

COMPARISON OF FISH ASSEMBLAGES AND HABITAT USE OF NATIVE AND NON-  
NATIVE ESTUARINE SPECIES IN A FISHPOND COMPLEX IN HILO, HAWAI'I

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## Abstract:

Estuaries are highly productive systems that provide refugia for juveniles of many exploited nearshore fish species and represent essential nursery habitat. Traditional Hawaiian fishponds, called loko i‘a, were situated on areas to exploit the increased productivity due to the mixing of nutrient rich groundwater with seawater. These structures are essentially artificial estuaries; however, due to their impounded nature and varying levels of management, loko i‘a have the potential to differ in their ecologic role relative to the natural estuaries. I selected three fishponds located in Hilo, Hawai‘i: Hale O Lono, Loko Waka, and Waiāhole and embayment of Hilo Bay shared by all ponds. These locations represent a broad range in size, salinity regime, habitat, and management strategy. I utilized temporally and spatially robust sampling, mark recapture methods, and habitat mapping to elucidate the effects of environmental conditions within a fishpond complex on fish assemblage habitat association and population parameters of five important game species: Striped Mullet *Mugil cephalus*, Kanda *Osteomugil engeli*, Yellowstripe Goatfish *Mulloidichthys flavolineatus*, Reticulated Flagtail *Kuhlia sandvicensis*, and Hawaiian Flagtail *Kuhlia xenura*. I found that a salinity and mud habitat proportion gradient had the greatest explanatory power on the composition of fish assemblages in this system. The embayment and Hale o Lono comprised one physicochemical and habitat grouping, whereas Waiāhole and Loko Waka ponds comprised a second, disparate grouping. The bay and Hale O Lono grouping comprised of species rich mesohaline conditions, whereas Waiāhole and Loko Waka grouping was depauperate and spring-water dominated. Populations parameters of game species were observed to vary with location and habitat. Differences in apparent survival among locations appear to be the result of differences in habitat with mud being negatively associated with survival in most species. The fish populations in the embayment and fishponds do share some degree of connectivity as movement of Yellowstripe Goatfish was observed between Hale O Lono and the embayment; and Kanda movement was observed between Loko Waka and Waiāhole. Results indicate that limited connectivity to the marine environment results in conditions too osmotically challenging to support most native species. These findings can assist in prioritizing rehabilitation efforts in similarly spring fed ponds to reduce non-native species abundance and potential increase fish production.

## Introduction:

Estuaries are a critical habitat in the early life history of many exploited nearshore fish species because they are highly productive systems, often with a reduced number of predators compared to habitats used by adults (Rozas and Hackney 1984). On oceanic islands, the amount of estuarine habitat can be very limited which can restrict the productivity of nearshore waters (Dürr et al. 2011, Kim et al. 2011). For example, the amount of estuarine habitat in the main Hawaiian Islands is minimal, estimated to be little as 100-200 km<sup>2</sup> by Maragos et al. (1975), though application of more modern definitions of estuarine habitat substantially increases this estimate (K. Payton, Hawai'i Division of Aquatic Resources, *pers. comm.*). Moreover, Hawaiian estuaries tend to be small and unevenly distributed among the islands. Despite this, Hawaiian estuaries support a number of species important to subsistence and recreational fisheries such as: Striped Mullet ('ama'ama) *Mugil cephalus*, Hawaiian Flagtail (āholehole) *Kuhlia xenura*, Pacific Threadfin (moi) *Polydactylus sexfilis*, Milkfish (awa) *Chanos chanos*, and Longjaw Bonefish ('ō'iō) *Albula virgate* (Potter et al. 2006, McRae et al. 2011, Bagarinao, 1991). The importance of estuarine habitats to these fisheries was recognized by native Hawaiians, who developed an advanced aquaculture technology centered around augmenting existing or creating new estuarine habitats through the construction of fishponds.

Traditional Hawaiian fishponds, i.e., loko i'a, were strategically placed to make use of nutrient inputs from surface water flow and submarine discharge of ground water. The enclosed structure may have also played a role in retaining these inputs resulting in an increase of productivity. In terms of their hydrology and geomorphology, Hawaiian fishponds are essentially artificial estuaries, but their ecology remains largely unexamined. These artificial structures have the potential to play an important role in the productivity of nearshore fisheries. For example, juveniles of game species are commonly associated with fishponds suggesting that these ponds may be functioning as estuarine nursery habitat and attracting these species (Costa-Pierce 1987).

Loko i'a were a fundamental component of food production of Hawaiian civilization prior to European contact. These culturally important aquaculture systems served to enhance food production by passively generating animal protein. These structures ranged in their construction and location from upland river irrigated ditches, to earthen berms or stacked rock walls that encircled a portion of marine coastline. Regardless of location and construction type, loko i'a



achieved high levels of productivity despite not being actively fertilized (Kikuchi 1976). These systems were often integrated with other forms of agriculture, such as the production of taro, and primarily relied on passive recruitment of invertebrates and fishes that entered through a gated canal (makahā). Juvenile fishes and invertebrates thrived in loko i‘a, receiving protection from predators and abundant food resources. By design, fishes were prevented from exiting once they reached a sufficient size by the gate and were available for harvest.

Prior to European contact in 1778, an estimated 488 ponds were actively managed and producing fish (DHM 1990). These ponds, of various configurations, covered 2,700 ha and produced an estimated minimum annual yield of 900,000 kg (Costa-Pierce 1987). Fishponds represented an important food source and a means to selectively raise prized species. Unfortunately, these structures did not fare well in the tumultuous changes in land use and ownership that occurred in the 19<sup>th</sup> Century (Kikuchi 1976). Many of these ponds fell into disrepair or were filled in and built over for other structures. Although there is a considerable grassroots effort to preserve and restore these structures, only 38 ponds are in current use with many more in various stages of disrepair (KUA, 2017). Despite the impaired state of many of these ponds, they may still be serving an important role in the ecology of nearshore waters, such as nursery habitat for game species. However, the degree to which the fish assemblage in fishponds differ from that in adjacent, natural estuarine habitats is largely unknown. It is not clear whether fishes recruiting into fishponds move between the pond and the adjacent estuary. Furthermore, as these structures are repaired or rebuilt their internal assemblages and the degree to which they contribute to the adjacent areas is likely to change (Carswell et al. 2015). The scale of connectivity between actively managed fishponds, inactive fishponds, and natural estuarine habitats has not been assessed. This connectivity could be problematic as it may serve as a mechanism aiding the establishment and persistence of non-native species.

There is evidence that fishponds can serve as habitat for non-native species. Known species that use fishponds as refugia include, red mangrove *Rhizophora mangle* (Allen 1998, Chimner et al. 2006), Kanda *Osteomugil engeli* (Randall 2007), Blacktail Snapper *Lutjanus fulvus* (Randall 2007); Mozambique Tilapia *Oreochromis mossambicus* (Nishimoto et al. 2015), and various poeciliids (Hiatt et al. 1947a, 1947b). Moreover, there is concern that restoration efforts may provide opportunities for invasion; as disturbance events are often a precursor to invasion in

aquatic environments (Moyle and Light 1996, Sakai et al. 2001, Marchetti et al. 2004). Disturbances can also precipitate later invasion of already-introduced species that are not currently at nuisance levels (Rilov and Gasith 2004). It is not well understood if loko i'a offer a more conducive habitat for native or introduced species. Ikejima et al. (2006) compared abandoned aquaculture ponds to adjacent natural habitats and found that the modified habitat had lower species diversity and differed in fish assemblage structure. In particular, Kanda was found to preferentially occur more in disturbed habitat and abandoned ponds than adjacent natural habitat.

This preference by Kanda for abandoned pond habitat is of particular interest to resource managers in Hawai'i. Kanda were an unintentional introduction that occurred when Marquesan sardines were introduced to Hawai'i and have been found to occupy fishponds (Randall 1987). A consistent theme in discussions with Hawai'i Division of Aquatic Resources (DAR) and private resource managers was the observation that Kanda were on the rise. The concern raised is that the culturally important Striped Mullet, may be outcompeted by Kanda. To address this concern, and similar dynamics of native and non-native species, five species of interest were selected. Striped Mullet (native) and Kanda (non-native) were selected as they share a similar habitat are observed to be in direct competition for food and habitat resources (Nishimoto 2007). While Striped Mullet are an important game species with high market value, Kanda is relatively small and is seen as commercially worthless (Randall 1987). The resource managers of these ponds have in the recent past invested in stocking their ponds with Striped Mullet, to control for this intervention and accurately assess native/non-native dynamics, two additional species with no history of stocking were selected for further investigation. Reticulated Flagtail (native), and Hawaiian Flagtail (native) were both selected due to the difficulty in identification at the size classes encountered during this study (Randall 2007). Kuhliid flagtails also represent an important fishery and have been historically important family of fishes in Hawaiian fishponds due to their flexibility, as they are euryhaline during all phases of their life cycle (Benson and Fitzsimons 2002). Yellowstripe Goatfish were selected as they are abundant in these locations, and are one of the few reef species that have demonstrated an ability to occupy mesohaline conditions (Brock 1980)

Additionally, these partially enclosed estuary proxies were designed attract juveniles and impede their dispersal; acting as ecological traps (Robinson and Jennings 2012). Therefore, the goal of this study is to evaluate the role of fishponds on the productivity and connectivity of nearshore fisheries in Hawai'i to inform permitting decisions and best management practices. To further this goal, the objectives of the proposed study are as follows: 1) compare the abundance and species composition of the fishes inhabiting a complex of Hawaiian estuary ecotypes consisting of an inactive fishpond, two fishponds actively under production, and the adjacent natural estuary; and 2) assess the survival, recruitment, movement, and habitat use of the young-of-year of five fish species commonly associated with fishponds and natural estuaries: Striped Mullet, Kanda, Yellowstripe Goatfish, Reticulated Flagtail, and Hawaiian Flagtail using mark-recapture methods.

## **Methods:**

### **Study area:**

The study was conducted in a complex of three fishponds and the adjacent portion of Hilo Bay along the Keaukaha coastline located along the northeastern shore of the island of Hawai'i (Figure 1). The Keaukaha coastline is characterized by large amounts of both river flux and submarine groundwater discharge (SGD). This SGD plays an important role on Hawai'i Island in general and this location specifically as the SGD is estimated to exceed surface runoff (Schopka and Derry 2012). The abundance of nutrient-rich SGD was likely noted and opportunistically exploited by native Hawaiians as evidenced by the construction of numerous fishponds along the Keaukaha coastline that occurred over a 500-year period prior to European contact. I selected three Keaukaha fishponds that were incorporated into this study, Loko Waka, Hale O Lono, and Waiāhole, as they represent a diversity in size, salinity regime, habitat, and management strategy (Table 1), but have connections to the same 8.6-ha embayment of Hilo Bay (Figure 1). This close proximity and range of characteristics allowed for the identification of abiotic factors affecting fish habitat use as they share a common pool of natural recruits arriving to the embayment. Loko Waka and Waiāhole are classified as loko pu'uone, estuarine ponds constructed of earthen barriers. Both ponds historically had several mākāhā (sluice gates) connecting these ponds to the ocean (> 3). However, after the construction of State Highway 137 (Kalanianaʻole Avenue) bisected the fishponds and the coastline, Loko Waka and Waiāhole were each limited to a single

mākāhā with a long, i.e., > 40 m, 'auwai (sluice or culvert). The construction of SH-137 also physically separated Waiāhole from Hale O Lono. To the best of local knowledge, Loko Waka and Waiāhole have always been separate ponds, but are suspected to be connected overland during heavy rainfall and/or spring high tide events. Hale O Lono is a loko kuapā, or estuarian pond, constructed of stacked rock walls that extend into Hilo Bay. This pond currently contains three mākāhā, and its walls are regularly breached during spring high tides and storm events. Waiāhole and Hale o Lono are both actively managed for the production of Striped Mullet and kuhliid flagtails by Kamehameha Schools and Edith Kanaka'ole Foundation (EKF) respectively and serve as important cultural and educational facilities. Loko Waka is not currently managed for fish production and is leased from the state of Hawai'i by owners of the restaurant located on the eastern shore of the pond (Figure 1). The shared embayment is bordered by two popular county parks and experiences regular recreational fishing pressure. Each of fishponds also experience some level of illegal fishing based on surveillance video and conversations with the fishpond managers of Hale O Lono and Waiāhole.

Sampling stations ( $n = 30$ ) were haphazardly distributed amongst the pond and adjacent embayment based on their surface areas. Center points for stations were placed along the shoreline, while maintaining a  $\geq 40$ -m buffer between adjacent stations. A minimum of three sampling stations was delineated in each pond with an additional sampling station added per each 1.0 ha of pond surface area. Each sampling station consisted of a 40-m diameter area centered on a selected point along the shore, sampling with net casts occurred at any point within this area. Stations were distributed into three blocks based on their distance from the culvert connecting the pond to the embayment, with an equal number of stations in each block. These blocks ranged from 0-100 m, 100-200 m and > 300 m, away from each ponds culvert.

