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Research Paper

Diversity and community structure of fish in the Bulgarian Black Sea shelf area

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ABSTRACT : - *The diversity and structure of the fish communities in the Bulgarian Black Sea shelf area were examined in spring, summer and autumn seasons during the period 2010 – 2012. We analyzed data from 146 demersal trawl hauls collected during four research surveys. Temporal patterns in structure of fish agglomerations were assessed using a combination of diversity measures (species richness, Shannon diversity and evenness) and multivariate analyses. In total, 35 fish species were identified, distributed among 23 families. The diversity and evenness indices were the highest in summer and autumn seasons and decreased in spring. Three main assemblages along the Bulgarian coast were recognized by cluster analysis and multidimentional scaling. Our study provides the first description of current diversity pattern in the Bulgarian Black Sea shelf area and baseline for future monitoring of the fish diversity and community structure.*

Keywords: - *Bulgarian Black Sea shelf zone, diversity, fish assemblages*

I. INTRODUCTION

Black Sea is isolated, semi-enclosed basin connected with the Mediterranean Sea and the Sea of Azov through the Bosphorous and the Kerch Straits. The drainage area of Black Sea is five times greater than the sea surface, leading to the organic enrichment and the high primary production [1]. Permanent density stratification of the water column and the permanent anoxic conditions below the depth 140-200 m [1][2][3] limited the distribution of the marine biota to the deeper areas. The specific characteristics of the basin determine the low number of fish species in the Black Sea (193), which is 2.3 times lower compared to the number of fish species in the Mediterranean - 500 [4] and the high sensitivity of the basin to the anthropogenic stress. Eutrophication, alien species and the excessive commercial fishing in the shelf area has exerted significant pressure on the fish populations and their habitats since the 1970-ties [2][5] and have become the critical ecological problems for the Black Sea ecosystem that have resulted in long-term decline in the species abundance and diversity [6].

Black Sea ichthyofauna included fish species divided into three groups - brackish Ponto-Caspian relicts, cold-water species with Boreal-Atlantic origin and warm - water species with Mediterranean origin [7]. The last two groups include the most widely spread and commercially important fish species in the Black Sea. The cold-water species with Boreal-Atlantic origin (*Sprattus sprattus*, *Merlangius merlangus*, *Scophthalmus maximus* etc.) spawns during the autumn – winter season and warm - water species with the Mediterranean origin (*Engraulis encrasicolus*, *Trachurus mediterraneus*, *Sarda sarda*, *Pomatomus saltatrix* etc.) – during the summer in the surface layers of the North – Western Black Sea shelf zone.

Bulgarian Black Sea area amounted at 34 523 km^2 including Exclusive economic Zone (EEZ) up to 200 nautical miles, from which the shelf zone down to 200 m depth represented 12 105 km^2 [8]. First investigations of the fish fauna in the Bulgarian Black Sea waters were initiated in early 20s years of XX century and generally were descriptive, giving the rough idea about the species composition, which at this time listed 92 species [9]. Later, the 135 species belonging to the 49 families were recorded, including 23 fresh water species inhabiting the coastal lakes and the rivers mouths, which enter into the Black Sea [10]. Recent studies identify 134 fish species belonging to 44 families, which inhabit permanently, seasonally or sporadically Bulgarian Black Sea coastal waters [11][12][13]. From all 134 species, 23 are Ponto-Caspian relicts, 10 originate from the Atlantic and 100 are Mediterranean immigrants. Approximately 64 species in the Bulgarian waters migrate towards the shore and back and all over the Black Sea, Sea of Azov and the Mediterranean. Although the taxonomic studies on the fish diversity in the Bulgarian Black Sea are relatively plentiful

[10][11][12][13], specialized studies on the fish assemblages and temporal community structure in the Bulgarian shelf zone are deficient. Species diversity and community structure is of great importance in enclosed and semi-enclosed marine ecosystems, such as the Black Sea, which is highly sensitive to human impacts and activities, as fisheries, shipping and tourism, which are concentrated over the shelf zone [2][3].

The goal of the present study is to provide description of the fish communities' diversity, structure and distributional patterns in the Bulgarian Black Sea shelf area in seasonal aspect by application of diversity measures and community similarity analysis.

