



Rapid changes and long-term cycles in the benthic megafaunal community observed over 24 years in the abyssal northeast Pacific



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ARTICLE INFO

Article history:

Received 2 December 2013

Received in revised form 11 April 2014

Accepted 14 April 2014

Available online 20 April 2014

ABSTRACT

The abyssal seafloor community in the NE Pacific (Station M, ~4000 m depth) was studied between 2006 and 2012 using remotely operated vehicles (ROVs) as part of a continuing 24-year time-series study. New patterns continue to emerge showing that the deep-sea can be dynamic on short time scales, rather than static over long periods. In just over 2 years the community shifted from a sessile, suspension-feeding, sponge-dominated community to a mobile, detritus-feeding, sea cucumber-dominated assemblage. In 2006 megafaunal diversity (Simpson's Diversity Index, SDI) was high, yet the community was depauperate in terms of density compared to later periods. Over an 18-month period beginning in spring 2011, the densities of mobile organisms increased by nearly an order of magnitude while diversity decreased below 2006 levels. In late 2012 four sea cucumbers (two *Peniagone* spp., *Elpidia* sp. A, and *Scotoplanes globosa*) were at the highest densities recorded since investigations began at Station M in 1989. For a group of 10 echinoderms investigated over the entire study period, we saw evidence of a long-term cycle spanning 2 decades. These changes can be tied to a variable food supply originating in shallow water. Large variations over decadal-scales indicate that remote abyssal communities are dynamic and likely subject to impacts from anthropogenic changes like ocean warming, acidification, and pollution manifested in the upper ocean. The degree of dynamism indicates that one-time or short-term investigations are not sufficient for assessing biological community structure in conservation or exploitation studies in the deep sea.

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1. Introduction

Understanding the ecological dynamics of the deep sea, and especially the vast abyssal area covering 75% of seafloor (Ramirez-Llodra et al., 2011), will be increasingly necessary in order to assess the impacts of large-scale changes to the world ocean such as warming temperatures (Smith et al., 2009, 2013), acidification (Barry et al., 2013), mineral mining (Ramirez-Llodra et al., 2010), pollution (Paull et al., 2002), and anthropogenic debris (Schlining et al., 2013).

Most abyssal areas appear relatively homogenous and less disturbed by physical processes compared to continental shelves, submarine canyons, seamounts, hydrothermal vents, and other deep-sea habitats. Large-scale habitat disturbances like turbidity flows or mass wasting (Okey, 1997) are infrequent in abyssal areas. Near constant pressure, temperature, and oxygen levels, plus aphotic conditions, and the rarity of fast, sediment-eroding currents allow for relative seabed stability (Ramirez-Llodra et al., 2010). While multiple factors control the demographics of deep-sea

megafauna, with the advent of investigations at Station M in the northeast Pacific Ocean (Smith et al., 2009, 2013), the Porcupine Abyssal Plain (PAP, 48° 50' N, 16° 30' W; Iken et al., 2001; Wigham et al., 2003a; Sweetman and Witte, 2008; Billett et al., 2010) and the Atlantic Ocean and Fram Strait in the Arctic (78° 0' N, 0° 0' W; Meyer et al., 2013), we are learning that episodic input of organic carbon from surface waters (POC) comprises a major disturbance to the abyss.

The impact of POC on deep-sea animals has been a long-term area of research (Smith, 1987; Wigham et al., 2003a; Robison et al., 2005; Smith et al., 2009; Lampitt et al., 2010; Tecchio et al., 2013). Food supply is known to influence organism abundance, food web structure, and the diversity of communities (Smith and Druffel, 1998; Bett et al., 2001; Smith et al., 2002, 2009; Wigham et al., 2003b; Ruhl and Smith, 2004; Sweetman and Witte, 2008; Ruhl, 2008; Tecchio et al., 2013). However, the impacts of atypically large food influxes (i.e. those observed only once or a few times in a record) on megafaunal community composition are largely unknown. The California Current overlying Station M exhibits long-term oscillations in oceanographic and ecosystem properties extending from years to decades (e.g. Rykaczewski and Checkley, 2008; Norton and Mason, 2005).

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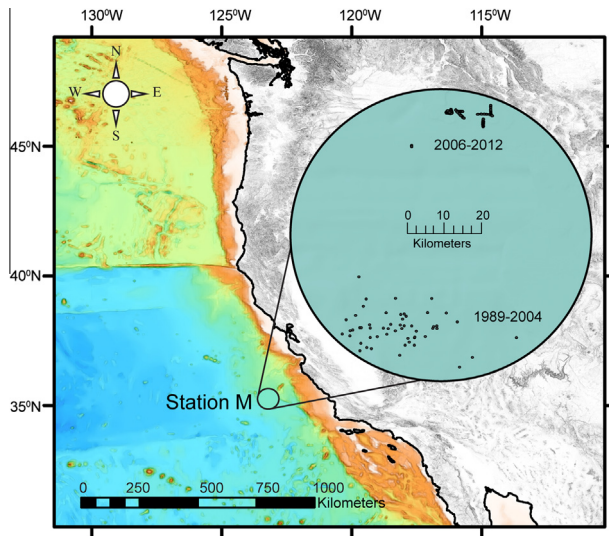


Fig. 1. Map showing Station M in the northeast Pacific, 220 km off the California coast. Inset: areas sampled during investigations. Black circles indicate the start point of transects. ROV studies conducted from 2006 to 2012 are shown to the northeast, while 1989–2004 camera sled sampling took place about 40–50 km to the southwest. Bathymetric layer: http://services.arcgis.com/ArcGIS/services/Ocean_BaseMap 2013.

Because the deep sea food supply relies on surface water processes with interannual or longer variations, we might expect some cyclicity to translate to abyssal depths, as changes in climate drive highs and lows in supply, which in turn influence the species-specific responses that drive community structure. Likewise, atypical fluxes might lead to excursions from such cyclicity.

The current study was conducted at Station M in the northeast Pacific Ocean (Fig. 1) and is a continuation of a long time series study of the megafauna community begun in 1989 (Lauerman et al., 1996; Smith and Druffel, 1998; Smith et al., 1998, 2002, 2006; Ruhl and Smith, 2004). This investigation extends the time series to 24 years and seeks to examine variation on time scales from annual to decadal in epibenthic megafauna. Station M is located at the base of the Monterey Canyon abyssal fan at ~4000 m depth and the overlying water mass is influenced by the California Current with distinct seasonal upwelling events, leading to pulses of primary production (Smith and Druffel, 1998). With the advent of new technologies like ROVs and high definition video we were able to continue the study, documenting changes over a 7-year period, 2006–2012, documenting the entire visible megabenthos community.

Our goals were to (1) investigate changes in megafaunal community composition structure in terms of diversity and functional group composition for the megabenthos community from 2006 to 2012, (2) examine how changes in the dominant echinoderm populations relate to observed changes across a broader range of taxa and functional groups than addressed previously, and (3) to examine the data for long-term and potentially cyclical changes in the densities and dominance of 10 mobile echinoderm taxa studied since 1989. We interpret observed changes with regard to observations of particulate organic carbon flux to the seafloor.

2. Methods

2.1. Surveys

Between 2006 and 2012, Station M (35° 10' N, 122° 59' W; Fig. 1) was surveyed nine times using the Monterey Bay Aquarium Research Institute's (MBARI) R/V *Western Flyer*, equipped with

Table 1

Quantitative transects. For ROV dive number, T indicates ROV *Tiburon* and D for ROV *Doc Ricketts*. The bin column denotes the number of 20 m² subsamples. Note that in February 2009, ROV navigation quality did not allow the transect to be reliably subsampled. We observed substantial detritus on the seafloor during three periods.

Year	Date	ROV dive	Combined transect area (m ²)	#Bins
2006	December	T1067	1120	056
2007	February	T1077, 1080	220	011
2007	June	^a T1094	80	004
2007	September	^a T1141, 1143	420	021
2009	February	D008	1560	001
2011	May	D230, 231, 232	4500	225
2011	November	D321, 323, 324	2640	132
2012	June	^b D403	400	020
2012	November	D442, 443	2600	130

^a Phytodetrital aggregates present.

