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MANGROVES IN CHANGING ENVIRONMENTS

Fish communities and juvenile habitat associated with non-native *Rhizophora mangle* L. in Hawai'i

Stacia D. Goecke · Susan M. Carstenn

Abstract There are many well-documented ecosystem services for which mangroves have received protection globally; however, in Hawai'i, where no species of mangroves are native, these services have not been thoroughly evaluated. Twelve permanently open stream mouth estuaries on O'ahu were sampled from September to October 2014. Abiotic factors and fish community data were correlated with percent mangrove cover and the Landscape Development Intensity Index to examine potential relationships among mangroves, humans, and fish communities. The three most abundant species, of 20 species caught, were *Kuhlia xenura*, *Mugil cephalus*, and *Mulloidichthys flavolineatus*. Of these three native species, 99% of the individuals caught were juveniles indicating the overall importance of stream mouth estuaries as juvenile habitat. Non-metric multidimensional scaling analysis of fish community data showed that *K. xenura*, *M. cephalus*, and *Lutjanus fulvus* were more abundant in shallower sites with lower salinity and higher percent mangrove cover. Stream mouth estuaries with mangroves are important juvenile habitats for the native *K. xenura* and *M. cephalus* and the non-native *Osteomugil engeli*. These species, two of which are important in recreational and subsistence fisheries, will be most likely affected by mangrove removal based on abundance and distribution in mangrove-dominated stream mouth estuaries.

Keywords Landscape development intensity index · *Kuhlia xenura* · *Mugil cephalus* · Stream mouth estuaries · Juvenile abundance · Invasive species

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Introduction

In Hawai'i, there are two types of estuaries: bays or saturated river valleys, and tidally influenced stream mouths (Kam et al., 1975), also referred to as stream mouth estuaries (SMEs). These SMEs may be perennial or permanently open, discharging into the ocean year-round, or intermittently open, discharging seasonally, or only after heavy rain (Kam et al., 1975). The stream mouth of permanently open SMEs is permanently connected to the ocean from the freshwater source. Stream modifications and diversions used for development and agriculture now prevent or minimize stream flow to the full downstream extent and into many historical stream mouths. SMEs, in the context of this study, include embayment areas where

there is an open connection between freshwater sources and the ocean along the coastline; some of these freshwater sources are natural (streams) and some are anthropogenic drainage. Mangroves are often associated with SMEs.

Land use/human impacts can alter environmental conditions, particularly along watersheds. Less developed areas with more vegetation cover have slower heat increases and smaller temperature fluctuations, whereas developed areas result in overall warmer temperatures and larger temperature fluctuations (Weng, 2001; Brasher, 2003; Weng et al., 2004). Surface temperatures increase with increased impervious surface (concrete/asphalt) due to reductions in vegetation canopy cover and shading. Areas that are more developed often have increased stream and groundwater diversion and impervious surfaces, limiting the amount of freshwater reaching the SME. This decreases fluvial and groundwater influences, leaving the SMEs more affected by tidal influences, thereby increasing salinity. Streams, rivers, and run-off connect the entire watershed allowing resulting effects of disturbances throughout the watersheds to accumulate in the SMEs. SMEs and their inhabitants are thus especially vulnerable to disturbances, including human impacts (e.g., land use/land cover alterations and stream water diversion), and particularly important subjects for research and coastal management.

Mangroves require tidal flushing (Lugo & Snedaker, 1974; Schaeffer-Novelli et al., 1990; Harris et al., 2010), yet sea-level rise, storm surges or rough water conditions can damage, stress, or kill mangroves and affect their distribution (Lugo & Snedaker, 1974; Doyle et al., 1995; Gilman et al., 2007; Smith et al., 2009). Primary productivity of *Rhizophora mangle L.* decreases with increased salinity (Lugo & Snedaker, 1974), but it is more tolerant of salt water than other species in Hawai'i, e.g., *Bruguiera sexangula* (Lour.) Poir. (Clough, 1992). Increased salinity decreases proxies for photosynthetic rates (leaf stomatal conductance and leaf chlorophyll fluorescence induction) in *R. mangle* suggesting an optimal salinity of less than 20 ppt for increased photosynthesis (Biber, 2006). Optimal growth of a closely related species, *R. mucronata*, was at 50% seawater (16–18 ppt), with decreased growth in salinity higher than 16–18 ppt (Aziz & Khan, 2001). SMEs on O'ahu are a balanced combination of calm, brackish water, ideal for *R. mangle*. This species was first introduced to

southwestern Moloka'i in 1902 and to He'eia, O'ahu in 1922 (Allen, 1998). It is now well-established in many coastal areas of Hawai'i, including SMEs. All mangroves in Hawai'i are non-native and *R. mangle* is considered invasive.

Mangroves influence physical and chemical properties. Mangroves are highly productive and therefore add more vegetation (stand structure and propagules) and detritus (leaf litter, wood debris) to SMEs than native plants found in similar habitats in Hawai'i (Allen, 1998; Cox & Allen, 1999; Demopoulos et al., 2007). Decomposition of these materials may lower dissolved oxygen and increase particulate and dissolved organic matter. Mangrove vegetation can reduce water flow, velocity, and tidal drainage (Kitheka, 1997), decrease tidal currents (Furukawa et al., 1997), and limit water exchange (Wu et al., 2001). Mangroves may cause complete blockages of the stream channel, further limiting water mixing within the estuary (Wu et al., 2001). In Hawai'i, some of the concerns regarding mangroves include drainage impedance, poor aesthetic qualities, reduction of habitat for native shorebirds, and damage to archeological sites (Allen, 1998; Rauzon & Drigot, 2002). The latter two have motivated efforts around the Hawaiian Islands, including Kaloko-Honokōhau National Historic Park in Kona, Hawaii, Marine Corps Base (MCBH) on the Makapu'u peninsula, Kāne'ohe, O'ahu, and Pearl Harbor National Wildlife Refuge, Pearl Harbor, O'ahu, to remove the mangroves and restore native vegetation. Proper planning and a thorough understanding of specific mangrove areas throughout Hawai'i are essential to better inform management and minimize expense, effort, and potential disturbance when considering mangrove removal in SMEs.

In their native range, leaf litter and shading from mangrove canopy cover creates refuge for fish (Ellis & Bell, 2004). The extensive stand structure and organic sediment from mangroves provide nursery habitat for fish and shellfish species targeted in recreational and commercial fisheries (Vidy, 2000). Juvenile fish dominated total catch in mangrove studies in Brazil, West Africa, and Taiwan (Kuo et al., 1999; Vidy, 2000; Krumme et al., 2004). Mangroves support fish populations by providing refuge and food, especially for juveniles (Nagelkerken & Faunce, 2008). A nursery habitat has previously been defined as "any habitat that makes a greater than average contribution

to the recruitment of adults" (Beck et al., 2001). Nursery function may be measured as the dominance of species in juvenile stages (Nagelkerken et al., 2000). Beck et al. (2001) states that any combination of four factors (density, growth, survival of juveniles, and movement into adult habitats) may be considered to assess contribution to adult recruitment and thereby identify nursery habitat. The definition of nursery habitat continues to evolve. Two papers published after the current study was conducted, Nagelkerken et al. (2015) and Sheaves et al. (2015), expand this list to include assessment of connectivity and complexity within potential nursery habitats as well as with adjacent coastal areas to determine nursery value. Despite being well-documented as essential nursery habitat in their native range worldwide, the function of non-native mangroves specifically as nursery habitats in Hawai'i's SMEs has not been studied.