### **Habitat characterization:**

Benthic habitat composition was characterized using a HumminBird Helix 7 G2 side scan sonar unit (Johnson Outdoors Marine Electronics, Inc. Eufaula, Alabama) mounted on the starboard side of a kayak. The sonar unit was configured for shallow saltwater with side scan range of 30m to either side at 455 kHz, with GPS readings at 2 s intervals. A perimeter path was first established to capture the pond edges. Total coverage was achieved with multiple parallel passes across the longest axis with repeat coverage perpendicular to previous transects. In shallow areas

that limited the effectiveness of sonar, multiple passes along with written descriptions of composition were used to classify habitat. The sonar imagery was georeferenced and the substrates classified following methods adapted from those described by Kaesar and Litts (2010). Georectified images were synthesized from raw bathymetric video files and GPS points using SonarTRX v.17.1 (Leraand Engineering Inc., Honolulu, Hawai'i). From these benthic maps, habitat was manually classified into six habitat types, converted to polygons, and rasterized using Arc Map 10.4 (Environmental Systems Research Institute, Redlands, California) (Appendix 3). Habitat classification was verified using 100 random points from the delineated habitat and ground-truthed using visual confirmation of substrate. Classification across these 100 points was accurate for 96% of points with the final four points falling at or near the boundary of habitat and due to the limitations in precision of handheld GPS these points were deemed to be sufficiently accurate.

### **Fish assemblage surveys and mark-recapture:**

My capture methods were developed through consultation with biologists from Hawai'i DAR and fishpond managers. The managers of Hale O Lono and Waiāhole raised concerns about decreased water quality due to excessive sediment disturbance resulting from seining. Further, biologists at Hawai'i DAR use cast nets to collect fishes as part of their routine statewide estuarine monitoring program. Therefore, we deployed 6-m diameter nylon cast nets with 0.63 cm mesh to minimize disturbance to sediments and to produce results comparable to the data collected by DAR monitoring protocols. While not as commonly used as other gear types, cast nets are an effective method for sampling nekton in estuarine habitat and are frequently used to target estuarine species in Hawai'i by recreational and subsistence fishers (Stein et al. 2014; Sakihara et al. 2017; Schemmel et al. 2019).

Sampling was conducted following the robust design as described by Pollock (1982). Sampling occurred monthly between May 2018 – March 2019, encompassing 10 primary sampling events occurring monthly. Each primary sampling event consisted of three secondary sampling events ( $n = 30$ ), during which all 30 stations were sampled. Secondary sampling events within a primary event occurred over 3-4 consecutive days. However, during eight secondary samplings unsafe ocean and weather conditions prohibited sampling at two stations exposed to high wave action (Figure 1).

Collection at each station consisted of three non-overlapping net casts located at any location within the 40-m station with casts occurring in as quick succession as possible given the reloading of the net. This sampling procedure was usually completed in ~15 minutes per station depending on catch size. Casts were targeted at any visible fishes. If no fishes were visible in the first two minutes of observation, casts were performed on likely habitat. In stations with high water clarity and depths that limit net efficacy, a single net cast was targeted at likely habitat; and supplemented with a five-minute visual survey by two observers. The presence of all fishes that could be positively identified, but were not susceptible to capture in the cast net, were recorded. In stations that contained small-bodied fishes that were not sensitive to the gear, such as poeciliids like Western Mosquitofish *Gambusia affinis*, their presence was noted when they could be positively identified. All captured fishes were held in aerated 36-L coolers until station processing was completed. All captured fishes were identified to species, measured for total length (TL) to the nearest mm and released. All Striped Mullet, Kanda, Yellowtail Goatfish, Yellowstripe Goatfish, and kuhliid flagtails were scanned for the presence of a passive integrated transponder (PIT) tag using a handheld GPR Plus tag reader (Biomark, Inc.). Due to the difficulty in identification at the size classes encountered during this study, for analysis both species of kuhliid flagtails were grouped together for analysis. If no PIT tag was found, captured individuals of these species  $\geq 90$  mm TL received an 8.4 x 1.29mm 134.2-kHz ISO FDX-B PIT tag (Biomark, Inc., Boise, Idaho) via insertion into the peritoneal cavity at the pelvic girdle (Figure 2), and released (Prentice et al. 1990; Fraiola and Carlson 2016). The tag weight in air was 0.1 g.

### **Data analysis:**

Fish assemblage composition and habitat associations were analyzed using canonical correspondence analysis (CCA; Ter Braak 1986). This method synthesizes both ordination technique of correspondence analysis with multiple regression (Ter Braak 1986). Prior to analysis, the habitat data and environmental measurements were evaluated for normality and natural log (ln +1) transformed where needed. To control for rare occurrences, species occurring in less than 5% of secondary sampling sessions were removed from analysis. These variables were then assessed for severity of multicollinearity using variance inflation factor (VIF), but none of the variables included exceed the threshold of >4. CCA was performed in R v. 3.5.1 (R

Core Team 2018) using the “vegan” package 8 (Oksanen et al. 2019). Significance of the resultant CCA model was evaluated by permutational ANOVA using 1000 iterations.

The population dynamics of flagtails, Striped Mullet, Kanda, and Yellowstripe Goatfish in this pond complex were assessed using a robust mark/recapture design (Pollock 1982). The encounter histories of these species were analyzed separately using MARK v. 8.2 (White and Burnham 1999) to estimate population parameters such as survival, detection, emigration, and immigration. These parameters were estimated through generation of competing Huggins p and c models that incorporate habitat parameters to differing degrees (Huggins 1989). A set of candidate models were constructed a priori and informed by the results of CCA. Only the environmental variables that were included in the CCA model were considered for inclusion. Covariates within models selected to avoid correlation and address specific habitat questions raised by resource managers. These candidate models are detailed in Table 3. These models were evaluated for their strength evidence using Akaike information criteria corrected for small sample sizes ( $AIC_c$ ). Where appropriate,  $\Delta AIC_c$  values were used to evaluate the support for inferences and across multiple models and to quantify pairwise comparisons with models  $\Delta AIC_c > 10$  used as strong support for the model with the lower  $AIC_c$  (Burnham and Anderson 2004). The most parsimonious models were selected using values of  $\Delta AIC_c < 2$  and averaged for the parameter estimates model.

## **Results:**

A total of 3331 fishes representing 53 species were captured during the study (Table 4); with the bay contributing the largest total number of species (47), the most species not found at the other locations (25), and the lowest proportion of non-native species encountered at 2.1%. Hale O Lono retains greater marine influence; however, the species richness decreased by half (20) with only four species unique to this location, and an increase of non-native proportion to 15.0%. Waiāhole contained 11 species, one unique species and a non-native proportion of 54.0%. Half of the 12 species captured at Loko Waka were non-native, with none of these species being unique to Loko Waka. The most abundant fish captured during the study was Yellowstripe Goatfish; however, this species was only found at bay and Hale O Lono stations. In contrast, the second most abundant species, Mexican Molly *Poecilia sphenops*, was absent from only bay stations. Kanda was the most abundant mugilid and was present at all four locations. Striped

Mullet was found only in the ponds and had the widest range of total length, with individuals  $\geq 400$  mm TL encountered relatively frequently. However, most fishes captured were  $< 130$  mm TL. Many of the species differed in relative abundance and total length among ponds with smaller individuals generally being found in the pond locations in comparison to the embayment (Table 4).

A total of 1592 tags were deployed across the seven species (Table 5). Of these tagged fish, 66 individuals were recaptured at least once. With four of these individuals recaptured a third time for a recapture rate of 4.62%. Yellowstripe Goatfish were the most numerous recaptures with seven recaptures at bay stations and 29 within Hale O Lono. With one individual being recaptured within a Hale O Lono in October and recaptured a month later in a bay station. Kanda was the second most frequent recaptured species with 31 Kanda recaptured within Hale O Lono stations. One of the four recoveries of Kanda in Waiāhole in was originally tagged in Loko Waka in July was recovered in September. Striped Mullet were only recaptured in Loko Waka.

Canonical correspondence analysis indicated the presence of two distinct habitat types and associated fish assemblages within the study area ( $Df = 8$ ,  $\chi^2 = 1.132$ ,  $F = 5.027$ ,  $P = 0.001$ ). The first canonical axis explained 60.94% of the variation along gradient of salinity, temperature, and proportion of mud substrate (Table 6). The stations in Hilo Bay and Hale O Lono were characterized with warmer temperatures, higher salinities and less proportion of mud habitat. In contrast Loko Waka and Waiāhole represent the other endpoint with very low salinity, and high associations with large woody debris and mud habitat (Figure 5). There was a similar division in the fish assemblage. The fishes associated with lower salinities and temperatures and a greater proportion of mud substrates were mostly introduced species such as the poeciliids, Grass Carp *Ctenopharyngodon idella* and Mozambique Tilapia *Oreochromis mossambicus*, that were encountered exclusively in Loko Waka and Waiāhole. The species associated exclusively with Hilo Bay and Hale O Lono were primarily reef fishes representing the families Chaetodontidae, Labridae, and Acanthuridae. Mugilids and khuliids did not show particularly strong associations with the first or second canonical axis (Figure 5), suggesting that their occurrence in the study area is less constrained by environmental conditions.

The second canonical axis was associated with distance to culvert and proportion of rubble substrate and explained about 17.56% of the variability in the dataset. The second canonical axis



is primarily associated with the differences in hard substrates among stations, with rubble and lava flow being unassociated with one another. Large woody debris and rubble substrate were negatively associated with one another.

The result of model selection generally indicates strong support for the influence of availability of mud and lava flow substrates on survival (Table 7). The top models for Striped Mullet, Kanda, and Yellowstripe Goatfish all contained at least one habitat variable and in the case of Yellowstripe Goatfish and Kanda, models containing these covariates were indistinguishable  $\Delta AICc$  of  $\leq 2$ . Flagtails did not display the same support for the influence of substrate, with top models only containing environmental variables present during capture. The top models estimated temporary immigration as random ( $\gamma(.)$ ) and all immigration and emigration as constant across secondary sampling events, but allowed to vary across primary sampling. While there are model formulations that allow for these parameters to vary across time and detect specific movement behaviors, the combination of small sample sizes per location and low recapture rates limit the ability to extract useful information from these more complex models. The model averaged estimates for apparent survival of flagtails and Striped Mullet indicate that these models may be data deficient and unable to accurately parameterize survival. These estimates are close to the upper and lower the bounds of probability and have standard errors close to zero and, thus, have low utility. Kanda and Yellowstripe Goatfish both display differing survival estimates based on location.

All four species displayed differing responses of apparent survival to the two covariates of total length and salinity (Table 12). Flagtails apparent survival was high across most salinities ( $\Phi=0.999\pm0.002$ ), but decreased for large individuals in low salinities. Striped Mullet displayed a relationship between apparent survival and total length ( $\beta= -7.85\pm30.57$ ) similar to that seen in flagtails, but an inverse relationship between apparent survival and salinity ( $\beta= -2.41\pm14.45$ ). Apparent survival of Kanda generally was high across most conditions, with the lowest apparent survival estimates occurring for small individuals in estuarine conditions (Figure 5). Overall, apparent survival of Yellowstripe Goatfish was generally high ( $\Phi= 0.75\pm0.31$ ); however, it was notably lower for larger individuals in low-salinity environments (Figure 5).

The top models gave strong support of the influence of substrate availability and environmental conditions on parameter estimates, particularly apparent survival and temporary emigration.

Apparent survival of flagtails and both mullet species was negatively associated with total length. However, it is unclear if this is due to actual mortality, emigration, or to larger fishes becoming less sensitive to capture after their first encounter. The influence of total length on Yellowstripe Goatfish survival is the conventionally expected relationship with larger bodied fishes associated with increased survival. Only Striped Mullet displayed a positive relationship between survival and the availability of mud substrate (Table 12).

## **Discussion:**

Understanding the roles of habitat availability and physicochemical conditions in structuring fish assemblages in estuarine ecosystems is an essential part in nearshore fisheries management. My results demonstrate a strong influence of salinity and habitat on species composition and abundance. The two main groupings represent disparate endpoints, one of highly temporally variable estuarine conditions and the other of more homogeneous spring water conditions. The natural embayment is the source of high salinity but oligotrophic water and is unencumbered to the recruitment and movement of fishes. While rich in reef-associated species, the abundance of species of interest was low. It is not clear if observed patterns in habitat and species abundance is driven by taxa resource requirements, reduced productivity, or the relatively high fishing pressure in the bay. At the other extreme, stations were dominated by nutrient rich but depauperate freshwater springs. At the lowest salinity stations, conditions were likely osmotically challenging for most fish species. This is demonstrated by the rapid decline in species diversity and increasing proportion of non-native species associated with increasing freshwater input. This trend of decreasing diversity is well documented in coastal marshes where manmade structures disrupt water movement (Rogers et al. 1992). These barriers can create harsh conditions and limit connectivity thus decreasing the pool of species that can recruit (Herke et al. 1992; Kneib 1997; Robinson and Jennings 2014). In Loko Waka and Waiāhole extremely fresh conditions are not being effectively utilized by estuarine species, resulting in stations with salinities  $< 4$  ppt being dominated by non-native species. In these ponds the small size of the connection limits mixing of spring water and sea water.

The abundance of freshwater spring conditions may also be limiting overall productivity of these ponds. Previous work in Hale O Lono and Waiāhole indicated primary productivity was

significantly correlated with salinity, but this association was not nutrient-driven as nutrient availability was similar among ponds (Anthony et al. 2018). The lower primary productivity in the hyposaline stations could indicate that the benthic autotroph community in these stations are osmotically limited (Admiraal 1976). An increase in the connectivity to the ocean could improve primary productivity as estuarian benthic microalga growth is limited at  $< 4$  ppt and achieves a maximum at  $\sim 20$  ppt (Williams 1964). Increasing primary productivity has direct implications for improving fish production. Furthermore, this increase in salinity is likely to increase native species diversity through widening the pool of species that can occupy habitat within the pond. Systems with greater native diversity are associated with increased ecosystem function, higher resilience to disturbance, and increased resistance for further invasions (Stachowicz et al. 1999; Chapin et al. 2000; Englund 2002).

