ICES Journal of Marine Science, 59: 1215–1227. 2002
doi:10.1006/jmsc.2002.1294, available online at http://www.idealibrary.com on IDEAL®

Effects of large-scale habitat variability on condition of demersal exploited fish in the north-western Mediterranean

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Lloret, J., Gil de Sola, L., Souplet, A., and Galzin, R. 2002. Effects of large-scale habitat variability on condition of demersal exploited fish in the north-western Mediterranean. – ICES Journal of Marine Science, 59: 1215–1227.

We examine the variation in condition of ten exploited fish species as an indicator of large-scale habitat quality in the north-western Mediterranean. To determine fish condition, we used morphometric (Fulton's K) and physiological (hepatosomatic, HSI; digestivesomatic, DSI; and gonadosomatic, GSI) indices. Generalized linear models (GLMs) were applied to assess the influence of depth, latitude, length, year, sex and reproductive status on condition. The GLMs incorporating all independent variables accounted for between 25 and 74% of the variance in Fulton's K condition factor, 15–77% of the variance in HSI, 14–35% of the variance in DSI, and 77% of the variance in GSI. The mean condition factor of the species studied showed considerable interannual fluctuations along with an increasing trend over the time series (1994–2001). Length is an important explanatory variable in explaining condition of fish species. Condition typically increased with fish length and explained 72% of the deviance in GSI of *M. barbatus.* For some species, there were differences in condition due to sex and reproductive status, with adults being usually better in condition than juveniles and, among adults, females better than males. The influence of latitude and depth on condition of a given species varied according to the index used to assess condition. When there was a significant effect, fish with the highest condition factor, HSI and/or DSI inhabited the shallowest and northernmost parts of the area of study. Considering that condition influences growth, reproduction and survival of fish, our results support the importance of shallow habitats to productivity of demersal stocks in the Mediterranean Sea.

Keywords: Mediterranean, habitat, spatial and bathymetric variability, fish condition, Fulton's K condition factor, hepatosomatic index, gonadosomatic index, digestivesomatic index.

Received 16 February 2002; accepted 9 July 2002.

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Introduction

Despite evidence of important ecological linkages between habitat and fishery production, the management of most commercial resources world-wide has historically concentrated on assessing stock size and controlling fishing mortality (Benaka, 1999). However, the conservation and management of fishery habitat is becoming an important fishery management tool (Fogarty, 1999; Minello, 1999). According to this, a key element in moving toward sustainable fisheries is the identification of essential fish habitats, i.e. high quality habitats for fish species (Benaka, 1999). Many studies have addressed the role of key ecological communities in coastal waters and estuaries such as seagrass beds and rocky-algal reefs as essential spawning and nursery habitats for commercially and recreationally marine species (see e.g. Able, 1999; Minello, 1999; Packer and Hoff, 1999). In addition to this, juveniles of many demersal species occur predominantly within the inshore

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soft bottoms along the coast (Dalley and Anderson, 1997; Bertrand *et al.*, 1999), where some ecological processes that enhance their survivorship takes place (Kaiser *et al.*, 1999). Accordingly, much of the essential marine fish habitat of concern is in shallow coastal waters and estuarine wetlands, even though some deep habitats such as rocky submarine canyons may constitute natural refuges for large individuals of some demersal species (Yoklavich *et al.*, 1999).

Condition or health is a particular important attribute of fishes and future population success because it has a large influence on growth, reproduction and survival (Krivobok and Tokareva, 1972; Love, 1974; Kjesbu *et al.*, 1992; Lambert and Dutil, 1997; Adams, 1999; Marshall and Frank, 1999; Marshall *et al.*, 1999; Shulman and Love, 1999; Lambert and Dutil, 2000). The condition of a fish is a measure of physical and biological circumstances during some previous period, and is affected by interactions among food availability, physical factors, parasitic infections, and the physiology of the fish (Love, 1974; Parrish and Mallicoate, 1995; Francis, 1997; Shulman and Love, 1999; Lee and Khan, 2000; Lloret and Rätz, 2000; Yaragina and Marshall, 2000; Okuda, 2001). The condition of fishes can be assessed by a variety of criteria ranging from morphometric (weight–length) and physiological (liver and gonad weights) measures to biochemical measures such as lipid or protein content. Lipid storage and dynamics within the organism, however, are a particular important feature of fish condition (Adams, 1999). In many benthic and demersal fishes the main reserve of fat is stored in liver (Schulman and Love, 1999). Therefore, physiological and biochemical measures such as the hepatosomatic index and the fish fatness are accurate measures of the energy reserves of fish (Adams, 1999; Shulman and Love, 1999). Morphometric indices, which assume that heavier fish of a given length are in better condition, are simple indicators of energy storage, even though they are used reiteratively because they are constructed with simple weight and length data.

Different populations display different levels of condition according to the characteristics of their habitats such as food availability or environmental conditions (De Silva *et al.*, 1998; Lee and Khan, 2000; Vila-Gispert and Moreno-Amich, 2001; Rätz and Lloret, 2002). The quality of a given habitat has been shown to be related to fish population's conditions in freshwater ecosystems, i.e. the higher the quality of the habitat, the higher the fish condition (De Silva *et al.*, 1998; FitzGerald *et al.*, 1998; Vila-Gispert and Moreno-Amich, 2001). Fish condition has seldom been used to assess habitat quality in marine ecosystems, where most of research dealt with differences in abundance and biomass between habitats (see e.g. Benaka, 1999). Few studies have examined the geographic and bathymetric differences in condition of marine fishes (e.g. Love, 1974; Grecay and Targett, 1996; Brodeur *et al.*, 2000; Lee and Khan, 2000; Chouinard and Swain, 2001; Rätz and Lloret, 2002). Apart from the Black Sea, where physiological and biochemical indicators are widely applied in the assessment of commercial fish stocks (Shulman and Love, 1999), research on fish condition in the Mediterranean Sea has been conducted sporadically (e.g. Shulman, 1972). Recently, condition of some coastal species in the north-western Mediterranean has been documented (Mosconi and Chauvet, 1990; Planes *et al.*, 1997). Apart from these studies on wild fish, there are numerous studies on condition of reared fish for pisciculture purposes (e.g. Eisawy and Wassef, 1984).

