Effects of Interannual Environmental Changes on Juvenile Fish Settlement in Coastal Nurseries: The Case of the Adriatic Sea

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This study tested generality in the settlement and recruitment patterns of juvenile fish in the coastal Mediterranean as driven by interannual environmental differences. A multivariate analysis of juvenile fish community data, sampled over three consecutive years, was conducted to elucidate the interannual changes of new settlers' occurrence and abundance in different nurseries along the eastern Adriatic coast. Sites were assigned to four groups of nurseries based on water type (marine or transitional) and geographical position (north or south). Statistically significant interannual differences were found in temperature but not in salinity. In general, species occurrence significantly fluctuated between years and seasons. The highest total abundance of juveniles was observed in the significantly warmer year 2018 within all study groups. Defined groups expressed significant annual differences in species richness and abundance related to variations in water temperature and salinity as environmental factors for the same consecutive years. Nurseries within transitional waters in the north are more prone to interannual water temperature changes. The associated community composition differed most from those recorded in southern marine waters, where groups were mostly defined by salinity influence and were least sensitive to interannual temperature fluctuations. The cold and rainy spring in 2019 caused late settlement and longer retention of specific economically and ecologically important fish species in the nurseries. The results suggested that settlers' delay or retention due to negative temperature deviation in the spawning period were linked to the nurseries located in the northern transitional waters that are under a stronger coastal influence. These delays can have ecological consequences on population dynamics and on inter- and intraspecific relationships within specific nursery communities.

Keywords: juvenile fish, community, settlement, nurseries, interannual changes

INTRODUCTION

Coastal areas are commonly acknowledged as highly productive and valuable ecosystems that provide many favourable habitats for fish, while also supporting fundamental ecological links with other environments (Duarte, 2000; Beck et al., 2001; Hinz et al., 2019). Their role in early life stages, and also as foraging and spawning grounds for non-coastal fish species (Harmelin-Vivien, 1984;

Francour et al., 1999) is recognised throughout the Mediterranean and worldwide (Francour, 1997; Deudero et al., 2008). There is ambiguous evidence for the importance of habitat characteristics in driving patterns of population dynamics (Vasconcelos et al., 2013). Highly valuable habitats generally provide shelter and an abundance of food to juveniles that may facilitate their survival and growth processes, thus contributing to overall production and population stability (Scharf et al., 2006; Dahlgren and Eggleston, 2014; Cheminée et al., 2016). Knowing the role of habitat use is particularly valuable from a conservation and management perspective, since the vulnerability of coastal habitats to anthropogenic stressors is increasing (Sala, 2004; Halpern et al., 2008; Sala et al., 2012). Marine ecosystems have been degraded in many areas, particularly in the Mediterranean, and many critical coastal habitats are no longer available or adequate to provide nursery, feeding, or reproductive functions, with negative consequences on production and renewal of populations (Guidetti et al., 2002; Barbier et al., 2011; Matić-Skoko et al., 2020).

Population dynamics, as a complex process including reproduction, growth, survival, and demographic rates, are under environmental influences (Vasconcelos et al., 2013) and therefore they are reflected in the fisheries dynamics of exploited species (Hixon and Johnson, 2009). However, the variability of spawning success and the relationship between spawning and recruitment are among the least understood aspects of fish population dynamics. The process starts with the transition between pelagic and benthic stages (Brothers et al., 1983). Settler supply and nursery habitat availability are key factors affecting settlement and recruitment processes, determining the renewal of populations and shaping the structure of adult assemblages (Cheminee et al., 2011). In the Mediterranean, a variety of fish species inhabit coastal nurseries, some of them for life while others just for a part of life (Dulčić et al., 2007; La Mesa et al., 2011; Félix-Hackradt et al., 2014; Cheminée et al., 2017).

Settlement of juvenile fishes occurs year-round, though most species have a settlement peak between early spring and late summer (García-Rubies and Macpherson, 1995; Dulčić et al., 1997, 2007; Biagi et al., 1998). Specific settlers often have strict microhabitat requirements for potential nurseries. After settling until recruitment, their survival within a habitat largely depends on the environmental conditions encountered at the site of settlement (Beck et al., 2001). This makes temperature, salinity and bottom depth preferences even more important when choosing a nursery area. Global warming or climate change has driven significant changes in marine ecosystems in recent decades, particularly in coastal areas facing compositional and structural changes. Specifically, alterations in species distributions and ranges, composition of species assemblages, and biodiversity have all been convincingly linked to rising temperatures (Bellard et al., 2012; Doney et al., 2012) in regions where climate change has substantially altered the physical environment (see Barceló et al., 2016 and references therein). These are the main biological responses to temperature and salinity as factors of environmental modifications. Generally, changes in growth rates, shifts in the spawning season, and shifts in the spawning area (latitude) are expected after a rise

in sea temperature due to global warming. Recently, shifts in the physical and biological regimes of the Adriatic Sea were connected with the climate change in the northern hemisphere (Grbec et al., 2015). Matić-Skoko et al. (2020) highlighted the importance of investigating temporal changes in littoral juvenile fish assemblages through responses to environmental factors as important causal factors of habitat modifications due to climate change. These responses represent the environmental tolerances of individual species (Martins et al., 2019). Further, the absence or occurrence of certain species may be a signal of a poleward shift in the spawning area and a temporal shift in spawning timing to avoid higher temperatures (Shoji et al., 2011).

Previous studies have generally focused on the intrinsic ecological functions of microhabitats at a local scale, e.g., for sparids along the rocky shore of Marseilles (NW Mediterranean) (Cheminee et al., 2011). The whole eastern Adriatic coast represents a mosaic of different coastal nurseries, from coastal lagoons to shallow, semi-closed coves with varying annual influence of freshwater springs, which is highest in the winter-spring period after snow melt and intensive rain (Novosel et al., 2005). These coves were previously identified as having higher fish species richness (Dulčić et al., 1997) than coastal lagoons, due to the wide connection with the sea that favours the inflow of fish eggs, larvae and young of-the-year by the tides and currents from spawning areas (Blaber et al., 1995; Potter et al., 2010; Araújo et al., 2016). However, the extent of interannual differences in settler supply along the coast and across different habitats is unknown, and little is also known about which habitats and consequently which fish species are most sensitive to such changes. Several hypotheses have thus been defined for the main aims of this study: (1) there are significant interannual variations in species presence and species abundance of settled juvenile fish along the eastern Adriatic coast, (2) different habitat types (related to water type and geographical position) respond differently to interannual changes of environmental factors, and (3) estuarine nursery areas are more susceptible to such changes than marine ones. The present study aims to further understand the relative importance of interannual changes of environmental parameters and nursery attributes at different spatial scales in settlement and post-settlement processes and how they influence recruitment level.

MATERIALS AND METHODS

Sampling Procedure

Sampling on a seasonal basis (March, June, September, and December) was conducted in three consecutive years (2017, 2018, and 2019) at 20 sites (**Table 1** and **Figure 1**) across marine and transitional waters along the eastern Adriatic coast. The specific ecological characteristics of each site are presented in **Table 1**. All sites were selected based on knowledge where juvenile fish occurrence had been previously described (Dulčić et al., 1997, 2005, 2007; Matić-Skoko et al., 2007) over a similar biotope characterised mainly by sandy (S1, S3, S5, S6, S9, S10, S12, S15, S18, and S20), rocky (S11 and S16), or mixed sandy-rocky-pebbles (S2, S4, S7, S8, S13, S14, S17, and S19) substrata covered

TABLE 1 | Summary of sampling data for juvenile fish communities along the eastern Adriatic coast within selected sites in the period 2017–2019.

