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Coupling remote sensing with *in situ* surveys to determine reef fish habitat associations for the design of marine protected areas

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ABSTRACT: Nearshore fish populations are in decline in the main Hawaiian Islands, and effective, sustainable management is needed. There has been increasing emphasis on the value of ecosystem-based management and the conservation of essential fish habitat, but policy is encumbered by a lack of supporting information. This study uses science and technology to support traditional knowledge in identifying juvenile fish habitats, providing a basis for effective resource management in a rural Hawaiian community. Building on existing local knowledge of nearshore resources, we quantitatively assessed juvenile fish–habitat associations. We conducted fine-scale *in situ* ecological surveys of juvenile reef fishes and their habitats, and produced detailed benthic habitat maps using GIS and interpretation of satellite imagery, from which we extracted multiscale seascape variables. Canonical correspondence analysis was used to assess fish–habitat relationships at multiple scales. Depth, coral cover, structural complexity, scattered rock and coral habitat, and distance to shore emerged as primary factors associated with juvenile reef fish abundance. We identified the habitat associations of 2 important food resource species in the study area of Hāʻena, Kauaʻi: the convict tang *Acanthurus triostegus sandvicensis*, an endemic subspecies, and the redlip parrotfish *Scarus rubroviolaceus*. Results from this study played an important role in the successful approval of the Hāʻena community-based fishery management plan by the state governing agency. We argue that an ecosystem-based co-management approach, informed by conventional survey methods, remote sensing technology, and traditional knowledge, can help to ensure the sustainability of fisheries worldwide.

KEY WORDS: Nursery habitat · Fish–habitat relationships · Habitat mapping · Remote sensing · Juvenile fishes · Hawaiʻi · Resource management · Spatial fisheries management

INTRODUCTION

Nearshore marine ecosystems around the globe are under great pressure from environmental and anthropogenic stressors such as habitat destruction, overfishing, climate change, invasive species, nutrient runoff, and sedimentation (Hughes et al. 2003, 2007, Lotze et al. 2006). As a result, marine resources are in decline worldwide (Jackson et al. 2001, Hilborn et al. 2003, Bellwood et al. 2004). Identification and protection of essential fish habitats is vital in the effort to conserve fisheries resources (Rieser 2000), and research that expands our understanding of ecological dynamics can help inform management.

Habitat use and nursery habitats

Fishes use a variety of habitats within and across different stages of their life (Lindeman et al. 2000). Habitat use is largely determined by the requirements of a fish at a given time, which change over

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their lives (Cocheret de la Morinière et al. 2003, Nemeth 2009). Ontogenetic habitat shifts, or movement of fishes from one habitat to another at certain life stages, is assumed to be a strategy that provides advantages to individuals during these life stages, which in turn increases lifetime fitness (Dahlgren & Eggleston 2000). In early life stages, fishes experience a suite of pressures, such as high predation intensity (Hixon 1991) and food scarcity (Jones 1986). These pressures can impact the demography of post-settlement fish assemblages (Tolimieri 1998), and ultimately impact the composition and distribution of adult assemblages (Jones 1990). Previous studies have revealed the importance of juvenile habitats to local reef fish density and biomass (Mumby et al. 2004a, Nagelkerken et al. 2012), and there is a growing understanding of the value of these areas to conservation objectives.

Some habitats, termed nursery habitats, serve the role of juvenile habitat more effectively than others, providing a disproportionately higher contribution of individuals to adult populations (Beck et al. 2001). Focusing management efforts on these areas with a pronounced ecological role can be a cost-efficient way to protect biodiversity and fisheries resources (Beck et al. 2001). Nagelkerken et al. (2012) found that proximity of reef fish communities to nursery habitats increased biomass of large-bodied nursery species by 139%. The United States Sustainable Fisheries Act of 1996 (Public Law 104-297) mandated conservation and enhancement of essential fish habitat such as nurseries, calling for 'scientific evaluation of the best available information, to describe the type of habitat… needed by all life stages' of managed species. Extensive research has been done in recent years on the value of mangroves (Mumby et al. 2004a), seagrass beds (Nagelkerken et al. 2000), and backreef lagoons (Adams & Ebersole 2002) as nursery habitats. However, investigations of fish nursery habitats in Hawaiian reef systems are limited, often having addressed only a single species or genus, rather than a local assemblage (Leber et al. 1996, Smith & Parrish 2002; but see DeMartini 2004, DeMartini et al. 2010).

While scientific studies of nursery habitats in Hawai'i are few, the value of nursery habitat protection was recognized by indigenous Hawaiians, who would minimize disturbance in areas known to support juvenile fishes so that they could replenish adult stocks that fed the community (Maly & Maly 2003b, Poepoe et al. 2007). Over the past decade, the community in Hā'ena, Kaua'i has sought to incorporate their customary knowledge into a state-sanctioned community-based fisheries management plan proposing to protect an area known by community members to be critical for supporting fishes in early life stages. In the state of Hawai'i, nearshore resources are severely depleted (Friedlander & DeMartini 2002, Friedlander et al. 2015) and the development of effective management is critical. This study applies conventional ecological methods and explores the utility of remote sensing technology in order to provide a quantitative assessment of juvenile reef fish habitat associations in the Hā'ena coastal reef ecosystem, lending a foundation on which monitoring and legislation could be based (Lindeman et al. 2000, Tissot et al. 2009).

This study differs from many previous nursery habitat investigations in that it recognizes the importance of combinations of habitat variables. Fish assemblages are influenced not simply by a single habitat type, but by the landscape of surrounding habitats, or more appropriately the 'seascape' (Kendall et al. 2004). The evaluation of suitable nursery habitat should thus incorporate the spatial characteristics of the mosaic of habitat types, in addition to assessing individual habitats.

Remote sensing and habitat mapping

Remote sensing technology has become a powerful tool in the investigation of ecological dynamics within coral reef systems (Mumby et al. 2004b), providing information for coastal management that is cost-effective, time-efficient, and replicable (Wedding et al. 2011a). Remote sensing has been successfully used to create accurate benthic habitat maps (Roelfsema & Phinn 2010), which can then be used to predict resource distributions and aid in identification of high priority areas for management (Purkis et al. 2008). Remote sensing methods are also enhancing the incorporation of seascape ecology concepts into research and resource management. Technological advances in geospatial tools allow for quantitative studies of the correlations between the mosaic of habitats in an area and the assemblage structure of reef fishes, strengthening an understanding of species–habitat linkages (Pittman et al. 2007, Wedding et al. 2011a).

