

It has come to our attention that site names, Kamiloloa and Kamalo, were switched in the text. We apologize for any inconvenience and/or confusion caused by this error. We are in the process of publishing a formal correction with Coral Reefs.

Please make the following corrections:

- **Page 295, Table 1, change site name Kamalo with Kamiloloa, and Kamiloloa with Kamalo.**
- **Page 296, paragraph 1, change Kamalo with Kamiloloa.** Text should read “. . .0.8% at Kamiloloa (10m) to a high of 89.0% at Molokini (13m) (Table 1).”
- **Page 296, paragraph 3, change Kamiloloa with Kamalo.** Text should read “ Rugosity measurements ranged from a low of 1.12 at Papaula Pt. (10m) to a high of 2.46 at Kamalo (10m) (Table 1).”
- **Page 298, paragraph 1, change Kamiloloa with Kamalo.** Text should read, “The deep and shallow Kamalo sites on the south shore of Molokai were classified as south-sheltered locations based on their wave exposure, but had fish assemblages more similar in ordination space to south- and north-exposed locations.”

A. M. Friedlander · E. K. Brown · P. L. Jokiel
W. R. Smith · K. S. Rodgers

Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago

Received: 12 April 2002 / Accepted: 26 March 2003 / Published online: 16 August 2003
© Springer-Verlag 2003

Abstract The relationships between fish assemblages, their associated habitat, and degree of protection from fishing were evaluated over a broad spatial scale throughout the main Hawaiian islands. Most fish assemblage characteristics showed positive responses to protection whether it was physical (e.g. habitat complexity), biological (e.g. coral cover growth forms), or human-induced (e.g. marine reserves). Fish biomass was lowest in areas of direct wave exposure and highest in areas partially sheltered from swells. Higher values for fish species richness, number of individuals, biomass, and diversity were observed in locations with higher substrate complexity. Areas completely protected from fishing had distinct fish assemblages with higher standing stock and diversity than areas where fishing was permitted or areas that were partially protected from fishing. Locations influenced by customary stewardship harbored fish biomass that was equal to or greater than that of no-take protected areas. Marine protected areas in the main Hawaiian islands with high habitat complexity, moderate wave disturbance, a high percentage of branching and/or lobate coral coupled with legal protection from fishing pressure had higher values for most fish assemblage characteristics.

Keywords Reef fish assemblages · Marine protected areas · Essential fish habitat · Hawaiian archipelago · Community-based management

Introduction

Diversity, quality, and areal extent of habitat are among the most important environmental determinants of coral reef fish distribution, abundance, and diversity (Bellwood and Hughes 2001). The association of coral reef fish diversity and physical habitat has been demonstrated by a number of authors (Luckhurst and Luckhurst 1978; Carpenter et al. 1981; Roberts and Ormond 1987; Grigg 1994; Friedlander and Parrish 1998a). In Hawaii, habitats with low spatial relief and limited shelter were found to be associated with low biomass of reef fishes, while highly complex habitats harbored high fish biomass (Friedlander and Parrish 1998a).

Physical disturbance from waves is the primary natural mechanism controlling coral reef community structure in Hawaii (Dollar 1982; Grigg 1983). Surf height and degree of wave exposure have been shown to have a negative relationship with several measures of fish assemblage organization in Hawaii (Friedlander and Parrish 1998b). This relationship suggests that habitats protected from highest wave energies maintain larger fish populations with greater richness and diversity of species.

Coral reefs have always been an important component of human existence in Hawaii. These reefs once provided the majority of the protein for the Hawaiian people, and today consumptive uses of reef resources include subsistence, commercial, and recreational activities. Coastal fisheries are facing overexploitation and severe depletion on a global scale (Food and Agriculture Organization 1998; National Research Council 1999) and Hawaii is no exception. This decline in fish abundance and size, particularly around the more populated areas of the state, is likely the cumulative result of years of chronic

A. M. Friedlander (✉)
NOAA/NOS/National Centers for Coastal and
Ocean Science–Biogeography Program,
Makapuu Point/41–202 Kalanianaʻole Highway,
Waimanalo, Hawaii 96795, USA
E-mail: afriedlander@oceanicinstitute.org
Tel.: +1-808-2593165
Fax: +1-808-2595971

A. M. Friedlander
Oceanic Institute, Makapuu Point/41–202
Kalanianaʻole Highway, Waimanalo,
Hawaii 96795, USA

E. K. Brown · P. L. Jokiel · W. R. Smith · K. S. Rodgers
Hawaii Coral Reef Assessment and Monitoring Program,
Hawaii Institute of Marine Biology,
University of Hawaii at Manoa,
P.O. Box 1346, Kaneohe,
Hawaii 96744, USA

overfishing (Shomura 1987; Gulko et al. 2000; Friedlander and DeMartini 2002). Fishing pressure on near-shore resources in heavily populated areas of the main Hawaiian islands (MHI) appears to exceed the capacity of these resources to renew themselves (Smith 1993).

In the United States, one-half of fish stocks for which information is available are overfished or approaching overfishing (National Marine Fisheries Service 2001). Worldwide the situation is even worse, with 69% of fish stocks estimated to be fished to or beyond their maximum capacity (Food and Agriculture Organization 1998). Current fisheries management strategies throughout the world are primarily directed at restrictions or controls of fishing by focusing on bag limits, size restrictions, limited entry, or seasonal closures for particular species or small groups of species. These strategies do not address the habitats required by these species and therefore may not be appropriate for the long-term sustainability of these resources. Identification and protection of high-quality fisheries habitat is an important consideration for sustaining fisheries production and in the conservation of these resources for non-consumptive purposes (Schmitt 1996).

The poor performance of conventional fisheries management worldwide has led to increased interest in marine reserves as a solution to the problems of overfishing (Dugan and Davis 1993; Rowley 1994; Bohnsack 1996, 1998; Murray et al. 1999). Successful enhancement of localized fish stocks by establishing closed areas and marine reserves is well documented (Alcala and Russ 1990; Russ 1991; Roberts and Polunin 1991; 1993, Roberts 1995; Russ and Alcala 1996a, 1996b; Halpern 2003). Marine reserves create a protected population, which in theory can provide greater stability in the dynamics of the exploited population and can be incorporated into a management system as a buffer against uncertainty (Sladek Nowlis and Roberts 1999; Sladek Nowlis 2000; Sladek Nowlis and Friedlander 2003). Marine reserves are an effective management strategy that can help protect and maintain the complexity and quality of fish habitat as well as mitigate the direct effects of fishing (Bohnsack 1996; Bohnsack and Ault 1996; Auster and Shackell 1997; Yoklavich, 1998). By protecting habitats and their associated fish populations, reserves can provide a precautionary approach to management that reduces the risks against overexploitation of fish stocks (Murray et al. 1999).

Despite their gaining popularity and historical use, there is still disagreement about how to effectively design marine reserves and the larger marine protected areas (MPAs). Successful implementation of marine reserves requires knowledge of the location, distribution, and extent of habitats necessary for components of the ecosystem to perform basic life-cycle functions (Dugan and Davis 1993; Friedlander and Parrish 1998a; Murray et al. 1999). If reserves are to maintain system integrity and structure, all components necessary to ensure system function must be included within the reserve design, either by networking smaller areas

or by creating large all-encompassing areas (Appeldoorn et al. 1997, 2003). To be effective, it is generally accepted that MPA networks should be distributed along environmental gradients and should protect representative species and habitat types (Ballantine 1997; Murray et al. 1999), although rare and vulnerable habitat types should be represented more fully (Sladek Nowlis and Friedlander 2003). Because coral reef ecosystems will only function properly when a mosaic of habitat types is connected biologically (Ogden 1988; Ogden 1997; Appeldoorn et al. 2003), MPA networks should strive to include a range of habitat types in an interconnected manner.

Closing areas to fishing is far from a new idea in the management of marine resources. Pacific islanders traditionally used a variety of marine resource management practices, including fishery closures (Johannes 1978, 1981, 1997; Ruddle 1996). These closures were often imposed to ensure large catches for special events or as a cache for when resources on the regular fishing grounds ran low. The traditional system in Hawaii emphasized social and cultural controls on fishing with a code of conduct that was strictly enforced (Friedlander et al. 2002). Marine resource management was based on identification of the specific times and places where fishing could occur so it would not disrupt basic processes and habitats of important food resources, rather than on quotas or gear restrictions.

There are a variety of marine areas in Hawaii that have some type of protected status (Gulko et al. 2000). Historical sampling of fish assemblages from a select group of marine reserves in Hawaii suggests that no-take MPAs with good habitat diversity and complexity can have a positive effect on fish standing stock, whereas other areas with limited protection or poor habitat quality result in relatively depauperate fish assemblages (Friedlander 2001). Despite their proven effectiveness, less than 1/5 of 1% (0.2%) of all coral reef habitats around the main Hawaiian islands have complete no-take MPA status (Gulko et al. 2000).

To date, no study has undertaken an extensive survey of the shallow-water reef fish assemblages across the entire main Hawaiian islands archipelago in reference to habitat parameters and levels of protection from fishing. Management units are typically on the scale of an island or the entire state, and resource evaluation should therefore be conducted on a similar scale. This study evaluates the relationship between fish assemblages, their associated habitat, and degree of protection from fishing on a scale consistent with the patterns of both the resources and their users. The purpose is to determine the relative importance of particular reef characteristics in explaining fish assemblage parameters over a large spatial scale (100 km) and to permit prediction of fish populations from practical measurements of reef characteristics. Owing to the wide range of protection and habitat quality of MPAs in Hawaii, it is critical that the efficacy of various protected areas be compared and evaluated.

Methods

Study sites

The study sites originated from the Hawaii Coral Reef Assessment and Monitoring Program (CRAMP). This program was initiated in 1998 in order to better understand the ecology of Hawaiian coral reefs at a spatial and temporal scale consistent with the management of these resources. The experimental design involved the selection and installation of 30 permanent sites at two depth strata (60 locations total) on Kauai, Oahu, Maui, Molokai, Kahoolawe, and Hawaii. The overall network provides a cross section of reefs across the main Hawaiian islands with regard to habitat type, direction of wave exposure, perceived environmental stress, and degree of protection from fishing (Fig. 1).

The 60 locations surveyed were categorized according to the direction of wave exposure based on wave models derived from the US Naval Oceanographic Office and long-term observations by the authors. Categories included: locations exposed to north swells (N), north-facing locations sheltered from swell (NS), locations exposed to south swells (S), south-facing locations sheltered from swell (SS), and locations within Kaneohe Bay, an embayment sheltered from all swells (SH).

