

Spatial and vertical patterns in the tidepool fish assemblage on the island of O`ahu

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Abstract The microtides, wave regimes, and relative isolation of the Hawaiian archipelago may provide unique environmental and biogeographic effects that shape the structure of tidepool fishes. We sampled fishes across a narrow gradient at low tide from 6 sites on the island of O`ahu. We tested predictions of the hypotheses that environmental conditions (pool depth, volume, macroalgal cover, temperature, and salinity) would result in a vertically structured tidepool fish assemblage unique to basalt or limestone rocky shores. 343 fish were recorded from 40 pools, and 19 species from 10 families were identified. Tidepool fish diversity (H' : O`ahu=2.4; Sites Average=0.0–0.9) was typical for tropical islands, with members from Gobiidae (5 species), Blenniidae (4 species), Pomacentridae (3 species), Acanthuridae (2 species) and Kuhliidae (2 species)

among the most common. Endemism (32%) was higher than other well studied assemblages yet similar to Hawaiian reef fishes (25%). Assemblage abundance varied among shores with basalt or limestone substrate, among sites, and vertically among high, mid, and low pools. In general, blenniids occurred at higher proportions on limestone shores and gobiids were more common on basalt shores. High pools were characterized by an abundance of a small sized (29.0 mm median standard length) blenniid *Istiblennius zebra*, while the blenniid *Entomacrodus marmoratus* and wrasses *Thalassoma* spp. were more common in low pools. Temperature was the best environmental predictor of assemblages and this relationship warrants further investigation. Our findings indicate that assemblages can vary across a narrow geographical range and intertidal shore.

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Introduction

Intertidal fish assemblages are known to vary in composition across latitudes and continents, between regions, and within individual localities (Gibson and Yoshiyama 1999). Geographic patchiness, dispersal abilities, and evolutionary history explain the distribution of species across latitudes and continents, while abiotic factors often contribute to patterns at

regional and local scales (Gibson and Yoshiyama 1999). Vertical gradients in temperature, air exposure, wave action, and salinity can occur across the shore. As water recedes during low tide, fishes that reside in pools (residents) are more tolerant to these variable conditions and the most physiologically tolerant species occur higher on-shore (Yoshiyama et al. 1986; Zander et al. 1999). Substrate type also can contribute to patterns in tidepool fish assemblages. Examples can be found in central California, U.S.A., where stichaeids and pholids are found in tidal boulder fields while heavy vegetated pools are often dominated by cottids and clinids (Yoshiyama et al. 1986) and in the Mediterranean where rock structures affect the species composition (Macpherson 1994). Pool rugosity, volume, and depth can further contribute to tidepool fish community patterns (Griffiths 2003). Isolated oceanic island chains, like the Hawaiian Islands, provide an opportunity to explore the importance of abiotic factors and biogeography in shaping fish assemblage structure in these islands, as has been done for numerous continental shores.

Tidepool fish assemblages are known to exhibit distinct biogeographic affinities resulting from the dispersal abilities of larvae and the degree of geographic connectedness between populations (Prochazka et al. 1999). For example, central California and southern Chile have similar environmental regimes but distinct intertidal fish fauna (Boyle and Horn 2006). Similarly, islands often have different flora and fauna in contrast to nearby mainland populations. The marine waters surrounding the Hawaiian archipelago contain many tropical fish species that co-occur throughout the Indo-West Pacific and presumably these islands serve as a stepping stone for dispersal across a vast oceanic barrier (Randall 2007). However, the isolation allows for a high number of endemic fish species; 25% of the Hawaiian island marine fish fauna are endemic (Randall 2007). Therefore, the isolated nature of Hawaiian intertidal zones in combination with the typically harsh environmental conditions may facilitate speciation and result in a unique assemblage of intertidal fishes.

The tropical location and tidal conditions in the state of Hawaii may influence the vertical and spatial patterns of fishes in the intertidal zone. Tides in Hawaii are considered microtidal with an amplitude of less than 1 m (Gosline 1965; Abbott 1999). The islands of Hawaii are located in the trade wind belt

and seasonally directed winds drive wave height and determine which shores (north, south, east, or west) experience wave swell at different times of the year (Gosline 1965; Abbott 1999; Bird 2006). The combination of microtides and surge limit air exposure for intertidal organisms and the vertical span of the intertidal zone is much reduced in comparison to the extensive vertical span of other well studied intertidal shores (Gosline 1965; Abbott 1999). Nonetheless, pools are abundant along Hawaiian shores (Gosline 1965) and are apparent on spring low tides that occur in summer daylight hours when temperatures are at their peak. Additionally, O`ahu has both basalt and carbonate based shores (Gosline 1965; Abbott 1999). Basalt shores are often barren of lush macroalgae unlike rough and porous limestone shores (Abbott 1999), thus these types of shores may provide different habitats best suited for the survival of different species of fishes.

During the approximately 35 years since the first observational description of Hawaiian intertidal fishes (Gosline 1965), much has changed in the near shore environment. Changes include the invasion of palatable and unpalatable alien algae (Stimson et al. 2001; Smith et al. 2002), increased fishing pressure (Friedlander and DeMartini 2002), and altered temperatures and sea level from global warming (Jokiel and Brown 2004). However, it is not known if these changes have impacted the fish assemblages in the intertidal habitat. Additionally, comparable descriptive studies on tropical and temperate intertidal zones focus on quantification of resident fishes found in pools during the low tide (Horn et al. 1999). Gosline (1965) detailed observations of fishes on high and low tides in these coastal zones but robust quantification was not provided.

The aims of this study were to describe the tidepool fish assemblage for the island of O`ahu and examine fish assemblage structure across and among shores. We tested the hypothesis that tidepool fishes would be vertically distributed. Further, we tested the hypothesis that intertidal fish communities would vary among shores with different substrate type (basalt or limestone). Lastly, the isolation of the Hawaiian archipelago is hypothesized to result in a tidepool fish community for the island of O`ahu with high species abundance but low richness and high endemism.

Materials and methods

To describe assemblage patterns and abundances of tidepool fishes on O’ahu, six rocky intertidal sites were chosen for sampling: `Ewa Beach, Turtle Bay, Nānākuli, Sandy Beach, Makapu`u and Diamond Head (Fig. 1). These sites were selected to ensure a representative sample of fishes and to test the hypothesis that substrate type correlates with structure. Sites are located on the south, east, west, and north shores and included tidal benches composed of basalt or limestone (Table 1).

