Bottom trawling and oxygen minimum zone influences on continental slope benthic community structure off Vancouver Island (NE Pacific)

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ABSTRACT

Understanding responses of benthic ecosystems to cumulative impacts of natural stressors, long-term ocean change and increasing resource exploitation is an emerging area of interest for marine ecologists and environmental managers. Few, if any, studies have quantitatively addressed cumulative effects in the deep sea. We report here on a study from the continental slope off Vancouver Island (Canada) in the northeast Pacific Ocean, where the Oxygen Minimum Zone impinges on seabed habitats that are subjected to widespread bottom trawling, primarily by the fishery for thornyhead (*Sebastolobus* ssp.). We examined how the benthic megafauna in this area was influenced by varying levels of dissolved oxygen and trawling activity, along a depth gradient that was also likely to shape community composition. Continuous video and sonar records from two ROV surveys (50 linear km total; depth range 300–1400 m) respectively provided data on faunal attributes (composition, abundance and diversity) and the frequency of trawl door marks on the seabed. Faunal and trawl data were compiled in a geo-referenced database along with corresponding dissolved oxygen data, and pooled into 500 m segments for statistical analysis. Trawl mark occurrence peaked between 500 and 1100 m, corresponding to areas of slope subjected to hypoxia (< 1.4 ml l^{-1}) and severe hypoxia (< 0.5 ml l^{-1}). A combined total of 266,251 megafauna organisms from 87 taxa were enumerated in the two transects. Significant megafaunal assemblages according to depth, trawling intensity and bottom water dissolved oxygen concentration were identified by PERMANOVA analyses, with characterizing taxa identified for all three factors. Depth, dissolved oxygen and trawl mark density accounted for 21% to 52% of the variability in benthic community structure according to multiple regression (DISTLM) models. Species richness was highest at intermediate depths and in areas subject to intermediate levels of trawling, and higher under hypoxia than under severe hypoxia. These statistically significant trends demonstrate that the structuring influences of bottom trawling on deep-sea benthic communities can be observed even where communities are being shaped by strong environmental gradients.

1. Introduction

The deep sea, when considered as waters deeper than 200 m, is the largest ecological region on Earth, occupying 65% of the planet's surface (Thistle, 2003) and up to 90% of the oceans in terms of volume (Harris et al., 2014). Deep-sea benthic ecosystems occupy many sub-habitats (e.g., sedimented slopes, cold seeps, canyons, oxygen minimum zones (OMZs), abyssal plains, hydrothermal vents, ridges, seamounts, and trenches) with unique abiotic and biological characteristics supporting high biodiversity and delivering important ecosystem services (Hessler and Sanders, 1967; Grassle and Maciolek, 1992; Danovaro et al., 2008; Smith et al., 2008; Rex and Etter, 2010; Thurber et al., 2014). Until the early 1970s, direct human impacts in the deep

sea were mainly related to waste disposal (i.e., sewage, dredge spoils, low-level radioactive waste, munitions and pharmaceuticals), affecting limited spatial extents of a few habitat types (Ramirez-Llodra et al., 2011). The human footprint in the deep sea has increased substantially in the past few decades as technological developments and economic drivers have combined to extend fisheries, and hydrocarbon and mineral extraction to depths below 2000 m (Glover and Smith, 2003; Levin and Sibuet, 2012; Van Dover et al., 2012; Mengerink et al., 2014), affecting most, if not all, deep-sea habitats (Halpern et al., 2008; Ramirez-Llodra et al., 2011). Bottom trawling represents the single most pervasive human activity affecting the deep-sea floor and its ecosystems (Ramirez-Llodra et al., 2011). At a global scale, most deep-sea bottom trawling occurs on sedimented slopes at the edges of

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continental margins, where predicted expansion of oxygen minimum zones and increases in coastal eutrophication (Helly and Levin, 2004; Ramirez-Llodra et al., 2011) will add to the effects of bottom trawling in the near future. Understanding and forecasting such large-scale cumulative impacts represent important future challenges for deep-sea biologists and environmental managers.

Direct effects of bottom trawling have been extensively reviewed and include scraping and ploughing of the substratum, sediment resuspension with a smothering impact on the fauna, destruction of non-target benthic species, and organic loading from the dumping of waste from at-sea processing (Hutchings, 1990; Jones, 1992; Auster et al., 1996; Collie et al., 2000). Documented indirect effects include post-fishing mortality and long-term, trawl-induced changes in the benthos, such as reduced diversity, evenness and biomass, and changes in community structure and habitat heterogeneity (Hutchings, 1990; Jones, 1992; Dayton et al., 1995; Jennings et al., 2001; Hall, 1999; Clark and Koslow, 2007). Such effects can be quantified. In a comparative study off Oregon, USA, Hixon and Tissot (2007) found that benthic invertebrate density was six times higher in untrawled areas, and the total number of fish species was 30% higher, versus areas of seafloor subjected to bottom trawling. The same study also reported an increase in abundances of mobile scavenging fishes (eg., hagfish and eelpouts) in trawled areas, which tended to aggregate along trawl-door furrows, possibly exploiting exposed infaunal macro-benthos. In contrast, slow-growing, long-lived, suspension-feeding, sessile invertebrates, such as corals, sea pens and sponges, dominated untrawled areas. In another study, Clark and Rowden (2009) found significant differences in macrobenthic assemblage composition between fished and unfished seamounts in New Zealand, with live, habitat-forming stony corals such as *Solenosmilia variabilis* and *Madrepora oculata* rarely occurring on heavily fished seamounts (Clark and Rowden, 2009). Opportunistic and early colonizing taxa, like many nematodes, oligochaetes and amphinomid polychaetes were collected in much higher abundances in heavily trawled areas of Monterey Bay, California, and when compared with lightly trawled areas, showed a clear effect of trawling disturbance on community succession (Engel and Kvitek, 1998). The same study also reported high densities of many ophiuroid species in heavily trawled areas. However, the latter could not be categorized as opportunists but rather were thought to be taxa resilient to the physical damage of the trawl nets (Engel and Kvitek, 1998).

dditional long-term and widespread effects of trawling may include changes in sedimentary processes. Turbidity currents can be triggered by heavy otter boards (weighting up to 1.3 t each; Pere Puig, Instituto de Ciencias del Mar, ICM-CSIC, Barcelona, personal communication) dragging through soft muddy sediments (Palanques et al., 2006). Where entire trawler fleets concentrate their operations in optimum mono-specific fishing grounds at the edges of submarine canyons (Palanques et al., 2006), already active submarine canyon currents act synergistically to distribute the sediments resuspended by trawling over extensive areas of the canyon seafloor. Such processes, integrated over decades of intense fishing activity, have completely changed the nature of the seabed in some Mediterranean submarine canyons by modifying the physical properties of surficial sediments, altering the dynamics of water-sediment chemical exchanges, and dramatically reducing the organic matter content of sediments available for the epi- and infaunal benthos (Martín et al., 2008, 2014; Puig et al., 2012).

Off British Columbia, Canada, deep-sea bottom trawling began in the 1990s in response to growing market demand for two species, the shortspine thornyhead (*Sebastolobus alascanus*) and the longspine thornyhead (*Sebastolobus altivelis*) (Haigh and Schnute, 2003). The depth distribution of *S. altivelis* ranges from 500 to 1600 m, while *S. alascanus* occurs over a broader range, from 90 to 1460 m. Relevant bycatch taxa from this fishery, in terms of captures and biomass, include macrourid fishes, sablefish (*Anoplopoma fimbria*), dover sole (*Microstomus pacificus*), deep-sea sole (*Embassichthys bathybius*),

zoarcids (eelpouts), and a variety of invertebrates such as the grooved tanner crab (*Chionoecetes tanneri*), sea stars, gastropods, octopus and squid (Haigh and Schnute, 2003).

Bottom trawling remains an important and lucrative method of fishing in British Columbia (Driscoll et al., 2009) despite public concern and scientific evidence from other locations, about potential physical disturbance of seafloor habitats and associated communities (Jamieson and Chew, 2002; Ardron et al., 2007; Finney, 2009), and high by-catch rates (Haigh and Schnute, 2003; Ardron et al., 2007). Bottom trawling data from Canada's Department of Fisheries and Oceans (DFO) spanning from 1996 to 2005 show that the fishery footprint extends over a 38,000 km^2 area along Canada's Pacific coast at depths ranging between 115 and 1100 m meters (Sinclair, 2007). The impacts of the various types of fishing gear used in Canada, as well as the economic importance of each individual fishery were investigated by Fuller et al. (2008). While bottom trawling had the highest catch volume with 296,992 t of fish accounting for $377 million, pot and trap gear types yielded a higher economic value with $1117 million despite a lower total catch, 167,151 t (data from 2005). In more recent data (2014), the commercial fisheries landings for groundfish reached 167,318 metric tons in Canada, which had a total economic value of over $302 million (Canada Department of Fisheries and Oceans, Commercial Fisheries Statistics: http://www.dfo-mpo.gc.ca/stats/commercial/sea-maritimes-eng.htm).

Evaluation of the impact of the trawl fishery on benthos of the continental slope off British Columbia must contend with the potentially confounding, and little studied (in this region) influence of bottom water hypoxia on faunal abundance and community composition. An Oxygen Minimum Zone (OMZ) impinges on the continental slope in the 600−1200 m depth range off Vancouver Island (Supplementary Fig 1). We present here a study of the cumulative impacts of trawling and hypoxia, and their separate effects on the megabenthos, across a broad depth range on the continental slope. We made opportunistic use of seafloor video and scanning sonar records from remotely-operated vehicle (ROV) cable route surveys in this area, and modelled bottom water dissolved oxygen using data from nearby water column profiles and ROV dives. We quantitatively assessed depth-related patterns in the distribution and community structure of the epibenthic megafauna from the shelf break down to the deep slope, in relation to natural environmental stressors (namely dissolved oxygen availability) and human-induced disturbances caused by bottom trawling. Additionally, since shelf-break and slope epibenthic megafauna community structure patterns have not been described for this area of the NE Pacific, we sought to provide a first comprehensive community and species richness assessment that will aid comparisons with OMZ faunas described elsewhere.

Coupled ocean-atmosphere models predict substantial dissolved oxygen reductions in the global ocean's interior as surface water warming reduces dissolved oxygen solubility and increases thermal stratification thereby decreasing ocean ventilation (Brewer and Peltzer, 2009; Shaffer et al., 2009; Keeling et al., 2010; Stramma et al., 2010; IPCC, 2014). Naturally occurring OMZs, such as the one centered in the NE Pacific, are thought to be the regions where large-scale oxygen reductions will occur at faster paces (Brewer and Peltzer, 2009; Shaffer et al., 2009; Keeling et al., 2010; IPCC, 2014; Chu and Tunnicliffe, 2015). Therefore, this study also serves as a baseline for future investigations of the synergistic effects of human-induced impacts such as bottom trawling, OMZ expansion, ocean acidification and eutrophication.

