A year in Barkley Canyon: A time-series observatory study of mid-slope benthos and habitat dynamics using the NEPTUNE Canada network

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ABSTRACT

Understanding long-term trends in species abundance and distribution represents an important challenge for future research in the deep sea, particularly as management of human impacts becomes a more important concern. However, until natural higher frequency variability is better understood, it will be difficult to interpret any long-term trends that may be apparent in data sets. We present here the results of the first year of observations at the NEPTUNE Canada cabled observatory site in Barkley Canyon, off the coast of Vancouver Island, in the northeast Pacific Ocean. Presence/absence and abundance data for 28 faunal groups were extracted from daily video records from an observatory camera. Concurrent CTD and current meter data were collected from co-located instruments. Water mass properties, currents and faunal community composition exhibited notable seasonal trends. Distinct seasonal faunal groupings were observed, together with summer and winter trends in temperature, salinity and current patterns. Variations in abundance of decapod crustaceans and fishes were responsible for most differences between faunal groups. We suggest that faunal composition may have been responding to seasonal variations in food availability, together with direct and indirect physical influences on predator and prey abundance.

1. Introduction

The study of deep-sea benthic ecosystems has traditionally relied on the collection of data and physical samples by oceanographic vessels and submersibles (Thiel et al., 1994). Ship-based surveys have been essential to the development of our understanding of the biodiversity and distribution of deep-sea organisms, culminating in the recently completed Census of Marine Life. Knowledge of processes that shape and change deep-sea benthic communities has advanced at a slower pace. Several studies have reported long-term, inter-annual trends in species composition and abundance (reviewed in Glover et al. (2010)), but causation is difficult to determine without experimentation or continuous observation. Deep-sea ecosystems are subject to a variety of environmental influences from cyclic phenomena such as tides, to disturbances acting at multiple temporal and spatial scales. These influences act on biological processes at corresponding time scales. Semi-diurnal tides are known to affect the behavior and activity of fishes and benthic invertebrate species (Aguzzi et al., 2011a). Over several days, benthic storms, generated by changes in current structure or biological activity can resuspend sediment,

which in turn can affect biogeochemical exchanges at the sediment–water interface (Thistle et al., 1991; Yahel et al., 2008). Seasonal scale variations in organic matter input from the surface ocean control food availability for deep-sea benthic organisms and influence reproductive cycles (Billett et al., 2010). At decadal scales, variations in environmental conditions related to phenomena such as the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO; Blanchard et al., 2010) may cause changes in species abundance, as may changes in ocean climate related to global warming. Understanding decadal and longer-term trends in species abundance and distribution represents an important challenge for future research in the deep sea, particularly as management of human impacts becomes a more important concern. But until natural higher frequency variability is better understood, it will be difficult to interpret any long-term trends that may be apparent in data sets (Smith et al., 2008).

Variability in particulate food input from the photic zone is an important driver of seasonal and longer-term change in deep-sea benthos. Surface productivity and related food supply are widely studied in deep-sea ecology and have been shown to shape benthic communities from the continental slope to the abyssal plain, including submarine canyons (Cunha et al., 2011; Billett et al., 2010; Leduc et al., 2012). Much of our understanding of seasonal variability in deep-sea faunal communities comes from work at long-term study sites such as Station M in the eastern

North Pacific Ocean and the Porcupine Abyssal Plain in the North Atlantic, where researchers have used a combination of seasonal sampling and autonomous instrument platform deployments (Gage and Tyler, 1992; Smith and Kaufmann, 1999; Billett et al., 2001; Ruhl and Smith, 2004). These studies have identified seasonal variations in the quality and quantity of food imports and some temporal trends in faunal composition and abundance (Billett et al., 2010). However, literature contains few integrated studies that examine the influence of multiple environmental variables on the composition and abundance of deep-sea benthos (Mamouridis et al., 2011). Some progress in understanding the relationship between multiple habitat variables and faunal properties has also come from habitat mapping studies that use cameras to examine megafaunal distribution in relation to environmental factors (Buhl-Mortensen et al., 2012).

Time series observations can also be used to study the influence of multiple environmental variables on benthic communities in the deep sea. The recent development of cabled seafloor observatories, with real-time communications and 'unlimited' power capabilities is providing new opportunities for time-series studies of deep-sea ecology. Cabled observatories are being established or are currently in operation in several areas of the world ocean. Some have seismic or single discipline missions while others are multidisciplinary. The NEPTUNE Canada and VENUS networks, operated by Ocean Networks Canada, are examples of multi-disciplinary cabled observatories that support the simultaneous observation of benthic fauna and habitat variables. In their first months and years of operations, continuous imagery and data from these networks have been used to study seasonal and higher frequency variability in benthic ecosystems (Matabos et al., 2012; Aguzzi et al., 2011b; Matabos et al., in preparation). As observatory data accumulate, high-resolution studies of longer-term trends will become possible.

The NEPTUNE Canada (NC) cabled undersea network, off Vancouver Island, Canada supports continuous observations of faunal and habitat variables at several deep-water sites. Instrument platforms connected to the NC network have been recording daily data and video imagery since May, 2010. The pilot study presented here examines the first complete year (2011) of data from a NC site in Barkley Canyon (800–1000 m depth), a submarine canyon that incises the continental shelf off Vancouver Island. The NC community science experiment in Barkley Canyon was designed specifically to study benthic-pelagic coupling in a submarine canyon, mid-slope setting. The primary goal of this study was to develop baseline knowledge of the seasonal dynamics of the benthic faunal communities inhabiting the Barkley Canyon site and to explore their relationship to environmental factors over an entire year. A companion study (Matabos et al., in preparation) examined hourly-scale variability in habitat and faunal properties at this same site, during the month of December, 2011. The specific goals of this study were to:

(i) identify temporal patterns in the composition of the epi-benthic megafauna from daily video observations,
(ii) quantify variability in the physical environment using continuously recorded data, and
(iii) examine relationships between physical processes and observed biological patterns.

Previous studies of seasonal and inter-annual variability in megafaunal composition and abundance in the deep ocean and on continental shelves and slopes have used sample data and imagery from camera tows or time-lapse camera deployments. At abyssal depths echinoderms, especially holothurians, are known to exhibit substantial temporal differences in abundance and biomass (Billett et al., 2010; Lauermann and Kaufmann, 1998), whereas abundance changes of more mobile organisms such as

fishes and crustaceans appear to be the most prominent feature of megafaunal dynamics on continental shelves and slopes (Sardà et al., 1994; Moranta et al., 2008; Aguzzi et al., 2009; Papiol et al., 2012). We therefore hypothesized that these latter groups would dominate seasonal scale changes in abundance of the Barkley Canyon megafauna, and that these changes would be related to seasonal shifts in water mass properties that could be measured by the in situ instruments at this site. Waters off Vancouver Island, as elsewhere along the northwest coast of North America, are influenced by summertime northerly winds that cause intermediate depth, oxygen-depleted water that lies along the continental slope, to upwell onto the shelf, particularly through submarine canyons (Hsieh et al., 1995; Keeling et al., 2010).

2. Methods

2.1. Study area

The NEPTUNE Canada Barkley Canyon node supports four instrument arrays (sites): an upper slope site outside of the canyon (396 m depth); a mobile, tracked instrument platform in a gas hydrate field; a pair of instrument platforms near the base of the north wall of the canyon (890 m depth); and a single platform in the canyon axis (Fig. 1). Each instrument platform carries a suite of instruments for environmental and biological data acquisition (Table 1). This study used data acquired by the paired platforms (Pods 3 and 4), which were installed in May, 2010. Several previous studies have documented the physical oceanography and biological productivity of the water column in and around Barkley Canyon (Freeland et al., 1984; Thomson and Allen, 2000; Allen et al., 2001).

