Introduced Mangroves Along the Coast of Moloka'i, Hawai'i may Represent Novel Habitats for Megafaunal Communities[1]

Bryan A. Nakahara,[2] Amanda W. J. Demopoulos,[3,8] Yoshimi M. Rii,[4]
Rosanna A. Alegado,[5,6] Kauaoa M. S. Fraiola,[7] and Craig R. Smith[5]

Abstract: Mangrove forests are prevalent along tropical/subtropical coastlines and provide valuable ecosystem services including coastline stabilization, storm impact reduction, and enhanced coastal productivity. However, mangroves were absent from the Hawaiian Islands and their introduction to Moloka'i in 1902 has provided an opportunity to examine their unique influence on coastal landscapes. Previous studies indicate an inability of native detritivores to utilize tannin-rich substrates, yielding poor cycling of mangrove-derived detritus in Hawaiian tidal zones. We hypothesize that in addition to altering detrital inputs, introduced mangroves facilitate the persistence of introduced species in the Hawaiian coastal zone by providing novel habitat for juvenile megafauna. To determine whether mangrove-dominated tidal zones harbor megafaunal assemblages distinct from open sandflats, we sampled in two mangrove (M1 and M2) and two adjacent sandflat (S1 and S2) sites along the southern coast of Moloka'i, where the most mature mangrove forests occur in Hawai'i. There were no statistical differences in total abundances between M1 and M2 or S1 and S2; therefore, results from individual deployments were pooled across the sites in order to conduct between-habitat (mangrove vs. sandflat) comparisons. Our mangrove study site had significantly higher abundances of megafauna, including several shrimp and crab species, compared to the sandflat site. The community composition within the mangrove site differed from the sandflat site, including higher abundances of non-native mangrove crabs (*Scylla serrata*), as well as native fish *Bathygobius cocosensis* and crustaceans (*Thalamita crenata*, *Palaemon pacificus*, *P. debilis*) than in the sandflat site, indicating that the mangrove site may provide niches for both invasive and native species. In addition, mean body length for several similar species was smaller in the mangrove site than in the sandflat site, suggesting that these mangroves may be providing a habitat for juvenile species. While our study was spatially limited to two mangrove and two adjacent sandflat sites, our results suggest that introduced mangroves in Moloka'i may support small-bodied, native, and non-native megafauna, influencing coastal Hawaiian trophic dynamics. Our case study provides a baseline for megafaunal fish and invertebrate communities

[1]Manuscript accepted 8 January 2021.
[2]Hawaiian Electric Corporation, Honolulu, HI, USA.
[3]Wetland and Aquatic Research Center, U.S. Geological Survey, Gainesville, FL, USA.
[4]Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kāne'ohe, HI, USA.
[5]Department of Oceanography, University of Hawai'i at Mānoa, Honolulu, HI, USA.
[6]Sea Grant College Program, University of Hawai'i at Mānoa, Honolulu, HI, USA.
[7]Marine National Monuments in the Pacific, U.S. Fish and Wildlife Service, Honolulu, HI, USA.
[8]Corresponding author (e-mail: ademopoulos@usgs.gov).

present prior to non-native mangrove removal as well as for monitoring potential community changes following expansion of mangrove habitats due to climate change.

Keywords: mangroves, novel ecosystem, megafauna, non-native, juvenile habitat

MANGROVE FORESTS ARE KEY COMPONENTS of low-latitude coastal ecosystems, occupying greater than 60% of tropical and subtropical coastlines, and are among the most productive marine habitats (Wester 1981, Duke 1992). Native mangrove forests provide vital habitat for a wide variety of species (Odum and Heald 1972, Odum et al. 1982, Thayer et al. 1987, Faunce and Serafy 2006) and their effects on microclimate, water level fluctuations, nutrient runoff, and wave energy can influence invertebrate community composition and distribution (Duke 1992). Many estuarine species make transient use of mangrove canopies and aerial roots for foraging, roosting, and breeding, amongst other activities. Previous studies indicate the importance of mangroves as nursery habitats for juveniles of commercially valuable fish species and crustaceans (Staples and Vance 1985, Robertson and Duke 1987, Parrish 1989, Laegdsgaard and Johnson 1995, Vance et al. 1996, Mohan et al. 1997, Primavera 1997, Ronnback et al. 1999, Nagelkerken et al. 2000*a*,*b*, 2002, Nagelkerken and van der Velde 2002). It has been postulated that juvenile fish and crustaceans enter mangroves to avoid predators, or become trapped in mangroves as larvae, and experience enhanced food availability (Odum and Heald 1972, Orth et al. 1984, Parrish 1989, Primavera 1997, Nagelkerken et al. 2000*b*, Laegdsgaard and Johnson 2001, Verweij et al. 2006). Accumulation and retention of mangrove leaf litter may support a productive detrital food web for species adapted to utilize these substrates (Odum and Heald 1975, Robertson et al. 1992, Robertson and Blaber 1992). Thus, mangroves may contribute to megafaunal (fish and invertebrates >1 cm, Grassle et al. 1975, de Montaudouin et al. 2018) adult recruitment by increasing juvenile (1) density, (2) growth rates, (3) survival, and/or (4) movement to adult habitats (Beck et al. 2001).

Impact of Introduced Mangrove in the Hawaiian Islands

Because of geographic isolation, the intertidal zone of the Hawaiian Islands evolved with few intertidal vascular plants (Wester 1981). Mangroves were introduced on Moloka'i Island in 1902 to help stabilize the coastline and retain soil eroded from changes in land use, agricultural development, and pasturelands (Munro 1904, MacCaughey 1917). The dominant species, *Rhizophora mangle*, is now present on six of the main Hawaiian Islands, with two other species, *Bruguiera* spp. and *Conocarpus erectus*, also occurring (Allen 1998). While the beneficial contributions of native mangroves to coastal ecosystem services are well documented, few studies have examined the impact (positive or negative) of mangrove introduction in non-native habitats such as in Hawai'i.

Mangrove invasion in Hawai'i dramatically altered a variety of ecologically important coastline characteristics (Allen 1998), thus providing a "novel ecosystem" in Hawai'i (e.g., Hobbs et al. 2006, Ewel et al. 2013, Lewis et al. 2019). Novel ecosystems are the result of intentional or accidental human action that also result in new species combinations that may lead to changes in ecosystem functioning (Hobbs et al. 2006). Mangroves in Hawai'i substantially altered the structural complexity of the benthic habitat, and, as a result, facilitated the persistence of non-native benthic invertebrates (Demopoulos 2004, Demopoulos et al. 2007, Demopoulos and Smith 2010). The increase in solid substrata, combined with tannin-rich detritus, low water flow, and high turbidity, can exclude native Hawaiian fauna adapted to open coast conditions (Demopoulos et al. 2007, Demopoulos and Smith 2010, Sweetman et al. 2010). Mangroves may also limit recovery of endangered waterbird populations by

out-competing flora used by the birds for foraging and nesting habitats, and by providing shelter for introduced waterbird predators (U.S. Fish and Wildlife Service 1985, Rauzon and Drigot 2002). Thus, mangroves may provide a foothold for invasive species, threatening marine and estuarine benthic species endemic to Hawaiʻi (Walsh 1967).