2. Materials and methods

2.1. Study area

The study was conducted in two NE Pacific continental slope areas off Vancouver Island, British Columbia, Canada (Fig. 1). An OMZ
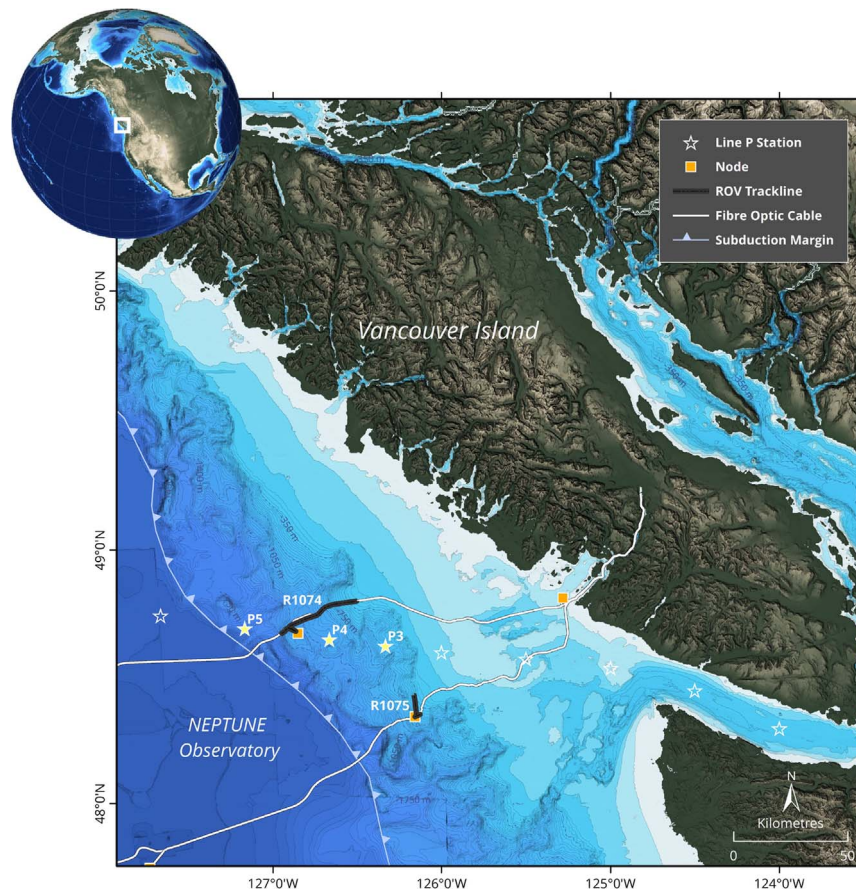
Fig. 1. Map showing the study area on the continental slope, about 60–100 km off the West Coast of Vancouver Island, Canada. Combined video and sonar transect R1074 ranged from 300 to 1400 m, and R1075 from 340 to 650 m. Base map was sourced from Smith and Sandwell, 1997.

impinges on the continental margin in the study area with its core (lowest dissolved oxygen concentrations) situated between 600 m and 1200 m depth (e.g., Supplementary Fig. 1 and 2). Time series data show the OMZ in this area to be relatively stable, except for the dynamic of the upper boundary (Supplementary Fig 1) driven by interannual variations in water column respiration and physical forcing by upwelling and downwelling (Whitney et al., 2007; Crawford and Peña, 2013). During summer months, with prevailing upwelling-favorable winds, low oxygen water is drawn onto the shelf. Downwelling-favorable winds predominate during winter, resulting in wind-driven mixing that forces oxygen rich surface waters downward to the seafloor at shelf depths (Whitney et al., 2007).

The Vancouver Island continental slope has been subjected to bottom trawling activity since 1994, over a wide bathymetric range from shelf depths (~150 m) to the deep slope (~2,000 m) (Kulka and Pitcher, 2001; Sinclair, 2007). Records of accumulated trawling activity obtained from the Canadian Department of Fisheries and Oceans show trawls to be widely distributed within the management areas that encompass the two study sites (Supplementary Fig 3).

2.2. Video and sonar surveys

2.2.1. Benthic megafauna

Video transects for this study were carried out from the Canadian Coast Guard Ship J.P Tully using the remotely-operated vehicle (ROV) ROPOS from the Canadian Scientific Submersible Facility on August 3–7, 2007, during Ocean Networks Canada cable route surveys in preparation for the installation of the NEPTUNE observatory (Fig. 1). Two transects were conducted in separate dives, R1074 and R1075. Transect R1074 covered 30.8 linear kilometers beginning at the 1300 m isobath on the mid slope, running in a NE direction, and

ending at 300 m at the shelf-break (Fig. 1). Transect R1075 covered 12 linear km, in a V-shaped pattern, starting NW of Barkley Canyon at 650 m, and running in a SW direction along the continental slope for 1.8 km and then in a N-NW direction for the remaining of the transect reaching a final depth of 340 m (Fig. 1). The video camera system used was a 3 sensor CCD DXC 990 Sony with standard definition (SD) video, mounted obliquely in front of the ROV at a 45° tilt angle. Video was recorded on MiniDV tapes and transferred to DVDs following the survey. The protocols for acquiring the video footage were as follows: ROPOS flew along a transect at an altitude of approximately 1.5 m above the seafloor, following the support vessel at approximately 0.5 knots (0.25 m/s). Average altitude and speeds for each transects were calculated from ROV position and altimeter records. Transect R1075 had a mean altitude of 1.4 m (s.d.=0.4, n=1236) while mean altitude for transect R1074 was 1.7 m (s.d.=0.4, n=734).

Faunal analysis, which consisted of assigning unique taxon identies and making individual counts, was performed in video playback mode in the laboratory at the University of Victoria. Animals were counted as they crossed a horizontal line in the centre of the video image (i.e., perpendicular to the direction of movement of the ROV), that transected two parallel laser (10 cm separation) points projected onto the seafloor. ROV position, depth and time (UTC) were always visible on the video screen and were added to the annotation database along with individual faunal counts. Digital still photos as well as frame grabs from close-up video were taken along the transects to help with further taxonomic identifications of benthic organisms.

A geo-referenced faunal database was created by merging ROV navigation data with the faunal counts from the video analysis, using the time stamps from the video (Sameoto et al., 2008). Individual faunal observations were thus assigned a unique latitude, longitude and depth combination. Where faunal abundances in video images were too

high for accurate individual counting, with taxa occupying 25% or more of the field of view, taxa density was determined by extracting frame grabs from the video and counting all individuals in 10–15 sequential frames, and then extrapolating average values to adjacent video segments where the aggregates were present. In practice, faunal aggregates were composed of the echinoid *Strongylocentrotus fragilis*, ophiuroids (not possible to identify to species level) and two holothurians, *Scotoplanes globosa* and *Pannychia moseleyi*. Both individual taxa and faunal aggregates were only counted along the transects when image quality permitting discernment of individuals larger than 5 cm. Faunal counts in the database were then amalgamated into 500-m length sample units, to match the spatial scale at which trawling intensity was estimated using sonar (see below), as well as to giving more weight to less abundant species when performing the community statistical analysis. Latitude, longitude and depth were assigned to each 500 m sample unit using data from the midpoint.

2.2.2. Trawl marks

The intensity of bottom trawling at the seafloor was evaluated using digital records from a 1171 series Kongsberg single beam scanning sonar (675 KHz frequency) mounted on the front of the ROV. The high-resolution sonar detected the linear furrows in the seabed scoured by trawl doors (Fig. 2). The 50-m sonar radius covered a total area of approximately 2793 m^2 of the seafloor as it scanned a forward-looking sector of 128° width. While trawl marks were also visible in the video, a single sonar sweep sampled a much larger area of seafloor, > 1000-fold greater than that covered by a video frame (Fig. 2). Kongsberg MS 1000 post-processing software was used to annotate sonar scan files from dives R1074 and R1075 to count trawl marks, identify their location and record their orientation. Annotated and geo-referenced sonar images were then exported to the database and abundances of trawl marks were grouped into 500-m long linear transect bins along the survey direction in both transects. The 500-m linear sample units proved to be the optimal spatial scale in which trawl marks could be individually identified and counted, and then converted into density categories (adapted from Smith et al., 2007).

2.3. Ancillary environmental data

Dissolved oxygen was not measured during the 2007 survey dives. Dissolved oxygen data in milliliters per liter (ml/l) were sourced from the Line P- Ocean Station Papa time series that has been maintained by the Canadian Department of Fisheries and Oceans for several decades (https://www.waterproperties.ca/linep/). For transect R1074, we used dissolved oxygen data from station P5 (19 km west, Fig.1) from May

Fig. 2. Example of high-resolution scanning sonar output showing trawl marks in the seabed. Image is to scale showing also the ROV platform in the centre, and the relative size of the field of view of the video camera.

2007 (no data available for August 2007), while dissolved oxygen data for transect R1075 came from August 2007 profiles at Station P3, 24 km northeast (Fig.1). Oxygen data were joined to the faunal database through depth (bottom depth for the midpoint of each faunal sample unit, and corresponding water column depth from the Line P dataset).

We employed a two-step approach to ensure that Line P dissolved oxygen data were representative of bottom water conditions experienced by the benthic megafauna at the time of the 2007 surveys. The first validation used data from station P4 (Fig. 1), which has a more complete time series than stations P3 and P5. A time series compilation (2004–2014) of Station P4 dissolved oxygen profiles collected in May/ June of each year, confirmed the inter-annual consistency of dissolved oxygen values and profiles for the area (Supplementary Fig 1). The second validation used ROV-mounted oxygen sensor data from June 2012 ROPOS dives at locations corresponding to the areas of the two 2007 ROPOS transects. These data confirmed the general correspondence of water column dissolved oxygen profiles between the transects and the corresponding Line P stations (Supplementary Fig 3), with differences (0.2–0.4 ml/l) attributable to a consistent offset between the ROV dissolved oxygen sensor and the sensor used for the Line P profiles.

Mean dissolved oxygen data for each 500 m transect section were then grouped into three categories (Normoxia,[0_2] > 1.4 ml/l; Hypoxia, $1.4 < [0_2] < 0.5$ ml/l; Severe hypoxia, $[0_2] < 0.5$ ml/l) following the criteria of both Tyson and Pearson (1991) and Levin et al. (2001). We acknowledge that the applicability of these general thresholds is context-dependent because of varying responses to oxygen deficit across multiple taxa (Vaquer-Sunyer and Duarte, 2008) and the effects of seasonal variability in temperature on oxygen solubility (Brewer and Hofmann, 2014). In addition, recent findings suggest that NE Pacific taxa may be more resilient than Atlantic taxa, responding to lower sub-lethal and lethal thresholds (Chu and Tunnicliffe, 2015). However, the latter study was carried out in a semi-confined and shallow fjord (Saanich Inlet, 230 m of maximum depth), and therefore subject to different dissolved oxygen seasonal dynamics compared to the OMZ in the slope of Vancouver Island.

2.4. Data analysis

2.4.1. Benthic megafauna community structure

Three separate PERmutational Analysis of Variance (PERMANOVA) tests were employed to verify significant differences in megabenthic community structure as a function of the following factors: (1) depth strata [upper slope (299–450), deep upper slope (451–600 m), mid slope (600–900 m) and deep slope (900–1400 m), (2) trawl intensity [low (1–20 trawl marks), low-moderate (21–40), moderate-high (41–60) and high (> 61), and (3) dissolved oxygen (as per above, normoxia, hypoxia, and severe hypoxia) in a one-way design with fixed levels for each factor. The three *a priori* factors were analyzed separately to mitigate the unbalanced sample design. This analysis was based on a resemblance matrix using the Bray Curtis similarity index after square root transformation of the abundance data. The transformation procedure allowed all species to contribute to the similarity matrix while still giving the most common species greater weight (Warwick, 1993). A non-metric multidimensional scaling (n-MDS) ordination technique, based on the square root transformed abundance data, was used to visualize faunal patterns and evaluate coherence with results obtained from the PERMANOVA. In the n-MDS plots, a group-average cluster analysis method was used to overlay faunal groups that were significantly different at 50, 65 and 80% similarity levels.

