Deep–Sea Research I 176 (2021) 103603

Contents lists available at ScienceDirect

Deep-Sea Research Part I

journal homepage: www.elsevier.com/locate/dsri

Potential factors influencing the condition of demersal sharks in the Mediterranean deep sea ecosystems

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ARTICLE INFO

Keywords:
Demersal sharks
Galeus melastomus
Fish condition
Feeding
Productivity
Bottom trawl footprint

ABSTRACT

The Alboran Sea and the Balearic Islands are two contrasting areas in terms of primary productivity. The former is among the most productive areas of the whole Mediterranean Sea, whereas the Balearic Islands is among the less productive ones in the western Mediterranean. The two areas also show different patterns in the bottom trawl fishing footprint. In the Alboran Sea, the fishing effort on the upper slope is much higher than in Balearic Islands. However, the opposite applies to the middle slope, the vast majority of it remaining unexploited in Alboran Sea, whereas a widespread fishery targeting blue and red shrimp *Aristeus antennatus* develops in Balearic Islands.

Galeus melastomus is a small demersal shark species inhabiting slope bottoms, where adults and juveniles are segregated and concentrate in the middle and upper slope, respectively. It feeds intensively on mesopelagic preys which, in turn, feed on low trophic level organisms close to primary producers. In this work we aimed to study the effect of surface primary production on the condition of deep sea demersal communities. We compared the condition, diet and potential intra- and inter-species competition for feeding resources in the juveniles of *G. melastomus* between Alboran Sea and Balearic Islands. The comparisons of Le Cren's relative condition factor, and hepatosomatic and digestivosomatic indices evidenced an opposite pattern to that a priori expectable: better condition in the less productive area. The analysis of stomach contents showed similar diets in both areas, but lower food ingestion in Alboran Sea than in Balearic Islands. Different abundances of potential intra- and inter-specific competitors for feeding resources in the two areas, apparently linked to the different fishing footprints, seems the most likely explanation for the better nourished individuals in Balearic Islands. Whereas juveniles of *G. melastomus* dominate the shark community in the Balearic Islands upper slope, where the presence of adults of this species is almost negligible, in Alboran Sea this stratum is dominated by adults and potential competitors of other small demersal shark species. All shark species together, including *G. melastomus*, showed abundances 38% higher in Alboran than in Balearic Islands. Our results show that condition of deep sea demersal fish is ruled by complex inter-relationships among different factors, needing the combination of biological, ecological and fisheries knowledge to understand its variability.

1. Introduction

The deep sea is the largest biome of planet Earth, representing about 90% of the ocean (Ramírez-Llodra et al., 2010). It presents peculiar environmental conditions (Gage and Tyler 1991), like the absence of light, high pressure and low temperature (with some exceptions such as the Mediterranean), among others. Due to this uniformity of physical factors, the deep sea ecosystems had been considered as stable environments and habitats, where physical and biological processes remained unchanged over time. However, there is now evidence that

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https://doi.org/10.1016/j.dsr.2021.103603
Received 5 September 2020; Received in revised form 28 February 2021; Accepted 15 July 2021
Available online 20 July 2021

physical disturbances occur, causing important biological responses (Rogers 2015). In relation to the energy that supports deep sea ecosystems, their faunal communities depend firstly on surface primary production and then from the energy and carbon transfer along the water column (Angel 1990). Oceanographic features and geo-morphologic structures such as submarine canyons and seamounts affect this transfer (e.g. Ivanov et al., 2004; Clark et al., 2010; Fernández-Arcaya et al., 2017), which is largely mediated by the vertical displacements of organisms (Brierley 2014).

The Mediterranean Sea is characterized by its oligotrophy. At a large scale, there is a decreasing west-east trend in the availability of nutrients and the western and eastern basins are considered oligotrophic and ultraoligotrophic, respectively (Stambler 2013). This trend also applies to the primary production, limited by the low nutrient concentrations, particularly of inorganic phosphorus and nitrogen (Estrada 1996; Bosc et al., 2004; Stambler 2013). Despite the general oligotrophic condition, in the western basin several mesoscale hydrographic features produce a spatial heterogenic distribution of nutrients (Estrada 1996; Bosc et al., 2004): e.g. presence of shelf/slope fronts and vertical convection in the northwestern basin, upwelling driven by northerly winds in the Gulf of Lions, exchange of Mediterranean and Atlantic waters in the Strait of Gibraltar and the presence of important rivers such as Rhône, Po and Ebro in the northern coast. The Mediterranean Sea below 200 m depth is characterized by a high degree of environmental stability for both temperature and salinity: ~13 °C and ~38.5, respectively (Hopkins 1985). The general oligotrophy of this sea is more pronounced in its deep sea ecosystems. Available estimations give the annual primary production in the northwestern basin as between 77 and 100 gC/m^{-2}/year^{-1} (Minas et al., 1988), although only about 1–5 gC/m^{-2} may reach the benthic ecosystems at 800 to 1000 m depth (Miquel et al., 1994). However, it is known that Mediterranean deep sea ecosystems are more dynamic than previously thought, linked to upper water column processes through the varying (in both space and time) influx of organic matter, driven by geomorphological and oceanographic features, and benthic communities have been shown to react very rapidly to seasonal or/and episodic sedimentation of organic matter (Sardà et al., 2004). Mesopelagic crustaceans, cephalopods and fishes play an important role in these fluxes, due to their vertical migrations in search of food near the surface during the night and of shelter in deep waters during the day (Cartes et al. 2001, 2009; Granata et al., 2001; Olivar et al., 2012; Valls et al., 2017).

Fish condition is a widely used term to refer to the overall physiological status or health of an individual (Lloret et al., 2014). Several factors can affect fish condition such as temperature, primary production, density dependent processes, fishing impacts on trophic webs and habitat quality (Rätz and Lloret, 2003; Basilone et al., 2006; Lloret et al., 2007; Hiddink et al., 2011; Ordines et al. 2015, 2019). Condition, in turn, affects key biological traits such as reproduction, growth and mortality of species (Marshall and Frank 1999; Dutil and Lambert 2000; Dutil et al., 2006; Ordines et al., 2009), and consequently fisheries productivity (Rätz and Lloret 2003). Among the various methods used to determine fish condition, biochemical analyses are considered the most accurate ones, because they supply direct information on key indicators, such as the lipid and protein reserves (Shulman and Love 1999). However, this methodology is time-consuming, expensive and, therefore, not suitable for large numbers of individuals (Crossin and Hinch 2005). For this reason, morphometric indicators of fish condition based on length and weight data have been widely used, due to the quick and easy collection of the data and its almost immediate availability for analysis. These indicators are based on the premise that a fish of a given species and length should weigh as much as a standard for its length, and variations from this standard are taken as an indication of the relative fitness of this individual (Lloret et al., 2014). These indexes can be complemented with organosomatic or bioenergetic indicators of condition, which are directly related to the physiological composition of body tissues and provide a more precise measure of actual fitness in terms of stored energy. These indicators are calculated as the ratios of the tissue weight where individuals store energy and the weight of the individual, being the most common ones those based on liver, mesenteric fat and digestive tract weights (Lloret et al., 2014).

The application of condition indices to sharks has been limited (Hussey et al., 2009). The Mediterranean is no exception, and despite being key species of benthic and nekto-benthic communities in the deep-sea ecosystems of the Mediterranean (e.g. Moranta et al., 1998; 2008; Massutí et al., 2004; D'Onghia et al., 2004), studies about condition indices of sharks are scarce compared with teleosts, mostly due to the relatively smaller participation of sharks in the Mediterranean fishery production, since they mostly occur as an important fraction of by-catch and discards of deep water trawling (Moranta et al., 2000; Guijarro et al., 2012).