Of the 60 locations surveyed, 18 had some level of protection from fishing associated with them. Hanauma Bay ($n=2$), Honolua Bay ($n=2$), and Molokini Crater ($n=2$) are all no-take Marine Life Conservation Districts (MLCDs) that prohibit all fishing activities from occurring within their boundaries. Moku o Loe (Coconut Island-Hawaii Marine Laboratory Refuge) is fully protected from fishing, although limited take for scientific purposes is permitted ($n=2$). Locations within the Kahoolawe Island Reserve (Hakioawa; $n=2$) were considered partially protected with customary stewardship due to the limited take permitted for cultural, spiritual, and subsistence purposes authorized by the Kahoolawe Island Reserve Commission. Ahihi-Kinaiu Natural Area Reserve (Kanahena Bay and Kanahena Point) was also considered partially protected with customary stewardship due to the extremely limited take by a single family for cultural purposes ($n=4$). Nenué Point ($n=2$) on the island of Hawaii is designated as a Fishery

Replenishment Area (FRA) which prohibits the collection of aquarium fish but permits all other types of fishing activities. Pupukea, on the north shore of Oahu ($n=2$), is also classified as an MLCD, yet a wide variety of fishing methods are permitted within the district boundaries. These activities include hook-and-line fishing, spearfishing without SCUBA, collection of seaweeds, and gillnetting in a portion of the MLCD. For the reasons stated above, the Pupukea MLCD and the Nenué Point FRA were only considered to have partial protection from fishing in this analysis.

Locations were categorized according to their level of protection from fishing based on current state regulations. These included no-take areas completely protected from fishing (NT), partially protected areas that allow certain fishing activities to occur (PP), partially protected areas where customary stewardship is in effect (CS), and areas fully open to fishing (O).

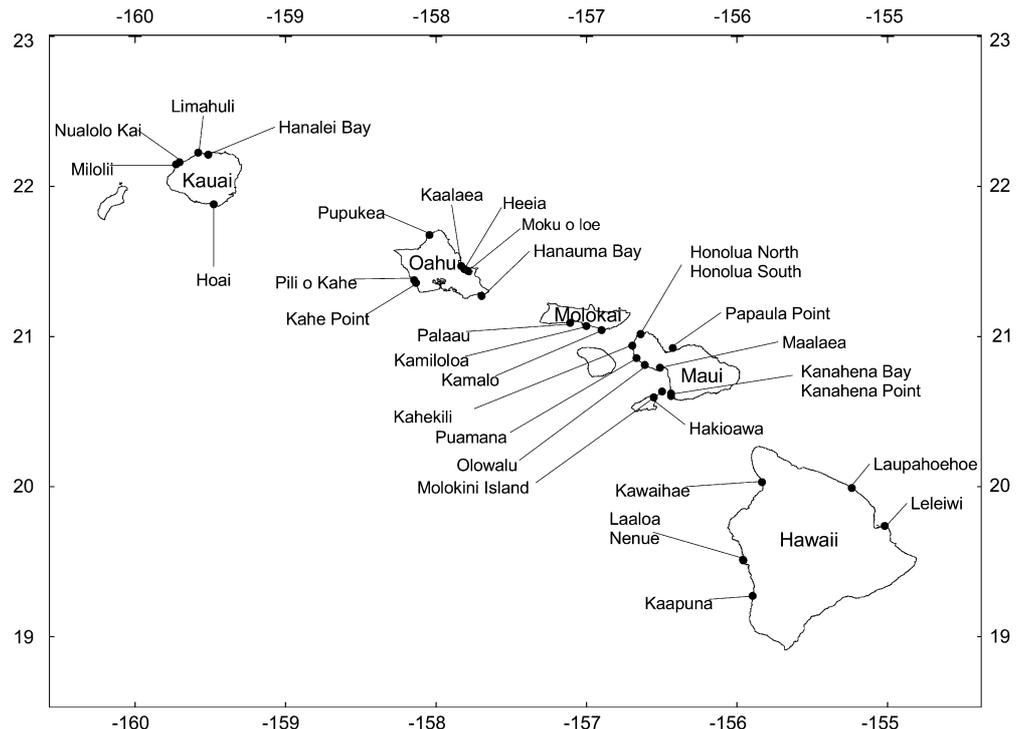
Benthic survey techniques

Benthic habitat characteristics at each location were assessed along ten randomly assigned permanent transects at two depths (generally 3 and 10 m) along a 2x100-m grid. Each transect was 10 m in length. Digital video was used to record images along each benthic transect at a height of 0.5 m above the substrate. Twenty randomly selected, non-overlapping video frames were selected and processed using PointCount99 software (Dustan et al. 1999) to develop estimates for coral and substrate types.

To examine the role that coral morphology played in structuring fish assemblages, we grouped percent live coral cover of various species for each site into three growth form categories: plate/encrusting, branching, and lobate. Plate/encrusting growth forms included *Cyphastrea ocellinus*, *Leptastrea purpurea*, *Montipora capitata*, *M. flabellata*, *M. patula*, *M. studeri*, *Pavona varians*, *Porites rus*, and *Psammocora nierstrazi*. Branching species included *Pocillopora damicornis*, *P. ligulata*, *P. edouxyi*, *P. meandrina*, and *Porites compressa*. The lobate growth forms included *Pavona duerdeni*, *Porites brighami*, *P. evermanni*, and *P. lobata*.

To measure reef rugosity or surface relief, a chain of small links (1.3 cm per link) was draped along the full length of the centerline of each transect (Risk 1972). Care was taken to ensure that the

Fig. 1 Location of sampling sites in the main Hawaiian islands. Shallow (1–5 m) and deep (6–13 m) locations were sampled at each survey site



chain followed the contour of all natural fixed surfaces directly below the transect centerline. A ratio of distance along the reef surface contour to linear horizontal distance gave an index of spatial relief or rugosity. The ten randomly selected transects within a grid were all measured in this manner to produce an average rugosity for the transect location.

Fish sampling methodology

Fish assemblages at each location were assessed using standard underwater visual belt transect survey methods (Brock 1954; Brock 1982). A SCUBA diver swam each 25x5-m transect at a constant speed and identified to the lowest possible taxon all fishes visible within 2.5 m to either side of the centerline (125-m² transect area). Swimming duration varied from 10–15 min depending on habitat complexity and fish abundance. Nomenclature followed Randall (1996). Transects were located along the centerline of the previously established CRAMP benthic survey grids. Four transects, separated by 5-m gaps, were conducted at each location. Total length (TL) of fish was estimated to the nearest centimeter. Length estimates of fishes from visual censuses were converted to weight using the following length–weight conversion: $W = aSL^b$; the parameters a and b are constants for the allometric growth equation, where SL is standard length in millimeters and W is weight in grams. Total length was converted to standard length (SL) by multiplying standard length by total length fitting parameters obtained from FishBase (www.fishbase.org). Length–weight fitting parameters were available for 150 species commonly observed on visual fish transects in Hawaii (Hawaii Cooperative Fishery Research Unit, unpublished data). This was supplemented by using information from other published and web-based sources. In the cases where length–weight information did not exist for a given species, the parameters from similar-bodied congeners were used. All biomass estimates were converted to metric tons per hectare (t/ha) to facilitate comparisons with other studies in Hawaii. Finally, fish taxa were categorized into six trophic categories (herbivores, mobile invertebrate feeders, sessile invertebrate feeders, piscivores, zooplanktivores, and detritivores) according to various published sources and FishBase (www.fishbase.org).

Accuracy assessment of visual census methods

To compare observer variability, two divers (A.M.F. and E.K.B.) swam 12 parallel 25x5-m transects in a similar habitat separated by 10 m on the forereef at Hoai Bay, Kauai, in December 1999. There were no significant differences in number of species ($t = 0.206$, $P = 0.839$), number of individuals ($t = 1.800$, $P = 0.086$), or biomass ($t = 0.133$, $P = 0.895$) observed between the two divers, and all subsequent visual census fish data were collected using only these two observers.

Biomass estimates derived from underwater estimates of fish lengths during the study were carefully calibrated to improve the accuracy associated with these measurements. This was accomplished by comparing observer length estimates with those of plastic-laminated fish models. Seventeen fish models ranging in size from 5–30 cm and utilizing several different species with varying morphologies were haphazardly attached to a weighted line using snap swivels. On the first trial, each diver swam along a transect line ca. 2.5 m from the parallel line with the attached fish models and estimated the total length of each model. The divers then returned along the fish model transect line and measured the actual length of each model. On the second trial, six additional fish were added and the locations of all existing models were haphazardly changed. A third trial was conducted with all 23 fish models again being haphazardly changed along the transect. For both observers pooled, the mean difference in estimated vs. actual length was greatest for the first trial (2.23 cm) and became progressively lower with each subsequent run (trial 2 = 0.89 cm; trial 3 = 0.71 cm). The mean difference in estimated vs. actual length was not significantly different between trial 2 and 3 ($P > 0.05$).

This experiment showed that with minimal training, divers could learn to estimate fish lengths underwater. Both observers obtained accuracy of less than 1 cm in estimating actual fish length after only two trials.

Statistical analysis

Species diversity was calculated from the Shannon-Weaver Diversity Index (Ludwig and Reynolds 1988): $H' = -\sum (p_i \ln p_i)$, where p_i is the proportion of all individuals counted that were of species i . An index of relative dominance (IRD) for each fish taxa was created by multiplying the percent frequency of occurrence of the taxa on each transect by the relative percent biomass of that taxa $\times 100$ (Greenfield and Johnson 1990).

Coral species richness and reef rugosity among different wave exposure regimes were analyzed using one-way ANOVA tests ($\alpha = 0.05$) with unplanned comparisons conducted using Bonferroni Multiple Comparison Procedures. Percentages of live coral cover by morphological grouping were arcsin square-root transformed for all analyses (Zar 1984).

Since fish transects within locations were spatially autocorrelated, mean values for all transects at each location were used in all statistical analyses. Fish assemblage characteristics (species richness, number of individuals, biomass, and diversity) between shallow and deep depth strata were compared using students' t -test. Fish assemblage characteristics among different wave exposure regimes and level of protection from fishing were analyzed using one-way ANOVAs. Number of individuals and biomass were $\log_e(x)$ transformed for all statistical analyses to normalize distributions and homogenize variances to permit parametric testing. Size of fishes under different levels of protection from fishing was also compared using one-way ANOVAs.

Detrended correspondence analysis (DCA) was used to identify clusters of similar locations in ordination space. A matrix of sample units (60 locations) by fish species (mean number or mean weight per location) was created for use in this analysis. Values were $\log_e(x)$ transformed with rare species downweighted. Those taxa that occurred in less than 20% of the number of stations than the most common taxon occurs were downweighted. The amount that the species was downweighted was inversely related to its frequency of occurrence. This type of ordination results in an arrangement of samples of species in a low-dimensional space such that similar samples are in close proximity to one another (Gauch 1982). Wave exposure regime and level of protection from fishing were defined a priori and then overlaid on the station clusters created by DCA.