In addition, mangroves have distinct morphological adaptations (e.g., aerial prop roots and cable roots) that promote stability of soft/muddy sediments (Tomlinson 1986), and enhance the accumulation of fine, organic-rich sediments by reducing water flow (Duke 1992, Demopoulos and Smith 2010), leading to some ecological benefits in Hawaiʻi. Within the oldest stands on Molokaʻi, mangroves reduce suspended-sediment loads in coastal waters, decreasing turbidity, potentially serving as sinks for nutrients and pollutants from terrestrial sources (Walsh 1967), and protecting adjacent coral reefs from sedimentation (D'Iorio 2003). Mangroves serve as significant carbon sinks and may have sediment accretion rates that keep pace with current rates of sea level rise, potentially providing important protection to coastal environments for some effects of climate change (Soper et al. 2019).

Benthic demersal megafaunal communities in Hawaiian mangrove habitats remain under-sampled (Walsh 1967, MacKenzie and Kryss 2013, Goecke and Carstenn 2017). Two recent studies focusing on mangrove-associated fishes indicate that mangroves may provide habitat for juvenile fishes, including native and non-native species (MacKenzie and Kryss 2013, Goecke and Carstenn 2017). However, in ecologically important tidepool systems on Hawaiʻi Island, there was no difference in the abundance of non-native species in tidepools surrounded by mangroves versus native vegetation. Additionally, there was a prevalence of native fishes in tidepools surrounded by mangroves (MacKenzie and Kryss 2013), suggesting that exotic mangroves may not be restricting certain native fish assemblages in Hawaiʻi. Mangroves may support juveniles of native fishes important for subsistence fishing (e.g., *Kuhlia xenura*, *Mugil cephalus*, and *Mulloidichthys flavolineatus*) in estuaries at stream mouths on Oʻahu (Goecke and Carstenn 2017). However, these previous assessments of mangrove-associated megafaunal communities were limited to fish and were conducted within small mangrove environments surrounding tidepools (MacKenzie and Kryss 2013), or in adjacent stream environments (Goecke and Carstenn 2017). Thus, megafaunal (fish and invertebrate) communities associated with the oldest and most extensive mangrove forests that occur in Hawaiʻi remain poorly characterized.

Mangrove introduction in Hawaiʻi provides an opportunity to understand their role in creating a novel ecosystem. Here, we compared the abundance, composition, and species richness of megafauna in two mangrove sites and two nonmangrove (sandflat) sites on Molokaʻi, Hawaiʻi, to test the following hypotheses: (1) Hawaiian mangroves harbor higher abundances of megafauna compared to nearby sandflats at similar elevation relative to zero tide, (2) mangrove habitats harbor a greater abundance of fish and invertebrate megafaunal species alien to Hawaiʻi compared to nearby sandflats, and (3) mangroves contain higher proportions of smaller fish and crabs, including commercially important species, than nearby sandflat habitats.

MATERIALS AND METHODS

Study Site

This study was conducted on the southern coast of Molokaʻi, which has the oldest, most extensive mangrove stands in the Hawaiian archipelago (Wester 1981). Megafaunal species were sampled in two different habitat types: extensive, mature *R. mangle* mangrove stands located near Kapuaiwa Grove, Molokaʻi (21° 05′ 52″ N, 157° 03′ 10″ W), and sandflats of similar elevation relative to zero tide level located ≥100 m to the east of the mangrove stands along the south shore of Molokaʻi (Figure 1*A*,*B*). Two randomly located replicate plots were sampled within each habitat type: S̲andflat 1, S̲andflat 2, M̲angrove 1, and M̲angrove 2. The replicate plots were selected from with one contiguous mangrove stand and the sandflat adjacent to its eastern edge.
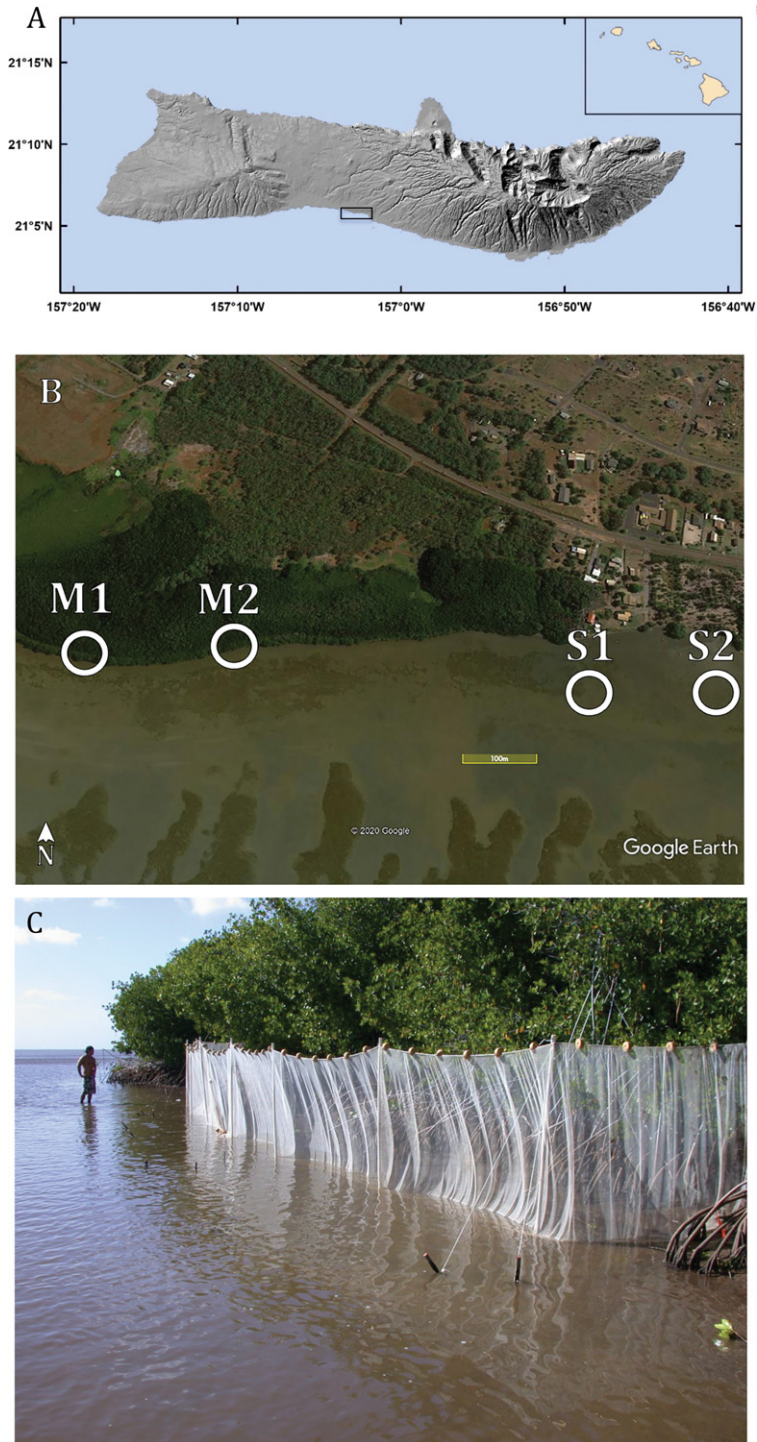
FIGURE 1. Study site and sample collection set up. (A) Study area (black rectangle) on Molokaʻi Island, Hawaiian Archipelago, modified from USGS 10-m Digital Elevation Model (DEM): Hawaii: Molokai: Hillshade. (B) Approximate locations for the habitat sample sites: sandflat (S1, S2) and mangrove (M1 and M2), modified from Google Earth. (C) The drop net in lowered position in the mangrove habitat during ebb tide.

