ESTABLISHING SPECIES-HABITAT ASSOCIATIONS FOR 4 ETENE SNAPPERS USING A BAITED STEREO-VIDEO CAMERA SYSTEM

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAIʻI AT MĀNOA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

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ABSTRACT

Deepwater Eteline snappers in the Hawaiian Islands are part of a complex of commercially valuable bottomfish that has been subject to recent overfishing. The lack of ecological data on deepwater bottomfish makes it difficult to define their essential fish habitat (EFH), an integral concept in ecosystem-based fisheries management. This study makes use of a baited stereo-video camera system to quantitatively define the habitat associations of four of these species (Pristipomoides filamentosus, P. sieboldii, Etelis coruscans, and E. carbunculus) and expand our understanding of their ecology. Relative abundance, length, and habitat data from six locations in the main Hawaiian Islands that encompass a Bottomfish Restricted Fishing Area (BRFA) were evaluated and species- and size-specific differences were identified. Depth was a major factor influencing bottomfish distributions and habitat preferences were found to be species-specific. Pristipomoides filamentosus and E. carbunculus associated with hard bottom, low slope habitats. Etelis coruscans was found over both hard-low and hard-high habitats while the distribution of P. sieboldii was not significantly different between the four habitat types sampled. Pristipomoides filamentosus showed an ontogenetic increase in habitat depth while P. sieboldii, and E. coruscans, in addition to P. filamentosus, exhibited size-related shifts in habitat type, with two of the species moving from hard bottom, low slope to hard bottom, high slope environments. No ontogenetic shifts were found for E. carbunculus as only a limited number of juveniles were recorded. Regional variations in relative abundance and length distributions were also observed. In establishing species-habitat associations, it is imperative that the influence of life stage, mode of habitat utilization, and environmental variables on bottomfish distributions be assessed on a species level to better understand these intricate relationships.
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INTRODUCTION

Deepwater fisheries are composed of a multitude of species that are found on continental slopes and deep topographic oceanic structures such as seamounts, ridges, and banks to depths below 2000 m. In 2004, the total commercial landings of deep-sea fisheries species in the Atlantic, Pacific, and Indian Oceans combined peaked at 3.7 million tons (FAO, 2011). In the Pacific, deepwater snappers (*Lutjanidae*), groupers (*Serranidae*), and jacks (*Carangidae*) that inhabit deep slopes and seamounts between 100 and 400 m make up a major component of this fishery. Hawaii’s deepwater handline or “bottomfish” fishery also targets these groups of fishes (Haight et al., 1993a). Most of the commercially important bottomfish species have a relatively high age of maturity, long life span, and slow growth rate which make them highly susceptible to overfishing (Haight et al., 1993a). In 1998, an assessment by the National Marine Fisheries Service found that stocks of two species of deepwater snapper, onaga (*Etelis coruscans*) and ehu (*Etelis carbunculus*), were approaching a low spawning potential ratio in the main Hawaiian Islands. To ensure long term-sustainability of bottomfish stocks, the State of Hawaii’s Department of Land and Natural Resources created bottomfish restricted fishing areas (BRFAs) where catching these fish was prohibited (Parke, 2007) (Figure 3). However, identifying geographic areas containing high quality bottomfish habitat has been difficult with little species-specific habitat data available. Information of this type is hard to obtain in most deepwater fisheries due to the logistical constraints involved in sampling the deep sea.

Several environmental factors have been related to the distribution of fish species, namely depth, substrate complexity, food availability, water quality, the presence of current, wave exposure, shelter availability, and coral cover (Williams, 1991). According to Friedlander and Parrish (1998), structural features on a reef may provide shelter from physical stress, restrain foraging predators and interfering competitors, and modify the availability of resources and their rate of acquisition. It can be expected that certain species show an affinity for specific habitat types based on ecological needs and how a habitat may be utilized to meet those needs. Fish-habitat association studies on demersal reef fish assemblages have shown strong relationships between fish abundance and depth.
(Friedlander and Parrish, 1998), substrate type (Bouchon-Navarro et al., 2005), relief (Parrish and Boland, 2004), topographic complexity (Friedlander and Parrish, 1998), or a combination of these habitat variables (Friedlander and Parrish, 1998; Williams and Bax, 2001; Moore et al., 2009). On deeper continental shelf habitats, Stein et al (1992) found that habitat variability was a fundamental cause of heterogeneity among fish assemblages but species occurrences were also related to specific substrates. A similar study done by Anderson and Yoklavich (2007) on the continental shelf within southern Monterey Bay found strong relationships between demersal fish abundance and habitat stratum and relief. Hard stratum habitats with high relief had the highest overall densities of fish which could be attributed to their greater habitat complexity. Fish densities decreased with decreasing habitat complexity (Anderson and Yoklavich, 2007).

In Hawaiian waters, information on fish-habitat associations for deepwater bottomfish is limited. Video and fishing surveys have found that some species associate with areas of high relief, such as underwater headlands, ledges, outcrops, and pinnacles (Ralston et al., 1986; Moffitt and Parrish, 1996; Haight et al., 1993a). More recent ROV and submersible surveys have suggested that substrate type may be an important habitat factor that influences bottomfish distributions (Kelley et al., 2006). These studies have identified habitats with hard substrates and high slopes as being preferred by the adults of many bottomfish species. However, less is known about the habitat preferences of juveniles. Juvenile opakapaka, *Pristipomoides filamentosus*, have been found in association with soft substrates with little to no relief (Moffitt and Parrish, 1996; Parrish et al., 1997). This is the only instance where a change in habitat with life stage has been observed for a bottomfish species in Hawaii. Variations in adult and juvenile habitats may exist among other species of deepwater bottomfish but these differences, if any, have yet to be identified. If habitat usage changes with size, it can have large management implications.

