Impacts of Human Disturbances on Biotic Communities in Hawaiian Streams

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Streams throughout the tropics have been altered by water diversion, channel modification, introduced species, and water quality degradation. The Hawaiian Islands, with watersheds ranging from the relatively pristine to the highly degraded, offer an opportunity to examine the impacts of human disturbance on native stream communities. For example, urbanization is often accompanied by stream-channel modification and reduced canopy cover, resulting in higher water temperatures and greater fluctuations in daily temperature. Even in relatively pristine watersheds, stream diversions can result in decreased flow velocity and water depth, reducing habitat availability. Dewatering of stream reaches can also inhibit downstream dispersal of larvae and upstream migration of juveniles and adults of native species. Many nonnative aquatic species are better adapted than native species to degraded habitats; once established in these habitats, they can cause further reduction in native populations through competition, predation, and the introduction of parasites or diseases. Understanding the relationship between habitat alteration and aquatic community structure is critical for developing sound management strategies.

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tream habitats on tropical islands are undergoing substantial alteration as human population increases and watersheds become far different from those that once sustained native stream communities. Effects of habitat alteration can occur simultaneously at different scales, such as landscape (watershed), stream reach, and microhabitat. For example, urbanization (a landscape-scale process) is typically accompanied by channelization and the removal of riparian canopy cover (a reach-scale process), resulting in higher water temperatures, increased daily temperature fluctuations, increased siltation, and decreased substrate size (microhabitat-scale processes). Even in relatively pristine watersheds not yet affected directly by modern urban development, stream diversions can result in reduced flow velocity and water depth, thereby changing habitat conditions and potentially reducing habitat availability. Dewatering of stream reaches can also inhibit downstream dispersal of larvae and upstream migration of postlarvae, which are critical to the life cycles of many native species. Nonnative generalist species are typically better adapted than native species to degraded habitats; once established in these habitats, they can cause further reduction in native populations directly and indirectly through competition, predation, and the introduction of parasites and diseases.

With continuing development of tropical island ecosystems, the potential for watershed modification remains substantial. Understanding the relationship between habitat alteration and aquatic community structure is critical for developing sound management strategies. The Hawaiian Islands, with watersheds ranging from the relatively pristine to the highly degraded, offer an opportunity to examine the impacts of different types of habitat alteration on native stream communities. These islands also serve as an example of what may eventually happen in other tropical island systems that have yet to experience the level of human impact that has occurred in Hawaii.

Hawaii is the most isolated island archipelago in the world, located 4000 kilometers from the nearest continent. Historically, the isolation of the Hawaiian archipelago prevented large-scale colonization of stream systems because of the limited dispersal mechanisms of most freshwater species; consequently, most native stream species most likely derived from those that arrived from the ocean. This has resulted in a native stream fauna that consists of relatively few species (see Font 2003). For example, there are no native

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representatives of the widespread insect orders Ephemeroptera (mayflies), Plecoptera (stoneflies), or Trichoptera (caddisflies) (Howarth and Polhemus 1991). However, as discussed below, the native fauna that does occupy Hawaiian streams is highly endemic and unique. For example, of the five native fish species, each is from a separate genus (Kinzie 1990, McDowall 2003), and the damselflies (Odonata) have radiated from a single ancestor to form 26 separate species within the genus *Megalagrion* (Polhemus and Asquith 1996).

Climate characteristics of a tropical ecosystem

The climate of Hawaii is characterized by mild temperatures, which vary little between seasons. The small temperature difference between the warmest and coolest months is largely attributable to the influence of the surrounding ocean, the persistence of cool trade winds, and the small seasonal variation in solar radiation (Sanderson 1993, Oki and Brasher 2003). Daylight hours also change little from season to season. The length of the longest day and the shortest day of the year varies by only 2 hours and 34 minutes. This lack of seasonality in temperature and day length is reflected in the reduction of seasonality in the invertebrate life cycles in Hawaiian streams, compared with similar life cycles in many temperate continental streams (Kondratieff et al. 1997, Wolff 2000). For example, species that reproduce only once each spring in temperate streams may reproduce repeatedly throughout the year in Hawaii.