To examine the vertical structure of tidepool fishes across the shore, six to eight pools distributed in an on-offshore direction within the intertidal habitat at each site were chosen haphazardly for collection of fishes. Because the Hawaiian Islands have microtides and a limited range of vertical intertidal zonation, tidal height was not obvious, hence pools were sampled as high, mid, or low depending on their location to the water at time of peak low tide. Pools located near the water’s edge or subtidal zone and usually covered in fleshy macroalgae were referred to as low, whereas barren pools near terrestrial vegetation and above the gastropod *Nerita* spp. and within the gastropod *Littoraria* spp. zone were referred to as high. Any pools found between the high and low

pools were referred to as mid. Pools in the high zone were within the intertidal and not supratidal as these pools are submersed on the incoming high tide (personal observations TEC). Fishes were collected from at least two pools in each position (high, mid, low) at each site for a total of 6–8 pools.

Each site was visited once and sampled for fishes in high, mid, and low pools (Table 1). All sampling occurred during the summer months May–August 2008, on a spring low tide. Multiple sites could not be sampled in 1 day as microtidal conditions quickly limits access to pools. Summer months were chosen for the sampling period because this is when spring low tides co-occur in daylight hours. These spring low tides ranged from -0.12- to -0.06 m. The peak low tides during the sampling period occurred in the morning hours 06:00–10:11. Sampling began at least 1 h prior to peak low tide and continued until high tide prevented accessibility of pools. High, mid and low pools were haphazardly sampled during each site visit.

Non-destructive sampling was preferred as it lessens the impact on the tidepool community and studies on methodology in other intertidal habitats have found similar results regardless of techniques (Gibson 1999; Griffiths 2000). A battery operated submersible bilge pump and various sized buckets

Fig. 1 Map of the island of O’ahu with the location of six intertidal sites

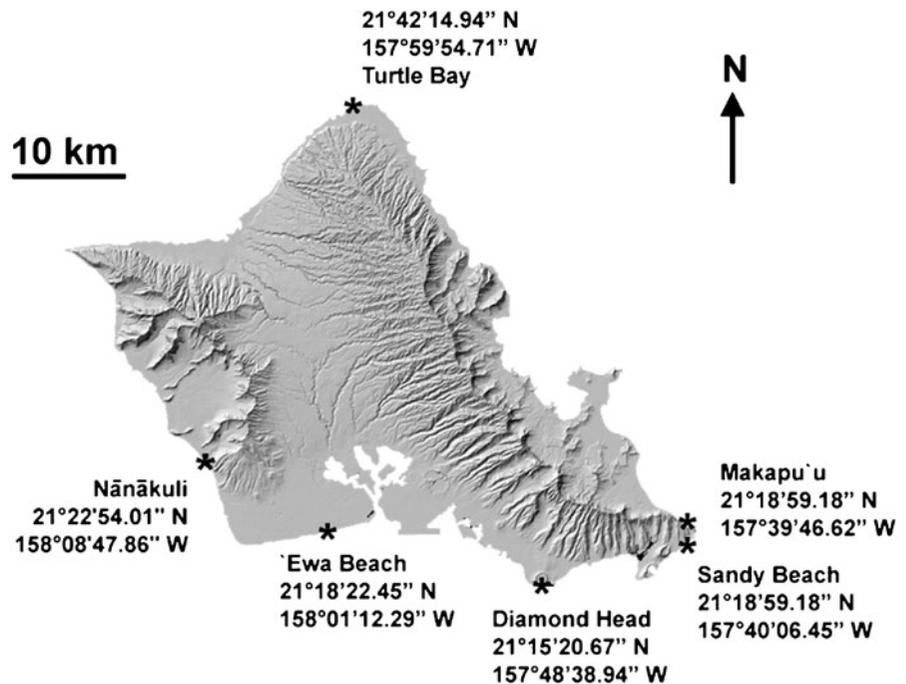


Table 1 Site name, substrate type, location and date, tidal height sampled

| Sites | Abbreviation | Substrate Type | O'ahu Shore Location | Date Sampled in 2008 | Low Tide Height (m) |
|--------------|--------------|----------------|----------------------|----------------------|---------------------|
| Diamond Head | D | Basalt | Southeast | August 1 | -0.06 |
| Makapu'u | M | Basalt | East | June 30 | -0.12 |
| Sandy Beach | S | Basalt | East | May 30 | -0.09 |
| ʻEwa Beach | E | Limestone | Southwest | June 3 | -0.15 |
| Nānākuli | N | Limestone | West | July 2 | -0.12 |
| Turtle Bay | T | Limestone | North | June 5 | -0.12 |

were used to drain and bail each pool of seawater. Any fishes present were scooped up by hand or with hand-net. A chopstick or finger was used to probe gently into holes and crevices to ensure the capture of small cryptic fishes. Captured fishes were kept alive and placed in aerated buckets of seawater for identification and measurements.

To determine the abundance and diversity of fishes each individual collected was counted, identified, and measured prior to release. In the field, fishes were anesthetized in buckets of seawater with MS-222 and then identified to the lowest possible taxon using dichotomous keys of Hawaiian Shore Fishes (Randall 2007). A hand lens was used to view any diagnostic features difficult to observe with an unaided eye. Once the species was identified and recorded, the standard length of fishes greater than 15 mm SL was measured. Each individual was assigned an id number, and its size and locality (both site and pool position) recorded. To minimize impact to the tide-pool community, fishes were revived in aerated seawater and released to the tidepool from which they were collected after pools were inundated from rising tides or to a nearby location. Fishes were kept in buckets until all sampling had concluded to avoid re-sampling. On rare occasions, fishes were returned while sampling was ongoing but any sampled pools were >20 meters from release site.

The statistical software package Primer-E (Clarke and Warwick 2001) was used to analyze the spatial distribution and abundance of fishes among and across shores. Because of the difficulty in identifying small *Bathygobius* spp. a conservative approach was taken and in this analysis all *Bathygobius* spp. were grouped into one taxonomic category. However, results did not differ when all *Bathygobius* were grouped by genus or when those identified to species level were considered separately. These counts of

fishes were expressed as a proportion of total number of individuals found per pool and each pool was considered a replicate of position (high, mid, or low) nested within a site. Abundances were square-root transformed to down-weight common species and account for the patchy nature of tidepool species (Gibson and Yoshiyama 1999). These data were then used to construct Bray-Curtis similarity matrix between sites and pool position. Dendrograms were used to visualize the similarity of fishes by site, shore substrate type, and pool position. Further, PERMANOVA with pool position nested within sites and sites nested within substrate was used to statistically test the hypothesis that fishes were vertically and spatially distributed. A series of one-way SIMPERs were used to analyze which species contributed to the observed similarity patterns.

To examine if sizes of fishes varied across the shore we compared the standard length (mm) of the most abundant species that occurred on O'ahu: *Abudefduf sordidus*, *Bathygobius cocosensis*, *Entomacrodus marmoratus*, and *Istiblennius zebra*. Sizes of fishes across sites were pooled for each tide pool position and differences between length medians were tested with Kruskal-Wallis or Mann-Whitney tests.

