Parasites of Hawaiian Stream Fishes: Sources and Impacts

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Abstract

Introduced freshwater fishes impact native Hawaiian stream fishes in two important ways. In addition to direct negative effects associated factors such as predation, competition, and interference, indirect effects may occur when exotic fishes transfer their parasites to native hosts. Six species of helminths that have been introduced with alien live-bearing fishes, including guppies, green swordtails, shortfin mollies, and mosquitofish which now parasitize the five species of gobioids that occur naturally in Hawaiian streams. Some of these exotic parasites form large populations and produce heavy infections in native fishes that can result in disease. Sources, host specificity, distribution, and life cycles of these parasites were studied to assess their potential for pathogenicity and to aid in the formulation of comprehensive conservation and management plans for native stream species in Hawai'i.

Introduction

Vitousek *et al.* (1997) regarded introduced species to be second only to habitat destruction as a threat to biodiversity. Although he was referring to the global distribution of alien species, his experience with the negative impacts of introductions was gained through his extensive research in Hawai'i. Much research has been conducted on species introduced either accidentally or deliberately into terrestrial ecosystems within the archipelago by humans. Maciolek (1984) and Devick (1991) addressed the problem of introduced species in Hawaiian streams. In addition to providing a list of introduced aquatic animals, they presented a chronology of introductions, details pertaining to the sources of each species, and reasons for which exotics were brought to the archipelago. Negative impacts of exotic fishes on native species have been documented globally for many species. Among the most well studied species, the mosquitofish *Gambusia affinis* has been introduced worldwide, principally for mosquito control, and has resulted in the reduction or elimination of populations of several native fish species (Rupp, 1996). Adverse factors that affect native fishes include predation, competition for food or other resources, and disruption of normal reproduction. Significantly, Devick (1991) raised the specter of an additional threat posed by exotic fishes, i.e. the possibility that they had introduced parasites or diseases that could affect native Hawaiian stream fishes. He was responsible for insuring that parasitology research was included in the ongoing comprehensive research program of the Hawaii Division of Aquatic Resources designed for the conservation and management of native stream fishes. That parasitology research program initiated in 1993 resulted in the first report of parasites of native Hawaiian freshwater gobioids and the association of some of these parasites with live-bearing fishes introduced into Hawaiian streams (Font & Tate, 1994).

Subsequent papers have provided the identity of both native and exotic parasites of Hawaiian stream fishes. Geographic distribution of these parasites in Hawaiian streams has been determined at different scales, both within streams and among streams throughout the archipelago (Font, 1997, 1998, 2003). Host specificity and seasonal dynamics of parasite populations was reported by (Vincent & Font, 2003a, b). The impact of parasites of near-shore coral reef fishes on stream fishes was studied by Rigby & Font (1997).

The objective of this paper is to integrate new findings regarding parasites in Hawaiian streams with information gained from prior studies in order to add to our understanding of the biology of these parasites and to appreciate the role that these parasites play in the conservation of Hawaii's native stream fishes.

Materials and Methods

Techniques for collecting fishes included using small shrimp seines ('ōpae net) or baited hand lines while snorkeling, dip nets, traps, and spears. Most fish were transported alive in aerated buckets and maintained in aquariums until examined for parasites, usually within 3 days of collection. Other fishes were preserved immediately in 10% formalin for subsequent examination. Standard parasitological techniques for necropsy and specimen preparation were employed (Pritchard & Kruse, 1982). Voucher specimens have been deposited in the United States National Museum Parasite Collection, Beltsville, Maryland.

Ecological terms are used in accordance with recommendations of Bush *et al.* (1997). Prevalence is the percentage of fish infected with a parasite. Abundance is the average number of helminths per fish.

Results and Discussion

Table 1 lists the 5 native gobioid stream fishes and the 4 species of introduced poeciliid fishes that were examined for helminth parasites. The 14 species of helminths parasitizing native Hawaiian gobioid stream fishes include both species that are native to the archipelago and species that have been introduced in association with anthropogenic activities. Two sources of native parasites have been discovered: Hawaiian marine fishes and native Hawaiian piscivorous birds. Non-native freshwater fishes, principally livebearers in the family Poeciliidae, have been implicated as sources of helminths that now parasitize native stream gobioids. Table 2 provides a summary of which helminths occurring in Hawaiian streams are native and which are exotic, as well as the sources of each, the manner in which stream fish become infected, life cycle stage that develops in the fish, and whether the fish serves as definitive (= final) or intermediate host for the parasite.

