

TARGETED INVASIVE SPECIES REMOVAL CASCADES TO REDUCE NON-
TARGET INVASIVE SPECIES THROUGH APPARENT FACILITATION

A Thesis

by

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This thesis meets the standards for scope and quality of
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ABSTRACT

Invasion biologists often focus on facilitative interactions between non-native species. These facilitative interactions can result in invasional meltdown, a positive feedback loop where naturalized species facilitate other non-natives to establish to the detriment of native ecosystem structure and function. In order to understand the effects of restoration efforts via the removal of non-native species it is important to quantify the beneficial impacts to the ecosystem when feedback loops are broken by removing key linkages between invasive species. To address this, I tracked the responses of benthic stream invertebrates to invasive fish removal in Hawai'i. Invasive fishes were removed in April of 2016 from 12 freshwater streams on the island of O'ahu, Hawai'i, USA. Following fish removal, I collected 96 macroinvertebrate samples (4 replicates from each treatment [Experimental + Control] at 12 sites) using a 30.48 x 30.48 cm Surber sampler. The invertebrates were sorted, identified to the lowest taxonomic resolution and enumerated. Visual surveys of fish communities were performed monthly at each site and invertebrates were collected and processed as before in monthly cycles from November 2016 through August 2017. I observed that the removal of poeciliids, a numerically dominant family of non-native fishes in Hawai'i, led to reduced predation pressure on native midge larvae (Chironomidae). As the relative abundance of chironomids increased, there was a decrease in abundance of the non-native caddisfly *Cheumatopsyche analis*, possibly due to competition for resources. These results demonstrated that targeted invasive species removal can benefit native species through cascading interactions. In this case the results showed reducing predation pressure on native invertebrates and reversing the effects of invasional meltdown. By understanding the relationships between multiple

native and non-native organisms can lead to effective and cost-efficient management in areas that have multiple invasive species.

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CHAPTER I: INTRODUCTION

1.1 Species invasion

As globalization continues, the introduction of species to new environments is occurring at an exponential rate (Ricciardi et al., 2013), often with extreme and harmful results (Jeschke et al., 2013). Exotic invaders are the leading cause of changes in biodiversity globally, both via homogenization of flora and fauna across regions and as a leading cause of native species extinctions (Zavaleta et al., 2001; Richardson and Ricciardi, 2013). Effective resource management requires the development of improved methods to predict the impacts of these introductions, manage removal after the invasion has occurred, and maximize ecosystem recovery once the invasive species are removed.

In the 1950's, Charles Elton, an early pioneer in the study of invasive organisms, urged scientists to look at species invasion historically, ecologically, and from a conservation perspective (Elton, 1958). However, studies of biological invasion near the turn of the century were still focused on patterns rather than processes; with no attempts of defining a mechanistic hypothesis to help improve the understanding of invasion impact (Ricciardi, 2001). Since the turn of the twenty-first century, invasion ecology has developed beyond its founding discipline, branching out into multiple fields of studies (Richardson, 2011).

1.1.1 Defining terms in ecological invasion

Native species are found naturally in a geographical location and are either endemic or indigenous (Carlton, 1996). Endemic species are range-restricted, often isolated by great barriers such as large mountain ranges or oceans, vs. widely distributed

indigenous species that are native to multiple regions (Carlton, 1996). Species introduced into a new geographical location through anthropogenic means are considered alien species (Pysek et al., 2008).

The term “alien species” is an umbrella word that encompasses all other terms associated with nonindigenous species whether benign or harmful (Blackburn et al., 2011). The three classifications of introduced species are; casual, naturalized, and invasive. Casual species rely on repeated introductions to maintain a continued presence in the area. Naturalized species are those that have become self-propagating for several generations but do not meet the definition of invasive (Pysek et al., 2008). In order to be considered invasive, a species must have a proficient fecundity rate over several cycles, spread into new areas (Thompson et al., 1995; Carlton, 1996; Davis and Thompson, 2000; Valery et al., 2008), and negatively impact native species and the ecosystem that the alien species has invaded (Alpert et al., 2000). It is important to note that not all naturalized species become invasive and that some native species become invasive.

1.1.2 Stages of Invasion

There are three distinct stages of the invasion process: introduction, establishment, and spread (Puth and Post, 2005). Globalization has brought with it the introduction of non-native species to new regions of the world, both intentionally and non-intentionally (Vander Zanden, 2005). As humans move around the world, they often take with them the comforts of home, transporting food and other agricultural goods, such as leather, timber, and fur, into new areas. Other types of transport include the live food trade, bait fish, aquarium/ornamental, and animals introduced for biological control. Accidental introductions are the unintentional byproduct of shipping goods around the

world. Introduced species travel through new dispersal corridors such as shipping channels and canals, attach themselves to the transport vehicles, or stow-a-way in ballast water, and shipping containers. Once a non-native species has been introduced to a new region, the new species must produce viable offspring and become established in the new zone.

Establishment and spread are challenging. To become established, an alien species must adapt to the new environment, reproduce, and create a self-sustaining population. Spread requires dispersal capabilities, allowing movement beyond the area where the non-native species was introduced. The naturalized species then needs to establish itself in habitats along the expanding range edge. It is estimated that approximately 10% of introduced species become naturalized, 10% of naturalized species spread and propagate to establish an invasive population, and 10% of invasive species cause a negative impact. This is known as the 10's rule (Vander Zanden, 2005).

A system that is high in diversity is often less vulnerable to invasion due to biotic resistance (Lake and O'Dowd 1991; Green et al., 2011). Diverse communities have greater competition and predation which creates resistance to invasion. An opening in a community functional feeding group gives an alien species the ability to fill the open niche and become established. Once established the naturalized species often change the ecosystem biotic and abiotic components. Changes in the system allow exotic invaders to displace indigenous taxa, continue to alter habitats, change the dynamics of community structure, and drive the loss of biodiversity and ecosystem functions.

1.1.3 Impacts

Alien invaders systematically change ecosystems at multiple levels. Impacts on native species are diverse, ranging from subtle or indirect impacts such as altering behavior, causing morphological changes, and exposure to new parasites or diseases (Ricciardi et al., 2013), to direct impacts such as interference competition and predation. These individual impacts scale up to communities resulting in alterations to species composition, richness, and evenness (Ricciardi et al., 2013). Alterations to each level of an ecosystem, from single organisms to community, change how energy and nutrients cycle through the system allowing facilitation to occur (Ricciardi et al., 2013). Facilitation occurs when one non-native species directly aids in the establishment and spread of another non-native species. As each invasive species alters the ecosystem in ways that benefit another non-native species such that it becomes established, an invasional meltdown occurs (Simberloff and Von Holle, 1999; Ricciardi, 2005; Ricciardi, 2013).

1.2 Hawai‘i as a study site

The streams of the Hawai‘ian archipelago are an excellent example of the potential impacts of species invasion. Fish released initially on the islands for mosquito control, primarily poeciliids which include mollies (*Poecilia mexicana*), guppies (*Poecilia reticulata*) and green swordtail (*Xiphophorus hellerii*) (Englund, 1999), have proliferated and invaded most of the stream networks (Brasher et al. 2006). This group is believed to have a detrimental impact on the native and highly endangered O‘ahu Odonata, the *Megalagrion* damselflies (Englund, 1999). Other species were introduced to the islands through aquarium release or through government agencies to enhance

fisheries; these taxa include the suckermouth catfish – watawata group (*Hypostomus* sp.), the banded jeweled and convict cichlids (*Hemichromis elongatus* and *Archicentrus nigrofasciatus* respectively), and the smallmouth bass (*Micropterus dolomieu*) (Englund 1999). The list of invasive stream species also includes the Asiatic clam (*Corbicula fluminea*), the Tahitian prawn (*Macrobrachium lar*), Louisiana swamp crayfish (*Procambarus clarkii*), along with two frogs, the Japanese wrinkled frog (*Rana rugose*), the American bullfrog (*Rana catesbeiana*), and the cane toad (*Bufo marinus*).

The Hawai‘ian archipelago is located in the Pacific Ocean, just south of the Tropic of Cancer and approximately halfway between the East Coast of mainland Japan and the West Coast of the United States. The island chain is comprised of small volcanic landmasses drifting northwest with the Pacific Plate and is the most isolated archipelago in the world (Smith et al., 2003; Brasher 2004). Over millions of years, new islands continually formed over the volcanic hotspot, while the older islands drift northwest slowly losing land mass via erosion (McDowell, 2003). One of the most highly invaded islands in the chain is the island of O‘ahu.

O‘ahu maintains mild temperatures year-round that are credited to the lack of variation in seasonal solar radiation and the continual effects of the trade winds that bring more cooling oceanic breezes (Blumenstock and Price, 1967; Sanderson, 1993; Brasher et al., 2003). Although temperature variations among seasons are mild, rapid changes in the topography of the island generate multiple microclimates. The climate ranges from tropical to subtropical on the island with three significant ecoregions, tropical moist broadleaf forest, tropical dry broadleaf forest, and tropical grasslands, savannas &

shrublands (Bailey, 1980), and three main classifications of land use which are urban, agricultural, or forested (Brasher et al., 2003).

The trade winds that blow across the island also give O‘ahu two physiographic zones, the windward and leeward (Brasher et al. 2003). As in most mountainous regions, the island of O‘ahu receives more rainfall with smaller drainage basins on the windward side while the leeward side receives less rainfall and encompasses larger watersheds (Brasher et al., 2003; Oki and Brasher, 2003). O‘ahu experiences a rainy season and a dry season which runs October through April and May through September, respectively. However, heavy rainfall can occur at any time of the year (Blumenstock and Price 1967; Sanderson 1993; Brasher et al., 2003) with rainfall often reaching 25.4 – 50.8 cm in one 24-hour storm period (Giambelluca et al., 1984; Brasher et al., 2003). Due to the rainfall patterns and the island's small drainage basins, most O‘ahu streams are considered flashy (large fluctuations in streamflow due to steep drainage basins and rapid, high volume rainfall events) by nature, although streamflow characteristics are temporally and spatially variable (Brasher et al., 2003).

