Depth zonation and bathymetric trends of deep-sea megafaunal scavengers of the Hawaiian Islands

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ABSTRACT

The deep sea has been shown to exhibit strong depth zonation in species composition and abundance. Examination of these patterns can offer ecological insight into how organisms adapt and respond to changing environmental parameters that co-occur with depth. Here we provide the first tropical study on bathymetric zonation and other depth-related trends (size, abundance, and species richness) spanning shelf to abyssal depths of scavenging megafauna. Baited time-lapse free-vehicle cameras were used to examine the deep-sea benthic and demersal scavenging communities of the Hawaiian Islands, an area for which the biology and ecology have remained poorly studied below 2000 m. Twenty-two deployments ranging in depth from 250 to 4783 m yielded 37 taxa attracted to bait, including the first known occurrence of the family Zoarcidae in the Hawaiian Islands. Cluster analysis of Bray–Curtis similarity of species peak abundance (n_{max}) revealed four main faunal zones (250–500, 1000, 1500–3000, and $\geqslant 4000$ m) with significant separation (ANOSIM, global $R = 0.907$, $p = 0.001$) between designated depth groups. A major faunal break was identified at the 500–1000 m transition where species turnover was greatest, coinciding with the location of the local oxygen minimum zone. Dominance in species assemblage shifted from decapod crustaceans to teleosts moving from shallow to deeper faunal zones. Significant size differences in total length with depth were found for two of the four fish species examined. A logarithmic decline was observed in scavenger relative abundance with depth. Evidence of interaction between scavenging species was also noted between *Synaphobranchus affinis* and *Neolithodes* sp. (competition) and *Histiobranchus* sp. and aristeid shrimp (predation), suggesting that interactions between scavengers could influence indices of abundance generated from baited camera data.

1. Introduction

Life in most of the deep sea is ultimately dependent on surface-derived organic matter for energy to fuel growth, metabolism, and reproduction. Food supporting deep-sea ecosystems descends from the overlying water column in several forms including phytodetritus, macrophyte detritus, fecal pellets, marine snow, and carrion. A suite of animals have demonstrated the ability to utilize this last source to supplement their diets (Britton and Morton, 1994), with some able to survive over a year without feeding (Tamburri and Barry, 1999). These scavengers can play an important role in deep-sea community ecology as both predators—which can affect prey populations and control food web dynamics through top-down effects—and rapid dispersers of large food falls (Priede et al., 1991). Highly mobile megafaunal scavengers break up and distribute large point sources of organic material (dead fish, whales, fisheries bycatch, etc.) through sloppy feeding and defecation, making food available to the

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background community in the form of particulate and dissolved organic matter (Smith, 1985; Stockton and DeLaca, 1982). By definition, megafaunal scavengers are attracted to bait, and information on their identity, size, abundance, and behavior can be determined with baited cameras (Henriques et al., 2002; Jones et al., 2003; King et al., 2006).

Continental margins of the world's oceans are unique habitats in that they encompass extensive vertical ranges where steep gradients of environmental parameters such pressure, temperature, and light exist. Accordingly, the effects of depth on the community structure of marine biota have been the focus of numerous deep-sea studies. For example, species richness has been shown to display a parabolic trend for fish and invertebrate megafauna with depth off the New England coast, reaching a maximum at mid-slope regions (Rex, 1981). The abundance of benthos, measured as either biomass or population density, has displayed exponential decrease with depth throughout the world's oceans (Rowe, 1983; Gage and Tyler, 1991). Body size trends with depth have also been reported but with varying relationships for different taxonomic groups (Thiel, 1975; Polloni et al., 1979; Rex and Etter, 1998; Moranta et al., 2004; Collins et al., 2005).

Species have been shown to occupy discrete depth bands and progressively replace each other moving from shelf to abyssal depths (Carney et al., 1983; Carney, 2005). Distinct bathymetric faunal zones, or vertical regions of species homogeneity enclosed by transitions with rapid species turnover, have been identified by the characteristic vertical distributions and associated abundances of marine animals across all taxa and size classes (Cartes and Sarda, 1993; Haedrich et al., 1980; King et al., 2006; Aldea et al., 2008). Causes of zonation have been mainly attributed to gradients in environmental parameters (i.e. light, temperature, food availability) that co-occur with depth—which affect the biology and physiology of marine organisms—and ecological interactions between taxa (Rex, 1976; Carney, 2005). For example, larvae of the echinoid *Echinus echinus* have been found to require pressures of at least 1000 dbar for development (Tyler and Young, 1998), suggesting larval dispersal and recruitment may be confined vertically by pressure boundaries. Trophic interactions, such as competition between scavenging fishes, have also been postulated to affect zonation. In the northeast Atlantic lower abundances of *Corphaenoides armatus* (Macrouridae) were observed shallower at 2500 m, where its vertical distribution overlapped with that of the competing scavenger, *Antimora rostrata* (Moridae), compared to at abyssal depths where this competitor is absent (Collins et al., 1999). Although zonation of species assemblages offers insight into how marine animals interact with each other and how they adapt to changes in their surroundings, driving forces behind this phenomenon may be more complex than ecological or environmental factors alone.

The deep-sea benthic and demersal fauna of the Hawaiian Islands is understudied, in part because of difficulties encountered in trawling topographically challenging island and seamount flanks. Surveys focusing on systematics of Hawaiian ichthyofauna have ranged in depth from 40 to 2000 m (Struhsaker, 1973; Borets, 1986; Chave and Mundy, 1994). Below 2000 m, only scant trawling within the archipelago has been conducted (Gilbert, 1905). Outside the islands, a handful of studies have been performed on the abyssal plain 900 miles east and 450–600 miles north of Oahu (Shulenberger and Hessler, 1974; Smith et al., 1979; Ingram and Hessler, 1983; Smith et al., 1992). Mundy (2005) provides the most comprehensive list available for Hawaiian ichthyofauna. Only 2% of the 1224 verified fish species within this inventory occur at depths of 2000 m or greater, reflecting a combination of dearth in sampling effort in the deep regions of the Hawaiian exclusive economic zone (EEZ) and a low in species richness of fish in the deep sea. The scarcity of data at these depths calls for further exploration in order to expand the limited knowledge on the composition and ecology of deep-sea communities in this region. Furthermore, the majority of studies on faunal zonation in the deep sea have been conducted in temperate productive areas. The current lack of data from tropical settings is a restriction to understanding if and how depth zonation occurs in warmer and more oligotrophic regimes, where food supply and thermal structure differ from those in temperate areas. The steepness of the Hawaiian ridge (transition from coastal areas to the abyssal plains in <50 nautical miles at steepest regions) makes it especially suited for the study of depth-related patterns associated with deep-sea fauna by exploiting an expansive vertical study area while simultaneously minimizing horizontal habitat variability.

The focus of this research was to investigate depth-related trends pertaining to scavengers of the Hawaiian Islands using time-lapse free-vehicle cameras to circumvent the difficulties encountered when attempting to trawl this area. Here we aim to accomplish the following: (1) identify the benthic and demersal megafaunal scavenging communities of the Hawaiian region, (2) observe any evidence of depth zonation in the vertical distribution of scavengers, and (3) explore depth-related trends in species richness and scavenger abundance and size. We expect to find new or unidentified species due to paucity of sampling effort in the area. Based on the considerable body evidence from the literature, we expect to identify faunal zones with a distinct scavenger assemblage—though these zones may differ in composition and depth when compared to other regions of the world (Haedrich and Merrett, 1990)—and anticipate depth-related declines in species richness and scavenger abundance and size.

2. Materials and methods

2.1. Data collection

Two free-vehicle camera systems were used to acquire photographic data on the deep-sea scavenging community of Oahu and the Northwestern Hawaiian Islands (NWHI). The instrument package of each system included a camera and strobe, floatation, ballast, and dual release mechanisms. A surface float assembly (3.5 m mast and flag, radio beacon, and xenon flasher) was attached to

each instrument package to aid in recovery upon surfacing. The instrument package was suspended 2 m above the seafloor, anchored by ~90 kg of ballast. Bait consisted of either two whole adult mackerel (~1.5 kg total) or one adult skipjack tuna (~2 kg) attached to 1 m × 1 m reference scale bars and ballast. Although bait species changed during this study because of availability and cost, both were scombrid fishes and used in similar amounts. A 4.0 megapixel digital stills camera and strobe (Scorpio Plus, Insite Pacific) mounted to the instrument package were aimed obliquely downward (22.6° from vertical) at the bait parcel, imaging ~2.0 m² of seafloor. Images were taken at 2-min intervals to maximize the amount of data that could be collected in a 24-h period. For 6 deployments, one camera system was equipped with a current meter (Aquadopp, Nortek, USA) that recorded 2D current velocity, pressure, and temperature at 30-s intervals at 2 m above the seafloor.

