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Article

Molluscs from Tidal Channels of the Gulf of Gabès (Tunisia): Quantitative Data and Comparison with Other Lagoons and Coastal Waters of the Mediterranean Sea

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Abstract: The present study analyses the spatio-temporal structuration of the molluscan fauna from four tidal channels of the Gulf of Gabès. A total of 26 stations were sampled at four seasons from March 2016 to January 2017, leading to the identification of 2695 individuals and 57 species. The species richness and abundances are higher in autumn than in other seasons. The fauna is dominated by seven species, three gastropods [*Cerithium scabridum* Philippi, 1848, *Bittium reticulatum* (da Costa, 1778) and *Tricolia speciosa* (Megerle von Mühlfeld, 1824)] and four bivalves [*Abra alba* (W. Wood, 1802), *Loripes orbiculatus* Poli, 1791, *Varicorbula gibba* (Olivi, 1792) and *Peronaea planata* (Linnaeus, 1758)], which are characteristic of habitats with detritus accumulation and seagrass meadows. These dominant species are commonly recorded in lagoons and coastal shallow waters of the Mediterranean Sea. The structure of the molluscan fauna is linked to the location of tidal channels in the Gulf of Gabès. Abundances are lower in the Mimoun channel than in the other channels, especially the Maltine channel which shows a great accumulation of organic matter and high abundances of molluscs. Low abundances are found in high-energy hydrodynamic zones with gravel sediment; conversely, the presence of macrophytes (mainly in seagrass meadows) increases molluscan diversity. Comparisons with other sites in the shallow waters of the Tunisian coast and lagoons show that the taxonomic diversity of molluscs of the tidal channels of the Gulf of Gabès is equivalent to that reported elsewhere, but the abundance per m² is among the lowest levels recorded here. Moreover, most of the dominant species found in the Gulf of Gabès tidal channel are reported as dominant in other studies covering the Mediterranean Sea. A distance-based redundancy analysis shows that depth, sediment type and the presence of marine phanerogams and filter-feeder bivalves on fine sands and gravels account for the structure of mollusc assemblages associated with each channel.

Keywords: subtidal macrobenthos; molluscan assemblages; spatio-temporal variations; seagrasses



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1. Introduction

Molluscs are among the predominant and most abundant components of the benthic macrofauna of the shallow waters and lagoons of the Mediterranean Sea [1–8]. Moreover, many of the non-indigenous species in the Mediterranean Sea are molluscs [9–11].

In the Mediterranean Sea, Ref. [12] recorded 2113 mollusc species that represent 19.3% of all invertebrates known to occur in this basin. Therefore, studies of molluscan assemblages can be considered as representative for understanding the ecological status and dynamics of benthic communities in coastal Mediterranean areas [13]. Many ecological studies have been carried out on molluscan faunas along the Tunisian coastline [5,8,14–17]. Other ecological studies have mentioned mollusc species in the context of bionomic studies [6,7,14,17–37].

Most of the studies on molluscs in Tunisia have been carried out by considering sea grass meadow habitats [3,8,38,39] or the macrozoobenthos in lagoons and shallow coastal waters [6,7,14,29,30,40–43].

Ref. [44] analysed the malacological fauna of 25 samples (8 dredging and 17 cores) collected between 13 and 300 m depth in the Gabès Gulf and its surrounding area (Pelagian Sea). Later, Ref. [45] studied in particular the Testaceous Molluscs of the mediolittoral and infralittoral bottoms (0 to 20 m depth) of the Kerkennah plateau; he identified 150 species, without specifying the species which had been found alive and which only in thanatocoenosis. He identified four types of habitats: (1) *Posidonia oceanica* meadow with 71 molluscan species, (2) *Cymodosea nodosa* meadow (56 molluscan species), (3) *Caulerpa prolifera* meadow (47 molluscan species), and finally (4) soft bottoms without vegetation (fine sands, gravels, mixed sediment) with a molluscan diversity included between 19 and 42 species. Ref. [46] had studied the macrofauna of the bottoms of the Gulf of Gabès, particularly those of the Kerkennah Islands and Djerba Island; according to these authors, the malacological diversity of these areas reached 148 species.

The subtidal macrobenthos of the tidal channels of the Gulf of Gabès had been previously investigated by [36,37,47]. This ecosystem is unique in the Mediterranean Sea as it is associated with a high-energy environment with a tidal range >2.2 m at spring tide similar to that occurring in the North of the Adriatic Sea [48,49]. These tidal conditions favour the circulation of seawater, sediments, organic matter, nutrients and pollutants between terrestrial and coastal marine environments not only in the tidal channels but also in the shallower parts of the Gulf of Gabès [48,49].

In the framework of our investigations of the macrobenthic communities from tidal channels in the Gulf of Gabès [47], we obtained a large collection of molluscs. Therefore, the aims of the present study are (1) to describe the spatio-temporal patterns of the mollusc populations in four tidal channels sampled at four dates from spring 2016 to winter 2017; (2) to compare the mollusc diversity, abundances and predominant species found in the subtidal tidal channels of the Gulf of Gabès, with those recorded in intertidal zones around the Kneiss Island and other Tunisia sites in the Gulf of Gabès; and (3) to compare the molluscs population found in the Gulf of Gabès with other results reported from shallow waters and lagoons of the Mediterranean Sea.

2. Materials and Methods

2.1. Study Area

The Gulf of Gabès is a shallow embayment located on the southern coast of the central Mediterranean Sea, covering an area of about 36,000 km². It is characterized by very pronounced annual water temperature cycle (13 °C in winter to 29 °C in summer) [50] and an unusually high tidal amplitude reaching 2.3 m, the highest range observed in the Mediterranean Sea [51].

In their review, Ref. [49] pointed out that the functioning of the Gulf of Gabès ecosystem is influenced by several interacting factors: the climate, water circulation, seasonal variations of sea water temperature and salinity, as well as the oligotrophic conditions. Several studies were dedicated to the impact of human activities on the benthic communities such as bait digging, clam harvesting, fishing operations in the tidal channel of the Kneiss Islands, dredging operations in the channels between the major port of Sfax and the offshore Kerkennah Islands, industrial discharge due to the phosphate industry and the relating discharge of metals, and hydrocarbon contamination (see [47] and references therein). These works suggested that the pollution effects remained moderate and only had a local impact on the benthic structure, in spite of consistent emissions going back several decades.

In spite of its exposition to numerous anthropogenic pressures, the Gulf of Gabès hosts important biological resources as well as some rich coastal and marine ecosystems, while its natural environment is also probably sensitive to climatic change [49].

In our study, four tidal channels were selected as representative of the influence of human activities in the north-western part of the Gulf of Gabès [47,49,52]: the Maltine Channel, the Kneiss Islands Channel, the Ben Khlaf Channel and the Mimoun Channel. Further details and descriptions of these channels are available in [47,52].

2.2. Sampling and Laboratory Procedures

Sampling stations were positioned from the shallow upstream to the deeper downstream parts of four tidal channels [47] (Figure 1). Seven stations were sampled in the Mimoun Channel (CM) and six stations from the Kneiss Channel (CK), the Maltine Channel (CML) and the Ben Khlaf Channel (CP), with a supplementary station in September 2016 and January 2017, for a total number of 26 stations (Table 1).

