universität wien

DIPLOMARBEIT / DIPLOMA THESIS

Titel der Diplomarbeit / Title of the Diploma Thesis

„Temporal dynamics of molluscan assemblages in the Levantine basin under the pressure of the Erythrean invasion“

verfasst von / submitted by

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angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Magistra der Naturwissenschaften (Mag.rer.nat.)

Wien, 2018 / Vienna, 2018

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	A 190 445 344
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Lehramtstudium UF Biologie und Umweltkunde UF Englisch
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1. Introduction

1.1. The Mediterranean Sea and the Suez Canal

Over the past decades, the dramatic spread of alien species in the Mediterranean Sea has gained increased interest as it was recognized to have severe impacts on human health and economy (Galil and Zenetos 2002; Streftaris and Zenetos 2006; Galil 2012). But jellyfish affecting tourism, fisheries and coastal installations are only the tip of the iceberg of a bioinvasion whose effects and magnitude are still only little understood. So far, research has shown that over the last hundred and fifty years hundreds of tropical and subtropical marine species have entered the Mediterranean Sea. Accordingly, the Mediterranean Sea is under the pressure of the most impactful contemporary marine bioinvasion. It holds the record not only in number of alien species recorded and in duration of invasive processes, but also in the unprecedented rate of introduction (Safriel 2013). Although it can be assumed that the intentional and unintentional transport of marine organisms into the Mediterranean dates back several thousand years (Galil 2012), it was the man-made connection of the Mediterranean Sea with the Red Sea via the Suez Canal in 1869 that unleashed a bioinvasion of the magnitude we are witnessing today.

1.2. The Erythrean invasion

For decades, this bioinvasion was known as the “Lessepsian migration”, a term that was coined by Por (1969). “Lessepsian” refers to Ferdinand Lesseps who developed the project of the Suez Canal. The term “migration”, however, may be misleading as in ecological context it describes seasonal movement. Therefore, it is more accurate to use the term “invasion” which is used in ecology when an alien species is by means of human actions introduced into a new habitat, which lies outside its potential range, and survives, reproduces and disperses there (Richardson and Pyšek 2008). Hence, today the term “Lessepsian migration” is widely replaced by the term “Erythrean invasion”, where Erythrean points towards the biogeographic origin of the invading species.

In its early days, only few species were reported to pass the Suez Canal, but the situation has changed. The canal is an economically important and highly navigated waterway; therefore, it has undergone continuous enlargement. Starting at a length of 164km and a cross sectional area of 304m² in 1869, it measured a length of 193km and the cross sectional area was increased by the factor of 17 to 5200m² in 2010 (Suez Canal Authority 2017). The abiotic factors in the channel have always been challenging for marine life, foremost the high but unstable levels of salinity (El-Sabh 1968; Por 1964). Initially, the high salinity of the Bitter Lakes, which contribute to the canal system, provided an insurmountable

barrier for most species; however, today the increase of the canal's cross section and the subsequent decrease of salinity in the Bitter Lakes facilitate the passage for marine life (Hewitt et al. 2006). There are various possible pathways for marine organisms to transit the canal, but the route and means of alien species introduction are rarely known from direct evidence. On the one side, nektonic species can actively swim through the canal. On the other side, crossing the canal can be achieved by planktonic larvae which are carried by the currents, or by successfully invading the canal itself or both (Safriel 2013). Additionally, there is human-assisted transport, which includes transport of ship fouling species on vessels and planktonic larvae in ship's ballast water (Safriel 2013).

The exchange between the two artificially connected seas is strikingly one-sided; far more species originating from the Red Sea reach the Mediterranean Sea than the other way round. There are various reasons for this asymmetry. First, species that are native to the Red Sea are adapted to higher degrees of salinity (~ 42‰) (Lieske and Myers 2010), and are therefore more likely to survive inside the canal. Second, it was suggested that the environmental conditions and the community structure in the Mediterranean favor Erythrean invaders as these are adapted to wider temperature ranges, higher maximal sea surface temperature, as well as higher levels of salinity (Safriel 2013; Por 2010). In contrast, colonizers from the Mediterranean, which are adapted to salinity levels of ~39‰, struggle to establish in the Red Sea (Por 1978). In general, it was found that ecosystems with environmental conditions similar to the native habitat of invasive species, which are in addition characterized by habitat disturbances, low species diversity, few natural enemies and high environmental heterogeneity, are more susceptible to invasions (Chan and Briski 2017). Hence, Red Sea species encounter favorable conditions in the Mediterranean Sea, whereas Mediterranean species meet various abiotic and biotic obstacles in the Red Sea. Last, the current system inside the Suez Canal was found to favor the transport of propagules from the Red Sea to the Mediterranean (Agur and Safriel 1981).

Over 660 non-native marine metazoan species have already passed the Suez Canal and settled in the eastern Mediterranean Sea, and sightings of new aliens are recorded every month (Galil 2009). The highest number of alien species can be found in the Levantine basin which is in close proximity to the opening of the Suez Canal, but various alien Levantine species have been recorded from the westernmost Mediterranean (Galil 2012) and a further spread of already established but also new alien species must be expected. Already in the early 20th century, researchers claimed that the invaders have the capacity to disrupt the stability of the Mediterranean basin (Galil 2012). However, the complexity of the Mediterranean ecosystems impedes efforts to document the magnitude of effects of even single Lessepsian aliens. Hence, there is little knowledge on the impact of these newcomers on food web interactions, physical alterations of habitats, or competitive exclusion of native

species. Moreover, there is only data for conspicuous species, i.e. jellyfish, fish, and larger molluscs, that are easily distinguished from the native biota, and that occur along a frequently sampled or fished coast (Bariche, Letourneur, and Harmelin-Vivien 2004; Mienis 2002; Galil and Goren 2014). And although first records of alien species were published shortly after the opening of the Suez Canal, their spatial and temporal coverage was limited. Moreover, data for many of the small sized invertebrate phyla is entirely absent because of limited search effort, and taxonomic and biogeographic resolution (Galil 2012).

1.3. Current state of quantitative research

Only in the second half of the 20th century systematic studies started to quantitatively address the distribution and abundance of alien species. A brief overview of quantitative studies conducted in the Levantine basin will be provided in the following summary.

In 1981, Galil and Lewinsohn investigated the composition and distribution of soft-bottom benthic invertebrate assemblages offshore the Israeli coast. Their classificatory analysis revealed five large topographically coherent groups of organisms. But as those groups were only vaguely related to the substrate of the sampling site, the authors suggest that these benthic communities show a complex gradient related to their distance to the shore. Furthermore, Galil and Lewinsohn describe that sandy-mud associations were characterized by the absence of typical Atlantic-Mediterranean species and the presence of Indo-Pacific species which build thriving populations; 26 (10%) of the 245 identified species were found to be of Indo-Pacific origin (Galil and Lewinsohn 1981).

Another quantitative study was published by Tom and Galil in 1991. Its aim was to monitor the changing faunal composition, distribution and relative abundance of microbenthic fauna in Haifa Bay. Similar to the findings of Galil and Lewinsohn (1981), their study suggests that the spatial distribution of faunal associations tend to be overlapping and continuous, and furthermore, faunal assemblages are connected to sediment properties (Tom and Galil 1991). In addition, this study confirmed massive penetration of Indo-Pacific species of the sampling sites, and the authors conclude that the fauna of the collected samples might not be truly indicative of the sampled environment.

In 2011, Çinar et al. published a study on the spatio-temporal distributions of zoobenthos in Mersin Bay (Turkey), Levantine Sea. They found that the zoobenthic communities were dependent on spatial variables such as water depth and sediment structure, but were not significantly affected by seasonal changes. Moreover, the community was found to be rich of alien molluscs; aliens species accounted for 12% of the total number of species, and 31% of the total number of individuals (Çinar et al. 2012). The most dominant species were identified as *Cerithidium diplax, Corbula gibba, Bittium reticulatum*, and *Nassarius pygmaeus*, whereas *C. diplax* was also the most abundant alien species.

In 2014, Leshno et al. investigated the influence of waste-water onto the molluscan assemblages of the Israeli shelf. Their study suggests that the increasing sewage pollution caused by increasing urbanization of the Israeli coasts impacts the molluscan community. It results in a dominance of deposit feeding species which are more tolerant to water pollution, and a loss of sensitive species (Leshno et al. 2015). Regarding the composition of the molluscan assemblage, the authors found that 17% of the total of species was alien species.

The most recent quantitative study was conducted by Guarnieri et al. (2017) who quantified the patterns of invasion of shelled molluscs in soft-bottom assemblages along the Israeli coast. In comparison to the previous studies, Guarneri et al. found a strikingly higher amount of alien species (32 (30%) of 106 molluscan species were non-indigenous). Moreover, their study revealed that significant changes had taken place in the molluscan assemblages over the past ten years, which can be ascribed to a general increase of non-indigenous species. Additionally, Guarneri et al. state that both alien and native molluscan assemblages showed prominent fluctuations in abundance in space and time which might be due to interspecific competition or reactions to disturbances or environmental stress, e.g. pollution (Guarnieri et al. 2017).

In sum, quantitative research proofs the increasing abundances and impact of alien species on the benthic assemblages of the Mediterranean Sea.

1.4. Paleoecological research methods

Although quantitative sampling has been scarce, new insight into the temporal course of the Erythrean invasion can be gained from the investigation of paleoecological data. Paleoecological data yields quantitative records over temporal scales that enable us to assess long-term processes (Kosnik and Kowalewski 2016). Marine sediments are highly valuable sources of paleoecological data. The investigation of calcareous shelly remains in sediments enables us to reconstruct ecological changes and developments of the past. Countless marine organisms, like molluscs, have durable mineralized skeletons which steadily accumulate on the sea floor and contribute to marine sediments. Naturally accumulated death assemblages were shown to reliably reflect the original composition of the living assemblage, and are therefore crucial for the investigation of time-series of sedimentary cores (Kidwell 2001). Furthermore, death assemblages of molluscs have shown to be fully representative of the biodiversity of the living species from all habitat types (Warwick and Turk 2002). Thus, the investigation of molluscan shells in Mediterranean sediments has the potential to reveal processes and effects of the Erythrean invasion, and to trace back developments that occurred decades or even centuries ago.

1.5. Research questions

The aim of this project is to overcome the lack of direct records of the temporal dynamics of the Erythrean invasion by exploring a unique dataset of quantitative samples that allows insight into the past. Therefore, I have analyzed the molluscan remains of a sediment core taken on the Israeli shelf in 2017. My study provides quantitative information on the composition of the benthic molluscan assemblages at different stages of the invasion, and on how the benthic molluscan assemblages responded during the massive introduction of alien species. The long-term assessment of benthic assemblages on a large scale is essential for understanding the spread, establishment and expansion of alien species in the Mediterranean which gives reason to major ecological and socio-economical concerns.

The following research questions will be addressed:

- Are there alien species present in the core and to which sediment depths can they be found?
- Does the diversity of the molluscan assemblages change within the core?
- Which factors affect the overall diversity of the molluscan assemblage?
- Are there differences in the abundance of alien species in the different depths of the core?

2. Material and methods

2.1. Study area

The sampling was conducted on the Israeli shore, at the southeastern corner of the Mediterranean Sea, and in proximity to the opening of the Suez Canal and the Nile Delta (Fig. 1 and Fig. 2). The sampling area is located on a shallow shelf that consists of sediments transported by the Nile, and therefore the sea floor is characterized by sandy and muddy substrates. The sample (SC30) was taken at a water depth of 30 m.

