RESEARCH ARTICLE

Drivers of zooplankton community composition in a novel ecosystem: Hawai'i mangroves as a case study

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Abstract

1. Management of established non-native plants is challenging because removal is expensive and can produce negative consequences, yet establishment can create novel ecosystems. Red mangrove propagules were introduced to Moloka'i, Hawai'i, in 1902 to mitigate the effects of soil erosion and have since spread along the coast and to adjacent islands creating novel habitat.

2. We compared zooplankton communities between novel mangrove and historical non-mangrove habitat both within fishponds and along open coastline to examine environmental factors, including mangrove presence, affecting zooplankton community composition.

3. Community composition patterns were driven by lunar cycle and site characteristics, including fishpond structure, mangrove and open-coast shoreline length, percent of mangrove shoreline length, total percent mangrove leaf carbon and upstream watershed disturbance.

4. Our findings indicate that during the tropical summer reproductive season, non-native mangroves support diversity, richness and community composition similar to non-mangrove areas, though some widespread taxa have lower abundance, and some rare taxa are more abundant in mangroves.

5. Additionally, fishpond zooplankton community structure is significantly different from open-coast areas, indicating fishponds, themselves, create novel habitat.

6. *Synthesis and application*. In the face of declining fisheries, threatened reef habitat and changing climatic conditions, non-native mangroves may provide, rather than impede, zooplankton habitat availability in novel locations.

KEYWORDS

disturbance, invasive, light trap, management, non-native, plankton tow, red mangrove, *Rhizophora mangle*

1 | INTRODUCTION

Globally, ecosystems are being transformed into configurations that differ in composition and function from historical systems (Hobbs et al., 2009). These changes can result from altered species distributions (extinction and invasion) and environmental modification through climatic and land use changes (Harris et al., 2006; Hobbs et al., 2009; Root & Schneider, 2006; Truitt et al., 2015).

Species invasions can threaten ecosystems (Wilcove et al., 1998), with the United States alone spending over $100 billion annually in economic damages and control (Pimentel et al., 2005). Despite growing recognition that non-native species may provide

ecosystem services in areas where climate and land use are rapidly changing, bias against non-native species exists (Davis et al., 2011; Gozlan, 2008; Schlaepfer et al., 2011; Shackleton et al., 2007). Perhaps because invasive species can damage new environments, their potentially beneficial role in supporting new or replacing previously lost ecosystem services in novel ecosystems is rarely studied (Charles & Dukes, 2007, but see Shackleton et al., 2007 ; Dickie et al., 2014 ; Vaz et al., 2017). Yet non-native species often provide positive effects on some component of native biodiversity or ecological functioning (Gozlan, 2008; Katsanevakis et al., 2014; Vaz et al., 2017). Additionally, unintended consequences may result from restoration that removes established non-native species, attempting to return ecosystems to a previous state (Hobbs et al., 2009; Zavaleta et al., 2001). For example, non-native eucalyptus trees in California support native butterflies where original host plants have disappeared; eucalyptus management strategies now consider this role (Graves & Shapiro, 2003). For many species, such as coastal mangroves, similar assessments remain to be conducted.

Mangroves are salt-tolerant (halophyte) plants adapted to life in harsh intertidal zone conditions in tropical and subtropical regions (Giri et al., 2011; Wester, 1981). Where mangroves occur naturally, they provide numerous well-documented ecological functions and services of considerable value to human society (Ewel et al., 1998; Odum et al., 1982) including flood protection, erosion control, nutrient uptake and transformation, carbon sequestration, water quality improvement, plant products and habitat for a diverse array of fish and invertebrates (Ewel et al., 1998; Mcleod et al., 2011). Worldwide, mangroves are declining due to agriculture, aquaculture, tourism, urban development and overexploitation (Field et al., 2007; Giri et al., 2011; Goldberg et al., 2020) with an estimated 35% loss between 1980 and 2000 (MA, 2005). Yet in a few locales, mangroves have been introduced because of the services they provide (Allen, 1998). For example, on south central Moloka'i, Hawai'i, United States, *Rhizophora mangle* (red mangrove) was introduced in 1902 to stabilize eroding coastal mudflats and protect adjacent coral reefs (Wester, 1981) from degradation resulting from historical cattle ranching, feral animal grazing and subsequent plantation agriculture (Field et al., 2007; Roberts, 2000). Mangroves have since spread along the intertidal zone of Moloka'i and adjacent islands creating novel habitat (Allen, 1998).

The spread of *R. mangle* into mudflat habitat has created a novel ecosystem with beneficial and detrimental ecosystem impacts (Allen, 1998). Although mangroves have not displaced native wetland plant communities directly and have a generally positive influence on sediment retention and water quality (Allen, 1998), they may threaten ancient Hawaiian fishponds, the local aquaculture (Clark & Rechtman, 2010; US EPA, R. 9, n.d.). Numerous alien species and a few native bird species (black-crowned night heron—*Nycticorax nycticorax hoactli* and great blue herons—*Ardea herodias*) use mangroves for nesting and foraging (Allen, 1998). Yet, four endemic waterbirds (Hawaiian duck—*Anas wyvilliana*, Hawaiian coot—*Fulica alai*, Hawaiian stilt—*Himantopus mexicanus knudseni*, Hawaiian moorhen—*Gallinula chloropus sandvicensis*) that use mudflats for foraging and nesting have suffered large declines due to anthropogenic stressors, and mangrove encroachment on mudflats may limit their recovery (Allen, 1998; Meyerson & Reaser, 2003).

Little research exists on the effects non-native mangroves have on marine community structure. Research outside of their native range provides an opportunity to better understand effects and functional roles of a non-native plant on tropical coastal ecosystems (Allen, 1998; Meyerson & Reaser, 2003). Specifically, do non-native mangroves provide larval/juvenile nursery habitat, as they do in their native range (Allen, 1998; Meyerson & Reaser, 2003; Wester, 1981), and might non-native mangrove removal alter zooplankton community structure, including larval coral reef fish abundance as in mangroves' native range (Granek & Frasier, 2007; Mumby et al., 2004; Nagelkerken et al., 2001)?

