



The effects of submarine canyons and the oxygen minimum zone on deep-sea fish assemblages off Hawai'i

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ABSTRACT

Submarine canyons are reported to be sites of enhanced fish biomass and productivity on continental margins. However, little is known about the effects of canyons on fish biodiversity, in particular on oceanic islands, which are imbedded in regions of low productivity. Using submersibles and high-definition video surveys, we investigated demersal fish assemblages in two submarine canyons and slope areas off the island of Moloka'i, Hawai'i, at depths ranging from 314 to 1100 m. We addressed the interactions between the abundance, species richness and composition of the fish assemblage, and organic matter input and habitat heterogeneity, testing the hypotheses that heterogeneous bottom habitats and higher organic matter input in canyons enhance demersal fish abundance, and species density, richness and diversity, thereby driving differences in assemblage structure between canyons and slopes. Sediment type, substrate inclination, water-mass properties (temperature and dissolved oxygen) and organic matter input (modeled POC flux and percent detritus occurrence) were put into multivariate multiple regression models to identify potential drivers of fish assemblage structure. A total of 824 fish were recorded during ~13 h of video yielding 55 putative species. Macrouridae was the most diverse family with 13 species, followed by Congridae (5), Ophidiidae (4) and Halosauridae (3). Assemblage structure changed markedly with depth, with the most abrupt change in species composition occurring between the shallowest stratum (314–480 m) and intermediate and deep strata (571–719 m, 946–1100 m). *Chlorophthalmus* sp. dominated the shallow stratum, macrourids and synphobranchid eels at intermediate depths, and halosaurs in the deepest stratum. Assemblages only differed significantly between canyon and slope habitats for the shallow stratum, and the deep stratum at one site. Dissolved oxygen explained the greatest proportion of variance in the multivariate data, followed by POC flux and percent organic-detritus occurrence. Fish abundances were generally higher in canyons but only statistically significant for the deepest stratum. Reduced fish abundances both in canyon and slope transects occurred at intermediate depths within the core of the oxygen minimum zone (OMZ). Species density, diversity and richness and abundance were usually higher in the canyons, but only statistically higher in the deepest stratum. Possible causes for increased abundance and species densities and richness in the deepest stratum in canyons include reduced disturbance at deeper depths. We conclude that submarine canyons on oceanic islands are likely to be sites of enhanced fish abundance and species richness, but that these enhancing effects are offset when oxygen concentrations fall below $\sim 0.7 \text{ ml l}^{-1}$ in OMZs.

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1. Introduction

Submarine canyons are topographic features that can receive high organic-matter inputs by channeling and trapping coastally-derived and surface-produced organic detritus (Vetter and Dayton, 1998, 1999), focusing nekton and zooplankton scattering layers

(Greene et al., 1988; Lavoie et al., 2000; Genin, 2004) and enhancing local primary productivity by inducing upwelling (Klinck, 1996; Hickey, 1997; Sobarzo et al., 2001; Allen and Hickey, 2010). Typically, the seafloor of canyons is topographically complex, yielding a mosaic of habitat types (Gardner et al., 2003; Schlacher et al., 2007, 2010). Both the input of organic matter and habitat heterogeneity can be fundamental drivers of biodiversity in faunal assemblages (Rosenzweig, 1995; Tews et al., 2004).

High-resolution bathymetric data indicate that there are well over 660 submarine canyons globally (De Leo et al., 2010); a very

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recent tabulation based on satellite altimetry suggests that the number of submarine canyons exceeds 5800 (Harris and Whiteway, 2011). A small number of these submarine canyons (45, or less than 0.7%) has been studied to evaluate the effects detrital input and habitat heterogeneity on faunal diversity and community structure (Rowe et al., 1982; Houston and Haedrich, 1984; Vetter, 1994; Hargrave et al., 2004; Schlacher et al., 2007; Escobar-Briones et al., 2008; Tyler et al., 2009; Vetter et al., 2010; Bianchelli et al., 2010; De Leo et al., 2010; McClain and Barry, 2010; Ingels et al., 2011; Paterson et al., 2011). Some of these studies (e.g., Stefanescu et al., 1994; Harrold et al., 1998; Vetter and Dayton, 1998; Vetter et al., 2010) conclude that enhanced detrital accumulation is responsible for elevated invertebrate and fish abundances in canyons compared to slope environments. For example, De Leo et al. (2010) reported in Kaikoura Canyon, New Zealand, the highest benthic invertebrate biomass ever observed for non-chemosynthetic ecosystems deeper than 500 m in the ocean, mostly composed of deposit-feeding megafauna. Furthermore, these authors hypothesized that this extraordinary biomass has a direct trophic link to demersal fish communities by enhancing prey availability for benthic-feeding fish species, which also exhibited significantly higher abundances in the canyon (De Leo et al., 2010). The strength of this “canyon effect” of enhanced abundance of benthic macro- and megafauna has shown varying trends along depth gradients i.e., remaining constant (Houston and Haedrich, 1984), or showing maxima in benthic abundance either in canyon heads (Vetter and Dayton, 1998) or at intermediate depths (Duineveld et al., 2001; Escobar-Briones et al., 2008). It appears that in canyon systems fueled largely by coastally-derived organic detritus, the enhancement of canyon benthos may decrease exponentially with depth as organic material is consumed downslope (Vetter and Dayton, 1998). Alternatively, when canyons are large enough to extend far onto the continental slope, primary production over the outer shelf/slope may be enhanced by canyon-hosted meso-scale eddies, yielding mid-depth peaks in organic carbon flux and benthic community abundance in submarine canyons (Duineveld et al., 2001; Escobar-Briones et al., 2008).

Habitat heterogeneity provided by the broad range of substrate types and complex topography inside submarine canyons has also been invoked to explain enhanced benthic invertebrate diversity at both local and regional scales compared to more homogenous open slopes (Schlacher et al., 2007, 2010; Tyler et al., 2009; Buhl-Mortensen et al., 2010; Vetter et al., 2010; Ingels et al., 2011; Paterson et al., 2011; De Leo et al., in preparation). The habitat-heterogeneity hypothesis assumes that structurally complex habitats lead to an increase in species diversity by providing a higher number of niche dimensions, including a wider range of resources (MacArthur and Wilson, 1967). Only a few studies, however, have investigated relationships between small-scale seafloor habitat heterogeneity (Brodeur, 2001; Uiblein et al., 2003) and diversity (Yoklavich et al., 2000) of demersal fish communities inhabiting submarine canyons. For example, Brodeur et al. (2001) found higher densities of rockfish (*Sebastes alutus*) in the Pribilof Canyon, Bering Sea, when contrasted to open slope sites. They suggested that higher densities resulted from the presence of sea whip “forests” (*Halipterus willmoesi*), arguing that rockfish use these three-dimensional habitats as refuges from predators. Uiblein et al. (2003) found that demersal species inhabiting the Bay of Biscay (NE Atlantic) occurred preferentially on hard, highly structured substrates associated with canyon floors. Finally, Yoklavich et al. (2000) found highest canyon rockfish diversity in complex habitats composed of a mixture of rocks, cobbles and mud.

While organic detrital input and habitat heterogeneity can lead to differences in benthic communities between canyons and

slopes, a variety of other environmental factors can also influence these patterns. For example, the frequency and intensity of disturbance such as flushing events (Bosley et al., 2004; Hargrave et al., 2004; Company et al., 2008) and sediment slumps at the base of canyon walls (McClain and Barry, 2010), water mass properties such as temperature variability and oxygen concentrations (Vetter and Dayton, 1998), as well as the vertical flux of particulate organic carbon (POC) (Goody and Turley, 1990; Levin et al., 2001, 2010; Levin and Dayton, 2009) can differ between canyons and open slopes. It is essential that any attempt to determine the influence of organic detritus input and seafloor habitat heterogeneity on benthic assemblages should account for the full range of environmental factors that act in concert to generate environmental variability on continental and island-margin settings.

Few quantitative distribution data exist for the demersal fish fauna of the Hawai’ian Islands, a major slope habitat in the central North Pacific. While quantitative surveys have been conducted on island and atoll flanks to depths of ≤ 300 m (Kelley et al., 2006), most information about the fish fauna inhabiting the deeper slopes of the archipelago comes from trawl surveys (Gilbert, 1905; Struhsaker, 1973) and qualitative video/photographic observations made from submersibles (Chave and Mundy, 1994). Therefore, as for seamounts deeper than 300 m (Menezes et al., 2009) the deep demersal fish assemblages of the Hawai’ian Archipelago are very poorly described.

We studied fish assemblages in two submarine canyons and on adjacent areas of the slope north of the island of Moloka’i, in the main Hawai’ian archipelago, to investigate the potential role of habitat heterogeneity and enhanced detrital input on the structure of demersal fish communities in submarine canyons. We hypothesized that (1) fish community structure differs between canyon and slope habitats due to a combination of environmental drivers, including differences in the amount of detritus and seafloor habitat heterogeneity; (2) fish abundance is greater in canyon than slope habitats as a result of higher inputs of organic material from terrestrial and macroalgal sources (that we assume yield, directly or indirectly, greater food resources for fish); (3) demersal fish abundance decreases less rapidly with depth in canyons than on open slopes due to detrital transport down canyons; (4) fish species richness is positively correlated with habitat heterogeneity, and is therefore higher in the more heterogeneous settings of canyons.

This study of demersal fish assemblages on the submarine flanks of Moloka’i was part of a broader project to investigate the roles of Hawai’ian submarine canyons in enhancing fish and invertebrate diversity and abundance on the slopes of oceanic islands imbedded in an oligotrophic ocean (the North Pacific Subtropical Gyre). Patterns of diversity and abundance of invertebrate mega- and macrofauna in canyon versus slope habitats are reported in Vetter et al. (2010) and De Leo et al. (in preparation), respectively.

2. Materials and methods

2.1. Study area

The Hawai’i Undersea Research Laboratory (HURL) Pisces IV and V submersibles were used to survey submarine canyon and nearby slope habitats off the north coast of the island of Moloka’i, located in the main Hawai’ian Islands. Abundance and taxonomic richness of bottom fish assemblages were surveyed by means of high-definition video surveys within three different depth strata (shallow, 314–464 m; intermediate, 571–719 m; deep, 946–1100 m); The two studied canyons, Pelekunu and Kawanui

