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Abstract—In this study, the growth pattern of juvenile European hake (*Merluccius merluccius*) was analyzed in relation to oceanographic and ecological factors in the Ligurian Sea and northern Tyrrhenian Sea, both part of the Mediterranean Sea. The ages of juvenile European hake, collected during a trawl survey in June 2011, were estimated by reading otolith daily growth rings. The growth pattern (length–age relationship) of juvenile European hake recruited to the population (<1 year old) was analyzed by fitting a multivariate generalized additive model with explanatory variables: depth, bottom temperature, sea-surface temperature, scalar wind speed, chlorophyll-*a* concentration, and fish density (number of individuals per square kilometer). A significant effect of density on the length–age relationship was found, and an increased growth rate at densities >3000 individuals km^{-2}. This observed positive effect of density on growth could be argued to be a consequence of favorable environmental conditions, such as food availability and temperature, where both fish density and growth are maximized. Conversely, areas of lower density correspond to habitats of low suitability, where growth is impaired.

Modeling the growth of recruits of European hake (*Merluccius merluccius*) in the northwestern Mediterranean Sea with generalized additive models

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The European hake (*Merluccius merluccius*) is a demersal fish widely distributed in the Mediterranean Sea and in the northeastern Atlantic (Murua, 2010). In the Mediterranean Sea, it is a major component of the demersal fish assemblages on both the continental shelf and the upper slope (Orsi Relini et al., 2002; Colloca et al., 2004). Juvenile European hake aggregate in nursery areas located on the continental shelf break (Maynou et al., 2003; Abella et al., 2005; Bartolino et al., 2008a; Hidalgo et al., 2008), and adult fish can be found in a wider depth range from the shelf to the upper slope (Aldebert et al., 1993; Sbrana et al., 2007; Cartes et al., 2009; Bartolino et al., 2011). Because of its abundance and wide spatial distribution, the European hake is one of the most highly exploited species in the Mediterranean Sea, targeted by multigear fisheries. The bulk of the catch of this species is obtained from trawl fisheries, which mainly exploit the youngest portion of the population (≤30 cm in total length [TL]). However, there are still relatively high discard rates of undersize fish (Cardinale et al., 2011) despite an amendment in 2010 in the European Union Council Regulation to increase trawl codend mesh size (European Union Council Regulation 1967/2006). The adult fraction (>40 cm TL) is exploited by gillnet and longline fisheries (Sbrana

et al., 2007; Bartolino et al., 2011). This pattern results in high exploitation rates across the entire population, from small individuals (<15 cm TL) to large females (>60 cm TL) in spawning aggregations (Aldebert et al., 1993) and highlights the importance of management measures to reduce the catch of both juveniles and spawning adults (Drouineau et al., 2010).

The very high concentration of juvenile European hake along the coasts of Italy in the Ligurian and Tyrrhenian Seas indicates that these areas are the main European hake nurseries in the northwestern Mediterranean basin (Orsi Relini et al., 2002; Colloca et al., 2009). Orsi Relini et al. (2002) estimated mean densities of European hake recruits to be up to 8 times higher than densities reported for other nurseries in the Mediterranean Sea. In the Tyrrhenian Sea, at the boundary between the continental shelf and the upper slope, densities >25,000 individuals km^{-2} have been observed (Colloca et al., 2009).

Despite many studies of the biology of European hake in the Mediterranean Sea, the growth pattern of juveniles is still controversial (Drouineau et al., 2010). It is not clear whether the reported variability in the growth rate of European hake juveniles is due to methodological differences in the approaches used for age determination or due to natural variability in growth processes.

Atmospheric processes and oceanographic features are known to have a key role in recruit condition and recruitment strength of other fishes. A link between environmental variables (e.g., climate variability, temperature, and phytoplankton production) and recruitment of Atlantic cod (*Gadus morhua*) in the North Sea and northeastern Atlantic has been described previously (Köster et al., 2005; Steingrund and Gaard, 2005; Stige et al., 2006; Beggs et al., 2014). Furthermore, increases in temperature in the North Sea have been reported to affect growth dynamics of haddock (*Melanogrammus aeglefinus*) (Baudron et al., 2011). Thermal conditions have been reported to affect recruitment and distribution of Pacific cod (*Gadus macrocephalus*) in the eastern Barents Sea (Hurst et al., 2012), of Pacific hake (*Merluccius productus*) along the western coast of North America (Agostini et al., 2008), and of Chilean hake (*Merluccius gayi gayi*) in the south Pacific (San Martín et al., 2013). Within-year variability in growth of recruits of Argentine hake (*Merluccius hubbsi*) in response to environmental variables was found by Norbis et al. (1999) along Uruguayan coasts, and interannual variability in growth was found in Pacific hake (Woodbury et al., 1995).

Density-related growth relationships also have been described for a range of species: Bromley (1989) found a negative relationship between growth and fish density in both 1-year-old (I group) and 2-year-old (II group) Atlantic cod, whiting (*Merlangius merlangus*), and haddock in the North Sea: fish in areas of low density were larger than fish in areas of high density, possibly because of feeding competition in high density areas.

Although environmental and oceanographic features are known to affect recruit condition and recruitment strength of European hake (Alvarez et al., 2001; Maynou et al., 2003; Olivar et al., 2003; Abella et al., 2008; Bartolino et al., 2008a; Hidalgo et al., 2008), understanding of the effect of those factors on the growth dynamics of juvenile European hake is still limited.

The aim of the present study was to model the growth of European hake juveniles to determine the effects of environmental variables (i.e., sea-surface temperature, bottom temperature, depth, scalar wind speed, chlorophyll-*a*) and population factors (i.e., fish density) using a generalized additive model (GAM) (Hastie and Tibshirani, 1990).

Materials and methods

Study area

For this study, the growth pattern of juvenile European hake was analyzed in northwestern Italian waters, which include the Ligurian Sea and the northern Tyrrhenian Sea (Fig. 1). The Tyrrhenian Sea is generally considered a distinct entity within the western Mediterranean basin because it is semi-enclosed between the islands of Corsica, Sardinia, and Elba and the mainland (Italy) and is separated from the rest of the western basin by a channel of moderate depth, about 1500 m (Orfila et al., 2005). Along the central western Italian coasts, the Tyrrhenian Current, also called the Eastern Corsica Current, flows northward through the Corsica Channel into the Ligurian Sea. The Corsica Channel is the passage between the islands of Corsica and Elba that connects the northern Tyrrhenian Sea to the southern Ligurian Sea. It plays a key role for water circulation in the northwestern Mediterranean Sea because the water exchange that runs through it involves the whole water column (Gasparini et al., 1999).

The general seasonal pattern of phytoplankton dynamics is typical of subtropical areas, with a bloom period of maximum productivity from February to April and a period of minimum productivity in summer months. The intensity of this winter–spring bloom varies significantly between years. In the Ligurian Sea, a substantial positive correlation links the intensity of the phytoplankton winter–spring bloom with a strong autumn–winter water turbulence (which is mainly driven by winds), and reduced wind mixing in March (Nezlin et al., 2004).

