Effect of intra-specific competition, surface chlorophyll and fishing on spatial variation of gadoid's body condition

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Abstract.   Fish condition indices can be used as biological indicators of the health of individuals and are influenced by numerous external and internal drivers. Like most essential biological traits, they are very sensitive to the spatial heterogeneity occurring in marine ecosystems, which appears at many observational scales. This brings out different ecological processes that can only be revealed either regionally or locally. The scale-dependent spatial variability concerns not only environmental factors, but also anthropogenic activities such as fishing. Understanding these relationships is crucial for improving the spatial management of marine resources, because fish condition considerably affects the sustainability of populations. We explore the influence of density-dependent (intra-specific competition) and density-independent variables (surface chlorophyll *a* concentration and fishing impact) on fish condition of three species of harvested gadoids (*Merluccius merluccius*, *Phycis blennoides* and *Micromesistius poutassou*) of the benthopelagic communities off the Balearic Islands (western Mediterranean). This area is characterized by high spatial heterogeneity in the environmental processes and fishing impact. Results show contrasting responses in body condition to the investigated covariates, with species-specific and ontogenetic differences sensitive to the spatial scale of analysis. Some of these responses occur at regional level, while others are more sensitive to local variation. Intra-specific competition shows a very clear effect, which depends on the ontogeny, identifying aggregation areas for recruits and limitation of resources for older individuals. Surface chlorophyll *a* has always a species-specific regional effect, despite gadoids have a more benthic behavior. Fishing effort displays a heterogeneous impact on fish condition. While spatially contrasting effects are observed at local scale, non-linear regional patterns occur, with positive effects of fishing pressure at intermediate levels. Models analyzing the influence of external drivers in essential fish biological traits such as body condition should consider the spatial variation in responses, especially in highly heterogeneous areas where anthropogenic activities occur. Failing to do so may hide local ecological processes that can be crucial for the persistence of fish populations, which is of paramount relevance for the regional assessment and spatial management of marine exploited resources.

Key words: environmental drivers; fish condition; fishing; habitat heterogeneity; local and regional effects; *Merluccius merluccius*; *Micromesistius poutassou*; ontogeny; *Phycis blennoides*; spatial scale; varying-coefficient models; western Mediterranean.

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INTRODUCTION

Fish condition indices measure the amount of energy stored within an individual, thus reflecting the health of the fish, because energy reserves have a direct influence on essential biological processes such as growth, reproduction and survival (Marshall and Frank 1999, Lloret et al. 2002). Therefore, fish condition is an important factor for the sustainability of harvested populations, which has clear implications for stock assessment and fisheries management as it can be considered an indicator of habitat quality (Lloret and Planes 2003, Lloret et al. 2014). Many studies have focused on identifying the environmental drivers that influence fish condition, but very few have addressed the spatial variation of such interactions (Casini et al. 2014), thus missing key ecological applications for assessment and management purposes due to the influence of the surrounding environmental and habitat conditions on fish health.

The spatial variability in ecological responses is often difficult to explore, because the interactions between the species and their surrounding environment are complex and change depending on the scale of analysis, that is, different observational scales bring out different aspects of such interactions (Huston 1999, Ciannelli et al. 2008, Bartolino et al. 2012). Recent efforts in marine systems have addressed the spatial effect of ecological responses by developing analytical techniques to detect scale-dependent processes on habitat selection (Bacheler et al. 2009, Bartolino et al. 2011, 2012, Ciannelli et al. 2012, Llope et al. 2012). Despite the cumulating evidence of contrasting local-scale effects on populations' abundance and biomass, the spatially variant responses of fish condition have, to our knowledge, not been investigated. This is of essential interest, because local effects of environmental drivers on fish condition that might be considered for assessment and management (Schindler et al. 2010, Rogers et al. 2011) could be ignored when searching for general responses at large scales. Thus, analytical techniques of fish condition may allow including both local and regional scale effects.

While numerous studies have demonstrated the regional influence of density-dependent and environmental variables on fish condition, comparatively fewer have investigated the potential effect of anthropogenic activities, such as fishing pressure (Appendix: Table A1). However, despite the regional density-dependent, environmental and anthropogenic influence on fish condition, general patterns are often elusive with contrasting responses observed between systems and species. This influence varies with the type of condition index analyzed (i.e., morphometric, physiological or biochemical index; Lloret et al. 2002), the species analyzed and the biogeographic location (Appendix: Table A1). For example, intra-specific competition has shown opposite influences on body condition, from positive (Orlova et al. 2010, Kjesbu et al. 2014) to negative (Casini et al. 2006, Sandeman et al. 2008) or not significant (Carscadden and Frank 2002, Kjesbu et al. 2014). The effect of surface chlorophyll a is often positive (Basilone et al. 2006, Rueda et al. 2014), though its influence is observed at different temporal lags (Hidalgo et al. 2008, Rueda et al. 2014). In addition, several authors described a negative effect of fishing on body condition (e.g., Choi et al. 2004, Hiddink et al. 2011, Lloret et al. 2014), whereas others have detected positive effects at low levels of fishing pressure (Giacalone et al. 2010) or absence of a statistical significant relationship (Lloret and Planes 2003, Giacalone et al. 2010).These contrasting effects prove the complexity of such interactions and suggest the necessity of addressing the influence of the density-dependent, environmental and anthropogenic drivers on body condition in an integrative manner.

Moreover, the sensitivity of fish condition to the aforementioned influence may vary across the lifespan of the species (Bartolino et al. 2011, Lloret et al. 2014). Indeed, ontogeny plays a crucial role in the allocation of the energy stored by individuals due to trade-offs between the main biological processes (e.g., changes in diet, foraging behavior or reproduction activity) resulting in inter- and intraspecific ontogenetic differences in fish condition (Gunderson 1997, Hidalgo et al. 2008). Thus, ontogeny may indirectly affect the sensitivity of fish condition to the external biological, environmental or anthropogenic drivers.

The purpose of the present study is to investigate both regional and local scale effects of density-dependent (intraspecific competition)

and density-independent variables (surface chlorophyll *a* concentration and fishing effort) influencing body condition of three species of gadoid fish harvested in the western Mediterranean: European hake (*Merluccius merluccius*), greater forkbeard (*Phycis blennoides*) and blue whiting (*Micromesistius poutassou*). We first hypothesize that the three species should display contrasting responses due to their differences in the bentho-pelagic behavior and their different sensitivity to the investigated drivers. In addition, we specifically expect to find density-dependent effects due to limitation of resources, a positive effect of chlorophyll concentration as a result of the trophic cascade and a negative effect of fishing effort. Due to the high hydrographic heterogeneity around the islands we also expect to find local sensitivity to these effects. Hence we apply spatially explicit models, which allow distinguishing both regional effects around the islands as well as the local changes in the responses. Finally, because the response of fish condition to external drivers depends on the ontogenetic stage, which have been reported for these species (Macpherson 1978, Massutí et al. 1996, Hidalgo et al. 2008), we have accounted for such ontogenetic variability by analyzing the investigated effects for each life history stage separately and, thus, being able to detect both regional and local processes across species and ontogeny.

