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Comparative study of spawning pattern and reproductive potential of the Northern and Southern stocks of Argentine hake (*Merluccius hubbsi*)

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ABSTRACT

The reproductive biology of the Northern (Bonaerense) and Southern (Patagonian) stocks of *Merluccius hubbsi* in the Argentinean Sea is analyzed, including information on spawning areas, estimates of abundance and size composition of spawning females, fecundity, spawning frequency and egg quality. Samples of Argentine hake were obtained during the period of peak reproductive activity; May and January for the Northern and Southern stocks, respectively.

The size of the reproductive area for the Northern stock (35–38°S) was clearly smaller than the one estimated for the Southern population (43°30′–46°S), being 23,770 km^2 and 52,460 km^2 respectively. Spawning females from the Northern reproductive area were smaller (modal values between 35 and 40 cm TL) than those from the Southern stock (modal values between 38 and 50 cm TL), and they were also less abundant in number and had a lower spawning frequency (8–13 days and 5–7 days between partial spawning for the Northern and Southern stocks respectively). No differences in batch and relative fecundity between stocks were recorded (mean values of 526 and 530 hydrated oocytes g^{-1}), but the dry weights of hydrated oocytes from females of the Northern group were higher (3.08 mg for 100 hydrated oocytes) than those of the Patagonian stock (2.84 mg) for the same total length range. The egg production during the month of peak spawning of the Northern group depended mostly on the smaller females (<50 cm TL) and was in average 1 to 2 orders of magnitude lower than that estimated for the Southern stock (9×10^{12}–22×10^{12} eggs and 692×10^{12}–1295×10^{12} eggs for the Northern and Southern stocks respectively). Those differences in egg production and the high productivity and retentive characteristics described for the spawning area and nursery ground in Patagonian waters would justify the greater abundance and resilience of the Southern stock of Argentine hake. The low abundance of females in spawning capable stage observed during the reproductive season of the Northern group (autumn–winter), led us to postulate that currently it does not exist a pronounced reproductive peak in this stock similar to the one observed for the Southern hake group during the summer.

1. Introduction

Argentine hake (*Merluccius hubbsi*) is a demersal species distributed from 22°S to 55°S at depths mainly between 50 and 500 m (Cousseau and Perrotta, 1998). This is the main fishery resource for the Argentine and Uruguayan bottom trawler fleet (FAO, 2003), with an abundance of around one million tons, as estimated in 2012 (Irusta and D´Atri, 2013; Santos and Villarino, 2013). In Argentina, two main hake stocks were identified: the Northern or Bonaerense group (between 34°S and 41°S), which is shared with Uruguay into the Argentine–Uruguayan Common Fishing Zone, and the Southern or Patagonian group ranging between 41°S and 55°S. Studies of ichtyoplankton distribution (Ehrlich, 2000; Ehrlich and Ciechomski, 1994; Gonçalves Torres-Pereira, 1983) and gonadal maturity of Argentine hake individuals (Louge, 1996; Rodrigues and Macchi, 2010) showed that the reproductive activity of the Northern stock takes place mainly during autumn and winter, with a main peak in May, mostly at north of 38°30′S. As the reproductive period progresses spawning females move toward the northern area (Ehrlich, 2000; Rodrigues and Macchi, 2010), reaching Brazilian waters (32–34°S), where hake eggs have been observed during late winter (Gonçalves Torres-Pereira, 1983). Martos et al. (2005) define this region as a mixed water area, with a strong influence of the Rio de la Plata discharge (which conform a permanent saline front of large-scale) and characterized by a high primary productivity, driven mainly by the nutrient input from river discharges and by the high vertical stability of the water column (Acha et al., 2004; Viñas et al., 2002).

