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# Factors Affecting the Density of *Metabetaeus lohena* (Decapoda: Alpheidae) at a High-Density Anchialine Pool Environment on the Kona Coast of the Island of Hawai'i<sup>1</sup>

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Abstract: Caridean shrimps (Caridea) are the dominant macroinvertebrates in most anchialine ecosystems. Hawaiian anchialine ecosystems, primarily composed of shallow surface pools connected to the ocean via hypogeal networks of cracks, tubes, and other voids, support 10 caridean shrimp species, including two federally listed as endangered. Little is known about most of these species. The objective of this study was to identify factors that affect the abundance and distribution of Metabetaeus lohena (Alpheidae), an uncommon species found across the Hawaiian Archipelago, at Kaloko-Honokohau National Historical Park, Island of Hawai'i. This park supports the highest concentration of anchialine pools in the State of Hawai'i and is critical to protecting this threatened ecosystem. During 2017, we measured the density of M. lohena during nighttime surveys, as well as a variety of other biological, physical, and chemical parameters, in 130 pools. Metabetaeus lohena occupied 71.5% of the pools surveyed, with a mean density of 7.32 individuals/ $\hat{m}^2$  (95% CI = 5.14–9.49). Invasive fish and the endemic shrimp Halocaridina rubra (Atvidae) had the strongest effects on M. lohena density, with negative and positive relations, respectively. In the first estimate of M. lohena density at this scale, our data indicate that Kaloko-Honokohau supports about 11,480 shrimp (95% CI = 8,054-14,906) in the pools surveyed. Furthermore, our models predict that this park could support an additional 1,695 individuals (95%) CI = 955-3,008) for a population of about 13,175 shrimp if fish were removed from 19 pools in which *M. lohena* are absent.

Keywords: density estimate, anchialine pool, shrimp, invasive fish, Hawai'i

ANCHIALINE ECOSYSTEMS are globally distributed, but geographically restricted, brackish water habitats generally found in caves, cenotes, blue holes, grietas, lakes, and other coastal locations (Holthuis 1973, Iliffe 1991, Becking et al. 2011). The definition of anchialine has evolved with time (Holthuis 1973, Stock et al. 1986) but was recently defined as "a tidally influenced subterranean estuary located within crevicular and cavernous terrains" (Bishop et al. 2015). Because anchialine habitats consist of mixtures of fresh and salt water, most are found in porous or chemically eroded landscapes dominated by basaltic or limestone (karst) substrates (Brock and Kam 1997, Bishop et al. 2015). Anchialine ecosystems often support unique and biologically rich microbial and invertebrate communities with high proportions of endemic taxa (Sket 1999, Seymour et al. 2007,

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Humphreys et al. 2009, Martínez-García et al. 2009, Calderón-Guitérrez et al. 2018). A wide variety of invertebrates are found in anchialine ecosystems, but caridean shrimp often dominate these communities (Bishop et al. 2015).

Although some anchialine habitats are entirely hypogeal, others include small surface openings that receive sunlight and direct inputs of organic materials from emergent and peripheral vegetation (Dudley et al. 2014). These epigeal anchialine pools (sometimes also referred to as ponds) are globally distributed, with concentrations in the tropical and subtropical Atlantic (Thomas et al. 1991, Gonzalez et al. 2011), the Indo-Pacific (Holthuis 1973, Hamner and Hamner 1998, Cerrano et al. 2006, Becking et al. 2011), the Mediterranean (Benovic et al. 2000), as well as other regions (Iliffe 1991). However, the highest density of pools is found in the Hawaiian Islands (Brock 1985). Most Hawaiian anchialine pools are shallow (<1 m deep) and situated in basaltic substrates across the relatively young landscapes of Maui and the Island of Hawai'i, but some anchialine pools also exist within limestone caverns formed on the geologically older island of O'ahu. Connectivity to the ocean and the water table is through subterranean cracks, crevices, and other voids that dissect these substrates. Hawaiian anchialine pool communities are dominated by species restricted to brackish water; however, species typically found in nearshore marine habitats sometimes occur, including several fish species such as Mugilidae, Kuhliidae, and Gobiidae (Brock 1977). Distinctive bacterial and micro-eukaryotic assemblages have been identified in these ecosystems (Hoffman et al. 2018, Sterling et al. 2022), but the most notable macrofauna include species of Decapoda, Gastropoda, and Odonata (Chai et al. 1989, Brock and Bailey-Brock 1998, Sakihara 2009, Marrack and Beavers 2011, Tango et al. 2012, Peck and Nash 2022). Native Hawaiians have strong cultural ties to anchialine pools as they have historically been used for bathing, sources of drinking water, refrigeration, containment of food and bait fish, and spirituality and healing (Adler and Ranney 2018, Gibson et al. 2022).

Caridean shrimp are abundant and ecologically important macroinvertebrates found in healthy Hawaiian anchialine pools (Dalton et al. 2013, Sakihara et al. 2015), with 10 species reported (Sakihara 2012, Yamamoto et al. 2015). Two species, Procaris hawaiana Holthuis, 1973 and Vetericaris chaceorum Kensley and Williams, 1986 (both Procarididae) are federally listed as endangered (USFWS 2013, 2016, respectively) and largely restricted to a small set of pools on the southern coast of the Island of Hawai'i (Sakihara 2012). Metabetaeus lohena Banner and Banner, 1960, a widespread Hawaiian anchialine shrimp (Russ et al. 2010), was a candidate for endangered species protection (USFWS 2006) but was removed from listing (USFWS 2015) because a population was discovered in an anchialine pool at Rapa Nui, Chile (Anker 2010), indicating that it is not endemic to the Hawaiian Archipelago. Regardless, M. lohena typically occur in low abundance and is vulnerable to population declines across its Hawaiian range. In contrast, Halocaridina rubra Holthuis, 1963 is found in many pools across the archipelago and is often locally abundant (Sakihara 2012, Marrack et al. 2015). Despite broadly overlapping ranges, M. lohena and H. rubra differ in size, larval feeding strategies, and population structures. Little genetic structure was found for M. lohena across the main Hawaiian Islands, indicating considerable dispersal capabilities of their planktotrophic larvae (Russ et al. 2010), a pattern that greatly contrasts to that found for H. rubra (Santos 2006).