In a national mapping effort, the NOAA National Ocean Service Biogeography Branch created benthic habitat maps for the Hawaiian Islands, delineating distinct seafloor habitat classes at a scale of 1:6000, with a minimum mapping unit of 1 acre (0.4 ha; Battista et al. 2007). Previous maps produced with this same resolution (but with a slightly different classification hierarchy) (Coyne et al. 2003) have proven beneficial to the evaluation of region-level function of marine protected areas (MPAs) in Hawaiʻi (Friedlander et al. 2007). However, to assist management efforts at a local scale, higher resolution maps are necessary (Wedding et al. 2011a). In order to establish useful knowledge of fish distribution patterns in relation to habitat, maps must contain appropriate spatial and thematic detail, created at a resolution that allows for the detection of fish–habitat interactions in the system (Kendall et al. 2004). In an effort to better understand ecological patterns at the scale of the Hāʻena community fishery, we created a higher-resolution map, and assessed correlations of fish assemblages with characteristics of the surrounding seascape.

Data from our remote sensing mapping efforts characterized the broad-scale geomorphological structure of the study area, while *in situ* methods provided fine-scale data on biological cover. The combination of benthic mapping with *in situ* ecological surveys facilitates the identification of habitat characteristics important for structuring fish assemblages (Pittman et al. 2007), and allows for a clear and robust evaluation of fish distributions in a seascape framework.

Here we seek to: (1) investigate combinations of habitat variables with which species of juvenile fishes are associated, with the *a priori* hypotheses that: (a) juvenile fish distributions are associated with specific habitat variables, and (b) these associations vary between species; (2) combine data from 2 different approaches, which produce data at different spatial scales, in order to achieve a more complete understanding of juvenile fish–habitat associations; and (3) make recommendations for future juvenile habitat studies and the conservation of these habitats.

The integrative methods applied in this study helped to develop a better understanding of the ecological dynamics that impact Hawaiian reef resources, and our results directly contributed to the policy-making process and informed local fishery management. The approaches used herein can serve as a template for future resource management efforts around the state of Hawaiʻi and elsewhere.

MATERIALS AND METHODS

Study site and sample design

The study was conducted in Hāʻena, located on the north shore of the island of Kauaʻi, at the northwest end of the chain of the inhabited Hawaiian Islands (Fig. 1a). The Hāʻena coastline is a highly dynamic ecological setting, exposed to large ocean swells and storms (Bodge & Sullivan 1999), heavy annual rainfall (Nullet & Mcgranaghan 1988), and high alluvial and groundwater input (Knee et al. 2008). Biological surveys were carried out on 2 adjacent coastal reefs, Kēʻē and Makua, which are divided by a channel approximately 500 m wide. The crest of these fringing reefs is several hundred meters offshore, dividing them into distinct fore- and backreef zones (Fig. 1a). Forereef zones (5 to 15 m depth) extend from the reef crest seaward, and are characterized by high exposure to waves, wind, and swell energy. Backreef zones (≤5 m depth) are directly shoreward of the reef crest, are more protected from wave energy, and have less water movement.

To ensure sufficient sampling to capture the variations in conditions, we randomly stratified our surveys across the different zones (forereef and backreef zones of Makua and Kēʻē reefs), with the number of samples proportional to the area of each zone. A total of 126 surveys were conducted over 2 sampling periods, July 2013 and August 2014. All survey start-points within each sample year were separated by ≥60 m. Additional nearshore zones were sampled in the second sampling period, in order to include representation of a characteristically distinct habitat recognized during the first sampling period (Fig. 1a). Nearshore areas, located within 50 to 60 m from the shoreline, are shallow, low relief rock benches, often exposed at low tides. The Makua nearshore zone has sections of sandy bottom adjacent to the shoreline (≤1.5 m depth), and Kēʻē has a small sandy-bottom lagoon (ca. 0.67 ha) adjacent to shore.

Boundaries of the forereef zones were based on contiguous areas of hard-bottom, pavement habitat structure, as delineated by the previous NOAA benthic habitat mapping efforts (Battista et al. 2007). The seaward extent was limited to roughly the 8 m depth contour, as determined from LiDAR (light detection and ranging) bathymetry (Irish & Lillycrop 1999). Division of distinct zones was based on locally recognized reef identifications, visual interpretation of satellite imagery, and area boundaries outlined in the proposed Hāʻena Community Based Subsistence Fishing Area (CBSFA), Hawaiʻi Administrative Rules documentation (HAR § 13-60.8-2 2013). Survey data were pooled across sampling periods (July 2013 and August 2014) after an analysis of similarities (ANOSIM) showed data between years to be similar (R = 0.05) (Clarke & Warwick 2001).