Instruments are maintained once a year; during this study Pods 3 and 4 were lifted to the surface, cleaned, failed instruments swapped, and redeployed at the same location. Environment Canada maintains a surface meteorological buoy on La Perouse Bank, located NNE of the Barkley Canyon study area.

2.2. Data collection

Data from all instruments are archived and available online in near real-time using the Oceans 2.0 software interface (dmas.uvic.ca). The cameras can be operated by investigators from shore or set on automated schedule. All videos and still imagery are archived and available through Oceans 2.0. Temperature (°C), salinity (psu), density, pressure (dbar), chlorophyll fluorescence, and turbidity were acquired by instruments deployed on the canyon wall benthic platforms at 890 m depth (Table 1). The two platforms were separated by 70 m. Each instrument sampled at a rate of one measurement per minute. An upward-looking 150 kHz ADCP provided information on water column currents.

Images were collected using a 470 Line ROS Inspector low light, color camera, equipped with an 18 × optical zoom. A pan/tilt unit allowed complete coverage of seafloor (± 90° Tilt and ± 180° Pan) and light was available on demand from two Deep-Sea Power and Light variable intensity lamps.

Following a commissioning phase, data acquisition from this site began in December, 2010 and continued until the camera failed in January, 2012. A replacement camera was installed in June, 2012 but not used in this study. Videos were recorded daily, except during the maintenance cruise (8–27 July, 2011). Since the camera was being tested by several research projects, there was no standardized image acquisition protocol during this first year. The length of video records varied from 9 s to 1 h and 57 min in the period from December 29, 2011 to January 2, 2012. Some videos included a full sweep of the area, while for others the camera remained in a fixed position. Zoom level was also variable over the
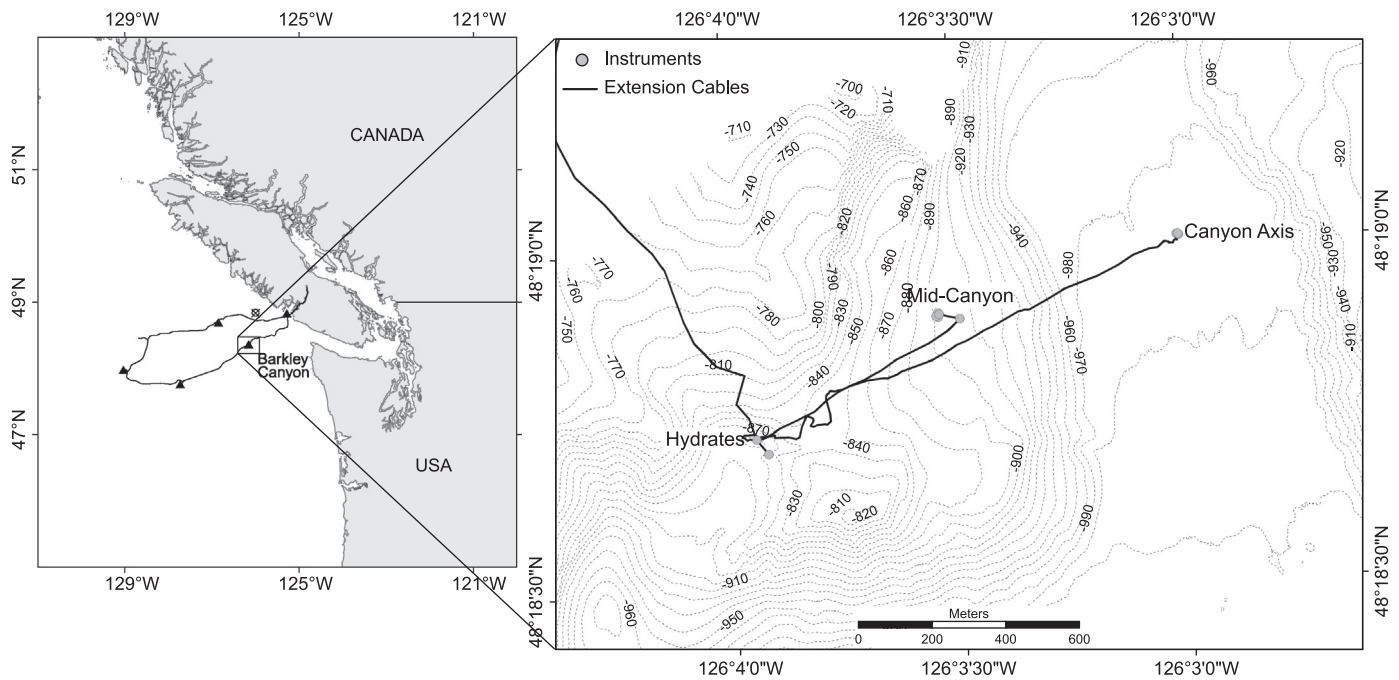
Fig. 1. Location of NEPTUNE Canada (NC) camera/instrument site in Barkley Canyon. Left panel inset shows the NEPTUNE Canada network with the five nodes. Right panel illustrates instrument pod installations within Barkley Canyon (upper slope site not shown). All NC data used in this study are from Pods 3 and 4 at mid-canyon site. Square symbol north of Barkley Canyon in left panel indicates location of meteorological buoy on La Perouse Bank, the source of atmospheric data used in this study.

Table 1

List of instruments used for this study from the two benthic platforms at the study site near the base of the wall of Barkley Canyon, North East Pacific. Instruments from which the data were not used are not reported.

Site	Instruments	Type	Water property
POD 3	ADCP 150 kHz	RDI	Water column currents
POD 4	Camera system	ROS 'Inspector'	Seafloor imagery
	Fluorometer	WET Labs	Chlorophyll, turbidity
	CTD	Sea-Bird	Temperature, conductivity, pressure

year. Variations in lighting duration may have affected the number and type of species in the area, with species attracted by the lights while others will avoid them. In order to mitigate variability and bias related to the non-systematic acquisition of imagery, only videos satisfying the three following rules were analyzed: (i) camera must be in a fixed position; (ii) seafloor must constitute more than half of the image area; and (iii) camera must be zoomed out (wide field of view). When all three rules were met, 5 min of video were analyzed per day and individuals counted to the lowest taxonomic level possible. Video analysis data were pooled according to the fortnightly tidal cycle, determined from pressure data recorded by the camera platform CTD. Pooling data in this way augmented sample size for statistical analysis and mitigated possible aliasing effects from the tidal cycle. Measured tides were mixed semidiurnal/diurnal with the M2/S2 dominating to give a pronounced ∼14-day, spring-neap cycle.

2.3. Data analysis

2.3.1. Environmental characterization

A Seabird 16+ CTD and a Wetlabs fluorometer collected water property data in near-real time. Both instruments sampled at 1-min intervals. To mitigate time stamp jitter for time series analysis, the CTD data were binned to one hour on the hour. These data were then analyzed for tidal constituents and, for some

analyses, low-pass filtered to remove the effects of tidal currents. Hourly pressure data were low-pass filtered with a 72-h, Kaiser–Bessel window designed filter to remove higher frequency tidal effects (Emery and Thomson, 1997). The fluorometer measured backscattered fluorescence at 695 nm from a 470 nm source. Turbidity was measured as the overall backscattered intensity at 700 nm.

Deep-sea current data were collected by an upward facing 150 kHz RDI Acoustic Doppler Current Profiler (ADCP) on Pod 3. Five-meter bins were used with the center of the first bin at 9 m above bottom with a useable range of up to 50 bins or 259 mab. The data were collected as single pings in radial coordinates and converted to earth coordinates and 15-minute averages of about 450 pings on shore. These data were then resampled with anti-aliasing filtering to hourly data, and filtered with a 30 h low-pass filter. All filtering was done using a Kaiser–Bessel window designed filter.

