

Marine Resource Assessment of Moloka'i's North Coast (ʻĪlio Point – Kalaupapa)

A comprehensive baseline assessment of the nearshore marine resources along the north shore of Moloka'i was conducted to document and evaluate the current status of the nearshore marine ecosystem, and to help guide future management actions



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Executive Summary

This report summarizes data gathered by the State of Hawai'i's Division of Aquatic Resources, the Kaulapapa National Historic Park, NOAA Pacific Islands Fisheries Science Center, and the Fisheries Ecology Research Lab of the University of Hawai'i at Manoa during two separate sampling periods in May and August, 2017. Surveys were conducted in order to gather baseline ecological data to characterize the nearshore ecosystems of the North Shore of the island of Moloka'i.

The North Shore of Moloka'i is a dynamic environment, exposed to dominant winds and heavy winter swells. The challenging conditions along this shoreline, in conjunction with low nearby human population density, results in low fishing pressure and a marine ecosystem that harbors some of the highest reef fish biomass in the State of Hawaii. These natural resources are important to livelihoods of the local communities on Moloka'i, and efforts are being made to protect and preserve the nearshore marine ecosystem and associated local fisheries by establishing Community Based Subsistence Fishery Management regulations.

This comprehensive assessment of the nearshore marine resources along the north shore of Moloka'i characterizes the fish and benthic communities of Moloka'i's North Shore. This is intended to serve as a baseline to describe the current nearshore ecosystem, from which future monitoring may be measured and management efforts may be assessed.

Main conclusions and observations

- North Moloka'i has some of the highest biomass of reef fish in the State of Hawaii, with resource species biomass nearly 3.5X higher than the statewide average, and nearly 3X higher than other northern coastlines.
- Target species important to the community also show higher mean biomass than similar northern shorelines (~ 1.5 to 2X higher for kole, kumu, and uhu).
- Sizes of species of interest (kole and kumu) are generally larger on Moloka'i's north coast than elsewhere in the MHI.
- Benthic habitat in the study area is dominated by turf algae. Rock and boulder habitats have greater benthic diversity than other habitats, with coralline algae, *Porites lobata*, and *Pocillipora meandrina* also comprising portions of the benthic cover.
- The northern coastline of Moloka'i has healthy fisheries resources, and fishery management actions in this area have the potential to preserve these resources for the future.

Introduction

Fisheries declines in Hawai'i

The State of Hawai'i's nearshore fisheries are in decline, a result of chronic overexploitation (Friedlander et al., 2003; Friedlander and DeMartini, 2002; Shomura, 1987; Smith, 1993) and habitat degradation (Hunter and Evans, 1995). A growing human population, the use of efficient and/or destructive fishing techniques (monofilament gillnets, Scuba equipment, spear guns, power boats, sonar fish finders), and loss of traditional conservation practices are putting increasing pressure on nearshore fisheries (Brock et al., 1985; Friedlander et al., 2003; Lowe, 1996). If long-term sustainability of fishery stocks is to be achieved, actions must be taken to address these pressures and conserve existing coastal fisheries.

North Moloka'i subsistence fishing

The local nearshore fisheries of the north coast of Moloka'i are a bright spot in Hawai'i. With a long history of subsistence fishing and gathering, communities of North Moloka'i follow practices of community self-management, with natural resources managed by those that use them and know them best (Poepoe et al., 2007). This subsistence-fishery management approach, in conjunction with the rugged, remote, and inaccessible character of Moloka'i's northern shoreline, has been thought to have prevented North Moloka'i's nearshore fisheries from slipping into the same state of decline as elsewhere in the main Hawaiian Islands.

Mo'omomi's History

Marine resources along Moloka'i's north-west coast are primarily harvested by a community of native Hawaiians who reside in the nearby Ho'olehua Hawaiian Homestead. Opened in 1924, Ho'olehua was established in 1924 after the US Congress passed the Hawaiian Homes Commission Act in 1921, and act intended to return Hawaiians to the land. The community has a population of about 1,000 native Hawaiians (Hui Malama o Mo'omomi, 1995), and retains a strong communal identity defined by shared cultural heritage and a system of interdependence and social reciprocity (Poepoe et al., 2007). Residents of Ho'olehua Homestead depend highly on subsistence farming and fishing, which provide a third of the food consumed by the community (Governor's Moloka'i Subsistence Taskforce, 1994). Most Ho'olehua households include active fishers, and it has been estimated that the average household consumes nearly 11 kg of seafood per week, or about ten times as much as on O'ahu (Poepoe et al., 2007).

Strong social cooperation and dependence on subsistence harvesting foster a collective interest in proper resource use and conservation (Hui Malama o Mo'omomi, 1995), to be promoted to local resource users as well as to fishermen who come from elsewhere to harvest within the area. In the past, when certain fish species such as kumu (*Parupeneus porphyreus*) were

targeted for their high commercial value in markets in Honolulu, high exploitation by fisherman from Molokaʻi and elsewhere led to a decline in the stock of this species. This served as a clear example of the consequences of deviating from traditional subsistence fishing practices and resource conservation norms. Recognition of the importance of community-based resource management led to the formation of Hui Malama o Moʻomomi (Hui Malama o Moʻomomi, 1995).

In 1994, the Hawaii State Legislature established a process, codified as Hawaiʻi Revised Statute (H.R.S.) §188-22.6, for designating community-based subsistence fishing areas, allowing communities to manage shoreline marine resources in nearby areas for subsistence fishing (Governor's Moloka'i Subsistence Taskforce, 1994). In response to this legislation, the Hui Malama o Moʻomomi prepared a fishery management plan for the north-west coast of Molokaʻi (Hui Malama o Moʻomomi, 1995), with objectives to:

- establish a marine resource monitoring program that integrates traditional and science-based techniques
- foster consensus about how fishing should be conducted to restore community values and care-taking
- revitalize a locally sanctioned code of fishing conduct.

In a two-year experimental period, the State Department of Land and Natural Resources (DLNR) designated Moʻomomi and Kawaʻaloa Bays, a small portion of the community's fishing grounds, as a community subsistence fishing area, with fishing gear restrictions and monitoring of resources and fishing activities (DLNR, 1996). After the experiment, the state drafted regulations for permanent government designation of a subsistence fishing area limited to the two bays. In October 2000, the DLNR held a public hearing on Molokaʻi, at which community leaders expressed ambitions for a much larger special area. They proposed a traditional *ahupuaʻa* framework (Smith and Pai, 1992), in which land and sea would be managed as interconnected units. The Hui proposed to manage local fisheries according to mutually agreed standards that would allow the state to evaluate the community's management performance (Poepoe et al., 2007). However ultimately, the CBSFA management plan proposed by the Hui was rejected.

Current proposed management

Despite the passage of CBSFA legislation more than 20 years ago, the Moʻomomi CBSFA remains to be established with an approved management plan. Hui Mālama O Moʻomomi continues to advance a renewed proposal to make traditional subsistence harvesting practices legally enforceable in the designated area of Molokaʻi's north shore.

Current proposed CBSFA regulations aim to reaffirm and protect Native Hawaiian traditional and customary subsistence fishing, cultural, and religious practices, and to protect the diversity, abundance, and accessibility of the marine resources upon which these practices rely. The

proposed management area extends from Kalaeokaʻīlio (ʻĪlio Point) in the west to Nihoa Flats in the east, with the eastern boundary lining up with the western boundary of Kalaupapa National Historical Park, from the shoreline out to one nautical mile. Proposed regulations include a mix of bans, bag limits, size limits, and seasonal closures for certain species of interest. It also bans night diving, spearfishing on scuba, and commercial fishing (with exemptions for trolling for pelagic species, and for deep bottomfishing outside of 40 fathoms). A special protection area is proposed for Kawaʻaloa Bay, an important nursery area for many species, areas which traditionally were left alone to allow fishes to rest and replenish. The protected nursery area would limit fishing and recreational activity, with certain exceptions.



