

Geomorphology, Development of Running Water Habitats, and Evolution of Black Flies on Polynesian Islands

DOUGLAS A. CRAIG

Running water habitats develop in concert with the age of hotspot volcanic islands. This study tracks the geologic and hydrologic processes involved in this development for the Society Islands, French Polynesia. Over a period of about 6 million years, these islands have rafted northwest on the Pacific Plate and eroded from high islands with many stream systems to atolls with no running water. Black flies that require running water for their immature stages have undergone a species radiation into a wide array of running water habitats on Tahiti. From there, black flies appear to have dispersed to older islands farther west. The reduction of running water habitat with the island's increasing age has had consequences for the biogeography of these insects. The habitat generalist species are the most widespread. Species with dependence on cascades cannot colonize islands where cascade habitats have eroded away.

Keywords: islands, running water, habitats, evolution, black flies

Rivers and streams on continents tend to be relatively consistent in their development. There is always ample geological material for the water to erode and redistribute. Hence, continental flowing water can achieve commonality worldwide in characteristics such as slope of profile, branching pattern (order), meander wavelength, and floodplain in relation to volume of discharge (e.g., Gordon et al. 1992). However, this predictable development is different for running waters on volcanic islands, where the type of running water is closely linked to the age of the island. In large part, the erosive force of water leads to eventual formation of diverse habitats and creates opportunities for organisms to adapt to a complex topography over evolutionary time. Erosive forces, however, eventually lead to the demise of the island and of the running water itself.

In his classic book on islands worldwide, Menard (1986) showed that altitude, prevailing wind, and consequent rainfall were important aspects in the general development of streams and rivers in relation to erosion on volcanic islands. Haynes (1990) also found strong correlations between altitude, area, and diversity and the size of freshwater habitats on oceanic islands. Resh and de Szalay (1995) compiled information on streams and rivers of the islands of Oceania (those in the tropical Pacific Ocean). In addition to useful images of landscapes and streams of Moorea, one of the Society Islands (figure 1), they provide tables of information on the islands' geology, climate, and biota and discuss their

interactions. They note that the Hawaiian Islands are the most studied, while information on the stream and river systems of other tropical Pacific islands is variable.

The evolution of streams and rivers on hotspot islands has implications for aquatic insects and their biogeography. My observations of these interactions (figure 2) are based mainly on the islands of French Polynesia, with emphasis on the Society Islands. I focused on the taxonomy (e.g., Craig 1987, 1997, Craig and Joy 2000) of Polynesian black flies (Simuliidae) of the subgenus *Inseliellum*. These black flies are separately distributed across the Pacific Ocean, occurring in Guam and Chuuk (Micronesia), in Rarotonga (Cook Islands), and in the Marquesas Islands, Society Islands, and Austral Islands (French Polynesia). An analysis of the historical biogeography of *Inseliellum* (Craig et al. 2001) shows that the stage of fluvial geomorphic development on an island in large part determines the species composition of black flies inhabiting the island. In this article, I consider (a) the volcanic processes involved in island development, (b) the effects of changes in hydrological processes related to underlying geological conditions on the development of running water

Douglas A. Craig (e-mail: d.craig@ualberta.ca) is a professor emeritus, Department of Biological Sciences, University of Alberta, Edmonton, T6G 2E9, Canada. His research is mainly broadly based investigation of the biology of Simuliidae (black flies). © 2003 American Institute of Biological Sciences.

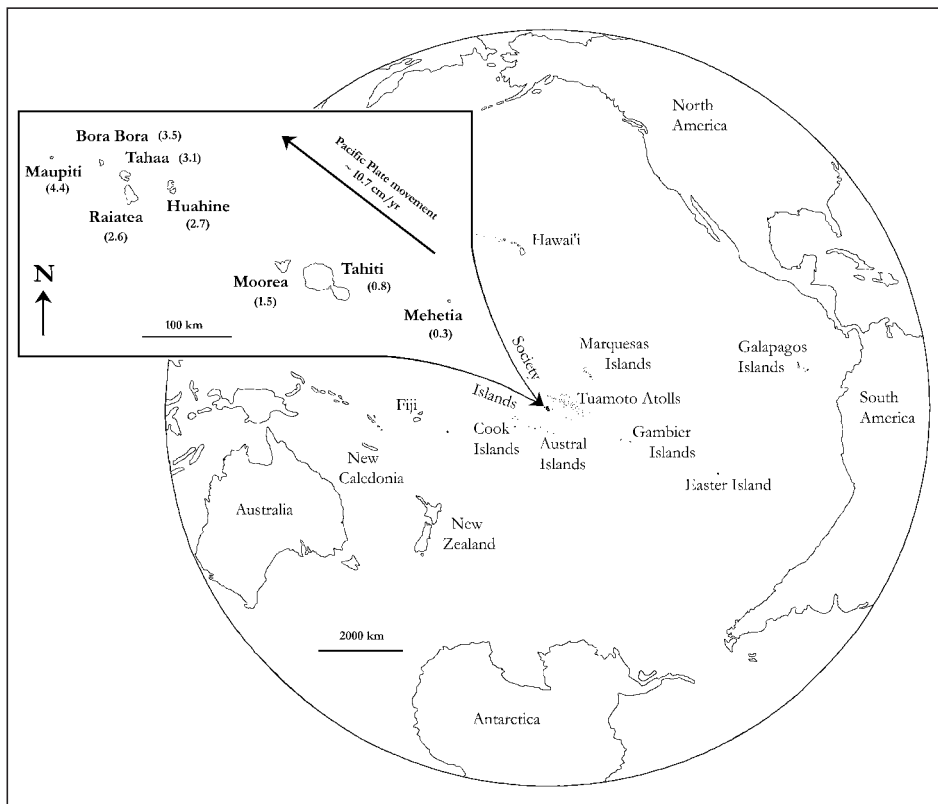


Figure 1. Map of the Pacific Ocean, centered on Tahiti, French Polynesia. The inset shows the Society Islands at a finer scale and the direction of movement of the Pacific Plate. The average age of the islands is indicated (in millions of years). Adapted from ORSTOM (1993).

habitats, (c) the characteristics of aquatic habitats as they relate to black fly larvae and some other organisms that depend on running water, (d) the geomorphic changes as an island ages and the effect of these changes on running water habitats (in relation to the biogeography of *Inseliellum*), and (e) the impact of human activities on running water habitats in Polynesia.