Two studies in Hawai'i have assessed fish communities correlated to mangroves, either in un-vegetated areas (MacKenzie & Kryss, 2013) or adjacent mud flats (Nakahara, 2007). The results of these studies suggest that mangroves in Hawai'i may be providing nursery habitat, as fish in mangrove-dominated habitats are predominantly juveniles. On the island of Hawai'i, significantly smaller individuals of both the native Hawaiian flagtails (*Kuhlia* spp.) and the exotic mollies (*Poecilia* spp.) were collected in tide pools with mangroves than in tide pools with native vegetation (MacKenzie & Kryss, 2013). On Moloka'i, three of four fish species had higher relative abundance of juveniles in mangroves than on adjacent sand flats (Nakahara, 2007). There is considerable debate on whether or not mangroves are benefiting coastal environments in Hawai'i, though these studies suggest that mangroves may provide nursery function in Hawai'i as they do elsewhere.

Physical and chemical parameters may explain variability in fish distribution and community structure within and among SMEs. These parameters affect the quality and suitability of habitat for particular species or age classes. Though abiotic factors and fish communities have been studied throughout Hawai'i, the correlation between percent mangrove canopy cover with SME conditions and fish communities has yet to be evaluated. In the current study, we explored differences in the fish community among SMEs on O'ahu based on gradients of percent mangrove cover and human impact. The Landscape Development

Intensity Index (LDI) is a weighted measure of potential disturbance to an ecosystem that is used to quantify a gradient of human impact based on land use (Brown & Vivas, 2005). It was hypothesized that SMEs with higher percent mangrove cover would exhibit lower diversity of native species, species richness and evenness, and higher overall biomass and relative abundance of individual fish, specifically juveniles. It was also hypothesized that SMEs with higher LDI would exhibit lower diversity of native fish species, fish species richness and species evenness, and higher diversity, biomass, and relative abundance of non-native fish species.

Analyses of correlations among percent mangrove cover, LDI, abiotic factors, and fish communities assess the suitability of SMEs as nursery habitat, which is a beneficial ecosystem service. The value of mangroves in SMEs for juvenile and nursery fish habitat, especially for native species valued in recreational and subsistence fisheries, should be evaluated alongside potential detrimental effects to better manage SMEs. There are many abiotic factors attributing the suitability of juvenile habitat for specific species (salinity, depth, temperature, structure for refuge). While it is not possible to determine direct influence of mangroves on fish communities in Hawai'i's SMEs, this study assesses which species are more abundant in and may be benefiting from SMEs with higher percent mangrove cover and which will be most impacted by mangrove removal efforts based on distribution.

Materials and methods

Site selection

Twelve permanently open SMEs (Fig. 1) on O'ahu, Hawai'i, located near 21.4667°N, 157.9833°W, were sampled during September and October 2014. Sites were selected based on a gradient of percent mangrove canopy cover, LDI, accessibility, and permitting.

Sampling methods

Each SME was sampled in three approximately equal sections designated lower, middle, and upper, using a stratified random sampling approach (Fig. 2) at low tide. The stream mouth was delineated as a straight line connecting the two farthest points of land on the
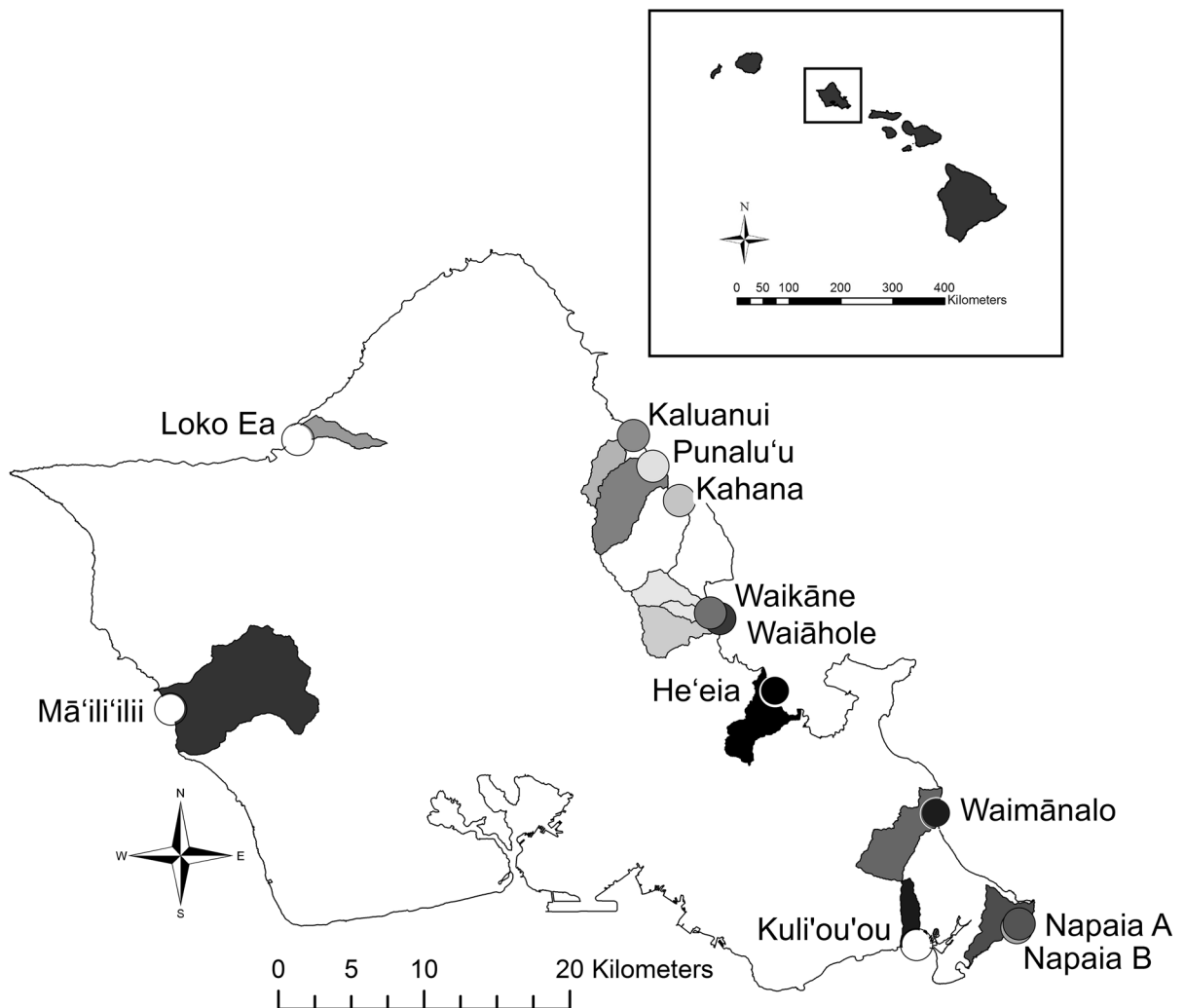
Fig. 1 Map of sampling sites on Oʻahu. Corresponding watersheds for each stream mouth are *color coded white to black* from lowest to highest Landscape Development Intensity index values. The range of LDI values for sample sites is 1.62 (Kahana) to 18.33 (Heʻeia), on a logarithmic scale. *Circle markers* for each site indicate the percent mangrove cover of the stream mouth estuary, *color coded white to black* from lowest to highest percent mangrove cover. The range of mangrove cover for sample sites is 0 (Māʻiliʻilii and Kuliʻouʻou) to 97.10 (Heʻeia)