The decreased productivity and fish abundance in the spring-fed portions of Loko Waka and Waiāhole are likely symptomatic of limited connectivity to the marine environment. However, this limited connectivity also has consequences on the physical habitat available to fishes. The slower flushing, lower salinity, and high abundance and biomass of non-native plants contribute to the formation and retention of unconsolidated sediments (Portnoy 1999). The proportion of mud habitat in these ponds was associated with decreased apparent survival in all of the tagged species except for Striped Mullet (Table 9). While Striped Mullet production is a stated goal of these ponds, there exist potential to increase production of Striped Mullet, in addition to other game species. In these ponds, unconsolidated mud overlays lava flow bedrock. These contiguous shelves of lava flow was strongly positively associated survival in Striped Mullet and flagtails, indicating that restoration efforts to remove soft sediments may not negatively impact this species in relations to habitat utilization. In addition to physical removal of soft sediment by increased flushing, restoration of tidal influence has been associated with enhanced organic decomposition through increased sulfate reduction (Portnoy 1999; Van Proosdij et al. 2010).

The embayment and fishponds are physically connected through several different modes that vary in their frequency, size, and direction. In addition to the permanent connections such as makahā, ephemeral connections can occur due to high tide or storm events. The relative importance of these modes of connectivity is unknown; however, the fish populations in the embayment and fishponds do share some degree of connectivity. Yellowstripe Goatfish

movement was observed between the embayment and Hale O Lono. Given the current regularity that this pond's wall is breached by high tides and storm conditions, these locations likely share a population. There were observed differences in apparent survival of Yellowstripe Goatfish between these two locations. The models of Yellowstripe Goatfish do display some location specific effects on survival (Table 10). When modeling both bay and Hale O Lono as a single location for survival model fitness decreased, giving strong support delta ( $\Delta AIC_c > 10$ ) that populations in these locations behave differently. This difference may be driven by the negative response of lava and mud habitat on survival. The bay is composed of more rubble and sand habitat and, while not explicitly modeled, the differences in response of Yellowstripe Goatfish could be a result different habitat requirement compared to the other species modeled. Movement of Kanda was observed between Waiāhole and Loko Waka. This connectivity likely took place directly overland during storm/flooding conditions during Hurricane Lane that occurred between encounters. The modeling of Kanda did not display support for the populations behaving differently as all location specific models were equally fit ( $\Delta AIC_c < 2$ ). This connectivity has management implications, as any non-native species control methods should consider reinvasion risk from adjacent ponds. This connectivity is likely to increase as restoration efforts to remove invasive grasses and sediments from ponds may reduce the obstructions, and these overland connections could become more frequent. The survival of Kanda was higher in Hale O Lono and identical in the two spring fed ponds. The lack of difference in survival in the Loko Waka and Waiāhole suggest that management level does not dramatically impact the survival of Kanda.

The three ponds and the embayment differ greatly in their management level (Appendix 1). Loko Waka serves as an illustration of the current state of similar unmanaged fishponds throughout the state. It is evident that unmanaged ponds are still attractive to new recruits (Table 4). If the remnant structures of the abandoned ponds are able to sufficiently restrict movement, these structures may behave as ecological sinks; as juveniles recruit, but are unable to emigrate out of harsh conditions or complete their lifecycle (Rogers et al. 1992).

These fishponds and the embayment that they share are interacting one another on several levels. First, these structures influence one another in their hydrology and geomorphology. As seen in this fishpond complex, differing degrees of connectivity and proximity to the marine environment and can have dramatic effects on the salinity regime. Where Loko waka and

Waiāhole are limited to a single long makahā, are more similar to one another than to Hale O Lono or the embayment. Hale O Lono, as an impounded section of the bay displays higher retention of low salinity water and the highest abundance of game species. The embayment serves as the supply of recruits and receives the freshwater output of the fishponds. The fish assemblies and populations of these ponds are interacting and impacting one another in complex ways. With species specific movement that differ in their destination indicating that the connectivity between and among these structures is likely to differ between fish guilds in response to habitat or resources requirements. Each of these display differing characteristics, limitations, and require differing management strategies. Effective management of any of these structures and similar arrangements of ponds across Hawai'i requires the not only proper considerations to each pond, but management of these structures as an interconnected whole.

### **Management implications:**

Loko i'a can be highly variable in their physiochemical conditions and this has direct implications for the fish assemblages within and around these structures. These dynamic conditions are driven by the relative inputs of water from both the marine and terrestrial environments. It is important to understand how changes to the degree of connectivity of a pond to either of these sources will change the fish community. In this study area, ponds experience large amounts of freshwater input. If these locations are limited in their connectivity to the marine environment, an imbalance occurs and produces conditions that are unfavorable to many native species. These oligohaline conditions leave these ponds and similar estuaries across the landscape vulnerable to invasions and propagation of non-native species. If fishponds are to continue to operate as intended, management efforts must include plans to mitigate an imbalance of inputs.

On the landscape scale, abandoned or unmanaged ponds are functioning as artificial estuaries. The large population of non-native species, low diversity, and lower survival of game species make abandoned fishponds important targets for nearshore fisheries management. These structures need to be assessed for their vulnerability to invasion and proactive efforts must be taken to limit further propagation of non-native species. Preventing abandoned ponds as acting as stepping stone populations can play an important role in limiting range expansion. (Shigesada et

al. 1995; Apte et al. 2000). This mitigation strategy may be important for taxa, such as cichlids and poecilids, whose dispersion is likely driven by adult movement rather than larval dispersion.

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1 **Table 2.** Characteristics of Waiāhole, Hale o Lono, Loko Waka fishponds, and the embayment they share located along the Keaukaha  
2 coast of Hilo, Hawai'i. Area and perimeter were estimated using satellite imagery (DigitalGlobe 1/9/2016). Depth measurements  
3 extracted from boat mounted down imaging sonar surveys.

<b>Location</b>	<b>Area (ha)</b>	<b>Perimeter (m)</b>	<b>Maximum depth(m)</b>	<b>Average depth (m)</b>	<b>Status</b>	<b>Resoration start date</b>	<b>Number of culverts</b>
Loko Waka	8.12	1747	4.1	1.9	Unmanaged		1
Waiahole	1.12	918	2.6	1.3	Managed	2012	1
Hale o Lono	0.62	513	1.7	0.5	Managed	2002	3
Bay	8.65	1563	11.4	2.0	Unmanaged		N/A

7 **Table 2.** Benthic habitat categories and their definitions used to manually classify substrate within a fishpond complex on the  
8 Keaukaha coastline in Hilo, Hawai'i from side scan sonar imagery collected between December 2018 – July 2019.

Substrate type	Definition
Mud (MU)	Substrate composed of very fine particles < 0.1 mm
Lava flow (LF)	Substrate composed of large contiguous shelves of basalt
Rubble (RU)	Substrate composed of unconsolidated rock > 2 mm and <1m
Tree (LWD)	Submerged Large woody debris
Sand (SA)	Substrate composed of particles size < 2 mm

9

**Table 3.** Candidate models for parameterizing Huggins p and c for the estimation under a robust design of population parameters of flagtails *Kuhlia* spp., Striped Mullet *Mugil cephalus*, Kanda *Osteomugil engeli*, and Yellowstripe Goatfish *Mulloidichthys flavolineatus* captured and tagged between May 2018 – March 2019 in Waiāhole, Hale O Lono, Loko Waka fishponds, and the adjacent embayment of Hilo Bay along the Keaukaha coast of Hilo, Hawai'i. Apparent survival ( $S$ ,  $\phi$ ) was modeled as constant ( $\cdot$ ) and covaried with salinity (SAL), total length (TL), and percent habitat coverage at capture site (LAVA, or MUD). Temporary immigration and emigration was modeled constant ( $G$ ,  $\gamma(\cdot)$ ,  $G'$ ,  $\gamma'(\cdot)$ ). Capture and recapture were modeled functions of distance from the culvert (CUL) and temperature (TEMP). Capture and recapture were modeled as either behavior dependent (P, C) or behavior independent (P=C). Kanda (OSEN) and Yellowstripe Goatfish (MUFL) had sufficient captures between locations to be modeled by location. Models that are location specific are denoted by location codes Hale O Lono (H), Waiāhole(W), Loko waka (L) a bar ( $\bar{\cdot}$ ) indicates the locations modeled separately for each location, locations with (=) denotes modeled as a common location.

Number	General Models
1	Total Model
2	Null model
3	$S(\cdot)$
4	$P=C$
5	$S(\cdot) P=C$
6	$S(\cdot) G'(\cdot) G''(\cdot) P=C$
7	$S(\cdot) G'(\cdot) G''(\cdot) P(\cdot) C(\cdot)$
8	$S(TL) G'(\cdot) G''(\cdot) P=C$
9	$S(TL) G'(TL) G''(TL) P(\cdot) C(\cdot)$
10	$S(TL, SAL) G'(\cdot) G''(\cdot) P=C$
11	$S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P=C$
12	$S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P(CUL) C(CUL)$
13	$S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P(TEMP) C(TEMP) P=C$
14	$S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P(TEMP, CUL) C(TEMP, CUL) P=C$
15	$S(TL, SAL, MUD) G'(TL, SAL, MUD) G''(TL, SAL, MUD) P(TEMP, CUL) C(TEMP, CUL) P=C$
16	$S(TL, SAL, LAVA) G'(TL, SAL, LAVA) G''(TL, SAL, LAVA) P(TEMP, CUL) C(TEMP, CUL) P=C$
MUFL Location models	
1	$S(\cdot) G'(\cdot) G''(\cdot) P=C S(B=H)$
2	$S(TL, SAL, MUD) G'(TL, SAL, MUD) G''(TL, SAL, MUD) P(TEMP, CUL) C(TEMP, CUL) P=C S(B=H)$
3	$S(TL, SAL, LAVA) G'(TL, SAL, LAVA) G''(TL, SAL, LAVA) P(TEMP, CUL) C(TEMP, CUL) P=C (B=H)$
OSEN Location models	
1	$S(\cdot) G'(\cdot) G''(\cdot) P=C S(H=W=L)$
2	$S(\cdot) G'(\cdot) G''(\cdot) P=C S(H W=L)$
3	$S(TL, SAL, MUD) G'(TL, SAL, MUD) G''(TL, SAL, MUD) P(TEMP, CUL) C(TEMP, CUL) P=C S(H=W=L)$
4	$S(TL, SAL, LAVA) G'(TL, SAL, LAVA) G''(TL, SAL, LAVA) P(TEMP, CUL) C(TEMP, CUL) P=C S(H W=L)$

21 **Table 4.** Number of individuals of each species captured from the complex of fishponds along the Keaukaha coast of Hilo, Hawai'i  
 22 between May 2018 – March 2019. Percent total is the proportional contribution to the overall abundance of captured fishes. Rank  
 23 indicates the ordering of each species based on percent contribution.

Species code	Common name	Scientific name	Bay			Hale O Lono			Loko Waka			Waiahole			Total abundance	% of	
			Range (mm)	n	Mean ± SD	Range (mm)	n	Mean ± SD	Range (mm)	n	Mean ± SD	Range (mm)	n	Mean ± SD		Total	Rank
MUFL	Yellowstripe Goatfish	<i>Mulloidichthys flavolineatus</i>	111.0- 240	240	136.1± 19.3	97- 299	678	154.1± 35.1	--	0	--	--	0	--	918	27.59	1
POSP	Mexican Molly	<i>Poecilia sphenops</i>	--	0	--	92- 118	9	104.3± 9.1	60- 94	54	82.6± 6.9	59- 146	820	89.0± 7	883	26.54	2
OSEN	Kanda Mullet	<i>Osteomugil engeli</i>	193.0- 242	28	213.6± 12.6	83- 255	317	120.6± 20.5	110- 207	126	147.6± 20.2	84- 220	136	131.6± 31.5	607	18.24	3
MUCE	Striped Mullet	<i>Mugil cephalus</i>	--	0	--	99- 383	50	174.1± 76.9	109- 690	23	283.1± 180.5	97- 544	124	247.0± 120.9	197	5.92	4
KHSP	Flagtail	<i>Kuhlia xenura</i> or <i>Kuhlia sandwicensis</i>	80.0- 201	27	129.2± 40.1	54- 280	128	122.7± 39.6	--	1	341 -	81- 228	26	170.4± 50.8	182	5.47	5
ACTR	Convict tang	<i>Acanthurus triostegus</i>	50.0- 220	146	133.4± 32.4	46- 167	25	124.4± 32.2	--	0	--	--	0	--	171	5.14	6
STBA	Belted Wrasse	<i>Stethojulis balteata</i>	86.0- 123	62	101.3± 15.1	--	1	106 -	--	0	--	--	0	--	63	1.89	7
ABVA	Indo-pacific sargent	<i>Abudefduf vaigiensis</i>	57.0- 121	32	80.7± 18.2	68- 127	5	87.8± 27.2	--	0	--	--	0	--	37	1.11	8
MUVA	Yellowtail Goatfish	<i>Mulloidichthys vanicolensis</i>	60.0- 174	32	137.8± 18.8	--	0	--	--	0	--	--	0	--	32	0.96	9
THDU	Saddle Wrasse	<i>Thalassoma duperrey</i>	99.0- 173	26	112.2± 14.1	107- 188	4	137.0± 36.7	--	0	--	--	0	--	30	0.90	10*
ELSA	Hawaiian sleeper goby	<i>Eleotris sandwicensis</i>	--	0	--	--	0	--	--	1	109 -	55- 184	29	127.0± 32.1	30	0.90	10*
ABAD	Hawaiian Sargent	<i>Abudefduf abdominalis</i>	63.0- 141	8	108.9± 23.9	100- 205	11	171.9± 31.4	--	0	--	--	0	--	19	0.57	11
CAME	Bluefin Trevally	<i>Caranx melampygus</i>	85.0- 186	14	126.1± 33.7	100 -	1	100 -	--	0	--	--	0	--	15	0.45	12*
STMA	Hawaiian Gregory	<i>Stegastes marginatus</i>	63.0- 141	15	108.9± 23.9	--	0	--	--	0	--	--	0	--	15	0.45	12*
CASE	Bigeye Trevally	<i>Caranx sexfasciatus</i>	84.0- 210	9	141.3± 49.3	--	0	--	--	2	395.0± 25.9	--	0	--	11	0.33	13
NELE	Sharpnose Mullet	<i>Neomyxus leuciscus</i>	--	0	--	95- 106	10	99.4± 4.2	--	0	--	--	0	--	10	0.30	14
STHA	Naniha oopu	<i>Stenogobius hawaiiensis</i>	--	0	--	--	0	--	--	0	--	80- 149	8	116.6± 21.6	8	0.24	15*
NESA	Spotfin Squirrelfish	<i>Neoniphon sammara</i>	88.0- 167	3	110.3± 45	156- 171	5	163.7± 3.5	--	0	--	--	0	--	8	0.24	15*
CAIG	Giant Trevally	<i>Caranx ignobilis</i>	91.0- 100	3	94.7± 4.7	--	1	86	390- 730	3	505.0± 194.9	--	0	--	7	0.21	16
PLIM	Brighteye damselfish	<i>Plectroglyphidodon imparipennis</i>	61.0- 165	6	84.0± 45.3	--	0	--	--	0	--	--	0	--	6	0.18	17*
ZACO	Moorish Idol	<i>Zanclus cornutus</i>	81.0- 185	6	119.7± 48.7	--	0	--	--	0	--	--	0	--	6	0.18	17*
CHLU	Raccoon Butterflyfish	<i>Chaetodon lunula</i>	68.0- 105	5	86.5± 26.2	--	1	110 -	--	0	--	--	0	--	6	0.18	17*
CTID	Grass Carp	<i>Ctenopharyngodon idella</i>	--	0	--	--	0	--	115- 960	4	673.8± 380.6	--	1	310 -	5	0.15	18



