



Trophic Ecology of Deep-Sea Megafauna in the Ultra-Oligotrophic Southeastern Mediterranean Sea

Tamar Guy-Haim*, Nir Stern and Guy Sisma-Ventura*

National Institute of Oceanography, Israel Oceanographic and Limnological Research, Haifa, Israel

OPEN ACCESS

Edited by:

Sylvie Marylène Gaudron,
Sorbonne Universités, France

Reviewed by:

Gilles Lepoint,
Fonds National de la Recherche
Scientifique (FNRS), Belgium
Jeffrey C. Drazen,
University of Hawaii at Manoa,
United States

*Correspondence:

Tamar Guy-Haim
tamar.guy-haim@ocean.org.il
Guy Sisma-Ventura
guy.siv@ocean.org.il

Specialty section:

This article was submitted to
Deep-Sea Environments and Ecology,
a section of the journal
Frontiers in Marine Science

Received: 18 January 2022

Accepted: 03 June 2022

Published: 27 July 2022

Citation:

Guy-Haim T, Stern N and
Sisma-Ventura G (2022)
Trophic Ecology of Deep-Sea
Megafauna in the Ultra-Oligotrophic
Southeastern Mediterranean Sea.
Front. Mar. Sci. 9:857179.
doi: 10.3389/fmars.2022.857179

The trophic ecology of fourteen species of demersal fishes and six species of demersal decapod crustaceans from the continental slope and rise of the Southeastern Mediterranean Sea (SEMS) was examined using stable isotope analysis. Mean $\delta^{13}\text{C}$ values among fish species varied by ca. 4.0‰, from -20.85‰ (*Macroramphosus scolopax*) to -16.57‰ and -16.89‰ (*Conger conger* and *Centrophorus granulosus*), showing an enrichment in ^{13}C as a function of depth (200 – 1400 m). Mean $\delta^{13}\text{C}$ values of the crustaceans showed smaller variation, between -18.54‰ (*Aristeus antennatus*) and -16.38‰ (*Polychaetes typhlops*). This suggests a shift from pelagic to regenerated benthic carbon sources with depth. Benthic carbon regeneration is further supported by the low benthic-pelagic POM- $\delta^{13}\text{C}$ values, averaging $-24.7 \pm 1.2\text{‰}$, and the mixing model results, presenting relatively low contribution of epipelagic POM to the deep-sea fauna. Mean $\delta^{15}\text{N}$ values of fish and crustacean species ranged $7.91 \pm 0.36\text{‰}$ to $11.36 \pm 0.39\text{‰}$ and $5.96 \pm 0.24\text{‰}$ to $7.73 \pm 0.46\text{‰}$, respectively, resulting in trophic position estimates, occupying the third and the fourth trophic levels. Thus, despite the proximity to the more productive areas of the shelf, low number of trophic levels ($\text{TL} \sim 1.0$) and narrow isotopic niche breadths ($\text{SEA}_C < 1$) were observed for demersal crustaceans ($\text{TL} = 2.94 \pm 0.18$) and fishes ($\text{TL} = 3.62 \pm 0.31$) in the study area – probably due to the ultra-oligotrophic state of the SEMS resulting in limited carbon sources. Our results, which provide the first trophic description of deep-sea megafauna in the SEMS, offer insight into the carbon sources and food web structure of deep-sea ecosystems in oligotrophic marginal seas, and can be further used in ecological modeling and support the sustainable management of marine resources in the deep Levantine Sea.

Keywords: stable isotope analysis, trophic level, vertical vs. lateral transport, Bayesian mixing models, benthic carbon regeneration, carbon limitation, continental slope and rise

INTRODUCTION

Deep-sea ecosystems cover much of the oceans seafloor and play a major role in large-scale biogeochemical cycles (Walsh, 1991; Drazen and Sutton, 2017). They provide ecosystem services that are important to humans, including carbon sequestration, nutrient recycling and burial, waste accumulation and fisheries production (Danovaro et al., 2008; Mengerink et al., 2014; Thurber et al., 2014). Recent studies have shown that an increasing number of stressors, including climate change (warming), deoxygenation, ocean acidification, as well as, overfishing, and natural resource extraction

(e.g., Stramma et al., 2008; Yasuhara et al., 2008; Stramma et al., 2010; Helm et al., 2011; Tecchio et al., 2015) are expanding into deep environments, thus threatening the diversity and stability of deep-sea ecosystems. Consequently, studying the status of deep-sea communities and describing deep-sea ecosystem structures are currently gaining more and more attention.

Continental slopes account for ~11% of the total ocean floor (Ramirez-Llodra et al., 2010), connecting the shallow shelf productive areas with the abyssal plains along steep seabed gradients. Covering large bathymetric ranges (~200–2000 m), these dynamic habitats exhibit strong spatial differences in temperature, salinity, nutrient concentrations, sedimentological features, like organic carbon content, and consequently, in habitat suitability (Koslow, 1993; Gordon et al., 1995; Neat et al., 2008; Bergstad, 2013; Pajuelo et al., 2016). Bathyal habitats also support diverse deep-sea fauna (Gordon and Swan, 1997; Kelly et al., 1998; Menezes et al., 2006; Neat et al., 2008), even in ultra-oligotrophic basins, such as the easternmost Mediterranean Sea (Goren et al., 2008). In deep-sea benthic ecosystems, fish can play key ecological and biogeochemical roles (Drazen and Sutton, 2017) by regulating nutrient limitation and zooplankton populations (Hopkins and Gartner, 1992; Pakhomov et al., 1996).

Deep-sea benthic ecosystems largely rely on particulate organic matter (POM) that passively sinks from the surface waters or by lateral transport as a primary source of nutrients (Tecchio et al., 2013). Marine organisms that carry out vertical diel migrations through the water column (Trueman et al., 2014) and occasional sink of large animal carcasses is another important food source to deep-sea ecosystems (Smith and Baco, 2003). Each of these primary food sources may carry a distinct isotopic signature that reflects its origin, resulting from different chemo-physical processes. Thus, by knowing the isotopic composition of the food sources that fuels a specific food web, it is possible to reconstruct the trophic structure and dynamics of specific habitats (Post, 2002).

Stable isotope analysis (SIA) has been used successfully to study trophic level, important prey types, and trophic niche breadth in deep-sea ecosystems (e.g., Boyle et al., 2012; Shipley et al., 2017a). Nitrogen stable-isotope composition ($\delta^{15}\text{N}$) is used to determine the trophic position of an animal, as it preferentially fractionates as a function of its diet, where the heavy isotopes are retained in the consumers in respect to their prey by 2–4‰ (Post, 2002). Carbon stable isotopes ($\delta^{13}\text{C}$) fractionate much less with each trophic step (<1‰), but can be effectively used to infer basal sources of carbon. Moreover, SIA provides an integrated view of an organism's diet over time-scales relevant to tissue turnover rates rather than digestion rates (Peterson and Fry, 1987; Post, 2002), thereby providing estimates of the trophic position of an organism within a specific food web.

Knowledge of food web structure and dynamics is key to our understanding of ecological communities and their functioning (Polis and Strong, 1996; Winemiller and Polis, 1996). This fundamental information is, however, lacking in many oceanographic regions, including the Southeastern Mediterranean Sea (hereafter, SEMS) (Parzanini et al., 2019)

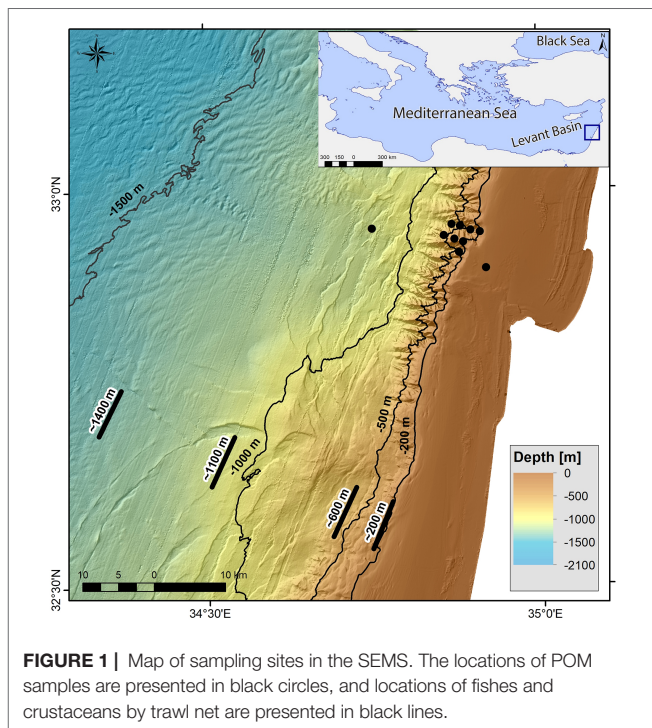
— one of the most oligotrophic, nutrient-impoverished marginal basin, worldwide (Kress et al., 2014). This basin exhibits extremely low open water primary production ($\sim 60 \text{ g C m}^{-2} \text{ y}^{-1}$) merely half of that measured in other oligotrophic areas of the ocean (Hazan et al., 2018), resulting in limited energy sources to its deep-sea habitats (Rahav et al., 2019). The greatest fraction of particulate flux to the SEMS deep-seafloor is transported laterally from the continental shelf at intermediate depths (Katz et al., 2020) and is considered to be highly refractory (Rubin-Blum et al., 2022). The SEMS, therefore, provides a miniature model of processes occurring in vast oligotrophic marginal seas, an ideal location to study food web structure and functioning under severe nutrient limitation. Furthermore, the SEMS is one of the regions where sea surface temperatures are rising at the fastest rates under recent climate changes (Sisma-Ventura et al., 2014; Ozer et al., 2017) and is one of most vulnerable marine regions to species invasions (Rilov and Galil, 2009), which have been also reported from deep-sea habitats (Galil et al., 2019). Understanding deep-sea community structure and functioning is of prime importance for developing better predictions regarding the ecological effects of future climate change. The main objective of this study was to elucidate the energy sources that sustain the deep-sea food-webs of the SEMS.

To date, much of the research describing the trophic ecology of the Eastern Mediterranean Sea has focused on zooplankton groups (Koppelman et al., 2003; Koppelman et al., 2009; Hannides et al., 2015; Protopapa et al., 2019), shallow rocky reefs (Fanelli et al., 2015), and on anthropogenically-influenced coastal environments (Grossowicz et al., 2019), while less attention has been paid to deep-sea fishes and crustaceans that occupy higher trophic levels. Here we used bulk carbon and nitrogen stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of demersal and bathybenthic fishes and crustaceans from the southeast Mediterranean continental slope and rise. We explored potential factors that may explain the variability in stable isotope values across species. These data offer insights into the carbon sources and trophic complexity of deep-sea ecosystems in oligotrophic marginal seas.

MATERIALS AND METHODS

Study Sites and Sampling Design

Sampling campaigns were conducted in the course of three oceanographic cruises during 2017–2019, as part of the national deep-water monitoring program of the Israeli Mediterranean Sea performed by Israel Oceanographic and Limnological Research (IOLR). Sampling sites were divided to three major benthic habitats: (1) the end of the continental shelf, with an average depth of 200 m; (2) the continental slope with depth range of 500–600 m; and (3) the deep bathyal plateau (continental rise) with depth range of 1000–1400 m (**Figure 1**). Specimens were collected onboard the R/V *Bat-Galim*, using a semi-balloon trawl net with an opening of eight meters and mesh size of 10 mm. Once the trawls were retrieved, specimens were sorted, enumerated, weighted and visually identified to species level. The



total length (cm) of each specimen was recorded. Specimens for SIA were selected and frozen whole at -20°C until processed at the IOLR.