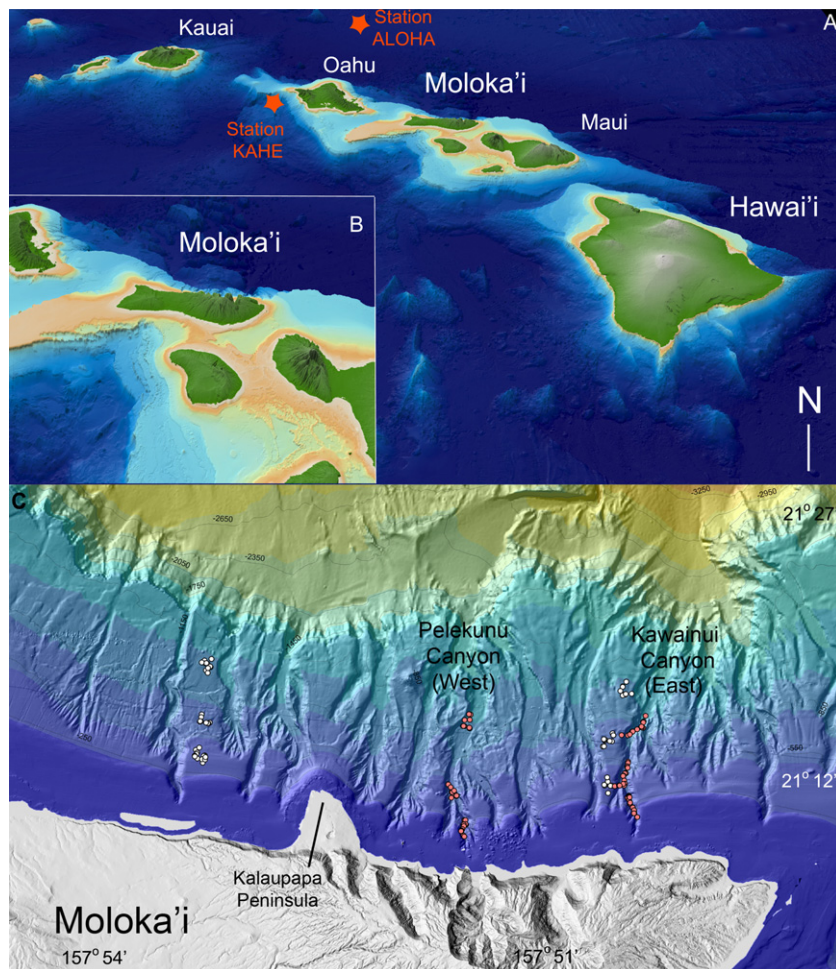


Fig. 1. Map of the study area. (A, B) 3D-view of bathymetry and relief of the Main Hawai'ian Islands with detail of Moloka'i (imagery from Main Hawai'ian Islands Multibeam Synthesis, SOEST, University of Hawai'i, <http://www.soest.hawaii.edu/HMRG/Multibeam/index.php>). Hawai'ian Ocean Time Series (HOT) stations ALOHA and KAHE are indicated (Temperature, Oxygen and POC flux data from Station ALOHA were used in this study). (C) Pisces V dive locations were video transects that were conducted (white symbols, slopes; pink or gray, canyons). Numbers represent depth in meters. (Detailed multi-beam bathymetric data provided by C. Kelley and J. Smith, from Hawai'ian Undersea Research Laboratory (HURL).) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Canyons and the two adjacent slope sites studied occurred along the north shore of Moloka'i (Fig. 1). High sea cliffs reaching 600–800 m altitudes with lush vegetation and high annual precipitation (200–400 cm) dominate the north shore off Moloka'i (Culliney, 2006), especially east of the Kalaupapa Peninsula. A large number of coastal embayments provide direct connections between drainage basins along Moloka'i's north shore and the heads of several submarine canyons, which reach depths as shallow as 150 m (Fig. 1; Shepard and Dill, 1966). For this reason, the input of terrestrial material into canyons is enhanced relative to the open slope, as indicated by large concentrations of decomposing plant material along the floors of both of these canyons (Vetter et al., 2010).

2.2. Demersal fish assemblages and habitat composition

Fish were identified to the lowest possible taxonomic level, generally putative species. We determined the number of different fish taxa and individuals from a total of 45 video transects using a high-8 digital camera mounted on the submersible. The video and light sources on the submersible had the same settings during all dives and transects, thus standardizing the quality of the footage obtained (Kelley et al., 2006; Vetter et al., 2010). When obstacles to navigation were encountered (e.g., canyon

walls), transects were suspended and resumed when seafloor morphology allowed submersible navigation and transect observations (see Vetter et al., 2010). Also, in order to survey a range of bottom habitats within both canyon and open-slope areas, transects were performed both parallel and perpendicular to isobaths as described in Vetter et al. (2010). A summary of all submersible dive information, with geographical positions, dive duration and total area surveyed is presented in Table 1. The total area surveyed per transect was calculated using the standard submersible speed (2 knots) and transect duration (9–27 min) to determine transect length, which was multiplied by the average width-of-view of each transect. Video transect widths were estimated using parallel laser scale markers (10 cm) in at least 60 frame grabs per transect with the image analysis software Image J[®] (Rasband, 2009). Fish abundances per transect were determined by dividing the total number of individuals in each video by its total area, and normalizing it to an area of 100 m² (0.01 ha). To obtain species density, the total number of fish species per transect was divided by the transect duration in minutes. Rarefaction curves were calculated using Hulbert's (1971) modification of Sanders (1968), to estimate diversity as a function of number of individuals. Because species accumulations did not reach asymptotic values for any of our depth strata in either canyon or slope settings, we used nonparametric species richness

Table 1

Summary of Pisces dive information: depth, habitat, geographical coordinates and total sampling effort for video transects taken to the north of Moloka'i island, in the main Hawaiian archipelago.

Pisces dive	Depth (m)	Habitat	Initial position (dec. degree)		Final position (dec. degree)		No. of transects and minutes surveyed			Total area covered	
			Lat (N)	Long (W)	Lat (N)	Long (W)	N	Min.	Tot min.	m ²	ha
P4159	1000	Pelekunu Canyon (canyon West)	21.25845833	156.8842617	21.25174833	156.8884033	3	16+18+16	50	9259.5	0.93
P5661	650	Pelekunu Canyon (canyon West)	21.21772833	156.8972217	21.21407333	156.8938233	4	13+13+25+27	78	14,444.82	1.44
P5662	350	Pelekunu Canyon (canyon West)	21.196825	156.887835	21.18726	156.8878967	3	16+18+18	52	9629.88	1.22
P5663	1000	Slope control (West)	21.28998833	157.0391567	21.28892	157.04082	3	21+17+17	55	10,185.45	1.33
P5664	650	Slope control (West)	21.25854667	157.040775	21.25457667	157.0416683	3	15+16+18	49	9074.31	0.91
P5665	350	Slope control (West)	21.23783833	157.0442333	21.23399333	157.0448167	4	18+17+18+14	67	12,407.73	1.24
P5666	1000	Kawainui Canyon (canyon East)	21.257745	156.7823633	21.24855167	156.78978	4	22+15+17+17	71	13,148.49	1.31
P5667	650	Kawainui Canyon (canyon East)	21.23094833	156.7925583	21.21801833	156.7954317	5	10+16+18+16+10	70	12,963.3	1.29
P5668	350	Kawainui Canyon (canyon East)	21.210035	156.7928783	21.19857	156.7871667	4	17+13+21+19	70	12,963.3	1.29
P5669	350	Slope control (East)	21.21855	156.8043617	21.21703667	156.7975183	4	17+15+15+21	68	12,592.92	1.25
P5670	650	Slope control (East)	21.24754833	156.8016033	21.24682333	156.7914983	4	15+16+14+23	68	12,592.92	1.25
P5671	1000	Slope control (East)	21.27763667	156.793635	21.27062833	156.7904967	4	17+18+17+14	66	12,222.54	1.22

estimators (Chao 1 and Chao 2) to estimate total species richness within canyon and slope depth strata (Colwell and Coddington, 1994).

Bottom habitat characteristics were also determined for each transect based on the video footage. Substrate type (unrippled mud, unrippled sand, sand/mud with ripples, sand/mud with boulders, rock outcrops, rock walls) and seabed inclination (gentle, moderate or steep slope, *sensu* Greene et al., 1999) were visually assessed, and % areas of each substrate and inclination type within each transect were calculated using Image J[®] software. The total number of bottom habitats (substrate types and bottom inclination) along each transect was also determined from this assessment.

2.3. Water mass variables, estimated vertical carbon flux and organic detritus input

Temperatures measured in situ during submersible video transects were well correlated ($R^2=0.947$; $p=0.002$) with yearly averages obtained from the 23-year long record from the Hawaiian Ocean Time-series (HOT) station ALOHA, ~130 km north of Moloka'i (Fig. 1). Therefore, to estimate annual means and standard deviations for in situ temperature within our depth strata, we used HOT data for the year 2006 (HOT cruises #177–188), when our cruise took place (<http://hahana.soest.hawaii.edu/hot/hot-dogs/interface.html>; Fujieki, 2007). This allowed evaluation of differences in water mass climatology between depth strata. The dissolved oxygen values obtained with the Pisces submersibles were not usable due to probe malfunction (J. Smith, HURL, personal communication) so we also used dissolved oxygen data from station ALOHA, averaged over the same period. Note that this approach assumes low spatial (horizontal) variability in these variables across the study area (spanning ~35 linear kilometers). Oxygen profiles at KAHE Station (Fig. 1) on the south side of Oahu (measured as part of the HOT program) show patterns very similar to Station ALOHA, with similar oxygen concentrations and an OMZ at ~650–700 m. This indicates that the OMZ is broadly distributed around the main Hawaiian Islands.

Regional sinking flux of particular organic carbon (POC) flux within depth strata was estimated using the 2006-average sediment trap (at 150 m) data record from station ALOHA (Fujieki, 2007). An export-flux power function, based on results from the VERTIGO experiment (Buesseler et al., 2007), was applied to the HOT data to estimate regional POC flux at the depths of video transects. The average depth along each transect was used in the

equation: $F/F_{150}=(z/150)^{-b}$, where F =carbon flux at transect depth; F_{150} =carbon flux into the sediment trap located at 150 m depth; $-b$ =the exponent derived from replicate deployments of neutrally buoyant sediment traps (Buesseler et al., 2007). This approach estimated POC flux to the seafloor at particular depths across the region, evaluating the background POC flux regime in which the canyons are imbedded.

Percent occurrence of terrestrial plant and macroalgae detritus on the seafloor was evaluated by means of image analysis of video frame grabs using a modification of the methods of Vetter and Dayton (1999). Briefly, a single frame grab was gridded with squares 44.72 pixels on a side (each 2000 pixels in area), in which only the central 99 squares were used for the analysis. This step eliminated the least illuminated edges of video frame grabs. Percent detritus occurrence was then measured by counting the number of squares in which plant detritus (leaves, trunks, seeds, etc.) occurred and dividing it by 99 (the total number of squares assessed). It is important to note that while this grid approach samples greater seafloor area in the background than the foreground of each frame, this bias was internally consistent across transects, allowing between-transect comparisons within this study. Biases could also result from differences in within-square patchiness between depth strata and sites. However, differences in detritus occurrence, especially between canyons and slopes, were so large that any effects of such bias were very small.

2.4. Data analysis and statistics

The structure of demersal fish assemblages was investigated using the multivariate statistical analysis software package PRIMER v.6 with the PERMANOVA+ add on (Clarke and Gorley, 2006; Anderson et al., 2008). Distance-based PERMutational Multivariate ANalysis Of VAriance (PERMANOVA, McArdle and Anderson, 2001) was employed to test for significant differences in fish assemblage structure (hypothesis 1) as a function of the following factors: (1) *habitat* (canyons × slopes), (2) *site* (east × west Moloka'i) and (3) *depth* (shallow, intermediate and deep strata) in a three-way crossed design with fixed levels for each factor. This analysis was based on a resemblance matrix using the Bray–Curtis similarity index after square-root transformation of the abundance data. This matrix consisted of individual fish species abundances from replicate transects normalized by sample effort (number of transect minutes). The transformation procedure allowed for all species to contribute to the similarity matrix while still giving the most common species greater weight (Warwick, 1993). A non-metric multi-dimensional scaling (MDS)

ordination technique, based on the same similarity resemblance matrix, was used to visualize the faunal patterns and to evaluate the coherence with the results provided by PERMANOVA. A SIMilarity PERcentage analysis (SIMPER) was subsequently employed to reveal which species contributed the most to the similarity/dissimilarity within/between assemblages identified by the PERMANOVA analysis to be significantly different. Characterizing and discriminating species were ranked by their average contribution (%) to the within- and between-assemblage similarity and dissimilarity and the ratio of the similarity/dissimilarity and standard deviation (SD), respectively. Species are considered a good characterizing/discriminating species if the ratio of the mean to the standard deviation of the contribution of each species to the overall similarity/dissimilarity between assemblages is ≥ 1.3 (Clarke and Warwick, 2001).