The blackmouth catshark (*Galeus melastomus*) is a small-sized shark species no usually exceeding 70 cm in total length. It is widely distributed in the north-east Atlantic, from Norway to Senegal, including the Mediterranean Sea (Ebert and Stehmann 2013), where inhabits the continental slope bottoms, preferentially between 200 and 800 m depth (Moranta et al., 1998; Rey et al., 2005; Ordines et al., 2011), although its bathymetric range extends to more than 1500 m (Stefanescu et al., 1992; Massutí et al., 2004). In the Mediterranean, this species segregates bathymetrically depending on size, with juveniles (individuals smaller than 50 cm in total length, i.e. the length at first maturity in the western Mediterranean) mainly dwelling in the upper slope bottoms shallower than 600 m depth, whereas larger ones live mainly below that depth, in the middle slope (Massutí and Moranta 2003; Ramírez-Amaro et al., 2015). It is one of the dominant fish species dwelling in the slope bottoms (Moranta et al., 1998; Farriols et al., 2019), and the most important by-catch of the bottom trawl fishery targeting blue and red shrimp (*Aristeus antennatus*) in the middle slope of the western Mediterranean (Moranta et al., 2000; Guijarro et al., 2012). In this area, the bathymetric distribution of *G. melastomus* overlaps with that of the small sharks *Galeus atlanticus* (only in the Alboran sea; Rey et al., 2010), *Scyliorhinus canicula* and *Etmopterus spinax*, the latter two being typical components of the demersal communities from the continental shelf to the upper slope and on the middle slope, respectively (Stefanescu et al., 1992; Moranta et al., 1998; Massutí and Moranta 2003; Ordines et al., 2011; Ramírez-Amaro et al., 2015; Farriols et al., 2019). There is no information on diet of *G. atlanticus*, but it has been studied in *S. canicula* and *E. spinax* and both species present an important trophic overlap with *G. melastomus* (Macpherson 1980; Valls et al., 2011).

Galeus melastomus feeds intensively on mesopelagic preys which are typical components of the benthic boundary layer, with myctophid fishes, euphausiids and decapod crustaceans, and cephalopod mollusks being the most important components of its diet (Macpherson 1980; Olaso et al., 2005; Neves et al., 2007; Fanelli et al., 2009; Anastasopoulou et al., 2013; Valls et al. 2011, 2017). We hypothesize the diet of *G. melastomus* can establish a trophic link with the production in the pelagic environment, making this demersal bathyal shark a good candidate to study the effect of surface primary production on the condition of deep sea demersal fish communities. Whether this link exists, the condition of *G. melastomus* should be affected by the highly contrasting primary productivity between Alboran Sea and Balearic Islands. To study this effect, we compare the condition, diet and the potential intra- and inter-species competition for feeding resources in juveniles of this species between both areas, which are also subject to different levels of fishing effort.

2. Material and methods

2.1. Study area

In the western basin, the Alboran Sea and the Balearic Islands can be considered two highly contrasting areas in terms of primary productivity. The north Alboran Sea is nutrient enriched by several main hydrographic features: turbulent mixing in the Strait of Gibraltar, which recovers for the euphotic zone nutrients transported by deep Mediterranean waters; upwelling and frontal systems; and the effects of the Atlantic current, which has higher nutrient content than surface Mediterranean water (Estrada 1996). On the contrary, no such enrichment features have been reported for the Balearic Islands area, which is neither affected by the presence of rivers that could locally enhance the content of nutrients in the Archipelago. In fact, the Alboran Sea is one of the areas with the highest values of annual primary productivity in the whole Mediterranean, contrasting with the Balearic Islands which are among the areas presenting the lowest values in the western Mediterranean (Bosc et al., 2004; D'Ortenzio and D'Alcalá 2009; Uitz et al., 2012; Basterretxea et al., 2018).

Primary productivity is not the only contrasting feature between Alboran Sea and Balearic Islands. The slope bottoms of these areas also show different fishing footprints. In the Alboran Sea, the fishing effort exerted by the trawl fleet at bottoms deeper than 500 m is restricted to the most eastern area and the Alboran Island, where the fleet targets *Aristeus antennatus*, leaving unexploited the vast majority of the middle slope bottoms (Gil de Sola 1993; results herein). On the other hand, off the Balearic Islands the highest trawl fishing pressure takes place in the middle slope bottoms, where the fishing fleet targeting for *A. antennatus* has an ubiquitous presence, covers most of the surface between 500 and 800 m depth and shows the highest fishing effort levels around the Archipelago (Farriols et al., 2017).

2.2. Sampling

Data and samples were collected during the annual MEDITS surveys performed on 2016 and 2018 taking place in spring/summer. The sampling gear used, the bottom trawl GOC73, and the sampling scheme and procedure applied are described in detail in Bertrand et al. (2002) and Spedicato et al. (2019). A total of 238 sampling stations were considered (Fig. 1), covering a depth range from 50 to 800 m depth along the Alboran Sea (136 sampling stations from the Strait of Gibraltar to Cape of Gata) and Balearic Islands (102 sampling stations around Mallorca and Menorca). The experimental hauls were conducted in spring (23 April to 23 June) during daylight hours, with durations of 30 to 60 min, depending on the depth stratum. The average towing speed was about 3 knots and the net's arrival at and departure from the bottom, as well as its horizontal and vertical openings (usually ranging from 16 to 22 m and 2.5 to 3.2 m, respectively) were measured in real time using acoustic monitoring systems attached to the sampling gear.

In each sample, the catch was sorted out by species. Then, their abundance and biomass, as well as length frequency distribution (in case of fish and main commercial decapod crustaceans and cephalopod mollusks) were determined. Abundances were standardized to 1 km^2 by dividing the number of individuals by the area sampled in each haul, which was estimated from the distance covered and the horizontal opening of the net.

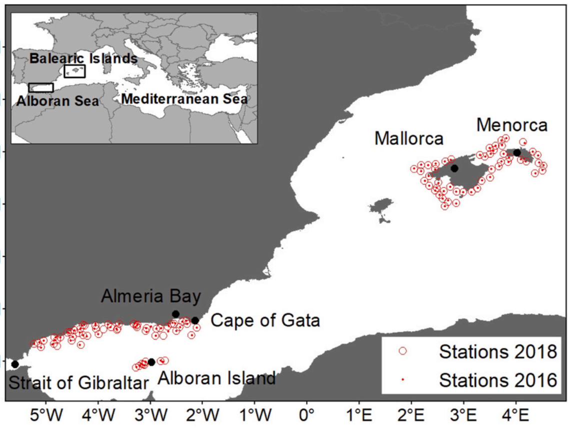

Fig. 1. Map of the study areas showing the stations sampled in 2016 (circles) and 2018 (dots).

Individual biological data of *Galeus melastomus* was also collected on a sample basis. This biological sampling was restricted to juvenile individuals in order to reduce the variability in condition attributed to different stages of gonad development, which requires energy investment mostly supplied by the mobilization of stored reserves, mainly from the liver (Lloret et al., 2014). Although individuals could be considered juveniles when they were smaller than the length at first maturity (in both areas around 50 cm total length TL for males and females together; Ramírez-Amaro et al., 2015), only those not showing any significant development of the gonad were selected. Since increases in the volume of the gonads were detected in individuals larger than 32 cm TL, we restricted our biological samplings, and considered hereafter as 'juveniles', individuals up to 30 cm TL. We performed biological samplings of a representative number of juveniles from every haul, including individual sex, maturity stage, TL (to the lower mm), total weight (TW), eviscerated weight (EW), liver weight (LW) and digestive tract weight (DW). All these weights were measured to the nearest 0.1 g. The stomach of a representative number of individuals was removed in each sampling station for content analysis. This was also done for the co-generic species *G. atlanticus* from Alboran Sea, the only area where this species is present in the Mediterranean (Rey et al., 2005).

2.3. Fish condition

The Le Cren's relative condition factor (K_n; Le Cren 1951), which compares the actual length of an individual to a standard weight predicted by the length-weight relationship of the population analyzed, was used to obtain individual length-independent measures of condition. This index was calculated following:

$$K_n = \frac{W}{W_t} * 100$$

where W was the observed individual weight and W_t the individual theoretical weight estimated from the length-weight relationship. We calculated this index based on the eviscerated weight in order to avoid the effect of viscera and gonad weight (Lloret et al., 2014). To prevent the effect of sexual dimorphism on K_n, this index was calculated based on length-weight relationships by sex.

The information obtained from the K_n index was complemented with the calculation of two organosomatic indicators: the hepatosomatic (HSI) and the digestivosomatic (DSI) indices, based on the liver and digestive tract weights (including stomach, duodenum, valvular intestine, colon and cloaca), respectively. Both indices were calculated as a ratio of the tissue weight (LW or DW) and the eviscerated weight (*EW*) of the individual as follows:

$$I = \frac{T_i W}{EW}$$

where I is the organosomatic index to be calculated based on the specific tissue weight (T_iW). Individuals presenting regurgitated stomachs or livers that suffered damage during the capture were not considered for the calculation of these indicators.