Geological considerations

The Hawaiian Islands provide the classic model for island chains formed by volcanic hotspots (Carson and Clague 1995). The island chains of Polynesia are more complex than the Hawaiian Islands, having more than one hotspot, and they are not in such a simple lineament (Craig et al. 2001). Of these island chains, the Society Islands have the simplest linear arrangement, but even so, they appear to include at least two hotspots in addition to the recently active hotspot island of Mehetia. The formation of such islands is well understood (Duncan and McDougall 1976); however, the underlying mechanism of hotspots is currently in dispute (Jones 2003, Kerr 2003). In the first stage of island formation, a magma plume is thought to produce a volcano on the Pacific Plate, which is traveling to the northwest at approximately 10.7 centimeters per year (figures 1, 2). The early building phase, in which the volcano rises above sea level, is rapid. Moving

northwest on the Pacific Plate, the island is gradually separated from the magma plume, and volcanic activity decreases. If the island is of sufficient altitude to generate its own weather and concomitant rainfall, erosion of material covering the magma chamber allows renewal of volcanicity. Nuku Hiva in the Marquesas Islands and some deeply eroded valleys in Tahiti offer clear examples of the resultant layered basalt. Such renewed volcanicity has occurred in Tahiti regularly every 2000 years (Duncan et al. 1994). With further reduction of overburden, the roof of the magma chamber eventually collapses to form a caldera. As discussed later, these last two processes have important consequences for the development of two particular running water habitats and for the evolution of Tahitian black flies.

The weight of the island depresses the underlying ocean crust; consequently, as erosion lightens the island, it tends to rise through isostatic rebound. This rebound is offset, however, by cooling and shrinking of the underlying crust as it moves away from the hotspot magma plume; this subsidence occurs faster than does the rebound. On balance, the island subsides at 2 to 6 millimeters (mm) per year (Menard 1986). With that subsidence, coral reef formation takes place around the island circumference, and with continued subsidence, by an age of 4 million to 6 million years, little of the original island is left above sea level (Paulay 1994). Excellent examples

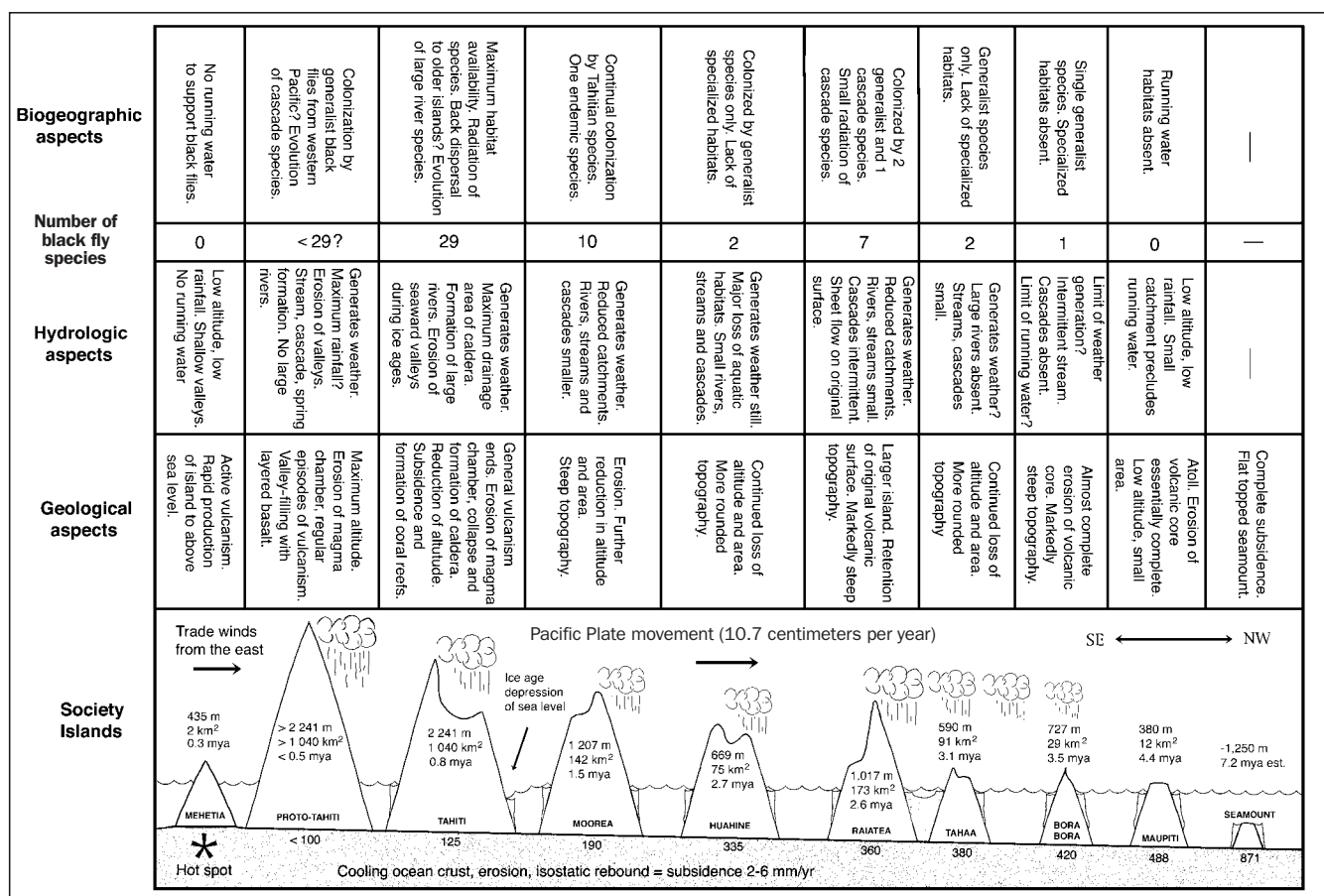


Figure 2. Schematic of the formation of the Society Islands, development of running water habitats, and biogeography of black flies. Distance (in kilometers) of each island from the hotspot is indicated below the island. Altitude (in meters), area (in square kilometers), and average age (in millions of years) are given for each edifice. Not all of the Society Islands are shown, but an earlier, hypothetical stage of Tahiti is indicated. Islands are not to scale. Based on ORSTOM (1993) and Craig and colleagues (2001).

of this stage are Bora Bora (Society Islands) and Mangareva (Gambier Islands) (figure 1). By the time an island reaches 6 million to 7 million years of age, only an atoll is left, and by 8 million to 9 million years of age, the seamount is totally submerged (ORSTOM 1993). The majority of Polynesian islands are consistent with this conceptual model (figure 2).