ocean edge across the stream. The lower section started closest to the ocean at the mouth of the SME and the upper section ended at the farthest accessible extent of the SME, or where the marine influence on salinity was no longer detectable, whichever was closest to the mouth. This study included four different approaches to describe the SMEs: one to measure physical and chemical water characteristics and three (cast nets, traps, and lay nets) to assess fish assemblages.

Measurement and identification protocol was the same for all fish catching methods. Total length

(TL) and (wet) mass of each fish was measured and recorded before the catch was returned to the SME. Photographs were taken of all individuals to ensure proper identification. All individuals were identified to the lowest possible taxonomic group. Species of the Cichlidae family commonly referred to as tilapia (regardless of proper genus), were identified in this study as *Tilapia* complex and assumed to be one of the seven species found by Wu and Yang (2012): *Oreochromis aureus* (Steindachner 1864), *O. mossambicus* (Peters 1852), *O. niloticus* (Linnaeus 1758), *Sarotherodon melanotheron* (Rüppell 1852),

Fig. 2 Schematic diagram of sampling divisions and methods, indicating placement of cast nets, lay net, traps, and multi-parameter measurements, within each site. Each section of the estuary was sampled. Diagram adapted from Ratana (2014)
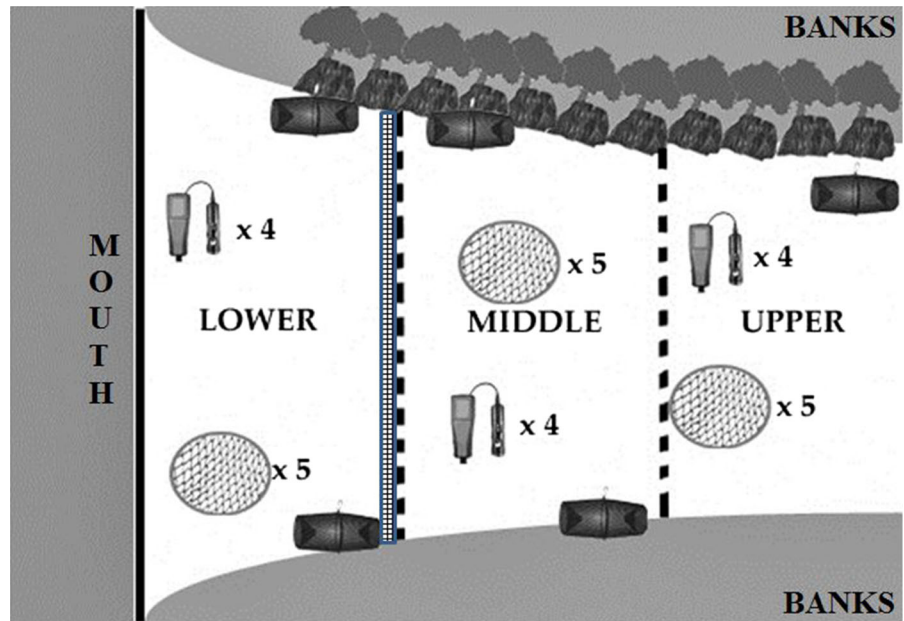
O. urolepis (Norman 1922), *Tilapia rendalli,* and a hybrid of *O. mossambicus* and *O. niloticus.* Since these species are non-native to Hawai'i and some hybridize, individuals were grouped together as *Tilapia* complex, without further effort to identify the species.

Physical and chemical measurements

Temperature, salinity, percent oxygen saturation, pH, and turbidity were recorded using an Orion A239 multi-parameter meter and a Hach 2100Q Portable Turbidimeter. Stratified random sampling included four measurements taken mid-depth in the water column per SME section: two near the middle of the channel of the SME and two near the banks in at least 10 cm water. Water depth was recorded where the parameters were measured.

Cast nets

Fish abundance and density were sampled using two cast nets: a standard 16 foot (4.88 m) diameter, ¼ inch (0.64 cm) un-stretched mesh, and a 6 foot (1.83 m) diameter ¾ inch (1.91 cm) stretched mesh. The larger net was used primarily but the smaller net was used selectively for shallower, narrower areas within SMEs for which the larger

net was ineffective. Five random casts were employed in each section.

Fish traps

Five baited fish traps (3 cm opening diameter, 0.5 cm mesh) were secured at each sample site, giving preference to areas having emergent vegetation, when present. Total soak time for each site was recorded.

Lay nets (gill nets)

An 11 foot (3.4 m) long, 6.7 foot (2 m) high, lay net with 2.5 inch (6.35 cm) mesh was deployed in stream mouths targeting adult fishes at all sites. Protocols followed Department of Land and Natural Resources (DLNR) regulations HAR section §13-75-12.4 or special provisions granted in a special activity permit provided by the State of Hawai'i DLNR's Division of Aquatic Resources. Total soak time was recorded.

Data acquisition

SME size

SME size was delineated in ArcGIS 10.2 using the USGS National Hydrography Dataset and Digital Globe 2010 World View 2 aerial imagery. Sites were

delineated from the mouth to the furthest upstream extent based on physical and/or legal access and from the center of the stream to 15 meters from the stream bank on both sides (Dunn, 2015).

Percent mangrove canopy cover

Percent mangrove canopy cover for this study was estimated using Digital Globe 2010 World View 2 aerial imagery and ArcGIS 10.2 zonal statistics tool. Mangrove canopy identified in the imagery of each SME, as delineated for SME size, was included in the calculation of percent mangrove cover for each SME (Dunn, 2015).

Landscape development intensity index (LDI)

LDI has been correlated to biotic conditions of adjacent coral reefs (Oliver et al., 2011; Ku'ulei et al., 2012), wetlands (Brown & Vivas, 2005; Mack, 2006; Reiss & Brown, 2007; Lin et al., 2013), O'ahu's SMEs (Ratana, 2014), and Hawai'i's bays and estuaries (Jenzen, 2014). It is calculated based on intensity factors that are the measurements of non-renewable energy use per unit area. Calculated values are on a Log_{10} scale where a value of zero represents no human impact. The following equation was used to calculate the index (Reiss et al., 2014):

$$\mathrm{LDI} = 10 \times \log_{10}(\mathrm{AEI_{Total}}/\mathrm{AEI_{Ref}}), \quad (1)$$

where *LDI* Landscape Development Intensity index for a watershed, AEI_{Total} total areal empower intensity within a watershed, AEI_{Ref} renewable areal empower intensity within a watershed.

