Does the Intermediate Disturbance Hypothesis apply to the deep-sea benthic communities in Monterey Canyon?

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ABSTRACT

The most influential model explaining the effects of disturbance on diversity is the Intermediate Disturbance Hypothesis (IDH), which proposes a maximum diversity at intermediate levels of disturbance frequencies or intensities while diversity is low at both ends of a disturbance continuum. To test if this model can predict patterns of biodiversity in deep-sea benthic communities we conducted a field experiment at 7 study sites in the Monterey Canyon. Disturbance, in the form of sediment movement, occurs naturally along the canyon and no additional experimental disturbance was applied. Infauna was collected by taking sediment push cores and megafauna was recorded with video transects using the Tiburon, a remotely operated vehicle (ROV) developed at the Monterey Bay Aquarium and Research Institute (MBARI). Mean richness of megafauna peaked at intermediate distance from the canyon head, where intermediate physical disturbance as sediment movement would occur, and where the abundance of dead plant material (Phyllospadix and Laminares) also was at intermediate levels. However, distance from the canyon head will also mean increase in depth. Effects of disturbance on diversity were not separable from effects of resource enrichment or factors associated with depth (i.e. oxygen) possibly affecting benthic communities.

Key words: *community structure; competitive exclusion; disturbance; benthic community; infauna; megafauna; resource availability*

INTRODUCTION

The high diversity of plants and animals that exist in natural communities, and especially the difference in diversity between communities, have always fascinated biologists and naturalists. More recently much attention has been shifted towards the deep-sea benthos due to technological advances allowing this formerly unavailable area to be explored by scientists. According to Gage (1996) the question of how this seemingly food-poor and apparently featureless habitat can hold such a high biological diversity provides one of the most intriguing and challenging problems in marine biology. An abundance of studies and experiments on variability in diversity along spatial and temporal gradients has been conducted for a long time and has given rise to a variety of explanatory theories and hypothesis throughout the last century. Earlier efforts to explain spatial patterns in diversity include: the time theory (Fischer, A. G. 1960), the theory of spatial heterogeneity (Miller, A. H. 1958, MacArthur and MacArthur 1961), the competition hypothesis (Dobzhansky, T. and Pavan, C. 1950), the predation hypothesis (Paine, R. T. 1966.), the theory of climatic stability (Klopfer, P. H., 1959, Klopfer, P. H., and R. H. MacArthur, 1961) and the productivity theory (Connell and Orias 1964). Theories explaining patterns in biodiversity where later divided into equilibrium and nonequilibrium hypothesis. According to equilibrium hypotheses the species composition of communities is usually in a state of equilibrium and high diversity is maintained without continual changes in species composition, while the nonequilibrium hypotheses predict high diversity to be maintained only when the species composition is continually changing and that the species composition of communities is seldom in a state of equilibrium. Equilibrium hypotheses include: the niche diversification hypothesis (Schoener, 1974), the circular networks hypothesis (Buss and Jackson,1979) and the compensatory mortality hypothesis (Janzen, 1970), whereas the gradual change hypothesis (Hutchinson, 1941), the equal chance hypothesis (Sale, 1977) and the Intermediate Disturbance Hypothesis (Connell, 1978) are examples of nonequilibrium hypotheses.

The Intermediate Disturbance Hypothesis (henceforth referred to as the IDH) predicts that diversity patters in nature can be explained by different responses to disturbance. Disturbance has been recognized as a structuring force in ecological communities since the beginning of the last century (Cooper, 1926), although it is not until recently disturbance has received much attention as an important mechanism affecting patterns of biodiversity (e.g., Buckling et al. 2000, Huxham et al. 2000, Mackey and Currie 2001, Molino and Sabatier 2001, Gutt and Piepenburg 2003, Roxburgh et al. 2004, Lenz et al. 2004). There is a rich variety of mechanisms and processes that are defined as agents of disturbance in ecological studies and they are usually divided into two major groups; physical disturbance and biological disturbance. Physical disturbance is most often characterized by what is commonly known as "natural" disturbances, such as fire (Eggeling 1947), wind (Molino and Sabatier 2001), wave action (McGuinness 1987), grounding of icebergs (Gutt and Pipenberg 2003), drifting logs (Dayton 1971), floods (Lake et al. 1989), sediment movement (Cowie et al. 2000), disease (Ayling 1981), temperature (Flöder and Sommer 1999), patchy input of organic material (Smith 1986), and emersion of aquatic organisms (Lenz et al. 2004), but also anthropogenic activities such as trawling (Lindegarth et al. 2000) and even warfare (Rapport et al. 1985). Biological disturbance is most often recognized plainly as predation (Talbot et al. 1978) and/or grazing (Agard et al. 1996), but some authors add trampling (Eggeling 1947) and burrowing (Guo 1996) by animals as examples of biological disturbance. There is also a broad range of theoretical definitions of disturbance, from Grime's (1977) simple definition of disturbance as "partial or total destruction of biomass", to a more complex definition by Pickett and White (1985), where disturbance is "any relative discrete event in time that disrupts ecosystems, community, or population structure and changes resources, substrate availability, or the physical environment". The disturbance applied on the communities in this experiment, was removal of biomass from a certain area of the settlement panel, thus, additionally freeing substratum for settlement, and is therefore coherent with the definition of disturbance by Sousa (1984): "disturbance is a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established". Because the definitions of disturbance are highly variable in ecological studies, this can be an important source of bias when results are compared among studies with different disturbance definitions. Ecological studies with the same general data may draw entirely different conclusions depending on what definition of disturbance that is used. Thus, the definition of disturbance may be as important as either the experimental set-up or the statistical analyses for the result of an ecological study.

The IDH has become established in ecological thinking and has had a major influence on many management plans, for instance the Yellowstone National Park fire policy (Wootton 1998). There has recently been a rather strong debate on the origin of the IDH (e.g. Wilkinson 1999) where the first signs are reaching back to 1925 (Underwood 2000). The most common, although not necessarily the most appropriate, paper cited is that by Connell (1978). The IDH is based on the basic proposition that diversity is low at both ends of a disturbance continuum with a unimodal peak at the intermediate level, yielding the characteristic hump-back curve (Fig 1.) of Connell (1978). The underlying mechanisms for the hump-back curve is often explained by the "shifting mosaic theory" for between-patch mechanisms (e.g. Sousa 1979, 1980, Wilson 1990) and by the set back of a patch's "successional clock" for within-patch mechanisms (e.g. Connell 1978, Osman 1977, Collins and Glenn 1997).

According to the within-patch explanation of IDH patches that are frequently and/or intensely disturbed are expected to exhibit low species richness because fewer species are able to

colonize the patch during the brief period between disturbances or tolerate the high intensities of disturbances. At the other end of the continuum patches with infrequent and/or low intensity of disturbances are also expected to be low in species number because they become dominated by competitively superior species. The highest species richness will then occur at intermediate levels and/or intensities of disturbance because both rapid colonizers and more competitive species coexist in the patch (Osman, 1977). The highest diversity within in a patch will also occur at intermediate lengths of time following a disturbance event, although this has suggested to be an independent and unrelated prediction of the IDH (Collins et al., 1995, Collins and Glenn, 1997).