Hydrological considerations and habitat formation

The erosion of an island is caused mostly by water (Menard 1986). Streams and rivers on a lineament of hotspot volcanic islands will change in concert with the ongoing geomorphic development stages of the islands, and aquatic habitats will differ among islands in the line (figure 2). The formation of hill slope drainage networks for the West Coast of North America has been examined by Montgomery and Dietrich (1989) and by Gomi and colleagues (2002). In general, downward mass movement of substrate forms an unchanneled hollow. Saturated subsurface flow then causes an erosional break in the soil where a channel (with a defined bank) will begin. For gentle slopes, abrupt channel commencement is determined by such seepage erosion and also

by overland flow. The observations for Polynesia below are consistent with the general observations above, albeit the surface slopes for the islands under consideration are often markedly steeper.

The original process of stream formation in the Society Islands can only be surmised, because there is now no original volcanic surface left on any island, with the exception of a little heavily weathered original surface high on Raiatea. On Mehetia, however, some 120 kilometers (km) southeast of Tahiti, formed only 0.3 million years ago and considered the active hotspot for the Society Islands, early valley formation processes may be seen. Aerial photographs show that the island, volcanically active in historic times and covered in lava and scoria (loose volcanic debris), already has very shallow, vegetated valleys, but surface water is absent. This development of the landscape is similar to developments in the better-known Hawaiian Islands (Craig et al. 2001), where the volcanic material is initially too porous to support running surface water. The rainwater simply percolates down through the substrate (Menard 1986). Typically, such a situation lasts until vegetation becomes well established and soil

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Figure 3. A young stream in the Fareteuira Valley, Tahiti, characterized by a low volume of flow running over rough lumps of lava basalt and shaded by low vegetation. Photograph: Douglas A. Craig.

develops, with consequent water retention and infiltration. Groundwater seeps downward in the upper slopes via shallow hollows, macropores, and flow paths, eventually coalescing and forming a true channel. The converged flow then begins eroding channels on the middle and lower slopes of the volcano (Craig et al. 2001). In the Society Islands, such young streams on middle slopes tend to be overhung with vegetation that shades the channel and also provides organic input to the stream from the riparian canopy (figure 3). Some Polynesian black fly species are only found in such heavily shaded habitats.

The initial formation of valleys appears to take place rapidly, as on the hotspot island of Mehetia. This island, with an altitude of only 435 meters (m), is probably too low to generate its own weather; hence, its rainfall is little more than that of the surrounding ocean, 470 to 570 mm per year (ORSTOM 1993). However, full-scale erosion of Mehetia by running water and formation of larger valleys will most likely not occur unless the island is raised higher by geologic processes. A more recent example is seen in the Krakatau Archipelago in Indonesia. Rakatau Island, 800 m high, with heavy rainfall (3200 mm per year) but only 120 years since its eruption, already has semipermanent standing water and deeply incised,

wet, heavily vegetated valleys, although it has no permanent running water (Thornton 1995, Zabka and Nentwig 2002). Another, equally dramatic example of rapid valley formation is that of Mount St. Helens, Washington, which, with a good supply of water, already has well-eroded waterfalls and rivers only 23 years since its last eruption (Findley 2000). These last two well-known volcanoes, however, produced mainly ash, so their erosion has been more rapid than it would be on basaltic islands.

A variant on the early development of running water on volcanic islands is water spread over smooth lava and flowing in broad, nonincised beds. Such flow is not currently present in French Polynesia, except for small flows high on the Temehanirahi Plateau, Raiatea, where some of the original volcanic surface remains. Such flows are more common in Hawaii (Craig et al. 2001). These broad channels have no shade except at their margins. The difference between Hawaii and the Society Islands is probably due to the viscosity of the lava, which is very low for Hawaiian volcanoes and higher for those in Tahiti. Slopes in Tahiti are 8° to 10° steeper than in Hawaii, and faster erosion has removed the original surface (Duncan and McDougall 1976).

With increased catchment area of valley walls, including seepage from riparian vegetation and soils, erosion increases and stream networks develop. In Tahiti, a middle stage of stream development tends toward a stair-step profile, with steep valley walls, fast runs leading to high falls, and deep plunge pools below. Good examples are the Fautaua Cascade (figure 4) and the Trois Cascades (figure 5). Such falls generally represent the edge of a basalt layer down to which the water has eroded. Typically, these streams have markedly variable discharges and high velocities (Resh and de Szalay 1995). Discharge fluctuations lead to finer material being flushed away, leaving unstable loose boulders and cobble (e.g., figure 6).

During the younger stream phase, however, before a valley is fully eroded, a stream such as that at the Grottes de Maraa, Tahiti, may occupy a bedrock-floored channel more or less to its seaward terminus, where water falls straight into the lagoon. As a stream progresses in age, it cuts back into the island more deeply, forming a seaward reach with a bed of alluvium that extends inland to a cascade. Streams of this type are common in Hawaii (Craig et al. 2001). In Tahiti, the Utuofai River and its cascade provide a good example (figure 7). Flow in these alluvial-bedded terminal reaches may be completely hyporheic (flowing through the substrate). The streambeds will appear dry, with flowing water appearing only at transverse bedrock ridges. Most such alluvial streams in Polynesia flow out to the sea as surface water. In Hawaii, alluvial channels can be overhung by riparian forest, since they are usually bordered by gentle to moderate slopes. In the Society Islands and the Marquesas Islands, however, valley sides are steeper, and alluvial rivers are normally wide open to full sunlight. In Tahiti, such sunlit rivers are the preferred habitat of the black fly *Simulium tahitiense* (Craig et al. 2001).



Figure 4. Fautaua Cascade, Tahiti, at low flow. Regular layers of lava basalt can be seen on the lower vertical rock wall. Lateral springs, arising from between basalt layers, are high in the upper right (not in view). Photograph: Douglas A. Craig.

Present-day alluvial-filled valleys were probably produced during the last ice age, when sea levels were depressed 120 m (Voris 2000) and seaward valleys were deeply eroded. As the sea rose to modern levels, the valleys backfilled with alluvium. During the ice age, the length of valleys and rivers extended (Voris 2000) and formed networks no longer in existence. Tahiti consists of two parts (figure 1), the larger Tahiti-nui and the smaller Tahiti-iti, presently connected by a low isthmus at Taravao with no running water. In the last ice age, the two parts would most likely have been better connected, probably by contiguous streams. Joined streams, now separated, might be of biogeographical significance to the distribution of black flies in Tahiti (Joy et al. 2003). Farther west, the islands of Raiatea and Tahaa, now barely separated by a shallow lagoon (figure 2), were probably connected by land and by contiguous streams.

Full development of vegetation and soil with concomitant retention of water is important for reasons other than simply providing water for upper and middle stream reaches. Seepage over bedrock, covered with mosses, ferns, and other vegetation, forms habitats referred to by Craig and colleagues (2001) as “grottos” (figure 8). These are very specialized habitats for the *castaneum* species-group of black flies in Tahiti (Craig and Currie 1999), the larvae of which prefer thin films of flowing water.

