ecological research does not become a "waste of time" (Allan 1984).

The need for descriptive taxonomic studies cannot be overlooked. In particular, taxonomic surveys provide essential baseline information used for comparison following management, conservation, and restoration efforts. This is especially true for undescribed systems and/or areas of great ecological concern, such as the Northern Channel Islands of southern California. These islands are managed by the National Park Service and the Nature Conservancy, with both agencies involved in island management, monitoring, and restoration projects. To document the degree of success and recovery rates in response to these restoration programs, baseline information must be available.

Although adequate taxonomic documentation exists for some island animal groups (Tables i.1 and i.2), other groups are poorly known. For instance, information for several insect groups (e.g., aquatic orders) is minimal or completely lacking (Miller and Menke 1981, Miller 1985a). With notable exceptions (Rentz and Weissman 1982, Miller and Miller 1985), most published accounts of California Channel Island insect groups do not include identification keys (Miller 1985a). Additional species lists, detailed distributional data, identification information, and voucher specimens are needed to support further research.

In particular, aquatic insect groups have received little attention on the California Channel Islands. This may be because most entomologists tend to focus on terrestrial taxa. Other contributing factors may include the narrow taxonomic focus of many entomologists, the short-lived nature of many aquatic adults, and the difficulty in identifying aquatic larval stages. Current National Park Service invertebrate biomonitoring programs for the Northern Channel Islands focus exclusively on terrestrial groups (Fellers and Drost 1991). On Santa Cruz Island, the Nature Conservancy has initiated terrestrial, but not aquatic, invertebrate monitoring in conjunction with restoration efforts. Monitoring programs for aquatic macroinvertebrates could be of great value in restoration projects, especially if combined with data regarding riparian restoration, stream health, or watershed recovery from grazing and/or exotic plant and animal removal.

This portion of my study provides baseline taxonomic information about aquatic insect groups on Santa Cruz Island and offers the first comprehensive list of aquatic taxa for one of the California Channel Islands. I will provide voucher specimens from my surveys to the Santa Cruz Island Reserve (University of California) and the Santa Barbara Museum of Natural History. The availability of voucher specimens should aid future aquatic research efforts and also enable other researchers to verify or correct identifications made from this collection.

STUDY AREA

Collections were taken from several locations on Santa Cruz Island (longitude 119° 55' 44" W to 119°31' 10" W, latitude 34°04' 39" N to 33° 57' 33" N), the largest and most topographically diverse of the California Channel Islands. Santa Cruz is the only California Channel Island with a central valley. This valley, oriented along the east-west axis of the island, formed as a result of movement along the Santa Cruz Island fault (Figure 1.1). The mountain ridges paralleling the north and south sides of the valley attain elevations of 753 m and 464 m, respectively.

Human occupation on Santa Cruz Island dates back to at least 5,000 years B.C. (Glasow 1980). European impacts on the island began over 140 years ago with the establishment of cattle and sheep ranching. Pigs were also introduced to Santa Cruz at this time. During the 1880's, cultivation of fruit trees, vegetables, and grapes was established (Junak et al. 1995). Cattle and sheep grazing was eliminated on much of the island in the late 1980's.

Santa Cruz Island is dominated by a Mediterranean climate and experiences cool wet winters and warm dry summers. Mean monthly temperatures taken from the Stanton Ranch (in the Central Valley, from 1961-1971) range from 20.9 °C in August to 11.7 °C in December (Junak et al. 1995). Mean monthly precipitation is highly variable, ranging from approximately 114 mm in February to 0.25 mm in July (Stanton Ranch, 1904-1993; Junak et al. 1995). This climatic regime is moderated on the island's coastal slopes by maritime influences, resulting in cool foggy summers and mild winters (Philbrick and Haller 1977, Hochberg 1980). In contrast, the central valley, isolated from moderating maritime influences by mountain ridges to the north and south, experiences higher summer temperatures (maximum 36°C) and lower winter temperatures (minimum -4°C, Stanton Ranch, 1961-1978; Junak et al. 1995).

Relative to the other California Channel Islands, Santa Cruz exhibits a high level of ecological diversity. This diversity results in part from the island's topographic and microclimatic complexity. The island supports a variety of vegetative communities and a number of endemic plants. Junak et al. (1995) described 16 plant communities and 37 California Channel Island endemics on Santa Cruz. Eight additional species are endemic to Santa Cruz Island alone. Generally, the Santa Cruz Island flora "appears harmonic and balanced" in comparison to the mainland (flora comparable to a similar area on nearby mainland); however, the island riparian woodland communities are noticeably less diverse than nearby comparable mainland communities (Junak et al. 1995).

The surface of Santa Cruz Island is covered by several watersheds of varying size. Considering only drainages with areas greater than ca. 1 km^2, thirty streams flow north into the Santa Barbara Channel, twenty flow south into the Pacific Ocean, thirteen flow west into the Santa Cruz Channel, and eight flow east into the Anacapa Channel. The largest watershed (ca. 35 km^2), flows from the Central Valley into Prisoners stream which then flows into the Santa Barbara Channel. Several streams flow year-round, fed by springs; however, most streams sustain flow only after storm events.

Discharge was calculated using stream cross-section and velocity measurements. The cross-sectional area was measured with a tape measure stretched across the stream (perpendicular to the stream bank). Ten depth measurements were taken at evenly spaced intervals along the tape (each interval equal to the stream width x 0.10). Velocity was measured (with either a Global Flow Probe or Marsh - McBirney Model 201D Portable Current Meter) concurrently with the depth measurements (ten per cross-section) at a depth 0.60 of the distance from the water surface to the stream bed. Baseflow discharge in permanent streams ranged from 0.1 to 8.8 liters/second. Following winter storms, discharge may exceed baseflow levels by a factor of 10 or more.

Water temperatures, measured over the course of this study (1992-1997) during collections and with minimum-maximum thermometers, ranged from 11 to 17 °C in the winter months (December 22 through March 20) and from 16 to 24.5 °C in the summer (June 20 through September 23). In unfiltered water samples taken during this study, orthophosphate levels in the streams ranged from 0.36 to 2.93 μmole/liter and nitrite+nitrate concentrations ranged from 0.28 to 48.36 μmoles/liter. Other water chemistry data were not available.

METHODS

To adequately characterize aquatic invertebrate communities in Santa Cruz Island streams, I collected from a variety of island streams during all seasons.

Collections were taken from the following streams: Black Point (5 sites), Coches Prietos (5 sites), Christy's (1 site), Horquetta (4 sites), Laguna (6 sites), North Diablo (1 site), Prisoners (6 sites), Sauces (4 sites), Water Canyon (2 sites), and Willows (3 sites; Figure 1.2, Tables I.1 and I.2).

In addition to collecting aquatic stages directly from island streams, adult insects were collected with a black light at the Santa Cruz Island field station. The black light station consisted of a black light hanging on an outside wall over a plain white ground cover. The light was turned on after sunset to attract adult insects. Throughout the evening, the ground cover and wall were examined for the presence of aquatic adult insects. These insects were then preserved in 70% ethanol or pinned and added to the reserve collection.

To account for temporal variation in insect availability I collected insects over a period of seven years (Table I.3). From 1990 to 1992 collections were sporadic, taken opportunistically from a variety of streams. Many of the streams and sites were not included in later years of the study. The collections taken from 1990 to 1992 were not standardized. These collections consisted of hand picking insects from streams and using nets of various mouth area (300 cm^2 to 650 cm^2) and mesh sizes (0.3 mm to 1 mm) to collect benthic, water column, and surface insects.

From 1993 through 1994, the sample sites, timing, and methods of collection were standardized. Two to three sites were chosen at each of seven streams (Black Point, 3 sites; Coches, 3 sites; Horquetta, two sites; Laguna, 3 sites; Prisoners, 2 sites; Sauces, 3 sites; Willows, 2 sites; Figure 1.2, Tables I.1 and I.3). To account for longitudinal variation, the sites encompassed a variety of elevations on each stream. To account for seasonal variation in insect presence and abundance, sampling visits to the island (consisting of 3 to 4 days each) were conducted monthly. This sampling strategy insured that each site was visited, at the least, every other month.

Because the primary goal of this study was to collect as many taxa as possible, I took semi-quantitative samples. As suggested by Elliot (1979), I used standardized kick samples over a given area (1 meter) for a given amount of time (30 seconds) to obtain samples of benthic taxa. In addition, I employed standardized net sweeps (5 sweeps of 1 meter each) to collect surface and water column taxa. I used a 300 micron mesh dip net with mouth dimensions of 15 cm by 20 cm to collect kick and sweep samples. A sweep and kick sample were each taken from a pool and a riffle at each site. Each sample was preserved in the field with 70% ethanol.

From 1995 through 1998, additional samples were taken from the seven streams to compensate for sampling inequities and to include additional sites (Figure 1.2, Tables I.2 and I.3). I collected these samples using the standardized methods described above. In all, more than 1000 samples were taken over 75 collection days (over 800 samples were processed).

Aquatic specimens were processed by sieving samples through 1 mm and 500 micron mesh sieves. I sorted insects retained on these sieves by eye and identified them with a dissecting microscope (8.4 to 36x power). I processed the material passing through the 500 micron mesh under a dissecting microscope (8.4 to 36x power). Because of the great volume of samples, the 300-500 micron fraction was given low processing and identification priority. The primary identification keys used were Merritt and Cummins (1984) and Usinger (1971). In addition, I employed various taxon-specific keys (Table I.4).

To estimate the adequacy of my sampling efforts, I constructed a curve of cumulative taxa per cumulative sampling effort (indicated as visits; number of samples taken varied per visit). Previous studies illustrate that the cumulative number of taxa collected increases with the number of samples taken (Hellawell 1986); however, as sampling effort increases, fewer new taxa are added. If my sampling efforts were adequate, I would expect that the cumulative number of taxa collected would rise rapidly then level off with very few species added as sampling effort increased (Hellawell 1986, Allan 1995). In constructing this curve I used only taxa taken from Santa Cruz Island stream habitats, excluding Chironomidae and non-aquatic stages (flying adults).

I examined material from other collections to supplement my data . Many of the specimens in these collections, housed at the Santa Cruz Island Reserve Field Station, Santa Barbara Museum of Natural History, and Natural History Museum of Los Angeles County, were unidentified. I assumed that the unidentified insects were not included on any previously published lists. I also compared my taxa list with previously published occurrences (Miller and Menke 1981, Miller 1985b, Miller 1993) and an unpublished list provided by Scott Miller of the Bishop Museum, Hawaii. Richard Bauman (personal communication) provided information regarding collections of the stonefly *Mesocapnia projecta* (Family: Capniidae) from Santa Cruz Island.

RESULTS

My surveys yielded many taxa previously undescribed for Santa Cruz Island (Figure 1.3, Table I.5). Prior to this investigation, 71 aquatic insect taxa were recorded from Santa Cruz. In all, 82 aquatic taxa were collected from Santa Cruz Island streams (excluding Chironomidae) during this study. In addition, 3 taxa were identified from terrestrial collections and previously unidentified museum/reserve specimens. Of these 85 taxa, 47 were new records for Santa Cruz Island (based on literature records, museum collections, and the unpublished Miller list). Forty-one of these taxa were unrecorded from any of the California Channel Islands.

In addition, I tentatively identified 16 Chironomidae genera from Santa Cruz Island. Previous records indicate only one species from the island, *Paraclunio alaskensis* (Miller, unpublished list), an intertidal species not collected during this survey. Due to the difficulty of identifying chironomid larvae to genus, I have not processed enough specimens to give a comprehensive account of their taxonomic richness on the island. Therefore, these organisms were not included in the taxa vs. effort curve. I expect that several chironomid genera will be added to this list as sample processing continues. This sampling effort also yielded several non-insect macroinvertebrates (Table I.5).

This collection, combined with unpublished accounts (unidentified museum specimens and Bauman stonefly records), adds one insect order (Plecoptera), four caddisfly families (Philopotomidae, Hydroptilidae, Lepidostomatidae, Sericostomatidae), five aquatic beetle families (Gyrinidae, Haliplidae, Hydroscaphidae, Scirtidae, Elmidae), and five aquatic dipteran families (Psychodidae, Simulidae, Dixidae, Empididae, Sciomyzidae) to the list of Santa Cruz Island aquatic insects. Several of these also represent new records for the California Channel Islands.

As sampling progressed, the number of new taxa collected increased at a decreasing rate (Figure 1.4). Of the 82 taxa taken from the streams (excluding Chironomidae and terrestrial stages), 37% were collected during the first visit (July 1990). Before initiating a standardized sampling procedure in 1993, I had collected 70% of the taxa. By the start of the 1994 sampling year (11th visit), 98% of the taxa had been collected. During the last eight months of standard collecting (from the spring of 1994 to 1995), no new taxa were found.

My efforts did not find 48 taxa previously collected and identified from Santa Cruz Island (Tables I.6 and I.7). Most of these taxa (28) were identified to a greater level of taxonomic resolution than I employed (Table I.6). In addition, I did not collect eleven genera and one family reported in previous collections (Table I.7). Likewise, I did not find several species recorded for Santa Cruz Island, even though I collected their congeners.

DISCUSSION

This collection effort yielded a considerable amount of new information about the Santa Cruz Island stream fauna. In all, this study contributes 47 new taxa records (including one order and 14 families) for Santa Cruz Island, adding to the general entomological knowledge of the California Channel Islands. This chapter presents not only results from my collections, but also a compilation of scattered reports of aquatic taxa from Santa Cruz Island (Table I.5). These results provide foundational data for the following chapters as well as future island research

From the cumulative number of taxa vs. sample visits curve, it appears that this collection effort provided a good estimate of taxonomic richness for aquatic insects from the targeted Santa Cruz Island streams. Several studies of stream taxonomic richness illustrate similar trends (Hellawell 1986, Allan 1995), namely, that as sample efforts increase, new taxa are added at a decelerating rate (Figure 1.4). Because the taxa vs. effort curve for Santa Cruz Island streams plateaus, and only two taxa were added in the final year of standardized collection (1994), I feel confident that the majority of insects inhabiting the sampled streams have been identified.

The taxa per effort curve shows stepped increases rather than the expected smooth and gradual increase in the number of taxa, this is probably due to changes in sampling effort prior to 1993. At the beginning of this work, my sampling efforts were sporadic and methods inconsistent. I used standardized methods at set sample sites after January, 1993 (visit 6, Figure 1.4). Following this change, the curve shows an abrupt rise and a more characteristic shape.

Nineteen taxa (not including those identified to a greater level of taxonomic resolution) previously collected from the island did not appear in my collections

(Table I.7), but the specimens found in this study did include congeners of seven of these "missing" taxa (Table I.5). Although some of these congeners may have been misidentified in earlier studies, two (*Anax junius* and *Notonecta kirbyi*) were presumably identified correctly. Santa Cruz Island collections at the University of California Reserve Station and/or in museums included these two species. By checking identifications of my congeners (*Anax walsinghami* and *Notonecta hoffmanni*) against museum specimens, these congeners also appeared to have been correctly identified. I did not find the other five "missing" congeners from Santa Cruz Island (*Notonecta unifasciata*, *Hydraena arenicola*, *H. circulata*, *Cymbiodyta punctatostriata*, and *Tropisternus californicus*) in any other collections. A check of the species, *Cymbiodyta dorsalis* and *Tropisternus ellipticus*, from my collections, against museum specimens revealed that these beetles had been correctly identified.

Of the remaining "missing" taxa, three (*Tramea* sp., *Protochauliodes* sp. and *Hydrophilus triangularis*) were found in the University of California Reserve collection. These specimens lacked identification labels, indicating why earlier island lists omitted them. The hemipteran, *Corisella decolor*, did not appear in my collections but does appear in museum collections from Santa Cruz Island. It is unlikely that this lentic hemipteran would be taken in lotic samples.

Seven taxa not represented in my collections were dipterans. The midge, *Paraclunio alaskensis*, inhabits saline environments (Merritt and Cummins 1984);

therefore, it would not have occurred in streams. *Sargus viridis*, a soldier fly species and the mosquitoes, *Anopheles franciscanus* and *Culiseta* spp., typically inhabit lentic habitats (Merritt and Cummins 1985) and not the lotic habitats sampled in this project. The other missing dipteran taxa are two cranefly species. I did not collect these species, although their larvae occur in lotic habitats.

In addition to the above 19 taxa not collected in my study, 28 other species were identified by others to greater levels of taxonomic resolution than used in my study (Table I.6). Most of those 28 taxa were probably identified from adult specimens. By contrast, my samples focused on larval stages, where identification below family (Ceratopogonidae, Dolichopodidae, Ephydridae) or genus level is often difficult. Also several of these organisms may not typically inhabit the freshwater lotic environments studied in this project. For example, *Ephydra millbrae* is found in saline environments, and the typical habitats for *Scatella*, *Aedes*, *Culex*, and *Culiseta* are lentic (Merritt and Cummins 1984).

CONCLUSION

This portion of the study accomplished several goals. It increased the amount of entomological data for the California Channel Islands and substantially added to records of aquatic taxa. Although my efforts provided baseline information, I expect that this taxa list can be increased by the following measures:

1. identification of more chironomid larvae.
2. increased taxonomic resolution via collection of adult stages and/or rearing immatures to adult stages.
3. expanding collection efforts to include additional streams as well as standing water environments.

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Table I.1. Characteristics of primary collection sites (used in standardized sampling after 1993).[a]

	Stream Description:					Collection Site Description:						
Stream	Total Catchment (km^{2})	Baseflow^{b} (liters/s)	Stormflow^{b} (liters/s)	Phosphate (um/liter)^{b}	Nitrate+Nitrite (um/liter)^{b}	Elevation (m)	Catchment Area (km^{2})	Slope^{c}	Mean Width (m)	Mean Depth (m)	Substrata^{d}	Canopy^{e}
Black Point	1.09	0.24	n/a	0.77	6.91							
						61	0.64	13%	0.89	0.05	Gravel/Macrophytes	PC
						107	0.36	21%	0.28	0.02	Sand/Macrophytes	PC
						212	0.21	21%	<0.30^{f}	<0.03^{f}	Bedrock/Bedrock	O
Horquetta	1.83	1.37	n/a	n/a	n/a							
						38	1.07	4%	0.75	0.01	Bedrock/Sand	C
						61	0.76	6%	0.69	0.02	Bedrock/Gravel	PC
Coches Prietos	5.04	2.33	n/a	0.36	1.52							
						22	4.57	5%	<0.40^{f}	<0.03^{f}	Sand/Gravel	C
						34	3.64	6%	1.52	0.09	Sand/Roots	C
						65	2.71	10%	1.23	0.05	Sand/Roots	PC
Sauces	5.86	n/a	n/a	0.58	8.30							
						8	5.64	3%	<0.75^{f}	<0.03^{f}	Rock/Sand	O
						31	5.43	5%	<0.60^{f}	<0.05^{f}	Sand/sand	O
						52	4.36	3%	<0.40^{f}	<0.05^{f}	Sand/Gravel	O
Willows	6.32	9.44	32.08	0.36	48.36							
						75	5.50	6%	1.19	0.05	Rock/Gravel	PC
						100	2.78	6%	1.29	0.02	Roots/Roots	C

Table 1.1. Continued.

Stream	Stream Description: Total Catchment (km^2)	Baseflow[b] (liters/s)	Stormflow[b] (liters/s)	Phosphate (um/liter)[b]	Nitrate+Nitrite (um/liter)[b]	Collection Site Description: Elevation (m)	Catchment Area (km^2)	Slope[c]	Mean Width (m)	Mean Depth (m)	Substrata[d]	Canopy[e]
Laguna	12.16	0.59	n/a	1.22	0.28							
						68	2.28	5%	<0.30[f]	<0.03[f]	Sand/Gravel	PC
						98	1.14	6%	0.95	0.07	Sand/Sand	O
						123	0.78	7%	0.33	0.02	Sand/Gravel	PC
Prisoners	34.66			1.76	6.48							
		5.26	52.11			66	25.06	2%	1.78	0.02	Sand/Gravel	PC
		0.64	12.72			314	2.77	5%	0.23	0.01	Sand/Bedrock	O

[a] These sites represent the primary collection sites in each stream. Additional collection sites are described in Table 1.2.

[b] Not available for all streams

[c] Calculated from topographic maps using elevation increase from 0.25 km below to 0.25 km above collection site.

[d] Pool substrate/Riffle substrate

[d] C = closed; PC = partially closed; O = Open

[f] Estimated

Table I.2. Locations of secondary collection sites. These sites were either used prior to standardization of collection sites and methods (1990-1992) or, employed standardized sampling methods but sites were not consistently sampled (1993-1997).

	Site Description:			Collection Dates:	
Stream	Elevation (m)	Substrata	Canopy Cover	1990-1992	1993-1997
Black Point	138	Bedrock	Open	x	
	161	Bedrock,Sand	Open	x	
Christy's	92	Gravel	Partially Closed	x	
Coches Prietos	100	Gravel	Closed	x	
	131	Bedrock,Sand	Closed	x	
Horquetta	105	Gravel	Closed		x
	111	Gravel	Closed		x
Laguna	8	Sand,Gravel	Open		x
	89	Bedrock	Open	x	x
(Sierra Blanca drainage)	108	Gravel, Bedrock	Partially Closed	x	
North Diablo	215	Bedrock	Partially Closed	x	
Prisoners	8	Sand,Gravel	Open	x	x
	100	Sand,Gravel	Open	x	
	223	Gravel	Partially Closed	x	x
(Puertosuello drainage)	246	Gravel	Partially Closed	x	
Sauces	69	Sand,Gravel	Partially Closed	x	x
Water Canyon	69	Bedrock	Closed	x	
	80	Bedrock	Partially Closed	x	
Willows	15	Sand,Gravel	open	x	x

Table I.3. Time line of sampling effort by stream. All visits after 1992 (except experiments) utilized standardized sample collection methods.

Sampling Visits * Year	19 90				19 91				19 92				19 93				19 94				19 95				19 96				19 97			
Season**	W	Sp	Sm	F	W	Sp	Sm	F	W	Sp	Sm	F	W	Sp	Sm	F	W	Sp	Sm	F	W	Sp	Sm	F	W	Sp	Sm	F	W	Sp	Sm	F
Stream:																																
Black Point						x				x			x	xx	x	xx	xxx	xxx	xxx	xx												
Christy's						x																										
Coches Prietos			x			x				x	x		x	x	x	xx	xx	xxx	xxx	x	x				x							
Horquetta											x				xx	x	x	xx	xx	x			x		x							
Laguna						x		x			xx		x	x	xx	xx	xx	xxx	x	x					x							
North Diablo						x																										
Prisoners			x	x	x	xx					x		x	xx	x	xx	xx	xx	xxx	xx	x			E	x		x		E	E		
Sauces								x		x				xx	xx	xx	xx	xxx	xxx	x												
Water Canyon								x					x	x																		
Willows										x				x	xx	xx	xx	xxx	xx	x	x				x							

* x = sampling visit
E = experiment

** W = Winter Sm = Summer
Sp = Spring F = Fall

Table I.4. Identification keys used for specific taxonomic groups of aquatic macroinvertebrates.

Taxon	Key:
Ephemeroptera	Edmunds et al. 1976
Baetis	Morihara and McCafferty 1979
Odonata	Walker 1953, Walker 1958
Anisoptera	Needham and Westfall 1954
Zygoptera	
Enallagma	Garrison 1984
Plecoptera	Jewett 1960
Hemiptera	Menke 1979
Megaloptera	Chandler 1954
Trichoptera	Wiggins 1977
Non-insect macroinvertebrates	Pennak 1978 Thorp and Covich 1991

Table I.5. Results of this survey of Santa Cruz Island stream taxa compared with literature records and museum/reserve collections.

Taxa:	Furlong Collection[a]	Literature References[b]	Other Collections[b]: NHMLAC	SBNHM	SCIR
Ephemeroptera					
Baetidae					
Baetis bicaudatus	●				
B. tricaudatus	●				
Callibaetis	○	Cru			
C. pictus	●				
Centroptilum	●				
Caenis					
Caenis	○				
Leptophlebiidae					
Paraleptophlebia associata	○	Cru			
Odonata					
(Anisoptera)					
Aeshnidae					
Aeshna walkeri	○	Cru			Cru
Anax junius		Cru, Ana, Mig	Cru,Ana	Mig	
A. walsinghami	●				

Table I.5. Continued

	Furlong	Literature	Other Collections[b]:		
Taxa:	Collection[a]	References[b]	NHMLAC	SBNHM	SCIR
Libellulidae					
Libellula saturata	○	Cru	Cat	Cru	Cru
Paltohemis lineatipes	●		(Cru)		(Cru)
Pantala flavescens	●				(Cru)
Sympetrum corruptum	●	Ana, Bar, Cat	Ana,Cat	Ana,Bar	
Tramea					(Cru)
(Zygoptera)					
Lestidae					
Archilestes		Cru			
A. californica	○				Cru
Coenagrionidae					
Argia sedula	●				
A. vivida	○	Cru, Cat, Ros		Cru,Ros	
Enallagma carunculatum	○	Cru			Cru
E. cyathigerum	○	Cru, Ros		Ros	
Plecoptera					
Capniidae					
Mesocapnia projecta	●	Baumann, Personal Communication			

Table I.5. Continued

	Furlong	Literature	Other Collections[b]:		
Taxa:	Collection[a]	References[b]	NHMLAC	SBNHM	SCIR
Hemiptera					
Saldidae					
Saldula pexa	○	Cru, Cat			
Veliidae					
Microvelia beameri	○	Cru, Cat, Ros	Cru		
Gerridae					
Aquarius remigis	○	Cru,Cat, Cle, Ros	Cru,Cat,Ros	Cru,Cat,Ros	
Corixidae					
Corisella decolor		Cru	Cru	Cru,Ros	
Graptocorixa uhleri	○	Cru	Cru,Ros	Cru	
Notonectidae					
Notonecta hoffmanni	●				
N. kirbyi		Cru	Cat		
N. unifasciata		Cru, Cat	Cat		
Megaloptera					
Corydalidae					
Neohermes filicornis	○	Cru, Cat	Cru,Cat		
Protochauliodes					(Cru)

Table I.5. Continued

Taxa:	Furlong Collection[a]	Literature References[b]	Other Collections[b]: NHMLAC	SBNHM	SCIR
Trichoptera					
Philopotamidae					
Wormaldia	●				
Psychomyiidae					
Tinodes	○				
T. schusteri		Cru			
Polycentropodidae					
Polycentropus	○				
P. halidus		Cru			
P. variegatus		Cru			
Hydropsychidae					
Hydropsyche	○				
H. californica		Cru			
H. philo	○	Cru,Cat			
Hydroptilidae					
Hydroptila	●				
Ochrotrichia	●				
Lepidostomatidae					
Lepidostoma	●				
Sericostomatidae					
Gumaga	●				

Table I.5. Continued

	Furlong	Literature	Other Collections[b]:		
Taxa:	Collection[a]	References[b]	NHMLAC	SBNHM	SCIR
Lepidoptera					
Pyralidae					
Pterophila sp.	●				
Synclita ?	●				
Coleoptera					
Gyrinidae					
Gyrinus plicifer	●		(Cat)		(Cru)
Haliplidae					
Peltodytes simplex	●		(Cat)		
Dytiscidae					
Agabinus glabrellus	●	Other			
A. sculpturellus	●				
Agabus discors	●				
A. seriatus intersectus	○	Cru		Cru	
Deronectes striatellus	○	Cru, Ros	Cat	Ros	
Hydroporus vilis	●	Cat, Ros			
Hydrovantus brevipes	●				
Rhantus gutticollis	●	Cat,Cle,Nic,Ros		Cat,Cle,Ros	

Table I.5. Continued

	Furlong	Literature	Other Collections[b]:		
Taxa:	Collection[a]	References[b]	NHMLAC	SBNHM	SCIR
Hydroscaphidae					
Hydroscapha natans	●				
Hydrophilidae					
Anacaena signaticollis	●				
Berosus punctatissimus	●	Ros	(Cat)	Ros	
Cymbiodyta dorsalis	○	Cru,Cat,Mig, Nic,Ros			
C. punctatostriata		Cru			
Enochrus pectoralis	○	Cru			
Helochares normatus	●				
Hydrobius fuscipes	●				
Hydrochara lineata	○	Cru,Ros	Cru	Cru	
Hydrophilus triangularis					(Cru)
Laccobius californicus	○	Cru			
L. ellipticus	○	Cru,Cat,Ros			
Tropisternus californicus		Cru,Cat		Cru	
T. ellipticus	○	Cru,Cat,Nic,Ros	Cru,Cat,Ros	Cru,Ros	
Hydraenidae					
Hydraena arenicola		Cru			
H. circulata		Cru			

Table I.5. Continued

Taxa:	Furlong Collection[a]	Literature References[b]	Other Collections[b]: NHMLAC	SBNHM	SCIR
H. vandykei	○	Cru			
Ochthebius interruptus	●				
O. puncticollis	○	Cru			
Scirtidae	●				
Elmidae					
Ordobrevia nubifera	●				
Diptera					
Tipulidae					
Dicranota	●				
Erioptera pallipes		Cru,Ros		Ros	
Hexatoma	●				
Holorusia hespera	○	Cru,Ros			
Limonia	○				
L. defuncta defuncta		Cru			
Rhabdomastix		Cru			
Tipula	○				
T. hastingsae diperona		Cru			
T. inusitata		Cru			
T. santaecruzae		Cru			

Table I.5. Continued

Taxa:	Furlong Collection[a]	Literature References[b]	Other Collections[b]: NHMLAC	SBNHM	SCIR
T. capistrano		Cru			
T. lygropis		Cru			
T. praecisa		Cru,Ros			
T. vestigipennis	○	Cru,Ana,Mig,Ros			
Culicidae					
Aedes	○				
A. sierrensis		Cru,Cat			
Anopheles franciscanus		Cru,Cat			
Culex apicalis	○	Cru,Cat			
C. erythrothorax		Cru			
C. peus		Cru,Cat			
C. tarsalis		Cru,Cat,Nic			
C. thriambus		Cru			
Culiseta incidens		Cru,Cat,Cle,Ros			
C. inornata		Cru,Ana,Cat,Cle, Nic,Ros			
Psychodidae					
Maruina	●				
Ceratopogonidea	○				
Culicoides baueri		Cru			

Table I.5. Continued

Taxa:	Furlong Collection[a]	Literature References[b]	Other Collections[b]: NHMLAC	SBNHM	SCIR
C. cacticola		Cru,Ana,Cat,Cle			
C.copiosus		Cru,Cat			
C. sitiens		Cru,Cat			
Palpomyia linsleyi		Cru			
Simulidae		Ana			
Simulium aureum	●				
S. latipes	●				
S. piperi	●				
S. virgatum	●				
Chironomidae					
(Tanypodinae)					
Ablabesmyia	●				
Labrundinia	●				
Pentaneura	●				
Procladius	●				
Zaverlimyia	●				
(Orthocladiinae)					
Cardiocladius	●				
Corynoneura	●				
Cricotopus	●				

Table I.5. Continued

	Furlong	Literature	Other Collections[b]:		
Taxa:	Collection[a]	References[b]	NHMLAC	SBNHM	SCIR
Eukiefferiella	●				
Microspecta	●				
Orthocladuis	●				
Paraclunio alaskensis		Cru,Cle,Mig,Nic			
Thienemanniella	●				
(Chironminae)					
Chironomus	●				
Kiefferulius	●				
Rheotanytarsus	●				
Tanytarsus	●				
Dixidae					
Dixa (Dixa)	●				
D. (Meringodixa)	●				
D. (Paradixa)	●				
Stratiomyidae					
Euparyphus	○				
E. proxipalus proxipalus		Cru			
Odontomyia	○	Cru			
Sargus virdis		Cru,Cat			

Table I.5. Continued

Taxa:	Furlong Collection[a]	Literature References[b]	Other Collections[b]: NHMLAC	SBNHM	SCIR
Tabanidae					
Chrysops	●				
Tabanus	○				
T. punctifer		Cru,Cat,Ros		Ros	
Dolichopodidae	○				
Dolichopus talus		Cru			
Empididae	●				
Ephydridae	○				
Ephydra millbrae		Cru			
Scatella triseta		Cru			
Sciomyzidae	●				
Muscidae					
Limnophora	○				
L. discreta		Cru			
Non-insect taxa:					
Ph. Platyhelminthes, *Dugesia*	■				
Ph. Nematomorpha	■				
Ph. Mollusca					
Cl. Gastropoda, *Physa*, *Valvata?*	■				
Cl. Bivalvia, *Sphaerium?*	■				

Table I.5. Continued

Taxa:	Furlong Collection[a]	Literature References[b]	Other Collections[b]: NHMLAC	SBNHM	SCIR
Ph. Arthropoda					
Cl. Arachnida (mites)	■				
Cl. Ostracoda	■				
Cl. Copepoda	■				
Cl. Malacostraca, *Hyallela azteca*	■				

[a] ● =New record for Santa Cruz Island
○ =Previously records exist for Santa Cruz Island
■ = May be a new record for Santa Cruz Island

[b] Ana =Anacapa Island
Bar = Santa Barbara Island
Cat = Santa Catalina Island
Cle = San Clemente Island
Cru = Santa Cruz Island
Mig = San Miguel Island
Nic = San Nicholas Island
Ros = Santa Rosa Island
( ) = Indicates a new record from unidentified specimen in collection
NHMLAC =Specimen from Natural History Museum of Los Angeles County collection
SBNHM =Specimen from Santa Barbara Natural History Museum collection
SCIR =Specimen from Santa Cruz Island Reserve collection

Table I.6. Santa Cruz Island aquatic insect taxa identified to greater taxonomic resolution in previous studies compared to this study.

Taxa:	Comments:	Habitat*:
Trichoptera		
Hydropyschidae		
Hydropsyche californica	This study primarily identified to genus.	Lotic
Polycentropidae		
Polycentropus halidus	This study identified to genus only.	Lotic
P. variegatus		
Psychomyiidae		
Tinodes schusteri	This study identified to genus only.	Lotic
Diptera		
Ceratopogonidae	This study identified to genus only.	
Culicoides baueri		Lentic and lotic margins
C. cacticola		
C. copiosus		
C. sitiens		
Palpomyia linsleyi		Lotic
Culicidae		
Aedes sierrensis	This study identified to genus only.	Lentic
Culex erythrothorax	This study primarily identified to genus.	Lentic
C. peus		
C. tarsalis		
C. thriambus		
Dolichopodidae	This study identified to family only.	
Dolichopus talus		Lentic and lotic margins
Ephydridae	This study identified to family only.	
Ephydra millbrae		Saline
Scatella triseta		Saline
Muscidae		
Limnophora discreta	This study identified to genus only.	Lotic
Stratiomyidae		
Euparyphus proxipalus proxipalus	This study identified to genus only.	Lotic
Tabanidae		
Tabanus punctifer	This study identified to genus only.	Lentic and lotic
Tipulidae		
Limonia defuncta concinna	This study identified to genus only.	Lotic and lentic

Table I.6. Continued.

Taxa:	Comments:	Habitat*:
Tipula hastingsae *T. inusitata* *T, santaecruzae* *T. capistrano* *T. lygropis* *T. praecisa* *T. vestigipennis*	This study identified to genus only.	Lotic and lentic

* Habitat designations as listed in Merritt and Cummins 1984.

Table I.7. Records of Santa Cruz Island aquatic insects not collected during this study.

Taxa:	Source*:	Comments:
Odonata		
Aeshnidae		
Anax junius	NHMLAC	Congener collected.
Libellulidae		
Tramea	SCI Reserve Collection	Previously unidentified, new record.
Hemiptera		
Corixidae		
Corisella decolor	Lauck 1979, SBNHM, NHMLAC	
Notonectidae		
Notonecta kirbyi	Truxal 1979	Congener collected.
N. unifasciata	Miller List	Congener collected.
Megaloptera		
Corydalidae		
Protochauliodes	SCI Reserve Collection	Previously unidentified, new record.
Coleoptera		
Hydraenidae		
Hydraena arenicola	Perkins 1981	Congener collected.
H. circulata	Perkins 1981	Congener collected.
Hydrophilidae		
Cymbiodyta punctatostriata	Smetana 1974	Congener collected.
Hydrophilus triangularis	SCI Reserve Collection	Previously unidentified, new record.
Tropisternus californicus	Miller List	Congener collected.
Diptera		
Chironomidae		
Paraclunio alaskensis	Miller List	Found in intertidal habitats.
Culicidae		
Anopheles franciscanus	Miller List	Found in lentic habitats.

Table I.7. Continued.

Taxa:	Source*:	Comments:
Culiseta incidens	Miller List	Found in lentic habitats.
C. inornata	Miller List	Found in lentic habitats.
Stratiomyidae		
Sargus virdis	Miller list	Found in lentic habitats.
Tipulidae		
Erioptera pilipes	Miller list	
Rhabdomastix sp.	Miller list	

* Miller List = unpublished list provided by Scott Miller, Bishop Museum
NHMLAC = Natural History Museum of Los Angeles County Collection
SBNHM = Santa Barbara Natural History Museum Collection

Figure 1.1. Map of Santa Cruz Island.

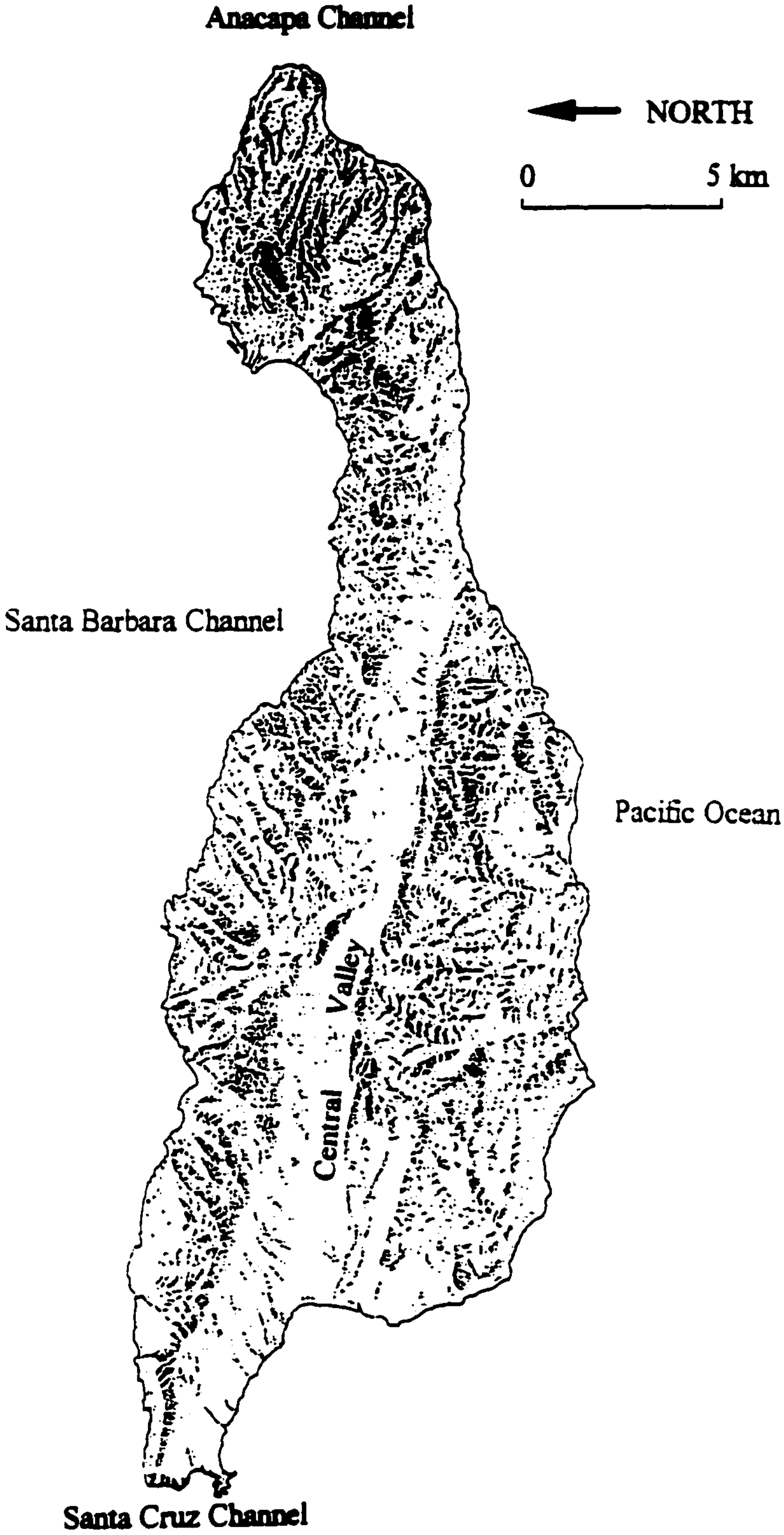

Anacapa Channel
NORTH
0
5 km
Santa Barbara Channel
Pacific Ocean
Central Valley
Santa Cruz Channel

Figure 1.2. Locations of streams and sample sites used for Santa Cruz Island macroinvertebrate collections (⊙ indicates primary sampling site, O indicates secondary sampling site). Minor tributaries are not shown.

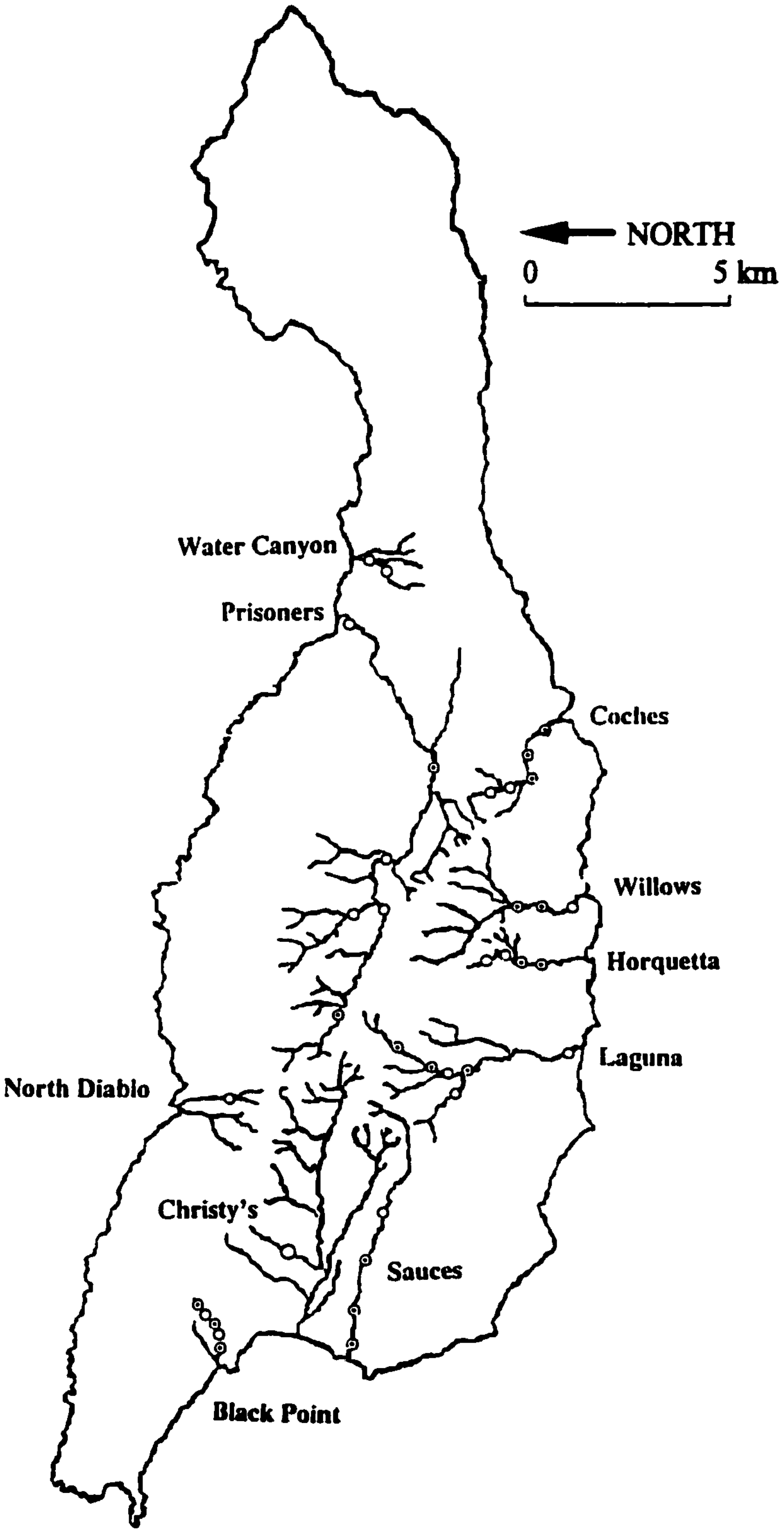

NORTH
0
5 km
Water Canyon
Prisoners
Coches
Willows
Horquetta
Laguna
North Diablo
Christy's
Sauces
Black Point

Figure 1.3. Sources of information used in constructing the list of Santa Cruz Island stream insects.