In order to investigate the influence of the measured and modeled environmental variables (depth, substrate type, seabed inclination, dissolved oxygen, temperature, POC flux, organic detritus occurrence, number of different bottom habitats) on fish assemblage structure (hypothesis 1), a distance-based linear model (DISTLM) multiple regression was employed (McArdle and Anderson, 2001; Anderson et al., 2008). We used the BEST selection procedure to arrive at the best model because this procedure examines the values of selection criteria for all possible combinations of predictor variables (Clarke and Gorley, 2006; Anderson et al., 2008). The models were run using the AIC_c (Akaike's Information Criterion corrected) selection criterion. The AIC_c was devised to handle situations where the number of samples (N) is small relative to the number (ν) of predictor variables ($N/\nu < 40$), which applies to our data set ($N=45$, $\nu=14$, $N/\nu=3.21$) (Anderson et al., 2008 and references therein). The resemblance matrix used in DISTLM analyses was based on the Bray–Curtis similarity of square-root transformed abundance data.

Before the DISTLM models were run, the existence of highly correlated variables and any need for data transformation was assessed using a draftsman plot. Depth, as expected, was highly negatively correlated with POC flux ($r = -0.93$) since this variable uses depth in its exponential function and with temperature ($r = -0.98$). The latter was highly correlated with oxygen concentration ($r = 0.94$) and POC flux ($r = 0.99$). As a result, depth and temperature were not included as variables in the analysis. The seabed inclination variable % steep slope and % detritus occurrence required $\log(1+\nu)$ transformation prior to the multiple regression analysis because they had a high degree of skewness (Clarke and Gorley, 2006). Normalization of variables prior to the analysis was automatically performed within the DISTLM routine (Anderson et al., 2008).

A distance-based redundancy analysis (dbRDA) was used to visualize the DISTLM results. This analysis consisted of a constrained principal coordinate ordination analysis (PCoA, Gower, 1966) of the fish assemblage and species richness data, using the Bray–Curtis similarity and Euclidean distance resemblance matrices, respectively, where the projected axes are directly and linearly related to the significant fitted predictor variables (Legendre and Anderson, 1999). The dbRDA analysis has been presented as an advantageous method appropriate for use in ecology with two main strengths: (1) it can be based on any distance measure (including the semi-metric Bray–Curtis measure), and (2) it can provide a multivariate partitioning to test any individual term in a multifactorial ANOVA experimental design (McArdle and Anderson, 2001).

Three-way crossed univariate PERMANOVA tests were performed to verify differences on percent detritus occurrence, normalized fish abundance, species density, ES(5) and ES(10) between groups of samples (transects) from canyon and slope

habitats, depth strata and sites (hypotheses 2, 3 and 4). For the detritus cover and normalized abundance tests used the square-root transformed data to generate the resemblance matrix using Bray–Curtis dissimilarity. All the remaining tests also used square-root transformed data however employing Euclidian-distance as resemblance measure (Anderson et al., 2008). Since Chao 1 and Chao 2 species estimators are obtained by pooling the transect replicates, not enough terms in each of the three pre-defined factors were available to perform the PERMANOVA test. Nevertheless we evaluated the confidence intervals generated in the calculation of those estimates (Chao, 1987; Cowell, 2000) to verify statistical significance (Cowell, 2000; Magurran, 2004).

General linear models (GLMs) were applied to examine the relationships between fish abundance and percent detritus occurrence and depth (hypotheses 2 and 3) and also between species density, rarefaction diversity, species richness estimates and the total number of habitats present in each transect (measure of habitat heterogeneity) (hypothesis 4).

3. Results

3.1. Environmental setting

Fourteen environmental variables relating to sediment type, bottom inclination, water-mass characteristics and organic input were estimated or measured for each transect (Supplementary Table). Dive localities generally differed in landscape characteristics, as evidenced by between-site differences in the proportions of substrate type and inclination (Fig. 2). While both slope environments are characterized almost entirely by flat bottoms covered by sand or mud, the canyons have a variety of bottom types, including flat, medium and steep inclination with boulders, rock outcrops and rock walls. Ripple marks were evident in 50% and 80% of the total area in Pelekunu Canyon in intermediate and shallow strata, respectively, indicating strong bottom currents. In Kawaiui Canyon, ripple marks are even more widespread, occurring on 87% and 96% of the seafloor in intermediate and shallow strata, respectively. Ripples also occurred over 21% of the canyon area at 1000 m, indicating that bottom currents still affect the canyon habitat at the greatest depths studied (Fig. 2).

A number of environmental variables, including temperature, dissolved oxygen, organic detritus occurrence and estimated POC flux varied with depth (Fig. 3). The shallowest transects (314–464 m) fall within the thermocline, the depth zone with the highest variability in temperature, dissolved oxygen and POC flux values. Temperature within this 314–464 m depth stratum ranges from 12 to 7.8 °C, dissolved oxygen ranges from 4.48 to 2.85 ml l⁻¹ and POC flux ranges from 3.57 to 2.19 g C m⁻² yr⁻¹. At the intermediate depths (571–719 m) and deepest depths (946–1100 m), these environmental variables remained within much narrower ranges (Fig. 3, Supplementary Table 1). The percent occurrence of organic detritus (mostly decomposing vascular plant material such as leaves, branches and accumulations of kukui nuts (*Aleurites moluccana*)) varied significantly with depth ($p=0.0001$), but no differences were observed between the West and East sites (Table 2). The influence of habitat was not included in the statistical test since organic detritus was completely absent at all depths at slope sites (Fig. 3, Supplementary Table 1).

3.2. Fish species composition

A total of 824 fishes in 30 families, totaling 55 putative species, were observed during ~13.3 h of video transects (Table 3). Another 17 species were also observed from the submersible during other activities (baited stations or scavenger trap

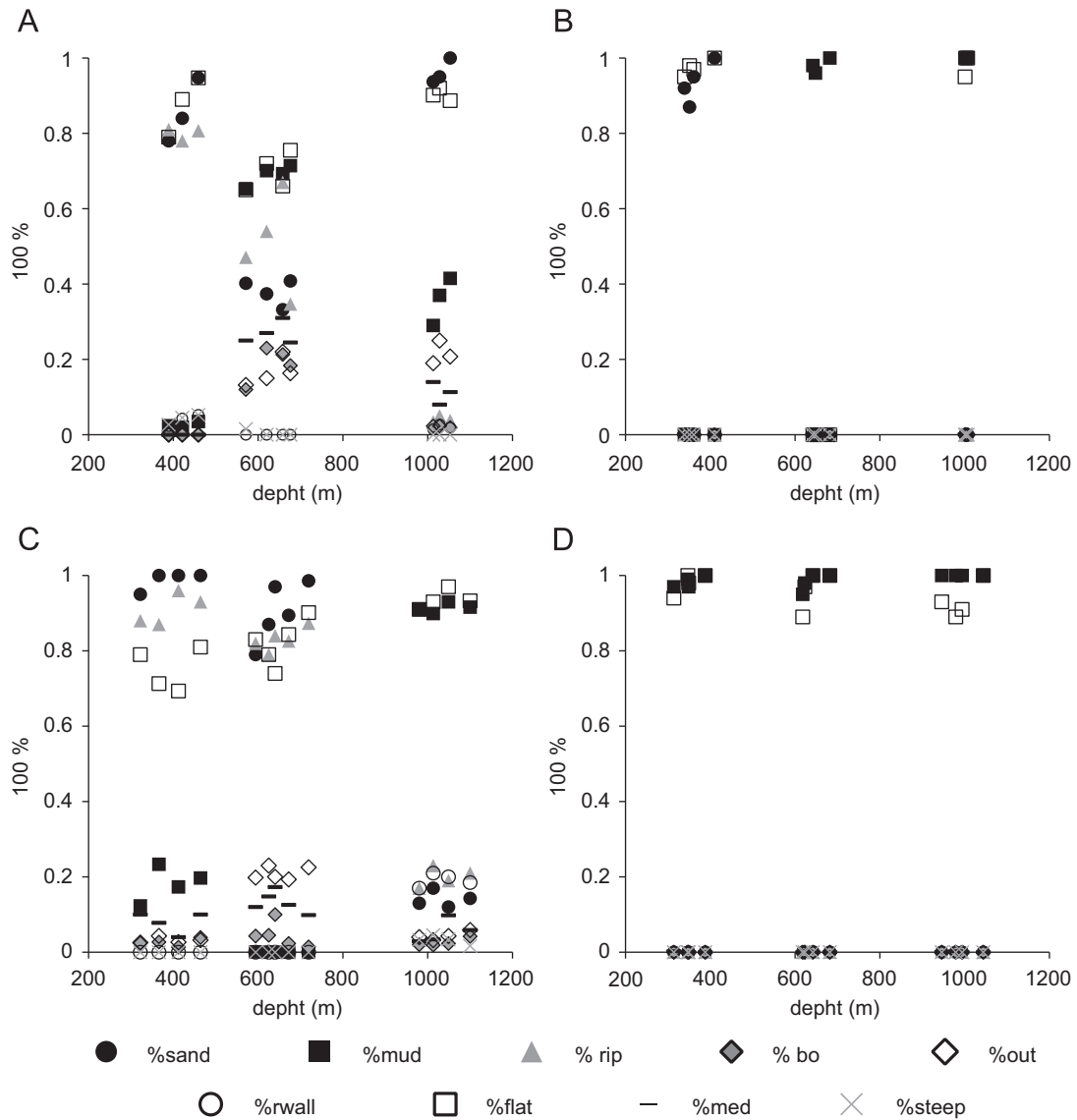


Fig. 2. Proportion of each substrate type and inclination. (A) Pelekunu Canyon. (B) Pelekunu Slope. (C) Kawainui Canyon. (D) Kawainui Slope. Symbols are mean values from replicate transects (see Table 1); % rip=ripple marks; % bo=boulders; % out=outcrops; % rwall=rocky walls; % flat=flat slope; % steep=steep slope; % med=medium slope.

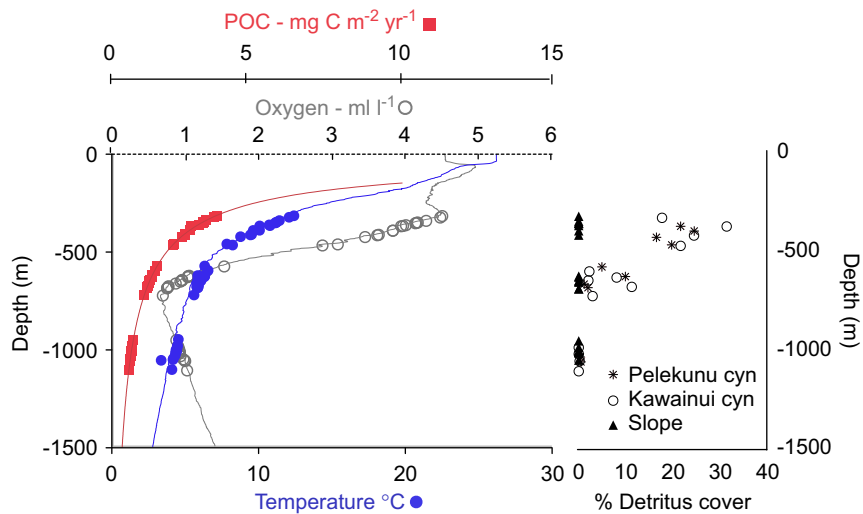


Fig. 3. Water mass properties (temperature, dissolved oxygen, POC flux) (left), and percent seafloor occurrence of organic detritus (right). Symbols represent values at mean video transect depths (see text for data sources). Integrated lines are 2006 mean values from station ALOHA (see Fig. 1). Refer to Table 2 for number of frames analyzed and standard deviation of % of detritus occurrence.

Table 2
Results from the univariate PERMANOVA analysis for differences in % detritus occurrence.