Hawai'ian non-native mangroves provide a unique case study to assess the habitat role and ecosystem services of non-native species that create novel habitats. Since zooplankton are a key component of marine ecosystems, near the base of marine food webs (Johnson & Allen, 2012; Turner & Tester, 1997), and since native mangroves provide important habitat for tropical zooplankton, we examined watershed and environmental drivers of zooplankton diversity, abundance and community composition in non-native mangrove versus native non-mangrove habitat both in fish ponds and along open coastline on Moloka'i, Hawai'i, to (a) determine whether zooplankton diversity, richness and community composition differ significantly between established mangrove and non-mangrove shoreline habitat, and (b) assess factors driving differences in zooplankton community assemblages.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted adjacent to Moloka'i in the Hawaiian Archipelago, North Pacific Ocean. The shore is characterized by open coastline and numerous Polynesian fishponds ranging in size from <1 to ~15 ha. The coast is primarily dominated by either *R. mangle* (non-native red mangrove), *Prosopis pallida* (non-native mesquite/kiawe tree), *Thespesia populnea* (milo tree, possibly introduced by Polynesians; Wagner et al., 1990), *Hibiscus tiliaceus* (hau tree, unknown native status) or sandy beach. With the exception of the eastern-most ponds, fishponds have been partially or completely filled with mangroves, ranging from mangroves lining the edges to fully overgrown.

Ten paired sites along the southeast coast of Moloka'i, Hawai'i, were selected based on accessibility (Figure 1; Table 1). Paired sites consisted of an area of mangrove habitat and an adjacent open-coast area (representing historical coastline conditions). Site types included seven paired sites within fishponds (partially lined with mangrove and partially open coastline; Figure 1b) and three paired sites outside of fishponds (Figure 1c). All accessible sites on Moloka'i with stretches of at least 100 m of mangrove shoreline

FIGURE 1 (a) The island of Moloka'i and its location in the Hawaiian Islands. Examples of (b) a paired site within a fishpond and (c) a paired open-coast site outside a fishpond. *M* open-coast mangrove, *O* open-coast non-mangrove, *PM* fishpond mangrove, *PO* fishpond non-mangrove
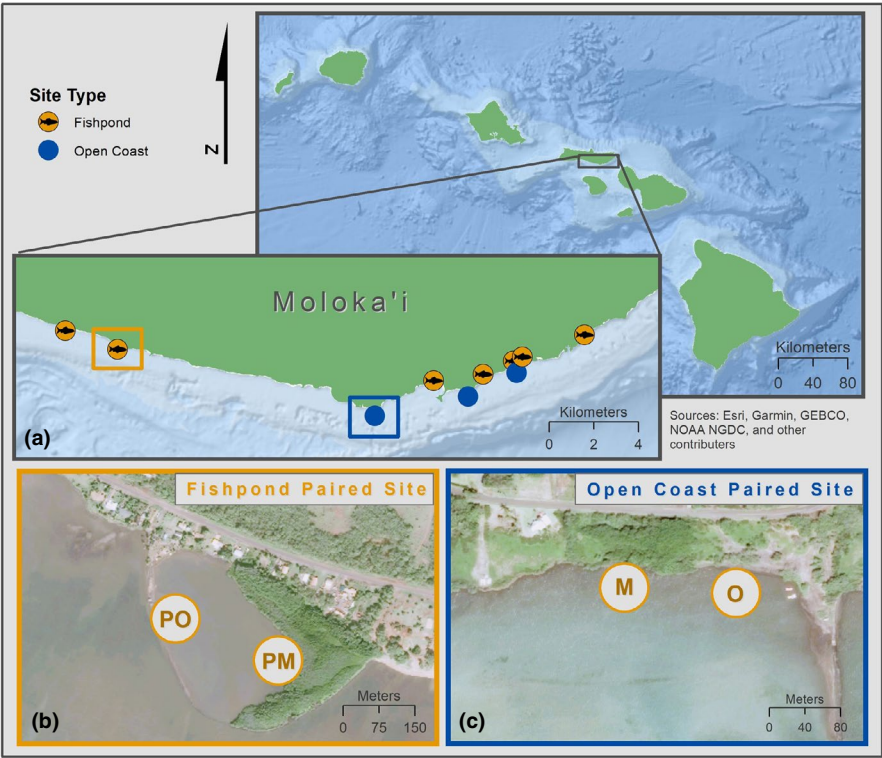
TABLE 1 Sample site names from west to east, habitat type, GPS coordinates and dates sampled

Site name	Habitat type (Fishpond/Open-coast)	GPS coordinates		Date(s) sampled
Kaloko'eli	Fishpond	21.07767	−157.000767	6/7/2015, 6/12/15, 6/13/15
Ali'i	Fishpond	21.07013	−156.979733	6/7/2015, 6/12/15, 6/13/15
Kamalo Wharf	*Open-coast*	21.04688	−156.876133	6/8/15
Keawanui	Fishpond	21.05745	−156.852417	6/8/15
Manawai	*Open-coast*	21.05462	−156.838582	6/10/15
Ualapue	Fishpond	21.05997	−156.832522	6/10/15
Kaope' ah'hina Pond	Fishpond	21.06535	−156.820333	6/6/15
Kaope' ah'hina Open	*Open-coast*	21.06425	−156.819017	6/6/15
Nia'u Pala	Fishpond	21.06708	−156.816665	6/11/15
Kupeke	Fishpond	21.07587	−156.79175	6/9/15

adjacent to at least 100 m of open-coast (Granek & Frasier, 2007), as measured in Google Earth, were included in the study, leading to an unbalanced design between open-coast and fishpond sites. The primary road of Moloka'i (Kamehameha V Hwy) along the southeast coast, ranging from ~10 to 600 m from shore, provided accessibility.