Trawl sampling and environmental data

Specimens of juvenile European hake were collected from 13 of the 120 trawl stations sampled in June 2011 during an experimental bottom trawl survey, the Mediterranean International Trawl Survey (MEDITS; see Bertrand et al., 2002, for technical specifications) in the Ligurian and northern Tyrrhenian Seas (Fig. 1). To
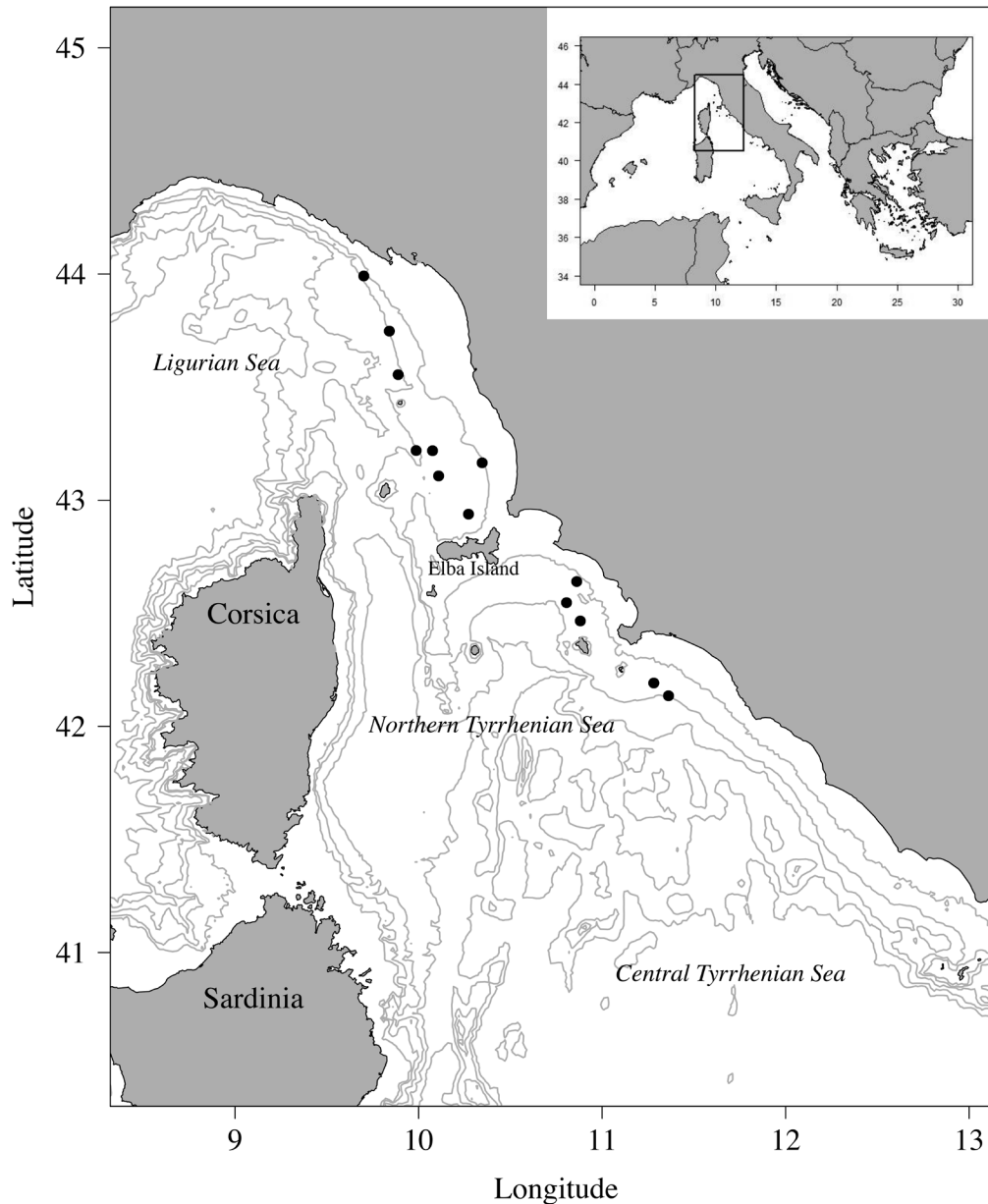
Figure 1

Map of the study area in the Ligurian Sea and northern Tyrrhenian Sea. Black circles indicate the 13 sites where European hake (*Merluccius merluccius*) were sampled in June 2011 during the Mediterranean International [bottom] Trawl Survey (MEDITS). Gray lines show the 100-, 200-, 500-, 1000- and 1500-m isobaths.

cover the relevant nursery areas, identified by Colloca et al. (2009), 5 of the 13 stations from which specimens were collected were located in the Tyrrhenian basin and 8 were located in the Ligurian Sea.

For each station, a suite of oceanographic and ecological variables that potentially affect growth processes of the European hake was obtained (Table 1). Satellite data at a fine spatial scale for sea-surface temperature (SST, degrees Celsius), scalar wind speed (meters per second), and chlorophyll-*a* concentration (milligrams per cubic meter) were used (MyOcean follow-on project, http://www.myocean.eu); daily data were averaged for the period of January–March 2011. Bottom temperature (degrees Celsius) was measured and mean depth (meters) was recorded at each station by using a DST centi-TD[1] temperature and depth probe, with

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[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Environmental and ecological variables used in the generalized additive model (GAM) of environmental effects on growth of juvenile European hake (*Merluccius merluccius*) in the northwestern Mediterranean Sea. European hake were sampled in June 2011 in the Tyrrhenian Sea (Tyr) and Ligurian Sea (Lig). Latitude (Lat.) and longitude (Long.) of the mean point of each haul are shown, as well as the number of specimens (otoliths), mean bottom temperature (Bottom temp.), mean depth, and recruit density (number of individuals per square kilometer) recorded in each haul, the mean sea-surface temperature (SST), mean wind scalar speed, and mean concentration of chlorophyll-*a* (chl-*a*) used in the GAM.

Haul code	Area	Lat.	Long.	Number of otoliths	Bottom temp. (°C)	Mean depth (m)	Recruit density (individuals km^{-2})	SST (°C)	Mean scalar wind speed (m s^{-1})	Chl-*a* (mg m^{-3})
42	Tyr	4208.07	1121.43	14	13.9	156	3214.0	14.00	6.53	0.449
43	Tyr	4211.32	1116.55	22	14.0	124	3571.0	14.00	6.53	0.443
59	Tyr	4227.59	1052.53	24	13.9	131	8319.0	13.80	6.31	0.438
62	Tyr	4237.86	1051.43	22	13.9	109	6631.0	13.87	6.31	0.413
63	Tyr	4232.51	1047.81	23	13.8	164	7377.0	13.83	6.31	0.424
91	Lig	4255.79	1015.80	21	13.7	113	1008.0	13.87	5.57	0.457
94	Lig	4313.11	958.73	21	13.6	251	3159.0	13.50	7.74	0.448
98	Lig	4332.80	952.79	19	13.5	241	6835.0	13.42	7.74	0.441
100	Lig	4312.68	1003.93	20	13.6	153	1819.0	13.63	7.74	0.408
103	Lig	4306.27	1006.32	28	13.6	150	1378.0	13.62	7.74	0.426
115	Lig	4344.53	950.26	18	13.4	205	3197.0	13.42	8.54	0.449
126	Lig	4309.57	1020.49	22	13.8	101	1072.0	13.59	7.74	0.434
131	Lig	4359.29	941.66	17	13.4	140	2003.0	13.48	8.54	0.414

supporting SeaStar software (Star-Oddi, Gardabaer, Iceland), attached to the trawl net. European hake juveniles were identified according to the morphological features described by Murua (2010). At each station, density (number of individuals per square kilometer) of juvenile European hake was computed as the ratio between the number of recruits and the swept area (unit of measurement km²).

Otolith reading

All specimens of European hake that were caught at the 13 selected stations were measured in TL to the nearest 0.5 cm; otoliths (sagittae) were removed from a subsample of 318 individuals that ranged in size from 4.5 to 18.0 cm TL. The upper size limit of 18.0 cm TL was used to define European hake recruits (fish in their first year of life) (Belcari et al., 2006). The length-frequency distribution of the specimens caught at the 13 stations was broken down into normal components by using Batthacharya's method (Bhattacharya, 1967).
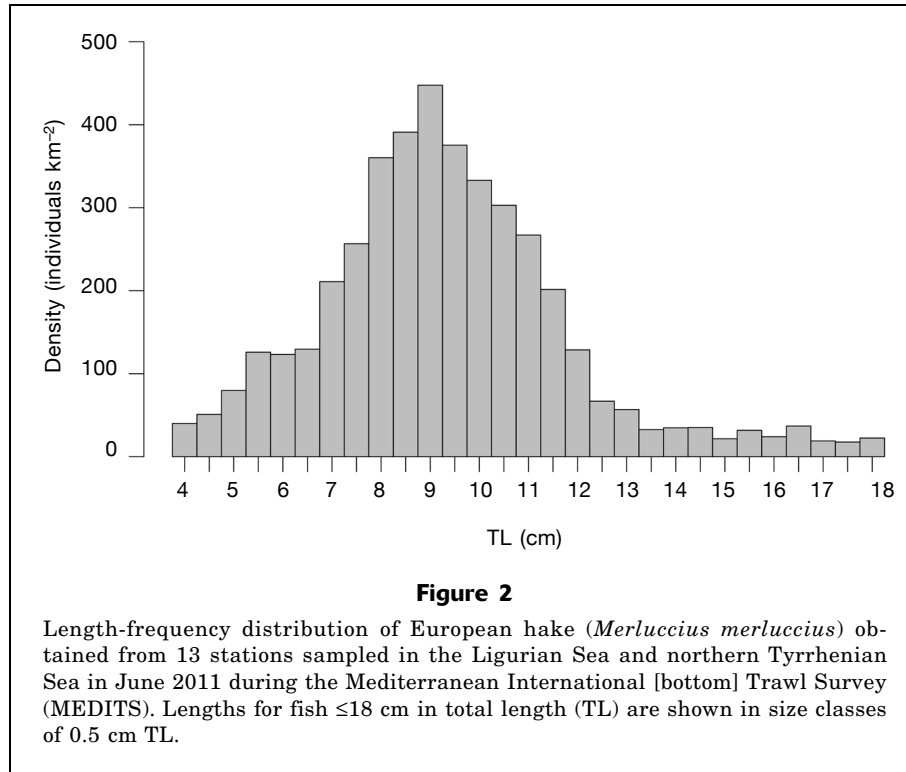
Left sagittae were ground on wet sandpaper, polished on abrasive cloth with alumina slurry, and mounted external-side up on glass slides with a 2-component epoxy resin; a second grinding and polishing procedure was performed to obtain thin frontal sections (Belcari et al., 2006). Microstructure analysis (counting of daily growth rings) of otolith sections was carried out with a compound green-light, polarizing microscope with

