STREAM FAUNA OF SANTA CRUZ ISLAND

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ABSTRACT

Records indicate that entomologists have collected insects from the California 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 39 taxa previously undescribed from the California 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 94 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.

Keywords: Aquatic insects, stream fauna, biogeography, disharmony, dispersal, Santa Cruz Island.

INTRODUCTION

A basic knowledge of the system under consideration is an essential component to ecological, evolutionary, and biogeographical research. In particular, taxonomic surveys provide essential baseline information used for monitoring, management, and conservation purposes. This is especially true for undescribed systems and/or areas of great ecological concern, such as the Northern Channel Islands. With multiple agencies involved in management and restoration projects on the islands, the availability of baseline data is essential for the documentation of the success of these programs. Although adequate taxonomic documentation exists for some island animal groups, others are poorly known. Information for several insect groups is minimal or completely lacking (Miller 1985). In particular, aquatic insect groups have received scant attention on the California islands. Monitoring aquatic macroinvertebrates could be of great value in management and restoration programs, especially if combined with data regarding watershed recovery from grazing and/or exotic plant and animal removal. A primary goal of this study is to provide baseline knowledge of aquatic insect assemblages for Santa Cruz Island streams.

In addition, this research compares the stream insect assemblage of Santa Cruz Island with those found in nearby mainland streams. 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 organisms. Species with good dispersal and/or colonization abilities (such as bats and/or strand plants) are often over-represented on islands compared to the mainland (Carlquist 1974), whereas those with poor dispersal ability across oceans (such as freshwater fishes and large mammals) are under-represented. 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 more easily observed on distant oceanic islands but evident on the California islands as well. Savage (1967) noted that the California island herpetofaunas "are depauperate and composed of vagile forms." In reference to land vertebrates, Wenner and Johnson (1980) noted that the assemblages present on the Northern Channel Islands do not represent a random assortment, but are "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 also become established on an island through random events. Though freshwater species rarely disperse across salt water, most stream insects possess winged adult forms allowing for aerial transport. It is also possible that these organisms may raft to islands on debris originating from stream banks. 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).

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 of some islands may also contribute to the depauperate nature of their biotas. These and other factors combine to produce a biota that may have a very different composition than 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 project explores three aspects of the Santa Cruz Island stream fauna. First, the study provides baseline information regarding the stream insect assemblage on Santa Cruz. Second, it examines to what degree mainland stream insects are represented on Santa Cruz Island. Third, this work investigates whether the island stream insect assemblage appears to be a random subset of mainland assemblages or represents a disharmonic assemblage.

MATERIALS AND METHODS

Collections were taken from several locations on Santa Cruz Island (34° 04' 39" N to 33° 57' 33" N, 119° 55' 44" W to 119° 31' 10" W), the largest and most topographically diverse of the California islands. The surface of Santa Cruz Island is divided by a number of watersheds varying in size from less than 1 km^2 to nearly 35 km^2. Several streams flow year around, fed by emergent groundwater. However, most drainages sustain flow only following storm events. The majority of island collections were taken from the following watersheds: Black Point, Coches, Horquetta, Laguna, Prisoners, Sauces, and Willows (Figure 1). The watershed area of these streams varies from 1.09 km^2 (Black Point) to 34.66 km^2(Prisoners). In addition to collections taken directly from island streams, adults forms of stream insects were collected utilizing a black light at the Santa Cruz Island field station. Mainland collections were taken from three coastal Santa Barbara County streams: Rattlesnake-Mission Creek (34° 27' 30" N, 119° 41' 30" W), Refugio Creek (34° 30' 00" N, 120° 3' 30" W), and Jalama Creek (34° 32' 30" N, 120° 27' 30" W). Detailed information regarding island and mainland collection sites may be found in Furlong (1999).

To maximize opportunities for obtaining the greatest number of taxa, collections from both island and mainland streams took place during all seasons. Island collections were conducted from 1990 to 1997; mainland samples were taken during 1997. The number of sampling sites per stream ranged from three to five. Both pool and riffle habitats were sampled at each site (for detailed site descriptions see Furlong 1999). In all, this sampling effort included over 75 collection dates with over 800 samples taken. As suggested by Elliott (1979), we employed standardized kick samples over a given area (1 m) for a given amount of time (30 seconds) to obtain semi-quantitative samples of benthic taxa. In addition, standardized net sweeps (five sweeps of 1 m each) were used to collect surface taxa. All collections were taken with a 300 micron mesh dip net. Occasionally, insects were collected by hand-picking with forceps. Insects collected in this study will be vouchered at the Santa Barbara Museum of Natural History.