26 Table 4. (Continued).

															Total abundance	% of Total	Rank
			Bay			Hale O Lono			Loko Waka			Waiahole					
Species code	Common name	Scientific name	Range (mm)	n	Mean ± SD	Range (mm)	n	Mean ± SD	Range (mm)	n	Mean ± SD	Range (mm)	n	Mean ± SD			
CAAM	Ambon Toby	<i>Canthigaster amboinensis</i>	72.0- 115	4	87.8± 20.5	--	0	--	--	0	--	--	0	--	4	0.12	19*
THTR	Christmas wrasse	<i>Thalassoma trilobatum</i>	95.0- 111	4	106.3± 7.5	--	0	--	--	0	--	--	0	--	4	0.12	19*
TYCR	Crocodile needlefish	<i>Tylosurus crocodilus</i>	242.0- 436	4	358.8± 84.3	--	0	--	--	0	--	--	0	--	4	0.12	19*
ORMO	Mozambique tilapia	<i>Oreochromis mossambicus</i>	315.0- 402	0	--	--	0	--	--	1	291 -	--	3	347.3± 47.6	4	0.12	19*
CAJA	Whitespot Toby	<i>Canthigaster jactator</i>	62.0- 134	4	83.0± 34.2	--	0	--	--	0	--	--	0	--	4	0.12	19*
LUFU	Blacktail Snapper	<i>Lutjanus fulvus</i>	--	0	--	114 154	3	129.7± 21.4	--	0	--	--	0	--	3	0.09	20*
POLA	Sailfin molly	<i>Poecilia latipinna</i>	--	0	--	--	0	--	--	1	60 -	87- 88	2	87.5± 0.7	3	0.09	20*
THPU	Surge wrasse	<i>Thalassoma purpureum</i>	95.0- 105	3	100.0± 7.1	--	0	--	--	0	--	--	0	--	3	0.09	20*
CHAU	Threadfin Butterflyfish	<i>Chaetodon auriga</i>	143.0- 200	2	171.5± 40.3	--	1	53 -	--	0	--	--	0	--	3	0.09	20*
PAPO	Whitesaddle goatfish	<i>Parupeneus porphyreus</i>	105.0- 194	3	158.3± 47.1	--	0	--	--	0	--	--	0	--	3	0.09	20*
CAFE	Barred Jack	<i>Carangoides ferdau</i>	76.0- 113	2	94.5± 26.2	--	0	--	--	0	--	--	0	--	2	0.06	21*
ABSO	Blackspot sargent	<i>Abudefduf sordidus</i>	142.0- 143	2	142.0± 1.4	--	0	--	--	0	--	--	0	--	2	0.06	21*
ACNF	Brown Surgeon	<i>Acanthurus nigrofuscus</i>	134.0- 175	2	154.5± 29	--	0	--	--	0	--	--	0	--	2	0.06	21*
ACBL	Ringtail Surgeonfish	<i>Acanthurus blochii</i>	--	0	--	122- 123	2	122.5± 0.7	--	0	--	--	0	--	2	0.06	21*
DIHY	Spotted Porcupinefish	<i>Diodon hystrix</i>	--	0	--	250- 390	2	320.0± 99	--	0	--	--	0	--	2	0.06	21*
CIPI	Stocky hawk fish	<i>Cirrhitus pinnulatus</i>	50.0- 109	2	79.5± 41.7	--	0	--	--	0	--	--	0	--	2	0.06	21*
GAAF	Misquito fish	<i>Gambusia affinis</i>	--	0	--	--	0	--	--	1	20 -	--	1	22 -	2	0.06	21*
CHAG	Agile Chromis	<i>Chromis agilis</i>	--	1	64 -	--	0	--	--	0	--	--	0	--	1	0.03	22*
KYHA	Bicolor Chub	<i>Kyphosus hawaiiensis</i>	--	1	282 -	--	0	--	--	0	--	--	0	--	1	0.03	22*
CHQU	Fourspot butterflyfish	<i>Chaetodon quadrimaculatus</i>	--	1	82 -	--	0	--	--	0	--	--	0	--	1	0.03	22*
CHAU	Golden Trevally	<i>Gnathanodon speciosus</i>	--	1	168 -	--	0	--	--	0	--	--	0	--	1	0.03	22*
SYUL	Brown lizardfish	<i>Synodus ulae</i>	--	1	210 -	--	0	--	--	0	--	--	0	--	1	0.03	22*
CTHA	Chevron tang	<i>Ctenochaetus hawaiiensis</i>	--	1	144 -	--	0	--	--	0	--	--	0	--	1	0.03	22*
RHAF	Lagoon triggerfish	<i>Rhinecanthus aculeatus</i>	--	1	237 -	--	0	--	--	0	--	--	0	--	1	0.03	22*
NALI	Orange-spine unicornfish	<i>Naso lituratus</i>	--	1	268 -	--	0	--	--	0	--	--	0	--	1	0.03	22*
SAPU	Peppered Squirrelfish	<i>Sargocentron punctatissimum</i>	--	1	109 -	--	0	--	--	0	--	--	0	--	1	0.03	22*
SEBA	Ballieu's Scorpion fish	<i>Sebastapistes ballieui</i>	--	1	109 -	--	0	--	--	0	--	--	0	--	1	0.03	22*
OSME	Spotted boxfish	<i>Ostracion meleagris</i>	--	1	103 -	--	0	--	--	0	--	--	0	--	1	0.03	22*
CACA	Stareye Parrotfish	<i>Calotomus carolinus</i>	--	1	394 -	--	0	--	--	0	--	--	0	--	1	0.03	22*
Total				706			1254			217		--	1150		3327		
* indicates shared rank																	

27

28

29 **Table 5.** The amount and distribution of PIT tags deployed and recaptured across seven species captured in Waiāhole, Hale o Lono,  
 30 Loko Waka fishponds, and the adjacent embayment of Hilo Bay along the Keaukaha coast of Hilo, Hawai'i.

Species	Bay		Hale o Lono		Loko Waka		Waiahole	
	Deployed	Recaptured	Deployed	Recaptured	Deployed	Recaptured	Deployed	Recaptured
Flagtail	13	0	77	0	1	0	24	0
Striped Mullet	0	0	47	0	10	3	81	0
Kanda Mullet	24	0	274	31	123	0	119	4
Yellowstriped Goatfish	169	7	576	29	0	0	0	0
Yellowtail Goatfish	20	0	0	0	0	0	0	0
Hawaiian Sleeper Goby	0	0	0	0	1	0	23	0
Sharpnose Mullet	10	0	0	0	0	0	0	0
Total	236	7	974	60	135	3	247	4

31

32 **Table 6.** Summary of A) environmental components and B) canonical axis significance testing of CCA model of species found in  
 33 Waiāhole, Hale O Lono, Loko Waka Fishponds, and the embayment they share located along the Keaukaha coast of Hilo, Hawai'i  
 34 between May 2018 and April 2019. Testing was performed using permutational ANOVA with 1000 iterations.

A

Environmental variable	Df	ChiSquare	F	P-Value	Abbreviation
Temperature	1	0.10	3.65	0.01	Temp.
Salinity	1	0.55	19.60	0.00	SAL.
Proportion Mud habitat	1	0.09	3.31	0.00	Mud
Proportion Lava flow habitat	1	0.07	2.44	0.00	Lava F
Proportion Large woody debris habitat	1	0.04	1.56	0.08	LWD
Proportion Rubble habitat	1	0.12	4.33	0.00	Rubble
Distance to culvert	1	0.12	4.17	0.00	DTC
Tide Height	1	0.03	1.14	0.28	Tide Height
Residual	547	15.40			

B

Axis	Df	ChiSquare	F	P-Value	Eigenvalue	Percentage of variation explained
CCA1	1	0.690	24.507	0.001	0.6899	60.94
CCA2	1	0.199	7.061	0.001	0.1988	17.56
CCA3	1	0.069	2.442	0.047	0.06874	6.07
CCA4	1	0.060	2.136	0.085	0.06014	5.31
CCA5	1	0.041	1.438	0.548	0.04048	3.58
CCA6	1	0.032	1.117	0.841	0.03145	2.78
CCA7	1	0.024	0.848	0.947	0.02386	2.11
CCA8	1	0.019	0.665	0.917	0.01872	1.65
Residual	547	15.40				

**Table 7.** Summary of model selection based on second order Akaike Information Criterion for small sample sizes ( $AIC_c$ ) to assess the parameterization of Huggins  $p$  and  $c$  for flagtails (*Kuhlia* spp.), Apparent survival ( $\phi$ ) was modeled as constant ( $\cdot$ ) and covaried with salinity (SAL), total length (TL), and percent habitat coverage at capture site (LAVA or MUD). Temporary emigration was modeled as a constant ( $\gamma'' = \gamma'$ ). Capture and recapture were modeled functions of distance from the culvert (CUL) and temperature (TEMP). Models with  $\Delta AIC_c$  of  $\leq 2$  were averaged for the final parameter estimates. All averaged models did not include a behavioral component ( $P=C$ ).

Number	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
14	S(TL SAL) G'(TL SAL) G''(TL SAL) P(CUL, TEMP) C(CUL, TEMP) P=C	262.12	0.00	0.48	1.00	23	204.11	204.11
13	S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P(TEMP) C(TEMP) P=C	262.91	0.80	0.32	0.67	23	204.91	204.91
16	S(TL SAL, LAVA) G'(TL SAL, LAVA) G''(TL SAL, LAVA) P(CUL, TEMP) C(CUL, TEMP) P=C	265.13	3.01	0.11	0.22	23	207.13	207.13
15	S(TL SAL, MUD) G'(TL SAL, MUD) G''(TL SAL, MUD) P(CUL, TEMP) C(CUL, TEMP) P=C	265.49	3.37	0.09	0.19	23	207.49	207.49
9	S(TL) G'(TL) G''(TL) P(.) C(.)	277.73	15.62	0.00	0.00	23	219.73	219.73
8	S(TL) G'(. ) G''(. ) P=C	278.31	16.20	0.00	0.00	23	220.31	220.31
12	S(TL SAL) G'(TL SAL) G''(TL SAL) P(CUL) C(CUL)	279.20	17.09	0.00	0.00	23	221.20	221.20
7	S(. ) G'(. ) G''(. ) P(.) C(.)	285.55	23.44	0.00	0.00	23	227.55	227.55
10	S(TL, SAL) G'(. ) G''(. ) P=C	286.72	24.61	0.00	0.00	33	193.94	193.35
6	S(. ) G'(. ) G''(. ) P=C	291.32	29.20	0.00	0.00	33	197.95	197.95
3	S(. )	292.34	30.22	0.00	0.00	68	265.31	265.31
11	S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P=C	294.78	32.66	0.00	0.00	13	265.21	265.21
5	S(. ) P=C	363.31	101.20	0.00	0.00	48	197.10	197.10
4	P=C	417.36	155.24	0.00	0.00	56	197.15	197.15
2	Null model	533.11	270.99	0.00	0.00	5	197.45	197.45
1	Full model	649.11	387.00	0.00	0.00	76	197.01	197.01

**Table 8.** Summary of model selection based on second order Akaike Information Criterion for small sample sizes ( $AIC_c$ ) to assess the parameterization of Huggins  $p$  and  $c$  for Striped Mullet (*Mugil cephalus*). Apparent survival ( $\phi$ ) was modeled as constant ( $\cdot$ ) and covaried with salinity (SAL), total length (TL), and percent habitat coverage at capture site (LAVA or MUD). Temporary emigration was modeled as a constant ( $\gamma'' = \gamma'$ ). Capture and recapture were modeled functions of distance from the culvert (CUL) and temperature (TEMP). Kanda and Yellowstripe Goatfish had sufficient captures across multiple locations for the assessment of differences of survival, immigration, emigration, capture, and recapture. Models with  $\Delta AIC_c$  of  $\leq 2$  were averaged for the final parameter estimates. All averaged models did not include a behavioral component ( $P=C$ ).