2.2 | Environmental variables

Watershed relief, percent of mature tree cover, mean annual precipitation, percent of impervious surface area, and percent of developed land were calculated using StreamStats (U.S. Geological Survey, 2012). Mature tree cover is defined as 'areas dominated by trees generally >5 m tall, >20% of total vegetation cover, more than 75% of the tree species maintain their leaves all year and canopy is never without green foliage' (Homer et al., 2007).

Leaves were collected at each mangrove site to evaluate biologically available nitrogen and carbon to assess sewage inputs, distinguishable from other nitrogen sources entering marine ecosystems by their elevated $\delta^{15}N$ signature (Costanzo et al., 2001). Upon collection, two green leaves from different trees were composited, oven-dried and ground to a fine powder. Nitrogen and carbon were analysed by an elemental analyser interfaced to a continuous flow isotope ratio mass spectrometer (EA-IRMS) for tissue %N/%C and $\delta^{15}N/\delta^{13}C$ isotopic signatures at the University of California

Davis Stable Isotope Facility following methods from Costanzo et al. (2001).

2.3 | Zooplankton sampling

Marine zooplankton, including both holoplankton (permanent members of the plankton) and meroplankton (fish and invertebrate larvae that settle out of the plankton at a future life-history stage), larger than 210 μm (sampling mesh diameter) were sampled during the reproductive season of the tropical summer. Mesh diameter was selected to collect a majority of ecologically relevant zooplankton in the community based on previous studies (e.g. Granek & Frasier, 2007). Community composition sampled in light traps and plankton tows differs due to the range of swimming abilities and photosensitivity across zooplankton species (e.g. Doherty, 1987; Granek & Frasier, 2007; Porter et al., 2008). Therefore, light traps, which attract photopositive but not photonegative species, and plankton tows, that capture only those zooplankton in the path of the tow without discrimination by phototaxis, were used simultaneously to assess a more complete array of the zooplankton community at each site.

Sampling was conducted for eight consecutive nights in June 2015 (Walsh, 1987) to capture peak spawning season during two lunar cycle phases following peak spawning, with sample period limited by resource availability. Therefore, this study does not capture variability across all seasons and lunar phases. Each night two paired sites were sampled simultaneously using both traps and tows. To determine the role of lunar phase, two sites were sampled repeatedly during different lunar cycle phases—for a total of three nights each (Table 1).

2.4 | Light traps

The light trap design, modelled after Granek and Frasier (2007), consisted of an inverted 3.8-L (1 gal) transparent blue-tinted plastic water jug, with side funnels and a removable cod end constructed of 220-μm mesh-lined PVC tubing (Appendix Figure A3). A white LED light stick (Trident Long Life LED Glow Stick Dive Light) suspended from the top inside each trap was the light source. Two funnel-shaped entry points on the bottle's sides led inward to an ~1 cm diameter hole providing access points for phototactic zooplankton. The small entry point limited both the size of individuals entering the trap and the ability of captured zooplankton to leave the traps. When light traps were lifted from the water, zooplankton were flushed into the mesh-lined cod end.

Traps were deployed for 1 hr at sunset. In mangrove areas, light traps were anchored within the root structure; using weights tied to a line, air was removed from traps until the top of the trap was just above the surface of the water. In non-mangrove areas within fishponds, traps were deployed near the fishpond wall, and in open-coast areas, traps were deployed off beach areas in water depths comparable to adjacent mangrove areas.

2.5 | Plankton tows

Plankton nets were towed alongside waders near the light traps for 1 min (for a standardized length of ~20 m along shore) during the light trap deployment (Granek & Frasier, 2007). Plankton nets had 210 μm mesh, a 30-cm mouth diameter and were 120 cm long. Mesh size was selected to capture a broader size range of holo- and meroplankton. In mangrove areas, the tow was pulled through water as close to the mangrove root structure as possible while tows near the fishpond walls and open-coast mirrored the topography of the paired habitat. All tows were pulled at a similar speed to control for water volume sampled.

2.6 | Sample processing

Contents of light trap and plankton tow cod ends were fixed in 2%–4% formalin solution then transferred to a 70% ethanol solution for preservation. A dissecting light microscope was used for sample identification. When feasible, all individuals were counted in each sample and identified following methods in Granek and Frasier (2007) unless further identification was possible. For crabs, larvae were identified to stage: zoea, megalope or post larval. A Folsom splitter was used on highly dense samples (>2,000 individuals; average individuals per sample = 11,040, $SD = 36,646$) and abundances were scaled up to estimate total number (Milroy, 2015). Subsamples had a mean of 898 individuals (minimum = 483, $SD = 337$). Split samples were fully scanned for rare species.

2.7 | Data analysis

Separate analyses were conducted for each sampling method (light traps and plankton tows). To characterize zooplankton assemblages among habitat types (open-coast mangrove, open-coast non-mangrove, fishpond mangrove, fishpond non-mangrove), relative abundance of each taxon to the sample's total organism count was calculated. Individual-based rarefaction and extrapolation curves of species richness were constructed for each habitat type (Appendix Figure A1; e.g. Chao et al., 2014; Colwell et al., 2012; Hortal et al., 2006). For rarefaction curves, bootstrap replicates estimated 95% confidence intervals with estimates obtained using the ɪNEXT package in ʀ (Hsieh et al., 2016). For each sample, taxa with multiple developmental life stages were aggregated, then richness and Shannon diversity (both based on lowest identifiable taxon) were calculated. We compared richness and diversity at (a) all mangrove sites to all non-mangrove sites, (b) mangrove to non-mangrove sites only within fishponds and (c) mangrove to non-mangrove sites only outside of fishponds using paired t-tests to assess the hypothesis that richness and diversity in mangroves are greater than in non-mangrove habitat. With zooplankton data (natural) log transformed to reduce the influence of dominant taxa, all groups met assumptions of normality and equal variance.