The implementation of the Magnuson-Stevens Fishery Conservation and Management Act of 1996 required federal fishery management plans to identify the essential fish habitat (EFH) for their fishery species. This act defines an EFH as “*those waters and substrate necessary for fish spawning, feeding, or growth to maturity*” (Rosenberg et al., 2000). The overall EFH definition for Hawaii’s bottomfish fishery is
“depths from 0 to 400 meters”. The lack of information available on the ecology of these species has resulted in this very broad definition (Parks, 2002). The Hawaii bottomfish EFH has recently been divided by species complexes making use of known differences in specific depth ranges. Shallow (0 to 240 m), intermediate (40 to 320 m), and deep (80 to 400 m) bottomfish complexes have been identified by Kelley and Moriwake (2011). Kelley et al (2006) and Parke (2007) suggested that suitable habitat for adult bottomfish is a depth between 100 and 400 m, a slope of greater than 20 degrees, and a hard bottom. These definitions have yet to incorporate species-specific habitat requirements, when in fact these requirements probably differ between bottomfish species and ontogenetic stage. EFH definitions are designed, among other reasons, to guide management decisions on the protection and sustainable exploitation of fishery resources and, therefore, need to be as complete and as specific as possible (Kelley et al., 2006).

Eteline snappers of the genus *Pristipomoides* and *Etelis* are widely distributed throughout the Indian and Pacific Oceans (Randall, 2007) at depths between 40 and 400 m. Common shallow water stock assessment techniques such as diver swum transects and catch and release methods are not logistically feasible at these depths. This has led to the emergence of baited camera systems as tools for estimating relative abundances of fish species within this depth range (Ellis and DeMartini, 1995; Priede and Merrett, 1996; Merritt et al., 2011). Eteline snappers are also among the most commercially valuable species that make up a major component of the deepwater fishery in areas such as Hawaii, Guam, CNMI, and American Samoa (WPRFMC, 2005). *Pristipomoides filamentosus* (pink snapper, opakapaka) and *E. coruscans* (flame snapper, onaga) rank first and second in total landed weight and value while the smaller species *E. carbunculus* (ruby snapper, ehu) and *P. sieboldii* (lavender snapper, kalekale) are abundant but lower in value and landings in the Hawaiian Islands (WPRFMC, 2005). These four species (Figure 1) are the focus of this paper.

With the use of a baited stereo-video camera system, this study aims to improve our understanding of the species-habitat associations, within different size classes, of 4 species of bottomfish in the main Hawaiian Islands. This type of species-specific data can be used to assess the amount of ideal habitat present in restricted fishing areas and relate species catch per unit effort (CPUE) data to habitat. Most importantly, by expanding our
understanding of the ecology of selected bottomfish, a better definition of the essential fish habitat for each species can be forged and ecosystem-based management strategies can be further developed.

Figure 1. BotCam images of A) *Pristipomoides filamentosus* (opakapaka); B) *P. sieboldii* (kalekale); C) *Etelis coruscans* (onaga); and D) *E. carbunculus* (ehu).

**METHODS**

The Bottom Camera Bait Station (BotCam; Figure 2), developed by Danny Merritt (Merritt, 2005) and NOAA’s Pacific Islands Fisheries Science Center (PIFSC) Coral Reef Ecosystem Division (CRED), is a remote fully automated baited stereo-video camera system designed specifically for non-extractive fishery-independent sampling of bottomfish species in their habitat and depth range (Merritt et al., 2011). The BotCam makes use of ambient light which allows for an operating depth of up to 300 m but restricts sampling to daytime hours. It is operational on multiple bottom types including steep slopes and high relief. Upon deployment, the BotCam unit sits parallel to the seafloor at about 3 m off the bottom generating a horizontal field of view of the bottom environment. Depending on depth of deployment, amount of light, and water clarity, the field of view may expand or contract. Moore et al (in revision) estimated the visual area sampled to be between 4 and 400 m². The BotCam recorded 30-45 minutes of continuous
video at each deployment location. Depth data was taken from a Sea-Bird CTD profiler attached to the system. The BotCam’s bait canister was filled with approximately 800 grams of ground anchovy and squid which is similar to the bait used by bottomfish fishermen (Merritt et al., 2011). The BotCam is a means by which dynamic bottomfish abundance estimates within actual bottomfish habitats can be made, fish lengths can be accurately measured, and habitats can be visually characterized.

![BotCam system with labeled parts and BotCam deployment schematic](image)

Figure 2. BotCam system with labeled parts from Moore et al. (in revision) (A) and BotCam deployment schematic from NOAA-PIFSC CRED website (B).

Habitat types were characterized using multibeam and sidescan sonar data from the main Hawaiian Islands collected by the Pacific Islands Benthic Habitat Mapping Group, the University of Hawaii Undersea Research Laboratory (HURL), and the Hawaii Mapping Research Group. Depth, substrate hardness, and slope are all habitat variables that can be determined from bathymetry and multibeam backscatter data. Habitats were classified into four simplified types: hard substrate with high slope (hard-high), hard substrate with low slope (hard-low), soft substrate with high slope (soft-high), and soft substrate with low slope (soft-low). Backscatter values varied depending on the multibeam system used. A single boundary value was determined for each system to classify substrate as either hard or soft. A slope of 20 degrees or greater from a range of 0
to 90 degrees was considered a high slope. Using ArcGIS, the area in and around BRFAs were divided into 200 x 200 m grids and each assigned a habitat type corresponding to the habitat covering the majority of the grid. The 200 x 200 m grid size was chosen on the assumption that there would be no attraction of fish from outside this area to the bait.