Fig 1. (a) Proposed boundary for Mo'omomi CBSFA, and (b) proposed Kawa'aloa Bay Nursery Area

Species of interest

Uhu pālupaluka and 'ele'ele (Redlip parrotfish, *Scarus rubroviolaceus*)

Two of Hawai'i's largest parrotfish species are uhu 'ele'ele (male Redlip parrotfish, *Scarus rubroviolaceus*) and the endemic uhu uliuli (male Spectacled parrotfish, *Chlorurus perspicillatus*) (Hoover, 2008). For *S. rubroviolaceus*, L50, or the length at which 50% of the population has reached sexual maturity, is around 13 inches fork length (FL), which is larger than the current State rule of minimum catch size of 12 inches. This means that fish that may be legally caught and kept might still not be reproductively mature, thus contributing to population declines. In the Mo'omomi area, as in much of the state, declines of uhu populations have been observed over the last 15 years.

Kūmū (Whitesaddle Goatfish, *Parupeneus porphyreus*)

Kūmū is Hawai'i's only endemic shallow-water goatfish, and is highly prized and targeted, reputed to be the best tasting of the Hawaiian goatfish. Traditionally, kūmū was used as an offering to the gods. Growing up to 20 inches, it is typically low in the water column, associated with the bottom where they forage over sand and rubble. Due to heavy exploitation in the past few decades, kūmū in the Mo'omomi area is considered to be depleted.

Recent trends for Kūmū and Pālupaluka (uhu 'ele'ele)

Data since 2006 from Kalaupapa National Historical Park for kūmū and pālupaluka (uhu 'ele'ele) show promising patterns. While the trend in kūmū abundance and biomass is slightly negative, the relationship does not appear to be statistically significant. Pālupaluka abundance has increased moderately since 2006, with a significant increase in biomass, indicating larger fish are now present.

Kole (Goldring surgeonfish, *Ctenochaetus strigosus*)

Kole is a territorial, group-spawning species found in shallow sub-surge zones of coral, rock, and boulders. Due to the rough conditions much of the year on Moloka'i's north coast, kole at Mo'omomi are highly targeted in the summer months when the conditions are calm. Given their life history characteristics, they are easily exploited and often overharvested, and when groups of large, reproductive individuals are greatly reduced (i.e. spawning group is harvested), recovery can be slow.

Objectives of this report

This report aims to summarize baseline ecological data gathered on the North Shore of the island of Moloka'i by the State of Hawai'i's Division of Aquatic Resources, the Kaulapapa National Historic Park, NOAA Pacific Islands Fisheries Science Center, and the Fisheries Ecology Research Lab of the University of Hawai'i at Manoa. In addition to characterizing the nearshore

ecosystems of North Moloka'i, this report also focuses on key species important to the local communities, and describes the marine resources relative to other locations in the State.

Efforts to establish regulations for the Mo'omomi Community Based Subsistence Fishery Area have long been underway, and have been informed by local knowledge and customs. The summary evaluation presented herein serves to contribute to these efforts by providing a quantitative ecological analysis conducted using scientific methods. Furthermore, this baseline assessment provides a platform from which future monitoring efforts and evaluations may be based.

Mo'omomi and the north coast of Moloka'i seek to establish CBSFA regulations to ensure food, economic, and cultural sustainability. CBSFA designation would bring the rich local knowledge and traditions of the Mo'omomi community together with the formal rule making authority and enforcement capabilities of the DLNR. The CBSFA process is an important new tool that the state can use to work with communities to protect Hawai'i's marine resources, and develop management activities that support ecological and cultural sustainability.

Methods

Surveys took place in May and August of 2017 and extended from Kalaeokaʻilio in the west to Nihoa Flats in the east (Fig 2). Surveys were conducted using a stratified random sampling design, restricted to habitats with > 50% hard bottom based on NOAA Benthic Habitat maps (Battista et al., 2007), with the study area stratified into segments from east to west to ensure spatially comprehensive representation. Furthermore, Kawaʻaloa Bay served as a separate stratum, to ensure thorough sampling of this area of interest.

A total of 141 surveys were conducted, following standard underwater visual census (UVC) methods in which observers recorded species, size (total length, TL), and abundance of all observed fishes within 25 x 5 m transects. The habitat was classified at each transect start, as was a ranking of complexity, on a scale of 1 to 5, with 1 being flat pavement and 5 being large complex boulders or other types of habitat with large caves, overhands and/or ledges. Benthic data were also collected along the transects using photo-quadrat methods, where photos of the benthos were taken from 1 m above the substrate at every meter along the transect line.

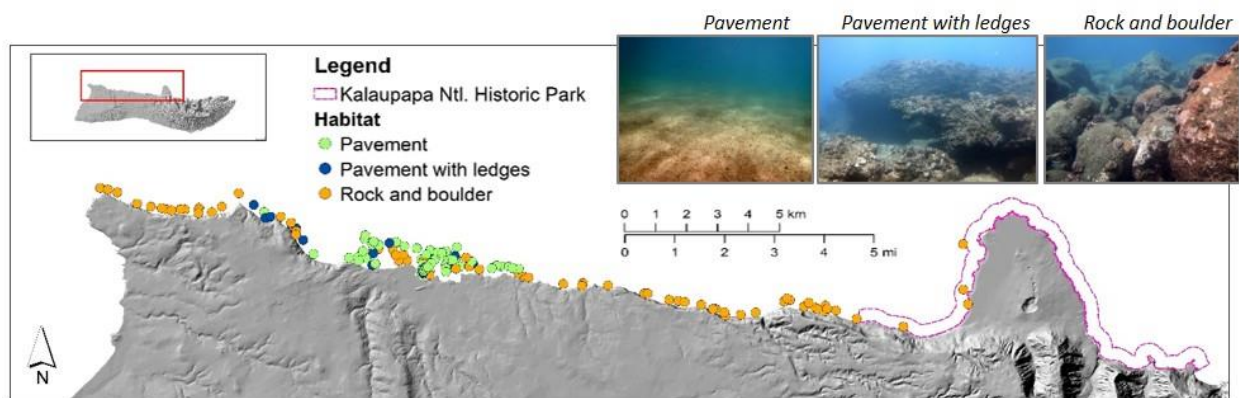


Fig 2. Underwater visual census survey points (n = 141) from May and August 2017 sampling periods; classified by habitat type, as determined *in situ* during sampling.