Sample Collection

Megafaunal community composition in each habitat type (sandflat and mangrove) was sampled 14 times with a drop net and baited crab traps (7 drops each within mangrove sites M1, M2, and within sandflat sites S1, and S2, including both night and day deployments) between January 2003 and July 2006 (Supplemental Table 1). The net was deployed a total of 22 times during daylight hours, with 11 replicate deployments in each habitat type (Supplemental Table 1). Three night deployments each were conducted in darkness (between astronomical twilights). Sample collections were conducted at peak spring tides to allow for the maximum utilization of the mangrove habitat by marine species. At each sampling, the drop net was deployed (dropped) at peak high tide and recovered at lowest low tide. If the low tide following deployment did not drain the site, or if there was not enough light to recover and collect specimens, recovery occurred during the next low tide, which resulted in differences in deployment duration. The total number of organisms caught was compared across samples under the assumption that no organisms would be able to enter or leave the area once the net was dropped.

Plots measuring 19 m × 19 m were sampled in each habitat type using a drop net (Vance et al. 1990). The net measured 85 m long by 2 m high (5 mm square mesh with float line and bottom lead line) (Figure 1C). To prepare the sites for net deployment, mangrove branches and prop roots were manually removed down to the sediment surface in 1-m wide swaths surrounding each sampled plot. Due to the extent of the disturbance by the chainsaws, the cleared areas were allowed to settle for one day prior to the initial net deployment. At low tide, PVC pipes (213 cm tall) reinforced by rebar were inserted into the sediment (40 cm). The net was strung around the sample area, enclosing the entire plot, and bundled and attached to the top of the PVC pipes >1 m above the high tide level. For the mangrove sites, the interior edge of the mangrove forest (also the high tide mark) served as one of the boundaries for each 19 m × 19 m square plot. The float line was secured ∼7 cm below the tops of the pipes, and the net was loosely bundled and tied using a running slipknot. The ends of the slipknot were fastened to pegs pounded into the sediment 5 m away in sandflats, or to mangrove roots 4-m outside the sample area. At the peak high tide, the net was deployed by pulling the ends of the slipknot from several meters away, which lowered the net around the plot from the front border to the back, allowing the weight of the lead line to pull the bottom of the net down to the sediment. Once the net was dropped, the bottom of the net was manually secured to the seafloor using wire pegs and by pushing the lead weights on the bottom line into the sediment.

Three baited crab traps were deployed in each sample area; two with a 17-cm diameter opening, and one with a 27-cm opening to accommodate larger crustaceans. Each trap was baited with dead fish, wrapped in 5 mm diameter welded wire, weighted down and placed inside the enclosure near the seaward edge of the plot. At low tide, the mangrove roots were exposed, allowing the easy collection of animals that had accumulated on the seaward edge of the net. Animals found in the traps were collected, and scoop nets (20.32 cm diameter with 6.35 mm mesh) were used to capture the fish, shrimp, and crabs trapped inside the net. Collections of animals lasted between 20 and 35 min for each deployment. Trap and drop-net collections were combined for analysis. All animals were preserved in 10% formalin-seawater solution.

Species Identification and Size Measurements

All animals captured within the nets were identified to species and measured for length. Fish were measured for total length (TL; forward tip of the nose to most posterior part of tail or caudal peduncle). Crabs were measured for carapace width, and shrimp were measured from the forward end of the rostrum to the posterior tip of the telson. To test whether smaller megafaunal individuals are preferentially utilizing mangrove habitats,

size frequency distributions of dominant species were compiled and compared between habitats.

Statistical Analyses

All data presented are means ($\pm$ 1 standard error). Statistical analyses were conducted using the R package (version 4.0.1) "car" (Fox and Weisberg 2019) to compare total megafaunal community composition first between habitat types, then by the time of sampling per habitat type. Because of the high variability in species composition, unequal variance, and nonnormal distributions, nonparametric one-way ANOVA (Kruskal–Wallis) were run to determine whether there were significant differences between the two sites within each habitat (i.e., M1 vs. M2, S1 vs. S2), habitat types (mangrove vs. sandflat) in the numbers of individuals, or mean size of species collected. Corrections (5 total) for multiple testing were calculated using the Dunn–Sidak correction in Holm's procedure (Holm 1979) as follows: All (mangroves vs. sandflat), day (mangroves vs. sandflat), night (mangroves vs. sandflat), and day versus night (sandflat or mangroves).

Megafaunal community analyses were conducted with the PRIMER Statistical Software (Clarke and Gorley 2015). The following diversity metrics were calculated: number of species (S), normalized species richness per site ($d = S - 1/\ln N$, where $N =$ number of individuals), the Shannon–Weiner Information index (H'; log base 2), evenness (J') per site, and ES(n) rarefaction (Hurlbert 1971). Similarities and differences in megafaunal communities were examined using non-metric multidimensional scaling (NMDS) analysis based on Bray-Curtis similarity indices of square-root transformed assemblage data. Comparisons of megafaunal communities with respect to habitat type (sandflat vs. mangrove) and time of sampling (day vs. night) were examined using one-way Analysis of Similarity (ANOSIM). Similarity of percentage (SIMPER) analyses were conducted to identify the species responsible for discriminating between communities. An alpha level of 0.05 was used as the criterion for statistical significance.