Due to the volcanic formation, isolated location, and age of the Hawai‘ian Archipelago, local evolution and adaptive radiation have created one of the richest collections of indigenous species in the world (Eldredge and Evenhuis, 2003; McDowell, 2003; Englund, 2007). The same isolation that helped promote an environment with such unique fauna has also left the Hawai‘ian Islands endemically species poor (McDowell, 2003; Brasher, 2004). Continental tropical streams typically have greater crustacean and fish diversity, but lower insect biodiversity than temperate streams (Allen and Flecker,

1993). However, insular tropical streams do not follow the same trend as continental tropical tributaries and show low speciation and simplistic community structure (Smith et al., 2003).

In the Hawai‘ian Archipelago, many benthic freshwater taxa are so rare that they are only found in patchy habitats in few streams, limiting most areas to less than a dozen species (Englund et al., 2007). On average, native macroinvertebrate species richness has approximately 45 taxa (Yamamoto, 2000; Nishida, 2002; Englund et al., 2007), whereas, reference condition mainland streams may have hundreds of species when dipterans are included (Reece and Richardson, 2000). The low native diversity in the freshwater streams on the islands results in simplistic food webs compared to continental streams, leaving niche spaces open within the functional feeding groups and some functional groups such as insect shredders absent (Resh and De Szalay, 1995; Larned, 2000; Holitzki et al., 2013).

1.2.1 Native fauna

Although there are over 130 endemic and indigenous aquatic native insect species across the Hawai‘ian Archipelago, many are so rare they are only found in a few remote streams, often on only one island. Key native species in Hawai‘ian freshwater ecosystems include two species of dragonflies Common Green Darner Dragonfly (*Anax junius*) and the Giant Hawai‘ian Dragonfly (*Anax strenuus*) and one damselfly, Blackburn ’s Hawai‘ian Damselfly (*Megalagrion blackburni*). The Hawai‘ian Islands only freshwater species in the chironomid genus *Telmatogeton* (*T. abnormis*, *T. fluviatilis*, *T. hirtus*, *T. japonicus*, *T. torrenticola*, and *T. williamsi*) are endemic. *Telmatogeton* sp. along with

other native Chironomidae such as the Hawai‘ian midge (*Chironomus Hawai‘iensis*), likely evolved in local intertidal estuaries from saltwater tolerant species (Tokunaga, 1935; Wirth, 1947; Newman, 1977; Newman, 1988; Benbow 2003). Native freshwater fishes include five gobioid species, ‘o‘opu akupa (*Eleotris sandwicensis*), ‘o‘opu nopili (*Sicyopterus stimpsoni*), ‘o‘opu ‘alamo‘o (*Lentipes concolor*), ‘o‘opu naniha (*Stenogobius hawaiiensis*), ‘o‘opu nākea (*Awaous guamensis*). Native crustaceans include one shrimp know as ‘opae kala‘ole or ‘opae kuahiwi (*Atyoida bisulcata*), and one freshwater prawn, ‘opae ‘oeha‘a (*Macrobrachium grandimamus*). All seven of these native fish and crustaceans are amphidromous. Fishes and invertebrates that display migratory patterns spawn in freshwater, then migrate in their larval stage to marine habitats where they spend their early life before returning to freshwater habitats for their adult cycle (Closs et al., 2013).

1.3 Thesis outline and aims

I explored the effects that large-scale pulse removals of invasive species have on stream benthic communities and how the benthic communities responded post-removal. Providing an improved understanding of how invasive species alter and change the community structure of freshwater ecosystems is critical for effective management. This study will help local and regional ecosystem managers and key stakeholders understand:

- i. How the presence of non-native species alters species interactions within stream benthic communities
- ii. How pulsed removal of non-native fish and crustaceans from stream reaches affects benthic communities

- iii. If one-time removal of non-native species can have lasting positive outcomes for native species and ecosystem health

CHAPTER II: Targeted invasive species removal cascades to reduce non-target invasive species through apparent facilitation

2.1 Abstract

Positive and potentially synergistic interactions between non-native species can result in invasional meltdowns that negatively affect native biota. Accordingly, there is interest in understanding whether management interventions can be executed that impede or reverse meltdowns. To address this, I tracked responses of native and non-native benthic invertebrates to invasive fish and crustacean removal. Invasive species were removed in April 2016 from 13 freshwater streams on the island of O‘ahu (Hawai‘i, USA). Following removal, monthly visual surveys of fish communities and invertebrate collections in 2-3-month intervals from November 2016 through August 2017 were completed. Each month, macroinvertebrate samples were collected (4 replicates from each treatment [Experimental + Control] at 13 sites) using a 30.48x 30.48 cm Surber sampler. Samples were sorted, invertebrates identified to the lowest taxonomic resolution possible and then enumerated. I observed that removal of poeciliids, one of the dominant invasive fish groups in Hawai‘ian streams, correlated with an increase in native midges and a decrease in non-native caddisfly *Cheumatopsyche analis*. This suggests that poeciliid predation of native midges indirectly favors non-native caddisfly abundance via competitive release, and that removal of poeciliids allows native midges to outcompete non-native caddisflies. This indicates that management of non-native poeciliids in Hawai‘i can be an effective strategy for promoting native benthic invertebrate populations. Understanding direct and indirect relationships between species in invaded

ecosystems can guide management of invasive species to maximize benefits to native biota.

2.2 Introduction

Species invasion; a global problem

Invasive species, considered to be one of the chief causes of biodiversity loss, change ecosystem dynamics in ways that often lead to detrimental ecological and economic impacts (Zavaleta *et al.*, 2001; Richardson and Ricciardi, 2013). Negative impacts species introductions vary over time, often with rapid initial impacts that level off in the long term (Richardson and Ricciardi, 2013). Impacts on ecosystems by alien species often fluctuate in severity due to variation in environmental conditions and are exacerbated by overlapping stressors such as alterations to carbon, nitrogen and other cycles, as well as climate change, land use change, and natural disturbances (Parker *et al.*, 1999; Ricciardi *et al.*, 2013). Aided by the rapid technological advancements in the ease of transporting goods and services around the world, globalization of trade and commerce has become a key player in species invasion. Global trade, along with intentional release of pets, has allowed the introduction of alien species to new regions to occur at an exponential rate, often with drastic results to the new region and the species that live there (Vitousek *et al.* 1997, Lowe *et al.* 2000, Mooney and Cleland 2001; Holitzki *et al.*, 2013).

Native species, naturally adapted to the region where they are indigenous, can often resist alien invasion. However, disturbances may decrease native biotic resistance to invasion (Diez *et al.*, 2012) allowing non-natives to exploit open habitat. Systems with

reduced amounts of native biodiversity may be more prone to invasion, creating additional changes to the system that then aid additional exotics in the naturalization process (Ricciardi, 2001; Lockwood et al., 2009). This progression, also known as facilitation, is when the activity of one species helps another species to establish, spread, or impact a native species (Green et al., 2011) forming commensal relationships and driving additional habitat modification (Ricciardi, 2001).

An invasional meltdown occurs as changes to a system create a positive feedback loop where naturalized species facilitate other non-natives to establish, often resulting in low native biodiversity (Simberloff and Von Holle, 1999; Ricciardi, 2005; Ricciardi, 2013). For example, on Kiritimati Island in the Indian Ocean, the ability of the non-native giant African land snail (*Achatina (Lissachatina) fulica*) to spread and invade via predation is repressed by the high abundance of the native red land crab (*Gecarcoidea natalis*) (Lake and O'Dowd 1991; Green et al., 2011). However, the alien taxa groups, the yellow crazy ant (*Anoplolepis gracilipes*) and honeydew-secreting scale insects (*Tachardina aurantiaca* and *Coccus* spp.), exhibit a facilitative interaction that allows the ants to form high-density supercolonies which attack and kill the red land crabs, decreasing the crab population and allowing the spread of the invasive giant African land snail (Green et al., 2011). In the Willamette Valley of Oregon, USA, the presence of bluegill (*Lepomis macrochirus* Rafinesque), helped facilitate the invasion of the non-native bullfrog tadpoles (*Rana catesbeiana*), creating a trophic cascade to lower trophic levels by consuming the nymphs of native dragonflies *Aeshna multicolor*, *Aeshna californica*, and *Anax junius* (Adams et al. 2003). This suggests that in cases where multiple invasive species are facilitating one another, the removal of one or more key

invasive species could result in a cascade of interactions that are detrimental to other invaders and beneficial to native species. Such a targeted approach to species removal may be more cost-effective than alternatives where all invasive species are equally targeted in removal efforts.

Hawai‘ian streams provide an excellent study system for evaluating the efficacy of a targeted invasive species removal. Hawai‘ian streams are naturally species-poor and contain a high proportion of indigenous and endemic threatened fishes (Lisi *et al.*, 2018) and invertebrate species (Englund *et al.*, 2007). These streams are the only place where dipterans in genus *Telmatogeton* (*T. abnormis*, *T. fluviatilis*, *T. hirtus*, *T. japonicus*, *T. torrenticola*, and *T. williamsi*), and the species *Chironomus hawaiiensis* (Tokunaga, 1935; Wirth, 1947; Newman, 1977; Newman, 1988; Benbow 2003), and critically endangered damselflies in genus *Megalagrion* are found.

