Research Article

Benthic macro-faunal abundance and diversity and sediment distribution in Akhziv submarine canyon and the adjacent slope (eastern Levant Basin, Mediterranean Sea)

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Abstract

The Israeli coastline is generally characterized by a broad and shallow continental shelf. Akhziv submarine canyon (ASC), in its northern reach, creates a locally unique marine ecosystem. The present study is the first to investigate the benthic macro-fauna of ASC, in order to assess its importance as a potential productivity 'hotspot' within its ultra-oligotrophic surroundings. Seven research cruises were conducted during 2010-2013, along ASC's two channels and at iso-bathic control sites on the adjacent slope (AS), encompassing 8 sampling stations, at depths of 40-450 m. Bottom samples were collected by a Van Veen Grab, gravity corer and a GOMEX box corer. The infauna ($\geq$500 µm) were counted and identified to the lowest possible taxonomic level. Sediments were analysed for grain size & composition and total organic carbon concentration. Mean benthic macro-faunal abundance (individuals/500ml ± SD) was higher inside the canyon (13.0±19.4) compared to the AS (2.9±3.3) (p=0.004), as was estimated true taxon richness (Chao1): 42.2 versus 10, respectively. Sediments' mode grain size was found to be significantly higher in ASC's eastern channel compared to AS (p=0.028), along with sand enrichment of up to 36%. The higher macrofaunal abundance and taxon richness may relate to a more heterogeneous sea bed provided by the higher diversity in grain size existing inside ASC. A relatively rich benthic realm, such as that observed in the ASC, may serve as a refuge for certain species and by hosting a relatively diverse assemblage, stands a better chance of adapting to changing conditions such as climate change.

Keywords: Submarine canyon; Israeli Mediterranean slope; granulometry; total organic carbon; nepheloid layer.

Introduction

Submarine canyons play an important role in the functioning of deep sea ecosystems (Danovaro *et al.*, 2010; Würtz, 2012; De Leo *et al.*, 2014). This may be achieved through: (1) the channeling of currents between shallow continental shelf and deep habitats, with potential exchange between ecological communities (Klinck, 1996; Hickey, 1997; Sobarzo *et al.*, 2001; Allen & Durrieu de Madron, 2009) (2) transport of organic matter (Vetter & Dayton, 1998; Genin, 2004; Canals *et al.*, 2006; Company *et al.*, 2008; Amaro *et al.*, 2015) and/or sediments (de Stigter *et al.*, 2007; Oliveira *et al.*, 2007; Tesi *et al.*, 2008; Canals *et al.*, 2009) from coastal zones to the deep ocean, (3) their bathymetric features that funnel and concentrate diel vertical migrators (Greene *et al.*, 1988; Genin, 2004) and (4) their providing enhanced seafloor habitat heterogeneity (Brodeur, 2001; Azzellino *et al.*, 2008; Vetter *et al.*, 2010).

The northern Levant continental margins of the Israeli Mediterranean are a warm, hyper-saline (minimum temperature and salinity: 13.60 °C and 38.75 PSU; Kress *et al.*, 2014) and extremely oligotrophic marine environment due to limited vertical mixing and very low river runoff. This situation intensified after the damming of the Nile River (Herut *et al.*, 2000). The continental shelf narrows from a width of 3 km north of Haifa Bay, to a negligible shelf off the coast of southern Lebanon. This is accompanied by a steepening of the continental slope (Ben-Avraham, 1978; Ben-Avraham *et al.*, 2006; Carton

et al., 2009) and the existence of a series of submarine slope canyons. This unique geomorphological province differs conspicuously from the southern province (south of Haifa Bay), which is characterized by a generally smooth relief and gentle gradients, with numerous slump scars along the margin (Mart, 1989; Katz *et al.*, 2015). Transport and depositional processes are far more intense over the steep northern continental slope of Israel, and especially along its canyons, than over the gentle southern slope (Almagor & Schilman, 1995; Schattner *et al.*, 2015; Schattner & Lazar, 2016).

The steep continental slope of the northern Levant is incised by ten major mature canyons (Almagor, 1993), defined by Harris & Whiteway (2011) as 'type 2' canyons in active margins. Those are "shelf incising canyons with no clear bathymetric connection to a major river system, in margins that are often influenced by tectonism and basement structure'. The Akhziv submarine canyon (ASC) is the southernmost of these canyons. It was formed as a result of erosional processes caused by sediment transport along fixed paths over the slope (Almagor, 1993). From a depth of 1200 m, two canyon heads cut backwards into the continental shelf, delineating a triangular stretch of the continental margin opposite the Sulam-Sour sea cliff (Fig. 1) (Almagor, 1993). The northern one trends roughly E-W and meanders to a depth of about 50 m, some 3 km offshore. The other trends obliquely south-southeast, cutting backwards to about 8 km offshore.