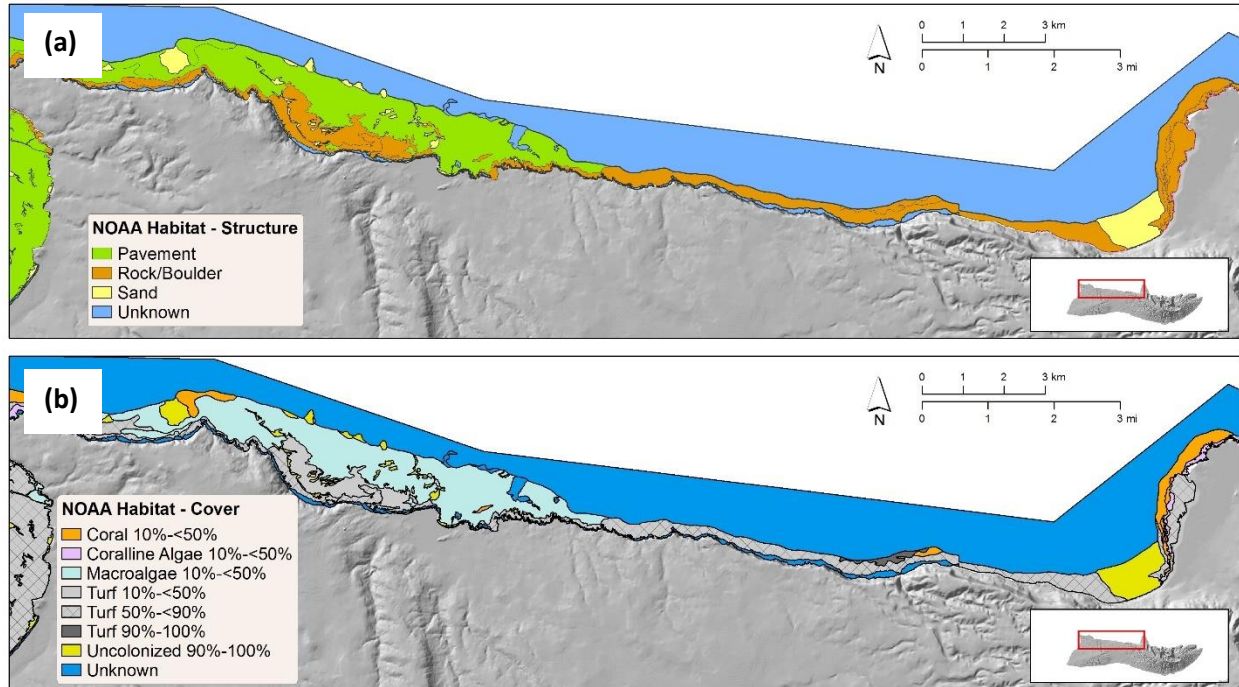


Fig 3. NOAA benthic habitat maps of study area, depicting classes of (a) geomorphological structure, and (b) biological cover (Battista et al., 2007).

Results

Fish

Reef fish biomass

Mean total biomass of reef fish on North Moloka'i was $172 (\pm 14) \text{ g / m}^2$, with samples ranging from 0.9 to 840 g / m^2 . Biomass of resource species of reef fish $145 (\pm 13) \text{ g / m}^2$, with samples ranging from 0 to 829 g / m^2 . Resource biomass on North Moloka'i was high relative to other areas in the State of Hawai'i; approximately 3 times higher than that of other north-exposed shorelines, and nearly 3.5 times that of the main Hawaiian Islands (MHI) in general (Fig 5). Mean biomass of resource species estimated from May and August 2017 survey data is consistent with estimates from Friedlander et al.'s (2018) analysis of resource biomass by moku (Fig 6), which indicated that North Moloka'i had the highest estimated biomass of resource species in the state.

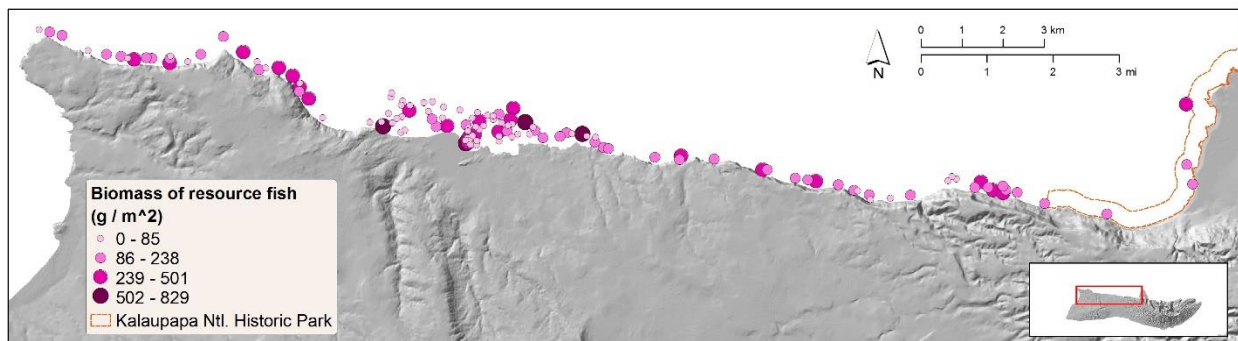


Fig 4. Biomass of resource fish across study area.

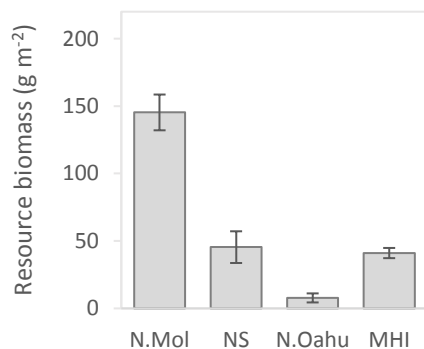


Fig 5. Resource species biomass (with 95% confidence intervals), for N. Moloka'i, other north shores in the MHI, N. Oahu, and all MHI (data for other sites from HIMARC 2017 and Friedlander et al. 2017).

PAVL), while mobile invertivores are more highly represented in pavement with ledges (26%) than other habitats (17% in ROB, 12% in pavement). Rock and boulder had the most even diversity of the habitat types in the study area, but was still dominated by herbivores, as were the other habitats.

Table 1. Mean fish assemblage metrics, by habitat type (\pm st. err.).

	Total reef fish biomass (g/m ²)	Resource species biomass (g/m ²)	Density (indiv/ 100m ²)	Spp richness (no. spp)
Pavement	102.41 (23.2)	93.69 (23.1)	72.88 (6.2)	11.80 (0.7)
Pavement with ledges	214.54 (33.2)	189.43 (30.7)	119.79 (14.8)	18.67 (1.3)
Rock and boulder	223.41 (17.4)	180.88 (16.3)	164.7 (10.0)	25.78 (0.7)

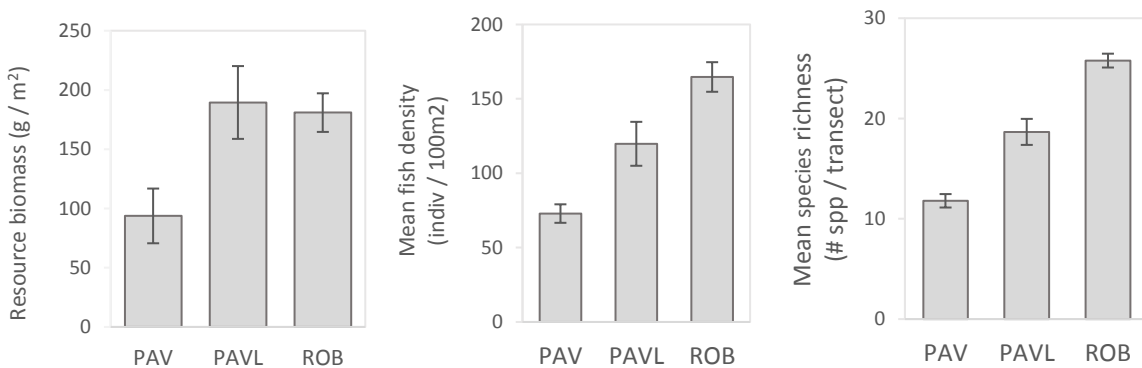


Fig 7. (a) Resource fish biomass (g / m²), (b) mean fish density (no. indiv / 100 m²), and (c) mean species richness (no. species / transect), by habitat type (\pm st. err.)

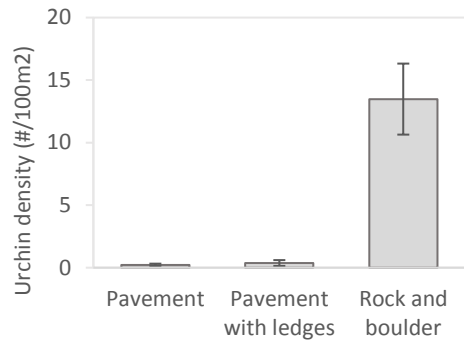


Fig 8. Mean sea urchin density (\pm st. err.), by habitat.