2.3.2. Biological data

Organism abundance data for all video recordings were compiled at the lowest taxonomic level. Prior to any analysis, a Hellinger transformation was applied to the abundance data to mitigate effects of differences in sample size. This transformation is the square root of the relative abundance of each species in each observation (i.e., tidal period). After this transformation, Euclidean-based methods of analysis will preserve the Hellinger distance among observations. This distance is more appropriate than Euclidean distance for ordination or MRT analysis of community composition data containing many zeros (Legendre and Gallagher, 2001). Temporal breaks over the year were identified using a multivariate regression tree (MRT; De'ath, 2002). This method was used to define groups of dates that had similar faunal composition and were temporally adjacent. The MRT is a partitioning method of the multivariate response data matrix (i.e., species) constrained, in this study, along a single explanatory variable (i.e., time) to generate temporally consistent groups. The multivariate tree is grown by successive binary splitting of the data, with each split chosen to minimize the total multivariate sum of squares within the
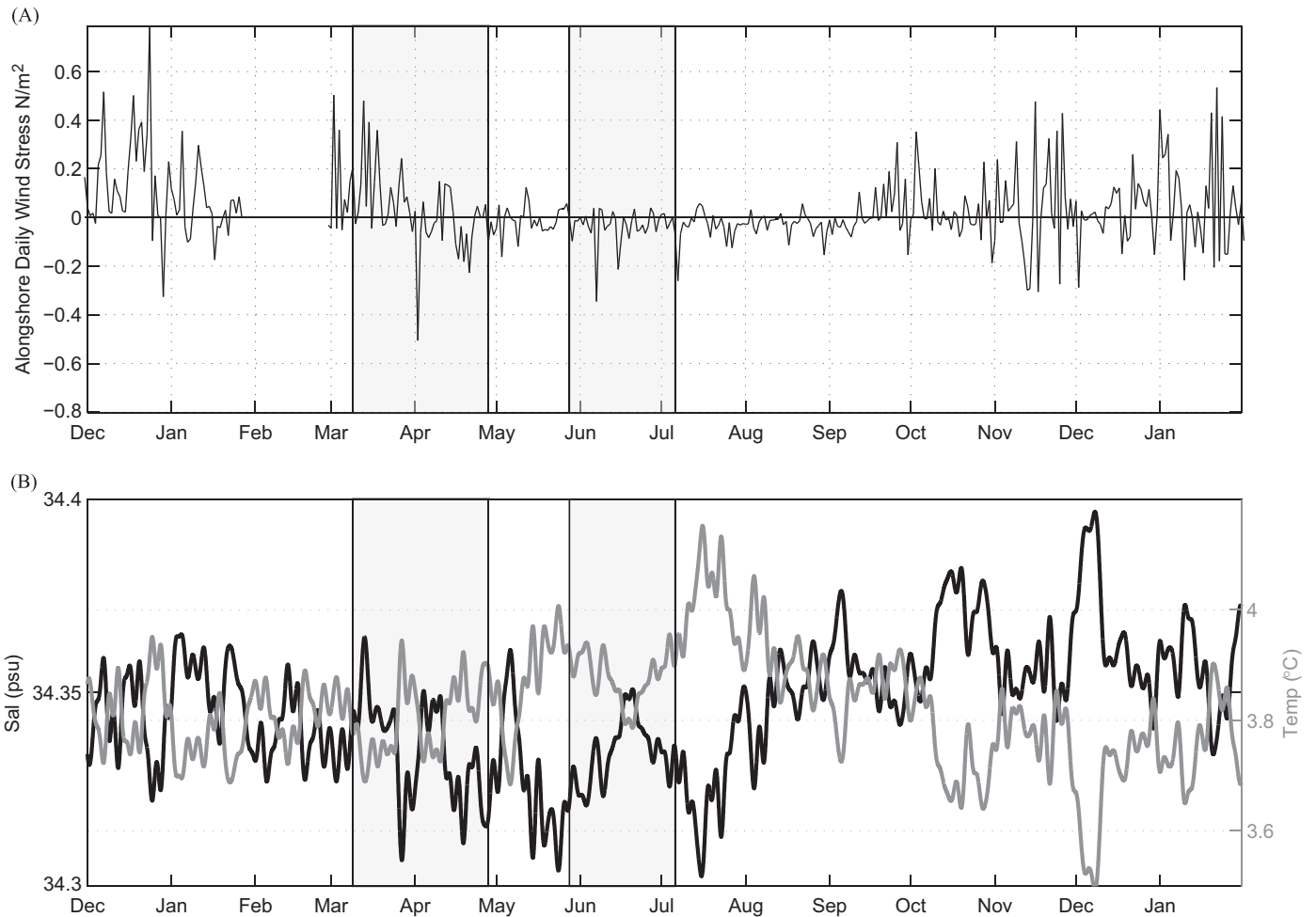
(A)

(B)

Fig. 2. Time-series of wind stress (a), and salinity and temperature characteristics (b) during the 2011 study period. Wind data are from the La Perouse Bank meteorological buoy, while water property data are from Pod 4 in Barkley Canyon. Gray shaded periods in (b) indicate pulses of fluorescence as detected by the fluorometer on Pod 4. Data in (b) filtered to remove tidal effects, as described.
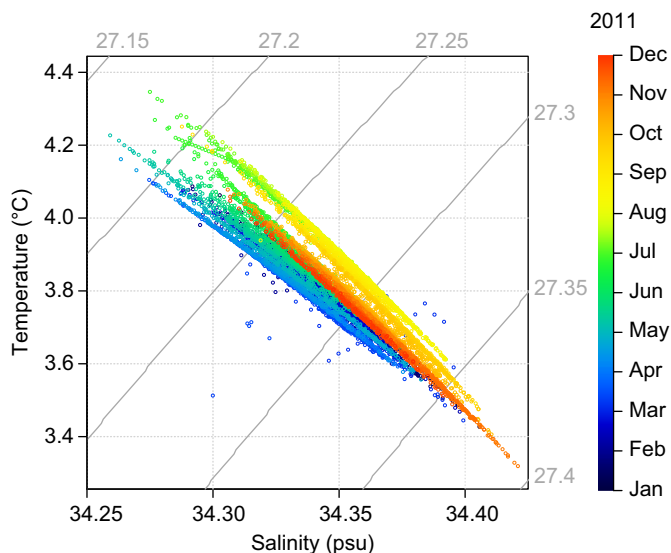

Fig. 3. Scatter plot of hourly temperature–salinity values for 2011 at Barkley Canyon study site. Data not filtered for tidal effects.

two groups formed. Each cluster is defined by the multivariate mean of its sites, the number of sites, and the explanatory variable value that explained it, in this study the time. The tree was generated using the

'mvpart' package (De'ath, 2002) in the R statistical language (R Development Core Team, 2008).

The computation of a Bray–Curtis index among observation periods generated a distance matrix subsequently used for ordination methods. The distance matrix was computed on both raw abundance data (not shown) and on Hellinger-transformed data. To represent ecological distances between observation periods we applied a dendrogram, computed using the Ward's (1963) method, and a non-metric, multidimensional scaling (NMDS). Environmental variables vectors were fitted onto the ordination. The arrows show the direction of the increasing gradient and the length of the vector is proportional to the correlation between the variable and the ordination. The significance of the fitted vectors was assessed using 999 permutations of the environmental variables. A SIMPER analysis (Similarity Percentage) helped identify species contributing the most to the differences among the clusters detected in the dendrogram. All analyses were conducted using the package 'Vegan' in the R language library (Oksanen et al., 2008; R Development Core Team, 2008).