The percent of the land area within a watershed of each land use was estimated using ArcGIS 10.2 and data layers from the Honolulu Department of Planning, 2011 NOAA Coastal Change Analysis Program (C-CAP), and 2010 City and County of Honolulu Zoning Designations, and assigned an intensity factor following Brown and Vivas (2005) and Brown and Reiss (2010).

Data analyses

PC-ORD 6.19, SPSS 21, and Sigmaplot 11.0 were used for analyses. Data, even with transformations, did not meet the parametric assumption of normality; therefore, non-parametric analyses were used. Results

were considered statistically significant with a significance value of $P \leq 0.05$. Two multivariate statistical methods, non-metric multidimensional scaling (NMS) and polar ordination, were used to assess differences among SMEs.

NMS ordination was performed to explore differences among sites based on fish community data ($n = 11$ sites) and Juvenile/Adult Abundance and Biomass (JAAB) data ($n = 10$ sites). For NMS analyses, similarity matrices were constructed using the relative Sorensen (Bray–Curtis) distance measure. The number of axes from the NMS analyses was chosen to minimize stress. Solutions were not accepted if the stress value was greater than 10 (Clarke, 1993; McCune et al., 2002). Significance values were determined from Monte Carlo randomization tests, using 999 runs. The resulting plot is a visual depiction of differences among study sites.

Polar ordination supports hypothesis testing by choosing an abiotic gradient and evaluating differences among sites and species based on this gradient. The better the selected gradient explains the variance in the dataset, the higher the percent variance explained by the subjectively selected axis. Polar ordination was performed to evaluate the variance explained by percent mangrove cover versus other, objectively selected gradients. For polar ordination, similarity matrices were constructed using the variance-regression end point selection method (Beals, 1984), relative Sorensen (Bray–Curtis) distance measure, and City Block Axis Projection. Percent variance between sites was based on the comparison of both subjective and objective end points in order to determine which best explained the differences in the fish community and JAAB among SMEs. Ordination scores are the coordinates for each site along respective axes indicating the calculated distances between sites/species along the axis (based on how similar or different the sites/species are with respect to a specific gradient). There is one score or number (coordinate value) for each site/species for each axis. For objective axes, these scores were then correlated using Kendall's rank (Tau) correlation with abiotic variables to explore relationships of these objective gradients to the abiotic data. Axes from NMS and polar ordination analyses were correlated with abiotic factors including salinity, percent oxygen saturation, water temperature, depth, pH, turbidity,

SME size, percent mangrove canopy cover, LDI, and effort by fishing method.

Results

A total of 509 individuals, representing 20 fish species (Table 1), were caught across twelve sites. There was a total of 15 native species and 5 non-native species caught, indicating the dominance of native species richness in SMEs. Despite small sample size, clear and significant patterns were found in this study. These results only reflect findings of the sampled SMEs during low tide during the time of sampling. Interpretation should not be extended to all seasonal and temporal scales in these highly variable systems but rather represent a "snap-shot" of some occurring patterns.

The following species each had more than 5% relative abundance and comprised 88% of the cumulative abundance: *Kuhlia xenura* (Jordan & Gilbert 1882), *Mulloidichthys flavolineatus* (Lacepède 1801), *Mugil cephalus* Linnaeus, 1758, *Osteomugil engeli* (Bleeker 1858), and *Tilapia* complex. Of these species, 90% of the individuals caught were juveniles based on L50 values, the length at which 50% of the individuals within the population are able to reproduce (Tong, 2004; Nishimoto et al., 2007; McRae et al., 2011; Niyonkuru & Laleye, 2012). Of the three native species, all of which are important targets in recreational fisheries in Hawai'i, 99% of individuals caught were juveniles.

SMEs with lower LDI had a greater abundance and species richness of non-native species (non-native species abundance: $\tau = -0.425$, $P \leq 0.05$, and non-native species richness: $\tau = -0.499$, $P \leq 0.05$). Also, juveniles of the five most abundant species were more abundant in sites with lower LDI ($\tau = -0.412$, $P \leq 0.05$). There were no significant correlations between percent mangrove cover and fish community metrics, including total abundance ($\tau = 0.063$, $P > 0.05$), total biomass ($\tau = 0.078$, $P > 0.05$), juvenile abundance ($\tau = 0.047$, $P > 0.05$), juvenile biomass

Table 1 List of species caught in order of relative catch abundance, from most to least abundant, and whether each is native or non-native to Hawai'i

Species	Common name	Total catch	Native	Non-native
Kuhlia xenura	Hawaiian flagtail/Āholehole	162	×	
Mulloidichthys flavolineatus	Yellowstripe goatfish/Weke 'ā (adults)/'Oama (juveniles)	94	×	
Mugil cephalus	Striped mullet/'Ama'ama	96	×	
Osteomugil engeli	Kanda mullet	50		×
Tilapia complex	Tilapia	46		×
Caranx ignobilis	Giant trevally/Ulua aukea	10	×	
Atherinomorus insularum	Hawaiian silverside/'Iao	10	×	
Acanthurus triostegus	Convict surgeonfish/Manini	9	×	
Naso unicornis	Bluespine unicornfish/Kala	5	×	
Acanthurus nigrofuscus	Brown surgeonfish/Lavender tang/Mā'i'i'i	3	×	
Caranx melampygus	Bluefin trevally/'Ōmilu	3	×	
Poecilia sp.	Mollies/Guppies	3		×
Eleotris sandwicensis	Sandwich island sleeper/O'opu akupa	2	×	
Lutjanus fulvus	Blacktail snapper/Flametail snapper/To'au	2		×
Pterygoplichthys multiradiatus	Long-fin armored catfish/Orinoco sailfin catfish	2		×
Rhinecanthus rectangulus	Reef triggerfish/Picasso triggerfish/Humu humu nukunuku apua'a	2	×	
Saurida nebulosa	Nebulous lizardfish/Clouded lizardfish/'Ulae	2	×	
Bothus pantherinus	Panther flounder/Leopard flounder/Pāki'i	1	×	
Echidna nebulosa	Snowflake moray/Starry moray/Puhi kāpā	1	×	
Upeneus arge	Bandtail goatfish/Finstripe goatfish/Nightmare goatfish/Weke pueo	1	×	

($\tau = 0.047$, $P > 0.05$), species richness ($\tau = 0.065$, $P > 0.05$), or evenness ($\tau = -0.388$, $P \leq 0.10$).

