Favoring exchanges between the sea and the lagoons: a necessary support for the restoration of the functional role as fish nursery in the saltmarshes of Hyères (Provence, France)

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FAVORING EXCHANGES BETWEEN THE SEA AND THE LAGOONS: A NECESSARY SUPPORT FOR THE RESTORATION OF THE FUNCTIONAL ROLE AS FISH NURSERY IN THE SALTMARSHES OF HYÈRES (PROVENCE, FRANCE)

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SALTMARSHES
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EXPERIMENTAL FISHING
NURSERY
FISH JUVENILES

ABSTRACT. – The salt exploitation of the saltmarshes of Hyères (*Salin des Pesquiers* and *Vieux Salins* sites) has led to the isolation of the lagoon from the sea to control evaporation. The question of whether or not the saltmarshes' ecological functioning is impaired with regard to the fish population is one aspect that has been studied at the ecosystem scale. During 2018-2019, 4 samplings with 4 mm-mesh size fyke nets (24 h fishing duration) confirmed that the two saltmarshes still have a relictual nursery role. If juvenile fishes were numerically dominant in the catches, adults were also present. A few euryhaline and permanent small-sized taxa (Atherinidae, Gobiidae, Syngnathidae) contributed to 90 % of the total abundance in the catches. The amphihaline migrator *Anguilla anguilla* (mainly adult stages) was the main contributor to the biomass of catches. Juveniles of commercial species such as *Dicentrarchus labrax, Sparus aurata,* Mugilidae and Soleidae were caught in autumn and spring when going back and forth between the lagoon and the sea. Their tolerance of a wide range of salinity enables them to benefit temporarily from good environmental conditions for their growth. However, considering the low connectivity and the high salinity of most of the ponds, most of those marine fish juveniles are probably trapped inside the lagoon. In both lagoons, the closer the sampling sites were to the open sea, the higher were the species richness and density of the juveniles, suggesting that other parts of the lagoons function as an ecological sink. The diversity of the fish assemblages of the saltmarshes of Hyères is directly dependent on the effectiveness of the connection with the open sea. Among the different actions emerging from this study, the introduction of a sluice gate between the northern pond (*Salin des Pesquiers*) and the input channel could significantly enhance exchanges and potentially provide support for fish resources at sea.

INTRODUCTION

The current management strategy for the Hyères saltmarshes (*Salin des Pesquiers* and *Vieux Salins* sites) is driven by the optimization and enhancement of the sustainability of biological functions at both sites. As a migratory stage for European birds, the Hyères saltmarshes are also an important site for their reproduction and feeding. The decades-old management of water circulation for the salt exploitation of the saltmarshes and the influence of bird protection NGOs has led to the isolation of both lagoons from the sea in order to control evaporation. Among numerous abiotic and biotic characteristics shared with other Mediterranean lagoons, the Hyères saltmarshes shelter a fish population, with numerous juveniles, and crustaceans (mainly crabs and shrimps). For the coastal marine species of the eastern part of the French Mediterranean coast, the saltmarshes of Hyères are the only lagoon sites in the Var, with the Villepey ponds near Fréjus (Provence, France) that they can frequent.

To determine, whether or not, their ecological functioning was altered, with regard to the fish population, was one of the aspects studied at the ecosystem scale. Some marine species need to spend a certain duration of their lifetime in estuarian or lagoon brackish waters, especially as juveniles, in order to grow, then, go back to the sea for adult life and reproduction. The nursery role of the Hyères saltmarshes has already been recognized by Poizat *et al*. (2004), Rosecchi *et al*. (2004), CREOCEAN (2011), but has not been studied. Only particular abiotic conditions of the water (temperature, salinity) and suitable habitats may sustain this functionality. The significant cover of a diverse aquatic vegetation, including the occurrence) of *Ruppia spiralis* Linnaeus ex Dumortier meadows (Astruch *et al*. 2019, 2020, Massinelli *et al*.

2020), has also been considered as an indicator of suitable habitats for the juvenile fish fauna in the present work.

In 2018-2019, four surveys were conducted to sample the juvenile population of teleost fishes in the saltmarshes. The periods when juveniles were present in the ponds and those when they migrated between the lagoons and the sea were identified: in May (spring), when eggs, larvae and juveniles of marine species enter (also adults), and in October (autumn), when fish juveniles and adults leave and go back to the open sea. During summer, they had enjoyed favorable conditions (warm, calm waters, light, fewer predators, see Beck *et al*., 2001) for growing within the marshes.

In the present paper, we examine which species were present in the saltmarshes, the taxonomic richness and abundance of the teleost fishes sampled as juveniles or young adults according to their location within the saltmarshes. On this basis, we discuss how to facilitate exchanges with the sea in order to allow the life cycle of the concerned species to be achieved. The importance of the functional role of the saltmarshes as nursery for marine species in the central part of the Var is highlighted.

MATERIAL AND METHODS

The four scientific fishing campaigns were organized with the help of the manager of the Hyères saltmarshes and several local fishermen in May 2018, October 2018, March 2019 and May 2019. (Fishing has long been banned within the saltmarshes, but artisanal fishing is a traditional activity in the neighboring coastal zone). Qualitative sampling was conducted with a beach seine and quantitative sampling with fixed nets (both 4 mm mesh size), in channels and ponds where the depth allowed their deployment. At each site, sampling was carried out at 6 stations accessible from the paths (Figs 1, 2). At each station, 3 replicates of 24 h fishing duration were done on 3 consecutive days (4 replicates in March 2019). The temperature and the salinity of the water were measured at each station with a multi-parameter probe before hauling the nets. Other bi-monthly measurements taken by the managers of the sites at respectively 15 stations in the Salin des Pesquiers and 10 stations in the Vieux Salins, from 2013 to 2019, were used as reference. Species nomenclature is based on International Commission on Zoological Nomenclature and on International Code of Nomenclature for algae, fungi and plants.