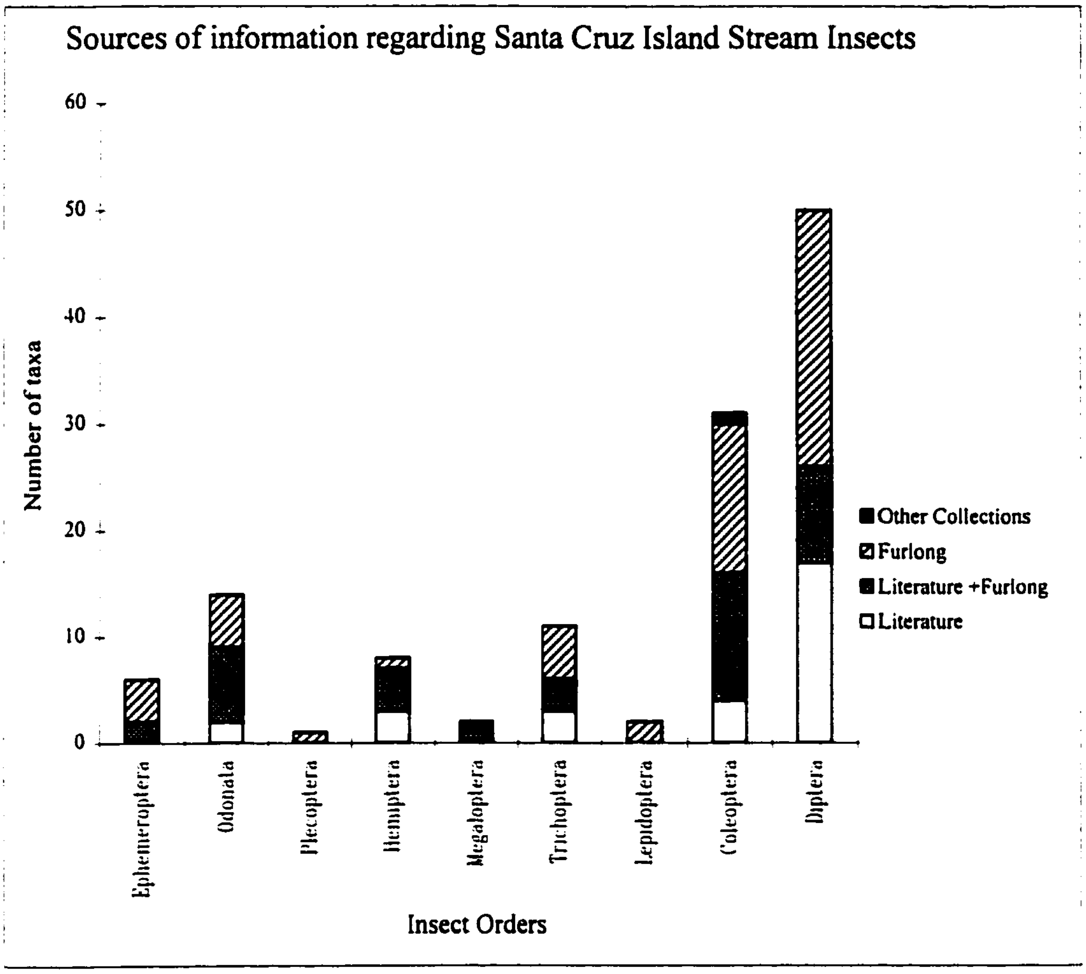
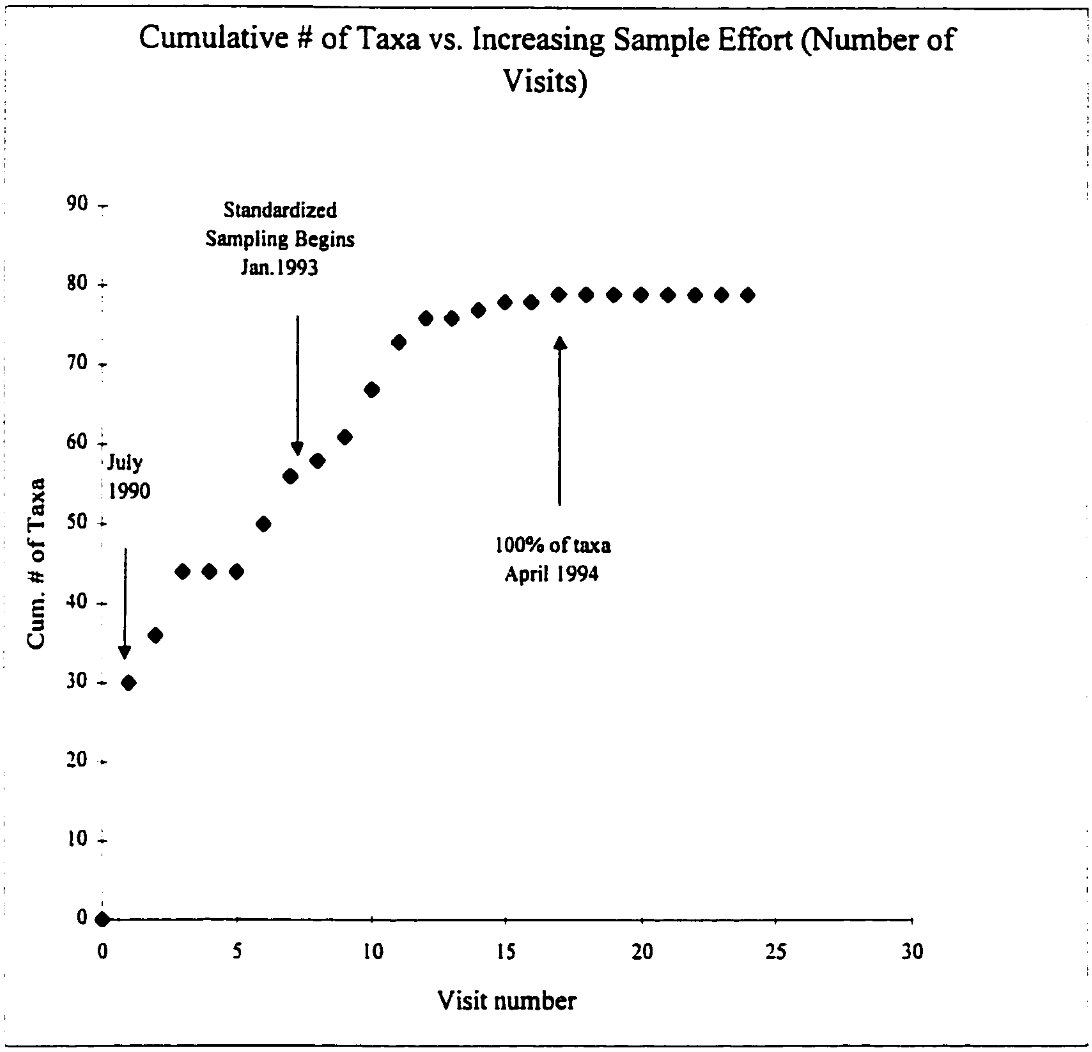

Sources of information regarding Santa Cruz Island Stream Insects
Number of taxa
60
50
40
30
20
10
0
Ephemeroptera
Odonata
Plecoptera
Hemiptera
Megaloptera
Trichoptera
Lepidoptera
Coleoptera
Diptera
Insect Orders
■ Other Collections
▨ Furlong
■ Literature +Furlong
☐ Literature

Figure 1.4. Cumulative number of insect taxa versus sampling effort (indicated as number of visits). This represents the cumulative number of taxa for all sampled and does not include chironomid taxa.


Cumulative # of Taxa vs. Increasing Sample Effort (Number of Visits)
Cum. # of Taxa
90
80
70
60
50
40
30
20
10
0
0
5
10
15
20
25
30
Visit number
Standardized Sampling Begins Jan.1993
July 1990
100% of taxa April 1994

CHAPTER II

COMPARISON OF MAINLAND AND SANTA CRUZ ISLAND STREAM TAXA

INTRODUCTION

Early observations of the flora and fauna of islands revealed that islands typically have fewer species compared to the nearest mainland. In addition, islands, especially oceanic islands, typically support non-random subsets of organisms found in source areas. Carlquist (1974) and Pielou (1979) proposed that this phenomenon results from the differential dispersal and colonization abilities of different organisms.

Species with good dispersal and/or colonization abilities (such as bats or strand plants) are often over-represented on islands compared to the mainland, whereas those with low dispersal ability across oceans (such as freshwater fish and large terrestrial mammals) are under-represented (Carlquist 1974). Therefore, island biotas are characteristically disharmonic, "containing only a small proportion of the basic adaptive types found in surrounding source regions" (MacArthur and Wilson 1967).

This phenomenon is most easily observed on distant oceanic islands but is evident on the California Channel Islands as well. Savage (1967) noted that the California Island herpetofaunas "are depauperate and composed of vagile forms." Wenner and Johnson (1980) observed that the assemblages of land vertebrates present on the Northern Channel Islands did not represent a random assortment of species from nearby mainland areas, but were "the sorts of animals one might associate with an Indian culture or which could have rafted to the islands."

As discussed by Wenner and Johnson (1980), species with poor dispersal and colonization abilities may become established on an island through random events. Freshwater species rarely disperse across salt water. For stream insects, however, the presence of winged adult forms, and the possibilities of aerial transport and rafting to the island on debris, may provide for some dispersal. The presence of aquatic insects on distant oceanic islands, such as the Hawaiian Archipelago, is evidence that some aquatic groups are capable of long distance dispersal (Howarth and Polhemus 1991). However, the high level of endemicity among Hawaiian aquatic insect taxa indicates that these organisms have been genetically isolated from mainland populations for some time.

Once a colonizing species reaches an island, appropriate habitat and adequate resources must be available for the organism to become established (Carlquist 1974). Therefore, the relative ecological poverty (i.e. lack of resources or habitat) of some islands may also contribute to their depauperate biotas. These factors combine to produce a biota that may have a very different composition from that of the mainland. The depauperate nature of islands makes them particularly interesting for general ecological studies, because the systems are often simplified versions of those on the mainland.

This chapter of my thesis explores two aspects of the Santa Cruz Island stream fauna. First, to what degree are mainland stream insects represented on Santa Cruz Island? Second, do the stream insect taxa present on the island represent a random subset of mainland taxa or do they represent a disharmonic assemblage?

STUDY AREAS

Insects were collected from both Santa Barbara County mainland and Santa Cruz Island streams (Figure 2.1). See Chapter I for a description of the island collection sites. The Santa Barbara County mainland collections were taken from three coastal streams: Mission-Rattlesnake Creek, Refugio Creek, and Jalama Creek. Although other mainland streams are more comparable to Santa Cruz Island streams with respect to watershed size, lack of fish, composition of riparian vegetation, etc., one cannot expect a perfect match. Instead, target streams exhibited the following characteristics: 1) Collections from Mission-Rattlesnake and Refugio Creeks permitted a check of my samples against published lists (Wenner et al. 1977, Cooper et al. 1986). 2) The Jalama watershed is similar to Santa Cruz Island in that it has been heavily grazed by cattle. 3) These streams were also chosen for their accessibility. After the ease of obtaining permission to sample from island streams, I was surprised to find that permission to sample mainland streams, many of which cross private land, was so difficult to obtain. After trying, unsuccessfully, to obtain access to several mainland streams, I opted for streams accessible to the public.

Jalama Creek (latitude 34°32'30"N, longitude 120°27'30"W), the most northern and western of the three creeks, originates at elevations approaching 554 meters in the Santa Ynez Mountains north of Point Conception and runs east-west. Jalama Creek drains a watershed which is the largest of those sampled on the mainland (approximately 66.70 km^2). Sample sites were located at various elevations (2, 15, 92 meters) on the creek (Figure 2.1). Creek width, measured at the sampling sites, ranged from 1.6 to 7.5 meters. Discharge measurements taken during sampling varied from near 0 to 106.1 liters/second (Table II.1).

Refugio Creek (latitude 34°30'00"N, longitude 120°3'30"W) is located approximately 30 km southeast of Jalama Creek. The Refugio headwaters lie in the Santa Ynez mountains at an elevation of 861 meters. The stream runs from north to south, with a watershed area of 21.46 km^2. Sample sites on Refugio were located at elevations of 7, 70, 110, and 139 meters (Figure 2.1). At those four sites, creek widths ranged from 3.6 to 0.4 meters. Discharge measurements at these stations ranged from 3.7 to 40.1 liters/second (Table II.1).

Mission-Rattlesnake Creek (latitude 34°27'30"N, longitude 119°41'30"W), located approximately 30 km east of Refuigo Creek, also originates in the Santa Ynez Mountains and runs north-south. However, this stream originates at higher elevations (1067 meters, Cooper et al. 1986) and has a total watershed area of 19.46 km^2. Sample sites were located at various elevations on the stream (at approximately 62, 108, and 260 meters, Figure 2.1) and stream widths at these sites varied between 1 and 3.5 meters (Table II.1). Discharge measurements taken during these 1997 collections at the sample sites ranged between 22.7 and 40.1 liters/second. The narrow discharge range is due to the lack of discharge readings from the summer and fall; however, Cooper et al. (1986) recorded discharges as low as 3 to 4 liters/second.

The upper reaches of Mission-Rattlesnake and Refugio Creeks drain relatively undisturbed chaparral and southern oak woodland communities (Parikh and Davis 1986, Kücher 1988). The lower reaches of these creeks pass through urban (Rattlesnake-Mission) and agricultural developments (Refugio). The Jalama Creek watershed supports southern oak woodland (upper reaches) and coastal sage (near mouth) communities (Kücher 1988). Cattle grazing occurs throughout the Jalama watershed. The banks of all three creeks support well-developed riparian woodland communities, dominated by sycamore (*Platanus racemosa*), willow (*Salix* spp.), and alder (*Alnus rhombifolia*), interspersed with oaks (primarily *Quercus agrifolia*).

MATERIALS AND METHODS

The mainland portion of the study involved qualitative sampling which attempted to obtain as many taxa as possible. The Santa Cruz Island list represented a seven year effort with approximately 800 samples processed. Santa Cruz Island collection methods were noted in Chapter I.

Three (Mission-Rattlesnake and Jalama) or four (Refugio) sample sites at varying elevations were established for each stream. Five samples were taken from each site, usually two from a riffle habitat (a kick and a sweep sample), two from a pool habitat (a kick and a sweep sample), and one from a stream macrophyte bed or area where water cascaded over large boulders (a kick sample). Mainland sample collections took place during March, June, and September of 1997. Sample processing procedures were the same as those used for island samples described in Chapter I. Unfortunately, in the winter of 1998, a large tree fell and destroyed our garage and more than half of the mainland samples. Therefore, the mainland list is based on approximately 90 samples taken in March and June of 1997.

In addition to island and mainland samples taken during the course of this study, literature records (Wenner et al. 1977, Cooper et al. 1986), and museum specimens and records (Santa Barbara Museum of Natural History) permitted the compilation of a more complete list of mainland taxa. The Wenner et al. (1977) list was developed from 60 summer samples. Cooper et al. (1986) constructed their list from approximately 4 years of qualitative sampling throughout the year. For additional literature sources and collections used to compile the list for Santa Cruz Island see Chapter I. To avoid possible errors in, or absence of, species-level identifications, counts of island and mainland taxa were done at the generic level unless otherwise noted.

Collections and records for the families Leuctridae (Plecoptera) and Scirtidae (Coleoptera), as well as the dipteran families Ceratopogonidae, Dolichopodidae, Empididae, Ephydridae, and Sciomyzidae were not identified below the family level; therefore, records of these families from collections and lists were counted as one genus each. Santa Cruz Island records of aquatic insects that occurred primarily in lentic and saline habitats (see Tables I.6 and I.7) were not indicated on this taxon list and were not included in counts.

To determine if island taxa represent a random subset of all (mainland and island) taxa, the Kolmogorov-Smirnov goodness-of-fit metric, D_{max}, was calculated for the observed distribution of island taxa across orders compared to the expected distribution (Zar 1984). This metric evaluates the deviation found between a cumulative observed (F_i) and cumulative expected ($\hat{F}_i$) frequency:

$$\text{Kolmogorov-Smirnov } D_{max} = \frac{|F_i - \hat{F}_i|}{n}$$, where n is the sample size.

The null hypothesis (observed and expected frequencies do not differ significantly) is rejected if the Kolmogorov-Smirnov D_{max} value exceeds the critical value for an *a priori* level of significance (Pimental 1990). The expected distribution was determined by calculating the proportion of total taxa (mainland and island) found on the island (# of taxa on island / # of total taxa). The total number of taxa per insect order was multiplied by this figure to obtain the expected number of island taxa per order. Therefore, if 25% of the taxa are found on the island, then I would expect 25% of total taxa within each order to be represented on the island.

Life history information for aquatic taxa was obtained from Usinger 1971, Edmunds et al. 1976, Wiggins 1977, Menke 1979, Merritt and Cummins 1984, and Thorp and Covich 1991. Guild assignments (from Merritt and Cummins 1984) permitted comparisons of island and mainland Plecoptera and Trichoptera guilds.

RESULTS

Mainland and island collections and records yielded a total of 161 genera (Tables II.2 and II.3). Including species-level identifications, that figure rises to 220 taxa. Regardless of the level of taxonomic resolution, dipterans exhibited the greatest overall richness, accounting for approximately 31% of the total taxa (Table II.2, Figure 2.2). The proportion of island genera which were dipterans (42%), was higher than that found on the mainland (29%, Table II.2, Figure 2.2). Though not as pronounced, the same pattern was observed in the richness of coleopteran taxa; beetles contributed 20.5% of the total genera (23.6% of the species) and comprised a greater proportion of the island genera (23.7%) than of the mainland genera (19.3%).

Genera in the orders Megaloptera and Lepidoptera contributed little (1 to 2%) to the richness of total, mainland, and island assemblages. Genera in the order Plecoptera contributed the least to island richness (1%), but contributed more than 7% of the taxa to the mainland assemblage (Table II.2, Figure 2.2).

Of the total 161 taxa (generic level), 145 (90%) occurred in mainland streams and 97 (60.5%) in island streams. The greatest disparity in richness occurred within the orders Plecoptera and Trichoptera. Mainland records contained 11 and 22 genera within the orders Plecoptera and Trichoptera, respectively;

however, only one stonefly and eight caddisfly taxa were collected from Santa Cruz Island streams (Table II.3). In all, 28 families and 64 genera of aquatic insects found in mainland streams did not occur in Santa Cruz Island samples. By contrast, 3 families and 15 genera collected or recorded from Santa Cruz Island were absent in mainland records and collections. One species, the caddisfly *Tinodes schusteri*, is considered to be endemic to Santa Cruz Island (Miller 1985).

Mainland aquatic taxa varied considerably in their distribution among and within the sampled streams (Table II.4 and Figure 2.3). Of the taxa occurring on the mainland and island, 80% were found in 3 or more mainland streams and 20% were found in only one or two mainland streams. Considering taxa occurring only in mainland streams, a greater proportion had narrow distributions among the five streams (60% in one or two streams only) and a smaller proportion had wide distributions among mainland streams (40% in four or five streams). In addition, the taxa occurring on the mainland and island exhibited broader distributions within mainland streams with 83% occurring in both up and downstream sampling sites compared to 56% of taxa with exclusive mainland distributions. The taxa "missing" from the island also occupy a narrower habitat range. Taxa exclusively found on the mainland predominately occupy lotic habitats only (75%). In contrast, the majority of taxa collected from mainland + island streams were taxa occupying both lotic and lentic habitats (61%; Table II.4, Figure 2.3).

Life history characteristics also varied between mainland taxa found on Santa Cruz Island and those exclusively found in mainland streams (Table II.4 and Figure 2.3). The majority of island and exclusively mainland taxa are bi- or univoltine (55% and 64% respectively). However among taxa occurring on Santa Cruz Island, 35% are multivoltine compared with only 7% of taxa occurring only on the mainland. A greater proportion of exclusively mainland taxa have generations exceeding one year compared with island taxa (29% and 10% respectively). Seasonal emergence patterns did not differ greatly between the two groups.

For most insect orders, the number of island genera observed within each order approximates the number expected (Table II.5, Figure 2.4). The number of taxa expected was much higher than that observed for the orders Trichoptera (13 expected, 8 observed) and Plecoptera (7 expected, 1 observed). The numbers of dipteran and coleopteran taxa observed exceeded the expected (Diptera: 31 expected, 41 observed; Coleoptera: 20 expected, 23 observed). The Kolmogorov-Smirnov goodness-of-fit metric, Dmax, calculated for observed versus expected richness within orders was significant ($D_{max\ n=8,k=98} = 14$, $P < 0.01$).

Within the Plecoptera, shredders appeared to be under-represented on the island compared to the mainland (Table II.6). Seven of the eleven mainland stonefly taxa are primarily shredders (Merritt and Cummins 1984). Of these seven mainland shredder genera, only one was found on Santa Cruz Island (the only plecopteran genera on Santa Cruz Island). This same pattern was not observed for trichopterans. Of the 22 trichopteran genera collected from mainland streams, six (27%) are designated as shredders (Merritt and Cummins 1984). Caddisfly shredders account for 25% of the island genera (2 of 8 genera; Table II.6). By comparison, within the Trichoptera, collector genera were well-represented on the island compared to the mainland, accounting for half of the island caddisfly genera (4 out of 8 genera) and approximately 25% of mainland taxa (6 out of 22 genera).

DISCUSSION

Depauperate Nature of Santa Cruz Island Biota

A comparison of mainland and island biotic richness poses many problems. One can assume, given the difficulties of overwater dispersal, that islands will only support a subset of mainland organisms; however, factors other than dispersal may result in a depauperate, or what appears to be a depauperate, biota. Limited resources or habitat may also limit the number of organisms that establish on an island (MacArthur and Wilson 1967). For example, animals may encounter a depauperate flora or lack of suitable prey taxa. In addition, island organisms may experience increased rates of extinction due to small population sizes, low genetic variability, and/or the introduction of exotic species (Carlquist 1974). Island biotas may also "appear" depauperate due to sampling bias. For example, island organisms are often not as well known or as thoroughly studied as their mainland counterparts. Contrasting island richness with large areas of the mainland introduces an additional source of bias due to differing sizes of sampled areas. In spite of the difficulties inherent in comparing the richness of mainland and island biotas, such comparisons continue to interest researchers.

Although Santa Cruz Island is only 30 kilometers from the mainland and supports 16 different plant communities (Junak et al. 1995), its fauna is notably depauperate (Table II.7). Santa Cruz Island supports only 45% of the herpetofauna found in comparable habitats in Ventura County (Savage 1967) and 12% of land mammal species (excluding bats) observed on the coastal mainland (van Bloeker 1967, Wenner and Johnson 1980). With respect to breeding land birds, 39 species occur on the island compared with 160 species in comparable mainland habitats (Diamond and Jones 1980).

The richness of Santa Cruz Island insects varies by group (Table II.7). The 37 orthopteran taxa, probably the most thoroughly studied of all island insect orders, comprise only 53% of those collected from the Santa Monica Mountains (Rentz and Weissman 1982, Weissman 1985). A survey comparing the Santa Cruz Island Lepidoptera fauna with that at the Big Creek Reserve (Monterey, California) revealed that 543 taxa were found on the island compared with 901 species at Big Creek (Powell 1994). The results of surveys by Rust et al. (1985) and Thorp et al. (1994) revealed that the Santa Cruz Island bee fauna (6 families) was composed of only 19% (105 species) of the species from the southern California Coast Ranges (an estimated 520). This value appears low compared to Orthoptera and Lepidoptera figures, and Thorp et al. (1994) suggested that island figures "considerably underestimate" the actual number of bee species.

The number of stream insect genera recorded for Santa Cruz Island accounts for approximately 60% of the total number of island and mainland stream insect genera (Table II.2). Island Plecoptera exhibit very low richness compared with the mainland, with the island supporting only 9%, or one out of the eleven mainland genera. Trichoptera genera numbers were also low compared to the mainland (Table II.2). Island representation in the groups Ephemeroptera, Odonata, and Hemiptera (aquatic) was comparable to that of orthopterans and terrestrial lepidopterans (Table II.7). Compared to other insect groups, aquatic beetles, flies, and megalopterans are well represented on the island; however, this effect was small within the Coleoptera and only a few Megaloptera taxa were collected.

Overwater dispersal may be difficult for freshwater organisms; however, very few island stream insects are strictly aquatic. The majority possess a winged and/or terrestrial adult stage. Some aquatic forms disperse readily, with odonates and aquatic members of the orders Hemiptera, Coleoptera, and Diptera occurring on the Hawaiian Islands (Table II.8, Howarth and Polhemus 1991). Ephemeroptera and Trichoptera occur on islands as far as 300 km from the mainland in the Atlantic (Malmqvist 1993). On South Pacific islands one can find these groups 600-700 km from possible colonization sources (Winterbourn 1980). Plecopterans have been collected from the islands Snares, Auckland, and Campbell (approximately 100-600 km south of New Zealand); however, these stoneflies consist of taxa with terrestrial nymphs and apterous adults and are closely related to New Zealand species. The origin of these islands may be continental; therefore the stoneflies may not have dispersed overwater (Winterbourn 1980). Other than these records, plecopterans are rarely recorded for oceanic islands.

Records indicate that some aquatic insects have crossed distances much greater than the Santa Barbara Channel (30 km). In addition, the distance to the Northern Channel Islands from the mainland was even less in the past. During periods of low sea level, the lowest occurring approximately 17,000-18,000 years ago, the Northern Channel Islands formed the super-island Santarosae (Vedder and Howell 1980), and the width of the Santa Barbara Channel at that time was only 6 km (Wenner and Johnson 1980). The expanded island area, combined with the reduced overwater dispersal distance, increased the probability of immigration occurring from the mainland and of the establishment and expansion of the island populations.

Given the overwater dispersal capabilities of some aquatic insects and the relatively narrow barrier to dispersal presented by the Santa Barbara Channel, factors other than dispersal distance could contribute to the low richness of Santa Cruz Island aquatic insects. Also, one might interpret the above data in light of the difficulties associated with making island-mainland comparisons.

As noted earlier, the ecological poverty (i.e., lack of resources or habitat) of islands may contribute to their depauparate biota. Junak et al.(1995) noted that the Santa Cruz Island flora appears "harmonic and balanced compared to regional floras of comparable size on the adjacent mainland, with a few conspicuous exceptions." Among those "exceptions" is the absence or limited distributions of several riparian tree species that dominate mainland riparian woodlands. Alder (*Alnus rhombifolia*), sycamore (*Plantanus racemosa*), and California bay (*Umbellaria californica*) do not, with the exception of a few introduced sycamores, occur on the island (Junak et al. 1995). Riparian woodlands supporting cottonwood (*Populus* spp.) occur in a few isolated island drainages, primarily on the inaccessible north side of the island and in a few south draining watersheds (Coches, Laguna Alamos, personal observations, Junak et al. 1995). Willows (*Salix* spp.) and mulefat (*Baccharis salicifolia*) dominate the majority of Santa Cruz Island riparian corridors. If mainland insect groups (such as plecopteran shredders) rely heavily upon alder, sycamore, and cottonwood leaves as food sources, these groups might be unable to establish on Santa Cruz Island.

Once organisms reach an island and become established, their populations face the possibility of extinction due to such factors as low genetic variability (Carlquist 1974) and relatively small population sizes (Pielou 1979). These factors also contribute to the depauperate nature of island biotas. In reference to Santa Cruz Island, insects may have crossed the Santa Barbara Channel repeatedly, as birds have (Diamond and Jones 1980). Those immigrants would therefore contribute to the island gene pool, reducing the risk of extinction for island populations. Research comparing the genetic variability of aquatic insect taxa collected from mainland and island populations would be of great use in determining the relative degrees of genetic homogeneity among island aquatic insect groups.

Small habitat areas support small populations, making them susceptible to extinction (MacArthur and Wilson 1967). The size of Santa Cruz Island and possibly the magnitude of stream flow have not been static. During periods of high sea level, the probability of island extinctions increased as island surface area and perhaps stream flows decreased and distances from source populations increased. In addition to island-wide extinctions, localized extinction events may also occur on Santa Cruz Island. Winter storm events often result in stream scour, which might result in the local extinction of aquatic insect populations.

Through various activities, humans also contributed to island extinctions (Carlquist 1974, Marshall 1988). The introduction of sheep, cattle, and pigs in the mid 1880's decimated native plant communities, with up to 48 plant species lost from Santa Cruz Island (Peart et al. 1994). Introduced grasses gradually replaced the native flora in heavily grazed areas (Junak et al. 1995). In addition to the loss of native plant cover, livestock grazing, and the activities of feral pigs resulted in increased erosion. Sheep and cattle grazing on Santa Cruz Island ended in 1988, but feral pigs continue to affect island communities. Although not well-documented on Santa Cruz Island, the activities of grazing animals and pigs may have degraded riparian habitats, perhaps contributing to the depauperate nature of the stream fauna. Portions of the three mainland streams, however, are more affected by human activities (urban development, farming, grazing) than those on the island.

The richness of island biotas may be underestimated due to sampling bias. Islands are relatively inaccessible; therefore, studies of island biotas may not be conducted as frequently or thoroughly as those in mainland sites. In addition, mainland surveys may encompass a larger area and consequently a greater range of habitats. Together, these factors contribute to a mainland bias in taxonomic richness. In this study, I tried to avoid these biases, taking island samples over the course of seven years from seven streams (see Chapter I). Mainland collections were taken from three streams over the course of only 6 months; however, I also used additional mainland lists for these and additional streams. The Wenner et al. (1977) list also included samples from Cold Springs and San Jose Creeks; however, samples from these streams added no additional taxa to the mainland records.

The studies used for the mainland list do not appear to have used a greater sampling effort compared with the effort used to develop the Santa Cruz Island list. The Wenner et al.(1977) list was developed from 60 summer samples. Cooper et al. (1986) constructed their list from approximately 4 years of qualitative sampling throughout the year. My mainland list was produced from approximately 90 samples. The Santa Cruz Island list represented a seven year effort with approximately 800 samples processed. Overall, the richness of Santa Cruz Island stream insects may be overestimated compared to the mainland. It is likely that the mainland sampling efforts were incomplete and underestimated mainland richness.

A possible bias could result due to the relative distances between mainland streams. The distances between Jalama and Refugio Creeks and between Mission-Rattlesnake and Refugio Creeks are approximately 30 km. In contrast, Santa Cruz Island is only 38 km in length. In addition, the size of the Jalama watershed is much larger than any watershed on Santa Cruz Island.

In all, it appears that the depauperate nature of the Santa Cruz Island aquatic insect assemblage may not be due solely to difficulties associated with overwater dispersal. One must also consider the potential roles of the low diversity of island riparian vegetation and potentially high island extinction rates. In addition, a mainland bias in taxonomic richness may result because mainland samples were taken over greater area (60 km) compared to the island (less than 38km).

Disharmony of Santa Cruz Island Biota

Ecological and physical barriers limit the distributions of organisms. Saltwater serves as a barrier to terrestrial and freshwater organisms, but the presence of non-marine species on oceanic islands indicates that a subset of organisms can cross this barrier. There are limited means for the dispersal of these organisms to islands. They must disperse aerially or on water. Aerial dispersal results from active flight, passive movement caused by wind currents, or via presence on or within aerially-dispersing organisms (Simberloff and Wilson 1969). Dispersal on water by floating, swimming, or rafting may also occur (Carlquist 1974, Wenner and Johnson 1980). Following the dispersal event, a combination of insular conditions and attributes of the colonizing organism determine whether or not the organism becomes established.

Differential dispersal abilities and ecological tolerances among taxa result in disharmonic island biotas, dominated by species with "positive adaptations for long-distance dispersal and for establishment" (Carlquist 1974). The determination of dispersal ability (to islands) can be assessed by determining a propagule's ability to stay suspended in air, its tolerance to cold, desiccation and salt water, its ability to float or raft, its reproductive characteristics (asexual vs. sexual reproduction), and its ecological requirements. The work of Carlquist (1974) has contributed much to our understanding of the dispersal abilities of plants. However, other than comparing the characteristics of animals successfully colonizing islands vs. those restricted to mainlands, the determination of the dispersal abilities of animals is somewhat circular. In general, those animals that have colonized isolated islands have been considered good dispersers.

Santa Cruz Island, as Santarosae Island, has been separated from the mainland by as little as 6 km. In spite of this relatively narrow barrier to dispersal, portions of its fauna appear disharmonious. For example, only 12% of mainland mammals and 45% of mainland herpetofauna are found on the island. According to records compiled by Darlington (1957) and Carlquist (1974), maximum known dispersal distances for reptiles (lizards - 3200 km, snakes - 960 km) and amphibians (800 km) generally exceed those of land mammals (rodents - 960 km, small non-rodents - 322 km, large mammals 40 km). Compared with the herpetofauna, the overall low proportion of mammals and complete absence of large mammals on islands, leads to the inference that these patterns resulted from differential dispersal abilities. Given that the Northern Channel Islands have supported and continue to support sizable populations of introduced large mammals and have supported mammoth populations in the past (Wenner and Johnson 1980), deleterious ecological conditions presumably did not prevent the establishment of large native mammals on these islands.

In regards to aquatic insects, I would expect "good" dispersers and colonizers to be strong fliers and/or small bodied (passive wind dispersal), and have either long-lived adults or multivoltine generations (adults present many times of year). In addition, I would expect the "good" dispersers and colonizers to be widely distributed among and within mainland streams and occupy a broad range of aquatic habitats (generalists rather than specialists). Care must be taken when determining these characteristics for mainland taxa because limited ranges may be due to the lack of adequate mainland sampling rather than limited dispersal abilities and/or narrow habitat ranges of individual taxa. The following discussion addresses only taxa from the five mainland streams used for comparison.

When comparing taxa present on the mainland and island with those found only on the mainland, several trends become apparent (Table II.4, Figure 2.3). Taxa found on the island tend to be broadly distributed on the mainland (80 % found in three or more streams), whereas those found only in mainland streams exhibited a narrower distribution (60% found exclusively in one or two streams). In addition, the taxa found on the island had a broader mainland distribution within mainland streams, with 70% found in both upstream and downstream mainland sites. Of those taxa found exclusively on the mainland, a large proportion (48%) were found at upstream sites. The breadth of habitats occupied by taxa also varied, with the taxa found on the island typically occupying a greater range of habitat types (61% occupy lentic + lotic habitats) than those on the mainland only (21% occupy lentic + lotic habitats). In addition, a greater proportion of island taxa are multivoltine (35% vs. 7% of taxa on mainland alone). In short, island taxa are broadly-distributed, multivoltine, habitat generalists. The remaining characteristics will be discussed for individual orders.

The expected number of taxa per order differed significantly from observed values. The numbers of observed Coleoptera and Diptera taxa exceeded the expected numbers (Table II.5, Figure 2.4). Taxa in the orders Plecoptera and Trichoptera exhibited the opposite trend, and these results generally corresponded to published dispersal distances for these orders (Table II.8). The expected numbers in the remaining orders approximated those observed.

Aquatic coleopterans and dipterans (as well as odonates and aquatic hemipterans) occur on islands as distant as Hawaii (3200 km from the nearest mainland, Howarth and Polhemus 1991) and dipterans occur on new or harsh islands such as Surtsey (recent volcanic island, Lindroth et. al. 1973) and Macquarie (subantarctic island, Marchant and Lillywhite 1994). Coleopteran and dipteran families present on the mainland, but missing on Santa Cruz Island include those with narrow distributions among (Dryopidae) or within (Psephenidae, Blephariceridae) mainland streams. In addition, Psephenidae and Blephariceridae have very narrow habitat specificities, occurring only in erosional stream habitats (Merritt and Cummins 1984).

Trichopterans and ephemeropterans are not found on islands as distant as Hawaii, but have been collected from numerous South Pacific Islands (although several are continental). Plecopterans have not been collected from islands more distant than Santa Cruz Island, with the exception of continental islands south of New Zealand. Stonefly adults usually crawl rather than fly and have fairly short-lived adult stages (less than two weeks); therefore, it is not surprising that so few occur on islands. In addition, based on observations of the families occurring on the Santa Barbara mainland, stoneflies exhibit narrow distributions among and/or within streams (Table II.4). Although trichopterans have a longer adult stage (to one month) than plecopterans, they also exhibit lower than expected richness on Santa Cruz Island. Several of the trichopteran families "missing" from Santa Cruz Island have narrow mainland distributions among (Brachycentridae, Limnephilidae, Leptoceridae) and/or within (Rhyacophilidae, Glossosomatidae, Limnephilidae, Leptoceridae) mainland streams.

Based on the characteristics of the Order Ephemeroptera, one would not expect to find many on islands. These insects have a very short-lived adult stage and are weak fliers. However, three of the seven families found on the mainland occur on Santa Cruz Island (Table II.4) and observed island richness (5 genera) within this order does not differ greatly from expected richness (7 genera). The island families (Baetidae, Caenidae, and Leptophlebiidae) have broad habitat ranges and are widely distributed among and within mainland streams. In contrast, families found exclusively on the Santa Barbara mainland have narrow habitat ranges (Heptageniidae), are not widely distributed among (Siphlonuridae, Ephemerellidae) or within (Siphlonuridae) mainland streams. Caenidae and Tricorythidae have very similar distributions and characteristics; however only Caenidae occur on Santa Cruz Island.

Odonates are strong fliers with fairly long-lived adults. These insects are found on oceanic islands as distant as the Hawaiian Archipelago (Table II.8); however, the high degree of endemism in Hawaiian odonates indicates long isolation from mainland populations. Compared with mainland records, odonates are well represented on Santa Cruz Island (4 of 7 families; 9 genera observed, 10 genera expected). The three families missing from the island are either narrowly distributed within (Gomphidae, Cordulegaster, Calyopterygidae) or among

(Cordulegaster, Gomphidae) streams. In addition, Gomphidae and Calyoptergidae are weak fliers. Families occurring on Santa Cruz Island are strong fliers (Libellulidae, Coenagrionidae), widely distributed among and within mainland streams (Lestidae, Coenagrionidae), and have wide habitat ranges (Aeshnidae, Libellulidae, Lestidae, Coenagrionidae). Members of the Aeshnidae, Libellulidae, and Coenagrionidae also occur on islands more distant than Santa Cruz (Brönmark et al. 1984, Howarth and Polhemus 1991).

Although the number of observed Hemiptera genera closely corresponds with the expected, one can compare the taxonomic composition of the island's hemipteran assemblage with data from other islands (Table II.8). Australia's continental hemipteran fauna (possible source populations for south Pacific islands) consists of many of the same families found on the California mainland, including Mesoveliidae and Hydrometridae (not collected during this study). The families Hebridae, Naucoridae, and Nepidae do not occur on islands in the southwestern Pacific (Winterbourn 1980). Although belostomatids are found on New Caledonia, New Caledonia is a continental island. These results parallel those of this study. The Belostomatidae, Hebridae, Hydrometridae, Naucoridae, and Nepidae are missing from Santa Cruz Island and oceanic islands in the South Pacific implying that these families may lack dispersal capabilities enabling them to cross salt water barriers. In addition, the families Hebridae, Nepidae, and Naucoridae exhibit narrow ranges among and within Santa Barbara mainland streams and belostomatids have narrow habitat ranges (Table II.4).

Aerial and shipboard trapping also contribute to our knowledge of aquatic insect dispersal. A shipboard trapping program, supported by the Hawaiian Bishop Museum from 1957 to 1966, included cruises in the Pacific, Atlantic, Antarctic and Indian Oceans. These cruises used a variety of trap types ranging from "wind-sock" type nets suspended from the ships' railing to suction traps. Insects collected during that program included 11 aquatic dipteran families, 6 aquatic hemipteran families, 5 aquatic coleopteran families, 2+ families of odonates, one family of ephemeropterans, and 2 unidentified trichopterans (Holzapfel and Harrell 1968).

Published data from another set of Pacific cruises conducted in 1965 included distance information. During this cruise, aquatic Diptera (Ceratopogonidae) were trapped 540 km from the nearest land (Holzapfel and Perkins 1969). The majority of aquatic families trapped during both studies are a subset of those collected from Santa Cruz Island during this study and listed for other islands (Table II.9).

The Bishop Museum also conducted an aerial trapping program over the Pacific Ocean from 1966 to 1969 (Table II.9). These collections were taken at altitudes up to 2745 m; however no insects were collected above 1525 m. The majority of trapped insects (93 of 101 specimens) were recovered from samples taken soon after take-offs and landings (Holzapfel 1978). The only aquatic taxa recovered by these efforts were Chironomidae (Diptera).

Because distance data were not consistently published with the aerial and shipboard trapping results, one cannot draw conclusions regarding dispersal distances. Several groups, however, found on Santa Cruz Island and more distant islands were recovered by the aerial and shipboard trapping efforts. Conversely, with few exceptions, these efforts did not collect many groups that were not recorded from Santa Cruz and other islands (Table II.9).

If published dispersal distances and trapping efforts truly represent the differential dispersal capabilities of aquatic groups, then these differences may contribute to the unbalanced nature of Santa Cruz Island's aquatic insects assemblages. Coleopterans and dipterans exhibit the ability to disperse farther than other orders. These groups are over-represented on Santa Cruz Island compared to the mainland. In contrast, Plecoptera and Trichoptera appear to possess very limited dispersal capabilities. Plecoptera and Trichoptera are under-represented on Santa Cruz Island compared to the mainland. It is important, however, to consider the possible effects of ecological conditions on these under-represented groups.

The depauperate nature of riparian vegetation might exclude functional groups (plecopteran shredders) that feed on sycamore, alder, bay, and cottonwood leaves. However, willow and mule fat provide alternative sources of allochthonous input in Santa Cruz Island streams. Shredding taxa account for a large proportion of mainland plecopteran (64%); however, this trend was not apparent for trichopteran taxa (32%; Table II.6). Of shredder taxa, only one of eight Plecoptera occur on Santa Cruz Island. These anecdotal observations indicate that the depauperate nature of Santa Cruz Island's riparian vegetation may play a role in the lower than expected richness of island Plecoptera.

CONCLUSION

A comparison of Santa Cruz Island and nearby mainland streams indicates that the island has a depauperate stream insect fauna. Only 60% of the total number of collected and listed mainland and island insects were found on the island. Comparisons of mainland taxa present vs. absent on Santa Cruz Island indicate that taxa shared with Santa Cruz Island have more generations per year, broader distributions among and within mainland streams, and broader habitat requirements than taxa found only on the mainland.

Coleopterans and dipterans compose a greater proportion and Trichoptera and Plecoptera a lower proportion of island stream taxa compared with their proportions in mainland streams. The patterns of generic richness in various aquatic insect orders differed significantly between the island and the mainland.

Several factors may contribute to the depauperate and disharmonic nature of Santa Cruz Island stream insect fauna. Although limited overwater dispersal is often cited to account for the depauperate and disharmonic nature of island biotas, problems associated with making comparable collections from similar mainland habitats and with the relatively depauperate nature of riparian vegetation on Santa Cruz Island may also play a role.

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Table II.1. Characteristics of mainland collection sites.

Stream	Stream Description:			Collection Site Description:						
	Total Catchment (km^2)	Baseflow[a] (liters/s)	Stormflow[a] (liters/s)	Elevation	Slope[b]	Mean Width (m)	Mean Depth (m)	Substrata	Canopy[c]	Land Use[d]:
Jalama	66.70	2.67	65.47							
				2	1%	6.65	0.11	Sand + Macrophytes	PC	R
				15	2%	2.10	0.09	Gravel	C	R
				92	2%	2.30	0.09	Gravel + Sand	PC	R
Refugio	21.46	4.78	22.27							
				7	2%	2.20	0.08	Sand + Macrophytes	O	A
				70	2%	1.95	0.08	Gravel	PC	A
				110	3%	0.86	0.11	Gravel + Cobbles	PC	A
				139	6%	0.98	0.04	Bedrock	C	N
Rattlesnake-Mission	19.46	3 to 4[e]	31.40							
				62	2%	3.20	0.06	Sand + Gravel	PC	U
				108	4%	3.50	0.05	Cobbles	C	P
				260	9%	1.00	0.05	Gravel + Cobbles	C	N

[a] Calculated from stream cross-sections and current velocity measurements; stormflow from March 1997.

[b] Calculated from topographic maps using elevations from 0.5 km below to 0.5 km above collection site

[c] C = closed; PC = partially closed; O = open

[d] A= avocado and lemon orchards; N = natural landscape; P = park; R = cattle ranching; U = urban

[e] From Cooper et al. 1986

Table II.2. Number and percent of taxa per order from records and collections of mainland Santa Barbara County and Santa Cruz Island streams.

Order	Total Genera		Total Species		Mainland Genera		Island Genera	
	Genera per Order	% of Genera per Order	Taxa per Order	% of Taxa per Order	Genera per Order	% of Genera per Order	Genera per Order	% of Genera per Order
Ephemeroptera	11	6.8	13	5.9	11	7.6	5	5.2
Odonata	16	9.9	27	12.3	16	11.0	9	9.3
Plecoptera	11	6.8	11	5.0	11	7.6	1	1.0
Hemiptera	12	7.5	18	8.2	11	7.6	6	6.2
Megaloptera	3	1.9	3	1.4	3	2.1	2	2.1
Trichoptera	22	13.7	26	11.8	22	15.2	8	8.2
Lepidoptera	2	1.2	2	0.9	1	0.7	2	2.1
Coleoptera	33	20.5	52	23.6	28	19.3	23	23.7
Diptera	51	31.7	68	30.9	42	29.0	41	42.3
Total Taxa	161	100.0	220	100.0	145	100.0	97	100.0

Table II.3. Insect taxa of Santa Cruz Island and coastal Santa Barbara County streams. This table does not include island records of aquatic insects occurring in non-lotic habitats as noted in Tables I.6 and I.7.

Taxa:	**Location:** Mainland					Santa Cruz Island			
Source*:	Cooper	Wenner	Furlong	Other	Combined	Literature	Furlong	Other	Combined
Ephemeroptera									
Siphlonuridae									
Ameletus	○	○	○		●				
Baetidae									
Baetis	○		○		●		○		●
B. bicaudatus	○	○					○		
B. tricaudatus	○						○		
Callibaetis	○	○	○	○	●	○	○		●
C. pictus							○		
Centroptilum			○		●		○		●
Heptageniidae									
Epeorus (Iron)	○		○	○	●				
E. sancta-gabriel		○							
Heptagenia	○		○	○	●				
H. rubroventris		○							
Ephemerellidae									
Drunella	○		○		●				
Ephemerella	○		○	○	●				
E. flavilinea		○							
Tricorythidae									
Tricorythodes	○		○		●				
T. fallax		○		○					
Caenidae									
Caenis	○		○	○	●		○		●
C. tardata		○							
Leptophlebiidae									
Paraleptophlebia	○		○	○	●				●
P. altana		○							
P. associata						○	○		
Number of Genera:					**11**				**5**

Table II.3. Continued.

	Location:								
	Mainland					Santa Cruz Island			
Taxa: **Source*:**	**Cooper**	**Wenner**	**Furlong**	**Other**	**Combined**	**Literature**	**Furlong**	**Other**	**Combined**
Odonata									
(Anisoptera)									
Cordulegastridae									
Cordulegaster dorsalis	○	○	○	○	●				
Gomphidae									
Octogomphis specularis	○	○	○	○	●				
Aeshnidae									
Aeshna				○	●				●
A. interrupta interna		○							
A. multicolor				○			○		
A. umbrosa occidnetalis		○							
A. walkeri	○	○				○	○	○	
Anax					●				●
Anax junius				○		○		○	
A. walsinghami							○		
Libellulidae									
Erythemis collocata		○		○	●				
Erythrodiplax funera		○			●				
Libellula					●				●
L. pulchella				○					
L. saturata						○	○	○	
Pachydiplax longipennis		○		○	●				
Paltohemis lineatipes	○	○	○	○	●		○	○	●
Sympetrum					●				●
S. corruptum		○		○			○		
S. illotum				○			○	○	
Tramea					●			○	●
T. lacerata		○		○					
(Zygoptera)									
Calopterygidae									
Hetarina		○		○	●				
Lestidae									
Archilestes				○	●	○			●
A. californica	○	○					○	○	
A. grandis	○	○		○					

Table II.3. Continued.

