Changes in size at maturity of European hake Atlantic populations in relation with stock structure and environmental regimes

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Abstract

European hake (*Merluccius merluccius*) female size at maturity is estimated on an annual basis for Bay of Biscay and Galician coast, which are parts of the distribution of the Northern and Southern stocks, respectively. Clear trends in this reproductive parameter are observed along the time series and the potential factors affecting these trends have been investigated. Total biomass, different indexes of SSB, age diversity index, fishing mortality at age, NAO winter index, upwelling index and temperature were included in multiple regressions models to assess the relative importance of each of them on shifts in size at maturity.

Bay of Biscay and Galician coast hake have followed different evolution in patterns of changes in size at maturity. In Bay of Biscay, a steadily decline of 15 cm has been observed from 1987 to 2004, which is well predicted by fishing mortality and age diversity, but also the environment may have played an important role. However, on the Galician coast a drastic decline of 16 cm from 1980 to 1988 was followed by a rapid increase in size at maturity during the next 10 years to original values and a stable period in the last 6 years. Decreasing biomass may explain the decline in size at maturity in the first period. However, total biomass and spawning biomass declined even during the period when size at maturity increased, which is contrary to compensatory theory. Shifts in environmental regime, NAO and upwelling, may have contributed to a decelerated growth during this period that might explain the later maturation.

Keywords

Size at sexual maturity, Population structure, Environmental effects, Gadoid fisheries, Hake, *Merluccius merluccius*, Bay of Biscay, Galician Coast

1. Introduction

One of the basic goals of fisheries management is to conserve sufficient reproductive potential in a stock to allow for sustainable exploitation. To achieve this, most of the stocks are managed based on maintaining certain levels or limit thresholds of Spawning Stock Biomass

(SSB) on the assumption this is an indicator of the 'viability' of the stock. Therefore assessment and management of fish populations currently rely on correct estimation of the SSB (Hilborn and Walters, 1992), which is based on accurate maturity ogives of the population. Those ogives are usually calculated from a macroscopic evaluation of the gonad maturity. However, macroscopic analysis may overestimate the proportion of mature females (Murua et al., 2003; Vitale *et al.*, 2006).. Moreover, in most scientific assessments of European marine fish stocks, SSB is calculated using a fixed maturity ogive, ignoring the inter-annual variability in this parameter.

Most of the European marine fish resources are outside safe biological limits or overexploited. In spite of the several technical measures taken to recover the stock status, most have failed. This has raised again the debate (Anon., 2004) as to whether fishing is the main factor causing the decline of stocks, or whether environmental factors are the main cause (Cook and Heath, 2005). To demonstrate that environment plays important role on population dynamics is a hard task, firstly because its effect is often mixed with those produced by fishing and the inherent difficulty to discern between them; but, secondly due to lack of good quality data that can produce robust statistical results. Still, some environmental parameters are well known to affect fish biology. Temperature could influence patterns of maturity, either directly or through changes in growth (Beacham, 1983; Brander, 1995; Cardinale and Modin, 1999). The onset of maturation requires that certain conditions are fulfilled at a specific times in the life cycle, either with respect to size or accumulations of energy stores, or both, thus growth is considered a prerequisite for maturation Saborido-Rey and Kjesbu, in press).

Size and age at maturity are highly plastic parameters that change under external pressure, particularly with a decrease in the population abundance (Adams, 1980; Gunderson, 1980; Wootton, 1990). Shifts in age at maturity have been more often identified as a density-dependent response to abundance variations, mostly decreasing maturity with declining abundance (Beacham, 1983; Cardinale and Modin, 1999; Hutchings, 2004; Jørgensen, 1990; Morgan and Brattey, 1996; Saborido-Rey and Junquera, 1998, 1999). However, although decreasing size at maturity still can be a density-dependence effect, it normally provides an indicator that a fish population is coming under stress from too high rates of exploitation (Trippel, 1995). Barot *et al.* (2004) used reaction-norms to identify a downward shift in maturation at size in Georges Bank and Gulf of Maine stocks of Atlantic cod (*Gadus morhua*) supporting the hypothesis that an evolutionary trend, probably caused by high fishing mortalities, is partially responsible for the observed decrease in age and size at maturation in these cod stocks (Olsen *et al.*, 2005). Regardless the causes of maturation variation, this population characteristic can have large effects on the reproductive output of a stock. For example, shifts to maturation at smaller sizes and younger ages affect fecundity (Rijnsdorp 1991, Kraus *et al.* 2002, Marteinsdottir and Begg 2002), egg and larval size and viability (Trippel *et al.*, 1997).

The Atlantic population of European hake (*Merluccius merluccius*) Atlantic population supports a major fishery (Casey and Pereiro, 1995). Currently the existence of two stocks is recognized, the so-called Northern and the Southern stocks (ICES Divisions VIIIc and IXa) (ICES, 2005). Both stocks are outside safe biological limits and EU has developed recovery plans that for the Northern stock being implemented in 2004. Current assessment procedures use a a fixed maturity ogives for both sexes combined for the whole time series in the Northern stock, and annual maturity ogives for both sexes combined for the Southern stock. Both are based on macroscopic observations.

In this paper, we have estimated the annual female maturity ogives for Bay of Biscay (Northern stock) and Galician Coast and Cantabric Sea (Southern stock); which form part of the distribution of the Northern and Southern stock, respectively. We have investigated different number of factors that could affect trends in size at maturity, broadly grouped into:

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stock characteristics, fishing pattern and environmental factors. Specifically, the following factors were utilized: total biomass, total SSB, female only SSB, age diversity index, fishing mortality at age, NAO winter index, upwelling index and temperatures.

2. Material and methods

2.1 Biological data

The sampling of hake gonads was carried out in two different areas, namely Bay of Biscay (ICES Divisions VIIIabd) and Galician Coast (ICES Division IXa) in the north and northwest Spain.

Maturity data for the Galician coast was available for the years 1980 to 2004 from both spring and autumn surveys (although the same survey was not available every year) and from landing samplings (usually monthly sampling, but all months were not necessarily covered in all years). In the case of Bay of Biscay, maturity data was collected over the periods 1987-1990, 1996-2004, but always based on port sampling or directly collected by observers on commercial vessels. Maturity was assessed based in macroscopic observations (Table 1). The fact that the data come from very different sources (surveys, landings, observers onboard, as well from different months) created complexity in the data matrix, which was checked and revised to harmonize differences. In 2003 and 2004 maturity ogives were additionally based on histological observations and compared with the macroscopic ogives for the same years (Dominguez *et al.*, 2005). The comparison showed than in a number of cases postspawning fish had been staged as immature. Because the proportion of postspawning/resting fish is higher in autumn, special care was taken when revising the data for those particular months. Unusually high numbers of large immature fish or an unusually large number of postspawning small fish were found in a few hauls. This type of clear inconsistency leads to the removal of the whole haul/sampling/day. Data for 1981 and 1987 in Galician coast were very limited (2 and 34 specimens). For these years an average of the size at maturiy of females in the preceding and subsequent years was used. The estimates were derived from 13,840 and 16,702 individuals for Galician coast and Bay of Biscay respectively (Table 2).