RESULTS

Variability in Abundance and Diversity Indices Between Habitat Types

A total of 205 individuals from 13 species were collected in the sampled sandflats, while 666 individuals from 17 species were captured at the mangrove sites. There were no differences in total abundances between M1 and M2 (Kruskal–Wallis, $p = 0.798$ [All], $p = 0.394$ [Day only]), S1 and S2 ($p = 0.745$), so deployments were pooled across the sites in order to conduct between-habitat comparisons. From here on, pooled habitat sites (e.g., M1 and M2) are referred to as "site." Total megafaunal abundance within the sandflat site (28.3 ± 7.3 individuals per deployment, range: 14–111) was significantly lower than from within the mangrove site (66.1 ± 6.7 individuals per deployment, range: 20–121; $p = 0.002$, Kruskal–Wallis; Table 1). While there was a high degree of variation, typically a result of certain species being present only during some of the sampling events, the abundance of several species was significantly different between the two habitat sites (Table 1, day and nighttime samples pooled together). The fish, *Bathygobius cocosensis*, was more abundant in the mangrove site ($p = 0.020$), while *Kuhlia sandvicensis* had greater numbers in the sandflat site ($p = 0.033$). The crustaceans, *Thalamita crenata*, *Scylla serrata*, *Palaemon pacificus*, and *P. debilis* (Table 1, $p < 0.001$ to 0.016) were more abundant in the mangrove site, while *Portunus sanguinolentus* had higher abundances in the sandflat site ($p = 0.012$). While total abundances of all the fish species did not differ between sites ($p = 0.250$), abundances of shrimp ($p = 0.004$) and crabs ($p = 0.005$) were significantly higher within the mangrove site.

For daytime collections, mean megafaunal yields were higher within the mangrove site (60.6 ± 6.4 individuals per deployment, range: 20–95 individuals) compared to the sandflat site (18.6 ± 1.3 individuals per deployment, range: 14–27 individuals, $p = 0.001$, Kruskal–Wallis test). Daytime sampling results

TABLE 1

Mean Megafaunal Abundance (Number of Individuals Per Net Deployment)

	Sandflat				Mangrove				p-Values, Sandflat vs. Mangrove		
	All	Day	Night	p-Values, Day vs. Night	All	Day	Night	p-Values, Day vs. Night	All	Day	Night
Species	N = 14	N = 11	N = 3		N = 14	N = 11	N = 3				
Fish											
Mugil cephalus	3.93 ± 1.94	2.82 ± 1.48	8.00 ± 8.00	1.000	0.43 ± 0.23	0.36 ± 0.28	0.67 ± 0.33	0.677	0.681	0.656	1.000
Neomyxus leuciscus	–	–	–	–	0.14 ± 0.14	–	0.67 ± 0.67	–	–	–	–
Kuhlia sandvicensis	1.93 ± 1.26	0.82 ± 0.26	6.00 ± 6.00	1.000	0.07 ± 0.07	–	0.33 ± 0.33	–	[b]0.033	–	1.000
Sphyraena barracuda	0.50 ± 0.17	0.55 ± 0.21	0.33 ± 0.33	1.000	0.38 ± 0.13	0.27 ± 0.14	0.67 ± 0.33	1.000	1.000	1.000	1.000
Saurida nebulosa	2.43 ± 0.55	2.82 ± 0.64	1.00 ± 0.58	0.534	0.86 ± 0.23	0.82 ± 0.26	1.00 ± 0.58	1.000	0.148	0.117	1.000
Bathygobius cocosensis	1.43 ± 0.44	1.45 ± 0.47	1.33 ± 1.33	0.973	7.57 ± 1.85	8.91 ± 2.17	2.67 ± 1.45	0.356	[b]0.020	[b]0.021	0.973
Caranx sexfasciatus	0.07 ± 0.07	0.09 ± 0.09	–	–	0.29 ± 0.22	0.36 ± 0.28	–	–	1.000	1.000	–
Ctenochaetus sp.	–	–	–	–	0.14 ± 0.14	0.18 ± 0.18	–	–	–	–	–
Conger cinereus	–	–	–	–	0.07 ± 0.07	0.09 ± 0.09	–	–	–	–	–
Caranx ignobilis	0.07 ± 0.07	0.09 ± 0.09	–	–	–	–	–	–	–	–	–
Acanthurus triostegus	0.07 ± 0.07	0.09 ± 0.09	–	–	–	–	–	–	–	–	–
Arothron hispidus	0.07 ± 0.07	0.09 ± 0.09	–	–	0.07 ± 0.07	0.09 ± 0.09	–	–	1.000	1.000	–
Bothus mancus	–	–	–	–	0.07 ± 0.07	0.09 ± 0.09	–	–	–	–	–
[a]*Poecilia* sp.	0.21 ± 0.15	–	1.00 ± 0.58	–	4.93 ± 3.42	2.27 ± 2.08	14.7 ± 14.7	1.000	1.000	–	1.000
Total Fish	**10.7 ± 3.21**	**8.82 ± 1.67**	**17.7 ± 13.2**	**1.000**	**15.0 ± 3.03**	**13.5 ± 2.14**	**20.7 ± 13.2**	**1.000**	**0.250**	**0.250**	**1.000**
Crabs											
Thalamita crenata	2.21 ± 0.62	2.09 ± 0.5	2.67 ± 2.67	0.689	16.8 ± 2.52	18.6 ± 2.90	10.3 ± 3.53	0.364	[b]0.000	[b]0.000	0.364
Portunus sanguinolentus	5.71 ± 0.87	6.55 ± 0.91	2.67 ± 1.33	0.716	1.93 ± 0.64	2.18 ± 0.77	1.00 ± 1.00	0.716	[b]0.012	[b]0.013	0.716
[a]*Scylla serrata*	0.21 ± 0.21	–	1.00 ± 1.00	–	0.86 ± 0.21	1.00 ± 0.23	0.33 ± 0.33	0.364	[b]0.016	–	0.796
Total Crabs	**8.14 ± 0.73**	**8.64 ± 0.68**	**6.33 ± 5.04**	**0.469**	**19.6 ± 2.93**	**21.7 ± 3.28**	**11.7 ± 4.81**	**0.303**	**[b]0.005**	**[b]0.003**	**0.469**
Shrimp											
Atyoida bisulcata	–	–	–	–	0.07 ± 0.07	–	0.33 ± 0.33	–	–	–	–
Palaemon pacificus	1.50 ± 0.67	0.36 ± 0.24	5.67 ± 1.20	[b]0.008	5.36 ± 0.85	5.36 ± 1.01	5.33 ± 1.76	1.000	[b]0.007	[b]0.002	1.000
Palaemon debilis	7.93 ± 4.78	0.82 ± 0.50	34.0 ± 16.0	[b]0.037	24.6 ± 5.11	18.3 ± 2.76	48.0 ± 17.5	0.103	[b]0.004	[b]0.000	0.827
Penaeus marginatus	–	–	–	–	0.79 ± 0.19	0.82 ± 0.23	0.67 ± 0.33	0.798	–	–	–
[a]*Gonodactylaceus falcatus*	–	–	–	–	0.71 ± 0.24	0.91 ± 0.29	–	–	–	–	–
Total Shrimp	**9.43 ± 5.34**	**1.18 ± 0.74**	**39.7 ± 16.5**	**[b]0.017**	**31.6 ± 5.42**	**25.4 ± 3.45**	**54.3 ± 18.6**	**0.147**	**[b]0.004**	**[b]0.000**	**0.827**
Total Individuals	**28.3 ± 7.29**	**18.6 ± 1.25**	**63.7 ± 28.0**	**0.729**	**66.1 ± 6.70**	**60.6 ± 6.35**	**86.7 ± 18.9**	**0.729**	**0.002**	**0.001**	**0.729**
Range	14 to 111	14 to 27	14 to 111		20 to 121	20 to 95	56 to 121				