Watershed characteristics of an island ecosystem

Drainage basins in Hawaii are small compared with continental watersheds, and the streams are "flashy" in nature, responding rapidly to storm rainfall (Craig 2003). In addition, streamflow characteristics are highly variable, both spatially and temporally. A rainy season occurs in Hawaii from October through April, and a dry season from May through September; however, rains and storm flows can occur throughout the year (Oki and Brasher 2003). Hawaiian streams are flashy because of high-intensity rainfall, small drainage basins, steep basin and stream slopes, and little channel storage. Stream stage can rise and fall several feet over a few hours in response to rainfall (Oki and Brasher 2003). Native stream species in Hawaii (and in other tropical island systems) are adapted to these flashy conditions (McDowall 1995), while introduced species are typically unable to withstand such flow regimes.

Highly specialized native stream fauna

The native Hawaiian freshwater fish fauna consists of one indigenous (native to Hawaii and elsewhere) goby, *Awaous guamensis* (oopu nakea); one endemic (occurring only in Hawaii) eleotrid, *Eleotris sandwicensis* (oopu akupa); and three endemic gobies, *Lentipes concolor* (oopu alamoo), *Sicyopterus stimpsoni* (oopu nopili), and *Stenogobius hawaiiensis* (oopu naniha) (Kinzie 1990). The native stream fauna is well adapted to the flashy nature of Hawaiian streams and the steep topography of the watersheds. All of the native gobies have

fused pelvic fins, allowing them to cling to the substrate during torrential flows and to climb steep waterfalls (Ford and Kinzie 1982).

Native crustaceans occurring in Hawaiian streams include the mountain shrimp *Atyoida bisulcata* (opae kalaole) and the estuarine prawn *Macrobrachium grandimanus* (opae oehaa). Native gastropods (snails) in Hawaiian streams include the limpetlike *Neritina granosa* (hihiwai), the estuarine *Theodoxus vespertinus* (hapawai), and snails in the family Lymnaeidae. The latter are present in some streams and, more frequently, along stream banks and in adjacent springs and seeps.

Native stream fishes (gobies) and the larger crustaceans and mollusks in Hawaii derived from stream species elsewhere in the Indo-Pacific, which in turn originally derived from marine species. These Hawaiian species have retained an oceanic larval life stage (McDowall 2003). In this type of diadromy (where part of the life cycle is spent in the stream and part in the ocean), called amphidromy, the adult life is spent in streams, and larval periods are spent as marine or estuarine zooplankton (Ford and Kinzie 1982, Kinzie 1988, McDowall 1988). Adults of these amphidromous species all reproduce in upstream habitats, and the larvae drift downstream into estuaries or the ocean, eventually returning to the stream as bottom-dwelling postlarvae and migrating upstream to grow and reproduce (Kinzie 1990, 1993). Such communities in island streams generally appear to be structured by the species' differing abilities for colonization and upstream migration (Lyons and Schneider 1990) as well as the unpredictable recruitment (successful return to a stream) of larvae (Kinzie 1988). A critical feature of the amphidromous life cycle is the need for unimpeded access to and from the ocean for downstream dispersal of larvae and upstream migration of postlarvae (Resh et al. 1992, McDowall 1995, Brasher 1996, Benstead et al. 1999, Fievet 2000, McIntosh et al. 2002).

Amphidromous species spawn in the stream and, with the possible exception of the goby A. guamensis (Ego 1956, Kinzie 1990, Ha and Kinzie 1996), there is little evidence that the adults make a downstream migration to spawn. When the newly hatched larvae drift downstream, they remain in the water column by alternately swimming upward and passively sinking back down as they are carried toward the sea (Bell and Brown 1995, Lindstrom 1998). Larvae spend from 1 to 5 months as oceanic plankton before returning to freshwater (Radtke and Kinzie 1987, Radtke et al. 1988, 2001, Bell and Brown 1995, Bell et al. 1995, Benstead et al. 1999). Although initially there was local phyletic evolution to produce the four Hawaiian endemic goby species, there has apparently been no local radiation to produce single-island endemics across the archipelago (McDowall 2003). Studies on some of the Hawaiian amphidromous gobies indicate that adult populations are genetically undifferentiated throughout their range, that recruitment is from a well-mixed pool of larvae, and that larvae do not return to the stream where they were born (Fitzsimons et al. 1990). Once in the stream,

different species of gobies have been shown to have distinct habitat preferences and may exhibit a longitudinal separation along the stream gradient (Kinzie 1988, Nishimoto and Kuamoo 1991, Fitzsimons et al. 1993, Brasher 1996, 1997).