Oxygen concentration data ([O_2], µmol kg^{-1}, ml l^{-1}) were taken from Station ALOHA (23°45'N, 158°00'W) near Oahu from cruises 178, 181, 184, and 188 of the Hawaiian Ocean Time Series (HOTS, Fujieki, 2007) that occurred between February and December 2006 and submersible dives P5-688 thru P5-690, P5-695, P5-696, and P5-670 conducted near French Frigate Shoals and Twin Banks (NWHI) in November 2007 (Hawaii Undersea Research Lab, unpublished data).

2.2. Data quantification

Following Britton and Morton (1994), only animals observed either feeding on or actively attracted to bait were recognized as scavengers. Megafaunal (>2 cm) scavengers were identified to the lowest taxonomical level based on diagnostic morphological characteristics using standard keys and texts in conjunction with consultation from taxonomic specialists. Taxa new to the Hawaiian Islands were designated as such based on verification with Mundy (2005).

For each deployment, the first arrival time, t_0 (the time required for the first individual to arrive at bait after vehicle touchdown), and peak abundance, n_{max} (maximum number of a species observed in any single image throughout the deployment), were recorded for all scavenging species observed. Although deployment duration varied throughout the study, n_{max} was reached for most species well before the end of all deployments except during PEN1 and LIS1 where the bait was removed almost immediately. Relative scavenger abundance (# of individuals deployment^{-1}) was measured by summing n_{max} across all scavenging taxa for each deployment. This provided a conservative measure of the number of scavengers attracted to bait while avoiding double counts of individuals.

Teleost densities (# individuals km^{-2}) were estimated using the model proposed by Priede and Merrett (1996) incorporating t_0, fish swimming speed (V_f), and current speed (V_w):

$$N(\text{# fish} \cdot \text{km}^{-2}) = \frac{0.3849(V_f^{-1} + V_w^{-1})^2}{t_0^2}$$

Because it was not possible to quantify V_f, measured swimming speeds of 0.077 m s^{-1} for *Coryphaenoides armatus* (Henriques et al., 2002), 0.213 m s^{-1} for *A. rostrata* (Collins et al., 1999), and calculated V_f of 0.169 m s^{-1} for *Synaphobranchus kaupi* (King et al., 2006) were assumed for the congeners *C. longicirrhus, C. yaquinae, C. rudis, A. rostrata, S. affinis,* and *S. brevidorsalis* observed in this study. Fish swimming speed varies interspecifically, but can even display variation within the same species depending on fish length, depth of occurrence, and season (Bainbridge, 1958; Priede et al., 1994; Uiblein et al., 2002). Variations in V_f (and V_w), however, influence density estimates less than changes in t_0.

For the 6 deployments in which current data were available, mean V_w for the first 30 min was used for abundance estimation. For deployments lacking V_w data, the mean current velocity from available current data of 0.043 m s^{-1} was assumed. This value is very close to the value used by other investigators ($V_w = 0.050$ m s^{-1}) at similar depths where current data have been unavailable (Armstrong et al., 1992; Priede and Merrett, 1996).

Total length (TL) was measured for individual scavenging fishes along the dorsal fin base using image analysis software (ImageJ 1.38X, NIH) calibrated to the scale bars in each image. TL was measured only when the fish was above the seafloor at the same height as the scale bars and when positioned parallel to the plane of the scale bars (evaluated by comparing distances between shadow and target for both criteria). Mean percent error for this method was determined to be $3.62 \pm 1.98\%$ based on measurement of objects of known length ($n = 20$) in the plane of the scale bars. Effort was made not to measure the same fish twice by inspecting each individual for distinguishable characteristics (damaged fins, mottling, scarring, etc.) and allowing 10 images between measurements (in most cases, distinctly identifiable fish were not present for more than 10 images); however, this did not eliminate the possibility of repeat measurements.

2.3. Statistical analyses

Similarity in scavenger community structure was examined using PRIMER 5 (version 5.2.9) software based on Bray–Curtis (1957) similarity of square root transformed n_{max} for all species across all deployments. This approach factors in presence/absence of a species and its abundance when pair-wise similarity between deployments is assigned. Square-root transformation was employed to prevent rare or low abundance species from being masked by the few numerically dominant species when similarity was calculated (Clarke and Green, 1988). Group-averaged hierarchical cluster analysis of similarity data produced a dendrogram and allowed for depth groups to be defined (30% similarity level). The biota and environmental matching procedure (BIOENV) was used to verify that depth—as opposed to other environmental variables (latitude, longitude, time of year, deployment duration)—best explained similarity between deployments. Significance testing of separation between depth groupings was performed using ANOSIM, while

contribution of each species to the similarity within a depth grouping was assessed by SIMPER analysis.

Significance of depth-related trends in scavenger relative abundance was examined with ANOVA for both linear and non-linear trends (MINITAB, Release 14). Intraspecfic changes in TL between depths were assessed non-parametrically (Mann–Whitney U Test, Statistica 7) to allow for non-normal distributions and small/uneven sample sizes. Comparison of average scavenger size (across all taxa) with depth was not possible because of the inability to determine length for most animals. In addition, length is a poor measurement of size inter-specifically because of varying length–weight relation-ships between species (biomass is a more appropriate metric). Length–weight regressions were available for very few species to transform length data to biomass.

Rarefaction curves (Sanders, 1968) were generated (PRIMER 5, v5.2.9) for pooled n_{max} data for each of the seven target depths to evaluate species richness between depths. Comparison of ES_n (estimated species at n individuals) between depths allowed for species richness comparisons to be made while constraining the influence of variation in sample size.

3. Results

Data were collected from a total of 22 camera deployments conducted between 18 February 2006 and 17 July 2007 off of Oahu and the NWHI of Nihoa, Lisianski, Laysan, and Pearl and Hermes Atoll spanning several different cruises (Fig. 1). A summary of deployment information is presented in Table 1. Deployment depth ranged from 250 to 4783 m, targeting seven discrete depths: 250, 500, 1000, 1500, 2200, 3000, and $\geqslant 4000$ m. Duration of data collection ranged from 10:40 to 29:12 (hh:mm). Bait was removed within the first 12 and 8 min during deployments PEN1 and LIS1, respectively, poten-tially causing underestimation of the composition and abundance of scavengers that would have been observed with longer bait duration. These data were therefore omitted from the abundance analysis. Technical difficul-ties were experienced on 6 deployments. The field of view was not centered on the bait parcel for LIS3 and ALO2 because of uneven ballasting of the camera frame. The focal length was set too high for MAK1 and MAK2, reducing the field of view to 0.4 m^2 of seafloor. As a result, n_{max} for these deployments may have been potentially underestimated. No images were captured on LIS5. Images from WAI1 were out of focus.

