

SUBMARINE CANYONS: HOTSPOTS OF DEEP-SEA BENTHIC ABUNDANCE  
AND BIODIVERSITY

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## ABSTRACT

Submarine canyons are abundant features along continental and oceanic island margins that connect continental shelves to deep ocean basins. Patterns of benthic community structure and productivity have been studied in a small number (45, or less than 0.7%) of submarine canyons globally. Previous findings suggest that enhanced habitat heterogeneity and organic input in canyons are responsible for enhancing benthic biodiversity and creating biomass hotspots. However, because of the physical complexity of canyon habitats, predictions concerning the effects of canyons on local (alpha), turn-over (beta), and regional (gamma) diversity are not straightforward since a variety environmental and physical characteristics (e.g., topography, current regime, sediment availability, and quantity and quality of organic matter supply) interact, often non-monotonically, in canyon habitats. Very few studies have systematically considered a broad range of habitat heterogeneity characteristics and their influence on canyon benthic biomass and biodiversity. Based on an extensive literature review, here I devise a conceptual model that helps to predict mechanistically the effects of environmental drivers on patterns of benthic community structure and biodiversity in canyons. Subsequently, testable hypotheses are proposed based on this conceptual model. The model framework employs the intermediate disturbance hypothesis (Connell, 1978) and meta-community model theory (reviewed in Leibold et al., 2004) to make predictions. Two central hypotheses ('The Habitat Heterogeneity Hypothesis' and the Organic Enrichment Hypothesis') were then tested for submarine canyons in the Hawaiian Islands and on the eastern New Zealand Margin. The set of canyons studied encompasses a wide range in physical habitat characteristics as well as boundary constraints, which is suitable for testing a general canyon-biodiversity-hotspot hypothesis. The Hawaiian canyons are embedded in the oligotrophic North Pacific Subtropical Gyre (NPSG) while canyons in New Zealand experience one of the highest reported sediment inputs from major riverine systems, as well as large inputs of coastal and pelagic organic matter. Within the Hawaiian archipelago, despite the predominantly oligotrophic conditions, canyons in the main high islands (MHI) (Oahu and Moloka'i) receive higher loads of coastal detritus (terrestrial plants and macroalgae) than canyons in the low Northwest Hawaiian Islands (NWHI), which are carbonate platforms and atolls. The first primary hypothesis that submarine canyons harbor enhanced habitat heterogeneity at multiple spatial scales relative to open slope habitats was supported for most of the canyon systems investigated. Exceptions to this general rule were evident in the submarine canyons off the low NWHI, Maro Reef and Nihoa Island, where 'canyon effects' on benthic macrofaunal community structure and overall abundance were not perceived. The Kaikoura Canyon system off the eastern New Zealand margin harbors a high degree

of habitat heterogeneity from spatial scales ranging from meters to a few kilometers related to macrofaunal and megafaunal bioturbation activity. The second main hypothesis stating that canyons show enhanced organic matter enrichment relative to slopes was also supported for most but not all the canyons studied. As for the ‘habitat heterogeneity hypothesis’, organic enrichment was evident in the form of higher macrofaunal abundances in Kaikoura Canyon and also in the three canyons (Pelekunu, Kawainui and Kaneohe canyon) off the MHI, but not for the canyons off Maro Reef and Nihoa Island (NWHI). The lack of ‘canyon effects’ in the NWHI both in terms of abundance, alpha and beta-diversity is thought to result from reduced habitat heterogeneity and sparse detrital organic enrichment, resulting from relatively weak forcing on canyons from low islands/reefs. Absence of ‘canyon effects’ on fish and macrobenthic invertebrate community structure, abundance and diversity in canyons off Moloka‘i and Oahu are attributed to a mid-depth oxygen minimum zone and to enhanced physical disturbance (strong bottom currents) at the heads of these canyons. For those canyon systems where enhanced habitat heterogeneity and organic enrichment were indicated, the overall benthic biodiversity was higher than on slopes, particularly at beta scales. These results further demonstrate that canyons often enhance faunal abundance and diversity at local scales (where physical disturbance is moderate) but more significantly at beta scales. This information has strong implications for marine spatial planning and conservation, and inclusion of entire canyon features in marine protected areas aimed at the protection of biodiversity hotspots.

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# **Chapter 1**

## **Introduction: environmental drivers and mechanistic underpinnings of patterns of benthic biodiversity in submarine canyons**

### **1.1 Background**

Continental margins are considered major reservoirs of marine biodiversity (Sanders and Hessler, 1969; Rex, 1983; Etter and Grassle, 1992; Snelgrove et al., 1992; Levin et al., 2001; Brandt et al., 2007 and have been, albeit controversially, compared to the most diverse terrestrial and shallow water marine habitats (Rex et al., 1983; Etter and Grassle, 1992; Grassle and Maciolek, 1992). Although biodiversity patterns are still poorly described on most continental margins, recent studies indicate that margin biodiversity is correlated with a variety of ecosystem functions and services (Danovaro et al., 2007; Levin and Sibuet, 2012).

The enormous reservoir of biodiversity on continental margins, summed across many margin habitat types (e.g. cold seeps (Cordes et al., 2008, 2010), coral mounds (Buhl-Mortensen et al., 2008, 2010), foraminifera beds (Gooday et al., 1998, 2010), oxygen minimum zones and open slopes (Levin et al., 2010) is facing increasing threats from human activities such as bottom fishing, oil and gas extraction, and sewage dumping, as anthropogenic influences penetrate into the deep sea (Smith et al., 2008; Ramirez-Llodra et al., 2010; Levin and Sibuet, 2012). Therefore, attempts to describe and quantify continental margin biodiversity patterns are crucial to identifying biodiversity hotspots and to developing conservation strategies, which may include designation of areas for permanent protection within marine protected areas (Smith et al., 2008; Ramirez-Llodra et al., 2010; Levin and Sibuet, 2012).

A recent study estimates that total marine eukaryotic biodiversity to be 2.2 million (+/- 0.8 million SE) species (Mora et al., 2011). If this estimate is reasonable, it means that ~91% of marine species (or ~2 million species) are yet to be described (Mora et al., 2011). The 10-year effort of the international project Census of Marine Life (CMOL) collected 6,000 potential new species, and completed new descriptions of 1,200 species (Ausubel et al., 2010). If the above (Mora et al., 2011)

predictions are correct and we roughly extrapolate the likelihood of finding new species by the total area of continental margins relative to the word's oceans (11% in area; Janhke, 2010), we may estimate another 200,000 species to be found on continental margin habitats. This estimate is, of course, a rough generalization as species distribution and diversity patterns are related to a range of environmental and biological factors (reviewed in Levin et al., 2001).

Submarine canyons are abundant and ubiquitous features along continental and oceanic island margins that connect continental shelves to deep ocean basins (Shepard and Dill, 1966). Roughly 20% of the NE Pacific shelf edge between Alaska and the Equator is interrupted by steep, narrow and abrupt submarine canyons (Hickey, 1997). The first global review on canyon distribution, origin, geology and sedimentation patterns dates from 1966 (Shepard and Dill, 1966) and mapped 96 major canyons around the world. High-resolution bathymetric data indicate that there are well over 660 submarine canyons globally (De Leo et al., 2010/Chapter 2); and very recent tabulation based on satellite altimetry, suggests that the number of submarine canyons could exceed 5800 (Harris and Whiteway, 2011), although the definition of canyons used by Harris and Whiteway (2011) is more inclusive than those of previous authors.

Patterns of benthic community structure and productivity have been studied in a small number (45, or less than 0.7%) of submarine canyons (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). The majority of findings suggest that enhanced habitat heterogeneity and organic matter deposition in canyons are responsible for enhancing benthic biodiversity and creating biomass hotspots (Vetter, 1994; Vetter and Dayton, 1998, 1999; Schlacher et al., 2007, 2010; Vetter et al., 2010). Enhanced local fishery production in canyons, when contrasted to regular slope environments, has also been reported and attributed to a 'canyon effect'; simply, the channeling and concentrating of detrital organic matter and pelagic animal populations in canyons (Vetter and Dayton, 1999; Yoklavich et al., 2000; Ramirez-Llodra et al., 2008). Many other unusual ecological characteristics have been attributed to canyons such as concentrating diel vertical migrators (Greene et al., 1988; Mackas et al., 1997), displacing deep-water species to coastal zones (King et al., 1987), promoting topographically induced upwelling (Sorbazo et al., 2001; Ryan et al., 2005) and enhancing diapycnal mixing via internal wave generation (Thurnherr, 2006; Kunze et al., 2011).

Canyons can be complex topographic features often characterized by complicated patterns of hydrography, flow, and sediment transport and accumulation (Shepard et al., 1974; Oliveira et al., 2007; Garcia et al., 2008). Unusual physical oceanographic conditions inside canyons can be

caused by topographic effects such as accelerated currents and dense-water cascades, which increase suspended particulate concentrations and transport organic matter from coastal zones to deeper regions of the margin (Bosley et al., 2004; Genin, 2004; Canals et al., 2006). These phenomena can be responsible for enhancing both pelagic and benthic productivity inside canyon habitats as well as the biodiversity of many benthic faunal groups (Schlacher et al., 2007; Vetter et al., 2010).

Because of the physical complexity of canyon habitats, predictions concerning the effects of canyons on local (alpha) and regional (gamma) diversity are not straightforward since a variety environmental and physical characteristics (e.g., topography, current regime, sediment availability, and quantity and quality of organic matter supply) interact often non-monotonically in canyon habitats. For example, at moderate rates of flow and sediment deposition, suspension- and deposit-feeding macrobenthos can be enhanced in abundance and/or diversity in canyons (Vetter and Dayton, 1998) whereas at high rates of flow and sediment accumulation (e.g., from accelerated bottom currents or extremely high sedimentation rates near river mouths), canyon fauna can become impoverished yielding low species richness and high dominance by a few tolerant species (Haedrich et al., 1980, Rowe et al., 1982; Gage et al., 1995; Vetter and Dayton, 1998).

While some studies have reported levels of local (alpha) and turn-over (beta) megafaunal biodiversity in canyons rivaling seamounts (Schlacher et al., 2007), in other cases high disturbance rates (Rowe et al., 1982) and absence of stable habitat heterogeneity lead to faunal impoverishment compared to adjacent slope environments (Vetter et al., 2010). Nevertheless, very few studies have focused on comparing canyon effects on biodiversity at several spatial scales: i.e., at local or within habitat (alpha diversity), across different habitat types (beta diversity), and regional scales (gamma diversity). Beta diversity is thought to be a particularly important component of biodiversity when selecting priority areas for conservation, because it can be used to identify heterogeneity in species assemblages along environmental gradients as well as biodiversity hotspots (Magurran, 2005).

## 1.2 Rationale

Very few studies have systematically considered a broad range of habitat heterogeneity characteristics and their influence on canyon benthic biomass and biodiversity. Thus, a systematic overview of the drivers by which submarine canyons structure continental margin benthic habitats is urgently needed as fisheries and conservation strategies shift focus to these widespread, often productive and diverse deep-water habitats (Smith et al., 2008; Ramirez-Llodra et al., 2011; Levin and Sibuet, 2012). The lack of comprehensive studies is not surprising considering the diversity of canyons in terms of their primary physical properties (shape, size, vertical relief, water masses and physical oceanographic forcing, etc.) and also their boundary constraints (quality and quantity of

organic matter inputs, sediment availability, background coastal and oceanic productivity) and the complex interactions among these factors in affecting benthic communities.

Habitat heterogeneity is recognized to have an important influence on, and to be correlated with, biodiversity (Rozsenzweig, 1995; Tews et al., 2004). This generalization seems to hold across numerous terrestrial and marine environments (Rozsenzweig, 1995; Levin et al., 2001). The habitat heterogeneity hypothesis assumes that structurally complex habitats lead to an increase in species diversity by providing a higher number of distinct niche dimensions including ways of exploiting resources (MacArthur and Wilson, 1967). Many aspects of heterogeneity across habitats can be quantitatively (or qualitatively) measured by the variation, number or extent (percentage cover, height, volume) of a variety of physically structuring elements (sediment types, organic-rich patches, oxygen levels, etc.) (Cordes et al., 2010). The quantification of a specific metric of habitat heterogeneity can be correlated with a biodiversity measure (for the same spatial scales considered) to test their relationship along environmental gradients (Tews et al., 2004).

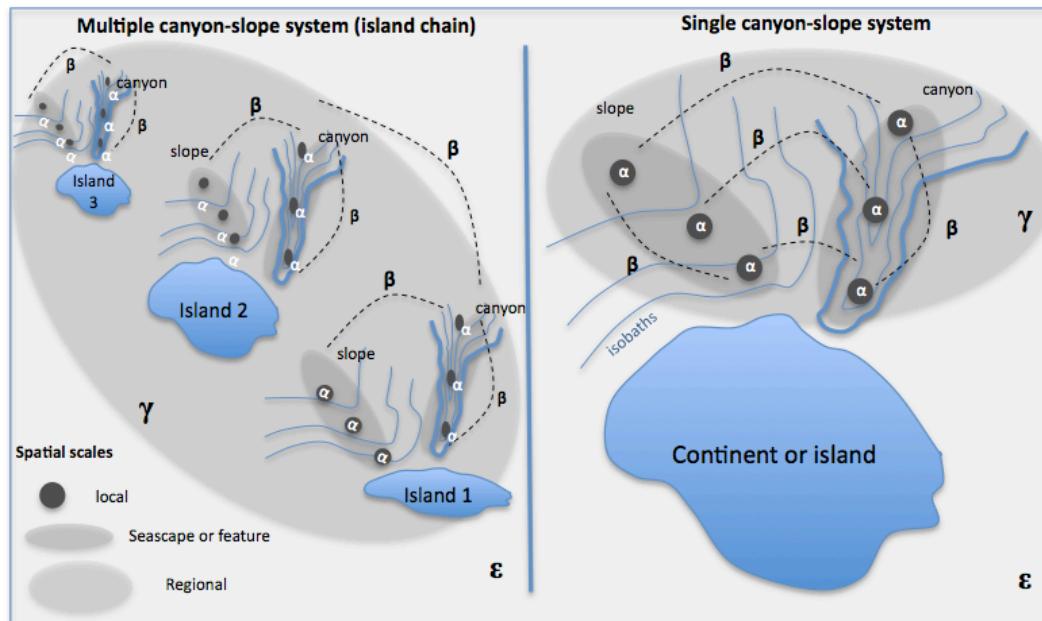
A productivity gradient, for example, can be viewed as a heterogeneity factor affecting species distributions and abundance patterns. For example, in fresh water pond systems, the shapes of productivity-biodiversity relationships are found to be linear at larger (regional) spatial scales while hump-shaped on smaller (local) spatial scales (Chase and Leibold, 2002). However, in studies of deep-sea benthic communities, a hump-shaped relationship between productivity and diversity has been documented at large spatial scales along depth gradients from the shelf to the abyss, alongside with the exponential decrease in food supply (Rex, 1983; Rex et al., 2006). In some cases, local ( $\alpha$ ), and turn-over ( $\beta$ ) diversity peak at intermediate depths on continental margins, a pattern that has been postulated to result in part from intermediate disturbance rates and source-sink processes in a heterogeneous landscape (Rex, 1983; Snelgrove and Smith, 2002; Rex et al., 2006).

In order to understand the influence of habitat heterogeneity on the complex and diverse array of canyon systems, we need to create a conceptual model to predict (mechanistically) how different environmental factors will affect habitat heterogeneity and benthic biodiversity in canyons. Such a model will provide a framework for predicting the existence of biodiversity hotspots and to help in planning conservation and management efforts.

### **1.3 Defining spatial scales and proper diversity measures**

Here I briefly define what I will consider as local, landscape and regional scales and the most appropriate metrics to measure biodiversity at each of these scales when studying canyon and slope benthic habitats. The limits of these scales, as suggested by many reviews in community ecology, are not straightforward since boundaries between different biological assemblages,

communities, meta-populations and biogeographical provinces are not always easy to draw (Rex, 1983; Magurran, 2004). Here I use a biodiversity scale scheme commonly used in ecological studies (summarized in Magurran, 2004) (Fig. 1.1).



Scale	Spatial units	Biological units	Examples	Biodiversity Metrics
local	10-100's of m	Assemblages (mix of populations)	site	$\alpha$ , Shannon, Simpson
feature	10's of km	Communities	Canyon	$\beta$ , Species Accum. curves, sp. estimators, Anosim, Sorenson
regional	100's of km	Metapopulations	Whole margin	$\gamma$ , Gamma, species richness
Biogeographical province	1000's of km	All metapopulations	Archipelagum	$\epsilon$ , Epsilon, species rich.

**Figure 1.1** Definition of spatial scales and appropriate biodiversity measures, here specifically applied to megafaunal organisms (animals larger than 3 cm or visible in photographs).

## 1.4 Literature review

The goal of this literature review is to summarize what is known about patterns of benthic biodiversity and abundance in submarine canyons, and to select the most relevant environmental drivers to include in a mechanistic/conceptual model.

Based on published literature and results and discussions from the workshop *Roles of habitat heterogeneity in generating and maintaining continental margin biodiversity* (sponsored by COMARGE and hosted at Scripps Institute of Oceanography in September of 2008), I have selected

the main environmental factors that have been shown to influence habitat heterogeneity in submarine canyons and in turn used to explain benthic biodiversity and biomass/abundance patterns. A total of 35 peer-reviewed articles comprising studies performed in 41 submarine canyons worldwide was used in this literature review. These factors (1- terrain and substrate heterogeneity; 2- organic matter supply/quality; 3- physical energy/levels of flow disturbance; 4, levels of sediment loading; 5- bioturbation of the substrate by infauna and epifauna; 6- spatial distance between canyons) were tabulated to enumerate the peer-reviewed articles in which they were selected as important environmental drivers of benthic abundance and biodiversity. When multiple drivers were assigned in a single study, a count for each was tabulated. Although published papers on meio-, macro- and megafauna communities were tabulated, they were comprised mostly of studies on the two larger faunal size fractions. The output of this tabulation is shown in Table 1.1. The direction of the effects of these factors on benthic community biodiversity and biomass (or abundance) are highlighted and qualitatively assigned as positive, negative, variable or not studied; or simply identified as affecting the community composition/structure (or beta diversity). For biodiversity in particular, the effects are assigned to the spatial scale observed, but as for most of studies to date, alpha (local) diversity is the main scale investigated.

The result of this literature survey allows me to rank the four most important drivers of benthic abundance/biomass and biodiversity patterns in submarine canyon systems. These are, in order of importance: 1) Organic matter supply/quality (26 references); 2) Terrain and substrate heterogeneity (15 references); 3) Physical energy/levels of disturbance (14 references); 4) Sediment loading (8 references); 5) Bioturbation of the substrate by infauna and epifauna (1 reference); 6) Spatial connectivity between canyons (1 reference) (Refer to Table 1.1).

Based on this literature review, the most important driver affecting biodiversity and biomass/abundance patterns in canyons is organic matter input (sources, quantity and quality) and is mostly related to coastal detrital inputs (kelp and other macrophytic debris) or pelagic productivity regimes (upwelling, meso-scale eddies, zooplankton aggregations) (Table 1.1 for references).

Seafloor terrain and substrate heterogeneity altogether account for the second most important driver of benthic biodiversity in submarine canyons (i.e., the physical canyon structure such as bottom types and sedimentary structure, presence of hard substrates, grain size distributions, shape and relief of the canyon, etc). One of these factors, sediment grain size, can be considered as a ‘super-parameter’ (Etter and Grassle, 1992) since it directly or indirectly reflect local physical energy and sedimentation patterns (See Table 1.1 for references).

**Table 1.1** Literature review of environmental drivers of benthic biodiversity and abundance/biomass on submarine canyons

Forcing type	Character type	Underlying mechanism	Effects on benthic				Published literature	
			$\alpha$	$\beta$	$\gamma$	B/A	Article/ pub. year	Canyon
<b>Biological - Organic matter supply/quality (26 references)</b>								
Coastal Macrophytic Productivity		Creates microhabitats for macro and megafauna and provide food for macrofauna detritivores. May decrease alpha-diversity locally due to enrichment effect and dominant species, but increases beta and gamma diversity	+	+	ns	+	Vetter & Dayton, 1998, 1999 Harrold et al., 1998 Ramirez-Lodra 2007; Tudela et al., 2003 Sabatini 2007 Curdia et al., 2003; Amaro et al., 2010; Paterson et al., 2011; Cunha et al., 2011 Vetter et al., 2010	Scripps La Jolla Carmel Blanes Quirra Nazare Setubal Cascais Pelekunu Kawaihui Kaneohe Nihoa Maro Hudson Carson Lacaze-Duthiers Cap de Creus Adriatic Cascais Nazare MidAtlantic bight
		Less food for detritivores fauna	0	0	ns	0	Rowe et al., 1982	
			0	0	ns	0	Houston & Haedrich, 1984 Bianchelli et al., 2010	
			0	+	+	0		
			0	0	ns	0	Auster et al., 2005	
Upwelling induced phytoplankton productivity and POC flux		Intense organic enrichment causes sediment hypoxia and reduced community complexity - dominant species predominate	0	ns	ns	+	Maurer et al., 1995	Newport
			+	+	ns	+	Duineveld et al., 2001	Whittard
		Particulate organic material serves as food for benthos and concentrate pelagic prey	+	+	ns	+	Hargrave et al., 2004	Gully
			+	+			McClain and Barry, 2010	Monterey
			0	ns	ns	+	Escobar-Briones et al., 2008	Campeche
Riverine and along-shore OM		Intense turbidity flows disturbing some faunal groups	ns	ns	ns	ns	Bosley et al., 2004	Astoria
		Organic-rich sediments but also depending on the intensity (IDH)	0	0	ns	0	Griggs et al., 1969	Cascadia
			-	-	ns	+	Bianchi 2001	Mississippi
							Gerino et al., 1999; Sorbe et al., 1999; Sarda et al.,	Cape-Ferret Merengue era
			+	+		+	Wei et al., 2010	Mississippi Alaminos Hudson
			0	+	+	+ or 0	Haedrich et al., 1980; Rowe et al., 1982	
			0	+	ns	0	Huston and Haedrich, 1978	Carson
			+	+	+	+	Galeron et al., 2009	Congo
			0	+	ns	+	King et al., 2008	Nazare
Distance from shore		Impacts the amount of coastal derived organic material. Usually have a negative effect on canyon	+	ns	ns		Vetter and Dayton, 1998	Scripps La Jolla
Small			+	ns	ns		Duineveld et al., 2001	Whittard

Large		head communities due to high frequency disturbances (lowers alpha diversity locally) Large distances limit the amount of coastal organic matter transported to benthic communities	+ + -	ns ns 0	ns ns -	De Leo et al., 2010 Gerino-Patriti et al 1999 Rowe et al 1982	Kaikoura Cape-Ferret Hudson	
			- -	ns ns	-	Houston & Haedrich, 1984	Hudson	
			-	-	ns	-	McClain and Barry	
			-	-	-	-	Monterey	
<b>Physical/Geological – Terrain and Substrate Heterogeneity (15 references)</b>			$\alpha$	$\beta$	$\gamma$	B/A	Article/ pub. year	Canyon
<b>Canyon shape</b>	V-shaped	A 'v' shaped canyon is usually associated with high-energy currents, sediment slumps that can expose hard substrates enhancing habitat heterogeneity and favoring mobile and sessile megafauna suspension feeders. On the other hand can promote sediment scouring disturbing macro-infauna	+ + - - -	+ ns ns ns ns	ns ns ns ns -	Schlacher et al., 2007 (Tasmanian canyons) Vetter and Dayton 1998, 1999 Vetter et al., 2010, De Leo et al., 2012 Rowe et al., 1983	Pieman LindHole King Island BigHorse shoe Scripps La Jolla	
	U-shaped	Affects sediment deposition and can potentially be a proxy of organic enrichment. For example, fine organics can deposit in 'u' shaped wider and with gentle sloping walls and flat thalweg enhancing food availability. Homogeneous conditions prevent 3-dimensional habitat structuring but allows organic matter retention	+ - - +	ns - ns ns	ns - me + me + me	De Leo et al., 2010 De Leo et al., 2010 Hargrave et al., 2004 Schlacher et al., 2007 (Tasmanian canyons)	Kaikoura Kaikoura Gully Pieman LindHole King Island BigHorse shoe	
<b>Substrate Types</b>	Mosaic type habitats (soft mixed with hard substrates) favors niche partitioning and increased	+ + -	+ + -	ns ns ns	+ both ns - both	Hargrave et al 2004 Paterson et al., 2011 Vetter and Dayton 1998	Gully Nazare Scripps	
	Reduced habitat heterogeneity	-	ns	ns	-	De Leo et al., 2010	Kaikoura	
	Frequent habitat disturbance	- +	ns ns	ns ns	- both	Duineveld et al., 2001 Maurer et al., 1995	Whittard Newport	
	Reduced habitat heterogeneity	- - - - +	- - - - +	ns ns ns ns ns	0 0 0 0 0	Griggs, 1967 Rowe et al., 1971 Haedrich et al., 1980 Houston and Haedrich, 1984 Bianchelli et al., 2010	Cascadia Hatterras Hudson Carson Lacaze-Duthiers Cap de Creus Adriatic Cascais Nazare	
			+ +	ns ns	0	Ingels et al., 2010 Buhl-Mortensen et al., 2009	Whittard Gollum 5 Norwegian Canyons	

<b>Canyon Size</b>	large	Species x Area relationships. The larger the area, the more species will be capable of colonizing the various habitats within that area.	+	+	+	+	De Leo et al (Chapter 4)	Kawaiinui Pelekunu Kaneohe MaroReef Nihoa
	small	Opposite as above	-	-	-	-		
<b>Physical – Physical Energy/levels of Disturbance (14 references)</b>		$\alpha$	$\beta$	$\gamma$	B/A	Article/ pub. year	Canyon	
wind/wave energy	Periodicity and intensity of bottom flow regimes affecting sediment deposition and community succession.	+	0	ns	+	Okey, 1997	Monterey	
turbidity flows	Margin activity affecting mass wasting events. Dense shelf water cascading affecting sediment slumps and organic matter inputs.	+	0	ns	ns	Rowe et al., 1971; 1982	Hudson Hatteras	
margin activity	Dense shelf water cascading affecting sediment slumps and organic matter inputs.	0	0	ns		Maurer et al., 1995	Newport	
bottom currents	Final classification as erosional x depositional. Depositional favors macrofauna and erosional favors megafauna. However, faunal diversity (alpha-local) should peak on intermediate disturbance conditions (Intermediate disturbance hypothesis theory).	+	ns	ns	+ ma - me	De Leo et al., 2010	Kaikoura	
dense water cascading		ns	ns	ns	- me	Canals, 2006	Blanes	
		-	ns	ns	-	Haedrich et al., 1980	Hudson	
		-	ns	ns	-	Rowe et al., 1982	Hudson	
		-	ns	ns	-	Koho et al., 2008	Nazare	
		-	ns	ns	-	Vetter and Dayton, 1998	Scripps La Jolla	
		-	+	ns	-	Vetter et al., 2010	Kawaiinui Pelekunu Kaneohe MaroReef Nihoa	
		-	+	ns	-	McClain and Barry, 2010	Monterey	
		-	+	ns	-	Hargrave et al., 2004	Gully	
		-	+	ns	-	Paterson et al., 2011	Nazare Setubal Cascais	
<b>Physical/Geological – Sediment Loading (8 references)</b>		$\alpha$	$\beta$	$\gamma$	B/A	Article/ pub. year	Canyon	
	High sediment loading is observed in shelf-incising canyons providing large and steady supplies of sediments that reach the canyon heads and are transported down canyon. High sedimentation is often associated with high organic content	+	+	ns	+	Houston & Haedrich, 1984	Carson	
		+	+	ns	+	Maurer et al., 1995	Newport	
		+	0	ns	+	Curdia et al., 2003	Nazare Setubal Cascais	
		+	ns	ns	+	Amaro et al., 2010	Nazare	
		+	ns	ns	+	Bianchelli., 2011	Lacaze-Duthiers	
		+	ns	ns	+	Wei et al., 2010	Mississippi Alaminos	
		+	ns	ns	+	Ramirez-Llodra et al., 2008	Blanes	
		+	ns	ns	+	Escobar-Briones et al., 2008	Campeche	
<b>Spatial Connectivity* (1 reference)</b>	Larval dispersal and colonization among nearby canyons	ns	+	+	ns	Schlacher et al., 2007	Pieman LindHole King Island BigHorse shoe	
Related to canyon spacing								

Notes: me, megafauna; ma, macrofauna; ns, not studied;  $\alpha$ , alpha-diversity;  $\beta$ , beta-diversity;  $\gamma$ , gamma diversity; B/A, Biomass/Abundance; Refer to the Reference list at the end of the chapter for

## **1.5 Conceptual model: environmental drivers and mechanistic understanding of patterns of benthic biodiversity in submarine canyons**

To explain how these heterogeneity factors influence benthic biodiversity and abundance at local and regional scales, I use theoretical models derived from the General Hypothesis of Diversity proposed by Huston (1979), as well as meta-community models reviewed by Leibold et al (2004), to build a conceptual canyon model (Fig. 1.2).

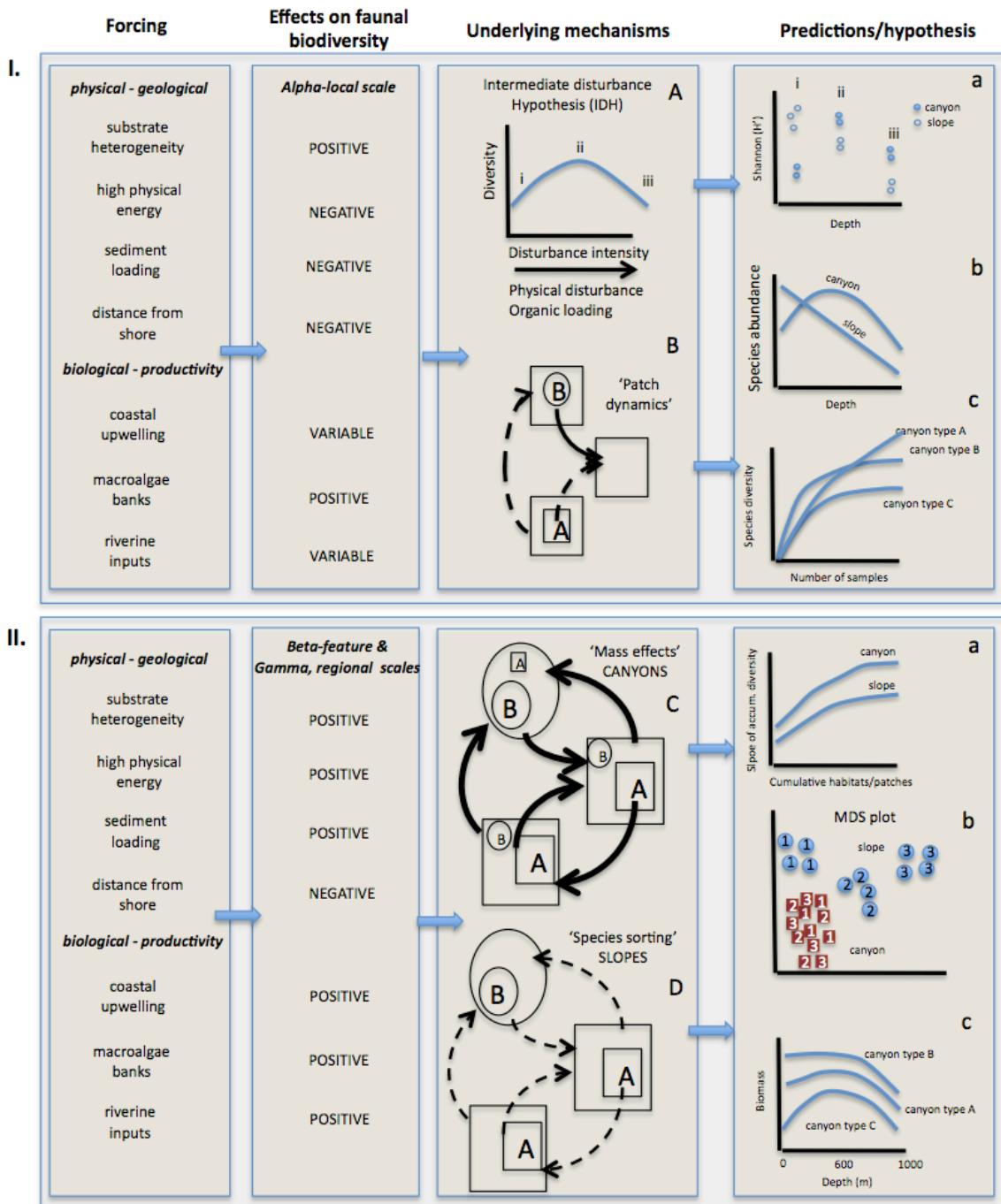
The upper panels (I) predict the effects of forcing on abundance and diversity in canyons relative to slopes at local scales (10-100's meters, Figure 1.1). According to the Intermediate Disturbance Hypothesis (IDH) of Connell (1978) and modified by Huston (1979), the frequency of population reductions (density-independent) relative to population growth rates has a major effect on the maintenance of diversity. At low population reduction rates (or disturbance rates), diversity is reduced by competitive displacement (k-strategists replace r-strategists; Panel A-i). At intermediate disturbance rates (in space and time) alpha-diversity is high due to individual patches and beta diversity is elevated by the presence of a mosaic of patches in various stages of succession (Panel A-ii). Finally, if disturbance frequency is high, only a few species have population growth rates high enough to maintain viable populations, and diversity is reduced (Panel A-iii). The predicted response in local diversity measured by the Shannon diversity index in canyons versus slopes is shown in the graph at the top of the right panel (a). The value of the Shannon index is predicted to be reduced in canyons, particularly at shallow depths because disturbance rates from strong bidirectional bottom currents are expected to be higher than on open slopes. The effect on community abundance is depicted in the middle of the panel (I.b). The hump-shaped pattern for canyons depicts two responses: 1) reduced abundance at shallow depths resulting from higher disturbance frequency, 2) higher abundance at intermediate and deeper depths (relative to slopes) due to channeling and concentration of organic matter. Panel I.c shows a comparison among different canyons in terms of physical regimes. Diversity is predicted to be higher in intermediate energy regimes (e.g., hypothetically canyon type A) while reduced in high-energy physical regimes (e.g., canyon type C).

The meta-community model depicted in I.B (the 'patch dynamics model') depicts situations where biodiversity may be maintained by patchy disturbance (i.e., population reductions) in relatively physically homogeneous slope environments, where habitat patches are similar (represented by the square symbols). Species A is a better competitor (depicted by its shape: a square) than Species B in this square patch type but species B is a better colonizer (higher immigration rates depicted by the solid arrows). Here, homogeneity, which is, in general, predicted

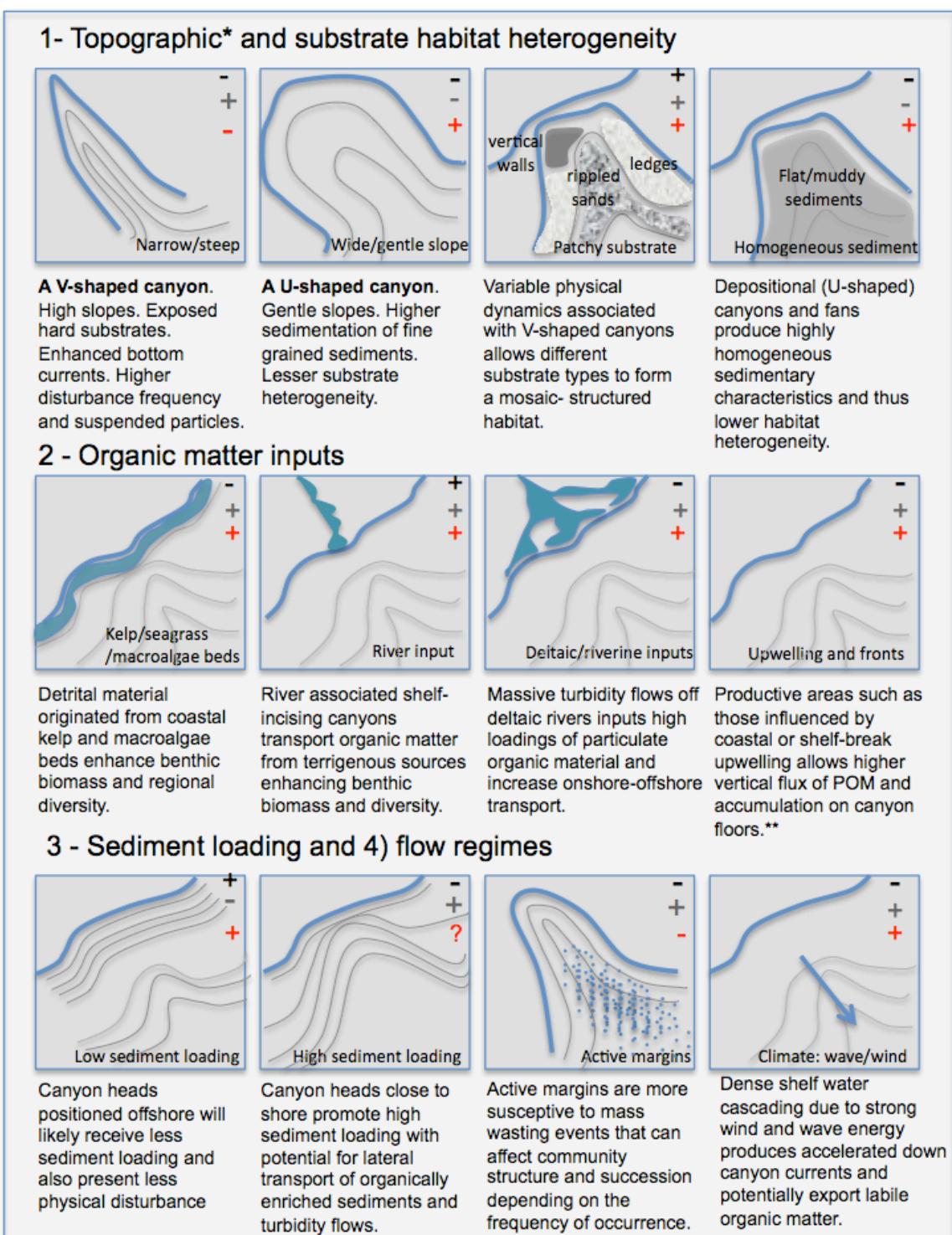
to be greater on slope sedimentary environments, contrasts with the predicted multi-habitat types and variable physical regimes of canyons.

The lower panels II, in contrast, predict biodiversity at landscape (beta) and regional (gamma) scales. Here I employ two other meta-community models. The ‘mass effects’ model (Panel C), for example, can be used to predict diversity and community structure at landscape scale within canyons. This model, which is also encapsulated in broader source-sink models, predicts that high landscape-scale diversity is maintained by high exchange of individuals by dispersal between different sub-populations. In this panel, the smaller letters and symbols represent sub-populations. The different shapes (oval and squares) represent different local habitats. In canyons, in particular those subjected to high-energy regimes, the model predicts communities with higher diversity due to higher exchange of individuals (via dispersion by strong bi-directional flow regimes) among different sub-populations (a). Along a bathymetric gradient, canyons are also predicted to have less structured communities, meaning higher species similarity from shallow to deeper areas due to the homogenizing effects of along-axis transport (II.b). In contrast, slope communities are predicted to have more bathymetric turnover or heterogeneity since the predominant depth zonation will prevail in the absence of strong across isobath currents. In this case, the most appropriate meta-community model to account for diversity is the ‘species sorting’ model (Panel D). In this scenario, species occupy their most favorable niches and the weak dispersal capabilities of both species A and B (depicted by the dashed arrows) prevent niche overlap and allow coexistence on the landscape scale. In terms of biomass (panel II-c), the decrease-with-depth trend also is predicted to vary according to disturbance/energy gradients.

Based on the literature review and using my conceptual model, I draw up a scheme that presents several examples where different canyon landscapes, varying in shape, size, axis slope, distance from shore, background productivity are predicted to modulate the effects of these drivers on faunal (e.g., beta) diversity and biomass patterns (Fig. 1.3).



**Figure 1.2.** Conceptual mechanistic model drawing relationships between environmental forcing and submarine canyon abundance and biodiversity patterns. [Notes: In Panel I-A the impact of organic loading affects diversity by dominance patterns rather than competitive exclusion; Canyon types (A=intermediate disturbance levels; B= low disturbance, C=high disturbance); in Panel II, right-hand column, panel b: numbers 1,2 ad 3 represent groups of samples taken in different depths inside canyons (square symbols) and on slopes (circles).]



**Figure 1.3.** Canyon habitat heterogeneity showing the most relevant physical and biological boundary conditions. Effects on benthic community structure are qualitatively assigned as: (+, -) factor has a positive or negative effect on faunal diversity (alpha-black; beta-grey) and on biomass (red); ?, heterogeneity effect is dependent on intensity scale (variable). Consideration: Many of the factors described in this scheme can work together to affect benthic faunal patterns. \* Canyon orientation relative to the shoreline may also be important as to determine sedimentary inputs and

physical energy by tidal currents; \*\* Diel vertical migrators may also be an important enrichment factor in canyons in productive areas.

## 1.6 Objective

The main objective of the present study is to use a predictive mechanistic model to test hypotheses regarding the role of submarine canyons as sources of habitat heterogeneity and in producing hotspots of benthic biodiversity and abundance/biomass. Testing of these hypotheses will help to determine whether canyons are margin landscape features requiring special consideration in ecosystem management and conservation.

The following chapters examine benthic diversity (especially beta diversity) and abundance patterns at local, landscape and regional scales in several submarine canyon (and adjacent slopes) systems located in two distinct oceanographic settings: (1) the Main and Northwest Hawaiian Islands, (2) the Eastern New Zealand Margin. This set of canyons encompasses a wide range in physical habitat characteristics as well as boundary constraints, which is suitable for testing a general canyon-biodiversity-hotspot hypothesis. For example, Hawaiian canyons are embedded in the oligotrophic North Pacific Subtropical Gyre (NPSG) while canyons in New Zealand experience one of the highest reported sediment inputs from a major riverine system, as well as large inputs of benthic and pelagic organic production. Within the Hawaiian archipelago, despite the predominantly oligotrophic conditions, canyons in the main high islands (e.g., Oahu and Moloka'i) receive higher loads of coastal detritus (terrestrial plants and macroalgae) than canyons in the low Northwest Hawaiian Islands (NWHI), which are carbonate platforms and atolls.

## 1.7 Testable hypotheses

Two basic hypotheses are to be tested:

**H1: Habitat heterogeneity is greater in submarine canyons due to substrate heterogeneity at a variety of spatial scales and to variable flow dynamics promoted by steep topography – ‘The Habitat Heterogeneity Hypothesis’.**

**H2: Organic loading is higher in canyons that receive large fluxes of pelagic and coastal inputs of organic detritus – ‘The Organic Enrichment Hypothesis’.**

Nested in those two basic hypotheses is a subset of hypotheses formulated based on predicted relationships between habitat heterogeneity/organic loading effects on benthic faunal abundance and biodiversity:

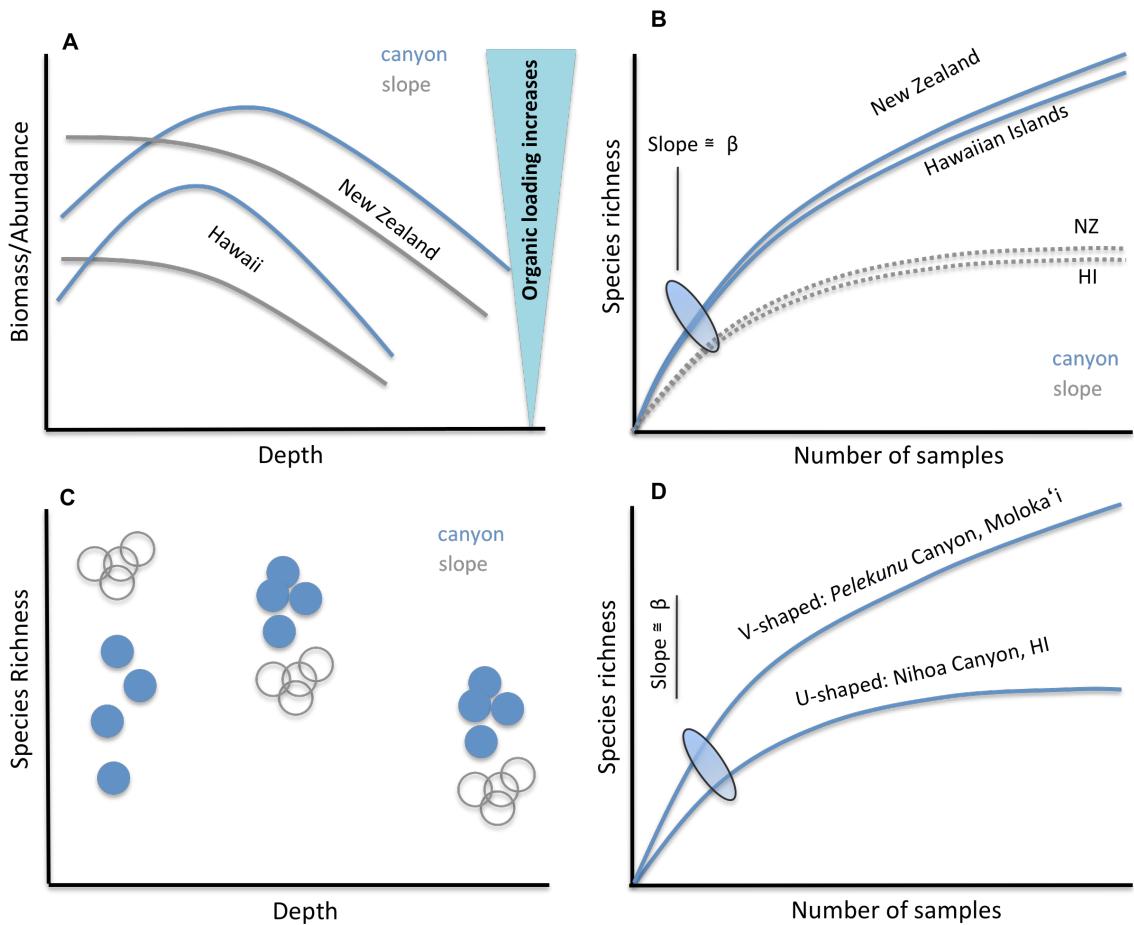
**H<sub>1</sub>:** All canyon systems will show greater faunal abundances (macro- and megafauna) and *beta* diversity than adjacent slopes due to higher habitat heterogeneity (e.g., mosaic of sediment and landscape-terrain types, variable current regimes);

**H<sub>2</sub>:** Canyons with high organic input will show higher macrofauna abundance (or biomass) and species dominance than canyons with little organic input (either pelagic or benthic) (e.g.1., Kaikoura Canyon, NZ versus Main Hawaiian Island Canyons; e.g.2, Main Hawaiian Island Canyons versus Northwest Hawaiian Island Canyons);

**H<sub>3</sub>:** Local (alpha) diversity and macrofauna abundances will be reduced at shallower depths in canyons, particularly in those subjected to higher energy regimes (e.g., 'V' shaped canyons);

**H<sub>4</sub>:** Steep-walled (V-shaped) canyons produce higher habitat heterogeneity than smooth cross-profile (U-shaped) canyons and show higher beta-diversity

A few predictions based on these hypotheses are summarized in figure 5.