The hypothesis that mangrove presence affects zooplankton community composition was tested using permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001). PERMANOVA was performed on all samples from the four habitat groups using 'adonis' function in VEGAN R package (Oksanen et al., 2015). Prior to using PERMANOVA, homogeneity of multivariate dispersions among habitats was assessed with Bray–Curtis dissimilarity measure using 'betadisper' function in VEGAN R package (Oksanen et al., 2015). Zooplankton abundance was (natural) log transformed prior to analysis to reduce the influence of dominant taxa on dissimilarity patterns. The unbalanced design between habitat types dictates cautious interpretation of results.

To visually examine differences in zooplankton community assemblages among habitats and in community composition over time at sites sampled multiple times, we performed nonmetric multidimensional scaling (NMDS; Clarke, 1993). Zooplankton abundance was log transformed to dampen the impacts of dominant species on the ordination analysis. Multiple developmental life stages within a taxon were separated for this analysis to understand how community assemblages vary both by taxa and developmental stages. Rare taxa (<1% mean relative abundance) were included as they may clarify community patterns, since 98% of regionally rare fish species (and possibly other taxa) support highly vulnerable ecosystem functions in coral reefs (Mouillot et al., 2013). Bray–Curtis dissimilarity index values were calculated among the samples and plotted using NMDS. NMDSs for each sampling method were related to measured environmental variables using the 'envfit' function in VEGAN R package (Oksanen et al., 2015). This function fits explanatory variables in the ordination space defined by the species data (Oksanen et al., 2015). Each environmental variable was analysed independently and a permutation test (permutations = 1,000) assessed the importance of each vector using a squared correlation coefficient (r^2; Oksanen et al., 2015; Pan et al., 2016). Prior to envfit analysis, a principal components analysis (PCA) was conducted on highly correlated variables to reduce repetition by creating a summary variable related to human disturbance (see Appendix Figure A2). All analyses were performed using R version 3.3.2 (R Core Team, 2016).

To understand differences in community composition and their relationship to environmental variables (particularly mangrove metrics), Spearman correlation coefficients were calculated comparing taxa abundances to mangrove and open shoreline length and percentage of mature forest in the watersheds. Additional NMDS plots were created to assess temporal variation and differences between samples collected within and outside of fishponds.

3 | RESULTS

3.1 | Environmental conditions

Environmental conditions varied between fishpond and open-coast habitat (Table 2). Fishponds were generally larger than open-coast sites (fishponds: median = 12.65 ha and open-coast median: 1.76 ha),

leading to longer mangrove and non-mangrove shoreline lengths in fishponds. However, in both fishponds and open-coast sites, the percentage of shoreline colonized by mangroves was similar (~50%). Mangrove leaf nutrients averaged 45.72% carbon (range of 42.62%–48.34%) and 1.05% nitrogen (range of 0.87%–1.31%), though fishpond mangroves had lower % carbon and greater % nitrogen than open-coast mangroves.

Watershed conditions also varied (Table 2). Most watersheds draining into fishpond sites had greater human disturbance than open-coast sites, with fishponds having a lower median percent of mature forest (fishponds = 6.0%; open-coast = 32.5%) and a higher median percentage of impervious surfaces (1.7%–0.4% respectively) and developed land (13.2%–3.3% respectively). For environmental and watershed conditions by site, see Appendix Table A2.

3.2 | Zooplankton assemblages: trends by sampling method and habitat type

During the sampling period, 28 zooplankton taxa were identified with copepods in the greatest abundance (light traps = 15%–26%; plankton tows = 25%–32%) followed by shrimp larvae (light traps = 14%–17%; plankton tows = 14%–20%), combined developmental stages of crabs (light traps = 12%–16%; plankton tows = 7%–12%) and amphipods (light traps = 11%–20%; plankton tows = 6%–8%; Figure 2). Other taxa with >5% abundance were isopods (8%–11%) in light traps and ostracods (5%–9%) and bivalves (4%–9%) in plankton tows. In light traps, the largest abundances were collected the first two sampling nights, but tows saw relatively large abundances later in the lunar cycle.

Richness did not vary significantly among site types (Figure 3a,b; Appendix Table A4), possibly due to small sample size. There were 6–15 taxa per site (taxa per sample: mean = 10.8, SD = 2.4). Open-coast mangroves (outside fishponds) sampled with light traps had the greatest mean richness (15.3); in plankton tows, non-mangrove open-coast sites had the greatest mean richness (11.7; Figure 3a,b). Except in open-coast mangroves sampled with light traps, rarefaction curves reached asymptotes, indicating species diversity in open-coast mangroves may be higher than that sampled (Appendix Figure A1).

Diversity varied across sites from 0.04 to 1.68 (average Shannon diversity per sample = 0.90, SD = 0.49), but did not differ significantly among site types (Figure 3c,d; Appendix Table A4). Open-coast mangrove light trap samples had the greatest mean Shannon diversity (1.184), and in plankton tow samples, non-mangrove fishpond sites had the greatest mean diversity (0.995; Figure 3c,d).

Zooplankton community composition was highly similar within pairs (Figure 4; PERMANOVA: light traps: $df = 3$, $F = 1.12$, $p = 0.31$, stress = 0.16; plankton tows: $df = 3$, $F = 1.15$, $p = 0.28$, stress = 0.19). Thus, further analyses focus on overall sites and environmental variables to understand drivers in zooplankton community composition.

Zooplankton community composition in light traps varied by mangrove shoreline length and mangrove leaf carbon ($p < 0.001$),