	Source	df	SS	MS	Pseudo-F	p (perm)	Unique perm
Detritus	si	1	3.8369	3.8369	0.82925	0.3855	9834
	de	2	1098.4	549.18	118.69	0.0001	9952
	sixde	2	10.294	5.1468	1.1123	0.3644	9939
	Res	33	152.69	4.6269			
	Total	44	3081.5				

PERMANOVA 3-factor model. Bold values indicate significant differences at $p < 0.05$. si, site; de, depth; sixde, represents interaction terms; df, degrees of freedom; SS, sum of squares; MS, mean squares; perm, permutations. Data was fourth-root transformed and resemblance calculated using Euclidian Distance.

deployments), and therefore were not part of our analyses. Among those were species that occurred primarily in canyons (e.g., *Hexanchus griseus*, *Etelis carbunculus*, *Laemonema* sp., *Luciobrotula* sp., *Dendrochirus barbieri*), primarily on slopes (e.g., *Coelorinchus doryssus*) or in both habitats (e.g., *Setarches* sp.). In the case of the six-gill shark *Hexanchus griseus*, it is easy to understand its absence from video surveys since this species is less likely to be disturbed by a stationary submersible during a bait station than by a moving submersible running a transect. For the species that were seen only in canyon habitats, all but *H. griseus* were found associated with hard substrates close to crevices and boulders. This agrees with the literature that describes their main habitat of occurrence (Chave and Mundy, 1994; Mundy, 2005) and indicates that excluding them from our analyses did not impair a good species–habitat characterization as far as separating canyon from non-canyon fauna.

Macrouridae was the most diverse family with 13 species, followed by Congridae (5 spp.), Ophidiidae (4 spp.) and Halosauridae (3 spp.). The most abundant species over the entire study area were *Chlororhynchus* sp. ($n=312$), Macrourid sp. 1 (81), Congrid sp. 1 (57), Black halosaur (48), *Aldrovandia phalacra* (39), Halosaurid (33), *Synagrops* sp. (25), *Squalus mitsukuri* (20), *Chironema* sp. 1 (19) and *Coelorinchus doryssus* (19) (Table 3).

3.3. Assemblage structure

The PERMANOVA results indicate significant differences in fish assemblage between habitat (canyon \times slopes) ($p-F=6.1$; $p=0.0001$), sites (east \times west) ($p-F=4.1$, $p=0.0001$) and depth (three strata) ($p-F=19.1$, $P=0.001$) with the last factor being the most influential (Table 4). However, significant interactions among the factors called for pair-wise comparisons between habitats within sites and depths. We found that at the west sites, significant differences in assemblage structure between canyons and slopes are restricted to the shallowest stratum (~ 314 – 459 m) ($t=1.734$, $p=0.029$). At the east sites, however, canyon and slope assemblage structure differed significantly in the shallowest ($t=3.801$, $p=0.027$) the deepest ($t=2.597$, $p=0.029$) strata (Table 4). This pattern of assemblage structure is evident in the MDS output (Fig. 4), which shows transects from both habitats and sites at intermediate depths clustering together, as do transects from both canyon sites for the shallow stratum. Transects from the deep stratum at the east slope site form a distinct cluster, while west slope sites group together with east canyon and slope sites for this depth stratum. Overall, the MDS plot indicates a higher separation (higher degree of dissimilarity) between the demersal fish fauna from the shallowest stratum (314–459 m) (right side of plot) and the other two deeper strata (571–719 m and 946–1100 m) (left side of plot).

The results of the SIMPER analysis (Supplementary Table 2) revealed the most important species contributing to the similarity within groups (characterizing species) and dissimilarity between groups (discriminating species) of transects that were verified to be significantly different by the PERMANOVA analysis. The species that better discriminated between the shallow depth stratum of Pelekunu Canyon and slopes were *Chlorophthalmus* sp., *Seriola dumerilii*, *Polymixia* sp. and *Epigonus* sp., which occurred at higher abundance or exclusively in the canyon; *Chascanopsetta* sp. and *Poecilopsetta Hawai'iensis*, which occurred exclusively on the slope. At the east site, also in the shallow stratum, the best discriminating species between canyon and slopes were *Seriola dumerilii*, which occurred exclusively in the canyon, and *Squalus mitsukuri*, Unidentified flatfish, *Epigonus* sp., *Glossanodon* sp. and *Chironema chryseres*, which occurred only on the slope (Supplementary Table 2). Interestingly, *Chlorophthalmus* sp., the single most abundant species in the shallow depth stratum, was more abundant in the canyon and the west site but much more abundant on the slope in the east (Supplementary Table 2). Finally, discriminating species that contributed the most to the average dissimilarity between canyon and slope at the deepest depth stratum were Halosaurid, Macrourid sp. 1, *Sphagemacurus* sp., Congrid sp. 1, *Gadomus melanopterus* and *Synaphobranchus affinis*, which were restricted or more abundant in the canyons and Congrid with white fins, which occurred only on the slope.

3.4. Environmental predictors of fish assemblage structure

The multivariate multiple linear regression (DISTLM) model using the AIC_c criterion explained up to 50.4% of the variation in the demersal fish assemblages off Moloka'i, and attributed the variation to 6 significant variables (Table 5). Dissolved oxygen contributed the highest percentage (25.71%), followed by POC flux (9.26%), percent detritus occurrence (6.21%), % sand (4.31%), % rock outcrops (2.87%) and % rock walls (2.06%) (Table 5).

The ten best models were all significant as AIC_c values ranged apart less than one unit from each other (Anderson et al., 2008; Table 6). The combinations of variables (between 5 and 7 variables) included in each model and explaining the largest variability in the multivariate data cloud almost always contained dissolved oxygen concentration, POC flux, detritus input, % sand, % ripple marks, % boulders, % of rock outcrops, % rocky walls, % medium slope (Table 6).

The dbrDA plot emphasized the vectors that correspond to the variables selected in the best models (i.e., the lowest AIC_c values) (Fig. 5). The length and direction of the vectors indicate strength and direction of the relationship. Relatively good agreement is evident between the constrained (dbrDA) and the unconstrained ordination (MDS) methods (compare Figs. 4 and 5), indicating a good fit for the DISTLM models.

A first examination of the dbrDA plot shows that essentially three main gradients can be modeled by the selected environmental variables (Fig. 5). The first largely distinguishes among samples from both canyons and slopes in the shallow stratum where oxygen concentration is high and samples from intermediate and deep strata where oxygen concentrations are lower. The second gradient is related to modeled POC flux to the seafloor; samples from canyons and slopes in the intermediate stratum where POC shows middle values and some samples from the shallow stratum (mainly from canyon sites) where POC is slightly higher are distinguished from the remainder of samples. The third gradient correlated with percent occurrence of detrital organic matter, which helps to separate some shallower, mainly canyon sites, from deeper canyon and slope sites (Fig. 5). The variables % sand, % rock outcrops and % of rock walls also contribute a small amount to separate canyon from slope transects, particularly for the intermediate and deepest depth strata.

Table 3
Abundance of the 55 putative fish species identified from video transects taken to the north of Moloka'i Island, in the main Hawai'ian archipelago.

TAXA			Pelekunu Cyn			Slope west			Kawainui Cyn			Slope east			Tot
Family	Putative species		s	i	d	s	i	d	s	i	d	s	i	d	
1	Scyliorhinidae	<i>Apristurus spongiceps</i>	0	0	0	0	0	0	0	0	1	0	0	0	1
2	Squalidae	<i>Squalus mitsukuri</i>	0	0	0	1	0	0	0	0	0	3	0	0	4
3	Echinorhinidae	<i>Echinorhinus cookei</i>	1	0	0	0	0	0	0	0	0	0	0	0	1
4	Etmopteridae	<i>Centroscyllium</i> sp.	0	0	2	0	0	0	0	1	0	0	0	0	3
5		<i>Etmopterus</i> sp.	0	0	0	0	0	0	0	1	0	0	0	0	1
6	Plesiobatidae	<i>Plesiobatis daviesi</i>	0	2	0	0	0	0	0	2	0	0	1	0	5
7	Halosauridae	<i>Aldrovandia phalacra</i>	0	0	10	0	0	2	0	0	22	0	0	4	38
8		Black halosaur	0	0	13	0	0	13	0	0	16	0	0	6	48
9		Halosaurid	0	0	2	0	0	2	0	0	28	0	0	1	33
10	Synphobranchidae	Synphobranchid	0	2	1	0	0	1	0	1	0	0	0	0	5
11		<i>Synphobranchus affinis</i>	0	2	0	0	0	0	0	2	4	0	0	1	9
12	Congridae	Congrid sp. 1	1	12	2	0	5	0	2	18	5	0	12	0	57
13		Congrid w white fins	0	0	0	0	0	0	0	0	0	0	3	0	3
14		<i>Bathycongrus guttulatus</i>	0	0	0	0	3	0	0	0	0	0	0	0	3
15		<i>Uroconger lepturus</i>	0	0	0	0	0	2	0	0	0	0	0	0	2
16		<i>Bathyroconger vicinus?</i>	0	0	0	0	0	0	0	2	1	0	1	0	4
17	Nettastomatidae	<i>Nettastoma</i> sp.	0	0	2	0	0	0	0	0	1	0	0	0	3
18	Argentinidae	<i>Glossanodon</i> sp.	0	0	0	0	0	0	0	0	0	7	0	0	7
19		<i>Ijimaia plicatellus</i>	0	1	0	0	0	0	0	1	0	0	0	0	2
20	Alepocephalidae	Alepocephalid?	0	0	0	0	1	0	0	0	0	0	0	0	1
21	Chlorophthalmidae	<i>Chlorophthalmus</i> sp.	32	0	0	4	0	0	42	0	0	234	0	0	312
22	Ipnopidae	<i>Bathytrophops marionae</i>	0	0	1	0	0	0	0	0	0	0	0	0	1
23	Polymixiidae	<i>Polymixia</i> sp.	5	0	0	1	0	0	0	0	0	0	0	0	6
24	Macrouridae	<i>Coelorinchus</i> sp.	0	0	0	0	2	0	0	0	0	0	0	0	2
25		<i>Coelorinchus doryssus</i>	0	0	0	0	0	1	0	5	5	0	2	4	17
26		<i>Coryphaenoides longicirrus</i>	0	0	0	0	0	0	0	0	1	0	0	0	1
27		<i>Gadomus melanopterus</i>	0	0	1	0	1	1	0	0	5	0	0	0	8
28		<i>Sphagmacrurus</i> sp.	0	0	0	0	0	0	0	4	4	0	3	0	11
29		Macrourid sp. 1	0	21	2	1	15	5	0	12	15	0	9	0	80
30		Macrourid sp. 2	0	1	0	0	0	0	0	0	0	0	0	0	1
31		<i>Hymenocephalus</i> sp.	0	1	0	0	0	1	0	3	0	0	0	0	5
32		<i>Ventrifossa</i> sp.	0	0	0	0	4	0	0	5	0	0	7	0	16
33		<i>Nezumia</i> sp. 1	0	0	0	0	0	1	0	5	0	0	2	0	8
34		<i>Nezumia burragei</i>	0	0	0	0	1	0	0	0	0	0	0	0	1
35		Bathygadid	0	0	0	0	0	0	0	0	0	0	0	1	1
36		<i>Bathygadus</i> sp.	0	0	0	0	0	0	0	3	0	1	2	0	6
37	Ophidiidae	Ophidiid	0	0	2	0	0	0	0	0	0	0	0	0	2
38		<i>Lamprogrammus brunswegii</i>	0	0	1	0	0	0	0	0	1	0	0	0	2
39	Lophiidae	<i>Sladenia remiger</i>	0	0	0	0	0	1	0	0	1	0	0	0	2
40	Chaunacidae	<i>Chaunax umbrinus</i>	1	0	0	0	0	0	0	0	0	0	0	0	1
41	Berycidae	<i>Beryx decadactylus</i>	0	0	0	0	0	0	2	1	0	0	0	0	3
42	Peristediidae	<i>Satyrichthys</i> sp.	1	0	0	2	0	0	2	0	0	10	1	0	16
43		<i>Satyrichthys hians</i>	0	0	0	0	0	0	0	1	0	0	0	0	1
44	Acropomatidae	<i>Synagrops</i> sp.	0	0	0	0	0	0	3	1	0	20	0	0	24
45	Epigonidae	<i>Epigonus</i> sp.	2	0	0	0	0	0	0	0	0	0	0	0	2
46	Carangidae	<i>Seriola dumerilii</i>	1	0	0	0	0	0	8	0	0	0	0	0	9
47	Percophidae	<i>Chironema</i> sp.	0	0	0	1	0	0	2	0	0	16	0	0	19
48		<i>Chironema chryseres</i>	0	0	0	0	0	0	0	0	0	2	0	0	2
49	Gempylidae	<i>Gempylidae</i> sp.	0	0	0	0	0	0	1	0	0	0	0	0	1
50		<i>Rexea nakamurai</i>	0	0	0	0	0	0	2	0	0	0	0	0	2
51	Bothidae	<i>Chascanopsetta</i> sp.	0	0	0	2	0	0	2	0	0	0	0	0	4
52	Pleuronectidae	<i>Poecilopsetta hawai'iensis</i>	0	0	0	0	0	0	0	0	0	1	0	0	1
53	Triacanthodidae	<i>Hollardia goslinei</i>	1	0	0	0	0	0	0	0	0	0	0	0	1
54	??	Eel	0	2	7	0	1	1	2	0	1	0	3	0	17
55	??	Unid. Flatfish	0	0	0	1	0	0	0	0	0	8	0	0	9
Total			57	52	53	18	39	36	74	74	119	352	60	22	824
Total no. per min. ^a			0.81	0.67	0.80	0.25	0.79	0.53	1.04	1.06	1.7	5.17	0.88	0.33	
Total no. per 100 m ² (0.01 ha) ^b			44.1	36.1	43.4	13.5	42.9	29.1	56.5	57.4	92.2	281.6	48	18.0	