Abundant introduced species in Hawaiian streams

Today more than 50 species of introduced fish, invertebrates, reptiles, amphibians, and aquatic plants are established in streams and reservoirs in Hawaii (Yamamoto and Tagawa 2000). For mollusks alone, 22 freshwater snails and slugs have been introduced to the Hawaiian Islands (Cowie 1997), and 12 are known to be established (Cowie 1998). Many of the nonnative species were intentionally released because they were expected to be beneficial; others were simply dumped into streams with little consideration of the consequences (Yamamoto and Tagawa 2000). Introductions of larger aquatic organisms, such as fish, into Hawaiian streams occurred in four waves (as summarized in Maciolek 1984, Devick 1991, Eldredge 1992, Brown et al. 1999). A number of species were introduced before 1900, primarily as food, by immigrant workers from Asia. Between 1900 and World War II, mosquito control and recreation were the major reasons for fish introductions. From 1946 to 1961, numerous species were introduced for the control of aquatic plants, for aquaculture, as bait fish, and for recreational fishing. For example, the introduced Tahitian prawn (Macrobrachium lar) is present throughout the state; a popular food item, it was first released in Hawaii in 1956 and has since spread to every stream system (HCPSU 1990, Devick 1991). Most recently, numerous introductions have apparently resulted from amateur home aquarium owners releasing unwanted pets into streams and other aquatic environments. Introduced fish are often accompanied by smaller invertebrates and plants that become established in the system as well.

The impact of introduced species on aquatic ecosystems in Hawaii ranges from relatively benign to highly detrimental. Not only are the introduced species well suited for disturbed habitat conditions, some actually create such conditions. For example, introduced catfish and crayfish dig holes in stream banks, causing erosion and increasing water turbidity (Yamamoto and Tagawa 2000). Other species, such as smallmouth bass, introduced as a sport fish, are voracious predators that feed on native fish and shrimp (Yamamoto and Tagawa 2000). One introduced carnivorous snail (Euglandina rosea) actually dives underwater to prey on the native aquatic lymnaeid snails (Kinzie 1992). Many aquarium pets, such as the cichlids, are also very aggressive and predatory. Even seemingly innocuous species, such as guppies and mollies, are known to carry parasites that can infect native fishes (Bunkley-Williams and Williams 1994, Font and Tate 1994, Font 2003) and are prolific breeders that reproduce large numbers very rapidly (Yamamoto and Tagawa 2000).

Habitat alteration

Urbanization and streamflow diversion are two major sources of habitat alteration of watersheds in tropical island settings today. Examples of the impacts of these human-caused disturbances are common in the Hawaiian Islands and can provide information for implementing management strategies in less-developed areas where such habitat alterations are also becoming prevalent.

Urbanization. Honolulu, the capital city of Hawaii on the island of Oahu, is currently ranked the most densely populated city in the United States (Fulton et al. 2001). Associated with population growth and urbanization is an increase in the implementation of flood control projects and in the number of road crossings over streams and channels realigned around housing projects. Early forms of channel modifications on Oahu, during the 1930s to 1950s, were primarily the result of bridge building; they included clearing riparian vegetation, realigning channels, and reinforcing the altered banks (Norton et al. 1978, Timbol and Maciolek 1978). Subsequent channelization has generally been a result of flood control projects, with their straightened, concrete-lined channels (Hathaway 1978).