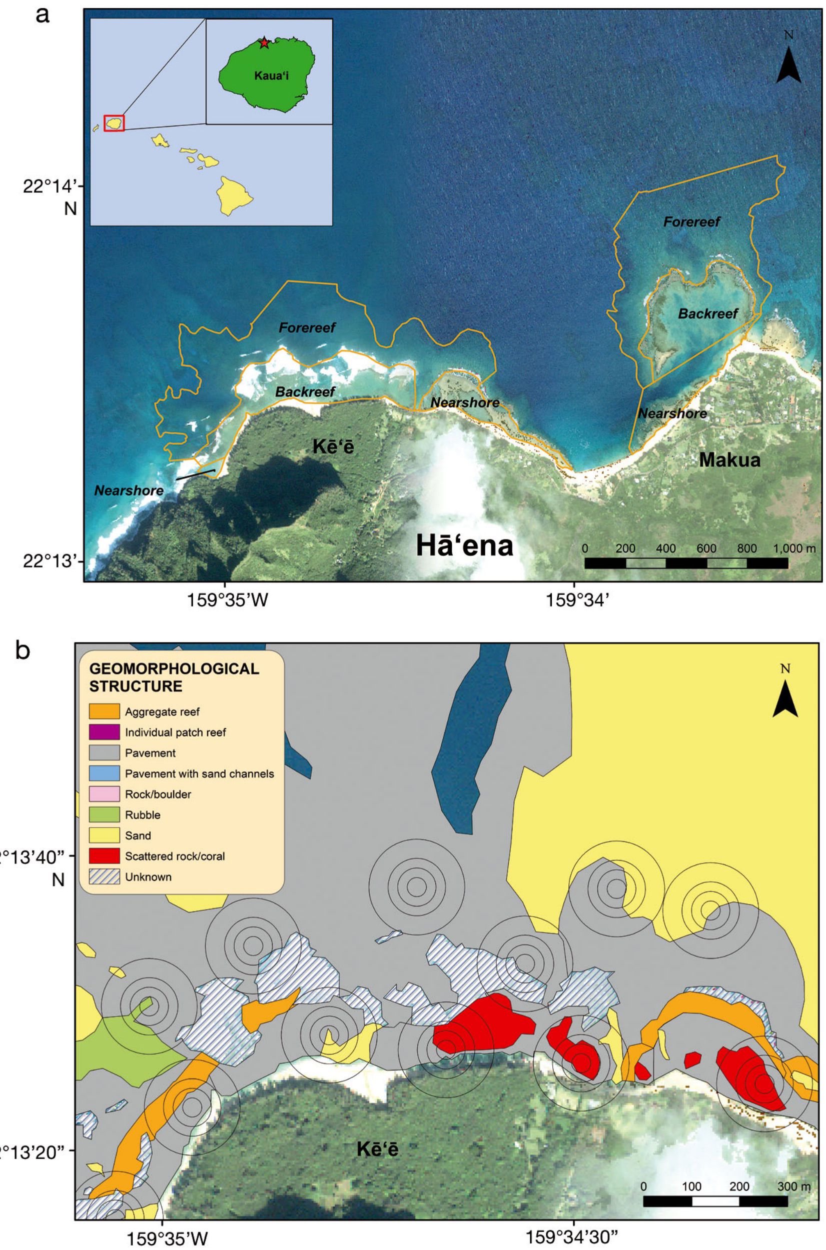


Fig. 1. (a) Study site: Hāʻena, Kauaʻi. Two study reefs, Kēʻē and Makua, with forereef, backreef, and nearshore sampling zones. (b) Process for extracting remotely sensed habitat data, displayed in a portion of the study area. Eight geomorphological structure habitat classes were present in the study area (not all are displayed within this area; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m588p121_supp.pdf for habitat map of whole study site). Cover area for each habitat class was quantified within concentric buffer zones of 20, 40, 60, 80, 100, 150, 200, and 300 m radii. Only radii of 20, 40, 60, and 100 m are displayed for clarity

In situ juvenile fish surveys

Juvenile fish data were collected via underwater visual census surveys, along transects of 25 × 2 m (Brock 1954). A single diver swam the transect line, following a bearing that roughly followed the depth contour. Surveyors recorded all observed fishes <10 cm within 2 m to the right of the transect line, identifying to the lowest taxonomic level possible and estimating fork length to the nearest cm. To further refine the count data so as to more accurately represent abundance of true juveniles, we applied post-hoc species-specific maximum size criteria prior to analysis. Of the species included in the analyses, we removed observations of *Coris venusta*, *Stegastes marginatus*, and *Macropharyngodon geoffroy* >5 cm, and of *Gomphosus varius*, *Thalassoma duperrey*, *Stethojulis balteata*, *Plectroglyphidodon imparipennis*, and *Chromis vanderbilti* >3 cm. A maximum size of 10 cm was retained for *Acanthurus leucopareius*, *A. triostegus sandvicensis*, and *Scarus rubroviolaceus*.

In situ habitat data

Data for habitat variables came from 2 sources: *in situ* benthic surveys and remotely sensed habitat class data from a benthic habitat map produced for this study. For *in situ* surveys, benthic community composition was characterized along the same transect lines as the fish surveys, using quadrat point-intercept methods (Reed 1980). Randomly stratified quadrats of 0.5 m^2 were placed along the right side of the transect line, with 2 quadrats per 5 m segment for a total of 10 per transect. Quadrats were strung with a grid of 10 cm^2, and the underlying benthic substrate (e.g. coral, algae) was identified to the lowest possible taxonomic level at each of the 16 intersection points. The quadrats were strung with a double-layered grid to avoid surveyor bias and eliminate parallax (Preskitt et al. 2004). Point-intercept data were converted to percent cover for each transect by dividing the number of occupied points by the total number of intersections. Taxa or substrates were pooled into 5 benthic cover types: live coral, macroalgae, coralline algae, turf algae, or substrate (sand, mud, rubble).

Depth was recorded at the start of each transect, and rugosity — an index of structural complexity — was measured using a chain-link method (Risk 1972). A small link chain was laid serially along the transect line for the entire length of the transect, ensuring that it followed the contours and features of the seafloor. The final distance covered by the length of the chain was recorded, and the ratio of that length to the linear distance of the transect (25 m) provided a measure of rugosity (Friedlander et al. 2003). The Shannon-Wiener diversity index (H') was also calculated for each transect, based on the spatial proportion of benthic cover types represented in the transect area (Coppedge et al. 2001).

Remotely sensed habitat data

The habitat map of geomorphological structure classes of the Hāʻena coastal area was created in ArcGIS 10.1 using visual interpretation of multispectral satellite imagery. The imagery used in the mapping process was WorldView-2 panchromatic multispectral 8-band imagery, with a spatial resolution of 4 × 4 m. Remotely sensed data were projected in UTM Zone 4 NAD 1983. The map was created using the NOAA Habitat Digitizer extension for ArcGIS 10 (Environmental Systems Research Institute [ESRI] 2011), a tool developed to assist previous NOAA benthic mapping efforts. Habitat boundaries were digitized into polygons, delineated at a minimum mapping unit (MMU) of 100 m^2. During the digitizing process, the scale was locked at 1:2000 to ensure a consistent level of detail in the delineation (Wedding et al. 2011a). Polygons were attributed with classes of geomorphological structure (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m588p121_supp.pdf), following a hierarchical classification scheme adapted from the NOAA National Ocean Service Biogeography Program for coral reef mapping efforts in the main Hawaiian Islands (Coyne et al. 2003, Battista et al. 2007). Visual interpretation was informed by training with NOAA benthic habitat maps, and by *in situ* training surveys conducted prior to mapping to ensure accuracy of the photo-interpreted classifications determined in the production of the map.