s—shallow (314–459 m); i, intermediate (571–719 m); d, deep (946–1100 m); tot, total.

^a Abundance normalized by the total number of video transect minutes (refer to Table 1).

^b Abundance normalized by the total area surveyed in each depth-habitat (refer to Table 1).

3.5. Abundance patterns

Fish abundance was statistically significantly different between canyons and slopes ($p=0.0425$; Table 7). Further pairwise comparisons reveals that this difference is restricted to the deepest stratum (946–1100 m), where canyon abundance is greater (Supplementary Table 3). After removing two data

outliers (representing two shallower transects performed at slope east where a single species, *Chlorophthalmus* sp., was present at extraordinary abundances compared to the whole study; Fig. 6A), overall test significance increases ($p=0.033$) and average abundances in the canyon also become comparatively higher, and statistically significant ($p=0.046$) than on the slopes for the shallowest depth stratum (Supplementary Table 3). No significant

Table 4
Output of the PERMANOVA analysis based on the resemblance matrix of fish abundance data from video transects taken to the north of Moloka'i island, in the main Hawaiian archipelago. Pair-wise tests of factors habitat (canyon × slopes), sites (east × west) and depth (shallow, intermediate, deep) are also shown.

Source	df	SS	MS	Pseudo-F	p (perm)	Unique perm	ECV
Main test							
Habitat	1	9501.9	9501.9	6.0916	0.0001	9914	362.17
Site	1	6392.5	6392.5	4.0982	0.0001	9939	220.38
Depth	2	59567	29,784	19.094	0.0001	9924	1928.1
Habitat × site	1	4576.4	4576.4	2.9339	0.0004	9909	275.13
Habitat × depth	2	12,740	6370	4.0838	0.0001	9891	657.22
Site × depth	2	10,087	5043.4	3.2333	0.0001	9885	475.97
Habitat × site × depth	2	6265	3132.5	2.0082	0.0023	9878	429.76
Residual	33	51,474	1559.8				1559.8
Total	44	162,240					
Source	df			t-stat	p (perm)	Unique perm	
Pair wise tests							
Habitat × site							
Within level 'west'	14			1.6932	0.0023	9931	
Within level 'east'	19			2.6399	0.0001	9938	
Habitat × site × depth							
Within 'west' and 's'	5			1.7347	0.0291	25	
Within 'west' and 'i'	5			1.0987	0.3094	35	
Within 'west' and 'd'	4			1.6905	0.1006	10	
Within 'east' and 's'	6			3.8015	0.0277	35	
Within 'east' and 'm'	7			1.0954	0.2666	126	
Within 'east' and 'd'	6			2.5976	0.0294	35	

PERMANOVA 3-factor model. Bold values indicate significant differences at $p < 0.05$. s, shallow (314–459 m); i, intermediate (571–719 m); d, deep (946–1100 m); df, degrees of freedom; SS, sum of squares; MS, mean squares; perm, permutations; ECV, estimated component of the variation.

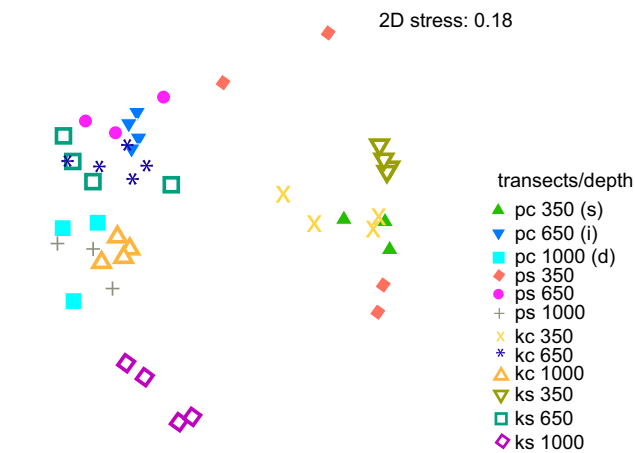


Fig. 4. Multidimensional scaling plot of Bray-Curtis similarity matrix based on square root-transformed abundance data of the 55 putative fish species identified from video transects taken to the north of Moloka'i island, in the main Hawaiian archipelago. Each point represents replicate video transects (pc, Pelekunu Canyon; ps, Pelekunu Slope; kc, Kawaiinui Canyon; ks, Kawaiinui Slope; s, shallow (350 m); i, intermediate (650 m); d, deep (1000 m)—depth strata).

differences in fish abundances were observed between the two sites sampled (Table 7). No significant correlations were observed between the percent occurrence of seafloor organic detritus and fish abundance (Fig. 6B).

While canyon fish abundances increased slightly with depth ($R^2=0.23$, $p=0.019$), no significant trend was observed for slopes ($R^2=0.14$, $p=0.07$), even with the presence of two outliers (Fig. 6). In the deepest depth stratum, fish abundances reach their highest values in canyons but decline to their lowest values on the slopes. The transition zone at the intermediate depth stratum (571–719 m) overlaps the core of the oxygen minimum zone (Fig. 6A).

Table 5

Results of the multivariate multiple regression (DISTLM), using the BEST selection procedure, of fish species abundance and environmental data obtained for study locations to the north of Moloka'i island, in the main Hawaiian archipelago. Percentage of variation explained by individual axes.

Criterion	% Explained variation (fitted model)		% Explained variation (total)	
	Indiv.	Cum.	Indiv.	Cum.
AICc				
Axis				
Dissolved O ₂	50.98	50.98	25.71	25.71
POC flux	18.36	69.34	9.26	34.96
% Detritus	12.32	81.66	6.21	41.18
% Sand	8.55	90.21	4.31	45.49
% Outcrop	5.7	95.91	2.87	48.36
% Rock wall	4.09	100	2.06	50.43

Indiv., individual; Cum., cumulative.

3.6. Species density, diversity and estimated species richness × habitat heterogeneity

Species density is statistically different between canyons and slopes ($p=0.0015$; Table 7), being higher on both canyons only at the deepest sites (940–1100 m) (see Supplementary Table 3 for pairwise tests; Fig. 7A). Overall site effects are highly statistically significant ($p=0.0001$) with greater species density occurring on east sites.

Because fish abundances were very low on some transects (min=3; max=104; mean=20), patterns in species density were largely driven by patterns of abundance. We thus used rarefaction diversity to remove biases from large differences in sample size. At ES₅ (i.e., expected species per 5 individuals), species diversity showed no significant differences neither between canyon and slope habitats nor between sites east and west (Table 7; Fig. 7B). However ES₅ values varied significantly with depth ($p=0.0014$), with differences found between all depth strata but between the

intermediate and deep-strata (Supplementary Table 3, Fig. 7B). It is important to note that 7 transects (all but one from slope sites) had fewer than 5 individuals and could not be included in the ES₅ analysis. At ES₁₀, 14 transects could not be included (again all but one from slope sites), however differences in species diversity between canyon and slope become more evident (Fig. 7C). Overall ES₁₀ values do not show statistical differences neither between canyon and slopes nor between east and west sites (Table 7). The higher ES₁₀ in the canyons, although not statistically significant at any depth strata, shows a more realistic estimation of species diversity agreeing with the pattern observed for species density. The complete lack of slope transects at the deepest depth stratum (all with less than 10 individuals per transect), however, precludes a full comparison of those trends employing species density and diversity. These shortcomings and also the fact that ES₅ values were often close to 5 species stressed the relevance of also employing the species estimator indexes, Chao 1 and Chao 2.

Table 6
Overall best solutions of the multivariate multiple regression (DISTLM), using the BEST selection procedure, for fish species abundance and environmental data obtained for study locations to the north of Moloka'i island, in the main Hawai'ian archipelago.

AICc	R ²	RSS	No. vars	Selections (variables)
354.01	0.50425	80,428	6	1,5,6,13–15
354.13	0.53465	75,497	7	1,4–6,13–15
354.16	0.50255	80,704	6	2,5,6,13–15
354.3	0.46877	86,185	5	1,5,13–15
354.33	0.53261	75,828	7	2,4–6,13–15
354.37	0.46796	86,317	5	5,6,13–15
354.4	0.49993	81,129	6	1,4,5,13–15
354.42	0.46736	86,415	5	2,5,13–15
354.43	0.53156	75,998	7	1,5,6,8,13–15
354.46	0.46692	86,485	5	1,6,13–15

Predictor variables (Vars): 1, % sand; 2, % mud; 3, % ripple marks 4, % bolders; 5, % outcrops; 6, % rock walls; 7, % flat slopes; 8, % medium slope; 9, % steep slope; 11, depth range; 13, dissolved oxygen; 14, modeled POC flux; 15, % detritus occurrence.

Bold faces represent values of both AICc and BIC within the range of best acceptable models (Anderson et al., 2008).

The nonparametric species richness estimator Chao 1 predicts a higher number (statistically different based on the calculated confidence intervals) of species for the canyon east site only in the deepest depth stratum (42 species versus 11 species on the slope; Fig. 8A and B), in a trend similar that for species density. Chao 2 predicts higher species richness for canyons at intermediate depths (west: 16 species × 8 species on the slope; east: 41 species × 27 species on the slope), and in the deepest stratum for Kawaiui Canyon (31 species × 11 in the slope (Fig. 8C and D)).

Habitat heterogeneity (measured as the number of different substrate and bottom inclination types observed along each video transect) shows a positive correlation with species density, rarefaction diversity (ES₁₀) and estimated species richness (Fig. 9). The strength of the linear regression model is weak (R²=0.12) for species density, but the relationship is still statistically significant (p=0.015) and clearly driven by differences between homogeneous bottom habitats on slopes and the more heterogeneous habitat structure inside canyons (Fig. 9A). The trends for both rarefaction (R²=0.19) and estimated species richness (Chao 1, R²=0.26; Chao 2, R²=0.23) are stronger, but only the correlations between ES₁₀ (p=0.01) and Chao 2 (p=0.04) were statistically significant. Again, these patterns are clearly driven by higher habitat heterogeneity within canyons (Fig. 9B and C). However, it is important to note that, for rarefaction, the correlation excludes those data points (transects) that had less than 10 individuals (mostly slope transects).