TABLE 2 Key environmental and watershed variables by site type

| Variable	Site Type											
	All sites				Fishponds				Open-coast			
	Min	Median	Max	SD	Min	Median	Max	SD	Min	Median	Max	SD
Site characteristics												
Mangrove shoreline (m)	110.17	488.19	1,138.49	371.04	288.80	571.43	1,138.49	316.28	110.17	143.81	143.82	19.42
Non-mangrove shoreline (m)	116.87	436.90	710.83	216.33	402.46	550.85	710.83	122.73	116.87	131.79	206.72	48.15
% mangrove shoreline	28.89	52.75	70.86	13.27	28.89	53.32	70.86	14.49	34.77	52.18	55.17	11.02
$\delta^{13}C$ mangrove leaves	−32.14	−28.91	−26.53	1.63	−30.71	−28.48	−26.53	1.43	−32.14	−29.34	−27.73	2.23
%C mangrove leaves	42.62	45.96	48.34	1.92	42.62	45.66	48.34	2.07	44.73	46.55	48.00	1.64
$\delta^{15}N$ mangrove leaves	1.02	2.17	3.77	0.89	1.02	2.51	3.77	0.82	1.55	1.76	3.77	1.23
%N mangrove leaves	0.87	0.96	1.31	0.18	0.90	0.96	1.31	0.18	0.87	0.89	1.18	0.17
Watershed characteristics												
Relief of watershed (m)	133.20	665.99	1,499.62	440.88	133.20	627.89	1,499.62	233.65	679.70	1,402.08	1,499.62	447.89
% mature tree cover	2.00	10.00	48.00	15.38	2.00	6.00	48.00	5.50	27.00	32.47	48.00	10.89
Mean annual precipitation (cm)	48.77	132.34	177.29	38.90	48.77	103.63	177.29	33.82	136.91	163.07	177.29	20.48
% impervious area	0.21	0.89	7.25	2.17	0.59	1.74	7.25	2.36	0.21	0.41	0.51	0.15
% of land use/developed	1.37	5.08	36.60	11.08	3.56	13.20	36.60	11.78	1.37	3.34	4.35	1.52
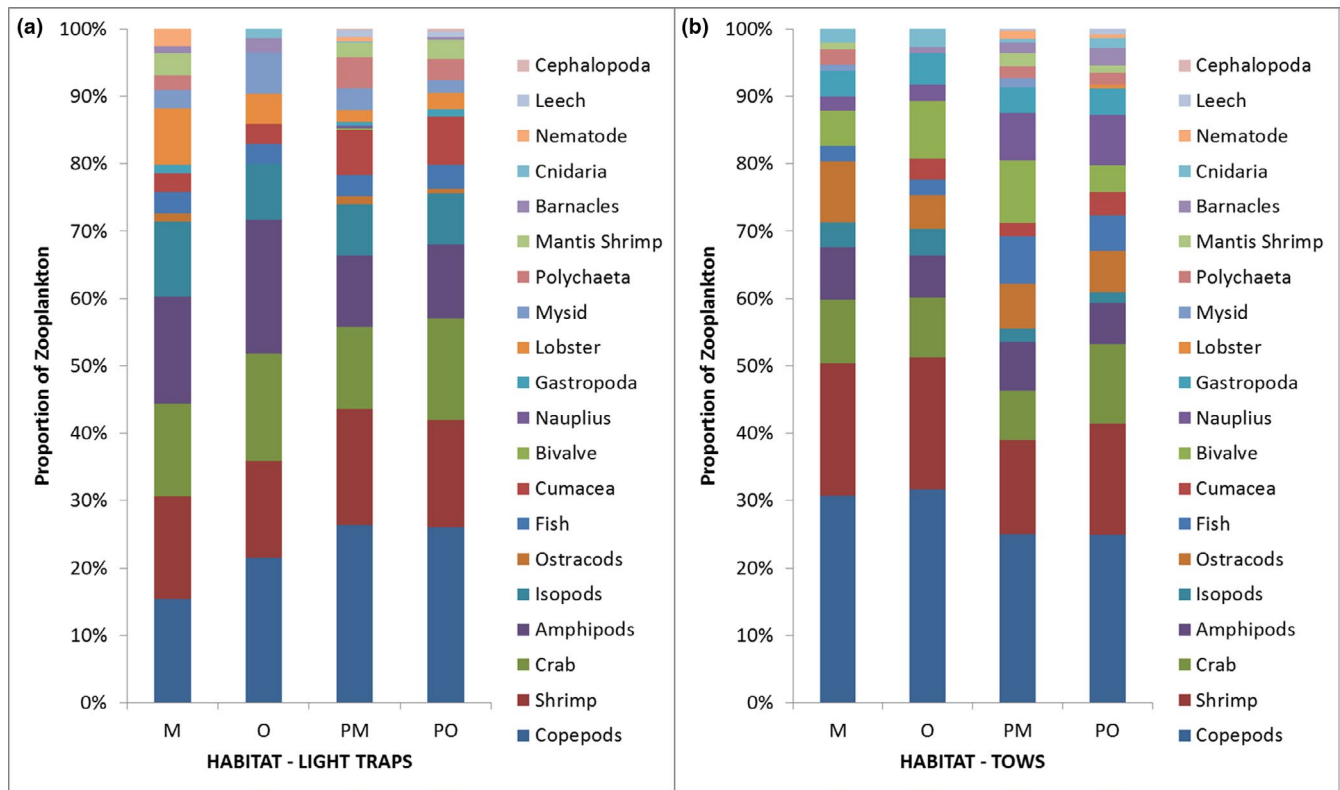
FIGURE 2 Comparison of proportional abundance values of major zooplankton groups among habitat type using (a) light traps and (b) plankton tows during June 2015. *M* open-coast mangrove, *O* open-coast non-mangrove, *PM* fishpond mangrove, *PO* fishpond non-mangrove