The health and integrity of Hawaiian anchialine pools are threatened by a wide range of physical and biological phenomena. Most notable threats include land development (Brock 1977, Hoover and Gold 2006), nutrient-loading from groundwater inputs (Hoover and Gold 2006, Marrack and Beavers 2023), contamination from recreational use (Chai et al. 1989, Sakihara 2009, Marrack and Beavers 2011), and predation and competition from invasive species (Chai et al. 1989, Weijerman et al. 2008). Additionally, sealevel rise is expected to inundate many existing pools, shifting this habitat to slightly higher

# elevations over the next century (Marrack and O'Grady 2014, Johnson et al. 2015, Marrack 2016).

Introduced fish have particularly strong negative effects on Hawaiian anchialine pool ecosystems, primarily through predation. The introduced species tilapia (often Oreochromis mossambicus [Peters, 1852] or Sarotherodon melanotheron [Ruppell, 1852]), guppies (Poecilia reticulata Peters, 1859), and western mosquitofish (Gambusia affinis [Baird and Girard, 1853]) were documented in anchialine pools in 1977 (Brock 1977) and increased their range within pool habitats in recent years (Brock and Kam 1997, Mackenzie and Bruland 2012, Havird et al. 2013). Oreochromis mossambicus were first introduced to Hawai'i as early as the 1950s, primarily to control vegetation, as a fisheries bait, and for aquaculture (Wu and Yang 2012). In contrast, P. reticulata and G. affinis were introduced in 1922 and 1905, respectively, to control mosquito populations (Brock 1960, Nico et al. 2013). Mechanisms and rates by which these species spread across the archipelago are poorly documented, but each is now widespread and occupy a wide range of habitats (Neil 1966, Moody et al. 2017, Peck et al. 2023). These opportunistic predators affect H. rubra and M. lobena abundances where fish and shrimp populations are found together. Notably, shrimp are often absent from pools with fish (Brock 1977, Capps et al. 2009, Dalton et al. 2013, Marrack et al. 2015, Seidel et al. 2016), are physically larger when they co-occur with fish (Capps et al. 2009), or change their behavior to avoid fish predators such as feeding at night when fish are less active (Carey et al. 2011, Havird et al. 2013, Seidel et al. 2016).

The overall goal of this study was to estimate the population size of *M. lohena* in anchialine pools at and immediately adjacent to Kaloko-Honokōhau National Historical Park, Island of Hawai'i (hereafter collectively referred to as Kaloko-Honokōhau), and identify factors that influence their distribution and abundance across this area. The work was conducted at Kaloko-Honokōhau because

the park supports one of the highest concentrations of anchialine pools in the state and is critical to protecting this threatened habitat across the archipelago. This study builds on earlier efforts to understand factors affecting anchialine pool shrimp populations (Marrack et al. 2015) by using *M. lohena* density, rather than presence or absence, as the primary response variable. Density is a preferred response metric because it provides more information about shrimp populations and how they interact with their environment than occupancy. Our primary objective was to compare shrimp density to several physical, chemical, and biological variables measured in pools. Secondarily, we tested two hypotheses that we thought may help explain M. lohena population patterns. First, we hypothesized that M. lohena density would increase with substrate age because older substrates have more time to develop conditions conducive to autochthonous and allochthonous inputs of organic matter that provide resources for pool inhabitants (Drake and Mueller-Dombois 1993). Time may be particularly important to pools at Kaloko-Honokohau due to the relatively low amount of rainfall that occurs on the leeward sides of the high islands of the archipelago (Giambelluca et al. 2013), which generally results in slow vegetation development (Aplet et al. 1998). Second, we hypothesized that *M. lohena* density would decrease with increasing geographic distance from the ocean, possibly due to lower salinity (Bauer 2003) or reduced hypogeal connectivity that may be expected from occlusions or other physical disconnections among cracks and crevices within the basaltic landscape. This potential barrier of geographic distance may be particularly strong for *M. lohena* due to its planktotrophic larvae and connection to the ocean for dispersal (Russ et al. 2010). A priori, we expected invasive O. mossambicus, P. reticulata, and G. affinis to be an important factor affecting M. lohena pool occupancy at Kaloko-Honokōhau (Marrack et al. 2015), but the extent to which they affect shrimp (i.e., shrimp density) at this park has yet to be determined.

#### MATERIALS AND METHODS

#### Study Site

Kaloko-Honokōhau National Historical Park is located about 6 km (3.6 mi) north of Kailua-Kona on the arid western coast of the Island of Hawai'i (16.80° N, -156.03° W) (Figure 1). Honokōhau Small Boat Harbor, Queen Ka'ahumanu Highway, and the Kohanaiki Private Club Community border the park on the south, east, and north, respectively. Kaloko-Honokōhau occupies about 5 km<sup>2</sup> (1,200 acres) of coastal land (Marrack and Beavers 2011) and protects a rich assemblage of archaeological, cultural, and historical features. Brackish wetland habitat within the park includes over 180 anchialine pools (Marrack and Beavers 2011), and Kaloko and 'Aimakapā Fishponds. Anchialine pools range in size from 0.2 to  $105.5 \text{ m}^2$ , are shallow (typically <1 m deep), vary in salinity (0.5–35 ppt), and many dewater during low tide (Figure 1). Kaloko and 'Aimakapā Fishponds are considerably larger, occupying about 4.5 ha and 12 ha, respectively.