To describe the assemblage and test diversity hypotheses, species richness (S) and Shannon (H') indices were computed for each pool position at each shore and for the island of O'ahu. For site and position comparisons, each pool was considered a replicate sample and computed values were compared statistically with a two-way ANOVA (sites and position). Prior to testing data were log transformed to meet parametric requirements and alpha values were adjusted to account for multiple comparisons. To determine S and H' for the island of O'ahu all species were pooled from every site and values reported.

To characterize conditions experienced by tidepool fishes in O’ahu, a snapshot sample of physical conditions and surroundings were collected from tidepools during the sampling period. Prior to fish collection, the maximum pool depth, length, and width was measured with a transect tape and were used to calculate a rough estimate of pool volume. Salinity measurements (‰) were collected with a handheld refractometer, and a visual estimate was made of algal percent cover within and along the edges of pools. The surface water temperature was recorded with 2–3 Hobo temperature loggers placed in sampled and unsampled pools during the low tide window. At some sites measurements were not collected because of instrument failure or observer oversight, thus only sites with all measurements were included in analyses.

To test if any of these physical features were related to observed fish assemblage patterns a distance based redundancy ordination analysis (dbRDA) was used in combination with a distance based linear model. The distance based linear model (DISTLM function in PRIMER-E) models the relationship between predictor variables and the multivariate data cloud based on a multiple regression. This routine finds the linear combination of variables that best explains the greatest variation in the data cloud and the amount of variance each covariate explains separately providing a pseudo-F statistical value. dbRDA is an ordination analyses that visualizes these results. Predictors that best explain the data cloud are viewed as vectors in a biplot. The longer the vector the larger the effect of the predictor (Anderson et al. 2008).

Table 2 Proportion and total # of fish species by family (F) that were collected and identified in the high, mid, and low pools at the 6 sites. *B. spp* = *Bathygobius*, *E. spp* = *Entomarcodus*, *T. spp* = *Thalassoma*; see Table 3 for other taxonomic abbreviations

| Taxa | F | Diamond Head | | | Makapu’u | | | Sandy Beach | | | ’Ewa Beach | | | Nānākuli | | | Turtle Bay | | | Total # |
|------------------------|----|--------------|-----|-----|----------|-----|-----|-------------|-----|-----|------------|-----|-----|----------|-----|-----|------------|-----|-----|---------|
| | | H | M | L | H | M | L | H | M | L | H | M | L | H | M | L | H | M | L | |
| <i>B. cocosensis</i> | G | – | 0.6 | 0.6 | – | 0.6 | 0.0 | – | 0.8 | 0.3 | – | – | – | – | – | – | 0.3 | 0.1 | 0.3 | 64 |
| <i>I. zebra</i> | B | 0.3 | – | – | 0.7 | 0.1 | 0.0 | 0.1 | 0.2 | 0.2 | 0.2 | 0.4 | – | 1.0 | – | – | 0.2 | 0.2 | 0.4 | 63 |
| <i>A. sordidus</i> | P | 0.8 | 0.3 | 0.2 | – | 0.1 | 0.2 | – | – | – | – | 0.1 | 0.1 | – | 1.0 | 1.0 | – | 0.0 | – | 51 |
| <i>B. spp.</i> | G | – | – | 0.2 | 0.3 | – | 0.1 | 0.7 | – | 0.2 | 0.5 | – | – | – | – | – | 0.3 | 0.2 | 0.3 | 46 |
| <i>E. marmoratus</i> | B | – | 0.1 | 0.0 | – | – | – | – | – | – | 0.1 | 0.4 | 0.7 | – | – | – | – | 0.1 | 0.1 | 36 |
| <i>A. triostegus</i> | A | – | – | – | – | 0.1 | 0.2 | – | – | 0.3 | – | – | – | – | – | – | 0.1 | 0.1 | – | 20 |
| <i>K. sandvicensis</i> | K | – | – | – | – | – | 0.1 | – | – | – | – | – | – | – | – | – | – | 0.0 | – | 7 |
| <i>B. coalitus</i> | G | – | – | – | – | – | – | – | – | – | 0.2 | 0.1 | 0.0 | – | – | – | – | 0.0 | – | 6 |
| <i>E. spp.</i> | B | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 0.1 | 0.1 | – | 6 |
| <i>K. xenura</i> | K | – | – | – | – | – | 0.1 | – | – | – | – | – | – | – | – | – | – | – | – | 5 |
| <i>T. purpureum</i> | L | – | – | – | – | – | – | – | – | – | – | – | 0.1 | – | – | – | – | 0.0 | – | 5 |
| Creediidae | C | – | – | – | – | – | 0.1 | – | – | – | – | – | – | – | – | – | – | – | – | 3 |
| <i>M. cephalus</i> | M | – | – | – | – | – | 0.1 | – | – | – | – | – | – | – | – | – | – | – | – | 3 |
| <i>B. cotticeps</i> | G | – | – | – | – | – | 0.0 | – | – | – | – | – | – | – | – | – | – | – | – | 2 |
| <i>T. spp.</i> | L | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 0.0 | – | 2 |
| <i>A. abdominalis</i> | P | – | – | – | – | – | 0.0 | – | – | – | – | – | – | – | – | – | – | – | – | 1 |
| <i>B. gibbifrons</i> | B | – | – | – | – | – | – | – | – | 0.1 | – | – | – | – | – | – | – | – | – | 1 |
| <i>C. lunula</i> | Ch | – | – | – | – | – | 0.0 | – | – | – | – | – | – | – | – | – | – | – | – | 1 |
| <i>C. obscurus</i> | B | – | – | – | – | – | – | – | – | – | – | – | 0.0 | – | – | – | – | – | – | 1 |
| <i>D. griessingeri</i> | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 0.0 | – | 1 |
| <i>G. anjerensis</i> | G | – | – | – | – | – | – | 0.1 | – | – | – | – | – | – | – | – | – | – | – | 1 |
| <i>P. imparipennis</i> | P | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 0.1 | – | – | 1 |
| <i>S. balteata</i> | L | – | – | – | – | 0.1 | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 |
| Total # | | 12 | 15 | 25 | 6 | 14 | 45 | 7 | 12 | 19 | 11 | 17 | 23 | 18 | 3 | 18 | 16 | 50 | 16 | 327 |

Results

A total of 343 fishes were recorded and 327 individuals actually captured from six sites (40 sampled tidepools) on the island of O`ahu. Fishes that were observed but not captured were often young-of-the-year gobies or blennies. Of the 327 captured, 25 taxa were recorded and 19 species ($H^{\prime}=2.5$) identified from 10 families (Tables 2 and 3). Those taxa identified to only the

family or genus level were of small size and belonged to the genera *Bathygobius*, *Entomacrodus*, *Thalassoma*, or Family Creediidae.