The between-patch explanation differs from the within-patch explanation only regarding species number at different successional stages. According to the between-patch explanation of the IDH, different patches are at different successional stages but they still contain the same species number, although a different set of species. Early successional patches will show a higher proportion of r-selected species and late successional patches will have a higher content of K-selected species, thus together increasing diversity in a shifting patch mosaic (Sousa, 1979).

The IDH have been tested extensively by field studies in both terrestrial (e.g. Molino and Sabatier 2001) and marine (e.g. Talbot et al. 1978) ecosystems as well as in laboratory experiments (Buckling et al. 2000, Cowie et al. 2000) and by mathematical modelling (Levin and Paine 1981, Dial and Roughgarden 1998). However, there have not been many field studies testing the IDH on macro- and megafaunal communities in submarine canyons.

The aim of this project was to test whether the IDH is applicable to, not only terrestrial and shallow aquatic environments, but also deep-sea benthic communities in submarine canyons. The degree of sediment movement (i.e. physical disturbance) declines with distance from canyon head (e.g. depth) in the Monterey canyon and 7 different sites, ranging from 400 to 3800 m depth, along the canyon were compared with regard to abundance and diversity of macro- and megafauna. The diversity of the different sites was estimated from counting and identifying infauna from sediment samples and megafauna from video transects taken with a R.O.V. (remotely operated vehicle) over a period of 5 years ranging from December 2000 to July 2005.

STUDY SITE

The Monterey Canyon is the largest submarine canyon on the California coast (Xu et al. 2002), and it lies within the Salinian block, a Cretaceous basement block that has been tectonically slivered into its current position (Barry et al. 1996). The Monterey Canyon head extends very close to shore, and the canyon follows a winding path for 75 km across the shelf and slope to a depth of approximately 3000 m, where the canyon connects with Monterey fan valley, known as the Monterey Fan (McHugh et al. 1992). Monterey canyon is large enough to have a great variety of physical dimensions along its entire length and the deep, steep-walled canyon is eroded through relatively hard sedimentary, igneous and metamorphic rocks, whereas the more subdued fan valley is incised in relatively soft and young fan deposits (Xu et al. 2002). A variety of investigations have shown that sediment transport in Monterey Canyon is a very active process and that internal tides are strong enough to transport sediment in the canyon (Xu et al. 2002). Evidence of sediment transportation in Monterey Canyon includes the recent Loma Prieta earthquake, where transponders deployed in the canyon moved 2 km down-canyon, suggesting some type of gravity current (Garfield et al. 1994) and

observations by Okey (1997) which have shown that sediment ponds near the canyon head are periodically released in sudden failures caused by fall-winter storms.

MATERIALS AND METHODS

Infauna samples were collected and video transect were recorded in the Monterey Canyon and the Monterey Fan at 7 different sites at depths from 400-4000 m under a period of 5 years, from December 2000 to July 2005. The remotely operated vehicles (R.O.V) Tiburon and Ventana, developed at the Monterey Bay Aquarium Research Institute (MBARI), were used to take 3 cylindrical push cores (7 cm diameter) and approximately 3 x 10 minute video transects from each site. The Tiburon was used for taking the samples from sites at 1860 m (122°10'W/36°70'N), 2310 (122°15'W/36°60'N), 3050 m (122°58'W/36°57'N), 3260 m (122°67'W/36°37'N), 3670 m (123°24'W/36°08'N) and 3890 m depth (123°00'W/35°54'N), while the Ventana was used for taking the samples from one site at 400 m depth (121°88'W/36°79'N).

The cylindrical tube push cores were sectioned vertically for infaunal analyses, yielding 0-3, 3-5 and 5-10 cm fractions for the site at 3.6 km depth and 0-5 and 5 -10 cm fractions for samples from all other sites. All samples were live-sieved through 300 µm screen on board ship and preserved in formalin. Samples were transferred to 100 or 70 % ethanol within 48 hours of collection. Infauna were sorted from the top 10 cm of core samples at 12-50 x magnification using a dissecting microscope.

Video transects were taken by letting the remotely operated vehicles (R.O.V) Tiburon and Ventana., equipped with HMI (metallogen metal halide arc lamp) lighting, a high-resolution color digital camera (three chip Panasonic WVE550)(Goffredi et al. 2004), film while cruising along a straight course close to the bottom for approximately 3 x 10 minutes at each site. Laser pointers spaced 30 cm apart were used in order to make accurate estimations of the length of each transect. Video transects were later annotated for species identification and abundance of megafauna with the aid of VARS software (Video Annotation and Reference System).

RESULTS

INFAUNA

The nematodes and polychaetes were the most abundant infaunal invertebrates in the push core samples for all sites and especially abundant at 2.3 and 3.2 km depth, 48.8 and 127 km of distance from the Monterey Canyon head, respectively (Table 1, Fig. 1). The sites at 2.3 and 3.2 km depth also had the highest number of individuals in total from all groups (Fig. 1). Crustaceans, mostly benthic copepods and Tanaid sp.2, were most abundant at 3.2 km depth 127 km from the Monterey Canyon head (Table 1, Fig 1.).

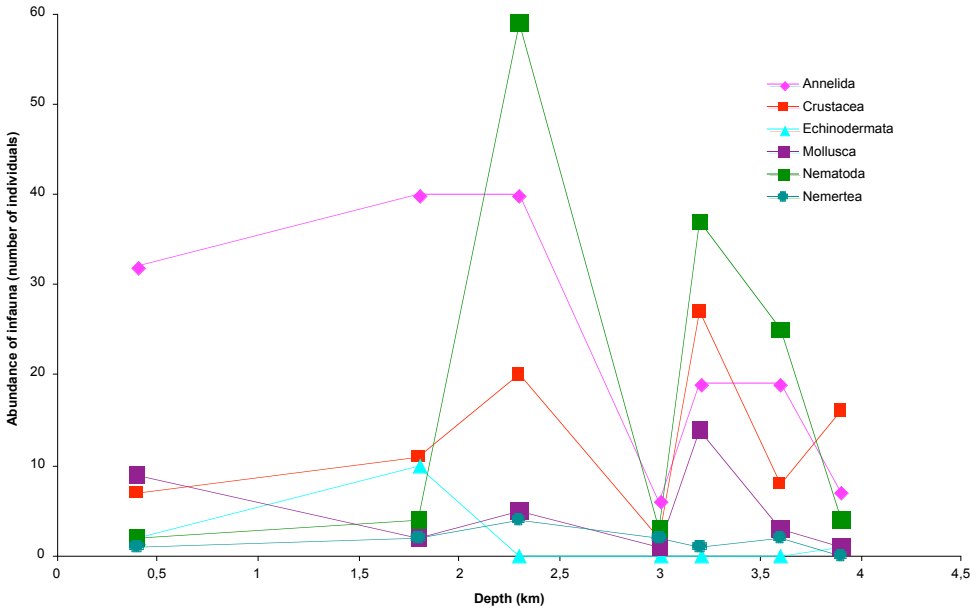

Figure 1 Total abundance of infauna (number of individuals) for all sites plotted against kilometers of depth from surface.

Table 1 Total abundance of infaunal species for all sites. Numbers in bold indicates depth and normal numbers indicates distance from Monterey Canyon head.