3. Results

3.1. Physical environment

Summer time (May through September) surface winds in the region showed distinctly different characteristics from wind

Table 2

Temporal range of organisms encountered in the camera field of view in Barkley Canyon, from 2 weeks observation period points. Organisms were identified to the lowest taxonomic level possible. Shaded groups separate taxa from the same phylum the following order: arthropods, chordates, mollusks, echinoderms, cnidarians and ctenophores. The striped bars represent periods when no data were available.
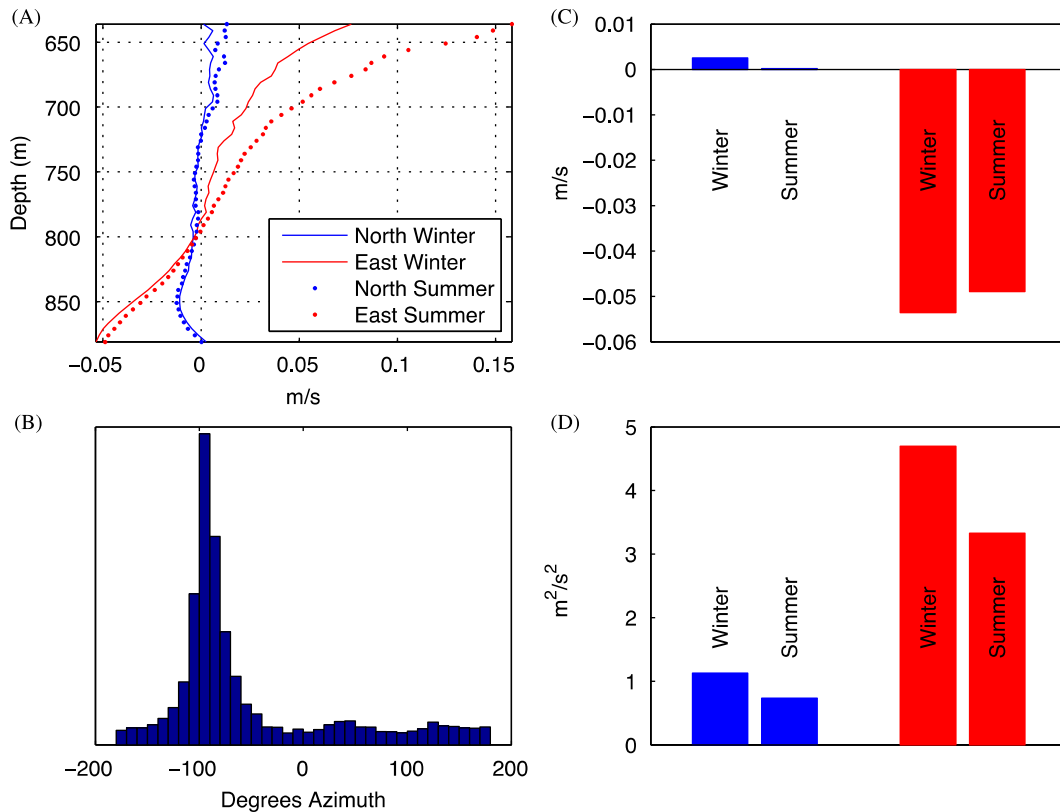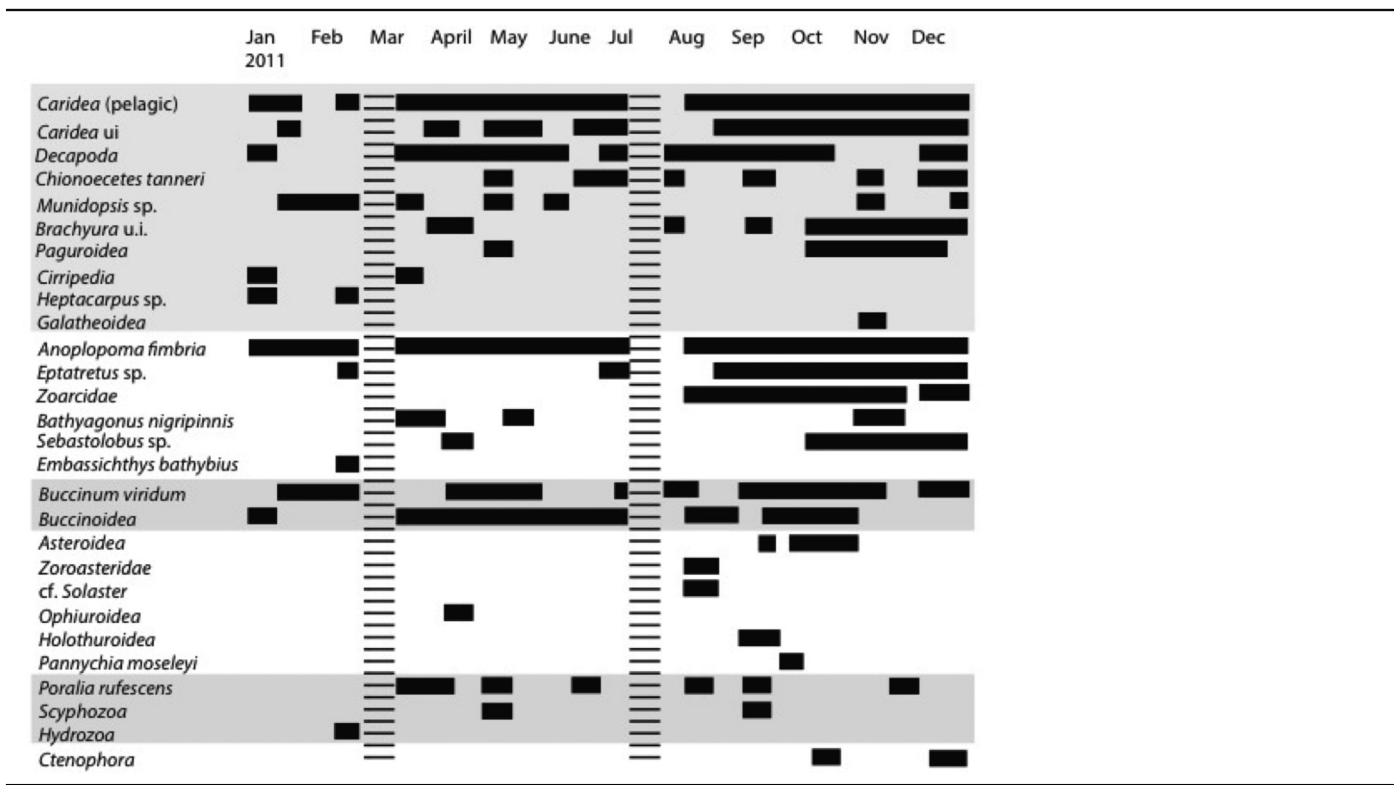

Fig. 4. Current data from 150 kHz ADCP on Pod 3 in Barkley Canyon. (a) Vertical profiles of North and East current vectors, in summer and winter. (b) Principle direction of currents in bottom bin (9–14 mab) of ADCP profile, for entire year. Bar graphs show mean velocity (c) and variance (d) of North (blue) and East (red) current vectors in bottom bin (9–14 mab) of ADCP profile, during summer and winter months. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

patterns at other times of the year (Fig. 2a). Winds were lighter and more northerly in direction during summer months. Temperature/salinity data (Fig. 2b) showed a seasonal trend that approximately mirrored the wind pattern, with a generally warmer and fresher water mass present at the study site during summer months (May through September). In addition, fluorometer data (not shown) had distinct, sustained pulses of near-bottom fluorescence in spring (April–May) and summer (June–July, Fig. 2b). Turbidity data (not shown) exhibited frequent spikes suggestive of brief resuspension events but no seasonal pattern could be identified. Some of the turbidity spikes were related to illumination of the camera lights, which occasionally caused fish to make sudden movements resuspending sediment. The camera lights also appear to have been responsible for anomalous fluorescence and turbidity readings in the sensors' optical detector, depending on the direction of camera pans. For these reasons, we do not offer any further interpretation of the fluorescence and turbidity data.