No	Sites	Geographic position	Type of water	Bottom* and vegetation	Number of species			Number of individuals			Mean annual temperature (°C)			Mean annual salinity (‰)		
					2017	2018	2019	2017	2018	2019	2017	2018	2019	2017	2018	2019
S1	Prapratna	South	Marine	S/No	17	12	9	269	373	488	19.4	20.1	19.8	36.6	31.4	29.9
S2	Duba Stonska	South	Marine	R-S/Yes	13	9	16	40	94	130	18.4	19.9	18.1	37.2	34.0	36.2
S3	Mala Neretva	South	Transitional	S/Yes	30	23	19	177	241	100	20.0	21.4	20.0	28.6	24.8	22.5
S4	Drvenik	South	Marine	R-S/No	22	24	9	128	127	147	18.5	20.9	18.7	33.1	34.3	28.8
S5	Cetina ušće	South	Transitional	S/Yes	37	31	25	883	1222	452	18.4	18.7	19.1	25.3	28.7	19.6
S6	Duće	South	Transitional	S/Yes	27	21	18	370	189	424	19.1	21.4	18.5	34.1	31.6	20.9
S7	Grljevac	South	Marine	S-R/Yes	17	23	19	923	2023	540	18.3	20.0	18.4	36.0	34.2	30.9
S8	Kašjuni	South	Transitional	S-R/Yes	16	21	23	322	269	217	18.6	19.2	18.1	33.1	36.1	36.2
S9	Pantan	South	Transitional	S/Yes	21	23	22	281	578	130	19.7	22.3	18.4	34.6	26.6	28.2
S10	Stari Trogir	South	Marine	S/Yes	29	30	24	237	1008	619	19.9	20.4	17.9	37.8	35.4	37.9
S11	Primošten	North	Marine	R/Yes	22	20	16	407	627	522	19.3	20.4	19.5	38.5	38.5	38.3
S12	Žaborić	North	Marine	S/Yes	27	23	23	375	234	162	19.5	21.7	20.6	38.3	30.1	35.7
S13	Jadrija	North	Transitional	P/Yes	16	14	18	913	1125	611	17.8	17.3	19.2	18.5	14.2	19.4
S14	Sovlja	North	Marine	S-R/Yes	34	31	27	227	214	270	18.3	19.6	19.4	38.2	38.0	38.3
S15	Prosika	North	Transitional	S/Yes	29	22	22	198	268	173	18.8	19.9	19.6	34.5	28.9	33.0
S16	Sukošan	North	Marine	R/Yes	22	23	18	404	765	545	18.6	20.1	19.2	37.8	37.9	37.6
S17	Petrčani	North	Marine	S-P/Yes	22	22	21	809	348	374	18.6	19.7	18.8	38.3	35.6	38.4
S18	Nin	North	Transitional	S/No	20	15	10	262	259	185	17.6	18.8	18.4	37.4	32.1	36.8
S19	Maslenica	North	Transitional	P/Yes	17	23	10	232	184	40	16.3	17.9	16.4	17.2	17.5	19.5
S20	Karišnica	North	Transitional	S/Yes	16	17	14	353	476	263	16.2	18.5	17.0	18.7	16.6	17.2

Sites are listed as S1–S20 from south to north (border: Cape Ploča 43°29.648′N; 15°58.184′E) (Bottom: S-sandy; R-rocky, P-pebbles).*

by photophilic algae alternating with patches of *Cymodocea nodosa* seagrass beds. At each site, three replicates separated by tens of meters were performed with a specially constructed small shore seine (L = 25 m; minimum mesh size 4 mm). To ensure comparability, the same net was used during the entire study period at all sites. Hauls were also performed in the same bathymetric range, from 0 to 2.2 m depth. A total of 36 samples per site were taken over a 3-year period. Sites were divided into four groups of five locations based on water type (marine or transitional) and geographical position (north or south): transitional north (T_N), transitional south (T_S), marine north (M_N), and marine south (M_S). The border between the northern and southern sites is Cape Ploča (43°29.648′N; 15°58.184′E) as the most prominent point of land along the eastern Adriatic coast. This cape represents the geographic and climatological boundary between the northern and the southern Adriatic, and is often characterised by strong sea currents and swells as weather systems from the north and the south come in contact (Gloginja and Mitrović, 2021). Surface and bottom temperature (°C) and salinity (‰) measurements were performed using a multi-parameter probe model YSI 85. All fish individuals were identified to the species level according to Jardas (1996) and Dulčić and Kovačić (2020), measured (total length to the nearest 0.1 cm) and weighed (total body weight to the nearest 0.1 g). Sampling covered all stages of fish, but only juveniles were selected for further analysis. Further on, the species *Atherina* sp. were excluded, since they were the most dominant and most common species in all samples, and the majority of specimens were adults, while *Sardina pilchardus* and *Engraulis encrasicolus*
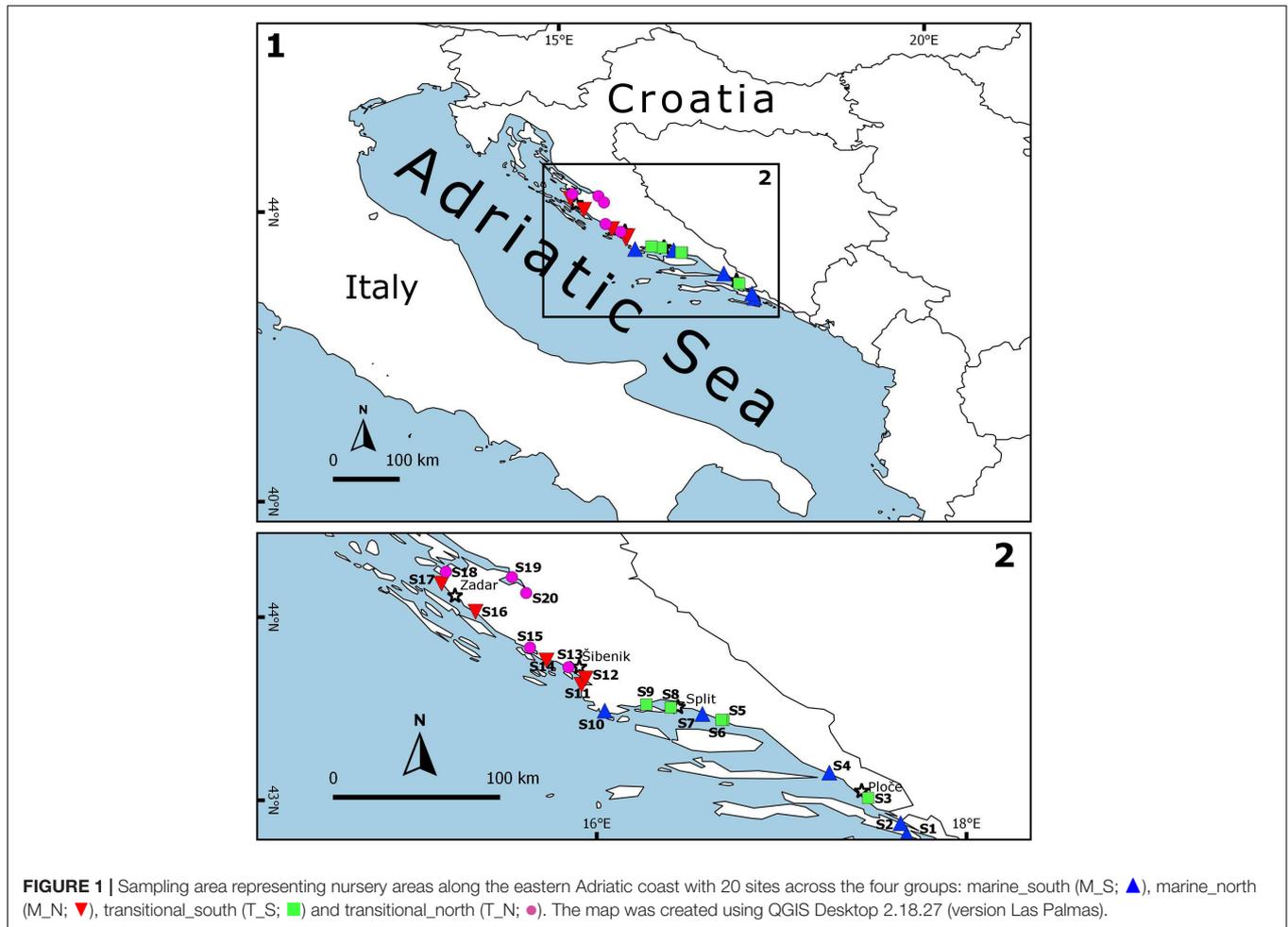
were caught only sporadically in high abundance, thus skewing the results. The following species were excluded from further analysis as only adults, and no juvenile specimens, were caught: *Lichia amia*, *Pseudocaranx dentex*, *Sciena umbra*, *Uranoscopus scaber*, and *Zeus faber*.

Data Analysis

Total abundance (A), as the number of individuals (N) per species, and species richness (R), as the number of species (S), were counted, while the mean number of individuals and species per haul were recorded for each site and each period.

All analyses were performed using PRIMER-E software (Clarke and Gorley, 2015) with the add-on package PERMANOVA+ (Anderson, 2001; Anderson et al., 2008). Graphs were prepared using SigmaPlot (v. 13.0; Systat Software Inc., San Jose, CA, United States).

Multivariate statistical testing of abundance data for juvenile fish assemblages used a four-factor design [Year (Ye)/Season (Se)/Geographic position (Ge)/Type of water (Ty)], within one factor Period (1–12): 2017 (1–4), 2018 (5–8), and 2019 (9–12) constructed for cyclicity purposes. Factors Ye and Se were considered fixed while factors Ge and Ty were randomly nested in Se. The additional factor Period_Type of water_Geographic position was combined. Data sets for each site were imported in the PRIMER workspace and combined into a single matrix. Variability in the numbers of individual species in the samples was used to carry out dispersion weighting for each species. The dispersion-weighted data was transformed by a milder square-root transformation, as demonstrated by Clarke et al. (2014) for

FIGURE 1 | Sampling area representing nursery areas along the eastern Adriatic coast with 20 sites across the four groups: marine_south (M_S; ▲), marine_north (M_N; ▼), transitional_south (T_S; 🟩) and transitional_north (T_N; 🔴). The map was created using QGIS Desktop 2.18.27 (version Las Palmas).

fish communities, particularly those in estuaries and nearshore coastal waters, where the prevalence of juvenile and small schooling species is high. Bray–Curtis similarity was then calculated on the dispersion weighted, transformed data.