	9.9 km **0.4 km**	48.8 km **1.8 km**	61.4 km **2.3 km**	104 km **3 km**	127 km **3.2 km**	220 km **3.6 km**	288 km **3.9 km**
Annelida							
Capitella sp.	0	0	0	0	6	0	0
Pogonophoridae sp. 1	0	0	0	0	2	0	0
Polychaet sp. 1	0	7	2	0	0	7	0
Polychaet sp. 2	0	0	4	0	0	0	0
Polychaet sp. 3	0	0	2	0	0	0	1
Polychaet sp. 4	5	2	2	0	0	4	1
Polychaet sp. 5	0	0	10	0	0	0	0
Polychaet sp. 6	0	0	3	0	0	1	0
Polychaet sp. 7	0	0	1	0	0	0	0
Polychaet sp. 8	0	8	2	1	0	2	0
Polychaet sp. 9	0	1	7	1	0	0	1
Polychaet sp. 10	0	0	2	0	0	1	0
Polychaet sp. 11	0	0	1	0	0	0	1
Polychaet sp. 12	0	0	2	0	0	0	0
Polychaet sp. 13	0	0	1	0	0	0	0
Polychaet sp. 14	0	1	1	0	0	0	0
Polychaet sp. 15	0	0	0	0	0	0	1
Polychaet sp. 16	0	0	0	0	0	1	2
Polychaet sp. 17	0	0	0	1	0	0	0
Polychaet sp. 18	0	0	0	2	0	0	0
Polychaet sp. 19	0	0	0	1	0	0	0
Polychaet sp. 20	0	1	0	0	0	0	0
Polychaet sp. 22	0	3	0	0	0	0	0
Polychaet sp. 25	0	1	0	0	0	0	0
Polychaet sp. 26	0	3	0	0	0	0	0
Polychaet sp. 27	0	2	0	0	0	0	0
Polychaet sp. 28	0	1	0	0	0	0	0
Polychaet sp. 30	6	0	0	0	0	0	0
Polychaet sp. 31	2	0	0	0	0	0	0
Polychaet sp. 32	1	0	0	0	0	0	0
Polychaet sp. 33	1	0	0	0	0	0	0
Polychaet sp. 34	1	0	0	0	0	1	0
Polychaet sp. 35	1	0	0	0	0	0	0

Polychaet sp. 36	0	0	0	0	0	2	0
Polychaet sp. 37	0	0	0	0	11	0	0
Crustacea							
Ampeliscidae	0	0	0	0	0	1	0
Amphipod sp.3	1	1	0	0	0	0	0
Amphipod sp.5	0	4	0	0	0	0	0
Amphipod sp.6	0	3	0	0	0	0	0
Bathymedon sp.	0	2	4	0	0	0	0
Campylapsis sp.	0	1	0	0	0	0	0
Copepoda	0	0	6	0	14	2	6
Desmosomatidae	0	0	0	0	3	0	0
Eudorella sp.	0	0	1	0	0	1	0
Harpiniopsis epistomata	0	1	3	0	0	1	0
Ischnomesidae sp. A	0	0	1	0	0	0	0
Isopod sp. A	0	0	1	0	0	0	0
Leptostylis sp.	0	1	0	0	0	0	0
Myodocopid sp. 1	0	0	0	0	0	1	0
Myodocopid sp. 2	0	0	0	0	0	0	3
Oedicerotidae sp. 1	0	0	0	0	1	0	0
Ostracoda	0	0	0	1	0	0	0
Ostracoda sp. 1	0	0	0	0	0	6	0
Ostracoda sp. 2	0	0	0	1	0	0	3
Ostracoda sp. 3	7	0	0	0	0	0	0
Tanaid sp.1	0	0	1	0	0	0	0
Tanaid sp.2	0	0	5	0	9	1	1
Valletiopsis sp.	0	0	0	0	0	0	1
Echinodermata							
Holothurian sp.1	0	0	0	0	0	0	1
Ophiacantha sp.	0	3	0	0	0	0	0
Ophiura sp.	2	6	0	0	0	0	0
Mollusca							
Adontorhina cyclia	0	0	3	1	2	0	2
Adontorhina lynnae	0	0	0	0	2	0	0
Bivalvia	1	1	1	0	0	1	0
Calyptogena juvenile	7	0	0	0	0	0	0
Camptonectidae juvenile	0	0	0	0	1	0	0
Lasaeidae	0	0	0	0	2	0	0
Mendicula ferruginosa	0	0	0	0	0	1	0
Mohnia vernalis	0	0	0	0	1	0	0
Neilonella mexicana	0	0	0	0	1	0	0
Nuculana nov. sp.	0	1	0	0	0	0	0
Spathoderma californicum	0	0	0	0	3	0	0
Tindaria	0	0	0	0	0	1	0
Tindaria Juvenile	0	0	0	0	1	0	0
Tindaria kennerlyi	0	0	1	0	0	1	1
Nematoda							
Nematoda	3	2	60	3	37	18	4
Nemertea							
Nemertea	1	2	4	2	1	2	0
Sipuncula							
Sipuncula sp.	0	1	0	0	1	0	1
Total	39	59	131	14	98	56	30

Looking at the relative distribution of higher taxon invertebrates groups the annelids (polychaetes) are decreasing with depth and the crustaceans are increasing with depth (Fig. 2). The nematodes are more common at intermediate depths and distances from the Monterey Canyon head, while all others groups are fairly constant and low in abundance (Fig. 2).

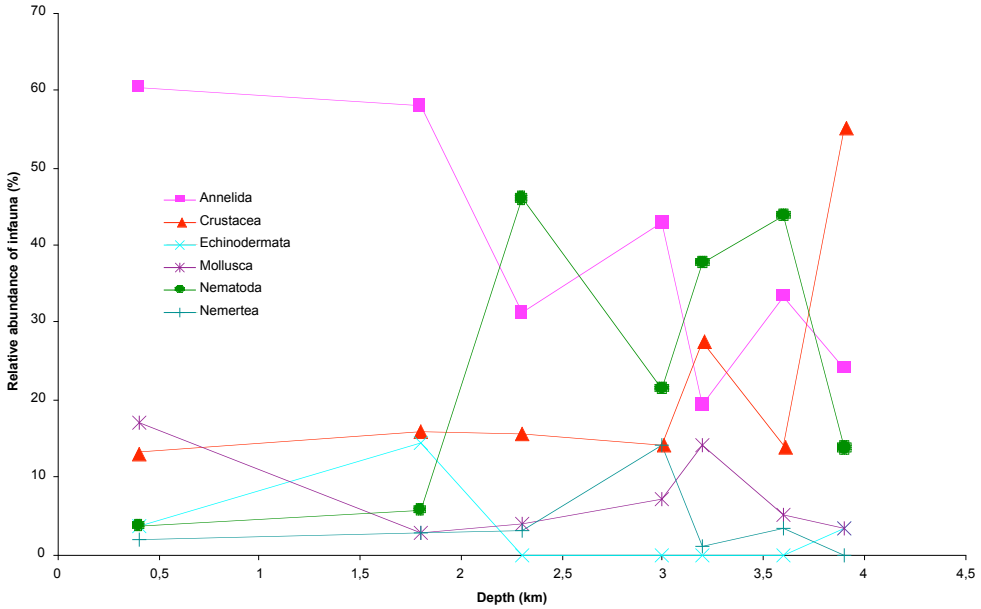

Figure 2 Relative abundance of infauna in percentage for all sites plotted against kilometers of depth from surface.

