A survey of fishes associated with Hawaiian deep-water *Halimeda kanaloana* (Bryopsidales: Halimedaceae) and *Avrainvillea* sp. (Bryopsidales: Udoteaceae) meadows

Ross C Langston Corresp., [1], **Heather L Spalding** [2]

[1] Department of Natural Sciences, University of Hawaii- Windward Community College, Kaneohe, Hawaii, United States

[2] Department of Botany, University of Hawaii at Manoa, Honolulu, Hawaii, United States

Corresponding Author: Ross C Langston
Email address: langston@hawaii.edu

The invasive macroalgal species *Avrainvillea* sp. and native species *Halimeda kanaloana* form expansive meadows that extend to depths of 80 m or more in the waters off of O'ahu and Maui, respectively. Despite their wide depth distribution, comparatively little is known about the biota associated with these macroalgal species. Our primary goals were to provide baseline information on the fish fauna associated with these deep-water macroalgal meadows and to compare the abundance and diversity of fishes between the meadow interior and sandy perimeters. Because both species form structurally complex three-dimensional canopies, we hypothesized that they would support a greater abundance and diversity of fishes when compared to surrounding sandy areas. We surveyed the fish fauna associated with these meadows using visual surveys and collections made with clove-oil anesthetic. Using these techniques, we recorded a total of 49 species from 25 families for *H. kanaloana* meadows and surrounding sandy areas, and 28 species from 19 families for *Avrainvillea* sp. habitats. Percent endemism was 28.6% and 10.7%, respectively. Wrasses (Family Labridae) were the most speciose taxon in both habitats (11 and six species, respectively), followed by gobies for *H. kanaloana* (six species). The wrasse *Oxycheilinus bimaculatus* and cardinalfish *Apogonichthys perdix* were the most frequently-occurring species within the *H. kanaloana* and *Avrainvillea* canopies, respectively. Obligate herbivores and food-fish species were rare in both habitats. Surprisingly, the density and abundance of small epibenthic fishes were greater in open sand than in the meadow canopy. In addition, species richness was also higher in open sand for *Avrainvillea* sp. We hypothesize that the dense holdfasts and rhizoids present within the meadow canopy may impede benthic-dwelling or bioturbator species, which accounted for 86% and 57% of individuals collected in sand adjacent to *H. kanaloana* and *Avrainvillea* sp. habitats, respectively. Of the 65 unique species recorded in this study, 16 (25%) were detected in clove oil stations alone, illustrating the utility of clove-oil

anesthetic in assessing the diversity and abundance of small-bodied epibenthic fishes.

A Survey of Fishes Associated with Hawaiian Deep-water *Halimeda kanaloana* (Bryopsidales: Halimedaceae) and *Avrainvillea* sp. (Bryopsidales: Udoteaceae) Meadows

Ross C. Langston[1], Heather L. Spalding[2]

[1]Department of Natural Sciences, University of Hawai‘i Windward Community College, 45-720 Keaahala Rd., Kāne‘ohe, HI 96744

[2]Department of Botany, University of Hawai‘i at Mānoa, 3190 Maile Way, Room 101, Honolulu, HI 96822

Corresponding Author:

Ross Langston[1]

45-720 Keaahala Rd, Kāne‘ohe, HI, 96744

Email address: langston@hawaii.edu

ABSTRACT

The invasive macroalgal species *Avrainvillea* sp. and native species *Halimeda kanaloana* form expansive meadows that extend to depths of 80 m or more in the waters off of O‘ahu and Maui, respectively. Despite their wide depth distribution, comparatively little is known about the biota associated with these macroalgal species. Our primary goals were to provide baseline information on the fish fauna associated with these deep-water macroalgal meadows and to compare the abundance and diversity of fishes between the meadow interior and sandy perimeters. Because both species form structurally complex three-dimensional canopies, we hypothesized that they would support a greater abundance and diversity of fishes when compared to surrounding sandy areas. We surveyed the fish fauna associated with these meadows using visual surveys and collections made with clove-oil anesthetic. Using these techniques, we recorded a total of 49 species from 25 families for *H. kanaloana* meadows and surrounding sandy areas, and 28 species from 19 families for *Avrainvillea* sp. habitats. Percent endemism was 28.6% and 10.7%, respectively. Wrasses (Family Labridae) were the most speciose taxon in both habitats (11 and six species, respectively), followed by gobies for *H. kanaloana* (six species). The wrasse *Oxycheilinus bimaculatus* and cardinalfish *Apogonichthys perdix* were the most frequently-occurring species within the *H. kanaloana* and *Avrainvillea* canopies, respectively. Obligate herbivores and food-fish species were rare in both habitats. Surprisingly, the density and abundance of small epibenthic fishes were greater in open sand than in the meadow canopy. In addition, species richness was also higher in open sand for *Avrainvillea* sp. We hypothesize that the dense holdfasts and rhizoids present within the meadow canopy may impede benthic-dwelling or bioturbator species, which accounted for 86% and 57% of individuals collected in sand adjacent to *H. kanaloana* and *Avrainvillea* sp. habitats, respectively.

Of the 65 unique species recorded in this study, 16 (25%) were detected in clove oil stations alone, illustrating the utility of clove-oil anesthetic in assessing the diversity and abundance of small-bodied epibenthic fishes.

INTRODUCTION

Macroalgal meadows constitute important habitats for reef- and nearshore fish species. Many are important grazing areas for herbivorous fishes (Lobel and Ogden 1981) and may also serve as spawning sites for recreationally important food fishes such as parrotfish and wrasses (Colin and Bell 1991). Macroalgae may also serve a key role in ontogenetic habitat shifts in post-settlement fish (Eggleston 1995, Dahlgren and Eggleston 2000). Relative to surrounding habitats, which are often sandy and of low-relief, macroalgal meadows constitute highly-complex and rugose habitats which may afford protection to juvenile and small-bodied reef fish species alike.

Until recently, most detailed studies of reef fish diversity have been limited to 30 m or less (e.g., Randall 1998, Greenfield 2003), which is the generally accepted limit for conventional SCUBA diving. However, with the recent advent of Closed Circuit Rebreathers (CCR) and mixed-gas diving technology, properly-trained researchers are now able to work at depths of 100 m or more (e.g., Pyle 2000, Lesser et al. 2009, Khang et al. 2010, Kane et al. 2014, Kosaki et al., 2016 and Simon et al. 2016). Recent work has focused on the mesophotic zone, which extends from 30-150 m (Henderstein 2010). Much of this work has focused on coral reef habitats and their associated fauna. Few studies have investigated the fauna of mesophotic macroalgae, despite the fact that several meadow-forming species occur at depths of 50 m or more in tropical and subtropical waters (Huisman et al. 2007, Spalding 2012, Pyle et al. 2016).

In this paper, we describe the fish fauna associated with two deep-water macroalgal species, *Avrainvillea* sp. and *Halimeda kanaloana*, from Hawaiian waters. *Avrainvillea* sp. and *H. kanaloana* are siphonous green macroalgae which form predominantly monospecific meadows over large areas of sandy substrate from shallow (1 m) to deep (>80 m) waters in the Main Hawaiian Islands (Spalding 2012). *Halimeda kanaloana* is a calcified alga native to Hawai‘i with multiple branched axes up to 30 cm in height (Verbruggen et al. 2006). *Avrainvillea* sp., an invasive species that was previously misidentified as *A. amadelpha* (Wade and Sherwood 2015), forms dense, mat-like beds with bladed canopies approximately 10 cm in height (Spalding 2012). *Avrainvillea* sp. first appeared off Kahe Point, O‘ahu in 1981, and subsequently spread to Maunalua Bay, O‘ahu (Brostoff 1989), where it outcompeted native algae and seagrasses (Peyton 2009, Abbott and Huisman 2004). Both species have been reported to support a greater diversity of epibenthic or infaunal invertebrates when compared to surrounding sandy habitats (Fukunaga 2008; Magalhaes and Bailey-Brock 2014); however, little is currently known about the role these assemblages may play in the creation/loss of unique habitat for fishes. Because *Avrainvillea* sp. and *H. kanaloana* occupy similar habitats in Hawai‘i (sandy substrate in moderate to low wave environments), they offer an opportunity to determine the effects of canopy type on the composition of the associated fish fauna.