In Tahiti, another important and specialized habitat depends on the development of cascades (figures 4, 5). The regular outbursts of volcanism that took place on average every 2000 years, between 1.3 million and 0.6 million years ago (Duncan et al. 1994), produced stacked layers of lava, very noticeable at places such as the Fautaua Cascade (figure 4) and the Trois Cascades (figure 5). Unconformities, or junctions, between the basalt layers, when exposed on the cascade face,



Figure 5. The first of the Trois Cascades, Fareteuira Valley, Tahiti, showing the lower one-third with very low flow. Here, regular layers of basalt show poorly on the rock face, but springs from between layers can be seen high on the right. Such springs produce thin films of water with very constant flow (see figure 9). Photograph: Douglas A. Craig.

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Figure 6. Upper Viriviriterai River, a main tributary of the Papanoo River. The vertical wall of the Papanoo caldera below Mount Urufa (altitude 1493 meters) is immediately above the background. Photograph: Douglas A. Craig.

almost always produce springs to the side and high up the cascade (figure 5). Water from such springs flows down the vertical rock face of the cascade as a thin film of water (about 2 to 10 mm in depth) and is known as *madicolous flow*. Unlike the discharge in the cascade proper, which can vary markedly, discharge from the springs varies little; hence, the madicolous flow is very stable. Such flows are the preferred specialized habitat for species such as *Simulium catartarum*, rarely found elsewhere (figure 9; Craig and Currie 1999).

Erosion of overburden caused the collapse of the magma chamber of Tahiti about 0.87 million years ago (Menard 1986, Craig et al. 2001), producing a caldera opening to the north, from which the Papanoo River drains. This river, the largest on Tahiti, may represent the mature phase of running-water development in the Society Islands. Without the large drainage area of the caldera, a river of that size could not develop; therefore, it is likely that such large rivers are the most recent habitat on the island. This places an upper age on the

speciation of *S. tahitiense*, larvae of which are only found in such fully developed, sunlit rivers (Craig et al. 2001).

A characteristic of streams and rivers on volcanic islands is that they are of short length (Resh and de Szalay 1995). The Papanoo River, although of substantial discharge (maximum 2000 m³ per second), is only about 20 km long and only a fifth-order river. The walls of the caldera are vertical in places, but there is sufficient rainfall (up to 8000 mm per year; Craig et al. 2001) that even such vertical surfaces have running water (e.g., figure 10). Thence the water gathers quickly into small cascades, then into tributary streams and small rivers with steep slopes (figure 6).

In the lower reaches of the Papanoo Valley, the river, now at least 60 m wide, has a well-developed meander pattern. That pattern is, however, constrained in places by the valley walls. In these lower reaches the valley, with a broad gravel floodplain, is sufficiently wide (300+ m) that the riparian vegetation does not influence the running water overall. Such large rivers, including the Punaruu (figure 11) on the western side of Tahiti-nui and the Vaitepiha and Tirahi Rivers on the smaller Tahiti-iti, were probably not historically much larger, having at present their maximum catchment area. Further erosion in the future can only decrease the catchment.

As an island further ages and erodes, its altitude is lowered and its surface area reduced (Menard 1986). Hence, rivers senesce, as on Mooréa (1.5 million years of age). Although this island has mature rivers (e.g., Opunohu) with upper cascades, middle reaches, and meandering alluvial regions, their discharges are lower than in Tahiti, because the catchment is reduced (ORSTOM 1993). Huahine (2.7 million years of age), farther to the west, which is markedly eroded, has streams that are all small (about 1 m wide). Raiatea (2.6 million years of age), the second largest of the Society Islands, although one-tenth the area of Tahiti (figure 2), still maintains considerable altitude, but its running water habitat diversity is reduced. At high altitude (1017 m) on the Temehanirahi Plateau, groundwater draining from the weathered original volcano surface produces shallow sheets of water that coalesce within meters to form small streams (Spironello and Brooks 2003), feeding cascades that plunge immediately down to sea level at the narrow coastal plain. With its considerable altitude, Raiatea produces its own weather, and it rains along the mountain ridge of the island on most days during the wet season. This frequent rainfall keeps some cascades flowing that would otherwise be dry (figure 10). There are a few small rivers (about 5 to 6 m wide), none longer than 5 km. Probably because the island has subsided so far into the sea, the alluvial seaward portions of these rivers are heavily influenced by the sea and are more estuarine than not. This situation on Raiatea presages the eventual fate of a Society Islands stream. Such is seen on Bora Bora (3.5 million years of age), which has little of the original volcano left, albeit with steep topography. Here, the largest stream, the Faanui, about 0.3 m in width, has only a small flow of water in a series of pools and low drops (figure 12). During drier periods the stream is intermittent, but

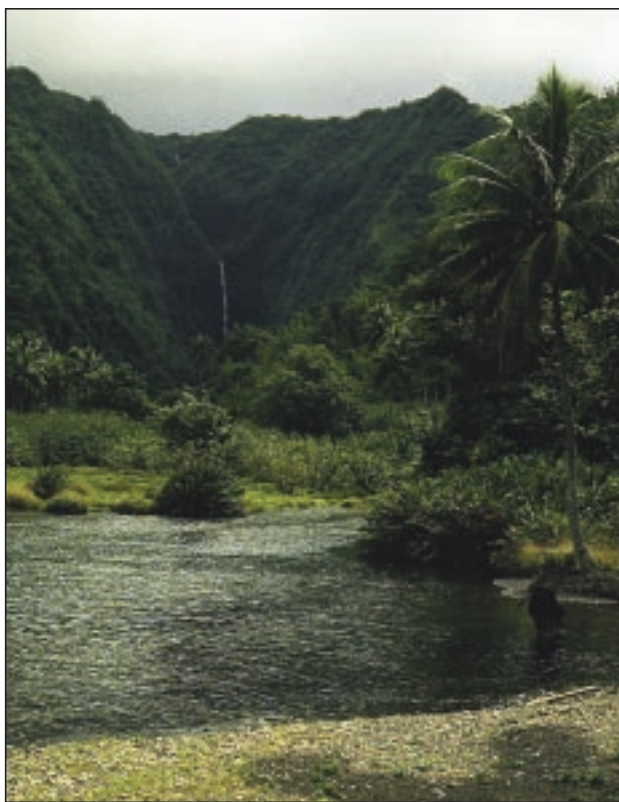


Figure 7. Utuofai River, Tahiti, from sea level, showing an alluvium-filled valley below the cascade. Photograph: Douglas A. Craig.

it still maintains one species of black fly, *Simulium malardei* (Craig 1997).