A ROV (Remotely operated vehicle) study (Spanier *et al.*, 1991) of the epibenthic megafauna at the shallow end of Akhziv canyon (100-150m) showed substrate, rich in trace fossils and extensively bioturbated by megafaunal epibenthic species, mainly decapods and fish. A comprehensive biotic characterization of ASC is so far unavailable.
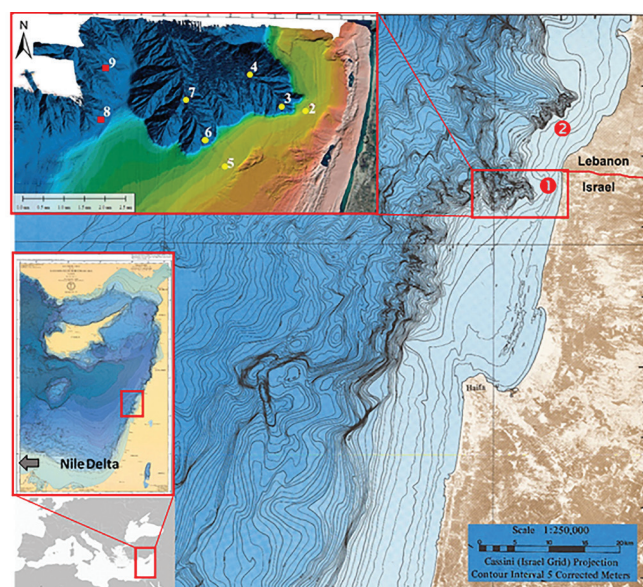

Fig. 1: Map of study area on the northern Israeli coastline, eastern Mediterranean (Almagor & Hall, 1984; Sade *et al.,* 2006). Sampling stations marked by numbers. Stationdepths are specified in Table 2.
🟡 ASC sampling stations
🟥 AS sampling stations

Pending the latter and hastened by recent steps to include the canyon in a new extended National Marine Protected Area, the present study was launched in order to provide preliminary, semi-quantitative data on the infaunal biota of the canyon and its surroundings. As such, and due to operational and budgetary constraints which limited the sampling cruises to a single day per season, multiple samplings at given stations were sacrificed in favor of visiting all sampling sites per cruise.

Accordingly, the study was devised in the form of a strict comparison between the sedimentology and the macro-benthic community of ASC and that of the adjacent slope (AS) to the west.

If the ASC were shown to enhance or funnel sediment transport and particulate organic matter through its channels, resulting in a richer and more diverse fauna, it would be of regional importance as a possible biological recruitment source and as a potential biological refuge in the case of habitat deterioration.

Materials and Methods

Sampling strategy

Seven single day sampling cruises (Table 1) were carried out over a period of two and a half years (November 2010 - May 2013) to ASC and the slope to its southwest, on board EcoOcean's R/V *Mediterranean Explorer*. Two cruises were performed per season, except during winter which was sampled only once (2012) due to technical reasons.

Eight sampling stations were assigned in the study area, as specified in Table 2 and depicted in Figure 1. These included two stations along each of the two channels of ASC at bottom depths of 150-160m (shallow) and 420-450m (deep) and two stations at similar depths on the adjacent slope (AS).

At each sampling station, sediments were taken from the top 10cm of the seafloor for invertebrate content, total organic carbon (TOC) assay and granulometry. Sediment sampling was carried out with a Van Veen Grab (15L, dimentions:136 x 36 x 35cm) (fall 2010, summer 2011), gravity corer (4-inch diameter; sleeve length 50cm) (fall 2011, winter and spring 2012, spring 2013) and a GO-MEX box corer (25 x 25 x 50cm) (summer 2012). The reason for the use of different sampling gear was the availability of the equipment that happened to be on board, as dictated by other uses of the ship. During each cruise, all samples were obtained using the same gear. In order to sample all stations, each site was sampled once only. A second attempt was rarely made upon failure to retrieve

Table 1. Cruise dates sorted by season of the year.

Fall	30/11/2010	23/10/2011
Winter	05/02/2011	
Spring	29/04/2012	06/05/2013
Summer	20/07/2011	13/08/2012

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Table 2. Sampling stations (2 to 9) in the study area, indicating seafloor depth, coordinates and a description of the location.

Station number	Depth (m)	Location		
		LAT	LONG	
2	46	33⁰ 03›53N	035⁰04›32E	Canyon, east, entrance
3	160	33⁰ 03›70N	035⁰03›67E	Canyon, east channel, shallow
4	420	33⁰ 04›44N	035⁰02›74E	Canyon, east channel, deep
5	47	33⁰ 02›19N	035⁰01›99E	Canyon west, entrance
6	160	33⁰ 02›86N	035⁰01›41E	Canyon, west channel, shallow
7	450	33⁰ 03›79N	035⁰00›89E	Canyon, west channel, deep
8	150	33⁰ 03›21N	034⁰58›19E	Slope, shallow
9	450	33⁰ 03›85N	034⁰57›63E	Slope, deep

a sample (sediments running out of the grab, non-penetration of the corer) and if also unsuccessful, the vessel moved on. Due to vessel drift, the actual sampling depth (sounded at the time of impact) was often different from the value specified in Table 2. Actual sampling depths are provided in the relevant tables below. Regardless of the mode of sampling, only sediments recovered with an undisturbed appearance were considered acceptable and subsamples were removed from these.