The most abundant fishes were from 4 families and include (in order of abundance) *Bathygobius cocosensis* (Gobiidae), *Istiblennius zebra* (Blenniidae), *Abudefduf sordidus* (Pomacentridae), *Entomacrodus marmoratus* (Blenniidae), and *Acanthurus triostegus* (Acanthuridae) (Tables 2 and 3).

Table 3 Distribution, habitat, and resident status of tidepool species and their families (family abbreviation follows) with a comparison to assemblage determined by Gosline (1965). R = resident species (permanent inhabitants), PR = partial residents

(spend part of life in intertidal), T = transients (visitors); + = present - = absent in Gosline (1965) splash zone assemblage. Distribution and habitat according to Randall (2007), definitions follow Gibson (1982)

| Family <i>Genus species</i> | Biogeographic Distribution | Habitat | Resident Status | Presence/Absence in Gosline (1965) |
|--|--------------------------------------|--|--------------------|---------------------------------------|
| Acanthuridae (A) | | | | |
| <i>Acanthurus triostegus</i> | Indo-Pacific, Tropical E. Pacific | Juveniles in tidepools, adults shallow water | PR | + |
| Blenniidae (B) | | | | |
| <i>Blenniella gibbifrons</i> | Indo-Pacific | 1–3 m | R | – |
| <i>Cirripectes obscurus</i> | Hawaiian Islands | 1–6 m | R | – |
| <i>Entomacrodus marmoratus</i> | Hawaiian Islands | Tidepools | R | + |
| <i>Istiblennius zebra</i> | Hawaiian Islands | High tidepools | R | + |
| Chaetodontidae (Ch) | | | | |
| <i>Chaetodon lunula</i> | Indo-Pacific | 1–158 m on coral reefs | T | – |
| Creediidae (C) | | | | |
| | N/A | 15–20 m | ? | – |
| Gobiidae (G) | | | | |
| <i>Bathygobius coalitus</i> | Indo-Pacific, W. Pacific | Intertidal zone | R | – |
| <i>Bathygobius cocosensis</i> | Indo-Pacific | Tidepools | R | + |
| <i>Bathygobius cotticeps</i> | Indo-Pacific, W. Pacific | Rocky tidepools, lower intertidal | R | – |
| <i>Discordipinna griessingeris</i> | Indo-Pacific | 1–37 m | ? | – |
| <i>Gnatholepis anjerensis</i> | Indo-Pacific | Usually occurs in >2 m, tidepools | R | – |
| Kuhliidae (K) | | | | |
| <i>Kuhlia sandvicensis</i> | Indo-Pacific | Shallow-water | PR | + |
| <i>Kulia xenura</i> | Hawaiian Islands | Juveniles occur in tidepools, adults offshore | PR | – |
| Labridae (L) | | | | |
| <i>Stethojulis balteata</i> | Hawaiian Islands & Johnston Atoll | Shallow-water to 22 m | T | – |
| <i>Thalassoma purpurum</i> | Indo-Pacific | Rocky shores shallow-water | T | + |
| Mugilidae (M) | | | | |
| <i>Mugil cephalus</i> | Circumglobal warm-waters | Inshore protected waters | T | – |
| Pomacentridae (P) | | | | |
| <i>Abudefduf abdominalis</i> | Hawaiian Islands & Johnston Atoll | Young often in tidepools, adults inshore | PR | – |
| <i>Abudefduf sordidus</i> | Indo-Pacific | Young often in tidepools, adults inshore | PR | + |
| <i>Plectroglyphidodon imparipennis</i> | Indo-Pacific | Reefs usually >4 m | R | – |

The nMDS and dendrograms (Fig. 2) reveal a large amount of overlap in assemblage similarity among sites and pool position, although the centroid based nMDS plot (Fig. 2, top) shows clusters of sites based on substrate type (basalt or limestone). The limestone sites are less clustered than basalt sites as the pool samples from Nānākuli are more distinct. Furthermore, site assemblages differed among high, mid, and low pools (Fig. 2, bottom). Results from the PERMANOVA support significant differences among pool positions, sites, and sites with different substrate types (Table 4).

Different abundances of the common fishes contribute to the dissimilarity among tested groups (Tables 2 and 5). Although the presence of species was similar among basalt and limestone based shores, there were significant differences in the proportion of blennies and gobies. *Bathygobius* spp. occurred at higher proportions on basalt shores while the blennies *I. zebra* and *E. marmoratus* occurred at higher proportions at limestone shores (Table 5). Within the basalt shores (Diamond Head, Makapu`u, Sandy Beach) roughly 20% of community dissimilarity was accounted for by the differing proportions of *I. zebra* and *Bathygobius* spp. (Table 2). *Abudefduf sordidus* was absent from Sandy Beach but abundant at both Diamond Head and Makapu`u. This species

accounts for 30% difference between Sandy Beach and Diamond Head and 12% of the differences between Sandy Beach and Makapu`u. Assemblages also varied among limestone sites. Nānākuli assemblage was most dissimilar from other limestone sites (84% dissimilar from Turtle Bay, 88% dissimilar from `Ewa Beach) as it has a higher proportion (0.7) of *I. zebra* (which accounted for ~20% of said dissimilarities). The composition at `Ewa Beach and Turtle Bay were only 65% dissimilar and the abundance of *E. marmoratus* accounted for 20% of this dissimilarity.

The composition of fishes varied vertically across the shore (Fig. 2). Assemblages differences were greatest between high and low pools (Fig. 2; Table 5). *Istiblennius zebra* was more common in high pools and *E. marmoratus*, *A. triostegus*, and *Thalassoma* spp. were more common in low pools (Table 5). Also, out of four common species examined (*A. sordidus*, *Bathygobius* spp., *E. marmoratus*, and *I. zebra*) the median SL (mm) of *I. zebra* was smaller in high pools (Kruskal-Wallis, p -value<0.001, Dunn's Method, p -value<0.05) (Fig. 3). High pools can therefore be characterized by a high number of small sized individuals of *I. zebra*.