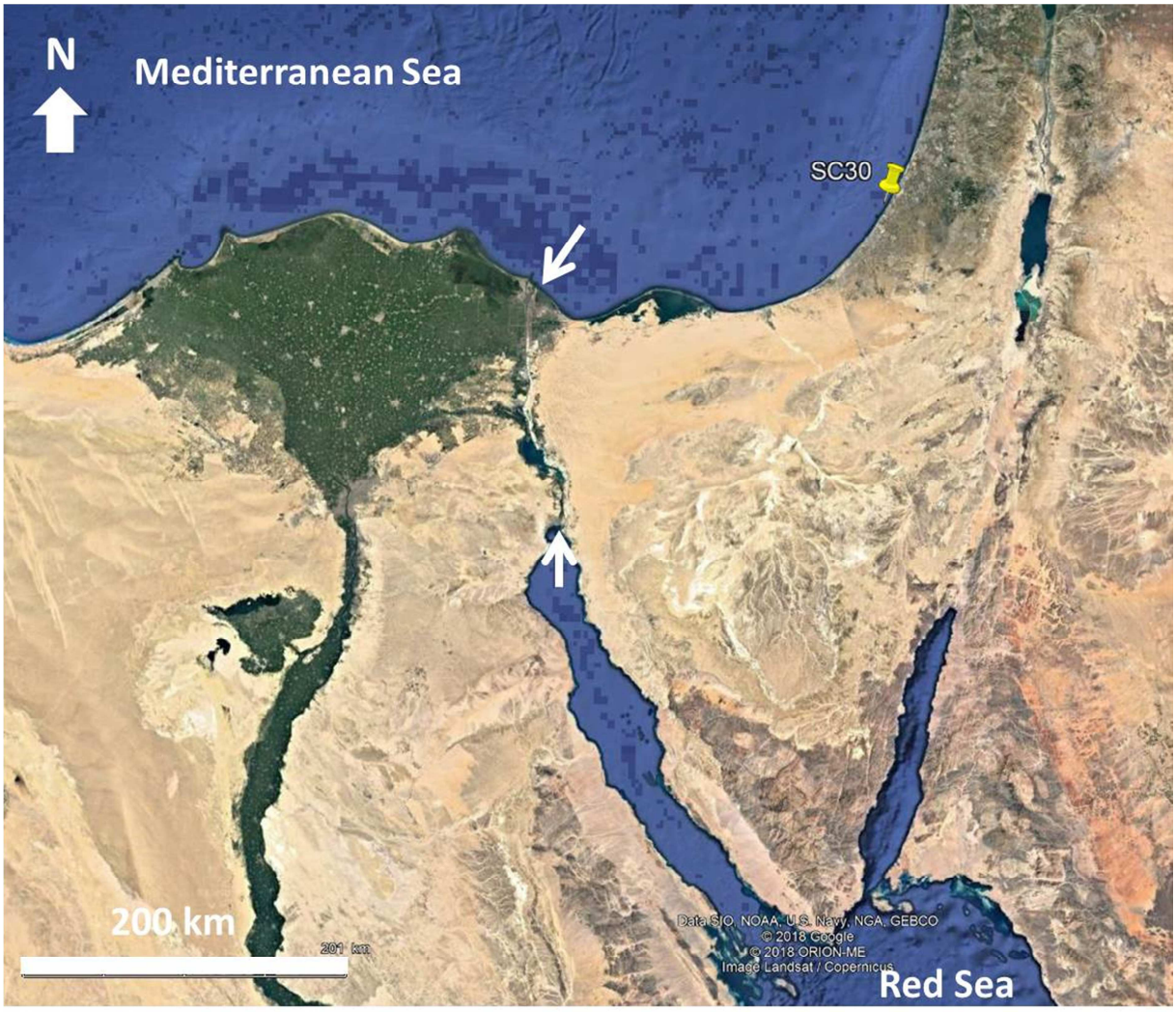

Figure 1. The sample site (SC 30) was located on the Israeli shore in the Mediterranean Sea. The openings of the Suez Canal are indicated by arrows, the River Nile and the Nile Delta are characterized by its green vegetation.

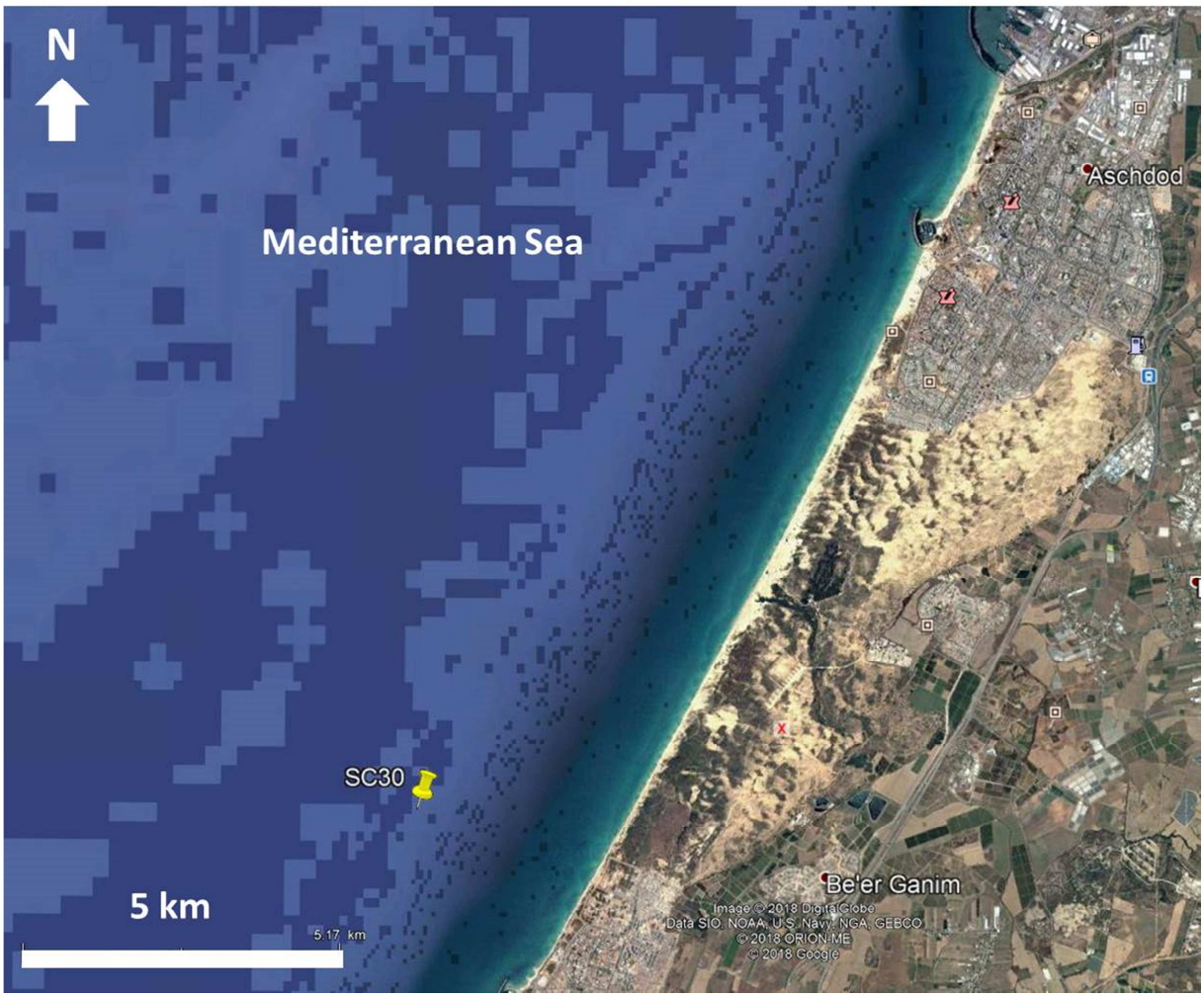

Figure 2. Sample site SC30 was located close to the Israeli coast at a water depth of 30m.

2.2. Sampling

The material for this research was provided by a research cruise in spring 2016, which was part of the project *Historical ecology of Lessepsian migration*. The sediment core was taken from a vessel at a water depth of 30 m using a metal corer. The sampling position (31°42'36.29"N, 34°32'25.98"E) was recorded by means of a global positioning system (GPS). For further processing, the core was separated into 1cm slices. The slices were dried, weighed, sieved with mesh openings of 63µm and 500µm. The fraction with particles bigger than 500µm was sorted for hard shelled organisms, and molluscs were kept separately for subsequent analysis and identification.

2.3. Species identification and counting

For efficiency reasons, only 49 out of 123 core slices were further analyzed. In order to get a representative overview of the whole core, samples were picked ever 2 to 3 cm

(represented by the slices 3, 5, 8, 10, 13, 15 …120, 123). All molluscs were identified to species level (Cossignani and Ardovini 2011; Zuschin and Oliver 2003; Smriglio 2001; D'Angelo and Gargiullo 1979; Cossignani et al. 1992; Poppe and Goto 1991, 1993) except of those individuals which were extremely broken or worn so that identification was impossible. One representative individual of each species was photographed using a microscope camera and ZEN software in order to create a collection of visual material that would optimize species identification of the project.

Due to the overall low abundance of shells within the sample, all shells that could be identified to species level were taken into account. Single bivalve shells were counted as 0.5 individual, intact bivalves, gastropods and scaphopods as 1 individual.

2.4. Statistical analysis

Univariate and multivariate statistical analyses were performed on the whole core data, between four subsections of the core, and between the assemblages of sand- and mud-dominated slices. Statistical analysis was performed with Microsoft Excel and the package PAST (Hammer, Harper, and Ryan 2001). Diversity was calculated for the overall community by comparing the total number of species and the individuals per sample; alien species diversity was illustrated as the number of alien species compared to the total number of species. Moreover, standardized species diversity was calculated by dividing the number of species by the number of individuals per sample.

In order to reduce the multispecies complexity of assemblage data into a single number, diversity indices were calculated. First, the Shannon index takes into account the number of individuals as well as the number of taxa; it varies from 0 (communities with a single taxa) to high values (communities with numerous taxa but few individuals). This index was used because it is affected by species in the middle of the rank sequence of species (at base of 10 [$H' = - S_i\ p_i\ log\ (p_i)$]; p_i is the proportion of the total count arising from the i^{th} species). Second, the Simpson index [$1\text{-}D = 1\text{-}(S\ p_i\ ^2)$] measures 'evenness' of the community from 0 to 1. It is affected by the 2-3 most abundant species. Last, evenness was calculated based on the Probability of Interspecific Encounter (PIE= $[N / (N - 1)]\,(1 - \sum_{i=1}^{S} pi^2)$; N is the number of individuals per sample, p_i is the proportion of species i in the sample)) (Olszewski and Kidwell 2007). As the PIE is not biased by sample size it allows direct comparison of evenness without the need for sample size correction (Gotelli and Graves 1996).

Non-metrical multidimensional scaling (nMDS) is a means of visualizing the level of similarity of individual cases of a dataset. All pairwise distances among samples were calculated with the Bray-Curtis distance measure. nMDS uses non-metric algorithms,

respecting only the relative ordering of the input dissimilarities (Clarke and Warwick 1997).The nMDS ordination was performed on a 2-dimension distance matrix; stress (representing goodness of the fit) was calculated with the Kruskal's method (Clarke and Warwick 1997). PERMANOVA is a non-parametric test which was used to investigate significant differences between two or more groups (Anderson 2001). Calculations were based on Bray-Curtis distance measure. SIMPER (Similarity Percentage) assesses which taxa are primarily responsible for an observed difference between groups of samples (Clarke 1993).

As the number of individuals per sample was highly variable, data for non-metric multidimensional scaling (nMDS) was standardized (i.e., relative abundances were used) and square-root transformed to deemphasize the importance of the most abundant species (Clarke and Warwick 1997). Diversity indices, PERMANOVA and SIMPER were calculated with the original data.

3. Results

3.1. Characterization of the core sediments

The core was characterized by sandy (grain size 63-500µm) and muddy (grain size <63µm) sediments. In the upper (1-41cm) and lower part (113-123cm) of the core the sediment was dominated by sand. In the middle part (42-112cm) the percentage of mud shows a considerable increase with levels from 60 to 97%.

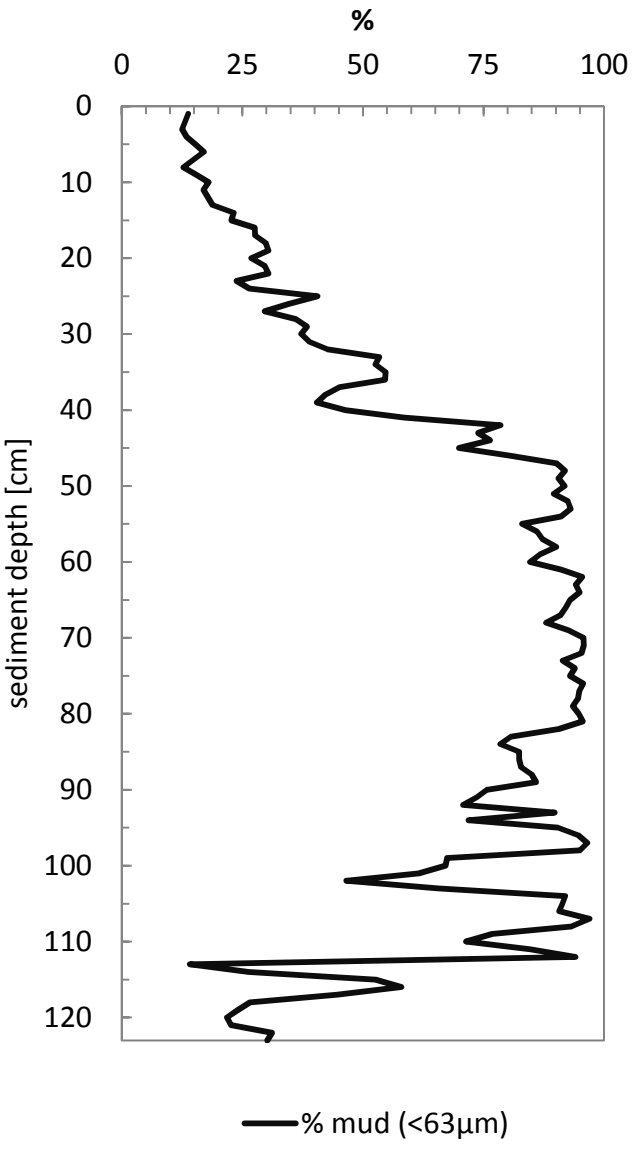

Figure 3. The percentage of mud is lower than 60% in the upper (1-41) and lower (113-123) slices, but increases to over 90% (maximum 97%) in the middle part of the core.

