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Changes in the juvenile fish assemblage of a Mediterranean shallow *Posidonia oceanica* seagrass nursery area after half a century

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Abstract

The within-year dynamics of the juvenile fish community in a shallow seagrass-dominated nursery habitat (*Posidonia oceanica*) in a Mediterranean bay were compared between two surveys separated by 50 years (1960 and 2012-2013). A nocturnal survey over depths ranging from 2 to 10 m over patchy seagrass meadows was conducted for one year (2012-2013) through 72 epibenthic tows spread fortnightly in 4 nearby stations, mimicking a survey conducted in 1960 in terms of sampling intensity, sampling zone, temporal coverage and sampling gear. Although a large proportion of the fish species were similar among surveys, remarkable and statistically significant differences were detected. A striking feature was that one of the most common and abundant Sparidae species currently, *Diplodus annularis*, did not appear in 1960. Other strong differences included the nonappearance of the European eel *Anguilla anguilla* in the recent survey. Furthermore, one of the most valuable species for artisanal fisheries in the area, the black scorpionfish *Scorpaena porcus*, was almost 10 times less abundant in 1960. A finer-scale study of the 2012-2013 survey allowed a quantitative analysis between species composition and potential environmental drivers through redundancy analysis that well described the current pattern of time-dependent recruitment pulses in nearshore meadows of the area throughout the year, with marked effects of surface temperature and photoperiod. The comparison between surveys suggests that some major differences between surveys are not likely to be attributable to interannual stochasticity in recruitment or environmental variability but may be related to i) unaccounted-for habitat transformation and/or ii) the strong decrease in juvenile fishing mortality in this shallow nursery area since the enforcement of bans on littoral epibenthic trawling activities characteristic of this area.

Keywords: Seagrass meadow; nursery habitat management; juvenile fish assemblages.

Introduction

Many littoral fish species in temperate areas have a bipartite life cycle in which adults live in a small territory or home range (Alós *et al.*, 2014 a,b) but spawn floating eggs that become pelagic larvae for a relatively long period (Raventós *et al.*, 2001). Once these larvae reach an adequate size, they swim to (and/or settle in) benthonic nearshore habitats during the settlement phase (Beck *et al.*, 2001; Leis & McCormick, 2002). The processes that regulate the success of this transitional phase are complex and can act as bottlenecks of recruitment into adult populations (Macpherson & Raventós, 2005; Sponaugle & Grorud-Colvert, 2006; Nash & Geffen, 2012). Nursery habitats vary in complexity and extent depending on the habitat-forming species, topography and fish species us-

ing them. Optimal nursery habitats are generally found where there is equilibrium between predation and feeding trade-offs (Heck *et al.*, 2003; Sheaves *et al.*, 2014). These areas often occur in relatively narrow coastal strips, which in some instances can be severely altered by anthropogenic actions that alter the structure of the habitat and the survival of fish within these transitional environments (Munsch *et al.*, 2016).

In the Mediterranean Sea, the main settlement habitats differ among species (Garcia-Rubies *et al.*, 1995), even within the same fish family. For example, within Sparidae, the white seabream *Diplodus sargus* and the two-banded seabream *Diplodus vulgaris* settle mainly in sand and pebble coves, recruiting later to rocky deeper reefs when they attain a certain size (Vigliola *et al.*, 1998; Casado, 2015; Di Franco *et al.*, 2015), while other spar-

ids such as the annular seabream *Diplodus annularis*, the black seabream *Spondyliosoma cantharus* and the salem *Sarpa salpa* settle mainly on seagrass meadows. In the north-western Mediterranean, these meadows are formed mostly by *Posidonia oceanica* and to a lesser extent by *Cymodocea nodosa* and *Zostera noltii* (Fourqurean *et al.*, 2007), in addition to the macrophyte *Caulerpa prolifera*, which also forms meadows in small protected bays (Box Centeno, 2008). The key nursery role of coastal habitats such as seagrass meadows and rocky reefs has been reviewed several times (Beck *et al.*, 2001; Heck *et al.*, 2003). In the Mediterranean, the nursery role (here defined as the capacity of a given habitat to host higher a juvenile density than that in the surrounding habitats, Beck, *et al.*, 2001) of the endemic seagrass *P. oceanica* is paramount as it covers approximately 23% of the coastal shallow habitats (Pasqualini *et al.*, 1998) with an approximate extension of 2.5 to 5.5 million hectares (Buia *et al.*, 2000). To guarantee successful recruitment into adult populations, settlers and juveniles must find not only shelter but also adequate food, which is available in the form of invertebrates and epiphyte algae from the complex and dense canopies of *P. oceanica* (Orth *et al.*, 1984; Larkum *et al.*, 2006). Moreover, the distribution of *P. oceanica* from very shallow nearshore habitats (from 1 to 43 metres (Marbà *et al.*, 2002)) offers in many places an easy transition from juvenile to adult habitats, which confers advantages for growth, survival and recruitment (Heck *et al.*, 2003; Igulu *et al.*, 2011).

The alteration of nursery areas has been the object of numerous studies (Marbà *et al.*, 2002; Seitz *et al.*, 2014; Ruiz *et al.*, 2015). In the case of *P. oceanica*, meadows are threatened (Diaz-Almela *et al.*, 2007) due to multiple anthropogenic factors from pollution to fishing (Coll *et al.*, 2010). In some Mediterranean areas, such as the Balearic Islands, anthropogenic pressure in littoral areas is high due not only to tourism and to an increasing local population but also to the combined effect of both artisanal and recreational fisheries, which has been notably increasing in the last years (Morales-Nin *et al.*, 2005; Cardona *et al.*, 2007; Cardona & Morales-Nin, 2013). Until the 1970s, in the Balearic Islands, a common practice to obtain bait for recreational and artisanal fishing relied on the use of small epibenthic trawls, called “gànguil” by the locals, over the littoral *P. oceanica* and *C. prolifera* meadows. The obtained catch was composed mainly of small Decapoda from the genera *Processa*, *Hippolyte* and *Palaemon* (Sánchez-Jerez *et al.*, 2000), which were sold as bait.