MEGAFAUNA

The megafauna is most abundant, by far, at 3.2 km depth, where Cnidarians and Echinoderms had strong peaks in abundance. The jellyfish Benthocodon contributed most to the abundance of the cnidarians (Figure 3, Table 2).

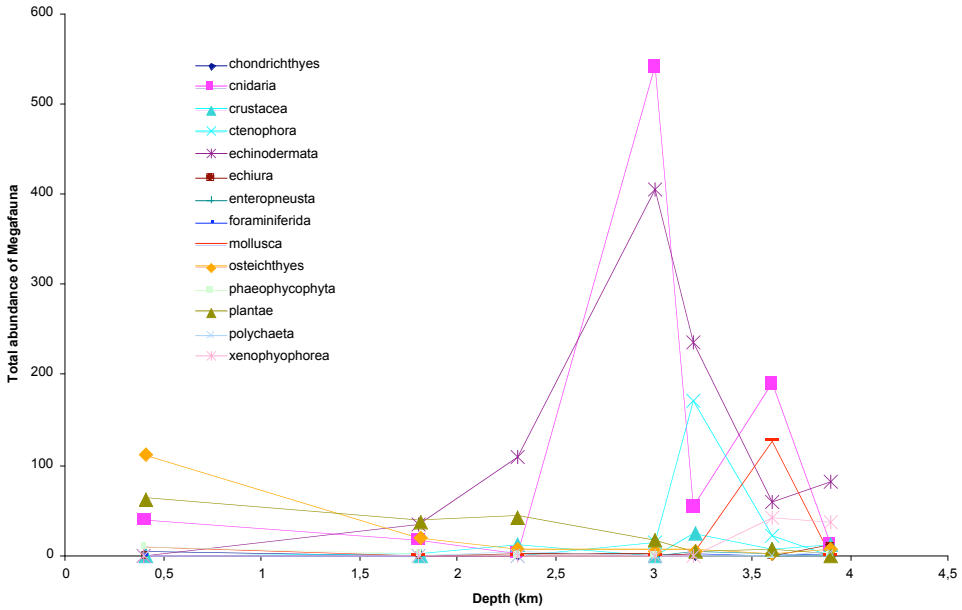

Figure 3 Total abundance of megafauna divided in higher taxon groups for all sites plotted against kilometers of depth from surface.

The relative abundance of megafauna shows that Osteichthyes are decreasing with depth, while Molluscs and Cnidarians are increasing at deeper sites and the Echinoderms are more abundant at intermediate depths (Figure 4). Megafauna divided into 3 separate groups depending on potential speed to colonize an empty patch cleared by disturbance gives a more clear pattern of functional differences of the different megafaunal groups. The mobile species are more abundant at shallow sites where disturbance is high and slow moving taxa are increasing with depth where disturbance are less likely to have a strong impact, whereas the species with medium colonization speed have a peak in abundance at intermediate depths (Figure 5).

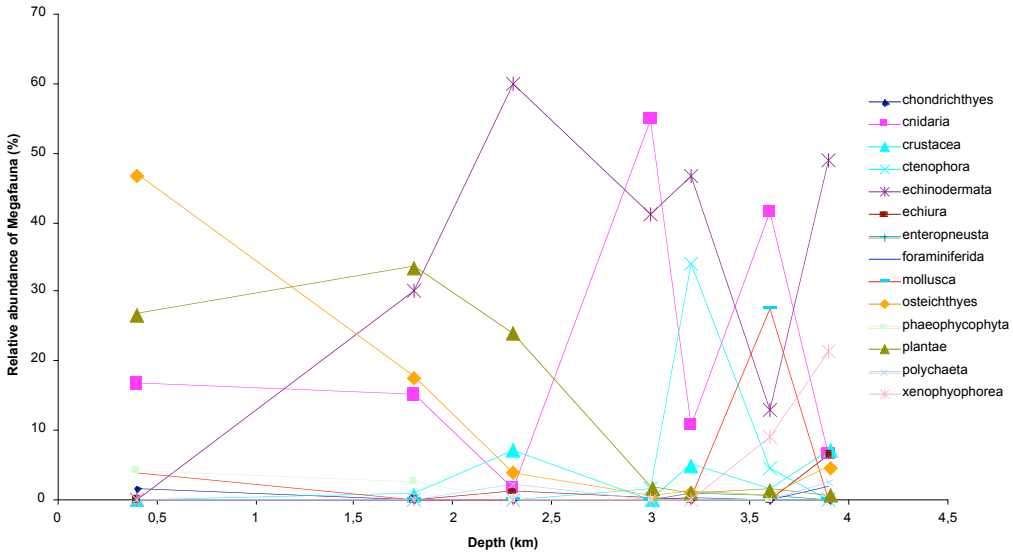

Figure 4 Relative abundance of megafauna divided in higher taxon groups in percentage for all sites plotted against kilometers of depth from surface.

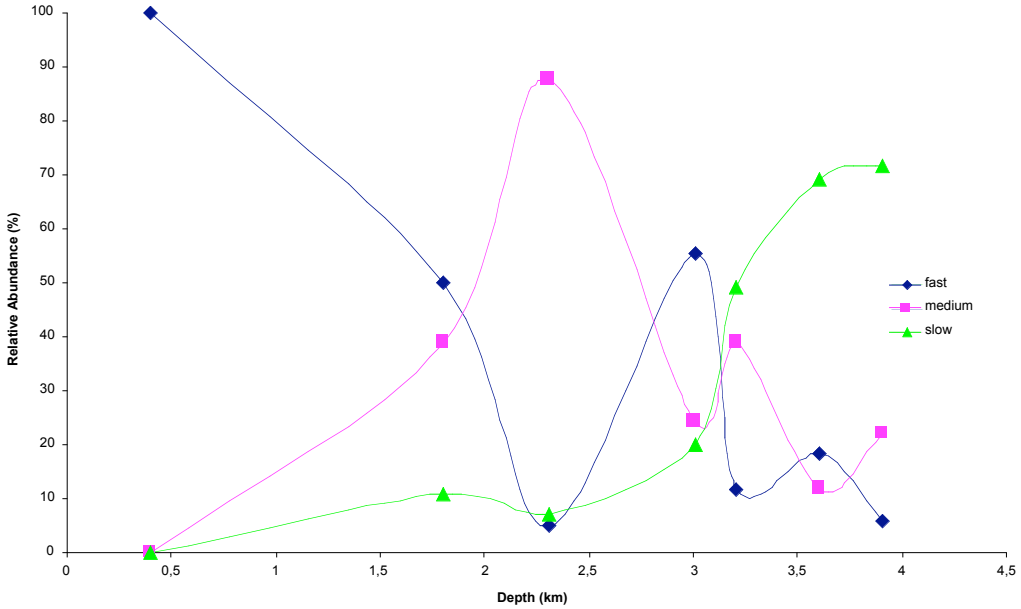

Figure 5 Relative abundance of megafauna divided into 3 separate groups of potential colonization speed (fast (blue), medium (pink) and slow (green)) for all sites plotted against kilometers of depth from surface.