3.2. Basic structure of the molluscan assemblage

A total of 2920.5 individuals (calculated from articulated and disarticulated bivalves, gastropods, and scaphopods) were collected in the core. These shells represent 212 species from 70 families. A total of 54 individuals (2.02% of the total of individuals) belonging to 20 (9.43% of the total number of species) alien species were found.

3.3. Abundance of species

The species with the highest abundances were all native to the Mediterranean Sea. The most abundant species were the bivalve *Corbula gibba* and the gastropod *Ringicula auriculata* (Tab. 1). In addition, there were 9 alien bivalve species represented by 18 disarticulated and articulated shells, and 11 alien gastropod species represented by 36 individuals (Tab. 2). The most abundant alien species was *Cerithidium diplax* with a total of 15 individuals which was first recorded as an Erythrean alien in Israel in 1961.

Table 1. The ten most abundant species (each contributing more than 50 individuals (n)) were all native to the Mediterranean Sea.

Class	Family	Genus	Species	Author	n
Bivalvia	Corbulidae	*Corbula*	*gibba*	(Olivi, 1792)	668
Gastropoda	Ringiculidae	*Ringicula*	*auriculata*	(Ménard de la Groye, 1811)	339
Gastropoda	Nassariidae	*Tritia*	*pygmaea*	(Lamarck, 1822)	210
Gastropoda	Cerithiidae	*Bittium*	*reticulatum*	(da Costa, 1778)	203
Bivalvia	Nuculanidae	*Lembulus*	*pella*	(Linnaeus, 1758)	192
Scaphopoda	Dentaliidae	*Antalis*	*sp. 2*		119
Bivalvia	Semelidae	*Abra*	*alba*	(W. Wood, 1802)	104.5
Bivalvia	Nuculidae	*Nucula*	*nitidosa*	Winckworth, 1930	65.5
Bivalvia	Veneridae	*Pitar*	*rudis*	(Poli, 1795)	60.5
Bivalvia	Veneridae	*Chamelea*	*gallina*	(Linnaeus, 1758)	50.5

Table 2. A total of 20 alien species were present. The alien assemblage consisted of 9 alien bivalve species (36 individuals), and 11 alien gastropod species (18 individuals).

Class	Family	Genus	Species	Author	n	Year of first record in Israel
Gastropoda	Cerithiidae	*Cerithidium*	*diplax*	(Watson, 1886)	15	1961
Gastropoda	Cerithiidae	*Rhinoclavis*	*kochi*	(Philippi, 1848)	7	1963
Gastropoda	Pyramidellidae	*Syrnola*	*fasciata*	Jickeli, 1882	5	1949
Bivalvia	Veneridae	*Microcirce*	cf. *dilecta*	(Gould, 1861)	4	2016
Gastropoda	Scaliolidae	*Finella*	*pupoides*	A. Adams, 1860	4	1958
Bivalvia	Tellinidae	*Pseudometis*	sp.		3.5	2008
Gastropoda	Cerithiidae	*Cerithidium*	sp.		3	1961
Bivalvia	Mactridae	*Mactra*	*lilacea*	Lamarck, 1818	2.5	2001
Bivalvia	Pteriidae	*Pinctada*	*imbricata radiata*	(Leach, 1814)	2.5	1899
Bivalvia	Ungulinidae	*Transkeia*	*bogii*	van Aartsen, 2004	2	1982
Gastropoda	Retusidae	*Pyrunculus*	*fourierii*	(Audouin, 1826)	2	1989
Bivalvia	Veneridae	*Gouldiopa*	*consternans*	(Oliver & Zuschin, 2001)	1.5	2011
Bivalvia	Veneridae	*Microcirce*	sp. 2		1	2016
Gastropoda	Pyramidellidae	*Syrnola*	*lendix*	(A. Adams, 1863)	1	1994
Gastropoda	Fasciolariidae	*Fusus*	sp.		1	2016
Gastropoda	Trochidae	*Pseudominolia*	*nedyma*	(Melvill, 1897)	1	1966
Gastropoda	Pyramidellidae	*Turbonilla*	*edgarii*	(Melvill, 1896)	1	1984
Gastropoda	Amathinidae	*Amathina*	*tricarinata*	(Linnaeus, 1767)	1	2005
Bivalvia	Cardiidae	*Fulvia*	*fragilis*	(Forsskål in Niebuhr, 1775)	0.5	1955
Bivalvia	Veneridae	*Paratapes*	*textilis*	(Gmelin, 1791)	0.5	1946

3.4. Diversity of the molluscan assemblage

Species diversity is depicted as the number of species per sample (Fig. 4). High numbers of species paired with low numbers of individuals suggest high diversity. Species diversity varies considerably throughout the core. At the sediment depth of 113cm, diversity reaches its maximum of 55 species. Overall, species diversity is high in the upper part (1-45cm) and in the lowest part of the core (113-123cm), and low in the middle part of the core. In the latter, two samples (65 and 80cm) did not contain a single species.

A similar pattern can be observed in the abundance of individuals. Maximum numbers of individuals were counted in the upper part of the core with 219 individuals at the depth of 23cm and 12 individuals at the depth of 28cm, and in the lower part of the core with 286.5 individuals at 113cm sediment depth. The middle part of the core was poor in individuals, especially the interval from slice 48 to slice 98 where numbers of individuals ranged between 0 and 18.

Standardized species diversity illustrates the ratio between the number of species and the number of individuals (Fig. 5). This measure indicates peaks of diversity in the middle part (48-108cm) of the core, except slices 65 and 80, which contained zero individuals and thus result in zero standardized species diversity.

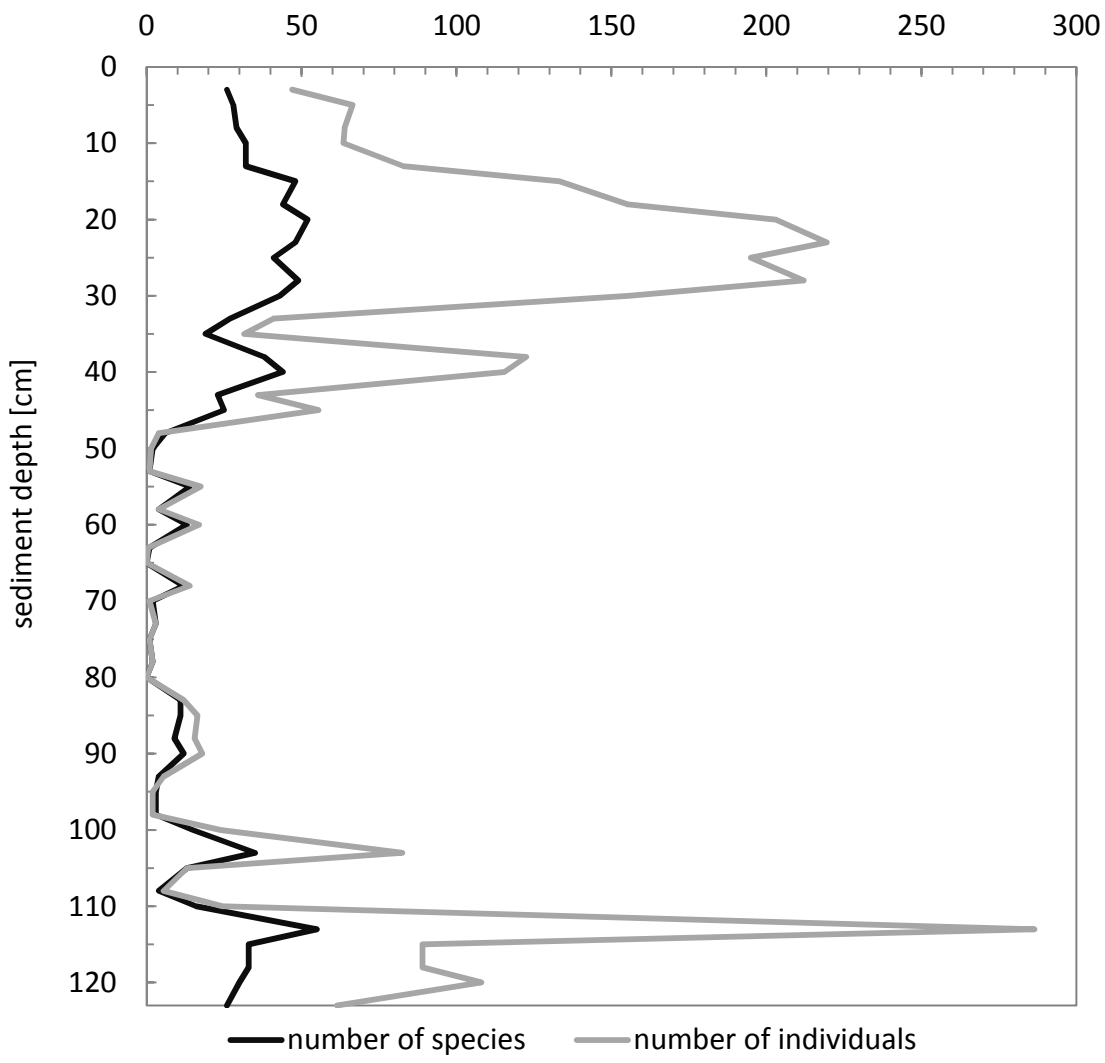

Figure 4. The number of species and the number of individuals is higher in the upper part (1-30cm) and the lowermost part (100-123cm) than in the middle part of the core.

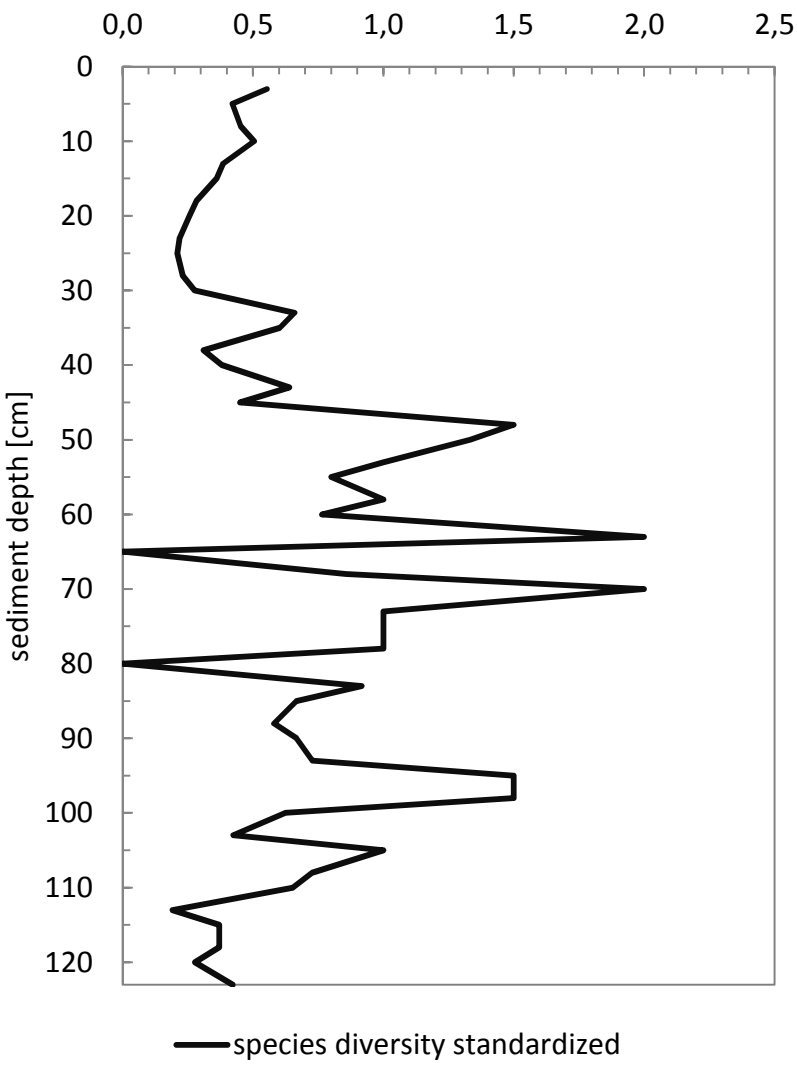

Figure 5. Standardized species diversity (number of individuals/number of species) shows high fluctuations between sediment depths of 45cm to 108cm.