POM was collected during three research expeditions in winter 2018, summer 2020, and winter 2021, across the shelf, slope and rise of the SEMS (Figure 1 and Table 1). POM samples were collected throughout the water column using 8-L Niskin bottles. Water samples were then filtered on pre-combusted 47-mm glass fiber filters (Whatman) in duplicates at low pressure and dried at 60°C for 24 h prior to isotope analysis.

Stable Isotopes Analysis

SIA was conducted on 86 fish and 46 crustacean specimens as well as 77 POM samples (Table 1). White muscle tissue for SIA was dissected from the dorsal musculature of fishes and from the abdominal segment of the crustaceans. Samples were rinsed with deionized water, frozen, and lyophilized for 48 h. Freeze-dried samples were homogenized using a mortar and pestle, weighed, and shipped to the Stable Isotope Facility at Cornell University (USA) for SIA analysis. The isotopic composition of organic carbon and nitrogen was determined by the analysis of CO_2 and N_2 continuous-flow produced by combustion on a Carlo

TABLE 1 | Sample descriptions and bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope data (mean \pm SD).

Sample type/Species(abbreviation)	n	Depth (m)	Total length (cm)	Total weight (g)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C/N	
Fish								
<i>Bathypterois mediterraneus</i> (Bm)	3	200	9.73 \pm 1.63	5.00 \pm 2.08	-17.76 \pm 0.21	9.62 \pm 0.01	2.94 \pm 0.02	
<i>Centrophorus granulosus</i> (Cg)	1	600	n/a	n/a	-16.89	9.55	2.39	
<i>Coelorinchus caelorhincus</i> (Cc)	3	200	18.47 \pm 4.00	26.33 \pm 18.88	-17.88 \pm 0.32	10.88 \pm 0.56	3.02 \pm 0.02	
<i>Coelorinchus caelorhincus</i> (Cc)	8	600	12.63 \pm 0.68	n/a	-19.18 \pm 0.77	9.40 \pm 0.49	3.02 \pm 0.02	
<i>Conger conger</i> (CCo)	1	1000	87	1296	-16.57	11.25	3.03	
<i>Dentex macropthalmus</i> (Dm)	12	200	13.67 \pm 0.97	42.00 \pm 8.96	-18.67 \pm 0.65	9.22 \pm 0.45	3.38 \pm 0.26	
<i>Etmopterus spinax</i> (Es)	3	1100	30.67 \pm 1.17	121.00 \pm 15.31	-17.61 \pm 0.05	8.83 \pm 0.33	2.62 \pm 0.20	
<i>Galeus melastomus</i> (Em)	4	1100	33.53 \pm 4.99	114.00 \pm 39.62	-17.75 \pm 0.28	7.97 \pm 0.13	2.42 \pm 0.10	
<i>Helicolenus dactylopterus</i> (Hd)	14	500, 600	17.50 \pm 1.75	95.00 \pm 29.88	-17.99 \pm 0.27	8.82 \pm 0.28	3.09 \pm 0.16	
<i>Hoplostethus mediterraneus</i> (Hm)	6	500, 600	16.00 \pm 1.41	62.00 \pm 5.66	-17.49 \pm 0.20	10.29 \pm 0.67	3.04 \pm 0.16	
<i>Lepidotrigla cavillone</i> (Lc)	6	200	10.03 \pm 0.60	14.00 \pm 2.22	-19.13 \pm 0.25	8.35 \pm 0.35	3.10 \pm 0.25	
<i>Lophius budegassa</i> (Lb)	2	1000	65.55 \pm 21.14	37.00 \pm 2.12	-17.17 \pm 0.18	9.80 \pm 0.46	3.09 \pm 0.01	
<i>Macroramphosus scolopax</i> (Ms)	5	200	9.08 \pm 0.79	5.00 \pm 1.48	-20.85 \pm 0.46	7.91 \pm 0.36	4.48 \pm 0.72	
<i>Nezumia</i> sp. (Ns)	4	500	n/a	n/a	-17.24 \pm 0.30	10.76 \pm 0.36	3.31 \pm 0.07	
<i>Nezumia</i> sp. (Ns)	9	1100	17.39 \pm 1.44	14.33 \pm 3.60	-17.09 \pm 0.24	11.36 \pm 0.39	3.06 \pm 0.09	
Decapod crustaceans								
<i>Acanthephyra eximia</i> (Ae)	11	1400	12.04 \pm 2.19	13.18 \pm 7.49	-17.59 \pm 0.30	6.95 \pm 0.64	2.90 \pm 0.11	
<i>Aristaeomorpha foliacea</i> (Af)	3	1400	9.83 \pm 1.53	5.36 \pm 1.54	-17.97 \pm 0.87	7.68 \pm 0.68	2.90 \pm 0.06	
<i>Aristeus antennatus</i> (Aa)	6	600	12.02 \pm 0.43	9.37 \pm 0.95	-18.54 \pm 0.17	7.62 \pm 0.14	2.87 \pm 0.03	
<i>Aristeus antennatus</i> (Aa)	10	1100, 1400	11.50 \pm 1.49	8.01 \pm 3.66	-18.09 \pm 0.59	7.73 \pm 0.46	2.84 \pm 0.18	
<i>Parapenaeus longirostris</i> (Pl)	7	200	10.17 \pm 0.82	4.34 \pm 1.18	-18.45 \pm 0.10	6.72 \pm 0.19	2.94 \pm 0.08	
<i>Plesionika edwardsii</i> (Pe)	3	200	11.37 \pm 1.35	4.05 \pm 0.56	-17.72 \pm 0.13	5.96 \pm 0.24	2.66 \pm 0.09	
<i>Plesionika edwardsii</i> (Pe)	3	600	13.43 \pm 0.81	7.56 \pm 0.66	-17.66 \pm 0.23	6.33 \pm 0.30	2.74 \pm 0.15	
<i>Polychaetes typhlops</i> (Pt)	3	1100, 1400	6.93 \pm 0.81	2.86 \pm 0.58	-16.38 \pm 0.21	7.67 \pm 0.18	3.36 \pm 0.05	
POM								
Shelf	surface	8	0-5	n/a	n/a	-24.32 \pm 0.72	1.61 \pm 0.92	9.42 \pm 1.83
	bottom	9	60-250	n/a	n/a	-24.27 \pm 1.24	1.09 \pm 0.95	10.23 \pm 3.34
Slope	surface	4	0-5	n/a	n/a	-24.73 \pm 0.82	1.26 \pm 0.75	11.18 \pm 2.29
	bottom	10	400-800	n/a	n/a	-25.45 \pm 1.50	2.76 \pm 0.85	15.19 \pm 3.76
Deep basin	surface	9	0-5	n/a	n/a	-23.98 \pm 1.05	-0.77 \pm 1.34	8.43 \pm 2.68
	bottom	15	>1000	n/a	n/a	-23.91 \pm 2.10	6.64 \pm 2.96	10.25 \pm 3.32

n/a denotes data not available.

Erba NC2500 connected on-line to a DeltaV isotope ratio mass spectrometer coupled with a ConFlo III interface.

Measured stable isotope ratios are reported in the δ -notation, i.e., as the deviation in per mill (‰) from the international standards:

$$\delta_{\text{Sample}} = \left(\frac{R_{\text{Sample}}}{R_{\text{Standard}}} - 1 \right) \times 10^3$$

where, R represents the $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ ratio. Stable isotope data are expressed relative to international standards of Vienna PeeDee belemnite and atmospheric N_2 for carbon and nitrogen, respectively. The analytical precision for the in-house standard was $\pm 0.04\text{‰}$ [1σ] for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The C/N ratios of fishes and crustaceans in this study were low (species mean C/N ranged between 2.33 – 4.48; where in 97% of individuals C/N < 4.0, see **Supplementary Figures 1, 2**), suggesting that lipids did not significantly affect the $\delta^{13}\text{C}$ interpretation (Post et al., 2007). Therefore, all data analyses were performed on uncorrected $\delta^{13}\text{C}$ values. To determine if the isotopic signatures of POM samples changed with depth, we used collection depth to classify POM samples as epipelagic (0 – 200 m), mesopelagic (200 – 800 m), or bathypelagic (>800 m).

Data Analysis

We estimated and compared modal trophic position (TP) and 95% credibility interval (i.e., 95% of modeled estimates of TP) for each species using the R package tRophicPosition (version 0.7.7; Quezada-Romegialli et al., 2018) according to the following equation:

$$\delta^{15}\text{N}_c = \delta^{15}\text{N}_b + \Delta\text{N}(\text{TP} - \lambda)$$

Where $\delta^{15}\text{N}_c$ corresponds to the nitrogen stable isotope value from the consumer that the TP is estimated, $\delta^{15}\text{N}_b$ represents the nitrogen stable isotope value of the baseline consumer; ΔN corresponds to the trophic discrimination factor (TDF) for nitrogen and λ the TP from baseline consumer. We used the average $\delta^{15}\text{N}$ in zooplankton ($3.9 \pm 1.8\text{‰}$) measured by Koppelman et al. (2009) in the Eastern Levantine Basin as the baseline ($\lambda=2$) using the oneBaseline model option and applied the trophic discrimination factor $\delta^{15}\text{N}$ of $3.15 \pm 1.28\text{‰}$, which was previously used to calculate the trophic level of meso- and bathypelagic fish (Valls et al., 2014; Richards et al., 2018).

Least-squares linear regression analysis was conducted for each species to explore the relationship between fish length and the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Spatial variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of both fishes and crustaceans was investigated using least-squares linear regression between stable isotopic values and depth. All statistical analyses were performed in R v. 4.0.5 (R Core Team, 2020).

The trophic breadth of each species ($n \geq 5$) and trophic similarity among species were assessed by calculating Standard Ellipse Area (SEA) using the R package SIBER v. 2.1.6 (Jackson

et al., 2011; Jackson and Parnell, 2021). Size-corrected SEAs (SEAc) and Bayesian estimate of SEAs (SEA_B) were calculated for each species, which adjusts for underestimation of ellipse area at small sample sizes and allows for inter-study comparison of ellipse sizes (Jackson et al., 2011). Fish and crustacean community metrics were calculated based on Layman et al. (2007).

Bayesian mixing models were applied using R package MixSIAR v. 3.1.12 (Stock et al., 2018; Stock et al., 2021) to estimate the relative contribution of shelf, slope, and deep-basin surface vs. bottom POM to each species. These models are sensitive to variable discrimination factors (Bond and Diamond, 2011; Olin et al., 2013), which may be influenced by diet (Caut et al., 2009), tissue type (Malpica-Cruz et al., 2012), temperature (Britton and Busst, 2018), and species-specific metabolic rates (Pecquerie et al., 2010). Since the modeled species are predators and do not feed directly on POM, the total trophic fractionation per species was calculated as follows:

$$\text{TEF}_{\text{species}} = \text{TEF}_{\text{TL}} \times (TL_{\text{species}} - TL_{\text{source}})$$

Where, $\text{TEF}_{\text{species}}$ is the total trophic fractionation in the consumer relative to its basal source, TEF_{TL} is the mean enrichment per trophic level, TL_{species} is the trophic position of the consumer, and TL_{source} is the trophic position of the source. To evaluate the contribution of the basal sources to the studied species, we have assigned to POM $TL_{\text{source}} = 1.0$, since POM- $\delta^{13}\text{C}$ values are compatible of the lowest size fraction (pico-phytoplankton) measured in the Western Mediterranean Sea (Hunt et al., 2017).