From an economic point of view the Southern group of *M. hubbsi* is the most important one, with an abundance of about 80% of the total biomass estimated for this resource in Argentina (Santos and Villarino,

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2013). Its reproductive activity takes place mainly in waters off the Chubut province, between 43° and 45°30′S at depths from 50 to 100 m. However, unlike the Northern stock, spawning occurs during spring and summer with a main peak in January (Macchi et al., 2004; Pájaro et al., 2005). The hydrography of the north Patagonian shelf is characterized by a frontal system produced as a result of the dynamics of tides. This tidal front separates homogeneous coastal waters from the stratified ones (Glorioso, 1987), and it is characterized by a high biological productivity caused by phyto-plankton blooms and large aggregations of copepods (Ramírez et al., 1990). In the Patagonian region the formation of this oceanographic structure occurs in spring and summer, during the spawning of the Southern hake stock. Therefore, this scenario clearly creates a suitable habitat for spawning and survival of the early life stages of this species (Sánchez and Ciechomski, 1995).

Since the 1990s both stocks of *M. hubbsi* have been exposed to high levels of exploitation and their biomass has decreased drastically, in particular the Northern group (Aubone et al., 2000; Irusta and D´Atri, 2013; Pérez, 2000; Santos and Villarino, 2013). Additionally, changes have been recorded on the length and age structure of both stocks (Irusta and D´Atri, 2013; Santos and Villarino, 2013) and in the location of spawning shoals for the Southern group (Macchi et al., 2005).

In this context, we hypothesize that changes in the parental stock structure may have consequences on the reproductive potential of hake, considering the relationship between the size of spawners and the quantity and quality of produced eggs (Trippel, 1998; Marshall et al., 1998). These changes should have been more significant in the Northern group, taking into account that the fishing activity on this stock has been much more intense during the last years and began earlier than in the Patagonian region. Therefore, the main goal of this paper was to compare the spawning pattern and reproductive potential of the Northern and Southern hake stocks, by estimating the egg production and oocyte quality. These variables were analyzed in relation to the size structure of spawners during the main reproductive peak of each stock, between 2009 and 2012.

2. Materials and methods

2.1. Spawning area, abundance and length distributions of active females

Samples of *M. hubbsi* were obtained from bottom trawls during 7 research surveys conducted by the National Institute for Fisheries Research and Development (INIDEP) during the reproductive peak of both Argentine hake stocks; three of them were carried out in the area of Buenos Aires Province (Northern or Bonaerense stock) in May 2009, 2011 and 2012, and the other four in the Patagonian area (Southern or Patagonian stock) in January 2009, 2010, 2011 and 2012 (Table 1; Fig. 1).

The fishing trawls were distributed in transects perpendicular to the bathymetry, covering the main reproductive areas of both stocks. Argentine hake specimens were captured at depths between 50 and 300 m using a bottom trawl with a mouth width of about 20 m, a height of about 4 m, and with a 20-mm mesh size at the inner lining of the codend.

Table 1
Number of Argentine hake (*Merluccius hubbsi*) specimens sampled during the research surveys carried out in autumn (Northern stock) and summer (Southern stock) between 2009 and 2012.

Stock	Year	Trawls	Research surveys date	*N* individuals sampled
Northern	2009	66	May 15–Jun 2	5287
	2011	77	May 17–Jun 7	7542
	2012	75	May 15–Jun 4	5980
Southern	2009	86	January 15–January 29	15813
	2010	83	January 22–February 2	19683
	2011	72	January 24–February 9	13487
	2012	89	January 11–January 22	19362

From each specimen it was recorded: total length (TL) in centimeters, total weight (TW), gutted weight (GW), and liver weight (LW) in grams, sex and macroscopic gonad maturity stage. For this, a visual maturity key of five stages was used: (1) immature, (2) developing, (3) spawning capable, (4) regressing and (5) regenerating (Macchi and Pájaro, 2003; Brown-Peterson et al., 2011). This scale was validated for females by histological analysis of 6425 ovaries (1922 from the Northern stock and 4503 from the Southern stock). The ovaries collected were preserved in 10% formalin during the cruise, and later they were weighed (GW) and a portion of tissue was removed from the center of each gonad, dehydrated in methanol, cleared in xilol and embedded in paraffin. Sections were cut at approximately 5 μm thick and stained with Harris' hematoxylin followed by eosin counterstain. Histological staging of ovaries was based on the stage of oocyte development, the occurrence of postovulatory follicles (POF) and atresia, following the classification described for the Southern stock of Argentine hake (Macchi et al., 2004).