Abundance at age was obtained from the data compiled by the ICES Working Group on the Assessment of Hake, Monk and Megrim (ICES, 2006). Female numbers at age were derived by applying the sex-ratios to the Working Group numbers-at-age estimates. Sex-ratios for the Bay of Biscay were available for the period 1987-1994 and 1998-2004, from extensive annual market sampling carried out in the Basque Country fishing harbors. This sampling covered the main fishing fleets targeting European hake in ICES Divisions VIIIabd and Sub-area VII. In addition to the market sampling over the period 1998-2004, samples obtained from observers onboard commercial fishing vessels within two EU projects, "Biological Studies of Demersal Fish: megrim, hake and anglerfish" (BIOSDEF) and "New assessment and biology of the main commercial fish species: Hake and anglerfishes of the Southern shelf demersal stocks in the South of the western Europe" (DEMASSES), were also used to estimate female sex-ratios. The current analysis extended back to 1980, therefore, a 3-year average of the closest years (1987-90) was used to extend sex ratios back to this year. For the period of 1995-1997, where sex-ratio data were not available, the mean of the closest three years was used. Sex-ratios for Galician coast were not available and Bay of Biscay data was used for this area. SSB and females only SSB were estimated from mean weight at age in the catch (as

used by the Working Group) and the two abundance data sets described above, together with the maturity ogives specifically estimated for this analysis.

The age diversity of the spawning stock was estimated using the Shannon diversity index (Marteinsdottir and Thorarinsson 1998):

$$H = (n\log(n) - \sum_{i=1}^{k} f_i \log(f_i)) / n$$

The logarithmic base of 10 was used to compute H, where k is the number of age groups, n is the total number of mature fish in all age groups, and f_i is the number of mature fish in each age group. Unlike biomass and SSB, this diversity index is relatively independent of stock size as it is estimated from both the number of cohorts contributing to spawning biomass and relative abundance of each age class comprising SSB.

Fishing mortality was obtained from the ICES Working Group VPA estimates (ICES 2005). Mortalities from ages 1 to 7 were selected, since those covered more than 97% of the population abundance. Data from 1980 to 2004 were used.

2.2 Environmental data

Temperatures for the Bay of Biscay are sea surface temperatures, estimated as a mean for the whole year, for the period 1982 to 2004. Temperatures for the Galician Shelf were obtained from monthly CTD transects and hence estimated by 50 m depth intervals from the sea surface to 300 m. However, temperature in this area was only available for the period 1986 to 2000.

Annual upwelling indexes were estimated from geostrophic winds and Qx as the average of the values from March to July for the period 1982-2004. However, for the Galician Shelf monthly data of temperature and upwelling was available. In order to assess trends in these environmental factors, temperature and upwelling (expressed as –Qx) data were interpolated to create a 3D mesh plot using inverse distance as the smoother and month and year as the X,Y variables. An upwelling index was available for 1965 to 2004.

North Atlantic Oscillation (NAO) data were obtained from NOAA. Only winter NAO was used, as the mean of the January to March values. To compare with trends in the reproductive potential of the stock (SRP), besides mean winter NAO, standardized winter NAO was produced as 3, 5 and 10 year running means.

2.3 Analysis and modeling caveats

Maturity ogives were adjusted to a logistic curve as described by Ashton (1972):

$$\hat{P} = \frac{e^{a+bL}}{1+e^{a+bL}} \qquad\qquad \text{Eq. (1)}$$

and the logit transformation:

$$\ln\frac{\hat{P}}{1-\hat{P}} = a + bL \qquad\qquad \text{Eq. (2)}$$

where $\hat{P}$ is the predicted mature proportion, a and b the estimated coefficients of the logistic equation and L the length.

The maximum-likelihood method was considered to be the most satisfactory methodology for estimating length and age at maturity (Welch and Foucher, 1988; Hosmer and Lemeshow, 1989). Error variances across the range of the x variable were checked and found to be equal. The goodness-of-fit was assessed using a chi-square test for maximum likelihood. Size and age at maturity were estimated as the minus ratio of the coefficients (-a/b) by substituting $\hat{P}$=0.5 in Equation (2).

To study the influence of the different fisheries, biological and environmental variables on size at maturity a set of forward stepwise multiple linear regressions were performed; F to enter was fixed to 1.00 and F to remove fixed to 0.99, and tolerance at 0.0001. The r^2 and the ANOVA of the relationship between the dependent variable and the selected set in independent variables were used to assess the overall goodness of fit. However, the correlation between the observed and the predicted size at maturity was also used as a good indicator of the prediction power of the model.

Statistica for Windows 6.1 (StatSoft, Inc., 2004) was used to fit both the logistic and the multiple linear regression models, as well as to estimate the correlations.

For both stocks the data used was limited to a reduced area compared with the theoretical distribution of the stock. Northern European hake stocks is distributed through ICES Division IIIa, Subareas II, IV, VI and VII and Divisions VIIIa,b,d, from Bay of Biscay to Norway. However, the data used in this modeling exercise was limited to a reduced part of the distribution of the Northern stock (Bay of Biscay with a northern limit at 48°N and a Southern limit of the Basque Coast). The Southern stock, which is distributed from the Cantabrian Sea to Morocco, data was limited to the Galician shelf. Therefore, the results cannot be extrapolated to the whole stock and should be treated with caution. In addition, a number of assumptions have been made in relation to missing data or the way data was compiled, which further underline the need for caution in the interpretation of the results and conclusions. In particular, spatial analyses have not been conducted, and shifts in spatial distribution of hake and/or changes on fishing pattern may affect the estimation of size at maturity, as well as many other stock parameters.

3. Results and discussion

3.1. Maturity ogives

Size at maturity for each analyzed year and both stocks are given in Fig. 1. For the Southern Stock, with the longer time series, size at maturity declined from 55 cm in 1980 to 39.5 cm in 1988, the lowest value observed. Since then, size at maturity progressively increased to the largest value of 53 cm in 1998. In recent years, size at maturity of southern hake has been stable at around 46.5 cm. Thus, for this particular stock, three different periods can be identified; from 1980 to 1989 with a progressive decline in size at maturity; from 1989 to 1998 with a steady increase and finally from 1999 to the present a stable size at maturity.

The results suggest that the size at maturity in the Southern Stock declined 16 cm in 9 years, and increased 14 cm over another 10 years. Moreover, in the two year period from 1998to 2000 size at maturity declined by 7 cm.

The number of years for which data are available for the Bay of Biscay is much more restricted (Fig. 1). Observed as a whole, there has been a progressive decline in size at maturityh from 1987 to 2004. Only 1990, 2000 and 2001 break this decreasing trend. The decline in size at maturity in the Bay of Biscay from 1987 to 2004 was of 15 cm (56 to 41 cm), but from 51.6 to 41.4 cm in 1996-2004, i.e. 10 cm in 9 years.