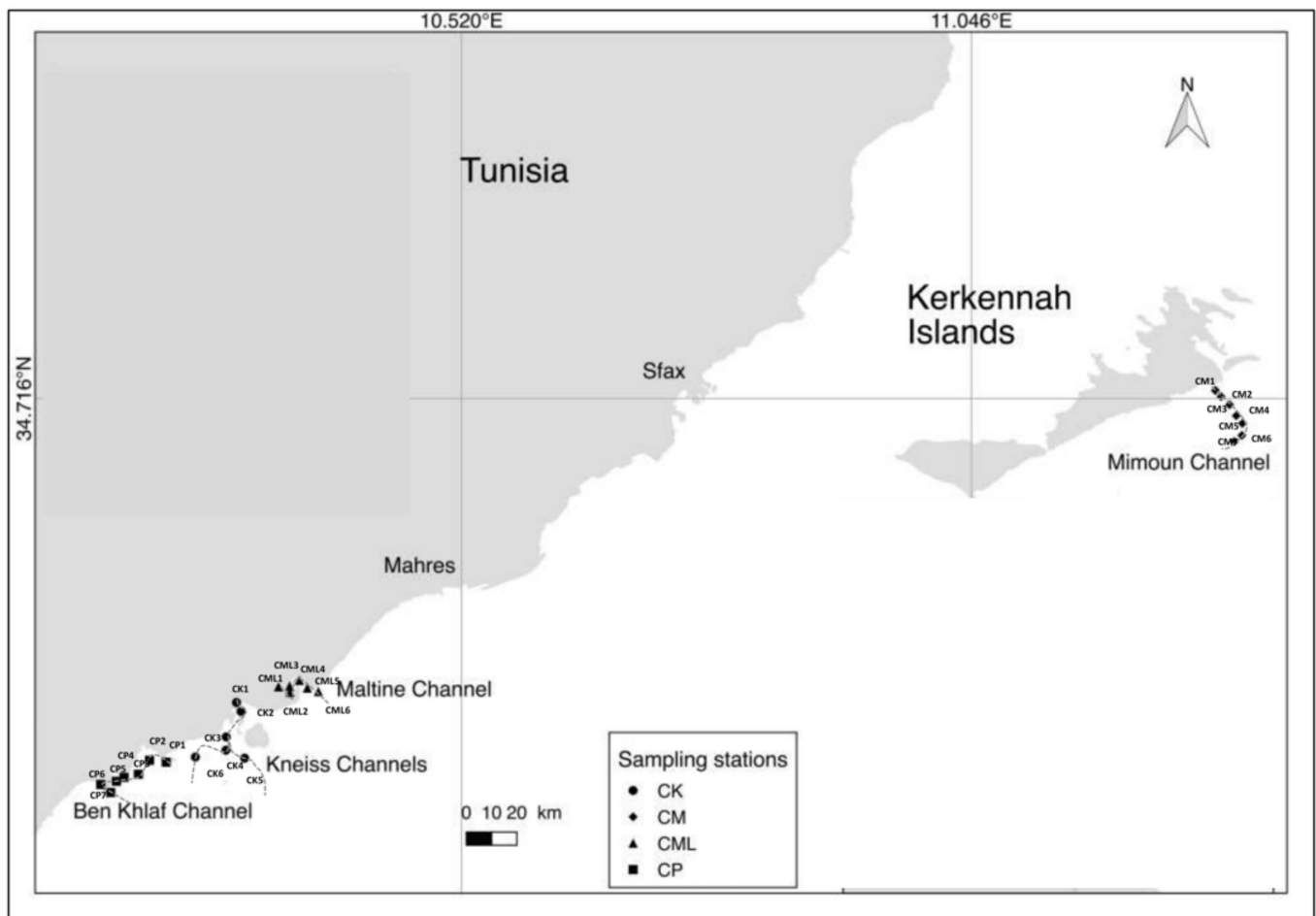


Figure 1. Study area showing the location of sampling stations in the four channels traversing the Gulf of Gabès (Adapted from [47]).

Stations were sampled (yielding four 0.1 m² Van Veen replicates) in four seasons: i.e., March, July and September 2016 as well as in January 2017. In our study, the prospected channels are not *Posidonia oceanica* meadow or other marine phanerogams but soft-bottoms (see Table 1): 11 stations with fine or medium sands or sands and gravel as sediments while the other 15 stations corresponded to fine or medium sands, or sands and gravel with sparse or rare tuft of marine phanerogams. This is a typical soft-bottom substrata where the use of a Van Veen grab is suitable for collecting the characteristic macrofauna of such soft-substrate. The sediment was sieved on a 1-mm mesh a regular sieve-mesh used in most of the benthic studies from the Mediterranean Sea; after sorting, only the living molluscs were identified under a binocular microscope.

Table 1. Main characteristics of the sampling stations in the four tidal channels (mean \pm standard deviation). Gravel ($>1000 \mu\text{m}$), sand ($63\text{--}1000 \mu\text{m}$), silt and clay ($<63 \mu\text{m}$); OM: Organic Matter. The four channels are labelled as follows: CP: Ben Khlaf; CML: Maltine; CK: Kneiss; CM: Mimoun (from [47]).

Station	Depth (m)	Gravel (%)	Sand (%)	Silt-Clay (%)	OM %	Sediment Type	Phanerogams
CP 1	3.5	2.0	84.8	12.6	2.8	Fine sand	<i>Cymodocea nodosa</i> , <i>Zostera noltei</i>
CP 2	2.8	1.7	96.6	1.5	0.9	Fine sand	<i>Cymodocea nodosa</i>
CP 3	3.2	76.3	18.5	4.8	2.4	Gravelly sand	<i>Cymodocea nodosa</i>
CP 4	6.1	7.9	87.8	3.8	1.1	Fine sand	-
CP 5	7.6	3.7	83.6	12.3	1.9	Fine sand	-
CP 6	11.9	2.1	62.4	34.9	7.3	Silty sand	-
CP 7	0.9	2.0	95.3	2.4	1.9	Fine sand	-
CML 1	1.0	22.2	49.8	27.6	9.3	Silty sand	<i>Zostera noltei</i>
CML 2	2.1	57.2	35.4	7.0	3.1	Shell and gravelly sand	<i>Zostera noltei</i> , <i>Cymodocea nodosa</i> , <i>Halophila stipulacea</i>
CML 3	2.1	67.6	26.4	5.8	1.7	Shell and gravelly sand	<i>Cymodocea nodosa</i>
CML 4	3.1	80.6	17.8	1.5	1.5	Gravelly sand	<i>Halophila stipulacea</i> , <i>Posidonia oceanica</i>
CML 5	4.4	4.3	93.5	1.7	1.4	Fine sand	-
CML 6	3.7	30.7	66.9	2.0	1.5	Coarse sand	<i>Halophila stipulacea</i>
CK 1	2.0	1.6	89.8	8.5	4.2	Fine sand	<i>Cymodocea nodosa</i> , <i>Halophila stipulacea</i>
CK 2	8.5	18.1	78.5	3.1	0.7	Medium sand	-
CK 3	5.3	2.3	90.3	6.9	2.4	Fine sand	<i>Cymodocea nodosa</i>
CK 4	7.4	17.5	78.5	3.6	1.6	Medium sand	-
CK 5	5.3	2.6	94.9	2.5	1.7	Fine sand	<i>Cymodocea nodosa</i> , <i>Zostera noltei</i>
CK 6	8.3	4.0	80.9	14.4	5.8	Silty sand	<i>Cymodocea nodosa</i>
CM 1	3.3	24.1	67.7	7.6	5.8	Medium sand	-
CM 2	3.3	14.6	78.1	6.6	5.2	Fine sand	<i>Cymodocea nodosa</i>
CM 3	3.6	35.8	57.4	6.1	4.9	Medium sand	<i>Posidonia oceanica</i>
CM 4	4.1	62.8	36.5	0.4	1.7	Gravelly sand	-
CM 5	10.0	61.6	36.6	1.5	1.8	Gravelly sand	-
CM 6	13.5	75.7	21.6	2.4	2.5	Gravelly sand	-
CM 7	15.0	5.7	86.7	6.8	5.4	Fine sand	<i>Posidonia oceanica</i>

The molluscs were identified following the morphological characteristics and keys given in [53–67]. They were stored at the University Caen Normandy in the ‘Morphodynamique Continentale et Côtère’ laboratory. Their classification of the species in trophic group came from [35].

Species names were checked using the World Register of Marine Species list (<http://www.marinespecies.org> accessed on 31 May 2022).

In addition, measurements of temperature, salinity and pH were all carried out in situ close to the seabed [47,52].

Sediment from each sample was homogenized and wet-sieved through sieves with mesh sizes of 1000, 500, 250, 125 and 63 μm for 10 min to separate the different grain-size fractions. Then, three sediment fractions were considered: gravel ($>1000 \mu\text{m}$), sand ($63\text{--}1000 \mu\text{m}$), silt and clay ($<63 \mu\text{m}$), leading to the identification of the following sediment types: silty sand, fine sand, medium sand, coarse sand, gravelly sand and shells with gravelly sand. Organic matter content was determined on powder samples by ‘loss on ignition’ at 450 $^{\circ}\text{C}$ for 4 h.

More details on the main characteristics of the 26 sampled stations are available in [47,52] and summarized in Table 1.

2.3. Statistical Analysis of Biological Parameters

Two-way ANOVA was used to investigate spatio-temporal changes (factors involving channels and seasons) in species richness and total abundance of molluscs in the Gulf of Gabès. A Shapiro-Wilk normality test and a Bartlett test for homogeneity of variances were used. The Tukey Honestly Significant Difference test was applied when ANOVA showed significant differences. The R software package (version R 3.4.3. for Windows, Auckland, New Zealand) was used to perform ANOVAs as well as the Shapiro, Bartlett and Tukey tests.