Eruptions from Hualālai volcano paved Kaloko-Honokōhau with lava most recently during three time periods: 1,500–3,000, 3,000–5,000, and 5,000–10,000 years before present (Wolfe and Morris 1996). Where anchialine pools are found, the youngest and oldest flows are dominated by the relatively smooth or ropy pahoehoe, and the intermediateaged flow is composed primarily of rubbly or



FIGURE 1. Location of Kaloko-Honokōhau National Historical Park on the western coast of the Island of Hawai'i. Anchialine pools (yellow and black dots) are primarily clustered in five general areas located in lava substrate deposited during three time periods. Pools containing invasive fish are indicated with black dots. Note that numerous pools are adjacent to Kaloko and 'Aimakapā Fishponds (indicated in blue) and are connected to the fishponds during extreme high tides. Source of base map: ESRI, World Imagery, 2022.

clinkery 'a'ā, although some patches of pahoehoe exist in the 3,000-5,000-year substrate (Richmond et al. 2008). Soil on both lava substrates is thin and poorly developed due to their relatively young age and dry climate (Richmond et al. 2008). Topography slopes gently seaward with the highest elevation being about 25 m asl. Pool bottom surfaces range from silt, sand, pebbles, cobbles, to rock slabs, and often include leaves and twigs that fall into pools from nearby vegetation. Types and amounts of vegetation immediately peripheral to pools vary with milo (in Hawaiian, or portia tree, Thespesia populnea Sol. Ex Corrèa, 1807), Christmasberry (Schinus terebinthifolia Raddi, 1820), and beach naupaka (Scaevola taccada

(Gaertn.) Roxb., 1814) most common. Emergent vegetation, where present, primarily includes makaloa (in Hawaiian, or smooth flatsedge, Cyperus laevigatus L., 1771), 'ākulikuli (in Hawaiian, or shoreline seapurslane, Sesuvium portulacastrum (L.) L., 1759), and turtleweed (Batis maritima L., 1759) (Figure 2). Invasive fish occupy many pools within Kaloko-Honokohau (Figure 1). Oreochromis mossambicus are firmly established in 'Aimakapā Fishpond and populate numerous adjacent pools. Poecilia reticulata and G. affinis are found in pools adjacent to both fishponds and at the southern end of Kaloko-Honokōhau. Because P. reticulata and G. affinis are difficult to differentiate in the field, hereafter they are referred to as poeciliids (Poeciliidae).



FIGURE 2. Anchialine pools at Kaloko-Honokōhau National Historical Park at the southern end of the park (A; 1,500–3,000 years lava flow); on the northwestern side of Kaloko Fishpond (B; 3,000–5,000 years lava flow); in the Kaloko-Honokōhau area of the park (C; 5,000–10,000 years lava flow); and on the northwestern side of 'Aimakapā Fishpond (D; 5,000–10,000 years lava flow). Note that the shallow pool in (C) often dewaters during low tides, precluding the existence of fish. Pool (B) contains poeciliids and (D) contains tilapia and poeciliids; no shrimp were detected in either of those pools. Photos by Robert Peck.

# Pool Parameters

Several physical, chemical, and biological variables were measured in each pool included in this study during 17 August-12 September 2017. Water temperature, salinity, pH, and oxygen concentration were measured on one occasion near high tide during the survey period using a calibrated YSI Sonde (YSI Incorporated, Yellow Springs, Ohio) placed at two locations on the pool bottom. The physical structure of each pool was determined by estimating the proportion of the pool bottom composed of substrate within the following categories: impervious, sand, and cobbly. Impervious substrate consisted of silt, sand, and very fine pebbles (<2 mm); each were considered to be a barrier to the passage of shrimp. Sandy substrate included sand and very fine to very coarse pebbles (2–64 mm). Cobbly substrate described the larger rocks of cobbles (64-128 mm), boulders (128-512 mm), and slabs (>512 mm). Additionally, we estimated the amount of pool bottom covered by leaves and twigs (lying on top of the substrates). Pool substrates and leaves and twigs were estimated by visual assessment of cover to the nearest 5%.

The age of the substrate on which pools were located was determined by overlaying geography coordinates (in Universal Transverse Mercator [UTM]) for each pool with a geographic information system (GIS) layer delimiting lava substrate in the park (Wolfe and Morris 1996). The distance between each anchialine pool and the nearest large body of water (the coast, or either Kaloko or 'Aimakapā Fishpond, whichever was closest) was measured using the Distance tool in ArcMap (release 10.1, ESRI 2013). Due to proximity to the coast and large size relative to the anchialine pools, we considered the two fishponds to pose little resistance to the dispersal of larval shrimp and therefore considered them as "coastal" in our analysis. Pool size  $(m^2)$  was determined by the National Park Service (K. Annandale, Kaloko-Honokōhau NHP, written communication, 2017). Fish were identified by poolside observers to genus or species, when possible, but not counted.

# Shrimp Survey

Metabetaeus lohena density was estimated in each pool by counting the number of individuals observed during nighttime visual searches lasting 5-15 min. The duration of each survey depended on the size of the pool as follows:  $<5 \text{ m}^2 = 5 \text{ min}; 5-10 \text{ m}^2 = 10$ min;  $>10 \text{ m}^2 = 15 \text{ min.}$  Durations were sufficient to allow for thorough examination of the pool for shrimp. No pool was large enough to require entry. Because it was not possible to see the bottom of some pools due to dense vegetation (primarily *B. maritima*), the size of searchable area for each pool was estimated visually to the nearest 5%. We then calculated the density of shrimp in the pool by dividing the number of individuals observed by the area searched. Randomly placed quadrats, often used to estimate benthic invertebrate density, were deemed infeasible due to the complex, three-dimensional structure of many pool bottoms and the rarity of M. lohena.