3.5. Diversity indices

Shannon diversity is high and shows stable values in the upper part of the core from 1 to 45cm and the lowest part from 110 to 123cm (Tab. 3 and Fig. 6). In contrast, there are great fluctuations of the index values between the sediment depths from 48 to 108cm. The Simpson index (here given as 1-D) shows high values in the same parts of the core as the Shannon diversity index; moreover, the Simpson index shows its lowest values between 48 and 108 cm. This result indicates a strong dominance of few species in the middle part of the core, whereas the diversity in upper and lower part of the core is higher and less dominated by single species (Tab. 3 and Fig. 6).

Probability of Interspecific Encounter (PIE) shows stable values from 1 to 45cm and from 113 to 123cm sediment depth which indicates that the assemblages in that part are

characterized by high evenness (Tab 3. and Fig. 7). In contrast, in the middle part of the core between 50 and 108cm the PIE shows high variations with a maximum value of 2.07.

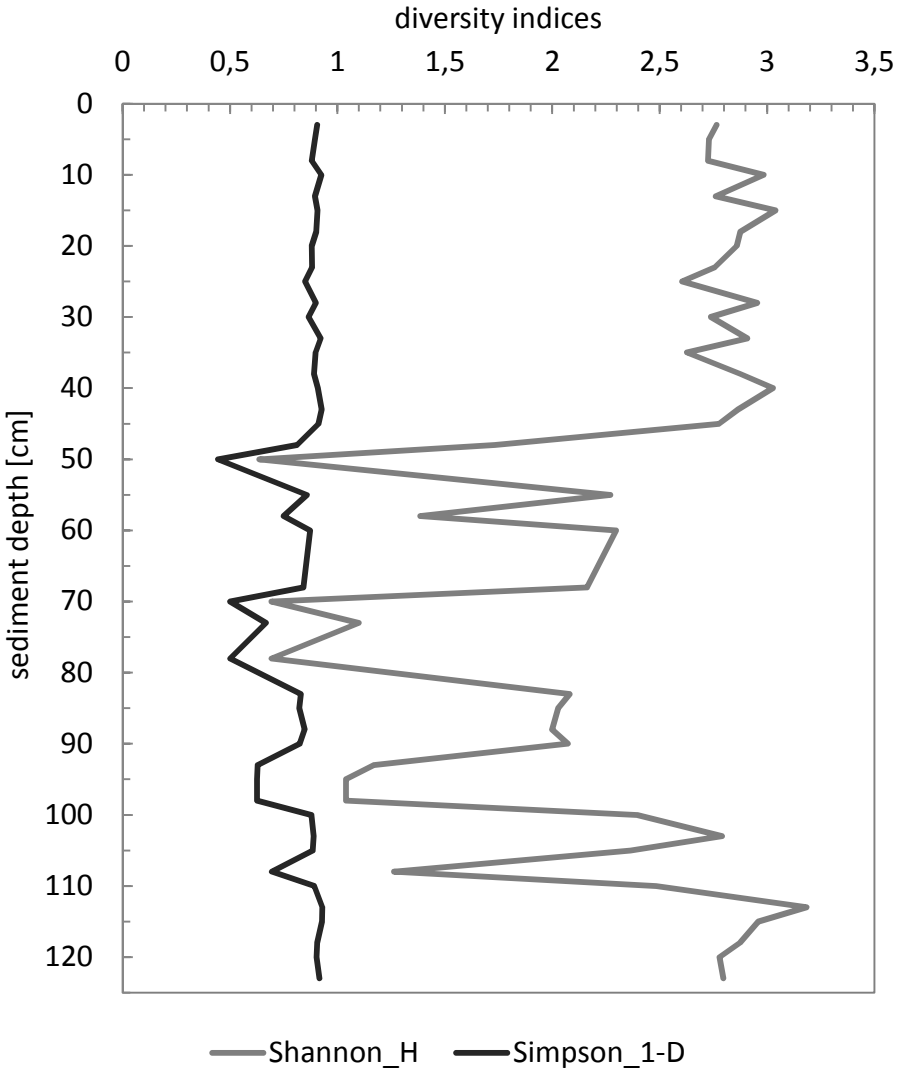

Figure 6. The Shannon index indicates high levels of diversity in the upper and lower part of the core; the Simpson (1-D) index illustrates that those samples show low dominance of single species.

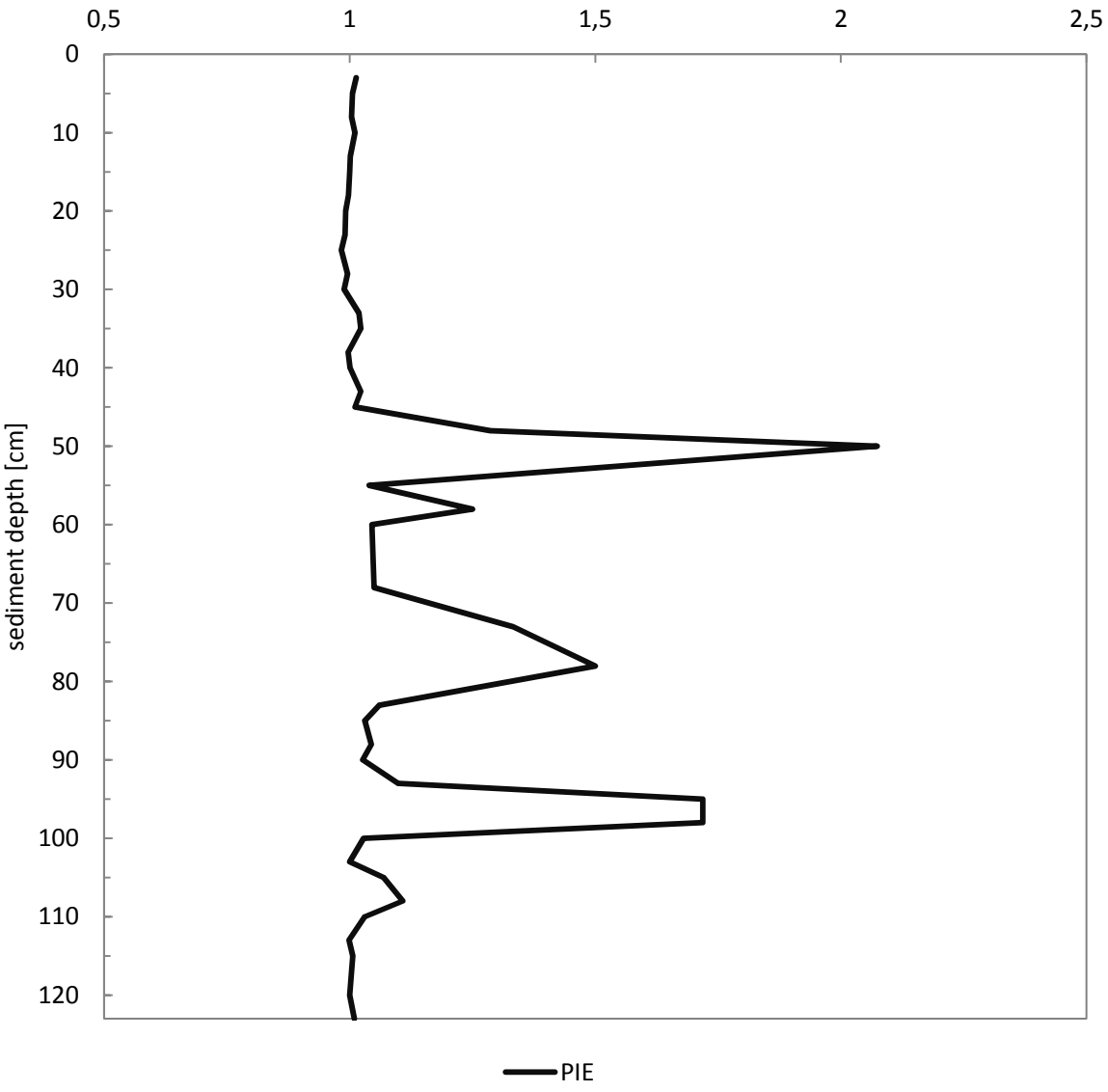

Figure 7. Probability of Interspecific Encounter (PIE) shows stable values of evenness from 1 to 45cm and from 113 to 123cm sediment depth, in between the values show high variations. Samples containing zero or one individual were excluded.

Table 3. Number of taxa and individuals, Shannon diversity index, Simpson diversity index, and PIE are depicted for each sediment depth.

sediment depth [cm]	number of taxa	number of individuals	Shannon	Simpson (1-D)	PIE
3	26	47.00	2.77	0.91	1.01
5	28	66.50	2.73	0.90	1.01
8	29	64.00	2.73	0.88	1.00
10	32	63.50	2.98	0.93	1.01
13	32	83.00	2.76	0.90	1.00
15	48	133.00	3.04	0.91	1.00
18	44	155.00	2.88	0.90	1.00
20	52	203.00	2.86	0.88	0.99
23	48	219.50	2.76	0.88	0.99
25	41	195.00	2.61	0.85	0.98
28	49	212.00	2.96	0.90	1.00
30	43	155.50	2.74	0.86	0.99
33	27	41.00	2.91	0.92	1.02
35	19	31.50	2.63	0.90	1.02
38	38	122.50	2.88	0.89	1.00
40	44	115.50	3.03	0.91	1.00
43	23	36.00	2.87	0.93	1.02
45	25	55.50	2.78	0.91	1.01
48	6	4.00	1.73	0.81	1.29
50	2	1.50	0.64	0.44	2.07
53	1	1.00	0.00	0.00	-
55	14	17.50	2.27	0.86	1.04
58	4	4.00	1.39	0.75	1.25
60	13	17.00	2.30	0.87	1.05
63	1	0.50	0.00	0.00	0.00
65	0	0	-	-	-
68	12	14.00	2.16	0.84	1.05
70	2	1.00	0.69	0.50	-
73	3	3.00	1.10	0.67	1.33
75	1	1.00	0.00	0.00	-
78	2	2.00	0.69	0.50	1.50
80	0	0	-	-	-
83	11	12.00	2.08	0.83	1.06
85	11	16.50	2.03	0.82	1.03
88	9	15.50	2.00	0.85	1.04
90	12	18.00	2.07	0.83	1.03
93	4	5.50	1.17	0.63	1.10
95	3	2.00	1.04	0.63	1.72
98	3	2.00	1.04	0.63	1.72
100	15	24.00	2.40	0.88	1.03
103	35	82.50	2.79	0.89	1.00
105	13	13.00	2.37	0.88	1.07
108	4	5.50	1.26	0.69	1.11
110	16	24.50	2.49	0.89	1.03
113	55	286.50	3.18	0.93	1.00
115	33	89.00	2.96	0.93	1.01
118	33	89.00	2.87	0.91	1.00
120	30	108.00	2.78	0.90	1.00
123	26	61.50	2.80	0.92	1.01

3.6. Alien species abundance and diversity

Alien species were found from the uppermost slices of the core down to a sediment depth of 115cm (Fig.8). Most alien individuals were found in the upper part of the core; only three samples below a sediment depth of 45cm contained any alien individuals (1 to 2 individuals). Alien species diversity was highest in the upper part of the core from 1 to 28cm sediment depth (Fig. 9). In the uppermost investigated layer (3cm), the contribution of alien species was 18%. Although some alien species were found in sediment depth below 28cm, alien species diversity was very low there, ranging between 0 and 2.