The species accumulation was plotted with the permuted option with 999 permutations (i.e., random order repeated 999 times and with the curve being averaged across the repeats at each point) on the Species Presence/Absence (1/0) matrix, using the PRIMER 6 package.

The spatial and temporal changes considering all molluscs (abundance matrix) were analysed separately by group-average sorting classification, using a hierarchical clustering procedure (CLUSTER mode) based on the Bray-Curtis similarity index with a square-root transformation of abundances (total abundance of the four replicates, i.e., for 0.4 m²) using the PRIMER v6 software package [67].

Distance-based Redundancy Analyses (db-RDA) [68] were performed to investigate the relationship between benthic assemblage in terms of abundance (i.e., total numbers of individuals found in the four seasons at the 26 stations) and the abiotic factors. The following abiotic factors were included in the analyses: depth, bottom water temperature (temperature), bottom water salinity (Salinity), pH, seawater transparency (Transparency) % of gravel (Gravel), % of sand (Sand), % of silt-clay (Silt-Clay), Organic Matter (OM). The presence of four marine phanerogams: *Cymodocea nodosa*, *Halophila stipulacea*, *Posidonia oceanica* and *Zostera noltei*. db-RDA allows us to model the effect of environmental variables on the entire malacofauna, rather than on species richness. The abundances of the species were transformed with the Hellinger distance. Only species present on at least three stations were retained for the db-RDA (i.e., 28 species out of a total of 56).

2.4. Environmental Parameters

The patterns of the environmental parameters had been investigated in a previous study [47]. We reported here the main results of these analyses. No differences were detected between the water temperatures in the tidal channels: the mean annual sea temperature ranged from 21.8 to 23.8 °C. The water temperatures show a seasonal pattern with minimum values recorded during the winter (12–13 °C) and a maximum in summer and autumn (27–28 °C) [47]. Water salinity varies from 36 to 47, being significantly higher in the CML channel (mean salinity > 40.0) than in the three other channels, although there are no significant changes across the seasons [47].

The pH values of the sea water are significantly higher in the CML channel than at the three other sites, while there are no changes in Water transparency with season and no difference can be detected between the channels. The organic matter content in sediment samples remains high at all times of the year at the three shallow stations CP6, CML1 and CK1, and is still high in the wintertime at the deeper station CK6. Values are significantly higher in winter, but no difference is observed between these stations, while the two stations CM1 and CM2 show high mean values [47].

The stations located in the shallowest depth are mainly characterized by sand, whilst gravel is found at the intermediate-depth stations, and the deeper stations are dominated by fine sediment (Table 1). There is no seasonal difference in the percentage of fine particles between the stations [47]. Moreover, the percentage of sand and gravel is different between the two channels CML and CM, the latter showing a higher percentage of gravel, whereas sediment in the CK and CP channels are dominated by sand [47].

A total of 14 out of the 26 stations on diverse sediment types show the presence of four species of seagrasses (Table 1): *Cymodocea nodosa* at 10 stations from 2.1 to 8.3 m depth,

Halophila stipulacea at three stations from 2.1 to 3.7 m, *Posidonia oceanica* at three stations from 3.1 to 13.5 m and *Zostera noltei* at three stations from 1 to 5.3 m.

3. Results

3.1. General Characteristics of the Molluscan Fauna

Fifty-six species belonging to three classes were identified (Table 2). The most diverse class was Bivalvia (32 species), followed by Gastropoda (22 species) and then Polyplacophora (two species). The species richness differed between the channels: 32 for CK, 30 for CM, 29 for CML and 21 for CP, with Bivalvia being the dominant taxon in all channels. Moreover, the total number of species was higher in autumn (35), closely similar in spring (32) and winter (29) and very low in summer (21).

A total of 2695 individuals had been collected during the sampling period. More than 55% of the individuals were assigned to the gastropod class, containing two dominant species (*Bittium reticulatum* and *Cerithium scabridum*), while 43% of the individuals were represented by Bivalvia with only one species (*Abra alba*) occurring in abundance (Table 2).

The species accumulation curve (Figure 2) shows no signs of stabilizing towards an asymptote, which illustrates high diversity of molluscs and the continued recording of additional species after a sampling effort of 11, 20 m² (CM 28 samples of 0.4 m²). Three of the channels show similar species (CK, CM and CML) curve accumulations while this of CP is lower.

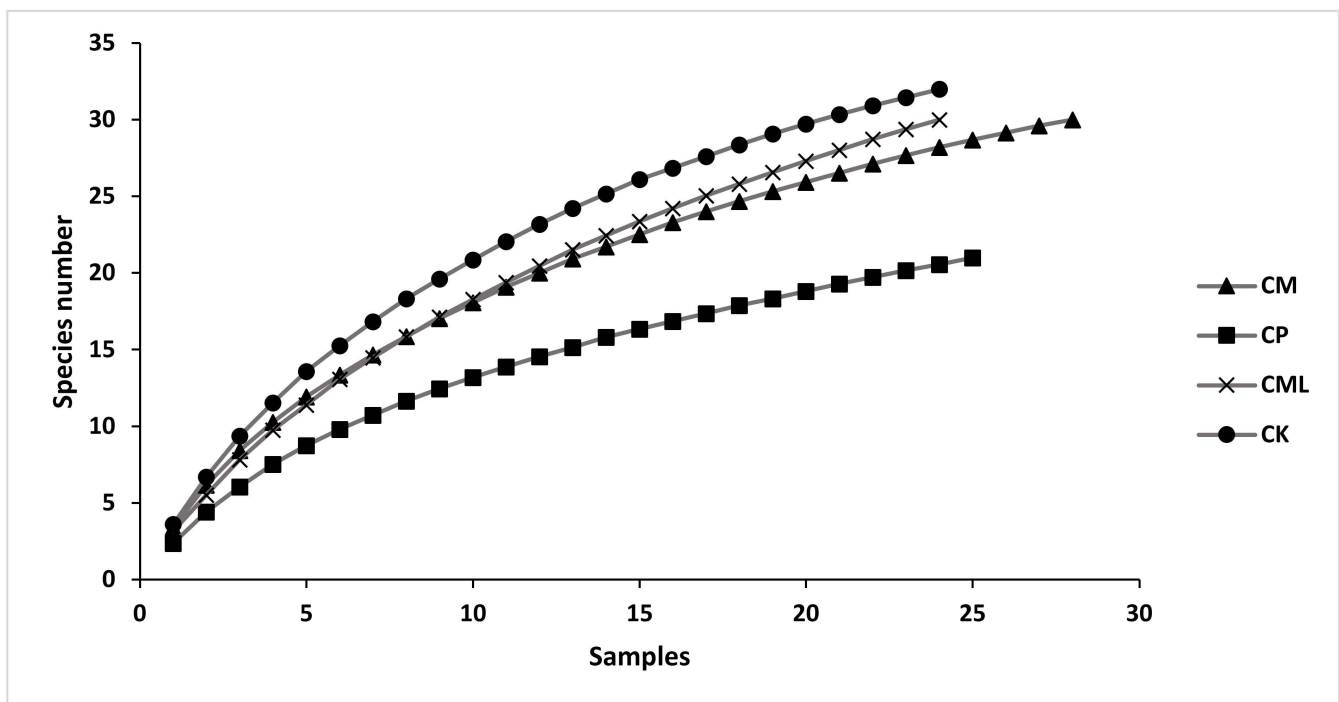


Figure 2. Species accumulation curve (Species Numbers) in the four channels sampled four times from spring 2016 to winter 2017. CP: Ben Khlaf; CML: Maltine; CK: Kneiss; CM: Mimoun.

Out of the 106 samples, nineteen yield no molluscs and eleven others show only one individual in each sample. These samples correspond mainly to those collected in summer and at gravelly stations in the four channels. Seven samples show abundances of more than 100 individuals per 0.4 m², with a maximum at station CML1 (1 m depth on mixed sediment) in summer (382 individuals per 0.4 m²).

Table 2. Numbers of molluscs collected in each channel during the four seasons. 2017/01: January 2017 (winter: win), 2016/09: September 2016 (autumn: aut), 2016/07: July 2016 (summer: sum), 2016/04: April 2016 (spring: spr). Sampling area at each season, CK and CML: 2.4 m²; CM and CP: 2.8 m² except CP 2.4 m² in spring and summer.