Multiple regression models (general linear models, GLM) were used to examine the contribution of various physical, biological, and management parameters to fish assemblage structure. Continuous independent variables included percent live coral cover by morphological type (plate/encrusting, branch, and lobate) and rugosity. Rugosity was $\log_e(x)$ transformed for these analyses. Categorical independent variables included depth [shallow (1–5 m) and deep (6–13 m)]; wave exposure (exposed, partially sheltered, and embayments); and level of protection from fishing. No-take and customary tenure were classified as protected from fishing for this analysis, while open access and partial protection were classified as not protected. Dependent variables included number of species, number of individuals, biomass, and species diversity.

Results

Site characteristics

Percent live coral cover averaged 25.1% (SD = ± 21.2) across all 60 sample sites (Table 1), with the deeper sites (29.8%) having a higher percent cover than the shallow sites (20.9%). Live coral cover ranged from a low of

Table 1 Physical, biological, and management characteristics of sampling location, Sub-habitat types based on National Ocean Service main Hawaiian islands habitat classification scheme (Coyne et al. 2001). *O* Open access; *PP* partially protected; *NT* no-take; *CS* customary stewardship *N* north; *S* south; *NS* north sheltered; *SS* south sheltered; *SH* sheltered

| Island | Site | Depth (m) | Rugosity | Wave exposure direction | Percent live coral cover | | | Total coral cover (%) | Coral sp. richness (total no.) | Legal status | Sub-habitat |
|-----------|---------------|-----------|----------|-------------------------|--------------------------|-----------|--------|-----------------------|--------------------------------|--------------|--|
| | | | | | Plate/encrusting (%) | Branching | Lobate | | | | |
| Kauai | Hanalei | 3 | 1.24 | N | 13.92 | 1.22 | 0.99 | 16.13 | 9 | O | Colonized pavement |
| | | 8 | 1.53 | N | 24.5 | 1.31 | 2.26 | 28.07 | 7 | O | Colonized pavement with sand channels |
| | Hoai Bay | 3 | 1.61 | S | 0.07 | 2.85 | 8.21 | 11.13 | 4 | O | Colonized volcanic rock/boulder |
| | | 10 | 1.50 | S | 0.01 | 2.82 | 0.48 | 3.31 | 5 | O | Uncolonized volcanic rock/boulder |
| | Limahuli | 1 | 1.24 | N | 3.02 | 0.06 | 11.82 | 14.9 | 7 | O | Colonized pavement |
| | | 10 | 1.60 | N | 16.47 | 0.68 | 2.36 | 19.51 | 8 | O | Aggregated coral heads |
| | Miloli | 3 | 1.54 | N | 0.6 | 0.42 | 2.67 | 3.69 | 7 | O | Uncolonized pavement with sand channels |
| | | 10 | 1.74 | N | 7.78 | 0.63 | 5.62 | 14.03 | 8 | O | Colonized pavement |
| | Nualolo Kai | 3 | 1.51 | N | 1.19 | 0.31 | 1.33 | 2.83 | 7 | O | Uncolonized volcanic rock/boulder |
| | | 10 | 1.47 | N | 9.63 | 1.83 | 9.22 | 20.68 | 7 | O | Colonized pavement |
| Oahu | Hanauma | 3 | 2.00 | SS | 0.65 | 0.68 | 22.28 | 23.61 | 8 | NT | Colonized pavement |
| | | 10 | 2.25 | SS | 0.02 | 11.93 | 14.79 | 26.74 | 4 | NT | Aggregated coral heads |
| | Heeia | 2 | 2.31 | SH | 1.82 | 34.52 | 0 | 36.34 | 4 | O | Patch reef (aggregated) |
| | | 8 | 1.64 | SH | 2.64 | 5.12 | 0 | 7.76 | 4 | O | Scattered coral/rock in unconsolidated sediments |
| | Kaalaea | 2 | 1.95 | SH | 0.34 | 61.81 | 0 | 62.15 | 5 | O | Patch reef (individual) |
| | | 8 | 1.36 | SH | 1.82 | 0.01 | 0.01 | 2.64 | 5 | O | Scattered coral/rock in unconsolidated sediments |
| | Kahe Pt | 3 | 1.44 | S | 1.15 | 5.73 | 4.99 | 11.87 | 6 | O | Colonized pavement with sand channels |
| | Moku o Loe | 2 | 2.25 | SH | 21.77 | 9.15 | 0 | 30.92 | 2 | NT | Aggregated coral heads |
| | | 8 | 1.35 | SH | 7.3 | 0.34 | 0 | 7.64 | 4 | NT | Scattered coral/rock in unconsolidated sediments |
| | | 3 | 1.36 | S | 1.01 | 2.12 | 5.83 | 8.96 | 11 | PP | Uncolonized pavement with sand channels |
| Molokai | Pupukea | 4 | 1.22 | N | 2.57 | 0.98 | 6.76 | 10.31 | 6 | PP | Colonized volcanic rock/boulder |
| | | 8 | 1.30 | N | 4.83 | 2.96 | 2.96 | 8.31 | 7 | PP | Uncolonized volcanic rock/boulder |
| | Kamalo | 3 | 1.33 | SS | 0.02 | 3.51 | 0.11 | 3.64 | 10 | O | Aggregated coral heads |
| | | 10 | 1.37 | SS | 0.39 | 0.12 | 0.33 | 0.84 | 8 | O | Aggregated coral heads |
| | Kamiloloa | 3 | 2.34 | SS | 69.63 | 1.89 | 3.08 | 74.6 | 5 | O | Uncolonized pavement with sand channels |
| | | 10 | 2.46 | SS | 49.68 | 25.3 | 0.24 | 75.22 | 6 | O | Uncolonized pavement with sand channels |
| | Palaau | 3 | 1.92 | SS | 9.62 | 6.99 | 13.03 | 29.64 | 8 | O | Aggregated coral heads |
| | | 10 | 2.07 | S | 45.63 | 25.33 | 1.45 | 72.41 | 8 | O | Aggregated coral heads |
| | Hakioawa | 3 | 1.50 | SS | 10.43 | 9.69 | 14.31 | 34.43 | 8 | CS | Aggregated coral heads |
| | | 10 | 1.81 | SS | 36.21 | 16.24 | 9.55 | 62.00 | 6 | CS | Aggregated coral heads |
| Maui | Honolua North | 3 | 1.47 | NS | 4.77 | 1.5 | 8.98 | 15.25 | 12 | NT | Aggregated coral heads |
| | Honolua South | 3 | 1.67 | NS | 15.38 | 1.83 | 3.65 | 20.86 | 11 | NT | Aggregated coral heads |
| | Kahekili | 3 | 1.58 | NS | 7.51 | 12.99 | 23.02 | 43.52 | 9 | O | Aggregated coral heads |
| | | 7 | 1.40 | NS | 3.31 | 8.03 | 18.82 | 30.16 | 5 | O | Aggregated coral heads |
| Kahoolawe | Kanahena Bay | 1 | 1.30 | SS | 1.40 | 0.71 | 9.23 | 11.34 | 6 | CS | Colonized volcanic rock/boulder |
| | | 3 | 1.60 | SS | 5.16 | 2.42 | 14.03 | 21.61 | 7 | CS | Aggregated coral heads with sand channels |
| | Kanahena Pt | 3 | 1.23 | SS | 1.62 | 1.31 | 0.61 | 3.54 | 6 | CS | Uncolonized volcanic rock/boulder |
| | | 10 | 1.56 | SS | 27.16 | 12.28 | 1.21 | 40.65 | 10 | CS | Aggregated coral heads with sand channels |
| Molokini | Maalaea | 3 | 1.20 | S | 2.68 | 1.50 | 17.83 | 22.01 | 9 | O | Aggregated coral heads |
| | | 6 | 1.28 | S | 6.94 | 0.86 | 5.60 | 13.40 | 9 | O | Aggregated coral heads |
| | | 7 | 1.63 | SS | 32.62 | 7.30 | 24.08 | 64.00 | 9 | NT | Aggregated coral heads |
| | | 13 | 1.54 | SS | 78.19 | 6.29 | 4.50 | 88.98 | 6 | NT | Aggregated coral heads |
| Olowalu | | 3 | 1.52 | S | 10.30 | 4.79 | 7.82 | 22.91 | 12 | O | Aggregated coral heads with sand channels |
| | | 7 | 1.90 | S | 36.24 | 3.32 | 15.85 | 55.41 | 10 | O | Aggregated coral heads with sand channels |

Table 1 (Contd.)

| Island | Site | Depth (m) | Rugosity | Wave exposure direction | Percent live coral cover (%) | | | Total coral cover (%) | Coral sp. richness (total no.) | Legal status | Sub-habitat |
|-----------------------|-------------|-----------|----------|-------------------------|------------------------------|-----------|--------|-----------------------|--------------------------------|---------------------------------|-----------------------------------|
| | | | | | Plate/encrusting (%) | Branching | Lobate | | | | |
| Hawaii | Papaula Pt | 4 | 1.14 | N | 18.33 | 0.70 | 8.46 | 27.49 | 5 | O | Colonized Volcanic Rock/Boulder |
| | | 10 | 1.12 | N | 41.50 | 0.43 | 8.39 | 50.32 | 8 | O | Colonized Volcanic Rock/Boulder |
| | | 3 | 1.31 | S | 0.99 | 8.78 | 5.16 | 14.93 | 7 | O | Spur and grove |
| | Puamana | 13 | 1.12 | S | 0.18 | 0.77 | 1.59 | 2.54 | 8 | O | 10–50% Macroalgae |
| | | 4 | 1.46 | S | 0.34 | 4.65 | 2.72 | 7.71 | 4 | O | Uncolonized volcanic rock/boulder |
| | Kaapuna | 10 | 1.68 | S | 1.62 | 2.52 | 5.69 | 9.83 | 6 | O | Colonized volcanic rock/boulder |
| | | 3 | 1.81 | NS | 2.58 | 9.55 | 9.02 | 21.15 | 8 | O | Aggregated coral heads |
| | | 10 | 1.77 | NS | 0.83 | 25.22 | 6.06 | 32.11 | 9 | O | Spur and grove |
| | Laaloa | 3 | 1.99 | S | 1.56 | 12.45 | 17.60 | 31.61 | 9 | O | Colonized volcanic rock/boulder |
| | | 10 | 1.94 | S | 0.85 | 3.83 | 35.51 | 40.19 | 6 | O | Aggregated coral heads |
| | Laupahoehoe | 3 | 1.78 | N | 2.15 | 2.94 | 6.51 | 11.60 | 8 | O | Colonized volcanic rock/boulder |
| | | 10 | 1.22 | N | 3.10 | 0.43 | 6.57 | 10.10 | 5 | O | Colonized volcanic rock/boulder |
| | Lelewi | 3 | 1.69 | N | 2.59 | 2.33 | 7.18 | 12.10 | 8 | O | Colonized volcanic rock/boulder |
| | | 10 | 1.63 | N | 2.58 | 9.11 | 19.36 | 31.05 | 8 | O | Aggregated coral heads |
| | Nenu Pt | 5 | 1.70 | S | 0.50 | 1.76 | 5.37 | 7.63 | 6 | PP | Uncolonized volcanic rock/boulder |
| 10 | | 1.71 | S | 0.51 | 1.94 | 13.29 | 15.74 | 7 | PP | Colonized volcanic rock/boulder | |
| Average for all sites | | 1.60 | | 10.97 | 6.46 | 7.64 | 7.12 | | | | |

0.8% at Kamalo (10 m) to a high of 89.0% at Molokini (13 m) (Table 1). Coral growth forms were dominated by the plate/encrusting corals (11.0%) followed by lobate (7.6%) and branching corals (6.1%). At deeper sites (> 5 m) plate/encrusting forms averaged more than twice the cover (15.8%) compared to the other two predominant growth forms (lobate, 7.7%; branching, 5.6%). In contrast, the various growth forms were relatively equivalent (lobate, 7.6%; plate/encrusting, 6.3%; and branching, 6.6%) at the shallower sites.