Recorded number of "All" ("Day" and "Night" pooled), "Day," and "Night" animals collected from sandflat and mangroves, and p-values of Kruskal–Wallis tests comparing mean abundances of species within and between sandflat and mangrove sites. N = total number of deployments within each site. Species selected for statistical tests consisted of samples sizes large enough to produce more robust results. Information in bold represents summary statistics for each major category: Total Fish, Total Crabs, Total Shrimp, and Total Individuals. [a]Species non-native to Hawaiʻi. [b]p-values significant at an experiment-wise alpha level of 0.05 from Kruskal Wallis tests, calculated using the Sequential Bonferroni Corrections in Holm's procedure (Holm 1979).

mirrored the results from the "All" analyses (Table 1), where abundances of shrimp ($p < 0.001$) and crabs ($p = 0.003$) were significantly higher within mangrove site, and total abundances of all the fish species did not differ between sandflat and mangrove sites ($p = 0.250$). The crab, *T. crenata*, and shrimp species, *P. pacificus* and *P. debilis* were significantly more abundant in the mangrove site when compared to the sandflat site (Table 1, $p < 0.001$–0.002), whereas *P. sanguinolentus* were more abundant in the sandflat site ($p = 0.013$). Only one fish species, *B. cocosensis*, was more abundant ($8\times$) in the mangrove site ($p = 0.021$), while *K. sandvicensis* had greater numbers in the sandflat site and were absent from the mangrove site during daytime.

A total of three deployments were conducted during night hours for each of the two habitat sites. These three deployments produced 260 animals in the mangrove site and 191 in the sandflat site and captured a few species not collected in a particular site during daytime. For our mangrove site, these included two fish species (*Neomyxus leuciscus* and *K. sandvicensis*) and one shrimp species (*Atyoida bisulcata*), while one additional fish species (*Poecilia* sp.) and one crab species (*S. serrata*) were found in the sandflat site (Table 1). Megafaunal yields for the night samples were 86.7 ± 18.9 (range: 56–121) per deployment within the mangrove site, and 63.7 ± 28.0 individuals per deployment in the sandflat site (Table 1; range: 14–111). No single species was found to be significantly different in abundance at night between mangrove and sandflat sites, likely due to the small number of nighttime deployments (Table 1).

Species richness in terms of number of species (S) of "All" ("day" and "night" pooled) and "day" samples was higher within the mangrove site (Supplemental Table 2, $p = 0.002$ [All], $p = 0.004$ [day]). However, while evenness (J') was slightly higher in the sandflat site, none of the other diversity indices (J', H', d) differed significantly between sites (Supplemental Table 2).

Individual-based rarefaction curves for separate net drops showed a broader range for the sandflat sites, with the mangrove curves falling within this range (Supplemental Figure 1A). Thus, there was no indication of differences in central tendencies between mangrove and sandflat rarefaction diversity, implying that there was no significant difference in rarefaction diversity between sites based on individual samples, similar to other diversity metrics' tests. However, sample-based rarefaction diversity was higher for the mangrove than the sandflat site (Supplemental Figure 1B). The sample-based rarefaction curves did not reach asymptotes, suggesting that species richness was undersampled for both sites.

Variability in Megafaunal Community Composition between Mangrove and Sandflat Sites

There were no community differences between the sites for sandflats (S1 and S2; ANOSIM, $R = -0.006$, $p = 0.454$) or mangroves (M1 and M2; ANOSIM, $R = 0.001$, $p = 0.449$), so replicate samples for each habitat type were combined for subsequent analyses. A total of 22 species were found, with 13 species common to both sites (Table 1). Six species were found only within the mangrove site, while two were exclusive to the sandflat site.

Non-metric multidimensional scaling revealed that sandflat and mangrove sites were significantly different (Figure 2; ANOSIM, $R = 0.655$, $p = 0.001$), indicating that each site contained a distinct community, with the exception of two "night" sandflat samples falling within the mangrove cluster. These night deployments contained higher abundances of one crab species (*T. crenata*) and another crab species that was not present in the sandflat daytime sampling (*S. serrata*).

SIMPER analysis indicated that assemblages within the mangrove site were more similar (~63%) than within the sandflat site (~45%). Overall, dissimilarity between the two sites was high (~67%), with higher abundances of *P. debilis*, *P. pacificus*, *T. crenata*, and *B. cocosensis* in the mangrove site, and higher abundances of *P. sanguinolentus*, *M. cephalus*, and *S. nebulosa* in the sandflat site.
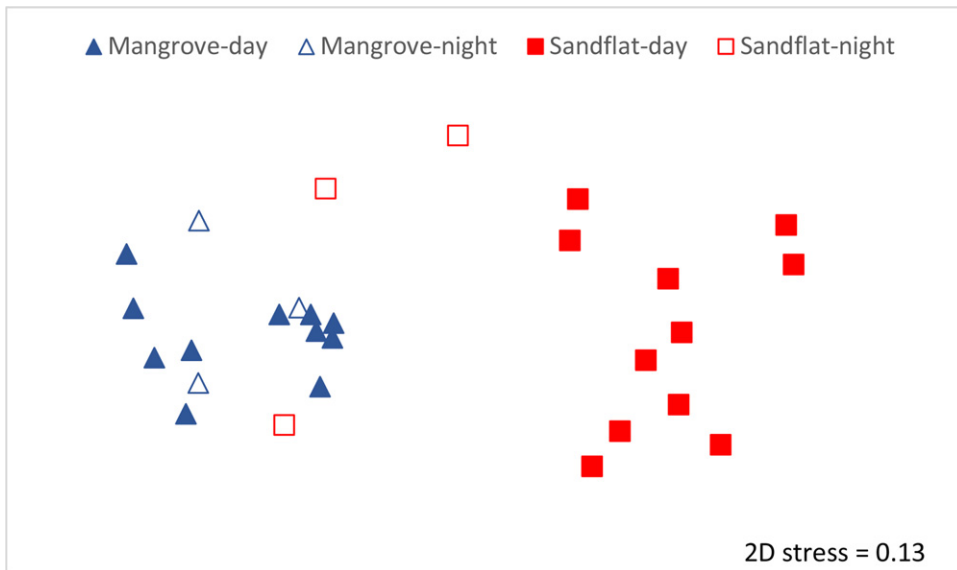
FIGURE 2. Non-metric Multi-Dimensional Scaling (NMDS) plot showing distinct sandflat and mangrove communities.

Distribution of Non-native Species in Sandflat and Mangrove Sites

The mangrove site contained all three non-native species collected in this study (*Poecilia* sp., *S. serrata*, and *Gonodactylaceus falcatus*), whereas the sandflat site contained two of these species. The abundance of introduced *S. serrata* crabs were significantly higher in mangrove site than in sandflat site ($p = 0.016$; Kruskal–Wallis). In contrast, abundances of non-native fish were not significantly different between mangrove and sandflat sites (Table 1).