3.1. Community composition

A total of 37 taxa were identified as scavengers in this study including fishes, decapod shrimps and crabs, echinoderms, and one species of cephalopod (Fig. 2). Species identifications are considered tentative until future trapping efforts produce specimen material for verification purposes. Scavenger peak abundances and depths of occurrence are listed in Table 2. The fish fauna consisted of 22 species—16 teleosts, six elasmobranchs, and one Myxiniforme—from 13 families. Of these, the Synaphobranchidae (*Histiobranchus* sp., *Meadia abyssalis*, *Simenchelys parasitica*, *S. affinis*, and *S. brevidorsalis*) were the most speciose and covered the greatest vertical distribution (Table 2), with five species collectively spanning a range of 250–4000 m. As a family, the synaphobranchids were also the most numerous fishes observed. *Synaphobranchus affinis* and *Histiobranchus* sp. reached peak abundances (n_{max}) of 19 and 13, respec-tively, the highest of all fish species (Table 2). The Ophidiidae and Macrouridae were the other dominant scavenging fish families, with multiple species occurring at several depths. Ophidiidae 1 sp. (*Apagesoma/Bassozetus* sp.?) reached an n_{max} value of 13 individuals, and along with *Histiobranchus* sp. was the second most abundant fish attracted to bait based on n_{max}. Consistency of
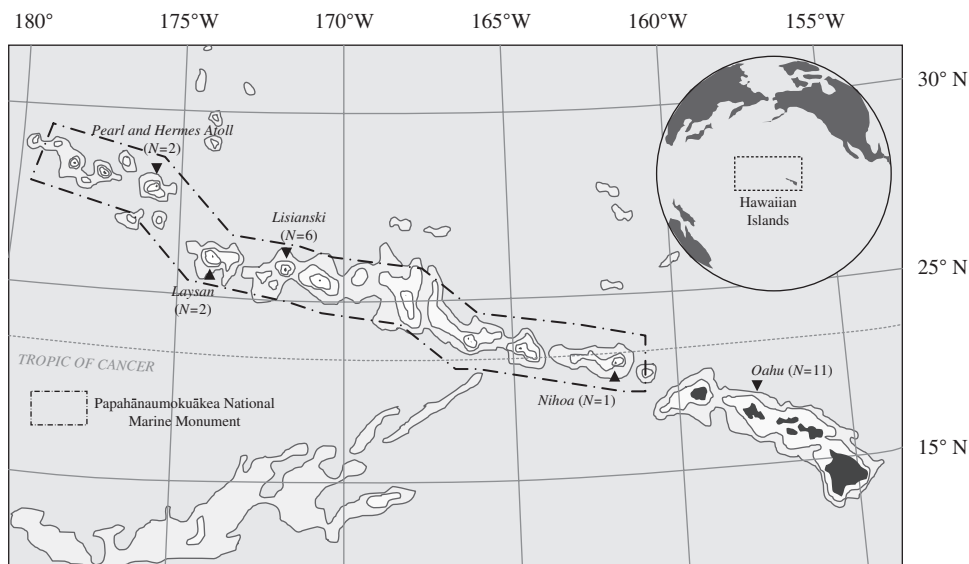

Fig. 1. Study area and island locations where camera systems were deployed.

Table 1
Summary of deployment information

Deployment	Location	Date	Lat. (N)	Long. (W)	Depth (m)	Duration (hh:mm)	V_c (m s^{-1})	Comments
PEN1	S Oahu	26-Dec-06	21 01.463	157 45.928	250	21:14	–	Bait removed in first 12 min
PEN2	S Oahu	27-Dec-06	21 01.514	157 45.812	250	23:18	–	
MAK1	E Oahu	22-May-07	21 21.647	157 36.750	500	15:50	–	Reduced field of view
MAK2	E Oahu	24-May-07	21 20.940	157 45.812	500	15:50	–	Reduced field of view
LIS1	Lisianski	13-Jul-07	26 3.892	173 46.633	508	14:28	0.028	Bait removed in first 8 min
LIS2	Lisianski	13-Jul-07	26 6.514	173 46.247	500	12:34	–	
ALO1	NW Oahu	18-Feb-06	21 42.800	158 18.800	1000	29:08	–	
ALO3	NW Oahu	19-Mar-07	21 42.843	158 20.069	1000	39:10	–	
WAI4	W Oahu	20-Sep-07	21 23.101	158 15.527	1000	22:33	–	
LIS 5	Lisianski	15-Jul-07	26 11.200	173 51.740	1489	16:58	0.044	No images, camera malfunction
LIS 6	Lisianski	15-Jul-07	26 13.502	173 53.699	1500	17:52	–	
WAI2	W Oahu	23-Mar-06	21 26.913	158 22.048	2200	21:28	–	
LIS4	Lisianski	14-Jul-07	25 49.085	173 55.824	2200	27:06	–	
LIS3	Lisianski	14-Jul-07	25 48.322	173 52.814	2205	24:34	0.043	Field of view not centered on bait
NIH1	Nihoa	8-Jul-07	22 56.310	161 57.660	2348	22:16	0.042	
WAI1	W Oahu	22-Mar-06	21 10.944	158 21.466	3000	18:08	–	Out of focus
ALO2	NW Oahu	25-May-06	21 54.311	158 16.305	3000	20:36	–	Field of view not centered on bait
LAY2	Laysan	24-Jul-07	25 47.025	172 01.583	3000	17:06	–	
LAY1	Laysan	24-Jul-07	25 49.932	172 03.588	3003	17:10	0.062	
P&H1	Pearl and Hermes	17-Jul-07	27 38.547	175 42.267	3987	29:12	0.039	
P&H2	Pearl and Hermes	17-Jul-07	27 37.327	175 38.121	4000	28:14	–	
ALO4	N Oahu	4-May-07	22 41.027	157 59.957	4753	10:40	–	

Where current velocity data were unavailable, $V_c = 0.043$ m s^{-1} (mean) assumed.

scavenger arrival to bait varied throughout the study. Some species such as *Conger oligoporus* and *Gymnothorax nuttingi* were observed only once. In contrast, *C. longicirrhus* (Macrouridae) and the blue hake, *A. microlepis* (Moridae), were present during every deployment within their observed depth distribution (Table 2).

Elasmobranch scavengers included five shark and one ray species, none occurring deeper than 2200 m. In general, elasmobranch presence was infrequent, typically with a single individual observed at a time. Only the Pacific sleeper shark, *Somniosus pacificus*, the six-gill shark, *Hexanchus griseus*, and the dogfish shark, *Squalus mitsukurii*, were observed at more than 2 deployments (Table 2).

Fifteen species of invertebrate scavengers were recorded. The decapod shrimp *Heterocarpus ensifer* (Pandalidae) and crab *Neolithodes* sp. (Lithodidae) reached the highest peak abundances in the study with n_{max} values of 70 and 34 individuals, respectively (Table 2). Although their depth ranges were narrow (*H. ensifer*, 250–500 m, *Neolithodes* sp., 1000–1500 m; Table 2), these scavengers were found commonly and in high abundance. Unidentified aristeid shrimp were recorded during all deployments between 1000 and 4753 m (Table 2), the largest observed depth range for any scavenger in this study. Numerous smaller shrimp similar in appearance were present throughout this depth range: it is possible these were either juveniles of the same larger species or multiple aristeid species were present. Without specimen material in hand, these shrimp were treated as a single species. In contrast, the majority of the other crustaceans were observed infrequently (1–2 deployments) throughout the study. Additional non-crustacean invertebrate scavengers included the asteroids *Ceramaster bowersi* and *Meadiaster ornatus* and the octopus *Enteroctopus* n. sp.

3.2. Depth zonation

Cluster analysis of the deployments based on n_{max} data (Table 2) revealed four distinct faunal groups corresponding to four well-defined depth zones (Fig. 3): Group A—upper slope (250–500 m), group B—middle slope (1000 m), group C—lower slope/upper rise (1500–3000 m), and group D—abyssal ($\geqslant$4000 m). BIOENV confirmed that depth was the variable primarily responsible for similarity between deployments. ANOSIM confirmed significance of separation when all designated groups were considered (global $R = 0.907$, $p = 0.001$). All pair-wise comparisons between individual groups yielded significant differences ($p \leqslant 0.005$) with the exception of group B vs. D ($p = 0.100$)—probably a result of small sample sizes of both groups ($n = 3$ vs. $n = 3$).