A random stratified sampling approach was used to locate BotCam sampling locations. While the purpose of this study was to evaluate species-habitat associations, one main goal of the larger project was to evaluate population changes inside and outside of BRFAs. This affected the sampling design. However, it was not anticipated that any effects of protection would be seen since the system of BRFAs was put in place the year this work began. This study uses data from 625 BotCam deployments conducted inside and outside of 6 of the 12 current BRFAs (Figure 3) between May 2007 and June 2009. The BRFAs sampled were located off Niihau (BRFA B), Kaena Point (BRFA D), Makapuu (BRFA E), Penguin Bank (BRFA F), Pailolo Channel (BRFA H), and Hilo (BRFA L). The 100 to 300 m depth range was sampled 32 times inside and 32 times outside but adjacent to each BRFA for each year it was sampled. Although the EFH for Hawaii’s deep bottomfish extends from 100 to 400 m, the BotCam has cameras which work under ambient light to only 300 m, therefore limiting the sampling depth range. Sampling effort was weighted towards known preferred bottomfish habitats. This was done to ensure greater replication where fish densities were expected to be higher. 12 hard-high, 8 hard-low, 8 soft-high, and 4 soft-low grids were targeted inside and outside each BRFA. In regions where a given habitat type was not present, sampling intensity was increased in the next most suitable habitat. BotCam deployments targeted centroids of the randomly selected 200 x 200 m grids.
Figure 3. Map of the current Bottomfish Restricted Fishing Areas (BRFAs) in the main Hawaiian Islands (Moore et al., in revision). Red letters indicate BRFAs sampled in this study.

Relative Abundance

BotCam videos were reviewed in the laboratory to estimate relative abundance (MaxNo) of the four most abundant and commercially important bottomfish species, *Pristipomoides filamentosus*, *P. sieboldii*, *Etelis coruscans*, and *E. carbunculus*. MaxNo is the highest count of a species observed in a single frame of video. Through the use of MaxNo, the potential problem of counting the same fish twice as it enters and re-enters the camera’s field of view can be avoided. Many studies have found that MaxNo positively correlated with fish density (Ellis and DeMartini, 1995; Priede and Merrett, 1996; Willis et al., 2000; Willis and Babcock, 2000; Yau et al., 2001; Cappo et al., 2003). This parameter also correlated best with the traditional CPUE parameter used in fishing surveys (Ellis and DeMartini, 1995).
Permutational analysis of variance (PERMANOVA) in Primer 6.0 with PERMANOVA+ (Anderson et al., 2008) was used to analyze the data. With the unbalanced experimental design and multiple zero counts leading to a highly skewed (non-normal) relative abundance distribution, a PERMANOVA was deemed appropriate as it does not assume that the data is normally distributed. It is known that not all of the species considered occupy the entire depth range sampled (Polovina et al., 1985; Haight, 1989; Everson et al., 1989; Merritt et al., 2011). To constrain the data to an appropriate range for each species, the depths at which each species had its greatest MaxNo had to be identified. For the initial analysis, depth was divided into seven 30 m bins from 90 to 300 m. Relative abundance values were square-root transformed to down weight the effect of numerous zero counts and few very large numbers. A Euclidean distance matrix was used in the statistical test with a type III sum of squares. If a significant difference (p<0.05) was found across depth bins, a subsequent pair-wise PERMANOVA was performed to determine the preferred depths of each species. Subsequent analyses (MaxNo and lengths) were then constrained to 90 to 210 m for P. filamentosus, 180 to 270 m for P. sieboldii, and 210 to 300 m for both E. coruscans and E. carbunculus.

In identifying habitat preferences, the influence of location (BRFA) and protection (inside versus outside a BRFA) could not be overlooked. A 3-way crossed design PERMANOVA was used to determine how location (BR, 6 levels, fixed), protection (PR, 2 levels, fixed), habitat type (HA, 4 levels, fixed), and the interaction of these factors affected each species’ relative distribution. MaxNo values were square-root transformed and the PERMANOVA was run on a Euclidean distance matrix with type III sum of squares. Where significant results (p<0.05) occurred, pair-wise testing was done to identify specific differences.

Fork Length

Fork lengths were measured for individual fish visible in both BotCam cameras using stereogrammetric measurement software (Visual Measurement System (Geomsoft, Victoria, Australia) and PhotoMeasure / EventMeasure (SeaGIS Pty Ltd)). Measurements of individual fish were taken at the point of MaxNo or where the most fish could be
measured. This was done to ensure that individuals were not repeatedly measured at various times during the video. Replicate measurements were taken for each individual fish measured a few frames before or after the identified measurement time to increase the precision and accuracy of the measurement. A LED light device was used to ensure synchronicity of the left and right camera video files. Measurements with a root mean squared (RMS) error or residual parallax greater than 10 mm and a precision to fork length ratio of greater than 10 percent were removed from the analyses. RMS error and residual parallax are measures of quality of the intersections of the two points that define the endpoints of a length measurement which directly affect precision. The same 3-way crossed PERMANOVA design from the relative abundance analysis (BR, PR, HA) was used to test fork lengths for each species. Transformation of fork lengths, however, was not necessary as these data typically were normally distributed.

Since the above approach only evaluated the variations in mean length, additional analyses were done to investigate size-related changes in habitat association. A linear regression was used to evaluate the relationship between depth and fork length for each of the 4 species studied to identify ontogenetic shifts with depth. In determining ontogenetic shifts across habitat types, a contingency table (tested with Pearson chi-square test) was used to determine whether the size class distribution of each species was independent of habitat type. Fork lengths were grouped into 10 cm bins. This size interval was chosen to maximize the number of observations in each size bin. In testing fish measurements from BotCam video, Merritt et al (2011) found measurements to be accurate to within 0.3 to 0.9 cm making such a grouping very robust.