Both stocks have undergone different temporal variation in size at maturity. The Southern stock size at maturity decreased notably during the 80's, and then it increased at similar rate during the 1990s, and finally remained stable in recent years. On the contrary, Bay of Biscay hake showed a higher size at maturity in early years with a decrease through 1990s, then showing a further decrease in recent years. In 2000 and 2001 both maturity ogives were similar and not statistically different. However, in 2003 and 2004 the ogives were statistically different. This suggests that both stocks have responded differently to fluctuating situations, supporting the identity of two different stocks. Currently, ICES consider both as management units based on two main criteria; the first is the presence of a geographical barrier, Cape Breton Canyon, which separates Spanish waters from France in the extreme corner of the Bay of Biscay (ICES, 2006). The second reason is the observation of two spawning areas, one located from the French coast to the Celtic Sea and the other located on the northwest coast of the Iberian Peninsula. However, some controversy exists about the stock structure of European hake in the Atlantic. Some authors consider that there is no separation between traditional Northern and Southern stock because of intense gene flow related to the current systems of this area (Balado *et al*., 2003) Recent studies based on genetic and biological parameters and incidence of identified parasites used as tags for stock identification suggest that only one stock is really differentiated in the North-east Atlantic; although probably two sub-populations exist and are separated by the Cape Breton Canyon (Lo Brutto *et al*., 2004; Mattiucci *et al*., 2004; Castillo *et al*., 2005). These results are relevant for management purpose and the boundary between these stocks should be reconsidered based on biological evidence.

Estimated total biomass, based on the Working Group figures is much greater in Bay of Biscay than in Southern Stock (Fig. 2a). Nevertheless, both have shown a progressive decline in biomass since the early 1980s to early 1990s. Since then the Northern Stock has shown signs of recovery, whereas the Southern Stock declined progressively until 2001.In 2004 an increase in biomass was observed as consequence of recruitment, but this result. should be considered as preliminary until the high recruitment is confirmed by further data. SSB based on females only and using the maturity ogives estimated in the project (see previous section) showed a similar trend (Fig. 2b). Both stocks underwent a sharp decrease in SSB in the 1980s, earlier in the case of Southern Stock. In 1994, the Northern Stock SSB reached its lowest value, but has shown a slow recovery since then. The Southern stock reached the minimum recorded spawning biomass in 1998, but no recovery has been observed and SSB remains at a low level.. Recruitment in Northern hake, based in Working Group estimates at age 0, did not show any major variations up to 1990 (with an average of 200-250 millions of recruits) then showed a period of higher recruitment up to 1995, decreasing thereafter up to 2000 (Fig. 2c). In recent years, except for 2002, recruitment was lower, at around 160 millions. The trend in Southern stock is quite different. Recruitment dropped from 100 millions in 1986 to 40 millions in 1991, reaching a new low value, 30 millions, in 2000 (Fig. 2c). In recent years,

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however, strong year classes seem to have occurred. In both stocks recruitment in 2004 has been estimated at extremely high values (600 and 132 millions for north and south stock respectively). The Working Group has considered these figures to be unrealistic, and awaits better estimates, thus it has not been considered in the current analyses.

On the Galician shelf, recruitment was positively and significantly correlated with the size at maturity two and one year earlier (r^2=0.87 and 0.61 respectively) in the period 1980-1990. However, for the period between 1990 and 1998, when size at maturity increased, recruitment was significantly, but negatively correlated with size at maturity two years earlier (r^2=0.61). Similarly, the relationships between SSB and size at maturity showed the same trend separately for each period. During the 1980s the decrease in biomass may explain the decline in size at maturity, as reduced biomass may favor accelerated growth as a compensatory response. Reduced size at maturity during the 1980s was not, however, enough to compensate for the lost biomass, and SSB continued decreasing in the 1990s in spite of increasing size at maturity and hence so did recruitment.

Changes in maturity ogives have been recorded by several authors in different species. Haug and Tjemsland (1986) studied Atlantic halibut from Norwegian waters and observed that while age at maturity decreased, size at maturity remained more or less constant. Junquera *et al*. (1999) described similar results for size at maturity of Greenland halibut from the Northwest Atlantic, and suggest that this species is relatively resilient to environmental changes, and that its reproductive parameters remain stable despite unfavourable conditions, although age at maturity was not considered in their study. Engelhard and Heino (2004a) observed in Norwegian herring that during a collapse of the population, age at maturity diminished, whereas size at maturity increased slightly, probably as a compensatory response. Marteinsdottir and Begg (2002) described for Atlantic cod a decrease in size and age at maturity, not only between years due to overexploitation, but also between Northern and Southern stocks, probably as a consequence of changes in temperature.

3.2. Changes in maturity in response to fishing pressure

Fishing mortality at age showed notable differences between stocks, but also among ages within the studied period (Fig. 3). Age 1 in the Southern Stock showed relative high levels of mortality before 1990, but reduced levels since then. In contrast, the Northern Stock showed the highest levels at this age during 1990-1997. At ages 2-4 (Fig. 3) fishing mortality was constant during the whole period for Northern Stock (F=0.25). For the same ages, in the Southern Stock two different periods can be identified, from 1982 to 1994 with a mean F of 0.4, and since 1995 to the present with a mean F of 0.6. For both periods fishing mortalities have been considerably higher in Southern Stock compared with Northern Stock. Ages 5-7 (Fig. 3) in Northern Stock showed the highest F values during the period 1988-1996, with a mean F of 0.6, over the rest of the period the mean was 0.3. Only for the period 1989-1992, was the fishing mortality of the Southern Stock lower than that of the Northern Stock. The difference is especially marked in the decade 1992 to 2002, when the Southern stock reached the highest F estimated in 1995 with a fishing mortality of 1.

Age diversity of the female only SSB based on the Shannon diversity index, was used as proxy for stock structure, and hence the consequences of fishing mortality. In Fig. 4 the diversity index for both stocks since 1982 to 2004 is presented. With the exception of 1982, age diversity was higher in Southern Stock. Age diversity fluctuated from 1982 to 1990 in Northern Stock, but has been at the same level since then with a value of 0.68. There was

evidence of an increasing trend in recent years, at the same time that size at maturity decreased steadily. In this period the variables were negatively correlated (r=0.96), although the time series of maturity ogives is too short to draw conclusions; for the whole available time series the correlation dropped to 0.76. Age diversity in Southern stock fluctuated across the whole period. However, particular time periods can be distinguished. Between 1982 and 1990, age diversity increased progressively from 0.75 to 0.87. During the period of decreasing size at maturity (1982-1988), this reproductive parameter was negatively correlated with age diversity (r=0.96). This result indicates that, in both stocks, a reduction in size at maturity enriched the age diversity of SSB. Increasing age diversity increases the SRP if no other changes in the stock occur (Trippel *et al.*, 1997; Bleil and Oeberst, 2005). The diversity index of the Southern Stock decreased sharply in 1992 and 1993. This was likely a consequence of increasing size at maturity. However, diversity in 1994-1998 was at high levels, in spite of increasing size at maturity. During this period fishing mortality-at-age was particularly high, especially at older ages, with the exception of age 1 (Fig. 3). Although increasing size at maturity will reduce the number of year classes in the SSB, reducing the diversity index, the reduction of abundance at all ages increased the diversity index. Thus, this index alone is not a good proxy for the reproductive potential of the stock, and changes in it are not explained exclusively by observed changes in size at maturity.