A SIMilarity PERcentage analysis (SIMPER) was subsequently employed to identify which taxa contributed the most to similarity/ dissimilarity within/between communities that the PERMANOVA analysis identified as significantly different. Characterizing and
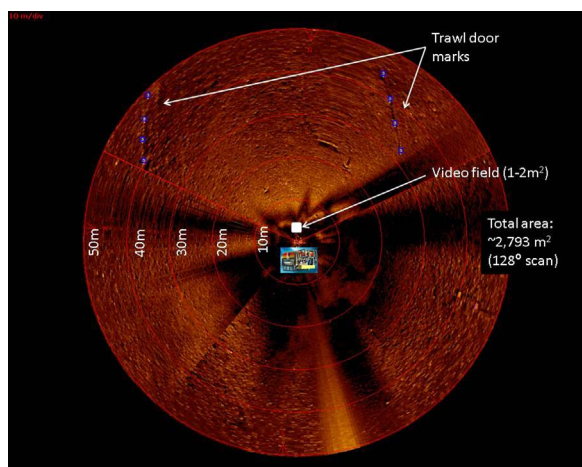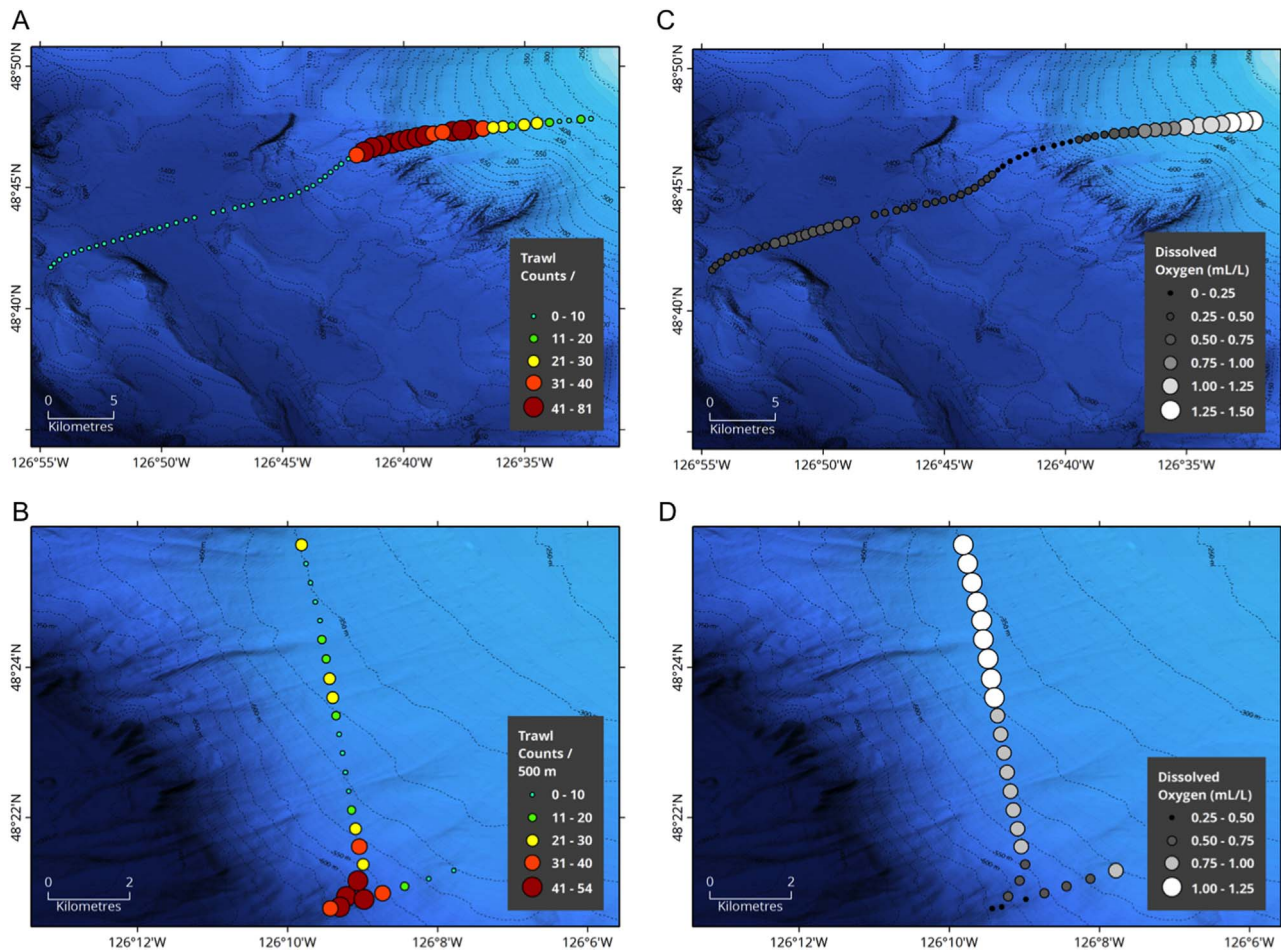
Fig. 3. Maps showing trawl counts (A,B) and dissolved oxygen (C,D) in ml l $^{-1}$ along transects R1074 (top panels) and R1075 (lower panels). High-resolution bathymetry data (UW TN175) were sourced with consent from J.R. Delaney, D.S. Kelley, and D. Glickson, University of Washington.

discriminating taxa were ranked by their average contribution (%) to within and between community similarity and dissimilarity, and the ratio of the similarity/dissimilarity and standard deviation (SD), respectively. Taxa are considered good characterizers/discriminators if the ratio of the mean to the standard deviation of the contribution of each to overall similarity/dissimilarity between communities is ≥1.3 (Clarke and Warwick, 2001).

2.4.2. Modeling the effects of trawling and environment on the community structure

A DISTance-based Linear Model (DISTLM) multiple regression was employed to examine the influence of environmental variables and trawling intensity on megafaunal community structure (McArdle and Anderson, 2001; Anderson et al., 2008). The variables originally included in the model were: latitude, longitude, depth, temperature, dissolved oxygen, and trawl mark abundance. We included latitude and longitude in the regression models to quantify (%) explanation by spatial autocorrelation in the community structure (Legendre, 1993). In ecological and biogeographic data, assemblages that are geographically closer to one another tend to be more similar for extrinsic (e.g., spatially defined environmental gradients) or intrinsic (e.g., interspecific competition) factors, violating statistical assumptions that samples are independent from one another (Legendre, 1993; Dormann et al., 2007). We used the BEST selection procedure as it identifies the best model based on the AICc (Akaike's Information Criterion) selection criterion for all possible combinations of predictor variables (Clarke and Gorley, 2006; Anderson et al., 2008). The AICc was devised to handle situations where the number of samples (N) is small relative to

the number of predictor variables (v) such that N/v < 40, which applies to our data set (N=90, v≤6, N/v=15) (Anderson et al., 2008 and references therein). The existence of highly correlated variables and any needs for data transformation were assessed using a draftsman plot. The variable 'temperature' was therefore removed from the modeling procedure because of its high linear correlation with depth (r= 0.98). Normalization of variables prior to the analysis was automatically performed within the routine of DISTLM (Anderson et al., 2008).

All multivariate statistical analyses (PERMANOVA, n-MDS, cluster analysis, SIMPER and DISTLM) were performed using the software PRIMER version 6.0 with the PERMANOVA+add-on package (Clarke and Gorley, 2006; Anderson et al. 2008).

2.4.3. Effects of trawling and dissolved oxygen in species turnover

To quantify potential effects of trawling intensity and dissolved oxygen on megafauna species turnover at larger spatial scales (beta-diversity), we evaluated the slope of randomized species accumulation curves after pooling samples within levels of factors (i.e., 1-depth strata, 2-trawling intensity, 3-dissolved oxygen levels, see Section 2.4.2); first within dive R1074 and then after pooling both transects together (Ugland et al., 2003; De Leo et al., 2014). The analysis was not performed on data from dive R1075 (shorter, V-shaped transect) alone because of an insufficient number of samples within individual levels of some of the factors.
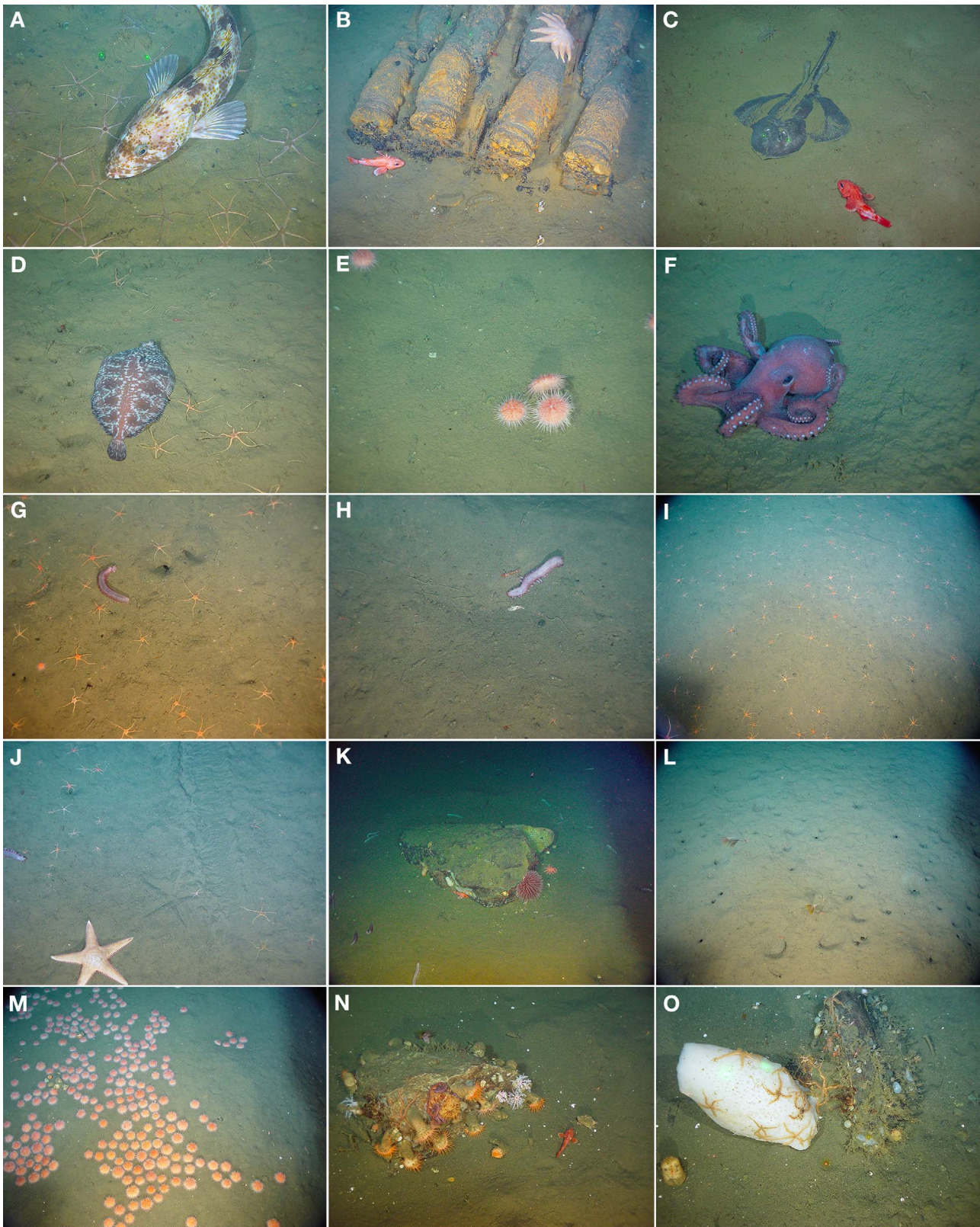
Fig. 4. Photo atlas of common taxa and general seascape observed in the slopes offshore Vancouver Island, NE Pacific. **A-F**, transect R1074. **G-O**, transect R1075. **A**, Lingcod, *Ophiodon elongatus* and ophiuroid aggregations (Ophiuroidea sp.1); **B**, seastar *Pycnopodia helianthoides* and rockfish *Sebastes* spp. near an ammonition pallet; **C**, *Bathyraja abyssicola* and *Sebastes* spp.; **D**, deep-sea sole *Embassichthys bathybius*; **E**, small aggregation of the pink sea urchin *Strongylocentrotus fragilis*; **F**, octopus *Graneledone borepacifica*; **G**, the holothurian *Pannychia moseleyi* sourrounded by ophiuroids (Ophiuroidea sp. 2); **H**, *P. moseleyi*, shrimp *Pandalopsis* sp.; **I**, high densities of ophiuroids; **J**, unidentified seastar, its resting mark, *P. moseleyi*, ophiuroids and a nearly a faded trawl mark; **K**, dropstone with *Liponema* sp. and other attached anemones, seastars and ophiuroids, and several *P. moseleyi* in the background; **L**, unidentified Cerianthid anemones and bioturbation marks by sea urchins; **M**, large aggregation of *S. fragilis*; **N**, dropstone with several anemones, giant Pacific octopus *Enteroctopus dofleini*, gastropod *Fusitriton oregonensis*, sessile holothurian *Psolus* spp. (white tentacles); *Sebastes* spp.; **O**, unidentified Hexactinellid songe, Ophiuroidea sp. 2., Brachiopoda sp., anemone.
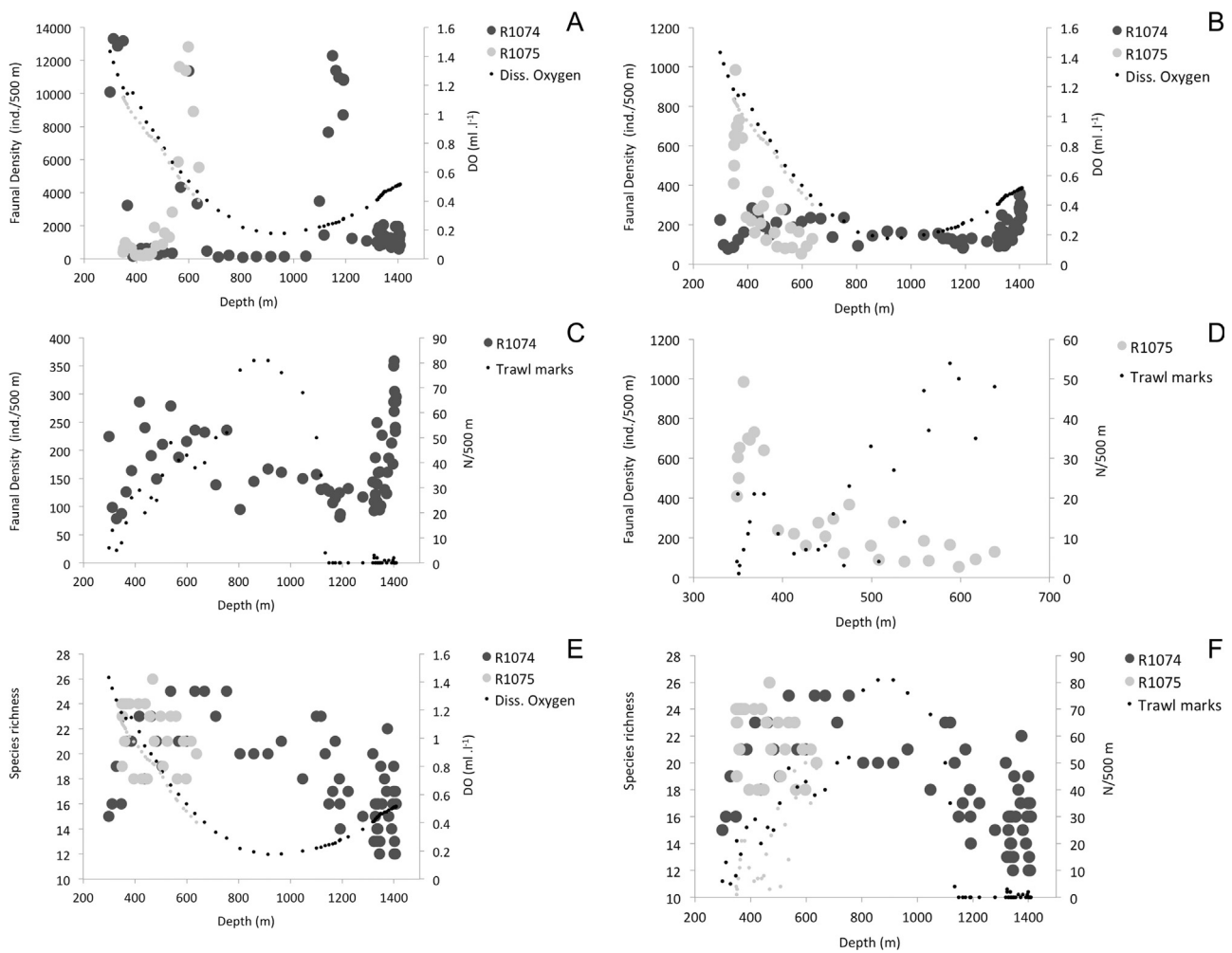
Fig. 5. A-D, Total benthic megafauna densities (left Y-axis, large symbols), dissolved oxygen and trawl mark counts (right Y-axis, small symbols) along the bathymetric gradient. Panel A includes faunal aggregates (i.e., ophiuroids, *S. fragilis*, *S. globosa* and *P. moseleyi* – refer to Section 2.2.1 in the Methods). E-F, Species richness (number of taxa per 500 m transect segments) plotted against dissolved oxygen (E) and trawl mark counts (F).