Coral species richness ranged from a low of two species at Moku o Loe to a high of 12 species at Honolua and Olowalu. Differences in coral species richness were marginally significant among different exposure regimes ($F_{4,53} = 2.6$, $P = 0.049$). Sites subjected to greater wave exposure regimes (north, north sheltered, and south) generally had higher average species richness (7.2, 9.3, and 7.4, respectively) than more protected sites (south sheltered, 7.0; sheltered, 5.7).

Rugosity measurements ranged from a low of 1.12 at Papaula Pt. (10 m) to a high of 2.46 at Kamiloloa (10 m) (Table 1). Northern exposure sites had the lowest rugosity (mean \pm SD = 1.43 ± 0.22), while sheltered sites had the highest rugosity measurements (mean \pm SD = 1.86 ± 0.43). Rugosity was significantly different among different wave exposure regimes ($F_{4,55} = 2.51$, $P = 0.05$), with north-exposed locations significantly lower ($P < 0.05$) than all other exposures except south-exposed locations.

Fish assemblage composition

Endemic species accounted for 35% of numerical abundance and 22% of the total fish biomass observed over all locations. The brown surgeonfish, *Acanthurus nigrofuscus*, was the most dominant species over all study sites based on IRD (Table 2). It occurred on over 81% of all transects and accounted for 6.3% of the total fish biomass. This species was followed in importance by the black triggerfish (*Melichthys niger*), which accounted for over 13% of the total reef fish biomass but only occurred on 36% of the transects. The endemic goldring surgeonfish (*Ctenochaetus strigosus*), the endemic saddle wrasse (*Thalassoma duperrey*), and the orangespine surgeonfish (*Naso lituratus*) comprised the remaining top five species based on IRD. The endemic saddle wrasse was the most ubiquitous species observed during the study, appearing on nearly all transects (99.6%).

Surgeonfishes accounted for six of the top ten species and comprised over 38% of the total reef fish biomass and 32% of the total number of individuals. Parrotfishes were the next most important family based on biomass, accounting for 16% of the total weight of fishes and 12% of the total number, followed by triggerfishes which comprised a little over 16% of the total reef fish biomass but only 3.6% of the total numerical abundance. Damselfishes followed surgeonfishes in numerical abundance with 23.0% of the total, but only accounted

Table 2 Top 20 fish species overall at all 60 locations surveyed. *Freq.* Frequency of occurrence (total number of transects = 231). Number and biomass are percentages of the total. Species are ordered by index of relative dominance (*IRD*) = (frequency of occurrence × percent biomass) × 100

| Family | Taxon name | Hawaiian name | Common name | Freq. | Number | Biomass | IRD |
|---------------|--|-----------------------|-------------------------|-------|--------|---------|--------|
| Acanthuridae | <i>Acanthurus nigrofuscus</i> | Maiii | Brown surgeonfish | 81.59 | 11.98 | 6.28 | 512.07 |
| Balistidae | <i>Melichthys niger</i> | Humuhumu elele | Black triggerfish | 36.82 | 2.31 | 13.25 | 487.72 |
| Acanthuridae | <i>Ctenochaetus strigosus</i> ^a | Kole | Goldring surgeonfish | 62.76 | 7.35 | 6.52 | 408.95 |
| Labridae | <i>Thalassoma duperrey</i> ^a | Hinalea lauwili | Saddle wrasse | 99.58 | 11.67 | 3.40 | 338.27 |
| Acanthuridae | <i>Naso lituratus</i> | Umaumalei | Orangespine unicornfish | 49.37 | 1.34 | 4.39 | 216.65 |
| Scaridae | <i>Chlorurus sordidus</i> | Uhu | Bullethead parrotfish | 39.33 | 2.02 | 3.95 | 155.29 |
| Acanthuridae | <i>Acanthurus leucopareius</i> | Maikoiko | Whitebar surgeonfish | 28.87 | 2.29 | 5.10 | 147.27 |
| Scaridae | <i>Scarus rubroviolaceus</i> | Palukaluka | Redlip parrotfish | 23.01 | 0.31 | 4.42 | 101.68 |
| Acanthuridae | <i>Zebrosoma flavescens</i> | Lauipala | Yellow Tang | 34.31 | 2.37 | 2.68 | 92.10 |
| Acanthuridae | <i>Acanthurus triostegus</i> ^b | Manini | Convict tang | 24.27 | 3.31 | 3.66 | 88.87 |
| Acanthuridae | <i>Acanthurus olivaceus</i> | Naenae | Orangeband surgeonfish | 31.38 | 0.95 | 2.72 | 85.23 |
| Scaridae | <i>Scarus psittacus</i> | Uhu | Palenose parrotfish | 39.75 | 2.45 | 1.71 | 67.86 |
| Scaridae | <i>Chlorurus perspicillatus</i> ^a | Uhu uliuli | Spectacled parrotfish | 15.90 | 0.44 | 4.18 | 66.40 |
| Pomacentridae | <i>Abudefduf abdominalis</i> ^a | Mamo | Sergeant Major | 17.57 | 4.11 | 3.42 | 60.13 |
| Pomacentridae | <i>Stegastes fasciolatus</i> | | Pacific Gregory | 69.46 | 3.10 | 0.76 | 52.83 |
| Mullidae | <i>Parupeneus multifasciatus</i> | Moano | Manybar goatfish | 48.95 | 0.84 | 0.87 | 42.38 |
| Serranidae | <i>Cephalopholis argus</i> ^c | | Blue spot grouper | 23.43 | 0.26 | 1.75 | 40.99 |
| Acanthuridae | <i>Naso unicornis</i> | Kala | Bluespine unicornfish | 9.62 | 0.32 | 3.58 | 34.42 |
| Balistidae | <i>Rhinecanthus rectangulus</i> | Humuhumunukunukuapuaa | Reef triggerfish | 34.73 | 0.56 | 0.96 | 33.28 |
| Pomacentridae | <i>Chromis vanderbilti</i> | | Blackfin chromis | 48.12 | 9.09 | 0.59 | 28.29 |

^aEndemic species,

^bRegarded as an endemic subspecies—*Acanthurus triostegus sandvicensis*,

^cIntroduced species

for 6.4% of the total biomass. Wrasses were the next most important family, numerically comprising 17.6% of the total but with a much lower contribution to the total fish biomass (5.6%).

Herbivores were the most important feeding guild and accounted for 65.8% of the biomass and 44.9% of the total number of individuals observed. The next most important feeding guild were the mobile invertebrate feeders, constituting 12.3% of the biomass and 22.6% of the numerical abundance of reef fish observed on transects. Planktivores comprised 7.4% of the biomass and 19.6% of the total number of individuals. Approximately 7% of the biomass and numerical abundance consisted of detritivores. This trophic category was made up almost exclusively of the endemic goldring surgeonfish. Piscivores were rare and accounted for only 4.7% of the biomass and 1.4% of the total number of fishes.

Depth comparisons

There were no significant differences ($P > 0.05$) in all fish assemblage characteristics (e.g., species richness, number of individuals, biomass, and diversity) between shallow-water locations (range 1–5 m) and deeper locations (range 6–13 m) for 60 locations surveyed around Kauai, Oahu, Maui, Kahoolawe, and Hawaii (Table 3). Despite the lack of statistical differences in some major fish assemblage characteristics, the number of species, number of individuals, and biomass all tended to be

Table 3 Comparison of fish assemblage variables by depth strata. Shallow locations range from 1–5 m, deep locations range from 6–13 m. Values are mean number per transect (125 m²) except for biomass which is reported in t/ha. Standard deviation of the mean is in parentheses. Statistical results from student's t-test

| Assemblage characteristic | Deep (n = 28) | Shallow (n = 28) | t | P |
|---------------------------|------------------|---------------------|------|------|
| Species | 17.9 (5.5) | 18.9 (5.6) | 0.67 | 0.50 |
| Number | 105.4 (50.5) | 149.6 (97.1) | 1.86 | 0.07 |
| Biomass (t/ha) | 0.5 (0.3) | 0.9 (0.8) | 1.13 | 0.26 |
| Diversity | 2.2 (0.4) | 2.1 (0.3) | 0.61 | 0.54 |

higher at the shallower locations, while diversity was higher at the deeper locations.

The same top five species occurred in both the shallow and deep locations, but their relative rank varied among depth strata. The black triggerfish (*Melichthys niger*) was the most dominant species by weight at the shallow and deep sites, accounting for 15 and 11% of the fish biomass, respectively. It occurred in 43% of the samples at the shallow locations but at only 26% of the transects at the deeper locations. The goldring surgeonfish was the most numerically abundant species at the deep locations, accounting for 11% of the total number of individuals, while it ranked sixth and accounted for 5% of the abundance at the shallow locations. The brown surgeonfish (*Acanthurus nigrofuscus*) was numerically dominant at the shallow locations, accounting for 14% of the number of individuals, while ranking fourth at the deep locations, representing 9% of the total numerical abundance.

Comparison of wave exposure among locations

Detrended correspondence analysis (DCA) of fish census data for number of individuals and biomass identified groupings that corresponded to the different wave regimes defined a priori (Fig. 2). The DCA first axis shows a gradual shift in fish assemblage structure along an environmental gradient from the sheltered locations within Kaneohe Bay to the locations that received the greatest degree of wave exposure. There was clear separation in fish assemblage structure between Kaneohe Bay, sheltered from all swells, and all other types of exposures based on both the numbers and weight of species. There was also good concordance among locations within Kaneohe Bay. Although there was a good deal of overlap in assemblage structure among all other locations, south-sheltered and north-sheltered locations had higher concordance than north- and south-exposed locations. South- and north-sheltered locations tended to have fish assemblage structure that was more similar to the sheltered embayment of Kaneohe

ohe than to the more exposed locations. The deep and shallow Kamiloloa sites on the south shore of Molokai were classified as south-sheltered locations based on their wave exposure, but had fish assemblages more similar in ordination space to south- and north-exposed locations. The low coral cover and habitat heterogeneity at this site appears more similar to sites with higher wave exposure, which may help to explain the similarity of these fish assemblages with more exposed locations. North-exposed locations appeared to be more dissimilar to the Kaneohe Bay sheltered locations compared with south-exposed, south-sheltered, and north-sheltered locations.