Two stepwise multiple regressions were performed on each hake stock to assess the variation in size at maturity as a function of i) fishing mortality at different ages and the age diversity index; and ii) adding different biomass indexes, i.e. total biomass, SSB and female only SSB. The multiple regression i) conducted for Northern hake indicated that fishing mortality at age 2, 4 and 5 has an impact on size at maturity, although the fit was poor (F=5.53, p=0.020, multiple r^2=0.65). Predicted size at maturity, however, correlated significantly with observed values (p<0.001), with an r of 0.81 (Fig. 5a). In the case of the Southern stock, multiple regression indicated that fishing mortality or age diversity had no significant impact on size at maturity (F=3.01, p=0.075, multiple r^2=0.25). Predicted versus observed size at maturity correlated poorly (p=0.165), with an r of 0.30 (Fig. 5a).

When biomass indexes were incorporated into the model (ii), prediction improved considerably. For Northern hake, the multiple regression indicated that in addition to fishing mortality at age 2, 4 and 5, as in previous case, total biomass and SSB had a significant impact on size at maturity (F=14.11, p=0.002, multiple r^2=0.91). Predicted sizes at maturity from multiple regression were very close to observed values (Fig. 5b) yielding an r of 0.95 (p<0.001). In the case of the Southern stock, the three indexes of biomass and the age diversity index were significantly related to size at maturity (F=16.37, p<0.0001, multiple r^2=0.90). The model outputs correlated well with actual size at maturity, with an r of 0.87 (p<0.001) (Fig. 5b). Similar observations were made by Marteinsdottir and Thorarinsson (1998) who detected that inclusion of a stock age diversity index in Icelandic cod assessment improved the stock-recruitment relationship, and variation of recruitment explained by the model increased from 15% to 31% when age composition was considered. Furthermore, Saborido-Rey *et al*. (2004) not only analysed effects of including age composition of spawner stock in stock-recruitment models, but also considered sex ratio and presence of skip spawners that directly affected estimates of SSB; it was observed that recruitment predictions improved when these variables were included in the model. Marshall *et al*. (1998) suggested that survey-based indices of total abundance and reproductive potential should be incorporated into the analytical assessment of stock status to indicate the quantity and quality of old spawners, because models based on SSB-recruitment relationship are not sensitive to the true variation in reproductive potential of the stock.

The reproductive system of fish reacts to any changes in life conditions, consequently variations in growth and reproduction dynamics of fish populations substantially affects fish production not only quantitatively but also qualitatively (Godø and Haug, 1999; Oven, 2004; Saborido-Rey and Kjesbu, in press). Fishing pressure may act as a stress factor by removing older and larger individuals from the spawning stock and causing changes in age and size at maturity. In this situation, intra-specific competition is diminished and smaller fish have more available food, grow at higher rates and reach maturity at younger ages. Morgan and Brattey (2005) propose two possible explanations; on the one hand, they consider that this may be the response to a stock biomass reduction, and on the other, suggest it could be a genetic response to increased mortality. Stressing factors, like fishing, exert a biased selection of individuals, and if they continue for a long time, can fix genetic changes that are reflected in variations of reaction norm (Jørgensen, 1990; Engelhard and Heino, 2004b; Ernande *et al.*, 2004; Barot *et al.*, 2005). This seems to be the case for Flemish Cap cod whose size and age at maturity have decreased, and show no signs of recovery despite the moratorium on fishing only for cod (Saborido-Rey and Junquera, 1999). Bowering (1989) detected a decrease in size at maturity in witch flounder but an increase of age at maturity; the former could be explained by overexploitation but not the latter. Something similar was observed in striped bass (*Morone saxatilis*) in coastal Rhode Island waters during 1985-1987, where a decrease in size at maturity was accompanied by a slight increase in age at maturity. In contrast, *Catostomus commersoni* from acidified lakes exhibited late age and large size at sexual maturity despite declines in population size (Trippel, 1995). Although a certain phenotypic plasticity exists, Helser and Brodziak (1998) emphasize that from determined fishing mortality (F=0.5-0.6), a stock compensatory response disappears or is very slow.

All these changes in maturity parameters affect stock reproductive potential, because smaller and younger females have different reproductive attributes than larger and older individuals (Solemdal, 1997; Trippel *et al.*, 1997). Maternal physiological status, spawning experience (recruit or repeat spawners) or food rations during gametogenesis are all known to alter fecundity, egg and larval quality, as well as duration of the spawning season (Hislop *et al.*, 1978; Kjesbu *et al.*, 1991; Trippel, 1999; Marteinsdottir and Begg, 2002). Fecundity and relative fecundity generally increase with body size (Wootton, 1979; Kjesbu *et al.*, 1998). Consequently, at the population level, the annual population fecundity (total egg production) will, in addition to the number of mature fish, depend not only on size (age) structure, but also on fish condition (Marshall *et al.*, 1998). Change in stock structure entails a compensatory response of age/size at maturity because depletion of large fish can be compensated for by an increased egg production by young fish (Trippel, 1995). If this compensatory response does not occur a stock could reach a critical stage. Consequently, to improve fisheries assessment, it is necessary to account for compensatory mechanisms of stocks and the variability of maturation parameters (Domínguez, 2007).

3.3. Changes in maturity ogives in response to environmental fluctuations

Reduced population biomass normally as a consequence of high fishing exploitation, usually leads to a reduction in the plastic parameter of age at maturity. In the case of the Southern Stock of hake, size at maturity increased over a long period (1988-1998) in spite of continuously decreasing total biomass, SSB and female SSB. Thus, changes in size at maturity are not the only consequence of reduced SSB. However, in the Northern Stock the trend of size at maturity seems to be related to the trend on SSB, which has slowly, but steadily increased since 1995, although with important fluctuations during this period (Fig.

