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High densities and depth-associated changes of epibenthic megafauna along the Aleutian margin from 2000–4200 m

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The Aleutian margin is a dynamic environment underlying a productive coastal ocean and subject to frequent tectonic disturbance. In July 2004, we used over 500 individual bottom images from towed camera transects to investigate patterns of epibenthic megafaunal density and community composition on the contiguous Aleutian margin (53°N 163°W) at depths of 2000 m, 3200 m and 4200 m. We also examined the influence of vertical isolation on the megafaunal assemblage across a topographic rise at 3200 m, located 30 km from the main margin and elevated 800 m above the surrounding seafloor. In comparison to previous reports from bathyal and abyssal depths, megafaunal densities along the Aleutian margin were remarkably high, averaging 5.38 ± 0.43 (mean ± 1 standard error), 0.32 ± 0.02 to 0.43 ± 0.03 and 0.27 ± 0.01 individuals m^{-2} at 2000 m, 3200 m and 4200 m, respectively. Diversity at 2000 m was elevated by 15–30% over the deeper sites (3200–4200 m) depending on the metric, while evenness was depressed by ~10%. Levels of richness and evenness were similar among the three deeper sites. Echinoderms were the most abundant phylum at each depth as ophiuroids accounted for 89% of individuals in photographs at 2000 m, echinoids were dominant at 3200 m (39%), and holothurians dominated at 4200 m (47%). We observed a 26% reduction in megafaunal density across the summit of the topographic rise relative to that documented on the continental slope at the same depth; however, the two communities at 3200 m were very similar in composition. Together, these data support the modified 'archibenthal zone of transition' framework for slope community patterns with distinct communities along the middle and lower slope (the upper slope was not evaluated here). This study fills a geographical gap by providing baseline information for a relatively pristine, high-latitude, deep-sea benthic ecosystem. As pressures grow for drilling, fishing and mining on high-latitude margins, such data can serve as a reference point for much-needed studies on the ecology, long-term dynamics, and anthropogenically induced change of these habitats.

Keywords: Aleutian margin, megafauna, community composition, deep-sea photographs, density, diversity, archibenthal zone of transition, TowCam, Unimak, echinodermata

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INTRODUCTION

High-latitude continental margins such as the Aleutian margin in the North Pacific Ocean often lay beneath productive surface waters influenced by strong seasonality (Larrance, 1971). As such, the deep-sea fauna within these environments have the potential to be influential in the oceanic carbon cycle (Rex *et al.*, 2000), exploited for the harvest of natural resources (Smith *et al.*, 2008a), and subject to distinct faunal shifts related to climate fluctuations (Ruhl & Smith Jr, 2004). We examined community patterns of the epibenthic megafauna along the Aleutian margin acknowledging several questions related to latitudinal and bathymetric expectations, as well as recognizing the mosaic of deep-sea environments within the region (Rathburn *et al.*, in press). These fauna play important roles in nutrient cycling and trophic pathways (Ruhl & Smith Jr, 2004), bioturbation (Dayton & Hessler, 1972) and habitat provision (Levin *et al.*, 2001a), and this study offers valuable baseline data for deep-sea megafaunal communities of the Aleutian margin in the far northern Pacific.

Decrease in species diversity with increasing latitude is a predominant biogeographical pattern identified in terrestrial and marine ecosystems (Willig *et al.*, 2003). Even in the deep sea, where there is greater uniformity among benthic habitats in temperature and energy flux, deep-sea taxa such as the Gastropoda, Bivalvia and Isopoda demonstrate inverse latitude-diversity relationships (Rex *et al.*, 1993, 2000). For instance, isolated environments like the high-latitude Norwegian Sea can be sites of high abundance but low diversity (Grassle, 1989). Because many high-latitude slopes lie underneath productive coastal seas, examples like those from the Norwegian Sea are thought to reflect the negative relationship between density/standing biomass and diversity in highly productive systems (see Levin *et al.*, 2001b and references therein). However, recent exploration in the Weddell Sea of Antarctica between 800 and 6000 m

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has revealed an unexpected wealth of species richness and diversity among deep-sea invertebrates (Brandt *et al.*, 2007). This finding challenges the paradigm of depressed diversity in productive, high-latitude environments. Thus, questions remain about the character of high-latitude, deep-sea biota including the megafauna.

For deep-sea megafauna, there are also a number of expectations regarding depth-related density and assemblage trends for slope communities. In their meta-analysis of deep-sea density and biomass patterns, Rex *et al.* (2006) found significant and relatively predictable decreases in megafaunal abundances with depths from 200–5500 m. In addition to density gradients, continental margins are also zones of faunal transition. Carney (2005) reviewed the evidence for depth zonation globally, and listed many of the factors thought to restrict individual species and specific assemblages to particular depth bands. These included pressure physiology, food availability, temperature, oxygen levels, and transport of larvae. Based on these factors, Carney (2005) modified the concept of the 'archibenthal zone of transition' of Menzies *et al.* (1973) and proposed a three-transition model for continental slopes. In this simplified version, slope species can be divided into three groups: upper boundary biota (UBB), interboundary biota (IBB) and lower boundary biota (LBB).

Based on global patterns, we expected the Aleutian margin to have higher density and lower diversity than less productive areas. We also expected to see some changes in community structure across depths, owing to changes in pressure, dissolution rates or geomorphology. However, we anticipated dramatically different communities between the slope at 3200 m and a topographic rise at the same depth due to vertical isolation across the rise summit. Furthermore, we expected that depth-related changes in density might be dampened due to a release from food limitation that could result from high regional productivity, oxygen depletion along the slope (Helly & Levin, 2004; Paulmier & Ruiz-Pino, in press) or disturbance (see directly below). If true, these results would suggest that the Aleutian margin is poorly described by the modified 'archibenthal zone of transition' (Carney, 2005).