Metric Multidimensional Scaling (mMDS) ordination used data at the same level of sample averaging for each Period, Geographical position, and Type of water combination to visualise the extents to which ichthyofaunal composition differed across Period_Type of water_Geographic position. All plots were constructed by calculating the distances between each pair of group centroids, i.e., the relevant average in the "Bray–Curtis space" of all samples (Anderson et al., 2008).

The RELATE statistic (P) was employed to test whether the pattern of temporal catch composition change conformed to cyclicity. If there is no tendency to cyclicity, then P will be close to zero (Clarke and Warwick, 2001). Separate two-way crossed analysis of similarities ANOSIM was used to interpret the relative size of the overall spatio-temporal effects on fish compositions, using the same resemblances as for the PERMANOVA tests. The species that mainly contribute to the separation between the factor Period_Type of water_Geographic position were determined by the SIMPER procedure, which shows the average contribution of each species to the dissimilarity between the

groups. The results were presented for the specific season along all three consecutive years, characterised by most significant changes in communities.

To explore the data further, we used canonical variate plot (CAP) analysis. CAP is a routine for performing canonical analysis by calculating principal coordinates among groups of samples to predict group membership, positions of samples with another single continuous variable, or finding axes having maximum correlations with another set of variables (Anderson and Willis, 2003). This was initially run separately for each of the two factors: "Geographic position" and "Type of water" and then merged into a scatter plot. Particularly, CAP was used to estimate the accuracy of fish composition and environmental variables (temperature and salinity).

RESULTS

Interannual Variations of Abiotic Factors

The mean monthly variation in water temperature and salinity averaged over four groups (M_S, M_N, T_S, and T_N) are shown in **Figure 2**. The observed sea surface temperatures followed a seasonal cycle, with the highest temperatures in June-September
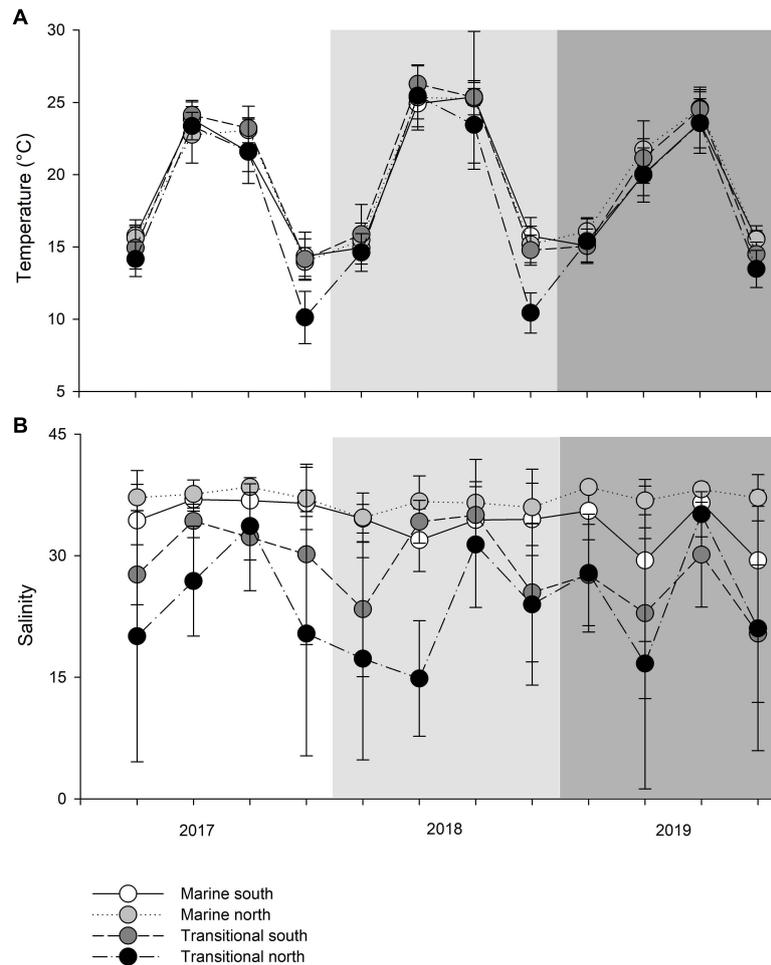
FIGURE 2 | Mean seasonal values of **(A)** temperature (°C) and **(B)** salinity (‰) among transitional and marine waters in the north and south (M_S, M_N, T_S, and T_N).

(particularly in 2018) and the lowest in December in all three years (**Figure 2A**). Observing the differences between marine and transitional waters, less variation was observed among waters in the south, regardless of the type of water (**Supplementary Table 1**). The mean seasonal temperature in T_N was always lower than in the remaining groups, though this is especially evident in December when higher and more similar results were recorded in the other three groups compared to T_N. Namely, northern transitional waters had the lowest mean values recorded in December 2017 ($10.12 \pm 1.81°C$) and December 2018 ($10.44 \pm 1.39°C$). It is evident that the mean temperature in December 2019 was higher for the T_N group than in the two previous years, and this was much more uniform among the groups (**Figure 2A**). Further, the mean temperature in June 2019, regardless of water type, was 2.78°C lower than in 2017 and 4.78°C lower compared to 2018. Analysis of variance revealed significant differences in temperature between years (PERMANOVA: Pseudo-F = 10.371; P = 0.0004), seasons (Pseudo-F = 50.181; P = 0.0013), interactions of years and seasons (Pseudo-F = 10.624; P = 0.0002), and among groups (M_S, M_N,

T_S, and T_N) in relation to seasonal changes in temperature (Pseudo-F = 4.6813; P = 0.0008) (**Table 2**).

As expected, the measured salinity values showed greater variation between water types such that marine areas showed less seasonal fluctuations and continuous higher values (**Figure 2B** and **Supplementary Table 1**). Lower salinity values were observed for northern transitional waters (mean salinity value across the sampling period was $23.53 \pm 6.23‰$) than southern transitional waters. Two negative peaks of mean salinity values were observed in June and December 2019, regardless of water type. The mean salinity was always higher in 2017 and 2018 in the south, regardless of water type, while an inversion occurred in 2019 and mean salinity values were higher in the north in both types of waters. Also, every September in all three years, the mean salinity values were highest and most similar among the groups following the summer drought (**Figure 2B**). However, analysis of variance did not reveal significant differences in salinity between years, seasons, type of waters, and geographic position and their interactions, except for strong statistically significant annual variations among water type/geographic position groups (M_S,

TABLE 2 | Summary of PERMANOVA results for the multivariate analysis of the overall matrix constructed from seasonal temperature data measured in three consecutive years (2017, 2018, 2019) along the eastern Adriatic coast for 20 sites with assigned affiliation according to water type (marine or transitional) and geographic position (south or north).

	df	MS	Pseudo-F	P
Year (Ye)	2	1.896	10.731	**0.0004**
Season (Se)	4	49.157	50.181	**0.0013**
Geographic position (Ge)	5	0.406	0.838	0.5693
Water type (Ty)	5	0.641	1.323	0.3743
Interactions				
Ye × Se	5	1.876	10.624	**0.0002**
Ye × Ge (Se)	7	0.122	1.429	0.3213
Ye × Ty (Se)	7	0.062	0.738	0.6461
Ge (Se) × Ty (Se)	5	0.485	4.681	**0.0008**
Ye × Ge(se) × Ty (Se)	7	0.085	0.823	0.5728
Residuals	192	0.104		
Total	239			

Statistically significant values (P < 0.05) marked in bold.

TABLE 3 | Summary of PERMANOVA results for the multivariate analysis of overall matrix constructed from seasonal salinity data measured in three consecutive years (2017, 2018, 2019) along the eastern Adriatic coast for 20 sites with assigned affiliation according to water type (marine or transitional) and geographic position (south or north).

	df	MS	Pseudo-F	P
Year (Ye)	2	2.229	2.431	0.0776
Season (Se)	4	3.906	0.494	0.8206
Geographic position (Ge)	5	0.550	0.186	0.9520
Water type (Ty)	5	13.816	4.679	0.0669
Interactions				
Ye × Se	5	1.465	1.736	0.1713
Ye × Ge (Se)	7	0.753	1.701	0.2491
Ye × Ty (Se)	7	0.346	0.782	0.615
Ge (Se) × Ty (Se)	5	2.953	4.913	**0.0005**
Ye × Ge (Se) × Ty (Se)	7	0.443	0.737	0.646
Residuals	192	0.601		
Total	239			

Statistically significant values (P < 0.05) marked in bold.

M_N, T_S, and T_N) in relation to seasonal changes in salinity, i.e., as nested in season (Pseudo-F = 1.9354; P = 0.0001) (**Table 3**).