plan apochromatic objectives. The number of daily increments deposited within the primordium, the central area of the otolith (Morales-Nin and Moranta, 2004), was recorded to estimate the duration of the presettlement period of this species (Arneri and Morales-Nin, 2000; Morales-Nin and Moranta, 2004; Belcari et al., 2006).

Otolith readings were used to back-calculate the hatching-date distribution by subtracting the fish age from the date of capture. An indirect validation of the periodicity of increment formation was obtained by comparing the estimated hatching-date distribution with the spawning period of the species (Arneri and Morales-Nin, 2000; Panfili et al., 2002; Belcari et al., 2006). To estimate the age-frequency distribution and to back-calculate the hatching-date distribution, the age-length key that resulted from the readings was applied to the length-frequency distribution that was obtained from the 13 stations that were sampled. In addition, a subsample of 40 otoliths was reread by the same operators for evaluation of the match between the readings (Belcari et al., 2006).

Data analysis

A multivariate GAM with Gaussian distribution was used to describe the growth of juvenile European hake, specifically the length–age relationship and environmental covariates. For the initial model that was used

Figure 2
Length-frequency distribution of European hake (*Merluccius merluccius*) obtained from 13 stations sampled in the Ligurian Sea and northern Tyrrhenian Sea in June 2011 during the Mediterranean International [bottom] Trawl Survey (MEDITS). Lengths for fish ≤18 cm in total length (TL) are shown in size classes of 0.5 cm TL.

to define the length–age relationship with covariates, the following equation was used:

$$Length = \alpha + f_1(Age) + f_2(bottom\ T) + f_3(density)$$
$$+ f_4(depth) + f_5(SST) + f_6(wind) + f_7(chl\text{-}a)$$
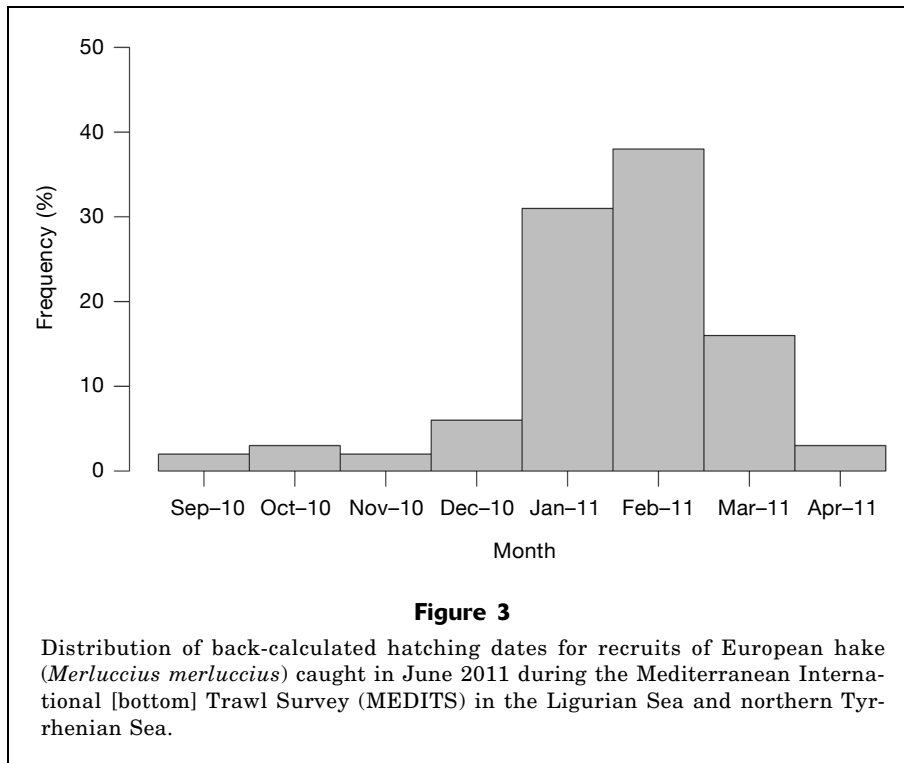$$+ f_8(depth\text{:}density) + factor(Area) + \varepsilon_t, \quad (1)$$

where bottom T, density, and depth = the bottom temperature, European hake recruit density, and depth from each station, respectively; and *SST*, *wind*, and chl-*a* = sea-surface temperature, scalar wind speed and chlorophyll-*a* concentration averaged over the period of January–March 2011.

To evaluate possible differences in recruit growth patterns, the area (Ligurian Sea or Tyrrhenian Sea) was included in the analysis and treated as a factor (*Area*). Following the findings by Bartolino et al. (2008b), which included observation of a stable pattern of depth preference by juvenile European hake, the interaction between depth and fish density (f_8) was also included in the GAM.

Two forms of this model were constructed. With the first, a continuous variable of density was assumed; this first form was compared with a second model in which density was treated as a 3-level factor: low (<2000 individuals km^{-2}), medium (2000–4000 individuals km^{-2}) and high (>4000 individuals km^{-2}). Then, the fit of these models was compared. Analysis of variance was used to test for a significant difference in model fit, and

the model with the lowest Akaike's information criterion (AIC) was selected as the best model, which is the model that best fits the set of data.

The degree of collinearity between explanatory variables was tested with plots of paired variables (pairplots), a matrix of scatter plots that show the bivariate relationships of variables, and variance inflation factor (VIF) values (Zuur et al., 2009). Variables with a high Pearson's correlation coefficient (r) (>0.8, absolute value) and a high VIF value (>3) were considered correlated, and one of the pair was removed. A backward stepwise model selection procedure based on analysis of variance and on the AIC was used to identify the most parsimonious model with the greatest explanatory power. The significance of each variable in the GAM was determined by means of analysis of variance (*F*-test). The levels of constraints (k) for splines were reduced from a maximum, but still achieving convergence to 1. The level of constraint for the number of splines that were used in the final analysis was selected by a comparison of AIC scores. Model residuals were tested for assumptions of homogeneity and normality (Zuur et al., 2009). A multiple linear regression model that used the final selected explanatory variables also was compared with the GAM model by using analysis of variance and AIC. Data exploration and analyses were carried out with the package R, vers. 2.15.2, and the associated mgcv package (R Core Team, 2012). An assumed significance level of 5% was used in all statistical analyses.

Figure 3

Distribution of back-calculated hatching dates for recruits of European hake (*Merluccius merluccius*) caught in June 2011 during the Mediterranean International [bottom] Trawl Survey (MEDITS) in the Ligurian Sea and northern Tyrrhenian Sea.

Results

At the 13 selected stations, 3123 specimens of European hake were caught during the 2011 MEDITS in the Ligurian Sea and northern Tyrrhenian Sea. Sizes ranged from 4.0 to 41.0 cm TL; the length-frequency distribution of the specimens belonging to the first year class (up to 18 cm TL) is shown in Figure 2. The length-frequency distribution showed a single normal component with mean size of 9.0 cm TL (standard deviation [SD] 2.0).