Besides latitude- and depth-associated influences, the Aleutian margin fauna may also be significantly affected by disturbance, particularly tectonic activity, as the Aleutian margin is adjacent to a subducting trench. Rathburn *et al.* (in press) documented a suite of heterogeneous environments that could affect faunal patterns. These features included deeply incised canyons along the upper slope, uplifted blocks at mid-slope depths that collect sediment from shallower depths, and a lower slope defined by a highly faulted sediment prism. The discovery of methane seeps along the central Aleutian margin (Levin & Mendoza, 2007), as well as the dominance of crustaceans, rather than polychaetes, among the macrofauna also suggest that disturbance could have a significant effect on the biological communities in this region (Rathburn *et al.*, in press). Within the Aleutian Trench at 7300 m, Jumars & Hessler (1976) found a dense macrofaunal community with low species diversity, and concluded that disturbance (sediment instability), rather than a productivity/diversity relationship, was likely responsible for this observation. In particular, this region of the Aleutian margin has been a focus of study because this sector has been proposed as the site of a submarine slide that caused the devastating 1946 tsunami that had lethal effects in both Alaska and Hawaii (Fryer *et al.*, 2004). Based on GLORIA imagery, a large elevated (800 m) feature south of the slope was identified as a potential toe of the 1946 slide. However, recent analyses of multibeam data and samples taken during 'Jason II' dives (from the same cruise we base our dataset on) showed that the feature in the study area identified from previous GLORIA images as the 'Ugamak Slide' (Fryer *et al.*, 2004) was not a slide triggered by the 1946 earthquake. Rather than a 50-km scale disturbance event, the feature was a fault-bounded block (an uplifted basement high we refer to as a topographic rise) located within the main Aleutian terrace basin. With these processes in mind, we also considered the role of disturbance in structuring the Aleutian margin megafauna, particularly across the summit of the false 'slide toe' where vertical isolation was an issue (hereafter referred to as a topographic rise).

The deep megafauna are difficult to sample quantitatively given their seclusion, density and mobility. As such, a consensus has developed for the use of seabed photographs to explore the abundance and diversity of megafauna in the deep sea (Rice *et al.*, 1982; Fujita & Ohta, 1990; Gage & Tyler, 1999; Smith & Rumohr, 2005). Here, we present quantitative data generated from photo-transects on the community characteristics of megafauna along the Aleutian margin south of Unimak Island, AK. Specific questions addressed for megafauna included: (1) what are the density and diversity of the Aleutian margin megafauna from 2000–4200 m, and how do these measures compare with other deep-sea communities across biogeographic scales?;(2) do changes in the megafaunal assemblage with increasing depth support current slope transition models?; and (3) does the megafaunal community on an isolated topographic rise at 3200 m differ from that on the nearby (~30 km) continental slope at the same depth, and in general, what role does disturbance have in driving community patterns along the Aleutian margin?

MATERIALS AND METHODS

An interdisciplinary cruise to examine the Aleutian margin for evidence of large-scale disturbance and document an unexplored region of the sea floor took place aboard the RV 'Roger Revelle' during July 2004 (Rathburn *et al.*, in press). The cruise utilized the ROV 'Jason II', a Kongsberg Simrad seafloor mapping system, and a towed camera array to examine bathyal seafloor stations along Unimak Island (53°N 163°W). Bottom photographs taken with the towed camera were advantageous both as reconnaissance for planning 'Jason II' dives, and to document the megafaunal communities of this region (operationally defined as the organisms large enough to be visible in seabed photographs; Gage & Tyler, 1999). It is within this larger experimental context that we present our megafaunal observations.

Seabed photographs were obtained between July 12 and July 19, 2004, from four transects over the Aleutian margin: along the continental slope at 2000 m and 3200 m, across the summit of a topographic rise at 3200 m that was elevated ~800 m above the abyssal sea floor (not defined as a seamount since it was elevated < 1 km above the surrounding seafloor), and over the abyssal plain terrace at 4200 m (Table 1; Figure 1). Photo-transects were made using the Woods Hole Oceanographic Institution's TowCam (Fornari, 2003). This towed camera system consisted of a downward-facing, internally recording digital camera with two oblique strobes. It also

Table 1. Logistic and environmental summaries of TowCam survey transects across the Aleutian margin.

Feature Traversed	**Slope**	**Slope**	**Topographic Rise**	**Abyssal Plain**
Depth Range (m)	**1904–2016**	**3168–3378**	**3162–3348**	**4235–4238**
Date (Tow Start)	July, 16 2004	July, 16 2004	July, 12 2004	July, 19 2004
Start Latitude	N 53°40.7684′	N 53°30.0458′	N 53°17.8995′	N 53°25.0000′
Start Longitude	W 163°22.4380′	W 163°25.6481′	W 164°04.0006′	W 163°19.9980′
Stop Latitude	N 53°41.4281′	N 53°32.0867′	N 53°17.8995′	N 53°26.0141′
Stop Longitude	W 163°23.5618′	W 163°26.1127′	W 164°00.7294′	W 163°21.4541′
Transect Length (km)	9.0	9.8	10.2	7.2
Seabed Photographs (#)	1800	1800	1750	1200
Photographs Analyzed (#)	130	105	153	120
Mean Photograph Area (m^2)	12.45	19.16	15.00	17.35
Bottom Area Surveyed (m^2)	1618.50	2011.80	2295.00	2082.00
T(°C)	1.96	1.47	1.49	1.49
Salinity	34.57	34.67	34.67	34.69
Oxygen (ml l^{-1})	1.11	2.51	2.72	3.02
Bottom Type	100% Soft-sediment	88% Soft-sediment, 12% Rocky	100% Soft-sediment	100% Soft-sediment