Group A, the shallowest assemblage, included 6 deployments from two depths (250 and 500 m) and was least similar to other groups. Twenty-one scavenging species were observed from these sites; however, only two species, *H. ensifer* and *S. mitsukurii*, accounted for 80.7% of the within-group similarity. Deployment PEN1 at 250 m was extremely dissimilar to the rest of group A. Complete bait removal occurred within 12 min of touchdown; thus, the number of species that would have arrived at this station is likely underestimated. Even with this deployment removed, clustering still revealed the least similarity between group A and all other depths. Group B included only 1000 m deployments. *Neolithodes* sp., *S. affinis*, and *Acanthephyra* sp. were present during every deployment and responsible for 74.1% of group similarity. Group C was the largest group with 9 deployments and spanned the greatest vertical range of 1500–3000 m. Aristeid shrimp and *C. longicirrhus* were present during every deployment of this group, and contributed most (30.8% and 18.1%,

Fig. 2. Scavenging taxa of the Hawaiian Islands.

respectively) to within group similarity. Other contributions came from *Eptatretus carlhubbsi* (14.1%), *S. brevidorsalis* (10.6%), and *Histiobranchus* sp. (10.5%). Group D

included the three deepest deployments. Only five scavenging species were found ≥4000 m. Aristeid shrimp and Ophidiidae 1 sp. (*Apagesoma/Bassozetus* sp.?) were the
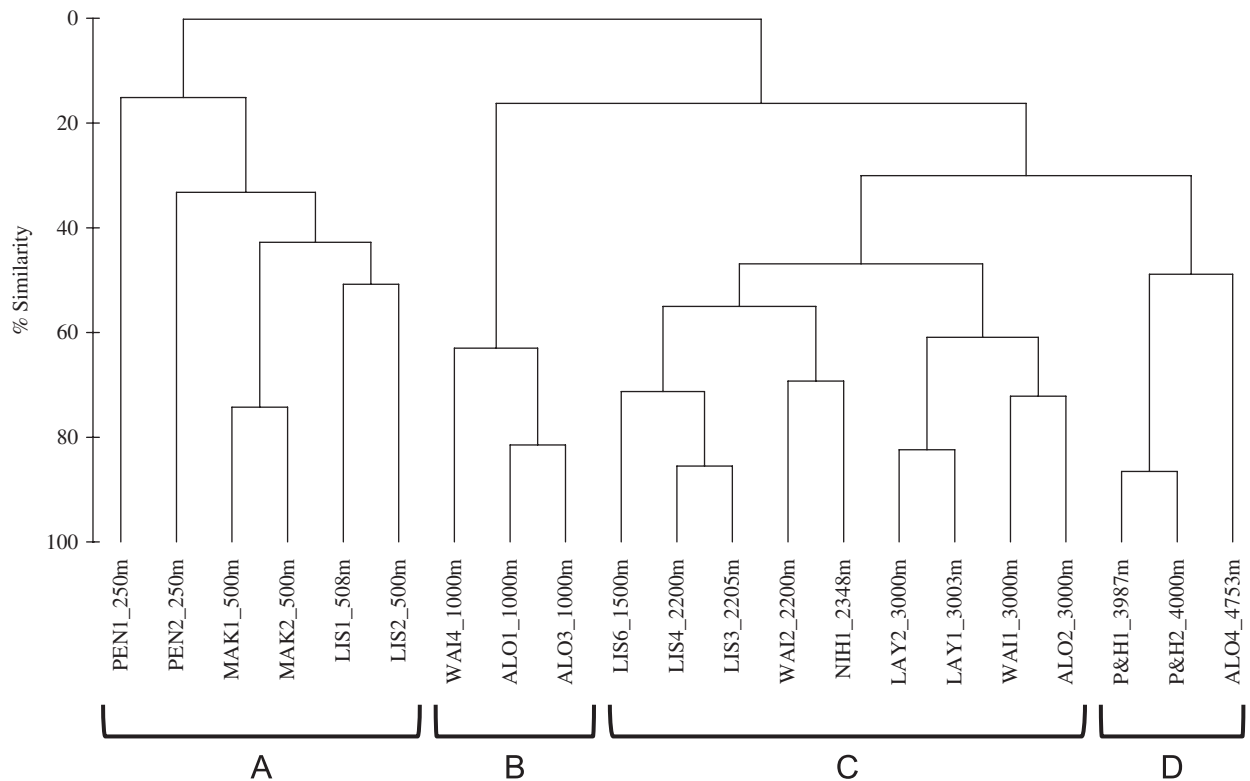
Table 2
Scavenger peak abundance (n_{max}) listed by increasing deployment depth

Deployment	Depth (m)	Teleost															Elasmobranch							Shrimp				Crab											Total
		Antimora microlepis	*Coryphaenoides longicirrhus*	*Coryphaenoides rudis*	*Coryphaenoides yaquinae*	*Barathrites* sp.	*Ophidiidae 1* sp.	*Ophidiidae 2* sp.	*Pachycara* sp.	*Conger oligoporus*	*Gymnothorax nuttingi*	*Histiobranchus* sp.	*Meadia abyssalis*	*Simenchelys parasitica*	*Synaphobranchus affinis*	*Synaphobranchus brevidorsalis*	*Plesiobatis davisi*	*Squalus mitsukurii*	*Somniosus pacificus*	*Echinorhinus cookie*	*Hexanchus griseus*	*Psuedotriakis microdon*	*Eptatretus carlhubbsi*	*Acanthephyra* sp.	Aristeidae	*Heterocarpus ensifer*	*Heterocarpus laevigatus*	*Cancer macrophthalmus*	*Lithodes nintokuae*	*Mursia hawaiiensis*	*Neolithodes* sp.	*Paramola* sp.	*Randallia distincta*	*Sympagurus birkenroadi*	*Sympagurus dofleini*	*Ceramaster bowersi*	*Mediaster ornatus*	*Enteroctopus* n. sp.	
PEN1	250		1								1		2					3														1			1		8	2	7
PEN2	250		1							2			5					1		1						8									2		1	2	28
MAK1	500																1	2								36													56
MAK2	500																1	1								70	14								1	1			76
LIS1	508																				1					24	4												27
LIS2	500																	5			1					14		4		3		4	2			2			32
ALO1	1000														6				1					9	2						4								22
ALO3	1000														19				1					5	2						12								39
WAI4	1000														3						1	1	1	2	1						34								44
LIS 6	1500	1		2										3		1			1			1	2		20						4								36
WAI2	2200	1	1									1				4							3		5									1					13
LIS4	2200	1	1	1										2		2							4		6														16
LIS3	2205	2	1				1							2		2			1						8														21
NIH1	2348	1	2				1					1				1							7		3				2					1					19
WAI1	3000		1					1	1			3				1							1		2														9
ALO2	3000		1					1	1			2													2									2					9
LAY2	3000		1	2			1	1				13				2							4		3														27
LAY1	3003		1	1				1				7				1							3		4									1					19
P&H1	3987					2	13					2													16														33
P&H2	4000					2	3					3													20														28
ALO4	4753				2		2																		5														9

Fig. 3. Faunal zones identified based on group-averaged cluster analysis of Bray–Curtis similarities from $\sqrt{}$-transformed n_{max}: Group A (250–500 m), Group B (1000 m), Group C (1500–3000 m), and Group D ($\geqslant$4000 m).

dominant scavengers in terms of n_{max} and frequency of occurrence contributing 54.4% and 30.1%, respectively, to group similarity.

Each faunal zone consisted of varying contributions from three main taxonomic groups: teleosts, elasmobranchs, and invertebrates (Fig. 4). Invertebrates dominated species richness in Group A (59% of all species) and decreased in contribution with increasing depth group. In contrast, teleosts were the smallest component of groups A and B, but increased in contribution with increasing depth group to a maximum of 80% in group D. Elasmobranchs showed greatest contribution at middepths in group B and lesser importance in groups A and C.

3.3. Scavenger abundance and size

Relative scavenger abundance (n_{max}) by species for all deployments is reported in Table 2. Relative abundance for all scavenging taxa, expressed as $\sum n_{max}$ across all species per deployment, declined significantly with depth ($p = 0.010$, $R^2 = 0.389$) in a logarithmic relationship (Fig. 5). The peak mean number of scavengers to arrive at bait was 48 individuals found at 500 m, largely because of high abundance of the shrimp H. ensifer and other invertebrates while the lowest was nine individuals at 4753 m. Estimated teleost density based on t_0, V_f, and V_w are presented in Table 3. Interestingly, no scavenging teleosts were observed during any of the 500 m deployments.
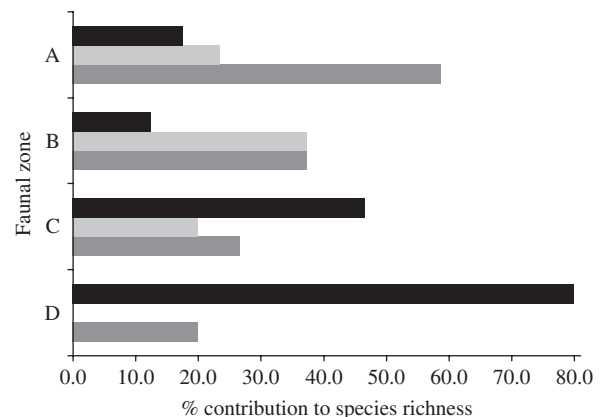
Fig. 4. Percent contribution to species richness by faunal zone of major taxonomic groups—teleost (black), elasmobranch (light gray), and invertebrates (dark gray).