2.4. Diet

In the stomach content analyses, preys were identified to the lowest possible taxonomic level, counted and their volume was measured using a calibrated device consisting in graduated semi-cylinders used in previous studies (e.g. Olaso et al., 1998; Valls et al., 2011). Fresh preys susceptible to have been eaten in the net were not taken into account. The diet of juveniles of *G. melastomus,* and for the whole population of

G. atlanticus, was described using the following indices: 1) frequency of occurrence (%F), as percentage of stomachs with a specific type of prey in relation to the total number of stomachs containing food; 2) numerical (%N) and volumetric (%V) composition, expressed as the percentage contribution of each prey to the whole content in number or volume, respectively; 3) index of relative importance $IRI = \%F^* \, (\%N + \%V)$, which according to Cortes (1997) was standardized as follows $\%IRI = \left(\frac{IRI}{\sum IRI}\right)^*100$; and 4) vacuity index, as the percentage of empty stomachs. To calculate these indexes, all preys were included, even those identified only to a high taxonomic level.

To facilitate diet comparisons between individuals caught in the Alboran Sea and those caught in the Balearic Islands, eleven major prey categories were established: siphonophoran, euphausiids, amphipods, isopods, mysids, stomatopods, decapod crustaceans, cephalopods, polychaetes, thaliaceans and teleosts.

In order to detect differences in the relative volume of preys ingested, cumulative frequency curves of the ratio of repletion, estimated as the total volume of preys (in ml) in the stomach of the individual, relative to EW (in g), were plotted by year and area.

2.5. Fishing effort

Data from Vessel Monitoring by Satellite System (VMS) of the Alboran Sea and the Balearic Islands bottom trawl fleets during 2016–2018 were analyzed. In this system, each fishing vessel sends a signal every 2 h including position and instantaneous velocity. This data were filtered in order to just consider the positions where the fleet was fishing and avoiding signals corresponding to navigation. Only instantaneous velocities ranging from 2 to 3.6 knots, corresponding to bottom trawling velocities, were taken into account. Maps of the VMS density were created using ArcGis software v. 10.5.1 by defining a spatial grid in which nodes were separated at a 0.01°. Each VMS signal was associated to the nearest grid node and the number of signals per node was mapped. Moreover, the fishing trips (fishing days) were calculated for each year, area and stratum. To do so, depth was assigned to each VMS signal using the Emodnet bathymetry (https://www.emodnet-bathymetry.eu/). Then, we assigned the strata in which a particular boat had operated each day. The surface of each depth strata in each area was also calculated in ArcGis by using the 50, 100, 200, 500 and 800 m isobaths from Emodnet bathymetry.

The fishing effort in each sampling station was calculated counting the annual number of VMS signals in a 0.03° grid whose center was the midpoint of the transect covered in each haul. This counting was done using the R software (R Core Team, 2018).

2.6. Data analysis

Bathymetric distribution models of the standardized abundance of juveniles and adults of *G. melastomus*, and for the whole population of *G. atlanticus, Scyliorhinus canicula* and *Etmopterus spinax* were produced using Generalized Additive Models (GAM; Hastie and Tibshirani, 1990). In these models, the dependent variable was the log-transformed standardized abundance in each haul, whereas the explanatory variable was the smoothed function of the depth.

GAM models were also used to test the effect of the area on each of the different condition indicators calculated for juveniles of *G. melastomus*. In these models, the dependent variable was the individual value of the condition indicator analyzed, whereas the explanatory variables included two categorical factors, area and year of sampling, and three continuous predictors, depth (m), fishing effort (number of VMS signals in each sampling station) and the standardized abundance of juveniles of *G. melastomus*. Starting the models including all explanatory variables and removing those which were not significant, the most parsimonious model was selected on the basis of the lowest generalized cross-validation (GCV) value. A Gaussian family distribution was used. The assumption of normal distribution of residuals was checked graphically for each model. The GAM analyses were performed using the *mgcv* package (Wood 2006) in R software (R Core Team, 2018). The effect of the abundance of the other small sharks which are potential competitors for trophic resources (*G. atlanticus*, *S. canicula* and *E. spinax*) was not included in the models, due to this abundance clearly depended on the area. This was also the case of the adult population of *G. melastomus*.

The *t*-test was used to compare between areas the mean depth of the sampled individuals, and the mean total abundance of individuals of small shark species in sampling stations with presence of juveniles of *G. melastomus*. The non-parametric two-sample Kolmogorov-Smirnov (K–S) test was used to compare the cumulative frequency curves of the ratio of repletion relative to EW between years within each area and between areas. Bubble maps were produced with ArcGis version 10.5.1 program to show the distribution of the abundance and average values of condition indicators of juveniles of *G. melastomus* in each sampling station.

3. Results

A total of 1040 and 681 biological samplings and 444 and 304 stomach content analyses of juveniles of *Galeus melastomus* were performed in Alboran Sea and Balearic Islands, respectively. Tables 1 and 2 show the length parameters of the individuals analyzed in the biological samplings and stomach content analyses, respectively. The individuals analyzed were distributed as evenly as possible by year, sex and throughout the length range (16–30 cm TL) sampled in both areas. The depth range of the samples in which individuals were collected was wider in Alboran Sea, where the mean depth of the individuals sampled was slightly, but significantly deeper (around 35 m; $t_{1708} = 5.79$, $p<0.0001$), than in the Balearic Islands.

The length parameters of the 174 individuals of *Galeus atlanticus* sampled for stomach content analyses in Alboran Sea are shown in Table 2. For this species, due to its lower abundance and the lack of information on its diet, the whole length range was considered.

3.1. Diet

The analysis of the stomach contents revealed that the most important preys, in terms of %F, %N, %V and %IRI, for juveniles of *G. melastomus* in both Alboran Sea and Balearic Islands were teleosts, cephalopods, euphausiids and decapod crustaceans, with the rest of groups not reaching 1% IRI. The only exceptions were thaliaceans and siphonophorans, which in the Balearic Islands during 2018 accounted for 2.6 and 1.7% IRI, respectively (Table 3).

In the Alboran Sea, teleosts were the most important group in both years in terms of %IRI and most especially in %V (50 and 47% in 2016 and 2018, respectively). Decapod crustaceans and cephalopods alternate as the second most important group, with very similar values of %V in both years (26 and 17%, respectively). Euphausiids were the fourth group in terms of %F, %V and %IRI in both years, showing very low inter-annual variation (Table 3).

In the Balearic Islands, the diet composition varied between the two years. In 2016, cephalopods showed the highest values of all indexes except for %N (for which euphausiids showed the maximum value and ranked second in %IRI) and accounted for nearly 50% IRI. However, the importance of cephalopods dropped for all indexes in 2018, when they accounted for 14% IRI. That year the most important groups were the euphausiids for all indexes, except for %V, and teleosts ranking seconds for all indices (Table 3).

For the most important taxonomic groups of preys, the species or taxa composition was similar for both areas and years (Supplementary Material Tables 1–4). Myctophidae clearly dominated the teleosts, and

Table 1
Size descriptors (total length; TL) and number of juvenile individuals (N) of *Galeus melastomus* with biological sampling by sex (F: females; M: males), area and year. The depth range (DR) of the sampling stations and the mean depth (Mean D) are also shown. Standard deviations are shown between brackets.

Area	Sex	TL Range (cm)	Mean TL (cm)	N	N		DR(m)	Mean D(m)
					2016	2018		
Alboran Sea	F	16.0–30.9	23.1 (4.0)	530	540	500	234–658	452.9 (110.8)
	M	16.0–30.8	22.9 (3.8)	510				
Balearic Islands	F	16.8–30.4	22.2 (2.9)	337	340	341	301–600	428.1 (66.7)
	M	16.0–30.2	21.7 (3.0)	344				

Table 2
Size descriptors (total length; TL) and number of individuals (N) of juveniles of *Galeus melastomus* with stomach content analysis by sex (F: females; M: males), area and year. The information is also given for *Galeus atlanticus* from Alboran Sea. Standard deviations are shown between brackets.

Area	Species	Sex	TL Range (cm)	Mean TL (cm)	N	N	
						2016	2018
Alboran Sea	*G. melastomus*	F	16.0–30.8	24.5 (3.8)	164	184	260
		M	16.1–30.8	23.9 (3.5)	163		
	G. atlanticus	F	18.5–38.5	28.1 (4.4)	72	46	128
		M	18.0–40.4	28.3 (5.0)	78		
Balearic Islands	*G. melastomus*	F	16.8–30.3	22.6 (3.5)	149	147	157
		M	16.8–30.2	22.5 (3.1)	152		

Paralepididae was also present in both areas and years. Cephalopods could not be frequently identified to a low taxon, but in both areas the most important preys were squids (Teuthida) and sepiolids. In both areas and years, decapod crustaceans preys were dominated by species of the *Pasiphaea* genus and Sergestidae family, while euphausiids were dominated by the species *Meganychtiphanes norvegica*.