Class/Family/Species	Kerkennah (CM)					Maltine (CML)					Kneiss (CK)					Ben Kelaf (CP)					Total	
	Spr	Sum	Aut	Win	Total	Spr	Sum	Aut	Win	Total	Spr	Sum	Aut	Win	Total	Spr	Sum	Aut	Win	Total		
Polyplacophora																						
Tonicellidae Simroth, 1894																						
<i>Lepidochitona cinerea</i> (Linnaeus, 1767)						21					21										21	
Acanthochitonidae Pilsbry, 1893																						
<i>Acanthochitona crinita</i> (Pennant, 1777)		1		1	2																	2
Gastropoda																						
Fissurellidae Fleming, 1822																						
<i>Diodora graeca</i> (Linnaeus, 1758)			1	2	3																	3
Trochidae Rafinesque, 1815																						
<i>Clanculus cruciatus</i> (Linnaeus, 1758)			1	3	4																	4
Phasianellidae Swaison, 1840																						
<i>Tricolia pullus</i> (Linnaeus, 1758)													1	1					2	2		3
<i>Tricolia speciosa</i> (Megerle von Mühlfeld, 1824)								11	16	27			131	9	140							167
<i>Tricolia tenuis</i> (Michaud, 1829)													1	1								1
Neritidae Rafinesque, 1815																						
<i>Smaragdia viridis</i> (Linnaeus, 1758)	1				1	1		3	5	9			1	1	2							12
Cerithiidae Fleming, 1822																						
<i>Bittium reticulatum</i> (da Costa, 1778)	1				1	8	429			437	4		2	6	4				1	5		449
<i>Cerithium scabridum</i> Philippi, 1848		1		2	3	17		665	22	704			18	18	3					3		728
Littorinidae Children, 1834																						
<i>Melarhaphé neritoides</i> (Linnaeus, 1758)								1		1												1
Rissoidae Gray, 1847																						
<i>Alvania</i> sp																1					1	1
<i>Rissoa auriscalpium</i> (Linnaeus, 1758)													5	5								5
<i>Setia sciutiana</i> (Aradas & Benoit, 1874)													4	4								4
Velutinidae Gray, 1840																						
<i>Lamellaria perspicua</i> (Linnaeus, 1758)													90	90								90
Columbellidae Swaison, 1840																						
<i>Amphissa acutecostata</i> (Philippi, 1844)					2					2												2
Nassariidae Iredale, 1916																						
<i>Tritia mutabilis</i> (Linnaeus, 1758)											2			2								2
<i>Tritia varicosa</i> (W. Turton, 1825)				4	4	4				5												9
Muricidae Rafinesque, 1815																						
<i>Bolinus brandaris</i> (Linnaeus, 1758)											4			4								4
<i>Hexaplex trunculus</i> (Linnaeus, 1758)				1	1	1				1	1		1	2								4
Tudicidae Cossmann, 1901																						

Table 2. Cont.

Class/Family/Species	Kerkennah (CM)					Maltine (CML)					Kneiss (CK)					Ben Kelaf (CP)				Total	
	Spr	Sum	Aut	Win	Total	Spr	Sum	Aut	Win	Total	Spr	Sum	Aut	Win	Total	Spr	Sum	Aut	Win		Total
<i>Moerella distorta</i> (Poli, 1791)									1	1		2			2		3	5	25	33	36
<i>Moerella pulchella</i> (Lamarck, 1818)												12			12	1				1	13
<i>Peronaea planata</i> (Linnaeus, 1758)												126			126						126
Donacidae J. Fleming, 1828																					
<i>Donax semistriatus</i> Poli, 1795							1			1											1
Semelidae Stoliczka, 1870																					
<i>Abra alba</i> (W. Wood, 1802)		1	6	14	21	3	6	7	73	89		2	93	57	152		24	4	34	62	324
<i>Abra segmentum</i> (Récluz, 1843)			1		1																1
<i>Abra tenuis</i> (Montagu, 1803)						9				9				6	6				2	2	17
Veneridae Rafinesque 1815																					
<i>Gouldia minima</i> (Montagu, 1803)	1			5	6	1	2			3			2	2	4	1			1	2	15
<i>Pitar rudis</i> (Poli, 1795)												1			1						1
<i>Ruditapes decussatus</i> (Linnaeus, 1758)			3	2	5				3	3	29	1	1		31				1	1	40
Corbulidae Lamarck, 1818																					
<i>Varicorbula gibba</i> (Olivi, 1792)	1	2			3			1		1	16	1	8	2	27	87	4	7	8	106	137
Pharidae H. Adams & A. Adams, 1856																					
<i>Pharus legumen</i> (Linnaeus, 1758)						1				1					1	1				43	43
Total	33	22	86	81	222	83	446	698	130	1357	317	13	357	89	786	110	36	24	160	330	2695

There are significant differences in abundances between seasons (Table 3): 1059 individuals were collected during the autumn (39% of total collected individuals), and fewer during spring (510), summer (479) and winter (248). The abundances at CML (1357 individuals) are significantly higher than in the three other channels (CK: 786, CP: 330, CM: 222; Table 3).

Table 3. Results of ANOVA tests on mollusc abundance and species richness, Shannon-Weaver Diversity (H') and Pielou’s Evenness (J'). CP: Ben Khlaf; CML: Maltine; CK: Kneiss; CM: Mimoum (df: degree of freedom; F: F test, the mean square of each independent variable divided by the mean square of the residuals; p : p value).

		df	F	p	Tukey Test
Species richness	Season	3	3.11	<0.05	Sum \neq Spr; Aut; Win
	Channel	3	2.07	0.11	-
Abundance	Season	3	1.66	0.18	-
	Channel	3	4.87	<0.01	CML \neq CP; CM
J'	Season	3	1.27	0.29	-
	Channel	3	5.62	<0.01	CML \neq CM
H'	Season	3	1.43	0.24	-
	Channel	3	3.48	<0.05	CM \neq CP
	Σ	98			

3.2. Spatial Patterns

The main patterns that can be clearly seen include the higher abundances at the CML stations (chiefly the shallow stations CML1 and CML2 on mixed sediment), and, conversely, the low abundances at all the stations of both channels CM and CP (Figure 3). The mean abundance decreases clearly in both CK and CML channels from the shallow stations towards the deeper stations (Figure 2). The mean abundances in both CM and CP are more erratic without any spatial pattern. While a low species richness is observed at some stations (CK4 at 7.4 m on sand sediment, CM5 at 10.0 m on gravel, CML1 at 1 m on mixed sediment, CP2 at 2.8 m on sand and CP7 at 0.9 m on sand), values are highest for CK3 at 5.3 depth on sand. No clear spatial patterns of species richness could be observed in the four channels according to water depth or sediment type (Table 3).

At a level of 30% of similarity, the dendrogram based on abundance data allows us to identify nine groups of stations (Figure 4). Six stations (namely CP1, CP2, CP7, CM5, CK4 and CK5) remain unique without any links to the other stations. The stations CML1 to CML4 form a single group, while the CM stations (except station CM5) form another distinct group, with the rest of the stations forming another group of 10 stations. This last group can be divided into three sub-groups corresponding to three channels: i.e., the stations CP3 to CP6, the stations CK1, CK2, CK3 and CK6, while both of the deeper stations CML5 and CML6 belong to a separate sub-group. Generally speaking, there is little similarity between the stations (lower than 60%) or between sets of stations according to their location in any given channel (Figure 4).

There are no significant differences regarding Species Richness, J' and H' between stations, but differences in abundance are observed between CML and CP as well as between CM and CK (Table 3).