II. MATERIAL AND METHODS

2.1. Study area

The study area embraces Bulgarian Black Sea continental shelf up to 200 m – Fig.1. The Black Sea basin is characterized with the specific hydrology and strong vertical stratification into two layers with different hydrological characteristics, divided by a constant picnocline (halocline) and anoxic conditions under 150 – 200 m [1][2]. The upper layer waters are characterized by a predominantly cyclonic, strongly time-dependent and spatially-structured basin wide circulation [3], which mixing the Mediterranean underflow (characterized typically by temperature of 13-14^{o}C and salinity of 35-36‰) and the freshwater river input.

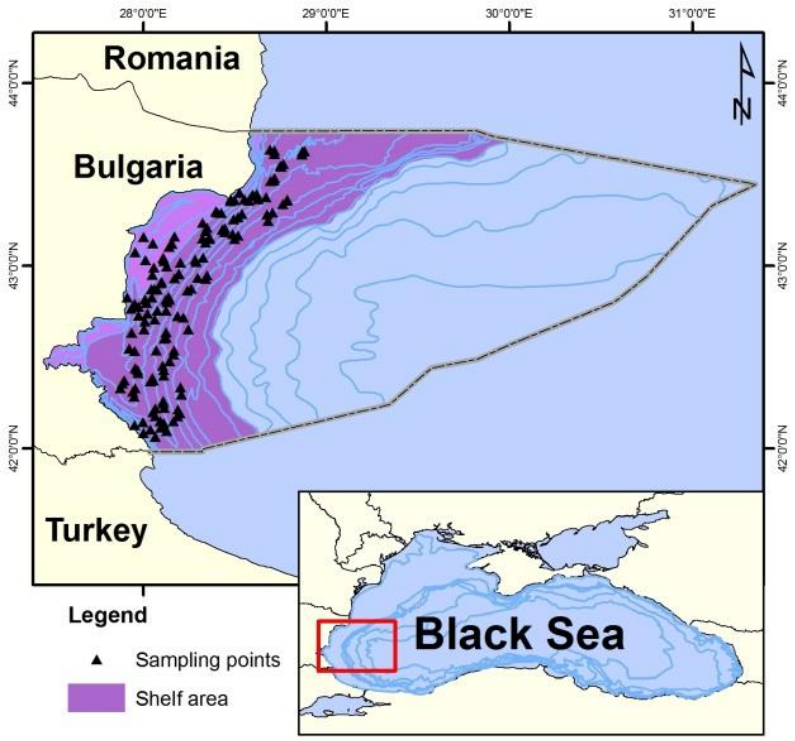

Figure 1. Study area and sampling points in the Bulgarian Black Sea shelf zone.

The temperature regime follows the seasonal alterations in the solar intensity. During the winter season, the intensive water exchange leads to temperatures of 2.0 – 3.0^{o}C in the whole water column over the shelf zone [14]. In spring, the surface layer starts to warm up to the average temperature of 24.5 – 25 C, followed by the thermocline formation [14]. In summer, the thermocline drop to the depths of 25 – 40 m, after which the water temperatures are about 6 - 8^{o}C.

The salinity of the surface waters in front of the Bulgarian coast fluctuated between 16 ‰ - 18 ‰, at depths about 100 m increased to 20 ‰ and at depth of 2000 m reached 22 - 24 ‰ [15][5].

Specific hydrological and hydrochemical peculiarities of the Black Sea significantly influenced the composition and abundance of the fish fauna, which is less abundant compared to the Mediterranean Sea [4].

2.2. Sampling methods

The distribution and the community structure of the fish fauna in the Bulgarian Black Sea shelf area were investigated during four consecutive surveys in spring, summer and autumn seasons during the period 2010 - 2012 (October 2010, November 2011, May 2012 and July 2012). The sampling was accomplished by

bottom trawl with the stretched mesh size of the net codend - 8 mm. Overall, 146 hauls with standard duration of 1 hour were carried out between depths of 15 m and 100 m. The number of hauls ranged between 32 and 37 per survey. The catch at each location was sorted and the fishes were identified to the species level, weighted and counted.

2.3. Statistical analyses

Prior to the analysis, the raw data of abundance by species and stations were standardized to the number of individuals per 1 km^2. The standardized abundance data was used for the calculation of three common metrics of functional diversity by seasons: species richness (S) – the number of species within a community, Shannon – Wiener diversity index (H') - weights species by abundance and evenness (Pielou's J) - measure of the degree to which the abundances are divided equally among the species present. The mean values of the diversity indices were calculated and compared across the studied seasons using one-way analysis of the variance (ANOVA). Numbers of species were analyzed as numbers of species per haul. The frequency of occurrence (FO) by species was calculated as percentage of occurrence of each species in the hauls.