**Interval MaxNo**

Changes in the numbers of fish present at the camera throughout the deployment were estimated by recording MaxNo at one minute intervals for the first 40 minute period of video. The rate at which each species arrived and the time it took to reach their maximum numbers were determined as these could be indicative of schooling behavior and habitat preference. Earlier arrival and larger peak abundances may be observed when a species has a strong association with a given habitat type and, thus, highlight habitat
preference. MaxNo from each minute interval was averaged by habitat type for each species to visualize the data. Interval MaxNo data was collected only during the first year of sampling (378 BotCam deployments) because the process was extremely time consuming. The data was further constrained to the identified preferred depths of each species. Having already analyzed MaxNo against habitat (see relative abundance section), the mean time it took for a species to reach MaxNo in each habitat type was compared using a PERMANOVA.

RESULTS

A total of 625 successful BotCam deployments were analyzed from 6 BRFA regions (Table 1). BRFA D and L were only sampled during the first year of the project giving these areas half the number of deployments compared to other BRFA regions. In BRFA D, there were not enough hard-high and soft-high classified habitats to meet the sampling design. These deployments were thus assigned to hard-low habitats which were considered to be the next most suitable. BRFA H had no high slope habitats which led to an increased sampling of hard-low habitats.

<table>
<thead>
<tr>
<th>BRFA</th>
<th>hard-high</th>
<th>hard-low</th>
<th>soft-high</th>
<th>soft-low</th>
<th>Total</th>
</tr>
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<tr>
<td>B (Niihau)</td>
<td>47</td>
<td>31</td>
<td>32</td>
<td>16</td>
<td>126</td>
</tr>
<tr>
<td>D (Kaena)</td>
<td>12</td>
<td>34</td>
<td>10</td>
<td>8</td>
<td>64</td>
</tr>
<tr>
<td>E (Makapuu)</td>
<td>40</td>
<td>36</td>
<td>36</td>
<td>16</td>
<td>128</td>
</tr>
<tr>
<td>F (Penguin Bank)</td>
<td>45</td>
<td>30</td>
<td>30</td>
<td>15</td>
<td>120</td>
</tr>
<tr>
<td>H (Pailolo Channel)</td>
<td>0</td>
<td>110</td>
<td>0</td>
<td>16</td>
<td>126</td>
</tr>
<tr>
<td>L (Hilo)</td>
<td>21</td>
<td>16</td>
<td>16</td>
<td>8</td>
<td>61</td>
</tr>
<tr>
<td>Total</td>
<td>165</td>
<td>257</td>
<td>124</td>
<td>79</td>
<td>625</td>
</tr>
</tbody>
</table>
Relative Abundance

For all species studied, significant differences in relative abundance were found across depth bins (PERMANOVA, p<0.05). Pair-wise comparisons of MaxNo from the seven depth bins highlighted each species’ depth preference (Figure 4). MaxNo was highest from 90-210 m for *Pristipomoides filamentosus* (post-hoc PERMANOVA, p<0.05). The preferred depths of *P. sieboldii* ranged from 180-270 m while both *Etelis* species had the deepest range of highest MaxNo from 210-300 m (post-hoc PERMANOVA, p<0.05).

Within each species’ preferred depths, location (BR), habitat type (HA), or the interaction of these two factors (BRxHA) had an effect on relative abundance (Table 2). Protection (PR) and the interaction of all other factors with protection, however, did not (PERMANOVA, p>0.05). For *P. filamentosus*, BRFA L had the highest relative abundance of this species among BRFAs and hard-low habitats had higher mean MaxNo compared to other habitat types (Figure 5; post-hoc PERMANOVA, p<0.05). While there were no significant location or habitat effects for *P. sieboldii*, the interaction of location and habitat was marginal (p=0.0564, Table 2) as two of the largest counts of this species (100 and 85 individuals) occurred on hard-high habitats in BRFA B leading to a high mean MaxNo (Figure 5). Habitat type was the only factor that affected the relative abundance of *E. coruscans*. Hard substrate habitats with either high or low slope had greater mean MaxNo compared to soft substrate habitats (Figure 5; post-hoc PERMANOVA, p<0.05). *E. carbunculus* had its highest relative abundance in BRFA H and lowest in BRFA B, D, and E (Figure 5; post-hoc PERMANOVA, p<0.05). Hard-low habitats had a mean MaxNo greater than other habitat types overall. By region, hard-low habitats had a higher mean MaxNo compared to soft-low habitats in BRFA H. In BRFA F, hard-high, hard-low, and soft-high habitats had equally as many recorded *E. carbunculus* on average. BRFA B and D differed from the others in that hard-high had greater MaxNo than hard-low.
Figure 4. Mean relative abundance (MaxNo) with standard error by species across 7 depth bins. By species, columns that share a letter are not significantly different from each other (p>0.05, post-hoc PERMANOVA testing).

Table 2. Permutational analysis of variance (PERMANOVA) for relative abundance data (MaxNo) testing the factors: location (BR), protection (PR), and habitat type (HA).

<table>
<thead>
<tr>
<th>Source</th>
<th>P. filamentosus (90-210m)</th>
<th>P. sieboldii (180-270m)</th>
<th>E. coruscans (210-300m)</th>
<th>E. carbunculus (210-300m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Source</td>
<td>df</td>
<td>F</td>
<td>p</td>
<td>df</td>
</tr>
<tr>
<td>BR</td>
<td>5</td>
<td>2.860</td>
<td>0.024</td>
<td>5</td>
</tr>
<tr>
<td>PR</td>
<td>1</td>
<td>9.000</td>
<td>0.096</td>
<td>1</td>
</tr>
<tr>
<td>HA</td>
<td>3</td>
<td>8.282</td>
<td>0.000</td>
<td>3</td>
</tr>
<tr>
<td>BRxPR</td>
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<td>0.629</td>
<td>0.659</td>
<td>5</td>
</tr>
<tr>
<td>BRxHA</td>
<td>13</td>
<td>1.642</td>
<td>0.076</td>
<td>12</td>
</tr>
<tr>
<td>PRxHA</td>
<td>3</td>
<td>0.617</td>
<td>0.587</td>
<td>3</td>
</tr>
<tr>
<td>BRxPRxHA</td>
<td>12</td>
<td>1.019</td>
<td>0.417</td>
<td>10</td>
</tr>
</tbody>
</table>
Figure 5. Mean relative abundance (MaxNo) with standard error by location (BRFA), by habitat, and by habitat in each BRFA (brfa x habitat) within each species’ preferred depths. By factor, columns that share a letter (upper case for BRFA; bold lower case italics for habitat; lower case for brfa x habitat) are not significantly different from each other (p>0.05, post-hoc PERMANOVA testing). Number below each column is the number of BotCam deployments.