To calculate the enrichment factors from POM to the top consumers included in this study, we have used two discrimination factor levels — from POM to zooplankton, and from zooplankton to the studied species. Based on average $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ between POM to zooplankton measured in the Western Mediterranean Sea, we set the basal enrichment factors of $1.40 \pm 1.15\text{‰}$ for $\delta^{15}\text{N}$ and $4.10 \pm 1.63\text{‰}$ for $\delta^{13}\text{C}$ (Hunt et al., 2017). The enrichment from zooplankton to the studied species was done using discrimination factors of $3.15 \pm 1.28\text{‰}$ for $\delta^{15}\text{N}$ and $0.97 \pm 1.08\text{‰}$ for $\delta^{13}\text{C}$ (Sweeting et al., 2007), which have been previously used to study the trophic structure of meso- and bathypelagic fishes in the Gulf of Mexico (Richards et al., 2018) and in the Western Mediterranean Sea (Valls et al., 2014).

Each model was run with identical parameters (number of MCMC chains = 3; chain length = 300000; burn in = 200000; thin = 100), and model convergence was determined using Gelman-Rubin and Geweke diagnostic tests (Stock et al., 2018).

RESULTS

Stable Isotopes

Species-specific mean $\delta^{13}\text{C}$ values ranged from -20.85 to -16.89‰ for fish and from -18.54 to -16.38‰ for crustaceans. Fish mean $\delta^{13}\text{C}$ values differed by 3.96‰, separating the most depleted (*Macrorhamphosus scolopax*: $-20.85 \pm 0.46\text{‰}$,

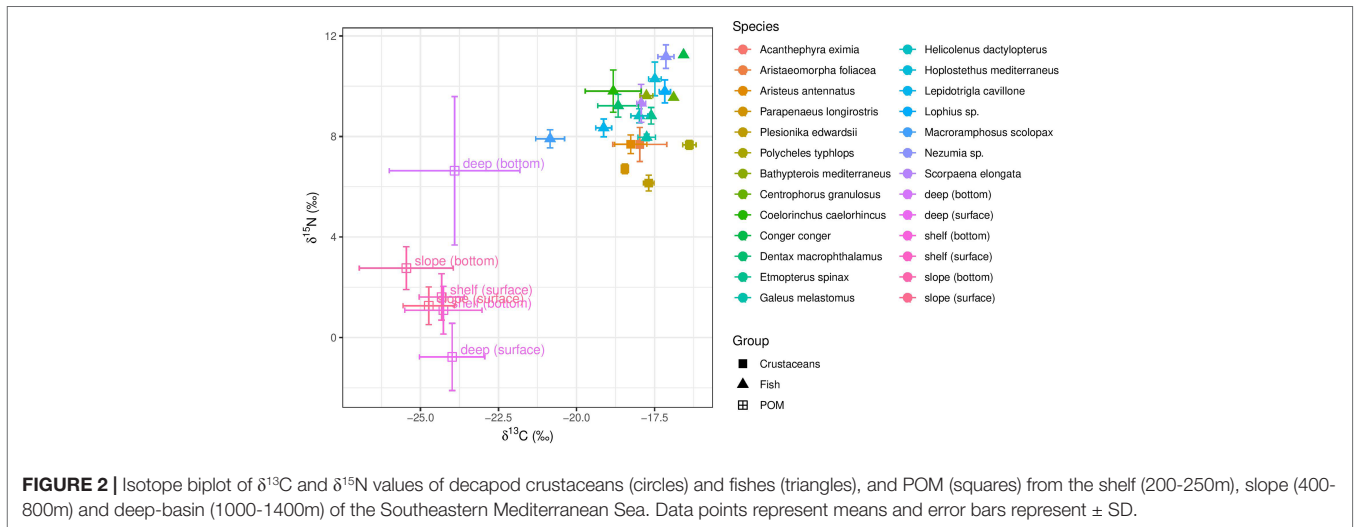


FIGURE 2 | Isotope biplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of decapod crustaceans (circles) and fishes (triangles), and POM (squares) from the shelf (200-250m), slope (400-800m) and deep-basin (1000-1400m) of the Southeastern Mediterranean Sea. Data points represent means and error bars represent \pm SD.

sampling depth of 200 m) and the most enriched species (*Centrophorus granulatus* and *Conger conger*: -16.89 and -16.57‰ , respectively, sampling depth of $\sim 1000\text{m}$) (Table 1 and Figure 2). Crustaceans species-specific mean $\delta^{13}\text{C}$ varied by 2.18‰ , where the most depleted species was *Aristeus antennatus* ($-18.54 \pm 0.17\text{‰}$, sampling depth of 600 m) and the most enriched species was *Polycheles typhlops* ($-16.38 \pm 0.21\text{‰}$, sampling depth of ~ 1400 m). Species-specific differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were significant for both fish (MANOVA, $F_{13,144} = 19.73$, $p < 0.001$) and crustaceans (MANOVA, $F_{5,78} = 14.62$, $p < 0.001$).

Species-specific mean $\delta^{15}\text{N}$ values varied from $7.91 \pm 0.36\text{‰}$ (*M. scolopax*, 200 m depth) to $11.36 \pm 0.39\text{‰}$ (*Nezumia* sp., 1100 m depth) in fish and from $5.96 \pm 0.24\text{‰}$ (*Plesionika*

edwardsii; 200 m depth) to $7.73 \pm 0.46\text{‰}$ (*Aristeus antennatus*; 1100 – 1400 m depth) in crustaceans. Fish mean $\delta^{15}\text{N}$ values positively correlated with the $\delta^{13}\text{C}$ values ($r^2 = 0.6$, $p < 0.001$, Figure 2 and Supplementary Figure 1) and varied among species (ANOVA, $F_{13,72} = 24.22$, $p < 0.001$). Crustaceans, however, did not show this correlation between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ($r^2 = 0.002$, $p > 0.05$, Figure 2 and Supplementary Figure 2), observed in fish from similar depths. Due to limited spatial coverage within each species (the specimens of most species were sampled from the same depth), spatial variation could not be tested within each species, and therefore, spatial trends were tested by addressing all fish species together. Fish $\delta^{13}\text{C}$ values positively varied with bottom depth ($r^2 = 0.42$; $P < 0.01$, Figure 3), where the most enriched samples were found at the continental rise (> 1000 m)

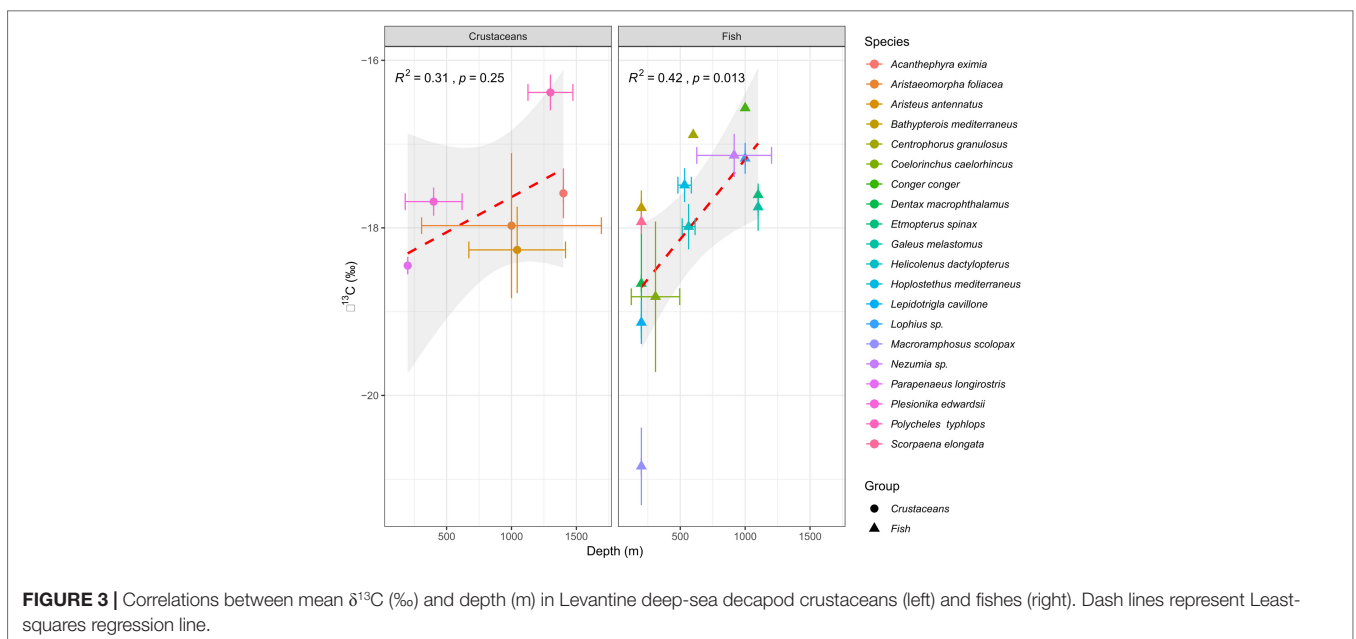
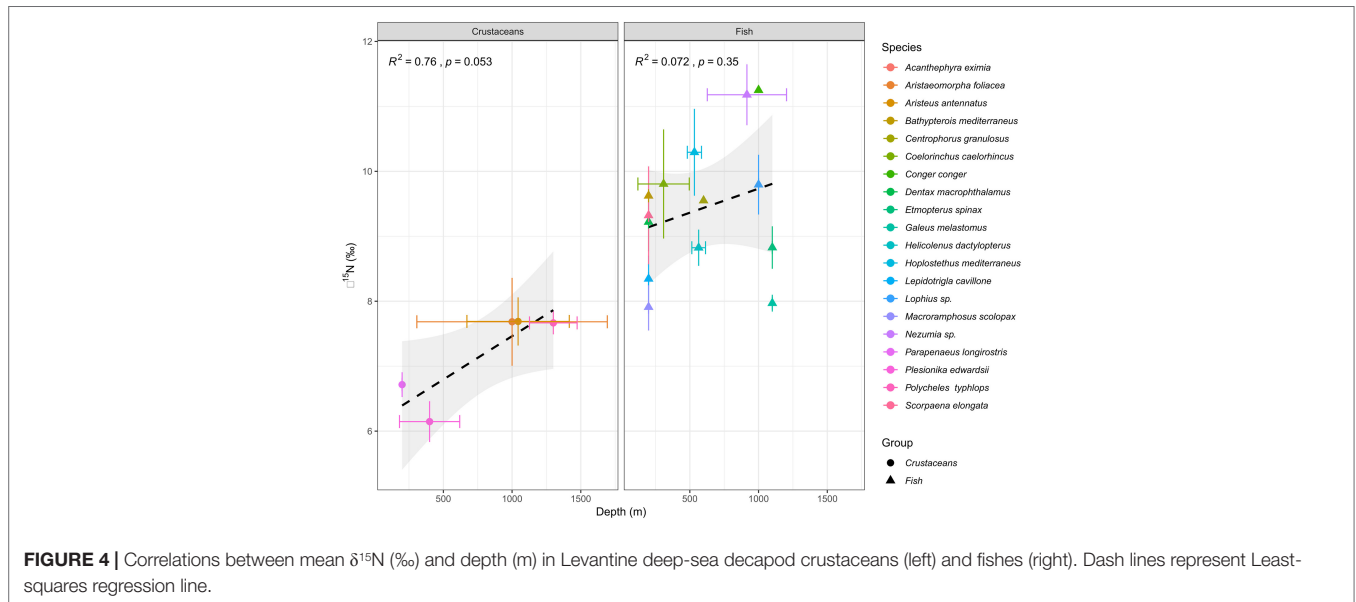


FIGURE 3 | Correlations between mean $\delta^{13}\text{C}$ (‰) and depth (m) in Levantine deep-sea decapod crustaceans (left) and fishes (right). Dash lines represent Least-squares regression line.