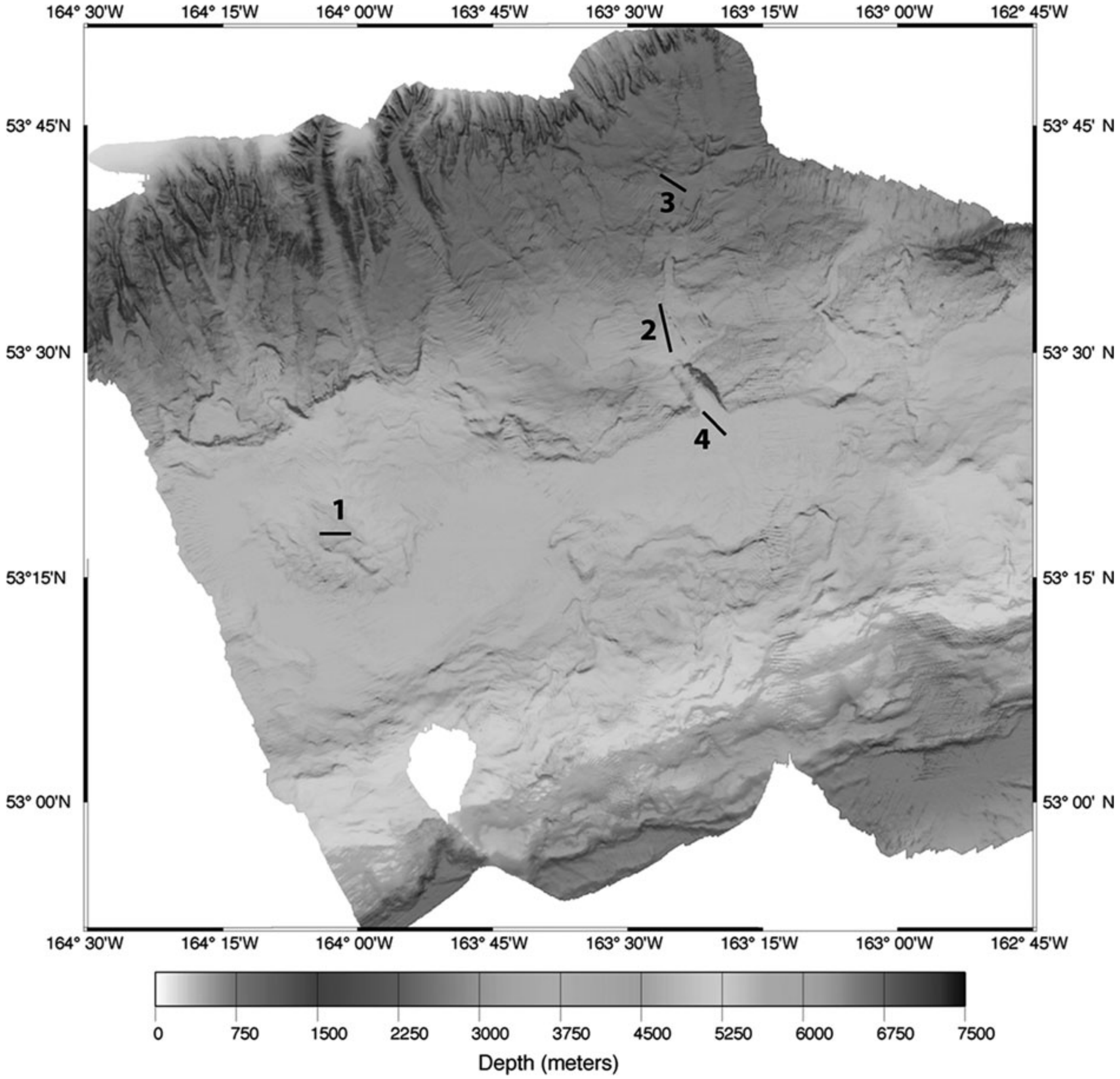

Fig. 1. Locations of photo-transects along the Aleutian margin captured via TowCam. In the order they were conducted, photograph samples covered a deep-sea underwater topographic rise at 3200 m (1), along the continental slope at 3200 m and 2000 m (2 and 3, respectively), and over the abyssal plain terrace at 4200 m (4). See Rathburn *et al.* (in press) for detailed cruise maps.

included two 5.0 l Niskin bottles as well as a CTD to record water properties. TowCam was towed from the ship using coaxial CTD sea cable, therefore allowing an operator to 'fly' the system above the bottom using forward and downward facing sonar to monitor depth and altitude. The instrument produced 3.3 megapixel digital images of the bottom that could be used for investigating megafaunal community composition. Each tow lasted approximately 4 hours from deployment to recovery, and the system was set to record seabed photographs every 10 seconds once the system reached the bottom. Bottom transects were between 7.2 and 10.2 km in length, and between 1200 and 1800 bottom photographs were captured during each tow (Table 1).

Following system recovery, digital bottom photographs were downloaded onto a laptop computer, and imported into Adobe Photoshop 5.0 for analysis. We selected photographs for analysis based upon two conditions: first, up to six serial photos could overlap the same seafloor, and therefore we only analysed every 8-12th (randomly determined) photograph taken by TowCam to quantify community composition. Second, even with the shipboard controls and real-time flight information, it was not always possible to maintain the altitude of the system above the bottom. Therefore, we only analysed photographs taken at 3–5 m above the bottom to help standardize photograph area and resolution (586–352 pixels m^{-1}). As a result, 100–200 photographs were available for analyses from each transect. Each image we selected was divided into a 3×3 grid, and each grid cell was enlarged (300% zoom) to aid in identification. Organisms were classified to the lowest taxonomic level possible and entered into an Excel database. Identification was aided by comparisons to specimens collected during 'Jason II' dives as well as consultations with taxonomic experts. Using bottom features such as holes and man-made debris, we concluded that our resolution was approximately 2 cm. Using the system's altitude we calculated the area of visible bottom using a conversion provided by TowCam's developers: photograph area = 1.02*altitude^2, and megafaunal densities were then estimated.

We investigated differences in megafaunal densities (total and broken down by phyla, class or order; see Figure 2 for representative megafaunal images) by Kruskal–Wallis tests on untransformed data, in which site was considered fixed. F_{max} tests revealed significant heteroscedasticity in densities ($\alpha = 0.05$) for the majority of the taxa, and data transformations failed to reduce differences in variances among groups.

We examined patterns of species diversity among sites by computing the following measures for each individual photo: S, the minimum number of species observed; $ES_{(20)}$, the minimum species richness rarefied to 20 individuals; H', the minimum Shannon–Weiner diversity index ($\log_e$); and J', the minimum Pielou's evenness measure (PRIMER 5.2.2 software; PRIMER-E Ltd; Clark & Gorley, 2001). Since identification was not typically made to the species level, we only calculated minimum diversity indices for photographs. Differences among sites for each of these measures were examined by ANOVAs conducted on raw data (as well as Fisher's post-hoc comparisons in cases with statistically significant results), as variances were stable among groups. All univariate tests were conducted using StatView 5.0.1 software (SAS Institute Inc).

