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Hawaiian Freshwater Polychaeta: a Potentially Substantial Trophic Component of Stream Depositional Habitats

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Abstract—In this paper we report the widespread occurrence of large annelids (Polychaeta: Nereididae) in Hawaiian stream depositional habitats, drawing attention to the lack of knowledge of Hawaiian stream energetics. Specimens of *Namalycastis* sp. were collected from five Hawaiian Islands from May–July 1995 and from the island of Maui from July–December 1999 and April–July 2000. Most specimens collected were *N. hawaiiensis,* while two specimens of *N. abiuma* were collected from a single site on the island of Molokai. Specimens were collected from elevations ranging from 3–240 m; several collections were from sites above at least one major (> 15 m high) waterfall. Habitats were characterized by slow-moving or stagnant water, water temperatures ranging from < 18–29 C, mixed gravel and sand substrates with organic detritus. Specimens were found among roots of vegetation along stream edges, in small lava pockets, buried in loose gravel, and in depressions between, under, and inside porous rocks. Body lengths of preserved specimens ranged from ~ 9 to 150 mm among islands and streams between years and seasons. Polychaetes were usually abundant in these habitats indicating a nearly ubiquitous distribution of *Namalycastis,* and suggesting ecological importance for stream benthic trophic dynamics throughout the Hawaiian archipelago.

Introduction

Of 85 families in the class Polychaeta, only 10 have representatives in brackish and freshwater habitats (Klemm 1985). There are more than 6,000 identified species in this class, with < 2% classified as euryhaline or freshwater (Ushakov

1972) and < 50 species restricted to freshwaters (Pennak 1989). Most freshwater or euryhaline representatives are within the Nereididae (Ushakov 1972, Klemm 1985), which is predominantly a marine family (Hartman 1959b). However, there are other families containing euryhaline and freshwater species (i.e., Sabellidae, Serpulidae, and Ampharetidae, see Klemm 1985). Over half of the 50 euryhaline and freshwater species of Nereididae are located in the tropical and subtropical western Pacific region (Johnson 1903, Hartman 1938, Ryan 1980), while only 10 species are found in North America. Freshwater and euryhaline Polychaeta have been reported from North America, including Alaska (Holmquist 1967), California (Johnson 1903, Hartman 1938), Georgia (Rasmussen 1994), the Great Lakes (Krecker 1939, Rolan 1974), New York (Spencer 1976), caves of Mexico (Solis-Weiss & Espinasa 1991), the Philippines (Berkeley & Berkeley 1964), Canada (Mackie & Qadri 1971), in addition to Papua New Guinea and Fiji (Glasby et al. 1990), New Zealand (Estcourt 1967a, Estcourt 1967b, Winterbourn 1969), the Amazon (Correa 1948), Japan (Izuka 1908, Takahasi 1933), China (Chamberlin 1924), India (Singh et al. 1988), and Hawai'i (Johnson 1903, Glasby et al. 1998). Most freshwater or brackish polychaete habitats were once geographically connected or are presently connected to the ocean (Hartman 1959b). In addition, almost all specimens have been collected within ~ 32 km of the ocean (Pennak 1989), supporting a theory of recent evolution into freshwater (Hartman 1959b).

Johnson (1903) was the first to document the occurrence of freshwater polychaetes in Hawai'i, but that study only reported taxonomic descriptions of two specimens collected from a single spring near Honolulu. *Namalycastis hawaiiensis* can be found in both freshwater and brackish habitats, but most of the Hawaiian representatives have been collected in freshwater (Glasby et al. 1998). There are no other published studies specifically addressing freshwater polychaetes in Hawai'i except a recent species documentation by Glasby et al. (1998). Other literature on Hawaiian freshwater polychaetes reference Johnson's (1903) report (Hartman 1938, Correa 1948, Hartman 1959b, Hartman 1959a, Klemm 1985, Pennak 1989, Solis-Weiss & Espinasa 1991).