Counts of otolith daily increments from microstructure analysis ranged from 77 to 340. The number of increments within the primordium of the otolith ranged between 36 and 70, with an average of 50 (SD 5). The results of the rereading of 40 otolith slides used by Belcari et al. (2006) showed no discrepancies larger than 10%, a proportion that is considered a reading precision threshold (Arneri and Morales-Nin, 2000), providing further support for the reading method used in the present study.

Back-calculation of hatching dates provided estimates of the main hatching period to be from December 2010 to March 2011, with a peak during January–February 2011 (Fig. 3).

A subsample of 271 individuals was used to fit the growth model by means of GAM. The 271 individuals were born during the main hatching period (December 2010–March 2011) with a size range between 4.5 and 13 cm TL and an age range between 77 and 205 days (Fig. 4); therefore, they represented a single cohort.

Data exploration highlighted collinearity between area, bottom temperature, SST, and scalar wind speed (Fig. 5), supported by $r > 0.8$ and VIF values >3. Therefore, area, SST, and scalar wind speed were removed from the model, and a model containing age, bottom temperature, fish density, depth, chlorophyll-*a*, and the second-order interaction depth:density as explanatory variables was tested by means of analysis of variance and backward selection:
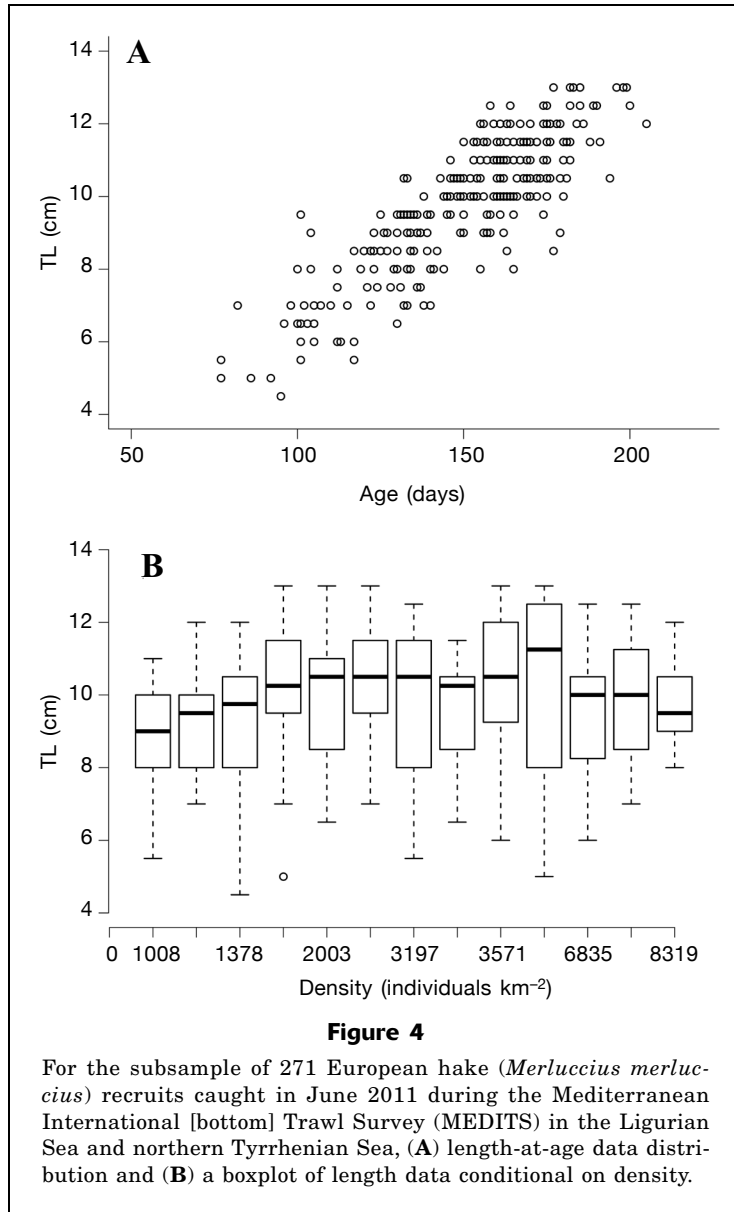
$$Length = \alpha + f_1(Age) + f_2(bottom\ T) + f_3(density) + f_4(depth) + f_5(\text{chl-}a) + f_6(depth{:}density) + \varepsilon_i. \quad (2)$$

Based on backward selection, the best model (Table 2), with variables significant only at the 5% level and with the lowest AIC (689.3), contained only age and density as explanatory variables:

$$Length = \alpha + f_1(Age) + f_2(density) + \varepsilon_i. \quad (3)$$

That final model explained 81% of the total deviance, with a generalized cross-validation score of 0.727. The multiple linear regression model fitted with the same explanatory variables had heterogeneity within the model residuals, as well as a higher AIC (704.2). The analysis of variance between these models was significant ($F=9.221$, $P<0.05$), indicating that the smoothers were not linear.

The explanatory variable *age* had a linear effect, although with some fluctuations, especially in the first

Figure 4

For the subsample of 271 European hake (*Merluccius merluccius*) recruits caught in June 2011 during the Mediterranean International [bottom] Trawl Survey (MEDITS) in the Ligurian Sea and northern Tyrrhenian Sea, (**A**) length-at-age data distribution and (**B**) a boxplot of length data conditional on density.
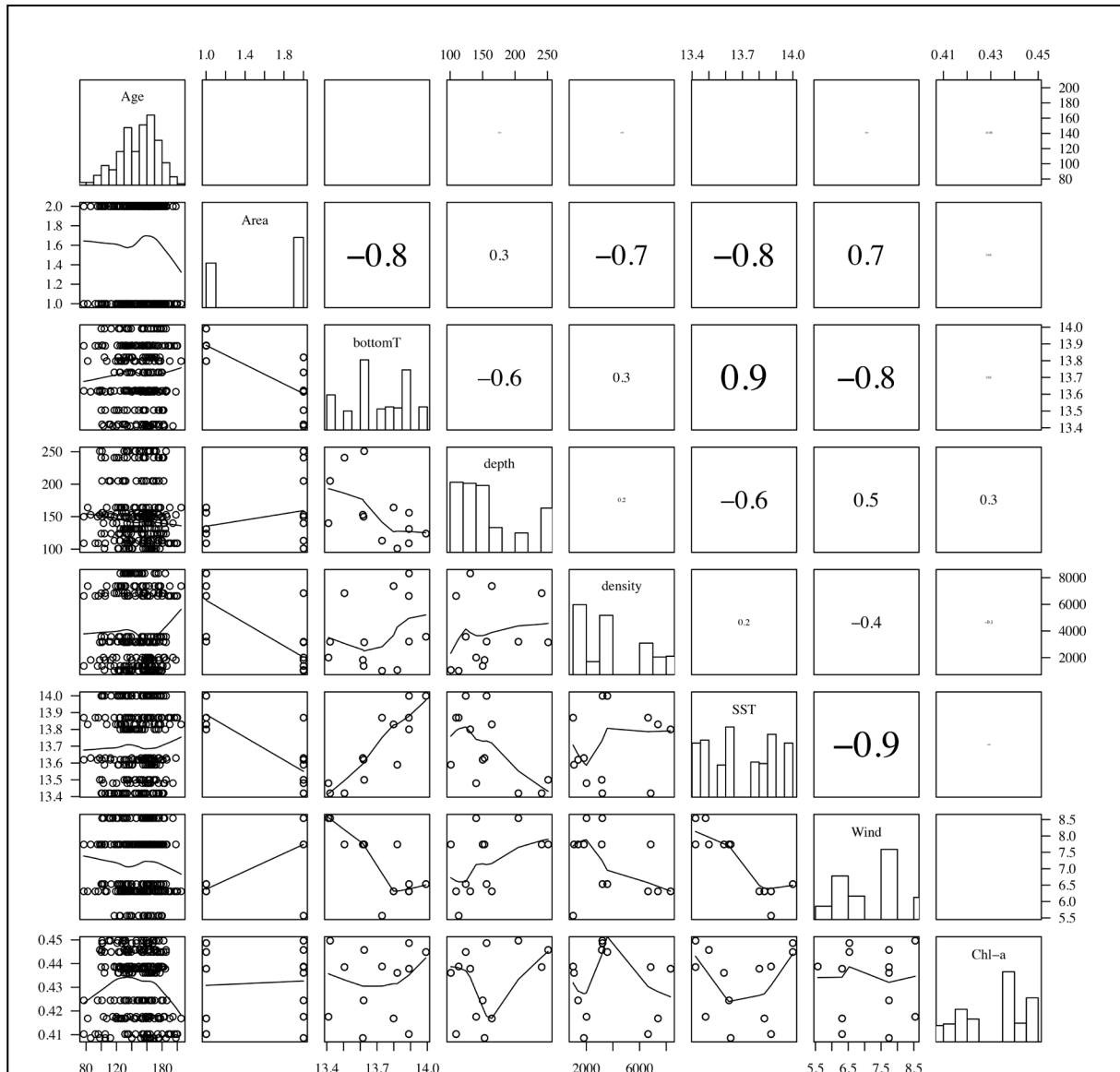
of density showed an increasing trend up to 3700 individuals km^{-2} and then a rather constant pattern at higher densities, limiting the effect caused by fitting the model in the area where values of density were missing in the database. Further, the use of the variable density as a factor (3-level factor) was tested. The results were similar to those obtained with the model that had a continuous variable of density: increasing growth rate with density, although with a slight decrease at very high densities. However, this model had a higher AIC and, therefore, was less suitable in its fit to the data than the model that used density as a continuous variable and a k value of 4. An inspection of the graphs for the model (Fig. 7) shows that there was no evidence of a pattern within the model residuals.