A 500ml subsample was taken from the upper 10 cm of the retrieved sediments for infaunal invertebrate analysis. Two additional 50ml sediment samples were taken from the upper 10cm and frozen (-18 °C) for total organic carbon (TOC) content and grain size analysis.

Two additional very shallow (45-46m) stations set at the entrances to the canyon's channels (St. 5 in the west and St. 2, in the east) were included in the sampling scheme, in an attempt to shed some light on the dynamics of the sedimentological processes in ASC. Sediments from these entrance stations were sampled 5 times by SCUBA diving (Nitrox-SAFEAIR), co-temporally with the research cruises (whenever possible); 0.25L of the upper 10 cm of sediments were collected manually with a scoop and sampled for granulometry and TOC only. The results, ambiguous in respect to the above-mentioned intention, will not be reported on in the manuscript, but are presented in supplementary data (Fig S1; Table S4) in order to complete the overall picture.

At stations deeper than 100m (Fig. 5, Table 2), water column CTD profiles were obtained. In winter, spring and summer of 2012, turbidity was derived from CTD data as the light scattered by suspended particles, and expressed in Formazin Turbidity units (FTU).

Sample processing

For infaunal invertebrate analysis, samples were labelled and fixed in 4% formaldehyde (in sea water) on board for at least 24h and subsequently, washed in the laboratory with tap water over a 500µm sieve to remove the formaldehyde and mud. The sample retained on the sieve was re-suspended in 70% ethanol and stained with 2gr/l Rose Bengal solution for 24 hours in order to facilitate detection and isolation of small organisms within the sediment. These were then examined under a Nikon SMZ800 Stereomicroscope (zoom range 1x-6.3x) and every individual was identified to the lowest taxonomic level possible, and counted.

For granulometry, sediment samples were heat-dried, gently crumbled and mixed. 1-3g of sediments were suspended in 20 ml of distilled water and stirred for 30 minutes. In order to remove organic matter, samples were then oxidized by gradual addition (slow dripping) of 20mL aliquots of 30% H_2O_2 until bubbling ceased (generally 5 days). 10% HCl was added to half of the sample for 2-3 hours, in order to dissolve calcium carbonate. Samples were rinsed with distilled water. Single measurements of 0-2000µm grains were performed separately for samples containing carbonate and for those without, using a Beckman Coulter particle analyzer (LS 13320).

For TOC content determinations, aliquots from the samples (1-2mg) were placed in silver capsules (5mm x 8mm) and exposed to HCl vapor for 16 hours at room temperature in order to remove carbonates. Samples were then heated in an oven for 1 hour at 60°C to remove residual HCl and then combusted at 1700°C in an Elemental Analyzer (1112 Flash EA, Thermo-Finnigan) to determine organic carbon content.

Data analysis

Generalized linear modelling (gamma probability distribution, log link function) was applied, with depth (covariate) and site and season (factors) as independent explanatory variables. For benthic invertebrate analysis, samples from the two ASC channels were pooled and compared to AS and the dependent variables were abundance (# organisms/500 ml), taxon richness (number of different taxa in sample), taxon diversity and phylum diversity. The latter two were expressed by the Shannon Diversity Index *(H')*, calculated with PAST 2.17c (Hammer *et al.*, 2001). For both taxon richness and diversity, samples with <2 organisms were excluded. Results are reported as "significant" if the probability *p* of the null hypothesis was less than 0.05 and "highly significant" if *p*< 0.01. For sedimentology, the compared sites were ASC's east channel, west channel and AS and dependent variables were TOC, mode grain size, % sand content and % biogenic sand content.

Following normality tests (Shapiro-Wilk), correlation tests (parametric or non-parametric, as appropriate) were also performed to look for potential relationships between continuous variables. All tests were carried out using IBM SPSS Statistics version 19.

The asymptotic approach, through the non-parametric Chao1 estimator (Chao, 1984, Colwell & Coddington, 1994, Chao & Chiu, 2016), was used to infer the lower bound of the true species richness from the observed taxon richness in samples from ASC and AS communities (Estimate-S version 9.1.0; Colwell, 2013).

Results

Benthic macro-fauna (BMF)

Total macro-faunal abundances in sediments ranged from 0 to 96 individuals/500ml (mean=13.0; SD=19.4) inside the canyon and from 0 to 10 individuals/500ml (mean=2.9; SD=3.3) on the slope (Table S1). Polychaetes dominated the macrofauna in terms of abundance in both canyon and slope samples (55% and 54%, respectively), being more abundant at the shallower stations. Site and season affected BMF abundance and taxon richness (Table S2). The effect of site was expressed by ASC samples having overall higher BMF abundance and taxon richness than AS samples and the effect of season, by summer samples showing higher values than both spring and fall. No interaction was found between the explanatory variables. The same effect of season, with summer significantly higher than all other seasons, pertained for phylum biodiversity, while no explanatory factor had a significant effect on taxon diversity (Table S2). All dependent biogenic indices except phylum diversity (not shown in Table S3 in supplementary data) were highly inter-correlated (Spearman's-rho: p<0.001; r values ranging between 0.736-0.945). As also evident in Table S3, correlations of biogenic with non-biogenic variables were confined to % sand content (total abundance) and to the biogenic fraction of sand (total abundance and taxon richness). There was no correlation between BMF attributes and depth, mode grain size or TOC.