Table 2 Mean abundance of megafaunal species per 10 m of video transect for all sites. Numbers in bold indicates depth and normal numbers indicates distance from Monterey Canyon head.

	9.9 km **0.4 km**	48.8 km **1.8 km**	61.4 km **2.3 km**	104 km **3 km**	127 km **3.2 km**	220 km **3.6 km**	288 km **3.9 km**
Chondrichthyes							
Bathyraja kincaidii	0,02	0,00	0,00	0,00	0,00	0,00	0,00
Raja-rhina	0,04	0,00	0,00	0,00	0,00	0,00	0,00
Rajiformes	0,02	0,00	0,00	0,00	0,00	0,00	0,00
Cnidaria							
Actiniaria	0,00	0,00	0,01	0,67	0,00	1,65	0,00
Benthocodon	0,87	0,10	0,00	51,00	2,36	1,44	0,04
Ceriantharia sp.2	0,00	0,00	0,00	0,17	0,00	0,00	0,00
Cerianthidae	0,00	0,00	0,02	0,00	0,00	0,00	0,00
Dofleinia	0,00	0,00	0,00	0,00	0,00	0,04	0,00
Gorgonacea	0,00	0,00	0,00	0,00	0,00	0,02	0,00
Kophobelemnidae	0,00	0,00	0,00	0,00	0,00	0,04	0,02
Liponema brevicornis	0,00	0,10	0,00	0,00	0,00	0,00	0,00
Pennatulacea	0,00	0,00	0,00	0,00	0,05	0,19	0,17
Poralia rufescens	0,00	0,30	0,00	0,00	0,00	0,00	0,00
Umbellula	0,00	0,00	0,00	0,00	0,05	0,00	0,00
Crustacea							
Amphipoda	0,00	0,00	0,00	0,00	0,00	0,04	0,00
Caridea	0,00	0,00	0,06	0,00	0,00	0,00	0,00
Galatheidae	0,00	0,00	0,00	0,00	0,18	0,07	0,00
Mysidae	0,00	0,00	0,00	0,00	0,00	0,00	0,23
Paralomis	0,00	0,70	0,00	0,00	0,00	0,00	0,00
Paralomis verrilli	0,00	0,00	0,10	0,00	0,00	0,00	0,00
Pycnogonida	0,00	0,00	0,00	0,00	0,00	0,02	0,02
Storthyngura	0,00	0,00	0,00	0,00	0,91	0,00	0,00
Tjalfiella tristoma	0,00	0,00	0,00	1,17	7,64	0,37	0,00
Echinodermata							
Abyssocucumis abyssorum	0,00	0,00	0,00	0,33	0,09	0,18	0,29
Aporocidaris milleri	0,00	0,00	0,00	0,00	0,00	0,00	0,04
Asteroidea	0,00	0,10	0,01	0,00	0,00	0,00	0,00
Benthodytes	0,00	0,00	0,00	0,83	0,09	0,00	0,02
Brisaster	0,00	0,00	0,00	0,00	0,00	0,04	0,00
Brisingidae	0,00	0,60	0,00	0,00	0,00	0,00	0,00
Cystechinus loveni	0,00	0,00	0,00	0,00	0,55	0,00	0,00
Cystocrepis setigera	0,00	0,00	0,00	0,83	2,05	0,09	0,63
Echinocrepis rostrata	0,00	0,00	0,00	0,00	0,00	0,05	0,27
Holothuroidea	0,00	0,00	0,00	0,00	1,73	0,37	0,02
Ophiuroidea	0,00	0,00	0,00	5,17	0,23	0,00	0,13
Paelopadites confundus	0,00	0,00	0,00	11,17	1,00	0,00	0,00
Pannychia moseleyi	0,00	2,60	1,27	0,00	0,00	0,00	0,00
Peniagone leander	0,00	0,00	0,00	0,00	2,05	0,07	0,17
Pteraster	0,00	0,00	0,00	3,33	0,09	0,00	0,00
Scotoplanes globosa	0,00	0,00	0,00	8,67	2,68	0,21	0,00
Echiura							
Echiura	0,00	0,00	0,02	0,00	0,00	0,00	0,23
Enteropneusta							
Enteropneusta	0,00	0,00	0,00	0,00	0,18	0,04	0,00
Foraminiferida							
Bathysiphon	0,00	0,00	0,00	0,00	0,09	0,00	0,06
Mollusca							
Benthoctopus leioderma	0,00	0,00	0,00	0,00	0,05	0,00	0,00
Calyptogena elongata	0,00	0,00	0,00	0,00	0,00	2,18	0,00
Octopus rubescens	0,09	0,00	0,00	0,00	0,00	0,00	0,00
Opisthoteuthis californiana	0,11	0,00	0,00	0,00	0,00	0,00	0,00
Solemya	0,00	0,00	0,00	0,00	0,00	0,05	0,00
Osteichthyes							
Anoplopoma fimbria	0,22	0,00	0,00	0,00	0,00	0,00	0,00
Antimora microlepis	0,00	0,30	0,00	0,00	0,00	0,00	0,00
Coryphaenoides acrolepis	0,00	0,20	0,02	0,00	0,00	0,00	0,00
Coryphaenoides armatus	0,00	0,00	0,00	0,17	0,18	0,04	0,17
Coryphaenoides cinereus	0,00	0,40	0,00	0,00	0,00	0,02	0,00
Coryphaenoides filifer	0,00	0,00	0,00	0,33	0,05	0,00	0,00

Glyptocephalus zachirus	0,09	0,00	0,00	0,00	0,00	0,00	0,00
Liparidae	0,43	0,00	0,00	0,00	0,00	0,00	0,00
Lycenchelys	0,00	0,60	0,05	0,33	0,05	0,00	0,00
Lycodapus	0,00	0,10	0,00	0,00	0,00	0,00	0,00
Lycodes cortezianus	0,33	0,00	0,00	0,00	0,00	0,00	0,00
Lycodes diapterus	0,39	0,00	0,00	0,00	0,00	0,00	0,00
Merluccius productus	0,07	0,00	0,00	0,00	0,00	0,00	0,00
Microstomus pacificus	0,48	0,00	0,00	0,00	0,00	0,00	0,00
Ophidiidae	0,00	0,10	0,00	0,00	0,00	0,00	0,00
Pleuronectiformes	0,24	0,00	0,00	0,00	0,00	0,00	0,00
Serrivomer	0,20	0,00	0,00	0,00	0,00	0,00	0,00
Osteichtyhes	0,00	0,00	0,01	0,00	0,00	0,00	0,00
Polychaeta							
Flota	0,00	0,00	0,00	0,00	0,00	0,00	0,04
Polynoidae	0,00	0,00	0,05	0,00	0,00	0,00	0,00
Sabellidae	0,00	0,00	0,00	0,00	0,00	0,00	0,04
Urochordata							
Octacnemidae	0,00	0,00	0,00	0,00	0,00	0,02	0,00
Xenophyophorea							
Psamminidae	0,00	0,00	0,00	0,00	0,00	0,74	0,73
Total	3,59	6,20	1,63	84,17	22,32	7,93	3,31

The mean richness of the megafauna per 10 m of video transect has a peak at intermediate distance from the Monterey Canyon head, where the disturbance by sediment movement quite possibly also are at intermediate levels compared to the highly disturbed shallow sites near the canyon head and to the calm deep sites (Figure 6).
Total abundance of dead plant and algae debris (Phyllospadix and Laminares) are high near the canyon head and decrease with increasing depth (Figure 7). The mean richness of megafauna has its peak not only at intermediate distance from the canyon head, but also at intermediate abundance of Plantae (Phyllospadix and Laminares)(Figure 7).