**Figure 1.4.** Predictions based on the conceptual model and working hypotheses. **A.** Canyon benthic abundance/biomass predicted along a depth and productivity gradient. **B.** Beta diversity is higher on canyons due to enhanced habitat heterogeneity and organic loading. **C.** Alpha-diversity is higher on submarine canyons except in areas (or depths) where physical disturbance is frequent (canyon heads). In Hawaii, an oligotrophic system, slope and canyon signatures diverge more visibly than California and New Zealand Systems, where highly productive pelagic ecosystems input POM indiscriminately on canyons and slopes.

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# **Chapter 2**

## **Submarine canyons as hotspots of benthic biomass and productivity in the deep-sea: a study case of Kaikoura Submarine Canyon, New Zealand**

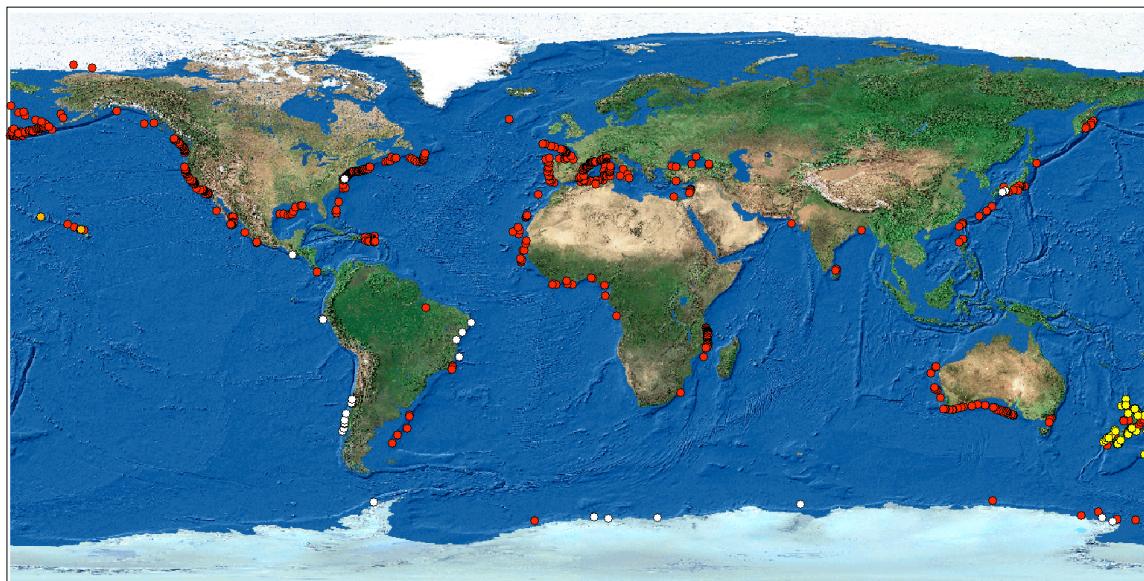
### **2.1 Abstract**

Submarine canyons are dramatic and widespread topographic features crossing continental and island margins in all oceans. Canyons can be sites of enhanced organic-matter flux and deposition through entrainment of coastal detrital export, dense shelf-water cascade, channelling of resuspended particulate material, and focusing of sediment deposition. Despite their unusual ecological characteristics and global distribution along oceanic continental margins, only scattered information is available about the influence of submarine canyons on deep-sea ecosystem structure and productivity. Here we show that deep-sea canyons such as the Kaikoura Canyon on the eastern New Zealand margin ( $42^{\circ} 01' S$ ,  $173^{\circ} 03' E$ ) can sustain enormous biomasses of infaunal megabenthic invertebrates over large areas. Our reported biomass values are 100-fold higher than previously reported for deep-sea (non-chemosynthetic) habitats below 500 m in the ocean. We also present evidence from deep-sea towed camera images that areas in the canyon which have the extraordinary benthic biomass also harbor high abundances of macrourid (rattail) fishes likely to be feeding on the macro- and megabenthos. Bottom-trawl catch data also indicate that Kaikoura Canyon has dramatically higher abundances of benthic-feeding fish than adjacent slopes. Our results demonstrate that Kaikoura Canyon is one of the most productive habitats described so far in the deep sea. The importance of such deep-sea canyons as potential hotspots of production and commercial fisheries yields merits substantial further study.

**Keywords:** submarine canyons; benthic biomass hotspots; molpadiid holothurians; macrourid fishes; Eastern New Zealand margin.

## 2.2. Introduction

Continental margins are considered major reservoirs of marine biodiversity and productivity (Sanders & Hessler 1969; Rex 1983; Snelgrove *et al.* 1992; Levin *et al.* 2001; Brandt *et al.* 2007) and have been, albeit controversially, compared to the most diverse terrestrial and shallow-water marine habitats (Rex 1983, Etter & Grassle 1992). Submarine canyons are abundant and ubiquitous features along continental and oceanic island margins that connect continental shelves to deep ocean basins (Shepard & Dill 1966). Roughly, 20% of the NE Pacific shelf edge between Alaska and the equator is interrupted by steep, narrow and abrupt submarine canyons (Hickey 1997). The single global review available on canyon distribution, origin, geology and sedimentation patterns dates from 1966 and mapped 96 major canyons around the world (Shepard & Dill 1966). Today's more detailed, readily available bathymetric data (still far for being comprehensive, and compiled in the present work for the first time) show at least 660 canyons crossing continental margins globally (Fig. 2.1).



**Figure 2.1.** Global distribution of submarine canyons counted in this study (total of 660 canyons). Three data sets were used. (1) Red circles (named) and white (unnamed) canyons from the Google-Earth (SIO, NOAA, U.S. Navy, NGA, GEBCO) databases; (2) Light-yellow circles from an unpublished database of New Zealand canyons (Thompson 2001) and (3) Orange circles from Vetter *et al.* (2010).

Patterns of benthic community structure and productivity have been studied in relatively few submarine canyons (e.g., Vetter 1994; Vetter & Dayton 1999; Hargrave *et al.* 2004; Schlacher *et al.* 2007). Some findings suggest that increased habitat heterogeneity in canyons is responsible for enhancing benthic biodiversity and creating biomass hotspots (Rowe 1983; Vetter 1994; Vetter *et al.*

2010). Enhanced local fishery production in canyons, when contrasted to regular slope environments, has also been reported and attributed to the channelling and concentrating of detrital organic matter and pelagic animal populations (Yoklavich *et al.* 2000; Brodeur 2001; Tudela *et al.* 2003; Company *et al.* 2008). Many other unusual ecological and physical have been attributed to canyons such as concentrating diel vertical migrators (Greene *et al.* 1988), displacing deep-water species to coastal zones (King 1987), promoting topographically induced upwelling (Klinck 1996; Hickey 1997; Sorbazo *et al.* 2001), enhancing dyapicnal mixing via internal wave generation (Kunze *et al.* 2002), and focussing of internal tidal bores (Vetter & Dayton 1999).

Canyons are complex topographic features often characterized by complicated patterns of hydrography, flow, and sediment transport and accumulation (Shepard *et al.* 1974; Oliveira *et al.* 2007; Garcia *et al.* 2008). Unusual physical oceanographic conditions inside canyons, such as accelerated currents and dense-water cascades, can be caused by topographic and climate forcing, increasing suspended particulate matter concentrations and transport of organic matter from coastal zones to the deep ocean (Bosley *et al.* 2004; Genin 2004; Billet *et al.* 2006; Canals *et al.* 2006; Company *et al.* 2008). These phenomena can be responsible for enhancing both pelagic and benthic productivity inside canyon habitats as well as biodiversity of many benthic faunal groups (Rowe 1983; Schlacher *et al.* 2007; Vetter *et al.* 2010).

Here we study the deep-sea Kaikoura submarine canyon on the eastern New Zealand margin ( $42^{\circ} 01' S$ ,  $173^{\circ} 03' E$ ) as part of the RENEWZ (Exploration of Chemosynthetic Habitats of the New Zealand Region) and NIWA's "Impact of resource use on vulnerable deep-sea communities" research projects. We report extraordinary megafaunal biomasses in this poorly explored deep-sea submarine canyon; patterns of benthic community structure and biodiversity in Kaikoura will be described elsewhere. Our quantitative samples and photographic surveys from the sediment-covered canyon floor indicate one of the most productive benthic habitats described so far in the deep-sea. Trawl data obtained in Kaikoura Canyon and in control areas on the open slope also show evidence of elevated demersal fish abundances associated with the canyon floor, especially of benthic-feeding species. We hypothesize that the high benthic invertebrate biomass and estimated productivity, as well as the higher benthic-feeding fish abundance, are produced by a combination of high pelagic productivity (i.e., export of phytodetrital material from the Subtropical Front System (Nodder *et al.* 2007), and high macrophyte detrital export from shallow coastal areas, channelled and deposited on flat, low-energy areas of the Kaikoura Canyon floor.

## 2.3 Materials and Methods

### 2.3.1 Sampling of macro- and megafauna

During the research cruise TAN0616 aboard NIWA's *R/V Tangaroa* (Nov 01–20 of 2006), a framed, 0.2-m<sup>2</sup> van Veen grab was used to collect four quantitative samples (Eleftheriou & McIntyre 2005) for infaunal megabenthos at depths of 1000-1040 m inside Kaikoura Canyon (figure 2.2; table 2.1). On shipboard, sediment samples were washed on a 2-mm mesh size sieve (mega-infauna) and the residue stored in 80% ethanol for quantitative analysis of abundance and biomass. Standard protocols for wet weight biomass were used (van der Meer et al. 2005). Briefly, animals were blotted dry on GF/F glass fibre filters and weighed individually on a 0.001-g precision balance after removing excess ethanol by strong suction using a peristaltic pump. Wet weights in grams of wet tissue were converted to grams of carbon per m<sup>2</sup> using the conversion factor of 4.3% (Rowe 1983). Four multiple-core deployments, each collecting 3 tubes 10 cm in diameter by 40 cm in deep, provided quantitative samples of infaunal macrobenthos in Kaikoura Canyon at depths of ~1000 m (figure 2.2; table 2.1). Samples were sieved on 300 µm mesh and residues stored in 4% buffered formaldehyde-seawater solution. Macrofauna were sorted using a dissecting microscope. During a second cruise (KAH0706) aboard NIWA's *R/V Kaharoa*, similar multiple-core samples were collected in a control area on the slope off Wairarapa basin (41° 46' S; 175° E) at two depths, 1000 and 1600 m (figure 2.2; table 2.1). A deeper station (~1600 m) located inside Kaikoura Canyon was also sampled. A beam trawl was used to provide qualitative information on megafaunal community structure (e.g., species lists and material for taxonomic identification).

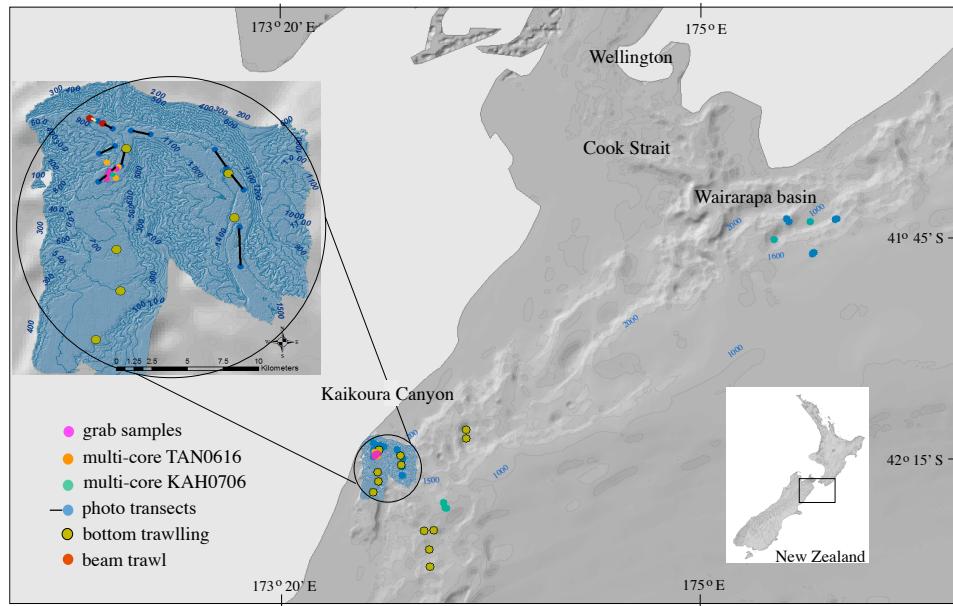
### 2.3.2 Seafloor photographic surveys

The towed camera platform (NIWA's "Deep Towed Imaging System" or DTIS) took digital photographs oriented perpendicular to the seafloor every 20 seconds along transects that varied from 0.65 to 1.6 km in length (11 transects, 464 total photographs analyzed; table 1). A total of 8 transects were positioned inside Kaikoura Canyon in two depth zones (900-1100 m and 1200-1300 m), and 3 transects positioned in a control area on the slope off Wairarapa basin at depths ranging from 1027 to 1064 m (figure 2.2; table 2.1). Photographs with frames covering an area between 1.6 and 2.5 m<sup>2</sup> of the seafloor were analyzed. Frames with areas outside of this range (when camera was either too close or too far from the seafloor) were excluded from the analysis. The total area of the seafloor analyzed in the photographs 920.4 m<sup>2</sup> in canyon and 280.8 m<sup>2</sup> in slope transects, respectively. We employed image analysis software (Image J; Rasband 2009) to determine the abundance of megafauna (invertebrate and fish) as well as of bioturbation features (*lebensspuren*) from the images. The area of the seafloor imaged by each photograph was determined with the aid

**Table 2.1.** Detailed information about the oceanographic stations where macro- and megabenthic communities were sampled off Kaikoura Canyon and Wairarapa slope (dtis, Deep Towed Imaging System).

cruise code	station n.o	date	area	gear	deployment duration (min.)	latitude South (deg.&mins)	longitude East (deg.&mins)	depth gear start (m)	depth gear end (m)	distance covered (km)	n.o photos analysed/cores sorted
<b>Kaikoura canyon sampling</b>											
TAN0616	106	17-11-06	canyon	grab	-	42° 31.20	173° 37.18	1020	-	-	-
TAN0616	107	17-11-06	canyon	grab	-	42° 31.06	173° 37.32	1029	-	-	-
TAN0616	108	17-11-06	canyon	grab	-	42° 31.39	173° 37.14	1014	-	-	-
TAN0616	109	17-11-06	canyon	grab	-	42° 30.98	173° 37.61	1028	-	-	-
TAN0616	92	16-11-06	canyon	dtis	58	42° 30.85	173° 37.86	1055	1087	0.64	42
TAN0616	100	16-11-06	canyon	dtis	66	42° 30.91	173° 37.62	1044	993	0.9	40
TAN0616	104	17-11-06	canyon	dtis	62	42° 30.35	173° 36.76	899	1035	0.65	51
TAN0616	94	16-11-06	canyon	dtis	57	42° 29.41	173° 38.34	1039	1185	0.74	31
TAN0616	97	16-11-06	canyon	dtis	60	42° 29.32	173° 37.46	1076	1015	0.65	30
TAN0616	90	15-11-06	canyon	dtis	54	42° 30.93	173° 43.13	1296	1200	0.86	55
TAN0616	102	17-11-06	canyon	dtis	62	42° 31.84	173° 43.97	1348	1300	0.91	60
TAN0616	95	16-11-06	canyon	dtis	48	42° 35.01	173° 43.82	1376	1390	1.63	45
TAN0616	98	16-11-06	canyon	multi-core	-	42° 30.71	173° 37.95	1061	-	-	1
TAN0616	101	17-11-06	canyon	multi-core	-	42° 30.90	173° 37.61	1041	-	-	2
TAN0616	103	17-11-06	canyon	multi-core	-	42° 31.12	173° 37.42	1033	-	-	1
TAN0616	105	17-11-06	canyon	multi-core	-	42° 31.37	173° 37.26	1020	-	-	1
KAH0706	3	11-06-07	canyon	multi-core	-	42° 41.27	173° 54.46	1808	-	-	4
KAH0706	6	12-06-07	canyon	multi-core	-	42° 31.15	173° 37.33	1040	-	-	5
TAN0616	99	16-11-06	canyon	beam trawl	15	42° 29.10	173° 36.92	1079	1023	0.51	-
<b>Wairarapa slope sampling</b>											
TAN0616	75	13-11-06	slope	dtis	16	41° 46.82	175° 23.85	1027	1058	0.8	38
TAN0616	76	13-11-06	slope	dtis	45	41° 47.03	175° 23.79	1041	1055	0.33	34
TAN0616	77	13-11-06	slope	dtis	35	41° 47.22	175° 24.63	1051	1064	0.36	36
KAH0706	12	13-06-07	slope	multi-core	-	41° 50.82	175° 14.79	1628	-	-	4
KAH0706	14	13-06-07	slope	multi-core	-	41° 47.40	175° 23.65	1077	-	-	4

of two scaling laser beams (20 cm apart) attached to the DTIS. Animal and bioturbation feature densities measured from each frame were then normalized to 1 m<sup>2</sup> of the sea floor and plotted along the transect length. Transects performed within similar depth ranges and in close proximity were pooled (transects 92, 100 and 104; 94 and 97; 90 and 102; 75-77; table 2.1).



**Figure 2.2.** Map showing the areas sampled in the Eastern New Zealand margin. Coloured symbols show positions of grab, multi-cores, DTIS photo-transects and bottom trawl samples in Kaikoura Canyon and Wairarapa slope.

### 2.3.3 Multi-beam data and GIS analysis

A digital terrain map of Kaikoura Canyon floor was produced using bathymetric data collected during the TAN0616 cruise by a multi-beam echo sounder (EM300). We used the high-resolution bathymetry to estimate the total area of the canyon that could be considered the invertebrate infaunal megabenthos hotspot. We based this estimate on biomass measurements from grab samples collected in the upper arm of the canyon and from the abundances of invertebrate and bioturbation features observed in photographic transects. We assumed that the high-biomass assemblages were restricted to depositional canyon-floor regions with gentle slopes of  $\leq 10$  degrees, similar to the sites where infauna were sampled, and within the depth range where the greatest concentration of animal feeding and moving traces were observed in photographs, i.e., 900-1100 m. The areal calculation was then performed using the functions ‘reclassify’ and ‘sum raster’ of the *Spatial Analyst* tool kit of ArcGIS 9, as follows: the original bathymetry grid data file (20x20 m cell-size) was first used to create another grid with the average slope of each cell (> spatial analyst > surface analysis > slope). This new grid file was then

reclassified to provide only the cells in which slopes were  $\leq$ 10 degrees. The next reclassification step used the original bathymetry grid to produce a new layer with only cells filled by depths between 900 and 1100 m. The two new layers generated, i.e., (1) depths of 900-1000 m and (2) slopes of 10 degrees or less, where then overlaid. The total number of 20 x 20 m cells in the overlaid layer were counted (74,297) and multiplied by the area of a single cell (0.0004 km<sup>2</sup>), to reach a total area of 29.719 or ~30 km<sup>2</sup>.

### 2.3.4 Bottom-fish trawl data

Research trawl survey data from the area of 42°00' – 43°00' S, 173°20' – 174°00' E were extracted from the New Zealand Ministry of Fisheries database *Trawl*. Several bottom-trawl surveys for orange roughy were carried out in the 1980s and 1990s, and trawls were taken on cruise TAN0616 (RENEWZ I). All cruises employed the standard NIWA rough-bottom orange roughy trawl net and gear set-up. Data from a total of 12 trawls from the canyon and nearby continental slope met the criteria of similarities in depth, slope and apparent bottom type. Six trawls came from the canyon; three from the upper, western side of the canyon head at about 700 m depth, and three from 1300–1400 m on the northern and eastern sides of the canyon head. Six tows were available from similar depths away from the canyon to the south and east on the adjacent slope (figure 2; table 2). The catch composition of the 12 trawls included 66 fish and squid species, which were considered demersal rather than pelagic, and to be sufficiently large-bodied to be fully captured and retained by the trawl gear for valid comparison. These were then categorized as benthic feeders (22 species) or bentho-pelagic feeders (44 species) based on a combination of dietary data from NIWA gut content studies, and morphology of the fish species (e.g. mouth position). Catch rate analyses were carried out on the species combined into the two ecological feeding groups (table 2.2).

### 2.3.5 Data analysis and statistics

Analysis of variance was employed to verify significant differences between faunal parameters (invertebrate megafauna, fish and bioturbation-feature abundances) between all sites sampled. The groups of photographic transects compared were: (1) Kaikoura Canyon head, transects 92, 94, 97, 100 and 104 (n =190 photographs); (2) deep Kaikoura Canyon, transects 90, 95, 102 (n = 160 photographs); (3) Wairarapa slope control site, transects 75, 76 and 77 (n = 108 photographs). Normality and homoscedasticity of variances were tested prior to analysis using parametric one-way ANOVA. The alpha-level was corrected with Holm's modification of the sequential Bonferroni correction to an experiment-wise p = 0.05 to avoid inflation of type-I error from multiple testing. Student's t-test was used to compare the log transformed mean total catch and catch rates between bottom trawls inside Kaikoura Canyon (n =6) versus in slope reference areas (n =6).

### 2.3.6. Worldwide inventory of submarine canyons.

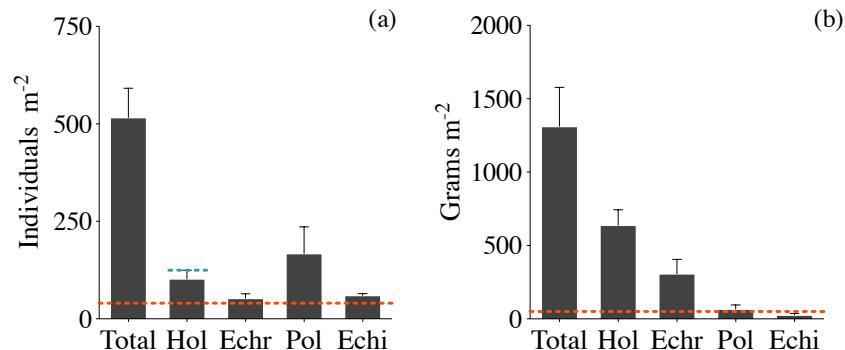
To estimate the number of submarine canyons potentially harbouring biomass hotspots such as Kaikoura, we include a worldwide inventory of submarine canyons. To the best of our knowledge, this is the first such inventory in the scientific literature. Using the online available databases for seafloor bathymetry in Google-Earth (data sources: SIO, NOAA, U.S. Navy, NGA, GEBCO), currently mapped submarine canyons can be viewed when activating the layer '*Boarders and Labels*' in the layers' panel of the Google-Earth applicative. Spatial coordinates can be then extracted. We employed a fly through over continental margins globally, using an 'eye altitude' distance of a maximum of 25 miles, enabling discernment of the smallest canyon features mapped. Available names and geographical coordinates for all canyons observed are provided in table S1 in the electronic supplementary material. A smaller proportion of geo-referenced submarine canyons were identified from unpublished databases cited in the scientific literature, such as the canyons in New Zealand (Thompson 2001) and the Hawaiian Archipelago (e.g. Vetter *et al.* 2010). It is clear that the online bathymetric data still fail to provide a comprehensive global inventory of submarine canyons because of the extremely patchy distribution (figure 2.1). For example, the eastern and western continental margins of South America lack detailed bathymetry data; however, the lower resolution bathymetry data available still reveals major canyons in those areas. In addition, major gaps occur along the margins of Africa, India and Southeast Asia. Therefore, our current inventory should be considered a conservative estimate.

**Table 2.2.** Bottom trawling samples collected inside Kaikoura Canyon and in control areas of the adjacent slope (b-pelagic = benthopelagic)

Cruise	Station n.o	date	area	deplom. (min.)	latitude	longitude	depth gear	depth (m)	distance (km)	total catch	total catch	catch rate	catch rate
												(kg. Km <sup>-1</sup> )	(kg. Km <sup>-1</sup> )
TAN0616	91	15-11-06	canyon	22	42° 30.14	173° 38.09	1130	1088	0.94	218.8	1552.8	14	46.9
TAN0616	93	16-11-06	canyon	12	42° 31.16	173° 43.22	1285	1305	0.43	124.2	480.5	19.5	35.5
TAN0616	96	16-11-06	canyon	11	42° 32.98	173° 43.52	1360	1365	0.23	25	376.9	6.5	80.4
TAN9403	25	20-03-98	canyon	36	42° 36.02	173° 37.81	740	642	2.05	255.8	318.8	6.1	5.6
TAN9403	46	22-03-98	canyon	34	42° 36.82	173° 36.57	625	736	2	204.7	233.6	5.5	4.2
WIL8901	20	26-09-93	canyon	73	42° 34.09	173° 37.60	773	633	3.19	135.5	638.5	3.8	5.7
TAN9403	22	19-03-98	slope	36	42° 27.94	173° 57.83	765	800	1.94	69.6	157.7	2.8	2.8
TAN9403	23	19-03-98	slope	36	42° 29.77	173° 57.91	877	859	2.01	23.9	590.7	1.1	8.8
TAN9403	26	20-03-98	slope	36	42° 45.16	173° 52.99	1208	1425	2	17.7	381.9	1	6.4
TAN9403	27	20-03-98	slope	33	42° 46.88	173° 49.18	1050	1105	2	5.9	210.1	0.5	4.4
WIL8901	18	26-03-93	slope	64	42° 46.58	173° 49.16	1004	1106	3.09	335.4	46	2402.2	1.3
WIL8901	19	26-03-93	slope	63	42° 45.58	173° 52.62	1222	1446	2.67	95.1	79.9	903.8	2.3

## 2.4 Results and Discussion

The multiple remote sampling devices (grab samples, multi-cores, beam trawls and photographic transects) employed on the sediment covered Kaikoura Canyon floor revealed extremely dense populations of large burrowing holothuroids, echiurans, polychaete worms and irregular urchins at depths of 900-1100 m. The mean ( $\pm$  s.e.) abundance of infaunal megabenthos (animals retained on a 2-mm sieve) was  $516 \pm 75.2$  individuals  $m^{-2}$  (figure 2.3a), i.e., roughly 10-fold higher than ever measured in detritus-based (i.e., non-chemosynthetic) habitats deeper than 500 m in the ocean (Rex et al. 2006). Megafaunal biomass, measured as wet weight, ranged from 0.8 to 2.1 kg  $m^{-2}$ , averaging  $1.31 \pm 0.26$  kg  $m^{-2}$  (figure 2.3b). Biomass dominants included the mound-building, conveyor-belt deposit feeding (Wheatcroft et al. 1989) holothuroid *Molpadia musculus* (50% of biomass), the mound building, deposit feeding echiuran *Alomasoma nordpacificum* (24%), and the conveyor-belt deposit feeding polychaete, *Maldane theodori* (5%). When converted to grams carbon, the average megabenthic biomass ( $89 \pm 18$  g C  $m^{-2}$ ) in Kaikoura Canyon is extraordinary for detritus-based habitats in the deep-sea, exceeding by 100-fold the highest megabenthic biomass previously recorded at depths below 500 m (Rex et al. 2006).



**Figure 2.3.** Kaikoura Canyon megafaunal abundance and biomass from van Veen grab samples (Hol, holothurians; Echr, echiurans; Pol, polychaetes; Echi, echinoids. (a) Average abundance (+ s.e.). (b) Average wet weight biomass (+ s.e.). Dashed red lines represent the maximum total megafaunal abundance and biomass previously reported in the scientific literature primarily for non-canyon habitats at depths > 500 m (Rex et al. 2006). Dashed green line represents holothurian densities at 3500 m in canyon (Portugal), from unpublished literature (cruise report of the National Oceanography Center, Southampton, UK, cited in Amaro et al. (2009)).

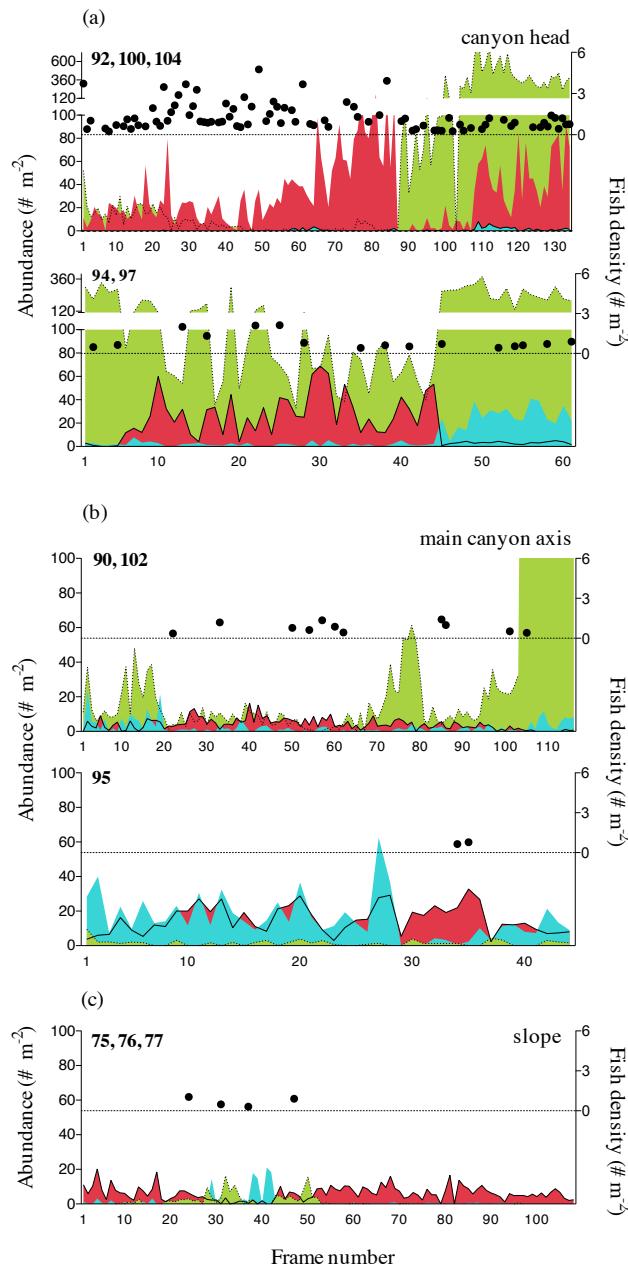
The physical setting (low relief with muddy sediments) of the main study area in the canyon head (900-1100 m depths) appears suitable for trapping particulate organic matter (POM) derived from pelagic production and coastal detrital export. The overall biomass and organic loading patterns suggest that Kaikoura Canyon is a low energy depocenter for POM derived from the

Subtropical Front System (Nodder *et al.* 2003, 2007) as well as from riverine and terrestrial inputs (Lewis & Barnes 1999). These conclusions from previous studies are corroborated by observations from the present study of macroalgal detritus in the shallowest photographic transects near the canyon head (900 m) and the absence of sediment ripples or other evidence of sediment transport in all canyon photographs from 900-1100 m.

Our benthic biomass measurements were concentrated in one arm of Kaikoura Canyon head (figure 2.2) but analysis of seafloor photographic transects indicates that this high-biomass community was widespread throughout canyon-floor sediments at depths of 900-1100 m. The eight seafloor photographic transects conducted in the canyon, extending over ~7 linear km and covering an area of 11,200 m<sup>2</sup>, revealed in all images analyzed (920.4 m<sup>2</sup> of the seafloor) high densities ( $33 \pm 2.5 \text{ m}^{-2}$ ) of bioturbation features characteristic of the biomass dominants *Molpadius musculus* and *Alomasoma nordpacificum*, including faecal mounds, feeding traces and burrows (figure 4). Feeding and mobility traces of megafauna in this part of the canyon are an order of magnitude more abundant (significant one-way ANOVA,  $p=0.001$ ) than at similar depths on the nearby slope ( $6 \text{ m}^{-2} \pm 0.4 \text{ s.e.m.}, n=108$ ), and at greater depths (1200-1400 m) within the canyon ( $7.2 \text{ m}^{-2} \pm 0.5 \text{ s.e.m.}, n=160$ ) (figure 2.4; see also figure 2.5 for more details on the abundance and types of bioturbation features). The bioturbation features formed by megafauna in the Kaikoura Canyon head area are also strikingly abundant when compared to general deep-sea depositional habitats, where biogenic structures such as feeding traces, faecal mounds and animal tracks are common features in the ocean floor (Gage & Tyler 1996). Our mean value ( $33 \text{ m}^{-2}$ ) is at least 7 times higher than reported from North Atlantic non-canyon habitats (mean  $4.5 \text{ m}^{-2} \pm 0.25$  confidence interval) where a similar towed camera platform was employed over similar depth ranges and spatial scales (Jones *et al.* 2007). In addition, the remarkable densities observed for the foraminiferan *Bathysiphon* sp. ( $127 \text{ m}^{-2} \pm 12 \text{ s.e., } n=195$ ) in the canyon head (3-fold higher than at deeper areas in the canyon and 50-fold higher than at the open slope control site; figure 2.4) also indicate organic-rich, bioturbated sediments, as observed elsewhere in continental margin depositional environments (Gooday *et al.* 1992).

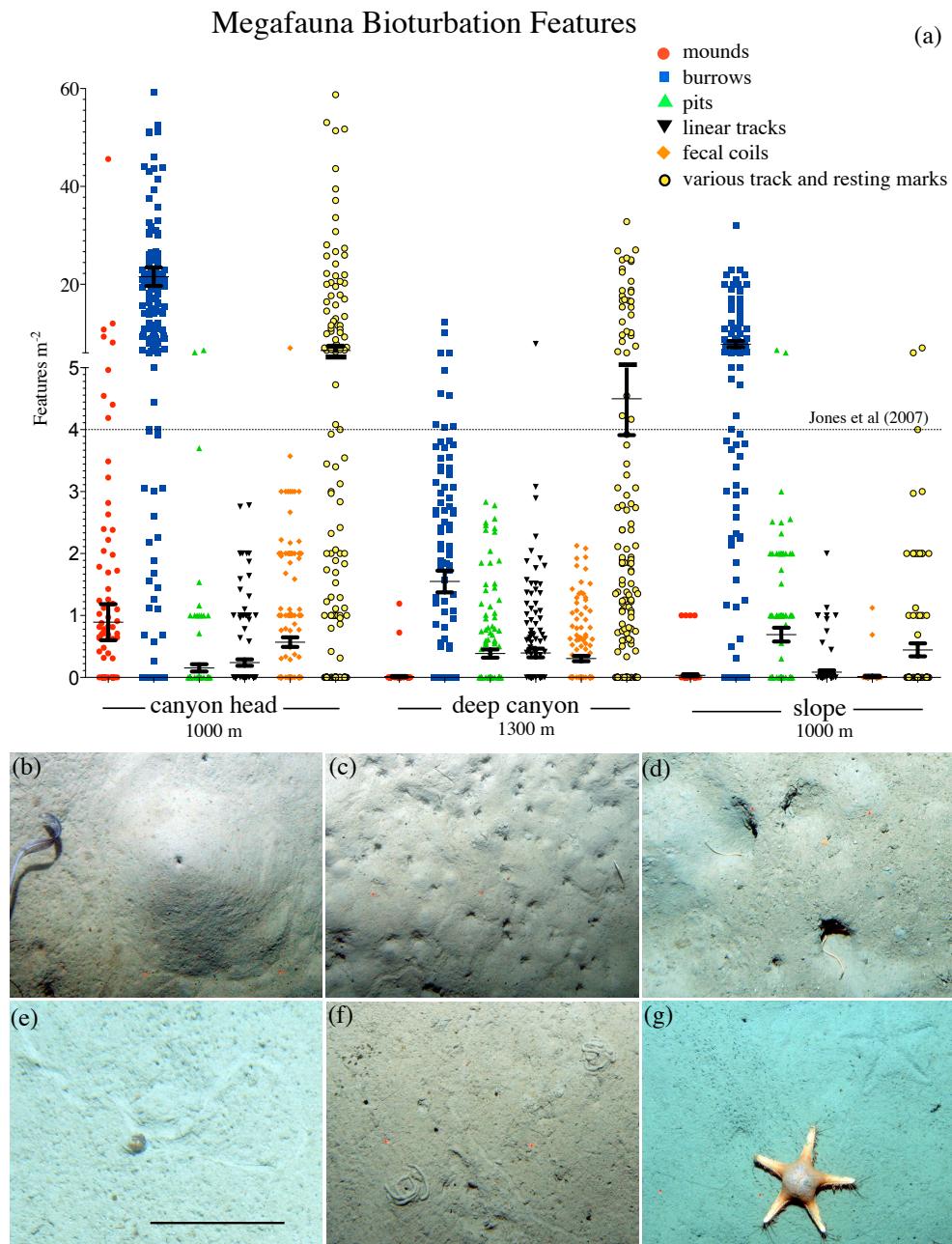
GIS spatial analysis applied to a digital terrain map of Kaikoura Canyon revealed a total area of ~30 km<sup>2</sup> of the canyon floor between depths of 900 and 1100 m with gentle slopes of < 10 degrees in which we expect the high biomass megafaunal assemblages to be found (figure 2.6; refer to section 2.3.3). Assuming an average infaunal biomass of  $1.31 \text{ kg m}^{-2}$  (based on grab samples) for this 30 km<sup>2</sup>, we estimate total infaunal megabenthic biomass for this 'biomass hotspot' in the Kaikoura Canyon to be  $\sim 3.9 \times 10^4$  tonnes wet weight. Assuming conservatively that this megafaunal biomass in Kaikoura Canyon turns over once every ~20 years (Gage & Tyler 1996), the biomass hotspot is likely to produce of order  $2.0 \times 10^3$  tonnes of megafaunal biomass yr<sup>-1</sup>. To place this

production estimate in a regional fishery context, the estimated annual production of Kaikoura megabenthic invertebrates exceeds a recent estimate of the production of orange roughy (*Hoplostethus atlanticus*) for the entire Mid-East Coast stock of the New Zealand fishery, which is derived from an area of  $>10^5 \text{ km}^2$  (New Zealand Ministry of Fisheries Report, 2009).



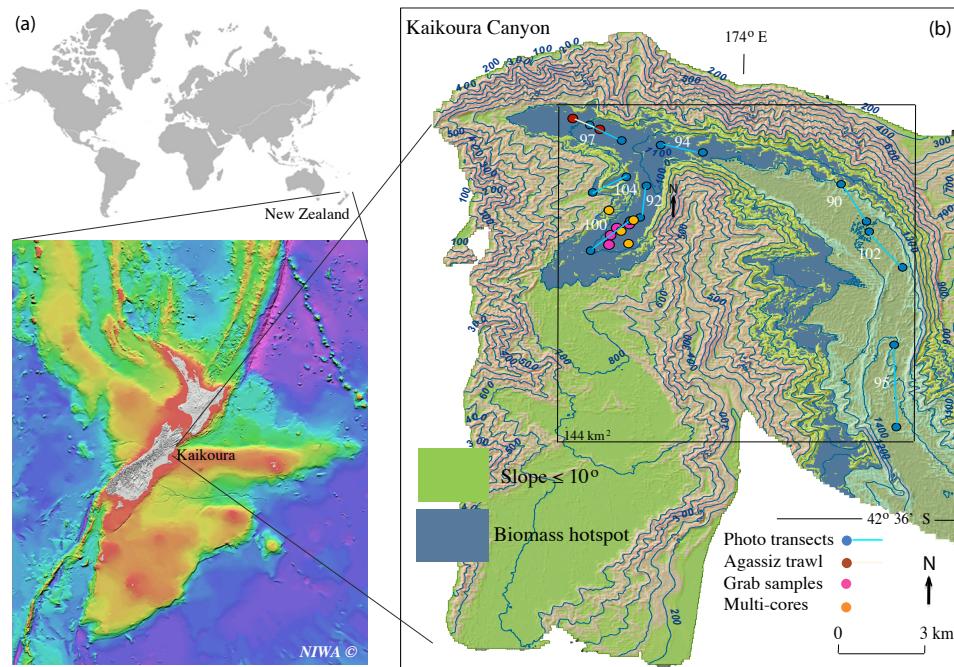
**Figure 2.4.** Abundance of epibenthic megafauna, bioturbation features, and the foraminiferan *Bathysiphon* sp. (left y-axis), and demersal fish (4 macrourid species, right y-axis). Epifaunal invertebrate megabenthos (blue shading), bioturbation features characteristic of infaunal megabenthos (red shading), demersal fish (black dots) and *Bathysiphon* sp. (green shading) from

photographic transects (with station numbers for the 11 transects indicated at top-left of charts). (a) Canyon head (900–1100 m; n = 195). (b) Main canyon axis (1100–1300 m; n = 160). (c) Wairarapa open slope site (900–1100 m; n = 108). Frame numbers represent individual photographs and indicate the total taken in each depth zone. Transects performed in close proximity within the same depth zones were pooled (e.g., transects 92, 100 and 104 were all conducted within one branch of the canyon head; see figure 2.6). Note left y-axis gaps in the upper (canyon head) panels.



**Figure 2.5. Megafauna bioturbation marks (*lebensspuren*) diversity and abundance.** (a) Counts per frame converted into  $\# \text{ m}^{-2} (\pm \text{s.e.})$  of the six categories of bioturbation marks: mounds (b), burrows(c), pits (d), linear tracks (e), fecal coils (f). The sixth category (various, g) includes sea star resting and tracking marks, paired burrows (u-shaped burrows), fish-feeding marks and unidentified tracks. b, Mound, c, Burrows, d, Pits, e, Linear tracks (generally made by the naticid gastropod

*Falsilunaria powelli*) f, Fecal coils, g, Sea star resting (R) and tracking (T) marks. All photographs besides (e) (scale bar, 10 cm) shows the DTIS laser marks (20 cm apart) for scaling. Dashed line represents average ( $\pm$  95% confidence intervals) bioturbation mark densities from North Atlantic (Faroe-Shetland channel) non-canyon sediments at 1300 m<sup>15</sup>.



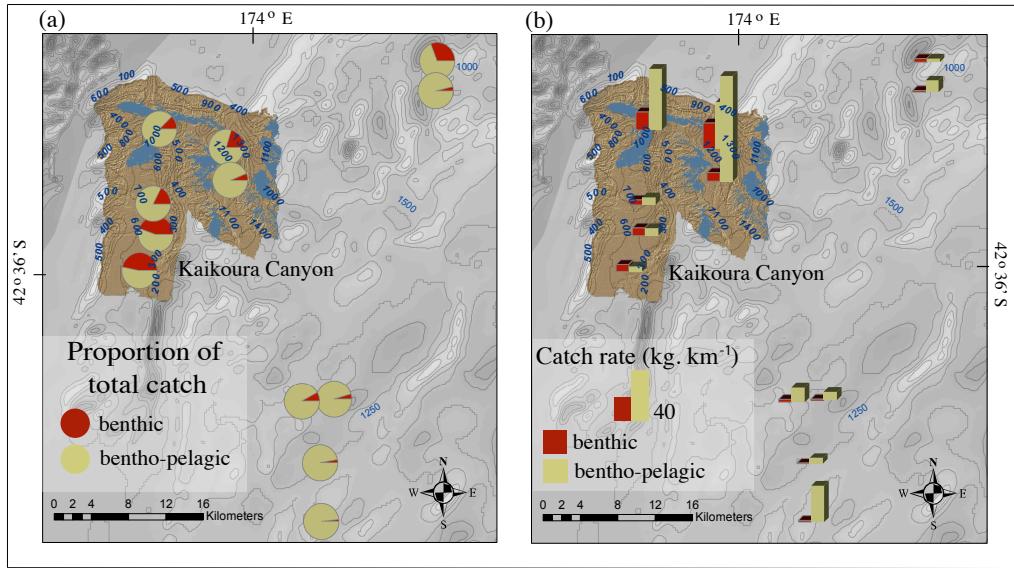
**Figure 2.6.** Kaikoura Canyon (42° 01' S, 173° 03' E), eastern New Zealand margin. (a) World map and TOPO altimetry map showing bathymetry of New Zealand continental margins and highlighting the surveyed area. (b) Detailed multi-beam bathymetry map of the canyon seafloor showing sampling sites and highlighting the estimated extent of the megafaunal biomass hotspot obtained from the GIS analysis.

Higher local benthic invertebrate biomasses have been recorded at depths of 10-60 m in submarine canyons; e.g., a maximum of ~10 kg wet weight m<sup>-2</sup> in detrital mats in Scripps Canyon on the Californian margin (Vetter 1994). However, these high-biomass detrital mats extended over relatively small areas (~0.01 km<sup>2</sup>) and therefore the total invertebrate biomass concentrated in detrital mats in Scripps Canyon (~100 tonnes wet weight) is roughly two orders of magnitude lower than estimated at 900-1100 m in Kaikoura Canyon head. In addition, very high abundances of infaunal megabenthic holothuroids similar to those in Kaikoura Canyon have been reported at 3500 m depths in Nazare Canyon off the coast of Portugal, although the biomass and areal extend of these holothuroid populations have not been documented (Amaro et al. 2009).