Multivariate community analysis was carried out with the statistical package PRIMER 6 [16]. Hierarchical cluster analysis was used to separate groups of stations with similar species assemblages. The data matrix of abundances for all fish species was square root transformed and a resemblance matrix based on the Bray-Curtis similarity coefficient (Bray-Curtis, 1957) was employed to assess the similarity between every pair of samples depending on the season. The possible seasonal effect on fish structures was tested for each season through a one-way nonparametric analysis of similarity (ANOSIM). Hierarchical agglomerative clustering procedure using group-average linking and ordination by Multidimensional Scaling (MDS) were performed on the pairwise similarities matrix to study the community pattern and differentiation of communities [17]. The percentage contribution of each species to the similarity within a group was determined by taking the average over all pairs of samples within a group by means of SIMPER analysis [17] and the typical species of the community were defined statistically.

III. RESULTS

3.1. Species composition

Overall, 35 species belonging to 23 families were identified – Table 1. The most abundant families were Gobiidae, Clupeidae and Blenniidae. The number of species per sampling location varied from 1 to 16. In terms of the number of species per family, Gobiidae (7 species) was the most diverse followed by Clupeidae (3 species) and Blenniidae (3 species), (Table 1). Most of the fish species were small-sized and non-migratory pelagic and demersal dwellers. Considering the origin of the species, 22 were Mediterranean immigrants (63%), 7 species (20%) were Ponto – Caspian relicts and 6 species (17%) were Boreal – Atlantic relicts (Table 1). The most common species in the Bulgarian shelf area were *M. merlangus*, *S. maximus* and *N. melanostomus* observed with the frequency of occurrence over 50 %.

Table 1: List of species collected over the Bulgarian Black sea shelf area. P – C: Ponto – Caspian relict, B – A: Boreal – Atlantic relict, M – Mediterranean immigrant, FO: frequency of occurrence of each species (%).

Family	Species	Origin	FO
SQUALIDAE	*Squalus acanthias* Linnaeus, 1758	B - A	21.23
RAJIDAE	*Raja clavata* Linnaeus, 1758	B - A	19.18
DASYATIDAE	*Dasyatis pastinaca* (Linnaeus, 1758)	B - A	4.11
CLUPEIDAE	*Sprattus sprattus* (Linnaeus, 1758)	B - A	42.47
CLUPEIDAE	*Alosa immaculata* Bennett, 1835	P - C	49.32
CLUPEIDAE	*Alosa tanaica* (Grimm, 1901)	P - C	3.42
ENGRAULIDAE	*Engraulis encrasicolus* (Linnaeus, 1758)	M	5.48
BELONIDAE	*Belone belone* (Linnaeus, 1761)	M	0.68
LOTIDAE	*Gaidropsarus mediterraneus* (Linnaeus, 1758)	M	24.66
GADIDAE	*Merlangius merlangus* (Linnaeus, 1758)	B - A	89.73
SYNGNATHIDAE	*Syngnathus variegatus* Pallas, 1814	M	1.37
SYNGNATHIDAE	*Hippocampus guttulatus* Cuvier, 1829	M	6.16

Family	Species	Origin	FO
POMATOMIDAE	*Pomatomus saltatrix* (Linnaeus, 1766)	M	30.82
CARANGIDAE	*Trachurus mediterraneus* (Steindachner, 1868)	M	34.93
MULLIDAE	*Mullus barbatus ponticus* Essipov, 1927	M	48.63
LABRIDAE	*Symphodus roissali* (Risso, 1810)	M	2.05
LABRIDAE	*Symphodus cinereus* (Bonnaterre, 1788)	M	1.37
TRACHINIDAE	*Trachinus draco* Linnaeus, 1758	M	47.26
URANOSCOPIDAE	*Uranoscopus scaber* Linnaeus, 1758	M	4.11
BLENNIIDAE	*Parablennius sanguinolentus* (Pallas, 1814)	M	1.37
BLENNIIDAE	*Parablennius tentacularis* (Brunnich, 1768)	M	0.68
BLENNIIDAE	*Coryphoblennius galerita* (Linnaeus, 1758)	M	2.05
OPHIDIIDAE	*Ophidion rochei* Muller, 1845	M	1.37
SCORPAENIDAE	*Scorpaena porcus* Linnaeus, 1758	M	18.49
GOBIIDAE	*Pomatoschistus minutus* (Pallas, 1770)	M	0.68
GOBIIDAE	*Gobius niger* Linnaeus, 1758	M	19.18
GOBIIDAE	*Ponticola cephalargoides* (Pinchuk, 1976)	P - C	2.74
GOBIIDAE	*Neogobius melanostomus* (Pallas, 1814)	P - C	52.74
GOBIIDAE	*Neogobius ratan* (Nordmann, 1840)	P - C	1.37
GOBIIDAE	*Neogobius gymnotrachelus* (Kessler, 1857)	P - C	0.68
GOBIIDAE	*Mesogobius batrachocephalus* (Pallas, 1814)	P - C	4.79
TRIGLIDAE	*Chelidonichthys lucerna* (Linnaeus, 1758)	M	2.74
SCOPHTHALMIDAE	*Scophthalmus maximus* (Linnaeus, 1758)	M	53.42
PLEURONECTIDAE	*Platichthys flesus* (Linnaeus, 1758)	B - A	42.47
SOLEIDAE	*Pegusa lascaris* (Risso, 1810)	M	5.48