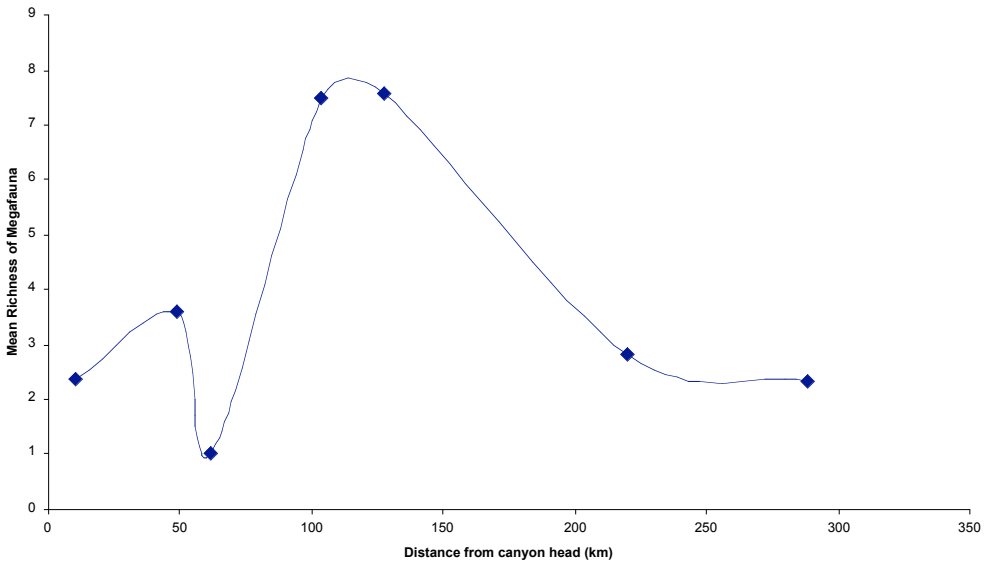

Figure 6 Mean Richness of megafauna per 10 m of video transect for all sites plotted against distance (km) from Monterey Canyon head.

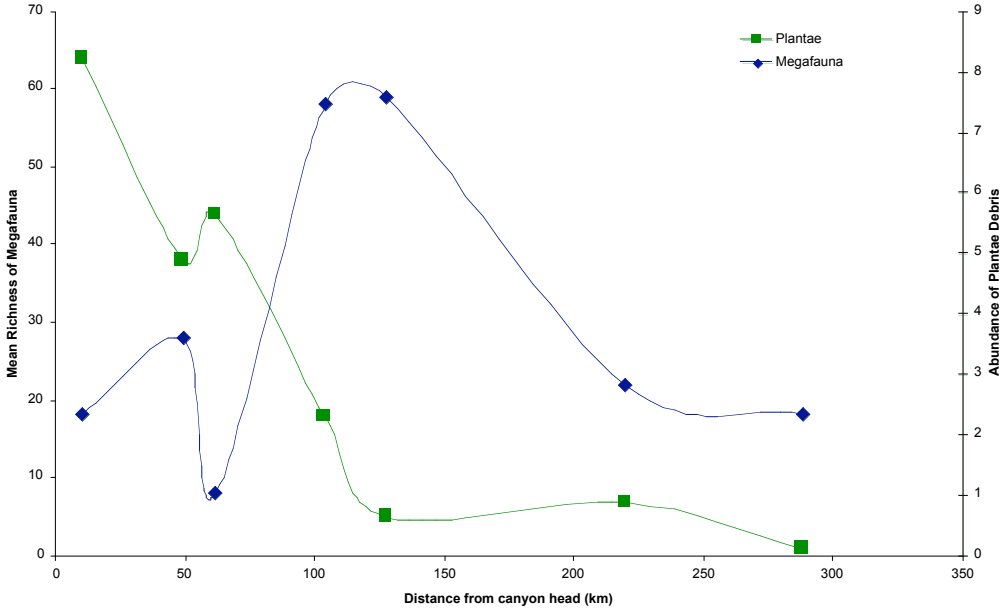

Figure 7 Mean Richness of megafauna per 10 m of video transect (red) and total abundance of dead plant and algae (green) for all sites plotted against distance (km) from Monterey Canyon head.

The total abundance of megafauna peaks at the depth where the infauna has its lowest abundance. Correspondingly the infauna is most abundant at depths where the megafauna is low in abundance (Figure 8)

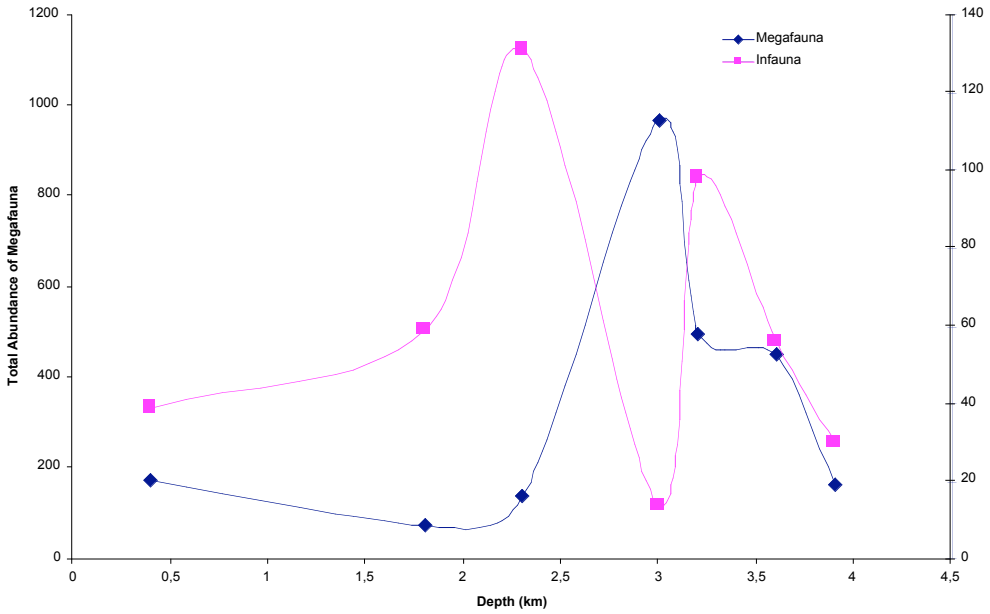

Figure 8 Abundance of infauna (pink) and megafauna (blue) for all sites plotted against depth (km) from surface.