^b Dead/dying pelagic salps present.

remotely operated vehicles (ROV) *Tiburon* (2006–2007) and *Doc Ricketts* (2009–2012; Fig. 1, Table 1). We conducted video transects within a 40 km² area of seafloor at 4000 m depth (±40 m). Multiple combined transects conducted in what we define as a “sampling period” were recorded within 3 days and from within an approximately 2 km area, reducing unintended temporal or spatial variation. Benthic and demersal megafauna (organisms large enough to be identified in seafloor images, about 1 cm in size or larger) were quantified by annotating video recorded with Ikegami high-definition cameras fitted with HA10Xt.2 Fujinon lenses. Camera models and visual resolution from lighting did not vary between ROVs. Two lasers mounted on the ROVs, with parallel beams spaced 29 cm apart, were used to measure a consistent meter-wide strip in the video. MBARI's Video Annotation and Reference System (VARS) was used to manually annotate video (Schlining and Stout, 2006). To further ensure a consistent meter-wide strip in the oblique view, we only counted organisms that passed the lasers, visible in the lower 75% of video. Transects were divided into 20 m subsections, which were analyzed as replicate sample units to calculate mean densities. This sample size was used to minimize the effect of our known ROV navigation data resolution, while maximizing the detection of variation in density.

2.2. Taxonomic and functional group assignment

Identification was performed to the lowest practical taxonomic level, and because the identification of organisms on video can be uncertain, we were conservative in our assignment of taxonomic names. When possible, specimens were collected for positive identification. Observed taxa were assigned a mobility category (sessile, functionally sessile, mobile) and a feeding-type category (suspension feeder, surface deposit feeder, subsurface deposit feeder, or predator/scavenger), based on stable isotope analysis for select deep-living benthic organisms (Iken et al., 2001).

2.3. Dominant echinoderm community change (24-year time series)

We compared the density of organisms observed in these ROV surveys with the densities of 10 mobile megafaunal organisms (Ruhl, 2007) quantified from towed camera-sled images during previous Station M studies conducted between 1989 and 2004. These early transects occurred 40–50 km to the southwest (34° 50' N, 123° 00' W, 4100 m) and about 100 m deeper than the current site (Fig. 1). The shifted location was necessary due to the depth limits of ROVs *Tiburon* and *Doc Ricketts*. The expected difference in downward POC flux between these depths would be only about 2% on the basis of the Martin curve of POC flux attenuation (Martin et al., 1987), a quantity greatly out-scaled by temporal

variability of the area. As a second indication of site compatibility, we found that all dominant animals were present at both sites.

In order to understand the compatibility between the methods in terms of the detectability of fauna, we measured 3300 of the smallest sea cucumber (holothurian) species (*Elpidia* sp. A) from recent video and compared the length of the animals to the lengths from the earlier study. We found that the smallest sized *Elpidia* sp. A on video was 7.8 mm, and the average smallest observed size in the previous study was 8.9 mm (± 1.3 mm 95% confidence interval) in the monthly estimates from the camera sled data spanning 1989–2004.

Higher-resolution imagery and additional specimen sampling over time have allowed us to recognize multiple species that look very similar to each other and might have been indistinguishable in earlier studies. Therefore we combined *Peniagone* sp. A, *P. gracilis*, and *P. papillata* as *Peniagone* sp. A complex for comparison to historic data, in which these species would have been identified as *Peniagone vitrea* in previous work. *Peniagone* sp. 1, and *Peniagone* sp. 2 were combined as *Peniagone* sp. B complex, in which these species would have been identified as *Peniagone diaphana* in previous work.

2.4. Data analysis

2.4.1. Megafaunal density (2006–2012)

After testing variances using Bartlett tests for homogeneity on $\log(x + 1)$ and square-root transformed taxa-level data by sampling period, we conducted non-parametric Kruskal–Wallis and two-sample Kolmogorov–Smirnov (KS) tests using Systat v.13 (2009).

To test differences in densities by phylum-level groups, we also conducted a Friedman 2-way analysis of rank abundance with post hoc tests (Friedman Multiple Comparisons). We performed diversity measures and species richness estimators (Chao et al., 2009) with PRIMER-E v.6 on untransformed data. Simpson's Diversity Index ($1 - \lambda$, SDI) was chosen to reduce the effects of varying sample sizes (Olabarria, 2006) over time. We also compared Pielou's Evenness (J') and Shannon Index (H') for each sampling period.

2.4.2. Dominant echinoderm community change (24-year time series)

To examine similarities in community composition, we used PRIMER-E v.6 for hierarchical cluster analysis and non-metric multidimensional scaling analysis (MDS) based on a Bray Curtis dissimilarity index using square-root-transformed mean densities. To test for annual cycles (distance based on number of years between samples), we ran a PRIMER RELATE analysis.

3. Results

3.1. Surveys

The total benthic habitat quantitatively surveyed by ROV from December 2006 to November 2012 was 13,570 m², with transect areas varying between 80 and 4500 m² (Table 1). Based on ROV CTD instruments one meter above the seafloor, mean water temperature (1.50 °C, range = 1.49–1.52) and salinity (mean = 34.60 - PSU, range = 34.40–34.70) were relatively consistent during the study. Winkler tests indicate that oxygen levels at the site were not limiting (3.04 ml l⁻¹).

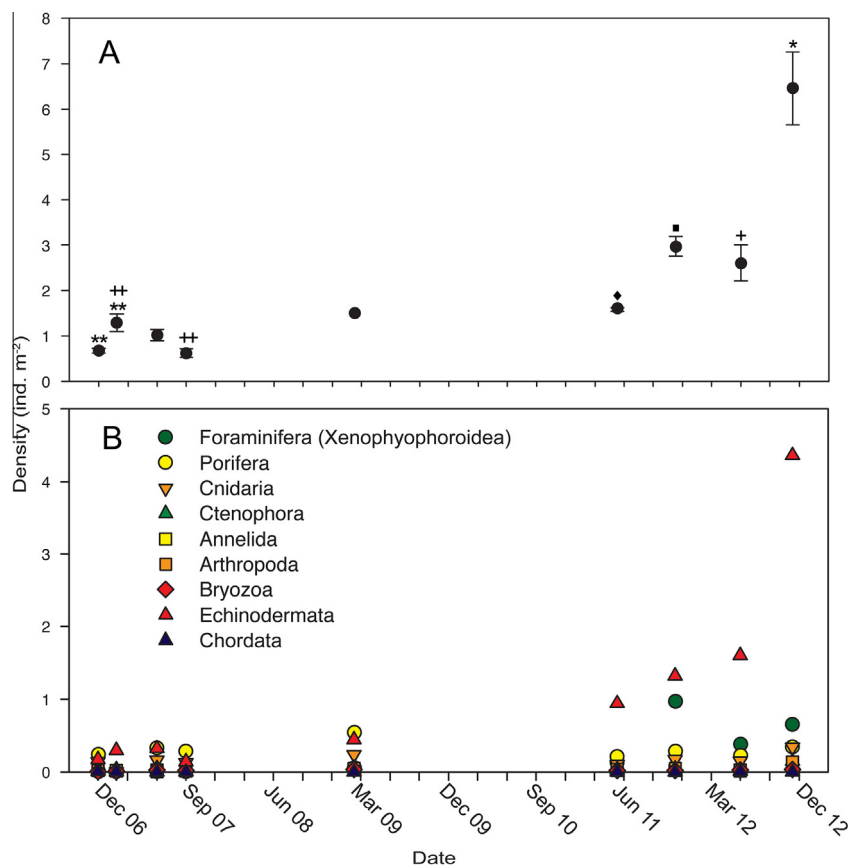


Fig. 2. Density of organisms observed during nine ROV sampling periods between 2006 and 2012. (A) Overall density of organisms (error bars = SE). Note that in February 2009, ROV navigation quality did not allow the transect to be reliably subsampled. Significant results of the two-sample KS test ($p < 0.05$): ** December 2006 \times vs. February 2007 \blacklozenge vs. all periods except December 2006 and September 2007 \blacksquare vs. all periods except June 2007 \blacklozenge vs. all periods except February 2007 and November 2011 \blacklozenge vs. all other periods. (B) Overall density for phylum-level categories. Friedman post hoc tests indicate that there were significant differences ($p < 0.05$) in the ranks among all phyla except for Cnidaria vs. Echinodermata, Cnidaria vs. Porifera, and Echinodermata vs. Porifera.