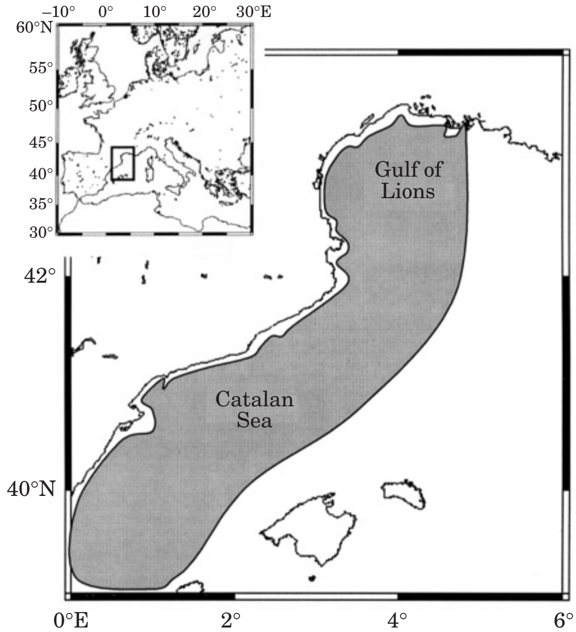

Figure 1. Map of the study area (shadowed): the soft bottoms of the Gulf of Lions and the Catalan Sea platforms (NW Mediterranean).

The purpose of this paper is to examine bathymetric and spatial variation in condition of ten exploited fish species. Condition will be used as an indicator of large-scale habitat quality in the north-western Mediterranean. Interspecific, interannual, sexual and size variability in condition are considered too because condition of many fish species changes from year to year and tends to increase with age/length (Lilly, 1996; Shulman and Love, 1999; Lloret and Rätz, 2000). This study was conducted at two areas showing marked differences in productivity: the Gulf of Lions and the Catalan Sea (Figure 1). The Gulf of Lions, situated at the western and northernmost part of the Mediterranean, is one of the most productive areas of the Mediterranean Sea owing to a number of hydrographic features, including a wide shelf, river run-off, strong vertical mixing in winter, and occasional coastal upwelling. The Catalan Sea, located south of the Gulf of Lions, has a lower productivity (Ben-Tuvia, 1983; Champalbert, 1996; Estrada, 1996). Because there is also a decreasing trend in productivity with depth, deeper areas of distribution of a given species may represent a marginal habitat in terms of food resources (Chouinard and Swain, 2001).

Materials and methods

Weight and length measurements of individual fish were derived from European Union groundfish surveys ("MEDITS" program) covering the soft bottoms of the shelf and the continental slope of the western Mediterranean. The surveys, which were performed in spring, started in 1994, and followed the technical specifications given in Bertrand *et al.* (1997). Total length (cm) and total (whole body) weight ($\pm$0.01 g) of all individuals in the catch were measured in the period 1994–2001. For analysis, we selected data of individuals measuring more than 10 cm of ten important demersal fish species of the western Mediterranean: *Lophius budegassa, Lophius piscatorius, Merluccius merluccius, Micromesistius poutassou, Phycis blennoides, Trisopterus minutus capelanus, Mullus barbatus, Mullus surmuletus, Pagellus acarne* and *Pagellus erythrinus.* The first six species are demersal offshore species that inhabit relatively deep waters (typically down to 500–900 m), while the other four species can be considered as demersal inshore species that inhabit down to 300–500 m. Individuals were classified as juveniles and adults. Adults were classified according to sex (males/females) and reproductive status (maturing, spawning and post-spawning/resting). Sex and reproductive status were combined into a single categorical variable that considered the following groups: juveniles, maturing males, maturing females, spawning males, spawning females, post-spawning/resting males and post-spawning/resting females. While *M. barbatus* was spawning during the yearly sampling, *P. acarne* and *P. erythrinus* were maturing. The rest of the species (*L. budegassa, L. piscatorius, M. merluccius, M. poutassou, M. surmuletus, P. blennoides* and *T. minutus capelanus*) were in the post-spawning/resting stage. Because data were collected during the same season (spring) year after year, the seasonality in condition of any given species due to reproductive and feeding cycles was not considered for the analyses. Juveniles of *M. barbatus* were disregarded in the analyses because the low number of samples collected. Morphometric data in 1994 lacked for the following species: *M. barbatus, P. acarne, P. erythrinus, P. blennoides* and *T. minutus capelanus*. During the 2000 and 2001 surveys, livers of *L. budegassa, M. merluccius, M. barbatus, M. surmuletus, P. acarne and P. erythrinus* were sampled, the digestive tracts (stomach + intestine + food content) of the last four species were weighted and gonad weights of female spawners of *M. barbatus* were recorded. Additionally, we collected data in spring 2000 and 2001 on board fishing vessels and during experimental trawls in shallow soft bottoms down to 60 m (same measurements, methodology and species as before). All data was combined together to cover a wide range of depths (15 m–800 m) and latitudes (39°N–43°N) within the study area.