Since little information is currently available for these habitats, our primary goal was to provide baseline information on the fish fauna associated these meadows. As part of this goal, we sought to document the most common and abundant species in both habitats. We also sought to identify any commercially- or recreationally important fish species so that resource managers can determine if these meadows merit additional study or protection. Based on surveys from shallow-water meadows (e.g., Lobel and Ogden 1981; Francini-Filho et al., 2010), we

hypothesized that deepwater *H. kanaloana* and *Avrainvillea sp.* meadows might be important feeding areas for herbivorous species such as surgeonfishes or parrotfishes, many of which are important food-fish species in Hawai‘i. In addition, we also attempted to calculate the level of endemism in both macroalgal habitats. Given that deep reefs in the Northwestern Hawaiian Islands (NWHI) support a greater number of endemic species than their shallow-water counterparts (Kane et al. 2014), we hypothesized that deep water macroalgal meadows might likewise support a greater proportion of endemic species than shallow habitats in the Main Hawaiian Islands (MHI).

Our final goal was to compare the abundance and diversity of small-bodied epibenthic fishes between open sand and meadow canopy subhabitats. Because both macroalgal species form structurally complex three-dimensional canopies, we hypothesized that they would support a greater abundance and diversity of fishes when compared to surrounding sandy habitats, which are typically of low relief and complexity. This hypothesis is supported by the work of Chittaro (2004), who found that fish abundance and species richness in Tague Bay, St. Croix were positively correlated with *H. incrassata* habitats and negatively correlated with open sand and pavement. Likewise, Ornellas and Coutinho (1998) found that fish diversity in sublittoral areas of Cabo Frio Island (Brazil) was greater in *Sargassum furcatum* beds than in surrounding sandy habitats. Thus, it seems likely that *H. kanaloana* and *Avrainvillea* meadows should support a greater diversity and abundance of fishes than adjacent sandy areas.

MATERIALS AND METHODS

We utilized CCR technical diving to survey fish assemblages during a total of 20 dives (four in *Avrainvillea* sp. habitats and 16 in *H. kanaloana* habitats). *Avrainvillea* sp. habitats were surveyed at a single site off west O'ahu and *H. kanaloana* habitats were surveyed at three sites off of south and west Maui (Figure 1). All surveys were conducted between June 14th, 2005 and June 12th, 2006. Initial surveys consisted of visual censuses supplemented by collections made with pole spears. All other surveys were conducted using tandem visual surveys combined with collections using clove-oil anesthetic in order to better assess the numbers of small epibenthic fishes (Figure 2). For these collections, an anesthetic solution of 10% clove oil in 90% ethanol was aspirated from a squirt bottle beneath a 1.5 m weighted plastic tarp. The tarp was placed haphazardly over either sand or canopy. The solution was allowed to work for a period of 10 minutes, during which the diver conducted visual- and photographic surveys of larger-bodied fish species (see below). After the 10 minutes had elapsed, the divers removed the weighted tarp and used fine-mesh nets to collect the fishes, which were photographed and preserved in 10% formalin for subsequent identification. Because fishes caught in the clove oil stations were collected from a known area (1.5 m), we were able to compare the species richness and abundance (average number of species and individuals per 1.5 m collection) between sand and canopy sub-habitats.

<<Figure 1 near here>>

Conventional transect-based visual surveys were impractical given the limited bottom-time, mobility, and task-load of diver teams. Instead, large-bodied fishes were surveyed using a stationary point count (SPC) in which a diver recorded all fishes that resided or passed through a

159 visually estimated 10 m cylinder centered on the diver's location (the weighted tarp). The survey
160 time for each SPC was typically 10 minutes. Additional species were collected or surveyed via
161 opportunistic spearfishing and photographs. All fish collections were performed in accordance
162 with a University of Hawaii Institutional Animal Care and Use Protocol (# 06-058). Permission
163 to use clove oil anesthetic was granted by the Hawaii Department of Land and Natural Resources
164 (Permit #s PRO 2006-28 and PRO 2007-47).

165 <<Figure 2 near here>>

166 *Data Analysis*

167 All specimens were identified to species or lowest-possible taxon and classified as endemic
168 (restricted to the Hawaiian Islands, Midway, and Johnston Atoll) or non-endemic using available
169 references (e.g., Randall 2007 and Mundy 2005). For both clove oil collections and visual
170 surveys, we recorded the abundance (N) of each species as well as the habitat (meadow-forming
171 species) and sub-habitat (canopy or sand & rubble) where each species was observed or
172 collected. We used this information to calculate the species richness (S) and a Shannon-Wiener
173 diversity index (log e; H') for each sub-habitat. We calculated percentage occurrence (%Occ) as
174 the proportion of collections made within each sub-habitat in which a species was recorded, and
175 percentage relative abundance (%RA) as the number of individuals of a species recorded within
176 a sub-habitat divided by the total number of individuals that were collected or observed in that
177 sub-habitat. We follow Randall (1996) in calculating the percent endemism by dividing the
178 number of endemic species by the total number of species present in a particular habitat. We also
179 used available references (Randall 1996, 2007) and personal observations to identify species that
180 reside-upon or feed within the sediment as benthic associates or bioturbators (B) in order to

181 determine if abundance of these species differed between sub-habitats. For clove oil collections,
182 we estimated the density (D) of fishes collected by dividing the number of individuals of each
183 species by the total area of the substrate that was sampled. We compared the median abundance
184 (N_x), density (D_x), and species richness (S_x) within each sub-habitat using the Mood Median
185 Test, as the resulting data did not meet the assumptions necessary to use parametric statistical
186 tests.

187 RESULTS

188 We conducted a total of 14 visual surveys and 51 tandem surveys (visual surveys + collections
189 using clove oil anesthetic) in *Avrainvillea* sp. and *H. kanaloana* habitats (Table 1).
190 *<<Table 1 near here>>*
191 *Percent occurrence and relative abundance of fishes in* H. kanaloana *meadows*
192 A total of 49 species from 25 families were recorded from *H. kanaloana* meadows and
193 surrounding sandy areas (Table 2). Overall species richness and diversity were nominally
194 greater in canopy (S = 31 species, H' = 2.523) than in open sand (S= 29 species, H'= 2.064).
195 Wrasses (Family Labridae) were the most speciose taxon within both sub-habitats followed by
196 Gobies. Wrasses were also the most abundant taxon within meadow canopy, accounting for
197 54.8% of individuals collected or observed. In contrast, gobies comprised only 15.9% of
198 individuals surveyed in the *H. kanaloana* canopy. The most abundant and frequently-occurring
199 species within meadow canopy was the Two-spot wrasse, *Oxycheilinus bimaculatus*. Other
200 commonly-occurring species included the goby, *Gnatholepis* spp., and the wrasses
201 *Pseudojuloides cerasinus* and *Cymolutes praetextatus*. The latter species was previously
202 unknown east of the Marshall Islands, and thus constitutes a new record for Hawai'i (see Randall
203 et al. 2006).

In contrast to *H. kanaloana* canopy, adjacent sandy areas were numerically dominated by goby species (Total %RA = 56.9%), whereas wrasses only accounted for 4.9% of individuals surveyed within this sub-habitat. The three most commonly-occurring species were gobies: *Gnatholepis* spp., *Opua nephodes*, and *Psilogobius mainlandi*.

<<*Table 2 near here*>>

Percent occurrence and relative abundance of fishes in Avrainvillea sp. *meadows*

A total of 28 species from 19 families were recorded from *Avrainvillea* meadows and adjacent sandy habitats (Table 3). Overall species richness and diversity were nominally greater in open sand (S = 19 species, H' = 2.74) than in meadow canopy (S= 13 species, H'= 1.871). Wrasses were the most speciose and abundant taxon in both sub-habitats. All other taxa were represented by two species or fewer.

The most commonly occurring species within meadow canopy was the cardinalfish *Apogonichthys perdix*. This species was recorded only from clove oil collections and was never observed in visual surveys. Other common species found in *Avrainvillea* sp. canopy include the wrasses *O. bimaculatus* and *Pseudocheilinus evanidus*. The two most abundant species were the unicorn fish *Naso caesius* and Hawaiian Flame Wrasse, *Cirrhilabrus jordani*, however, these species were recorded from a single collection each.