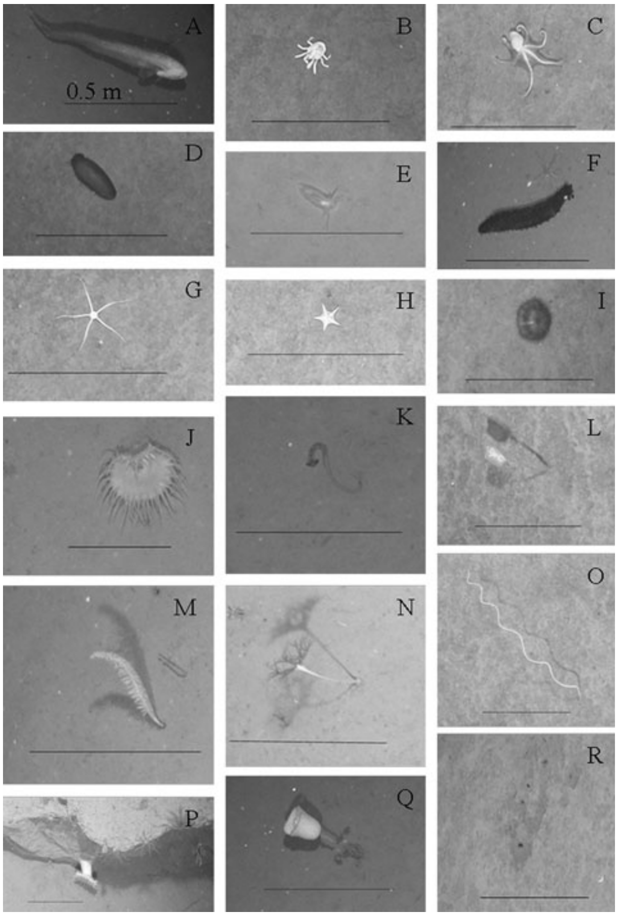

Fig. 2. Images of common Aleutian margin taxa used in community analyses. (A) Class Actinopterygii; (B) order Decapoda; (C) order Octopoda; (D–F) class Holothuroidea; (G) class Ophiuroidea; (H) class Asteroidea; (I) class Echinoidea; (J) order Actinaria; (K) class Enteropneusta; (L) class Ascidiacea; (M–N) order Pennatulacea; (O) order Antipatharia; (P) rocky bottom covered by megafauna, including the class Crinoidea; (Q) phylum Porifera; (R) lebensspuren.

We also analysed similarities and differences among megafaunal communities along each transect using non-metric multidimensional scaling (MDS), based on Bray–Curtis similarity indices among all individual photos (4th root-transformed data). Pairwise comparisons between transects were conducted with analysis of similarity (ANOSIM) and similarity (or dissimilarity) percentages (SIMPER) using PRIMER 5.2.2 software. Photographs revealed three distinct bottom types along the 3200 m slope transect: completely soft-sediment (N = 88), sediment-outcrop mix (N = 6) and completely rocky outcrop (N = 11). Therefore, we also examined how these differences in bottom type affected overall megafaunal density (using Kruskal–Wallis), as well as similarities and differences among megafaunal communities (using MDS, ANOSIM and SIMPER). Because each statistical test applied to separate and easily distinguishable hypotheses, we made no corrections to experiment-wise alpha during this study (Hurlbert & Lombardi, 2003).

RESULTS

Bottom temperature and salinity varied little among depths; the average transect values were 1.5–2.0°C for temperature and 34.6–34.7 for salinity. Oxygen levels ranged from 1.11 ml l^{-1} at 2000 m to 3.02 ml l^{-1} at 4200 m, reflecting the presence of midwater hypoxia (<1.42 ml l^{-1}) and a shallower oxygen minimum zone (<0.5 ml l^{-1}) along the margin (Table 1) (see also: Helly & Levin, 2004; Paulmier & Ruiz-Pino, in press). Based on TowCam images, 100% of the seafloor along the slope at 2000 m, topographic rise summit, and abyssal plain was soft-sediment bottom. The slope at 3200 was 88% soft-sediment bottom, while rocky bottom was observed covering 12% of the seafloor (Table 1).

Lebensspuren in photographs consisted of burrows, mounds and tracks (e.g. Figure 2R), and the abundance of these animal traces was statistically different among transects (df = 3; H = 327.362; $P < 0.001$). Highest densities of lebensspuren were recorded at 2000 m (16.42 traces m^{-2}), while the slope at 3200 m and abyssal plain had one-third to one-fifth the number of traces that we observed along the 2000 m transect, respectively (Table 2). We observed the lowest densities of lebensspuren over the summit of the topographic rise (0.91 traces m^{-2}).

Representatives of 8 phyla and a minimum of 83 species were observed in the seabed photographs. These included the Porifera, Cnidaria and Echiura (only along the slope sites), Arthropoda, Mollusca, Echinodermata and

Table 2. Mean densities (with standard error) and proportional representation of megafauna observed during TowCam surveys along the Aleutian margin (slope at 2000 m, slope at 3200 m, topographic rise at 3200 m and abyssal plain at 4200 m). Statistical probabilities among transects were based on Kruskal–Wallis tests, and are included for each taxon (as well as total megafauna, phyla and lebensspuren).

Taxonomic Group	Slope 2000 m		Slope 3200 m		Topographic Rise 3200 m		Abyssal Plain 4200 m		Kruskal-Wallis prob.
	Ave. Den (SE) (# m^{-2})	Prop. of total	Ave. Den (SE) (# m^{-2})	Prop. of total	Ave. Den (SE) (# m^{-2})	Prop. of total	Ave. Den (SE) (# m^{-2})	Prop. of total	
TOTAL MEGAFAUNA	5.380 (0.427)		0.432 (0.029)		0.318 (0.017)		0.265 (0.011)		**<0.001**
PORIFERA									**<0.001**
Unid. Porifera	0.010 (0.004)	0.002	0.020 (0.004)	0.046	0.001 (0.001)	0.001	0.021 (0.003)	0.079	<0.001
CNIDARIA									**<0.001**
Anthozoa									
Hexacorallia									
Actinaria	0.006 (0.002)	0.001	0.034 (0.005)	0.079	0.023 (0.004)	0.072	0.030 (0.004)	0.113	<0.001
Antipatharia	0.004 (0.002)	0.001	0.002 (0.001)	0.005	0.014 (0.003)	0.044	0 (0)	0.000	0.069
Unid. Hexacorallia	0.018 (0.004)	0.003	0.004 (0.002)	0.009	0.001 (0.001)	0.001	0.042 (0.004)	0.158	<0.001
Octocorallia									
Pennatulacea	0.338 (0.032)	0.063	0.007 (0.002)	0.016	0.009 (0.002)	0.028	0.001 (0.001)	0.004	<0.001
Unid. Octocorallia	0.036 (0.008)	0.007	0 (0)	0.000	0 (0)	0.000	0 (0)	0.000	0.001
ECHIURA									**0.778**
Unid. Echiura	0.006 (0.002)	0.001	0.001 (0.001)	0.001	0 (0)	0.000	0 (0)	0.000	0.778
ARTHROPODA									**0.001**
Pycnogonida	0.001 (0.001)	0.001	0 (0)	0.000	0.003 (0.001)	0.009	0 (0)	0.000	0.959
Crustacea									
Malacostraca									
Decapoda	0.037 (0.008)	0.007	0.004 (0.001)	0.009	0.002 (0.001)	0.006	0.002 (0.001)	0.008	0.001
MOLLUSCA									**0.16**
Gastropoda	0.016 (0.004)	0.003	0 (0)	0.000	0 (0)	0.000	0 (0)	0.000	0.109
Cephalopoda									
Coleoidea									
Octopoda	0 (0)	0.000	0.001 (0.001)	0.002	0.002 (0.002)	0.006	0.001 (0.001)	0.004	0.997
ECHINODERMATA									**<0.001**
Crinoidea	0.033 (0.005)	0.006	0.036 (0.015)	0.083	0 (0)	0.000	0.007 (0.002)	0.026	0.001
Stelleroidea									
Ophiuroidea	4.767 (0.406)	0.886	0.090 (0.016)	0.208	0.074 (0.008)	0.233	0 (0)	0.000	<0.001
Asteroidea	0.016 (0.004)	0.003	0.003 (0.001)	0.007	0.003 (0.001)	0.009	0.002 (0.001)	0.008	0.338
Echinoidea	0.016 (0.004)	0.003	0.170 (0.013)	0.394	0.127 (0.010)	0.399	0.014 (0.002)	0.053	<0.001
Holothuroidea									
Apodida	0 (0)	0.000	0.004 (0.003)	0.009	0.003 (0.001)	0.009	0.049 (0.005)	0.185	<0.001
Elasipodida	0.057 (0.008)	0.011	0.052 (0.007)	0.120	0.021 (0.003)	0.066	0.076 (0.007)	0.287	<0.001
HEMICHORDATA									**0.601**
Enteropneusta	0 (0)	0.000	0 (0)	0.000	0 (0)	0.000	0.005 (0.002)	0.019	0.601
CHORDATA									**0.001**
Urochordata									
Ascidiacea	0.002 (0.001)	0.000	0 (0)	0.000	0.021 (0.003)	0.066	0.011 (0.002)	0.042	0.002
Vertebrata									
Osteichthyes									
Actinopterygii	0.017 (0.004)	0.023	0.006 (0.002)	0.014	0.013 (0.003)	0.041	0.004 (0.002)	0.019	0.205
LEBENSSPUREN	16.420 (1.272)		3.889 (0.270)		0.912 (0.054)		5.363 (0.259)		**<0.001**