Size Frequency Community Analyses

Size-frequency analysis was conducted on nine species that had more than one individual collected within each of the sites. Day versus night size frequency distributions within sites were not significantly different for most species (Supplemental Table 3). However, *M. cephalus* ($p < 0.001$) was significantly smaller at night in the sandflat site and *T. crenata* was significantly larger at night in the mangrove site ($p = 0.037$; Supplemental Table 3). However, size differences between day and night sampling events may be related to time of year or season, since all the night sampling occurred in January–March, whereas daytime samples were collected from May to July.

In contrast, when all samples collected within each habitat were pooled (All, day + night deployments), all but *P. pacificus*, *P. debilis*, and *S. barracuda* exhibited statistically significant ($p < 0.05$) differences in size frequency distributions between the sandflat and mangrove sites (Figure 3, Supplemental Table 3). Most of these differences were driven by daytime samples, since the organisms collected during night did not display statistically significant differences between the sites, except for *M. cephalus*.

Significantly smaller individuals of the fishes *S. nebulosa* and *B. cocosensis* were found within the mangrove site compared to the sandflat site ($p \leq 0.001$); only *M. cephalus* was represented by larger individuals in the mangrove site ($p < 0.001$; Figures 3 and 4, Supplemental Table 3). The crabs *T. crenata*
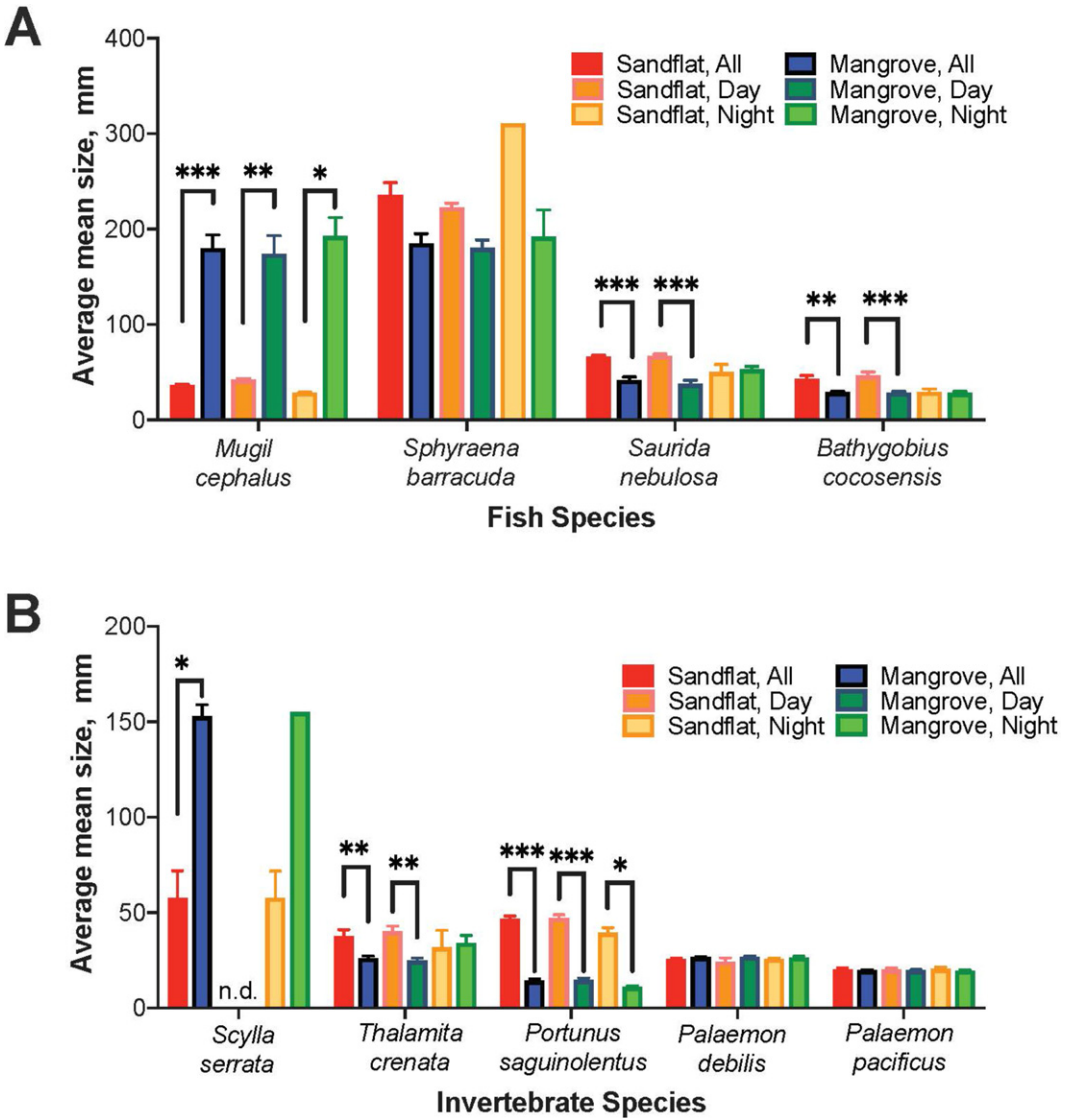
FIGURE 3. Mean size (±1 standard error) of species with more than one individual collected in each of habitats for "All," "Day," and "Night," samples. n.d. = not determined. *p*-values: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, exact significance between sandflat versus mangrove sites and Day versus Night samples, in Supplemental Table 3.

and *P. sanguinolentus* were both significantly smaller in the mangrove site (Figures 3 and 4, $p = 0.002$ for *T. crenata*, $p < 0.001$ for *P. sanguinolentus*). In contrast, *S. serrata* were larger in the mangrove site than in the sandflat site ($p = 0.028$).

DISCUSSION

Mangrove and Sandflat Sites Exhibited Distinct Community and Abundance Patterns

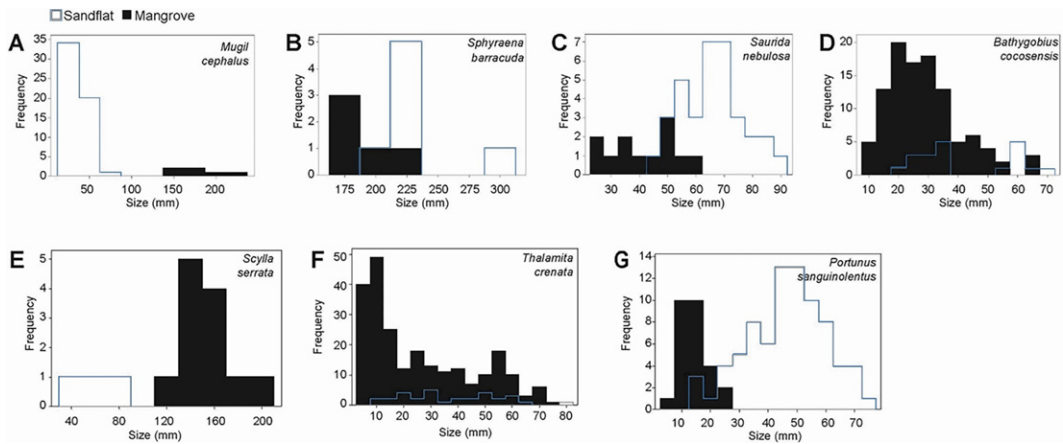Megafaunal densities were significantly higher in our mangrove site, consistent with