	Location:								
	Mainland					Santa Cruz Island			
Taxa: **Source*:**	**Cooper**	**Wenner**	**Furlong**	**Other**	**Combined**	**Literature**	**Furlong**	**Other**	**Combined**
Coenagrionidae									
Argia			○	○	●				●
A. emma	○	○							
A. sedula	○						○		
A. vivida	○	○	○			○	○	○	
Enallagma					●				●
E. canuculatum						○	○	○	
E. cyathigerum						○	○		
E. praevarum		○							
Zoniagrion exclamationis		○			●				
Number of Genera:					**16**				**9**
Plecoptera									
Taeniopterygidae									
Taenionema	○		○		●				
Nemouridae									
Malenka	○		○		●				
Leuctridae	○				●				
Capniidae									
Capnia	○				●		○		●
Eucapnopsis brevicauda		○			●				
Isocapnia	○				●				
Mesocapnia	○				●				
Perlidae									
Calineuria californica	○	○	○	○	●				
Perlodidae									
Isoperla	○	○	○	○	●				
Chloroperlidae									
Alloperla		○		○	●				
Sweltsa			○		●				
S. pacifica	○								
Approximate Number of Genera:**					**11**				**1**
Hemiptera									
Saldidae									
Saldula pexa						○	○		●

Table II.3. Continued.

	Location: Mainland					Santa Cruz Island			
Taxa: **Source*:**	**Cooper**	**Wenner**	**Furlong**	**Other**	**Combined**	**Literature**	**Furlong**	**Other**	**Combined**
Hebridae									
Merragata hebroides			○		●				
Veliidae									
Microvelia	○			○	●				●
Microvelia beameria		○	○			○	○	○	
M. californiensis		○	○						
Gerridae									
Aquarius remigis	○	○	○	○	●	○	○	○	●
Nepidae									
Ranatra brevicollis			○	○	●				
Belostomatidae									
Abedus indentatus	○	○	○	○	●				
Corixidae									
Corisella					●				●
C. decolor						○		○	
C. inscripta		○							
Graptocorixa				○	●				●
G. uhleri	○	○	○			○	○	○	
G. uhleroides	○	○							
Trichocorixa reticulata		○			●				
Naucoridae									
Ambrysus californicus bohartorum			○		●				
Notonectidae									
Buenoa	○			○	●				
Notonecta					●				●
N. hoffmanni	○	○	○	○			○		
N. kirbyi			○	○		○			
N. shooteri		○							
N. unifasciata						○			
Number of Genera:					**11**				**6**
Megaloptera									
Sialidae									
Sialis			○		●				
S. californica	○	○							

Table II.3. Continued.

	Location: Mainland					Santa Cruz Island			
Taxa: **Source*:**	**Cooper**	**Wenner**	**Furlong**	**Other**	**Combined**	**Literature**	**Furlong**	**Other**	**Combined**
Corydalidae									
Neohermes filicornis			○		●	○	○	○	●
Protochauloides	○	○			●			○	●
Number of Genera:					**3**				**2**
Trichoptera									
Philopotamidae									
Wormaldia	○	○	○	○	●		○		●
Psychomyiidae									
Tinodes	○	○	○	○	●		○		●
T. provo						○			
T. schusteri						○			
Polycentropodidae									
Polycentropus	○	○	○	○	●		○		●
P. halidus						○			
P. variegatus						○			
Hydropsychidae									
Cheumatopsyche		○			●				
Hydropsyche	○	○	○	○	●		○		●
H. californica						○			
H. oslari	○								
H. philo						○	○		
Rhyacophilidae									
Rhyacophila	○	○	○	○	●				
Glossosomatidae									
Agapetus	○	○	○		●				
Hydroptilidae									
Hydroptila	○		○	○	●		○		●
Neotrichia		○	○		●				
Ochrotrichia	○	○	○		●		○		●
Brachycentridae									
Micrasema	○	○	○		●				
Lepidostomatidae									
Lepidostoma	○	○	○	○	●		○		●
L. unicolor		○							

Table II.3. Continued.

	Location: Mainland					Santa Cruz Island			
Taxa: **Source*:**	**Cooper**	**Wenner**	**Furlong**	**Other**	**Combined**	**Literature**	**Furlong**	**Other**	**Combined**
Limnephilidae									
Clostoeca disjunctus		○			●				
Dicosmoecus	○				●				
Neophylax	○			○	●				
Neothremma		○			●				
Pseudostenophylax		○			●				
Psychoglypha	○				●				
Sericostomatidae									
Gumaga			○		●		○		●
G. nigricula	○	○							
Odontoceridae									
Marilia flexuosa		○			●				
Helicopsychidae									
Helicopsyche borealis	○	○	○	○	●				
Leptoceridae									
Oecetis	○	○		○	●				
Number of Genera:					**22**				**8**
Lepidoptera									
Pyralidae			○		●				●
Pterophila							○		
Synclita							○		
Coleoptera									
Gyrinidae									
Gyrinus	○				●				●
G. plicifer		○	○				○		
Haliplidae									
Haliplus	○				●				
Peltodytes simplex	○	○	○	○	●		○		●
Dytiscidae									
Agabinus					●				●
A. glabrellus		○	○				○		
A. sculpturellus							○		
Agabus	○		○	○	●		○		●
A. discors			○				○		

Table II.3. Continued.

	Location: Mainland					Santa Cruz Island			
Taxa: **Source*:**	**Cooper**	**Wenner**	**Furlong**	**Other**	**Combined**	**Literature**	**Furlong**	**Other**	**Combined**
A. disintegratus		○							
A. ilybiiformis		○							
A. obsoletus		○							
A. regularis				○					
A. seriatus intersectus						○	○	○	
Bidessus quadripustulatus			○		●				
Deronectes	○				●				●
D. deceptus		○	○						
D. griseostriatus		○							
D. striatellus		○	○			○	○		
Hygrotus medialis		○			●				
Hydroporus	○				●				●
H. vilis			○				○		
Hydrovantus brevipes			○		●		○		●
Liodessus	○				●				
Rhantus					●				●
R. gutticollis				○			○		
R. hoppingi		○							
Hydroscaphidae									
Hydroscapha natans							○		●
Hydrophilidae									
Anacaena	○				●				●
A. signaticollis							○		
Berosus			○	○	●				●
B. punctatissimus							○		
Crenitis seriellus		○			●				
Cymbiodyta			○		●				●
C. dorsalis		○				○	○		
C. imbellus		○							
C. punctatostriata		○				○			
Enochrus			○		●				●
E. hamiltoni pacificus		○							
E. pectoralis						○	○		
Helochares normatus		○			●		○		●
Hydrobius fuscipes							○		●
Hydrochara lineata				○	●	○	○	○	●

Table II.3. Continued.

Location:	Mainland					Santa Cruz Island			
Taxa: **Source*:**	**Cooper**	**Wenner**	**Furlong**	**Other**	**Combined**	**Literature**	**Furlong**	**Other**	**Combined**
Hydrophilus triangularis								○	●
Laccobius	○				●				●
L. californicus						○	○		
L. ellipticus						○	○		
Tropisternus			○		●				●
T. californicus						○		○	
T. ellipticus			○			○	○	○	
T. salsamentus		○							
Hydraenidae		○							
Hydraena					●				●
H. arenicola						○			
H. circulata						○			
H. vandykei			○			○	○		
Ochthebius					●				●
O. interruptus						○	○		
O. puncticollis			○			○	○		
Psephenidae									
Eubrianix edwardsi	○	○	○	○	●				
Dryopidae									
Helichus spp.	○		○		●				
H. immsi		○							
H. suturalis		○							
Scirtidae							○		●
Elmidae									
Heterlimnius koebeli	○		○		●				
Optioservus	○				●				
Ordobrevia nubifera							○		●
Zaitzevia parvula	○				●				
Approximate Number of Genera:					**28**				**23**
Diptera									
Blephariceridae									
Blepharicera			○	○	●				
B. micheneri	○								
Tipulidae									
Antocha	○	○		○	●				

Table II.3. Continued.

	Location:								
	Mainland					Santa Cruz Island			
Taxa: **Source*:**	Cooper	Wenner	Furlong	Other	Combined	Literature	Furlong	Other	Combined
Dicranota	○		○	○	●		○		●
Erioptera pallipes				○	●	○			●
Hexatoma	○	○	○	○	●		○		●
Holorusia hespera			○		●	○	○		●
Limonia				○	●		○		●
L. defuncta defuncta						○			
Pedicia				○	●	○			●
Rhabdomastix						○			●
Tipula	○	○	○	○	●	7 spp.	○	○	●
Culicidae									
Aedes	○				●		○		●
A. sierrensis						○			
Anopheles	○				●	○			●
Culex	○		○		●		○		●
Culex apicalis						○			
C. erythrothorax						○			
C. peus						○			
C. tarsalis						○			
C. thriambus						○			
Psychodidae									
Maruina	○	○	○	○	●		○		●
Pericoma	○				●				
Ceratopogonidae	○		○		●	○	○		●
Culicoides baueri						○			
C. cacticola						○			
C. copiosus						○			
C. sitiens						○			
Palpomyia linsleyi						○			
Simulidae									
Simulium					●				●
S. argus			○						
S. aureum			○				○		
S. bivittatum			○						
S. canadense	○								
S. latipes							○		
S. piperi	○		○				○		
S. virgatum	○		○				○		

Table II.3. Continued.

Taxa:	**Source*:**	**Location:** Mainland Cooper	Wenner	Furlong	Other	Combined	Santa Cruz Island Literature	Furlong	Other	Combined
Chironomidae										
(Tanypodinae)										
Ablabesmyia								○		●
Labrundinia								○		●
Pentaneura								○		●
Procladius								○		●
Rheopelopia		○				●				
Zaverlimyia								○		●
(Orthocladiinae)										
Brillia		○				●				
Cardiocladius		○				●		○		●
Corynoneura		○	○			●		○		●
Cricotopus		○				●		○		●
Eukiefferiella		○				●		○		●
Limnophyes		○				●				
Microspectra								○		●
Orthocladuis		○				●		○		●
Paratrichocladius		○				●				
Thienemanniella		○	○			●		○		●
Tvetenia		○				●				
(Chironominae)										
Calospectra			○			●				
Chironomus			○			●		○		●
Kiefferulius								○		●
Polypedilum		○				●				
Rheotanytarsus		○	○			●		○		●
Tanytarsus								○		●
Dixidae										
Dixa		○			○	●				●
D. (Dixa)				○				○		
D. (Meringodixa)			○	○				○		
D. (Paradixa)								○		
Stratiomyidae										
Euparyphus		○	○	○	○	●		○		●
Odontomyia			○	○	○	●	○	○		●
Stratiomys					○	●		○		●

Table II.3. Continued.

	Location:								
	Mainland					**Santa Cruz Island**			
Taxa: **Source*:**	**Cooper**	**Wenner**	**Furlong**	**Other**	**Combined**	**Literature**	**Furlong**	**Other**	**Combined**
Tabanidae									
Chrysops	○	○			●		○		●
Tabanus	○	○			●		○		●
T. punctifer						○			
Dolichopodidae	○		○		●		○		●
Dolichopus talus						○			
Empididae	○		○		●		○		●
Ephydridae			○		●	○	○		●
Sciomyzidae	○				●		○		
Muscidae									●
Limnophora	○		○	○	●		○		●
L. discreta						○			
Approximate Number of Genera:					**42**				**41**

*Source:

Combined	= Combined records
Cooper	= Cooper et al. 1986
Furlong	= Furlong collections from mainland Santa Barbara County streams/Santa Cruz Island streams
Literature	= Published and unpublished sources as described in Chapter 1.
Other	= Mainland- Santa Barbara Natural History Museum collection and records; literature records. = Santa Cruz Island - Santa Barbara Natural History Museum, Natural History Museum of Los Angelos County, and Santa Cruz Island Reserve collections.
Wenner	= Wenner et al. 1977

** Some specimens only identified to family level.

Table II. 4. Distributions and characteristics of aquatic insect taxa in mainland streams. Local distribution records from Wenner et al. (1977), Cooper et al. (1986), Santa Barbara Museum of Natural History, and Furlong collection. Information regarding taxon characteristics from Usinger (1971), Edmunds et al. (1976), Wiggins (1977), Menke (1979), Merritt and Cummins (1984), and Thorp and Covich (1991). Taxa present only on the mainland are indicated by boldface type.

Taxon:	Streams[a]:	Elevation:		Adult Characteristics:					Habitat Range[c]:		
		<100 m	> 100 m	Duration	Body Size[b]	Flight[c]	Season of Emergence[d]	Generation Time (years)	Lentic	Lentic & Lotic	Lotic
Ephemeroptera				< 4 days		Weak					
Siphlonuridae	Rt Rf		x		Medium		Sp-Sm	<1 to 1			x
Baetidae	C Rt S Rf J	x	x		Small-Medium	1 mile	Sp-Fl	< 0.5		x	
Heptageniidae	C Rt S Rf J	x	x	2-4 days	Medium		Sp-Fl	<1			x
Ephemerellidae	Rt Rf	x	x		Medium		Sp-Sm	<1 to 1			x
Tricorythidae	Rt S Rf J	x	x		Small		Sp-Sm	< 0.5		x	
Caenidae	C Rt Rf J	x	x	3-4 hours	Small		Sp-Sm	< 0.5		x	
Leptophlebiidae	C Rt S Rf J	x	x		Small		Sp-Fl	<1 to 1			x
Odonata				2-4 weeks		Strong					
Cordulegastridae	C Rt Rf		x		Large	Strong	Sp-Sm	3 to 4			x
Gomphidae	Rt S		x		Large	Weak	Sp-Sm	1 to 4			x
Aeshnidae	Rt		x		Large	Strong	Sm	2 to 4	x		
Libellulidae	C Rt Rf	x	x		Large		Sp-Fl	1 to 4		x	
Calyopterygidae	Not Given				Large	Near Water	Sp-Fl	1 to 2			x
Lestidae	C Rt S Rf J	x	x		Large		Fl	< 0.5 to 1		x	
Coenagrionidae	C Rt S Rf J	x	x		Medium	Far	Sp-Fl	0.5 to 1		x	
Plecoptera				< 2 weeks		Weak		1 to 3			
Taeniopterygidae	Rt J	x	x		Small-Medium		W-Sp	1			x
Nemouridae	Rt Rf J	x	x		Small		Sp-Fl	1			x
Leuctridae	Rt		x		Small		Sp	1			x
Capniidae	Rt		x		Small		W-Sp	1			x
Perlidae	Rt Rf		x		Medium		Sp	1 to 3			x

Table II. 4. Continued.

Taxon:	Streams[a]:					Elevation:		Adult Characteristics:					Habitat Range[e]:		
						<100 m	> 100 m	Duration	Body Size[b]	Flight[c]	Season of Emergence[d]	Generation Time (years)	Lentic	Lentic & Lotic	Lotic
Perlodidae		Rt			J	x	x		Small-Medium		Sp	1			x
Chloroperlidae		Rt		Rf			x		Small		Sp-Sm	1 to 2			x
Hemiptera								3-4 months							
Saldidae									Small	Strong	Sm-F			x	
Hebridae				Rf		x	x		Small	Far	Sm-F	<0.5 to 1	x		
Veliidae	C	Rt	S	Rf	J	x	x		Small	Strong	Sm-F	0.5 to 1		x	
Gerridae		Rt	S	Rf		x	x		Medium-Large		Sm-F	0.5 to 1		x	
Nepidae					J	x			Large		Sm-F	0.5 to 1		x	
Belostomadidae	C	Rt	S	Rf		x	x		Large	To Light	Sm-F	0.5 to 1			x
Corixidae	C	Rt		Rf		x	x		Medium	Far				x	
Naucoridae		Rt			J	x			Medium	Rare		1		x	
Notonectidae	C	Rt		Rf	J	x	x		Medium	Far	Sm-F	0.5 to 1		x	
Megaloptera															
Sialidae		Rt		Rf		x	x		Large	Rare	Sm-F	1 to 2		x	
Corydalidae		Rt		Rf		x	x		Large	Far	Sp-Sm	2 to 5			x
Trichoptera								1 month		To Light		<1 to 1			
Philopotamidae	C	Rt	S	Rf		x	x		Small		Sp-Sm	1			x
Psychomyiidae		Rt	S	Rf	J	x	x		Small-Medium		Sp-Sm	0.5 to 1			x
Polycentropodidae	C	Rt		Rf	J	x	x		Small		Sm	1			x
Hydropsychidae	C	Rt	S	Rf	J	x	x		Small-Medium			0.5 to 1			x
Rhyacophilidae	C	Rt	S	Rf			x		Small-Medium			1			x
Glossosomatidae	C	Rt		Rf			x		Small		Sp-Sm	1			x
Hydroptilidae		Rt	S	Rf	J	x	x		Small			<1			x
Brachycentridae		Rt		Rf		x	x		Small-Medium		Sp-Fl	1			x
Lepidostomatidae	C	Rt	S	Rf	J	x	x		Small-Medium			1			x

Table II. 4. Continued.

Taxon:	Streams[a]:	Elevation:		Adult Characteristics:					Habitat Range[e]:		
		<100 m	> 100 m	Duration	Body Size[b]	Flight[c]	Season of Emergence[d]	Generation Time (years)	Lentic	Lentic & Lotic	Lotic
Limnephilidae	Rt		x		Small-Medium			<1			x
Sericostomatidae	C Rt Rf J	x	x		Small-Medium			1			x
Odontoceridae	Not Given				Small-Medium			<1			x
Helicopsychidae	C Rt Rf	x	x		Small-Medium		Sm	1		x	
Leptoceridae	Rt		x		Small-Medium			1		x	
Lepidoptera											
Pyralidae	C Rt S J	x	x					< 0.5		x	
Coleoptera											
Gyrinidae	Rt Rf J	x	x	3-4 months	Small-Medium		F	1		x	
Haliplidae	C Rt S Rf J	x	x	3-4 months	Small			1		x	
Dytiscidae	C Rt S Rf J	x	x	3-4 months	Small-Large	Readily	F	0.5 to 1		x	
Hydroscaphidae	Not Given				Small			<1			x
Hydrophilidae	Rt Rf J	x	x	3-4 months	Small-Large			1		x	
Hydraenidae	Rf		x	3-4 months	Small	None				x	
Psephenidae	C Rt S Rf		x		Small			1 to 2			x
Dryopidae	Rf J	x	x		Small	15 miles		1			x
Scirtidae	Not Given			Short-lived	Small				x		
Elmidae	Rt S Rf J	x	x	1 year	Small	Rare		2			x
Diptera											
Blephariceridae	Rt S Rf		x	1-2 weeks	Small						x
Tipulidae	C Rt S Rf J	x	x	Short	Small-Large			<0.5 to 1		x	
Culicidae	Rt J	x			Small			<0.5 to 1		x	x
Psychodidae	Rt S Rf	x	x		Small					x	x
Ceratopogonidae	Rt Rf J	x			Small					x	
Simulidae	C Rt S Rf J	x	x		Small	Far		<0.5 to 1		x	x

Table II. 4. Continued.

Taxon:	Streams[a]:	Elevation:		Adult Characteristics:					Habitat Range[e]:		
		<100 m	> 100 m	Duration	Body Size[b]	Flight[c]	Season of Emergence[d]	Generation Time (years)	Lentic	Lentic & Lotic	Lotic
Chironomidae	C Rt S Rf J	x	x	< 2 weeks	Small			< 0.5		x	
Dixidae	C Rt S Rf	x	x		Small						x
Stratiomyidae	C Rt S Rf J	x	x		Small-Medium					x	
Tabanidae	Rt		x		Medium			0.5 to 1.5		x	
Dolichopodidae	Rt S Rf	x			Small-Medium					x	
Empididae	Rt Rf	x	x		Small					x	
Ephydridae	Rf	x			Small				x		
Sciomyzidae	Not Given				Small					x	
Muscidae	C Rt Rf	x	x		Small						x

[a] C= Cold Springs; J = Jalama; Rf = Refugio; Rt = Rattlesnake/Mission; S = San Jose; Not Given = Records exist but stream not specified

[b] Small = < 10 mm; Medium = 10 to 20 mm; Large = > 20 mm

[c] Most references give strength of flight in descriptive terms

[d] Sp = Spring; Sm = Summer; F = Fall; W = Winter

[e] Habitat range for collected and/or listed genera within orders, Merritt and Cummins 1984

Table II.5. Number of insect genera per order observed for mainland streams and number of genera observed and expected for Santa Cruz Island streams.

Order	Total	Mainland	Island Observed	Island Expected
Ephemeroptera	11	11	5	7
Odonata	16	16	9	10
Plecoptera	11	11	1	7
Hemiptera	12	11	6	7
Megaloptera	3	3	2	2
Trichoptera	22	22	8	13
Lepidoptera	2	1	2	1
Coleoptera	33	28	23	20
Diptera	51	42	41	31
Total Taxa	161	145	97	97

Table II.6. Functional guilds for genera of Santa Barbara County and Santa Cruz Island Trichoptera and Plecoptera.

	Functional Group:*					
	Non-Shredder/Collector		Shredder		Collector	
	Mainland	Island	Mainland	Island	Mainland	Island
Plecoptera:						
Taenionema			X +			
Malenka			X +			
Leuctridae			X			
Capnia			X	X		
Eucapnopsis			X			
Isocapnia			X			
Mesocapnia			X			
Calineuria	X					
Isoperla	X					
Alloperla					X+?	
Sweltsa	X					
% of taxa per guild	**27**	**0**	**64**	**100**	**9**	**0**
Trichoptera						
Wormaldia					X	X
Tinodes					X +	X +
Polycentropus	X	X				
Cheumatopsyche					X	
Hydropsyche					X	X
Rhyacophila	X					
Agapetus	X					
Hydroptila	X	X				
Neotrichia	X					
Ochrotrichia					X +	X +
Micrasema			X +			
Lepidostoma			X	X		
Clostoeca			X +			
Dicosmoecus	X +					
Neophylax	X					
Neothremma	X					
Pseudostenophylax			X +			
Psychoglypha					X +	
Gumaga			X+	X+		
Marilia			X			
Helicopsyche	X					
Oecetis	X					
% of taxa per guild	**46**	**25**	**27**	**25**	**27**	**50**

* = Functional group assignments according to Merritt and Cummins 1984

\+ = Taxa also assigned to other functional groups

? = Designation unclear

Table II.7. Comparison of California Channel Island and mainland fauna.

	Number of Mainland Taxa	Number of Island Taxa	% of Mainland Taxa*	Source
Vertebrate Fauna:				
Herptofauna	20 (Ventura County)	9 (Northern Channel Islands)	45%	Savage 1967
		9 (Santa Cruz Island)	45%	
Breeding Land Birds	160 (Nearby Southern California Mainland)	56 (California Channel Islands)	35%	Diamond & Jones 1980
		39 (Santa Cruz Island)	24%	
Land Mammals (excluding bats)	38 (Coastal California)	4 (Northern Channel Islands)	12%	van Bloeker 1967 Wenner and Johnson 1980
		4 (Santa Cruz Island)	12%	
Terrestrial Insects:				
Orthoptera	70 (Santa Monica Mnts.)	54 (California Channel Islands)	77%	Rentz and Weissman 1974
		37 (Santa Cruz Island)	53%	Weissman 1985
Lepidoptera	901 (Big Creek Reserve Monterey, California)	726-760 (California Channel Islands)	80-84%	Powell 1994
		543+ (Santa Cruz Island)	60%	
Bees	520 estimated (Southern California Coast Ranges)	161 (California Channel Islands)	31%	Rust et al. 1985 Thorp et al. 1994
		105 (Santa Cruz Island)	19%	
Stream Insects:	Mainland	Santa Cruz Island		Wenner and Busath 1977
Ephemeroptera	11	5	45%	Cooper et al. 1986
Odonata	16	9	56%	Furlong Collection
Plecoptera	11	1	9%	Museum/Reserve Collections
Hemiptera	11	6	55%	
Megaloptera	3	2	67%	Literature Sources (Appendix I)
Trichoptera	22	8	36%	
Lepidoptera	2	2	100%	Miller (unpublished list)
Coleoptera	28	23	82%	
Diptera	42	41	98%	
Total	146	97	66%	

* Percentages are biased toward island(s) as endemics and taxa exclusively occurring on island(s) are included in the counts.

Table II. 8. The distribution of aquatic insects on islands.

Island:*	S	B	SCI	T	C	F/S	C/S	M	NC	H
km from nearest possible source:	18	26	38	300	600	700	700-800	800	1200	3200
Taxa										
Ephemeroptera	-	x	x	x	ng	x	x	-	x	-
Odonata					ng	ng	ng		ng	
Aeshnidae	-	-	x	x				-		-
Libellulidae	-	-	x	x				-		x
Coenagrionidae	-	-	x	-				-		x
Plecoptera	-	x	x	-	x	-	-	-	-	-
Hemiptera					ng					
Gerridae	-	x	x	x		x	x	-	x	-
Veliidae	-	x	x	x		x	x	-	x	-
Notonectidae	-	-	x	x		x	x	-	x	-
Mesoveliidae	-	-	-	-		x	-	-	x	x
Corixidae	-	-	x	x		-	-	-	x	-
Pleidae	-	-	-	-		-	-	-	x	-
Hydrometridae	-	-	-	x		-	-	-	x	-
Belostomatidae	-	-	-	-		-	-	-	x	-
Hebridae	-	-	-	x		-	-	-	-	-
Saldidae	-	-	x	-		-	-	-	-	-
Naucoridae	-	-	-	-		-	-	-	-	-
Nepidae	-	-	-	-		-	-	-	-	-
Megaloptera	-	-	x	-	-	-	-	-	-	-
Trichoptera	-	x	x	-	x	x	-	-	x	-
Coleoptera	x	x	x	x	ng	ng	ng	-	ng	x
Diptera	x	x	x	x	x	x	x	x	x	x

* Island	Location of nearest possible source populations:
S = Surtsey	South of Iceland, "born" 1963, ecologically young (Lindroth et al. 1973)
B = Bornholm	South of Sweden, possibly continental (Bronmark et al. 1984)
SCI = SCI	West of California (See Table II.5)
T = Tenerife	West of Morocco (Malmqvist et al. 1993)
C = Campbell	South of New Zealand, continental (Winterbourn 1980)
F/S = Fiji/Samoa	East of New Caledonia, Fiji is continental (Winterbourn 1980)
C/S = Cook/Societies	East of Fiji/Samoa (Winterbourn 1980)
M = Macquarie	South of Campbell, continental? (Marchant and Lillywhite 1994)
NC = New Caledonia	East of Australia, continental (Winterbourn 1980)
H = Hawaii	West of California (Howarth and Polhemus 1991)

x = Present
- = Absent
ng = Information not given

Table II.9. Results of shipboard and aerial trapping for aquatic insects (Holzapfel and Harrell 1968, Holzapfel and Perkins 1969, Holzafpel 1978) compared with families collected from islands.

Taxa recovered by shipboard and aerial trapping:			Family recovered on islands:* (references in Table II.8)			
Order		**Family**	Santa Cruz	Tenerife	Southwest Pacific**	Hawaii
Ephemeroptera						
		Palingeniidae	-	-	x	-
Odonata					ng	
	Zygoptera					
		Coenagrionidae	x	-		x
	Anisoptera					
		Libellulidae	x	x		x
Hemiptera						
		Corixidae	x	x	-	-
		Gerridae	x	x	x	-
		Mesoveliidae	-	-	x	x
		Pleidae	-	-	-	-
		Saldidae	x	-	-	-
		Veliidae	x	x	x	-
Trichoptera			x	x	-	-
Coleoptera					ng	
		Dytiscidae	x	x		x
		Gyrinidae	x	x		-
		Haliplidae	x	x		-
		Hydrophilidae	x	x		x
		Noteridae	-	-		-
Diptera					x	
		Ceratopogonidae	x	x		x
		Chironomidae	x	x		x
		Culicidae	x	x		i
		Dolichopodidae	x	-		x
		Empididae	x	x		-
		Ephydridae	x	-		x
		Muscidae	x	-		x
		Psychodidae	x	-		x
		Simuliidae	x	x		-
		Stratiomyiidae	x	x		i
		Tipulidae	x	x		x

* x = present
- = absent
i = introduced
ng = not given

** Southwest Pacific islands = oceanic islands: Samoa, Cooks, Societies

Figure 2.1 Location of sampled mainland streams (● indicates approximate location of mainland sample sites, Figure 1.2 shows island sample sites).

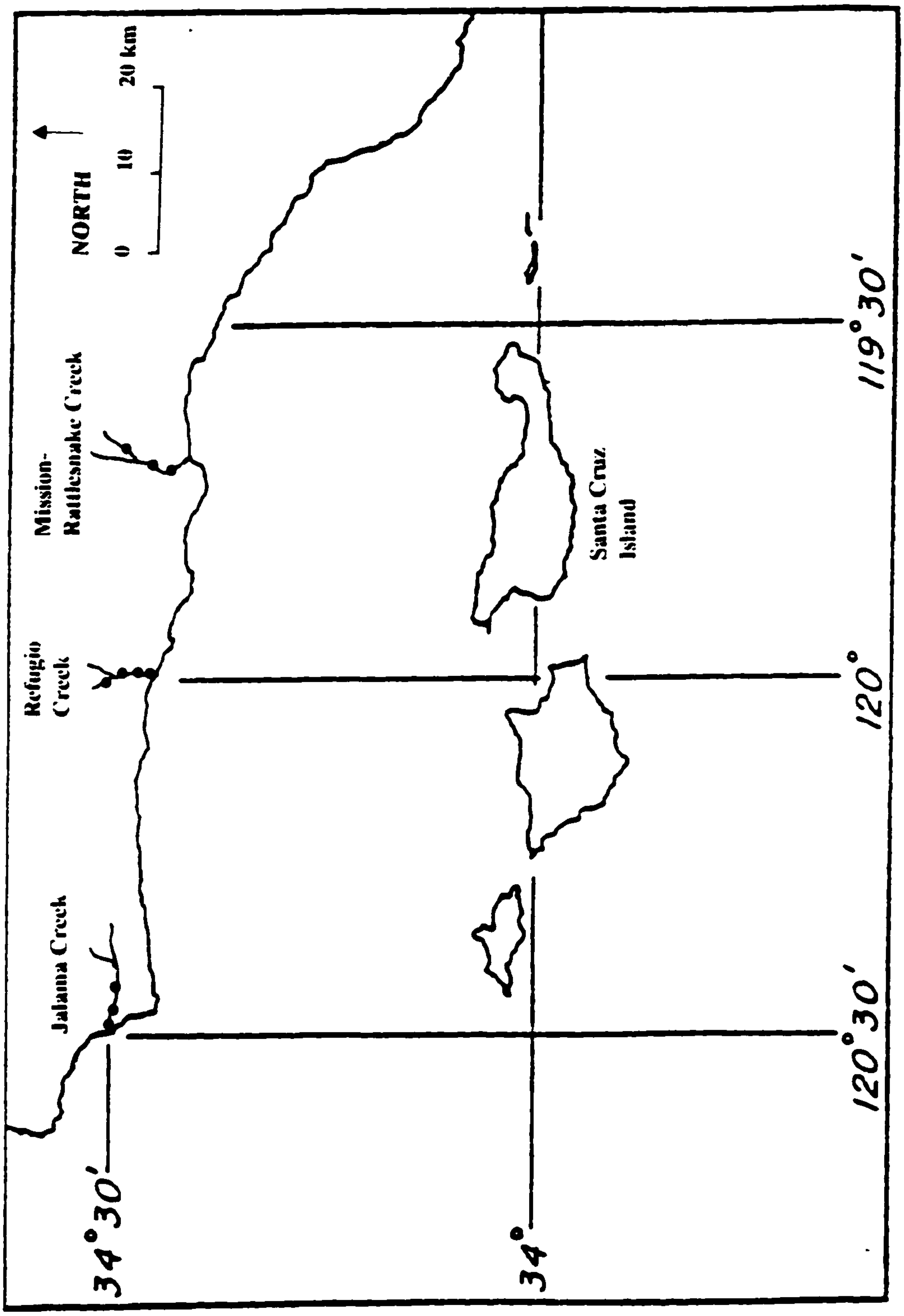

Jalama Creek
Refugio Creek
Mission-Rattlesnake Creek
NORTH
0
10
20 km
Santa Cruz Island
34°30'
34°
120°30'
120°
119°30'

Figure 2.2. Differences in the representation of total, mainland, and island taxa per insect order. Percentages are given for total (mainland + island) taxa at two levels of taxonomic resolution. Percentages are also given for mainland and island genera alone. The percentages of genera in the orders Dipteran and Coleopteran were higher on island than mainland streams, whereas the opposite was observed for the orders Trichoptera and Plecoptera.

Figure 2.2. Percent of total, mainland, and island taxa per order

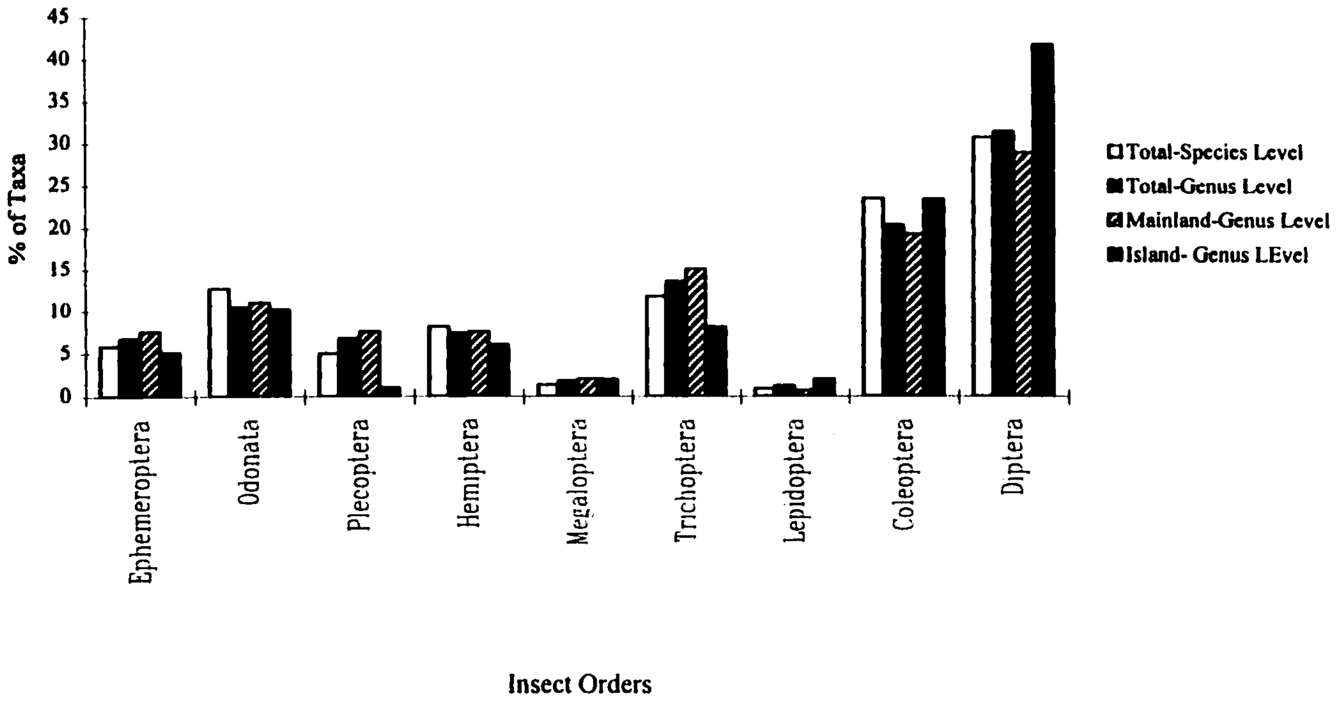


Figure 2.3. Comparisons of the distributions and life history characteristics of mainland taxa found on Santa Cruz Island vs. taxa occurring on the mainland alone.

Figure 2.3 Distributions and characteristics of taxa occurring on the mainland and island vs. mainland alone

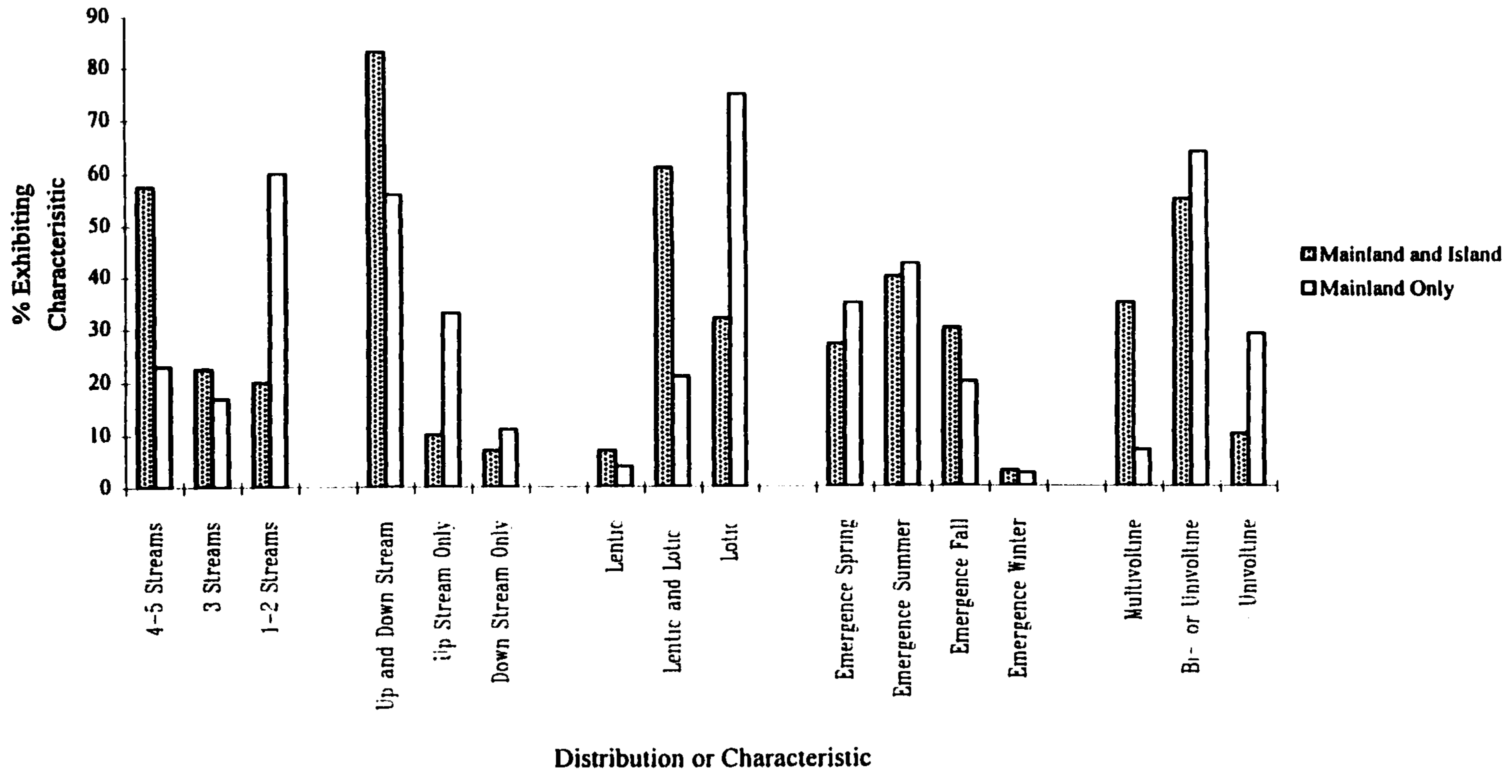
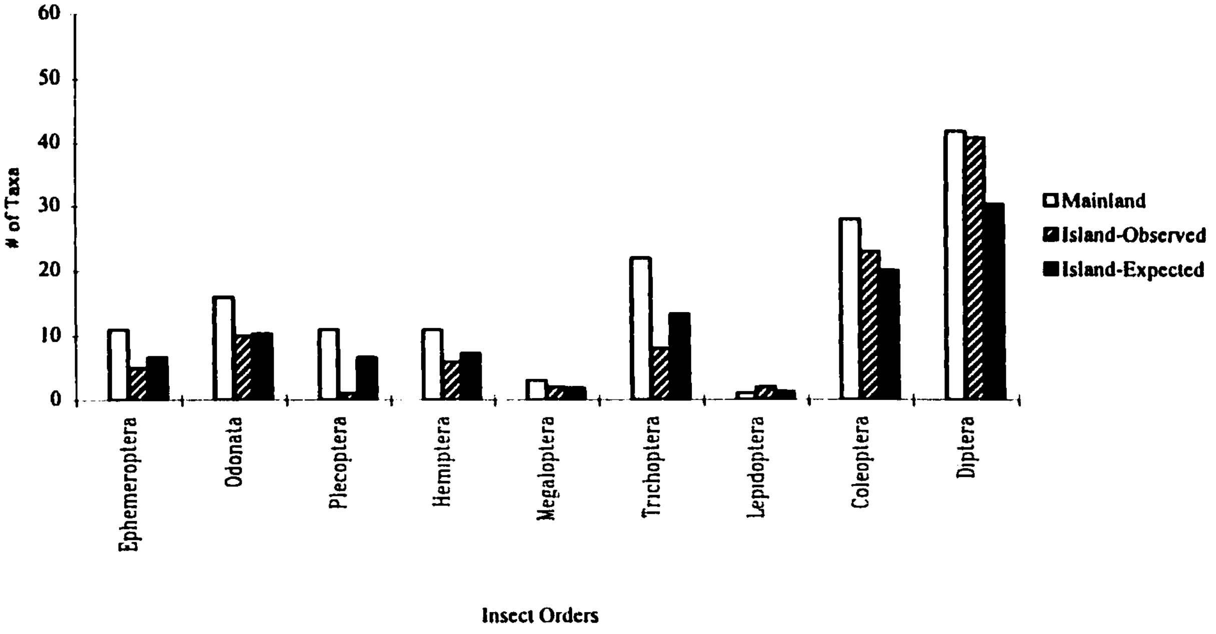


Figure 2.4. Number of insect genera per order from Santa Cruz Island and mainland Santa Barbara County stream collections and records. The number of genera collected and recorded from the mainland is compared to the number of taxa collected and recorded from Santa Cruz Island. In addition, the expected number of island taxa per order is compared to the observed number of island taxa per order. The expected values were calculated as 60% of the total (mainland + island) taxa per order (Table II.5). In most orders, the expected and observed values were fairly close; however, observed values exceed expected values for island Diptera and Coleoptera. Observed values were lower than those expected for the orders Plecoptera and Trichoptera.

Figure 2.4. Number of insect taxa per order from Santa Cruz Island and mainland Santa Barbara County stream collections and records.



CHAPTER III

SPATIAL AND TEMPORAL VARIATION OF STREAM INVERTEBRATE COMMUNITIES ON SANTA CRUZ ISLAND

INTRODUCTION

Ecologists attempt to recognize patterns in communities and determine the processes that generate those patterns (Townsend 1989). Ecological work is complicated because abiotic and biotic processes influence communities at different scales of time and space, resulting in patchy, or uneven, distributions of organisms (Legendre and Demers 1984, Cooper et al. 1997). At large spatial scales, lotic systems vary regionally, due to differences in climate, vegetation, topography and land use; they also varylongitudinally from head to mouth (Hynes 1970, Vannote et al. 1980, Poff and Ward 1985, Grubaugh et al. 1996). These large-scale spatial patterns are superimposed upon finer grained spatial heterogeneity such as alternating riffles and pools within a reach, differing flow regimes within the water column and bottom, and local variation in substrate size and texture (Rabeni and Minshall 1977, Stazner and Higler 1986, Dudley and D'Antonio 1991, Cooper et al. 1997 and 1998). Temporal variation in streams range from geological time spans to diurnal activity cycles and insect movements (Minshall 1988). Many studies that address temporal heterogeneity have focused on the roles of disturbance frequency and intensity, seasonal flow variation, and their concomitant influences on community structure and function (e.g., Poff and Ward 1989, Delucchi 1988, Delucchi and Peckarsky 1989, Boulton et al. 1992a, Flecker and Feifarek 1994).

The need to simultaneously investigate temporal and spatial variation in community structure stems from the realization that variability in time and space occurs simultaneously (e.g., Hawkins and Sedell 1981, Boulton and Lake 1992a and 1992b, Closs and Lake 1994, Maridet et al. 1996). Most stream studies have addressed time spans of less than one year, and range spatially from within habitats (pools or riffles) to entire streams (Resh and Rosenberg,1989). Although phenomena operating at large scales may dominate some aspects of community structure, small scale heterogeneity (such as small scale variation in velocity or substrate size) contributes to patchiness at local scales.

This chapter focuses on a description of the taxonomic composition of Santa Cruz Island stream communities at varying spatial and temporal scales. Spatial scales addressed include all seven study streams collectively, individual streams, and habitat types (pools vs. riffles). Because this project aimed to collect as many taxa as possible, streams were selected from widely separated areas of the island.

In addition, the streams drain varied landscape types and differ in watershed size, gradient, aspect, vegetation, and lithology. Because of spatial heterogeneity among the streams, I would expect the streams to differ markedly in their taxonomic composition. I also would expect to find variation in taxonomic assemblages in pools versus riffles due to habitat-level differences (flow regime, water depth, substrata).

The temporal scales addressed included the 1993 to 1996 sampling effort (see Table I.3) and seasonal differences in taxonomic composition. Due to seasonal changes in environmental conditions, most notably stream flow, I would expect to find seasonal differences in taxonomic composition. Temporal phenomena should influence all streams on the island in the same way because they share the same climate. Due to the interplay of spatial and temporal heterogeneity, however, temporal changes in physical factors (such as winter scour) may affect each stream differently. For example, streams with smaller watersheds may escape severe damage by winter storm events compared to those with larger watersheds (Poff and Ward 1989). In short, this portion of the study describes patterns of community composition at varying temporal and spatial scales.

METHODS

Samples used for this part of the study were taken primarily in 1993 and 1994 (supplemental samples were taken in 1995 and 1996). Descriptions of the sampling sites, standard sampling methods, and sample processing were given in Chapter I. A sweep and kick sample from each habitat type (pool and riffle) at each site were grouped and treated as a single sampling unit for calculations of mean taxonomic richness. I used Jaccard's similarity coefficient to analyze taxonomic similarity across streams, habitats and seasons. Jaccard's similarity coefficient = a/(a+b+c), with "a" being the number of taxa common to both sites and "b" and "c" the number of taxa occurring exclusively in each of the two sites (i.e. b = number of taxa occurring only in site 1 and c = number taxa occurring only in site 2, Pielou 1979). Guild assignments for collected taxa were determined from Merritt and Cummins (1984). Occasionally, insects were assigned to more than one functional guild, due to ontogenetic changes in food habits, catholic diets, or lack of taxonomic resolution.