To investigate the variation of condition with latitude, depth, year, sex and reproductive status, generalized linear models (GLMs; McCullagh and Nelder, 1989) were used. To determine fish condition, we used both morphometric and physiological data. Morphometric measures were based on the analysis of length-weight data collected during 1994–2001. We computed the Fulton's K condition factor with the formula $K = 100(W/L^3)$, where W is the total weight and L is the total length. The stated formula, with the constant = 3, assumes an isometric growth in fish (i.e., the b-value of the weight–length relationship must be close to 3). However, this is often not the case, and there appear correlations between the condition factor and length (Bolger and Connolly, 1989; Cone, 1989). The b-parameters computed from the weight–length relationships of the 10 species studied are close but not exactly 3 (Table 1). A way to avoid the problems that this could create is to compare populations with similar length structures only. However, as for many other demersal species, bathymetric and spatial distribution of the species studied is related to length and age (Relini *et al.*, 1999; Gil de Sola *et al.*, 2001). For the GLMs, we took condition factor (K) as the response variable; year and the sex/reproductive status as categorical predictor variables and depth, latitude and fish length as continuous predictor variables. The following GLM was therefore used:

$$K = \mu + Y + S + D + G + L$$

where K is the Fulton's condition factor, μ is the intercept, Y is the effect of the year (1994–2001), S is the effect of sex and reproductive status combined, D is the effect of depth, G is the effect of latitude and L is the effect of fish length. Because the present paper concentrates on the primary impact of the factors influence condition, we will not consider interactions between explanatory variables. The GLM was performed by species in order to observe the effect of the same factors (year, sex, depth, latitude and length) in each of the ten species. K frequencies of *L. piscatorius, P. acarne* and *P. blennoides* were skewed to the left and followed a gamma distribution function (K-S test, $p > 0.05$), which were used explicitly in the GLMs. K frequencies for the rest of species were normally distributed. Identity-link

Table 1. Parameters of the weight–length relationships for the species studied in the NW Mediterranean (all data together, 1994–2001).

Species	b	a	r^2	n
Lophius budegassa	2.844	− 3.772	0.984	559
Lophius piscatorius	2.923	− 3.958	0.993	251
Merluccius merluccius	3.216	− 5.605	0.987	3663
Micromesistius poutassou	3.228	− 5.732	0.991	1504
Mullus barbatus	3.360	− 5.534	0.960	3387
Mullus surmuletus	3.190	− 5.006	0.970	489
Pagellus acarne	3.231	− 5.020	0.966	1083
Pagellus erythrinus	2.961	− 4.263	0.983	790
Phycis blennoides	3.230	− 5.668	0.994	850
Trisopterus minutus capelanus	3.209	− 5.564	0.981	849

functions were used to relate the condition indices to the predictors. Analysis of deviance to evaluate the significance (F-test) of the factors in the model was performed by a stepwise procedure. The final models were checked through inspection of the scatterplots showing he relationships between residuals and predicted values and the histograms of residuals.

Two physiological indices were considered to evaluate the condition of *M. barbatus, M. surmuletus, P. acarne and P. erythrinus* during 2000 and 2001: a liver index (hepatosomatic index, HSI) and a digestive index (digestivesomatic index, DSI). We also computed the HSI of *L. budegassa* and *M. merluccius*, and a gonad index (gonadosomatic index, GSI) for females of *M. barbatus*.

The HSI, DSI and GSI were calculated as:

$$HSI = 100(LW/W)$$

$$DSI = 100(DW/W)$$

$$GSI = 100(GW/W)$$

where LW, DW, GW and W represent liver, digestive tract (stomach + intestine + food content), ovary and somatic (eviscerated) weights, respectively. We pooled data from 2000 and 2001 because there were not significant differences in these indices between both years. HSI, DSI and GSI frequencies were skewed to the left and followed a gamma distribution function (K-S test, $p > 0.05$), which were used explicitly in the GLMs.

The following generalized linear models were therefore used:

$$HSI = \mu + S + D + G + L$$

$$DSI = \mu + S + D + G + L$$

$$GSI = \mu + D + G + L$$

where μ is the intercept, S is the effect of sex and reproductive status combined, D is the effect of depth, G is the effect of latitude and L is the effect of fish length.

Results

Weight–length measure: Fulton's K condition factor

The GLMs incorporating all independent variables explained between 25% (*L. piscatorius*) and 74% (*T. minutus capelanus*) of the deviance of condition factor (Table 2). There was a significant relationship between length and condition factor that accounted for 1–45% of the deviance in condition factor (Table 2). Condition factor was positively related to length with the exception of *L. budegassa*, *L piscatorius* and *P. erythrinus*, where a negative relationship was found.

A significant effect of year was detected through the GLMs in condition factor of all species (Table 2). There are also significant differences in condition factor between sexes of *L. budegassa*, *M. merluccius*, *M. poutassou, M. barbatus, M. surmuletus, P. blennoides* and *T. minutus capelanus* (Table 2). Interannual fluctuations in mean condition factor (adjusted to the length, latitude and depth) are significant (Figure 2). With the exception of *L. budegassa* and *M. surmuletus*, adults are better conditioned than juveniles (Figure 2). Among adults, females of *L. budegassa, M. merluccius, M. barbatus* and *M. surmuletus* are better conditioned than males. Figure 2 also shows the existence of interspecific variability in condition factor not only between species belonging to different families (e.g. between *M. barbatus* and *L. piscatorius*) but also between species belonging to the same genus (e.g. condition values of *M. surmuletus* are higher than those of *M. barbatus*).