Sampling strategy: The selection of the ponds to be sampled was made according to several criteria, such as: (i) the presence of *Ruppia spiralis* meadows and associated macroalgae community based on previous inventory and mapping (Massinelli *et al*. 2020) (50 ha meadows/550 ha in the Pesquiers lagoon; 14 ha meadows/330 ha in the Vieux Salins); (ii) the water circulation; (iii) the depth of channels and ponds; (iv) our ability to deploy fishing gear (depth, access, ground resistance); and (v) scientific knowledge (previous works on the Hyères saltmarshes by Poizat *et al*. (2004) and CREOCEAN (2011), mainly dedicated to adult fishes but also mentioning juveniles).

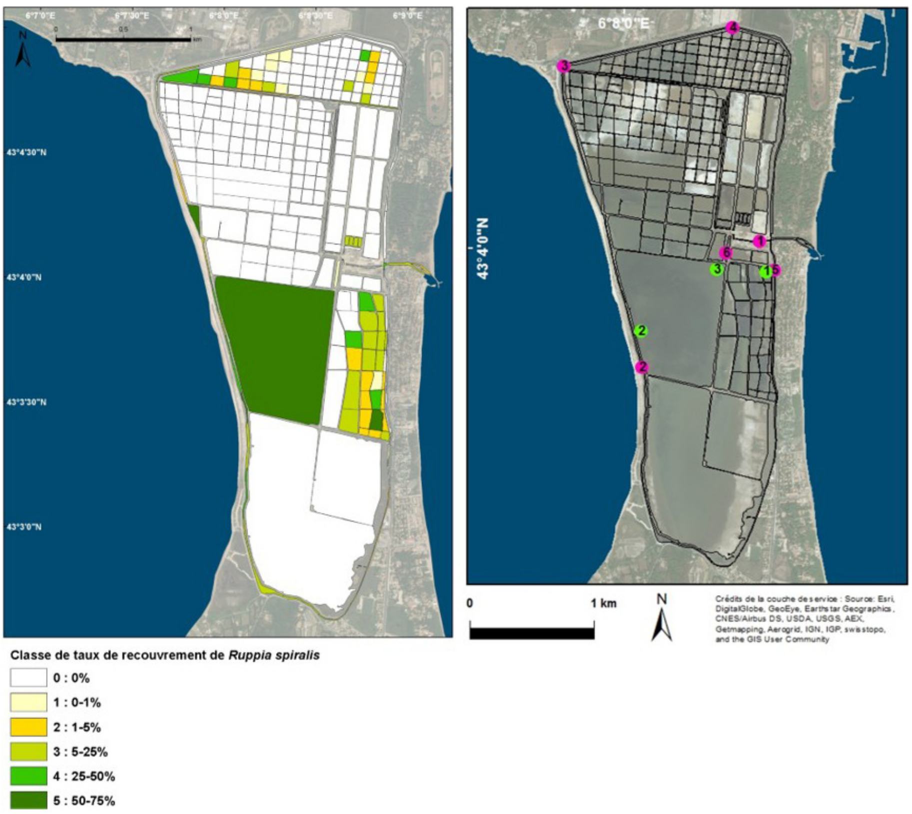

Fig. 1. – Localization of sampling stations in the Pesquiers lagoon according to the presence of *Ruppia spiralis* (% of covering by *Ruppia* is divided into 5 classes), depth and circulation of water (fixed nets sampling stations are in pink and beach seine sampling stations are in green).

The water circulation, in the Salin des Pesquiers, was mostly driven by gravity and led towards the irrigation of the northern pond, which was the deepest basin of the lagoon. The seawater entered at La Capte (station 1 in the middle of the western part, Fig. 1) and in the eastern part of the site by infiltration or driven by winter storms. For decades, the exchange of water between the sea and the lagoon had been made difficult by the requirements of the salt industry, by the constraints linked to the conservation of the historic salt works and to the conservation of nesting areas for birds. That was also the case in the Vieux Salins (Fig. 2).

Data analysis: The occurrence of species or families was calculated as catches per unit effort (CPUE) expressed in abundances per season per site and for each season at each site. Non-parametric comparison tests (U Test and Kruskal Wallis test) were used to compare the daily catches between sites (2), stations (6 at each site) and seasons (4 seasonal data collections). The variations were declared statistically significant when p was < 0.1). A principal components analysis (PCA) (Benzecri 1976a, b *in* Scherrer 2009) was performed on the basis of the daily log (CPUE+1) in abundance per taxa in order to evidence patterns of the juvenile assemblage according to sites, stations, seasons, and stations at each site.

RESULTS

Results of catches

In the catches, 39 taxa were recorded, among them 30 fish taxa and invertebrates: Carcinidae (crabs), Palaemonidae and Penaeidae (several shrimps), Sepiolidae (cephalopods), but fishes were dominant. The abundances in fish catches showed 98 % juveniles and adults of 'small size' species (*i.e.*, with a size of less than 15 cm) (Table I). The faunistic list encompasses typical taxa from the lagoon environment with numerous individuals, and other species such as *Z. ophiocephalus*, *Mullus*, *Engraulis,* with individuals occasionally present. The number of migratory species originating from peripheral environments (*i.e.*, brackish or marine waters) was higher than the number of sedentary species, underlining the importance of exchanges with the marine environment. The number of marine and freshwater species remained inferior to the number of species present in the nearby marine and freshwater environments.

Two species stand out for their abundance or their contribution to the caught biomass*: Atherina boyeri* (*Atherina* sp. *sensu stricto* because the number of *Atherina* was so high that each individual could not be identified to species level. But we are sure that *Atherina boyeri* was largely dominant in our catches) was dominant in abundance (CPUE catches per unit effort), its occurrence per site and per season was higher than 90 %. *Anguilla anguilla* (diadromous species protected by a national management plan) occurred at all stations, all seasons and dominated biomass in the catches. Caught individuals were mainly adults, up to 1 m in maximum total length (TL). Other species were caught as adult stage, in large numbers, or showed high occurrences in the catches. They belonged to euryhaline species such as *Sparus aurata,* several species of Mugilidae (*Chelon auratus, C. ramada and* Mugilidae) and Soleidae. However, the abundance of 98 % of the catches was composed of juveniles and adults of species smaller than 15 cm TL.