Many Hawai‘ian streams are invaded by fish in the family Poeciliidae which were introduced to control mosquito populations and include mollies (*Poecilia mexicana*), guppies (*Poecilia reticulata*), mosquitofish (*Gambusia affinis*), and green swordtail (*Xiphophorus hellerii*) (Englund, 1999). Poeciliids, as a group, are one of the most widely distributed invasive species in freshwater systems worldwide (Holizki *et al.*, 2013). While the majority of documented impacts are attributed to the western mosquitofish (*Gambusia affinis*) in temperate climates, other members of this group have been found to cause a variety of impacts in tropical streams (Pyke, 2008).

In Hawai‘i, naiveté of native taxa to poeciliid foraging may put them at a disadvantage. Englund (1999) found that immature damselfly species that are native to

the Hawai‘ian Islands swam to the surface of the experimental tank of introduced fishes whereas the introduced larval Odonata, Rambur’s forktail (*Ischnura ramburii*) and roseate skimmer (*Orthemis ferruginea*), dove down and hid in the substrate in response to the presence of these predatory fish. This behavior led to the survival of the introduced Odonata and complete mortality of the native species (Englund, 1999). This suggests that non-native poeciliid predation may benefit non-native invertebrates via competitive releases. Field observations provide further support for this mechanism. Hawai‘ian streams are heavily invaded by non-native *Cheumatopsyche analis*, a numerically dominant species that have few native competitors (Brasher *et al.*, 2004). Holitzki *et al.* (2013) observed that streams with large numbers of invasive poeciliids tended to have reduced numbers of native Chironomidae and greater numbers of non-native *Cheumatopsyche analis*. This observation is suggestive that poeciliids are preferentially consuming native dipterans to the benefit of non-native caddisflies. Impacts may extend to non-insect taxa as well. On Maui and the island of Hawai‘i, the introduction of poeciliids has caused endemic shrimp to modify their diel migration patterns to a nocturnal regime, resulting in impacts on the anchialine pool ecosystems (Havird and Weeks, 2013). Overall, Hawai‘ian streams invaded by poeciliids differ significantly from uninvaded streams in terms of benthic species composition and nutrient dynamics (Holitzki *et al.* 2013).

Conservation programs around the globe are removing aquatic invasive species from streams and rivers to slow the loss of native biodiversity. Mirroring global efforts, the state of Hawai‘i has made the removal of alien species a management priority. However, it is uncertain how effective removal efforts are at reducing densities of

invaders and restoring native communities and ecosystem functions. Two fundamental questions in ecosystem management in this region are to determine precisely how these stream ecosystems have been altered and whether management actions such as large-scale efforts to remove invasive species can have positive outcomes on native species and their ecosystem. Poeciliids may play a key role in facilitating other non-native species by disrupting native food webs, therefore targeted removal of these species may be an effective strategy to shift food webs to a native-species dominated state. To address this question, thirteen streams on the island of O‘ahu were manipulated as part of an invasive species management experiment. Invasive fish, amphibians, and large crustaceans were removed on a large-scale from a study reach in each stream and biota, and ecosystem functions in the experimental stream reach and paired upstream control reaches were monitored through time.

The focus of this study was to evaluate the effects of the invasive species removal on the native and non-native benthic invertebrates in each stream reach. I hypothesized that based on field studies of invaded and uninvaded streams on the Hawai‘ian Islands, Hawai‘ian chironomids, many of which are believed to be native in O‘ahu streams, will increase while the non-native *Cheumatopsyche analis* will decline. Higher elevations should have greater abundances of native fish and macroinvertebrate taxa than lower stream reaches both before and after removal.

2.3 Methods

2.3.1 Study sites

Thirteen streams on the Island of O‘ahu, Hawai‘i, USA (Fig. 1) were chosen to accurately reflect several natural and anthropogenic gradients found throughout the

island. Rainfall varies greatly among microclimates of the island. In contrast to the high biodiversity and invertebrate abundance that healthy forested streams display in the continental United States, forested Hawai‘ian tributaries exhibit lower abundance and diversity than the islands urban tributaries due to species invasions and the island’s limited number of indigenous species (Brasher, 2003). Study streams were chosen to represent a variety of aquatic invasive species (AIS) densities along different land use and rainfall gradients. The design was intended to allow for analysis of possible interactions between precipitation, land use, and the effects of the AIS removal. Sites within each stream were chosen to accurately represent the typical stream habitat along the river corridor and were bounded by natural barriers (e.g., cascades) that would help limit the ability of the AIS to reestablish the removal area.

2.3.2 Catchment information (slope, land-use, etc.)

O‘ahu experiences a rainy season from October through April and a dry season which runs May through September. However, heavy rainfall can occur at any time of the year (Blumenstock and Price 1967; Sanderson 1993; Brasher et al., 2003). The watersheds of each stream were delineated and characteristics including watershed size, land use, percent impervious surface, percent development, hill slope, underlying geology, and mean annual precipitation were extracted from appropriate databases (DAR and USGS). Watersheds varied greatly in size with eight streams (He‘eia, Kahalu‘u, Kalihi, Kawa, Kea‘ahala, Waianu, Waikāne, and Waimānalo) having drainage basins less than 5 km², three streams (Halawa, Mānoa, and Punalu‘u) between 5 – 10 km², and two streams with drainage basins < 15 km² (Kīpapa and Waimea). The mean basin slope was between 70-89%, with the exception of Waimānalo at 44% and Kawa at 15% (Table 1).

Elevation maps (10 m digital resolution) from the National Elevation Dataset (Gesch et al., 2002) were used to obtain slope and area of each stream watershed catchment. All thirteen study systems have maximum elevation heights between 708 m and 941 m except Kawa, which sits at approximately 286 m. The elevation at the study sites ranged from 148 to 379 m. Most of the study areas of the streams have a boulder/cobble or cobble/gravel substrate with two sites falling into silt/gravel. Average annual precipitation was calculated using the “Online Rainfall Atlas of Hawai’i” (Giambelluca et al., 2013), whereas the precipitation gradient that follows O‘ahu’s windward and leeward geomorphic stream catchment features and hydrology followed Lau & Mink (2006). Nine of the stream sites are located on the windward side of the island and four streams on the leeward (Table 1). Changes in substrate material follow the changes in elevation with higher proportions of boulder and cobble substrate at higher elevations and greater proportions of silt and gravel at lower elevations. Except for Kawa and Waimānalo, study sites receive over 2.54 meters of rain annually. The Halawa site was dropped from the analysis after the initial removal due to inadequate sampling collections and stream flow.

The National Land Cover Dataset (2001), classes 21-24 (Homer et al., 2007), while ArcGIS (ArcGIS Desktop: Release 10.1, ESRI, Redlands, CA, USA) was used to measure and quantify (in percentage) different land developmental usages such as agriculture, canopy cover, development intensity (high and medium), bare land and open spaces. Open spaces included areas with light construction with vegetation planted for recreational, aesthetic, and erosion control. Medium developmental intensity ranged from 0 to 28% with the majority of streams below 5%. Kawa was the exception with 28% of

the land around the stream falling into the medium building intensity category. Open space accounted for 3-11% of stream area with the exceptions of three streams (Mānoa, Waimānalo, and Kawa) that had 17%, 21%, and 37% respectively (Table 1).

2.3.3 Experimental design & removal method

Streams were divided into two 100 m reaches separated by a 25 m buffer. The downstream reach was treated as the experimental reach, whereas the upstream reach was used as an experimental control. In March of 2016, all invasive fish, crustaceans, and amphibians were removed from a 100 m reach in 12 of the streams. In July of 2017, the invasive species removal was performed in a thirteenth site, Punalu‘u stream. Each removal reach was bounded by an upstream and downstream block net to prevent invasive species from escaping the reach. Before AIS removals, native species were hand-netted out of the removal reach by snorkelers and held in aerated buckets stream side during the removal process to reduce the likelihood of injury to native animals. Removals were performed by multi-pass electrofishing with a backpack electrofisher (LR-24 Smith-Root, Vancouver, WA). The fishing team then walked through the control reaches with the electrofisher off to simulate the disturbances effect caused by multiple persons walking through the reach.

Taxa removed from each reach were identified and enumerated. Within 24 hours, a spectrum of individuals from each species was measured for total and standard lengths as well as wet mass. Native species were returned to the stream in the same location within the reach that they were removed from, while all AIS were humanely euthanized using five-gallon buckets of stream water containing a high dose of MS-222 or tricaine methanesulfonate. Twenty-one invasive species, in total, were identified throughout the

thirteen study reaches. These twenty-one species included three species of catfish, five poeciliids, three chichlids, one species small mouth bass, one swamp eel, and one loach, as well as three crustaceans – shrimp, and three amphibian – frogs. The catfish are locally known as the bristlenosed/bearded catfish (*Ancistrus temmincki*), suckermouth/armored catfish (*Hypostomus watwata*), and the whitespotted clarias/Chinese catfish/puntat or its Hawai‘ian name ‘o‘opu kui (*Clarias fuscus*). The poeciliids that were removed included the Western mosquitofish (*Gambusia affinis*), shortfin/mexican molly (*Poecilia mexicana*), guppy or rainbow fish (*Poecilia reticulata*), and *Poecilia* sp. which include hybrid complexes of the *salvatoris/mexicana* group, along with the green swordtail (*Xiphopjorus helleri*). Data collected was then used to calculate species composition and biomass.

2.3.4 Water chemistry & nutrients

Water samples for dissolved nutrients were collected in the center of the stream channel and field filtered through a glass fiber filter (Whatman GFX; 0.45 μm), placed on ice, and then stored frozen until analyzed. Samples were shipped to Clackamas, Oregon, USA for analysis by standard colorimetric methods on an Astoria-Pacific Autoanalyzer II for soluble reactive phosphate (SRP), total phosphorus (TP), ammonium (NH_4^+), nitrate (NO_3^-) and total nitrogen (TN). 1 to 3 L of water was collected from the stream on pre-weighed, precombusted filters (ProWeigh) and stored frozen until drying (48 hr, 60 °C) and weighing for assessment of total suspended solids (TSS).