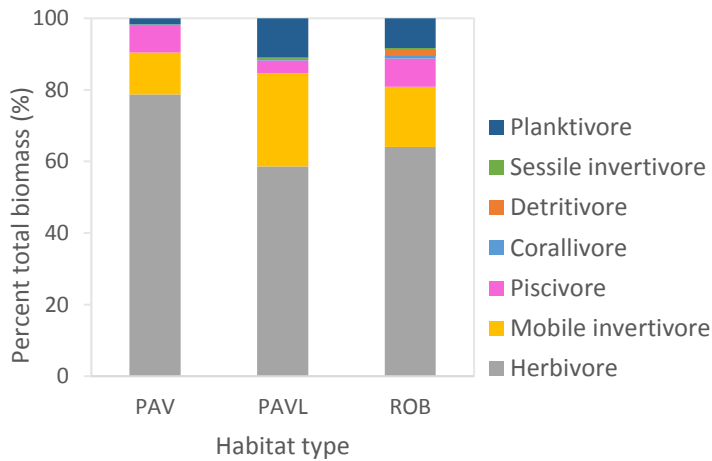


Fig 9. Trophic structure of fish communities, by habitat

Given the clear difference in fish assemblage metrics between habitat types, biomass comparisons between locations were further assessed by habitat type. Survey data from other locations were attributed with habitat types based on NOAA Benthic Habitat Map structure classes (Battista et al., 2007). Assessment of resource biomass for Rock and Boulder and Pavement habitats showed consistent patterns with those previously presented. Biomass of resource fish in Rock and Boulder habitats on North Moloka'i is substantially higher than that of similar habitats on coastlines of similar exposures. With a mean of $180.9 (\pm 16.3) \text{ g m}^{-2}$, Rock and Boulder habitats on North Moloka'i have greater than 5X the biomass of resource species than those of other northern coastlines in the main Hawaiian Islands, and nearly 40X the biomass of North O'ahu (Fig. 10a). While the differences were not as pronounced in Pavement habitats, North Moloka'i still exhibited higher resource biomass in this habitat, 3-5X higher than Pavement habitats elsewhere in the MHI (Fig. 10b). A closely analogous structure class was not available for Pavement with Ledges.

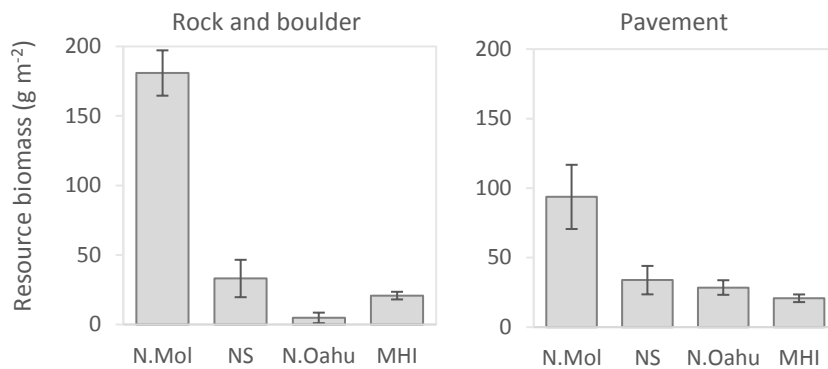


Fig 10. Mean biomass (g m^{-2}) of resource species in (a) rock and boulder habitats, and (b) pavement habitats (\pm st. err.). North Moloka'i compared to all other north shores in the MHI, nearby North Oahu specifically, and statewide mean. Data source for comparisons: HIMARC 2018

Species of interest

Mean biomass of selected resource species (kole, *Ctenochaetus strigosus*; kumu, *Parupeneus porphyreus*; and uhu, *Scarus rubroviolaceus*) varied substantially by habitat (Fig). Kole occurred exclusively in rock and boulder habitat. Kumu was observed in rock and boulder habitat, as well as pavement with ledges and cracks, but had very low biomass in flat pavement habitats, a pattern similarly observed in uhu. *Chlorurus perspicillatus*, also a species of interest in the study area, was not abundant enough in surveys to be included in the analyses of uhu.

Rock and boulder habitats and pavement areas with ledges and overhangs have greater structural complexity than flat pavement habitats. Higher complexity provides more holes and spaces that fish can use for refuge, and these patterns of higher biomass in habitats of greater structural complexity are further supported by analyses of rugosity rankings (Fig. 12).

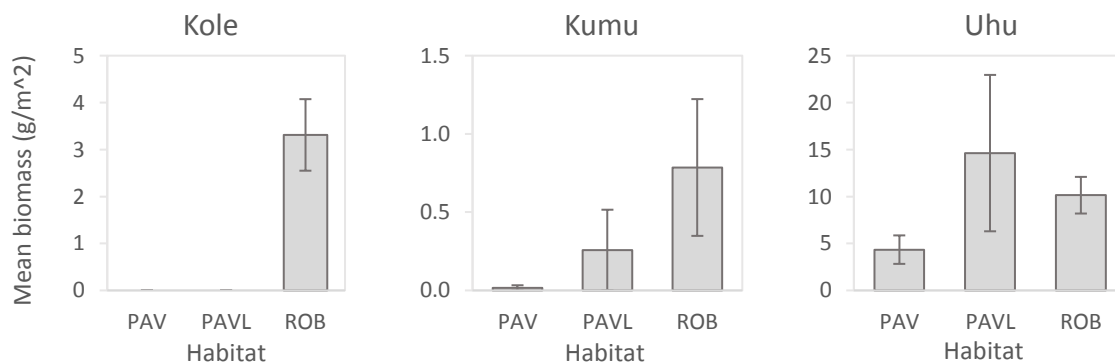


Fig 11. Mean biomass of species of interest, by habitat type. PAV = pavement, PAVL = Pavement with ledges, ROB = rock and boulder.

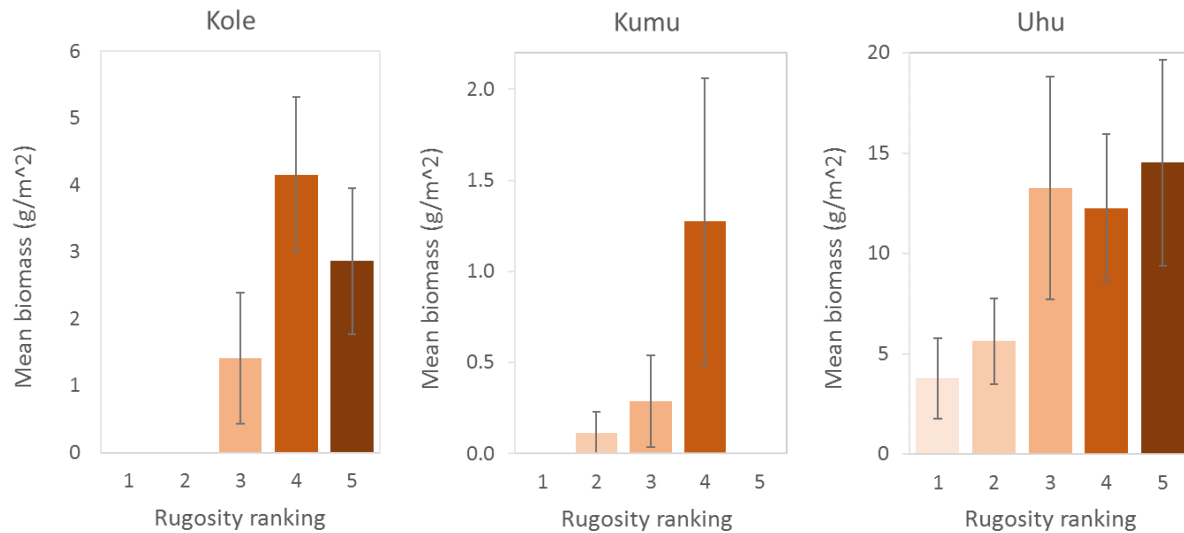


Fig 12. Mean biomass of resource species, by rugosity ranking. Rugosity estimates are on a scale of 1 to 5, with 1 being flat pavement and 5 being large complex boulders or other types of habitat with large caves, overhands and/or ledges.

