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Coastal Fish Fauna in the *Cystoseira s.l.* Algal Belts: Experiences from the Northern Adriatic Sea

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Abstract: *Cystoseira s.l.* forests are recognised as important habitats which host diverse coastal fish assemblages. Many fish species use such habitats as feeding, breeding, and nursery grounds. Since the coastal fish community depends on the availability of dense macroalgal belts, the decline of these habitats in the Mediterranean Sea also affects the density of coastal fish species. We studied the coastal fish assemblage in *Cystoseira s.l.* forests in three consecutive years 2019–2021 in the Gulf of Trieste (Adriatic Sea). Data on coastal fish fauna were collected by visual counts conducted by SCUBA diving. Data on algal cover and habitat types were obtained by recording with a video camera. Similarities and differences in the fish community were analysed in terms of habitat and substrate preferences. A total of 34 species were recorded in *Cystoseira* forests. The results of the present study show that the different algal cover and associated depth gradient have different effects on the fish assemblage in coastal waters, affecting species composition and abundance. For many species, particularly labrids and sea breams, there is a decreasing temporal trend in frequency of occurrence and density. However, fish community trends can be used as a good “proxy” to evaluate the algal belt status. Our results indicate that rapid conservation and restoration actions are needed to stem the decline of *Cystoseira s.l.* forests.

Keywords: *Cystoseira s.l.* forests; fish assemblage; fish biodiversity; habitat preference; macroalgal belt; Mediterranean Sea



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1. Introduction

Coastal brown macroalgae of the genus *Cystoseira sensu lato* (Fucales, Phaeophyta) (hereafter referred to as *Cystoseira*), recently subdivided into the three genera *Cystoseira*, *Ericaria*, and *Gongolaria* [1], are habitat-builder species that can thrive from intertidal to circalittoral bottoms. In the Mediterranean Sea, they form dense and highly structured habitats over rocky bottoms, which resemble forest-like habitats that are among the most productive communities in the Mediterranean coastal area. *Cystoseira* forests have been recognised as important habitat builders in the euphotic zone of the Mediterranean [2]. They are known to host diverse and rich associated invertebrate fauna [3–6]. Ecosystem services provided by brown algal forests also include high primary production [7,8], a long-term carbon sink [9], and the production of numerous bioactive metabolites that have therapeutic properties [10].

Many coastal fish species inhabit *Cystoseira* forests and complete their entire life cycle within such algal belt [11,12]. They are also recognized as crucial nursery areas for some wrasses (genus *Symphodus*, *Coris julis*) and combers (genus *Serranus*) [13,14].

Recently, the biocenosis of photophilic algae faced a dramatic decline in many areas of the Mediterranean Sea [15,16]. Brown algal forests has been reported to be especially

vulnerable [13] to various anthropogenic factors, such as marine pollution, boat anchoring, coastal urbanisation, dredging, date mussel fishing, and others [17–19]. Human stressors also negatively impact connectivity in the marine environment, leading to habitat fragmentation and loss and genetic disjunction, even at small spatial scales [20]. Moreover, seawater warming and thermal anomalies are leading to changes in reproductive phenology, early stages growth, and viability of *Cystoseira* spp. [21,22].

Cystoseira s.l. species are listed in (i) Habitats Directive 92/43/EEC as Habitat of Community Interest (Habitat code 1170); (ii) Bern Convention as strictly protected in Annex I; (iii) Barcelona Convention in Annex II. All *Cystoseira* spp. are also under surveillance by international organizations (IUCN, SPA/RAC, MedPAN).

A sharp decline of canopy-forming species has also been reported in the northern Adriatic Sea [23–25], leading to displacement by smaller and persistent so-called turf-forming species in shallow waters. The increasing coverage of such low-lying algae is mainly related to human-induced hydromorphological changes to the shoreline (construction of piers, platforms, seawalls, marinas, etc.) and high sediment resuspension rates (also due to maritime traffic and dredging of the seabed) [24]. Currently, *Gongolaria barbata* (Stackhouse) Kuntze and *Cystoseira compressa* (Esper) Gerloff and Nizamuddin are present in the Gulf of Trieste only along the Slovenian coastline, while they have almost disappeared on the Italian side of the gulf. Other *Cystoseira s.l.* species are already rare in Slovenian waters and extinct in Italian waters of the Gulf of Trieste [23–25]. In Slovenian coastal waters, *G. barbata* belts grow mainly in a depth range of 1 to 3 m; then, they are replaced by *C. compressa* and dense *Padina pavonica* (L.) Thivy belts [24], and below 4 m, by precoralligenous formations and *Cystoseira corniculata* (Turner) Zanardini [25]. Cormaci and Furnari (2003) [26] concluded that *C. compressa* dominates unperturbed sites with low pollution levels, while Vukovič (1980) [27] reported that *G. barbata* grows also at sites with mild sedimentation rates and low organic pollution. The red algae *Halopithys incurva* (Hudson) Batters, also considered a canopy-forming species, was also reported to adapt to unsteady biotopes [26]. The latter is in Slovenian coastal waters, dominant at sites with high sedimentation rates [24]. Since the coastal fish community depends on the availability of suitable algal belts, provided by canopy-forming macroalgae [28], the decline of these habitats also affects the density of fish species in coastal areas. Previously, few papers were published on the coastal fish community in the Slovenian part of the Adriatic Sea; however, these works dealt with the situation twenty years ago, when the *Cystoseira* forests were still in rather good health [29,30].

The aims of this study are to: (1) analyse relative habitat use and preference of coastal fish species in areas with high macroalgal coverage; (2) identify temporal changes in fish communities, also considering single species frequencies and abundances; and (3) verify the influence of the following factors: time, depth, habitat type and substrate on the overall fish community's structures, density, richness, and diversity.

2. Materials and Methods

2.1. Study Area

The Gulf of Trieste (Figure 1) is a shallow semi-enclosed basin in the northernmost part of the Adriatic Sea with a maximum depth of 33 m. It is characterized by the largest tidal amplitudes (67 cm on average [31]) and the lowest winter temperatures (7 °C on average [32]) in the Mediterranean Sea [33]. The area is known by high oscillations in temperature and salinity and the important stratification of the water column in the warmer period of the year. Salinity, which is, on average, around 37‰ [32], is influenced by freshwater inputs, mainly from the Isonzo River [34], while the water circulation is mainly counter clockwise in the lower layer and clockwise in the surface layer [35]. The rocky bottom is made mainly of Eocene Flysch layers with alternating solid sandstone and soft marl [36]. The Slovenian coastal sea covers the southern part of the Gulf of Trieste, with the coastline approximately 46 km long.