3. Results

3.1. Trawl marks and dissolved oxygen

The total number of trawl marks identified in the sonar images followed a clear pattern along the depth gradient, with a peak in trawl mark occurrence between 500 and 1100 m for transect R1074 (Fig. 3A) and between 500 and 650 m for the shorter, shallower transect R0175 (Fig. 3B). The overall pattern clearly coincides with the almost decade long history of bottom trawling activity that preceded the 2007 surveys, depicted in Supplementary Fig 3, with sharp boundaries in trawling activity representing distribution patters for the main target species, the rockfish *Sebastes* spp., and the short and longspine thornyheads, *Sebastolobus alascanus* and *Sebastolobus altivelis,* respectively.

With respect to bottom water dissolved oxygen concentrations, conditions of normoxia only occurred in the shallowest sections of transect R1074 (~300 m depth) on the upper slope. From mid slope, dissolved oxygen decreased steadily to hypoxic levels until about 630 m, where it reached the threshold of severe hypoxia (< 0.5 ml.l^{-1}) (Fig. 3C). At around 1200 m depth, oxygen levels returned to hypoxic levels where they remained until the deepest extent of the transect at about 1,400 m. The trend was similar for the shorter transect, where hypoxic waters were present between 350 and 580 m, and severe hypoxia occurred below 600 m (Fig. 3D).

3.2. Faunal density, species richness and community structure

The two video transects combined yielded a total of 90 samples (500 m sections), 266,251 individual megafaunal organisms, and 87 taxa. Transect R1074 alone had a total abundance of 193,434 individuals and 56 taxa, while transect R1075 had 72,817 individuals from 51 taxa. These values include the estimated abundances of faunal aggregates, i.e., the echinoid *Strongylocentrotus fragilis*, the holothurians *Scotoplanes globosa* and *Pannychia moseleyi* and an unidentified ophiuroid (Ophiuroidea sp. 1). Furthermore, still considering the faunal aggregates, echinoderms accounted for 96% of the total abundance of transects combined, and 35% and 95% of abundance in transects R1074 and R1075, respectively. Other represented taxa in R1074, in terms of total abundance, were an unidentified sea whip (Gorgonian, Alcyonacea) with 3,001 individuals, the asteroid *Henricia sanguinolenta* (962 individuals), rockfishes (672 ind.), Macrouridae sp.1 (566 ind.), *Fusitriton oregonensis* (504 ind.), Anemone sp. 1 (384 ind.), the sea pen *Umbellula lindahli* (304), Anemone sp. 2 (245 ind.), and the thornyhead *Sebastolobus altivelis* (212 ind.). For transect R1075 the most represented taxa after the echinoderms were mostly unidentified: Anemone sp. 3 (2,942), Anemone sp. 4 (1,026 ind.), the Gastropod sp. 1 (894 ind.), Anemone sp. 5 (411 ind.), and Anemone sp. 6 (174 ind.). A few of the most abundant species responsible for the groupings in the multivariate analysis are shown in the photo atlas in Fig. 4.

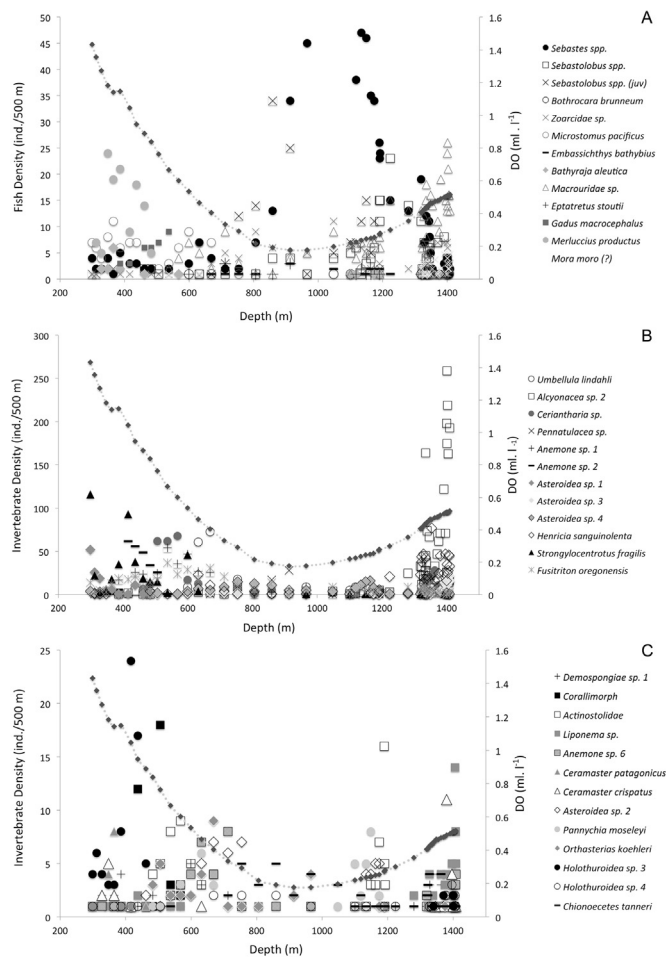Megafauna density showed a bimodal distribution with depth for

Fig. 6. Benthic megafauna densities by taxa in transect R1074 (left Y-axis, larger symbols) and dissolved oxygen concentration (right Y-axis, small diamond symbols) along the bathymetric gradient. Data excluding faunal aggregates (i.e., ophiuroids, *S. fragilis*, *S. globosa* and *P. moseleyi*. A, fish. B, invertebrates with moderate densities. C, invertebrates with low densities.

Fig. 7. Benthic megafauna densities by taxa in transect R1075 (left Y-axis, larger symbols) and dissolved oxygen concentration (right Y-axis, small diamond symbols) along the bathymetric gradient. Data excluding faunal aggregates (i.e., ophiuroids, *S. fragilis*, *S. globosa* and *P. moseleyi*. A, fish. B, invertebrates with moderate densities. C, invertebrates with low densities.

transect R1074 (Fig. 5A). However, this trend is not apparent when faunal aggregates are removed (Fig. 5B). There was a sharp decrease in faunal density coincident with the increase in trawling intensity (most marked between 600 and 1100 m) as well as with entry into the core of the OMZ (800–1100 m) (Fig. 5A and B). For the shorter transect R1075 megafauna increased with depth peaking at 500–600 m when including the faunal aggregates (mostly ophiuroids and the sea urchin *Strongylocentrotus fragilis*) (Fig. 5A). However, an opposite trend is observed when data from faunal aggregates are removed; lowest densities then occur within areas most impacted by trawling and low dissolved oxygen concentrations (Fig. 5B and D).

Species richness for the longest transect increased with depth until about 754 m, peaking at 24 taxa, and then decreasing again reaching 12 taxa at 1405 m. (Fig. 5E). What resembles a bell-shaped curve pattern with depth is interrupted by lower species richness coinciding with both high trawling intensity and the core of the OMZ (Fig. 5E,F). For transect R1075, species richness increased with depth reaching 26 species at 469 m and decreasing again to 20 species at 638 m (Fig. 5E).