Bora Bora is probably at the lower limit of size and altitude to produce running water, and by itself it might not be able to do so. But, positioned only 40 km northwest of Tahaa and Raiatea, Bora Bora captures storm clouds, and hence rain, from the downwind wake caused by easterly trade winds blowing over those first two islands (figure 2). Such a downwind wake is well known for the Hawaiian Islands (Xie et al. 2001). On smaller older islands, such as Maupiti (4.4 million years of age; figures 1, 2) and Manuae (6.8 million years of age) farther northwest, the lack of catchment area and altitude precludes running water—the islands are now too eroded. This sequence is in full agreement with Haynes (1990), who showed a close correlation between island area, height, and available freshwater habitat.

The Marquesas Islands, some 1500 km to the northeast of Tahiti, have a range of ages similar to that of the Society Islands, but they do not form such a simple lineament of islands (Craig et al. 2001). Rivers and streams there, however, follow the scheme for the Society Islands closely. The Marquesas Islands receive less than half the rainfall of the Society Islands (ORSTOM 1993). In comparison with the Society Islands, they are large for their age, not having eroded as rapidly, again in general agreement with Menard (1986). Most streams in the Marquesas are smaller and at



Figure 8. Surface water seepages produce specialized running water habitats—here, a grotto in the Vaitamanu Valley, Tahiti. Such habitats have more species of black fly than any other in Tahiti. Photograph: Douglas A. Craig.

most only a few meters wide; they are densely shaded, but with enough flow to produce a pool-riffle sequence. Small cascades (e.g., figure 7) are numerous, but larger ones (e.g., figure 4) are few. The occasional large river (e.g., Taipivai on Nuku Hiva, with a bankfull width greater than 15 m) can be considered mature, but none have discharges approaching those of larger Tahitian rivers.

In Rurutu, one of the Austral Islands, some 600 km south of Tahiti (figure 1), cascades have been eroded away, and now water flows over small smooth chutes into hard rock pools (figure 13). Such water flows are indicative of old age; Rurutu (0.3 million to 12.8 million years of age) has a complex geological history, having been raised above sea level after full subsidence. Like the streams in Bora Bora, these waters support a single species of black fly. The island of Tubuai (10.6 million years of age), east of Rurutu, which lacks

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Figure 9. A thin film of water (madicolous flow) on a vertical rock face is the preferred specialized habitat of the black fly *Simulium cataractarum*, whose larvae can be seen in the middle. They attach by their posterior end and use head fans to capture food particles from the water flow. Arrow indicates direction of flow. Scale bar = 5.0 millimeters. Photograph: Douglas A. Craig.

black flies, has never been below sea level. Streams on Tubuai are few, less than a meter across; they lack any chutes and are densely shaded, superficially reminiscent of the original state of streams (figure 3) but with a lower slope of bed. Farther east of Tubuai are the high islands of Raivavae (6.5 million years of age) and Rapa (5.0 million years of age). Neither of these islands has black flies (Englund 2003), but both have running water habitats reminiscent of those in Bora Bora, Tahaa, and Huahine. Black flies appear not yet to have reached these islands.

Water quality characteristics

With heavy rainfall and rapid runoff, water in the high Society Islands (Tahiti, Mooréa, and Raiatea) is pure. The



Figure 10. Western face of Mount Tefatua (1017 meters in altitude), Raiatea, showing the Eereo Cascades immediately after a torrential rainfall. Within hours most of these cascades are reduced to trickles and are normally dry. Those that do maintain a flow are the habitats for *Simulium castaneum*, a species closely related to *Simulium cataractarum*, the larvae of which inhabit cascades in Tahiti. Photograph: Douglas A. Craig.

conductivity of the water is low; Resh and colleagues (1990) reported a measurement of 30 microsiemens (μS) for a cascade in Mooréa. Higher conductivity (250 μS), however, has been recorded in Tahiti at the Maroto River, an upper tributary of the Papanoo River, deep in the caldera and influenced by the input of sulfurous water from springs (Craig 1997). With little dissolved material in the water, buffering is low, and pH measurements tend to show a diurnal pattern, influenced by carbon dioxide uptake by mosses and algae during photosynthesis. In that process, carbon dioxide is taken out of the water and is replaced by hydroxyl ions, raising the pH (Ruttner 1974). As noted by Resh and de Szalay (1995), high pH may indicate high primary productivity of aquatic vegetation. In a 24-hour study (Craig 1997) at the Trois



Figure 11. *The Punaruu River, Tahiti (shown in 1974) is a mature river with meanders and a small floodplain. Such fully sunlit habitats with very fast water flow are the preferred habitat of larvae of the black fly *Simulium tahitiense*. This river is now fully used for human activity and flows to the sea only after heavy rain. Photograph: Douglas A. Craig.*

Cascades, Tahiti (figure 5), the pH dropped from 9.0 to 7.8 between sunset and sunrise, rising rapidly to 9.3 during daylight hours (6:00 a.m. to 6:00 p.m.) as mosses and algae on the cascade face began photosynthesis. The highest pH reading (10.2) taken in the Society Islands was at the Afareiatu Cascade, Mooréa. In all such instances, high pH was associated with a thin film of water flowing over moss and algae on a rock face in full sunlight. Conductivity showed the reverse pattern, dropping from 117 μ S to 77 μ S during the rapid increase in pH values, presumably as ions in the water were absorbed for metabolism associated with photosynthesis. Particulate material, or seston (mainly diatoms), larger than 0.45 micrometers in diameter was at a maximum of 27 milligrams (mg) per liter (L) at 1:00 p.m., dropping to 6.3 mg per L at 3:00 a.m. and then rising again during daylight.

In general, pH measurements in Polynesia are alkaline and conductivity is low. In Hawaii, while conductivity is similarly low, pH tends to be slightly acidic (Resh and de Szalay 1995), perhaps indicating the influence of a different type of underlying basalt or, as suggested by Resh and de Szalay (1995), a measure of higher primary productivity in Polynesian running-water systems.

Resh and colleagues (1990) reported 2.6 mg per L of seston (mainly diatoms) at a headwater cascade in Mooréa, with the concentration decreasing rapidly within 2.5 km of the cascade to 0.5 mg per L in the middle reaches of the stream. Craig (1987) noted order-of-magnitude differences in seston richness between cascades and rivers. Although not quantified, seston in the middle reaches of streams and rivers



Figure 12. *The Faanui Stream in Bora Bora is the end of the road for running water in the Society Islands. This stream, while intermittent, supports larvae of a single black fly species, *Simulium malardei*, a habitat generalist that is widespread in the Society Islands. On this island there are no habitats remaining for habitat-specialized black fly species. Photograph: Douglas A. Craig.*

was mainly snail feces and undetermined fine material, a marked change in quality from seston in the cascades.