Pools were searched by individual observers for 30–120 min following sunset because M. lohena are naturally more active at night (Sakihara 2012), and shrimp often take refuge from fish under rocks or in crevices during the day (Capps et al. 2009, Carey et al. 2011, Dalton et al. 2013, Havird et al. 2013). Surveys were conducted within about 2 h of high tide to minimize the loss of surveyable pools due to dewatering at low tide. Five to seven trained observers conducted M. lohena surveys over four evenings from 16 May to 13 July 2017. Surveyors used flashlights to illuminate the bottom of the pools, which did not appear to affect shrimp behavior. Observers slowly moved around the perimeter of each pool if necessary to search the entire pool.

At pools in which *M. lobena* were not observed, or could not be searched (e.g., deep, narrow cracks in the substrate), 1-3 traps baited with 5-10 g of canned tuna were deployed on the pool bottom for about 60 min as an additional measure to assess their presence or absence in the pool. Trapped shrimp were released back into the pool immediately after being identified. Results from trapping were not used in density estimations or in modeling but were included in counts of pools in which *M. lohena* were detected.

Halocaridina rubra were also surveyed during our study. However, logistical constraints required about one-half (49%) of the pools to be surveyed for this species during daylight hours, which may have reduced their abundance relative to nighttime surveys (Carey et al. 2011). This temporal mismatch, coupled with a lack of spatial independence among pools (i.e., groups of nearby pools tended to be surveyed together during night or day) that would confound an analysis that considered time as a factor, led to us exclude estimates of H. rubra density from the analysis. The presence or absence of *H. rubra* and two other caridean shrimp species, Macrobrachium grandimanus (Randall, 1840) and Palaemon debilis Dana, 1852, were recorded.

Overall, 130 pools were surveyed for M. lohena during the study. Our primary goal was to evaluate anchialine pools at Kaloko-Honokohau, but we included four pools located on state land adjacent to the southern edge of the park in the analysis because of their proximity ( $\leq$ 55 m) and because they likely share environmental conditions (Figure 1). For ease in reading, these pools are hereafter referred to as part of the park. Numerous other pools at Kaloko-Honokohau were omitted from the study because they were fully obscured by B. maritima, could not be located, or had dewatered at the time of the survey. Many of the unsampled pools were adjacent to Kaloko and 'Aimakapā Fishponds, although several pools were south of the Honokohau small boat harbor, and elsewhere across the park. Summaries of M. lohena densities in relation to the presence or absence of *H. rubra* and fish were based on this dataset.

# Statistical Analysis

To identify the relationship of physical and biological parameters associated with *M. lohena* density within pools, we fitted a set of univariate variable regression models

and used Akaike information criterion (AIC) to rank the models to identify predictor variables with the most explanatory power. Predictors included presence or absence of fish, presence or absence of *H. rubra*, substrate age, pool size, distance to the coast, water temperature, pH, salinity, oxygen concentration, percent composition of pool bottom substrate, and percentage of the pool bottom substrate covered by leaves and twigs. The variables were entered into a multiple variable regression model using a forward selection algorithm and added in order of their AIC rank following methods described in Burnham and Anderson (2002). At each step, AIC was computed, and the process stopped when no additional variables produced a decrease in AIC. The shrimp *M. grandimanus* and *P. debilis* may prey on M. lohena to some extent, but were not analyzed as a predatory factor because they were generally uncommon (12 of 130 and 10 of 130 pools, respectively), in low density (M. grandimanus:  $2.16 \pm 0.41$  SE individuals in pools in which they were seen; P. *debilis* were not counted), are primarily scavengers or detritivores (Fonds et al. 1981), and to our knowledge, have not been documented to prey on M. lohena. Missing physical or biological data precluded the use of some pools (n = 31) for which M. lohena were surveyed, resulting in a model-analyzed sample size of 119 pools. We predicted densities of *M. lohena* to the range of pool characteristics at Kaloko-Honokohau fitted to models of the most informative variables. All analyses were conducted in the R Statistical Software Environment version 4.0.3 (R Core Team 2022), with data manipulation and graphing conducted with the package 'tidyverse' (ver. 1.3.1; Wickham et al. 2019) and 'ggplot2' (ver. 3.4.0; Wickham 2016), respectively.

We also evaluated our *a priori* hypotheses that substrate age and distance to large water bodies influenced *M. lohena* density independently of the AIC model selection process described above. Because the influence of the two large fishponds was unknown, analyses were conducted comparing shrimp density to both the distance to the ocean and to the nearest large body of water (ocean or fishpond, whichever was closer to the pool). Due to the negative influence of introduced fish on M. lobena, only pools in which fish were absent were included in these analyses (n = 93 of 130 pools). A Kruskal–Wallis *H* test was used to compare M. lohena densities among substrate ages, and linear regression was used to test for relationships between shrimp density and distance to the ocean and to the nearest large body of water. P-values associated with these three tests were adjusted to a critical P-value of 0.017 using a Bonferroni correction for multiple comparisons. Additionally, we tested for differences in pool parameters between pools with fish and without fish using Mann-Whitney U tests, and for relationships between pool salinity and distance to coast or nearest body of water using linear regression; a critical P-value of 0.05 was used for these tests. Mean values reported throughout include  $\pm$ SE.