Only three collections were made in sandy habitats adjacent to *Avrainvillea* meadows. Overall, wrasses were the most abundant taxon in open sand (%RA=23.3%). The most frequently-occurring species was the wrasse *O. bimaculatus*, followed by the sandperch *Parapercis schauinslandii*, which was also the most abundant species.

<<Table 3 near here>>

227 *Abundance, species richness, and diversity of epi-benthic fishes from clove oil anesthetic*
228 *collections*

229 A total of 105 individuals from 19 species were collected from *H. kanaloana* habitats
230 using clove oil anesthetic (Table 4). The eyebar goby, *Gnatholepis anjerensis*and wrasse *O.*
231 *bimaculatus*, were the most abundant and frequently-collected species in *H. kanaloana* canopy.
232 In contrast, the cloud goby, *Opua nephodes*, and Hawaiian shrimp goby *Psilogobius mainlandi*
233 were the most abundant fishes in in open sand, and were rarely collected from meadow canopy.

234 The median abundance and density of fishes was significantly higher in open sand (N_x =
235 4.00 individuals/collection, D_x = 2.67 fish per m^2) when compared to the meadow canopy (N_x
236 = 1.00, D_x = 0.67; Chi-Square = 13.41, DF = 1, P = 0.000 for both tests). Total species richness
237 was also nominally higher in open sand (15 vs. 10 species); however, median species richness
238 did not differ significantly between sub-habitat types (Chi-Square = 0.63, DF = 1, P = 0.426).
239 We calculated Shannon Weiner Diversity Index values of 2.2474 and 1.5013, respectively for
240 open sand and canopy.

241 *<<Table 4 near here>>*

242 A total 16 species and 42 individuals were collected from *Avrainvillea* sp. sub-habitats
243 using clove oil anesthetic (Table 5). The cardinalfish *Apogonichthys perdix* was the most
244 abundant species collected from *Avrainvillea* canopy whereas the sandperch *Parapercis*
245 *schauinslandii* was most abundant species collected in open sand.

246 As with collections made in *H. kanaloana* meadows, fishes from *Avrainvillea* collections
247 were more abundant and densely-distributed within open sand (N_x = 7.00 individuals/collection,
248 D_x = 4.67 fish per m^2) when compared to meadow canopy (N_x = 2.50, D_x = 1.67; Chi-Square
249 = 11.00, DF = 1, P = 0.001 for both tests). Median Species Richness was also significantly

250 greater in open sand (S_x = 6.00 species/collection) when compared to meadow canopy (S_x =
251 2.00; Chi-Square = 11.00, DF = 1, P = 0.001). The Shannon Weiner Diversity Index was
252 likewise higher in open sand (H' = 2.3667) vs. meadow canopy (H' = 1.4383).

253 *<<Table 5 near here>>*

254 **Discussion**

255 Deep-water *Avrainvillea* sp. and *H. kanaloana* meadows form complex three-dimensional
256 habitats in an otherwise two-dimensional sandy environments. This structure provides habitat
257 and shelter for numerous fish species. Of the two habitat types, *H. kanaloana* was most diverse
258 supporting a total of 49 species from 25 fish families. In contrast, *Avrainvillea sp.* meadows
259 contained 28 species from 19 families, though it is likely that the lower numbers for this species
260 may be due to the lower sample size for this species. Within-canopy diversity (H') was
261 nominally greater for *H. kanaloana* (2.52) than *Avrainvillea* sp. (1.87). In comparison,
262 Friedlander and Parrish (1998) estimated that fish diversity on a shallow Kauai reef ranged
263 between 1.72 to 2.54. Therefore, it would appear that the diversity of these deep-water
264 macroalgal meadows is similar to that of shallow Hawaii reefs.

265 Wrasses (Family Labridae) were the most speciose taxon in both habitats (11 and six
266 species, respectively), followed by gobies for *H. kanaloana* (six species). The wrasse
267 *Oxycheilinus bimaculatus* and cardinalfish *Apogonichthys perdix* were the most frequently-
268 occurring species within the *H. kanaloana* and *Avrainvillea* canopies, respectively. These
269 species were considerably less common and abundant in open sand, indicating as strong habitat
270 preference for the meadow canopy. Other common species that showed strong associations with
271 meadow canopy include the toby, *Canthigaster jactator* (*H. kanaloana*) and the wrasses
272 *Cymolutes lecluse* and *C. praetextatus* (*H. kanaloana*) and *Pseudojuloides cerasinus* (both

273 species). With the exception of *A. perdix*, which is nocturnal, we observed each of these species
274 actively foraging within the meadow canopy on numerous occasions. Thus, meadow canopy
275 appears to be an essential habitat for these species.
276 Most of the other common species were epibenthic sand-dwellers (e.g., gobies,
277 dragonettes, sandperch, and flatfishes). Many of these species also occur in sandy areas near
278 coral reefs (see Greenfield, 2003). In most cases, these species were actually more abundant in
279 open sand rather than canopy (Tables 2 & 3), suggesting that their association with the meadows
280 is incidental rather than a result of any inherent habitat preference.

281 *Percent Endemism*

282 We estimate the percent endemism for fishes living in *H. kanaloana* and *Avrainvillea* habitats
283 (including adjacent sandy areas) to be 28.6% and 10.7%, respectively. Given that approximately
284 25% of Hawaii's fish species are considered to be endemic (Randall 2007), *H. kanaloana*
285 meadows harbor a slightly greater proportion of endemic species than would be expected by
286 chance. In comparison, approximately 46% of fishes surveyed within mesophotic depths in the
287 NWHI are endemic (Kane et al., 2014), and endemism may reach 100% in some areas (Kosaki et
288 al., 2016). Thus, compared to mesophotic habitats in the NWHI, these macroalgal meadows
289 have proportionally fewer endemic species. We speculate that the nominally higher endemism
290 documented for *H. kanaloana* habitats could be a result of coevolution; *H. kanaloana* is native to
291 Hawai'i, with the largest meadows reported from the Maui-Nui complex (Spalding 2012). It is
292 possible that some of these endemic fish species may have evolved a commensal relationship
293 with the alga. Although only five of the 14 endemic species regularly reside in *H. kanaloana*
294 meadows, it is possible that some of the sand-dwelling endemics may occasionally dart into the
295 canopy to avoid predators or may opportunistically exploit the new habitat created when

296 blowouts (barren areas) are formed by the scour of winter swells. In contrast, *Avrainvillea sp.* is
297 an invasive species which was first reported off Kahe Point, O'ahu in 1981 (Brostoff 1989).
298 This species supports only three endemic species, with two (*C. jordani* and *Bodianus*
299 *albotaeniatus*) recorded from canopy and one (*Aseraggodes borehami*) recorded from open sand.
300 Given its supposed recent arrival, it is possible that endemic fish species have had less time to
301 adapt to this unique habitat.
302 *Abundance of Herbivores and Food fish*
303 Contrary to our hypothesis that *H. kanaloana* and *Avrainvillea sp.* meadows may serve as
304 foraging grounds for herbivorous fish species, we found that obligate herbivores were quite rare
305 in both meadow types and were represented by only two species: the angelfish *Centropyge*
306 *fisheri* (*H. kanaloana)* and the surgeonfish *Acanthurus blochii* (*Avrainvillea* sp.). Neither
307 species was common or abundant, nor do they feed on macroalgae. *Centropyge fisheri* is an
308 obligate herbivore (Thresher and Collin 1986) that likely feeds on turf algae, whereas *A. blochii*
309 typically feeds primarily on benthic algae on reefs or algal films covering sand (Randall 2005).
310 Surprisingly, parrotfishes (Family Scaridae) and Blennies (Family Bleniidae) were completely
311 absent from the deepwater meadows, despite the fact that we have observed them in shallow-
312 water (<1 m) *Avrainvillea sp.* meadows (R. Langston, Pers. Obs). Six species (*Rhinecanthus*
313 *aculeatus, Aluterus scriptus*, *Ostracion meleagris*, *Arothron hispidus, Canthigaster jactator*, and
314 *C. coronata*) from *H. kanaloana* meadows and two from *Avrainvillea* sp. meadows (*A. hispidus*
315 and *C. coronata*) are reported to be omnivorous, and occasionally consume algae. However,
316 given their small size and limited abundance, it is unlikely that they consume significant amounts
317 of macroalgal biomass. These results corroborate the work of Spalding (2012) who found little
318 evidence of feeding scars on plants collected from deep-water *H. kanaloana* meadows. The

absence of herbivores in these habitats may, in part, be due to their extreme depths. Several studies (e.g., Brokovich et al., 2010, Fukunaga et al., 2016, Larkum et al., 1967 and Thresher and Colin, 1986) report that herbivorous fish species are rare below 30 m. In addition, the lack of herbivory may be due to the low digestibility of the algae; both *Avrainvillea* sp. and *Halimeda sp.* contain numerous compounds which may deter herbivory (Meyer et al. 1994; Hay et al. 1990; Paul and van Alstyne 1992). In addition, the partial calcification of *H. kanaloana* may serve as an added impediment to herbivory (Schupp and Paul 1994).