A scatter plot of the temperature-salinity data (Fig. 3) reveals two notable features of these water mass properties. In addition to the summer-winter pattern described above, higher frequency, across-isopycnal pulsing occurred at all times of year.

Current data were separated into summer (April through September) and winter (October through March) seasons based on patterns observed in water mass properties, in an effort to understand relationships between water mass changes and lower water column current patterns. Mean currents in the N–S direction were near zero in both seasons and throughout the depth range of the ADCP (Fig. 4a). Mean currents were stronger along the East–West vector, which corresponds to the general direction of the main axis of Barkley Canyon. Mean flow 10 m above bottom the seafloor was predominantly easterly, shifting to a westerly flow higher in the water column with an inflection point near 800 m depth (Fig. 4a). For mean bottom currents along both axes, there was little summer-winter difference in direction or velocity (Fig. 4b and c), but there was a notable decrease in variance of current speed in summer (Fig. 4d).

3.2. Fauna

Twenty-eight different morphotypes, belonging to 6 phyla (i.e. cnidarians, ctenophores, arthropods, echinoderms, mollusks and chordates), were observed in a total of approx. 17.5 h of video recordings (5 min × 210 observations). Faunal identification from video imagery was challenging and individuals were occasionally difficult to discriminate at the species or genus levels. To minimize errors, uncertain lower level identifications were made to a higher taxonomic level (e.g. brachyuran and hydrozoa). For example, the unidentified decapoda order (decapoda) was used for squat lobsters (Munidopsis sp.), crab or shrimp that were too far from the camera to permit discrimination, appearing as red 'dots' in the camera field of view. The brachyura category probably included a mixed assemblage of crab species. Several morphologically similar shrimp occur along the west coast of North America (Zimmermann, 2006), but we are confident that most observed shrimp are from the family hippolytidae.

Some species such as the sablefish (Anaplopoma fimbria) and a buccinid gastropod (Buccinum viridum) occurred all year round but most of the taxonomic units were sporadically present in the field of view (Table 2). No echinoderms were observed during the summer from May through July or in the winter in December/January.

There were no discernable seasonal patterns in species richness or rarefaction indices through the year (Table 3). Species richness for the fortnightly observation periods ranged from 3–14, while the calculated rarefaction index for a sample of 36 individuals ranged from 3.0 to 9.8 (Table 3). There was a significant correlation

Table 3
Faunal counts from 5-min video recordings for fortnightly tidal periods in Barkley Canyon during 2011, together with corresponding species richness and rarefaction indices.

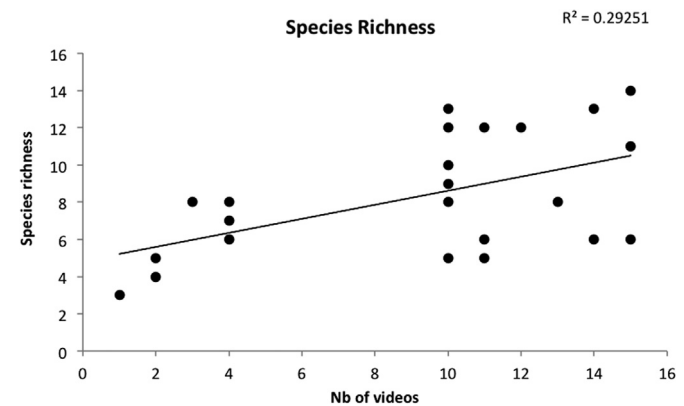| Observation period	Number of videos	Total no. individuals	Species richness	Rarefaction (36 ind.)
29 Dec.–13 Jan.	4	36	6	6.0
14–28 Jan.	2	51	5	4.5
29 Jan.–12 Feb.	1	16	3	3.0
13–26 Feb.	3	93	8	6.4
14–28 Mar.	4	43	7	6.3
28 Mar.–12 Apr.	10	124	10	6.8
13–26 Apr.	10	121	5	4.8
27 Apr.–11 May	10	54	12	9.8
12–26 May	11	91	6	5.4
27 May–10 Jun.	11	108	5	3.5
11–24 Jun.	14	152	6	4.2
25 Jun.–9 Jul.	10	106	8	5.1
25 Jul.–8 Aug.	2	6	4	4.0
9–22 Aug.	13	135	8	5.2
23 Aug.–6 Sept.	15	164	6	4.6
7–21 Sept.	15	259	14	6.3
22 Sept.–6 Oct.	10	123	9	6.4
7–21 Oct.	11	163	12	7.3
22 Oct.-4 Nov.	14	179	13	7.9
5–19 Nov.	10	161	13	7.4
20 Nov.–4 Dec.	4	42	8	7.4
5–19 Dec.	15	170	11	6.8
20 Dec.–2 Jan.	12	127	12	8.1

Fig. 5. Relationship of species richness to the total number of videos pooled for each per fortnightly sampling period.

(Fig. 5) between species richness and sample size (number of observations per fortnightly period).

The multivariate regression tree (MRT; Fig. 6) identified three groups of observation period, explaining a total of 37.2% of the variation in the relative abundance dataset. The first split separated the four observation periods prior to February 27, from the remainder of the year. Following this first split, two further groups emerged, separated at October 21. Inspection of the MRT bar plots revealed that the first group is determined by the presence of Munidopsis sp. and Heptacarpus sp., the second group by the presence of decapods and group 3 by carideans (Fig. 6).