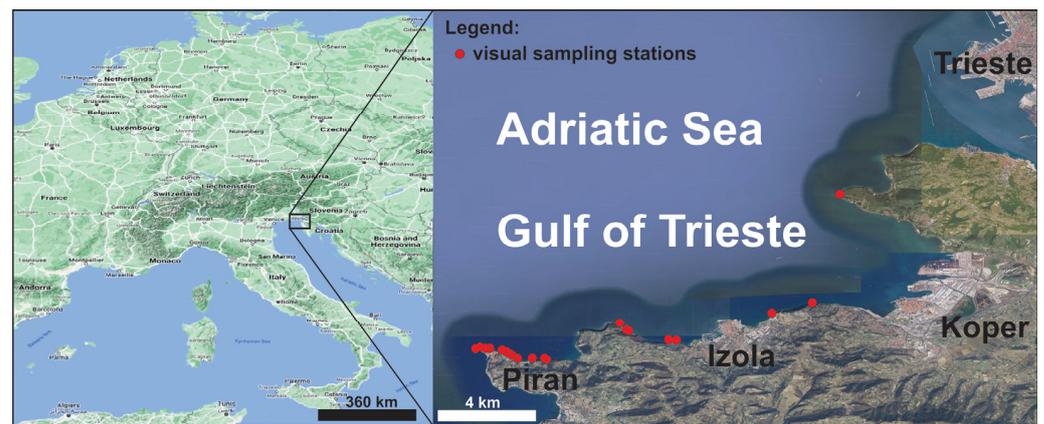


Figure 1. The geographic position of the study area with the stations for the visual sampling of the fish assemblage within *Cystoseira s.l.* algal belts.

2.2. Fieldwork

2.2.1. Fish Assemblage Composition and Abundance

Field data were collected by visual censuses carried out using SCUBA diving [30,37–39]. Such techniques are currently recognized as standard sampling methods for studying fish ecology [40]. They provide a suitable methodology for a rapid and non-destructive inventory of fish communities in coastal waters. Although some biases have been attributed to this method, the visual census has many advantages, of which the negligible impact on the environment is one of the most important [41]. Moreover, with the increasing number of marine protected areas in the Mediterranean, traditional fishing gear—prohibited in protected areas—must be replaced by visual counts carried out by SCUBA diving when a fish assemblage is to be studied or monitored [42–45].

The fish community in vegetated habitats along the Slovenian coast (Gulf of Trieste, Figure 1) was studied for three consecutive years, from 2019 to 2021. The fieldwork was conducted in late spring and summer as some dominant coastal fish groups, such as labrids, have been shown to be less active in winter [46]. At 22 sampling stations (8 in 2019 and 2020 and 6 in 2021), the fish community and habitat structure were visually assessed by an experienced diver, who swam along 50 m long and 1 m wide horizontal transects at more or less constant speed [47–49]. A total of 190 visual transects were conducted, 66 in 2019, 70 in 2020, and 52 in 2021. Transects ran parallel to the coast with more or less constant depths ranging from 1.5 to 5 m. Only fishes bigger than 2 cm were included in the counts. All visual transects were performed between 10:00 and 13:00. Environmental variables were measured after the visual fish counts. A second diver filmed the transects to assess the algal coverage and the habitat types.

2.2.2. Habitat Types

Habitat composition along the transects was characterized based on abiotic and biotic factors (Table 1). The former is represented by the geomorphological features, such as rocks, boulders, platforms, overhangs, crevices, burrows, and others (*sensu* Gimenez-Casalduero et al. [50]), while the latter include different vegetation types or biogenic formations [51]. The following microhabitat variables, adapted from Larssonneur 1977, were considered [52]: bottom substrate composition [boulders (>2 m; 2–1 m; 1–0.50 m), rocks (30–50 cm), pebbles (10–30 cm), gravel (2–0.2 cm), sand (0.2–0.05 mm), and mud (<0.05 mm)], water depth, and the presence of biological structures, such as macroalgae (*Cystoseira* spp., *Halopithys incurva*, *Padina pavonica*, precoralligenous algae, and algal turf). To reduce the bias associated with the sampling season, the sampling period was chosen to correspond to the time of maximum development of *Cystoseira s.l.* species and *H. incurva* [24]. The height of these canopy-forming species, on average, was around 20–30 cm. In addition, the category substrate structure was divided into four smaller habi-

tat types, such as K1-stones from 1–10 cm, K2a-stones from 10–20 cm, K2b-stones from 20–30 cm, and rock 30–50 cm. The coverage of each habitat type was assessed by analysing the filmed material and expressed as a percentage of the surveyed area.

Table 1. The checklist of habitat types encountered in the study area in the period 2019–2021.

Habitat Type-Algal Cover	Code
Rocks with dense <i>Cystoseira s.l.</i>	Cy3
Rocks or boulders with dense <i>Padina pavonica</i>	Cy4
Terrace with dense <i>Cystoseira s.l.</i>	Cy5
Boulder with dense <i>Cystoseira s.l.</i>	Cy6
Rocks, terraces, or boulders with <i>Halopithys incurva</i>	Hinc
Rocks/boulders with precoralligenous communities	PKG
Habitat Type-Substrate Structure	
Rough sand <0.5 cm	P1
Bare stones 0.5–10 cm	K1
Bare stones 10–20 cm	K2a
Bare stones 20–30 cm	K2b
Bare or turf vegetated rocks 30–50 cm	K3
Bare or turf vegetated terrace >50 cm	K5
Bare or turf vegetated boulders >50 cm	K6

2.3. Data Analysis

In the first step, fish species abundance and composition per habitat type (algal cover (Cy3, Cy4, Cy5, Cy6, Hinc, and PKG) or substrate structure (K2a, K2b, K3, K5, K6, and P1)) was studied by organizing all collected data into a frequency table. Frequency of occurrence (FO% = $100 \times A/a$, where a is the number of transects where certain species was caught, and A is the total number of transects) and relative abundance (N% = n/N ; as the number of individuals of certain species divided with the abundance of specimens of all species) was calculated to distinguish between rare (<1%) and dominant (>10%) species [53,54]. In addition, mean and maximum fish density ($d = 100 \times (n/S)$, as the number of fish individuals (n) per 100 m² of the sampled area (S)) for the consecutive year, were calculated as well to detect trends in fish occurrence and density. Next, the relative habitat use of all fish species was measured with Ivlev's electivity index (s) [55–57]. The electivity index was calculated as $E = (r_i - p_i)/(r_i + p_i)$, where r_i is the percentage of fish species using a given habitat and p_i is the total percentage of habitat type in the studied environment [58]. The s values for each fish species per habitat type (algal cover or substrate structure) varied between -1.0 (never used) and $+1.0$ (exclusively used), with 0.0 representing no habitat preference [55,59]. Moreover, the relationship between habitat types (algal cover (Cy3, Cy4, Cy5, Cy6, Hinc, and PKG) or substrate structure (K2a, K2b, K3, K5, K6 and P1)) and coastal fish species were further explored with the Canonical Correspondence Analysis (CCA) and the redundancy analysis (RDA) with the *vegan* package in the R environment [60]. We tested how much variation in fish assemblage could be explained by habitat type (algal cover) and substrate structure. Prior to ordination analysis, fish abundance data were Hellinger transformed by applying the *decostand* algorithm in the *vegan* package. Thus, the weight of abundant species was reduced while Euclidean distances between samples in the multidimensional space were simultaneously preserved [61]. The significance of constraints in the produced CCA model (by = "term") were tested with the *anova* function within *vegan*, which automatically chooses the correct variant for the result of constrained ordination.