Indices of abundance of active females per length class were estimated by stock and year of the period analyzed, during the main spawning peak of each hake population (May and January for the Northern and Southern stock respectively). The information obtained from sampling of the trawl catch was weighted in order to obtain estimates of abundance (number of individuals per length class) in the spawning area as detailed by Macchi et al. (2004). It was calculated by multiplying the number of hake within each length class by the proportion of active females for that length class (Marshall et al., 1998). The sum of values estimated across the size range was an index of the total number of active females for each year during the reproductive peak of each hake stock.

Length distributions of active females or spawning capable (Brown-Peterson et al., 2011) were analyzed, considering in these stages only those individuals capable of spawning at the time of capture or within this spawning season (Hunter et al., 1992).

2.2. Spawning frequency

The spawning frequency (number of days between partial spawnings) was estimated from the daily proportion of spawning females sampled for each year during the reproductive peak of each stock. This variable was determined by the incidence of females with day 1 POF (between 24 and 48 h from spawning), owing to that 48 h after spawning postovulatory follicles could not be consistently identified because of their rapid degeneration. On the other hand, the occurrence of postovulatory follicles less than 24 h old is affected by hour of sampling and sexual composition of the school (Hunter and Goldberg, 1980). Mean and variance were calculated according to the equations developed by Picquelle and Stauffer (1985).

2.3. Fecundity

Batch fecundity (BF: number of hydrated oocytes released per spawning) and relative fecundity (RF: number of hydrated oocytes per gram of body weight) were estimated gravimetrically with the hydrated oocyte method on fixed ovarian samples (Hunter et al., 1985), using only ovaries that showed no evidence of recent spawning (i.e., no POF). For these determinations were selected 141 ovaries of females from the Northern stock and 371 ovaries from the Southern stock. Three pieces of ovary, approximately 0.1–0.2 g each, were removed from the anterior, middle, and posterior parts of one gonad and weighed to the nearest 0.1 mg, and hydrated oocytes were counted. Batch fecundity for each female was the product of the mean number of hydrated oocytes per unit of weight and the total weight of the ovaries. Relative fecundity was determined as the batch fecundity divided by female weight (without ovary).

The relationships of BF to TL obtained first among years and later between stocks were compared on the basis of overlapping length ranges