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2b). Size and age at maturity depends not only on the maturation process by itself but also on growth and survival conditions (Olsen *et al.*, 2004) that seems to be conditioned by population abundance. For example, age at maturity of cod from the Irish Sea diminished when SSB decreased, although growth rates did not change (Armstrong *et al.*, 2004). In similar way, size and age at maturity of American plaice from Northwest Atlantic has decreased since the 1960s coinciding also with a decrease of SSB, the maturation of cohorts being related to total abundance of the stock over the whole life history of the cohort (Morgan and Colbourne, 1999). However, Rätz and Lloret (2005) suggest that for Greenland cod population density only affects growth of younger age groups. On the contrary, in this study it was observed that for the Southern Stock of hake the reduction in size at maturity has no or little effect on SSB, which did not recover in spite of the dramatic decline in size at maturity which,was probably, at least in part, caused by the impact of fishing mortality on SSB. However, as mentioned, size at maturity increased during the 1990s in spite of declining SSB, which is contrary to compensatory theory. The lack of compensatory response is known as depensation. According to Liermann and Hilborn (2001) four mechanisms of depensation exist: i) reduction of fertilization probability, ii) alterations of group dynamics, iii) environmental influences and iv) saturation of predators. These four mechanisms are responsible for lack of acompensatory response, even if stock density and intraspecific competition decrease. This phenomenon could be the explanation for absence of recovery of the Northern cod after 15 years of moratorium (Shelton and Healey, 1999).

Changes in size at maturity must reflect shifts in growth rate of the different cohorts, and since biomass (abundance) has no or little effect on growth, the hypothesized changes in growth rate must be coupled with environmental factors. This might be supported by the fact that the observed changes in size at maturity occurred over a very short time period. If size at maturity changes as a consequence of growth rates, the results presented here should support a highest growth rate than that traditionally used. This hypothesis has been confirmed by the growth rates resulting from tagging experiments of Northern Stock (Lucio *et al.*, 2000; de Pontual *et al.*, 2003).

Environment may play an important role in these changes, affecting growth rate of different cohorts. Three key oceanographic factors have been analyzed in this study: upwelling, NAO and temperature. The upwelling index fluctuated considerably during the study period in both areas (Fig. 6). In general upwelling was relative weak in 1983-1988 and 1998-2004 in Bay of Biscay, and strong during the central period, i.e. 1989-1997. The pattern in the Galician shelf is not so clear, and years of strong upwelling are followed by years of relative weak upwelling. However, since 1991 the upwelling index has declined. For the particular case of the Galician shelf, monthly values of upwelling allowed the creation of an interpolated smooth mesh plot, where the trend is more easily observed (Fig. 7). Upwelling was very strong in spring and summer during the 1970s and early 1980s. Spring upwelling has declined considerably since then, and today is at a low level. Summer upwelling strength has also progressively declined. NAO winter index (Fig. 8) showed positive values during the whole period except in 1985, 1987, 1996 and 2001 and the highest values occurred during the 1990s. When considering the standardized running mean, however, some interesting trends are observed. Firstly, from 1984 to 1988 there was a decline in NAO index from positive to negative values, from a 3 year running mean. This trend is also observed with 5 and 10 year running means, but smoothed. In 1990 the NAO index increased to positive values, remaining at this level for 4, 7 or 12 years depending on the running mean considered (Fig. 8). After this period NAO was negative again until 2004. In general 1987-1988 showed the lowest values

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after a declining period, which coincides with the lowest size at maturity estimated for Southern Stock.

Mean annual surface temperatures were only available for the Bay of Biscay. These temperatures are not only affected by current systems, upwelling and other factors that may alter the SRP, but are very much affected by solar irradiation, as can be observed for the Galician shelf where monthly and annual patterns were very different from those at greater depths (Fig. 9). This figure indicates that during the summer, temperatures were lower than in winter at all the depths analyzed. During the late 1980s the difference between summer and winter temperature was lower, or in other words, in recent years (up until 2000), winters have been warmer than in previous ones. This warming effect persisted at all depths over temporal series, but was higher at relatively shallower depths, i.e. 50-150 m (Fig. 9). The impact of temperature on fish physiology and behavior has been documented for several species. Many studies have described the effects of sea temperature on fish metabolism (Tyler and Colow, 1985; Solemdal, 1997; Martínez *et al.*, 1999; Harvey, 2005; Stevens *et al.*, 2006), growth rates (Rätz *et al.*, 1999; Dutil *et al.*, 2003), condition (Krohn *et al.*, 1997), reproduction (Fedorov, 1971; Wootton, 1990; Jonsson and Jonsson, 2003; Privalikhin, 2003; Basilone *et al.*, 2006; Coombs *et al.*, 2006) or offspring survivorship (Lambert *et al.*, 2003; O´Brien *et al.*, 2003; Abdoli *et al.*, 2005). Furthermore, water temperature also conditions fish population dynamics (Marshall *et al.*, 2000; Armstrong *et al.*, 2004; Yoneda *et al.*, 2006) and distributions (Louge, 1996; Gordoa *et al.*, 2000; Pájaro *et al.*, 2005).

Stepwise multiple regressions were performed for each hake stock to assess the variation in size at maturity as a function of environmental factors, i.e., NAO and the upwelling index. Temperature was not used, firstly because temperature at different depths was not available for Bay of Biscay and secondly because the time series only covered part of the period for which size at maturity data were available. NAO winter index, the three running means and upwelling index of the same year and from the previous year were included in the model. The multiple regression conducted for the Bay of Biscay indicated that the 5 year NAO running mean and upwelling in the preceding year and 10 year NAO running mean of the same year has a significant correlation with size at maturity (F=8.33, *p*<0.005, multiple r^2=0.74). Predicted size at maturity from the multiple regression correlated significantly with observed values (r=0.86, p<0.001) (Fig. 5c). In the case of the Southern Stock, the multiple regression indicated that the 10 year NAO running average and upwelling in the preceding year, and the 5 year NAO running mean, upwelling index and winter NAO of the same year has a significant impact on size at maturity (F=7.12, *p*<0.001, multiple r^2=0.70). Predicted versus observed size at maturity correlates less well compared with Northern stock but is still significant (r=0.84, p<0.001) (Fig. 5c).

Althoug temperature was not used in the multiple regression analysis, it is known that it impacts on age and size at maturity (Armstrong *et al.*, 2004; Drinkwater, 2005), although the responses of fish to this factor varies between species (Cook and Heath, 2005). Rose (2005) suggests that small pelagics respond quickly and strongly to climate changes because of their physiological limits and fast potential growth. Moreover, temperature may influence the fish maturation process indirectly through alterations of ecosystem composition, resource availability or hydrographic conditions (Kell *et al.*, 2005; Orlova *et al.*, 2005; Rätz and Lloret, 2005; Rose, 2005). The upwelling process causes a rise of cold deep water rich in nutrients (Wooster *et al.*, 1976; Fraga, 1981) during summer. The increase in nutrients is translated into higher ecosystem productivity and more available food for hake. In these circumstances, females achieve a better condition for the next spawning season, producing higher quality

