Temporal and spatial dynamics of hake *Merluccius merluccius* recruitment in the Tyrrhenian and Ligurian Sea (Mediterranean)

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Joint Research Doctoral Thesis

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LIST OF PUBBLICATIONS

I. **Bartolino V.**, Ottavi A., Colloca F., Ardizzone G.D., Stefansson G. 2008. Bathymetric preferences in hake juveniles (*Merluccius merluccius*). *ICES J. Mar. Sci.*, 65(6): 963-969, doi: 10.1093/icesjms/fsn079

II. Colloca F., **Bartolino V.**, Jona Lasinio G., Maiorano L., Ardizzone G.D. 2009. Identifying fish nurseries using fish density and persistence measures. *Mar. Ecol. Progr. Ser.*, 381: 287-296, doi: 10.3354/meps07942

III. **Bartolino V.**, Colloca F., Sartor P., Ardizzone G.D. 2008. Modelling recruitment dynamics in hake, *Merluccius merluccius*, in relation to key environmental variables. *Fish. Res.*, 92: 277-288, doi: 10.1016/j.fishres.2008.01.007

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INTRODUCTION

In exploited fish populations, large part of the variance in the stock size can be related to high variability in recruitment (Fogarty et al., 1991). Highly variable recruitment is a direct consequence of the life history strategy of many exploited marine species. Population fecundity and random variation in survival rates during the early life stages, provide the bases for recruitment fluctuations.

Understanding temporal and spatial dynamics of recruitment and the role played by coupling physical and biological processes has been one of the main topics of interest for fisheries science during the last decades. Moreover, the study of the relationship of recruitment with the stock size and environmental variability has been made more difficult by the confounding effect of fishery.

In this respect, European hake in the Mediterranean sea is relevant and of interest considering also the central ecological (Colloca et al., 2003; Carpentieri et al., 2005) and economic (FAO, 2008) role played by this species in the demersal community.

The European hake fishery in the Mediterranean is a very old story of exploitation started since the beginning of the 20th century . As for most fisheries worldwide, the advent of steam trawlers in the '50s and '60s changed the hake exploitation in the Mediterranean that assumed very soon the characteristics of an unsustainable use of the resource. Furthermore, the common use of very small mesh size and a market able to appreciate small size individuals (much below the mean length of maturity) made the hake fishery in the Mediterranean mostly a juvenile fishery (Aldebert et al., 1993; Colloca et al., 2000).

Although the hake population showed very soon clear signs of overexploitation such as a reduction in the adult portion of the stock (Abella and Serena, 1998), there are some key features in the biology of this species related to its high reproductive potentiality that make the hake fishery still productive and the species still a prime in the commercial landings in terms of quality, quantity and economic value.

The lack of any evident decreasing trend in hake recruitment, as found for some other marine species, could represent a 'recruitment paradox' (Rothschild, 1986) but at the same time a key aspect of the biology of this species worth of investigation to understand its high productivity. The large variability in hake recruitment is particularly evident in the Tyrrhenian and Ligurian sea (fig. 1) where some of the highest concentrations of the whole Mediterranean occur.

Different studies showed the importance of the western coasts of Italy for the recruitment of hake in the western basin (Ardizzone and Corsi, 1997; Orsi Relini et al., 2002; Abella et al, 2005). Even though, there is a lack of data on the spatial migration pattern of hake from recruitment areas, we cannot exclude a spillover effect over a wider geographical area.

Many species of the genus *Merluccius* show well defined ontogenetic phases across their life cycle (Alheit and Pitcher, 1995). Resolution of the temporal and spatial dynamics of these phases is the first step towards the understanding of the mechanisms and processes that determine these

dynamics and can improve possibilities for management and conservation of resources (Sparre et al., 1989).

The main objectives of this thesis can be summarised as follows:

- identification of recruit and juvenile post-recruit stages in the European hake according to bathymetric preferences
- modelling spatial distribution of hake recruits
- identification of nursery areas
- identification of the length of migration from nursery areas and its inter-annual variability
- modelling temporal dynamics of hake recruitment in relation to key environmental variables
- modelling hake population structure and dynamics
- identification of no-take marine protected areas through a multi-species approach that includes specific conservation targets for hake and other commercial species
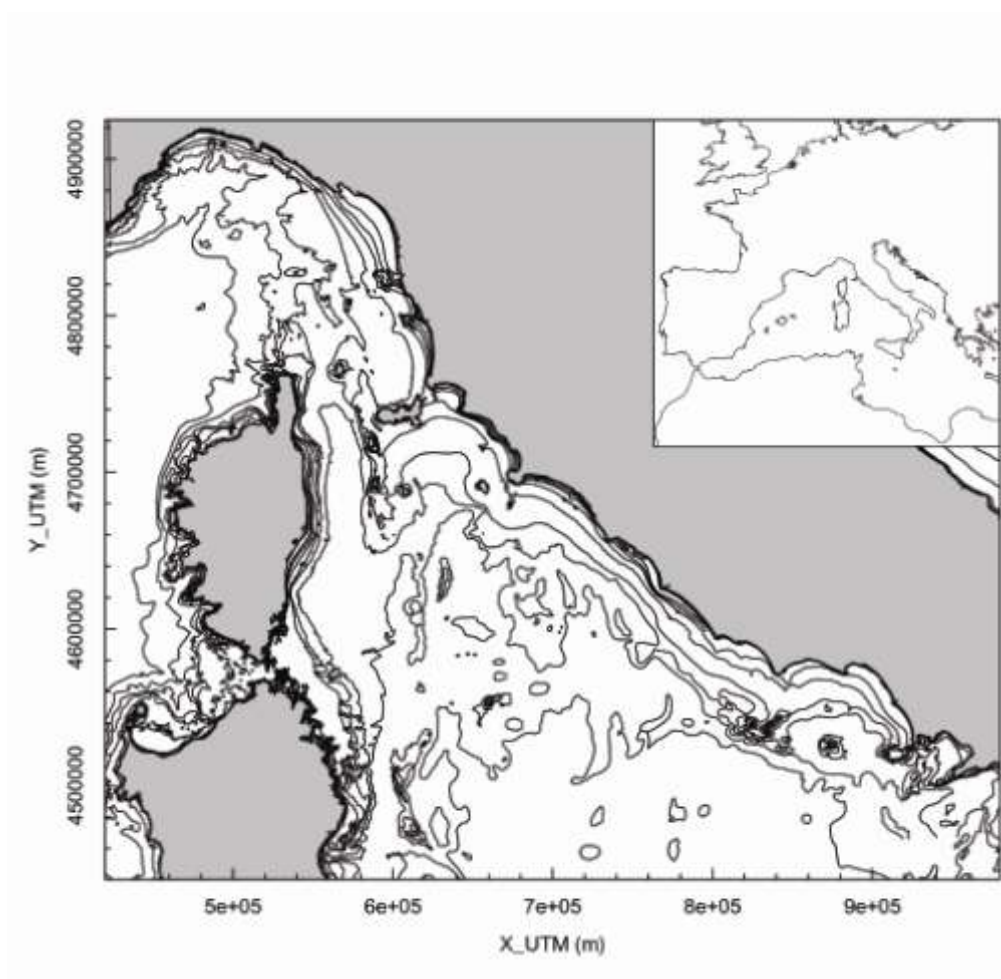

Fig. 1 - Map of the study area.

RECRUIT AND JUVENILE POST-RECRUIT LIFE STAGES OF HAKE

In fish populations ontogenetic differences can be particularly strong and many species show several well defined phases during their life. The environment that fish occupy throughout their life history may involve large differences between different stages (Sullivan et al., 2000). The identification of these life stages that characterise the life history of exploited marine species is of fundamental importance in our understanding of fish behaviour and to improve possibilities for management and conservation of resources (Sparre et al., 1989). Particular attention has been spent to the so defined "crucial stages" during which fish are more vulnerable to natural and/or anthropogenic factors that can drastically modify their survival or potentiality to reproduce or to reach the reproductive age and finally to renewal and maintain the population throughout time. Although recruitment is widely recognised as one of these crucial phases (Fogarty et al., 1991), a great confusion still exists around the theoretical and practical definition of what a fish recruit is. The most diverse and ambiguous definitions can be found in literature on the concept of recruit, and also for a highly studied species like the European hake there is no consensus or accepted approach.

If we consider that hake is highly exploited by the Mediterranean fisheries and that a large portion of landings, especially trawl-landing, is represented by juveniles or more generally by immature individuals, we can understand the importance of a proper definition of recruits of hake and the identification of the boundaries between different phases.

Although no specific analysis was carried on the bathymetric preference of the European hake, indirect information came from studies on its spatial distribution (i.e. Abella et al., 2005; Fiorentino et al., 2003). An ontogenetic pattern of distribution was reported by Abella et al. (2005), with age0 fish that were distributed mostly at depths between 100 and 250 m, whilst age1 individuals were mainly concentrated in shallower waters on the shelf. But most of previous analyses are not specifically applied to identify different life stages and largely rely on growth estimations, thus introduce biases related to our ability to correctly estimate hake growth (growth rate estimation is under a strong debate of the scientific community, i.e. Garcia-Rodriguez and Esteban, 2002).

A new approach based on the use of thin plate spline was developed for this purpose (paper I). The great flexibility of this non-parametric regression technique made its application very easy and suitable for ecologists very often more interested in data analysis rather than formal statistical testing.

The analysis is divided in three steps:
- Calculation indices of abundance (n km^{-2}) from autumn trawl survey data for each haul and 1-cm length class
- Compilation a depth x length matrix based on the calculation of a relative depth preference index ($Y_{l,d}$)
- Fitting a two-dimensional surface over the length x depth matrix

Hake showed a stable pattern of depth preference in the 6-year dataset examined, with two distinct depth-length clusters (fig. 2). Small hake below a certain threshold length were found over the continental slope, while large hake preferred shallower waters, on the shelf.

Small hake below a certain threshold length had the highest preference for 170-220 m depth and appear to move slightly deeper when they reached 10 cm in length. Large hake persisted on the continental shelf with a preference for 70-100 m depth, especially when fish reached 18-20 cm in total length.
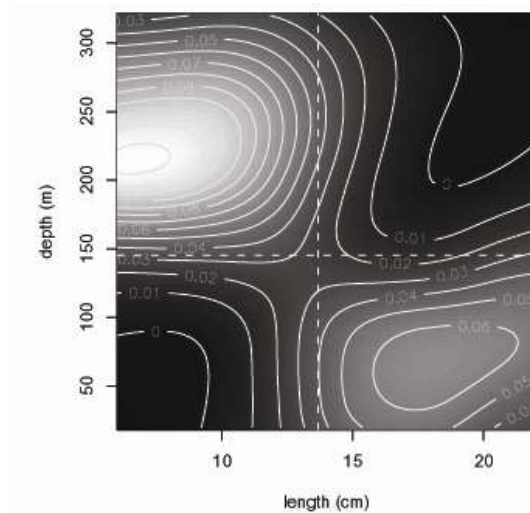

Fig. 2 - Length-depth surface estimated for hake in 2002.

Length and depth of migration have been defined as the length at which the minimum depth preference was shown and it ranged between 12.4 and 15.8 cm depending on the year. This length represents a clear and objective threshold between two immature stages of the life cycle of hake and was interpreted as the real end of the recruit phase (paper I).

These outcomes well fit previous results on the trophic ecology of hake (Giuchet, 1995; Carpentieri et al., 2005) and allow a more clear interpretation of the ecology of this species (fig. 3). Results from stomach data collected in the same area and analysed by our laboratory (Carpentieri et al., 2005) demonstrated an important shift in the diet of hake when fish reach approximately 15-16 cm in total length. Small hake are zooplanktivorous, feeding on euphausiids and mysiids (mainly *Nictiphanes couchi* and *Lophogaster typicus*) that are followed together with other epiplanktonic crustaceans during they wide nictemeral migrations (Casanova, 1970; Franqueville, 1971; Vallet and Dauvin, 2001). Sabatés *et al*. (1989) associated high concentrations and peaks of zooplankton with the existence of permanent frontal systems offshore that consequently can attract zooplanktivorous predators, such as recruits of hake. Shelf break bottoms along the Tyrrhenian coasts have been reported as areas characterized by the occurrence of large patches of macrozooplanktonic organism (Colloca *et al*. 2004). A similar dynamic was observed off the coast of California, near the shelf break, where large shoals of Pacific hake (*M. productus*) overlap large patches of euphausiids (Swartzman, 1999).
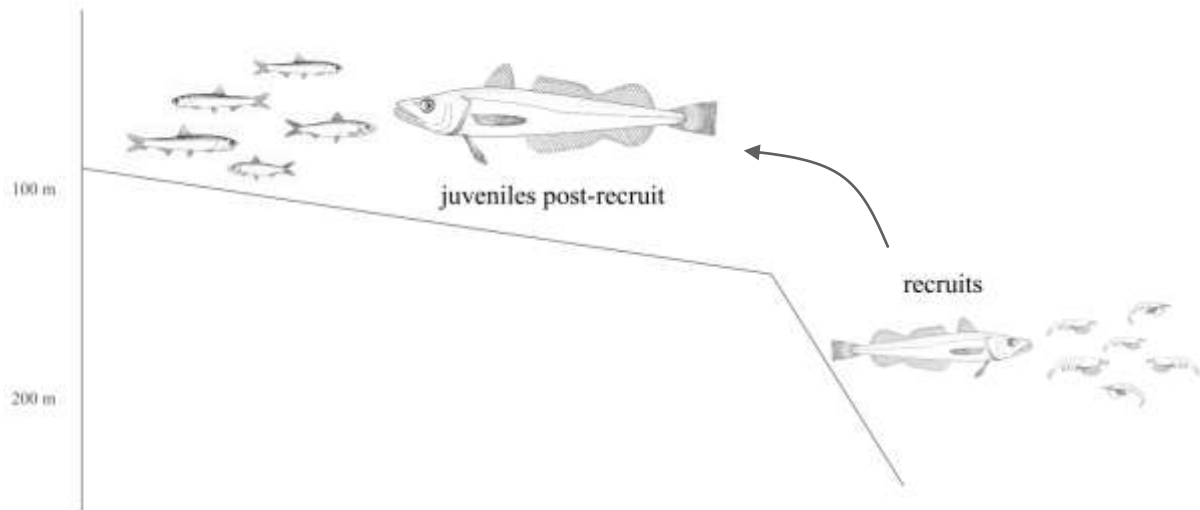
Fig. 3 - hake recruits and post-recruits bathymetric segregation with migration from the continental slope (170-220 m) to the shelf (<120m) and the associated main preys.

Above the 15-16 cm length, hake drastically change its diet mostly toward small pelagic fish preys (Carpentieri et al., 2005). *Sardina pilchardus* and *Engraulis encrasicolus* are the main preys and the bathymetric preference observed for hake larger than 15 cm strongly agrees with the clupeids behaviour of forming schools largely distributed on the coastal continental shelf (Fisher et al., 1987).

SPATIAL DISTRIBUTION OF HAKE RECRUITS

A geostatistical model was built to study the spatial distribution of hake recruits in the Tyrrhenian and Ligurian sea (paper II). Within a Bayesian framework, we implemented preliminary analyses on the distribution of hake for the same area based on ordinary kriging procedure (Colloca et al., 2006). Previous studies revealed a fairly complex spatial pattern in the distribution of hake recruits (i.e. Ardizzone and Corsi, 1997) and a strong localisation of areas with elevated concentration of recruits (Colloca et al., 2006; Abella et al., 2005).

Because available data come from trawl surveys not specifically designed for geostatistical analyses (MEDITS and GRUND projects, for more details see respectively Bertrand et al., 2002 and Relini, 1998) the development of high resolution models for recruits of hake had to face the problem of having sparse observations both in space and time.
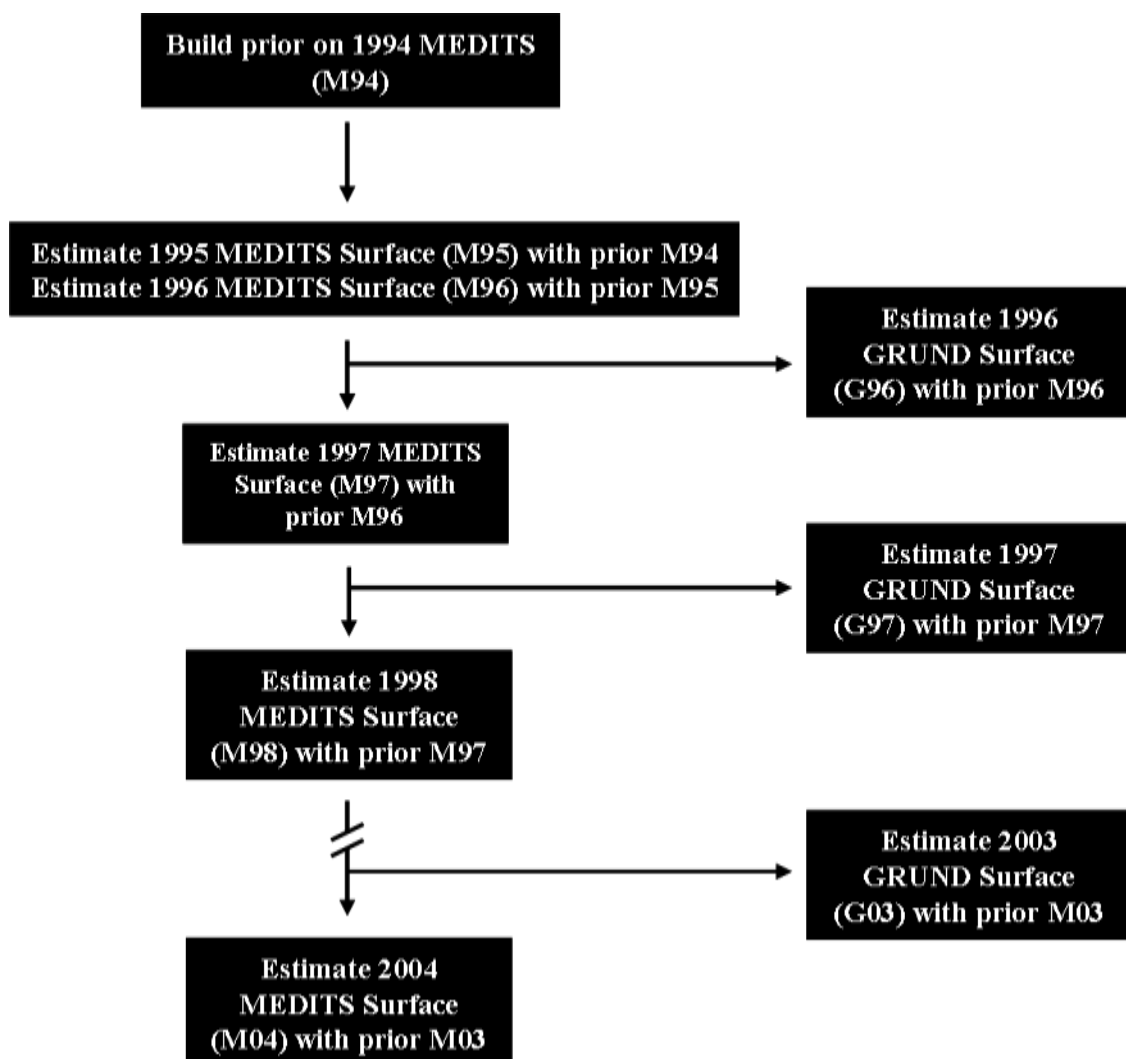

Fig. 4 - Bayesian estimation chain to map hake recruits distribution from 1994 to 2004.

One of the main advantages of the Bayesian inference is related to the use of a biological prior information that can be used explicitly and quantitatively within the model. This important feature provided a way to integrate the data from the two annual surveys within the same analytical procedure allowing a better use of the information available.

In practice the distribution of recruits estimated from the late spring-early summer survey was used as prior for the estimation on the autumn survey, through an estimation chain from 1994 to 2004 (fig. 4).

Identification of nursery areas

The problem of identifying areas with high concentration of hake recruits was of primary importance in this research and the possibility offered by the Bayesian approach to have two annual estimations (one for each trawl survey) allowed to recognize seasonal hot-spots of aggregation. No biological threshold is currently known to define hake nurseries, also considering that in a variable environment and under strong recruitment fluctuations it would be impossible and meaningless defining a single density threshold for different years. Thus we tried to identify hot-spots looking at the spatial structure of the estimated surfaces using geostatistical aggregation curves (Matheron, 1981; Petitgas, 1997, 1998).

Areas of major concentration of recruits (nursery areas) were identified at that point where the spatial distribution passed from an aggregated to a dispersed pattern through the development of a specific approach as presented in paper II (fig. 5).
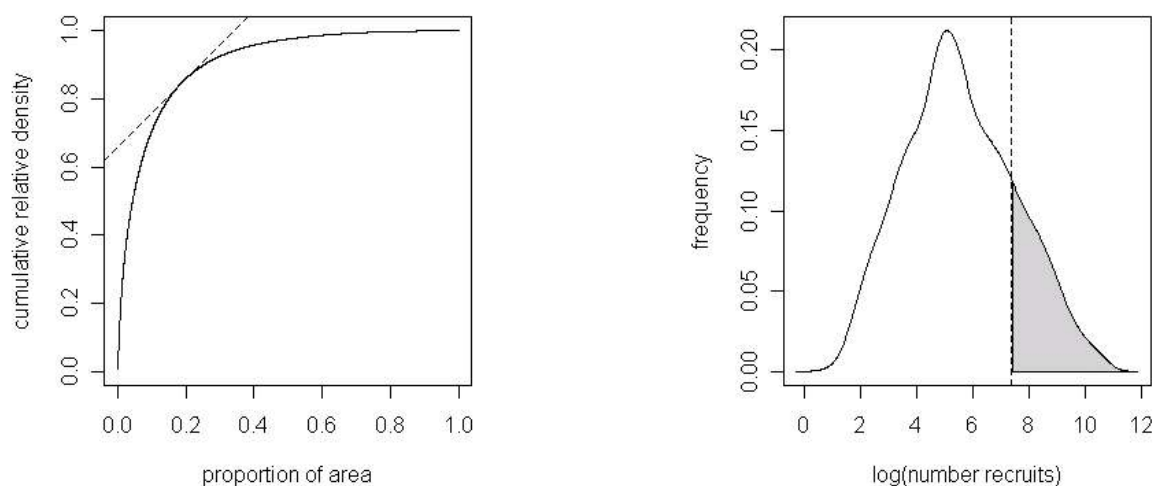
Fig. 5 - Relative geostatistical aggregation curve showing the tangent to the curve with 45° slope (left). Frequency distribution of estimated hake density with the related percentile (shade area) corresponding to the proportion of cells above the identified density threshold (right).

Time series density maps of hake recruits obtained using the Bayesian kriging procedure revealed that the distribution of recruits is clearly characterized by patchiness which appear

rather stable throughout the study period. A certain stability was also observed across the two season examined (late spring-early summer and autumn). The main temporal differences in the spatial distribution pattern are related to the dimension of the observed patches that increased in size in period of higher recruit density.
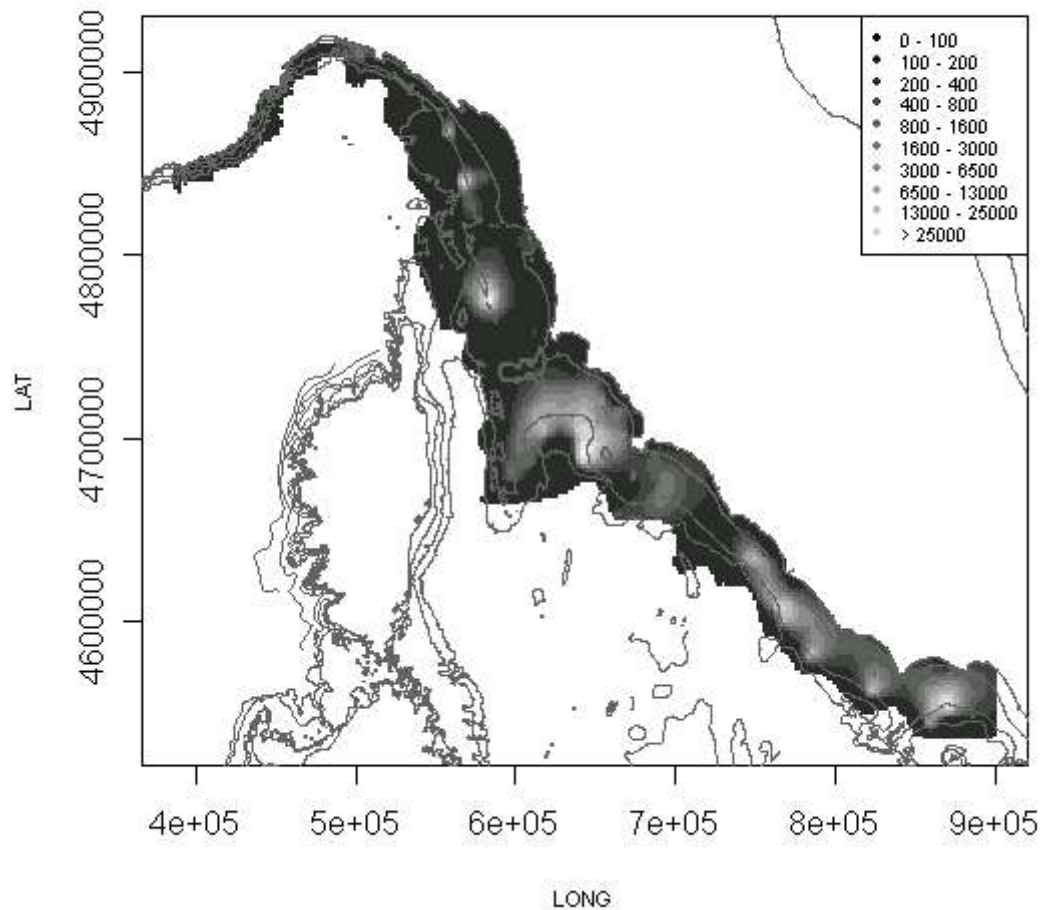

Fig. 6 - Density map of hake recruits from the early summer survey (MEDITS) in 2001.

The bathymetric preference of hake recruits for grounds deeper than 150 m (paper I) was confirmed by the spatial model (paper II) that located highest abundance of fish around the continental shelf-break and upper-slope (fig. 6). Hot-spots are found both in the northern Tyrrhenian Sea and Ligurian Sea (fig. 6) in agreement with previous studies (Colloca et al., 2006; Abella et al., 2005). The importance of these areas for bottom settlement of hake can be related to the northward pattern of current (fig. 8), that flows along the Tyrrhenian and Ligurian sea, and to the topography of the continental margin.

In the north Tyrrhenian a very high density of recruits have been found around the shelf-break, with very localised hot-spots respectively off the north-west coast of Giglio island and the southern coasts of Elba island. In the Ligurian Sea two main areas appeared regularly, between 150 and 300 m depth, north-east of Capraia island and off-shore the coast between La Spezia and

Livorno. In the central Tyrrhenian the identified hotspots are smaller and scattered along the shelf-break. The main areas have been detected south-east the Argentario cape and between Gaeta and the Pontine islands. Other small areas appeared in some years off-shore the main capes along the shore between Anzio and Civitavecchia (see time series maps in paper II).

The estimated average density of hake recruits showed large fluctuations throughout the period of study between 300 (Medits 1994) and 2479 (Medits 1998) fish km^{-2}. Recruit density changed widely also in the same year between the two surveys, in agreement with the existence of multiple recruitment peaks throughout the year.

The density threshold used to separate nursery from non-nursery areas varied between 246 and 3390 fish km^{-2} for the late spring survey and between 568 and 2835 fish km^{-2} for the autumn survey. The identified nurseries covered a surface variable from survey to survey between 18 and 30% of the total area. Years with higher recruitment were characterised by both higher densities and larger dimension of the main nursery area.

Temporal persistence of nursery areas

The method adopted allowed to classify each portion of the study area for its role as hake nursery during the study period (paper II). Results showed the occurrence of highly persistent nurseries (fig. 7), revealing their importance for the recruitment success of hake in the area (Table 1).

Persistence	%A	%R
$I > 40\%$	20.6	82.9
$I > 60\%$	12.4	65.6
$I > 80\%$	5.3	39.2

Table 1 - Estimated average proportion of nursery areas on the study area (%A) and mean proportion of recruits in the nurseries over the total estimated number of recruits (%R) for different levels of persistence.

The seasonal and annual stability observed in the spatial distribution of the main hake nurseries can be interpreted as a result of the quite stable water circulation pattern (fig. 8) that characterises the Tyrrhenian and Ligurian sea (Artale et al., 1994). The occurrence of oceanographic features, such as thermal fronts and upwelling allow transport, retention and survival of fish larvae in well distinct and productive areas according to the 'fundamental ocean triad' (Bakun, 1996, 1998; Agostini and Bakun, 2002; Abella et al., 2008).

We can expect that these habitats, also characterized by very high densities of macro-epibenthic invertebrates, such as crinoids (Colloca et al., 2004), can have a significant impact on survival rates of hake recruits.

During the study period nurseries generally expanded or contracted according to fluctuations in recruits abundance maintaining rather stable core areas.
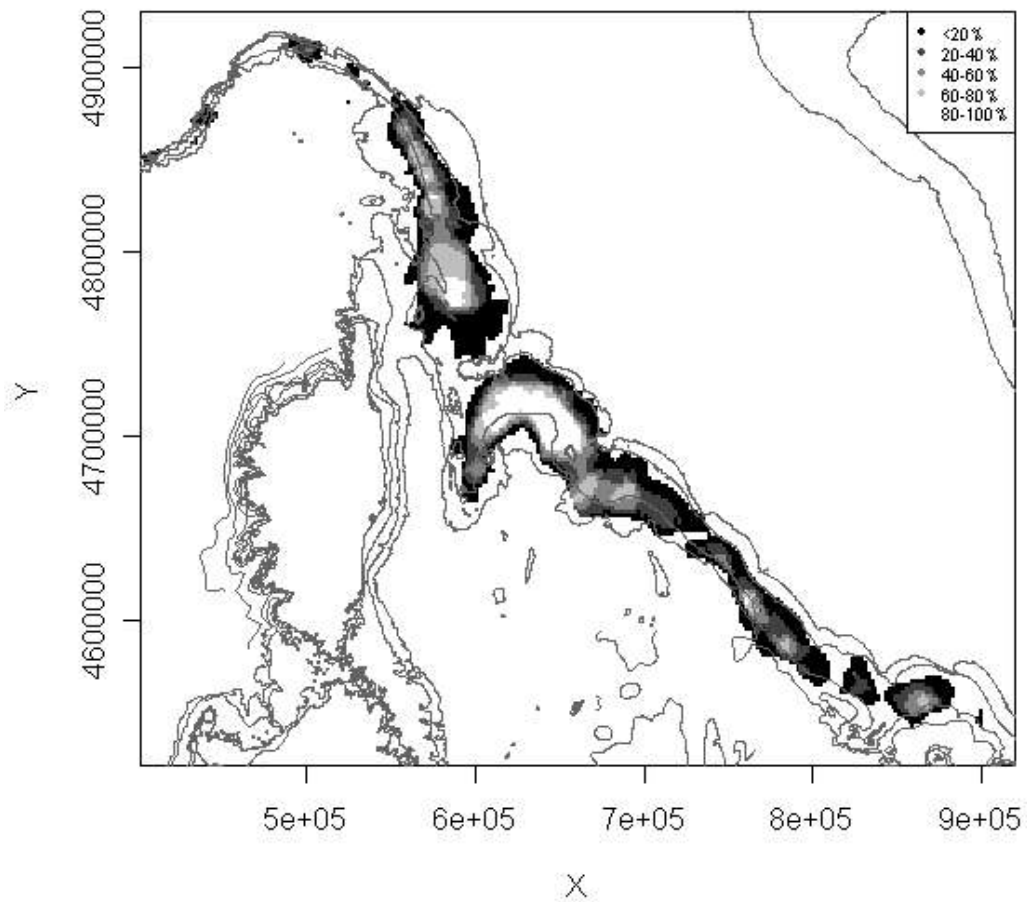

Fig. 7 - Temporal persistence of the estimated nurseries in the period 1994-2004.