Visible scavengers ranged in size from 2 cm (unidentified amphipods, body length) to an estimated TL of 391 cm for S. pacificus (pectoral length = 41.2 cm) based on morphometric regressions (Ebert et al., 1987). Four fish species were observed in high frequency in an orientation necessary to permit accurate length measurement: E. carlhubbsi, Histiobranchus sp., S. parasitica, and S. brevidorsalis. These species were abundant and spanned multiple depths to allow for statistical comparison of size

with depth. Their length–frequency distributions are shown in Fig. 6. Significant differences in TL between depths were found for *S. brevidorsalis* (2200 vs. 3000 m, $p = 0.028$) and *S. parasitica* (1500 vs. 2200, $p = 0.034$), but not for *Histiobranchus* sp. (3000 vs. 4000 m, $p = 0.306$) and *E. carlhubbsi* (2200 vs. 3000 m, $p = 0.748$). Interestingly, *E. carlhubbsi* displayed a bimodal distribution in TL, possibly indicative of the presence of two different species. *Synaphobranchus brevidorsalis* were larger deeper with mean TL = 83.5 ± 17.98 at 2200 m compared to mean TL = 98.4 ± 16.41 cm at 3000 m. Surprisingly, *S. parasitica* displayed the opposite trend and were larger shallower with mean TL = 37.2 ± 6.53 cm at 1500 m compared to mean TL = 30.6 ± 5.59 cm at 2200 m.

3.4. Species richness

Peaks in cumulative species richness were evident at 500 and 2200 m (12 scavenging species) as displayed in Fig. 7. When species are separated into general taxonomic groups, it is apparent that the bimodal maxima are due to different contributions to species richness from fish (teleosts and elasmobranchs) and invertebrates at both peaks. The invertebrate fauna is largely responsible for the shallower peak (75% of all species) while the fish contribution is largely responsible for the deeper peak (75% of all species). Plotted in the secondary axis in Fig. 7
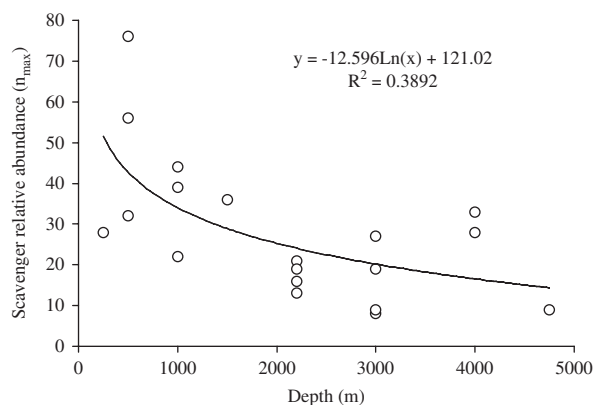
Fig. 5. Scavenger relative abundance (for all taxa) vs. depth.

is oxygen concentration ($[O_2]$, μmol kg^{-1}) from HOTS cruise 188 at Station ALOHA, 60 nautical miles north of Oahu. The steep drop in $[O_2]$ between ~400 and 750 m followed by an oxygen minimum zone (OMZ) of ~28 μmol kg^{-1} (~0.62 ml l^{-1}) between 750 and 850 m coincides with the local minimum in species richness. Oxygen data from additional HOTS cruises spanning ~1 year in conjunction with Hawaii Undersea Research Lab (HURL) $[O_2]$ data from the NWHI confirm that the OMZ is a permanent feature both spatially and temporally.

Fig. 8 shows the change in the scavenger assemblage as the result of new species encountered or species lost from the prior adjacent sampling depth. Species gain between stations declined with increasing depth from a maximum of +7 species at the 250–500 m transition to +1 between 4000 and 4783 m. Species loss was greatest at the 500–1000 m (-11 species) and 3000–4000 m (-7 species) transitions. The most dramatic change in species richness took place between 500 and 1000 m (again, coinciding with the OMZ), where the largest shift in assemblage (a total of 17 species either gained or lost) occurred.

Because of limitations in shiptime, sample sizes varied between 1 and 4 deployments for each target depth. The number of individuals observed also varied between deployments. The question then arises whether the maxima and local minimum found in scavenger diversity is a result of sampling effort. Rarefaction curves shown in Fig. 9 provide a look at the estimated number of species that would have been observed if each target depth consisted of a standard sample size of n individuals (ES_n). If sample size was standardized to the smallest number of observed individuals for any target depth (ES_{36}), lowest species richness occurs at 1000 and $\geqslant 4000$ m, suggesting our findings of richness minima at these depths were not a result of variation in sample sizes.

3.5. Scavenger–scavenger interactions

On two occasions, interaction between scavenging species was noticeable. During Station ALO3 at 1000 m, abundance at bait of the crab *Neolithodes* sp. and eel *S. affinis* were negatively correlated (Spearman's rank correlation; $R = -0.39$, $p < 0.05$)—crab numbers were highest when eel numbers were lowest and vice versa (Fig. 10A).

Table 3
First arrival times and associated estimated densities (hh:mm; # individuals km^{-2}) for the genera *Antimora*, *Coryphaenoides*, and *Synaphobranchus*

| Deployment	Depth (m)	A. microlepis	C. longicirrhus	C. rudis	C. yaquinae	S. affinis	S. brevidorsalis
ALO1	1000					0:38; 50	
ALO3	1000					0:10; 718	
WAI4	1000					0:12; 499	
LIS6	1500	0:28; 83	0:30; 129	0:32; 114			0:10; 718
WAI2	2200	1:54; 5	4:08; 2				0:24; 125
LIS4	2200	0:26; 96	1:46; 10				0:14; 366
LIS3	2205	0:14; 424	4:00; 2				0:20; 227
NIH1	2348	0:22; 178	1:26; 20				3:54; 2
WAI1	3000		3:26; 3				0:36; 55
ALO2	3000		2:54; 4				
LAY2	3000		7:06; 1	7:22; 1			0:14; 366
LAY1	3003		7:56; <1	9:10; <1			3:38; 1
ALO4	4753				4:56; 1		
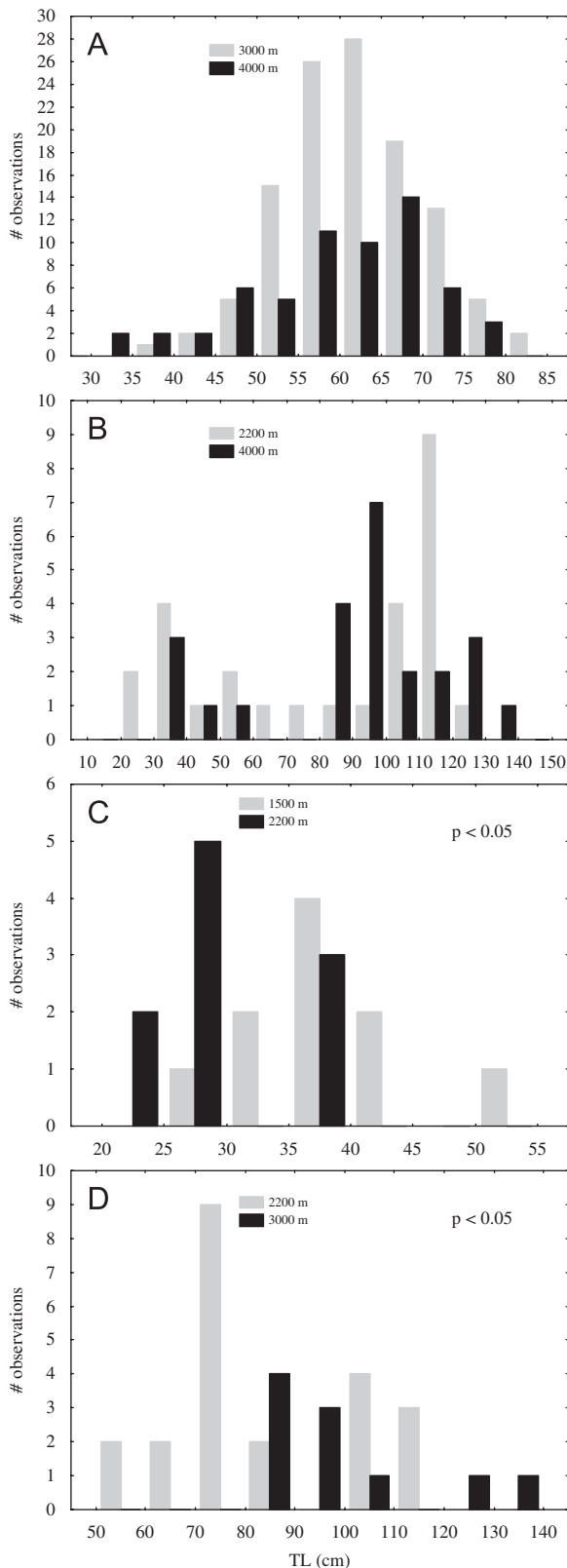
Fig. 6. Length–frequency distributions (TL, cm) of (A) *Histiobranchus* sp., (B) *Eptatretus carlhubbsi*, (C) *Simenchelys parasitica*, and (D) *Synapho-branchus brevidorsalis* by depth.