3.2. Benthic megafaunal community (2006–2012)

A total of 36,599 organisms from 102 taxa were quantified, and an additional 19 taxa were present in the immediate area but observed only outside of transects (Appendix). The majority of megafauna observed quantitatively were echinoderms (56.8%), xenophyophores (13.9%), sponges (11.1%), and cnidarians (6.9%). Overall megafaunal densities ranged from a mean of $0.67 \text{ ind. m}^{-2} \pm 0.048$ ($\pm \text{SE}$) in December 2006 to $6.46 \text{ ind. m}^{-2} \pm 0.81$ in November 2012, an order of magnitude increase (Fig. 2a). The Kruskal–Wallis test indicated a significant ($H = 269.7(8)$, $p < 0.001$) difference in the mean rank of megafaunal density among all nine sampling periods. The two-sample KS test showed that density was significantly higher in 2012 than in all other periods (Fig. 2a). Echinoderms were responsible for the sharp rise in densities (Fig. 2b). According to the Friedman's test ($X^2 = 111.9$, (15), $p < 0.001$) there was a significant difference in the ranks of phyla among sampling periods (Fig. 2b). Pair-wise post hoc tests showed that there were significant differences ($p < 0.05$) in the ranks among all phyla except for Cnidaria vs. Echinodermata, Cnidaria vs. Porifera, and Echinodermata vs. Porifera (Fig. 2b).

Alpha, or local scale, community diversity was high at the start of the ROV time series in December 2006, as indicated by $\text{SDI} = 0.92$ (Fig. 3). Species richness may be underestimated for the June 2007 sampling period due to a short transect as was reflected in Chao2 species accumulation curves. Nevertheless, an overall trend of lower diversity began in 2007 (Fig. 3). Diversity gradually increased again, peaking in February 2009 ($\text{SDI} = 0.93$). Diversity declined with the large increase of holothurian density in May 2011 ($\text{SDI} = 0.91$) and then sharply declined 6 months later as xenophyophores and two species of holothurians continued to dominate ($\text{SDI} = 0.85$). In June 2012, SDI began to rise again, but with an overall shift from a sponge to a holothurian-dominated community (Fig. 3). Community evenness (Pielou's, J') was lower for all sampling periods after May 2011 (Fig. 3). Species diversity based on the Shannon Index (H') was highest in March 2009. By May 2011, diversity was reduced, reaching the lowest level in November 2011 (Fig. 3).

3.3. Sessile vs. mobile organisms (2006–2012)

In 2006, early 2007 and during 2009, sessile (e.g. sponges, tunicates, anemones), and functionally sessile organisms (e.g. brisingid seastars, crinoids) comprised 59.2–68.4% of the megafaunal community (Fig. 4a). There was a decline in sessile fauna density during the 12-month period beginning in Fall 2011, and in Fall 2012 their contribution dropped to 26.9%. Conversely, the number of observed mobile animals (e.g. holothurians, ophiuroids) became more abundant by Fall 2012 (73.1%).

3.4. Feeding strategies (2006–2012)

From 2006 to 2009 the majority of observed organisms were suspension feeders (54.0–74.2%; Fig. 4b), which included animals such as sponges, tunicates, anemones, and sea pens (Appendix). A persistent, notable drop in the absolute density of suspension feeders occurred in the spring of 2011 when surface deposit feeders (mostly holothurians), subsurface deposit feeders (holothurians, sipunculids), and xenophyophores, which appear to have a mixed feeding strategy that includes obtaining nutrition from the water column and from sediments (Riemann et al., 1993), comprised 70.3–78.3% of the community (Fig. 4b).

3.5. Community dominants (2006–2012)

Echinoids *Cystocrepis loveni* and *C. setigera* were dominants before May 2011 (Table 2). While high density in *C. setigera* was

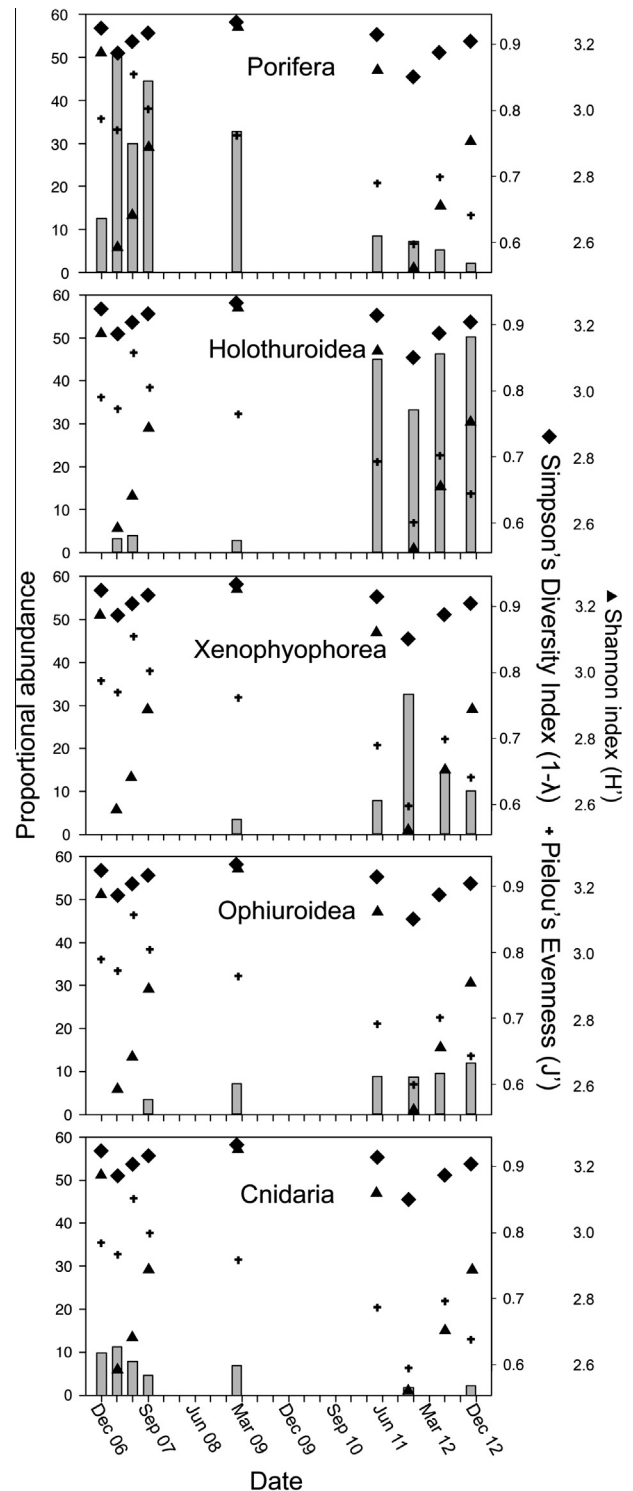


Fig. 3. Relative proportion (as a percent) of higher-taxa groups having the most effect on community structure, based on ROV surveys between 2006 and 2012 (bars). We show Simpson's Diversity Index (SDI), Pielou's Evenness and the Shannon Index (right axis) for each period. Note that due to the short transect length, species richness for June 2007 is likely underestimated.

only observed for the first 3 months of the study, *C. loveni* increased in density for more than 2 years. As with most of the sponges, the echinoids had a large drop in density in May 2011, with no rebound.

Visible xenophyophores were rare until November 2011 when density peaked at $0.97 \text{ ind. m}^{-2} \pm 0.15$ (Table 2). After an