Hemichordata (only on the abyssal plain) and Chordata (Table 2). Total megafaunal densities were significantly different among sites (df = 3; H = 252.492; $P < 0.001$), ranging from 5.38–0.27 (individuals m^{-2}) from shallowest to deepest. Also, densities of the Porifera (df = 3; H = 25.026; $P < 0.001$), Cnidaria (df = 3; H = 168.879; $P < 0.001$), Arthropoda (df = 3; H = 18.228; $P = 0.001$), Echinodermata (df = 3; H = 276.345; $P < 0.001$), and Chordata (df = 3; H = 19.767; $P = 0.001$) were significantly different among sites (Table 2). The Echinodermata were the dominant phylum along each site, making up 90.3%, 73.8%, 71.6%, and 55.9% of the megafauna over the slope at 2000 m, the slope at 3200 m, the topographic rise summit at 3200 m, and abyssal plain at 4200 m, respectively. Within the Echinodermata, dense beds of ophiuroids (88.6%) dominated at 2000 m, while echinoids (39.4–39.9%) and ophiuroids (20.8–23.3%) shared dominance at the 3200 m sites. Over the abyssal plain at 4200 m, soft-bodied megafauna belonging to the Holothuroidea (47.2%) and Actinaria (11.3%) were most abundant (see Table 2 for taxa-specific densities and statistical results).

There was a single peak in species richness (S; $F_{3.504} = 26.949$; $P < 0.001$), rarefied diversity ($ES_{(20)}$; $F_{3.504} = 53.388$; $P < 0.001$) and Shannon–Weiner diversity (H'; $F_{3.504} = 13.870$; $P < 0.001$), with highest values (≥20% greater) at the shallowest site (Figure 3). However, because of the high dominance of ophiuroids at 2000 m, evenness (J') was lowest (≥10% lower) at that site ($F_{3.504} = 345.933$; $P < 0.001$; Figure 3). Among the three sites at 3200–4200 m, there were some statistical differences in diversity measures based on Fisher's post-hoc analyses (see Figure 3), but these differences were generally small in magnitude (<5%) and there were no clear trends among sites or depths across the various diversity indices.

Megafaunal assemblages were distinct among depths, and ophiuroid densities accounted for the largest proportion of these differences (see: Table 3 for ANOSIM and SIMPER, Global R = 0.537; Figure 4 for MDS). The sites at 2000 m and 4200 m were most distinct from one another, while the two sites at 3200 appeared transitional between our minimum and maximum study depths (Figure 4). Nearly all pairwise comparisons indicated that the communities were well separated (Table 3). Only the slope at 3200 m and summit of the topographic rise showed little difference between megafaunal communities (R = 0.066), although total megafaunal densities were notably higher over the slope site (0.43 ± 0.03 versus 0.32 ± 0.02 individuals m^{-2}). Within-site heterogeneity ranged from ~40–60%. Surprisingly, the 3200-m slope site had the second highest within-group similarity despite the presence of soft- and hard-bottom seafloor (Table 3). This was predominately due to uniformly high echinoid counts within photographs taken from this site. Overall, taxa belonging to the Echinodermata were most important for measuring community similarity and dissimilarity along this continental margin, followed by the Pennatulacea (Table 3).

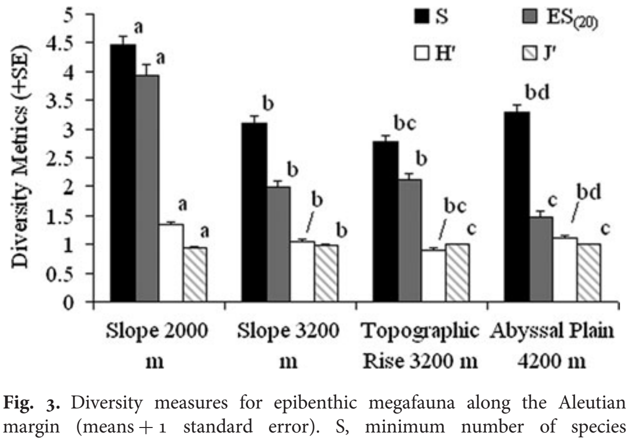

Fig. 3. Diversity measures for epibenthic megafauna along the Aleutian margin (means + 1 standard error). S, minimum number of species observed in each photograph; $ES_{(20)}$, minimum species richness rarefied to 20 individuals; H', minimum Shannon–Weiner diversity index ($\log_e$); J', minimum Pielou's evenness measure. Values of each metric that were not significantly different from one another among sites, based on Fisher's post-hoc tests, share the same letter (a–d).