4. Discussion

4.1. General assemblage composition

The bathyal demersal fish assemblage off the north side of Moloka'i is generally consistent both in terms of its geographic and bathymetric distributions, with previous trawl and baited camera studies (Gilbert, 1905, Struhsaker, 1973; Chave and Mundy, 1994; King et al., 2008; Yeh and Drazen, 2009). However, two species were observed outside previously reported depth ranges: *Ijimaia plicatellus* (Ateleopopidae), occurred deeper than its previously reported depth-distribution (265–500 m), at 650 m, while *Sladenia remiger* (Lophiidae) occurred shallower (at 650 m

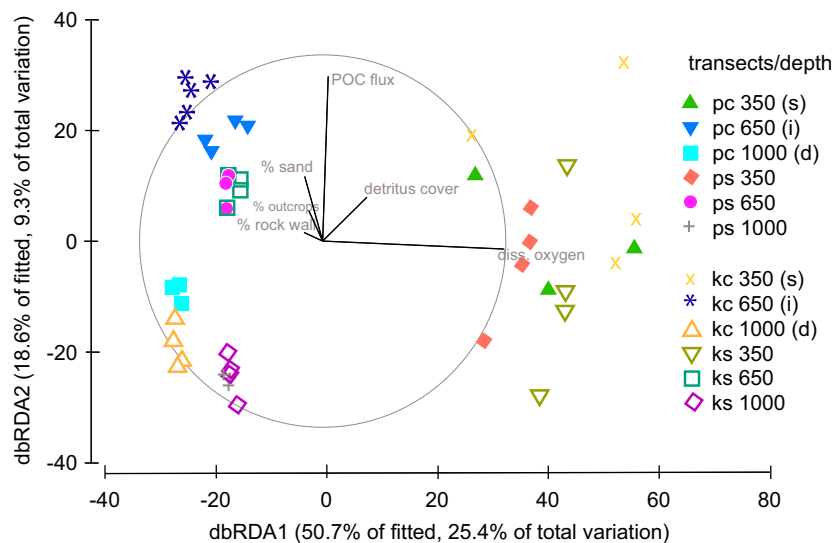


Fig. 5. Results of the distance-based multivariate multiple regression (DISTLM) of fish species abundance overlaid with the partial correlations of the significant environmental variables identified by models using two selection criteria. (A) AICc criterion; B BIC. Color legend represents group of replicate transects within sites (pc, Pelekunu Canyon; ps, Pelekunu Slope; kc, Kawaiui Canyon; ks, Kawaiui Slope; s, shallow (350 m); i, intermediate (650 m); d, deep (1000 m)—depth strata). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 7

Results from the univariate PERMANOVA analysis for differences in normalized fish abundance (N), species density (S) and rarefaction (ES(5), ES(10)).

	Source	df	SS	MS	Pseudo-F	p (perm)	Unique perm	p (perm)*	
N	ha	1	862.01	862.01	3.7871	0.0425	9949	0.0337	9924
	si	1	577.48	577.48	2.537	0.1104	9939	0.2556	9906
	de	2	776.08	388.04	1.7048	0.1841	9951	0.5734	9949
	haxsi	1	1077	1077	4.7316	0.0316	9932	0.0383	9904
	haxde	2	647.31	323.65	1.4219	0.2386	9943	0.493	9942
	sixde	2	363.86	181.93	0.79927	0.4686	9948	0.7354	9949
	haxsixde	2	1626.3	813.16	3.5725	0.0331	9959	0.0104	9950
	Res	33	7511.5	227.62					
	Total	44	13,666						
	S	ha	1	0.0694	0.0694	13.2250	0.0015	9838	
si		1	0.1869	0.1869	35.6270	0.0001	9837		
de		2	0.0508	0.0254	4.8409	0.0153	9952		
haxsi		1	0.0073	0.0073	1.3960	0.2502	9820		
haxde		2	0.1477	0.0738	14.0740	0.0002	9943		
sixde		2	0.0144	0.0072	1.3679	0.2631	9944		
haxsixde		2	0.0727	0.0364	6.9292	0.0020	9967		
Res		33	0.1731	0.0052					
Total		44	0.7718						
ES(5)		ha	1	0.0199	0.0199	0.0979	0.7565	9823	
	si	1	0.3482	0.3482	1.7143	0.1969	9813		
	de	2	3.4221	1.7111	8.4241	0.0014	9952		
	haxsi	1	2.2827	2.2827	11.238	0.0024	9844		
	haxde	2	0.7216	0.3608	1.7763	0.1923	9939		
	sixde	2	2.9768	1.4884	7.3279	0.0029	9936		
	haxsixde	2	1.5019	0.7509	3.6971	0.0368	9949		
	Res	26	5.281	0.2031					
	Total	37	20.009						
	ES(10)	ha	1	0.0149	0.0149	3.7114	0.0721	9831	
si		1	0.0001	0.0001	0.0205	0.8898	9835		
de		2	0.1017	0.0508	12.6630	0.0003	9944		
haxsi		1	0.0049	0.0049	1.2085	0.2904	9831		
haxde**		1	0.0004	0.0004	0.1019	0.7486	9825		
sixde		2	0.0260	0.0130	3.2377	0.0587	9953		
haxsixde**		0	0.0000		No test				
Res		22	0.0883	0.0040					
Total		30	0.3304						

PERMANOVA 3-factor model. Bold values indicate significant differences at $p < 0.05$. ha, habitat; si, site; de, depth; haxsi, haxde, sixde, haxsixde represent interaction terms; df, degrees of freedom; SS, sum of squares; MS, mean squares; perm, permutations.

Data was fourth-root transformed and resemblance calculated using Bray–Curtis (N) and Euclidian-Distance (S, ES(5) and ES(10)). See Supplementary Table 3 for results on posteriori pairwise comparisons.

* p -Value obtained after outliers removed (two shallow-stratum transects in slope East).

** Missing terms.

compared to a previous depth range of 780–1540 m (Mundy, 2005)).

We cannot ignore potential observational limitations due to low abundances but our large sampling effort (~13 h of footage equally distributed among canyon and slope habitats (see Table 1)) makes us confident that the differences in community composition and structure observed are real and reproduce habitat-related structuring parameters and not artifacts, for example, of pseudo-endemism. Vetter et al. (2010) present a list of species (mostly invertebrate megafauna) that occurred exclusively in canyon habitats as well as exclusively in slope habitats. There were many more canyon-restricted species and the authors argued that despite observational limitations, those species may be using canyons preferentially due to higher abundance of prey.

4.2. Assemblage structure: any noticeable canyon effect?

The PERMANOVA test revealed that the greatest significant difference in fish assemblage structure was among depth strata. The highest degree of assemblage dissimilarity occurred between the shallowest (314–459 m) and intermediate and deepest depth strata (571–1100 m) transects, suggesting a transition zone in

faunal composition occurs around 500 m. While depth may be one of the most important correlates of fish assemblages both within canyons and along the open slopes off Moloka'i Island, we have assessed the influence of factors likely to be more directly driving assemblage change by looking at modeled POC flux and dissolved oxygen, both of which are negatively correlated with depth (refer to Section 2.3). This strategy is more sensible because POC flux and dissolved oxygen are more likely to be mechanistically related to faunal change than depth, which is a proxy for other environmental variables including temperature, POC flux, pressure, light, dissolved oxygen, etc. (Carney, 2005; Rex et al., 2006; Rowden et al., 2005; Smith et al., 2008; O'Hara and Tittensor, 2010). Both dissolved oxygen and modeled POC flux were selected in the multivariate multiple regression model (DISTLM) as the most important predictor variables and appear to be important drivers of the patterns of dissimilarities among transects across the examined depth gradient. Above the transition zone identified, the fish assemblages are affected by comparatively wider ranges in temperature (12–7.8 °C) and POC flux (3.6–2.2 g C m⁻² yr⁻¹). Dissolved oxygen concentrations also vary across a wider range above this transition zone (4.48–2.85 ml l⁻¹), but remain above the threshold (~1.4 ml l⁻¹)

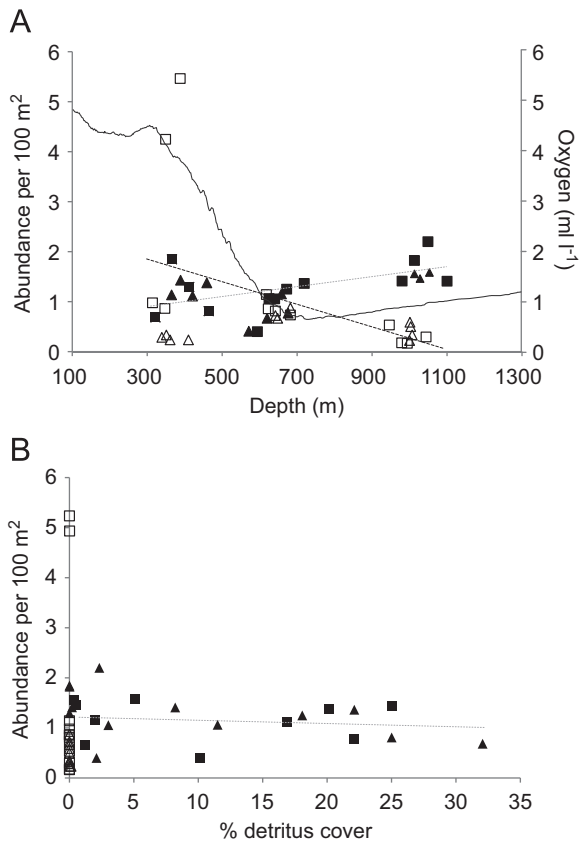


Fig. 6. Fish abundance (#/100 m²) plotted against depth (A), and % detritus cover (B). (canyon, solid symbols; slopes empty symbols; squares, east site; triangles, west site). Linear regressions in A: Pelekunu and Kawainui canyons combined (gray dotted line): $y=0.0009x+0.6352$, $R^2=0.23302$; Pelekunu and Kawainui slopes combined (dashed line): $y=-0.0019x+2.2326$, $R^2=0.14639$. 2006 average of station ALOHA dissolved oxygen concentration (solid gray line) vs. depth plotted in the secondary y-axis. Linear regression in B: overall, $y=-0.0022x+1.1139$, $R^2=0.00038$.

at which oxygen levels are thought to become stressful for coastal fishes (Vaquer-Sunyer and Duarte, 2008; Keller et al., 2010).

Below this transition zone, temperature (6.6–4.1 °C) and POC flux (1.64–0.67 g C m⁻² yr⁻¹) are more homogeneous, but dissolved oxygen falls to the lowest values in the core of the OMZ at 650–1000 m (1.52–0.69 ml l⁻¹) (Fig. 3). Dissimilarities in assemblage structure between 571 and 719 m and 946 and 1100 m transects are much smaller than with the shallowest depths, consistent with a transition into more stable environmental conditions (Carney, 2005; King et al., 2006). This degree of uniformity in assemblage composition below the major faunal compositional shift (between 459 m and 571 m) can largely be explained by the presence of many macrourid, synbranchid and congrid species, which occurred within the two deepest strata (571–719 m, 946–1100 m), but not in the shallowest stratum (314–459 m).