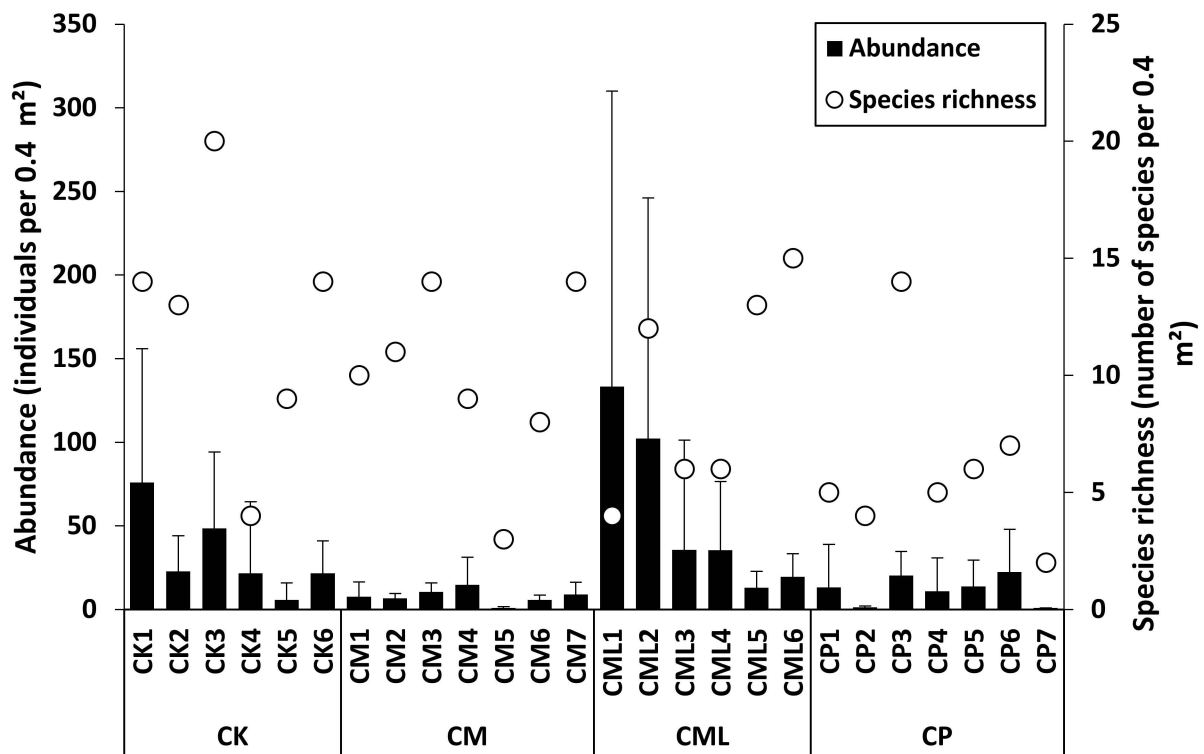


Figure 3. Mean Mollusca abundance (ν) (with standard deviation) and total species richness (μ) per 0.4 m² at the 26 stations of the four channels sampled four times from spring 2016 to winter 2017. CP: Ben Khlaf; CML: Maltine; CK: Kneiss; CM: Mimoun.

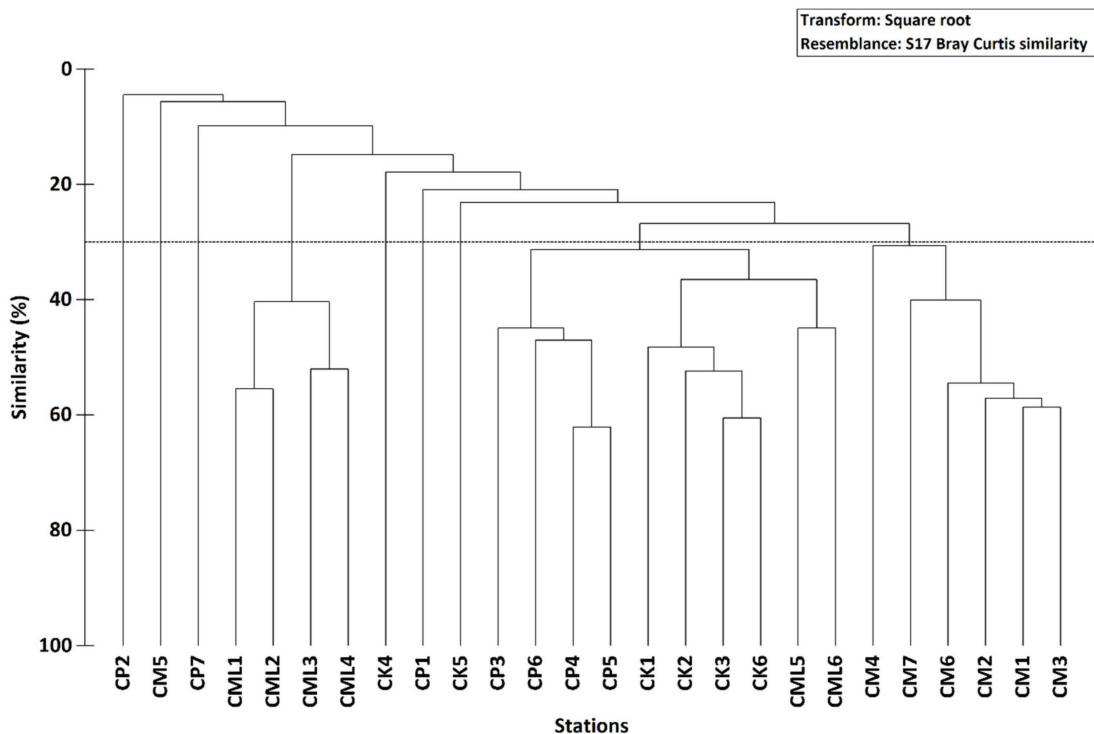


Figure 4. Cluster dendrogram showing distribution of mean abundances (for the four seasons at each of the 26 stations) as a function of the Bray-Curtis similarity index after square-root transformation of the abundances of the 57 mollusc species. CP: Ben Khlaf; CML: Maltine; CK: Kneiss; CM: Mimoun.

3.3. Seasonal Patterns

Figure 5 shows the seasonal variation in species richness and mean abundance of molluscs from the four channels (i.e., four seasons × four channels). There is a clear pattern of species enrichment in the channels in winter, except for CK, with a very low abundance throughout the year in CM and low abundances at CP. Both CM and CP show higher abundances in winter than during the other seasons, while high abundances are observed in summer and autumn at CML and in spring and autumn at CK. The H' values vary between 0.32 and 0.41 at CML in summer and autumn (due to the predominance of the Gastropod species *Bittium reticulatum* and *Cerithium scabridum*) and rises to 3.44 in winter at CM (Table 4). The evenness J' shows the same pattern, with low values for CML in summer and autumn (0.11) and high values for CM in winter (0.84) (Table 4). Nevertheless, we note a significant seasonal difference only in the case of Species Richness (Table 3).

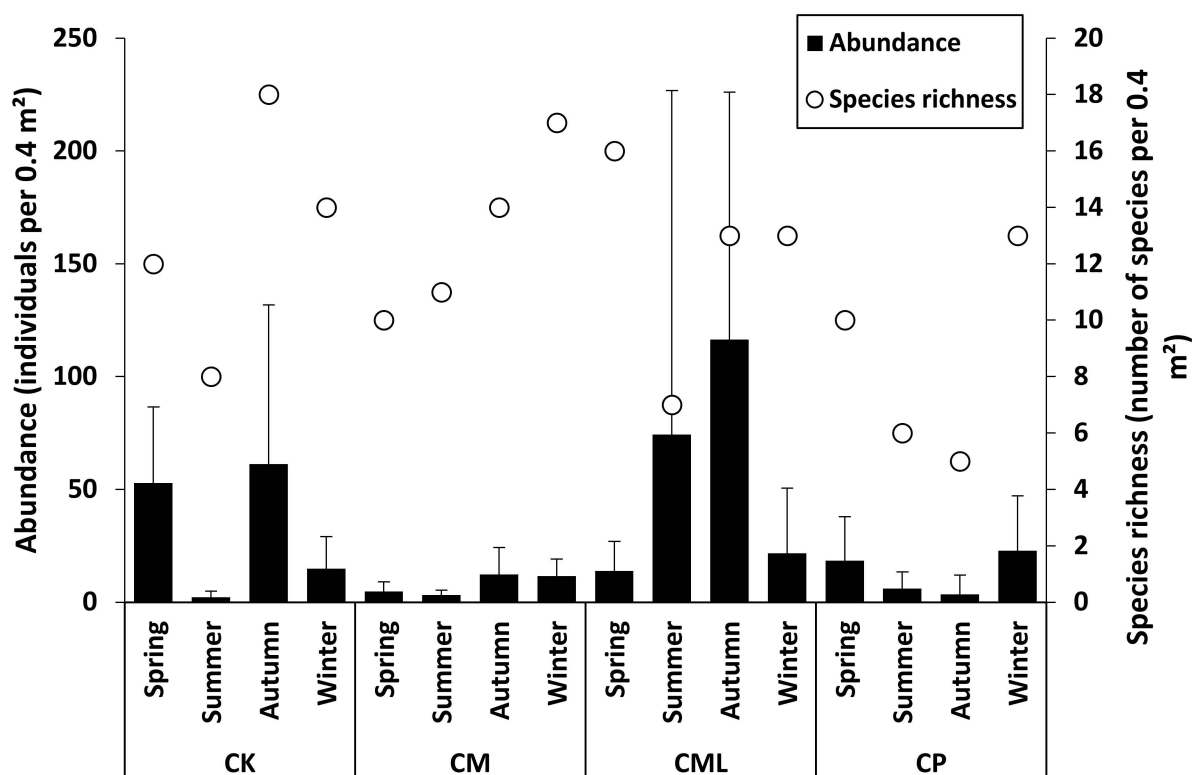


Figure 5. Mean Mollusca abundance (ν) (with standard deviation) and total species richness (μ) per 0.4 m^2 in the four channels sampled during the four sampling seasons from spring 2016 to winter 2017. CP: Ben Khlaf; CML: Maltine; CK: Kneiss; CM: Mimoun.