Environmental data were extracted from the produced benthic habitat map using ArcMap 10.1 (ESRI 2011) (see Table S1 in the Supplement). Data were extracted at varying spatial scales to explore the strength of relationships and identify a scale at which juvenile fishes were most strongly associated with the seascape (Kendall et al. 2011). Area of habitat classes were quantified within buffers around transect midpoints, using concentric circles of 20, 40, 60, 80, 100, 150, 200, and 300 m radii (Fig. 1b), and were calculated as a percentage of the total buffer area, excluding land and unknown classes. At increasing spatial coverage, buffer rings around transects began to overlap one another, as will happen with sampling in any constrained geographical area (Pearman 2002). We explored differences between analyses with full datasets and reduced datasets, in which one out of every pair of spatially overlapping samples was removed. Results between full and reduced datasets were consistent, so we used the full datasets.

Remotely sensed habitat variables also included distance to shore, distance to reef edge, slope of slope (a measure of structural complexity), and depth. Polygons for shoreline and reef edge were delineated in ArcMap 10.1, and the Generate Near Table tool was used to calculate the closest distance between each transect midpoint and shoreline or reef edge. A slope of slope raster was created from LiDAR data using the Slope tool in the Spatial Analyst toolbox for ArcMap 10 (ESRI 2011). The Focal Statistics and Sample tools were then used to extract mean values of slope of slope for a circular area with 20 m radius around each transect mid-point. Measures of mean depth were derived from bathymetric data using the Sample tool to extract values for 6 points along the transect survey lines — the start point and every 5 m to the end of the transect. We also included a Shannon-Wiener diversity index (H') for remotely sensed habitat data in order to examine the influence of habitat diversity at the seascape scale in addition to the finer-scale diversity within transects.

Statistical analysis

We applied canonical correspondence analysis (CCA) using CANOCO 5 statistical software (ter Braak 2012) to investigate multivariate associations between juvenile fish assemblages and their surrounding habitat. Non-linear methods were most appropriate for our response data, which were compositional and had a gradient >2 SD units, indicating that the data were heterogeneous. CCA is an eigenvalue-based ordination method that assumes a unimodal response function of response variables. Principal ordination axes are constrained to be a linear combination of environmental descriptors, where the first axis is a linear combination that best explains variation in community data, and additional orthogonal axes explain the remaining variance (ter Braak 1986).

CCA does not strictly assume multivariate normality, although normality is required for the statistical inference test of the significance of each canonical function (Hair et al. 1998). Therefore, each explanatory variable was evaluated for normality, and transformed as necessary (see Table S1 in the Supplement). For each analysis, statistical significance ($p < 0.05$) of the individual axes as well as of the overall analysis was determined with Monte Carlo permutation tests (Coppedge et al. 2001). Environmental data were centered and standardized in CANOCO 5 to have zero mean and unit variance (Šmilauer & Lepš 2014). In order to identify environmental characteristics most strongly represented by the ordination axes, intraset correlations, or the correlation between CCA axis scores and seascape variables, were calculated in CANOCO 5 (Coppedge et al. 2001).

Our study was designed to address the management objectives of a subsistence fishery, for which rare species are not the primary focus. As such, and due to the influence of rare species on chi-squared distances used in the CCA ordination, species that were observed in ≤11 (~10%) of the sample surveys were excluded from the analysis (cf. Lepczyk et al. 2008). Similarly, habitat variables that occurred in <10% of the sample surveys were excluded from analyses. Habitat variables for all datasets were examined for covariance ($\rho \geq 0.8$; see Table S2 in the Supplement at www.int-res.com/articles/suppl/m588p121_supp.pdf), and highly correlated variables were removed to allow for more direct ecological interpretation of species–habitat relationships (Pillsbury & Miller 2008). Juvenile fish abundances were square-root transformed to down-weight the contribution of a few highly abundant species on assemblage structure.

Initial analyses were performed on *in situ* variables independently and remotely sensed datasets of varying spatial scales (20, 40, 60, 80, 100, 150, 200, and 300 m radii) in order to assess the scale at which juvenile fish–habitat relationships were strongest, based on highest percent of explained variance. The spatial scale at which response variables were most strongly associated was then selected for an integrated analysis, in which remotely sensed and *in situ* habitat data were combined in a single model. This final analysis was then used to interpret juvenile fish associations with broad-scale geomorphological structure, as well as fine-scale biological cover variables. As such, the integrated dataset included measures of Shannon-Wiener habitat diversity from both scales, in order to assess biological cover diversity at the transect level, as well as geomorphological structure diversity at the seascape-scale. Correlations between all modeled habitat variables were investigated to assist in interpretation of the results.