Fork Length

In evaluating mean lengths, location, protection, and habitat type were all important factors and the interactions between these were sometimes significant (Table 3). BRFA B had the largest *P. filamentosus* on average (65.29 cm) among locations while BRFA L had the smallest (28.35 cm; Figure 6; post-hoc PERMANOVA, p<0.05). The smallest individual in the BRFA L region measured approximately 16 cm while the largest found in BRFA B was 79 cm. *Pristipomoides filamentosus* from outside protected areas had a mean fork length of 42.89 cm and were larger than those found inside (40.53 cm; PERMANOVA, p<0.05). The smallest mean lengths of this species were found over hard-low habitats when comparing habitat types overall, habitats at each BRFA location, and habitats either inside or outside a particular BRFA (Figure 6; Table 4; post-hoc PERMANOVA, p<0.05). Pair-wise comparisons for *P. sieboldii* showed that this species had its smallest mean fork length (23.64 cm) in the BRFA D region, was largest in hard-high (31.46 cm) and smallest in soft-low habitats (8.64 cm, n=2), and larger inside BRFA F and H and outside BRFA L (Figure 6; Table 4; post-hoc PERMANOVA, p<0.05). The
smallest individual *P. sieboldii* measured, however, was 7.63 cm in the BRFA B region. Mean fork length for *E. coruscans* was smallest in the BRFA H region (42.80 cm) compared to other locations (Figure 6) and larger inside BRFA H than outside of the protected area (Table 4; post-hoc PERMANOVA, p<0.05). The smallest individual measured was 15.05 cm. Although the interaction of location and habitat and the interaction of location, protection, and habitat had significant results for *E. coruscans*, no clear trends were seen. Location was the only factor that had an influence on mean length for *E. carbunculus* (Table 3; PERMANOVA, p<0.05). Overall, mean sizes were very similar for this species but were smallest in the BRFA E and L regions (Figure 6).

### Table 3. Permutational analysis of variance (PERMANOVA) for length data testing the factors: location (BR), protection (PR), and habitat type (HA).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>F</th>
<th>p</th>
<th>df</th>
<th>F</th>
<th>p</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>P. filamentosus</strong> (90-210m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR</td>
<td>5</td>
<td>36.037</td>
<td>0.000</td>
<td>5</td>
<td>28.197</td>
<td>0.000</td>
<td>4</td>
<td>11.046</td>
<td>0.000</td>
</tr>
<tr>
<td>PR</td>
<td>1</td>
<td>14.236</td>
<td>0.000</td>
<td>1</td>
<td>1.4291</td>
<td>0.230</td>
<td>0</td>
<td>No test</td>
<td>0.000</td>
</tr>
<tr>
<td>HA</td>
<td>3</td>
<td>11.393</td>
<td>0.000</td>
<td>3</td>
<td>18.381</td>
<td>0.000</td>
<td>1</td>
<td>0.4781</td>
<td>0.491</td>
</tr>
<tr>
<td>BRxPR</td>
<td>5</td>
<td>2.0229</td>
<td>0.079</td>
<td>3</td>
<td>16.568</td>
<td>0.000</td>
<td>3</td>
<td>4.8170</td>
<td>0.002</td>
</tr>
<tr>
<td>BRxHA</td>
<td>9</td>
<td>7.6621</td>
<td>0.000</td>
<td>4</td>
<td>1.1566</td>
<td>0.328</td>
<td>1</td>
<td>23.693</td>
<td>0.000</td>
</tr>
<tr>
<td>PRxHA</td>
<td>2</td>
<td>0.4536</td>
<td>0.636</td>
<td>2</td>
<td>0.2065</td>
<td>0.815</td>
<td>2</td>
<td>0.4810</td>
<td>0.612</td>
</tr>
<tr>
<td>BRxPRxHA</td>
<td>5</td>
<td>3.4213</td>
<td>0.005</td>
<td>2</td>
<td>0.2100</td>
<td>0.809</td>
<td>1</td>
<td>13.258</td>
<td>0.000</td>
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<tr>
<td>Res</td>
<td>419</td>
<td>446</td>
<td></td>
<td>242</td>
<td>274</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| **P. sieboldii** (180-270m) |    |     |         |    |     |        |    |     |         |
| **E. coruscans** (210-300m) |    |     |         |    |     |        |    |     |         |
| **E. carbunculus** (210-300m) |    |     |         |    |     |        |    |     |         |
**E. carbunculus** (210-300m; d=117; n=296)

![Figure 6](image)

**Figure 6.** Mean fork length with standard deviation by location (BRFA), by habitat, and by habitat in each BRFA (brfa x habitat) within each species’ preferred depths. By factor, columns that share a letter (upper case for BRFA; bold lower case italics for **habitat**; lower case for brfa x habitat) are not significantly different from each other (p>0.05, post-hoc PERMANOVA testing). Number below each column is the number of fish measured. For protection effects refer to table 4.