Overall biomass of species of interest on Moloka'i's north coast was high compared to other locations around the State (Fig 83). Kumu and uhu showed higher mean biomass on North Moloka'i than the statewide average. Comparing to shorelines of comparable exposure, mean biomass of kole, kumu, and uhu on Moloka'i's north shore was higher than the north shores of other islands. A particularly strong contrast was observed in the comparison of the north shores of Moloka'i and O'ahu; resource fish biomass on North Moloka'i was drastically higher (10-20X) than on neighboring O'ahu, an area of high fishing pressure.

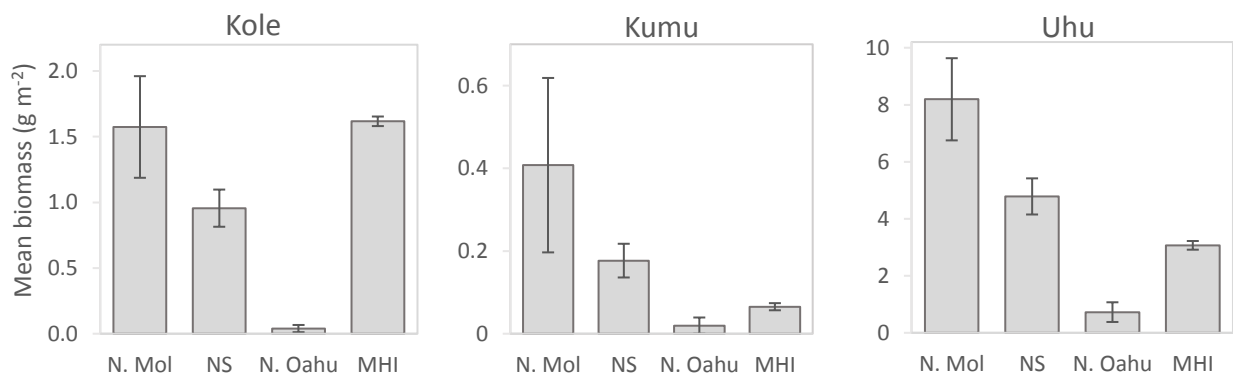


Fig 8. Mean biomass (\pm SE) of species of interest; North Moloka'i compared to all other north shores in the MHI, nearby North Oahu specifically, and statewide mean. Data source for comparisons: HIMARC 2018

Differences in fish communities were also apparent in the size structure of species of interest. Sizes of kole, kumu, and uhu of North Moloka'i were generally larger than those of the MHI as a whole (Fig 94, Fig 105, Fig 116).

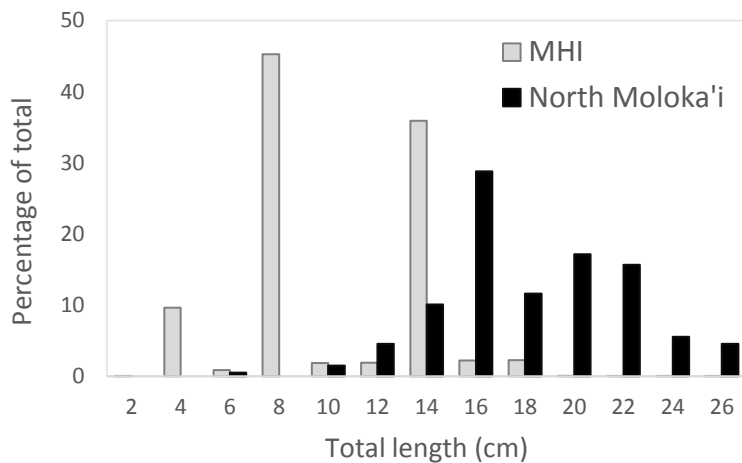


Fig 9. Size distributions of kole; North Moloka'i vs. MHI.

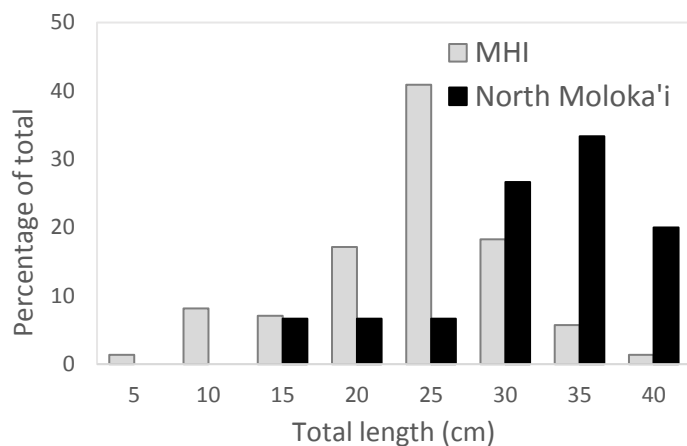


Fig 10. Size distributions of kumu; North Moloka'i vs. MHI.

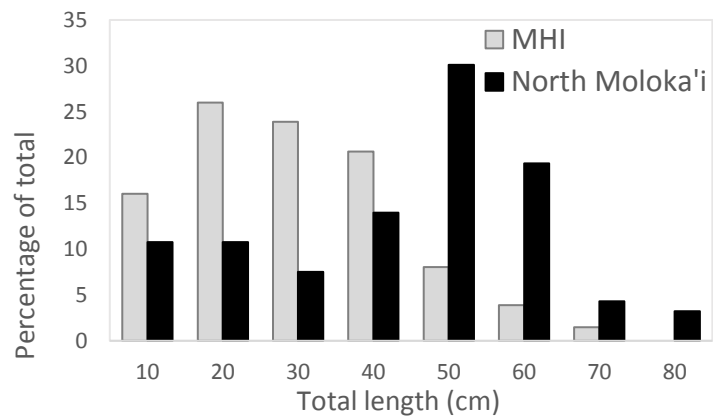


Fig 11. Size distributions of uhu; North Moloka'i vs. MHI.

Benthic habitat

The benthic community of North Moloka'i was dominated by turf algae cover, with low cover of coralline algae, coral (primarily *Porites lobata* and *Pocillopora meandrina*), and macroalgae. There was some variation in community composition by habitat type (Table 2, Fig. 17). Pavement and Pavement with ledges were primarily turf and sand cover, ~87-89% and ~4-5%, respectively. Hard coral cover was low in all habitats, ranging from 3-6% cover, the highest cover occurring in Rock and Boulder habitats. Coralline algae ranged from 1% cover in Pavement habitats to 11% cover in Pavement with Ledges habitats. Rock and boulder had a more diverse benthic community, with turf comprising 78% cover, coralline algae 11%, and coral 6% cover.

Table 2. Top benthic categories (mean percent cover \pm st. err.).