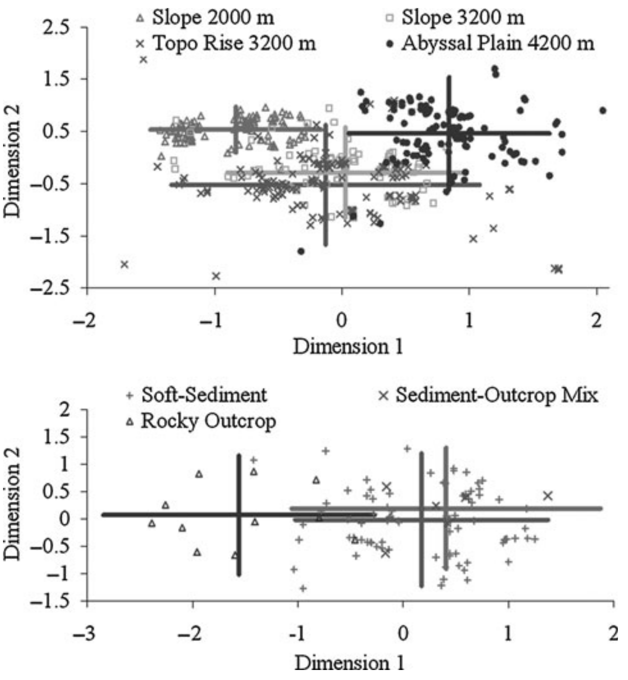

Fig. 4. Multidimensional scaling (MDS) plots of megafauna assemblages over: (A) the continental slope at 2000 m, the continental slope at 3200 m, a deep-sea topographic rise at 3200 m and the abyssal plain terrace at 4200 m; and (B) soft sediment, sediment-outcrop mixed and rocky outcrop bottoms at 3200 m. MDS stress = 0.17 and 0.21 for A and B, respectively. Each data point represents one photograph taken to document the epibenthic megafaunal community.

Among the three bottom types we observed over the slope at 3200 m, there were no statistical differences in megafauna abundances (df = 2; H = 5.290; $P = 0.071$), although the mean density was elevated ~2x over rocky outcrops (0.92 individuals m^{-2}) as compared to sediment-outcrop mix (0.40 individuals m^{-2}) and soft-sediment bottoms (0.37 individuals m^{-2}). Also, community composition appeared different among bottom types as ophiuroids and crinoids dominated the megafauna community over rocky outcrops, and as a result this habitat was distinct from both soft-sediment and sediment–outcrop mix bottoms (see: Table 3 for ANOSIM and SIMPER; Figure 4 for MDS). Conversely, multivariate tests indicated no meaningful difference between communities of soft-sediment and sediment–outcrops mix habitats (Table 3). Echinoids were most consistently observed over soft-sediment and sediment-outcrop mixed bottoms, along with elasipods (soft-sediment) and the Porifera (sediment–outcrop mix). All three habitats

Table 3. Comparisons of community structure among the four TowCam transect sites (the slope at 2000 m, the slope at 3200 m, across the summit of a topographic raise at 3200 m and the abyssal plain at 4200 m) as well as the three bottom types observed at 3200 m along the slope (soft-sediment, sediment–outcrop mix and rocky outcrop). Matrix entries within the upper right of each box include R-values and significance probabilities from ANOSIM analyses (global $R = 0.537$ and 0.446, respectively). Lower-left entries are pairwise dissimilarity percentages between groups (from SIMPER), including the three taxa most responsible for differences between groups. Entries along the matrices diagonals are within-group similarity percentages calculated by SIMPER. Similarity percentages are followed by the two taxa most consistently found (generally at high densities) in seabed photographs at each site or over each bottom type.

	Slope 2000 m	Slope 3200 m	Topo Rise 3200 m	Abyssal Plain 4200 m
Slope 2000 m	59.93% Ophiuroidea (61.50%) Pennatulacea (23.22%)	R = 0.752 0.001	R = 0.631 0.001	R = 0.828 0.001
Slope 3200 m	77.83% Ophiuroidea (28.54%) Pennatulacea (14.99%) Echinoidea (12.73%)	46.22% Echinoidea (57.22%) Elasipodida (15.04%)	R = 0.066 0.001	R = 0.489 0.001
Topo Rise 3200 m	78.76% Ophiuroidea (28.38%) Pennatulacea (15.47%) Echinoidea (11.35%)	60.10% Ophiuroidea (17.51%) Echinoidea (14.85%) Elasipodida (14.70%)	39.98% Echinoidea (55.89%) Ophiuroidea (25.74%)	R = 0.576 0.001
Abyssal Plain 4200 m	88.58% Ophiuroidea (31.42%) Pennatulacea (13.97%) Elasipodida (7.11%)	76.50% Echinoidea (19.38%) Elasipodida (12.32%) Apodida (11.72%)	84.46% Echinoidea (16.01%) Elasipodida (13.08) Ophiuroidea (11.89%)	41.06% Elasipodida (35.92%) Apodida (22.78%)

	Soft-Sediment	Sediment-Outcrop Mix	Rocky Outcrop
Soft-Sediment	50.80% Echinoidea (60.94%) Elasipodida (15.79%)	R = -0.33 0.057	R = 0.613 0.001
Sediment-Outcrop Mix	47.73% Porifera (20.11%) Elasipodida (18.87%) Ophiuroidea (17.14%)	47.58% Echinoidea (71.02%) Porifera (10.87%)	R = 0.68 0.002
Rocky Outcrop	73.86% Ophiuroidea (19.58%) Crinoidea (18.13%) Echinoidea (15.46%)	74.19% Ophiuroidea (18.15%) Crinoidea (17.52%) Echinoidea (15.45%)	51.07% Ophiuroidea (59.07%) Crinoidea (25.34%)

demonstrated comparable within-habitat similarities ranging between 47 and 51% (Table 3).