Yeh and Drazen (2009) also reported a faunal shift in scavenger assemblage composition (fish and invertebrates) at depths ranging from 500 to 1000 m in the main and northwest Hawaiian Islands, including diminished abundances of scavengers within the core of the oxygen minimum zone. However, Yeh and Drazen (2009) only studied scavenger communities, which had little species overlap (6 species) with fish assemblages (55 species) observed in our video transects. However, agreement among Yeh and Drazen (2009), Struhsaker (1973) and the present study in the depths of a major shift in faunal composition, despite differences in sampling methods, provides robust evidence that

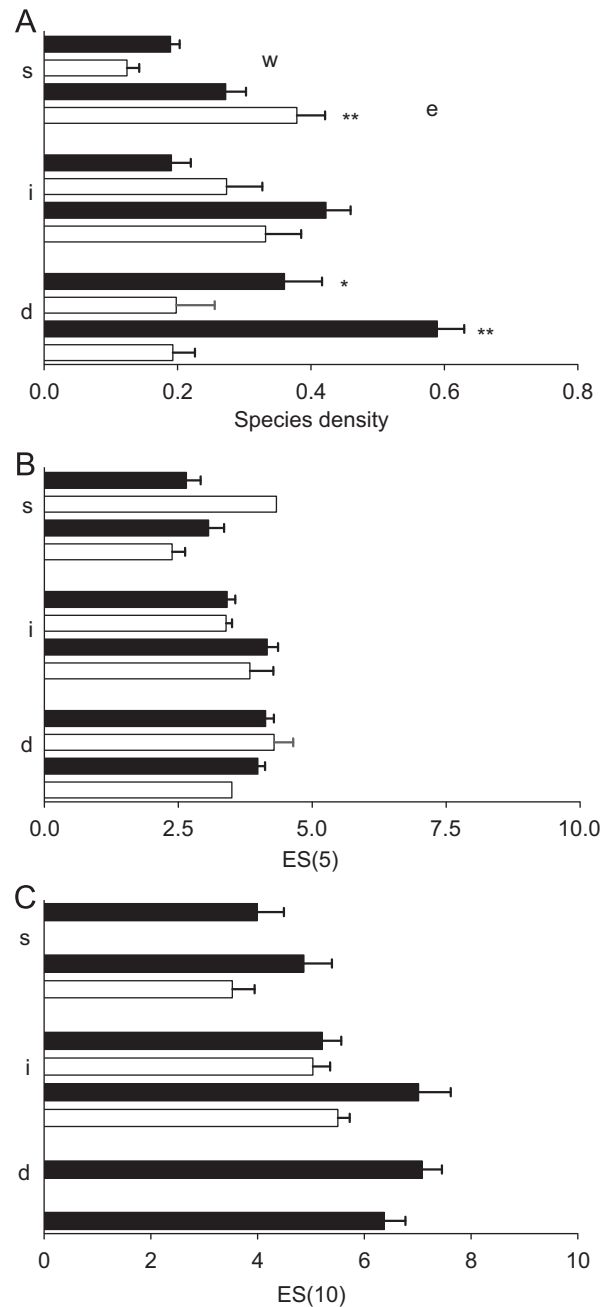


Fig. 7. Fish species density (A) and rarefaction diversity at ES₅ (B) and ES₁₀ (C). Canyon, solid bars; slope empty bars; s, shallow, i, intermediate, d, deep depth strata; w, west, e, east sites. Asterisks indicate statistical significance at $p < 0.5$ (*) and $p < 0.05$ (**).

the communities studied are responding to similar environmental gradients.

The results of the PERMANOVA analysis also provided an indication of a “canyon effect” on community structure (*sensu* Vetter and Dayton, 1998, 1999); pairwise comparisons revealed that the assemblage structure of canyons and slopes was different within the shallowest stratum at both sites, and between the deepest stratum for one of the study sites (east). No canyon effect was observable at intermediate depths. We speculate that the lack of canyon effects at intermediate depths could be caused by oxygen stress from the OMZ, which might equally affect fish communities inside and outside canyons and yield a homogenizing effect on species composition. Noteworthy, however, canyon

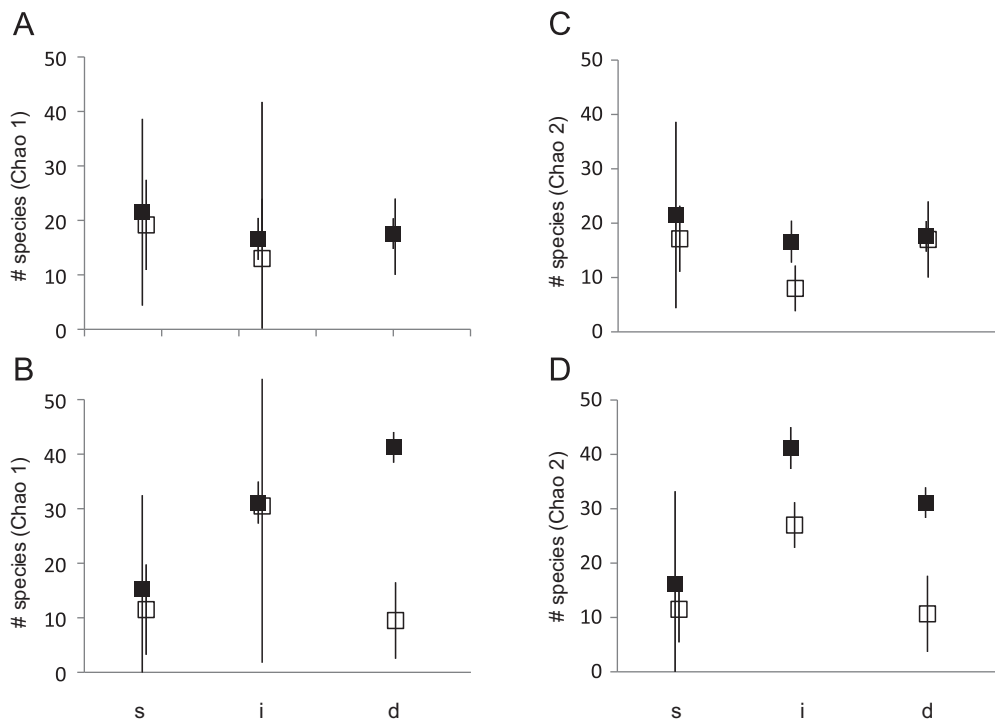


Fig. 8. Estimated species richness using (A, B) Chao 1, and (C, D) Chao 2 based on pooled transects performed at individual sites. Top charts are from Pelekunu Canyon and Slope; bottom charts from Kawaiinui Canyon and Slope (canyon, solid symbols; slopes empty symbols). Vertical bars represent confidence intervals.

effects were in fact observable at intermediate depths for mobile invertebrate megafauna off Moloka'i, which showed higher abundances and diversity within the canyons when contrasted with slopes (Vetter et al., 2010). This discrepancy between our results and those presented by Vetter et al. (2010) may suggest that the demersal fish fauna has a lower tolerance for low oxygen concentrations than does the invertebrate megafauna, consistent with higher metabolic demands due to enhanced locomotory capacity (Seibel, 2007; Seibel and Drazen, 2007).

The DISTLM analysis indicated that the amount of organic detritus may also be a driver of assemblage structure. This finding agrees with our first hypothesis that the amount of detritus would be implicated in explaining any observable differences in fish assemblages between canyons and slope. Other studies in temperate regions have demonstrated that inputs of coastally derived detritus composed mostly of macroalgae and has a crucial effect in determining tropho-dynamics (Harrold et al., 1998) and thus assemblage structure (Vetter and Dayton, 1998, 1999) in submarine canyons. For example, in Carmel Canyon, near Monterey, California, the sea urchin *Allocentrus fragilis* relies heavily on macroalgae sources, compared with areas of the open slope, where this species feeds mostly upon macrofaunal crustaceans and other types of detritus. In our study, the organic detritus was predominantly composed of relatively refractory material, such as decomposing wood and large masses of *Kukui* nuts. Despite the likely lower nutritional value of this material compared with macroalgal sources (McLeod and Wing, 2007), the input of this detrital organic matter also appears to influence the fish assemblage, most probably through an indirect effect of increasing sediment macrofaunal prey availability (discussed in the next Section 4.3).

While the contribution of terrestrial detritus appears to be important, we cannot ignore the contributions of fresh material derived from pelagic productivity depositing on floors of Hawai'ian canyons. However, this contribution may be rather modest in the oligotrophic waters of the Hawai'ian Archipelago if compared to canyons on more eutrophic continental margins.

4.3. Abundance patterns: result of organic enrichment in the canyons?

Steep and V-shaped canyons (*sensu* Shepard and Dill, 1966) can enhance the transport and accumulation of detrital and sedimentary organic material, ultimately providing a surplus of organic carbon for the system (Stefanescu et al., 1994; Vetter et al., 2010; De Leo et al., unpublished). We predicted higher fish abundances in the canyons, but canyon abundances were significantly higher only in the deepest (946–1100 m) strata. The lack of enhanced fish abundance in canyons at shallow and intermediate depths may be related to the homogenization effects of the OMZ discussed previously, but further (e.g., physiological) studies are needed to test this hypothesis.

We hypothesized greater fish abundance in canyons based on the argument that the terrigenous organic detritus yields nutrient subsidies for the benthic invertebrates inside canyons, providing enhanced prey availability for benthic-feeding fish at canyon floors (De Leo et al., 2010). The link between the amount of organic detritus and fish abundances was not directly established but we have strong evidence that increased fish abundance in the canyons is associated with increased benthic prey availability. Enhanced invertebrate megafaunal abundances have been observed at similar depths in Hawai'ian submarine canyons, including both Moloka'i canyons (Vetter et al., 2010). In faunal macrobenthos in Pelekunu (west) and Kawaiinui (east) Canyons off Moloka'i also exhibit higher densities (highly statistically significant) compared to the slope sites (De Leo et al., unpublished). The coincidence in abundance patterns between macro-invertebrates (mostly polychaetes, bivalves and peracarid crustaceans) and demersal fish assemblages at these sites (De Leo et al., unpublished) provides support for our hypothesis. Furthermore, many small macrourid species (e.g., *Coelorhincus* spp.) and halosaurs (such as *Aldrovandia phalacra*), which were more abundant in mid and deeper strata in the canyons, are known to consume small benthic infauna and epifauna (Mauchline and

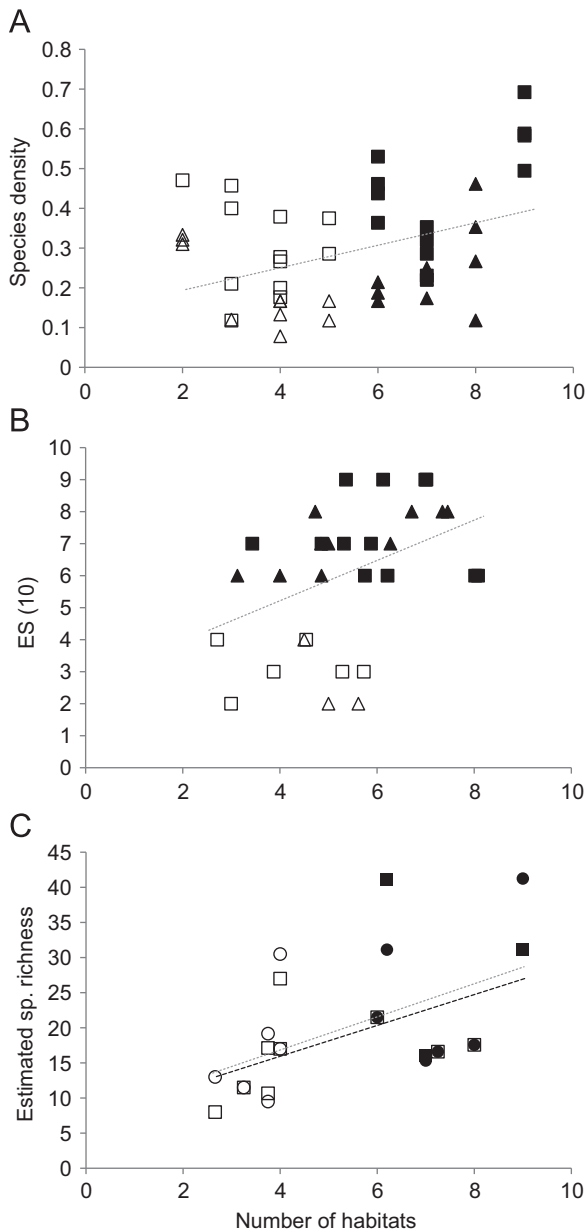


Fig. 9. Fish species density (A), rarefied diversity ES_{10} (B) and estimated species richness (C) plotted against the total number of habitat features (sediment and substrate inclination types) present along video transects. (canyon, solid symbols; slopes empty symbols; squares, Kawaiinui/east; triangles, Pelukunu/west). Linear regression overall (gray dotted line): in A, $y=0.0243x+0.1677$, $R^2=0.12277$; in B, $y=0.6882x+2.2788$, $R^2=0.19787$; in C, for Chao 1 (squares), $y=2.321x+7.7924$, $R^2=0.26852$, for Chao 2 (circles), $y=2.173x+7.8663$, $R^2=0.2335$.