Habitat	Benthic ID	Percent cover (st. err)
Pavement	Turf Algae	88.6 (1.6)
	Sand	3.84 (1.3)
	Coral	3.37 (0.7)
	Macroalgae	2.40 (0.5)
	Coralline Algae	1.18 (0.3)
Pavement with ledges	Turf Algae	86.7 (3.4)
	Sand	4.81 (2.6)
	Coralline Algae	4.16 (1.7)
	Coral	2.77 (1.0)
	Macroalgae	1.27 (0.7)
Rock and boulder	Turf Algae	77.6 (2.0)
	Coralline Algae	10.6 (1.9)
	Coral	5.73 (1.0)
	Sand	3.08 (0.7)
	Macroalgae	1.86 (0.7)

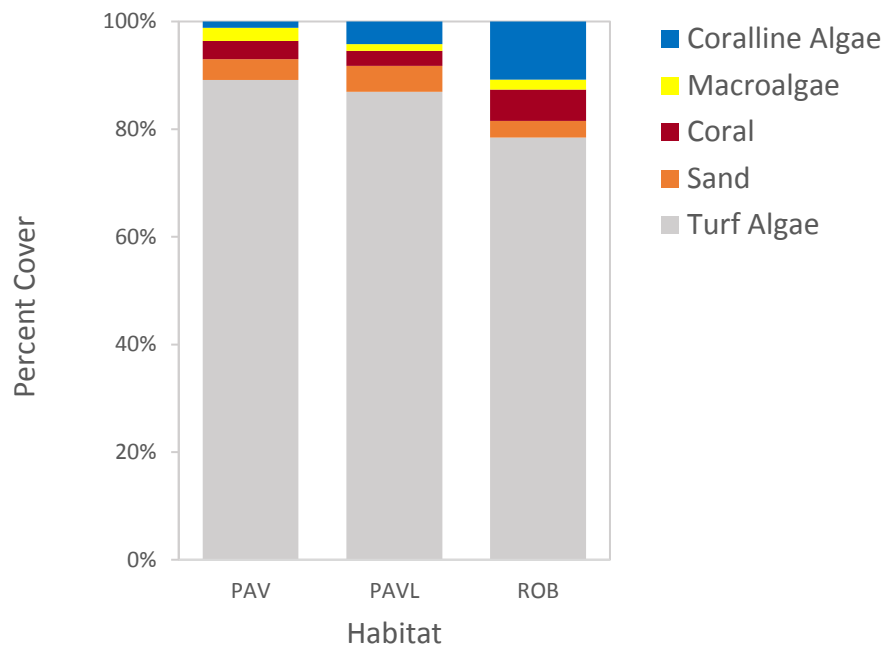


Fig 12. Benthic composition, by habitat type.

Discussion

The north shore of Moloka'i has some of the healthiest nearshore ecosystems and highest biomass of reef fish in the state. The exposure of this shoreline to powerful waves and consistent rough water, as well as the limited shoreline access, has historically kept fishing pressure low, but this may not keep these statewide resources protected from fishing forever. Concerns within the community about recent declines in overall catches and declining fish sizes have highlighted the timely need to address Moloka'i's fishery management in order to sustain these marine resources into the future.

As resources throughout the state decrease, it is likely additional pressure will be placed on the resources of this area, potentially causing declines in the marine resources of the area. In an analysis of fishery catch data from 2004 to 2013, the total annual catch of reef fish per unit area of hardbottom habitat was estimated to be 0.64 metric tons $\text{km}^{-2} \text{ year}^{-1}$ for the island of Moloka'i (McCoy et al., 2018). In contrast, the island of Oahu had an estimated 1.84 metric tons $\text{km}^{-2} \text{ year}^{-1}$ of fish extracted from the nearshore environment. O'ahu, the most populated island in the State, is an area of high fishing pressure. The highest estimates of shore-based fishing effort are on Oahu (Delaney et al., 2017), and Oahu has the highest estimated number of fishing trips of any of the main Hawaiian Islands (McCoy et al., 2018). Furthermore, Oahu has the highest boat ownership and most launch ramps, and catch levels for boat-based fisheries appear to be driven by island-scale population density (Wedding et al., 2018). Population density and shoreline accessibility are drivers of Hawaii's nearshore fishery (Wedding et al., 2018), and in locations such as the north shore of Moloka'i, with low population density and limited access to the shore, fishing pressure and total catch is low, and fish biomass is high.

It is increasingly important to set up management plans that will help maintain the quality of North Moloka'i's nearshore ecosystem in the face of increasing fishing effort. In nearby Kalaupapa National Historic Park, an area with no (or negligible) catch (Delaney et al., 2017), fish biomass has shown to remain stable over time (Fig. 18; National Park Service, 2015). This part of the coastline is of similar habitat to the study area, subjected to the same rough conditions. The stability of the marine resources within Kalaupapa NPS is suggestive of the potential stability that could be achieved along the rest of the coastline.

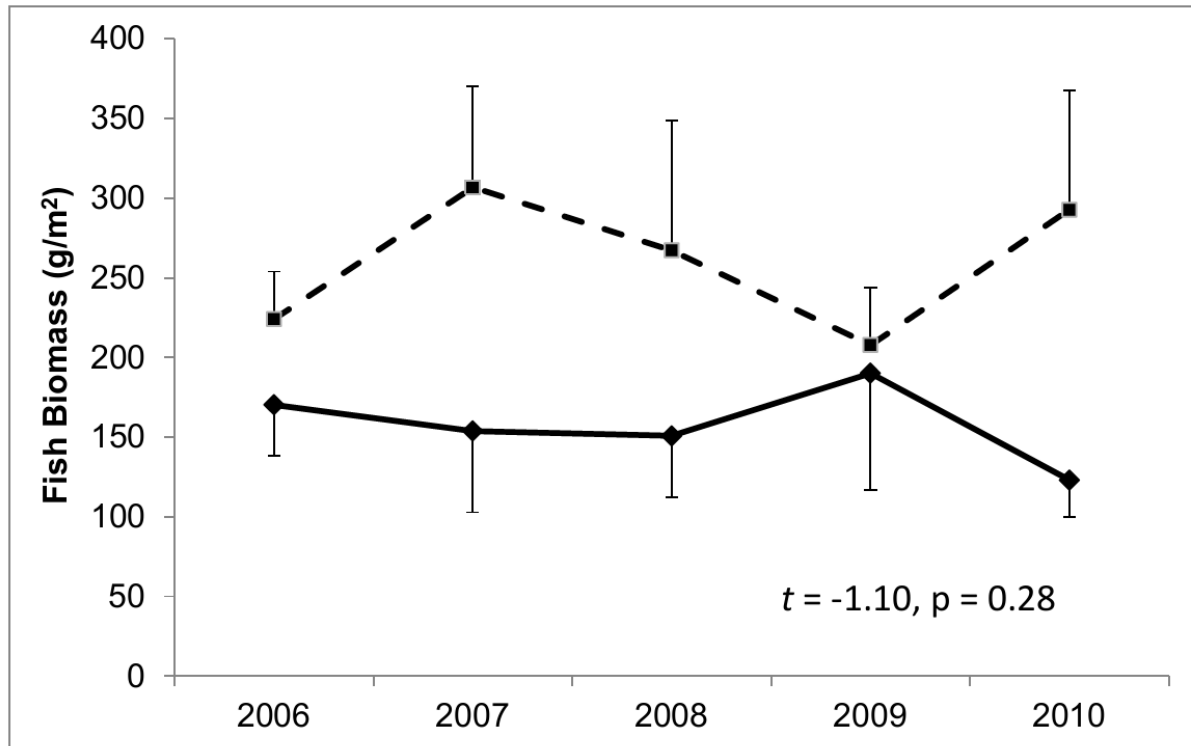


Fig 138. Fish biomass (\pm SE) in Kalaupapa National Historical Park, at monitoring sites from 2006-2010 (solid line = fixed sites, dashed line = temporary sites) (National Park Service, 2015)

In addition to higher fish biomass and abundance on North Moloka'i, individual fish were also generally larger. The size distributions of key species of interest were shifted toward larger sizes compared to the rest of the main Hawaiian Islands. Currently, State regulations for minimum catch size is below the estimated size of sexual maturity for some species, potentially hindering the capacity of a population to reproduce and thus be a sustainable stock. For example, the estimated L50 for *Scarus rubroviolaceus* is 13 inches, or 33 cm. This is around the size at which uhu frequency drops off in MHI data (Fig. 16). However, the individuals in Moloka'i are reaching and surpassing this size, suggesting successful reproduction opportunities. In areas where fish are reaching reproductive sizes, fisheries have greater potential to maintain sustainable yields, and management tools such as slot limits can provide further assurance that these populations remain sustainable.