#### RESULTS

### **Pool Parameters**

Physical, chemical, and biological parameters of pools varied considerably across Kaloko-Honokōhau (Table 1). Pools were generally large  $(12.1 \pm 2.6 \text{ m}^2)$  and warm  $(23.9 \pm 0.2 \text{ °C})$  with relatively high salinity  $(13.4 \pm 0.3\%),$ neutral рH  $(7.92 \pm 0.03),$ high dissolved oxygen  $(6.4 \pm 0.2 \text{ mg/l})$ , and with relatively large amounts of leaves and twigs  $(8.0 \pm 1.6\%)$ . Cobbly substrate cover was most common  $(69.3 \pm 1.2\%)$ , followed by impervious substrate  $(23.0 \pm 1.6\%)$  and sand  $(7.7 \pm 3.2\%)$ . Significant differences in pool parameters between pools with fish and without fish were found for pool size (Z = 4.236; P < 0.0001), temperature (Z = 4.623; P < 0.001), dissolved oxygen (Z = -3.170; P = 0.002), leaves and twigs (Z = 3.485; P = 0.005), impervious substrate (Z = 4.118; P < 0.001), sand (Z =-2.864; P = 0.004), and cobbly substrates (Z = -2.646; P = 0.008). Pools with fish were larger, warmer, and substrates were more impervious than pools without fish. In contrast, pools without fish had more dissolved oxygen, more leaves and twigs, and the pool substrates were more sandy and cobbly.

# Shrimp Density

Metabetaeus lohena were visually detected and counted in 93 of 130 pools surveyed (71.5%). The mean density of *M. lohena* was  $7.32 \pm 1.12$  shrimps/m<sup>2</sup>. In addition, we documented *M. lohena* using traps in six pools in which they were not observed during the surveys.

*Halocaridina rubra* were present in 112 of the 130 pools surveyed (86.2%). In general, *H. rubra* occupied the same pools as *M. lobena* but were found in 15 pools that did not contain *M. lobena*, and two pools contained *M. lobena* but not *H. rubra*. *Metabetaeus lobena* density was higher in pools with *H. rubra* than in pools without *H. rubra* (8.49  $\pm$  1.26 and 0.03  $\pm$  0.03 individuals/m<sup>2</sup>, respectively; Mann–Whitney *U* test, *Z* = 5.51, *P* < 0.001).

*Macrobrachium grandimanus* was detected in 12 pools (9.2%), *P. debilis* was observed in 10 pools (7.7%), and undetermined shrimp (neither *M. lohena* nor *H. rubra*) were seen in four pools (3.1%).

Fish were observed in 37 of the 130 pools surveyed (28.5%). Poecilia reticulata were most prevalent, being found in 32 of these pools. Oreochromis mozambicus, along with P. reticulata, were found in four pools. Native fish were found in five pools: a goby (Family Gobiidae) in two pools, unidentified silver schooling fish (likely Kuhlia sp.) in three pools, and manini (Acanthurus triostegus L., 1758) and chub (Kyphosus sp.) together in one pool (a pool that also included P. reticulata). Metabetaeus lohena were found in 14 of 37 pools that contained fish (37.8%) and 85 of 93 pools without fish (91.4%). Metabetaeus lohena were absent from 8 pools that did not contain fish (8.6%). Metabetaeus lohena density was lower in pools that contained fish than in pools without fish  $(2.23 \pm 1.19 \text{ and } 9.34 \pm 1.44)$ shrimps/m<sup>2</sup>, respectively; Mann–Whitney Utest,  $\vec{Z} = -5.47$ ,  $\hat{P} < 0.001$ ). Halocaridina rubra were observed in 22 pools with fish (59.5%), 90 pools without fish (96.8%), and were absent from three pools that also lacked fish.

Physical,	Chemical, and Biol	logical Parameter:	s (Mean ± SE, Ra	nge) of Anchial National His	ine Pools With Fish, V torical Park	Vithout Fish, ar	nd for All Pools a	ıt Kaloko-Honc	okõhau
							Pool Su	bstrate Covera	ge (%)
Fish Present?	Pool Size (m <sup>2</sup> )	Temp. (°C)	Salinity (‰)	Hq	Dissolved Oxygen (mg/l)	Leaves & Twigs (%)	Impervious	Sand	Cobbly
Yes	$22.2 \pm 8.0^{a}$ 0.6-295.3	$25.6 \pm 0.4^{a}$ 20.8-31.3	$13.1 \pm 0.7$ 5.0-26.2	$7.8 \pm 0.10$ 6.9-8.6	$5.3 \pm 0.4^{a}$ 1.7-12.1	$7.8 \pm 2.4^{a}$ 0.0-80.0	$42.0 \pm 7.2^{a}$ 0.0-95.0	$3.5 \pm 1.5^{a}$ 0.0-30.0	$54.5 \pm 6.8^{a}$ 5.0-100.0
No	$8.0 \pm 1.5^{\rm b}$ 0.1-105.5	$23.3 \pm 0.2^{\rm b}$ 20.4–28.8	$13.6 \pm 0.4$ 7.8-24.6	$8.0 \pm 0.03$ 7.0-8.6	$6.9 \pm 0.2^{\rm b}$ 2.6-10.3	$8.0 \pm 2.0^{\rm b}$ 0.0-85.0	$15.3 \pm 3.2^{\rm b}$ 0.0-95.0	$9.3 \pm 1.6^{\rm b}$ 0.0-65.0	$75.4 \pm 3.1^{\rm b}$ 5.0-100.0
All pools	$12.1 \pm 2.6$ 0.1-295.3	$23.9 \pm 0.22$ 0.4-31.3	$13.4 \pm 0.3$ 5.0-26.2	$7.9 \pm 0.03$ 6.9-8.6	$6.4 \pm 0.2$ 1.7-12.1	$8.0 \pm 1.6$ 0.0-85.0	$23.0 \pm 3.2$ 0.0-95.0	$7.7 \pm 1.2$ 0.0-65.0	$69.3 \pm 3.1$ 5.0-100.0

TABLE 1

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The presence of fish, and their effect on M. lohena density, varied across the park (Figures 2 and 3). The highest mean densities of M. lohena were located in pools at South Harbor  $(n = 35, 12.2 \pm 3.0)$ , 'Ai'ōpio  $(n = 26, 12.2 \pm 3.0)$ , 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'ōpio ( $n = 26, 12.2 \pm 3.0$ ), 'Ai'opio ( $n = 26, 12.2 \pm 3.0$ ), ' 11.6  $\pm$  3.3), and Kaloko Fishpond (n = 25,  $10.4 \pm 3.2$ ), and the lowest mean densities were at Kaloko  $(n = 71, 4.4 \pm 0.9)$  and 'Aimakapā Fishpond (n = 16,  $3.4 \pm 2.5$ ). Oreochromis mossambicus were found in two pools each along the northern and northwestern edges of 'Aimakapā Fishpond. Poeciliids were present in numerous pools at Kaloko and 'Aimakapā Fishponds (n = 8 and n = 10, respectively) and South Harbor (n = 10), and at several pools at Kaloko-Honokōhau (n = 4). Two pools at KalokoHonokōhau contained only a native goby, and three pools at Kaloko Fishpond contained only small native schooling fish (likely *Kuhlia* sp.).