RESULTS AND DISCUSSION

Results and discussions are unified in this section, addressing spatial and temporal patterns in total richness (total number of taxa), mean richness (number of taxa per sample unit), and compositional similarity of Santa Cruz Island stream insect communities.

General Spatial Patterns

Overall, this study yielded 82 taxa (primarily genera, excluding Ceratopogonidae, Chironomidae, Dolichopodidae, Empididae, Ephydridae, and Sciomyzidae which were identified to family; each family was counted as one genera). The numbers of taxa collected per sample unit (combined kick and sweep sample), were quite variable (mean = 8.86 , SD = +/-4.02, Table III.1). The distribution of taxa among sample units was uneven, with 20 of the 80 taxa found in less than 1% of the sample units and only 2 taxa found in more than 50% of the sample units (Table III.2). As observed in other studies, most taxa occurred rarely and only a few were common (Allan 1995). Given the adequacy of sampling efforts indicated by taxa per cumulative sampling effort curves (Chapter I, Figure I.4.), these data may indicate a patchy distribution of organisms within and among the seven Santa Cruz Island streams rather than differences in sampling effort. Consequently, sampling of additional island streams could yield more taxa.

Each of the seven sampled streams accounted for various subsets of the collective taxonomic pool. Overall taxonomic richness per stream ranged from 35 to 53 taxa (Table III.1). Mean number of taxa per sample for each of the streams ranged from 5.12 (SD = +/-3.23) to 11.28 (SD = +/- 4.08). Two streams, Sauces and Willows, had low mean richness compared to the remaining five streams (Table III.1). Willows, Sauces, and Horquetta had lower overall richness compared to the remaining streams.

Increasing taxonomic richness presumably correlates with increasing habitat heterogeneity, which is assumed to be correlated with increasing habitat area (e.g., Williamson 1988). That pattern did not emerge in this study (see Chapter IV). Rather, the stream with the smallest watershed area (Black Point, Table I.1, Chapter I) had the greatest taxonomic richness.

The taxonomic composition of the streams varied considerably, with similarity coefficients ranging from 0.41 to 0.70 (Figure 3.1). The mean similarity coefficient (0.51) of the seven streams indicated that, on average, the streams shared approximately 50% of the taxa collected at any one time. Insect orders with low numbers of taxa and low habitat specificity (found equally in riffles and pools) had the highest similarities between streams (Table III.3, Figure 3.1). Similarity was low within orders having many, uncommon taxa. For example, Ephemeroptera (5 taxa) and Trichoptera (8 taxa) had mean similarities of 0.84 and 0.72 respectively. By contrast, coleopterans (21 taxa) and dipterans (20 taxa), had the lowest mean similarities (0.43 and 0.46, respectively; Figure 3.1).

Pools vs. Riffles

Samples were collected from two habitat types, pools and riffles, at each stream site. Island-wide (seven streams combined), pool habitats exhibited a higher degree of overall richness than riffle habitats (74 taxa in pools, 64 taxa in riffles, Table III.1). In addition, the mean number of taxa per sample was greater for pools than riffles, with values of 9.72 (SD = +/- 4.42) and 8.03 (SD = +/- 3.40) taxa, respectively. Taxonomic richness in the pools and riffles of individual streams generally corresponded with the combined results noted above. In five of the seven streams, total richness in pool habitats exceeded that of riffle habitats (Table III.1); however, pool and riffle richness (33 taxa) was identical in Coches Stream and the number of riffle taxa exceeded pool taxa in Horquetta Stream. The mean numbers of pool taxa per sample exceeded the mean for riffles in all streams, with mean number of pool taxa ranging from 5.82 to 13.33 and riffle taxa ranging from 4.38 to 10.12 (Table III.1).

The results of this study agree with those obtained by other researchers. Boulton and Lake (1992a) found greater numbers of taxa in pool than in riffle habitats in intermittent streams. They concluded that pools may provide refuges from dessication during periods of drying. They found that taxonomic similarity was greater between riffles and pools in streams that frequently stopped flowing (Boulton and Lake 1990). Some studies from permanent streams also reported a greater or similar number of taxa and/or greater densities in pools as opposed to riffles (Logan and Brooker 1983, McCulloch 1986). Therefore, factors other than intermittency may influence observed patterns of community structure. Departures from island-wide patterns in richness between pool and riffle habitats observed in Coches and Horquetta Streams may relate to differences in flow patterns; however, both streams have premanent flow.

Over 18 taxa occurred more commonly in pools, the majority of these being predatory insects such as odonates, hemipterans, and beetles (Table III.3). In contrast, only 5 taxa occurred more commonly in riffles; these taxa were a mixture of collectors, scrapers, and predators (Table III.3). The overall similarity in composition of the pool and riffle habitats was high (Jaccard's similarity coefficient = 0.80); however, mean richness of predatory taxa in pools (4.84) exceeded that in riffles (3.02, Table III.4). The mean richness of prey taxa in pools did not differ greatly from that of riffles. As in the pooled results, mean predator richness was higher in pools compared to riffles for the majority of streams (Black Point, Coches, Laguna, Prisoners, and Willows, Table III.4). In only one case did any functional group other than predators show notably higher mean richness in one habitat. Collectors had higher mean richness in Coches Stream riffles compared with pools (Table III.4).

The above results support the concept that faunal assemblages can vary between pool and riffle habitats in the same stream (Rabeni and Minshall 1977, Cooper et al. 1986, Allan 1995). It is unclear whether biotic or abiotic factors are most responsible for these differences. Pools and riffles differ in both water depth and flow. Pools are characterized by deep water and slow currents, riffles by shallow water and relatively rapid currents. The difference in current velocity results in sediment sorting, with riffles typified by coarser substrata. The greater surface area and interstices of the coarse riffle substrate provides surface area for algal growth and zones of detrital build-up. That, in turn provides food resources for guilds of shredding, collecting and scraping insects (Rabeni and Minshall 1977, Flecker and Allan 1984). In addition, sedimentation is lower and oxygen content may be higher in riffles than in pools.

Biotic factors contributing to taxonomic differences between pools and riffles may be related to predator avoidance by prey animals. Predators typically occupy pools; therefore, prey animals that occupy riffle zones may avoid predation

(Bowlby and Roff 1986). In addition, the coarse substrata of riffles may provide additional cover for prey animals (Peckarsky 1986). Even though the overall similarity in taxonomic composition for riffles and pools was high, predatory taxa, such as odonates, hemipterans, and coleopterans, occurred more often in pools than in riffles (Table III.3, Table III.4). In contrast, prey taxa did not exhibit notably greater mean richness in riffles compared to pools (with one exception). Overall, higher taxonomic richness in pools vs. riffles may be related to the net downstream movement of riffle organisms (prey source) into the depositional pool habitats (prey sink) combined with a higher number of predator taxa in pools than in riffles. In addition, riffle organisms of intermittent streams may use pool habitats as refuges during dry period when flow ceases (Boulton and Lake 1992a).

Temporal Patterns

Total faunal richness varied seasonally, ranging from 57 (spring and fall) to 46 (winter) taxa (Table III.5). Total richness during the summer was similar to spring and fall, with 54 taxa. Mean taxonomic richness exhibited seasonal variation, ranging from 6.83(SD = +/-3.18) in the winter to 9.83(SD = +/-4.34) in the spring (Table III.5). Mean values for summer and fall samples were 9.06(SD = +/-3.59) and 8.92(SD = +/-3.78) respectively. The overlap in taxonomic composition between consecutive seasons (example winter vs. spring) ranged from 58% for fall and winter samples to 73% for spring and summer samples (Jaccard's similarity coefficient, Figure 3.2). Mean similarity for all seasons was 63% (Figure 3.2).

Seasonal variation in community structure generally correlates with, among other factors, seasonal changes in discharge (Cooper et al. 1986, Boulton and Lake 1992b, Closs and Lake 1994). This is especially true of streams in regions, such as southern California, that experience summer drought alternating with winter scour (Poff and Ward 1989). In these streams, richness and abundance is reduced in the winter by flood disturbances (Cooper et al. 1986, Boulton and Lake 1992b). Richness and abundance typically increase through spring, summer, and fall, until drought conditions result in a decrease in habitat area (Delucchi and Peckarsky 1989, Boulton and Lake 1992b). These trends may vary from year to year, depending on whether or not winter flooding occurs in the stream. The results observed in this study (all streams combined) generally agree with those observed by Boutlon and Lake (1992b), with lowest total richness and mean richness occurring in the winter; total richness and mean taxonomic richness did not vary greatly from spring to fall.

Temporal-Spatial Patterns

Seasonal observations of taxonomic richness in different habitats and streams provide insights regarding the interactive effects of spatial and temporal variablity in community structure. Overall taxonomic similarity for all streams across seasons combined was quite high (63%); however, mean taxonomic similarity of individual streams across seasons was decidedly lower, ranging from 37% to approximately 51% (Figure 3.2). Streams with overall low richness (Willows, Sauces, and Horquetta) also exhibited the lowest taxonomic similarity across seasons. In contrast, Black Point, with the higherst overal richness, had the highest taxonomic similarity across seasons.

In the previous section, differences in total and mean richness for winter samples versus samples from other seasons were observed at an island-wide scale. Although this general pattern occurred at the scale of most individual streams, Prisoners Stream exhibited higher richness in the winter (total and mean) compared to summer and fall; winter richness (total and mean) equalled fall richness in Sauces Stream (Table III.5)

Island-wide patterns in seasonal composition and richness do not adequately portray patterns found in individual streams. This disparity may illustrate why results of studies addressing seasonal variations in taxonomic composition among streams are often contradictary and emphasizes the need consider the effects of scale in ecological studies. To build a complete list of island stream insects, streams chosen for this study varied greatly in degree of intermittency, watershed area, aspect, and tendency to scour during winter flooding. Therefore, it is not surprising that general seasonal patterns in taxonomic similarity and richness cannot be readily applied to all seven streams.

For individual streams, total richness across seasons in pool and riffle habitats ranged from 36 to 54 and 35 to 47, respectively (Table III.5). In both pools and riffles, richness was lowest in winter and highest in the spring and fall. In all seasons, pools generally supported higher total and mean richness than riffles. These results correspond to temporal and spatial trends in total taxonomic richness observed in other studies (i.e., greater richness in pools, Boulton 1989, Boulton and Lake 1992b) and larger scale observations in this study.

Taxonomic similarity between pools and riffles across streams, as indicated by Jaccard's similarity coefficients, varied seasonally (Table III.6). Fall pool and riffle communites differed the most, with a Jaccard's coefficient of 0.49; spring pool and riffle assemblages exhibited the greatest degree of taxonomic overlap (Jaccard's coefficient = 0.75). Mean seasonal similarity of riffles and pool was approximately 61%. If riffle taxa migrate into pools during periods of drying, as suggested by Boulton and Lake (1992b), one might expect to find greater taxonomic similarity between these habitats during the summer and fall; however, the streams of this study are a combination of permanent and partially intermittent streams. Results from this "mixture" of stream types may not be comparable to results obtained from intermittent stream studies. In addition, the abiotic differences between pool and riffle habitats may be more pronounced in late summer and fall; these differences would be less pronounced during periods of high flow.

At the scale of individual streams, the island-wide pattern of seasonal similarity between pools and riffles (highest similarity in spring, lowest similarity in fall) was not observed (Table III.6, Figure 3.2). For example, only three streams exhibited highest similiarity between pools and riffles in the spring and lowest similarity in the fall was observed in only one stream. Winter pool-riffle similarity was highest in two streams and lowest in three streams. The same pattern was observed for summer poo-riffle similarities. These differences in seasonal pool-riffle similarities may be due to several interacting factors. These results may reflect differences in seasonal flow patterns found in individual streams, with some streams subjected to winter scour and/or periods of partial intermittency. In addition, the physical differences between pool and riffle habitats may vary among the individual streams, with pool and riffle habitats similar in one stream but very different in another. Quantitative sampling and experimental manipulations would give better indications of which environmental factors contribute to temporal-spatial patterns observed in individual streams.

CONCLUSION

Addressing the total and mean taxonomic richness of stream insects at varying temporal and spatial scales produced interesting patterns and anomalies. By describing how the insect communities of Santa Cruz Island streams vary in terms of overall richness, mean richness, and composition, this chapter illustrates the importance of considering patterns on a variety of temporal and spatial scales. The patchy distribution (between streams, habitats, and seasons) of the majority of taxa resulted in differences between large-scale and small-scale patterns. Although island-wide (seven streams combined) patterns of total and mean richness in pools versus riffles were observed in individual streams, island-wide patterns in seasonal richness and taxonomic composition were not observed in individual streams. These differences may be related to variations in flow regime (occurrence and degree of intermittency and scour) of individual streams.

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Table III.1 Total and mean (taxa per sampling unit) taxonomic richness of Santa Cruz Island stream insects (excluding genera of Ceratopogonidae, Chironomidae, Dolichopodidae, Empididae, Ephydridae, and Sciomyzidae, which are counted as one genera each). Each sample unit consists of a combined kick and sweep sample.

Stream: (catchment area)	Habitat Type:	Total taxa	Mean number of taxa (St.Dev.)	Number of Sampling Units
Island-wide				
(n.a.)	All pools	74	9.72 (+/-4.42)	110
	All riffles	64	8.03 (+/-3/40)	110
	Combined	80	8.86 (+/-4.02)	220
Black Point				
(1.09 km^2)	Pools	47	13.33 (+/-4.47)	18
	Riffles	29	9.22 (+/-2.29)	18
	Combined	55	11.28 (+/-4.08)	36
Coches				
(5.04 km^2)	Pools	33	11.31 (+/-2.52)	16
	Riffles	33	10.12 (+/-3.72)	17
	Combined	53	10.7 (+/-3.21)	33
Horquetta				
(1.83 km^2)	Pools	28	9.46 (+/-4.01)	15
	Riffles	30	8.53 (+/-3.04)	17
	Combined	35	8.96 (+/-3.49)	32
Laguna				
(12.16 km^2)	Pools	41	10.47 (+/-4.09)	17
	Riffles	37	9.63 (+/-3.16)	16
	Combined	50	10.06 (+/-3.64)	33
Prisoners				
(34.66 km^2)	Pools	44	9.75 (+/-4.01)	16
	Riffles	31	7.57 (+/-2.82)	14
	Combined	49	8.73 (+/-3.61)	30
Sauces				
(5.86 km^2)	Pools	34	5.82 (+/-3.88)	17
	Riffles	25	4.38 (+/-2.53)	16
	Combined	38	5.12 (+/-3.23)	33
Willows				
(6.32 km^2)	Pools	28	6.92 (+/-2.87)	11
	Riffles	24	6.33 (+/-2.41)	12
	Combined	35	6.59 (+/-2.59)	23

Table III.2 Frequency of occurrence of taxa in samples

Taxa	Number of Samples	% of Samples	Taxa	Number of Samples	% of Samples
Total # of samples	492	100			
Ephemeroptera			*Deronectes*	33	6.7
Baetis	331	67.3	*Hydroporus*	21	4.3
Callibaetis	163	33.1	*Hydrovantus*	2	0.4
Centroptilum	1	0.2	*Rhantus*	17	3.5
Caenis	138	28.0	*Hydroscapha*	21	4.3
Paraleptophlebia	16	3.3	*Anacaena*	3	0.6
Odonata			*Berosus*	11	2.2
Aeshna	8	1.6	*Cymbiodyta*	6	1.2
Anax	2	0.4	*Enochrus*	26	5.3
Libellula	28	5.7	*Helochares*	12	2.4
Paltohemis	51	10.4	*Hydrobius*	15	3.0
Sympetrum	3	0.6	*Hydrochara*	4	0.8
Archilestes	23	4.7	*Laccobius*	75	15.2
Argia	281	57.1	*Tropisternus*	50	10.2
Enallagma	41	8.3	*Hydraena*	2	0.4
Plecoptera			*Ochthebius*	9	1.8
Mesocapnia	4	0.8	*Ordobrevia*	3	0.6
Hemiptera			**Diptera**		
Microvelia	127	25.8	*Dicranota*	8	1.6
Aquarius	112	22.8	*Hexatoma*	10	2.0
Saldula	4	0.8	*Holorusia*	2	0.4
Graptocorixa	17	3.5	*Limonia*	7	1.4
Notonecta	81	16.5	*Tipula*	10	2.0
Megaloptera			*Aedes*	1	0.2
Neohermes	5	1.0	*Culex*	2	0.4
Trichoptera			*Maruina*	2	0.4
Wormaldia	7	1.4	Ceratopogonidae	4	0.8
Tinodes	44	8.9	*Simulium*	126	25.6
Polycentropus	15	3.0	Chironomidae	220	44.7
Hydropsyche	162	32.9	*Dixa*	32	6.5
Ochrotrichia	52	10.6	*Euparyphus*	108	22.0
Hydroptila	74	15.0	*Odontomyia*	13	2.6
Lepidostoma	47	9.6	*Chrysops*	1	0.2
Gumaga	130	26.4	*Tabanus*	1	0.2
Lepidoptera	6	1.2	Dolichopodidae	5	1.0
Coleoptera			Empididae	5	1.0
Gyrinus	30	6.1	Ephydridae	11	2.2
Peltodytes	41	8.3	Sciomyzidae	2	0.4
Agabinus	25	5.1	*Limnophora*	9	1.8
Agabus	10	2.0			

Table III.3. Insect taxa collected in pool and riffle habitats by season. These taxa were collected using standardized collection techniques from 1993-1995.

Taxa:	Guild*	Season:**							
		Winter		Spring		Summer		Fall	
		P	R	P	R	P	R	P	R
EPHEMEROPTERA									
Baetidae									
Baetis	C,Sc	○	○	○	○	○	○		
Callibaetis	C	●	○	●	○	●	○	●	○
Centroptilum	C,Sc		⊙						
Caenidae									
Caenis	C,Sc	○	○	○	○	○	○	○	○
Leptophlebiidae									
Paraleptophlebia (probably) associata	C,Sc	○	○	○	○				
ODONATA									
(Anisoptera)									
Aeshnidae									
Aeshna	P	●		●	○	●	○	●	
Anax walsinghami	P								⊙
Libellulidae									
Libellula saturata	P			●		●	○	●	○
Paltohemis lineatipes	P	●		●	○	●	○	●	○
Sympetrum corruptum	P	⊙	⊙			⊙			
(Zygoptera)									
Lestidae									
Archilestes (probably)californica	P			●		●			

Table III.3. Continued.

Taxa:	Guild*	Season:** Winter P	R	Spring P	R	Summer P	R	Fall P	R
Coenagrionidae									
Argia spp.	P	○	○	○	○	○	○	○	○
Enallagma cyathigerum	P		○	●	○	●		●	
PLECOPTERA									
Capniidae									
Mesocapnia projecta	Sh	⊙	⊙	⊙	⊙				
HEMIPTERA									
Veliidae									
Microvelia beameri	P	○	○	○	○	○	○	○	○
Gerridae									
Aquarius remigis	P	●	○	●	○	●	○	●	
Corixidae									
Graptocorixa uhleri	P	●		●		●	○	●	
Notonectidae									
Notonecta hoffmanni	P	●	○	●	○	●		●	
Saldidae									
Saldula pexa	P			⊙			⊙	⊙	
MEGALOPTERA									
Corydalidae									
Neohermes filicornis	P		○	●		●●			

Table III.3. Continued.

Taxa:	Guild*	Season:** Winter		Spring		Summer		Fall	
		P	R	P	R	P	R	P	R
TRICHOPTERA									
Philopotamidae									
Wormaldia	C			○	●				●
Psychomyiidae									
Tinodes	Sc,C	○		○	○	○	○	○	○
Polycentropodidae									
Polycentropus	P,C,Sh	○	○	○	○		○	○	
Hydropsychidae									
Hydropsyche	C	○	●	○	●	○	●	○	●
Hydroptilidae									
Hydroptila	R,Sc	○	○	○	○	○	○	○	○
Ochrotrichia	C,R	○	○	○	○	○	○	○	○
Lepidostomatidae									
Lepidostoma	Sh		○	○	○	○	○	○	○
Seriocostomatidae									
Gumaga	Sc,Sh	○	○	○	○	○	○	○	○
LEPIDOPTERA									
Pyralidae									
Petrophila	Sc				●	○			●
Synclita?	Sh		⊙						

Table III.3. Continued.

Taxa:	Guild*	Season:**							
		Winter		Spring		Summer		Fall	
		P	R	P	R	P	R	P	R
COLEOPTERA									
Gyrinidae									
Gyrinus plicifer	P	●		●	○	●		●	
Haliplidae									
Peltodytes simplex	R,Sh,P	●		●	○	●	○	●	○
Dytiscidae									
Agabinus spp.	P	○	○	○	○				○
Agabus seriatus intersectus	P			●	○	●		●	○
Deronectes striatellus	P	●		●	○	●		●	
Hydroporus vilis	P			●	○	●			
Hydrovantus brevipes	P	⊙						⊙	
Rhantus gutticollis	P	○	○	○	○			○	
Hydroscaphidae									
Hydroscapha natans	Sc			●		●	○	●	○
Hydrophilidae									
Anacaena signaticollis	P,C?					⊙	⊙		
Berosus punctatissimus	R,C	●		●	○	●			○
Cymbiodyta dorsalis	P,C?			●	○				
Enochrus spp.	C,R			○	○	○	○	○	
Helochares normatus	P,C?					○	○	○	○
Hydrobius fuscipes	P,C?			○		○	○	○	○
Hydrochara lineata	P,C?			○	○	○	○		

Table III.3. Continued.

Taxa:	Guild*	Season:**								
		Winter			Spring		Summer		Fall	
		P	R		P	R	P	R	P	R
Laccobius spp.	R	○	○		○	○	○	○	○	○
Tropisternus ellipticus	P,C,R	○			○	○	○	○	○	○
Hydraenidae										
Hydraena vandykei	P,Sc,C				⊙					
Ochthebius spp.	P,Sc,C	○		○	○				○	
Elmidae										
Ordobrevia	C,Sc?		⊙							⊙
DIPTERA										
Tipulidae										
Dicranota	P				○	○	○	○		
Hexatoma	P	○	○				○	○		○
Holorusia hespera	Sh						⊙		⊙	
Limonia	Sh				○		○	○	○	○
Tipula	Sh,C		○		○	○		○	○	○
Culicidae										
Aedes	C								⊙	
Culex	C								⊙	
Ceratopogonidae	P,C				⊙	⊙			⊙	
Simuliidae										
Simulium	C	○	○		○	○	○	○	○	○
Chironomidae	C,P	○	○		○	○	○	○	○	○
Dixidae										
Dixa spp.	C				○	○	○	○	○	○

Table III.3. Continued.

Taxa:	Guild*	Season:** Winter		Spring		Summer		Fall	
		P	R	P	R	P	R	P	R
Stratiomyidae									
Euparyphus	C,Sc	○	○	○	○	○	○	○	○
Odontomyia	C	●	○	○	○	●			
Tabanidae									
Chrysops	C								⊙
Tabanus	P								⊙
Dolichopodidae	P	○	●		●	○	●		
Empididae	P,C		●		○	●		○	●
Ephydridae	C,Sc, Sh,P	○	○	○		○		○	
Muscidae									
Limnophora	P	○		○	○		○	○	○
Sciomyzidae	P		⊙					⊙	

* Guild Assignments (Merritt and Cummins, 1984):

C=Collector R=Piercer (herbivore) Sh=Shredder
P=Predator Sc=Scraper ?=Assignment uncertain for this taxa

**P =pool, R =riffle
○ = taxa found in this habitat type
● = taxa predominantly (in >2x number of samples) found in this habitat type or only in this habitat type
⊙ = taxa rare, found in 4 or fewer samples

Table III.4. Mean richness of taxa in various functional groups in pool and riffle habitats.

Functional Group	Stream	Pool Mean Richness	St. Dev.	Riffle Mean Richness	St. Dev.
Predators					
	All Combined	4.84	2.89	3.02	1.90
	Black Point	6.61	3.45	3.06	1.51
	Coches	6.20	2.04	3.82	2.72
	Horquetta	3.36	1.74	3.87	1.85
	Laguna	6.05	2.46	3.56	1.63
	Prisoners	5.93	2.63	2.50	1.55
	Sauces	1.81	1.56	1.88	1.31
	Willows	3.00	1.13	2.40	1.68
All Prey					
	All Combined	12.11	5.02	10.67	2.81
	Black Point	8.33	2.72	10.41	3.36
	Coches	8.33	2.72	10.41	3.36
	Horquetta	8.93	3.83	7.87	2.95
	Laguna	9.00	4.89	9.25	3.73
	Prisoners	8.47	4.75	7.69	3.26
	Sauces	5.75	3.30	4.25	2.11
	Willows	6.67	3.70	6.20	2.08
Collectors					
	All Combined	4.63	2.20	4.67	1.89
	Black Point	6.00	2.25	5.67	1.41
	Coches	4.27	0.80	5.41	1.70
	Horquetta	4.93	1.90	4.53	1.73
	Laguna	4.79	2.64	5.44	2.00
	Prisoners	4.87	2.26	4.50	2.00
	Sauces	3.25	1.95	2.81	1.56
	Willows	4.00	2.17	4.13	1.36

Table III.5. Continued

Functional Group	Stream	Pool Mean Richness	St. Dev.	Riffle Mean Richness	St. Dev.
Scrapers					
	All Combined	1.98	1.14	1.88	1.12
	Black Point	2.67	1.08	2.72	1.36
	Coches	2.07	1.22	2.53	1.12
	Horquetta	2.21	0.89	1.73	0.70
	Laguna	1.74	1.24	1.69	1.25
	Prisoners	2.07	1.39	1.88	0.81
	Sauces	1.56	0.81	1.13	0.62
	Willows	1.42	0.79	1.27	0.70
Shredders					
	All Combined	0.94	0.96	0.75	0.90
	Black Point	1.83	1.25	1.33	1.03
	Coches	1.53	0.92	1.82	0.73
	Horquetta	0.57	0.76	0.53	0.74
	Laguna	0.95	0.62	0.63	0.50
	Prisoners	0.53	0.64	0.38	0.62
	Sauces	0.19	0.40	0.00	0.00
	Willows	0.75	0.75	0.40	0.74
Piercers (herbivores)					
	All Combined	1.06	1.27	0.83	0.96
	Black Point	1.61	1.29	0.94	0.73
	Coches	0.47	0.83	0.65	0.86
	Horquetta	1.21	1.31	1.07	1.03
	Laguna	1.53	1.71	1.50	1.41
	Prisoners	1.00	1.31	0.94	1.00
	Sauces	0.75	0.77	0.31	0.48
	Willows	0.50	0.80	0.40	0.51

Table III.5. Seasonal total and mean (taxa per sampling unit) taxonomic richness of Santa Cruz Island stream insects (excluding genera of Ceratopogonidae,Chironomidae, Dolichopodidae, Empididae, Ephydridae, and Sciomyzidae which are counted as one genera each). Each sample unit consists of a combined kick and sweep sample.

Stream:	Season:	Habitat Type:	Total taxa	Mean per Sample Unit (N)	St.Dev.
All Streams	Winter	Pool	36	7.11(21)	3.45
		Riffle	35	6.57(21)	2.98
		Combined	46	6.83(44)	3.18
	Spring	Pool	54	11.12(33)	5.03
		Riffle	47	8.68(35)	3.76
		Combined	57	9.83(68)	4.54
	Summer	Pool	50	9.67(27)	3.58
		Riffle	38	8.29(21)	3.52
		Combined	54	9.06(48)	3.59
	Fall	Pool	46	9.86(29)	4.35
		Riffle	39	8.03(31)	2.97
		Combined	57	8.92(60)	3.78
Black Point	Winter	Pool	19	9.67(3)	0.58
		Riffle	12	9.00(3)	1.73
		Combined	24	9.33(6)	1.21
	Spring	Pool	34	14.50(6)	5.58
		Riffle	25	10.00(6)	3.29
		Combined	42	12.25(6)	4.96
	Summer	Pool	18	11.33(3)	4.16
		Riffle	15	8.00(3)	1.73
		Combined	25	9.67(6)	3.39
	Fall	Pool	19	15.00(3)	3.79
		Riffle	20	9.17(3)	1.72
		Combined	35	12.08(6)	4.14
Coches Prietos	Winter	Pool	15	8.67(3)	1.53
		Riffle	16	7.25(4)	1.50
		Combined	20	7.86(7)	1.57
	Spring	Pool	22	13.33(6)	1.97
		Riffle	28	12.43(7)	3.82
		Combined	32	12.85(13)	3.02
	Summer	Pool	22	9.75(4)	1.71
		Riffle	15	9.33(3)	4.04
		Combined	25	9.57(7)	2.64
	Fall	Pool	20	12.00(3)	1.73
		Riffle	15	9.33(3)	3.21
		Combined	24	10.67(6)	2.73

Table III.5. Continued.

Stream:	Season:	Habitat Type:	Total taxa	Mean per Sample Unit (N)	St.Dev.
Horquetta	Winter	Pool	13	5.00(4)	4.24
		Riffle	10	4.50(4)	0.71
		Combined	17	4.75(8)	2.50
	Spring	Pool	18	10.33(3)	5.13
		Riffle	19	8.75(4)	3.77
		Combined	25	9.43(7)	4.08
	Summer	Pool	19	10.50(4)	4.04
		Riffle	19	11.00(3)	3.00
		Combined	24	10.71(7)	3.35
	Fall	Pool	16	10.00(4)	2.94
		Riffle	15	8.50(6)	1.87
		Combined	19	9.10(10)	2.33
Laguna	Winter	Pool	12	7.00(3)	2.65
		Riffle	15	9.00(3)	2.65
		Combined	22	8.00(6)	2.61
	Spring	Pool	29	13.75(4)	4.50
		Riffle	21	9.50(4)	3.32
		Combined	35	11.63(8)	4.31
	Summer	Pool	32	12.25(4)	3.59
		Riffle	34	11.00(3)	5.00
		Combined	34	11.71(7)	3.90
	Fall	Pool	24	8.83(6)	3.06
		Riffle	21	9.33(6)	3.01
		Combined	33	9.08(12)	2.91
Prisoners	Winter	Pool	18	10.00(3)	4.58
		Riffle	15	7.67(3)	4.73
		Combined	26	8.83(6)	4.36
	Spring	Pool	34	12.33(6)	3.98
		Riffle	25	7.40(5)	2.41
		Combined	36	10.09(11)	4.11
	Summer	Pool	15	9.00(2)	0.00
		Riffle	13	6.00(3)	2.65
		Combined	20	7.20(5)	2.49
	Fall	Pool	15	7.00(4)	3.37
		Riffle	14	7.00(4)	3.16
		Combined	25	7.00(8)	3.02

Table III.5. Continued.

Stream:	Season:	Habitat Type:	Total taxa	Mean per Sample Unit (N)	St.Dev.
Sauces	Winter	Pool	8	3.67(3)	2.31
		Riffle	7	4.00(3)	1.73
		Combined	9	3.83(6)	1.83
	Spring	Pool	14	5.00(5)	3.39
		Riffle	11	4.67(6)	2.34
		Combined	17	4.82(11)	2.71
	Summer	Pool	29	8.33(6)	4.89
		Riffle	17	5.00(4)	3.27
		Combined	33	7.00(10)	4.45
	Fall	Pool	7	4.33(3)	1.15
		Riffle	8	3.33(3)	3.51
		Combined	9	3.83(6)	2.40
Willows	Winter	Pool	6	4.00(2)	2.83
		Riffle	6	3.67(3)	1.53
		Combined	11	3.80(5)	1.79
	Spring	Pool	15	6.50(3)	1.91
		Riffle	17	7.50(3)	2.43
		Combined	19	7.10(6)	2.18
	Summer	Pool	14	7.67(3)	2.08
		Riffle	10	6.00(3)	1.00
		Combined	15	6.83(6)	1.72
	Fall	Pool	16	8.67(3)	4.16
		Riffle	11	7.00(3)	2.65
		Combined	24	7.83(6)	3.25

Table III.6. Taxonomic similarity between pool and riffle fauna by season. Taxonomic similarity determined with Jaccard's similarity coefficient (1 = habitats share all taxa, 0 = habitats share no taxa).

Stream:	Similarity Coefficient:				
	Winter	Spring	Summer	Fall	Mean
All	0.54	0.75	0.62	0.49	0.61
Black Point	0.54	0.48	0.39	0.53	0.49
Coches	0.55	0.56	0.42	0.46	0.50
Horquetta	0.44	0.61	0.65	0.63	0.58
Laguna	0.27	0.47	0.56	0.36	0.42
Prisoners	0.33	0.54	0.31	0.21	0.35
Sauces	0.63	0.53	0.38	0.56	0.53
Willows	0.33	0.76	0.38	0.39	0.47

Figure 3.1. Calculated Jaccard's similarity coefficients for the insect assemblages in seven Santa Cruz Island streams. A coefficient of 1 indicates complete similarity of assemblages. Similarity coefficients were calculated for all taxa and taxa within individual orders (excluding Plecoptera, Megaloptera, and Lepidoptera due to low numbers of taxa).

Keys:

Streams:
BP= Black Point
C= Coches Prietos
H= Horquetta
L= Laguna
P= Prisoners
S= Sauces
W= Willows

Similarity ranges:
0.00-0.19 □
0.20-0.39 ░
0.40-0.59 ▒
0.60-0.79 ▨
0.80-1.00 ■

Figure 3.1. Jaccard's similarity coefficients for insect taxa of seven Santa Cruz Island streams.

All Taxa	BP	C	H	L	P	S	W
BP	x	▒	▒	▨	▨	▒	▒
C	0.54	x	▒	▒	▨	▒	▒
H	0.48	0.42	x	▒	▒	▒	▒
L	0.70	0.44	0.51	x	▨	▨	▒
P	0.67	0.60	0.43	0.60	x	▒	▒
S	0.52	0.41	0.54	0.60	0.44	x	▒
W	0.53	0.41	0.52	0.41	0.51	0.41	x
mean	0.51						
range	.41-67						

Ephemeroptera	BP	C	H	L	P	S	W
BP	x	▨	■	■	▨	■	■
C	0.75	x	▨	▨	■	▨	▨
H	1.00	0.75	x	■	▨	■	■
L	1.00	0.75	1.00	x	▨	■	■
P	0.60	0.80	0.60	0.60	x	▨	▨
S	1.00	0.75	1.00	1.00	0.60	x	■
W	1.00	0.75	1.00	1.00	0.60	1.00	x
mean	0.84						
range	.60-1.00						

Odonata	BP	C	H	L	P	S	W
BP	x	▨	░	▒	▒	▒	░
C	0.67	x	░	▒	▨	░	░
H	0.33	0.22	x	▒	░	▨	■
L	0.57	0.56	0.40	x	■	▨	▒
P	0.50	0.67	0.33	0.83	x	▒	░
S	0.50	0.33	0.67	0.60	0.50	x	▨
W	0.33	0.22	1.00	0.40	0.33	0.67	x
mean	0.51						
range	.22-1.00						

Hemiptera	BP	C	H	K	P	S	W
BP	x	▨	▒	■	▨	■	▒
C	0.60	x	▨	▨	■	▨	▨
H	0.40	0.67	x	▒	▨	▒	■
L	1.00	0.60	0.40	x	▨	■	▒
P	0.60	1.00	0.67	0.60	x	▨	▨
S	0.80	0.75	0.50	0.80	0.75	x	▒
W	0.40	0.67	1.00	0.40	0.67	0.50	x
mean	0.66						
range	.40-1.00						

Figure 3.1. Continued

Trichoptera	BP	C	H	L	P	S	W
BP	x	■	▨	▨	■	▒	■
C	1.00	x	▨	▨	■	▒	■
H	0.71	0.71	x	■	▨	▨	▨
L	0.71	0.71	1.00	x	▨	▨	▨
P	1.00	1.00	0.71	0.71	x	▒	■
S	0.43	0.43	0.60	0.60	0.43	x	░
W	0.88	0.88	0.63	0.63	0.88	0.38	x
mean	0.72						
range	.38-1.00						

Coleoptera	BP	C	H	L	P	S	W
BP	x	▒	▒	▨	■	▒	░
C	0.42	x	░	░	▒	░	░
H	0.50	0.38	x	░	░	▒	░
L	0.68	0.35	0.35	x	▨	▒	
P	0.88	0.47	0.39	0.67	x	▒	░
S	0.50	0.39	0.56	0.50	0.40	x	░
W	0.31	0.25	0.25	0.17	0.36	0.21	x
mean	0.43						
range	.17-.88						

Diptera	BP	C	H	L	P	S	W
BP	x	▒	░	▨	▒	▒	▨
C	0.41	x	░	░	▒	░	░
H	0.37	0.33	x	▒	░	▒	▒
L	0.65	0.29	0.50	x	▒	▨	▒
P	0.53	0.43	0.38	0.50	x	▒	▒
S	0.47	0.29	0.41	0.63	0.41	x	▒
W	0.67	0.33	0.53	0.47	0.53	0.47	x
mean	0.46						
range	.29-.67						

Figure 3.2. Jaccard's similiarity coefficients for insect assemblages among seasons in Santa Cruz Island streams.

Key to similarity ranges:

0.20-0.29	□
0.30-0.39	░
0.40-0.49	▒
0.50-0.59	▨
>0.60	■

Figure 3.2 Jaccard's similarity coefficients for insect taxa by season.

Stream: All Streams

Season	Spring	Summer	Fall	Winter
Spring	X	■	■	■
Summer	0.734	X	■	▨
Fall	0.652	0.657	X	▨
Winter	0.609	0.563	0.585	X

Mean similarity= 0.633

Black Point

Spring	Summer	Fall	Winter
X	▓	▨	▓
0.447	X	▨	▨
0.500	0.533	X	▨
0.457	0.538	0.555	X

0.505

Coches Prietos

Season	Spring	Summer	Fall	Winter
Spring	X	▨	▓	■
Summer	0.552	X	░	▓
Fall	0.471	0.357	X	▓
Winter	0.621	0.400	0.400	X

Mean similarity= 0.467

Horquetta

Spring	Summer	Fall	Winter
X	▓	▓	░
0.455	X	▓	░
0.433	0.433	X	▓
0.346	0.259	0.450	X

0.396

Stream: Laguna

Season	Spring	Summer	Fall	Winter
Spring	X	▨	▓	░
Summer	0.537	X	▓	░
Fall	0.412	0.432	X	▓
Winter	0.378	0.366	0.414	X

Mean similarity= 0.432

Prisoners

Spring	Summer	Fall	Winter
X	▓	▓	▓
0.455	X	▓	░
0.486	0.448	X	▓
0.432	0.344	0.468	X

0.439

Stream: Sauces

Season	Spring	Summer	Fall	Winter
Spring	X	▓	░	░
Summer	0.421	X	▨	
Fall	0.352	0.500	X	
Winter	0.375	0.278	0.267	X

Mean similarity= 0.366

Willows

Spring	Summer	Fall	Winter
X	▓	▓	▓
0.415	X	▓	
0.400	0.478	X	
0.412	0.278	0.260	X

0.374

CHAPTER IV

APPLICATION OF THE SPECIES-AREA RELATIONSHIP TO SANTA CRUZ ISLAND STREAMS

INTRODUCTION

Biogeographical studies often focus on species distributions and the relationship between species richness and spatial and temporal habitat heterogeneity (Williamson 1988). In general, habitat heterogeneity increases with increases in habitat area. Correspondingly, biogeographers frequently find a positive relationship between area and species number. Botanists recognized species-area relationships as early as the 1920's, observing a linear relationship between species number (Gleason 1922), or the logarithm of species number (Arrhenius 1921), and the logarithm of area.

Hypotheses explaining the significance of the species-area relationship take three forms. Preston (1962) suggested that the species-area relationship could result from a sampling effect, reflecting the tendency of species abundances to follow log-normal distributions (species richness plotted against the log of abundance per species approximates a normal curve). He proposed that if species having different abundances are distributed randomly across the landscape, then greater number of species will be found with increasing sample area. MacArthur and Wilson (1963, 1967) applied the species-area relationship to islands to explain variation in species richness on oceanic islands of varying size. They asserted that larger areas allow for greater habitat diversity, "...which in turn controls species diversity" (MacArthur and Wilson 1967). In addition, the MacArthur-Wilson equilibrium model of island biogeography incorporates the effects of island area and distance from mainland populations on species immigration and extinction rates (i.e., nearer and larger islands provide closer and larger "targets"). The MacArthur and Wilson model assumes that if enough time has passed then the species richness for a given island will approach an equilibrial balance between immigration and extinction rates. Subsequently, numerous workers (i.e., Wilcox 1980, Diamond 1972, Wilson 1988, Powell 1994) examined island biotas for agreement with the general formula: $S = cA^z$, with S = species number, A = area, and c and z being constants. For islands, the slope constant, z, usually falls within the range of 0.2 to 0.35, although the meaning and importance of "z" is debatable (Williamson 1988).

The species-area relationship has been extended to habitat patches isolated from one another by intervening regions of dissimilar habitat, with the resultant formation of "ecological islands." Examples of ecological or habitat islands include caves (Culver 1970, Vuilleumier 1973), desert mountaintops (Brown 1971), lakes (Barbour and Brown 1974), river basins (Allan 1995), and coastal streams (Sepkoski and Rex 1974, Brönmark et al. 1984). Attempts to apply the species-area relationship and other aspects of the equilibrium theory of island biogeography to natural reserve design has resulted in a renewed interest in, and a critical re-assessment of, these concepts (Simberloff 1994).

Results from studies of some California Channel Island animal groups (primarily insects) have corresponded well with the predicted correlation between taxon richness and island area (e.g., Wilcox 1980, Powell 1985, Rust et al. 1985, Weissman 1985, Powell 1994). In addition, studies of river and stream system species-area relationships also show the predicted relationship between richness and stream drainage area for freshwater mussels (Sepkoski and Rex 1974), macroinvertebrates (Brönmark et al. 1984), and fish (Allan 1995).

Streams on the California Channel Islands, separated from each other by terrestrial habitat surrounding each stream as well as open ocean at the stream mouths, can be viewed as ecological islands. The present study thus included an investigation of the possible relationship between numbers of aquatic insect taxa in Santa Cruz Island streams and their catchment areas, which are assumed to be correlated with habitat size and diversity (Allan 1995). In addition, I examined the species-area relationship using the catchment area above individual sample sites on the streams. This chapter also explores the relationship between number of insect taxa collected and island stream distances from mainland source populations.

MATERIALS AND METHODS

Seven Santa Cruz Island streams with catchment areas ranging from 1.09 to 34.66 km^2 were chosen for this study (Figures 1.3 to 1.5, Table I.1). Two or three sample sites located at different elevations on each stream were visited at least bi-monthly from 1993 to 1994 and, occasionally, in 1995 and 1996 (Table I.3). Catchment areas above these sites ranged from 0.21 to 25.06 km^2. The standardized sampling methods and sample processing are described in Chapter I. Most insects collected were immatures and were identified only to the genus level. Coleopterans and hemipterans were often collected as adults, permitting identification to the species level. Due to inadequate identification of some dipteran families (Ceratopogonidae, Chironomidae, Dolichopodidae, Empididae, Ephydridae, and Sciomyzidae), they were included in the taxon count at the family level of resolution rather than the genus level.

I plotted curves of the cumulative number of taxa against sampling effort (cumulative number of sampling visits through time) for each stream to determine if most taxa likely present at the sample sites had been collected. Exponential lines were fitted to these data. For each stream, I also regressed the number of taxa against the number of samples taken to assess whether differences in sampling effort (number of samples) among streams might bias the results of the species-area relationship. All regression analyses in this chapter are Model I regressions using the least squares method to fit lines. Regression analyses of the $\log_{10}$ of number of taxa (total and within orders) for entire streams against the $\log_{10}$ of catchment area (with and without Black Point, a possible outlier) were used to determine the adequacy of catchment area to predict aquatic insect richness in these streams. In addition, regression analyses of the $\log_{10}$ of number of taxa (total and within orders) against the $\log_{10}$ of catchment area above individual collections sites were performed.

Distances from source populations may also influence the number of taxa on an island or island-type habitat (MacArthur and Wilson 1967); therefore, number of total taxa and taxa within orders were regressed against the distance of island streams from possible mainland source populations. The distances of island streams from mainland populations were estimated using Arroyo Burro and

Refugio Creeks as colonist sources (Figure 4.1. and Table IV.1.). These streams are located closest to Santa Cruz Island (straight line), assuming the arrival of colonists on the island's north side. I assumed that immigrants arriving from Refugio Creek would colonize the Black Point stream via a track from West Point moving south along the island coast (avoiding a mountain range). From Black Point, immigrants could colonize the Sauces stream. Immigrants arriving at drainages on the north slopes of Santa Cruz Island from Arroyo Burro Creek could move up-canyon, colonizing the upper portion of the Prisoners catchment. Colonization from upper to lower Prisoners Creek was assumed to occur from the downstream drift of insects. From the upper portions of the Prisoners catchment, insects could colonize Laguna (via up-canyon movement) and the mid and lower reaches of the Prisoners stream. From the mid-reach of Prisoners, insects could colonize (via up-canyon movement) the perennial portions of Willows, and then from Willows, move into the Horquetta catchment via Willows side-branches. Insects in the lower portion of the Prisoners stream (near the Stanton Ranch) could move up-canyon into the Coches Prietos catchment.

Multiple regressions of $\log_{10}$ species richness (total and within orders) against $\log_{10}$ of distance and $\log_{10}$ of catchment of area were conducted to assess the relationship between richness and each of these variables while controlling for the effect of the other.

RESULTS

The number of insect taxa collected from Santa Cruz Island streams varied from 53 in the Black Point stream, to 35 in Horquetta and Willows streams (mean taxa/stream = 43, Table IV.2). Most taxa were coleopterans (mean across all 7 streams = 13 taxa/stream, range 5-17) and dipterans (mean = 12 taxa/stream, range 9-15). The mean number of dipteran taxa would be much greater if taxa within the families Ceratogponidae, Chironomidae, Dolichopodidae, Empididae, Ephydridae, and Scimyzidae were identified to a greater level of taxonomic resolution. Aquatic taxa of the orders Plecoptera, Megaloptera, and Lepidoptera had the narrowest distributions and lowest richness in Santa Cruz Island streams (Table IV.2).