FIGURE 3 Box plots of richness (a, b) and Shannon diversity (c, d) by habitat types and sampling method. *M* open-coast mangrove (*n* = 3), *O* open-coast non-mangrove (*n* = 3), *PM* fishpond mangrove (*n* = 7), *PO* fishpond non-mangrove (*n* = 7)
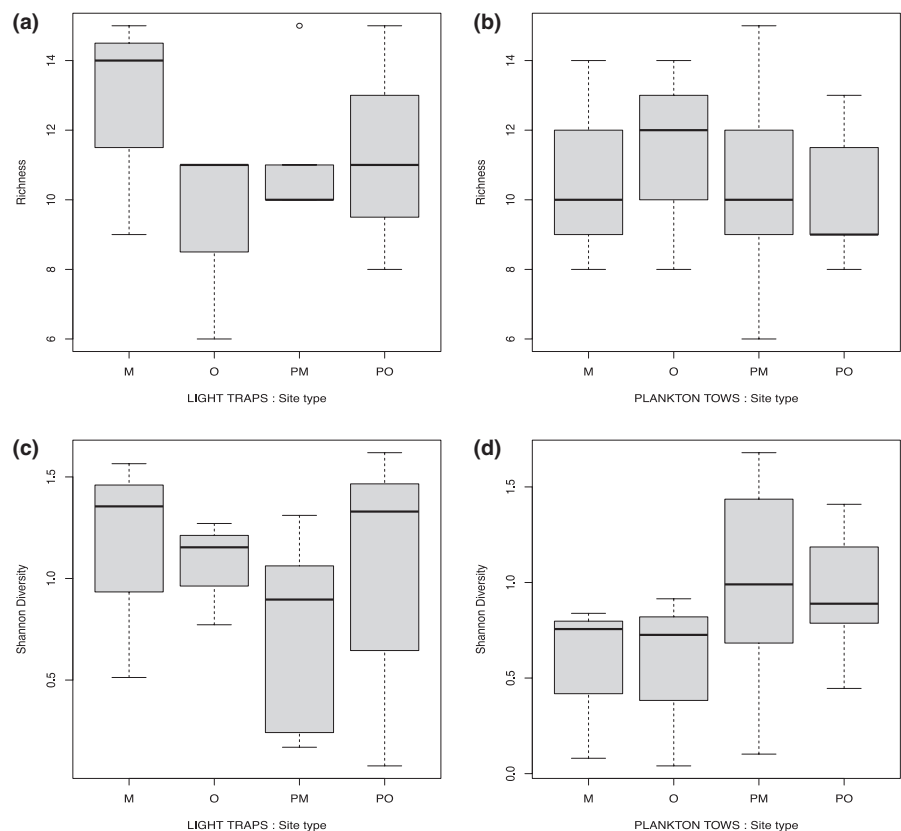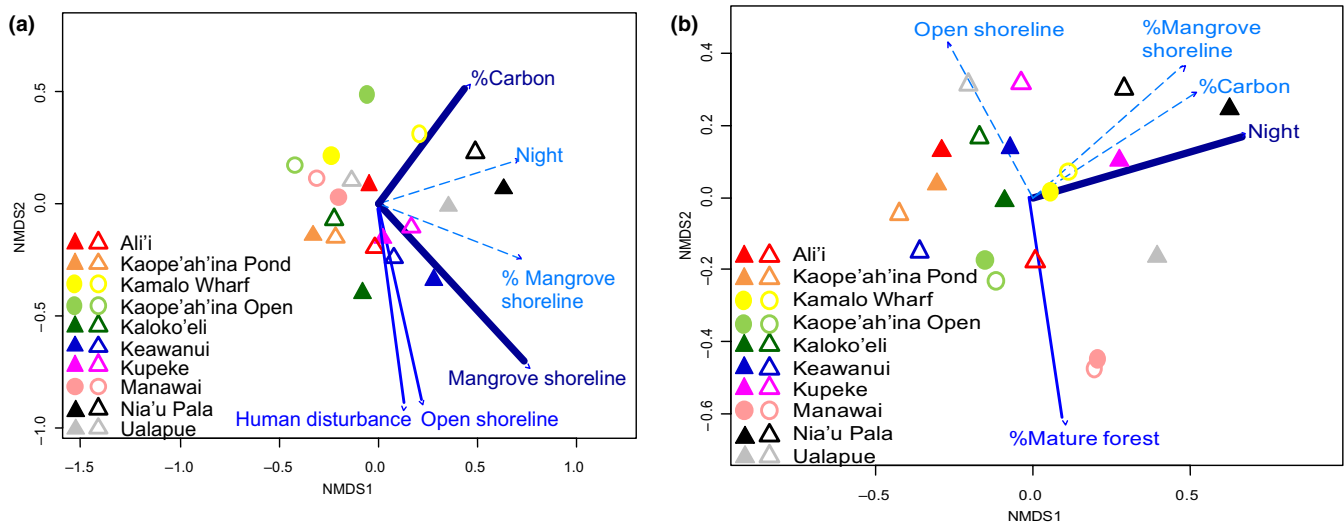
FIGURE 4 Nonmetric multidimensional scaling (NMDS) comparing zooplankton assemblages collected in (a) light trap samples and (b) plankton tows across site locations and habitat types and including environmental vectors driving community assemblages (▲ = fishpond mangrove, △ = fishpond non-mangrove, ● = open-coast mangrove, ○ = open-coast non-mangrove, dark thick line—$p = 0$–0.0001, thin line—$p = 0.001$–0.01, light dotted line—$p = 0.01$–0.05)

and by non-mangrove shoreline length, sampling night, percent of mangrove shoreline length and human disturbance gradient ($p < 0.05$; Figure 4a). Within the human disturbance gradient, undisturbed sites were characterized by greater watershed relief, higher percent mature forest and higher annual precipitation, while more disturbed sites had a greater percent of both watershed impervious surface and developed land. Zooplankton community composition in plankton tows varied by sampling night (lunar cycle; $p < 0.001$), and by percent mature tree cover in the watershed, mangrove leaf carbon and percent non-mangrove and mangrove shoreline length ($p < 0.05$; Figure 4b).

3.3 | Fishponds create novel habitat

Zooplankton community composition differed inside versus outside of fishponds (Figure 5; PERMANOVA: light traps: $df = 1$, $F = 2.55$, $p = 0.01$, stress = 0.16; plankton tows: $df = 1$, $F = 1.70$, $p = 0.09$, stress = 0.195), overshadowing any potential differences in community composition between mangrove and non-mangrove sites.

4 | DISCUSSION

During the study period, zooplankton diversity, richness and community composition did not differ between mangrove and non-mangrove sites on Moloka'i, in contrast to patterns found in mangroves' native range (Granek & Frasier, 2007). However, trends in diversity and abundance among habitat groups (Figure 3) indicate that the lack of significance may be due to the small sample size available on Moloka'i. Specifically, rarefaction analysis of open-coast

mangrove light trap samples not reaching asymptote indicate underrepresentation of mangrove richness in our dataset (Appendix Figure A1) and open-coast mangrove sites had the highest richness while open-coast non-mangrove sites had the lowest, with fishpond samples at intermediate diversity.