TEMPORAL DYNAMICS OF HAKE RECRUITS

Evidences suggest that successful recruitment of European hake depends on the interaction of biological and physical processes, but few studies tried to evaluate the extent and nature of these relationships (i.e. Abella et al., 2005; Maynou et al., 2003; Morales-Nin and Moranta, 2004; Olivar et al., 2003).

Some studies, mostly on other hake species and outside the Mediterranean, have found that temperature for instance can influence *Merluccius* spp. life history at various stages, i.e. larval growth and mortality (Palomera et al., 2005; Grote et al., 2007), growth (Steves and Cowen, 2000), maturity (Alvarez et al., 2001), spawning patterns and regimes (Horne and Smith, 1997; Alvarez et al., 2001) and egg viability (Horne and Smith, 1997). Temperature is also known to influence the production and distribution of plankton (e.g. Beaugrand et al., 2002) and subsequently, the food resource for juveniles and adults.

Hydrographical structures such as currents and eddies can have important effects on the displacement of either hake eggs and larvae (Sánchez and Gil, 2000; Olivar et al., 2003). These oceanographic features act as important processes in favour or against the recruitment success by controlling the drift of larvae to either nursery areas or offshore (Agostini and Bakun, 2002). Mesoscale oceanographic processes, driving the dispersion and retention of plankton, strongly affect ocean productivity patterns with a consequent effect on higher trophic levels (Harrison and Parsons, 2000).

Oceanography of the study area

In the northern and central Tyrrhenian Sea, the circulation is organized in a series of cyclonic (counter-clockwise) and anticyclonic (clockwise) gyres determined by the wind effect (fig. 8; Artale et al., 1994). Three main gyres, characterized by cold water inside, two cyclonic and one anticyclonic have been discerned. They undergo significant seasonal changes, particularly the central anticyclonic gyre that spreads over most of the basin in spring and summer and almost disappears in autumn and winter.

Due to the occurrence of the gyres, the northern part of the basin exerts a crucial role in the general water mass budget on the Tyrrhenian Sea. A principal effect is that the related upwelling provides a mixing of the MAW (Modified Atlantic Water) and the LIW (Levantine Intermediate Water) below, with a corresponding modification of the water properties. Moreover, the northern part of Tyrrhenian Sea is one of the main places for concentration of the basin's chemical resources (Nair et al., 1992).
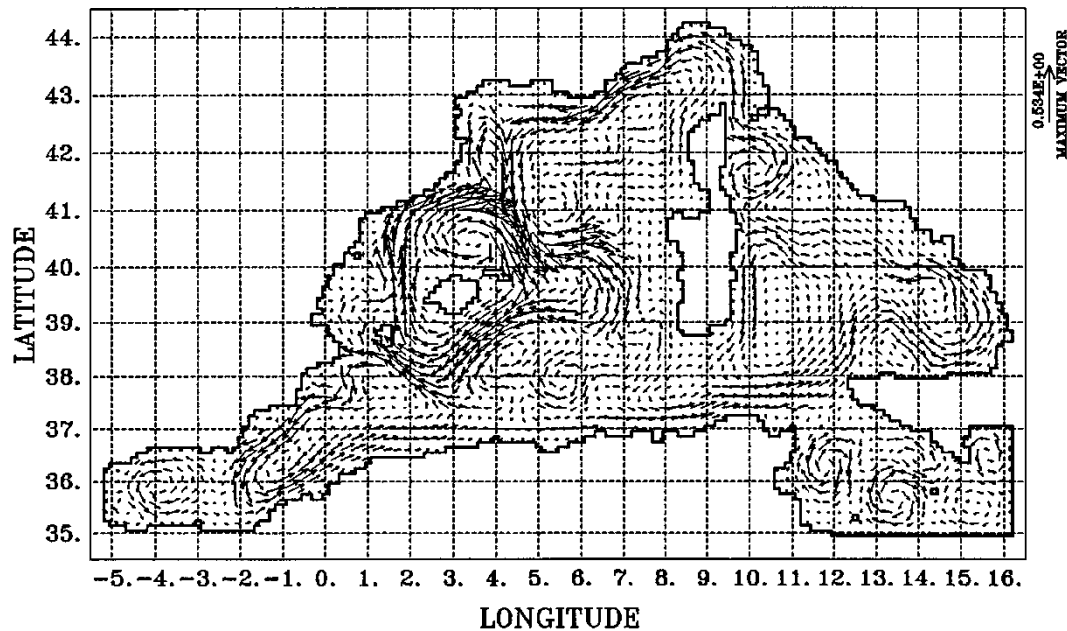
Fig. 8 - Main circulation pattern in the western Mediterranean Sea (from Herbaut et al., 1997).

The general pattern of phytoplankton seasonal dynamics was typical of subtropical areas with a maximum in cold season from October to April and a minimum in summer months (Longhurst, 1995). Mediterranean intermediate (LIW) and deep waters (DMW) have a constant temperature between 12.8-13 °C, thus higher water turbulence (mainly driven by winds) and deeper convection during autumn-winter period enriched the upper layer with nutrients. Reduced wind mixing in March enhances thermocline formation allowing more intense phytoplankton bloom to occur. Moreover, the temperature and density profiles show that in years of rather warm and not windy March the seasonal thermocline was formed faster (Nezlin et al., 2004). A secondary but not less important effect of deepening of the mixed layer and the following high input of nutrients to the surface layer is represented by the storage of nutrients for the summer period (in favourable weather conditions) that results in higher phytoplankton production in deeper layers in summer despite strong stratification. Diatoms peaked in May (February-March in other western Mediterranean areas) and October (Nezlin et al., 2004).

Effect of environmental variables

Our results (paper III) suggested that sea temperature, probably at a medium regional scale is responsible for increasing or decreasing hake recruitment throughout the Tyrrhenian, but that other variables (wind driven processes) account for local patterns, too.

A negative almost linear effect of maximum water temperature in summer was found to reduce deeply the abundance of recruits in autumn. Water temperature plays an important role in egg development and larval growth and survival of several hake species (Steves and Cowen, 2000). In the Mediterranean Morales-Nin and Moranta (2004) found the main abundance of recruits in a temperature interval of 13.5-14°C.

The thermal anomaly that characterised summer months in 2003 has been particularly strong in the central Mediterranean and the Tyrrhenian basin was one of the most affected areas (Marullo and Guarracino, 2003). Along the Catalan coast strong vertical temperature and salinity gradients in autumn 1998, with sea surface temperatures higher than the seasonal mean, reduced water mixing and intrusion of warmer and less saline Atlantic waters, produced anomalous oceanographic conditions that indirectly affected hake recruitment (Olivar et al., 2003).

It can be hypothesised that the summer anomalous oceanographic scenario observed in 2003, could negatively affect recruit abundance in autumn through the combination of different mechanisms: increasing mortality rates of eggs and larvae during higher temperature peaks, enhancing water stratification with relative lower phytoplankton production and modifying gyres and water circulation systems that are probably involved in larval transport and retention processes of hake larvae in the nursery areas.

In the Tyrrhenian, sea surface temperature enhances a process of nutrient enrichment of water masses (Nezlin *et al*., 2004) with a positive effect of low late winter temperature on the late winter-early spring recruitment.

A clear effect of wind driven water mixing processes on recruitment was observed only in the central Tyrrhenian. Elevated water mixing weakens the spring thermocline formation with a consequent negative effect on the spring productivity process. But the dome-shaped relationship (fig. 9) that we found suggests also a negative effect of sea conditions dominated by very low water turbulence during the same spring month that well fits the interpretation of "optimal environmental windows" firstly proposed by Cury and Roy (1989). Intermediate wind mixing situations can represent a compromise between enhanced spring phytoplankton production and appropriate larval drift to feasible recruit retention areas (nursery areas, see paper II). A similar functional response was found by Grote at al. (2007) for *Merluccius capensis* and *Merluccius paradoxus* in the Benguela upwelling region.
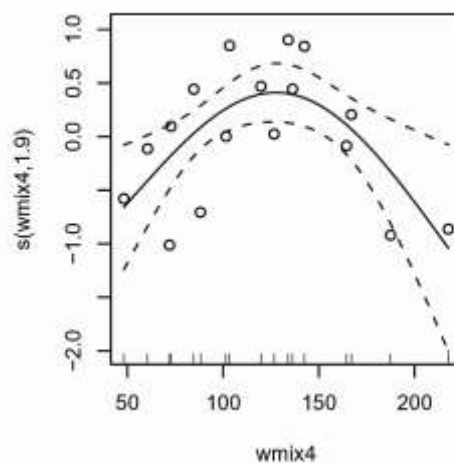

Fig. 9 - Effect of water mixing on hake recruitment as found in the central Tyrrhenian model.

In the northern Tyrrhenian the upwelling mechanism is more related to the main pattern of currents that is dominated by the northward Tyrrhenian current that moving parallel to the coast across the whole Tyrrhenian Sea to create a wide gyre over the large continental shelf southern Elba island (Nair et al., 1992). Thus, the northern Tyrrhenian works as a place of nutrient enrichment (Nair et al., 1992) and hake recruit abundance is less dependent on spring wind driven processes. This interpretation could also explain the elevated temporal stability of the hake nurseries in this area respect the smaller and less persistent ones that occur in the central Tyrrhenian sea.

Population structure model

An age-length structured model (paper IV) was built for hake in the central and north Tyrrhenian, using Gadget (Begley and Howell, 2004; Begley, 2006). Gadget is the Globally applicable Area Disaggregated General Ecosystem Toolbox developed to model marine ecosystems, and it is able to integrate species interaction and the impact of fisheries exploiting the stocks of that species (Taylor et al., 2007). As specified by Stefansson and Palsson (1998), Gadget has been developed as a forward simulation model using statistical estimation through weighted combinations of several log-likelihood criteria.

Among the main advantages of Gadget there are its flexibility, through simulation low data-demanding requirements, and possibility to integrate into the same model uncompleted time series of data at different aggregation level. All features that helped to implement the hake model in the Tyrrhenian sea and that allowed to combine different sources of information at quite different scale.

The Gadget framework consists of three main parts:

- simulation of a process or temporal dynamics
- comparison of model output to the data
- optimisation procedure for the estimation of model parameters

A series of equations characterised by some parameters enclose most of the information that define the model (fig. 10). Gadget runs a model based on these equations and parameters, and then compares the outputs from the model to the observed data to get likelihood scores as a goodness of fit of each model component. Through a combination of different minimisation algorithms (Simulated Annealing, Hooke & Jeeves, BFGS) parameters are adjusted until a minimum in the overall likelihood score is found (best fit of the model to the data). A fundamental part of the parameter estimation procedure consists in assigning a weight to each source of information to define its contribute to the overall sum of squared error. We adopted the weighting method proposed by Stefansson (1998, 2003) where the importance assigned to each source of information or component is proportional to how well the model fits the data and to the size of the component itself.

The basic conceptual model (paper IV) includes two stock components representing small (2-40 cm in TL, age0-3) and large (40-100 cm in TL, age1-4+) hake.

The growth process (fig. 11) was implemented on the base of a simplified version of the Von Bertalanffy growth equation as follow:

$$\Delta L_i = (L_\infty - L_i)(1 - e^{-k\Delta t})$$

$$\Delta W_i = q_1[(i - \Delta L_i)^{q_2} - L_i^{q_2}]$$

where L is fish length, t is time and W is fish weight. Growth parameters (L_∞= 100 cm; k = 0.21; q_1 = 0.59*10^5; q_2 = 3.0595) were fixed according to the fast growing hypothesis proposed for hake (Garcia-Rodriguez and Esteban, 2002) on the base of recent results from tagging experiments (Pinero et al., 2004; de Pontual et al., 2006), reinterpretation of otholit rings (Belcari et al., 2006; Kacher and Amara, 2005; Morales-Nin and Moranta, 2004) and bioenergetic considerations (Jobling, 1994; Because, 2007). The effects of a new growth estimation, almost twice faster respect that generally used in previous assessments (i.e. SAC, 2003), represents an important improvement and change.
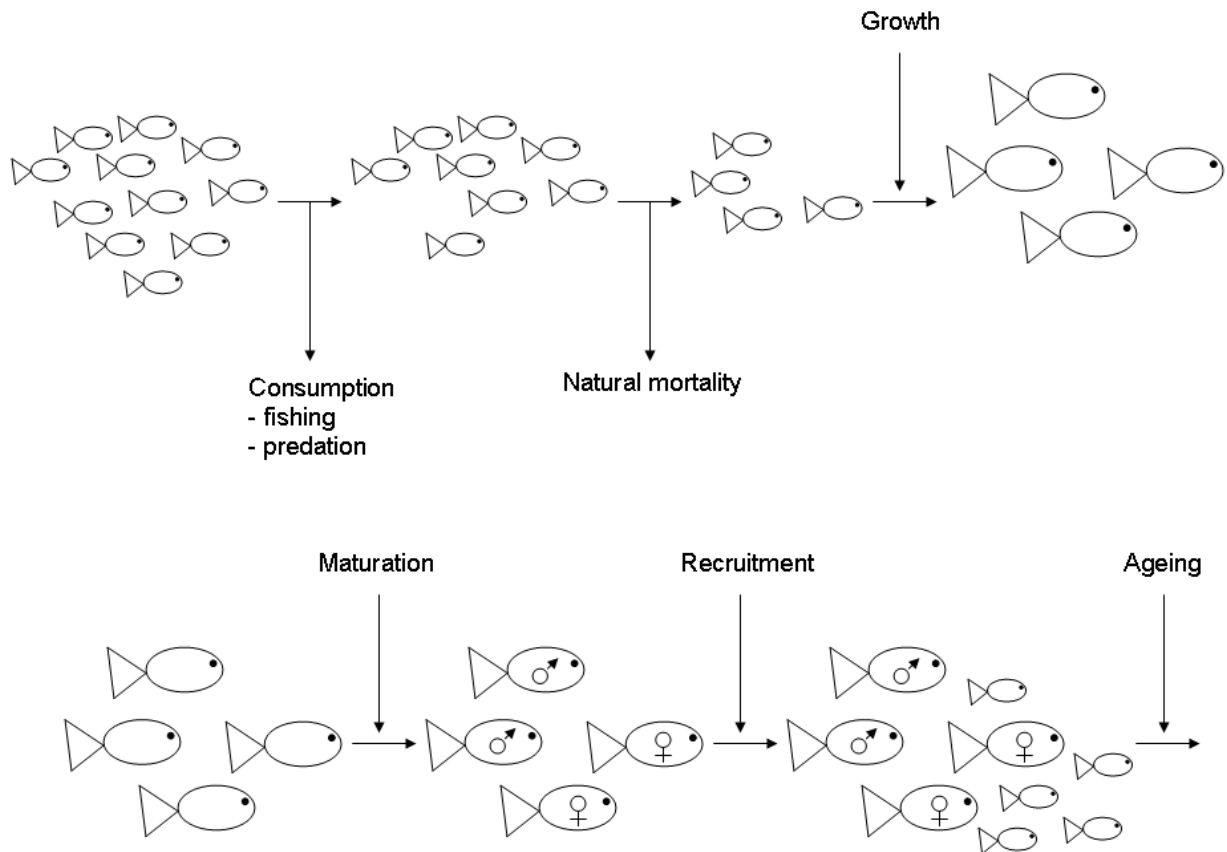

Fig. 10 - Order of the main processes included in each timestep of the hake Gadget model.

A natural mortality vector (M_0=1.3; M_1=0.8; M_2=0.4; M_3=0.3; M_{4+}=0.2) was adopted to simulate more elevated values for the first age classes as a consequence of higher predation mortality and more intense density-dependent mechanisms affecting recruits and juveniles (Caddy, 1993; Caddy and Abella, 1999; SGMED, 2008).

Maturation was simulated with a fixed length maturity function that determine the number of fish that in each timestep reach a specified length (40 cm) and can "move" to the mature part of the stock (in this case the large hake stock component). This approach assumes that the length of maturation is the same for each year.

The model has a time aggregation in quarters for a time span of 14 years (from 1994 to 2007).

Two recruitments are simulated in the first and second time step every year. They have the same pattern based on the number of recruits estimations from the spatial model (paper II) but different level (scale factor estimated within Gadget, fig. 11).

Two fishing fleets are simulated in the model, the trawler and gillnet fisheries. Reduction of animals by fishing in the model is given by the combination of the fishing level (effort) and the suitability function (gear selection). Annual fishing levels for the two fleets were obtained from IREPA national statistics, and described the greater effort exerted by trawlers respect gillnets and a moderate reduction in the fishing effort during the last decade. Trawlers and gillnets displayed also a different pattern of selectivity (fig. 11), targeting different portion of the stock, that was approximated through gear-specific parameters. The suitability function for both the fishing gears was a combination of a Gamma and a constant function:

$$S(L) = \alpha$$

$$S(L) = \left(\frac{L}{(\alpha - 1)^{\beta\gamma}}\right)^{\alpha - 1} e^{\frac{\alpha - 1 - L}{\beta\gamma}}$$

Estimation and monitoring of adult fish biomass is considered one of the most important aspect of fish stock assessment and management (Francis, 1997), because in spawner fish is concentrated the potentiality of a stock to renewal and persist in time (SSB paradigm), large fish often occupy higher levels of the trophic web, and because large fish are generally economically more valuable than small ones. Age2+ group, mostly composed by mature fish, shows a strong decrease during the time period investigated (1994-2007). A minimum is observed in 2003 with a spawning stock biomass approximately half of the initial value in 1994.

Although deterministic models are known for producing only a single realisation and development of the system, also in the case of forward simulations, some sources of stochasticity can be still considered. Multiple sources of uncertainty have been recognised in modelling biological systems and processes (Charles, 1998; Harwood and Stokes, 2003) and simulations invariably include stochastic elements in which random variation around one or more model

components can be included. Monte-Carlo simulations were used to explore forward projections of our hake model, to assess part of the uncertainty of the model and the implications of some management strategies.

Resampling was carried out assuming recruitment as gamma distributed (Shelton, 1992; Taille et al., 1995) according to the recruitment variation observed in the previous years.

Running the forward simulations a sufficient number of times (for computational reasons we limited the number of simulations to 100) we got a summary information of the confidence interval associated to the predictions, thus an estimation of uncertainty.

8-years forward projections of the modelled hake stock, assuming a stable fishing effort based on 2007, have been done (fig. 11). After a further decrease in 2008 and 2009, SSB is expected to have a progressive increase in the following years, possibly obtaining from 2014 values greater than the average biomass calculated over the observed recruitment. Few runs simulated multiple consecutive low recruitments that would produce a further decrease in SSB.
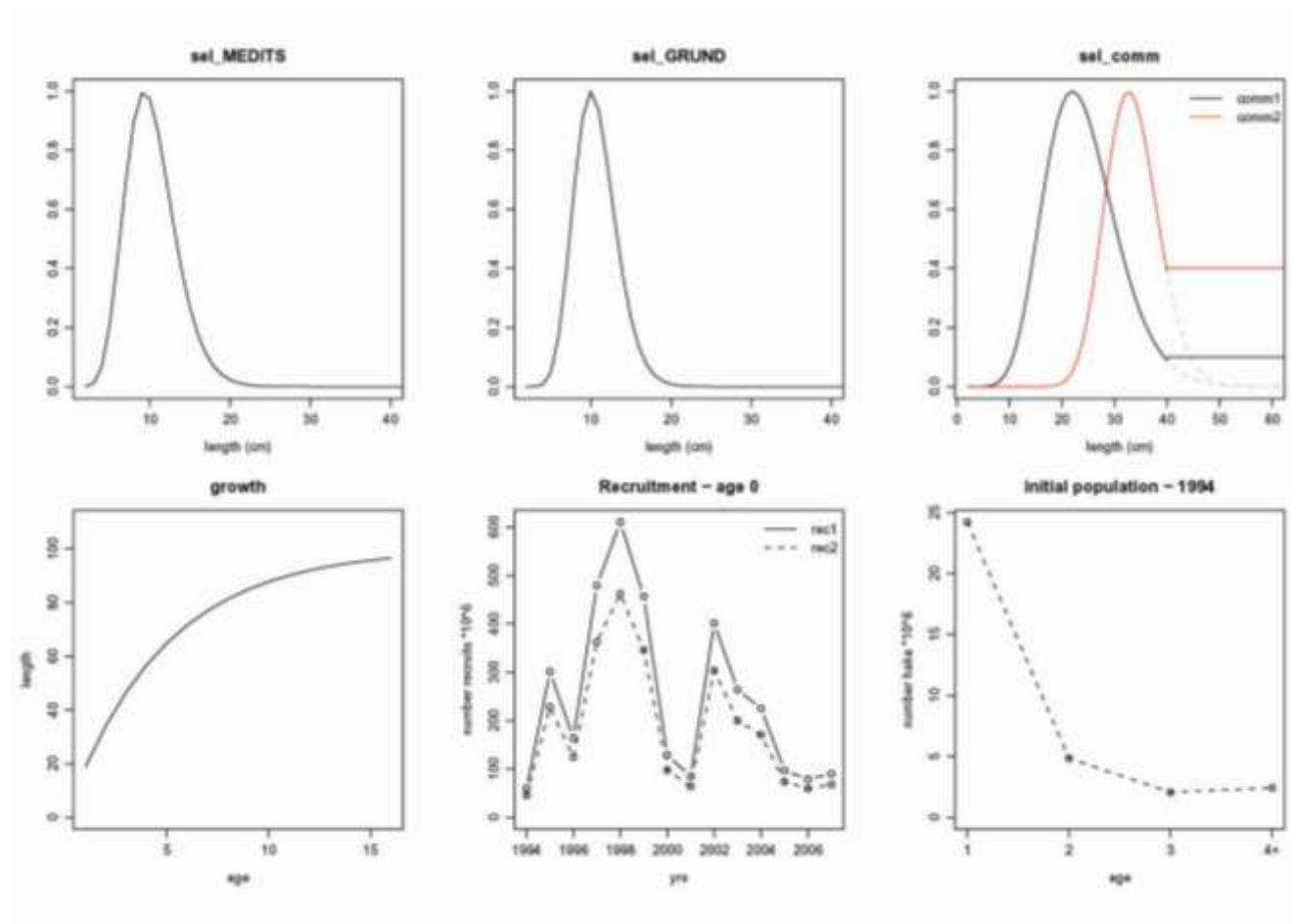
Fig. 11 - Main parameters and function of the hake Gadget model, (from top left) selectivity pattern of the early spring survey (MEDITS), selectivity pattern of the autumn survey (GRUND), selectivity pattern of the commercial fleet (trawlers in black and gillnets in red), Von Bertalanffy growth function, number of recruits coming into the model, age structure of the initial population (timestep 1, year 1994).

Fig. 12 - Annual estimated biomass (timestep 4) by age-class (age0, age1, age2, age3, age4+, age2+) from the hake Gadget model from 1994 to 2007 and boxplot of the SSB projections (100 runs) up to 2015.

MANAGEMENT

Total Allowable Catch (TAC) has been the most commonly used tool to conserve fish stocks worldwide. In the last decade it has been realised that whereas the TAC can be a very effective management tool in the control of a single species fishery fished in isolation, it is less effective when it comes to mixed fisheries bein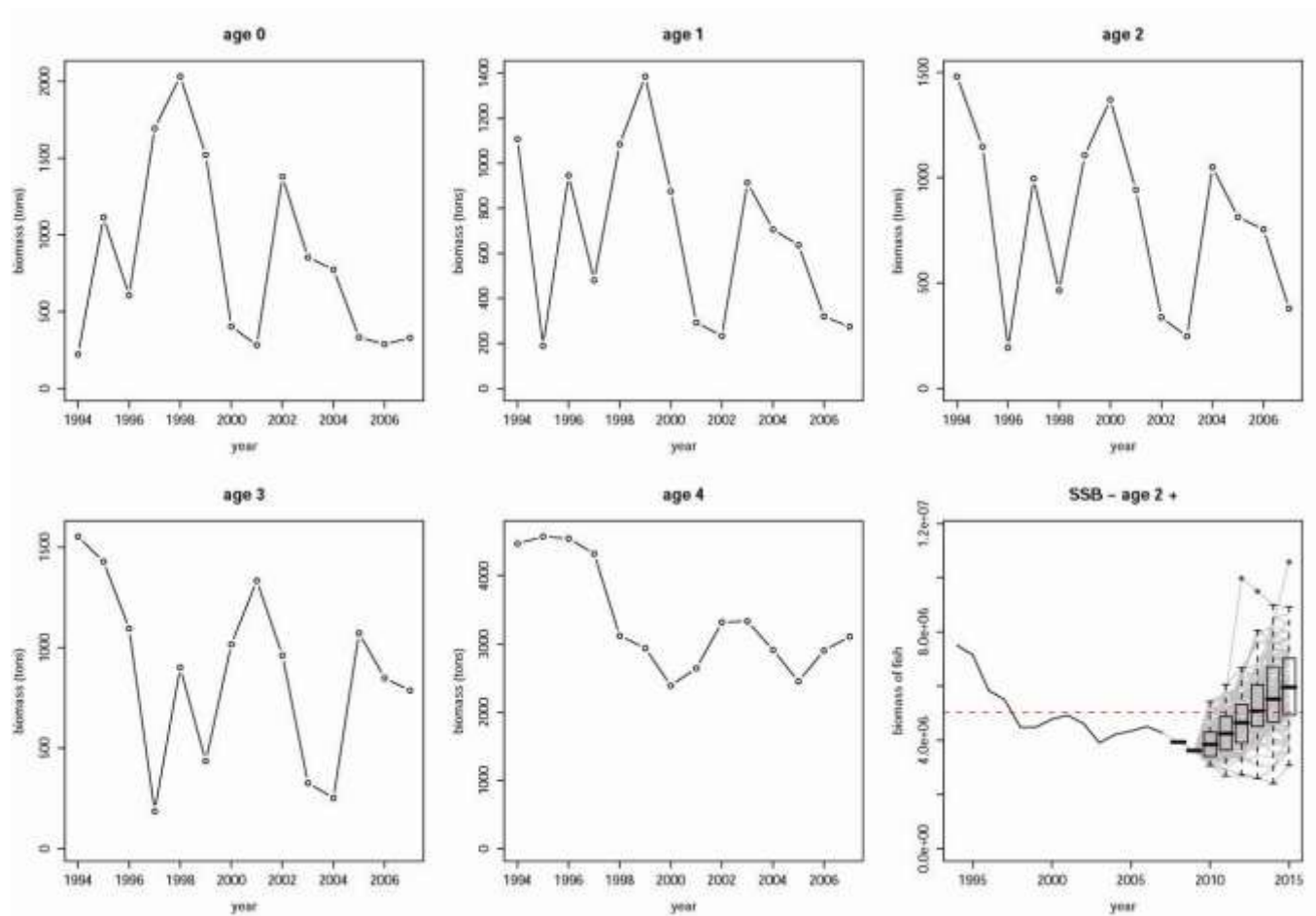g fished by more than one country (Mercer, 1982; Holland and Maguire, 2003) hence the need for technical measures (Bjordal, 2002) to supplement the basic TAC regulations.

Mediterranean fishery is strongly characterised for being mostly a multi-species fishery. Mediterranean trawlers and gillnets generally target a multitude of species that mostly reflects the high marine diversity of the Mediterranean basin. This aspect had important effects on the development of appropriate management measures and represented one of the main reasons of the limited success of traditional management tools (Tudela, 2004; Lleonart, 2005). Considering the high variability of hake recruitment it would be very difficult to set a reasonably precise and accurate TAC (Pope, 1983) in the Mediterranean.

The recognition of the importance of high-quality habitats for the persistence of fish populations, introduced in the U.S. with the Magnusus-Stevens Act in 1996, and the introduction in management plans of Essential Fish Habitats (EFH) for each managed species, offered to the ecologists new perspectives to investigate the effects of habitat protection on fish populations and communities.

Simulation of alternative management measures

According to our geostatistical model (paper II) the closure of highly persistent nurseries (80-100% persistence) would determine a small reduction of the exploitable fishery area (5.3%) and the protection of a consistent fraction (39.2%) of the total estimated recruits (Table 1). Such findings clearly show the potential of spatial measures for the reduction of fishing mortality on hake juveniles and to rebuild the hake stock, with an expected very limited effect on the fishing effort pattern in the area.

The effect of alternative management strategies on the stock structure was also evaluate through the implemented hake Gadget model (paper IV). The ability of Gadget to model several sub-processes and mechanisms combined with its flexibility, offered an extensive control of a large number of the model components. Medium term (8-years forward) projections allowed to simulate multiple scenarios based on different management strategies and the effects on the adult stock biomass (SSB) and on the landings were evaluated (fig. 12).

The following management measures were tested:

- establishment of no-fishery areas on hake nursery grounds, under different conservation scenarios as presented in the geostatistical model (a protection range between 39% and 83% of recruits)

- reduction of the fishing pressure (20% and 40% decrease)

Although all our projections are characterised by extremely high variability as consequence of the high variability and uncertainty associated to the recruitment predictions, the expected mean effect on the mature part of the stock is largely different between the alternative management scenarios. Limited increase in SSB has been observed when a reduction in fishing mortality was restricted to recruits, as in the case of closed areas in correspondence the main hake nurseries. Also in the most conservative scenario (closure of 21% of area and protection of 83% of recruits) the estimated increase in SSB was only moderately affected by the simulated management strategy (in 2015 SSB under recruits protection scenario is only 6.4% greater than without management).