Examination of the benthic megafauna community composition data revealed how densities of individual taxa changed over the depth gradient (Figs. 6 and 7). In transect R1074, for fish species in particular, only thornyheads, rockfishes, Zoarcids, macrourids and the deep-sea sole (*E. bathybius*) occurred at the core of the OMZ (Fig. 6A), and where trawl mark density was higher (Supplementary Fig 4). Thornyheads and rockfishes completely dominated the community composition between 800 and 1200 m, with other groups
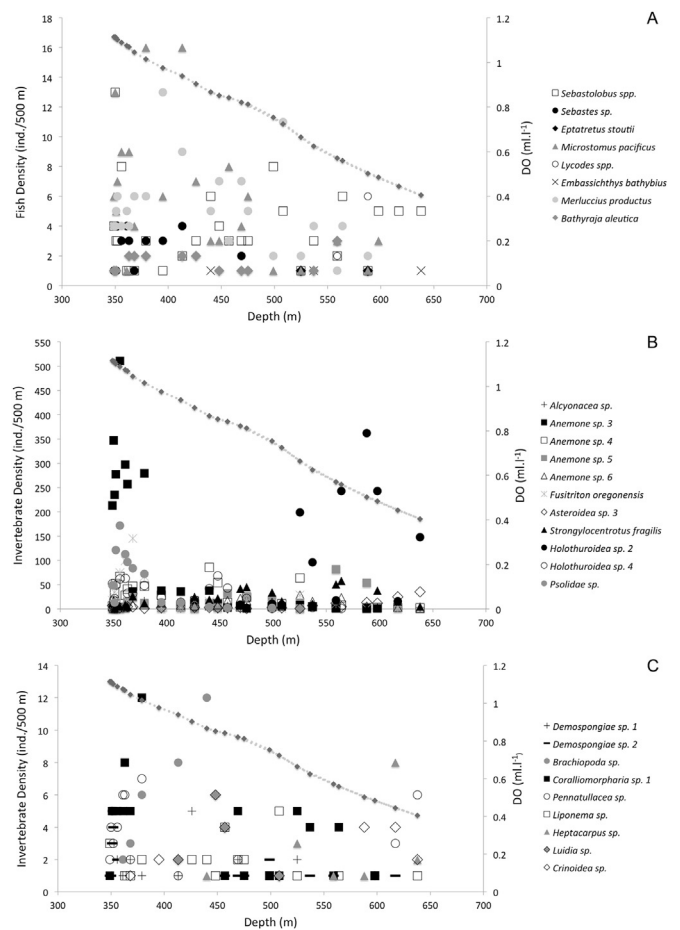
showing depressed densities. Taxa richness and densities increased both shallower and deeper from the aforementioned depth zone. For invertebrates, the overall pattern was similar (Fig. 6B-C). Pennatulids and seastars were the groups occurring at the center of the OMZ, with only moderate abundances (Fig. 6B), followed by the grooved tanner crab *C. tanneri*, the seastar *O. koehleri.*, Anemone sp. 3, *Liponema* sp., and the holothurians *P. modeleyi* and Holothuroidea sp. 4 (Fig. 6C). Once again, taxa richness and densities increased above and below this zone, which was also subject to the highest level of trawling (see Supplementary Fig 4). For the shorter transect R1075, megafauna followed the same initial trend as the longer transect, with individual taxa densities decreasing from upper to deep-upper slope (Fig. 7A-C). Both fish and invertebrate taxa had their lowest densities between 437 and 638 m, where severe hypoxic conditions began to dominate (Fig. 7), and where bottom trawling intensity reached its highest values. (Supplementary Fig 5).

In a first exploratory assessment of the multivariate data cloud (i.e., taxa x samples) we analyzed the two transects combined. However, there were notable differences in community structure between the two transects, which were spatially separated by ~60 km and covered unequal depth ranges (300–1200 m versus 323–600 m) (Supplementary Fig 6). Additionally, transect R1074 covered a greater distance (~30 km) in a predominantly W-E upslope direction as opposed to transect R1075, which ran for ~12 km in a more along-slope, S-N direction. Comparatively therefore, transect R1075 encountered a narrower range of depth, dissolved oxygen concentrations and trawling intensity. These distinct differences between transects con-

Table 1

Output of the one-way PERMANOVA analysis based on the resemblance matrix of megafauna abundance data for transect R1074. *A priori* factors were analyzed separately due to an unbalanced sample design: *depth strata* (upper slope, deep upper slope, mid slope, deep slope), *trawling* (low, low-moderate, moderate-high, high), *dissolved oxygen* (normoxia, hypoxia, severe hypoxia).

R1074	Source	df	SS	MS	Pseudo-F	p(perm)	Unique permutations
Main test	**Depth Strata**	3	45500	15167	20.363	**0.0001**	9930
	Residual	59	43945	744.83			
	Total	62	89445				
	Trawling	3	27970	9323.2	8.9479	**0.0001**	9912
	Residual	59	61475	1041.9			
	Total	62	89445				
	Diss. Oxygen	2	15137	7568.5	6.1112	**0.0001**	9913
	Residual	60	74308	1238.5			
	Total	62	89445				
Pair wise tests	Source	df			t-statistic	p(perm)	Unique permutations
Depth St.	DS, MS	46			4.348	**0.0001**	9944
	DS, DUS	46			4.179	**0.0001**	9926
	DS, US	47			5.328	**0.0001**	9956
	MS, DUS	12			3.536	**0.0006**	1707
	MS, US	13			5.976	**0.0003**	5090
	DUS, US	13			2.861	**0.0002**	5023
Trawling	L, LM	50			3.165	**0.0001**	9950
	L, MH	48			2.747	**0.0001**	9930
	L, H	47			3.587	**0.0001**	9891
	LM, MH	12			1.440	0.0913	2889
	LM, H	11			3.142	**0.002**	1287
	MH, H	9			1.914	**0.017**	462
Diss. Oxygen	SH, H	60			3.211	**0.0001**	9947
	SH, N	38			1.712	**0.0244**	40
	H, N	22			1.009	0.4587	24

PERMANOVA *one-way model.* Bold values indicate significant differences at p < 0.05. DS, deep slope, MS, mid slope, DUS, deep upper slope, US, upper slope; L, low, LM, low-moderate, MH, moderate-high, H, high; SH, severe hypoxia, H, hypoxia, N, normoxia. df, degrees of freedom, SS, sum of squares, MS, mean sum of squares, p(perm), p-value derived from permutations.

founded the identification of the environmental drivers of community structure in the combined data. Subsequent statistical analysis therefore separately considered data from each of the two transects.

Significant differences between megabenthic communities according to depth (factor depth strata, p-F =20.26, p=0.0001), trawling intensity (p-F=8.94, p=0.0001), and bottom water dissolved oxygen regimes (p-F= 6.11, p=0.0001) were verified for transect R1074 from the PERMANOVA analysis (Table 1). All pairwise comparisons between depth strata were significant, i.e., community structure differed significantly between upper slope, deep upper slope, mid slope and deep slope (Table 1). For the trawling intensity factor, all but one pairwise comparison was statistically significant. Megafauna community structure was not statistically different between the groups of samples subjected to low-moderate and moderate-high trawling intensity (Table 1). Similarly, for dissolved oxygen, all but one pairwise comparison was statistically significant, with community structure not differing between communities subject to normoxia and hypoxia (Table 1). Depth contributed the most to the partitioning of total multivariate variability (higher pseudo-F statistic), with trawling and dissolved oxygen, contributing progressively less. These results can be visualized and corroborated in the n-MDS ordination diagram (Fig. 8), where depth appears to strongly influence community structure, separating highly-similar sample clusters between upper slope, deep upper slope, mid slope and deep slope (Fig. 8). The effects of trawling and dissolved oxygen were not as strong in the two-dimensional n-MDS space (Fig. 8B-C).

Benthic megafauna community structure on transect R1075 was also significantly influenced by all three factors, depth (p-F=18.6, P=0.0001), trawling (p-F=4.64, p=0.0001) and dissolved oxygen (p-F=6.93, p=0.002) (Table 2). Depth was once again the predominant factor in between-group sample differences, but now followed by dissolved oxygen, and then trawling (Table 2). All but one pairwise

comparison between levels of depth, dissolved oxygen and trawling intensity was statistically significant. The exception was megafauna community structure comparisons between samples subjected to low and low-moderate levels of trawling (Table 2). The n-MDS plot visualizes these patterns, and corroborates the PERMANOVA results (Fig. 9).

The most important taxa contributing to similarity within groups (characterizing taxa) for all three factors (depth, trawling, dissolved oxygen), and for each transect separately are presented in Tables 3 and 4. For depth, there were taxa consistently (i.e., across both transects) representative of upper slope communities (the pink sea urchin, *S. fragilis*, the North Pacific hake, *M. productus*, the dover sole *M. pacificus*) and deep-upper slope (Ophiuroidea sp. 1, *S. fragilis*, and six anemone species). In terms of oxygenation, taxa consistently representing severe hypoxic conditions were the thornyheads *Sebastolobus* spp., the seastar *Henricia sanguinolenta*, and Ophiuroidea sp. 1. While rockfish *Sebastes* spp. were highly abundant at the OMZ core (severe hypoxia) in transect R1074, they were absent in those conditions in transect R1075. Lastly, only *Sebastolobus* spp., consistently characterized assemblages subject to moderate to moderate-high trawling conditions (proxied by trawl mark counts in sonar records).

3.3. Effects of bottom trawling and environment in the community structure

The results of the DISTLM multiple regression model for transect R1074 are summarized in Supplementary Table 1. The marginal tests show the contribution of explanatory variables to benthic megafauna community structure when considered individually in the model. While depth alone contributed 31% of the model variability, longitude (considered to represent spatial auto-correlation) contributed 28%, dissolved oxygen 23%, and trawl mark density 21% (Supplementary
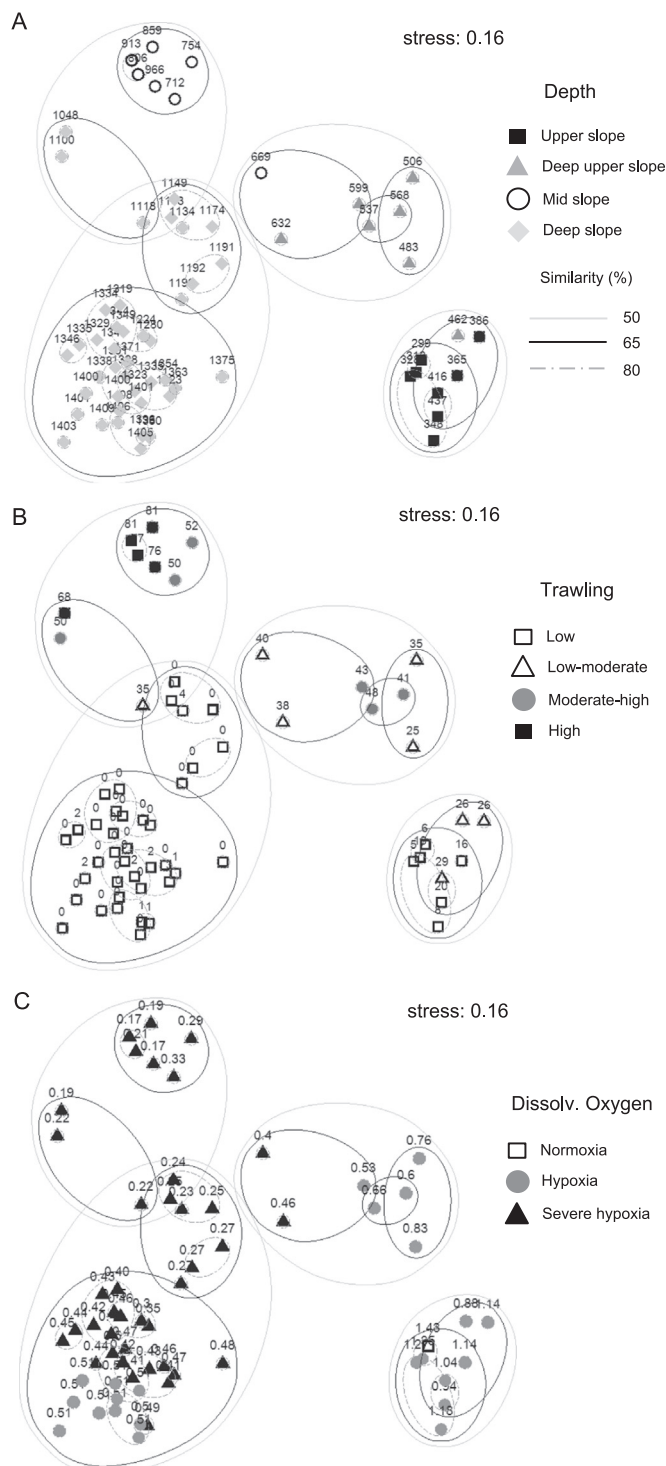
Fig. 8. Non-metric multidimensional scaling (n-MDS) plot of Bray–Curtis similarity matrix based on square root-transformed abundance data of benthic megafauna taxa sampled along transect R1074 (grouped by 500 m sample units). Circles represent group-average clusters at 50%, 65% and 80% of similarity. Panels A through C display sample labels according to factors depth strata, trawling intensity and levels dissolved oxygen.