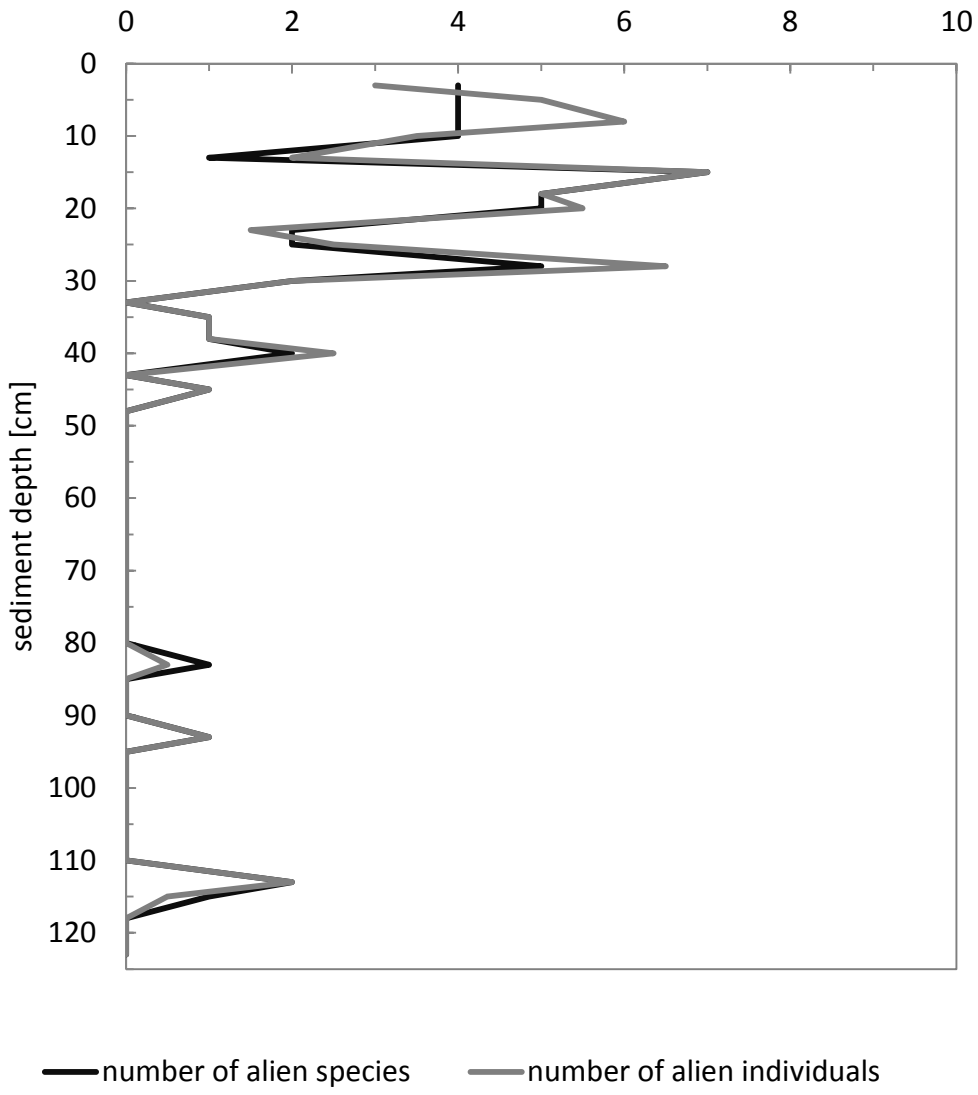

Figure 8. Highest abundances of alien individuals were present at sediment depths above 45cm.

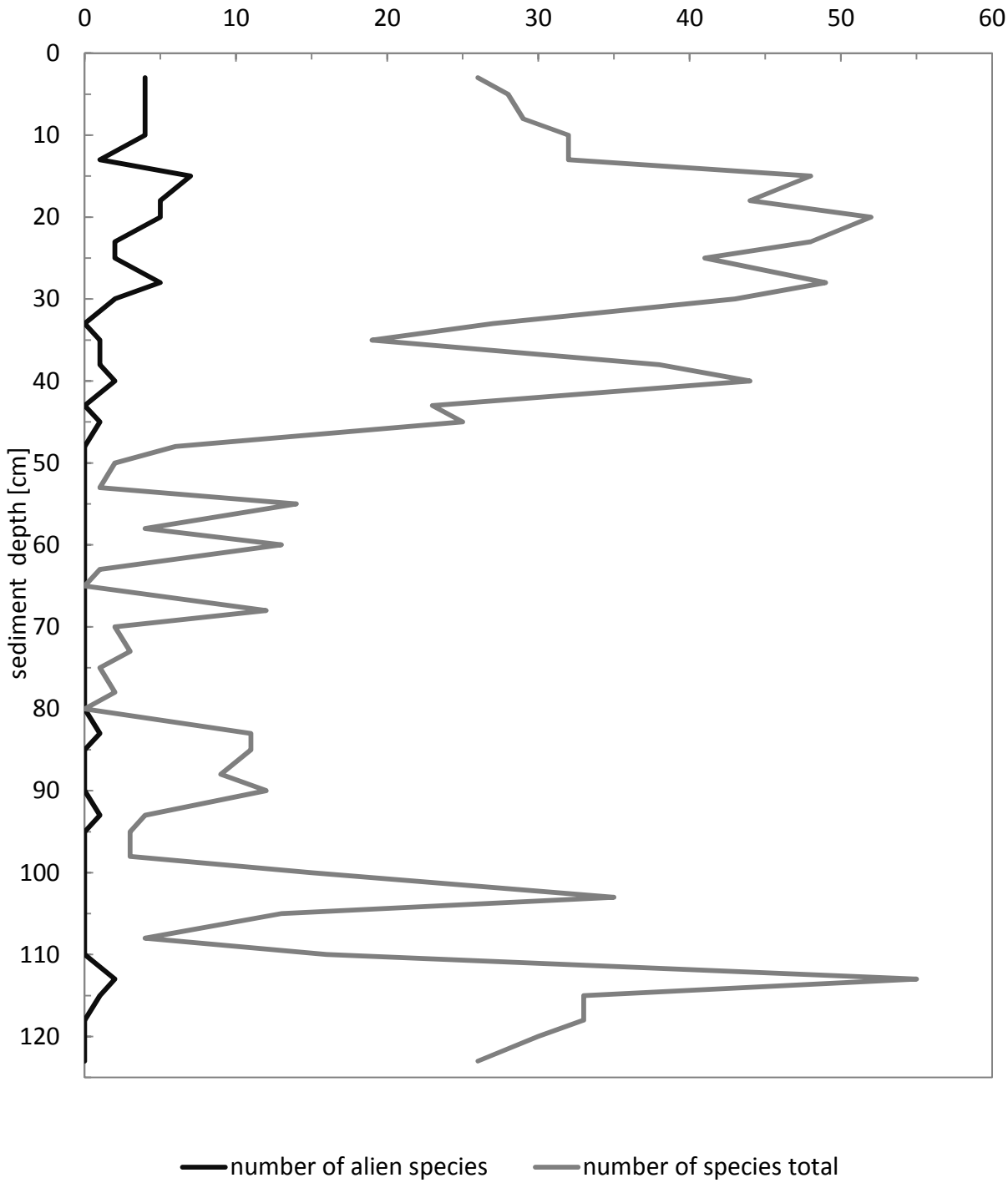

Figure 9. Alien species diversity is highest between 1-25cm sediment depths. This fraction of the core is also characterized by the highest overall species diversity.

3.7. Influence of sediment depth on the molluscan assemblage

Temporal changes of the molluscan assemblages are directly related to sediment depth. Therefore, the core was separated into four subsections which are assumed to represent four distinct periods of sedimentation. The first subsection (S1) comprises slices 3-30, the second (S2) the slices 33-60, the third (S3) the slices 63-90, and the last subsection (S4) the slices 93-123.

NMDS revealed differences in the molluscan assemblages among these four subsections (Fig. 10). Samples of the uppermost quarter of the core plot in close distance to each other as well as to some of the samples of the lowermost quarter. The samples of S3 are well separated from S1 which indicates highly distinct species compositions in these two subsections. Some samples of S2, S3, and S4 are dispersed in the ordination. This is caused by their heterogeneous molluscan compositions which are different from all other samples. NMDS stress value was 0.1495.

PERMANOVA proved that S1, the uppermost subsection was significantly different to S2 ($p=0.0002$), to S3 ($p=0$), and to S4 ($p=0.0018$) (PERMANOVA; $p<0.0001$, F: 3.812 , Bonferroni corrected, Tab. 4). Moreover, S2 was significantly different to S3 ($p=0.036$), and S3 was significantly different to S4 ($p=0.0147$). The only subsections which were not significantly different were S2 and S4.

Finally, SIMPER analysis revealed that those species that contributed most to the differences between the subsections were *Corbula gibba, Tritia pygmaea, Ringicula auriculata, Bittium reticulatum* (Tab. 5-10). These are all native Mediterranean species. Only two alien species, the gastropods *Cerithidium diplax* and *Amathina tricarinata*, were found among the twenty species that contributed most to group difference, but they were ranking low in all cases (Tab. 5, Tab. 6, Tab. 7, Tab. 10).

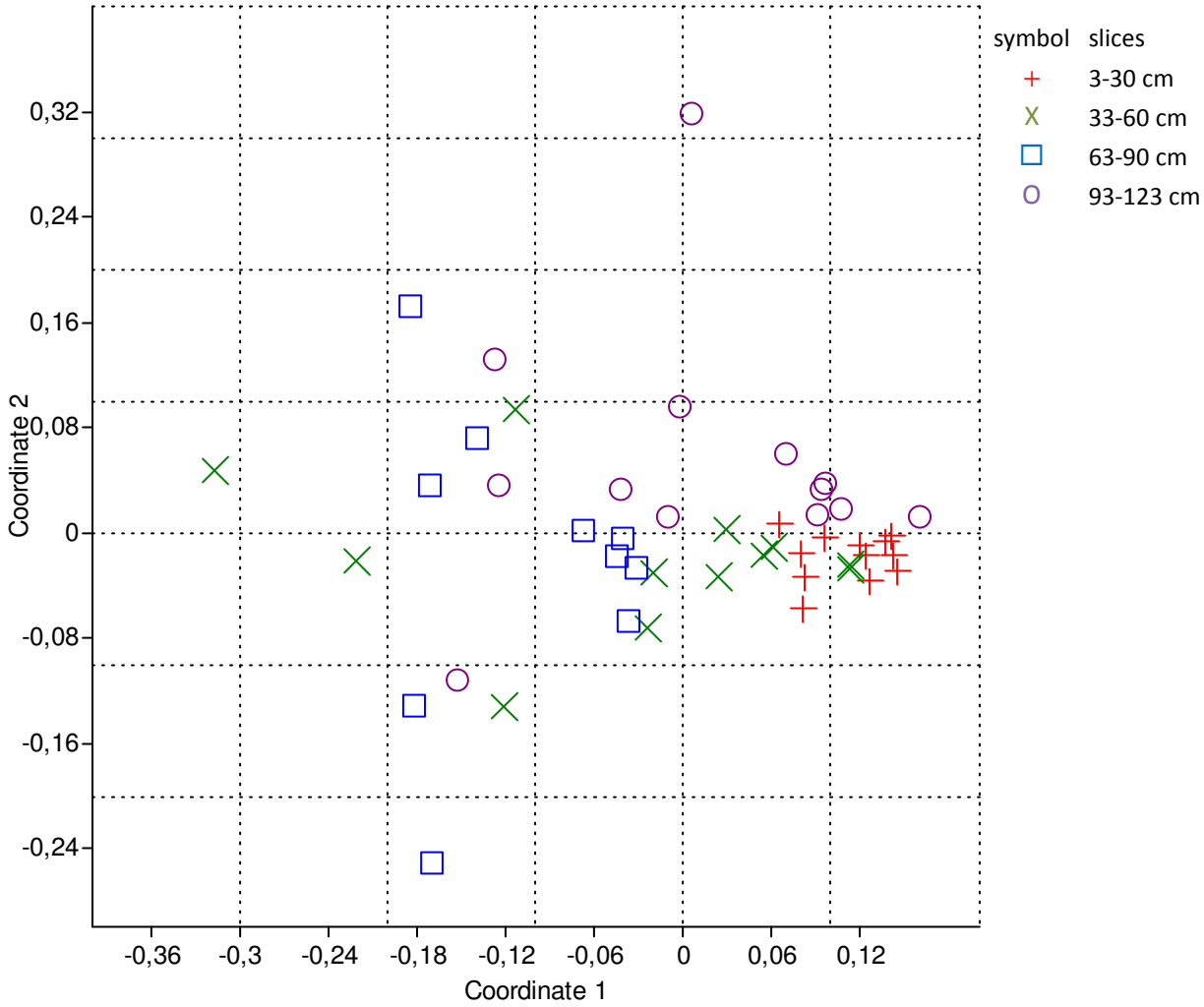

Figure 10. NMDS plots samples of the uppermost quarter of the core (red crosses) plot in close distance to each other as well as to some of the samples of the lowermost quarter (purple circle). The samples of the third quarter (blue squares) are well separated from the first quarter which indicates distinct species compositions (stress value 0.1495).

Table 4. PERMANOVA pairwise comparisons of the four subsections S1, S2, S3 and S4 ($p<0.0001$, F: 3.812, Bonferroni corrected). Significant comparisons are in bold.

Subsection	S1	S2	S3
S2	**0.0002**		
S3	**0**	**0.0360**	
S4	**0.0003**	0.2596	**0.0147**

Table 5. SIMPER reveals, which 20 species contribute most to differences among S1 and S2; alien species represented in bold.