Differences in community assemblages between open-coast and fishpond sites (Figure 5) suggest that fishponds create microcosms with unique community assemblages. Although the four most dominant species were similar between fishponds and open-coast areas, less abundant species differed. Specifically, in light trap samples, cumaceans were more abundant and lobster larvae less abundant in fishponds; in tow samples, larval fish, nauplii and nematodes were more abundant and isopods and cnidaria less abundant in fishponds compared to open-coast sites (Figure 2). The novel habitat in fishponds may be partially due to accumulation of mud and sediment within ponds that are not actively cleared (Kepler & Kepler, 1991; Roberts & Field, 2008). Moreover, fishpond walls create habitat complexity that limits flow and entry by larger species, while providing protection for zooplankton. Since non-mangrove fishpond sites were collected along structurally complex fishpond walls, and not in sandy habitat, as at open-coast sites, community composition along pond walls may be more similar to mangrove habitat than open-coast habitat, possibly explaining the observed similarity in community composition between the two fishpond habitats. Additionally, paired pond sites may experience extensive mixing or spillover between pond mangrove and non-mangrove areas, masking any differences in community composition.

Open-coast sites had more variable communities of photosensitive (light trap sampling) zooplankton. Specifically, mangrove light traps collected several species not collected by open-coast non-mangrove light traps including ostracods, gastropoda, polychaeta,
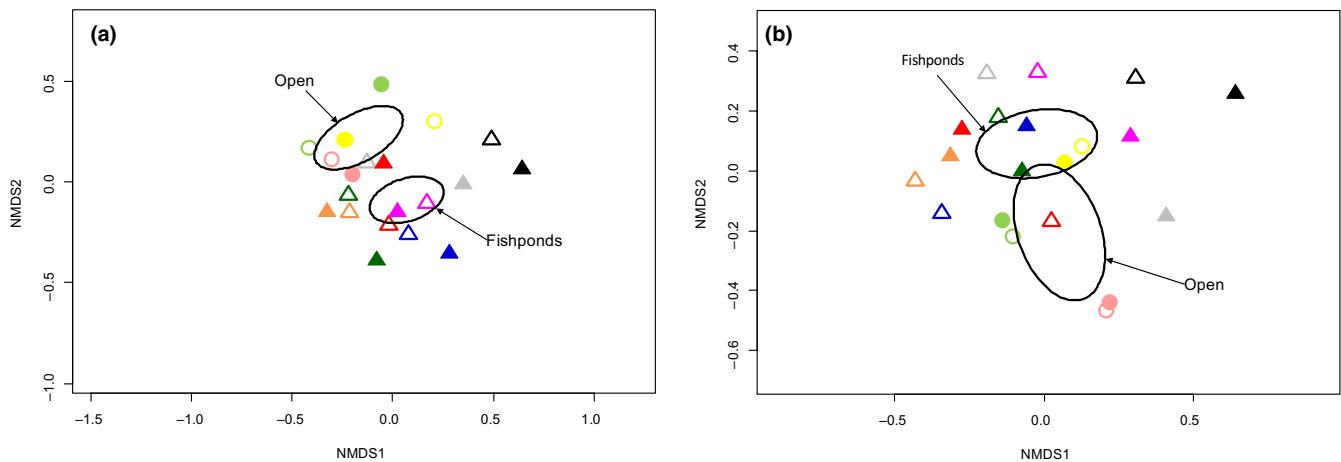
FIGURE 5 Nonmetric multidimensional scaling (NMDS) comparing zooplankton assemblages between open sites and fishpond sites in (a) light traps (stress = 0.16; PERMANOVA comparing habitat types: $df = 1$, $F = 2.55$, $p = 0.01$) and (b) plankton tows (stress = 0.195; PERMANOVA comparing habitat types: $df = 1$, $F = 1.70$, $p = 0.09$). Ellipses represent 95% confidence intervals. ▲ = fishpond mangrove, △ = fishpond non-mangrove, ● = open-coast mangrove, ○ = open-coast non-mangrove

mantis shrimp and nematodes; similarly, mangrove plankton tows collected mysids, polychaeta and mantis shrimp, species not collected in non-mangrove open-coast sites, though plankton tows in this habitat type collected cumaceans and barnacles—not detected in mangrove tows. These differences and rarefaction curves, indicating that we may not have captured the full diversity of zooplankton in open-coast mangroves, indicate that open-coast mangroves may provide habitat not offered by historical open-coast habitat.

Zooplankton community composition varied by night of the lunar cycle and by a suite of environmental factors, including mangrove shoreline length. In general, paired sites were more similar to each other than to other sites of that habitat category, though paired sites sampled across different periods of the lunar cycle revealed notable within-site temporal variability in community composition (Figure 4, Appendix Figure A4). Based on repeat sampling at Ali'i and Kaloko'eli fishponds (Table 1), differences among sites may be an artefact of lunar cycle rather than a reflection of actual differences in community composition (see Figure 5, Appendix Figure A4), suggesting a shortcoming of our sampling design that only covered part of the lunar cycle during a single year (missing seasonal and interannual variability).

4.1 | Habitat complexity

Zooplankton community composition differed by length of non-mangrove open shoreline within a site for both sampling methods and by mangrove shoreline length in light trap samples. In light traps, taxon abundances either decreased or were not affected as the length of mangrove shoreline increased (Appendix Table A5), contrary to patterns in native mangrove habitat in which abundances of certain taxa and overall diversity increase by more than 50% in mangrove relative to non-mangrove habitat (Granek & Frasier, 2007).