Other evidence of community enrichment at depths around 1000 m in Kaikoura Canyon comes from the data on infaunal macrobenthos obtained from the multiple-core samples. Densities

in the canyon ( $n=10$ ) are twice as high (significant one-way ANOVA,  $p=0.0085$ ) relative to the slope ( $n=4$ ), with the average of  $51,500 \text{ m}^{-2}$  ( $n=10$ ; s.e. =  $5,500$ ) being 10-fold higher than average macrofaunal abundances at the same depths (obtained from a global-scale analysis of macrobenthic standing stock (Rex *et al.* 2006).

The abundant macro- and megafaunal taxa in Kaikoura Canyon play well-documented roles in sediment reworking and carbon burial (e.g., Smith *et al.* 1986; Wheatcroft *et al.* 1990) and can also serve as important prey for demersal fishes (Issacs & Schwartzlose 1975; Drazen 2002; Jones *et al.* 2008). Research trawls from similar depth ranges inside the canyon and on the adjacent slope reveal that benthic-feeding fish constitute a much higher proportion of the fish catch in the canyon (21%) than on the open slope (5%) (figure 2.7a). In addition, total catch rates of demersal (bottom associated) fish species in Kaikoura are 7-fold higher than at comparable depths on the open slope (figure 2.7b) - this difference is highly statistically significant ( $t=-5.033$ ,  $p=0.001$ , d.f.=10). Among the most abundant demersal fish trawled inside the canyon, the rattails (macrourids) *Coelorinchus bollonsi*, *C. innotabilis*, *Trachyrinchus* spp., and *Coryphaenoides subserrulatus* were consistently present in our bottom photographs, and particularly abundant at 900-1100 m depths (figure 2.8). Rattail densities from photographic transects at 900-1100 m depths in the canyon head are very high, with 141 specimens observed over  $273 \text{ m}^2$  of seafloor, i.e., a density of  $5,000 \text{ ha}^{-1}$ . This exceeds by one order of magnitude total fish abundance estimated for well-studied bathyal slopes in the Northeast Atlantic (Bailey *et al.* 2009) ( $\sim 120\text{-}220 \text{ ha}^{-1}$ ) and off central California ( $\sim 50\text{-}500 \text{ ha}^{-1}$ ) (Cailliet *et al.* 1999). Frequently, our photographs revealed multiple rattails in a single frame in head-down positions consistent with feeding on sediment infauna and/or epifauna (figure S2 in the electronic supplementary material). These observations suggest that the high invertebrate macro- and megabenthic abundance/biomass is exploited by bottom-feeding fishes in Kaikoura Canyon, which historically has been an important area of major deepwater fishery catch off New Zealand (Clark *et al.* 2003).

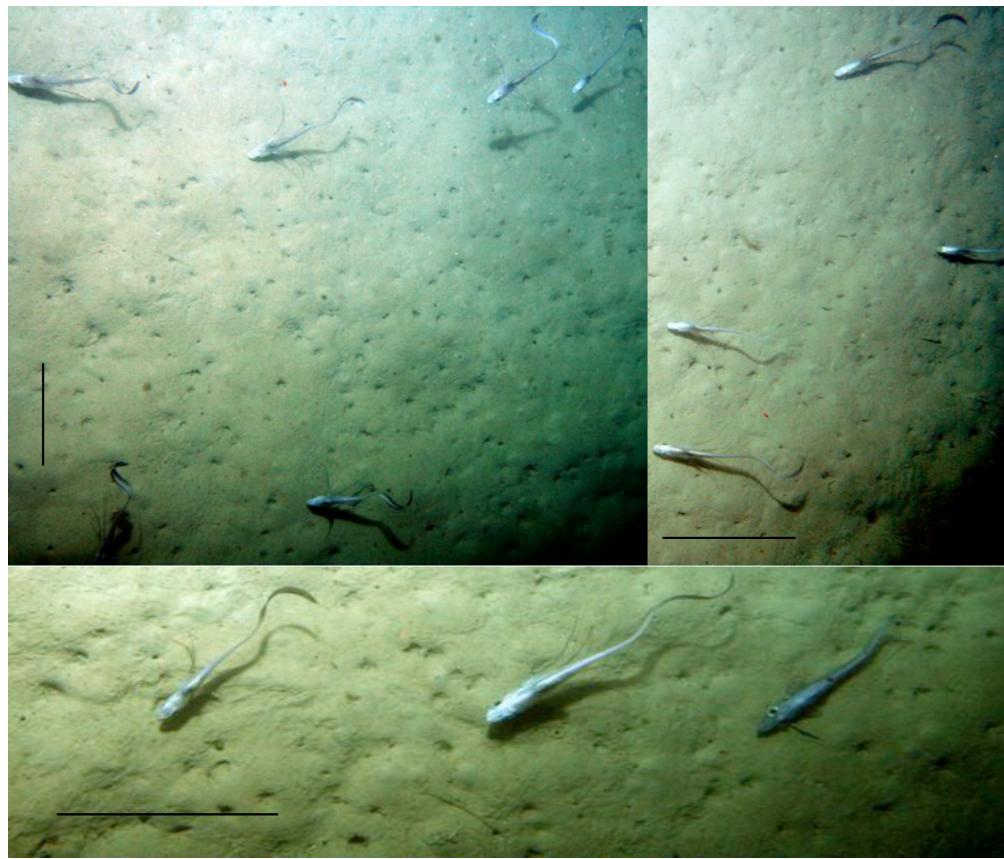


**Figure 2.7.** Total catch and catch rates of benthic and benthopelagic fish trawled in Kaikoura Canyon and adjacent slopes. (a) Proportion of benthic-feeding fish (red fill) relative to benthopelagic feeding fish (beige fill) in trawl catches in the areas indicated. (b) Catch rates ( $\text{kg km}^{-1}$ ) of combined benthic (red) and benthopelagic (beige) fish species (see table 2 for catch and catch rate values). Blue shaded areas represent megafaunal biomass hotspots calculated from the GIS analysis (section 2c, fig. 4).

Our findings suggest that Kaikoura Canyon is one of the most productive benthic habitats known for the deep-sea and may contribute significantly to deep-sea ecosystem production in the immediate canyon vicinity, which includes deep commercial fisheries for hoki (*Macruronus novaezealandiae*) and orange roughy (*Hoplostethus atlanticus*) (Clark *et al.* 2003). Whether Kaikoura Canyon production is important for fish residing temporarily in the canyon but commercially exploited more broadly remains to be ascertained.

Submarine canyons are globally numerous but very poorly sampled, which may explain why biomasses similar to those in Kaikoura Canyon have not been previously recorded for the deep sea. How common are biomass hotspots such as Kaikoura Canyon likely to be on ocean margins? Approximately 15% of the 96 submarine canyons whose physical and geological features have been reviewed in detail (Shepard & Dill 1966) exhibit characteristics similar to those of Kaikoura Canyon (and Nazare Canyon off Portugal margin, as potentially another example (Amaro *et al.* 2009) including: (1) heads positioned in coastal embayments with high loads of terrestrial material, (2) U-shaped canyon cross sections, and (3) substantial inputs of coastal sediments (Lewis & Barnes 1999; Oliveira *et al.* 2007). Thus, on the order of 15% of submarine canyons globally may support intense deep-sea biomass hotspots. Recent global bathymetry data made available on Google-Earth<sup>®</sup> (refer to section 2f) indicate that there are  $\geq 647$  submarine canyons cutting across the world's continental

margins, excluding Antarctica (which exports little terrestrial organic material to the ocean) (figure 1 shows the first available map with submarine canyon distribution in continental and island margins worldwide; see table S1 in the electronic supplementary material for canyon geographic coordinates). This suggests that globally there could be on the order of  $0.15 \times 647 = 97$  deep-sea canyons harboring biomass hotspots like Kaikoura Canyon. Clearly, the role of submarine canyons as hotspots of benthic biomass and potential fisheries production in the deep- sea merits further investigation, especially due to the steadily increasing human footprint on deep-sea ecosystems (Smith *et al.* 2008).



**Figure 2.8. Benthic-feeding fish foraging on invertebrate megafauna.** Seabed photographs taken inside Kaikoura canyon (DTIS 92, 100,104) showing high concentration of macrourid fish (rattails) in an orientation consistent with foraging and feeding; also visible are the high density of burrows and mounds made by large mega-invertebrate infauna scale bars = 20 cm at the seafloor. Most of the individuals shown in the pictures belong to the *Coryphaenoides subserrulatus* species, with the exception of a single specimen of *Coelorinchus innotabilis*, appearing in the lower panel (bottom-right).

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## 2.6. Appendix

**Supplementary Table 2.3.** Names and geographical coordinates of all submarine canyons mapped in the databases of Google-Earth (SIO, NOAA, U.S. Navy, NGA, GEBCO), in an unpublished database of New Zealand, and in Vetter et al 2010. (-) Represent West longitudes and South latitudes.

US/Canada East Coast	Latitude			Longitude			US/Canada East Coast	Latitude			Longitude		
	Deg	Min	Seg	Deg	Min	Seg		Deg	Min	Seg	Deg	Min	Seg
Great Abaco	27	4	40.26	-76	59	34.11	Veatch	39	51	57.53	-69	35	52.12
Little Abaco	26	40	54.99	-76	45	3.7	Shallop	39	55	58.69	-69	7	8.26
Jacksonville	27	35	1.73	-76	45	25.8	Hydrographer	40	11	57.89	-69	3	22.83
Blake	30	12	59.32	-76	3	18.83	Dogbody	40	2	56.2	-68	47	14.12
Pamlico	34	19	53.1	-74	33	38.39	Clipper	39	59	58.12	-68	40	4.9
Hatteras	34	39	58.16	-74	0	26.04	Sharpshooter	40	2	0.25	-68	35	29.95
Washington	37	26	58.19	-74	29	13.19	Welker	40	14	59.19	-68	34	17.08
Keller	35	32	54.44	-74	41	8.33	Heel Tapper	40	7	57.79	-68	15	5.19
Norfolk	37	3	57.53	-74	40	20.77	Oceanographer	40	29	54.3	-68	9	50.89
Hull	37	15	0.04	-74	18	17.01	Filebottom	40	11	4.07	-67	59	24.08
Accomac	37	46	0.26	-74	2	21.49	Chebbaco	40	12	1.9	-67	57	18.39
Leonard	37	45	54.14	-73	51	10.48	Gilbert	40	17	59.16	-67	55	12.61
Phoenix	37	49	54.93	-73	43	56.18	Lydonia	40	27	54.71	-67	42	3
Warr	37	54	56.33	-73	34	8.77	Powell	40	19.33	58.33	-67	22	4.31
Baltimore	38	2	55.1	-73	44	6.88	Munson	40	37	59.94	-67	2	19.94
South Vries	38	4	57.92	-73	40	10.14	Nygren	40	38	57.35	-66	30	12.02
South Heyes	38	13	0.94	-73	34	14.38	Georges	41	15	57.18	-66	16	5.56
North Heyes	38	14	57.94	-73	32	9.04	Corsair	41	19	59.6	-66	11	11.6
South Wilmington	38	15	57.64	-73	28	15.07	Verril	42	49	54.03	-61	15	6.59
Wilmington	38	21	1.22	-73	31	29.67	Dawson	42	59	59.82	-61	5	15.62
Spencer	38	33	56.78	-73	8	6.1	Bonne'camps	43	4	57.28	-60	25	9.66
Lindenkohl	38	45	57.65	-72	57	11.1	Logan	43	14	56.4	-59	50	14.44
Carteret	38	51	56.5	-72	50	5.85	The Gully	44	14	57.72	-59	15	4.42
Berkeley	38	57	1.92	-72	45	30.51	Shortland	43	49	54.95	-58	15	21.51
South Toms	38	59	0.22	-72	41	18.76	Haldimand	43	59	56.85	-57	58	23.53
Middle Toms	39	0	2.53	-72	37	24.36	DesBarres	44	0	3.3	-53	27	20.22
Toms	39	6	57	-72	42	3.72	Treworgie	43	45	6.27	-52	48	37.32
Mey	39	7	0.43	-72	26	8.69	Jukes	43	15	58.93	-52	1	12.73
Hendrickson	39	6	54.8	-72	30	52.63	Whitebourne	42	54	5.6	-51	12	23.16
Hudson	39	27	2.12	-72	12	22.69	Denys	42	46	59.72	-50	16	15.15
Jones	39	26	54.57	-71	56	8.22	Cameron	43	0	1.53	-49	35	20.23
Babylon	39	29	56.31	-71	56	7.16	Jackman	43	15	58.3	-49	28	11.75
Emery	39	33	55.98	-71	48	0.23	Guy	43	30	3.65	-49	18	18.77
Uchupi	39	36	56.31	-71	45	18.67	Hoyles	43	33	5.28	-49	5	21.48
Ryan	39	41	55.35	-71	39	1.57	Kettle	43	59	2.78	-49	0	22.1
McMaster	39	43	55.28	-71	37	0.08	Clifford Smith	44	35	14.79	-49	5	30.44
Block	39	49	55.15	-71	16	6.82	Lilly	44	51	59.36	-49	0	9.01
Alvin	39	51	56.37	-70	30	18.27	Carson	45	27	0.25	-48	39	24.4
Atlantis	39	51	58.08	-70	12	10.74							

Nantucket	39	49	56.49	-69	55	14.66												
	Latitude			Longitude				Latitude			Longitude							
	Deg	Min	Seg	Deg	Min	Seg		Deg	Min	Seg	Deg	Min	Seg					
<b>Arctic</b>							<b>Mexico/US/Canada West Coast</b>											
Barrow	72	29	27.73	-153	59	40.16	Fuerte	25	32	59.24	-109	31	48.89					
Hanna	73	29	45.2	-159	59	41.37	Pescadero	23	48	0.32	-109	35	35.31					
<b>Caribbean</b>							Palmas	23	44	57.47	-109	34	47.54					
Anegada	19	20	7.26	-64	37	15.51	Santiago	23	39	59.52	-109	35	39.38					
Molinos	18	37	51.83	-65	24	58.29	Soledad	23	39	58.27	-109	31	37.57					
Bandera	18	43	55.73	-65	37	13.96	Pulmo	23	26	57.39	-109	21	51.64					
Mameyes	18	26	56.13	-65	43	28.71	Saltito	23	24	57.88	-109	19	55.67					
Loiza	18	40	3.36	-65	53	58.85	Los Frailes	23	22	1.74	-109	19	29.01					
Pin~ones	18	27	59.65	-65	57	12.12	Salado	23	16	59.29	-109	20	48.53					
San Juan	18	49	34.47	-66	5	23.73	Santa Maria	22	49	53.35	-109	45	31.14					
Arecibo	18	43	0.002	-66	39	27.29	San Jose	22	44	56.98	-109	50	2.9					
Guajataca	18	44	8.26	-66	51	19.05	San Lucas	22	44	51.18	-109	55	25.69					
Mona	19	0	43.1	-67	22	0.08	Vigia	22	46	56.11	-109	55	0.29					
Engano	18	52	43.66	-67	48	14.53	Cardonal	22	51	1.97	-109	59	42.3					
Desecheo	17	57	40.23	-67	28	2.67	Outer Candelaria	23	0	0.44	-110	14	9.87					
Monito	17	56	53.76	-67	37	11.77	Inner Candelaria	23	1	52.38	-110	10	54.27					
Guayanilla	17	45	4.49	-66	45	43.94	San Pablo	27	14	57.29	-114	34	44.77					
Investigator	17	47	2.22	-66	16	16.95	Coronado	32	30	26.89	-117	21	45.25					
Shepard	17	45	2.59	-64	58	8.88	Loma	32	45	51.8	-117	29	14.83					
Sprat Hall	17	44	42.79	-64	55	52.37	La Jolla	32	53	7.15	-117	17	41.72					
Frederiksted	17	40	57.35	-65	1	16.69	Scripps	32	52	2.21	-117	16	49.61					
Long Point	17	30	29.88	-64	52	58.36	Carlsbad	33	5	56.27	-117	24	5.47					
Krause	17	33	1.4	-64	41	26.18	San Clemente	32	44	56.49	-118	12	55.03					
Turner Hole	17	35	16.46	-64	23	30.65	Newport	33	34	49.47	-117	55	32.84					
<b>Gulf of Mexico</b>							San Gabriel	33	33	58.13	-118	3	50.46					
Alaminos	26	29	54.09	-94	35	8.69	Catalina	33	22	58.9	-118	32	46.74					
Keathley	26	24	56.81	-93	26	36.08	Redondo	33	48	56.63	-118	28	9.39					
Bryant	25	59	56.99	-91	56	31.09	Santa Monica	33	54	59.49	-118	37	44.37					
Corte's	26	2	53.67	-91	17	58.98	Dume	33	57	55.46	-118	48	4.64					
Farnella	26	27	56.09	-90	53	23.58	Mugu	34	2	52.9	-119	5	24.87					
Green	27	2	57.21	-90	26	41.66	Hueneme	34	5	54.1	-119	14	16.76					
Mississippi	28	29	57.96	-89	44	26.86	Santa Cruz	33	54	39	-119	49	18.53					
Dorsey	28	52	55.47	-88	1	40.11	Arguello	34	20	42.06	-121	4	58.16					
Sounder	29	3	57.59	-88	7	38.49	La Cruz	35	42	57.88	-121	24	47.68					
De Soto	28	59	56.39	-87	29	45.09	Villa	35	47	58	-121	29	54.94					
<b>Mexico/US/Canada West Coast</b>							Mill Creek	35	57	14.45	-121	34	25.04					
Burica	7	59	57.18	-82	44	52.79	Lucia	35	58	1.75	-122	0	0.97					
Unnamed	13	24	6.72	-90	43	42.77	Partington	36	7	58.66	-121	44	49.04					
Lazaro Cardenas	17	7	50.05	-101	58	15.46	Sur	36	5	55.36	-122	3	59.3					
Petacalco	17	29	57.97	-101	59	44.42	Carmel	36	32	2.87	-121	58	18.4					
Banderas	20	30	27.51	-105	46	4.45	Monterey	36	39	57.11	-122	4	57.68					
Vinorama	25	26	45.69	-109	53	28.63	Soquel	36	47	40.22	-122	0	17.44					
Sinaloa	25	13	59.33	-109	5	42.12	Cabrillo	36	48	57.25	-122	17	45.17					
Ignacio	25	29	58.35	-109	29	48.54	Ano Nuevo	36	50	59.68	-122	24	7.34					

	Latitude			Longitude				Latitude			Longitude		
	Deg	Min	Seg	Deg	Min	Seg		Deg	Min	Seg	Deg	Min	Seg
<b>Mexico/US/Canada West Coast</b>				<b>Iberian Peninsula/Celtic Sea</b>									
Ascencion	36	54	59.6	-122	27	50.98	Arosa	42	23	0.46	-9	25	8.49
Pioneer	37	17	16.39	-123	15	15.11	Mugia	42	59	56.92	-9	45	9.41
Bodega	38	14	0.7	-123	34	56.84	Lage	43	34	2.67	-10	30	5.43
Arena	38	57	52.94	-124	7	4.7	El Ferrol	44	2	58.91	-9	15	4.19
Navarro	39	5	50.99	-124	6	44.94	Avile's	43	55	0.19	-6	19	14.6
Noyo	39	31	9.99	-124	20	23.46	Lastres	43	52	5.48	-4	33	7.2
Vizcaino	39	39	46.99	-124	29	42.74	Llanes	43	40	13.2	-4	23	13.8
Delgada	40	2	9.92	-124	10	14.1	Torrelavega	44	10	2.78	-4	0	10.04
Spanish	40	6	20.73	-124	18	18.61	Santander	44	10	12.78	-3	35	13.35
Mattole	40	16	47.47	-124	26	49.45	Cap Breton	43	39	49.82	-1	50	1.65
Mendocino	40	22	15.36	-124	28	5.99	Cap Ferret	44	42	7.42	-2	30	11.39
Eel	40	38	41.66	-124	34	48.73	La Rochelle	45	37	52.81	-3	46	57.88
Trinidad	41	8	43.11	-124	49	45.79	Sables s'Olonne	45	53	43.59	-4	2	58.17
McArthur	45	47	53.58	-124	53	8.96	Noirmoutier	46	0	14.28	-4	15	9.9
Astoria	46	14	40.13	-124	30	8.53	Saint-Nazaire	46	10	40.27	-4	28	30.43
Willapa	46	24	19.14	-124	45	22.52	Belle-ile	46	19	47.25	-4	47	23.03
Guide	46	36	19.93	-124	47	2.74	Blavet	46	36	49.85	-4	51	38.68
Grays	46	54	59.97	-124	52	34.15	Odet	46	39	56.33	-5	8	0.44
Quinault	47	21	32.83	-125	8	23.77	Gulvinec	46	43	53.04	-5	15	17.63
Quillayute'	47	43	16.19	-125	15	27.99	Penmarch'h	46	56	51.13	-5	40	8.8
Juan de Fuca	47	50	28.47	-125	30	28.89	Black Mud	47	39	53.63	-7	42	33.03
Nitnat	48	8	46.37	-125	50	40.54	Shamrock	47	44	53.51	-8	45	26.52
Barkley	48	15	36.06	-126	11	5.71	Whittard	48	34	48.9	-10	47	1.1
Loudoun	48	34	42.79	-126	19	56.24	King Arthur	48	29	54.38	-11	30	13.49
Father Charles	48	39	34.93	-126	30	7.3	Loury	56	25	57.48	-22	0	25.28
Clayoquot	48	59	23.15	-126	36	16.27	<b>West Mediterranean</b>						
Esperanza	49	39	29.6	-127	29	17.24	Annaba	37	6	54.72	7	39	54.92
Kyuquot	49	39	33.95	-127	47	37.32	Skikda	37	7	51.2	6	46	52.88
Crowther	49	47	37.36	-127	45	6.83	El Kebir	37	1	56.87	6	7	55.06
Oucukinsh	49	59	27.45	-128	0	13.96	Nil	36	53	50.75	5	57	47.48
Quatsino	50	9	21.29	-128	10	8.58	Bejaia	36	54	55.26	5	22	2.62
Noyes	55	9	55.36	-134	22	18.14	Sebaou	37	4	51.76	3	42	44.15
<b>Iberian Peninsula/Celtic Sea</b>							Alger	36	53	52.68	3	27	47.96
Faro	36	20	2.9	-8	0	4.28	Sefsaf	36	48	48.48	3	32	38.03
Portimao	36	54	56.76	-8	30	2.63	Guelta	36	29	57.22	0	43	53.56
Lagos	36	32	3.66	-9	5	4.67	Khadra	36	25	50.25	0	28	34.3
Sao Vicente	36	57	14.02	-9	25	13.23	Gibraltar	36	9	10.01	5	24	19.94
Setubal	38	14	57.58	-9	15	7.71	Ceuta	35	55	3.31	5	18	2.92
Lisboa	38	20	9.88	-9	20	4.95	Almeria	36	33	9.45	2	30	17.63
Cascais	38	20	12.9	-9	35	8.77	Gata	36	40	0.37	1	41	6.97
Nazare	39	36	8.28	-9	20	10.41	Palomares	37	4	23.19	1	29	32.72
Sao Pedro	39	49	56.73	-10	0	5.06	Cartagena	37	41	5.48	0	4	43.24
Aveiro	40	46	39.8	-9	44	1.98	Alicante	37	59	20.3	0	5	31.97
Porto	41	18	3.61	-9	30	5.92	Benidorm	38	13	6.92	0	28	43.35

	Latitude			Longitude				Latitude			Longitude			
	Deg	Min	Seg	Deg	Min	Seg		Deg	Min	Seg	Deg	Min	Seg	
<b>West Mediterranean</b>				<b>West Mediterranean</b>				<b>West Mediterranean</b>				<b>West Mediterranean</b>		
Pitiusas	38	30	8.13	1	36	40.12	Oristano	39	44	10.77	7	59	43.29	
Benicasim	40	8	6.82	1	24	42.82	San Antioco	38	39	50.03	8	5	1.2	
Oropesa	40	10	8.15	1	18	42.47	Toro	38	29	58.85	8	12	54.34	
Torreblanca	40	13	10.13	1	20	44.17	Teulada	38	30	12.98	8	37	40.71	
Alcalá de Chivert	40	13	52.92	1	25	0.77	Spartivento	38	30	9.97	8	55	43.53	
Peníscola	40	18	57.1	1	19	53.73	Cagliari	38	55	1.49	9	26	56.59	
Benicarló	40	21	3.16	1	21	46.72	Bizerte	38	23	5.96	9	59	47.89	
Tortosa	40	49	6.37	1	34	40.44	San Lorenzo	39	30	2.96	9	46	51.24	
Tarragona	40	50	8.57	1	59	42.89	Arbatax	39	57	0.81	9	52	48.91	
Llobregat	41	16	14.91	2	10	21.26	Orosei	40	12	6.16	9	53	46.28	
Barcelona	41	14	6.26	2	31	46.31	Gonone	40	18	10.75	9	52	44.21	
Mataró	41	19	11.37	2	38	38.88	Posada	40	44	9.39	9	56	45.89	
Blanes	41	29	11.12	2	53	38.23	Caprera	41	25	1.8	9	57	52.21	
Palamos	41	37	6.72	3	29	47.11	Napoli	40	35	6.01	14	6	50.7	
Fonera	41	52	10.29	3	26	36.15	Stromboli	38	50	2.74	15	23	55.76	
Cabo Creus	42	21	16.71	3	28	37.39	Patti	38	48	59.32	15	23	50.72	
Lacaze-Duthiers	42	25	20.78	3	30	10.34	San Vito	38	18	54.04	12	57	59.74	
Bourcat	42	35	10.7	3	44	35.63	Messina	37	42	3.41	15	47	50.97	
Marti	42	40	5.13	3	59	43.89	<b>East Mediterranean</b>							
Septe	42	42	15.21	4	12	36.83	Alexandria	31	44	2.18	29	59	48.86	
Montpellier	42	46	20.35	4	25	34.82	Antalya	36	39	56.57	30	39	59.13	
Petit Rhône	42	50	12.05	4	39	40.15	Junieh	34	4	58.25	35	29	50.95	
Grand Rhône	42	46	19.22	4	59	30.36	Saint Georges	33	55	7.72	35	28	45.71	
Marseille	43	0	11.21	5	3	40.52	Beirut	33	54	49.5	35	10	50.55	
Cassis	43	0	14.52	5	24	36.64	Zahrani	33	54	56.43	35	9	1.52	
Stoechades	43	7	9.63	6	39	38.49	Saynīq	33	32	56.76	35	18	54.18	
Saint-Tropez	43	16	57.06	6	56	46.2	Akhziv	33	4	57.25	35	2	54.81	
Cannes	43	25	6.1	7	9	44.04	<b>Black Sea</b>							
Var	43	34	3.79	7	15	46.45	Bosporus	41	30	3.92	29	22	46.48	
Roia	43	45	11.18	7	38	43.1	Sakarya	41	19	41.93	30	40	17.61	
Taggia	43	45	4.4	7	53	45.4	Kızılırmak	42	5	31.78	35	44	24.82	
Verde	43	47	11.3	7	53	40.75	Chorokh	41	50	3.21	41	11	55.51	
Ligurian	43	45	8.31	8	34	45.74	Enguri	42	15	47.15	41	11	9.62	
Genova	44	0	3.69	8	45	49.23	Kumani	44	39	32.92	37	12	43.83	
Lle Rousse	42	47	54.58	8	54	58.13	Bosporus	41	30	3.92	29	22	46.48	
Calvi	42	39	4.85	8	41	44.3	<b>Gulf of Alaska/Aleutian Trench</b>							
Galeria	42	29	8.47	8	32	46.84	Smith	58	54	17.74	-146	13	11.01	
Porto	42	16	10.56	8	25	42.15	Adak	51	26	1.3	-177	6	43.52	
Sagone	42	0	4.28	8	26	47.3	Kanaga	51	12	44.99	-177	59	16.23	
Ajaccio	41	49	1.72	8	36	49.35	Pchnoi	51	59	43.9	-179	29	39.67	
Valinco	41	39	6.26	8	35	45.28	Bowers	52	49	34.93	-179	24	52.81	
Des Moines	41	31	3.79	8	40	53.52	Usof	53	4	24.52	-166	39	0.05	
Castelsardo	41	18	10.12	8	27	39.46	Tanaga	51	46	59.78	-178	29	52.11	
Il Catalano	39	55	2.35	7	47	54.11	Amatignak	51	8	18.38	-179	28	31.71	

	Latitude			Longitude				Latitude			Longitude		
	Deg	Min	Seg	Deg	Min	Seg		Deg	Min	Seg	Deg	Min	Seg
<b>Gulf of Alaska/Aleutian Trench</b>													
Anchitka	51	15	20.92	-179	52	11.75	Carlisle	53	28	28.41	-170	15	20.7
Ward	51	3	44.72	-179	18	39.12	Umnak	53	46	21.96	-169	58	46.99
Karius	51	8	50.49	-178	50	44.45	Uliaga	53	38	11.29	-169	41	0.34
Makar	51	9	13.18	-178	54	34.04	Okmuk	53	49	50	-169	20	32.35
Seymour	51	11	43	-178	45	21.83	Inanudak	53	59	47.11	-168	54	17.67
Bird	51	23	55.32	-178	15	30.35	Bering	54	7	39.21	-168	14	8.55
Thurmond	50	47	53.42	-178	3	30.83	Bristol	54	54	50.18	-168	59	27.6
Ayugadak	51	29	43.15	-178	7	18.1	Baranof	54	59	48.92	-137	31	0.11
Rat Island	51	29	27.82	-177	51	15.98	Bogoslof	53	54	36.78	-167	47	53.37
Krysi	51	27	47.81	-177	46	15.1	Saint George	56	0	21.14	-172	0	16.68
Bukhti	51	46	45.02	-177	33	30.58	Pribilof	55	34	47.23	-169	59	39.17
Sobaka	51	29	42.12	-177	13	19.44	Zhemchug	57	29	46.29	-175	19	28.25
Vega	51	30	6.58	-177	8	38.16	Saint Matthew	58	28	38.65	-177	20	11.68
James	50	51	18.64	-177	11	17.92	Middle	58	36	47.75	-175	44	33.7
Saint	51	30	3.07	-176	55	40.04	Navarin	60	29	44.52	-179	45	30.61
Murray	51	30	9.5	-176	49	33.14	Litke	57	54	53.18	-163	55	41.74
Coulee	51	41	59.02	-176	21	36.04	Pokatyy	56	53	5.74	-163	17	23.94
Broad	51	11	50.57	-175	51	33.87	Wildcat	58	37	9.03	-146	22	19.32
Tahoma	51	44	31.77	-175	23	19.35	<b>Japan-RyuKyu Trenches</b>						
Pennant	51	54	45.48	-175	5	34	Nerpich'y'e	55	48	30.42	162	41	35.92
Heck	52	14	49.78	-175	0	26.09	Chazhma	55	9	19.86	161	59	25.24
Agattu	52	22	52.89	-172	35	33.67	Kozlova	54	32	8.17	161	59	41.41
Abrahan	52	36	44.51	-172	20	27.78	Kronotskaya	53	59	27.04	160	37	11.14
Stalemate	52	49	39.94	-171	25	31.69	Zhupanova	53	32	22.33	160	20	29.26
Etienne	52	39	54.59	-171	19	9.83	Kushiro	42	20	1.51	144	56	26.53
Strandberg	52	26	24.87	-176	44	25.66	Katakai	35	13	58.65	141	2	7.12
August	52	29	47.2	-176	51	29.07	Kamogawa	35	3	13.21	140	12	19.57
Cargo	52	26	46.57	-176	30	18.13	Habuto	35	0	10.21	140	11	1.15
Segula	52	11	57.8	-177	54	36.44	Kottono	34	51	39.15	140	4	8.87
Sitkin	52	15	8.09	-178	20	32.03	Mera	34	51	54.3	139	42	5.31
Grenell	52	18	47.42	-179	2	36.12	Inoko	34	54	39.41	134	34	59.52
Roberts	52	26	44.35	-179	19	55.5	Tatemaya	35	0	16.49	139	44	33.74
Rude	53	18	17.05	-178	44	39.68	Suno Saki	34	56	31.91	139	34	36.84
Bobrof	51	56	44.1	-177	31	42.34	Tokio	35	2	29.22	139	43	54.78
Aganak	51	54	46.37	-177	17	41.58	Jogashima	35	5	33.41	139	32	5.99
Koniuji	52	14	41.57	-175	16	45.59	Misaki	35	7	45.38	139	30	24.47
Korovin	52	44	38.58	-174	4	5.24	Miura	35	9	47.89	139	28	7.34
Atka	52	44	45.07	-173	46	28.98	Hayama	35	13	11.71	139	27	50.83
Amlia	52	53	56.65	-173	14	21.25	Enoshima	35	14	13.14	139	25	11.39
Seguam	52	39	42.48	-172	35	44.01	Sagami	35	14	42.77	139	22	11.33
Amukta	53	9	40.34	-171	44	24	Iro	34	23	18.49	138	53	38.48
Chagulak	53	15	8.58	-171	21	14.01	Suruga	34	43	19.19	138	34	36.81
Yunaska	53	15	17.31	-170	50	39.77	Zenisu	33	44	24.09	138	55	6.37
Herbert	53	24	42.39	-170	39	37.09	Tenryu	34	0	10.7	137	34	5.7

	Latitude			Longitude				Latitude			Longitude		
	Deg	Min	Seg	Deg	Min	Seg		Deg	Min	Seg	Deg	Min	Seg
<b>Japan-RyuKyu Trenches</b>							<b>Australia/Tasmania</b>						
Shionomisaki	33	9	33.47	135	57	31.68	Vancouver	-35	29	18.02	118	27	28.06
Unnamed 1	33	34	51.03	135	15	4.99	Albany	-35	30	22.46	118	9	33.39
Unnamed 2	33	34	25.58	135	2	6.2	Wilson	-35	30	19.41	117	9	44.09
Unnamed 3	33	37	10.54	134	51	59.85	Broke	-35	25	16.14	116	9	37.27
Unnamed 4	33	20	37.29	133	53	32.69	D'Entrecasteaux	-35	20	8.85	115	49	4.88
Tonbi	28	42	45.49	130	37	57.51	Leeuwin	-35	15	15.65	115	29	27.2
Okinoerabu	27	14	4.47	128	59	41.13	Perth	-31	47	8.9	114	31	56.76
Kerama	25	43	37.9	126	41	53.04	Pelsaert	-29	28	58.56	113	34	12.7
Shih-t'i Pi	23	30	41.74	121	30	38.87	Geraldton	-29	15	15.22	112	54	45.91
Wu-shih Pi	23	12	40.01	121	25	20.45	Wallabi	-29	0	43.46	112	35	19.66
Hsin-i	23	1	39.8	121	21	44.33	Houtman	-28	24.64	24.64	112	28	49.37
Tung-chiang	22	21	28.85	120	16	9.27	Carnavon	-23	56	5.94	111	15	59.69
Cagayan	18	25	48.43	121	35	38.18	Cloates	-22	8	28.08	112	50	1.02
Abra	17	30	26.56	120	21	18.85	Cape Range	-21	52	18.49	112	55	18.15
Santa	17	28	39.52	120	23	59.2	<b>New Zealand</b>						
<b>Australia/Tasmania</b>							Aiguilles	-35	3		176	3	
Everard	-38	19	44.32	149	27	30.4	Albatross	-49	43		179	0	
Bass	-38	40	21.86	149	4	42.21	Arawhata	-43	51		168	23	
Flinders	-39	38	21.36	148	49	39.7	Breaksea	-45	35		166	30	
Gantheaume	-37	27	27.76	137	31	55.51	Brodie	-46	20		170	40	
Kangaroo	-37	15	49.51	137	31	26.36	Cascade	-44	0		168	15	
Seal	-37	8	24.4	137	17	1.08	Colville	-36	10		176	38	
Sprigg	-37	1	36.94	136	49	46.24	Five Fingers	-45	50		166	10	
Du Couedic	-37	0	29.37	135	59	57.83	Foulwind	-41	55		169	40	
Althorpe	-36	37	20.1	135	44	45	Haast	-44	0		167	55	
Gambier	-36	29	26.48	135	39	47.33	Haast channel	-44	50		167	0	
Neptune	-36	30	8.38	135	30	16.42	Hurunui	-42	57		173	45	
Spencer	-36	17	24.89	135	12	53.88	Jackson	-43	55		168	27	
Lincoln	-36	25	20.38	135	11	42.93	Kaipara	-36	44		173	48	
Topgallant	-36	5	20.34	135	6	48.99	Karetu	-34	25		171	45	
Whidbey	-36	10	16.21	134	46	46.06	Matheson	-42	30		179	40	
Pearson	-36	12	15.55	134	13	39.59	Milford	-44	35		167	40	
Nuyts	-35	57	15.82	133	49	10.34	Mokohinai	-35	45		176	15	
Fowlers	-35	42	23.12	133	16	25.77	Molyneux	-46	31		170	20	
Ceduna	-35	45	13.91	132	44	29.31	Murimoto	-34	2		172	55	
Adieu	-35	35	28.06	132	11	39.48	Ngatoro	-36	50		176	50	
Yalata	-34	46	24.96	131	41	37.99	Nicholson	-41	28		174	48	
Nullarbor	-34	57	30.37	131	11	12.13	North Cape	-32	22		173	10	
Eucla	-34	10	32.08	128	40	47.4	Okains	-43	22		173	57	
Eyre	-33	50	20.22	126	19	3.25	Pallister	-41	44		175	5	
Pasley	-34	24	8.51	124	14	3.47	Paparoa	-42	22		169	53	
Esperance	-34	40	5.1	121	46	41.83	Rakitu	-35	55		176	30	
Stokes	-34	49	44.41	121	0	44.51	Ranfurly	-37	34		178	41	
Bremer	-35	0	20.36	119	54	54.78	Rekohu	-42	30		176	30	

	Latitude			Longitude				Latitude			Longitude		
	Deg	Min	Seg	Deg	Min	Seg		Deg	Min	Seg	Deg	Min	Seg
New Zealand							India						
Ruahine	-35	38		176	8		Swatch of no ground	21	13	29.21	89	25	51.48
Secretary	-45	10		166	42		North Trinco	8	40	10.46	81	36	59.38
Surville	-34	7		173	5		South Trinco	8	51	43.74	81	24	47.58
Sutherland	-44	36		167	20		Trincomalee	8	32	19.14	81	16	32.85
Tataweka	-35	28		175	54		Africa						
Tauranga	-37	24		176	53		The Swatch	23	16	0.46	67	13	30.58
Tokomairiro	-46	25		170	32		Lindi	-9	38	0.67	40	12	31.42
Wairarapa	-41	28		174	58		Mikindani	-9	49	18.52	40	25	1.62
Waitaki	-45	10		171	35		Rovuma	-10	25	46.62	40	29	40.45
Yates	-44	27		167	38		Quionga	-10	31	32.49	40	39	14.07
Cavalli	-38	47	8.56	174	2	33.2	Mebuisi	-10	35	40.91	40	41	42.23
Parengarenga	-34	30	20.45	173	24	15.77	Tungue	-10	43	44.3	40	39	38.34
Northen Viti	-38	59	36.39	172	29	38.48	Afungi	-10	47	20	40	46	55.8
Central Viti	-39	3	10.71	172	26	27.05	Vamizi	-10	57	18.71	40	44	59.96
Southern Viti	-39	7	17.4	172	27	8.51	Metundo	-11	5	18.86	40	43	38.19
Hokitika	-42	19	33.84	169	45	42.3	Macunga	-11	9	46.21	40	46	40.83
Moeraki east	-44	35		171	21		Niuni	-11	12	39.73	40	44	52.56
Moeraki west	-43	36.181		168	51.847		Suna	-11	17	42.02	40	45	21.62
Haast	-44	4	36.01	167	59	28.52	Tambuzi	-11	25	23.01	40	43	45.97
Cook	-43	17	33.86	169	33	19.5	Kero Niuni	-11	35	14.41	40	41	39.05
Mason	-46	57	18.12	167	19	59.38	Medjumbe	-11	44	11.86	40	41	33.68
Taieri	-46	15	30.18	170	46	46.18	Macaole	-11	54	45.01	40	39	40.77
Hoopers	-46	6	24.66	170	59	48.2	Pantalon	-11	56	8.78	40	47	1.23
Saunders	-45	58	26.96	171	0	2.95	Montepuez	-12	32	44.49	40	39	35.87
Papanui	-45	53	17.72	171	5	8.09	Amelia	-12	53	17.09	40	39	35.51
Taiaroa	-45	46	14.63	171	10	3.54	Lurio	-13	29	18.51	40	35	41.42
Karitane	-45	38	30.9	171	9	58	Membra	-14	8	16.36	40	39	16.12
Pukaki	-42	20	18.07	174	0	16.2	Fernao Veloso	-14	21	41.58	40	47	22.04
Pegasus	-43	14	43.15	173	41	6.11	Janga	-14	36	42.24	40	52	56.06
Kaikoura	-42	35	22.1	173	44	45.55	Conducia	-14	55	18.42	40	49	34.59
Opauawae	-41	45	18.19	175	22	53	Mocambo	-15	9	40.89	40	43	40.48
Cook Strait	-41	20	10.56	174	35	38.08	Mucalanga	-15	35	16.73	40	36	50.84
Pahaua	-41	41	48.75	175	49	6.78	Namaete	-15	43	38.06	40	32	50.19
South Honeycomb	-41	27	17.97	175	50	10.91	Congolene	-16	5	41.87	40	13	18.96
North Honeycomb	-41	23	47.33	175	52	37.65	Zambezi	-18	46	52.7	39	32	12.28
Whareama	-41	7	16.99	176	23	0.43	Tugela	-30	3	47.04	32	10	35.44
Turnagain	-40	55	22.77	176	47	4.28	Congo	-5	59	39.57	11	49	56.73
Madden	-40	38	18.7	177	19	0.55	Gabon	0	31	13.13	8	18	45.76
Hawke	-39	38	20.77	177	51	53.12	Calabar	3	51	50.19	8	13	29.09
Poverty	-39	0	21.56	178	14	18.9	Mahin	5	59	43.71	4	24	43.33
Gisborne	-38	45	19.89	178	49	36.3	Avon	6	9	37.76	3	54	52
White Island	-37	9	30.68	177	31	49.9	Baoule	4	3	39.54	-2	5	9.22
Hauraki	-35	20	3.83	175	35	0	Aby	4	14	36.52	-3	40	21.17

							Le Trou Sans Fond	5	11	19.15	-3	59	18.12
	Latitude			Longitude				Latitude			Longitude		
	Deg	Min	Seg	Deg	Min	Seg		Deg	Min	Seg	Deg	Min	Seg
<b>Africa</b>													
Tabou	3	53	38.41	-7	11	7.18	Amazon	-3	22	39.54	-48	25	22.51
Grand Cess	3	57	46.01	-8	20	21.99	Rio de La Plata	-37	8	55.04	-53	42	45.79
Bijagos	11	1	46.58	-18	20	30.99	Mar del Plata	-37	39	27.8	-53	40	6.26
Geba	11	27	34.11	-18	15	2.86	Bahia Blanca	-41	23	1.84	-54	23	9.44
Qualo	11	48	18.77	-17	59	51.4	Ameghino	-43	40	48.3	-57	21	38.91
Mandingo	12	12	39.72	-18	25	25.82	Almirante Brown	-46	10	46	-59	2	26.88
Dakar	14	45	59.32	-17	47	43.13	San Antonio	-33	40	33.18	-72	16	9.94
Kayar	14	58	1.98	-17	17	15.01	Unnamed 1	-42	29	38.15	-74	43	24.48
Mauritania	16	51	53.1	-16	49	56.63	Unnamed 2	-41	29	22.86	-74	22	21.89
Nouakchott	18	1	45.29	-16	34	1.18	Unnamed 3	-40	7	20.29	-74	13	9.31
Tanoudert	20	1	9.89	-18	57	54.53	Unnamed 4	-39	45	3.08	-74	13	38.74
Arguin	20	40	57.74	-20	49	13.19	Unnamed 5	-38	55	15.14	-74	7	26.07
Nouadhibou	21	13	4.88	-18	47	5.65	Unnamed 6	38	26	2.66	-74	12	36.18
Corveiro	22	5	8.35	-19	15	38.58	Unnamed 7	-36	42	40.48	-73	39	47.19
Chtoukane	25	14	6.98	-16	44	34.3	Unnamed 8	-33	26	40.58	-72	5	16.32
Nwayfadh	25	32	34.25	-16	31	58.04	Unnamed 9	-32	17	8.33	-71	47	41.86
Lamjaybir	25	47	32.65	-16	19	51.24	Unnamed 10	-6	46	54.7	-81	8	26.49
Cordero	25	58	21.52	-16	21	9.17	Unnamed 11	-7	6	6.25	-80	54	17.39
Agadir	32	29	59.8	-12	50	1.64	Unnamed 12	-18	49	43	-37	51	31.29
<b>Hawaiian archipelago</b>													
Nonopu	22	9.67	159	-159	42	31	Unnamed 14	-10	57	46.92	-36	48	8.85
Kailiu	22	14	44.33	-159	37	7.28	Unnamed 15	-7	55	40.41	-33	59	18.93
Kaneohe	21	33	55.57	-157	45	32.92	Unnamed 16	-64	55	57.74	-64	55	57.74
Sampan	21	31	14.98	-157	44	22.58	Unnamed 17	-69	57	20.03	9	18	29.4
Kailua	21	28	45.56	-157	38	39.16	Unnamed 18	-69	30	38.65	4	53	15.8
Mokio	21	18	41.09	-157	12	55.28	Unnamed 19	-69	41	34.5	24	53	23.59
Naiwa	21	14	6.13	-157	3	43.69	Unnamed 20	-69	51	12.54	165	33	3.63
Kalvanui	21	13	45.84	-157	0	55.68	Unnamed 21	-70	56	19.72	168	47	57.93
Waihanau	21	13	45.53	-156	59	46.93	Unnamed 22	-65	25	4.93	70	1	41.94
Waialeia	21	13	9.38	-156	57	42.73	<b>Antarctica</b>						
Waikolu	21	13	17.66	-156	55	23.74	Wegener	-70	44	46.21	-13	59	16.55
Waipu	21	14	23.68	-156	53	47.38	Porpoise	-64	19	14.88	131	2	22.29
Waiehu	21	12	46.13	-156	51	13.13	Terra Nova	-68	59	55.83	158	59	56.13
Wailau	21	13	23.33	-156	48	41.54	Oates	-67	58	54.9	164	28	50.14
Kawainui	21	12	41.93	-156	47	16.1	Borchgrevink	-70	15	14.08	170	17	47.79
Halawa	21	12	32.09	-156	43	6.23	Wilson	-70	32	36.2	176	18	35.9
Nihoa	23	11		-161	54	23							
Maro	25	32		-170	24	25							

Note: Entries in shaded yellow are from the unpublished database on New Zealand canyons (Thompson 2001); in blue are unnamed canyons from the Google-Earth database; and in orange from Vetter et al. (2010).