Table 4. Values of Shannon-Weaver Diversity (H') and Pielou’s Evenness (J') for the four seasons and four channels. CP: Ben Khlaf; CML: Maltine; CK: Kneiss; CM: Mimoun.

	Spring				Summer				Autumn				Winter			
	CM	CP	CML	CK	CM	CP	CML	CK	CM	CP	CML	CK	CM	CP	CML	CK
H'	2.46	1.34	3.28	2.62	2.86	1.65	0.32	2.78	2.71	2.13	0.41	2.39	3.44	2.83	2.13	2.10
J'	0.74	0.40	0.82	0.73	0.82	0.64	0.11	0.93	0.71	0.92	0.11	0.57	0.84	0.76	0.57	0.55

The similarity between the channels is illustrated using a dendrogram based on abundance data (Figure 6). Winter is clearly discriminated from the other seasons by the absence of any changes in the structuration of the molluscan community. The four channels show a clear distinction between samples according to the season rather than spatial location.

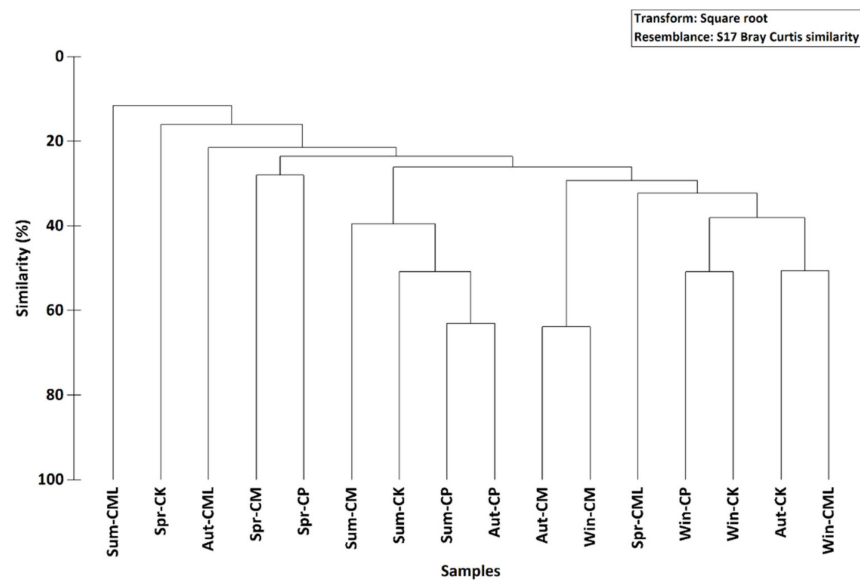


Figure 6. Cluster dendrogram showing distribution of mean abundances (at stations sampled in each of the four channels at the four seasons) as a function to the Bray-Curtis similarity index after square-root transformation of the abundances of amphipod species. CP: Ben Khlaf; CML: Maltine; CK: Kneiss; CM: Mimoun. Win: winter; Aut: autumn; Sum: summer; Spr: spring.

Nevertheless, the structure of the molluscan fauna shows a greater similarity between autumn and winter than between spring and summer, but still lacks any clear pattern.

3.4. Role of Environmental Factors

The db-RDA reveals that the first two factors (Depth and Temperature) explain 27.1% of the variance, with 14.8% for the first axis and 12.4% for the second axis (Figure 7). The stations of the four channels can be clearly separated according to environmental factors and characteristic species.

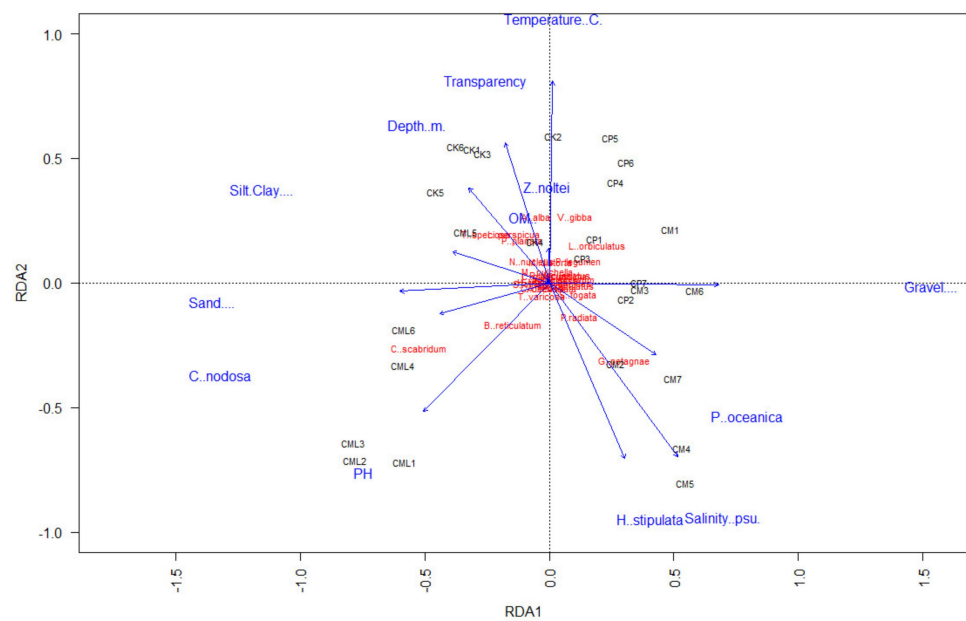


Figure 7. Distance-based Redundancy Analysis (db-RDA) for abundance of 39 benthic species at 26 stations in the four channels constrained by 13 abiotic factors: Depth, Temperature, Salinity, OM, Gravel, Sand, Silt-Clay, pH, Transparency, and presence of four phanerogams *Cymodocea nodosa*, *Halophila stipulacea*, *Posidonia oceanica* and *Zostera noltei*. In red, the name of the species, in Black the stations and in blue the environmental parameters.

The CP stations plot in the positive field of both axes, associated with the gravel and temperature factors, as well as the presence of suspension-feeder species such as *Loripes orbiculatus*, *Pharus legumen* (Linnaeus, 1758) and *Varicorbula gibba*.

The CK stations plot in the positive field of axis 1 and the negative field of axis 2, being linked with temperature, the silt-clay and sand fraction of the sediment, along with the presence of *Zostera noltei* as well as the suspension-feeder species *Moerella pulchella* (Lamarck, 1818), *Peronea planata*, *Abra tenuis*, *Nucula nucleus* (Linnaeus, 1758), *Lembulus pella* (Linnaeus, 1758) and *Cerastoderma glaucum* (Brugière, 1789), species such as deposit feeders *Abra alba* and the grazer species *Tricolia speciosa*.

The CM stations plot in the positive field of axis 1 and negative field of axis 2 and are associated with salinity, gravel and the presence of *Posidonia oceanica* and *Halophila stipulacea* as well as suspension-feeders such as *Gregariella petagnae* (Scacchi, 1832), *Gouldia minima* (Montagu, 1803), and *Pinctada radiata* (Leach, 1814) or the mixed suspension-deposit feeder *Ctena decussata* (O.G. Costa, 1829) which is a symbiont-bearing species [69].

Finally, the CML stations near the centre of the db-RDA plot in the negative field of both axes, being linked with sand sediment, the phanerogam *Cymodocea nodosa*, pH, and the gastropod grazer species *Bittium reticulatum* and *Cerithium scabridum*.

Thus, the db-RDA shows that the structure of molluscan assemblages in each channel can be explained by depth, sediment type and the presence of marine phanerogams associated in most cases with filter-feeder bivalves characteristic of fine sands and gravels.

4. Discussion

4.1. Main Characteristics of the Malacofauna of the Tidal Channel of the Gulf of Gabès

Despite recent studies mainly in Tunisia waters [3,5,11,14,16,17] (see Figure 8), there is still relatively little published research on molluscs from the coastal waters of southern Tunisia, including the Gulf of Gabès [6,7,28–37].