Materials and Methods

Case study

Gadoids were collected during the annual Mediterranean bottom trawl surveys MEDITS developed from 2007 and 2012 around the waters off Majorca and Menorca (Balearic Islands), which are situated in the western Mediterranean (Fig. 1A). The waters around the Balearic Archipelago show a more pronounced oligotrophy than other areas in the western Mediterranean (Fig. 1B), due to the absence of nutrients supply from land runoff (Estrada, 1996). Its topography and oceanographic processes are complex, resulting in a spatial environmental variability, which has relevant ecological implications (Balbín et al. 2012) and affect the occurrence and abundance of harvested species, influencing the spatial and seasonal variation of fishing pressure (Fig. 1C).Technical specifications

regarding the MEDITS surveys are reported in Bertrand et al. (2002).

The selected species show contrasting life histories, habitat and trophic preferences. *Merluccius merluccius* and *Micromesistius poutassou* make daily vertical migrations moving off-bottom at night, whereas *Phycis blennoides* has a more demersal and benthic behavior. In addition, *M. merluccius* is more common at shallower waters, when compared with *M. poutassou* and *P. blennoides*. These characteristics affect the diet, with *P. blennoides* being a species mostly benthic feeder, while *M. poutassou* is more related to the pelagic realm. However, ontogenetic shifts in diet occur for these species, feeding on small crustaceans when they are recruits and switching to a predominantly ichtyophagous diet when reaching adulthood (Cohen et al. 1990, Massutí et al. 1996, Hidalgo et al. 2008).

Fish condition and intra-specific competition

For each species, the total weight and number of individuals captured by haul were collected. In addition, total length (TL) of each individual was measured to the lower half cm and weighted to the nearest 0.1 g. The relative condition index (K_n; Le Cren 1951) was used as a proxy of body condition. We used $\log W' = \log a + b \log TL$ to predict the weight at a given length. K_n for each individual was calculated as $K_{ni} = 100(W_i/W_i')$, where W_i is the actual weight and W_i' is the predicted weight. We computed the length-weight regression equations using ordinary least squares (OLS). As certain authors have addressed the inadequacy of the OLS methods, (Sokal and Rohlf 1995, Green 2001), we also used reduced major axis regression (RMA; Legendre and Legendre 1998) and tested for significant differences between both the regression methods.

The species were separated in ontogenetic stages (Table 1) for statistical analysis taking into account: the previous knowledge in the species life history, the sampled length frequency distributions and the mean ontogenetic pattern of K_n (Fig. 2). Differences in the energy allocation patterns among the species display contrasting species-specific strategies according to the ontogenetic stage. There is an increase in morphometric body condition of recruits and juveniles, who maximize body growth, except for *M. poutassou*, whose body condition is maximized
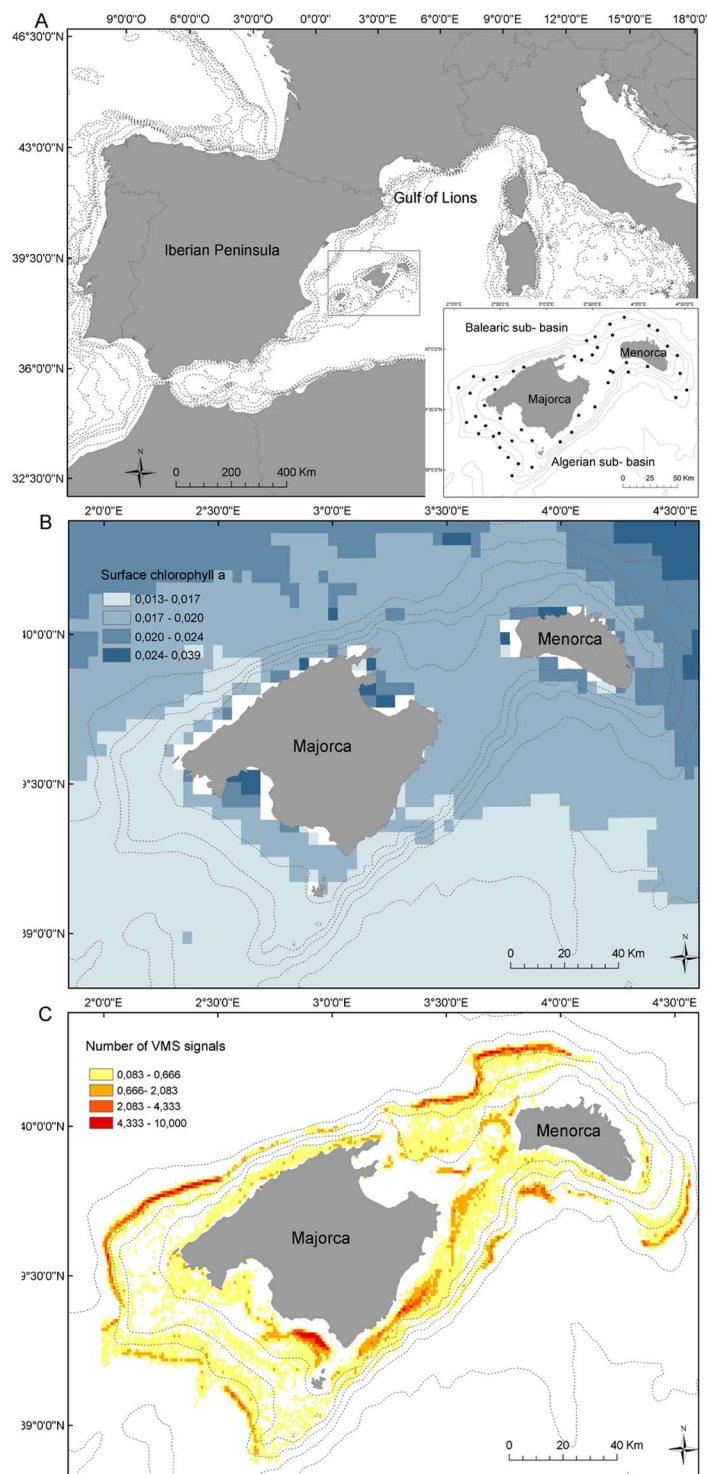
Fig. 1. (A) Balearic Islands (western Mediterranean Sea). Black dots represent the fixed stations conducted yearly during the MEDITS surveys. (B) Mean surface chlorophyll a concentration (mg/m^3) at 0.05 degrees spatial resolution. (C) Average number of signals of bottom trawl fishing effort in 2012 for a 1-km^2 grid, estimated from the vessel monitoring system (VMS).