# **Chapter 3**

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

### **3.1 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, Hawaii, 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 hours 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 synaphobranchid 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 significantly so 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.

**Keywords:** submarine canyons, demersal fish, Hawaii, habitat heterogeneity, species richness, organic matter input, oxygen minimum zone

## 3.2 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; Sorbazo 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 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., in press). 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., in press; 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 (*Sebastodes 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” (*Halipteris willmoei*), arguing that rockfish use these three-dimensional habitats as refuges from predators. Ublein 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 mix 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 et al., 1998), as well as the vertical flux of particulate organic carbon (POC) (Gooday 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 Hawaiian Islands, a major slope habitat in the central North Pacific. While quantitative surveys have been conducted on island and atoll flanks to depths of  $\leq 300$  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 Hawaiian 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 Hawaiian archipelago, to investigate the potential role of habitat heterogeneity and of 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.

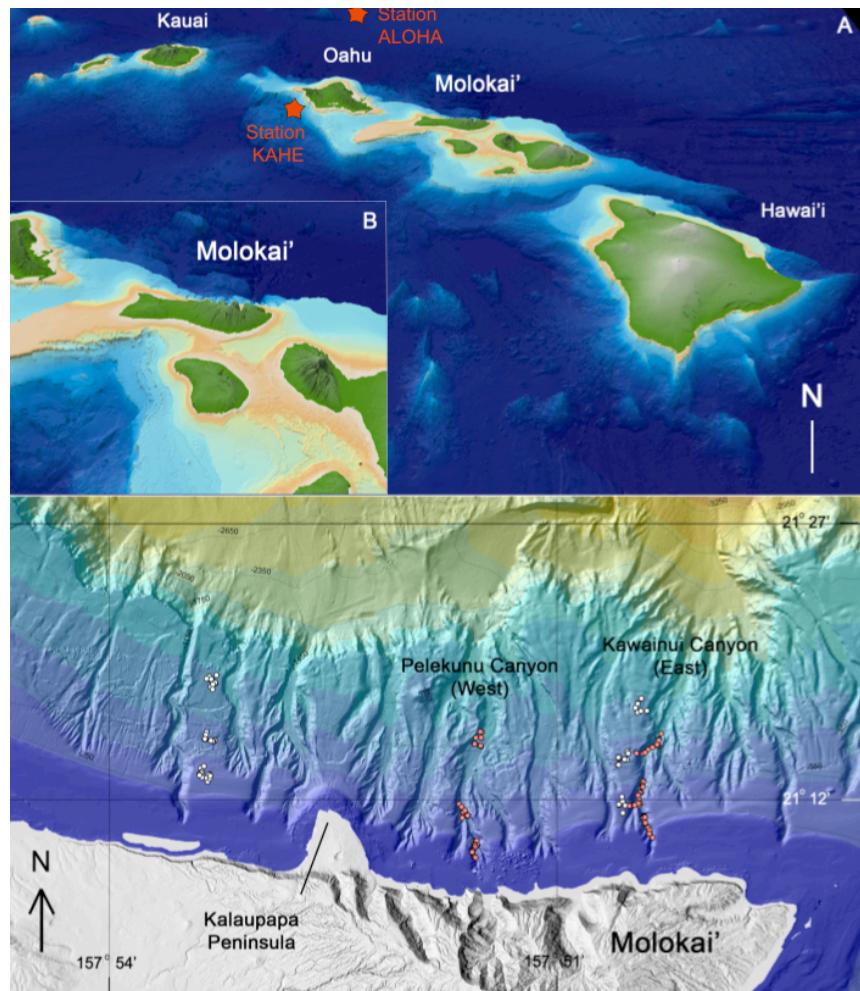
This study of demersal fish assemblages on the submarine flanks of Moloka'i was part of a broader project to investigate the roles of Hawaiian submarine canyons in enhancing fish and invertebrate diversity and abundance on the slopes of oceanic islands imbedded in an oligotrophic ocean (the North Pacific Subtropical Gyre). Patterns of diversity and abundance of invertebrate mega- and macrofauna fauna in canyon versus slope habitats are reported in Vetter et al (2010) and De Leo et al (in Chapter 4), respectively.

### **3.3. Materials and Methods**

#### **3.3.1 Study area**

The Hawaii 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 Hawaiian 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 Kawainui Canyons and the two adjacent slope sites studied occurred along the north shore of Moloka'i (Fig. 3.1). 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. 3.1; 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).



**Figure 3.1** Map of the study area. A-B, 3D-view of bathymetry and relief of the Main Hawaiian Islands with detail of Molokai' (imagery from Main Hawaiian Islands Multibeam Synthesis, SOEST, University of Hawaii, <http://www.soest.hawaii.edu/HMRG/Multibeam/index.php>). Hawaiian 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 were conducted (white symbols, slopes; pink or grey, canyons). Numbers represent depth in meters. [Detailed multi-beam bathymetric data provided by C. Kelley and J. Smith, from Hawaiian Undersea Research Laboratory (HURL)].

### *3.3.2 Demersal fish assemblages and habitat composition*

Fish were identified to the lowest possible taxonomic level, generally to 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 3.1. 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 (10cm) 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 m<sup>2</sup> (0.01 hectare). 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 estimators (Chao1 and Chao2) to estimate total species richness within canyon and slope depth strata (Cowell and Coddington, 1994).

**Table 3.1** 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	depth	habitat	initial position (dec. degree)		final position (dec. degree)		No. of transects & minutes surveyed			total area covered	
dive	(m)		Lat (N)	Long (W)	Lat (N)	Long (W)	N	min.	tot min.	m <sup>2</sup>	ha
P4159	1000	<i>Pelekunu Canyon</i> (canyon West)	21.25845833	156.8842617	21.25174833	156.8884033	3	16+18+16	50	9259.5	0.93
P5661	650	<i>Pelekunu Canyon</i> (canyon West)	21.21772833	156.8972217	21.21407333	156.8938233	4	13+13+25+27	78	14444.82	1.44
P5662	350	<i>Pelekunu Canyon</i> (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	10185.45	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	12407.73	1.24
P5666	1000	<i>Kawainui Canyon</i> (canyon East)	21.257745	156.7823633	21.24855167	156.78978	4	22+15+17+17	71	13148.49	1.31
P5667	650	<i>Kawainui Canyon</i> (canyon East)	21.23094833	156.7925583	21.21801833	156.7954317	5	10+16+18+16+10	70	12963.3	1.29
P5668	350	<i>Kawainui Canyon</i> (canyon East)	21.210035	156.7928783	21.19857	156.7871667	4	17+13+21+19	70	12963.3	1.29
P5669	350	slope control (East)	21.21855	156.8043617	21.21703667	156.7975183	4	17+15+15+21	68	12592.92	1.25
P5670	650	slope control (East)	21.24754833	156.8016033	21.24682333	156.7914983	4	15+16+14+23	68	12592.92	1.25
P5671	1000	slope control (East)	21.27763667	156.793635	21.27062833	156.7904967	4	17+18+17+14	66	12222.54	1.22

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.

### 3.3.3 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 3.1). 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. 3.1) 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 by 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.

### 3.3.4 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 x slopes), (2) *site* (east x 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  $\geq 1.3$  (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<sub>c</sub> (Akaike's Information Criterion corrected) selection criterion. The AIC<sub>c</sub> was devised to handle situations where the number of samples (N) is small relative to the number (v) of predictor variables ( $N/v < 40$ ), which applies to our data set ( $N=45$ ,  $v=14$ ,  $N/v = 3.21$ ) (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+v) 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

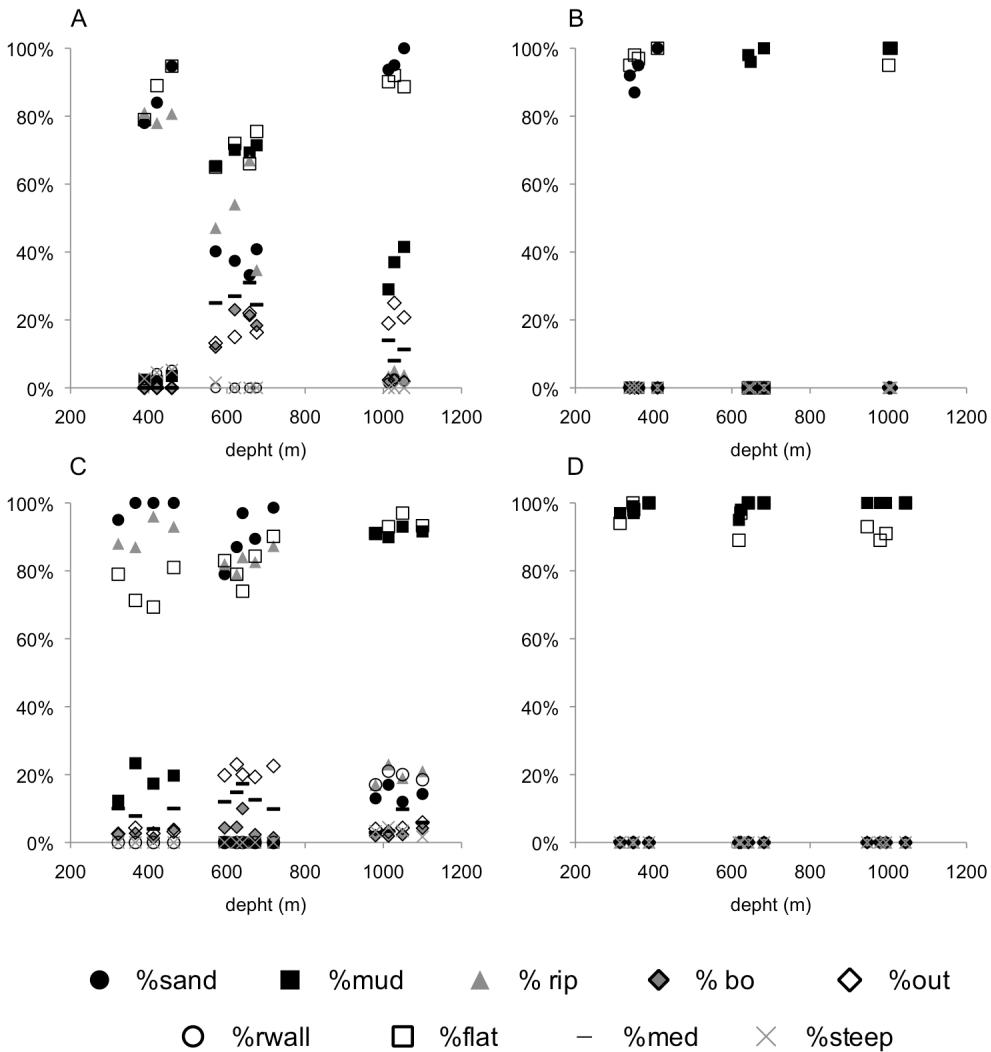
to generate the resemblance matrix using Bray-Curtis dissimilarity. All the remaining tests also used square-root transformed data however employing Euclidian-distance as resemblance measure (Anderson et al., 2008). Since Chao 1 and Chao 2 species estimators are obtained by pooling the transect replicates, not enough terms in each of the there 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, Colwell, 2000) to verify statistical significance (Colwell, 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).

## 3.4 Results

### 3.4.1 Environmental setting

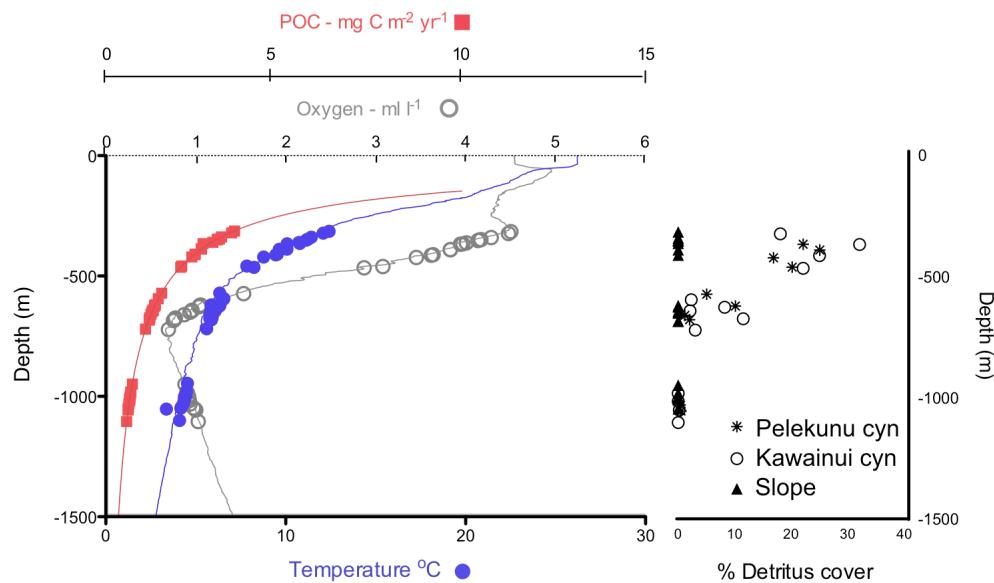
Fourteen environmental variables relating to sediment type, bottom inclination, water-mass characteristics, and organic input were estimated or measured for each transect (Supplementary Table 3.8). Dive localities generally differed in landscape characteristics, as evidenced by between-site differences in the proportions of substrate type and inclination (Fig. 3.2). 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 Kawainui 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. 3.2).



**Figure 3.2** 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.

A number of environmental variables, including temperature, dissolved oxygen, organic detritus occurrence, and estimated POC flux varied with depth (Fig. 3.3). 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 oC, 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. 3.3, Supplementary Table 3.8). 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 3.2). The influence of habitat was not included in the statistical test since organic detritus was completely absent at all depths at slope sites (Fig. 3.3, Supplementary Table 3.8).



**Figure 3.3** 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 3.2** Results from the univariate PERMANOVA analysis for differences in % detritus occurrence.

	Source	df	SS	MS	Pseudo-F	p(perm)	Unique perm
<b>Detritus</b>	si	1	3.8369	3.8369	0.82925	0.3855	9834
	de	2	1098.4	549.18	118.69	<b>0.0001</b>	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, 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 Euclidian Distance.

### 3.4.2 Fish species composition

A total of 824 fishes in 30 families, totaling 55 putative species, were observed during ~13.3 hours of video transects (Table 3.3). Another 17 species were also observed from the submersible during other activities (baited stations or scavenger trap 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 *Chlorophthalmus* 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), *Chrionema* sp. 1 (19) and *Coelorinchus doryssus* (19. (Table 3.3)

**Table 3.3** Abundance of the 55 putative fish species identified from video transects taken to the north of Moloka'i Island, in the main Hawaiian archipelago.

TAXA family	Putative species	Pelekunu Cyn			slope west			Kawainui Cyn			slope east			tot	
		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	Etomopteridae	<i>Centroscyllium sp.</i>	0	0	2	0	0	0	0	1	0	0	0	0	3
5		<i>Etomopterus sp.</i>	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
1	Synaphobranchida	Synaphobranchid	0	2	1	0	0	1	0	1	0	0	0	0	5
1		<i>Synaphobranchus affinis</i>	0	2	0	0	0	0	0	2	4	0	0	1	9
1	Congridae	Congrid sp. 1	1	12	2	0	5	0	2	18	5	0	12	0	57
1		Congrid w white fins	0	0	0	0	0	0	0	0	0	0	3	0	3
1		<i>Bathycongrus guttulatus</i>	0	0	0	0	3	0	0	0	0	0	0	0	3
1		<i>Uroconger lepturus</i>	0	0	0	0	0	2	0	0	0	0	0	0	2
1		<i>Bathyuroconger vicinus?</i>	0	0	0	0	0	0	0	2	1	0	1	0	4
1	Nettastomatidae	<i>Nettastoma sp.</i>	0	0	2	0	0	0	0	0	1	0	0	0	3
1	Argentinidae	<i>Glossanodon sp.</i>	0	0	0	0	0	0	0	0	0	7	0	0	7
1		<i>Ijimaia plicatellus</i>	0	1	0	0	0	0	0	1	0	0	0	0	2
2	Alepocephalidae	Alepocephalid?	0	0	0	0	1	0	0	0	0	0	0	0	1
2	Chlorophtalmidae	<i>Chlorophthalmus sp.</i>	32	0	0	4	0	0	42	0	0	234	0	0	312
2	Ipnopidae	<i>Bathytyphlops marionae</i>	0	0	1	0	0	0	0	0	0	0	0	0	1
2	Polymixiidae	<i>Polymixia sp.</i>	5	0	0	1	0	0	0	0	0	0	0	0	6
2	Macrouridae	<i>Coelorinchus sp.</i>	0	0	0	0	2	0	0	0	0	0	0	0	2
2		<i>Coelorinchus doryssus</i>	0	0	0	0	0	1	0	5	5	0	2	4	17
2		<i>Coryphaenoides</i>	0	0	0	0	0	0	0	0	1	0	0	0	1
2		<i>Gadomus melanopterus</i>	0	0	1	0	1	1	0	0	5	0	0	0	8
2		<i>Sphagmacrurus sp.</i>	0	0	0	0	0	0	0	4	4	0	3	0	11
2		Macrourid sp. 1	0	21	2	1	15	5	0	12	15	0	9	0	80
3		Macrourid sp. 2	0	1	0	0	0	0	0	0	0	0	0	0	1
3		<i>Hymenocephalus sp.</i>	0	1	0	0	0	1	0	3	0	0	0	0	5
3		<i>Ventrifossa sp.</i>	0	0	0	0	4	0	0	5	0	0	7	0	16
3		<i>Nezumia sp. 1</i>	0	0	0	0	0	1	0	5	0	0	2	0	8
3		<i>Nezumia burragei</i>	0	0	0	0	1	0	0	0	0	0	0	0	1
3		Bathygadid	0	0	0	0	0	0	0	0	0	0	0	0	1
3		<i>Bathygadus sp.</i>	0	0	0	0	0	0	0	0	3	0	1	2	6
3	Ophidiidae	Ophidiid	0	0	2	0	0	0	0	0	0	0	0	0	2
3		<i>Lamprichthys sp.</i>	0	0	1	0	0	0	0	0	1	0	0	0	2
3	Lophiidae	<i>Sladenia remiger</i>	0	0	0	0	0	1	0	0	1	0	0	0	2
4	Chaunacidae	<i>Chaunax umbrinus</i>	1	0	0	0	0	0	0	0	0	0	0	0	1
4	Berycidae	<i>Beryx decadactylus</i>	0	0	0	0	0	0	2	1	0	0	0	0	3
4	Peristediidae	<i>Satyrichthys sp.</i>	1	0	0	2	0	0	2	0	0	10	1	0	16
4		<i>Satyrichthys hiatus</i>	0	0	0	0	0	0	0	1	0	0	0	0	1
4	Acropomatidae	Synagrops sp.	0	0	0	0	0	0	3	1	0	20	0	0	24
4	Epigonidae	<i>Epigonus sp.</i>	2	0	0	0	0	0	0	0	0	0	0	0	2
4	Carangidae	<i>Seriola dumerilii</i>	1	0	0	0	0	0	8	0	0	0	0	0	9
4	Percophidae	<i>Chrionema sp.</i>	0	0	0	1	0	0	2	0	0	16	0	0	19
4		<i>Chrionema chrysereis</i>	0	0	0	0	0	0	0	0	0	2	0	0	2
4	Gempylidae	Gempylidae sp.	0	0	0	0	0	0	0	1	0	0	0	0	1
5		<i>Rexea nakamurai</i>	0	0	0	0	0	0	2	0	0	0	0	0	2
5	Bothidae	<i>Chascanolopsetta sp.</i>	0	0	0	2	0	0	2	0	0	0	0	0	4
5	Pleuronectidae	<i>Poecilopsetta hawaiiensis</i>	0	0	0	0	0	0	0	0	0	1	0	0	1
5	Triacanthodidae	<i>Hollardia goslinei</i>	1	0	0	0	0	0	0	0	0	0	0	0	1
5	??	Eel	0	2	7	0	1	1	2	0	1	0	3	0	17
5	??	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. -			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(0.01 ha) -			44.1	36.1	43.4	13.5	42.9	29.1	56.5	57.4	92.2	281.	48	18.0	

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

<sup>a</sup> abundance normalized by the total number of video transect minutes (refer to Table 1)

<sup>b</sup> abundance normalized by the total area surveyed in each depth-habitat (refer to Table 1)

### 3.4.3 Assemblage structure

The PERMANOVA results indicate significant differences in fish assemblage between habitat (canyon x slopes) ( $p\text{-}F=6.1$ ;  $p=0.0001$ ), sites (east x west) ( $p\text{-}F=4.1$ ,  $p=0.0001$ ) and depth (three strata) ( $p\text{-}F=19.1$ ,  $P=0.001$ ); 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 3.4). This pattern of assemblage structure is evident in the MDS output (Fig. 3.4), 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).

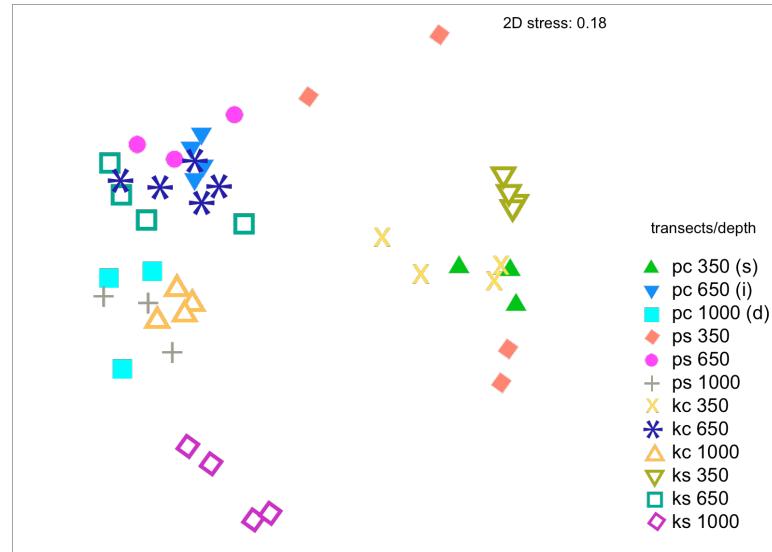
**Table 3.4** Output of the PERMANOVA analysis based on the resemblance matrix of fish abundance data from video transects taken to the north of Moloka'i island, in the main Hawaiian archipelago. Pair-wise tests of factors habitat (canyon x slopes), sites (east x west) and depth (shallow, intermediate, deep) are also shown.

	Source	df	SS	MS	Pseudo-F	p(perm)	Unique perm	ECV
<b>Main test</b>								
	habitat	1	9501.9	9501.9	6.0916	<b>0.0001</b>	9914	362.17
	site	1	6392.5	6392.5	4.0982	<b>0.0001</b>	9939	220.38
	depth	2	59567	29784	19.094	<b>0.0001</b>	9924	1928.1
	habitat x site	1	4576.4	4576.4	2.9339	<b>0.0004</b>	9909	275.13
	habitat x depth	2	12740	6370	4.0838	<b>0.0001</b>	9891	657.22
	site x depth	2	10087	5043.4	3.2333	<b>0.0001</b>	9885	475.97
	habitat x site x depth	2	6265	3132.5	2.0082	<b>0.0023</b>	9878	429.76
	residual	33	51474	1559.8				1559.8
	total	44	162240					
<b>Pair wise tests</b>								
	Source	df		t-stat		p(perm)	Unique perm	
	<u>Habitat x site</u>							
	within level 'west'	14			1.6932	<b>0.0023</b>	9931	
	within level 'east'	19			2.6399	<b>0.0001</b>	9938	

Habitat x site x depth					
within 'west' and 's'	5	1.7347	<b>0.0291</b>	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	<b>0.0277</b>	35	
within 'east' and 'm'	7	1.0954	0.2666	126	
within 'east' and 'd'	6	2.5976	<b>0.0294</b>	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.

The results of the SIMPER analysis (Supplementary Table 3.9) 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; and *Chascanopsetta* sp. and *Poecilopsetta hawaiiensis*, 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 *Chrionema chrysereis*, which occurred only on the slope (Supplementary Table 3.9). 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 3.9). 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, *Sphagmacrurus* 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.



**Figure 3.4** 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, Kawainui Canyon; ks, Kawainui Slope; s, shallow (350 m), i, intermediate, (650 m) and d, deep, (1000 m) – depth strata).

#### 3.4.4 Environmental predictors of fish assemblage structure

The multivariate multiple linear regression (DISTLM) model using the AICc 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 3.5). 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 3.5).

The ten best models were all significant as AICc values ranged apart less than one unit from each other (Anderson et al., 2008; Table 6). The combinations of variables (between 5-7 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 3.6).

The dbRDA plot emphasized the vectors that correspond to the variables selected in the best models (i.e., the lowest AICc values) (Fig. 3.5). 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 Fig. 3.5 and Fig. 3.4), indicating a good fit for the DISTLM models.

**Table 3.5** 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.
<b>AICc</b>				
Axis				
dissolved O <sub>2</sub>	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

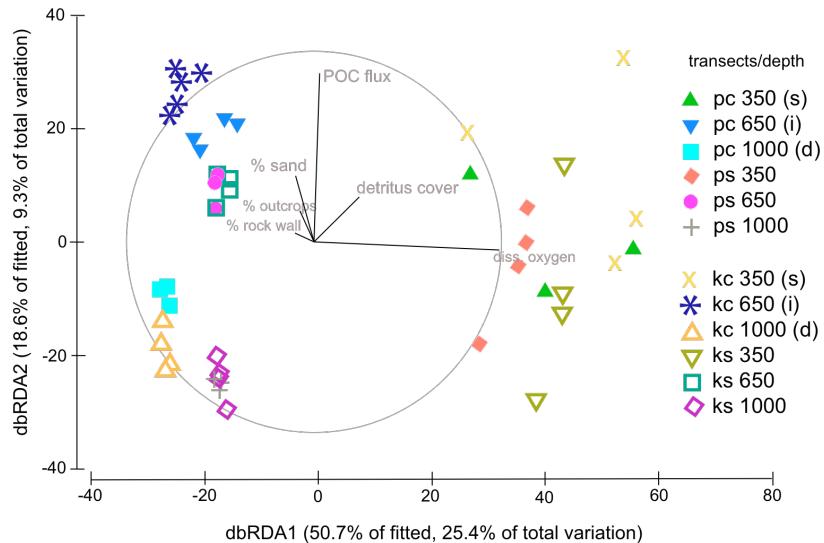
Indiv., individual; Cum., cumulative

**Table 3.6** 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 Hawaiian archipelago.

AICc	R <sup>2</sup>	RSS	No. Vars	Selections (Variables)
<b>354.01</b>	0.50425	80428	6	1,5,6,13-15
<b>354.13</b>	0.53465	75497	7	1,4-6,13-15
<b>354.16</b>	0.50255	80704	6	2,5,6,13-15
<b>354.3</b>	0.46877	86185	5	1,5,13-15
<b>354.33</b>	0.53261	75828	7	2,4-6,13-15
<b>354.37</b>	0.46796	86317	5	5,6,13-15
<b>354.4</b>	0.49993	81129	6	1,4,5,13-15
<b>354.42</b>	0.46736	86415	5	2,5,13-15
<b>354.43</b>	0.53156	75998	7	1,5,6,8,13-15
<b>354.46</b>	0.46692	86485	5	1,6,13-15

Predictor variables (Vars): 1, % sand; 2, % mud; 3, % ripple marks 4, (% boulders); 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).



**Figure 3.5.** 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, Kawainui Canyon; ks, Kawainui Slope; s, shallow (350 m), i, intermediate, (650 m) and d, deep, (1000 m) – depth strata).

A first examination of the dbRDA plot shows that essentially three main gradients can be modeled by the selected environmental variables (Fig. 3.5). 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. 3.5). 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.

### 3.4.5 Abundance patterns

Fish abundance was statistically significantly different between canyons and slopes ( $p=0.0425$ ; Table 3.7). Further pairwise comparisons reveals that this difference is restricted to the deepest stratum (946-1100 m), where canyon abundance is greater (Supplementary Table 3.10). 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. 3.6A), 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 3.10). No significant differences in fish abundances were observed between the two sites sampled (Table 3.7). No significant correlations were observed between the percent occurrence of seafloor organic detritus and fish abundance (Fig. 3.6B).

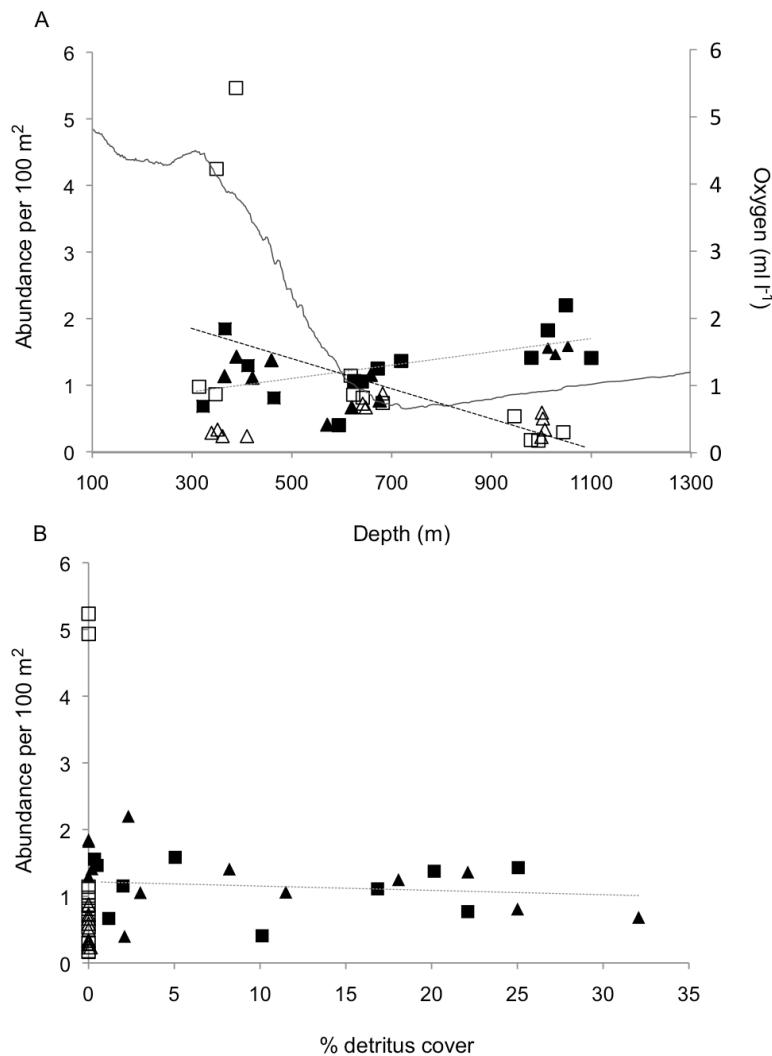
**Table 3.7** Results from the univariate PERMANOVA analysis for differences in normalized fish abundance (N), species density (S) and rarefaction (ES(5), ES(10)).

	Source	df	SS	MS	Pseudo-F	p(perm)	Unique perm	p(perm)*
<b>N</b>	ha	1	862.01	862.01	3.7871	<b>0.0425</b>	9949	<b>0.0337</b>
	si	1	577.48	577.48	2.537	0.1104	9939	0.2556
	de	2	776.08	388.04	1.7048	0.1841	9951	0.5734
	haxsi	1	1077	1077	4.7316	<b>0.0316</b>	9932	<b>0.0383</b>
	haxde	2	647.31	323.65	1.4219	0.2386	9943	0.493
	sixde	2	363.86	181.93	0.79927	0.4686	9948	0.7354
	haxsixde	2	1626.3	813.16	3.5725	<b>0.0331</b>	9959	<b>0.0104</b>
	Res	33	7511.5	227.62				
	Total	44	13666					
<b>S</b>	ha	1	0.0694	0.0694	13.2250	<b>0.0015</b>	9838	
	si	1	0.1869	0.1869	35.6270	<b>0.0001</b>	9837	
	de	2	0.0508	0.0254	4.8409	<b>0.0153</b>	9952	
	haxsi	1	0.0073	0.0073	1.3960	0.2502	9820	
	haxde	2	0.1477	0.0738	14.0740	<b>0.0002</b>	9943	
	sixde	2	0.0144	0.0072	1.3679	0.2631	9944	
	haxsixde	2	0.0727	0.0364	6.9292	<b>0.0020</b>	9967	
	Res	33	0.1731	0.0052				
	Total	44	0.7718					
<b>ES(5)</b>	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	<b>0.0014</b>	9952	
	haxsi	1	2.2827	2.2827	11.238	<b>0.0024</b>	9844	
	haxde	2	0.7216	0.3608	1.7763	0.1923	9939	
	sixde	2	2.9768	1.4884	7.3279	<b>0.0029</b>	9936	
	haxsixde	2	1.5019	0.7509	3.6971	<b>0.0368</b>	9949	
	Res	26	5.281	0.2031				
	Total	37	20.009					
<b>ES(10)</b>	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	<b>0.0003</b>	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. \* p-value obtained after outliers removed (two shallow-stratum transects in slope East); \*\* missing terms. Data was fourth-root transformed and resemblance calculated using Bray-Curtis (N) and Euclidian-Distance (S, ES(5) and ES(10)). See Supplementary Table 3.10 for results on posteriori pairwise comparisons.

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

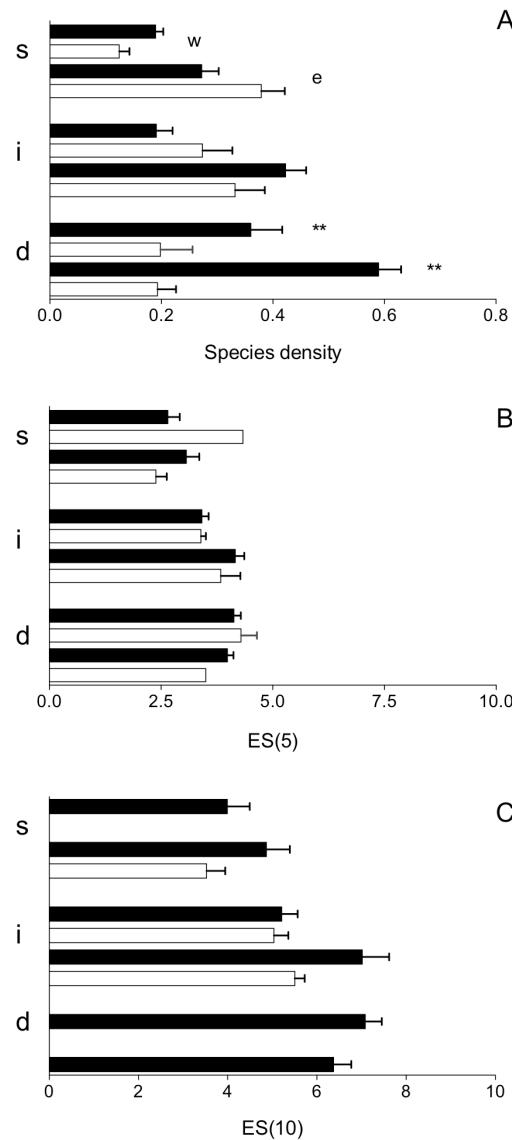
(Fig. 3.6). In the deepest depth stratum, fish abundances reach their highest values in canyons but decline to their lowest values on the slopes. The transition zone at the intermediate depth stratum (571-719 m) overlaps the core of the oxygen minimum zone (Fig. 3.6A).



**Figure 3.6** Fish abundance (# /100 m<sup>2</sup>) 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 (grey 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,  $y = -0.0022x + 1.1139$ ,  $R^2 = 0.00038$ .

### 3.4.6 Species density, diversity and estimated species richness x habitat heterogeneity

Species density is statistically different between canyons and slopes ( $p=0.0015$ ; Table 3.7); being higher on both canyons only at the deepest sites (940-1100m) (see Supplementary Table 3.10 for pairwise tests; Fig. 3.7A). Overall site effects are highly statistically significant ( $p=0.0001$ ) with greater species density occurring on east sites.

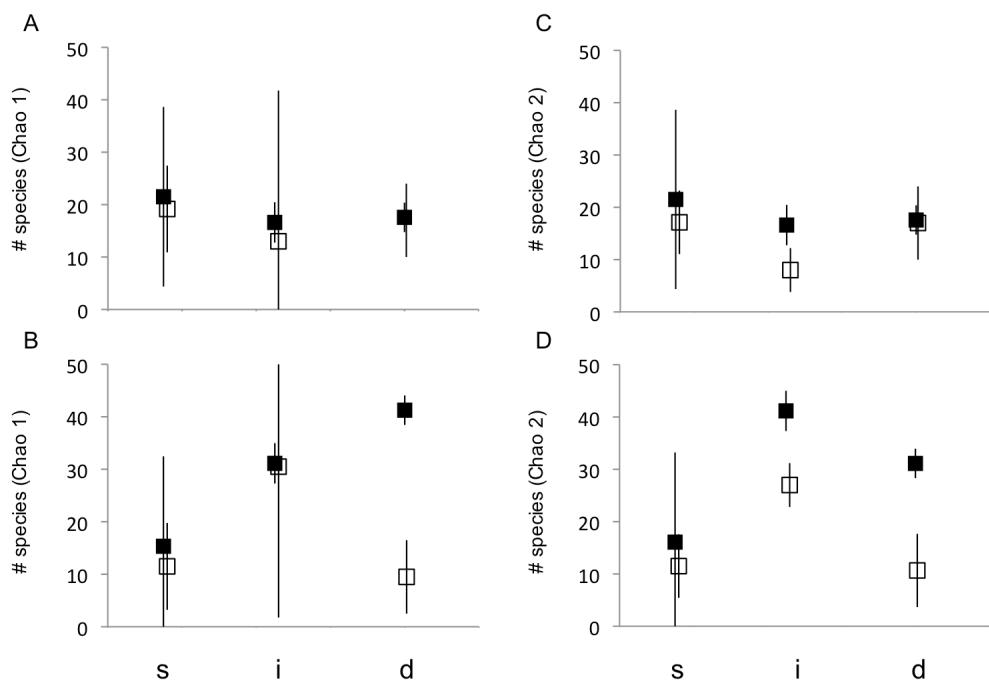


**Figure 3.7** Fish species density (A) and rarefaction diversity at ES-5 (5 individuals) (B), and ES10 (C). Canyon, solid bars; slope empty bars; s, shallow, i, intermediate, d, deep depth strata; w, west, e, east sites. Asterisks indicate statistical significance at  $p < 0.5$ (\*) and  $p < 0.05$ (\*\*).

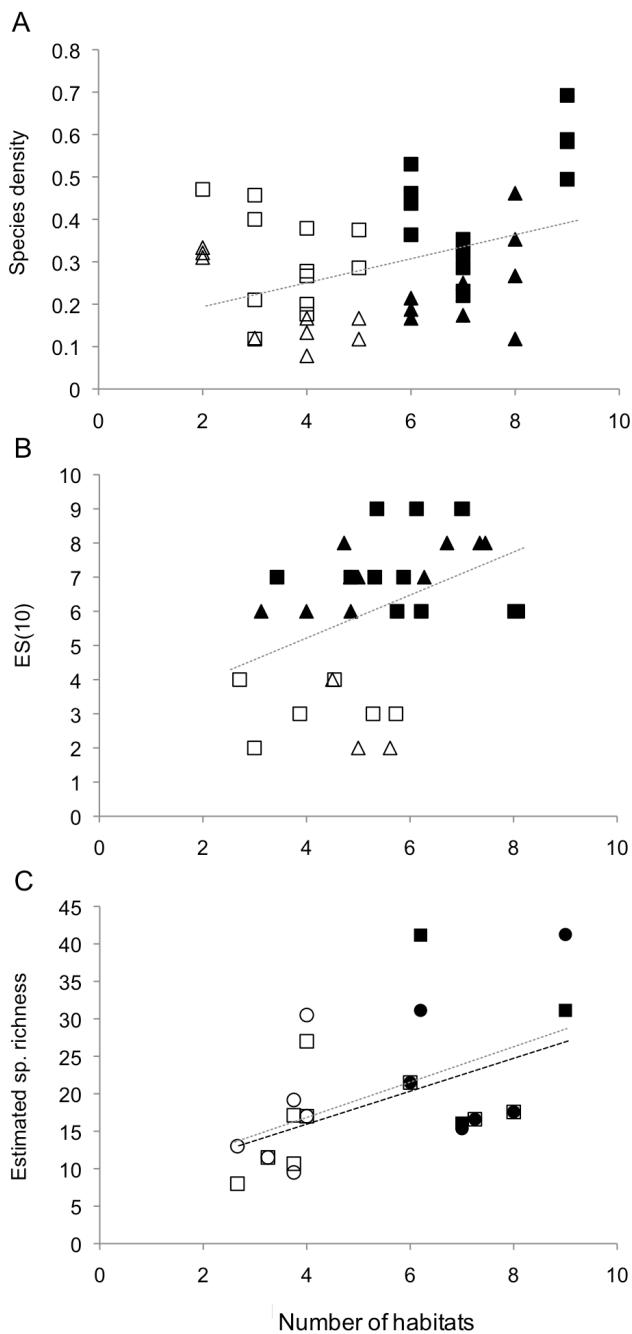
Because fish abundances were very low on some transects (min=3; max=104, mean=20), patterns in species density were largely driven by patterns of abundance. We thus used rarefaction diversity to remove biases from large differences in sample size. At ES5 (i.e., expected species per 5 individuals), species diversity showed no significant differences neither between canyon and slope habitats nor between sites east and west (Table 3.7; Fig. 3.7B). 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 3.10, 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. 3.7C). Overall ES10 values do not show statistical differences neither between canyon and slopes nor between east and west sites (Table 3.7). The higher ES10 in the canyons, although not statistically significant at any depth strata show 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.

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. 3.8A-B), in a trend similar that for species density. Chao 2 predicts higher species richness for canyons at intermediate depths (west: 16 species  $\times$  8 species on the slope; east: 41 species  $\times$  27 species on the slope), and in the deepest stratum for Kawaiinui Canyon (31 species  $\times$  11 in the slope (Fig. 3.8C-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. 3.9). The strength of the linear regression model is weak ( $R^2=0.12$ ) 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. 3.9A). The trends for both rarefaction ( $R^2=0.19$ ) and estimated species richness (Chao 1,  $R^2=0.26$ ; Chao 2,  $R^2=0.23$ ) 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. 3.9B-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).



**Figure 3.8** 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 Kawainui Canyon and Slope (canyon, solid symbols; slopes empty symbols). Vertical bars represent confidence intervals.



**Figure 3.9** Fish species density (A), rarefied diversity ES10 (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, Kawainui/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),  $y = 2.173x + 7.8663$ ,  $R^2 = 0.2335$ .

## 3.5 Discussion

### 3.5.1 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 of 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 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 [ $\sim$  13 hours 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.

### 3.5.2 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 3.3.4). 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<sup>-2</sup> yr<sup>-1</sup>). Dissolved oxygen concentrations also vary across a wider range above this transition zone (4.48-2.85 ml l<sup>-1</sup>), but remain above the threshold (~1.4 ml l<sup>-1</sup>) 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<sup>-2</sup> yr<sup>-1</sup>) 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<sup>-1</sup>) (Fig. 3.3). Dissimilarities in assemblage structure between 571-719 m and 946-1100 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, synaphobranchid 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 500-1000 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 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 of canyons and yield a homogenizing effect on species composition. Noteworthy, however, is that canyon 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 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 macroalage 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, 3.5.3).

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

### *3.5.3 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 in 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 Hawaiian submarine canyons, including both Moloka'i canyons (Vetter et al., 2010). Infaunal macrobenthos in Pelekunu (west) and Kawainui (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 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 Hawaiian 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., in preparation). 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 et al., 1999; Paterson et al., in press). 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 et al., 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.

### *3.5.4 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; Willians 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 Hawaiian 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 Hawaiian 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 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 et al, 2011).