Native parasites

Although the number of species of native parasites exceeds the number of species of exotic parasites, the population sizes, distribution, and adverse impacts of exotics is actually greater than that of natives. With few exceptions, native helminths are rare in stream gobioids; most have a prevalence of less than 1% and a mean abundance of less than 1 worm per fish. Because the pathogenicity of a helminth parasite is often correlated with intensity (i.e., the number of worms per infected fish) and its biomass, the small number of native helminths infecting individual gobioids is unlikely to produce disease in their hosts (Font, 1997). Furthermore, the distribution of native parasites differs from that of exotic parasites. Although the distribution of native parasites spans the entire archipelago from Kaua'i to Hawai'i, Font (1997) reported that, in general, they were found in far fewer streams than exotic parasites. The distribution of native hosts accounts, in large measure, for the distribution of native parasites. Marine fishes parasitized by didymozoid trematodes and *Scolex polymorphus* cestodes are cosmopolitan in their distribution, and these offshore species may occasionally infect larval gobioids that eat infected intermediate hosts during the marine phase of their amphidromous life cycles. Thus, the rare and apparently random parasitization of these larval fishes results in their sporadic occurrence among streams with no obvious geographic patterns of distribution. Similarly, it is the vagility of piscivorous birds that accounts for other native parasites to be distributed among streams throughout the entire archipelago. Furthermore, it is likely that the pattern of visitation of streams and feeding on stream fishes by native birds such as the black crowned night heron that explains the sporadic distribution of these native helminths among streams.

Two species of native helminths are somewhat exceptional in that they are either more common than other native parasites or they display a different distributional pattern. Font (1997, 2003) showed that the native acanthocephalan *Southwellina hispida* is nearly as common as two of the most abundant introduced parasites and infects fish in approximately one-third of all Hawaiian streams that have been surveyed. Although over 50 of the bright orange cystacanths may be found in large specimens of hosts such as *Eleotris sandwicensis*, each parasite is about the size of a rice grain and has its attachment organ, the proboscis, retracted within its body. Cystacanths are non-

Table 1. Scientific and common names of native gobioid and exotic poeciliid fishes from Hawaiian streams that were examined for parasites.

Scientific Name	Common Name
Native Fishes	
Awaous guamensis	ʻoʻopu nākea
Lentipes concolor	ʻoʻopu ʻalamoʻo
Sicyopterus stimpsoni	ʻoʻopu nōpili
Stenogobius hawaiiensis	ʻoʻopu naniha
Eleotris sandwicensis	ʻoʻopu ʻakupa
Introduced Fishes	
Poecilia reticulata	guppy
Poecilia mexicana	shorttail molly
Xiphophorus helleri	green swordtail
Gambusia affinis	mosquitofish

motile; they attach to connective tissues along the outside of the intestinal track, and feed by absorption of nutrients. No host tissue damage is associated with these cysts and the amount of host nutrients that are absorbed is minimal, therefore pathogenicity seems unlikely at infection levels that have been recorded in native gobioids. This parasite, however, does have the potential for pathogenicity in fish-eating birds such as black crowned night herons that serve as definitive (= final) hosts in which the acanthocephalan becomes a sexually mature adult. An epizootic in Kanahā Pond near Kahului, Maui resulted in the deaths of black crowned night herons from which large numbers of adult *Southwellina* sp. were recovered with their spinous proboscises embedded in the intestinal mucosa (Thierry Work, USGS, National Wildlife Health Research, Honolulu, pers. comm.). Some effort, therefore, has been devoted to life cycle studies of *S. hispisda* in Hawaiʻi. Cystacanths are often found attached to the outside of the intestinal wall in the abdomen of crayfishes examined in my laboratory Louisiana. However, I have failed to find cystacanths in the red swamp crawfish *Procambarus clarkii* introduced into Hawaiian streams, nor have I found infections in *Atyoida bisulcata*, *Macrobrachium grandimanus,* or *M. lar* collected from streams where native gobioids harbor cystacanths. The search for the decapod crustacean host of this acanthocephalan in Hawaiian streams will continue. The discovery of rare infections of cystacanths in green swordtails and shortfin mollies, but only in the very largest specimens of these fishes, may provide a clue regarding the size of crustaceans that may host *S. hispida.*

The second parasite species that deviates from the pattern of rare occurrence and sporadic distribution of native stream species is the nematode *Spirocamallanus istiblenni*. This roundworm occurs commonly in many near shore coral reef fishes. Where estuarine conditions exist in stream mouths (*muliwai*), this parasite can become abundant in *E. sandwicensis* (Rigby & Font, 1997). In general, heaviest infections occur in larger estuaries where opportunities for transmission from marine fishes to stream fishes are greater. The discovery of *S. istiblenni* in blue-lined snappers or *taʻape* (*Lutjanus kasmira*) introduced into the Hawaiian archipelago from the Marquesas Islands caused Rigby & Font (1997) to question the native status of *S. istiblenni.* They considered the possibility that this parasite should be regarded as cryptogenic in the sense of Carlton (1996), that is, a species that is neither demonstrably native nor introduced. More recently, the introduced black tailed snapper or *toʻau* (*L. fulvus*) and native Hawaiian flagfin or *āholehole* (*Kuhlia xenura*) from the Wailoa River estuary in Hilo, occurring syntopically with infected *E. sandwicensis,* were found to harbor *S. istiblenni.*

One final species of native parasite that displays a distinct pattern of distribution and can attain large population sizes is the leech *Aestabdella abditovesiculata*. Originally misidentified by Font *et*

Table 2. Helminth parasites of stream fishes: sources, means by which fish host obtains its infection, life cycle stage that develops in the fish, and role of fish in parasite's life cycle (type of host).