In this paper, we give qualitative observations of the occurrence, size ranges, and habitat of Hawaiian freshwater polychaetes, that were otherwise undocumented in polychaete literature. Our findings suggest that Hawaiian freshwater Polychaeta are found in patchy, depositional habitats that have never received research attention in Hawaiian streams. The presence of large annelids in these habitats suggests that the depositional areas of Hawaiian streams may contribute more to the food web than decomposition alone. There have been few Hawaiian stream studies addressing anything beyond the endemic gobies, shrimp, freshwater limpets, and insects (particularly only the Odonata). An understanding of Hawaiian stream energetics is completely lacking. We hope that this paper will draw attention to the occurrence of freshwater Polychaeta in Hawai'i, the heretofore ignored depositional habitats of these streams, and to the lack of knowledge concerning endemic and non-endemic freshwater invertebrate assemblages.

Methods

Habitat and Site Selection

The chance capture of a single polychaete worm from a Makamaka-‘ole Stream drift sample (21 December 1993), taken at an elevation > 200 m above several waterfalls, prompted a qualitative investigation into the occurrence and habitat of these organisms. This was the only polychaete caught during hundreds of stream drift samples (some drift sample sequences represented 24 h protocols ~ 6 h apart) in 15 streams on three of the major Hawaiian Islands (Hawai‘i, Maui, Moloka‘i) over six years. The drift samples were collected under median base-flow conditions; not during flood events. In 1994, initial collection attempts to find polychaetes on Maui were unsuccessful; however, over several months during the summers of 1994 and 1995 on Maui, the sampling procedure was refined and optimal polychaete habitat was identified and characterized (see *Results and Discussion* below for habitat parameters) so that numerous specimens were collected in 1995. Based on these preliminary investigations, typical polychaete

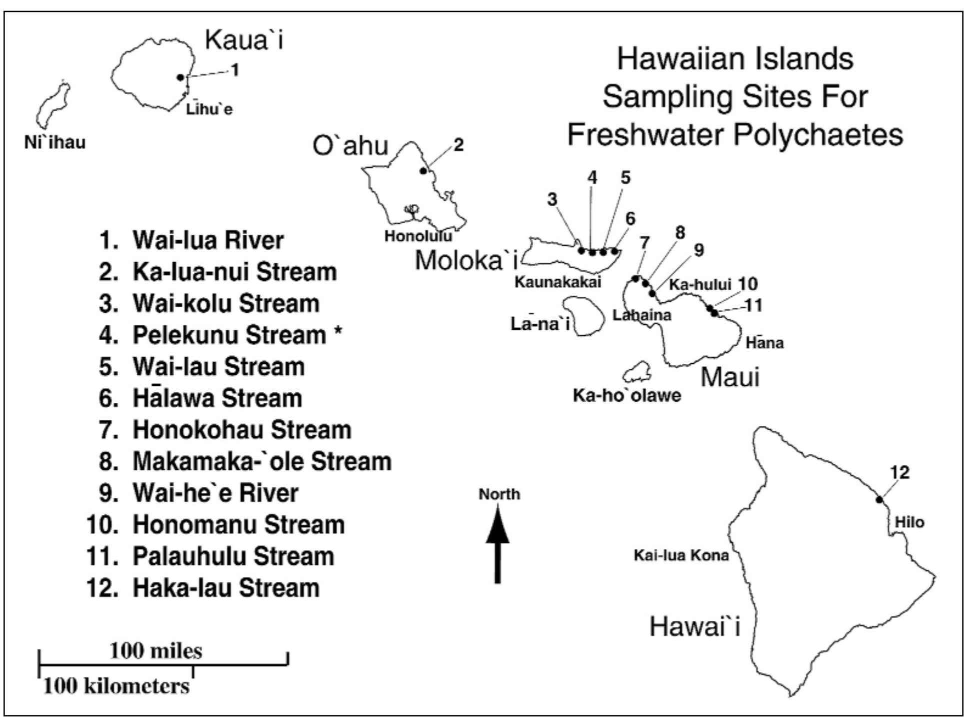

Figure 1. Map of freshwater Polychaeta sampling locations on the five major Hawaiian Islands. Coordinates of sampling locations are given in Table 1. *Specimens are *Namalycastis abiuma*. Representative specimens from other streams were identified as *N. hawaiiensis*; see Glasby et al. (1998).

Table 1. Polychaete collection sites on the major Hawaiian Islands. Location, number of worms collected and habitat notes^.