### 3.6 Summary and Conclusions

Our first hypothesis of a canyon effect on the structure of demersal fish assemblages off Moloka'i Island, Hawaii, 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 affect 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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## 3.8 Appendix

**Supplementary Table 3.8.** Measured and modeled environmental variables associated with individual Pisces IV and V video transects.

transect <sup>a</sup>	Sediment type, bottom geomorphology												Water mass and organic input					
	av dph	dph r	san d	mu d	ripp les	bol d	out cr	rwa ll	flat	me d	ste ep	d. O <sub>2</sub> <sup>b</sup> ml l <sup>-1</sup>	temp °C	POC <sup>d</sup> g C m <sup>-2</sup> yr <sup>-1</sup>	Detritus occurrence <sup>e</sup>			
	m	m	%	%	%	%	%	%	%	%	%	ml l <sup>-1</sup>	°C	g C m <sup>-2</sup> yr <sup>-1</sup>	mean	sd	n	
P5_662_1 c	459	40	0.95	0.04	0.81	0.00	0.00	0.05	0.95	0.00	0.05	3.06	7.84	2.19	20.15	4.36	50	
P5_662_2 c	421	50	0.84	0.02	0.78	0.00	0.00	0.04	0.89	0.00	0.05	3.43	8.77	2.47	16.85	3.35	55	
P5_662_3 c	389	36	0.78	0.02	0.81	0.00	0.00	0.02	0.79	0.00	0.03	3.81	9.64	2.74	25.05	3.78	58	
P5_662_4 c	365	29	0.73	0.15	0.74	0.00	0.00	0.13	0.83	0.00	0.01	3.95	10.78	3.00	22.11	0.40	41	
P5_661_1 c	676	41	0.41	0.71	0.35	0.18	0.16	0.00	0.76	0.24	0.00	0.76	5.78	1.30	2.01	2.27	51	
P5_661_2 c	658	43	0.33	0.69	0.67	0.21	0.22	0.00	0.66	0.31	0.00	0.86	5.81	1.34	1.18	0.72	42	
P5_661_3 c	620	49	0.37	0.70	0.54	0.23	0.15	0.00	0.72	0.27	0.00	1.03	5.86	1.46	10.12	0.07	53	
P5_661_4 c	571	45	0.40	0.65	0.47	0.12	0.13	0.00	0.65	0.25	0.02	1.52	6.33	1.64	5.05	5.07	50	
P4_159_1 c	1053	24	1.00	0.42	0.04	0.02	0.21	0.02	0.89	0.11	0.00	0.99	3.36	0.71	0.50	0.10	37	
P4_159_2 c	1028	13	0.95	0.37	0.05	0.02	0.25	0.03	0.92	0.08	0.00	0.93	4.32	0.73	0.35	2.17	48	
P4_159_3 c	1013	14	0.94	0.29	0.03	0.02	0.19	0.01	0.90	0.14	0.00	0.92	4.37	0.75	0.12	1.91	54	
P5_665_1 s	410	49	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	3.62	9.53	2.56	0.00	0.00	53	
P5_665_2 s	361	40	0.95	0.00	0.00	0.00	0.00	0.00	0.97	0.00	0.00	3.99	10.73	3.05	0.00	0.00	42	
P5_665_3 s	351	5	0.87	0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.00	4.11	11.13	3.17	0.00	0.00	32	
P5_665_4 s	339	41	0.92	0.00	0.00	0.00	0.00	0.00	0.95	0.00	0.00	4.26	11.43	3.29	0.00	0.00	43	
P5_664_1 s	682	12	0.00	1.00	0.00	0.00	0.00	0.00	0.96	0.00	0.00	0.74	5.87	1.29	0.00	0.00	31	
P5_664_2 s	648	7	0.00	0.96	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.92	6.06	1.37	0.00	0.00	25	
P5_664_3 s	642	16	0.00	0.98	0.00	0.00	0.00	0.00	0.79	0.00	0.00	0.95	6.09	1.40	0.00	0.00	36	
P5_663_1 s	1007	23	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.91	4.41	0.75	0.00	0.00	41	
P5_663_2 s	1003	2	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.91	4.36	0.76	0.00	0.00	39	
P5_663_3 s	1001	27	0.00	1.00	0.00	0.00	0.00	0.00	0.95	0.04	0.00	0.91	4.42	0.77	0.00	0.00	26	
P5_663_4 s	1000	23	0.00	1.00	0.00	0.00	0.00	0.00	0.93	0.04	0.00	0.91	4.38	0.77	0.00	0.00	35	
P5_668_1 c	412	46	1.00	0.17	0.96	0.01	0.03	0.00	0.69	0.04	0.00	3.60	9.45	2.56	25.01	1.97	55	
P5_668_2 c	366	43	1.00	0.23	0.87	0.03	0.04	0.00	0.71	0.08	0.00	3.92	10.08	2.78	32.07	2.66	46	
P5_668_3 c	464	15	1.00	0.20	0.93	0.04	0.03	0.00	0.81	0.10	0.00	2.85	8.24	2.16	22.11	1.80	48	
P5_668_4 c	322	33	0.95	0.12	0.88	0.02	0.03	0.00	0.79	0.10	0.00	4.45	12.09	3.57	18.07	1.79	39	
P5_667_1 c	719	24	0.99	0.00	0.87	0.01	0.23	0.00	0.90	0.10	0.00	0.69	5.61	1.19	3.02	3.93	49	
P5_667_2 c	672	34	0.89	0.00	0.83	0.02	0.19	0.00	0.84	0.13	0.00	0.76	5.92	1.31	11.50	4.77	50	
P5_667_3 c	640	7	0.97	0.00	0.84	0.10	0.20	0.00	0.74	0.17	0.00	0.95	6.11	1.40	2.10	1.24	43	
P5_667_4 c	625	31	0.87	0.00	0.79	0.05	0.23	0.00	0.79	0.15	0.00	1.02	6.32	1.44	8.21	2.06	55	
P5_667_5 c	594	18	0.79	0.00	0.82	0.04	0.20	0.00	0.83	0.12	0.00	1.28	6.57	1.54	2.32	4.71	48	
P5_666_1 c	1100	46	0.14	0.92	0.21	0.04	0.06	0.18	0.93	0.06	0.02	1.02	4.10	0.67	0.01	4.56	52	
P5_666_2 c	1049	34	0.12	0.93	0.19	0.02	0.04	0.20	0.97	0.10	0.03	0.98	4.17	0.71	0.20	3.96	50	
P5_666_3 c	1013	33	0.17	0.90	0.23	0.02	0.03	0.21	0.93	0.03	0.05	0.92	4.37	0.75	0.00	2.89	42	
P5_666_4 c	980	43	0.13	0.91	0.17	0.02	0.04	0.17	0.91	0.03	0.03	0.89	4.47	0.79	0.01	0.79	55	
P5_669_1 s	388	44	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	3.81	10.07	2.73	0.00	0.00	49	
P5_669_2 s	349	4	0.00	0.97	0.00	0.00	0.00	0.00	0.98	0.00	0.00	4.13	11.20	3.17	0.00	0.00	45	
P5_669_3 s	347	27	0.00	0.99	0.00	0.00	0.00	0.00	1.00	0.00	0.00	4.15	11.23	3.23	0.00	0.00	48	
P5_669_4 s	314	1	0.00	0.97	0.00	0.00	0.00	0.00	0.94	0.00	0.00	4.48	12.41	3.65	0.00	0.00	49	
P5_670_1 s	682	40	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.74	5.87	1.29	0.00	0.00	47	
P5_670_2 s	642	6	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.95	6.09	1.40	0.00	0.00	42	
P5_670_3 s	623	3	0.00	0.98	0.00	0.00	0.00	0.00	0.97	0.00	0.00	1.03	6.33	1.44	0.00	0.00	37	
P5_670_4 s	618	44	0.00	0.95	0.01	0.00	0.00	0.00	0.89	0.00	0.00	1.05	6.34	1.46	0.00	0.00	39	
P5_671_1 s	1044	48	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.97	4.20	0.72	0.00	0.00	44	
P5_671_2 s	994	13	0.00	1.00	0.00	0.00	0.00	0.00	0.91	0.00	0.00	0.91	4.43	0.77	0.00	0.00	48	
P5_671_3 s	979	33	0.00	1.00	0.00	0.00	0.00	0.00	0.89	0.00	0.00	0.89	4.48	0.78	0.00	0.00	46	
P5_671_4 s	946	25	0.00	1.00	0.00	0.00	0.00	0.00	0.93	0.00	0.00	0.87	4.54	0.83	0.00	0.00	40	

**Supplementary Table 3.9.** Results of the SIMPER analysis for fish assemblages at canyons and slopes habitats to the north of Moloka'i island, in the main Hawaiian archipelago.

WEST (shallow)							EAST (shallow)							
canyon	Av similarity: 71.74%						canyon	Av similarity: 53.71%						
Species	Av N	Av	Sim/	% C	Cum		Species	Av N	Av	Sim/	% C	Cum		
			Sim	SD	%					Sim	SD	%		
<i>Chlorophthalmus</i> sp.	0.8	38.7	8.3	53.9	53.9		<i>Chlorophthalmus</i>	0.8	25.9	8.4	48.1	48.1		
<i>Seriola dumerilii</i>	0.4	16.4	13.1	22.9	76.8		<i>Seriola dumerilii</i>	0.3	13.6	11.2	25.3	73.4		
<i>Polymixia</i> sp.	0.3	13.1	6.7	18.2	95.0		<i>Chrionema</i> sp.	0.2	4.4	0.9	8.2	81.7		
<b>slope</b>	Average similarity: 17.02						<b>slope</b>	Average similarity: 82.86						
Species	Av N	Av	Sim/	% C	Cum		Species	Av N	Av	Sim/	% C	Cum		
			Sim	SD	%					Sim	SD	%		
<i>Chlorophthalmus</i> sp.	0.2	5.1	0.4	29.8	29.8		<i>Chlorophthalmus</i>	1.8	34.5	6.6	41.7	41.7		
<i>Satyrichthys</i> sp.	0.1	4.8	0.4	28.0	57.8		<i>Synagrops</i> sp.	0.6	10.4	20.2	12.5	54.2		
<i>Chascanopsetta</i> sp.	0.1	3.6	0.4	21.1	78.9		<i>Chrionema</i> sp.	0.5	9.3	20.2	11.2	65.4		
<i>Poecilopsetta</i>	0.1	3.6	0.4	21.1	100		Unid. Flatfish	0.4	6.6	20.2	7.9	73.3		
<b>canyon x slp</b>	Average dissimilarity = 82.32%						<i>Glossanodon</i> sp.	0.3	5.8	6.8	7.0	80.3		
	cny	slp					<b>canyon x slope</b>	Average dissimilarity = 67.08%						
Species	Av N	Av N	Av.D	Diss/	% C	Cum			cny	slp				
			Diss	SD	%									
<i>Chlorophthalmus</i> sp.	0.8	0.2	21.6	2.7	26.2	26.2		Species	Av N	Av N	Av	Diss/	% C	Cum
<i>Seriola dumerilii</i>	0.4	0.0	11.8	8.2	14.3	40.5						Diss	SD	%
<i>Polymixia</i> sp.	0.3	0.1	8.8	2.1	10.6	51.2	<i>Chlorophthalmus</i>	0.8	1.8	14.6	2.8	21.8	21.8	
<i>Epigonus</i> sp.	0.2	0.0	5.3	1.3	6.4	57.6	<i>Squalus mitsukuri</i>	0.0	0.5	5.9	1.7	8.8	30.6	
<i>Satyrichthys</i> sp.	0.1	0.1	4.4	1.0	5.3	62.9	<i>Synagrops</i> sp.	0.1	0.6	5.5	3.2	8.2	38.8	
<i>Chascanopsetta</i>	0.0	0.1	4.0	0.9	4.9	67.8	Unid. Flatfish	0.0	0.4	4.7	15.0	7.0	45.8	
<i>Poecilopsetta</i>	0.0	0.1	4.0	0.9	4.9	72.7	<i>Seriola dumerilii</i>	0.3	0.0	4.7	9.0	6.9	52.7	
<i>Hollardia goslinei</i>	0.1	0.0	3.1	0.7	3.7	76.4	<i>Epigonus</i> sp.	0.0	0.3	4.5	1.7	6.6	59.3	
<i>Echinorhinus cookei</i>	0.1	0.0	2.4	0.7	2.9	79.3	<i>Glossanodon</i> sp.	0.0	0.3	4.3	6.8	6.5	65.8	
Congrid sp.	0.1	0.0	2.4				<i>Chrionema</i> sp.	0.2	0.5	4.2	2.3	6.2	72.1	
<b>EAST (deep)</b>	Average similarity: 67.49%						<i>Satyrichthys</i> sp.	0.1	0.3	3.7	1.9	5.5	77.6	
<b>canyon</b>	Average similarity: 67.49%						<i>Chrionema</i>	0.0	0.2	2.5	1.7	3.7	81.3	
Species	Av N	Av	Sim/	% C	Cum									
			Sim	SD	%									
<i>Halosaurid</i>	0.6	14.2	6.5	21.1	21.1									
<i>Aldrovandia phalacra</i>	0.6	12.0	5.5	17.8	38.9									
Black halosaur	0.5	11.1	7.4	16.5	55.4									
Macrourid sp. 1	0.5	9.9	7.8	14.6	70.0									
<i>Synaphobranchus affinis</i>	0.2	5.6	7.4	8.3	78.3									
<i>Sphagmacrurus</i> sp.	0.2	5.6	7.4	8.3	86.5									
<b>slope</b>	Average similarity: 39.62%													
Species	Av N	Av	Sim/	% C	Cum									
			Sim	SD	%									
<i>Aldrovandia phalacra</i>	0.2	27.4	3.6	69.2	69.2									
Congrid w white fins	0.1	5.5	0.4	13.8	82.9									
<b>canyon x slope</b>	Average dissimilarity = 78.47%													
	cny	slp												
Species	Av N	Av N	Av	Diss/	% C	Cum								
			Diss	SD	%									
<i>Halosaurid</i>	0.6	0.0	12.8	4.4	16.3	16.3								
Macrourid sp. 1	0.5	0.0	9.2	6.7	11.8	28.1								
Black halosaur	0.5	0.1	7.3	2.1	9.3	37.4								
<i>Aldrovandia phalacra</i>	0.6	0.2	6.4	3.1	8.1	45.5								
<i>Sphagmacrurus</i> sp.	0.2	0.0	4.8	5.5	6.2	51.7								
Congrid sp.	0.2	0.0	4.1	1.5	5.3	57.0								
<i>Coelorinchus doryssus</i>	0.2	0.1	4.0	1.1	5.1	62.0								
<i>Synaphobranchus affinis</i>	0.2	0.1	3.7	1.7	4.7	66.7								
<i>Gadomus melanopterus</i>	0.2	0.0	3.6	0.9	4.6	71.4								
<i>Bathygadus</i> sp.	0.2	0.1	2.6	1.0	3.3	74.7								

Congrid w white fins	0.0	0.1	2.5	0.9	3.2	77.9
Gempylidae sp.	0.1	0.0	2.1	1.0	2.7	80.6

cny, canyon; slp, slope; Av N, average abundance, Av Sim, average similarity, Sim/SD, similarity divided by the standard deviation; Av Diss, average dissimilarity; % C, percent contribution; Cum %, cumulative percentage;

**Supplementary Table 3.10.** Results from the univariate PERMANOVA analysis for differences in normalized fish abundance (N), species density (S) and rarefaction ( $ES_5$ ,  $ES_{10}$ ).

	Source	df	t stat	Unique	p(perm)*
				p(perm)	perm
<b>N</b>					
	<u>haxsixde</u>				
	wxi	5	2.1434	0.4327	25
	wxm	5	1.5165	0.1933	25
	wxd	4	1.3881	<b>0.0295</b>	10
	exi	4	1.0739	0.5360	15
	exm	7	1.0949	0.2954	126
	exd	6	1.4055	<b>0.0197</b>	35
<b>S</b>					
	<u>haxde</u>				
	ha x i	11	0.1386	0.8948	9836
	ha x m	12	0.0932	0.9306	9847
	ha x d	10	5.7515	<b>0.0008</b>	9816
	<u>haxsixde</u>				
	haxw - s	5	2.4791	0.0869	35
	haxw - i	5	1.3785	0.2587	35
	haxw - d	4	4.0371	<b>0.0197</b>	10
	haxe - s	6	2.0432	0.0805	35
	haxe - i	7	1.4659	0.1817	126
	haxe - d	6	7.1885	<b>0.0279</b>	35
<b>ES<sub>5</sub></b>					
	<u>de</u>				
	sxi	19	2.9471	<b>0.0076</b>	9807
	sxd	15	3.8301	<b>0.0014</b>	9857
	idx	18	1.5469	0.1408	9842
<b>ES<sub>10</sub></b>					
	<u>de</u>				
	sxi	17	3.2981	0.0038	9822
	sxd	13	4.7163	0.0006	9825
	idx	14	1.6859	0.1108	9824

PERMANOVA 3-factor model. Bold values indicate significant differences at  $p < 0.05$ . ha, habitat; si, site; de, depth; haxsi, haxde, haxsixde represent interaction terms; 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. \* p-value obtained after outliers removed (two shallow-stratum transects in slope East); Data was fourth-root transformed and resemblance calculated using Bray-Curtis (N) and Euclidian-Distance (S,  $ES_5$  and  $ES_{10}$ ).

# **Chapter 4**

## **Spatial scale-dependent habitat heterogeneity influences submarine canyon macrofaunal abundance and diversity off the Main and Northwest Hawaiian Islands**

### **4.1 Abstract**

The mapping of biodiversity on continental margins on landscape scales is highly relevant to marine spatial planning and conservation. Submarine canyons are widespread topographic features on continental and island margins that enhance benthic biomass across a range of oceanic provinces and productivity regimes. However, it remains unclear whether canyons enhance faunal biodiversity on landscape scales relevant to marine protected area (MPA) design. Furthermore, it is not known which physical attributes and heterogeneity metrics can provide good surrogates for large-scale mapping of canyon benthic biodiversity. To test mechanistic hypotheses evaluating the role of different canyon-landscape attributes in enhancing benthic biodiversity at different spatial scales we conducted 34 submersible dives in 6 submarine canyons and nearby slopes in the Hawaiian archipelago sampling infaunal macrobenthos in a depth-stratified sampling design. We predicted that, in canyons, organic enrichment by macroalgae and terrestrial plant sources would yield greater macrofaunal abundance, and that enhanced habitat heterogeneity would yield greater beta diversity. In addition, we predicted reduced alpha diversity in canyons due to sustained physical disturbance and enhanced dominance associated with organic enrichment. We employed multivariate multiple regression models to evaluate sediment and topographic heterogeneity, canyon transverse profiles, and overall water mass variability as potential drivers of macrobenthic community structure and species richness. We find that variables related to habitat heterogeneity at medium ( $0.13 \text{ km}^2$ ) and large ( $15-33 \text{ km}^2$ ) spatial scales such as slope, backscatter reflectivity and canyon transverse profiles, are often good predictors of macrobenthic biodiversity, explaining 16-30% of the variance. Particulate organic carbon (POC) flux and distance from shore are also important variables, implicating food supply as a major predictor of canyon biodiversity. Canyons

off the high Main Hawaiian Islands (Oahu and Moloka'i) are significantly affected by organic enrichment, showing enhanced infaunal macrobenthos abundance, whereas this effect is imperceptible around the low Northwest Hawaiian Islands (Nihoa and Maro Reef). Variable canyon alpha-diversity and high rates of species turnover (beta-diversity), particularly for polychaetes, suggest that canyons play important roles in maintaining high levels of regional biodiversity in the extremely oligotrophic system of the North Pacific Subtropical Gyre. This information is of key importance to the process of MPA design, suggesting that canyon habitats be explicitly included in marine spatial planning.

**Keywords:** submarine canyons; infaunal macrobenthos, Hawaii, beta-diversity, deep-sea, marine spatial planning.

## 4.2. Introduction

Environmental variability can be remarkably high in continental margin settings when contrasted with continental shelves and abyssal plains (Levin et al., 2001; Snelgrove and Smith, 2002; Levin and Dayton, 2009; Williams et al., 2009; Levin et al., 2010). Benthic species diversity also often peaks along continental margins at depths between 1,500 and 2,500 m (Rex, 1983; Grassle and Maciolek, 1992; Levin et al., 2001; Rex and Etter, 2010). The midslope diversity maximum, observed at both alpha- (local species richness) and beta-diversity (species turnover) scales, occurs for benthic macrofauna such as crustaceans, mollusks and polychaetes, as well as for invertebrate megafauna and fishes (Rex, 1983; Carney, 2005). Although this pattern is hypothesized to be driven by changes in (1) sediment heterogeneity, (2) water mass properties and (3) seafloor particulate organic carbon flux with depth (Levin et al., 2001; Rex and Etter, 2010), the shape of this diversity versus depth curve varies with continental margin setting (Menot et al., 2010). This suggests that depth-related environmental gradients and habitat variability may differ significantly across regions (Menot et al., 2010). The roles of continental margins as sources of habitat heterogeneity over a range of spatial scales (Levin et al., 2001), the theoretical underpinnings of habitat heterogeneity-diversity relationships (Levin and Dayton, 2009; Menot et al, in preparation), and the increasing human impacts on continental margin biodiversity (Glover et al., 2003; Smith et al., 2008; Ramirez-Llodra et al., 2011; Levin and Sibuet, 2012) have recently been reviewed, showing a high demand for better understanding processes in this major deep-sea habitat.

Submarine canyons are major sources of habitat heterogeneity in continental margin settings (Vetter, 1994; Vetter and Dayton, 1998, 1999; Levin et al., 2001, 2010; Genin, 2004; Schlacher et al., 2007; 2010; Escobar-Briones et al., 2008; Tyler et al., 2009; De Leo et al., 2010;

Menot et al., in prep). Although canyons are distributed widely along ocean and island margins (De Leo et al., 2010; Harris and Whiteway, 2011), benthic community structure, standing stock, species richness and diversity have been investigated in only a small proportion (< 0.5%) of the worlds canyons (e.g., Rowe et al., 1982; Maurer et al., 1995; Vetter and Dayton, 1998, 1999; Curdia et al., 2004; Hargrave et al., 2004; Rowe et al., 2008; Ramirez-Llodra et al., 2010; Vetter et al., 2010; Buhl-Morthensen et al., 2010; Schlacher et al., 2007, 2010, Amaro et al., 2009, Tyler et al., 2009, Bianchelli et al., 2010; De Leo et al., 2010; 2012; McClain and Barry, 2010; Wei et al., 2010; Cunha et al., *in press*; Ingels et al., 2011, Patterson et al., 2012). *Infaunal* macrobenthos have been studied in even fewer submarine canyons (Rowe et al., 1982; Gage et al., 1995; Maurer et al., 1995; Vetter and Dayton, 1998; Gerino et al., 1999; Sorbe et al., 1999; Curdia et al., 2004; Escobar-Briones et al., 2008; McClain and Barry, 2010; Cunha et al., *in press*; Paterson et al., *in press*), even though this size class of benthos accounts for a large proportion of the known metazoan species diversity at the ocean floor (Snelgrove, 1999; Ebbe et al., 2010).

Canyons can enhance habitat heterogeneity on the margin and affect faunal communities in a variety of ways: (1) by channeling currents and promoting topographically induced upwelling (Klinck, 1996; Hickey, 1997); (2) by entraining particulate organic matter (Vetter, 1994; Vetter and Dayton, 1998; Harrold et al., 1998; Company et al., 2008; Rowe et al., 2008; De Leo et al., 2010, 2012), (3) by transporting shelf sediments to slopes in episodic turbidity currents or mass wasting events (de Stiger et al., 2007; Oliveira et al., 2007; Arzola et al., 2008), (4) by acting as topographic features that funnel and concentrate diel vertical migrators (Greene et al., 1988; Lavoie et al., 2000; Genin, 2004), and (5) by providing enhanced seafloor habitat heterogeneity (Brodeur, 2001; Yoklavish et al., 2001; Ublein et al., 2003; Buhl-Morthensen et al., 2010; Vetter et al., 2010; De Leo et al., 2012).

The enhancement of macro- and megabenthic abundance and biomass relative to open slope habitats seems to be a widespread effect of canyons, as a consequence of organic enrichment (e.g., Vetter, 1994; Vetter and Dayton, 1998, 1999; De Leo et al., 2010). Low biomass exceptions occur at particular depths within canyons subjected to frequent physical disturbance (e.g., bedload transport, sediment scour) from energetic flows, such as tidal currents (De Leo et al., 2012; Paterson et al., 2011), or from high sedimentation rates associated with turbidite deposition (Vetter and Dayton, 1999; Cunha et al., 2011; Paterson et al., 2011). Differences in species structure between canyon and non-canyon habitats are also well established for many canyon-slope systems, with canyons often exhibiting a high dominance by opportunistic species in organically-enriched settings (Vetter and Dayton, 1998; Curdia et al., 2003; Wilson et al., 2008; Cunha et al., 2012; Paterson et al., 2012). In spite of these marked effects on faunal abundance and community structure, the influence of canyons on species richness and evenness are poorly defined (i.e., weak patterns) at

local (alpha) scales. A few studies have indicated reduced species richness in highly disturbed canyon soft-sediment environments. For example, macrofauna species richness near cliff walls in Monterey canyon was reduced on a scale of hundreds of meters, possibly resulting from increased sedimentation and/or bioturbation disturbance near the canyon walls (McClain and Barry, 2010). Vetter and Dayton (1998) reported reduced alpha-diversity at shelf-depths and at the head of La Jolla canyon when compared with control sites on nearby slopes and attributed this pattern to the high dominance by opportunistic species such as *Capitella capitata* (polychaete), *Orchomene limodes* (amphipod) and *Nebalia* sp. (leptostracan), responding to enrichment by kelp and surfgrass detritus.

Most of the studies dealing with benthic communities, in particular the macrobenthos, in submarine canyons have focused on local habitat heterogeneity and alpha-diversity at spatial scales ranging from 0.1 to 10 km (Rowe et al., 1982; Vetter and Dayton, 1998; Cunha et al., 2012, Paterson et al., 2012). The focus of those studies has often been to measure a small subset of environmental variables (e.g. depth, sediment grain size, detrital cover/ input, quantity or quality of sedimentary organic matter, etc) thought *a priori* to be correlated with alpha diversity, and therefore potentially indicating drivers of local biodiversity patterns. In recognition that cause of local and regional diversity may be linked (e.g., Leibold et al., 2004), recent studies have addressed canyons as landscape features in continental margin settings that can enhance beta- and gamma diversity (Schlacher et al., 2007, 2010; Williams et al., 2009; 2010; Vetter et al., 2010; McClain and Barry, 2010; Menot et al., 2010). This approach considers habitat heterogeneity throughout entire canyons, and the influence of this heterogeneity on beta- diversity (or species turnover between habitat patches) and allows for greater ecological insight (Schlacher et al., 2007, 2010; Williams et al., 2009, 2010; Vetter et al., 2010). Such an approach is essential to map biodiversity at larger spatial scales for the purposes of marine spatial planning (e.g., implementation of networks of marine protected areas (MPAs) in the deep-sea) (Levin and Sibuet, 2012; Menot et al., 2010; Van Dover, 2011). As the human footprint increases in continental margin environments (e.g., fishing, hydrocarbon and mineral extraction, ocean acidification, etc), identification of key landscape features, and their influence on beta and gamma diversity, is essential for identifying likely biodiversity hotspots (Rowden, et al, 2005; Vierros et al., 2008; Clark and Rowden, 2009; O'Hara et al., 2011; Ramirez-Llodra et al., 2011, Levin and Sibuet, 2012; Van Dover et al., 2012). Furthermore, as well established principles for MPA design include: 1) conserving biodiversity hotspots, and 2) maximizing representativeness of species communities and habitats (Stevens, 2002; Nowlis and Friedlander, 2004), characterization of landscape scale drivers of habitat heterogeneity and beta diversity is critical.

Here I evaluate the importance of habitat heterogeneity, and other environmental variables, at differing spatial scales in driving benthic macrofauna community structure (including abundance and diversity) in submarine canyons at island margin settings along the Hawaiian archipelago, in the North Pacific Ocean. While benthic megafauna (invertebrate and fish) along Hawaiian slopes and canyons have been moderately well investigated (Struhsaker, 1973; Chave and Mundy 1994; Mundy, 2005) with recent new contributions (Kelley et al., 2006; Yeh & Drazen 2009, Vetter et al. 2010, De Leo et al., 2012), virtually no information on the sediment dwelling macroinvertebrate fauna along Hawaiian slopes is available. We employed geographic information system (GIS) spatial analysis to evaluate landscape metrics of habitat structure, including seafloor rugosity, steepness and canyon transverse profiles, with the goal of determining how these metrics are related to benthic community structure and diversity. Here we address four main hypotheses:

- 1) Macrofaunal abundance is greater in canyon than slope habitats as a result of trapping and downslope transport of allochthonous organic material from terrestrial and macroalgal sources, which we assume yield, directly or indirectly, greater food resources for benthic fauna;
- 2) Macrofaunal 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;
- 3) Macrofaunal species richness is positively correlated with habitat heterogeneity, and is therefore higher in the more heterogeneous settings of canyons; although reduced at the head of the canyons where physical disturbance is known to be higher;
- 4) Species turnover or beta-diversity of macrofaunal communities is greater at canyon than slope habitats, and is related to the higher habitat heterogeneity of canyons at a landscape scale.

## 4.3 Materials and Methods

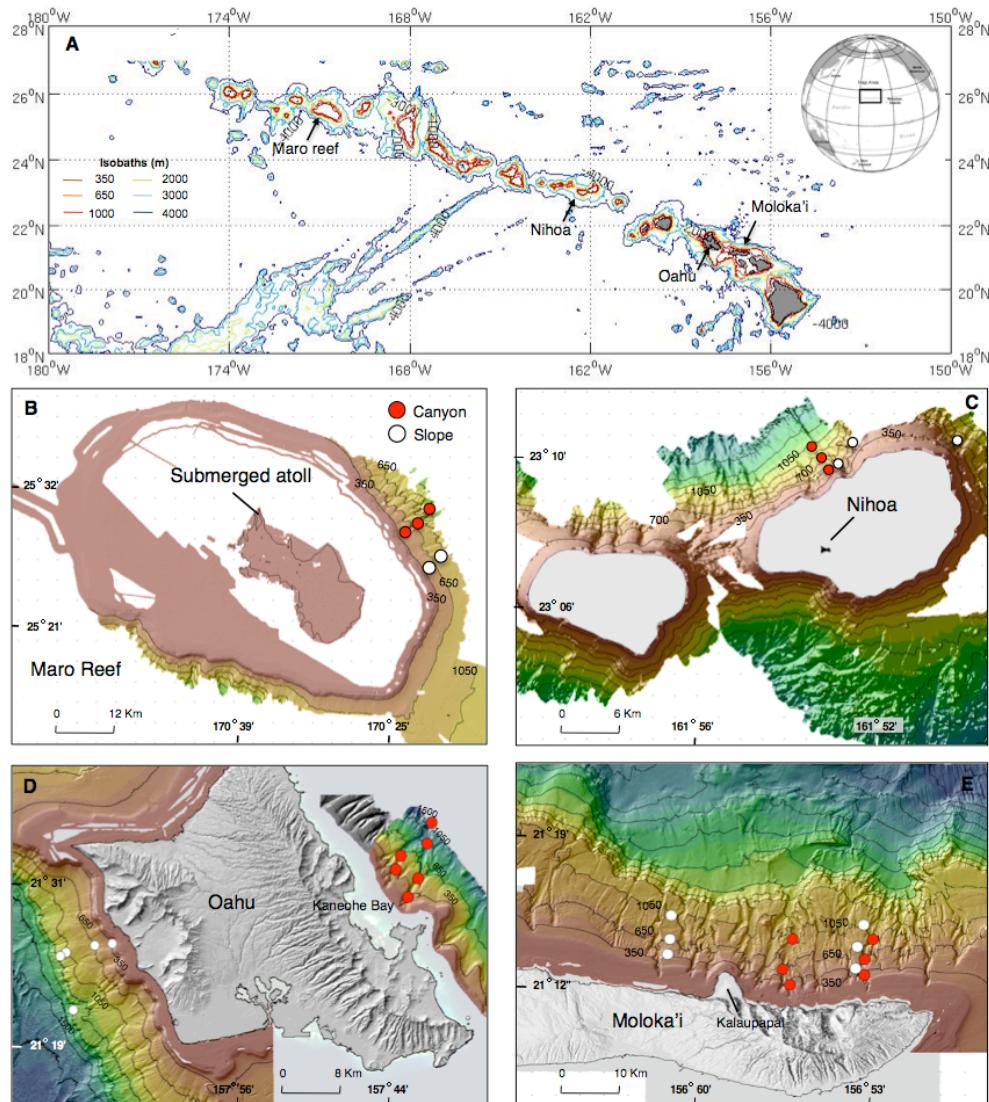
### 4.3.1 Study Area

The canyons studied here are distributed along 1,500 km of the Hawaiian Archipelago, in the oligotrophic North Pacific Subtropical Gyre System (NPSG) (Karl et al. 1996). This enables comparisons with sub-tropical and temperate submarine canyons located on CMs where thus far nearly all such studies have taken place. A relatively weak oxygen minimum zone (OMZ) affects the Hawaiian archipelago between depths of 600 and 700 m, with minimum oxygen concentrations of

0.6 ml l<sup>-1</sup> [O<sub>2</sub>] around 650 m (Yeh and Drazen, 2009; De Leo et al., 2012). Recent observations have postulated that the OMZ off Hawaii may partially account for lower abundances of scavenging teleosts and total demersal fish, although with no significant effects observable on species richness and diversity (Yeh and Drazen, 2009, De Leo et al., 2012).

The study was performed on the margins of two of the main Hawaiian Islands (Oahu and Moloka'i), and Nihoa and Maro reef in the Northwest Hawaiian Islands (NWHI), (Fig. 1a). The later two belong to the *Papahānaumokuākea* Marine National Monument, a conservation area of 273,409 km<sup>2</sup>, and recognized in 2010 as a UNESCO World Heritage Centre (<http://whc.unesco.org/en/list/1326>) (Fig. 1a). The environmental settings for the canyons ranged from high islands with relatively large terrestrial and marine sources of organic matter (Oahu and Moloka'i), through a low, dry island with very limited terrestrial detrital input (Nihoa), to an extensive submerged atoll (Maro Reef), considered functionally to be similar to a small, low 'island' (Vetter et al., 2010).

Off the NE shore of Oahu (21.557 ° S; 157.760 ° W), we sampled the Kaneohe Canyon, which has two shallow extensions separating at about 1000 m and terminating near the 100 m isobaths. Two sites were sampled and hereafter are referenced as Kaneohe Canyon North and South, respectively. Both canyons have heads positioned close to the 100 m isobath off Kaneohe Bay and extend 15 km (Kaneohe Canyon North) and 13 Km (Canyon South) offshore (Fig. 4.1b,c). A mosaic of benthic habitats characterizes the shallow Kaneohe Bay including patches of coral reef, coralline algae and macroalgae banks (NOAA, 2007). Macroalgae banks cover up to 40% of the plan area in the inner and middle parts of the Bay. We therefore expected high export rates of macroalgae detritus to deeper areas offshore since the region is subjected to strong wave action and wind-driven currents (Concklin and Smith, 2005; Ostrander et al., 2008). Two sandy channels connect the bay directly to the heads of the studied canyons (Fig. 4.1c). Oahu slope sites were located on the SW side of Oahu because a massive (~7 m) northeast swell prevented submersible work off the NE shore of Oahu during half of our cruise (Fig. 4.1d).



**Figure 4.1** Map showing Pisces dive locations where infaunal macrobenthos was sampled (from Vetter et al 2010).

Off Moloka'i, *Pelekunu* and *Kawainui* Canyons, both extending ~16 km offshore, were sampled along the north shore of the island ( $21.2^{\circ}$  S;  $156.9^{\circ}$  W) (Fig. 4.1e-g). Both canyons lie to the east of Kalaupapa Peninsula, a landmark that divides Moloka'i's north shore into two main landscapes, with an uniform, dry and low-elevation flat coastline to the west (Fig. 4.1e) and a complex high-elevation, forested coastline with a system of embayments to the east (Fig. 4.1g). The eastern portion of the coast contains 600-800 m sea cliffs with valleys carved by intense precipitation that ranges from 200-400 cm  $y^{-1}$  (Culliney, 2006). Sites on the open slope were located to the west of each of the canyons (Figure 4.1e-g).

In addition, two submarine canyons in the NWHI Islands were studied. Both canyon systems off Nihoa Island ( $23.18^{\circ}$  N;  $161.89^{\circ}$  W; Fig. 4.1h,i) and Maro Reef ( $25.5^{\circ}$  N;  $170.4^{\circ}$  W; Fig 4.1j,k) originate on the edges of large carbonate platforms at depths of around 200 m, extending for ~7-8 km offshore and reaching maximum depths of 2000 m. Slope sites at Nihoa were immediately north-west of the canyon, while at Maro Reef they were to the south-east of the canyon (Fig 4.1h,k).

#### *4.3.2 Macrofauna Sampling and Processing*

Three cruises onboard R/V *Ka'imikai-o-Kanaloa* allowed for a total of 34 dives using the Hawaii Undersea Research Laboratory's (HURL) Pisces IV and V submersibles, from which we conducted sediment macrofaunal community sampling in different depth strata (nominally, ~350, ~650, ~1000 m) inside the submarine canyons and at same depths on nearby slopes. In the NWHI, two depths were sampled because soft sediment occurred only at these depths: 'shallow'; ~350 m and 'intermediate'; ~650 m in Nihoa; 'intermediate' and 'intermediate-deep'; ~1000 m, in Maro Reef. In the main islands at least three depths were sampled (~350, ~650, ~1000 m) in Moloka'i, with a fourth 'deep' stratum (~1500 m) sampled off Oahu. Sediment push cores (6.8 cm of internal diameter, 0.0036 m<sup>2</sup> of area) employed using Pisces manipulators sampled benthic macrofauna in suitable soft-sediment flat areas of the canyon and slope. Within a site, cores were collected along random headings with sampling locations spaced at random distances of 1-10 m. Cores were inserted to a depth of ~15 cm, or until they were stopped by underlying bedrock. Five to eight core samples were collected in each depth stratum at each canyon or slope site, totalling 177 samples (Table 4.1).

Once shipboard, entire core samples were washed gently on 300-μm sieves and stored in 10% formaldehyde solution in seawater buffered with sodium hydroxide. In the laboratory samples were transferred to 80% ethanol solution in deionized water prior to sorting. Macrofauna was first sorted into main taxonomic groups and further identified with the help of taxonomic experts (see acknowledgements). Because most species appeared to be undescribed, most animals were assigned to operational taxonomic units, which differentiated putative species based on morphology. The number of individuals for each putative species was determined for each core.

**Table 4.1** Summary of R/V KOK cruises and Pisces dive information: depth, habitat, geographical coordinates and macrofaunal sampling effort.

Cruise/Pisces dive/date	Depth (m)	Site and habitat	Coordinates (dec. degree)		Sampling effort	
			Lat (N)	Long (W)	N	m <sup>2</sup>
<b>KOK-1 July 22-Aug 15, 2003</b>						
P4-90	431	Nihoa canyon	23.17914	161.88675	1	0.0036
P4-91	429	"	23.17913	161.88675	1	0.0036
P4-92	443	"	23.17955	161.88905	4	0.0144
P4-93	365	"	23.19939	161.87139	4	0.0144
P4-93	357	Nihoa slope	23.17683	161.86500	2	0.0072
P4-94	339	Nihoa canyon	23.17353	161.88316	2	0.0072
P4-94	368	Nihoa slope	23.18000	161.88000	3	0.0108
P4-95	620	"	23.19927	161.71450	5	0.018
P4-97	983	Maro canyon	25.53360	170.39920	7	0.0252
P4-98	834	"	25.53097	170.40230	7	0.0252
P4-99	631	"	25.51756	170.41514	1	0.0036
P4-100	635	"	25.51787	170.41567	3	0.0108
P4-101	657	Maro slope	25.48917	170.35167	7	0.0252
P4-102	968	"	25.48491	170.37162	3	0.0108
<b>KOK-2 Nov 3-21, 2003</b>						
P4-109	1579	Waianae slope	21.41639	158.31053	5	0.018
P4-110	1194	"	21.42703	158.28942	5	0.018
P4-111	348	"	21.43373	158.21650	2	0.0072
P4-111	358	"	21.43347	158.21768	1	0.0036
P4-111	356	"	21.43364	158.21704	2	0.0072
P4-112	1507	Kaneohe canyon (North)	21.60227	157.71353	5	0.018
P4-113	1023	"	21.57228	157.71947	4	0.0144
P4-113	1001	"	21.57417	157.72258	4	0.0144
P4-114	659	"	21.55719	157.76011	5	0.018
P5-115	372	"	21.52474	157.77728	5	0.018
P4-116	645	"	21.52177	157.73361	8	0.0288
P4-117	352	Kaneohe canyon (South)	21.49096	157.75256	4	0.0144
P4-118	653	Waianae slope	21.43549	158.23973	5	0.018
P4-119	1011	"	21.42605	158.28699	6	0.0216
<b>KOK-3 Aug 15-31, 2006</b>						
P5-661	636	Pelekunu canyon (canyon West)	21.21773	156.89722	6	0.0216
P5-662	345	"	21.19683	156.88784	6	0.0216
P5-663	1008	slope (West)	21.28999	157.03916	6	0.0216
P5-664	655	"	21.25855	157.04078	5	0.018
P5-665	343	"	21.23784	157.04423	6	0.0216
P5-666	1043	Kawainui canyon (canyon East)	21.25775	156.78236	6	0.0216
P5-667	643	"	21.23095	156.79256	7	0.0252
P5-668	320	"	21.21004	156.79288	6	0.0216
P5-669	348	slope (East)	21.21855	156.80436	6	0.0216
P5-670	647	"	21.24755	156.80160	6	0.0216
P5-671	985	"	21.27764	156.79364	6	0.0216

### *4.3.3 Environmental variables - measures of habitat heterogeneity*

#### *4.3.3.1 Water mass variability characteristics*

Temperature was measured *in situ* by Pisces IV and V sensors. The temperature values 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) oceanographic Station ALOHA. Therefore, we used the Station ALOHA annual mean and standard deviation for the years 2003 (KOK-1,2; HOT cruises # 144-154) and 2006 (KOK-3; HOT cruises #177-188) in which our cruises took place (<http://hahana.soest.hawaii.edu/hot/hot-dogs/interface.html>; Fujieki, 2007). This ensured good representation of the variability in water mass climatology. 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 periods (2003 and 2006). Note that this approach assumes low spatial (horizontal) variability in these variables across the study area (spanning ~ 1,500 linear kilometers). Oxygen profiles at KAHE Station (Fig. 3.1) 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 at least around the main Hawaiian Islands. Salinity data were not used as a measure of environmental variability as previous studies have shown a very small range in values (10-year variability from station ALOHA: 34.1 to 34.6 at all depths) that are not biologically significant for macrobenthic communities (Tyler, 1995).

#### *4.3.3.2 Organic matter input*

Particulate organic carbon (POC) flux at the seafloor was obtained by using a vertically explicit export productivity model mapped to the sample depth (Lutz et al., 2007) and used as a proxy of food availability for the macrobenthos. The model is based on net primary production derived from remotely sensed estimates and from export flux functions derived from global sediment trap data (Lutz et al., 2007). The POC flux data was gridded in an 18-km resolution to match the bathymetry data layer. In an attempt to provide an overall POC flux climatology for the region of the Main Hawaiian Islands, POC flux data obtained from the Lutz et al model was compared with long-term particle flux measurements at Station ALOHA, obtained from neutrally-buoyant sediment traps (Buesseler et al., 2008).

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). Video data was recorded along transects that were performed to study benthic megafaunal communities. Transects were conducted within the same depth strata where push cores were collected (Vetter et al., 2010; De Leo et al., 2012). 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 (cf. Vetter et al., 1999). 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.

#### *4.3.3.3 Sediment particle characteristics*

Because of limited sampling capacity of the submersibles, we were unable to collect samples specifically for granulometry. We thus evaluated sediment particle heterogeneity using macrofaunal sample residues (particles retained on a 300  $\mu\text{m}$  sieve, i.e.,  $\geq$  fine sand). Particle size heterogeneity in sand sized fractions has been shown to be correlated with deep-sea species diversity, and hence is an important environmental variable (Etter and Grassle, 2002). Our analyses provided a quantitative measure of local habitat heterogeneity that was internally consistent across all samples. Five replicate aliquots of 0.05 ml of sediment per core were evenly distributed in small Petri dishes using a vortex at 150 rpm. These were photographed using a Canon-A60 digital camera mounted on a stereomicroscope using either black or white backgrounds, depending on the nature of the sediment. A 10-mm ruler was placed in view for scaling. The following procedures were undertaken using the image analysis software Image J (Rasband, 2009): (1) images were cropped to a central area in which the number of particles to be measured varied between 200 and 800. The minimum of 200 particles, used as the threshold for robust statistical representation of the particle size spectra, was derived from Kennedy and Mazzullo (1991); (2) color images of Petri dishes were transformed into 8-bit images (Image J>image>type) and their background removed (Image J>process>remove background); (3) images were thresholded (image J>adjust>threshold) and scaled (Image J>analyze>set scale>10 mm) prior to particle analysis. Six particle heterogeneity metrics were extracted from each sediment core pooling all the replicate photographs: (i) mean and (ii) standard deviation of particle area; (iii) mean and (iv) standard deviation of diameter length (maximum and minimum diameter lengths were derived by fitting an ellipsoid function to each particle (Image J>analyze>set measurements>fit ellipse); (v) mean and (vi) standard deviation of the ratio between min and max diameters. Sediment particle characteristics were analyzed for all sites but the ones located in the island of Oahu, where sediment residues were not available.

#### 4.3.3.4 Seafloor terrain characteristics

Post-processed high-resolution ( $20 \times 20$  m grid) bathymetry and backscatter reflectivity for all the areas sampled with the Pisces submersibles was obtained from various mapping cruises (PIs D. Clague, 1998; C. Kelley, 2002, B. Applegate, 2005) for the MHI and from the National Geophysical Data Center (NGDC) at NOAA (National Ocean and Atmospheric Administration) (<http://www.ngdc.noaa.gov/mgg/bathymetry/relief.html>) for the NWHI. The Simrad EM120, EM300 and EM1002 multi-beam sonar systems mounted in the R/V Kilo Moana and in the M/V Ocean Alert were employed for gathering of all data sets.

Several metrics of seafloor terrain heterogeneity were extracted from both the multi-beam and backscatter data layers at four spatial scales. Those scales, progressively increasing in area, were denominated: scale A, at the grid cell where cores were sampled ( $20 \times 20$  m, or  $0.0004 \text{ km}^2$ ); scale B, 8 nearest grid cells (or  $0.0064 \text{ km}^2$ ); scale C, two hundred meters in radius from the center of the central cell (or  $0.12 \text{ km}^2$ ); and scale D, the whole canyon projected area and equivalent areas on the adjacent open slope, which ranged between 15 to  $33 \text{ km}^2$  (Fig. 4.2a). The total plan area of a canyon was calculated by employing *Hydrology* functions in Arc Map 9.3.1 (ESRI Spatial Analyst 9.3.1). The functions *Basins*, *Watershed*, and *Flow Direction* primarily delimited the canyon rims, as all the terrain declivity would converge to a lowest elevation point within a single basin (Fig. 4.2b). The *Stream Network* function was employed to find the main thalweg along the canyon axes and its distributaries (Fig. 4.2c). This is equivalent to finding the network of streams and rivers that would flow through the lowest elevation paths within a watershed in subaerial canyons or valleys (ESRI Spatial Analyst 9.3.1). All the raster layers (bathymetry and backscatter reflectivity) were then clipped using the area of the canyons as a masking feature (>spatial analyst>raster>extract>using mask) (Fig. 4.2d). Mean and standard deviation of slope, aspect (measure of terrain rugosity, Lassueur et al., 2006; Moore et al., 2010) and backscatter reflectivity (measure of substrate type, Goff et al., 2000; Kloser et al., 2001; Durand et al., 2006) were obtained for all the spatial scales aforementioned.