Table 1. Final models of ontogenetic and species-specific effects on fish condition for *Merluccius merluccius*, *Phycis blennoides* and *Micromesistius poutassou*, captured during the MEDITS surveys between 2007 and 2012 around the Balearic Islands.

Species and size	Size range (TL, cm)	K_n	N	Model
M. merluccius†,‡				
Recruits	≤17.9	75.79–139.04	2694	s(TL) + s(lon, lat)log(d) + s(3m-ch) + s(lon, lat)12m-vms + s(lon, lat)
Juveniles	18–32.9	78.09–140.46	1542	s(TL) + s(3m-ch) + s(12m-vms) + s(lon, lat)
P. blennoides§				
Recruits	≤14.9	86.74–117.33	730	s(log(d) + s(3m-ch) + s(12m-vms)
Juveniles	14.9–32.9	74.17–122.67	561	s(TL) + s(3m-ch)) + s(12m-vms)
Adults	>32.9	74.16–118.56	52	s(log(d))
M. poutassou¶				
Recruits	≤18.9	85.32–119.01	240	s(TL) + s(log(d)) + s(lon, lat)6m-vms + s(lon, lat)
Adults	>18.9	69.65–155.07	920	s(TL) + log(d) + s(5m-ch)

Notes: TL: total length; K_n: relative condition index; N: number of individuals analyzed.
Size ranges derived from † Hidalgo et al. (2008); ‡ Cartes et al. (2009); § Cohen et al. (1990); ¶ Nadal (1983).

at the adult stage.

In order to explore intra-specific competition, the density per haul for each species and ontogenetic stage was calculated by dividing the total number of individuals of the same stage by the swept area of the haul (N/km^2).

Chlorophyll a data

Weekly average of sea surface chlorophyll *a* concentration (mg/m^3) at 0.05 degrees spatial resolution from the MODIS sensor were downloaded between 2007 and 2012 from the web site of NOAA CoastWatch Program and NASA's Goddard Space Flight Center (http://coastwatch. noaa.gov/). The average concentration of chlorophyll *a* for each haul within a 9 km radius circle was calculated to capture local variations in chlorophyll *a* among the different sampling stations. In order to explore the effect of time-lag of chlorophyll *a* on fish condition the mean concentration was computed for two months (1 February–31 March), three months (1 March–30 May) and five months (1 January–31 May). These averages included the highest annual peak in primary production corresponding to the spring bloom, which takes place between January and March in the area (Fernández de Puelles et al. 2007, Rueda et al. 2014).

Fishing impact

Fishing effort data were derived from the Vessel Monitoring System (VMS) records from 2007 to 2012 for the study area. We accounted only for VMS signals from bottom trawlers, as these species are mainly caught with this type of gear in the study area. Only signals with speed between 1.5 and 5.0 knots were included, which correctly identify fishing activity (e.g., Guijarro and Massutí 2006). In order to account for the effect of fishing effort intensity on body condition, we averaged the sum of signals for each haul within a 3 km radius circle. Due to the pronounced bathymetric gradient (Fig. 1A), hauls were assigned to different depth strata: inner shelf (<100 m), middle shelf (100–200 m), shelf edge (200–500 m) and upper slope (>500 m). These strata delineate contrasting demersal communities (Massutí and Reñones 2005), as well as bottom trawl fishing tactics related to the VMS data used (Palmer et al. 2009).

Because ontogenetic changes in habitat use related to depth are known for these species (Cohen et al. 1990, Massutí et al. 1996, Hidalgo et al. 2008), only VMS signals within the same bathymetric range were included in the monthly average per haul. To assess the degree of lasting fishing impact, we explored accumulated effects of effort intensity on fish condition in the longer scale (1 yr), calculating the annual mean of the monthly averages before the survey for each haul. To account for a potential recent impact at shorter scale, we calculated the mean over a half-year before the survey.

Statistical analysis

We applied generalized additive mixed models (GAMM) with a Gaussian distributed error. The response variable was the natural logarithm of the relative condition index, K_n. The 1% shortest and largest outliers in K_n for each species and
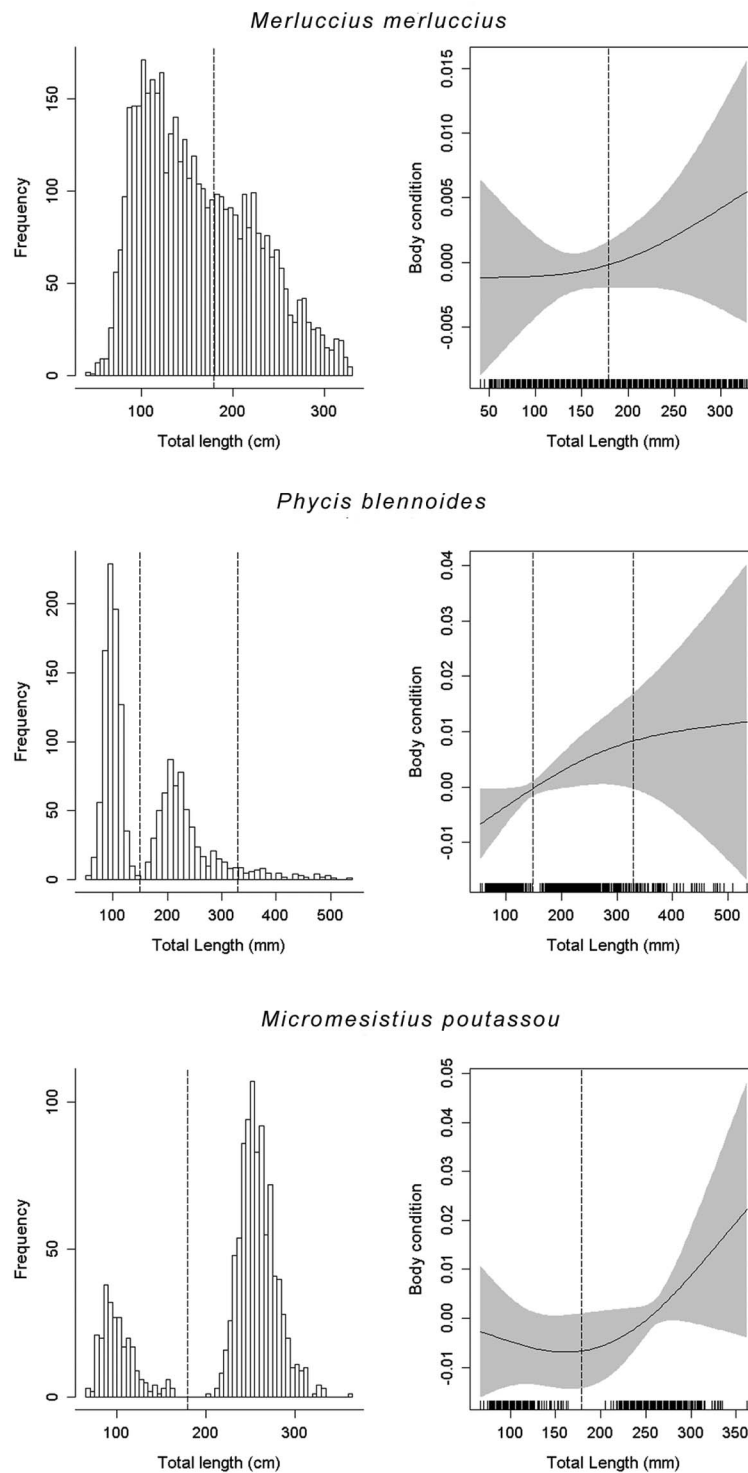
Fig. 2. Left: Length frequency distribution of individuals of *Merluccius merluccius, Phycis blennoides* and *Micromesistius poutassou*, captured during the 2007–2012 MEDITS surveys Right: Smoothed functions of body condition and total length. Dashed lines indicate the ontogenetic groups considered for analysis.