To visualize potential differences in fish assemblage composition in regard to factors year (2019, 2020 and 2021), depth (<3 m and >3 m), and algal cover (Cy3, Cy4, Cy5, Cy6, Hinc, and PKG), the non-metric multidimensional scaling analysis (NMDS) was performed by applying *vegdist* (method = bray) and *metaMDS* functions in the *vegan* package [62]. The multivariate permutation analysis of variance (PERMANOVA; 999 permutations) revealed in the next step if above mentioned factors significantly contributed to coastal

fish community differentiation. In addition to the PERMANOVA function *adonis* in the *vegan* package, the *betadisper* and *permutest* algorithms were applied to test the multivariate homogeneity of group and permutation dispersion. If both tests were insignificant ($p > \alpha$; $\alpha = 0.05$), the *simper* function was used to find key contributors to the discovered differences in the fish community by factors (year, depth, and algal cover).

To further explore and understand the fish community–environment interaction, variables fish density, number of species, and Shannon index [63,64] were calculated for each transect, then compared by factors year (2019, 2020, and 2021), depth (<3 m and >3 m) and habitat type (algal cover (Cy3, Cy4, Cy5, Cy6, Hinc, and PKG) or substrate structure (K2a, K2b, K3, K5, K6, and P1)). Accordingly, a two-factor analysis of variance (ANOVA) for each combination (year–depth, algal cover–depth, and substrate structure–depth) was performed (after testing for normality and homogeneity of variances) in the R statistical environment [60] to identify potential differences in fish density and diversity in the studied environment. This interdependence was further tested with a generalized linear model (a *glm* function in the R environment) to evaluate the effect of selected variables/factors (year, depth, and habitat type (algal cover)) on coastal fish density and diversity.

3. Results

3.1. Coastal Fish Assemblage Composition and Abundance

Altogether, 34 coastal fish species were recorded in shallow algal belts, with 30 species detected in 2019, 29 species in 2020, and 26 species in 2021. Among them, 8 were labrids, 7 sparids, 7 blennies, and 4 gobies (other families with less than 3 species). The most frequent species were *Serranus scriba* (FO% from 94.2 to 97.2), *Gobius fallax* (FO% from 62 to 92.5), *Diplodus vulgaris* (FO% from 50.0 to 98.5), *Symphodus cinereus* (FO% from 59.6 to 82.1), and *Chromis chromis* (FO% from 50.0 to 77.6), respectively (Table 2). The most abundant species were *C. chromis*, with mean density from 28.48 in 2019 to 6.65 ind. 100 m⁻² in 2021, *Gobius fallax*, with 11.22 to 13.12 ind. 100 m⁻², and *S. scriba*, with 8.81 to 8.08 ind. 100 m⁻².

Table 2. Frequency of occurrence (FO%), relative abundance (N%) and mean (d), and maximum (max) densities (ind. 100 m⁻²) of coastal fish species along the Slovenian coast between 2019 and 2021.

Family	Species	2019				2020				2021			
		FO%	N%	d	Max	FO%	N%	d	Max	FO%	N%	d	Max
Labridae	<i>Coris julis</i>	16.40	0.66	0.60	8.00	15.50	1.32	0.68	10.00	3.90	0.28	0.62	4.00
	<i>Labrus merula</i>	3.00	0.07	0.06	2.00	1.40	0.06	0.03	2.00	3.90	0.19	0.08	2.00
	<i>Symphodus cinereus</i>	82.10	4.37	3.94	12.00	60.60	6.49	3.32	18.00	59.60	5.43	2.23	14.00
	<i>Symphodus doderleini</i>	1.49	0.03	0.03	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Symphodus mediterraneus</i>	3.00	0.10	0.09	4.00	0.00	0.00	0.00	0.00	1.90	0.37	0.15	8.00
	<i>Symphodus ocellatus</i>	32.80	1.66	1.49	18.00	26.80	5.78	2.96	44.00	5.80	1.03	0.42	12.00
	<i>Symphodus roissali</i>	7.50	0.20	0.18	4.00	9.90	0.50	0.25	6.00	0.00	0.00	0.00	0.00
	<i>Symphodus rostratus</i>	13.40	1.13	1.01	18.00	8.50	0.33	0.17	4.00	1.90	0.09	0.04	2.00
	<i>Symphodus tinca</i>	89.60	10.69	9.64	34.00	52.10	5.39	2.76	14.00	19.20	1.78	0.73	6.00
Blenniidae	<i>Microlipophrys dalmatinus</i>	23.90	0.89	0.81	8.00	2.80	0.11	0.06	2.00	13.50	0.65	0.27	2.00
	<i>Parablennius gattorugine</i>	23.90	0.66	0.60	6.00	19.70	0.88	0.45	4.00	19.20	0.94	0.38	2.00
	<i>Parablennius incognitus</i>	13.40	0.43	0.39	6.00	2.80	0.11	0.06	2.00	3.90	0.19	0.08	2.00
	<i>Parablennius rouxi</i>	19.40	0.63	0.57	8.00	16.90	1.10	0.56	8.00	0.00	0.00	0.08	2.00
	<i>Parablennius sanguinolentus</i>	9.00	0.33	0.30	6.00	7.00	0.94	0.48	8.00	5.80	0.37	0.15	4.00
	<i>Parablennius tentacularis</i>	0.00	0.00	0.00	0.00	7.00	0.44	0.23	4.00	1.90	0.09	0.04	2.00
	<i>Parablennius zvonimiri</i>	11.50	0.03	0.03	2.00	2.80	0.44	0.23	8.00	0.00	0.00	0.00	0.00
Sparidae	<i>Diplodus annularis</i>	26.90	0.93	0.84	6.00	9.90	0.61	0.31	6.00	3.90	0.37	0.15	6.00
	<i>Diplodus vulgaris</i>	98.50	13.37	12.06	42.00	71.80	9.47	4.85	26.00	50.00	8.79	3.62	32.00
	<i>Diplodus puntazzo</i>	32.80	1.06	0.96	8.00	23.90	1.38	0.70	8.00	11.50	1.40	0.58	10.00
	<i>Diplodus sargus</i>	0.00	0.00	0.00	0.00	1.40	0.11	0.06	4.00	3.90	0.19	0.08	2.00
	<i>Oblada melanura</i>	4.50	0.13	0.12	4.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Sarpa salpa</i>	20.90	3.67	3.31	54.00	8.50	1.10	0.56	14.00	1.90	2.06	0.85	44.00
	<i>Spondylliosoma cantharus</i>	10.50	0.46	0.42	8.00	1.40	0.06	0.03	2.00	1.90	0.09	0.04	2.00

Table 2. Cont.