Commercially- or recreationally-important food-fish species were likewise rare in surveys of either meadow habitat. Three species each were recorded from *H. kanaloana* (*Caranx melampygus*, *Aprion virescens*, and *Mulloidichthys* sp.) and *Avrainvillea* sp. habitats (*Caranx lugubris*, *Parupeneus multifasciatus,* and *A. virescens*), however, each of these records was based on a single individual (Tables 2 and 3). In contrast, our surveys do indicate that deep-water *Avrainvillea* sp. meadows may be an important habitat for the flame wrasse, *C. jordani*, which is important in the Hawai‘i aquarium fish trade. According to Walsh et al. (2003), commercial fishers in the state reported catches of 13,919 *C. jordani* between the years1976 and 2003. They estimated total wholesale value for the catch to be $133,116. Based on our review of two online fish sellers (liveaquaria.com and petsolutions.com- July 2016), *C. jordani* retails for $130 (juvenile female) to $300 (adult male) each. Assuming the extraordinary price of *C. jordani* is a result of high demand among aquarium enthusiasts, it is possible that aquarium fishers may eventually target deep-water *Avrainvillea* sp. meadows as a potential source for this species.

Abundance, species richness, and diversity of epi-benthic fishes from clove oil anesthetic collections

Our clove oil surveys detected significantly higher abundances and densities of epibenthic fishes in open sand when compared to meadow canopy for both *H. kanaloana* and *Avrainvillea* sp. Median species richness was also significantly higher in sand vs. meadow canopy for *Avrainvillea* sp. , and diversity (H') was nominally higher in open sand for both species. These results are surprising given that several studies (e.g., Chittaro 2004; Omena and Creed 2004; and Ornellas and Coutinho 1998) have documented that diversity and abundance of fishes and invertebrates are usually highest within meadow canopy. Moreover, two recent surveys of the invertebrate fauna of *H. kanaloana* and *Avrainvillea* sp. meadows further support this hypothesis. Magalhaes and Bailey-Brock (2014) found that infaunal polychaetes were considerably more abundant and diverse in shallow *Avrainvillea* meadows, when compared to adjacent sandy areas. Fukunaga (2008) likewise found that polychaetes were more abundant and diverse within *H. kanaloana* canopy. She also reported that epibenthic invertebrates were more diverse and speciose within meadows, but that abundance did not differ significantly between the two sub-habitats.

It is possible that the greater abundance of fishes in open sand may, in part, reflect a sampling bias. Fish inhabiting dense canopy are more likely to be overlooked by visual surveys when compared to individuals occurring on bare sand. Similarly, fish anesthetized in clove oil stations are more easily recovered in bare sediment than in dense canopy (this is particularly true for *Avrainvillea sp.* meadows given their dense, bladed morphology). Alternatively, it is possible that the greater abundance of some species on open sand may be related to differences in habitat preference or sediment composition between vegetated and non-vegetated areas. For

example, within *Halimeda kanaloana* meadows, the Hawaiian shrimp goby, *P. mainlandi* was collected almost exclusively on bare sediment. This species lives in burrows constructed by the snapping shrimps, *Alpheus rapax* and *A. rapicida* (Randall, 2007). In a concomitant study of the epibenthic invertebrates from the same *H. kanaloana* meadows, Fukunaga (2008) recorded a total of 131 *A. rapax* in sand patches and only three individuals within the meadow canopy. Given this, it is not surprising that *P. mainlandi* was also rare within meadow canopy; without the presence of its invertebrate symbiont, the goby would have a difficult time finding shelter. We believe that the dearth of *A. rapax* burrows within meadow canopy may be related to sub-surface algal growth. Each *H. kanaloana* plant has a large, bulbous holdfast over 8 cm in length that penetrates deeply into the substrate, forming a network of stringy rhizoids that extend out into the surrounding sediment (Verbruggen et al. 2006). In addition, most *H. kanaloana* meadows contain several hundred plants per m^{-2} (Spalding 2012), thus forming a dense concentration of rhizoids and holdfasts in the sediment that may be difficult for burrow-forming species, such as *A. rapax*, to penetrate. In contrast, *Avrainvillea* has a dense and spongy holdfast that forms a terraced, penetrating mat over the sediment (Huisman et al. 2007). These mats sequester fine sediments under their holdfast, forming anoxic mounds of sediment (Littler et al. 2005). It is possible that these structures may likewise negatively impact benthic-dwelling and bioturbator speces. Other published studies support this hypothesis. For example, Milazzo et al. (2004) found that numbers of Bucchich's goby, *Gobius bucchichi* increased significantly in plots where the algal biomass was experimentally reduced. This feeds primarily on benthic mollusks and prefers open sandy habitats (Fasola et al. 1997). Thus, it is not surprising that its abundance would increase when more suitable habitat was made available through the algal removal experiments. Neira et al. (2005) likewise documented a similar shift in the invertebrate

macrofauna for tidal flats invaded by a hybrid cordgrass. They found that the densities of macroinvertebrates were 75% lower in the vegetated flats, when compared to un-vegetated areas, and that species richness was also lower in the vegetated areas. Although we did not experimentally manipulate the algal biomass in this study, it does appear that benthic-dwelling and bioturbator species are numerically more abundant in open sand. Within *H. kanaloana* habitats (Table 4), these species accounted for 86% of individuals collected within open sand vs. 61% collected meadow canopy. A similar relationship is evident for *Avrainvillea* sp. collections (Table 5); 57% of individuals collected from open sand were from benthic-dwelling or bioturbator species, whereas only five percent of those collected from canopy were classified as such. Thus, we suggest that the presence of surface- and subsurface algal growths may negatively impact the abundance and diversity of small epi-benthic fishes by reducing the amount of favorable habitat and feeding areas utilized by these species.

Advantage of Clove Oil Collections

The use of clove oil anesthetic greatly enhanced our ability to estimate the fish diversity within *H. kanaloana* and *Avrainvillea* sp. meadows. Of the 65 unique species recorded in this study, 16 (25%) were detected only in clove oil stations alone. Thus, the use of clove oil anesthetic increased our overall estimate of species richness by 32.7%. It also enabled us to more accurately estimate the abundance and species richness of small-bodied fishes (gobies, scorpion fishes, cardinalfishes, dragonettes, and small wrasses), many of which are difficult to identify to species without the use of a dissecting scope. In some cases, species collected with clove oil but missed by visual surveys were also quite common. For instance, the cardinalfish *Apogonichthys perdix* was found to be the most frequently-occurring species in *Avrainvillea* sp. canopy (Table

3) though, due to its cryptic coloration and nocturnal nature, it was never observed in visual surveys. In a related study, Fukunaga (2008) measured the diversity and abundance of epibenthic invertebrates within *H. kanaloana* meadows using both visual surveys and clove-oil collections. She recorded 15 species of invertebrates in the visual surveys and 20 additional species in the clove-oil surveys. In this case, the use of clove oil anesthetic increased her ability to detect small epibenthic invertebrates by 133%. Together, these data highlight the utility of anesthetics (or ichthyocides) in estimating the diversity and abundance of small-bodied fishes and epibenthic invertebrates.