Island	Stream/River	U.S.G.S. Map Quadrangle	Location	Elevation ~ m	No. Worms	Habitat Description (depositional channel edges or pool/'backwater' areas)
Kaua'i	Wai-lua	Ka-pa'a	22°02.29´N, 159°22.71´W	67	11	~30 m upstream of Wai-lua Falls in small lava pockets with decaying detritus at channel edges
O'ahu	Ka-lua-nui	Hau'ula	21°34.86´N, 157°55.00´W	103	6	~100 m downstream of plunge pool for Sacred Falls along channel edges
Moloka'i	Wai-kolu	Moloka'i East	21°10.37´N, 156°55.93´W	9-10	2	along channel edge or under large, loose rocks in slow flow with sand, gravel and organic detritus
		Moloka'i East	21°08.97´N, 156°55.23´W	240	36	coarse sand around submerged roots and detritus
	Pelekunu *	Moloka'i East	21°08.89´N, 156°52.87´W	8-9	2	see description for Wai-kolu Stream
	Wai-lau	Moloka'i East	21°09.87´N, 156°49.93´W	5	3	see description for Wai-kolu Stream
	Halawa	Moloka'i East	21°09.52´N, 156°44.94´W	10-15	1	see description for Wai-kolu Stream
Maui	Honokohau^	Na-pili	21°01.44´N, 156°36.69´W	3-4	15	lower elevation: see description for Wai-kolu Stream, ~30 m upstream of mouth (no canopy)
	Honomanu	Honolua	20°51.62´N, 156°10.18´W	3-4	12	see description for Wai-kolu Stream
	Makamaka-'ole^	Ka-haku-loa	20°57.63´N, 156°32.30´W	226	102	above several waterfalls in pools with woody detritus, much canopy, and mixed gravel
	Wai-he'e^	Wai-luku	20°57.07´N, 156°30.80´W	5	6	~150 m upstream from mouth (no canopy), much leaf and wood detritus and sand
	Palauhulu	Ke-'anae	20°51.54´N, 156°08.94´W	45	1	above several waterfalls in a large pool with leafy detritus in sand under a bank overhang
Hawai'i	Haka-lau	Papa'a-loa	19°54.06´N, 155°08.08´W	3-4	20	see description for Wai-kolu Stream, along rooted vegetation of instream island and channel edges

*Specimens are *Namalycastis abiuma*. Representative specimens from other streams are *N. hawaiiensis* (see Glasby et al. 1998).

^These stream sites also include collections made from June–December 1999 and April–July 2000.

habitat was qualitatively sampled in streams on the island of Maui over the 1995 summer. In a concentrated effort to determine inter-island distribution, we made one or two day sampling trips to streams on the other four, main islands in July 1995. During these trips, streams were selected for logistical ease and identifiable polychaete habitat at elevations near sea-level and above major waterfalls. The streams sampled during these trips are given in Table 1 and Figure 1. Practical and financial limitations did not permit us to do a more comprehensive survey of additional streams on islands other than Maui.

Collection dates in 1995 for each site are as follows (island name is given first followed by respective streams and date): Kaua‘i, Wai-lua River (25 July); O‘ahu, Ka-lua-nui Stream (26 July); Moloka‘i, Wai-kolu Stream upper elevation (23 May and 14 June), Wai-kolu Stream lower elevation, Pelekunu Stream, and Wai-lau Stream (all three 19 July), Halawa Stream (18 July); Maui, Honokohau Stream (24 July), Makamaka-‘ole Stream (29 May), Wai-he‘e River (26 June), Palauhulu Stream (10 July); Hawai‘i, Haka-lau Stream (22 July). Additonal sampling on Maui occurred from June–December 1999 and April–July 2000 in Wai-he‘e River, Honokohau Stream, Honomanu Stream, and Makamaka-‘ole Stream.

Specimen Collection and Body Length Measurements

Polychaetes were collected using two methods. Initially, a standard wash bucket with a 0.5 mm mesh screen bottom was used to sift through bottom substrates excluding large rocks. The bucket was used to scoop up substrate, which was allowed to settle, and larger rocks were rinsed with stream water and removed until only pebbles or sand remained. The remaining material was hand swirled and polychaetes were carefully removed and placed into containers with stream water until preservation. This process proved to be cumbersome and limited the substrate types that could be sampled. Furthermore, if the bucket was left standing for a few minutes to allow for increased water clarity, it was noted that any disclosed worms would quickly burrow back into the substrate. The bucket was not used in later collections.