**Table 4.** Summary of significant post-hoc PERMANOVA comparisons of fork lengths for location (BR), protection (PR), habitat type (HA), and the interaction of these factors.

<table>
<thead>
<tr>
<th>Species</th>
<th>BR</th>
<th>PR</th>
<th>HA</th>
<th>BRxPR</th>
<th>BRxHA</th>
<th>PRxHA</th>
<th>BRxPRxHA</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. filamentosus</em></td>
<td>Largest in B</td>
<td>Larger outside</td>
<td>Smallest in HL</td>
<td>NS</td>
<td>(D) largest in SH, smallest in HL</td>
<td>NS</td>
<td>(D) in SH&gt;HL</td>
</tr>
<tr>
<td><em>P. sieboldii</em></td>
<td>Smallest in D</td>
<td>NS</td>
<td>Largest in HH</td>
<td>(F) larger inside (H) larger inside (L) larger outside</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td><em>E. coruscans</em></td>
<td>Smallest in H</td>
<td>No test</td>
<td>NS</td>
<td>(H) larger inside</td>
<td>(B) larger in HL than HH</td>
<td>NS</td>
<td>(B) in HL&gt;HH</td>
</tr>
<tr>
<td><em>E. carbunculus</em></td>
<td>Similar mean size</td>
<td>No test</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>No test</td>
</tr>
</tbody>
</table>

*HH = hard-high; HL = hard-low; SH = soft-high; SL = soft-low; NS = not significant*
Size-related shifts in species-habitat associations were evident. The linear regressions of depth against fork length for each species showed that *P. filamentosus* increased in size with depth ($R^2=0.438$, $p<0.01$) while the other 3 species did not (Figure 7). In evaluating the proportion of fish measured in each habitat type by size class, it was clear that habitat associations varied by size for *P. filamentosus*, *P. sieboldii*, and *E. coruscans* (Figure 8). *Etelis carbunculus* had very similar habitat associations in all size classes and did not show any habitat shifts with size (Pearson chi-square, $p>0.05$). *Pristipomoides filamentosus* had a shift from hard-low habitats to hard-high habitats with an increase in size. There was a greater proportion of sexually mature individuals ($\geq 43$ cm; Kikkawa, 1984) for this species over hard-high habitats while individuals less than 43 cm were mostly in hard-low habitats. For *P. sieboldii*, although less evident, a shift to hard-high from other habitat types was observed within the 25-35 cm size class. The length at which this species reaches sexual maturity is 29 cm (DeMartini and Lau, 1999). *Etelis coruscans* and *E. carbunculus* were recorded mostly in hard-low habitats in all size classes. For *E. coruscans*, however, the smallest individuals (<55 cm) were found only in hard-low habitats and as size increased, hard-high habitats were equally dominant. According to Everson et al (1989), the onset of sexual maturity for this species occurs at 61 cm.
Figure 7. Fork length versus depth within each species’ preferred depths (d = # of BotCam deployments; n = # of fish measured).
Figure 8. Proportion of fish measured in each habitat type by size class within each species’ preferred depths (d = # of BotCam deployments; n = # of fish measured).
Interval MaxNo

The results of the interval MaxNo analysis (Figure 10) showed that patterns of MaxNo over time varied by species and habitat type. The relative elevations of each line correspond to overall habitat mean MaxNo values in figure 5 but the shape of the lines provides some information about behavior of the fish in each habitat type. Schooling was identifiable by a rapid increase in MaxNo in a relatively short period of time followed by a rapid decline in numbers. *Pristipomoides filamentosus, P. sieboldii,* and *E. coruscans* all exhibited a schooling behavior in hard-high habitats as numerous individuals arrived at the BotCam unit within a few intervals and dissipated as members of the group started leaving. The same schooling pattern was also evident in hard-low habitats for *E. coruscans.* *Etelis carbunculus,* on the other hand, had a consistently increasing interval MaxNo in hard-high, hard-low, and soft-high habitat types. In comparing the time to MaxNo by habitat type for each species (Figure 9), no differences were detected (PERMANOVA, *p*> 0.05). There were many instances where only a single observation of a species was made during a deployment (MaxNo = 1). Often times these single observations occurred much later in the video increasing mean time to MaxNo. This metric, therefore, does not coincide with the observed peaks in figure 10 which are driven by interval counts.

![Figure 9. Time to MaxNo in minutes with standard error by species across habitat types within each species’ preferred depths (d = # of deployments) (PERMANOVA, *p*> 0.05).](image)
Figure 10. Mean MaxNo in 1 minute intervals by habitat type within each species’ preferred depths (d = # of BotCam deployments). Note difference in mean MaxNo scale.
DISCUSSION

Depth has a significant influence on the distribution of bottomfish. Two distinct depth groupings were seen within the sampling range of this study. *Pristipomoides filamentosus* was dominant in the shallower end of the sampling depths (<200 m) while *P. sieboldii, Etelis coruscans, and E. carbunculus* were found more frequently towards the deeper end (>200 m). The depth ranges that were identified within which the bottomfish species were most abundant were consistent with previous studies in Hawaii (Haight, 1989; Everson et al., 1989; Merritt et al., 2011) and the findings of Polovina et al (1985) in the Marianas Islands and Guam. When establishing species-specific differences in distribution, depth must be the first factor evaluated.