DISCUSSION

Our research is among the first to characterize bathyal megafaunal communities of the high-latitude North Pacific outside of ground fish and commercially valuable crustacean surveys (e.g. Drazen, 2007), recognizing the mosaic of habitats resulting from changes in depth, isolation and disturbance along the Aleutian margin. Examination of photo-transects along the continental slope at 2000 m and 3200 m, across the summit of a topographic rise at 3200 m, and over the abyssal plain terrace at 4200 m led to the following answers for the questions posed in the introduction:

What are the density and diversity of the Aleutian margin megafauna from 2000–4200 m, and how do these measures compare with other deep-sea communities across biogeographical scales? Benthic photographs revealed dense megafaunal assemblages (peaking at 5.38 individuals m^{-2}) at each depth we surveyed. Rex *et al.* (2006) reviewed > 100 reports of total megafaunal densities taken from non-reducing settings at bathyal and abyssal depths across all major ocean basins (200–5500 m). They were limited, however, by large spatial voids in published studies from much of the southern hemisphere (all latitudes), as well as relatively remote locations such as the northernmost Pacific Ocean (an approximately 12° latitude gap in their analysis). Increased spatial resolution in benthic density/biomass estimates is a requisite for fully understanding the global carbon cycle and exploring animal–habitat relationships in the deep sea (Rex *et al.*, 2006). Compared against their meta-analysis, the 2000-m Aleutian margin is one of the three most dense megafaunal communities ever sampled below 1000 m (Table 2) (for trends in the Atlantic Ocean, also see Levin & Gooday, 2003). Additionally, the densities observed at 3200 m on the slope and topographic rise were both greater than any previous value measured below 3000 m, while megafauna on the abyssal plain terrace (4200 m) represented the highest density recorded below 4000 m. Notably, macrofaunal densities along the Aleutian margin at comparable depths are also higher than in many other regions (Jumars & Hessler, 1976; Rathburn *et al.*, in press), and are even comparable to densities in sediments influenced by methane seepage (Levin & Mendoza, 2007).

There are several, likely co-occurring, explanations for above-average abundances of megafauna along this high-latitude margin. The subarctic sea south of Unimak Island is a region of high local productivity (Larrance, 1971; also evidenced by the oxygen profile we observed), and the relationship between high surface production and benthic biomass has been well documented for deep-sea fauna (Rowe, 1971; Ruhl *et al.*, 2008; Smith *et al.*, 2008b). Alternatively, pulsed seasonal blooms at high latitudes may decouple annual primary production from pelagic feeding and increase the export of organic material to the deep-sea benthos (Rowe, 1983). In highly seasonal, high-latitude environments this could allow more, or higher quality, phytodetritus to reach deep communities during episodic events such as spring blooms. Proximity to land (i.e. ice-melt runoff) may also contribute to episodic pulses of carbon.

Densities at 2000–4200 m also may have been elevated, particularly among the ophiuroids, due to an 'edge' effect associated with the midwater oxygen minimum zone and hypoxic conditions at depths shallower than 2000 m, as the Aleutian margin is defined by a relatively strong O_2 mimimum at ~1100 m depth (Levin, 2003; Paulmier & Ruiz-Pino, in press). Murty *et al.* (in press) observed an ophiuroid-dominated abundance peak along the Pakistan Margin at ~1100 m, and ascribed this to a strong oxygen minima that had its lower boundary near that same depth (maximum megafaunal densities were 2.7 individuals m^{-2} in that study). Although we did not sample on the Aleutian margin immediately below the boundary of the oxygen minimum zone (0.5 ml l^{-1}), a shallower zone of depleted oxygen could have excluded fauna and subsequently allowed an elevated flux of carbon to reach 2000–4200 m without aerobic restrictions on local metabolism at those depths (Levin *et al.*, 1991; Levin, 2003).

Our observation of maximal megafaunal diversity at 2000 m is consistent with a unimodal depth–diversity relationship found in fish, other megabenthos, and macrobenthos (Stuart *et al.*, 2003). The majority of these cross-slope transect analyses have yielded diversity maxima at 1500–2500 m (Levin *et al.*, 2001b; Carney, 2005). A number of factors have been invoked to explain this general pattern, including habitat heterogeneity, productivity gradients and null models related to vertical boundary constraints of species' depth-ranges (Levin *et al.*, 2001b). Despite limits on the taxonomic resolution of this study, our data allow us to comment on latitudinal or productivity-related diversity gradients. Although we observed a dense (productive) macrofaunal community, we also observed a much more evenly represented fauna (J′ ~1.0 at all depths) than Rex *et al.* (2000) reported for the Bivalvia, Gastropoda and Isopoda across all latitudes in the North Atlantic. Measures of minimum S and H′ for total megafauna along the Aleutian margin did fall within the range of values reported by Rex *et al.* (2000) for these same taxa near N53°. However, the minimum expected number of species rarefied to 20 individuals ($ES_{(20)}$: a metric standardized for sample size) ranged between 3.0 and 4.5, and these values are comparable to diversities reported by Levin *et al.* (2001a) for total *macro*fauna along the margins of Oman and Peru. Thus, the megafaunal community along the Aleutian margin (consisting of ≥83 species) appears to be relatively diverse despite high local abundances (at N53°).

We did observe a characteristic abundance–depth relationship in which average density decreased with depth following a negative power function ($r^2 = 0.93$): density = $9^*10^{14}(\text{depth})^{-4.33}$. Since we confined our analyses to megafauna at every depth, this also suggests an exponential decline in biomass along the Aleutian margin, as predicted by Rowe (1983) for continental slopes. Thus, a depth-related decline in density (and likely biomass) was not dampened along the Aleutian margin due to high productivity or disturbance as we had hypothesized. The Aleutian margin also appeared to be a typical continental margin in that we observed high dominance of ophiuroids at 2000 m. This was predictable given that many studies have reported dense beds of this taxon at bathyal depths from multiple ocean basins and latitudes (e.g. Fujita & Ohta, 1990; Murty *et al.*, in press).

Do changes in the megafaunal assemblage with increasing depth support current slope transition models? The Echinodermata dominated at all depths we surveyed, and were the key group for explaining community composition (Table 3). There was a clear shift from ophiuroids to echinoids to holothurians as depth increased from 2000 to 3200 to 4200 m (Table 3). Ophiuroids are tolerant of relatively low oxygen/low pH conditions (Levin, 2003) and this may explain their high dominance at the hypoxic 2000-m site. Alternatively, maintaining calcium carbonate shells or ossicles becomes more metabolically taxing with increasing hydrostatic pressure (Gooday, 2002). In the North Pacific, Peterson (1966) experimentally showed that the depth at which $CaCO_3$ rapidly decreased in sediments (lysocline) occurred between 3600 and 4000 m. This is another potential explanation for the shift from the heavily ossified ophiuroids and echinoids towards the soft-bodied holothurians at depths > 4000 m. The shift in taxa may also be indicative of changes in trophic or feeding mode strategies, with scavengers and suspension feeders on the upper and mid slope being replaced by deposit and suspension feeders along the lower slope and continental rise (Gage & Tyler, 1999). This would be consistent with the exponential decline we observed in megafaunal densities with depth, perhaps reflecting changes in food availability. The role of temperature in structuring deep-sea assemblages can also be considered (Carney, 2005); however, the static temperatures we observed during TowCam deployments at depths > 2000 m (Table 1) and strong zonation of fauna along this high-latitude continental margin (Figure 4) suggest that temperature was not a key driver of community patterns.