2.3.5 Benthic invertebrate community

Benthic invertebrates were collected in replicate ($n = 4$) within the treatment reach and the upstream control reach of each study stream using a 0.093 m^2 Surber

sampler. Samples were taken within two weeks after AIS removal and then at two to five-month intervals (referred to as “cycles”). For the 12 streams that received the treatment in spring of 2016, the first benthic invertebrate samples were collected from the removal and upstream control reaches in April 2016, within a month of the invasive fish removal, and then in sampling cycles from November 2016 through August 2017. For Punalu‘u, sampling occurred 6 times prior to removal and then directly after invasive fish removal in July of 2017.

Invertebrate samples were preserved in 80% ethanol, then later drained, shipped to the Limnology Lab at TAMUCC, refilled with ethanol, and then sorted under a dissecting scope at 40x magnification. All invertebrates were picked from the sediment, identified to the lowest possible taxonomic resolution (typically genus or species) using Merritt and Cummins (2011), Knezovic et al. (2015), Landcare Research (2017), and CPIE Project (2011), and then enumerated. Due to the difficulties of identifying Hawai‘ian Chironomidae in their larval stages, taxa in the Chironomidae family were classified as native species, because most of these non-biting midge species are known to be native in Hawai‘i. In their 2007 study on using aquatic insect taxa as stream health indicators, Englund et al. determined sixteen of the eighteen chironomids they observed were either indigenous or endemic to the Hawai‘ian islands.

2.3.6 Statistical analyses

Data from the twelve streams that underwent removal in March 2016 were analyzed independently from Punalu‘u, as removals in Punalu‘u occurred approximately 16 months after the rest of the streams, and data were collected pre- and post-removal in Punalu‘u as opposed to the post-removal sampling only in the other 12 streams.

Community analysis was performed via NDMS (non-metric multidimensional scaling), using the metaMDS function in Vegan Library in R (Oksanen 2013). Ordinations were fit using two axes for ease of interpretation and n=1000 iterations to maximize fit.

Following the ordinations, we performed PERMANOVA tests to evaluate the effects of treatment (removal vs control), cycle (i.e., sampling period), and stream.

To explore the relationships between environmental covariates and community composition among streams, I performed a CCA (constrained correspondence analysis) using the Vegan library in R (Oksanen 2013). The original dataset contained over 100 covariates that included land use, elevation, slope, topography, number of taxa removed, litter decomposition rates, and nutrients. Prior to the CCA, the complete dataset was paired down to the top ten variables using Ordination fit in R, that maximized explanatory power and were not redundant with one another: medium development land cover, open land cover, NH_4^+ , mean basin slope greater than 30%, max temperature, mean temperature, total suspended solids, poeciliid abundance, and annual precipitation. The research focus on poeciliids was based on prior work showing the many factors this group of livebearers have on benthic communities and revealing the need to identify what has the potential for the greatest effect.

To test for the effect of treatment and sampling period (cycle) on benthic invertebrate response variables including Shannon diversity, total abundance, taxonomic richness, and the abundance of common taxa, we ran mixed effects models using lme function in the nlme package in R. In all of the models, stream identity was treated as a random effect with autocorrelation structure of 1. Significant treatment effects were then explored among the streams by relating treatment effect size for each stream to among-

site differences in residence fish communities and environmental variables using generalized linear models. To test for the predicted relationships between native and introduced benthic invertebrates, I ran mixed effects models testing for the effect of cycle and invasive species abundance on native species abundance, treating site as a random effect with an autocorrelation structure of 1. A mixed effect model was conducted to test the interactions between *C. analis* and poeciliids densities in removal reaches.

2.4 Results

2.4.1 Water chemistry

Mean water temperature at study streams ranged from 20.6 - 24.7 C° with maximum temperatures peaking as high as 31.9 C° at Waimānalo. Ammonium was variable throughout the study streams ranging between 2.4 to 8.4 µg for Kahalu‘u, Waikāne, Waimea, Kea‘ahala, He‘eia, Waianu, Kīpapa, and Kalihi whereas concentrations in the other four streams had were two to four times greater (Table 1). Waimānalo has the largest concentrations of NH_4^+ at 45.88 µg. Coinciding with the high levels of NH_4^+ , total suspended solids (TSS) in Waimānalo were more than three times the amount in the other streams at 14.15 µg. The other eleven streams have TSS levels between 0.973 and 4.42 mg (Table 1).

2.4.2 Seasonal changes in invertebrate composition

After excluding Mollusca from the species list there were eight taxa that were the most common in all streams: *Cheumatopsyche analis*, Chironomidae, Ostracoda, Oligochaeta, Tricladida, *Hyaella azteca* sp., *Hemerodromia stellaris*, and *Hydroptila* sp. (Fig. 2). There were slight temporal variations in community composition in the study streams and some taxa were only observed during the wet or dry season.

Seven taxa (*Caenis punctate*, Coleoptera, Culicidae, Homoptera, Myodocopina, Nematoda, and Turbellaria) were collected during the 2016 dry season but not in the 2017 dry season. The relative abundance of the most common taxa changed between years. The relative abundance of *Cheumatopsyche analis* and Chironomidae was less in 2017 than in 2016. However, the relative abundance of Chironomidae starts to rebound in the Dry 2017 season while *C. analis* relative abundance continues to decline. In Punalu'u, Cheumatopsyche were the largest proportion of the community near the start of the dry season (December) comprising 37% of the macroinvertebrate community (Fig. 2b); by the beginning of the rainy season, they were < 2% (Fig. 2b).

2.4.3 Spatial variation in invertebrate communities

Overall community composition varied among the study streams. However, five dominant species are commonly found. The dominant taxa include *Cheumatopsyche analis*, Chironomidae, *Hydroptila* sp., Oligochaeta, and Ostracoda (Table 2). Eighteen of the twenty-seven macroinvertebrate taxa found in O'ahu streams are rare that together they only constitute around 1% of abundance in stream communities.

The non-metric multidimensional scaling model had a stress level of 0.222 indicating a reasonable fit of the data (Oksanen 2013). The first NMDS axis contained the largest proportion of variation in stream community composition (Fig. 4). The variables in the constrained correspondence analysis on the relationships between the covariates and stream communities explained between 9.7-24.51% of the variation in community composition (Table 3) and identified two groups of diametrically opposed predictors. Temperature, NH_4^+ , landcover, and TSS are oriented in a vector that is positive with NMS1 and NMS2, whereas precipitation, slope, and poeciliids are oriented

in the opposite direction in a wider spread (Fig. 3). Subsequent analysis to explore the covariation in drivers negatively associated with NMDS1 identified poeciliids as being correlated with precipitation and slope metrics, with more poeciliids removed in streams with greater slope and rainfall (Fig. 4). More poeciliids were removed from the seven streams where 70% or more of the basin had a slope of $> 30\%$ and an average annual rainfall of $> 3.41 \text{ (m)} \pm \text{SE } 0.31 \text{ (m)}$ vs. streams with $<$ basin slope and rainfall.

2.4.4 Treatment effects on invertebrate communities

Results of the PERMANOVA indicate that there are significant positive interactions between Site and Cycle ($P = 0.01$), a significant positive interaction between Treatment and Site ($P = 0.04$), and a three-way interaction between Site, Treatment, and Cycle ($P = 0.04$) on stream invertebrate community abundance, richness, and diversity (Table 4a). Whereas in Punalu'u, both Treatment ($P = 0.02$) and Cycle ($P = 0.01$) had direct effects on community composition; but no interaction between factors (Table 4b). The changes in Punalu'u community dynamics include greater abundances of *C. analis* and *Hyalella Azteca* sp. and lower abundance of *Oligochaete* in the dry season. The reverse is true in the rainy season.

There were significant positive interactions of Sampling Period on individual species Richness for all streams (Table 5a/5b). For Punalu'u there was a non-significant effect of Sampling Period on Shannon Diversity ($P=0.06$) (Table 5c). However, there was no significant treatment effect on any of these responses. We observed a significant positive effect of treatment on *Cheumatopsyche analis* in all study streams (Punalu'u excluded) with populations decreasing directly after removal ($P = 0.01$), and a significant negative treatment effect on amphipod abundance ($P = 0.02$) (Table 5d, 5e). On the first

sampling date the abundance of *C. analis* was less in removal reaches than the control reaches in two of the nine sites. Caddisfly abundance continued to decline, or remain depressed, in six of the nine sites. The six streams that showed declines had an average decrease in poeciliid density of -1.0333 ± 0.352 SE after the removal event, whereas the remaining three that did not show declines in *Cheumatopsyche analis* had an average decrease in poeciliid density of -0.4222 ± 0.294 SE (Fig. 5). The size of the reduction in density of poeciliids due to the removal explained 95% of the variation in *Cheumatopsyche analis* response magnitude ($P < 0.001$, $F=95.34$, $df=2,7$; Fig. 5). The size of the reduction in density of poeciliids due to the removal explained 95% of the variation in *Cheumatopsyche analis* response magnitude ($P < 0.001$, $F=95.34$, $df=2,7$; Fig. 5).

Treatment did not have a significant positive effect on chironomid abundance ($P = 0.142$, $df= 1,275$), however, chironomids increased in removal reaches relative to control reaches in four of the nine streams. The streams where chironomids increase were the same streams where the largest declines in *Cheumatopsyche analis* abundance were recorded. The abundance of *C. analis* exerted a significant negative effect on Chironomidae ($P < 0.001$, $df=1,275$, $F=198.85$). This effect varied temporally and was greater where poeciliid densities were higher ($P < 0.001$, $df=4,275$, $F=8.54$).