Family	Species	2019				2020				2021			
		FO%	N%	d	Max	FO%	N%	d	Max	FO%	N%	d	Max
Gobiidae	<i>Gobius cobitis</i>	16.40	0.40	0.36	4.00	9.90	0.39	0.20	2.00	13.50	1.12	0.46	10.00
	<i>Gobius cruentatus</i>	23.90	0.53	0.48	2.00	56.30	8.31	4.25	20.00	21.20	2.34	0.96	10.00
	<i>Gobius fallax</i>	92.50	12.45	11.22	42.00	62.00	7.93	4.06	24.00	88.50	31.90	13.12	52.00
	<i>Pomatoschistus bathi</i>	14.90	1.62	1.46	14.00	21.10	2.15	1.10	10.00	26.90	3.55	1.46	12.00
Serranidae	<i>Serranus hepatus</i>	0.00	0.00	0.00	0.00	16.90	0.83	0.42	6.00	0.00	0.00	0.00	0.00
	<i>Serranus scriba</i>	95.50	9.76	8.81	24.00	97.20	20.91	10.70	46.00	94.20	19.64	8.08	22.00
Tripterygiidae	<i>Tripterygion delaisi</i>	37.30	1.66	1.49	10.00	9.90	0.50	0.25	4.00	15.40	0.84	0.35	4.00
	<i>Tripterygion tripteronotus</i>	11.90	0.46	0.42	8.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Syngnathidae	<i>Hippocampus guttulatus</i>	1.50	0.03	0.03	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pomacentridae	<i>Chromis chromis</i>	77.60	31.58	28.48	200.00	50.70	21.63	11.07	44.00	50.00	16.18	6.65	36.00
Soleidae	<i>Solea solea</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.90	0.00	0.04	2.00
Mugilidae	<i>Liza aurata</i>	0.00	0.00	0.00	0.00	4.20	0.77	0.39	16.00	0.00	0.00	0.00	0.00

A decreasing temporal trend in the frequency of occurrence is evident for many species (Table 2), especially those from the genera *Diplodus* (*D. annularis*, *D. vulgaris*, and *D. puntazzo*) and *Symphodus* (*S. cinereus*, *S. tinca*, *S. rostratus*, and *S. ocellatus*). The same is true for their abundances, expressed as density (ind. 100m⁻²). The overall mean density of the coastal fish decreased from 45.09 ind. 100 m⁻² in 2019 to 25.59 ind. 100 m⁻² in 2020 and to 20.56 ind. 100 m⁻² in 2021. Even if we do not consider gregarious species, such as *Chromis chromis*, the trend is still evident. Among the different families, labrids showed the most marked negative trend. Their total densities decreased from 8.52 ind. 100 m⁻² (2019) to 5.08 ind. 100 m⁻² (2020) and to 1.88 ind. 100 m⁻² (2021).

3.2. Coastal Fish Habitat Preference and Trends

Some wrasses, such as *S. ocellatus*, *S. cinereus*, and *C. julis*, show preferences for *Cystoseira* algal belts. Simultaneously, these species prefer sandy areas (P1) and environments with bare stones (K2a, K2b) (see the electivity index in Figure 2).

Family	Species	n	Cy3	Cy4	Cy5	Cy6	Hinc	PKG	K2a	K2b	K3	K5	K6	P1
Labridae	<i>Coris julis</i>	94	0.30	0.17	-1.00	0.63	-1.00	0.74	-1.00	-1.00	0.25	-1.00	-0.46	-1.00
	<i>Symphodus cinereus</i>	352	0.32	-0.38	0.31	-0.27	0.55	-0.14	0.86	0.40	-0.26	0.33	-0.23	0.77
	<i>Symphodus ocellatus</i>	251	0.64	-0.13	-0.42	-0.32	0.64	-0.48	0.03	-1.00	0.15	-0.37	-0.20	-1.00
	<i>Symphodus rostratus</i>	82	-1.00	0.31	-1.00	-0.70	0.34	-1.00	0.78	-1.00	0.21	-1.00	-0.65	-1.00
	<i>Symphodus tinca</i>	872	-0.05	-0.12	0.12	0.16	0.59	0.26	-1.00	-1.00	-0.09	0.18	0.11	-1.00
Blenniidae	<i>Parablennius gattorugine</i>	89	0.09	0.12	-0.04	0.61	0.31	0.33	-1.00	0.60	0.13	-0.12	-0.32	-1.00
	<i>Parablennius incognitus</i>	34	0.07	-0.76	0.57	0.12	0.24	-1.00	-1.00	0.55	-0.50	0.65	0.01	-1.00
	<i>Parablennius rouxi</i>	78	-1.00	0.01	-1.00	0.01	-1.00	0.85	-1.00	-1.00	0.12	-1.00	-0.02	-1.00
	<i>Parablennius sanguinolentus</i>	45	0.57	-1.00	0.46	-0.22	0.43	-1.00	-1.00	0.83	-0.16	0.51	-0.32	-1.00
	<i>Parablennius zvonimiri</i>	114	-1.00	0.30	-1.00	-0.14	-1.00	-1.00	-1.00	-1.00	0.20	-1.00	-0.24	-1.00
Sparidae	<i>Diplodus annularis</i>	86	0.63	-0.01	-0.17	0.27	-1.00	-1.00	-1.00	-1.00	-0.09	-0.11	0.17	-1.00
	<i>Diplodus vulgaris</i>	1340	0.08	-0.21	0.23	0.14	-0.08	-0.31	-0.43	-1.00	-0.13	0.38	0.05	-0.13
	<i>Diplodus puntazzo</i>	143	-0.15	-0.31	0.07	0.29	0.08	-1.00	-1.00	-1.00	-0.17	0.13	0.20	-1.00
	<i>Sarpa salpa</i>	306	0.78	0.03	0.42	0.02	-1.00	0.55	-1.00	-1.00	-0.06	0.47	-0.09	-1.00
	<i>Spondyllosoma cantharus</i>	268	-0.27	0.17	0.03	-0.09	-1.00	-1.00	-1.00	-1.00	0.09	0.09	-0.14	-1.00
Gobiidae	<i>Gobius cobitis</i>	59	0.07	-0.43	0.64	-0.08	-0.36	-1.00	0.39	0.60	0.00	0.22	-0.19	-1.00
	<i>Gobius cruentatus</i>	384	-0.11	-0.18	0.65	-0.13	0.69	-1.00	0.52	0.57	-0.34	0.61	0.22	0.77
	<i>Gobius fallax</i>	1722	-0.31	0.10	0.10	-0.05	-0.29	-0.42	-0.62	0.16	0.05	-0.12	-0.05	0.04
	<i>Pomatoschistus bathi</i>	154	-1.00	-0.40	0.51	-0.83	0.75	-1.00	-1.00	0.64	-0.30	0.64	-0.17	-1.00
Serranidae	<i>Serranus hepatus</i>	30	-1.00	-0.03	-1.00	-0.16	0.70	-1.00	0.89	0.92	-1.00	-1.00	-0.02	-1.00
	<i>Serranus scriba</i>	1687	0.30	-0.10	0.16	-0.11	0.00	0.09	0.20	0.34	0.01	0.09	-0.10	0.19
Tripterygiidae	<i>Tripterygion delaisi</i>	136	-0.40	0.21	-0.54	-0.12	-1.00	0.44	-1.00	-1.00	0.18	-1.00	-0.16	-1.00
Pomacentridae	<i>Chromis chromis</i>	3040	-0.40	0.13	-0.76	0.05	-0.18	0.15	-1.00	-1.00	0.06	-0.86	0.07	-0.66
Soleidae	<i>Solea solea</i>	30	0.75	-0.73	-1.00	-0.35	-0.04	-1.00	-1.00	0.60	0.21	-1.00	-0.44	-1.00
Mugilidae	<i>Liza aurata</i>	82	0.58	-0.71	0.00	0.02	0.34	-1.00	0.81	-1.00	-0.06	0.06	-0.08	-1.00