Most collections were made by carefully digging and disrupting the benthic substrate by hand. This allowed collections to be made underneath large rocks, between roots of macrophytes in soft substrates, and in small pockets between large boulders. At deeper sites ($\geq$ 1 m), it was necessary to snorkel for collections. Any worms dislodged during the disturbance were collected. Few, if any, worms were lost downstream because of low water velocities in these habitats. Hand collections proved to be the most effective and efficient means of polychaete collection. Logistical and practical problems prevented using a net (e.g. Surber sampler) for collections. For both collection methods in 1995, polychaetes were placed in 3–4% neutral formalin before leaving the stream, or photographed live and then preserved. In 1999 and 2000 some specimens were perserved in 3–4% formalin or 70% isopropyl alcohol while in the field, while others were kept live in small bowls at room temperature for preliminary rearing experiments. At all sites, observational notes on habitat included the following: substrate and vegetation structure, water flow and clarity, canopy, amount and type of detrital material (odor of reducing conditions, relative abundance of leafy and woody debris, etc.), and weather conditions on the collection day. Water temperature was measured at some sites.

Polychaete body length measurements were made on 63 preserved whole specimens. Many times during field collections only pieces of worms were collected and preserved. These partial specimens were only counted if there was a head. Also, several specimens were shipped to experts for identification before body length measurements were made. Thus, size range data do not represent all specimens collected. The data presented in Table 2 are meant to give conservative body size distributions among islands, streams, and season.

Representatives voucher specimens (vouchers HAW 1–HAW 13) were deposited at Barry A. Vittor and Associates, 8060 Cottage Hill Rd., Mobile, AL.

Results and Discussion

Distribution, Habitat, and Abundance

Stream sampling sites are given in Figure 1. Only one stream was sampled from the islands of Hawai'i, Kaua'i, and O'ahu, and the lower elevation sites on Moloka'i were all sampled on the same day. Sampling trips were short to enable rapid determination of polychaete distribution across islands. Therefore, the sampling sites do not reflect a complete survey of every accessible stream. More extensive sampling occurred from streams on Maui and the upper elevation Moloka'i sites. Sampling site location, numbers of specimens, and habitat are given in Table 1.

Two species were identified and described by Glasby et al. (1998). Most specimens collected were *Namalycastis hawaiiensis*, exceptions being two specimens of *N. abiuma* from Pelekunu Stream (Table 1, Fig. 1). The absence of *N. abiuma* from other sites may be attributed to insufficient sampling effort and time in the more undisturbed streams of Moloka'i. The perinneal streams of Moloka'i that were sampled are relatively free of agricultural run-off and other anthropogenic disturbance, which may preclude the habitat requirements necessary for *N. abiuma* from the other Island streams that recieve relatively more disturbance (through diversions, development, agriculture, etc.). The immediate, benthic habitat of each species did not apper to be different, and there is no direct evidence (e.g., gut contents; see below) to show competitive exclusion. A clear explanation for the absence of *N. abiuma* in most of the sampling locations remains unknown.

Recent collections of *N. hawaiiensis* (i.e., July–December 1999 and April–August 2000) have been made on Maui with > 100 specimens taken from

Makamaka-‘ole (from the upper elvation and near the mouth at ~ 10–15m elevation) and Honokohau (near mouth elevation at ~ 2–3 m) Streams (Table 1). The total number of freshwater polychaete specimens from all sampling dates is ~ 200, with almost half collected from ~ 50 m reach of Makamaka-‘ole Stream (upper elevation) on Maui. Thus, although only one specimen was captured in a single drift sample, the populations appear to be extensive. This is probably due to the benthic habitat of these annelids. On every sampling occasion, worms were observed to quickly swim down to the substrate and re-burrow during and after the sampling disturbance, therefore, suggesting that the populations remain within the sand and gravel substrates with infrequent visits the surface.