2.5 Discussion

Invasional meltdown refers to the positive effects one non-native species has on the establishment and invasion of the new species (Simberloff and Von Holle 1999). Non-native species may facilitate the establishment of yet more non-native species, creating a positive feedback loop that accelerates the invasion rate, creating a meltdown

effect (Simberloff & Von Holle, 1999; Simberloff, 2006). Although the invasional meltdown theory has been investigated in many systems, I do not know how ecosystems that have experienced invasional meltdown will respond when invasive species that were key contributors to the feedback loop are removed. Analyses suggest that the invasional meltdown process can be reversed if the key invaders are removed. I observed that the removal of non-native poeciliid fishes, predator of native benthic invertebrates, resulted in reductions in the abundance of other non-native invertebrates. Mechanistically, the reduction in poeciliid predation allowed native midges to rebound and outcompete non-native hydropsychid caddisflies. The ecosystem response reveals that a key group of species are maintaining a component of invaded Hawai‘ian streams via predation on native species.

Community composition in freshwater habitats follows gradients that combine the multiple effects of physical and biotic factors (Wellborn et al., 1996). I observed that benthic invertebrate communities differed among streams and throughout time. Although other anthropogenic factors, such as NH_4^+ , temperature, and TSS, are correlated with densities of invasive fish species on the island of O‘ahu, it appears that slope and precipitation play a more important role in the distribution of both invasive and native species. I interpreted the water quality predictors to represent human impacts and their effect on stream biota, whereas the hydrological variables represent natural environmental gradients in rain and slope driven by the mountain range. The three streams with the highest number of invasive poeciliids removed (> 500 individuals) had mean basin slopes of 75% or higher. There was no trend between these factors and the

macroinvertebrate recovery. Invasive poeciliid abundance is positively correlated with slope: at the same time, slope contributes to species richness of invasive benthic taxa.

Due to natural variability in stream flow dynamics, seasonal variation in abundance without complete species replacement is common in subtropical streams (Mesa, 2012). Although spatial variations in O‘ahu stream communities can be attributed to natural and anthropogenic effects, seasonal effects could be partially responsible for temporal variation in benthic communities. Results show a similar seasonal change in invertebrate community structure in all streams with a negative trend between the seasonal sampling periods and non-native benthic invertebrates observed in all sites. However, I observed that a significant portion of the temporal variation can be attributed to the effect of the AIS removal as the composition of the taxa was altered once the main seasonal reproduction cycle began. Alien invertebrate species abundance continued to decline after the removal event in April 2016 until May 2017, which coincides with the beginning of the rainy season.

2.5.1 Fish removal effects on benthic invertebrates

I observed that benthic invertebrate invasive species richness declined at all sites after invasive fish and crustacean were removed, however, declines are more substantial in the removal reaches than the control reaches. Invasive invertebrates increase in abundance in control reaches after the seasonal decline relative to the experimental reaches. However, the abundance of non-native invertebrates in the removal reach declined again after their initial rebound. The loss of a synergistic effect between invasive fish and the non-native invertebrates could be a key driver in changes to invasive species richness and abundance. The impact of frequent monthly sampling and snorkel surveys is

likely responsible for the observed decline in AIS observed in both treatment and control streams. Swimming, walking, and disturbing each stream reach may have caused benthic organisms to enter the drift, reducing densities relative to pre-experiment amounts.

The significant negative effect of removal on non-native caddisfly (*Cheumatopsyche analis*) provides support for my hypotheses regarding cascading effects of AIS removal on other exotic species. After post-invasive fish were removed, I observed a steady decline in the relative abundance of *C. analis*, from approximately 40% of the community in the dry season of 2016 to only 17% in the dry season of 2017. This decline is especially impressive considering that *C. analis* in Hawaiian streams are multivoltine with continuous recruitment (Kondratieff et al., 1997). Thus, there is less potential for the results of this study to reflect a lag effect due to an annual reproductive cycle. Mechanistically, these results are well explained by the removal of predation pressure. Poeciliids prefer native Chironomidae prey (Arthington, 1989; Bassar et al., 2010; Holizki et al., 2013). This dietary specialty might be attributed to the limited gape size of the two dominant poeciliid species (*Poecilia reticulata* and *Xiphophorus helleri*). The gape size of these two species does not exceed 2.3 mm, making Chironomidae (mean length approximately 3.3 mm) easy to capture and swallow. In contrast, non-native *C. analis* (mean length approximately 7.3 mm) grow beyond the gape size of these primary predators while competing with Chironomids for space and food (Holizki et al., 2013). Thus, restriction in gape size highly influences competitive dynamics between chironomids and *C. analis* (Fig. 7). While this dynamic has been previously proposed and is supported by spatial observations in organism relative abundances (Holizki et al., 2013), these results, derived from a manipulative experiment, provide support for the

hypothesis. The post-hoc analysis relating *C. analis* response magnitude to the magnitude of the poeciliid removal further supports this interpretation. Streams in which the largest numbers of poeciliids were removed per unit area were in the most invaded state pre-experiment and had the greatest top-down pressure being exerted on the benthic community. Thus, these were the sites that had the greatest potential for change after invasives were eliminated.

For Punalu‘u stream, from which invasives were removed fifteen months after sampling had started, I observed the treatment effects on non-native hydroptilids was negative, lowering the species abundance, whereas ostracods responded positively. I also detected a negative temporal effect on *Cheumatopsyche analis* and hydroptilids and positive temporal effects on ostracods and amphipods. Although some of these effects may have been seasonal, the delay in response times of the invasive caddisflies suggests causal attribution to the removal. Once the predation pressure by poeciliids on small-bodied benthic invertebrates is eliminated, the larger *C. analis* faces greater competition for food and space from Chironomidae and hydroptilids. However, these trophic effects may not all be positive. *Hyaella azteca* sp., an invasive amphipod, nearly triples in abundance between 2016 and 2017 dry seasons in the experimental reaches, suggesting release from top-down predation pressure.

2.5.2 Spatial environmental effect

On Oah‘u, rapid changes in the topography drive climate variation, ranging from tropical to subtropical, with three major ecoregions: tropical moist broadleaf forest, tropical dry broadleaf forest, and tropical grasslands, savannas & shrublands (Bailey 1980). The geomorphology of each ecoregion, along with anthropogenic factors, affects

stream spatial invertebrate composition. However, I found that slope and elevation are correlated with densities of poeciliids and invasive benthic macroinvertebrates. Higher species richness of invertebrates in study sites was greater at elevations above 45 m and steeper slopes. Although this seems counterintuitive, ecosystems on Hawai‘i are naturally depauperate. While aquatic insect species can surmount dispersal barriers like plunges, dry stretches, and waterfalls during their adult flying stage, poeciliid dispersal is constrained by these features and their densities correlate positively with hill slope.

2.5.3 Caveats, considerations, and future work

Invasive freshwater fishes impact streams from both top-down and bottom-up mechanisms. Invasive prey species may attract predation of some species while releasing predation of others which results in higher native species richness and adds to the mortality rate of other stream species by apparent competition (Castorani and Hovel, 2015). Poeciliids, a group of predatory fishes, are a known threat to aquatic ecosystems across the Hawaiian Archipelago (Englund, 1999). Poeciliids change ecosystem geochemical structure and ecological functions in Hawai‘ian streams by altering biotic and abiotic factors (Holizki et al., 2013). The results of this study provide additional information about the role of poeciliids play in structuring communities through trophic interactions; in this case, poeciliids help facilitate other invasives. However, the results have broader implications as well.

My study shows that managing ecosystems that contain communities that are dominated by non-natives requires an understanding of the ways that species facilitate one another. By understanding how invasive species rely on one another, future decision making may be more effective if key invasive facilitators are targeted. Future studies that

include spatial and temporal data collected before as well as after the removal of non-native species and more frequent sampling following removal would allow more robust analysis and comparisons. Collecting invertebrate organisms prior to the removal of non-native invasive fish would elucidate the direct effect of electrofishing on invertebrates. Future studies that included more spatial data, especially the addition of removal sites at different elevations of the streams in concert with the added temporal data, might help researchers and managers better understand the covarying effect of elevation on the relationships between physical and biotic factors.

Although ample study has been devoted to Hawai‘ian terrestrial insects, research on freshwater insect and benthic macroinvertebrate fauna are scarce (Englund et al., 2007). In these early life stages identification to species is exceedingly difficult because there are few taxonomic keys or detailed illustrations to aid in the identification of insects in their larval stages (Englund et al., 2007). When DNA processing becomes more feasible, identification of the smallest stream invertebrates may improve, allowing researchers to more clearly understand the fine-scale details of freshwater food webs and the connections each species has within its ecosystem. For this study, it would have been beneficial to have taxonomic keys designed to aid in the identification of the Hawai‘ian Chironomidae facilitate a clearer understanding of the dynamics between native and non-native species. Further research should focus on the presence of other invasive species, the importance of their ecological interactions, and how apparent facilitation may be the key factor in that propagates non-native species into invasive species. Finding these connections could be the best way to deal with areas, such as Hawai‘i, where invasional meltdowns have occurred.

2.5.5 Summary

To slow the effects of invasive species on native fauna and ecosystems, the state of Hawai‘i has initiated a variety of plans to remove alien species. Two key questions in ecosystem management in this region are: 1) to determine exactly how stream ecosystems have been altered, and 2) whether management actions such as large system efforts to remove invasive species can have positive outcomes on native species and their communities. This study shows management that in ecosystems in which multiple non-native species have become dominant may benefit from an understanding of how interspecific interactions maintain the state of invasion and how positive interactions between non-native species can negatively impact the native biota and ecosystem processes.