Chao1 individual comparisons between sites (all samples at the two sites were pooled) estimated the true taxon richness in AS as 10 taxa (95% confidence interval: 9.1-18.7) and in ASC as 42.2 taxa (95% confidence interval:
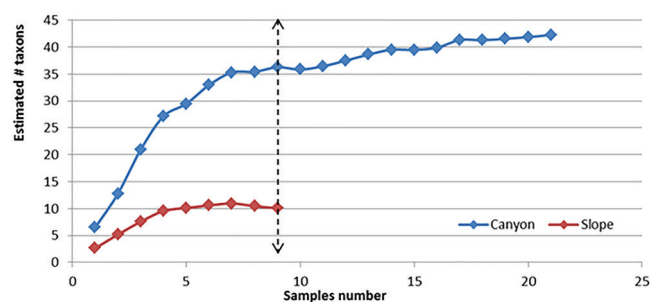
34.7-70.4) (Fig. 2). The lack of overlap in the confidence limits suggests a significant difference in taxon richness among ASC and AS (Chao & Chiu, 2016).

Thirty-three different benthic taxa, belonging to 8 phyla (Annelida, Arthropoda, Mollusca, Platyhelminthes, Nemertea, Sipuncula, Cnidaria and Foraminifera) were identified inside ASC and on the AS (Table 3). Noteworthy in respect to differences in composition were mollusks (Aplacophora and bivalves) (Fig. 3), which comprised 32% of the sampled canyon's infauna and were absent in samples from the slope.

Of the fourteen polychaete families identified in the canyon, Cirratulidae, Cossuridae, Spionidae and Maldanidae were more abundant, Representatives of the families Capitellidae, Chaetopteridae, Glyceridae, Lambrenidae, Nereidae, Nephtyidae, Onuphidae, Paraonidae, Serpulidae and Sigalionidae were found in lower abundances. The only two polychaete families identified on the slope were Chaetopteridae and Spionidae (Table 3). Most (75%) of the total polychaete assemblage could not be identified to family level due to its poor condition. The paucity of sampled organisms (several taxa were represented by single specimens) precluded a quantitative comparison of community composition between the two sites.

Total Organic Carbon (TOC)

TOC content varied between 0.69 - 1.18% inside the canyon and 0.64 - 1.07% on the slope (Table S4). Generalized Linear Modelling did reveal a highly significant effect of site on TOC content (Table S2), but this was due to samples from the western channel having a higher TOC content than from the eastern channel, with no differences between either channel and AS.

Sediment grain size and composition

Sediments inside the canyon and on the slope were predominantly muddy (79-99.8% of sediment volume), and silt (2-63μm) accounted for more than 60% of the sediment in most stations (Table S4).
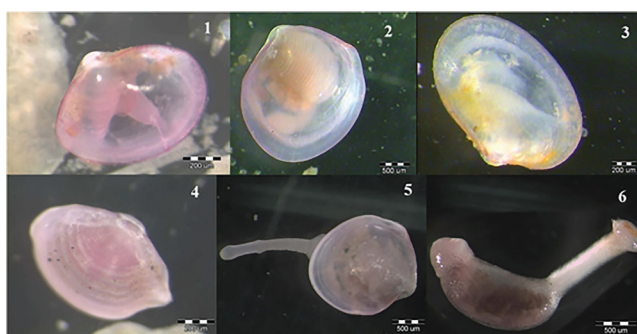
A bimodal distribution of grain size, with one peak in

Fig. 2: Taxa cumulative curve, all samples pooled (Chao-1, EstimateS).

Fig 3: Mollusc species found only inside ASC: (1) *Thyasira oblonga* (2) *Thysira alleni* (3) *Kurtiella bidentata* (4) *Saccella commutata*, (5) *Thyasira* sp. and (6) *Falcidens* sp.

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Table 3. List of taxa and preponderance. Taxon identity level ranges from phylum to species. Dispersion represents the number of different stations the taxon was found in; Repetition stands for the number of different cruises in which the taxon was found.