In addition, some canyon-specific measures were determined. These included two canyon transverse-profile indexes extracted from the bathymetry data. These metrics were used to compare variability in cross-section terrain profiles between canyons. V-shaped and U-shaped canyons are hypothesized to have different current flow regimes, being much more intense in V-shaped canyons (Shepard and Dill, 1966; Klinck, 1989), differentially affecting and yielding different benthic boundary layer structure. In order to calculate those profile indices, the seafloor terrain slope was extracted from the bathymetry data layer along parallel profile lines separated by 0.5 Km (NWHI) or 1 km (MHI) from each other, using the 3D Analyst toolkit in ArcMap (Fig. 4.2d-e). For the first

profile index, the average and standard deviation of slope along the profile lines were obtained, and finally the average of all profile lines constituted the Profile Index 1 (Fig. 4.2f). The second index computed the angle between the deepest point in the canyon thalweg and every other point along the profile line to both sides of the thalweg. Once again, the total average of all profiles angle averages constituted the Profile Index 2 (Fig. 4.2g). While the first index provides information on the variability in (multidirectional) slope along the profile lines and thus a measure of topographic variability, the second focuses on the unidirectional (perpendicular to the thalweg line) change in the terrain inclination angle along the profile lines. Those two metrics are meant to provide topographic abruptness indexes that likely translate into varying levels of physical energy and therefore the likelihood of substrate remobilization and faunal disturbance.

Finally, the total linear perpendicular distances between coring sites and the shoreline were measured as a proxy for organic loading (macroalgae and plant detrital material). The distance between coring sites and the canyon thalwegs were measured as a way to predict effects of bottom currents on faunal disturbance (e.g., reduced alpha-diversity, changes in community structure), likely to be higher in the proximity of canyon's maximum point of physical energy- (Shepard and Dill, 1966). Those two metrics were obtained using the measuring tool in ArcMap 9.3.1.

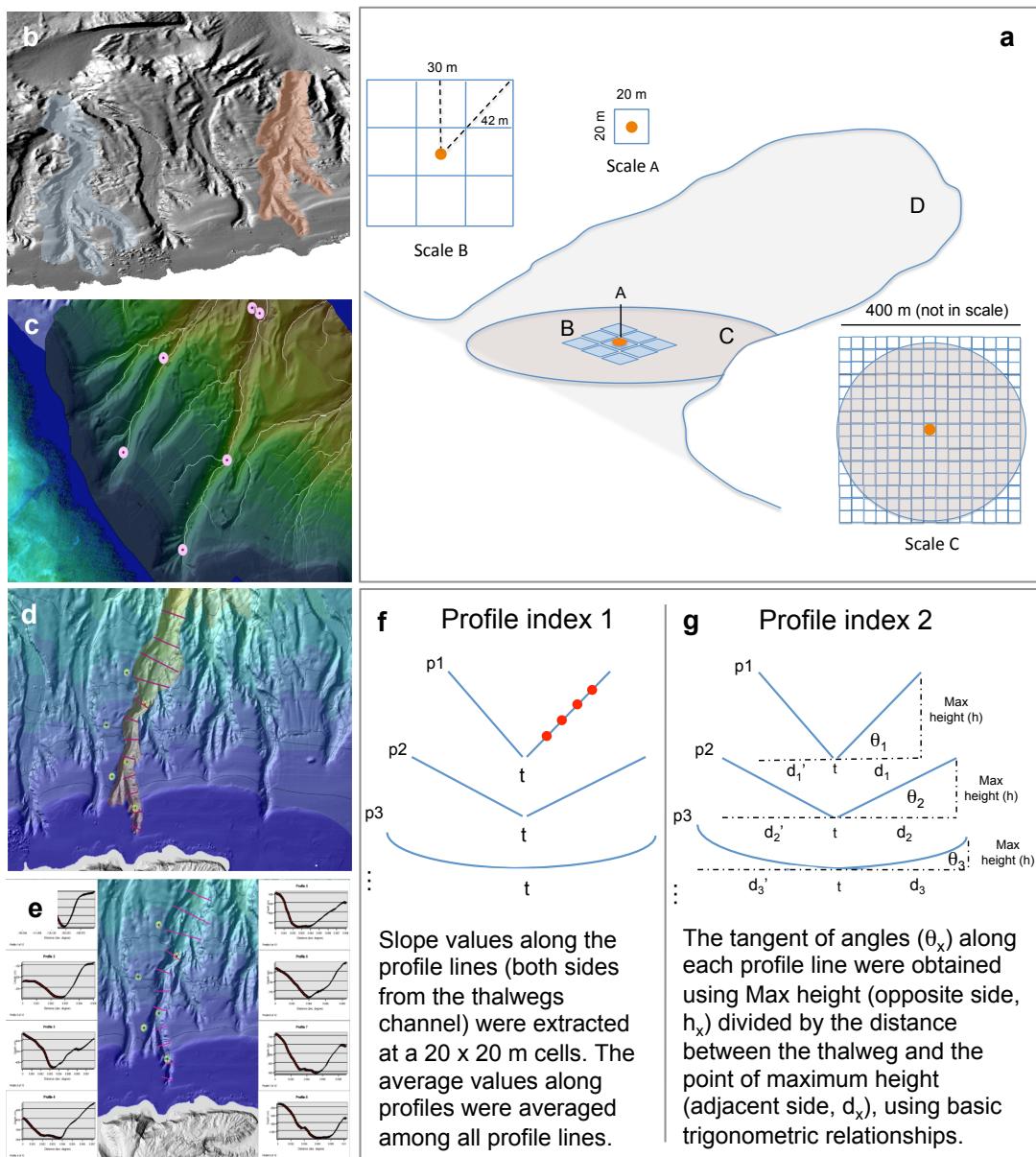
#### 4.3.4 Data and statistical analysis

##### 4.3.4.1 Abundance patterns and organic matter input (*Hypothesis 1*)

Three-way crossed univariate PERMANOVA tests were performed to determine differences in percent detritus occurrence, POC flux and macrofauna abundance between groups of samples from canyon and slope habitats, depth strata and sites. For this test the square-root transformed data to generate the resemblance matrix using Bray-Curtis dissimilarity was used. General linear models (GLMs) were applied to examine the relationships between estimated species richness and the most important predictor variables selected in the DISTLM regression models.

##### 4.3.4.2 Community structure patterns and environmental drivers (*Hypothesis 2*)

Distance-based PERMutational Multivariate ANalysis Of VAriance (PERMANOVA, McArdle and Anderson, 2001) was employed to test for significant differences in macrofaunal communities as a function of the following factors: (1), *habitat* (canyons x slopes), (2) *sites* (Oahu, Moloka'i, Nihoa and Maro Reef), and (3) *depth* (~350, ~650, ~1000 and ~1500 m 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. The transformation procedure allowed 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



**Figure 4.2** Measuring canyon habitat heterogeneity. a) Spatial scales investigated; (A, 0.0004 km<sup>2</sup>, B, 0.0064 km<sup>2</sup>, C, 0.13 km<sup>2</sup>, D, 15-33 km<sup>2</sup>); b) output of mask-clipping whole canyons from the bathymetry dataset; c) Thalwegs obtained using hydrology functions in ArcMap (canyons off Kaneohe Bay, Oahu are shown); d) Selection of masking clip (canyon East off Moloka'i is shown); e) Extraction of transverse-profile lines in ArcMap; f, g) Computation of two canyon transverse-profile indexes (p, profile; t, thalwegs; d, distance from thalweg to canyon edges).

(MDS) ordination technique, based both on the square root transformed abundance data and on presence-absence, were used to visualize the faunal patterns and 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

communities identified by the PERMANOVA analysis to be significantly different. Characterizing and discriminating species were ranked by their average contribution (%) to the within- and between community 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 communities is  $\geq 1.3$  (Clarke and Warwick, 2001).

In order to examine the influence of environmental variables on macrofaunal community structure, a DISTance-based Linear Model (DISTLM) multiple regression was employed (McArdle and Anderson, 2001; Anderson et al., 2008). A summary of all environmental variables available for the DISTLM routine, and their derivation, is provided on Table 4.2. We used the *BEST* selection procedure as it selects the best model based on the selection criterion (the  $AIC_c$ , Akaike's Information Criterion) for all possible combinations of predictor variables (Clarke and Gorley, 2006; Anderson et al., 2008). The  $AIC_c$  was devised to handle situations where the number of samples ( $N$ ) is small relative to the number of predictor variables ( $v$ ) such that  $N/v < 40$ , which applies to our data set ( $N=177$ ,  $v\leq 15$ ,  $N/v=10.4$ ) (Anderson et al., 2008 and references therein) (Table 4.2).

Three different runs of the DISTLM routine had to be applied to the data, as some environmental variables were available only for some data sets. The first run included all core samples in the analysis, but only water mass, organic matter and seafloor terrain data were included as predictor variables (refer to Table 4.2 for further clarification). The second run included all samples other than those from Oahu, and also used sediment particle data as predictor variable (Table 4.2). For the third and final run only samples taken from submarine canyons were included, as the canyon morphology profiles were appropriate for comparisons of habitat heterogeneity between canyons. For this run, water mass, organic matter and seafloor terrain predictor variables were also included (Table 4.2).

Before the DISTLM models were run, the existence of highly correlated variables and any need for data transformation was assessed using a draftsman plot. No more than 15 predictor variables were input into the model runs, as computational time would excessively increase without adding explanatory power to the models (R. Clarke, pers. communication). For this reason, the exploratory steps of removing redundant variables were fundamental prior to running the analysis. Normalization of variables prior to the analysis was automatically performed within the routine of DISTLM (Anderson et al., 2008). Replicate core samples had to be pooled in order to match the spatial-resolution in the measures of habitat heterogeneity related to seafloor terrain. For example, most of the core samples were taken randomly at distances  $\leq 10$  meters from each other, all falling within one pixel cell of the bathymetry data grid.

A distance-based redundancy analysis (dbRDA) was used to visualize the DISTLM results. 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).

The multivariate statistical routines MDS, PERMANOVA, SIMPER, DISTLM, dbRDA were run using PRIMER version 6.0 with the PERMANOVA+ add-on (Clarke and Gorley, 2006; Anderson et al., 2008).

**Table 4.2** List of 47 predictor variables available for the DISTLM models

Variable type	Id #	Name	Source	Unit
SEAFLOOR/TERRAIN HETEROGENEITY	1	Sample depth	bathymetry (20 x 20 m)	
	2	Distance to shore	Arc measuring tool	
	3	Slope (slp) A	bathymetry (20 x 20 m)	degrees
	4	slp B, m	bathymetry (20 x 20 m)	degrees
	5	slp B, sd	bathymetry (20 x 20 m)	degrees
	6	slp C, m	bathymetry (20 x 20 m)	degrees
	7	slp C, sd	bathymetry (20 x 20 m)	degrees
	8	slp D, m	bathymetry (20 x 20 m)	degrees
	9	slp D, sd	bathymetry (20 x 20 m)	degrees
	10	Aspect (asp) A*	bathymetry (20 x 20 m)	degrees
	11	asp B*, m	bathymetry (20 x 20 m)	degrees
	12	asp B*, sd	bathymetry (20 x 20 m)	degrees
	13	asp C*, m	bathymetry (20 x 20 m)	degrees
	14	asp C*, sd	bathymetry (20 x 20 m)	degrees
	15	asp D*, m	bathymetry (20 x 20 m)	degrees
	16	asp D*, sd	bathymetry (20 x 20 m)	degrees
	17	Backscatter (ss) A	backsctatter (20 x 20 m)	decibels
	18	ss B, m	backsctatter (20 x 20 m)	decibels
	19	ss B, sd	backsctatter (20 x 20 m)	decibels
	20	ss C, m	backsctatter (20 x 20 m)	decibels
	21	ss C, sd	backsctatter (20 x 20 m)	decibels
	22	ss D, m	backsctatter (20 x 20 m)	decibels
	23	ss D, sd	backsctatter (20 x 20 m)	decibels
CANYON MORPHOLOGY <sup>a</sup>	24	Canyon total area	Arc 3D Analyst	m <sup>2</sup>
	25	Surface area	Arc 3D Analyst	m <sup>2</sup>
	26	Volume	Arc 3D Analyst	m <sup>3</sup>
	27	Surface Area/Volume	Arc 3D Analyst	m <sup>-1</sup>
	28	Linear length	Arc 3D Analyst	km
	29	Profile index 1, m	Arc 3D Analyst	degrees
	30	Profile index 1, sd	Arc 3D Analyst	degrees
	31	Profile index 2, m	Arc 3D Analyst	pure
	32	Profile index 2, sd	Arc 3D Analyst	pure
	33	Distance to thalweg	Arc measuring tool	km
SEDIMENT CHARACTERISTICS <sup>b</sup>	34	Sed part. area, m	Image analysis (> 300 µm)	mm
	35	Sed part. area, sd	Image analysis (> 300 µm)	mm
	36	Sed part. diameter, m	Image analysis (> 300 µm)	mm
	37	Sed part. diameter, sd	Image analysis (> 300 µm)	mm
	38	Sed part. diameter ratio,	Image analysis (> 300 µm)	mm
	39	Sed part. diameter ratio,	Image analysis (> 300 µm)	mm
	40	Temp annual, m	from station ALOHA	°C
	41	Temp annual, sd	from station ALOHA	°C
	42	Oxy annual, m	from station ALOHA	ml l <sup>-1</sup>
	43	Oxy annual, sd	from station ALOHA	ml l <sup>-1</sup>
	44	POC Lutz annual, m	from station ALOHA	g C m <sup>-2</sup>

45	POC Lutz, sd	(2003/2006) from station ALOHA	$\text{yr}^{-1}$ $\text{g C m}^{-2}$
46	% detritus occurrence, m	Pisces video transects/image	%
47	% detritus occurrence, sd	Pisces video transects/image	%

<sup>a</sup> restrained analysis to canyon samples only

<sup>b</sup> samples from Oahu lacking

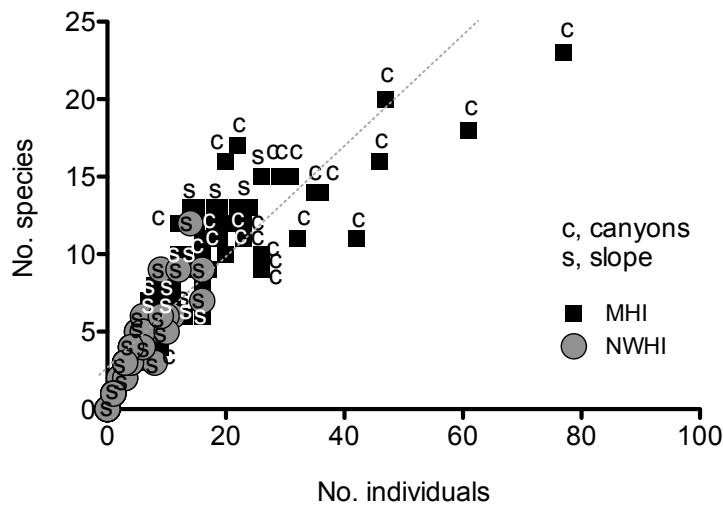
\* Because aspect is a circular variable, it was transformed into two variables, northness (calculated as  $\cos(\text{aspect})$ ), and eastness (calculated as  $\sin(\text{aspect})$ ). These variables described sites of north–south aspect and sites of east–west aspect.

m, mean, sd, standard deviation, part, particle.

Spatial scales: A, 0.0004 km<sup>2</sup>, B, 0.0064 km<sup>2</sup>, C, 0.13 km<sup>2</sup>, D, 15–33 km<sup>2</sup>.

#### 4.3.4.3 Species richness and habitat heterogeneity (*Hypothesis 3*)

Three-way crossed univariate PERMANOVA tests were performed to determine differences sediment particle characteristics between groups of samples from canyon and slope habitats, depth strata and sites. Species richness was measured using three descriptors: (1) total number of species per core (i.e., sample species richness, S), (2) estimated species richness using the estimators Chao 1 and Chao 2 (Colwell and Coddington, 1994; Magurran, 2004), and (3) rarefaction species richness (ES<sub>10</sub>). Although the area of each sample (0.0036 m<sup>2</sup> core) was constant, we used species richness estimators (Chao 1 and Chao 2) because the low macrofauna abundances caused sample species richness to be highly density dependent; i.e., variations in sample species richness were almost entirely explained by number of individuals in the sample (Fig. 4.3). Since Chao 1 and Chao 2 species estimators are obtained by pooling the transect replicates, not enough terms in each of the 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, Colwell, 2000) to verify statistical significance (Colwell, 2000; Magurran, 2004). The DISTLM routine was run as a univariate multiple regression model to evaluate the effects of habitat heterogeneity variables (and other predictor variables) on estimated macrofaunal species richness (Chao 1 and Chao 2 indexes) (Anderson et al., 2008 and references therein). For this analysis, a Euclidian-distance resemblance matrix was constructed based on the dissimilarities between groups of replicate samples pooled (Anderson et al., 2008). General linear models (GLMs) were applied to examine the relationships between estimated species richness and the most important habitat heterogeneity variables selected in the DISTLM regression models.



**Figure 4.3** Macrofaunal abundance *vs* species richness per core.

#### 4.3.4.4 Species turnover and habitat heterogeneity (*Hypothesis 4*)

Species turnover or beta-diversity at the landscape-scale was measured by evaluating the slope of randomized species accumulation curves after pooling samples within single canyon or slope sites (Ugland et al., 2003). To examine the relationship between beta-diversity and habitat heterogeneity accumulation curves were also generated for each possible combination of habitat-patches (i.e., the depth stratum for most cases) within a habitat, within a site (Cordes et al. 2010). Curves were rarefied by quantifying the number of species present in an increasing number of individuals, randomly selected without replacement from the available pool of samples avoiding distortions in the curves due to variations in species abundance and sampling effort (Gotelli and Colwell, 2001).

Species accumulation curves were also calculated for canyons and slopes by pooling all samples from all sites within each habitat to determine the gamma diversity of the island margin, i.e., an accumulation curve was made by pooling all samples from both canyon and slope habitats.

## 4.4 Results

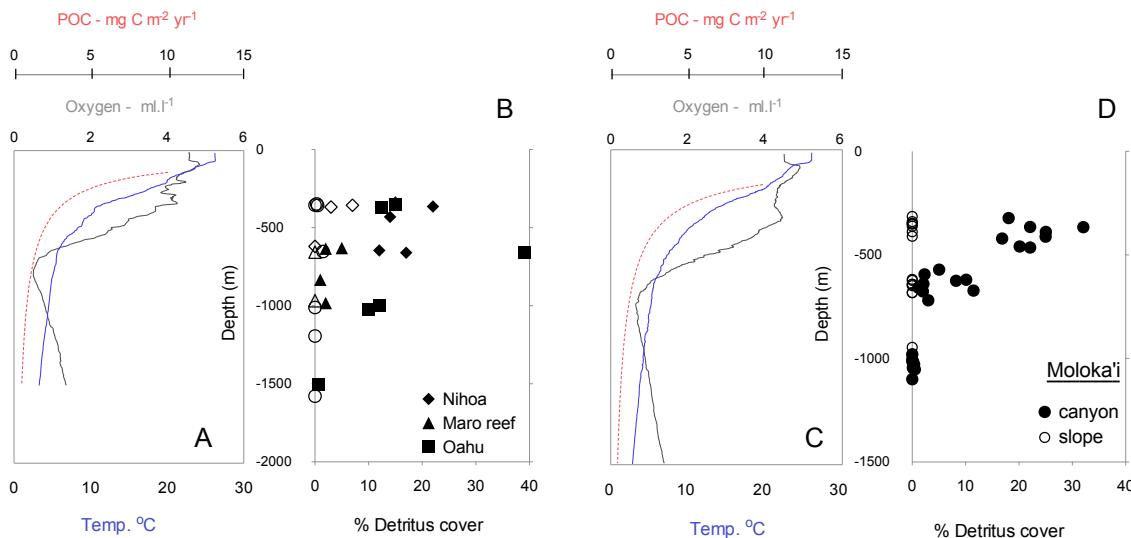
### 4.4.1 Environmental Variability

#### 4.4.1.1 Water mass characteristics

Yearly averaged temperature and oxygen profiles changed little from 2003 to 2006, when our study took place (Fig. 4.4). While a thermocline extended roughly between 50 and 600 m (~26° C at the top, ~6° C at the base), oxygen values declined rapidly from 350 m to 750 m, establishing an oxygen minimum zone with lowest values between 0.5-0.65 ml [O<sub>2</sub>] l<sup>-1</sup> at around 750 m.

#### 4.4.1.2 Organic matter input

Modeled POC flux varied significantly with depth, but not between canyon and slope habitats (Table 4.3). The island of Oahu showed higher POC flux at the seafloor when compared to all other islands ( $t=29.279$ ,  $p=0.0001$ , pairwise statistics not shown in Table 4.3). Percentage occurrence of detritus showed an overall decreasing trend with depth (Fig. 4.4b,d). In Oahu, while detritus occurrence peaked (~40%) at intermediate depths (~650 m), it also showed the highest overall values observed in the 650 to 1000 m strata (10-12%, Fig. 4b). In Molokai, we observed the highest detritus occurrence in the shallow stratum (18-32%) (Fig. 4.4d). Percentages of detritus occurrence on canyon floors were statistically higher than on slopes in all systems (MHI and NWHI) surveyed (Table 4.3). Complete absence of detritus was observed at various depths of the open slope sites (Fig. 4.4).



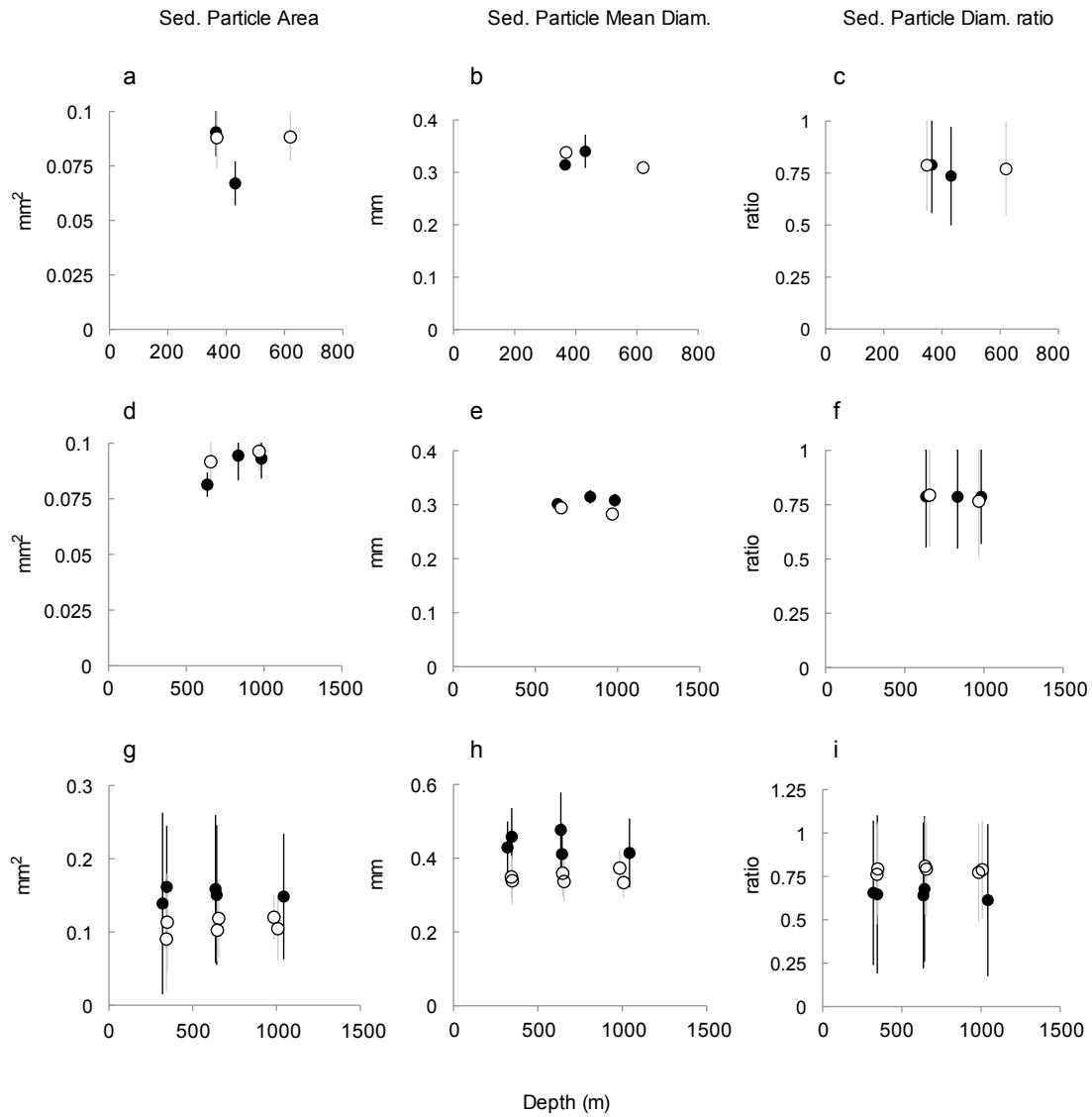
**Figure 4.4** Water Mass (mean annual temperature and dissolved oxygen, from Station ALOHA), POC flux (annual mean modelled based on Buesseler et al., 2007) and % detritus occurrence data. A-B, 2003 KOK1-2 cruises with annual means from station ALOHA data. C-D, data matching 2006 KOK-3 cruise. Symbols indicate depths where core samples were taken (A,C) or mean video transect depths for % detritus occurrence measurements (B,D, diamonds, Nihoa, triangles, Maro Reef, circles, Molokai). Dark symbols, canyons; empty symbols, slopes.

**Table 4.3** Univariate PERMANOVA tests for differences in POC flux and % detritus occurrence between a priori factors defined: ha, habitat (canyon x slopes), si, sites (Maro reef, Nihoa, Oahu, Moloka'i) and depth. \*\* Missing terms.

Tested variable	Source	df	SS	MS	Pseudo-F	p(perm)	Unique permutations
<b>POC flux</b>	Habitat (ha)	1	0.00	0.000	0.1971	0.6516	9811
	Site (si)	3	1.26	0.420	422.21	<b>0.0301</b>	9960
	Depth (de)	3	2.56	0.856	859.74	<b>0.0001</b>	9949
	haxsi	3	0.72	0.242	243.83	<b>0.0251</b>	9943
	haxde	3	0.25	0.084	84.65	0.0924	9951
	sixde**	4	0.72	0.182	182.72	0.3251	9941
	haxsixde**	4	0.21	0.053	53.26	<b>0.0135</b>	9948
	Res	156	0.15	0.001			
	Total	177	8.79				
						No test	
<b>Detritus</b>	Habitat (ha)	1	744.	744.3	464.5	<b>0.0074</b>	9423
	Site (si)	3	704.	234.8	146.58	<b>0.0001</b>	9958
	Depth (de)	4	287	717.5	447.74	<b>0.0001</b>	9975
	haxsi**	1	246.	2.46E	153.54	<b>0.0087</b>	9554
	haxde**	1	68.1	68.14	42.524	<b>0.0065</b>	9523
	sixde**	4	183	457.9	285.74	<b>0.0001</b>	9957
	haxsixde**	0	0				
	Res	4	6.41	1.602			
	Total	18	661				

#### 4.4.1.3 Sediment particle characteristics

Sediments from NWHI were mainly composed of carbonate sands (reef sands and foraminiferan oozes). The particle metrics derived from image analysis showed no statistical differences for mean particle area and diameter with depth, habitat (canyon or slopes) and sites (Nihoa Island and Maro Reef) (Fig. 4.5a,b,d,e). The metric of particle diameter ratio (small diameter/larger diameter in a fitted ellipsoid function) also showed little variability, meaning most particle grains are approaching spherical shapes (in 2 dimensions) and thus relatively well sorted at the NWHI sites (Fig. 4.5c,d). On the other hand, sediments sampled off Moloka'i (MHI) were composed of a range of siliceous mineral grains, organic debris (fragmented seeds, leaves, wood), as well as carbonate sands (foraminiferans and shell rubble). This larger diversity in particle types and shapes were well represented by the three particle metrics, with small but observable differences in particle spectra between canyons and slopes (Fig. 4.5g-i). Mean and standard deviations of particle area and diameter were significantly higher in canyons of MHI, indicating larger overall particle heterogeneity (Table 4.4). Standard deviations of particle diameter ratio also showed marked differences between canyon and slope samples and were largely due to amorphous organic (wood and leaf debris) fragments with low sphericity in shape.



**Figure 4.5** Sediment particle characteristics ( $> 300 \mu\text{m}$ ). Mean and standard error of particle area (left), diameter (center) and diameter ratio (right-column). Sample sizes equal 5 photographs were 200-800 particles were counted and measured. Island of Nihoa (a-c), Maro Reef (d-f), Moloka'i (g-i). Filled circles, canyons; open circles, slopes (with standard error bars in grey). Slight offsets between symbols relate to small differences in depth from where samples were collected. The lack of error bars represents small SE values.

**Table 4.4** Univariate PERMANOVA tests for differences in mean sediment particle characteristics (area, diameter and diameter ratio) between *a priori* factors defined: ha, habitat (canyon x slopes), si, sites (Maro reef, Nihoa, Oahu, Moloka'i) and depth (s, i, i-d, d, refer to footnotes).

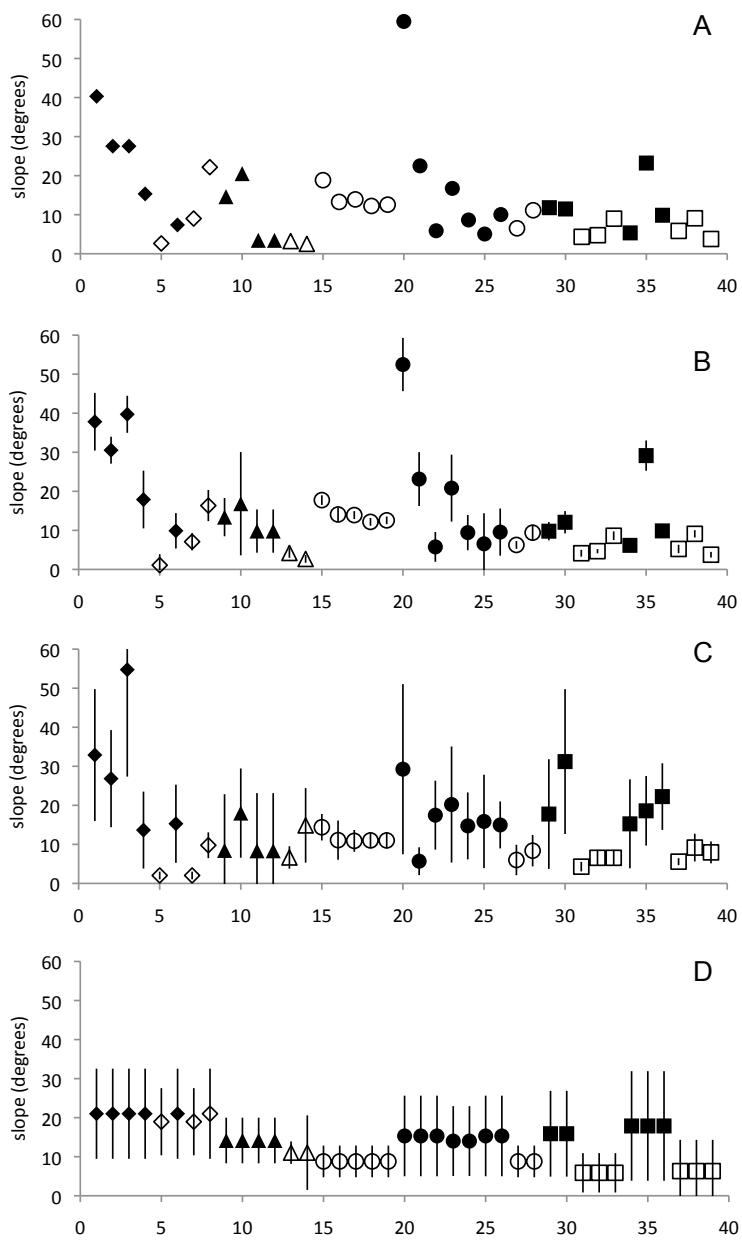
Tested variable	Source	df	SS	MS	Pseudo-F	p(perm)	Unique permutations
<b>Area (A)</b>	Habitat (ha)	1	0.001	0.001	0.969	0.334	997
	Site (si)	2	0.022	0.011	8.214	<b>0.002</b>	999
	Depth (de)	2	0.000	0.000	0.005	0.996	997
	haxsi	2	0.001	0.000	0.305	0.728	998
	haxde	2	0.001	0.001	0.414	0.676	998
	sixde**	2	0.000	0.000	0.050	0.953	999
	haxsixde**	2	0.000	0.000	0.051	0.95	996
	Res	58	0.079	0.001			
	Total	71	0.114				
<b>Diameter (D)</b>	Habitat (ha)	1	0.004	0.004	1.773	0.175	998
	Site (si)	2	0.082	0.041	16.393	<b>0.001</b>	998
	Depth (de)	2	0.004	0.002	0.711	0.492	999
	haxsi	2	0.026	0.013	5.167	<b>0.005</b>	998
	haxde	2	0.002	0.001	0.388	0.696	997
	sixde**	2	0.004	0.002	0.753	0.49	998
	haxsixde**	2	0.003	0.001	0.507	0.605	998
	Res	58	0.145	0.002			
	Total	71	0.374				
<b><math>D_1:D_2</math> ratio</b>	Habitat (ha)	1	0.031	0.031	10.522	<b>0.002</b>	997
	Site (si)	2	0.176	0.088	29.560	<b>0.001</b>	997
	Depth (de)	2	0.007	0.003	1.094	0.349	999
	haxsi	2	0.044	0.022	7.404	0.002	998
	haxde	2	0.001	0.001	0.206	0.787	998
	sixde**	2	0.008	0.004	1.378	0.265	999
	haxsixde**	2	0.000	0.000	0.041	0.958	999
	Res	58	0.173	0.003			
	Total	71	0.674				

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.\*\* missing terms. s, shallow (314-459 m); i, intermediate (571-719 m); i-d, intermediate-deep (946-1100 m); deep (1400-1500 m). Data was square-root transformed and resemblance calculated using Bray-Curtis.  $D_1$  and  $D_2$  are the smaller and larger particle diameter in an ellipsoid fitted function to each particle (see section 4.3.3).

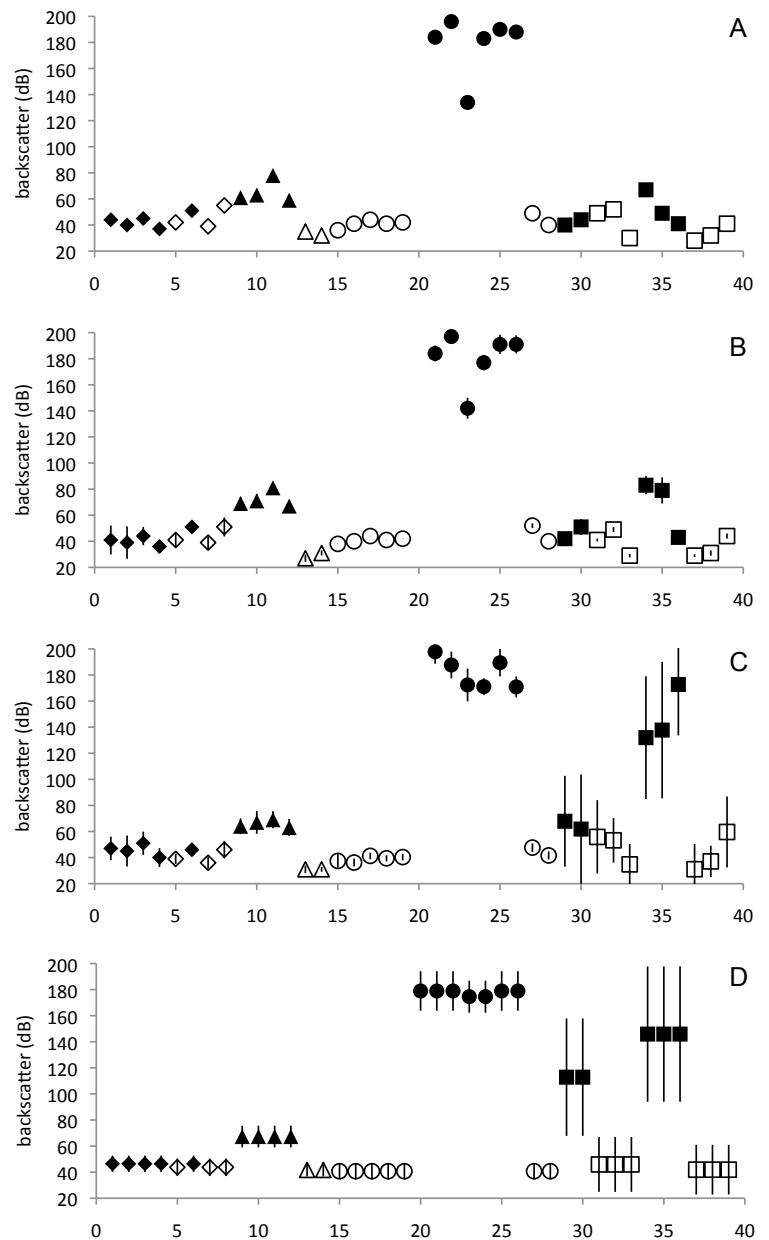
#### 4.4.1.4 Seafloor terrain characteristics

In terms of seafloor terrain characteristics, canyon and slope areas varied among all islands. As expected, within-site comparisons revealed higher mean values and variability in bathymetric slope in the canyons as opposed to slope sites (Fig. 4.6). Moreover, the extent of that variability remained higher on canyons across all scales from A ( $0.0004 \text{ km}^2$ ) to D ( $15-33 \text{ km}^2$ ) (Fig. 4.6).

The backscatter reflectivity also showed higher mean values and higher variability inside canyons, indicating a higher degree of substrate type heterogeneity (Fig. 4.7). This trend, however, was not strongly evident at Nihoa Island where both slope and canyon had similarly low backscatter values (Fig. 4.7), indicating this was homogenous soft sediment.



**Figure 4.6** Slopes extracted from the  $20 \times 20$  m grid resolution bathymetry. A-D, varying spatial scales: A,  $0.0004 \text{ km}^2$ , B,  $0.0064 \text{ km}^2$ , C,  $0.13 \text{ km}^2$ , D,  $15-33 \text{ km}^2$ . Diamonds, Nihoa; triangles, Maro Reef; circles, Moloka'i; squares, Oahu. Filled symbols = canyons, open symbols = slope sites. Standard deviations are shown for all scales except at the cell grid ( $20 \times 20$  m) scale, scale A.



**Figure 4.7** Backscatter reflectivity extracted from the  $20 \times 20 \text{ m}$  grid resolution bathymetry. A-D, varying spatial scales: A,  $0.0004 \text{ km}^2$ , B,  $0.0064 \text{ km}^2$ , C,  $0.13 \text{ km}^2$ , D,  $15-33 \text{ km}^2$ . Diamonds, Nihoa; triangles, Maro Reef; circles, Molokai; squares, Oahu. Filled symbols = canyons, open symbols = slope sites. Standard deviations are show for all scales except at the cell grid ( $20 \times 20 \text{ m}$ ) scale, scale A.

#### 4.4.2. Abundance patterns and organic matter input (Hypothesis 1)

Macrofaunal abundances ranged from 313-25,000 individuals m<sup>-2</sup> across the whole area sampled (Mean= 3,227; SD=3,454). Abundances were comparatively higher in canyons relative to slopes in the MHI (Table 4.5, pairwise tests for *habitat x site* interaction term), with highly significant differences at 650 m and 1000 m off Oahu, and at 650 m off Moloka'i (Table 4.5, pairwise test for *habitat x site x depth* interaction term). In the NWHI sites, however, lower abundances were generally found both on canyons and slopes, with no significant differences between the two habitats (Table 4.5).

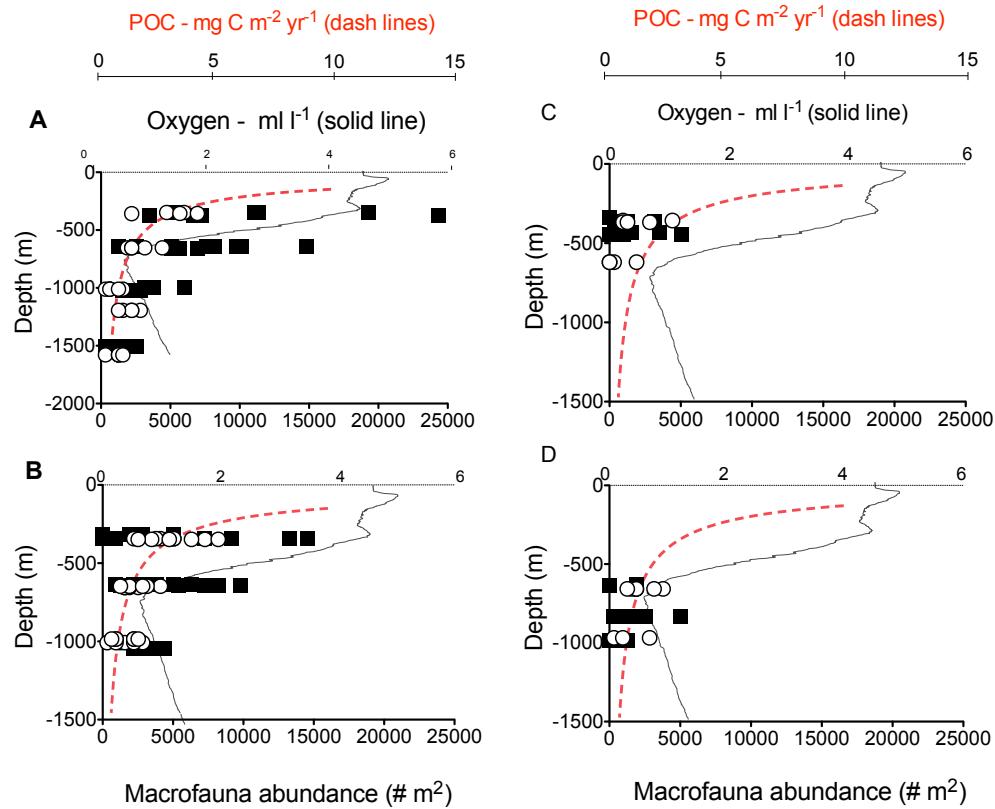
**Table 4.5** Univariate PERMANOVA tests for differences in macrofaunal abundance (i.e., number of individuals per core sample) between *a priori* defined factors: *ha*, habitat (canyon x slopes), *si*, sites (Maro reef, Nihoa, Oahu, Moloka'i) and *de*, depth (s, i, i-d, d, refer to footnotes).

Macrofaunal abundance	Source	df	SS	MS	Pseudo-F	p(perm)	Unique perm
<b>Main test</b>							
	Habitat (ha)	1	41.7	41.75	0.17	0.0523	999
	Site (si)	3	8,197	2,732.5	11.2310	<b>0.0010</b>	998
	Depth (de)	3	12.35	4,119.8	16.93	<b>0.0010</b>	999
	haxsi	3	1,466	488.74	2.01	<b>0.0431</b>	998
	haxde	3	1,717	572.34	2.35	<b>0.0450</b>	999
	sixde**	4	1,652	413.13	1.70	<b>0.0120</b>	999
	haxsixde**	4	600.6	150.15	0.62	<b>0.0178</b>	999
	Res	14	34,54	243.30			
	Total	16	70,99				
<b>Pair wise tests</b>							
	Source	df		t-stat	p(perm)	Unique perm	
<u>ha x si</u>							
	Nihoa (ni)	14		0.354	0.841	999	
	Maro Reef (ma)	19		0.189	0.935	998	
	Moloka'i (mo)	56		2.663	<b>0.0008</b>	998	
	Oahu (oa)	53		3.1941	<b>0.0001</b>	999	
<u>ha x si x de</u>							
	Moloka'i (s)	10		0.112	0.987	112	
	Moloka'i (i)	4		0.624	<b>0.019</b>	15	
	Moloka'i (i-d)	6		0.2354	0.022	5	
	Oahu (s)	13		0.278	0.948	84	
	Oahu (i)	20		0.773	<b>0.007</b>	980	
	Oahu (i-d)	20		2.525	<b>0.023</b>	981	
	Oahu (d)	16		2.994	0.445	652	
	Nihoa (s)	12		1.897	0.079	723	
	Nihoa (i)	16		2.655	0.679	845	
	Maro (i)	17		3.3434	1	753	
	Maro (i-d)	8		0.205	0.845	30	

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.\*\* missing terms. s, shallow (314-459 m); i, intermediate (571-719 m); i-d, intermediate-deep (946-1100 m); deep (1400-1500 m). Data was square-root transformed and resemblance calculated using Bray-Curtis.

For Oahu and Moloka'i (MHI), an exponential decrease in macrofaunal abundances with depth is evident both for canyons and slopes, following the exponential decrease in POC flux with

depth (dotted lines in Fig. 4.8). However, a larger scatter and overall higher values of macrofauna abundance is observed in the canyons of the MHI. Macrofaunal abundances did not seem to be affected by the presence of the oxygen minimum zone (OMZ) at ~750 m (Fig. 4.8).