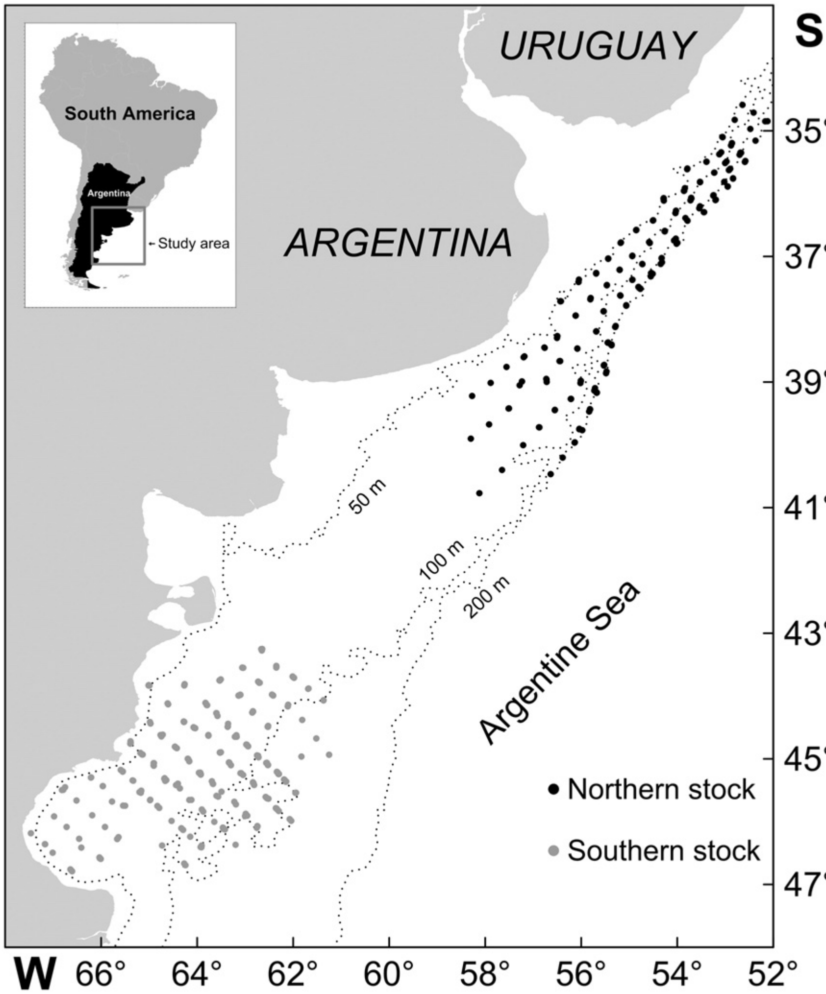

Fig. 1. Spatial distribution of demersal trawl stations in the spawning area of *M. hubbsi*: Northern stock (sampled in autumn) and Southern stock (sampled in summer), between 2009 and 2012.

of the females (38–80 cm TL), by using an analysis of covariance on the log-transformed data (Draper and Smith, 1981). A two-way ANOVA procedure was applied to examine the effect of the years sampled and stocks on the mean values of relative fecundity.

After that comparison, the relationships of BF and RF to TL, gutted weight, HSI (hepatosomatic index), and Kn (relative condition factor) were described through the use of simple regression analysis, because the variation in size or condition of spawning females could influence both fecundity and egg production (Brooks et al., 1997; Kurita et al., 2003; Lambert et al., 2003). Normal probability plots of the residuals were used to assess normality of distribution.

HSI, which provides an indication of the status of energy reserves in the liver, was defined by the following equation: $HSI = (LW / GW) * 100$. For these determinations the gutted weight (GW) was used because fish weight may be greatly influenced by the stomach content and fullness of the gut.

Relative condition factor (Kn), was expressed as a proportion between the observed GW and the GW determined by the relationship of TL versus GW for each year and stock (Le Cren, 1951).

2.4. Oocyte dry weight (DW)

A sample of 100 hydrated oocytes was removed from each gonad of 154 females from the Northern stock and 230 female from the Southern stock; they were rinsed in distilled water to remove formaldehyde remnants, dried for 24 h at 60 °C, and weighed to the nearest 0.1 mg. The oocyte dry weight (DW) was considered an index of egg quality for the hake spawning females, taking into account that dry mass is associated with the quantity of yolk reserves stored in oocytes (Macchi et al., 2006; Mehault et al., 2010). Although we are aware (Hislop and Bell, 1987) that this procedure to determine oocyte dry weight is biased due to losses while stored in formaldehyde, it was the only option for ovaries preserved at sea and the best available for our application. Finally, the relationships between DW and the different morphophysiological variables (TL, GW, HSI, and Kn) were evaluated with simple regression analysis.

2.5. Egg production

The egg production during the main reproductive peak of each stock (May and January) was based on the estimates of three variables during each month: the abundance of active females per 3 cm length size class, the BF–size relationship and the spawning frequency. The egg production by length was estimated by multiplying the number of active females in each length class by the fecundity estimated for that length class and the number of spawning by month (Macchi et al., 2004). The sum of values estimated across the size-range was an index of the total egg production for the month of peak reproductive activity of each stock. This variable was estimated for each year of the period analyzed (2009–2012).

3. Results

3.1. Spawning area, abundance and length distributions of active females

To determine the main reproductive areas of the Northern and Southern Argentine hake stocks the spatial distribution of females showing evidence of spawning was considered, with hydrated oocytes and/or new postovulatory follicles (day 1) in the ovaries, obtained for different years (Figs. 2 and 3).

Samples of the Northern stock collected during May showed that females near spawning or with recent POF were concentrated inshore, in waters close to the 50 m isobath, mainly between 35° and 38°S. In 2011 and 2012, some females in spawning stage were observed at south of 38°S and also near 50 m depth (Fig. 2). In general, the location of spawning females was not coincident with the spatial distribution of the more dense schools of hake, which were mainly observed at waters deeper than the 100 m isobath (Fig. 2).The size of the reproductive area for this stock was estimated in 23,770 km^2.