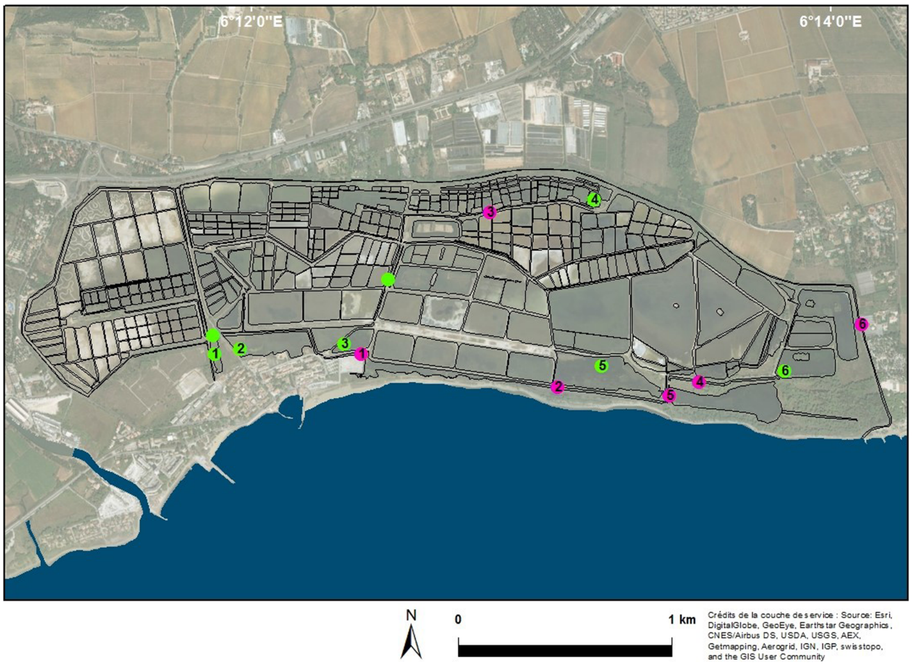

Fig. 2. – Sampling stations with fixed nets (pink) and with beach seine (green) in the Vieux Salins saltmarsh.

Table I. – Frequency of occurrence in the catches per 24 h sampling per taxon: species and families. Reproduction habitat of each taxon: M: marine water, F: fresh water, B: brackish water. Category of taxon according to its reproduction habitat. Kind of lagoon taxon. (Species nomenclature is based on International Commission on Zoological Nomenclature).

Species	Family	Reprod habitat	Category	Lagoon species	Occurrence per site		Occurrence per season				Occurrence per station											
											Pesquiers						Vieux Salins					
					Pesquiers	Vieux Salins	May-18	Oct-18	Mar-19	May-19	P1	P2	P3	P4	P5	P6	V1	V2	V3	V4	V5	V6
Anguilla anguilla	Anguillidae	M	Marine migrant	Characteristic	8%	20%	30%	3%	0%	14%	0%	0%	44%	0%	0%	10%	0%	11%	22%	44%	11%	33%
Atherina sp.	Atherinidae	F/B/M	Sedentary or marine migrant or freshwater migrant	Characteristic	90%	98%	94%	94%	100%	92%	85%	89%	67%	100%	100%	100%	100%	100%	100%	100%	100%	89%
Buglossidium luteum	Soleidé	M	Marine migrant	Complementary	3%	7%	0%	0%	0%	17%	0%	11%	0%	0%	0%	10%	22%	0%	0%	0%	0%	22%
Monochirus hispidus	Soleidé	M	Marine migrant	Complementary	13%	0%	0%	0%	67%	0%	31%	0%	0%	0%	31%	0%	0%	0%	0%	0%	0%	0%
Solea solea	Soleidé	M	Marine migrant	Characteristic	2%	2%	3%	0%	0%	3%	0%	11%	0%	0%	0%	0%	11%	0%	0%	0%	0%	0%
Chelon auratus	Mugilidae	M	Marine migrant	Characteristic	41%	15%	3%	33%	83%	31%	31%	56%	56%	33%	38%	40%	0%	22%	33%	33%	0%	0%
Chelon labrosus	Mugilidae	M	Marine migrant	Characteristic	8%	2%	6%	6%	8%	3%	8%	0%	11%	22%	8%	0%	11%	0%	0%	0%	0%	0%
Chelon ramada	Mugilidae	M	Marine migrant	Characteristic	22%	4%	6%	11%	58%	8%	8%	11%	56%	11%	31%	20%	0%	11%	0%	0%	0%	11%
Chelon saliens	Mugilidae	M	Marine migrant	Characteristic	8%	2%	0%	14%	0%	3%	0%	22%	33%	0%	0%	0%	0%	0%	0%	0%	0%	11%
Mugilidae indet.	Mugilidae	M	Marine migrant	Characteristic	32%	31%	64%	8%	33%	25%	46%	11%	33%	44%	38%	10%	44%	22%	11%	33%	33%	44%
Dicentrarchus labrax	Moronidae	M	Marine migrant	Characteristic	6%	11%	12%	0%	0%	17%	0%	11%	0%	33%	0%	0%	0%	22%	0%	0%	0%	44%
Dicentrarchus punctatus	Sparidae	M	Marine migrant	Rare	2%	0%	0%	3%	0%	0%	0%	0%	0%	0%	8%	0%	0%	0%	0%	0%	0%	0%
Diplodus puntazzo	Sparidae	M	Marine migrant	Characteristic	5%	2%	3%	0%	25%	0%	15%	0%	0%	0%	8%	0%	11%	0%	0%	0%	0%	0%
Diplodus sargus	Sparidae	M	Marine migrant	Characteristic	0%	4%	0%	0%	0%	6%	0%	0%	0%	0%	0%	0%	0%	11%	0%	0%	0%	11%
Diplodus vulgaris	Sparidae	M	Marine migrant	Characteristic	8%	15%	6%	3%	42%	14%	15%	0%	0%	0%	23%	0%	11%	11%	0%	11%	22%	33%
Sarpa salpa	Sparidae	M	Marine migrant	Characteristic	2%	9%	0%	0%	8%	14%	0%	0%	0%	0%	8%	0%	0%	22%	0%	0%	0%	33%
Sparus aurata	Sparidae	M	Marine migrant	Characteristic	32%	20%	36%	17%	25%	28%	8%	56%	33%	56%	31%	20%	11%	33%	33%	0%	0%	44%
Gambusia holbrooki	Poecillidae	F	Sedentary	Complementary	21%	2%	12%	17%	8%	8%	0%	0%	100%	22%	15%	0%	11%	0%	0%	0%	0%	0%
Lepomis gibbosus	Centrarchidae	F	Freshwater migrant	Complementary	0%	2%	3%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	11%
Gobiidae indet.	Gobiidae	B/M	Sedentary	Characteristic	21%	9%	30%	11%	17%	6%	8%	11%	33%	56%	15%	10%	0%	11%	0%	22%	11%	11%
Gobius cruentatus	Gobiidae	B/M	Sedentary	Characteristic	0%	15%	24%	0%	0%	0%	0%	0%	0%	0%	0%	0%	11%	33%	0%	22%	22%	0%
Gobius niger	Gobiidae	B/M	Sedentary	Characteristic	0%	2%	0%	0%	0%	3%	0%	0%	0%	0%	0%	0%	11%	0%	0%	0%	0%	0%
Gobius paganellus	Gobiidae	B/M	Sedentary	Characteristic	0%	2%	0%	3%	0%	0%	0%	0%	0%	0%	0%	0%	11%	0%	0%	0%	0%	0%
Pomatoschistus marmoratus	Gobiidae	B/M	Sedentary	Characteristic	6%	2%	0%	0%	33%	3%	0%	0%	0%	0%	31%	0%	11%	0%	0%	0%	0%	0%
Pomatoschistus microps	Gobiidae	B/M	Sedentary	Characteristic	11%	4%	0%	3%	25%	14%	8%	11%	11%	11%	15%	10%	0%	11%	0%	0%	11%	0%
Pomatoschistus sp.	Gobiidae	B/M	Sedentary	Characteristic	19%	50%	33%	3%	25%	67%	8%	22%	0%	11%	31%	40%	33%	44%	44%	56%	67%	56%
Zosterisessor ophiocephalus	Gobiidae	B/M	Sedentary	Complementary	5%	0%	0%	0%	25%	0%	8%	0%	0%	0%	15%	0%	0%	0%	0%	0%	0%	0%
Engraulis encrasicolus	Engraulidae	B/M	Marine migrant	Complementary	2%	0%	0%	3%	0%	0%	8%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
Salaria pavo	Blenniidae	B/M	Sedentary	Characteristic	0%	13%	6%	0%	0%	14%	0%	0%	0%	0%	0%	0%	33%	11%	33%	0%	0%	0%
Syngnathus abaster	Syngnathidae	B/M	Sedentary	Characteristic	11%	39%	30%	6%	25%	36%	8%	22%	0%	11%	23%	0%	22%	44%	33%	56%	56%	22%