Phylum	Taxon	Canyon			Slope		
		Total number of individuals	Dispersion	Repetition	Total number of individuals	Dispersion	Repetition
Annelida	Unidentified Polychaeta	111	4	7	10	2	4
	Capitellidae	1	1	1	-	-	-
	Chaetopteridae	1	1	1	1	1	1
	Cirratulidae	8	3	5	-	-	-
	Cossuridae	6	3	3	-	-	-
	Glyceridae	2	2	2	-	-	-
	Lambrenidae	1	1	1	-	-	-
	Maldanidae	4	2	3	-	-	-
	Nereidae	2	2	1	-	-	-
	Nephtyidae	1	1	1	-	-	-
	Onuphidae	1	1	1	-	-	-
	Paraonidae	3	2	2	-	-	-
	Serpulidae	1	1	1	-	-	-
	Sigalionidae	1	1	1	-	-	-
	Spionidae	6	4	5	2	2	2
Arthropoda	Amphipoda	6	3	4	-	-	-
	Unidentified Decapoda	2	1	1	2	1	1
	Paguridae	2	1	1	-	-	-
	Isopoda	1	1	1	1	1	1
	Tanaidacea	2	2	1	-	-	-
Mollusca	*Falcidens* sp.	2	2	2	-	-	-
	Kurtiella bidentate (Montagu, 1803)	1	1	1	-	-	-
	Austronucula perminima (Monterosato, 1875)	1	1	1	-	-	-
	Thyasira sp.	5	3	4	-	-	-
	Thyasira oblonga (Monterosato, 1878)	64	2	1	-	-	-
	Thyasira alleni (Carrozza, 1981)	9	2	2	-	-	-
	Saccella commutata	4	1	1	-	-	-
Cnidaria	Unidentified Hydrozoa	7	3	3	1	1	1
	Hydractiniidae	1	1	1	-	-	-
Foraminifera	*Lenticulina* sp.	1	1	1	2	1	2
Nemertea		9	3	3	3	1	1
Platyhelminthes		1	1	1	-	-	-
Sipuncula		3	2	2	2	1	2

the fine silt size range and the other in the course silt-fine sand range, was evident in most samples from stations deeper than 100m, in both ASC and AS (Fig. 4). Grain sizes in these samples typically did not exceed 150µm. Exceptions to this were found in the east channel of ASC, where some particles reached 350µm in the summer season (summer 2011 at St.3 and summer 2012 at St.4). The sample from St.4 during summer 2012 was exceptional in having roughly 36% sand. In the majority of samples (including all samples on the AS) mode grain size was in the range of fine silt and in others (including all deep east channel samples), it reflected the larger size category
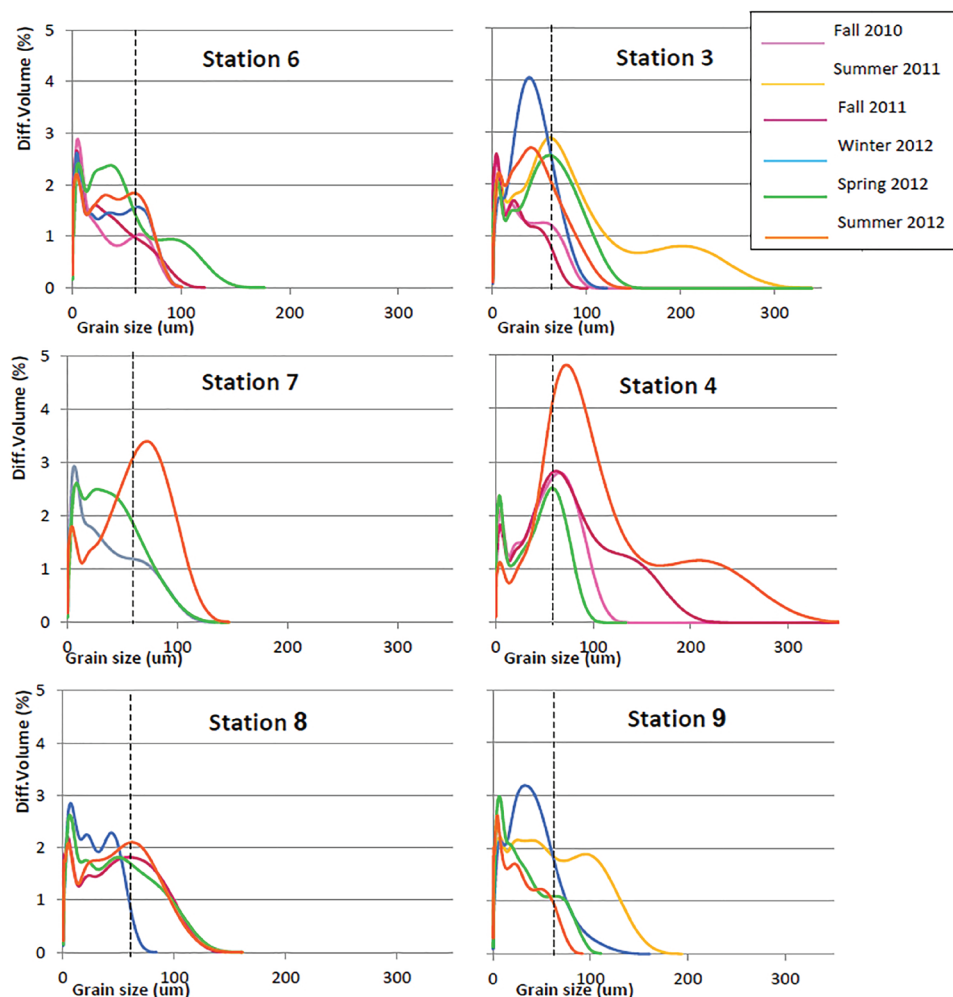
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Fig. 4: Grain size relative volumes in ASC (St. 3, 4, 6, 7) and at AS (St. 8, 9) by seasons. West channel on the left, East channel on the right. Broken lines represent the boundaries between grain type categories (clay and silt < 63μm, sand = > 63μm). Representations of %volume along the X axis are not equally spaced (the counter issues a value after counting a given number of particles) such that the area under the curve gets exaggerated at larger (and less frequent) grain sizes and the contribution of sand is over-portrayed. Therefore, one cannot visually compare areas under different curves in a panel, even though they all sum up to 100%.