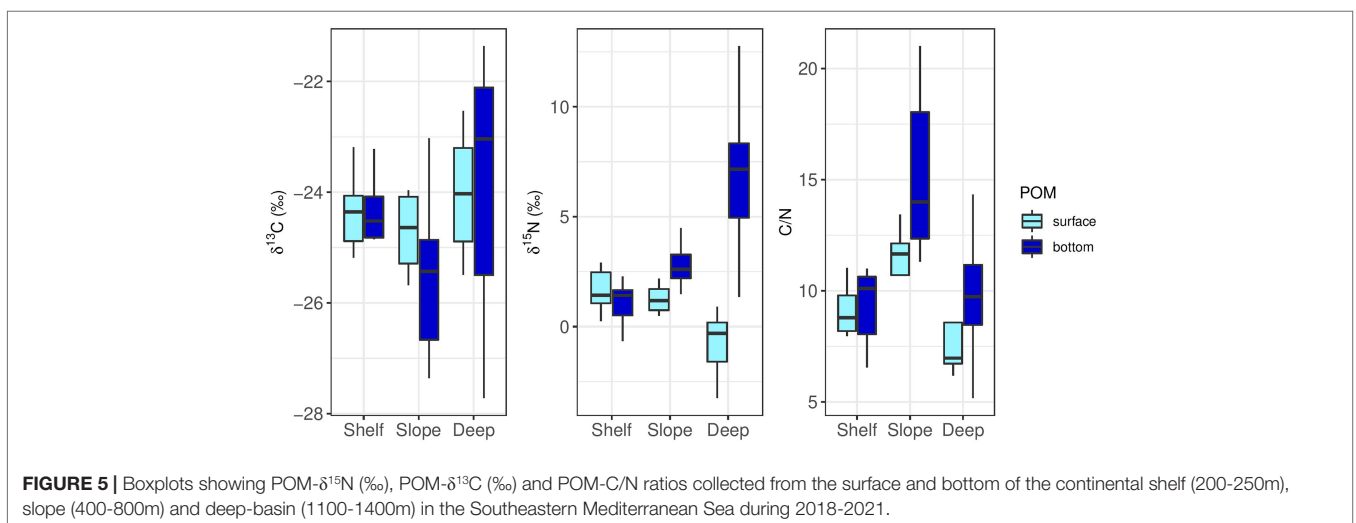
and the most depleted at the shallow slope (200 m) at the edge of the shelf. This pattern was less clear in the case of fish $\delta^{15}\text{N}$ values (Figure 4), where species-specific mean values seem more variable in the continental rise (> 1000 m). Crustaceans mean $\delta^{15}\text{N}$ values positively correlated with depth ($r^2 = 0.76$, $p = 0.053$, Figure 4), while their mean $\delta^{13}\text{C}$ values showed no such correlation (Figure 3).

POM collected from depths ranging from 0 to 1135 m over the continental shelf, slope and rise exhibited a wide $\delta^{13}\text{C}$ range (-27.72 to -21.36‰) and $\delta^{15}\text{N}$ range (-3.25 to 12.76‰), with POM samples generally becoming more enriched in ^{15}N and more depleted in ^{13}C at bottom depths (Figure 5). Significant differences in POM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among the zones and depths were observed (MANOVA, $F_{5,98} = 7.15$, $p < 0.001$). POM- $\delta^{13}\text{C}$ and C/N ratio exhibited a significant negative correlation (Pearson

correlation, $r = -0.566$, $p < 0.001$, Supplementary Figure 3), which was not observed in POM- $\delta^{15}\text{N}$ and C/N ratio.

Trophic Position Estimates

We used the average $\delta^{15}\text{N}$ value of Eastern Levantine zooplankton (3.9 ± 1.8 ‰) obtained from Koppelman et al. (2009) as a baseline ($\lambda=2.0$) for estimating species-specific TL. Based on the low $\delta^{15}\text{N}$ values of zooplankton in the eastern Mediterranean, it was assumed that the primary food source, namely smaller zooplankton, phytoplankton and particles have a $\delta^{15}\text{N}$ value around zero (Koppelman et al., 2009). Large mesozooplankton (333- μm mesh size, upper water column) $\delta^{15}\text{N}$ values in the EMS showed an enrichment trend across a west-east transect (SE Crete mean $\delta^{15}\text{N}$ value ~ 2.0 ‰ and SE Cyprus mean $\delta^{15}\text{N}$ value ~ 4.0 ‰, Koppelman et al., 2009). Using these data to set the baseline,



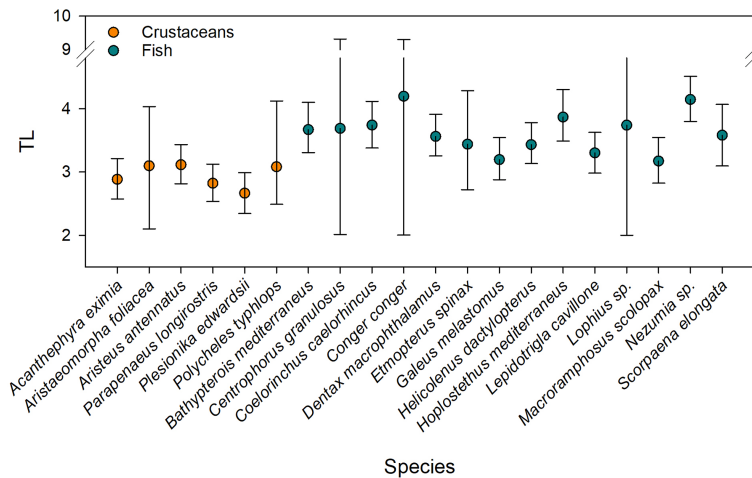


FIGURE 6 | Trophic level (TL) Bayesian estimates based on $\delta^{15}\text{N}$ data of deep-sea Levantine decapod crustacean (orange, $n=6$) and fish (blue, $n=14$) species using zooplankton of the Eastern Levantine Basin (Koppelman et al., 2009) as an isotopic baseline. Error bars denote 95% confidence intervals.

fish modal TL ranged from 3.17 (*M. scolopax*; 200 m depth) to 4.19 (*C. conger*; 1000 m depth), while the average modal TL of all fish species was 3.62 ± 0.31 (Figure 6). Crustaceans- $\delta^{15}\text{N}$ values yielded modal TLs between 2.66 (*P. edwardsii*; 200-600 m depth) and 3.11 (*A. antennatus*; 600 – 1400 m), with an average of 2.94 ± 0.18 (Figure 6).

Of the species examined, only few enabled an estimation of ontogenetic effect (Figure 7). This is due to the low range of body size within individual species that were sampled in this study. Nevertheless, the crustaceans *A. eximia* ($r^2 = 0.82$; $p < 0.001$) and *P. edwardsii* ($r^2 = 0.72$; $p < 0.05$) exhibited a positive relationship between length and $\delta^{15}\text{N}$ values. Size and $\delta^{13}\text{C}$ values did not yield significant correlations. Positive relationship between size and $\delta^{15}\text{N}$ values was also observed for the fish *D. macrophthalmus* ($r^2 = 0.59$; $p < 0.05$).

Trophic Niche Breadth

Isotopic niche breadth, calculated using size-corrected standardized ellipse area SEA_C (Supplementary Table 1 and Figure 8), was largest for the fish collected from the shallow continental slope *C. caelorrhynchus* ($\text{SEA}_C = 2.04$), *D. macrophthalmus* ($\text{SEA}_C = 0.94$) and *M. scolopax* ($\text{SEA}_C = 0.66$), and for the shrimps *A. antennatus* ($\text{SEA}_C = 0.63$) and *A. eximia* ($\text{SEA}_C = 0.56$), both opportunistic carnivores. The smallest isotopic niche breadth belonged to the deep-water rose shrimp *P. longirostris* ($\text{SEA}_C = 0.07$). Fish and crustacean assemblage metrics (Table 2A) showed a contrasting trend of isotopic niche size with depth, where fish isotopic niche size was largest in the shelf assemblage ($\text{SEA}_C = 1.81$) and crustaceans isotopic niche size was largest in the deep assemblage ($\text{SEA}_C = 1.43$). As a trophic guild (Table 2B), the fish showed higher convex hull area

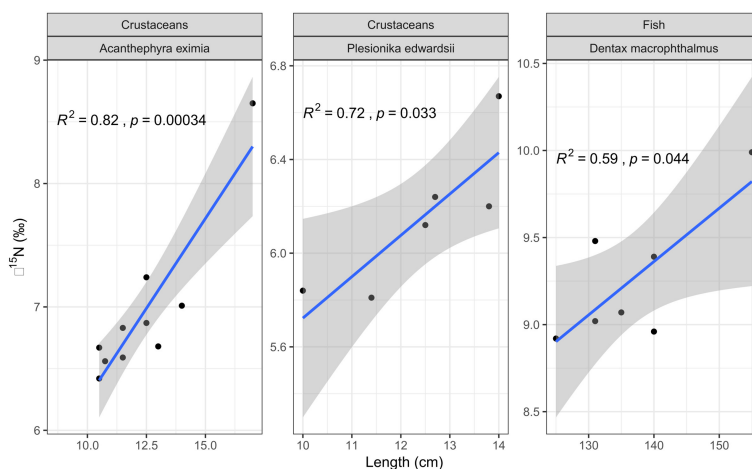


FIGURE 7 | Least-squares regression analysis between total length (cm) and $\delta^{15}\text{N}$ values in the decapod crustaceans *A. eximia* ($n=10$) and *P. edwardsii* ($n=6$), and the fish *D. macrophthalmus* ($n=7$).