Collections from the Los Angeles County Museum of Natural History, Santa Barbara Museum of Natural History,

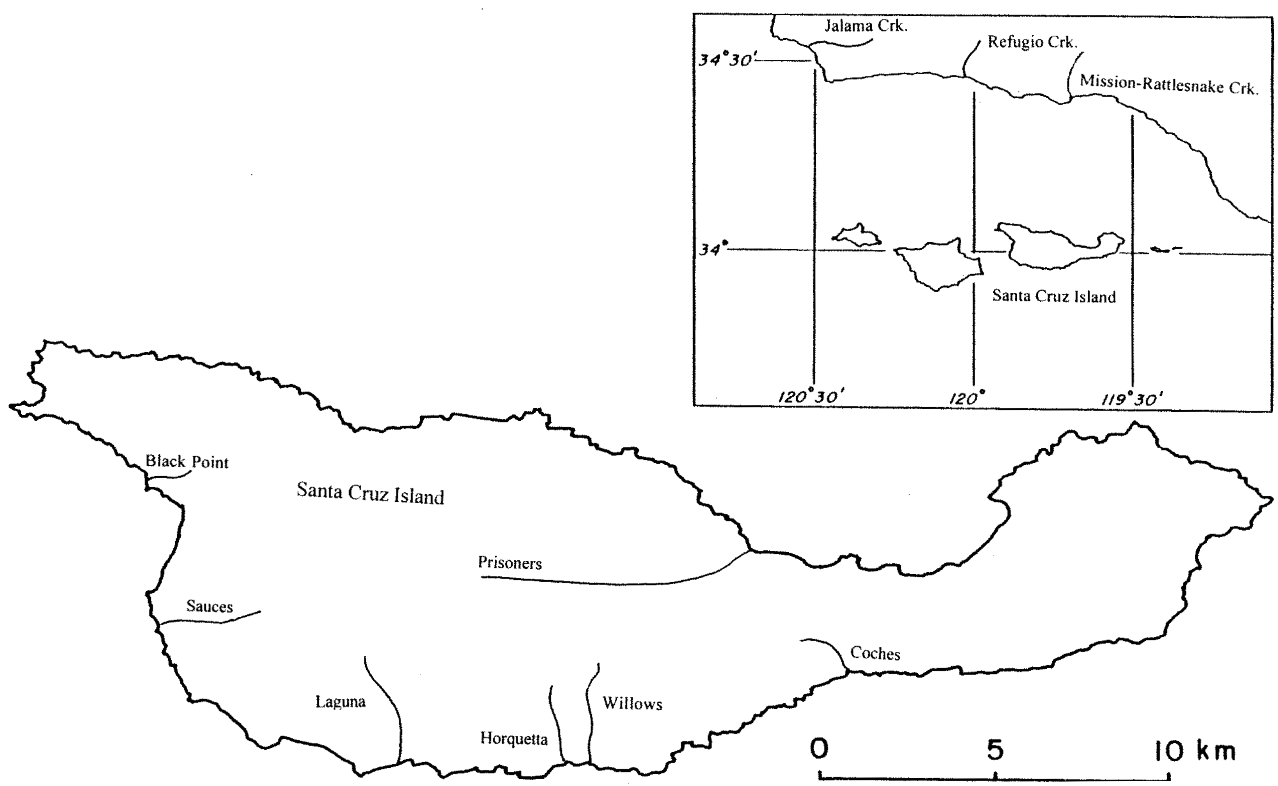

Figure 1. Location of mainland and Santa Cruz Island streams used for aquatic insect collection.