Fish assemblage characteristics differed significantly among locations with different degrees of wave exposure (Fig. 3). Species richness differed significantly ($F_{4,55}=3.20$; $P=0.02$) and was highest at the north-sheltered locations. The south-sheltered locations,

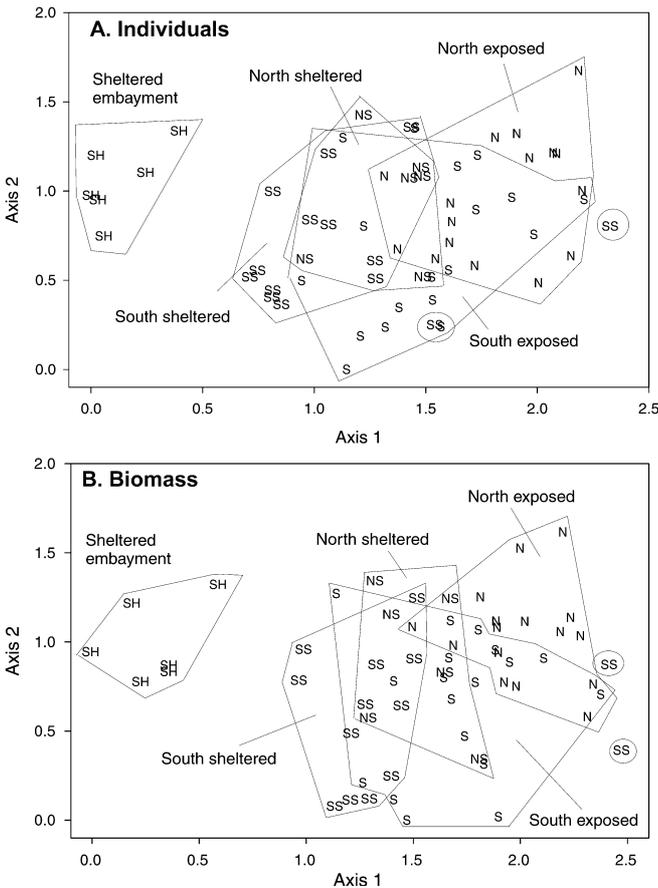


Fig. 2 Relationships among fish assemblages at 60 locations across the main Hawaiian islands relative to their degree of wave exposure. Results of detrended correspondence analysis with input values $\log(e)$ transformed and rare species downweighted for **A** number of individuals and **B** biomass. Polygons group locations with the same wave exposure. N North exposed; S south exposed; NS north sheltered; SS south sheltered; SH sheltered

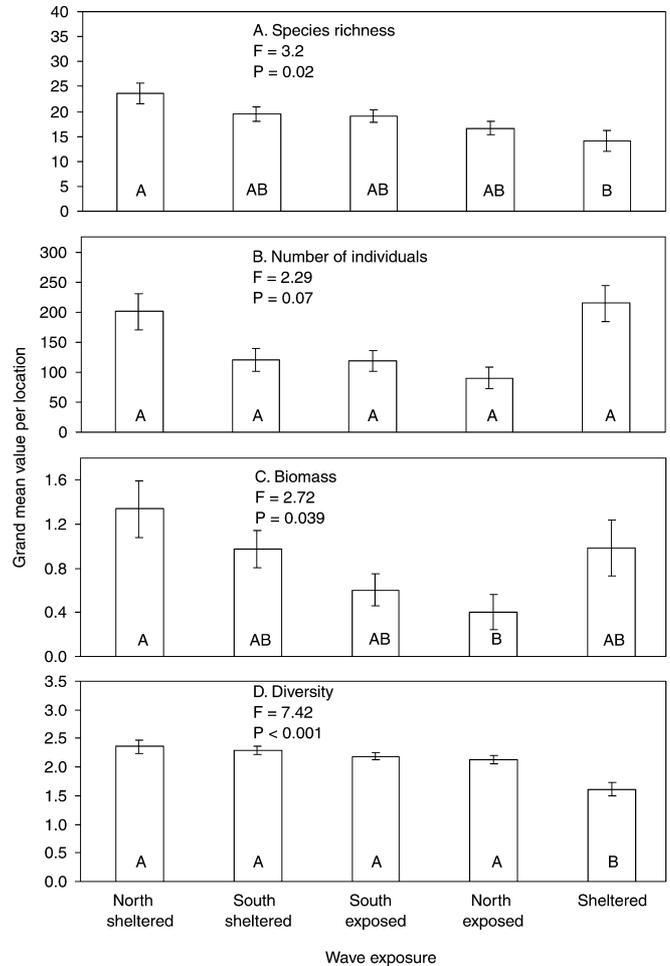


Fig. 3 Comparisons of fish assemblage characteristics with various degrees of wave exposure. Grand mean values per location. All values are based on 125-m² transect except biomass, which is reported in t/ha. Error bars are one standard error of the mean. Statistical results of one-way ANOVA are shown. Exposures with the same letter designation are not significantly different (Bonferroni adjusted multiple comparisons test, $\alpha=0.05$). Note differences in y-axis scales

south-exposed, north-exposed, and sheltered areas in Kaneohe Bay had lower species richness, respectively, but were not significantly different from one another ($P > 0.05$). The total number of individuals was not significantly different among sites ($F_{4,55} = 2.29$; $P = 0.07$). Kaneohe Bay (sheltered embayment locations) had the greatest number of individuals observed on transects, followed by the north-sheltered locations. The north-exposed locations had the lowest number of individuals. Total fish biomass was also significantly different ($F_{4,55} = 2.72$; $P = 0.039$) among locations based on wave exposure, with the south-sheltered, north-sheltered, and sheltered locations having the highest standing stocks of fish present. Fish biomass was more than three times higher at north-sheltered locations compared to the north-exposed locations and nearly two times higher than at the south-exposed locations. Despite these large differences in standing stock, the only significant test result was between the north-exposed locations and the north-sheltered locations ($P < 0.05$), due to the high variance associated with these biomass values ($CV = 90\%$). Species diversity was significantly different among locations ($F_{4,55} = 7.42$; $P < 0.001$). North- and south-sheltered locations had the highest diversity but were not significantly different from the south- and north-exposure locations ($P > 0.05$). Sheltered locations within Kaneohe Bay had significantly lower species diversity compared with all other locations sampled ($P < 0.05$).

Comparison of marine protected areas

For both number of individuals and biomass, fish assemblage structure in areas fully protected from fishing (no-take areas) tended to be different from those assemblages observed in areas where various levels of fishing are permitted (Fig. 4). Fish assemblage structures within partially protected areas with customary stewardship had high concordance with fully protected areas. Partially protected areas had concordance with both fully protected sites and areas partially protected with customary stewardship. Moko o Loe (Coconut Island, The Hawaii Marine Laboratory Refuge) possessed a fish assemblage structure similar to other non-protected areas within Kaneohe Bay where fishing was permitted.

Due to the differences in fish assemblage structure and assemblage characteristics between Kaneohe Bay and all other locations, analyses comparing levels of protection from fishing were conducted excluding all locations within this sheltered embayment. Species richness, biomass, and diversity were significantly different ($P < 0.05$) among no-take areas, areas with customary stewardship, partially protected areas, and locations with open access (Fig. 5). Values for all assemblage characteristics were higher in no-take areas and areas with customary stewardship compared to partially protected and open access areas. No-take areas had the highest values for species richness, number of individuals, and diversity, followed

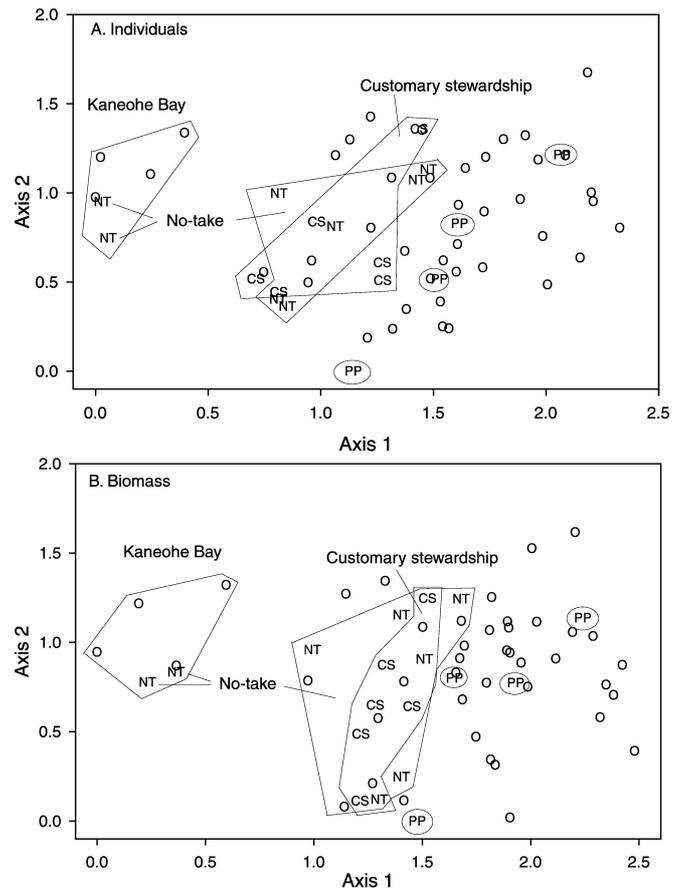


Fig. 4 Relationships among fish assemblages at 60 locations across the main Hawaiian islands relative to their protection from fishing. Results of detrended correspondence analysis with input values $\log(e)$ transformed and rare species downweighted for **A** number of individuals and **B** biomass. Polygons group locations with the same level of protection from fishing. NT No-take; CS customary stewardship; PP partial protection; O open access

by customary stewardship, partially protected, and finally open-access areas having the lowest values. Biomass was highest in locations with customary stewardship followed by no-take areas. The biomass in these two areas was more than 2.5 times greater than partially protected and open access sites, yet this difference was not significant from partially protected sites ($P > 0.05$) due to the low sample size at these locations ($P = 0.57$). Fish standing stock was lowest in the partially protected areas but not significantly different from locations without protection from fishing.