Class	Family	Genus	Species	Author	Contribution
Bivalvia	Corbulidae	*Corbula*	*gibba*	(Olivi, 1792)	17.29
Gastropoda	Nassariidae	*Tritia*	*pygmaea*	(Lamarck, 1822)	6.40
Gastropoda	Ringiculidae	*Ringicula*	*auriculata*	(Ménard de la Groye, 1811)	6.22
Gastropoda	Cerithiidae	*Bittium*	*reticulatum*	(da Costa, 1778)	5.82
Bivalvia	Nuculanidae	*Lembulus*	*pella*	(Linnaeus, 1758)	3.15
Bivalvia	Semelidae	*Abra*	*alba*	(W. Wood, 1802)	3.06
Scaphopoda	Dentaliidae	*Antalis*	sp. 2		2.97
Bivalvia	Veneridae	*Pitar*	*rudis*	(Poli, 1795)	1.78
Bivalvia	Nuculidae	*Nucula*	*nitidosa*	Winckworth, 1930	1.55
Scaphopoda	Dentaliidae	*Antalis*	sp. 1		1.19
Gastropoda	Creseidae	*Creseis*	*clava*	(Rang, 1828)	1.05
Gastropoda	Cerithiidae	*Bittium*	*submamillatum*	(de Rayneval & Ponzi, 1854)	0.85
Gastropoda	Cerithiidae	***Cerithidium***	***diplax***	(Watson, 1886)	**0.80**
Bivalvia	Veneridae	*Chamelea*	*gallina*	(Linnaeus, 1758)	0.78
Bivalvia	Semelidae	*Abra*	*nitida*	(Müller O.F., 1776)	0.78
Bivalvia	Veneridae	*Dosinia*	cf. *lupinus*	(Linnaeus, 1758)	0.77
Bivalvia	Glycymeridae	*Glycymeris*	*nummaria*	(Linnaeus, 1758)	0.71
Bivalvia	Montacutidae	*Kurtiella*	*bidentata*	(Montagu, 1803)	0.59
Bivalvia	Cardiidae	*Acanthocardia*	*paucicostata*	(Sowerby G.B. II, 1834)	0.54
Gastropoda	Pyramidellidae	*Megastomia*	*conoidea*	(Brocchi, 1814)	0.52

Table 6. SIMPER reveals, which 20 species contribute most to differences among S1 and S3; alien species represented in bold.

Class	Family	Genus	Species	Author	Contribution
Bivalvia	Corbulidae	*Corbula*	*gibba*	(Olivi, 1792)	21.91
Gastropoda	Nassariidae	*Tritia*	*pygmaea*	(Lamarck, 1822)	8.66
Gastropoda	Ringiculidae	*Ringicula*	*auriculata*	(Ménard de la Groye, 1811)	7.77
Gastropoda	Cerithiidae	*Bittium*	*reticulatum*	(da Costa, 1778)	7.13
Bivalvia	Nuculanidae	*Lembulus*	*pella*	(Linnaeus, 1758)	3.99
Scaphopoda	Dentaliidae	*Antalis*	sp. 2		3.84
Bivalvia	Semelidae	*Abra*	*alba*	(W. Wood, 1802)	3.68
Bivalvia	Veneridae	*Pitar*	*rudis*	(Poli, 1795)	2.21
Bivalvia	Nuculidae	*Nucula*	*nitidosa*	Winckworth, 1930	2.05
Bivalvia	Veneridae	*Chamelea*	*gallina*	(Linnaeus, 1758)	1.13
Gastropoda	Cerithiidae	***Cerithidium***	***diplax***	(Watson, 1886)	**1.00**
Gastropoda	Cerithiidae	*Bittium*	*submamillatum*	(de Rayneval & Ponzi, 1854)	0.92
Scaphopoda	Dentaliidae	*Antalis*	sp. 1		0.90
Bivalvia	Veneridae	*Dosinia*	cf. *lupinus*	(Linnaeus, 1758)	0.89
Bivalvia	Glycymerididae	*Glycymeris*	*nummaria*	(Linnaeus, 1758)	0.87
Gastropoda	Creseidae	*Creseis*	*clava*	(Rang, 1828)	0.82
Bivalvia	Semelidae	*Abra*	*nitida*	(Müller O.F., 1776)	0.65
Gastropoda	Pyramidellidae	*Megastomia*	*conoidea*	(Brocchi, 1814)	0.61
Bivalvia	Montacutidae	*Kurtiella*	*bidentata*	(Montagu, 1803)	0.61
Bivalvia	Mytilidae	*Modiolus*	sp. 2		0.58

Table 7. SIMPER reveals, which 20 species contribute most to differences among S1 and S4; alien species represented in bold.

Class	Family	Genus	Species	Author	Contribution
Bivalvia	Corbulidae	*Corbula*	*gibba*	(Olivi, 1792)	15.89
Gastropoda	Nassariidae	*Tritia*	*pygmaea*	(Lamarck, 1822)	5.82
Gastropoda	Ringiculidae	*Ringicula*	*auriculata*	(Ménard de la Groye, 1811)	5.74
Gastropoda	Cerithiidae	*Bittium*	*reticulatum*	(da Costa, 1778)	5.23
Bivalvia	Nuculanidae	*Lembulus*	*pella*	(Linnaeus, 1758)	3.25
Bivalvia	Semelidae	*Abra*	*alba*	(W. Wood, 1802)	2.92
Scaphopoda	Dentaliidae	*Antalis*	sp. 2		2.68
Bivalvia	Veneridae	*Pitar*	*rudis*	(Poli, 1795)	1.64
Bivalvia	Nuculidae	*Nucula*	*nitidosa*	Winckworth, 1930	1.61
Bivalvia	Veneridae	*Chamelea*	*gallina*	(Linnaeus, 1758)	1.09
Bivalvia	Glycymerididae	*Glycymeris*	*nummaria*	(Linnaeus, 1758)	0.88
Gastropoda	Pyramidellidae	*Megastomia*	*conoidea*	(Brocchi, 1814)	0.78
Gastropoda	Cerithiidae	*Bittium*	*submamillatum*	(de Rayneval & Ponzi, 1854)	0.78
Gastropoda	Cerithiidae	***Cerithidium***	***diplax***	(Watson, 1886)	**0.76**
Gastropoda	Cerithiidae	*Cerithium*	sp. 3		0.75
Bivalvia	Veneridae	*Dosinia*	cf. *lupinus*	(Linnaeus, 1758)	0.73
Gastropoda	Rissoidae	*Alvania*	*mamillata*	Risso, 1826	0.66
Scaphopoda	Dentaliidae	*Antalis*	sp. 1		0.66
Gastropoda	Creseidae	*Creseis*	*clava*	(Rang, 1828)	0.63
Bivalvia	Semelidae	*Abra*	*nitida*	(Müller O.F., 1776)	0.59

Table 8. SIMPER reveals, which 20 species contribute most to differences among S2 and S3.

Class	Family	Genus	Species	Author	Contribution
Bivalvia	Corbulidae	*Corbula*	*gibba*	(Olivi, 1792)	14.1
Gastropoda	Ringiculidae	*Ringicula*	*auriculata*	(Ménard de la Groye, 1811)	9.29
Bivalvia	Nuculanidae	*Lembulus*	*pella*	(Linnaeus, 1758)	7.52
Gastropoda	Nassariidae	*Tritia*	*pygmaea*	(Lamarck, 1822)	6.58
Scaphopoda	Dentaliidae	*Antalis*	sp. 1		4.32
Bivalvia	Semelidae	*Abra*	*alba*	(W. Wood, 1802)	2.84
Scaphopoda	Dentaliidae	*Antalis*	sp. 2		2.64
Bivalvia	Semelidae	*Abra*	*nitida*	(Müller O.F., 1776)	2.10
Gastropoda	Creseidae	*Creseis*	*clava*	(Rang, 1828)	1.93
Bivalvia	Nuculidae	*Nucula*	*nitidosa*	Winckworth, 1930	1.75
Gastropoda	Eulimidae	*Eulima*	*glabra*	(da Costa, 1778)	1.52
Gastropoda	Cerithiidae	*Bittium*	*reticulatum*	(da Costa, 1778)	1.52
Bivalvia	Montacutidae	*Kurtiella*	*bidentata*	(Montagu, 1803)	1.39
Bivalvia	Veneridae	*Pitar*	*rudis*	(Poli, 1795)	1.29
Bivalvia	Veneridae	*Chamelea*	*gallina*	(Linnaeus, 1758)	1.19
Bivalvia	Ostreidae	*Ostrea*	sp. 2		0.94
Bivalvia	Cardiidae	*Acanthocardia*	*paucicostata*	(Sowerby G.B. II, 1834)	0.94
Gastropoda	Rissoidae	*Alvania*	*mamillata*	Risso, 1826	0.76
Gastropoda	Cerithiidae	*Cerithium*	sp. 3		0.72
Gastropoda	Iravadiidae	*Hyala*	*vitrea*	(Montagu, 1803)	0.70

Table 9. SIMPER reveals, which 20 species contribute most to differences among S2 and S4.

Class	Family	Genus	Species	Author	Contribution
Bivalvia	Corbulidae	*Corbula*	*gibba*	(Olivi, 1792)	11.24
Gastropoda	Ringiculidae	*Ringicula*	*auriculata*	(Ménard de la Groye, 1811)	9.95
Bivalvia	Nuculanidae	*Lembulus*	*pella*	(Linnaeus, 1758)	5.34
Gastropoda	Nassariidae	*Tritia*	*pygmaea*	(Lamarck, 1822)	5.14
Gastropoda	Cerithiidae	*Bittium*	*reticulatum*	(da Costa, 1778)	3.42
Scaphopoda	Dentaliidae	*Antalis*	sp. 2		3.20
Scaphopoda	Dentaliidae	*Antalis*	sp. 1		2.44
Bivalvia	Veneridae	*Chamelea*	*gallina*	(Linnaeus, 1758)	2.10
Bivalvia	Semelidae	*Abra*	*alba*	(W. Wood, 1802)	2.02
Gastropoda	Cerithiidae	*Cerithium*	sp. 3		1.75
Bivalvia	Nuculidae	*Nucula*	*nitidosa*	Winckworth, 1930	1.51
Bivalvia	Semelidae	*Abra*	*nitida*	(Müller O.F., 1776)	1.45
Gastropoda	Creseidae	*Creseis*	*clava*	(Rang, 1828)	1.25
Bivalvia	Veneridae	*Pitar*	*rudis*	(Poli, 1795)	1.09
Bivalvia	Glycymerididae	*Glycymeris*	*nummaria*	(Linnaeus, 1758)	1.02
Gastropoda	Rissoidae	*Alvania*	*mamillata*	Risso, 1826	1.01
Gastropoda	Pyramidellidae	*Megastomia*	*conoidea*	(Brocchi, 1814)	0.87
Bivalvia	Montacutidae	*Kurtiella*	*bidentata*	(Montagu, 1803)	0.87
Gastropoda	Eulimidae	*Eulima*	*glabra*	(da Costa, 1778)	0.86
Bivalvia	Donacidae	*Donax*	*venustus*	Poli, 1795	0.76

Table 10. SIMPER reveals, which 20 species contribute most to differences among S3 and S4; alien species represented in bold.

Class	Family	Genus	Species	Author	Contribution
Gastropoda	Ringiculidae	*Ringicula*	*auriculata*	(Ménard de la Groye, 1811)	13.23
Bivalvia	Corbulidae	*Corbula*	*gibba*	(Olivi, 1792)	11.95
Bivalvia	Nuculanidae	*Lembulus*	*pella*	(Linnaeus, 1758)	7.07
Gastropoda	Nassariidae	*Tritia*	*pygmaea*	(Lamarck, 1822)	5.69
Scaphopoda	Dentaliidae	*Antalis*	sp. 2		4.39
Gastropoda	Cerithiidae	*Bittium*	*reticulatum*	(da Costa, 1778)	4.00
Bivalvia	Veneridae	*Chamelea*	*gallina*	(Linnaeus, 1758)	3.09
Gastropoda	Cerithiidae	*Cerithium*	sp. 3		2.54
Bivalvia	Glycymerididae	*Glycymeris*	*nummaria*	(Linnaeus, 1758)	1.38
Bivalvia	Nuculidae	*Nucula*	*nitidosa*	Winckworth, 1930	1.20
Bivalvia	Mactridae	*Spisula*	*subtruncata*	(da Costa, 1778)	1.16
Gastropoda	Rissoidae	*Alvania*	*mamillata*	Risso, 1826	1.10
Bivalvia	Ostreidae	*Ostrea*	sp. 1		0.99
Gastropoda	Pyramidellidae	*Megastomia*	*conoidea*	(Brocchi, 1814)	0.99
Scaphopoda	Dentaliidae	*Antalis*	sp. 1		0.96
Bivalvia	Veneridae	*Callista*	*chione*	(Linnaeus, 1758)	0.92
Gastropoda	Pyramidellidae	*Parthenina*	sp. 5		0.90
Bivalvia	Donacidae	*Donax*	*venustus*	Poli, 1795	0.90
Bivalvia	Veneridae	*Pitar*	*rudis*	(Poli, 1795)	0.86
Gastropoda	Amathinidae	***Amathina***	***tricarinata***	(Linnaeus, 1767)	**0.75**

3.8. Influence of sediment type on the molluscan assemblage

As mentioned above, the sediment composition within the core was highly variable; some samples were dominated by mud and others by sand (Fig. 3). The influence of the sediment composition on the molluscan assemblages will be investigated in the following part of the results.