The faunal assemblages of continental margins generally transition across a series of depth sectors. Megafaunal assemblage structure along the Aleutian margin appeared to change dramatically with depth (Figure 4), although we only have true replicate depth data for 3200 m. We did observe a relatively high degree of cohesion among communities at 3200 m even when comparing photographs across large-scale (contiguous slope versus topographic rise) and small-scale (soft-sediment versus rocky outcrop bottom) habitat gradients at this single depth. These data are consistent with the modified framework for zonation along continental margins proposed by Carney (2005), with distinct communities along the middle (IBB) and lower slope (LBB) in addition to a separate abyssal megafaunal assemblage at 4200 m (Figure 4). Images shallower than 2000 m were not available to evaluate the presence of an UBB (or influence of the oxygen minimum zone boundary).

Does the megafaunal community on an isolated topographic rise at 3200 m differ from that on the nearby (~30 km) continental slope at the same depth, and in general, what role does disturbance have in driving community patterns along the Aleutian margin? When compared to photographs taken along the slope and abyssal plain, the megafaunal community at the summit of the topographic rise appeared similar to the community on the slope at 3200 m. Both sites at 3200 m appeared transitional between the shallowest and deepest sites (Figure 4). Topographically raised features such as seamounts are generally characterized by enhanced densities of suspension feeders, indicating the potential for higher food inputs or food fluxes (Genin, 1987). We did not observe this on the 3200-m rise; conversely, vertical isolation was associated with reduced megafaunal density across the summit of the topographic rise when compared to the continental slope at 3200 m (depressed by 26%). We expect this result was driven by the presence of outcropped bottom habitat along the slope, which supported ~2x higher megafaunal densities relative to soft-sediment bottom. Specifically, the Porifera, which were slightly depressed in density on outcropped bottoms as compared to soft-sediment bottoms on the slope site (by 0.1 individuals m^{-2}), and the Crinoidea, which were elevated on outcropped bottoms as compared to soft sediment bottoms on the slope site (by 0.3 individuals m^{-2}), represent suspension/filter feeding taxa that were greatly reduced on the topographic rise (Table 2). Even if currents were elevated around the topographic rise, the relative absence, compared to the slope site at 3200 m, of suitable hard substrate for attachment (Table 1) may have excluded the Porifera and Crinoidea from this site. However, we still observed a 12% decrease in total megafaunal densities on the topographic rise even when just comparing soft-sediment communities between the two sites. Across all taxa, only the Ascidiacea and Antipatharia had elevated densities across the summit site relative to the slope at 3200 m (Table 2).

The topographic rise summit appeared distinct from all other sites in having comparatively low lebensspuren densities (Table 2). Several large-scale or small-scale disturbance factors could have contributed to this, including: (1) strong topography-generated currents (Genin, 1987) that either limit the abundance of benthic fauna, or rework sediment to remove lebensspuren; or (2) predation pressure from the Osteichthyes over the topographic rise summit that may have reduced benthic faunal densities. The role of top-down regulation is only beginning to be explored in deep-sea communities (e.g. Micheli *et al.*, 2002), but the topographic rise transect was observed to have the second highest densities of fish (second to the 2000-m slope site), and the highest proportional abundance of fish (although there were no statistically significant differences among transects; Table 2).

Although the topographic rise was revealed to not be a major disturbance event, disturbance may still dramatically impact the Aleutian margin biota. During July, 2004, total organic carbon sampled during 'Jason II' dives at nearby stations was variable, ranging from low values of ~0.42% at the summit of the topographic rise to a high of ~2.2% along the slope at 2000 m, but without clear depth trends (Rathburn *et al.*, in press). Both Rathburn *et al.* (in press) and Jumars & Hessler (1976) suggested that disturbance caused by the vertical displacement of sediments could also influence depth gradients in organic matter input, and subsequently affect faunal patterns. While the impacts of this cannot be fully discounted in promoting elevated densities of megafauna at every depth we surveyed, the evidence is not clear. For instance, we did observe an order of magnitude decreased in megafaunal densities with depth, as well as changes in the Echinodermata that suggested a decrease in suspended food at the 4200-m site. Methane seeps (often exposed following slides) observed during 'Jason II' dives could provide another source of energy fuelling this deep-sea benthic food web and contributing to the high standing crop of megafauna (Levin & Mendoza, 2007). Although no seeps were observed in the TowCam photographs, they were reported within 5 km of the 3200 m photo-transect by Rathburn *et al.* (in press). Seep production might be incorporated by vagrant predators or scavengers and then moved off site (MacAvoy *et al.*, 2003).

Disturbance may have also contributed to the distinct UBB, LBB and abyssal communities we observed along the Aleutian margin. Rathburn *et al.* (in press) conducted geological assessments at the same depths we studied the megafauna via TowCam, and found that the upper slope was best described by sediment loss and canyons, while the lower slope was characterized as collecting most of the sediment lost from the upper slope. Unfortunately, our surveys were not designed to rigorously determine how much effect this had on the composition of the communities we observed at 2000 m, 3200 m and 4200 m.

CONCLUSIONS

Deep-sea sediments are among the most abundant habitats on Earth. Recently, it has been shown that communities in this environment at high latitudes can store huge amounts of diversity and represent significant ecological/evolutionary opportunity related to food-web structure and dynamics (Brandt *et al.*, 2007). Our investigation revealed a remarkably dense assemblage of megafauna over the Aleutian margin, with strong community shifts corresponding to the gradient in depth across the continental slope and likely influenced by mesoscale disturbance. Given the mounting pressure for offshore oil exploration of natural resources in the deep sea (Smith *et al.*, 2008a), as well as changing climate regimes and carbon fluxes in the North Pacific (Ruhl & Smith Jr, 2004; Ruhl *et al.*, 2008; Smith *et al.*, 2008b), there is a growing imperative to understand controls on megafaunal taxa regarding standing crops, temporal patterns (over seasonal and decadal scales), trophic relationships and roles in biogeochemical cycling.

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