In the Patagonian region, during January, most of the females in spawning condition were also located between the 50 and 80 m depths, but the spawning area was double in dimension in comparison with the Northern group, covering 52,460 km^2 between 43°30′ and 46°S. During 2009 and 2010 some small reproductive groups were also observed in deeper waters, close to 100 m depth (Fig. 3). Nevertheless, in contrast to the Northern stock, during the spawning peak the highest abundances of hake in the Patagonian region were observed in most coastal waters, mostly coinciding with the spawning schools (Fig. 3).

The abundance of active females estimated within each reproductive area during the peak spawning showed that it is approximately 30 times higher for the Southern stock in comparison to the Northern group. This was also reflected in the hake density estimated by trawl sampling for each stock, i.e. tons of hake per square nautical mile were much higher in the Southern stock (Table 2). In both populations mean values of hake density were higher in 2012 (Table 2; Figs. 2 and 3).

Length distribution of active females from the Northern hake stock obtained for the 3 years analyzed varied between 25 and 87 cm TL. During 2012 there was a greater abundance of active females, with a main size mode in 36 cm TL. In previous years the length distributions showed not so clearly a group of main sizes, although they were generally dominated by individuals smaller than 50 cm TL (Fig. 4). Regarding the Southern stock, the range of active females for all years analyzed varied between 25 and 95 cm TL, showing different modal values for each year ranging between 38 cm and 50 cm TL (Fig. 4). Besides the difference in abundance observed for each stock, great difference in the size structure was observed. The Northern spawning stock was mainly characterized by younger adult individuals (<50 cm TL), with regard to the Southern group.