Diversity of fishes measured as species richness and H' did not statistically (at adjusted $\alpha=0.025$)

Fig. 2 Non-metric multidimensional scaling ordinations (nMDS plots) on the basis of Bray-curtis dissimilarity measure of each pool (top left symbols = sites, see Table 1 for abbreviation of site names; bottom left symbols = position) and of centroids (right) of sites (top right) and pool position nested within sites (bottom right symbols = sites). Dendrograms in upper left corners are the similarity distance between the centroids of sites (top left) and pool position (bottom left) and serve as a legend for symbols in nMDS plots. Note the differences shown as distance between basalt and limestone based shores, sites, and pool position

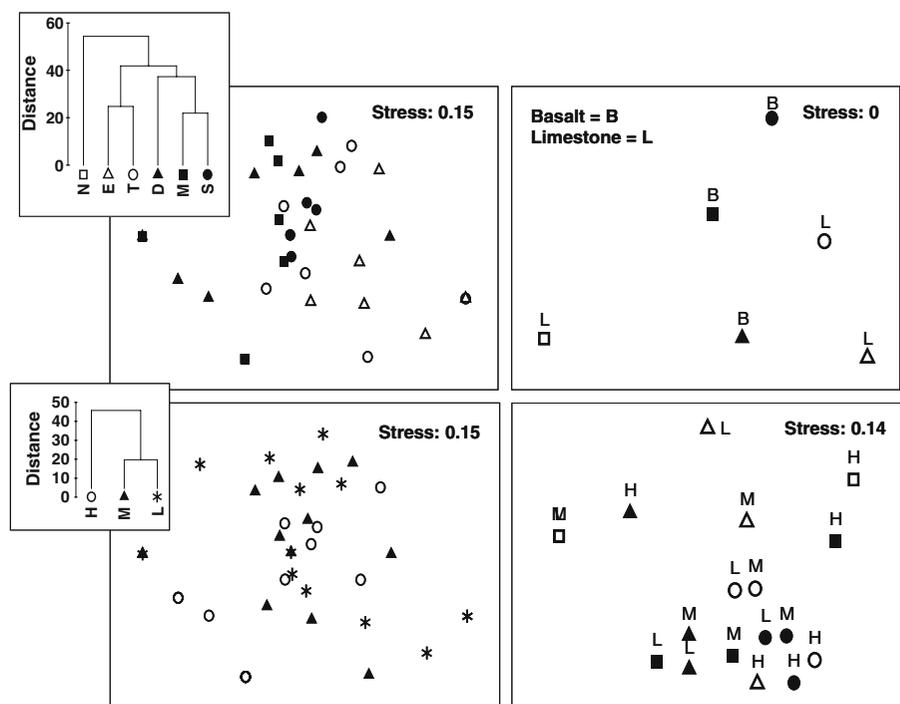


Table 4 Results of PER-MANOVA showing the significant assemblages of fishes. Results are out of 1,000 permutations

| Source of variation | df | SS | MS | Pseudo-F | P (perm) | Unique Perms |
|-----------------------|----|---------|--------|----------|----------|--------------|
| Substrate = Su | 1 | 5742.7 | 5742.7 | 3.9 | 0.01 | 999 |
| Sites (Su) | 4 | 20119.0 | 5029.8 | 3.4 | 0.001 | 998 |
| Position (Sites (Su)) | 12 | 41222.0 | 3435.2 | 2.4 | 0.001 | 997 |
| Residual | 22 | 32114.0 | 1459.7 | | | |

vary across shores but did vary among sites (S: Two-way ANOVA, p -value <0.01 ; H' : two-way ANOVA, p -value <0.001) (Fig. 4). Nānākuli ($S=1.0\pm 0.2$ SE, $H'=0.0\pm 0.0$ SE) had low species richness and H' index but was within range of values determined for Diamond Head ($S=2.0\pm 0.3$ SE, $H'=0.5\pm 0.2$) and Sandy Beach ($S=2.3\pm 0.2$ SE, $H'=0.7\pm 0.1$ SE).

Diversity was higher for Makupu`u ($S=3.5\pm 0.6$ SE, $H'=0.9\pm 0.3$ SE), Ewa Beach ($S=3.2\pm 1.3$ SE, $H'=0.9\pm 0.2$ SE) and Turtle Bay ($S=3.7\pm 0.7$ SE, $H'=0.9\pm 0.2$ SE).

Measured conditions experienced by fishes during sampling period varied between high, mid, and low pools (Table 6). Temperature varied notably as pool

Table 5 Results from SIMPER analyses showing the species and their proportions that contribute to ~80.0% of the dissimilarity among basalt and limestone shores and across high, mid, and low pools

| Species | Dissimilarity=71.3% | | Av. Dissimilarity (Stdev) | % Contribution | Cumulative% |
|--------------------------------|---------------------|-----------|---------------------------|----------------|-------------|
| | Basalt | Limestone | | | |
| | Av. Abund | Av. Abund | | | |
| <i>Bathygobius</i> spp. | 0.6 | 0.3 | 16.3 (1.2) | 22.9 | 22.9 |
| <i>Istiblennius zebra</i> | 0.3 | 0.4 | 14.3 (1.1) | 20.1 | 43.0 |
| <i>Abudefduf sordidus</i> | 0.3 | 0.2 | 11.8 (0.8) | 16.5 | 59.5 |
| <i>Entomacrodus marmoratus</i> | 0.1 | 0.3 | 10.3 (0.8) | 14.5 | 74.0 |
| <i>Acanthurus triostegus</i> | 0.1 | 0.1 | 3.5 (0.5) | 4.9 | 78.9 |
| | Dissimilarity=67.3% | | | | |
| | High | | | | |
| | Av. Abund | Av. Abund | Av. Dissimilarity (Stdev) | % Contribution | Cumulative% |
| <i>Istiblennius zebra</i> | 0.6 | 0.3 | 17.6 (1.2) | 26.2 | 26.2 |
| <i>Bathygobius</i> spp. | 0.3 | 0.6 | 16.6 (1.2) | 24.7 | 50.9 |
| <i>Abudefduf sordidus</i> | 0.2 | 0.3 | 12.6 (0.8) | 18.6 | 69.5 |
| <i>Entomacrodus marmoratus</i> | 0.0 | 0.2 | 6.4 (0.7) | 9.5 | 79.0 |
| <i>Acanthurus triostegus</i> | 0.0 | 0.1 | 1.0 (0.5) | 2.8 | 81.8 |
| | Dissimilarity=67.1% | | | | |
| | Mid | | | | |
| | Av. Abund | Av. Abund | Av. Dissimilarity (Stdev) | % Contribution | Cumulative% |
| <i>Bathygobius</i> spp. | 0.6 | 0.5 | 14.4 (1.1) | 21.4 | 21.4 |
| <i>Entomacrodus marmoratus</i> | 0.2 | 0.3 | 12.5 (0.9) | 18.7 | 40.1 |
| <i>Abudefduf sordidus</i> | 0.3 | 0.2 | 11.8 (0.9) | 17.6 | 57.7 |
| <i>Istiblennius zebra</i> | 0.3 | 0.1 | 9.7 (1.0) | 14.4 | 72.1 |
| <i>Acanthurus triostegus</i> | 0.1 | 0.1 | 4.6 (0.6) | 6.8 | 78.9 |
| <i>Thalassoma purpurum</i> | 0.0 | 0.1 | 2.2 (0.5) | 3.3 | 82.1 |
| | Dissimilarity=79.5% | | | | |
| | Low | | | | |
| | Av. Abund | Av. Abund | Av. Dissimilarity (Stdev) | % Contribution | Cumulative% |
| <i>Istiblennius zebra</i> | 0.1 | 0.6 | 20.9 (1.4) | 26.4 | 26.4 |
| <i>Bathygobius</i> spp. | 0.5 | 0.3 | 14.6 (1.2) | 18.4 | 44.7 |
| <i>Entomacrodus marmoratus</i> | 0.3 | 0.0 | 11.5 (0.7) | 14.4 | 59.2 |
| <i>Abudefduf sordidus</i> | 0.2 | 0.2 | 10.2 (0.8) | 12.9 | 72.0 |
| <i>Acanthurus triostegus</i> | 0.1 | 0.0 | 4.3 (0.5) | 5.4 | 77.4 |
| <i>Thalassoma purpurum</i> | 0.1 | 0.0 | 1.7 (0.4) | 2.2 | 79.6 |