The cumulative frequency curves of the ratio of repletion relative to eviscerated weight (EW) showed clear differences, with up to 93 and 95% of the individuals with values of this ratio lower than 0.05 in Alboran Sea in 2016 and 2018, respectively, whereas only 75 and 71% of the individuals in the Balearic Islands showed such low values in both years, respectively (Fig. 2). Moreover, up to 10–11% of the individuals in the Balearic Islands showed values of the ratio >0.1 (1 g per ml of preys volume would represent ingestions of at least 10% of the weight of the predator), whereas only 0.5–1.5% of individuals in Alboran Sea reached this value. In Alboran Sea, there were significant differences between years in these curves ($D_{260,184}$ = -0.30; $p<0.001$), with higher ratios in 2018. This can be related to the difference in the vacuity index, as the maximum differences between 2016 and 2018 curves were detected when the ratio was equal to zero (Fig. 2). In the Balearic Islands, no significant differences were detected between years ($D_{157,147}$ = -0.12). The cumulative frequency curve resulting from joining 2016 and 2018 individuals in the Balearic Islands (not shown in Fig. 2 for clarity) showed significant differences with respect to the Alboran Sea curves for 2016 ($D_{304,184}$ = -0.26; $p<0.001$) and 2018 ($D_{260,304}$ = -0.29; $p<0.001$), with higher ratios of repletion relative to EW in the Balearic Islands (Fig. 2). The vacuity index was higher and showed higher difference between areas in 2016 (45.1 and 26.4 in Alboran Sea and Balearic Islands, respectively) than in 2018, when values were very similar (15.0 and 17.2 in Alboran Sea and Balearic Islands, respectively).

In the case of *G. atlanticus*, the most important taxonomic groups of preys were cephalopods and decapod crustaceans (43.3 and 37.5% IRI, respectively), both of them with very similar values of all the trophic indexes analyzed. Teleosts preys ranked third for all indexes except %N (16.1), which was slightly lower than the %N of euphausiids (17.7). The rest of groups showed a very low contribution to the diet (Table 3). Regarding the composition of each of the most important groups of preys (Supplementary Material Table 5), Myctophidae, Teuthida, Pasiphaeidae and Sergestidae, and *M. norvegica* dominated among teleosts, cephalopods, decapods crustaceans and euphausiids, respectively.

3.2. Spatial and bathymetric distribution

The juveniles of *G. melastomus* were widely distributed throughout both areas (Fig. 3). Although some variability was observed between years, the pattern was similar, with the deepest values closer to the Strait of Gibraltar and around the Alboran Island in Alboran Sea, and southwestern Mallorca and Menorca Channel in the Balearic Islands.

A significant effect of depth on the abundance of *S. canicula*, *G. melastomus* and *E. spinax* was detected (all GAM models were significant at $p<0.001$). The predictions based on these models for these three species showed deeper maximum abundances in Alboran Sea than in Balearic Islands, excepting adults of *G. melastomus* (Fig. 4). For *S. canicula*, depth explained 29 and 58% of the deviance of its abundance in Alboran Sea and Balearic Islands, respectively. Predictions for this species showed maximum abundances around 260 m depth in Alboran Sea and 150 m depth in Balearic Islands, respectively, with maximum predicted values in the latter area three times higher than in Alboran Sea. For juveniles of *G. melastomus*, depth explained 47 and 78% of the deviance of their abundance in Alboran Sea and Balearic Islands, respectively. Predictions for these individuals showed maximum abundance around 500 and 440 m depth in Alboran Sea and Balearic Islands, respectively, again with maximum predicted values in the latter area three times higher than in Alboran Sea. For *E. spinax*, depth explained 65 and 60% of the deviance of its abundance in Alboran Sea and Balearic Islands, respectively. The bathymetric distribution of this species showed differences between areas, with an almost linear increasing trend, starting at around 300 m depth in Alboran Sea and a unimodal distribution, with a maximum around 540 m depth in Balearic Islands. For adults of *G. melastomus*, depth explained 69 and 81% of the deviance of their abundance. The bathymetric distribution of these individuals showed a different pattern between areas. In Alboran Sea, the maximum was around 680 m depth, while in Balearic Islands it was detected an increasing trend, with very low abundances shallower than 600 m depth and steeply increasing below 700 m depth until the end of the bathymetric range sampled. The maximum predicted values of adults of *G. melastomus* in Alboran Sea were almost twice those in Balearic Islands. Depth explained 21% of the deviance of the abundance of *G. atlanticus* in Alboran Sea. Its maximum abundance was detected at around 560 m depth. This species showed the lowest predicted maximum values (around 560 m depth) of all species, not reaching 20 individuals/km^2, despite the high values (up to 4000 individuals/km^2) observed in some samples.

Table 3
Diet composition of juveniles of *Galeus melastomus* by year and area. The diet composition of *Galeus atlanticus*, only present in the Alboran Sea, is given for both years altogether due to the lower number of individuals analyzed. Preys are ordered according to their percentage of the Index of Relative Importance (IRI). %F: frequency of occurrence; %N and %V: numerical and volumetric percentage composition, respectively.

Species (area and year)	%F	%N	%V	IRI	%IRI
G. melastomus (Alboran Sea, 2016)					
Teleosts	42.59	28.86	49.55	3339.36	45.00
Decapods	42.59	26.37	25.41	2205.26	29.72
Cephalopods	30.56	17.91	18.13	1101.26	14.84
Euphausiids	25.93	24.88	4.92	772.57	10.41
Thaliaceans	0.93	0.5	0.95	1.34	0.02
Amphipods	0.93	0.5	0.32	0.76	0.01
Polychaetes	0.93	0.5	0.12	0.57	0.01
G. melastomus (Alboran Sea, 2018)					
Teleosts	40.72	24.03	47.16	2898.95	38.39
Cephalopods	44.8	28.64	17.45	2064.77	27.35
Decapods	39.37	21.36	26.9	1899.6	25.16
Euphausiids	26.7	20.63	4.15	661.5	8.76
Amphipods	3.62	1.94	1.16	11.21	0.15
Polychaetes	3.17	1.7	0.92	8.3	0.11
Thaliaceans	1.81	0.97	1.71	4.85	0.06
Isopods	1.36	0.49	0.2	0.93	0.01
Stomatopods	0.45	0.24	0.37	0.28	0.003
G. atlanticus (Alboran Sea, 2016 & 2018)					
Cephalopods	61.33	32.28	35.17	4136.69	43.27
Decapods	55.33	29.43	35.33	3583.5	37.49
Teleosts	32.67	16.14	22.81	1272.2	13.31
Euphausiids	26.67	17.72	3.09	554.84	5.8
Isopods	2.67	1.27	0.83	5.58	0.06
Amphipods	2	1.27	0.33	3.19	0.03
Thaliaceans	1.33	0.63	0.66	1.72	0.02
Stomatopods	0.67	0.32	1.39	1.14	0.01
Siphonophorans	0.67	0.32	0.18	0.33	0.003
Polychaetes	0.67	0.32	0.12	0.29	0.003
Mysids	0.67	0.32	0.1	0.28	0.003
G. melastomus (Balearic Islands, 2016)					
Cephalopods	50	23.42	47.54	3548.17	49.35
Euphausiids	34.91	46.47	8.17	1907.34	26.53
Teleosts	26.42	11.15	29.19	1065.64	14.82
Decapods	25.47	11.9	12.39	618.61	8.6
Mysids	5.66	2.6	0.95	20.13	0.28
Thaliaceans	5.66	2.23	0.81	17.22	0.24
Amphipods	4.72	1.86	0.81	12.6	0.18
Siphonophorans	1.12	0.20	2.83	3.75	0.05
Isopods	0.94	0.37	0.13	0.47	0.01
G. melastomus (Balearic Islands, 2018)					
Euphausiids	46.92	55.26	9.42	3035.08	46.1
Teleosts	34.62	11.72	36.76	1678.22	25.49
Cephalopods	30.77	10.53	19.75	931.54	14.15
Decapods	24.62	8.13	18.25	649.44	9.87
Thaliaceans	9.23	8.37	10.43	173.54	2.64
Siphonophorans	11.54	4.78	5.1	114.03	1.73
Mysids	1.54	0.48	0.19	1.03	0.02
Amphipods	0.77	0.24	0.03	0.21	0.003

The scatter plots and bathymetric models (Fig. 4) showed clear differences between Alboran Sea and Balearic Islands in terms of overlap between juveniles and adults of *G. melastomus* and the other two species. This overlap was much more important in Alboran Sea than in Balearic Islands, where juveniles of *G. melastomus* dominated in most sampling stations. In this sense, juveniles of *G. melastomus* showed the highest abundances in 86% of all the sampling stations shallower than 660 m depth in which they appeared, whereas in Alboran Sea this percentage was reduced to 37%. Furthermore, in these sampling stations, the total abundance of individuals of small shark species (pooling *G. melastomus*, *G. atlanticus*, *S. canicula* and *E. spinax*) was higher in Alboran than in Balearic Islands (3797 ± 57 and 2364 ± 99 sharks/km^2, respectively; $t_{95} = 1.99$, $p<0.05$).