The scenario based on a reduction of 20% of the fishing effort over all the length groups showed an important positive effect on the predicted SSB. Under no management scenario expected SSB in 2015 is approximately 6000 tons, while it exceed 9100 tons under 20% reduction of the fishing effort). The reduction in the effort has the immediate effect of decreasing the expected landing (2008 landing is 17% smaller in the management scenario), but the stronger increase in the stock size produces a progressive increase in the catch per unit effort and consequently a more rapid increase of landings. In the last three years (2013-2015) the highest quality of the catch under the management scenario produces a higher landed biomass although a 20% reduction in the fishing effort (2420 tons against 2190 tons in 2015).
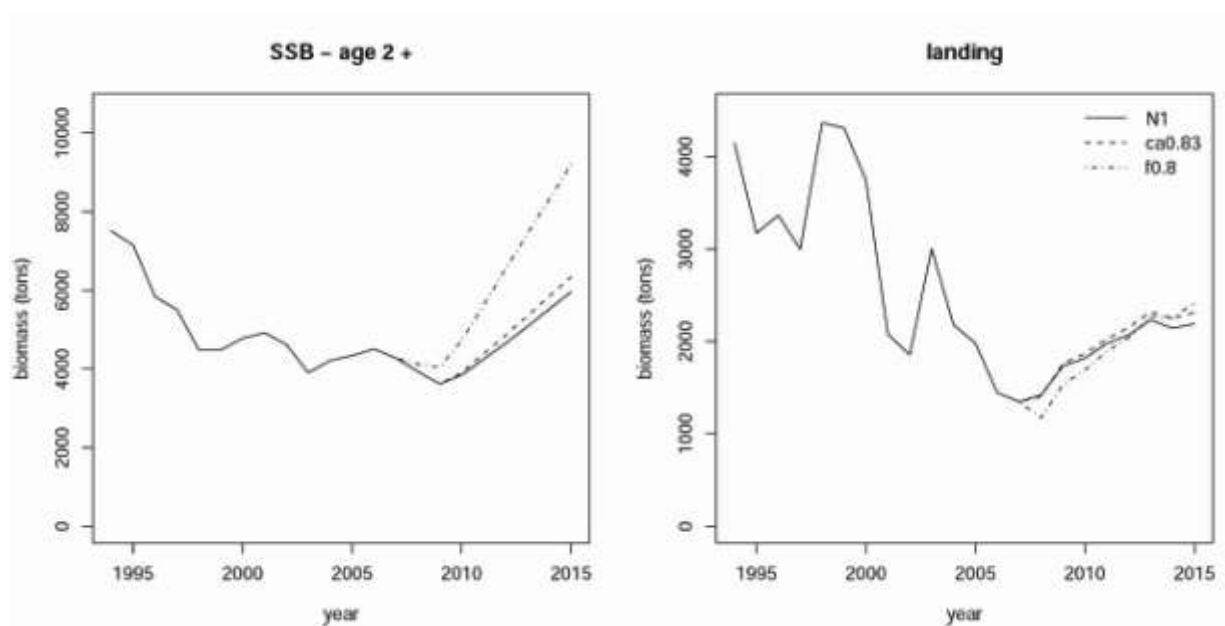

Fig. 12 - Average projections (up to 2015) of SSB and total commercial landing for the hake Gadget model under no management scenario (N1), with protection of 83% of recruits through the establishment of 21% closed areas over nurseries (ca0.83) and reducing total fishing effort of 20% (f0.8).

Although the current high levels of fishing mortality on recruits can be easily considered far from any sustainable exploitation scenario (SGMED, 2008) and moreover risky considering the possible occurrence of repeated failed annual recruitments, a reduction of F only for recruits would provide rather limited effects on the stock. Also the most precautionary scenario based on closed areas (protection of 83% of recruits) poorly performed in terms of fish that were able to grow up to the mature size. This can be explained mainly by the high natural mortality (M) that characterised the first year class. As a consequence the total mortality (Z) of age-0 hake is more strongly influenced by M rather than F. Thus, even if closed areas would provided positive results their effect alone would be as much limited as natural mortality is high compared fishing mortality:

$$\text{if } M \gg F \qquad \rightarrow \qquad Z = M + F \sim M$$

This result should not be interpreted as a reason against the implementation of closed areas to fishery, but it demonstrates that the positive effects that should be looked for in protecting hake nursery grounds are only limitedly related to a reduction in hake recruits fishing mortality.

Hake within a systematic conservation plan

A part from the portion of the population directly protected by the establishment of no-fishing areas, spatially based management measures offer the important advantage to extend their effects to entire communities of organisms and to habitats. Juvenile classes are often strictly related to specific seafloor habitat conditions for feeding and protection from predators (Diaz et al., 2003; Hook et al., 2003; Scharf et al., 2006). Moreover, according to the definition of EFH, specific grounds have fundamental importance during crucial phases of the life cycle of marine species, for instance during recruitment and spawning. Thus, the effects of protection of these habitats is generally hard to be predicted but their preservation has been strongly recommended for conservation purposes also in the Mediterranean (Council Regulation EC No. 1967/2006*).

Although the biologically sound-based definition of EFH and the statement of their importance for management purposes in the Magnusus-Stevens Act, some objective difficulties exist behind the real application of the Act's principles. One of the main problem related to the management of marine resources within a multi-species fishery context, rely on the fact that the direct cumulative addition of habitats identified as important for different species would easily cover wide areas. A step forward a more rational choice of areas of interest for conservation and management is oriented toward those life-history stages that would benefit more from the habitat protection (Cook and Auster, 2005).

* Council regulation (EC) No. 1967/2006 - concerning management measures for the sustainable exploitation of fishery resources in the Mediterranean Sea, amending Regulation (EEC) No 2847/93 and repealing Regulation (EC) No 1626/94.

Systematic conservation planning (Margules and Pressey, 2000) represents a relatively new, structured and rational approach to conservation (paper V). Commercially exploited fish populations, such as hake, are among the natural resources that would be included within an ideal systematic conservation plan for the western Mediterranean.

We developed a case study for the Tyrrhenian and Ligurian Sea, in which conservation targets for 10 species (*Merluccius merluccius*, *Micromesistius potassou*, *Phycis blennoides*, *Pagellus erythrinus*, *Mullus barbatus*, *Nephrops norvegicus*, *Parapenaeus longirostris*, *Octopus vulgaris*, *Eledone cirrhosa* and *Illex coindetii*) are fulfilled both minimising the area required for conservation and reducing the economic conflict with fishery activities. Rather than defining separate areas for potential conservation for each of the 10 species considered we selected the planning units (PUs) necessary for the conservation of all species using a multispecies approach based on the concept of irreplaceability (the likelihood that an area will be needed to achieve an explicit conservation goal; Pressey et al., 1994) and on the definition of species specific conservation targets. Irreplaceability values range from 1 (totally irreplaceable area that cannot be substituted by any other area in the conservation scheme) to 0 (area that does not contain any species in a density that is needed to achieve the conservation objective).

Two conservation targets have been tested (paper V): 20% and 40% of protection of the individuals for each species. Taking into account also information on the spatial distribution of the trawler commercial fleet (Vessel Monitoring System data, VMS), we were able to include into two of the conservation scenarios presented a flexible measure to mitigate the potential conflict with fisheries (excluding *a priori* from the conservation scheme some of the commercially most important fishing grounds).
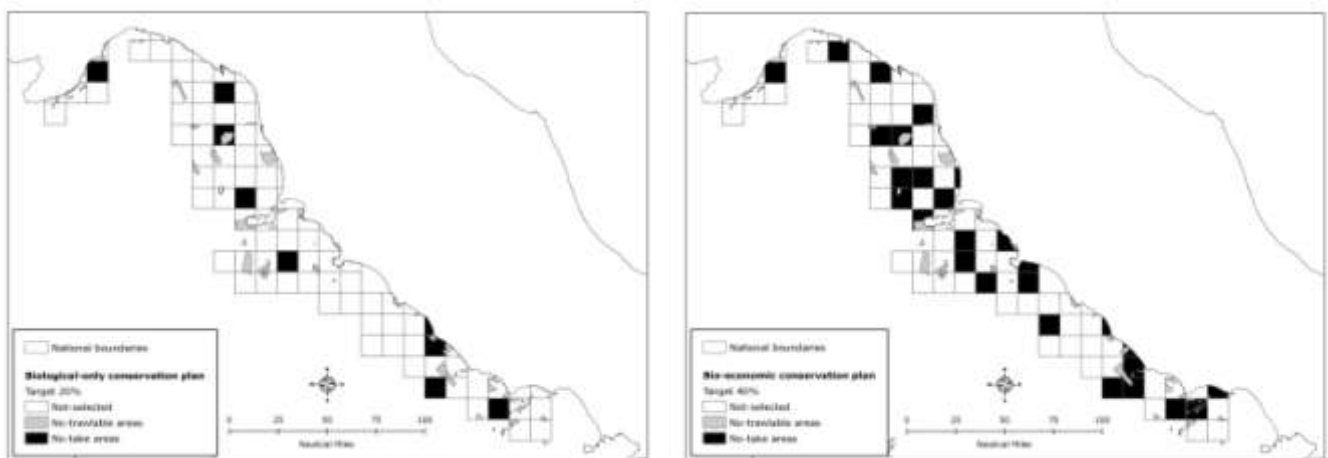
Fig. 13 - Possible conservation plans obtained considering 20% representation target and no conflict with fishery (left) and considering 40% representation target and mitigating the conflict with fishery (right).

Considering the wide ecological range given by the whole group of species included in the analysis, selected PUs were located both on the continental shelf and along the slope, in the Tyrrhenian as well as the Ligurian Sea (fig. 13). In the less conservative scenario (20% protection for each species and no compromise with the commercial fleet activity) 9 PUs were selected (12% of the whole study area) to achieve the conservation target. In the most conservative scenario (40% protection for each species and mitigation measure of the conflict with the commercial fleet) 27 PUs were selected (35% of the whole study area).

CONCLUSIONS

Two distinct post-planktonic life stages have been found to occur during the first year of life of immature juvenile hake. These two phases, representing the recruit and post-recruit stages, have been detected according to different bathymetric preferences. Hake recruits showed high preference for the continental slope (170-220 m depth), while juvenile post-recruits were more abundant on the continental shelf (70-100 m depth). This result is in agreement with the trophic ecology of the species and with bioenergetic considerations related to the maturation process. Length of migration between the two phases showed some inter-annual variations in the range 12.4-15.8 cm in total length.

Spatial distribution of hake recruits was mapped. Seasonal density hot-spots of recruits have been identified and interpreted as nursery areas. The distribution of nurseries across the shelf-break showed a patchy pattern related to the main oceanographic features of the Tyrrhenian and Ligurian sea. The main identified nurseries showed also an elevated seasonal and annual stability.

Temporal dynamics of recruitment was explained by late-winter, early spring oceanographic processes that enhance marine productivity and through 'optimal environmental windows' promote exceptionally high recruitments in some years. On the other side, the stable feature of nutrient enrichment that characterises the northern Tyrrhenian well agrees with the high persistency of the large nursery area found southern Elba island.

Survival of recruits was also putted in relation with thermal anomalies that occasionally occur during summer months, such as in 2003 summer. As expected for a cold species like hake particularly high temperature has been found to have a negative effect on its recruitment.

A first length structured model of hake was built in the central and north Tyrrhenian. The model included new fast growth parameters for hake and simulates trawler and gillnet fleets. Some of the model parameters have been estimated within the optimisation step, fitting model outcomes with experimental survey and commercial landing data.

Monte Carlo simulations were used to run short and medium term projections. Due to a progressive reduction in the fishing effort since 2000, an increase in the spawning stock biomass is expected in the next years. Simulations of alternative management options, such as closed areas specifically design to protect hake recruits and a further reduction in the fishing effort, demonstrated an improvement in the stock recovery process. The effects of a reduction of recruit fishing mortality would have limited effect on the stock due to the high natural mortality of hake recruits and to the partial selectivity of trawlers for very small fish. This outcome support the idea that spatially based management measures should be adopted in the Mediterranean to manage hake population, and other species with a high reproductive potentiality, mainly in relation to the importance that certain grounds (the so called essential fish habitats) have for some crucial stages of species life cycle.

According to this idea, methodologies developed in systematic conservation planning have been adopted to define multispecies management scenarios including hake in the Tyrrhenian and Ligurian sea. Information on the fishing effort spatial distribution were taken into account to develop some management scenarios with a lower impact on fishing activities.

Synthesis of the main results (in Roman numbers the related paper):

- recruit and juvenile post-recruit stages have been identified in the European hake according to marked differences in their bathymetric preferences (I)
- the spatial distribution of hake recruits has been modelled (II)
- density hot-spots of hake recruits have been identified as nursery areas (II)
- nursery areas showed elevated temporal persistence (II)
- the proportion of recruits and area included in the nurseries for different levels of persistence was calculated (II)
- inter-annual variability in the length of migration from the nursery areas have been identified (I)
- late winter-early spring marine productivity and summer thermal anomalies have been found as two of the main key processes affecting hake recruitment (III)
- a length-based model of hake was built for the central and north Tyrrhenian including a multi-fleet component (IV)
- several management scenarios have been simulated, including closed areas, reduction of the fishing effort and alternative fishing selectivity patterns (IV)
- identification of no-take marine protected areas through a multi-species approach that included specific conservation targets for hake and other commercial species (V)

Future work and next developments should include:

- Understanding of the importance of recruits migration from the nurseries to the continental shelf and the consequent trophic shift toward a highly energetic diet, based on small pelagic fish, especially in relation to the gonad development of post-recruit hake.
- Development of spatial models that include a spawner-recruit relationship and environmental factors.
- Implementation of the simple length structured model presented through the simulation of maturity process and predator-prey relationships, with particular regards to cannibalism and interaction with small pelagic fish.
- Systematic conservation planning based on a larger number of species, including non commercial ones, and biologically sound-based species-specific conservation targets.

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I

Bathymetric preferences of juvenile European hake (*Merluccius merluccius*)

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The concept of a recruit is a basic notion in fisheries science, but it is still far from being an unequivocal term, and many diverse, even ambiguous, definitions can be found in the literature. We propose a more objective and biologically meaningful way to define the length range of recruits for species that have clear bathymetric segregation during the early stages of their life cycle. The bathymetric distribution of juvenile European hake was studied by fitting a thin plate spline to data from the national autumn trawl survey. Hake showed a stable pattern of depth preference in the 6-year dataset examined. Small hake had the greatest preference for depths of 170–220 m and appeared to move slightly deeper when they reached 10-cm total length. Larger hake persisted on the continental shelf with a preference for water 70–100 m deep, especially when they reached 18–20 cm long. The length at migration was defined as the length at which the minimum depth preference was shown, and it ranged between 13.2 and 15.8 cm depending on the year. There was a relationship between length at and depth of migration, and we provide a full description of the depth preference of juvenile hake, and test the effectiveness of the analytical approach used.

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Introduction

The spatial distribution of marine organisms is generally not homogeneous in space, and different aggregation phases can be recognized in the life cycle of many species (Shima *et al.*, 2002). The environment fish occupy throughout their life often differs between the larval and the adult stages (Sullivan *et al.*, 2000), and size-class relationships for many species are not yet well resolved at a regional or ecosystem level (Methratta and Link, 2007).

Ontogenetic differences in fish populations are often evident, many species having several well-defined phases during their life. Marked variations in morphology and physiology (McCormick, 1998; Fisher *et al.*, 2005), in trophic behaviour (Werner and Gilliam, 1984), and in spatial distribution (Ardizzone and Corsi, 1997) can represent transitions between the different phases. Fish move deeper or shallower, to the surface or the seabed, to feed, to avoid predation, or to reproduce (Neilson and Perry, 1990). Understanding such movements can help us understand fish behaviour better, and improve management and conservation of the resources (Sparre *et al.*, 1989).

Many species of the genus *Merluccius* make extensive migrations during one or more phases of their life cycle (Cohen *et al.*, 1990; Alheit and Pitcher, 1995). Although no specific analysis was carried out on the bathymetric preference of the European hake

(*Merluccius merluccius*), indirect information came from studies on its spatial distribution (Ardizzone and Corsi, 1997; Fiorentino *et al.*, 2003; Abella *et al.*, 2005). An ontogenetic pattern of distribution was reported by Abella *et al.* (2005), fish aged 0 being concentrated mostly at between 100 m and 250 m deep, and fish aged 1 year being distributed mainly in shallower water over the shelf.

Although a proper understanding of hake migration from the nursery areas is basic to defining the phase of recruit during which fish concentrate before dispersal, no study has described this process in detail. A better comprehension of hake juvenile distribution would be of particular importance, considering that fisheries such as that for hake in the Mediterranean Sea exploit recruits as a large proportion of the total landings of a species or stock (Abella *et al.*, 1997).

The term recruit has been defined in many different ways in the literature, including the scientific literature. Descriptions differ in the meaning and in relation to the context in which they are used. Scientific fisheries management defines recruits to the fished stock as those fish entering the exploitable component (FAO, 1997). Other biological definitions generally refer to recruits as age 0 fish (e.g. Fiorentino *et al.*, 2003), fish of the youngest cohort (e.g. McBride and Conover, 1991), or simply immature fish.

The purpose of the present study was to analyse the bathymetric distribution of juvenile hake in the Mediterranean Sea with regard to their migration from nursery areas, using an easily applied analytical approach based on thin plate spline (tps) surfaces. A model of bathymetric preference will sharpen the definition of the concept "recruit" if clear size- or age-dependent bathymetric preferences can be identified.

Historically, spline methods were methods of interpolation, basically interpolating functions between observations (Wahba, 1990; Green and Silverman, 1994). The main issue becomes how to weight measurements at different distances from the prediction point. A common method for such interpolation to estimate a process in one or more dimensions is kriging, which uses a variogram to estimate the process variation, giving the weights to be used (Wahba, 1990; Mardia *et al.*, 1996). Smoothing splines have been popularized through generalized additive models (GAMs; Hastie and Tibshirani, 1990). These smoothing splines do not need to go through the data points themselves (nor does kriging with a "nugget effect"). The virtue of GAMs and kriging methods over parametric methods such as generalized linear models (GLMs) lies largely in their flexibility, one no longer needing to specify a functional relationship which has to be valid across the entire space. Instead, GAMs require specification of the degrees of freedom (or knots), which specify how flexible the surface can be. A tps is a recent method in the flora of methods, and is particularly well suited when one cannot easily specify this flexibility *a priori*. Instead, a smoothness criterion is used (minimization of a penalty function which measures the amount of "wiggliness", controlling the trade-off between data fitting and smoothness), along with cross-validation. On the negative side, it is not obvious how one should conduct formal significance testing, so the method should be considered data analysis rather than formal statistical inference. Here, we were not interested in formally modelling the bathymetric migration of juvenile hake, which can be more appropriately approached with other regression techniques (i.e. a GLM), but we wanted to investigate variations in bathymetric preference and segregation during the first years of life.

Material and methods

Our study area covered the continental shelf and the upper slope of the central Tyrrhenian Sea, from Cape Argentario to the mouth of the Garigliano River (Figure 1).

Data were collected in September/October during the Italian national trawl survey project (GRUND), from 1998 to 2004 (no survey was conducted in 1999). The randomized stratification scheme for the surveys was based on five bathymetric strata (10–50, 51–100, 101–200, 201–500, and 501–700 m; for more detail, see Relini, 1998). The hauls, selected randomly, were fixed in the first year and repeated in the following years. Hauls from the first three strata and part of the fourth, up to 330 m deep, were considered for this analysis, to include both the continental shelf and the upper slope, where immature hake are mainly distributed (Table 1).

The number of hake juveniles analysed each year ranged between 3582 and 24 606, respectively, in 2003 and 1998 (length distributions are shown in Table 2). Indices of abundance were calculated from each haul as the number of fish per swept area ($n \, km^{-2}$) for 1-cm length classes in the length range 5–22 cm; this interval was selected because the focus of the study was on the first year of hake life (Garcia-Rodriguez and Esteban, 2002; Morales-Nin
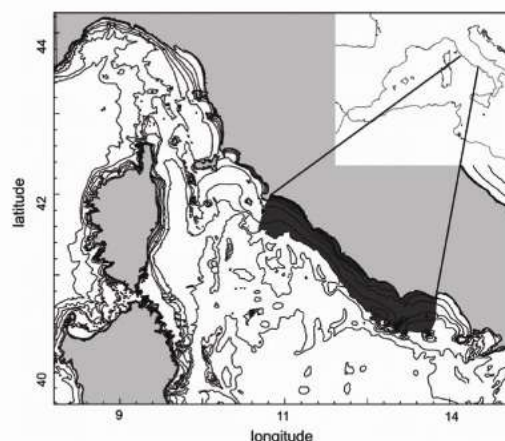

Figure 1. Map of the study area.

and Moranta, 2004; Belcari *et al.*, 2006). The abundance values by haul were averaged by 10-m depth classes to obtain a depth × length matrix of fish density, because the mean is more appropriate than the sum for density data. Finally, to reduce the large differences in the number of fish in different length classes, depth–frequency distributions by 1-cm length class were calculated by normalizing to 1 any column of the depth × length matrix, so obtaining a relative depth preference index ($Y_{l,d}$) as follows:

$$Y_{l,d} = \frac{N_{l,d}}{\sum N_l},$$

where N is the number of fish per swept area, by length l and depth d.

tps were used to smooth a surface over the depth preference matrix for each year separately. The Thin plate splines function, implemented in the fields package of R (freely available at http://www.r-project.org/), fits a tps surface to data spaced irregularly. The spline interpolator is based on the kriging estimator, assuming the covariance to be the radial basis function. The smoothing parameter is selected by generalized cross-validation. The function assumed an additive model:

$$Y_{l,d} = f(l, d) + \varepsilon,$$

where $f(l, d)$ is a two-dimensional surface defined by the independent variables length and depth.

This non-parametric method of regression has been used extensively in a variety of specific applications of fish biology, such as morphometrics (e.g. Loy *et al.*, 1999; Valentin *et al.*, 2002), and in the study of spatial and abundance data (e.g. Wood and Horwood, 1995; Augustine *et al.*, 1998; Fox *et al.*, 2000; Howell and Kobayashi, 2006).

Given the resulting bivariate surface, fitted to length and depth, univariate functions describing density as a function of either depth or length can be constructed by alternatively eliminating the other variable. This method, also referred as density profiling, takes the maximum value of the surface for each fixed length, and plots these maxima as a function of length (and similarly for

Table 1. Hauls, mean depth, and number of hake caught in the length range 5–22 cm for each year analysed.

Haul code	Depth (m)	Number of hake 5–22-cm long caught					
		1998	2000	2001	2002	2003	2004
1	322	288	81	118	1 122	–	–
2	176	409	1 784	246	542	296	348
3	141	202	210	33	64	281	316
4	319	313	48	19	118	–	–
5	41	16	–	–	–	2	14
6	85	34	136	80	108	66	150
7	148	536	22	130	1 090	121	392
8	33	168	2	–	1	–	9
9	83	234	73	264	422	68	187
10	162	802	718	608	121	81	19
11	159	3 660	1 096	114	1 282	219	222
12	102	286	145	402	447	–	–
13	82	530	97	461	206	174	55
14	20	–	–	–	19	–	–
15	31	352	–	–	194	–	–
16	249	535	478	245	2 250	–	–
17	154	869	226	84	173	–	–
18	198	1 686	5 340	728	270	316	1 828
19	33	–	–	162	369	–	–
20	98	79	73	395	280	–	–
21	92	160	170	496	260	113	276
22	171	549	206	2 801	730	96	357
23	111	29	39	289	66	–	–
24	320	1 148		40	753	–	–
25	145	100	139	189	1 691	200	945
26	130	548	50	88	326	–	–
27	101	82	64	90	94	–	–
28	91	77	50	166	160	–	–
29	73	82	1	58	170	172	128
30	43	207	39	223	49	30	120
31	81	580	159	101	153	110	129
32	170	870	435	1 852	1 026	228	2 352
33	164	4 859	–	2 844	1 236	712	1 218
34	168	800	352	596	882	–	–
35	317	1 186	26	53	697	54	3 248
36	41	220	–	4	86	–	–
37	83	522	212	235	485	243	772
38	126	186	2 043	32	236	–	–
39	200	1 402	306	1 290	3 736	–	–

Table 2. Number of hake analysed by length class and year.

Length (cm)	Number of hake analysed					
	1998	2000	2001	2002	2003	2004
5	8	4	3	1	0	1
6	45	121	20	61	1	27
7	111	851	117	371	14	178
8	301	2 644	331	1 240	30	467
9	686	3 329	1 192	3 782	72	1 295
10	2 018	3 260	3 140	6 153	295	2 481
11	4 349	2 037	3 634	4 932	659	3 129
12	5 708	1 012	2 719	2 578	833	2 669
13	4 709	568	1 740	1 107	589	1 546
14	3 086	318	839	657	339	613
15	1 624	136	553	421	230	238
16	760	117	382	219	168	143
17	410	109	317	128	108	82
18	305	77	254	90	69	87
19	221	90	144	42	66	62
20	136	68	66	57	38	35
21	96	44	60	48	50	18
22	33	35	25	27	21	14

depth). The modes of the original surface are clearly reflected as modes in the univariate plots. The lower values in the density profile with respect to fish size represent the length at which the lower bathymetric preference is observed. Conversely, the minima in the density–depth plots indicate the depth at which the two length groups are better discriminated.

Results

Two distinct depth–length clusters were shown in all annually estimated surfaces (Figure 2). The clusters had different shape and value in the density peak, but described a common situation throughout the time-series: small hake below a certain length were found over the continental slope, and larger hake preferred shallower water over the shelf. The small hake group (total length, TL, <13–16 cm) had the greatest preference for water 170–220 m deep. In some years, the right side of this cluster was skewed towards deeper water (>220 m), and in 2004, the largest length classes of the small hake cluster moved towards the deeper part of the upper slope (280–300 m). The length minima in the length-density profile plots were found in the 13.2–15.8 cm length range, in 2000 and 1998. For each year, they represented the length class at which the less marked depth preference was observed. The depth at which the two length classes were better discriminated ranged between 117 and 150 m in 1998 and 2000, respectively.

The larger hake length class persisted on the continental shelf with a preference for water 70–100 m deep, especially when fish reached 18–20 cm TL.

A sharp depth change distinguished the two length classes identified in most years except 2000 and 2003, when depth migration appeared to have been more gradual. However, two clusters were found during 2000 and 2003 at 13.2 cm TL and 150 m depth and at 14.1 cm and 125 m, respectively, but the estimated surfaces showed a progressive migration towards shallower water for hake of intermediate length (12–17 cm TL).

A significant linear relationship ($r = 0.77$, $p < 0.05$) was found between the estimated length and depth of migration (Figure 3). The two clusters were also discriminated by shallower water in years when hake were predicted to migrate at a larger size, as opposed to when the length-at-migration was expected to be smaller. The year 2003 showed the largest residual from the fitted linear model, and hake recruits were smaller than expected or simply more concentrated in shallower water.
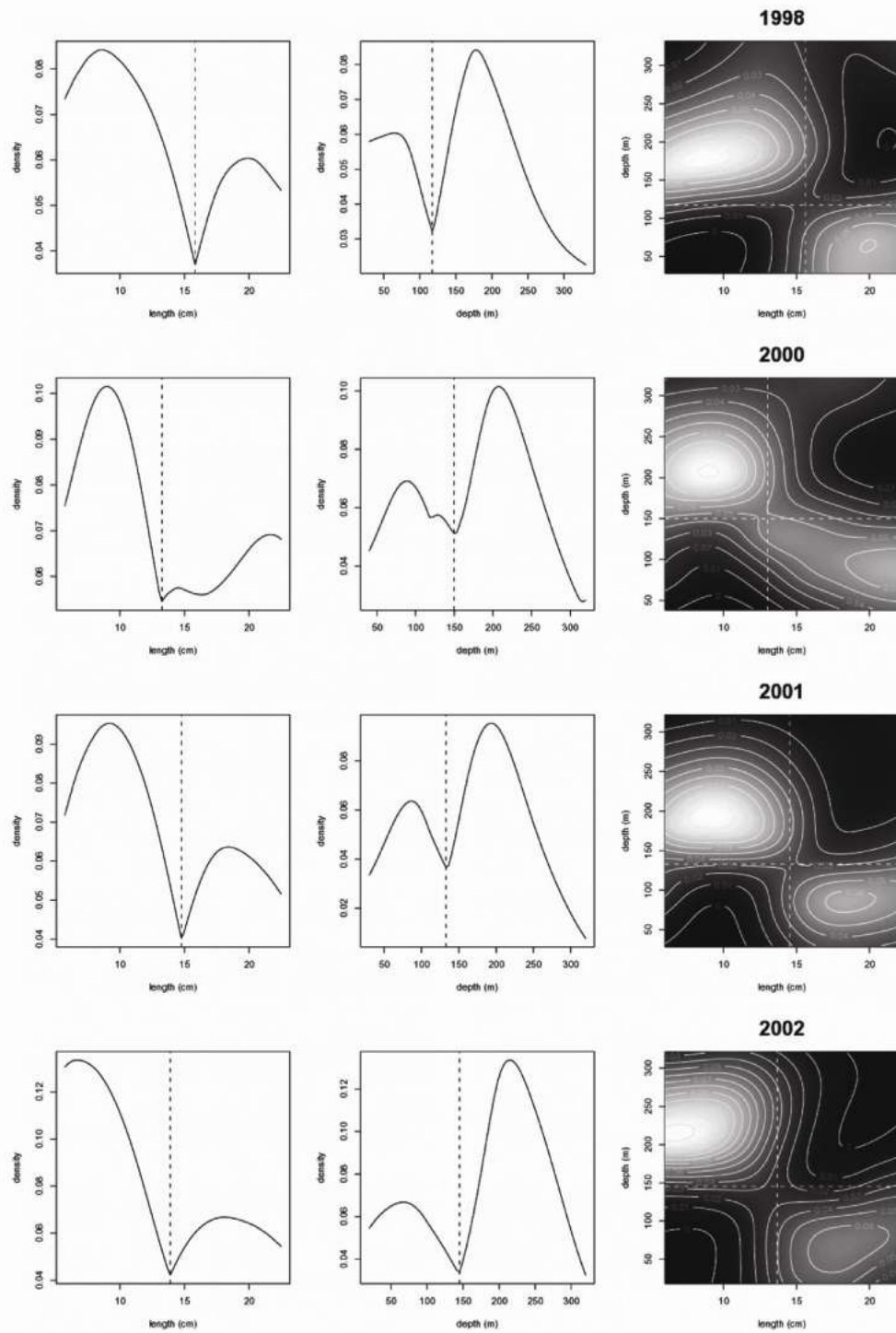
Figure 2. Density profiles with respect to length and depth and estimated length–depth surfaces, 1998–2004.
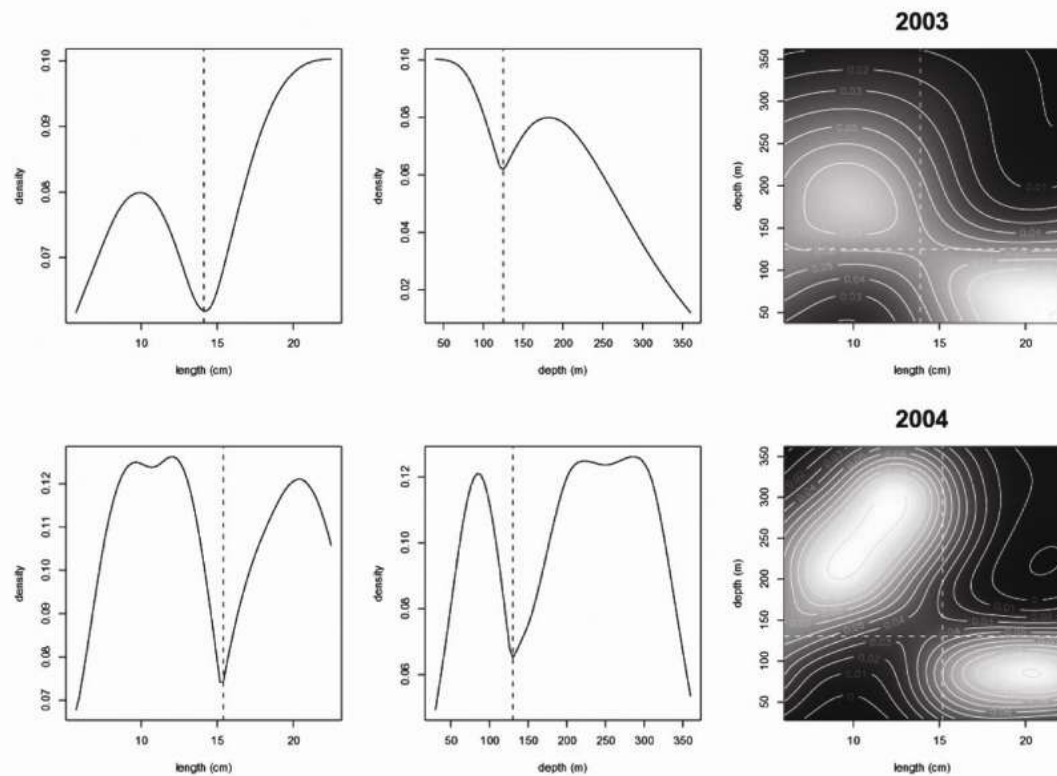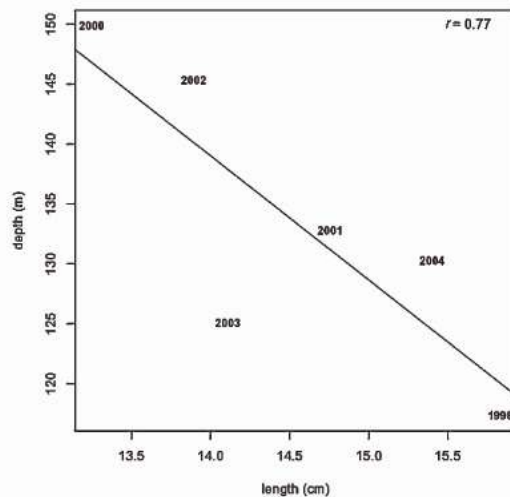
Figure 2. *Continued*

Figure 3. Bivariate regression of the estimated length and depth of migration of European hake in the Mediterranean Sea, 1998–2004.