In the 1960s, Massuti acknowledged the potential impacts of this non-regulated bait-collection practice on the juvenile fish population in Palma Bay (Mallorca) by analysing the juvenile catch within an experimental time-series of night trawling using a “gànguil” over the course of one year (1960) (Massuti, 1965). This study did not specifically test impact (e.g., by using control areas or a before-after impact design) but suggested that the littoral area swept every night was large and that most fish caught were juvenile specimens, which provoked the enforcement of existing (but rarely observed) laws banning

this coastal trawling (BOE, 1941). As a consequence, during the early 1970s, this trawling activity declined rapidly after the enforcement of the ban. Furthermore, another work from 1966 evaluated the impact of a similar but larger bottom trawl on deeper *P. oceanica* meadows (15-20 metres) (Oliver, 1966); this work and Massuti’s work from 1965 offer a snapshot of the fish communities inhabiting *P. oceanica* meadows 50 years ago.

The main objective of this study is to compare the current composition of juvenile fish over seagrass meadows in the shallow (1-10 metres) zone of Palma Bay with that in the original data from Massuti (1965), following a similar methodology. We hypothesize that after 50 years, and concurrently with the observed change in human pressures (e.g., changes in fishing activity, habitat transformation, pollution, etc.), the juvenile fish assemblage may have changed.

Material and Methods

Sampling

In his published work in 1965, Massuti described a whole year (1960) of sampling of the fish community in shallow (mostly seagrass-covered) nursery areas using the same epibenthic trawl (“gànguil”) as the local fishermen in Palma Bay. Briefly, the “gànguil” is a lightweight epibenthic trawl with an incorporated rolling stainless steel cylinder in the bottom of the mouth that protects the *P. oceanica* leaves from snagging and tearing while the trawl is in operation [see details for design in Catalán *et al.*, (2014)]. Before the ban enforcement in the 1970s, night trawling over seagrasses in the nearshore could concentrate up to 200 small boats in Palma Bay (a mid-size bay of ca. 20 km wide, Fig. 1) that trawled at low

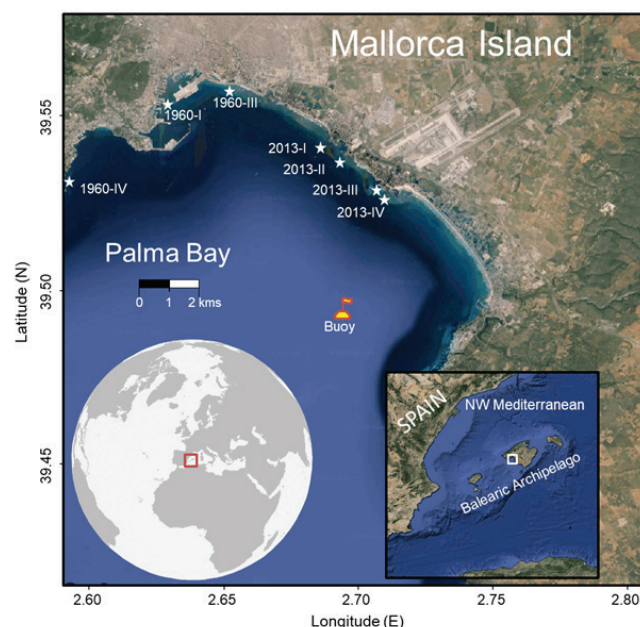


Fig. 1: Centroids of the sampling areas and environmental variable collection spots (oceanographic buoy). Stations I and II from 1960 were inside the actual commercial port. Additionally, station II was not considered for comparative studies.

speeds over depths of approximately 1-10 metres using oars or small engines. To reproduce that sample design, we conducted a fortnightly survey for one year (2012-2013) using almost the same gear over areas close to those surveyed by Massutí (Fig. 1). The exact same locations could not be sampled due to restrictions on access to and increased anthropization associated with the commercial harbour; therefore, we selected nearby areas with bottom characteristics and depths similar to those reported in the surveys in 1960 (Table 1). Care was taken to include *P. oceanica* meadows that were sparsely patched with sand and few rocks; this condition was checked visually prior to the surveys, taking advantage of the low depth and high water transparency. One of the stations in 1960 was excluded for comparative purposes due to its proximity to a sporadic freshwater source from a dry riverbed. The remaining sites were otherwise comparable to those sampled in 1960 and covered a stretch of approximately 2.5 km of littoral zone over *P. oceanica*. Fish were collected after sunset (as in 1960) using two epibenthic bottom trawls, “gànguils”, whereas only one trawl was used in 1960. To avoid possible between-survey differences due to fishing operation skills, the surveys in 2012-2013 were performed with the aid of an experienced traditional fisherman on his own boat authorised for scientific sampling by the local administration. The two gears were towed in parallel, covering an elliptical trajectory of 700-1000

m. This sampling methodology is the same as that used in the traditional bait fishery and has been proven to be adequate to sample juvenile fish with low size ranges close to settlement size (Catalán *et al.*, 2014). After approx. 20 minutes of trawling at approx. 1 knot (Table 1), samples were sorted on board. Endangered species (i.e., *Sygnathidae*) were immediately released to reduce post-release mortality due to handling for measurements or identification; they were not recorded and thus not included in the analyses. The remaining catch was frozen at -20°C and processed in the laboratory for identification and measurement of total length (to the closest mm) and weight (to the nearest mg). Additionally, the data on the scorpaenid *Scorpaena porcus* were not available in July, August and September 2012. Therefore, *Scorpaenidae* were not included in the multivariate analyses (see below), and between-year data of *S. porcus* were analysed independently.

For the detailed analysis of the settlement pulses in 2012 and 2013, a wide range of environmental variables were obtained from different sources: daily surface temperature (SST, °C) data were obtained from the CMEMS high resolution L4 reprocessed SST product (marine.copernicus.eu). In particular, the 4 km² area centred at 2.62°E/39.37°N was extracted and considered representative of the SST in Palma Bay. SST anomalies (SST_A) with respect to the annual cycle were also computed. Sa-

Table 1. Details of the epibenthic trawl surveys in 1960 and 2012-2013. In April 1960, there was no sampling due to problems with the boat.