The multiple variable regression model with both *H. rubra* and fish had the lowest AIC value, accounting for 94.1% of the cumulative weight (Table 2). Univariate models with *H. rubra* and fish alone accounted for 3.2% and 2.7% of the model weights, respectively. Of the other physiochemical pool variables measured, only models containing substrate age and pool size contributed more than the null model, but with model weights <0.1%.

Based on the multiple variable regression model, the predicted densities of *M. lohena* in the presence and absence of *H. rubra* and fish



FIGURE 3. Density (no./m<sup>2</sup>) of *Metabetaeus lobena* at five general areas across Kaloko-Honokōhau National Historical Park, including Kaloko Fishpond (*A*), Kaloko-Honokōhau (*B*), 'Aimakapā Fishpond (*C*), 'Ai'ōpio (*D*), South Harbor (*E*), and for all pools combined (*F*). These areas are identified in Figure 1. Note that the *y*-axis differs for all pools combined panel (*F*).

#### TABLE 2

Results of Regression Analysis Identifying Anchialine Pool Parameters Best Explaining *Metabetaeus lohena* Density at Kaloko-Honokōhau National Historical Park

Model	Κ	AICc	ΔAICc	Weight	Log Likelihood	Cumulative Weight
HalRub + Fish	4	403.0543	0.000000	94.1%	-197.3517	94.1%
HalRub (yes or no)	3	409.8411	6.786833	3.2%	-201.8162	97.3%
Fish (yes or no)	3	410.1505	7.096213	2.7%	-201.9709	100.0%
Substrate age	4	420.4781	17.423874	0.0%	-206.0636	100.0%
Size	3	430.1906	27.136306	0.0%	-211.9909	100.0%
Null	2	432.1036	29.049340	0.0%	-214.0001	100.0%

*Note*: The number of parameters (*K*), Akaike's information criterion adjusted for small sample size (AICc) values, change in AICc (AAICc) values, model weights (Weight), negative log likelihood (Log likelihood), and cumulative model weights (Cumulative weight) are presented for the six best-fit models. Predictor variables *Halocaridina rubra* (HalRub; presence/absence), fish (presence/ absence), and substrate age (1,500–3,000, 3,000–5,000, and 5,000–10,000 years before present) were categorical variables while pool size was a continuous variable.

are as follows: *H. rubra* absent (1.13 individuals/m<sup>2</sup>; 95% CI = 0.50–2.52); *H. rubra* present (3.85 individuals/m<sup>2</sup>; 95% CI = 2.94– 5.04); fish present (0.39 individuals/m<sup>2</sup>; 95% CI = 0.21–0.72); and fish absent (5.36 individuals/m<sup>2</sup>; 95% CI = 3.02–9.51). These predicted densities differ from observed values because the models account for the influence of *H. rubra* when estimating the density of *M. lobena* in the presence or absence of fish.

#### Substrate Age

Substrate age had a significant influence on M. lohena density in pools without fish (Kruskal–Wallis *H* test;  $X^2 = 14.72$ , *P* < 0.001). Mean density was highest in the oldest substrate (5,000-10,000 years; n = 18; $17.9 \pm 3.8$  shrimps/m<sup>2</sup>), intermediate in the substrate (1,500-3,000 years; youngest  $n = 21; 11.7 \pm 3.8 \text{ shrimps/m}^2$ ), and lowest in the middle-aged substrate (3,000-5,000 years; n = 57;  $5.3 \pm 1.3$  shrimps/m<sup>2</sup>). A significant difference in shrimp density was found between the oldest and the middleaged substrates ( $P \leq 0.001$ ). In contrast, there was no difference in the amount of leaves and twigs among substrate ages (Kruskal-Wallis *H* test;  $X^2 = 5.25$ , P = 0.07).

# Distance from Ocean

No relationship was found between *M. lohena* density and distance from the coast

 $(R^2 = 0.003, F = 0.29, P = 0.59)$  or to the nearest large body of water (the coast, Kaloko Fishpond, or 'Aimakapā Fishpond, whichever was closest to the pool)  $(R^2 = 0.04, F = 3.93, P = 0.05)$ . In contrast, significant relationships were found between pool salinity and both distance to coast and distance to nearest large body of water  $(R^2 = 0.26, F = 40.09, P < 0.001$  and  $R^2 = 0.26, F = 40.95, P < 0.001$ , respectively).

#### DISCUSSION

Results from our study indicate that Kaloko-Honokohau supports a robust population of M. lohena, a species once considered a candidate for endangered species protection (USFWS 2006). Metabetaeus lobena was found to be widespread in the park, occupying 76.2% of the 130 anchialine pools surveyed. This occupancy rate is considerably higher than the 16% (27 of 172) of pools surveyed about 10 years earlier at Kaloko-Honokohau by Marrack and Beavers (2011). The greater proportion of pools containing M. lohena in our study was likely due to higher detectability of the shrimp at night compared to during the day, rather than landscape level changes in shrimp abundance. At a broader scale, Maciolek and Brock (1974) found M. lohena in 31% of 305 pools along the western and southern coasts of the Island of Hawai'i, and Marrack et al. (2015) found M. lohena to occupy 13% of 398 pools surveyed over much

of the same study area. Both of these studies surveyed pools for shrimp during daylight hours.