Discussion

Depth is one of the major environmental gradients in marine ecosystems, influencing the vertical pattern of species distribution both in abundance and size (Macpherson and Duarte, 1991; Clain and Rex, 2000; Moranta *et al.*, 2004). The analytical approach fitting a tps over depth–frequency distribution data gave an accurate description of the bathymetric preference of hake during their early years of life. For hake aged 0, two length aggregations were discriminated by the bathymetric distribution. During the period of the study, the ontogenetic migration between these two groups was in the length range 13.2–15.8 cm. We recognized in the small hake group the true recruits, because those fish concentrated in the nursery areas over the upper slope. In contrast, the larger hake group was formed by juveniles that were no longer true recruits because they were widely dispersed over the continental shelf.

Orsi-Relini *et al.* (2002) found that hake biomass and abundance were affected by depth, but their analysis did not investigate the relationship between depth and length. They observed greatest abundance coinciding with the 100–200-m depth stratum (five depth strata were analysed), where most nursery grounds of hake in the Mediterranean Sea are located. Similar results were found by other authors in different areas and with a variety of spatial analytical approaches (Ardizzone and Corsi, 1997; Abella *et al.*, 2005).

Our results supported the hypothesis that bathymetric changes are related to a change in diet that would coincide with the migration of juvenile hake from nursery areas on the shelf break and upper slope to the mid-shelf (Andaloro *et al.*, 1985; Ardizzone and Corsi, 1997). Carpentieri *et al.* (2005) observed a clear change in the diet of European hake in the Mediterranean Sea at 15–16 cm TL. Therefore, migration and a changed bathymetric distribution agree with a shift in diet from small planktonic crustaceans (Euphausiacea) to small pelagic fish such as *Sardina pilchardus* and *Engraulis encrasicolus*, which inhabit the coastal continental shelf and form schools usually deeper than 25 m (Fischer *et al.*, 1987). Moreover, such trophic shifts coincide with an increase in the area of the inner ear of hake responsible for the detection and location of objects, which takes place approximately at the same critical size of 14–15 cm (Lombarte and Popper, 1994); this sensorial area could be important in the location of mobile prey such as fish.

Although there are noticeable differences in recruitment strength (Bartolino *et al.*, in press) and growth rate (Morales-Nin and Moranta, 2004) between years and seasons in the central and western Mediterranean, the distribution of hake nurseries was stable and consistent in both space and time, within and throughout years (Abella *et al.*, 2005). As a result, nursery areas were identified mainly along the shelf break and the upper slope. This supports the assumption that spatial and consequently the bathymetric distribution of hake recruits is relatively independent of the time of the year. Therefore, the bathymetric distribution of hake during their first year of life is strongly related to fish size, with a clear depth preference for each length class, and the predicted surfaces can be considered to be a good approximation of the ontogenetic migration hake undertake from the nursery areas to the continental shelf.

A negative linear relationship was found between depth and the length at which fish migrate annually. This relationship suggests that recruits migrate before or at smaller size in years in which nursery areas are deeper. This statement is supported by the departure of the year 2003 from the proposed length–depth model and by the thermal anomaly observed in the Mediterranean during that summer (Marullo and Guarracino, 2003). Perhaps, during summer 2003, hake recruits did not grow sufficiently to reach the size at migration predicted by the simple linear model, or maybe nursery areas were located in shallower water. An increase in water temperature, coupled with reduced hydrodynamics and water stagnation, could have had negative effects on the marine production that consequently affected hake recruitment size and growth during summer and autumn of that year (Bartolino *et al.*, in press). It is not clear, however, how the plankton distribution pattern could have been altered by this thermal anomaly, although it could have influenced the availability and distribution of prey and consequently the growth and bathymetric distribution of hake recruits.

The results of this study suggest that the tps approach is a successful descriptive one to study the bathymetric preference of juvenile European hake. It allowed is to investigate the depth distribution of fish by length during their first year of life, revealing the existence of two distinct bathymetric phases separated by a migration at 12–16 cm TL. The development of an objective and easily applicable protocol to define the length that discriminates pre- and post-migration phases from nurseries could have useful management applications in fisheries science. It could also represent an approach for a more natural and widely

acceptable definition of which fish, although still juveniles, cannot be described as recruits, because they are no longer concentrated in nursery areas on the shelf break and slope.

Further developments of this approach will focus on how fast fish move between slope and shelf, and which density-dependent and/or environmental processes can explain the annual variations in length at migration. We believe too that the analytical approach proposed here could be productively applied to explore the depth distribution by length of other phases of the life cycle of hake and other species.

Acknowledgements

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II

Identifying fish nurseries using density and persistence measures

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ABSTRACT: We propose a 3-step methodological approach to identify and classify fish nurseries for fisheries management purposes. We applied our approach to juvenile European hake *Merluccius merluccius* in the central Mediterranean Sea. Time series of trawl-survey fish-density data were used to map juvenile hake distribution with Bayesian kriging, while geostatistical aggregation curves were used to find density hot-spots. Persistence measures were adopted to identify nurseries on the basis of their spatio-temporal persistence. We found that areas with a high density of juvenile hake showed a high temporal persistence on both a seasonal and annual basis, with the most persistent nursery areas covering about 5% of the study areas while including about 39% of hake recruitment (averaged over 10 yr). We believe the persistence of these areas is indirect evidence of their importance to the productivity of the population, with many potentially important implications for fisheries management. The approach that we developed to identify hake nurseries can be applied to different species and life stages to improve knowledge of the role of habitat for populations and communities.

KEY WORDS: Nurseries · *Merluccius merluccius* · Mediterranean Sea · Bayesian kriging · Geostatistical aggregation curves · Persistence measure

INTRODUCTION

Fisheries worldwide are experiencing a general failure of many widely used management systems; roughly 76% of the 441 stocks or species groups assessed can be considered fully exploited or depleted, while only 3% are underexploited (Csirke 2005). The main causes of such failure are intrinsically linked to the high uncertainty associated with the different steps of any fisheries management process, including the variability and complexity of marine ecosystems, the dynamic nature of fish populations, the impact of fishing activities, and the difficulties in achieving adequate monitoring and harvesting control in marine fisheries (Harwood & Stokes 2003).

In the Mediterranean Sea, fisheries management must cope with the particularly high complexity and heterogeneity of fish habitats and a high number of commercial fish species and by-catches (Bianchi &

Morri 2000). Fisheries are dominated by small and medium-sized vessels dissipated along the coasts and operating with a wide array of fishing gears (Lleonart 2005). Almost all management strategies in this context are limited to the control of fishing capacity or to the application of technical measures, like mesh size regulation, establishment of a minimum landing size and closures of areas and seasons for fishing.

Although Mediterranean fisheries have shown a surprisingly high resilience to human exploitation compared to some Atlantic fisheries, the most important commercial species are now fully exploited or overexploited (Lleonart 2005), and important negative impacts have also been measured at the level of habitats and communities (Tudela 2004). To address these problems, the scientific community is currently evaluating the introduction in the Mediterranean of the so-called ecosystem approach to fisheries (EAF), which should supply the necessary tools to protect and

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restore ecosystems, including commercial species and their habitats, with the ultimate objective of ensuring the sustainability of fisheries in the long term (Goñi et al. 2000, Pauly et al. 2002).

The Council Regulation of the European Community (EC reg. no. 1967/2006) provides some guidelines for the implementation of EAF in the Mediterranean, with particular attention devoted to the protection of nursery areas. The regulation has the potential to yield important conservation benefits and is based on 2 assumptions: (1) juvenile fish are particularly vulnerable to fine mesh trawl fishery (Caddy 1993), especially when they concentrate in nursery areas, and (2) a reduction in fishing mortality of immature fish represents a fundamental prerequisite for sustainable fisheries (Beverton & Holt 1957).

The implementation of management measures aimed at reducing the effects of fishing on juveniles and their habitats requires the spatial identification of nurseries. Usually, any area where juveniles occur in relatively high densities has been considered as a nursery (Dahlgren et al. 2006) but without providing a clear definition. Some recent attempts to establish a definition of nurseries within a general conservation framework have been developed mainly for coastal species. Beck et al. (2001) defined a nursery as a habitat that, compared to other habitats on a per-unit-area basis, gives a greater contribution to the adult population of a given species; Dahlgren et al. (2006) introduced the concept of Effective Juvenile Habitats, referring to habitats that make a greater than average overall contribution to the adult population. Many authors agree that the most effective way of assessing the importance of a specific habitat in terms of juvenile production is to directly measure the movement of individuals from juvenile habitats to the adult population (Beck et al. 2001, Gillanders et al. 2003). This strategy has been applied mainly to coastal species, using different techniques from mark-recapture (Pihl & Ulmestrand 1993) to analyses of trace elements in fish otoliths (Tomás et al. 2006). Most of these techniques, however, cannot be applied to large populations of deep-water species, whose nurseries are often located on deep continental shelves or upper slopes, as is the case with the European hake *Merluccius merluccius*, which, after a larval planktonic stage, settles down over the shelf-break (between 100 and 200 m in depth; Fiorentino et al. 2003, Colloca et al. 2004). Estimating the contribution of nurseries to the adult population of this species would require large field experiments, often far beyond the current economic possibilities of most national research systems.

As a practically feasible alternative we suggest that the spatial abundance of juvenile fish and the persistence over time of density hot-spots can be used to identify nursery areas. Our approach is based on the assumption that the average contribution to the adult population can be expected to be higher for nurseries with higher juvenile density and higher spatio-temporal stability. In fact, maintenance of a population depends on successful recruitment of young fish to nursery areas and from nursery areas back to the parent population (Hinckley et al. 2001). The location of nursery areas is therefore an integral component of the adaptation of marine fish life cycles to their environments. In this context, the stability of a density hot-spot of fish juveniles in a given area can be assumed to be indirect evidence of the importance of that area to the recruitment success of the population. Furthermore, the temporal persistence of the characteristics of an area is a fundamental prerequisite for its inclusion in a conservation network, as commonly considered in terrestrial ecosystems (Early et al. 2008).

We propose a 3-step approach to identify and classify nursery areas for conservation purposes. In particular, using European hake as a model species, we (1) estimated the distribution of juvenile densities using Bayesian kriging (Diggle & Ribeiro 2007) and trawl survey data, (2) identified density hot-spots using geostatistical accumulation curves and (3) produced measures of persistence to identify nurseries.

We selected hake as a case study because it is among the most important commercial species in the Mediterranean, suffering from high fishing pressure and currently overexploited (Lleonart 2005). Standard assessments indicated the need for drastic reduction of the fishing mortality in juveniles, which are particularly exposed to trawl fishery after the bottom settlement stage, when they congregate over nursery grounds (Aldebert et al. 1996).

MATERIALS AND METHODS

Study area and trawl survey data. We considered 42410 km² off the central-western coast of Italy, corresponding to the FAO fisheries management geographical sub-area 9 (central-western Tyrrhenian and Ligurian Seas; Fig. 1). Data on juvenile hake density were collected during 2 different trawl survey projects, the EU-funded MEDIterranean Trawl Survey (MEDITS; Bertrand et al. 2002), carried out in spring to early summer (May to July) and the GRUppo Nazionale Demersali (GRUND; Relini 1998), conducted in autumn. MEDITS started in 1994 and was carried out every year and GRUND was carried out from 1985 to 1987 and from 1996 to 2006 (no data available for 1999). Both projects used a stratified sampling design based on depth (5 bathymetric strata: 10–50, 51–100, 101–200, 201–500 and 501–700 m) and geographical

Fig. 1. Study area

sub-area. Depth strata were adopted to cover as much as possible of the distribution ranges of the species commercially exploited or potentially exploitable in each geographical sub-area. Sampling stations (153 for MEDITS and 210 for GRUND) were placed randomly within each stratum at the beginning of the projects and were sampled in all subsequent years. Each haul, conducted during daytime hours (06:00 to 18:00 h), lasted from 30 min (hauls up to 200 m in depth) to 60 min (hauls below 200 m in depth) for MEDITS, and 60 min for GRUND. The towing speed of the vessels was about 5.6 km h^{-1} for both projects. The distance covered by the net on the bottom was calculated with a Global Positioning System (GPS).

The area swept in each haul, calculated from direct measurements of the horizontal opening of the net detected by SCANMAR equipment, ranged between 0.03 and 0.18 km^2, according to the depth and the duration of the hauls.

We included in the analyses all available data from both MEDITS and GRUND collected from the 1980s to 2004. For each haul, we calculated inds. km^{-2}, considering only hake recruits, defined as those individuals less than 14 cm in total length (Bartolino et al. 2008).

Estimating spatial distribution of juvenile hake. We adopted a Bayesian kriging model (Diggle & Ribeiro 2007) to calculate a pair of density estimates for each year (an early summer estimate based on MEDITS and an autumn estimate based on GRUND) over a 2 km × 2 km estimation grid covering the whole study area (7290 cells). Data from all hauls were log(y+1) transformed to improve normality.

A prerequisite of any Bayesian analysis is the choice of prior distributions to be used for the estimation of

model parameters (McCarthy & Masters 2005). Given a time series of survey data, an earlier survey can provide informed priors for the calculation of the posterior parameter distribution covering the entire time span considered (Fig. 2).

We used the available data from the 1980s to build an informative prior structure for the early summer estimation of 1994. In the subsequent step of our estimation chain, the estimated 1994 posterior distribution was used to define the prior for the following year, and we proceeded in the same way for all early summer surveys, building an estimation chain from 1995 to 2004. Starting from 1996, we also used the early summer estimated posterior distributions to define the prior distribution for the autumn survey data (Fig. 2), building a second estimation chain from 1996 to 2004.

The 2 estimation chains described above are based on the assumption that the spatial distribution and abundance of juvenile hake in early summer are highly indicative of the distribution and abundance of juvenile hake in autumn of the same year and in the early summer of the subsequent year. A pattern of this type can be generated by the usual recruitment dynamics of hake in the central Mediterranean Sea. In fact, a main recruitment event occurs in winter-spring (Belcari et al. 2006), and then the spatial distribution of recruits remains constant for the following 6 to 10 mo
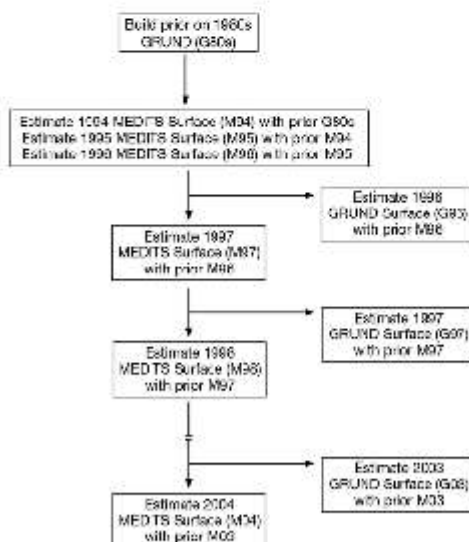

Fig. 2. Bayesian estimation procedure used to map juvenile hake in the central Mediterranean Sea employing trawl survey density data (inds. km^{-2})

(Bartolino et al. 2008). This implies that every year the 2 surveys (MEDITS and GRUND) sampled the same age class at 2 time intervals. In contrast, distribution and abundance measured in autumn are not necessarily indicative of the distribution and abundance during early summer of the following year, because a new recruitment event has occurred between the GRUND and MEDITS surveys.

The general model structure that we adopted can be formalised mathematically as:

$$Y(s) = \mu(s) + \varepsilon(s) \qquad (1)$$

where $Y(s)$ is the observed value at location s, $\mu(s)$ is the spatial trend (or large-scale variation), and $\varepsilon(s)$ is the small-scale variation (Cressie 1993). We performed an exploratory analysis of spatial variability considering first- and second-order trend models. A first-order model was selected because the second-order model absorbed most of the spatial variation (trend overfitting). The choice of a linear trend was also supported by a maximum likelihood ratio test (performed for each year and each survey) that clearly demonstrated no significant difference (p > 0.05) between first- and second-order models.

To explore possible differences in the spatial structure in our entire estimation chain, we performed an exploratory analysis, calculating for each year and for each survey an empirical variogram, formalised mathematically as:

$$\gamma(h) = \frac{1}{2n(h)} \frac{1}{n} \sum_{k=1}^{n} \delta_{ij}[y(s_i) - y(s_i + h)]^2 \qquad (2)$$

where $\gamma(h)$ is the experimental variogram for distance h, $n(h)$ is the number of points separated by distance h, and $y(s_i)$ is the fish density value at point s_i. A monotonic increase of the variogram with increasing distance separating the sampling locations indicates the presence of a spatial autocorrelation (Cressie 1993). The exploratory analysis, performed using the geoR library of the R statistical software (R Development Core Team 2007), confirmed a relatively stable spatial structure. In particular, we fitted different variogram models (exponential, spherical, Gaussian) using maximum likelihood (Cressie 1993), and the combination of an exponential variogram model with a first-order trend provided the best results in terms of cross-validation and the Bayesian Information Criterion (Schwarz 1978).

Identifying density hot-spots. To identify areas that host high annual densities of juvenile hake (i.e. annual nursery areas), we built a geostatistical aggregation curve for the estimated spatial distribution of each early summer and autumn. Geostatistical aggregation curves were originally defined by Matheron (1981), and subsequently elaborated by Petitgas (1998), to describe spatial distribution changes as a function of variations in population abundance. Here we used geostatistical aggregation curves to identify annual nursery areas.

A geostatistical aggregation curve relates the relative abundance of individuals $P(y)$ to the area $T(y)$ occupied by those individuals for densities greater than y. For calculation of the aggregation curve, all cells are ranked according to their density from maximum to minimum. Along this gradient, it is possible to calculate for each cell the cumulative abundance as a proportion of the total abundance, $P(y)$, and the proportion of the total area, $T(y)$. Both $P(y)$ and $T(y)$ range from 0 to 1, and the resulting curve describes the accumulation abundance with increasing area. $P(y)$ and $T(y)$ can be formalised mathematically as:

$$P(y) = \sum_{i=1}^{k} \frac{n_i}{N} \qquad (3)$$

$$T(y) = \sum_{i=1}^{k} \frac{a_i}{A} \qquad (4)$$

where n_i is the number of fish in the density class i, a_i is the area occupied by those fish for each class i and N is the total number of fish in the total area A.

We calculated a relative geostatistical aggregation curve $P(T)$ for each annual estimated spatial distribution combining Eqs. (3) & (4). For each geostatistical aggregation curve, we identified the location where the tangent line to the curve had a 45° slope. The tangent point was adopted as a threshold for the identification of nurseries over each annual estimated surface. Each curve up to the 45° tangent point included a specific percentage of cells. This percentage was used to find the corresponding percentile of the estimated fish density distribution and thus the nursery density threshold (Fig. 3).

The geometrical properties of the 45° tangent to the relative aggregation curve correspond to a change in the spatial distribution of fish from a dispersed distribution pattern to an aggregated pattern. For fish densities lower than the above identified threshold, a relative increase in the area is followed by a proportionally lower increase in the number of fish included. Conversely, above the threshold the relative increase is higher in the number of fish than in the area.

Persistence of nurseries. For each cell in the study area, we calculated an Index of Persistence (I_i), measuring the relative persistence of the cell i as an annual nursery (Fiorentino et al. 2003). Let $\delta_{ijk} = 1$ if the grid cell i is included in a nursery in year j and in survey k, and $\delta_{ijk} = 0$ otherwise. We computed I_i as follows:

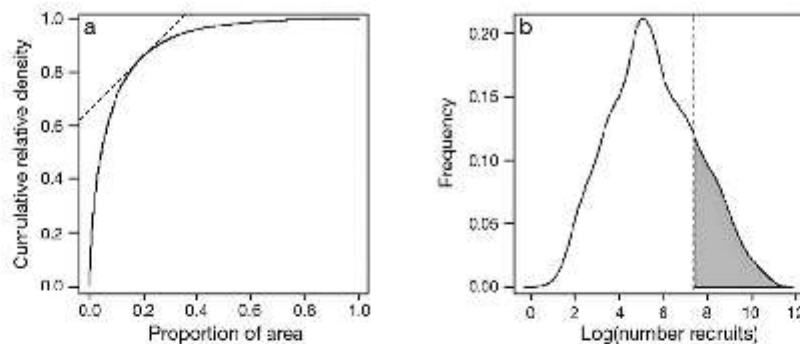$$I_i = \frac{1}{n} \sum_{k=1}^{n} \delta_{ij} \qquad (5)$$

Fig. 3. *Merluccius merluccius*. (a) Relative geostatistical aggregation curve (cumulative relative density of hake juveniles versus proportion of study area) showing the tangent (dotted line) to the curve with 45° slope. (b) Frequency distribution of estimated fish density with the related percentile (shaded area) corresponding to the proportion of cells above the identified density threshold

where n is the number of surveys considered. I_i ranges between 0 (cell i never included in an annual nursery area) and 1 (cell i always included in an annual nursery area) for each cell in the study area. Using different levels of I_i, we calculated the area occupied by nurseries and the proportion of hake recruits included in the nurseries.

RESULTS

Spatial distribution of juvenile hake

For the 1994 early summer estimate, we used the following prior settings: (1) variogram range with a uniform distribution (2 to 250 km with 1 km increments), (2) nugget to sill ratio fixed to 0, (3) diffuse priors (Gaussian and inverse Gamma) for trend parameters and overall variance. All other estimates (both early summer and autumn) were based on early summer posterior estimates (of the previous year or of the same year, respectively) used as priors. Exponential variogram models had a nugget between 0 and 3.83, partial sill ranging from 4.88 to 15.17, and range between 6.31 and 15.44 km (Table 1).

Juvenile hake distribution (Figs. 4 & 5) was clearly patchy in all years considered, with a fairly consistent spatial pattern and with differences only in the size of the observed patches. The estimated average density of hake recruits showed large fluctuations throughout the sampling period, ranging

from 300 fish km^{-2} (for MEDITS 1994) to 2479 fish km^{-2} (for MEDITS 1998). Recruit density also changed widely between the 2 surveys within the same year (Table 2).

Distribution of density hot-spots

The geostatistical aggregation curves showed a relatively stable spatial distribution pattern for hake in the

Table 1. *Merluccius merluccius*. Trend coefficients (β_0, β_1, β_2) and variogram parameters (partial sill, range, nugget) estimated for hake recruits (log-densities) for MEDITS (early summer) and GRUND (autumn) surveys

Year	β_0	β_1	β_2	Partial sill	Range	Nugget
MEDITS						
1994	−27.106	0.010	0.005	7.358	12.831	2.616
1995	−27.106	0.010	0.005	7.358	12.831	2.616
1996	−67.300	0.015	0.013	11.456	14.376	0.798
1997	−36.190	0.011	0.007	12.035	11.349	0.000
1998	−7.241	0.007	0.001	12.077	15.447	1.481
1999	−38.756	0.007	0.008	15.176	9.529	0.000
2000	−3.742	0.006	0.001	12.909	9.547	0.000
2001	−25.281	0.012	0.004	10.036	8.896	0.000
2002	−13.631	0.005	0.003	11.559	7.588	0.000
2003	−11.967	0.004	0.003	14.247	12.086	0.000
2004	−22.935	0.006	0.005	12.367	11.498	0.000
GRUND						
1996	−33.317	0.011	0.007	15.059	6.547	0.000
1997	−17.133	0.010	0.003	11.320	12.977	1.429
1998	−33.317	0.011	0.007	12.273	6.315	0.000
2000	−14.236	0.005	0.003	9.678	13.809	3.832
2001	10.790	−0.002	−0.001	9.255	7.171	0.000
2002	−31.982	0.010	0.007	6.682	11.961	2.644
2003	7.098	0.004	−0.001	4.888	11.395	3.286
2004	34.609	−0.003	−0.006	15.059	6.547	0.000

Hake density (n/km²)
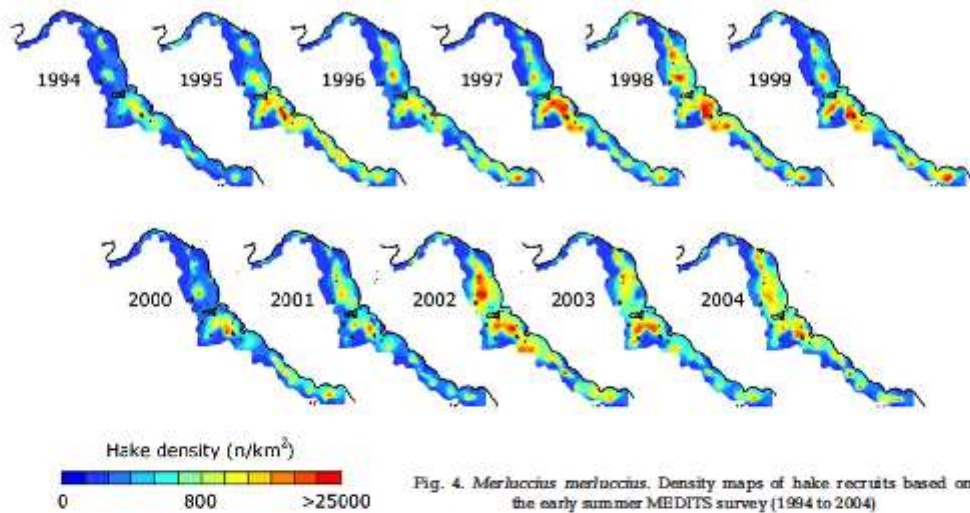
0   800   >25000

Fig. 4. *Merluccius merluccius*. Density maps of hake recruits based on the early summer MEDITS survey (1994 to 2004)

study area, despite the large density fluctuations from survey to survey. The curves clearly indicated a strong aggregation of recruits, with about 80% of them concentrated in 18 to 26% of the study area during early summer, and in 20 to 30% of the study area in autumn (Table 2, Fig. 6).

The different nursery thresholds varied between 245.9 and 3389.7 fish km^{-2} for the MEDITS survey,

and between 568.3 and 2834.7 fish km^{-2} for the GRUND survey. The nurseries identified by these thresholds covered 18 to 30% of the total study area. The nurseries with the largest recruit density were located north (south Ligurian Sea) and south of the Isle of Elba (northern Tyrrhenian Sea), while smaller high-density patches were widespread along the
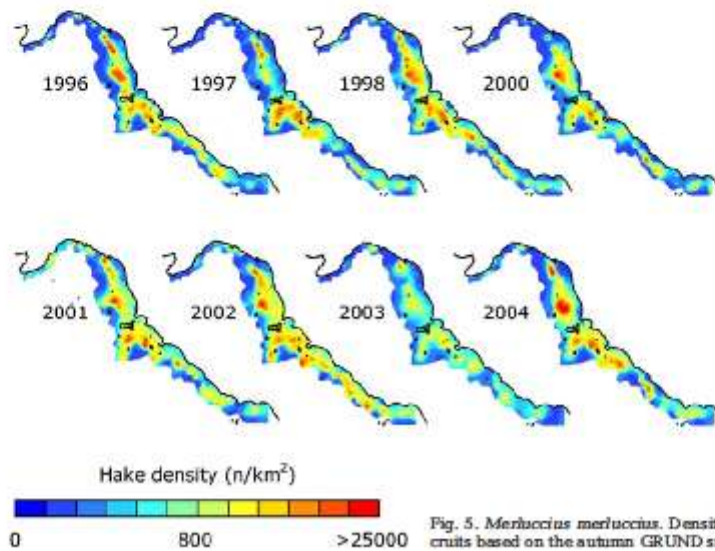

Hake density (n/km²)

0   800   >25000

Fig. 5. *Merluccius merluccius*. Density maps of hake recruits based on the autumn GRUND survey (1996 to 2004)

Table 2. *Merluccius merluccius*. Estimated size, percentage of the study area and percentage of recruits for the identified hake nurseries off the central-western coast of Italy. M: MEDITS survey (early summer), G: GRUND survey (autumn)

Survey	Nursery area (km²)	Study area (%)	Recruits (%)
1994M	4264	22.3	82.1
1995M	6024	25.1	81.8
1996M	5748	25.1	81.5
1996G	6104	25.9	82.8
1997M	4392	19.1	86.5
1997G	5680	23.7	84.4
1998M	5136	20.4	82.8
1998G	6876	27.0	82.5
1999M	4576	19.2	85.2
2000M	3988	18.1	81.2
2000G	5724	24.1	83.3
2001M	4888	21.8	80.4
2001G	6800	25.0	76.9
2002M	5244	20.5	80.1
2002G	8024	29.8	78.3
2003M	4960	19.9	79.5
2003G	7460	29.7	73.9
2004M	6544	26.3	79.2
2004G	5016	19.8	80.7

shelf-break (120 to 250 m depth) across the entire study area (Figs. 4 & 5).

Nursery persistence

The largest nursery areas showed a highly persistent core, surrounded by areas with lower persistence (Fig. 7). Smaller nurseries appeared sporadically along the shelf-break (150 to 250 m). Different levels of persistence produced different scenarios in terms of proportion of recruits included within nursery areas. Highly persistent nurseries ($I_s > 80\%$) covered 5.3% of the study area and included on average 39.2% of recruits (proportion calculated over the entire study period). Nurseries occurring in at least 60 to 80% of surveys included 12.4% of the whole area and 65.6% of recruits.

DISCUSSION

We proposed a conceptual and methodological framework for the identification of fish nurseries on the basis of their spatio-temporal persistence, which can be helpful when quantitative data on the contribution of nursery habitats to the adult population are lacking.