Condition factor of *L. budegassa*, *L. piscatorius*, *M. merluccius*, *M. barbatus*, *M. surmuletus*, *P. acarne*, *P. erythrinus*, *P. blennoides* and *T. minutus capelanus* increased with latitude, as demonstrated by the positive and significant coefficients (Table 2). Individuals of these species were better conditioned in the northern parts of the study area than in the southern parts. In these cases, latitude explained up to 16% of the variability in condition factor. Condition factor of *L. budegassa*, *M. merluccius*, *M. poutassou*, *M. surmuletus*, *P. acarne*, *P. erythrinus*, *P. blennoides* and *T. minutus capelanus* decreased with depth, as demonstrated by the negative and significant coefficients (Table 2). Depth explained up to 45% of the variability in condition factor of these species.

Physiological measures: hepatosomatic (HSI), digestivesomatic (DSI) and gonadosomatic (GSI) indices

The GLMs incorporating all independent variables accounted for 15–77% of the deviance of HSI and between 14% and 35% of the variability in DSI of the species considered (Table 2). There was a significant positive relationship between length and HSI of *M.*

Table 2. Analysis of deviance tables for generalized linear models fitted to Fulton's K condition factor of 10 species of the NW Mediterranean (1994–2001), to hepatosomatic index (HSI) of 7 species (2000–2001), to digestivesomatic index (DSI) of 4 species (2000–2001) and to gonadosomatic index (GSI) of female spawners of *M. barbatus* (2000–2001). Analysis compare full models with models incorporating the corresponding tested effect. Model estimates (regression coefficients) for the continuous predictors are shown.

Variable	Source	d.f.	Estimate	s.e.	p	Residual deviance	% Explained
Species: *Lophius budegassa*							
K	NULL					32.87	
	Length	1	− 0.0007	0.0001	<0.0000	28.83	12.30
	Depth	1	− 0.0004	0.0001	<0.0000	28.42	1.24
	Latitude	1	0.0420	0.0090	<0.0000	26.46	5.96
	S (J, PM, PF)	2			0.0103	25.97	1.50
	Year	7			<0.0000	24.19	5.42
	Intercept		− 0.1540	0.3620	0.6700		
	Model					24.19	26
HSI	NULL					13.92	
	Length	1	− 0.0044	0.0220	0.8440	13.31	4.38
	Depth	1	− 0.0013	0.0013	0.3060	12.04	9.12
	Latitude	1	0.5440	0.2520	0.0310	11.27	5.53
	S (J, PM, PF)	2			0.3060	10.85	3.02
	Intercept		− 20.2760	10.3690	0.0510		
	Model					10.85	22
Species: *Lophius piscatorius*							
K	NULL					6.08	
	Length	1	− 0.0004	0.0001	0.0005	5.47	10.00
	Depth	1	− 0.0001	0.0001	0.6700	4.46	0.03
	Latitude	1	0.0465	0.0127	0.0002	5.21	4.16
	S (J, PM, PF)	2			0.5500	5.17	0.66
	Year	7			0.0100	4.55	10.20
	Intercept		− 0.3040	0.526	0.5600		
	Model					4.55	25
Species: *Merluccius merluccius*							
K	NULL					34.93	
	Length	1	0.0005	0.0000	<0.0000	27.28	21.90
	Depth	1	− 0.0002	0.0000	<0.0000	26.85	1.23
	Latitude	1	0.0070	0.0020	0.0001	26.57	0.80
	S (J, PM, PF)	2			<0.0000	26.24	0.94
	Year	7			<0.0000	24.00	6.41
	Intercept		0.3500	0.0721	<0.0000		
	Model					24.00	31
HSI	NULL					34.12	
	Length	1	0.1311	0.0270	<0.0000	20.22	40.74
	Depth	1	− 0.0036	0.0018	0.044	19.54	2.00
	Latitude	1	− 0.0330	0.1550	0.830	19.48	0.18
	S (J, PM, PF)	2			0.162	18.81	1.96
	Intercept		1.470	6.3220	0.817		
	Model					18.81	45
Species: *Mullus barbatus*							
K	NULL					57.91	
	Length	1	0.0011	0.0000	<0.0000	44.21	23.66
	Depth	1	− 0.0001	0.0001	0.700	43.77	0.76
	Latitude	1	0.0205	0.0026	<0.0000	43.21	0.97
	S (SM, SF)	1			<0.0000	38.61	7.94
	Year	7			<0.0000	32.71	10.19
	Intercept		0.0620	0.104	0.548		
	Model					32.71	44
HSI	NULL					49.71	
	Length	1	0.0610	0.0240	<0.0000	34.06	31.48
	Depth	1	− 0.0030	0.0010	0.029	31.73	4.70
	Latitude	1	0.0250	0.0370	0.500	31.58	6.30
	S (SM, SF)	1			<0.0000	11.41	40.58
	Intercept		0.3070	1.4670	0.835		
	Model					11.41	77

(*continued on next page*)