The size of all fishes within areas under various levels of protection (excluding Kaneohe Bay) was significantly different from one another ($F_{3,6949} = 62.3$, $P < 0.001$). No-take reserves (mean \pm SD = 13.9 ± 0.2 cm) and areas under customary stewardship (mean \pm SD = 13.3 ± 0.2 cm) were not significantly different from each other ($P > 0.05$) but were significantly greater ($P < 0.05$) than both partially protected (mean \pm SD = 10.2 ± 0.3 cm) and open access sites (mean \pm SD = 11.6 ± 0.1 cm). The size of fishes in areas open to fishing was significantly greater than areas partially protected from fishing ($P < 0.05$).

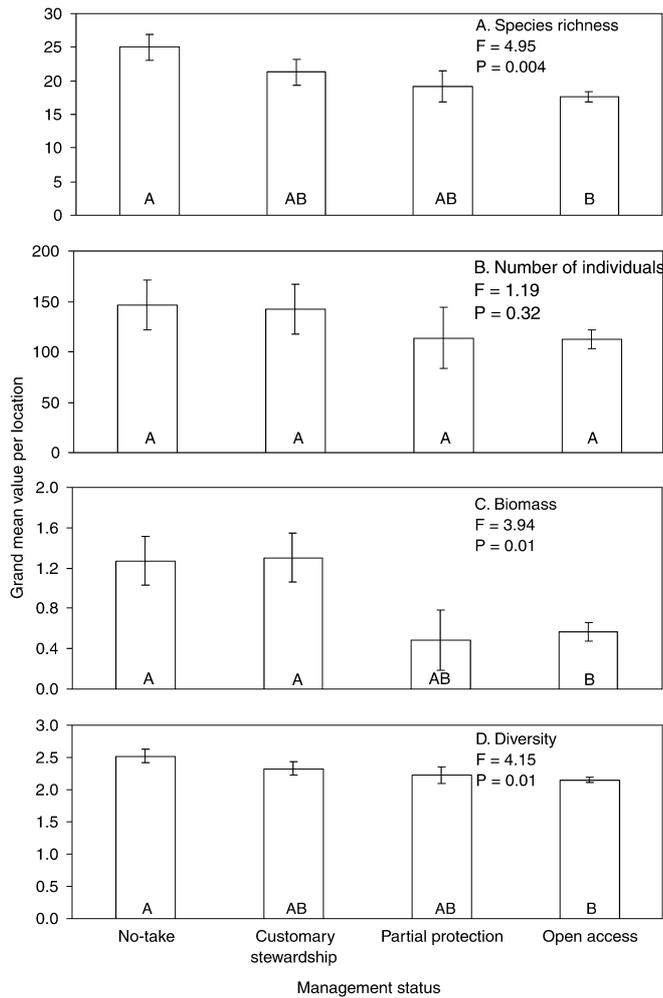


Fig. 5 Comparisons of fish assemblage characteristics with various levels of protection from fishing. Grand mean values per location. All values are based on 125-m² transect except biomass, which is reported in t/ha. Error bars are one standard error of the mean. Statistical results of one-way ANOVA are shown. Levels of fishing protection with the same *letter* designation are not significantly different (Bonferroni adjusted multiple comparisons test, $\alpha=0.05$). Note differences in *y-axis* scales

Fish assemblage characteristics varied greatly among no-take areas and areas under customary stewardship (Fig. 6); however, no statistical analyses were conducted on these data due to small sample sizes at most locations. When data was pooled within a site, species richness was highest at the no-take reserves at the Hanauma Bay site on Oahu, and Honolulu Bay on Maui. Species richness at the no-take Moku o Loe (Coconut Island) site on Oahu was 1.8 times lower than the highest site, possibly reflecting the limited habitat provided by patch reefs in Kaneohe Bay. Biomass followed a similar trend, with Hanauma Bay having the highest standing stock and Moku o Loe having the lowest (1.5 times lower than Hanauma Bay), although variability within sites was high. Diversity was also lowest at Moku o Loe and highest at Honolulu Bay and Molokini Island off of Maui. Despite having the lowest standing stock, diversity, and species richness of any marine reserve

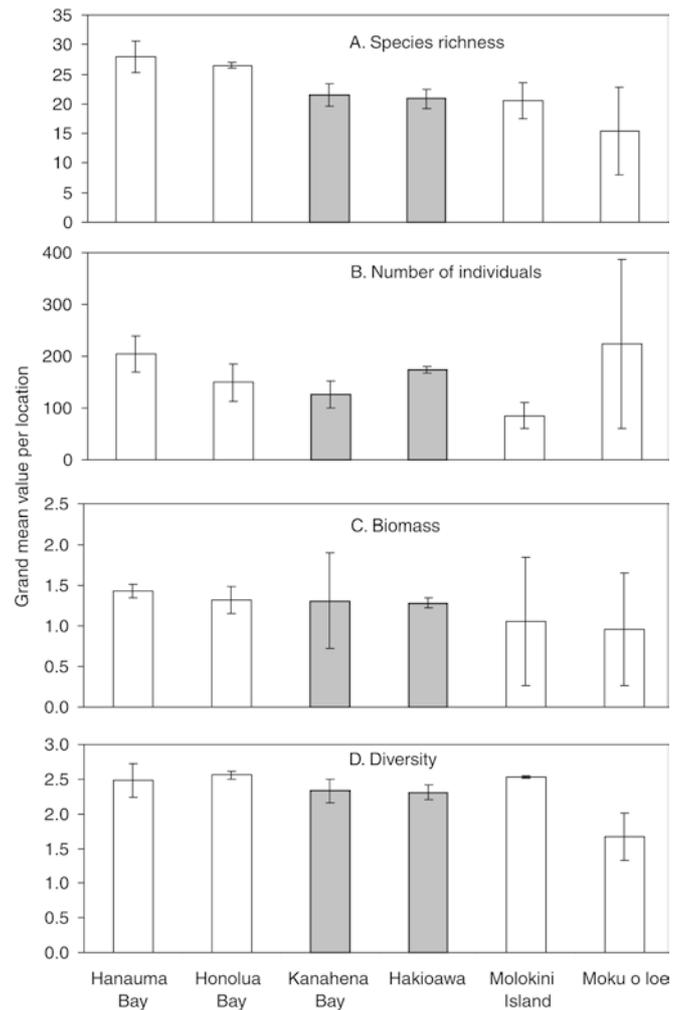


Fig. 6 Comparisons of fish assemblage characteristics in no-take protected areas (*open bars*) and locations under customary stewardship (*shaded bars*). Grand mean values per location. All values are based on 125-m² transect except biomass, which is reported in t/ha. Error bars are one standard error of the mean. Note differences in *y-axis* scales

in the study, Moku o Loe had the highest number of individuals observed among these sites. The fish assemblage structure at Moku o Loe was not common to the other protected sites and was dominated by juvenile parrotfish and small-bodied fishes. These included endemic species like Hawaiian sergeants (*Abudefduf abdominalis*), Domino damselfishes (*Dascyllus albisella*), and saddle wrasses (*Thalassoma duperrey*).

Relationships between fish assemblage structure and environmental parameters and management regimes

Environmental parameters and management regimes influenced the fish assemblage characteristics in different ways (Table 4). General linear models were used to assess the importance of various environmental parameters and fisheries management regimes on fish

Table 4 Influence of various environmental variables and management regimes on fish assemblage characteristics in the main Hawaiian islands. Results of multiple regression models (GLM). Overall model results appear in text

| Parameter | Species | | Number | | Biomass | | Diversity | |
|--------------------------|---------|-------|--------|-------|---------|-------|-----------|--------|
| | F | P | F | P | F | P | F | P |
| Physical | | | | | | | | |
| Depth | 0.02 | 0.893 | 3.39 | 0.072 | 0.63 | 0.431 | 1.16 | 0.287 |
| Rugosity | 7.70 | 0.007 | 4.62 | 0.036 | 4.92 | 0.031 | 4.11 | 0.048 |
| Wave exposure | 2.80 | 0.080 | 0.65 | 0.526 | 0.06 | 0.945 | 11.50 | <0.001 |
| Biotic | | | | | | | | |
| Coral cover—plate | 2.31 | 0.135 | 0.71 | 0.402 | 1.42 | 0.239 | <0.01 | 0.955 |
| Coral cover—branching | 2.03 | 0.161 | 6.14 | 0.017 | 2.71 | 0.106 | 1.30 | 0.260 |
| Coral cover—lobate | 5.48 | 0.023 | 5.42 | 0.024 | 3.09 | 0.085 | 1.02 | 0.319 |
| Management regime | | | | | | | | |
| Protected status | 11.70 | 0.001 | 2.40 | 0.128 | 7.02 | 0.011 | 7.58 | 0.008 |

assemblage characteristics. All locations, including Kaneohe Bay, were used in developing these models. Rugosity, live lobate coral cover, and areas protected from fishing (no-take areas and areas under customary tenure) were all significant parameters in explaining the variability in species richness among locations ($F_{8,51}=6.73$, $P<0.001$). Rugosity, live branching, and lobate coral cover were significant parameters in explaining the variability in the number of individuals ($F_{8,51}=5.57$, $P<0.001$). Rugosity and protected status were the only parameters that were significant in explaining the variability in biomass ($F_{8,51}=4.86$, $P<0.001$). Diversity was explained by rugosity, the degree of wave exposure (exposed, sheltered, and embayments), and protected status ($F_{8,51}=7.42$, $P<0.001$).

Depth strata were not significant in explaining the variability in any fish assemblage characteristics; however, numerical abundance was much higher in the shallow depth strata ($t=1.84$, $P=0.072$). There was a significant positive relationship with rugosity and species richness ($P=0.007$), number of fish ($P=0.036$), biomass ($P=0.031$), and diversity ($P=0.048$). Exposure only explained a significant portion of the variability in diversity ($P<0.001$).

Live coral cover morphology generally did not explain significant portions of variation in the various fish assemblage characteristics, with two notable exceptions. Branching corals significantly explained the variation in the number of individuals ($P=0.017$), while lobate corals significantly explained the variation in species richness ($P=0.023$) and number of individuals ($P=0.024$). In both cases these were positive relationships, with higher cover of branching coral associated with higher values for number of individuals and higher lobate coral cover related to greater species richness and higher number of individuals.

Finally, locations with protected status explained the finding of significant portions of variation in species richness ($P=0.001$), biomass ($P=0.01$), and diversity ($P=0.008$). For each of these characteristics, locations protected from fishing (NT and CS) had higher numbers of species, greater biomass, and higher diversity. Numerical fish abundance did not vary significantly ($P>0.05$) between protected and unprotected locations.

Discussion

This study examined the relationship between fish assemblages and their associated habitat on a scale consistent with the patterns of both the resources and their users. Direction of wave exposure, amount of habitat complexity, and the level of protection from fishing all proved to be important determinants of reef fish assemblage structure and standing stock. Greater numbers of fishes were observed in the shallow depth strata, but high variability in the abundance of schools of small juveniles in this strata masked statistical differences due to low power.