Interannual Variations of Juvenile Fish Composition

At all sites, a total of 720 small beach seine samples were taken across three consecutive years (**Tables 1**, **4**). A total of 24,807 fish juveniles belonging to 23 families and 92 species were included in this survey. The most abundant species were *Sarpa salpa* (2,805 individuals in total), *Pomatoschistus marmoratus* (2,028), *Pagellus acarne* (1,806), *Chelon ramada* (1712), *Diplodus annularis* (1,683), *Chelon auratus* (1,550), and *Diplodus vulgaris* (1,074), which together comprised 51.03% of the total sample. A high number of species were sporadically present throughout the 3-year study period (though with <30 individuals). Some species, such as *Symphodus roissali* and *Chelidonichthys lucerna*, were completely absent in 2019. Although the collection effort

(as the total number of samples per year, month and site) was the same, the total number of species and individuals clearly fluctuated across sites (**Table 4**, **Figure 3**, and **Supplementary Table 2**) and across groups. The number of species varied among sites from 1 (at S18 and S19 in June and September 2019, respectively) to 24 species (at S16 in June 2018) and among the groups from 1 (T_N in December 2019) to 25 species (M_N in June 2018). The number of species varied less over the 3-year period at marine stations than at transitional ones, with the largest interannual changes observed in the T_N group. Moreover, PERMANOVA analysis of the number of juvenile fish species found significant differences along three consecutive years (Pseudo-F = 1.7459; P = 0.0362), across seasons among years (Pseudo-F = 1.4222; P = 0.0406) and among groups [M_S, M_N, T_S, and T_N, as Ge(Se) × Wa (Se) interactions] in relation to seasonal changes in the number of species (Pseudo-F = 2.0571; P = 0.0002) (**Table 5**).

Similar to the number of species, abundance fluctuated considerably less in marine waters and more in transitional ones, especially in the north. The abundance of individuals was the highest in 2018, and the highest in M_N group (4067 individuals). On the contrary, abundance was lowest in 2019, especially in the M_S (1,317) and T_N groups (1,407). Although some fluctuations in abundance were evident, especially the 52.5% reduction in the M_N group in 2019 (1,930), PERMANOVA analysis of juvenile fish abundance for all sites found no significant differences for the three consecutive years, seasons, type of water and geographical position together with their interactions, except among groups in relation to seasonal changes in the number of individuals (Pseudo-F = 1.9354; P = 0.0001) (**Table 6**). Regarding species, the abundance of *Boops boops*, *Pagellus acarne*, *Pagellus erythrinus*, *Symphodus tinca*, and *S. roissali* was drastically decreased in 2019 compared to previous years (**Table 4**). Additionally, *P. acarne* was only present in southern marine waters in 2017 and 2018.

On the metric MDS ordination plot, derived from the distance among centroid matrices, four groups were defined, clearly separating both geographical position and type of waters (**Table 3** and **Figure 3**) ordinating groups from transitional to marine and then from north to south (T_N, T_S, M_N, and M_S), indicating that the greatest differences were found between the groups T_N and M_S (**Figure 4**). The cyclicity of abundance data, obtained from the RELATE test, following a seasonal pattern and was less visible for T_N. It seems that there were similar patterns for marine groups, namely between M_S in 2017 (Rho = 0.621, P = 0.839) and 2018 (Rho = 0.414, P = 0.665) and M_N in 2017 (Rho = 0.828, P = 0.335) and 2018 (Rho = 0.828, P = 0.333) while in the final year of the study period, similarity dropped drastically. Interestingly, there was no similar pattern between the three consecutive years at T_S (Rho = 0.014, P = 0.365). Species composition in T_N was governed by a similar pattern in 2018 (Rho = 0.414, P = 0.679) and 2019 (Rho = 0.414, P = 0.035). Two-way crossed ANOSIM tests showed and confirmed that the fish fauna composition was significantly related to both factors, types of water (R = 0.106, P = 0.001) and geographic position (R = 0.188, P = 0.001), with the latter factor more prominent. Moreover, one-way ANOSIM for the interaction type of water_geographic

TABLE 4 | Summary of abundance data (number of individuals) for 92 juvenile fish species sampled in three consecutive years (2017–2019) along the eastern Adriatic coast with assigned affiliation to four groups according to water type (marine or transitional) and geographic position (south or north): M_S, M_N, T_S, and T_N.

		2017				2018				2019			
		M_S	M_N	T_S	T_N	M_S	M_N	T_S	T_N	M_S	M_N	T_S	T_N
Species	**Family**												
Arnoglossus laterna	Bothidae	21	26	44	2	15	22	26	2	8	11	12	3
Arnoglossus thori	Bothidae	2	0	0	0	1	0	0	0	0	0	0	0
Belone belone	Belonidae	1	8	0	1	3	2	0	4	5	42	0	0
Blennius ocellaris	Blenniidae	0	0	0	2	0	0	0	0	1	0	0	0
Boops boops	Sparidae	0	4	16	9	5	0	82	0	29	0	2	0
Bothus podas	Bothidae	38	0	17	0	56	0	20	0	25	0	0	0
Callionymus pusillus	Callionymidae	3	27	5	9	1	9	3	5	1	7	1	13
Callionymus risso	Callionymidae	3	21	36	7	10	51	8	22	0	12	6	8
Chelon labrosus	Mugilidae	43	13	0	22	3	56	1	17	2	29	6	21
Chelidonichthys lucerna	Triglidae	0	2	3	0	1	5	2	0	0	0	0	0
Chelon auratus	Mugilidae	154	188	34	350	38	80	5	558	51	79	1	12
Chelon ramada	Mugilidae	79	144	2	379	67	434	80	170	37	80	7	233
Chelon saliens	Mugilidae	5	5	3	22	15	64	2	5	14	301	0	39
Chromis chromis	Pomacentridae	0	0	0	0	1	0	10	0	0	1	0	0
Coris julis	Labridae	8	1	18	0	0	0	8	0	0	1	0	0
Deltentosteus collonianus	Gobiidae	0	0	1	0	0	0	0	0	0	0	0	0
Deltentosteus quadrimaculatus	Gobiidae	0	0	5	0	0	0	1	1	0	0	0	0
Dentex dentex	Sparidae	3	1	0	0	1	1	8	0	0	1	0	0
Dicentrarchus labrax	Moronidae	0	49	0	20	0	29	1	10	1	4	0	8
Diplodus annularis	Sparidae	32	378	85	9	59	692	80	23	63	133	124	5
Diplodus puntazzo	Sparidae	42	73	58	10	88	46	106	11	33	66	76	21
Diplodus sargus	Sparidae	0	0	1	0	0	0	10	0	0	0	0	0
Diplodus vulgaris	Sparidae	63	127	182	22	48	12	117	7	101	71	303	21
Echiichthys vipera	Trachinidae	1	8	0	3	0	1	2	1	0	1	0	2
Epinephelus costae	Serranidae	1	0	0	0	0	0	0	0	0	0	0	0
Gobius cobitis	Gobiidae	5	0	7	6	5	0	2	23	2	3	7	33
Gobius couchi	Gobiidae	3	24	33	2	10	0	126	3	1	0	33	2
Gobius cruentatus	Gobiidae	0	0	2	0	0	0	2	0	0	0	5	0
Gobius fallax	Gobiidae	0	2	11	0	0	0	43	0	0	0	19	0
Gobius geniporus	Gobiidae	3	3	0	22	1	0	1	0	0	0	1	0
Gobius niger	Gobiidae	8	136	154	104	15	326	94	182	25	124	38	160
Gobius paganellus	Gobiidae	0	0	0	0	0	2	1	0	0	0	1	0
Hippocampus hippocampus	Syngnathidae	2	0	1	1	0	0	0	0	1	0	0	0
Hippocampus ramulosus	Syngnathidae	0	0	2	0	0	0	0	0	0	0	0	0
Knipowitschia kavcasica	Gobiidae	0	0	0	0	0	0	0	2	0	0	0	0
Knipowitschia panizzae	Gobiidae	0	0	0	121	0	0	0	65	0	0	0	17
Labrus merula	Labridae	0	1	0	0	0	0	0	0	1	0	0	0
Labrus viridis	Labridae	0	0	0	1	0	0	0	0	0	0	0	0
Lichia amia	Carangidae	0	0	1	0	0	0	0	0	0	0	0	0
Lipophrys trigloides	Blenniidae	3	0	3	0	0	0	0	0	0	0	0	0
Lithognathus mormyrus	Sparidae	36	17	140	20	57	78	53	5	366	120	51	13
Monochirus hispidus	Soleidae	0	0	1	0	0	0	1	1	0	1	0	0
Microlipophrys dalmatinus	Blenniidae	1	2	0	0	0	0	0	0	0	1	0	0
Mullus barbatus	Mullidae	80	69	34	43	298	81	20	61	36	93	18	29
Mullus surmuletus	Mullidae	34	0	9	0	7	0	1	0	1	1	0	0
Nerophis maculatus	Syngnathidae	0	13	0	1	0	1	0	0	0	0	0	0
Nerophis ophidion	Syngnathidae	0	2	0	0	1	5	0	0	0	4	0	1
Oblada melanura	Sparidae	2	0	3	0	3	0	1	5	1	1	0	0
Oedalechilus labeo	Mugilidae	61	0	23	0	83	2	214	0	15	2	153	2
Pagellus acarne	Sparidae	450	8	172	74	864	90	74	0	73	0	1	0
Pagellus bogaraveo	Sparidae	0	1	0	0	0	0	0	0	0	0	0	0
Pagellus erythrinus	Sparidae	126	2	2	1	33	3	14	3	2	0	10	0
Pagrus pagrus	Sparidae	6	0	9	0	9	0	1	0	63	0	2	0
Parablennius gattorugine	Blenniidae	0	0	0	1	2	0	2	0	0	0	0	0