The Bray–Curtis distance dendrogram (Fig. 7a) generally agreed with the MRT, separating January/February observations (Group 1) from the rest (except for 25th July), and then splitting post-October 22, 2011 observations (Group 2) from the remainder. With one exception (December 29, 2010), the split of Groups 3 and 4 separates observations in early spring (Group 3) from those in late spring, summer and early autumn (Group 4). The MDS (Fig. 7b) supported the grouping highlighted by the dendrogram, with a stress value of 0.11. Temperature was the only environmental variable with a
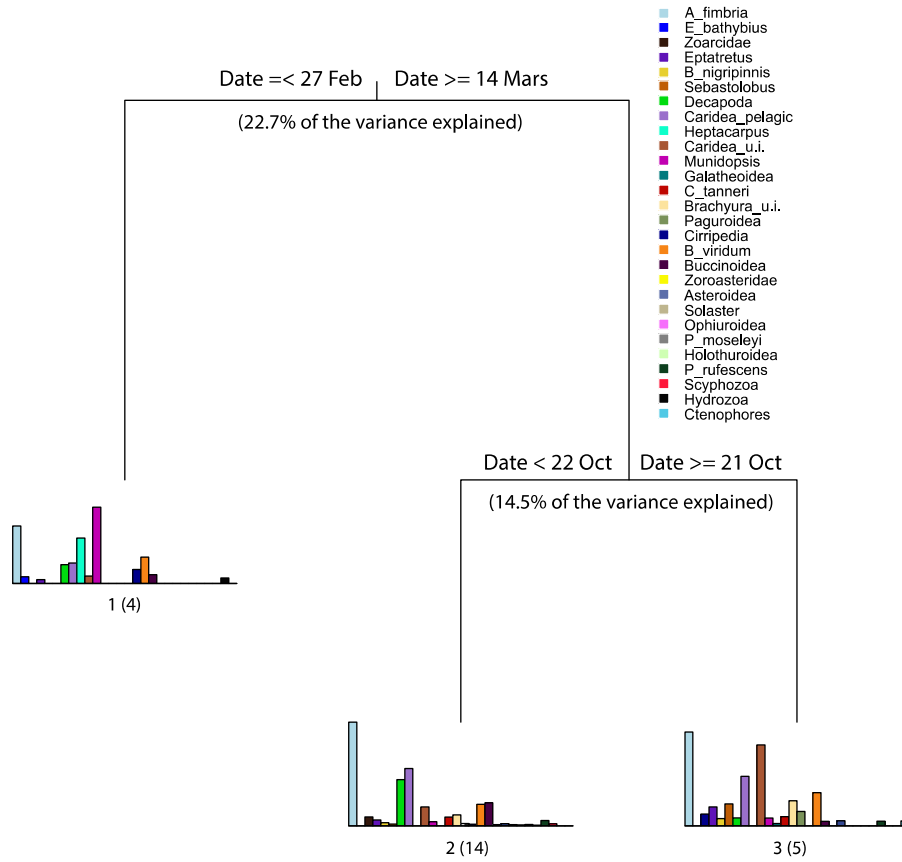
Fig. 6. Multivariate Regression Tree (MRT) using Hellinger transformed faunal abundance data. Numbers in parentheses indicate the number of observations included in Groups 1, 2 and 3. Note absence of data between February 28 and March 14 (see Table 2).
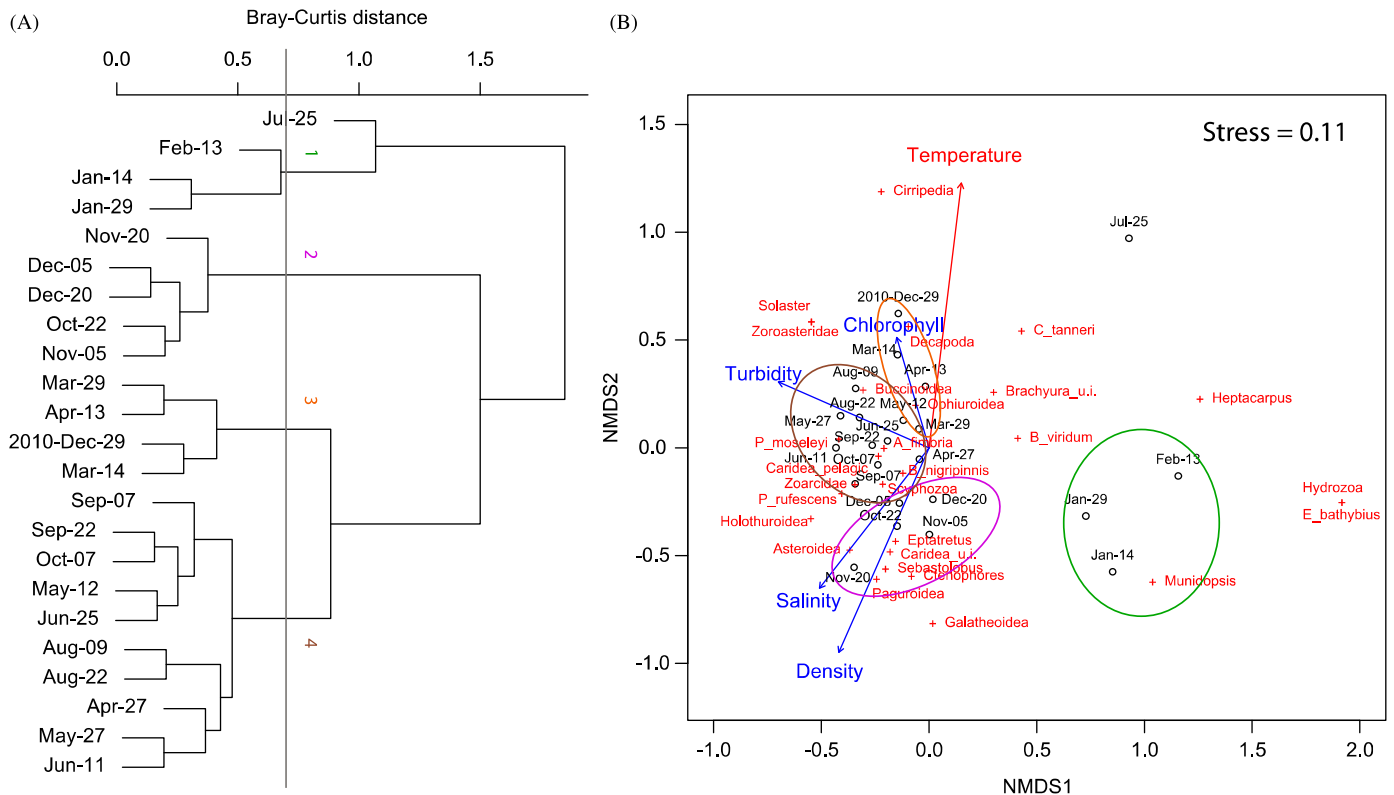

Fig. 7. Graphic ordination of observation periods using Bray–Curtis coefficients, based on Hellinger transformation of quantitative counts of fauna in the camera field of view in Barkley Canyon. (a) Dendrogram. (b) Non metric multidimensional scaling (NMDS) showing groups (colored ellipses) identified by the dendrogram. Environmental variables vectors were fitted onto the ordination. Arrows show the direction of increasing gradients for environmental variables. Length of each vector is proportional to the correlation between the variable and the ordination. Red arrows identify significant correlations with the ordination. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

significant influence on the NMDS ordination (Fig. 7b), where it aligned with the axis of separation of Groups 2, 3 and 4.

Munidopsis sp. relative abundance contributed 44% of the difference between the two main groupings (Group 1 versus Groups 2–4), followed by *Heptacarpus* sp. with 22% and the sablefish *A. fimbria* (12%). Groups 2 and 3 were distinguished by decapod abundance (31%) followed by unidentified *Caridea* (24%), *A. fimbria* (13%) and pelagic carideans (6%). Relative abundance of the Decapod taxon accounted for 31% of the difference between Groups 3 and 4, followed by *A. fimbria* (19%) and pelagic carideans (14%).

The relative importance of *Munidopsis* sp. in the first division of the Bray–Curtis dendrogram agrees with the first MRT split where the mean relative abundance of *Munidopsis* sp. for the first group was 51%, compared with 5% or less in Groups 2 and 3. The *Munidopsis* sp. taxon also grouped closely with the Group 1 dates in the NMDS (Fig. 7b). This relative dominance of *Munidopsis* sp. in Group 1 was also reflected in the mean abundance of *Munidopsis* sp. for this period (6.3 individuals ($n=10$) per sample), which was significantly (Mann–Whitney U test, $p=2.13 \times 10^{-13}$) greater than the mean of 0.04 individuals ($n=200$) per sample for the remainder of the year. For dates after February 27th (in fact, March 14th, because of a data gap), no more than one individual *Munidopsis* sp. was seen in any of the 200 observation periods. Sablefish also showed a similar pattern of relative and real abundances. Mean sablefish abundance per observation period before February 27 was 2.4 ($n=10$), significantly lower than the mean of 6.1 ($n=200$) for the remainder of the year (Mann–Whitney U test, $p=0.005$).

3.3. Discussion

The strong seasonal patterns in the distribution of several faunal groups are the most prominent biological feature of our year of observation. While there were some consistent, year-round residents at the study site, the dendrogram and multidimensional scaling determinations identified winter (pre-February 27 and post-October 22) and extended summer (mid-March to mid-

October) assemblages. Most of these patterns can be explained as motile organisms moving in and out of the field of view of the camera, and presumably the general vicinity of our observing system, at a time scale of weeks. These include pelagic and demersal organisms such as shrimp, gelatinous plankton and fish, as well as slower moving, entirely benthic galatheid crabs and echinoderms. The three sessile organisms that were occasionally observed (sponge, anemone, and barnacle) were attached to gastropod shells, so that their movements are those of their hosts.