Number	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
16	S(TL, SAL, LAVA) G'(TL, SAL, LAVA) G''(TL, SAL, LAVA) P(TEMP, CUL) C(TEMP, CUL) P=C	305.05	0.00	0.56	1.00	33	218.47	218.47
14	S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P(TEMP, CUL) C(TEMP, CUL) P=C	306.94	1.88	0.22	0.39	33	220.35	220.35
15	S(TL, SAL, MUD) G'(TL, SAL, MUD) G''(TL, SAL, MUD) P(TEMP, CUL) C(TEMP, CUL) P=C	307.45	2.39	0.17	0.30	33	220.86	220.86
12	S(TL SAL) G'(TL SAL) G''(TL SAL) P(CUL) C(CUL)	307.63	2.58	0.13	0.28	33	221.05	221.05
11	S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P=C	312.06	7.00	0.02	0.03	33	225.47	225.47
13	S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P(TEMP) C(TEMP) P=C	312.19	7.14	0.02	0.03	33	225.60	225.60
9	S(TL) G'(TL) G''(TL) P(.) C(.)	312.94	7.88	0.01	0.02	23	257.66	257.66
10	S(TL, SAL) G'(. ) G''(. ) P=C	313.30	8.25	0.01	0.02	33	226.71	226.71
8	S(TL) G'(. ) G''(. ) P=C	317.43	12.37	0.00	0.00	33	230.84	230.84
7	S(.) G'(. ) G''(. ) P(.) C(.)	319.99	14.94	0.00	0.00	23	264.71	264.71
6	S(.) G'(. ) G''(. ) P=C	320.12	15.07	0.00	0.00	33	233.54	233.54
5	S(.) P=C	378.85	73.80	0.00	0.00	48	232.81	232.81
2	Null model	383.07	78.01	0.00	0.00	5	372.63	372.63
4	P=C	418.39	113.33	0.00	0.00	56	232.15	232.15
3	S(.)	493.49	188.43	0.00	0.00	68	230.68	230.67
1	Full model	559.55	254.50	0.00	0.00	76	230.22	230.22

**Table 9.** Summary of model selection based on second order Akaike Information Criterion for small sample sizes ( $AIC_c$ ) to assess the parameterization of Huggins  $p$  and  $c$  for Kanda (*Osteomugil engeli*). Apparent survival ( $\phi$ ) was modeled as constant ( $\cdot$ ) and covaried with salinity (SAL), total length (TL), and percent habitat coverage at capture site (LAVA or MUD). Temporary emigration was modeled as a constant ( $\gamma'' = \gamma'$ ). Capture and recapture were modeled functions of distance from the culvert (CUL) and temperature (TEMP). For models with separate locations and are denoted by location codes Hale O Lono (H), Waiāhole(W), Loko waka (L) a bar ( $\bar{\cdot}$ ) indicates the locations modeled separately for each location, locations with (=) denotes modeled as a common location. Models with  $\Delta AIC_c$  of  $\leq 2$  were averaged for the final parameter estimates. All averaged models did not include a behavioral component ( $P=C$ ).

Number	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
12	S(TL,SAL) G'(TL,SAL) G''(TL,SAL) P(CUL) C(CUL) P=C	747.14	0.00	0.18	1.00	99	505.04	505.04
11	S(TL,SAL) G'(TL,SAL) G''(TL,SAL) P=C	747.21	0.07	0.18	0.97	99	505.11	505.11
O1	S(.) G'(. ) G''(. ) P=C S(H=W=L)	748.19	1.05	0.11	0.59	99	506.09	506.09
O3	S(TL,SAL, MUD) G'(TL,SAL, MUD) G''(TL,SAL, MUD) P(TEMP,CUL) C(TEMP,CUL) P=C S(H=W=L)	748.28	1.14	0.10	0.56	99	506.19	506.19
O4	S(TL,SAL, MUD) G'(TL,SAL, MUD) G''(TL,SAL, MUD) P(TEMP,CUL) C(TEMP,CUL) P=C S(H   W=L)	748.39	1.25	0.10	0.54	99	506.29	506.29
O2	S(.) G'(. ) G''(. ) P=C S(H   W=L)	748.49	1.35	0.09	0.51	99	506.39	506.39
16	S(TL,SAL, LAVA) G'(TL,SAL, LAVA) G''(TL,SAL, LAVA) P(TEMP,CUL) C(TEMP,CUL) P=C	751.72	4.57	0.02	0.10	99	509.62	509.62
10	S(TL,SAL) G'(. ) G''(. ) P=C	765.89	18.75	0.00	0.00	99	523.79	523.79
14	S(TL,SAL) G'(TL,SAL) G''(TL,SAL) P(TEMP,CUL) C(TEMP,CUL) P=C	771.97	24.83	0.00	0.00	99	529.87	529.87
13	S(TL,SAL) G'(TL,SAL) G''(TL,SAL) P(TEMP) C(TEMP) P=C	772.17	25.03	0.00	0.00	99	530.07	530.07
8	S(TL) G'(. ) G''(. ) P=C	778.76	31.62	0.00	0.00	99	536.66	536.66
15	S(TL,SAL, MUD) G'(TL,SAL, MUD) G''(TL,SAL, MUD) P(TEMP,CUL) C(TEMP,CUL) P=C	782.17	35.03	0.00	0.00	99	540.07	540.07
9	S(TL) G'(TL) G''(TL) P=C	783.28	36.14	0.00	0.00	99	541.18	541.18
6	S(.) G'(. ) G''(. ) P=C	784.92	37.78	0.00	0.00	99	542.82	542.82
5	S(.) P=C	894.49	147.35	0.00	0.00	144	503.12	503.12
4	P=C	985.85	238.71	0.00	0.00	168	500.42	500.42
3	S(.)	1134.55	387.41	0.00	0.00	204	483.41	483.41
7	S(.) G'(. ) G''(. ) P(.) C(.)	1244.18	497.04	0.00	0.00	69	1086.02	1086.02
1	Total model	1264.21	517.07	0.00	0.00	228	481.88	481.88
2	Null model	1493.63	746.49	0.00	0.00	5	1483.52	1483.52

**Table 10.** Summary of model selection based on second order Akaike Information Criterion for small sample sizes ( $AIC_c$ ) to assess the parameterization of Huggins  $p$  and  $c$  for Yellowstripe Goatfish (*Mulloidichthys flavolineatus*). Apparent survival ( $\phi$ ) was modeled as constant ( $\cdot$ ) and covaried with salinity (SAL), total length (TL), and percent habitat coverage at capture site (LAVA or MUD). Temporary emigration was modeled as a constant ( $\gamma'' = \gamma'$ ). Capture and recapture were modeled functions of distance from the culvert (CUL) and temperature (TEMP). For models with separate locations and are denoted by location codes Hale O Lono (H), Bay(B) a bar (|) indicates the locations modeled separately for each location, locations with (=) denotes modeled as a common location. Models with  $\Delta AIC_c$  of  $\leq 2$  were averaged for the final parameter estimates. All averaged models did not include a behavioral component ( $P=C$ ).

Number	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
15	S(TL, SAL, MUD) G'(TL, SAL, MUD) G''(TL, SAL, MUD) P(TEMP, CUL) C(TEMP, CUL) P=C	1771.71	0.00	0.47	1.00	66	1626.69	1626.69
16	S(TL, SAL, LAVA) G'(TL, SAL, LAVA) G''(TL, SAL, LAVA) P(TEMP, CUL) C(TEMP, CUL) P=C	1772.36	0.65	0.34	0.72	66	1627.34	1627.34
14	S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P(TEMP, CUL) C(TEMP, CUL) P=C	1775.09	3.38	0.09	0.18	66	1630.06	1630.06
12	S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P(CUL) C(CUL) P=C	1776.45	4.74	0.04	0.09	66	1631.43	1631.43
13	S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P(TEMP) C(TEMP) P=C	1777.20	5.49	0.03	0.06	66	1632.18	1632.18
10	S(TL, SAL) G'(. ) G''(. ) P=C	1779.85	8.14	0.01	0.02	66	1634.82	1634.82
11	S(TL, SAL) G'(TL, SAL) G''(TL, SAL) P=C	1780.02	8.31	0.01	0.02	66	1634.99	1634.99
M3	S(TL, SAL, LAVA) G'(TL, SAL, LAVA) G''(TL, SAL, LAVA) P(TEMP, CUL, MUD) C(TEMP, CUL) P=C S(B=H)	1782.73	11.02	0.00	0.00	65	1640.11	1640.11
M1	S(. ) G'(. ) G''(. ) P=C S(B=H)	1782.73	11.02	0.00	0.00	65	1640.11	1640.11
M2	S(TL, SAL, MUD) G'(TL, SAL, MUD) G''(TL, SAL, MUD) P(TEMP, CUL) C(TEMP, CUL) P=C S(B=H)	1782.74	11.03	0.00	0.00	65	1640.12	1640.12
8	S(TL) G'(. ) G''(. ) P=C	1785.09	13.38	0.00	0.00	66	1640.07	1640.07
6	S(. ) G'(. ) G''(. ) P=C	1785.14	13.42	0.00	0.00	66	1640.11	1640.11
5	S(. ) P=C	1848.33	76.62	0.00	0.00	96	1627.63	1627.63
4	P=C	1891.95	120.24	0.00	0.00	112	1627.97	1627.97
3	S(. )	1941.63	169.92	0.00	0.00	136	1608.44	1608.44
9	S(TL) G'(TL) G''(TL) P(. ) C(. )	1944.76	173.05	0.00	0.00	46	1846.57	1846.57
7	S(. ) G'(. ) G''(. ) P(. ) C(. )	1945.69	173.98	0.00	0.00	46	1847.50	1847.50
2	Null model	1987.65	215.94	0.00	0.00	5	1937.99	1937.99
1	Full model	1989.18	217.47	0.00	0.00	152	1606.74	1606.74

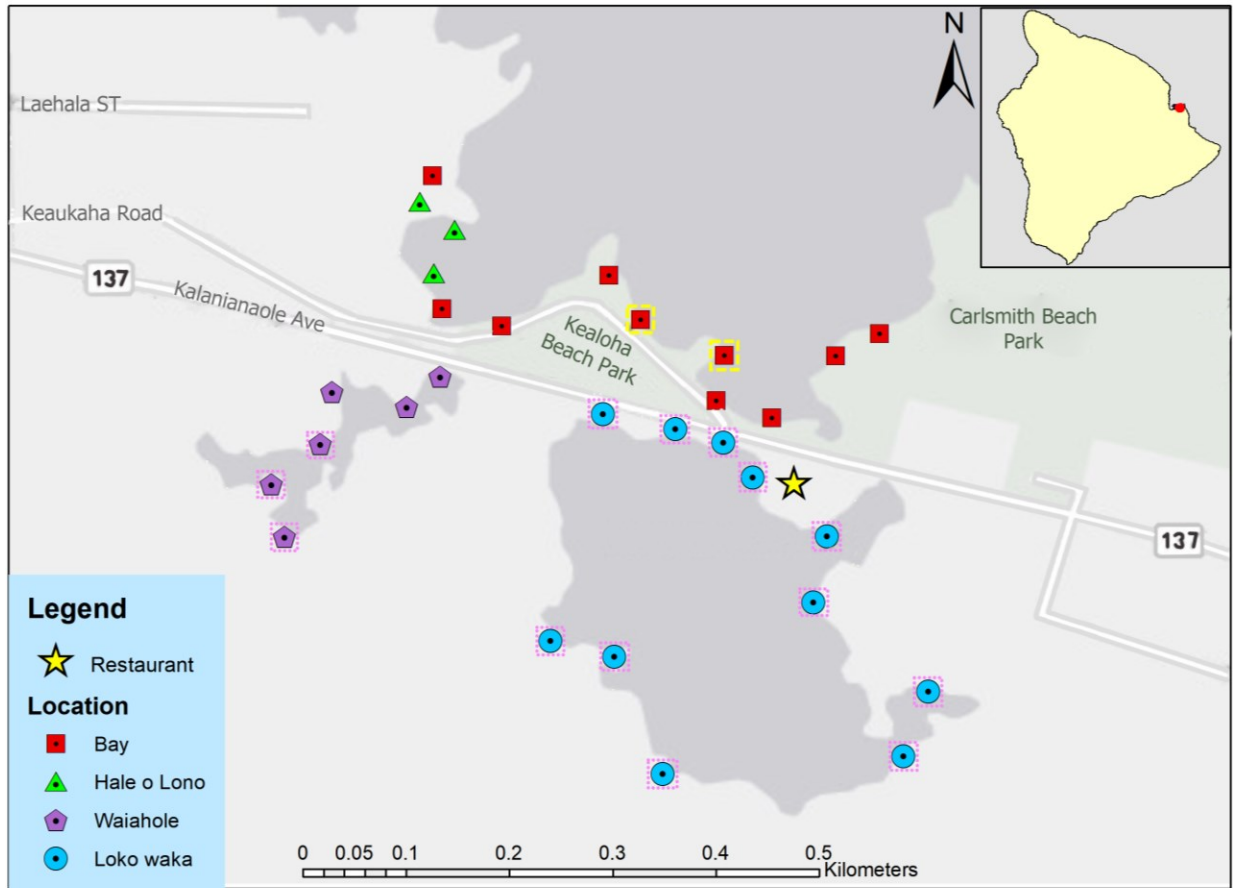
79 **Table 11.** Averaged estimates of apparent survival ( $\phi$ )  $\pm$  SE for A) Flagtails (*Kuhlia* spp.), B) Striped Mullet (*Mugil cephalus*), C)  
80 Kanda (*Osteomugil engeli*), and D) Yellowstripe Goatfish (*Mulloidichthys flavolineatus*) including 95% confidence intervals.