Although previous studies have suggested that habitats with hard substrates and high slopes such as headlands and promontories (Ralston et al., 1986) are preferred by many bottomfish species (Ralston and Polovina, 1982; Parrish, 1987; Kelley et al., 2006; Parke, 2007), this study has found that other habitat types, such as hard-low habitats, are important to Eteline snappers and species-specific differences in habitat preference do exist. It is hypothesized that high slope areas form localized zones of turbulent vertical water movement that may increase the availability of prey for bottomfish species (Haight et al., 1993a). Kelley et al (2006) proposed that this increase in water flow that is also observed over large topographic features may be important only to some species while substrate type and finer habitat characteristics may be important to others. The results of this study show that, in the main Hawaiian Islands, Eteline snappers are not predominantly found over a single habitat type. It is apparent that hard-low habitats are important to 3 of the 4 species studied. The overall habitat preference of *P. filamentosus* based on relative abundance is low-sloping hard substrates. *E. coruscans* is associated with hard-high and hard-low habitats while *E. carbunculus* has an affinity for hard-low habitats. For *E. carbunculus*, this trend could be driven by the lack of habitat types other than hard-low in BRFA H (Pailolo Channel) where many observations of this species were made. In BRFA F (Penguin Bank), high slope habitats were similarly important to this species in addition to hard-low (Figure 5). The sampling design may have influenced the pattern of habitat preference observed for *E. carbunculus* but the results do highlight
the importance of the deep hard-bottom flats of Pailolo Channel to this species. The observed association of juvenile *P. filamentosus* and *E. coruscans* with hard-low habitats may be driving each species preference for this habitat type. When assessing species-habitat associations, an understanding of the changes in habitat utilization by life stage is, therefore, necessary.

Clear ontogenetic shifts in habitat association were evident in 3 of the 4 species studied. For *P. filamentosus*, there is a distinct ontogenetic progression in the habitat association that extends previous studies. The known habitat for juveniles of this species from 7 to 20 cm in fork length is shallow low-sloping soft substrates. Juvenile *P. filamentosus* have been found at depths between 65 and 100 m offshore of Kaneohe Bay (Parrish, 1989; Moffitt and Parrish, 1996) and more recently off Waikiki, Oahu between 37 and 42 m (Drazen, unpublished data). These juveniles move out of their nursery grounds and presumably merge with the adult schools in deeper waters after about 1 year (Parrish et al., 1997). Within the preferred depth range identified for *P. filamentosus* (90-210 m), the smallest mean lengths were found over hard-low habitats in 4 of the 6 regions sampled. This study shows that *P. filamentosus* as small as 16 cm live in the adult depth range but over low-sloping hard substrates. Based on growth curves from DeMartini et al (1994), these juveniles are just under a year old and could be recent migrants from a surrounding nursery area. The results of this study show that these fish continue to stay in hard-low habitats until they reach a length of 45 cm or ~5 years of age then increasingly utilize hard-high habitats. It is possible that this species utilizes hard substrates with low slopes as a transitional habitat prior to moving into hard-high habitats. *Pristipomoides filamentosus* reaches sexual maturity at approximately 43 cm (Kikkawa, 1984). The shift in habitat from hard-low to hard-high could be a response to reproductive maturity which will be discussed below.

Size-related habitat shifts were also evident for *P. sieboldii* and *E. coruscans* but without a change in their depth of occurrence. Previous studies also showed a lack of depth changes with size for these species (Kelley et al., 1997; Ikahara, 2006). The move into hard-high habitats with increasing size roughly coincides with the onset of sexual maturity in both species. This occurs between 3 to 6 years of age for *P. sieboldii* (Williams and Lowe, 1997) and 5 to 6 years for *E. coruscans* (Everson et al., 1989). In
contrast to the other 3 species, no size-related habitat shifts were observed for *E. carbunculus*. This species matures at a small size similar to *P. sieboldii*. But unlike *P. sieboldii*, very few juveniles of this species were measured (min. length = 24 cm). Juvenile *E. carbunculus* along with other smaller bottomfish are highly vulnerable to predation by demersal carnivores such as *Seriola* spp. (Humphreys and Kramer, 1984). Despite possibly being in the vicinity of the bottom cameras, juveniles may remain closer to the bottom for protection and out of the BotCam’s field of view. Until very small *E. carbunculus* (i.e. 5-15 cm) can be observed regularly, a complete ontogenetic assessment of habitat will not be possible. However, it is important to note that the size range harvested by the fishery is represented in this study.

The drivers of the ontogenetic habitat shifts observed could be related to shifts in diet, increasing reproductive output, and predator avoidance at smaller sizes. Szedlmayer and Lee (2004) found a shift in the diet of the shallow-water juvenile red snapper (*Lutjanus campechanus*) from crustaceans to fish and cephalopods with increasing size. This change in diet was associated with the migration from nursery habitats to coral reefs. For deepwater snappers, diet shifts have yet to be documented. DeMartini et al (1996) examined the diet of juvenile *P. filamentosus* from the Kaneohe Bay nursery and found that it was composed of crustaceans, jellies, nekton, and benthos (demersal octopods, echinoids, and microgastropods). With the exception of benthic prey, a similar diet was found for *P. filamentosus* caught between 100 and 300 m in Penguin Bank by Haight et al (1993b). It is possible that smaller individuals of this species associate with low-sloping hard bottom habitats to feed on the benthos and then shift to a pelagic diet when they move into hard-high habitats where the postulated increase in water flow increases prey availability (Ralston et al., 1986; Haight et al., 1993a; Kelley et al., 2006). However, further studies are still needed to determine whether ontogenetic diet shifts do occur for *P. filamentosus* and other deepwater snappers.