3.2. Diversity pattern

The spatial pattern in the distribution of species richness showed clear seasonality (Fig. 2). The average species richness was the highest during the autumn seasons of 2010 and 2012 (Table 2) and the lowest – during the spring season of 2012. The maximum of 16 fish species registered per station was recorded in the summer of 2012. The difference between estimated average values by seasons was statistically significant ($p<0.005$, ANOVA).

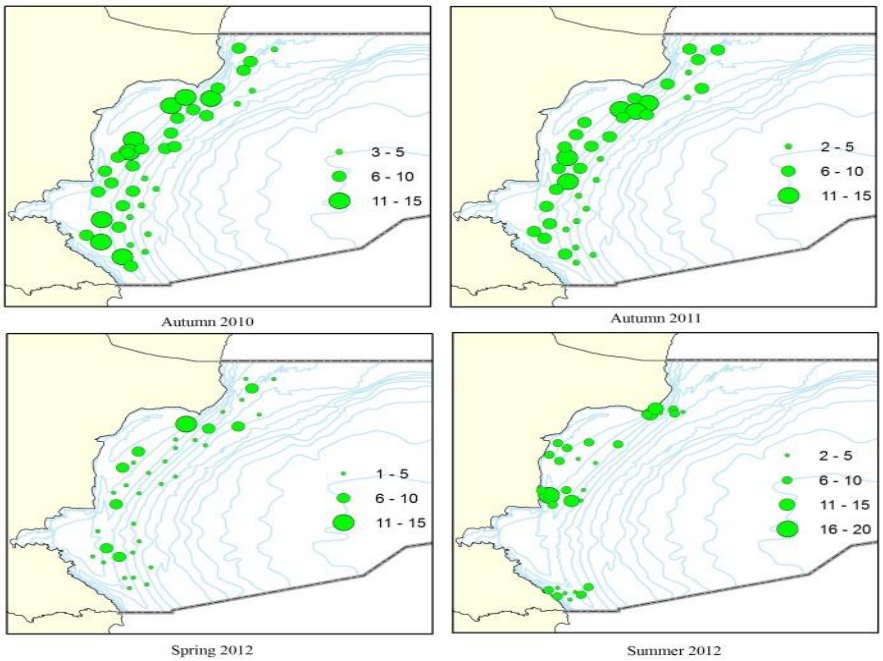

Figure 2. Species richness (S) by seasons in the Bulgarian Black Sea shelf area.

Table 2: Functional diversity of fish community by seasons in the Bulgarian Black Sea shelf area.

Metrics	*Autumn 2010*	*Autumn 2011*	*Spring 2012*	*Summer 2012*
Species richness (S)	7.75	7.38	3.97	6.69
Shannon – Wiener diversity (H')	1.09	0.84	0.44	0.75
Evenness (Pielou's J)	0.38	0.28	0.28	0.30

In the present study, the index of Shannon – Wiener diversity (H') showed significant ($p<0.001$, ANOVA) variation across seasons – Fig. 3, with the higher values during the autumn seasons of 2010 and 2011 and the lowest value in spring 2012 (Table 2).

Fish communities along the Bulgarian coast were characterized with low equitability and high dominance – Fig. 4. Calculated evenness (Pielou's J) was the highest in autumn season of 2010 and during the rest of the studied period ranged between 0.28 – 0.30 (Table 2).