Table 1). Consequently, depth was the best explanatory variable for a single variable model. For the best two-variable model, depth and dissolved oxygen explained 50% of model variability, and the best three-variable model (longitude, trawl mark density and depth) explained about 58% (Supplementary Table 1). In the overall best model solution (smallest AICc coefficient), all four explanatory variables accounted for 63% of the variance (Supplementary Table 1).

Fig. 10A shows the constrained ordination output from the redundancy analysis (dbRDA), with the length and direction of the vectors representing individual variables. The first two RDA axes accounted for 52% of the total variation and 83% of the variation of the fitted model.

For transect R1075, marginal tests revealed that depth explained a large portion of model variability (52%, Supplementary Table 2). However, dissolved oxygen had the same weight, also accounting for 52% of the model variability (again note that marginal tests provide variable contributions when considered alone in the model). Latitude (representing effects of spatial autocorrelation) explained about 45%, and trawl mark density about 32% of model variability (Supplementary Table 2). For the best one-variable model once again depth was the best predictor of megafauna community structure. The best two-variable model, accounting for 61% of the variability, included latitude and depth, and the best three-variable model included the latter two variables plus trawl mark density (Supplementary Table 2). With respect to best overall model solutions for this transect, latitude was the most important variable, appearing in all models, followed by depth and dissolved oxygen, which were present in three of the best models, and trawl mark density, present in two. Fig. 10B shows the constrained ordination output from the redundancy analysis method (dbRDA). The first two RDA axes accounted for 61% of the total variation and 93% of the variation of the fitted model.

3.4. Taxa turnover

Taxa turnover against depth, trawling intensity, and bottom water dissolved oxygen are presented in Fig. 11. When considering the R1074 transect alone, taxa turnover was higher at intermediate depths (deep upper slope and mid slope) and lower both above (upper slope) and below (deep slope) (Fig. 11A). When data from the two transects were pooled, the same trends were apparent, to a lesser degree, with the exception of taxa turnover for mid slope, that was reduced relative to deep upper slope samples (the other intermediate depth strata) (Fig. 11D). When trawling intensity was considered, species accumulation curves showed higher species turnover at intermediate levels (low-moderate, moderate-high) of trawling intensity (Fig. 11B). This pattern was also seen in pooled data from the two transects. (Fig. 11E). Lastly, when beta diversity was related to dissolved oxygen categories, samples that were under hypoxic conditions showed higher taxa turnover than samples from areas subject to severe hypoxia (Fig. 11C). The pattern was sustained, and was even more evident when samples from both transects were pooled (Fig. 11F).

4. Discussion

The cable route surveys analyzed in this study were not optimally designed for parsing the separate effects of depth, dissolved oxygen and trawling on slope benthic communities. Dissolved oxygen concentration showed depth-related trends that changed sign part way through the longest transect, as did indications of trawling intensity, with a peak of trawling occurring mid-slope, in areas where hypoxia was most severe. Additionally, spatial autocorrelation, a perennial problem in transect surveys (e.g., Fortin and Dale 2005; Dormann et al., 2007), also influenced the results obtained, as evidenced by the variability attributable to the factors 'latitude' and 'longitude' in the statistical analyses. Despite these potentially confounding factors, statistically significant and plausible trends emerged from the > 50 km of continuous observations, with 21 to 52% of the total variability in the multivariate space (community structure) explained by either depth, trawling intensity, or dissolved oxygen (Supplementary Tables 1 and 2 Fig. 10).Therefore, influences of bottom trawling on structuring deepwater benthos can be observed even where communities are being shaped by strong environmental gradients. Our data revealed evidence of higher trawling intensity at mid-slope depths (600–900 m), largely

Table 2

Output of the one-way PERMANOVA analysis based on the resemblance matrix of megafauna abundance data for transect R1075. *A priori* factors were analyzed separately due to an unbalanced sample design: *depth strata* (upper slope, deep upper slope, mid slope, deep slope), *trawling* (low, low-moderate, moderate-high, high), *dissolved oxygen* (normoxia, hypoxia, severe hypoxia).

R1075	Source	df	SS	MS	Pseudo-F	p(perm)	Unique permutations
Main test	**Depth Strata**	1	11385	11385	18.601	**0.0001**	9925
	Residual	25	15301	612.04			
	Total	26	26686				
	Trawling	2	7448.7	3724.3	4.6465	**0.0017**	9934
	Residual	24	19237	801.54			
	Total	26	26682				
	Diss. Oxygen	1	5792.2	5792.2	6.9306	**0.0002**	2831
	Residual	25	20893	835.74			
	Total	26	26686				
Pair wise tests	Source	df			t-statistic	p(perm)	Unique permutations
Depth St.	DUS, US	2			4.3129	**0.0001**	9939
Trawling	L, LM	21			1.2592	0.1605	9844
	L, MH	17			3.2354	**0.0001**	3585
	LM, MH	10			1.8184	**0.0485**	495
Diss. Oxygen	H, SH	25				**0.0004**	2814

PERMANOVA*one-way model.* Bold values indicate significant differences at p < 0.05. DS, deep slope, MS, mid slope, DUS, deep upper slope, US, upper slope; L, low, LM, low-moderate, MH, moderate-high, H, high; SH, severe hypoxia, H, hypoxia, N, normoxia. df, degrees of freedom, SS, sum of squares, MS, mean sum of squares, p(perm), p-value derived from permutations.
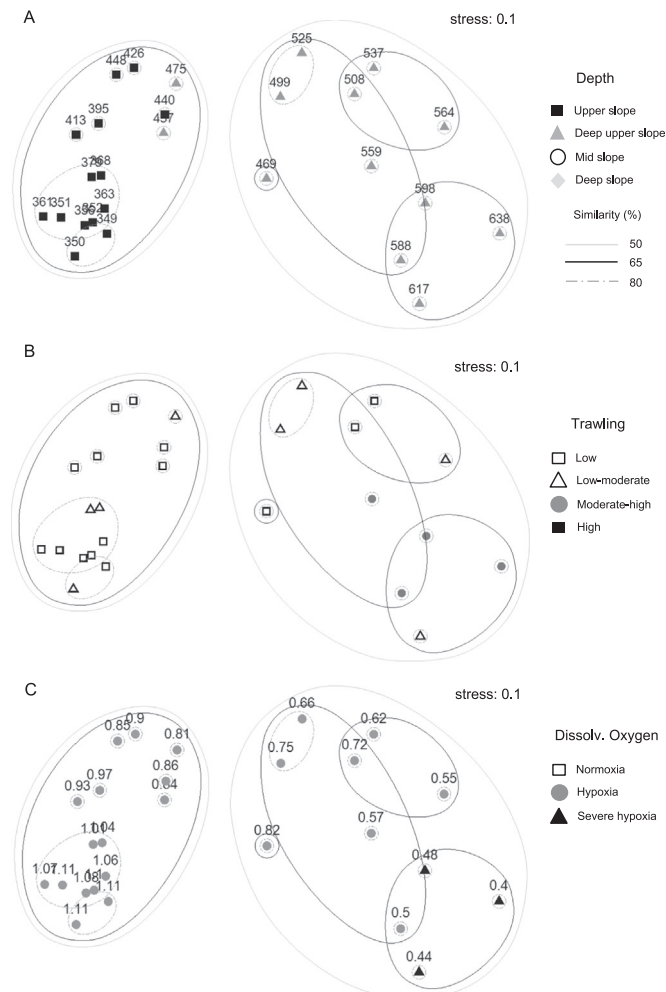

Fig. 9. Non-metric multidimensional scaling (n-MDS) plot of Bray–Curtis similarity matrix based on square root-transformed abundance data of benthic megafauna taxa sampled along transect R1075 (grouped by 500 m sample units). Circles represent group-average clusters at 50%, 65% and 80% of similarity. Panels A through C display labels according to factors depth strata, trawling intensity and levels dissolved oxygen.

corresponding to optimal areas for the commercial capture of the main targeted species, the shortspine thornyhead (*Sebastolobus alascanus*) and the longspine thornyhead (*Sebastolobus altivelis*) (Haigh and Schnute, 2003). Megafaunal densities (both invertebrates and fish), with exception of the aforementioned target species, were much lower at those depths, particularly if we consider the longer R1074 transect, which covered a wider depth range on the slope (Fig. 5, Supplementary Fig 4). This trend is consistent with previous observations of the direct and indirect effects of trawling on faunal mortality and recruitment, habitat destruction (Hutchings, 1990; Jones, 1992; Auster et al., 1996; Collie et al., 2000), and changes to the sedimentary environment that reduce the quantity and quality of deposited organic matter (Palanques et al., 2006; Martín et al., 2008, 2014; Puig et al., 2012).

The low abundance and species richness of suspension feeders in the most heavily trawled areas are in agreement with results from previous studies. Clark and Rowden (2009) found decreased abundances of slow-growing, long-lived suspension-feeding species such as corals, sea pens and sponges in heavily-trawled areas of New Zealand seamounts. However, we must use caution when comparing with these seamount studies, since the slope habitats surveyed here were covered mostly by unconsolidated sediments, which often host a distinct fauna with intrinsic adaptations to an unstructured seafloor environment compared with the fauna inhabiting highly structured seamount habitats. Another effect in the communities subject to higher trawling activity was the noticeable reduction in abundance of fish groups such as the macrourids and species such as the dover sole *M. pacificus*, and the North Pacific hake *M. productus*. These are all taxa listed as important components of the bycatch by the established bottom trawl fishery off Vancouver island (Haigh and Schnute, 2003).

Data obtained from the Canadian Department of Fisheries and Oceans (DFO) showed a relatively constant level of trawling activity in the area since record keeping began in 1996, with a total of 501 detectable 'events' (between 1996 and 2007) crossing transect R1074 (summarized in Supplementary Fig 3). Considering that the two trawl-doors from the bottom nets would be visible in the sonar, the counted number of trawl-door marks crossing transect R1074 (1,007) correlates well with the fishing events data, suggesting that trawl marks can remain visible on the seabed for at least 10 years in this environment. In the absence of confidential information that would allow the dating of trawling activity (i.e., single events) in each of the 500 m transect segments that were used in our data analysis, the observed faunal

Table 3

Output of SIMilarity PERcentage (SIMPER) analysis showing characterizing taxa contributing to similarity within groups of samples for transect R1074.