Acknowledgements

We are grateful to D. Pence, A. Fukunaga, S. Hau, K. Peyton, and C. Stobeneau for assistance with field surveys and logistical support. Small boat support was kindly provided by the Hawai‘i Department of Aquatic Resources, Department of Land and Natural Resources on Maui.

Literature Cited

Abbott IA, Huisman JM. 2004. *Marine green and brown algae of the Hawaiian Islands*. Honolulu, Hawaii: Bishop Museum Press.

Brokovich E, Ayalon I, Einbinder S, Segev N, Shaked Y, Genin A, Kark S, Kiflawi M. 2010. Grazing pressure on coral reefs decreases across a wide depth gradient in the Gulf of Aqaba, Red Sea. *Marine Ecology Progress Series* 399:69-80.

Brostoff WN. 1989. *Avrainvillea amadelpha* (Codiales, Chlorophyta) from O‘ahu, Hawai‘i. *Pacific Science* 43:166-69.

Chittaro PM. 2004. Fish-hanitat associations across multiple spatial scales. *Coral Reefs*. 23:235-244. DOI 10.1007/s00338-004-0376-z

Colin PL, Bell LJ. 1991. Aspects of the spawning of labrid and scarid fishes (Pisces: Labroidei) at Enewetak Atoll, Marshall Islands with notes on other families. *Environmental Biology of Fishes* 31:229-60.

Dahlgren CP, Eggleston DB. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81:2227-2240.

Eggleston DB. 1995. Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. *Marine Ecology Progress Series* 124:9-22.

Friedlander AM, Parrish JD. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *J. Exp. Mar. Biol. Ecol.* 224:1-30.

Fukunaga A. 2008. Invertebrate community associated with the macroalga *Halimeda kanaloana* meadow in Maui, Hawaii. *International Review Hydrobiology* 93(3):328-341.

Fukunaga A, Kosaki RK, Wagner D, Kane C. 2016. Structure of mesophotic reef fish assemblages in the Northwestern Hawaiian Islands. PLoS ONE 11(7): e0157861. Doi:10.1371/journal.pone.0157861.

Fasola M, Canova L, Foschi F, Novelli O, Bressan M. 1997. Resource use by a Mediterranean rocky slope fish assemblage. *Marine Ecology* 18(1):51-66.

Francini-Filho R, Ferreira C, Coni E, De Moura R, Kaufman, L. 2010. Foraging activity of roving herbivorous reef fish (Acanthuridae and Scaridae) in eastern Brazil: Influence of resource availability and interference competition. *J. Mar. Biol. Assoc. U.K.* 3:481-492. doi:10.1017/S0025315409991147

Greenfield DW. 2003. A survey of the small reef fishes of Kaneohe Bay, Oahu, Hawaiian Islands. *Pacific Science* 57(1):45-76.

476 Hay ME, Paul VJ, Renaud PE, Fenical W. 1990. Specialist herbivores reduce their
477 susceptibility to predation by feeding on the chemically defended seaweed *Avrainvillea*
478 *longicaulis*. *Limnol. Oceanogr*. 35(8):1734-1743.
479
480 Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, Zawada GG,
481 Appeldoorn R. 2010. Theme section on "Mesophotic coral ecosystems: characterization,
482 ecology, and management". *Coral Reefs* 29:247-51.
483
484 Huisman JM, Abbott IA, Smith CM. 2007. *Hawaiian reef plants*. Honolulu, Hawaii: University
485 of Hawaii Sea Grant College Program.
486
487 Kane C, Kosaki K, Wagner D. 2014. High levels of mesophotic reef fish endemism in the
488 Northwestern Hawaiian Islands. *Bulletin Marine Science* 90(2)693-703.
489
490 Kosaki RK, Pyle RL, Leonard JC, Hauk BB, Whitton RK, Wagner D. 2016. 100% endemism in
491 mesophotic reef fishes assemblages at Kure Atoll, Hawaiian Islands. *Mar. Biodiv*.DOI
492 10.1007/s12526-016-0510-5.
493
494 Khang SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L,
495 Toonen RJ. 2010. Community ecology of mesophotic coral reef ecosystems. *Coral Reefs*
496 29:255-275.
497
498 Larkum AWD, Drew EA, Crossett RN. 1967. The vertical distribution of attached
499 marine algae in Malta. *Journal Ecology* 55:361-71.
500
501 Lesser MP, Slattery M, Leichter JJ. 2009. Ecology of mesophotic coral reefs. *Journal*
502 *Experimental Marine Biology Ecology* 375:1-8.
503
504 Littler MM, Littler DS, Brooks BL. 2005. Extraordinary mound building *Avrainvillea*
505 (Chlorophyta): the largest tropical marine plants. *Coral Reefs* 24: 555-555.
506
507 Lobel PS, Ogden JC. 1981. Foraging by the herbivorous parrotfish *Sparisoma radians*.
508 *Marine Biology* 64:173-83.
509
510 Magalhaes WF, Bailey-Brock JH. 2014. Polychaete assemblages associated with the invasive
511 green alga *Avrainvillea amadelpha* and surrounding bare sediment patches in Hawaii. *Memoirs*
512 *Museum Victoria* 71:161-168.
513
514 Meyer KD, Paul VJ, Sanger HR, Nelson SG. 1994. Effects of seaweed extracts and
515 secondary metabolites on feeding by the herbivorous surgeonfish *Naso lituratus*. *Coral*
516 *Reefs* 13:105-12.
517
518 Milazzo M, Badalamenti F, Riggio S, Chemello R. 2004. Patterns of algal recovery and small-
519 scale effects of canopy removal as a result of human trampling on a Mediterranean rocky
520 shallow community. *Biological Conservation* 117:191-202.
521

522 Mundy BC. 2005. *Checklist of the fishes of the Hawaiian Archipelago*. Honolulu, Hawaii:
523 Bishop Museum Press.
524
525 Neira C, Levin LA, Grosholz ED. 2005. Benthic macrofaunal communities of three sites in San
526 Francisco Bay invaded by hybrid *Spartina*, with comparison to uninvaded habitats. *Marine*
527 *Ecology Progress Series* 292: 111–126.
528
529 Omena E, Creed JC. 2004. Polychaete fauna of seagrass beds (*Halodule wrightii* Ascherson)
530 along the coast of Rio de Janeiro (Southeast Brazil). *Marine Ecology* 25:273–288.
531
532 Ornellas AB, Coutinho R. 1998. Spatial and temporal patterns of distribution and abundance of
533 a tropical fish assemblage in a seasonal *Sargassum* bed, Cabo Frio Island, Brazil. *J. Fish. Biol*.
534 53:198-208. doi:10.1111/j.1095-8649.1998.tb01027.x
535
536 Paul VJ, van Alstyne KL. 1992. Activation of chemical defenses in the tropical green
537 algae *Halimeda* spp. *Journal Experimental Marine Biology Ecology* 160:191-203.
538
539 Peyton KA. 2009. Aquatic invasive species impacts in Hawaiian soft sediment habitats. Ph.D.
540 dissertation. University of Hawaii at Manoa.
541
542 Pyle RL. 2000. Assessing undiscovered fish biodiversity on deep coral reefs using advanced self-
543 contained diving technology. *Marine Technology Society Journal* 34:82-91.
544
545 Pyle RL, Boland R, Bollick H, Bowen BW, Bradley CJ, Kane C, Kosaki RK, Langson R,
546 Longenecker K, Montgomery AD, Parrish FA, Popp BN, Rooney J, Smith CM, Wagner D,
547 Spalding HL. 2016. A comprehensive investigation of mesophotic coral ecosystems in the
548 Hawaiian Archipelago. *PeerJ* 4: e2475. DOI: https://doi.org/10.7717/peerj.2475
549
550 Randall, JE. 1996. *Shore fishes of Hawaii*. Natural World Press.

551 Randall JE. 1998. Zoogeography of shore fishes in the Indo-Pacific region. *Zoological Studies*
552 *Taipei* 37:227-268.