FIGURE 4. Size frequency distributions of selected fish (*A–D*) and crab (*E–G*) species for sandflats and mangrove sites from all deployments. Significance of distributions, $p < 0.001$.

our first hypothesis. This agrees with previous work on mangrove sediment macrofauna (Demopoulos and Smith 2010), where abundances were higher in mangroves (on Moloka'i and O'ahu) than in adjacent sandflats. In our study, multiple shrimp species were more abundant in the introduced mangrove study site, consistent with abundance patterns documented in native mangroves in other regions. For example, on Inhaca Island in Africa, 90% of penaeid shrimp, primarily *Penaeus indicus*, were captured within the mangroves, with higher abundances and wider size ranges of penaeid shrimp within the mangrove habitat than in sandflats (Ronnback et al. 2002). In Australia, Malaysia, and the Philippines, *P. indicus* and *P. merguiensis* were more abundant in mangroves than in adjacent seagrass meadows, algal beds, mudflats, or sandflats (Staples and Vance 1985, Robertson and Duke 1987, Chong et al. 1990, Vance et al. 1990, 1996, Primavera 1997).

While total abundances of fishes in our study did not differ between the two habitat sites (Table 1), megafaunal community structure differed between our mangrove and sandflat sites, driven by native species of fish and several crustaceans. Specific community-level differences based on SIMPER analysis included higher abundances of the fish *Bathygobius cocosensis* and the crustaceans (*P. debilis*

and *P. pacificus*, *T. crenata*) in the mangrove site, while *P. sanguinolentus*, *M. cephalus*, and *S. nebulosa* were more prevalent in the sandflat site. Given the smaller sizes of *B. cocosensis* and *T. crenata*, as well as the notably smaller individuals of *S. nebulosa* and *P. sanguinolentus* collected within mangrove site, certain native species may be using the Moloka'i mangroves as a juvenile refuge from predation. Other studies have shown that smaller individuals of *B. cocosensis* can be more abundant in the high intertidal (e.g., mangrove roots in this case) because they are excluded from the low intertidal due to predation and competition (e.g., Malard et al. 2016). The differences in size distributions of *B. cocosensis* in our study might be associated with their known tolerance for large variability in temperature and salinity (e.g., Pauly 1979, Hernández et al. 2002, White et al. 2015), which can fluctuate within mangrove forests.

Species richness (*S*) per sampling unit was higher within introduced mangrove study sites in Hawai'i than in sandflats for both macrofauna (Demopoulos and Smith 2010) and megafauna (this study). However, unlike the patterns found for sediment macrofauna, megafaunal diversity (*d*, Shannon–Weiner *H'*), evenness (*J'*), and rarefaction diversity did not differ significantly between our mangrove and sandflat sites. The high

variability in community composition among the net collections limited the power to detect diversity differences between the two environments. This variability may reflect the presence of transient species that are not well established in a particular habitat and move between them. There were very few species (4–9 species) and congeners (5) in common between our study and previous mangrove fish studies (MacKenzie and Kryss 2013, Goecke and Carstenn 2017), and other coastal wetlands in Hawai'i (MacKenzie and Bruland 2012), which may indicate site-specific or inter-island differences in megafaunal composition and environmental conditions (MacKenzie and Bruland 2012). However, the rarefaction curves (Supplemental Figure 1B) indicate that megafaunal species richness is underestimated within both our mangrove and sandflat study sites. Some species of fishes typically observed in shallow sandy coastal environments in Hawai'i (Randall 2007, MacKenzie and Bruland 2012, Peyton et al. 2016) were absent from our sandflat collections, including bonefish (Albulidae), milkfish (*Chanos chanos*), threadfins (Polynemidae), and ladyfish (*Elops hawaiiensis*) which may be a result of the collection method (net type and size) and/or sampling time of year. Additional collections at our sites, and in similar mangrove environments in Hawai'i, would improve our ability to quantify mangrove alpha, beta, and gamma diversity.

Although there were no significant differences in day versus night comparisons, perhaps due to limited sampling and time of year, communities collected in the few night catches in our sandflat site closely resembled those found in the mangrove site (Fig. 2). Previous research conducted in native mangroves indicates distinct diel trends in the utilization of the mangrove habitat by fishes (Thayer et al. 1987, Rooker and Dennis 1991, Nagelkerken et al. 2000b, Cocheret de la Moriniere et al. 2003), where species present in mangroves during the day may be reduced in number or absent at night (Rooker and Dennis 1991). Additional day-night sampling across seasons, as well as the incorporation of acoustic telemetry and chemical tags (e.g., stable isotopes), would improve estimates of diel patterns of Hawaiian mangrove habitat utilization and megafaunal movement (e.g., Huijbers et al. 2015).

Potential Role of Mangroves as a Habitat for Non-native Species

While mangrove introductions could result in niches for non-native species (Demopoulos and Smith 2010), only three of the 22 species found within the mangrove and sandflat study sites were non-native: *S. serrata*, *G. falcatus*, and *Poecilia* sp. We found that abundances of non-native fish and invertebrate megafaunal species in our mangrove site were not significantly higher than nearby sandflat site, inconsistent with our second hypothesis. Previous work on mangrove sediment infauna found that mangroves housed greater densities and proportions of cryptogenic and non-native species than sandflats (Demopoulos and Smith 2010; O'ahu, $p < 0.001$; Moloka'i, $p < 0.010$). On Hawai'i Island, fish assemblages in tidepools surrounded by vegetation, whether native or alien plants, also had higher densities of non-native species than nonvegetated tidepools, suggesting that the plants may either improve the habitat for invasive fish or degrade the habitat for native species (MacKenzie and Kryss 2013). However, the proportion of native versus introduced megafaunal species in coastal systems may differ among the Hawaiian islands; Moloka'i coastal environments may have a baseline community with fewer non-native species than other, more developed islands such as O'ahu, which have higher numbers of non-native species (Carlton and Eldredge 2009; Carlton et al. 2015).