Flagtail				
Location	$\Phi$	SE	Lower CI	Upper CI
All	0.999	0.002	0.830	1.000
Striped Mullet				
Location	$\Phi$	SE	Lower CI	Upper CI
All	0.007	0.027	0.000	0.060
Kanda Mullet				
Location	$\Phi$	SE	Lower CI	Upper CI
Hale O Lono	0.708	0.192	0.281	0.938
Loko Waka	0.569	0.388	0.056	0.967
Waiahole	0.587	0.383	0.060	0.969
Yellowstripe Goatfish				
Location	$\Phi$	SE	Lower CI	Upper CI
Bay	0.753	0.311	0.103	0.988
Hale O Lono	0.599	0.119	0.361	0.798



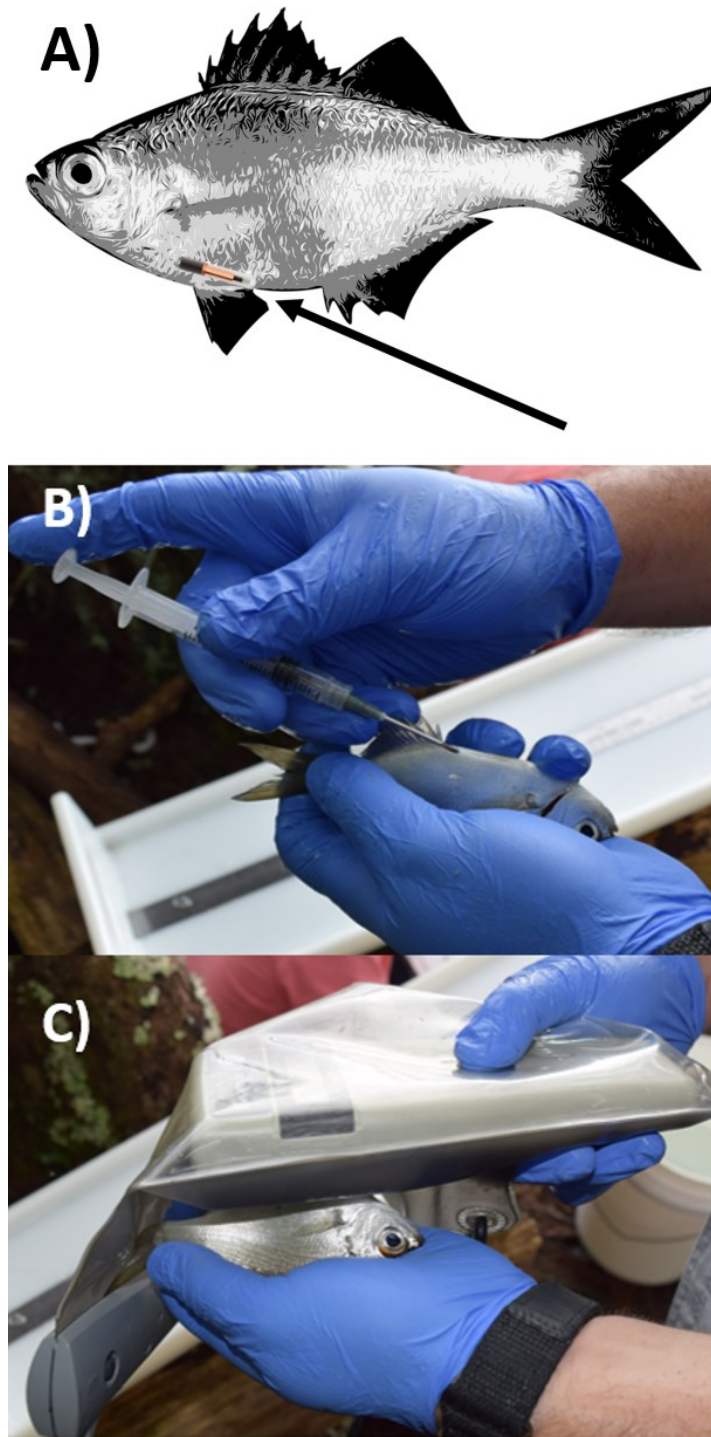
**Table 12.** Parameter estimates of beta coefficients for covariates  $\pm$  SE including 95% confidence intervals. Estimates are averaged from top models from model selection. Apparent survival ( $\phi$ ), temporary emigration and immigration were allowed to covary with proportion of lava flow habitat, mud habitat, and salinity. Capture and recapture probability were allowed to covary with distance from culvert and temperature.

Flagtail				
Parameter	Beta	SE	Lower CI	Upper CI
Distance from Culvert	-0.586	0.104	-0.790	-0.382
Lava flow habitat	5.835	10.907	-15.542	27.212
Mud habitat	-2.470	2.574	-7.516	2.575
Salinity	-0.091	1.679	-3.382	3.200
Temperature	6.353	0.552	5.271	7.435
Total length	-1.189	1.191	-3.523	1.145
Striped Mullet				
Parameter	Beta	SE	Lower CI	Upper CI
Distance from Culvert	-3.628	1.251	-6.080	-1.176
Lava flow habitat	6.967	14.452	-21.358	35.292
Mud habitat	12.648	18.001	-22.633	47.930
Salinity	-2.413	14.850	-31.518	26.692
Temperature	0.135	0.232	-0.320	0.590
Total length	-7.859	30.572	-67.779	52.062
Kanda Mullet				
Parameter	Beta	SE	Lower CI	Upper CI
Distance from Culvert	0.167	0.072	0.027	0.308
Lava flow habitat	17.421	13.999	-10.018	44.860
Mud habitat	-5.681	3.740	-13.011	1.650
Salinity	0.241	0.329	-0.404	0.886
Temperature	-0.141	0.143	-0.420	0.139
Total length	-0.119	0.489	-1.076	0.839
Yellowstripe Goatfish				
Parameter	Beta	SE	Lower CI	Upper CI
Distance from Culvert	-0.339	0.312	-0.950	0.273
Lava flow habitat	-0.424	0.266	-0.945	0.098
Mud habitat	-0.818	0.466	-1.731	0.094
Salinity	-0.949	0.500	-1.928	0.030
Temperature	0.249	0.221	-0.184	0.681
Total length	0.212	0.236	-0.250	0.675



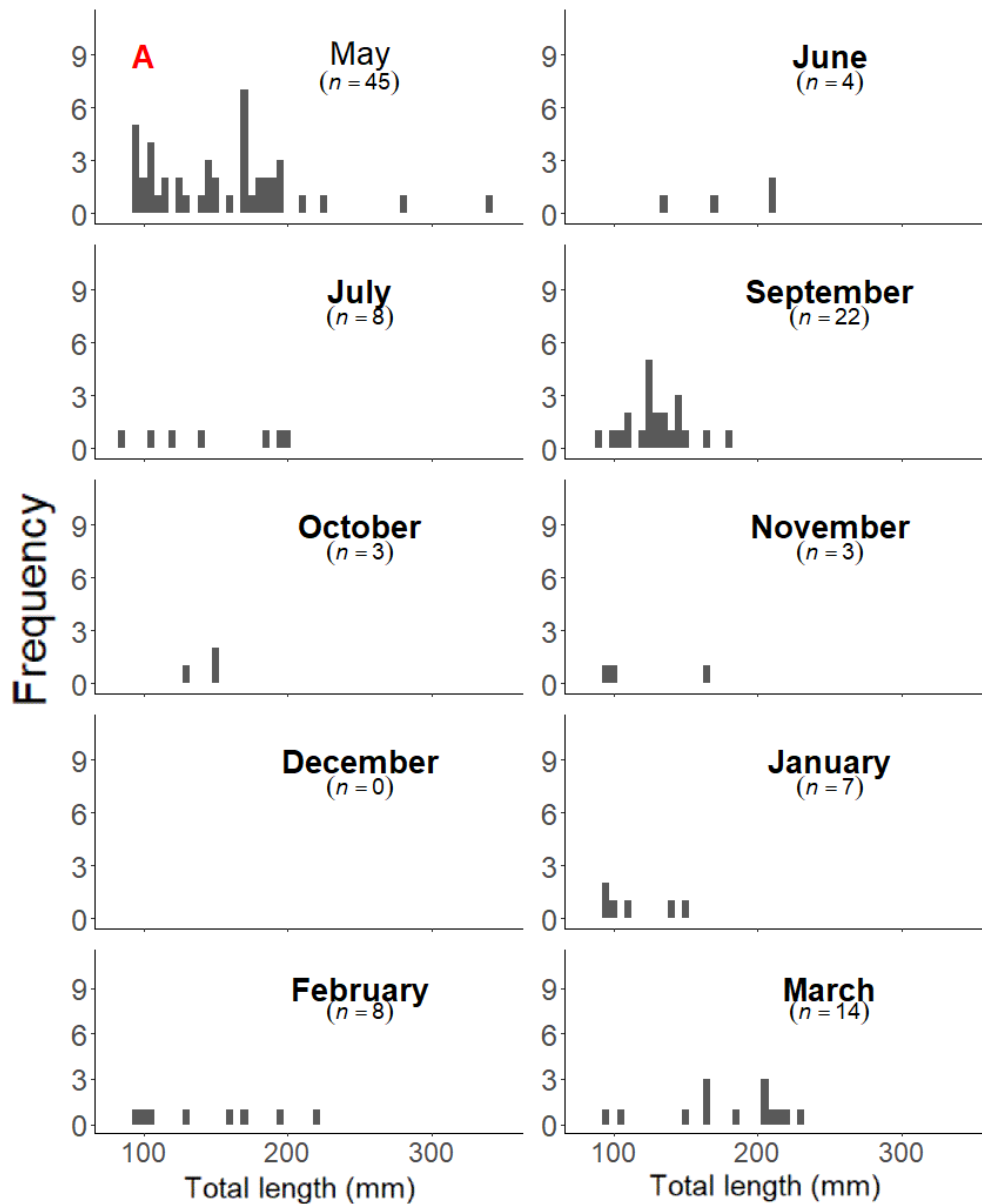
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**Figure 1.** Map detailing location and arrangement of sampling stations in Waiāhole, Hale O Lono, Loko Waka Fishponds, and the embayment they share located along the Keaukaha coast of Hilo, Hawai'i. Stations bounded by dashed lines were unsafe to sample during high surf and were unsampled on eight sampling days. Stations bounded by dotted lines were sampled by the two-observer method. Sampling was conducted during May 2018 – March 2019.