There were significant correlations between percent mangrove cover or LDI and individual species. *Kuhlia xenura* were significantly more abundant in SMEs with higher percent mangrove cover (abundance: $\tau = 0.476$, $P \leq 0.05$, biomass: $\tau = 0.476$, $P \leq 0.05$). *Mulloidichthys flavolineatus* were significantly more abundant in SMEs with lower percent mangrove cover (biomass: $\tau = -0.472$, $P \leq 0.05$). *Osteomugil engeli* were more abundant in SMEs with lower LDI (abundance: $\tau = -0.472$, $P \leq 0.05$, biomass: $\tau = -0.432$, $P \leq 0.05$).
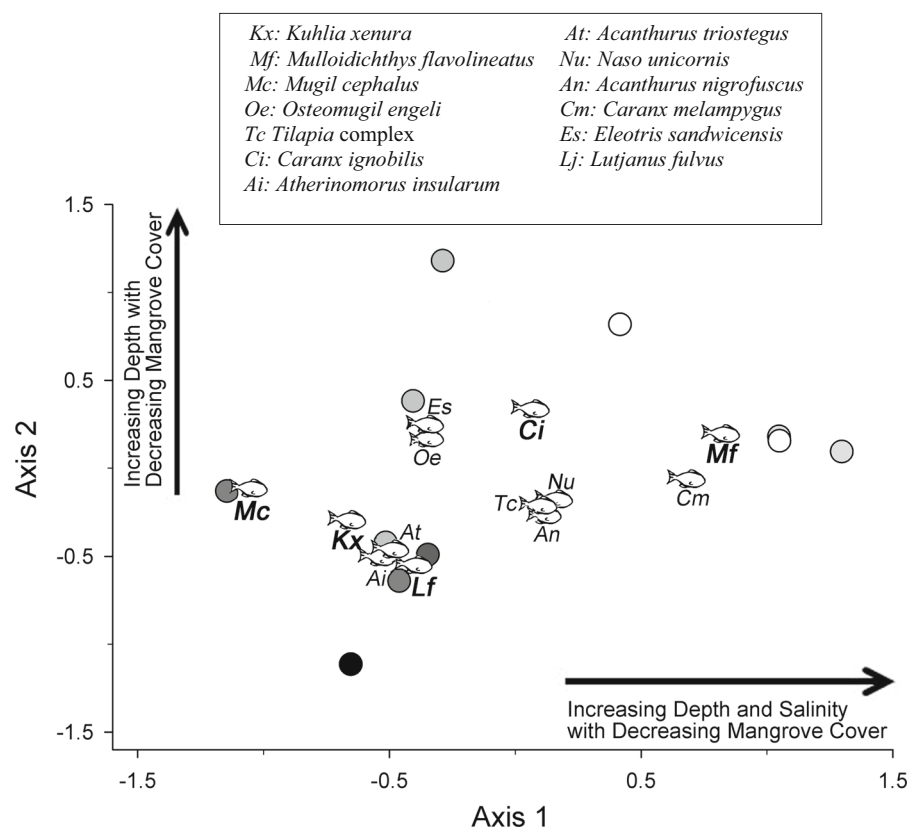
NMS of fish community data

NMS ordination of raw count fish community data produced a 2-dimensional solution with a stress value of 6.335 (Fig. 3). The 2-dimensional solution was significant ($P < 0.03$). The axes were orthogonal (88%), and cumulatively explained 89.5% of the variance in fish communities among sites. Percent mangrove cover (Axis 1: $\tau = -0.550$, $P < 0.05$; Axis 2: $\tau = -0.514$, $P < 0.05$) and depth (Axis 1: $\tau = 0.745$, $P < 0.001$; Axis 2: $\tau = 0.455$, $P < 0.05$) were significantly correlated to both axes. Salinity ($\tau = 0.564$, $P \leq 0.01$) was significantly correlated to Axis 1. Axis 1 represents a gradient of decreasing percent mangrove cover and increasing depth and salinity. Axis 2 represents a gradient of decreasing percent mangrove cover and increasing depth.

Kuhlia xenura was significantly correlated to both Axis 1 ($\tau = -0.663$, $P < 0.01$) and Axis 2 ($\tau = -0.422$, $P < 0.05$) indicating that it was more abundant in shallower SMEs with higher percent mangrove cover. *Mugil cephalus* (Axis 1: $\tau = -0.462$, $P < 0.05$) and *Lutjanus fulvus* (Forster 1801) (Axis 2: $\tau = -0.445$, $P < 0.05$) were also negatively correlated to Axis 1 and 2, respectively, indicating overlapping distributions with *K. xenura*.

Fig. 3 NMS 2-dimensional ordination of fish community data with fish species (*fish*) overlaid on sample sites (*circles*). Sites are color coded along the gradient from lowest to highest percent mangrove cover from *white to black*, respectively. Species significantly correlated to the axes are labeled in *bold* (*Kuhlia xenura*, *Mugil cephalus*, *Mulloidichthys flavolineatus*, *Caranx ignobilis*, and *Lutjanus fulvus*). Abiotic factors significantly correlated to each axis are described

Kx: Kuhlia xenura
Mf: Mulloidichthys flavolineatus
Mc: Mugil cephalus
Oe: Osteomugil engeli
Tc Tilapia complex
Ci: Caranx ignobilis
Ai: Atherinomorus insularum
At: Acanthurus triostegus
Nu: Naso unicornis
An: Acanthurus nigrofuscus
Cm: Caranx melampygus
Es: Eleotris sandwicensis
Lj: Lutjanus fulvus

Mulloidichthys flavolineatus (Axis 1: $\tau = 0.428$, $P < 0.05$) and *Caranx ignobilis* (Forsskål 1775) (Axis 2: $\tau = 0.442$, $P < 0.05$) were positively correlated with Axis 1 and 2, respectively. This indicates that the abundance of these species was greater in sites with higher salinity and depth and with lower percent mangrove cover.

NMS of JAAB data

NMS ordination of JAAB data produced a 3-dimensional solution with a stress value of 1.887 (Fig. 4). The 3-dimensional solution was highly significant ($P \leq 0.003$). The three axes were highly orthogonal (89.3%, $r = -0.327$ for axis pair 1 and 2, 99.0%, $r = 0.100$ for axis pair 1 and 3, and 99.8%, $r = 0.045$ for axis pair 2 and 3) and cumulatively explained 78% of the variance in juvenile and adult abundances and biomass by species among sites.