(Continued)

TABLE 4 | (Continued)

		2017				2018				2019			
		M_S	M_N	T_S	T_N	M_S	M_N	T_S	T_N	M_S	M_N	T_S	T_N
Parablennius sanguinolentus	Blenniidae	1	1	11	0	1	10	5	0	3	0	3	0
Parablennius tentacularis	Blenniidae	5	12	38	3	2	10	29	5	4	17	17	4
Pomatoschistus bathi	Gobiidae	0	8	15	11	0	0	26	6	1	4	7	0
Pomatoschistus canestrinii	Gobiidae	0	0	0	0	0	0	0	0	0	0	0	1
Pomatoschistus marmoratus	Gobiidae	12	172	72	430	3	218	210	339	7	133	122	310
Pomatomus saltatrix	Pomatomidae	0	0	0	0	0	0	0	0	0	0	0	1
Pseudaphya ferreri	Gobiidae	0	0	0	4	1	3	0	0	0	0	6	0
Pseudocaranx dentex	Carangidae	1	0	0	0	0	0	0	0	0	0	0	0
Salaria pavo	Blenniidae	0	18	1	12	2	68	1	82	0	27	1	8
Sarpa salpa	Sparidae	2	141	469	39	138	659	375	85	179	272	241	205
Sciaena umbra	Sciaenidae	0	0	1	0	0	0	0	0	0	1	0	0
Scorpaena notata	Scorpaenidae	0	0	0	0	0	0	0	0	0	0	0	0
Scorpaena porcus	Scorpaenidae	4	9	23	0	2	5	19	0	4	5	13	0
Serranus cabrilla	Serranidea	0	0	1	0	0	0	0	0	0	0	0	0
Serranus hepatus	Serranidea	4	1	22	0	7	0	40	1	0	0	13	2
Serranus scriba	Serranidea	5	15	6	1	4	13	16	1	2	12	14	0
Solea kleini	Soleidae	1	0	3	2	0	0	1	0	0	0	1	0
Solea solea	Soleidae	2	6	0	4	1	21	0	3	0	6	2	3
Sparus aurata	Sparidae	1	20	4	30	3	20	7	26	0	11	2	5
Sphyraena sphyraena	Sphyraenidae	1	8	1	0	1	2	1	0	0	0	2	0
Spicara flexuosa	Centracanthidae	2	0	0	0	0	0	0	1	0	0	0	0
Spicara smaris	Centracanthidae	6	1	49	2	0	393	111	13	1	3	87	0
Symphodus cinereus	Labridae	39	207	212	17	57	262	315	27	82	127	191	6
Symphodus ocellatus	Labridae	18	61	31	119	18	125	35	56	14	62	77	166
Symphodus roissali	Labridae	0	4	0	18	0	0	0	2	0	0	0	0
Symphodus rostratus	Labridae	2	3	0	0	4	7	0	0	0	5	0	0
Symphodus tinca	Labridae	2	43	20	3	3	96	24	1	3	1	15	1
Syngnathus abaster	Syngnathidae	0	0	0	1	0	0	0	0	0	1	0	9
Syngnathus acus	Syngnathidae	0	5	1	10	0	2	0	10	0	3	1	5
Syngnathus tenuirostris	Syngnathidae	1	11	8	0	3	2	14	6	0	2	5	0
Syonodus saurus	Synodontidae	0	0	0	0	1	0	0	0	1	0	0	0
Syngnathus typhle	Syngnathidae	3	14	6	8	2	27	6	2	1	11	3	4
Trachinotus ovatus	Carangidae	38	0	2	0	4	0	6	0	57	0	26	0
Trachinus draco	Trachinidae	2	2	1	1	0	0	3	0	0	0	11	1
Trachinus radiatus	Trachinidae	0	0	1	0	0	0	0	0	0	0	0	0
Trigla lyra	Triglidae	0	1	0	0	0	0	0	0	0	0	0	0
Tripterygion tripteronotum	Tripterygiidae	0	0	4	0	0	0	2	0	0	0	1	0
Zosterisessor ophiocephalus	Gobidae	0	22	1	81	0	32	0	180	0	38	0	33
Number of samples		20	20	20	20	20	20	20	20	20	20	20	20
Number of species		54	54	60	48	51	43	58	44	37	46	46	37
Number of individuals		1471	2140	2120	2060	2057	4067	2468	2032	1317	1930	1738	1407

position confirmed that the magnitude of difference was lower between groups in 2017 ($R = 0.419$; $P = 0.001$) and 2018 ($R = 0.458$; $P = 0.001$), and highest in 2019 ($R = 0.899$; $P = 0.001$).

We additionally ran a CAP analysis and related the environmental data to the community composition information. Temperature and salinity values for the four water types/geographic position groups of factors were plotted as distances among centroids based on community data (**Figure 5**), revealing that temperature had a prominent influence on community composition in T_N, less on T_S, while salinity had a positive effect on M_S and M_N. A separate CAP analysis was run for each of the two factors ("type of waters"

and "geographical position"), which also gave successful discrimination. In particular, 84.03 and 78.99% of samples from marine and transitional waters, respectively, were correctly allocated based on the community composition information. Further, 72.88 and 71.67% of samples were correctly allocated to north or south, respectively. These results suggested that transitional waters are more sensitive to interannual differences, especially in the north (**Figure 6**).

The SIMPER routine revealed that 14 species (**Table 7**) in varying order of percentage contribution were responsible for the most (>50%) dissimilarities in the interactions between the composition of juvenile fish sampled in June among the three

FIGURE 3 | Box plots of median values (± standard deviation) for the number of juvenile fish species and abundance across marine_south **(A,B)**, marine_north **(C,D)**, transitional_south **(E,F)**, transitional_north **(G,H)** groups during the sampling period (2017–2019) along the eastern Adriatic Sea.
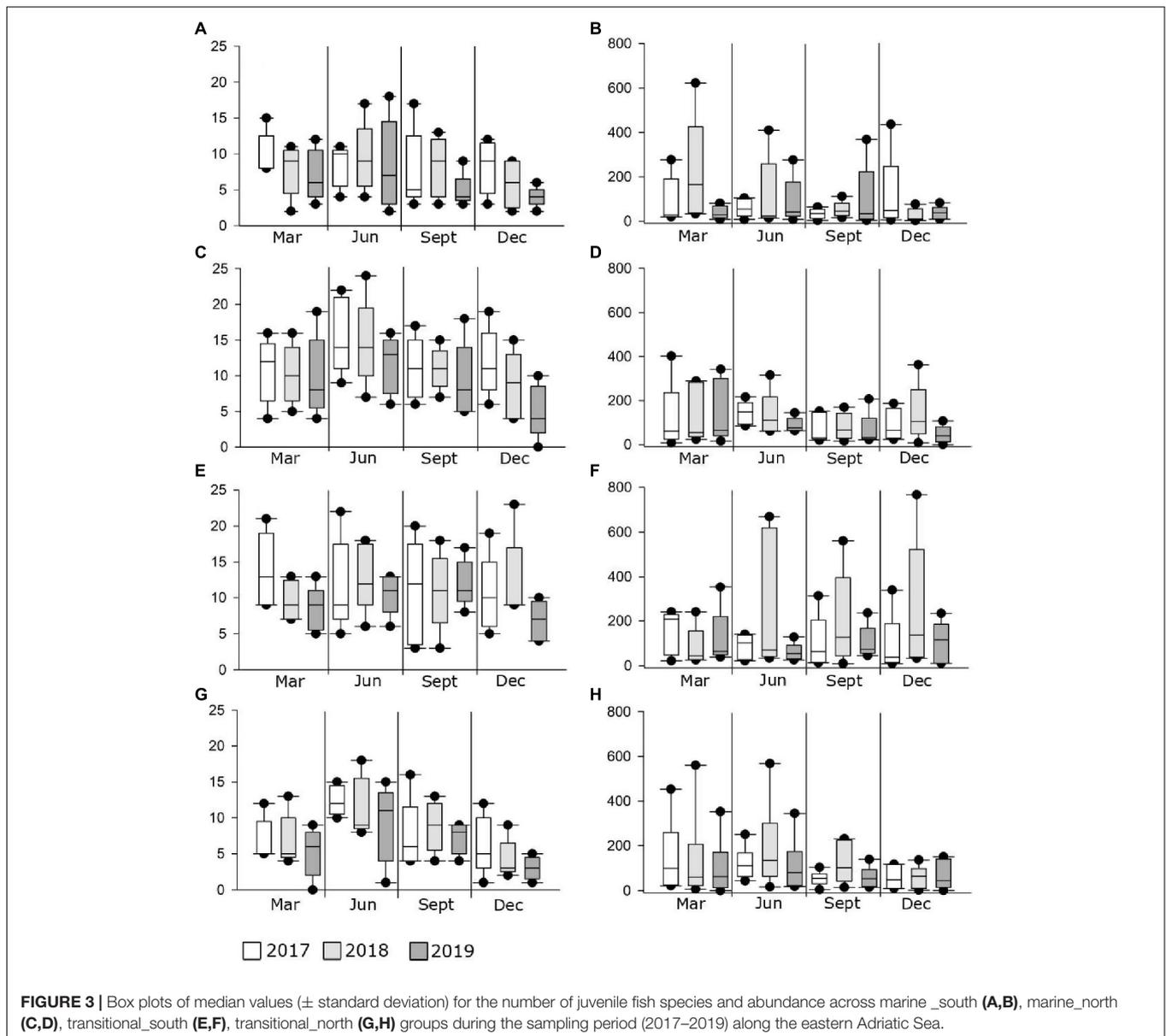
consecutive years. It was evident that five species that gave a significant contribution to T_N in 2017 (e.g., *Sparus aurata*, *Diplodus vulgaris*, and *Symphodus roissali*) were not present in 2018, while other species appeared (*Sarpa salpa* and *Chelon ramada*). SIMPER revealed that the average dissimilarity was highest between M_S and T_N (90.51%) while T_S and M_N were more similar (79.41%).