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offspring that grow at higher rates which results in a larger length at age, i.e. for the same age at maturity the size will be greater. Similarily, juveniles are able to grow more during summer to get into reproductive condition. This mechanism, in spite of its decrease in recent years, could be strong enough to neutralize the negative effect of SSB decrease on size at maturity in Southern Stock. Nevertheless, Castro *et al.* (1994) suggest that primary production on Galician Shelf may be carried offshore due to current system generated by the upwelling itself. In any case, it would be advisable to analyze historical trends of age at maturity if possible. Besides local physical conditions, there are large-scale climatic changes that may affect fish (Wells *et al.*, 2006); between these large-scale phenomena is NAO. The NAO index acts as integrator of several environmental factors that can have a synergistic effect on fisheries dynamics. NAO impacts on air temperature, wind and precipitation regime and on large water mass distribution and flow with the subsequent influence that all these factors have on ecosystems (Greene and Pershing, 2000; Köster *et al.*, 2005). For example in Northeastern USA high and low periods of yellowtail flounder recruitment were correlated with extreme values of NAO index (Sullivan *et al.*, 2005) and a decline in abundance of *Calanus finmarchicus* coincides with decrease in the NAO index (Greene and Pershing, 2000). So, NAO may act indirectly on size at maturity of hake in both stocks. Ottersen *et al.* (2001) has extensively reviewed the of ecological effects of the NAO, both in aquatic and terrestrial ecosystems.

A second set of multiple regressions were performed with both the environmental data and fishing mortality. Prediction improved with both datasets, although environmental data played the most important role. For the Northern Stock, the multiple regressions indicated that in addition to NAO and the upwelling index as before fishing mortality at age 6 had a significant impact on size at maturity but was less important than oceanographic factors. Predicted versus observed size at maturity (Fig. 5d) yielded a slightly higher correlation (r=0.91, p<0.001). In the case of the Southern Stock, in addition to environmental factors, which contributed with highest F values, fishing mortality at ages 1, 2, 6 and 7 were included in the final model as significant variables. The model predicted well the observed size at maturity, with an r of 0.91, p<0.001 (Fig. 5d). Impact of fishing mortality on size at maturity has been reported in other species such as cod from Irish and North Sea (Armstrong *et al.*, 2004; Kell *et al.*, 2005), however for Greenland cod no relationship was found between fishing intensity and length at age (Rätz and Lloret, 2005). Fishing activity usually removes larger individuals altering age and length composition of stocks that may result in selection of earlier maturing individuals (Olsen *et al.*, 2004). If it continues for long time it can cause the loss of genetic components (Shelton and Healey, 1999), although genetic changes can be explained by other factors such as, genetic flow between close stocks or selective natural predation (Chouinard *et al.*, 2005). In general, is postulated that fishing pressure may modulate fish stock dynamics over short-time scales while climatic change would have long-time scale effects (Kell *et al.*, 2005; Poulard and Blanchard, 2005; Rose, 2005).

A complex stock can include several sub-stocks that should be assessed and managed as independent units under the Precautionary Approach (Frank and Brickman, 2000). In the light of the present results on the dynamics of Northern and Southern Stocks of hake in recent years it seems that the European hake probably comprises a single population in North Atlantic but has different sub-populations. This hypothesis is supported by genetic and parasitological studies (Lo Brutto *et al.*, 2004; Mattiucci *et al.*, 2004; Castillo *et al.*, 2005)

4. Conclusions

Size at maturity of the Southern Stock hake declined drastically in a very short period during the 1980s but increased at the same rate over the next 10 years probably indicating that there have been no changes in reaction norm, since genetic changes are not easily reversed (Reznick, 1993; Heino *et al*., 2002a). However, it is very important not to confuse maturity ogives with reaction norms for age and size at maturation, as they describe different, although linked, features (Heino *et al*., 2002b). Shifts observed in size at maturity are more likely to be the consequence of changes in growth rate.

Decreasing biomass may explain the decline in size at maturity from 1980 to 1988. However, total and spawning biomass declined even during the period when size at maturity increased, which is contrary to compensatory theory. Shifts in environmental regime, NAO and upwelling, may have contributed to a decelerated growth during this period that explain the later maturation.

Evolution of size at maturity in Bay of Biscay has followed a different pattern, since a steady decline has been observed throughout the study period.. Shifts in size at maturity are well predicted by fishing mortality and age diversity, but the environment may also have played an important role. However, the low number of data available may affect the results of the multiple regressions.

Finally, it is worth mentioning that the data used in this modeling exercise was limited to a reduced part of the distribution of both the Northern and Southern Stocks and, therefore, the results should be treated with caution. In addition, a number of assumptions have been made in relation to missing data or the way data was compiled, which further underline that caution is required in interpreting the results and conclusions.

Acknowledgements

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Yoneda, M., Yamamoto, K., Yamasaki, S. and Matsuyama, M. 2006. Growth and maturation variability of female John Dory (*Zeus faber*) in the East China Sea in relation to thermal gradients. Journal of Marine Biology Association UK 86, 885-892.

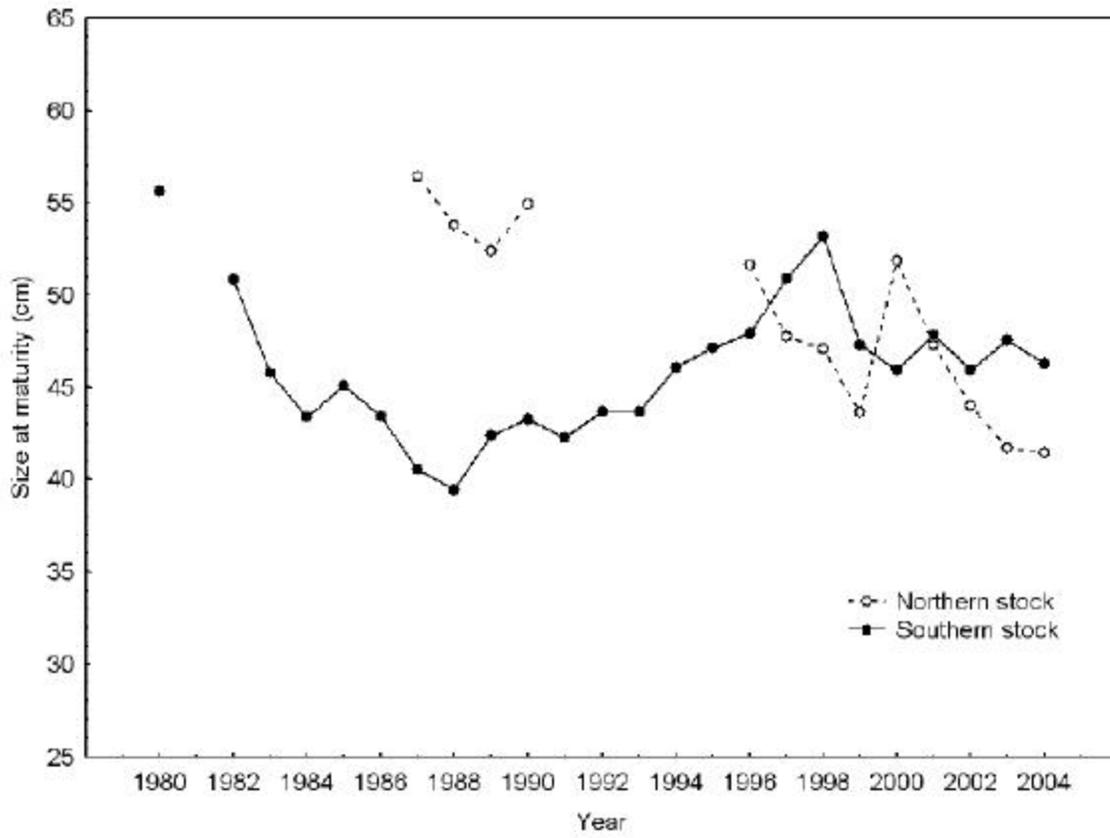Table 1. Macroscopic maturity classification criteria of female European hake