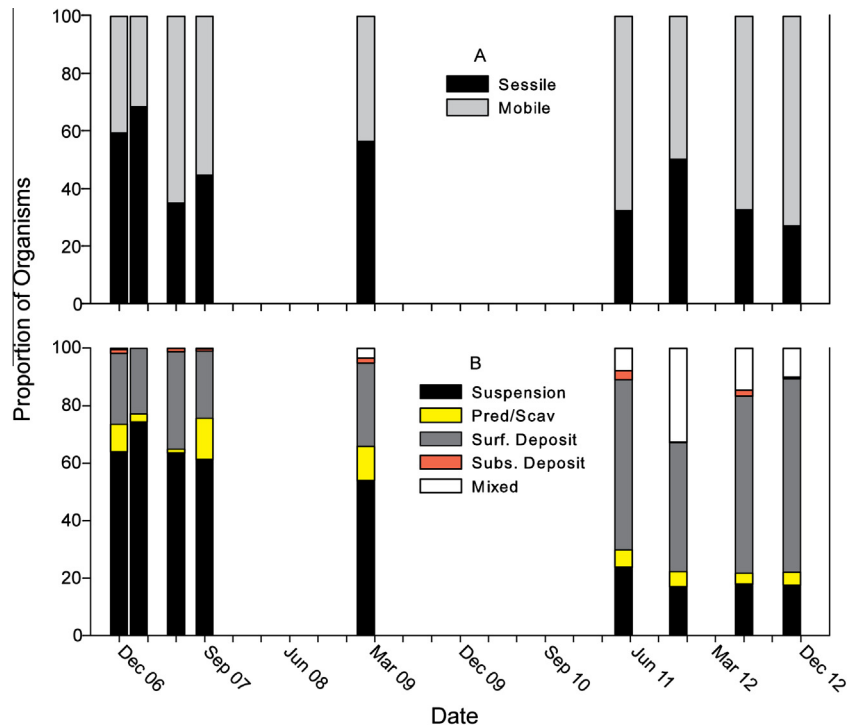


Fig. 4. (A) Mobility strategies of organisms. Proportion (as a percent) of sessile and functionally sessile vs. mobile organisms based on ROV surveys between 2006 and 2012. (B) Feeding strategies. Proportion of suspension feeders, predators and scavengers, surface deposit feeders, subsurface deposit feeders, and mixed feeding between 2006 and 2012. Categories after Iken et al. (2001).

ephemeral decrease 7 months later, densities began to rise again by November 2012. We saw no obvious size change in these organisms during the study.

Hexactinellid sponges (*Euplectellidae*, *Hyalonema bianchoratum*, and *Bathydorus laevis spinosus*) were community dominants until May 2011 when density dropped dramatically and remained low (Fig. 3). During the last sampling period in 2012, *B. l. spinosus* approached 2006–2007 densities. Plate sponges (*Bathydorus laniger* and *Docosaccus maculatus*) increased in density in 2007, dropped to very low numbers through June 2012, and then exhibited higher numbers as of the last sampling period in November 2012. *Cladorhiza* sp. A was the only sponge to increase in density over time (Table 2).

The sea pen *Pennatula* was consistently ranked in the top 10 dominants from December 2006 to February 2009 (Table 2) and then density dropped by more than 50% by May 2011. By November 2012, *Pennatula* had rebounded and was at the highest density ($0.07 \text{ ind. m}^{-2} \pm 0.02$) seen during the study period. The average density of the benthic ctenophore *Tjalfiella tristoma* fluctuated little until November 2012 when they more than quadrupled ($0.14 \text{ ind. m}^{-2} \pm 0.03$) within 6 months. A variety of rare and low-density tunicates were present at the site (Table 2). One particular epibenthic species (Order Stolidobranchia) was observed at low density throughout the study, and then spiked at $0.22 \text{ ind. m}^{-2} \pm 0.046$ in November 2012.

Macrourids (*Coryphaenoides* spp.) were the most frequently observed fishes. Densities ranged from zero to $0.007 \text{ ind. m}^{-2} \pm 0.010$ (December 2006).

3.6. Dominant echinoderm community change (24-year time series)

When considering the subset of 10 mobile echinoderm taxa we were able to track over the entire study period (1989–2012), we saw evidence of a single cycle, in which community structure in

2009–2012 was most similar to 1989–1998 (Fig. 5). The community structure variation was correlated to a model matrix with sinusoidal variation (1989–2009, $\text{Rho} = 0.279$, $p < 0.001$). The 2012 community state is among the more outlying points in terms of similarity, but it still more than 76% similar to community structures observed early in the time series. In November 2012, the holothurians *Peniagone* sp. A complex, *Peniagone* sp. B complex, *Elpidia* sp. A, and *Scotoplanes globosa* were at the highest densities recorded since mobile epibenthic megafaunal investigations began in 1989 (Fig. 6). Other fauna (four other holothurians, ophiuroids, and an echinoid), which were relatively abundant between 2001 and 2004, subsequently dropped in density (Fig. 6).

Peniagone sp. A complex began increasing in number in early 2011, after 22 years of relatively low density (Fig. 6). The holothurian *Elpidia* sp. A was the dominant megafaunal organism (peaking at 0.70 ind. m^{-2}) for at least a decade (1989–1999), but was nearly undetectable for the following 12 years. Beginning in 2011, *Elpidia* sp. A density increased and became the dominant organism within 18 months ($1.33 \text{ ind. m}^{-2} \pm 0.289$ in November 2012). *Peniagone* sp. B complex exhibited a similar, but temporally delayed pattern of being nearly undetectable for at least 7 years, followed by a large population size increase, comprising 9.5% of the total megafaunal population within just 6 months (2012). *Scotoplanes globosa* was in very low density from 1989 to 2011, but in 2012 it nearly tripled in density within 6 months. Ophiuroids were relatively abundant throughout the time series, but were observed in notably low numbers from 1995 to 1998 and from 2006 to early 2011 when densities started to rise again. The holothurian *Oneirophanta mutabilis* inhabited the area in low numbers for the first 9 years of the time series (1989–1998), then more than tripled in density by 2004. No trend was observed for the following 8 years. The echinoid *Echinocrepis rostrata* and holothurians *Psychropotes longicauda* and *Abyssocucumis abyssorum* were also observed in highest numbers between 2002 and 2004. Synallactid holothurian densities were

Table 2
Top 10 dominant taxa from Station M ROV surveys for sampling periods 2006–2012. Higher taxonomic group is denoted by (B) Bryozoa, (C) benthic Ctenophora, (E) Echinoid, (He) Hexacorallia, (H) Holothuroidea, (O) Ophiuroidea, (P) Pennatulacea, (Po) Porifera, (S) Sipuncula, (Si), benthic Siphonophorae, (T) Tunicata, (X) Xenophyophorae.