ontogenetic stage were excluded for the final analyses and hauls with less than 10 individuals of each species and ontogenetic stage were not considered. The explanatory variables were density (d) per haul, 2, 3 and 5 months chlorophyll *a* concentration means (hereafter 2m-ch, 3m-ch and 5m-ch, respectively) and half-year and annual fishing effort means (hereafter 6m-vms and 12m-vms, respectively). Total length was also included in the models as previous exploratory analysis showed a clear effect of length on body condition. Station was considered as random effect (Hiddink et al. 2011).

The analytical approach consisted of two steps. First, we developed *spatially invariant models*, where location (latitude and longitude) was incorporated in the best fully additive model by means of two-dimensional smoothing functions (Wood 2011). This formulation assumes that the effect of the explanatory variables on fish condition is invariant over space and thus allows capturing a regional pattern. And secondly, we used *spatially explicit models* to assess the potential spatially explicit effects of each of the covariates (i.e., local effects). In this case, latitude and longitude allow the effect of the explanatory variables to be spatially variant being able to capture local effects (e.g., Bartolino et al. 2012, Ciannelli et al. 2012). The advantage of these models is their ability to identify areas where body condition is expected to vary with an increase in the explanatory variables. Model selection strategy consisted of a forward selection to identify the best spatially invariant model.

Once we selected the best spatially invariant model, the spatially variant component was added to each explanatory variable of the best spatially invariant model alone as well as to all possible combinations of variables. The smoothing parameters were constrained to a basis dimension of three degrees of freedom. In all cases model selection was based on Akaike's information criterion (AIC) minimization as well as model diagnostics. Spatial autocorrelation was explored by means of variograms of residuals for each model (Zuur et al. 2009).

Statistical analyses were performed using the R version 3.0.2 (R Core Team 2013). GAMM models were implemented in the mgcv library (Wood 2011).

RESULTS

Gadoids were caught in 228 hauls conducted from 2007 to 2012 in 49 fixed stations in the study area (Fig. 1A). A total of 6739 individuals were measured and weighted (Table 1), being *Merluccius merluccius* the most abundant species, with 4236 individuals captured, followed by *Phycis blennoides* ($n = 1343$) and finally *Micromesistius poutassou* ($n = 1160$). We found no significant differences in the predicted values of the regression equations using OLS and RMA, hence condition indices were estimated from the predicted weight values of the OLS fitting.

Merluccius merluccius

The best model explaining the variations in K_n for small individuals included all the explanatory variables (density, chlorophyll *a* and fishing effort) and was spatially variant. That is, the model indicated spatial heterogeneity in body condition for the effect of density and fishing effort (Table 1, Fig. 3A). The local positive effect of density on body condition may indicate an aggregation effect generally observed in recruits in certain grounds around the islands. The best explanatory variable accounting for a regional effect of chlorophyll on condition was 3m-ch, which had a general positive but non-linear effect (Fig. 3A). 12m-vms showed a significant effect on fish condition with a clear latitudinal pattern (Fig. 3A). A positive effect was observed on the stations located on the north of the Islands whereas its effect on condition was negative in the south.

Juveniles had higher K_n values than recruits, evidencing the mentioned increase in body condition with ontogeny. The best model was spatially invariant with a non-linear regional effect of 3m-ch and a non-linear positive effect of 12m-vms (Table1, Fig. 3B).