Sampling characteristics	Year 1960	Year 2012-2013
Mesh size (mm)	5	5
Mouth aperture (cm)	70	80
Length of the net (m)	2.6	3
Number of stations	4	4
Name of the stations and type of habitat	1960-I: Patched <i>Posidonia</i> 1960-II: muddy [†] 1960-III: Patched <i>Posidonia</i> + sand 1960-IV: Patched <i>Posidonia</i>	2013-I: Patched (sand) <i>Posidonia</i> 2013-II: Patched <i>Posidonia</i> 2013-III: Patched (small rocks) <i>Posidonia</i> 2013-IV: Patched <i>Posidonia</i>
Depth range (m)	1.8-9	1.5-8
Period covered	January-December 1960	July 2012-June 2013
Number of trawls	76	72 [‡]
Mean trawls per month	6.3	6
Speed (knots)	<1	~1
Period	After sunset	After sunset
Duration (mins)	15-20	18-25
Environmental variables	Temperature	SST, Sal., SWH, WEWave, SCurrent, WECurrent, SNCCurrent, WindIntensity, WEWind, SNWind, SST _A , ModWECurrents, MoonPhase, Photoperiod and Depth.

[†] Station 1960-II was discarded for posterior analysis since it was directly situated on the mouth of a sporadic freshwater source (torrent) and over muddy bottoms, hence the fish community was not directly comparable with the rest of sampling sites. [‡]72 tows with 2 devices each, to a total of 144 samples. SST: Sea Surface Temperature; Sal.: Buoy Salinity; SWH: Significant Wave Height; WEWave: West-East Wave component; SCurrent: Surface Current; WECurrent: West-East Current component; SNCCurrent: South-North Current Component; WEWind: West-East Wind component; SNWind: South-North Wind component; SST_A: Sea Surface Temperature Anomaly; ModWECurrents: Modelled West-East Current component.

linity (psu), current intensity (m s^{-1}) and current direction (deg) at 1 m depth were collected from a nearby hydrographic buoy operated by SOCIB (www.socib.es) and located at $2.70^{\circ}\text{E}/39.49^{\circ}\text{N}$ (Fig. 1). The buoy also provided significant wave height (m), wave direction (deg), wind intensity (m s^{-1}) and wind direction (deg) data. The quality-controlled buoy data are provided at an hourly frequency, but to obtain a daily value, we averaged all values between 8.00 h and 20.00 h each day. The salinity records had large gaps due to the malfunctioning of the conductivity sensor. To fill those gaps, daily data from the CMEMS Mediterranean reanalysis was used. The temporal correlation of the modelled and observed salinity at 1 m depth was over 0.65 ($p < 0.05$). Additionally, model surface currents and the temperature at the buoy location were also considered.

Statistical analysis

We conducted two types of analyses. In the first approach, the two datasets (i.e., 1960 versus 2012-2013) were compared in terms of the multivariate species composition and relative abundances. For this comparison, downscaling of the 2012-2013 data was necessary, as some detailed information from 1960 was lacking (e.g., individual length data and environmental variables). In the second approach, the more detailed time series (2012-2013) was analysed in depth to gain an understanding of the settlement/recruitment dynamics in the area and to help interpret potential changes between surveys.

Historical comparison of the nursery area

Both surveys were conducted over the course of a full year, with over 70 tows in each year. All months were covered several times at each station except for April 1960 (Table 1). To compare the 1960 and 2012-2013 datasets, size information was downscaled to ranges of mean size (total length, mm) by month of sampling, which consisted of several trawls (Table 1). Furthermore, captures were standardized to percentages (of a given species) within a station per month. Species with relative abundances $< 0.5\%$ were considered rare and excluded from the comparative analyses to prevent bias in the multivariate community analysis. Although the individualised towing time was not available for 1960, the average towing time and speed (reported) of this traditional methodology enabled the assumption of comparability in the towing operation (Table 1). Potential differences between surveys and stations were analysed using a multivariate linear analysis via Redundancy Analysis (RDA, Borcard *et al.*, 2011). Furthermore, an Indicator Species Analysis (ISA, Cáceres *et al.*, 2010; De Cáceres and Legendre, 2009) was conducted to define the indicator species responsible for the differences between the groups identified through the RDA. In the case of the scorpaeids, their relative abundance per haul was compared between years through ANOVA after transforming the data

to meet the implicit assumptions (Zuur *et al.*, 2010) and by selecting the months common to both surveys.

Current dynamics of the nursery area associated with shallow seagrass meadows

During the 2012-2013 survey, abundance, individual size and weight and environmental variables were recorded. Fish abundances were standardised using the swept area method (Gunderson, 1993) and analysed with RDA, first, in terms of comparing concurrent trawls in each of the paired hauls, second, to analyse possible differences among the four locations, and finally, in terms of the environmental variables. As no differences were found in the port- and starboard-side tows, the data from both trawls from each haul were combined. The abundance of each species was binned into size classes that would represent ecologically relevant life stages for most of the species and at the same time facilitated the interpretation of multivariate data, following the available literature (Crec'hriou & Lenfant, 2015). The bins included “set-tlers” (< 30 mm), “juveniles” (31-60 mm) and “adults” (> 61 mm). Species under 0.5% abundance were considered rare and excluded for posterior analysis. Finally, the abundances were log transformed, and distances among sites were computed with Hellinger’s distance (Legendre & Gallagher, 2001). Therefore, a fish-by-size-range abundance matrix was used as the response and conditioned by the environmental matrix in an RDA model. In addition, for the most abundant species, the size distribution per month was plotted to visually assess the detailed size distribution of the species with regard to time over the shallow *Posidonia* meadow.

A total of twenty environmental variables (see Table S.1 for details) were first explored with a Pearson correlation analysis to reduce the dimensionality and avoid highly correlated variables. The variables included observations from the oceanographic buoy (10), satellite data (1), direct measures at each station (1), calculated magnitudes (2), and numerical models (6). Variables with correlation values $> 60\%$ were considered to be redundant, and one from each pair was discarded. The selected variables (Table S.1) were introduced as the explanatory matrix in the RDA model. In addition, each sampling date was coded as summer (June-September), autumn (October-November), spring (April-May) and winter (December-March) to aid in the visualization of the results.

All statistical analyses were carried out using the veg-an package (Oksanen *et al.*, 2013) in R software (www.r-project.org) (R Development Core Team, 2011). Specifically, Hellinger’s distances were calculated using the *decostand* function, and the selection of the environmental variables included in the final RDA model was realised with the *ordistep* function, which performs a forward stepwise selection of the variables from the null model without explanatory variables to the complete model (including all the variables) based on the P values (Blanchet *et al.*, 2008).