To begin with, Spearman's r_s showed that muddy sediments are significantly correlated to the number of individuals, the number of species, and the number of alien species in a sample (Tab. 11). First, the higher the content of mud in a sample, the less individuals were present (r_s= -0.88271; p<0.0001). Second, the higher the mud content in the sediment, the lower the overall species diversity of a sample (r_s= -0.87286; p<0.0001), and the lower the number of alien species in a sample (r_s= -0.65519; p<0.0001).

To further investigate the influence of sediment type on the molluscan assemblages the slices were assigned to two distinct groups. All slices with a proportion of mud higher than 60% were united to the group of mud-dominated samples (42 - 112cm); second, the rest of the samples formed the group of sand-dominated samples (1 - 40cm and 113 - 123cm). These two groups were used to plot an nMDS which visualizes similarities and differences among samples. The ordination shows muddy and sandy substrates as two distinct groups indicating distinct species composition in these two sediment types (Fig. 11). The samples of the sandy substrate plot close together, whereas the samples of the muddy substrate are more dispersed in the ordination, and thus indicate a more heterogeneous molluscan composition. However, two of the muddy samples (sediment depths 45 and 103cm) plot in close distance to the sandy samples signaling a high similarity of species composition. This is because both slices represent the boundaries of the two sediments types (see also Fig. 3). The stress value for the nMDS was 0.1495. Consequently, the scaling still gives a potentially usefully picture.

PERMANOVA confirmed that the differences between the molluscan assemblages in muddy and sandy substrates were significant (PERMANOVA; p<0.0001, F: 12.92 , Bonferroni corrected). SIMPER analysis was performed to investigate which species contributed most to the differences among muddy and sandy substrates. The species contributing most were *Corbula gibba*, *Ringicula auriculata*, *Tritia pygmaea* and *Bittium reticulatum*, which are all native to the Mediterranean Sea (Tab. 12).

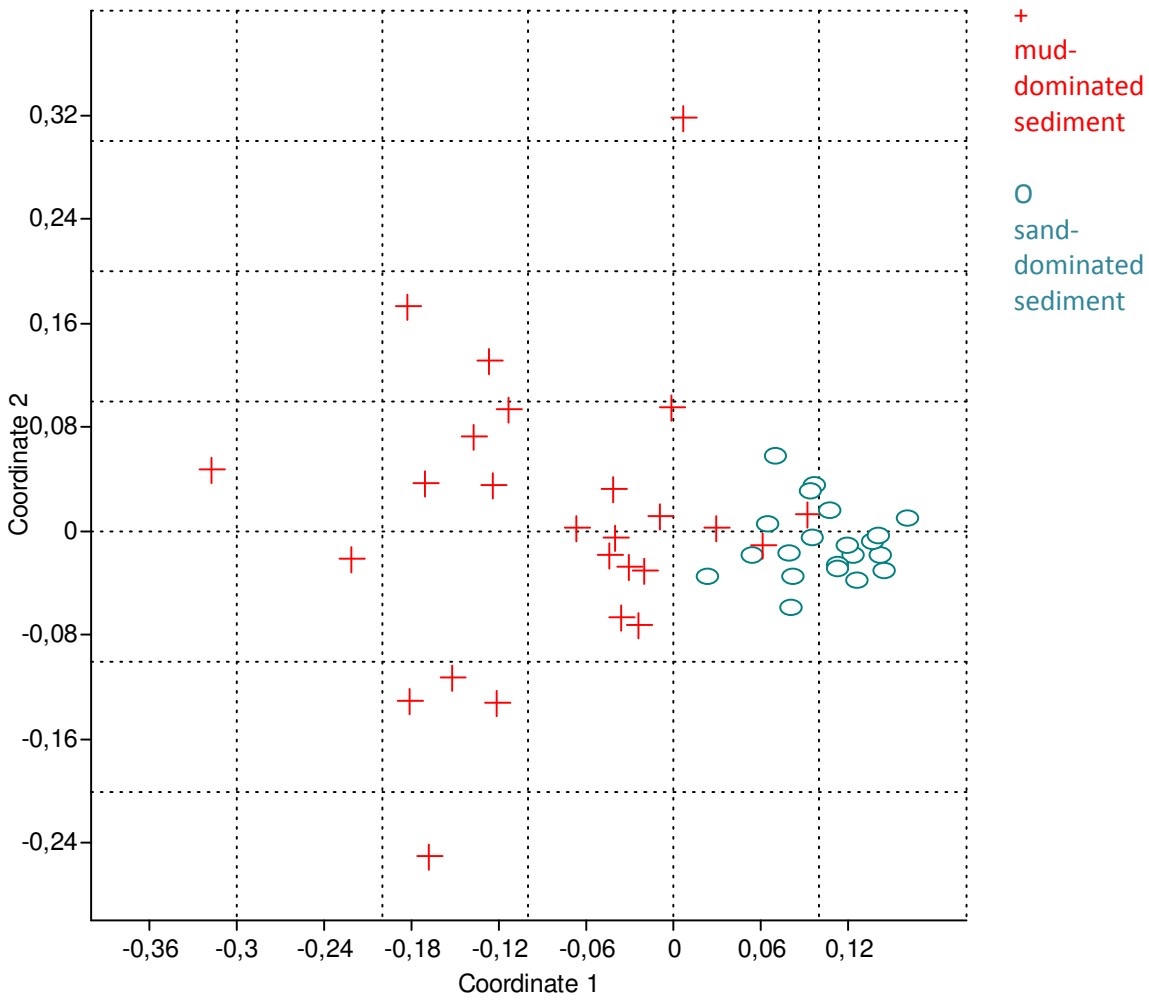

Figure 11. NMDS plots muddy (red crosses) and sandy (green circles) substrates as distinct groups (stress value 0.1495).

Table 11. Spearman's r_s indicates significant relations between muddy sediments and number of species, number of individuals, and number of alien species.

Spearman's r_s	muddy sediments (<63µm)	number of species	number of individuals	number of alien species
muddy sediments (<63µm)	0	**<0.0001**	**<0.0001**	**<0.0001**
number of species	-0.87286	0	**<0.0001**	**<0.0001**
number of individuals	-0.88271	0.98799	0	**<0.0001**
number of alien species	-0.65519	0.59571	0.58945	0

Table 12. SIMPER reveals that *Corbula gibba* contributes most to differences among muddy and sandy samples.

Class	Family	Genus	Species	Author	Contribution [%]
Bivalvia	Corbulidae	*Corbula*	*gibba*	(Olivi, 1792)	18.41
Gastropoda	Ringiculidae	*Ringicula*	*auriculata*	(Ménard de la Groye, 1811)	8.36
Gastropoda	Nassariidae	*Tritia*	*pygmaea*	(Lamarck, 1822)	6.62
Gastropoda	Cerithiidae	*Bittium*	*reticulatum*	(da Costa, 1778)	5.74
Bivalvia	Nuculanidae	*Lembulus*	*pella*	(Linnaeus, 1758)	4.94
Bivalvia	Semelidae	*Abra*	*alba*	(W. Wood, 1802)	3.29
Scaphopoda	Dentaliidae	*Antalis*	*sp. 2*		3.05
Bivalvia	Nuculidae	*Nucula*	*nitidosa*	Winckworth, 1930	1.84
Bivalvia	Veneridae	*Pitar*	*rudis*	(Poli, 1795)	1.77
Bivalvia	Veneridae	*Chamelea*	*gallina*	(Linnaeus, 1758)	1.60
Scaphopoda	Dentaliidae	*Antalis*	sp. 1		1.20
Bivalvia	Glycymerididae	*Glycymeris*	*nummaria*	(Linnaeus, 1758)	1.04
Bivalvia	Semelidae	*Abra*	*nitida*	(Müller O.F., 1776)	0.93
Gastropoda	Pyramidellidae	*Megastomia*	*conoidea*	(Brocchi, 1814)	0.87
Gastropoda	Rissoidae	*Alvania*	*mamillata*	Risso, 1826	0.84
Gastropoda	Creseidae	*Creseis*	*clava*	(Rang, 1828)	0.83
Bivalvia	Cardiidae	*Acanthocardia*	*paucicostata*	(Sowerby G.B. II, 1834)	0.78
Gastropoda	Cerithiidae	*Cerithium*	sp. 3		0.76
Bivalvia	Mactridae	*Spisula*	*subtruncata*	(da Costa, 1778)	0.68
Bivalvia	Veneridae	*Dosinia*	cf. *lupinus*	(Linnaeus, 1758)	0.67

4. Discussion

Surprisingly, the sediments of the core were characterized by highly variable proportions of sand and mud. These findings suggest that major changes must have affected the marine ecosystem of the Israeli coast. Until the middle of the last century, the continental shelf of Israel was characterized by high rates of sediments (Schilman et al. 2001); but, the completion of the Aswan high dam in 1965 has ceased the influence of the Nile floods which used to contribute large amounts of fine grained sediments to the Levantine basin (Krom et al. 1999; Stanley 1988). Accordingly, we expected the core, with a sediment depth of 123cm, to cover a time span exceeding 1869, the year of the opening of the Suez Canal. However, the presence of alien species in the lowermost part of the core indicates that the accumulation of the core sediment was different than expected. Reasons and consequences will be discussed in the following paragraphs.

4.1. Are there alien species present and to which depths can they be found?

As expected, various alien species were present in the sediment core. A total of twenty alien species were found from the top to the bottom of the core.

However, the findings of alien molluscs in the lowermost part of the core were unexpected, and suggest that either the lowermost part of the core does not predate the opening of the Suez Canal (because the sedimentation rates were higher than expected) or that there was a considerable degree of sediment mixing. Higher sedimentation rates would imply that all material of the core was deposited after the opening of the Suez Canal, and thus after the first introductions of Erythrean aliens to the Mediterranean Sea. Accordingly, a comparison to molluscan assemblages that thrived in the Mediterranean Sea before the Erythrean invasion is not possible with the data of this work; but it provides insight into the effects of the invaders on later communities. Another explanation for the occurrence of alien species in the lower depths of the core might be sediment mixing due to bioturbation, i.e. the reworking of the sediment by burrowing animals, or winter storms (Tom and Galil 1991) .

Although alien individuals contributed only 2.02% of the total of individuals, they provided 9.43% of the total of species. The percentage of alien species has its peak in the upper part of the core, and in the uppermost investigated layer (3cm sediment depth) the percentage of alien species was 18%. This result reflects the findings of other contemporary quantitative studies of molluscan assemblages on the Israeli shelf that investigated death assemblages of the top sediments; i.e. Leshno et al. (2015) reported a percentage of 17% alien species in their study, and Guarnieri et al. (2017) found even 30% of alien species in their samples. These findings confirm the important share of alien species on the molluscan

communities of the Levantine shelf. Nevertheless, it should be considered that differences in the abundance of alien species might be slightly influenced by different sampling methods, i.e. sample size, different water depths and sediment types, as well as different mesh sizes.

The presence of certain alien species compared to their first record on the Israeli shore was considered to provide insight into the temporal pattern of the core. One of the alien species that was found in the lowest part of the core was the bivalve *Gouldiopa consternans*. This bivalve was first recorded at the Israeli coast in 2011 (van Aartsen, Galil, and Bogi 2015). However, it is likely that this species was introduced to the Mediterranean Sea long before its first record but may have been overlooked due to its small size. This species was for example long unknown from its probable source region, the Red Sea, due to its small size (Oliver and Zuschin 2001). In general, the presence of small sized invertebrate phyla is rarely detected because of limited search effort, and taxonomic and biogeographic resolution (Galil 2012). Thus, this data cannot serve a valid estimation of the age of the core. Another alien species, the gastropod *Cerithidium diplax* which was also the most abundant alien species, was only found in the sediment depth of 45 cm and above. *C. diplax* was first recorded in the Mediterranean Sea in 1961 (Galil 2007). The absence of this species in deeper sediments might on the one hand be caused by the change of substrate from sandy to muddy sediments at that depth level which might not have suited the living conditions of this species. However, *C. diplax* is reported to be found in dense populations near harbors as its presence is mainly ship-mediated (Çinar et al. 2012; van Aartsen 2006). Thus, the sampling site of this study may also not have been within *C. diplax*'s main spatial range when the sedimentation of the deeper layers of the sediment core took place.

4.2. Does the diversity of the molluscan assemblage change within the core?

Species diversity was calculated for 49 representative depth layers and was found to be variable within the core. In general, evenness was high in the depths from 1-45cm and 110-123cm, and those depths were also characterized of a low dominance of few species. In contrast, the depths in-between showed low diversity and high dominance of single species.

The core was divided into four subsections to investigate time-related changes of the molluscan assemblage. PERMANOVA revealed that the molluscan composition of all four subsections of the core were significantly different to each other with the exception of subsection S2 and S4. Although this analysis focused on sediment depth, sediment type appears to exert a strong influence which must be taken into account. Those subsections which are significantly different to all other subsection, that is S1 and S3, are more homogeneous in their sediment composition (S1: dominated by sand; S3: dominated by

mud). Subsections S2 and S4 on the other hand, show variable amounts of sand and mud which might turn them significantly different to S1 and S4 but not to each other.