In this study, removal of one of the top invasive taxa (Poeciliidae) led to the decrease in abundance of another invasive taxon (caddisflies) by reducing predation pressure on the caddisflies competitor, chironomids. My data show that ecosystems that have suffered from multispecies invasion can benefit from understanding the apparent facilitation that species share with each other. In areas that must deal with multiple invasive species, understanding the relationships between organisms in their ecosystem will help effectively manage invasive species to maximize the removal control while streamlining cost. An important next step will be quantifying the full benefit to the ecosystem when positive interactions between invasive species are severed.

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APPENDIX A

Biota collected April 2016 through August 2018 for this study and their native or introduced status. [Status classification from Eldredge and Miller (1997), Yamamoto and Tagawa (2000), Nishida (2002), and Englund et al. (2007), Parham et al. (2008).]

Taxa	O.T.U	Status (N = Native; U * Undetermined; I = Introduced)
Native Aquatic Macroinvertebrates	<i>Atyoida bisulcata</i>	N
	<i>Ferrissa sharpi</i>	N
	<i>Namalycastis abiuma</i>	N
	<i>Neritina granosa</i>	N
	<i>Neritina vespertina</i>	N
	<i>Prostoma sp.</i>	N
Native Aquatic Insects	Chironomidae	N
	Collembola	N
	Homoptera	N
	<i>Limonia sp.</i>	N
Undetermined Aquatic Macroinvertebrates	Gastropoda	U
	<i>Glossiphonia weberi lata</i>	U
	Hirudinea	U
	Myodocopina	U
	Nematoda	U
	Oligochaeta	U
	Ostracoda	U
	Physidae	U
	Tricladida	U
	Turbellaria	U
Undetermined Aquatic Insects	Armadillidae	U
	Ceratopogonidae	U
	Coenagrionidae	U
	Coleoptera	U
	Collembola	U
	Gynacantha	U

**Introduced Aquatic
Macroinvertebrates**

<i>Barbronia weberi</i>	I
<i>Corbicula fluminea</i>	I
<i>Hyalella azteca</i> sp.	I
<i>Melanoides tuberculata</i>	I
<i>Neocaridina denticulata</i>	
<i>sinensis</i>	I
Physidae	I
<i>Procambarus clarki</i>	I
<i>Pseudosuccinea columella</i>	I
<i>Tarebia granifera</i>	I

Introduced Aquatic Insects

<i>Caenis punctata</i>	I
<i>Cheumatopsyche</i> sp.	I
Culicidae	I
<i>Hemerodromia stellaris</i>	I
<i>Hydroptila</i> sp.	I
<i>Oxyethira maya</i>	I

* Undetermined species are taxa that could not be identified to a species level as to verify their status or species that at the time my study was conducted had not yet been determined.

Table 1. Stream covariates. Invasive counts are per 100 m removal reach. Values of stream parameters post and pre removal of ammonium (NH4+), nitrate (NH3-), phosphorus (SRP), and total suspended solids (TSS) at removal (Rem) and upstream control (UC). Orographic effects are Windward (W) and Leeward (L)

Stream		He'eia	Kahalu'u	Kalihi	Kawa	Kea'ahala	Kipapa	Punalu'u	Mānoa	Waianu	Wikāne	Waimānalo	Waimea
Max Temp (C°)		23.45	25.03	23.74	29.05	24.45	28.46	25.61	29.52	24.55	25.90	31.88	29.55
Mean Temp (C°)		20.59	21.58	22.10	24.74	20.90	22.95	21.77	23.21	21.52	22.30	24.34	22.57
NH4+ Avg (µg)		5.95	2.38	10.06	27.56	3.64	8.38	0.00	21.08	6.89	2.68	45.88	3.13
NO3 Avg (µg)		34.18	92.31	40.77	710.31	141.98	20.25	13.35	74.56	43.61	69.27	411.46	7.51
SRP Avg (µg)		17.29	19.93	10.67	22.22	37.77	3.94	11.27	14.33	16.88	8.78	15.47	4.37
TSS Avg (mg)		1.75	0.97	2.49	3.55	3.09	2.02	2.37	4.41	2.83	2.55	14.15	1.20
Pre NH4+ (µg)	Rem	4.98	1.60	4.85	20.60	3.05	9.86	0	11.92	3.21	3.21	27.73	1.05
	UC	4.69	1.94	4.79	27.08	2.05	7.73	0	11.35	2.86	3.84	35.08	2.35
Post NH4+ (µg)	Rem	5.95	2.38	10.06	27.56	3.64	8.38	0	21.08	6.89	2.68	45.88	3.13
	UC	3.10	1.99	11.53	33.84	3.27	5.78	0	17.98	6.37	2.07	61.54	3.23
Pre NO3- (µg)	Rem	51.06	86.51	49.86	1031.01	210.15	54.03	0	12.42	13.99	89.85	275.08	5.11
	UC	48.41	133.66	29.69	556.26	212.82	0	0	7.44	57.00	71.52	193.75	2.10
Post NO3- (µg)	Rem	44.76	83.53	28.87	584.71	115.86	0	0	35.56	28.25	28.69	348.55	4.55
	UC	56.27	66.19	9.29	1223.43	200.29	0	0	14.92	79.79	35.24	264.54	3.17
Pre SRP (µg)	Rem	23.48	22.92	8.50	34.13	42.52	4.26	0	10.25	15.24	12.19	13.45	3.23
	UC	22.49	27.88	10.93	24.03	39.34	0	0	8.46	31.46	11.80	16.68	2.60
Post SRP (µg)	Rem	24.12	23.41	7.71	27.72	40.27	0	0	9.09	18.65	10.56	8.92	2.46
	UC	22.29	23.93	9.23	21.19	42.46	0	0	8.23	37.30	10.59	10.42	2.35
Pre TSS (mg)	Rem	1.63	0.57	1.37	2.15	3.6	2	0	6.53	3.5	1.8	15.7	0.25
	UC	3	0.63	1.33	3.55	1.62	0	0	6.05	3.3	1.85	13.4	0.65
Post TSS (mg)	Rem	1.55	0.67	1.17	2.29	3.8	15.37	0	3.85	5.25	1.35	10.23	1.9
	UC	1.25	0.85	1.52	2.36	2.5	0	0	4.95	5.9	1.5	13.83	0.65
Annual Precipitation (m)		2.58	3.06	3.03	1.70	2.55	3.25	4.72	3.10	4.17	3.75	1.65	2.83
Land Use (%)	Open	9	11	3	37	9	7	4	17	9	7	21	3
	Med Dev	2	2	1	28	3	5	0	12	0	0	4	0
	High Dev	0	0	0	10	1	2	3	0	0	0	2	0
	Bare	0	0	0	0	0	0	0	0	0	0	0	0
	Evergreen	3	30	89	23	35	70	60	76	62	79	60	90
	Crops	0	0	0	0	0	3	0	0	0	0	2	0
Mean Basin Slope		79.27	75.34	56.8	14.88	75.66	44.34	53.06	63.56	62.98	63.56	39.45	48.74
Elevation (m)	At Site	95	48	163	5	36	110	9	45	22	15	4	17
Orographic Effect		W	W	L	W	W	L	W	L	W	W	W	L
Poeciliids Count		881	524	172	6	812	99	1180	32	1257	402	1455	0
Natives		4	165	118	27	101	0	132	9	67	46	349	12

Table 2. Individual species ratio to the total sampled species that comprise of > 1% of the community composition in at least one site by stream. Taxa were sorted alphabetically top to bottom.

Taxa	Stream											
	He'eia	Kahalu'u	Kalihi	Kawa	Kea'ahala	Kipapa	Mānoa	Punalu'u	Waianu	Waikāne	Waimānalo	Waimea
<i>Babronia weberi</i>	0.017	0	0.028	0	0	0	0	0	0	0	0	0
<i>Cheumatopyche analis</i>	0.626	0.448	0.399	0	0.135	0.117	0.006	0.162	0.445	0.807	0.209	0.191
Chironomidae	0.063	0.125	0.051	0.061	0.451	0.1	0.031	0.063	0.385	0.054	0.051	0.238
<i>Corbicula fluminea</i>	0	0	0	0	0	0	0	0	0	0	0.168	0
<i>Hemerodromia stellaris</i>	0	0	0	0	0.013	0	0	0.013	0.018	0.008	0	0
<i>Hyaella azteca</i> sp.	0	0	0.097	0.097	0.119	0.032	0.165	0	0	0	0.008	0.024
<i>Hydroptila</i> sp.	0	0	0	0.444	0.01	0	0	0.169	0.015	0	0	0.024
<i>Melanoides tuberculata</i>	0	0	0	0	0.043	0.056	0.019	0	0	0	0.055	0.1
Myodocopina	0	0	0	0	0	0	0	0	0	0	0	0
<i>Namalycastis abiuma</i>	0.011	0	0.004	0.02	0	0	0.008	0	0	0.006	0.012	0.005
Nematoda	0.019	0	0.004	0.008	0	0	0	0	0	0	0	0
<i>Neocaridina denticulata sinensis</i>	0.013	0	0	0	0	0.004	0	0	0	0	0	0
Oligochaeta	0.151	0.29	0.322	0.028	0.092	0.639	0.271	0.544	0.004	0.056	0.327	0.348
Ostracoda	0.017	0.059	0.081	0.121	0.014	0.016	0.416	0.012	0.067	0.04	0.127	0.048
<i>Oxyethira maya</i>	0	0	0	0	0	0	0	0.012	0	0	0	0
Physidae	0	0	0	0.016	0	0	0.013	0	0	0	0	0
<i>Tarebia granifera</i>	0	0	0	0.177	0.011	0	0.018	0	0	0	0	0
Tricladida	0.042	0.04	0	0.008	0.098	0.028	0.022	0.023	0.06	0.011	0	0

Table 3. Results of constrained correspondence analysis

Predictor	NMDS1	NMDS2	R2	P-value
Medium Development Land in Watershed	0.98	0.2	0.245	< 0.001
NH ₄ ⁺ (mg/L)	0.917	0.398	0.222	< 0.001
% Watershed > 30% Slope	-0.999	-0.044	0.217	< 0.001
Maximum Water Temperature	0.912	0.41	0.18	< 0.001
Open Land in Watershed	0.993	0.118	0.15	< 0.001
Total Suspended Solids (mg/L)	0.982	0.189	0.149	< 0.001
Mean Temperature	0.781	0.625	0.14	< 0.001
Watershed Slope	-0.904	-0.428	0.123	< 0.001
Poeciliid Density	-0.63	-0.776	0.122	< 0.001
Annual Precipitation	-0.911	0.413	0.097	< 0.001

Table 4a. PERMANOVA of Site*Treatment*Sampling Period for all sites except Punalu'u.