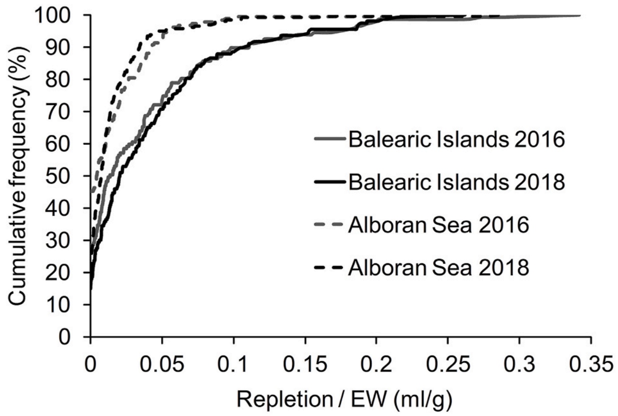

Fig. 2. Cumulative frequency curves of the ratio of repletion (ml) relative to eviscerated weight (g) of juveniles of *Galeus melastomus* by area and year.

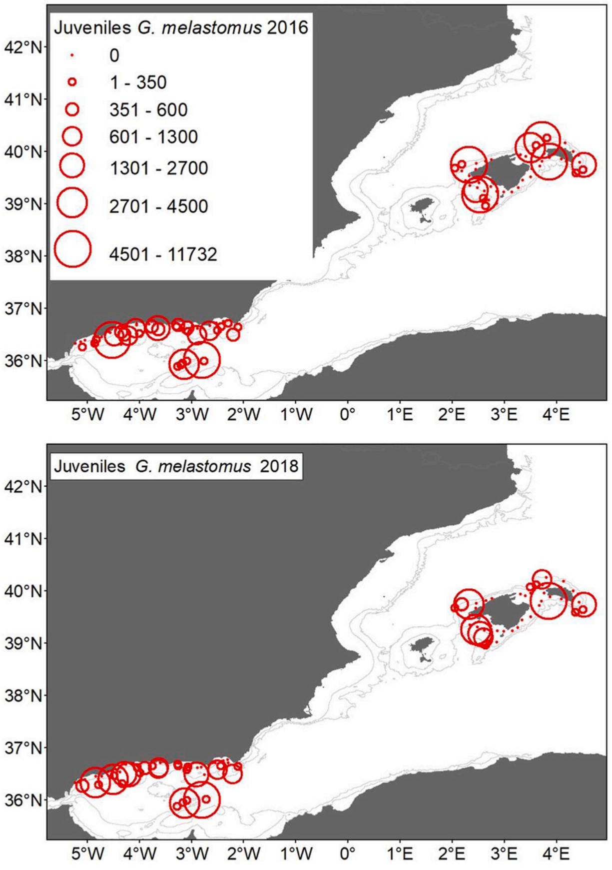

Fig. 3. Bubble maps of the abundance (individuals/km^2) of juveniles of *Galeus melastomus* observed in 2016 and 2018. The isobaths represent 200 and 800 m depth.

3.3. Fish condition

Bubble maps with mean values of individual K_n, HSI and DSI of *G. melastomus* showed that the majority of the lowest values were recorded in Alboran Sea (Fig. 5). The highest K_n and HSI values were recorded in Balearic Islands in 2018, whereas the highest values of DSI were recorded in Alboran Sea in 2016 (Fig. 5).

GAM models showed significant effects of area, year and abundance of juveniles of *G. melastomus* on these three condition indexes (Table 4). Fishing effort had significant effect only on K_n. Depth had a significant

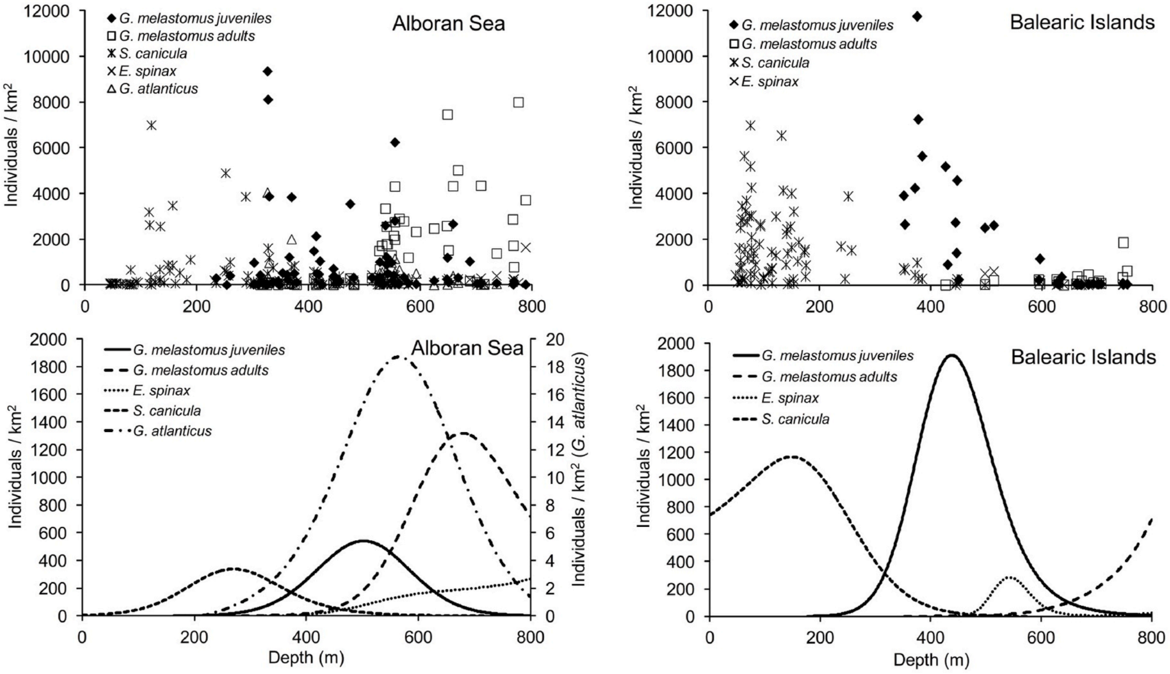

Fig. 4. Observed (top) and predicted (down) standardized abundance (individuals/km^2) by depth for juveniles and adults of *Galeus melastomus*, *Scyliorhinus canicula*, *Etmopterus spinax* and *Galeus atlanticus* in Alboran Sea (left) and Balearic Islands (right).