Based on our calculation of 7.3 individuals/  $m^2$ , we estimate the population of *M. lohena* to be about 11,454 within the observable, epigeal habitat of the 130 pools surveyed at Kaloko-Honokōhau. Additional M. lohena are expected to exist in pools that were not surveyed, although many of the unsurveyed pools were in areas where M. lohena abundance is likely low (e.g., in pools infested with invasive fish and B. maritima around Kaloko and 'Aimakapā Fishponds), possibly adding relatively few individuals to the total. Metabetaeus lohena also likely inhabit hypogeal habitat in the park but their abundance in this region is unknown. Regardless, to our knowledge, this is the first estimate of the M. lohena population across an area of this size in Hawai'i. Effects of invasive fish on M. lohena populations are clear as shrimp densities were 4.2 times higher in pools without fish compared to those with fish. Although the number of pools surveyed containing O. mossambicus was small (n = 4), no M. lohena were found in those pools, indicating stronger effect from that species.

We are uncertain how *M. lobena* densities at Kaloko-Honokōhau compare to other areas across the island, but if we extrapolate our results to the 29 pools in which Marrack et al. (2015) detected *M. lobena* outside of the park (all but three pools were without fish), then we can cautiously estimate an additional  $3,273 \pm 29.1$  *M. lobena* on south and west coasts of the Island of Hawai'i.

Metabetaeus lohena and H. rubra cooccurred in 70.0% (91 of 130) of the pools surveyed and was a strong predictor of M. lohena abundance. The positive association between the two species may be due to several non-mutually exclusive factors. For example, the two species may be responding in parallel, but independently, to factors such as water quality or habitat structure. However, none of the chemical or physical variables we measured contributed more than the null model indicating they had little influence on M. lohena abundance within the pools surveyed. Overall, both shrimp species occupied pools at or near the full ranges of salinity (5.0-24.6), temperature (20.4–28.8), and pH (7.0–8.6), indicating that most, if not all, pools surveyed across Kaloko-Honokōhau represent suitable habitat. The exception to this finding was the absence of shrimp in the five warmest pools (29.0–31.3 °C), and two pools with the lowest pH (6.9). Because each of these pools contained O. mossambicus and/or poeciliids, it is not possible to determine if the temperature and pH extremes or fish presence limited shrimp in these pools, which were adjacent to the northwestern edge of 'Aimakapā Fishpond. Regardless, the overall suitability of anchialine pools at Kaloko-Honokōhau is supported by Marrack et al. (2015) who also found these water parameters did not influence the occurrence of M. lohena.

Alternatively, the relationship between the two shrimp species may be largely unidirectional, with M. lohena responding to the presence of *H. rubra* due to the latter being a potential food source. Field observations indicate that M. lohena prey on H. rubra, but the importance of this prey is equivocal (Banner and Banner, 1960, Holthuis 1973, Chan and Fujii 1980) and other organic materials are also consumed. For example, Chan and Fujii (1980) dissected the digestive tracks of M. lohena and found detrital material including bacteria, diatoms, and small mineral particles, but found no evidence of shrimp cuticular matter. More recent work has shown that in some systems diets of M. lohena and microphagous grazing H. rubra (Bailey-Brock and Brock 1993, Sakihara et al. 2015) may overlap considerably. Seidel et al. (2016) found both shrimp species to have similar  $\delta$ <sup>15</sup>N isotope mean values (9.0 and 8.8 ppt for M. lohena and H. rubra, respectively) indicating little difference in trophic position. Of note, Brock (2004) found M. lohena to be an effective predator of mosquito larvae in low salinity pools, and it would be expected to find that M. lohena obtain animal food from allochthonous sources such as arthropods that fall from vegetation peripheral to the pools or are blown in from nearby habitat (Nakano et al. 1999). Overall, the limited information available for this species indicates that M. *lohena* is an opportunistic forager and its diet

may vary considerably across space and time. Information on *M. lohena* diet, and how food resources may affect shrimp abundance, is lacking and would be an important avenue for future research.

Our results add to the growing body of evidence showing that invasive fish are a primary factor limiting the distribution and abundance of shrimp in anchialine pools in Hawai'i (Capps et al. 2009, Carey et al. 2011, Havird et al. 2013, Marrack et al. 2015). We found shrimp density to be 4.2 times higher in pools without fish than in pools with fish. This ratio would have been even greater except that one pool at South Harbor (Figure 2) that contained poeciliids supported 41.3 shrimps/ m<sup>2</sup>, a density similar to three nearby pools that lacked fish (mean =  $35.3 \text{ shrimps/m}^2$ ), and nearly 4 times higher than the next highest pool containing both fish and M. lohena  $(11.5 \text{ shrimps/m}^2)$ . We did not measure fish abundance within the pools, and fish density may have been an important variable.

The relative importance of mechanisms by which fish may affect shrimp is unclear. Direct evidence of fish predation on shrimp in anchialine pools is lacking but studies have shown that G. affinis prey on small-sized H. *rubra* in a laboratory setting (Capps et al. 2009), and this shrimp reduces daytime activity in the presence of G. affinis (Capps et al. 2009, Carey et al. 2011). Due to its larger body size, and naturally being most active at night (Sakihara 2012), M. lobena may be less affected by predation from small fish like G. affinis and P. reticulata than H. rubra. The change in *M. lohena* temporal activity to avoid diurnal fish predators may help explain why our nighttime surveys detected M. lohena in considerably more pools that contained fish than did Marrack and Beavers (2011). Although adult *M. lohena* may be too large to be preved on by poeciliids, immature shrimp may be vulnerable to predation by these fish.