RESULTS

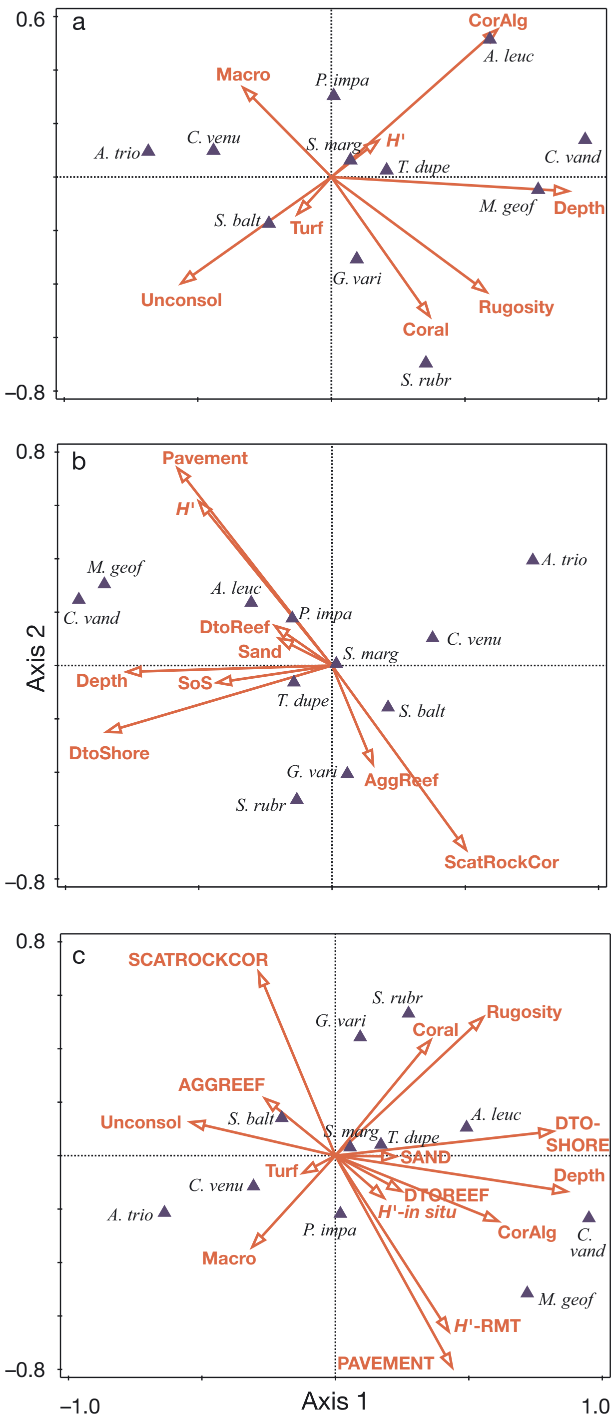
A total of 126 independent transect surveys were conducted over the 2 sampling periods, within which 2040 juvenile fishes were observed, representing 54 species from 15 families. The most abundant species were *Stethojulis balteata, Thalassoma duperrey,* and *Acanthurus triostegus sandvicensis*, together comprising 62.7% of the total number of individuals surveyed (see Table S3 in the Supplement at www.int-res.com/articles/suppl/m588p121_supp.pdf). Based on a criterion of occurrence in at least 10% of the sample surveys, 11 species of juvenile fishes, accounting for 90% of total fish abundance, were selected for inclusion in analyses. Of these species, *A. triostegus sandvicensis* and *Scarus rubroviolaceus* are considered important food resource species, harvested by the local community and throughout Hawai‘i.

A total area of 5.24 km^2 of benthic habitat was visually interpreted from satellite imagery, classified, and mapped for the coastal ecosystem of Hā‘ena, along 5.6 km of coastline and extending up to 1.7 km offshore. Seven different classes of geomorphological structure were delineated, 4 of which were included in analyses based on the criterion of a minimum 10% frequency of occurrence in samples. These (ordered from high to low structural complexity) were aggregate reef, scattered rock and coral, pavement, and sand.

Independent analyses

In the analysis of fine-scale *in situ* survey data, seascape variables explained 26.0% of the juvenile fish assemblage data variance. Both the first and second axes were significant, as was the overall analysis. Depth, coral cover, and rugosity were highly associated with juvenile fish assemblages, particularly with the resource species *S. rubroviolaceus* and *A. triostegus sandvicensis* (Fig. 2a). Results showed that juveniles of *S. rubroviolaceus* were more abundant in deeper areas with greater coral cover and structural complexity, while juveniles of *A. triostegus sandvicensis* were more abundant in shallow habitats with low rugosity.

Analyses of broad-scale remotely sensed data at all spatial scales showed significant relationships between juvenile fish assemblages and seascape characteristics (Table 1). The percentage of variance in response data explained by habitat variables ranged from 21.5 to 25.8%. The strongest relationships, based on percent variance explained, were detected at the 150 m scale, above which percent variance explained begins to decline. At this scale, results suggested a higher abundance of *A. triostegus sandvicensis* close to shore, and juveniles of *S. rubroviolaceus* to be more abundant in rugose coral habitat (Fig. 2b).



Integrated analysis

In the integrated analysis of *in situ* survey data and remotely sensed habitat data, seascape variables explained 34.6% of the juvenile fish assemblage data variance. Both the first and second axes were significant, as was the overall analysis. Axis 1, which explained 14.8% of the variance in response data, was most strongly correlated with depth, distance to shore, and coralline algae in the positive direction (r = 0.867, r = 0.815, and r = 0.610, respectively), and unconsolidated substrate in the negative direction (r = –0.542; Fig. 3). Axis 2 explained an additional 6.3% of the assemblage variance, most strongly correlated with pavement (r = –0.791), scattered rock and coral (r = 0.686), and broad-scale habitat diversity *H'* (r = –0.657). On Axis 1, *Chromis vanderbilti* and *Macropharyngodon geoffroy* were associated with deeper sites further from shore, characterized by coralline algae, while *A. triostegus sandvicensis* was associated with shallow unconsolidated or macroalgal habitats close to shore (Fig. 3). *S. rubroviolaceus* was most highly influenced by Axis 2, associated with coral cover and habitats of greater structural complexity. *Stegastes marginatus* and *T. duperrey* were oriented near the bi-plot origin, indicating minimal influence from seascape characteristics (Fig. 2c).