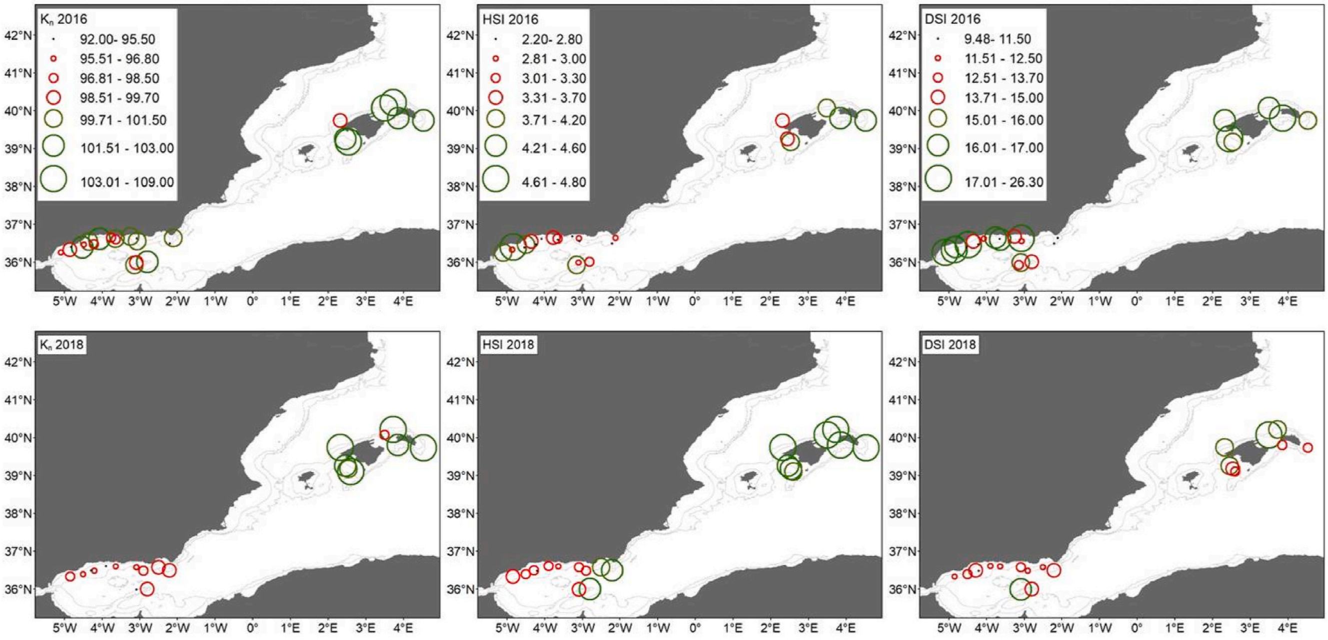

Fig. 5. Mean condition indices (K$_n$: Le Cren's relative condition factor, left; HSI: hepatosomatic index, middle; DSI: digestivosomatic index; right) values for juveniles of *Galeus melastomus*, estimated by sampling station and year (2016: top; 2018: down). The isobaths represent 200 and 800 m depth.

effect on HSI and DSI, but not on K$_n$. The highest percentage of deviance explained corresponded to HSI model, followed by K$_n$ and DSI, with values of 39, 15.3 and 8%, respectively (Table 4). The coefficient estimates (average predicted difference between the two levels of the categorical factor) for all three indexes showed that differences between areas were always due to higher values in Balearic Islands than in Alboran Sea (Table 4). Differences between years were due to lower values for K$_n$ and DSI in 2018 relative to 2016 and higher values for HSI in 2018 relative to 2016. The abundance of juveniles had a similar effect on K$_n$ and HSI, with both indexes increasing up to abundances between 6000 and 7000 individuals/km^2 and decreasing at higher abundances (Fig. 6). The trend was different for DSI, which showed a steep decreasing trend as abundance increased up to around 3000 individuals/km^2, with stabilization and also an increase in the 95% confidence intervals at higher abundances. K$_n$ showed a decreasing trend with increasing fishing effort. HSI and DSI showed a clear and similar decreasing trend towards deeper bottoms (Fig. 6).

Table 4

Summary of GAM models results considering the different condition indices for juveniles of *Galeus melastomus* (K_n: Le Cren's relative condition factor; HSI: hepatosomatic index; DSI: digestivosomatic index) as dependent variables and the smoothing terms, fishing effort (annual mean number of VMS signals), depth (D, in m) and standardized abundance of juveniles of *G. melastomus* (A, in individuals/km^2), and the categorical factors, geographic area (Alboran Sea and Balearic Islands) and year (2016 and 2018), as explanatory variables. The estimated degrees of freedom for each smoothing term, as well as the intercept and coefficient estimates (±standard error) for each categorical factor (corresponding to the levels Balearic Islands and 2018 for geographic area and year, respectively) are shown along with the significance level. DE: deviance explained (%); N: number of individuals. Significance levels are as follows: *: <0.05; **: <0.01; ***: <0.001; n.s.: not significant.

Index	Depth	VMS	A	Area	Year	Intercept	GCV	DE	N
K_n	n.s.	2.70**	2.83***	4.90 ± 0.4***	-1.12 ± 0.4**	98.87 ± 0.3***	41.9	15.3	1721
HSI	2.57***	n.s.	2.90***	1.24 ± 0.1***	0.95 ± 0.1***	2.83 ± 0.1***	0.1	38.9	1649
DSI	1.00***	n.s.	2.46*	2.48 ± 0.3***	-0.62 ± 0.3*	13.59 ± 0.2***	1.0	7.8	1625

3.4. Fishing effort

The spatial distribution of the bottom trawl fishing effort of the Alboran Sea and the Balearic Islands showed different bathymetric distribution patterns (Fig. 7). Whereas in the Alboran Sea major densities of VMS signals are found in the shallow shelf (50–100 m depth) and upper slope (200–500 m depth), in the Balearic Islands higher densities were found in the shallow shelf (50–100 m depth) and middle slope (500–800 m depth). The fishing effort on the upper slope is relatively homogeneous around both areas, but showing higher density values in the Alboran Sea. On the other hand, the fishing effort distribution on the middle slope of the Balearic Islands is distributed all around Mallorca and Menorca Islands, whereas in the Alboran Sea it concentrates in the Alboran Island and in front of Almeria Bay.

The mean total number of fishing trips per year in Alboran Sea is more than twice that in the Balearic Islands (23143 vs. 8746, respectively). In terms of percentage of fishing trips, the bottom trawl fleet in the Balearic Islands operates most of the days in the middle slope and shallow continental shelf, which account for 41 and 32% of the fishing days, respectively, whereas in Alboran Sea the effort is concentrated in the shallow shelf and upper slope, which account for 43 and 34% of the fishing days, respectively (Table 5). The total surface of all strata is similar in both areas, but the continental shelf is narrower in Alboran Sea than in Balearic Islands (2493 vs. 7504 km^2, respectively) whereas the opposite applies to the slope (9274 vs. 6101 km^2, respectively) (Table 5).

4. Discussion

Galeus melastomus is one of the dominant fish species in the slope bottoms of the western Mediterranean. The somatic condition of this shark has been compared between two highly contrasting areas of the western Mediterranean, in terms of primary production and different fishing footprints. We expected better condition, derived from higher food availability, in the most productive Alboran Sea than in Balearic Islands. However, the three condition indicators (K_n: Le Cren's relative condition factor; HSI: hepatosomatic index; DSI: digestivosomatic index) and the analyses of stomach contents of juveniles of *G. melastomus* evidenced the opposite pattern: better conditioned fish with enhanced diet were found in the Balearic Islands.

Depth showed a negative effect on both DSI and HSI, suggesting that food intake in juveniles is reduced with increasing depth, reducing in turn their reserves stored in the liver. This relation is expectable, because in the western Mediterranean the juveniles of *G. melastomus* have shown their preference for upper slope bottoms, tending to inhabit deeper bottoms as they grow (Massutí and Moranta 2003). This preference of the juveniles for upper slope bottoms also applies to the other two most common demersal shark species in the area, *Scyliorhinus canicula* and *Etmopterus spinax* (D'Onghia et al., 1995; Massutí and Moranta 2003; Ordines et al., 2011; Ramírez-Amaro et al., 2015). The potential role of the upper slope as an essential fish habitat where these species recruit is mediated, at least for *G. melastomus*, by a higher availability of food and hence healthier juvenile individuals than in deeper bottoms. However, depth did not show any effect on K_n. This may be related to the different nature of the HSI and K_n indices, the former being considered a more dynamic and sensitive measure of condition able to respond to short-term changes in feeding intensity and environmental conditions in both teleosts and sharks (Foster et al., 1993; Lambert and Dutil 1997; Hussey et al., 2009), and to the different patterns of response to density-dependent effects between these two indices and DSI. Whereas for K_n and HSI density only appear to have a negative effect on them at very high abundances of juveniles, for DSI, a negative correlation appears even at low abundances.

On the other hand, K_n was the only index affected by fishing effort. The lower sensibility of K_n to short-term changes in feeding intensity compared to HSI, may have allowed to detect the effects of long term regular stress induced by fishing activities. Similarly, the use of weight-at-length measures allowed detecting a negative effect of bottom trawling on the condition of plaice *Pleuronectes platessa* in an area of the Irish Sea showing a steep gradient of fishing effort (Hiddink et al., 2011). These authors attributed this effect to a bottom trawling induced reduction of the abundance of the main preys plaice feeds on, i.e. an indirect effect of bottom trawling caused by the impact on the ecosystem. However, our results showed that in *G. melastomus* the importance of benthic preys in the stomach contents is very low, suggesting other collateral effects of fishing could be involved. Trawling has been reported as the major driver of sediment resuspension and turbidity in muddy sedimentary bottoms at depths below the reach of storm waves (Martín et al., 2014). Although the effects the resuspended sediments on benthic communities have shown they cause benthic fauna smothering and prevent larvae settlement (Jones 1992 and references therein), their effect on demersal organisms has yet not been assessed. Whether these resuspended sediments influence the distribution of preys or the ability to find them by predators, it could negatively impact their condition.