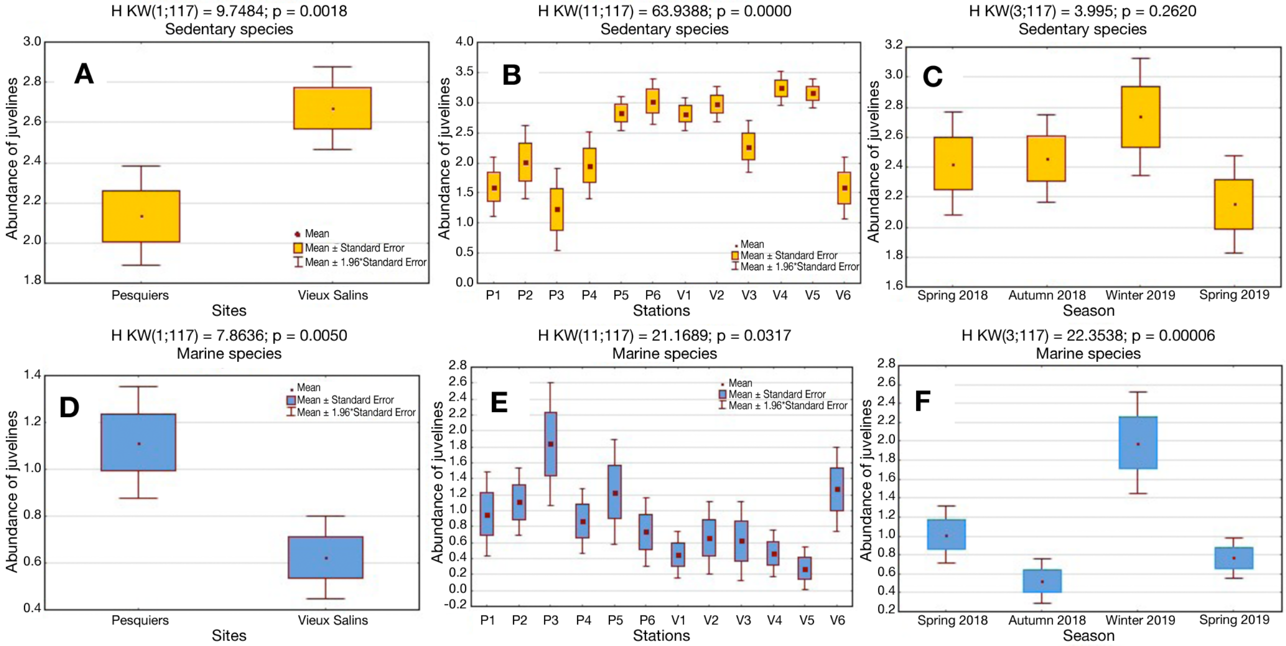

Fig. 3. – Abundance of fish juveniles in the catches according to sites, to stations and to seasons. Sedentary species are shown in the upper part, in yellow (**A**, **C**, **E**); marine migrants are shown in the lower part, in blue (**B**, **D**, **F**). Pesquiers stations: P1 to P5; Vieux Salins stations: V1 to V6.