This interaction appears to be one of competition, as a predator–prey relationship seems unlikely based on the morphology of either animal. Additionally, declines in aristeid shrimp abundance were observed shortly after a minimum of one individual of *Histiobranchus* sp. was present at Station P&H1 at 3987 m (Fig. 10B). Statistical testing was not applied to this event because of complexity of interaction. Several images from this deployment showed sediment clouds near the heads of *Histiobranchus* sp., with shrimps scattered away from the cloud. A single image shows two severed shrimp pleopods lying on the seafloor. These observations, combined with records of crustacean remains in *Histiobranchus bathybius* guts (Karmovskaya and Merrett, 1998) imply active predation on aristeid shrimp by this genus.

4. Discussion and conclusions

4.1. Systematics

The ubiquitous presence of bait-attending fauna throughout the broad depth range encompassed in this survey demonstrates an active scavenging component to the benthic and demersal communities of the Hawaiian Islands. Several of the observations from this study have contributed to species range extensions and represent putative first occurrences in the Hawaiian archipelago. A brief description of the diagnostic characteristics used to identify species new to the Hawaiian Islands or species with range extensions follows.

Histiobranchus sp. was identified based on the shape and size of the pectoral fin (rounded and small: pectoral length < 0.5 gape length), the location of the dorsal fin origin directly over the pectoral region, and posterior location of the anal fin origin near body mid-point (Sulak and Shcherbachev, 1997). *Simenchelys parasitica* (Sulak and Shcherbachev, 1997) was easily distinguishable from other anguilleformes due to the blunt and cylindrical head and small terminal mouth with gape falling well short of orbit. *C. yaquinae* (Wilson and Waples, 1983) was identified and distinguished from its congener of similar appearance, *C. armatus*, based on the number of dorsal and pelvic fin rays (9 and 10, respectively), ash-gray color, coarse scales, depressed snout, and depth of occurrence. *Somniosis pacificus* (Compagno, 1984) was identified based on the short rounded snout and thick, rough, and bristly head, posterior location of first dorsal fin (near mid-point of body), and blackish coloration. *E. carlhubbsi* (McMillan and Wisner, 1984) was identified based on the number of gill apertures (7) and presence of large prominent eyespots which distinguishes it from other congeners. *Barathrites* sp. (Nielsen et al., 1999) was identified by its short (head length $\frac{1}{3}$ of preanal length) and depressed head and pale white coloration. *Pachycara* sp. was identified based on its short head length, elongate tail, large head and mouth, and thick lips with a slight lobe in the lower lip (Anderson, 1994).

Prior to this work, the nearest record of the genus *Histiobranchus* was from 36°10′N, 178°E (*H. bathybius*, Karmovskaya and Merrett, 1998), several hundred miles
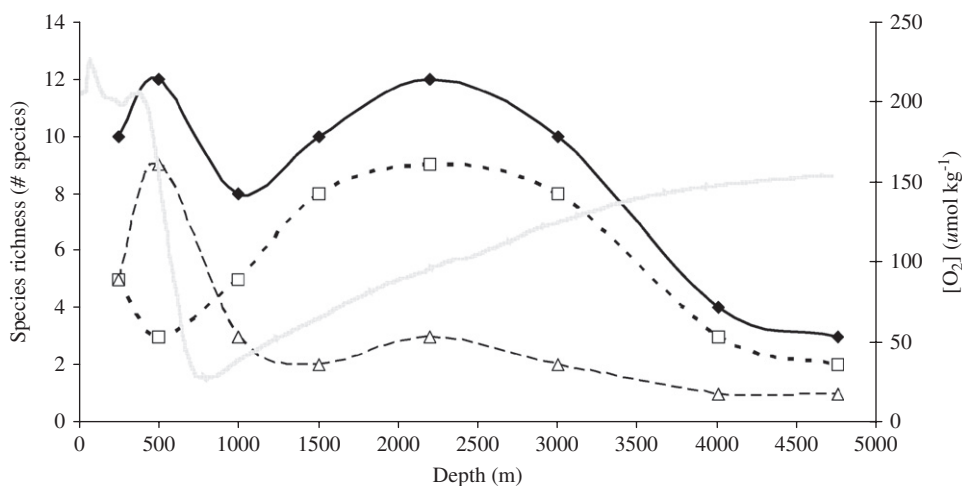
Fig. 7. Species richness vs. depth for all scavengers (solid black line), fish (teleosts and elasmobranchs, dotted line), and invertebrates (dashed line); Station ALOHA oxygen concentration ([O₂], μmol kg⁻¹, solid gray line) vs. depth plotted on secondary axis.
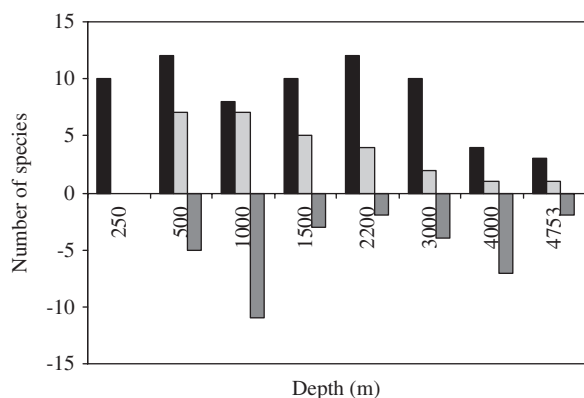

Fig. 8. Total number of species (black) by sampling depth. Species turnover shown as gain (light gray) or loss (dark gray) of species from the adjacent shallower depth.
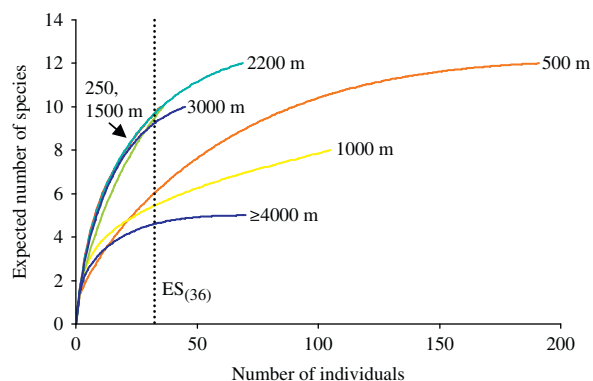