Parasite	Source	Mode of infection of fish	Stage in fish	Type of host
Trematoda				
Ascocotyle tenuicollis	exotic; poeciliid fishes	cercaria from snail penetrates fish	metacercaria	intermediate
Centrocestus formosanus	exotic; poeciliid fishes	cercaria from snail penetrates fish	metacercaria	intermediate
Didymozoidae	native; marine fishes	infected copepod eaten by fish (?)	larva	intermediate
Strigeoidea	native; birds (?)	cercaria from snail	metacercaria	intermediate
Cestoda				
Bothriocephalus acheilognathi	exotic; poeciliid fishes	infected copepod eaten by fish	adult	definitive
Cyclophyllidea	native; birds (?)	unknown	cysticercus	intermediate
Scolex polymorphus	native; marine fishes	infected copepod eaten by fish	plerocercoid	intermediate
Monogenea				
Salsuginus sp.	exotic; poeciliid fishes	larva attaches to fish gill	adult	definitive
Nematoda				
Camallanus cotti	exotic; poeciliid fishes	infected copepod eaten by fish	adult	definitive
Spirocamallanus istiblenni	native; marine fishes	infected copepod eaten by fish	adult	definitive
Acanthocephala				
Southwellina hispida	native; birds	infected decapod eaten by fish (?)	cystacanth	intermediate
Hirudinea				
Aestabdella abditovesiculata	native; marine fishes	direct attachment	adult	definitive
Cystobranchus sp.	native; marine fishes (?)	direct attachment	adult	definitive
Myzobdella lugubris	exotic; fishes or crustaceans	direct attachment	adult	definitive

al. (2002) and assumed to be introduced, the correct identification was provided to me by Eugene Burreson (pers. comm.) and reported (Font, 2003) as a native species that commonly infects Hawaiian marine fishes. Similar to the distribution of *S. istiblenni,* the leech is especially common in extensive estuaries and parasitizes mainly *E. sandwicensis,* but also occurs on other syntopic native gobies. Examination of fishes in streams leading into estuaries has shown that these fishes lose their leech infestations when salinity levels drop to zero parts per thousand. Experimental confirmation of the inability of this leech to survive prolonged exposure to pure freshwater was accomplished by placing *E. sandwicensis* heavily infested with *A. abditovesiculata* in aquariums containing stream water collected far upstream (*mauka*) of estuaries and recording leech detachment and subsequent mortality.

Two factors make specific identification and elucidation of life cycles of the remaining native helminth parasites problematic. First, most of these helminths are incompletely developed, anatomically undifferentiated larval stages of parasites that become adults in fish eating birds or marine fishes. Lack of definitive anatomical characteristics permits identification only to higher taxonomic categories and an understanding of life cycles and means of transmission consistent only with the broad patterns displayed by these higher taxa. Because of the immaturity and rarity of these helminths, classical techniques for determining specific identity and life cycles of these species are unlikely to be fruitful. However, newer molecular techniques that compare nucleic acid sequences of these larvae in stream gobioids with adult helminths in birds and marine fishes may prove to be a valuable tool to provide this information. Fortunately, these problematic species, because of their rarity in streams, are not a high priority concern for the conservation and management of native stream fishes.