The resources along the northern coastline of Moloka'i are important to the community, and they are currently some of the healthiest and highest biomass in the State. A community-based subsistence fishing area (CBSFA) is important way for the community to partner with the State and help ensure the sustainability of their fishery resources for future generations. Community-based resource management can be very effective at conserving marine resources and sustaining fish biomass that is equal to or greater than that in no-take reserves (Friedlander et al., 2003; Friedlander et al., 2013). Through sustainable fishing practices and traditional stewardship, CBSFAs can enhance fisheries management and ecosystem health in Hawai'i.

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Appendix

Table A1. Fish species observed in underwater visual census surveys; mean biomass (g/m² ± st. dev.) and density (individuals / 100 m² ± st. dev.).

	Taxa	Biomass g/m ² (sd)	Density indiv/ 100m ² (sd)
1	Kyphosus sp.	23.73 (45.5)	5.2 (9.6)
2	Acanthurus dussumieri	18.44 (75.6)	0.8 (2.9)
3	Naso unicornis	17.32 (44.5)	2.2 (4.5)
4	Acanthurus blochii	13.04 (41.9)	1.0 (2.7)
5	Naso lituratus	11.29 (16.3)	4.4 (7.0)
6	Caranx melampygus	8.46 (15.4)	2.4 (4.4)
7	Scarus rubroviolaceus	8.19 (17.1)	0.5 (1.0)
8	Acanthurus triostegus	7.74 (24.3)	6.4 (13.8)
9	Bodianus albotaeniatus	4.83 (6.4)	0.8 (1.0)
10	Acanthurus olivaceus	4.33 (12.9)	1.9 (4.8)
11	Lutjanus kasmira	4.28 (13.7)	2.4 (6.9)
12	Myripristis berndti	3.82 (15.4)	0.6 (2.4)
13	Naso hexacanthus	3.82 (21.0)	1.0 (5.3)
14	Mulloidichthys vanicolensis	3.75 (27.7)	1.2 (6.8)
15	Acanthurus leucopareus	2.85 (6.1)	15.9 (35.5)
16	Acanthurus nigrofusus	2.71 (3.5)	7.5 (8.4)
17	Monotaxis grandoculis	2.55 (8.0)	0.4 (1.2)
18	Lutjanus fulvus	2.25 (7.3)	0.7 (2.4)
19	Cephalopholis argus	1.92 (6.4)	0.2 (0.7)
20	Sufflamen fraenatus	1.68 (3.4)	0.3 (0.6)
21	Ctenochaetus strigosus	1.57 (4.6)	1.1 (3.4)
22	Rhinecanthus rectangulus	1.29 (3.5)	0.6 (1.0)
23	Mulloidichthys flavolineatus	1.20 (8.4)	0.6 (4.4)
24	Melichthys niger	1.16 (4.3)	0.3 (1.0)
25	Parupeneus multifasciatus	1.11 (2.1)	1.3 (2.3)
26	Thalassoma duperrey	1.09 (1.0)	13.2 (12.9)
27	Naso brevirostris	1.00 (7.9)	0.2 (1.4)
28	Chlorurus perspicillatus	0.93 (8.1)	<0.1 (0.2)
29	Aprion virescens	0.91 (10.9)	<0.1 (0.1)
30	Abudefduf sordidus	0.87 (2.7)	0.2 (0.6)
31	Abudefduf abdominalis	0.74 (7.2)	0.4 (2.4)
32	Parupeneus insularis	0.74 (2.0)	0.4 (0.9)
33	Thalassoma trilobatum	0.60 (1.2)	2.1 (3.8)
34	Sufflamen bursa	0.54 (1.4)	0.6 (1.2)
35	Chromis vanderbilti	0.53 (1.6)	24.4 (35)
36	Thalassoma ballieui	0.53 (1.8)	0.1 (0.4)
37	Decapterus macarellus	0.50 (2.9)	0.4 (2.1)
38	Kyphosus cinerascens	0.49 (4.2)	<0.1 (0.4)
39	Chaetodon miliaris	0.44 (3.0)	0.6 (3.6)
40	Chaetodon ornatissimus	0.43 (1.1)	0.2 (0.6)

41	<i>Chromis ovalis</i>	0.41 (2.9)	1.4 (8.8)
42	<i>Parupeneus porphyreus</i>	0.41 (2.5)	0.1 (0.5)
43	<i>Abudefduf vaigiensis</i>	0.40 (2.4)	1.0 (4.1)
44	<i>Scarus psittacus</i>	0.39 (1.3)	0.1 (0.5)
45	<i>Oplegnathus punctatus</i>	0.36 (4.2)	<0.1 (0.1)
46	<i>Melichthys vidua</i>	0.33 (2.2)	0.1 (0.3)
47	<i>Halichoeres ornatissimus</i>	0.32 (0.6)	1.0 (1.6)
48	<i>Parupeneus cyclostomus</i>	0.31 (1.7)	0.2 (0.6)
49	<i>Cantherhines dumerilii</i>	0.31 (2.3)	<0.1 (0.2)
50	<i>Anampses cuvier</i>	0.28 (0.9)	0.2 (0.6)
51	<i>Aphareus furca</i>	0.27 (1.3)	0.1 (0.5)
52	<i>Zanclus cornutus</i>	0.26 (0.8)	0.2 (0.6)
53	<i>Paracirrhites arcatus</i>	0.25 (0.5)	2.6 (4.1)
54	<i>Calotomus carolinus</i>	0.23 (1.0)	0.1 (0.3)
55	<i>Chaetodon quadrimaculatus</i>	0.22 (0.5)	0.5 (1.0)
56	<i>Acanthurus achilles</i>	0.19 (1.2)	0.2 (0.9)
57	<i>Zebrasoma flavescens</i>	0.18 (0.8)	0.2 (0.7)
58	<i>Zebrasoma veliferum</i>	0.17 (1.1)	<0.1 (0.2)
59	<i>Seriola dumerili</i>	0.17 (2.0)	<0.1 (0.1)
60	<i>Cirrhitus pinnulatus</i>	0.16 (0.6)	0.1 (0.4)
61	<i>Acanthurus nigroris</i>	0.15 (0.9)	0.2 (1.0)
62	<i>Stegastes marginatus</i>	0.15 (0.3)	0.8 (1.5)
63	<i>Chromis verater</i>	0.15 (1.7)	0.1 (1.4)
64	<i>Chaetodon lunula</i>	0.13 (0.4)	0.2 (0.6)
65	<i>Scomberoides lysan</i>	0.13 (0.7)	<0.1 (0.2)
66	<i>Diodon hystrix</i>	0.12 (1.0)	<0.1 (0.1)
67	<i>Plectroglyphidodon johnstonianus</i>	0.12 (1.1)	0.4 (1.5)
68	<i>Chaetodon auriga</i>	0.11 (0.5)	0.1 (0.3)
69	<i>Myripristis amaena</i>	0.10 (0.9)	<0.1 (0.3)
70	<i>Coris venusta</i>	0.10 (0.3)	0.9 (3.2)
71	<i>Paracirrhites forsteri</i>	0.10 (0.3)	0.3 (0.8)
72	<i>Chlorurus spilurus</i>	0.10 (0.7)	<0.1 (0.1)
73	<i>Myripristis kuntee</i>	0.10 (1.2)	<0.1 (0.5)
74	<i>Forcipiger flavissimus</i>	0.10 (0.3)	0.2 (0.6)
75	<i>Parupeneus pleurostigma</i>	0.09 (0.5)	0.5 (3.5)
76	<i>Chaetodon multicinctus</i>	0.07 (0.3)	0.2 (0.6)
77	<i>Chaetodon fremblii</i>	0.06 (0.1)	0.1 (0.3)
78	<i>Cantherhines sandwichiensis</i>	0.05 (0.2)	0.1 (0.2)
79	<i>Stethojulis balteata</i>	0.05 (0.2)	0.5 (1.1)
80	<i>Coris gaimard</i>	0.05 (0.2)	0.2 (0.6)
81	<i>Aulostomus chinensis</i>	0.04 (0.3)	<0.1 (0.1)
82	<i>Forcipiger longirostris</i>	0.04 (0.3)	<0.1 (0.3)
83	<i>Carangoides orthogrammus</i>	0.04 (0.4)	<0.1 (0.1)
84	<i>Plectroglyphidodon imparipennis</i>	0.04 (0.1)	2.8 (3.9)
85	<i>Ctenochaetus hawaiiensis</i>	0.03 (0.4)	<0.1 (0.1)
86	<i>Cirrhitops fasciatus</i>	0.03 (0.1)	0.3 (0.7)
87	<i>Chaetodon ephippium</i>	0.03 (0.3)	<0.1 (0.1)
88	<i>Neoniphon sammara</i>	0.02 (0.2)	<0.1 (0.2)