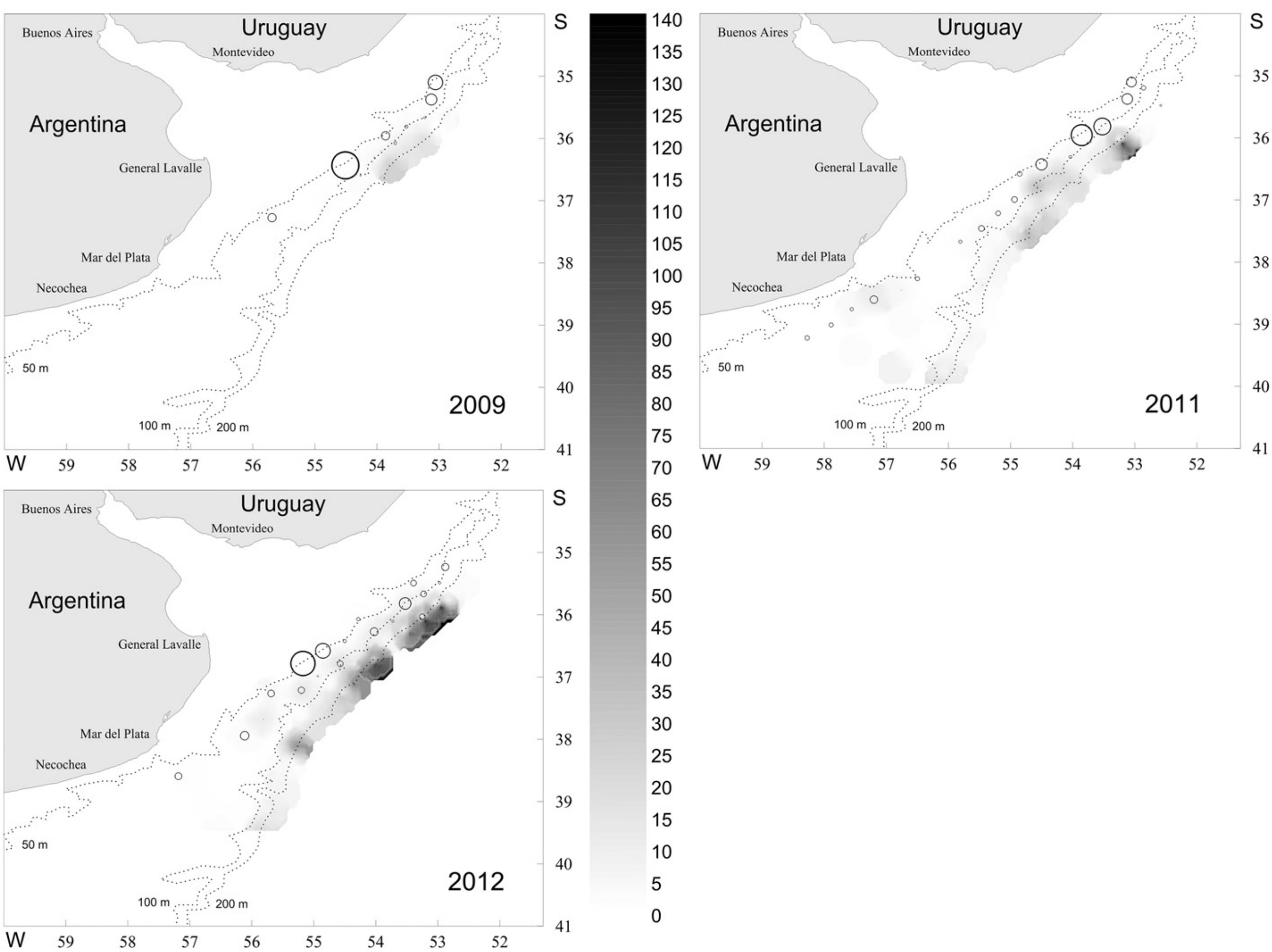

Fig. 2. *Merluccius hubbsi* abundance and spatial distribution of spawning females from the Northern stock. Symbols are proportional to percentage of females with hydrated oocytes or with POF 1 day (between 0% and 100%). Vertical shaded scale represents density (tons/nautical mile^2) of total hake estimated from each trawl surveys carried out in autumn 2009, 2011 and 2012.