(course silt-fine sand) (Table S4, Fig S1).

The Generalized Linear Modelling results and the correlation results are listed in Tables S2 and S3 in the supplementary data, respectively. Both site and depth had highly significant effects on mode grain size (Table S2), with interaction. Pairwise comparisons for the effect of site showed mode grain sizes in the two canyon channels to be similar, the eastern channel having a significantly (p=0.028) and the western channel a near significantly (p=0.053) larger mode grain size than the slope (Median test). The interaction between depth and site was evidenced by the positive correlation of mode grain size with depth (Spearman's-rho r=0.596; p=0.02) being mostly on account of all deep eastern channel samples showing mode sizes an order of magnitude higher than most samples elsewhere (Table S4). Mode grain size and sand content were positively correlated (Spearman's-rho r=0.468; p=0.018), yet, only depth had an effect on sand content, the two also being positively correlated (Spearman's-rho r=0.478; p=0.016) (Table S3).

Biogenic sand content, as derived from differences before and after acidification, ranged from 0.03-10.16%. None of the tested explanatory variables in the Generalized Linear Modelling had a significant effect on this measure.

Water column turbidity

CTD profiles in ASC's stations 4, 7 & 9 revealed higher turbidity (up to 0.45 FTU) in the upper section of the water column (240m in winter, 100m in spring and 80m in summer), decreasing with depth and then increasing again to varying degrees, towards the bottom (Fig. 5). A clear nepheloid layer above the bottom was evident on 5 occasions, mostly (4 out of 5) in ASC's eastern channel: Three times during spring 2012 (0.54FTU at a depth of 160m in St. 3, 0.32FTU at a depth of 350m in St. 4, 0.26FTU at a depth of 370m in St. 7) and twice in summer 2012 (1.07FTU at 120m depth in St.3 and 0.36 FTU at 400m depth in St.4). No similar elevations in turbidity were observed in AS stations.
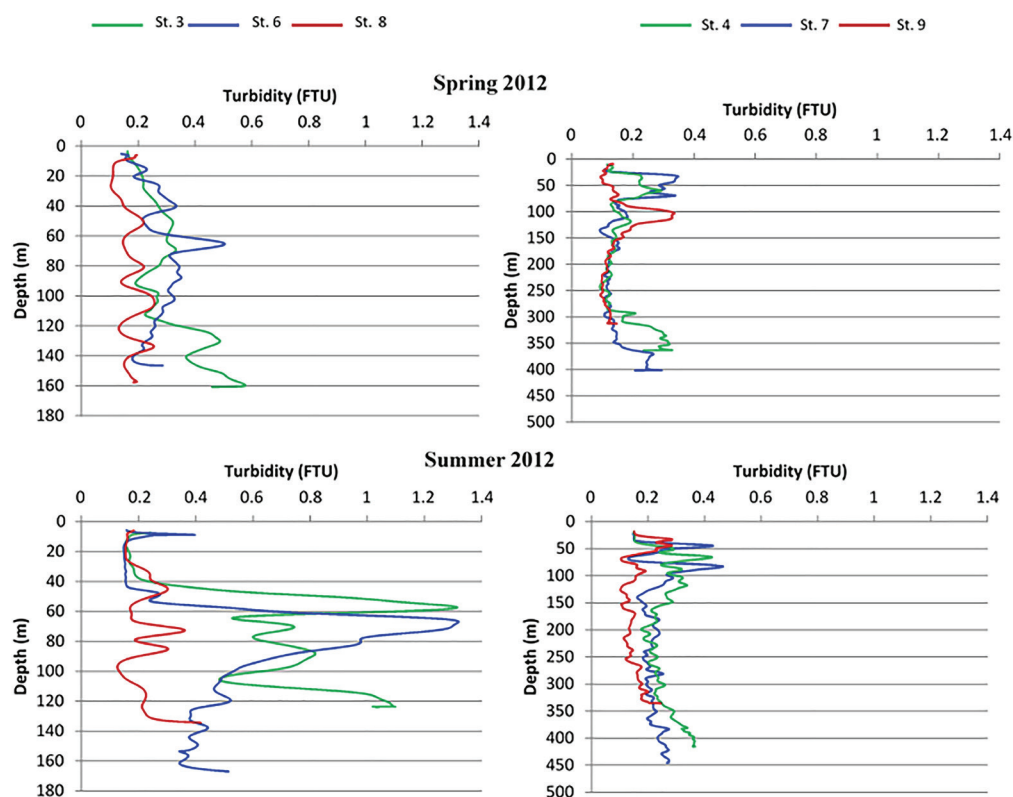
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Fig 5: Turbidity (FTU) profiles in spring (top) and summer (bottom) 2012 at 160 m (left) at stations 3, 6, 8 and at 400 m (right) at stations 4, 7, 9. ASC east channel in green, ASC west channel in blue, and AS in red.