Sites ranged from 3–240 m elevation, and two collections were above at least one large waterfall (ranging from 15–25 m high). Most polychaete habitats were found in steep, mountain streams that are frequently and unpredictably scoured by flash floods. This is in contrast to lentic-type aquatic habitats (i.e,. marshes and mangroves) where most freshwater and euryhaline polychaetes have been documented (Hiltunen 1965, Holmquist 1967, Pennak 1989). Relatively undisturbed (i.e., no diversions) Hawaiian streams are stair-step sequences of cascades and waterfalls, depositional pools, riffles and run habitats. Polychaetes within these large scale lotic systems were generally found in depositional pools or slow flow areas near the banks (i.e., in substrate associated with slow water flow or completely stagnant water). An exception was the site in Haka-lau Stream, on Hawaii, where water flow was more typical of a run or riffle habitat. Water temperatures ranged from < 18 C–29 C, substrate consisted of mixed gravel and sand, and water clarity was good (meaning the bottom substrate could be seen from the surface) at most sites. The exception was Halawa Stream on Moloka‘i, where the bottom could not be seen. Depths ranged from < 0.1 to > 1 m, with most collections in substrates from 0.3–0.5 m.

Specimens were also found among roots of vegetation along stream edges, in small lava pockets, buried in loose gravel and in depressions between, under, and inside porous rocks. All habitats were associated with fine organic detritus or decaying twigs and leaves. Many specimens were collected under large rocks that were loosely set in mixed gravel or sand, but never in compact mud or silt. When polychaetes were found along stream edges, the substrata were organic-loaded sand or silt held by roots. Substrata with organic debris were dominated by, or had evidence of, reducing conditions as indicated by the presence of black organic decay and odour (e.g., anoxic conditions). This may determine food resources and polychaete abundance and persistence in these habitats. In habitats containing organic detritus, specimens were generally collected in large numbers, indicating a habitat distribution pattern associated with the patchy nature of organic matter. Conditions of anoxia are known to be associated with *Namalycastis abiuma* habitat (Rasmussen 1994) and are probably not uncommon for most euryhaline and freshwater Polychaeta. Slow water flow in habitats with detrital material are common for other freshwater and euryhaline Polychaeta of estuaries and bays (Izuka 1908, Estcourt 1967b, Estcourt 1967a, Solis-Weiss & Espinasa 1991, Rasmussen 1994), and many populations are reported from lake (i.e., lentic) benthos (Hiltunen 1965, Holmquist 1967, Pennak 1989).

BODY SIZES AND ECOLOGY

Collected polychaetes ranged from ~ 9 to 150 mm in total body length with translucent to opaque bodies having an obvious dorsal blood sinus running the length of the body. The sizes were within the range of those reported by Johnson (1903); however, this is the first report of multiple body length measurements from specimens collected from each Hawaiian Island during different seasons between years. These data are conservative, as the measured number of individuals only represent ~ 20% of all worms collected. In addition, we probably missed many smaller (< 10 mm) individuals using the hand collecting technique. Thus, these body length ranges probably do not represent the smallest individuals of the populations.

Our observations indicated that Hawaiian freshwater polychaetes can move quickly over the substrate and through the interstitial spaces, burrowing into sand, moving into and between pockets or depressions of substrate; and they appear to be photonegative. Because of these seclusive movements, many of the smallest specimens were probably overlooked during collections. These worms also swim through the water with a distinct nereid (sinusoidal or undulatory wave) motion.

Table 2. Representative freshwater polychaete total body lengths (N = 63) among islands and streams of Hawaii. These data represent ~ 20% of total individuals collected. The condition of most preserved specimens did not permit measurements, and many live collections were not measured.

Island	Stream	Date Collected	Individual Body Lengths (mm)
Maui	Honokohau	24-Jun-95	7, 9, 15, 27
		9-Aug-99	17, 19, 19, 23, 24, 32, 50
		11-Oct-99	44, 46
	Makamaka-‘ole	29-May-95	31, 47, 66, 69
		12-Aug-99	28, 30, 62, 62, 65, 65
		8-Jul-99	45
		24-Nov-99	93
		15-Apr-00	47, 61, 92, 109, 122, 127
	Wai-he‘e	17-Aug-99	20, 36, 38
		17-May-99	20, 28, 33, 40
	Honomanu	7-Jul-99	44
Hawai‘i	Haka-lau	22-Jul-95	10, 15, 18, 23, 24, 26, 27, 27, 30, 33, 43, 57, 70
Kaua‘i	Wai-lua River	25-Jul-95	43, 88, 110, 115, 142, 150
O‘ahu	Ka-lua-nui	26-Jul-95	24, 28, 30, 46
Moloka‘i	Wai-lau	19-Jul-95	39

Many of these observations agree with those of Rasmussen (1994).