Fig. 2. Ordination bi-plots from separate analyses of relationships between juvenile fishes and benthic habitat types, described with (a) *in situ* survey methods, and (b) remotely sensed geomorphological structure, at a seascape spatial scale of 150 m radius around transect centers, and (c) an integrated dataset of both *in situ* and remotely (RMT) sensed seascape variables. Seascape variables are represented by vectors, where the length of the vector indicates the strength of the association with response variables. (▲) Species optima in ordination space. In the integrated analysis bi-plot (c), variables in lowercase letters are derived from *in situ* ecological survey methods; variables in uppercase letters are derived from remote-sensing methods. CorAlg: coralline algae, Macro: macroalgae, Unconsol: unconsolidated substrate (e.g. sand), ScatRockCor: scattered rock and coral, AggReef: aggregate reef, DtoShore: distance to shore, DtoReef: distance to reef, SoS: slope of slope (remote measure of rugosity), *H'*: Shannon-Wiener diversity index. For species names, see Table S3 in the supplement (www.int-res.com/articles/suppl/m588p121_supp.pdf)

Table 1. Strength of detected associations between juvenile fish assemblage and seascape variables, based on percent variation explained; comparison between data collection methods (*in situ* and remote sensing) and spatial scales. Monte Carlo permutation test results (pseudo-*F*-ratio, p-value). *Statistically significant ($p < 0.05$)

Dataset	Spatial scale (radius, m)	% Variation explained by seascape variables	% Variation explained by significant axes	Monte Carlo test: All axes	Monte Carlo test: Axis 1	Monte Carlo test: Axis 2
In situ		26.0	22.6	4.4, 0.001*	16.4, 0.001*	6.1, 0.007*
Remotely sensed geomorphological structure	20	21.5	12.7	2.8, 0.001*	13.3, 0.001*	4.3, 0.110
	40	22.0	17.6	2.9, 0.001*	13.5, 0.001*	5.3, 0.020*
	60	22.7	18.0	3.0, 0.001*	13.4, 0.001*	5.9, 0.009*
	80	24.0	18.26	3.2, 0.001*	13.6, 0.001*	6.1, 0.011*
	100	24.3	18.7	3.3, 0.001*	13.9, 0.001*	6.3, 0.003*
	150	25.8	19.0	3.6, 0.001*	14.5, 0.001*	6.1, 0.007*
	200	24.5	18.4	3.3, 0.001*	14.1, 0.001*	5.8, 0.013*
	300	23.8	18.02	3.6, 0.001*	13.8, 0.001*	5.8, 0.002*
Integrated dataset		34.6	21.13	3.3, 0.001*	16.2, 0.001*	7.4, 0.009*

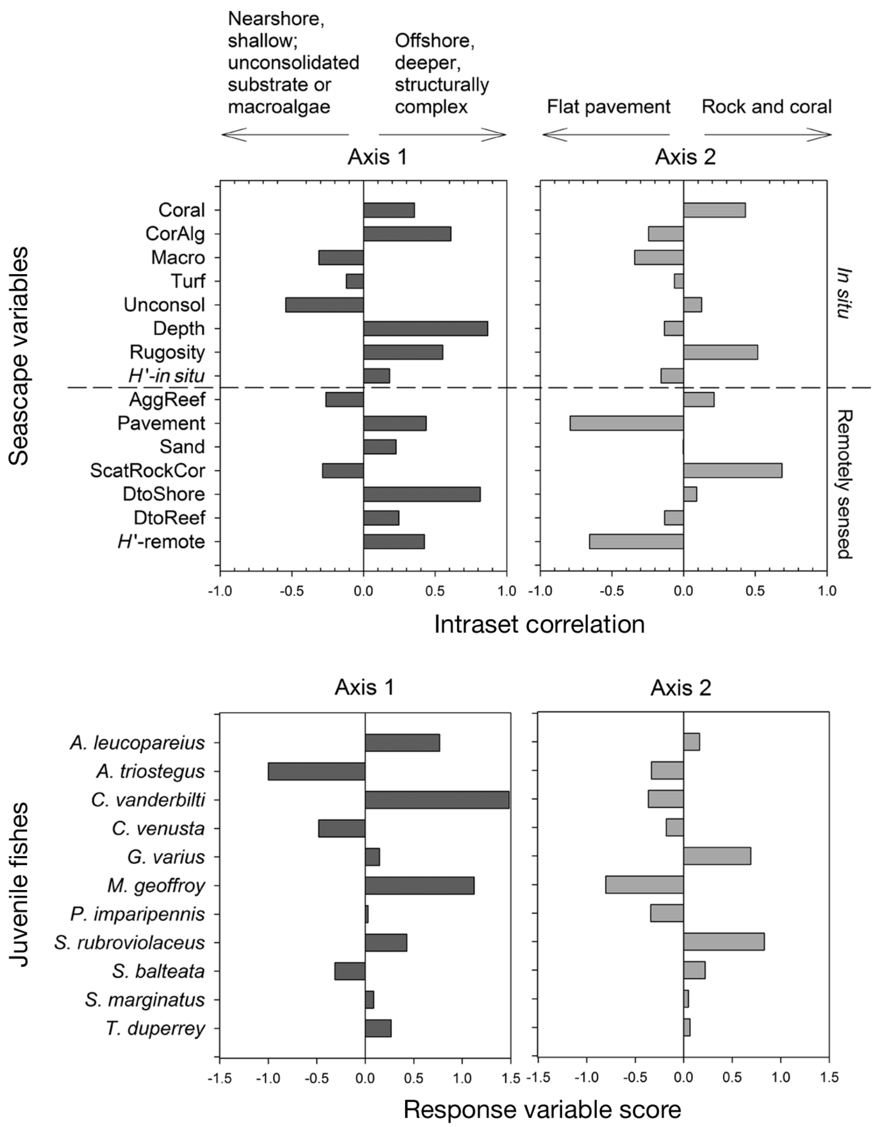


Fig. 3. Intraset correlations and response variable scores between variables and axes of the canonical correspondence analysis (CCA) for integrated dataset of seascape variables. Intraset correlations are the correlations between CCA axis scores and seascape variables, and help to describe the seascape characteristics represented by the axes (summarized above axes). Analogously, response variable scores represent correlations between axes and juvenile fish variables, and can be compared with the seascape correlations to interpret associations between juvenile species and seascape characteristics. Variables above dashed line are derived from *in situ* ecological surveys; variables below dashed line are derived from remote-sensing methods, at a spatial scale of 150 m radius around transect centers. CorAlg: coralline algae, Macro: macroalgae, Unconsol: unconsolidated substrate (e.g. sand), AggReef: aggregate reef, ScatRockCor: scattered rock and coral, DtoShore: distance to shore, DtoReef: distance to reef, *H'*: Shannon-Wiener diversity index. For full species names, see Table S3 in the Supplement (www.int-res.com/articles/suppl/m588p121_supp.pdf)

DISCUSSION

We applied geospatial tools and technology and *in situ* survey methods to describe patterns of distribution and abundance of juvenile fishes, and demonstrated the utility of incorporating remote-sensing methods in marine resource management. A combined approach in which fine-scale cover and broad-scale seascape data were integrated into a single analysis provided a more complete interpretation of juvenile fish–habitat relationships and greater explained variation than did separate analyses. Juvenile fish assemblages in the coastal reef ecosystem of Hāʻena were associated with certain habitat types and spatial configurations, and these associations varied among species. The described patterns of distribution contribute to a depauperate body of literature on juvenile reef fish–habitat associations in Hawaiʻi, and the study played an important role in the successful establishment of the community-based marine resource management area in Hāʻena.