Table 2. *Continued*

Variable	Source	d.f.	Estimate	s.e.	p	Residual deviance	% Explained
Species: *Mullus barbatus continued*							
DSI	NULL					19.10	
	Length	1	− 0.0555	0.0540	0.344	17.59	7.91
	Depth	1	0.0032	0.0340	0.406	17.53	0.31
	Latitude	1	− 0.0050	0.1060	0.638	17.52	0.05
	S (SM, SF)	1			<0.0000	12.85	24.43
	Intercept		6.8160	4.5980	0.137		
	Model					12.85	33
GSI	NULL					3.57	
	Length	1	0.3680	0.1100	<0.0000	3.04	72.22
	Depth	1	0.0070	0.0110	0.550	3.03	4.12
	Latitude	1	− 0.3400	0.3040	0.255	3.00	0.08
	Intercept		18.0040	12.4300	0.147		
	Model					3.00	77
Species: *Mullus surmuletus*							
K	NULL					6.96	
	Length	1	0.0013	0.0002	<0.0000	6.26	10.06
	Depth	1	− 0.0005	0.0001	<0.0000	5.50	10.92
	Latitude	1	0.0370	0.0050	<0.0000	4.69	11.64
	S (J, PM, PF)	2			0.0020	4.60	0.05
	Year	7			<0.0000	4.29	0.16
	Intercept		− 0.470	0.1910	0.0140		
	Model					4.29	38
HSI	NULL					4.53	
	Length	1	0.0280	0.0180	0.1050	3.20	29.36
	Depth	1	0.0020	0.0020	0.3940	3.03	3.75
	Latitude	1	0.1190	0.0520	0.0220	2.83	4.42
	S (J, PM, PF)	2			0.4500	2.75	1.77
	Intercept		− 4.3000	2.1060	0.0250		
	Model				0.0410	2.75	39
DSI	NULL					87.74	
	Length	1	0.0240	0.0690	0.7230	87.02	0.83
	Depth	1	− 0.0020	0.0080	0.8520	86.49	0.60
	Latitude	1	0.5610	0.2000	<0.0000	61.30	28.71
	S (J, PM, PF)	2			0.3050	57.29	4.57
	Intercept		− 17.9500	8.0090	0.0250		
	Model					57.29	35
Species: *Pagellus acarne*							
K	NULL					10.11	
	Length	1	0.0009	0.0001	<0.0000	8.89	12.06
	Depth	1	− 0.0007	0.0001	<0.0000	8.79	1.00
	Latitude	1	0.0600	0.004	<0.0000	7.21	15.62
	S (J, MM, MF)	2			0.230	7.19	0.20
	Year	7			0.0001	7.00	1.88
	Intercept		− 1.287	0.1780	<0.0000		
	Model					7.00	31
HSI	NULL					16.23	
	Length	1	0.0206	0.0090	0.020	15.11	6.90
	Depth	1	− 0.0030	0.0011	0.800	14.98	0.80
	Latitude	1	0.0904	0.0220	<0.0000	13.85	6.96
	S (J, MM, MF)	2			0.890	13.84	0.06
	Intercept		− 3.0380	0.9020	0.010		
	Model					13.84	15
DSI	NULL					10.07	
	Length	1	0.0530	0.0320	0.097	9.67	3.97
	Depth	1	− 0.0110	0.0040	0.011	8.95	7.15
	Latitude	1	0.2460	0.07600	0.001	8.30	6.45
	S (J, MM, MF)	2			0.4220	8.22	0.06
	Intercept		− 6.7600	3.0690	0.027		
	Model					8.22	18

Table 2. *Continued*

Variable	Source	d.f.	Estimate	s.e.	p	Residual deviance	% Explained
Species: *Pagellus erythrinus*							
K	NULL					10.00	
	Length	1	− 0.0002	0.0001	0.016	9.93	0.75
	Depth	1	− 0.0015	0.0001	<0.0000	8.69	12.35
	Latitude	1	0.0476	0.004	<0.0000	7.49	11.97
	S (J, MM, MF)	2			0.102	7.43	0.63
	Year	7			0.0003	7.18	2.50
	Intercept		− 0.5542	0.166	0.0008		
	Model					7.18	28
HSI	NULL					15.70	
	Length	1	− 0.016	0.009	0.061	15.54	1.02
	Depth	1	− 0.003	0.003	0.331	15.47	0.45
	Latitude	1	0.138	0.059	0.020	15.04	2.74
	S (J, MM, MF)	2			<0.0000	11.80	20.64
	Intercept		− 3.774	2.458			
	Model					11.80	25
DSI	NULL					4.99	
	Length	1	− 0.021	0.022	0.338	4.84	3.01
	Depth	1	− 0.017	0.007	0.019	4.30	10.82
	Latitude	1	0.0005	0.127	0.996	4.29	0.20
	S (J, MM, MF)	2			0.893	4.28	0.20
	Intercept		4.608	5.346	0.389		
	Model					4.28	14
Species: *Phycis blennoides*							
K	NULL					17.55	
	Length	1	0.0006	0.0000	<0.0000	9.62	45.19
	Depth	1	− 0.0002	0.0000	<0.0000	7.07	14.53
	Latitude	1	0.0090	0.0040	0.014	7.06	0.06
	S (J, PM, PF)	2			0.005	6.90	0.91
	Year	7			<0.0000	6.23	3.82
	Intercept		0.2897	0.151	0.055		
	Model					6.23	65
Species: *Trisopterus minutus capelanus*							
K	NULL					25.04	
	Length	1	0.0003	0.0000	<0.0000	23.17	7.46
	Depth	1	− 0.0004	0.0000	<0.0000	11.72	45.70
	Latitude	1	0.0871	0.0052	<0.0000	8.29	13.69
	S (J, PM, PF)	2			<0.0000	7.76	2.12
	Year	6			<0.0000	6.55	4.83
	Intercept		− 2.752	0.220	<0.0000		
	MODEL					6.55	74
Species: *Micromesistius poutassou*							
K	NULL					9.29	
	Length	1	0.0004	0.0000	<0.0000	6.06	34.77
	Depth	1	− 0.0001	0.0000	0.030	5.99	0.75
	Latitude	1	0.0015	0.0020	0.340	5.97	0.22
	S (J, PM, PF)	2			<0.0000	5.95	0.22
	Year	7			<0.0000	5.13	8.83
	Intercept		0.4940	0.1000	<0.0000		
	Model					5.13	45

Sex and reproductive status are combined into a single categorical variable (S) that includes the following groups: juveniles (J), maturing males (MM), maturing females (MF), spawning males (SM), spawning females (SF), post-spawning/resting males (PM) and post-spawning/resting females (PF). d.f. = degrees of freedom; s.e. = standard error.

merluccius, M. barbatus and *P. acarne* that accounted for 41, 32 and 7% of the variability in HSI of these species, respectively. Length was the only factor affecting significantly GSI of female *M. barbatus* (72% of the variability explained). Length and GSI of female *M. barbatus* follow a linear relationship (Figure 3). No significant relationships were found between length and DSI of any of the species considered (Table 2).