DISCUSSION

The present study focussed on the patterns of use of coastal nurseries by juvenile fish species along the eastern Adriatic coast. In particular, the study sought to answer whether species occurrence and density differed between habitats and sites over three consecutive years and whether certain sites or habitats

could be highlighted as important nursery areas for juveniles, and whether they are highly sensitive to environmental and other changes. Moreover, by modelling the response of juvenile occurrence and density to the environmental variables, this study identified which variables best explained the intra- and inter-coastal variability in juvenile fish distribution and abundance. Also, the strength of these parameter influences can characterise the features that define important sites for juveniles and how they varied among systems. Last but not least, more sensitive species in this context were defined.

Interannual Variations of Abiotic Factors

Generally, the determined fluctuations in sea temperature and salinity during the study period followed the well-known seasonal cycle specific to the Adriatic Sea (Grbec and Morović, 1997).

TABLE 5 | Summary of PERMANOVA results for the multivariate analysis of overall matrix constructed from juvenile fish species data sampled in three consecutive years (2017, 2018, 2019) along the eastern Adriatic coast for 20 sites with assigned affiliation according to water type (marine or transitional) and geographic position (south or north).

	df	MS	Pseudo-F	P
Year (Ye)	2	3944.3	1.746378	**0.0362**
Season (Se)	3	16518	1.345	0.2196
Geographic position (Ge)	4	5909.6	1.020	0.4856
Water type (Ty)	4	10682	1.844	0.1537
Interactions				
Ye × Se	6	2897.4	1.422	0.0406
Ye × Ge (Se)	8	2021.8	1.188	0.2784
Ye × Ty (Se)	8	1212.2	1.712	0.8607
Ge (Se) × Ty (Se)	4	5791.9	2.057	**0.0002**
Ye × Ge (Se) × Ty (Se)	8	1702.1	0.604	0.9973
Residuals	190	2815.6		
Total	237			

Statistically significant values (P < 0.05) marked in bold.

TABLE 6 | Summary of PERMANOVA results for the multivariate analysis of overall matrix constructed from juvenile fish abundances sampled in three consecutive years (2017, 2018, 2019) along the eastern Adriatic coast for 20 sites with assigned affiliation according to water type (marine or transitional) and geographic position (south or north).

	df	MS	Pseudo-F	P
Year (Ye)	2	3853.6	1.378	0.0894
Season (Se)	3	15921	1.329	0.1975
Geographic position (Ge)	4	6270.8	0.926	0.5656
Water type (Ty)	4	10800	1.595	0.1864
Interactions				
Ye × Se	6	3235.7	1.242	0.0886
Ye × Ge (Se)	8	2433.3	1.023	0.4533
Ye × Ty (Se)	8	2088.6	0.878	0.7242
Ge (Se) × Ty (Se)	4	6772.6	1.935	**0.0001**
Ye × Ge (Se) × Ty (Se)	8	2378.3	0.680	0.9995
Residuals	190	3499.3		
Total	237			

Statistically significant values (P < 0.05) marked in bold.

More pronounced interannual fluctuations in water temperature were found for transitional waters, especially those situated in the north. According to the Croatian Meteorological and Hydrological Service, mean monthly air temperatures for most of 2018 were above the average of the reference period 1961-1990, while in May 2019, temperatures were below the reference average along the entire coast. Specially in the area gravitating toward T_N, temperatures in May 2019 were nearly 5°C below average (DHMZ, 2019). Sites within this group are related to the transitional waters of the Zrmanja and Krka Rivers, whose water systems are more exposed to the mainland due to relief characteristics (heavy rains, snow melt from nearby mountains and cold north-easterly winds in spring) and the maritime influence is less pronounced. Usually, salinity fluctuations are associated with freshwater river flows, though the significantly lower temperatures of these waters, especially in the spring