Besides depth, fishing effort and density-dependent effects, area also showed a significant effect on the three condition indicators. Although in both areas the main preys in the diet of juveniles of *G. melastomus* were very similar within each of the exploited main taxonomic groups of feeding resources, the importance of these groups varied between areas. Teleosts, mainly Myctophidae, and cephalopods, which are high energetic prey items (Blaber and Bulman 1987; Madurell and Cartes 2005), were among the most important preys consumed in both areas, but the sum of %IRI of both groups was higher in Alboran Sea (60–63%) than in Balearic Islands (64% in 2016 and 40% in 2018). Hence, although better fish condition was expected in Alboran Sea due to diet composition, the contrary was observed. This can be explained by the fact that juvenile *G. melastomus* presented lower ratios of repletion in relation to their eviscerated weight and lower DSI values in Alboran Sea when compared to Balearic Islands.

The more reliable explanation is that even when diet composition should favor their better condition in Alboran Sea, this potential effect is taken away by the lower ingestion of food in this area compared to Balearic Islands. A lower abundance of preys in Alboran Sea than in Balearic Islands could explain the lower ingestion in the former area, but this is not a plausible hypothesis, due to the contrasting pattern of

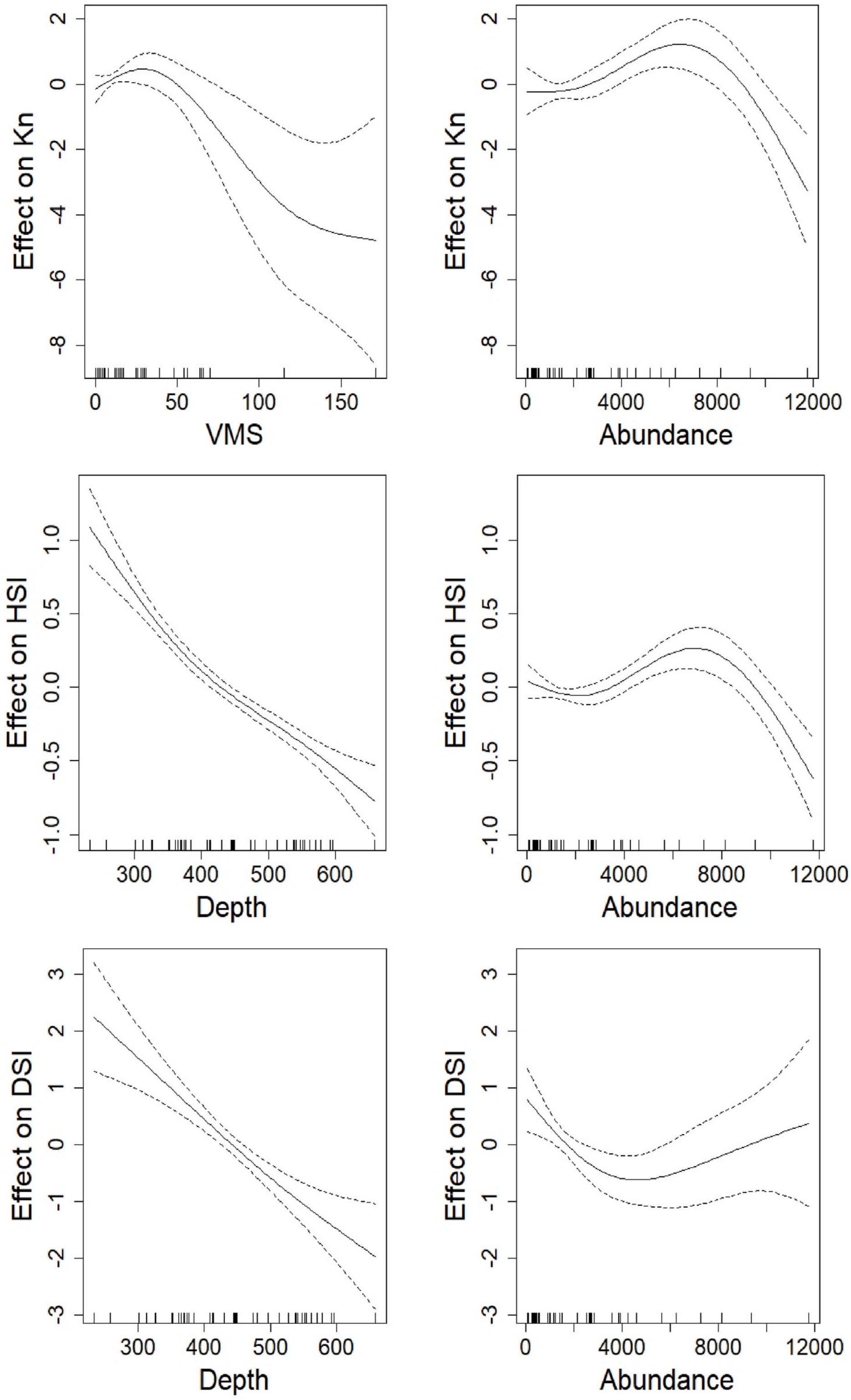

Fig. 6. GAM models showing the significant effects of the continuous predictors (fishing effort in number of annual satellite signals (VMS), depth in m, and standardized abundance of juveniles of *G. melastomus* in individuals/km^2) on the condition indices of juveniles of *Galeus melastomus* (K_n: Le Cren's relative condition factor, top; HSI: hepatosomatic index, middle; DSI: digestivosomatic index, down). The 95% confidence intervals are represented by dashed lines around the response curve (continuous line).

primary production between these areas (Bosc et al., 2004) and the nature of most preys for juvenile *G. melastomus*. These preys are mainly mesopelagic species, which undertake important vertical migrations to feed on preys belonging to low trophic levels close to primary producers near the surface (Foxton and Roe 1974; Andersen et al., 1998; Granata et al., 2001; Olivar et al., 2012; Saunders et al., 2019). The abundance of these preys should be favored by the highest productivity in Alboran Sea, which in turn should benefit deep water demersal fishes due to the highest availability of food. In fact, the abundance of *G. melastomus* in Alboran Sea is among the highest in the whole northern Mediterranean, pointing out this area represents a suitable habitat for the species (Bertrand et al., 2000; Farriols et al., 2019). However, we do not have suitable direct measures of abundance of the mesopelagic community in the two areas, which should be collected using other types of gears than the bottom trawl used in the present study, e.g. a midwater trawl (Olivar et al., 2012). Further studies of this community using suitable sampling

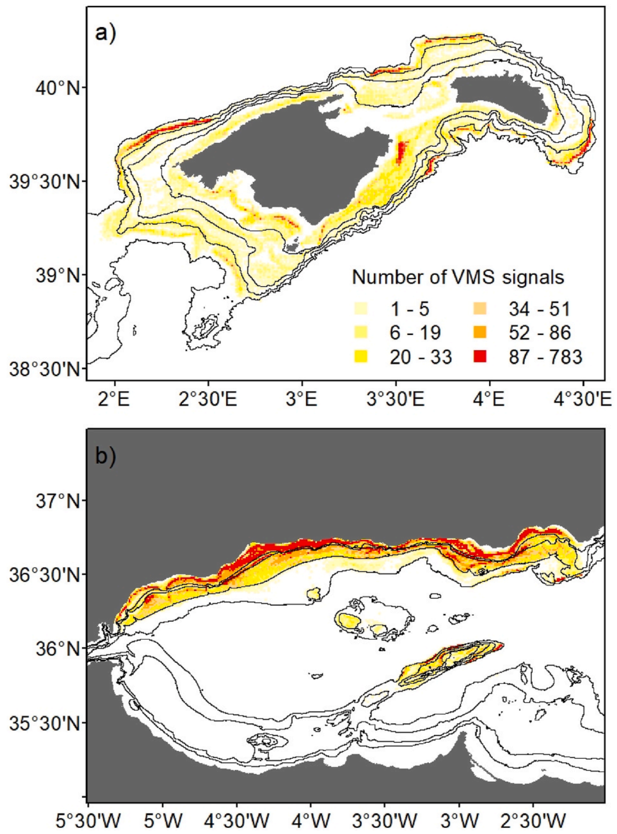

Fig. 7. Map of the study areas showing the density of Vessel Monitoring by Satellite System signals during the period 2016–2018 for: a) Balearic Islands; and b) Alboran Sea. The isobaths represent 100, 200, 500 and 800 m depth.