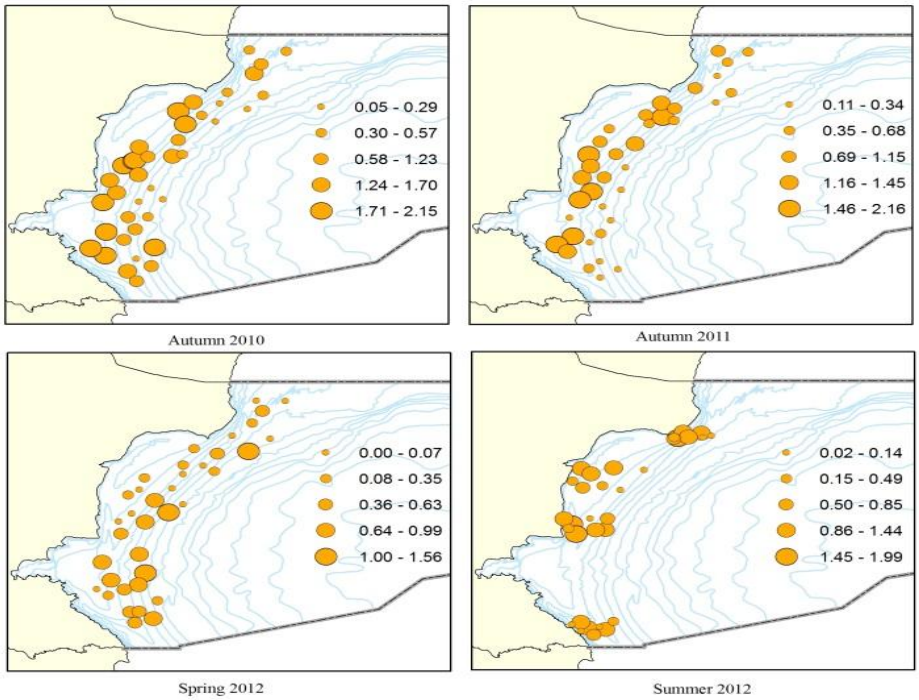

Figure 3. Shannon – Wiener diversity (H') by seasons in the Bulgarian Black Sea shelf area.

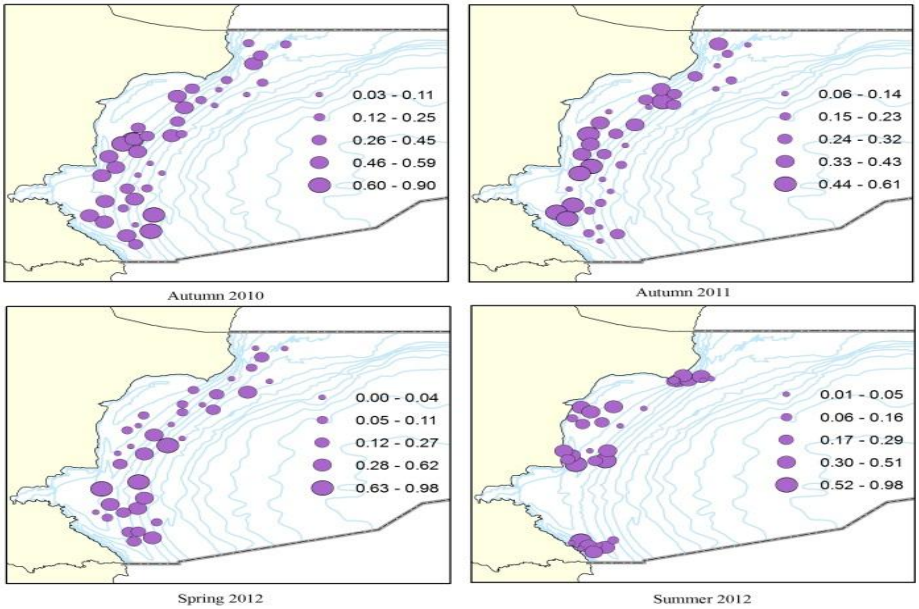

Figure 4. Evenness (Pielou's J) by seasons in the Bulgarian Black Sea shelf area.

3.3. Community structure

An analysis of similarities (one-way ANOSIM) revealed differences in the fish assemblage structures between the seasons ($R = 0.35$, $P < 0.001$). Therefore, three main assemblages along the Bulgarian coast were recognized by cluster analysis with the similarity level of 30% - Fig. 5. Samples separation in the MDS (2D stress=0.15) plot corresponded to the pattern revealed by cluster analysis, but overlapping of communities across seasons was observed.