Phycis blennoides

Recruit's body condition was determined by density, 3m-ch and 12m-vms and it showed a regional effect with no contrasting local patterns. The positive effect of density indicates the aggregation effect for recruits, which was not spatially recurrent due to the absence of a local effect. 3m-ch was also regionally homogeneous and positive while 12m-vms had a negative
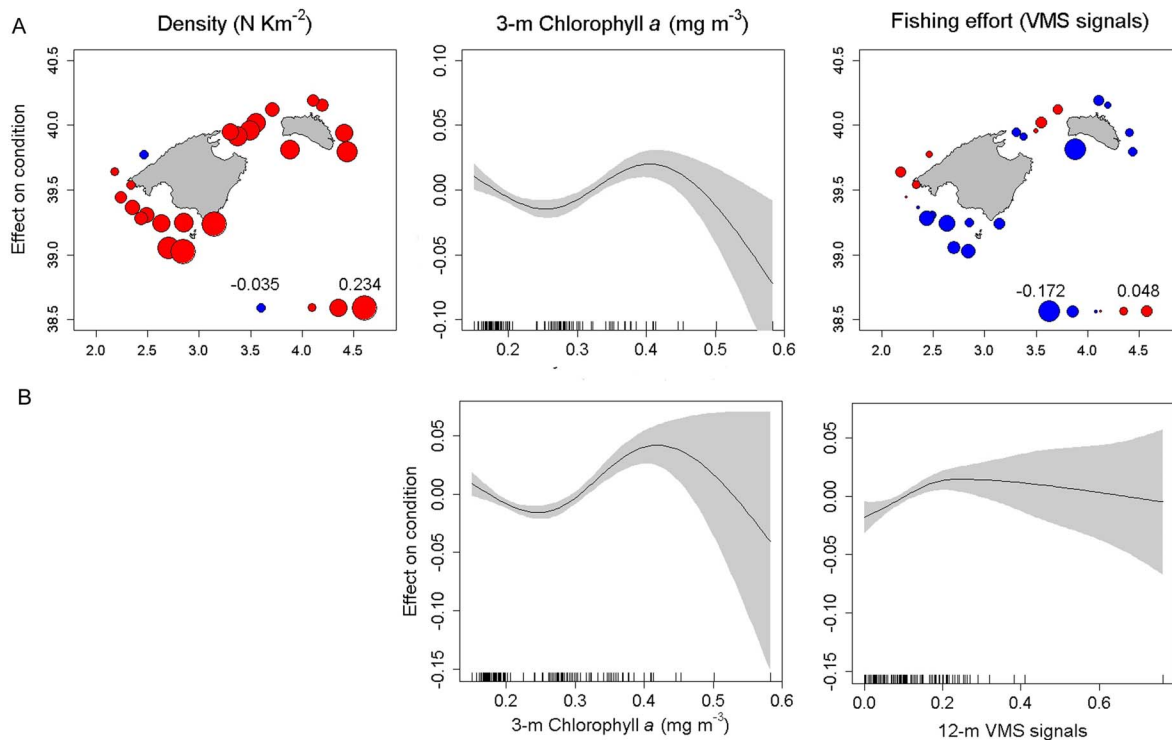
Fig. 3. Effects on body condition of the regional effects (spatially invariant) showed with smooth plots and local effects (spatially variant) showed with a map, included in the final model for (A) recruits and (B) juveniles of *Merluccius merluccius*. Shaded regions indicate the 95% confidence interval for the regional effects. Red and blue bubbles indicate an increase and decrease respectively in body condition for a unit increase of the explanatory variable with local effects.

regional effect on fish condition (Fig. 4A).

In juveniles, no significant local spatial effects were detected for the final response variables, which were 3m-ch and 12m-vms. K_n increased with increasing values of chlorophyll, stabilizing and slightly decreasing afterwards. On the contrary, it maximized at intermediate values of fishing effort and decreased afterwards (Fig. 4B).

Density was the unique significant variable explaining variations in body condition for adults (Fig. 4C), which decreased with increasing values in density, indicating plausible effects of intra-specific competition among adults.

Micromesistius poutassou

Density significantly influenced variations in K_n of recruits, which also increased with higher values of density. Fishing effort was also included in the final model, but recruits were more sensitive to recent impact (i.e., 6m-vms) rather

than annual accumulated impact. Moreover, our results suggest a spatial gradient in the response of K_n to this fishing pressure, with a negative effect in the stations located north of the Balearic Islands and positive in those further south (Fig. 5A).

Adults had, in general, higher condition than recruits. Final model displays a regional negative effect of density indicating intra-specific competition (Fig. 5B). 5m-ch showed a no linear effect on adult's body condition.

In all the models for any species and ontogenetic stage, residuals did not show spatial correlation.

Discussion

This study shows that body condition observed in harvested fish results from the combined influence, at both regional and local scale,
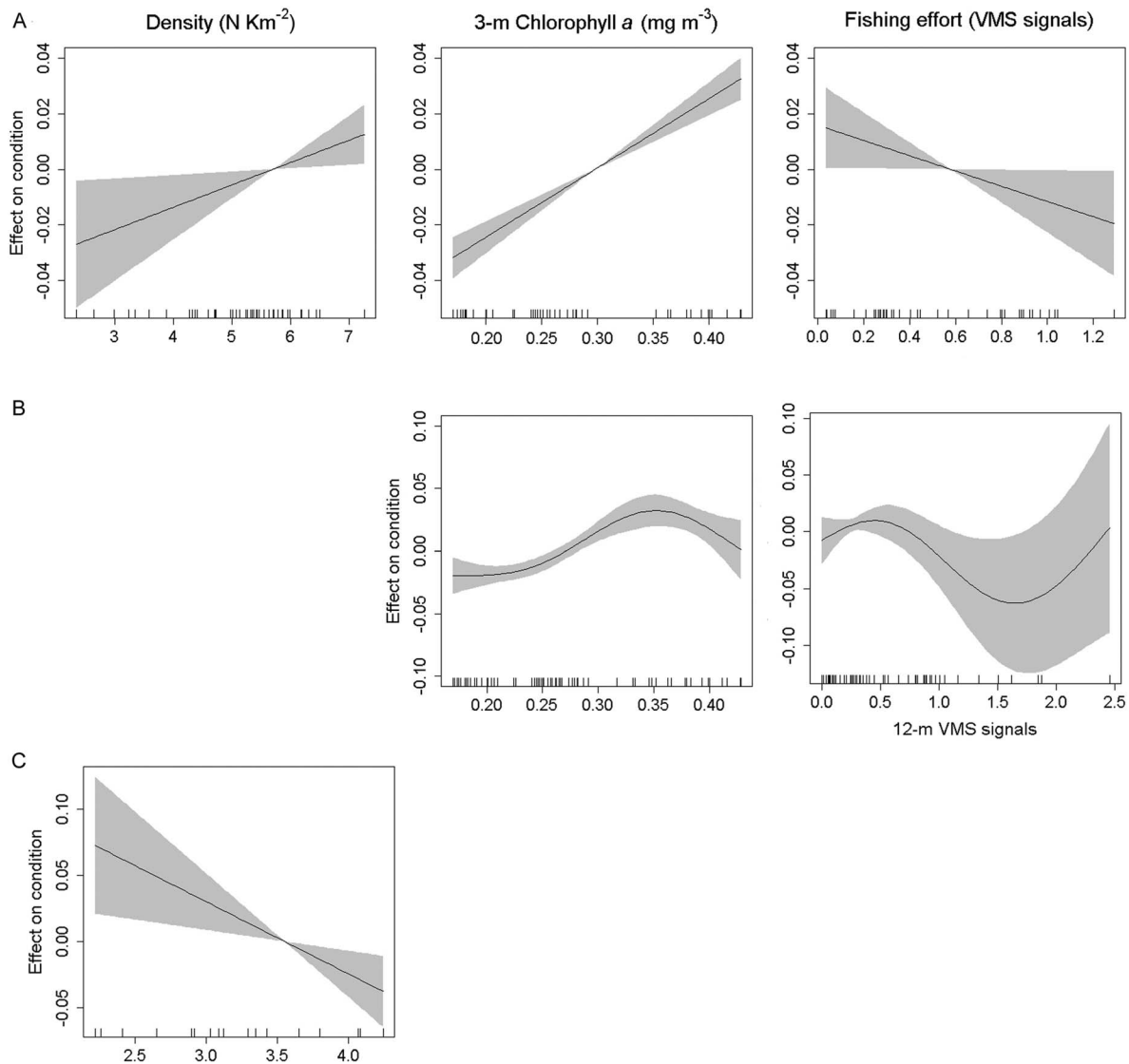
Fig. 4. Effects on body condition of the regional effects (spatially invariant) showed with smooth plots and local effects (spatially variant) showed with a map, included in the final model for (A) recruits, (B) juveniles and (C) adults of *Phycis blennoides*. Shaded regions indicate the 95% confidence interval for the regional effects. Red and blue bubbles indicate an increase and decrease respectively in body condition for a unit increase of the explanatory variable with local effects.