We applied our approach to hake recruits, using density data collected during 10 yr of trawl surveys in the central Mediterranean Sea (central-western coast of Italy). Trawl surveys represent one of the most important sources of data for the study of demersal fish (Bertrand et al. 2002), despite the inevitable inherent biases that characterise these datasets. A number of different methods are available for obtaining unbiased indices of abundance that account for trawl survey design, spatial autocorrelation and other spatial patterns and processes (Stefánsson 1996, Petitgas 2001). However, the application of geostatistical methods to such data to map species distribution (e.g. Maravelias et al. 1996) is often hampered by the low number of sampling stations relative to the area surveyed. Groundfish surveys tend to be spatially constrained because of high ship costs, and the resulting sampling points are usually scattered, with large areas that are
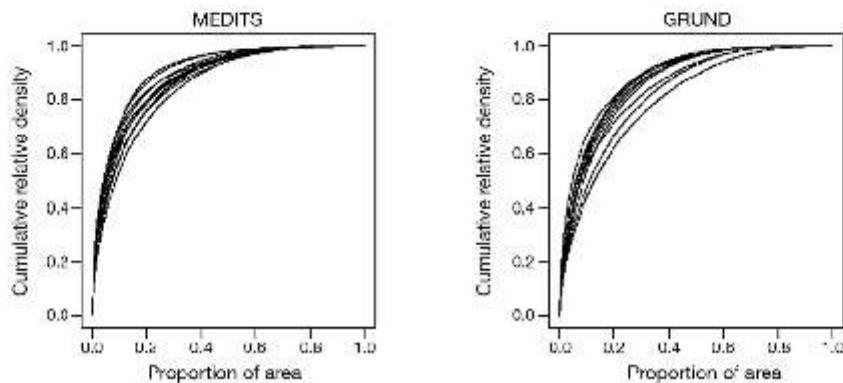

Fig. 6. *Merluccius merluccius*. Relative geostatistical aggregation curves (cumulative relative density of hake juveniles versus proportion of study area) for the early summer (MEDITS) and autumn (GRUND) estimations
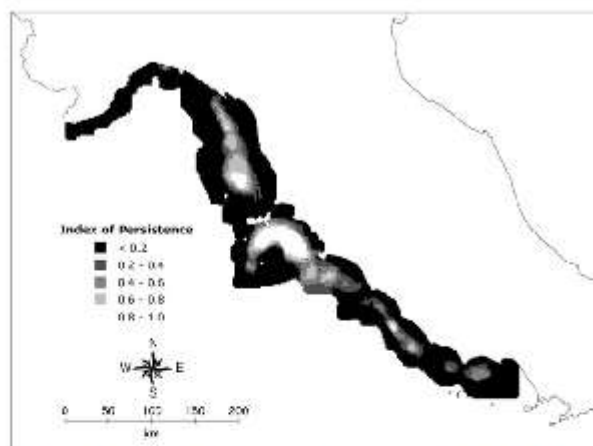
Fig. 7. Temporal persistence of the estimated nurseries in the period 1994 to 2004, based on data from the early summer and autumn surveys

not sampled. As a consequence, the variance associated with any index calculated through survey data is often extremely large, as is the uncertainty related to any spatial prediction (Rufino et al. 2006). In addition, the spatial distribution pattern of fish species is continuously changing as a consequence of density-dependent (MacCall 1990) and density-independent factors (Shepherd & Litvak 2004), with the latter generating large fluctuations in local abundance.

In classical geostatistical applications, the full range of uncertainties that is always associated with species distribution models is not correctly measured, as many parameters that are considered to be 'known' are actually estimated through the statistical model (Diggle & Ribeiro 2007), a potential cause of optimistic assessments of predictive accuracy. Using Bayesian kriging, we incorporated parameter uncertainty into the prediction process by treating the parameters as random variables. Even though our framework did not solve all problems linked to the lack of data, the existence of spatial clusters or variations in density-dependent and density-independent factors, Bayesian kriging has been increasingly used in ecological research (McCarthy & Masters 2005) to take advantage of biologically sound prior information.

For the identification of hot-spots of juvenile hake density, we coupled the Bayesian kriging estimates together with an innovative analysis of geostatistical accumulation curves. Previous studies that used the same technique focused on the analysis of spatial distribution changes in relation to variation in population abundance (Petitgas 2009). We clearly demonstrated

the potential of our approach for providing a simple alternative to traditional methods used for the spatial identification of hot-spots (Nelson & Boots 2008).

The spatial distribution of juvenile hake was similar to that already described in the same area through different mapping techniques (Ardizzone & Corsi 1997, Abella et al. 2005). Juvenile hake were patchily distributed around the shelf-break (150 and 250 m depth) and showed stable density hot-spots, which can be regarded as nursery areas, covering 18 to 30% of the study area, depending on the season and year considered. Three major physical processes explain the temporal stability of these high-density areas: (1) enrichment (e.g. upwelling, water mixing), (2) concentration (convergence, frontal formation, water column stability) and (3) retention within (or drift toward) appropriate habitat ('ocean triad'; Bakun 1998). In the Tyrrhenian and Ligurian Seas, both eddies and frontal systems retain larvae and juveniles of hake in areas of relatively high production (Abella et al. 2008), characterised by the occurrence of high biomass of macroepibenthic suspension feeders, such as crinoids (Colloca et al. 2004). A stable temporal pattern of hake nurseries was similarly observed in the Strait of Sicily (Fiorentino et al. 2003).

We considered the stability in space and time of high-density areas to be a useful measure to evaluate their importance as nurseries. Similarly, Fodrie & Levin (2008) showed that juvenile distribution over time was a good indicator of unit-area productivity of nursery areas of California halibut Paralichthys californicus.

The high spatial stability in time of the main hake nurseries can also represent a valuable feature for conservation and management purposes, ensuring, for instance, long-term effectiveness of no-take areas. In our study area, the closure of highly persistent nurseries ($I = 80$ to 100%) would result in a small reduction of the exploitable fishery area (5.3%) and the protection of a considerable fraction (39.2%) of the total estimated recruits. The impact on local fisheries of these measures could also be limited, given that the operating fleet does not concentrate on hake nursery areas owing to the high discard rate that trawling in these areas would imply (Abella et al. 2005). Using a theoretical model for European hake in the Mediterranean, Apostolaki et al. (2002) found that nursery protection led to an increase in resilience to fishing and in yields even when juvenile fish were targeted.

However, it is clear that other factors must be incorporated in any analysis aimed at quantitatively assessing the implications of no-take areas for fisheries. They include the effect of these areas on hake and other fish populations, also because of the reallocation of fishing effort after their establishment (Murawsky et al. 2005), and the economic consequences of no-take areas and their management plans (Edwards et al. 2009). Knowledge of the spatial and temporal distribution of juvenile fish is essential to closing the lifecycle in population dynamics models, and it is a prerequisite for the identification of spatial measures aimed at the protection of juveniles (Hinrichsen et al. 2009).

The analytical approach that we used here to document the persistence of spatial patterns in the distribution of juvenile hake can be extended to different species and life stages to improve knowledge of the role of habitat for populations and communities. This kind of information can be combined with data on the distribution of fishing fleets and with multiple species datasets (Maiorano et al. 2009) for an effective ecosystem approach to fisheries management in the Mediterranean.

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III

Modelling recruitment dynamics of hake, *Merluccius merluccius*, in the central Mediterranean in relation to key environmental variables

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Abstract

Hake recruitment has been examined in relation to environmental variables in two of the main reproductive areas of the central Mediterranean, the northern and central Tyrrhenian Sea. Seventeen years time series data from trawl surveys revealed high fluctuations in recruit abundance that could not be just explained by spawning biomass estimations. Generalized additive models were developed to investigate hake recruitment dynamics in the Tyrrhenian Sea in relation to spawner abundance and selected key oceanographic variables. Environmental data were explored in attempt to explain survival processes that could affect early life history stages of hake and that accounted for high fluctuations in its recruitment.

Thermal anomalies in summer, characterised by high peaks in water temperature, revealed a negative effect on the abundance of recruits in autumn, probably due to a reduction in hake egg and larval survival rates. In the northern Tyrrhenian, recruitment was reduced when elevated sea-surface temperatures were coupled with lower levels of water circulation. Enhanced spring primary production, related to late winter low temperatures could affect water mass productivity in the following months, thus influencing spring recruitment. In the central Tyrrhenian a dome-shaped relationship between wind mixing in early spring and recruitment could be interpreted as an "optimal environmental window" in which intermediate water mixing level played a positive role in phytoplankton displacement, larval feeding rate and appropriate larval drift. Results are discussed in relation to the decline in hake stock biomass and within the present climate change and global warming context.
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Keywords: Hake; Recruitment; Environmental factors; Generalized additive models; Mediterranean

1. Introduction

As the world fisheries' catches rapidly increased in the 1970s and 1980s (FAO, 2005), considerable emphasis was placed on understanding fishing effects on stocks abundance and persistence. A large amount of studies provided a valuable support for management decisions but they gave just a partial understanding of what really influences stock dynamics. In many cases fish populations declined by increasing fishing effort but unexpectedly they did not rise after that fishing pressure was reduced or completely removed (Savenkoff et al., 2003). Although environmental effects on population dynamics of fish have been recognized for a long time (i.e. Laevastu and Hayes, 1981; Cushing, 1982), a coordinated understanding, that accounted for oceans as dynamic systems in which changes have implications for marine organisms, was achieved only recently (Beamish et al., 2000).

Variations in temperature, salinity, winds and currents, can affect both the productivity and the distribution of fish stocks (e.g. Alheit and Hagen, 1997; Lehodey et al., 1997; Lloret et al., 2001). Early life history stage survival is largely influenced by environmental variability (i.e. Jennings et al., 2001).

The effect of climatic components on variability of Mediterranean fish has been largely overlooked (Agostini and Bakun, 2002). Evidences suggest that successful recruitment of European hake (*Merluccius merluccius*), that is both commercially and ecologically one of the most important species in the central-western Mediterranean, depends on the interaction of biological and physical processes, but few studies tried to evaluate the extent and nature of these relationships (i.e. Abella et al., 2005; Maynou et al., 2003; Morales-Nin and Moranta, 2004; Olivar et al., 2003).

Some studies, mostly on other hake species and outside the Mediterranean, have found that temperature for instance can

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influence *Merluccius* spp. life history at various stages, i.e. larval growth and mortality (Palomera et al., 2005; Grote et al., 2007), growth (Steves and Cowen, 2000), maturity (Alvarez et al., 2001), spawning patterns and regimes (Horne and Smith, 1997; Alvarez et al., 2001) and egg viability (Horne and Smith, 1997). Temperature is also known to influence the production and distribution of plankton (e.g. Beaugrand et al., 2002) and subsequently, the food resource for juveniles and adults.

Hydrographical structures such as currents and eddies can have important effects on the displacement of either hake eggs and larvae (Sánchez and Gil, 2000; Olivar et al., 2003). These oceanographic features act as important processes in favour or against the recruitment success by controlling the drift of larvae to either nursery areas or offshore (Agostini and Bakun, 2002). Mesoscale oceanographic processes, driving the dispersion and retention of plankton, strongly affect ocean productivity patterns with a consequent effect on higher trophic levels (Harrison and Parsons, 2000).

Although hake recruitment is almost continuous throughout the year due to multiple spawning (Orsi Relini et al., 1989), characteristic local peaks in spawning activity are found in different months in several sub-regions. In the central-western Mediterranean, recruitment peaks have been found in spring and autumn in the Ligurian Sea (Orsi Relini et al., 1989) and Gulf of Lions (Recasens et al., 1998), spring and summer in Catalan Sea (Maynou et al., 2003), Gulf of Valence and Alicante bay (Goñi et al., 2004), summer and autumn in Tyrrhenian Sea (Belcari et al., 2001) and winter and spring in Balearic Sea (Goñi et al., 2004).

Hake recruitment windows have been associated with inter-annual variability in oceanographic conditions in the western Mediterranean (Oliver and Massuti, 1995), but this hypothesis has not yet been tested. The lack of long time series of recruit abundance has been one of the main limitations increasing model uncertainty and reducing power forecast. Variations in the underlying structure of fish populations affect also stock properties, inevitably changing their functional responses to a variable environment (Dower et al., 2000). Thus, dynamics of fish populations are complex ecological processes affected by a multitude of inter-connected factors, whose effects are often non-linear (Bjørnstad and Grenfell, 2001).

The very high concentrations of hake recruits along the Ligurian and north-central Tyrrhenian coasts, FAO GFCM Geographic Sub-area 9 (GSA 9), suggested that these areas could represent the main nurseries of hake in the whole Mediterranean Sea. In GSA 9, Orsi Relini et al. (2002) estimated mean densities of hake recruits (n km^{-2}) also 8-fold higher than in the other nurseries identified in the rest of the Mediterranean basin. Concentrations higher than 25.000 recruits Km^{-2} are not unusual on the limit between the continental shelf and the upper slope into the GSA 9 (Colloca et al., 2006).

In the present study hake recruitment dynamics have been investigated in the Tyrrhenian Sea in relation to the adult hake abundance and key oceanographic variables through the development of non-parametric additive models. Environmental data are explored in attempt to explain survival processes that can affect early life history stages of hake and that account for high fluctuations in its recruitment.

2. Material and methods

2.1. Study area and oceanography

The study area covered the continental shelf and the upper and middle slope in the northern and central Tyrrhenian Sea. The northern Tyrrhenian extended from the Elba island to the cape of Argentario, while the central Tyrrhenian from this latter to the Garigliano river mouth (Fig. 1).

The Tyrrhenian Sea can be considered as a distinct entity within the central-western Mediterranean basin (Artale et al., 1994), because it is semi-enclosed between islands (Corsica, Sardinia and Elba) and mainland (Italy), and separated from the rest of the western basin by a channel of moderate depth.

In the northern and central Tyrrhenian Sea, the circulation is organized in a series of cyclonic (counter-clockwise) and anticyclonic (clockwise) gyres determined by the wind effect (Artale et al., 1994). Three main gyres, characterized by cold water inside, two cyclonic and one anticyclonic have been discerned. They undergo significant seasonal changes, particularly the central anticyclonic gyre that spreads over most of the basin in spring and summer and almost disappears in autumn and winter.

Due to the occurrence of the gyres, the northern part of the basin exerts a crucial role in the general water mass budget on the Tyrrhenian Sea. A principal effect is that the related upwelling provides a mixing of the MAW (Modified Atlantic Water) and the LIW (Levantine Intermediate Water) below, with a corresponding modification of the water properties. Moreover, the northern part of Tyrrhenian Sea is one of the main places for concentration of the basin's chemical resources (Nair et al., 1992).

The general pattern of phytoplankton seasonal dynamics was typical of subtropical areas with a maximum in cold season from October to April and a minimum in summer months (Longhurst, 1995). Mediterranean intermediate (LIW) and deep waters (DMW) have a constant temperature between 12.8 and 13 °C, thus higher water turbulence (mainly driven by winds) and deeper convection during autumn–winter period enriched the upper layer with nutrients. Reduced wind mixing in March enhances thermocline formation allowing more intense phytoplankton bloom to occur. Moreover, the temperature and density profiles show that in years of rather warm and not windy March the seasonal thermocline was formed more quickly (Nezlin et al., 2004). A secondary but not less important effect of deepening of the mixed layer and the following high input of nutrients to the surface layer is represented by the storage of nutrients for the summer period (in favourable weather conditions) that results in higher phytoplankton production in deeper layers in summer despite strong stratification. Diatoms peaked in May (February–March in other western Mediterranean areas) and October (Nezlin et al., 2004).
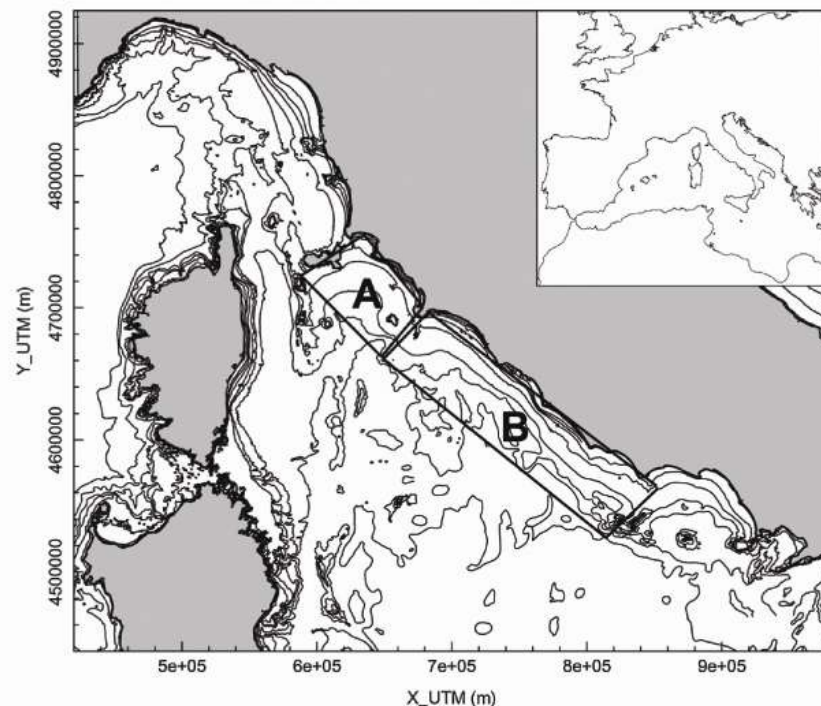
Fig. 1. Studied area: (A) northern Tyrrhenian and (B) central Tyrrhenian.

2.2. Trawl and environmental data

Time series trawl survey data comes from 1246 hauls conducted in autumn within the GRUND project (Relini, 1998) from 1985 to 2004 (in 1988, 1989 and 1999 no surveys took place). The randomized stratification scheme for these surveys was based on five bathymetric strata (10–50 m, 51–100 m, 101–200 m, 201–500 m, 501–700 m). An average of 22 hauls were yearly conducted into the 100–300 m depth range, where nursery areas are known to be located. Abundance data of hake, as mean number of individuals per squared kilometre ($n \, km^{-2}$), have been obtained for both recruits (<14 cm) and adults (>26 cm). The choice of the recruit length interval was based on the mean fish length of migration from nursery areas to the continental shelf (unpublished data). Considering that reproduction takes place throughout the year, with a spawning peak in late winter and that according to the relatively fast-growing hypothesis, in the Mediterranean small hake probably reach 15–16 cm length in 8–10 months (i.e. Belcari et al., 2006), abundance data on recruits account for most of the fish born in the year.

To investigate the effect of hydrological conditions on recruit abundance, a suite of environmental factors was selected that have an important influence on spring and summer primary production and that may potentially affect early life history stage survival. Time series of mean monthly values of remote sensing data (1985–2004, Table 1) of sea-surface temperature (SST, °C) and wind mixing index (W^3, $m^3 \, s^{-3}$)

were used, respectively from the Physical Oceanography Distributed Active Archive Center (PO.DAAC: http://podaac.jpl. nasa.gov/index.html) and the Pacific Fisheries Environmental Laboratory (PFEL: http://www.pfeg.noaa.gov/).

The turbulent energy transferred to the upper water layer generated by action of the wind on the sea-surface is roughly proportional to the cube of the wind speed. Hence, wind mixing index is calculated as the cube of the wind speed.

W^3 in April (wmix4), May (wmix5) and August (wmix8), SST in late winter (sstm.w) as mean temperature between February (sstm2) and March (sstm3), SST in August (sstm8) and maximum SST in August (sstmax8), have been selected as the main forces driving spring water productivity in the central Mediterranean basin and affecting hake early life history stages.

Low late winter SST was thought to positively affect spring primary production deepening the mixed layer and enhancing the following input of nutrients to the surface layer (Nezlin et al., 2004). This nutrient-enriched environment, followed by reduced water mixing in spring (wmix4 and wmix5), provides the storage of nutrients for the summer period that results in higher phytoplankton production in deeper layers in summer despite strong stratification (Nezlin et al., 2004).

Oceanographic features in August (sstm8, sstmax8 and wmix8) are also taken into account for their possible direct and indirect effects on hake recruit survival rates, considering that both young recruits and larvae are abundant during summer period.

Table 1
Data used in GAM modelling of hake recruitment for the northern (a) and central (b) Tyrrhenian

Year	Month	Recruits (n Km^{-2})	Spawners (n Km^{-2})	sstm2 (°C)	sstm3 (°C)	sstm8 (°C)	sstmax8 (°C)	wmix4 (m^3 s^{-3})	wmix5 (m^3 s^{-3})	wmix8 (m^3 s^{-3})
(a)										
1985	IX	6882.44	62.35	13.60	13.77	24.23	24.83	150.71	44.91	31.02
1986	IX	4246.05	64.02	13.52	14.12	26.63	27.75	102.64	13.46	15.57
1987	IX	23233.14	46.80	13.04	13.00	25.63	26.55	75.79	35.87	16.56
1990	X	7558.00	10.45	14.71	14.81	25.45	25.88	49.78	18.57	11.33
1991	X	9442.33	45.84	13.63	13.95	26.20	26.92	43.00	31.24	6.04
1992	XI	2302.79	36.87	13.25	13.66	26.90	28.80	157.12	31.82	8.47
1993	VII	5664.54	40.12	13.77	13.39	25.65	26.55	51.51	13.67	8.78
1994	X	3697.36	27.11	13.96	14.93	27.11	27.45	111.19	40.96	11.27
1995	X	3834.94	28.26	14.00	14.13	26.27	27.30	77.51	33.78	18.93
1996	X	2952.95	16.43	13.95	13.95	25.60	26.25	37.98	42.56	7.75
1997	IX	3411.86	16.45	14.10	14.25	25.66	26.25	179.42	71.65	24.94
1998	IX–X	2803.22	12.90	14.38	14.42	26.18	27.00	199.14	37.79	49.18
2000	IX	1871.79	12.39	13.64	13.98	25.00	26.33	132.61	45.04	16.26
2001	IX	3768.57	21.59	14.51	14.86	25.57	26.70	129.39	65.79	29.13
2002	IX	3939.69	17.06	14.00	14.32	25.21	26.33	138.11	72.77	49.25
2003	IX	1119.34	11.06	13.46	13.96	28.28	28.95	209.19	46.06	44.10
2004	IX	4273.78	12.80	13.66	13.70	25.83	26.70	85.85	87.30	21.86
(b)										
1985	IX	4051.79	74.60	13.72	14.00	24.98	26.33	164.45	62.20	46.75
1986	IX	2101.55	63.71	13.95	14.13	27.16	27.98	101.51	18.45	20.26
1987	IX	10057.70	234.40	13.69	13.36	26.30	26.92	103.38	45.22	14.94
1990	XII	720.91	8.20	15.05	15.19	26.47	27.23	88.15	28.29	15.01
1991	IX	860.97	29.63	13.94	14.32	26.72	27.52	71.98	67.87	8.42
1992	XII	659.23	29.19	13.52	13.72	27.70	29.25	187.49	31.00	7.62
1993	VII	2956.10	21.59	14.00	13.72	26.13	27.08	60.53	12.36	9.08
1994	XI	2330.60	37.26	14.56	15.21	27.93	28.73	133.98	57.11	8.96
1995	X	2236.54	37.01	14.61	13.96	27.53	28.58	84.67	45.70	17.34
1996	XII	1403.67	74.93	14.27	14.19	26.60	27.23	48.13	52.99	10.00
1997	X–XI	2752.39	49.04	14.40	14.47	26.46	27.19	166.93	52.82	22.25
1998	X–XI	3420.97	25.22	14.75	14.70	27.05	27.83	142.43	41.41	25.27
2000	X	2320.39	29.61	13.98	14.24	26.11	27.67	126.66	28.83	20.68
2001	X	1953.53	26.78	14.84	15.62	26.43	27.52	119.78	67.30	33.65
2002	IX	3592.77	25.55	14.46	14.95	25.89	26.70	136.24	66.67	45.02
2003	IX	470.81	25.70	13.99	14.36	28.88	29.40	217.67	39.71	54.46
2004	X	4064.49	17.63	13.86	13.90	26.39	26.77	72.78	91.72	19.94

2.3. Statistics

Principal component analysis (PCA) was applied in order to reveal possible correlation patterns in the environmental data and to reduce the number of variables to the first principal components (PCs) that are independent (orthogonal). All environmental variables were included in the PCA, except maximum sea-surface temperature (sstmax8) that as a proxy of summer extreme environmental conditions was explored separately. The newly derived PCs can be interpreted as empirical factors related to the main environmental and oceanographic properties of the investigated system.

Generalized additive models (GAM, Hastie and Tibshirani, 1990) are a highly flexible statistical approach that offers the main advantage to be able to model non-linearities that often relate biological data to environmental factors.

A Gaussian distribution of the log-transformed response variable was assumed.

Model fit and parsimony were evaluated through analysis of deviance using approximate F-test and generalized cross-validation (GCV) (Green and Silverman, 1994). Low values indicate the best compromise between model complexities (i.e. number of parameters) and fit to the observed data.

To avoid the problem of "collinearity", i.e. the inclusion of explanatory variables that are themselves correlated, two distinct formulations of GAMs were used. The first model included terms to model hake recruitment as a function of the spawner abundance and of the single environmental variables and took the form:

$$\log(\mathrm{recr}) \sim s(\mathrm{spawners}) + s(\mathrm{sstm.w}) + s(\mathrm{sstm8}) + s(\mathrm{sst\,max\,8})$$

$$+ s(\mathrm{wmix4}) + s(\mathrm{wmix5}) + s(\mathrm{wmix8})$$

where s is the thin plate regression spline smoothing function (Wood, 2003) which assesses the shape of the response variable as a function of the predictor.

In the second model, the two principal components were adopted as empirical factors and the model took the following form:

$$\log(\mathrm{recr}) \sim s(\mathrm{spawners}) + s(\mathrm{PC1}) + s(\mathrm{PC2}) + s(\mathrm{sst\,max\,8})$$

Statistical analyses were performed with R and the associated *mgcv* package (freely available at http://www.r-project.org/). The level of significance was set at 5% for all the statistical tests used in this study.

3. Results

Results from PCA summarised the regional environmental variability of the two examined sub-areas, revealing a similar pattern with late winter processes well distinguished by spring and summer events.

The first (PC1) and the second (PC2) principal components accounted respectively for the 33% and 27% of variance in the central Tyrrhenian and 38% and 27% in the northern Tyrrhenian (Fig. 2). Both sub-areas showed a clear distinction between late winter process of water mixing and thermocline deepening and
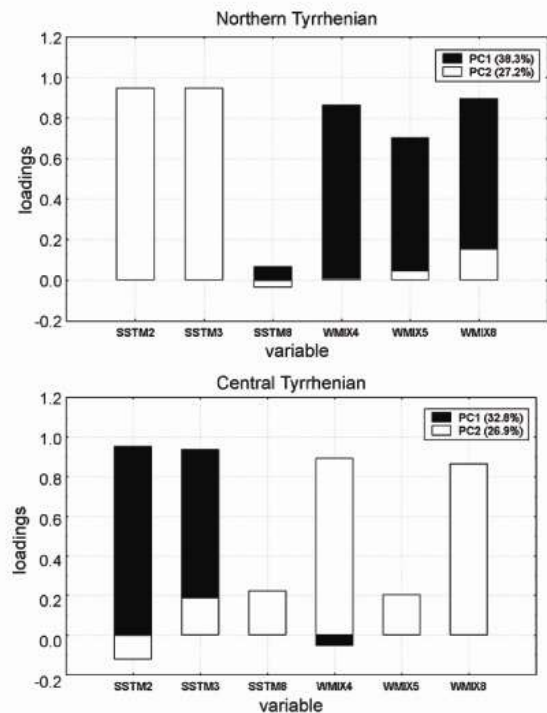

Fig. 2. Correlation of the environmental variables with the first two principal components (PC1 and PC2) in the northern (a) and central (b) Tyrrhenian Sea.

spring summer productivity processes. Sea-surface temperature in February and March was mainly explained by PC1 in central Tyrrhenian and PC2 in northern Tyrrhenian. On the other hand, wind variables and water temperature in August (that could be associated with wind driven circulation, reduced summer water circulation and elevated temperature values) were significantly correlated with PC2 in central Tyrrhenian and PC1 in northern Tyrrhenian.

The time series of abundance of adult hake in the two areas are both characterised by elevated values in the late '80s (Fig. 3), but a statistically significant negative trend ($r^2 = 0.57$, $P < 0.01$) was observed only in the northern Tyrrhenian (Fig. 3a). No decreasing trend was detected in the central Tyrrhenian (Fig. 3b).

3.1. Northern Tyrrhenian

The bivariate regression (Fig. 4a) showed a positive effect of spawners on the hake recruitment in the northern Tyrrhenian, with a regression coefficient $r^2 = 0.23$. The most significant effects on the abundance of recruits were the non-linear relationships with water temperature in winter (sstm.w, $r^2 = 0.29$, $P < 0.05$) and the negative linear relationship with wind mixing in April (wmix4, $r^2 = 0.30$, $P < 0.05$). Maximum water temperature in August had a linear negative effect on autumn recruitment (sstmax8, $r^2 = 0.2$, $P < 0.05$). The second principal component, related to late winter temperature pattern, showed the same but slightly weaker non-linear relation of sstm.w with recruitment
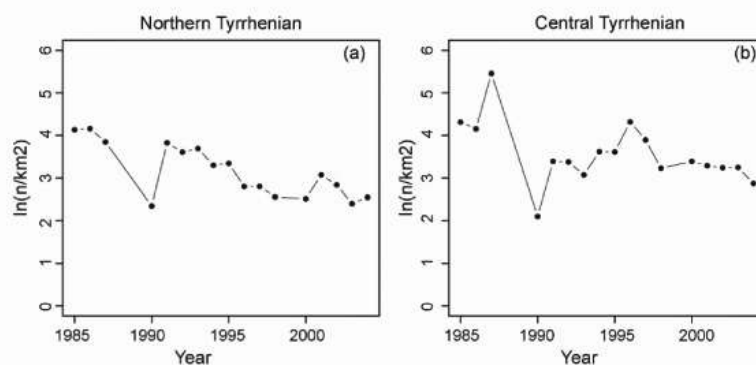
Fig. 3. Log indices of abundance of adult hake from 1985 to 2004 in the northern (a) and central (b) Tyrrhenian.