Artificially straightened stream reaches with concrete-lined, flat-bottomed channels and reinforced banks are now common in the urban areas of Oahu. Such modifications are often accompanied by a reduction in, or elimination of, substrate heterogeneity (through removal of large boulders) (Norton et al. 1978). Stream alterations can result in a wide, shallow, unshaded, and generally homogeneous stream reach (figure 1), a stark contrast to the steep, heavily vegetated, boulder-strewn reaches typical of the more pristine streams in forested areas of Hawaii (figure 2). Flat, concrete-lined channels provide no shelter for the benthic native organisms. The increased width and decreased depth associated with straightening and lining also can cause excessive solar heating (Timbol and Maciolek 1978, Shier 1998).

Stream water temperature on Oahu is associated with riparian vegetation characteristics, including canopy closure, canopy angle, and annual solar irradiation reaching the stream (Brasher et al. forthcoming). Cement-lined channels, lack of canopy cover, and reduced water depth act together to create higher water temperatures. On Oahu, urban streams, which tend to be shallow and have reduced or no riparian cover, have higher mean and maximum daily temperatures (figure 3) and substantially greater daily temperature fluctuations than streams in forested watersheds.

Overall, habitat characteristics vary greatly with land use in Oahu watersheds (Brasher et al. forthcoming). Forested streams on Oahu typically have more riffle habitat, greater canopy closure, and higher velocities than urban streams. Habitat variables associated with urban and agricultural streams include more straightened and channelized reaches, higher mean annual solar irradiance, and higher water temperatures. Such streams also typically have smaller substrates and higher levels of siltation than forested streams.

Distinct invertebrate assemblages are also associated with different land uses and can be used as an indication of habitat quality (Brasher et al. forthcoming). On Oahu, insects



Figure 1. Channelized urban stream on the windward side of the island of Oahu. Photograph: Anne M. D. Brasher.

typically make up more than 80% of the invertebrate species in forested watersheds; introduced Trichoptera (caddisflies) are the dominant insect. In contrast, insects typically make up only about half of the invertebrates collected at urban sites, with Diptera (true flies) more abundant than caddisflies. Introduced mollusks (snails and clams) are the most common noninsect invertebrate in channelized streams on Oahu (Brasher et al. forthcoming) but rarely occur in perennial streams in forested watersheds, where the native limpet (*N. granosa*) is often abundant. This pattern has also been documented in New Zealand, where a more pristine site was dominated by mayflies and caddisflies and a more disturbed site was dominated by Chironomidae (a type of true fly) and mollusks (Death 2000).

In addition to different types of invertebrates being associated with different habitat characteristics, the abundance of invertebrates also changes with habitat alteration. Invertebrate abundance (total number of individuals) is lower in degraded urban streams on Oahu than in forested ones (Brasher et al. forthcoming). Although abundance is lowest in degraded watersheds, species richness (the number of different taxa) and diversity show the opposite pattern (figure 4). Degraded watersheds on Oahu have many more taxa than forested watersheds (Brasher et al. forthcoming). This is a result of Hawaiian streams naturally having relatively few native species, with introduced species proliferating in the degraded conditions of altered watersheds.

Streamflow diversions. By 1978, at least 58% of the estimated 366 perennial streams in Hawaii had some type of streamflow alteration (Parrish et al. 1978). Streamflow can

be reduced by pumping ground water from wells or by directly diverting surface water. Results can vary from a slight reduction in discharge to complete drying of sections of the stream. This reduction in flow can be especially significant for amphidromous species that must migrate between the stream and the ocean to complete their life cycle. Larvae may be entrained (captured) by diversion weirs and ditch systems as they wash downstream (Benstead et al. 1999), and both downstream dispersal and upstream migration are impeded by dry stream reaches (March et al. 2003).

A study comparing two streams on the island of Molokai, one with a series of water diversions in its upper reaches (Waikolu Stream) and one with a natural flow regime (Pelekunu Stream), showed a substantial reduction in habitat availability in the diverted stream (Brasher 1997). With decreased discharge, channel width, depth, and water velocity in the diverted stream were reduced. There was also less variability in the range of depth and flow parameters. This reduction in habitat availability was reflected in lower densities of native fish and higher overlap in habitat use among species in the diverted stream (Brasher 1997). In addition, fewer fish were present in sampling areas above the water diversions, presumably because of the difficulty in traversing the periodically dry reach just downstream of the diversions (Brasher 1996, 1997).