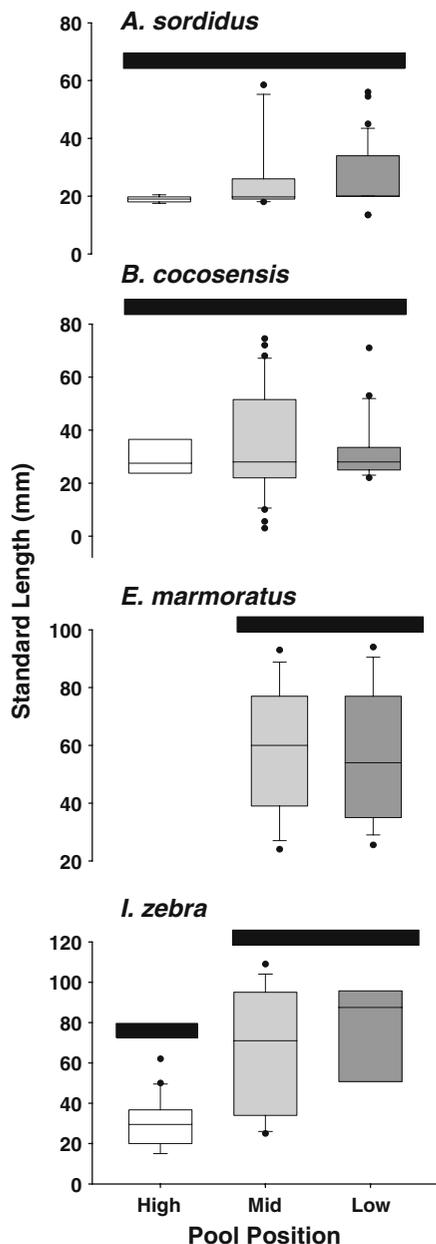


Fig. 3 Boxplots showing the distribution (median, quartiles, and outliers) of standard length (mm) for four common taxa *A. sordidus* ($n=51$), *B. cocosensis* ($n=63$), *E. marmoratus* ($n=34$), and *I. zebra* ($n=51$) collected from high, mid, and low pools. Bars above boxplots represent similar statistical groupings from Dunn’s multiple comparisons test when Kruskal–Wallis or Mann–Whitney test indicated significant differences among pool position

temperatures co-varied with substrate type. Basalt shores were warmer than limestone shores. The distance based linear model found temperature to be a significant predictor (Pseudo- $F=2.9$, p -value <

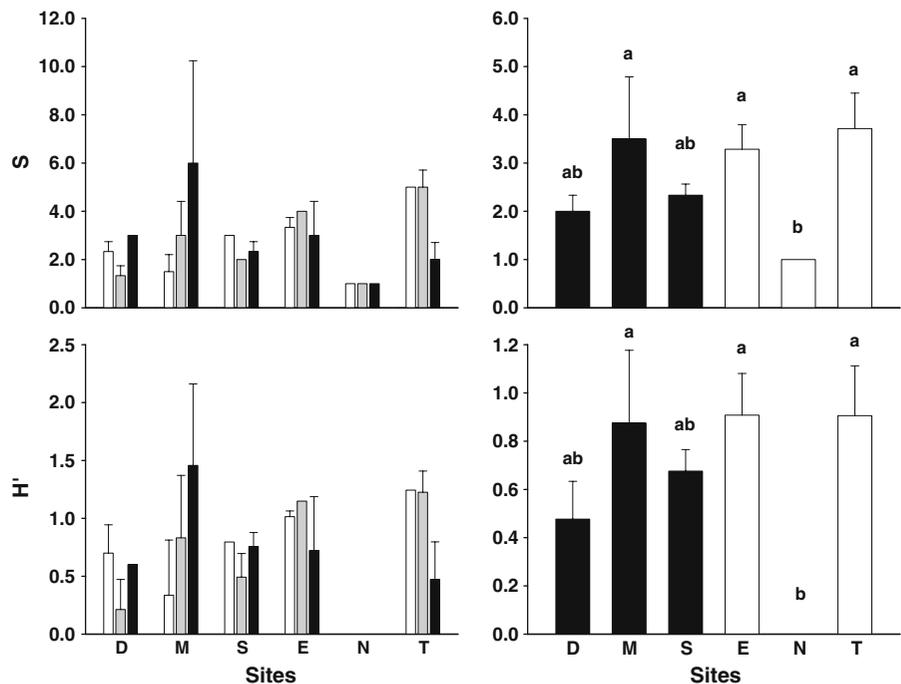
0.001) of assemblages but, the overall best model included all variables (pool volume, depth, salinity, macroalgal cover, and temperature). This can be seen in the dbRDA biplots (Fig. 5). The first three axes of the dbRDA explain 94% of the variation of the fitted model but only 25% of the total variation in the data pool. Tidepools at basalt and limestone shores fall along these axes varying with temperature and macroalgae; basalt shores tended to have a positive correlation with dbRDA axes 1 while limestone shores had a negative correlation with dbRDA axes 1. Sixty-eight percent of sampled tidepools had a full set of environmental measurements and were included in these multivariate analyses.

Discussion

Our study revealed a tidepool fish assemblage for O`ahu island composed of 19 species from 10 families. Results of this study support the hypothesis that basalt and limestone shores have distinct intertidal fish assemblages and that these assemblages are possibly related to temperature. Results also support the hypothesis that the tidepool fishes are vertically distributed. This vertical distribution coupled with the variation of assemblages among sites and substrate types, reveals a surprising amount of structure within a limited geographical area and across a narrow shore.