Discussion

Despite the ongoing debate about general issues of age estimation in European hake, reading daily growth rings on otoliths has proved to be a useful tool in the understanding of the first year of growth (Arneri and Morales-Nin, 2000). The use of annual rings on otoliths led to the assumption that the European hake grows slowly (Drouineau et al., 2010), but further studies on adult growth that have used tagging campaigns (de Pontual et al., 2003; Piñeiro et al., 2007) and analysis of otolith daily increments in juveniles (Arneri and Morales-Nin, 2000; Morales-Nin and Moranta, 2004; Kacher and Amara, 2005, Belcari et al., 2006; Piñeiro et al., 2008; Otxotorena et al., 2010) have revealed that the growth rate is probably much faster than previously thought.

Results from the present study are consistent with the main findings of recent studies on juvenile European hake growth in both the Atlantic and the Mediterranean Sea, which indicate a fast growth rate of about 0.6 mm day^{-1} during the first year of life (Morales-Nin and Moranta, 2004; Kacher and Amara, 2005; Belcari et al., 2006; Otxotorena et al., 2010). Also, the results of back-calculations of birth dates are in agreement with the available knowledge on spawning and recruitment of European hake in the western Mediterranean Sea (Maynou et al., 2003; Abella et al., 2005; Belcari et al., 2006; Recasens et al., 2008).

The present study is one of the first attempts to fit a recruit growth model for European hake with factors that could potentially affect growth dynamics. Through the application of a GAM on the length–age relationship, recruit density (number of individuals per square kilometer) was found to have a significant effect on the growth dynamics of European hake recruits; however,

part of the age range. However, in the older part of the age range, the smoothing function that describes the relationship between age and length flattened, indicating a decrease in growth rate. The effect of density on the growth rate was positive up to 3000 individuals km^{-2}, and had a weak negative effect at higher densities (Fig. 6). At the stations that had a recruit density higher than 3000 individuals km^{-2}, the length at age was on average 0.5 cm TL greater than the length at age observed at stations with lower densities.

The value of k selected for the final analysis of the effect of density, by comparison of AIC scores, was 4. The AIC was higher when values of $k > 4$ were used, and a "dome-shaped" effect caused by the lack of observations of densities between 3700 and 6000 individuals km^{-2} was evident. With k set at a value of 4, the effect

Figure 5

Pairs plot for all the explanatory variables in the data set used for this study of (*Merluccius merluccius*) in the northwestern Mediterranean Sea. The upper diagonal panel shows the Pearson's correlation coefficient, and the lower diagonal panel shows the scatterplots with a smoother added to visualize the pattern. The font size of the correlation coefficient is proportional to its estimated value.

no evidence of effects exerted by oceanographic features were found. Atmospheric processes and oceanographic features instead played a role in determining variations in recruitment strength of European hake (Alvarez et al., 2001; Maynou et al., 2003; Olivar et al., 2003; Abella et al., 2008; Bartolino et al., 2008a). Also, although Hidalgo et al. (2008) found spatial and temporal differences related to environmental and hydrographical variables in recruitment processes and condition of European hake around Balearic Islands,

they did not observe any differences in growth of this species.

The observed positive effect of recruit density could be interpreted as an optimal density window where growth is maximized. Fast growth was observed for densities of around 3000 individuals km^{-2}, and growth remained slightly constant at higher densities. Still, recruit growth remained greater in areas of high density of recruits than in areas with low density, which could correspond to habitats of low suitability, where

Table 2

Summary of the backward selection of the best model in the generalized additive model. The best model, with smoothers that are all significant and that has the lowest AIC value, is highlighted in bold. Explanatory variables included mean bottom temperature (temp.); mean depth; recruit density (number of individuals per square kilometer); mean concentration of chlorophyll-*a* (chl-*a*); and age (days). Depth:density is the interaction; "y" and "n" indicate the explanatory variables included and excluded in GAMs. Measures of model fitness were deviance explained (Dev. expl.), coefficient of determination (r^2), generalized cross-validation score (GCV), and Akaike's information criterion (AIC); ns=not significant: $P>0.05$; **=$P<0.01$; ***=$P<0.001$.

Mean bottom temp.	Mean depth	Chl-*a*	Recruit density	Age	Depth: density	Dev. expl. (%)	r^2	GCV	AIC
y^{ns}	y^{ns}	y^{ns}	y^{**}	y^{***}	y^{ns}	80.7	0.795	0.731	692.4
y^{ns}	y^{ns}	y^{ns}	y^{**}	y^{***}	n	80.7	0.794	0.734	691.1
n	y^{ns}	y^{ns}	y^{**}	y^{***}	n	80.6	0.794	0.737	692.3
n	n	y^{ns}	y^{***}	y^{***}	n	80.6	0.795	0.728	690.1
n	**n**	**n**	$\mathbf{y^{***}}$	$\mathbf{y^{***}}$	**n**	**80.7**	**0.795**	**0.727**	**689.3**

growth is impaired. Bromley (1989) found a negative relationship between density and growth in some gadoid (Atlantic cod, whiting, and haddock) juveniles in the North Sea.