Native fish in Hawaiian streams tend to separate longitudinally, with *A. guamensis* more abundant near the stream mouths, *S. stimpsoni* in the middle reaches, and *L. concolor* farthest upstream (Kinzie 1990, Brasher 1996). This is especially true on islands such as Maui, where steep waterfalls



Figure 2. Relatively pristine stream in a forested watershed on the island of Kauai. Photograph: Anne M. D. Brasher.

appear to act as a limiting factor in upstream migration for certain species. On Molokai, which lacks significant waterfalls in the lower reaches, there is substantially more longitudinal overlap of species; and when their distributions overlap, these species tend to use different microhabitats. For example, *S. stimpsoni* generally occurs in faster, shallower water and *A. guamensis* in slower, deeper water (Kinzie 1988, Brasher 1997). However, in diverted Waikolu Stream, in which the range of

available habitat is limited, Brasher (1997) found high overlap in habitat use by the three goby species, with all three species using similar depths and velocities. This overlap in habitat use could result in increased competition and predation, as well as more indirect impacts.

Overall, densities of the goby A. guamensis were much lower in Waikolu Stream than in Pelekunu Stream, and no A. guamensis were observed in the upper reaches of Waikolu Stream, where two dams and an additional reduction of flow resulting from groundwater withdrawal appear to have restricted upstream movement (Brasher 1996). At locations comparable to those below the diversions in Waikolu, there was little difference in S. stimpsoni abundance between the two streams, but at sampling locations equivalent to those above the diversions, there were significantly more S. stimpsoni in nondiverted Pelekunu Stream (figure 5). Additional analysis will be required to assess the statistical significance of these differences.

As observed in other Hawaiian streams, densities of the goby *L. concolor* increased with distance from the mouth in both streams. However, in diverted Waikolu Stream, *L. concolor* initially increased in density in the lower and middle reaches but decreased in the upper area, especially in the periodically dewatered section (Brasher 1996). At comparable locations below the water diversions, *L. concolor* was more abundant in Waikolu Stream than in Pelekunu Stream. However, Waikolu

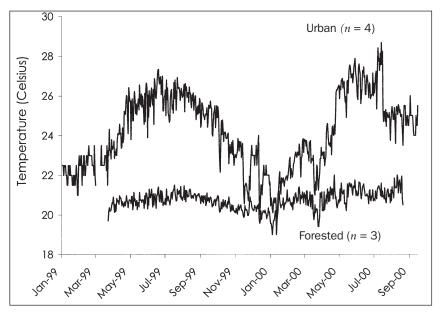


Figure 3. Average maximum daily water temperatures in four urban and three forested streams on the island of Oahu. Temperatures were recorded every 30 minutes for approximately 16 months. Adapted from Brasher and colleagues (forthcoming).

Stream had substantially fewer *L. concolor* in the area in and above the diversions (figure 5).

Similar to the effect of streamflow alteration on distribution and abundance of native gobies on the island of Molokai, composition and abundance of invertebrates and algae have been shown to be affected by water diversions on the islands of Maui and Kauai. A study conducted on the island of Maui, at sites above and below a major water diversion on Iao Stream, showed that a reduction in streamflow had significant negative impacts on species diversity and densities of macroinvertebrate communities (McIntosh et al. 2002). In addition, several invertebrate species that live in fast-flowing torrential habitats, such as the native shrimp *At. bisulcata*, were absent below the diversion structures (McIntosh et al. 2002). This was suggested to be the result of the lack of suitable riffle habitat at the sampling site below the diversion.