The patterns of the total macrofauna had been investigated in a previous study [47]. We give here the main results of the analyses in order to place the malacofauna in the context of the total macrofauna composition found in the four tidal channels studied in the Gulf of Gabès. With 2695 individuals collected during the sampling, the molluscs make up 11.5% of the total number of invertebrates collected during the study of the macrofauna of the tidal channels of the Gulf of Gabès and 18.3% of the taxa [47]. The polychaetes represent 52% and the crustaceans 32% of the abundance of macrofauna reported in the tidal channels during our study [47]. Measurements of the total abundance of molluscs reveal seasonal changes with maximum values in winter, spring, and lower numbers in summer similar to results for the other dominant groups of the macrofauna [47]. As observed for the molluscs, each tidal channel is characterized by specific features in the macrofauna, which is dominated by the polychaete *Cirratulus cirratus* (O.F. Müller, 1776), the amphipod *Microdeutopus anomalus* (Rathke, 1843) and the tanaids *Apeudopsis gabesi* Esquete, 2019 and *A. mediterraneus* (Bacescu, 1961). In a previous work, Ref. [47] had carried out a Hierarchical Ascendency Cluster Analysis on the 26 stations and the whole macrofauna; they showed that 85% of the stations are grouped according to their location in the four tidal channels. Moreover, they had performed a Principal Component Analysis on the same 26 stations to investigate the influence of each environmental parameter. They showed that sediment type is the most discriminant factor explaining the distribution of stations in each channel, while other factors such as depth, salinity, temperature and the presence of marine phanerogams played an important role in controlling the structuration of benthic macrofauna such as the mollusc assemblages observed in this present study. Molluscs such as *Bittium reticulatum* are among the dominant species in summer, while *Cerithium scabridum*, *Tricolia speciosa*, *Abra alba* and *Lamellaria perspicua* are dominant in autumn and *Abra alba* in winter. The dominance of the deposit surface feeder *Abra alba* reflects the presence of organic matter in the sediment in autumn and winter. Detritus in the tidal channels shows an increase in relation to the degradation of phanerogams during these periods and their accumulation in the channels. The high abundance of the grazer

Bittium reticulatum during the summer in the Maltine channel coincides with the abundance of macrofauna during this period. The grazer gastropods *Bittium reticulatum* and *Cerithium scabridum* are dominant in autumn in the Maltine channel, which is characterized by the presence of the phanerogams *Cymodocea nodosa*, *Zostera noltei* and *Halophila stipulacea* as well as macroalgae developed during the spring and summer.



Figure 8. Main sites where molluscs had been collected in Tunisian shallow waters (Map of Tunisia, from <https://d-maps.com/carte.php?numcar=1354&lang=fr>) (accessed on 30 January 2023).

4.2. Comparison with Other Mediterranean Malacofauna Assemblages

The present study has allowed us to record 56 species in the four tidal channels of the Gulf of Gabès, of which 28 are found in low numbers (1–4 individuals) and at only two stations (Table 2). For other Mediterranean coastal systems [70–75], a total of 87 species have been recorded in Lacco Ameno (Ischia, Italy) [72,73], 57 species in Porto Conte ((North-Western Sardinia, Italy) [74] and a maximum diversity of 136 species in the Stagnone di Marsala lagoon (Sicily) [75]. Nevertheless, it is recognized that the species richness of a particular area (whether of large extent or within a small zone) is related not only to the intrinsic global diversity of the considered area but also the sampling effort and the mesh sieve mesh used during a given campaign [76]. Consequently, it is difficult to compare

the species richness of different sites where different sampling coverage; nevertheless, Table 5 reports the taxonomic richness and abundance of molluscs and the total sampling surface for lagoons and shallow waters in the Gulf of Gabès as well as other Tunisian and Mediterranean sites [1–3,7,8,17,29–31,33,34,37,41–43,77–80].

For the intertidal zone of the Kneiss Islands, the diversity of molluscs reported in different studies (Table 5) ranges between 17 and 82 species in the *Zostera noltei* meadows. For the subtidal channels of the Skhira Bay, [37] reported 64 species, which is close to the number of species recorded in our study. In the shallow waters of the Boughara lagoon and south of Sfax, the species number is low: 26 and 19, respectively.

Studies on the northern Tunisian coast yield different assessments of species richness, varying from 13 in the Bizerte lagoon, 39 in the Bay of Tunis and 47 in the Cape of Zebib (Table 5). It is on the same order of magnitude in study on the malacofauna in other Mediterranean sites (Table 5), except along the south Spanish coast, where the species number is higher and ranges between 85 and 143. The mean abundances (69 ind. m^{-2} for the four channels in the tidal channels) is appallingly comprised between 22 (Mimoun Channel) and 142 (Maltine Channel (Table 5). The low abundances of molluscs found in the tidal channels of the Gulf of Gabès may be explained by the fact that the channels are constantly under strong currents, which remove the sediment and probably prevent the recruitment of juveniles. Furthermore, the mollusc abundance (76 ind. m^{-2}) in the Smir lagoon (Morocco) [1] is similar to that reported in our study, while the abundances were higher in other Mediterranean sites, reaching 2970 ind. m^{-2} in the Gialova lagoon (Greece) [80] (Table 5).

For the Skhira Bay in the Gulf of Gabès, Ref. [37] reports a mollusc abundance of 115 ind. m^{-2} for tidal channels of the Gulf of Gabès, confirming the low abundances in such high-energy environments. For the intertidal zone of the Kneiss Islands, the maximum density reaches 6000 ind. m^{-2} during spring, while the other mean values for the same intertidal area vary between 487 to 1913 ind. m^{-2} depending on the season and the presence of *Zostera noltei* meadows (Table 5). For the intertidal zone of the Kneiss Islands, a maximum abundance of 1010 per m^2 has been reported for *Scrobicularia plana* (da Costa, 1778), 866 for *Cerithium scabridum*, 812 for *Pirenella conica* (Blainville, 1829), 529 for *Loripes orbiculatus* and 392 for *Bittium reticulatum* [33]. These data on the Gulf of Gabès showed a higher abundance of mollusc on the intertidal zone than in the subtidal zone with high tidal currents. For other Tunisian areas, the abundance varies between 210 and 838 ind. m^{-2} (Table 5), while the abundance (76 ind. m^{-2}) in the Smir lagoon (Morocco) is similar to that reported in our study. Abundances are higher in other Mediterranean sites, reaching 2970 ind. m^{-2} in the Gialova lagoon (Greece) [81].

Eight species dominate the malacofauna in the tidal channels of the Gulf of Gabès: the bivalves *Abra alba* (324 specimens), *Cerastoderma glaucum* (66), *Loripes orbiculatus* (160), *Pinctada radiata* (53) and *Varicorbula gibba* (137), and three gastropods *Cerithium scabridum* (728), *Bittium reticulatum* (449) and *Tricolia speciosa* (167). To compare the dominant species found in our study with observations from other Mediterranean sites, top species per sites are reported in Table 6. Seventy-six species have been recorded, thus reflecting the high diversity of dominant species at the scale of the Mediterranean Sea (Table 6). Three species characterize the structure of the molluscan assemblages in the Mediterranean Sea: the bivalves *Cerastoderma glaucum* and *Loripes orbiculatus*, and the gastropod *Bittium reticulatum*.

Table 5. Taxonomic richness and abundance of molluscs (number of individuals per m²) and the total sampling surface and technique for lagoons and shallow waters in the Gulf of Gabès as well as other Tunisian and other Mediterranean sites. Depth in m; Nature of bottom-sediment and vegetation. References: 1. [7]; 2. [29]; 3. [17]; 4. [31]; 5. [33]; 6. [30]; 7. [31]; 8. [34]; 9. [2]; 10. [1]; 11. [79]; 12. [80]; 13. [8]; 14. [3]; 15. [77]; 16. [42]; 17. [43]; 18. [80]; 19. [41]; 20. [78]; 21. [37].