The different taxa could be grouped in 3 categories according to a combination of their reproduction habitat, their behavior and environmental preferences: the sedentary permanent species, the marine migrants and the freshwater species.

Sedentary, permanent species: euryhaline small-sized taxa contributed to 90 % of the total abundance in the catches. *Atherina* sp., *Pomatoschistus* spp. and other Gobiidae, Syngnathus (*Syngnathus abaster*) as juveniles or adults were always present in the catches and at all sites. They completed their entire life cycle in the saltmarshes. The juveniles of sedentary species were more abundant in the Vieux Salins than in the Salin des Pesquiers (Fig. 3A).

Freshwater species: *Gambusia holbrooki*, *Lepomis gibbosus* were only present at stations receiving freshwater (station 3 in the Salin des Pesquiers and station 6 in the Vieux Salins lagoon).

Marine migrant species: mainly euryhaline species as *Dicentrarchus labrax*, Mugilidae, Sparidae as *Diplodus* spp., *Sparus aurata* and Soleidae juveniles or adults were especially abundant in May and October, when the majority of individuals came into or left the saltmarshes. Those individuals contributed mainly to the biomass in catches and they needed to return to sea for spawning. That is why the CPUE were higher at stations close to the open sea at both sites. The juveniles of the marine species were caught during March and May, when they achieved their trophic migration and settlement in the salt marshes. Several species of mullet (*Mugil* and *Chelon* spp.) were caught, in the spring and in fall, when they entered or left the lagoons. These species are considered to be tolerant to salinity variations (Kara & Quignard 2018) and they were particularly frequent in the catches at different sizes. The juveniles of marine species were more abundant in the Salin des Pesquiers than in the Vieux Salins (Fig. 3B).

The significant differences in log (CPUE+1) abundances among sites, stations and seasons are reported in Table II for the different taxa. The total abundance was significantly different among sites ($p = 0.013$), among stations ($p = 0.017$) and among seasons ($p = 0.08$). When all taxa were considered together, the seasonal variations of the abundance were less marked than the spatial variations.

The specific composition highlighted some differences in the fish catches among sites, in that 12 taxa showed significant differences. At the scale of the stations, differences were less obvious, with 8 taxa showing significant differences among stations. The inter-station spatial variations in the Salin des Pesquiers concerned 8 taxa, which is more than in the Vieux Salins (5 taxa). Many more taxa showed variations between seasons (16), demonstrating seasonal patterns in the coastal species assemblage using the lagoon. The marine migrant species taken together displayed a highly significant seasonal variation ($p < 0.000$) as well as *Anguilla anguilla* ($p = 0.004$). Sedentary species and freshwater species did not show this pattern ($p = 0.262$ and $p = 0.679$, respectively; Table III).

Finally, 18 taxa showed non-significant inter-site variations, 22 taxa non-significant inter-station variations, 14 taxa non-significant inter-season variations, but the

Table II. – Summary of the ANOVA comparisons (non-parametric U test and Kruskal Wallis test) of log(CPUE +1) abundance of juveniles between sites, stations (all), seasons (all) and stations at each site. Reproduction habitat of each taxon: M: marine water, F: fresh water, B: brackish water. (Species nomenclature is based on International Commission on Zoological Nomenclature).

Total abundance			SITES		STATIONS		SEASONS		STATIONS			
			2 sites		All seasons, both sites, H(5, n = 117)		All stations, both sites, H(3, n = 117)		Pesquiers H(5, n = 63)		Vieux Salins H(5, n = 54)	
Species	**Family**	**Reprod habitat**	**p**		**p**		**p**		**p**		**p**	
			0.013	**	**0.017**	**	**0.080**	*	**0.002**	***	**0.000**	***
Anguilla anguilla	Anguillidae	M	0.049	**	0.014	**	0.004	***	0.001	***	0.214	
Atherina sp.	Atherinidae	F/B/M	0.002	***	0.000	***	0.209		0.000	***	0.000	***
Buglossidium luteum	Soleidé	M	0.306		0.144		0.002	***	0.450		0.131	
Monochirus hispidus	Soleidé	M	0.007	***	0.014	**	0.000	***	0.024	**	1.000	
Solea solea	Soleidé	M	0.922		0.557		0.703		0.306		0.415	
Chelon auratus	Mugilidae	M	0.001	***	0.507		0.000	***	0.735		0.074	*
Chelon labrosus	Mugilidae	M	0.143		0.532		0.863		0.474		0.415	
Chelon ramada	Mugilidae	M	0.003	***	0.319		0.000	***	0.153		0.538	
Chelon saliens	Mugilidae	M	0.141		0.087	*	0.035	**	0.014	**	0.415	
Mugilidae	Mugilidae	M	0.788		0.372		0.000	***	0.225		0.475	
Dicentrarchus labrax	Moronidae	M	0.324		0.025		0.049	**	0.012	**	0.006	***
Dicentrarchus punctatus	Sparidae	M	0.364		0.504		0.522		0.571		1.000	
Diplodus puntazzo	Sparidae	M	0.400		0.084	*	0.000	***	0.374		0.415	
Diplodus sargus	Sparidae	M	0.128		0.497		0.208		1.000		0.538	
Diplodus vulgaris	Sparidae	M	0.284		0.191		0.001	***	0.139		0.435	
Sarpa salpa	Sparidae	M	0.060	*	0.106		0.022	**	0.571		0.038	**
Sparus aurata	Sparidae	M	0.273		0.065	*	0.272		0.082	*	0.090	*
Gambusia holbrooki	Poecillidae	F	0.002	***	0.000	***	0.688		0.000	***	0.415	
Lepomis gibbosus	Centrarchidae	F	0.288		0.396		0.467		1.000		0.415	
Gobiidae	Gobiidae	B/M	0.071	*	0.350		0.023	**	0.030	**	0.582	
Gobius cruentatus	Gobiidae	B/M	0.002	***	0.255		0.000	***	1.000		0.230	
Gobius niger	Gobiidae	B/M	0.288		0.504		0.522		1.000		0.415	
Gobius paganellus	Gobiidae	B/M	0.288		0.504		0.522		1.000		0.415	
Pomatoschistus marmoratus	Gobiidae	B/M	0.224		0.017	**	0.000	***	0.006	***	0.415	
Pomatoschistus microps	Gobiidae	B/M	0.141		0.801		0.011	**	0.986		0.538	
Pomatoschistus sp.	Gobiidae	B/M	0.000	***	0.250		0.000	***	0.221		0.217	
Zosterissessor ophiocephalus	Gobiidae	B/M	0.108		0.306		0.000	***	0.380		1.000	
Engraulis encrasicolus	Engraulidae	B/M	0.364		0.504		0.522		0.571		1.000	
Salaria pavo	Blenniidae	B/M	0.003	***	0.082	*	0.067	*	1.000		0.058	
Syngnathus abaster	Syngnathidae	B/M	0.000	***	0.132		0.013		0.343		0.263	