	Mean (m ⁻²)	% Total		Mean (m ⁻²)	% Total
<i>December 2006</i>			<i>February 2007</i>		
Euplectellidae sp. indet. (Po)	0.141	21.0	Bathydorus laevis spinosus (Po)	0.277	21.6
Cystechinus loveni (E)	0.065	9.7	Euplectellidae sp. indet. (Po)	0.268	20.9
Pennatula sp. indet. (P)	0.046	6.8	Porifera sp. indet. (Po)	0.105	8.1
Epizoanthus stellaris (He)	0.045	6.7	Cystechinus loveni (E)	0.086	6.7
Hyalonema bianchoratum (Po)	0.033	4.9	Epizoanthus stellaris (He)	0.077	6.0
Cystocrepis setigera (E)	0.030	4.5	Cystocrepis setigera (E)	0.068	5.3
Bathydorus laevis spinosus (Po)	0.029	4.3	Pennatula sp. indet. (P)	0.059	4.6
Tunicata sp. indet. (T)	0.024	3.6	Elpidia sp. A (H)	0.041	3.2
Cladorhiza sp. A (Po)	0.022	3.3	Fungiacyathus marenzelle (He)	0.036	2.8
Tjalfiella tristoma (C)	0.021	3.2	Tjalfiella tristoma (C)	0.032	2.5
Total % attributable to dominants		68.0	Total % attributable to dominants		81.6
<i>June 2007</i>			<i>September 2007</i>		
Cystechinus loveni (E)	0.188	19.5	Bathydorus laevis spinosus (Po)	0.102	16.5
Bathydorus laevis spinosus (Po)	0.175	18.2	Euplectellidae sp. indet. (Po)	0.083	13.4
Pennatula sp. indet. (P)	0.075	7.8	Cystechinus loveni (E)	0.071	11.5
Hyalonema bianchoratum (Po)	0.063	6.5	Cladorhiza sp. A (Po)	0.067	10.7
Tjalfiella tristoma (C)	0.050	5.2	Pennatula sp. indet. (P)	0.045	7.3
Tunicata sp. indet. (T)	0.050	5.2	Epizoanthus stellaris (He)	0.029	4.6
Euplectellidae sp. indet. (Po)	0.050	5.2	Hyalonema bianchoratum (Po)	0.024	3.8
Abyssocucumis abyssorum (H)	0.038	3.9	Ophiuroidea spp. (O)	0.021	3.5
Echinocrepis rostrata (E)	0.038	3.9	Striatodoma dorothea (B)	0.017	2.7
Epizoanthus stellaris (He)	0.025	2.6	Echinocrepis rostrata (E)	0.014	2.3
Total % attributable to dominants		77.9	Total % attributable to dominants		76.3
<i>February 2009</i>			<i>May 2011</i>		
Bathydorus laevis spinosus (Po)	0.225	15.0	Peniagone sp. A (H)	0.359	22.4
Euplectellidae sp. indet. (Po)	0.178	11.8	Elpidia sp. A (H)	0.141	8.8
Cystechinus loveni (E)	0.163	10.8	Ophiuroidea spp. (O)	0.140	8.8
Ophiuroidea spp. (O)	0.108	7.2	Psamminidae sp. indet. (X)	0.126	7.9
Cladorhiza sp. A (Po)	0.090	6.0	Bathydorus laevis spinosus (Po)	0.095	5.9
Pennatula sp. indet. (P)	0.055	3.7	Peniagone gracilis (H)	0.088	5.5
Tjalfiella tristoma (C)	0.055	3.7	Peniagone vitrea (H)	0.084	5.2
Psamminidae sp. indet. (X)	0.053	3.5	Scotoplanes globosa (H)	0.051	3.2
Epizoanthus stellaris (He)	0.047	3.2	Sipuncula (S)	0.044	2.7
Peniagone vitrea (H)	0.044	2.9	Cladorhiza sp. A (Po)	0.042	2.6
Total % attributable to dominants		67.8	Total % attributable to dominants		72.9
<i>November 2011</i>			<i>June 2012</i>		
Psamminidae sp. indet. (X)	0.968	32.6	Peniagone sp. A (H)	0.545	20.9
Elpidia sp. A (H)	0.445	15.0	Elpidia sp. A (H)	0.465	17.8
Ophiuroidea spp. (O)	0.259	8.7	Psamminidae sp. indet. (X)	0.383	14.7
Peniagone sp. A (H)	0.233	7.8	Ophiuroidea spp. (O)	0.248	9.5
Peniagone gracilis (H)	0.163	5.5	Scotoplanes globosa (H)	0.125	4.8
Bathydorus laevis spinosus (Po)	0.117	3.9	Bathydorus laevis spinosus (Po)	0.083	3.2
Cladorhiza sp. A (Po)	0.097	3.3	Peniagone vitrea (H)	0.073	2.8
Peniagone vitrea (H)	0.081	2.7	Sipuncula sp. indet. (S)	0.055	2.1
Scotoplanes globosa (H)	0.063	2.1	Cladorhiza sp. A (Po)	0.053	2.0
Stephalia dilatata (Si)	0.050	1.7	Peniagone gracilis (H)	0.048	1.8
Total % attributable to dominants		83.3	Total % attributable to dominants		79.6
<i>November 2012</i>					
Elpidia sp. A (H)	1.335	20.7			
Ophiuroidea spp. (O)	0.767	11.9			
Peniagone sp. A (H)	0.747	11.6			
Psamminidae sp. indet. (X)	0.656	10.2			
Peniagone sp. 1 (H)	0.626	9.7			
Scotoplanes globosa (H)	0.289	4.5			
Peniagone vitrea (H)	0.247	3.8			
Tunicata sp. indet. (T)	0.220	3.4			
Tjalfiella tristoma (C)	0.143	2.2			
Bathydorus laevis spinosus (Po)	0.135	2.1			
Total % attributable to dominants		80.0			

highly variable, with numbers more than doubling at times within months (Fig. 6).

4. Discussion

In less than 27 months, this 4000 m deep abyssal ecosystem shifted from a sessile, suspension-feeding, sponge-dominated community to a mobile, detritus-feeding, holothurian-dominated

assemblage. Given these dynamic changes over a short period, it is clear that long-term ecological monitoring data are essential in understanding how emerging issues might elicit ecological change in this remote habitat.

In examining the densities of the 10 echinoderms tracked throughout the 24-year time series, there is now clearer evidence for a cyclical pattern in community composition. Variation in community composition of these mobile megafauna observed in the early 2000s has previously been linked to periodic El Niño

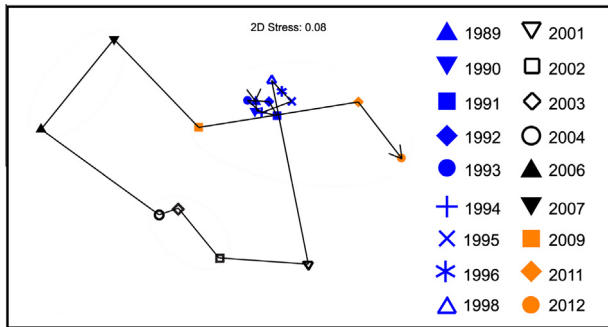


Fig. 5. Multidimensional scaling (MDS) plot for 10 echinoderm taxa followed from 1989 to 2012. The MDS is based on a Bray Curtis similarity index for square-root transformed mean densities and similarity is based on hierarchical cluster analysis (single linkage).

Southern Oscillation phenomena (Ruhl and Smith, 2004; Ruhl, 2008). However, it was not until about 2009 that community composition returned to an earlier state in the time series. Indeed the 1989–1991 period was one of the higher POC flux periods on record, yet these POC fluxes were not as high as those seen in 2012 when the community peaked in megafaunal density. Here only one putative cycle was observed; much longer time series will be needed in order to reliably determine the character of cyclicity and the degree to which it exhibits predictable behavior.

These major structural changes could potentially be due to large disturbances, changes in food availability, the presence of predators, and in-direct ecosystem changes. The observed changes have limited analogues to variation observed PAP megafaunal communities. There too, megabenthic communities had significant inter-annual scale variation where, for example, the sea cucumber *Amperima rosea* increased in density from a few ha^{-1} to several hundred ha^{-1} (Billett et al., 2010). Interestingly, an ‘*Amperima* event’ occurred twice (in 1997–1998 and 2002) during the analyzed record, which has 14 time points over 22 years (1989–2011; Ruhl et al., in press). The abundances of other fauna (echinoderms and infaunal polychaetes), and changes in size classes also varied in relation to these events. While statistical links between climate variations and seafloor community changes are less clear at PAP, there are important indications that both changes in the amount and type of available food supply are likely important (Smith et al., 2009; FitzGeorge-Balfour et al., 2010).

4.1. Benthic megafaunal response to changes in food supply

The faunal changes correspond to atypically large increases in food supply (organic carbon) reaching the seafloor as detailed by Smith et al., 2013. We observed three conspicuous depositions of food supply to the seafloor with the ROVs in the form of phytodetrital aggregates (June and September 2007) and carbon-rich dead pelagic salps (*Salpa* spp.) covering up to 98% of the seafloor (June 2012, Fig. 7). Detritus samples and additional photo documentation of the seafloor from a time-lapse camera at the site, showed one additional pulse of phytodetritus in September 2012, and that the dense salps were present on the seafloor for about 4 months (Fig. 6, Phytodetritus and Salp detritus). These large events comprised the largest influx of carbon to Station M documented in the past 24 years (Smith et al., 2013).

Recent large food inputs to Station M in 2011 and 2012 (Smith et al., 2013) appear to have fueled increased benthic megafaunal densities, but reduced megafaunal diversity. Sinking detritus provides food for abyssal detritus, passive suspension, and active filter feeders alike. However, sponges at Station M appear to have been negatively affected when atypically large pulses of phytodetritus

sank in 2007, and dead salps arrived on the seafloor in 2012. Plate sponges have been shown to benefit from inputs of POC (Kahn et al., 2012), but atypically large volumes of sinking detritus might smother sponges and other suspension feeders, severely reducing the number of organisms. A reduction in suspension and filter feeder diversity following large sedimentation events is not unprecedented in marine systems and can be caused by a variety of mechanisms that can lead to increased mortality and reduced reproductive success, a pattern that is well-documented in shallow ecosystems (Newcombe and MacDonald, 1991). Yahel et al. (2007) reported that many deep-living sponges filter bacteria from the water column. The amount and type of bacteria reaching sponges might have been altered while detrital aggregates and dead salps were present on the seafloor. By contrast, the increase in the density of the sponge *Cladorhiza* sp. A during these same time periods might suggest the ability of its very long spicules, held vertically and radiating from a central axis, to lessen or prevent the clogging of pores and oscula that affect rates of water flow through tissues. The increase in *C. sp. A*, which are carnivorous and prey on small crustaceans (Lehnert et al., 2005), might also suggest an increase in the abundance of their prey.

Beginning in January 2007 above average POC fluxes occurred for 19 continuous months (Smith et al., 2013). In conjunction with this increase in food supply, there was a dramatic reduction in SDI within 50 months due to the presence of large numbers of holothurians. Interestingly, some echinoderms, even congeners, appear to have responded to the influx of food differently. This might be due to variations in feeding strategy, food utilization, mobility, or disparities in the timing of reproduction and recruitment success.