California Academy of Sciences, and Santa Cruz Island Reserve were examined to verify identifications and supplement the inventory of mainland and island taxa. Additionally, California Channel Island insect records provided by Scott Miller (Bishop Museum) were utilized to draft a more complete account of Santa Cruz Island aquatic insects (Miller, pers. comm. 1996). Unpublished records of *Mesocapnia projecta* (Plecoptera) were provided by Richard Bauman (pers. comm. 1999). Published lists of mainland stream taxa provided additional information regarding the richness of mainland streams (Wenner and Busath 1977; Cooper et al. 1986). Island and mainland taxa were compared at the generic level to account for possible errors and differences in species-level identifications. Taxa identified to family level only were counted as one genus in mainland-island comparisons.

To determine if island taxa represent a random subset of total taxa, the Kolmogorov-Smirnov goodness of fit Dmax was calculated for the observed distribution of island taxa within Orders compared to the expected distribution (Zar 1984). The expected distribution was determined by calculating the percent of total taxa found on the island (at the generic level, excluding Chironomidae due to insufficient identification). The total number of taxa per insect Order was multiplied by this figure to obtain the expected number of island taxa per Order.

RESULTS

General Collection

This collection effort yielded many taxa previously undescribed for Santa Cruz Island (for full list of stream taxa see Furlong 1999). In all, 90 taxa were collected from island streams. In addition, 6 taxa were identified from our terrestrial collections and previously unidentified museum/reserve collections. Of these 96 taxa, 47 represent new records for Santa Cruz Island and 39 represent new records for the California Channel Islands (not including Chironomidae, Table 1). Several of these new records consist of identifications at greater levels of taxonomic resolution. This collection effort did not account for 52 aquatic or semi-aquatic taxa listed for Santa Cruz Island (Miller, pers. comm. 1996).

Several non-insect macroinvertebrates also were collected during this study. These include flatworms (*Dugesia*, Phylum Platyhelminthes), horsehair worms (Phylum Nematomorpha), bivalve molluscs (possibly Family Sphaeriidae), and the gastropod *Physa*. In addition, several non-insect arthropod taxa were encountered: water mites (Class Arachnida), seed shrimp (Class Ostracoda), copepods (Class Copepoda), and the amphipod *Hyallela azteca* (Saussure). The only vertebrate taxa occupying island streams were tadpoles of the Pacific tree frog (*Hyla regilla* Baird & Girard). Freshwater fishes do not occur in Santa Cruz Island streams.

Mainland vs. Santa Cruz Island

Mainland and island collections and records yielded a total of 161 taxa at the generic level (Furlong 1999). Dipterans exhibited the greatest overall richness, accounting for approximately 31% of all taxa (Table 2). The proportion of island stream taxa composed of dipterans, at 40%, was higher than that for the mainland, at 29%. The same pattern was observed in the richness of coleopteran taxa. Beetles, with a total of 20.5% of the total taxa, comprised a greater proportion of the island taxa (25%) compared to that found in the mainland assemblage (19%). Taxa in the Order Plecoptera contributed the least to island richness at 1%, while contributing more than 7% to the mainland assemblage (Table 2).

Of the total 161 taxa (generic level), 145 (90%) occurred in mainland streams and 94 (58%) in island streams. The greatest disparity in richness emerged within the orders Plecoptera and Trichoptera. Mainland records contained 11 and 22 taxa within the orders Plecoptera and Trichoptera, respectively (Table 2). However, only one stonefly and eight caddisfly taxa were collected from Santa Cruz Island streams. An additional 27 families of aquatic insects found in nearby mainland streams did not appear in samples from Santa Cruz Island. In contrast, three families recorded for Santa Cruz Island were absent in mainland records.

For most insect orders, the number of island taxa observed approximated the number expected (at the generic level, Figure 2). However, the expected number of taxa was much higher than observed for the orders Trichoptera (13 expected, 8 observed) and Plecoptera (6 expected, 1 observed). The number of dipteran and coleopteran taxa observed exceeded the expected number of taxa (Diptera: 29 expected, 37 observed; Coleoptera: 19 expected, 23 observed). The Kolmogorov-Smirnov goodness of fit Dmax calculated for overall observed versus expected richness within orders was significant ($Dmax_{n\ 8,\ k\ 92} = 12$) at the 0.05 level.