Discussion

Deep sea benthic fauna are generally reliant on extraneous food sources which usually arrive sporadically and in small amounts (Danovaro *et al.*, 1999). It is expected therefore that the flux of food to the seafloor is even more reduced in the oligotrophic eastern Mediterranean. Mean BMF density on the northern Israeli slope, as found in this study (289 individuals/m²), are below the range reported in the eastern Mediterranean, western Mediterranean and eastern North Atlantic (365-633 individuals/m²) (Table 4). Mean BMF densities found in ASC (2000 and 1053 individuals/m2 at depths of 100-220 and 280-440 m, respectively), on the other hand, are high on a local scale (means of 766 and 500 individuals/m2 at depths of 105-216 and 278-475 m, respectively; Lubinevsky, personal communication), Mediterranean scale (26-1,548 individuals/m², 250-3000 m depth; Stora *et al.*, 1999; Kroncke *et al.*, 2003) and even compared to some Atlantic canyons (189-4,600 individuals/m²; Cunha *et al.*, 2011) (Table 4). Higher BMF abundances inside submerged canyons as compared to the adjacent isobathic slopes have also been reported for submarine canyons in other regions (e.g. Paterson *et al.*, 2011). Such findings lend support to the hypothesis that the higher abundances in ASC and other type 2 slope canyons result from bathymetric features that enhance transport and accumulation of terrigenous and coastal detritus and organic-rich material (Vetter, 1994; Vetter & Dayton, 1998, 1999; De Leo *et al.*, 2010; Vetter et al., 2010).

Dominance of polychaetes, the rule in benthic infaunal communities *(e.g. Kroncke et al.*, 2003; De Leo et al.,

2010; Lubinevsky *et al.*, 2017), was prominent even when samples contained only few specimens. The high preponderance of Cirratulidae, Spionidae and Cossuridae within the assemblage is in line with findings further south along the Israeli continental shelf margine and upper slope (Lubinevsky *et al.*, 2017), yet, some taxons that were found in ASC were absent in the latter study, namely: Lambrenidae, Nereidae, Onuphidae and Serpulidae (Polychaeta), *Austronucula perminima* and *Abra* sp. (Mollusca), Paguridae (Decapoda) and *Eurydice* sp. (Isopoda).

The existence of a higher BMF abundance in ASC was expected to be accompanied by organic enrichment relative to the AS, as expressed by TOC data (Dauwe *et al.*, 1998; Kroncke *et al.*, 2003; Paterson *et al.*, 2011; Amaro *et al.*, 2015), but this was not the case. One may argue that in this ultra-oligotrophic setting, any surplus TOC in ASC is rapidly consumed and/or mineralized by bioturbating macro-fauna, such that a difference in TOC may not become evident. TOC levels in this study (range of 0.64 – 1.18%, both in ASC and AS) were similar to those reported by Kroncke *et al.*, (2003) and Lubinevsky *et al.*, (2017) in the SE Levantine basin. All values were lower than the average value of 2.2% found in the Nazaré submarine canyon, off the coast of Portugal (Pusceddu *et al.*, 2010), supporting this explanation.

Enhanced coarse sediment transport by currents is an important ecological factor which eventually influences macro-faunal bio-diversity by providing a more heterogeneous substrate (McClain & Barry, 2010). Temperature and sediment grain size are important factors that influence patterns of regional-scale species richness in soft bottom habitats (Gray, 2002). In an effort to link

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Table 4. Comparison of macro-benthic faunal abundance at different global sites, specifying mesh size used, range of seafloor depths, number of samples examined, mean macrofaunal abundance and the source.

Location	Size fraction used (µm)	Depth range (m)	Number of samples	Mean abundance (individuals/m²)	Source
Nazaré, Cascais and Setúbal submarine canyons,	500	897-1030	12	365	Cunha *et al.*, 2011
Toulon Canyon, Coast of Provence, NW Mediterranean Sea	500	canyon 250-2000	36	337	Stora *et al.*, 1999
		Slope 250-1500	30	532	
Ionian Sea towards the Levantine Basin	500	506-1945	17	822	Kroncke *et al.*, 2003
Levantine Basin	250	105-475	24	633	Lubinevsky, pers. comm.
Levantine Basin – **ASC**	500	135-460	22	1393	Present study
Levantine Basin – **AS**	500	130-360	9	289	Present study

between sediment grain size and species richness, Gray (2002) suggested that sediment characterized by high grain size diversity is more likely to support high species richness. Moreover, Levin & Gage (1998) demonstrated that changes in species richness may not in fact be related to depth alone but also to sediment properties while Etter & Grassle (1992) demonstrated that species richness in the Atlantic deep-sea correlated not only with depth, but also with particle size diversity.