Axis 2 was significantly correlated to pH ($\tau = -0.467$, $P \leq 0.05$) and Axis 3 was significantly correlated to salinity ($\tau = 0.467$, $P \leq 0.05$) and depth ($\tau = 0.733$, $P < 0.01$). This indicates that pH, salinity, and depth were the most influential abiotic factors with respect to JAAB data. Adult abundance and biomass of both species of mullet, *M. cephalus* (Abundance: $\tau = -0.596$, $P < 0.05$, Biomass: $\tau = -0.542$, $P < 0.05$) and *O. engeli* (Abundance and Biomass: $\tau = -0.609$, $P < 0.01$), were significantly correlated to Axis 2. This indicates an overlapping distribution of
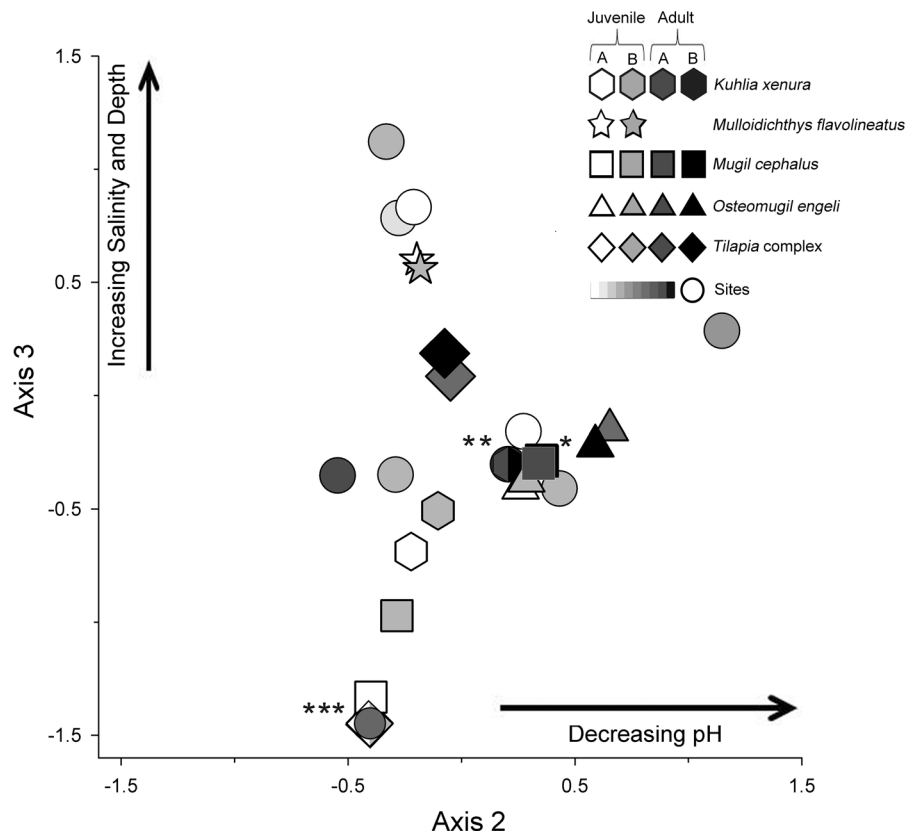

Fig. 4 NMS 2-dimensional ordination overlay of sites and JAAB data (dataset including species with at least 5% relative abundance of total catch). Only Axes 2 and 3, which explained the largest percent of the variance (17 and 53%, respectively), are shown, for simplification. Sites are color coded along the gradient from lowest to highest percent mangrove cover from *white to black*, respectively. Abiotic factors significantly correlated to each axis are described. All individuals of *Mulloidichthys flavolineatus* caught during this study were juveniles. Species abundance and biomass overlap are represented by the *half-shaded shapes and stars*. *Overlap of adult *Mugil cephalus* abundance and biomass. **Overlap of adult *Kuhlia xenura* abundance and biomass with sampling site Waimānalo. ***Overlap of juvenile *Tilapia* complex abundance and biomass with sampling site Waiāhole

the two species and that their abundance and biomass were greater in sites with lower pH. Juvenile abundance and biomass of *K. xenura* ($\tau = -0.680$, $P < 0.01$ and $\tau = -0.479$, $P < 0.05$, respectively) and *M. cephalus* ($\tau = -0.669$, $P < 0.01$) and juvenile abundance of *O. engeli* ($\tau = -0.596$, $P < 0.05$) were significantly correlated with Axis 3. Juveniles of these species were more abundant and overlapped in distribution in SMEs with lower salinity and depth.

Polar ordination

Polar ordination, using percent mangrove cover as a subjectively selected gradient, explained a larger percent of the variance in the data than any other objectively or subjectively selected axis (gradient).

LDI and other abiotic gradients considered in this study are less useful than percent mangrove cover in explaining patterns in fish community and JAAB data.

The percent mangrove cover gradient accounted for 72% of the variance in fish communities among sites (Fig. 5). Native species *K. xenura* ($\tau = -0.623$, $P < 0.01$) and *M. flavolineatus* ($\tau = 0.467$, $P \leq 0.05$) were significantly correlated with Axis 1. This indicates that *K. xenura* were more abundant in SMEs with greater percent mangrove cover whereas *M. flavolineatus* were more abundant in SMEs with lower percent mangrove cover. Objectively selected Axes 2 and 3, respectively, represented 16% and 9% of the variance in fish community data.

The percent mangrove cover gradient represented 50% of the variance in JAAB among sites (Fig. 6).
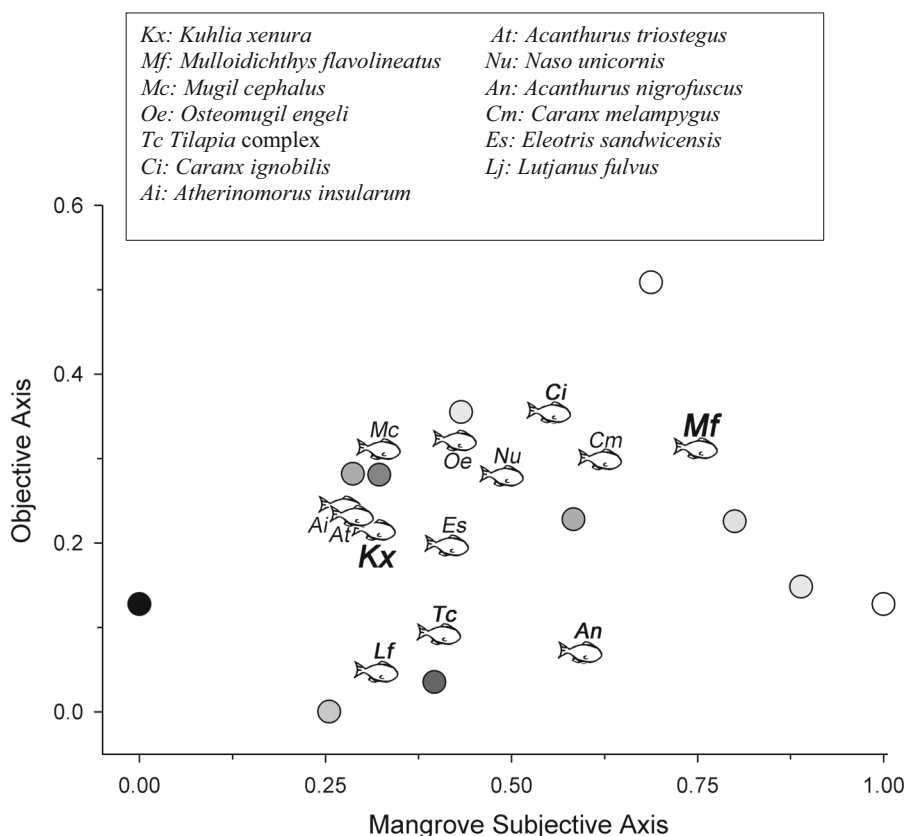