Figure 2. Electivity index values for coastal fish species (with more than 30 individuals [n]) regarding algal cover or substrate structure. Green colour stands for positive and red colour for negative index values.

The red triplefin, *Tripterygion tripteronotus*, prefers vegetated *Cystoseira* habitats, whereas the yellow triplefin, *T. delaisi*, prefers deeper parts of the rocky bottom where the pre-colligenous habitats occurs (Figure 2). Among blennies, the only species which seems to be related to vegetated environment is *Parablennius sanguinolentus*. The same relation was detected for *Sarpa salpa* (Sparidae), *Serranus scriba* (Serranidae), *Solea solea* (Soleidae), and *Liza aurata* (Mugilidae). Gobiids show a clear tendency towards rocks, terraces, or boulders with *Halopithys incurva* and bare stones (K2a and K2b).

The CCA ordination diagram (Figure 3) visualizes similarities and differences in the studied fish community in terms of habitat and substrate type preferences. The first two axes explained 36% of the variability of 34 coastal fish species. The permutation ANOVA analysis revealed that the CCA model is properly specified and all plotted environmental factors significantly contribute to the total constrained proportion. However, there was no significant improvement in the proportion of constrained values by applying RDA instead of CCA.

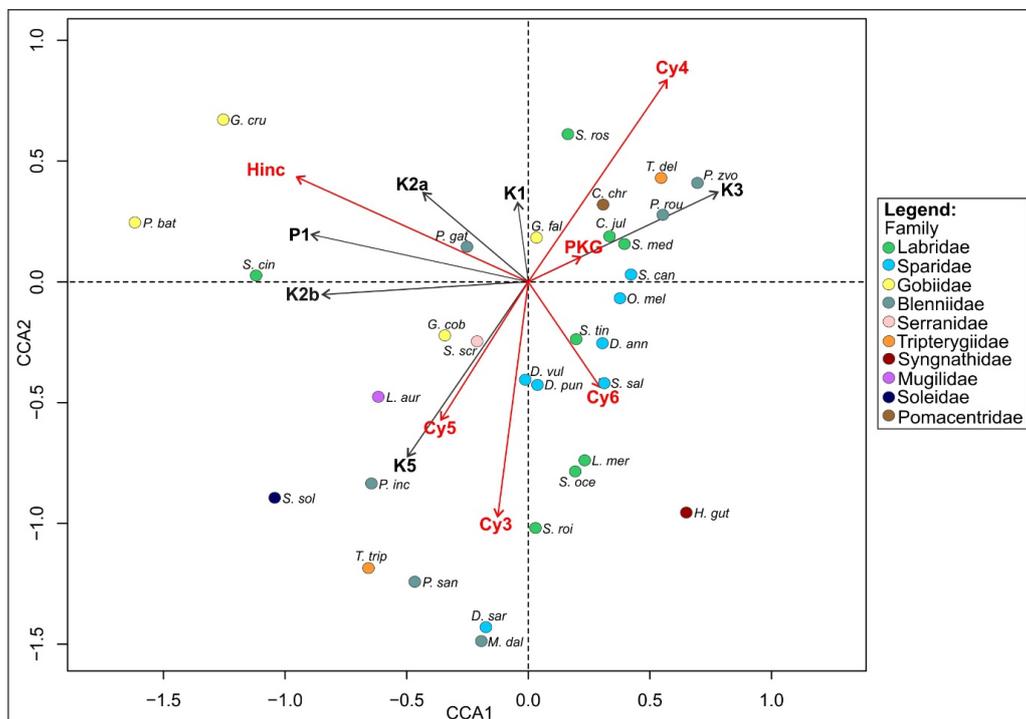


Figure 3. CCA analysis ordination between coastal fish assemblage and habitat types (algal cover) or substrate structure. The first axis loads 22% of variability, and the second axis 14%. Species names were systematically abbreviated to the first three letter of the species name in Table 1. C. chr—*Chromis chromis*; C. jul—*Coris julis*; D. ann—*Diplodus annularis*; D. pun—*Diplodus puntazzo*; D. sar—*Diplodus sargus sargus*; D. vul—*Diplodus vulgaris*; G. cob—*Gobius cobitis*; G. cru—*Gobius cruentatus*; G. fal—*Gobius fallax*; L. mer—*Labrus merula*; L. aur—*Liza aurata*; M. dal—*Microlipophrys dalmatinus*; O. mel—*Oblada melanura*; P. gat—*Parablennius gattorugine*; P. inc—*Parablennius incognitus*; P. rou—*Parablennius rouxi*; P. san—*Parablennius sanguinolentus*; P. ten—*Parablennius tentacularis*; P. bat—*Pomatoschistus bathi*; P. zvo—*P. zvonimiri*; S. sal—*Sarpa salpa*; S. hep—*Serranus hepatus*; S. scr—*Serranus scriba*; S. cin—*Symphodus cinereus*; S. med—*Symphodus mediterraneus*; S. oce—*Symphodus ocellatus*; S. roi—*Symphodus roissali*; S. ros—*Symphodus rostratus*; S. tin—*Symphodus tinca*; S. sol—*Solea solea*; T. trip—*Tripterygion tripteronotus*.