The fish assemblage structure in the sheltered embayment of Kaneohe Bay, Oahu, was distinct and differed greatly from all other fish assemblages around the state. Locations in Kaneohe Bay had the lowest species richness and diversity compared to all other types of exposure. Kaneohe Bay has been subjected to anthropogenic stresses in the past from both point source (Banner 1974; Smith et al. 1981; Hunter and Evans 1995) and non-point source (Jokiel et al. 1993; Hunter and Evans 1995) pollution. Small areal extent of live coral cover and low habitat complexity, particularly at the deeper locations in Kaneohe Bay (ca. 10 m), are a result of these anthropogenic impacts as well as habitat degradation associated with invasive algae. The poor quality of these habitats may help to account for the low species richness and diversity at locations within Kaneohe Bay.

Reef habitat complexity (rugosity) was important in explaining the variability in all reef fish assemblage characteristics in this study. Habitat complexity provides refuges and barriers that fragment the area, resulting in more heterogeneous assemblages (Sebens 1991). A number of authors have recognized the importance of habitat complexity in structuring fish assemblages (Luckhurst and Luckhurst 1978; Carpenter et al. 1981; Roberts and Ormond 1987; Holbrook et al. 1990; Grigg 1994; Friedlander and Parrish 1998a) and the results from this study clearly support these findings.

Species richness and diversity were highest in locations of moderate wave exposure. Fish biomass was lowest in locations exposed to north and south swells,

with locations protected from direct swell activity having higher standing stock of reef fishes. Elsewhere in Hawaii, surf height and degree of wave exposure have been shown to be negatively correlated with several measures of fish assemblage organization (Friedlander and Parrish 1998b). Fish populations may be depressed in these locations due to the seasonal variability in environmental conditions and the physiography of these reefs that tend to be dominated by encrusting corals and have lower habitat complexity compared to locations that receive less direct wave impacts.

Despite differences in habitat, locations protected from fishing formed distinct assemblages that had higher values for assemblage characteristics than areas where all fishing was permitted or partially restricted. Hanauma Bay on Oahu and Honolua Bay on Maui, two no-take areas with the highest levels of protection from fishing in the main Hawaiian islands, had the highest values for most fish assemblage characteristics. Both sites have either high coral cover, high coral species richness, or high reef complexity, suggesting that a combination of these parameters contributed to good fish habitat quality for reef fish in Hawaii. Moku o Loe had the lowest standing stock of reef fishes observed within areas protected from fishing, followed by Molokini Island. These locations are typified by having small-scale habitat complexity that harbors large numbers of small-bodied fish individuals but lacking in the large-scale habitat complexity necessary to support larger individuals.

A number of communities throughout Hawaii are currently strengthening local influence and accountability for the health and long-term sustainability of their marine resources through revitalization of local traditions and resource knowledge. The state of Hawaii has been encouraging community-based management of subsistence fishing areas since 1994, and a number of community-managed areas are now being established. The Ahihi-Kinau location has only recently been part of a harvesting effort involving customary and cultural take. There is only one permit issued by the Natural Areas Reserve Commission (to one family) that has only recently begun to exercise the take of some resources (mostly intertidal). It was the permittee's intent to teach the children the skills of the elders and not to fish for subsistence, so the harvested amounts are small. Similarly, Kahoolawe's resources are open to just a few people who are fishing for cultural and educational purposes only and are regulated by the Kahoolawe Island Reserve Commission. The remoteness of these locations combined with the light fishing pressure (on-island consumption only) and community oversight has resulted in high standing stock of reef fishes compared to other locations in Hawaii.

The Pupukeya MLCD and the Nenu Point FRA with limited protection from fishing had lower standing stock than areas where fishing was not restricted. Virtually all types of fishing are allowed in the Pupukeya MLCD and only ornamental fish collecting is restricted in the Nenu Point FRA. The existing management regime at the

Pupukeya MLCD does not appear to be enhancing fish stocks at this reserve in comparison with other no-take MPAs in the state (Friedlander 2001). The State of Hawaii, Department of Land and Natural Resources, Division of Aquatic Resources has just completed a modification to the Pupukeya MLCD that includes the expansion of existing boundaries and the restriction of most fishing activities within the reserve. The existing data will help to serve as a baseline to determine if these new regulations will enhance the fish assemblage within the reserve over time.

At a few locations, high biomass occurred in habitats with low rugosity that were protected from fishing (e.g., Honolua North and Kanahena Bay and Point shallow). This may be a result of migration from adjacent areas where fishing is permitted, but also suggests that protection from fishing may be as, if not more, important than habitat quality in sustaining and enhancing fish assemblages.

Locations characterized by high rugosity, moderate wave exposure, high percentage of lobate coral cover, and protection from fishing had higher levels of species richness. Embayments, on the other hand, typically had fewer numbers of species. Intuitively, increasing substrate complexity is beneficial to species richness by creating more niche space and thus a greater diversity of microhabitats. Even lobate corals when large enough appeared to create substantial refuge space under the edges of the colonies.

Higher fish abundance appeared to be influenced by higher rugosity, occurrence of embayments, and high cover of branching coral. Protection from fishing, however, did not make a difference in terms of number of fish. It is interesting to note that shallow water closer to the surge zone displayed higher numbers of fish regardless of size. This could be a function of refuge from predation due to the greater relief inshore or perhaps algal food availability was higher since herbivores were the dominant trophic group at these locations.

Only high rugosity and protection from fishing at a site showed higher levels of biomass. Wave exposure did not appear to play an important role in structuring size of fish within a community; however, sites with more refuge space and legal protection from fishing may mask this factor. The number of fish did not vary significantly among locations with or without legal protection, while biomass was significantly different among these locations. Fishing pressure tends to target the larger, more reproductively viable fish, with the resulting fish assemblage dominated by smaller sizes even though numbers of fish are equivalent (Jennings and Lock 1996; Jennings et al. 2001). Because of this, total population fecundity declines more quickly than numerical abundance (Post et al. 2002).

McGehee (1994) found that water movement energy in southwest Puerto Rico was the environmental parameter that had the strongest relationship with fish species distribution. McGehee did not, however, examine fish biomass and only sampled within a small depth strata

(1–3 m). Chabanet et al. (1997) discovered that coral variables for reefs at Reunion Island are most strongly correlated with species richness and diversity of fish assemblages. Friedlander and Parrish (1998a) in Hanalei Bay, Kauai, Hawaii, also noted that most of the variation in similar fish assemblage characteristics was explained by measures of holes in the substratum, rugosity, and depth. All of these studies, however, sampled over a small spatial scale along the same stretch of coastline, so consequently larger-scale inferences could not be made.

Clearly, protection, whether it is physical (e.g., rugosity), biological (e.g., coral cover growth forms), or human-induced (e.g. marine reserve), enhances fish assemblage characteristics in different ways. Ideally, essential fish habitat in the main Hawaiian islands should consist of an area with high rugosity or relief with moderate wave exposure that has a high percentage of branching and/or lobate coral coupled with legal protection from fish pressure. Habitats with these optimal characteristics should possess fish assemblages with high species richness, abundance, biomass, and diversity. New techniques [e.g., light detection and ranging instruments (LIDAR), hyperspectral imaging] that can rapidly discriminate habitats with these characteristics will aid scientists and managers alike in identifying areas that are important to protect and manage for the sustainability of nearshore fish populations in the Hawaiian Islands.

Marine reserve networks have the greatest chance of including all species, life stages, and ecological linkages if they encompass representative portions of all ecologically relevant habitat types (Ballantine 1997; Friedlander and Parrish 1998a; Murray et al. 1999). Wave exposure, live coral cover, and habitat complexity were all found to be ecologically important environmental parameters for fish assemblages in Hawaii and these parameters should be considered in future marine reserve design. We found several ecologically critical habitat types that it would be beneficial to represent more substantially in a marine reserve network in Hawaii. Locations sheltered from direct wave action and areas of high habitat complexity had higher values for most fish assemblage characteristics and therefore are worthy of greater protection. Areas with high percentages of branching coral provided small-scale structural relief and harbored large numbers of juvenile fishes. These areas may be important nursery habitats and their inclusion in reserve design should provide greater connectivity with adult habitats.

Habitat plays an important role in structuring fish assemblages, yet most studies of marine reserves fail to measure habitat quality (Cote et al. 2001). The high variance in fish assemblage characteristics among different habitat types and the unique fish assemblages associated with these different habitats means that sampling and statistical comparisons need to be stratified by habitat type for more robust statistical comparisons. Assessments of fished vs. protected areas must consider habitat and environmental variables when designing assessment programs in order to properly

examine MPA success. Once reserves are established, long-term monitoring programs can be implemented to help determine the effectiveness of the zoning plan and to guide future modifications to either the fishing regulations or the reserve boundaries.

Typically, ecological processes operate on geographic scales much larger than the majority of protected areas. The spatial scale of this study is beyond that of most other marine reserve studies yet it is the scale at which management decisions typically are made. Assessments of MPAs in other areas should try to examine multiple reserves and fished areas over a broad range of habitat types. A well-designed MPA assessment should first map the distribution and characteristics of benthic habitats within and outside the MPAs, followed by an inventory and assessment of the species of interest. Recent advances in analytical techniques and GIS tools to quantitatively define species habitat utilization patterns within and outside MPAs make a large-scale stratified random sampling design more attainable. Current studies on fish habitat utilization patterns using georeferenced benthic habitat maps have proven to be valuable in illuminating patterns of differential habitat utilization across the seascape, as well as identifying ontogenetic shifts in habitat selection within species (Christensen et al. 2003).

Marine reserve design must consider the habitat requirements and life histories of the species of interest as well as the extent of fishing pressure in the area and the degree of enforcement. If protective areas are to be effective, they must include the diversity of habitats necessary to accommodate the wide range of fish species. The kind of approach taken in this study, which attempts to make a functional match between habitats and fishes to be preserved, seems appropriate for selection, evaluation, and management of reserves. The results provide managers with a much better idea of how to select and manage reef habitat for maximum benefit to fish populations, with the attendant social benefits of improved fishery yield and/or improved results in preservation of fish populations and ecosystems quality.

Acknowledgments This work was supported with funds from the Hawaii Coral Reef Initiative (NOAA/NOS) and the US Geological Survey to the Hawaii Coral Reef Assessment and Monitoring Program. The Hawaii Institute of Marine Biology and the Oceanic Institute provided additional support for this project.