Holothurians in the genus *Peniagone* increased in numbers following recent periods of high food availability, although not all member species showed the same response. These congeners have broadly similar feeding structure morphologies and appear to be surface deposit feeders (Roberts and Moore, 1997), but nutrient stratification in sediments can impose species-specific food limitations. The composition of phytopigments present on the deep seafloor is variable (Smythe-Wright et al., 2010), and gut bacteria, and thus nutrient uptake ability, of deep-sea holothurians can be highly specialized (Amaro et al., 2009). Holothurians at Station M might have similar capabilities to other sea cucumbers, which can take advantage of specific phytopigments that other species cannot digest (Ginger et al., 2000; Bett et al., 2001; Wigham et al., 2003b,a; FitzGeorge-Balfour et al., 2010). Some components of phytodetritus, like carotenoids, cannot be synthesized by these animals but are essential to reproduction or other functions (FitzGeorge-Balfour et al., 2010). It is unknown how the quality, particle size, or digestibility of available food might benefit one species over another at Station M, allowing for niche partitioning in a variable resource environment. Mobility might be a factor in density changes over time for some megafauna as well. We saw the echinoid *Cystocrepis loveni* go from a dominant organism to being nearly absent from the community. Because of their relatively slow locomotion speed (Vardaro et al., 2009), this echinoid, along with *Echinocrepis rostrata*, and six other species of slower-moving holothurians, might not have been able to take the same advantage of large, episodic food pulses, as did some other taxa. Some abyssal organisms have been shown to alter their feeding behavior (active predator to scavenger) based on the availability of large food falls (Aguzzi et al., 2012).

4.2. Reproduction and recruitment

The life history of most of these deep-dwelling organisms is unknown, but we can hypothesize that some of them are capable of opportunistic reproduction. Preliminary results suggest that

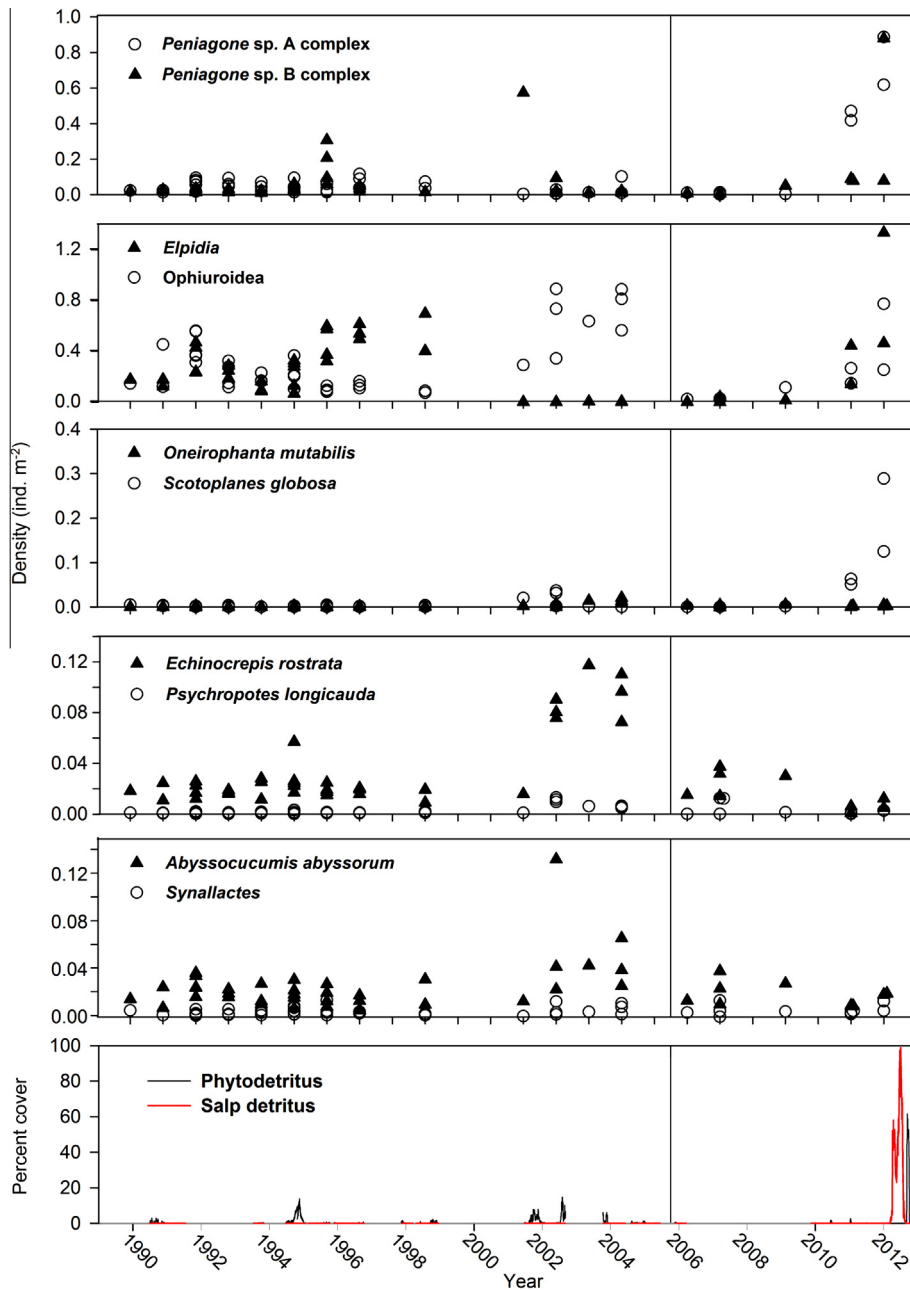


Fig. 6. Comparison of 10 mobile megafaunal taxa followed from 1989 to 2012, and percent cover of seafloor detritus from time-lapse camera images (gray x axis indicates no data; after Smith et al., 2013). Sampling dates to the left of the black bar indicate camera-sled sampling. Later periods were sampled via ROV transects. Note the vertical scale differences in the panels.

increases were likely due, at least in part, to recruitment. Small animals (likely juveniles) were frequently observed during these studies and larger animals often appeared gravid. In future work we hope to quantify size dispersion, biomass, and the reproductive state of organisms over time to understand more about how various species utilize episodic food events.

It is possible that immigration contributed to the large influx of holothurians. While we have evidence that small, local remnant populations of holothurians reproduced after feeding on the influx of food, we also observed *Peniagone* spp., known to be capable swimmers (Rogacheva et al., 2012), in the water column.

4.3. Potential ecosystem effects

Because abyssal megafauna are capable of turning over sediment on a time frame as short as a few weeks (Bett et al., 2001), the inferred increased rate of bioturbated sediment after May 2011 might have long-term effects on the ecosystem as a whole. The feeding activity of large numbers of deposit-feeding holothurians could serve to mix other nutrients deeper into the sediment, potentially making them available to infauna. Increased numbers of xenophyophores as well may redistribute nutrients as they use their pseudopodia to stir sediment around them (Riemann et al., 1993).