Study Area (Country)	Year	Depth (m)	Nature of Bottom-Sediment and Vegetation	Sampling Technique (Gear)	Sampled Area Per Station (m ²)	Total Sampled Area (m ²)	Taxonomic Richness	Abundance (ind./m ²)	Reference	
Gulf of Gabès, Tunisia	Four Tidal Channels: Maltine Channel, Kneiss Islands Channel, Ben Khlaf Channel and Mimoun Channel	Seasonally: March, July, September 2016, January 2017	3 to 15	Fine sand (FS), Gravelly sand with seagrass (<i>Cymodosa nodosa</i> , <i>Zostera noltei</i>) and macroalgae	Van Veen grab	0.4	40.8 Maltine: 9.6 Kneiss: 9.6 Ben Khlaf: 11.2 Mimoun: 10.4	56 29 32 30 21	69 (mean) 142 82 30 22	This study
	Boughrara lagoon	Seasonally: February 2012 to November 2013	0.2 to 3.1	FS	Scuba diving	0.75	9.75	26	112	1
	Kneiss Islands	January and March 2012	Intertidal	FS-Medium sand (MS) with <i>Zostera noltei</i>	Hand corer	0.032	0.608	24	639	2
	Kneiss Islands and Maltine Wadi	Seasonally: July 2013 to April 2014	Intertidal	FS-MS with <i>Zostera noltei</i>	Quadrat	1.25	10	82	487	3
	Kneiss Islands	September 2013 and December 2013	Intertidal	FS-MS with <i>Zostera noltei</i>	Hand corer	0.72	1.30	No data	Minimum 804 Maximum 1913	4
	Kneiss Islands	Spring 2013 and 2014	Intertidal	FS-MS with <i>Zostera noltei</i>	Hand corer	0.09	3.06	40	6000	5
	Kneiss Islands	March and April 2015	Intertidal	FS-MS with <i>Zostera noltei</i>	Hand corer	0.18	0.72	17	No data	6
	Kneiss Islands	April 2014 and Seasonally: October 2013, January, April and July 2014	Intertidal	FS-MS with <i>Zostera noltei</i>	Hand corer	0.09	3.06	46	No data	7
	Zone of South Sfax	Seasonally: April, July and October 2015, January 2016	1.5 to 8	FS-MS—Coarse sand Mud	Van Veen grab	0.2	9.6	19	No data	8
Others Mediterranean Sites Tunisia (others)	Skhira Bay	April 2010	1.5 to 24	FS-Coarse sand –Muddy sand Meadow of seagrass (<i>Cymodosa nodosa</i>) and macroalgae	Van Veen grab	0.2	5.6	64	115	21
	Bizerte lagoon (NE of Tunisia)	Monthly: September 2009 to September 2010	0.2 to 0.8	<i>P. oceanica</i> meadow	Scrapping	0.75	9	13	838	13
	Cap Zebib (NE of Tunisia)	Monthly: May 2007 to May 2008	3 and 12	<i>P. oceanica</i> meadow	Scuba diving	0.15	3.6	47	210	14
	Tunis Bay (N Tunisia)	May 2008	<5	Sandy mud	Scuba diving	0.4	4	39	No data	18
	Djerba Island (Gulf of Gabès, Tunisia)	July 2009	10 to 34	Sandy mud	Van Veen grab	0.36	3.96	3	No data	18
	Mellah lagoon (NE Algeria)	Seasonally: July 2008 to June 2009	1 to 5	FS with <i>Ruppia</i> spp.	Van Veen grab	0.3	18	11	188	9
	Smir lagoon (Mediterranean coast of Morocco)	Monthly: May 1999 to November 2000	1 to 2	FS-MS with macroalgae and seagrass (<i>Ruppia maritima</i> , <i>Zostera noltei</i>)	Hand corer	0.25	30	9	76	10
	Canuelo bay (Southern Spain)	Seasonally: June, September, December 2004 and March 2005	12–14	<i>Zostera marina</i> meadow	Scuba diving	0.32	1.27	85	1896	20
	Tyrrhenian Sea Ionian Sea (Southern Italia)	Spring 2015 summer 2015	10 to 20	FS <i>Posidonia oceanica</i> meadow	Airlift pump	0.48 0.75	1.92 3	36 38	355 135	15
	Calaburas (Southern Spain)	Seasonally: July, November 2007 and January, April 2008	2 to 3	<i>Posidonia oceanica</i> meadow	Airlift sampler	1.25 1.25	5 5	143 134	641 1101	11
	Calahonda (Southern Spain)	Seasonally: June, September, December 1995 and March 1996	0 to 1	Muddy sand with <i>Cymodocea nodosa</i>	Van Veen grab	0.25	7	23	2970	12

Moreover, five other species characterize the structure of the Tunisian malacofauna, the bivalves *Scobicularia plana* and *Ruditapes decussatus* (Linnaeus, 1758), along with the gastropods *Cerithium scabridum*, *Pirenella conica* and *Tricolia speciosa*. Apart from *Bittium reticulatum*, *Pirenella conica* and *Scobicularia plana*, the five other dominant species found in the Gulf of Gabès tidal channels have also been reported as dominant in other studies. Nevertheless, Refs. [36,37] have sampled numerous *S. plana* in the subtidal channels of the Kneiss Islands and the Ben Khlaf Channel. Moreover, although [37] recorded *Columbella rustica* (Linnaeus, 1758) at shallow depth in tidal channels of the Bay of Skhira and listed it among the dominant species, we failed to find this species in our study.

The dominant species found in our study are characteristic of areas of debris accumulation, associated with the presence of *Zostera*, *Halophila*, *Cymodocea* and *Posidonia* seagrass meadows. The molluscan fauna studied here is very similar to that of the shallow seagrass beds of Tunis Bay described by [16]. These authors reported a dominance of *Varicorbula gibba*, accompanied by most of the predominant species found in the current tidal streams of the Gulf of Gabès; in Tunis Bay, the temporal pattern of abundance is almost identical to that observed in the Gulf of Gabès, with maximum abundances in winter (January) becoming minimal in autumn (November). The distribution of molluscs in Tunis Bay is mainly related to depth, algae concentration and detritus availability. Similarly, most of the mollusc species recorded in Tunis Bay are also present in Bizerte lagoon [8] and in the Gulf of Gabès (this study). Plant components also play a key role in regulating the distribution and abundance of molluscs in these lagoons, where the mollusc community is typical of hydrodynamically influenced euryhaline lagoons.

Ref. [13] followed by [82] highlighted the fact that the mollusc fauna of the Gulf of Gabès shows a high level of endemism: i.e., 6–28% for the gastropods, while [46] gave a percentage of 7% for the molluscs. Nevertheless, in this study, we failed to find any endemic species in the tidal channels of the Gulf of Gabès, while the gastropods *Tricolia tenuis* (Michaud, 1829) and the three bivalves *Peronaea planata* (Linnaeus, 1758), *Moerella pulchella* (Lamarck, 1818), and *Pitar rudis* (Poll, 1795) are considered as endemic for the Mediterranean Sea [12,83].

Ref. [84] recorded 156 Non-Indigenous Species (NIS) of molluscs in the Mediterranean Sea, of which 17% are present in Tunisia. For Tunisian waters, [85] reported 26 molluscan NIS (17 gastropods, seven bivalves, two cephalopods and one polyplacophore). In our study, two NIS have been recorded: *Pinctada radiata* (53 individuals) and *Cerithium scabridum* (728 individuals). *Pinctada radiata* and *Cerithium scabridum* have been reported in the Bay of Tunis by [38] and in the Messina strait (Italy) by [86].

5. Conclusions

In conclusion, in the tidal channel of the Gulf of Gabès, the molluscs show four main patterns:

- (1) A decrease in species richness from the shallower to the deeper zones of the channels.
- (2) Seasonal changes in species richness and abundance, with higher values in autumn and winter than during the other two seasons. The seasons of autumn and winter appear favourable for the accumulation of algae and detritus in the channels after the period of macro-algae growth and reproduction.
- (3) Depth, sediment type and presence of the marine phanerogams are the main factors explaining the structuration of the malacofauna of the tidal channel of the Gulf of Gabès, forming four distinct assemblages. Fine sand and gravel suspension bivalve species account for the structure of the mollusc assemblages associated with each channel.
- (4) The Maltine channel shows higher abundances than the three other channels, which could be linked to the more extensive development of seagrasses and macroalgae at this site [47–52]. Moreover, a spatial pattern can be recognized in terms of species richness and abundance: the Maltine channel has the richest fauna, while the Mi-

moun channel has the poorest, with the Ben Khlaf and Kneiss channels showing intermediate values.

In the future, it would be interesting to study the mollusc population characteristics and their spatio-temporal changes in the long-term (>10 years), since molluscs are the main components of the macrofauna (along with polychaetes and amphipods) in intertidal and subtidal habitats of the Gulf of Gabès [47,52]. It will be a stimulating challenge to assess the future patterns of molluscan assemblages in relation to human activities (mainly over-fishing) in such sensitive ecosystems, which are under the pressure of climatic changes affecting the littoral and shallow environments of the Mediterranean Sea.

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