Because of the location of our instruments near the wall of a submarine canyon, on the continental slope, faunal movements out of the study area are likely to involve a depth change, and possibly a change in water mass properties. However, our data do not support the idea of organisms moving away from the study area to seek more hospitable water masses. The seasonal and higher frequency variations in water mass physical properties observed at this site were relatively minor, with the site being characterized by the 27.2–27.4 kg/m^3 isopycnal. The depth of the study site corresponds to the core of the oxygen minimum zone in the North Pacific, where oxygen concentrations are less than 0.5 ml O$_2$/l. Time series CTD-O$_2$ profiles at nearby Ocean Station P4 (http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/line-p/index-eng.htm) show only minor seasonal change in dissolved oxygen concentrations in the Sigma Theta 27.0 to 27.5 isopycnal range during 2011 (0.35 ml O$_2$/L in February, decreasing to 0.29 mL O$_2$/L in August). Although there were no dissolved oxygen sensors on the two Barkley Canyon instrument pods in 2011, ROV CTD-O$_2$ profiles (data not shown) during servicing dives to the site in July and September 2011 show close agreement with the P4 vertical profiles. Data from an oxygen sensor installed on Pod 4 in 2012 (not shown) show dissolved oxygen varying between 0.24 and 0.31 ml O$_2$/l from June 1, 2012 to February 20, 2013. Hourly averaging reduced this range (Fig. 8). These observations suggest that only minor changes in dissolved oxygen concentrations occurred at the study site in 2011, and that this seafloor location was below the depths affected by shelf-edge
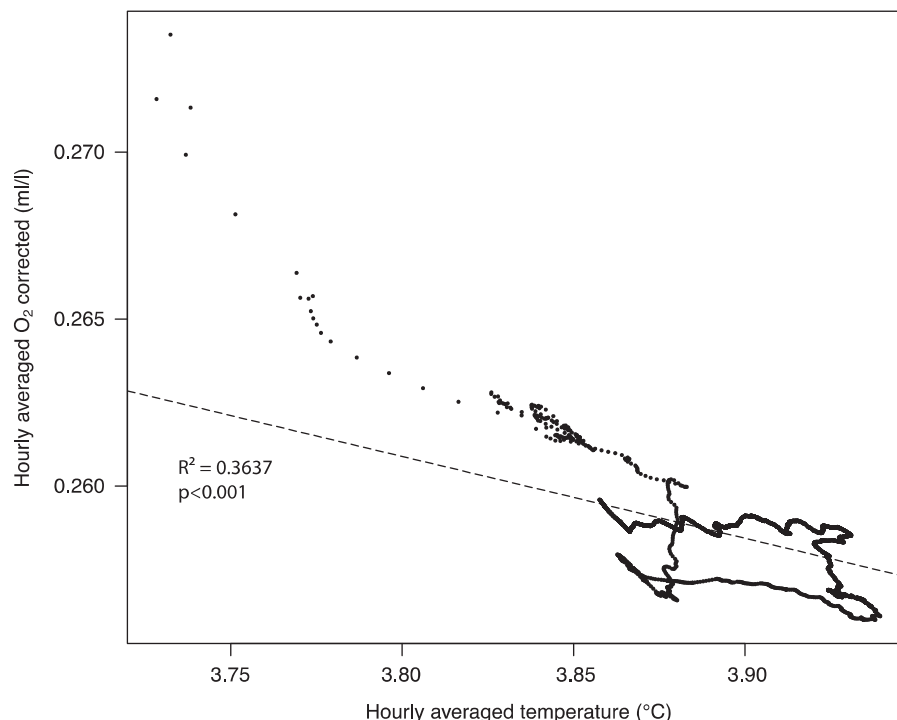

Fig. 8. Relationship of hourly averaged dissolved oxygen concentrations and temperature at Barkley Canyon Pod 4 location. Data are for the period June 1, 2012 through February 20, 2013, which followed the 2011 observations analyzed here. See text for explanation.

upwelling, at least during 2011. Nevertheless, the 2012–2013 dissolved oxygen concentrations were significantly correlated with temperature, indicating a relationship with water mass changes (Fig. 8).

Another potential habitat property that should be considered in explaining the movements of organisms through the study site is food availability. With growing evidence for seasonal and inter-annual variability in food supply to the seafloor, researchers often look to this factor to explain changes in faunal abundance (Billett et al., 2010). The spring and summer pulses in fluorometer data are indicative of periods of sporadic phytodetritus abundance at the study site, as would be expected during the phytoplankton growth season. This could be of some significance to deposit feeding organisms such as echinoderms, but it is difficult to attribute summer and wintertime absences of fish and deposit feeders to spring and summer peaks in phytodetritus. Further, the correspondence between suspended phytodetritus particles near the seafloor and the food richness in sediments being processed by deposit feeders at this site is not known.

Interest in the importance of seasonal variability in the deep sea was stimulated by the now classic time-lapse camera observations of phyto-detritus pulses accumulating on the seabed in the Porcupine Seabight in the North Atlantic (Lampitt, 1985). Since that time, a small number long-term sites have been established in the deep ocean that permit the study of seasonal patterns in faunal composition and activity, including reproduction, and causal roles of environmental variables (e.g. Tyler, 1988). Several studies have examined seasonal movements or changes in activity of benthic and bentho-pelagic megafauna on continental slopes. These studies consider possible links to food availability (Sardà et al., 1994; Moranta et al., 2008; Papiol et al., 2012) and predation pressure (Aguzzi et al., 2009) and note seasonal correlations with changes in temperature and salinity.

As discussed above, the relative minor fluctuations in water mass physical properties observed in Barkley Canyon make it unlikely that organisms showing seasonal signals in presence/absence or abundance, would be directly responding to changes in T, S (Papiol et al., 2012) or even dissolved oxygen (Matabos et al., 2012), at least as far as their physiological requirements are concerned. Indeed, higher frequency variations in water mass properties at this site exceeded the magnitude of seasonal changes (see Fig. 3). We suggest instead that these organisms were responding to a mixture of changes in food availability and indirect effects of water property changes. A similar conclusion was reached by Matabos et al. (2012) in a year long study of faunal and habitat dynamics at the VENUS observatory site in Saanich Inlet, a fjord on southern Vancouver Island. Like Barkley Canyon, the 104 m depth Saanich Inlet study site is characterized by hypoxic conditions, which in the latter case varied seasonally (0.1–1.27 mL/L), together with seasonal pulses in phytodetritus input and bacterial mat growth. In the Matabos et al. (2012) study, changes in the abundance of the shrimp Spirontocaris sica illustrate how organisms can respond to food availability and be indirectly influenced by water property changes. These shrimp were only present during the periods of lowest oxygen concentration, were they were observed 'resting' on the seafloor suggesting a bentho-pelagic life mode. High resolution ROV video imagery recorded this species feeding on microbial mats that were abundant during this low oxygen period. The abrupt departure of the shrimp from their camera site coincided with an increase in dissolved oxygen concentration, the disappearance of the bacterial mats and the arrival of potential predatory fish species in the area, which were less tolerant of low oxygen concentrations (Matabos et al., 2012).

In our Barkley Canyon study, 78% of the difference between the two major seasonal faunal groupings can be attributed to fish and crustaceans, which were the most mobile organisms observed at this site. Although predator–prey relationships in this area are not well known, it is conceivable that at least some of these movements were the result of predators (and directly or indirectly prey) being influenced by seasonal signals in water properties and food availability. Further statistical investigation of such cause and effect relationships will require an extensive, systematic quantification of faunal abundance in Barkley Canyon, in relation to habitat properties. The introduction of standard image acquisition protocols at this site in late 2011 and the addition of dissolved oxygen sensors in June 2012 should improve our ability to quantitatively examine relationships between faunal abundances and potential environmental drivers. The correlation between sample size and species richness (Fig. 5) for the fortnightly tidal periods provides guidance for the development of future observation protocols. Finally, while the study reported here considered seasonal-scale variations in fauna and habitat variables, there is no reason to exclude the possibility that some of the variability observed, particularly in faunal abundance, may be part of longer-term processes.