**Figure 4.8** Macrofaunal abundance (# indiv. m<sup>-2</sup>). A, Oahu, B, Moloka'i, C, Nihoa, D, Maro Reef. Canyon, solid squares; slopes, white circles. Two secondary x-axes depict vertical profiles of POC flux (top, mg C m<sup>-2</sup> yr<sup>-1</sup>, dash lines) and dissolved oxygen (ml l<sup>-1</sup>, solid lines) from station ALOHA.

#### 4.4.3 Community structure patterns and environmental drivers (Hypothesis 2)

##### 4.4.3.1 Community structure

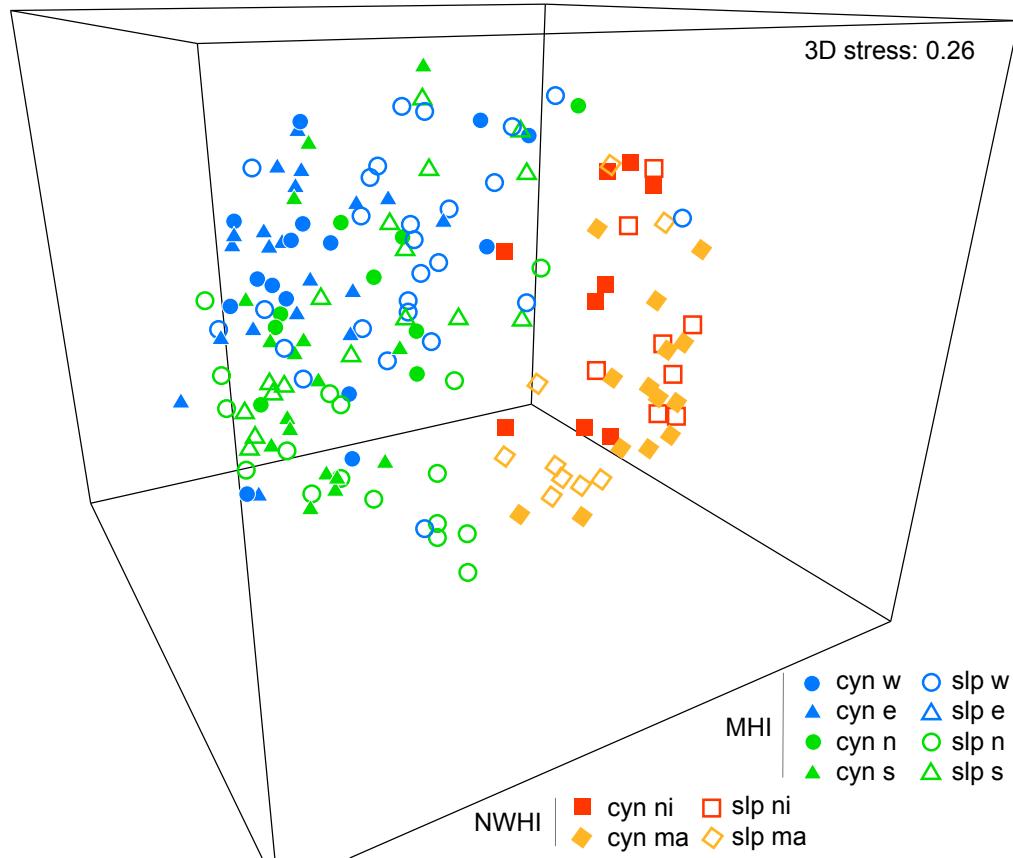
From a total of 1,836 individuals sampled from 177 core samples, 316 putative (morphotype) species were assigned. Specimens identified to known species level were only 13% in terms of the overall abundance and 1.5 % in terms of the total number of taxa. Identifications to generic level accounted for 7% of the overall abundance while 9% of the complete species list. Polychaetes dominated both in terms of abundance (63%) as well as in number of species (171 species, 54%). Mollusks represented 17% of the overall abundance and 11% of species list (35 sp.)

while crustaceans (decapods in early development stages, copepods, large ostracod and peracarids) accounted for only 14% of the overall abundance and 25% of the species (74 sp.). Copepods (20 sp.), tanaids (12 sp.), isopods (10 sp.) were relatively speciose. Rarer taxa, e.g., nemerteans, sipunculans, echinurans, bryozoans, echinoderms, accounted for 11% of the overall abundance and 11% of species (34 sp.).

Three new species are currently under description, including the two amphipods *Abyssorchromene* sp. nov. , *Orchomenopsis* sp. nov. (M. Thurston, person comm.), and the copepod *Pontostratiotes* sp. nov. (Kihara T.C., Natural History Museum, London, in preparation). The Spionid sp. 5 from the genus *Prionospio* is also a new species but has also been reported on the Portuguese margin and is being described at the Natural History Museum of London (A. Glover, G. Paterson, personal communication).

Among the most abundant families within the polychaete taxon were Spionidae (25%), Capitellidae (9.3%), Fauveliopsidae (8.5%), Syllidae (6.3%), Cossuridae (6.2%), Ophellidae (5.2%), Sigalionidae (4.2%), Cirratulidae (3.4%), Paraonidae (2.7%) and Flabelligeridae (1.8%).

The PERMANOVA results indicate significant differences in infaunal macrobenthic communities between habitats (canyon x slopes) ( $p\text{-}F=1.56$ ;  $p=0.0034$ ), sites (Nihoa, Maro, Moloka'i and Oahu) ( $p\text{-}F=5.14$ ;  $p=0.0001$ ) and depth (shallow, intermediate, intermediate-deep, and deep strata) ( $p\text{-}F=3.18$ ,  $p=0.0001$ ) (Table 4.6). The contrast analysis reveals that for the factor *site*, the greatest change in community structure lies between NWHI and MHI samples, followed by differences between the two MHI (Oahu and Moloka'i) (Table 4.6). These differences are reflected in the MDS plot, in which data clouds primarily segregate MHI from NWHI samples, and secondarily Oahu from Moloka'i, and less so Maro Reef from Nihoa samples (Fig. 4.10). A MDS analysis using the presence and absence data provided essentially the same results attesting that differences in community structure were related mostly to compositional patterns rather than abundance patterns. The significant interactions among the factors also called for pair-wise comparisons between *habitats* within *sites* and *depths*. For the *habitat* vs *site* interaction, we found that macrofaunal communities differed significantly between canyons and slopes in Moloka'i, Oahu and Maro reef, but not in Nihoa (Table 4.6). When further evaluating the *habitat* vs *site* vs *depth* interactions, we found canyon and slope differences in community structure restricted to two depths on Moloka'i (shallow and intermediate); three depths on Oahu (shallow, intermediate, intermediate-deep) and two depths at Maro Reef (intermediate and intermediate-deep). Depth alone significantly affected within site community structure both in canyons and slopes, but posteriori pair-wise tests (using the term *habitat* vs *site* vs *depth*, within levels of depth) revealed that this effect is restricted to the main islands.



**Figure 4.10** Multidimensional scaling plot of Bray-Curtis similarity matrix based on square root-transformed abundance data of the 317 putative macrofauna species sampled in the Main (MHI) and Northwest Hawaiian Islands (NWHI). Cyn, canyon, w, West, e, East, n, North, s, South, ni, Nihoa, ma, Maro Reef. Blue symbols Molokai', green, Oahu, red, Nihoa, orange, Maro Reef. Open and filled symbols are, respectively, slope (slp) and canyon (cyn) samples.

**Table 4.6** Output of the multivariate PERMANOVA analysis based on the resemblance matrix of macrofauna abundance data. *A priori* factors defined where: ha, habitat (canyon x slopes), si, sites (Maro reef, Nihoa, Oahu, Molokai') and depth (s, i, i-d, d, refer to footnotes).

Test step	Source	df	SS	MS	Pseudo-F	p(perm)	Unique permutations
Main test	habitat (ha)	1	5974.9	5974.9	1.5694	<b>0.0019</b>	9839
	site (si)	3	58781	19594	5.1465	<b>0.0001</b>	9720
	NW (MHI x NWHI)	1	28574	28574	6.9821	<b>0.0001</b>	9824
	Mo (Molokai' x Oahu)	1	20516	20516	5.7515	<b>0.0001</b>	9885
	Ni (Nihoa x Maro)	1	7975	7975	1.7968	<b>0.0009</b>	9853
	depth (d)	3	36299	12100	3.1781	<b>0.0001</b>	9730
Interactions	ha x si	3	23552	7850.6	2.062	<b>0.0001</b>	9726
	ha x NW	1	7519.6	7519.6	1.8374	<b>0.0003</b>	9811
	ha x Mo	1	10751	10751	3.0141	<b>0.0001</b>	9847
	ha x Ni	1	5964.7	5964.7	1.3439	<b>0.0464</b>	9836
	ha x de	3	23130	7710.1	2.0251	<b>0.0001</b>	9719
	si x de**	4	32150	8037.5	2.1111	<b>0.0001</b>	9700
	NW x de**	2	19483	9741.6	2.3804	<b>0.0001</b>	9757
	Mo x de**	2	15883	7941.3	2.2263	<b>0.0001</b>	9824

Ni x de**	0	0	No test			
ha x si x de**	4	27529	6882.2	1.8077	<b>0.0001</b>	9648
ha x NW x de**	2	15471	7735.4	1.8901	<b>0.0001</b>	9782
ha x Mo x de**	2	13147	6573.6	1.8429	<b>0.0001</b>	9834
ha x Ni x de**	0	0	No test			
Residual	156	5.94E+05	3807.2			
Total	177	8.25E+05				
Pair wise tests	Source	df		t-statistic	p(perm)	Unique permutations
ha x si						
Molokai	60		1.554	<b>0.0001</b>	9881	
Oahu	53		1.8504	<b>0.0001</b>	9898	
Nihoa	19		0.88162	0.8459	9886	
Maro	24		1.2739	<b>0.0136</b>	9895	
ha x si x de						
Molokai (s)	22		1.6349	<b>0.0002</b>	9835	
Molokai (i)	22		1.4969	<b>0.0016</b>	9874	
Molokai (i-d)	16		1.2037	0.0765	7695	
Oahu (s)	12		2.1761	<b>0.0005</b>	1987	
Oahu (i)	16		1.6503	<b>0.0017</b>	5860	
Oahu (i-d)	17		1.6498	<b>0.002</b>	9245	
Oahu (d)	8		1.1584	0.1069	31	
Nihoa (s)	12		1.0521	0.3177	832	
Nihoa (i)	7		0.90809	0.6849	16	
Maro (i)	9		1.476	<b>0.003</b>	162	
Maro (i-d)	15		1.2483	<b>0.0122</b>	243	

PERMANOVA 3-factor model. Bold values indicate significant differences at  $p < 0.05$ . s, shallow (~350 m); i, intermediate (~650 m); i-d, intermediate-deep (~1000 m) and d, deep (946-1100 m); df, degrees of freedom; SS, sum of squares; MS, mean squares; perm, permutations. \*\* term has one or more empty cells.

The results of the SIMPER analysis revealed the most important species contributing to the similarity within groups (characterizing species) and dissimilarity between groups (discriminating species) that were shown to be significantly different by the PERMANOVA analysis. For Moloka'i, in which canyon (or *habitat*) effects were statistically significant only at shallow and intermediate depth strata, the average similarity within groups (either canyon or slopes) as well as overall abundances were so low that it was difficult to assign good discriminating species for those two groups (Supplementary Table 4.9). For the shallow depth strata on Oahu, good discriminating species between canyons and slopes were Bivalvia sp. 6, Capitellidae sp. 4, Ophelliidae sp. 1, Fauvelliopsidae sp. 1, and Cossuridae sp. 1, which either occurred exclusively or more abundantly on canyons (Supplementary Table 4.9). In the intermediate depth stratum, only two good discriminating species were found, Sigalionidae sp. 3 and Spionidae sp. 8. The former occurred only in canyons while the latter more abundant in the canyons. For the intermediate-deep stratum (1000 m), a single species (Sipuncula sp. 3) proved to be a good discriminating species, with abundances almost 3-fold higher in the slope. For Maro Reef in the single canyon vs slope comparison assigned to be significantly different in the PERMANOVA output, Porifera sp. 1 and Tanaidacea sp. 6 were good discriminating species occurring both solely in the slope.

#### *4.4.3.2 Environmental predictors of community structure*

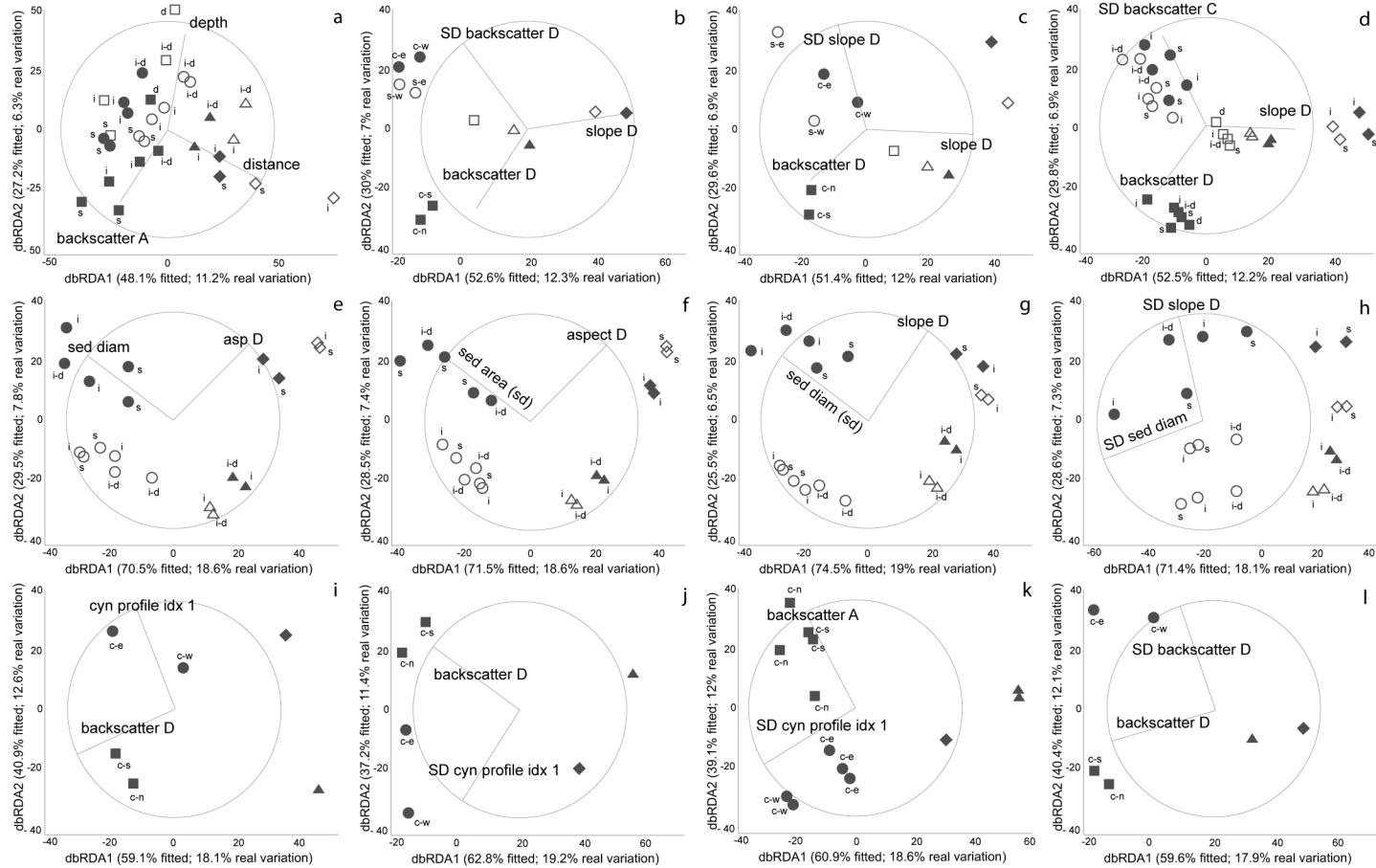
The best multivariate multiple linear regression models (DISTLM) explained up to 23%, 26% and 30% of the variation of the macrofaunal communities in the first, second and third DISTLM runs, respectively (Table 4.7). Variables directly (POC flux), or indirectly (distance from shore) associated with organic matter input, seafloor terrain (slope and backscatter reflectivity) often at the 0.13 km<sup>2</sup> (C) and 15-33 km<sup>2</sup> (D) spatial scales; sediment particle heterogeneity; and in the case of the canyon-only model, canyon curvature profiles explained a greater extent of the model variability (Table 4.7).

The results of the DISTLM analysis illustrated using the redundancy analysis dbRDA method, emphasize the vectors that correspond to the variables selected in the best (four) three-variable models (Fig. 4.13, Table 4.7). The length and direction of the vectors indicate strength and direction of the relationship. In the first run (Fig. 4.13a-d), besides the clear relationship of POC flux, distance from shore appears in one of the models that separates MHI from NWHI samples (Fig. 4.13a). This distinction occurred because both canyon and slope sampling sites of the NWHi islands are 8-25 km from the shorelines while for the MHI this distance was much shorter on average (range of 2-15 km). Mean and standard deviation of backscatter reflectivity (at scale A) separate MHI from NWHi samples, being higher in the MHI, as well as between canyon x slope habitats, being higher in the canyons (with the exception of the deepest depth stratum in the canyon off Oahu, which showed low backscatter values similar to the slope). High mean slope values segregated samples from Nihoa, and high variability in slope at scale D, and high variability in backscatter at scale D, isolated samples from Moloka'i. The best models in the second run largely separate the samples of Moloka'i from the ones in the NWHi based on sediment particle heterogeneity, and from canyons and slopes based on mean and standard deviation of slope at scale D (Fig. 4.13e-h). Higher mean and variability in particle area and diameter were observed in Moloka'i and higher mean and standard deviation of slopes observed in all canyons. The third model run, which considered only canyon samples separates samples from MHI and NWHi canyons, the former group representing samples from a quite different seafloor terrain (higher mean slope and backscatter) at the whole landscape scale (D). The canyon off Oahu has the highest values of backscatter signal at the 4 x10<sup>-4</sup> km<sup>2</sup> scale (A). In terms of the transverse-profiles, the canyons off Moloka'i and Nihoa have a much steeper profile on average and the former shows high variability in slope along the oblique profile lines (Fig. 4.13i-l).

**Table 4.7** Overall best solutions of multivariate DISTLM using the BEST selection procedure.

AICc	R <sup>2</sup>	RSS	No.Vars	Selections
<u>1st run</u> (B+WM+OM): 29 samples - 15 pred. variables				
<b>241.95</b>	0.10118	104450	1	2
<b>242.19</b>	0.16852	96621	2	2,17
<b>242.31</b>	0.16501	97030	2	1,2
<b>242.44</b>	0.16108	97485	2	2,33
<b>242.49</b>	0.23468	88933	3	8,22,23
<b>242.52</b>	0.23382	89033	3	8,9,22
<b>242.53</b>	0.15856	97779	2	8,22
<b>242.6</b>	0.2318	89267	3	1,2,17
<b>242.6</b>	0.2317	89279	3	8,21,22
<b>242.63</b>	0.15573	98107	2	2,22
<u>2nd run</u> (B+WM+SED+OM): 19 samples - 15 pred. variables				
<b>158.38</b>	0.17211	61718	1	35
<b>158.45</b>	0.16933	61925	1	37
<b>158.64</b>	0.16064	62573	1	34
<b>158.77</b>	0.1548	63008	1	2
<b>159</b>	0.26398	54869	2	15,37
<b>159.11</b>	0.25964	55192	2	15,35
<b>159.2</b>	0.13547	64449	1	23
<b>159.22</b>	0.25548	55503	2	8,37
<b>159.26</b>	0.2536	55643	2	9,37
<b>159.37</b>	0.24952	55947	2	8,23
<u>3rd run</u> (B+WM+OM+CYN): 15 samples - 15 pred. variables				
<b>125.48</b>	0.17511	46182	1	22
<b>125.5</b>	0.17422	46232	1	28
<b>125.57</b>	0.17039	46446	1	30
<b>126.06</b>	0.30667	38816	2	22,29
<b>126.07</b>	0.30615	38845	2	22,30
<b>126.07</b>	0.30602	38852	2	17,30
<b>126.2</b>	0.30001	39189	2	22,23
<b>126.21</b>	0.2998	39201	2	9,22
<b>126.21</b>	0.13413	48476	1	17
<b>126.23</b>	0.29875	39259	2	23,28

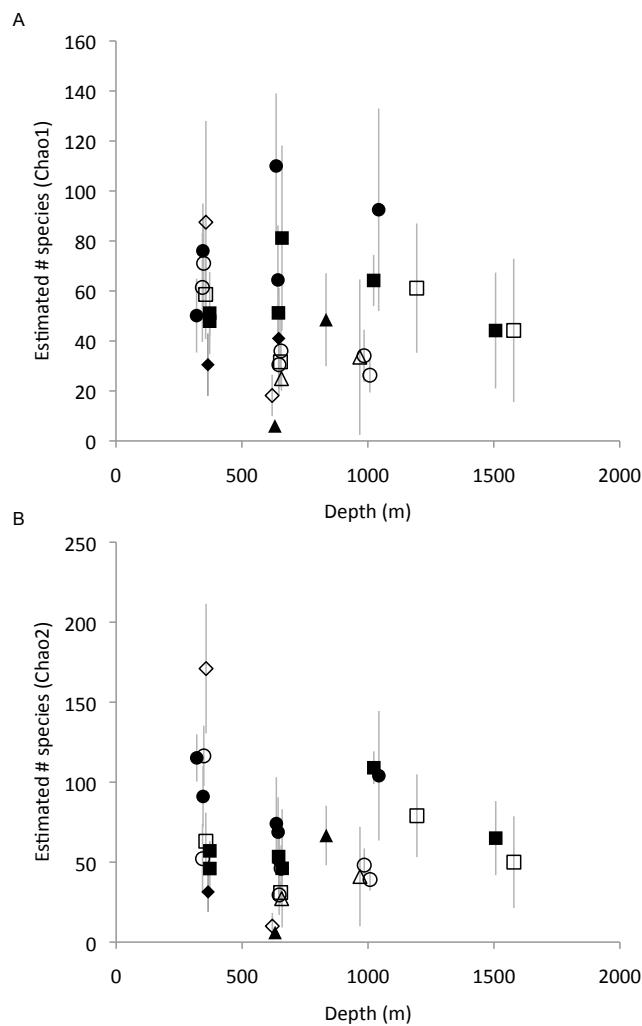
Bold face represents values of AICc within the range of acceptance for best models (Anderson et al., 2008). Refer to Table 2 for predictor variable information. Bold and underlined numbers represent variables with the single largest contribution to total model variability. B, bathymetry, WM, water mass, OM, organic matter input, CYN, canyon morphology variables.



**Figure 4.13** Results of the distance-based multivariate multiple regression (DISTLM) of macrofauna species abundance overlaid with the partial correlations of the significant environmental variables identified by models using the AICc selection criterion. Diamonds, Nihoa, triangles, Maro Reef, circles, Moloka'i, squares, Oahu. Empty symbols, slope samples. Depth strata: s, shallow (350 m), I, intermediate (650 m), i-d, intermediate-deep (1000 m), d, deep (1500 m). Four best models: A-D, first run, E-H, second run, I-L, third run (refer to methods section). Axes show % of fitted and real variation of data cloud.

#### 4.4.4 Species richness patterns and habitat heterogeneity (Hypotheses 3)

The use of raw species richness values or rarefaction was not effective for individual samples because in many instances few samples had  $> 10$  individuals. We therefore relied on the species estimators Chao 1 and Chao 2, for species richness comparisons between habitats. Chao1 and Chao 2 species richness estimates are higher in canyons mostly within intermediate (~650 m) and intermediate-deep (~1000 m) depth strata, but lower or similar within the shallow (350 m) and deepest (1500 m) depth stratum (Fig 4.9). However, none of these differences are statistically significant.



**Figure 4.9** Estimated macrofaunal species richness (Chao1) (canyon, solid symbols, slope, empty symbols; diamonds, Nihoa; triangles, Maro Reef, circles, Moloka'i, squares, Oahu). Light grey lines are standard deviations.

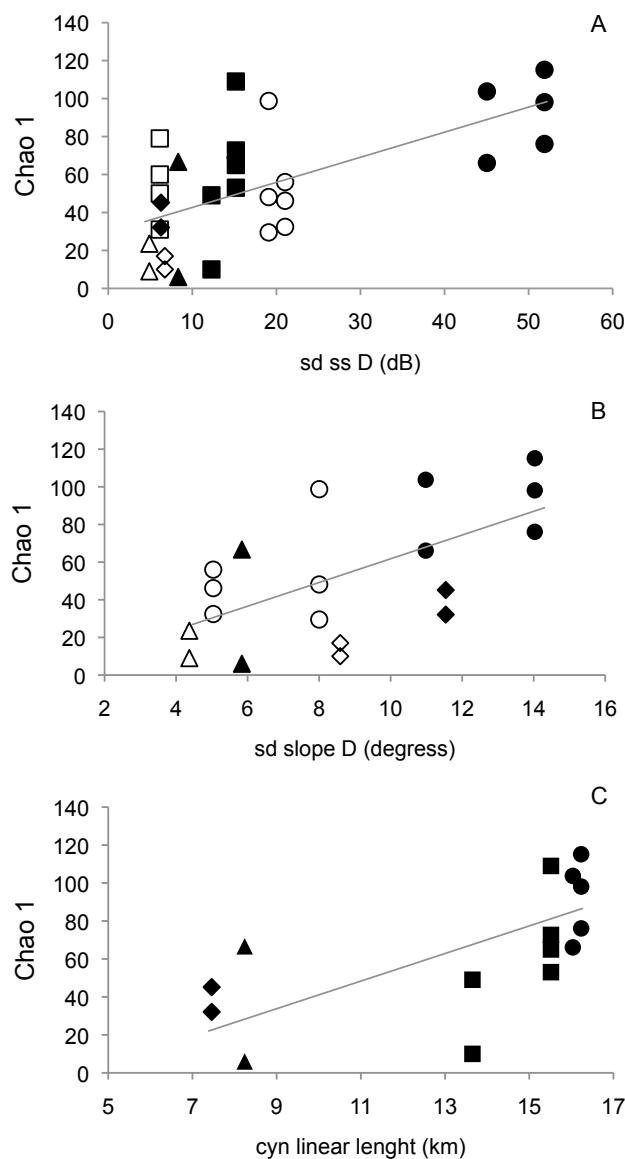
Univariate multiple linear regression (DISTLM) was used to select the best predictor variable models responding for the variability in the estimated species richness (Chao 1 and Chao 2) (Table 4.8). Once again three separate runs were employed as to accommodate for the lack of predictor variables and/or sub-sets of samples. Overall, a larger percentage of the variability was explained for the species estimator index Chao 1 than Chao 2, with 65, 88, and 69% of the variability being explained for first, second and third run respectively (Table 4.8). Most often implicated in these models were, for run 1 - standard deviation of the aspect at spatial scale B ( $0.0064 \text{ km}^2$ ), and standard deviation of the backscatter reflectivity at spatial scales C and D ( $0.13 \text{ km}^2$ ,  $15\text{-}33 \text{ km}^2$ ); for run 2 – depth, distance to shore, standard deviation of the slope at spatial scale D, mean aspect at spatial scale C, and standard deviation of detritus occurrence; for run 3 (canyon only) – linear length of canyon, and distance to thalweg.

**Table 4.8** Overall best solutions of univariate DISTLM analysis of species richness using the BEST selection procedure.

AICc	R <sup>2</sup>	RSS	No. Vars	Selections (var. code #)
<u>1st run</u> (B+WM+OM): 29 samples - 15 pred. variables				
Chao 1				
<b>183.56</b>	0.62252	10534	4	5,12,21, <b>23</b>
<b>183.82</b>	0.65904	9514.7	5	9,12,21, <u>23</u> ,43
<b>184.04</b>	0.65646	9586.6	5	5,12,19,21, <b>23</b>
Chao 2				
<b>40.706</b>	0.41047	84.573	3	2,22, <b>23</b>
<b>42.006</b>	0.44292	79.917	4	2,22, <u>23</u> ,44
<b>42.786</b>	0.36663	90.862	3	21, <u>23</u> , 44
<u>2nd run</u> (B+WM+SED+OM): 19 samples - 15 pred. variables				
Chao 1				
<b>111.61</b>	0.88234	2486.5	5	1,2, <u>9</u> ,13,47
114.48	0.89583	2201.4	6	1,2, <u>9</u> ,13,35,47
114.54	0.96936	647.44	9	1,2, <u>9</u> ,13,15,34,37,39,46
Chao 2				
<b>34.249</b>	0.39371	77.246	2	<b>8,36</b>
<b>35.458</b>	0.2493	95.646	1	<b>36</b>
<b>35.767</b>	0.34326	83.675	2	2, <b>36</b>
<u>3rd run</u> (B+WM+OM+CYN): 15 samples - 15 pred. variables				
Chao 1				
<b>98.249</b>	0.69813	4712.7	3	22, <u>28</u> ,33
<b>98.302</b>	0.69707	4729.2	3	17, <u>28</u> ,33
<b>98.577</b>	0.69146	4816.8	3	23, <u>28</u> ,33
Chao 2				
<b>13.974</b>	0.72315	17.11	3	23, <u>28</u> ,33
<b>14.324</b>	0.71662	17.513	3	<u>17</u> ,23,33
<b>14.924</b>	0.70505	18.229	3	17, <u>28</u> ,33

Bold face represents values of AICc within the range of acceptance for best models (Anderson et al., 2008). Refer to Table 2 for predictor variable information. Bold and underlined numbers represent variables with the single largest contribution to total model variability. B, bathymetry, WM, water mass, OM, organic matter input, CYN, canyon morphology variables.

Standard deviation of the backscatter reflectivity (i.e. substrate heterogeneity) at spatial scale D was the predictor variable that made the single largest contribution to the variability in the first model run (that includes the largest amount of samples distributed among both habitat types). For the second and third model runs the variables that accounted for the single largest contribution to the variability were standard deviation of slope at spatial scale D (Fig. 4.14 B) and the total canyon linear length (Fig. 4.14 C), respectively. Detail information on the regression lines is provided in figure 4.14.



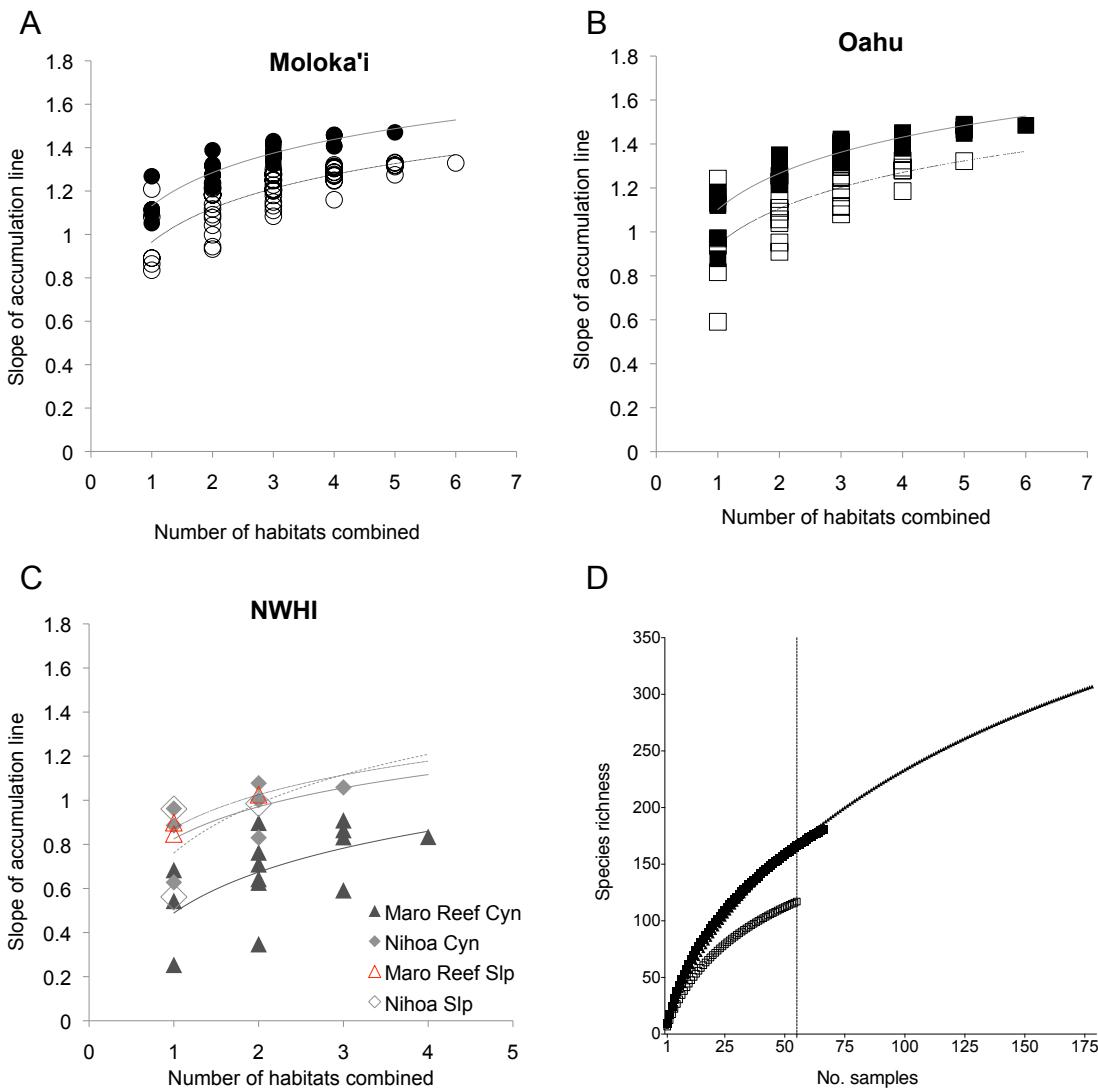
**Figure 4.10** Linear correlations between the best predictor variables and estimated species richness (Chao 1). A, First model run: standard deviation of the backscatter reflectivity (i.e. substrate heterogeneity,  $sd\ ss\ D$ ) at spatial scale D ( $15-33\ km^2$ ) - ( $p=0.0003$ ;  $y = 1.2802x + 30.419$ ,  $R^2 = 0.44$ ). B, Second model run: standard deviation of slope at spatial scale D ( $15-33\ km^2$ ) - ( $p=0.0001$ ;  $y = 1.0000x + 20.000$ ,  $R^2 = 0.44$ ). C, Third model run: total canyon linear length ( $km$ ) - ( $p=0.0001$ ;  $y = 0.6667x + 18.333$ ,  $R^2 = 0.44$ ).

0.39105); B, Second model run: standard deviation of slope at spatial scale D (15-33 km<sup>2</sup>) - (p=0.0025,  $y = 6.0633x - 0.7262$ , R<sup>2</sup> = 0.36046); C, Third model run: total canyon linear length - (p=0.0062,  $y = 5.8262x - 13.746$ , R<sup>2</sup> = 0.391112). Diamonds, Nihoa, triangles, Maro Reef, circles, Moloka'i, squares, Oahu. Back symbols, canyon samples; empty symbols, slope samples. sd, standard deviation; ss, backscatter reflectivity, dB, decibels.

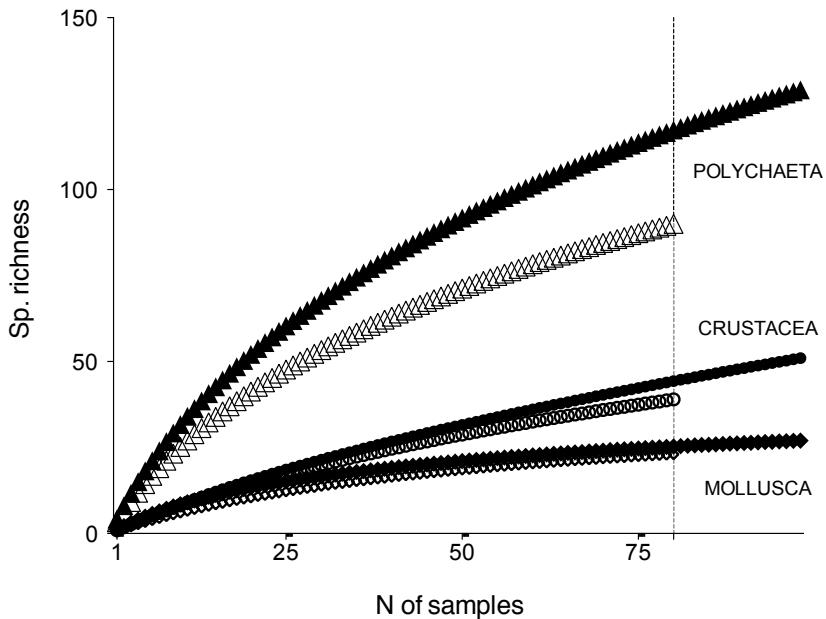
#### 4.4.5 Species turnover and habitat heterogeneity (*Hypothesis 4*)

Examining the rate at which new species accumulate after pooling multiple habitat patches within each habitat reveal elevated canyon macrofaunal beta-diversity relative to slope sites only in the MHI (Oahu and Moloka'i Islands) (Fig 4.11A-B). Beta-diversity in the canyon off Nihoa is comparable with non-canyon sites of MHI, higher than Maro Reef Canyon and no different than all NWHI slope sites altogether (Fig. 4.11C). In terms of gamma diversity, pooling all samples taken in all canyon systems *versus* samples taken in all control slope areas shows a clear influence of the abrupt topographic features in the observed increased species turnover (Figure 4.11D).

When species accumulation curves are plotted separately by different major faunal groups it becomes evident that the higher beta diversity in canyons is largely due to a higher number of species within Polychaeta (Fig. 4.12).



**Figure 4.11** Slopes of species accumulation curves plotted against of number of habitat patches sampled. A, Oahu; B, Molokai'i; C, Northwest Hawaiian Islands (NWHI); D, Species accumulation curves at a large (~1500 km) spatial scale (Gamma-diversity) after pooling all submarine canyon samples (dark symbols) and all open slope samples (empty symbols) and both habitats combined (thinner line). Vertical dotted line represents threshold of equal sampling effort.



**Figure 4.12** Randomized species accumulation curves (Ugland et al., 2004) plotted for different taxa. Canyons, dark symbols; slopes, empty symbols.

## 4.5 Discussion

### 4.5.1 Community structure and composition

The poorly described nature of the deep-sea invertebrate macrofauna off the Hawaiian islands becomes evident as 60% of our reported species are known only to family level. This is not surprising since this is the first study to sample macrobenthos over a relatively wide bathymetric range (314 -1500 m), and spanning ~1,500 km of the archipelago. The 4 newly described species (2 new species of amphipods, 1 new species of copepod, 1 new species of polychaete), and the remained large percentage of unresolved identifications point to the need for further studies of the taxonomic composition and biogeographic distribution of the deep-sea fauna of the Hawaiian archipelago.

The most abundant species spanning the whole study area were two polychaete species from the family Spionidae, *Auropisio dibrachiata* and *Spiophanes abyssalis*. Despite these two species having been reported as cosmopolitan distributional, occurring predominantly at bathyal to abyssal depths (Maciolek, 1981; Mincks et al., 2009), their occurrence at our shallower sites (350-650 m), with relatively higher abundance in the canyons off Oahu and Moloka'i, is worth

questioning. The role of canyons as conduits of faunal invasions from coastal-shallow waters to the deep-sea has been inferred from ecological (Snelgrove and Haedrich, 1985) as well as paleo-oceanographic studies (Parker, 1961). The potential for the opposite pathway, however, to the best of our knowledge, has not yet been hypothesized. The fact that Hawaiian slopes are characterized by sharp depth gradients over very short distances summed with high energy bottom currents (velocities exceeding 2 knots; calculated from video footage during sediment resuspension events) in canyons, may point to these features as potentially representing short-path conduits of larval stages and adults transported from deeper areas to mid and shallower depths in the canyon heads. This speculation, however, clearly needs further testing employing, above all, more intensive sampling and molecular genetic techniques.

The PERMANOVA analysis revealed that macrofaunal community structure differed across sites, depths, and habitats (canyon x slope) with the largest degree of community dissimilarity occurring between islands. Furthermore, the greatest macrofauna dissimilarity was between the Main (MHI) and the Northwest Hawaiian islands (NWHI), followed by relatively lower but still significant dissimilarities between the two MHI (Oahu and Moloka'i) islands. This indicates both high overall degrees of species turn-over (beta diversity) over a large regional spatial scale, spanning ~1,600 km, as well as between two islands that are separated by a short ~40 km channel distance. A recent multi-species connectivity study using genetic markers on scleractinean corals, mollusks, crustaceans, echinoderms, fish and marine mammals, found a high degree of genetic discontinuity (shared by more than 50% of species analyzed) over short linear distances along the Hawaiian archipelago (Toonen et al., 2011). These authors suggest at least four strong barriers to gene flow occur along the archipelago (Fig. 2 in Toonen et al., 2011). Interestingly, their proposed zones of faunal discontinuity are in close agreement with our observed highest rates of deep-sea macrofaunal turnover, with the largest separation occurring between the MHI and NWHI, but still very strong faunal structuring between Oahu and Moloka'i. Although these multi-species genetic discontinuities have been delimited for the Hawaiian archipelago, the basis for these shared genetic restrictions is poorly understood (Toonen et al., 2011). Furthermore, whether the deep-sea bathyal macrofauna populations studied here respond to the similar population structuring mechanisms as their shallow-water counterparts, or whether the environmental heterogeneity or even the differing patterns in abundance between sites sampled better corresponds to the striking changes in beta diversity, remains to be ascertained.

Strong faunal zonation between all depth strata was common only in the MHI. In addition, no OMZ effects were seen either in faunal composition and abundance, contrasting with demersal fish assemblages (De Leo et al., 2012/Chapter 3), which showed reduced abundances and a reduced canyon effect (i.e., lack of canyon vs slope differences) within the core of the OMZ (~650-

700 m). This suggests that sediment macrofaunal communities may better cope with reducing oxygen levels than the more metabolically active demersal fishes. Hypothesis # 1, i.e., that macrobenthic community structure differs between canyons and slopes, was supported on all islands but Nihoa, with effects largely restricted to shallow, intermediate and intermediate-deep depth strata. For example, for the deep depth stratum (1500 m), dissimilarities in community structure between the canyons off Kaneohe Bay in Oahu and the slopes at same depth are not significant. It could be that the differences exist off Oahu at 1500 m but enriched areas in the canyon becomes much more patchy at depth and is thus difficult to resolve with random sampling. We did observe “tumbleweeds” of detritus at the deepest depths in the canyons, but usually stuck in between rocks. In Moloka'i, the canyon effects terminate at the intermediate depth stratum (650 m). These results corroborate with past studies which suggest the organic enrichment in canyons dissipates with depth and distance from shore after most organic detrital resources are consumed by both macro- and megafauna (Vetter and Dayton, 1998, Escobar-Briones et al., 2008). The absence of canyon effects on the island of Nihoa could be partially explained by disturbance effects from high bottom current velocities ( $> 2$  knots) experienced in both shallow (350 m) and intermediate (650 m) depth strata, potentially leading to advective removal of macrofauna and detrital organic matter. Substantial amounts of drift algae were observed during our dives in Nihoa canyon; however, the macroalgae was typically moving along the bottom in the strong currents without settling on the seafloor. These strong currents are likely related to the abrupt topography of Nihoa Canyon, which shows, on average, the steepest slopes among all canyons studied, particularly along the canyon rim, where most core samples were collected. Vetter et al. (2010) reported a large proportion of the benthic megafauna inhabiting Nihoa canyon to be large suspension-feeder species such as sea pens, anemones and gorgonians and highly mobile species (teleosts, shrimps and hermit crabs), which are groups considered capable of dealing with the strong bottom currents (Vetter and Dayton, 1999; Vetter et al., 2010).

#### *4.5.2 Environmental drivers of community structure and species richness*

The environmental variables POC flux and distance from shore were often selected by the DISTLM models to explain a large proportion of the variability in macrofaunal community structure. Those two variables are related to organic loading in the study area, which is influenced by the vertical rain of POC to the seafloor, and by the horizontal advection of plant and macroalgae material from the coastal zone, which diminishes with distance offshore. It is important to highlight that the variable POC flux was highly correlated with depth ( $r=-0.92$ ), temperature ( $r=0.96$ ) and oxygen concentration ( $r=0.92$ ), making it difficult to tease out the effects of these environmental variables. The amount of organic detritus was clearly higher inside the canyons, decreasing with depth and concomitantly with distance from shore, almost disappearing within the intermediate-deep and

deep depth strata. The export of coastally derived carbon is more evident (based on our measures of % detritus occurrence) in the high-elevation (1000-1500 m maximum altitude) MHI, which has forested landscapes adjacent to the canyon heads, connected by significant drainage basins (Culliney, 2006). In contrast, the NWHI exhibited much less coastally derived detrital input, all derived from macroalgae. While macroalgae likely derived from shallow coral-reef systems were observed in Nihoa canyon at 350 m, on Maro Reef, very little terrestrial or macroalgal detritus was observed. This contrast between MHI and NWHI likely played a major role in structuring the infaunal macrobenthos, as it appeared to do for the benthic megafauna (Vetter et al., 2010), and may partially explain the large species turnover observed between MHI and NWHI discussed above. Total and highly-mobile invertebrate megafauna abundances were two to three times higher in the submarine canyons and slopes of the MHI contrasted with the NWHI (Vetter et al., 2010). These observations are consistent with our first hypothesis (i.e., that macrofaunal abundances are higher in canyons due to enhanced detrital export and accumulation via canyons).

Canyons may be particularly important in the very oligotrophic seascape of the Hawaiian Islands (Karl et al., 1996), particularly in the MHI, because they enhance organic-matter supply to the typically food-limited deep-sea. Vetter et al. (2010) suggest: "...canyons thus may harbor source populations in a 'source-sink system' in which dense, but localized, concentrations of breeding individuals broadcast larvae out to the surrounding slope, enhancing local and regional species diversity".