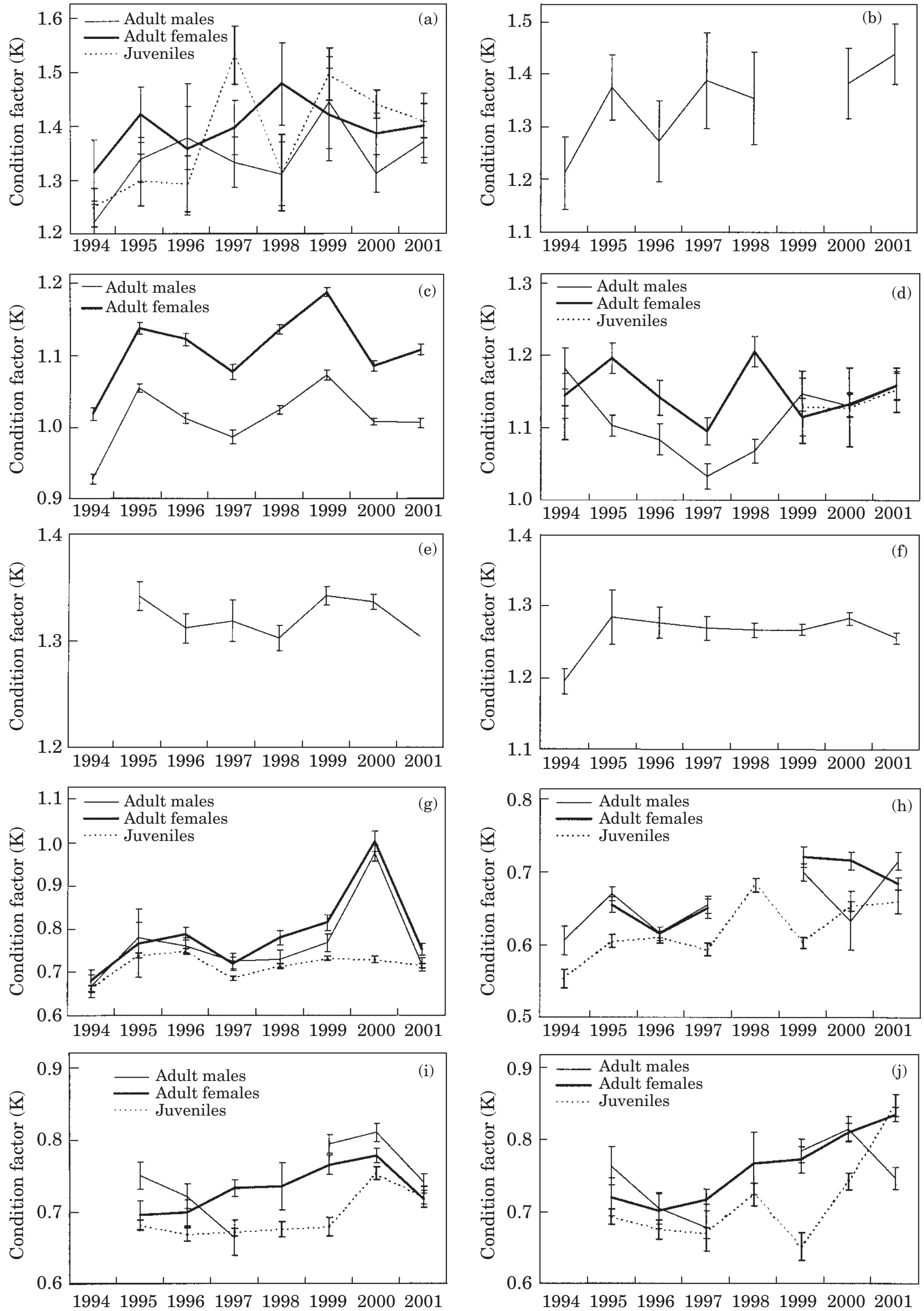

Figure 2. Interannual variations (adjusted means ± s.e.; 1994–2001) by sex/reproductive status in Fulton's K condition factor of ten demersal species: *L. budegassa* (a), *L. piscatorius* (b), *M. barbatus* (c), *M. surmuletus* (d), *P. acarne* (e), *P. erythrinus* (f), *M. merluccius* (g), *M. poutassou* (h), *P. blennoides* (i) *and T. minutus capelanus* (j). When the effect of sex/reproductive status is not significant, data from all sexes/reproductive stages were pooled together. Adjusted means are the means after adjusting for the variation of the covariables (length, depth and latitude).

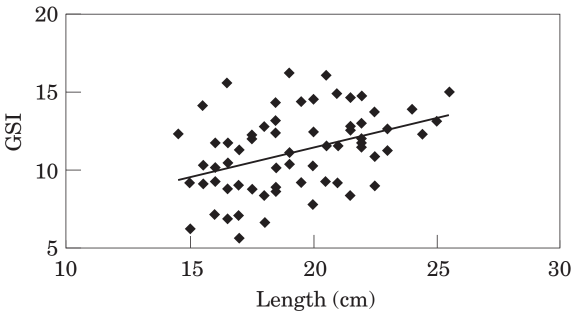

Figure 3. Linear relationship between GSI and length of female spawners of *M. barbatus* (2000–2001). GSI=4.010+0.374*Length.