Results

Historical comparison of nursery areas

Both surveys yielded similar mean numbers of individuals per trawl (16.8 ind. in 1960, 17.7 ind. in 2012-2013, Supplementary Fig. S.1 for mean number of individuals per month). The taxonomic composition was relatively similar in the number of species (27 species in 1960 vs 31 species in 2012-2013, see Table 2 for a complete list of species captured and size distribution) and

size ranges overlapped (Suppl. Fig. S.2), ensuring reasonably unbiased datasets for comparison between years. Moreover, the sea surface temperature from both years (the only environmental variable quantified in 1960) was reasonably similar despite being taken with a Negretti & Zambra thermometer in 1960 and from satellite measurements in 2012-2013 (Suppl. Fig. S.3).

The comparison of the relative abundances from both years using RDA showed that the effect of the *Year* ($F_{1,70}$; 17.99, $P < 0.001$) was much stronger than the effect of *Station* ($F_{5,70}$; 1.69, $P = 0.016$), and all of them explained

Table 2. Complete list of fish species found in shallow Posidonia meadows during the sampling season. Families are in bold, standard length (SL) range (Min and Max, of the averages of SL per month) in mm. Species not present in samples from one year are marked with “—”. Abundances from 2012/2013 are divided by two to make a comparison with captures with only one device. Species marked with † were captured mostly in single events in 1960. In addition, *Scorpaena porcus* and Syngnathidae were captured in both surveys.

Species	Year 1960			Year 2012-2013		
	Min SL	Max SL	n	Min SL	Max SL	n
Anguillidae						
<i>Anguilla anguilla</i>	74	125	27	—		
Apogonidae						
<i>Apogon imberbis</i>	—			48.95	70.58	2
Atherinidae						
<i>Atherina boyeri</i>	52	63	8	39.39	71.69	2
Bleniidae						
<i>Lipophrys trigloides</i>	—			27.8	27.8	1
<i>Parablennius gattorugine</i>	45	75.2	26	84.52	84.52	1
<i>Parablennius sanguinolentus</i>	—			54.34	100	1
<i>Parablennius tentacularis</i>	76	76	1	—		
Bothidae						
<i>Argonoglossus</i> spp.	29.8	29.8	31	30	96	4
<i>Bothus podas</i>	68	81	3	—		
Clinidae						
<i>Clinitrachus argentatus</i>	55	55	1	39.3	39.3	1
Gadidae						
<i>Gaidropsarus mediterraneus</i>	125	125	2	34.57	85.325	5
Gobiidae						
<i>Aphia minuta</i>	23.5	42.7	25	20.85	23.41	23
<i>Gobius bucchichi</i>	—			26.75	29.88	1
<i>Gobius cruentatus</i>	25	57	344	36.44	55.28	3
<i>Gobius paganellus</i>	52	80	35	31.36	106	20
Gobiesocidae						
<i>Lepadogaster lepadogaster</i>	30	35	11	—		
Labridae						
<i>Coris julis</i>	—			114.6	115.1	2
<i>Labrus merula</i>	67	77.4	12	153.05	178.02	1
<i>Labrus viridis</i>	—			24.87	111.31	10
<i>Symphodus bailloni</i>	82	82	1	61.53	129.3	31
<i>Symphodus cinereus</i>	36.5	85	46	29.1	29.1	1
<i>Symphodus ocellatus</i>	26.5	75	155	27.49	82.08	443
<i>Symphodus roissali</i>	—			42.92	90.44	12
<i>Symphodus rostratus</i>	65	75	18	26.78	121.34	47
<i>Symphodus tinca</i>	65	99.2	7	24.77	129.21	89
Mullidae						
<i>Mullus barbatus</i> †	47	64.2	36	—		
Ophidiidae						

continued

Table 2 continued

Species	Year 1960			Year 2012-2013		
	Min SL	Max SL	n	Min SL	Max SL	n
<i>Parophidium vassali</i>		—		43.34	147.64	11
Pomacentridae						
<i>Chromis chromis</i>	52.5	86	7	43.63	100.01	19
Serranidae						
<i>Serranus hepatus</i>		—		33.2	34.6	12
<i>Serranus scriba</i>	40	85	68	33.9	135.495	95
Sparidae						
<i>Diplodus annularis</i>		—		37.89	113.06	155
<i>Diplodus puntazzo</i>		—		60.65	60.65	1
<i>Diplodus sargus</i>	20	63	3	—	—	—
<i>Diplodus vulgaris</i>	35	50	12	19.6	89.77	135
<i>Lithognathus mormyrus</i> †	29.4	96	201	—	—	—
<i>Oblada melanura</i>		—		24.44	97.8	11
<i>Sarpa salpa</i>	42	42	1	23.64	103.27	156
<i>Spicara smaris</i>	55.2	56.2	9	—	—	—

an R^2 of 27.42% of the total variance. Accordingly, RDA Axis 1 separated the samples from Year with 73.05% of the explained variance, whereas the RDA2 attributed to station only explained 16.53% of the model variance (Fig. 2). Therefore, these two differentiated groups were selected for the ISA, which showed a clear shift in the species composition from 1960 to 2012-2013 (Ta-

ble 3). Selected indicator species were unique to one of the years (such as *Anguilla anguilla* or *Mullus barbatus* in 1960 or *Diplodus annularis* in 2012-2013) or were present in both years, but more abundant in one of them (e.g., *Gobius cruentatus* in 1960 or *Symphodus ocellatus* in 2012-2013). Moreover, 20 species were captured in