DISCUSSION

Faunal Survey

The limited scope of this collection effort, relative to the size of the island, yielded a considerable amount of new information regarding Santa Cruz Island stream fauna (Table 1). In all this study contributes 47 new records of Santa Cruz Island insects, of these 39 are new records for the California Channel Islands. A total of 52 aquatic and semi-aquatic insects recorded for Santa Cruz Island were not collected during this effort; however, many of these taxa occupy environments not encompassed by this study (intertidal, standing water, damp soil) and others were identified to a higher level of taxonomic resolution than employed in this effort. It is likely that more aquatic insects could be recorded for Santa Cruz Island if additional streams are sampled. Rearing studies and collections of terrestrial adult stages also would increase the degree of taxonomic resolution of several aquatic insects collected during this study.

Table 1. New records of aquatic insect taxa from Santa Cruz Island. This list was compiled from stream collections, terrestrial adult collections, unpublished records, and museum specimens. Excluding Chironomidae, this effort adds 47 records of insect taxa for Santa Cruz Island and 39 records for the California Channel Islands.

Taxa:			
Ephemeroptera			
	Baetidae		
			* *Baetis bicaudatus*
			* *B. tricaudatus*
			* *Callibaetis pictus*
			* *Centroptilum sp.*
	Caenidae		
			* *Caenis sp.*
Odonata			
	Aeshnidae		
			* *Anax walsinghami*
	Libellulidae		
			* *Paltothemis lineatipes*
			* *Pantala flavescens*
			Sympetrum corruptum
			* *Tramea sp.*
	Coenagrionidae		
			* *Argia sedula*
Plecoptera			
	Capniidae		
			* *Mesocapnia projecta*
Hemiptera			
	Notonectidae		
			* *Notonecta hoffmanni*
Megaloptera			
	Corydalidae		
			* *Protochauliodes simplus*
Trichoptera			
	Philopotamidae		
			* *Wormaldia sp.*
	Hydroptilidae		
			* *Hydroptila sp.*
			* *Ochrotrichia sp.*
	Lepidostomatidae		
			* *Lepidostoma sp.*
Trichoptera (continued)			
	Sericostomatidea		
			* *Gumaga sp.*
Coleoptera			
	Gyrinidae		
			Gyrinus plicifer
	Haliplidae		
			Peltodytes simplex
	Dytiscidae		
			Agabinus glabrellus
			* *A. sculpturellus*
			Agabus discors
			Hydroporus vilis
			* *Hydrovatus brevipes*
			Rhantus gutticollis
	Hydroscaphidae		
			* *Hydroscapha natans*
	Hydrophilidae		
			* *Anacaena signaticollis*
			Berosus punctatissimus
			* *Helochares normatus*
			* *Hydrobius fuscipes*
			* *Hydrophilus triangularis*
	Hydraenidae		
			* *Ochthebius interruptus*
	* Scirtidae		
	Elmidae		
			* *Ordobrevia nubifera*
Diptera			
	Tipulidae		
			* *Dicranota sp.*
			* *Hexatoma sp.*
	Psychodidae		
			* *Maruina sp.*
Diptera (continued)			
	Simuliidae (pupa used for species identification)		
			* *Simulium aureum*
			* *S. latipes*
			* *S. piperi*
			* *S. virgatum*
	Chironomidae (tentative identifications)		
		Tanypodinae	
			* *Ablabesmyia sp.*
			* *Pentaneura sp.*
			* *Procladius sp.*
		Orthocladiinae	
			* *Cricotopus sp.*
			* *Eukiefferiella sp.*
			* *Orthocladius sp.*
		Chironminnae	
			Chironomus sp.
			* *Kiefferulius sp.*
			* *Rheotanytarsus sp.*
	Dixidae		
			* *Dixa (Dixa) sp.*
			* *D. (Meringodixa) sp.*
			* *D. (Paradixa) sp.*
	Tabanidae		
			* *Chrysops sp.*
	Sciomyzidae		

* New record for California Channel Islands

Depauperate Nature of Santa Cruz Island Biota

Though Santa Cruz Island is only 30 km from the mainland and has 16 ecologically diverse plant communities (Junak et al. 1995), its fauna is notably depauperate. 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 breeding in comparable mainland habitats (Diamond and Jones 1980).