References

Aguzzi, J., Bahamon, N., Marotta, L., 2009. Modulation of activity rhythms in continental margin decapods by light availability and predatory behaviour of *Nephrops norvegicus*. Mar. Ecol. 30, 366–375.

Aguzzi, J., Company, J.B., Costa, C., Menesatti, P., Garcia, J.A., Bahamon, N., Puig, P., et al., 2011a. Activity rhythms in the deep-sea: a chronobiological approach. Front. Biosci. J. Virtual Libr. 16, 131–150.

Aguzzi, J., Costa, C., Robert, K., Matabos, M., Antonucci, F., Juniper, S.Kim, Menasatti, P., 2011b. Automated video-imaging for the detection of benthic crustaceans and bacterial mat coverage at VENUS cabled network. Sensors 11 (11), 10534–10556.

Allen, S.E., Vindeirinho, C., Thomson, R.E., Foreman, M.G., Mackas, D.L., 2001. Physical and biological processes over a submarine canyon during an upwelling event. Can. J. Fish. Aquat. Sci. 58, 671–684.

Billett, D.S.M., Bett, B.J., Rice, A.L., Thurston, M.L., Galéron, J., Sibuet, M., Wolff, G.A., 2001. Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). Prog. Oceanogr. 50, 325–348.

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 Res. II Top. Stud. Oceanogr. 57 (15), 1406–1417.

Blanchard, A.L., Feder, H.M., Hoberg, M.K., 2010. Temporal variability of benthic communities in an Alaskan glacial fjord, 1971–2007. Mar. Environ. Res. 69, 95–107.

Buhl-Mortensen, L., Buhl-Mortensen, P., Dolan, M.F.J., Dannheim, J., Bellec, V., Holte, B., 2012. Habitat complexity and bottom fauna composition at different scales on the continental shelf and slope of northern Norway. Hydrobiologia 685, 191–219.

Cunha, M., et al., 2011. Biodiversity of macrofaunal assemblages from three Portuguese submarine canyons (NE Atlantic). Deep Sea Res. II Top. Stud. Oceanogr. 58, 2433–2447.

De'ath, G., 2002. Multivariate regression trees: a new technique for modeling species–environment relationships. Ecology 83, 1105–1117.

Emery, W.J., Thomson, R.E., 1997. Data Analysis Methods in Oceanography. Elsevier, Amsterdam.

Freeland, H., Crawford, W.R., Thomson, R.E., 1984. Currents along the Pacific coast of Canada. Atmosphere—Ocean 22, 151–172.

Gage, J.D., Tyler, P.A., 1992. Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor. Cambridge University Press, Cambridge, UK.

Glover, A.G., 23 others, 2010. Temporal changes in deep-sea benthic ecosystems: a review of the evidence from recent time-series studies. Adv. Mar. Biol. Annu. Rev. 58, 1–95.

Hsieh, W.W., Ware, D.M., Thomson, R.E., 1995. Wind-induced upwelling along the west coast of North America, 1899–1988. Can. J. Fish. Aquat. Sci. 52, 325–334.

Keeling, R.F., Körtzinger, A., Gruber, N., 2010. Ocean deoxygenation in a warming-world. Annu. Rev. Mar. Sci. 2, 199–229.

Lampitt, R.S, 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent repercussion. Deep-Sea Res. 32A, 885–897.

Lauermann, L.M.L., Kaufmann, R.S., 1998. Deep-sea epibenthic echinoderms and a temporally varying food supply: results from a one year time series in the N.E. Pacific. Deep-Sea Res. II 45, 817–842.

Leduc, D., Rowden, A.A., Bowden, D.A., Probert, P.K., Pilditch, C.A., Nodder, S.D., 2012. Unimodal relationship between biomass and species richness of deep-sea nematodes: implications for the link between productivity and diversity. Mar. Ecol. Prog. Ser. 454, 53–64.

Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.

Mamouridis, V., Cartes, J.E., Parra, S., Fanelli, E., Saiz-Salinas, J.I., 2011. A temporal analysis on the dynamics of deep-sea macrofauna: influence of environmental variability off Catalonia coasts (western Mediterranean). Deep-Sea Res. I 58, 323–337.

Matabos, M., Tunnicliffe, V., Juniper, S.K., Dean, C., 2012. A year in hypoxia: epibenthic community responses to severe oxygen deficit at a subsea observatory in a coastal inlet. PLoS ONE 7 (9), e45626, http://dx.doi.org/10.1371/journal.pone.0045626.

Matabos, M., Bui, A.O.V., Mihály, S., Aguzzi, J., Juniper, S.K., Ajayamohan, R.S. High-frequency study of epibenthic megafaunal community dynamics in Barkley canyon: a multi-disciplinary approach using the NEPTUNE Canada network. J. Mar. Syst. (in preparation).

Moranta, J., Massutì, E., Stefanescu, C., Palmer, M., Morales-Nin, B., 2008. Short-term temporal variability in fish community structure at two western Mediterranean slope locations. Deep-Sea Res. I 55, 866–880.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Henry, M., Stevens, H.H., Wagner, H., 2008. The vegan Package. ⟨http://cran.r-project.org/⟩, ⟨http://vegan.r-forge.r-project.org/⟩.

Papiol, V., Cartes, J.E., Fanelli, E., Maynou, F., 2012. Influence of environmental variables on the spatio-temporal dynamics of bentho-pelagic assemblages in the middle slope of the Balearic Basin (NW Mediterranean). Deep-Sea Res. 61, 84–99.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing.

Ruhl, H.A., Smith, K.L., 2004. Shifts in deep-sea community structure linked to climate and food supply. Science 305, 513–515.

Sardà, F., Cartes, J.E., Company, J.B., 1994. Spatio-temporal variations in mega-benthos abundance in three different habitats of the Catalan deep sea (Western Mediterranean). Mar. Biol. 120, 211–219.

Smith, C.R., Levin, L.A., Koslow, A., Tyler, P.A., Glover, A.G., 2008. The near future of deep seafloor ecosystems. In: Polunin, N. (Ed.), Aquatic Ecosystems: Trends and Global Prospects. Cambridge University Press, pp. 334–351.

Smith, K.L., Kaufmann, R.S., 1999. Long-term discrepancy between food supply and demand in the deep eastern north Pacific. Science 284, 1174–1177.

Thomson, R.E., Allen, S.E., 2000. Time series acoustic observations of macro-zooplankton diel migration and associated pelagic fish abundance. Can. J. Fish. Aquat. Sci. 57, 1919–1931.

Thiel, H., Kirstein, K.O., Luth, C., Luth, U., Luther, G., Meyerreil, L.A., Pfannkuche, O., Weydert, M., 1994. Scientific requirements for an abyssal benthic laboratory. J. Mar. Syst. 6, 421–439.

Thistle, D., Ertman, S., Fauchald, K., 1991. The fauna of the Hebble site: patterns in standing stock and sediment-dynamic effects. Mar. Geol. 99, 413–422.

Tyler, P.A., 1988. Seasonality in the deep sea. Oceanogr. Mar. Biol. Annu. Rev. 26, 227–258.

Ward, J.H., 1963. Hierarchical groupings to optimize an objective function. J. Am. Stat. Assoc. 58, 236–246.

Yahel, G., Yahel, R., Katz, T., Lazar, B., Herut, B., Tunnicliffe, V., 2008. Fish activity: a major mechanism for sediment resuspension and organic matter remineralization in coastal marine sediments. Mar. Ecol. Prog. Ser. 372, 195–209.

Zimmermann, M., 2006. Benthic fish and invertebrate assemblages within the National Marine Fisheries Service US west coast triennial bottom trawl survey. Cont. Shelf Res. 26, 1005–1027.