The strong impact of sediment type was confirmed when comparing the assemblages of the mud- and sand-dominated core sections. Spearman's rho rank order correlation coefficient showed significant negative correlations between samples of muddy and sandy sediments. In other words, sandy sediments were richer in overall species diversity, as well as in alien species diversity and in abundance of individuals. Moreover, nMDS confirmed the differences of molluscan assemblages with the two different sediment types. Whereas an nMDS of the four subsections resulted in a rather dense patch of samples of the subsections S1, S2, and S4, the nMDS of the sediment types reveals a clearer pattern. Those samples plotting together in close distance are all sand-dominated core slices. Three of the mud-dominated samples which seemed to disturb the segregation turned out to be boarder cases of sediment type, as rather low percentages of mud (65-73%, threshold value for mud-domination: mud content >60%), and two of those samples are in close distance to the sand-dominated layers. Therefore, these slices could have been under the influence of sand-dominated environments, which might serve as an explanation for their similarity of their molluscan assemblages to the sand-dominated core slices.

4.3. Which factors affect the overall diversity of the molluscan assemblage?

The diversity within the samples did not correlate with the presence of alien molluscs. SIMPER showed that nearly all molluscs that contributed most to differences between subsections were all native of the Mediterranean Sea. Two alien species ranked amongst the twenty most impactful species, but they were on low ranks, and thus their influence can be neglected. In addition, although the abundance of alien species increased in the upper quarter of the core, there was no decrease of total species diversity.

In general, species diversity varied throughout the core. The variation in diversity between the samples is related to the great variations in sample size. Species diversity is strongly related to abundance of individuals in the samples and in this study the number of individuals per sample varied from 0 to 286.5. Especially, the middle interval of the core was very poor in shells which led to great variations in sample size.

As mentioned earlier, the abundance of species was found to be closely related to the types of substrate. The more mud a slice contained the less shells were present in the sample. Explanations for the strong impact of the core sediments on species diversity and abundance can be found in the close relationship between sediment type and habitat conditions, and differences in sedimentation rate and shell preservation.

First, many molluscan species are restricted to specific habitats and can even be used as indicators for different types of environments (Zuschin and Stachowitsch 2007). Moreover, earlier studies have found that the distribution of faunal assemblages on the shelf of Israel is closely linked to the properties of the sediment (Tom and Galil 1991). Thus, the lack of individuals in the mud-dominated layers might be explained by a shift in environmental conditions, which might have rendered the habitat unfavorable for the local fauna. Lastly, muddy substrates are reported to host different communities than sandy substrates. For instance, Ellingsen (2002) found that sediment properties such as the silt-clay content are one of the major environmental variables that influence marine communities. Moreover, Çinar et al. (2012) found that increasing percentages of sand significantly increased species diversity, whereas high percentages of mud decreased diversity and abundance of species.

Second, irregular sedimentation rates may lead to fluctuations in the abundances of shells. The more sediment is deposited in a certain time span, the fewer individuals will be present in a certain section of the sediment deposit. Hence, if the muddy sediments had been deposited in a shorter period of time than the sandy sediments this might have led to a dilution of abundances of shells. This argument is supported by the low abundances of the species *Corbula gibba* and *Lembulus pella* in the mud-dominated slices of the core. Usually *C. gibba* is abundant in silts and muddy gravels (Holmes and Miller 2006), and *L. pella* is a characteristic species of muddy fine sands and mixed coarse sand bottoms (Urra et al. 2011). However, in this study both species showed high abundances only in the sand-dominated parts. Moreover, previous studies found *C. gibba* and *L. pella* to be tolerant of low oxygen conditions (Diaz and Rosenberg 1996) and polluted environments (Simboura and Zenetos 2002; Borja, Franco, and Pérez 2000). This implies that even if environmental conditions changed as the sediment became muddier, and maybe richer in nutrients as this is a recent development due to the urbanization of the Israeli coast (Leshno et al. 2015), the abundances of *C. gibba* and *L. pella* should not have been affected on a major scale. Hence, the lack of these species in the middle part of the core points towards increased sedimentation rates and dilution of the assemblage.

Third, taphonomic conditions may differ in different sediments and sediment depths. On the one hand, preservation of shells may be poorer in muddy sediments than in sandy sediments. Aragonite, the main component of most molluscan shells, is reported to dissolve under certain circumstances of shallow burial in carbonate setting, especially in the taphonomically active zone where bacterial activities increase the acidity of the pore waters (Cherns, Wheeley, and Wright 2008). This might even lead to a dissolution of shells. Moreover, also sediment depth can impact the preservation of shells. Kidwell et al. (1991) report that the preservation of calcareous remains in marine sediments might be better in

upper layer, whereas different geochemical effects in deeper layers can have negative effects on the quality of shell preservation.

4.4. Are there differences in the abundance of alien species in different depths?

Only single specimens were found in the lower parts of the core, but the abundance of alien species increases towards the top of the core. It can be assumed that the absence of alien species in various samples is due to the great variation in sample size. Moreover, the impact of sediment type, which was discussed earlier, did not only influence the total species diversity but also the presence of alien species. Thus, the increase of alien species in the upper third of the core might be driven by the change to sand-dominated sediments.

Although it was not possible to estimate the temporal dimension of the sediment core, an increase of alien species in the upper sediments was expected because the continuous enlargement of the Suez Canal has facilitated the transport of Erythrean invaders through the canal. It can be assumed that the propagule pressure increases (Galil and Goren 2014); consequently, more alien species manage to successfully invade the Mediterranean Sea. Moreover, the ecosystem of the Levantine basin must be assumed to be increasingly affected by multiple stressors like eutrophication, pollution and overexploitation which frequently increases the chances of the Erythrean invaders (Galil and Goren 2014). In relation to the development of evolutionary adaptations anthropogenic disturbances happen fast. Nevertheless, they represent a strong selection pressure. Native species usually struggle to adapt instantly and suffer from a reduction of their fitness, whereas non-native species may be equipped with better adaptations to the disturbed environments and therefore outcompete native inhabitants (Byers 2002).

5. Conclusion

5.1. Main findings

- 20 species of alien bivalves and gastropods were found in the investigated sediment core. The presence of alien molluscs in the deepest layers of the core was unexpected.
- Species diversity and abundances of alien molluscs increased in the upper sections of the core.
- Species diversity of the molluscan assemblage was variable within the core.
- Molluscan species diversity was strongly related to sediment types.
- Molluscan assemblages of the mud-dominated assemblages were significantly less divers and had significantly lower abundances of individuals than the assemblages of the sand-dominated samples.
- Low abundances and hence low species diversity in the mud-dominated samples might be caused by higher sedimentation rates which had a diluting effect on the abundances, or a general change of environmental conditions.

5.2. Outlook

In this study, the influence of the sediment type on the molluscan assemblages was extremely strong, and may have disguised the impact of alien molluscs on the community. However, the increasing influence of Erythrean aliens can be assumed by their increase in abundance and diversity in the upper section of the core. Further conservation paleobiological work is necessary to understand the environmental processes and the biotic responses caused by the Erythrean invasion in the Mediterranean Sea at a temporal scale. The analysis of further cores will be necessary to understand the influence of the alien species on the native molluscan community. Moreover, it will be crucial to measure the sedimentation rate for the sampling site to clarify the variations in molluscan abundances.

6. Acknowledgements

I would first like to thank my thesis advisors Univ. Prof. Mag. Dr. Martin Zuschin and Dr. Paolo Giulio Albano, PhD of the Department of Palaeontology. The door to Dr. Albano's office was always open whenever I ran into a trouble spot or had a question about my research or writing. He consistently allowed this paper to be my own work, but steered me in the right the direction whenever he thought I needed it.

Finally, I must express my very profound gratitude to my parents for providing me with unfailing support and continuous encouragement throughout my years of study and through the process of researching and writing this thesis. This accomplishment would not have been possible without them. Thank you.

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8. Appendix

8.1. Abstract

This work investigates the molluscan remains within a sediment core taken 2017 on the Israeli shelf at a water depth of 30m. The dataset provides quantitative information on the composition of the benthic molluscan assemblages at different stages of the Erythrean invasion. A total of 2920.5 individual molluscs from 49 sediment slices (representing sediment depths from 3-123cm) were analyzed for species diversity and abundance in relation to alien species as well as sediment types and sediment depths.

Twenty alien species were present in the sediment core; they contributed 9.43% of the total number of species and 2.02% of the total number of individuals. The most abundant alien species was the gastropod *Cerithidium diplax*. Surprisingly, single alien individuals were discovered in the lowermost parts of the core, which implies that the material of this study was deposited after the opening of the Suez Canal. In addition, there was an increase of alien species in the upper sediments. This outcome was expected as the continuous enlargement of the Suez Canal as well as increasing anthropogenic pressure increases the chances of alien species to invade the Mediterranean Sea.

Species diversity was variable within the core and was strongly related to sediment type. The core was characterized by highly variable proportions of sand and mud. Sandy sediments were richer in overall species diversity, alien species diversity and abundance of shells than the mud-dominated sediments. This relation between sediment and molluscan assemblages might be influenced by the restriction of certain species to specific habitats, a dilution of abundance in the muddy sediments due to an increased sedimentation rate, or poorer taphonomic conditions in the mud-dominated samples. Next, species diversity was not related to the presence of alien molluscs. In contrast, all species that contribute most to the differences between different sediment depths but also between different sediment types were native to the Mediterranean. Here, the most impactful native species were the bivalves *Corbula gibba, Lembulus pella* and the gastropods *Ringicula auriculata* and *Tritia pygmaea*.

8.2. Zusammenfassung

In dieser Arbeit werden Molluskenschalen aus einem Sedimentkern analysiert, der 2017 vor der Küste von Israel in eine Wassertiefe von 30m entnommen wurde. Der so gewonnene Datensatz liefert Einblicke in die Zusammensetzung der Mollusken-Gesellschaften in verschiedenen Zeiträumen der Lessepsschen Migration („Erythrean Invasion“). Anhand von 2920,5 Molluskenindividuen aus 49 Sedimentschichten, welche Sedimenttiefen von 3-123cm repräsentieren, wurden Artenvielfalt und Individuenhäufigkeiten sowie deren Beziehung zu invasiven Arten, Sedimenttypen und Sedimenttiefe untersucht.

Insgesamt wurden zwanzig invasive Molluskenarten in der Probe gefunden. Der Anteil der invasiven Arten im Vergleich zur Diversität der gesamten Probe betrug 9,43%. Die Anzahl an Individuen, die einer invasiven Art angehörten, betrug 2,02% der Gesamtanzahl der Individuen in der Probe. Die häufigste invasive Art war *Cerithidium diplax*. Überraschenderweise wurden auch im untersten Bereich des Sedimentkerns einzelne invasive Mollusken identifiziert. Diese Funde implizieren, dass die Sedimente der analysierten Probe erst nach der Eröffnung des Sueskanals abgelagert wurden. Außerdem wurde eine Zunahme an invasiven Individuen in den oberen Schichten des Sedimentkerns festgestellt. Dieses Ergebnis bestätigt die Annahme, dass der zunehmende Ausbau des Sueskanals sowie der zunehmende anthropogene Stress die Überlebenschancen invasiver Arten im Mittelmeer erhöhen.

Die Artenvielfalt innerhalb der gesamten Sedimentprobe war variabel und stark abhängig vom Sedimenttyp. Der Sedimentkern zeichnete sich durch höchst variable Anteile an Sand und Schlamm aus. Sandige Sedimente wiesen dabei eine höhere Artenvielfalt, eine höhere Artenvielfalt invasiver Arten und höhere Anzahlen an Individuen als die von Schlamm dominierten Bereiche auf. Diese Abhängigkeit der Molluskengemeinschaft vom Sediment könnte durch mehrere Faktoren beeinflusst sein. Einerseits sind Molluskenarten meist auf einen speziellen Sedimenttyp spezialisiert, andererseits könnte eine erhöhte Sedimentationsrate zu einer Verringerung des Schalenanteils in den Schichten geführt haben. Letztlich könnten auch in den schlammigen Sedimenten ungünstigere taphonomische Bedingungen geherrscht haben. Weiters konnte festgestellt werden, dass die Artenvielfalt nicht von der Präsenz invasiver Arten beeinflusst war. Diejenigen Arten, welche am meisten zu einem Unterschied zwischen verschiedenen Sedimenttiefen und Sedimenttypen beitrugen, waren alles Mollusken, die im Mittelmeer als heimisch gelten. Die entscheidenden Arten waren hierbei die Bivalven *Corbula gibba, Lembulus pella* und die Gastropoden *Ringicula auriculata* and *Tritia pygmaea.*