months are due to their origin and flow through extremely mountainous terrain. On the contrary, the transitional waters of the Neretva and Cetina Rivers have wider mouths toward the open sea, especially the Neretva Delta, and thus are more influenced by the gentle maritime environment (Krvavica and Ružić, 2020). Unlike temperature, there were no prominent interannual fluctuations in salinity. However, reduced salinity was evident in the northern transitional waters for the same reasons as mentioned above. In late spring 2019, reduced salinity was recorded along the entire coast as a consequence of an extremely rainy period. For example, the amount of precipitation in May (120 mm) and November (210 mm) 2019 in the middle of study area (S8 and S9) was twice the average cumulative amount of precipitation in the reference period 1961–1990 for those months (DHMZ, 2019). In 2017 and 2018, the average salinity in the south, regardless of water type, was always higher than in the north, confirming the unusually high rainfall in the north (DHMZ, 2019). As expected, statistically significant interannual differences in mean seasonal water temperatures also led to a change in the species occurrence among the three consecutive years. Thus, June 2019 was characterised by markedly low salinity and low temperature after a cold and rainy winter and spring, which likely caused the absence of the following species: *B. boops*, *B. podas*, *P. acarne*, *P. erythrinus*, *S. tinca*, *S. roisalli*, and *C. auratus*. All these species, except *C. auratus*, spawn in spring (Bartulović et al., 2011; Dulčić and Kovačić, 2020) and their settlers likely delayed settlement due to the prevailing conditions. Interestingly, a significantly reduced abundance of *B. boops* and *B. podas* were observed in southern transitional waters (T_S) in the same period. These species also spawn in early spring (Dulčić et al., 2004; Matić-Skoko et al., 2007; Dobroslavić et al., 2017; Zorica et al., 2020) and apparently their juveniles did not yet inhabit the nursery areas by June. Late spawning and a longer retention in the nursery area could be the reason for increased abundance of *L. mormyrus* in September 2019. Increased abundance is most often a positive response to average warmer habitat conditions (Jones et al., 2009). It seems that the longer the spawning season for a population, the higher its probability of finding suitable conditions for larval survival, resulting in a higher recruitment level (Sale, 2006). This may imply that if environmental conditions change significantly, species with a shorter spawning period may experience a more pronounced shift in spawning time and consequently in settlement onset. Interannual variability in temperature has been linked with changes in fish year-class strength for a number of species (Planque and Fox, 1998; Laurel et al., 2017; Barbeaux and Hollowed, 2018). Temperatures affect the onset of spawning and spawning period, but also the ecology of early developmental stages of fish, thus defining the moment of their migration or entry into benthic nursery areas (García-Rubies and Macpherson, 1995; Dulčić et al., 1997, 2007; Biagi et al., 1998). Also, positive relationships between temperature and impacts on settlement and recruitment are generally observed in cold-temperate regions, whilst negative relationships are observed in warm-temperate regions (Planque and Fox, 1998; Barbeaux and Hollowed, 2018; Downie et al., 2021). Environmental changes at higher latitudes that are under greater coastal influence appear
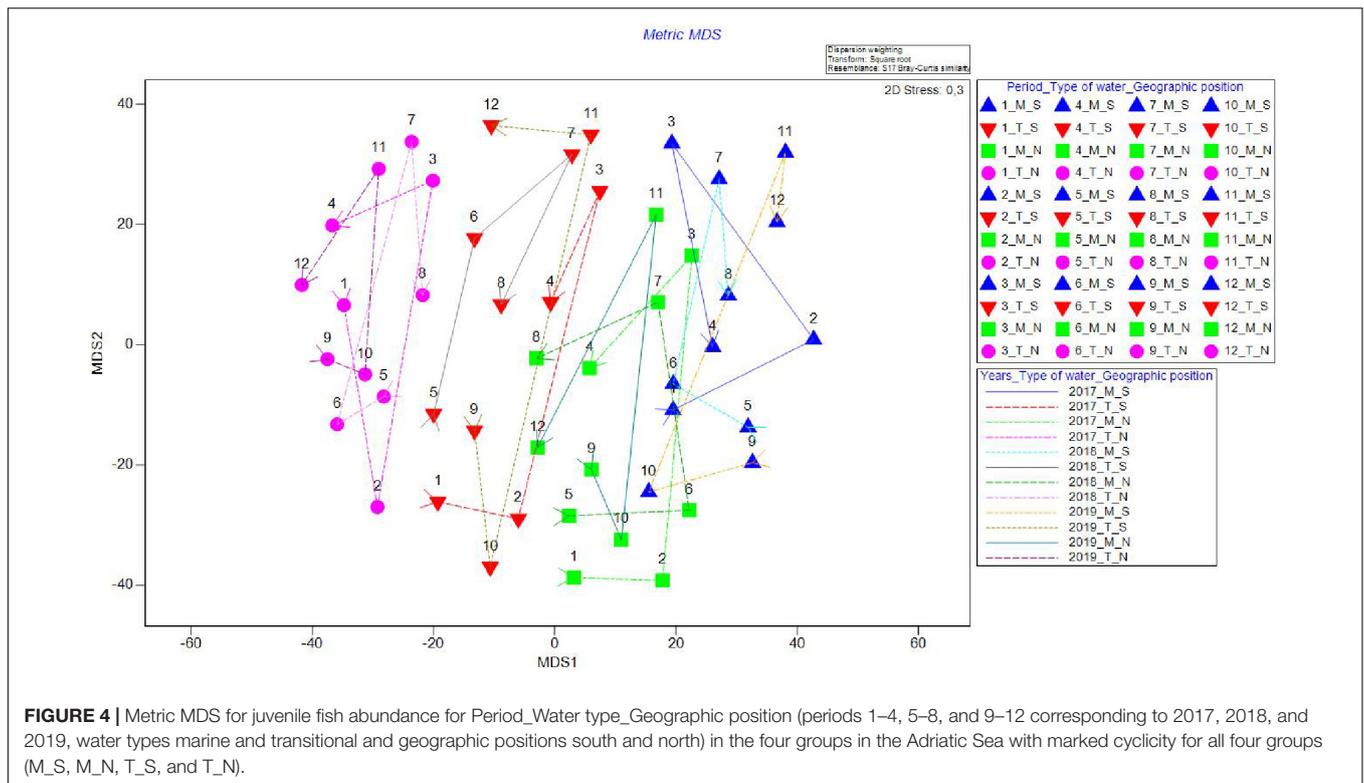
FIGURE 4 | Metric MDS for juvenile fish abundance for Period_Water type_Geographic position (periods 1–4, 5–8, and 9–12 corresponding to 2017, 2018, and 2019, water types marine and transitional and geographic positions south and north) in the four groups in the Adriatic Sea with marked cyclicity for all four groups (M_S, M_N, T_S, and T_N).

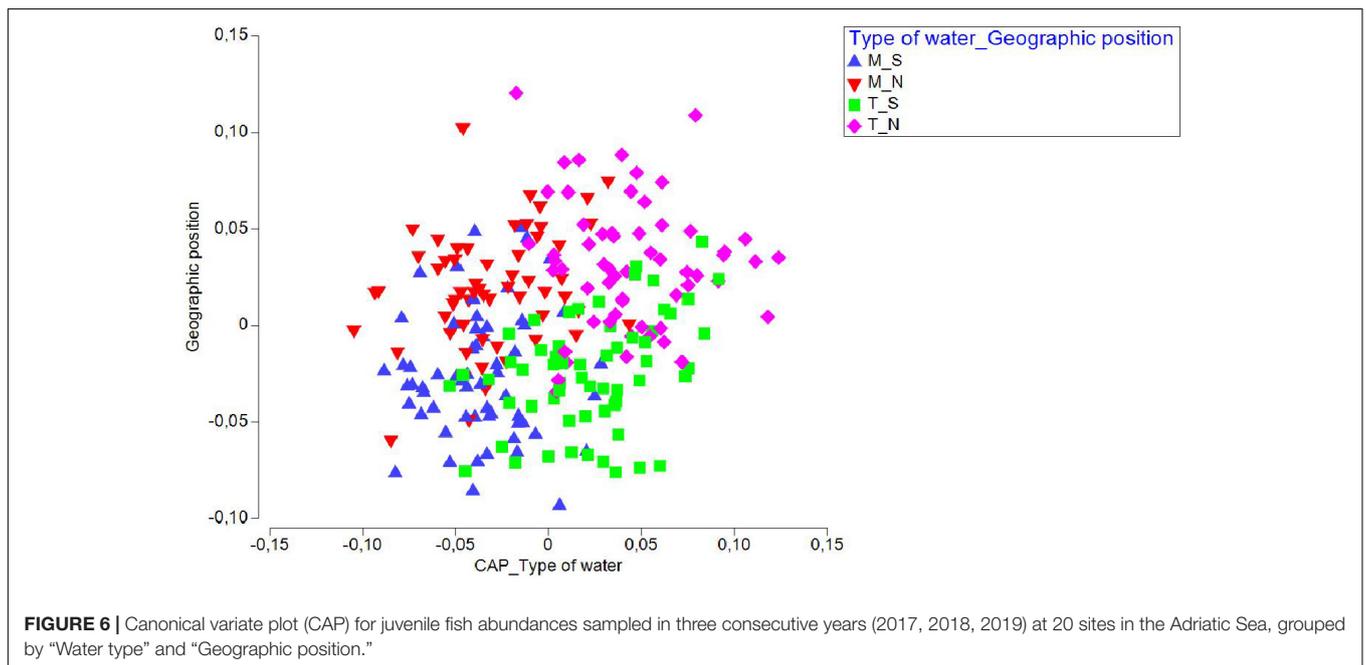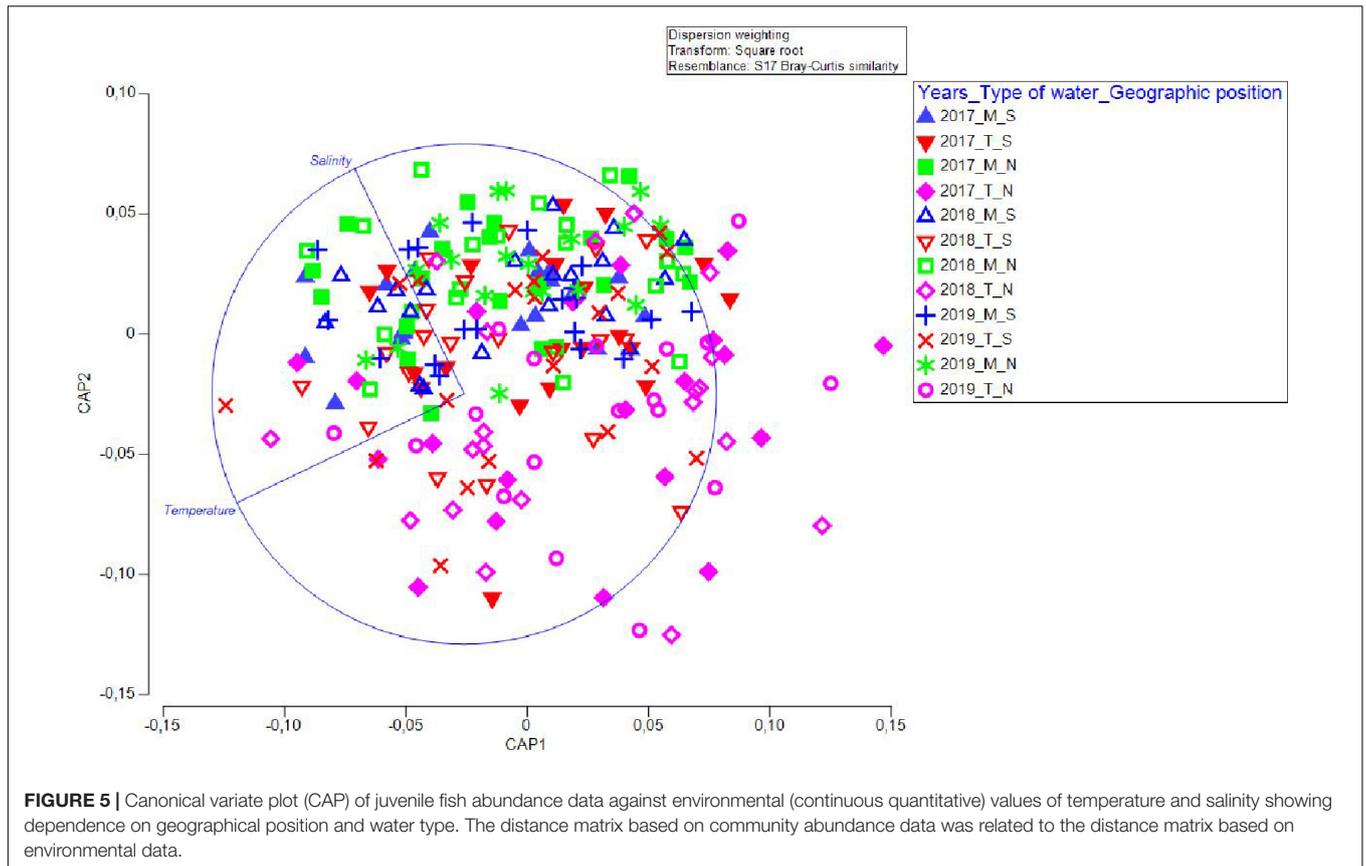to be more drastic or more rapidly reflected in changes at the community, species or individual level.