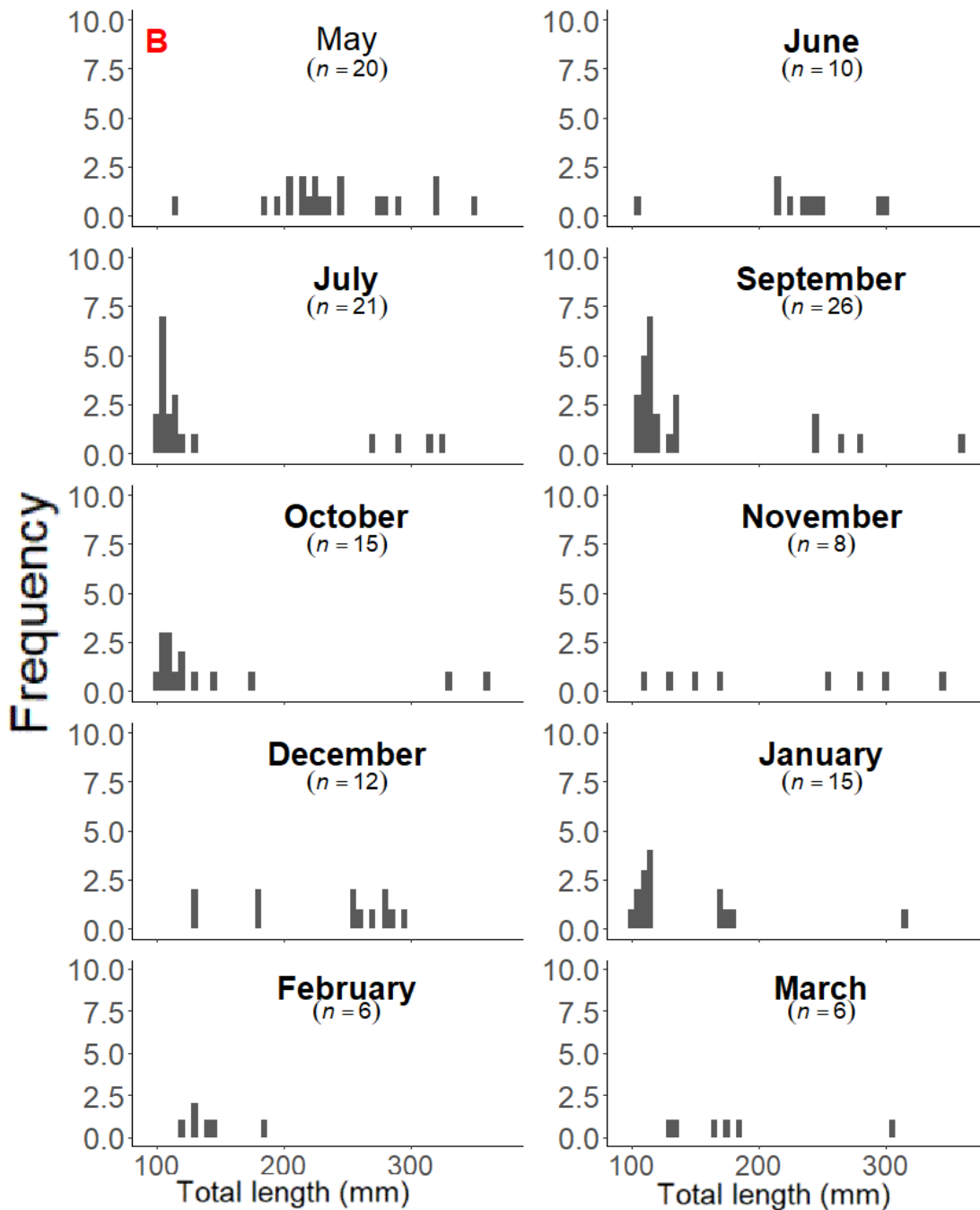


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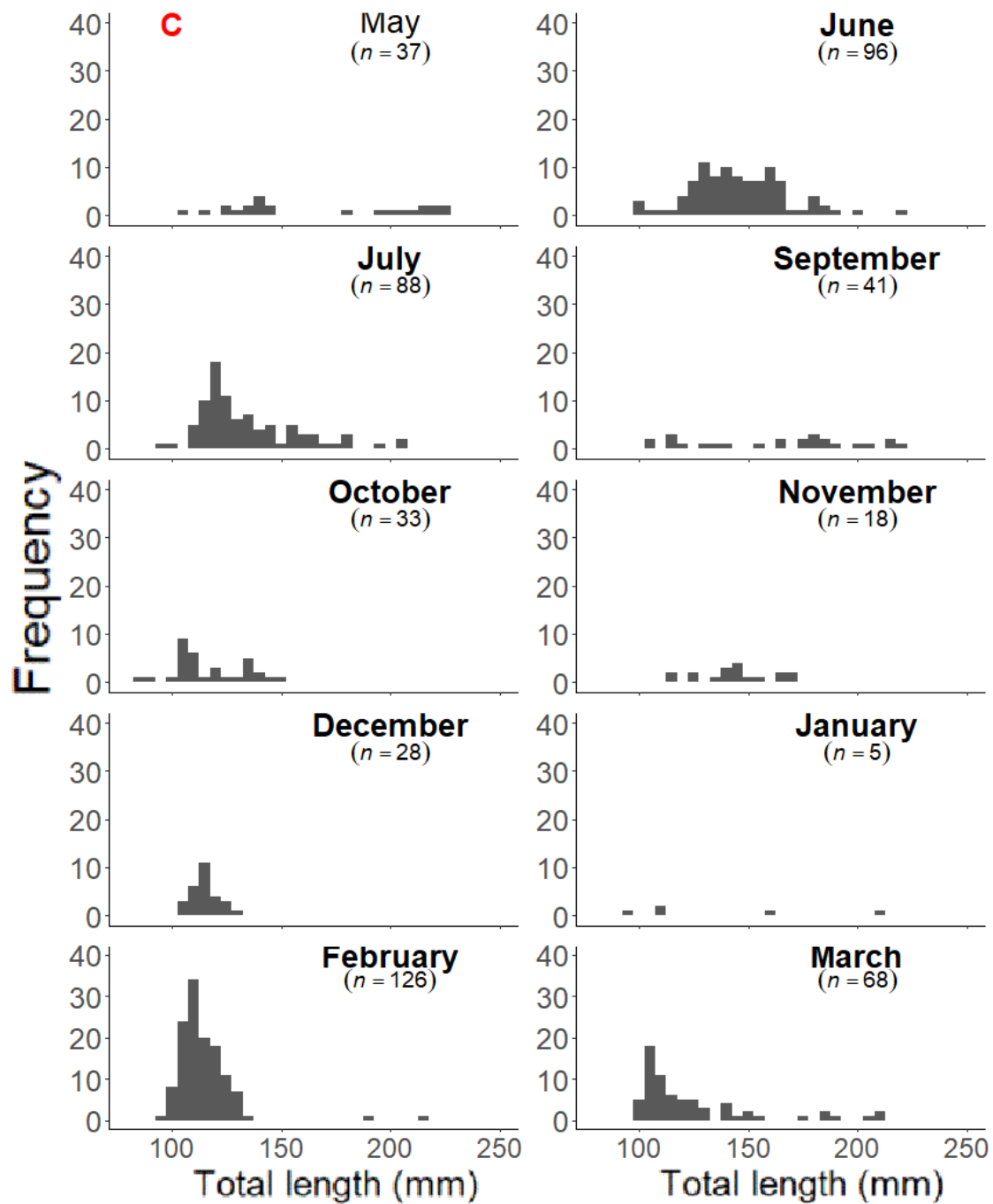
97 **Figure 2.** A) The location and direction of PIT tag insertion on the ventral surface into the  
98 peritoneal cavity at the pelvic girdle including final tag location. B) Tagging of juvenile flagtails.  
99 C) Scanning of tagged fish to obtain tag ID.



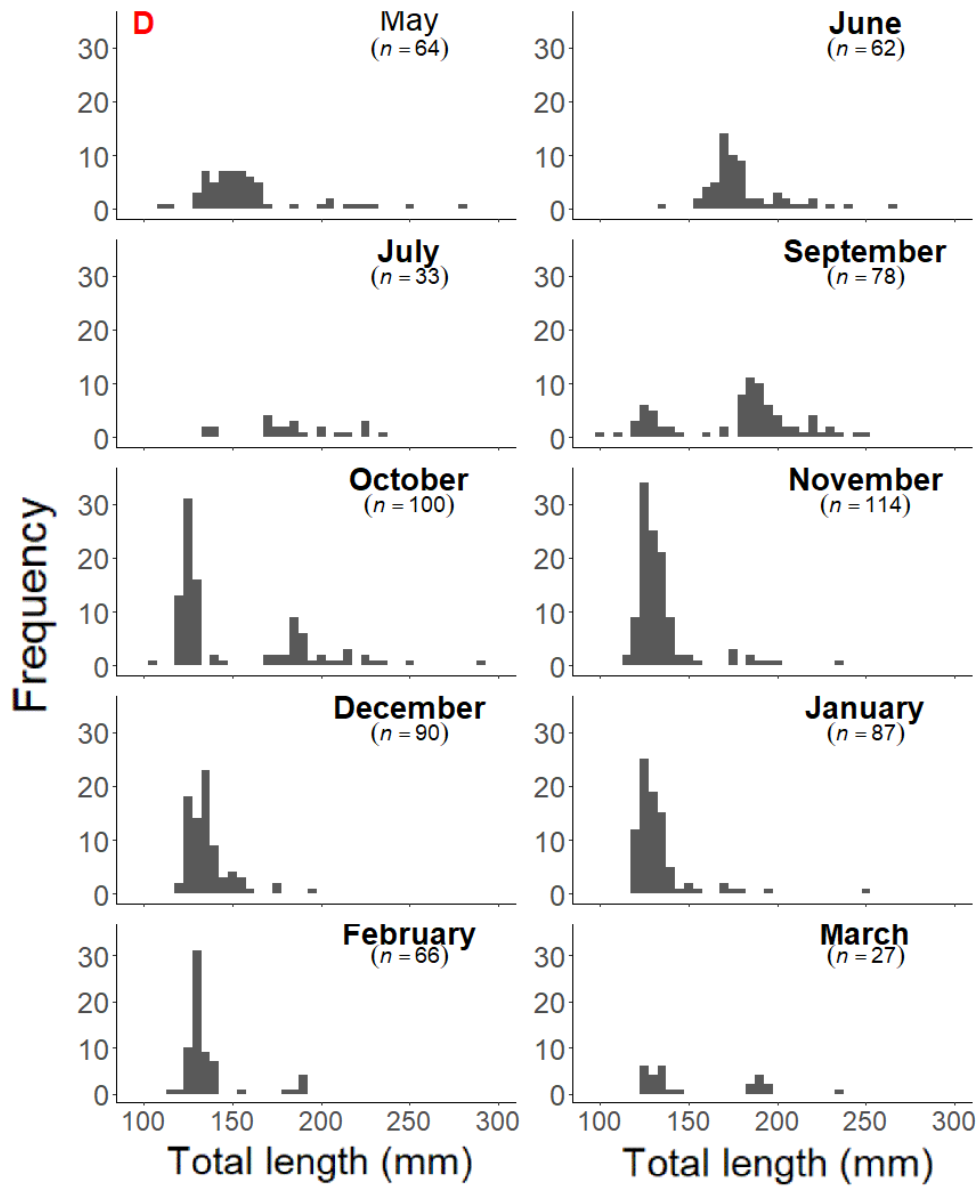
**Figure 3.** Length frequency distribution of flagtails *Kuhlia* spp., captured and tagged between May 2018 – March 2019 in Waiāhole, Hale O Lono, Loko Waka fishponds, and the adjacent embayment of Hilo Bay along the Keaukaha coast of Hilo, Hawai'i.



**Figure 4.** Length frequency distribution of Striped Mullet *Mugil cephalus* captured and tagged between May 2018 – March 2019 in Waiāhole, Hale O Lono, Loko Waka fishponds, and the adjacent embayment of Hilo Bay along the Keaukaha coast of Hilo, Hawai'i.

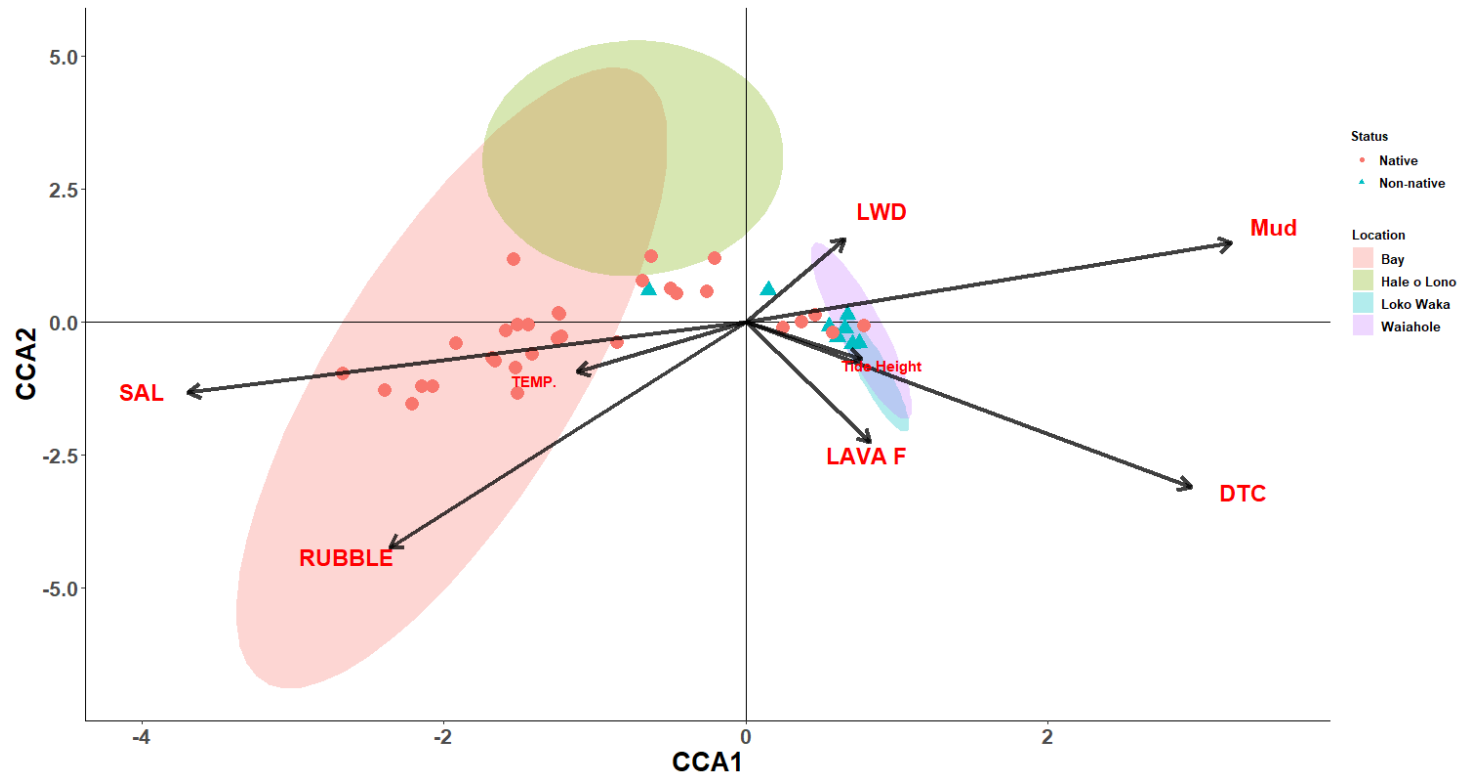


**Figure 5.** Length frequency distribution of Kanda *Osteomugil engeli* captured and tagged between May 2018 – March 2019 in Waiāhole, Hale O Lono, Loko Waka fishponds, and the adjacent embayment of Hilo Bay along the Keaukaha coast of Hilo, Hawai'i.