majority of those taxa were rare or presented a low occurrence per station.

The water temperature was recorded at the sampling sites at between 11.4 and 17.2 °C in March, 19.6 and 27.3 °C in May and 19.3 and 24.9 °C in October. Those relatively high temperatures are suited to juveniles' growth. The salinity in spring was between 26.7 and 28.7 $g.kg^{-1}$, and in autumn it was between 21.1 and 27.4 $g.kg^{-1}$, which are mean salinities lower than that of the Mediterranean Sea (about 38 $g.kg^{-1}$). The salinity measured in various other ponds could reach very high levels. The mean salinity of water calculated on a data set of 2 measurements per month in, respectively, 15 and 10 stations, from 2013 to 2019, was 74.8 $g.l^{-1}$ in the Salin des Pesquiers and 55.5 $g.l^{-1}$ in the Vieux Salins. The survival conditions for juveniles in shallow and over-salty ponds are undoubtedly limited for variable durations despite the high tolerance of the lagoon species for elevated salinities.

We performed a PCA analysis on the abundance of juvenile fishes in the catches. The descriptors of the sampling stations were salinity and temperature of the water at each sampling operation. The first two axes explained 23.21 % and 19.09 % of the variability respectively. Maps based on the first two axes (Fig. 4) showed differences between stations. The species mainly explaining variabil-

Table III. – Summary of the ANOVA comparisons (non-parametric U test and Kruskal Wallis test) of log(CPUE +1) abundance of juveniles between sites, stations (all), seasons (all) and stations at each site for families and categories according to the life traits. Reproduction habitat of each taxon: M: marine water, F: fresh water, B: brackish water. (Species nomenclature is based on International Commission on Zoological Nomenclature).

Taxon or category	Reproduction habitat	SITES All seasons		STATIONS All seasons, both sites, h(5, n = 117)		SEASONS All stations, both sites, h(3, n = 117)		STATIONS Pesquiers H(5, n = 63)		STATIONS Vieux Salins H(5, n = 54)	
Family		p		p		p		p		p	
Anguillidae	M	0.049	**	0.014	**	0.004	***	0.001	***	0.214	
Atherinidae	F/B/M	0.002	***	0.000	***	0.209		0.000	***	0.000	***
Blenniidae	B/M	0.003	***	0.082	*	0.067	*	1.000		0.058	*
Centrarchidae	F	0.288		0.396		0.467		1.000		0.415	
Engraulidae	B/M	0.364		0.504		0.522		0.571		1.000	
Gobiidae	B/M	0.057	*	0.000	***	0.000	***	0.005	***	0.053	*
Moronidae	M	0.496		0.064	*	0.130		0.046	**	0.006	***
Mugilidae	M	0.001	***	0.727		0.000	***	0.128		0.653	
Poeciliidae	F	0.002	***	0.000	***	0.688		0.000	***	0.415	
Soleidae	M	0.152		0.031	**	0.000	***	0.153		0.042	**
Sparidae	M	0.846		0.138		0.057	*	0.470		0.033	**
Syngnathidae	B/M	0.000	***	0.132		0.013	**	0.343		0.263	
Marine migrants		0.005	**	0.032	**	0.000	***				
Anguilla anguilla		0.049	**	0.006	**	0.004	***				
Sedentary species		0.002	***	0.000	***	0.262	ns				
Freshwater species		0.007	**	0.000	***	0.679	ns				

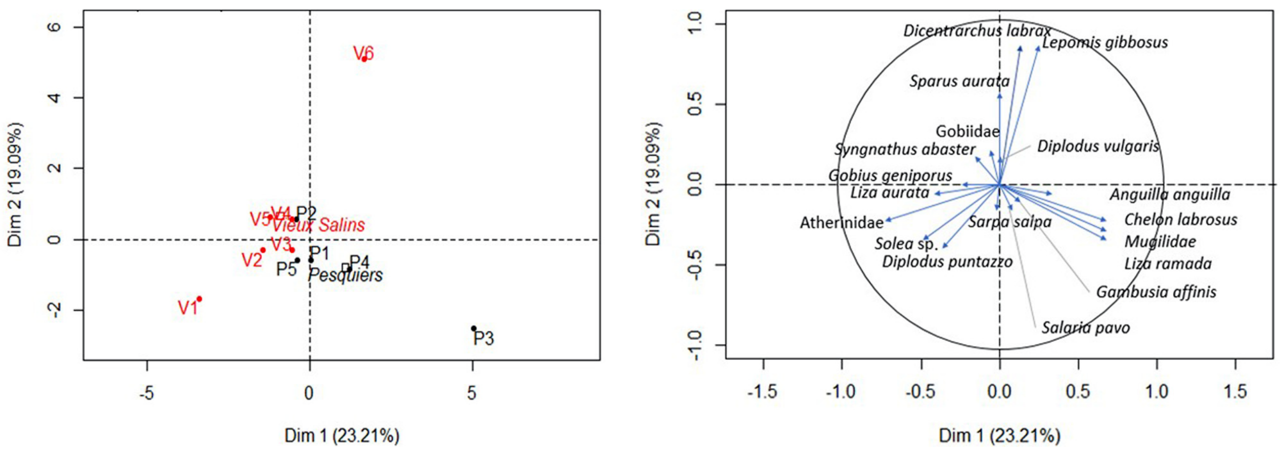

Fig. 4. – Principal Components Analysis of mean CPUE abundance per station (May, 2018). Pesquiers stations: P1 to P5; Vieux Salins stations: V1 to V6. The stations and taxa as supplementary vectors maps are defined by the first two factorial axes.

ity among stations were the seasonal marine migrants: the different species of Mugilidae, *S. aurata* and *S. solea* at both sites.