In all streams, the cumulative number of taxa collected initially rose rapidly with the number of sampling visits (Figure IV.2), with 71 to 98% of total taxa collected after five sampling visits (Table IV.3). No new taxa were added to most stream counts after the tenth visit (an exception: the thirteenth visit to the Willows stream, Table IV.3). The cumulative number of taxa increased with cumulative number of sampling visits. The relationships between these variables approximate curves of the number of species against the logarithm of sampling visits ($R^2 = 0.79$ to 0.97). There was no significant relationship between richness and the number of samples taken across streams (Figure 4.3; $y = 0.67x - 3.91$, $R^2 = 0.12$, $P = 0.45$).

A regression of the $\log_{10}$ of total richness against $\log_{10}$ of catchment area for the seven Santa Cruz Island streams (Figure 4.4a) was not statistically significant. Because the richness data for Black Point appeared to be an outlier, regressions were also calculated with this point removed. The removal of Black Point from the analysis resulted in an increased slope and better fit of the data to the regression line ($R^2 = 0.62$, $P = 0.06$; Figure 4.4b).

Regressing the $\log_{10}$ number of taxa in various orders against $\log_{10}$ of catchment area did not yield statistically significant species-area relationships (Figure 4.5, Table IV.4). The coefficients of determination (R^2) and slopes of these regressions ranged from >0 to 0.42 and -0.02 to 0.14, respectively. The removal of Black Point from the analysis resulted in overall increases in the coefficients of determination and slopes for most orders; however, none were significant.

The relationship between $\log_{10}$ number of taxa and $\log_{10}$ of catchment area above individual collection sites was negative but not significant (Table IV.4 and Figure 4.6). The relationship was also negative and not statistically significant, for the $\log_{10}$ of richness and $\log_{10}$ of catchment area above collection sites for the orders Hemiptera, Trichoptera, and Coleoptera (Table IV.4 and Figure 4.7). The relationship in the remaining orders was positive, but not significant (Table IV.4 and Figure 4.7).

There was no relationship between total richness and island stream distance from mainland source populations (Table IV.4 and Figure 4.8). These relationships tended to be negative and not signficant within the orders Ephemeroptera, Odonata, and Trichoptera (Table IV.4 and Figure 4.9). Richness within the orders Hemiptera, Coleoptera, and Diptera increased as distance from the mainland increased; however these relationships were not signficant (Table IV.4, Figure 4.9).

Multiple regressions of $\log_{10}$ total richness and richness within orders against $\log_{10}$ of catchment area and $\log_{10}$ of distance from the mainland were not significant. The multiple regression of richness within the order Trichoptera was significant for distance (Table IV.5)

DISCUSSION

Previous studies have revealed that the cumulative number of taxa collected in a given habitat usually increases to an asymptote with the number of samples taken (Allan 1995). If my sampling efforts were adequate, the cumulative number of taxa collected for each stream versus number of visits should have followed a pattern of rising rapidly and then leveling off as fewer taxa were added (i.e., very few species should be added as sampling effort increases above some sampling level). Logarithmic curves of the number of species against number of sampling visits fit the data well ($R^2 = 0.79$ to 0.97), indicating that as sampling in each stream progressed in this study, the number of new taxa collected did increase at a decreasing rate (Table IV.3, Figure 4.2). From the cumulative taxa vs. sample visit curves, it appears that my collection efforts provided good estimates of taxonomic richness for each of the seven streams.

The number of samples processed among streams varied from 66 to 77. A regression of number of taxa against number of processed samples across streams, however, did not result in a statistically significant correlation between number of taxa and sampling effort (Figure 4.3). I assumed, therefore, that sampling effort was reasonably equivalent among streams.

Before beginning the discussion of the regression results, it is necessary to comment on the limited statistical power of these analyses. For the regressions of richness against catchment area and against distance of streams from the mainland, the analyses are limited by the low number of observations (6 or 7 streams) and low number of taxa per order. The regression of richness against catchment areas above individual collection site were perhaps confounded by spatial autocorrelation (sites on the same stream not being independent of one another). The difficulties in estimating distances from island streams to mainland source populations will be discussed later. Overall, few analyses give high coefficients of determination (R^2) and none give significant slopes.

The results of the species-area relationships for total taxa and taxa per order occupying Santa Cruz Island streams do not indicate that increases in catchment area (and presumably habitat area) predict taxonomic richness. The removal of the outlier, Black Point, from the regression analyses generally increased the coefficients of variation. Although none of these regressions yielded statistically significant slopes, the P for the regression of total taxa decreases from 0.78 (including Black Point) to 0.06 (Black Point removed, Figures 4.4a and 4.4b, Table IV.4).

Overall, the slopes obtained from the above regressions are much lower than those reported for other studies of islands (i.e. Williamson 1988); however, those analyses addressed larger areas. Although significant stream species-area relationships have been observed in other stream studies, there were no significant species-area relationships across Santa Cruz Island. However, this study was limited by a comparatively low number of streams. By contrast, studies of freshwater mussel distribution in 49 North American Atlantic coastal rivers (Sepkoski and Rex 1974) and macroinvertebrate distributions in 22 Danish streams (Brönmark et al. 1984) both revealed significant relationships between species richness and catchment area (Sepkoski and Rex 1974) or stream area (discussed below, Brönmark et al. 1984). The work of Sepkoski and Rex (1974) may not be comparable to this study due both to the large catchments surveyed in their study (coastal rivers) and the limited dispersal capability of bivalves compared to aquatic insects. It is thus more appropriate to compare my results with those of Brönmark et al. (1984), because the catchment areas (estimated 1.04 to 36.86 km^2) in that study were similar to those examined in this study (1.09 to 34.66 km^2), both studies occurred on islands less than 50 km from the mainland, and both studies addressed the richness of aquatic insects. The area of the Danish island studied by Brönmark et al. (1984) was larger (572 km^2) than Santa Cruz Island (249 km^2).

The Brönmark et al. (1984) survey of 22 streams on a Danish island revealed that stream area was significantly related to stream invertebrate richness. Their study, however, used stream area (stream length multiplied by 1/2 stream width at mouth) rather than catchment area as the independent variable. By estimating catchment area with the formula $L = 1.4 (A)^{(0.6)}$, where L = stream length and A = catchment area (Allan 1995), I could directly compare their results to those from my study. A recalculation of the Brönmark et al. (1984) regression, using estimated catchment area, still gave a significant species-area relationship ($\log_{10} y = 0.18 \log_{10} x + 10.97$, $R^2 = 0.37$, $P < 0.01$). In contrast, this study of Santa Cruz Island streams did not yield a signficant species-area relationship.

Several factors (other than the statistical considerations listed above) may have contributed to the lack of relationships between richness and catchment area for Santa Cruz Island streams. Relative to mainland streams, Santa Cruz Island streams may be less heterogeneous. As noted by Junak et al. (1995), the island riparian flora is notably depauperate, lacking many dominant mainland species (sycamore, alder, cottonwood, bay). These species form canopies over mid- and upper-elevation mainland streams; therefore, as catchment area increases, differences in canopy cover and composition (habitat heterogeneity) are observed. These differences in canopy composition do not occur on Santa Cruz Island, although differences in canopy cover do occur; therefore, with respect to canopy characteristics, streams on Santa Cruz Island may be less heterogeneous than mainland streams.

In addition, habitat heterogeneity may not a crucial factor in the determination of richness in Santa Cruz Island streams due to the characteristics of the island stream fauna. Santa Cruz Island aquatic insects are a non-random subset of those found on the mainland (Chapter II). The majority of these insect taxa exhibit wide mainland distributions among and within streams, and low habitat specificity (Table II.4.); however larger streams may provide larger "targets" for colonizing insects. Following immigration to the island, those taxa with strong dispersal capabilities (i.e., odonates, flies, beetles) could easily disperse among drainages, resulting in non-significant relationships between catchment area and richness. In contrast, taxa with low dispersal capabilities (i.e., ephemeropterans, plecopterans, trichopterans) might arrive at a "target" and fail to disperse to other streams (see Chapter II). In this case, catchment area and/or distance from mainland source populations would be important determinants of richness.

In part, observations appear to support the "target" hypothesis. Stoneflies (weak fliers) only occur in the largest drainage, Prisoners, and mayflies (ephemeral adults, weak fliers) exhibit their highest richness in this stream. The ephemeropteran richness-area relationship exhibited a relatively high coefficient of determination ($R^2 = 0.42$) and was positive. I expected to observe similar results for caddisflies (weak fliers); however, catchment area was not a good predictor of richness within this order (Table IV.4, Figure 4.5). Several families within the orders Odonata, Hemiptera, Coleoptera, and Diptera possess strong dispersal capabilities and are able to colonize islands distant from the mainland; therefore, these insects could easily disperse among catchments. In these groups, catchment area was not a good predictor of richness (Table IV.4, Figure 4.5).

I also expected a negative relationship between distance to the mainland and richness. MacArthur and Wilson (1967) hypothesized that immigration rates, and therefore richness, would decrease as distance from the mainland increased. Regressions of total richness and richness within orders against distance of island streams from mainland source populations yielded non-significant results (Table IV.4, Figure 4.8 and 4.9). Richness within the orders Ephemeroptera ($R^2 = 0.49$, slope = -0.15, $P = 0.08$) and Trichoptera ($R^2 = 0.37$, slope = -0.29, $P = 0.15$) was negatively related to the distance of streams from the mainland. A multiple regression of species richness within these orders against both catchment area and distance from the mainland resulted in higher coefficients of determination and lower P values (Ephemeroptera: $R^2 = 0.66$, $P = 0.12$; Trichoptera: $R^2 = 0.74$, $P = 0.07$). For trichopterans, the partial regression coefficient for distance was negative ($\beta = -3.96$) and significiant ($P = 0.02$), indicating that distance from mainland source populations is a significant predictor of trichopteran richness in Santa Cruz Island streams after controlling for the effect of drainage area.

The estimated distances from the mainland to the island streams are based on several assumptions. First, the estimated distances are based on present conditions, although insects may have colonized the island during periods of lower or higher sea levels. Second, the assumed sources of colonists, Arroyo Burro Creek and Refugio Creek, may not be the actual sources of colonists and the mainland source populations may be located upstream, rather than downstream. Third, these estimates are based on straight-line aerial distances across the Santa Barbara Channel and do not take into account alternative colonization tracks or modes of colonization (i.e. rafting). Fourth, the estimated initial "landing" locations on the island are based on present conditions and may not represent actual (past or present) colonist "landings." Fifth, the estimated distances between island streams are based on either up-canyon dispersal or tracks along the coastline (to avoid mountains); however, other dispersal pathways between drainages may also occur. Finally, different taxa may vary in their dispersal routes and methods of dispersal.

Differences in the degree of environmental variability may contribute to the differences between the results of the Brönmark et al. (1984) study and my investigation. Several studies have addressed the influence of environmental variability (i.e., disturbance) on the structure of biological communities (i.e. richness; Menge and Sutherland 1976, Connell 1978, Pickett and White 1985). In stream systems, temporal and spatial variability in streamflow, particularly in flow predictability and flood frequency, are thought to influence the relative contributions of abiotic and biotic factors in structuring communities (Delucchi 1988, Grimm and Fisher 1989, Power et al. 1988, Poff and Ward 1989).

Streams in the southwestern United States are classified as "harsh intermittent" or "intermittent flashy" by Poff and Ward (1989) and typically experience long periods of zero or low flow and seasonal (winter) flooding. In Mediterranean streams, these cycles of intermittency and flooding may be seasonally predictable; however, the duration of intermittency and intensity of flooding varies from year to year. Both phenomena may decrease the relative contributions of biotic interactions to overall community structure and resultant communities should be low in species richness. By contrast, streams in more temperate regions may flood occassionally, but typically experience greater predictability in flow regime. This rather predictable flow may result in an overall increase in species richness (Poff and Ward 1989).

The degree of intermittency varies among Santa Cruz Island streams; however, intermittency does not appear to affect richness at the sampled sites. Of the seven sampled streams, only Coches experiences a notable decrease in richness during the summer and appreciable decreases from spring to fall do not occur in any of the streams (Table III.5). Due to the varying degrees of Santa Cruz Island stream intermittency, using the entire catchment area may not be appropriate for regression analyses of species-area relationships. Although the streams generally flow at and between the individual collection sites (drying occurred at a single site, the Laguna 68 meter elevation site, one time from 1993-1997; drying occurred between sites on Prisoners stream), the channels are usually dry above (Sauces, Willows) or below (Laguna, Prisoners, Willows) the collection sites. Therefore, it may be more appropriate to consider the catchment area above individual collection sites, rather than the catchment areas of entire streams. Regressions of the $\log_{10}$ of total richness and $\log_{10}$ of richness within orders at individual collection sites against the $\log_{10}$ of catchment areas at those collection sites were inconclusive (low R^2s and slopes not significant); however, inverse relationships (negative slopes) occurred between richness and area for several taxa (total richness, richness of hemipterans, trichopterans, and coleopterans; Table IV.4, Figures 4.6 and 4.7). If streams with smaller watersheds (Black Point) or individual sites with smaller watersheds, do not experience intense winter flood disturbance, these streams/sites may support relatively richer stream communities (Chapter V).

Observed relationships between species richness and winter stream flow variability agree more with expectations related to flow variability (i.e., increased flow variability should be negatively related to species richness) than to predictions based on catchment area. The Black Point stream (catchment area = 1.09 km^2), for example, experiences very little change in flow throughout the year (the small watershed results in only small changes during storm events) and exhibits the greatest taxonomic richness. By contrast, Prisoners stream (catchment area = 34.66 km^2) can experience extreme flooding during the winter. Although the Prisoners catchment area is much greater than that of Black Point, taxonomic richness in the Prisoners stream is lower. Taxa lacking life history characteristics that would enable them to withstand flooding (i.e., high mobility, terrestrial adults, and multivoltine life cycle) may simply not persist in Prisoners stream. However, data regarding the frequency and effects of flood disturbances in Santa Cruz Island streams are lacking at this point.

Distance from source populations, dispersal ability, and environmental variability may play more important roles than catchment area in determining taxonomic richness in Santa Cruz Island streams. Continued observations of patterns of richness in island streams combined with stream physical data and experimental manipulations are needed to determine the relative contributions of distance, dispersal ability, and enviromental variability to richness in Santa Cruz Island streams.

CONCLUSION

In general, taxon richness was not related to cacthment area and distance from the mainland. It appears that Santa Cruz Island streams were colonized by broadly-distributed, opportunistic generalists (Chapter II). After arrival, these taxa spread across the island. Given the dispersive nature of the majority of island stream insects and small differences in stream distances from the mainland, the appropriate target for these taxa would be the entire island rather than individual catchments. With the exception of caddisflies, weakly dispersive taxa, by and large, do not occur on Santa Cruz Island. Caddisfly richness was significantly and negatively related to stream distance from the mainland. Variations in hydrological regimes (i.e. intermittency, scour) among island streams may play an important role in stream insect establishment and dispersal.

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Table IV.1. Estimates of distances from mainland source populations to Santa Cruz Island Streams.

Colonization Track: From	Via	To	Distance (km)	Total distance to stream (km)	Catchment area (km^2)	# of taxa
Arroyo Burro Creek	Straight line over-water dispersal	North slope drainages of Santa Cruz Island	38.5			
North slope drainages of Santa Cruz Island	Up canyon dispersal	**Prisoners stream** (upper reaches)	3.7	42.2	34.7	48
Prisoners stream (upper reaches)	Up canyon dispersal	**Laguna stream** (upper reaches)	3.3	45.5	12.2	50
Prisoners stream (mid reach)	Up canyon dispersal	**Willows stream** (perennial reach)	3.7	45.9	6.3	35
Willows stream (perennial reach)	Dispersal across side branches	**Horquetta**	0.7	46.6	1.8	35
Prisoners stream (lower reach)	Up canyon dispersal	**Coches**	1.8	44.0	5	43
Refugio Creek	Straight line over-water dispersal	West Point, Santa Cruz Island	44.8			
West Point	Movement along coastline	**Black Point stream**	5.0	46.6	1.1	53
Black Point stream	Movement along coastline	**Sauces stream**	2.9	52.7	5.9	40

Table IV.2. Insect taxa collected from seven Santa Cruz Island streams (B = Black Point, C = Coches, H = Horquetta, L = Laguna, P = Prisoners, S = Sauces, W = Willows; Figures 1.3 to 1.5). These samples were collected from 1993 to 1996 using standardized collection techniques.

	Stream:						
Taxa:	B	H	C	S	W	L	P
Ephemeroptera							
Baetidae							
Baetis	●	●	●	●	●	●	●
Callibaetis	●	●	●	●	●	●	●
Centroptilum							●
Caenidae							
Caenis	●	●	●	●	●	●	●
Leptophlebiidae							
Paraleptophlebia associata			●				●
Total Ephemeroptera Taxa	3	3	4	3	3	3	5
Mean # of Ephemeroptera/stream = 3.4							
Odonata							
(Anisoptera)							
Aeshnidae							
Aeshna	●						
A. walkeri			●				
Anax walsinghami	●		●				
Libellulidae							
Libellula saturata	●		●			●	●
Paltohemis lineatipes	●	●	●	●	●	●	●
Sympetrum corruptum			●				
(Zygoptera)							
Lestidae							
Archilestes			●			●	●
Coenagrionidae							
Argia sedula			●				●
A. vivida	●	●	●	●	●	●	●
Enallagma sp.	●		●	●		●	●
Total Odonata Taxa	6	2	9	3	2	5	6
Mean # of Odonata/stream = 4.7							
Plecoptera							
Capniidae							
Mesocapnia projecta							●
Total Plecoptera Taxa	0	0	0	0	0	0	1
Mean # of Plecoptera/stream = 0.1							

Table IV.2. Continued.

	Stream:						
Taxa:	B	H	C	S	W	L	P
Hemiptera							
Saldidae							
Saldula pexa	●					●	
Veliidae							
Microvelia beameri	●	●	●	●	●	●	●
Gerridae							
Aquarius remigis	●	●	●	●	●	●	●
Corixidae							
Graptocorixa uhleri	●			●		●	
Notonectidae							
Notonecta hoffmanni	●		●	●		●	●
Total Hemiptera taxa	5	2	5	4	2	5	3
Mean # of Hemiptera/stream = 3.4							
Megaloptera							
Corydalidae							
Neohermes filicornis	●						●
Total Megaloptera taxa	1	0	0	0	0	0	1
Mean # of Megaloptera/stream = 0.3							
Trichoptera							
Philopotamidae							
Wormaldia					●		
Psychomyiidae							
Tinodes	●	●	●		●	●	●
Polycentropodidae							
Polycentropus	●		●		●		●
Hydropsychidae							
Hydropsyche	●	●	●	●	●	●	●
Hydroptilidae							
Hydroptila	●	●	●	●	●	●	●
Ochrotrichia	●	●	●		●	●	●
Lepidostomatidae							
Lepidostoma	●		●		●		●
Sericostomatidae							
Gumaga	●	●	●	●	●	●	●
Total Trichoptera taxa	7	5	7	3	8	5	7
Mean # of Trichoptera/stream = 6.0							

Table IV.2. Continued.

Taxa:	Stream: B	H	C	S	W	L	P
Lepidoptera							
Pyralidae							
Pterophila	●	●					
Synclita						●	
Total Lepidoptera taxa	1	1	0	0	0	1	0
Mean # of Lepidoptera/stream = 0.4							
Coleoptera							
Gyrinidae							
Gyrinus plicifer	●		●			●	●
Haliplidae							
Peltodytes simplex	●	●		●		●	●
Dytiscidae							
Agabinus	●	●	●		●		●
Agabus seriatus intersectus	●	●		●			
Deronectes striatellus	●		●	●		●	●
Hydroporus vilis	●		●			●	●
Hydrovantus brevipes						●	
Rhantus gutticollis	●	●	●	●	●		●
Hydroscaphidae							
Hydroscapha natans	●	●				●	●
Hydrophilidae							
Anacaena signaticollis		●	●	●			
Berosus punctatissimus	●					●	●
Cymbiodyta dorsalis	●			●		●	●
Enochrus pectoralis	●	●	●	●	●	●	●
Helochares normatus	●	●	●	●		●	
Hydrobius fuscipes	●			●		●	●
Hydrochara lineata		●		●		●	
Laccobius (larvae)	●	●					
L. californicus						●	
L. ellipticus				●	●	●	●
Tropisternus ellipticus	●	●	●	●		●	●
Hydraenidae							
Hydraena vandykei						●	
Ochthebius interruptus			●	●		●	
O. puncticollis				●			
Scirtidae			●				
Elmidae							
Ordobrevia nubifera	●					●	●
Total Coleoptera taxa	16	11	11	14	5	18	14
Mean # of Coleoptera/stream = 12.7							

Table IV.2. Continued.

	Stream:						
Taxa:	B	H	C	S	W	L	P
Diptera							
Tipulidae							
Dicranota		●		●	●		
Hexatoma	●	●			●	●	
Holorusia hespera				●	●		
Limonia	●	●		●	●	●	●
Tipula	●	●	●		●	●	●
Culicidae							
Aedes			●				
Culex			●	●			
Ceratopogonidae	●			●	●	●	
Simulidae							
Simulium	●	●	●	●	●	●	●
Chironomidae	●	●	●	●	●	●	●
Dixidae							
Dixa (Dixa)					●		●
D. (Meringodixa)	●				●		
D. (Paradixa)	●	●	●	●	●	●	●
Stratiomyidae							
Euparyphus	●	●	●	●	●	●	●
Odontomyia	●			●		●	●
Tabanidae							
Chrysops						●	
Tabanus		●					
Dolichopodidae		●		●		●	
Empididae	●		●		●		●
Ephydridae	●	●		●	●	●	●
Sciomyzidae	●		●				
Muscidae							
Limnophora	●			●	●	●	●
Total Diptera taxa	14	11	9	13	15	13	11
Mean # Diptera/stream = 12.3							
Total Number of Taxa	53	35	43	40	35	50	48

Table IV.3 . Cumulative number of taxa and cumulative percentage of taxa collected per number of sampling visits for 7 Santa Cruz Island Streams. Cumulative percentages are in parentheses.

Number of visits:	Streams: Black Point	Coches	Horquetta	Laguna	Prisoners	Sauces	Willows
1	26(49)	10 (23)	21 (60)	31 (62)	25 (52)	28 (70)	10 (29)
2	41(75)	22 (51)	24 (69)	41 (82)	42 (88)	30 (75)	12 (34)
3	46(83)	30 (70)	27 (77)	45 (90)	43 (90)	31 (78)	19 (54)
4	51(96)	39 (91)	27 (77)	47 (94)	44 (92)	31 (78)	19 (54)
5	51(96)	40 (93)	30 (86)	49 (98)	47 (98)	32 (80)	25 (71)
6	53 (100)	41 (95)	35 (100)	49 (98)	48 (100)	33 (83)	26 (74)
7	53 (100)	42 (98)	35 (100)	50 (100)	48 (100)	35 (88)	27 (77)
8	53 (100)	42 (98)	35 (100)	50 (100)	48 (100)	38 (95)	30 (86)
9		43 (100)	35 (100)		48 (100)	40 (100)	31 (89)
10					48 (100)	40 (100)	32 (91)
11					48 (100)	40 (100)	33 (94)
12							34 (97)
13							35 (100)
14							35 (100)
15							

Table IV. 4. Table of regression results for total richness and richness within orders against catchment areas of individual streams, catchment areas of individual streams excluding Black Point, catchment areas above individual collection sites, and distances from mainland source populations.

Dependent variable (x)	Independent variable (y) Richness	Coefficient of Determination (R^2)	Slope	Intercept
Catchment areas (log) of individual streams	Total (log)	0.02	0.02	42.5 ***
	Ephemeroptera (log)	0.42	0.12	2.76 ***
	Odonata (log)	0.04	0.14	3.28 *
	Hemiptera (log)	< 0.01	-0.002	3.23 *
	Trichoptera (log)	< 0.01	0.01	5.65 **
	Coleoptera (log)	< 0.01	0.02	11.58 ***
	Diptera (log)	0.02	-0.02	12.64 ***
Catchment areas (log) of individual streams, excluding Black Point	Total (log)	0.62	0.12	33.34 ***
	Ephemeroptera (log)	0.42	0.14	2.57 **
	Odonata (log)	0.27	0.33	2.02
	Hemiptera (log)	0.21	0.17	2.14
	Trichoptera (log)	0.07	0.09	4.62 *
	Coleoptera (log)	0.10	0.14	8.54 **
	Diptera (log)	0.01	0.02	11.45 ***
Catchment area (log) above individual collection sites	Total (log)	0.03	-0.03	29.12 ***
	Ephemeroptera (log)	0.01	0.03	2.97 ***
	Odonata (log)	< 0.01	0.03	2.98 ***
	Hemiptera (log)	0.20	-0.12	3.19 ***
	Trichoptera (log)	0.02	-0.04	4.77 ***
	Coleoptera (log)	0.08	-0.14	7.40 ***
	Diptera (log)	0.02	0.05	5.71 ***
Distance of streams from mainland source populations	Total	< 0.01	0.10	39.10
	Ephemeroptera	0.49	-0.15	10.39 *
	Odonata	0.21	-0.32	19.48
	Hemiptera	0.16	0.14	-2.98
	Trichoptera	0.37	-0.29	19.37
	Coleoptera	0.04	0.23	2.17
	Diptera	0.29	0.30	-1.79

* P = 0.05
** P = 0.01
*** P < 0.001

Table IV. 5. Summary of multiple regression analyses (regression parameters, +/- 1 SE, probability value of estimates in parentheses) for stream insect richness (total and within orders) in relation to watershed area and distance from mainland source populations. Richness, watershed area,and distance were $\log_{10}$ transformed before the analysis.

Order	Intercept	Area Slope	Distance Slope	R^2	F	P
All	2.65 ± 2.19	0.02 ± 0.09	0.02 ± 1.26	0.10	0.21	0.82
	(0.16)	(0.61)	(0.42)			
Ephemeroptera	2.56 ± 1.33	0.08 ± 0.06	-1.19 ± 0.78	0.66	3.84	0.12
	(0.07)	(0.12)	(0.11)			
Odonata	6.30 ± 5.69	0.01 ± 0.24	0.01 ± -0.48	0.24	0.06	0.58
	(0.18)	(0.83)	(0.39)			
Hemiptera	-1.45 ± 3.98	0.41 ± 0.17	1.22 ± 2.34	0.06	0.14	0.87
	(0.48)	(0.57)	(0.39)			
Trichoptera	7.55 ± 2.01	-0.10 ± 0.08	-3.96 ± 1.18	0.74	5.63	0.07
	(0.01)	(0.15)	(0.02)			
Coleoptera	-0.21 ± 5.28	0.06 ± 0.22	0.76 ± 3.10	0.02	0.05	0.95
	(0.82)	(0.54)	(0.57)			
Diptera	-0.66 ± 2.05	0.01 ± 0.09	1.06 ± 1.20	0.18	0.44	0.68
	(0.51)	(0.77)	(0.34)			

Figure 4.1. Estimated colonization tracks of aquatic insects from the mainland to streams on Santa Cruz Island. Dashed lines indicate intermmitent portions of streams.

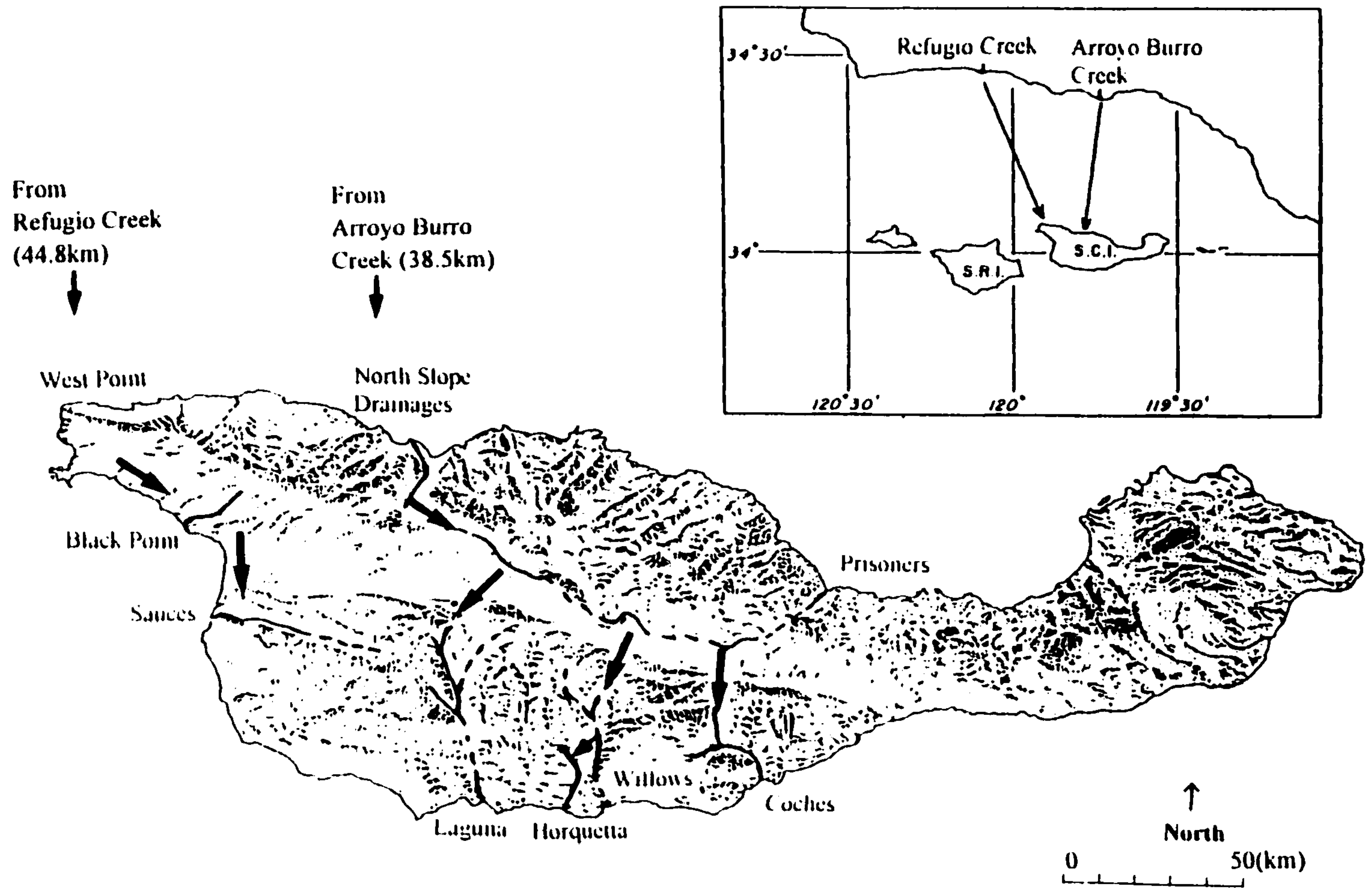

From
Refugio Creek
(44.8km)
From
Arroyo Burro
Creek (38.5km)
West Point
North Slope
Drainages
Black Point
Sauces
Prisoners
Laguna
Horquetta
Willows
Coches
North
0
50(km)
Refugio Creek
Arroyo Burro
Creek
34°30'
34°
S.R.I.
S.C.I.
120°30'
120°
119°30'

Figure 4.2. Cumulative number of insect taxa versus sampling effort (indicated as number of visits) for individual streams. These curves do not include individual genera within the families Ceratopogonidae, Chironimidae, Empididae Ephydridae, and Sciomyzidae.

a. Black Point, Coches Prietos, Willows
b. Horquetta, Laguna
c. Prisoners, Sauces

Figure 4.2a. Cumluative number of taxa colleced from Black Point (circle), Coches Prietos (square), and Willows (triangle) streams vs. cumulative number of sampling visits

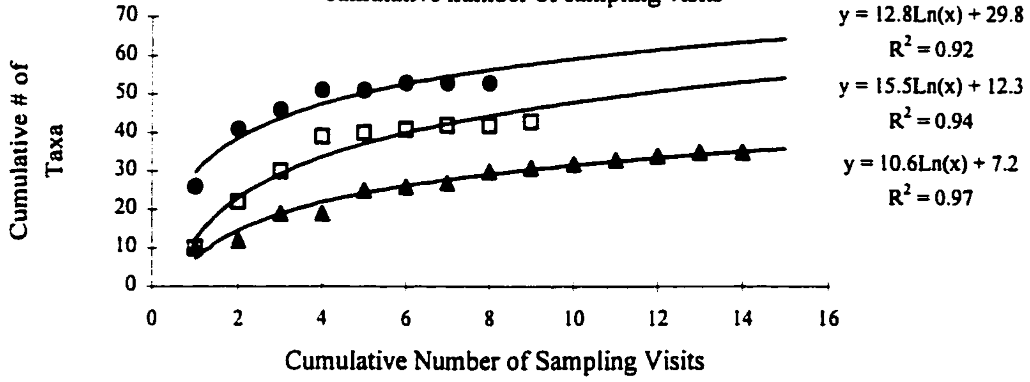


Figure 4.2b. Cumluative number of taxa colleced from Horquetta (circle) and Laguna (square) streams vs. cumulative number of sampling visits

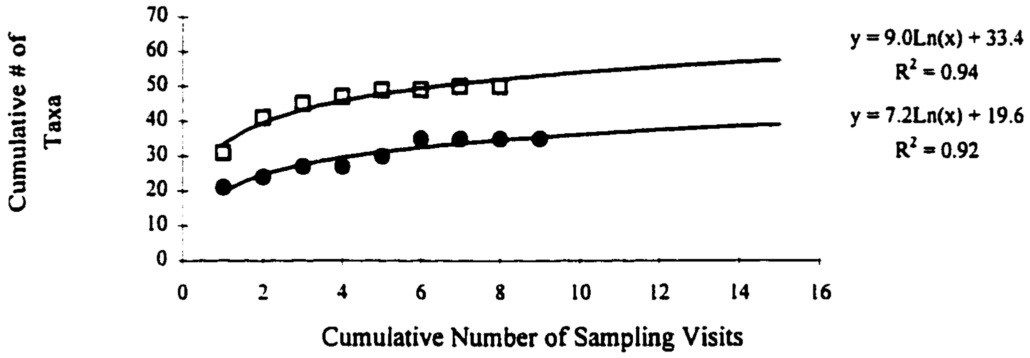


Figure 4.2c. Cumluative number of taxa colleced from Prisoners (circle) and Sauces (square) streams vs. cumulative number of sampling visits

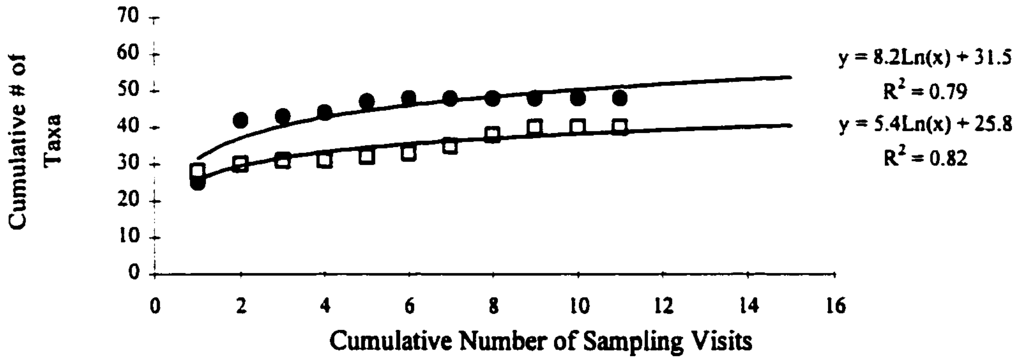


Figure 4.3. Regression of the total number of taxa against the number of processed samples per stream (BP = Black Point, C = Coches, H = Horquetta, L = Laguna, P = Prisoners, S = Sauces, W = Willows).

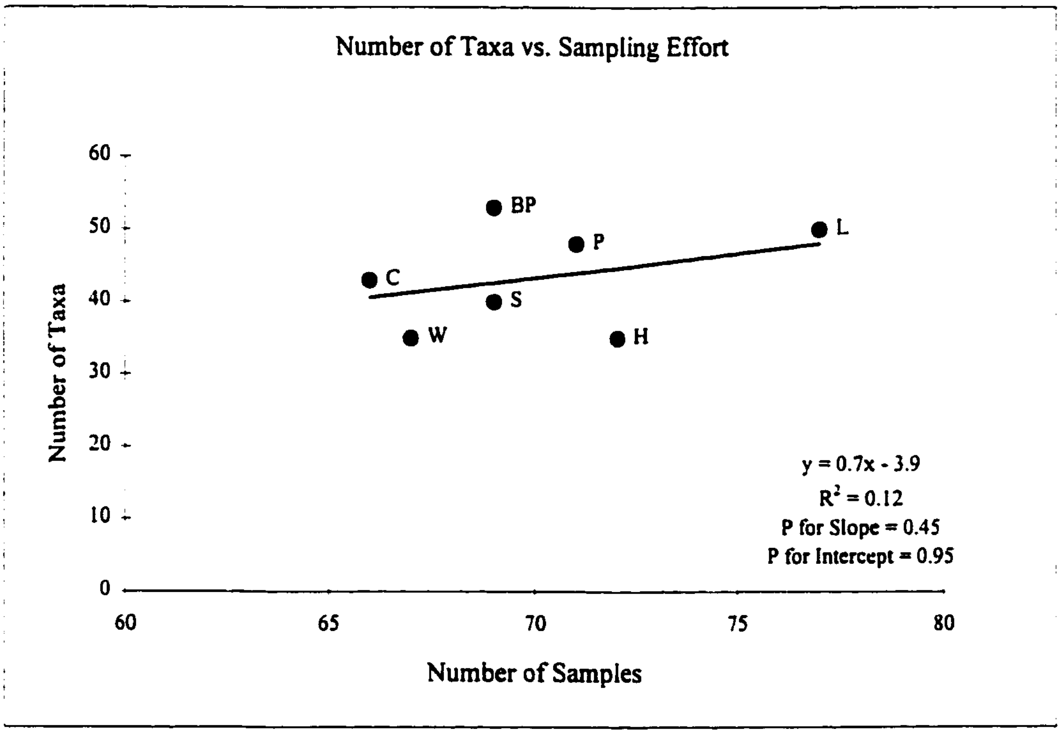

Number of Taxa vs. Sampling Effort
60
50
40
30
20
10
0
Number of Taxa
BP
P
L
C
S
W
H
y = 0.7x - 3.9
R² = 0.12
P for Slope = 0.45
P for Intercept = 0.95
60
65
70
75
80
Number of Samples

Figure 4.4. The log of number of taxa per stream plotted against the log of stream catchment area (BP = Black Point, C = Coches, H = Horquetta, L = Laguna, P = Prisoners, S = Sauces, Willows), including regression line and equation, coefficient of determination (R^2), and P values for t-teststhat the slopes and intercepts equalled 0.

a. All streams.
b. All streams, excluding Black Point

Figure 4.4a. Number of taxa vs. watershed area

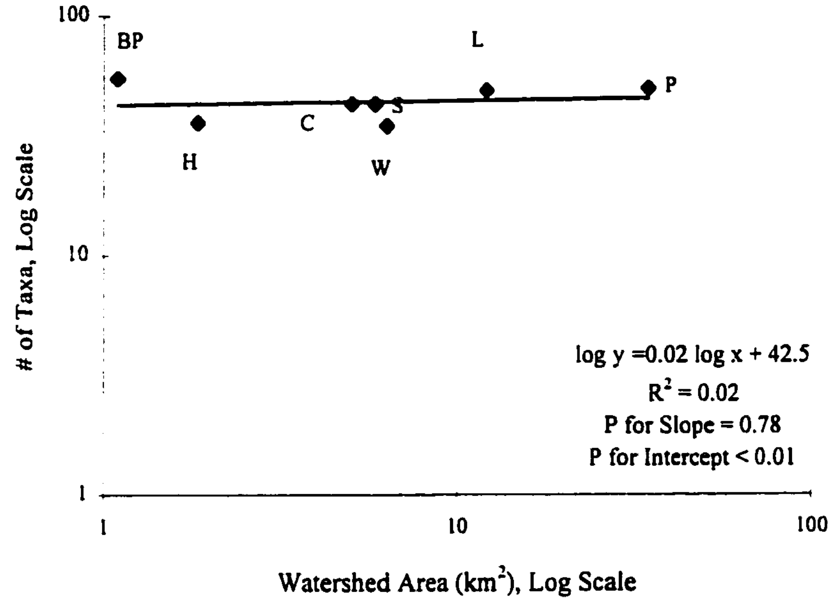


Figure 4.4b. Number of taxa vs. watershed area, excluding Black Point

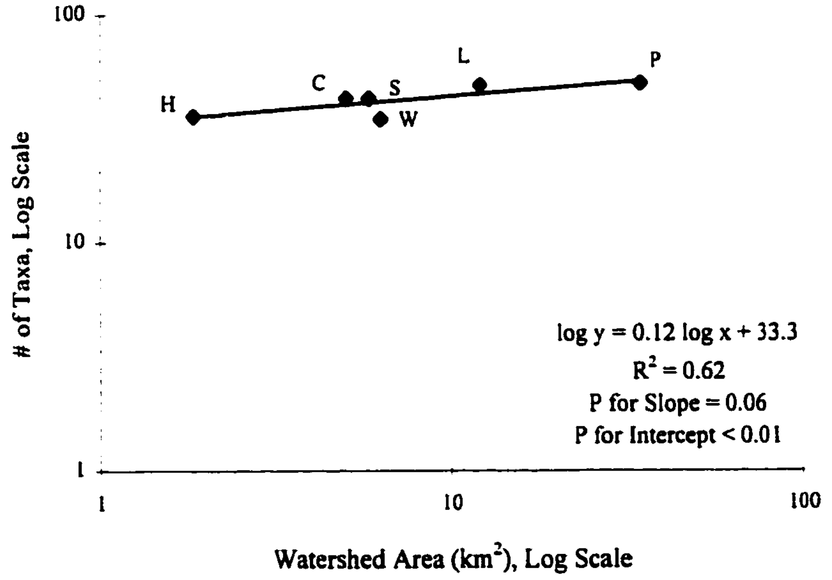
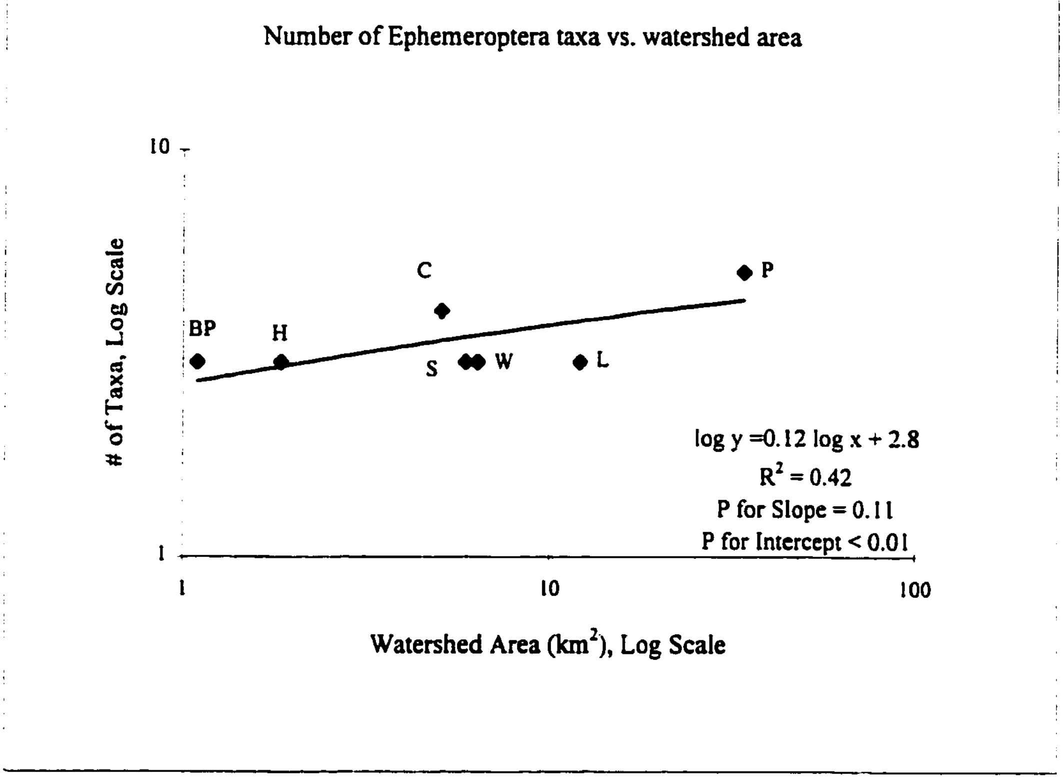


Figure 4.5. The relationship of log of number of taxa within orders per stream and the log of stream catchment area (BP = Black Point, C = Coches, H = Horquetta, L = Laguna, P = Prisoners, S = Sauces, W = Willows), including regression statistics as in Figure 4.4.

a. Ephemeroptera taxa, all streams
   Ephemeroptera taxa, Black Point excluded
b. Odonata taxa, all streams
   Odonata taxa, Black Point excluded
c. Hemiptera taxa, all streams
   Hemiptera taxa, Black Point excluded
d. Trichoptera taxa, all streams
   Trichoptera taxa, Black Point excluded
e. Coleoptera taxa, all streams
   Coleoptera taxa, Black Point excluded
f. Diptera taxa, all streams
   Diptera taxa, Black Point excluded

Figure 4.5a.