Results indicate that different fish species prefer different environments, which correlates with the electivity index values in Figure 2. Labrids and sparids inhabit *Cystoseira* belts, but they can also be found in deeper environments (PKG) with larger substrate (K3). Gobiids avoid densely vegetated habitats and prefer finer and smaller substrates. Blenniids are the most dynamic coastal fish group in terms of habitat preference. Some species

are linked to *Cystoseira* belts (e.g., *Parablennius incognitus* and *P. sanguinolentus*) on large substrate structures (K5), others can be found in deeper water near large rocks 30–50 cm bare or covered by turf (*P. rouxi* and *P. zvonimiri*) (K3), or in the shallows alongside small stones (*Parablennius gattorugine*) (K2a). Triplefin blennies clearly differ in habitat selection as well. *Tripterygion tripteronotus* can be found on sandstone terraces with dense *Cystoseira* (Cy5), whereas *T. delaisi* mostly utilizes the deeper-laying precoralligenous habitat (PKG).

3.3. Coastal Fish Community Differentiating Factors

Both the electivity index and the CCA ordination showed the preference of individual fish species for different habitat types in terms of algal cover and substrate type. However, given the negative trends in coastal fish occurrence and abundance (Table 2), the questions about differentiating factors and drivers of the changing fish community immediately arise. The NMDS (Figure 4) and PERMANOVA analysis proved that there were significant differences ($p < \alpha$; $\alpha = 0.05$) in the studied coastal fish community if we considered factors year (2019, 2020, 2021), depth (<3 m, >3 m) or habitat type (algal cover (Cy3, Cy4, Cy5, Cy6, Hinc1, and PKG)). Substrate structure (K2a, K2b, K3, K5, K6, and P1) did not affect species composition or abundance.

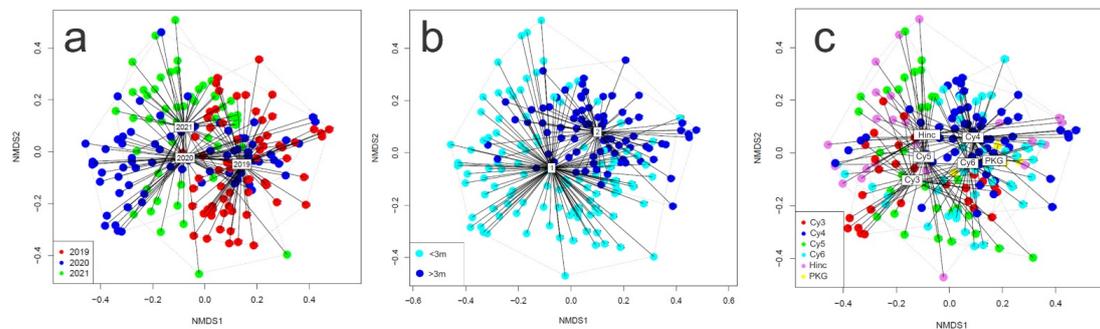


Figure 4. NMDS plots for the coastal fish assemblage in regard to factors year (a), depth (b), and habitat type (algal cover) (c).

The significant *betadisper* and *permutest* tests for the factor year indicated temporally different dispersion properties of the studied coastal fish community (Figure 4a). However, 2019 clearly differed from 2020 and 2021, when we had much greater dispersion but lower species diversity and density. Similar to factor year, fish species composition and abundance at different depths clearly differed, with differences in multivariate dispersion as well (Figure 4b). The major contributors are *C. chromis*, *G. fallax*, *S. tinca*, *D. vulgaris*, and *G. cruentatus*, all more abundant in deeper water (cumulative sum = 0.41). Significant differences between habitat types (algal cover) (Figure 4c), but no differences in the multivariate dispersion in the coastal fish assemblage were observed, which meant that the *simper* function could be fully trusted. Fish species mostly contributing to the significant difference between habitat types are shown in Table 3.

After identifying significant coastal fish community differentiating factors, the research focus turned to overall diversity. Figure 5 shows how the dependent variables: coastal fish density (number per 100 m⁻²), number of species and fish diversity (Shannon index), varied in relation to year, depth, and habitat type (algal cover). Coastal fish density was significantly higher ($p > \alpha$; $\alpha = 0.05$) in waters deeper than 3 m, with the exception of habitat types Cy3 (rocks with dense *Cystoseira s.l.*) and Hinc1 (rocks, terraces, or boulders with *Halopithys incurva*), and a marked decrease with years was observed in both depth categories. Species numbers clearly differed between depths only in habitats Cy3, Cy4, and Hinc1, and it showed an even more pronounced downward trend from 2019 to 2021. Species diversity did not differ significantly with depth but differed significantly among all habitat types and decreased dramatically over time. The highest coastal fish diversity was detected in habitats PKG and Cy4.

Table 3. Fish species mostly contribute to the significant difference between habitat types according to *simper* analysis, with indication of higher average abundance per habitat type and the cumulative sum of these species' contributions to the significant difference between habitat types. Legend in Figure 3.

	Cy3	Cy4	Cy5	Cy6	Hinc
Cy4	<i>C. chr</i> (>Cy4) <i>S. scr</i> (>Cy3) <i>G. fal</i> (>Cy4) 0.45				
Cy5	<i>G. fal</i> (>Cy5) <i>S. scr</i> (>Cy3) <i>D. vul</i> (>Cy5) 0.40	<i>C. chr</i> (>Cy4) <i>G. fal</i> (>Cy5) <i>S. scr</i> (>Cy5) 0.44			
Cy6	<i>C. chr</i> (>Cy6) <i>S. scr</i> (>Cy3) <i>G. fal</i> (>Cy6) 0.41	<i>C. chr</i> (>Cy4) <i>G. fal</i> (>Cy4) <i>D. vul</i> (>Cy6) 0.45	<i>G. fal</i> (>Cy5) <i>C. chr</i> (>Cy6) <i>D. vul</i> (>Cy5) 0.41		
Hinc	<i>S. scr</i> (>Cy3) <i>S. cin</i> (>Hinc) <i>C. chr</i> (>Hinc) 0.35	<i>C. chr</i> (>Cy4) <i>G. fal</i> (>Cy4) <i>S. cin</i> (>Hinc) 0.41	<i>G. fal</i> (>Cy5) <i>D. vul</i> (>Cy5) <i>S. cin</i> (>Hinc) 0.38	<i>C. chr</i> (>Cy6) <i>G. fal</i> (>Cy6) <i>S. cin</i> (>Hinc) 0.38	
PKG	<i>C. chr</i> (>PKG) <i>S. scr</i> (>Cy3) <i>S. oce</i> (>Cy3) 0.44	<i>C. chr</i> (>PKG) <i>G. fal</i> (>Cy4) <i>S. scr</i> (>PKG) 0.45	<i>C. chr</i> (>Cy5) <i>G. fal</i> (>Cy5) <i>S. tin</i> (>PKG) 0.46	<i>C. chr</i> (>PKG) <i>D. vul</i> (>Cy6) <i>G. fal</i> (>Cy6) 0.42	<i>C. chr</i> (>PKG) <i>S. cin</i> (>Hinc) <i>G. cru</i> (>Hinc) 0.39