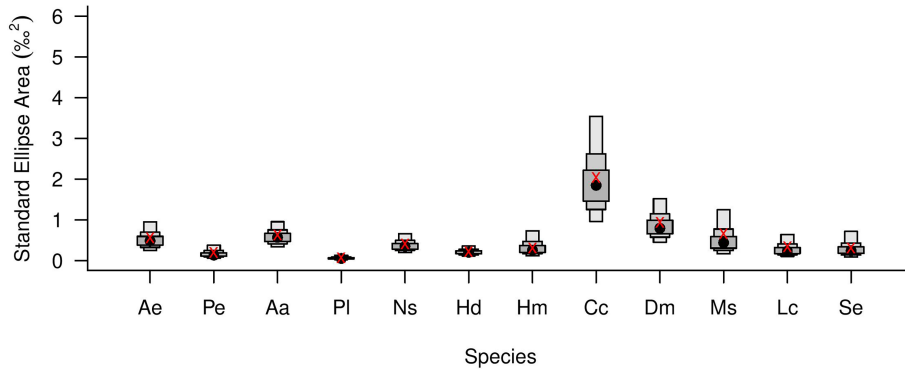


FIGURE 8 | Trophic niche breadth of Levantine fishes and decapod crustaceans ($n \geq 5$) estimated by size-corrected standard ellipse area (SEA_c) boxplots (showing 95, 75 and 50% credibility intervals). Black circles represent means; red x symbols represent the maximum likelihood estimates of SEA. Ae , *Acanthephyra eximia*; Pe , *Plesionika edwardsii*; Aa , *Aristeus antennatus*; Pl , *Parapenaeus longirostris*; Ns , *Nezumia* sp.; Hd , *Helicolenus dactylopterus*; Hm , *Hoplostethus mediterraneus*; Cc , *Coelorinchus caelorhincus*; Dm , *Dentex macropthalmus*; Ms , *Macroramphosus scolopax*; Lc , *Lepidotrigla cavillone*; Se , *Scorpaena elongata*.

(TA = 7.37) than the crustaceans (TA = 0.81), indicating a larger trophic community width (Layman et al., 2007).

Bayesian Mixing Models

The results of the mixing models indicated variable sources sustaining the deep-sea fish and crustacean consumers included in this study (Figure 9). The contribution of deep bathypelagic POM was highest in the decapod crustaceans *A. eximia* (74.8 ± 10.8%), *A. antennatus* (63.3 ± 9.5%) and *P. typhlops* (43.1 ± 1.7%), and in the rattail fish *Nezumia* sp. (66.3 ± 8.0%). The contribution of pelagic POM to the deep bathypelagic fauna spanned 26 ± 4%, increasing in the slope, varying between 24 and 61% (including both the shelf and slope surface POM). Whereas, the models showed an increased contribution of benthic POM to the deep-sea fauna (Figures 9G–O). For example, the benthic contribution

to the red shrimp *A. antennatus* was 20 ± 18.9% in the slope (Figure 9A) versus 63.3 ± 9.5% in the rise (Figure 9I). Therefore, the model results support a shift from pelagic to benthic source with increasing depth, i.e. with distance from shore.

DISCUSSION

This is the first attempt to elucidate the trophic ecology of deep-sea fish and crustacean species in the SEMs. The knowledge gained in this study provides insights into the main energy sources sustaining deep-sea food webs in one of the most oligotrophic, nutrient-improvised marine basins, worldwide. However, insights gained in this study are not limited to the SEMs alone, and can be relevant to many oligotrophic basins with limited carbon and nutrient sources.

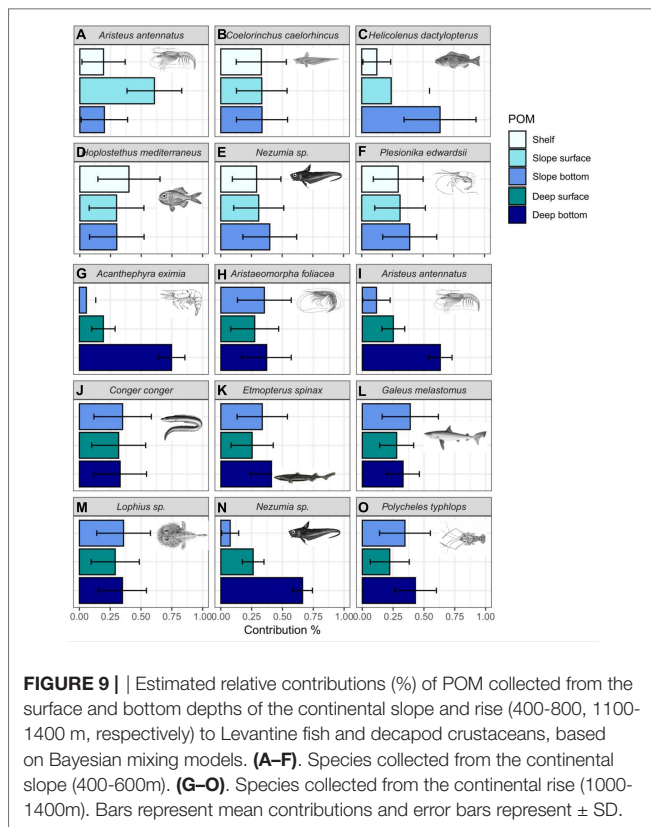
Our $\delta^{13}C$ and $\delta^{15}N$ values varied across fish species and as a function of depth, suggesting that depth and diet are controlling the trophic positions inferred from our stable isotope data. As expected, top predators such as the European conger eel *C. conger*, occupied the highest trophic position. The rattail *Nezumia* sp., a small macrourid fish that was collected from similar depths of >1000 m, yielded similar high $\delta^{15}N$ values. Both species occupied a maximum trophic position of 4.14 – 4.19 (modal TL). Polunin et al. (2001) found similar trophic position of 4.4 for both the shark *Centroscymnus coelolepis* and *Nezumia aequalis* in the continental slope of the Balearic Islands. High $\delta^{15}N$ values of *Nezumia* (11.09 ± 0.58‰ and 11.31‰) were also recorded by Fanelli and Cartes (2010) in the Archipelago of Cabrera (Algerian Basin) and by Papiol et al. (2013) in the Balearic Islands (Catalan Sea, West Mediterranean), respectively, and were attributed to the suprabenthic crustaceans and polychaetes that constitute the diet of this macrourid. Our TL data also agree well with that of benthic carnivorous fish from Bay of Banyuls-sur-Mer (northwest Mediterranean, France; Carlier et al., 2007). Among the fish, the lowest trophic position (3.17) was found in the snipefish *M. scolopax*, which feeds on hyperbenthic demersal zooplankton during daytime (Carpentieri et al., 2016). This was

TABLE 2 | Metrics for estimating assemblage and community (trophic guild) isotopic niche size in fish and decapod crustaceans from the Levantine deep-sea.

A) Assemblage type	TA	SEA	SEA _c
Crustaceans – Shelf	0.51	0.25	0.28
Crustaceans – Slope	0.79	0.44	0.51
Crustaceans – Deep	3.31	1.37	1.43
Fish – Shelf	7.04	1.77	1.81
Fish – Slope	3.50	1.12	1.17
Fish – Deep	2.77	1.16	1.22

B) Trophic guild	Crustaceans	Fish
$\delta^{13}C$ range	1.54	4.67
$\delta^{15}N$ range	2.07	3.71
TA	1.87	7.37
CD	0.81	1.29
MNND	0.75	0.82
SDMNND	0.43	0.52

(A) Assemblage metrics: TA, total area (‰²); SEA, standardized ellipse area (‰²); SEA_c, size-corrected standardized ellipse area. (B) Community metrics (Layman et al., 2007): TA, total area (‰²) encompassed by all data points of each trophic guild (crustaceans, fish); CD, mean distance to centroid (trophic diversity); MNND, mean nearest neighbour distance (trophic similarity); SDMNND, the standard deviation of MNND (trophic evenness).



also inferred from the results of the mixing models, indicating a relatively high contribution of mesopelagic POM to the diet of *M. scolopax*. Relatively to the fish, the bathybenthic crustaceans measured in this study occupied lower trophic positions — between 2.66 and 3.11, in agreement with the TL of deep benthic invertebrates of the Western Mediterranean (Carlier et al., 2007; Zorica et al., 2021).

The $\delta^{15}\text{N}$ values of the deep-sea decapods *A. eximia* and *P. edwardsii* increased significantly with length indicating an ontogenetic effect. Such trend was found in *A. eximia* from the Catalan Sea (Western Mediterranean), where gut content analysis indicated a dietary shift from scavenging and detritivory in small individuals to active predation in larger individuals (Cartes, 1993). Smaller sized *A. eximia* were suggested to be better adapted to regions where resources are scarce (Thiel, 1983; Pérès, 1985). Similar dietary preferences were observed in *P. edwardsii* (Cartes, 1993). The lower $\delta^{15}\text{N}$ that we measured in the smaller individuals of these decapods may indicate a detritivorous mode of feeding (Polunin et al., 2001). We found a similar ontogenetic effect in the demersal fish *D. macrophthalmus*. A gut analysis of this sparid fish off Angola and Namibia (South Atlantic Ocean) supports our finding, as the smaller fish tended to feed almost exclusively on polychaetes and euphausiids, but the larger fish preferred fish prey (Kilongo et al., 2007).

In the fish species examined here, mean $\delta^{15}\text{N}$ values spanned 3.45‰, about 1.1 TL, while in the crustacean species mean $\delta^{15}\text{N}$ values spanned 1.77‰, about 0.6 TL (assuming trophic enrichment factor of 3.15‰). Our observed ranges of

estimated trophic levels are in line with other studies examining Mediterranean (1.1 TL, Valls et al., 2014), Pacific (1.6 TL, Choy et al., 2015), and the Gulf of Mexico (0.62 TL, Richards et al., 2018). Different feeding strategies as well as different migration habits may explain wider range of $\delta^{15}\text{N}$ (Shiple et al., 2017a; Richards et al., 2020). Despite of the reliance on similar basal production, mesopelagic fishes from the Western Mediterranean were segregated by trophic position, between 2.9 for the small bristlemouth *Cyclothone braueri* to 4.0 for the lanternfish *Lobianchia dofleini* (Valls et al., 2014), and bathyal fishes off the Balearic Islands appeared to be foraging over two to three full trophic levels (Polunin et al., 2001). Our results support a much narrower trophic range for bathyal fish and bathybenthic decapod crustaceans in the SEMS. We attribute this narrow range to the ultra-oligotrophic state of the SEMS, resulting in limited carbon sources to sustain the deep-sea food webs, reflected by a general increase of $\delta^{13}\text{C}$ in fish as function of bottom depth. This pattern could be driven by a number of factors including shifting production sources, or shifts in community composition and feeding strategies, and or switching from benthic to pelagic prey (Fanelli et al., 2011; Trueman et al., 2014). For example, ^{13}C became more depleted in individuals captured at greater depths in the deep-sea island slope system of the Exuma Sound, the Bahamas (Shiple et al., 2017b). Inshore-to-offshore depletion in ^{13}C values were also apparent in epipelagic fishes in the northern California Current, where copepods, gelatinous zooplankton, and nekton showed a significant linear decrease in $\delta^{13}\text{C}$ with distance offshore (Miller et al., 2008). Our results show a different trend of increase in fish $\delta^{13}\text{C}$ as function of bottom depth, i.e., distance offshore.

The major carbon sources supporting deep-sea food webs are poorly defined, aside from oligotrophic open-ocean gyres, where sinking phytoplanktonic-POM is considered the main energy source (Shiple et al., 2017b). This was observed by a narrow range of $\delta^{13}\text{C}$ in meso- and bathypelagic predatory fishes in the Gulf of Mexico, indicating an exclusive epipelagic carbon source (Richards et al., 2018). Differently, the results of our mixing-model show increased contribution of bathypelagic POM and a reduction in the epipelagic source with increasing depth, i.e. distance offshore. This pattern agrees well with the extremely low primary production and carbon flux from the surface open water of the SEMS to the deep-seafloor (Katz et al., 2020). While most of the flux to the deep seabed is transported laterally.