The ecological factors that affect differences in growth between areas deserve further multiyear investigations, for example, through sampling to examine the abundance of prey, such as macrozooplankton, in the main nursery areas (Ferraton et al., 2007; Cartes et al., 2009). Indirect evidence of the environmental quality of European hake nurseries in the Mediterranean Sea has been inferred from their high spatiotemporal stability (Fiorentino et al., 2003; Colloca et al., 2009). In the Ligurian Sea and Tyrrhenian Sea, after 2 months spent in the pelagic environment (in the pres-
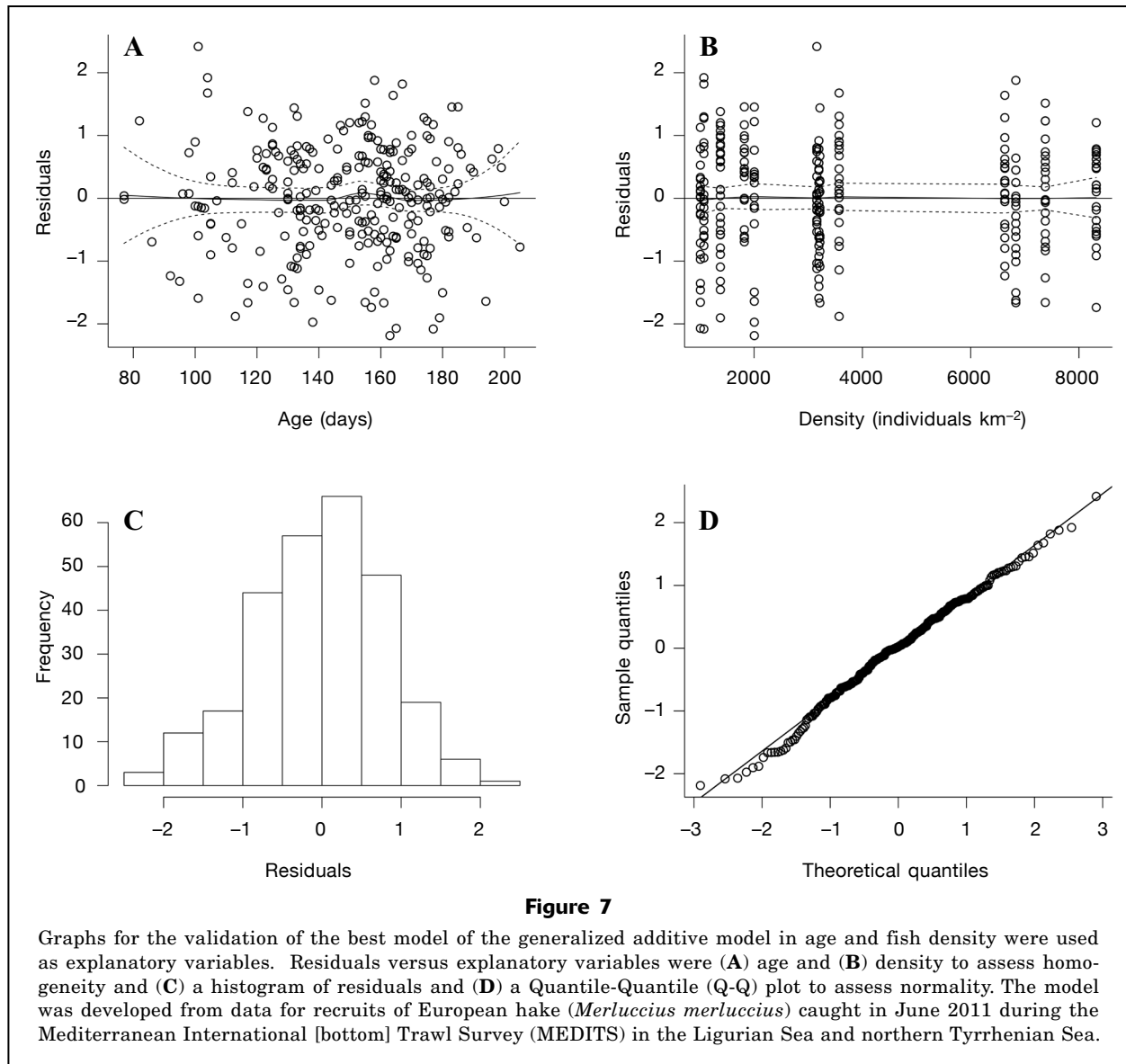
ent study; also, see Belcari et al., 2006), European hake larvae were transported by eddies and frontal systems to areas of relatively high planktonic production that resulted from upwelling (Abella et al., 2008). These areas are located along the shelf break (Colloca et al., 2004), where production is enhanced by upwelling and water turbulence, both of which increase the transport and nutrient input of organic matter into the water column (Pinazo et al., 1996). The entire trophic chain, therefore, is increased, including a positive effect on the main prey of European hake recruits, in particular euphausiids and mysids, which reach their highest diurnal abundance on the shelf break (Colloca et al., 2004).

The high spatial stability over time of the main hake nurseries in the Ligurian and Tyrrhenian Seas
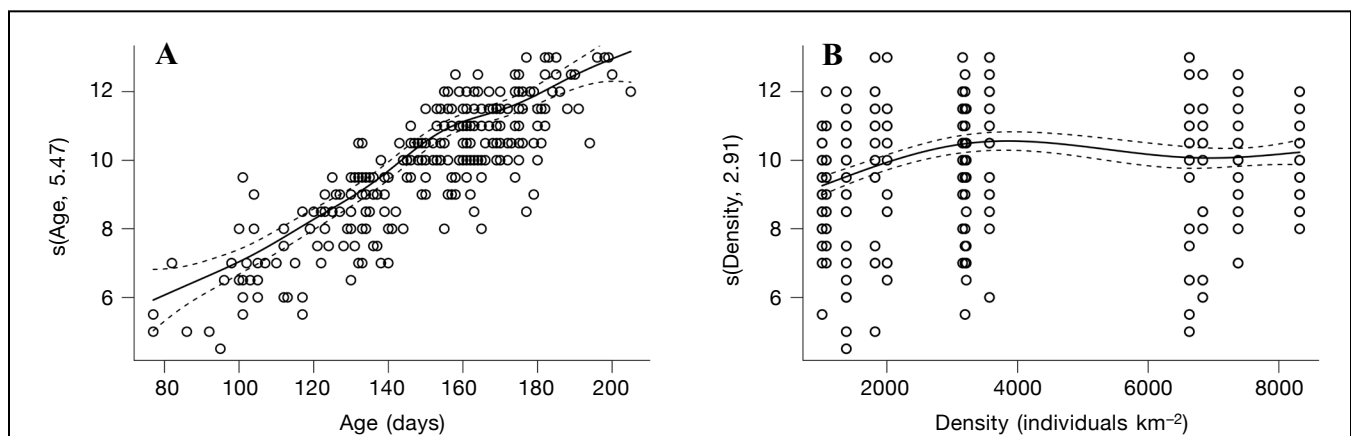
Figure 6

Estimated smoothing curves for the optimal generalized additive model representing the effects of (**A**) age (days) and (**B**) recruit density (number of individuals per square kilometer) on European hake (*Merluccius merluccius*) recruits caught in June 2011 during the Mediterranean International [bottom] Trawl Survey (MEDITS) in the Ligurian Sea and northern Tyrrhenian Sea.

Figure 7

Graphs for the validation of the best model of the generalized additive model in age and fish density were used as explanatory variables. Residuals versus explanatory variables were (**A**) age and (**B**) density to assess homogeneity and (**C**) a histogram of residuals and (**D**) a Quantile-Quantile (Q-Q) plot to assess normality. The model was developed from data for recruits of European hake (*Merluccius merluccius*) caught in June 2011 during the Mediterranean International [bottom] Trawl Survey (MEDITS) in the Ligurian Sea and northern Tyrrhenian Sea.

presents a potentially valuable feature for conservation and management purposes—one that, for instance, could be leveraged to ensure long-term effectiveness of no-take areas: Colloca et al. (2009) estimated that the closure of highly persistent nurseries would result in a small reduction of the exploitable fishery area (around 5%) and the protection of a considerable fraction (40%) of the estimated total number of recruits.

In a recent study, Cannella et al. (2011) found high hepatosomatic index values, a proxy for body condition, in recruits of European hake from areas of high density in the Tyrrhenian Sea, support the hypothesis that high-density nurseries around the shelf break are high-quality areas where juveniles find environmental conditions of food and temperature that are appropriate for survival and growth.

The present study is limited to growth estimation from a single year. However, although a longer time series of multiyear data is needed to sufficiently understand the role of environmental variables and density-based factors on growth, the results from the present study provide a first baseline and rationale in corroborating the key role played by high-quality nurseries for recruitment success. The results from this study indicate that European hake recruits grow faster inside their main nurseries than outside them, thereby increasing their chance to survive before they migrate to shallower areas on the continental platform. According to the definition by Dahlgren et al. (2006), these areas can be regarded as "effective juvenile habitats." In the areas that were identified as effective juvenile habitats, environmental characteristics (e.g., food avail-

ability and protection to predation) enhance juvenile condition and growth.

Juveniles of European hake are exposed to trawl fisheries after bottom settlement in their nursery grounds. Therefore, a reduction in fishing mortality of immature fish could be a fundamental prerequisite for sustainable fisheries. The implementation of the following requirements—use of a large mesh size, square-mesh panels, and selection grids in trawl fisheries—has reduced the bycatch of juvenile European hake (Sardà et al., 2004; Lucchetti, 2008). However, these measures may not be sufficiently effective in protecting juveniles and nursery areas. In fact, the use of gear selectivity as a fishery management tool without adequate research into the fate of escaping juvenile fish should be cause for concern for any fishery (Chopin and Arimoto, 1995). Moreover, trawling activities are known to cause alterations to the bottom of the seafloor, reducing habitat complexity and altering benthic community structure (Kaiser et al., 2002), both of which are fundamental components of habitat for juvenile European hake. Therefore, a deeper understanding of the importance of the quality of recruitment habitats (i.e., nurseries) on the growth and the survival of juveniles of European hake is a challenging task that could be relevant for conservation purposes (e.g., protection of nursery grounds).