	DF	Sums of Sqs	Mean Sqs	F.Model	R2	Pr(>F)
Site	11	20.05	1.823	6.882	0.199	0.01
Treatment	1	0.329	0.329	1.241	0.003	0.19
Sampling Period	4	3.914	0.979	3.695	0.039	0.01
Site: Treatment	10	3.412	0.341	1.288	0.034	0.04
Site: Sampling Period	26	11.949	0.46	1.735	0.119	0.01
Treatment: Sampling Period	4	0.856	0.214	0.808	0.009	0.78
Site: Treatment: Sampling Period	25	7.753	0.31	1.171	0.077	0.04
Residuals	198	52.44	0.265		0.521	
Total	279	100.708			1	

Table 4b. PERMANOVA of Treatment*Sampling Period for Punalu'u Stream

	DF	Sums of Sqs	Mean Sqs	F.Model	R2	Pr(>F)
Treatment	1	0.522	0.522	2.114	0.029	0.02
Sampling Period	6	5.945	0.991	4.016	0.331	0.01
Treatment: Sampling Period	6	1.617	0.27	1.092	0.09	0.32
Residuals	40	9.87	0.247		0.55	
Total	53	17.954			1	

Table 5. ANOVA values of effect of Cycle*Treatment on all study streams

5a. Richness of Sampling Period*Treatment for all streams except Punalu'u

	DF	F-value	<i>P-value</i>
(Intercept)	1	216.509	<.0001
Sampling Period	4	11.205	<.0001
Treatment	1	0.061	0.805
Sampling Period:Treatment	4	0.330	0.858

5b. Richness of Sampling Period*Treatment for Punalu'u

	DF	F-value	<i>P-value</i>
(Intercept)	1	40.852	<.0001
Sampling Period	6	4.426	0.002
Treatment	1	0.591	0.447
Sampling Period:Treatment	6	0.291	0.938

5c. Shannon Diversity of Sampling Period*Treatment for Punalu'u

	DF	F-value	<i>P-value</i>
(Intercept)	1	27.393	<.0001
Sampling Period	6	2.301	0.059
Treatment	1	3.195	0.084
Sampling Period:Treatment	6	0.699	0.653

5d. Sampling Period*Treatment on Cheumatopsyche analis

	DF	F-value	<i>P-value</i>
(Intercept)	1	2.260	0.134
Sampling Period	4	0.849	0.496
Treatment	1	6.703	0.010
Sampling Period:Treatment	4	1.669	0.158

5e. Sampling Period*Treatment on Halalella azteca

	DF	F-value	<i>P-value</i>
(Intercept)	1	5.401	0.021
Sampling Period	4	2.399	0.051
Treatment	1	5.899	0.016
Sampling Period:Treatment	4	0.993	0.412

FIGURE LEGEND

Figure 1. The 13 study sites on the Hawai‘ian Island of O‘ahu. Outline indicate study watersheds, greys indicate urban development intensity

Figure 2. Seasonal community composition of total taxa in O‘ahu study streams. The top eight taxa are listed while the “other” group contains species that contributed <1.5% of the vertebrate species. (a) Community composition in all streams minus Punalu‘u. (b) Community composition for only Punalu‘u

Figure 3. Results of constrained correspondence analysis for all streams show a relationship between environment and community that appear to be primarily oriented along the first ordination axis. Temperature, TSS, development, and nutrients positively associated with NMDS1 and precipitation, slope, and poecilid density at time of removal negatively associated with NMDS2

Figure 4. Relationship between Poecilid count and stream slope

Figure 5. Relationship between number of poecilids removed during the treatment application and the paired mean difference between the upstream control and the removal reach of *Cheumatopsyche analis*

Figure 6. Conceptual diagram for the relationship between Poecilids, Chironomids, and *Cheumatopsyche analis*

Figure 1.

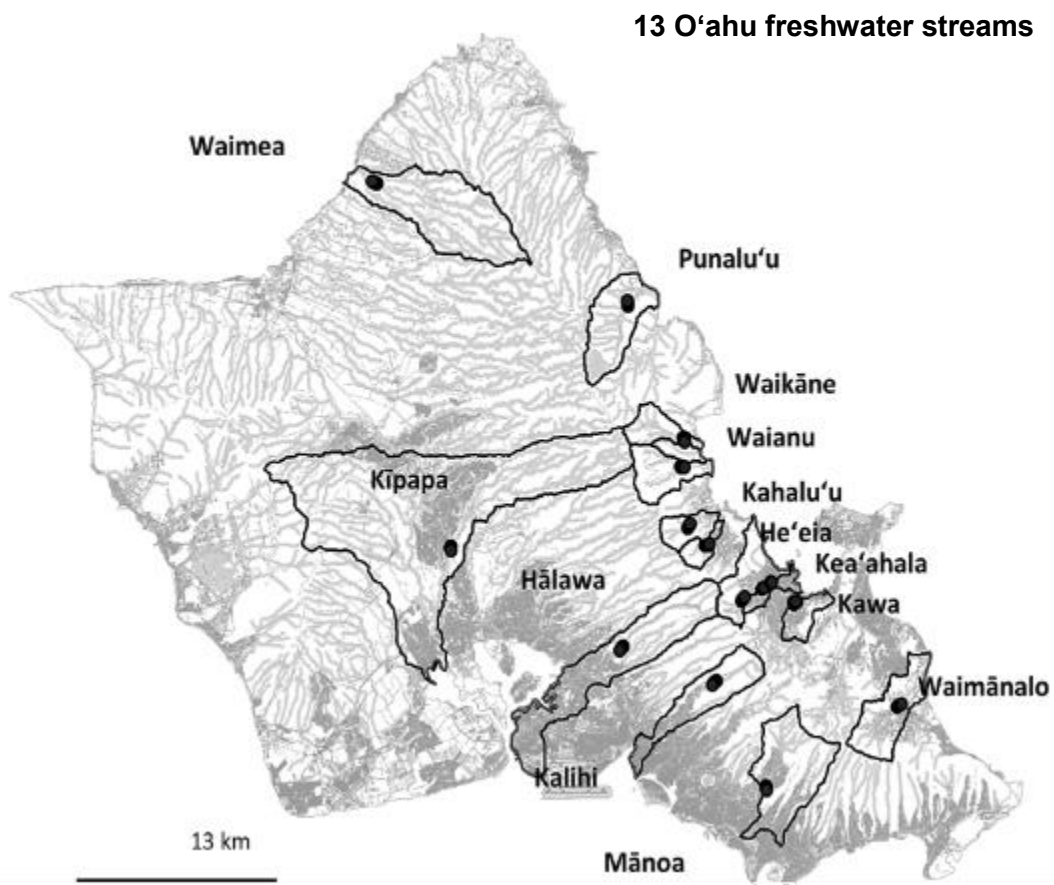


Figure 2.