Indeed, the majority of carbon supporting the species examined in this study is not derived from epipelagic sources. An alternative hypothesis is that the source of carbon in the deep-sea originates from the shelf. A significant proportion of neritic-derived primary production may be transported into deep-sea systems by currents (Suchanek et al., 1985; Sanchez-Vidal et al., 2012; Efrati et al., 2013), or via lateral transport (Fahl and Nöthig, 2007), and once assimilated into the food web, more enriched ^{13}C values are to be expected (Polunin et al., 2001; Fanelli et al., 2011). Katz et al. (2020) used deep-sea sediment traps in the Israeli Southeastern Mediterranean Sea and showed that lateral transport from the continental margin contributes the greatest fraction of particulate flux to the seafloor. Therefore, we suggest that lateral transport constitutes the main source of carbon to the

deep-sea food web in the Southeastern Mediterranean Sea. Our mixing model results and the relative decrease of C:N ratio in fish with increasing depth, indicating lower lipid content in deep-sea fish, further support a shift from pelagic to regenerated benthic carbon sources with depth. Given that the $\delta^{13}\text{C}$ of POM slightly vary between the different foraging habitats, it is likely that this shift in $\delta^{13}\text{C}$ occurs in the sediments water interface, by the enhanced bacterial regeneration of organic matter. This is likely driven by the high temperatures of the SEMS deep water near the seafloor ($\sim 13\text{--}14^\circ\text{C}$), compared to much lower temperatures of $\sim 4^\circ\text{C}$ at similar depths in most oceanic basins and despite the relatively low organic content of the SEMS sediments $<1\%$ (Ogrinc et al., 2007).

Since the carbon signature of primary producers can significantly vary between macroalgae and different phytoplankton groups (Fanelli et al., 2011; Grossowicz et al., 2019), food webs that show a linear relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are suggestive of a single food source (Polunin et al., 2001; Carlier et al., 2007). Generally weak $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ correlations were found in deep-sea macrozooplankton and micronekton off the Catalan slope likely due to the consumption of different kinds of sinking particles (e.g. marine snow, phytodetritus). Multiple recycling of POM constituted an enrichment effect on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of deep-sea macrozooplankton and micronekton (Fanelli et al., 2011). Our results yielded significant positive correlation between fish $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, further supporting a single food source.

Previous studies have shown that $\delta^{13}\text{C}$ fractionates less than 1.0‰ for each trophic position. The $\Delta^{13}\text{C}$ between the mean water column POM– $\delta^{13}\text{C}$ ($-24.13 \pm 1.56\text{‰}$) and fish/crustaceans $\delta^{13}\text{C}$ ($-18.10 \pm 0.93\text{‰}$) of the SEMS amounted to 6.04‰ (equal to at least six trophic positions), and therefore, cannot be attributed to trophic enrichment alone, but could be partly linked to the regeneration of benthic carbon sources, which may be relevant for detritus feeding animals, including all of the crustacean and some of the fish studied here. Moreover, our $\delta^{13}\text{C}$ –C/N data support the potential effect of microbially degraded phyto-detritus resulting in higher isotopic values of nitrogen and carbon in deep benthic food webs compared with pelagic food webs (Papiol et al., 2013; Romero-Romero et al., 2021).

Deep-sea ecosystems are subjected to exacerbating anthropogenic stressors, including overfishing, chemical pollution, mining, dumping, litter, plastics, and climate change (Davies et al., 2007). In oligotrophic environments such as the ultra-oligotrophic SEMS, deep-sea ecosystems are further vulnerable to reduced food availability (Kröncke et al., 2003). Regeneration of benthic carbon sources, supported by this study, provides oligotrophic deep-sea food webs with a greater ability to endure carbon limitation. Benthic carbon sources originating in lateral transport from the shallow shelf to the deep-sea, as indicated here, may hold important implications for marine spatial planning and the establishment of Marine

Protected Areas (MPAs) in the SEMS exclusive economic zones (EEZ), promoting the extension of protected areas from the shelf to the deep-sea in a continuum rather than the establishment of MPAs that are disconnected from the continental shelf and slope. Furthermore, lateral transport from the shelf to the deep sea may carry detrimental implications to the ecosystem via pollutant accumulation and biomagnification (Liu et al., 2020). This is particularly important in marginal seas that are prone to anthropogenic pollution (Kim et al., 2019; Shoham-Frider et al., 2020). Continuous studies should be undertaken to further unveil the implications of lateral transport and benthic carbon regeneration to deep-sea food webs.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in: Guy-Haim, Tamar; Stern, Nir; Sisma-Ventura, Guy (2022): Bulk stable isotopes of deep sea fish and crustaceans from the Southeastern Mediterranean Sea. PANGAEA, <https://doi.org/10.1594/PANGAEA.945321>.

ETHICS STATEMENT

The animal study was reviewed and approved by Israel National Institute of Oceanography Ethics Committee.

AUTHOR CONTRIBUTIONS

GS-V and TG-H conceived this study. GS-V, NS, and TG-H collected the data. NS provided species identification and measurements. GS-V and TG-H analyzed and modeled the stable isotope data. All co-authors contributed substantially to drafting the manuscript, and approved the final submitted manuscript.

ACKNOWLEDGMENTS

We wish to thank Mor Kanari for map preparation, and the captain and crew of R/V Bat-Galim, including onboard technical and scientific personnel for assistance in sampling. We also thank the two reviewers for critically reading the manuscript and suggesting substantial improvements. This work was supported by the National Monitoring Program of the Israeli Mediterranean waters.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.857179/full#supplementary-material>