Table 2

Analysis of deviance and calculated GCV of the main estimated GAMs for hake log recruitment, in the northern Tyrrhenian (a) and central Tyrrhenian (b)

Model	Response	Predictors	e.d.f.	p-Value	% Dev expl.	r^2	GCV	Edf
(a)								
mod1	log(recr)	spawners	1.00	0.006				
		sstm.w	1.94	0.001				
		sstm8	1.91	0.008	90.4	0.85	0.12	6.86
		sstmax8	1.00	0.002				
mod2	log(recr)	spawners	1.00	0.014				
		sstm.w	1.94	0.005				
		wmix4	1.00	0.072	86.9	0.80	0.15	6.53
		sstmax8	1.59	0.023				
mod3	log(recr)	spawners	1.00	0.007				
		sstm.w	1.94	0.004	84.5	0.78	0.15	5.78
		sstmax8	1.84	0.003				
mod4	log(recr)	spawners	1.00	0.003				
		PC2	1.95	0.003	85.8	0.80	0.14	5.85
		sstmax8	1.89	0.002				
Model	Response	Predictors	e.d.f.	p-Value	% Dev expl	r^2	GCV	Edf
(b)								
mod1	log(recr)	spawners	1.00	0.427				
		sstm.w	1.00	0.113				
		sstm8	1.00	0.201	77.5	0.64	0.37	6.90
		sstmax8	1.00	0.071				
		wmix4	1.90	0.031				
mod2	log(recr)	sstm.w	1.00	0.012				
		sstm8	1.00	0.082				
		sstmax8	1.00	0.020	76.6	0.66	0.32	5.94
		wmix4	1.94	0.006				
mod3	log(recr)	sstm.w	1.00	0.048				
		sstmax8	1.00	0.041	68.0	0.58	0.36	4.90
		wmix4	1.90	0.025				
mod4	log(recr)	sstm.w	1.00	0.396				
		sstmax8	1.00	0.009	41.6	0.33	0.49	3.00
mod5	log(recr)	sstm.w	1.00	0.037				
		wmix4	1.93	0.006	56.0	0.46	0.43	3.93

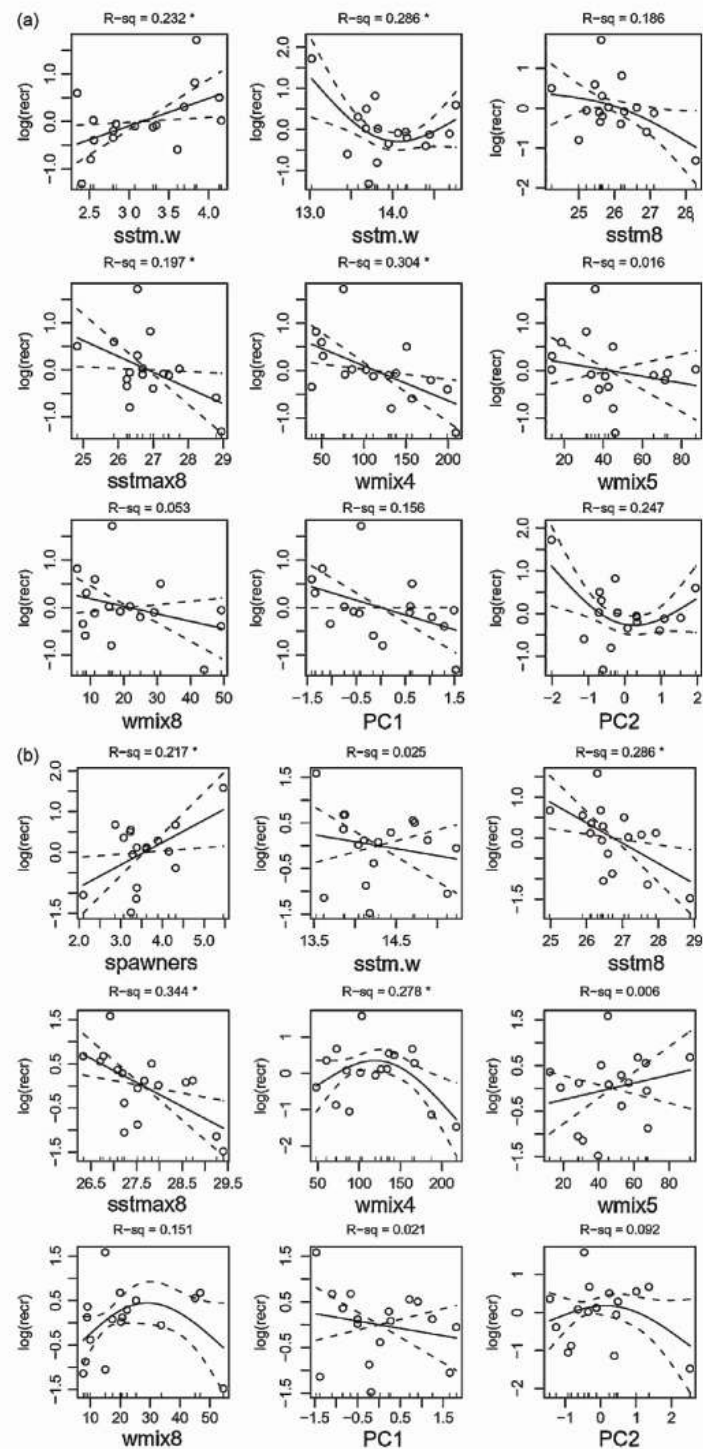Equivalent degrees of freedom are reported for the whole models (Edf) and for the single variables (e.d.f.).

Fig. 4. Scatterplots and regression spline smoothers of log recruitment of hake in the northern (a) and central (b) Tyrrhenian Sea against abundance of adults, sea-surface temperature in late winter, August, maximum sea-surface temperature in August, wind mixing index in April, May, August, first and second principal component. Each plot has associated its correlation coefficient marked with * for a statistical $P < 0.05$.
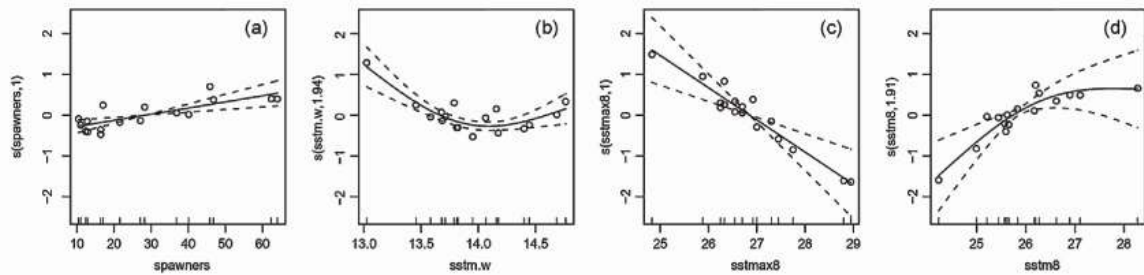
Fig. 5. Effects of: (a) spawners, (b) sstm.w, (c) sstmax8 and (d) sstm8 on hake recruitment in the northern Tyrrhenian (mod1).

(PC2, $r^2 = 0.25$, $P = 0.05$). The relationship with the first principal component was not significant.

Apart from the confirmed spawner–recruit relationship, hake recruitment in the northern Tyrrhenian was mostly a temperature driven process, highly influenced by late winter temperature and summer water warming (Fig. 5). Low late winter temperature had a positive effect as shown in the bivariate regressions (Fig. 5b). Wind mixing components are not represented in the best model (mod1, Table 2a) and although wind mixing in April (mod2, Table 2a) could have an effect on the abundance of recruits, it slightly increased the GCV score from 0.12 to 0.15, with a 3.5% reduction in the whole explained variance. Mean temperature in August had a strong positive effect on the abundance of recruits in autumn but it tended to an asymptote for values >27 °C (Fig. 5d). The effect of maximum temperature was linear and negative (Fig. 5c).

Together the spawner abundance, the second component and maximum temperature in August explained 85.8% of the variation in the hake autumnal recruitment. The second component effect resembled the relationships of late winter temperature (Fig. 6). High maximum temperatures in August confirmed their

negative consequences on autumnal recruitment but no effect was found in cooler years.

Although more parsimonious than mod1, 3 explanatory variables against 4, this second GAM (mod4) including empirical variables based on principal component analysis did not achieve any improvement in terms of GCV score and deviance explained.

The final model for hake recruitment in northern Tyrrhenian was: log(recr) $\sim$ spawners + sstm.w + sstm8 + sstmax8 (Fig. 7).

3.2. Central Tyrrhenian

Exploratory bivariate regressions of the recruit abundance against the adult abundance and the environmental variables (Fig. 4b), shows that the maximum water temperature in August was the most strongly correlated factor (sstmax8, $r^2 = 0.34$, $P < 0.01$), through a linear negative relationship. Significant relationships ($P < 0.05$) were also with spawner abundance ($r^2 = 0.22$), mean temperature in August (sstm8, $r^2 = 0.29$) and wind mixing in April (wmix4, $r^2 = 0.30$).

The dome-shaped curve of wind mixing in April (wmix4) suggested a positive effect of moderate wind in early spring that turned to negative, depressing recruitment for values higher than $\sim 150 \, m^3 \, s^{-3}$.
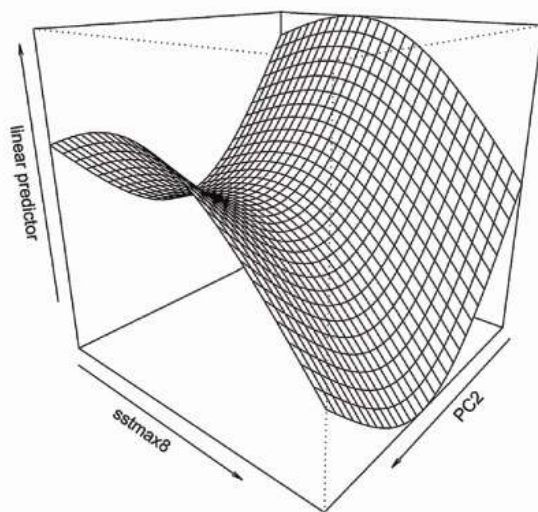

Fig. 6. Surface plot of the effect of PC2 and sstmax8 on hake recruitment in the northern Tyrrhenian from the GAM mod4 (GCV = 0.14).
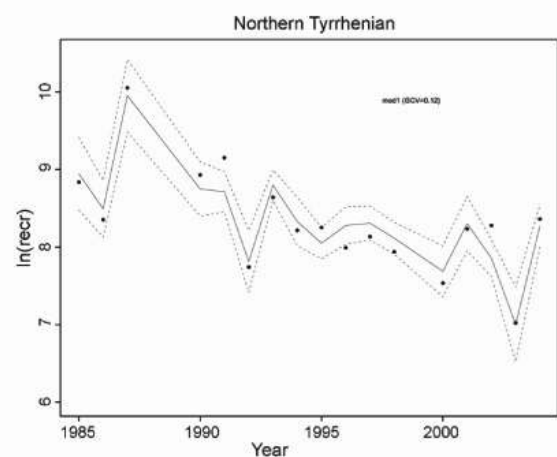

Fig. 7. Observed and predicted log recruitment from 1985 to 2004 in the northern Tyrrhenian, with 95% confidence interval.
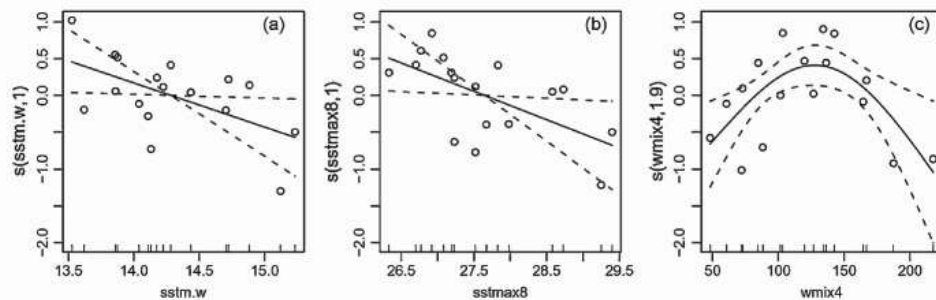
Fig. 8. Effects of: (a) sstm.w, (b) sstmax8 and (c) wmix4 on hake recruitment in the central Tyrrhenian (mod3).

No relationship was found with the first component, while the second component resembled the pattern of wind mixing in April and August but with a poor statistical significant level.

Several combinations of predictor variables were tested in GAMs and the best models were selected according to the lowest GCV and to biological criteria that allowed to exclude statistically good models but with no biological and ecological basis (Table 2).

The weak spawner–recruit relationship found in the exploratory analysis was rejected from the additive model because not significant ($P = 0.427$).

The reduced final model (GCV = 0.36) for log recruits from central Tyrrhenian (mod3, Table 2b) included late winter temperature, maximum temperature in August and wind mixing in April (log(recr) ~ sstm.w + sstmax8 + wmix4, Figs. 8 and 9). Surface temperature in late winter had a negative effect on the abundance of recruits (Fig. 8a). Maximum water temperature in August had a negative linear effect (Fig. 8b), while wind mixing in April confirmed the dome-shaped relationship of the bivariate regression (Fig. 8c).

No additive model, including principal components as explanatory variables, was selected.

Fig. 9. Observed and predicted log recruitment from 1985 to 2004 in the central Tyrrhenian, with 95% confidence interval.

4. Discussion

Results from this study helped to clarify the role played by some key environmental processes on hake recruitment dynamics in the central Mediterranean Sea.

The comparative examination of the two areas, suggested that mainly temperature, probably at a medium regional scale was responsible for increasing or decreasing hake recruitment throughout the Tyrrhenian, but that other variables (wind driven processes) accounted for local patterns, too.

Hake recruitment in the northern and central Tyrrhenian shared some similar responses to the considered predictors. A negative almost linear effect of maximum water temperature in summer was found to reduce deeply the abundance of recruits in autumn.

Water temperature plays an important role in egg development and larval growth and survival of several hake species (Steves and Cowen, 2000). In the Mediterranean Morales-Nin and Moranta (2004) found the main abundance of recruits in a temperature interval of 13.5–14 °C.

The thermal anomaly that characterised summer months in 2003 has been particularly strong in the central Mediterranean and the Tyrrhenian basin was one of the most affected areas (Marullo and Guarracino, 2003). Along the Catalan coast strong vertical temperature and salinity gradients in autumn 1998, with sea-surface temperatures higher than the seasonal mean, reduced water mixing and intrusion of warmer and less saline Atlantic waters, produced anomalous oceanographic conditions that indirectly affected hake recruitment (Olivar et al., 2003).

It can be hypothesised that the summer anomalous oceanographic scenario observed in 2003, could negatively affect recruit abundance in autumn through the combination of different mechanisms: increasing mortality rates of eggs and larvae during higher temperature peaks, enhancing water stratification with relative lower phytoplankton production and modifying gyres and water circulation systems that are probably involved in larval transport and retention processes of hake larvae in the nursery areas.

Although there are few data on phytoplankton and zooplankton communities in the studied areas, it is likely that the reduced upwelling process throughout the period of thermal stratification, late spring and summer, affected primary and secondary production and consequently, through a bottom-up effect, the
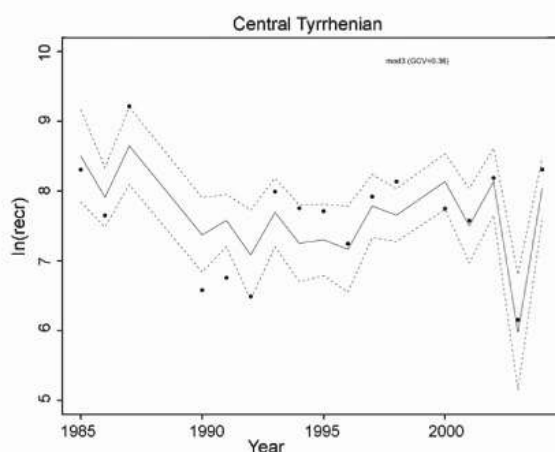
upper trophic levels. It has been previously observed in the Bay of Biscay that a reduction in nutrients recorded during years of low level upwelling, diminished the food availability for larvae and juveniles, negatively affecting hake recruitment (Sánchez and Gil, 2000).

In the Ligurian Sea late winter processes of thermocline erosion and nutrient mixing have a crucial role in supporting primary production in the following months (Nezlin et al., 2004). Deeper thermocline formation does not influence just spring phytoplankton production, that would affect recruitment during spring, but also summer productivity that could be more strictly related to summer and early autumn survival of larvae. In both northern and central Tyrrhenian, sea-surface temperature drives this enhanced nutrient enrichment process with a positive effect of low late winter temperature on the late winter-early spring recruitment.

The effect associated with the wind driven water mixing processes in April is evident in the central Tyrrhenian. Elevated water mixing reduces the effects of the upwelling mechanism mentioned above weakening the spring thermocline formation. This negatively affects spring productivity processes and deteriorates nutrient storage that can enhance also productivity through the following months. The negative effect of reduced wind mixing in April in the central Tyrrhenian probably reflects a more complex situation that could be interpreted in terms of "optimal environmental window" (Cury and Roy, 1989). A dome-shaped relationship between turbulence and larval feeding rate had been observed by MacKenzie and Miller (1994), demonstrating that larval fish ingestion rates are likely to be maximal at intermediate rather than high levels of turbulence. The same functional response was recently found by Grote et al. (2007) for the abundance of eggs and larvae of *M. capensis* and *M. paradoxus* in the Benguela upwelling region. The authors reported that to reduce the advection of larvae offshore into waters with unfavourable environmental conditions, these two species avoid spawning during time of minimal and maximal upwelling. Also in the central Tyrrhenian intermediate wind mixing can represent a compromise between enhanced spring phytoplankton production, and appropriate larval drift to feasible recruit retention areas (nurseries).

Because in the northern part of the Tyrrhenian Sea the high concentration of nutrients is more related to the general water circulation pattern and the large continental shelf southern Elba island (Nair et al., 1992), in this area recruit abundance is probably less dependent on spring wind driven processes. This could also explain the higher temporal stability of hake nurseries in the northern Tyrrhenian respect nursery areas in the central Tyrrhenian (Colloca et al., 2006).

In the Bay of Biscay for the European hake as well as in other areas for other hake species (i.e. Pacific hake, *M. productus*), oceanographic conditions contribute both to the dispersal and retention of early life history stages of hake and to the spatial dynamics of their planktonic food resources influencing relative year-class strength (Alvarez et al., 2001).

Although the hake spawning biomass has been reported to be highly depleted in the study area by several authors (Abella and Serena, 1998; Colloca et al., 2000), and the time series of abundance indices of adult fish examined in this study showed relatively high values in the '80s, evidences of a statistically significant decreasing trend in the time period investigated have been found only in the northern Tyrrhenian.

The linear spawner–recruit relationship found in the northern area could confirm a situation of recruitment overfishing characterised by low spawning biomass but the occurrence of yearly strong recruitment events would support the idea of an elevated reproductive potentiality of the remaining adult stock. Furthermore, currently no information would suggest any significant change in the fishing effort on hake in the Tyrrhenian Sea during the 20 years time span examined.

The apparent lack of a spawner–recruit relationship in the central Tyrrhenian could be interpreted as the dominance of environmental factors on the recruitment process but also as the fact that recruits replenishment in this area could originate from southern waters outside the study area. Aggregations of mature hake around and south of the Pontine islands were reported by fishermen and through the northward current hake recruits could be drifted and settle in the main nurseries of the central Tyrrhenian.

Climate fluctuations have always affected fish abundance, but their consequences on fish populations were very different when the confounding effects of fishing were not present (Larkin, 1996). Considering the present on-going global climate change, it is appropriate to stress the linkage between climate, the ocean ecosystem and fish population dynamics (Beamish et al., 2000).

The recruitment phase transition, to use the terminology suggested by Duffy-Anderson et al. (2005), observed in 2003, showed how small changes in a key-variable (e.g. maximum temperature in summer) can deeply depress hake recruitment.

In order to understand the complexities and to ameliorate the strategies of fishery management, it is necessary to study the nature of uncertainty associated with the abundance of fish stocks, the effects of fishing, and particularly the influence of the ocean environment (Rothschild et al., 2005).

Variations in recruitment and survival mechanisms may have profound ecological and management implications (Ciannelli et al., 2005) that should be taken into account in the face of possible incumbent climate changes.

Acknowledgements

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IV

First implementation of a Gadget model for the analysis of hake in the Mediterranean

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Introduction

One of the main objectives of statistical modelling is to integrate multiple sources of information and using them simultaneously to estimate parameters.

The advantages of using information from different datasets within the same single model fitting procedure have been clearly expressed by several authors (i.e. Demyanov et al., 2006; Methot, 1989) and widely recognised, but various problems are related to this issue and different solutions and approaches have been suggested. One of the main issue in combining multiple information is related to weighting of data sources.

The study of dynamics of fish populations require to incorporate a variety of processes and multiple datasets. Many widely used assessment models (e.g. XSA) do not consider this aspect and almost ignore combination of multiple datasets. An appropriate integration of different components of a model (e.g. stocks, fleets), generally described by different descriptors represented by different datasets, can pass through the use of so called likelihood components (Taylor et al., 2007). This provided also the basis for implementing rather complex and disaggregated models.

An age-length structured model was built for hake in the central and north Tyrrhenian, using Gadget (Begley and Howell, 2004; Begley, 2006). Gadget is the Globally applicable Area Disaggregated General Ecosystem Toolbox developed to model marine ecosystems, and it is able to integrate species interaction and the impact of fisheries exploiting the stocks of that species (Taylor et al., 2007). As specified by Stefansson and Palsson (1998), Gadget has been developed as a forward

simulation model using statistical estimation through weighted combinations of several log-likelihood criteria.

Among the main advantages of Gadget there are its flexibility, low data-demanding requirements, and the possibility to integrate into the same model uncompleted time series of data at different aggregation levels. All these features helped to implement the hake model for the Tyrrhenian sea (fig. 1) and allowed to combine different sources of information at quite different scale.

The complex ecology of hake, the key role it plays within Mediterranean demersal assemblages and its economic importance attracted the attention of marine ecologists and fisheries scientists since long time. This produced an extensive number of studies and literature on European hake during the last decades that made it probably one of the most studied species in the Mediterranean basin. Although this large amount of knowledge, very limited works of synthesis have been done for the development of population structure models (i.e. Apostolaki et al., 2002).

Hake represents one of the most important commercial species of the demersal fishery in the western Mediterranean. In the Tyrrhenian sea several different gears target hake, including trawlers, and gillnets with different mesh size.

Several studies demonstrated how trawlers and gillnets in the Mediterranean exploit mostly different portions of the hake stock according to their selectivity (e.g. Aldebert et al., 1993; Abella and Serena, 1998, Colloca et al., 2000). The common use in the Mediterranean of trawl nets with 40 mm and smaller cod-end mesh size, which finds an explanation in the high market value of small hake and other incidentally caught species, produces trawler catches dominated by small-sized hake mostly immature. Comparative fishing experiments with different mesh sizes (mentioned in Caddy, 1990) suggested that larger hake can be potentially less vulnerable to fine mesh gears or they can distribute over areas less vulnerable to trawling activity.

Studies of other fishing methods in the Gulf of Lions (i.e. Aldebert et al., 1993) showed that the old part of the hake stock, composed by mature fish and representing the spawning potential, is not normally caught by trawlers on the continental shelf. This limited pool of mature fish is however vulnerable to gillnets and longlines, especially along the edge between shelf and slope.

In the Tyrrhenian sea small scale fishery targets hake mainly through the use of gillnets (Abella et al., 1997). Trawlers exert a higher fishing effort respect small scale fishery and they catch considerably higher number of hake in the Tyrrhenian sea as well as in most of the north-western Mediterranean but, due to marked differences in the spectra of lengths targeted by the two gears, gillnet landings of hake reach comparable amounts in terms of biomass (IREPA official national statistics).

Estimation and monitoring of adult fish biomass is considered one of the most important aspect of fish stock assessment and management (Francis, 1997), because in spawner fish is concentrated the potentiality of a stock to renewal and persist in time (SSB paradigm), large fish often occupy higher levels of the trophic web, and because large fish are generally economically more valuable than small ones.

The main objective of this work is to develop a basic population structure model for hake in the Tyrrhenian Sea testing alternative model assumptions concerning recruitment, growth and fishing

effort. Furthermore, the basic model will be used to test the potential effects of implementing closed areas management scenarios in the hake nurseries as a specific tool to reduce fishing mortality on recruits.

Material and methods

A series of equations characterised by some parameters enclose most of the information that define the model (figs 2-3). Gadget runs a model based on these equations and parameters, and then compares the outputs from the model to the observed data to get likelihood scores as a goodness of fit of each model component. Through a combination of different minimisation algorithms (Simulated Annealing, Hooke & Jeeves, BFGS) parameters are adjusted until a minimum in the overall likelihood score is found (best fit of the model to the data). A fundamental part of the parameter estimation procedure consists in assigning a weight to each source of information to define its contribute to the overall sum of squared error. We adopted the weighting method proposed by Stefansson (1998, 2003) where the importance assigned to each source of information or component is proportional to how well the model fits the data and to the size of the component itself.

The basic conceptual model of hake (fig. 2) consists of two stock components represented by small (2-40 cm in TL, age0-3) and large (40-100 cm in TL, age1-4+) hake in a single area (central and northern Tyrrhenian). The model has a time aggregation in quarters for a time span of 14 years (from 1994 to 2007).

The growth process (G) was modelled on the base of a simplified version of the von Bertalanffy growth equation as follow:

$$\Delta L_i = (L_\infty - L_i)(1 - e^{-k \Delta t})$$

$$\Delta W_i = q_1((L_i + \Delta L_i)^{q_2} - L_i^{q_2})$$

where L is fish length, t is time and W is fish weight. Growth parameters (Linf = 100 cm; k = 0.21; q1 = 0.59*10^5; q2 = 3.0595) were fixed according to the most recent assessments (SGMED, 2008) and in agreement with the fast growth hypothesis proposed for hake (e.g. Garcia-Rodriguez and Esteban, 2002) on the base of recent results from tagging experiments (Pinero et al., 2004; de Pontual et al., 2006), reinterpretation of otholit rings (Belcari et al., 2006; Kacher and Amara, 2005; Morales-Nin and Moranta, 2004) and bioenergetic considerations (Jobling, 1994; Because, 2007).

Classical assessment has often assumed natural mortaliy as constant. This could be an appropriate assumption, although a simplification, considering for instance that many North Atlantic fish stocks are mostly exploited when fish are mature and that small fish are generally moderately selected by fishing gears or that they have no economic value. The lack of validity of these assumptions for most of the Mediterranean demersal fisheries, including hake fisheries, has been pointed out by

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several authors (i.e. Caddy, 1993; Caddy & Abella, 1999; Colloca et al., 2000). It is unreliable to assume a constant natural mortality rate for all age classes, mainly because younger individuals should be susceptible to higher predation mortality and more intense density-dependent mechanisms. The practical consequences are a rapid decline in natural mortality rate M in the first years of life to relatively constant natural mortality levels for adult fishes.

A natural mortality vector (M_a) was adopted according to recent assessment of the hake stock in the area (SGMED, 2008: M_0=1.3; M_1=0.8; M_2=0.4; M_3=0.3; M_{4+}=0.2).

Movement of fish (mat) from the small to the large hake component was simulated at the fixed length of 40 cm. Considering length-at-first maturity of female is 35 cm in TL (ref.) the large hake component approximately represents the mature portion of the stock.

Two recruitments (R) are simulated in the first and second time step every year. They have the same pattern based on standardised geostatistical estimations (Colloca et al., submitted) but different level (scale factor estimated within Gadget, fig. 3).

Two fishing fleets are simulated in the model, trawler and gillnet fisheries. Reduction of animals by the simulated fisheries is given by the combination of fishing level (effort) and suitability function (gear selection) disaggregated by gear. Time series of fishing effort (fig. 3) disaggregated by fishing gear were obtained from IREPA national statistics and are based on the combination of two main components, fishing capacity (*tsl*: gross weight of vessels measured in tons) and fishing activity (*gg*: mean number of fishing days by boat):

$$fishing \quad effort = \frac{tsl \cdot gg}{10^6}$$

Trawlers and gillnets displayed also a different pattern of selectivity (fig. 3), targeting different portion of the stock, that was approximated through gear-specific parameters. The suitability function for both the fishing gears was a combination of a Gamma and a constant function:

$$S(L) = \alpha$$

$$S(L) = \left(\frac{L}{(\alpha - 1)^{\beta \gamma}} \right)^{\alpha - 1} e^{\frac{\alpha - 1 - L}{\beta \gamma}}$$

Data and likelihood functions

For each observed data a corresponding fitted dataset can be generated by Gadget allowing direct comparison between modelled and observed population. This gives the possibility to properly evaluate the fitting of each model component to the available datasets.

The following data, data likelihood components in the Gadget terminology, from surveys and landing statistics have been used and associated to likelihood components for the estimation procedures:

- Summer trawl survey length distributions (MEDITS survey: Bertrand et al., 2003) on 1 cm length aggregation, from 1994 to 2007, were associated to the likelihood component LD1
- Autumn trawl survey length distributions (GRUND survey: Relini 1998) on 1 cm length aggregation, from 1994 to 2005, missing 1999, were associated to the likelihood component LD2
- Abundance indices on summer survey data (MEDITS survey: (Bertrand et al., 2003) based on 3 length classes, from 1994 to 2007, were associated to the likelihood components SI1.1, S1.2 and S1.3
- Abundance indices on autumn survey data (GRUND survey: Relini 1998) based on 3 length classes, from 1994 to 2005, missing 1999, were associated to the likelihood components SI2.1, SI2.2 and S2.3
- National official landings statistics (IREPA: Institute of Economic Researches on Fishery and Aquaculture) disaggregated by quarter for trawlers and mixed gillnets from 2004 to 2007, were associated to the likelihood components LN.trw and LN.gill
- Commercial catch length distributions (DCR: Data Collection Regulation) disaggregated for trawlers and mixed gillnets on 2 cm and 4 cm length aggregation respectively, from 1998 to 2007 (with several gaps), were associated to the likelihood components LD.trw and LD.gill

Modelled length distributions for both surveys and commercial fisheries components (LD1, LD2, LD.trw and LD.gill) were compared to the respective likelihood data through the sum of squares likelihood function:

$$l = \sum_{time} \sum_{age} \sum_{length} (P_{tal} - \pi_{tal})^2$$

where P_t is the proportion of the data sample for that time/age/length combination and π_t is the proportion of the model population for that time/age/length combination.

Three indices of abundance for each of the two experimental trawl surveys have been calculated. The length intervals have been considered from the observation of the length distributions from the surveys, in accordance with the main cohorts shown by the length structure (fig. 4):

- MEDITS: 2-12 cm, 12-20 cm, 20-80 cm
- GRUND: 5-16 cm, 16-26 cm, 26-80 cm

The likelihood components for the indices are the sum of squares of a log linear regression fitted to the difference between the modelled data (N_t) and the observed survey index (I_t). The slope has been fixed ($\beta = 1$), leaving Gadget to estimate the intercept.

$$I = \sum_{time} \left(I_t - (\alpha + \beta \ln N_t)\right)^2$$

Landing data are compared with fleet disaggregated overall catches with a log sum of squares function. Data are disaggregated by quarter and cover the 2004-2007 time interval.

$$I = \sum_{time}\sum_{fleet} \left(\ln(N_{tf} + \varepsilon) - \ln(v_{tf} + \varepsilon)\right)^2$$

where N_{tf} is the catch data for that time/fleet combination and v_{tf} is the modelled catch data for that time/fleet combination.

Model performances were also evaluated comparing the basic conceptual model (mod1) with alternative hypotheses and formulations such as:

- 1 recruitment in the first quarter (Alt1)
- 1 recruitment in the second quarter (Alt2)
- Estimating growth rate k under alternative assumptions of fishing effort (Alt3 and Alt4)
- Slow growth rate (Alt5)

Weighting procedure and parameters estimation

Independently from the criterion adopted to fit model to the data, maximum likelihood methods, sum of squared residuals or Bayesian methods, when multiple sources of information contribute to the overall sum of squared error each component will contribute proportionately to its associated relative weight. Several weighting protocols have been developed, but most of them generally try to consider the degree of uncertainty associated with the data or the statistic used (Haddon, 2001).

We adopted the weighting method proposed by Stefánsson (1998, 2003) where the minimum sum of squared error (sse) for each component is obtained through the estimation procedure applied to a very flexible model with each component one by one heavy weighted. The flexibility of the model is obtained leaving Gadget to estimate most of the parameters (see Stefánsson, 2003 for more details on the iterative re-weighting scheme).

The inverse of these minimum sse, multiplied by the degrees of freedom for each component, is used as a variance estimate to build the relative weight for each component. This means that greater the variability, less the relative weight.

The degrees of freedom represent the number of terms that constitute the data and are the number of potentially informative length cells for each year/step/age cell.

In the development of large models, it is generally a matter of choice to decide what should be estimated within the model and what should be taken as assumption or externally estimated. This is also what has been done here for the hake model into the Gadget framework. One of the main reasons for not leaving Gadget to estimate parameters for a too large number of processes, was to reduce the number of parameters to deal with. This was achieved through assumptions that constrained the model on some aspects of minor interest for the current work or for which more reliable information were available. For this reason estimation was mostly restricted to the scale factor for the initial population, the scale factor to size recruitments, fishing effort and growth rate.