Number of Ephemeroptera taxa vs. watershed area

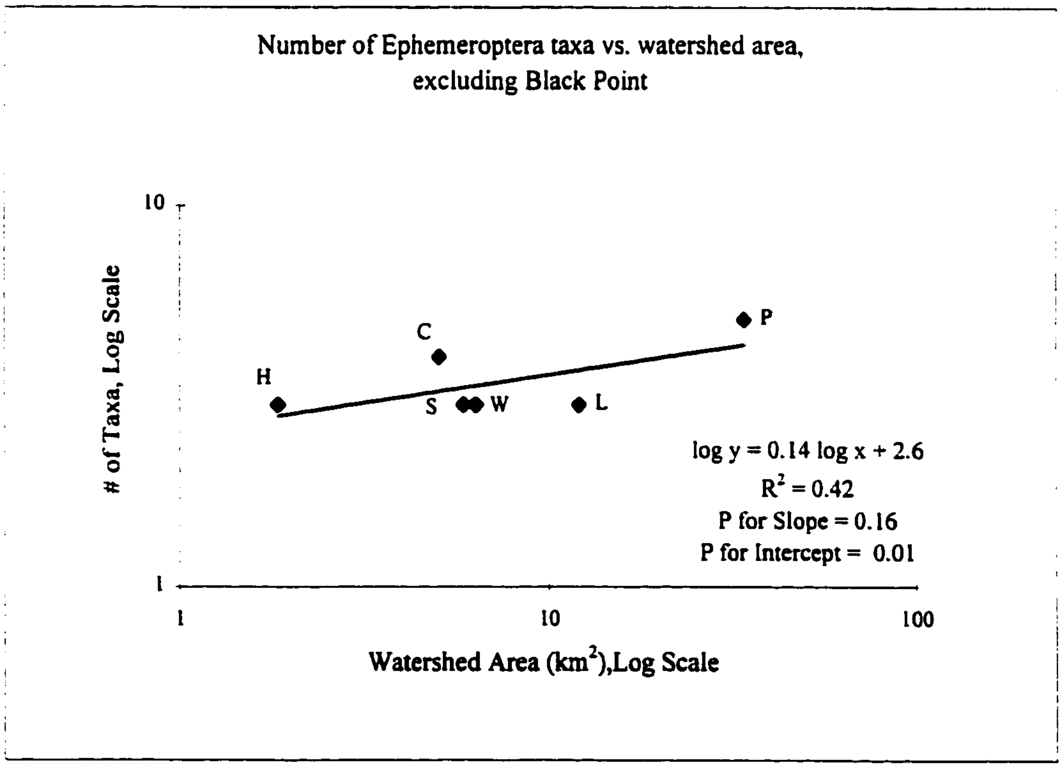
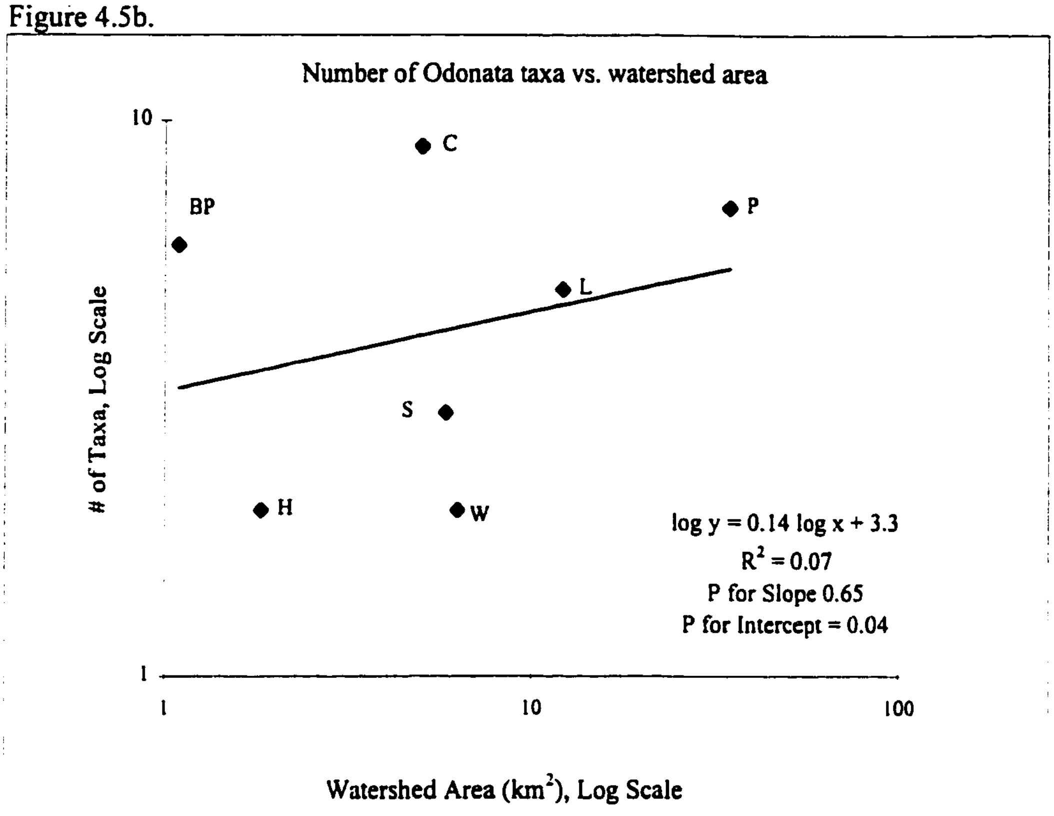

Number of Ephemeroptera taxa vs. watershed area, excluding Black Point

Figure 4.5b.


Number of Odonata taxa vs. watershed area

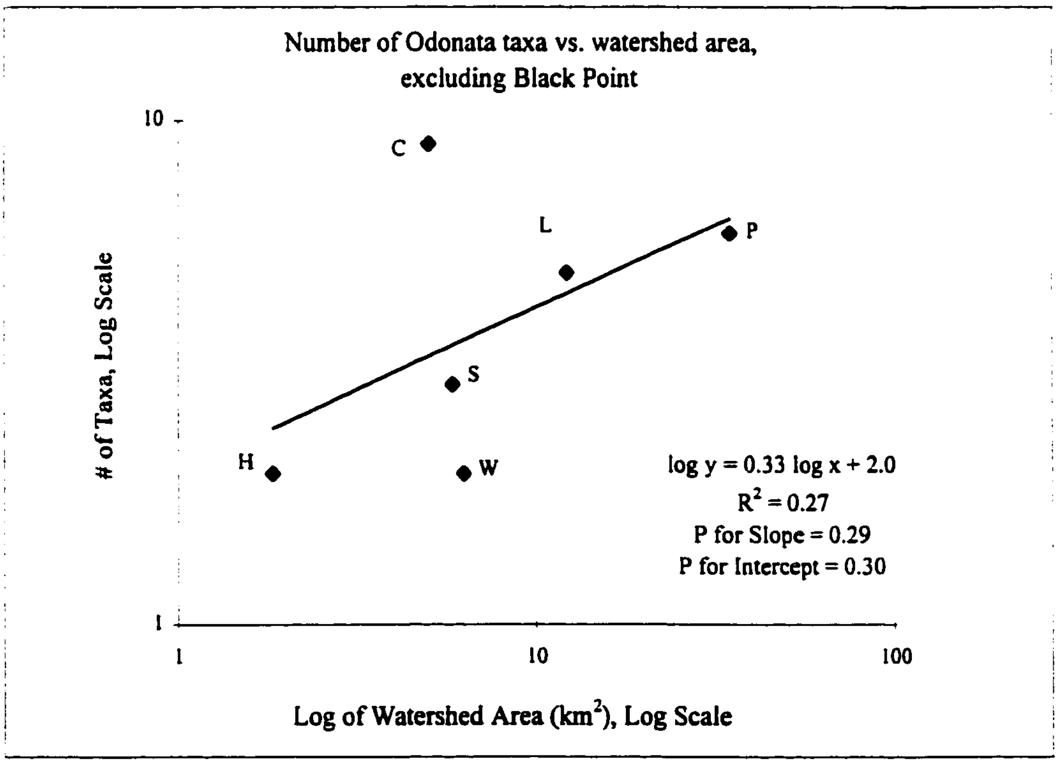
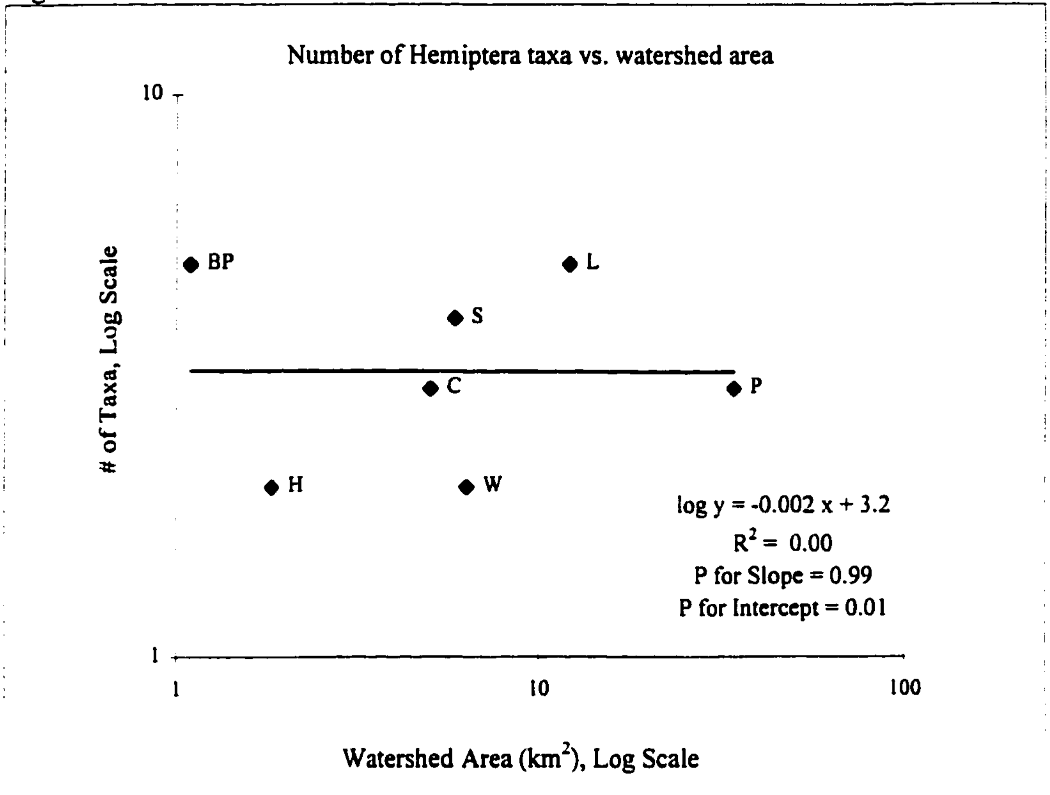

Number of Odonata taxa vs. watershed area, excluding Black Point

Figure 4.5c.


Number of Hemiptera taxa vs. watershed area
10
1
# of Taxa, Log Scale
BP
L
S
C
P
H
W
log y = -0.002 x + 3.2
$R^2 = 0.00$
P for Slope = 0.99
P for Intercept = 0.01
1
10
100
Watershed Area (km²), Log Scale

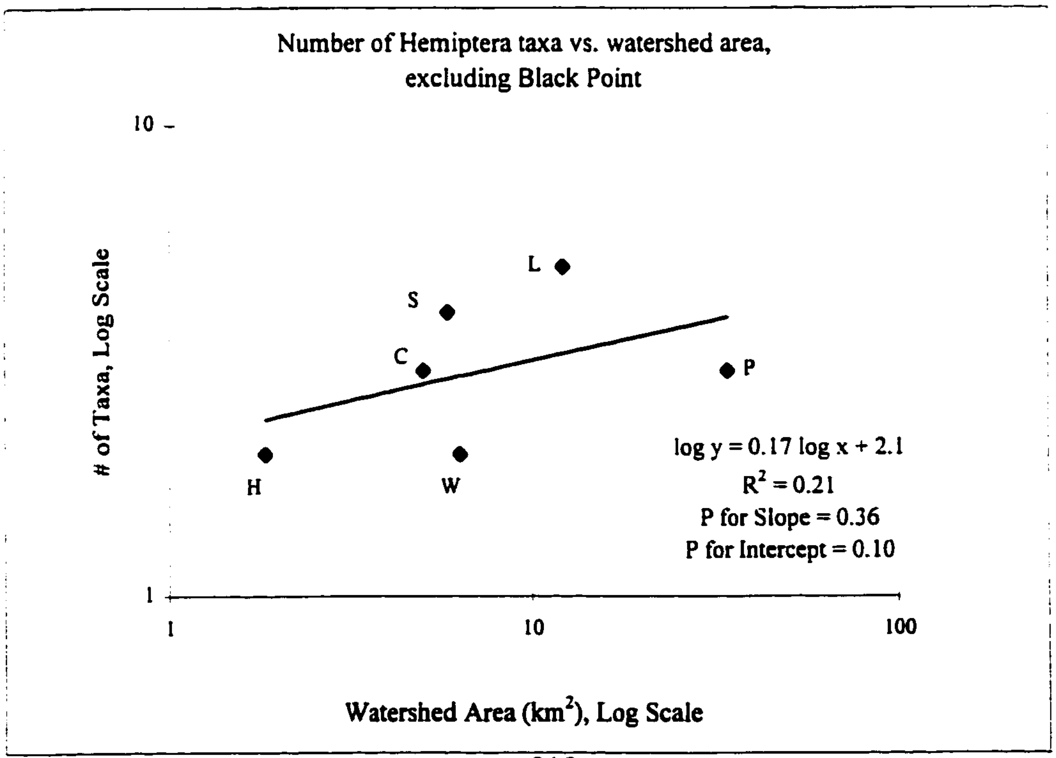
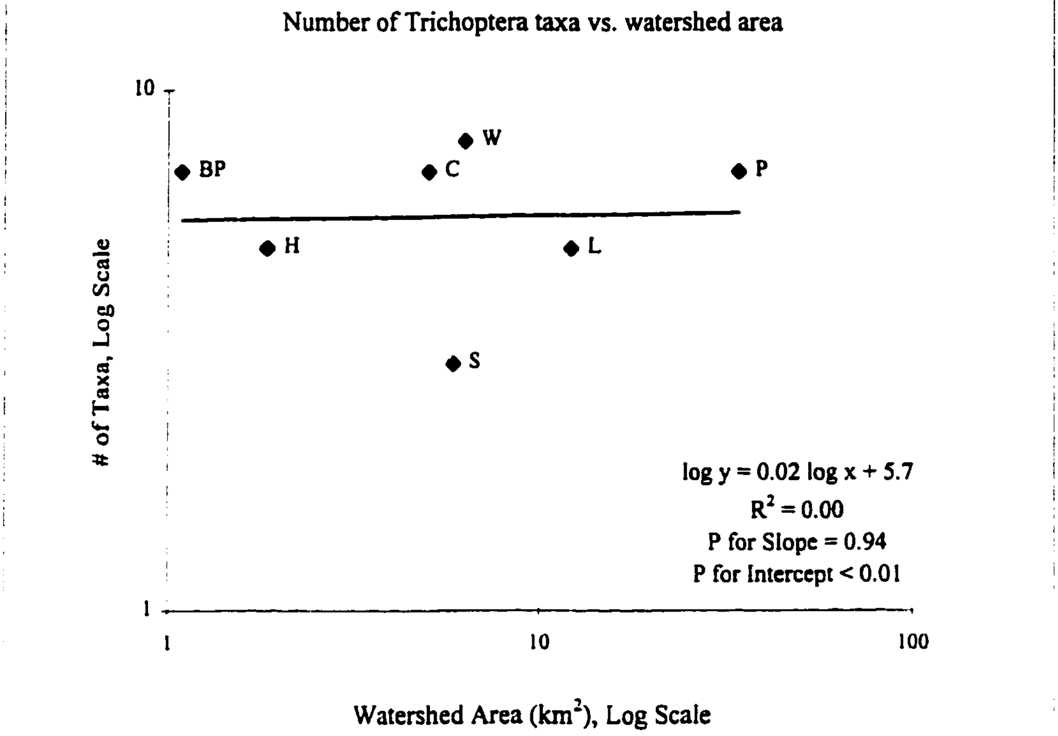
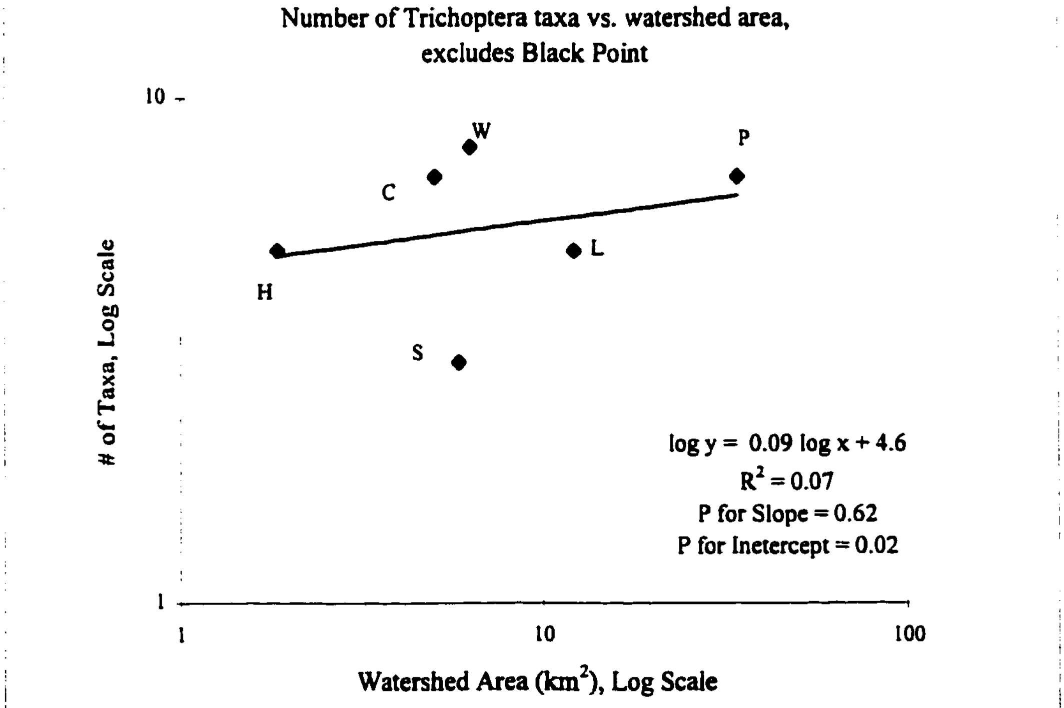

Number of Hemiptera taxa vs. watershed area, excluding Black Point
10
1
# of Taxa, Log Scale
L
S
C
P
H
W
log y = 0.17 log x + 2.1
$R^2 = 0.21$
P for Slope = 0.36
P for Intercept = 0.10
1
10
100
Watershed Area (km²), Log Scale

Figure 4.5d.

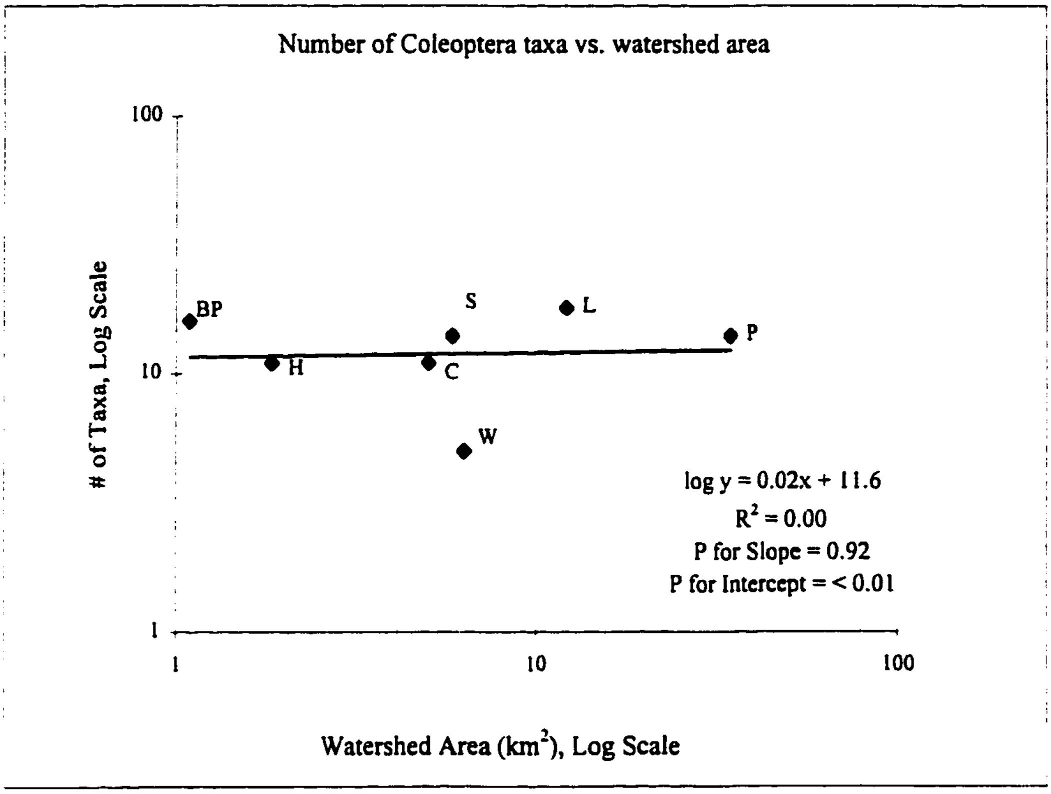


Number of Trichoptera taxa vs. watershed area
10
BP
W
C
P
H
L
S
# of Taxa, Log Scale
log y = 0.02 log x + 5.7
R² = 0.00
P for Slope = 0.94
P for Intercept < 0.01
1
1
10
100
Watershed Area (km²), Log Scale



Number of Trichoptera taxa vs. watershed area,
excludes Black Point
10
W
P
C
L
H
S
# of Taxa, Log Scale
log y = 0.09 log x + 4.6
R² = 0.07
P for Slope = 0.62
P for Inetercept = 0.02
1
1
10
100
Watershed Area (km²), Log Scale

Figure 4.5e.


Number of Coleoptera taxa vs. watershed area

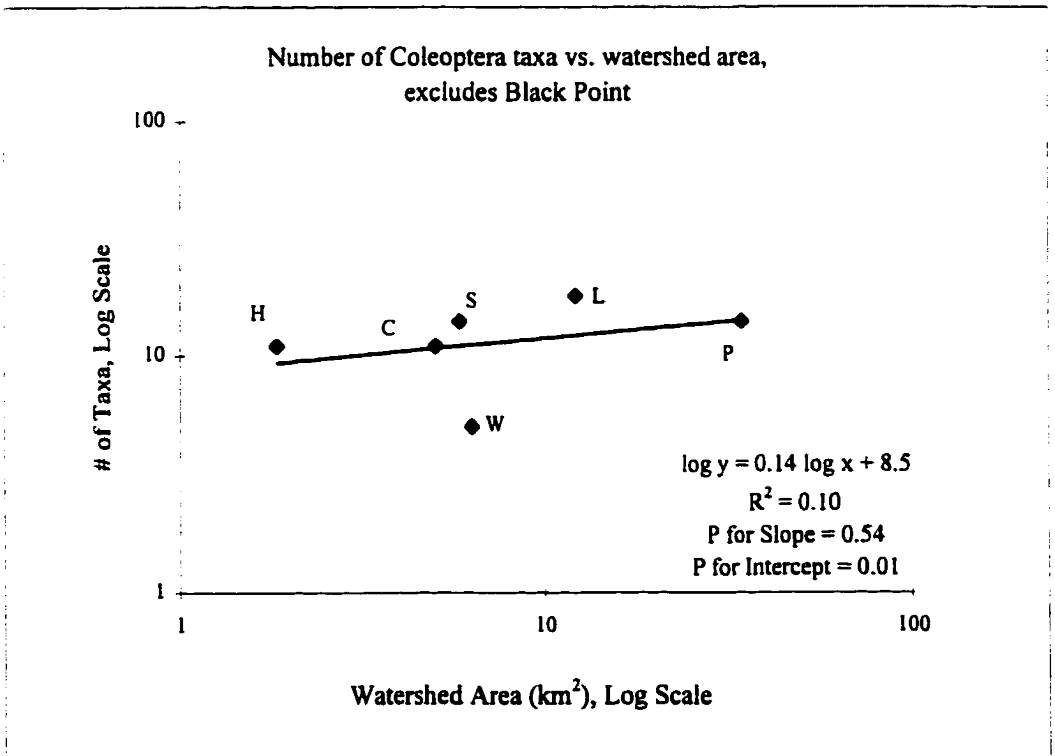
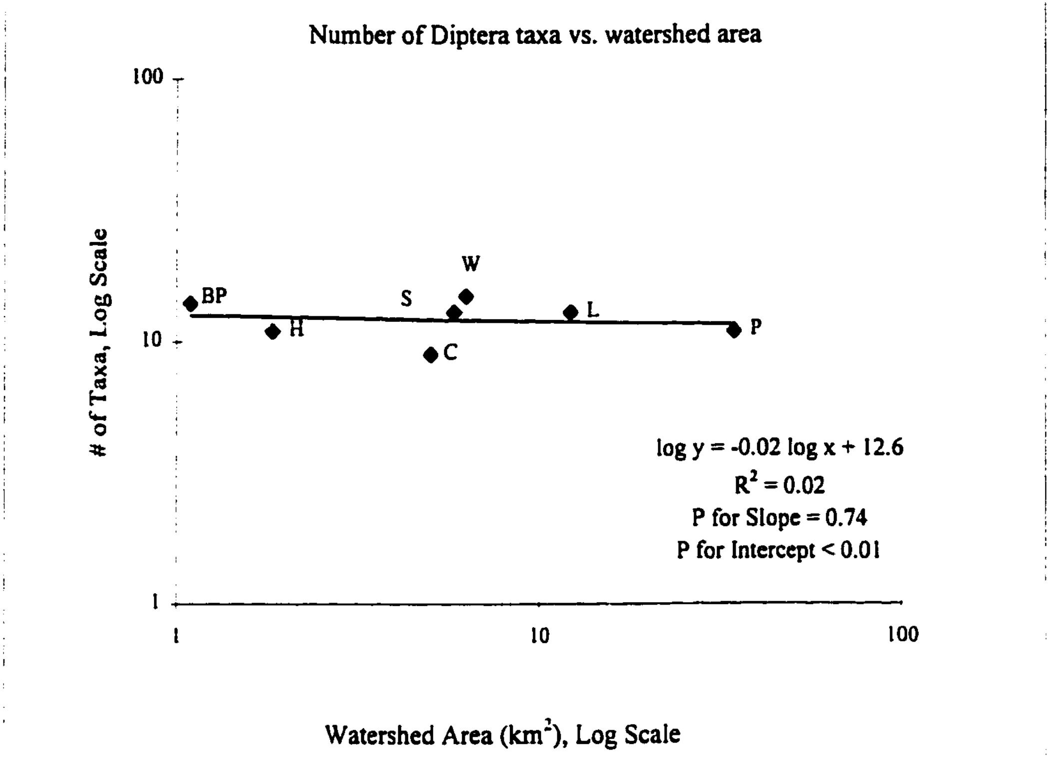

Number of Coleoptera taxa vs. watershed area, excludes Black Point

Figure 4.5f.


Number of Diptera taxa vs. watershed area
100
10
1
# of Taxa, Log Scale
BP
H
S
W
C
L
P
log y = -0.02 log x + 12.6
R² = 0.02
P for Slope = 0.74
P for Intercept < 0.01
1
10
100
Watershed Area (km²), Log Scale

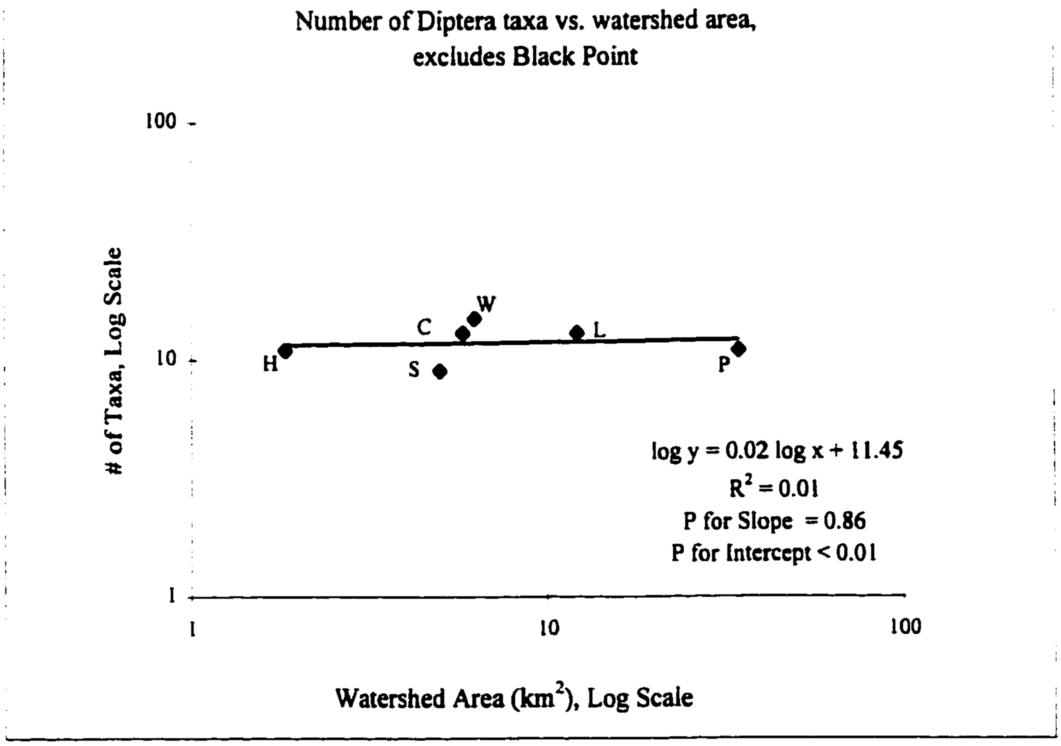

Number of Diptera taxa vs. watershed area, excludes Black Point
100
10
1
# of Taxa, Log Scale
H
C
W
S
L
P
log y = 0.02 log x + 11.45
R² = 0.01
P for Slope = 0.86
P for Intercept < 0.01
1
10
100
Watershed Area (km²), Log Scale

Figure 4.6. The relationship between the log of the number of taxa per sample site and the log of catchment area above individual sampling sites, including regression statistics as inFigure 4.4.

Legend:
Black Point = Open diamond
Coches = Open circle
Horquetta = Open square
Laguna = Closed circle
Prisoners = Closed triangle
Sauces = Cross
Willows = Closed diamond
Multiple records = Asterisk

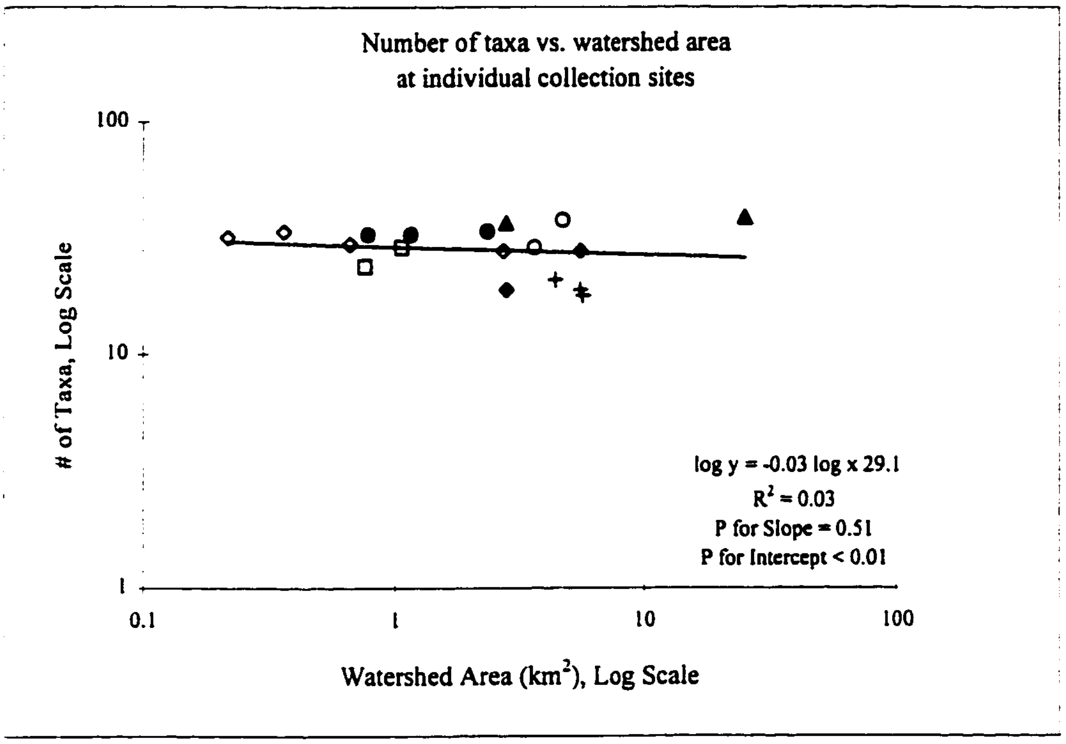

Number of taxa vs. watershed area
at individual collection sites
100
10
1
0.1
1
10
100
# of Taxa, Log Scale
Watershed Area (km^2), Log Scale
log y = -0.03 log x 29.1
R^2 = 0.03
P for Slope = 0.51
P for Intercept < 0.01

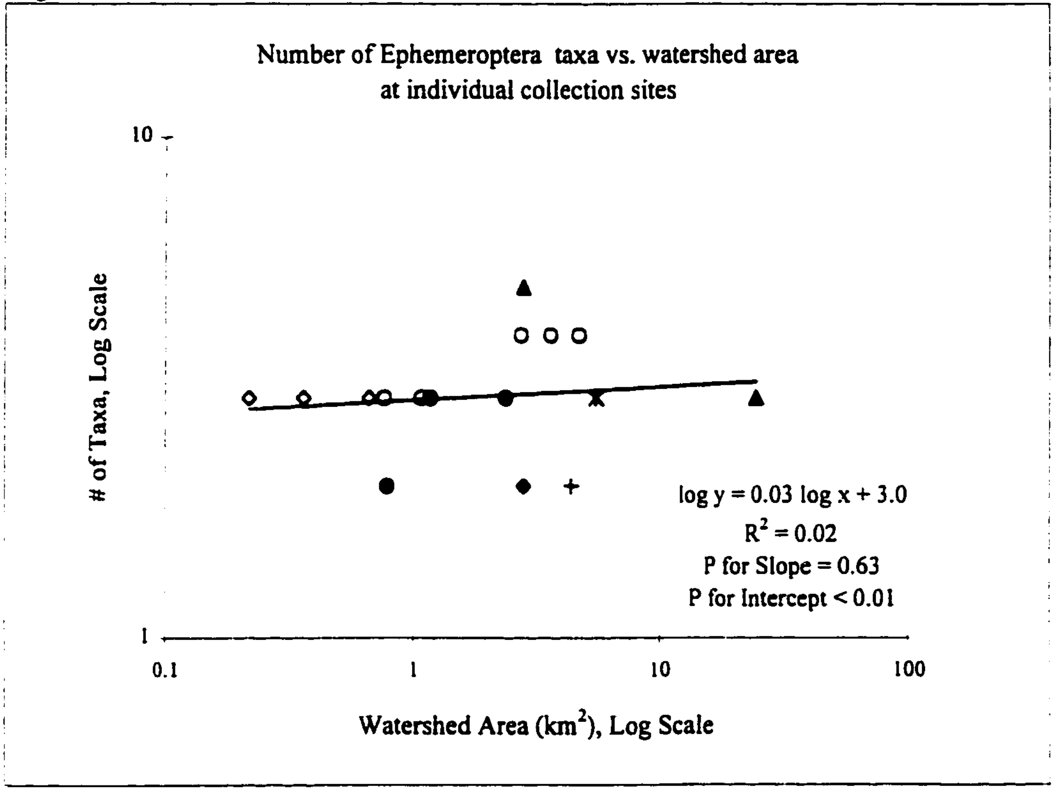
Figure 4.7. The relationship between the log of the number of taxa within orders per sampling site and the log of catchment area above individual sampling sites, including regression statistics as in Figure 4.4.

a. Ephemeroptera
b. Odonata
c. Hemiptera
d. Trichoptera
e. Coleoptera
f. Diptera

Legend:

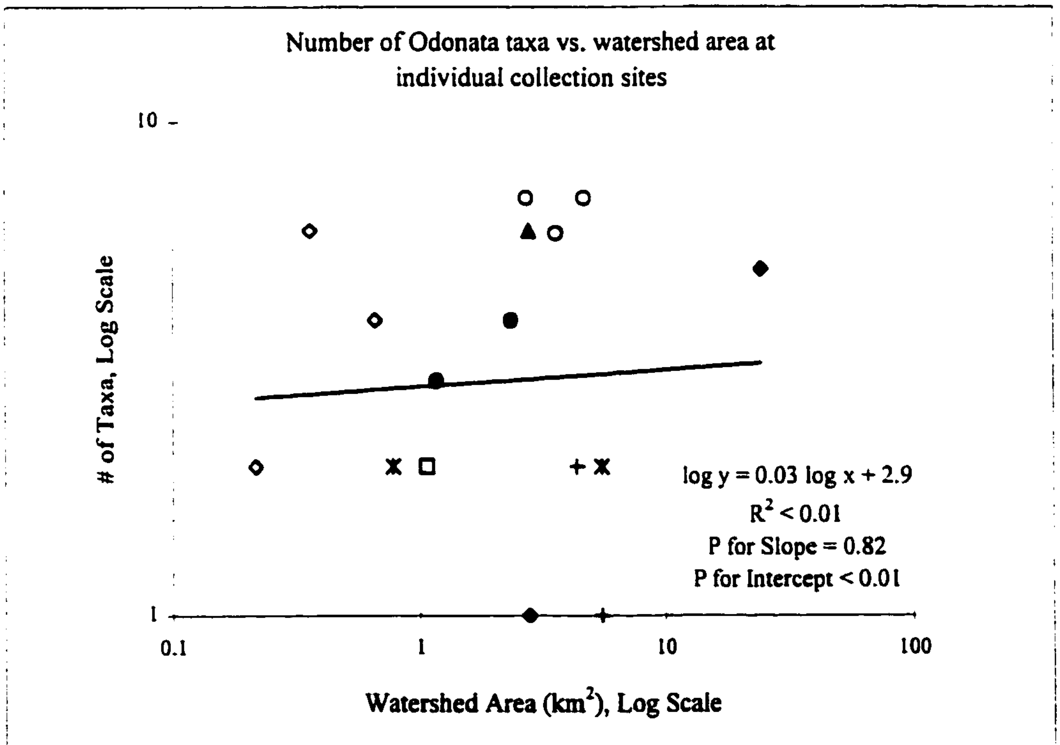
Black Point = Open diamond
Coches = Open circle
Horquetta = Open square
Laguna = Closed circle
Prisoners = Closed triangle
Sauces = Cross
Willows = Closed diamond
Multiple records = Asterisk

Figure 4.7a.



Number of Ephemeroptera taxa vs. watershed area at individual collection sites

Figure 4.7b.



Number of Odonata taxa vs. watershed area at individual collection sites

Figure 4.7c.

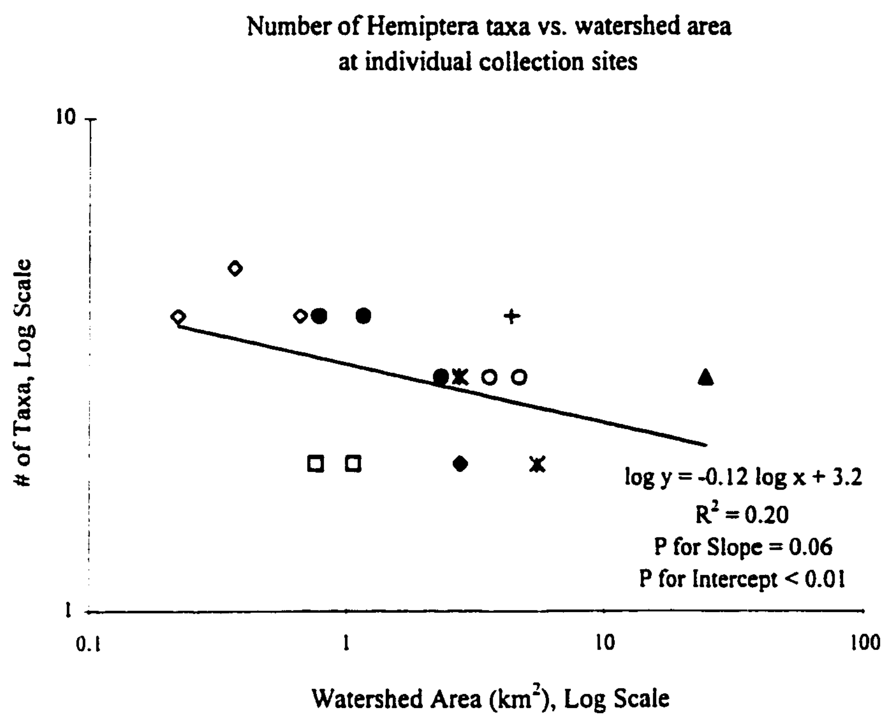


Figure 4.7d.

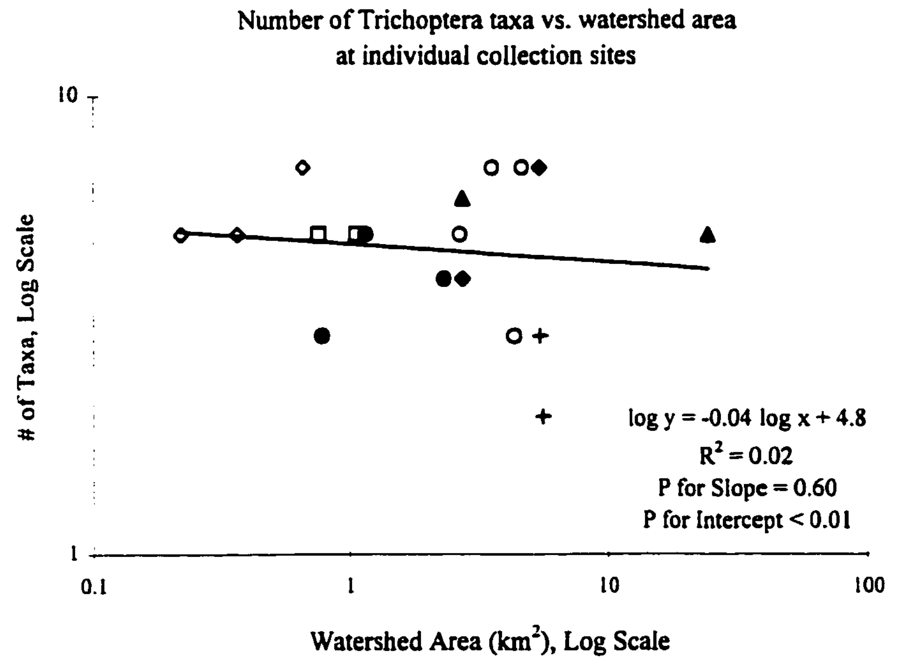


Figure 4.7e.

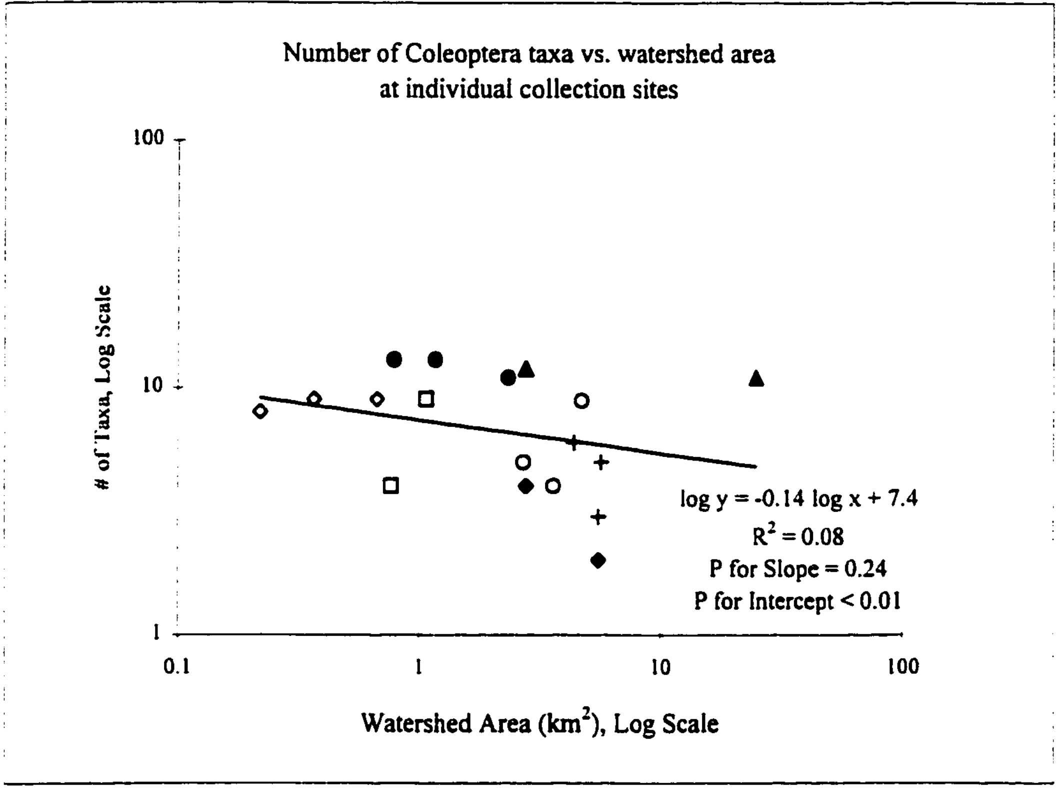


Figure 4.7f.

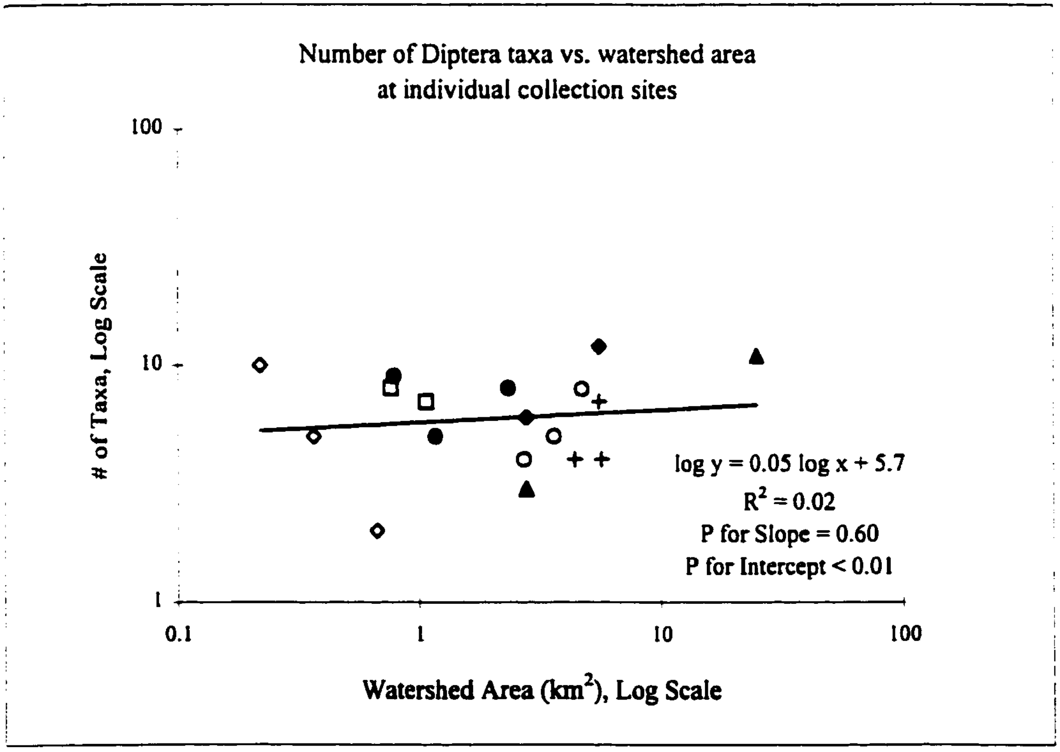


Figure 4.8. The relationship between the number of taxa per stream and the estimated distance from mainland source populations (BP = Black Point, C = Coches, H = Horquetta, L = Laguna, P = Prisoners, S = Sauces, W = Willows), including regression statistics as in Figure 4.4.