The richness of Santa Cruz Island insects varies by group. The 37 Orthoptera 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). In a survey comparing the Santa Cruz Island Lepidoptera fauna with that of the Big Creek Reserve (Monterey, California) only 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)

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

	Total Taxa Generic Level		Mainland Taxa Generic Level		Island Taxa Generic Level	
Order	Total Taxa per Order	% of Total Taxa	Taxa per Order	% of Taxa per Order	Taxa per Order	% of Taxa per order
Ephemeroptera	11	6.8	11	7.6	5	5.4
Odonata	17	10.6	16	11.1	10	10.9
Plecoptera	11	6.8	11	7.6	1	1.1
Hemiptera	12	7.5	11	7.6	6	6.5
Megaloptera	3	1.9	3	2.1	2	2.2
Trichoptera	22	13.7	22	15.3	8	8.7
Lepidoptera	2	1.2	1	0.7	2	2.2
Coleoptera	33	20.5	28	19.4	23	25.0
Diptera	50	31.1	42	29.2	37	40.2
Total Taxa	161	100.0	145	100.0	94	100.0

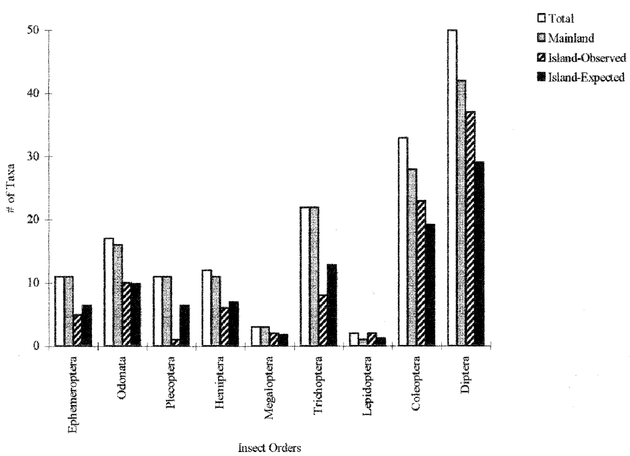

Figure 2. Comparison of total, mainland, and island richness of stream taxa per Order. Overall, Santa Cruz Island stream taxa account for 58% of the total taxa (at the generic level). Expected island richness per Order was estimated as 58% of total taxa per Order.

and Thorp et al. (1994) reveal that the Santa Cruz Island bee fauna accounts for only 19% (105 species) of mainland taxa (an estimated 520). This value appears low compared to Orthoptera and Lepidoptera figures, but Thorp et al. (1994) suggest that island figures "considerably underestimate" the actual number of bee species.

The number of stream insect taxa recorded for Santa Cruz Island accounts for approximately 58% of the total number of island and mainland stream insects (Table 2). Island Plecoptera exhibit very low richness compared with the mainland and with other island insect groups, with the island supporting only 9%, or one out of eleven mainland taxa. Trichoptera taxa also exhibit low richness compared to the mainland. Island representation within the groups Ephemeroptera, Odonata, and Hemiptera (aquatic) compares well with that of island orthopterans and terrestrial lepidopterans. Compared to other insect groups, aquatic beetles, flies, and megalopterans commonly occurred on the island.

Overwater dispersal may be difficult for freshwater organisms; however, very few island aquatic 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 (Howarth and Polhemus 1991). Ephemeroptera and Trichoptera occur as far as 300 km from the mainland in the Atlantic (Malmqvist 1993). On South Pacific islands one can find those forms 600 to 700 km from possible sources (Winterbourn 1980). Plecopterans have been collected from the subantarctic islands Snares, Aukland, and Campbell (approximately 100 to 600 km south of New Zealand). However, these stoneflies consist of taxa with terrestrial nymphs and apterous adults closely related to New Zealand species and may not have dispersed overwater (Winterbourn 1980).

Records indicate that aquatic insects have crossed distances much greater than the Santa Barbara Channel (30 km). In addition, the distance to the Northern Channel Islands was even less in the past. During periods of low sea level, the lowest occurring approximately 17,000 to 18,000 years ago, the Northern Channel Islands formed the island Santarosae (e.g., Vedder and Howell 1980). 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 would occur from the mainland and that island populations would establish and expand.