An 11-month restoration of natural flows over a hydropower weir on Kauai that was destroyed by a major hurricane also demonstrates the relationships among stream diversion, species composition, and community structure (Kido 1996). The undiverted stream segment was characterized by fewer species in higher densities, a pattern that is typical of native stream community structure in Hawaii. Species composition also varied, with species of *Cladophora* and *Nostoc* algae dominant in the unaltered habitat while *Spirogyra* species were dominant in the diverted reach (Kido 1996). Following flow restoration, invertebrate and algal biomass above the diversion reached nondiverted levels in just 8 weeks. Once flow diversion resumed, the densities of these species fell rapidly. Interestingly, overall community structure did not recover as rapidly, and differences between the altered and unaltered sites

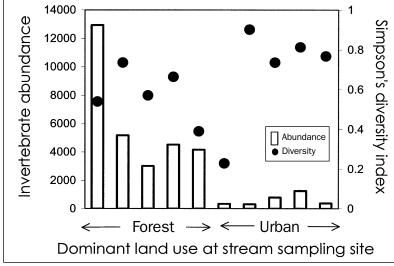


Figure 4. Invertebrate abundance (total number of individuals collected from five benthic samples of 0.25 square meters each) and invertebrate diversity at five sites in urban watersheds and five sites in forested watersheds on the island of Oahu. Simpson's diversity index = $\sum_{p_i^2}^{s} p_i^2$, where p_i is the proportion of species i in the community and i=1 s is the number of species. Adapted from Brasher and colleagues (forthcoming).

in numbers and abundances of individual species, dominant species, and colonization rate remained throughout the study period (Kido 1996).

In addition to the direct impacts of reduced velocities and depths caused by water diversions, the reduced streamflow in areas where streams have also been channelized can result in higher water temperatures and decreased levels of dissolved oxygen (Timbol and Maciolek 1978). Furthermore, sublethal or indirect impacts, including competition, predation, behavioral changes, changes in life history characteristics, and alterations of food chains, can all potentially result from streamflow alterations (Brasher 1997, McIntosh et al. 2002).

Discussion

Increasing human populations on tropical islands are introducing nonnative species, diverting water, modifying stream channels, and reducing flow in natural rivers. This has resulted in lower water quality and degraded physical habitats for many native stream species. Managing these intensely modified ecosystems requires much better understanding of how these cumulative stresses may result in localized extirpation or extinction of native species.

Habitat features resulting from stream alteration in Hawaii favor introduced fishes over native species (Norton et al. 1978). Surveys conducted on Oahu in 1978 showed that introduced fishes and crustaceans formed 87% of the fauna in altered streams and that native species were absent from cement-lined channels (Norton et al. 1978, Timbol and Maciolek 1978). Introduced species can compete with native species for food and shelter and may also prey on them.

Of the five native amphidromous fishes, only the two

species most tolerant of large variations in environmental conditions, *E. sandwicensis* and *St. hawaiiensis* (Hathaway 1978), are present in substantial numbers in some Oahu streams (HCPSU 1990, Kinzie 1990). The native fishes least tolerant to habitat degradation, *L. concolor* and *S. stimpsoni* (Hathaway 1978, Kinzie 1990), are rarely observed on Oahu (Timbol et al. 1980, Fitzsimons et al. 1990, Higashi and Yamamoto 1993). The two native (*M. grandimanus* and *At. bisulcata*) and one introduced (*M. lar*) amphidromous shrimp are present in many streams (Timbol and Maciolek 1978).

Although native species are relatively uncommon in Oahu streams, introduced species are abundant. At least one exotic fish or macrocrustacean species has been reported in all streams surveyed in Hawaii (Timbol and Maciolek 1978, HCPSU 1990), and the number of introduced species in Hawaiian streams is substantially larger than the number of native species (Devick 1991, Cowie 1998). A recent survey of benthic invertebrates at 10 sites in seven watersheds on Oahu identified 75 taxa, of which 40% were introduced and only 5% were native (Brasher et al. forth-

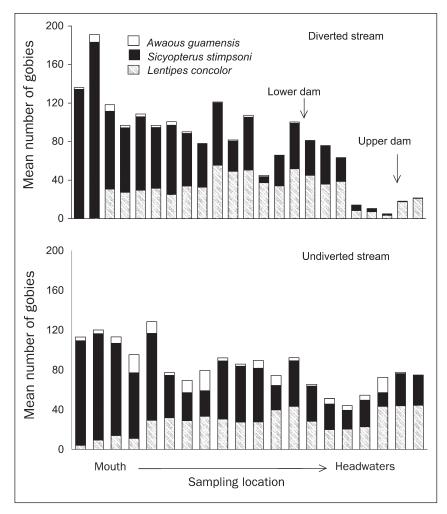


Figure 5. Longitudinal distribution and abundance of native gobies in two streams on the island of Molokai, one diverted and one undiverted. Data shown are the mean numbers of gobies in 10 quadrats (1 square meter each) at each sampling site during eight quarterly surveys over a 2-year period. Sites are arranged from the stream mouth to the headwaters, with corresponding sites in each stream at approximately the same location from the mouth. Adapted from Brasher (1996).