Results from the analysis of deviance also indicate that the observed differences in HSI between sexes of *M. barbatus* and *P. erythrinus* are significant (Table 2). Females of these species have higher HSI values than males (Figure 4). In addition to this, DSI values of female *M. barbatus* are significantly higher than those of males (Figure 4).

The HSI of *L. budegassa, M. surmuletus*, *P. acarne*, and *P. erythrinus*, as well as the DSI of *M. surmuletus* and *P. acarne* increased with latitude, as demonstrated by the positive and significant model coefficients (Table 2). Individuals of these species had higher condition values in the northern parts of the study area than in the southern parts. Latitude explained up to 7% and 29% of the variability in HSI and DSI, respectively. In addition to this, HSI of *M. merluccius* and *M. barbatus*, as well as DSI of *P. acarne* and *P. erythrinus* decreased with depth, as demonstrated by the negative and significant coefficients (Table 2). Depth explained up to 5% and 11% of the variability in HSI and DSI of these species, respectively (Table 2). The relationship between DSI of *P. acarne*, latitude and depth can be represented as a smooth linear function (Figure 5).

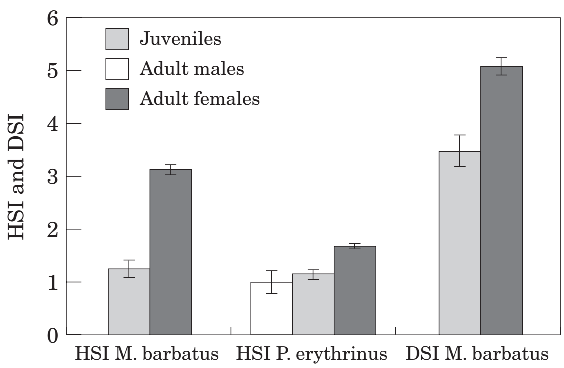

Figure 4. Adjusted mean (±s.e.; 2000–2001) HSI and DSI of adult males and females of *M. barbatus* and HSI of juveniles and adult males and females of *P. erythrinus*. Adjusted means are the means after adjusting for the variation of the covariables (length, depth and latitude).

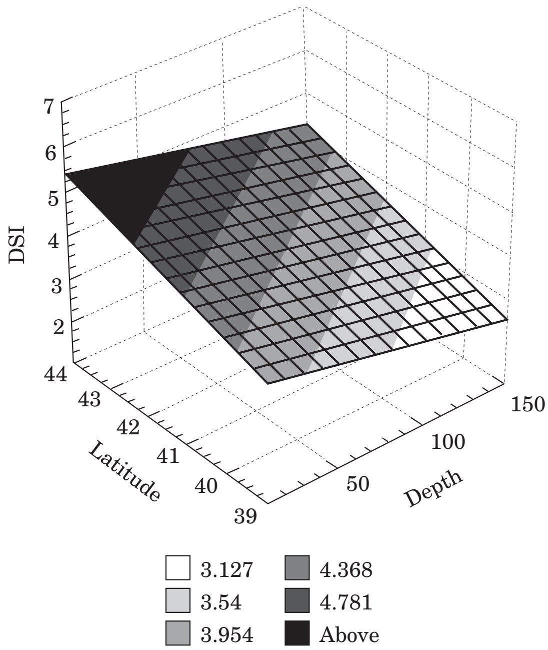

Figure 5. Linear relationship between digestivesomatic index (DSI) of *P. acarne*, depth and latitude (K = −8.993–0.008*Depth+0.328*Latitude). This 3-D graph displays a surface representing a linear smoothed image of overall data (all sexes/maturity stages and lengths are pooled together), divided in six uniform contours (step values used to draw contours are given in the legend).

Discussion

Condition, as a measure of energy reserves, is a particular important attribute of fishes and future population success because it has a large influence on growth, reproduction and survival. Inadequate energy reserves have been implicated in the reduced reproductive success of several fish species through reduced fecundity and/or quality of eggs and larvae quality (Kjesbu *et al.*, 1992; Adams, 1999; Marshall *et al.*, 1999; Lambert and Dutil, 2000). However, other studies have not found any relationship between maternal condition and egg viability (Ouellet *et al.*, 2001). Poor condition (i.e. lower available energy reserves) may also lower the chances of survival of big fish, leading to an increase of natural mortality (Krivobok and Tokareva, 1972; Love, 1974; Adams, 1999; Shulman and Love, 1999). Starvation due to exhaustion of energy reserves, particularly in smaller individuals and during the nonfeeding periods, weakens fish and also renders them more susceptible to predation and to a variety of environmental stressors (e.g. parasites, thermal effects and contaminant effects).

Our analyses reveal differences in condition factor from year to year and from species to species. Differences between forms that belong to different families, orders and even classes are probably not relevant (Shulman and Love, 1999). However, there are differences in condition between species belonging to the same genus, which may involve evolutionary processes and environmental factors that engender them (Shulman and Love, 1999). Interannual fluctuations of condition factor may be linked to environmental factors and food supply. Temperature data collected during some groundfish surveys were not sufficient to study the effect of temperature on fish condition.

We found a positive relationship between condition and length for most of the species studied. The relative body, liver, gonad and digestive tract weights increase as the fish grow. This is probably because since larger fish make greater demand on their resources, they lay up greater energy reserves (Shulman and Love, 1999). Length is an important variable in explaining condition of fish species. There is a strong correlation between GSI and length of female *M. barbatus* that probably reflects the increase in fecundity with age and size within this species and supports the importance of large spawners to total egg production and recruitment. For some species, we found that adult females were better conditioned than adult males and juveniles. Increased condition in adult fish, especially females, is more likely to act as an extra energy reserve at the spawning time to assist recovery (Shulman and Love, 1999).