553 Randall JE. 2005. *Reef and shore fishes of the South Pacific*. Honolulu, Hawaii: University of
554 Hawaii Press.

555 Randall JE. 2007. *Reef and shore fishes of the Hawaiian Islands*. Honolulu, Hawaii: Sea Grant
556 College Program.
557
558 Randall JE, Langston RC, Severns M. 2006. First record of the Labrid fish *Cymolutes*
559 *praetextatus* from the Hawaiian Islands. *Pacific Science* 60(4):549–553.
560
561 Schupp PJ, Paul VJ. 1994. Calcium carbonate and secondary metabolites in tropical seaweeds:
562 variable effects on herbivorous fishes. *Ecology* 75(4):1172-1185.
563
564 Simon T, Pinheiro HT, Moura RL, Carvalho-Filho A, Rocha LA, Martins AS, Mazzei E,
565 Francini-Filho RB, Amado-Filho GM, Joyeux JC. 2016. Mesophotic fishes of the Albrolhos

Shelf, the largest reef ecosystem in the South Atlantic. *Journal of Fish Biology* DOI: 10.1111/jfb12967.

Spalding HL. 2012. Ecology of mesophotic macroalgae and *Halimeda kanaloana* meadows in the Main Hawaiian Islands. Ph.D. Diss. University of Hawaii at Manoa.

Thresher RE, Colin PL. 1986. Trophic structure, diversity and abundance of fishes of the deep reef (30-300 m) at Enewetak, Marshall Islands. *Bull. Mar. Sci.* 38(1):253-272.

Verbruggen H, De Clerck O, N'Yeurt ADR, Spalding H, Vroom PS. 2006. Phylogeny and taxonomy of *Halimeda incrassata* , including descriptions of *H. kanaloana* and *H. heteromorpha* spp. nov. (Bryopsidales, Chlorophyta). *European Journal of Phycology* 41: 337-362

Wade RM, Tang Y, Sherwood AR. 2015. Morphological and molecular assessment of *Avrainvillea* (Ulvophyceae, Chlorophyta) and implications for invasive species management. p. 17 *In*: 50th Annual Meeting of the Phycological Society of America, 10-13 August 2015, Philadelphia, PA.

Walsh WA, Cotton SSP, Dierking J, Williams I. 2003. The commercial marine aquarium fishery in Hawaii 1976-2003. *In:* Status of Hawaii's Coastal Fisheries in the New Millennium Proceedings of the 2001 Fisheries Symposium American Fisheries Society, Hawai'i Chapter. 230 pp.

Figure 1

Map of the Main Hawaiian Islands showing the locations of the four survey sites.

Avrainvillea sp. meadows were surveyed off west Oahu. *Halimeda kanaloana* meadows were surveyed off south and west Maui.

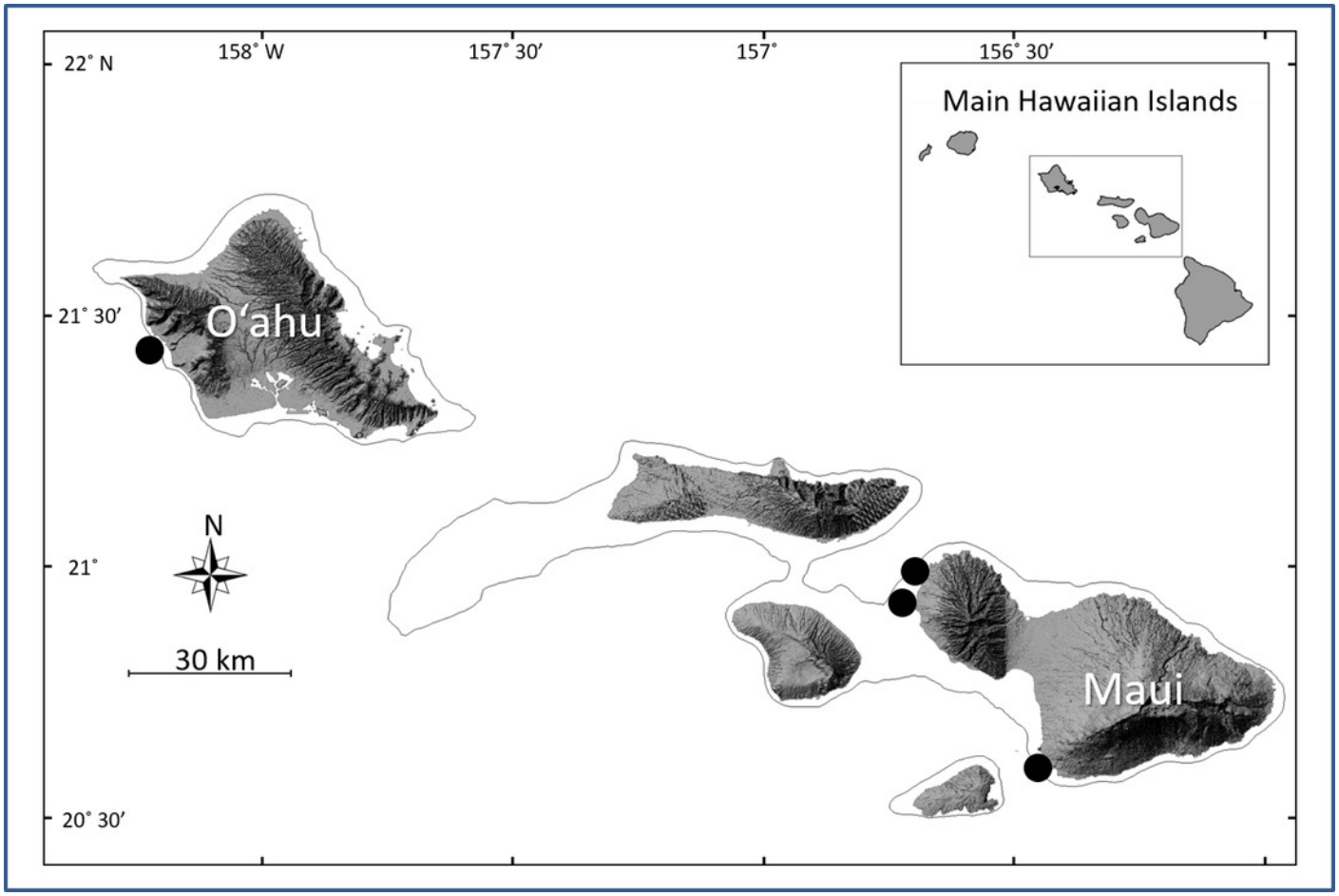

Figure 2

Survey techniques used in *Halimeda kanaloana* (A-D) and *Avrainvillea* sp. meadows.

Large-bodied species were surveyed visually (A) or photographically (B). Unidentified species were collected with small spears (C). Small-bodied epibenthic fishes were surveyed by injecting a clove-oil solution under a 1.5 m weighted tarp (D). The anesthetized fishes were collected with fine-mesh nets and preserved for subsequent identification. Diver conducting a visual survey of *Avrainvillea* sp. meadow (E). Note the denser canopy.