Observations of *N. hawaiiensis*' gut contents revealed mostly detrital material. This is consistent with *N. abiuma* reported by Rasmussen (1994) from Sapelo Island Georgia. Individual worms kept alive in containers were observed to process decaying organic matter in the form of passed feces. The feces were examined under a dissecting microscope and appreared to be balls of amorphous detritus and diatoms wrapped in a thin mucous sac. Based on these direct observations, it is estimated that once material is ingested, the total digestion time is less than 30 min. On several occasions, when three or more live worms were housed together in a closed, round container (approximately 20 cm diameter) with little or no detritus, there would be fewer individuals present after several days. Although not quantitative, we suspect that in the absence of a sufficient volume of detritus, the worms become aggressive predators and cannibals. Because of quick digestion, we were not able to examine the gut contents of remaining individual worms; however, on occasion, pieces of a dead worm were found among the remaining live worms, suggesting recent cannabilism. In the absence of a sufficient food source, the remaining worms would probably re-ingest their feces, thus eliminating direct evidence of canniblism. When several worms were placed into containers with at least 2 cm organic detritus, there was still evidence of canniblism; however, reduced numbers were not observed for at least one week, and then the number of individuals would remain constant. We hypothesize that the organic detritus acts 1) as a sufficient food source, and 2) to increase the immediate habitat heterogeneity in a closed system, thus, lowering the probability of chance encounters among individuals, that may result in predation.

This hypothesis is certainly plausable, like their marine relatives, these nereids have raptorial jaw structures that, in marine forms, are used for capturing prey. We propose that these freshwater polychaetes are omnivorous, with food sources of decaying organic matter, diatoms, small protozoans, oligochaetes, and immature insect larvae; and on chance occasions other polychaetes. This would be particularly advantageous during high discharge flooding when varieties of terrestrial and aquatic plant debris and macroinvertebrates are deposited into pools and slow flowing margins of the stream.

The nearly ubiquitous distribution and abundance of freshwater polychaetes in Hawaiian streams suggests that these organisms constitute a major portion of the macrobenthic community biomass and depositional trophic structure. Freshwater Polychaeta could potentially serve as predators by feeding on other stream invertebrates or a detritivore by ingesting organic material directly, or indirectly by conditioning the material, via digestion, for further decomposition by aquatic detritivore communities (e.g., bacterial and fungal). At several collection sites, polychaetes were associated with unidentified planarians and several aquatic annelids (i.e., a leech, *Metaphire schmardae*, and several oligochaetes, *Pontoscolex corethrurus*, *Amynthas diffringens*, *A. minimus*, two species of unidentified Ocnerodrilidae, and *Branchiura sowerbyi).* Therefore, freshwater polychaetes could be both predator and prey, providing a food source for Hawaiian freshwater gobies or other predators (e.g., prawns) found in depositional habitats. We speculate that freshwater polychaetes are an important component of depositional habitat secondary production and trophic structure.

Conclusion

We have collected freshwater polychaetes from the five largest islands in Hawai‘i. These polychaetes were found from the mouths of streams to high elevations above several waterfalls, indicating a complete freshwater existence with euryhaline tolerance. Our survey of their occurrence and persistence in Hawaiian depositional stream habitats has identified abundant populations. This may represent a nearly ubiquitous distribution in depositional, slow-flowing areas of streams throughout the Hawaiian archipelago. Because these annelids can be found in relatively large numbers, they are potentially an important part of the decomposing communities of Hawaiian streams and could also represent an important component of secondary production and trophic structure that has been largely ignored in Hawaiian stream studies. We are presently making collections for laboratory cultures to address several questions concerning feeding preference, life cycle, and microbial gut community and enzyme activity. We suggest quantitative field studies focusing on the habitat and biology of Hawaiian freshwater and euryhaline Polychaeta, and we call for more studies of Hawaiian stream energetics in general.

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