Our results also show that there are significant spatial and bathymetric differences in condition for demersal species inhabiting the soft bottoms of the north-western Mediterranean. The influence of latitude and depth on condition of a given species depends, however, on the index used to assess the condition. Thus, for example, depth affects HSI of *M. barbatus*, but not K, DSI or GSI of this species. When there was a significant effect of depth or latitude on condition of any species, better conditioned fish (highest condition factor, HSI and/or DSI) were always found at the shallow and northern parts of the study area. The negative relationship between condition and depth suggests that deeper areas of distribution of a given species represent a marginal habitat in terms of food resources (Chouinard and Swain, 2001). In contrast, shallow areas of distribution, where the best conditioned fish lives, may constitute essential fish habitats for some demersal species. In coastal areas there is often more food available than in the open sea, so fish tend to be better nourished (Love, 1974). Although many authors have documented a general trend for larger demersal fish to be found in deeper waters (Macpherson and Duarte, 1991; Swain, 1993; Dalley and Anderson, 1997; Relini *et al.*, 1999; Gil de Sola *et al.*, 2001), bathymetric patterns of condition have rarely been reported, with the exception of Atlantic cod (*Gadus morhua*) in the Gulf of St. Lawrence (Chouinard and Swain, 2001) and the North Sea (Love, 1974). The latitudinal gradient in the condition of some of the studied species, showing lower condition in the Catalan Sea relative to the Gulf of Lions, might be due to differences in productivity between the areas (Ben-Tuvia, 1983; Champalbert, 1996; Estrada, 1996). The Gulf of Lions appears to provide a good food supply as a result of upwelling, river runoff and wind mixing. Some of the demersal species in this northern region are heavier, have larger livers and digestive tracts (or more food inside) when compared with to specimens caught in the Catalan Sea. Similar results were reported by Shulman (1972), who found that small pelagics such as sprats and sardines of the Gulf of Lions had considerably higher fat content than that of sprats and sardines of other areas of the Mediterranean. In addition to this, he reported the existence of inter-population variability in condition of anchovies in the Mediterranean Sea that were supposed to be driven by food availability. There could be also a temperature effect on condition because the northern parts of the sampling area, where the higher condition fish are found, are colder than the southern parts. The higher condition of fish in the northern and shallow areas indicates that habitat suitability is highest there. Because foraging success is assumed commensurate with fish condition (Schoener, 1986), it seems that animals inhabiting these areas forage in a way that they maximize the amount of energy. Similarly, densities of many demersal species are highest in shallow areas of the Mediterranean and within the Gulf of Lions (Caddy *et al*., 1995; Bertrand *et al*., 1999; Gil de Sola *et al*., 2001). Therefore, foragers are not distributed among habitats so that foraging success is equal (as we would expect from the ‘‘ideal free distribution’’ hypothesis; Fretwell and Lucas, 1970). Although depth and latitude have minor effects on condition, the influence of both factors on condition is confirmed in this study using different morphometric and physiological measures such as weight–length relationships and hepatosomatic and digestivesomatic indices. We obtained the same results when using weight instead of condition factor, an approach similar to that proposed by Garcia-Berthou and Moreno-Amich (1993) and Chouinard and Swain (2001) to avoid the use of Fulton's condition factor. This approach consists in using weight (log-transformed) instead of condition factor as the response variable and length (log-transformed) as a covariate. All these condition indices, especially morphometric ones, are only gross measures of energy reserves, so that they can be easily biased (and differently biased amongst index and species). Biochemical indices such as fatness or protein content would assess condition more precisely (Shulman and Love, 1999). Moreover, a given index can be more relevant than another for a given species because the allocation of energy reserves among different tissues and organs depends on the fish species and the age and physiological status of the individuals (Shulman and Love, 1999). Apart from the general trends in condition we found (north–south and shallow-deep), there could be intermediate areas (e.g. rocks dispersed along the platform) where fish condition might be higher/lower than in the borders. These aspects could be important for fish condition and should deserve special attention in future investigations.

Our findings support the importance of shallow areas for condition of demersal fish species in the Mediterranean Sea. Shallow areas and the ecological communities therein (e.g. seagrass beds, rocky-algal reefs and soft bottoms) are important as providing habitat and nursery ground for numerous species, including commercially and recreationally fish species. This is not only valid for the Mediterranean (Francour, 1997; Bertrand *et al.*, 1999; García-Charton *et al.*, 2000; Guidetti, 2000; Planes *et al.*, 2000) but also world-wide (Dalley and Anderson, 1997; Benaka, 1999; Dunton, 1999; Kaiser *et al.*, 1999; Minello, 1999). Differences in fish condition between ecological communities using biochemical indicators such as fish fatness or protein content should be investigated to evaluate precisely the importance of specific habitats for fish productivity. Our results also support the importance of the Gulf of Lions for condition of demersal fish species. Whether the benefits of having well fit fish inhabiting the Gulf of Lions are exported or not to adjacent areas remains unknown.

Acknowledgements

The authors would like to thank the scientific staff and crew involved in the annual (1994–2001) research surveys "MEDITS" on board research vessels "Europe" (IFREMER, France) and "Cornide de Saavedra" (IEO, Spain), as well as crew of R/V "Nereis" (CNRS, France) for collection of data in 2001. We also thank two anonymous referees for their comments on the manuscript. The "MEDITS" groundfish surveys were financed by the D.G. Fisheries of the European Commission. Josep Lloret benefited from a Marie-Curie post-doc fellowship of the European Commission (program Quality of Life; contract QLK5-CT-2000-51950).

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