Black fly larvae are not known to be sensitive to variations in the pH, ionic composition, or conductivity of water (Crosskey 1990), but the quality of food is known to have a positive influence on growth (Thompson 1987). Further, rapidly assimilated food such as diatoms is known to determine the abundance of simuliid larvae (Martin and Edman 1993). Therefore, it has been assumed that high productivity of the aquatic vegetation on the cascades is significant for the evolution of the reduced larval head fans of cascade-dwelling species (Palmer and Craig 2000).

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Figure 13. A rocky chute, part of Vaipapa Stream (Rurutu, Austral Islands), represents the remnant of a cascade. Larvae of the single black fly species on this island occur in vast numbers on leaves stuck in the thin flow of water over the rock (center of photograph). Photograph: Douglas A. Craig.

Biological components of running water

Black flies are the best studied of any aquatic insect in Polynesia. Next best known are perhaps the dragonflies and damselflies (Polhemus et al. 2000, Englund 2003). Other aquatic organisms, though cataloged (Fossati and Marquet 1998), are less well studied.

Macroinvertebrate fauna. Streams and rivers of Polynesia have low diversity of macroinvertebrate fauna in comparison with most continental running waters (Resh and de Szalay 1995). Of the aquatic insects, mayflies, stoneflies, and caddisflies are absent. Larvae of midges are common, as are those of ephydrid flies—the latter, in particular, on cascades. Dragonfly and damselfly nymphs are not uncommon and often, surprisingly, occur in fast water. Black fly larvae dominate and can occur in astronomical numbers in some

situations. Of other arthropods, freshwater shrimp are very common and are found in all running water habitats, with *Atya* species dominating the upper courses and *Macrobrachium* species dominating the middle and lower reaches. Freshwater crabs are also sometimes observed (again, surprisingly) on cascades. Mites occur in all habitats but at low frequency. Of nonarthropods, snails (e.g., *Clithon*, *Neritina*) are ubiquitous. The Society Islands have the greatest diversity of macroinvertebrates of all the French Polynesian islands, followed by the Marquesas Islands and then the Austral Islands (Fossati and Marquet 1998). The lowest diversity known for running water invertebrates is on Rurutu. Absolutely nothing other than nymphs of dragonflies, damselflies, and black fly larvae were collected there in 2000 (Craig 2001). But black fly larvae densely covered every leaf in high-velocity water (figure 13).

Black flies. Black fly larvae require running water. Hatching from eggs laid on the substrate by the female adult, larvae attach their posterior end to a solid surface such as the bedrock, or roots and leaves, using a ring of hooks to hang onto a pad of salivary silk. The larva uses two elegant head fans consisting of numerous fine rays to filter particulate food material from the water flowing past (figures 14, 15). In Tahiti, the larvae of some black fly species have adapted to very specialized habitats. The more generalized larvae (e.g., *S. malardei*) that have fully developed head fans, as seen in figure 14, are found in smaller streams attached to grass and leaves. However, one species, *S. tahitiense*, while possessing generalized head fans, inhabits deep, very fast water of larger sunlit rivers such as the Punaruu (figure 11). The only obvious modifications for such an extreme habitat are an enlarged posterior abdomen and adaptive behavior in which the larvae form aggregations (figure 16). The function of the enlarged abdomen is not known, but the aggregation protects larvae from the full force of the current by producing skimming flow over the top of the group (Nowell and Jumars 1984). In contrast, larvae that prefer cascades, such as those of *S. cataractarum*, have smooth amphora-shaped bodies and a reduced number of fan rays (figure 15) and are typically evenly spaced on the substrate (figure 9).

Body shape and spacing are known to be used by black fly larvae to manipulate flow through the head fans (Chance and Craig 1986). Black fly larvae are known also to manipulate and maintain the amount of water flow through the fans, and hence the amount of food ingested, as flow conditions vary (Lacoursière and Craig 1993). Furthermore, the number of fan rays can vary among larvae developing under conditions of variable water velocity and amount of food (Zhang and Malmqvist 1997, Lucas and Hunter 1999). In Tahiti, water from cascades can have an order of magnitude more suspended food material than can water from streams and rivers (Craig 1987). Hence, it has been assumed (Craig 1987, Palmer and Craig 2000) that reduction in the number of larval fan rays of cascade-dwelling species, such as *Simulium clibanarium* (figure 17) and others, relates to

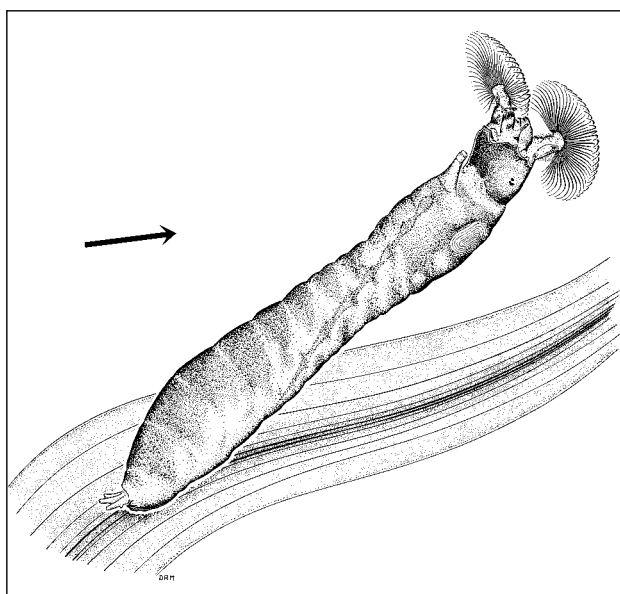


Figure 14. Drawing of a typical black fly larva. The posterior abdomen is attached to the substrate, here a grass blade, by means of a ring of hooks locked into a pad of salivary silk that the larva has deposited. The body is twisted lengthways to bring the head fans up into the water flow. The fans filter and capture particulate food material suspended in the water flowing past. The arrow shows the direction of the flow. Drawing courtesy of David Madison.

the high velocity and rich food of those habitats. Such species, although they can filter-feed, also browse the substrate; that practice is carried to an extreme in a small group of species that have almost completely reduced the head fans and live entirely by browsing. Not surprisingly, species with reduced larval head fans are essentially restricted to cascades. In general, for black fly larvae in the Society Islands, there is a close relationship between body shape, head fan structure, and habitat requirements.