Acknowledgments

Literature cited

Abella, A., F. Serena, and M. Ria.
   2005. Distributional response to variations in abundance over spatial and temporal scales for juveniles of European hake (*Merluccius merluccius*) in the Western Mediterranean Sea. Fish. Res. 71:295–310. doi: 10.1016/j.fishres.2004.08.036.
Abella, A., F. Fiorentino, A. Mannini, and L. Orsi Relini.
   2008. Exploring relationships between recruitment of European hake (*Merluccius merluccius* L. 1758) and environmental factors in the Ligurian Sea and Strait of Sicily (Central Mediterranean). J. Mar. Syst. 71:279–293. doi: 10.1016/j.jmarsys.2007.05.010.
Agostini, V. N., A. N. Hendrix, A. B. Hollowed, C. D. Wilson, S. D. Pierce, and R. C. Francis.
   2008. Climate–ocean variability and Pacific hake: a geostatistical modeling approach. J. Mar. Syst. 71:237–248. doi: 10.1016/j.jmarsys.2007.01.010.
Aldebert, Y., L. Recasens, and J. Lleonart.
   1993. Analysis of gear interactions in a hake fishery: the case of the Gulf of Lions (NW Mediterranean). Sci. Mar. 57:207–217.
Alvarez, P., L. Motos, A. Uriarte, and J. Egeña.
   2001. Spatial and temporal distribution of European hake, *Merluccius merluccius* (L.), eggs and larvae in relation to hydrographical conditions in the Bay of Biscay. Fish. Res. 50:111–128. doi: 10.1016/S0165-7836(00)00245-9.
Arneri, E., and B. Morales-Nin.
   2000. Aspects of early life history of European hake from the central Adriatic. J. Fish Biol. 56:1368–1380. doi: 10.1006/jfbi.2000.1255.
Bartolino, V., F. Colloca, P. Sartor, and G. Ardizzone.
   2008a. Modelling recruitment dynamics of Hake *Merluccius merluccius*, in the central Mediterranean in relation to key environmental variables. Fish. Res. 92:277–288. doi: 10.1016/j.fishres.2008.01.007.
Bartolino, V., A. Ottavi, F. Colloca, G. D. Ardizzone, and G. Stefánsson.
   2008b. Bathymetric preferences of juvenile European hake (*Merluccius merluccius*). ICES J. Mar. Sci. 65:963–969. doi: 10.1093/icesjms/fsn079.
Bartolino, V., F. Colloca, L. Taylor, and G. Stefansson.
   2011. First implementation of a Gadget model for the analysis of hake in the Mediterranean. Fish. Res. 107:75–83. doi: 10.1016/j.fishres.2010.10.010.
Baudron, A. R., C. L. Needle, and C. T. Marshall.
   2011. Implications of a warming North Sea for the growth of haddock *Melanogrammus aeglefinus*. J. Fish Biol. 78:1874–1889. doi: 10.1111/j.1095-8649.2011.02940.x.
Bhattacharya, C. G.
   1967. A simple method of resolution of a distribution into Gaussian components. Biometrics 23:115–135. doi: 10.2307/2528285.
Beggs, S. E., M. Cardinale, R. J. Gowen, and V. Bartolino.
   2014. Linking cod (*Gadus morhua*) and climate: investigating variability in Irish Sea cod recruitment. Fish. Oceanogr. 23:54–64. doi: 10.1111/fog.12043.
Belcari P., A. Ligas, and C. Viva.
   2006. Age determination and growth of juveniles of the European hake, *Merluccius merluccius* (L., 1758), in the northern Tyrrhenian Sea (NW Mediterranean). Fish. Res. 78:211–217. doi: 10.1016/j.fishres.2006.01.006.
Bertrand, J. A., L. Gil de Sola, C. Papaconstantinou, G. Relini, and A. Souplet.
   2002. The general specifications of the MEDITS surveys. Sci. Mar. 66(suppl. 2):9–17.
Bromley, P. J.
   1989. Evidence for density-dependent growth in North Sea gadoids. J. Fish Biol. 35(suppl. A):117–123. doi: 10.1111/j.1095-8649.1989.tb03052.x.
Cannella, M., F. Colloca, and G. D. Ardizzone.
   2011. Evaluation of habitat's role for recruitment's success of hake (*Merluccius merluccius*) in the Tyrrhenian Sea. Biol. Mar. Mediterr. 18:12–15.
Cardinale, M., H.-J. Rätz, and A. Charef (eds.).
   2011. Scientific, Technical and Economic Committee for Fisheries (STECF) assessment of Mediterranean Sea stocks—part 2 (STECF-11-14), 610 p. Publications Office of the European Union, Luxembourg. doi: 10.2788/13960.
Cartes, J. E., M. Hidalgo, V. Papiol, E. Massutí, and J. Moranta.
   2009. Changes in the diet and feeding of the hake *Merluccius merluccius* at the shelf-break of the Balearic Islands: influence of the mesopelagic-boundary community. Deep-Sea Res. Oceanogr., I 56:344–365. doi: 10.1016/j.dsr.2008.09.009.

Chopin, F. S., and T. Arimoto.
    1995. The condition of fish escaping from fish-
        ing gears—a review. Fish. Res. 21:315–327. doi:
        10.1016/0165-7836(94)00301-C.
Colloca, F., P. Carpentieri, E. Balestri, and G. D. Ardizzone.
    2004. A critical habitat for Mediterranean fish resources:
        shelf-break areas with *Leptometra phalangium* (Echino-
        dermata: Crinoidea). Mar. Biol. 145:1129–1142. doi:
        10.1007/s00227-004-1405-8.
Colloca, F., V. Bartolino, G. J. Lasinio, L. Maiorano, P. Sartor,
    and G. Ardizzone.
    2009. Identifyng fish nurseries areas using density and
        persistence measures. Mar. Ecol. Prog. Ser. 381:287–
        296. doi: 10.3354/meps07942.
Dahlgren, C. P., G. T. Kelliston, A. J. Adams, B. M. Gillanders,
    M. S. Kendall, C. A. Layman, J. A. Ley, I. Nagelkerken, and
    J. E. Serafy.
    2006. Marine nurseries and effective juvenile habi-
        tats: concepts and applications. Mar. Ecol. Prog. Ser.
        312:291–295. doi: 10.3354/meps312291.
de Pontual, H., M. Bertignac, A. Battaglia, G. Bavouzet, P. Mo-
    guedet, and A.-L. Groison.
    2003. A pilot tagging experiment on European hake
        (*Merluccius merluccius*): methodology and preliminary
        results. ICES J. Mar. Sci. 60:1318–1327. doi: 10.1016/
        S1054-3139(03)00149-8.
Drouineau, H., S. Mahévas, M. Bertignac, and D. Duplisea.
    2010. A length-structured spatially explicit model for
        estimating hake growth and migration rates. ICES J.
        Mar. Sci. 67:1697–1709. doi: 10.1093/icesjms/fsq042.
Ferraton, F., M. Harmelin-Vivien, C. Mellon-Duval, and A.
    Souplet.
    2007. Spatio-temporal variation in diet may affect condi-
        tion and abundance of juvenile European hake in the
        Gulf of Lions (NW Mediterranean). Mar. Ecol. Prog.
        Ser. 337:197–208. doi: 10.3354/meps337197.
Fiorentino, F., G. Garofalo, A. De Santi, G. Bono, G. B. Giusto,
    and G. Norrito.
    2003. Spatio-temporal distribution of recruits (0 group)
        of *Merluccius merluccius* and *Phycis blennoides* (Pi-
        sces, Gadiformes) in the Strait of Sicily (Central
        Mediterranean). Hydrobiologia 503:223–236. doi:
        10.1023/B:HYDR.0000008485.85468.ef.
Gasparini, G. P., G. Zodiatis, M. Astraldi, C. Galli, and S.
    Sparnocchia.
    1999. Winter intermediate water lenses in the Ligu-
        rian Sea. J. Mar. Syst. 20:319–332. doi: 10.1016/
        S0924-7963(98)00089-X.
Hastie, T. J., and R. J. Tibshirani.
    1990. Generalized additive models. Monogr. Stat. Appl.
        Prob ability 43, 335 p. Chapman & Hall, Boca Raton,
        FL.
Hidalgo, M., E. Massutí, J. Moranta, J. Cartes, J. Lloret, P.
    Oliver, and B. Morales-Nin.
    2008. Seasonal and short spatial patterns in European
        hake (*Merluccius merluccius* L.) recruitment process at
        the Balearic Islands (western Mediterranean): the role
        of environment on distribution and condition. J. Mar.
        Syst. 71:367–384. doi: 10.1016/j.jmarsys.2007.03.005.
Hurst, T. P., J. H. Moss, and J. A. Miller.
    2012. Distributional patterns of 0-group Pacific cod (*Ga-
        dus macrocephalus*) in the eastern Bering Sea under
        variable recruitment and thermal conditions. ICES J.
        Mar. Sci. 69:163–174. doi: 10.1093/icesjms/fss011.