Sediment particle heterogeneity is also selected in DISTLM models and explains part of the variability in macrofaunal community structure. While homogeneous carbonatic sands were observed in the NWHI, a mix of siliceous (land-based) and carbonate (marine-based) sediments mixed with various fragments of organic (mostly plant) material was observed in Moloka'i (MHI). Since we did not employ traditional grain size analysis, our results are not based on the full particle-size spectra. However, it is clear from our particle image analysis that larger and more heterogeneous sediments in Moloka'i containing organic debris (wood, seeds, *kukui* nut rash, for example) add to the ( $\geq 300 \mu\text{m}$ ) particle variability. Past studies have found positive correlations between sediment particle heterogeneity (sorting) and benthic macrofaunal diversity, besides influencing its composition and structure (Gray, 1974; Etter and Grassle, 1992). However, this relationship has not proven to be universal (Snelgrove and Butman, 1994; Levin et al., 2001). The pattern of higher sediment particle heterogeneity in Moloka'i relative to both islands of NWHI therefore may also account for the higher local macrofaunal species richness, increasing the number of sediment microhabitats.

Bottom habitat heterogeneity within canyons was clearly higher for most canyon vs slope comparisons, with large variability in slope and backscatter. Positive correlations between acoustic backscatter reflectivity and sediment particle size and variability have been reported (Goff et al., 2000; Collier et al., 2005), suggesting this remote mapping tool may be used to provide surrogates of habitat variability in marine benthic ecosystems. Backscatter reflectivity has been used to link benthic habitat variability (Le Godinec et al., 2003) and overall biodiversity in submarine canyons (Yoklavich et al., 2000; Schlacher et al., 2007), hydrothermal vents (Durand et al., 2006) and continental shelves (Kloser et al., 2001). For example, Schlacher et al. (2007) found a significant positive correlation between the variability of backscatter intensity and the total number of sponge species collected in 5 canyons off Southeastern Australia, suggesting that high habitat complexity in canyons, revealed by a mix of hard and soft substrates, provided more niches and consequently aided in the establishment of a speciose sponge fauna. Studies employing backscatter reflectivity as surrogates for benthic community structure and diversity are, however, still scant in the deep-sea literature. In the present study, while the values of backscatter reflectivity at the local scale (A: 0.0004 km<sup>2</sup>, i.e., one grid-cell in area) were implicated in a single DISTLM model, most of the best regression models implicated backscatter reflectivity at rather large spatial scales (C: 0.13 km<sup>2</sup>, and D: 15-33 km<sup>2</sup>), indicating the role of the broader landscape variability in influencing local community structure. The role of medium to large-scale landscape variability in influencing biological communities (species abundances and richness, home ranges, predator-prey and competitive interactions) has been largely investigated for terrestrial ecosystems (Kerr and Packer, 1997; Kie et al., 2002; Steffan-Dewenter et al., 2002; Fortin and Agrawal, 2005; Turner, 2005; Kumar et al., 2006), but is rarely addressed in deep-sea biodiversity studies. Many of these terrestrial ecology studies have demonstrated an overarching importance of landscape habitat heterogeneity over other environmental variables (such as energy, nutrient inputs, etc.) in predicting species richness and composition at various spatial scales (reviewed in Tews et al., 2004). For example, Kumar et al. (2006) found that landscape heterogeneity metrics (edge density, patch size and shape) at medium spatial scales (240 m in radius) provided the best explanation in the variability of distribution of native and non-native plant species richness inside 20 × 50 m plots sampled in the Rocky Mountain National Park, Colorado, USA. Local abundance and diversity of bees increased with increasing proportion of the surrounding semi-natural habitats demonstrating the role of structurally complex landscapes at larger spatial scales affecting local community structure (Steffan-Dewenter et al., 2002). Statewide mule deer spatial distributions (home ranges) in California were highly explained (up to 57% of variation) by landscape heterogeneity (edge density, mean patch-shape index, fractal dimension), with increasing correlation coefficients at progressively larger spatial scales. In a similar fashion, in the context of our study, we could argue that, if we consider a

whole canyon as a landscape unit crossing a continental (or in our case an island) margin sector, with increasing habitat complexity ranging from scales A (coring sites) through D (whole canyon), the sum of physical processes that generate habitat heterogeneity and are pertinent solely to the canyon landscape, could have an effect on how benthic communities are organized locally. This assumption follows the premises of mass effect models in the meta-community theory (reviewed in Leibold, 2004), where the regional pool ('source') of species (influenced by the regional-scale habitat heterogeneity), colonizes local ('sink') patches largely by increased immigration rate potential (high connectivity between varying habitat patches, which is supported in highly hydrodynamic canyon systems), balanced by low local competitive success. The result is the establishment of local communities with low population densities, large number of singletons, and doubletons, and high species turnover between patches at increasing spatial scales. Our medium-size spatial scale, C (200-m in radius from coring sites), for example, usually contained multiple habitats (from our submersible observations) such as highly disturbed canyon thalwegs often showing rippled sandy sediments, rock outcrops, rock ledges, rocky walls, all adding to the overall landscape habitat heterogeneity. Theoretically, such summation of different habitat patches would therefore contain the source metapopulation that eventually colonizes the smaller habitat (sink) patches.

The present study, to the best of our knowledge, is the first to attempt linking landscape heterogeneity metrics pertinent solely to submarine canyons with macrofauna community structure and species richness. We found, for example, that the size of the submarine canyons (linear length along the thalweg, variable code #28 on Table 4.7 and 4.8) has a positive and significant effect on macrofaunal species richness, largely agreeing with the species-area curve models (Rozwenweig, 1995). This observation, if proven to be consistent in future studies, may aid to the process of marine spatial planning and conservation of CM (or IM) settings, as a way to separate canyons in a rather simple quantitative geomorphology metric (which can also translate into a proxy of the amount of terrestrial/coastal organic input to the system). The employment of the canyon curvature (transverse) profiles is another example of such an attempt. The variability in those profiles was assigned to partially explain variability in macrofaunal community's structure among the different Hawaiian canyons, and is possibly reflecting the varying degrees of intensity and frequency of physical disturbance (mostly tidally-driven bottom currents). Canyons were once generically classified as having transverse profiles that are: 1) predominantly V-shaped; 2) V-shaped inner section, trough-('U') shaped outer canyon; 3) predominantly through shaped (Shepard and Dill, 1966). Predominantly V-shaped profile canyons are often assigned as having negative effects on infaunal macrobenthos as disturbance intensity and frequency are high; La Jolla Submarine Canyon is a typical example (Vetter and Dayton, 1998). However, explicit quantitative analysis relating

canyon current velocities and disturbances in macrofaunal communities are lacking. In contrast, U-shaped canyons are less prompt to promote strong tidally driven bottom currents (Shepard and Dill, 1966). For example, De Leo et al. (2010) report increased macro- and megabenthos biomass and abundance in Kaikoura Canyon, New Zealand, but only at deeper sections of the canyon (>1000 m <1600 m), where it attains a typical trough-shape transverse profile. Video and photographic transects at those depths in the canyon did not show any evidence of tidal flows, and the only sedimentary features observed are from several infaunal megabenthos- borrowing and tracking traces (De Leo et al., 2010). The extraction of those canyon transverse-profiles from high-resolution bathymetric maps is relatively straightforward (Goff, 2000, present paper) and may prove to be an effective method of classifying various canyons systems for marine spatial management purposes. In the present study, among the six canyons sampled, three had similar transverse profiles in terms of slope variability (Profile Index 1), the ones off Moloka'i (*Pelekunu* and *Kawaihau* Canyons) and the one off Nihoa (very steep at the head and rapidly smoothing towards the mouth). We implicated the very abrupt slopes at the mouth of Nihoa canyon as a possible 'culprit' for the lack of local canyon effects on macrofauna abundance and community structure due to the high disturbance frequency and intensity. This was also verified at the shallow heads of both Moloka'i canyons, where some replicate cores contained not a single macrofauna individual. Demersal fish abundances and species richness were also reduced at those shallow depths in those same canyons (De Leo et al., 2012; Chapter 3). This agreement indicates these transverse profile indexes may be promising landscape heterogeneity metrics to be employed in future studies relating environmental drivers of submarine canyons benthic biodiversity.

#### 4.5.3 Species richness and turn-over (beta) diversity

The lack of statistical support for greater canyon macrofauna alpha-diversity, agreeing with our third hypothesis, corroborates with several studies of macrobenthos in submarine canyons (Vetter and Dayton, 1998; McClain and Barry, 2010) which points to high disturbance frequency and local organic enrichment at small spatial scales in reducing local species richness (McClain and Barry, 2010, Cunha et al., in press; Paterson et al., in press). Local canyon macrofauna species richness and diversity has been reported to be particularly low at sites where bottom current regimes are the strongest at the head of highly 'active' (*sensu* Shepard and Dill, 1966) canyons. For example at the heads of La Jolla Canyon in California, Vetter and Dayton (1998) reported the lowest rarefied species richness at 100 m depth in the canyon, which was 3-fold lower than at same depths in the nearby slope, and 2-fold lower than at 200 m depth in the same canyon. In contrast, in an 'inactive' (*sensu* Shepard and Dill, 1966) canyon such as Hudson Canyon located at the East coast of the US, Rowe et al. (1982) report increased macrofaunal species richness and abundance at the head of the canyon (203 m) where they postulate maximum organic enrichment occurs concomitantly with

limited physical disturbance. Similarly high species richness at local scales is reported for Newport Canyon, California, where authors also evoke a ‘low-energy’ environment as facilitator for the establishment of climax (species-rich) benthic community (Maurer et al., 1994). Other types of physical disturbances on canyons have been described near cliff faces of the Monterey canyon system, California, where enhanced detrital deposition and subsequent increase in megafauna activity suppress infaunal macrobenthic communities, which often show reduced (fourfold) body size, number of species and evenness (McClain and Barry, 2010). The role of enhanced physical disturbance in canyons is therefore supported by our present study, in which despite of the lack of significant canyon *vs* slope differences in species richness throughout all depth strata, it negatively affects macrofauna (reduced species richness) particularly at the head of the canyons, supposedly the most energetic environment (Fig. 4.9A-B).

Changing the focus to beta diversity, our study demonstrates that the Hawaiian submarine canyons exert a much clearer role in the turnover of species community composition, agreeing with our fourth hypothesis. The observed higher habitat heterogeneity (topography, substrate rugosity, sediment particle heterogeneity) in the canyons, as discussed previously, is key in promoting niche diversification and allowing for different macrofaunal life strategies to colonize various patches in a structurally rich landscape. Two other key recent studies in the literature also verified high beta diversity on canyons both at small and large spatial scales (Schlacher et al., 2007; McClain and Barry 2010). The former study found levels of beta diversity of sponge assemblages of 5 Southeastern Australian canyons often exceeding or rivalling with those of often acclaimed biodiversity-oases seamounts, sampled in the nearby Coral and Tasman Seas and the northern Norfolk Ridge in New Caledonia (Schlacher et al., 2007). Canyon sponge species showed strongly compressed range sizes with 76% being restricted to a single site and 79% occurring in single canyons only. The latter study found that macrobenthic communities show high levels of ecological reorganization, which includes major shift in species compositions (~40%), over short (< 100 m) distances away from cliff faces of Monterey Canyon. Patchiness in food resources leading to varying megafauna density and bioturbation rates are postulated to regulate habitat heterogeneity at those small spatial scales, which ultimately promote high species turnover (beta diversity) and consequently increasing regional (gamma) diversity. Even though the results of these two studies lead to conclusive remarks about canyons positively affecting beta-diversity, they both lack samples collected in control areas outside the respective canyon systems investigated. In our study the sampling design was conceived to test, in particular, the ‘habitat heterogeneity’ hypothesis, including many areas in the slope that received a comparable sampling effort (which is extremely rare in the literature of benthic studies on submarine canyons). We therefore provide new, more

robust, evidence that canyons enhance beta-diversity, potentially increasing the regional species pool of infaunal macrobenthos by providing novel habitat heterogeneity.

## 4.6 References

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## 4.7 Appendix

**Supplementary Table 4.9** Output of Similarity Percentage (SIMPER) analysis.

Molokai' - Shallow						Maro Reef - Intermediate					
<b>Group canyon</b> Average similarity: 8.02%						<b>Group canyon</b> All the similarities are zero					
Species Av N Av Sim Sim/S D C % Cum %						<b>Group slope</b> Average similarity: 20.92%					
<i>Auropio dibranchiata</i> 0.8 3.1 0.5 38.5 38.5						Species Av N Av Sim Sim/S D C % Cum %					
Bivalvia sp. 2 0.5 0.8 0.3 10.0 48.5						<i>Sponge</i> sp. 1* 0.9 7.1 0.6 33.8 33.8					
Cirratulidae sp. 1 0.5 0.8 0.3 9.9 58.4						<i>Tanaidacea</i> sp. 1* 0.6 5.4 0.6 25.9 59.7					
Capitellidae sp. 1 0.3 0.7 0.2 8.5 66.9						<i>Hesionidae</i> sp. 2** 0.4 2.5 0.4 11.8 71.5					
Oligochaete sp. 1 0.3 0.4 0.2 4.9 71.8						<i>Tanaidacea</i> sp. 2* 0.3 1.1 0.2 5.4 76.9					
<i>Spiophanes cf. abyssalis</i> 0.3 0.4 0.2 4.9 76.7						<i>Magelonidae</i> sp. 1* 0.3 1.1 0.2 5.2 82.1					
Cossuridae sp. 1 0.5 0.3 0.2 4.1 80.8						<b>canyon x slope</b> Average dissimilarity = 98.71%					
<b>Group slope</b> Average similarity: 29.20%						cyn slp					
Species Av N Av Sim Sim/S D C % Cum %						Species Av N Av N Av Diss Diss/ SD C % Cum %					
<i>Capitellidae</i> sp. 2 1.5 8.2 0.8 27.9 27.9						<b>Sponge</b> sp. 1* 0.0 0.9 14.9 <b>1.0</b> 15.1 15.1					
<i>Auropio dibranchiata</i> 1.2 6.3 1.0 21.6 49.5						<i>Tanaidacea</i> sp. 1* 0.0 0.6 9.5 <b>1.0</b> 9.7 24.7					
Opheliidae sp. 1 0.9 4.9 1.0 16.6 66.2						<i>Hesionidae</i> sp. 2** 0.0 0.4 7.1 0.7 7.2 31.9					
Capitellidae sp. 1 0.9 3.5 0.6 12.1 78.3						<i>Tanaidacea</i> sp. 2* 0.0 0.3 7.0 0.6 7.0 39.0					
Lumbrineridae sp. 2 0.3 0.8 0.3 2.8 81.1						<i>Cossuridae</i> sp. 1* 0.3 0.3 5.7 0.7 5.8 44.8					
<b>canyon x slope</b> Average dissimilarity = 87.96%						<i>Magelonidae</i> sp. 1* 0.0 0.3 5.6 0.6 5.7 50.5					
Species Av N Av N Av Diss Diss/ SD C % Cum %						<i>Cumacea</i> sp. 1* 0.0 0.3 5.3 0.6 5.4 55.9					
<i>Capitellidae</i> sp. 2 0.1 1.5 8.7 <b>1.1</b> 9.9 9.9											
<i>Auropio dibranchiata</i> 0.8 1.2 5.7 <b>1.1</b> 6.4 16.3											
Capitellidae sp. 1 0.3 0.9 5.0 1.0 5.6 22.0											
Opheliidae sp. 1 0.3 0.9 4.9 <b>1.1</b> 5.6 27.5											
Molokai' - intermediate											
<b>Group canyon</b> Average similarity: 13.03%											
Species Av N Av Sim Sim/S D C % Cum %											
<i>Spiophanes cf. abyssalis</i> 1.1 2.9 0.6 21.9 21.9											
<i>Auropio dibranchiata</i> 0.7 2.0 0.5 15.1 37.0											
Nemertean sp. 1 0.5 1.8 0.5 13.5 50.5											
Bivalvia sp. 1 0.6 1.7 0.4 13.3 63.8											
Cirratulidae sp. 1 0.5 1.5 0.5 11.7 75.6											
Scaphopoda sp. 1 0.4 0.8 0.3 6.4 82.0											
<b>Group slope</b> Average similarity: 16.49%											
Species Av N Av Sim Sim/S D C % Cum %											
<i>Spiophanes cf. abyssalis</i> 0.6 3.3 0.4 20.1 20.1											
Syllidae sp. 2 0.5 2.6 0.5 15.6 35.7											
Unidenfied polych. sp. 2 0.6 2.1 0.3 12.6 48.3											
Bivalvia sp. 3 0.4 2.0 0.3 12.3 60.6											
Copepoda sp. 3 0.4 1.7 0.3 10.5 71.1											
<i>Auropio dibranchiata</i> 0.4 1.6 0.3 9.7 80.8											
<b>canyon x slope</b> Average dissimilarity = 90.60%											
Species Av N Av N Av Diss Diss/ SD C % Cum %											
<i>Spiophanes cf. abyssalis</i> 1.1 0.6 7.4 1.0 8.2 8.2											
Unidenfied polych. sp. 2 0.5 0.6 5.5 0.7 6.0 14.3											
Syllidae sp. 2 0.2 0.5 4.2 0.7 4.7 18.9											
<i>Auropio dibranchiata</i> 0.5 0.4 4.2 0.8 4.6 23.6											

cyn, canyon; slp, slope; Av N, average abundance, Av Sim, average similarity, Sim/SD, similarity divided by the standard deviation; Av Diss, average dissimilarity; % C, percent contribution; Cum %, cumulative percentage.

\* Maro Reef exclusive species, \*\* NWHI (Maro Reef and Nihoa) exclusive species. Bold face species and Diss/SD values represent relatively good discriminator species.

**Supplementary Table 4.9** continuation.

Oahu - Shallow						Oahu - Intermediate-Deep					
Group canyon		Average similarity: 35.66%				Group canyon		Average similarity: 11.01%			
Species	Av N	Av Sim	Sim/ SD	% C	Cum %	Species	Av N	Av Sim	Sim/S D	% C	Cum %
<b>Fauveliopsidae sp. 1</b>	2.09	5.82	<b>1.48</b>	16.33	16.33	<i>Aurospio dibranchiata</i>	0.73	2.8	0.5	25.46	25.46
<b>Bivalvia sp. 6</b>	1.75	5.82	<b>1.54</b>	16.32	32.65	<i>Aplacophora</i> sp. 1	0.5	2.15	0.5	19.48	44.94
<b>Cossuridae sp. 1</b>	1.34	4.47	<b>1.11</b>	12.54	45.19	Mite sp. 1*	0.38	1.23	0.34	11.13	56.07
<b>Opheliidae sp. 1</b>	1.25	3.62	<b>1.08</b>	10.15	55.34	<i>Copepoda</i> sp. 20*	0.38	0.94	0.34	8.52	64.59
<b>Capitellidae sp 4*</b>	1	3.03	<b>1.09</b>	8.51	63.85	<i>Cossuridae</i> sp. 1	0.38	0.92	0.34	8.36	72.95
Copepoda sp. 2	1.13	2.8	0.74	7.85	71.7	<i>Syllidae</i> sp. 8*	0.25	0.44	0.19	3.95	76.9
<i>Aplacophora</i> sp. 2	1.06	2.23	0.8	6.25	77.95	<i>Sipuncula</i> sp. 3	0.25	0.43	0.19	3.89	80.79
Gastropod sp. 6	0.73	1.5	0.56	4.2	82.15	<b>Group slope</b>	Average similarity: 19.22%				
<b>Group slope</b>	Average similarity: 27.14%					Species	Av N	Av Sim	Sim/S D	% C	Cum %
Species	Av N	Av Sim	Sim/ SD	% C	Cum %	<i>Sipuncula</i> sp. 3	0.87	14.2	0.84	74.14	74.14
<b>Cirratulidae sp. 1</b>	0.8	4.06	<b>1.16</b>	14.96	14.96	<i>Bivalvia</i> sp. 8*	0.4	1.98	0.34	10.28	84.42
<b>Spionidae sp. 3</b>	1.2	4.06	<b>1.16</b>	14.96	29.93	<b>canyon x slope</b>	Average dissimilarity = 93.03%				
<b>Lumbrineridae sp. 2</b>	0.8	4.06	<b>1.16</b>	14.96	44.89	Species	Av N	Av	Av Diss	Diss/S D	Cum %
Bivalvia sp. 2	0.8	2.53	0.61	9.3	54.2	<i>Sipuncula</i> sp. 3*	0.25	0.87	6.08	<b>1.22</b>	6.54
Gastropod sp. 4	0.6	2.05	0.62	7.54	61.74	<i>Aurospio dibranchiata</i>	0.73	0	5.9	0.94	6.34
Onuphidae sp. 2	0.68	2.03	0.62	7.47	69.22	<i>Aplacophora</i> sp. 1	0.5	0.18	3.84	0.94	4.12
Cossuridae sp. 1	0.6	1.99	0.62	7.32	76.54	<b>Mite</b> sp. 1*	0.38	0.27	3.54	0.85	3.8
Copepoda sp. 13	0.75	1.99	0.62	7.32	83.86						20.81
<b>canyon x slope</b>	Average dissimilarity = 86.97%										
Species	cyn Av N	slp Av N	Av Diss	Diss/ SD	% C						
<b>Bivalvia</b> sp. 6	1.75	0	5.21	<b>1.91</b>	5.99						
<b>Fauveliopsidae</b> sp. 1	2.09	0.6	5.03	<b>1.58</b>	5.78						
<b>Opheliidae</b> sp. 1	1.25	0	3.61	<b>1.6</b>	4.15						
Copepoda sp. 2	1.13	0	3.48	1.19	4.01						
<b>Cossuridae</b> sp. 1	1.34	0.6	3.15	<b>1.43</b>	3.62						
<b>Capitellidae</b> sp 4*	1	0	2.92	<b>1.71</b>	3.35						
Oahu - Intermediate											
Group canyon		Average similarity: 24.16%									
Species	Av N	Av Sim	Sim/ SD	% C	Cum %						
Sigalionidae sp. 3	1.1	5.29	1.4	21.9	21.9						
<i>Spiophanes wigley*</i>	1.42	5.14	0.87	21.28	43.18						
<i>Aurospio dibranchiata</i>	0.69	2.04	0.59	8.45	51.63						
Cossuridae sp. 1	0.58	1.66	0.45	6.86	58.49						
Fauveliopsidae sp. 1	0.83	1.48	0.45	6.11	64.61						
Acrocirridae sp. 1*	0.58	1.28	0.47	5.29	69.9						
Spionidae sp. 9*	0.53	1.24	0.37	5.14	75.04						
Capitellidae sp 4*	0.73	1.22	0.46	5.06	80.1						
<b>Group slope</b>	Average similarity: 17.77%										
Species	Av N	Av Sim	Sim/ SD	% C	Cum %						
Bivalvia sp. 8*	0.68	3.81	0.59	21.46	21.46						
Syllidae sp. 2	0.83	3.67	0.6	20.67	42.13						
<i>Prionospio</i> sp. *	0.48	1.88	0.32	10.56	52.69						
Ophiuroidea sp. 1*	0.4	1.73	0.32	9.73	62.42						
Ampharetidae sp. 2	0.4	1.1	0.32	6.17	68.59						
Polynoidae sp. 5*	0.48	1.04	0.32	5.85	74.44						
Scaphopoda sp. 1	0.4	1.04	0.32	5.85	80.28						
<b>canyon x slope</b>	Average dissimilarity = 87.95%										
Species	cyn Av N	slp Av N	Av Diss	Diss/ SD	% C						
<b>Prionospio</b> sp. *	1.42	0.48	5.74	<b>1.27</b>	6.52						
<b>Sigalionidae</b> sp. 3	1.1	0	5.12	<b>1.57</b>	5.82						
Syllidae sp. 2	0.34	0.83	3.72	1.04	4.23						

# Chapter 5

## Conclusions

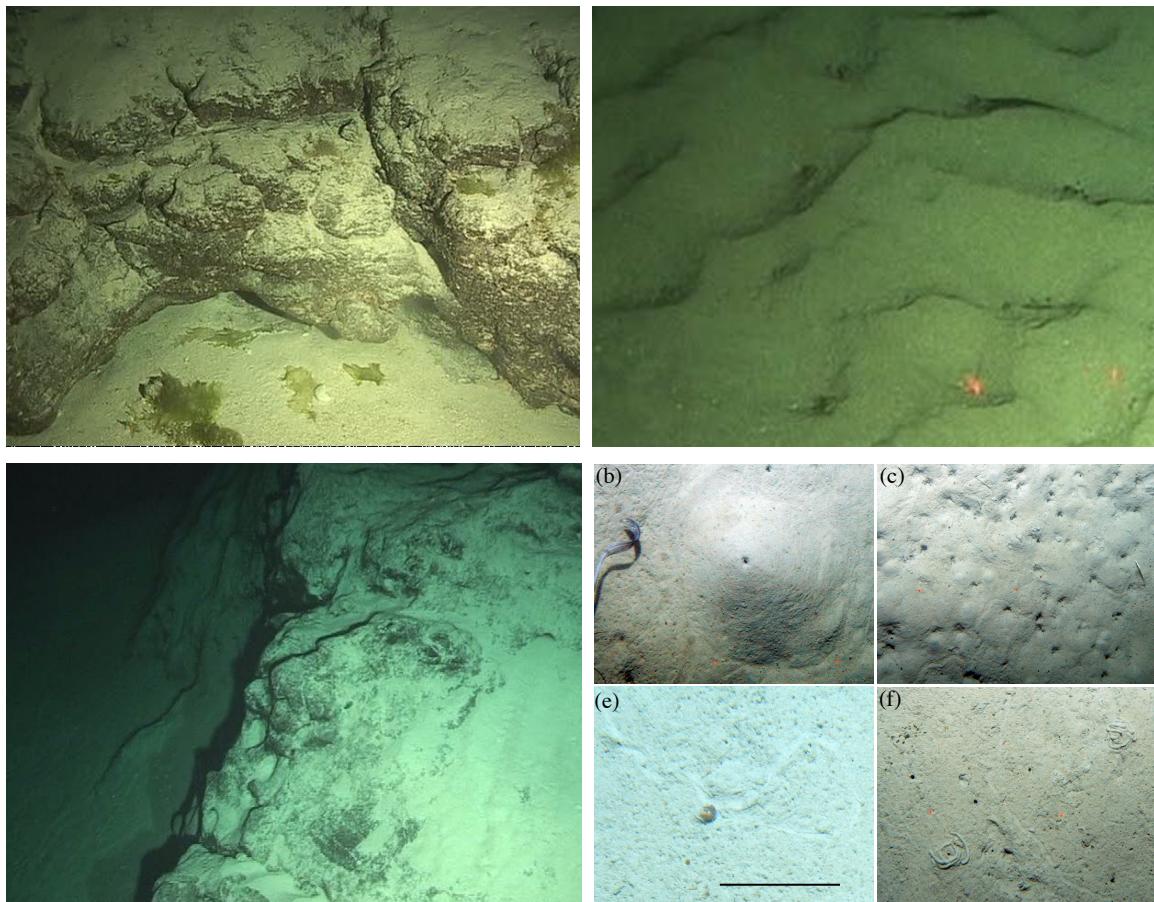
### 5.1 The Habitat Heterogeneity Hypothesis

The first primary hypothesis that submarine canyons harbor enhanced habitat heterogeneity at multiple spatial scales relative to open slope habitats was supported for most of the canyon systems investigated. Exceptions to this general rule were evident in the submarine canyons off the Northwest Hawaiian Islands (NWHI), Maro Reef and Nihoa Island, where ‘canyon effects’ of benthic macrofaunal community structure and overall abundance were not perceived.

The Kaikoura Canyon system on the eastern New Zealand margin harbors a high degree of habitat heterogeneity over spatial scales from meters to a few kilometers related to the density and diversity of macro-infauna and megafauna bioturbation features or *lebensspuren* (Fig. 5.1). *Lebensspuren* made by benthic macro- and megafauna are common features in deep-sea sediments (Jones et al., 2007), and are thought to have an important role in structuring benthic communities and maintaining high diversity (Kukert and Smith, 1992; Levin et al., 2001; Trush and Dayton, 2002; Widdicombe and Austen, 2005). The abundance of *lebensspuren* (used as a metric of substrate habitat heterogeneity) such as mounds, pits, burrows, resting and tracking marks made by holothurians, echiurans worms and gastropods were statistically significantly higher on Kaikoura Canyons sediments compared to the Wairarapa slope control site at comparable depths. This high degree of bioturbation is related to the accumulation of high quantities of organic matter from several pelagic and detrital sources. While this organic enrichment had strong positive effects on macro- and megafauna as well as on demersal fish abundances, a thorough study of these effects on the diversity of those communities is needed.

At larger spatial scales (10’s of kilometers), Kaikoura Canyon shows seafloor landscape homogeneity resulting from flat terrain (< 10 degrees in slope) and a sedimented (mostly muddy) seafloor. It appears that this homogeneity translates into low benthic megafauna diversity at beta scales. For example, from the 8 photographic transects conducted in the canyon, extending over ~7 linear km and covering an area of 11,200 m<sup>2</sup>, no more than 20 megafaunal species, dominated by

echinoderms, were observed, although megafaunal abundances were still much higher than in the slope.



**Figure 5.1** Sources of terrain and substrate habitat heterogeneity of Hawaiian canyons (top and bottom left panels) and sources of substrate habitat heterogeneity derived by faunal bioturbation in Kaikoura Canyon, New Zealand (bottom right panels).

In the chapter dealing with the demersal fish assemblages off two canyons (Pelekunu and Kawainui) off the North of Moloka'i Island in the Main Hawaiian Islands (MHI), a strong link was indicated between habitat heterogeneity and fish abundances, assemblage structure and diversity. The physical habitat (terrain and substrate) heterogeneity metrics measured showed that both canyons contained highly heterogeneous landscapes compared to nearby slopes, which were characterized by lower relief and mud or sand bottoms. Large rock walls, ledges, exposed bedrock, boulders and rippled sediments were common features of the canyons floors (Fig. 5.1; see also Fig. 3.2). It is also worth noting that high energy of bottom currents affected the benthic boundary layer in the canyons. The sediment ripple marks constituted a large percentage of the seafloor even at

1000 m (Fig 5.1 and Fig. 3.2). All these structural habitat heterogeneity parameters appeared to act in concert to explain the differences in fish assemblage structure between canyons and slopes. Nevertheless, the presence of the oxygen minimum zone at intermediate depths (~650-700 m) was an important environmental driver that overwhelmed these habitat heterogeneity effects, homogenizing both the structure and abundances of fish assemblages between canyons and slopes.

The canyons off the Northwest Hawaiian Islands showed a much lesser degree of substrate habitat heterogeneity both at small (meter) and large (kilometer) spatial scales. While features such as rock walls, ledges, and boulders were observed on the seafloor, they occurred much less frequently than in the canyons off the Main Hawaiian Islands. These observations were corroborated by the multi-beam backscatter signals, which were similar among canyon and open slope sites. At small spatial scales (meters), the sediments of both Nihoa and Maro Reef canyons were composed of well-sorted fine carbonate sands, with low variability in particle diameter.

Another indication that the canyons off the NWHI differ from those of the MHI is evident when all the ‘landscape’ metrics are evaluated. Maro Reef and Nihoa Canyons are smaller in their total length (7-8 km) than Moloka’i and Oahu canyons (15-16 km). The NWHI canyons are also farther from shore (10-12 km) than their MHI counterparts (2-3 km) and have smoother transverse vertical profile indices.

## 5.2 Organic Enrichment Hypothesis

The second main hypothesis stating that canyons show enhanced organic-matter enrichment relative to slopes was also verified for most but not all the canyons studied. I hypothesized greater fish and macroinvertebrate abundances in canyons based on the argument that the terrigenous organic detritus yields nutrient subsidies for the benthic invertebrates inside canyons, which in turn provide enhanced prey availability for benthic-feeding fish at canyon floors (Chapter 3 and references therein). The organic enrichment appeared to result in higher macrofaunal abundances in Kaikoura Canyon in New Zealand and also in the three canyons (Pelekunu, Kawainui and Kaneohe canyons) off the MHI (Oahu and Moloka’i), but not for the canyons off Maro Reef and Nihoa Island where only sparse detrital organic enrichment was observed. Higher demersal fish abundances were also reported for submarine canyons relative to slopes off Moloka’i (MHI).

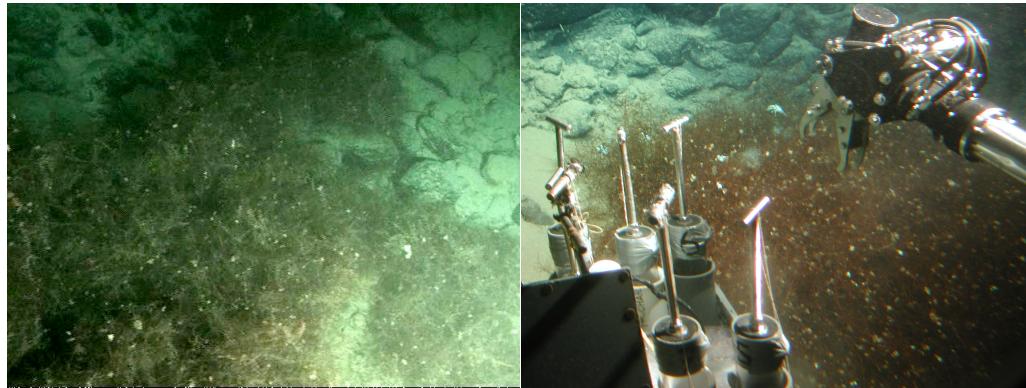
In Kaikoura Canyon, this organic enrichment has led to the remarkable biomasses reported for the infaunal macro- and megabenthos. As reported in Chapter 2, the biomass of infaunal megabenthos averaged  $1.3 \pm 0.26 \text{ kg m}^{-2}$  (max. of 2 kg), a value 100-fold higher than for the typical

deep-sea below 500 m depths. The high environmental stability, high sedimentation rates of particulate organic matter, and the import of detrital kelp material from near shore environments all help to explain the existence of these biomass hotspots. Submarine canyons are globally numerous but very poorly sampled, which may explain why biomasses similar to those in Kaikoura Canyon have not been previously recorded for the deep sea. How common are biomass hotspots such as Kaikoura Canyon likely to be on ocean margins? If we consider the most recent inventory on global distribution of submarine canyons (~5,800 canyons, Harris and Whiteway, 2011), 15% of these canyons have physical characteristics (low hydrodynamics, high POC sedimentation, high export and accumulation of kelp/macroalgae material, and low vertical relief) similar to Kaikoura Canyon. We thus may find on the order of  $0.15 \times 5,800 = 870$  deep-sea canyons harboring biomass hotspots like in Kaikoura.

The organic enrichment in the Kaneohe Canyons off Oahu was verified to be predominantly composed of macroalgae detritus. Patches of those organic falls or 'tumbleweeds' were found in abundance in the canyon up to depths of 1000 m, and less abundantly to 1500 m. Those algal 'clumps', often as large as 2 meters across in size, were composed of an ensemble of up to 10 algal species. These clump assemblages were sampled and described in the present study for the first time (Chapter 4). They consist of a mixture of red, green and brown algae, with some introduced (e.g., *Kappaphycus/Eucheuma* sp. complex) and some native Hawaiian species (*Ploclamium sandvicense*) (Fig. 5.2). Strikingly, those macroalgae detritus patches were virtually absent in the slope demonstrating that the steep topography of canyons act as conduit for this material from near shore to the deep-sea. Such conduits may be especially important in oligotrophic island settings.

In the Pelekunu and Kawainui Canyons off Moloka'i, large amounts of organic detritus were also observed during the Pisces submersible dives. The composition of this material was, however, quite different from the material observed and collected from Kaneohe Canyon in Oahu and composed of relatively refractory terrestrial plant material, such as decomposing wood and large masses of *Kukui* nuts (Fig. 5.3).

Patches of organic detritus were observed in much less abundance off the NWHI canyons. In fact, off Maro Reef Canyon, evidence of such organic material was virtually absent. In Nihoa Canyon, substantial amounts of fresh algal detritus were observed. However, algae detritus was often seen drifting along the bottom with the strong bottom currents.



**Figure 5.2** Images of the patches of macroalgae detritus at 650 m depth in the seafloor of Kaneohe Canyon.



**Figure 5.3** Upper panel: Seafloor patch of wood detritus and Kukui nut rash at 439 m off Pelekunu Canyon in Moloka'i. Lower panel: wood and leaf fragments on surface sediments of Pelekunu Canyon (Petri dishes are 4 cm in diameter – for scaling).

The results of enhanced macrofaunal and demersal fish abundances on Hawaiian canyons largely agree with results reported for the invertebrate megafauna (presented in Vetter et al., 2010). However, Vetter et al. (2010) also found higher benthic megafaunal abundances in the canyons of the NWHI, particularly for highly mobile species.

The overall results presented here can be generalized to submarine canyons receiving large and steady supplies of organic matter from coastal sources. Similar enrichment effects resulting in enhanced benthic abundance and/or biomass have been observed in other continental margin canyons worldwide (Mississippi and Campeche Canyons in the Gulf of Mexico, Nazaré and Portimão Canyons in Portuguese margins, and La Jolla, Scripps and Monterey Canyons in central and southern California are examples; Refer to Table 1.1 in chapter 1 for references). On the other hand, those organic enrichment effects in the benthos were weak or absent in another set of canyons (Hudson, Carson and Hatteras Canyons in the NW Atlantic, Newport Canyon in central California coast, and Merenguera and Blanes Canyons in the Mediterranean off Spain are examples. Table 1.1 for references). The reasons for those contrasting patterns in benthic abundance and biomass are clearly associated with the presence (or absence) of a ‘source’ of organic enrichment that in most cases is associated with coastal sources (benthic macroalgae, riverine input, etc.) (Vetter and Dayton, 1998; Vetter et al., 2010 and references therein).

Future studies on Hawaiian submarine canyons and elsewhere would highly benefit from employing stable carbon and nitrogen isotope data analysis coupled with mixing models to pinpoint the importance of plant and macroalgae carbon sources for demersal fish and macro-invertebrates.

### **5.3 Alpha diversity**

The hypothesis that canyons reduce alpha diversity at shallower depths where physical disturbance by bottom currents is higher was supported for canyons both off the MHI and NWHI. Species richness of benthic macrofauna was reduced at this shallower depth stratum in all Hawaiian canyons studied. Overall, macrobenthic species richness reached a maximum in canyons at intermediate depths. This result agrees with previous studies invoking the intermediate disturbance hypothesis as a mechanistic underpinning for canyon diversity patterns (Vetter and Dayton, 1998; Paterson et al., 2011). Higher (relative to slopes) benthic diversity is observed inside canyons where both organic enrichment and physical disturbance are at moderate levels (i.e., at intermediate depths). Towards the head of the canyons, particularly those with steep-walled V-shaped profiles, the intensity and frequency of physical disturbance from accelerated bottom currents appears to be often too high, disrupting surface sediments and ‘washing-out’ infaunal organisms. At greater depths

towards the mouths of the canyons, while physical disturbance is reduced, so is the amount accumulated detrital organic matter; benthic communities in the deepest parts of canyons resembled those outside of the topographic feature (i.e., a canyon effect is no longer perceivable). While this seems a very straightforward effect, not many studies to date have sampled along enough of the depth gradient (3 or more depth strata) to resolve this pattern (Vetter and Dayton, 1998 is an exception). This is, in my opinion, one of the merits achieved by the present research and should be a component of future studies.

The use of the landscape heterogeneity metrics (in Chapter 4) helped to resolve some variability between the canyons systems studied in terms of their shape, size, overall relief and substrate heterogeneity. The submarine canyons where faunal diversity was reduced at shallower depths coincided with those canyons that were narrower towards their heads, have steeper walls, and have high transverse-vertical profile indexes (Kawainui, Pelekunu and Kaneohe Canyons). Shepard and Dill (1969) classified the canyons off Mokoka'i for example as bearing typical V-shaped profiles with no indication of broad flat floors and less than 2 miles in width, therefore showing very steep slopes. While no current measurements were made during this study, high current velocities ( $> 2$  knots) were experienced at times in Moloka'i and Kaneohe canyons, particularly at the shallower sites, making submersible navigation difficult (F. De Leo, E. Vetter, C. Smith, pers. observations). This strongly supports the hypothesis that physical disturbance in canyons reduce faunal abundance and diversity in the shallower portions of canyons.

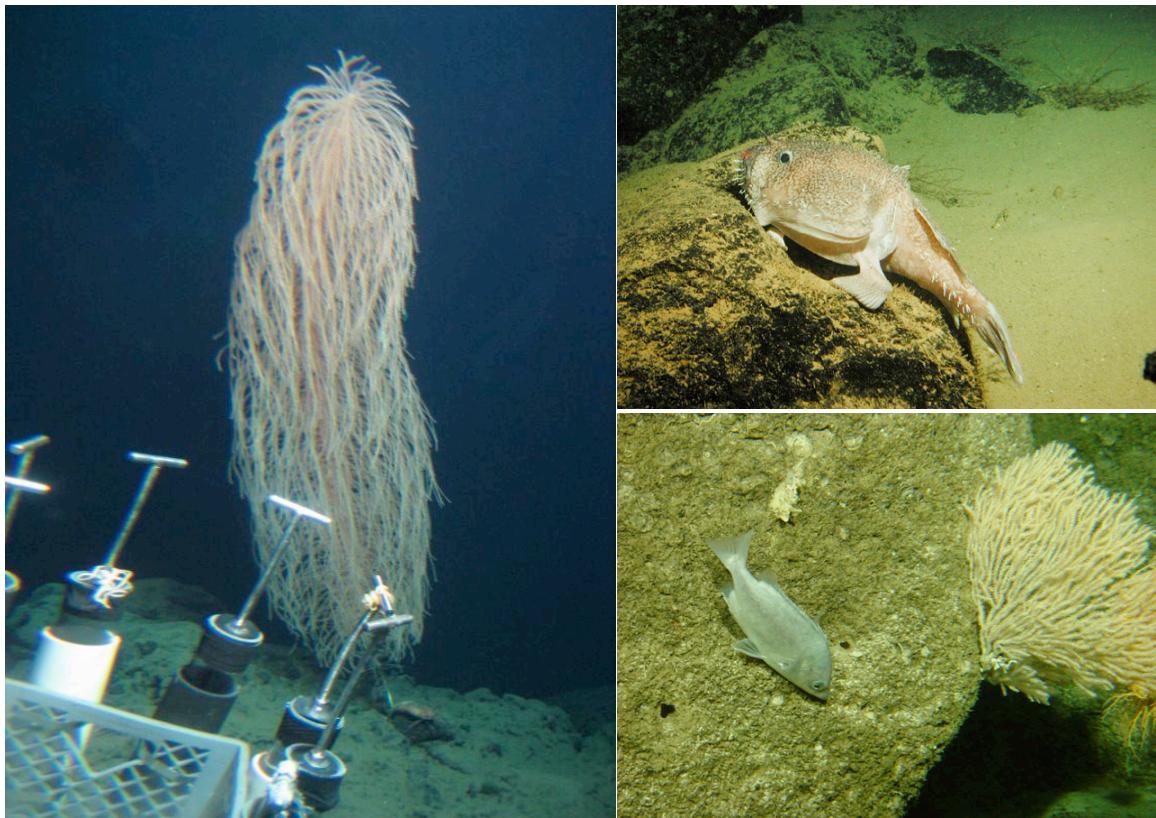
## 5.4 Beta diversity

A high degree of macrofaunal species turnover was also observed for most of the canyons studied, agreeing with the first primary hypothesis that habitat heterogeneity is enhanced in canyons at multiple spatial scales. However, once again this pattern was not observed for the NWHI canyons. The observed higher habitat heterogeneity (for topography, substrate rugosity, and sediment particle heterogeneity) in MHI canyons may be key to promoting niche diversification and allowing for different macrofaunal life strategies to colonize various patches in a structurally rich landscape. Although previous studies have investigated the positive effects of habitat heterogeneity in canyons on beta diversity (Schlacher et al., 2007; McClain and Barry, 2010), they all lack samples collected in control areas outside the respective canyon systems. In our study, the sampling design was conceived to test, in particular, the ‘habitat heterogeneity hypothesis’, and included many control areas on the slope that received a comparable sampling effort (which is extremely rare in the literature of benthic studies on submarine canyons). We therefore provide new, more robust,

evidence that canyons enhance beta-diversity, potentially increasing the regional species pool of infaunal macrobenthos by providing novel habitats.

The results presented here for fish and macrobenthic communities largely agree with the results reported by Vetter *et al* (2010) for benthic megafauna communities. Those authors found a high degree of community dissimilarity between slope and canyon habitats and a high percentage of species that were only found on canyons. Vetter *et al* state that the higher abundance and species richness of megabenthos (mostly fish and crustaceans) often found in the Hawaiian canyons suggest that canyons may also harbor larval-source populations and provide a critical habitat (including key-stone structures) for a variety of highly mobile species (Fig. 5.4). The higher macrofaunal abundances and often higher species richness in the canyons may allow source-sink mechanisms to play important roles in the colonization by macrofauna species of larger areas on the slope as well, further highlighting the ecological importance of these canyons.

The results in the present study further demonstrate that canyons enhance faunal abundance and diversity at local scales (where physical disturbance is moderate) but more significantly at beta scales. Canyons therefore can be considered as open systems that receive larval populations from the slope but also harbor important source populations that help to maintain regional (gamma) diversity. Thus, canyons should be considered of inclusion in marine protected areas in spatially based approaches designed to protect hotspots of biomass and biodiversity on continental and island margins (Van Dover *et al.*, 2011; present study). Moreover, since individual canyons harbor unique physical characteristics that translate into different faunal communities, protected areas on continental or island margins that harbor numerous canyons should include representative protected areas inside each canyon.



**Figure 5.4** Benthic megafauna using key-stone habitat features (bolders, rock ledges and crevices) as settlement or foraging habitats in Hawaiian Canyons. Left panel: large gorgonian observed at 650 m off Pelekunu Canyon off Moloka'i. Top right: A goosefish (*Sladenia remiger*) sits on a rock in a submarine canyon, using its modified dorsal fin to lure unsuspecting fishes to its mouth. Bottom right: Armorhead fish (*Pseudopentaceros wheeleri*) are most common in the Northwest Hawaiian Islands and are potential prey for the Hawaiian monk seals.

## 5.5 References

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