Model projections and alternative management measures testing

Although deterministic models are known for producing only a single realisation and development of the system, also in the case of forward simulations, some sources of stochasticity can be still considered. Multiple sources of uncertainty have been recognised in modelling biological systems and processes (Charles, 1998; Harwood and Stokes, 2003) and simulations invariably include stochastic elements in which random variation around one or more model components can be included.

Monte-Carlo approach was used to simulate forward projections of the model taking into account the uncertainty related to recruitment and evaluating its implications on the model under different management scenarios. Resampling was carried out assuming and statistically testing (Kolmogorov-Smirnov: D=0.160, p=0.868) recruitment as gamma distributed (Shelton, 1992; Taille et al., 1995) according to the recruitment variation observed in the 1994-2007 time interval.

Running the forward simulations a sufficient number of times (for computational reasons we limited the number of simulations to 100) we got a summary information of the confidence interval associated to the predictions, thus an estimation of uncertainty. 8-years forward projections of the modelled hake stock were done assuming a stable fishing effort based on 2007.

The effect of closed area management scenarios, aimed to reduce fishing mortality on recruits during their aggregation highly vulnerable phase, was evaluated on the basic model. Medium term projections allowed to simulate two different scenarios of protection of hake <15 cm in total length (Bartolino et al., 2008) from trawl fishery (40% and 60% levels) and the effects on the expected adult stock biomass (SSB) were evaluated.

Results

Basic hake model

The initial inverse weights and the weights determined from the iterative procedure are given in table 1 along with the ratio between the sum of squares from the final model and the minimum for each component. As a result of incorporating information from different data sources, the final sse for each component is typically greater than the minimum from the iterative weighting.

LD1 and LD2 likelihood components have the highest weights as expected from experimental data. Indices of abundance from the two surveys reveal an opposite weighting according to their fitting to the model dynamic, summer survey indices high weight the small hake length group SI1.1 while autumn survey indices high weight the large hake group SI2.3.

The estimated length distributions for both the surveys are dominated by the first cohort that produces an almost symmetric dome shape curve. During low recruitment years a second cohort appears in the summer survey component. As expected the first cohort mode is shifted from 8-9 cm to 11-12 cm from the summer to the autumn survey. This growth pattern appears correctly represented by the basic model. Residuals for length distributions (fig. 5) presented homogeneous dispersion for both trawl surveys for small hake. The model tends to overestimate mid-length and large fish.

The model has a very high fit for SI1.1 likelihood component (fig. 6) as expected from the high weight associated to this component (table 1). The indices from the two surveys showed comparable sum of square errors, thus fitting, for the intermediate length class, while the large hake group found better agreement with the autumn survey index SI2.3 (fig.6). The intercept of the assumed linear relationship can be interpreted as a relative measure to compare catchability between length groups and surveys. Length groups 2 and 3 show lower intercepts respect length group 1, as expected according to lower catchability of large fish. No sensible differences were found in the catchability of the two surveys.

Estimated length distributions from the commercial fleet components were found in agreement with data for most of the time steps available (fig. 7). The model simulates two distinct cohorts of trawl landings in time step 2 as generally observed in the data, with the second always larger than the first although large variations are observed in the data about their respective size. Length distributions of gillnet landings show a relatively simpler structure with a main mode at approximately 30 cm in fish total length.

Recruitment was spread between time step 1 and 2 with an estimated comparable size (only 5% difference, fig. 3).

Estimated fishing mortality F shows highest values in the first two age classes, as expected for a fishery mostly targeting immature fish, with a peak value of 1.02 ± 0.28 for age1 hake (table 2).

Spawning stock biomass (fig. 8) shows a strong decrease during the first five years (1994-1998) of the period investigated. A moderate reduction in biomass is found in the following period and a minimum is observed in 2003 with an estimated value less than half of the initial value of 1994.

Model comparison

Basic model (mod) overall likelihood score is the second best value after Alt5, with a value of 4284 against 4126. The other formulations range between 4448 and 7858.

Models were compared and evaluated according to their fit to the data but also considering the differences in the estimated population dynamics (fig. 8). Model runs can be divided in two distinct groups according to the estimated spawning stock biomass. Mod, Alt1 and Alt2 estimated much

higher values of SSB than the Alt3, Alt4 and Alt5 formulations, but at the same time lower relative reduction of mature fish throughout the time period investigated, approximately 50% reduction against 70-75% reduction.

Both single recruitment models require the estimation of large number of recruits coming into the models in a single time step to ensure the survival of a minimum number of fish to fit landings in the third and fourth quarter of each year. This penalises fitting of length structure components LDs from both fisheries and surveys (fig. 9).

Model alternatives including growth rate parameter optimisation (Alt3, Alt4, Alt5) are able to estimate alternative growth patterns that can improve parts of the hake stock dynamic matching with some of the survey-related likelihood components but they fail totally in fitting commercial catch, underestimating appropriate landings of large hake by gillnet fishery.

Nurseries closed areas scenario

8-years forward projections of the modelled hake stock have been done, assuming a constant fishing effort based on 2007 data. After a further decrease in 2008 and 2009 with a minimum of 3161 tons, SSB is estimated to have a progressive increase in the following years to reach 4853 tons in 2015. As expected forward estimations were characterised by consistent variability as consequence of the high uncertainty associated to recruitment predictions.

Reduction of recruits fishing mortality of 40% and 60% produced very limited effects on the predicted SSB from 2010. In 2015, after 8 years of simulated management scenarios, only a 3-5% improvement in SSB is estimated respect the scenario without further specific protection of hake recruits.

Discussion

The ability of Gadget to model several sub-processes and mechanisms combined with its flexibility, offered an extensive control of a large number of the model components.

The modelling framework was proved to perform successfully also in a landing data limited environment, as it often occurs in the Mediterranean.

Integration of new biological information such as the use of fast growth parameters for hake, almost twice respect those generally applied in previous assessments (i.e. SAC, 2003), represents an important aspect of improvement.

Weighting the different information available gave the possibility to prioritise the importance of the various data sources, high weighting specifically designed experimental surveys and low weighting commercial fisheries data. This framework allowed to consider also official statistics of commercial landing, known for being highly problematic due to the atomised characteristics of the Italian fisheries and for this reason generally omitted by most of modelling approaches. As shown in the results, low weight commercial landing components played a fundamental role in the hake model

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comparisons because allowed to identify models with SSB underestimation also in a limited data environment.

The reduction in the fishing effort observed during the last years, coupled with fast recovery features of the hake stock (r-selection), could have the potentiality for a moderate increase of the stock in the next years. Such possible increment in the stock size should be interpreted correctly at the light of the available short time series of data, thus considering the long history of exploitation of the stock in the area along the last fifty years with clear sign of overfishing since '80s.

Although the current high levels of fishing mortality on recruits can be easily considered far from any sustainable exploitation scenario (SGMED, 2008) and moreover risky considering the possible occurrence of repeated failed annual recruitments, a reduction of F only for recruits would provide rather limited effects on the stock.

Colloca et al. (submitted) demonstrated the occurrence of extremely high concentrations of hake recruits in the Tyrrhenian and Ligurian sea (60% of recruits are concentrated in only 10-11% of the area). The elevated spatio-temporal stability of the hake nurseries in this area (Colloca et al., submitted) would guarantee the effectiveness throughout time of the implementation of closed areas, but our population structure model showed how limited improvements in SSB should be expected even in the most precautionary scenario (60% level of recruits protection). This means that the a management measure specifically designed to protect hake recruits would perform poorly in terms of fish that would be able to grow up to the size of maturity.

This can be explained mainly by the high natural mortality (M) that characterises the first year class. As a consequence the total mortality (Z) of age-0 hake is more strongly influenced by M rather than F. Thus, even if closed areas would provided positive results their effect alone would be as much limited as natural mortality is high compared fishing mortality:

$$\text{if } M \gg F \quad \rightarrow \quad Z = M + F \sim M$$

This result should not be interpreted as a reason against the implementation of closed areas to fisheries, but it demonstrates that the positive effects that should be looked for in protecting hake nursery grounds are only limitedly related to a reduction in hake recruits fishing mortality. Other stages of hake life cycle could occur in the same areas where recruits congregate, being positively affected by a reduction of fishing activity on such grounds. Furthermore, a decrease in trawling impact over hake nurseries would ensure preservation of specific habitats of the shelf-break such as crinoids seabed (Colloca et al., 2004) that have been proved to play a key role in structuring important demersal assemblages (Cartes ...; Colloca et al., 2003) enhancing marine productivity.

Acknowledgements

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Tables

comp	1/ssem	ssef/ssem	scaled Wi
LN.trw	2.682	31.939	43
LN.gill	0.640	1.992	10
LD.trw	1.065	1.932	486
LD.gill	1.744	1.997	436
LD1	4.405	1.155	2344
LD2	6.378	1.654	2666
SI1.1	36.928	22.548	517
SI1.2	4.405	34.392	62
SI1.3	0.808	2.949	9
SI2.1	0.267	1.812	4
SI2.2	1.289	9.902	14
SI2.3	7.205	8.242	79

Table 1 - Component weights: the inverse minimum sums of squares, the scaled weights calculated from the iterative reweighting procedure and the ratio of the sum of squares from the optimised model (sse f) with the minimum from the weighting run (sse m).

age	F $\pm$ 95% CI
0	0.70 $\pm$ 0.19
1	1.02 $\pm$ 0.28
2	0.31 $\pm$ 0.10
3	0.29 $\pm$ 0.10
4+	0.29 $\pm$ 0.10

Table 2 - Estimated fishing mortality with 95% confidence interval by age class.

Figures
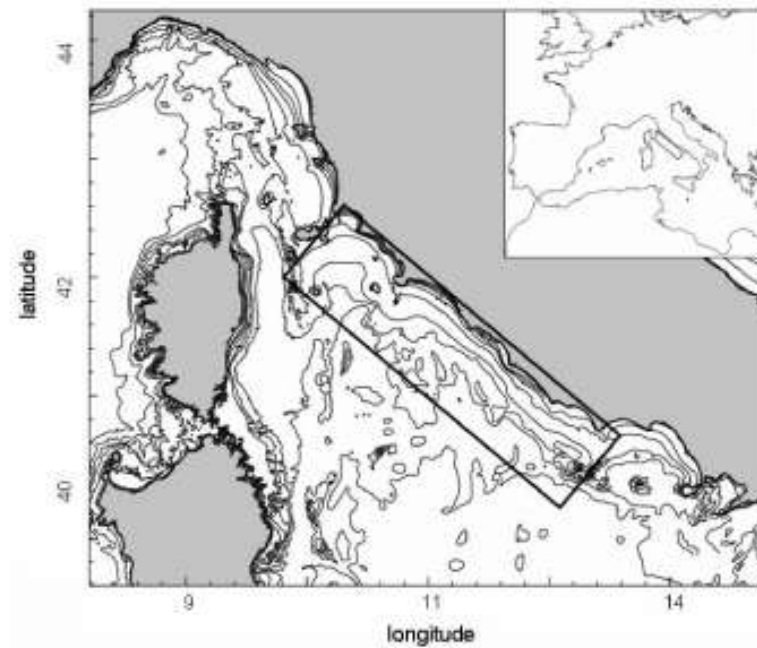
Fig. 1 - Map of the study area
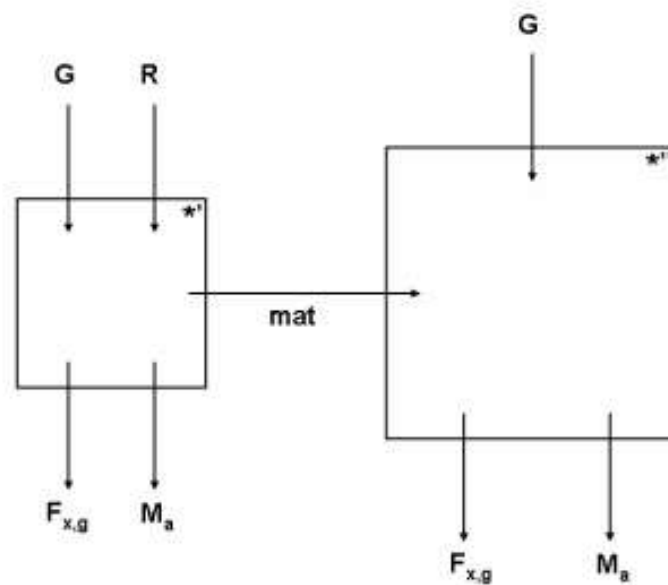
Fig. 2 - Basic conceptual model of hake simulating small (∗') and large (∗'') hake stock components and the processes of growth (G), recruitment (R), natural mortality by age (M_a), fishing mortality by fish length and fishing gear ($F_{x,g}$), movement of fish from the small hake to the large hake component (mat).
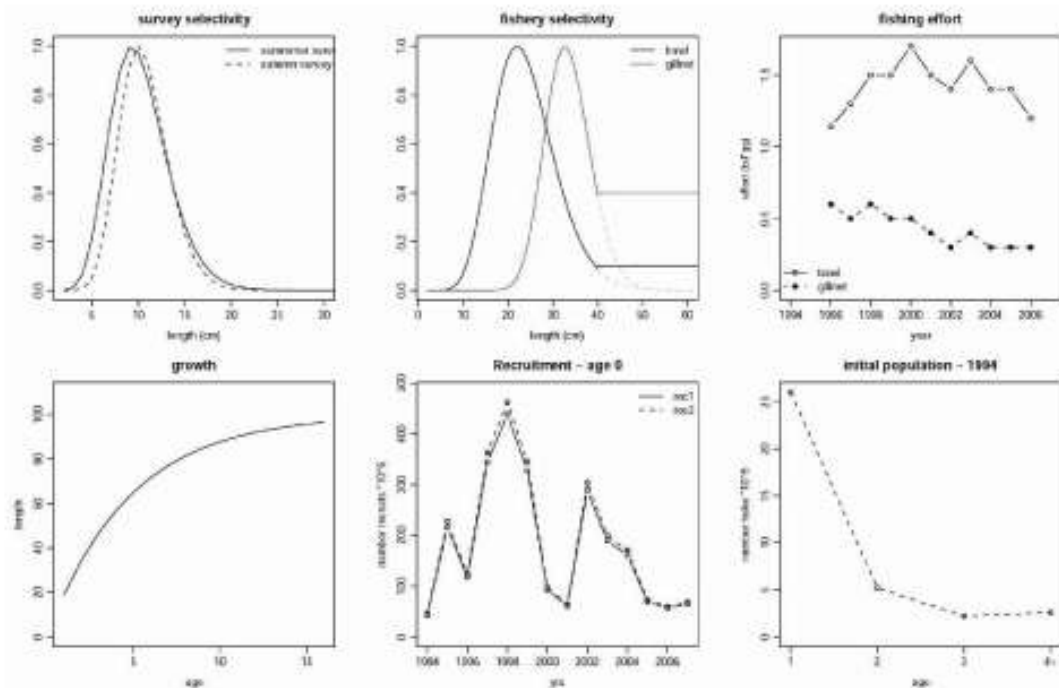
Fig. 3 - Main model relationships, (from top left) survey selectivity pattern, commercial trawler and gillnet selectivity pattern, trawler and gillnet fishing effort, von Bertalanffy growth function, number of recruits coming into the model, age structure of the initial population (timestep 1, year 1994).
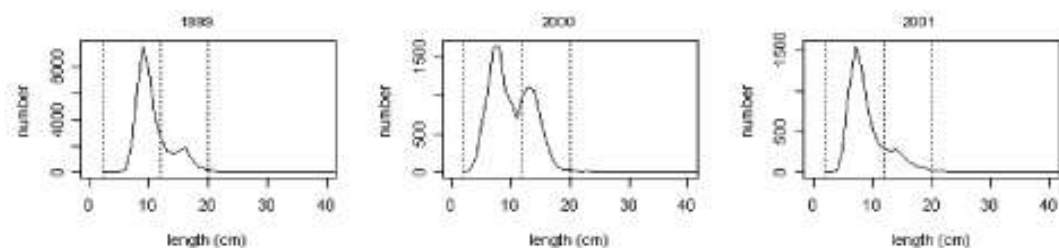
Fig. 4 - Length distributions from the summer survey for 1999, 2000 and 2001 with vertical lines indicating the length groups of aggregation to calculate the summer survey indices.

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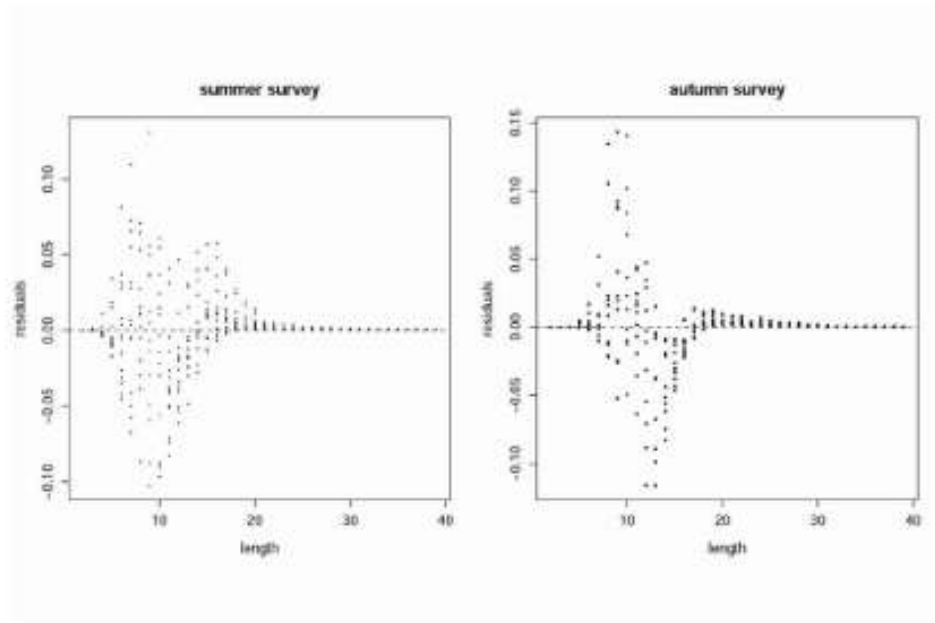
Fig. 5 - Length distribution residuals from summer (LD1) and autumn (LD2) trawl surveys.
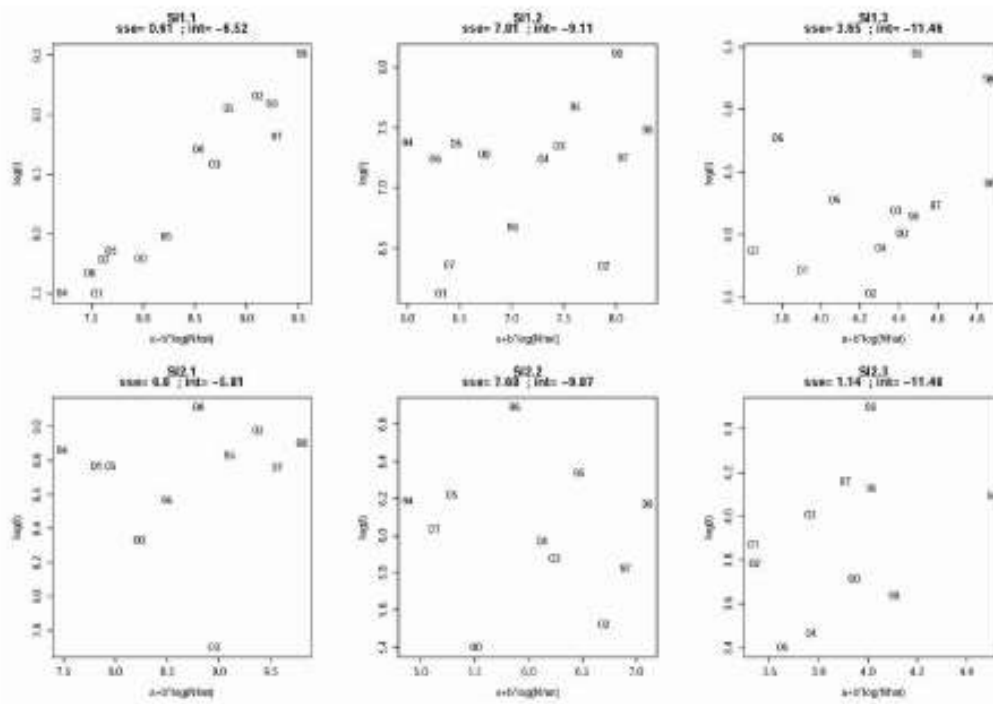
Fig. 6 - Plots of the log linear regression between survey indices from likelihood data and as estimated by gadget. ln(*I*) is the survey index and $\alpha + \beta \ln N_t$ is the fitted regression to the modelled fish population.
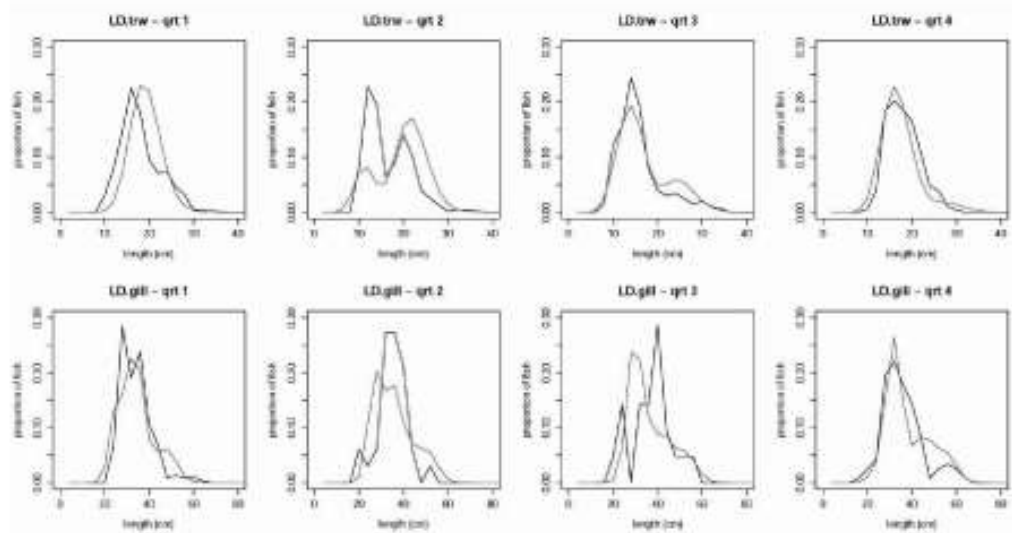
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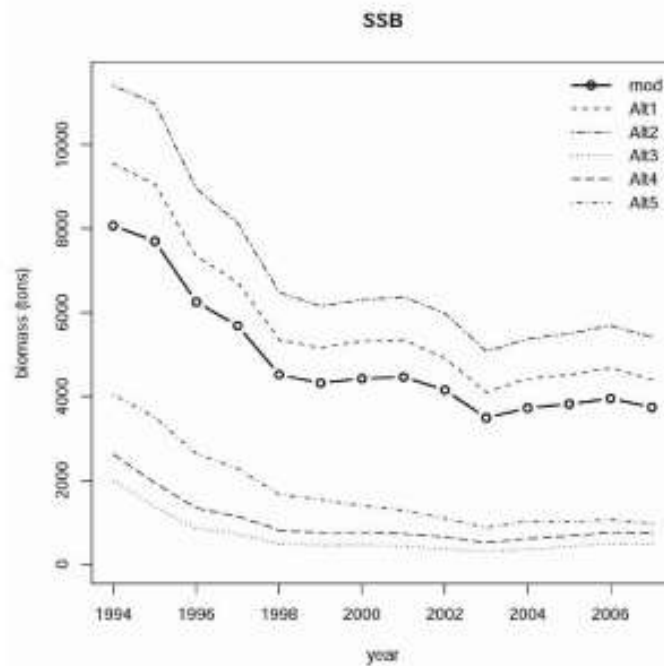

Fig. 8 - Estimated spawning stock biomass (timestep 4) from the basic and alternative models from 1994 to 2007.
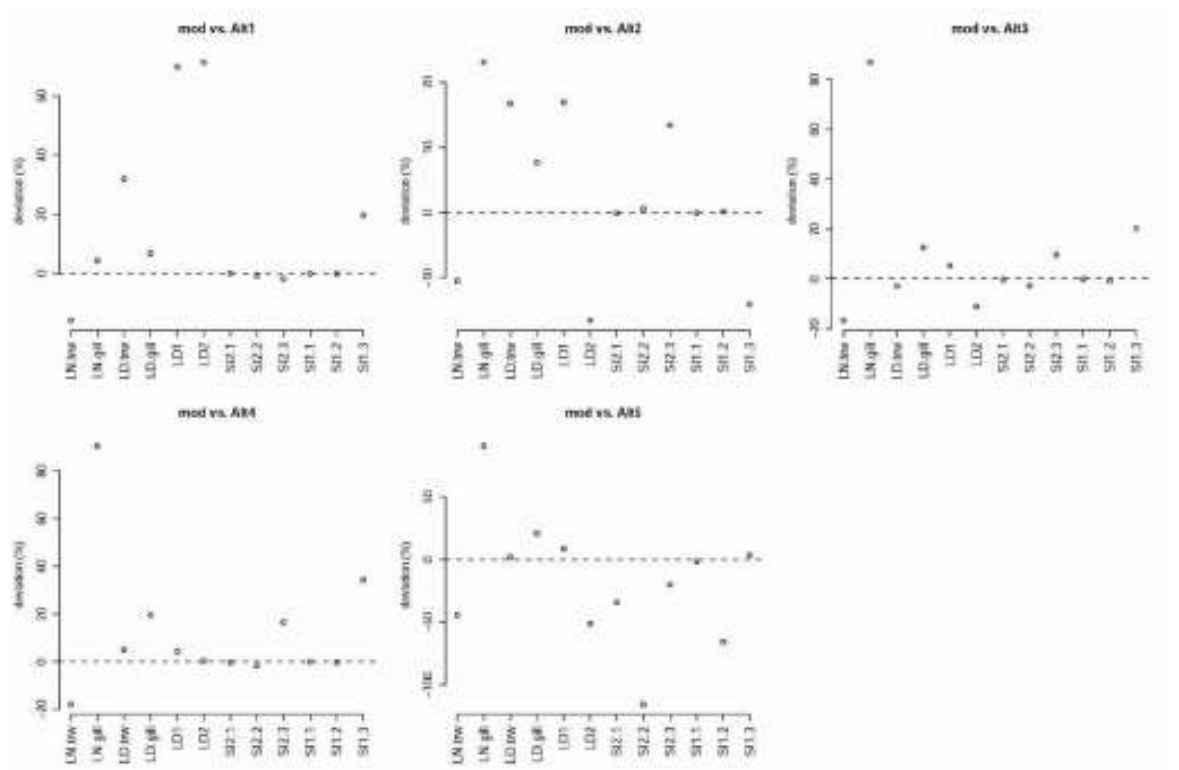
Fig. 9 - Likelihood component score deviations of the alternatives from the basic model and boxplot of the likelihood component scores of the basic hake model.
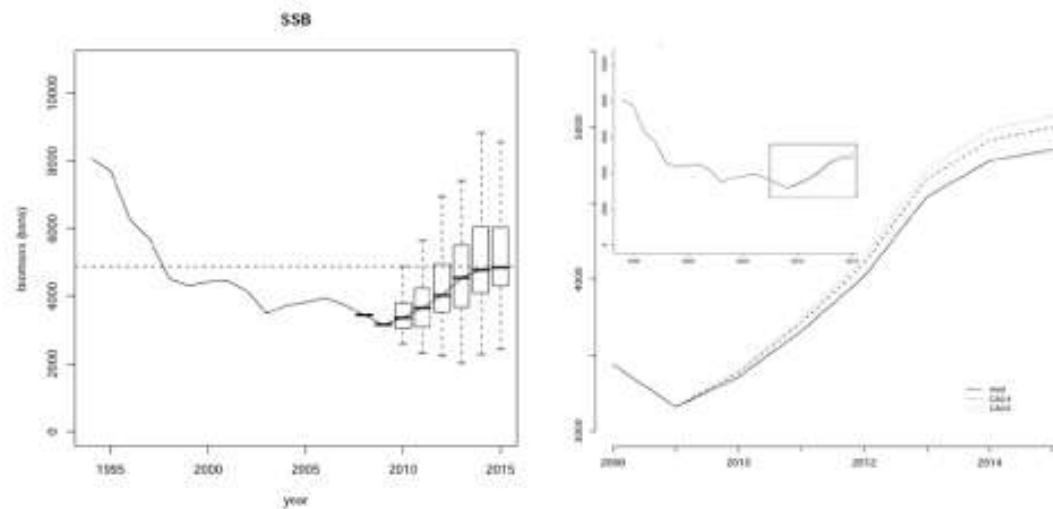

Fig. 10 - (a) Annual estimated spawning stock biomass (timestep 4) with boxplot of projections up to 2015 under no management scenario, dotted horizontal line mean

estimated SSB between 1994 and 2007. (b) Average projections of spawning stock biomass for the hake Gadget model under no management scenario (mod), and with 40% and 60% levels of protection of hake recruits (CA0.4 and CA0.6).

V

Systematic conservation planning in the Mediterranean: a flexible tool for the identification of no-take marine protected areas

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We propose the use of systematic conservation planning in the Mediterranean context for the identification of no-take marine protected areas (NTMPAs). We suggest a logical framework that should be used for the identification of areas to be targeted for multi-species, spatially explicit conservation actions. Specifically, we propose seven steps: (i) definition of the study area; (ii) selection of the species or habitats to be considered; (iii) definition of the planning units; (iv) measurement of the fishing effort; (v) definition of the conservation targets; (vi) review of the existing conservation areas; (vii) selection of additional NTMPAs. Moreover, we consider the potential impact of different conservation plans on existing fishing vessels. A working example is presented, focusing on a limited number of species and on a limited study area. This framework can be easily expanded to include datasets of different origin and to accommodate larger spatial scales. Such a process involves major data-collection and capacity-building elements, and conservation of productive commercial fisheries must be a priority.

Keywords: irreplaceability, Mediterranean, no-take marine protected areas, systematic conservation planning, vessel monitoring system.

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Introduction

Marine ecosystems and species face increasing threats from land- and sea-based anthropogenic activity, including pollution, climate change, and overfishing (Lubchenco et al., 2003). Mitigating these threats requires the adoption of multiple strategies, including incentives that encourage conservation and sustainability, building awareness of the value of biodiversity, and developing conservation plans for key species and ecosystems (Leslie, 2005).

In this context, protected areas are particularly important (Groves, 2003; Rosenzweig, 2003) for both terrestrial (Sinclair et al., 2002; Chape et al., 2005) and marine ecosystems (Lubchenco et al., 2003; Roberts et al., 2005; see Stefansson and Rosenberg, 2005, for a different view).

The main objectives for no-take marine protected areas (NTMPAs) are often the conservation of biodiversity (Groves et al., 2002) and the preservation of cultural and aesthetic values (e.g. particular scenic areas and/or areas with traditional activities) and ecosystem services (Daily et al., 2000). Socio-economic, aesthetic, and political criteria, however, have often driven the creation of protected areas, resulting in the selection of unrepresentative sites of lesser conservational value, both in the Mediterranean area (Maiorano et al., 2007) and worldwide (Scott et al., 2001; Rodrigues et al., 2004).