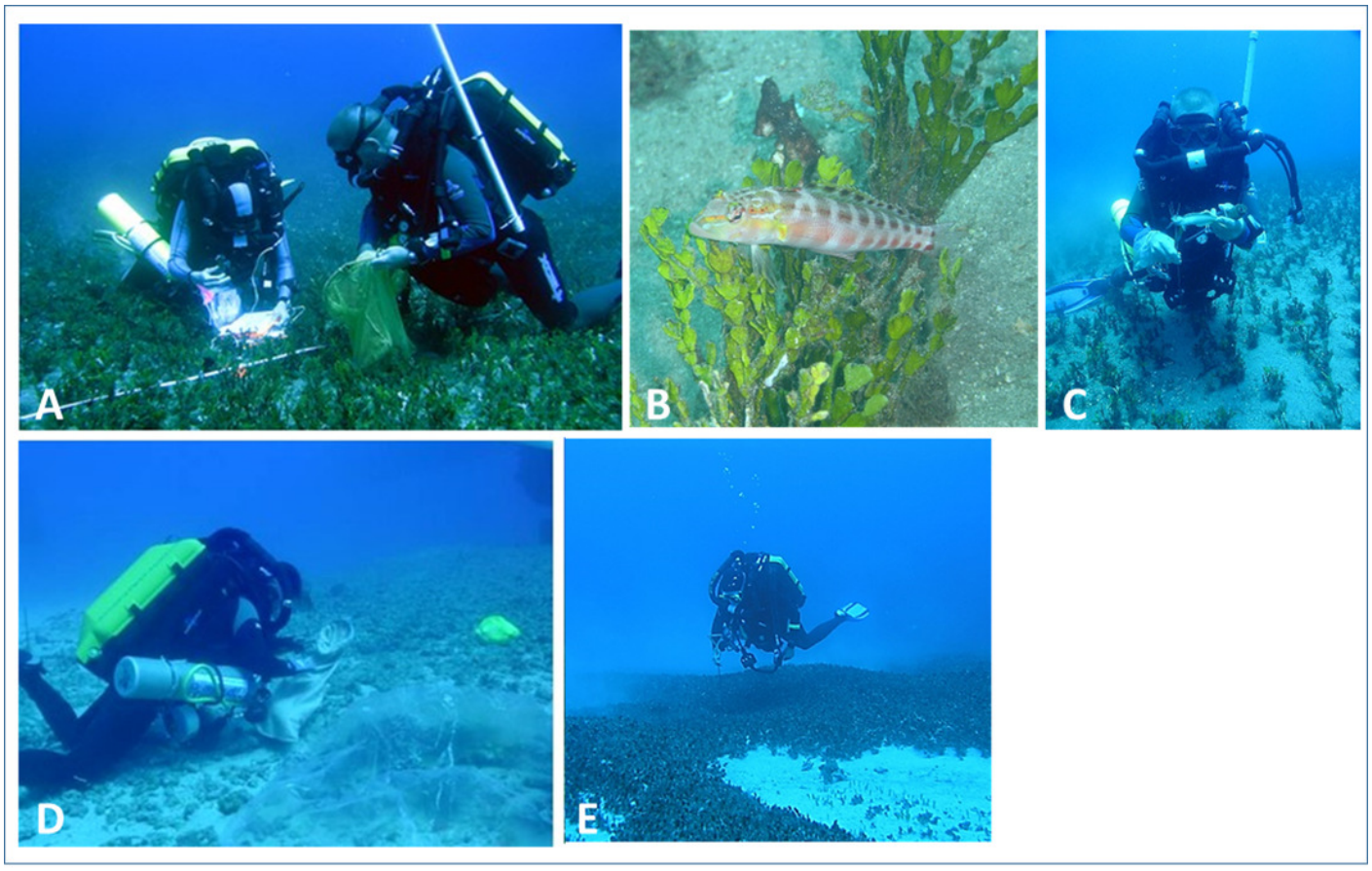

Table 1(on next page)

Summary of visual surveys and tandem visual+clove-oil collections by habitat type and location.

Table 1. Summary of visual surveys and tandem (visual+clove-oil) collections by habitat type and location.

	Avrainvillea sp.		*Halimeda kanaloana*	
Survey Type	Canopy	Sand/Rubble	Canopy	Sand/Rubble
Visual Only	2	0	8	4
Clove Oil + Visual	8	3	28	12
Depth Range	37-47 m		11-40 m	
Dates	10/26/2005-6/12/2006		5/15/06-5/23/06	
Collection Locations	Makaha, Oahu 21°26'50.22"N 158°12'42.24"W		Kahekili Beach Park, Maui 20°56'14.33"N 156°41'40.54"W Honokowai Beach Park, Maui 20°57'21.00"N 156°41'19.96"W Makena Beach Park, Maui 20°37'42.35"N 156°27'15.04"W	

Table 2 (on next page)

Checklist of fishes associated with deep-water *Halimeda kanaloana* meadows based on clove oil collections and visual surveys.

Sub-habitats are listed as Meadow Canopy (directly within vegetation) and Sand/Rubble (blow-outs and sandy meadow perimeters). Endemic species are indicated by “E” whereas those which rest directly upon- or feed within the substrate are indicated by “B”. CO(N) and V(N) indicate the numbers of each species collected or surveyed in clove oil collections or visual surveys, respectively. All other abbreviations are described in the methods.

Table 2. Checklist of fishes associated with deep-water *Halimeda kanaloana* meadows based on clove oil collections and visual surveys. Sub-habitats are listed as Meadow Canopy (directly within vegetation) and Sand/Rubble (blow-outs and sandy & meadow perimeters). Endemic species are indicated by "E" whereas those which rest directly upon- or feed within the substrate are indicated by "B". CO(N) and V(N) indicate the numbers of each species collected or surveyed in clove oil collections or visual surveys, respectively. All other abbreviations are described in the methods.

		Meadow Canopy				Sand/Rubble			
Species	E,B	CO(N)	V(N)	% Occ	% RA	CO(N)	V(N)	% Occ	% RA
Myliobatidae									
Aetobatus narinari							1	6.3	0.2
Manta birostris							1	6.3	0.2
Congridae									
Conger cinereus		1		2.8	0.3				
Synodontidae									
Synodus spp.	B		4	8.3	1.2				
Aulostomidae									
Aulostomus chinensis			2	2.8	0.6				
Fistulariidae									
Fistularia commersonii			6	8.3	1.8				
Apogonidae									
Foa brachygramma	B		5	5.6	1.5	2		6.3	0.4
Pristiapogon kallopterus	B		1	2.8	0.3		30	6.3	5.9
Carangidae									
Caranx melampygus			1	2.8	0.3				
Lutjanidae									
Aprion virescens							1	6.3	0.2
Mulllidae									
Mulloidichthys spp.	B						1	6.3	0.2
Scorpaenidae									
Pterois sphex	E					1		6.3	0.2
Scorpaenopsis diabolus	B		1	2.8	0.3				
Chaetodontidae									
Chaetodon miliaris	E						1	6.3	0.2
Heniochus diphreutes							1	6.3	0.2
Pomacanthidae									
Centropyge fisheri	E		2	2.8	0.6				
Pomacentridae									
Dascyllus albisella	E					2	50	12.5	10.2
Labridae									
Cheilio inermis		1	7	5.6	2.4		2	6.3	0.4
Cymolutes lecluse	E,B	1	8	11.1	2.7				
Cymolutes praetextatus	B		10	13.9	3.0				
Iniistius baldwini	B						1	6.3	0.2
Iniistius umbrilatus	E,B						1	6.3	0.2
Novaculichthys taeniourus	B		7	5.6	2.1				
Oxycheilinus bimaculatus		10	104	41.7	34.1	5		12.5	1.0
Pseudojuloides cerasinus		2	24	16.7	7.8	1	13	12.5	2.7
Pseudocheilinus evanidus							1	6.3	0.2
Pseudocheilinus tetrataenia							1	6.3	0.2
Stethojulis balteata	E,B		9	13.9	1.2				
Callionymidae									
Callionymus decoratus	E,B		2	2.8	0.6				
Synchiropus corallinus	B					2		6.3	0.4
Synchiropus rosulentus	E,B					6		6.3	1.2
Synchiropus spp.	B					1	79	12.5	15.7

Table 2 (continued)

		Meadow Canopy				Sand/Rubble			
Species	E,B	CO(N)	V(N)	% Occ	% RA	CO(N)	V(N)	% Occ	%RA
Pinguipedidae									
Parapercis schauinslandii	B		27	8.3	8.1	4	2	25.0	1.2
Gobiidae									
Eviota susanae	E,B					1		6.3	0.2
Gnatholepis spp.	B	21	1	33.3	6.6	13	1	37.5	2.7
Opua nephodes	B	1	28	11.1	8.7	15	151	31.3	32.5
Priolepis eugenius	E,B					1		6.3	0.2
Priolepis farcimen	E,B					1		6.3	0.2
Psilogobius mainlandi	E,B	2		5.6	0.6	11	96	31.3	21.0
Microdesmidae									
Gunnelichthys curiosus	B		4	8.3	1.2		2	6.3	0.4
Acanthuridae									
Acanthurus blochii			3	2.8	0.9				
Bothidae									
Bothus pantherinus	B		4	11.1	1.2		5	25.0	1.0
Balistidae									
Rhinecanthus aculeatus	B		2	2.8	0.6				
Monacanthidae									
Aluterus scriptus			1	2.8	0.3				
Ostraciidae									
Ostracion meleagris			2	5.6	0.6				
Tetraodontidae									
Arothron hispidus	B		4	5.6	1.2				
Canthigaster coronata	B		2	5.6	0.6				
Canthigaster jactator	E,B		23	19.4	6.9		3	6.3	0.6
Diodontidae									
Diodon hystrix	B		1	2.8	0.3				

Table 3(on next page)

Checklist of fishes found in association with deep-water *Avrainvillea sp*. meadows based on clove-oil collections and visual surveys.