Non-river-associated submarine canyon heads may trap highly diluted sediment density flows (<0.001vol% suspensions), generated by oceanographic processes such as longshore currents, tidal action, storms and internal waves, all of which re-suspend sediments into nepheloid layers. These fine-grained sediments are then transported down canyon by episodic slow (30cm/sec) turbidity currents that can last for several days and are subsequently deposited within the canyon as mud and fine sand. Episodes typically, but not as a rule, coincide with periods of large wave heights (Talling, 2014 and references therein). Such processes are expected to be more prominent in canyons that are close to shore.

Material transport by currents is inferred in ASC, mainly in the eastern channel, by: 1) the sediment grain size composition and 2) the presence of a nepheloid layer.

1. Sediment transport in the region is governed by the dynamics of the long-shore cyclonic current of the Levantine Jet System (Schattner *et al.*, 2015). As the shelf narrows northward and its slope increases, the current's velocity diminishes seawards and so does the carrying capacity for coarse suspended material, which is then deposited on the seafloor. In addition, crossing the bathymetric drop of ASC's channels, there is further considerable loss of energy and suspended sediments get trapped in the canyon, available to be transported basinwards through turbidity currents (Schattner *et al.*, 2015, Schattner & Lazar, 2016). Indirect evidence for such transport was the finding in summer of 2012 of two shallow benthic foraminifera, *Rosalina* sp. and *Porosononion* sp., (Avnaim-Katav *et al.*, 2013), in a vertical plankton tow sample taken from 150 m above the sea floor over the connecting point of ASC's two channels (680m depth) (Roditi-Elasar, 2015).

2. The existence of detached and bottom nepheloid layers in ASC is supported by turbidity profiles from 2012 (Fig. 5). It is also supported by the presence of mostly deep sea benthic foraminifera (*Adelosina* sp., *Globobulimina affinis, Gyroidina* sp., *Nonionella* sp., *Planorbulina mediterraneansis, Usbekistania charoides,* and 2 species of Miliolids; (Roditi-Elasar, 2015)) in vertical plankton tows, taken from 10m above the sea floor to the surface, at depths of 160m and 420m, along ASC's eastern channel. This phenomenon recurred in four different cruises (fall 2010, 2011 and summer 2011, 2012), suggesting strong bottom currents re-suspending sediments along the channel.

In the present study, sand is the major contributor to grain-size diversity of the predominantly fine-sediment bottom. Sand from ASC had a higher calcareous (biogenic) content, locally produced and/or transported from the shallower bottom. Whatever the manner by which ASC is enriched by sand, the latter would be expected to promote diversity of niches as well as dwellers. Indeed, a highly significant positive correlation between overall taxon richness and % sand (Pearson's r=0.573; p=0.003) was revealed (Table S3).

The finding of a significantly higher mode grain size at the deep station of ASC's eastern channel is not readily explained, nor is the related positive effect of depth on sand content. It may explain the lack of a negative depth effect on BMF abundance and diversity, a common finding in other studies (Kroncke *et al.,* 2003).

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Conclusions

This research is the first multiyear biologic and physical study in the Akhziv submarine canyon and the nearby slope, addressing benthic macrofaunal assemblages coupled with sedimentology. The preliminary results suggest that indeed, ASC's bathymetry and proximity to shore create a relatively rich and diverse benthic habitat, regional hyper-oligotrophy notwithstanding. Follow-up research should include infaunal composition analysis in addition to abundance and biodiversity, attempting to highlight the role of key organisms or indicators in the BMF community that may shed further light on the differences between canyon and slope habitats.

The second addressed issue, that enhanced abundance and diversity are reliant on preferential material transport to ASC, also receives support, but a more detailed study, including the placement of sand traps, is called for.

The enhanced abundance and diversity in ASC are of high importance as they stand and even more so in light of possible future threats. As climate models predict that the Mediterranean basin will be one of the regions most affected by the ongoing warming trend (Giorgi & Lionello, 2008) and as the carbon cycle is expected to be adversely affected by increased acidification, the low food availability in the Levantine Basin is expected to intensify, including in deep-sea habitats (Danovaro *et al.,* 2001). A relatively rich benthic realm, such as that observed in the ASC may therefore serve as a refuge for certain species and by hosting a relatively diverse assemblage it has a better chance of adapting to changing conditions.

It is hoped that the trends revealed by these preliminary findings will spur further research on the biogeographic distribution of the deep-sea benthic fauna in the studied region.

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The following supplementary information is available on line for the article:

Fig. 1S: Grain size relative volumes in ASC entrance stations (St. 2, 5) by seasons.
Table S1: Benthic samples (500 ml of wet sediment) list with bottom depth, season, number of taxa and specimens and Shannon's diversity index (H').
Table S2: Results (p values) of the Generalized Linear Modelling tests on granulometry, TOC and BMF Significant and highly significant effects are lightly and darkly shaded, respectively.
Table S3: Correlation matrix.
Table S4: Sediment granulometry and TOC.

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