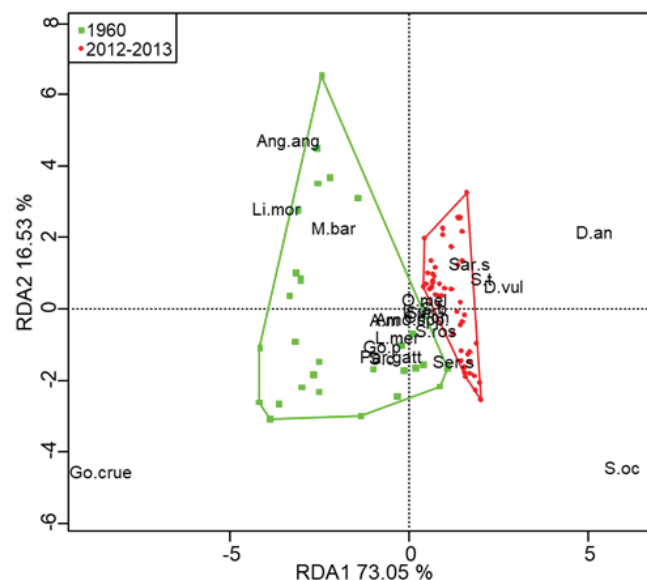


Fig. 2: Ordination plot of between-years RDA results. Symbols represent samples for each of the two years. Fish species names as follows: Ang.ang= *Anguilla anguilla*; A.m= *Aphia minuta*; Arno.spp.= *Argonoglossus* spp.; Ch.ch= *Chromis chromis*; D. an= *Diplodus annularis*; D.vul=*Diplodus vulgaris*; Go.cru= *Gobius cruentatus*; Go.p= *Gobius paganellus*; L. mer= *Labrus merula*; L.vir= *Labrus viridis*; Li.mor: *Lithognathus mormyrus*; O. mel= *Oblada melanura*; M.bar: *Mullus barbatus*; Par.gatt= *Parablennius gattorugine*; Sar.s=*Sarpa salpa*; Ser.s= *Serranus scriba*; S.b= *Symphodus bailloni*; S.c= *Symphodus cinereus*; S.ros= *Symphodus roissali*; S.oc= *Symphodus ocellatus*; S.r= *Symphodus rostratus*; S.t= *Symphodus tinca*.

Table 3. Indicator species analysis (ISA) results. IndVal_{ij} is the indicator value for the species in parts per unit. P values are based on 999 permutations. Significant indicator fish species for each sampling period are shown. Species marked with † are typically found in sandy bottoms.

	Species	Ind-Val _{ij}	P
Year 1960	<i>Gobius cruentatus</i>	0.92	0.005
	<i>Parablennius gattorugine</i>	0.554	0.005
	<i>Anguilla anguilla</i>	0.525	0.005
	<i>Lithognathus mormyrus</i> †	0.525	0.005
	<i>Symphodus cinereus</i>	0.509	0.005
	<i>Mullus barbatus</i> †	0.455	0.01
	<i>Labrus merula</i>	0.39	0.03
	<i>Diplodus annularis</i>	0.913	0.005
	<i>Symphodus tinca</i>	0.879	0.005
	<i>Symphodus ocellatus</i>	0.859	0.005
Year 2012-2013	<i>Serranus scriba</i>	0.815	0.005
	<i>Symphodus bailloni</i>	0.706	0.005
	<i>Symphodus rostratus</i>	0.682	0.015
	<i>Diplodus vulgaris</i>	0.665	0.01
	<i>Chromis chromis</i>	0.581	0.01
	<i>Sarpa salpa</i>	0.553	0.02
	<i>Labrus viridis</i>	0.479	0.015
	<i>Oblada melanura</i>	0.456	0.035
	<i>Symphodus roissali</i>	0.456	0.015

both sampling periods, although some were in very low abundances (e.g., *Diplodus vulgaris* and *Sarpa salpa* in 1960) (Table 2). The comparison of the *Scorpaena porcus* abundances for coincident months showed a significant increase in relative abundance in 2012-2013 (ANOVA $F_{1,14} = 11.65, P = 0.004^{**}$) (Fig. 3).

The comparison of the size distributions from 1960 and the recent survey was not further explored due to a lack of detailed observations at the individual level for 1960, which hampered a deeper comparison (but see Table 2 and Suppl. Fig. S.2).

Dynamics of the nursery area in 2012-2013

As no differences in the fish communities between the two tows per station trawl were observed (RDA, factor *Side* $F_{1,142} = 0.4215, P < 0.789$), we pooled the catches per trawl in order to maximize the representativeness of the size-species matrix. From the 20 available environmental variables, 14 were selected (Table S.1) for the RDA model ($R^2 = 32.76\%$). Six of the variables were found to be significant (Table 4) by forward stepwise selection. Selected variables in terms of decreasing explained variability were SST ($^{\circ}\text{C}$), photoperiod (h), dominant currents in the area (i.e., the dominant component of the surface current (West-East component)) from the oceanographic buoy (cm s^{-1}), temperature anomaly (SST_A $^{\circ}\text{C}$) and salinity (Fig. 4). Clearly, season-related variables such as SST, photoperiod and SST_A basically explained the ordination of species-size composition and particularly the settlement of species (Fig. 4), with additional significant influence of surface salinity and the direction of the surface currents (West-East component).

The detailed size distribution of the four more abundant species over time (Fig. 5) showed that the use of *P. oceanica* shallow habitats shifted among several species sequentially throughout the year: *Diplodus annularis* post-settlers appeared in July (~2.5 cm) and grew

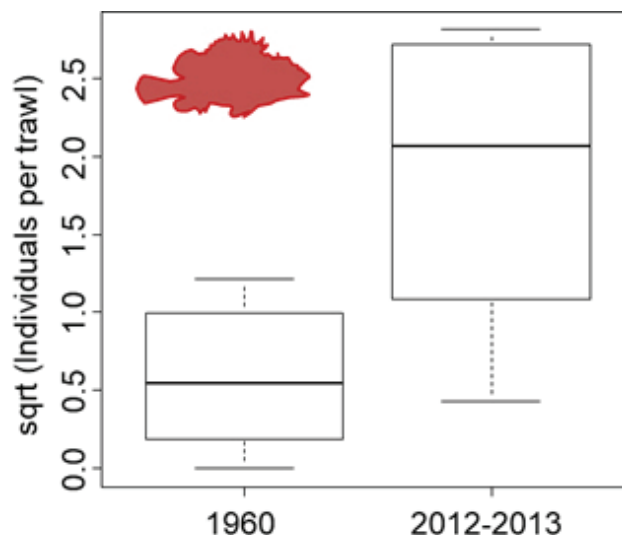


Fig. 3: Individuals of *Scorpaena porcus* per “gànguil” trawl in both surveys. Only common months are included (i.e., April 1960 + July, August and September 2012 are excluded).

over the summer season; *Symphodus ocellatus* juveniles ~4 cm were detected in the *Posidonia* shallow beds and stayed over autumn and winter months; *Sarpa salpa* settlers appeared from January until March, similar to *Diplodus vulgaris*, and settled down in late winter, growing over the spring season.