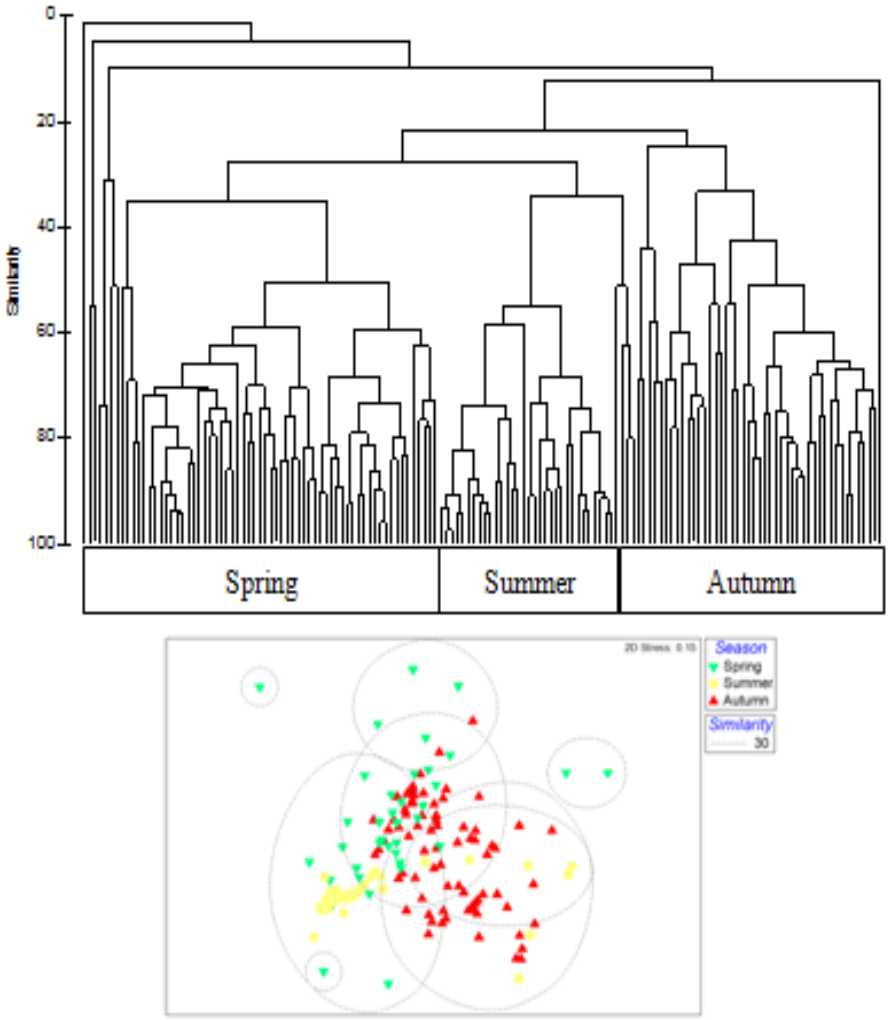

Figure 5. Dendrogram and two-dimensional MDS ordination based on abundance data from samples collected in the Bulgarian Black Sea shelf area during the period 2010 – 2012.

Using SIMPER, the species that most contributed within the groups by seasons was identified and the results were shown on Table 3. The main contributing species within autumn (2010 and 2011) group with the similarity of 39.84% were whiting (*M. merlangus*) and red mullet (*M. barbatus*). The fish community was composed by local, non-migratory species as whiting, greater weever (*T. draco*), round goby (*N. melanostomus*) and turbot (*S. maximus*) and migratory species as red mullet, bluefish (*P. saltatrix*) and horse mackerel (*T. mediterraneus*) , which left the Bulgarian Black Sea sector during the winter season. The migratory species are of high commercial interest and the main target species for the Bulgarian fisheries during the autumn season.

SIMPER analysis revealed that in spring samples of 2012, two species (*M. merlangus, S.sprattus*) contributed to the 94% of the average Bray–Curtis similarity (Table 3). These species are local, cold-water and migrate only to the open sea and backward through the year.

The community in summer season was characterized by the similarity of 46.37% between stations and the samples were dominated by whiting and sprat (92%).

Table 3: Species mostly contributing to within-group average similarity (cut-off: 95% of similarity level) and among groups dissimilarity. Av.SIM: Average similarity, Cont.%: Percentage contribution of each species, Cum.%: Cumulative contribution to similarity, Av.DISS: Average dissimilarity.