Introduced Parasites

Exotic freshwater fishes have been introduced into Hawaiian streams in association with anthropogenic activities. Devick (1991) has provided a thorough documentation with regard to the chronology, purpose, degree of success, and other details of these introductions. With regard to parasites that have been introduced by man into Hawaiian streams, the most important of these introductions are associated with poeciliid fishes. Among the several species of poeciliids that have been brought to the archipelago, the most widely distributed and abundant species are the guppy, *Poecilia latipinna,* the shortfin molly, *P. mexicana,* the green swordtail, *Xiphophorus helleri*, and the mosquitofish, *Gambusia affinis.* These live bearers were introduced into the majority of Hawaiian streams for control of mosquitoes and through aquarium releases. In association with the introduction of these fishes, the helminths that parasitized them at the time of their release into Hawaiian streams also became established in the streams. Furthermore, most of these helminths display broad host specificity and were able to infect the native gobioid fishes inhabiting these streams. What is not well appreciated is the fact that some of these parasites, in fact two of these species with the highest disease potential, are not only unnatural parasites of Hawaiian gobioids but do not occur naturally in these poeciliids either. The two parasites in question, the roundworm *Camallanus cotti,* and the tapeworm *Bothriocephalus acheilognathi* are native to Asia. The Asian fish tapeworm is a common parasite of carp in the Orient and has been introduced globally with carp aquaculture (Dove, 1998). Because of its broad host specificity, the tapeworm now infects many other fish hosts throughout its range of introduction. Similarly, the roundworm infects many fish throughout its native range in the Orient. The roundworm has been disseminated worldwide in association with the aquarium trade. Mark Rigby (pers. comm.) has established a web site for reports of *C. cotti* by freshwater aquarists, and has documented the occurrence of this parasite in aquarium fishes on all continents. There are also reports in the literature of populations of *C. cotti* that have escaped captivity and become established in nonaquarium habitats, e.g. Korea (Kim *et al.*, 2002). Because the poeciliids that now occur in Hawaiian streams are native to the New World, outside of the natural range of this roundworm and tapeworm, poeciliids did not bring these two parasites with them from North and South America. A more likely scenario is that the poeciliids introduced into Hawai'i first were parasitized by the roundworm and tapeworms in ponds on the archipelago where they were reared syntopically with parasitized Asian carp and other Oriental fishes. Only after acquiring these parasites in lentic habitats

were the poeciliids introduced into Hawaiian streams where native gobioids became infected.

Many other freshwater fishes have been introduced into Hawaiian streams (Devick, 1991; Yamamoto & Tagawa, 2000; Staples & Cowie, 2001) but their role in parasite transmission is largely unknown. A preliminary survey has found black chin tilapia *Sarotherodon melanotheron* from streams along the windward coast of Oʻahu infected with *C. cotti.* Exotic fish species are particularly prevalent in streams from urban areas (e.g., Mānoa Stream in Honolulu) but have not been surveyed for parasites. There is clearly a need for more research in this area to determine what other species of parasites occur in these exotic fishes, to document which of these parasites are capable of infecting native fish hosts, and to assess the potential for the spread of these parasites to other streams.

The six species of non-native parasites found in Hawaiian streams differ markedly from each other in their potential to cause disease in native stream gobioids, and thusly, differ in their importance to any program designed for the conservation and management of these fishes. Therefore, these parasites will be discussed in reverse order of their importance to fish conservation with the greatest disease threat associated with the roundworm *C. cotti* covered last.

Two of the helminths introduced into Hawaiian streams represent no conservation threat because they parasitize poeciliid fishes and do not infect the native stream gobioids. The first of these, *Salsuginus* sp., occurs on the gills of green swordtails. This helminth belongs to the Class Monogenea, Family Dactylogyridae, a taxon widely known for its extremely narrow host specificity. Syntopic gobioids taken from Hawaiian streams and even syntopic guppies and shortfin mollies do not harbor this parasite. The life cycle of this parasite is direct and involves fish to fish transmission. When infected green swordtails were maintained for 2 weeks in a 40 liter aquarium with *E. sandwicensis, Awaous guamensis, Lentipes concolor, Stenogobius hawaiiensis,* and *Sicyopterus stimpsoni*, none of the gobioids became infected.

Similarly, the heterophyid trematode *Centrocestus formosanus* infected only poeciliid fishes, with heaviest infections occurring in green swordtails. The species has broad host specificity and has been reported from reported from fishes belonging to several families including Eleotridae (Salgado-Maldonado *et al.*, 1995). Syntopic eleotrids and gobiids examined from localities where swordtails were infected have not revealed *C. formosanus* infections, although more specimens of native hosts will be examined as they become available.

In contrast, a second heterophyid trematode *Ascocotyle tenuicollis* previously reported only from the conus arteriosus of mosquitofish *G. affinis* was discovered in the conus of 3 of the 5 native gobioids that occurred syntopically with mosquitofish from Waiākea Pond in Hilo. The first intermediate host for this parasite in Hawaiʻi is the snail *Melanoides tuberculata* (Martin, 1958). Neither *L. concolor* nor *Si. stimpsoni* has been collected from habitats containing this snail; therefore their susceptibility to infection with *A. tenuicollis* is unknown. Because *M. tuberculata* has been introduced into so many Hawaiian streams, the potential for native species to be infected with this parasite is widespread. In Waiākea Pond where *M. tuberculata* is not abundant, native fishes harbored levels of infection too sparse to be considered pathogenic. However, in Louisiana, heavy infections in mosquitofish can result in the swelling of the conus arteriosus to several times its normal size. In Hawaiʻi, the potential for morbidity and mortality in native fishes is real wherever large populations of this snail occur.