Discussion

The fish communities associated with Mediterranean seagrasses and macrophytes are well described by numerous previous studies, usually using scuba diving (Harmelin-Vivien & Francour, 1992; Vigliola *et al.*, 1998; Guidetti, 2000; Guidetti & Bussotti, 2000; Félix-Hackradt *et al.*, 2013). In the Balearic archipelago, there have been several works describing the spatial variation of the fish

Table 4. Results of redundancy analysis (RDA) by variables and constrained axis computed for the fish community composition by size class (Fig. 4).

		Eigenvalue	Proportion explained	Variance	F	P	
Variables	SST			0.069	14.525	0.001	***
	Photoperiod			0.050	10.484	0.001	***
	BuoyWECcurrent			0.015	3.093	0.002	**
	BuoySurfaceCurrent			0.009	1.915	0.033	*
	SSTAnomaly			0.010	2.018	0.021	*
	BuoySalinity			0.010	2.109	0.022	*
	Residual			0.298			
Axis	RDA1	0.0783	0.5017	0.078	16.281	0.001	***
	RDA2	0.0514	0.3290	0.051	10.678	0.001	***
	RDA3	0.0163	0.1048	0.016	3.403	0.001	***
	RDA4	0.0100	0.0643	0.010	1.093	0.016	*
	Residual			0.2984			

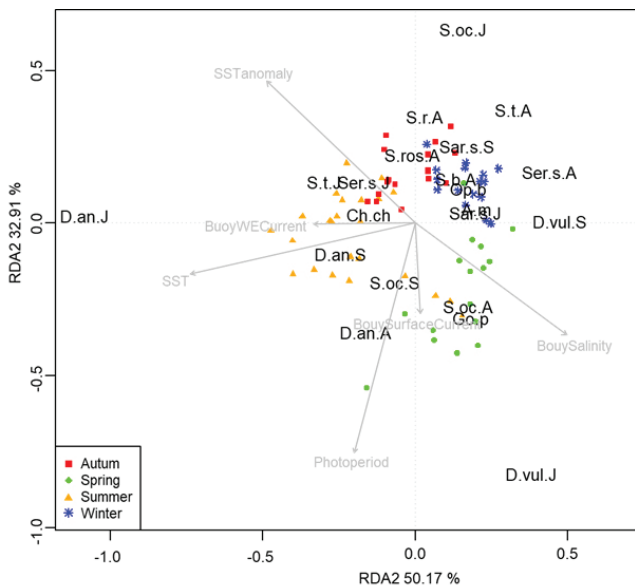


Fig. 4: Ordination plot of RDA results for 2012-2013. Axes depict the explained variance of the model. Grey arrows indicate the strength and direction of the different environmental variables selected in the RDA model. Symbols represent samples divided by sampling season. Fish species names are contracted, with the final letter showing the life stage: S for Settler, J for Juvenile, A for Adult. A.m= *Aphia minuta*; Ch.ch= *Chromis chromis*; D. an= *Diplodus annularis*; D.vul=*Diplodus vulgaris*; Go.p= *Gobius paganellus*; Op.b= *Ophidium barbatum*; Sar.s= *Sarpa salpa*; Ser.s= *Serranus scriba*; S.b= *Symphodus bailloni*; S.ros= *Symphodus roissali*; S.oc= *Symphodus ocellatus*; S.r= *Symphodus rostratus*; S.t= *Symphodus tinca*.

assemblages within deeper *P. oceanica* meadows (Oliver 1966; Moranta *et al.*, 2006), or for relatively short periods of time, for example, bimonthly over a year (Reñones *et al.*, 1995; Deudero *et al.*, 2008). These previous works were not only based on deeper meadows but also used larger mesh sizes than our study. The early work by Massutí (1965), which enabled the present comparative study, in addition to the works conducted in deeper meadows (Oliver, 1966; Moranta *et al.*, 2006; Deudero *et al.*, 2008), allow us to sketch a picture of the state of the fish assemblages half a century ago and to perform a static comparison of the annual dynamics of fish communities currently associated with the *P. oceanica* meadows in the Balearic archipelago.

The first description of the use of a small “gànguil” to capture crustaceans for bait dates back to 1897 in a description of Balearic Island customs and traditions by the German naturalist Ludwig Salvator, Archduke of Austria, although larger “gànguils” were used at least a century before that (Sañez Reguart, 1792). The use of this traditional fishing trawl was common until the first half of the twentieth century; despite being officially forbidden in 1941 (due to the small mesh size used [Spanish Official Bulletin (BOE), 1941]) in 1960 this fishing gear was still commonly used. Massutí (1965) described the fishing pressure to be approximately 330 to 1100 trawls per night on Saturdays and Sundays over the coastal strip. These figures are based on an average of 5.5 trawls (paired tows)

per night and an observed minimum of 60 boats operating during the night, with potential peaks of 200 boats only in Palma Bay. Assuming a conservative net mouth size of 70 cm, a mean speed of 1 knot and a mean duration of 30 minutes per haul, a range between 0.4 and 1.4 km² was swept each night. Because the target bait lives in seagrasses and the gear restricted the operations to shallow depths between approximately 1 and 10 m, the trawling pressure represented 10.8% of this shallow strip covered by patched seagrass, trawled at least twice per week. In that paper, Massutí related “it is important to highlight the damage caused by fishing enthusiasts on the development of the species that inhabit these habitats in their post-larval phase”. This observation in 1960, although lacking evidence of real effects on populations, promoted an effective reinforcement of the Spanish laws (this type of gear was regulated sequentially in 1962, 1973 and 1975 [BOE, 1962, 1973, 1975]) and a local enforcement that has been largely observed since then, except for a few residual licences that operated until 2000 (Regional Fisheries Management Department, pers. comm).