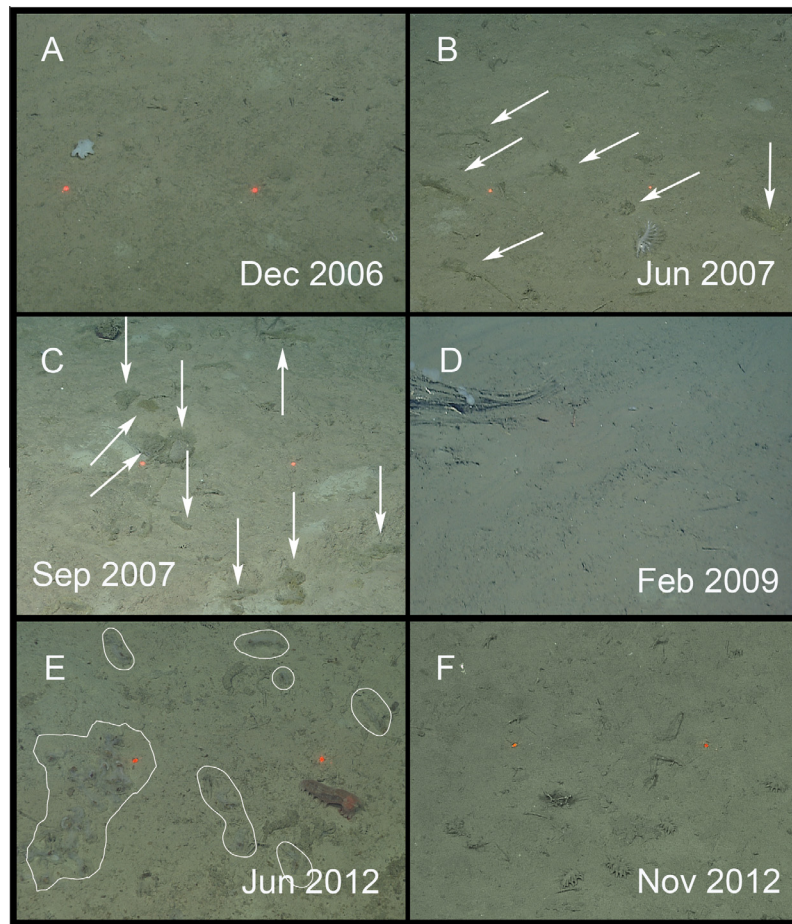


Fig. 7. Images showing seafloor conditions during various ROV surveys between 2006 and 2012. (A) Observations show the seafloor with little to no organic debris. A small Euplectellid sponge can be seen to the left of center. (B) In June 2007, detrital aggregates (white arrows) are apparent. The sea pen *Pennatula* is shown. (C) Three months later, the density and size of detrital aggregates (white arrows) became larger. (D) In February 2009, the seafloor had no detrital aggregates present. Dead *Hyalonema* sponge stalks with small sponges attached are shown in the upper frame. (E) In June 2012, dense numbers of dead/dying pelagic salps sank to the seafloor (white polygons). (F) Six months later organic debris was nearly gone, but the density of animals like the holothurian *Elpidia* was at its peak. ROV lasers (orange dots) are used for size reference, and are spaced 29 cm apart.

Biogenic structures provide both food and microhabitat for a diverse number of meio- and macrofauna, and we expect that the recent large increase in xenophyophore density, with their relatively fast-growing, persistent tests (Levin et al., 1986; Levin, 1991; Gooday et al., 1993), might facilitate cascading community changes. These large xenophyophores are known to positively influence the abundance and species richness of smaller organisms living on them and in surrounding sediment (Levin et al., 1986).

Top-down control of the community seems unlikely. Macrourids could be considered a top predator at this site, but in an evaluation of diet inferences based on lipid composition, they appear to feed mostly on amphipods, polychaete worms, and epipelagic carion (Drzen et al., 2009; Drzen et al., 2012). During the current study, the maximum density of *Coryphaenoides* spp. was observed in December 2006 when the remainder of the community was diverse but depauperate. Other predators of holothurians include seastars and crustaceans (Francour, 1997), both of which were observed in very low abundance.

While differences in methods occurred during the overall 24-year study and could have affected our results, dominant organisms were always large enough to be clearly seen in the evaluated imagery. Other small organisms might not always be visible in either camera-sled images or video (i.e. echiurans, sipunculids), and ophiuroids and animals that burrow or are otherwise cryptic, are difficult to reliably quantify (Booth et al., 2008). While earlier Station M studies took place up to 100 m deeper and 40–50 km

distant, our data support that the same biological community exists at both of these locations with no evidence for relevant differences in food supply or sediment type.

5. Conclusions

This long-term study shows that time-series investigations are important for understanding abyssal plain community structure. Major changes in the density and diversity of species and functional group shifts at Station M suggest that there is no constant community state, probably due to disturbance in the form of episodic food events from the far-removed overlying water column. With further study we expect to see a cyclical pattern of overall diversity like that suggested for dominant echinoderms (1989–2012). Many questions still remain as to how this abyssal site and others will change with continued, and perhaps increasing, anthropogenic change in the upper ocean.

Acknowledgements

We would like to thank the crew of the R/V *Western Flyer* and the *Tiburón* and *Doc Ricketts* ROV pilots. Many thanks to David Pawson, Andrey Gebruk, and Antonia Rogacheva for help in identifying specimens. This research was funded by the David and Lucile Packard Foundation and contributes to the CCE-LTER program of the National Science Foundation. We very much

appreciate the suggestions and helpful enhancements suggested by anonymous reviewers.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.pocan.2014.04.007>.