Group Autumn			**Group Spring**		
Av. SIM = 39.84			**Av. SIM = 30.48**		
Species	**Cont.%**	**Cum.%**	**Species**	**Cont.%**	**Cum.%**
M. merlangus	58.96	58.96	*M. merlangus*	79.39	79.39
M. barbatus	11.33	70.3	*S. sprattus*	14.36	93.76
T. mediterraneus	9.27	79.57	*M. barbatus*	2.33	96.09
A. immaculata	5.35	84.91			
P. saltatrix	4.98	89.9			
T. draco	2.74	92.63			
N. melanostomus	2.22	94.85			
S. maximus	1.49	96.34			
Group Summer			**Groups Autumn & Spring**		
Av. SIM = 46.37			**Av. DISS = 71.76**		
Species	**Cont.%**	**Cum.%**	**Species**	**Cont.%**	**Cum.%**
M. merlangus	66.35	66.35	*M. merlangus*	35.6	35.6
S. sprattus	25.48	91.83	*S. sprattus*	17.34	52.94
N. melanostomus	4.25	96.08	*M. barbatus*	12.87	65.81
			T. mediterraneus	12.22	78.03
			P. saltatrix	6.68	84.71
			A. immaculata	3.13	87.85
			N. melanostomus	2.48	90.33
			T. draco	2.29	92.62
			S. maximus	1.27	93.88
			P. flesus	1.24	95.12
Groups Autumn & Summer			**Groups Spring & Summer**		
Av. DISS = 78.26			**Av. DISS = 73.09**		
Species	**Cont.%**	**Cum.%**	**Species**	**Cont.%**	**Cum.%**
M. merlangus	40.44	40.44	*M. merlangus*	47.91	47.91
S. sprattus	27.77	68.21	*S. sprattus*	32.81	80.71
M. barbatus	9.1	77.31	*M. barbatus*	5.96	86.68
T. mediterraneus	6.89	84.2	*N. melanostomus*	5.4	92.08
N. melanostomus	4.13	88.33	*S. maximus*	1.05	93.13
P. saltatrix	3.83	92.16	*T. mediterraneus*	0.91	94.03
A. immaculata	1.37	93.53	*T. draco*	0.8	94.84
T. draco	1.07	94.6	*P. flesus*	0.76	95.6
S. maximus	0.89	95.49			

IV. DISCUSSION

In the present study, the Bulgarian Black Sea shelf area was investigated during the spring, summer and autumn seasons, focusing on the seasonality in fish diversity and assemblage structure. The study showed that the Bulgarian shelf zone is inhabited by variety of fish species with the commercial and conservation importance. In the current study, 35 fish species were identified, corresponding to the 27.78 % of the total number of species (n = 126), reported for the Bulgarian Black Sea coast [11]. Seasonal alterations in the Black Sea environment influenced the fish diversity and community structure which is composed by local and migratory species with the specific preferences to the surrounding environment. In general, the dominant and most abundant species as *M. merlangus*, *S.maximus*, *N. melanostomus* and *S. sprattus* are non-migratory and spend their life cycle in the Black Sea. The demersal species as turbot make only limited movements along the coast and to the offshore areas and backward related to the reproduction and feeding processes. The benthopelagic (*M.merlangus, S.acanthias*) and pelagic boreal species (*S. sprattus*) migrate to the offshore areas during the summer and autumn seasons and return in the shelf zone during the winter and spring for the reproduction [10]. The migratory species with the Mediterranean origin (*P. saltatrix*, *T.mediterraneus*, *E. encrasicolus*), inhabit Bulgarian shelf area in spring, summer and autumn seasons and left the area for the wintering in the southeast areas [2].

Three distinctive fish assemblages were identified in the study area associated with the seasonality of the environment and composed by species of commercial interest. The autumn assemblages in 2010 and 2011 were characterized by the predominance of the species like *M. barbatus, T. mediterranus, P. saltatrix* and *A. immaculata* which are the main target for the Bulgarian fisheries in that season. The main determining feature associated with the structure of the fish assemblages is the temperature and the drop triggered the wintering migrations of these species.

In spring season of 2012, the fish agglomerations in the shelf zone were composed by non-migratory species as sprat (*S.sprattus*) and whiting (*M.merlangus*), which contribute to the 94% within-group average similarity (Table 3) and by the less abundant species as *S. maximus, N. melanostomus, T.draco, A.immaculata, R. clavata* and *S.acanthias*. During the summer 2012, the local species were present and the migratory species like *M.barbatus, T. mediterraneus* and *E.encrasicolus* were recorded.