The tidepool fish assemblage in O`ahu is similar to other isolated tropical islands which have low species richness and a high number of endemic species, yet assemblage members are from taxonomic families that occur throughout the tropics. The tidepool species on O`ahu were largely distributed across the Indo-West Pacific (68%) and 32% were endemic to Hawaii and Johnston Atoll. This level of endemism is within range of the 25% determined by Randall (2007) for all marine fishes in Hawaii and it is higher than percentages recorded for most regions (Prochazka et al. 1999) yet it is lower than 61.7% of endemic rockpool fishes (mostly tripterygiids) that occur in cool temperate New Zealand waters (Paulin and Roberts 1993). The most abundant fish families were Gobiidae (5 species) >Blenniidae (4 species) >Acanthuridae (2 species) >Pomacentridae (3 species), and Kuhliidae (2 species). Most of these families are common in studied tropical intertidal habitats throughout the world except kuhliids which are absent in the west Atlantic (Hiatt and

Fig. 4 Comparison of species richness (S , top) and diversity (H' bottom) for tidepool fishes among six shores (right: black = basalt, white = limestone shores) and among high (white), mid (gray), low (black) pools nested within site (left) on the island of O'ahu. Letter groups above bars represent similar statistical groups (Two-way ANOVA with an adjusted $\alpha < 0.025$)



Strasburg 1960; Gosline 1965; Lee 1980; Greenfield and Johnson 1990; Duhart and Ojeda 1994; Mahon and Mahon 1994; Prochazka et al. 1999; Greenfield 2003). Notable differences include the absence of serranids, muraenids, and gobiesocids. Gobiesocids are common in many temperate intertidal regions and are found in a few tropical localities but are absent in Hawaii (Prochazka et al. 1999). Serranids are mostly absent in shallow-water collections in Hawaii except for a non-indigenous grouper that is common on coral reefs (Randall 2007). In the Indo-West Central Pacific province (where Hawaii is located) (Duhart and Ojeda 1994) muraenids are commonly found in tidepool communities. Also muraenids are prominent in tidepool collections from Barbados (Mahon and Mahon 1994) and the Marshall Islands (Hiatt and Strasburg 1960) and have been observed in Hawaiian tidepools. The absence of eels in this study could be because of their high mobility and that they are likely to occur in relatively low densities or are likely to be in larger pools that are only isolated from the ocean on the lowest of low tides. It is also possible that more tidepool species on O'ahu would be found if sampling occurred across the year, however, the tropics lack strong seasonality and tropical fish assemblages can be stable over short temporal scales (Chang et al. 1973; Castellanos-Gallindo et al. 2005). Similar

species richness is observed in tidepools at other isolated island chains. For instance, five species were recorded from a study on Easter Island (Duhart and Ojeda 1994), and 23 species were reported in the Seychelles (Prochazka et al. 1999), where as Taiwan, also located in the Indo-West Pacific, has 122 species (Prochazka et al. 1999). Thus it is more likely that low species richness is due to the isolated nature of the island chain and the dispersal ability of fishes.

We found many of the same species in O'ahu's tidepools that Gosline (1965) observed in the intertidal zone for the main islands of Hawaii yet, this study quantifies nearly double the number of species in the intertidal zone. Species richness in exposed rockpools on O'ahu is likely still higher than we determined as a few species, such as holocentrids, were observed but not sampled. Most of the fishes recorded during this study but not included by Gosline (1965) were transient or cryptic. Differences in methodology and definition of habitat possibly account for the discrepancy in species composition between studies. Gosline (1965) made observations of near-shore fishes for the Hawaiian Islands and refers to a spray, splash, and a surge zone. The splash zone is strictly intertidal and the surge zone he describes can be above or below the mean tidal level. This study

Table 6 Average (SE) of environmental variables collected across the shore at 6 sites

| | Approximate Volume (m ³) | Depth (cm) | Temperature (°C) | Salinity (‰) | Algal Cover (%) |
|--------------|--------------------------------------|--------------|------------------|--------------|-----------------|
| Diamond Head | | | | | |
| High | 0.5 (±0.1) | 33.8 (± 2.0) | 28.1 (±0.7) | 33.2 (±0.7) | 22.2 (±14.5) |
| Mid | 0.2 (±0.1) | 42.3 (± 5.0) | 27.4 (±0.5) | 33.5 (±0.3) | 60.7 (±16.0) |
| Low | 1.0 | 40.0 | 28.1 | 33.0 | 100.0 |
| Makapu'u | | | | | |
| High | 0.0 (±0.0) | 20.0 (± 0.0) | 27.3 (±2.8) | 33.2 (±0.7) | – |
| Mid | 0.3 (±0.3) | 27.1 (±21.2) | 25.0 (±1.0) | 32.9 (±1.4) | 16.4 (±10.6) |
| Low | 1.9 (±1.3) | 37.3 (± 7.1) | 25.0 (±0.8) | 38.5 (±1.4) | 5.3 (±14.1) |
| Sandy Beach | | | | | |
| High | 0.3 | 30.0 | 24.2 | 47.0 | – |
| Mid | 1.0 (±0.3) | 40.0 (±14.1) | 24.2 (±0.3) | 40.3 (±6.4) | 35.0 (±42.4) |
| Low | 1.1 (±0.7) | 29.7 (± 7.4) | 24.4 (±0.4) | 40.8 (±3.2) | 77.2 (± 3.5) |
| Ewa Beach | | | | | |
| High | 0.5 (±0.2) | 27.3 (± 2.0) | 22.7 (±0.0) | 36.7 | – |
| Mid | 1.0 | 45.0 | 23.8 | 35.0 (±0.4) | 20.0 |
| Low | 0.1 (±0.1) | 20.3 (± 8.9) | 24.1 (±0.3) | 41.0 (±3.6) | 90.0 |
| Nānākuli | | | | | |
| High | 0.5 (±0.3) | 43.3 (± 2.9) | – | 34.7 (±0.3) | 0.0 (± 0.0) |
| Mid | 0.4 | 35.0 | – | 35.0 | 0.0 (± 0.0) |
| Low | 0.6 | 35.0 | – | 35.0 | 0.0 (± 0.0) |
| Turtle Bay | | | | | |
| High | 0.2 | 15.0 | 25.0 | 35.0 | 25.0 |
| Mid | 0.5 (±0.2) | 18.1 (±12.7) | 25.3 (±1.3) | 33.1 (±0.7) | 59.5 (± 30.1) |
| Low | 0.2 (±0.2) | 12.9 (± 2.9) | 25.3 (±0.7) | 33.6 (±0.4) | 74.1 (± 18.7) |

quantitatively samples fishes in pools at mean low water for O'ahu and thus distinguishes the boundary between intertidal and subtidal zones.