REFERENCES

- Bergstad, O. (2013). North Atlantic Demersal Deep-Water Fish Distribution and Biology: Present Knowledge and Challenges for the Future. *J. Fish. Biol.* 83, 1489–1507. doi: 10.1111/jfb.12208
- Bond, A. L. and Diamond, A. W. (2011). Recent Bayesian Stable-Isotope Mixing Models are Highly Sensitive to Variation in Discrimination Factors. *Ecol. Appl.* 21, 1017–1023. doi: 10.1890/09-2409.1
- Boyle, M., Ebert, D. and Cailliet, G. (2012). Stable-Isotope Analysis of a Deep-sea Benthic-Fish Assemblage: Evidence of an Enriched Benthic Food Web. *J. Fish. Biol.* 80, 1485–1507. doi: 10.1111/j.1095-8649.2012.03243.x
- Britton, J. R. and Busst, G. M. (2018). Stable Isotope Discrimination Factors of Omnivorous Fishes: Influence of Tissue Type, Temperature, Diet Composition and Formulated Feeds. *Hydrobiologia* 808, 219–234. doi: 10.1007/s10750-017-3423-9
- Carlier, A., Riera, P., Amouroux, J.-M., Bodiou, J.-Y. and Grémare, A. (2007). Benthic Trophic Network in the Bay of Banyuls-sur-Mer (Northwest Mediterranean, France): An Assessment Based on Stable Carbon and Nitrogen Isotopes Analysis. *Estuarine. Coast. Shelf. Sci.* 72, 1–15. doi: 10.1016/j.ecss.2006.10.001
- Carpentieri, P., Serpetti, N., Colloca, F., Criscoli, A. and Ardzzone, G. (2016). Food Preferences and Rhythms of Feeding Activity of Two Co-Existing Demersal Fish, the Longspine Snipefish, *Macroramphosus scolopax* (Linnaeus 1758), and the Boarfish *Capros aper* (Linnaeus 1758), on the Mediterranean Deep Shelf. *Mar. Ecol. Prog. Ser.* 37, 106–118. doi: 10.1111/maec.12265
- Cartes, J. (1993). Feeding Habits of Ophiurid Shrimps in the Deep Western Mediterranean. *J. Mar. Biol. Assoc. United Kingdom.* 73, 193–206. doi: 10.1017/S0025315400032720
- Caut, S., Angulo, E. and Courchamp, F. (2009). Variation in Discrimination Factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): The Effect of Diet Isotopic Values and Applications for Diet Reconstruction. *J. Appl. Ecol.* 46, 443–453. doi: 10.1111/j.1365-2664.2009.01620.x
- Choy, C. A., Popp, B. N., Hannides, C. C. and Drazen, J. C. (2015). Trophic Structure and Food Resources of Epipelagic and Mesopelagic Fishes in the North Pacific Subtropical Gyre Ecosystem Inferred from Nitrogen Isotopic Compositions. *Limnology. Oceanogr.* 60, 1156–1171. doi: 10.1002/lno.10085
- Danovaro, R., Dell'anno, A., Corinaldesi, C., Magagnini, M., Noble, R., Tamburini, C., et al. (2008). Major Viral Impact on the Functioning of Benthic Deep-Sea Ecosystems. *Nature* 454, 1084–1087. doi: 10.1038/nature07268
- Davies, A. J., Roberts, J. M. and Hall-Spencer, J. (2007). Preserving Deep-Sea Natural Heritage: Emerging Issues in Offshore Conservation and Management. *Biol. Conserv.* 138, 299–312. doi: 10.1016/j.biocon.2007.05.011
- Drazen, J. C. and Sutton, T. T. (2017). Dining in the Deep: The Feeding Ecology of Deep-Sea Fishes. *Annu. Rev. Mar. Sci.* 9, 337–366. doi: 10.1146/annurev-marine-010816-060543
- Efrati, S., Lehahn, Y., Rahav, E., Kress, N., Herut, B., Gertman, I., et al. (2013). Intrusion of Coastal Waters Into the Pelagic Eastern Mediterranean: *In Situ* and Satellite-Based Characterization. *Biogeosciences* 10, 3349–3357. doi: 10.5194/bg-10-3349-2013
- Fahl, K. and Nöthig, E.-M. (2007). Lithogenic and Biogenic Particle Fluxes on the Lomonosov Ridge (central Arctic Ocean) and their Relevance for Sediment Accumulation: Vertical vs. Lateral Transport. *Deep. Sea. Res. Part I.: Oceanogr. Res. Papers.* 54, 1256–1272. doi: 10.1016/j.dsr.2007.04.014
- Fanelli, E., Azzurro, E., Bariche, M., Cartes, J. E. and Maynou, F. (2015). Depicting the Novel Eastern Mediterranean Food Web: a Stable Isotopes Study Following Lessepsian Fish Invasion. *Biol. Invasions.* 17, 2163–2178. doi: 10.1007/s10530-015-0868-5
- Fanelli, E. and Cartes, J. E. (2010). Temporal Variations in the Feeding Habits and Trophic Levels of Three Deep-Sea Demersal Fishes from the Western Mediterranean Sea, Based on Stomach Contents and Stable Isotope Analyses. *Mar. Ecol. Prog. Ser.* 402, 213–232. doi: 10.3354/meps08421
- Fanelli, E., Cartes, J. E. and Papiol, V. (2011). Food Web Structure of Deep-Sea Macrozooplankton and Micronekton Off the Catalan Slope: Insight From Stable Isotopes. *J. Mar. Syst.* 87, 79–89. doi: 10.1016/j.jmarsys.2011.03.003
- Galil, B. S., Danovaro, R., Rothman, S., Gevili, R. and Goren, M. (2019). Invasive Biota in the Deep-Sea Mediterranean: an Emerging Issue in Marine Conservation and Management. *Biol. Invasions.* 21, 281–288. doi: 10.1007/s10530-018-1826-9
- Gordon, J. D., Merrett, N. R. and Haedrich, R. L. (1995). “Environmental and Biological Aspects of Slope-Dwelling Fishes of the North Atlantic,” in *Deep-Water Fisheries of the North Atlantic Oceanic Slope* (Dordrecht, Springer), 1–26.
- Gordon, J. and Swan, S. (1997). “Deep-Water Demersal Fishes: Data for Assessment and Biological Analysis. Final Report of European Commission”. EUROPEAN COMMISSION.
- Goren, M., Mienis, H. and Galil, B. (2008). Not so Poor—More Deep-Sea Records From the Levant Sea, Eastern Mediterranean. *Mar. Biodiversity Records* (Cambridge University Press, Cambridge) 1, 1–4. doi: 10.1017/S1755267206005203
- Grossowicz, M., Sisma-Ventura, G. and Gal, G. (2019). Using Stable Carbon and Nitrogen Isotopes to Investigate the Impact of Desalination Brine Discharge on Marine Food Webs. *Front. Mar. Sci.* 6, 142. doi: 10.3389/fmars.2019.00142
- Hannides, C. C., Zervoudaki, S., Frangoulis, C. and Lange, M. A. (2015). Mesozooplankton Stable Isotope Composition in Cyprian Coastal Waters and Comparison with the Aegean Sea (Eastern Mediterranean). *Estuarine. Coast. Shelf. Sci.* 154, 12–18. doi: 10.1016/j.ecss.2014.12.009
- Hazan, O., Silverman, J., Sisma-Ventura, G., Ozer, T., Gertman, I., Shoham-Fridler, E., et al. (2018). Mesopelagic Prokaryotes Alter Surface Phytoplankton Production During Simulated Deep Mixing Experiments in Eastern Mediterranean Sea Waters. *Front. Mar. Sci.* 5, 1. doi: 10.3389/fmars.2018.00001
- Helm, K. P., Bindoff, N. L. and Church, J. A. (2011). Observed Decreases in Oxygen Content of the Global Ocean. *Geophys. Res. Lett.* 38, 1–6. doi: 10.1029/2011GL049513
- Hopkins, T. and Gartner, J. (1992). Resource-Partitioning and Predation Impact of a Low-Latitude Myctophid Community. *Mar. Biol.* 114, 185–197. doi: 10.1007/BF00349518
- Hunt, B. P., Carlotti, F., Donoso, K., Pagano, M., Dortenzio, F., Taillandier, V., et al. (2017). Trophic Pathways of Phytoplankton Size Classes Through the Zooplankton Food Web Over the Spring Transition Period in the North-West Mediterranean Sea. *J. Geophys. Research.: Oceans.* 122, 6309–6324. doi: 10.1002/2016JC012658
- Jackson, A. L., Inger, R., Parnell, A. C. and Bearhop, S. (2011). Comparing Isotopic Niche Widths Among and Within Communities: SIBER—Stable Isotope Barycenter Ellipses in R. *J. Anim. Ecol.* 80, 595–602. doi: 10.1111/j.1365-2656.2011.01806.x
- Jackson, A. and Parnell, A. (2021). *Package 'SIBER'. R Package Version 2.1.4.*
- Katz, T., Weinstein, Y., Alkalay, R., Biton, E., Toledo, Y., Lazar, A., et al. (2020). The First Deep-Sea Mooring Station in the Eastern Levantine Basin (DeepLev), Outline and Insights Into Regional Sedimentological Processes. *Deep. Sea. Res. Part II.: Topical. Stud. Oceanogr.* 171, 104663. doi: 10.1016/j.dsr2.2019.104666
- Kelly, C., Connolly, P. and Clarke, M. (1998). *The Deep Water Fisheries of the Rockall Trough: Some Insights Gleaned From Irish Survey Data.* CES CM. O:40, 22 pp.
- Kilongo, K., Barros, P. and Diehdiou, M. (2007). Diet of Large-Eye Dentex *Macrophthalmus* (Pisces: Sparidae) Off Angola and Namibia. *Afr. J. Mar. Sci.* 29, 49–54. doi: 10.2989/AJMS.2007.29.1.4.69
- Kim, H., Lee, K., Lim, D.-I., Nam, S.-I., Hee Han, S., Kim, J., et al. (2019). Increase in Anthropogenic Mercury in Marginal Sea Sediments of the Northwest Pacific Ocean. *Sci. Total. Environ.* 654, 801–810. doi: 10.1016/j.scitotenv.2018.11.076
- Koppelman, R., Böttger-Schnack, R., Möbius, J. and Weikert, H. (2009). Trophic Relationships of Zooplankton in the Eastern Mediterranean Based on Stable Isotope Measurements. *J. Plankton. Res.* 31, 669–686. doi: 10.1093/plankt/fbp013
- Koppelman, R., Weikert, H. and Lahajnar, N. (2003). Vertical Distribution of Mesozooplankton and its $\delta^{15}\text{N}$ Signature at a Deep-sea Site in the Levantine Sea (Eastern Mediterranean) in April 1999. *J. Geophys. Research.: Oceans.* 108, 1–11. doi: 10.1029/2002JC001351
- Koslow, J. A. (1993). Community structure in North Atlantic Deep-Sea Fishes. *Prog. Oceanogr.* 31, 321–338. doi: 10.1016/0079-6611(93)90005-X
- Kress, N., Gertman, I. and Herut, B. (2014). Temporal Evolution of Physical and Chemical Characteristics of the Water Column in the Easternmost Levantine Basin (Eastern Mediterranean Sea) from 2002 to 2010. *J. Mar. Syst.* 135, 6–13. doi: 10.1016/j.jmarsys.2013.11.016
- Kröncke, I., Türkay, M. and Fiege, D. (2003). Macrofauna Communities in the Eastern Mediterranean Deep Sea. *Mar. Ecol. Prog. Ser.* 24, 193–216. doi: 10.1046/j.0173-9565.2003.00825.x
- Layman, C. A., Arrington, D. A., Montaña, C. G. and Post, D. M. (2007). Can Stable Isotope Ratios Provide for Community-Identities Measures of Trophic Structure? *Ecology* 88, 42–48. doi: 10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2
- Liu, M., Xiao, W., Zhang, Q., Shi, L., Wang, X. and Xu, Y. (2020). Methylmercury Bioaccumulation In Deepest Ocean Fauna: Implications For Ocean Mercury