of population density, environmental features and fishing impact, being their effect highly dependent on the species-specific life history. Generally, the influence of intra-specific competition had a clear ontogenetic effect, detecting aggregation areas for recruits and limitation of resources for older individuals. Surface chlorophyll *a* displayed a general positive influence, highlighting its importance in an oligotrophic system even for those species with a benthic behavior. Fishing activity had opposite effects, being positive in some cases at intermediate levels of fishing pressure as well as negative in other species and ontogenetic stages. However, these drivers showed contrasting responses that varied depending on the species, location and ontogenetic stage of the individuals, being consistent with previous results from other areas.
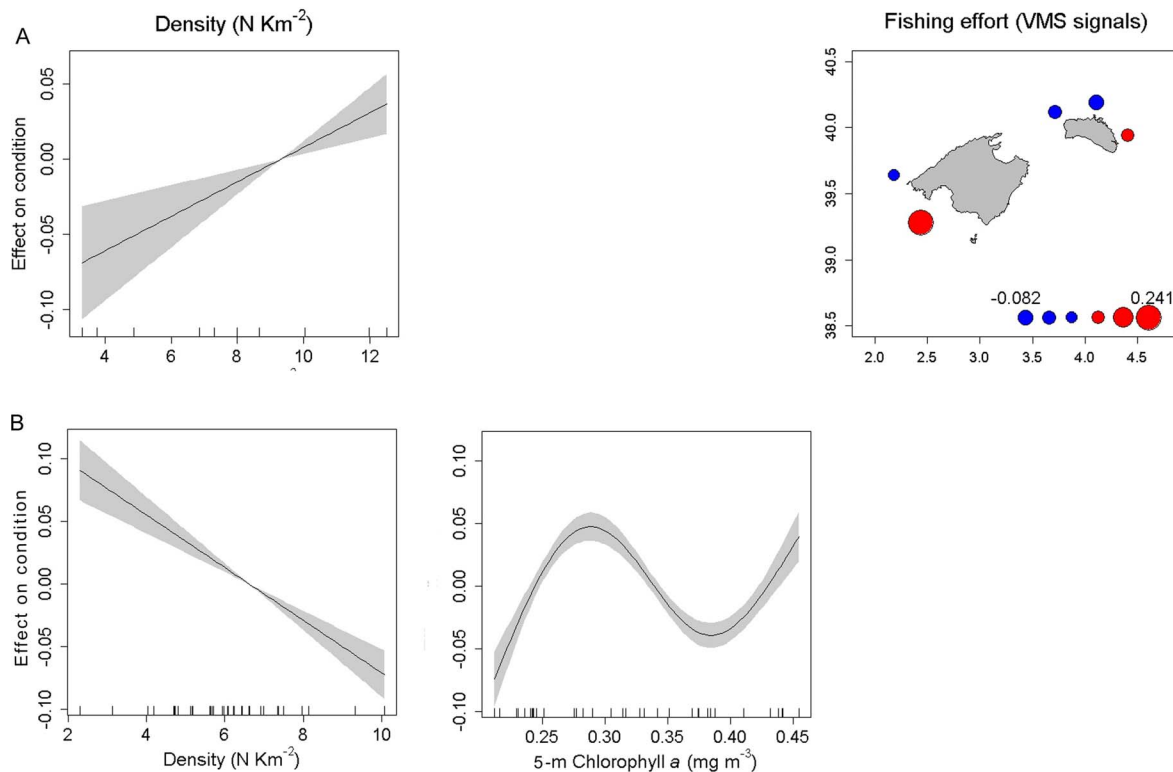
Fig. 5. Effects on body condition of the regional effects (spatially invariant) showed with smooth plots and local effects (spatially variant) showed with a map, included in the final model for (A) recruits and (B) adults of *Micromesistius poutassou*. Shaded regions indicate the 95% confidence interval for the regional effects. Red and blue bubbles indicate an increase and decrease respectively in body condition for a unit increase of the explanatory variable with local effects.

The more novel and relevant element of the study is the proved sensitivity of fish condition to both local and regional scale influence, evidencing the importance of including spatially explicit effects when investigating the impact of the environment variability and fishing on fish health.

The relationship between fish condition and total length revealed differences in the energy allocation pattern among the species with a clear ontogenetic component, which showed trade-offs between increments in age (i.e., body size) and energy storage (Sogard and Spencer 2004, Hidalgo et al. 2009). While *Merluccius merluccius* and *Phycis blennoides* invest energy in body weight from the very early recruit stage consistent with previous studies (Saborido-Rey and Kjesbu 2005), *Micromesistius poutassou* does not increase in body condition until they reach the juvenile

stage, which reveals a strategy to maximize length growth rather than weight to reduce the chance of being predated by maximizing swimming capacities (Payne et al. 2012). These ontogenetic differences in the trade-off in allocation of the surplus energy support that investigating the effect of density-dependent and density-independent mechanisms over different life-stages may veil the real contribution of these variables (e.g., Lloret et al. 2002, Sandeman et al. 2008).