References

- Aguzzi, J., Jamieson, A., Fujii, T., Sbragaglia, V., Costa, C., Menesatti, P., Fujiwara, Y., 2012. Shifting feeding behaviour of deep-sea buccinid gastropods at natural and simulated food falls. *Marine Ecology Progress Series* 458, 247–253. <http://dx.doi.org/10.3354/meps09758>.
- Amaro, T., Witte, H., Herndl, G.J., Cunha, M.R., Billett, D.S.M., 2009. Deep-sea bacterial variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic. *Progress in Oceanography* 50, 349–368.
- Billett, D.S.M., Bett, B.J., Reid, W.D.K., Boorman, B., Priede, I.G., 2010. Long-term change in the abyssal NE Atlantic: the “Amperima Event” revisited. *Deep Sea Research Part II: Topical Studies in Oceanography* 57, 1406–1417.
- Booth, J.A.T., Ruhl, H.A., Lovell, L.L., Bailey, D.M., Smith Jr., K.L., 2008. Size-frequency dynamics of NE Pacific abyssal ophiuroids (Echinodermata: Ophiuroidea). *Marine Biology* 154, 933–941.
- Chao, A., Colwell, R.K., Lin, C.-W., Gotelli, N.J., 2009. Sufficient sampling for asymptotic minimum species richness estimators. *Ecology* 90, 1125–1133.
- Drazen, J., Phleger, C., Guest, M., Nichols, P., 2009. Lipid composition and diet inferences of abyssal macrourids in the eastern North Pacific. *Marine Ecology Progress Series* 387, 1–14.
- Drazen, J.C., Bailey, D.M., Ruhl, H.A., Smith Jr., K.L., 2012. The role of carrion supply in the abundance of deep-water fish off California. *PLoS ONE* 7, e49332.
- FitzGeorge-Balfour, T., Billett, D.S.M., Wolff, G.A., Thompson, A., Tyler, P.A., 2010. Phytopigments as biomarkers of selectivity in abyssal holothurians: interspecific differences in response to a changing food supply. *Deep Sea Research Part II: Topical Studies in Oceanography* 57, 1418–1428.
- Francour, P., 1997. Predation on holothurians: a literature review. *Invertebrate Biology* 116, 52–60.
- Ginger, M., Santos, V., Wolff, G., 2000. A preliminary investigation of the lipids of abyssal holothurians from the north-east Atlantic Ocean. *Journal of the Marine Biological Association of the UK* 80, 139–146.
- Goody, A., Bett, B., Pratt, D., 1993. Direct observation of episodic growth in an abyssal xenophyophore (Protista). *Deep Sea Research Part I: Oceanographic Research Papers* 40, 2131–2143.
- Iken, K., Brey, T., Wand, U., Voigt, J., Junghans, P., 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Progress in Oceanography* 50, 383–405.
- Kahn, A.S., Ruhl, H.A., Smith Jr., K.L., 2012. Temporal changes in deep-sea sponge populations are correlated to changes in surface climate and food supply. *Deep Sea Research Part I: Oceanographic Research Papers* 70, 36–41.
- Lampitt, R.S., Billett, D.S.M., Martin, A.P., 2010. The sustained observatory over the Porcupine Abyssal Plain (PAP): insights from time series observations and process studies. *Deep Sea Research Part II: Topical Studies in Oceanography* 57, 1267–1271.
- Lauerman, L.M.L., Kaufmann, R.S., Smith Jr., K.L., 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. *Deep Sea Research Part I: Oceanographic Research Papers* 43, 1075–1103.
- Lehnert, H., Watling, L., Stone, R., 2005. *Cladorhiza corona* sp. nov. (Porifera: Demospongiae: Cladorhizidae) from the Aleutian Islands (Alaska). *Journal of the Marine Biological Association of the UK* 85, 1359.
- Levin, L.A., 1991. Interactions between metazoans and large, agglutinating protozoans: implications for the community structure of deep-sea benthos. *American Zoologist* 31, 886–900.
- Levin, L., DeMaster, D., McCann, L., Thomas, C., 1986. Effects of giant protozoans (class: Xenophyophorea) on deep-seamont benthos. *Marine Ecology Progress Series* 29, 99–104.
- Martin, J.H., Knauer, G.A., Karl, D.M., Broenkow, W.W., 1987. VERTEX: carbon cycling in the northeast Pacific. *Deep-Sea Research* 34, 267–285.
- Meyer, K.S., Bergmann, M., Soltwedel, T., 2013. Interannual variation in the epibenthic megafauna at the shallowest station of the HAUSGARTEN observatory (79° N, 6° E). *Biogeosciences* 10, 3479–3492.
- Newcombe, C.P., MacDonald, D.D., 1991. Effects of suspended sediments on aquatic ecosystems. *North American Journal of Fisheries Management* 11, 72–82.
- Norton, J.G., Mason, J.E., 2005. Relationship of California Sardine (*Sardinops sagax*) abundance to climate-scale ecological changes in the California Current system. *CalCOFI Reports* 46, 83–92.
- Okey, T.A., 1997. Sediment flushing observations, earthquake slumping, and benthic community changes in Monterey Canyon head. *Continental Shelf Research* 17, 877–897.
- Olabarria, C., 2006. Faunal change and bathymetric diversity gradient in deep-sea prosobranchs from Northeastern Atlantic. *Biodiversity and Conservation* 15, 3685–3702.
- Paull, C., Greene, H., Ussler, W., Mitts, P., 2002. Pesticides as tracers of sediment transport through Monterey Canyon. *Geo-Marine Letters* 22, 121–126.
- Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C.R., Levin, L.A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B.E., Smith, C.R., Tittensor, D.P., Tyler, P.A., Vanreusel, A., Vecchione, M., 2010. Deep, diverse and definitely different: unique attributes of the world’s largest ecosystem. *Biogeosciences* 7, 2851–2899.
- Ramirez-Llodra, E., Tyler, P.A., Baker, M.C., Bergstad, O.A., Clark, M.R., Escobar, E., Levin, L.A., Menot, L., Rowden, A.A., Smith, C.R., Van Dover, C.L., 2011. Man and the last great wilderness: human impact on the deep sea. *PLoS ONE* 6 (8), e22588. <http://dx.doi.org/10.1371/journal.pone.0022588>.
- Riemann, F., Tendaf, O.S., Gingele, F.X., 1993. *Reticulammina antarctica* nov. spec. (Xenophyophora, Protista) from the Weddell Sea, and aspects of the nutrition of xenophyophores. *Polar Biology* 13, 543–547.
- Roberts, D., Moore, H., 1997. Tentacular diversity in deep-sea deposit-feeding holothurians: implications for biodiversity in the deep sea. *Biodiversity & Conservation* 1505, 1487–1505.
- Robison, B.H., Reisenbichler, K.R., Sherlock, R.E., 2005. Giant larvacean houses: rapid carbon transport to the deep sea floor. *Science (New York, N.Y.)* 308, 1609–1611.
- Rogacheva, A., Gebruk, A., Alt, C.H.S., 2012. Swimming deep-sea holothurians (Echinodermata: Holothuroidea) on the northern Mid-Atlantic Ridge. *Zoosymposia* 224, 213–224.
- Ruhl, H.A., 2007. Abundance and size distribution dynamics of abyssal epibenthic megafauna in the northeast Pacific. *Ecology* 88, 1250–1262.
- Ruhl, H.A., 2008. Community change in the variable resource habitat of the abyssal northeast Pacific. *Ecology* 89, 991–1000.
- Ruhl, H.A., Smith Jr., K.L., 2004. Shifts in deep-sea community structure linked to climate and food supply. *Science (New York, N.Y.)* 305, 513–515.
- Ruhl, H.A., Bett, B.J., Hughes, S.J.M., Alt, C.J.S., Ross, E.J., Lampitt, R.S., Pebody, C.A., Smith Jr., K.L., Billett, D.S.M., in press. Links between deep-sea respiration and community dynamics. *Ecology*. <http://dx.doi.org/10.1890/13-0675.1>.
- Rykaczewski, R.R., Checkley, D.M., 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proceedings of the National Academy of Sciences of the United States of America* 105, 1965–1970.
- Schling, B.M., Stout, N.J., 2006. MBARI’s video annotation and reference system. In: *Proceedings of the Marine Technology Society/Institute of Electrical and Electronics Engineers Oceans Conference*, pp. 1–5.
- Schling, K., von Thun, S., Kuhnz, L., Schling, B., Lundsten, L., Jacobsen Stout, N., Chaney, L., Connor, J., 2013. Debris in the deep: using a 22-year video annotation database to survey marine litter in Monterey Canyon, Central California, USA. *Deep Sea Research Part I: Oceanographic Research Papers*.
- Smith Jr., K.L., 1987. Food energy supply and demand: a discrepancy between particulate organic carbon flux and sediment community oxygen consumption in the deep ocean. *Limnology and Oceanography* 32, 201–220.
- Smith Jr., K., Druffel, E., 1998. Long time-series monitoring of an abyssal site in the NE Pacific: an introduction. *Deep-Sea Research Part II* 45, 573–586.
- Smith Jr., K.L., Baldwin, R.J., Glatts, R.C., Kaufmann, R.S., Fisher, E.C., 1998. Detrital aggregates on the sea floor: chemical composition and aerobic decomposition rates at a time-series station in the abyssal NE Pacific. *Deep Sea Research Part II: Topical Studies in Oceanography* 45, 843–880.
- Smith Jr., K., Baldwin, R., Karl, D., Boetius, A., 2002. Benthic community responses to pulses in pelagic food supply: north Pacific subtropical gyre. *Deep Sea Research Part I* 49, 971–990.
- Smith Jr., K., Baldwin, R., Ruhl, H., 2006. Climate effect on food supply to depths greater than 4,000 meters in the northeast Pacific. *Limnology and Oceanography* 51, 166–176.
- Smith Jr., K.L., Ruhl, H.A., Bett, B.J., Billett, D.S.M., Lampitt, R.S., Kaufmann, R.S., 2009. Climate, carbon cycling, and deep-ocean ecosystems. *Proceedings of the National Academy of Sciences USA* 106, 19211–19218.
- Smith Jr., K.L., Ruhl, H.A., Kahru, M., Huffard, C.L., Sherman, A.D., 2013. Deep ocean communities impacted by changing climate over 24 y in the abyssal northeast Pacific. *Proceedings of the National Academy of Sciences* 110 (49), 19838–19841.
- Smythe-Wright, D., Boswell, S., Kim, Y.N., Kemp, A., 2010. Spatio-temporal changes in the distribution of phytopigments and phytoplanktonic groups at the Porcupine Abyssal Plain (PAP) site. *Deep Sea Research Part II: Topical Studies in Oceanography* 57, 1324–1335.
- Sweetman, A., Witte, U., 2008. Response of an abyssal macrofaunal community to a phytodetrital pulse. *Marine Ecology Progress Series* 355, 73–84.
- Tecchio, S., Coll, M., Christensen, V., Company, J.B., Ramirez-Llodra, E., Sardà, F., 2013. Food web structure and vulnerability of a deep-sea ecosystem in the NW Mediterranean Sea. *Deep Sea Research Part I: Oceanographic Research Papers* 75, 1–15. <http://dx.doi.org/10.1016/j.dsr.2013.01.003>.
- Vardaro, M.F., Ruhl, H.A., Smith Jr., K.L., 2009. Climate variation, carbon flux, and bioturbation in the abyssal North Pacific. *Limnology and Oceanography* 54, 2081–2088.

- Wigham, B.D., Hudson, I.R., Billett, D.S., Wolff, G.A., 2003a. Is long-term change in the abyssal Northeast Atlantic driven by qualitative changes in export flux? Evidence from selective feeding in deep-sea holothurians. *Progress in Oceanography* 59, 409–441.
- Wigham, B.D., Tyler, P.A., Billett, D.S.M., 2003b. Reproductive biology of the abyssal holothurian *Amperima rosea*: an opportunistic response to variable flux of surface derived organic matter? *Journal of the Marine Biological Association of the UK* 83, 175–188.
- Yahel, G., Whitney, F., Reiswig, H.M., Eerkes-Medrano, D.I., Leys, S.P., 2007. In situ feeding and metabolism of glass sponges (Hexactinellida, Porifera) studied in a deep temperate fjord with a remotely operated submersible. *Limnology and Oceanography* 52, 428–440.