The leech *Myzobdella lugubris* is unique among Hawaiian fish helminths in that it is the only parasite on native stream fishes that is known to both stream biologists and to the general public. Unlike other freshwater helminths in Hawaiʻi, leeches are ectoparasites, readily visible to the naked eye even upon casual inspection of fishes, and do not require dissection of the host or microscopical examination. The source of *M. lugubris* into Hawaiʻi is problematic. The leech is a common external parasite of many freshwater fishes throughout the southeastern United States, and also infests decapod crustaceans, grass shrimp *Palaemonetes pugio,* and blue crabs *Callinectes sapidus* from oligohaline estuaries of the Atlantic and Gulf of Mexico. Fishes are utilized by leeches as a source of nutrients, i.e., blood and tissue fluids, but crustaceans are used as hard substrate for leeches to deposit their egg cocoons in an environment consisting mostly of soft sediments (Overstreet, 1978). Because both freshwater fishes and blue crabs from the Southeast USA have been introduced

into the archipelago, it is not known which of these represents the original source of introduction. Ironically, in Hawai'i the behavior of this leech apparently has become modified. Stream dwelling crustaceans are unparasitized, presumably because the leeches cement their cocoons to the rocky substrate of stream beds. It is also extremely rare to find a poeciliid harboring *M. lugubris* whereas stream dwelling gobioids are often heavily infested. A probable explanation for this differential parasitism is the fact that gobioids are demersal and are much more likely to come into direct contact with a leech attached to a rock than is a nektonic poeciliid swimming higher in the water column. Because of their visibility, these leeches provide stream biologists with an opportunity for quantifying levels of infections without removing gobioid hosts from streams. In my experience, two areas of caution are warranted if these stream surveys are to be conducted. First, some leeches may attach within the mouth or inside the opercula of fishes and not be readily visible. In addition, based upon my experience in using microscopy to perform dissections to detect internal parasites, very small specimens of *M. lugubris* on fish skin or fins may go unnoticed unless the fish is examined with a stereomicroscope. Secondly, in oligohaline Hawaiian estuaries, *M. lugubris* may co-occur with *A. abditovesiculata*. With experience and with foreknowledge of their possible co-occurrence, however, these two species can be distinguished anatomically and by color pattern. *Myzobdella lugubris* has oral and caudal suckers with diameters that are less than or equal to the body width and is yellow-green. *Aestabdella abditovesiculata* has a caudal sucker that is greater in diameter than the body width and is dark brown-black. The method of attachment with the caudal sucker by these two leeches differs and offers some insight with regard to potential for pathogenicity. Although the caudal sucker of *A. abditovesiculata* is much more robust, it attaches weakly to the fishes' surface, does not produce tissue damage, and is readily removed with forceps. The caudal sucker of *M. lugubris* is embedded deeply into the fin or flesh of its fish host and produces a very visible lesion. Often this wound is surrounded by a white cloudy patch, presumably representing a secondary bacterial or fungal infection. These white patches are often visible in the absence of an attached leech and indicate the leeches may repeatedly move from place to place on its host producing multiple lesions. In addition to the tissue damage caused by the caudal sucker of *M. lugubris*, both species use the oral sucker for feeding on fish blood, and the bodies of these leeches are often red with blood that can be seen through their distended epidermis.

Because the Asian fish tapeworm *B. acheilognathi* parasitizes carp, a species that is of importance to the aquaculture industry, many studies on the biology of this parasite have been published, with particular emphasis on its pathology. Cyclopoid copepods serve as intermediate hosts, and transmission to the definitive host occurs when fishes eat infected copepods. The cosmopolitan distribution of these copepods, including streams in Hawai'i, and the broad specificity of the tapeworm for fish hosts is responsible for the invasiveness of this parasite. It currently is found wherever carp have been introduced for aquaculture or where poeciliids, another group of susceptible hosts, have been released for mosquito control. The Asian fish tapeworm is regarded as the most widely distributed freshwater fish tapeworm in the world. Poeciliids in Hawaiian streams are infected with this tapeworm and are responsible for its transfer to native stream fishes. Adult tapeworms parasitize *E. sandwicensis* and *A. guamensis* but have not been found in the other 3 species of stream gobies. The trophic ecology of *Si.stimpsoni* provides insight that explains the tapeworm's absence from this potential host. This goby feeds mainly on blue-green algae and diatoms attached to the surface of rocks. The absence of copepods from the diet of *Si. stimpsoni* (Kido, 1996; Fitzsimons *et al.*, 2003) has been confirmed by me through the examination of intestinal contents of over 50 specimens in the course of parasitological examination. In the laboratory, several juvenile *Si. stimpsoni* and *A. guamensis* were placed in 2-liter containers of stream water to which a concentrated sample of the copepods *Macrocyclops albidus* from Alenaio Stream, Hilo were added. When examined microscopically after two days, the intestines of *Si.stimpsoni* were empty, but the intestines of *A. guamensis* each contained over 100 copepods. The absence of *B. acheilognathi* from *St. hawaiiensis* and *L. concolor*, both of which feed upon copepods, is presently unexplained and requires further investigation.