All abbreviations follow table 2.

Table 3. Checklist of fishes found in association with deep-water *Avrainvillea sp.* meadows based on clove-oil collections and visual surveys. All abbreviations follow table 2.

		Meadow Canopy				Sand/Rubble			
Species	E,B	CO(N)	V(N)	% Occ	% RA	CO(N)	V(N)	% Occ	% RA
Muraenidae									
Gymnothorax spp.		1	1	20.0	2.2				
Serranidae									
Plectranthias nanus	B					1		33.3	2.3
Pseudanthias bicolor						2		66.7	4.7
Apogonidae									
Apogonichthys perdix		9		60.0	10.0	2		33.3	4.7
Carangidae									
Caranx lugubris			1	10.0	1.1				
Lutjanidae									
Aprion virescens			1	10.0	1.1				
Mulllidae									
Parupeneus multifasciatus	B						5	33.3	11.6
Scorpaenidae									
Iracundus signifer	B					2		66.7	4.7
Sebastapistes fowleri	B	1		10.0	1.1	2		66.7	4.7
Chaetodontidae									
Chaetodon kleinii						1		33.3	2.3
Pomacentridae									
Chromis leucura						1		33.3	2.3
Labridae									
Bodianus bilunulatus albotaeniatus	E		1	10.0	1.1				
Cirrhilabrus jordani	E		21	10.0	23.3				
Oxycheilinus bimaculatus		4		30.0	4.4	2	3	100.0	11.6
Pseudocheilinus evanidus		3		30.0	3.3		4	33.3	9.3
Pseudocheilinus octotaenia						1		33.3	2.3
Pseudojuloides cerasinus		1	14	20.0	16.7				
Callionymidae									
Synchiropus corallinus	B					1		33.3	2.3
Pinguipedidae									
Parapercis schauinslandii	B					6		66.7	14.0
Gobiidae									
Gnatholepis spp.	B						2	33.3	4.7
Acanthuridae									
Naso caesius			30	10.0	33.3				
Bothidae									
Bothus pantherinus	B						1	33.3	2.3
Soleidae									
Aseraggodes borehami	E,B					1		33.3	2.3
Balistidae									
Xanthichthys auromarginatus			1	10.0	1.1				
Monacanthidae									
Cantherhines dumerilii	B						2	33.3	4.7
Aluterus scriptus							3	33.3	7.0
Tetraodontidae									
Arothron hispidus	B		1	10.0	1.1				
Canthigaster coronata	B						1	33.3	2.3

Table 4(on next page)

Abundance and density of fishes from 1.5 m clove oil collections within *Halimeda kanaloana* canopy (n=28) and surrounding sand & rubble (n= 12) sub-habitats.

Median abundance (fish per 1.5 m collection, N), species richness (S), and a Shannon-Wiener diversity index (H') are included at bottom. All other abbreviations follow table 2. Note that the abundance of vagile species (*) may be underestimated as these species tend to swim away when the tarp is being deployed.

Table 4. Abundance and density of fishes from 1.5 m clove oil collections within *Halimeda kanaloana* canopy (n=28) and surrounding sand & rubble (n= 12) sub-habitats. Median abundance (fish per 1.5 m collection, N), species richness (S), and a Shannon-Wiener diversity index (H') are included at bottom. All other abbreviations follow table 2. Note that the abundance of vagile species (*) may be underestimated as these species tend to swim away when the tarp is being deployed.

Species	E,B	Meadow (N)	Meadow Density (fish per m^2)	Sand (N)	Sand Density (fish per m^2)
Congridae					
*Conger cinereus**		1	0.0238	0	0
Apogonidae					
*Foa brachygramma**	B	0	0	2	0.1111
Scorpaenidae					
*Unidentified**		1	0.0238	0	0
*Pterois sphex**	E	0	0	1	0.0556
Pomacentridae					
*Dascyllus albisella**	E	0	0	2	0.1111
Labridae					
*Cheilio inermis**		1	0.0238	0	0
*Cymolutes lecluse**	E,B	1	0.0238	0	0
*Oxycheilinus bimaculatus**		10	0.2381	5	0.2778
*Pseudojuloides cerasinus**		2	0.0476	1	0.0556
Callionymidae					
Synchiropus corallinus	B	0	0	2	0.1111
Synchiropus rosulentus	E,B	0	0	7	0.3889
Pinguipedidae					
*Parapercis schauinslandii**	B	0	0	4	0.2222
Gobiidae					
Eviota susanae	B,E	0	0	1	0.0556
Gnatholepis anjerensis	B	20	0.4762	12	0.6667
Gnatholepis cauerensis	E,B	1	0.0238	1	0.0556
Opua nephodes	E,B	1	0.0238	15	0.8333
Priolepis eugenius	E,B	0	0	1	0.0556
Priolepis farcimen	E,B	0	0	1	0.0556
Psilogobius mainlandi	E,B	1	0.0238	11	0.6111
Median Abundance (N_x)		1		4	
Median Species Richness (S_x)		1		1	
Total Species Richness (S)		10		15	
Diversity (H')		1.5013		2.2474	
Average Species Density m^2			0.0489		0.1930
Median Density of Fishes m^2			0.6667		2.6667
Average Density of Fishes m^2			0.9286		3.6667

Table 5(on next page)

Abundance and density of fishes from 1.5 m clove oil collections within *Avrainvillea sp.* canopy (n=8) and surrounding sand & rubble (n= 3) sub-habitats.

Median abundance (fish per 1.5 m collection, N), species richness (S), and a Shannon-Wiener diversity index (H') are included at bottom. All other abbreviations follow table 2. Note that the abundance of vagile species (*) may be underestimated as these species tend to swim away when the tarp is being deployed.

Table 5. Abundance and density of fishes from 1.5 m clove oil collections within *Avrainvillea sp.* canopy (n=8) and surrounding sand & rubble (n= 3) sub-habitats. Median abundance (fish per 1.5 m collection, N), species richness (S), and a Shannon-Wiener diversity index (H') are included at bottom. All other abbreviations follow table 2. Note that the abundance of vagile species (*) may be underestimated as these species tend to swim away when the tarp is being deployed.

Species	E,B	Meadow (N)	Meadow Density (fish per m^2)	Sand (N)	Sand Density (fish per m^2)
Muraenidae					
Gymnothorax spp.		1	0.0833	0	0
Serranidae					
Plectranthias nanus	B	0	0	1	0.2222
Pseudanthias bicolor		0	0	2	0.4444
Apogonidae					
Apogonichthys perdix		9	0.7500	2	0.4444
Scorpaenidae					
Iracundus signifer	B	0	0	2	0.4444
Scorpaenopsis fowleri	B	1	0.0833	2	0.4444
Unident		0	0	1	0.2222
Chaetodontidae					
Chaetodon kleinii		0	0	1	0.2222
Pomacentridae					
Chromis leucura		0	0	1	0.2222
Labridae					
Oxycheilinus bimaculatus		4	0.3333	2	0.4444
Pseudocheilinus evanidus		3	0.2500	0	0
Pseudocheilinus octotaenia		0	0	1	0.2222
Pseudojuloides cerasinus		1	0.0833	0	0
Callionymidae					
Synchiropus corallinus	B	0	0	1	0.2222
Pinguipedidae					
Parapercis schauinslandii	B	0	0	6	1.3333
Soleidae					
Aseraggodes borehami	E,B	0	0	1	0.2222
Median Abundance (N_x)		2.50		7.00	
Median Species Richness (S_x)		2		6	
Total Species Richness (S)		6		13	
Diversity (H')		1.4383		2.3667	
Average Species Density m^2			0.0990		0.3194
Median Density of Fishes m^2			1.6667		4.6667
Average Density of Fishes m^2			1.5833		5.1111