Due to the small sample size for both infauna and megafauna at all sites, rearefaction analysis was performed on species richness in order to estimate the true diversity in the areas. The rarefaction for the infauna and megafauna are shown by depth (Figure 9) as well as distance from the Monterey Canyon head (Figure 10). There is no clear pattern for either the rarefaction richness of infauna or megafauna, although they show similar patterns. The estimated richness of megafauna by rarefaction has its lowest values at 1.8 and 3.0 km depth, 48.8 and 104 km from the Monterey Canyon head respectively, whereas the highest richness is found at shallow and deep sites. The infauna has its highest richness at 2.3 and 3.6 km depth, 61.4 and 220 km from the canyon head respectively, and the lowest richness at the shallowest site as well as 48.8 km depth 104 km from the canyon head.

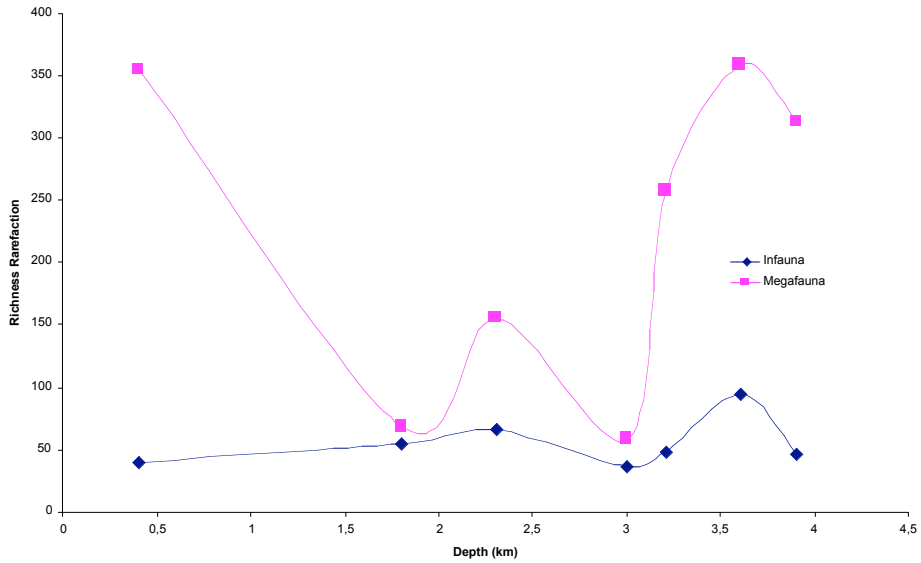

Figure 9 Richness derived from rarefaction analysis for megafauna (pink) and infauna (blue) for all sites plotted against depth (km) from surface.

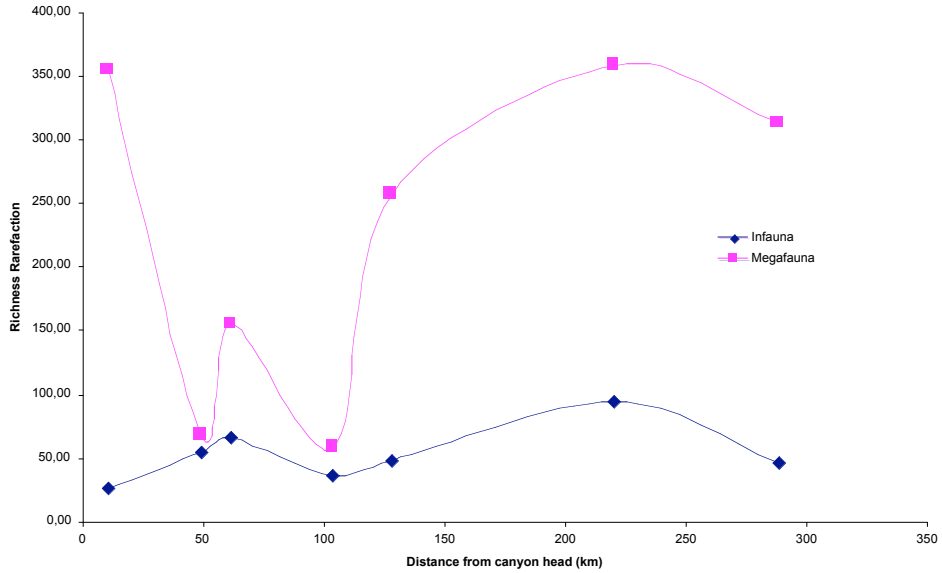

Figure 10 Richness derived from rarefaction analysis for megafauna (pink) and infauna (blue) for all sites plotted against distance (km) from Monterey Canyon head.

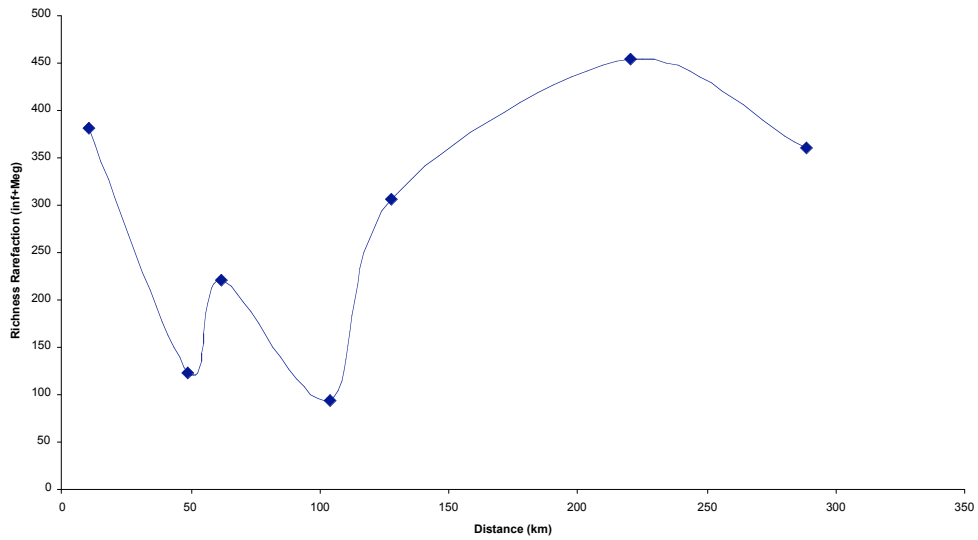

Figure 11 Pooled megafauna and infauna Richness derived from rarefaction analysis for all sites plotted against distance (km) from Monterey Canyon head.

DISCUSSION

Submarine canyons, like the Monterey Canyon, are among the most spectacular features found along continental shelves and they play an important role in the transport of sediment and organic matter from the shore to deep basins. Disturbance from periodically intense currents, debris transport, sediment slumps and turbidity flows are important community structuring mechanisms that are more likely to affect animals in canyons than in typical shelf and slope environments (Vetter and Dayton 1998).

It is however not always clear what actually constitutes a disturbance to benthic communities in submarine canyons. Many authors consider sediment movement to act as a disturbance (e.g. Cowie et al. 2000, Vetter and Dayton 1998) and some add patchy input of organic enrichment (Smith 1986) and yet others also consider predation as disturbance (Talbot et al. (1978). All these factors may possibly affect deep-sea benthic communities in different ways regardless of whether the factors are called disturbance or not. It is not always possible to distinguish between physical disturbance and organic enrichment, since currents transporting sediment may also bring debris with high organic content to a disturbed patch (Vetter and Dayton 1998). Grassle and Grassle (1976) did however distinguish between disturbance that adds labile organics to communities and disturbance that reduce competition without enhancing food availability. Gage (1996) argues that this distinction between disturbances is purely academic because a disturbance that smothers releases resources to the patch through organic enrichment from the animals killed by the disturbance. It is also possible to consider the debate of this from another point of view since most definitions of disturbance includes altering the availability of resources (e.g. Mackey and Currie 2000, Petraitis et al. 1989, Pickett and White 1985), and a mechanism not altering any resources would therefore not be a disturbance at all. In this study there is no data in order to tell whether organic enrichment has been associated with the sediment movement or not, sediment movement will therefore simply be referred to as physical disturbance without any distinctions.