Habitat associations

Structural complexity has previously been shown to be important for adult fish distributions (Hixon & Beets 1993, Pittman et al. 2007). Our study shows the importance of structural complexity for juvenile reef fish assemblages. Rugosity, a measure of fine-scale structure measured *in situ*, had a strong positive relationship with juvenile fish abundance. The observed importance of structural complexity to juvenile fish distributions is consistent with previous studies (Beukers & Jones 1998, Almany 2004). *Scarus rubroviolaceus*, an important food fish that also plays an important ecological role as a reef excavator in its adult phase, was more abundant in rugose habitats of higher coral cover. The association of *S. rubroviolaceus* with coral and rugose habitats has been found in previous studies (Berkström et al. 2012, Howard et al. 2013), but these studies did not address juvenile fish distributions specifically. In an examination of life history characteristics of parrotfishes, Taylor et al. (2014) found *S. rubroviolaceus* to be vulnerable to overexploitation, emphasizing the importance of establishing sustainable fishing practices and informed ecosystem-based management in order to maintain this resource.

Depth emerged as another strong predictor of juvenile distribution. The strong association with shallow habitats documented for juvenile *Acanthurus triostegus sandvicensis*, an endemic Hawaiian subspecies and important resource fish for Hāʻena, is consistent with local knowledge (Maly & Maly 2003a), as well as with studies from elsewhere in Hawaiʻi (Sale 1968, 1969). Distance to shore also had a strong influence on the distributions of juvenile fishes, with some species oriented further from shore and other species, such as *A. triostegus sandvicensis*, in greater abundance nearshore. Quantification of this seascape-scale metric was facilitated by remote sensing methods. One of the advantages of remote sensing methods is that they allow for evaluation of potential predictors that may otherwise be difficult to assess with *in situ* surveys. Tools and metrics that facilitate the examination of spatial ecological dynamics have been commonly applied to terrestrial landscape ecology (Turner 1989) and riverine systems (Wiens 2002), but the value of such tools in marine systems is still being explored and expanded (Wedding et al. 2011b). Broad-scale variables, such as cross-shelf location on the reef, have been previously shown to influence distributions of adult fishes (Christensen et al. 2003, Pittman & Brown 2011), and our results suggest that such variables are also correlated with juvenile distributions.

Our results from *in situ* and remotely sensed habitat datasets highlight the value of incorporating multiple scales in an analysis of fish associations with surrounding habitat. Separate analyses of *in situ* and remotely sensed data (150 m) both resulted in approximately 26% explained variation, while the integrated analysis resulted in 34.6% explained variation, a relative increase of 33%. It is noteworthy that the strongest predictors represent both the fine-scale (25 m) variables (i.e. coral cover, rugosity, depth, substrate) as well as broad-scale (150 m) remotely sensed variables (i.e. scattered rock and coral habitat, pavement, distance to shore). The combined importance of biological cover and geomorphological structure variables demonstrates the value of an integrated approach for management that considers both in management design. The two measures of Shannon-Wiener habitat diversity had different associations with the juvenile fish assemblage (Fig. 2c), with broad-scale habitat diversity more strongly associated with juvenile distributions than fine-scale biological cover diversity. This is interesting in that it highlights the importance of scale on this metric, and because previous work has shown habitat diversity to be a poor predictor of juvenile (and adult) reef fish abundance (Kendall et al. 2011). Overall, our integrated approach allowed for a more complete understanding of the variables that may be associated with juvenile reef fish distributions.

In the evaluation of how effective these methods are in identifying and explaining variation in juvenile distributions, it is prudent to recognize the differences in habitat associations among species. Typically, a large proportion of juvenile fish assemblages is made up of habitat generalists, species that are poorly associated with habitat variables (Brown 1984). This affects the overall measure of the strength of fish–habitat relationships, i.e. the percent of explained variance. In this study, the generalist species *Stegastes marginatus*, *Thalassoma duperrey*, and *Stethojulis balteata* made up a cumulative 62.7% of the total abundance of observed juveniles. Removal of these species in the analysis of *in situ* habitat data resulted in an increase from 33.4 to 39.4% variance explained by seascape variables. Acknowledging that a large portion of the response data represent species that do not exhibit strong relationships with any particular habitat variable, it is apparent that some species included in the analyses are likely more strongly influenced by habitat variables than the overall measure suggests. Studies like ours can be useful for identifying these species that are highly influenced by habitat, in order to focus efforts to further examine species-specific patterns relevant to ecosystem management objectives.

Limitations and data resolution

Given the dynamic characteristics of Kauai's northern coastline, with large ocean swells, high winds, and storms, sampling in the area is limited to the calmest periods of the year. Therefore, this study provides only a snapshot of the juvenile fish assemblage and is not a comprehensive assessment of recruitment dynamics. Our studies were conducted during the calm summer months, which is peak recruitment for most fish species in Hawaiʻi (Walsh 1987). However juvenile fish assemblages can vary substantially both seasonally and among years in Hawaiʻi and elsewhere (see review by Doherty & Williams 1988). We recommend that where feasible, similar studies should include multiple survey periods throughout the year and across a span of years, in order to capture different recruitment pulses and create a more comprehensive representation of the juvenile assemblage.