References

- Alcala AC, Russ GR (1990) A direct test of the effects of protective management on abundance and yield of tropical marine resources. *J Cons Int Expl Mer* 46:40–47
- Appeldoorn RS, Recksiek CW, Hill RL, Pagan FE, Dennis GE (1997) Marine protected areas and reef fish movements: the role of habitat in controlling ontogenetic migration. *Proc 8th Int Coral Reef Symp* 2:1917–1922
- Appeldoorn RS, Friedlander A, Sladek Nowlis J, Usseglio P, Mitchell-Chui A (2003) Habitat connectivity in reef fish

- communities and marine reserve design in Old Providence–Santa Catalina, Colombia. *Gulf Caribb Res* 14(2):61–78
- Auster PJ, Shackell NL (1997) Fishery reserves. In: Boreman JG, Nakashima BS, Powels HW, Wilson JA, Kendall RL (eds) Northwest Atlantic groundfish: perspectives on a fishery collapse. American Fishery Society, Bethesda, Maryland, pp 159–166
- Ballantine WJ (1997) Design principles for systems of “no-take” marine reserves. In: Proc Worksh on the Design and Monitoring of Marine Reserves, 18–20 Feb, Fisheries Centre, University of British Columbia, Vancouver, British Columbia, Canada
- Banner AH (1974) Kaneohe Bay, Hawaii: urban pollution and a coral reef ecosystem. *Proc 2nd Int Coral Reef Symp* 2:685
- Bellwood DR, Hughes TP (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science* 292:1532–1534
- Bohnsack JA (1996) Maintenance and recovery of reef fishery productivity. In: Polunin NVC, Roberts CM (eds) Reef fisheries. Chapman and Hall, London, pp 283–313
- Bohnsack JA (1998) Application of marine reserves to reef fisheries management. *Aust J Ecol* 23:298–304
- Bohnsack JA, Ault JS (1996) Management strategies to conserve marine biodiversity. *Oceanography* 9:73–82
- Brock RE (1982) A critique of the visual census method for assessing coral reef fish populations. *Bull Mar Sci* 32:269–276
- Brock VE (1954) A preliminary report on a method of estimating reef fish populations. *J Wildl Manage* 18:297–308
- Carpenter KE, Micalot RI, Albaladejo VD, Corpuz VT (1981) The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. *Proc 4th Int Coral Reef Symp* 2:497–502
- Chabanet P, Ralambondrainy H, Amanieu M, Faure G, Galzin R (1997) Relationships between coral reef substrata and fish. *Coral Reefs* 16:93–102
- Christensen JD, Jeffrey CFG, Caldwell C, Monaco ME, Kendall MS, Appeldoorn RS (2003) Cross-shelf habitat utilization patterns of reef fishes in southwestern Puerto Rico. *Gulf Caribb Res* 14(2):9–28
- Cote IM, Mosqueira I, Reynolds JD (2001) Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *J Fish Biol* 59(Suppl A):178–189
- Coyne MS, Monaco ME, Anderson M, Smith W, Jokiel P (2001) Classification scheme for benthic habitats: main eight Hawaiian Islands. Biogeography program. US Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Silver Spring, Maryland, 16 pp
- Dollar SJ (1982) Wave stress and coral community structure in Hawaii. *Coral Reefs* 1:71–81
- Dugan JE, Davis GE (1993) Applications of marine refugia to coastal fisheries management. *Can J Fish Aquat Sci* 50:2029–2042
- Dustan PJ, Leard J, Meier O, Brill M, Kosmynin V (1999) Point-Count 99 software. University of Charleston, South Carolina
- Food and Agriculture Organization (1998) The state of the world fisheries and aquaculture. FAO Fisheries Circ. FAO Fisheries Department, Rome, Italy
- Friedlander AM (2001) Essential fish habitat and the effective design of marine reserves: applications for marine ornamental fishes. *Aquarium Sci Conserv* 3:135–150
- Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Mar Ecol Prog Ser* 230:253–264
- Friedlander AM, Parrish JD (1998a) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *J Exp Mar Biol Ecol* 224:1–30
- Friedlander AM, Parrish JD (1998b) Temporal dynamics of the fish assemblage on an exposed shoreline in Hawaii. *Environ Biol Fish* 53:1–18
- Friedlander A, Poepoe K, Poepoe K, Helm K, Bartram P, Maragos J, Abbott I (2002) Application of Hawaiian traditions to community-based fishery management. *Proc 9th Int Coral Reef Symp* 2:813–818
- Gauch HG Jr (1982) Multivariate analysis in community ecology. Cambridge University Press, Cambridge
- Grigg RW (1983) Community structure, succession and development of coral reefs in Hawaii. *Mar Ecol Prog Ser* 11:1–14
- Grigg RW (1994) Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Mar Ecol Prog Ser* 103:25–34
- Greenfield DW, Johnson RK (1990) Community structure of western Caribbean blennioid fishes. *Copeia* 1990:433–448
- Gulko D, Maragos J, Friedlander A, Hunter C, Brainard R (2000) Status of coral reef in the Hawaiian archipelago. In: Wilkinson C (ed) Status of coral reefs of the world. Australian Institute of Marine Science, Cape Ferguson, Queensland, pp 219–238
- Halpern B (2003) The impact of marine reserves: do reserves work and does reserve size matter? *Ecol Appl* 13(Suppl 1):S117–S137
- Holbrook SJ, Schmitt RJ, Ambrose RF (1990) Biogenic habitat structure and characteristics of temperate reef fish assemblages. *Aust J Ecol* 15:489–503
- Hunter CL, Evans CW (1995) Coral reefs in Kaneohe Bay, Hawaii: two centuries of western influence and two decades of data. *Bull Mar Sci* 57:501–515
- Jennings S, Lock JM (1996) Population and ecosystem effects of reef fishing. In: Polunin NVC, Roberts CM (eds) Reef fisheries. Chapman and Hall, London, pp 193–218
- Jennings S, Kaiser MJ, Reynolds JD (2001) Marine fisheries ecology. Blackwell Science, Oxford
- Johannes RE (1978) Traditional marine conservation methods in Oceania and their demise. *Annu Rev Ecol Syst* 9:349–364
- Johannes RE (1981) Words of the lagoon: fishing and marine lore in the Palau district of Micronesia. University of California Press, Berkeley
- Johannes RE (1997) Traditional coral-reef fisheries management. In: Birkeland C (ed) Life and death of coral reefs. Chapman and Hall, New York, pp 380–385
- Jokiel PL, Hunter CL, Taguchi S, Watarai L (1993) Ecological impact of a fresh water “kill” on the reefs of Kaneohe Bay, Oahu, Hawaii. *Coral Reefs* 12:177–184
- Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef communities. *Mar Biol* 49:317–323
- Ludwig JA, Reynolds JF (1988) Statistical ecology. Wiley, New York
- McGehee MA (1994) Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. *Mar Ecol Prog Ser* 105: 243–255
- Murray SN, Ambrose RF, Bohnsack JA, Botsford LW, Carr MH, Davis GE, Dayton PK, Gotshall D, Gunderson DR, Hixon MA, Lubchenco J, Mangel M, MacCall A, McArdle DA, Ogden JC, Roughgarden J, Starr RM, Tegner MJ, Yoklavich MM (1999) No-take reserve networks: protection for fishery populations and marine ecosystems. *Fisheries* 24(11):11–25
- National Marine Fisheries Service (2001) Report to Congress: status of fisheries of the United States. US Department of Commerce, Silver Spring, Maryland
- National Research Council (1999) Sustaining marine fisheries. National Academy Press, Washington, DC
- Ogden JC (1988) The influence of adjacent systems on the structure and function of coral reefs. *Proc 6th Int Coral Reef Symp* 1:123–129
- Ogden JC (1997) Ecosystem interactions in the tropical coastal seascape. In: Birkeland C (ed) Life and death of coral reefs. Chapman and Hall, New York, pp 288–297
- Post JR, Sullivan M, Cox S, Lester NP, Walters CJ, Parkinson EA, Paul AJ, Jackson L, Shuter BJ (2002) Canada’s recreational fisheries: the invisible collapse. *Fisheries* 27(1):6–17
- Randall JE (1996) Shore fishes of Hawaii. Natural World Press, Vida, Oregon
- Risk MJ (1972) Fish diversity on a coral reef in the Virgin Islands. *Atoll Res Bull* 193:1–6
- Roberts CM (1995) Rapid build-up of fish biomass in a Caribbean marine reserve. *Conserv Biol* 9:815–826

- Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar Ecol Prog Ser* 41:1–8
- Roberts CM, Polunin NVC (1991) Are marine reserves effective in management of reef fisheries? *Rev Fish Biol Fish* 1:65–91
- Roberts CM, Polunin NVC (1993) Marine reserves: simple solutions to managing complex fisheries? *Ambio* 22:363–368
- Rowley RJ (1994) Case studies and reviews: marine reserves in fisheries management. *Aquat Conserv Mar Freshwater Ecosyst* 5:233–254
- Ruddle K (1996) Traditional management of reef fishing. In: Polunin NVC, Roberts CM (eds) *Reef fisheries*. Chapman and Hall, London, pp 315–336
- Russ GR (1991) Coral reef fisheries: effects and yields. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, pp 601–635
- Russ GR, Alcala AC (1996a) Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecol Appl* 6:947–961
- Russ GR, Alcala AC (1996b) Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Mar Ecol Prog Ser* 132:1–9
- Schmitt RA (1996) National Marine Fisheries Service: seeking partners for its National Habitat Plan and identifying essential fish habitats. *Fisheries* 21:4
- Sebens KP (1991) Habitat structure and community dynamics in marine benthic systems. In: Bell SS, McCoy ED, Mushinsky HR (eds) *Habitat structure, the physical arrangement of objects in space*. Chapman and Hall, New York, pp 211–234
- Shomura R (1987) Hawaii's marine fishery resources: yesterday (1900) and today (1986). Rep H-87-21. US Department of Commerce, NOAA, NMFS, Southwest Fisheries Science Center Administration, Honolulu, Hawaii, 14 pp
- Sladek Nowlis J (2000) Short- and long-term effects of three fishery management tools on depleted fisheries. *Bull Mar Sci* 66: 651–662
- Sladek Nowlis J, Friedlander AM (2003) Marine reserve design and function for fisheries management. In: Norse E, Crowder L (eds) *Marine conservation biology: the science of conserving the sea's biodiversity*. Island Press, Covelo, California (in press)
- Sladek Nowlis, J, Roberts CM (1999) Fisheries benefits and optimal design of marine reserves. *Fish Bull* 97:604–616
- Smith MK (1993) An ecological perspective on inshore fisheries in the main Hawaiian islands. *Mar Fish Rev* 55(2):34–49
- Smith SV, Kimmerer WJ, Laws EA, Brock RE, Walsh TW (1981) Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pac Sci* 35:279–395
- Yoklavich MM (1998) Marine harvest refugia for west coast rockfish. NOAA-TM-NMFS SWFSC-225. Pacific Fisheries Environmental Laboratory, National Marine Fisheries Service, Pacific Grove, California, 159 pp
- Zar JH (1984) *Biostatistical analysis*. Prentice Hall, Englewood Cliffs