Depth strata						Trawling					
Species	Av N	Av Sim	Sim/SD	C %	Cum %	Species	Av N	Av Sim	Sim/SD	C %	Cum %
Group US Average similarity: 68.65%						**Group L** Average similarity: 57.55%					
Sebastes spp.	7.54	22.3	2.45	31.11	31.11	Ophiuroidea sp. 1	6.3	16.9	3.29	28.3	28.3
Ophiuroidea sp. 1	7.54	16.7	1.73	24.38	24.38	*Scotoplanes globosa*	3.1	6.8	1.35	11.82	40.12
Strongylocentrotus fragilis	2.28	5.64	3.62	8.21	32.59	Alcyonacea sp. 2	2.21	5.08	1.18	8.83	48.95
Asteroidea sp. 1	1.93	5.18	7.4	7.55	40.14	*Henricia sanguinolenta*	1.8	4.7	1.55	8.16	57.11
Fusitriton oregonensis	1.77	4.68	4.85	6.82	53.83	Macrouridae sp. 1	1.62	4.4	1.64	7.64	64.75
Holothuroidea sp.1	1.62	4.33	8.71	6.31	60.13	*Fusitriton oregonensis*	1.25	3.22	1.77	5.59	70.34
Microstomus pacificus	1.62	4.71	14.68	6.86	47	*Sebastes* spp.	1.29	2.79	1.3	4.84	75.19
Merluccius productus	1.67	3.94	1.63	5.74	65.87	Zoarcidae sp. 1	1.07	2.62	1.48	4.56	79.74
Group DUS Average similarity: 59.39%						**Group LM** Average similarity: 54.13%					
Ophiuroidea sp. 1	5.6	10.7	3.95	18.12	18.12	Ophiuroidea sp. 1	4.35	9.47	4.15	17.5	17.5
Anemone sp. 1	2.33	5.72	10.14	9.64	27.76	*Fusitriton oregonensis*	2.01	5.29	8.67	9.77	27.27
Strongylocentrotus fragilis	2.74	5.04	4.97	8.49	53.96	Anemone sp. 1	2.01	5.08	4.3	9.38	36.65
Ceriantharia sp.	2.27	5.26	4.64	8.86	36.62	*Sebastes* spp.	1.34	2.65	1.67	4.89	46.78
Fusitriton oregonensis	2.11	5.26	10.28	8.85	45.47	Demospongiae sp. 1	1.03	2.2	1.64	4.06	50.84
Anemone sp. 2	1.45	3.5	5.46	5.89	59.85	Alcyonacea sp. 2	1	2.16	1.69	3.99	58.86
Orthasterias koehleri	1.11	2.33	1.51	3.93	63.78	Zoarcidae sp. 1	0.99	2.12	1.67	3.92	62.79
Demospongiae sp. 1	1	1.94	1.52	3.27	70.63						
Group MS Average similarity: 67.65%						**Group MH** Average similarity: 47.4%					
Asteroidea sp. 2	1.74	5.33	6.54	7.89	7.89	*Fusitriton oregonensis*	2.12	5.28	9.87	11.13	11.13
Fusitriton oregonensis	1.85	5.32	8.88	7.88	15.76	Macrouridae sp. 2	1.51	3.69	6.51	7.78	18.91
Sebastes spp.	1.76	4.67	3.36	6.92	22.68	Anemone sp. 1	1.81	3.24	1.28	6.84	25.75
Umbellula lindahli	1.93	4.49	3.72	6.64	36.24	Ceriantharia sp.	1.78	3.02	1.28	6.38	32.13
Zoarcidae sp. 1	1.5	4.67	6.84	6.92	29.6	Asteroidea sp. 3	1.32	2.47	1.23	5.2	37.33
Sebastolobus spp.	1.68	4.38	2.69	6.49	42.73	Zoarcidae sp. 1	1.28	2.2	1.36	4.63	41.97
Anemone sp. 1	1.53	4.17	6.92	6.18	48.91	Anemone sp. 3	1.1	2.09	1.33	4.4	50.86
Macrouridae sp. 1	1.31	3.71	6.58	5.49	54.4	*Orthasterias koehleri*	0.93	1.89	1.36	4	54.86
Henricia sanguinolenta	1.31	3.65	5.22	5.4	59.8	**Group H** Average similarity: 72.2%					
Group DS Average similarity: 62.26%						Sebastes spp.	2.27	7.12	5.78	9.86	9.86
Ophiuroidea sp. 2	5.57	14.1	2.3	22.67	22.67	Pennatulacea sp. 2	2.06	6.69	11.7	9.27	19.13
Scotoplanes globosa	3.66	9.03	2.34	14.51	37.17	Asteroidea sp. 3	1.68	5.65	8.71	7.83	26.95
Alcyonacea sp. 2	2.43	6.17	1.64	9.91	47.08	*Fusitriton oregonensis*	1.67	5.6	10.55	7.76	34.71
Macrouridae sp. 2	1.86	5.8	6.6	9.32	56.4	Zoarcidae sp. 1	1.62	5.59	12.77	7.74	42.45
Henricia sanguinolenta	1.86	4.98	1.59	8	64.39	*Sebastolobus* spp.	3.07	5.32	3.15	7.37	49.82
Fusitriton oregonensis	1.22	3.17	1.7	5.09	69.48	*Chionoecetes tanneri*	1.35	4.65	12.5	6.44	56.25
Zoarcidae sp. 1	1.16	2.96	1.72	4.75	74.23	*Umbellula lindahli*	1.31	4.19	8.27	5.81	62.06
Dissolved Oxygen						Macrouridae sp. 2	1.33	4.11	5.71	5.7	67.75
Group SH Average similarity 56.22%						Anemone sp. 1	1.27	3.97	8.79	5.5	78.92
Ophiuroidea sp. 1	4.86	9.73	1.16	17.31	17.31						
Scotoplanes globosa	3.02	5.86	1.08	10.42	27.73						
Macrouridae sp. 2	1.7	5.05	4.79	8.98	36.71						
Fusitriton oregonensis	1.5	4.19	3.35	7.46	44.17						
Henricia sanguinolenta	1.65	4.04	1.47	7.18	51.36						
Sebastes spp.	1.61	3.65	1.52	6.49	64.59						
Zorcidae sp. 1	1.24	3.28	2.11	5.83	70.42						
Sebastolobus spp.	1.26	3.11	1.61	5.53	75.95						
Group HY Average similarity 47.44%											
Ophiuroidea sp. 1	5.75	13.45	2.93	28.35	28.35						
Fusitriton oregonensis	1.38	2.81	1.33	5.92	40.4						
Sebastes spp.	0.97	2.18	1.21	4.6	55.32						

DS, deep slope, MS, mid slope, DUS, deep upper slope, US, upper slope; L, low, LM, low-moderate, MH, moderate-high, H, high; SH, severe hypoxia, HY, hypoxia; *Av N*, average abundance, *Av Sim*, average similarity, *Sim/SD*, similarity divided by the standard deviation; *% C*, percent contribution; *Cum%*, cumulative percentage.

characteristics must be assumed to be an unknown mixture of three possibly different faunal assemblages: 1) virgin assemblages on fragments of seafloor area untouched by trawling; 2) survivor assemblages of species that resisted the passage of the trawl and any resulting sediment redistribution; 3) recolonizing assemblages consisting of species best adapted for rapid recolonization of disturbed areas of the seafloor.

Depth was the single most important factor in determining benthic megafaunal community structure, i.e., accounting for the largest degree of community dissimilarity (PERMANOVA, Tables 1 and 2). This result does not come as a surprise as the deep-sea megabenthos is known to respond to depth, which is a co-variant of many other environmental variables such as hydrostatic pressure, temperature, and particulate organic carbon flux, all influencing assemblage composition, abundance and alpha diversity (Rex 1983; Levin et al., 2001; Carney 2005; De Leo et al., 2012, 2014). Megafaunal assemblages also differed (within each individual transect), however, as a function of trawling intensity and dissolved oxygen concentration, with smaller but still significant levels of variability partitioning explained among these two variables (Tables 1 and 2). Both dissolved oxygen and trawling intensity were also selected as important predictor variables in the output of the multiple regression models (DITLM analysis) for both transects studied, and can therefore be considered as important drivers of community structure patterns (Fig. 10, Supplementary Tables 1 and

Table 4

Output of SIMilarity PERcentage (SIMPER) analysis showing characterizing taxa contributing to similarity within groups of samples for transect R1075.

Depth strata						Trawling					
Species	Av N	Av Sim	Sim/SD	C %	Cum %	Species	Av N	Av Sim	Sim/SD	C %	Cum %
Group US - Average similarity: 72.09%						**Group L -** Average similarity: 64.24%					
Anemone sp. 7	3.47	8.41	4.07	11.67	11.67	Anemone sp. 7	2.86	6.36	2.97	9.9	9.9
Holothuroidea sp. 3	2.56	6.95	6.31	9.64	21.32	Holothuroidea sp. 3	2.33	5.99	3.77	9.33	19.23
Anemone sp. 5	2.4	6.23	5.45	8.64	29.95	Anemone sp. 5	2.31	5.75	3.91	8.95	28.18
Strongylocentrotuus fragilis	1.83	4.81	3.73	6.67	36.63	*Strongylocentrotus fragilis*	1.88	4.82	3.84	7.5	35.68
Holothuroidea sp. 4	2.36	4.75	1.47	6.59	43.22	Anemone sp. 4	1.68	4.45	5.38	6.94	42.62
Microstomus pacificus	1.65	4.43	7.82	6.14	49.37	*Merluccius productus*	1.53	4.11	8.13	6.4	49.02
Merluccius productus	1.52	4.18	9.19	5.79	55.16	Ophiuroidea sp. 1	2.14	3.8	1.79	5.91	54.93
Anemone sp. 4	1.55	4.16	4.79	5.77	60.93	*Sebastolobus* spp.	1.41	3.74	7.68	5.83	60.76
Group DUS Average similarity: 61.09%						Anemone sp. 6	1.41	3.36	2.12	5.24	65.99
Ophiuroidea sp. 1	6.22	10.9	1.72	17.93	17.93	*Microstomus pacificus*	1.39	3.23	1.65	5.04	71.03
Holothuroidea sp. 2	2.98	5.95	1.79	9.75	27.68	Asteroidea sp. 3	1.15	2.68	1.65	4.17	75.2
Strongylocentrotus fragilis	2.86	5.86	3.51	9.59	37.27	**Group LM -** Average similarity: 55.1%					
Anemone sp. 4	1.77	4.01	3.73	6.56	51.52	*Strongylocentrotus fragilis*	3.11	6.36	3	11.55	11.55
Anemone sp. 5	1.98	3.93	2.84	6.44	57.96	Anemone sp. 5	2.38	5.16	3.39	9.37	20.91
Asteroidea sp. 3	1.63	3.6	4.91	5.89	63.85	Anemone sp. 4	1.78	4.08	4.37	7.4	36.57
Sebastolobus spp.	1.36	3.26	5.91	5.34	69.19	Anemone sp. 6	1.53	3.61	4.45	6.55	43.12
Anemone sp. 6	1.43	3	2.04	4.91	74.11	Asteroidea sp. 3	1.5	3.4	4.04	6.17	49.3
Dissolved Oxygen						*Sebastolobus* spp.	1.41	3.31	4.77	6.01	55.31
Group HY Average similarity: 60.5						*Merluccius productus*	1.23	2.67	1.65	4.84	66.07
Anemone sp. 5	2.31	5.43	3.38	8.98	8.98	**Group MH -** Average similarity: 69.38%					
Anemone sp. 3	2.63	5.29	1.84	8.74	17.73	Ophiuroidea sp. 1	9.31	21.1	8.93	30.54	30.54
Strongylocentrotus fragilis	2.37	5.19	3.62	8.59	26.31	Holothuroidea sp. 2	3.87	8.95	15.2	12.9	43.44
Anemone sp. 4	1.72	4.28	5.06	7.08	33.39	*Strongylocentrotus fragilis*	2.45	4.98	3.58	7.18	57.93
Holothuroidea sp. 3	1.97	4.18	1.45	6.9	47.24	Asteroidea sp. 3	2.01	4.61	28.04	6.65	64.58
Merluccius productus	1.46	3.75	5.82	6.19	53.43	*Henricia sanguinolenta*	1.67	3.28	6.06	4.73	69.31
Anemone sp. 6	1.5	3.56	2.65	5.89	59.32	*Sebastolobus* spp.	1.29	2.84	5.08	4.09	73.4
Sebastolobus spp.	1.38	3.46	5.35	5.72	65.04	Anemone sp. 4	1.29	2.79	7.66	4.02	77.42
Microstomus pacificus	1.34	2.92	1.61	4.82	69.86	Anemone sp. 5	1.41	2.76	7.54	3.97	81.39
Asteroidea sp. 3	1.28	2.92	2.1	4.82	74.68						
Group SH Average similarity: 71.73											
Ophiuroidea sp. 1	9.4	22.6	7.83	31.53	31.53						
Holothuroidea sp. 2	3.55	8.67	24.35	12.08	43.61						
Asteroidea sp. 3	2.18	5.21	9.91	7.27	50.88						
Strongylocentrotus fragilis	1.99	4.38	5.09	6.1	56.98						
Sebastolobus spp.	1.5	3.93	50.85	5.47	68.08						
Pennatulacea sp. 3	1.75	3.5	5.55	4.88	72.96						
Anemone sp. 5	1.27	3.24	12.54	4.51	77.47						
Henricia sanguinolenta	1.39	3.12	50.85	4.35	81.82						
Pennatulacea sp. 4	1.29	2.9	6.4	4.04	85.87						
Anemone sp. 4	1.17	2.8	8.1	3.9	89.76						

DS, deep slope, MS, mid slope, DUS, deep upper slope, US, upper slope; L, low, LM, low-moderate, MH, moderate-high, H, high; SH, severe hypoxia, HY, hypoxia; *Av N*, average abundance, *Av Sim*, average similarity, *Sim/SD*, similarity divided by the standard deviation; *% C*, percent contribution; *Cum %*, cumulative percentage.

2). This first evaluation of the influence of environmental gradients along with bottom trawling effects on the megafauna community structure offshore Vancouver Island in the NE Pacific region provides baseline data for future investigations.