One of the responses of the scientific community to this situation has been the development of a new discipline called systematic conservation planning (SCP; Margules and Pressey, 2000). SCP can be defined as a structured conservation approach that provides the context needed to meet two basic objectives of any reserve system: representativeness, the need to protect the full variety of biodiversity at all its levels of organization; and persistence, the long-term survival of species inside a system of protected areas.

SCP has been used widely in both terrestrial and marine conservation (Leslie et al., 2003; Rodrigues et al., 2004; Fernandes et al., 2005; Halpern et al., 2006), but its usefulness for the Mediterranean Sea in the marine fishery context has not been explored.

Traditionally, Mediterranean fisheries have been orientated towards a multispecies complex, and the traditional management tools based on technical measures and fishing capacity control have mostly failed to ensure the long-term persistence of fish populations or the conservation of important habitats (Tudela, 2004; Lleonart, 2005). In this context, a multispecies, spatially explicit approach to the identification of NTMPAs would be a useful fishery management tool. Modelling approaches have suggested that NTMPAs can function as a hedge against the obvious limitations of traditional management strategies, thus promoting the long-term use of fishery resources (Lauck *et al.*, 1998). These models have been supported by field studies that clearly demonstrate the positive effect of NTMPAs on fish populations (Roberts *et al.*, 2001; Fisher and Frank, 2002; Russ *et al.*, 2004), although the real mechanism behind these processes is still the subject of debate (Hall, 1998; Hilborn, 2002; Gell and Roberts, 2003; Hilborn *et al.*, 2004). The establishment of NTMPAs is also recommended by the FAO Code of Conduct for Responsible Fisheries (FAO, 1995) as a tool to limit risks, provide refuges, and allow experimental comparisons with fished areas.

The protection of NTMPAs that effectively cover many different species usually requires the closure of large areas, as clearly demonstrated in the terrestrial context (Pressey *et al.*, 1993). Such a strategy is usually not compatible with high levels of economic activity, as is true in the Mediterranean. A step towards a more rational choice of areas of conservation and managerial interest is to consider the life-history stages that would benefit more from habitat protection (Cook and Auster, 2005), reducing the necessary conservation effort and hence the economic conflict. SCP provides the necessary framework for these tasks.

Here, we evaluate the potential of SCP as a tool for the identification of NTMPAs in the central Mediterranean. We use trawl survey data in a working example to obtain information on the distribution of juveniles and spawners of commercial demersal fish, cephalopods, and crustaceans. Moreover, we consider the potential impact of different conservation plans on existing fishing vessels. Our objective is to develop a framework that can be used to identify areas to be targeted for multispecies, spatially explicit conservation actions, while considering the socio-economic effects on local fisheries.

Material and methods

The selection of a biologically and economically effective conservation plan is conceptually simple and clear. We present a series of guidelines (modified from Margules and Pressey, 2000) for drafting a conservation plan, and we provide a practical example in the Mediterranean context.

Guidelines for SCP

We propose seven steps for SCP, which should be followed by a monitoring scheme to evaluate the effectiveness of the proposed conservation plan and that could be used in an adaptive management scheme (Margules and Pressey, 2000).

Step 1: define the study area

Theoretically, the study area should be defined following biological considerations that account for the spatial distribution of fish stocks and populations. However, social and economic factors often play an extremely important role. Management units and/or political boundaries, in fact, represent potential constraints for any conservation strategy.

Step 2: select the species/habitats to be considered in the conservation plan

The identification of potential NTMPAs requires the selection of a set of species or habitats towards which the conservation efforts should be directed. Several options are possible, ranging from the selection of all the species for which data are available to the selection of only the life-history stages that are more sensitive to fishing pressure.

Step 3: define the planning units to be used in the analysis

The planning units (PUs) are the foundation on which a conservation plan is built. PUs should be defined after considering the resolution of the available biological datasets, as well as the minimum management units that should be considered from a biological and political point of view.

Step 4: measure the fishing effort for each PU

Every conservation plan should consider the impact on local economic activities. This step is necessary if one of the objectives of the conservation plan is to avoid conflicts with fishing activities.

Step 5: define the conservation targets

The overall goals of an SCP (representativeness and persistence) have to be translated into more-specific, quantitative targets for operational use. Targets provide means to measure the conservation value of existing conservation areas, as well as of different PUs during area selection (Steps 6 and 7 below). A quantitative conservation target should be set for each species and/or habitat. Setting biologically sound targets can be difficult in practice because the environment is heterogeneous in space and time, and different species function at different spatial and temporal scales. However, different theoretical aspects in ecology and biogeography often provide useful guidelines (for a review, see Margules and Pressey, 2000).

Step 6: review the existing conservation areas

Building on already existing protected area systems represents a pragmatic approach to biodiversity conservation (Pressey, 1994; Groves, 2003), an approach that can be expanded easily to no-take areas and fishery management. The basic idea is to determine the degree to which the conservation targets (defined during Step 5) are already covered in existing NTMPAs, before identifying new elements that need further protection (Scott *et al.*, 1993; Margules and Pressey, 2000).

Step 7: select additional NTMPAs

The existing NTMPAs should be recognized not only for their contribution to the conservation target but also because they represent spatial constraints around which new NTMPAs are selected. The most convenient tools for the selection of the additional areas are algorithms working with explicit rules. These algorithms can be used to investigate various policy options, for example, to include or exclude NTMPAs and to compare different representation targets. They can also suggest whether or not the full set of targets is achievable and the extent to which trade-offs are necessary (e.g. between representation of all species and the requirements of the fishing industry). Moreover, they provide a
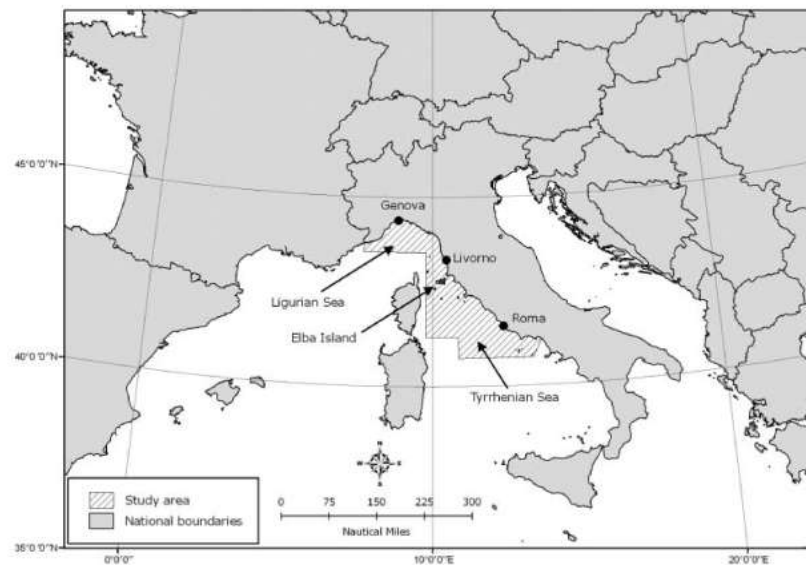
Figure 1. Location of the study area in the western Mediterranean basin.

basis for negotiation or refinement of the conservation plan by regional or local experts.

A working example

The study area was defined according to the availability of biological and socio-economic data, and it covers the continental shelf and the upper slope along the Ligurian and Tyrrhenian coasts (west-central Italy; Figure 1), corresponding to management geographical subarea 9 (GSA9), as defined by the FAO.

This area is under great fishing pressure, and the most important fish populations are generally overexploited. For hake (*Merluccius merluccius*) and red mullet (*Mullus barbatus*), an estimated reduction of fishing effort of 20–40% is required to move the stock towards a safer level of spawning biomass, assuming a direct proportionality between fishing effort and fishing mortality (e.g. Abella and Serena, 1998; Colloca *et al.*, 2000).

We obtained data on the abundance of fish, cephalopods, and crustacean species from 1704 hauls performed during an experimental trawl survey (MEDITS project), conducted in early summer from 1994 to 2005 (Bertrand *et al.*, 2002).

We considered only the most important species in the GSA9 from an economic point of view, corresponding to 70–80% of the trawl landings in 2006 (IREPA, 2006). We included mostly juveniles, because nursery grounds are considered among the most important areas for the management of fishery resources in the Mediterranean (EU Council Regulation, n. 1967/2006). Data on spawners were added for those species whose spawning period corresponded to the MEDITS survey (Table 1).

We divided the study area into 84 square PUs (20 × 20 km), looking for the finest spatial scale compatible with the number of available hauls, and requiring that each PU contained at least two hauls across the 12 years of available data (mean number of hauls = 20.1; s.d. = 13.8). All PUs were cut following the coastline and clipped using the boundaries of two existing NTMPAs and of 88 non-trawlable areas (Figure 2). Non-trawlable areas (4.5% of the

Table 1. Species and age classes considered in the analyses.

Species	Juveniles	Spawners
Merluccius merluccius	TL < 14.0	TL > 30.0
Micromesistius poutassou	TL < 12.0	–
Mullus barbatus	–	Mature individuals
Pagellus erythrinus	TL < 14.0	–
Phycis blennoides	TL < 12.0	–
Nephrops norvegicus	CL < 20.0	–
Parapenaeus longirostris	CL ≤ 2.0	CL > 2.0
Eledone cirrhosa	ML < 4.0	–
Illex coindetii	ML < 10.5	–
Octopus vulgaris	ML < 5.0	–

TL, total length (cm); CL, carapace length (cm); ML, mantle length (cm).

study area) are grounds not suitable for trawling because they are generally characterized by a hard bottom that would damage the nets. Although other kinds of fishing gear can operate on these grounds (i.e. gillnets, longlines), towed bottom-fishing gears were considered to have the most severe impact, so non-trawlable areas can be considered as naturally occurring NTMPAs.

Indices of abundance by haul were calculated for each species/age class (Table 1) as the number of individuals per swept-area ($n\,km^{-2}$), then used to estimate the mean abundance in each PU by species/age class. We assigned to each non-trawlable area the same abundances as estimated for each species in the PU inside which the non-trawlable area is found.

In all, 356 trawling vessels (≥15 m length) operate in GSA9 at 50–1000-m depth (IREPA, 2006). The spatial distribution of the fleet was analysed using data from a GPS vessel monitoring system (VMS) operating on board fishing vessels (FAO, 2005). A VMS (mandatory on fishing vessels ≥15 m) is a fully automated system commonly used to track the position of boats, querying each vessel hourly, and registering its position.
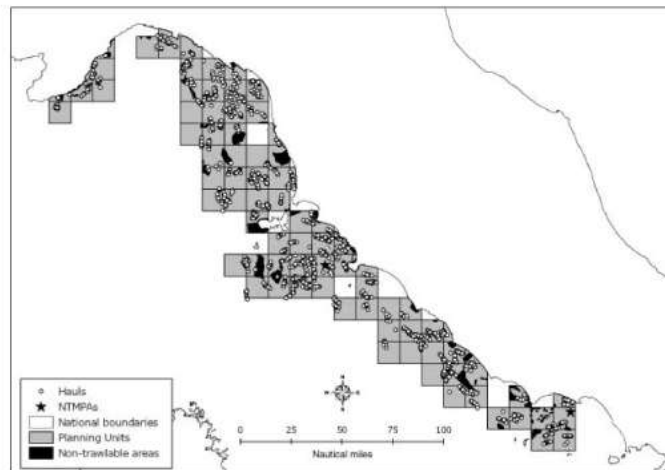
Figure 2. Subdivision of the study area into PUs. NTMPAs are indicated with fishing hauls considered in the analysis.

We calculated the importance of each PU for the trawling fleet using raw VMS data (including vessel position and operating speed) from the Italian Ministry of Agriculture, Food, and Forestry Policies. We excluded system errors (e.g. duplicate records) and records of non-fishing vessels (i.e. vessels with an operating speed >7.4 km h^{-1}) from the analysis. A simple index of presence was calculated for each PU by counting the mean number of records, using several months in 2006/2007, and assuming that PUs visited by a larger number of vessels are proportionately more important for the economy of the fishing fleet and are usually characterized by higher densities of fish.

Given that current biological knowledge does not allow for the definition of single species representation targets, we referred to the available data for GSA9 (e.g. Abella and Serena, 1998; Colloca *et al.*, 2000) to define two general conservation targets, using proportions (20 and 40%) of the cumulative abundance of each species within our study area.

No review of the existing conservation areas was performed, because only two small NTMPAs have been instituted in GSA9 for the conservation of juvenile hake (Figure 2). However, we also considered in our analyses non-trawlable areas as naturally occurring NTMPAs.

For the selection of additional NTMPAs, we used the concept of irreplaceability. Irreplaceability is a measure that reflects the importance of each PU in the context of the study area, for the achievement of a regional conservation goal: it is defined as the likelihood that a given site must be selected to achieve a specified set of targets or, conversely, the extent to which options for achieving those targets are reduced if the site is not selected (Pressey *et al.*, 1994). Possible values of irreplaceability range from 1, indicating a PU that is essential to achieving a given conservation target and therefore totally irreplaceable, to 0, indicating a PU that makes no contribution to the conservation target.

The calculation of irreplaceability for a PU$_x$ can be expressed as:

$$\text{Irr}_x = \frac{(R_{x\_included} - R_{x\_removed})}{(R_{x\_included} - R_{x\_excluded})},$$

where $R_{x\_included}$ is the number of possible conservation plans that include the PU$_x$ and satisfy the representation target, $R_{x\_excluded}$ is the number of possible conservation plans that do not include the PU$_x$ and satisfy the representation target, and $R_{x\_removed}$ is the number of possible conservation plans that include the PU$_x$ and that would satisfy the representation target even excluding site x (Ferrier *et al.*, 2000). We calculated irreplaceability using C-Plan 3.20 software (Pressey *et al.*, 2005), which implements the statistical estimation technique defined by Ferrier *et al.* (2000).

We used the results of irreplaceability analysis to find two sets of PUs (one for the 20% target and one for the 40% target) that would satisfy the representation target using the minimum possible area. We specifically asked C-Plan to create the two sets of areas (hereafter called biological-only conservation plans) through the MinSet function (an algorithm used to identify the "minimum set" of PUs that would fulfil a specific aim; for further details, see Pressey *et al.*, 2005), asking for the selection of PUs with the highest irreplaceability values. For these analyses, non-trawlable areas and the existing NTMPAs were considered as already protected, and therefore as areas that effectively contribute to the representation target.

To reduce potential conflicts with the trawling fleet, we proposed two additional scenarios (hereafter called bioeconomic conservation plans) where biological criteria were integrated with socio-economic considerations. In particular, we selected *a priori* (before the computation of the Min/Set function) the PUs where the mean number of fishing vessels was in the upper 5% of the distribution. In this way, the algorithm was forced to meet the representation targets selecting the PUs with the highest irreplaceability, but without considering the PUs where the potential conflict among conservation and economic activity was greater. Non-trawlable areas and the existing NTMPAs were included in the analysis as areas that effectively contributed to the representation target.

Results

The highest concentration of fishing vessels was located on the continental shelf of both the Tyrrhenian and Ligurian seas, with
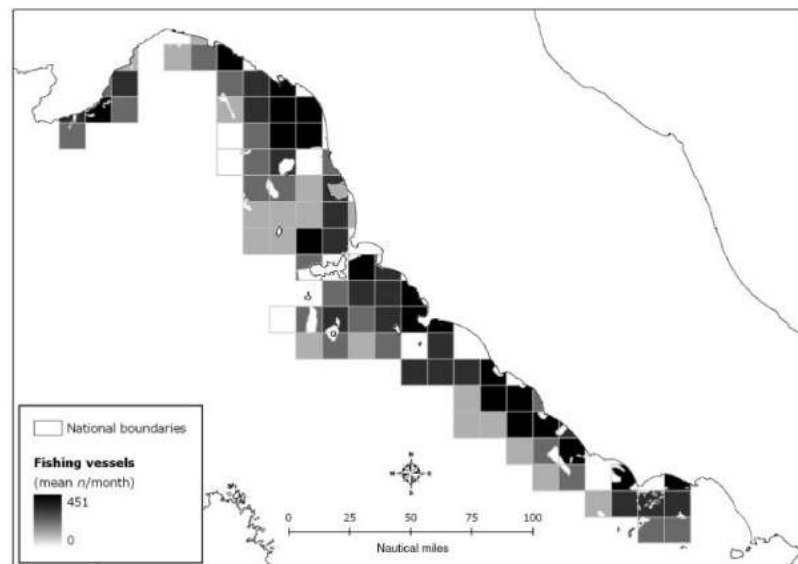
Figure 3. Mean number of fishing vessels per month measured for each PU using VMS data.

only three PUs that were never visited by the trawling fleet, located along the outer boundaries of GSA9 (Figure 3).

High irreplaceability values were distributed throughout the entire study area, considering both the 20 and 40% targets (Figure 4a and b). Obviously, the 40% target resulted in higher irreplaceability values, particularly for the PUs located on the continental shelf south of the Island of Elba.

Biological-only conservation plan

The biological-only conservation plan with a 20% representation target was achieved by selecting only nine PUs in addition to the non-trawlable areas and to the existing NTMPAs (Figure 5a). Considering a 40% representation target, 17 PUs were selected in addition to the non-trawlable areas and to the existing NTMPAs (Figure 5b). In general, the Tyrrhenian Sea was more important than the Ligurian Sea, with a larger number of PUs that should be closed for both targets (Ligurian Sea PUs: 40, Tyrrhenian Sea PUs: 44; target 20%: four PUs in the Ligurian Sea and five PUs in the Tyrrhenian Sea; target 40%: 6 PUs in the Ligurian Sea and 11 PUs in the Tyrrhenian Sea).

Bioeconomic conservation plan

The inclusion in the analyses of possible conflicts with fishing activities produced conservation plans requiring the protection of larger areas. The bioeconomic conservation plan with a 20% representation target was achieved with the selection of 11 PUs, in addition to the existing NTMPAs and non-trawlable areas (Figure 6a). The location of the additional PUs was different when compared with the biological-only conservation plan with a comparable target. In fact, many of the PUs with high irreplaceability value were also important for the bottom-trawling fleet so were not included in the conservation plan. In particular, the inclusion of economic constraints in the conservation plan caused

the reallocation of five PUs and the selection of two additional PUs, one in the Ligurian Sea and one in the Tyrrhenian Sea.

The bioeconomic conservation plan with a 40% representation target (Figure 6b) was achieved with 27 PUs in addition to the non-trawlable areas and the existing NTMPAs. Comparing this with the biological-only conservation plan, two PUs in the Ligurian Sea were removed because of economic constraints, and the number of PUs selected for closure increased to 12 (compared with the six selected only with biological criteria). In the Tyrrhenian Sea, seven PUs, included in the biological-only conservation plan, were excluded by the bioeconomic conservation plan and were replaced with 11 additional PUs, making a total of 15 PUs selected.

Discussion

Our proposal represents a first attempt at using the tools and criteria of SCP in the Mediterranean context for the identification of NTMPAs. Other authors have proposed slightly different schemes in different contexts (e.g. Margules and Pressey, 2000; Groves, 2003), but we tailored our framework to provide a set of guidelines that can be followed easily in practical applications.

The multispecies systematic approach that we propose provides an easy solution to the selection of no-fishing areas, and the computational procedure that we used looks for the most efficient solution that can satisfy species-specific conservation targets. Moreover, our approach has a short computational time, does not limit the number of species that can be included in the analysis, and can be used easily even with limited biological information.

Irreplaceability is a reasonable descriptor of the importance of each PU to the conservation of the group of species considered. In fact, studies using different methodological approaches identified roughly the same sites as important for conservation (Ardizzone
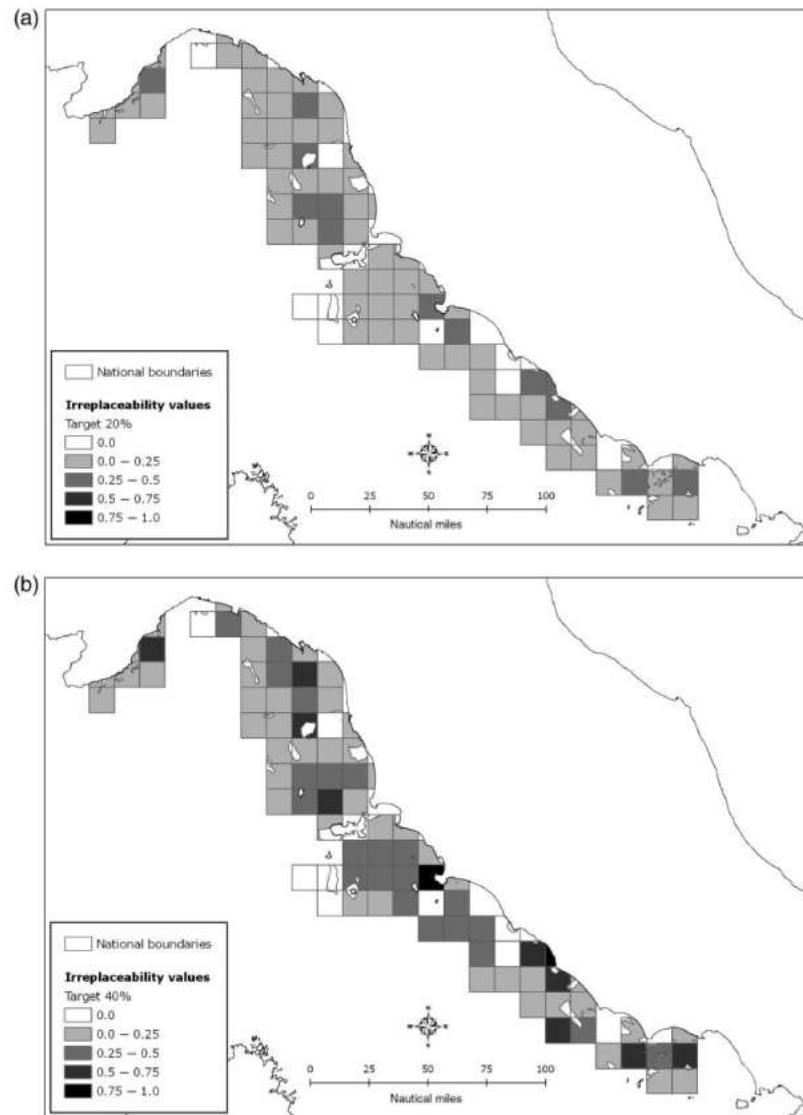
Figure 4. Distribution of irreplaceability values calculated using (a) a 20% target and (b) a 40% target.

and Corsi, 1997). Moreover, the importance of the selected PUs is demonstrated by their high densities for the target species.

The working example for the GSA9 provided valuable information for local conservation planners and clearly demonstrated the tool's potential. Comparing the two conservation plans obtained using biological-only criteria (one with a 20% target and the other with a 40% target), there is an obvious increase in the number of PUs selected that correspond to an increase in the representation target. However, most of the PUs selected using the 20% target were also selected with the 40% target, a stabilizing factor that provides a measure of their importance.

We recognize the obvious problem linked to the definition of generic conservation targets (as our 20 or 40% target), but the lack of explicit biological background for many species prevented the development of alternative solutions at this stage. In future, a better understanding of the exploitation status of marine resources will help us define more rational conservation targets on a multispecies level. Meanwhile, the arbitrary nature of our representation targets should be considered carefully while reading our results.

The conservation plans that we developed incorporating socio-economic criteria are of particular importance because
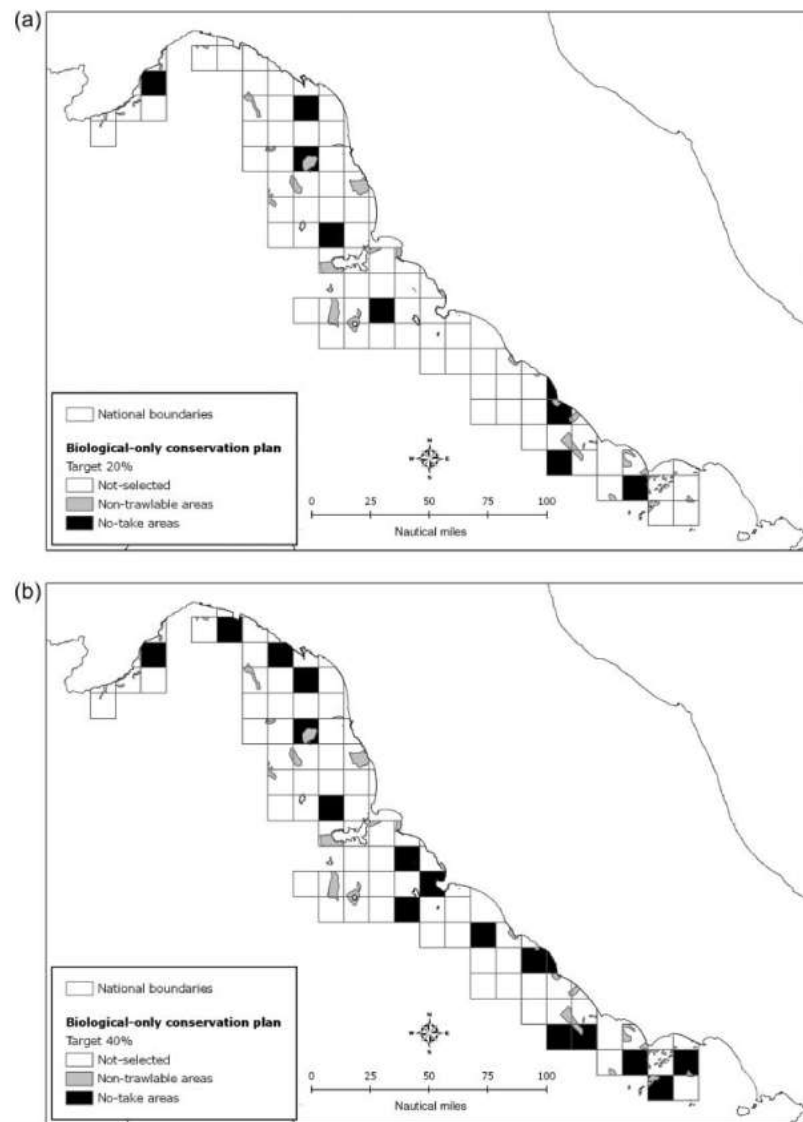
Figure 5. Possible conservation plans obtained considering two different representation targets (20 and 40%) and considering biological features only.

they allow attainment of conservation targets while minimizing conflicts with the fishing industry. Reserve selection exercises should have a solid biological background to be successful, and it has been suggested that they should precede socio-economic evaluations (Roberts *et al.*, 2003). However, reserve selection cannot ignore the general acceptance by resource users and the participation of stakeholders in the early stages of the reserve-design process (Richardson *et al.*, 2006). In this case, economic and social costs of conservation should be taken explicitly into account, and reserve design should integrate biological and

economic considerations. Although formally accepted, this integration is rarely realized, increasing the chance of conflict between parties.

The economic costs of establishing a reserve system are spatially heterogeneous (Smith and Wilen, 2003). The protocols that we applied incorporate fishery spatial dynamics in an attempt to mitigate potential conflicts, to limit the reallocation of fishing efforts that would impair the effect of the proposed conservation plan, and to look for alternative reserve selection schemes. They can offer a sound base for developing negotiation processes and
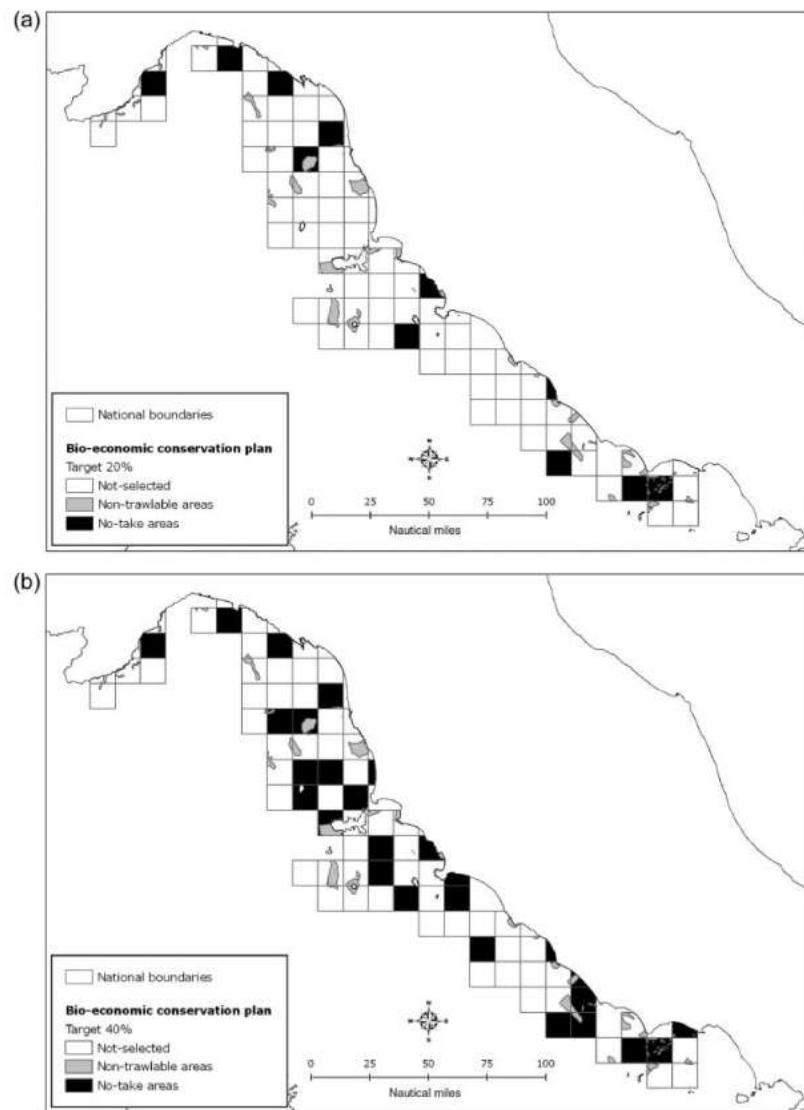
Figure 6. Possible conservation plans obtained considering two different representation targets (20 and 40%), and accounting for biological and economic features.

supporting decisions, with the possibility of discussing alternative conservation plans that could meet the same targets with different losses to the fishery. We chose an arbitrary threshold to define the PUs most frequented by the fishing fleet, but far from limiting our analysis, this clearly demonstrates its flexibility. In fact, the choice of the threshold can be used during negotiations between biologists, politicians, and the fishing industry about the design of a conservation plan that requires a predefined level of conservation while also considering economic factors.

Our analyses included juvenile age classes, which are often strictly related to specific seabed habitat conditions, either for

feeding grounds or for protection from predators (Diaz et al., 2003; Hook et al., 2003; Scharf et al., 2006). Therefore, it is reasonable to assume that our conservation plans present a spatially explicit solution that includes important portions of the Essential Fish Habitats (Benaka, 1999) for all ten species considered.

However, it must be emphasized that the current work provided an example application of methodology rather than a comprehensive conservation plan for the study area. An easy implementation of our framework could incorporate a larger study area and include additional information (e.g. environmental layers, data on the distribution of different species/age classes, data

on migration patterns, and other biological processes). Moreover, further developments can incorporate factors such as the spatial configuration of NTMPAs, considering different representation targets and/or measures related to the inherent uncertainty of irreplaceability. Such a process is currently being undertaken, and it involves major data-collection and capacity-building elements. It will be important not only from a biological standpoint; productive commercial fisheries are strictly related to healthy marine habitats, and the conservation of such habitats will help support fish communities in both the short and long terms.

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