The detailed analysis of the 2012-2013 survey allows us to further investigate potential explanations for the observed historical change. Our results from 2012-2013 showed that settlers and small juveniles of many species use shallow *P. oceanica* meadows as settlement habitats during the different seasons of a given year. The arrival of settlers of the different species was triggered by different environmental variables that modulate the fish community throughout the year. For example, higher sea surface temperature during summer, possibly in combination with photoperiod, is apparently related to *D. annularis* settlement, but these relationships cannot be assessed by only one year of sampling. Nevertheless, the RDA results showed differential use of this habitat by many species’ settlers during the different seasons of the year, coinciding with previous works in the Mediterranean (Garcia-Rubies *et al.*, 1995). These shallow *P. oceanica* meadows are spatially delineated by sandy areas or rocky reefs in proximity to the coastline and usually to deeper seagrass habitats. The rocky reefs are well characterized by an abundance of macrophytes such as Fucales, mainly of the genus *Cystoseira*, that also offer a good settlement niche (Ballesteros *et al.*, 1998; Cheminée *et al.*, 2013). Our ISA results selected several species that are considered indicators of the period 2012-2013, including the four species showing clear settlement pulses: *D. annularis*, *D. vulgaris*, *S. sarpa* and *S. ocellatus*. The shallowest area is characterized by the high abundance during summer of settlers of some species such as *S. ocellatus* that we found later in autumn in the shallow *P. oceanica* meadows in our samples. Conversely, the adults of *S. ocellatus* are very abundant in the deeper *P. oceanica* meadows; apparently, this labrid species uses the shallow seagrass habitats as feeding grounds during their juvenile stage (4-6 cm) (Gouraguine *et al.*, 2016) before moving to deeper habitats later in the season. On the other hand, the sparids *D. annularis*, *D. vulgaris* and *S. salpa* settled sequentially in summer, winter and early spring, showing a seasonal shift in the use of this nursery habitat.

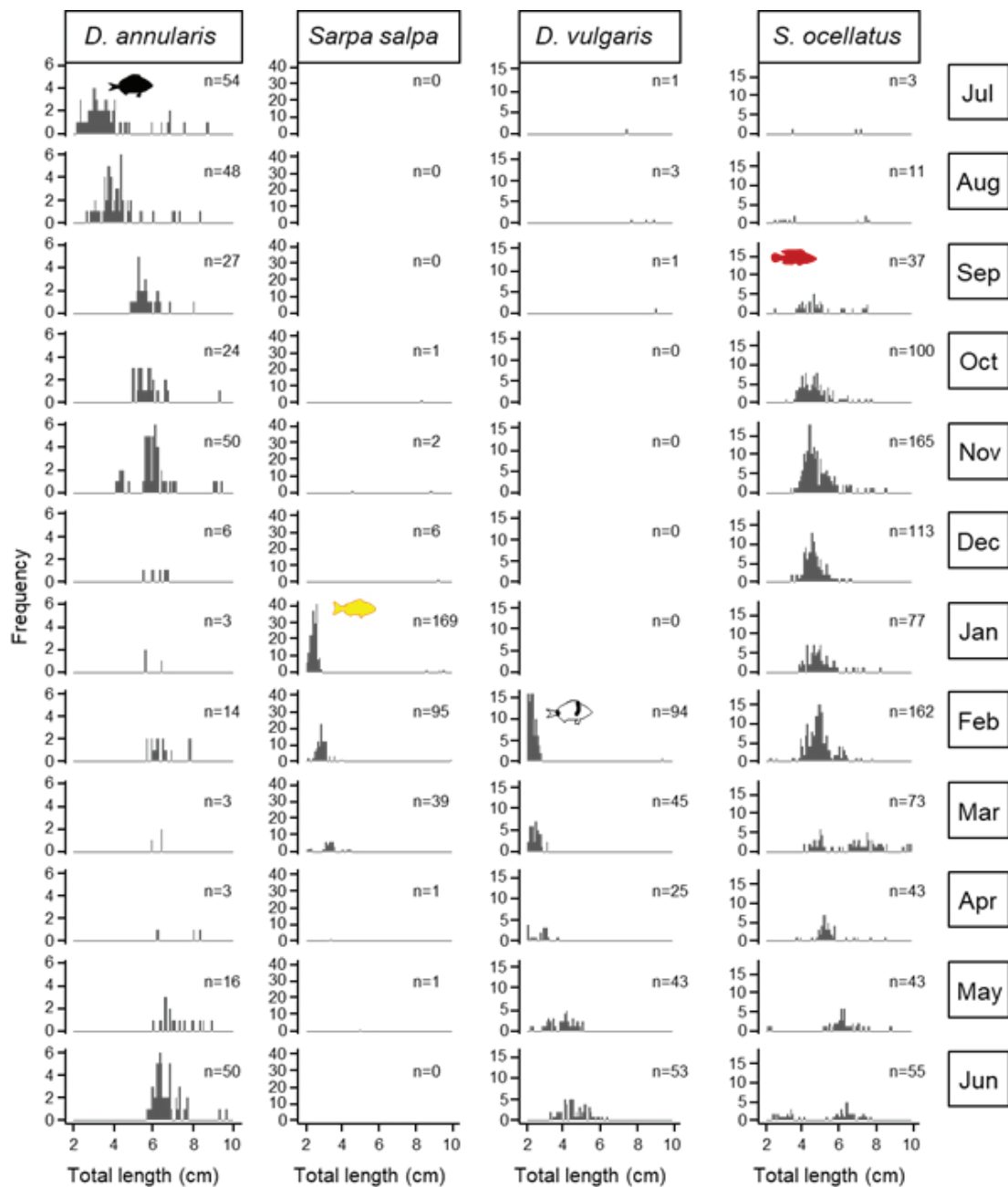


Fig. 5: Settlement pulses of the four most abundant species. *Diplodus annularis*, *Sarpa salpa*, *D. vulgaris* and *Symphodus ocellatus* throughout the whole sampling period (1 year). The number of individuals per sampling month and species is shown.

Despite capturing approximately the same number of individuals per trawl in 1960 and 2012-2013 (16.8 vs 17.7 ind./trawl), the community composition changed significantly, not only in species but also in size range. The comparison of the total species composition (27 species for 1960 and 31 in 2012-2013) revealed that some species had totally disappeared in 2012-2013, such as *Anguilla anguilla*, probably due to a degradation of the freshwater output habitat (see further), which is currently totally anthropized. This relationship has been observed in many other areas (Feunteun, 2002). Some differences in species composition might be attributed to sporadic hauls that captured a large number of individuals of species usually not present in *P. oceanica*; for example, one indicator species in 1960, *Lithognathus mormyrus*, is typically found in sandy bottoms, although it can dwell in

seagrass beds (Garcia-Rubies *et al.*, 1995). However, its capture was temporally and spatially infrequent because 91% of all individuals (183) were captured at a single station in that survey. Thus, this capture may be a signal of a fortuitous over-sand trawl and/or simply a catch of a sparse juvenile school. Moreover, the absence of this species in the following months of that survey reinforces this as a sporadic capture. In addition, the appearance of three individuals of *D. sargus* in 1960, whose juveniles tend to inhabit the shoreline and not *P. oceanica* (Casado, 2015), may be explained if some tows were extremely shallow; however, we do not believe that the bulk of the trawled area was in a different depth range or nursery habitat, not only according to their description of the methods but also because the range of sizes of the common species overlapped.