Interannual Variations of Juvenile Fish Composition

The influence of environmental factors on species composition or occurrence is specifically evident at the fish community level for both species richness and abundance. Moreover, water temperature appears to have a greater impact on transitional waters that are often retracted deep into the mainland. This is even more relevant since more than 64% of fish juveniles representing 68 species and 28 families were recorded in estuarine nurseries, and most are species of commercial interest (Dulčić et al., 2007). On the other hand, marine waters appear to be a less volatile environment, and the establishment of the juvenile fish community was defined primarily by salinity. This is supported by the fact that the same species were recorded in marine waters in all three years. Dulčić et al. (1997) investigated several shallow marine coves on distant islands and found a similar temporal pattern and the prevalence of five dominant species, suggesting that only a low amount of variation in the juvenile fish abundance in the real marine environment can be explained by temperature and salinity. The absence of certain species (e.g., *S. roissali* and *C. lucerna*) in 2019 in both marine and transitional waters could be regulated by a factor that is more regional in nature. Similarly, Stagličić et al. (2011) reported that species abundance within littoral fish assemblages could be a consequence of factors occurring on a wider spatial scale (i.e., fisheries mismanagement, pollution, climate change). Contrary, *C. saliens* and *S. salpa*

showed a higher abundance in northern marine waters (M_N) in 2019 and 2018, respectively, while *S. cinereus* was most abundant in T_S in 2018 in all four groups. However, there is the possibility that the sites where certain species were recorded are not essential or preferable nurseries for those species (i.e., poor site selection, low sample size, sampling gear selectivity). For example, *P. erythrinus* or *T. ovatus* were both lacking in southern marine areas in both 2018 and 2019. These species use other nursery areas, like marine coves on distant islands or at greater depths that are characterised by high and constant salinity (Dulčić et al., 1997; Biagi et al., 1998; La Mesa et al., 2011). In this study, *P. erythrinus* was found in 2017 exclusively at one station (S12) that is wide open toward the sea. Another typical marine species, *P. pagrus*, was also caught only at this site. The dispersal strategies of certain small migratory, shoaling species, such as *Spicara* sp. or *B. belone*, could also be the reason for their spatio-temporal absence (Hoare et al., 2000).

More Sensitive Species

If transitional waters geographically located at higher latitudes are more susceptible to interannual change, then the assumption is that more vulnerable species will select those waters for their nurseries, especially the more abundant species in the northern-central Adriatic (Dulčić et al., 2004; Matić-Skoko et al., 2007; Dulčić and Kovačić, 2020). Firstly, species of economic interest such as *D. labrax*, *S. salpa* and *S. aurata* should be highlighted here. It is also important to mention the small, resident species that also have ecological significance in the benthic communities of transitional waters, e.g., *Salaria pavo*,

FIGURE 5 | Canonical variate plot (CAP) of juvenile fish abundance data against environmental (continuous quantitative) values of temperature and salinity showing dependence on geographical position and water type. The distance matrix based on community abundance data was related to the distance matrix based on environmental data.

FIGURE 6 | Canonical variate plot (CAP) for juvenile fish abundances sampled in three consecutive years (2017, 2018, 2019) at 20 sites in the Adriatic Sea, grouped by "Water type" and "Geographic position."

S. ocellatus, and *Z. ophiocephalus,* as these herbivorous and omnivorous fishes seem to control both algae and invertebrates in rocky sub-littoral zones (Ruitton et al., 2000). *S. ocellatus* showed a significant association with an algal habitat, and

its abundance can certainly be related to the strong seasonal differences in algal cover (Hinz et al., 2019). If species preferring transitional waters at higher latitudes also spawn in winter and/or early spring, such as *D. vulgaris, D. sargus, S. aurata* and

TABLE 7 | SIMPER: species contributing most to the dissimilarity, in terms of abundance of juvenile fish abundances among transitional waters in the north (T_N) in June 2017 (Period 2), 2018 (Period 6) and 2019 (Period 10) in the Adriatic Sea.

Species	Co (%)	Cum (%)	Av. Diss	Co (%)	Cum (%)	Av. Diss
S. ocelatus	8.79	1.00	6.92	15.25	1.00	5.77
S. aurata	16.49	0.12	6.07	22.18	0.98	5.37
G. cobitis	23.06	0.98	5.18			
K. panizzae	28.80	0.18	4.53			
G. niger	34.46	0.67	4.46	7.80	0.67	6.04
S. roissali	38.40	0.00	3.11			
D. vulgaris	42.06	0.36	2.88			
S. acus	45.62	0.31	2.80			
Z. ophiocephalus	49.14	0.29	2.78	37.69	0.29	3.44
S. pavo				28.73	0.16	5.07
C. pusillus				33.24	0.37	3.49
S. salpa				41.80	0.46	3.18
C. ramada				45.84	0.24	3.13
C. risso				49.53	0.12	2.86

Co, contribution of species; Cumm, cumulative contribution; Av. Diss., average dissimilarity. Selected species contributed up to 50% of dissimilarity.
2_T_N & 10_T_N 6_T_N & 10_T_N

D. labrax, this makes them particularly sensitive to interannual differences in environmental conditions. As mentioned earlier, they can potentially be affected by late spawning, causing delays in settlement, leaving nurseries, or even causing individuals to remain in nurseries year round. Particularly, this delay can lead to the fact that at the moment of entry there is no prey of suitable size or in sufficient quantity for all incoming settlers (Machado et al., 2017). Decreased growth can make individuals too weak to join adult populations in the open seas that season (Lanier and Scharf, 2007). Since many marine species undergo long-distance dispersal during the pelagic larval phase before settling in benthic habitats where they remain (Di Franco et al., 2012), and many species also undergo further ontogenetic changes in restricted nursery grounds, pre- and post-settlement emigration by juveniles can then have significant population-level consequences (Vasconcelos et al., 2013). Sensitivity to physical-chemical changes of the aquatic environment, lack of suitable prey, and predation are the main causes of juvenile fish mortality (Guidetti, 2001; Cuadros et al., 2018).

CONCLUSION

Durrieu de Madron et al. (2011) highlighted the need to improve our understanding of species' distributions and ecological preferences to determine marine ecosystem responses to different anthropogenic impacts in the Mediterranean that affect juvenile survival in nursery areas. Matić-Skoko et al. (2020) suggested that significantly modified juvenile fish communities in recent decades may be the result of constant human embankment and marine infrastructure construction along the coast. Such an undesirable continuous practice on a wider spatial scale could potentially lead to biological homogenisation (Cacabelos et al., 2016; Pastro et al., 2016) due to changes in sediment or bottom type. In that sense, although there is a critical need to define the value of coastal habitats as nurseries for population abundance and growth of economically important or exploited species, quantifying the value of coastal habitats at the population level is a complex task (Beck et al., 2001; Duarte et al., 2008; Fodrie et al., 2009; Vasconcelos et al., 2011). The variability or similarity of structural features among different habitats illustrates species tolerance to available nursery conditions and should provide valuable information toward future spatially explicit predictions of species' distribution responses and resilience to potential changes in coastal conditions. Furthermore, variability of spatial and environmental use patterns in coastal areas should provide knowledge on the relevance of local regulation in defining nursery function. Ultimately, determining important sites for juveniles is a fundamental step toward the accurate identification of coastal nursery areas (Beck et al., 2001) that are essential for these species' metapopulations.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Ethics Committee of the Institute of Oceanography and Fisheries in Split.

AUTHOR CONTRIBUTIONS

SM-S, DV, HU and MP analysed the data end existing literature in collaboration with PT and DB. SM-S and DV wrote the draft of the manuscript. All authors conceived the research and participated in the improvement and revision of the document.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.849092/full#supplementary-material

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