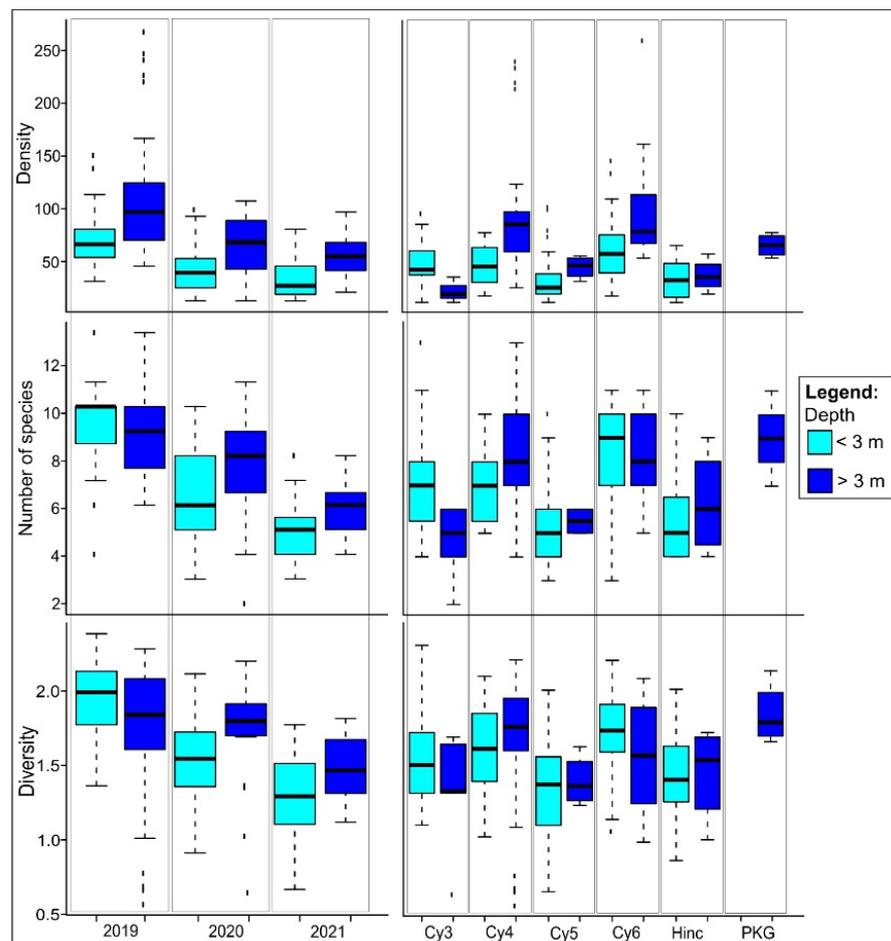


Figure 5. Two-factor boxplots (year-depth or habitat type-depth) for dependent variables fish density, species number and species diversity.

3.4. The Time-Depth-Habitat Type Effect on Coastal Fish Density and Diversity

In the next step, effects of these factors (year, depth, and habitat type (algal cover)) were measured with a generalized linear model. The number of species variable was omitted since it is correlated with species diversity represented by Shannon index values. The GLM results, represented in effect plots (Figure 6), showed that time has a significant negative impact ($p < \alpha$; $\alpha = 0.05$) on coastal fish density and diversity. The depth variable (here in continuous scale) positively influenced coastal fish density but simultaneously had a negative effect (marginally significant; $p < \alpha$; $\alpha = 0.10$) on fish diversity. The effect of habitat types (algal cover) had a similar pattern on fish density and diversity. Habitats Cy4, Cy6, and PKG significantly positively contributed to either coastal fish density or diversity.

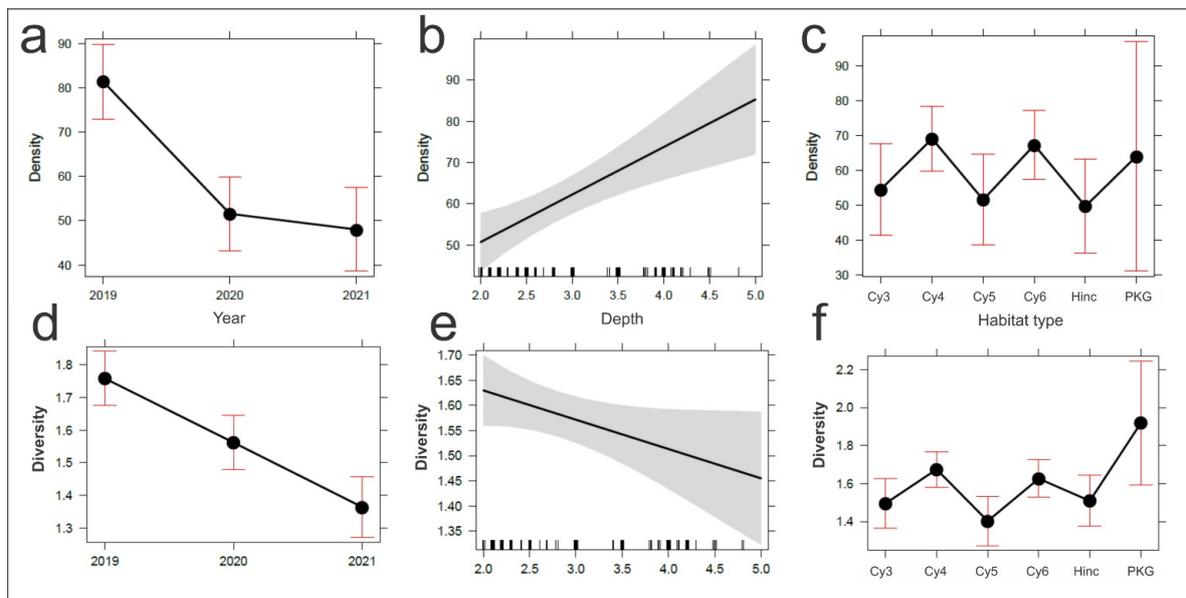


Figure 6. GLM effect plots of factors year (a,d), depth (b,e), and habitat type (algal cover) (c,f) with regard to fish density and diversity.

4. Discussion

As already pointed by Ruitton et al. [65], fish communities and algal vegetation are connected on two levels, namely, spatial (habitat selection) and feeding (prey availability). The richness of the fish community depends on the habitat heterogeneity [41] since structured habitats are known to host more abundant and diversified fish fauna [11,29,49]. The rocky subtidal in the Slovenian coastal sea is characterized by a high spatial heterogeneity (sensu Sala et al. [66]), which is evidenced by different macro and microhabitat types. The diversity of both affects many coastal fish families. In the Gulf of Trieste (Adriatic Sea), Orlando-Bonaca and Lipej [30] recorded the highest fish species richness in patches of *Cystoseira* spp. at 0.5–3 m depth compared to various other habitat-types differing in substrate type and/or algal cover. This pattern was confirmed also in other fish community studies in the Slovenian sea [29,67].