- Biotransport Through Food Webs. *Environ. Sci. Technol. Lett.* 7, 469–476. doi: 10.1021/acs.estlett.0c00299
- Malpica-Cruz, L., Herzka, S. Z., Sosa-Nishizaki, O. and Lazo, J. P. (2012). Tissue-Specific Isotope Trophic Discrimination Factors And Turnover Rates In A Marine Elasmobranch: Empirical And Modeling Results. *Can. J. Fisheries. Aquat. Sci.* 69, 551–564. doi: 10.1139/f2011-172
- Menezes, G. M., Sigler, M. F., Silva, H. M. and Pinho, M. R. (2006). Structure And Zonation Of Demersal Fish Assemblages Off The Azores Archipelago (Mid-Atlantic). *Mar. Ecol. Prog. Ser.* 324, 241–260. doi: 10.3354/meps324241
- Mengerink, K. J., Van Dover, C. L., Ardron, J., Baker, M., Escobar-Briones, E., Gjerde, K., et al. (2014). A Call For Deep-Ocean Stewardship. *Science* 344, 696–698. doi: 10.1126/science.1251458
- Miller, T. W., Brodeur, R. D. and Rau, G. H. (2008). Carbon Stable Isotopes Reveal Relative Contribution Of Shelf-Slope Production To The Northern California Current Pelagic Community. *Limnology. Oceanogr.* 53, 1493–1503. doi: 10.4319/lo.2008.53.4.1493
- Neat, F., Burns, F. and Drewery, J. (2008). The Deepwater Ecosystem Of The Continental Shelf Slope And Seamounts Of The Rockall Trough: A Report On The Ecology And Biodiversity Based On Frs Scientific Surveys. *Fisheries. Res. Serv. Internal Rep.*, 1–30.
- Ogrinc, N., Monperrus, M., Kotnik, J., Fajon, V., Vidimova, K., Amouroux, D., et al. (2007). Distribution Of Mercury And Methylmercury In Deep-Sea Surficial Sediments Of The Mediterranean Sea. *Mar. Chem.* 107, 31–48. doi: 10.1016/j.marchem.2007.01.019
- Olin, J. A., Hussey, N. E., Grgicak-Mannion, A., Fritts, M. W., Wintner, S. P. and Fisk, A. T. (2013). Variable $\Delta 15\text{N}$ Diet-Tissue Discrimination Factors Among Sharks: Implications For Trophic Position, Diet And Food Web Models. *PLoS One* 8, e77567. doi: 10.1371/journal.pone.0077567
- Ozer, T., Gertman, I., Kress, N., Silverman, J. and Herut, B. (2017). Interannual Thermohaline, (1979–2014) And Nutrient, (2002–2014) Dynamics In The Levantine Surface And Intermediate Water Masses, Se Mediterranean Sea. *Global Planetary. Change* 151, 60–67. doi: 10.1016/j.gloplacha.2016.04.001
- Pajuelo, J. G., Seoane, J., Biscoito, M., Freitas, M. and González, J. A. (2016). Assemblages Of Deep-Sea Fishes On The Middle Slope Off Northwest Africa (26–33 N, Eastern Atlantic). *Deep. Sea. Res. Part I.: Oceanogr. Res. Papers.* 118, 66–83. doi: 10.1016/j.dsr.2016.10.011
- Pakhomov, E., Perissinotto, R. and McQuaid, C. (1996). Prey Composition And Daily Rations Of Myctophid Fishes In The Southern Ocean. *Mar. Ecol. Prog. Ser.* 134, 1–14. doi: 10.3354/meps134001
- Papiol, V., Cartes, J. E., Fanelli, E. and Rumolo, P. (2013). Food Web Structure And Seasonality Of Slope Megafauna In The Nw Mediterranean Elucidated By Stable Isotopes: Relationship With Available Food Sources. *J. Sea. Res.* 77, 53–69. doi: 10.1016/j.seares.2012.10.002
- Parzanini, C., Parrish, C. C., Hamel, J.-F. and Mercier, A. (2019). Reviews And Syntheses: Insights Into Deep-Sea Food Webs And Global Environmental Gradients Revealed By Stable Isotope ($\Delta 15\text{N}$, $\Delta 13\text{C}$) And Fatty Acid Trophic Biomarkers. *Biogeosciences* 16, 2837–2856. doi: 10.5194/bg-16-2837-2019
- Pecquerie, L., Nisbet, R. M., Fablet, R., Lorrain, A. and Kooijman, S. A. (2010). The Impact Of Metabolism On Stable Isotope Dynamics: A Theoretical Framework. *Philos. Trans. R. Soc. B.: Biol. Sci.* 365, 3455–3468. doi: 10.1098/rstb.2010.0097
- Péres, J. (1985). History Of The Mediterranean Biota And The Colonization Of The Depths. *Western. Mediterr.* 1, 198–232.
- Peterson, B. J. and Fry, B. (1987). Stable Isotopes In Ecosystem Studies. *Annu. Rev. Ecol. systematics.* 18, 293–320. doi: 10.1146/annurev.es.18.110187.001453
- Polis, G. A. and Strong, D. R. (1996). Food Web Complexity And Community Dynamics. *Am. Nat.* 147, 813–846. doi: 10.1086/285880
- Polunin, N., Morales-Nin, B., Pawsey, W., Cartes, J. E., Pinnegar, J. K. and Moranta, J. (2001). Feeding Relationships In Mediterranean Bathyal Assemblages Elucidated By Stable Nitrogen And Carbon Isotope Data. *Mar. Ecol. Prog. Ser.* 220, 13–23. doi: 10.3354/meps220013
- Post, D. M. (2002). Using Stable Isotopes To Estimate Trophic Position: Models, Methods, And Assumptions. *Ecology* 83, 703–718. doi: 10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2
- Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J. and Montana, C. G. (2007). Getting To The Fat Of The Matter: Models, Methods And Assumptions For Dealing With Lipids In Stable Isotope Analyses. *Oecologia* 152, 179–189. doi: 10.1007/s00442-006-0630-x
- Protopapa, M., Koppelman, R., Zervoudaki, S., Wunsch, C., Peters, J., Parinos, C., et al. (2019). Trophic Positioning Of Prominent Copepods In The Epi-And Mesopelagic Zone Of The Ultra-Oligotrophic Eastern Mediterranean Sea. *Deep. Sea. Res. Part II.: Topical. Stud. Oceanogr.* 164, 144–155. doi: 10.1016/j.dsr2.2019.04.011
- Quezada-Romegialli, C., Jackson, A. L., Hayden, B., Kahilainen, K. K., Lopes, C. and Harrod, C. (2018). Trophic Position, An R Package For The Bayesian Estimation Of Trophic Position From Consumer Stable Isotope Ratios. *Methods Ecol. Evol.* 9, 1592–1599. doi: 10.1111/2041-210X.13009
- Rahav, E., Silverman, J., Raveh, O., Hazan, O., Rubin-Blum, M., Zeri, C., et al. (2019). The Deep Water Of Eastern Mediterranean Sea Is A Hotspot For Bacterial Activity. *Deep. Sea. Res. Part II.: Topical. Stud. Oceanogr.* 164, 135–143. doi: 10.1016/j.dsr2.2019.03.004
- Ramirez-Llodra, E., Brandt, A., Danovaro, R., Mol, B. D., Escobar, E., German, C. R., et al. (2010). Deep, Diverse And Definitely Different: Unique Attributes Of The World's Largest Ecosystem. *Biogeosciences* 7, 2851–2899. doi: 10.5194/bg-7-2851-2010
- R Core Team (2020). “R: A Language and Environment for Statistical Computing” (Vienna, Austria: R Foundation for Statistical Computing).
- Richards, T. M., Gipson, E. E., Cook, A., Sutton, T. T. and Wells, R. D. (2018). Trophic Ecology Of Meso-And Bathypelagic Predatory Fishes In The Gulf Of Mexico. *ICES. J. Mar. Sci.* 76, 662–672. doi: 10.1093/icesjms/tsy074
- Richards, T. M., Sutton, T. T. and Wells, R. (2020). Trophic Structure And Sources Of Variation Influencing The Stable Isotope Signatures Of Meso-And Bathypelagic Micronekton Fishes. *Front. Mar. Sci.* 7, 876. doi: 10.3389/fmars.2020.507992
- Rilov, G. and Galil, B. (2009). “Marine Bioinvasions In The Mediterranean Sea—History, Distribution And Ecology.” In *Biological Invasions In Marine Ecosystems* (Berlin Heidelberg, Springer-Verlag), 549–575.
- Romero-Romero, S., Miller, E. C., Black, J. A., Popp, B. N. and Drazen, J. C. (2021). Abyssal Deposit Feeders Are Secondary Consumers Of Detritus And Rely On Nutrition Derived From Microbial Communities In Their Guts. *Sci. Rep.* 11, 1–11. doi: 10.1038/s41598-021-91927-4
- Rubin-Blum, M., Sisma-Ventura, G., Yudkovski, Y., Belkin, N., Kanari, M., Herut, B., et al. (2022). Diversity, Activity, And Abundance Of Benthic Microbes In The Southeastern Mediterranean Sea. *FEMS Microbiol. Ecol.* 98, fiac009. doi: 10.1093/femsec/fiac009
- Sanchez-Vidal, A., Canals, M., Calafat, A. M., Lastras, G., Pedrosa-Pàmies, R., Menéndez, M., et al. (2012). Impacts On The Deep-Sea Ecosystem By A Severe Coastal Storm. *PLoS One* 7, e30395. doi: 10.1371/journal.pone.0030395
- Shipley, O. N., Brooks, E. J., Madigan, D. J., Sweeting, C. J. and Grubbs, R. D. (2017a). Stable Isotope Analysis In Deep-Sea Chondrichthyan: Recent Challenges, Ecological Insights, And Future Directions. *Rev. Fish. Biol. Fisheries.* 27, 481–497. doi: 10.1007/s11160-017-9466-1
- Shipley, O. N., Polunin, N. V., Newman, S. P., Sweeting, C. J., Barker, S., Witt, M. J., et al. (2017b). Stable Isotopes Reveal Food Web Dynamics Of A Data-Poor Deep-Sea Island Slope Community. *Food Webs.* 10, 22–25. doi: 10.1016/j.fooweb.2017.02.004
- Shoham-Frider, E., Gertner, Y., Guy-Haim, T., Herut, B., Kress, N., Shefer, E., et al. (2020). Legacy Groundwater Pollution As A Source Of Mercury Enrichment In Marine Food Web, Haifa Bay, Israel. *Sci. Total. Environ.* 714, 136711. doi: 10.1016/j.scitotenv.2020.136711
- Sisma-Ventura, G., Yam, R. and Shemesh, A. (2014). Recent Unprecedented Warming And Oligotrophy Of The Eastern Mediterranean Sea Within The Last Millennium. *Geophys. Res. Lett.* 41, 5158–5166. doi: 10.1002/2014GL060393
- Smith, C. R. and Baco, A. R. (2003). “Ecology Of Whale Falls At The Deep-Sea Floor,” in *Oceanography and Marine Biology, An Annual Review, Volume 41* (Florida, CRC Press), 319–333.
- Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L. and Semmens, B. X. (2018). Analyzing Mixing Systems Using A New Generation Of Bayesian Tracer Mixing Models. *PeerJ* 6, e5096. doi: 10.7717/peerj.5096
- Stock, B., Semmens, B., Ward, E., Parnell, A., Jackson, A. and Phillips, D. (2021). “Package ‘MixSIAR,’” in *Bayesian Mixing Models in R, Version 3*, 1.12.
- Stramma, L., Brandt, P., Schafstall, J., Schott, F., Fischer, J. and Körtzinger, A. (2008). Oxygen Minimum Zone In The North Atlantic South And East

- Of The Cape Verde Islands. *J. Geophys. Research.: Oceans*. 113, 1–15. doi: 10.1029/2007JC004369
- Stramma, L., Schmidtko, S., Levin, L. A. and Johnson, G. C. (2010). Ocean Oxygen Minima Expansions And Their Biological Impacts. *Deep. Sea. Res. Part I: Oceanogr. Res. Papers*. 57, 587–595. doi: 10.1016/j.dsr.2010.01.005
- Suchanek, T. H., Williams, S. L., Ogden, J. C., Hubbard, D. K. and Gill, I. P. (1985). Utilization Of Shallow-Water Seagrass Detritus By Caribbean Deep-Sea Macrofauna: $\delta^{13}C$ evidence. *Deep. Sea. Res. Part A. Oceanogr. Res. Papers*. 32, 201–214. doi: 10.1016/0198-0149(85)90028-7
- Sweeting, C., Barry, J., Barnes, C., Polunin, N. and Jennings, S. (2007). Effects Of Body Size And Environment On Diet-Tissue $\Delta^{15}N$ Fractionation In Fishes. *J. Exp. Mar. Biol. Ecol.* 340, 1–10. doi: 10.1016/j.jembe.2006.07.023
- Tecchio, S., Coll, M. and Sardà, F. (2015). Structure, Functioning, And Cumulative Stressors Of Mediterranean Deep-Sea Ecosystems. *Prog. Oceanogr.* 135, 156–167. doi: 10.1016/j.pocean.2015.05.018
- Tecchio, S., Van Oevelen, D., Soetaert, K., Navarro, J. and Ramírez-Llodra, E. (2013). Trophic Dynamics Of Deep-Sea Megabenthos Are Mediated By Surface Productivity. *PLoS One* 8, e63796. doi: 10.1371/journal.pone.0063796
- Thiel, H. (1983). Meiobenthos and nanobenthos of the deep sea. in: G. Rowe (ed.), *Deep-Sea Biology*. Wiley, New York. pp. 167–230
- Thurber, A. R., Sweetman, A. K., Narayanaswamy, B. E., Jones, D. O., Ingels, J. and Hansman, R. (2014). Ecosystem Function And Services Provided By The Deep Sea. *Biogeosciences* 11, 3941–3963. doi: 10.5194/bg-11-3941-2014
- Trueman, C., Johnston, G., O’hea, B. and Mackenzie, K. (2014). Trophic Interactions Of Fish Communities At Midwater Depths Enhance Long-Term Carbon Storage And Benthic Production On Continental Slopes. *Proc. R. Soc. B.: Biol. Sci.* 281, 20140669. doi: 10.1098/rspb.2014.0669
- Valls, M., Olivar, M. P., De Puellas, M. F., Molí, B., Bernal, A. and Sweeting, C. (2014). Trophic Structure Of Mesopelagic Fishes In The Western Mediterranean Based On Stable Isotopes Of Carbon And Nitrogen. *J. Mar. Syst.* 138, 160–170. doi: 10.1016/j.jmarsys.2014.04.007
- Walsh, J. J. (1991). Importance Of Continental Margins In The Marine Biogeochemical Cycling Of Carbon And Nitrogen. *Nature* 350, 53–55. doi: 10.1038/350053a0
- Winemiller, K. O. and Polis, G. A. (1996). “Food Webs: What Can They Tell Us About The World?” in *Food Webs* (New York, NY: Springer), 1–22.
- Yasuhara, M., Cronin, T. M., Demenocal, P. B., Okahashi, H. and Linsley, B. K. (2008). Abrupt Climate Change And Collapse Of Deep-Sea Ecosystems. *Proc. Natl. Acad. Sci.* 105, 1556–1560. doi: 10.1073/pnas.0705486105
- Zorica, B., Ezgeta-Balić, D., Vidjak, O., Vuletin, V., Šestanović, M., Isajlović, I., et al. (2021). Diet Composition And Isotopic Analysis Of Nine Important Fisheries Resources In The Eastern Adriatic Sea (Mediterranean). *Front. Mar. Sci.* 8, 183. doi: 10.3389/fmars.2021.609432

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s Note: All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Copyright © 2022 Guy-Haim, Stern and Sisma-Ventura. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.