coming). The origins of the remaining benthic species are currently unknown.

Stream alterations appear to have created habitats that are more suitable for introduced species than for native species (Maciolek 1977, Brown et al. 1999). The native species, which require sufficient streamflow to provide clean, cool, fresh water (Timbol and Maciolek 1978), are unable to maintain populations under degraded conditions (Brown et al. 1999), but introduced species, which have broader environmental tolerances, are able to flourish (Norton et al. 1978). The direct effects of introduced species on native species are unknown but may be extensive. In addition to whatever competition and predation they exert directly on native fishes in altered streams, introduced species can also serve as a source of introduced parasites, which then infest the native fish species (Bunkley-Williams and Williams 1994, Font and Tate 1994, Font 2003). Introduced fish are a source of a number of helminth

parasites previously unknown in Hawaii (Font and Tate 1994, Font 2003).

Throughout the tropics (Resh et al. 1992, Pringle 1997, Pringle and Ramirez 1998, Fievet 2000), including Hawaii (Timbol and Maciolek 1978, Kinzie and Ford 1982), modifications of stream ecosystems have been most severe at the lower altitudes. These reaches, in addition to being habitat for some species, are essential pathways for downstream dispersal of larvae and upstream migration of postlarvae of the native amphidromous species. Diversions and channelization may block these pathways, inhibiting the migrations required for successful completion of the life cycle (Brown et al. 1999, Fievet 2000). In addition, predation on postlarvae by introduced species may be substantial as the postlarvae attempt to migrate through altered habitat to the upstream reaches of streams or attempt to settle in such habitat (Brown et al. 1999, March et al. 2003).

Tropical island stream ecosystems around the world are being threatened by changes in water quantity and quality. Because these ecosystems are located in some of the more rapidly developing areas in the world, pressure on their natural resources is intense. With continuing development of tropical island ecosystems, watersheds are becoming far different from those that once sustained native stream communities. Throughout the world, land-use change is generally accompanied by habitat alteration and species introductions, resulting in increased homogenization of once-unique biogeographic regions (Cowie 1998, Scott and Helfman 2001, Kolar and Lodge 2002, Rahel 2002). With urbanization comes lower habitat heterogeneity and in-

creased abiotic variability, creating an environment more suitable for some introduced species (Schlosser 1991, Scott and Helfman 2001, McKinney 2002). In addition, even in relatively pristine areas, water diversions may result in decreased flow or even periodic dewatering of stream sections, reducing available habitat and inhibiting downstream dispersal and upstream migration. An extreme example of this comes from the temperate island of Gran Canaria, where water diversions have resulted in such extensive habitat loss that only three permanent streams exist on the island today, and all except one of the five endemic aquatic invertebrates are considered extinct or on the verge of extinction (Nilsson et al. 1998).

Effects of habitat alteration can be seen at different spatial scales, from landscape (e.g., urbanization) to reach (channelization, water diversion, temperature) to microhabitat (substrate, water depth, velocity). Changes in aquatic habitats are resulting in changes in species composition and abundance

at all scales and, most importantly, in a replacement of Hawaii's unique native fauna with tolerant, generalist introduced species. The initial isolation of the Hawaiian Islands resulted in a highly unique fauna that is especially vulnerable to habitat alteration and the establishment of nonnative species. Research to date in Hawaii has largely focused on describing the associations between different types of habitat alteration and the resulting changes in species composition and community structure. Future research should be directed at evaluating how specific management strategies can lessen the negative impacts of the seemingly inevitable continued development of isolated island ecosystems.

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