Our study has shown that remote sensing methods can contribute to investigations of juvenile fish distribution patterns. We created a map (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m588p121_supp.pdf) with a higher mapping resolution than the previous benthic habitat mapping efforts (MMU = 100 vs. 4047 m^2; Battista et al. 2007), which helped reveal seascape-scale fish-habitat patterns. However, the resolution is likely still too coarse to detect fine-scale, patchy distributions of juvenile fishes. Thus, we do not suggest that remote methods be used as the sole data collection method for juvenile studies, but rather we emphasize the value of integrating multi-scale data derived from a combination of methods.

Management and application

We identified seascape variables of particular importance to the juvenile fish assemblage in the Hāʻena coastal ecosystem, and this information played a key role in landmark management legislation. Of particular value to management efforts was the identification of habitat associations of locally important targeted species. The correlation of *A. triostegus sandvicensis* with shallow, nearshore areas was consistent with characteristics of the nursery area proposed by the Hāʻena community, as was the association of *S. rubroviolaceus* with structurally complex coral habitats (HAR § 13-60.8-2 2013). The proposed protected nursery area at Makua is a shallow backreef area close to shore, characterized by structurally complex rock and coral habitat. The preservation of resource species stocks is a priority for fishery management, and this study provided information corroborating the importance of the proposed spatial closures for species valuable to the subsistence fishery of Hāʻena.

In October 2014, the Hawaiʻi State Board of Land and Natural Resources approved Hāʻena's proposed Community Based Subsistence Fishery Area (CBSFA) management plan, making it the first community in Hawaiʻi to have state-sanctioned community-based marine resource management. This landmark decision has established a precedent, and as envisaged by Tissot et al. (2009), these successes provide an example from which other communities throughout the state can learn. The state of Hawaiʻi has taken important steps in recent years to empower communities to care for their own fisheries, but in order for further management efforts to be successfully sanctioned by government agencies, there is a great need for place-based quantitative ecological information.

The identification and mapping of essential fish habitat can be applied to inform reserve design in regions around the globe (Lindeman et al. 2000, Rieser 2000). Quantitative estimates of ecological linkages and associations are needed for management efforts, and an understanding of the relationships between fishes and the seascape is important for effective conservation (Doak & Mills 1994). Information on ecological functions provided by different habitat types and at different scales can help ensure that a proper suite of necessary habitats is protected and that the spatial design of reserves incorporates the seascape components influential to fish distributions (Boström et al. 2011).

It is important to acknowledge that the statistical approach used in this study involved the removal of rare species and habitats from the analysis, due to their influence on chi-squared distances used in the CCA ordination. In analyses which included rare species and habitats, explanatory power was substantially weaker, with only approximately 5% variation explained by significant axes, and clear fish–habitat patterns were not apparent. We feel that our approach was appropriate for the management objectives of the Hāʻena community, which are focused on the subsistence fishery, but we suggest that for management objectives focused on rare species, a different statistical approach is used.

In the context of climate change and conservation, it is important to consider the associations of juvenile fishes with habitat variables such as coral cover, macroalgae, and structural complexity. Changing ocean conditions can directly or indirectly change coral health (Hughes et al. 2003) and the level or composition of algal cover (Hoegh-Guldberg et al. 2007), which in turn could differentially affect fish species (Newman et al. 2015). Increases in macroalgal cover due to warmer waters and nutrient inputs could positively influence species such as *A. triostegus sandvicensis* that have an association with macroalgae. However, reductions in coral cover and thus structural complexity as a result of algal dominance and coral bleaching could negatively impact species such as *S. rubroviolaceus*. This study contributes an understanding of how different juvenile species populations may be affected by changing habitats, pertinent in the evaluation of ecosystem resilience in the face of a changing climate.

Recommendations and future studies

We have demonstrated the opportunity to develop a better understanding of juvenile fish habitat associations with the coupling of remote sensing and *in situ* ecological survey approaches, and we suggest that similar paired-approach methods are applied in other locations. The patterns that emerged from the different data collection methods highlight the value of a mixed-methods approach, and emphasize the importance of selecting the scale(s), resolution, and methods that are appropriate for the objectives of a study or management action. Juvenile fishes can be influenced by both micro-scale (Tolimieri 1998) and seascape characteristics (Drew & Eggleston 2008), so methods that incorporate multiple scales into assessments of associations will generate a more complete understanding of the ecological dynamics at play (Pittman et al. 2007).

Juvenile fishes generally have a smaller home range than adults, and are expected to be influenced by habitats at a different scale. Spatial scale and neighborhood size have been assessed for adult fishes (Kendall 2005, Kendall et al. 2011), but comparative evaluations of appropriate spatial scale for juvenile fishes remains a field for more exploration. Our results suggest a possible spatial threshold (150 m radius) at which juvenile reef fishes may be most strongly associated with geomorphological structure. Our analyses were limited by the small study area, but future studies may further examine seascape connections across broader scales in larger study areas so as to reduce the amount of spatial overlap of buffer areas. Additionally, we suggest that further studies examine micro-scale (within several meters) variations in habitat, so as to detect associated patchy distributions of juvenile fishes (sensu DeMartini et al. 2010). This would allow for a better understanding of a spatial scale that is still currently overlooked, and one which may further reveal ecological drivers of juvenile fish distribution.

CONCLUSIONS

In order to develop sustainable fisheries management, it is important to understand the habitat associations of the fishes within the management area. The identification of essential juvenile habitats helps guide delimitations of protected areas, and can be used to focus management on habitat specialist species, including important resource species such as *Acanthurus triostegus sandvicensis* and *Scarus rubroviolaceus.* We found juvenile fish assemblages as a whole to be associated with shallow, structurally complex habitats of mixed rock and coral, characteristic of sheltered backreef areas. These patterns were discernable with the integration of remote-sensing technology and *in situ* ecological methods, and the results from this study proved critical in the successful establishment of community-based fishery management in Hawaiʻi. Further studies coupling *in situ* and remote-sensing approaches can inform sustainable fishery management efforts around the globe. Advancements in technology will expand the opportunity to apply remote-sensing methods in marine ecology, and the effective application of such tools in the identification of essential fish habitat has substantial implications for MPA design and marine spatial planning worldwide.

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