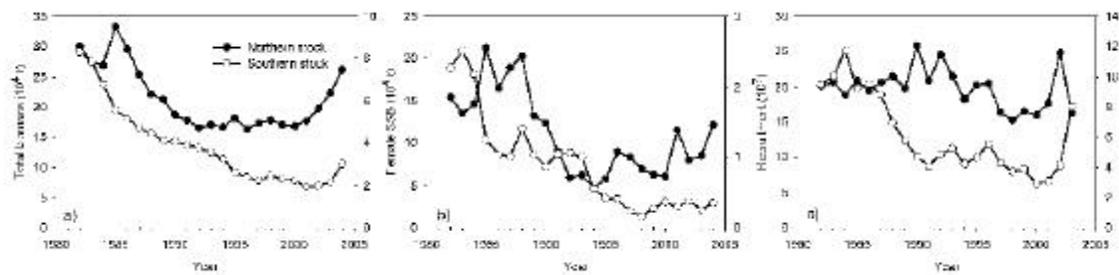| STAGE	DESCRIPTION
Immature	Ovaries emerge as tiny, paired organs in posterior body cavity; glassy orange-reddish and translucent. No opaque oocytes are observed.
Incipient maturation	Ovaries still small, opaque, orange to creamy yellow. Oocytes clearly visible.
Matures	Ovaries enlarge to mid body cavity, firm, orange to creamy yellow with some blood vessels. Oocytes are clearly visible and densely packed.
Hydrated	Ovaries fill most of body cavity, appear granulated pink to orange-reddish with mixture of opaque and transparent oocytes, prominent blood vessels. Lumen containing viscous fluid or hydrated eggs.
Advanced mature	Ovaries enlarge to mid body cavity, plump and flabbier than Matures with prominent blood vessels, opaque, orange to creamy yellow. Oocytes clearly visible and densely packed.
Spent	Ovaries shrunk to posterior body cavity, completely flabby with prominent blood vessels, dark red to purple. Opaque oocytes are few or absent.
Recovering	Ovaries contracted and somewhat uneven walls, slack, blurred translucent orange- to reddish-grey. Opaque oocytes absent, but single hydrated eggs or atretic oocytes (opaque, irregular granules) may occur.

Table 2.- Number of analyzed fish by year, quarter, area and source of the samples, including the length range and the number of immature and mature fish by year in Galician shelf

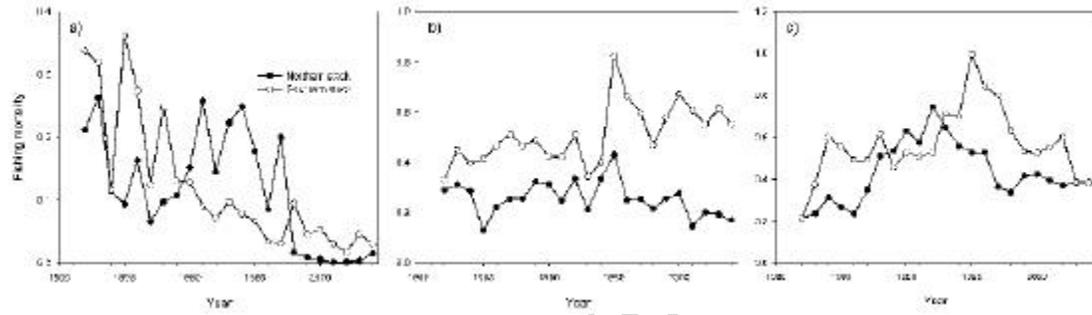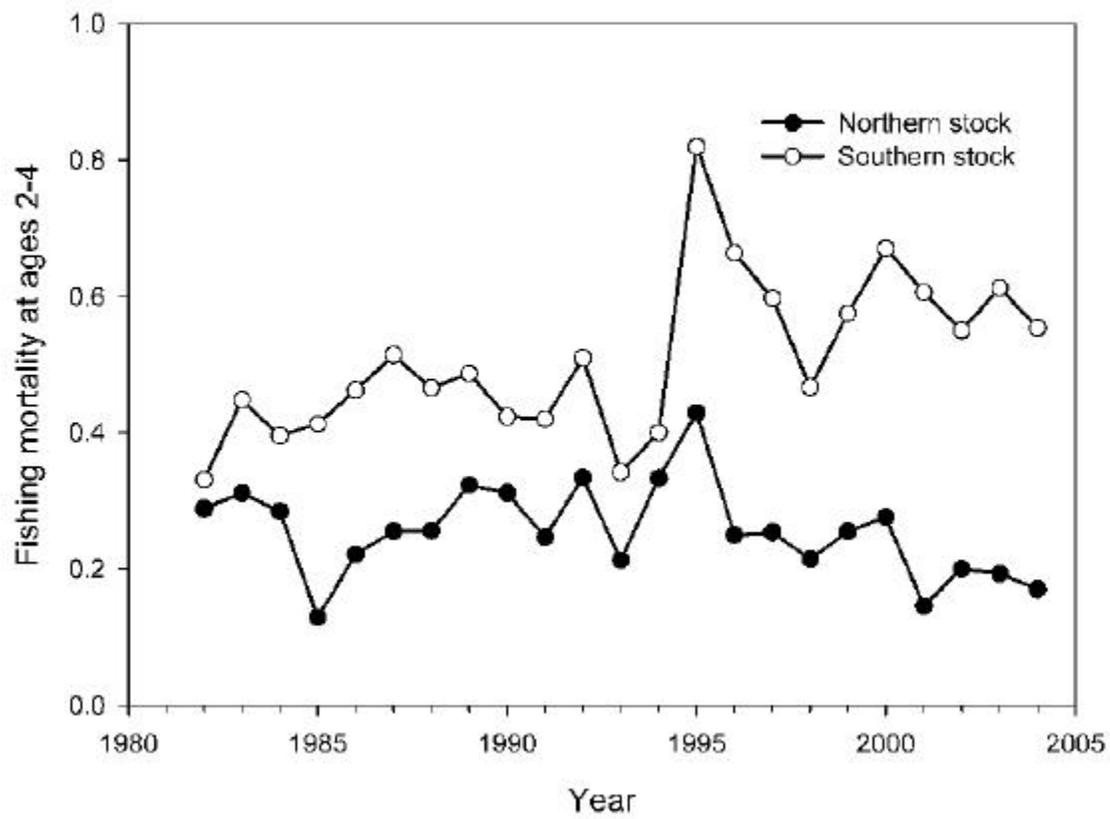|	Galician shelf											Bay of Biscay						
	Research surveys				Landing				Length	n°	n°	Landing				Length	n°	n°
Year /Quarter	1	2	3	4	1	2	3	4	range	immature	mature	1	2	3	4	range	immature	mature
1980						136	177	38	21-66	338	13							
1982					142	47	31		33-75	61	159							
1983					45	104			23-71	103	46							
1984					278	134	32	95	23-77	264	275							
1985					181	307	258	268	11-87	628	386							
1986					148		52	49	25-68	108	141							
1987													8	56	216	17-86	241	39
1988					30	149	270		15-63	369	80	201	365	429	482	10-87	1366	111
1989					153	310	102		15-70	322	243	140	201	333	469	13-66	1077	66
1990	311	324	226	226	80	76	42	39	14-70	1138	186	377	467	279	211	11-104	866	468
1991			131	152	52	190	67		14-65	406	186							
1992			332	164	52				14-66	528	20							
1993			58			107		16	16-53	160	21							
1994			123	261	81	95	12	85	15-78	583	74							
1995			5	289	115	142	57	24	13-70	526	106							
1996			155	538	112	169	252	29	14-75	949	306		816	417	650	14-91	819	1064
1997	69	127	137	185	68	135	75		10-79	662	134	813	466	191	145	22-92	634	981
1998			119	242	34	124	27		10-68	491	55	454	489	139	115	20-99	536	661
1999	24		89	232	27	59	2		9-71	369	64	123	103			21-55	162	64
2000	5			183	40	53	56	13	10-63	270	80	199	342	345	360	17-59	1160	86
2001	14	14	35	183	25	17			15-74	260	28	248	1536	599	68	17-101	589	1862
2002		145	55	241		231	128	38	12-75	601	237	310	375	532	817	8-110	1535	499
2003	52	75	76	146	59	191	201	62	16-69	691	171	475	224	121	147	32-84	137	830
2004	69	87	92	155	169	198	125	107	15-75	757	245	275	455	131		38-87	104	757
Total	544	772	1633	3197	1891	2974	1966	863		10584	3256						9220	7482