One of the most striking changes between both surveys is the absence of *D. annularis* in the samples from 1960. This species is currently one of the most abundant sparid species in Palma Bay, and within the bay, their adult phases were highly abundant in 1964-1965 in deeper *P. oceanica* habitats (Oliver, 1966) and in the early 1990s (Reñones *et al.*, 1995). Although we cannot discard the possible effect of climate and/or connectivity stochasticity as a driver of species shift, the similar temperature cycles in 1960 and 2012-2013 (Suppl. Fig. S.3) and the relatively high and constant retention rates in Palma Bay (Basterretxea *et al.*, 2012) suggest that other causes might explain the differences between juvenile fish assemblages in shallow seagrasses after 52 years. Although we are aware that we only have two one-year snapshots of juvenile fish composition, abundant literature shows that, irrespective of the year and area, juvenile *D. annularis* are always found in abundance over *P. oceanica* meadows (Oliver, 1966; Guidetti, 2000; Deudero *et al.*, 2008; Díaz-Gil *et al.*, 2017). Furthermore, we are confident that the basic benthic structure of the sampled habitat was comparable; although the spatial variability in the nursery areas can be large at relatively small scales, especially when affected by manmade structures (Bulleri & Chapman, 2010; Cheong *et al.*, 2013; Munsch *et al.*, 2016), we controlled for the effects of depth, bottom type, time period, and tows, which were integrated over hundreds of metres along a stretch of few kilometres. In addition, our data show that species typically found in *P. oceanica* (e.g., *Symphodus rostratus*, *Serranus scriba*, *Scorpaena porcus* and syngnathids, although the latter species were not included in the analyses) were frequent in both surveys; hence, our data support the fact that we are basically comparing the same habitat between surveys. Therefore, we propose two plausible explanations for the observed shift in key juvenile species, such as *Diplodus annularis*, between surveys:

i) Unaccounted-for habitat change. We acknowledge that habitat conservation status (density of *P. oceanica* shoots, quality of water) has changed (Ruiz *et al.*, 2015), but these effects would be confounded with other anthropogenic effects derived from the increment of the use of the seaside, such as construction of the seashore, yachting or recreational fishing (Miller, 1993; Morales-Nin *et al.*, 2005; Zahedi, 2008; Munsch *et al.*, 2016). However, due to the evidence noted above, this would not explain the lack of the currently extremely common juvenile *D. annularis*, whose adults were present in the area at greater depths, in the 1960s (Oliver, 1966).

ii) Direct and indirect fishing effects. The fishing effort in the 1960s was so strong and concentrated on the shallow seagrass nursery habitats that the abundance of the currently very abundant fish species was kept low. This can explain the fact that in the 1960s, the lower trophic fish species, such as Gobiidae and Blenniidae, that inhabited *P. oceanica* were more abundant. The striking lack of juveniles of *D. annularis* in the 1960s could be partly explained if fishing pressure lowered the abundance of these recruits at early stages (e.g., at the beginning of the settlement period), as low juvenile abundance

would be expected. This fraction, which should have existed in order to maintain the adult populations observed in deeper areas by Oliver (1966), might be found either in deeper *P. oceanica* meadows or at slightly different habitat configurations. Furthermore, the distance from the harbour was a major driver of where to fish, especially for boats without engines in the first half of the twentieth century. Consequently, the shallow seagrass meadows close to Palma harbour (and other minor marinas) were possibly affected by a strong fishing pressure on the juvenile stages of fish, with the adult populations maintained with individuals from nearby populations (Alós, Palmer, Catalán *et al.*, 2014). *D. annularis* was not the only case; the virtual absence from the 1960 samples of other species that use this nursery habitat for short periods of time during post-settlement, such as *D. vulgaris* or *S. salpa* (only 12 and 1 individuals in 1960, respectively), and, moreover, the lower abundance of species that had and have local economic value, such as *Serranus scriba* or *Scorpaena porcus* (Fig. 3), in 1960 reinforce the hypothesis of the intense fishing pressure on this shallow nursery habitats over half a century ago.

We cannot fully attribute the observed historical differences in juvenile fish assemblages between the 1960s and the recent survey to the decrease in the trawling pressure in shallow areas (hypothesis ii) because we cannot ignore that other concurrent effects were operating, including pressure on the adults' populations, anthropization of the nearshore habitats and/or water quality, as depicted above (hypothesis i, (Jones, 2014)). Moreover, we cannot discard the possibility of small differences among sampling sites in the old vs moderns survey. However, in this and other habitats, long-term fisheries have been shown to affect both community assemblages (Last *et al.*, 2011; Finigan *et al.*, 2018), size distributions and life history traits (Baum & Myers, 2004; Catalán *et al.*, 2018). In our case, many of the species that are currently common are also of interest for artisanal and recreational fisheries (e.g., *D. annularis*, *D. vulgaris*, *S. porcus* and *S. scriba*), and their increase in the shallow protected *P. oceanica* meadows might be thought to be positive for the sector. The increase in surveillance to enforce the prohibition of the use of "gànguils" to capture shrimps in the early 1970s can be regarded, albeit with caution, as a correct management measure with respect to the protection of the nursery function of shallow seagrass habitat in the Balearic Islands.

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The following supplementary information is available for the article:

Table S.1: Environmental variables used for the 2012/2013 analysis period. Variables marked with a No were highly correlated with others (>60%) and therefore not used in the RDA model.

Fig. S. 1: Mean captures per trawl during years 1960 and 2012-2013 (number of individuals).

Fig. S.2: Length range (TL) of individuals captured in 1960 and 2012-2013. Only species captured in both years (abundance >1 individuals) are shown. The rest of species and length ranges can be found in Table 2.

Fig. S.3: Temperatures (°C) along 1960 and 2012-2013 periods. Shaded areas represent min and max temperatures, solid lines are the mean temperatures of each period.