Given the overwater dispersal capabilities of aquatic insects and the relatively narrow barrier to dispersal presented by the Santa Barbara Channel, one might realize that other factors could contribute to the low richness of Santa Cruz Island aquatic insects. Also, it is necessary to interpret the above data in light of the difficulties associated with island-mainland comparisons. Ecological poverty may limit the number of organisms that occur on an island (Mac Arthur and Wilson 1967). For example, immigrating animals may encounter a depauperate flora or lack of specific prey taxa. In addition, island organisms may experience increased rates of extinction due to small population sizes, low genetic variability, and/or introduction of exotic species (Carlquist 1974). Island biotas may also "appear" depauperate due to sampling bias. Often, island organisms are not as well known or as thoroughly studied as their mainland counterparts. Contrasting island richness with larger areas of the mainland introduces an additional source of bias. In spite of the difficulties inherent in comparing the richness of mainland and island biotas, such comparisons continue to interest researchers.

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 species that dominate mainland riparian woodlands. Alder (*Alnus rhombifolia* Nutt.), sycamore (*Plantanus racemosa* Nutt.), and California-bay (*Umbellaria californica* Hook. & Arn.) 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, in Cottonwood Canyon, and in a few south draining watersheds (Junak et al. 1995; Furlong, pers. obs. 1995). Willows (*Salix* spp.) and mulefat (*Baccharis salicifolia* DC.) dominate the majority of Santa Cruz Island riparian corridors. Mainland insect groups relying heavily upon alder, sycamore, and cottonwood leaves as a food sources would 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 from the mainland and island could determine whether genetic restriction may contribute to the low richness of some island aquatic groups.

Small habitat areas support smaller populations, which in turn become more susceptible to extinction (MacArthur and Wilson 1967). The habitat size of Santa Cruz Island has not been static. During the Pleistocene, eustatic sea level fluctuations resulted in numerous expansions and contractions in the surface area of the Northern Channel Islands, as well as changes in the width of the Santa Barbara Channel (Vedder and Howell 1980). During periods of high sea level, the probability of island extinctions increased as island surface area 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. These events might result in occasional extinction of aquatic insect populations restricted to streams experiencing frequent winter scour.

Through various activities, man also contributes to island extinctions (Carlquist 1974; Marshall 1988). The introduction of sheep, cattle, and pigs in the mid 1880s decimated the 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, grazing and activities of feral pigs resulted in increased erosion. Sheep and cattle grazing on most of Santa Cruz Island ended in 1988, but feral pigs continue to impact island communities. Though not documented on Santa Cruz Island, the activities of the grazing animals and pigs may well have degraded riparian habitats and may to some extent contribute to the depauperate nature of the stream fauna. However, portions of the three mainland streams may be more impacted 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 of mainland sites. In addition, mainland surveys may encompass a greater range of habitats and a larger area. Together, these factors contribute to a mainland bias in taxonomic richness. In this study, we tried to avoid these biases, taking island samples over the course of seven years from seven streams. Mainland collections came from three streams over the course of six months. Additional mainland lists included these same streams, with one exception. The Wenner and Busath (1977) list included samples from Cold Spring and San Jose creeks. However, samples from these streams added no additional taxa to the mainland records.

The sources used for the mainland list do not appear to represent a greater sampling effort compared with the effort expended to develop the Santa Cruz Island list. The Wenner and Busath (1977) list was developed from 60 samples. Cooper et al. (1986) constructed their list from approximately four years of seasonal sampling. Our mainland list was produced from approximately 90 samples. The Santa Cruz Island list represents a seven-year effort with over 700 samples processed.

A possible bias could result due to the relative distance between mainland streams. The distances between Jalama and Refugio creeks and between Rattlesnake-Mission and Refugio are approximately 30 km. Jalama and Rattlesnake-Mission creeks are separated by approximately 60 km. The island, by contrast, 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 Santa Cruz Island aquatic insect taxa may not be due solely to difficulties associated with overwater dispersal. One must also consider the potential roles of the poverty of island riparian vegetation and island extinction rates. In addition, the greater area over which the mainland samples were taken may introduce a mainland sampling bias.