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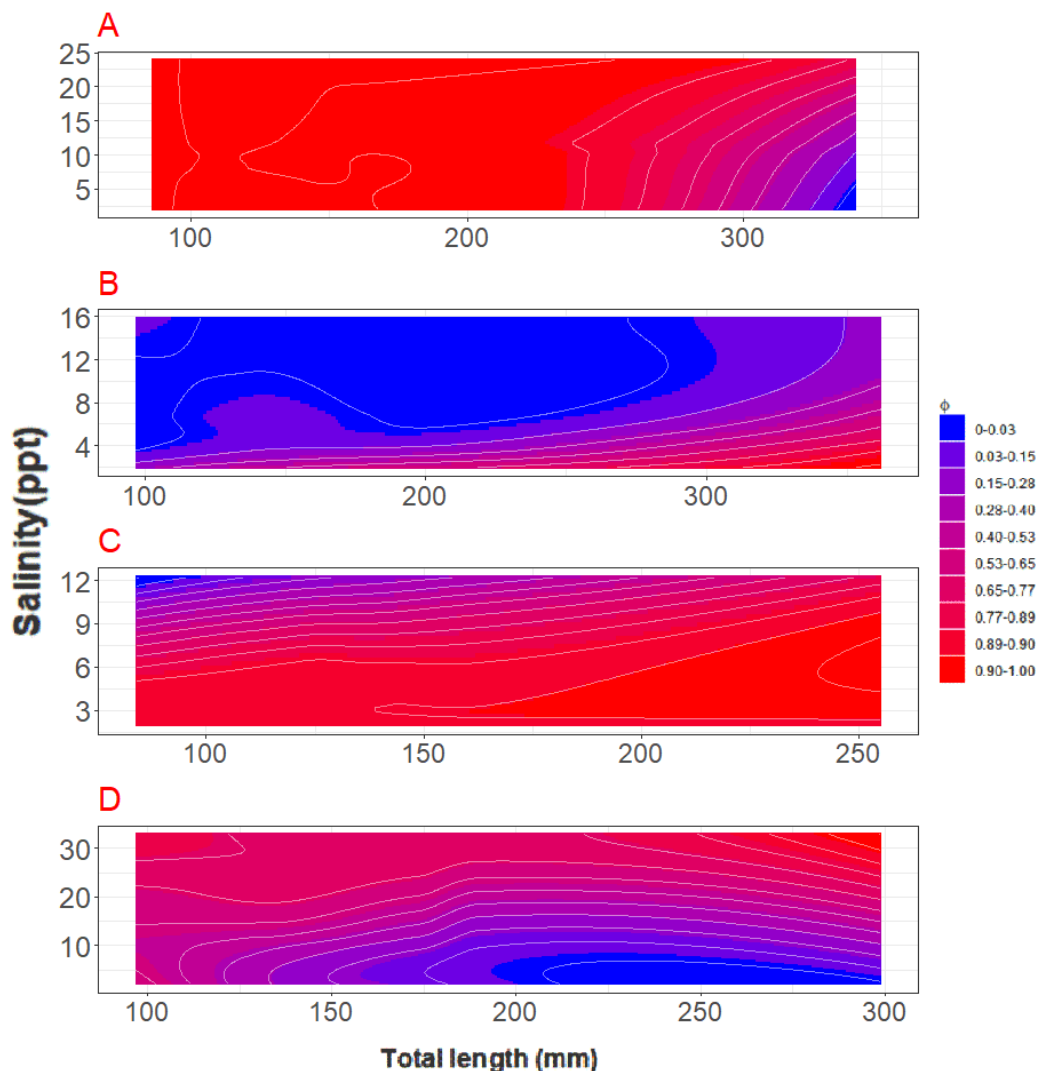
117 **Figure 6.** Length frequency distribution of Yellowstripe Goatfish *Mulloidichthys flavolineatus*  
 118 captured and tagged between May 2018 – March 2019 in Waiāhole, Hale O Lono, Loko Waka  
 119 fishponds, and the adjacent embayment of Hilo Bay along the Keaukaha coast of Hilo, Hawai'i.



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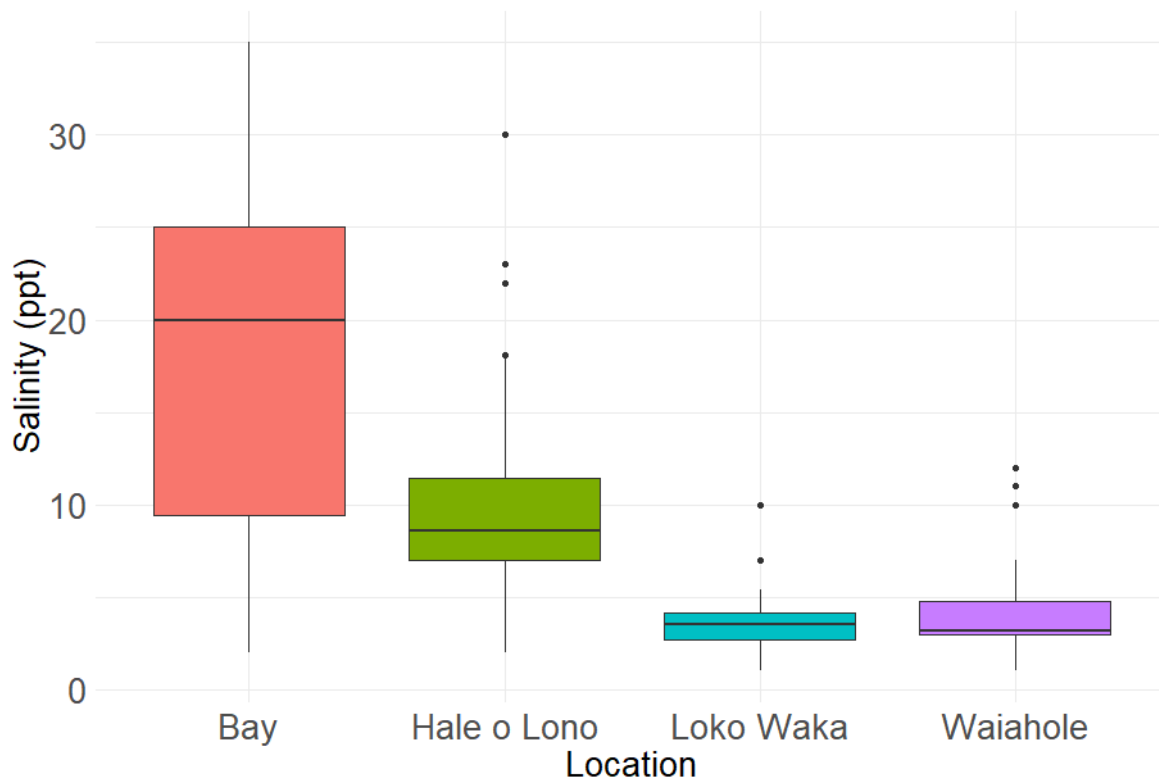
122 **Figure 7.** Canonical correspondence analysis biplots of species found in Waiāhole, Hale O Lono, Loko Waka Fishponds, and the  
 123 embayment they share located along the Keaukaha coast of Hilo, Hawai'i between May 2018 and April 2019. Species scores are  
 124 represented by points. Species introduction status indicated by shape of points. Environmental and habitat variables at the capture site  
 125 are represented by arrows and abbreviations listed in Table 6. CCA axis 1 describes 60.94% of the variance, with an eigenvalue of  
 126 0.689. CCA axis 2 explains 17.56% of the variance with and eigenvalue of 0.199. Ellipses represent the 95% confidence interval for  
 127 site scores for each location. Eigenvectors were multiplied by a factor of three for clarity.





129

130 **Figure 5.** Contour plot of the relationship among apparent survival ( $\phi$ ), salinity, and total length  
 131 of A) flagtails (*Kuhlia spp.*), B) Striped Mullet (*Mugil cephalus*), C) Kanda (*Osteomugil engeli*),  
 132 and D) Yellowstripe Goatfish (*Mulloidichthys flavolineatus*). Fish were captured and tagged  
 133 between May 2018 - March 2019 in Waiāhole, Hale O Lono, Loko Waka fishponds, and the  
 134 embayment they share located along the Keaukaha coast of Hilo, Hawai'i. Estimates of apparent  
 135 survival for each species are generated by the averaged top models of Huggins p and c.  
 136 Simulations of model predictions were conducted using 70000 iterations with covariates  
 137 bounded by the observed range of variables.



**Figure 6.** Box plot of salinity in Waiāhole, Hale O Lono, Loko Waka fishponds, and the embayment they share located along the Keaukaha coast of Hilo, Hawai'i. Between May 2018 – March 2019 The median is indicated inside each box by a dividing line. Lower and upper box boundaries define the upper 25th and lower 75th percentiles. Lower and upper error lines indicate 10th and 90th percentiles, respectively, filled circles indicate measurements that fall outside 10th and 90th percentiles.

145 **Appendix 1.** Management activities proposed and enacted across three fishponds locations.  
 146 Management activities noted from both communications with managers and permitting  
 147 applications with the state of Hawai‘i.

Location	Management activity					
	Rock wall repair	Invasive vegetation removal	Predator removal	Sediment dredging	Fish stocking	Invasive fish removal
Hale o Lono	x	x	x	x	x	x
Loko Waka					x	
Waiahole		x	x	x	x	x

148

149 **Appendix 2.** CCA axis scores of species found in Waiāhole, Hale O Lono, Loko Waka Fishponds,  
 150 and the embayment they share located along the Keaukaha coast of Hilo, Hawai'i between May  
 151 2018 and April 2019.

Species code	CCA1	CCA2	Status	Family	Common name	Scientific name
CAAM	-1.513	-1.336	Native	Tetraodontidae	Ambon Toby	Canthigaster amboinensis
STBA	-1.524	-0.853	Native	Labridae	Belted Wrasse	Stethojulis balteata
CASE	0.367	0.001	Native	Carangidae	Bigeye Trevally	Caranx sexfasciatus
ABSO	-2.077	-1.205	Native	Pomacentridae	Blackspot sargent	Abudefduf sordidus
LUFU	-0.645	0.593	Non-native	Lutjanidae	Blacktail Snapper	Lutjanus fulvus
CAME	-1.222	-0.273	Native	Carangidae	Bluefin Trevally	Caranx melampygus
PLIM	-2.208	-1.531	Native	Pomacentridae	Brighteye damselfish	Plectroglyphidodon imparipennis
ACNF	-2.670	-0.965	Native	Acanthuridae	Brown Surgeon	Acanthurus nigrofusus
CACA	-0.496	0.632	Native	Scaridae	Stareye Parrotfish	Calotomus carolinus
THTR	-1.916	-0.405	Native	Labridae	Christmas wrasse	Thalassoma trilobatum
CYCA	0.751	-0.394	Non-native	Cyprinidae	Common carp	Cyprinus carpio
ACTR	-1.589	-0.160	Native	Acanthuridae	Convict tang	Acanthurus triostegus
TYCR	-2.388	-1.278	Native	Belonidae	Crocodile needlefish	Tylosurus crocodilus
KHSP	-0.260	0.580	Native	Kuhliidae	Flagtail	Kuhlia xenura or Kuhlia sandwicensis
CAIG	0.249	-0.100	Native	Carangidae	Giant Trevally	Caranx ignobilis
CTID	0.704	-0.418	Non-native	Cyprinidae	Grass Carp	Ctenopharyngodon idella
STMA	-2.146	-1.216	Native	Pomacentridae	Hawaiian Gregory	Stegastes marginatus
SYUL	-1.677	-0.678	Native	Synodontidae	Brown lizardfish	Synodus ulae
ABAD	-1.439	-0.050	Native	Pomacentridae	Hawaiian Sargent	Abudefduf abdominalis
ABVA	-1.508	-0.045	Native	Pomacentridae	Indo-pacific sargent	Abudefduf vaiensis
OSEN	0.148	0.604	Non-native	Mugilidae	Kanda Mullet	Osteomugil engeli
POSP	0.550	-0.077	Non-native	Poeciliidae	Mexican Molly	Poecilia sphenops
GAAF	0.607	-0.281	Non-native	Poeciliidae	Misquito fish	Gambusia affinis
ZACO	-1.242	0.174	Native	Zanclidae	Moorish Idol	Zanclus cornutus
ORMO	0.657	-0.115	Non-native	Cichlidae	Mozambique tilapia	Oreochromis mossambicus
STHA	0.783	-0.067	Native	Gobiidae	Naniha oopu	Stenogobius hawaiiensis
CHLU	-1.231	0.150	Native	Chaetodontidae	Raccoon Butterflyfish	Chaetodon lunula
THDU	-1.249	-0.303	Native	Labridae	Saddle Wrasse	Thalassoma duperrey
POLA	0.674	0.135	Non-native	Poeciliidae	Sailfin molly	Poecilia latipinna
NELE	-0.625	1.246	Native	Mugilidae	Sharpnose Mullet	Neomyxus leuciscus
ELSA	0.574	-0.195	Native	Eleotridae	Hawaiian sleeper goby	Eleotris sandwicensis
DIHY	-0.204	1.201	Native	Diodontidae	Spotted Porcupinefish	Diodon hystrix
NESA	-0.458	0.536	Native	Holocentridae	Spotfin Squirrelfish	Neoniphon sammara
MUCE	0.463	0.131	Native	Mugilidae	Striped Mullet	Mugil cephalus
CHAU	-0.852	-0.390	Native	Chaetodontidae	Threadfin Butterflyfish	Chaetodon auriga
PAPO	-1.659	-0.732	Native	Mullidae	Whitesaddle goatfish	Parupeneus porphyreus
CAJA	-1.415	-0.604	Native	Tetraodontidae	Whitespot Toby	Canthigaster jactator
MUVA	-1.539	1.186	Native	Mullidae	Yellowtail Goatfish	Mulloidichthys vanicolensis
MUFL	-0.681	0.778	Native	Mullidae	Yellowstripe Goatfish	Mulloidichthys flavolineatus

**Appendix 3.** Benthic habitat composition of Waiāhole, Hale O Lono, Loko Waka Fishponds, and the shared embayment located along the Keaukaha coast of Hilo, Hawai'i. Benthic habitat was surveyed using boat mounted side-scan sonar video, georectified into an image, and manually classified.