The IDH predicts diversity to have an intermediate disturbance response, but diversity can also have a unimodal pattern with productivity (Abrams 1995). If effects of disturbance

cannot be separated from effects of productivity (e.g. food availability) the peak in diversity may instead be attributed to an intermediate organic content (productivity) in the benthic community. Huston (1979) predicted the effects of disturbance on diversity to be dependent on productivity. It would require a stronger disturbance to compensate for the increased competitive exclusion when the productivity is high, because the higher productivity will lead to increased growth-rates (Kondoh 2001). This pattern has been found in experiments from both terrestrial (Turkington et al. 1993) and benthic environments (Widdicombe and Austen 2001). Separating effects of disturbance and organic enrichment is usually not easy in studies of benthic communities in submarine canyons (Vetter and Dayton 1998), and Thistle (1981) was not certain whether the colonising fauna in marine soft bottom were responding to the absence of competitors or to the release of resources by the disturbance. However, Vetter and Dayton (1998) reports that the canyon enrichment effect decreases with depth because most detritus enters the canyon at its head and is consumed during transport downslope, whereas the canyon disturbance effect probably does not diminish as dramatically as the enrichment effect. Hence, the relative importance of enrichment should decrease with depth in canyons, compared with disturbance effects and the impact of disturbance increases relative to enrichment with depth. According to the dynamic equilibrium model (Huston 1979) diversity will peak at intermediate levels of disturbance when the productivity of the community also is at intermediate levels. This theory is coherent with the results of the mean megafaunal richness in this study where the peak of diversity occurred when both disturbance and abundance of organic debris were at intermediate levels.

The pattern of megafaunal mean diversity in this study can also be attributed to a variety of different mechanisms and processes. The mean diversity is showing an unimodal disturbance response when plotted against distance from canyon head, where the disturbance is difference in sediment movement along the canyon axis. However, distance from the canyon head is inevitably associated with depth and all the different factors depth may exert on ecological communities, such as difference responses of particular species or whole communities to pressure, light, temperature and particularly oxygen (Gage 2004).

Regions where oxygen is depleted typically occur between 100 and 1200 m depth and are usually formed beneath high productive, upwelled waters by degradation of organic matter and certain deep basins (e.g., off southern California) and fjords also contain permanently hypoxic or anoxic waters. The resulting hypoxic zones are referred to as oxygen minimum zones (OMZs) and they are defined as areas where $0_2 < 0.5$ ml/l, persist over geologic time (Levin et al. 2001). In an extensive review by Levin et al. (2001) it is stated that reduced oxygen availability can exert both direct and indirect negative effects on diversity. Species richness may be reduced directly through differential tolerance to hypoxia and also by the sulfides that build up in organic-rich hypoxic sediments. Hypoxic conditions may further impose habitat homogeneity that would contribute to spatially uniform assemblages of low species richness (Levin et al. 2001).

There are different responses to hypoxia both between and within meio-, macro- and megafauna. Sediments in areas with oxygen-depleted overlying bottom water often exhibit substantially reduced macrofauna diversity. The macrofauna within OMZs is often characterized by low species richness and very high dominance (Sanders 1969). Among the macrofauna, many molluscs, crustaceans, echinoderms, and cnidarians appear less tolerant of hypoxia than other taxa. No single taxon dominates the macrofauna of low oxygen settings, although annelid species are often more prevalent. Less information is available concerning the diversity responses to reduced oxygen concentrations of bacteria, small protists

(nanofauna), meiofauna or megafauna. A variety of larger metazoans (polychaetes, crustaceans, molluscs, echinoderms) all display abundance peaks close to OMZ bounderies. Where a range of faunal size groups have been compared, larger taxa (megafauna and macrofauna) exhibit density reductions within the most hypoxic portions of OMZs (Levin et al. 2001). In this study high abundance of megafauna was associated with low abundance of infauna and when infauna showed higher abundance the megafauna was not as abundant. The megafauna may control the infauna by predation, while affected by low oxygen in regions where the abundance of megafauna is low. In the absence of their predators the infauna may increase in abundance. The nematodes were among the most abundant groups responsible for the peaks in infaunal abundance and nematodes have been shown to be less affected by hypoxia than other macrofauna (Levin et al. 2001). Thus, both the higher tolerance of nematodes to low oxygen and the increase of infauna in the absence of megafauna may together explain the interesting pattern of opposed peaks in abundance of infauna and megafauna.

There was no clear pattern of the rarefaction analysis of the species/taxon richness of either infauna or megafauna, although the patterns of infauna and megafauna showed some similarities. Nor were there any changes in this pattern when infauna and megafauna rarefaction richness was pooled. The lack of an interpretable pattern might be due to the small sample size in this study as well as the difference in sample size of the megafauna from video transects of different length. It also shows the importance of scale, since the mean richness of megafauna does show an intermediate disturbance response, allowing for deep-sea communities at the 10 m scale to show a completely different pattern than when the true diversity of the areas are estimated by rarefaction analysis. It is however not uncommon to have different results for species richness and richness by rarefaction analysis, Wlodarska-Kowalczuk (2004) found that species richness declined with depth, whereas the rarefaction showed no clear pattern for deep-sea benthic communities in the North-Atlantic.

One of the complications of this study is the different levels of trophic structures as well as the difference in scales between macro- and megafaunal communities. Also this study included species that vary in mobility. Usually studies on effects of disturbance on diversity involve only one trophic level (Wotton 1998) and mobile species may not be affected by disturbance in a similar manner as sessile species, which is why the intermediate disturbance response by diversity is not often observed in communities with mobile species (Fuentes and Jaksic 1988). The peak in mean richness of megafauna occurred at depths where the most mobile species (such as fish and rays) were in low abundance compared to slower moving species that was more likely to be affected by disturbance, in the form of sediment movement, without being capable of moving fast enough to avoid it.

CONCLUSIONS/RECOMMENDATIONS

Although mean megafaunal richness peaked at intermediate distance from the canyon head, this was not necessarily caused by disturbance alone, if at all. Abundance of dead plant material (Phyllospadix and Laminares) was high on shallow sites and decreases with depth, which means that diversity would also be affected by the increase in available resources. Sediment movement may differ along the canyon axis, with highest levels near the canyon head, but distance from the canyon head will also mean increase in depth, which in turn adds a variety of factors possibly affecting benthic communities. Thus, effects of disturbance cannot be separated from factors associated with depth. Future experiments on disturbance should therefore be conducted in a manner which allows disturbance, as sediment movement, to be separated from depth related factors. Disturbance could be artificially applied at the

same depths and non-canyon control sites at the same depth as experimental sites in the canyon could help distinguish between effects of depth and disturbance on diversity.

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