Fig. 5 2-Dimensional polar ordination plot of fish community data with species (*fish*) overlaid on sampling sites (*circles*). Axis 1 was subjective representing the percent mangrove cover gradient and Axis 2 was objective. Sites are color coded along the gradient from lowest to highest percent mangrove cover from white to black, respectively. Species significantly correlated to the axes are labeled in bold (*Kuhlia xenura* and *Mulloidichthys flavolineatus*). The axes ordinate the sites using the selected end points and ordering the sites based on similarities/differences among sites between these chosen end points. The axes represent the calculated similarity distances between each site, as represented by the selected gradient and not the gradient empirically
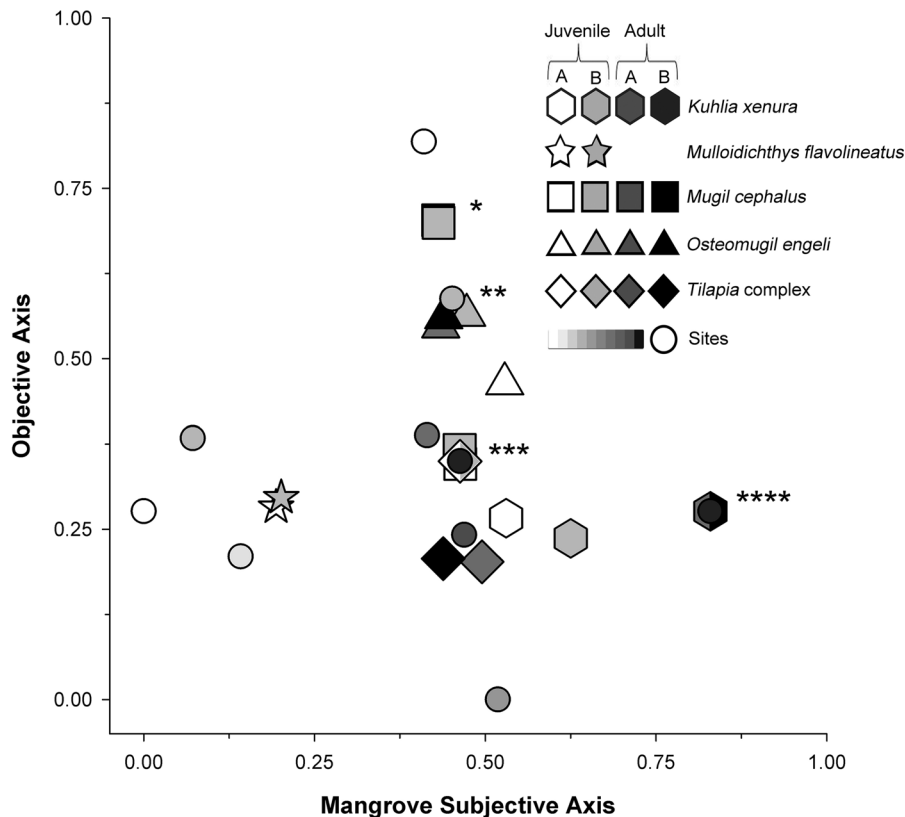
Fig. 6 2-D polar ordination plot of sites and JAAB variables for the five most abundant species. Axis 1 was subjective representing the percent mangrove cover gradient and Axis 2 was objective. Sites are color coded along the gradient from lowest to highest percent mangrove cover from *white to black*, respectively. The axes ordinate the sites using the selected end points and ordering the sites based on similarities/differences among sites between chosen end points. The axes represent the calculated similarity distances between each site, as represented by the selected gradient and not the gradient empirically. All individuals of *Mulloidichthys flavolineatus* caught during this study were juveniles. Species abundance and biomass overlap are represented by the half-shaded shapes and stars.*Overlap in adult *Mugil cephalus* abundance and biomass. **Overlap of adult *Osteomugil engeli* abundance and biomass, juvenile *Osteomugil engeli* biomass with sampling site Kahana. ***Overlap with juvenile *Mugil cephalus* and *Tilapia* complex abundance and biomass and sampling site Waiāhole. ****Overlap of adult *Kuhlia xenura* abundance and biomass and sampling site Waimānalo

Juveniles of native species *K. xenura* (Abundance: $\tau = 0.630$, $P < 0.01$, Biomass: $\tau = 0.832$, $P < 0.001$) and non-native species *O. engeli* (Abundance: $\tau = 0.646$, $P < 0.01$, Biomass: $\tau = 0.501$, $P < 0.05$) were significantly correlated with Axis 1, the mangrove gradient. This indicates that these species had greater abundance and biomass in SMEs with higher percent mangrove cover. Objectively selected Axes 2 and 3, respectively, represented 29 and 12% of the variance in JAAB data.

The LDI gradient, Axis 1, represented 47% of the variance in fish communities among sites. The native species *C. ignobilis* ($\tau = 0.569$, $P < 0.01$) was significantly correlated to Axis 1, indicating that this species was more abundant in less impacted SMEs (as indicated by a lower LDI value). Axis 1 ordination scores were negatively correlated with percent mangrove cover ($\tau = -0.514$, $P < 0.05$), further supporting the co-variability of mangrove cover and LDI. Objectively selected Axes 2 and 3, respectively, represented 39 and 11% of the variance in fish communities.

The LDI gradient, Axis 1, explained 23% of the variance in the JAAB among sites. No species were significantly correlated to Axis 1. This indicates that neither the number nor biomass of the top five most abundant species, for juveniles or adults, significantly correlated to LDI and that LDI is not a strong gradient

to explain patterns in JAAB data. Axes 2 and 3, respectively, explained 47 and 19% of the JAAB data. Kendall's Tau correlations of the polar ordination scores with abiotic variables show significant correlations of Axis 2 with salinity ($\tau = -0.494$, $P < 0.05$), water temperature ($\tau = -0.539$, $P < 0.05$), and depth ($\tau = -0.764$, $P < 0.01$), and that percent mangrove cover ($\tau = 0.477$, $P < 0.05$). Axis 3 was significantly correlated with pH ($\tau = -0.644$, $P < 0.01$). This indicates that other abiotic variables, including percent mangrove cover, are better indicators of juvenile and adult abundance and biomass than LDI.

Discussion

Though LDI was correlated with some fish community metrics, multivariate analyses suggest that LDI is a better predictor of abiotic factors and percent mangrove cover is a better predictor of fish communities. The difference is likely due to indirect relationships. Percent mangrove cover is likely influenced by abiotic factors (mangroves are more successful in optimal environments of specific abiotic conditions, i.e., brackish, calm water), as are the fish communities at the species level due to habitat suitability. Human activity (represented by LDI) directly affects abiotic factors, which then indirectly affects the fish communities, based on habitat suitability at the species level. Salinity was a main driver of juvenile and adult abundance in SMEs in this study.

Percent mangrove cover is significantly correlated to fish community data in O'ahu SMEs, but it is unlikely that the mangroves are causing these differences. More likely, mangroves are more successful in SMEs due to brackish salinity (Lugo & Snedaker, 1974; Blasco et al., 1996; Aziz & Khan, 2001; Biber 2006), lack of breaking waves, and calm shoreline conditions (Lugo & Snedaker, 1974; Doyle et al., 1995; Smith et al., 2009). Many of the fish inhabiting these areas, as the mangroves, also prefer this calm, brackish environment.