While most native mangrove environments support more diverse and abundant zooplankton communities than adjacent non-mangrove embayments (Kathiresan & Bingham, 2001; Robertson & Blaber, 1992), some mangrove environments demonstrate a different pattern. For example, Goswami (1992) reported lower zooplankton biomass in Goa, India's mangroves than in contiguous estuarine and neritic habitats due to the relatively harsh mangrove environment. The large tidal range in Moloka'i's mangroves is more similar to that in Goa than in the Caribbean, where mangroves are permanently flooded. As intertidal species, Moloka'i's mangroves only provide zooplankton and zooplanktivores habitat during higher tides, creating a harsher environment due to greater fluctuations in salinity and temperature.

4.2 | Lunar cycles

Zooplankton, influenced by lunar cycle, are generally most abundant in samples collected at the full moon; we observed variable community composition by sampling night, likely due to lunar phase and associated tides (Hernández-León, 1998; Hernández-León et al., 2002, 2004). Repeat sampling at two sites across three nights each allowed us to evaluate temporal differences by controlling spatial heterogeneity. These sites were first sampled during the middle of the third lunar quarter (5 days after the full moon) and then sampled twice more in the middle of the fourth lunar quarter. Community composition of sites sampled in the fourth lunar quarter had lower abundances and was more similar to each other than to samples from the same site collected during the third quarter (Appendix Figure A4, Appendix Table A1).

In the Canary Islands, zooplankton biomass decreased after the full moon due to the later rising moon (Hernández-León et al., 2002) that increases the period of darkness during the early hours of the

night. During these hours, diel vertical migrants, many of which are zooplankton predators, move to shallower waters and may reduce zooplankton biomass (Hernández-León et al., 2002). Diel vertical migration can increase predators in shallow waters by ~70% (Hernández-León et al., 2002; Longhurst & Williams, 1979). Similarly, we found abundances of (zoea, megalopa and post larval) crabs, shrimp larvae, Monstrillidae, isopods, fish larvae, hydropoids and jellies decreased the later after the full moon samples were collected (Figure 4, Appendix Table A1). This pattern may explain significant decreases in zooplankton abundance across habitat types during third quarter sampling and in community composition, abundance and diversity patterns across sites sampled on different nights after the full moon.

Crab abundance across diverse developmental stages declined significantly later in the lunar cycle, possibly due to larval release of crabs (Morgan & Christy, 1995), which increases during the largest amplitude nocturnal high tides of the lunar cycle to increase nocturnal larval transport from shore when predation by visual zooplanktivores is limited (Morgan & Christy, 1995). A large amplitude nocturnal high tide occurred prior to sample collection and another after sampling concluded. Crab reproduction patterns may explain why multiple crab developmental stages decreased significantly over time as the longer after reproduction, the greater the chances of larvae dispersing, dying or becoming prey. This pattern has been observed for other decapod crustaceans (Forward Jr, 1987) and may explain observed decreases in lobster larval abundance in both mangrove and non-mangrove sites.

4.3 | Human disturbance

In light trap samples, zooplankton community composition was correlated with human disturbance. Taxon abundance increased as the percent of mature tree cover in the watershed (lower human disturbance) increased (Appendix Table A6). For example, in light traps, amphipods, lobster larvae, *Lucifer* shrimp and megalopae had greater abundances as mature forest increased. This trend may indicate an environmental impact gradient whereby locations with lower anthropogenic impacts support more abundant populations of certain taxa than those with greater impacts, consistent with research on zooplankton sensitivity to human influences (Attayde & Bozelli, 1998; Micheli, 1999; Rogers & Greenaway, 2005). Additionally, greater mangrove shoreline length is strongly correlated with more disturbed watersheds (Appendix Table A3) perhaps indicating that mangroves are benefiting from terrestrial anthropogenic nutrient inputs. If so, detecting mangrove habitat benefits may be confounded by the negative anthropogenic watershed effects on zooplankton communities.

4.4 | Management implications

Overall, lunar cycles and site dynamics, including fishpond structure, mangrove and open shoreline length, percentage of mangrove shoreline length, total percent carbon in mangrove leaves and disturbance in upstream watersheds influenced zooplankton community composition. Mangrove influence on community assemblage is difficult to identify within fishponds, likely because of extensive mixing within these structures and/or the high structural complexity of the non-mangrove pond habitat we sampled (pond walls). Our findings indicate that non-native mangroves support community composition, richness and diversity *similar* to non-mangrove areas, though some widespread taxa have lower abundances in mangrove habitat, as found in mangroves' native range (Granek & Frasier, 2007). Additionally, study findings indicate that fishponds, themselves, create novel habitat, differing in environmental variables and community composition from native open-coast sites, and management approaches should recognize these differences.

These findings suggest that in the face of declining fisheries, threatened reef habitat and changing climatic and ocean conditions, non-native mangroves may provide, rather than impede, zooplankton habitat availability in novel locations, as found in native mangrove habitat. For non-native species established in an ecosystem, evaluating the suite of benefits and costs to conduct a risk assessment can facilitate comprehensive and cost-effective management decision-making. In addition to zooplankton habitat, the role non-native mangroves play in buffering adjacent coral reefs from sedimentation (Field et al., 2007; Ogston et al., 2004) and sequestering carbon (Alongi, 2012) is poorly understood. As climate change continues to affect physical, biological and chemical characteristics in marine environments, novel solutions may be necessary. For example, where mangroves' detrimental ecosystem effects are minimal (e.g. MacKenzie & Kryss, 2013) and as sea level rises and storm frequency and intensity increase, cost–benefit analyses are recommended for making decisions about non-native mangrove management. Species introductions are an ongoing global phenomenon, and cost–benefit or risk assessment analyses examining services and disservices provided under changing climatic and demographic conditions are needed to improve science-based decision-making for non-native species management.

AUTHORS' CONTRIBUTIONS
E.F.G. conceived the idea; C.L.L. and E.F.G. co-designed the study and conducted fieldwork; C.L.L. processed lab samples and analysed the data; C.L.L. led the writing process with significant input on drafts from E.F.G.

DATA AVAILABILITY STATEMENT
Data available via pdxscholar at https://doi.org/10.15760/geology-data.4 (Lewis & Granek, 2021).

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