In the present study, we showed that wrasses (family Labridae) and sparids are the families related most to *Cystoseira* spp. algal belts. Particularly wrasses are known to be closely associated with rocky bottoms with dense *Cystoseira s.l.* cover, since they find shelters and build nests inside such vegetation type [68]. Among wrasses that use *Cystoseira* forests as a nursery area, *Coris julis* prefers less complex habitats [69], while *Symphodus* spp. prefer more structurally complex habitats with canopy-forming algae, which offer them also abundant preys (amphipods and polychaetes) [65]. Additionally, Cheminee et al. [13] reported that densities of juvenile *Symphodus* were higher in *Cystoseira*-dominated habitats than in other erect macroalgae or bare areas. Moreover, Onofri [70] found eggs of *S. roissali* attached to *Cystoseira* thalli. Orlando-Bonaca et al. [71] also found a significant correlation

between the coverage (%) of *Cystoseira* and/or *H. incurva* and the density of *S. roissali*. In the past, this species inhabited mainly habitats with high vegetation cover, where the brown alga *G. barbata* was the dominant species [72], but also in shallow coastal areas [41,48]. Many funnel-shape nests of *S. roissali* were found in different localities within *Cystoseira* belts along the Slovenian coast [72]. In addition, *Cystoseira* s. l. and *H. incurva* represent important microhabitats for the lesser-known cryptobenthic blenny *Clinitrachus argentatus*.

With regard to feeding guilds, only a few herbivorous species were found in the present study, such as *Sarpa salpa*, *Parablennius sanguinolentus* [73,74], and, at least partially, *Diplodus puntazzo* [75]. The intensity of fish herbivory is highest on shallow sublittoral rocky bottoms, down to 5 m depth, as reported by Verges et al. [2]. The average density of *S. salpa* recorded in the three studied years was from 1.66 ind. 100 m⁻² in 2019, 0.28 ind. 100 m⁻² in 2020, and 0.42 ind. 100 m⁻² in 2021. Those values are very low; however, when we take into consideration the maximum density values, that are 54 ind. 100 m⁻² in 2019, 14 ind. 100 m⁻² in 2020, and 44 ind. 100 m⁻² in 2021, than our data are in line with values recorded by Gianni et al. [76] (20 ind. 100 m⁻²). On the other hand, the density of the painted comber (*Serranus scriba*), which is considered the dominant mesopredator of the littoral fish assemblage in the study area [77], showed no difference between habitats regarding its preference, which was also reported by Garcia Rubies and Macpherson [78] and Cheminee et al. [13] for juvenile specimens. Thiriet [51] showed that the higher densities of both prey and predatory fish in *Cystoseira* forests is related to their preference for the habitat structural-complexity provided by *Cystoseira* spp.

Canopy-forming species, such as *Cystoseira* s.l., are declining worldwide and the study area makes no exception. In 2006, the coverage of the canopy-forming taxa in the Slovenian coastal area was rather high [71], but a declining trend has been observed in the last decade [24,25]. At reference sites for macroalgae, during the period 2007–2019, the decline of total *Cystoseira* s.l. spp. coverage (%) was substantial, especially for spring samples, when coverage has decreased from 66.3% ± 12.8 SE in 2007 to 25.3% ± 9.7 SE in 2019 [25]. In addition to the aforementioned anthropogenic changes to the coastline, land–sea interaction due to runoff of pesticides and other chemicals is also considered to be among the causes of the decline of *Cystoseira* s.l. spp. [79]. In addition, the grazing effect of native herbivores was recently reported to be one of the main stresses on young thalli of *Cystoseira* spp. [21,80]. *Sarpa salpa* (Linnaeus, 1758), which is capable of drastically reducing algal and seagrass canopies, has been defined as an important ecosystem changer, as the smallest individuals have been found to feed primarily on macroalgae, while the largest individuals are known to feed exclusively on seagrasses [81]. Finally, increasing winter temperatures in the area [82] and exceptional wind periods [80] can lead to serious biological anomalies and loss of reproductive potential of canopy-forming species. For the nearest geographical area, the western Croatian coast of Istria, Iveša [83] hypothesized that high summer temperatures and benthic mucilage perform a crucial role in the decline of *Cystoseira* s.l. forests. These preliminary observations for the northern Adriatic Sea follow the reported negative impacts of increasing temperatures on marine algal forests in other Mediterranean regions [84].

The coastal fish fauna seems to follow this negative trend with the decrease in fish density and diversity. In particular, many sparid (genus *Diplodus*) and labrid species (genus *Symphodus*), strictly dependent on *Cystoseira* belts, decreased from 2019 to 2021 in terms of both density and frequency of occurrence. Conversely, other species, such as gobiids, showing clear preferences for rocks, *Halopithys incurva* and bare stones, did not show such a decreasing trend.

The replacement of *Cystoseira* belts with less complex belts of smaller algae due to the various anthropogenic factors was already reported to cause changes in the coastal fish fauna. Deza and Anderson [85] showed that habitat fragmentation and shrinkage of algal cover impact the abundance and survival of juvenile fish. Particularly the density of juvenile wrasses, such as *Symphodus ocellatus*, *S. roissali*, and *S. tinca*, is higher in *Cystoseira* forests [14].

To detect such a negative trend is fundamental to consider the different factors driving fish communities, which might otherwise mask temporal variability. In the present study, fish density and diversity varied in relation to depth, with higher values in waters deeper than 3 m, but the declining trend was observed in both shallow and deeper areas when considered separately. The preferences of individual fish species for different habitat types are also a crucial information for understanding why different species showed different trends in abundance over the time period studied.

The opening strategy to contain the decline of *Cystoseira s.l.* species was their protection through international agreements. However, there is little evidence of natural recovery of degraded brown algal forests in the Mediterranean Sea [86,87]. Therefore, rapid conservation and restoration actions are necessary, also in the context of UN Decade on Ecosystem Restoration (2021–2030) and EU Biodiversity strategy for 2030. In recent years, diverse restoration attempts for brown algal forests have been made in the Mediterranean region, through the transplantation of adult thalli [88], in situ restoration [89], and ex situ cultivation in laboratory conditions [21,80,90–92]. The latter two techniques are recommended for the recovery of endangered species to avoid depletion of donor populations. Yet, implementing successful restoration efforts needs exhaustive knowledge of the current and past distribution of lost habitats and species and the stressors that led to their decline [93].

The results of the present study show that different algal cover and associated depth gradient have different effects on the fish assemblage in coastal waters, affecting species composition and abundance. In the context of human impacts on the decline of canopy-forming algal species, future research on the relationships between algal belts and associated coastal fish assemblages should be planned, including to facilitate recently initiated restoration efforts.

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