Stations P3 and V6 differed from the others because they received some freshwater provided by runoff, and this explained the presence of *Lepomis gibbosus* and the relative abundance of *Gambusia holbrooki,* which are freshwater species. Station V1 was directly in connection with the sea and marine species were dominant and abundant there. *Anguilla anguilla* and the different taxa of Mugilidae were abundant in the Salin des Pesquiers. *Solea solea*, *Diplodus puntazzo* and *Chelon auratus* abundance characterized the Vieux Salins catches. The taxa belonging to the sedentary taxa such as Gobiidae, *Syngnathus abaster*, and also *A. anguilla* were positioned near the first two axes of the CPA because they were largely spread among the monitoring stations showing low spatial and low temporal variations.

During autumn, the Mugilidae (*Chelon auratus*, *C. labrosus* and *C. saliens*) were particularly abundant at the P2, V3 and V2, V4, V6 stations. In spring, the arrival of *Sparus aurata* and *Solea solea* structured the juvenile assemblage at P2, V2 and P6. *Chelon ramada* is a marine migrant species, which contributed to the P3, P4, and P5 assemblage in spring. All other species have shorter vectors that stay closer to the centre of the axis, such as Gobiidae, showing they are more regularly present in the saltmarshes and less discriminating.

DISCUSSION

In the saltmarshes of Hyères, the broad scale distribution pattern of fish juveniles was influenced by the circulation of water between ponds and the seawater inlet. The composition of the fish juveniles' assemblages at each station was mainly related to the water characteristics. The management team at both sites controlled the opening and closing of the traps according to the basin water level and to the inputs and outputs according to basin water level, rainfall, evaporation and barometric tides. The stations situated closed to the open sea or with effective connections presented higher abundances of juveniles and a higher taxonomic richness due to marine migrants. The water circulation was also observed to induce direct effects on the structure of both lagoon fish assemblages. The frequent changes in abiotic conditions induced high spatial and temporal variability in the survey variables (temperature and salinity of water and taxonomic richness, abundance of juveniles) at site and at station scales. Even behavior effects were observed such as fish swimming upstream when the seawater was entering the sites.

At the sampling stations in the Hyères saltmarshes, the abundance of marine migrants in the catches served as markers of seawater entry in spring. Their abundance in autumn in the stations closer to the sea showed their need to return to the sea and their departure when the water conditions in the saltmarsh were changing. The other sites, not sampled during this study, seemed to be unsuitable for survival during the warm season because of the high salinity level and eutrophication of the water.

According to our sampling, the fish populations of the two lagoons were not very different in composition. The Vieux Salins, localized along the seashore, had a lower salinity and a high proportion of marine species, but they were less abundant than in the Salin des Pesquiers. They presented all the features of other Mediterranean lagoons with sedentary species whose entire life cycle is completed within the lagoons, and species coming in from the sea, entering at different development stages (eggs, larvae, juveniles) (Bouchoucha 2010, Kara & Quignard 2018). The marine species (*Dicentrarchus labrax*; *Sparus aurata*, *Chelon* spp.) benefited from this favorable environment for their growth from late winter to the end of autumn. The presence of species that were rare in lagoons and abundant in the sea, of which only the year class 0+ (*i.e.*, individuals less than 1 year old) was present in the lagoons, showed the temporary carrying capacity of these two lagoon sites with respect to the peripheral environments. Adults were also present and they might use the saltmarshes for feeding and reproduction. Some freshwater species such as *Gambusia holbrooki* and *Lepomis gibbosus* contributed to the specific richness at stations where salinity conditions were particularly low (May).

The study has confirmed the nursery role of the Hyères saltmarshes, but the water salinity and the circulation conditions were shown to jeopardize fish survival in most of the saltmarsh ponds. Hydraulic management of the sites is complex and obviously governed by prior management constraints unsuited to the seasonal rhythms of the migrations of fishes between the lagoon and the sea. As compared to the seasonal functioning of other unconstrained estuarine systems (Le Diréach *et al*. 2010, 2013, Kara & Quignard 2018), these saltmarshes might produce disappointing results for species whose life scenario depends on those migrations.

The present work has provided an update on knowledge regarding the fish compartment with the sampling of juveniles and regarding the current functionality of the aquatic compartments of both lagoons. That could prove useful as a basis for a more functionally oriented management system with an ecosystem-based approach (Astruch *et al*. 2020). The work sessions organized with managers, fishermen and scientists have favored the sharing of knowledge and points of view. The increase in awareness of the interest of the aquatic compartment and its populations (fishes but also invertebrates: shrimps and crabs, which strongly contribute to the diet of waterfowl) was a goal of this work.

The ecosystem-based approach applied here has undoubtedly offered a clearer vision of the functioning of the sites both for managers and scientists, including the constraints of both sites and the vicinity of the city of Hyères (runoff, pollution from the watershed, management of the mosquito population, landscape conservation, mass tourism, education). The various possible solutions to facilitate the circulation of water and exchanges with the sea were discussed, among them: (i) the cleaning and dredging of the belt canal, (ii) permanent or temporary gravity-based circulation of the northern pond in the Salin des Pesquiers (*e.g*., decrease in mean salinity and eutrophication, reduction of pumping costs) and (iii) the use of a portion of channel as a lock.