Biogeographic considerations

Using morphological data, Craig and Currie (1999) attempted the first comprehensive phylogenetic analysis of Polynesian black flies, followed by another analysis with further information (Craig et al. 2001). These reconstructed phylogenies can be considered robust, because there was close concordance between them and other phylogenies, based on molecular data, by Joy (2001) and Joy and Conn (2001). In brief, two species from Micronesia evolved earliest of all species in *Inseliellum*. A distinct group that included species from Rarotonga (Cook Islands), Rurutu (Austral Islands), and the Marquesas Islands was next to evolve. *Simulium malardei* was ancestral to all species that occur in the Society Islands. The next species was *Simulium lotii*. Both these species occur only in the Society Islands and are widespread.

Using the reconstructed phylogeny, Craig and colleagues (2001) proposed a historical biogeography of *Inseliellum*.



Figure 15. A single larva of the black fly *Simulium cataractarum* in a smooth-flow trickle of water off moss hanging from a vertical rock face. The food sources here, mainly diatoms and moss spores, are quite rich. This larva has caught a fecal pellet from larvae in the flow above (see head fan on the right). Probably because of the rich food available, larvae of this species have a reduced number of fan rays, easily seen here. This is the most minimal habitat known for black fly larvae. The arrow indicates the direction of the flow; m/s = meters per second. Scale bar = 1.0 millimeters. Photograph courtesy of Simon Pollard.

They concluded that almost all species known from the Society Islands arose on Tahiti and that there was back dispersal of the highly modified cascade-dwelling species northwest to Mooréa and Raiatea. It was not possible, however, for Craig and colleagues to determine the direction of dispersal for the two widespread basal species, *S. malardei* and *S. lotii*. Such back dispersal, from younger to older islands, is well known for some biota of the Hawaiian Islands (e.g., Wagner

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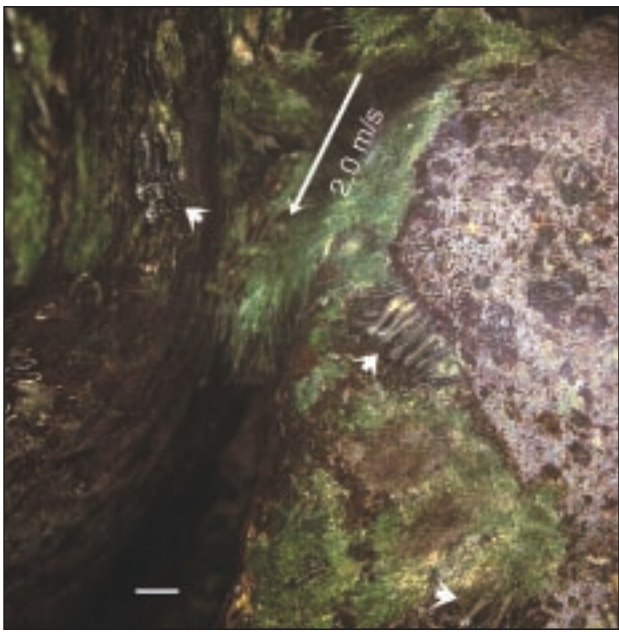


Figure 16. Underwater photograph of larvae of the black fly *Simulium tahitiense*, which prefers large, deep, fast-flowing, sunlit rivers. The velocity of the water is such that algae are scoured off rocks in unprotected areas. Note how the larvae (at the arrowheads) are clumped together for protection and located just out of the main flow. The arrow indicates the direction of the flow; m/s = meters per second. Scale bar = 5.0 millimeters. Photograph courtesy of Simon Pollard.

and Funk 1995). Colonizing organisms do not always disperse along an island chain from older to younger islands, as might be assumed.

The island biogeography theory of MacArthur and Wilson (1963, 1967) is a major hypothesis of dispersal, colonization, and evolution of island biota. The model predicts that the number of species on an island increases with new colonization but decreases through extinction. Equilibrium is reached when arrivals equal extinctions. The model predicts that species richness is influenced by distance from the species' source and by island area. That is, larger islands with more habitats available have fewer extinctions and therefore are more speciose than small islands. Islands near the source of animal and plant species are more heavily colonized and therefore more speciose than more distant islands.

MacArthur and Wilson (1963) hypothesized that "radiation zones" of adaptive radiation within an island are a major contributor to species richness and that this contribution may be greater on islands far from the source. Their rationale was that colonization to a far island, although rare, would allow colonists to be less influenced by gene flow from parental populations, which would hinder speciation. In an examination of the MacArthur and Wilson model, Heaney (2000) developed a series of phylogenetic predictions that Philippine islands close to a colonizing source would not show as much speciation of murid rodents as islands farther

removed. Similarly, Losos and Schluter (2000) showed that intra-island speciation rather than colonization was the primary source of new species of lizards on larger Caribbean islands.

MacArthur and Wilson's biogeographic model and radiation zone hypothesis were not invoked by Craig and colleagues (2001) in their biogeography of Polynesian black flies, although these black flies conform well to those basic models (Spironello and Brooks 2003). Larger islands such as Tahiti are more speciose (29 species) than smaller islands such as Mooréa (10 species). The more distant islands of Huahine and Bora Bora have two and one species, respectively. Mooréa, presumably close enough to Tahiti to be influenced by gene flow from that source island, has not undergone an intra-island species radiation, and it has only one endemic species, which is poorly known (Craig and Joy 2000). Raiatea, the second largest of the Society Islands, which is well removed from Tahiti, has undergone a moderate intra-island species radiation (four endemic species) but is close enough to Tahiti for some colonization (three species) (figure 2).

For the Society Islands, however, the size of an island is well correlated with its distance and age (figure 2), and older islands, because of their small size, do not have specialized running water habitat. Hence, there is no opportunity for species radiation into such habitats, nor are those habitats available for colonists requiring specialized conditions. Indeed, *S. malardei*, the one species that is widespread on all of the Society Islands with running water (Tahiti, Mooréa, Huahine, Raiatea, Tahaa, Bora Bora; figure 1), is a habitat generalist found in all running waters on Tahiti but most commonly in small shaded streams similar to those on smaller islands. *Simulium lotii*, although also widespread and a generalist, does not occur on Bora Bora.

The distribution of these two species, phylogenetically basal to all other Polynesian black flies, presented Craig and colleagues (2001) with the problem that direction of colonization along the Society Islands could not be determined. One assumption could be that basal species moved eastward along the Society Islands from older to younger islands, but the phylogeny does not support that idea. The molecular analysis by Joy (2001) on *Inseliellum* did not address that problem directly. That analysis and other molecular work (Craig et al. 2001, Joy et al. 2003), however, indicate that *Simulium oviceps*, a species with markedly reduced head fans (e.g., figure 17), is 1.8 million to 2.0 million years of age, significantly older than Tahiti. Hence, although the reconstructed phylogeny of Polynesian black flies (Craig et al. 2001) strictly indicates that *S. oviceps* arose in Tahiti, it more likely evolved on an older island such as Raiatea, where it does occur.