One of the most remarkable aspects of the biology of this tapeworm is the fact that this species that is found naturally in boreal climates is able to thrive in tropical waters. In the latter environment

tapeworm reproduction is not restricted to the warmer months of the year as is the case in the northern parts of its native range or even in temperate climates such as North Carolina where the species has been introduced (Granath & Esch, 1983). This ecological release, decoupling reproduction from its natural seasonal constraints may, to some extent, account for the successful worldwide spread of this parasite.

Of the 14 species of helminths found in Hawaiian streams, by far the most prevalent, abundant, and widely distributed is the invasive nematode, *Camallanus cotti* (Font & Tate, 1994; Font 1997, 1998). Because of its abundance and associated potential for causing disease in native stream fishes, its biology is especially relevant when considering research programs focused on the conservation of native fishes. Several aspects of the biology of this roundworm are remarkably similar to that of the Asian fish tapeworm. First, both species are native to the Orient and both have been introduced into Hawaiian streams concomitant with the release of poeciliid fishes that are native to the New World. Both the roundworm and tapeworm use cyclopoid copepods as intermediate hosts (i.e., in spite of their taxonomic differences they have the same basic life cycle pattern and mode of transmission). Both are very broadly host specific, and infect several families of freshwater fishes. Both produce disease in their fish hosts.

Long term monitoring of parasite populations in Waiāhole and Waianu Streams has provided us with an opportunity to study the host specificity, population dynamics, and seasonal aspects of the reproduction of this species (Vincent & Font 2003a, b). Our most important findings from those studies included the observation that all exotic poeciliids in those streams are efficient reservoirs for infections of native fishes. All ontogenetic stages of these fishes were found infected and roundworms were very abundant even in juvenile fishes. The observations indicate that immature fishes even as small as 10 mm standard length should not be overlooked in any survey for this parasite. Female roundworms were found in both summer and winter. Reproduction occurs throughout the year, and recruitment of new infections into the fish community is continuous. Over the span of 4 years from 1995 to 1999, *C. cotti* showed no yearly differences in prevalence or abundance and indicated that the population is established, persistent, stable, and unlikely to diminish spontaneously through natural causes. The conservation implications of these data are that reduction or elimination of *C. cotti* from Hawaiian streams is unlikely to occur naturally, but will require human intervention.

Additional multi-year monitoring of *C. cotti* populations was conducted in Hakalau and Nanue Streams on the Big Island. Study sites were located approximately 4 km upstream from the ocean and in these habitats the only fish present was *L. concolor*. Over 80% of gobies with mature gonads were infected with roundworms. The roundworm population was both persistent and stable, in spite of climactic changes associated with El Niño events that resulted in highly variable amounts of rainfall from year to year. Small specimens of *L. concolor* with immature gonads, presumably new arrivals at the upstream site, were rarely infected with roundworms (prevalence <10%). Because worm burdens increased after arriving upstream, it can be concluded that fish were becoming infected at the site and not downstream where juvenile *L. concolor* passed through populations of poeciliids and other species of gobioids that were heavily infected with roundworms. In a previous study, Font & Tate (1994) showed that juvenile *L. concolor* newly recruited from the ocean and collected near the mouth of Hakalau Stream were not infected with roundworms, whereas syntopic *A. guamensis* were parasitized. At the upstream sites in both Hakalau and Nanue Streams, we searched waters above the population of infected *L. concolor* for the presence of poeciliids that might serve as sources of roundworms that might infect these gobies; however, we found none. The conclusion that can be drawn from this study has ominous implications for conservation and management of native stream fishes. Once *C. cotti* has become established in native fishes, the continued presence of poeciliids is no longer necessary. The roundworm can persist in native fishes even if all infected exotic fishes are removed from the stream.

Camallanus cotti infects 3 of the 5 species of native stream gobioids. Infections are absent from *Si. stimpsoni* for the same reason that this fish is also uninfected with *B. acheilognathi*; it does not feed upon copepods that serve as intermediate hosts for both the roundworm and tapeworm. Lack of physiological suitability may explain the absence of mature roundworms in *St. hawaiiensis.* Careful

microscopical examination of the mucosa of the posterior intestine of this fish revealed the presence of dead, sclerotized mouthparts of *C. cotti* 3rd and 4th stage juveniles, devoid of the remainder of the body. It can be concluded that *St. hawaiiensis* can become infected, but that the roundworms cannot survive in that host.

A somewhat related observation was made when examining *C. cotti* infection data from *E. sandwicensis*. This fish harbored the largest numbers of the roundworm when compared with all other stream fishes; levels of infection often exceeded 100 worms. However, the vast majority of these specimens were 3rd or 4th stage juveniles. Rarely mature males and females were found in the intestine, but, among the thousands of *C. cotti* examined from this host, not a single gravid female worm was ever found. It may be concluded that *E. sandwicensis* represents a sink for *C. cotti* removing parasites from the stream without compensatory reproduction by the parasite.