The negative impacts of low dissolved oxygen concentrations on benthic megafauna densities species richness and turnover were evident in regions exposed to severe hypoxia conditions (i.e., dissolved oxygen concentrations lower than 0.5 ml l^{-1}, Figs. 5–7 and 11). This is in agreement with previous studies of the effects of oxygen minimum zones elsewhere in the Pacific and Indian oceans (reviewed in Levin, 2003; Gooday et al., 2010; and more recently in Gallo and Levin, 2016, specifically for fish species). Megafauna are mostly absent or nearly so in the cores of OMZs where bottom-water oxygen falls below 0.15 ml l^{-1} (Levin, 2003). For example, few taxa other than hermit crabs are found in the OMZ core off central California, where oxygen concentrations do not fall below 0.27 ml l^{-1} (Thompson et al., 1985). The core of the OMZ covering our study area of the NE Pacific reaches a minimum low of 0.17 ml l^{-1} in dissolved oxygen concentration between 900–

970 m, where aside from the hypoxia-tolerant taxonomic groups such as rockfishes, thornyheads and macrourids, only few other taxa are also present, such as sea pens and an unidentified sea star, but all at very low densities.

Another pattern we observed that is in agreement with previous observations is the presence of extraordinarily high densities of megafauna near the lower and upper boundaries of the OMZ. In our study, ophiuroids were overwhelmingly abundant at the upper (shallower) boundary (i.e., 580–620 m; diss. oxygen of 0.46–0.66 ml l^{-1}; temperature of 4.3–4.7 °C), as well as at the deeper boundary (i.e., 1100–1200 m; diss. oxygen of 0.22–0.30 ml l^{-1}; temperature of 3.06–3.27 °C), while the holothurian *Scotoplanes globosa* was extremely abundant only at the deeper boundary. For example, 3,359 individuals of *S. globosa* were counted in a 500 m transect segment at 1,100 m depth, just below the core of the OMZ. Levin (2003) has postulated that *edge effects* occur in those areas near the upper and lower boundaries of OMZs, where benthic faunal densities often exhibit a maximum at specific oxygen concentrations that may represent a physiological
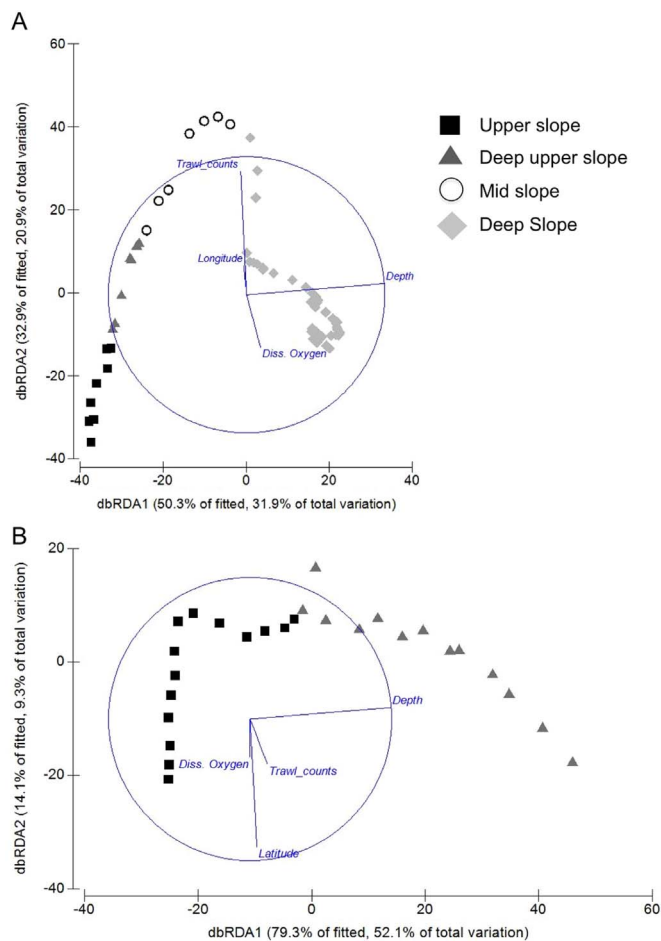
Fig. 10. Results of the distance-based multivariate multiple regression (DISTLM) of benthic megafauna abundance overlaid with the partial correlations of the significant environmental variables identified by the best models using the AIC$_c$ criterion. A) Transect R1074, B) Transect R1075. Sample labeling depicts levels of factor depth strata.

threshold. The author further discusses the idea that this response may reflect the interaction of a rich supply of organic matter with a release from oxygen limitation. One could argue that the occurrence of those high-density faunal aggregates in our study could also be related to the release from the highest trawling pressure, which somewhat coincides with the OMZ upper and lower boundaries. However, the peak in ophiuroid aggregations for transect R1075 does occur where trawl mark densities were the highest. This observation perhaps indicate that a dissolved oxygen deficit rather than high trawling pressure is the defining environmental gradient responsible for these OMZ edge effects, agreeing with Levin (2003).

5. Conclusion

Our results indicate that both trawling activity and hypoxia act cumulatively (or synergistically) in reshaping benthic megafauna community structure on the continental slope, offshore Vancouver Island, by reducing species densities, richness and turnover at larger spatial scales (beta diversity). These effects were particularly evident at mid-slope depths, where trawling was most concentrated and hypoxia was most severe. The long cable route survey transects that were our primary source of data were not ideally suited to resolving the effects of trawling and the influence of the OMZ. Our findings therefore represent a preliminary evaluation of the cumulative effects of trawling and hypoxia (and depth) on the slope benthos. Further investigation of identified trends will require more comprehensive surveys, including replicate cross-slope transects that hold depth and therefore dissolved oxygen constant while trawling intensity

varies. Such surveys could further resolve the individual and cumulative effects of these three factors. Extension of investigations to sediment infauna and microbial processes would provide a broader view of overall ecological effects, but would require sampling that followed a similar replicated cross-slope survey design. Additionally, the NEPTUNE cabled observatory network operated by Ocean Networks Canada (ONC) has fixed monitoring stations (seafloor instrument platforms) at the upper and lower boundaries of the OMZ (connected to the Barkley and Clayoquot Slope nodes, respectively; http://www.oceannetworks.ca/sights-sounds/maps), which could be used to monitor variability in water mass properties (dissolved oxygen, etc.) and related responses of the benthos. Previous studies have used time-series imagery and oceanographic sensor data from the Barkley instrument platforms to quantify surficial bioturbation by the slope megafauna (Robert and Juniper, 2012) and high-frequency and seasonal dynamics of the benthic megafaunal community in a nearby submarine canyon (Juniper et al., 2013; Matabos et al., 2014).

The poorly described nature of the benthic megafauna in this area of the NE Pacific, revealed by the low level of taxonomical resolution in our faunal identifications, is not surprising given the lack of previous studies in the region. This study represents a first contribution to knowledge of assemblage distribution, abundance, and overall diversity for the deep-sea benthic megafauna on the continental margin offshore Vancouver Island. Future studies that expand the taxonomic resolution of these faunal assemblages will help improve our understanding of the patterns observed here, and their relationship to the biology and ecology of individual species. For example, two taxa proved to be resilient to the apparent cumulative effects of trawling and hypoxia; the 'blood star' *Henricia sanguinolenta* and the thornyhead fishes (*Sebastes* spp.) occurred at moderate and high abundances, respectively, in oxygen concentrations of 0.2–0.4 ml l^{-1} and at peak trawl mark densities of 50–80 marks transect^{-1}. The predatory/scavenging *H. sanguinolenta* is distributed from intertidal to abyssal depths (0–2440 m; World Registry of Marine Species Aphia ID 123794) but no particular adaptations to hypoxia or disturbance by fishing gear have been documented. In contrast, blood pigment and metabolic adaptations of thornyhead fishes to hypoxic environments are well known in the physiological literature (e.g., Yang et al. 1992; reviewed in Gallo and Levin, 2016). The emergence of a commercial fishery targeting these species has resulted in the concentration of bottom trawling activity in the thornyhead habitat, where benthic communities are already subject to hypoxic and severe hypoxic stress. With predictions of spatial expansion of world's oceans dead zones, or OMZs, related to climate change and cultural eutrophication, there is a compelling need to improve our knowledge of how deep-sea organisms will respond to these foreseen changes, and to develop strategies for predicting and monitoring impacts on diversity and ecosystem functioning.
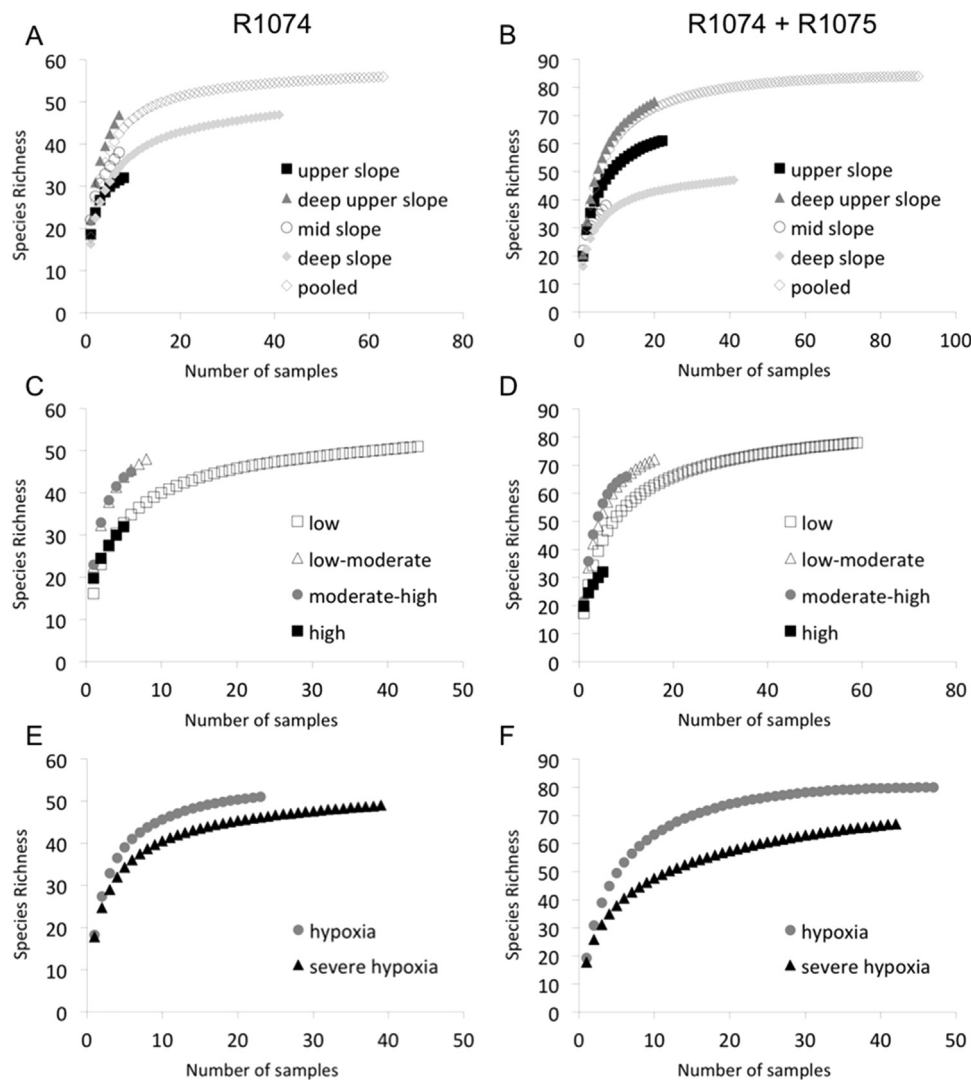
Fig. 11. Randomized species accumulation curves (Ugland et al., 2003) calculated for factors depth strata (A,B), trawling intensity (C,D) and dissolved oxygen (E,F). Left panels display curves computing only samples from transect R1074, and right panels display curves pooling samples from both transects.

in the manuscript derived from bathymetry and ROV survey data. Lastly, we thank L.A Levin and an anonymous reviewer for helping to substantially improve the manuscript. This manuscript is based on original M.Sc. research by M. Gauthier.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr2.2016.11.014.

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