An increase in reproductive output may be achieved in a habitat where there is an abundance of prey (Claisse et al., 2009), there is an aggregation of sexually mature individuals (Domeier and Colin, 1997), or environmental conditions are favorable for gamete release (Grimes, 1987). In Hawaiian coral reefs, the yellow tang (*Zebrasoma flavescens*) has been found to shift into habitats with increased food resources when they
reach reproductive size to possibly increase their reproductive ability (Claisse et al., 2009). With the hypothesized increase in bottomfish prey availability over hard-high habitats, it could be inferred that *P. filamentosus*, *P. sieboldii*, and *E. coruscans* move into this habitat type to increase foraging rate and maximize their reproductive output. Domeier and Colin (1997) describe the formation of spawning aggregations of many coral reef fish species including snappers. They found that these aggregations occurred seasonally with the same lunar periodicity and were site-specific. Grimes (1987) suggested that gamete release in Lutjanids is done where predation is less intense and there is suitable habitat for juvenile settlement. Other than seasonality, habitat and environmental parameters of bottomfish spawning have yet to be determined. No actual spawning events were recorded during daytime camera deployments as *P. filamentosus* and *E. coruscans* are known to spawn at night (Kelley, pers. comm.). It remains possible, however, that the observed ontogenetic habitat shifts occurred as a result of a reproductive cue given that the change in habitat roughly coincided with sexual maturity. Physical processes, such as currents, that influence prey availability and gamete dispersal should be looked into further. At the sampling depths of this study (100-300 m), it is likely that bottom currents are tidally driven. With the semi-diurnal tidal cycle in the Hawaiian Islands, future work should focus on characterizing the current regimes of sampled regions in addition to bottom camera deployments over a 24-hour period.

Another factor that may influence ontogenetic habitat shifts is habitat complexity. It is plausible that juveniles and smaller species of bottomfish use more complex habitats to avoid predation. Laidig et al (2009) found juvenile rockfish on the continental shelf off of central California associated with boulder and cobble habitats prior to moving into the adult slope habitats. The scale at which habitats were classified in this study, however, did not capture finer scale characteristics such as habitat complexity. Future work should investigate the role of habitat complexity on size distributions of bottomfish and look more closely into how specific habitat types are utilized.

Regional variations in relative abundance and mean length may be attributed to fishing or large-scale habitat factors. It can be expected that remote locations such as BRFA B (Niihau) would have less fishing pressure compared to those closer to major ports and, thereby, have increased relative abundances and lengths of target species.
Contrary to this expectation, the highest relative abundance of *P. filamentosus* was found in BRFA L (Hilo) and for *E. carbunculus* in BRFA H (Pailolo Channel). With both areas being easily accessible to fishing, other factors may be driving the observed distributions. Protection did not have an influence on the relative abundance of any of the four species studied. Given that this study uses data from the first two years after the establishment of the existing BRFAs and based on the results of Moore et al (in revision), a protection effect was not expected. For long lived species with a high age at maturity such as these deepwater snappers, it may take decades before an effect of protection on relative abundance is detected (Moore et al., in revision). In terms of mean length, the largest *P. filamentosus* being found in the BRFA B (Ni‘ihau) region could be due to the remote location and longevity of protection as BRFA B has been closed to fishing since 1998. The opposite may be true in BRFA L (Hilo) where the smallest *P. filamentosus* were found. Prior to the implementation of the 2007 system of BRFAs, fishing in the depth range of *P. filamentosus* was permitted because the BRFA boundary began at 200 m.

Understanding how protection and fishing pressure affect abundance and size distributions of bottomfish should be investigated further as these may confound any trends attributed to habitat or other environmental variables.

Mega-scale habitat features such as pinnacles, banks, terraces, and even featureless carbonate flats could also be influencing bottomfish distributions. In this study, juvenile *P. filamentosus* and *E. coruscans* were found to associate with low-sloping hard bottom habitats. The major terrace in BRFA L (Hilo) where most juvenile *P. filamentosus* were found and the flat hard-bottom channel of BRFA H (Pailolo Channel) where most *E. coruscans* juveniles were present are large-scale features that agree with the observed habitat preference of these species. However, because of the difference in habitat classification scale, establishing a conclusive connection between the observed bottomfish distributions and mega-scale bathymetric features still requires further investigation. In the case of BRFA H, previous fishing surveys suggested that this area was possibly a nursery ground for *E. coruscans* (Kelley, pers. comm.). With the smallest mean length and about 75 percent of all measured juveniles (<61 cm) in this study coming from the BRFA H region, it is highly likely that a nursery ground for *E. coruscans* exists in this area.
The metrics Interval MaxNo and Time to MaxNo do not appear to be effective measures for assessing differences in habitat preference. The amount of time it took each species to reach MaxNo for a given deployment was not significantly different among the four habitat types. The change in MaxNo over time, however, does highlight the schooling behavior in three of the four species studied and may thus be valuable in identifying behavioral trends. The observed schooling and non-schooling behaviors are consistent with what is known for these Eteline snappers (Ralston et al., 1986; Haight, 1989; Kelley and Moriwake, 2011). Also, as seen in figure 10 for *E. carbunculus*, a video recording time of 40 minutes may not be adequate in detecting MaxNo as these figures indicate a possible continued increase in abundance after the 40 minute mark. Increasing the recording length for future BotCam deployments may be necessary.

**CONCLUSIONS**

This study has improved our understanding of the species-specific ecology of four Eteline snappers in the main Hawaiian Islands. Habitat preferences based on relative abundance and length-frequency distributions showed that habitat types other than hard-high are important to each of these species often as a result of ontogenetic shifts in habitat utilization. Given that these species are found throughout the Indo-Pacific, these findings may provide the framework for predicting species distributions outside of Hawaii. With juveniles of *Pristipomoides filamentosus* and *Etelis coruscans* associated mostly with hard-low habitats, it is imperative that future definitions of the bottomfish essential fish habitat take into account habitat associations by life stage. Although some species share similar preferences, it is also clear that bottomfish distributions are species-specific and cannot be generalized for all members of Hawaii’s bottomfish fishery. By increasing our knowledge of individual species ecology, the results of this study can aid in the improvement of ecosystem-based management strategies and better define species-specific essential fish habitats. Future work should focus on assessing how much ideal bottomfish habitat is being protected by the current system of BRFAs and identifying high quality habitat areas that may be targeted as future BRFAs.
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