89	<i>Apolemichthys arcuatus</i>	0.02 (0.1)	<0.1 (0.1)
90	<i>Canthigaster amboinensis</i>	0.02 (0.1)	<0.1 (0.1)
91	<i>Thalassoma purpurum</i>	0.02 (0.2)	<0.1 (0.2)
92	<i>Canthigaster jactator</i>	0.02 (0.1)	0.2 (0.6)
93	<i>Ostracion meleagris</i>	0.02 (0.1)	0.1 (0.2)
94	<i>Dascyllus albisella</i>	0.02 (0.2)	<0.1 (0.3)
95	<i>Macropharyngodon geoffroy</i>	0.01 (0.1)	0.3 (1.8)
96	<i>Gomphosus varius</i>	0.01 (0.1)	0.1 (0.2)
97	<i>Chromis leucura</i>	0.01 (0.1)	<0.1 (0.1)
98	<i>Acanthurus nigricans</i>	0.01 (0.1)	<0.1 (0.2)
99	<i>Ptereleotris heteroptera</i>	0.01 (0.1)	0.3 (2.6)
100	<i>Acanthurus guttatus</i>	0.01 (0.1)	<0.1 (0.2)
101	<i>Plagiotremus goslinei</i>	0.01 (0)	0.9 (2.1)
102	<i>Plectroglyphidodon sindonis</i>	0.01 (0.1)	<0.1 (0.2)
103	<i>Xyrichtys pavo</i>	0.01 (0.1)	<0.1 (0.1)
104	<i>Oxycheilinus bimaculatus</i>	0.01 (0)	0.2 (0.7)
105	<i>Gunnellichthys curiosus</i>	<0.01 (0)	<0.1 (0.1)
106	<i>Novaculichthys taeniourus</i>	<0.01 (0)	<0.1 (0.2)
107	<i>Cirripectes vanderbilti</i>	<0.01 (0)	<0.1 (0.1)
108	<i>Apogon kallopterus</i>	<0.01 (0)	<0.1 (0.1)
109	<i>Neoniphon spp.</i>	<0.01 (0)	<0.1 (0.1)
110	<i>Exallias brevis</i>	<0.01 (0)	<0.1 (0.2)
111	<i>Centropyge potteri</i>	<0.01 (0)	<0.1 (0.1)
112	<i>Caracanthus typicus</i>	<0.01 (0)	0.1 (0.3)
113	<i>Chaetodon kleinii</i>	<0.01 (0)	<0.1 (0.1)
114	<i>Pseudocheilinus tetrataenia</i>	<0.01 (0)	<0.1 (0.2)
115	<i>Malacanthus brevirostris</i>	<0.01 (0)	<0.1 (0.1)
116	<i>Labroides phthirophagus</i>	<0.01 (0)	<0.1 (0.1)
117	<i>Pseudojuloides cerasinus</i>	<0.01 (0)	<0.1 (0.1)
118	<i>Plagiotremus ewaensis</i>	<0.01 (0)	<0.1 (0.2)
119	<i>Chromis agilis</i>	<0.01 (0)	<0.1 (0.3)
120	<i>Canthigaster coronata</i>	<0.01 (0)	<0.1 (0.1)
121	<i>Pseudocheilinus octotaenia</i>	<0.01 (0)	<0.1 (0.1)
122	<i>Chromis hanui</i>	<0.01 (0)	<0.1 (0.2)
123	<i>Sebastapistes ballieui</i>	<0.01 (0)	<0.1 (0.1)
124	<i>Synodus ulae</i>	<0.01 (0)	<0.1 (0.1)

Table A2. Benthic taxa observed in underwater visual census surveys; mean percent cover \pm st. err, by habitat type.

Habitat	Benthic ID	Percent cover (st. err)
Pavement	Turf Algae	88.6 (1.6)
	Sand	3.8 (1.3)
	Porites lobata	1.9 (0.5)
	Coralline Algae	1.1 (0.3)
	Rhodophyta	0.9 (0.3)
	Pocillopora meandrina	0.8 (0.3)
	Halimeda sp.	0.6 (0.1)
	Dictyota sp.	0.5 (0.1)
	Montipora capitata	0.3 (0.2)
	Other	0.2 (0.1)
	Asparagopsis taxiformis	0.2 (0.1)
	Porites compressa	0.2 (0.1)
	Unknown	0.2 (0.1)
	Porites lutea	<0.1 (<0.1)
	Mobile Invert	<0.1 (<0.1)
	Phaeophyta	<0.1 (<0.1)
Pavement with ledges	Turf Algae	86. (3.46)
	Sand	4.8 (2.6)
	Coralline Algae	4.1 (1.7)
	Porites lobata	1.3 (0.6)
	Pocillopora meandrina	1.2 (0.6)
	Rhodophyta	0.7 (0.5)
	Dictyota sp.	0.1 (0.1)
	Galaxaura sp.	0.1 (0.1)
	Liagora sp.	0.1 (0.1)
	Unknown	0.1 (0.1)
	Montipora patula	0.1 (0.1)
	Other	<0.1 (<0.1)
	Leptastrea purpurea	<0.1 (<0.1)
Rock and boulder	Turf Algae	77. (2.07)
	Coralline Algae	10. (1.9)
	Sand	3.0 (0.7)
	Porites lobata	2.7 (0.5)
	Pocillopora meandrina	2.6 (0.6)
	Unknown	0.6 (0.2)
	Asparagopsis taxiformis	0.4 (0.4)
	Galaxaura sp.	0.4 (0.2)
	Phaeophyta	0.3 (0.3)
	Rhodophyta	0.3 (0.1)
	Dictyota sp.	0.2 (0.1)

Halimeda sp.	0.1 (<0.1)
Zoanthid	0.1 (0.1)
Porites lutea	0.1 (<0.1)
Other	0.1 (0.1)
Pavona varians	<0.1 (<0.1)
Montipora capitata	<0.1 (<0.1)
Montipora patula	<0.1 (<0.1)
Porites brighami	<0.1 (<0.1)
Porites compressa	<0.1 (<0.1)
Substrate	<0.1 (<0.1)
Montipora flabellata	<0.1 (<0.1)
Porifera	<0.1 (<0.1)