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Figure captions

Fig. 1. Female size at maturity for Northern and Southern Stocks of hake

Fig. 2. Total biomass, female SSB and recruitment for Northern and Southern Stocks of hake.

Fig. 3. Fishing mortality at a) age 1; b) F_{med} for ages 2-4; and c) F_{med} for ages 5-7 for Northern and Southern Stocks of hake.

Fig. 4. Age diversity index for both hake stocks

Fig. 5. Size at maturity against predicted size at maturity from multiple linear regressions for each stock. Multiple regression were performed including in the initial model a) the fishing mortality at age (1 to 7), the F_{med} and the age diversity index; b) the variables used in previous panel together with the total biomass, SSB and the female SSB; c) the environmental data (Upwelling and Non-standarized and Standarized 3- 5- 10- years running mean winter NAO index and the same indexes lagged one year); and d) the environmental data as in previous panel together with fishing mortality at age 1 to 7, the F_{med} and the age diversity index.

Fig. 6. Annual upwelling index ($m^3 s^{-1} km^{-1}$ coast) for the sampling area of both stocks.

Fig. 7. Upwelling index ($m^3 s^{-1} km^{-1}$ coast) by month and year in the Galician waters (sampling area of the Southern stock)

Fig. 8. Non-standarized and Standarized 3- 5- 10- years running mean winter NAO index (mbar)

Fig. 9. 3D Mesh plot of the mean monthly temperatures by depth range in Galician shelf. Note the different Z-scale for the surface plot.
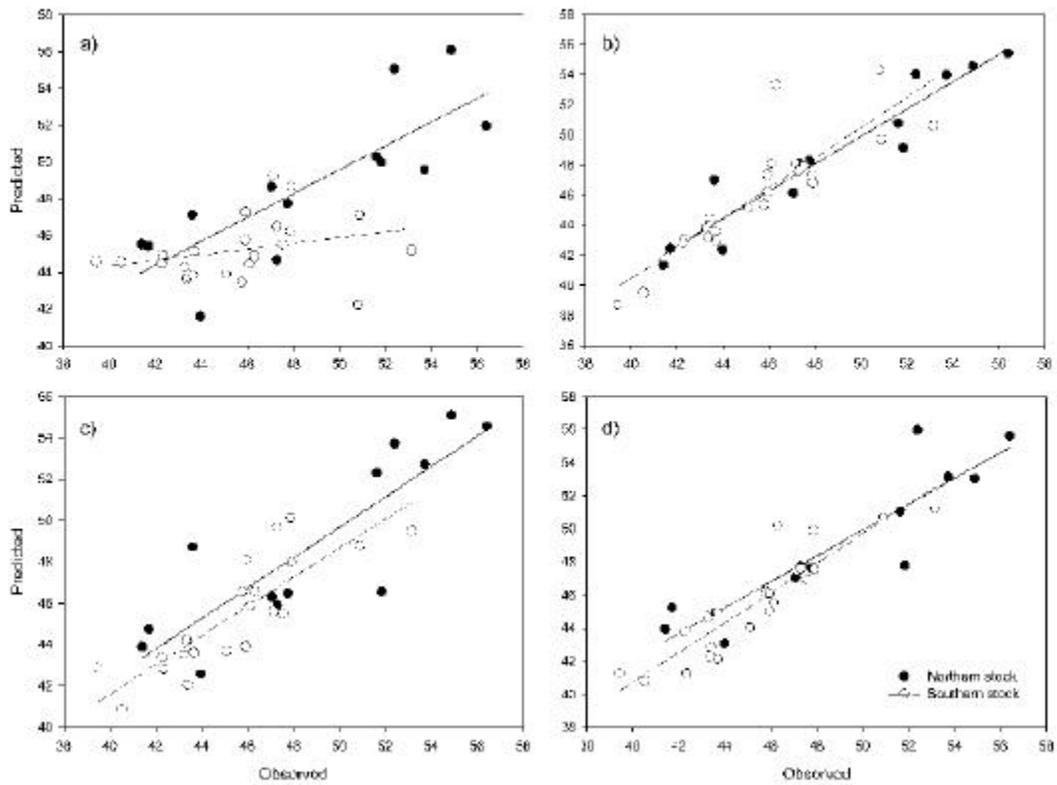
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