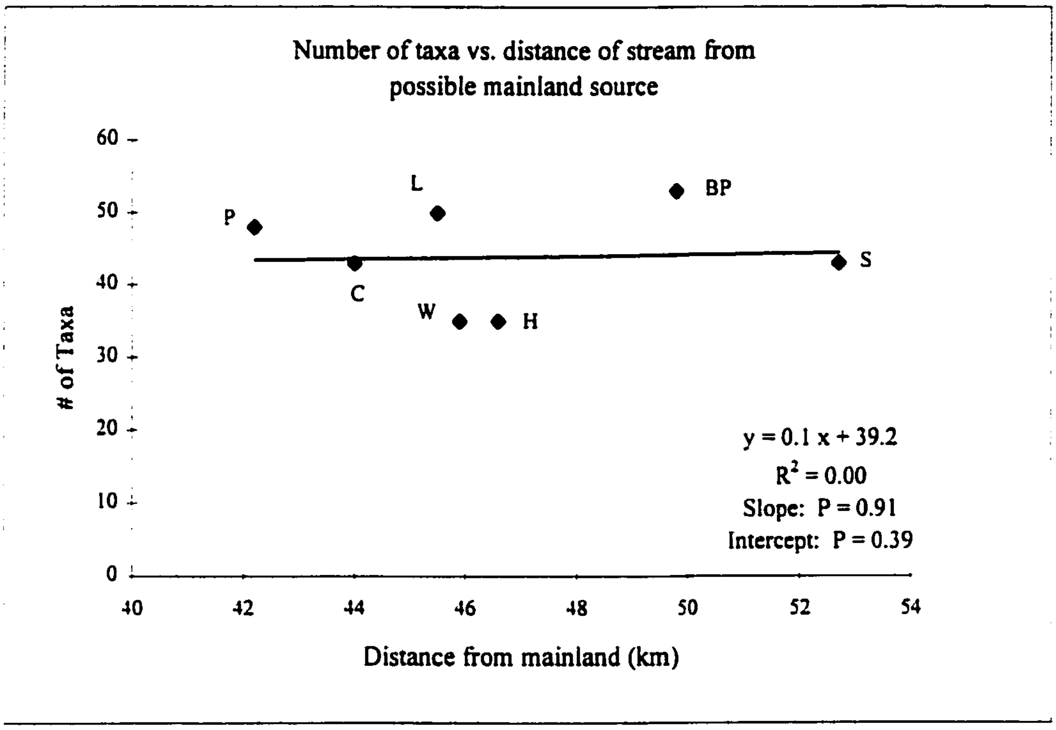

Number of taxa vs. distance of stream from possible mainland source
60
50
40
30
20
10
0
# of Taxa
P
L
BP
C
S
W
H
y = 0.1 x + 39.2
R² = 0.00
Slope: P = 0.91
Intercept: P = 0.39
40
42
44
46
48
50
52
54
Distance from mainland (km)

Figure 4.9. The relationship between the number of taxa with orders per stream and the estimated distance from mainland source populations (BP = Black Point, C = Coches, H = Horquetta, L = Laguna, P = Prisoners, S = Sauces, W = Willows), including regression statistics as in Figure 4.4.

a.	Ephemeroptera
b.	Odonata
c.	Hemiptera
d.	Trichoptera
e.	Coleoptera
f.	Diptera

Figure 4.9a.

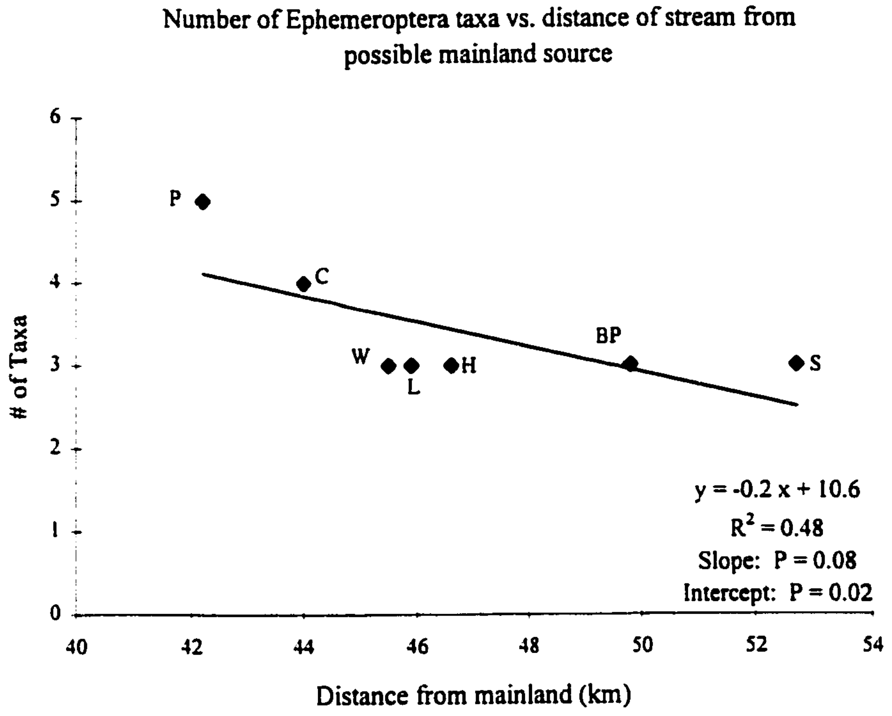


Figure 4.9b.

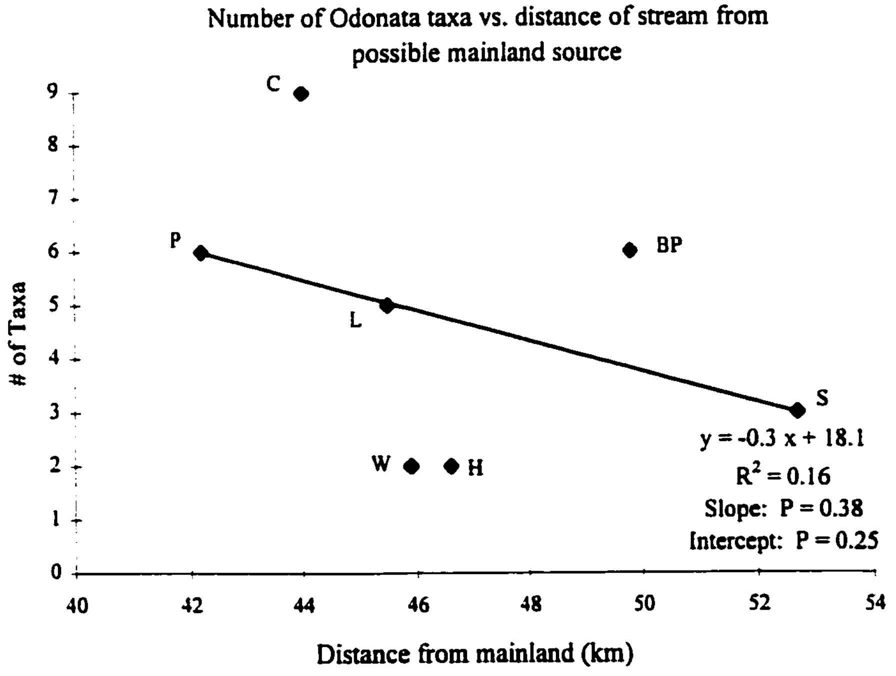


Figure 4.9c.

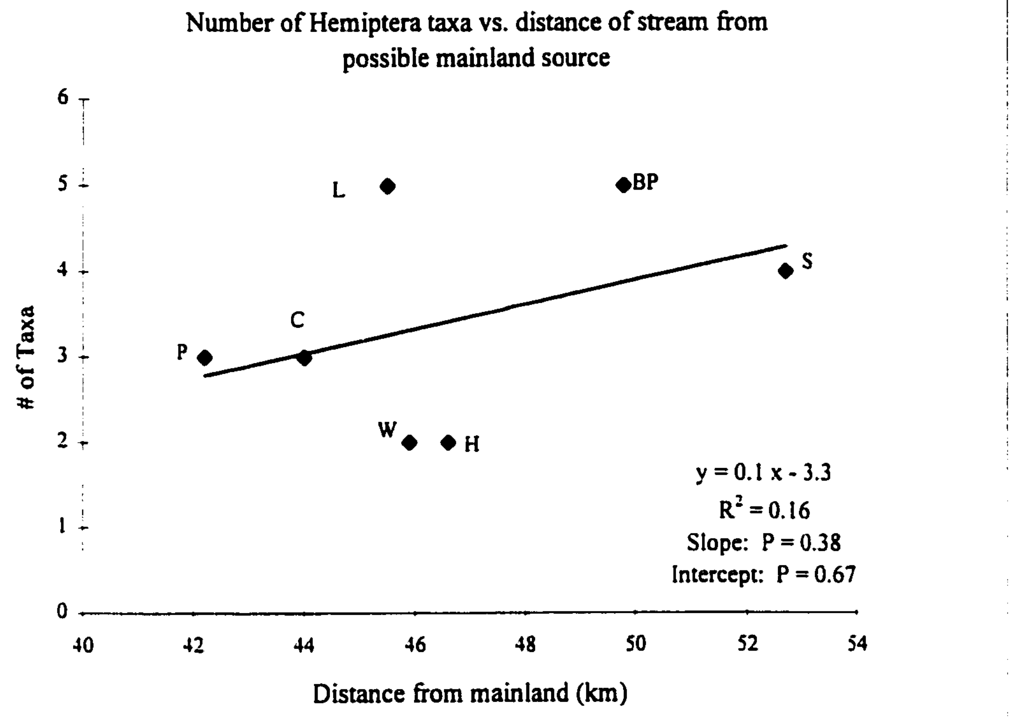


Figure 4.9d.

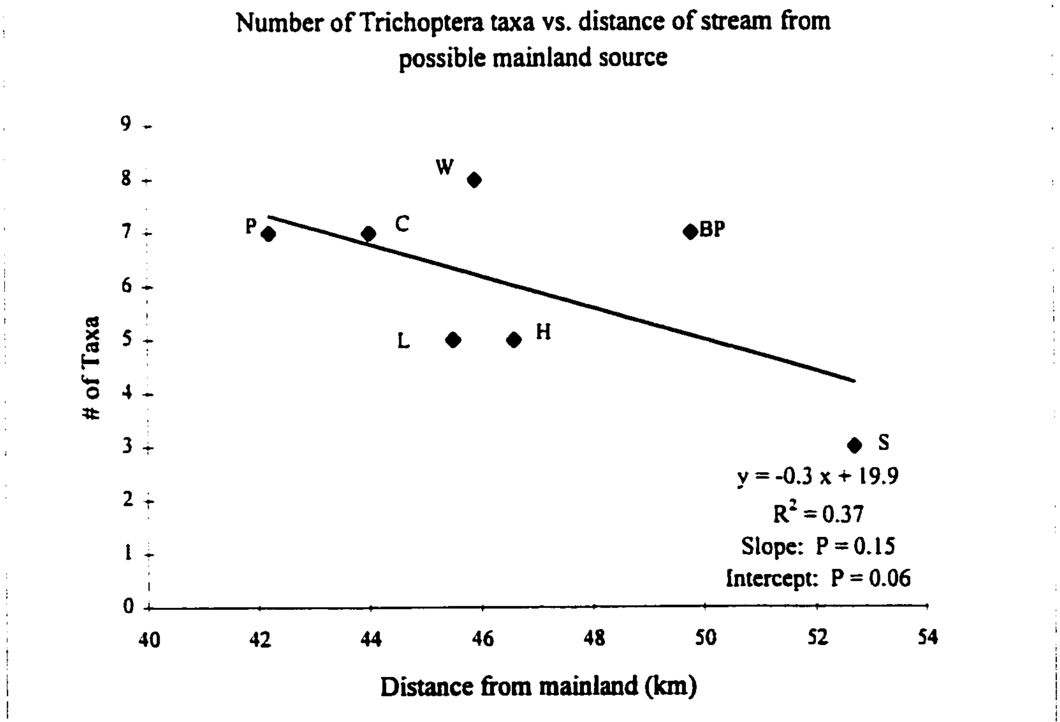


Figure 4.9e.

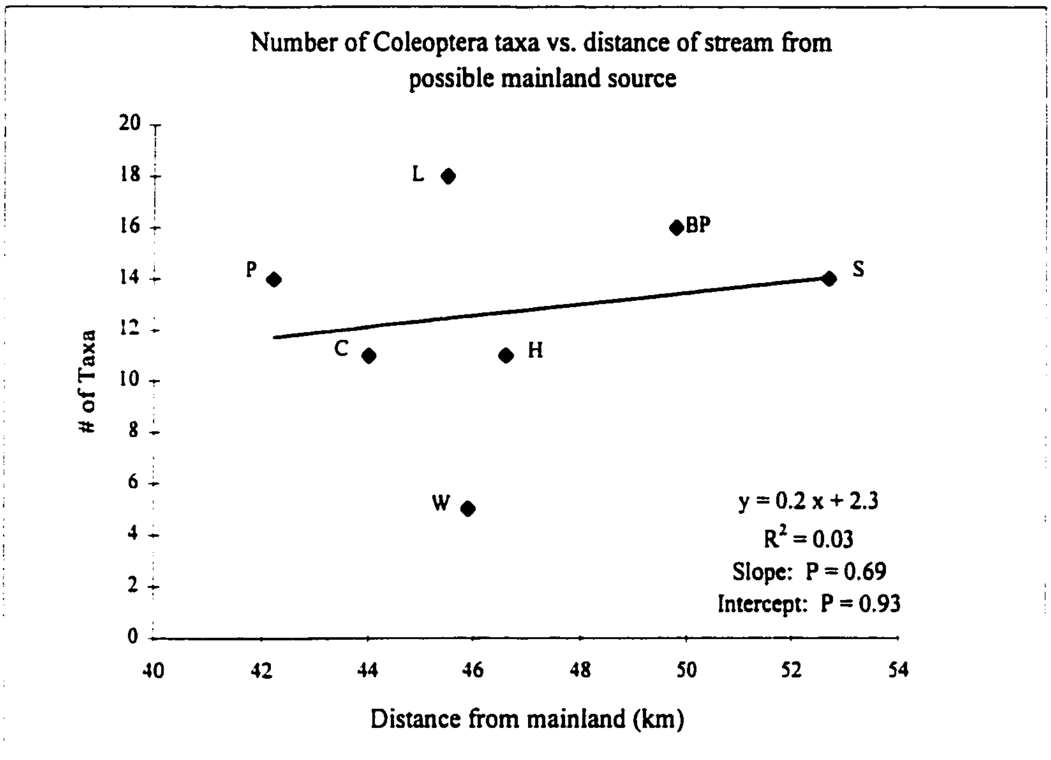
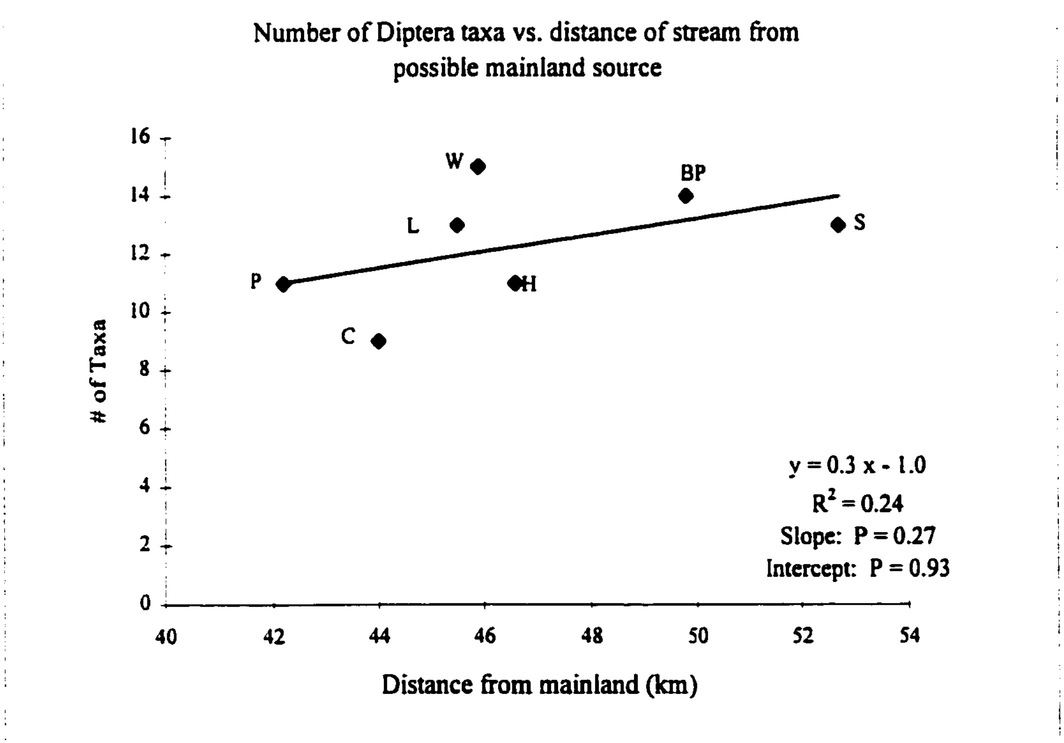


Figure 4.9f



CHAPTER V

EFFECTS OF PHYSICAL DISTURBANCE ON THE TAXONOMIC RICHNESS OF TWO STREAM REACHES

INTRODUCTION

Analyses of seven Santa Cruz Island streams revealed that increasing stream size (watershed area) alone is not significantly related to increasing taxonomic richness. For example, the stream with the smallest watershed, Black Point, exhibited the greatest overall taxonomic richness of the seven streams examined. Observations during the course of this study revealed that streams with small watersheds, and upstream sites on streams with large watersheds, rarely experienced winter scour and maintained relatively high invertebrate richness during winter months. This chapter examines the effects of scour and experimental disturbance on richness of the Santa Cruz Island stream fauna.

Physical disturbances influence the structure of many communities (Connell 1978, Huston 1979, Pickett and White 1985). In lotic systems, researchers often address the effects of disturbance resulting from discharge variations, such as floods and droughts, on community structure (e.g., Resh et al. 1988, Grimm and

Fisher 1989, Townsend 1989, Reice et al. 1990, Brooks and Boulton 1991, Boulton et al. 1992, Dudgeon 1993, Uehlinger et al. 1996, Matthaei 1997, Townsend et al. 1997b and 1997c). Depending on absolute increases in discharge following storm events, disturbances range in scale from dislodging organic matter and overturning stones to the scouring of entire channels with resultant large-scale substrate movement (Reice 1985). These events affect stream macroinvertebrates both directly, through scour, crushing, and catastrophic drift, and indirectly, through the loss of organic matter, including food resources (Grimm and Fisher 1989, Dudley and D'Antonio 1991).

The effects of spates on benthic communities have been studied phenomenologically (i.e., observations before and after spates, Scrimgeour et al. 1988, Brooks and Boulton 1991, Fisher et al. 1982, Boulton et al. 1992, Dudgeon 1993, Palmer et al. 1995, Uehlinger 1996, Townsend et al. 1997b), through the comparison of natural channels with differing flood regimes (Robinson et al. 1992), and through small-scale experimental manipulation (e.g., Hemphill and Cooper 1983, McAuliffe 1984, Boulton et al. 1988, Dudgeon 1991, Englund 1991, Matthaei et al. 1997). Each of these approaches has strengths and weaknesses (Townsend 1989). Phenomenological studies provide realism in terms of the scales and effects of flood events, but lack experimental controls and replication. Channel comparisons serve as natural experiments, with undisturbed channels acting as controls; however, variability among channels in factors other than disturbance can confound comparisons. By contrast, manipulations provide experimental control, and allow replication, but may lack realism (Fisher 1987, Minshall 1988).

Initially, the study outlined below attempted to incorporate all of the above approaches by conducting an experiment during the winter flood season in two channels differing in disturbance regimes. An exceptionally strong storm event, however, truncated the original experiment. I conducted an alternate experiment during the spring (not typically the season of scour). The objective of both experiments was to determine the effects of disturbance frequency on two types of faunal communities: one typically exposed to scour during the rainy season and one that is not. I hypothesized that channels exposed to seasonal scour might support only those taxa with adaptations enabling them to persist through disturbance events. In contrast, channels not experiencing scour would support a richer taxonomic assemblage consisting of "disturbance adapted" taxa as well as those more susceptible to scour. Santa Cruz Island's stream fauna is depauperate and "weedy": therefore, I would expect "disturbance adapted" taxa to persist even in the absence of disturbance due to a possible lack of competitive exclusion. I expected that the effects of experimental disturbance on richness would be greater in the channel that does not typically experience scour events.

DESCRIPTION OF STUDY SITES

For the comparison study, I chose two reaches of Prisoners Stream (Figure 1.2, primary sampling sites). The Prisoners Stream drainage is the largest on the island (catchment area = 34.66 km^2). The stream drains the central valley of the island, ultimately flowing north into the Santa Barbara Channel.

The upper reach (119° 46' W, 33° 60' N), at an elevation of 314 m, has a catchment area of 2.77 km^2. At this site, Prisoners is a second order stream with an average width of 1.5 m and a partially closed canopy of willow (*Salix* spp.) and mulefat (*Baccharis salicifolius*). The substrata consist primarily of cobbles and gravel underlain with sand. Previous observations indicate that the upper reach does not typically experience great absolute fluctuations in discharge, though large relative increases in discharge have occurred. Winter discharge ranged from to 1.67 to 32.22 liters per second (mean 11.99 l/s) in 1997. Spring 1997 discharge ranged from 0.33 to 5.78 liters/second (mean 2.39 l/s).

The lower reach (119° 41' W, 33° 59' N), at an elevation of 66 m, has a catchment area of 17.26 km^2. At this site, Prisoners is a fourth order stream with an average width of 2.5 m and a partially closed canopy of willow, mulefat and eucalyptus (*Eucalyptus globulus*). Substrata are similar to the upper reach but with some larger cobbles, approaching the size of small boulders. The lower reach typically experiences great absolute and relative fluctuations in discharge, with scouring stormflow during the rainy season (November-March). Discharge in the winter of 1997 ranged from 37.35 to 190.04 liters per second (mean 83.94 l/s). Spring 1997 discharges ranged from 1.24 to 93.00 liters per second (mean 26.98 l/s). Compared to the upper site, lower site pool and riffle habitats are less well defined; however, these differences in upper and lower site habitat characteristics have not been quantified.

Flow between the upper and lower reaches, which are 7 km apart, occurs only following substantial winter storm events and may continue for as long as three weeks. During this study, continuous flow occurred in December and following the January 1997 storm. During the spring of 1997, flow did not occur between the upper and lower reaches.

METHODS

Experiment I

At each site (upper and lower), four riffles within a 500 meter reach served as locations for experimental manipulations of natural (gravel, rock surface) and introduced (brick) substrata. On December 27, 1996, I placed three cement bricks (20 cm x 10 cm x 6 cm) in each of the 8 riffles (4 downstream and 4 upstream). Prior to brick placement, gravel substrata (approximating the volume of the brick) were agitated (via kicking) until cleared of organisms and organic matter, providing a clear space for recolonization. Materials dislodged into the water column were captured with a 300 micron mesh net placed immediately downstream, allowing an assessment of the initial faunal assemblage. In addition, in each riffle, an area of 200 cm^2 was marked with a chisel on the surface of 3 small boulders or on bedrock. I then cleared all surface material from the marked area (via vigorous brushing; material entering the water column captured with a 300 micron mesh net). All captured material was preserved in 70% ethanol.

Within each riffle, I randomly assigned one set of substrata (brick, cleared gravel, cleared rock) for disturbance at two week intervals, one set at four week intervals, and a third set to remain undisturbed for the eight weeks of the study. Disturbance included vigorous brushing (upper brick surface, marked rock surface) or agitation (vigorous stirring of gravel substrate with hands and cleaning individual stones with a brush). At each disturbance interval, control samples were taken from a 200 cm^2 area on randomly chosen rock surfaces and from gravel substrata (approximate volume of a brick) at each site for comparison with the experimental treatments. Materials dislodged by the disturbance treatments and random sample collections were retained in a 300 micron mesh net placed downstream and preserved in 70% ethanol. Interference among sample locations was avoided by sampling from downstream to upstream and capturing dislodged materials with a 300 micron mesh net.

An exceptionally strong winter storm occurred between the second (January 16, 1997) and fifth (February 6, 1997) weeks of the experiment. From January 20 to 27, the island received approximately 18 cm of rain. The subsequent flow at both sites removed or buried all but two of the twenty-four bricks. Most of the marked rocks were moved or buried in shifting substrata, resulting in the premature termination of the experiment. On this date, samples were taken from randomly chosen rock and gravel substrata, as noted above.

All samples were sorted by wet sieving on 1 mm and 500 micron mesh sieves. Macroinvertebrates were identified, to genus or species (insects) or less precise level of taxonomic resolution (other invertebrates), and counted. Mean richness was calculated as number of taxa per unit surface area of brick, rock, and gravel.

Experiment II

The second experiment (initiated March 19, 1997), essentially followed the design of the first experiment. This experiment differed somewhat from the first in terms of the use of rock substrata, intensity of substratum disturbance, and the collection of materials from experimental and control (random rock and gravel) substrata.

In the second experiment, I selected individual "brick-sized" rocks (length range: 7 to 22 cm; width range: 5.5 to 13.5 cm) from the stream banks to use as experimental rock substrates. Three 0.5 m^2 areas were cleared (substrata agitated by kicking until water ran clear) in each of the four upper and lower site riffles. A rock and cement brick (20 cm x 10 cm x 6 cm) were placed in the center of each of these cleared areas at the initiation of the experiment. Cleared gravel adjacent to each brick served as the gravel replicates for the experiment.

As in the first experiment, one set of substrata (brick, rock, and gravel) in each riffle was designated for disturbance at 2 week intervals, one set for disturbance at 4 week intervals, and one remain undisturbed for the 8 weeks of the study. Disturbance consisted of the removal of all organic matter from experimental substrate surfaces (rock, brick, gravel) and from an 0.5 m^2 area surrounding the disturbed substrata. Rock and brick substrata were cleared by vigorous brushing and scrubbing. Following disturbance on treatment substrata, I cleared the gravel substrata and a 0.5 m^2 area around the experimental substrata by agitating the gravel (via hands and kicking) until the water ran clear. In addition, the gravel substrata were scrubbed when necessary to remove algae. Interference with surrounding substrata was prevented by working from downstream to upstream and capturing dislodged materials in a 300 micron mesh net.

Organic materials (insects, particulate organic matter, algae) were collected from the rock and brick substrata by placing a 300 micron mesh net immediately downstream from the substrate units, placing the entire rock or brick into the net, and clearing materials from all surfaces. This procedure retained material associated with all surfaces of individual substrata. The surface area of each rock (treatments and controls) was estimated by covering the rock in foil. Surface area was calculated by comparing the weight of this foil with the weight of a known area of foil. Gravel samples (experimental and control) were obtained using a modified Surber sampling box with a 300 micron mesh net. Each gravel substrate sample approximated the volume of a brick (20 cm X 10 cm, to a depth of 6 cm).

Only samples collected at the end of the experiment (week 8, May 24, 1997) were processed. These samples were processed as noted in experiment I. In addition, I obtained the ash-free dry weight of particulate organic matter (>500 microns, includes algae) for each sample. The ash-free dry weight was calculated as the difference between the weight of POM dried at least 48 hours at 40°C and the weight after ashing (550°C for 4 hours). The ash-free dry weight provided a relative measure of the combined amount of detritus, microbes, and algae associated with each sample.

Statistical Analyses

One-way analyses of variance (ANOVAs) determined whether mean richness varied significantly with location (upstream vs. downstream) and disturbance frequency. In addition, one-way ANOVAs were used to detect significant differences between substratum types and to determine if POM varied significantly with disturbance frequency. Prior to analyses, the data were subjected to tests of normality and homogeneity of variance. Data were transformed ($\log_{10}$ or Box-Cox) when necessary to fulfill the assumptions of the analysis of variance (Pimental and Smith 1990). When comparing more than two treatments or substrata, Tukey's honestly significant difference tests determined which treatments were significantly different. I also used regression analyses to determine if there was a relationship between POM mass and the richness of macroinvertebrates.

RESULTS

Experiment I

On each of the three sampling dates (December 1996, January 1997, and February 1997) and for each of the three substratum types (rock, gravel, and brick), mean macroinvertebrate richness at the upper site exceeded that of the lower site (Figure 5.1). The differences were significant for the December samples (rock: lower site mean = 1.46 taxa/dm^2, SD ± 0.24, upper site mean = 2.96 taxa/dm^2, SD ±

0.54, $P = 0.02$; gravel: lower site mean = 1.29 taxa/dm^2, SD ± 0.22, upper site mean = 4.21 taxa/dm^2, SD ± 0.61, $P < 0.001$), January control gravel substrata (lower site mean = 1.88 taxa/dm^2, SD ± 0.24, upper site mean = 5.88 taxa/dm^2, SD ± 0.55, $P = 0.001$), and February samples (rock: lower site mean = 1.88 taxa/dm^2, SD ± 0.24, upper site mean = 3.88 taxa/dm^2, SD ± 0.31, $P = 0.002$). Experimentally disturbed gravel substrata also exhibited significantly higher mean richness at the upper site (lower site mean = 2.13 taxa/dm^2, SD ± 0.47; upper site mean = 7.50 taxa/dm^2, SD ± 1.95, $P = 0.04$). Mean richness did not vary significantly on brick substrata (lower site mean = 1.12 taxa/dm^2, SD ± 0.30; upper site mean = 2.61 taxa/dm^2, SD ± 0.48, $P = 0.06$) and rock treatment substrata (lower site mean = 2.00 taxa/dm^2, SD ± 0.29; upper site mean = 3.25 taxa/dm^2, SD ± 0.85, $P = 0.21$).

Despite the spate occurring between the January and February sample dates, control samples generally increased in richness from December to February (Figure 5.1). The increases in mean richness were significant at the lower site on gravel substrata, with February richness (mean = 3.38 taxa/dm^2, SD ± 0.63) significantly higher than December (mean = 1.29 taxa/dm^2, SD ± 0.22) and January (mean = 1.88 taxa/dm^2, SD ± 0.24, $P = 0.002$). January controls and treatments (both substratum types) did not differ significantly in mean richness.

Mean richness was lower on bricks (lower site= 1.12 taxa/dm^2, SD ± 0.30; upper site= 2.61 taxa/dm^2, SD ± 0.48) than on rock treatment substrata (lower site=

2.00 taxa/dm^2, SD ± 0.29; upper site= 3.25 taxa/dm^2, SD ± 0.83); however, these differences were not significant.

Experiment II

Overall patterns of richness-

A total of 56 macroinvertebrate taxa were collected from treatment and control substrata during this experiment (Table V.1). Dipterans made up the bulk of the total (16 taxa), followed by coleopterans (12 taxa), trichopterans (7 taxa), odonates (6 taxa), and ephemeropterans (4 taxa). In addition, several non-insect macroinvertebrate taxa were collected. Of the total taxa, 47 were collected from the lower site and 48 from the upper site. The greatest disparity in taxonomic richness between the sites occurred in the order Odonata (lower site = 2 taxa, upper site = 7 taxa). Other taxonomic groups were distributed over both sites. Within the Ephemeroptera, the riffle taxon, *Baetis* was abundant at the lower site, but rare to common at the upper site (Table V.1); the opposite pattern was observed for the pool taxa, *Caenis*, *Paraleptophlebia*, and *Callibaetis*. Overall, *Neohermes* (Megaloptera) and most coleopteran genera also occurred in a greater number of samples at the upper site.

Mean macroinvertebrate richness at the upper site surpassed that at the lower site for all substratum types (Figure 5.2). The difference between sites was significant for brick (lower site mean = 1.57 taxa/dm^2, SD ± 0.15, upper site mean = 2.14 taxa/dm^2, SD ± 0.16, $P = 0.01$) and gravel (lower site mean = 7.27 taxa/dm^2, SD ± 0.49 upper site mean = 8.63 taxa/dm^2, SD ± 0.36, $P = 0.03$) substrata. For three of the five dominant insect orders, Ephemeroptera, Odonata, Coleoptera, and Diptera, the upper site exhibited higher mean richness on brick, rock and gravel substrata than the lower site (Figures 5.3, 5.4, 5.6, and 5.7). Mean richness was significantly higher at the upper than lower site on brick and gravel substrata for ephemeropterans (brick: lower site mean = 0.20 taxa/dm^2, SD ± 0.0.02, upper site mean = 0.36 taxa/dm^2, SD ± 0.03, $P = 0.001$; gravel: lower site mean = 1.00 taxa/dm^2, SD ± 0.07, upper site mean = 1.31 taxa/dm^2, SD ± 0.13, $P = 0.04$), odonates (brick: lower site mean = 0.04 taxa/dm^2, SD ± 0.02, upper site mean = 0.17 taxa/dm^2, SD ± 0.02, $P < 0.001$; gravel: lower site mean = 0.23 taxa/dm^2, SD ± 0.07, upper site mean = 0.75 taxa/dm^2, SD ± 0.13, $P = 0.002$), and coleopterans (brick: lower site mean = 0.05 taxa/dm^2, SD ± 0.01, upper site mean = 0.28 taxa/dm^2, SD ± 0.06, $P = 0.001$; gravel: lower site mean = 0.20 taxa/dm^2, SD ± 0.10, upper site mean = 1.03 taxa/dm^2, SD ± 0.18, $P < 0.001$). In contrast, the mean richness of Trichoptera at the lower site exceeded that of the upper site on all substrata (Figure 5.5), with the mean significantly higher on gravel substrata (lower site mean = 1.50 taxa/dm^2, SD ± 0.18, upper site mean = 0.91 taxa/dm^2, SD ± 0.09, $P = 0.01$).

Regression analyses of total macroinvertebrate richness versus ash-free dry weight of particulate organic matter (POM) indicated a positive relationship at both sites and for all substratum types (Table V.2). This relationship was significant, however, only for rock substrata at the upper site. Within the five dominant insect orders, the relationship between richness and POM varied considerably, but was usually positive (Table V.2). Significant positive relationships were calculated for Ephemeroptera (rock substrata, upper and lower sites), Trichoptera (brick substrata, lower site; rock substrata, upper and lower sites), Coleoptera (brick substrata, lower site), and Diptera (rock substrata, upper site). In one instance the regression analyses indicated a significant negative relationship between ephemeropteran richness and POM (Table V.2).

Effects of experimental disturbance on richness-

Total macroinvertebrate richness increased significantly with decreasing disturbance frequency at both sites on rock substrata (lower site: mean richness of 2,4, and 8 week < control P = 0.002 THS test; upper site: mean richness of 2 week < 4 week, 8 week, and control, P 0.01 THS test) and lower site gravel substrata (mean richness of 2 week < 8 week, P = 0.03 THS test) substratum types (Figure 5.2). At the upper site, brick substrata disturbed at 2 week intervals had significantly lower richness than bricks disturbed at 4 and 8 week intervals (P = 0.02 THS test).

Analyses of richness within the dominant insect orders, revealed that patterns of mean richness varied considerably with disturbance frequency (Figures 5.3 to 5.7). Significant disturbance effects were primarily observed on rock substata (Ephemeroptera: upper site mean richness of 2 and 4 week < 8 week, control, P = 0.01 THS test; Trichoptera: lower site mean richness of 2 and 4 week < control, P = 0.01 THS test; Coleoptera: upper site mean richness of 2 and 4 week < 8 week, P = 0.02 THS test; Diptera: lower site, mean richness of 2, 4, and 8 week < control, P = 0.003 THS test; upper site mean richness of 2 and 4 week < 8 week and control, P = 0.002, THS test). Trichopterans exhibited a significant disturbance effect on lower site gravel substrata (P = 0.04, no significant subsets).

At both sites, brick substrata exhibited lower mean richness (lower site mean = 1.57, SD ± 0.15; upper site mean = 2.14, SD ± 0.29) than rock (lower site mean = 2.37, SD ± 0.24; upper site mean = 3.56, SD ± 2.58) and gravel (lower site mean = 7.33, SD ± 0.56; upper site mean = 8.96, SD ± 2.16) substrata (Figure 5.2). Richness on brick and rock substrata was significantly lower than on gravel substrata (lower site P <0.001 THS test; upper site P<0.001 THS test).

This pattern (richness on brick < rock < gravel) was also observed among the dominant insect orders (Figure 5.3 to 5.7). Gravel richness was significantly higher for the orders Ephemeroptera (lower site: brick mean = 0.20, SD ± 0.02 and rock mean = 0.42, SD ± 0.05, significantly lower than gravel mean = 1.00, SD ± 0.09, $P < 0.001$ THS test; upper site brick mean = 0.36, SD ± 0.03 and rock mean = 0.59, SD ± 0.08, significantly lower than gravel mean = 1.38, SD ± 0.15, $P < 0.001$ THS test), Odonata (lower site: brick mean = 0.04, SD ± 0.02 significantly lower than gravel mean = 0.25, SD ± 0.07, $P = 0.02$ THS test), Trichoptera (lower site: brick mean = 0.34, SD ± 0.02 and rock mean = 0.41, SD ± 0.08, significantly lower than gravel mean = 1.38, SD ± 0.51, $P < 0.001$ THS test; upper site brick mean = 0.28, SD ± 0.01 and rock mean = 0.27, SD ± 0.07, significantly lower than gravel mean = 0.92, SD ± 0.13, $P < 0.001$ THS test), Coleoptera (upper site: brick mean = 0.27, SD ± 0.04 and rock mean = 0.31, SD ± 0.21 significantly lower than gravel mean = 1.13, SD ± 0.55, $P < 0.001$ THS test), and Diptera (lower site: brick mean = 0.64, SD ± 0.05 and rock mean = 0.87, SD ± 0.15, significantly lower than gravel mean = 3.17, SD ± 0.97, $P < 0.001$ THS test; upper site brick mean = 0.71, SD ± 0.06 and rock mean = 1.41, SD ± 0.20, significantly lower than gravel mean = 3.50, SD ± 0.23, $P = 0.001$ THS test).

Disturbance treatments rarely effected richness on brick and gravel substrata (brick: significant for total richness, upper site; gravel: significant for total richness, lower site; Figure 5.2). In contrast, disturbance effects were frequently observed on rock substrata (significant effect for total richness, lower and upper sites;

Ephemeroptera, upper site; Trichoptera, lower site; Coleoptera, upper site; Diptera, both sites; Figures 5.3 to 5.7).

Effects of experimental disturbance on POM-

For the experimentally disturbed substrata, the ash-free dry weight of POM increased with decreasing disturbance frequency (Figure 5.8); however, these increases were not significant. POM mass was consistently higher on gravel substrata. The mass of POM did not differ significantly among the lower and upper sites on any of the substratum types (Figure 5.8).

DISCUSSION

Patterns of Richness

During the winter and spring, the lower and upper sites differed in discharge and disturbance frequency (scour). Over the past seven years I have observed that the lower site typically experiences winter scour following storms. The upper site rarely experiences these disturbances, although relative variability (proportional change) in discharge can be high. Scour may affect richness directly by removing organisms or by preventing taxa from establishing, or indirectly by removing food sources (algae and detritus). Most macroinvertebrate groups exhibited increasing richness with increasing quantities of POM in this study (Table V.2); however quantities of POM did not differ significantly between the two sites (Figure 5.8).

I expected, given differences in winter discharge and disturbance histories of both sites, that the lower site would support a comparatively depauperate fauna limited to those taxa able to withstand frequent disturbance or able to recolonize quickly following disturbance. Such taxa generally exhibit morphological, behavioral, and/or life history patterns that enable them to persist under frequent disturbance regimes or to recolonize rapidly following disturbance (Sagar 1986, Robinson and Rushforth 1987, Scrimgeour et al. 1988, Townsend et al. 1997a). Increasing disturbance frequency may disfavor sedentary, case building, and attached taxa (Sagar 1986). In addition, taxa with long lived aquatic stages may be disfavored in frequently disturbed channels (Power et al. 1988).

During the experimental period, mean macroinvertebrate richness at the upper site exceeded that at the lower site (Figures 5.1 and 5.2). Overall, the difference in mean richness was significant between sites, a pattern also observed within three of the five dominant insect orders, i.e., the Ephemeroptera (brick and gravel substrata, Figure 5.3), Odonata (brick and gravel substrata, Figure 5.4), and Coleoptera (brick and gravel substrata, Figure 5.6). Trichopterans exhibited the opposite pattern, with significantly greater richness at the lower than upper site on gravel substrata (Figure 5.5). Although both sites supported approximately the same number of taxa (47 taxa, lower site; 48 taxa upper site), several taxa occurred more frequently in upper compared to lower site samples (Table V.1).

Of the nine insect taxa unique to the upper site, over half were typical of depositional or lentic habitats, the majority being odonates. These organisms generally do not exhibit traits typical of macroinvertebrates occupying disturbed habitats. The "missing" odonate taxa were frequently collected from the lower site during the summer and fall, when discharge was low and scour absent. The six insect taxa unique to the lower site were a mix of those inhabiting erosional, depositional, and non-specific habitat types. In contrast to expectations, three of these taxa are sedentary and/or case builders (*Hydrospyche*, *Lepidostoma*, and *Ochrotrichia*). Two of the taxa are mobile (*Aquarius remigis* and *Graptocorixa*).

Several of the taxa within orders common to both sites occurred with different frequencies at the 2 sites. For example, *Callibaetis* occurred rarely in lower site samples (<10% of rock samples) and abundantly in upper site samples (>90% of all samples). The four taxa collected frequently at the lower but not upper site, *Baetis*, *Argia vivida*, *Hydroptila*, and *Euparyphus*, are not habitat specialists (i.e., they occur in both depositional and erosional habitats). *Baetis* and *Euparyphus* demonstrate characteristics of taxa typical of habitats experiencing frequent spates: frequent drift, rapid re-colonization, streamlined shape, high mobility. In contrast, three of the eight insect taxa that occurred more frequently in upper site samples exhibit specific habitat preferences; *Callibaetis*, *Caenis*, and *Rhantus*, inhabit depositional or lentic habitats.

In addition to differences in habitat characteristics (upper site with lower flow velocity and better defined pool and riffle habitats), the observed differences in taxonomic composition between the sites may result from a combination of the limited sampling effort of this study (85 samples) and the relative rarity of some taxa (Allan 1995); this may be the case for some rare taxa such as the beetles *Hydraena vandykei* and *Ordobrevia* and the tipulid, *Hexatoma*. Each of these organisms was present in only one sample.

Effects of disturbance on macroinvertebrate richness

Natural Disturbance-

The spate that occurred between the second and fifth weeks of my initial experiment enabled me to assess the impact of a natural spate on macroinvertebrate richness on two substratum types, rock and gravel (Figure 5.1). Despite the severity of this disturbance, richness increased after the spate on gravel control substrata at both the upper and lower sites. Richness on rock control substrata increased significantly at the upper site, but decreased at the lower site.

These results are consistent with those of other studies comparing pre and post-spate richness. Palmer et al. (1995) observed a change in taxonomic composition, but not numbers of chironomid and copepod taxa, following a spate. A summer flood resulted in the loss of five taxa from a desert stream; however, pre-flood richness levels were attained within two to three weeks after disturbance (Fisher et al. 1982). Matthaei et al. (1997) also observed recovery to pre-flood richness levels within 22 days in a Swiss river. The present study observed post-spate richness exceeding the pre-spate level within the 2 weeks following the spate.

The relatively rapid recovery to pre-disturbance richness levels and/or lack of significant change in richness may be due to the presence of microhabitat refuges within the stream (Lancaster and Hildrew 1993) combined with the resilience of the lotic biota (Grimm and Fisher 1989). Catastrophic disturbances (e.g., landslides, volcanic eruptions, debris flows) may result in longer recovery times to pre-disturbance levels (Lamberti et al. 1991, Wallace 1990).

Experimental Disturbance-

Experimental manipulations allow a great degree of control over the extent and frequency of disturbance (Minshall 1988). In addition, these manipulations enable direct comparisons of disturbance effects between sites and/or substrates. Despite the small sample sizes, this experiment yielded interesting results on the varied effects of disturbance on mean richness across sites, substrata, and taxa.

Significant disturbance effects on total taxonomic richness occurred on all substrata (Figure 5.2); however, these effects were most dramatic and consistent on rock substrata. Total richness on lower site rock substrata did not recover to control levels during the 8 week experiment; however, recovery of total richness to control levels occurred after 4 weeks on gravel (lower site), and upper site rock substrata. At the upper site, 2 week disturbance intervals significantly reduced richness compared to 4 and 8 week disturbance intervals. Within the orders Ephemeroptera (rock, upper site), Trichoptera (rock, lower site), Coleoptera (rock, upper site), and Diptera (rock, upper site), recovery from significant reductions in richness occurred after eight weeks (Figures 5.3 to 5.7). Recovery of dipteran richness to control levels did not occur on lower site rock substrata during the 8 week experiment.

Significantly positive relationships between POM and richness were observed for taxa significantly effected by disturbance (total taxa: rock, both sites; Ephemeroptera: rock, upper site; Trichoptera: rock, lower site; Diptera: rock, upper site; Table V.2). Increasing disturbance frequency reduced quantities of POM on all substrata at both sites; however, POM quantities among treatments and controls did not differ significantly (Figure 5.8). Although significant treatment effects on POM quantities were not observed, disturbance may affect some taxa indirectly through the removal of organic matter from substrata.