In addition to the management propositions, specific actions have resulted from the SALSA program. For the Salin des Pesquiers, those actions were: (i) optimizing the circulation between the northern pond and the belt channel; (ii) optimizing the gravity-based water circulation permanently or temporarily in the northern pond; (iii) building a sluice gate between the northern pond (Salin des Pesquiers) and the input channel; (iv) strengthening the seawalls and levees of various ponds (northern pond especially) to sustain a rise in their water level (about 30 cm rise). In the Vieux Salins, a closed channel was even linked to the Étang de l'Anglais in order to increase the water circulation. Those actions are included in the new management plan for the Hyères saltmarshes (BRLi 2018) but some of them still need funding and feasibility studies.

Before the study and in the previous management plan, the water circulation system was mostly inherited from mode of operation when the salt was still exploited at both sites (before 1995) and bird conservation a priority. The present study has provided new scientific knowledge for management purposes and greater attention will now be paid to the aquatic compartments in the new management plan. The main benefits of the program derive from the collaboration built up between the different stakeholders working on field data collection: the fishermen, the managers and the scientists. The time spent in discussions and in trying to better understand the different points of view in relation to the aquatic resources, the management priorities for the saltmarshes and the conservation of the different compartments was the price to pay for developing a new management approach.

The Salin des Pesquiers has suffered from breaches in their levees close to the sea and to seawater invasions over the centuries. Before the development of the salt industry, the site was a lagoon (named in French: *Étang des Pesquiers*) and an important fishing ground for local fishermen (Faget *et al.* 2021). At that time, fishes used the lagoon to accomplish their life cycle. Since the Pesquiers lagoon was transformed with the development of the salt industry, managers have devoted considerable effort to the reinforcement of the seawalls and levees and the control of the water level. The exchanges with the sea remain limited and the survival of fishes highly compromised by the high salinity conditions of the water. The restoration of the functionality of the Hyères saltmarshes will now depend on a compromise between the priorities of bird and heritage landscape conservation and a kind of natural restoration that will undoubtedly be given added urgency by Global change and its impact along the Mediterranean coast (*e.g.*, sea level rise, warming, invasive species, etc.).

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REFERENCES

Astruch P, Boudouresque CF, Changeux T, Faget D, Lascève M, Le Diréach L, Massinelli L, Moussy F 2019. From a species-centred to an ecosystem-based management approach. A case study of the saltmarshes of Hyères (Provence, France). *In* Gargiulo C, Zoppi C Eds, International Conference on Innovation in Urban and Regional Planning Academy 2019 – Planning, nature and ecosystem services, Cagliari (Italy), 24-26 June 2019: 29-38.

Astruch P, Boudouresque CF, Faget D, Changeux T, Lasceve M, Le Direach L, Gimond-Lanteri F, Massinelli L, Moussy F, Angles D'Ortoli N, Marchessaux G, Carlotti F, Belloni B, Guilloux L, Gomez MC, Simo M 2020. Improving the management of the saltmarshes of Hyères (Provence, France) using an ecosystem-based approach. Vie Milieu 70(3-4): 253-268.

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MR 2001. The identification, conservation and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51(8): 633-641.

Bouchoucha M 2010. Inventaire des peuplements de Poissons sur les milieux lagunaires corses – campagne 2009. Convention Agence de l'Eau RM&C / Ifremer n° 2009 4154: 36 p.

BRLi 2018. Document unique de gestion des sites du Conservatoire du Littoral sur la commune d'Hyères. État des lieux Diagnostic. BRL ingénierie, Nîmes: 561 p.

CREOCEAN 2011. Salins d'Hyères – Inventaire des peuplements piscicoles et analyses des résultats. Rapport d'étude. Contrat d'étude Communauté d'Agglomération Toulon Provence Méditerranée et Parc national de Port-Cros: 68 p.

Faget D, Réveillon E, Le Diréach L, Astruch P, Simo M 2021. La bordigue de la lagune de Giens (Hyères, France). Approche historique d'une zone humide méditerranéenne (Fin XVIIe-XXIe s.). *Sci Rep Port-Cros Natl Park* (in press).

Kara MH, Quignard JP 2018. Les Poissons des Lagunes et des Estuaires de Méditerranée. ISTE Editions, London.

Le Diréach L, Brosse L, Bonhomme P, Girard P, Bodilis P, Francour P 2010. Inventaire ichtyologique de l'étang de Berre (Rapport de seconde phase). Contrat GIPREB – GIS Posidonie. GIS Posidonie: 1-153 dont annexes.

Le Diréach L, Bonhomme P, Brosse L, Girard P, Bodilis P 2013. Inventaire ichtyologique de l'étang de Berre 2008-2009. *In* LAGUN'R – Rencontres Scientifiques autour de l'étang de Berre, 14-15 mars 2011, Aix-en-Provence, GIPREB: 233-255.

Le Diréach L, Astruch P, Moussy F, Abiven T, Boursault M, Brodu N, Changeux T, Charpentier M, Gimond F, Jehl C, Lascève M 2018. Programme NURSERHY : suivi du peuplement de poissons juvéniles et rôle de nurserie des Salins d'Hyères. Contrat GIS Posidonie – GALICA, GIS Posidonie, Marseille: 72 p.

Massinelli L, Astruch P, Lascève M, Boudouresque CF, 2020. Mapping of *Ruppia spiralis* meadows within the saltmarshes of Hyères (Provence, France): a key species for an ecosystem-based approach. *Vie Milieu* 70(3-4): 235-241.

Poizat G, Rosecchi E, Chauvelo P, Contournet P, Crivelli AJ 2004. Long-term fish and macro-crustacean community variation in a Mediterranean lagoon. *Estuar Coast Shelf Sci* 59(4): 615-624.

Rosecchi E 2004. Diagnostic écologique des anciens salins d'Hyères – Partie 2 : Inventaire des peuplements piscicoles. Parc National de Port-Cros, Ministère de l'Ecologie et du Développement Durable, Station Biologique de la Tour du Valat: 33 p + annexe.

Scherrer B 2009. Biostatistiques, Vol. 2, 2e édit. Gaetan Morin: 576 p.