Fig. 9. Rarefraction curves for each target depth (250 and 1500 m curves are masked by 2200 m curve); dashed line represents expected number of species at 36 individuals (ES₍₃₆₎).
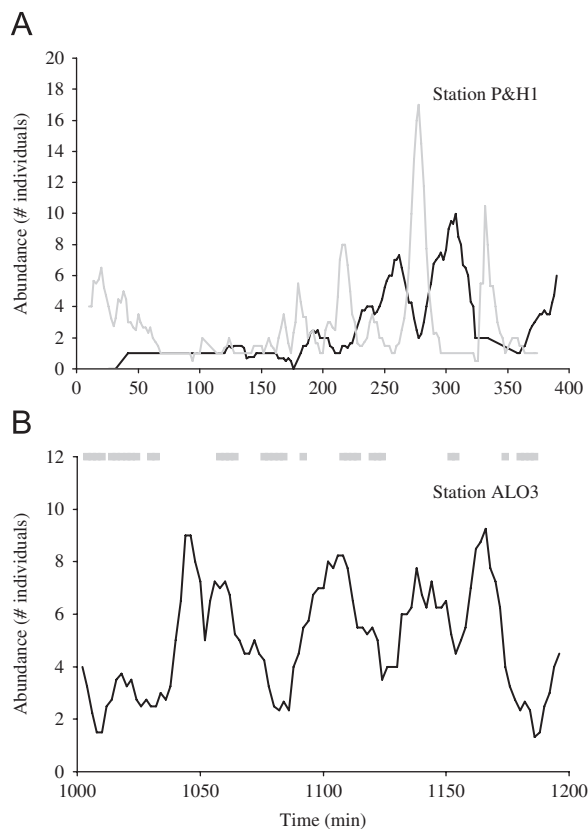
Fig. 10. Scavenger abundance (8 min moving average) vs. bottom time. (A) *Neolithodes* sp. (black line) and *Synaphobranchus affinis* (gray line) and (B) aristeid shrimp (black line) and *Histiobranchus* sp. (gray bar indicates ≥1 individual).

away from the northwest end of the NWHI, yet *Histiobranchus* sp. was observed frequently in this study from Oahu to Pearl and Hermes Atoll. In addition *S. parasitica*

was previously only known to occur in the vicinity of Hawaii at Darwin Guyot and near Wake Island (Solomon-Raju and Rosenblatt, 1971). *C. yaquinae* was reported over 500 nautical miles north of Oahu, but not directly within the archipelago (Smith et al., 1992). *Somniosis pacificus*, which had been documented only once locally at Hancock Seamounts (Wilson et al., 1985), was observed on every deployment from 1000 to 1500 m and once at 2200 m for a total of five occurrences. The hagfish *E. carlhubbsi*, another species previously considered uncommon, was also observed in high frequency (present at 8 deployments) from 1000 to 3000 m, greatly extending its known maximum depth of occurrence of 1574 m (McMillan and Wisner, 1984). Additionally, *Barathrites* sp. has not been documented anywhere near the Hawaiian Islands. Previously this genus has only been observed in the Atlantic Ocean. *Pachycara* sp. seen off NW Oahu at 3000 m is the first observation of any member of the Zoarcidae in the Hawaiian Islands. Two individuals of a currently undescribed octopus species of the genus *Enteroctopus* were also observed (E. Hochberg, pers. comm.).

4.2. Depth zonation and species richness

Bathymetric partitioning observed in the distribution of the scavenging community was not surprising as faunal zonation is a well documented phenomenon throughout the world's oceans (Haedrich et al., 1980; Carney, 2005; King et al., 2006). Faunal zones have shown coherence in species composition only on regional scales, however, and fail to display consistency when applied over broader areas (Haedrich and Merrett, 1990). Our results can be compared to the work of Struhsaker (1973) who examined the fish community from 90 to 700 m in the main Hawaiian Islands. The upper slope (250–500 m), middle slope (1000 m), lower slope/upper rise (1500–3000 m), and abyssal (≥4000 m) faunal zones identified in the present study complement and provide slight overlap with the shallower zones identified by Struhsaker (1973): outer shelf (91–150 m), upper slope (151–250 m), middle slope (251–500 m), and lower slope (501–700 m). Differences in nomenclature assigned to these zones vary from study to study and are of peripheral importance to their associated depths. Alignment at 250–500 m between investigations shows good agreement of zonation occurring between studies. The 1000 m zone identified in this study included 3 deployments from the same depth. It is possible that Struhsaker's 501–700 m zone is an extension of this 1000 m zone, filling in depths missed by our sampling regime. Despite agreement in zonation, species accounts are almost entirely different, with only one species, *C. oligoporus*, being common to both studies. This dissimilarity in faunal composition probably reflects a difference in sampling method rather than an actual difference in community structure. Struhsaker's trawl-based survey included only ichthyofauna and certainly missed some of the larger fishes such as elasmobranchs because of net avoidance. Our data, on the other hand, selected for scavenging species by design, included all taxa attracted to bait, and omitted non-scavenging

species. In contrast to our results, Chave and Mundy (1994) found no distinguishable faunal zones in a synthesis combining Struhsaker's work with submersible data extending to 2000 m from HURL. This claim was somewhat preliminary as it was made without statistical analyses. Recognition and identification of zonation patterns are dependent on sampling distribution, choice of taxa included, and methods of analysis applied (Carney, 2005). In our case zonation is clear and environmental and biological data allows us to speculate about the causes.

Of particular interest in this study is the major faunal break apparent from cluster analysis between 500 and 1000 m. At 500 m, 12 scavenging species were found compared to eight at 1000 m (Table 2), but only one species (*H. griseus*) was common to both depths, illustrating the massive shift in assemblage (seven species gained, 11 lost) taking place at the 500–1000 m transition (Fig. 9). Species richness was expected to peak at intermediate depths (Rex, 1981); therefore, the presence of two distinct maxima resulting from different taxonomic components and a local minimum of eight species at 1000 m was surprising (Fig. 7). Interestingly, this dramatic turnover in species turnover followed by a local minimum in species richness mimicked the oxygen profile found in this study area (Figs. 7 and 8). Similar sharp zonation boundaries (where rapid species turnover occurs) and low numbers of species of megafauna have been reported in OMZs off of Mexico and California (Levin, 2003). Although the OMZ is not truly hypoxic ($<0.50\,\mathrm{ml\,O_2\,l^{-1}}$), it appears low oxygen conditions are also influencing communities of active scavengers in Hawaii. Temperature is the other major environmental parameter that changes rapidly with depth that may contribute to zonation between 500 and 1000 m. The thermocline, however, is somewhat shallower (80–600 m) than the faunal break, suggesting that the role of temperature in affecting zonation boundaries (if any at all) is secondary to that of oxygen. A better understanding of the influence of environmental gradients on this zonation boundary is hindered by sampling resolution—deployments would ideally be spaced closely (≤100 m apart) at these depths. Struhsaker (1973) did sample the Hawaiian ichthyofauna from 61 to 869 m in high vertical resolution and found lowest species richness between 700 and 869 m, also coinciding with the OMZ.

Factors controlling the lower-slope/upper rise (1500–3000 m) and abyssal (≥4000 m) zones are not as clear. Carney (2005) speculates that pressure barriers are encountered at 500–1000 and 2000–3000 m for vertical larval dispersal. If these pressure limits are real, they align loosely with the upper boundaries of our mid-slope and abyssal zones and may at least partially explain why distinct species assemblages occur in these zones. Separation of the abyssal zone can also be rationalized from a food availability perspective over evolutionary time scales. The abyssal plains can be generalized as being a relatively food-deprived environment in comparison to other areas of continental margins. Consequently, some taxa are likely to have become specialized to extreme food limitation (Smith et al., 2008), resulting in a fauna particular to the abyssal plains.

Limited availability of primary production data constrained our investigation of depth zonation. Differences in scavenger community composition may be linked to spatial, seasonal, and/or interannual variation in primary production due to changing input to the benthos as a food source. The present study was conducted over 18 months and spanned a large geographic area—our data may be biased as a result. Seasonal pulses in primary production and carbon flux have been identified (although no correlation has been found between the two processes) at Station ALOHA (Karl et al., 1996) and a response in sediment community respiration rate to seasonality in deep-sea carbon export has been observed there as well (Smith et al., 2002). Drazen (2002), however, concluded that the nutritional condition for some scavenging fishes (*C. acrolepis*, *C. armatus*, and *C. yaquinae*) is not affected by seasonality in carbon export to the seafloor off the California coast, where extreme seasonal variations exist in surface production and particle flux. This finding implies that within the Hawaiian Islands, where seasonal fluctuations are much weaker, scavenger ecology is unlikely to be affected greatly by particle flux.