One other facet of the population dynamics of the roundworm in *E. sandwicensis* that deserves attention is the finding of the heaviest worm burdens in the largest specimens of this host species. These large sleepers are unlikely to utilize copepods as a food source at this stage in their life history; rather they prey mainly on small fishes. It seems reasonable to conclude that they acquire specimens of *C. cotti* from infected small fishes that are acting as paratenic (= transport) hosts. Experimental confirmation of this hypothesis is required to document the first example of paratenic transmission by a member of the genus *Camallanus*.

Parasites in Estuaries

The ecology of estuarine ecosystems in Hawai'i is understudied, but likely plays an important role in the interactions that occur in stream ecosystems. More research effort needs to be directed toward the study of *muliwai* dynamics where faunal interchange between ocean and streams take place (Robert T. Nishimoto, pers. comm.). This research focus is particularly important in archipelagoes such as the Hawaiian Islands where most species comprising the native stream fauna are amphidromous (Fitzsimons *et al.*, 2002; McDowall, 2003). Encouraged by Nishimoto, an emphasis on parasite ecology and transmission dynamics of parasites of native fishes occupying the *muliwai* has recently been initiated by focusing on the parasites of āholehole or Hawaiian flagfin (*Kuhlia xenura*), 'ama'ama or striped mullet (*Mugil cephalus*)*,* and 'o'opu 'akupa or sleeper, (*E. sandwicensis*)*.* The most important preliminary finding is that *K. xenura* and *E. sandwicensis* can become infected with both of the two closely related nematodes, the exotic freshwater roundworm *C. cotti* and the presumed native marine roundworm *S. istiblenni.* Some individuals of both fishes simultaneously hosted both species of roundworms. Several aspects of these dual infections require further study, perhaps the most significant of which might be their use as biological indicators of fish movements between marine to freshwater habitats. *Mugil cephalus* was not infected with either species of roundworm. However, most specimens of striped mullet from Waiākea Pond estuary in Hilo harbored monorchiid trematodes conspecific with specimens from the introduced *kanda* or Marquesan mullet (*Valamugil engeli*)*.* Whether these monorchiid trematodes are native to Hawai'i or introduced from the Marquesas is currently under investigation.

Future Directions

Parasites play important roles in Hawaiian stream ecosystems. In developing a plan for future research in stream biology in the archipelago, parasitology research should be included in any comprehensive program focusing on the biology of Hawaii's freshwater fauna. Although much basic parasitology research needs to be done in streams, I will emphasize studies that can be directly applied to the conservation and management of native stream fishes and invertebrates.

The most important questions involving the relationship of parasites and native Hawaiian stream fishes are questions of disease. Do the parasites known to occur in Hawaiian streams cause morbidity or mortality in native gobioids? Is fish fecundity reduced by these parasites as has been documented for other helminths infecting fishes (Heins *et al.*, 2004)? Do these parasites kill their fish hosts?

What seems like a simple question, "do parasites kill their hosts" is perhaps one of the most difficult for parasitologists to answer. Direct evidence of mortality is hard to obtain because only rarely

are major fish kills caused by helminth parasites where many infected hosts all die simultaneously and the fish kill is witnessed by humans. If fish are killed by parasites individually, here and there, now and then, the detection of these parasite induced kills is unlikely. Furthermore, small fish are more vulnerable to parasitic disease than are large fish harboring the same number (or biomass) of helminths. Detection of small fish that die from parasites is even more unlikely. More problematic is the fact that parasites weaken fish and make them more vulnerable to predators like piscivorous birds or carnivorous fishes. The differential predation of these weakened parasitized fish is virtually impossible to document in natural ecosystems.

Additional approaches to the study of fish disease include histopathological and pathophysiological studies to determine the nature and extent of damage to parasitized fishes. Currently, the histopathological changes to naturally infected Hawaiian gobies caused by *C. cotti* are underway in my laboratory in collaboration with John Fournie of the Environmental Protection Agency. A related avenue of study is to experimentally infect fishes in the laboratory in order to quantify levels of infection, i.e., number of worms required to kill a fish host. Studies of this nature are dependent upon the ability to complete the parasite's life cycle in the laboratory in order to experimentally infect fish with known numbers of parasites.