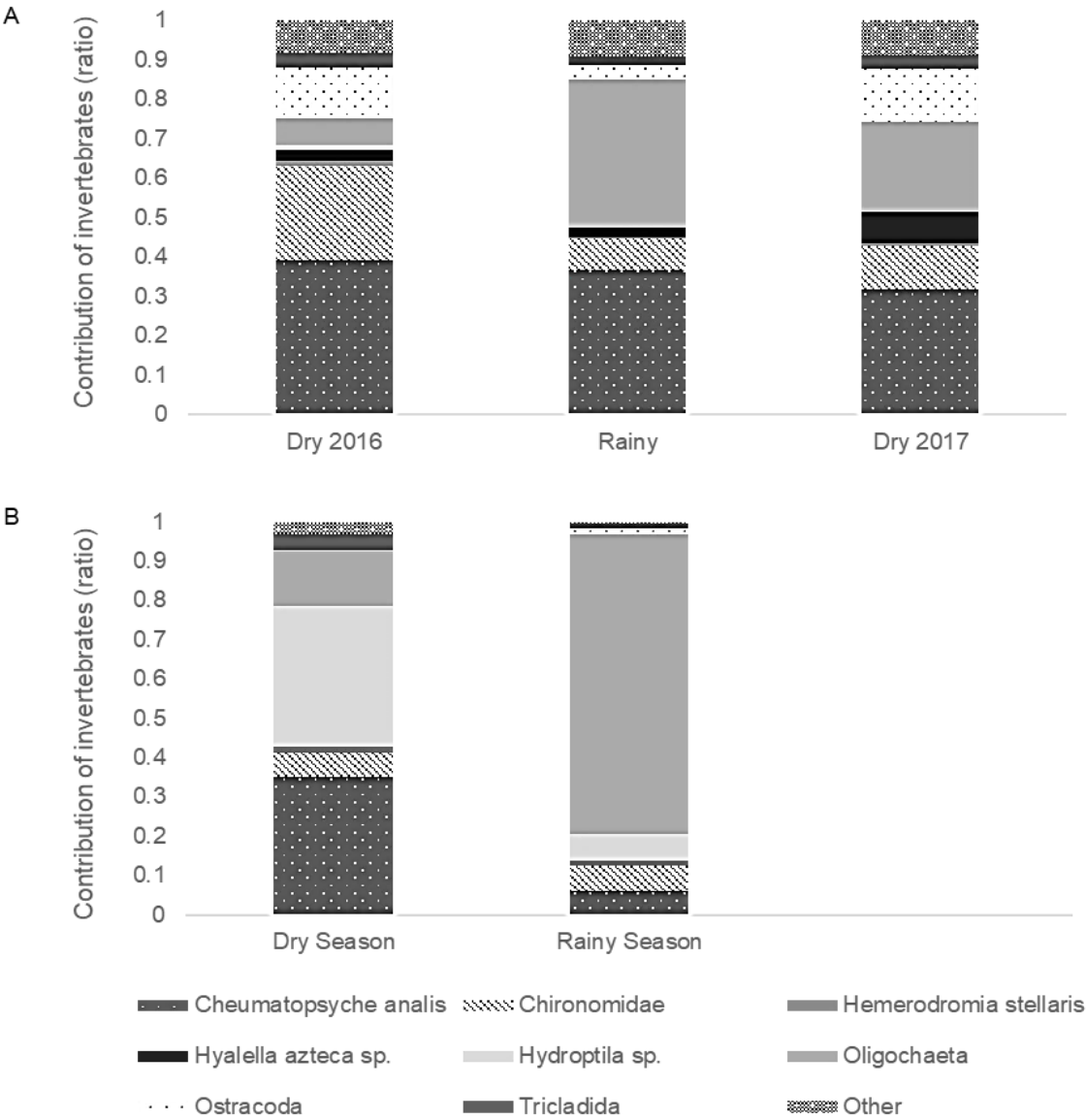


Figure 3.

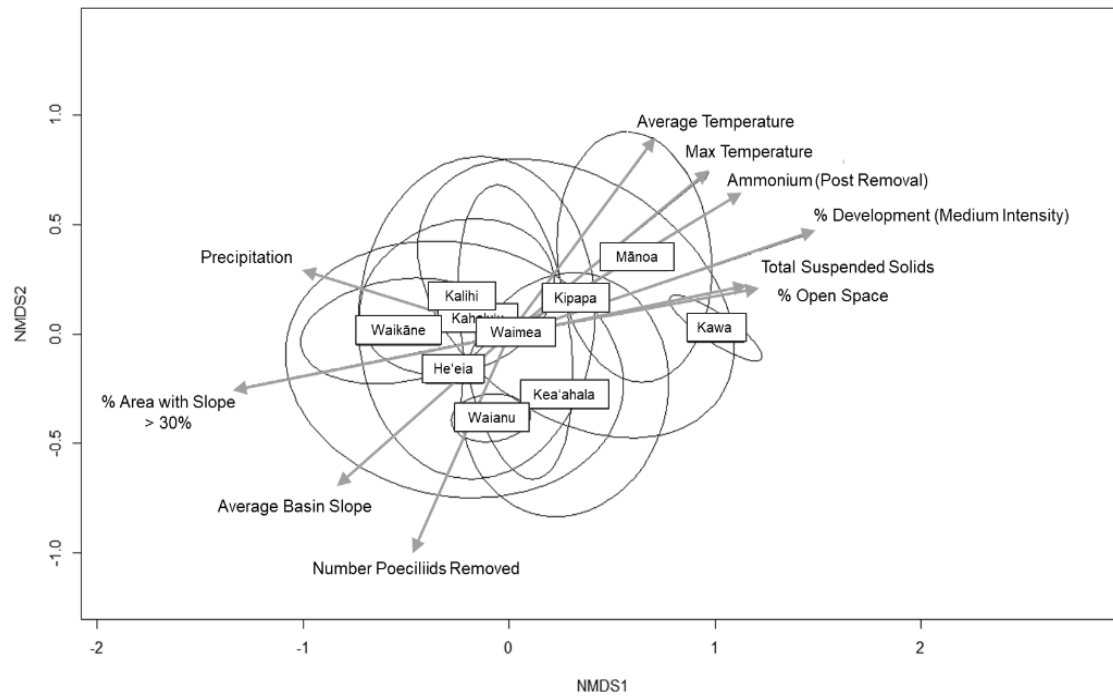


Figure 4.

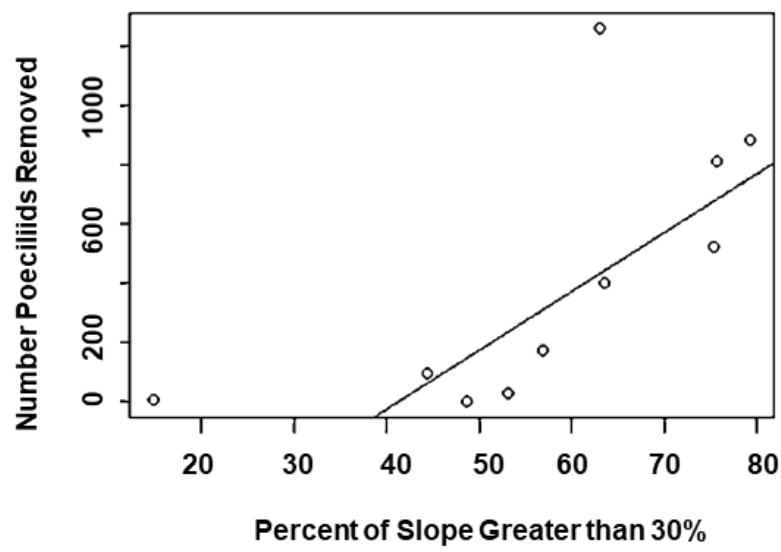


Figure 5.

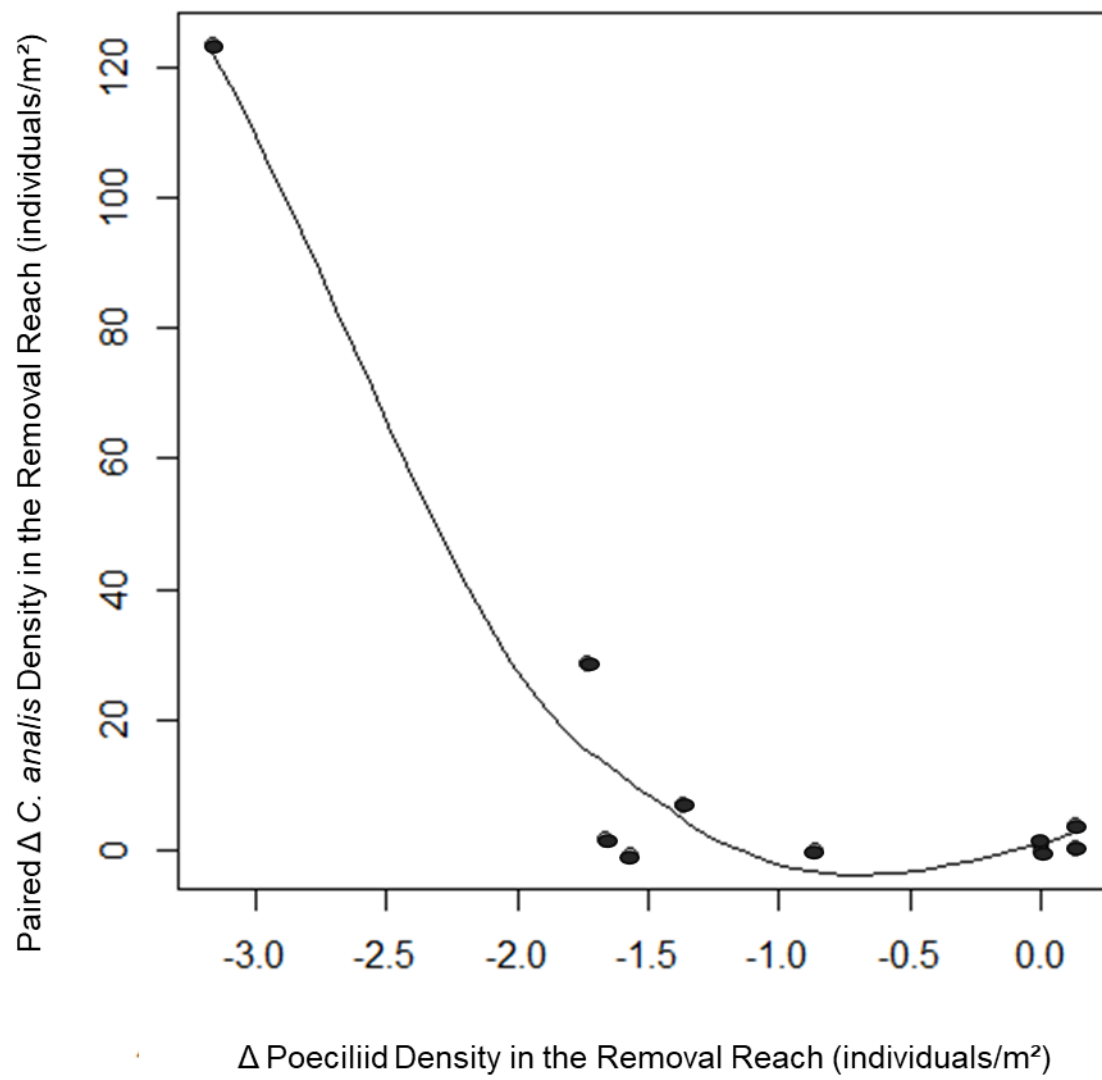


Figure 6.