4.3. Bathymetric trends in abundance

Low maximum numbers and long first arrival times found here (Tables 2 and 3) suggest a lower abundance of scavenging fish in the Hawaiian Islands compared to the NE Atlantic (though there is little overlap in species), where the majority of baited-camera studies have been performed. It is worth noting that this study incorporated slightly larger quantities of bait than work in the NE Atlantic, however, if abundance was affected by bait quantity, more bait would result in an overestimate. Scavenger abundance has been postulated to be affected in part by overlying primary production because of an indirect bottom-up control of food availability reaching the seafloor (Priede et al., 1994; Jansen et al., 2000). If this is true, it may explain why scavenging fish arrive slower and in lower numbers in the oligotrophic tropical regime where the Hawaiian Islands are situated.

A logarithmic decline with depth was observed for relative scavenger abundance (all taxa combined, Fig. 5), in accord with findings of Collins et al. (2005) from the NE Atlantic. Increased scavenger abundance at shallower depths was mainly the result of high numbers of decapod crustaceans found between 250 and 1000 m. It is important to recognize that our interpretations rely on n_{max}, which is a relative proxy for abundance that measures the maximum number present at bait at one instance. Whether n_{max} can be used to index actual abundance, or population density, has been a matter of debate. Ellis and Demartini (1994) and Willis et al. (2000) have demonstrated significant correlation between n_{max} (from baited video cameras) and catch per unit effort (CPUE) of multiple shallow-water fish species in Hawaii and New Zealand, concluding that maximum number can be used as an accurate index of abundance. Conversely, Priede and Merrett (1996, 1998) have found no significant relationship between n_{max} (from baited camera) and trawl abundance in the NE Atlantic at abyssal depths, and have

even suggested a negative correlation between n_{max} and fish abundance. From the standpoint of optimal foraging theory, low fish densities are found where food supply is scarce; however, more individuals arrive to bait to utilize a limited resource due to lack of alternative sources of food.

The absence of scavenging teleosts at 500 m noticed in this study is of considerable interest as they were observed at all other sampling depths. In reality scavenging teleosts are probably not completely absent at 500 m, but reduced in density. Two scavenging teleost species (*Spheroides pachygaster* and *Bathyuroconger* sp.) have been observed from bait stations in the Hawaiian Islands at slightly greater depths around 650 m (Smith et al., unpublished data), albeit very infrequently and in very low abundances/long arrival times. Diminished scavenging teleost presence at these depths may result from the sharp gradient in $[O_2]$ at these depths (Fig. 7) in conjunction with competition/predation from larger scavenging sharks, which are most abundant between 500 and 1000 m (Table 2).

Deficiencies in current data for several deployments and measured swimming speeds undoubtedly restricted the accuracy of t_0-derived population estimates. Of perhaps greater limitation were the long times of first arrivals encountered for most teleosts (60% of t_0's >2 h), potentially leading to density underestimation. The inverse-square model is hypersensitive at short arrival times and insensitive at longer first arrival times. For example, a difference between $t_0 = 5$ and 10 min (at $V_f = V_w = 0.050 \, \text{m s}^{-1}$) equates to a difference in density estimate of over 5000 fish km^{-2} while a difference between $t_0 = 200$ and 230 min is 1 fish km^{-2}. Consequently, results for several scavenging fish yielded $\leqslant 1$ fish km^{-2} (Table 3).

4.4. Bathymetric trends in fish size

Our findings of significant size differences with depth for some scavenging species (*S. parasitica* and *S. brevidorsalis*) and not others (*E. carlhubbsi* and *Histibranchus* sp.) suggest that the "bigger-deeper" trend cannot be generalized to apply to all scavenging fish. Additional studies in the Atlantic and Mediterranean have shown that some scavenging fish, such as *C. armatus*, increase in size (King et al., 2006) with depth, while others, like *Chalinura mediterranea*, do not (Jones et al., 2003). A surprising discovery of our size analyses was the "*smaller*-deeper" phenomenon—previously unreported for any scavenging fish—observed for *S. parasitica*. This beckons the question as whether it is truly a scavenger, but stomach content analysis (Anderson, 2005) and jaw/dental morphology (Robins and Robins, 1989) indicate that it is. It is difficult to use these preliminary data to postulate why *S. parasitica* would display this trend. Because the shallower depth (where larger individuals were found) for this species included only 1 deployment, it is possible that the size difference between depths may have resulted from horizontal rather than vertical location. Also worth noting is that for each species our size analyses are confined to a comparison of two extreme depths as opposed to examining a depth spectrum. As a result, any information

on what is occurring in the middle of a species vertical range is missed. Future work should be directed to exploring depths in between those explored in this study to corroborate the results presented here.

Size–depth trends have been identified and found to be undetectable for the same species, depending on the study. Baited camera length determinations for *S. kaupi* and *A. rostrata* displayed no depth trends (King et al., 2006), while trawl samples of the same species showed significant increase in individual biomass with depth (Collins et al., 2005). These conflicting results imply that intraspecific size–depth trends may be biased by sampling effort and methodology. For instance Collins et al. caught orders of magnitude more small specimens (mean mass by haul 5–10 g individual^{-1}) of both *S. kaupi* and *A. rostrata* by trawl than were ever observed by King et al. at bait stations (calculated mean wet weight 160 and 1090 g individual^{-1}, respectively). It is likely that these smaller individuals were juveniles. Absence of juvenile scavengers at baited cameras has been documented and may reflect their aversion to light (Raymond and Widder, 2007), a non-scavenging feeding mode at small size or early age (Drazen et al., 2001; Wagner, 2003), or the active avoidance of a location where large predators congregate. The possibility of avoidance of smaller size classes presents a disadvantage when baited cameras are used to address the size–depth relationships for scavengers.

4.5. Scavenger–scavenger interaction

Interactions between deep-sea animals attracted to baited cameras have been proposed before. In the Porcupine Seabight, declines in scavenger crab (*Mundiopsis crassa*) abundance were attributed to predation by the octopus *Benthoctopus* sp., although the octopus itself was never observed to directly utilize the bait (Kemp et al., 2006). Barry and Drazen (2007) also noted an inverse relationship in abundance between *Benthoctopus* sp. and fishes (zoarcids and an ophidiid). If interactions of any form do occur between scavengers at bait stations, they may influence first arrival times and affect density estimates derived from the inverse-square model (Priede et al., 1990) widely applied in baited camera literature. For example, in this study the presence of *Neolithodes* sp. may deter the competing scavenger *S. affinis* from attending to bait (despite already having arrived), overestimating t_0 and in turn underestimating animal density. Scavenger behavior, evaluated at the species level, should therefore be taken into account when population density based on t_0 is modeled.

In conclusion, the results presented here are the first description of scavenging communities in the Hawaiian Islands and offer the first survey of deep-sea fauna below 2000 m in over a century. This research has tentatively documented species new to the Hawaiian archipelago, extended known vertical ranges of some species, and provided length–frequency data previously not published for some species. In addition, this work represents the first statistical analysis of depth zonation and bathymetric trends in scavenger ecology in the region and contributes

to the very scant number of studies on zonation performed in the tropics. The scavenging fauna of the Hawaiian Islands is partitioned vertically, marked by compositional homogeneity within four faunal zones and rapid species turnover at transitions between boundaries: upper slope (250–500 m), mid-slope (1000 m), lower slope/upper rise (2200–3000 m), and abyssal ($\geqslant$4000 m). The presence of a major faunal break at the 500–1000 m transition coinciding with the location of the OMZ implies a response of the scavenging community to low [O_2] and reinforces the concept that zonation arises in part as a reaction to environmental parameters that change with depth. Knowledge on depth zonation and scavenger abundance gained may help guide future management of marine protected areas and assist in the conservation and preservation of living marine resources. This study has clearly demonstrated the ability of baited cameras to supplement information on deep-sea megafaunal communities where other sampling methods are not feasible because of either cost or terrain.

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