Life cycle studies on one of the most important exotic parasites in Hawai'i, the roundworm *C. cotti* are currently in progress at Southeastern Louisiana University. Levsen (2001) reported that he was able to transmit *C. cotti* directly from fish to fish in contradiction to all previous life cycle studies on *Camallanus* spp. that have demonstrated the necessity of a copepod intermediate host for successful completion of the life cycle. Such an unusual report requires independent verification which was tested in the laboratory at Southeastern Louisiana University. In three carefully controlled replicate experiments, fish exposed directly to 1st stage juveniles of *C. cotti* did not become infected whereas all fish exposed to copepods containing 3rd stage juveniles of *C. cotti* did become infected. Either Levsen was working with a strain of *C. cotti* that departs from all known species of *Camallanus* or his experiments were flawed in that, undetected by him, his aquarium systems were contaminated with copepods. In addition to the significance of this finding with regard to our knowledge of the basic biology of camallanid nematodes, there is an important practical conclusion that can be drawn from this experiment regarding the laboratory breeding of gobioids such as *L. concolor*. The production of laboratory reared gobies as potential sources of fishes for stream restocking programs would be unlikely if *C. cotti* had a direct life cycle because the infection of juvenile fishes from infected parents could not be prevented. However, confirmation of an indirect life cycle for this parasite demonstrates that uninfected laboratory-reared gobies can be obtained simply by taking the precaution of removing copepods from breeding aquariums. This precaution could be achieved simply by filtering the water through a fine mesh plankton net.

Theoretical aspects of the evolutionary biology of pathogens must be better understood by conservation biologists and managers. It is incumbent upon parasitologists and pathologists to adequately explain the nature of disease. Parasitologists have done a poor job of explaining aspects of host-parasite relationships, particularly with regard to parasite-induced disease, to both the general public and to other biologists. The future of stream research in Hawai'i must have an education component. Both scientists and laypersons need to be informed regarding the biology of Hawaiian streams, and parasitologists must become more actively involved in this educational process.

One misconception held by many non-parasitologists is that a good parasite never kills its host. While there are some examples of host-parasite relationships that support this notion, there are many exceptions. If the death of a host enhances the likelihood of parasite transmission and increased fecundity, then selection for increased parasite virulence or modified behavior may evolve (Ewald, 1994). For example, *Diplostomum spathaceum* is a trematode that becomes sexually mature in gulls. Larval *D. spathaceum* preferentially infect the eyes and brains of fishes. These parasitized fishes have reduced visual acuity, swim near the water's surface, and make predation by gulls and transmission of the parasite to the next life cycle host more probable.

Another aspect of the "common wisdom" regarding parasites is that ancient host-parasite relationships evolve toward coexistence and new host-parasite relationships display greater pathogenici-

ty. Although, once again, there is some support for this notion, there are many exceptions. As stated previously, the overriding factor regarding parasite pathogenicity is the whether increased virulence enhances or decreases parasite survival and fecundity. This concept is of particular relevance to exotic parasites in Hawaiian stream fishes. This "newness" argument is often stated, but is in fact irrelevant. *Camallanus cotti* and *B. acheilognathi* are not ancestral parasites of poeciliids and new parasites of Hawaiian gobioids. In fact, these Oriental parasites were newly acquired by New World poeciliids prior to their introduction in Hawaiian streams. If anything, the Hawaiian gobioids have amphidromous Indo-Pacific gobioids as ancestors, and indicate that for these two Oriental parasites they probably have an "older" relationship with Hawaiian gobioids than exotic poeciliids. Based upon this information, there is no reason to believe that the roundworm and tapeworm are more pathogenic to native Hawaiian stream fishes than to the exotic fishes that introduced them into the streams.

Helminth parasites of other exotic fishes represent a potential "Pandora's Box" for Hawaiian stream fauna. These alien fishes are virtually unstudied by parasitologists and may harbor helminths currently unknown from Hawai'i. It may be that these new parasites occur in exotic fishes in streams that are so degraded that they are presently uninhabitable by native gobioids. However, although these exotic parasites may not represent any current direct threat to native fishes, their presence in the archipelago may facilitate their transmission to streams where native fishes are present. In addition, the knowledge of the presence of these exotic parasites is instrumental to stream restoration if habitat quality of these degraded streams is to be improved in the future.

The concept of "parasite" is far broader than the current focus on helminth parasites in Hawaiian streams. In fact, in conducting helminth surveys, I have encountered several protistan parasites of native Hawaiian stream fishes. At least one of these protistans, *Ichthyophthirius multifilis* ("ich"), is a know fish pathogen. Perhaps even more importantly, no data have been collected with regard to viral, bacterial, and fungal pathogens in Hawaiian fishes. These taxa contain some of the most lethal of all fish parasites. It is strongly recommended that the parasitology research program for Hawaiian streams be expanded to include parasitologists who have the expertise to conduct research on other groups of parasites in addition to helminths.

Finally, the expansion of research by stream biologists to emphasize estuarine areas and stream mouths that represent the connection between stream and ocean is a clear need. This *muliwai* habitat is an integral component of the stream ecosystem and represents the focal point of faunal interchange between freshwater and the ocean. The leading researchers on amphidromy (Kinzie, 1991; Fitzsimons *et al.*, 2002; McDowall, 2003) have for years emphasized the importance of this key habitat, and it clearly is time that increased effort be devoted to its study.

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