Although the density of fishes varied among limestone and basalt based shores, it is unclear what causes the differing assemblages. In this study basalt shores tended towards higher temperatures and temperature was a predictor of assemblage variation. *Bathygobius* spp., more common on basalt shores, is known to have a high temperature tolerance (thermal maxima ~40°C) (Mora and Ospina 2001). However, a limited set of predictor variables were collected and used in the linear model and temperature alone did not explain a high amount of variation observed in the data pool. Further, *I. zebra* can tolerate conditions on basalt shores as it was present at all shores. Intertidal fishes commonly use holes and crevices for shelter and nesting (Duci et al. 2009). Limestone shores which maybe more easily eroded could provide

crevices that suit the recruitment or survival of blenniid species, like *I. zebra* and *E. marmoratus*. A similar conclusion was reached by Macpherson (1994) in the Mediterranean as a blenny species was absent in a habitat that lacked crevices in three separate sites. Alternatively, this assemblage difference between basalt and limestone shores could be the result of small number of sites sampled in this study. The addition of assemblages from more basalt and limestone shores could clarify the relationship between substrate and abundance patterns.

The among-site differences observed in this study are surprising given the small geographic distance between sites, the similarity in habitat within substrate groups, and the similar small number of species that occur in pools. These differences may be due to temporal recruitment of juveniles or the variation in the nearby subtidal habitat since the assemblages differed in number of partial resident and transient

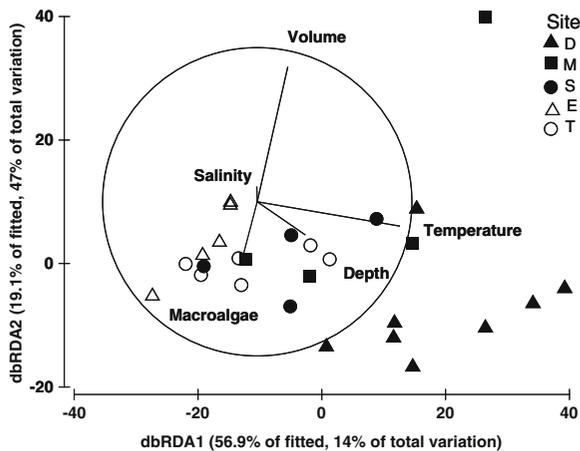


Fig. 5 dbRDA ordination plot displays the relationship between environmental predictors that best explain the variation among pools at different sites. The vectors within the circle show the “effect” of the predictor variables included in the model, the longer the vector from the center the larger the “effect”. Basalt pools are represented by solid symbols while limestone shores are represented by open symbols. Assemblages sampled from basalt pools tend to positively correlate with temperature while assemblages from limestone shores negatively correlated with temperature and fell along the macroalgae cover vector

species. *Acanthurus triostegus*, *A. sordidus*, and *A. abdominalis* are known to recruit to tidepools in summer months. These species grow quickly and move to lower pools and onto reefs as they mature (Randall 2007). Godinho and Lotufo (2010), in Brazil found sites to differ in intertidal fish assemblages and similarly suggested this relationship was due to recruitment differences over a small geographical scale. Seasonality and recruitment at the assemblage level has not been studied for intertidal fishes in Hawaii and no conclusive statements can be made.

Similar to several temperate intertidal environments (Zander et al. 1999; Griffiths et al. 2003), the tidepool fish assemblages in O’ahu were found to be vertically structured and these patterns in abundance are hypothesized to be related to tolerances to harsh conditions that vary across the shore. Diversity as H' and species richness did not vary statistically across the shore but, relatively small within-site sample sizes likely hindered the ability to detect such differences. For the island of O’ahu small sized *I. zebra* were abundant in high pools while most other species and larger sized *I. zebra* occurred in mid and low pools. This pattern suggests that harsh conditions are found near shore and that this “high” pool species may have

adaptations or morphological features which allow it to survive (Nakamura 1976; Horn and Riegler 1981; Martin 1995; Zander et al. 1999). Indeed another species of *Istiblennius*, *I. edentulus* which emerges into air in the wild have sense organs suited for intertidal life and behavioral characteristics that prevent rapid desiccation (Zander et al. 1999). In temperate latitudes, temperature, salinity, aerial exposure, ultraviolet radiation, and wave action are abiotic factors that often vary with shore height or pool depth (Metaxas and Scheibling 1992; Denny and Paine 1998; Zander et al. 1999). Hawaii’s microtidal regime combined with varying wave heights may alleviate or alter the type of harsh conditions experienced by tidepool fishes, especially in the mid to low pools. However, regardless of microtidal conditions temperature is likely to be a driving environmental factor in tropical localities as organisms experience some of the highest temperatures worldwide.

Biotic conditions, such as predation and competition, can also vary across the shore (Connell 1961) and can contribute to tidepool assemblages (Zander et al. 1999). For example, macroalgae that provides food and shelter for fishes varied in abundance across the sampled shores. Although herbivory tends to be more prominent in the tropics (Horn 1989; Floeter et al. 2005), the diets of many of these tidepool fishes are not known. In addition, macroalgal cover could be structured by similar physical factors and be unrelated to fish distributions. Another biotic condition that can structure communities is predation. Many have suggested that tidepools serve as a nursery for juvenile reef fishes providing a refuge from fish predators (Gibson and Yoshiyama 1999). Indeed, juveniles of the coral reef fishes *Abudefduf sordidus* and *Acanthurus triostegus* were common in mid and low pools. Partitioning through inter-specific competition or by different evolutionary histories could also result in co-occurring species living in different habitats (Zander et al. 1999; Davis 2000). On O’ahu, species within the genus *Bathygobius* seem to be partitioned into different zones or shores and two blennies *Istiblennius zebra* and *Entomacrodus marmoratus* are also distributed in different areas of the shore (high-mid and mid-low respectively). Additionally intra-specific competition could account for the skewed smaller median size of *I. zebra* in high pools as intra-competition outcomes usually depend on body size (Mayr and Berger 1992). It is also likely

that other fishes in this study had skewed body sizes with shore position but this could not be tested with our current sample sizes.

In conclusion, O`ahu's tidepool fish assemblage is represented by high endemism and low species richness similar in percentage and number to the general shallow reef fish assemblage in Hawaii. Additionally, O`ahu's tidepools are dominated by taxonomic families found in other tropical localities (gobiids, blenniids, pomacentrids, and acanthurids). Assemblages varied spatially among sites, among shores, and vertically across shores with pool position. High pool assemblages were the most distinct from low pools and were dominated by small sized *I. zebra*. Future experiments could expand on this study by investigating 1) temporal variation 2) the diets of common species 3) perform more quantitative measurements of physical conditions in pools 4) identify species tolerances to physical conditions and 5) investigate inter-specific and intra-specific competition.

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