Density-dependent variables such as intra- and inter-specific competition are local processes that affect the dynamics of species abundance and distribution (e.g., Huston 1999, Dingsør et al. 2007) and can have contrasting effects on condition (e.g., Orlova et al. 2010, Kjesbu et al. 2014). That is, competition can reduce fish condition via feeding rivalry (Casini et al. 2006,

Sandeman et al. 2008), but it can also be positively correlated if there is not food limitation and environmental conditions are adequate (Orlova et al. 2010, Kjesbu et al. 2014). Our study shows a consistent pattern in the effect of intraspecific competition for three species. Density was significant in the final models for recruits of the three gadoid species analyzed, either at the local or regional scale, indicating suitable areas of aggregation for recruits of these species in the study area. In case of *M. merluccius*, results are consistent with recent studies (Hidalgo et al. 2008, Colloca et al. 2015) that demonstrated the spatial heterogeneity in the recruitment process around the Balearic Archipelago. By contrast, adults were sensitive to negative density dependence effects with significant evidences of competition for resources in *P. blennoides* and *M. poutassou* at regional scale, which has been observed in other species (Casini et al. 2006, Sandeman et al. 2008). These results highlight the absence of limitation of resources around the islands for recruits.

Despite the influence of environmental factors and fish condition has been widely proved, few studies have accounted for the influence of surface chlorophyll *a* concentration (Appendix: Table A1). However, it played a key role on the body condition of gadoids analyzed, consistent with previous studies in the Mediterranean (e.g., Basilone et al. 2006, Rueda et al. 2014). Due to the high degree of oligotrophy in the Balearic Islands, chlorophyll *a* concentration had been proved to be crucial for the persistence of fish populations in the area with a high recruitment dependence on favorable trophic conditions in terms of fish survival and condition (Hidalgo et al. 2009). Here, we expand this relevance showing that its effect was generally species- and ontogenetic stage-specific. The effect was regional and generally positive even though it was not linear. The absence of local effects and the non-linearity can be explained by the high spatio-temporal (monthly and inter-annual) variability in chlorophyll values, though a general pattern of higher concentration is generally persistent in the north of the archipelago. In addition, interaction with other variables not considered here might explain the non-linear effect. The significance of chlorophyll proves a strong linkage between primary production and

the body condition of benthopelagic species such as gadoids. The effect of time-lag was clear, being the 3 months average chlorophyll *a* concentration the best variable representing such influence, consistent with previous studies in the area (Hidalgo et al. 2008). This time-lag would reflect the energy transfer efficiency of the trophic cascade, which depends on the complexity of the food web that vary at short scale in the Western Mediterranean (Fanelli et al. 2013).

The impact of trawling disturbance on the marine environment has been widely investigated, evidencing mostly negative effects from populations to ecosystems properties (e.g., Jennings et al. 2001, Kaiser et al. 2002, Hiddink et al. 2011, and references therein), including fish condition (e.g., Choi et al. 2004, Hiddink et al. 2011, Lloret et al. 2014). Conversely, positive effects of low levels of trawling have been either hypothesized (e.g., Rijnsdorp et al. 1991, Jennings et al. 2001, Daan et al. 2005) or proved (Hiddink et al. 2008, Giacalone et al. 2010, Walsh et al. 2012), mostly due to removal of the larger specimens and leading to three non-exclusive processes: (1) lower predation rates, resulting in higher benthic prey availability, (2) reduced competition among benthic fauna over food and space, which leads to increases in the production of the small benthos that fish feed on, and (3) proliferation of smaller, more productive benthic species ("farming the sea"). However, positive effects of low levels of fishing pressure on body condition by removal of intraspecific competitors (Giacalone et al. 2010) or predators (Walsh et al. 2012) were still very scarce. We here provide evidence of a regional positive influence on condition at intermediate levels of fishing impact for juveniles of *M. merluccius* and *P. blennoides*, suggesting the positive effect of intermediate levels of fishing-induced disturbance on fish condition (Daan et al. 2005, Hiddink et al. 2008, 2011, Giacalone et al. 2010). At these ontogenetic stages, these species are increasing their body condition by gaining weight (Fig. 2) and thus juveniles and young adults could be benefitting from reduced competition as well as the proliferation of benthic prey species. On the contrary, the effect of fishing effort on body condition of recruits of *P. blennoides* was negative, which could be explained by a reduction of their main prey as

observed in the recruitment grounds of other areas (Hiddink et al. 2011). Local effects of fishing effort on recruits of *M. merluccius* and *M. poutassou* present a consistent latitudinal gradient, with stations north and south of the Balearic Islands showing contrasting responses in body condition. Though a priori counter-intuitive due the opposed direction of the fishing impact in these two species, it suggests an identical pattern if one considers the contrasting energy allocation strategy of recruits of both species (Fig. 2). That is, positive effects of fishing effort on recruits of *M. merluccius* and negative on those of *M. poutassou* north off the Archipelago might be indicating a positive influence of the energy allocation strategy, growth in weight for the former and in length for the later. The most plausible explanation is that high levels of fishing removed recruits competitors in a small area where, at least, *M. merluccius* displays a high-specialized diet based on krill (Cartes et al. 2009).

In conclusion, the present study confirms the importance of targeting the spatial scales (or combination of scales) at which ecological processes and anthropogenic impacts occur. Species-environment interactions are complex, some of them happening at regional scales such as environmental gradients, while others being more sensitive to local variations (Huston 1999). Combining regional with local influence of variables has been proved as a powerful tool to investigate essential ecological processes such as survival, recruitment and trophic interactions (Bartolino et al. 2011, Hunsicker et al. 2013). Here, we take a step forward and prove the utility of this approach on fish condition, since local influence of the fishing impact and the environmental heterogeneity emerges in the gadoid species analyzed. This may have crucial implications for the conservation of marine living resources and the sustainability of fisheries, because fish condition is an important descriptor of the health of the fish that influences population viability (Marshall and Frank 1999, Lloret et al. 2014). Assuming regional responses can lead to incomplete conclusions, which could be relevant for the assessment and management of fish populations, especially in oligotrophic areas with high environmental heterogeneity and complexity such as the Balearic Islands. The

future challenge will be to implement this information on assessment and management schemes. For instance, spatial management measures such the protection of essential fish habitats will need to incorporate this information to properly account for the quality of marine habitats. Furthermore, standard procedures of stock assessment need to be implemented by including condition (Lloret et al. 2014) or life history (Hidalgo et al. 2014) information. Further ignoring the spatial heterogeneity offish health and the associated drivers will compromise the maintenance of population diversity and the natural complexity of marine ecosystems (Schindler et al. 2010), which are certainly a forefront goal for fisheries assessment and management.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Recent literature review (from year 2000 to present) of the effects of density-dependent, environmental and anthropogenic variables on different indices of fish condition and species. MI: Morphometric Index; PI: Physiological Index; BI: Biochemical Index (Lloret et al. 2002); n.s.: not significant.