Juveniles of *M. cephalus* (Whitfield et al., 2012) and *K. xenura* (Benson & Fitzsimons, 2002) prefer brackish habitats. *Mugil cephalus* juveniles are generally found in habitats with much lower salinity than adults (Cardona, 2000, 2006; Whitfield et al., 2012). *Osteomugil engeli* have overlapping habitat distribution with

M. cephalus, with juveniles preferring more brackish conditions and adults preferring marine conditions. The current study further supports this finding with juveniles of both species correlating to higher percent mangrove cover and lower salinity and depth. There were more adults of *O. engeli* (9) than *M. cephalus* (2), supporting the suggestion by Nishimoto et al. (2007) that adult *O. engeli* are not marine obligates as adults.

The fish community at Waiāhole had an anomalously large number of *M. cephalus* caught compared to all other sites. This abundant catch of *M. cephalus* is also consistent with a previous study, part of a mark-recapture stock assessment in Kāne'ohe Bay, where the mean number of wild (not cultured) individuals recovered in Waiāhole was 77.2 as averaged from 10 months of sampling (Leber et al., 1996). Not including Waiāhole, more *O. engeli* (40 total) were caught in this study than *M. cephalus* (12 total), suggesting that the introduced species of mullet is thriving and is more abundant than the native species in these SMEs.

Kuhlia xenura are found in freshwater reaches of streams and in tide pools (Benson, 2002; Benson & Fitzsimons, 2002), representing both ends of the salinity gradient, and even individuals found in upper freshwater reaches of streams have otolithic evidence of salt water exposure. *Kuhlia* spp. were also found to tolerate a large temperature range (Benson & Fitzsimons, 2002). Salinity is known to potentially affect immune function in *M. cephalus* (Fazio et al., 2013) and to affect *K. xenura* and *M. cephalus* growth rates, with optimal growth and development in brackish water. As in the current study, McRae et al. (2011) found juvenile *K. xenura* prefer shallower microhabitats with lower salinity and lower temperatures (McRae et al., 2011). Benson (2002) found that *K. xenura* were most common in windward SMEs, and that the smallest individuals were in SMEs whereas the largest individuals were caught in the ocean. This may explain the dominance of juveniles and the general absence of adults of *K. xenura* and *M. cephalus* in the current study.

We found a wide size range of juvenile *K. xenura* (caught individuals from 4.5 to 13.7 cm; only one individual was of adult size) and *M. cephalus* (caught individuals from 1.3 to 33.4 cm; only two individuals of adult size). SMEs with mangroves in Hawai'i may support juvenile growth (many sizes of juveniles present) and the movement of juveniles into adult

habitat, two of the criteria for nursery habitat by Beck et al. (2001). Additional studies are necessary to determine whether or not SMEs with higher percent mangrove cover provide nursery value and function for these species as defined in the latest literature. Such studies in growth rates of these species, trophic studies, and mortality rates of juveniles and connectivity between these SMEs with mangroves and adult habitat would greatly enhance the ability to prioritize these habitats for management (Beck et al., 2001; Nagelkerken et al., 2015; Sheaves et al., 2015).

This study suggests that native species *K. xenura* and *M. cephalus* share habitat with non-native *R. mangle*. Also, the native stream goby, *Eleotris sandwicensis* (Vaillant & Sauvage 1875), and non-native *L. fulvus* were only caught in SMEs with mangroves. *R. mangle* is likely affected by the abiotic properties of these SMEs (optimal conditions for growth and photosynthesis), but is also providing physical structure connected to the sediment. Previous studies where mangroves are native (Thayer et al., 1987; Laegdsgaard & Johnson, 1995; Lugendo et al., 2007) and in Hawai'i, where they are not native (Nakahara, 2007), suggest there was greater fish abundance and diversity in mangroves than in adjacent mud flat habitat. It is likely that the fish communities benefit from this added physical structure the mangroves provide. Many methods used in this study limited the ability to sample within the mangrove props roots, as opposed to the adjacent sand/mud flat areas of SMEs. Additional studies using visual surveys or time-lapse photography (Goecke, 2015) would be valuable in characterizing prop root (mangrove) use by specific species, including answering questions such as whether species valued in fisheries (e.g., *K. xenura* and *M. cephalus*) are using the prop root structure for habitat or if predators use these regions for finding prey. Visual surveys or time-lapse photography would also help to identify species using SMEs that may not be easily captured or identified using the other methods described and therefore may be underestimated or missed altogether in sampling. Four of the ten species identified within the prop roots in SMEs using time-lapse photography were not caught in the current study using traditional methods (Goecke, 2015).

Rapid mangrove removal will cause a disturbance to this habitat that may initially decrease fish abundance and species richness. In Belize, Taylor et al. (2007) documented significant decreases in both species richness and density of individuals where mangroves had been cleared versus adjacent habitat where mangroves were not cleared. Schooling species were more affected than non-schooling species, with densities almost 200 times less at the site with mangrove removal than the undisturbed site (*ibid*). Infaunal abundance of invertebrates increased gradually after mangrove removal in Hawai'i from 2007 to 2011 (Siple & Donahue, 2013). MacKenzie & Kryss (2013) found that in tide pools where mangroves were eradicated with herbicides, native fish densities recovered to pre-disturbance levels after one year. The effects of extended disturbance on fish communities in SMEs are yet to be studied. Recovery time of fish communities and the potential value of mangrove structure as habitat should be considered before commencing any mangrove removal or any other long-term disturbance.

Conclusion

This study found a co-existence of mangroves and fish communities, where mangroves may provide some benefit by adding structure and refuge. Native species, such as *K. xenura* and *M. cephalus*, that share this habitat are likely not reliant on mangrove presence and have inhabited SMEs since before mangrove introduction. Mangroves were introduced nearly 100 years ago to O'ahu and are now widespread and have become a fixed, structural feature of essential juvenile fish habitat. Due to their shared distribution in certain SMEs, these native species and mangroves are now linked and one cannot be disturbed without impacting the other.

Currently in Hawai'i, there are numerous efforts to remove invasive mangroves from SMEs. Mangrove removal in regions where they are native has decreased biodiversity (Fondo & Martens, 1998), fish density (Taylor et al., 2007), and increased algal biomass (Granek & Ruttenberg, 2008), and sedimentation (Victor et al., 2004). Mangroves are obvious habitats for fish in Hawai'i. Fish communities and mangrove habitats were strongly correlated; therefore, mangrove removal efforts have the potential to disturb fish habitat. The current study provides evidence of SMEs with mangroves providing suitable juvenile habitat for native, schooling species, like *K. xenura* and *M. cephalus*, which are important in recreational

and subsistence fisheries. These species are more abundant in sites with mangroves and are likely to be adversely impacted by mangrove removal.

Compliance with ethical standards

Conflict of interest Co-author Susan Carstenn (Hawai'i Pacific University), Eric Gilman (Lead Fisheries Science Advisor, The Nature Conservancy), and Keith Korsmeyer served on Stacia Goecke's Master's thesis committee and provided advisement on this research.

Ethical approval Protocols followed Department of Land and Natural Resources (DLNR) regulations HAR section §13-75-12.4 or special provisions granted in a special activity permit provided by the State of Hawai'i DLNR's Division of Aquatic Resources. Effort was taken to respect the welfare of animals caught for this study. Handling was minimized as much as possible. Fish were maintained in a well-aerated, cool environment after being caught and then were re-released into the environment after being weighed and measured.

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