If such molecular evidence is correct, the phylogenetic and biogeographic history of Polynesian black flies was much more complex than currently indicated (Craig et al. 2001). MacArthur and Wilson's model explicitly considers neither the geological history nor the phylogeny of island biota. Although the biogeography of black flies in the Society Islands

superficially agrees with that major biogeographic model, the model ignores important historical aspects. This problem has been discussed in detail by Lomolino (2000) and others.

Evolution of the cascade-dwelling species may have taken place on the now-older islands such as Bora Bora, with remnants (e.g., *Simulium castaneum*, *S. oviceps*) still left in Raiatea, with those lineages undergoing major species radiations in Tahiti. Extinctions of these habitat-specialized species, and others, on the older islands were probably forced by erosion of the islands with concomitant loss of running water habitats. Tahiti is the largest island at present (figure 2), with a plethora of running water habitats; however, its diversity may simply be a temporary result of the latest intra-island species radiation. As Tahiti ages and erodes away, it can be assumed that it too will lose species to extinction, with the now hotspot island of Mehetia, if it becomes larger and develops running water, undergoing its own blackfly species radiation.

Life for a running water organism on a Polynesian hotspot island is a tenuous affair. Some 4 million to 6 million years after arrival on a new hotspot island, with erosion by water, subsidence, and rafting some 500 km to the northwest, the island and its organisms will be gone (figure 2).

Conservation of Polynesian black flies?

To those familiar with the torment of the biting of female black flies, any thought of conservation of these insects seems counterintuitive. But the current state of knowledge of Polynesian islands and their black flies provides a fine system for examining evolution of insular aquatic insects. Spironello and colleagues (2002) and Joy and colleagues (2003) have used chromosomal and molecular analysis, respectively, to examine evolution and biogeography of some species of black flies in the Society Islands. Very recently, Spironello and Brooks (2003) examined the macroevolutionary implications of MacArthur and Wilson's model, using *Inseliellum*. Conservation of running water habitats on these islands, therefore, is of scientific importance. On many islands of Polynesia, human activities are having a detrimental effect on streams and rivers (Polhemus et al. 2000, Craig 2001). In the Marquesas Islands, almost every small stream has, at minimum, a pipe removing water, and most streams have a small dam or barrage to collect and divert flow. In Nuku Hiva, road building above the town of Taiohae is causing noticeable sedimentation in streams in the valley. In Rurutu, of the Austral Islands, water is a limiting factor for human activity; during dry periods almost all running water is collected for human use, and at such times little, or none, flows to the sea. Tahiti is perhaps the island most seriously affected by human activities (Craig 1997). There, to provide for increasing use of electricity, the Papanoo and Vaihiria river catchments have been markedly altered by hydroelectric dams and pipes. Indeed, much of the middle reach of the Papanoo River has been piped to produce electricity, and the type localities for *S. tahitiense* and *S. oviceps* have been destroyed, albeit these species are common in other rivers. The Punaruu River



Figure 17. Head of the larva of *Simulium clibanarium* showing the markedly reduced head fans. This species inhabits only cascades, and while the larvae can filter-feed, they normally browse the substrate. Scale bar = 0.25 millimeters.

(figure 11) is totally piped for industrial and potable use, and it flows to the sea only after heavy rainfall. But, with its multitude of running water systems, Tahiti still has many pristine habitats, and on Tahiti-iti the Vaitepiha River and its catchment are little altered.

Further research

There is much left undone in regard to black flies and the running water systems of Polynesia. Virtually nothing is known about black fly biology, including generation times, mating behavior, and, importantly, the flight range of the females. The latter might provide insights into the rate of colonization between adjacent islands.

Elsewhere in the world, black fly larvae, when in large numbers, are known to reduce the amount of particulate material in flowing water (e.g., Morin 1988, Malmqvist et al. 2001). Do the large numbers of *S. catartarum* that occur on cascades have an influence on the rich seston in the macicolous flow and hence affect the seston suspended in the flow farther downstream? Such questions relate to the river continuum concept (RCC; Vannote et al. 1980). This model of continental flowing waters deals with the relationship between stream size, energy inputs, and ecosystem function (Allan 1995). The applicability of the RCC to Polynesian running water systems is moot. The only studies invoking the RCC in Polynesia are those of Resh and colleagues (1990, 1992), which showed that,

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while there is a superficial agreement with the RCC in the distribution of organisms in the stream, other mechanisms may be the root cause of that distribution. The main problem in relating the RCC to Polynesian streams and rivers is the absence of leaf-shredding macroinvertebrates integral to RCC processes. In the absence of such invertebrates, how do leaves in Polynesian streams and rivers break down?

With their diversity of running water habitats, both pristine and altered, the Society Islands provide a fine template for examination of broader questions regarding the diverse processes that link aquatic communities along a gradient (Malmqvist 2002). Unlike their continental counterparts, island riverine systems have steeper environmental gradients and simpler biotic communities, examination of which might give insights into the processes that inexorably link communities within and along running water systems (Fisher 1997).

While the black flies of the Society Islands are taxonomically well known, and while their distribution can be related to biogeographic models and to the geological process associated with linear hotspot volcanic islands, the situation for black flies in the Marquesas Islands is less well understood. The southern Marquesas Islands, such as Fatu Hiva, have not been well sampled for black flies. Furthermore, the Marquesan black flies represent an earlier lineage of *Inseliellum* separate from those of the Society Islands (Craig et al. 2001). There has not been a radiation into specialized habitats, as in the Society Islands, and the larvae of most species are habitat generalists. Molecular and chromosomal examination might clarify the historical biogeography of the Marquesas black flies.

A fundamental question to be further examined is the origin of Polynesian black flies. Craig and Currie (1999) were of the opinion that Polynesian black flies were related to a black fly subgenus (*Nevermannia*) in Southeast Asia and New Caledonia, but Joy and Conn (2001) have molecular evidence that indicates a closer relationship to an endemic subgenus (*Hebridosimulium*) in Fiji and Vanuatu, a surprising observation considering that the two most basal species of *Inseliellum* are in Micronesia. Part of such a question concerns the mechanisms of dispersal over vast distance in the Pacific Ocean. Wind-assisted dispersal of up to 400 km is known for some adult black flies (Crosskey 1990), but that would only allow interisland colonization within an archipelago. Some of the adult female Marquesan black flies bite birds, so dispersal by birds cannot be discounted, even though there are no substantiated examples of this form of black fly dispersal (Craig et al. 2001). Of all the questions yet unanswered for Polynesian black flies, that of how such small flies manage to traverse such vast distances is perhaps the most intriguing.

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