The introduced species in our study included *Scylla serrata*, the mangrove crab, which was brought from Samoa to start a fishery in 1926 and 1935 (Brock 1960). The mangrove crab had become a dominant estuarine and prized fishery species by 1992 (Eldredge 1994). They also include the stomatopod, *G. falcatus*, which was first observed in 1954 in dead coral heads in Kāne'ohe Bay (Eldredge and Smith 2001). The third introduced species was the Molly fish, *Poecilia* sp. (hybrid complex *mexicana/*

reticulata), found in both our mangrove and sandflat study sites. Mollies were introduced to the streams of Hawai'i in the early to mid-1900s (Brock 1960, Englund 1999), and eventually made their way downstream to mangrove estuaries. When day and night deployments are considered, the mangrove crab and Molly species appear to utilize only our mangrove site during the day, with some movement onto the sandflat site at night. This diurnal movement could be associated with nocturnal foraging within sandflats by mangrove crabs (Bonine et al. 2008, Demopoulos et al. 2008). *Poecilia* sp. may use mangrove root structure as a refuge from visual predators (MacKenzie and Kryss 2013), which may explain their abundance in vegetated versus unvegetated environments. Mangrove roots might also provide a substrate for the periphyton and detritus on which *Poecilia* sp. feed (cf., Odum and Heald 1975, Chapman et al. 1991, Browder et al. 1994), and/or the reduced temperatures and salinity might serve as a refuge from environmental stress. While this study did not have a seasonal component, seasonal variation in habitat use has been noted in native mangrove forests, including significant differences in abundance and community structure of mangrove megafauna between wet and dry seasons (Robertson and Duke 1987, Thayer et al. 1987, Primavera 1997). Resolving potential seasonal patterns might help explain the high variation observed in this study.

Potential of Moloka'i Mangroves as Juvenile Habitats

While it was not feasible to consistently resolve juveniles (i.e., reproductively immature individuals) in the many different species examined, smaller-sized individuals for several species were more prevalent in mangrove than sandflat study sites, and we can infer that some of these individuals were juveniles. The functional role of mangroves as important juvenile habitat in other parts of the world has been well established, where they support higher abundances of smaller size classes than adjacent sandflats (e.g., Laegdsgaard and Johnson 2001, Cocheret de la Moriniere et al. 2003, Sheridan and Hays 2003, Dorenbosch et al. 2004, 2006, MacKenzie and Cormier 2012). Some of these studies also demonstrated that mangroves can provide habitat for pre-reproductive juveniles, supporting the nursery hypothesis (Thayer et al. 1987, Nagelkerken and van der Velde 2002). In our study, several species demonstrated this pattern in the pooled data from the two mangrove sites, which was consistent with our third hypothesis that mangroves contain higher proportions of smaller-sized fish and crabs (e.g., juveniles) than nearby sandflat sites.

All of the fish species in our study, except for *M. cephalus*, were considerably smaller within the mangrove site and could be using this habitat as a nursery. Smaller sizes of crabs were found in the mangrove habitats. For the blood-spotted crab, *P. sanguinolentus*, the smaller sizes were restricted to the mangrove site, and only the larger individuals were found in the sandflat site (Figure 4). The blue pincher, *T. crenata*, also had a wide size range in the mangrove site, with abundances dominated by smaller individuals (Figure 4). This pattern suggests that both *T. crenata* and *P. sanguinolentus* could be using the mangrove habitat as a nursery ground for juveniles. In contrast, the larger size of *S. serrata* in the mangrove site is consistent with previous studies showing *S. serrata* using mangroves as adult habitat (Hill et al. 1982, Bonine et al. 2008).

Our interpretation that mangroves serve as potential juvenile habitat for several species of fish and invertebrates is consistent with previous work on fish communities in streams adjacent to mangroves on O'ahu (Goecke and Carstenn 2017). However, our study was the first to collect quantitative samples directly from around the mangrove prop root system, isolating a large area, and enhancing our ability to examine mangrove-associated diversity within a spatially extensive, mature mangrove system.

Implications for Management in Hawai'i

Based on this study from one mangrove site, Moloka'i mangroves may have some positive

effects on the coastal environment by supporting native fish and invertebrate species, as well as potentially providing nursery areas for small fishes and crustaceans of commercial and recreational importance. Our mangrove study site harbors a higher abundance of native shrimp and crabs than the sandflat site and provides a habitat for species that support local fisheries, for example, *S. serrata*.

For the last two decades, coastal restoration projects in Hawai'i have focused on eradicating invasive plants like mangroves to restore the native fauna and flora of wetland and coastal habitats (e.g., Möhlenkamp et al. 2019). Our study serves as a case study of the fish and invertebrate communities associated with non-native mangroves (one study area) prior to mangrove removal. While one other study indicates that mangrove removal leads to an initial reduction in fish densities (Goecke and Carstenn 2017), densities of native fishes may return to preremoval levels over time (MacKenzie and Kryss 2013). Changes in benthic community function induced by mangroves can persist for years to decades following mangrove removal due to altered habitat structure and carbon remineralization dynamics (Demopoulos and Smith 2010, Sweetman et al. 2010, Siple and Donahue 2013, Soper et al. 2019). Climate warming is resulting in the latitudinal expansion of mangrove habitat in other parts of the globe (see Osland et al. 2017), facilitating mangrove invasion of wetlands where conditions are amendable to colonization. This expansion can have far-reaching impacts on coastal environments, including altering coastal megafaunal communities, as in our study.

Ongoing management of Hawaiian mangrove habitats involves trade-offs between high mangrove removal costs and long ecosystem recovery times (decades or longer; Ewel et al. 2013), versus the need for conservation and protection of native species (Lewis 2017, Lewis et al. 2019). In areas with extensive, mature mangrove systems, such as south Moloka'i in this study, it may be more cost effective to prevent further spread of mangroves, rather than removing large swaths of mangroves from the coastal environment.

In contrast, at culturally important sites, such as Hawaiian fishponds, mangrove removal and follow-up control may be required to ensure the full functionality of the historic fishpond system and associated watershed dynamics (e.g., Siple and Donahue 2013). Given our study was limited to one mangrove/sandflat area, comparisons of mangrove systems at multiple sites across the state, including along open coasts and within fishponds, are necessary to facilitate a robust understanding of the function of mangroves as novel ecosystems in Hawai'i, 100 years since their introduction.

CONCLUSIONS

While our study was limited to two mangrove and two adjacent sandflat sites, our results suggest that Moloka'i mangroves may serve as a novel ecosystem in Hawai'i for a variety of megafauna (both native and non-native species) and harbor higher abundances of several megafaunal species, including species supporting local fisheries, compared to nonmangrove habitats. For some of these species, higher abundances were represented by smaller individuals, which suggests that mangroves on Moloka'i may provide nursery habitats. The harboring of both native and non-native species in our mangrove sites suggests that mangrove removal in Hawai'i may have both positive and negative impacts on native Hawaiian and commercial species. However, due to potential differences in island-specific species composition, as well as the sampling limitations noted here (2 mangrove sites and 2 sandflat sites), future studies characterizing megafaunal communities in mangrove and nonmangrove habitats on a site-specific basis would provide the essential baseline information required by managers.

DEDICATION

'Ike 'ia no ka loea i ke kuahu. An expert is recognized by the altar she builds. We are inspired by the scholarship of Dr. Isabella Kauakea Aiona Abbott whose depth of knowledge of Hawaiian coastlines was unparalleled;

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