Gordon, 1984; Gartner et al., 1997; Anderson, 2005; Madurell and Cartes, 2005; Mundy, 2005). Stefanescu et al. (1994) reported increased fish abundance and biomass in Rec del Besós Submarine Canyon in the Catalan Sea (western Mediterranean) compared to the adjacent slope, in a comparatively eutrophic system. These authors attributed the higher abundances, and also an overall decrease in individual mean size, to an overall organic enrichment effect associated with the canyons, and suggested that these habitats act as nursery grounds for particular species. Scavenging fish populations may also be enhanced in canyons; King et al. (2008) concluded that scavenger first-arrival rates and staying times at the bait, as well as abundances, were elevated at bathyal and abyssal depths in Nazaré Submarine Canyon (off Portugal) due to organic enrichment in the canyon. Our studies of

scavengers in the Moloka'i canyons, as well as in four other canyon/slope systems in the Hawai'iian Islands, reveal faster first-arrival times at bait and higher scavenging rates in canyons relative to slopes, as would be expected in an organically-enriched habitat (Smith et al., unpublished). We also hypothesized that fish abundances would decrease with depth in both canyon and slope habitats, but more sharply along the relatively food-poor slope. This hypothesis is based on the assumption that the amount of organic carbon from surface water production reaching the seafloor decreases exponentially with increasing depth, which translates into a reduction in benthic standing stock (Rex et al., 2006), including benthic fish. We expected that terrestrially-derived detritus input would "dampen" this bathymetric gradient in canyons. Interestingly, the fish abundance in the canyons increased significantly with depth, while on the slopes abundance decreased (although not statistically significantly, a pattern driven to some extent by two data outliers). There could be a few reasons for the increase in fish abundance with depth in canyons including the higher rates of physical disturbance at the heads of the canyons. Higher physical disturbance associated with strong and frequent up- and down-canyon currents are common at those depths in V-shaped canyons (Shepard and Dill, 1966; Gage et al., 1995; Vetter and Dayton, 1999; Paterson et al., 2011). Previous studies have shown that shallow habitats at the head of submarine canyons are subject to frequent flushing events triggered by surface swells and currents from semi-diurnal internal tides, affecting both the abundance and diversity of benthic-boundary-layer invertebrate communities (Vetter and Dayton, 1998, 1999; Bosley et al., 2004; Hargrave et al., 2004). Thus, invertebrate prey items are likely to be less available for fish in these disturbed environments, which could limit fish abundance in the shallowest canyon strata. Furthermore, as the physical energy drops with increasing depth in the canyons and organic matter supply remains high (relative to the slopes), demersal fish communities are likely to experience both enhanced prey availability and more stable conditions, thereby promoting higher abundance at the deeper depths (Vetter and Dayton, 1999; De Leo et al., 2010). An alternative explanation for higher fish abundances at greater depths in canyons could be due to topographic interception and concentration of downward diel migrator species (such as euphausiids and myctophids) along canyon flanks, offering enhanced prey availability for fish at depth during day time (Genin, 2004). Thus, one could argue that the same topographic effect could cause higher fish abundances observed at depth in Moloka'i canyons. However, while a purely topographic effect on fish aggregation cannot be ruled out, there is evidence from other studies (e.g., off Kaikoura Canyon located in the New Zealand margin) that enhanced abundances of benthic-feeding fishes are directly correlated with enhanced prey availability in canyons, indicating more than topographic effects (De Leo et al., 2010). For the Moloka'i canyons in particular (which occur in an oligotrophic background compared to submarine canyons studied in other regions), we found evidence of enhanced canyon benthic macrofauna (De Leo et al., in preparation) and megafauna (Vetter et al., 2010) relative to the slopes. This is consistent with our hypothesis of organic enrichment leading to greater fish abundances by increasing prey availability in Moloka'i canyons.

4.4. Species density, diversity and richness versus habitat heterogeneity

Our findings confirm previous studies that canyons provide more complex benthic habitats than open slopes (Yoklavich et al., 2000; Schlacher et al., 2007, 2010; Williams et al., 2009, 2010; Tyler et al., 2009; Vetter et al., 2010). The canyons of Moloka'i

possessed a greater range of the proportions of the different substrate and inclination types than the slopes. Our fourth hypothesis predicted that species richness of the demersal fish assemblages would be higher in canyons compared to the open slopes due to higher habitat heterogeneity in the canyons. We found significant difference in species densities only in the deepest depth stratum (946–1100 m). Vetter et al. (2010) found that habitat heterogeneity in canyons was correlated with higher faunal species richness and diversity in Hawai'ian canyons. These authors suggested that different habitat features (e.g., rock outcrops, boulders, patches of organic detritus, etc.) are essential structuring variables for the invertebrate megabenthos, yielding large dissimilarities between canyon and slope assemblages, and leading to higher invertebrate species richness and diversity in Hawai'ian canyons. In our study, the significant correlation between the total number of habitat features (i.e., sediment types and geomorphological structures) and species density, rarefaction diversity, as well as estimated species richness (using Chao 2), provides further evidence for the role of habitat heterogeneity in canyons off Moloka'i in enhancing faunal species diversity. The secondary implication of such variables as % sand, % ripple marks, % boulders, % of rock outcrops, % rocky walls, % medium slope in the multiple regression (DISTLM) model also supports our habitat heterogeneity versus diversity hypothesis, and helped to distinguish canyon from slope fish communities. Habitat heterogeneity (high inclination, rock ledges and caves interspersed with muddy sediments) within canyons has been correlated previously with rockfish diversity off the California coast (Yoklavich et al., 2000). However, these authors concluded that higher habitat heterogeneity in canyons in their area (Soquel Canyon, Monterey Bay) reduced the accessibility of canyon habitats to fishing gear, providing fishing refugia and thus promoting high abundance and diversity. However, fishing pressure on the species in our study off Moloka'i is low, suggesting that habitat heterogeneity itself, rather than refugia from fishing, can promote high fish diversity in submarine canyons.

Positive correlations between habitat heterogeneity and benthic biodiversity have been demonstrated in other submarine canyon settings, particularly for the invertebrate benthic fauna (Schlacher et al., 2007, 2010; McClain and Barry, 2010). Schlacher et al. (2007) reported the occurrence of a diverse (at *alpha*- and *beta*- scales) deep-sea sponge assemblage that was directly correlated with high terrain complexity (measured by slope and sonar backscatter variability) within five Tasmanian canyons. In Monterey Canyon (off California), high species turnover of macrobenthic assemblages, at small spatial scales, (< 100 m) was explained by increased habitat heterogeneity related to substrate patchiness and physical disturbance (McClain and Barry, 2010).

In our study, fish species density and richness were not higher at all depths in the canyons, suggesting that other forces act in concert to determine fish species richness off Moloka'i. For example, lower species richness in the shallower depth strata in canyons may be related to higher physical disturbances inside canyons (Vetter et al., 2010). The high percent cover of ripple marks in canyons (50–96%) in shallow and intermediate depth strata indicates the presence of strong bottom currents at these depths. Similarly, extensive current ripple marks have been observed in other submarine canyons at relatively shallow depths (Shepard and Marshall, 1973; Inman et al., 1976; Vetter and Dayton, 1998, 1999; Tyler et al., 2009). While no current measurements were made during our study, we did at times experience high current velocities (> 2 knots) in canyons, making submersible navigation difficult (De Leo et al., pers. observations). Strong currents have been postulated to reduce fish species diversity on seamounts off New Zealand (Tracey et al., 2004). However, we know of no studies directly relating bottom currents

to species diversity of demersal fishes, so any causality between currents and fish diversity must remain speculative.

While patterns of fish species richness and diversity have been extensively investigated and positively correlated with enhanced habitat heterogeneity in shallow-water coastal systems (Curley et al., 2002; Friedlander et al., 2003; Grober-Dunsmore et al., 2008; Moore et al., 2010), studies of such diversity patterns for deep-sea fish communities are few. The present study provides new insights into relationships between habitat heterogeneity and fish diversity in the deep sea, highlighting the importance of submarine canyons on the landscape scale. Our results suggest that submarine canyons may be important sources of habitat heterogeneity for deep-sea fish communities on the landscape scale, and should be considered in ecosystem-based management approaches e.g., in the design of deep-sea marine protected areas (Smith et al., 2008; Van Dover, 2011) to mitigate biodiversity loss and other human impacts in deep-sea ecosystems (Danovaro et al., 2008; Smith et al., 2008; Clark and Rowden, 2009; Ramirez-Llodra et al., 2010; Van Dover, 2011).

5. Summary and conclusions

Our first hypothesis of a canyon effect on the structure of demersal fish assemblages off Moloka'i island, Hawai'i, was only partially confirmed by our multifactorial analysis. Multivariate regression analysis revealed that overall differences in assemblage structure in canyon and at slope sites were related largely to dissolved oxygen concentration, as well as POC flux, and to a lesser extent, detritus input. Differences in assemblage structure were detected between canyons and slopes in shallow strata (314–459 m), and in the deepest strata (946–1100 m) at one site. These differences, and the inclusion of detritus input in the multivariate regression analysis, indicate that some canyon effect is present. A break in assemblage structure, coincident with the core of the OMZ, suggests that low oxygen levels may override canyon effects on the Moloka'i margin. There was relatively little support for our second and third hypotheses, i.e., of higher fish abundances in canyons, and that decreases in abundance with depth would be less pronounced for canyons than slopes. Differences in abundance between canyons and slopes were only statistically significant at the deepest depth stratum, and contrary to expectation, canyon abundances were higher at deeper than shallower depths. We speculate that the lack of support for the second and third hypotheses is explained by a combination of the influence of the OMZ (which reduces canyon versus slope differences at intermediate depths), higher intensity and frequent disturbance in shallow canyon heads, and topographic interception of diel vertical migratory species. Habitat heterogeneity was greater in canyons than slopes, and was positively correlated with species density, rarefaction and estimated species richness. However, while species density was only statistically higher in canyons than slopes in the deepest strata, higher canyon species richness was limited to the intermediate and deepest strata. We speculate that higher currents (indicated by ripple marks) at shallow depths in canyons negatively affects fish-species densities and richness (by limiting the assemblage to only those species that can tolerate high current flow), overriding the positive effect of the higher habitat heterogeneity. Overall, submarine canyons on oceanic islands are likely to be sites of enhanced fish abundance and species richness, but these enhancing canyon effects (specifically, higher detritus input and habitat heterogeneity) may be offset by oxygen concentrations falling below $\sim 0.7 \text{ ml l}^{-1}$ in oxygen minimum zones, and canyon-related disturbance. These results demonstrate that canyon effects on fish abundance and community structure are not

restricted to temperate, eutrophic continental margins but also occur on oceanic islands in oligotrophic settings.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2012.01.014.

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