Kacher, M., and R. Amara.
    2005. Distribution and growth of 0-group European
        hake in the Bay of Biscay and Celtic Sea: a spatial and
        inter-annual analyses. Fish. Res. 71:373–378. doi:
        10.1016/j.fishres.2004.08.034.
Kaiser, M. J., J. S. Collie, S. J. Hall, S. Jennings, and I. R.
    Poiner.
    2002. Modification of marine habitat by trawling activi-
        ties: prognosis and solutions. Fish Fish. 3:114–136. doi:
        10.1046/j.1467-2979.2002.00079.x.
Köster, F. W., C. Möllmann, H.-H. Hinrichsen, K. Wieland, J.
    Tomkiewicz, G. Kraus, R. Voss, A. Makarchouk, B. R. MacK-
    enzie, M. A. St. John, D. Schnack, N. Rohlf, T. Linkowski,
    and J. E. Beyer.
    2005. Baltic cod recruitment—the impact of climate
        variability on key processes. ICES J. Mar. Sci. 62:1408–
        1425. doi: 10.1016/j.icesjms.2005.05.004.
Lucchetti, A.
    2008. Comparison of diamond- and square-mesh codends
        in the hake (*Merluccius merluccius* L. 1758) trawl fish-
        ery of the Adriatic Sea (central Mediterranean). Sci.
        Mar. 72:451–460.
Maynou, F., J. Lleonart, and J. E. Cartes.
    2003. Seasonal and spatial variability of hake (*Mer-
        luccius merluccius* L.) recruitment in the NW Medi-
        terranean. Fish. Res. 60:65–78. doi: 10.1016/
        S0165-7836(02)00062-0.
Morales-Nin, B., and J. Moranta.
    2004. Recruitment and post-settlement growth of juve-
        nile *Merluccius merluccius* on the western Mediterra-
        nean shelf. Sci. Mar. 68:399–409.
Murua, H.
    2010. Chapter two—the biology and fisheries of Euro-
        pean hake, *Merluccius merluccius*, in the north-east
        Atlantic. Adv. Mar. Biol. 58:97–154. doi: 10.1016/
        B978-0-12-381015-1.00002-2.
Nezlin, N. P., G. Lacroix, A. G. Kostianoy, and S. Djenidi.
    2004. Remotely sensed seasonal dynamic of phytoplank-
        ton in the Ligurian Sea in 1997–1999. J. Geophys. Res.
        109: C07013. doi: 10.1029/2000JC000628.
Norbis, W., M. I. Lorenzo, and G. J. Torres.
    1999. Intra-annual growth variations of young-of-the-
        year hake (*Merluccius hubbsi*) of the Uruguayan con-
        tinental shelf based on otolith analysis. Fish. Res.
        44:129–137. doi: 10.1016/S0165-7836(99)00059-4.
Olivar, M. P., G. Quílez, and M. Emelianov.
    2003. Spatial and temporal distribution and abundance
        of European hake, *Merluccius merluccius*, eggs and lar-
        vae in the Catalan coast (NW Mediterranean). Fish.
        Res. 60:321–331. doi: 10.1016/S0165-7836(02)00139-X.
Orfila, A., A. Alvarez, J. Tintoré, A. Jordi, and G. Basterrectxea.
    2005. Climate tele-connections at monthly time scales
        in the Ligurian Sea inferred from satellite data. Prog.
        Oceanogr. 66:157–170.
Orsi Relini, L., C. Papaconstantinou, S. Jukic-Peladic, A. Sou-
    plet, L. Gil de Sola, C. Piccinetti, S. Kavadas, and M. Rossi.
    2002. Distribution of the Mediterranean hake popula-
        tions (*Merluccius merluccius smiridus* Rafinesque, 1810)
        (Osteichthyes: Gadiformes) based on six years monitor-
        ing by trawl-surveys: some implications for manage-
        ment. Sci. Mar. 66(suppl. 2):21–38.
Otxotorena, U., G. Díez, E. López de Abechuco, M. Santurtún,
    and P. Lucio.
    2010. Estimation of age and growth of juvenile hake
        (*Merluccius merluccius* Linnaeus, 1758) of the Bay

of Biscay and Great Sole by means of the analysis of macro and microstructure of the otoliths. Fish. Res. 106:337–343. doi: 10.1016/j.fishres.2010.09.001.

Panfili, J., H. de Pontual, H. Troadec, and P. J. Wright (eds.).
2002. Manual of fish sclerochronology, 464 p. Ifremer-IRD coedition, Brest, France.

Pinazo, C., P. Marsaleix, B. Millet, C. Estournel, and R. Vélhil.
1996. Spatial and temporal variability of phytoplankton biomass in upwelling areas of the northwestern Mediterranean: a coupled physical and biochemical modelling approach. J. Mar. Syst. 7:161–191. doi: 10.1016/0924-7963(95)00028-3.

Piñeiro, C., J. Rey, H. de Pontual, and R. Goñi.
2007. Tag and recapture of European hake (*Merluccius merluccius* L.) off the Northwest Iberian Peninsula: first results support fast growth hypothesis. Fish. Res. 88:150–154. doi: 10.1016/j.fishres.2007.08.015.

Piñeiro, C., J. Rey, H. de Pontual, and A. García.
2008. Growth of Northwest Iberian juvenile hake estimated by combining sagittal and transversal otolith microstructure analyses. Fish. Res. 93:173–178. doi: 10.1016/j.fishres.2008.04.001.

R Core Team.
2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austira. [Available from http://www.r-project.org/.]

Recasens, L., V. Chiericoni, and P. Belcari.
2008. Spawning pattern and batch fecundity of the European hake (*Merluccius merluccius* (Linnaeus, 1758)) in the western Mediterranean. Sci. Mar. 72:721–732.

San Martín, M. A., R. Wiff, J. C. Saavedra-Nievas, L. A. Cubillos, and S. Lillo.
2013. Relationship between Chilean hake (*Merluccius gayi gayi*) abundance and environmental conditions in the central-southern zone of Chile. Fish. Res. 143:89–97. doi: 10.1016/j.fishres.2013.01.010.

Sardà, F., B. Molí, and I. Palomera.
2004. Preservation of juvenile hake (*Merluccius merluccius*, L.) in the western Mediterranean demersal trawl fishery by using sorting grids. Sci. Mar. 68:435–444.

Sbrana, M., P. Belcari, S. De Ranieri, P. Sartor, and C. Viva.
2007. Comparison of the catches of European hake (*Merluccius merluccius*, L. 1758) taken with experimental gillnets of different mesh sizes in the northern Tyrrhenian Sea (western Mediterranean). Sci. Mar. 71:47–56.

Steingrund, P., and E. Gaard.
2005. Relationship between phytoplankton production and cod production on the Faroe Shelf. ICES J. Mar. Sci. 62:163–176. doi: 10.1016/j.icesjms.2004.08.019.

Stige, L. C., G. Ottersen, K. Brander, K.-S. Chan, and N. C. Stenseth.
2006. Cod and climate: effect of the North Atlantic Oscillation on recruitment in the North Atlantic. Mar. Ecol. Prog. Ser. 325:227–241. doi: 10.3354/meps325227.

Woodbury, D., A. B. Hollowed, and J. A. Pearce.
1995. Interannual variation in growth rates and back-calculated spawn dates of juvenile Pacific hake (*Merluccius productus*). *In* Recent developments in fish otolith research (D. H. Secor, J. M. Dean, and S. E. Chipana, eds.), p. 481–496. Univ. S. Carolina Press, Columbia, SC.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith.
2009. Mixed effects models and extensions in ecology with R, 574 p. Statistics for biology and health. Springer, New York. doi: 10.1007/978-0-387-87458-6.