The effects of experimental disturbance on rock substrata vary considerably, depending on the intensity of the disturbance and the frequency of sampling following the disturbance. In a study comparing three levels of disturbance in which rocks were overturned, scrubbed, or acid scoured, richness was significantly reduced by disturbance but recovered within four to eight days on overturned and scrubbed rocks, respectively (Boulton et al. 1988). Recovery of assemblages on acid-scoured rocks did not occur within the 32-day study. Englund (1991) failed to observe any effects of disturbance (overturned stones); however, post-disturbance sampling did not commence until two months after the disturbance. McAuliffe's (1984) study, revealed that, in some instances, disturbance (brushing rock surfaces) resulted in an increase in richness on rock substrates (7 and 15 days following disturbance) by eliminating the dominant caddisfly, *Leucotrichia*.

The effect of experimental disturbance on rock substrata richness in this study approximated or exceeded that observed in other experimental studies, as well as for richness responses to disturbances from natural spates. In addition, the rates of richness recovery in this study approximated or exceeded times for colonization of introduced rock substrata recorded by Lamberti and Resh (1985). Possible explanations for differences in assemblage recovery rates observed in this study compared with others may be due to the intensity (clearing substrata around experimental substrata) and frequency of experimental disturbances. In this study, 0.5 m^2 areas around the rock substrata were also disturbed. Other studies disturbed only individual rock substrata and not surrounding substrata. The experiments noted above recorded recovery following a single disturbance, whereas this study observed recovery following one (=introduction of substrate), two, or four experimental disturbances.

The effects of experimental disturbance on brick substrata differed from the effects on rock substrata. Mean macroinvertebrate richness was significantly reduced by disturbance (2 week treatment significantly less than 4 and 8 week treatments) only on lower site brick substrata (figure 5.2). None of the five dominant taxa exhibited significantly reduced richness due to experimental disturbance on brick substrata (Figure 5.3 to 5.7); however, significant effects occurred on rock substrata for the orders Ephemeroptera, Trichoptera, Coleoptera, and Diptera. The rapid recovery in number of taxa on brick substrata, despite repeated disturbance, matched that found for Idaho streams (Robinson and Minshall 1986). As in this study, disturbance intervals of 27 days or more did not result in a significant decrease in richness.

Experimental disturbance studies also have used gravel substrates or gravel-filled baskets. In one such experiment, gravel-filled baskets were disturbed at varying frequencies by tumbling (Reice 1984, Reice 1985). Mean richness was reduced by frequent disturbance; however, the decrease in richness was not significant. Matthaei et al. (1997) disturbed large patches of gravel (9 m^2) in a Swiss river. In this study, disturbance significantly reduced richness, but richness recovered to control levels within three days. Recovery to control levels of mean richness occurred 33 days after repeated experimental disturbance in an Australian stream (Lake et al. 1989). The results of the present study parallel those of other experiments. Compared to the controls, macroinvertebrate richness on gravel was not significantly reduced by the experimental disturbances; however, lower site gravel assemblages did exhibit significant differences in richness between the two and eight week disturbance levels (Figure 5.2). Richness within the 5 dominant orders was not significantly decreased by experimental disturbance.

Several difficulties arise when extrapolating the results of small-scale experiments to large natural phenomena such as stream scour. The scales of experimental disturbances seem too small to simulate actual spates (Matthaei et al. 1997). That is, large scale recovery dynamics cannot be simulated by small experimental manipulations, resulting in an overestimation of colonization rates following disturbance (Minshall 1988, Lake 1990, Mackay 1992). Fisher (1987) also noted that experimental disturbances do not result in "appreciable mortality" of stream populations; therefore, "potential colonists, colonization distances," and the species composition of potential colonists are not affected by experimental disturbances. However, experimental disturbances may approximate small-scale natural disturbances, such as stone rolling (Peckarsky 1987). Despite the shortcomings of experimental disturbance studies, comparing some recovery rates of taxa from experimental and natural disturbances gives the impression that experimental studies overstate the effects of disturbances. In this study, richness increased following a natural disturbance (Figure 5.1), but was significantly decreased in many cases following experimental disturbance. The natural disturbance occurred in the winter, while the experiment occurred in spring, therefore, seasonal changes in species composition may, in part, account for these disparate results. Matthaei et al. (1997) proposed that the differences may be related to the more gradual onslaught of natural disturbances compared with experimental disturbances; however, this may not be true for flashy streams.

The results of natural and experimental disturbance studies vary depending upon the substrata examined, intensity of disturbance, and the frequency of disturbance. The richness of rock assemblages appear more sensitive to the impacts of disturbance than the richness assemblages on brick and gravel substrates (Figures 5.2 to 5.7). In addition, the frequency of natural and experimental disturbances is an important determinant of richness (Reice 1984, Reice 1985, Robinson and Minshall 1986, Robinson and Rushforth 1987, Robinson et al. 1990, Matthaei et al. 1997). The effects of disturbance can vary between sites on the same stream or between seasons at the same site (Robinson and Minshall 1986, Robinson et al. 1990). This study also illustrates that disturbance affects taxonomic groups differently.

Contrary to expectations, effects of experimental disturbance were not greater on upper than lower sites. Significant disturbance effects were observed equally at both sites for total taxa and dominant orders. The upper site supported more taxa typical of depositional habitats in comparison to the lower site, which supported more generalist taxa. Differences in disturbance regimes did not account for the significant differences in mean richness at the upper and lower sites. Differences may instead by related to differences in habitat characteristics, such as better defined pool and riffle habitats at the upper site; however, differences in habitat characteristics have not been quantified at the two sites.

CONCLUSION

In contrast to the predictions of the species area relationship (SAR), the largest Santa Cruz Island stream had lower macroinvertebrate taxonomic richness than smaller streams. This study examined an alternative explanation for observed patterns in richness by examining the effects of disturbance on taxonomic richness.

Connell (1978) asserted that higher taxonomic richness might be maintained at intermediate, as opposed to high and low, levels of disturbance. At intermediate disturbance levels, the community permits the coexistence of inferior and superior competitors by acting as an "ecotone" between the extremes of frequent disturbance (which favors colonizers) and lack of disturbance (which favors competitors).

The upper reaches of Prisoners Stream support relatively rich communities compared to the lower reaches. If disturbance frequency was a major determinant of differences in richness between the upper and lower reaches, then the lower reach communities should be limited to taxa adapted to frequent disturbance and the upper site would support a mixture of those taxa adapted and not adapted to disturbance. Therefore, I expected the lower site to be less susceptible to experimental disturbance than the upper site; however, I observed that the effects of disturbance on richness at the varied more with substrata, disturbance frequency, and taxonomic group, than with stream reach.

It is likely that the community richness of Santa Cruz Island stream reaches depends upon a complex set of interacting factors, including (but not limited to) habitat heterogeneity, random colonization events, and disturbance, which may operate over larger temporal and spatial scales than those addressed by this study.

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Table V.1. Overall patterns of richness and abundance observed for invertebrate taxa at the upper and lower experimental sites.

Presence and Occurrence Patterns of Macroinvertebrates*

Site:	Lower			Upper			Occurrence	
Substrata:	Brick	Gravel	Rock	Brick	Gravel	Rock	patterns	Habitat
# of samples:	12	15	14	12	16	16	per site	Comments**
Insect Taxa:								
Ephemeroptera								
Baetis	A	A	A	C	R	R	Lower	N
Callibaetis		vR		A	A	A	Upper	L
Caenis		vR	vR	C	vC	C	Upper	D
Paraleptophelbia		vR	vR	C	C	C	Upper	N
Odonata								
Archilestes				C	R	R	Upper Only	D
Argia vivida	R	C	C	R	R	R	Lower	N
A. sedula	vR			R	C	C	Upper	N
Enallagma				R	C	vR	Upper Only	D
Libellula saturata				R	vR	R	Upper Only	D
Paltohemis lineatipes						R	Upper On;ly	D
Aeshna interupta					vR		Upper Only	L
Hemiptera								
Aquarius remigis		vR					Lower Only	D
Microvelia beameri		vR		R			Equal	D
Graptocorixa		R					Lower Only	D
Megaloptera								
Neohermes californicus	R			C	vR	R	Upper	E
Trichoptera								
Tinodes	vR	C	R	vC	C	C	Upper	N
Polycentropus	C	A	C	C	C	C	Equal	N

Table V.1. Continued.

Presence and Occurrence Patterns of Macroinvertebrates*

Site:	Lower			Upper			Occurrence	
Substrata:	Brick	Gravel	Rock	Brick	Gravel	Rock	patterns	Habitat
# of samples:	12	15	14	12	16	16	per site	Comments**
Hydropsyche	C	vC	vC				Lower Only	E
Hydroptila	C	C	C	R	R	R	Lower	N
Ochrotrichia	vC	vC	vC				Lower Only	N
Lepidostoma	vR	R					Lower Only	N
Gumaga				C	C	R	Upper Only	D
Coleoptera								
Rhantus		vR		vR	C	C	Upper	D
Berosus	vR	vR		C			Equal	D
Enochrus				R	R	vR	Upper	L
Laccobius	vR			R	R	vR	Upper	D
Hydraena vandykei		vR					Lower Only	E
Ordobrevia					vR		Upper Only	E
Diptera								
Dicranota		R			vR		Equal	N
Hexatoma					vR		Upper Only	N
Simulium		R	R	vR		vR	Equal	E
Ceratopognidae	vR	vR			R		Equal	D
Euparyphus	vC			vR			Lower	N
Odontomyia		vR	vR		R	R	Equal	L
Limnophora		R	R	vR		vR	Equal	E
Ablabesmyia	C	vC	C	C	A	C	Equal	N
Pentaneura	A	A	vC	vC	A	A	Equal	N
Thienemanniella	vC	A	C	C	C	C	Equal	N
Labrundinia	C	vC	C	C	C	R	Equal	E
Microspecta	vC	vC	C	C	C	R	Equal	D

Table V.1. Continued.

Presence and Occurrence Patterns of Macroinvertebrates*

Site:	Lower			Upper			Occurrence	
Substrata:	Brick	Gravel	Rock	Brick	Gravel	Rock	patterns	Habitat
# of samples:	12	15	14	12	16	16	per site	Comments**
Rheotanytarsus	A	A	vC	A	A	A	Equal	E
Coryneura	vR	C	C	C	C	C	Equal	D
Chironomus	R	R	C	C	C	C	Equal	D
Cardiocladius	C	C	C	C	C	C	Equal	E
Non-Insect Taxa:								
Ph. Platyhelminthes	C	C	R			R	Lower	N
Ph. Nematomorpha	vR	vR					Lower	D
Ph. Mollusca								
Physa	vR		vR	C	C	C	Upper	D
Ph. Arthropoda								
Cl. Arachnida (mites)	vC	C	C	C	C	R	Equal	N
Cl. Ostracoda	C	vC	C	C	C	C	Equal	D
Cl. Copepoda	R		vR	R	R	R	Equal	D
Total Number of Taxa:	29	35	26	35	36	35		

* A = abundant, present in > 90% of samples
vC = very common, present in > 70% - 90% of samples
C = common, present in > 30 to 70% of samples
R = rare, present in 10 to 30% of samples
vR = very rare, present in <10% of samples

** Typical habitat of taxa (Merritt and Cummins 1984)
D = depositional
E = erosional
N = occurs in both depositional and erosional habitats
L = lentic
? = no information given

Table V.2. Summary of regression results: Taxonomic richness vs. ash free dry weight of particulate organic matter.

Taxa	Substratum Type	Site	Slope	Intercept	n	F value	r^2	P
All Macroinvertebrates								
	Brick	Lower	7.90	1.32	12	1.66	0.14	0.23
		Upper	3.82	2.02	12	1.57	0.14	0.24
	Rock	Lower	52.71	2.09	14	4.42	0.27	0.06
		Upper	21.85	2.83	16	13.01	0.48	0.003
	Gravel	Lower	1.43	6.90	12	0.81	0.06	0.38
		Upper	0.85	8.52	16	0.35	0.02	0.56
Ephemeroptera								
	Brick	Lower	0.02	0.19	12	3E-04	<0.001	0.99
		Upper	0.26	0.32	12	0.08	0.01	0.79
	Rock	Lower	8.59	0.35	14	9.19	0.43	0.01
		Upper	4.07	0.50	16	16.11	0.54	0.001
	Gravel	Lower	-0.54	1.05	14	9.71	0.43	0.002
		Upper	0.65	1.23	16	1.78	0.11	0.20
Odonata								
	Brick	Lower	-0.62	0.06	12	0.36	0.03	0.56
		Upper	-0.32	0.18	12	0.76	0.07	0.41
	Rock	Lower	-3.01	0.18	14	3.41	0.22	0.09
		Upper	-0.74	0.32	16	0.20	0.01	0.66
	Gravel	Lower	0.12	0.21	14	0.32	0.02	0.58
		Upper	-0.41	0.81	16	0.66	0.04	0.43
Trichoptera								
	Brick	Lower	2.44	0.26	12	2.07	0.17	0.18
		Upper	1.82	0.19	12	10.52	0.51	0.009
	Rock	Lower	20.90	0.27	14	13.06	0.52	0.004
		Upper	3.19	0.20	16	5.35	0.28	0.04
	Gravel	Lower	0.22	0.22	14	0.12	0.01	0.73
		Upper	0.27	1.06	16	0.53	0.04	0.43

Table V.2. Continued.

Taxa	Substratum Type	Site	Slope	Intercept	n	F value	r^2	P
Coleoptera								
	Brick	Lower	2.45	-0.03	12	10.78	0.51	0.009
		Upper	-0.55	0.30	12	0.22	0.02	0.65
	Rock	Lower	5.03	0.02	14	4.14	0.26	0.06
		Upper	3.90	0.18	16	4.26	0.23	0.06
	Gravel	Lower	0.16	0.23	14	0.06	0.02	0.80
		Upper	-0.25	1.06	16	0.12	0.009	0.73
Diptera								
	Brick	Lower	3.07	0.54	12	1.28	0.11	0.28
		Upper	2.06	0.64	12	3.17	0.24	0.11
	Rock	Lower	20.41	0.95	14	2	0.14	0.18
		Upper	9.86	1.19	16	16.57	0.54	0.001
	Gravel	Lower	1.07	2.83	14	2.1	0.14	0.17
		Upper	0.45	3.14	16	0.039	0.03	0.54

Figure 5.1. Mean richness (# taxa/dm ^{2}) at lower and upper stream sites from December 1996 to February 1997. Significant differences in richness determined via 1-way ANOVAs. Differences among controls at each site determined via Tukey's honestly significant difference and indicated by different letters above bars. Richness on control (hatched bars) and treatment (open bars) substrata not significantly different (rock: lower P=0.80, upper P=0.54; gravel: lower P=0.66, upper P=0.54).

a. Rock substrata
Significance of month: lower site, P=0.58; upper site, P=0.54

b. Gravel substrata
Significance of month: lower sire, P=0.002; upper site, P=0.053

Figure 5.1a. Mean richness on rock substrata at lower and upper sites from Dec. 1996 to Feb. 1997. Mean richness was significantly less at lower site in Dec. (P = 0.02) and Feb. (P = 0.002).

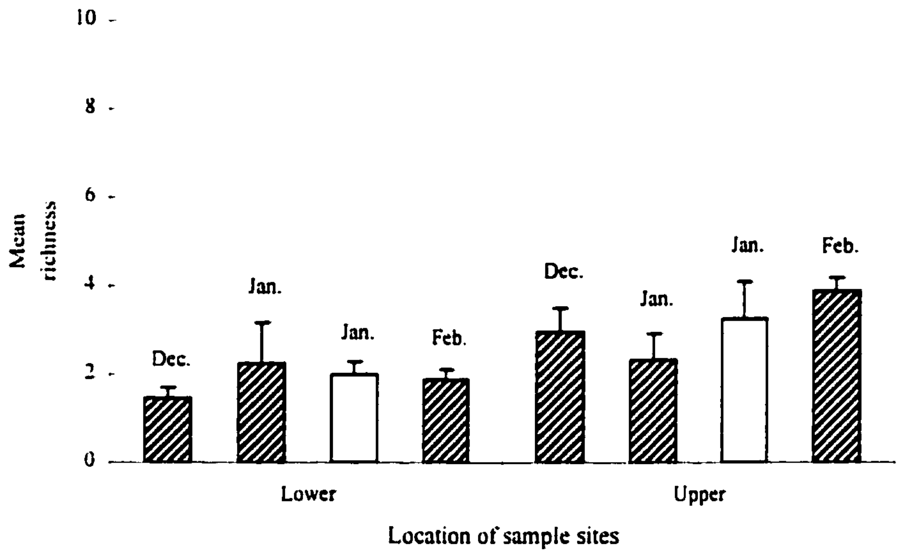

Figure 5.1b. Mean richness on gravel substrata at lower and upper sites from Dec. 1996 to Feb. 1997. Mean richness was significantly less at lower site in Dec. (P < 0.001), Jan. (P <0.001), Feb. (P = 0.01), and treatments (P=0.04).

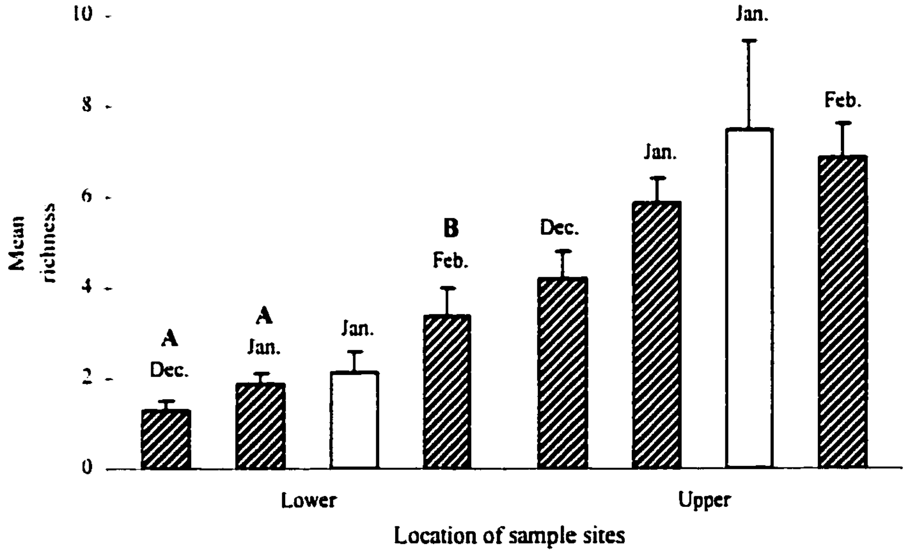

Figure 5.2. Mean macroinvertebrate richness (# taxa/dm^2) on brick, rock, and gravel substrata at varied disturbance frequencies (error bars indicate standard deviations). Significant differences in richness among sites determined via 1-way ANOVAs. Significant differences among treatments at each site determined via Tukey's honestly significant difference test and indicated by different letters above bars.

a. Mean richness on brick substrata.
Significance of treatment effects: lower site, $P = 0.62$; upper site, $P = 0.02$.

b. Mean richness on rock substrata.
Significance of treatment effects: lower site, $P=0.002$; upper site, $P=0.01$.

c. Mean richness on gravel substrata.
Significance of treatment effects: lower site, $P=0.03$; upper site, $P=0.16$.

Figure 5.2a. Macroinvertebrate richness at varied disturbance intervals on brick substrata. Mean richness significantly higher at upper site (P = 0.01).

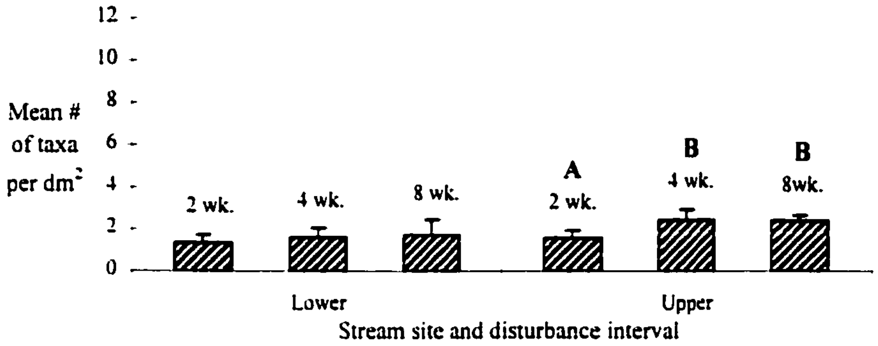

Figure 5.2b. Macroinvertebrate richness at varied disturbance intervals on rock substrata. Mean richness at lower and upper sites not significantly different (P = 0.23).

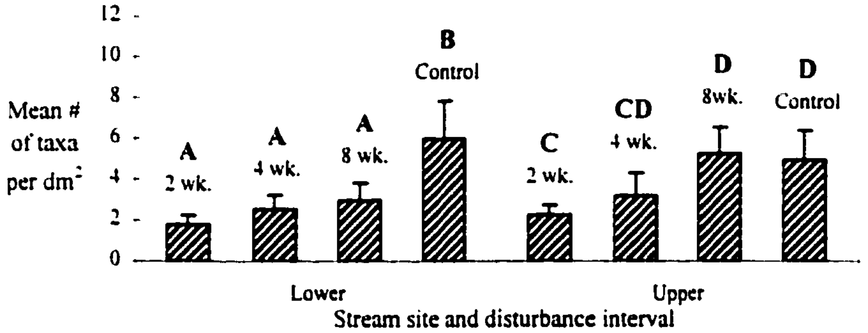

Figure 5.2c. Macroinvertebrate richness at varied disturbance intervals on gravel substrate. Mean richness significantly higher at upper site (P = 0.03).

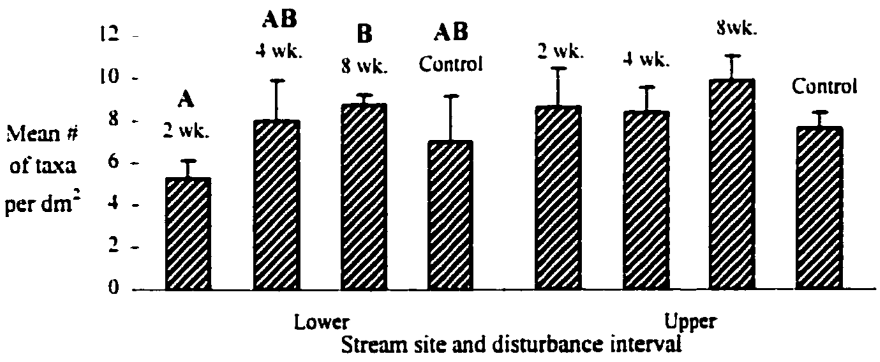

Figure 5.3. Mean ephemeropteran richness (# taxa/dm^2) on brick, rock, and gravel substrata at varied disturbance frequencies (error bars indicate standard deviations). Significant differences in richness among sites determined via 1-way ANOVAs. Significant differences among treatments at each site determined via Tukey's honestly significant difference test and indicated by different letters above bars.

a. Mean richness on brick substrata.
Significance of treatment effects: lower site, $P = 0.51$; upper site, $P = 0.57$.

b. Mean richness on rock substrata.
Significance of treatment effects: lower site, $P=0.11$; upper site, $P=0.01$.

c. Mean richness on gravel substrata.
Significance of treatment effects: lower site, $P=0.68$; upper site, $P=0.90$.

Figure 5.3a. Mean ephemeropteran richness at varied disturbance intervals on brick substrate. Mean richness significantly higher at upper site (P=0.001)

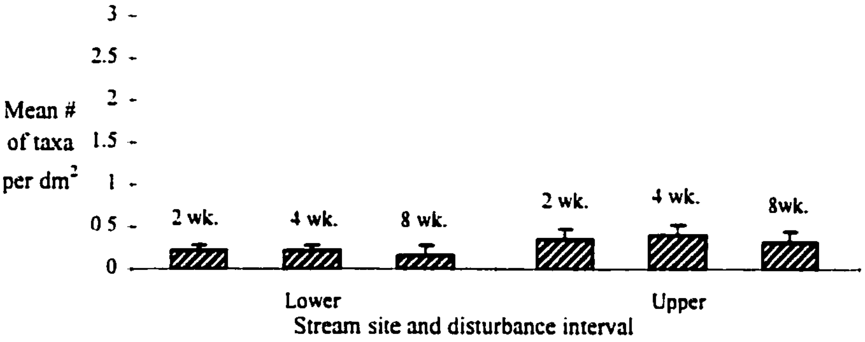

Figure 5.3b. Mean ephemeropteran richness at varied disturbance intervals on rock substrata. Mean richness among sites not significantly different (P=0.09).

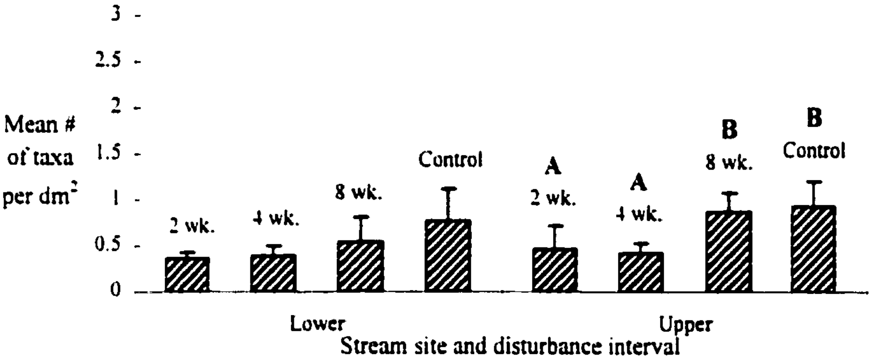

Figure 5.3c. Mean ephemeropteras richness at varied disturbance intervals on gravel substrate. Mean richness signficiantly higher at upper site (P=0.04).

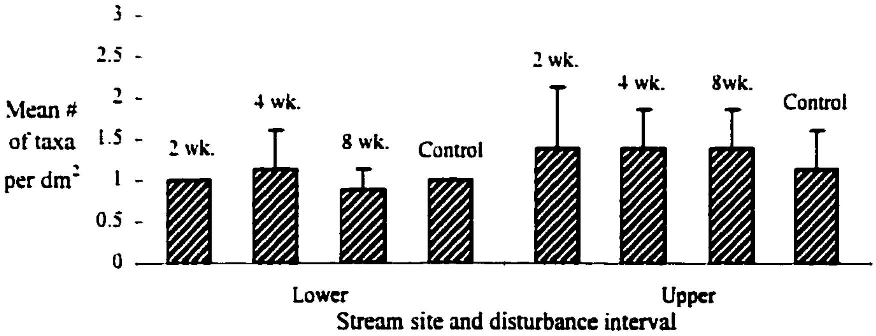

Figure 5.4. Mean odonate richness (# taxa/dm^2) on brick, rock, and gravel substrata at varied disturbance frequencies (error bars indicate standard deviations). Significant differences in richnessamong sites determined via 1-way ANOVAs. Significant differences among treatments at each site determined via Tukey's honestly significant difference test and indicated by different letters above bars.

a. Mean richness on brick substrata.
Significance of treatment effects: lower site, P = 0.27; upper site, P = 0.27.

b. Mean richness on rock substrata.
Significance of treatment effects: lower site, P=0.22; upper site, P=0.87.

c. Mean richness on gravel substrata.
Significance of treatment effects: lower site, P=0.60; upper site, P=0.09.

Figure 5.4a. Mean odonate richness at varied disturbance intervals on brick substrata. Mean richness significantly higher at upper site (P<0.001).

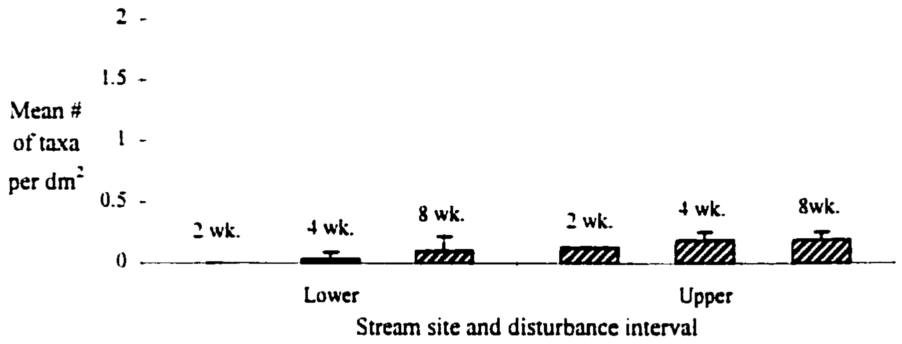

Figure 5.4b. Mean odonate richness at varied disturbance intervals on rock substrata. Mean richness not significantly different among sites (P=0.12).

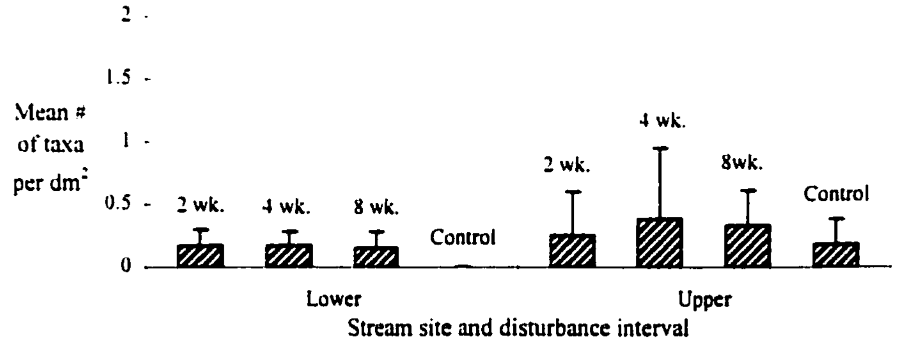

Figure 5.4c. Mean odonate richness at varied disturbance intervals on gravel substrata. Mean richness significantly higher at upper site (P=0.002).

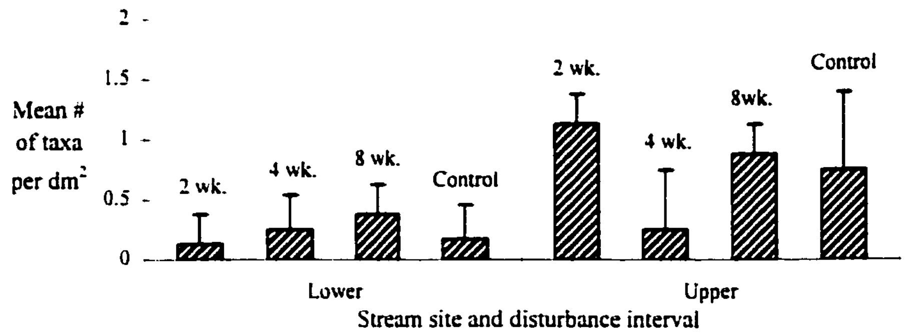

Figure 5.5. Mean trichopteran richness (# taxa/dm^2) on brick, rock, and gravel substrata at varied disturbance frequencies (error bars indicate standard deviations). Significant differences in richness among sites determined via 1-way ANOVAs. Significant differences among treatments at each site determined via Tukey's honest significant difference test and indicated by different letters above bars.

a. Mean richness on brick substrata.
Significance of treatment effects: lower site, $P = 0.51$; upper site, $P = 0.25$.

b. Mean richness on rock substrata.
Significance of treatment effects: lower site, $P=0.01$; upper site, $P=0.10$.

c. Mean richness on gravel substrata.
Significance of treatment effects: lower site, $P=0.04$; upper site, $P=0.60$.

Figure 5.5a. Mean trichopteran richness at varied disturbance intervals on brick substrata. Mean richness not significantly different among sites (P=0.26).

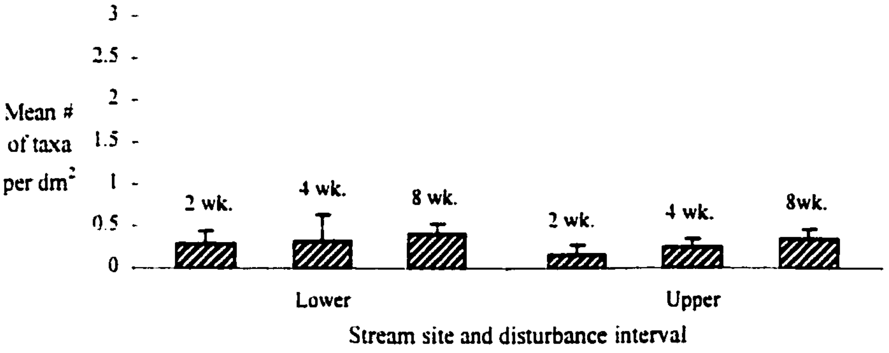

Figure 5.5b. Mean trichopteran richness at varied disturbance intervals on rock substrata. Mean richness not significantly different among sites (P=0.09).

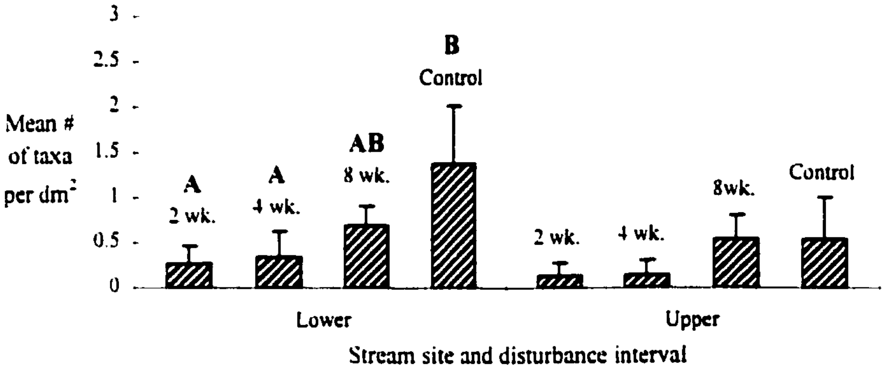

Figure 5.5c. Mean trichopteran richness at varied disturbance intervals on gravel substrata. Mean richness significantly higer at lower site (P=0.01).

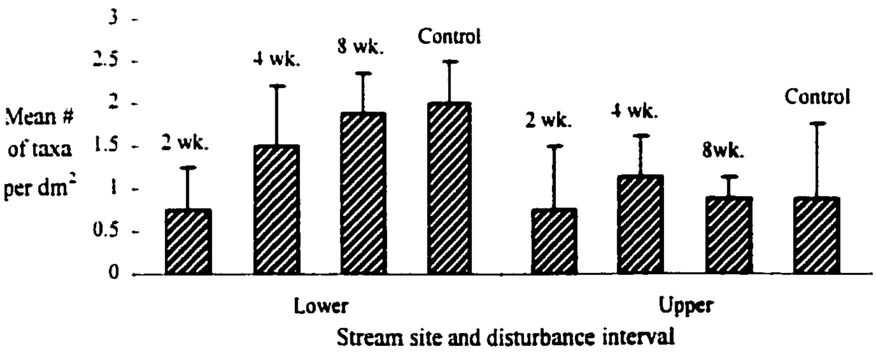

Figure 5.6. Mean coleopteran richness (# taxa/dm^2) on brick, rock, and gravel substrata at varied disturbance frequencies (error bars indicate standard deviations). Significant differences in richnessamong sites determined via 1-way ANOVAs. Significant differences among treatments at each site determined via Tukey's honestly significant difference test and indicated by different letters above bars.

a. Mean richness on brick substrata.
Significance of treatment effects: lower site, P = 0.53; upper site, P = 0.56.

b. Mean richness on rock substrata.
Significance of treatment effects: lower site, P=0.13; upper site, P=0.02.

c. Mean richness on gravel substrata.
Significance of treatment effects: lower site, P=0.68; upper site, P=0.82.

Figure 5.6a. Mean coleopteran richness at varied disturbance intervals on brick substrata. Mean richness significantly higher at upper site (P=0.001).

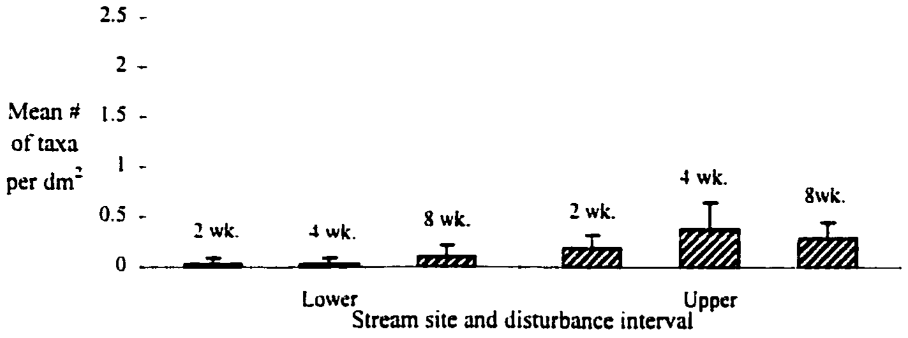

Figure 5.6b. Mean coleopteran richness at varied disturbance intervals on rock substrata. Mean richness not significanlty different among sites (P=0.07).

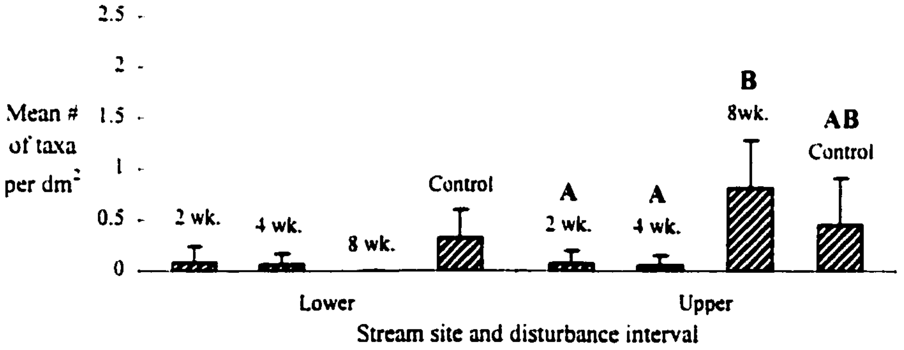

Figure 5.6c. Mean coleopteran richness at varied disturbance intervals on gravel substrata. Mean richness significantly higher at upper site (P<0.001).

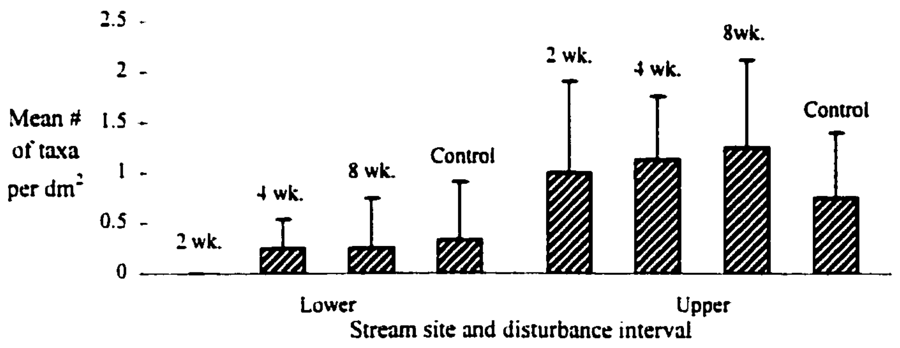

Figure 5.7. Mean dipteran richness (# taxa/dm^2) on brick, rock, and gravel substrata at varied disturbance frequencies (error bars indicate standard deviations). Significant differences in richness among sites determined via 1-way ANOVAs. Significant differences among treatments at each site determined via Tukey's honestly significant difference test and indicated by different letters above bars.

a. Mean richness on brick substrata.
   Significance of treatment effects: lower site, P = 0.57; upper site, P = 0.15.

b. Mean richness on rock substrata.
   Significance of treatment effects: lower site, P=0.003; upper site, P=0.002.

c. Mean richness on gravel substrata.
   Significance of treatment effects: lower site, P=0.17; upper site, P=0.20.

Figure 5.7a. Mean dipteran richness at varied disturbance intervals on brick substrata. Mean richness not significantly different among sites (P=0.51).

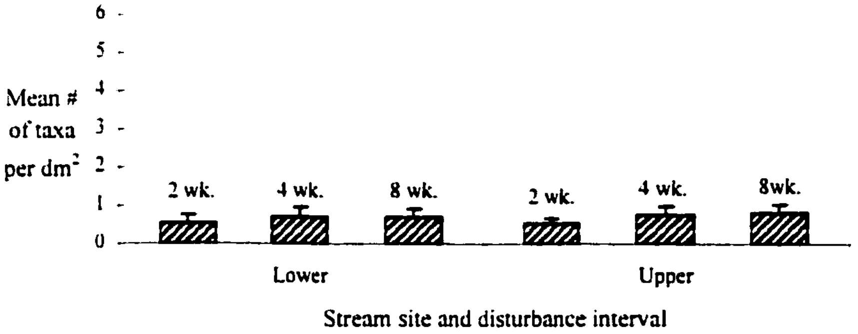

Figure 5.7b. Mean dipteran richness at varied disturbance intervals on rock substrata. Mean richness not significantly different among sites (P=0.32).

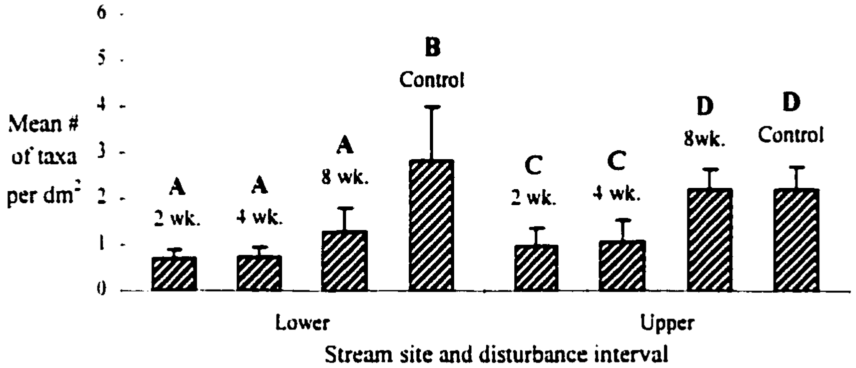

Figure 5.7c. Mean dipteran richness at varied disturbance intervals on gravel substrata. Mean richness not significantly different among sites (P=0.22).

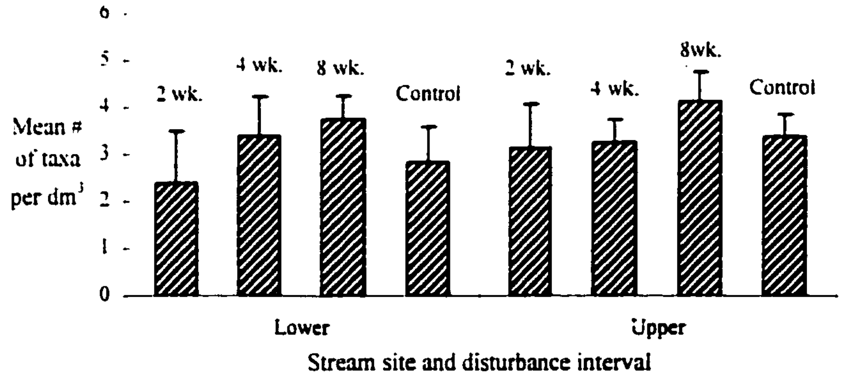

Figure 5.8. Mean mass of POM (grams/dm2) on substrata at lower and upper sites. POM mass did not differ significantly among sites and treatments for any substratum type. Standard deviations are represented by error bars.

a. POM mass on brick substrata.
   Significance of treatment effects: lower site P=0.51, upper site P=0.54

b. POM mass on rock substrata.
   Significance of treatment effects: lower site P=0.72, upper site P=0.39

c. POM mass on gravel substrata.
   Significance of treatment effects: lower site P=0.69, upper site P=0.70

Figure 5.8a. POM at lower and upper sites on brick substrata. POM mass not significantly different among sites (P=0.64).

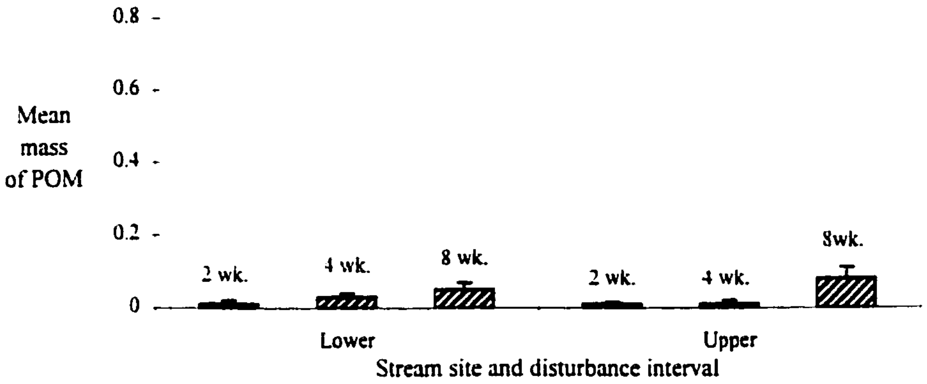

Figure 5.8b. POM at lower and upper sites on rock substrata. POM mass not significantly different among sites (P=0.65)

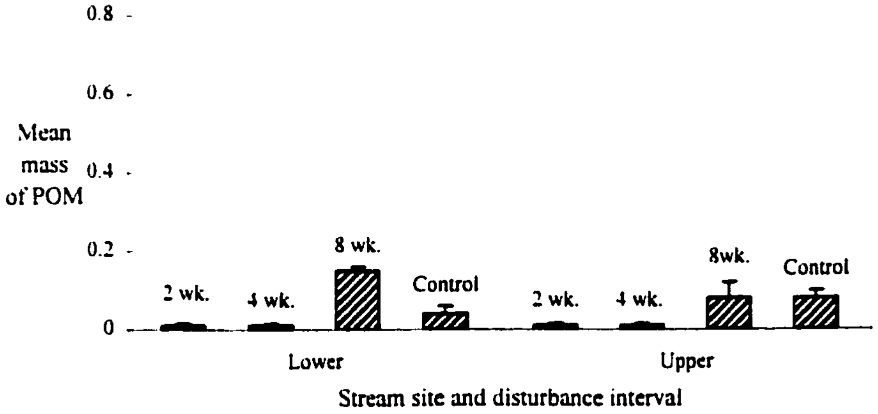

Figure 5.8c. POM at lower and upper sites on gravel substrata. POM mass not significantly different among sites (P=0.11).