Table 5
Mean number and standard deviation of fishing trips (FT) per year and depth strata in each studied area during the period 2016–2018. The mean percentage (%) represented by the fishing trips in each stratum as well as the surface of each stratum in each area is also shown.

Area	Depth strata	Depth range (m)	Surface (km^2)	Mean FT	% FT
Alboran	Shallow shelf	50–100	1627	9939 (416)	42.9
	Deep shelf	100–200	866	3372 (86)	14.6
	Upper slope	200–500	3692	7777 (259)	33.6
	Middle slope	500–800	5582	2055 (237)	8.9
Balearic Islands	Shallow shelf	50–100	4125	2854 (204)	32.6
	Deep shelf	100–200	3378	957 (142)	10.9
	Upper slope	200–500	3043	1365 (125)	15.6
	Middle slope	500–800	3057	3570 (167)	40.8

methods could corroborate the expected relationship between productivity and abundance of the mesopelagic preys of *G. melastomus*.

Whether this relation exists, two variables intrinsically included within the factor area could explain the unexpected results of higher condition in the less productive area: the different degrees of overlap with intra- and inter-specific competitors, and the fishing impact. In the Balearic Islands, juveniles of *G. melastomus* occurred in a relatively narrow bathymetric range where the presence of adults was negligible and where it was the most abundant shark species. The opposite was observed in Alboran Sea, where in most samples where juveniles of *G. melastomus* occurred, these samples were dominated by adults of these species and the other demersal small sharks *S. canicula*, *E. spinax* and *G. atlanticus*. Moreover, in these samples the total abundance of individuals of small shark species was higher (38% on average) in Alboran than in Balearic Islands. The trophic niche overlap between *G. melastomus* and both *S. canicula* and *E. spinax* is considered to be high in the western Mediterranean, where the main prey items for adult and juvenile *G. melastomus* are also coincident (Macpherson 1980; Valls et al. 2011, 2017). Moreover, the present results report a similar diet composition for juvenile *G. melastomus* and *G. atlanticus*. Thus, the lower abundance of competitors in Balearic Islands, at least of shark species, seems the most plausible difference able to explain the higher condition of juveniles of *G. melastomus* in this area with respect to the most productive Alboran Sea.

Additionally, the different fishing effort levels in both areas may also play a role in these results. Elasmobranchs are particularly vulnerable to the effects of fishing activities, due to their K-selected life history strategy, which involve traits such as slow growth, late sexual maturity and low fecundity (Stevens et al., 2000). Our results show that the bottom trawl fishing effort level, in terms of fishing days, is 5.7 times higher on the upper slope of the Alboran Sea than in the Balearic Islands, although this bathymetric stratum has similar surface in both areas. On the contrary, the fishing effort on the middle slope is 1.7 times higher in Balearic Islands than in Alboran Sea, where the surface of this bathymetric stratum is twice that of the Balearic Islands. Moreover, while this fishing effort is ubiquitous along the upper slope of the Alboran Sea, in its middle slope it is restricted to the Alboran Island and an area off Almeria Bay, leaving the vast majority of this stratum practically pristine. By contrast, trawl fishing activity in the middle slope off Balearic Islands, which is narrow except south-western Mallorca, is widespread and covers most of the area (Farriols et al., 2017).

The abundance of *G. melastomus* in the upper slope off Balearic Islands is among the highest along the northern Mediterranean Sea, with higher values only detected in Alboran Sea and around Corsica (Farriols et al., 2019). However, our results showed a sharp decrease of its abundance in the middle slope, which was not observed in Alboran Sea, where the abundance of adults in the middle slope was comparable to that of juveniles in the upper slope. These differences are coincident with the different fishing effort pattern in both areas and may explain the higher overlap of juveniles and adults below 500 m depth in Alboran Sea. By contrast, this overlap was negligible in the Balearic Islands, where the adult population is reduced, due to the impact of the fishery targeting for *Aristeus antennatus* in the middle slope, the most important trawling activity in the area, in which *G. melastomus* is the main by-catch (Guijarro et al., 2012).

The link between primary production and fisheries production is well established for pelagic species, which feed directly on primary or secondary producers. This has been also observed in the Mediterranean and Black Sea, particularly in areas influenced by river runoff (Lloret et al., 2004; Banaru and Harmelin-Vivien 2009; Martin et al., 2012). Demersal fish communities have also been linked to primary production, with productive areas enhancing their biodiversity and fisheries production (e.g. Ware 1992; Solanki et al., 2003; Leathwick et al., 2006; Alemany et al., 2014). These positive relations should be mediated through processes that have an effect at individual level, such as more food availability and the subsequent fish condition improvement. While this cause-effect relation is well documented for pelagic fish feeding on primary producers or preys linked with them by few trophic links, such as small pelagic fishes (e.g. Shulman 1972; Basilone et al., 2006; Banaru and Harmelin-Vivien 2009; Véron et al., 2020), it is not so clear for demersal fishes, whose feeding resources are separated from primary production by a larger number of trophic links, and much less clear in the case of deep water ecosystems, where the energy transfer between pelagic and benthic habitats is even more complex (Baustian et al., 2014; Griffiths et al., 2017).

Alemany et al. (2014) found that the degree of spatial association of fishing resources with oceanographic fronts which enhanced primary production depends upon the trophic level of the fishing resource, the lower this trophic level the higher the association. This result illustrates quite well the problem when dealing to find links between primary production and demersal resources, which is expected to get more difficult when investigating, not just abundance but also condition at an individual level. Nevertheless, several works comparing the condition of individuals of species mainly distributed on the continental shelf from highly contrasting areas or distributed through large productivity gradients, consistently evidenced this relation. Shulman (1974) found a clear decreasing trend in the fat content of juveniles of *Mullus surmuletus*, from the northernmost area of the Adriatic Sea, its most productive area under the influence off Po runoff, to the southernmost Strait of Otranto. Lloret et al. (2005) found a higher lipid content in *Pagellus acarne* and *Pagellus erythrinus* from the Gulf of Lions, a highly productive area, when compared to a less productive adjacent area off Catalan coast. At a smaller spatial scale, in the Balearic Islands, higher condition based on both morphometric indicators and lipid content, has been detected in *Scorpaena notata*, *Serranus cabrilla* and *Chelidonichthys lastoviza* from areas with high benthic primary production, when compared to individuals living in sandy bottoms, with low algal biomass (Ordines et al. 2009, 2015).

Our results show the opposite situation for demersal small sharks inhabiting the slope of two contrasting areas of the western Mediterranean in terms of primary production. In the deep water ecosystems of Alboran Sea and the Balearic Islands, where their feeding resources are separated from surface productivity not only by a large number of trophic links, but also by the water column, the competition for food can act as the most important factor. The lower competition for food in the Balearic Islands involved higher amounts of ingested food in juveniles of *G. melastomus* and hence a better condition than in Alboran Sea, despite the latter is a more productive area. Expected results based on the environmental settings in both areas are taken away by the different levels they present regarding competition for food. Similarly, Möllmann et al. (2005) showed for small pelagic fishes, that their condition not only depended on the productivity of food in the ecosystem, but also on the inter- and intra-specific competition for food. In the western Mediterranean, Ordines et al. (2019) found an increasing condition trend for the recruits of European hake (*Merluccius merluccius*) off north-eastern Iberian Peninsula, where the species is subjected to high over-exploitation levels. This has been explained by climatic favorable conditions but, most importantly, the clear decreasing trend in recruitment, leading to a lower intra-specific competition for food.

The results of the present study highlight the utility of condition indices to study the health or fitness of sharks and the influence of biotic and abiotic factors on that fishes. The condition of *G. melastomus* has turned out to be dependent on complex inter-relationships among different factors, needing the combination of biological, ecological and fisheries knowledge to disentangle the underlying causes behind its variability. Our results also demonstrate that condition indices of deep sea sharks could be useful tools to assess deep sea ecosystems and their state of exploitation and conservation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The MEDITS surveys included in the present work have been co-funded by the Instituto Españolde Oceanografía and the European Union through the European Maritime and Fisheries Fund (EMFF) within the National Programme of collection, management and use of data in the fisheries sector and support for scientific advice regarding the Common Fisheries Policy. SRA is supported by a postdoctoral contract co-funded by the Regional Government of the Balearic Islands and the European Social Fund.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2021.103603.

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