Competition for food resources between invasive fish and shrimp may also limit M. *lobena* densities. Diets of poeciliids and O. *mossambicus* are poorly documented in Hawaiian anchialine pools, but they are generally considered to be omnivorous, feeding on

benthic algae and detritus, as well as small invertebrates (De Silva et al. 1984, Capps et al. 2009, Zandoná et al. 2011). Indirect evidence of broad diet overlap between these fish and *M. lohena* was suggested by Seidel et al. (2016) based on not finding differences in  $\delta$  <sup>15</sup>N isotope mean values among these species. It is unclear if competition with fish for food is strong enough to affect shrimp abundance and this potential factor warrants further investigation.

Finally, the relatively large biomass of O. mossambicus found in many anchialine pools often results in considerable amounts of organic material accumulating on the bottoms of the pools. These soft sediments may be up to 23 cm thick (National Park Service Inventory and Monitoring Program, unpublished data, 2023) and often bury loose rocks and occlude the interstitial spaces in the lava that line the pools, eliminating places for shrimp to hide and reducing recruitment of shrimp into the pools. No M. lohena were observed in the four pools at Kaloko-Honokohau that contained O. mossambicus although it is not known if this is a result of predation or sedimentation.

Substrate age contributed little to the model, but its influence on M. lohena abundance may have been obscured by H. rubra and invasive fish. Metabetaeus lohena density in pools without fish did not support our hypothesis of increasing density with increasing substrate age. The highest density of *M. lohena* in pools without fish was found in the oldest substrate (5,000–10,000 years), as predicted, but the lowest density was found in the moderately aged substrate (3,000-5,000 years). It is possible that substrate structure, rather than age *per se*, had a greater influence on *M. lohena* densities within the moderately aged flow. Many of the pools that occur in this substrate were formed in an 'a'ā flow that overlies a slightly older pahoehoe flow (Richmond et al. 2008). Pools within this 'a'ā flow are generally devoid of both emergent and peripheral vegetation, resulting in little accumulation of organic material and relatively low food biomass. Metabetaeus *lohena* density was low in the 'a'ā flow despite many of the pools dewatering at low tide,

being generally distant from fishponds, and therefore lacking invasive fish. While *M. lohena* were found in many of the 'a'ā pools, they occurred at densities lower than in similarly aged pools of pahoehoe. For example, the five pools with the highest density of *M. lohena* (mean =  $31.1 \pm 13.7$  shrimps/m<sup>2</sup>) were found in pahoehoe; however, we did not document the lava type for all pools so we cannot quantify this observation across the park. The influence of lava type on *M. lohena* density warrants further study.

Our results did not support our hypothesis that M. lohena density would decrease with increasing distance from the coast, or to the nearest large body of water. Post hoc examination of these results also showed that M. lohena density in pools <100 m from the coast was similar to pools >100 m from the coast  $(7.48 \pm 12.4)$  and  $6.86 \pm 12.9$ shrimps/m<sup>2</sup>, respectively), and well within the confidence intervals describing the overall relationship. However, the  $R^2$  value characterizing the regression line that included the two fishponds in the analysis (nearest large body of water) was 13.4 times greater than for the regression line associated only with the coast, suggesting that the two fishponds may have some influence on shrimp density. Regardless, any such influence appears to be minor, and fails to provide evidence that distance from large body of water significantly affects M. lohena density.

As anticipated, we found salinity decreased significantly with distance from the coast, and from the nearest large body of water. However, the relationship only explained about 26% of the variation in both cases, indicating that factors other than distance per se influences salinity in the pools. But in general, this result is consistent with findings from the multivariate analysis suggesting that mechanisms other than salinity are the most important factors influencing M. lohena density. Pool salinity is determined by interactions between seawater and freshwater and is heavily influenced by substrate structure (e.g., fractures, lava tubes, dikes) and the topography of the land (Oki et al. 1999, Marrack 2015). Subterranean water movement in this area is surely complex, and seawater rarely moves linearly inland from the coast (or fishpond) as indicated by dye tracer and within-pool tidal fluctuation studies (K. Annandale, Kaloko-Honokōhau NHP, oral communication, 2023).

#### CONCLUSIONS

Kaloko-Honokohau provides important habitat for M. lohena, and likely supports a large proportion of the total population of this species on the western and southern coasts of the Island of Hawai'i. These results underscore the importance of Kaloko-Honokohau for this species as the largest concentration of anchialine pools on the island is found along these coasts (Marrack et al. 2015). The removal of invasive fish from the 32 anchialine pools included in our analysis is likely to have a strong, positive effect on the distribution and abundance of *M. lohena* in the park, and would be expected to increase overall abundances by about 21%. Halocaridina rubra is also likely to benefit from fish removal, further enhancing M. lohena population densities. While removing invasive fish is clearly important, minimizing effects from other threatening factors, such as invasive B. maritima that chokes out pools, water pollution, and drawdown of groundwater, may also be important to maintaining the M. lohena population. Impacts from groundwater pollution on anchialine pool water quality are poorly understood, but recent research has identified spatial relationships between upslope sewage sources and nitrogen in H. rubra tissues along the West Hawai'i coastal corridor (Marrack and Beavers 2023). Bottom-up effects of this anthropogenic input warrants further investigation. Sea level rise is projected to affect anchialine pools along the Kona coast, including at Kaloko-Honokōhau (Marrack 2015, 2016). While some anchialine pools are projected to be inundated permanently, or frequently during high tides and storm surges, other pools are expected to form in areas currently too high in elevation to form pools. If new pools do develop, preventing the establishment of invasive fish may help ensure that the habitat will remain viable for shrimp.

#### SUPPLEMENTARY DATA

Data and metadata associated with this paper are available at https://doi.org/10.5066/ P95N4HX1 (Peck 2024). Survey data from Marrack et al. (2015) were kindly shared by Lisa Marrack (University of Hawai'i at Hilo); these data were not publicly available.

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