Disharmony of Santa Cruz Island Biota

Differential dispersal abilities and ecological tolerances 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, its reproductive characteristics, and its ecological requirements. The work of Carlquist (1974) contributes much to our understanding of the dispersal abilities of plants. However, other than comparing the attributes of animals with those above features**,** the determination of the dispersal abilities of animals is somewhat circular. Those animals that have dispersed far are 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 are found on the island, compared with 45% of the herpetofauna. According to records compiled by Darlington (1957) and Carlquist (1974), maximum known dispersal distances of reptiles (lizards - 3,200 km, snakes - 960 km) and amphibians (800 km) generally exceed that of land mammals (rodents - 960 km, small non-rodents - 322 km, large mammals 40 km). Compared with the higher percentage of herpetofauna, the overall low proportion of mammals and complete absence of large mammals on Santa Cruz Island, leads to the inference that this lack of balance results 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 (e.g., Wenner and Johnson 1980), it is doubtful that ecological poverty precludes the establishment of large native mammals on these islands.

The distribution of aquatic insect within orders also appears disharmonic when compared to the mainland distribution. The expected (based on proportions of total taxa within orders) and observed distributions of taxa within insect orders differ significantly. The numbers of observed Coleoptera and Diptera taxa exceeded the expected (Figure 2). In addition, these groups account for a greater percent of island aquatic taxa compared with the mainland (Table 2). Taxa in the orders Plecoptera and Trichoptera exhibit opposite trends (Figure 2; Table 2). Aquatic coleopterans and dipterans occur on islands as distant as Hawaii (3,200 km distant; Howarth and Polhemus 1991) and aquatic dipterans occupy ecologically poor islands such as Surtsey (a recent volcanic island; Lindroth et al. 1973) and Macquarie (a subantarctic island; Marchant and Lillywhite 1994). In contrast, trichopterans do not occur on distant oceanic islands such as Hawaii, but have been collected from numerous islands in the South Pacific (Winterbourn 1980). However, many of these islands are considered continental (Carlquist 1974). Plecoptera are rarely collected from islands more distant than Santa Cruz Island (e.g., Winterbourn 1980; Malmqvist et al. 1993).

These observations appear to support the concept that aquatic beetles and flies disperse more readily and caddisflies and stoneflies disperse less readily to islands than other aquatic insect groups.

Aerial and shipboard trapping also contribute to our knowledge of aquatic insect dispersal capabilities. A shipboard trapping program supported by the Bishop Museum from 1957 to 1966 included cruises in the Pacific, Atlantic, Antarctic and Indian Oceans. Insects collected during that program included 11 aquatic Diptera families, 6 aquatic Hemiptera families, 5 aquatic Coleoptera families, 2+ families of odonates, one family of ephemeropterans, and 2 unidentified trichopterans (Holzapfel and Harrell 1968; Holzapfel and Perkins 1969). The these families are a subset of those collected during this study and listed for other islands. The Bishop Museum also conducted an aerial trapping program over the Pacific Ocean from 1966 to 1969 (Holzapfel 1978). These collections were taken at altitudes up to 2,745 m; however no insects were recovered above 1,525 m. The majority of trapped insects (93 of 101 specimens) were recovered from samples taken soon after takeoffs and landings. The only aquatic taxa recovered by these efforts were flies (Chironomidae). A single chironomid was collected at high altitudes.

Because distance data was not published with the aerial and shipboard trapping results, one cannot make assumptions regarding dispersal distances. However, several groups 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 recover many groups that were not recorded from Santa Cruz and other islands.

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. 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 do not appear to possess the dispersal capabilities observed in other aquatic orders. Plecoptera and Trichoptera rarely occur on Santa Cruz Island compared to the mainland. However, one must consider the possible effects of ecological poverty on these under-represented groups.

The depauperate nature of riparian vegetation might exclude functional groups (shredders) that feed upon sycamore, alder, and cottonwood leaves. Shredding taxa account for a large proportion of mainland plecopteran (73%) and trichopteran (41%) taxa. Of shredder taxa, only one of the eight Plecoptera and two of nine Trichoptera occur on Santa Cruz Island. Mainland trichopterans in the collector guild are well represented on Santa Cruz Island (five of seven taxa). This anecdotal observation indicates that the depauperate nature of Santa Cruz Island's riparian vegetation may also play a role in the lower than expected richness of island Plecoptera and Trichoptera.

The stage is now set for further studies of Channel Island aquatic insect ecology and biogeography. Studies of stream taxa on other islands and comparisons of richness between islands would be of interest. Using aquatic insects as biomonitors of watershed recovery might be an additional focus of island research.

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