In our study, the multivariate analyses detect seasonal changes in the overall structure of the fish assemblages between seasons. Results suggested that the local species (*M. merlangus, S. sprattus, S. maximus*) represent significant component of the fish communities all year round and during the warmer seasons the migratory species enhance the diversity. The overall structure of the fish communities presented here supports the previous studies [10][11][12][13] that the shelf zone is inhabited by diverse fish assemblages and represents very important spawning, feeding and nursery area for the most commercially important fish species. Therefore, the Bulgarian fishery is concentrated over the shelf zone and the fishing activities exerted negative impact on the communities.

V. CONCLUSION

The present study examines the seasonality in the diversity, distribution and structure of fish assemblages in the Bulgarian Black Sea shelf area. The obtained results showed that the observed communities were taxonomically rich and comprised by species with Mediterranean, Ponto – Caspian and Boreal – Atlantic origin. Our findings indicated variations in the structure of fish assemblages, different in composition and abundance between seasons. The most diverse and evenly distributed were the communities during the summer and autumn seasons and less diverse – in spring, when the agglomerations were composed mostly by local, non-migratory species.

The study results provide the first narrative of current diversity pattern in the Bulgarian Black Sea shelf area and baseline for future monitoring of the fish diversity and community structure. The findings could contribute to better fishery policy implementation and designation of marine protected areas at national and regional level.

REFERENCES

[1] M. E. Vinogradov, V. V. Sapoznikov, E. A. Shushkina, *The Black Sea Ecosystem* (Nauka, Moscow, 1992).

[2] K. Prodanov, K. Mikhaylov, G. Daskalov, K. Maxim, E. Ozdamar, V.Shlyakhov, A.Chashchin and A. Arkhipov, *Environmental management of fish resources in the Black Sea and their rational exploitation* (GFCM Studies and Reviews, Rome, 1997).

[3] BSC 2008, *State of the Environment of the Black Sea (2001-2006/7)* (Black Sea Commission Publications, Istanbul, 2008).

[4] B.E Zaika, Marine biological diversity of Black Sea and Eastern Mediterranean, *Marine ecology, 51,* 2000, 59-63.

[5] Yu. Zaitsev and V. Mamaev, *Marine biological Diversity in the Black Sea. A study of change and decline* (UN Publications, New York, 1997).

[6] TDA, *Black Sea Transboundary Diagnostic Analysis* (GEF Black Sea Environmental Programme publication, Istanbul, 2007).

[7] T.S. Rass, Modern views on the composition of fish fauna of the Black Sea and its changes, *Journal of Ichthyology, 27(2),* 1987, 179-187.

[8] E. Peneva, V. Slabakova and S. Moncheva, Pelagial, in S. Moncheva and V. Todorova (Ed.), *Initial assessment of the state of marine environment regarding art.8 of MSFD*, 1 (Ministry of Environment and Waters of Bulgaria, Varna, 2012) 30-34.

[9] P. Drensky, Contribution a etude des poisons de la Mer Noire, recoltes sur le cotes Bulgares, *Journal of Bugarian Acaemy of Sciences, 25*, 1923, 59-112.

[10] S. Stoyanov, Z. Georgiev, L. Ivanov, D. Hristov, P. Kolarov, K. Alexandrova, M. Karapetkova M., *Fishes in the Black Sea (Bulgarian coast)* (State press, Varna, 1963).

[11] K. Prodanov, K. Dencheva and L. Ivanov, Biodiversity of the ichthyofauna in the Bulgarian Black Sea waters, in *National Biological Diversity Conservation Strategy,* 1 (The Biodiversity Support program, Sofia, 1993) 547-566.

[12] M. Karapetkova and M.Zivkov, *Fishes in Bulgaria* (Publ. House"Gea-Libris", Sofia, 2006).

[13] T. Stefanov, Fauna and distribution of fishes in Bulgaria, in V. Fet and A. Popov (Ed.), *Biogeography and Ecology of Bulgaria,* (Springer, The Netherlands, 2007) 109-139.

[14] A. Konsulov, Trophic conditioning in the distribution of sprat – Sprattus sprattus sulinus (Antipa), *Proceedings of Institute of Fish Resources, 14*, 1975, 71-82.

[15] A. Rojdestvenski, *Hydrochemestry of the Bulgarian Black Sea sector* (Publ. House of Bulgarian Academy of Sciences, Sofia, 1986).

[16] K.R. Clarke and R.N. Gorley, *PRIMER v6: User Manual/Tutorial* (PRIMER-E, Plymouth, 2006).

[17] K.R. Clarke and R.M. Warwick, *Change in marine communities: an approach to statistical analysis and interpretation. 2nd edition* (PRIMER-E, Plymouth, 2001).