Variables	Effect	Type of index	Species	Sources
Density dependence				
Intra-specific competition				
	n.s.	MI	*Mallotus villosus*	Carscadden and Frank 2002
	n.s.	PI	*Gadus morhua*	Kjesbu et al. 2014
	+	BI	*Mallotus villosus*	Orlova et al. 2010
	+	PI	*Gadus morhua*	Kjesbu et al. 2014
	−	MI	*Clupea harengus, Sprattus sprattus*	Casini et al. 2006, 2011
	−	PI	*Gadus morhua*	Sandeman et al. 2008
	−	MI	*Sprattus sprattus*	Casini et al. 2014
Inter-specific competition				
	−	MI	*Clupea harengus, Sprattus sprattus*	Casini et al. 2006, 2011
	−	MI	*Clupea harengus*	Casini et al. 2010
Environment				
Bottom temperature				
	+	MI	*Gadus morhua*	Lloret and Rätz 2000
	+	MI	*Gadus morhua*	Rätz and Lloret 2003
	+	MI	*Gadus morhua*	Pardoe et al. 2008, Pardoe and Marteinsdóttir 2009
	−	PI	*Gadus morhua*	Pardoe et al. 2008, Pardoe and Marteinsdóttir 2009
Water temperature				
	n.s.	MI	*Mallotus villosus*	Carscadden and Frank 2002
	n.s.	MI, BI	*Solea solea*	Amara et al. 2007
	s	PI	*Gadus morhua*	Kjesbu et al. 2014
	+	MI	*Clupea harengus, Sprattus sprattus*	Casini et al. 2011
Sea surface temperature				
	n.s.	MI	11 Demersal fish spp.	Rueda et al. 2014
	+	PI	*Engraulis encrasicolus*	Basilone et al. 2006
	−	BI	*Sardina pilchardus*	Rosa et al. 2010
Sea surface temperatura anomaly				
	n.s.	BI	*Mallotus villosus*	Orlova et al. 2010
			Merluccius gayi peruanus	Ballón et al. 2008
Surface chlorophyll *a*				
	+	MI, PI	*Engraulis encrasicolus*	Basilone et al. 2006
	+	MI	11 Demersal fish spp.	Rueda et al. 2014
Dissolved oxygen				
	+	MI	11 Demersal fish spp.	Rueda et al. 2014
Depth				
	n.s.	BI	*Mullus barbatus, Mullus surmuletus, Pagellus acarne, Pagellus erythrinus*	Lloret et al. 2005
	s	MI, PI	*Diplodus sargus*	Lloret and Planes 2003
	s	MI	*Merluccius merluccius*	Ferraton et al. 2007
	+	PI	*Gadus morhua*	Pardoe et al. 2008, Pardoe and Marteinsdóttir 2009
	−	MI, PI	10 Demersal fish spp.	Lloret et al. 2002

Table A1. Continued.

Variables	Effect	Type of index	Species	Sources
		BI	*Mullus barbatus, Mullus surmuletus, Pagellus acarne, Pagellus erythrinus*	Lloret et al. 2005
		MI	*Gadus morhua*	Pardoe et al. 2008, Pardoe and Marteinsdóttir 2009
Salinity				
	n.s.	MI, BI	*Solea solea*	Amara et al. 2007
	+	MI	*Clupea harengus, Sprattus sprattus*	Casini et al. 2006
	+	MI	*Clupea harengus*	Casini et al. 2010, 2011
	+	MI	11 Demersal fish spp.	Rueda et al. 2014
Potential density				
	n.s.	MI	11 Demersal fish spp.	Rueda et al. 2014
NAO index				
	n.s.	PI	*Gadus morhua*	Sandeman et al. 2008
	−	BI	*Mallotus villosus*	Orlova et al. 2010
	−	PI	*Gadus morhua*	Kjesbu et al. 2014
Ekman transport				
	+	BI	*Sardina pilchardus*	Rosa et al. 2010
Bottom type (rocky habitat)				
	+	MI, PI	*Diplodus sargus*	Lloret and Planes 2003
Algal biomass				
	+	MI	*Scorpaena notata*	Ordines et al. 2009
Prey availability				
	n.s.	MI, BI	*Solea solea*	Amara et al. 2007
	n.s.	MI	11 Demersal fish spp.	Rueda et al. 2014
	+	MI	*Sprattus sprattus phalericus*	Shulman et al. 2005
	+	MI	*Clupea harengus, Sprattus sprattus*	Casini et al. 2006
	+	BI	*Mullus barbatus*	Lloret et al. 2007
	+	PI	*Gadus morhua*	Sandeman et al. 2008
	+	MI, PI	*Merluccius merluccius*	Hidalgo et al. 2008, 2009
	+	MI, PI	*Gadus morhua*	Pardoe et al. 2008, Pardoe and Marteinsdóttir 2009
	+	MI	*Pleuronectes platessa, Limanda limanda, Merlangius merlangius*	Hiddink et al. 2011
Prey availability				
	+	MI	11 Demersal fish spp.	Rueda et al. 2014
Type/quality of prey				
	s	MI, PI	*Gadus morhua*	Rideout and Rose 2006
Stomach content				
	+	MI, PI	*Gadus morhua*	Pardoe et al. 2008
	+	PI	*Gadus morhua*	Sandeman et al. 2008
Parasitic infection				
	n.s.	MI, BI	*Solea solea*	Durieux et al. 2007
River run-off				
	n.s.	BI	*Mullus barbatus*	Lloret et al. 2007
Fishing impact				
Protected area (no fishing)				
	n.s.	MI, PI	*Diplodus sargus*	Lloret and Planes 2003
	+	MI, PI	*Diplodus sargus*	Lloret and Planes 2003
	+	BI	*Diplodus sargus*	Lloret et al. 2005
Fishing effort				
	n.s.	MI	*Mullus barbatus, Merluccius merluccius*	Giacalone et al. 2010
	+	MI	*Mullus barbatus, Merluccius merluccius*	Giacalone et al. 2010
		MI, PI	5 reef-fish spp.	Walsh et al. 2012
	−	MI	*Groundfish spp.*	Choi et al. 2004
	−	BI	*Mullus barbatus*	Lloret et al. 2007
	−	MI	*Pleuronectes platessa, Limanda limanda, Merlangius merlangius*	Hiddink et al. 2011
Sediment contaminants				
	−	MI, BI	*Solea solea*	Amara et al. 2007