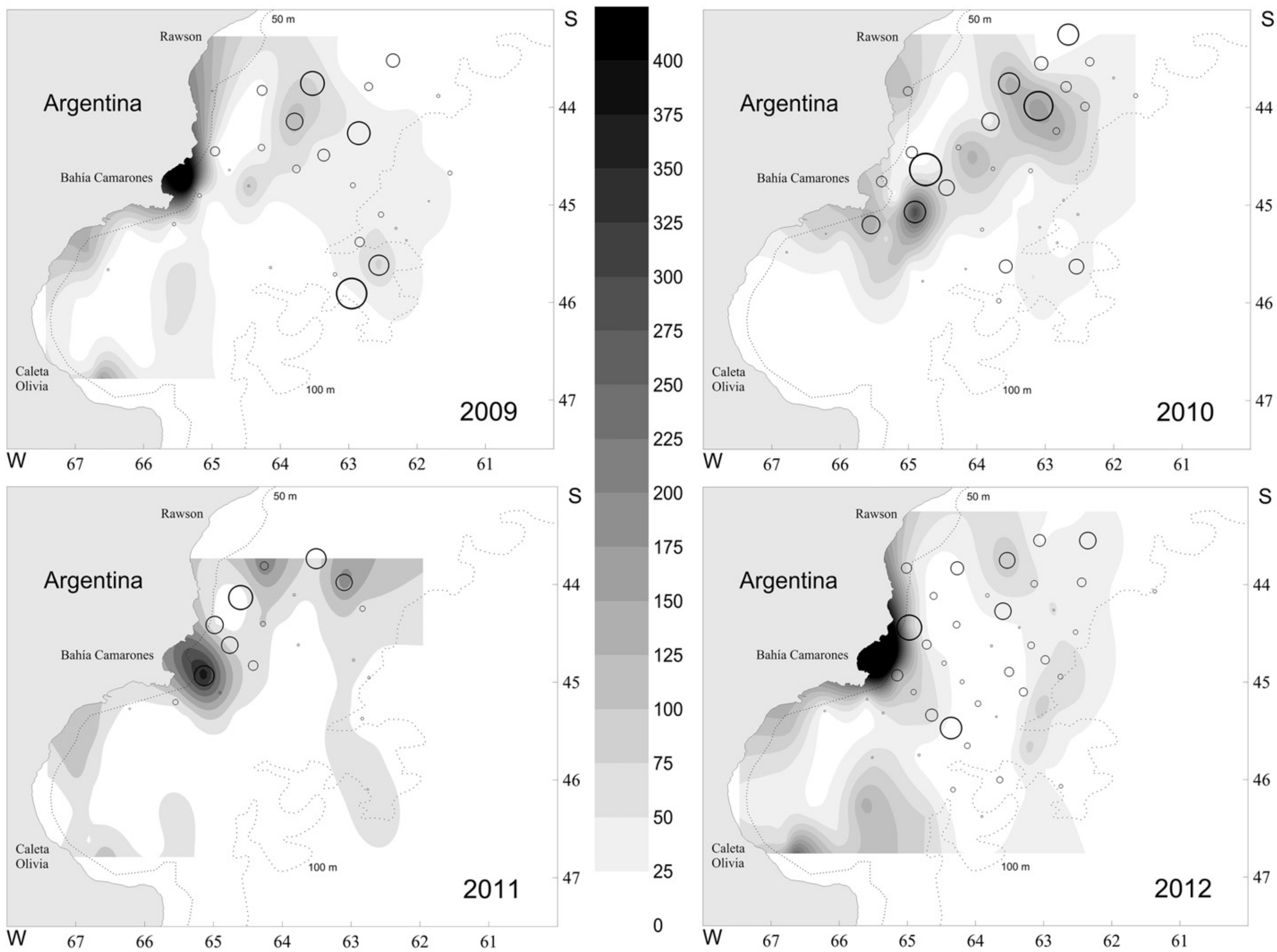

Fig. 3. *Merluccius hubbsi* abundance and spatial distribution of spawning females from the Southern stock. Symbols are proportional to percentage of females with hydrated oocytes or with POF 1 day (between 0% and 100%). Vertical shaded scale represents density (tonnes/nautical mile^2) of total hake estimated from each trawl surveys carried out in summer 2009, 2011 and 2012.

3.2. Spawning frequency

The spawning frequency was estimated from the mean proportion of females with day 1 POF sampled during the main reproductive peak of the Northern (May) and Southern (January) hake stocks in the period 2009–2012. During May 2009, 2011 and 2012, the proportions of females with day 1 POF were 0.07, 0.12 and 0.09, respectively. These results would indicate that Argentine hake spawned once every 8 to 10 days during May 2011 and 2012 (about 3 spawnings per month), while in 2009 the average interval between spawning was about 13 days during May (Table 3). Spawning frequency showed no statistical differences ($P > 0.05$) during the main reproductive peak within each stock.

In case of the Southern group, the daily proportion of spawning females during January 2009 was higher (0.19) than in 2010 (0.16), 2011 (0.15) and 2012 (0.15). These results would indicate that females of this stock spawned once every 5 to 7 days between January 2009 and 2012. Despite the variation observed between years, spawning frequency of the Southern hake was always higher than that estimated for the Northern stock (Table 3).

Table 2
Abundance (million) of active females and mean density (tons/nautical mile^2) of *M. hubbsi* estimated from different years and both stocks during the main peak of spawning.

Year	Northern stock		Southern stock	
	Abundance of active females	Mean density	Abundance of active females	Mean density
2009	9	3.24	341	52.36
2010	—	—	456	64.77
2011	10	3.25	302	41.07
2012	26	4.71	544	65.16

3.3. Fecundity

Batch fecundity obtained for the Argentine hake of the Northern stock during May 2009, 2011 and 2012 ranged between 74,244 and 2,716,655 hydrated oocytes for females between 30 and 89 cm TL. Batch fecundity obtained for the Southern stock during January 2009, 2010, 2011 and 2012 ranged between 40,673 and 2,674,279 hydrated oocytes for females between 29 and 95 cm TL. The analysis of covariance applied to compare the coefficients of the relationship of BF to TL obtained for each year by stock did not show statistical differences ($P > 0.05$); therefore, data from each hake stock were pooled to estimate all the regression analyses. Regarding the comparison between hake stocks, the analysis of covariance between the relationships BF to TL also did not show statistical differences ($P > 0.05$). In both stocks the relationship between BF and TL was curvilinear, fitting better to a power

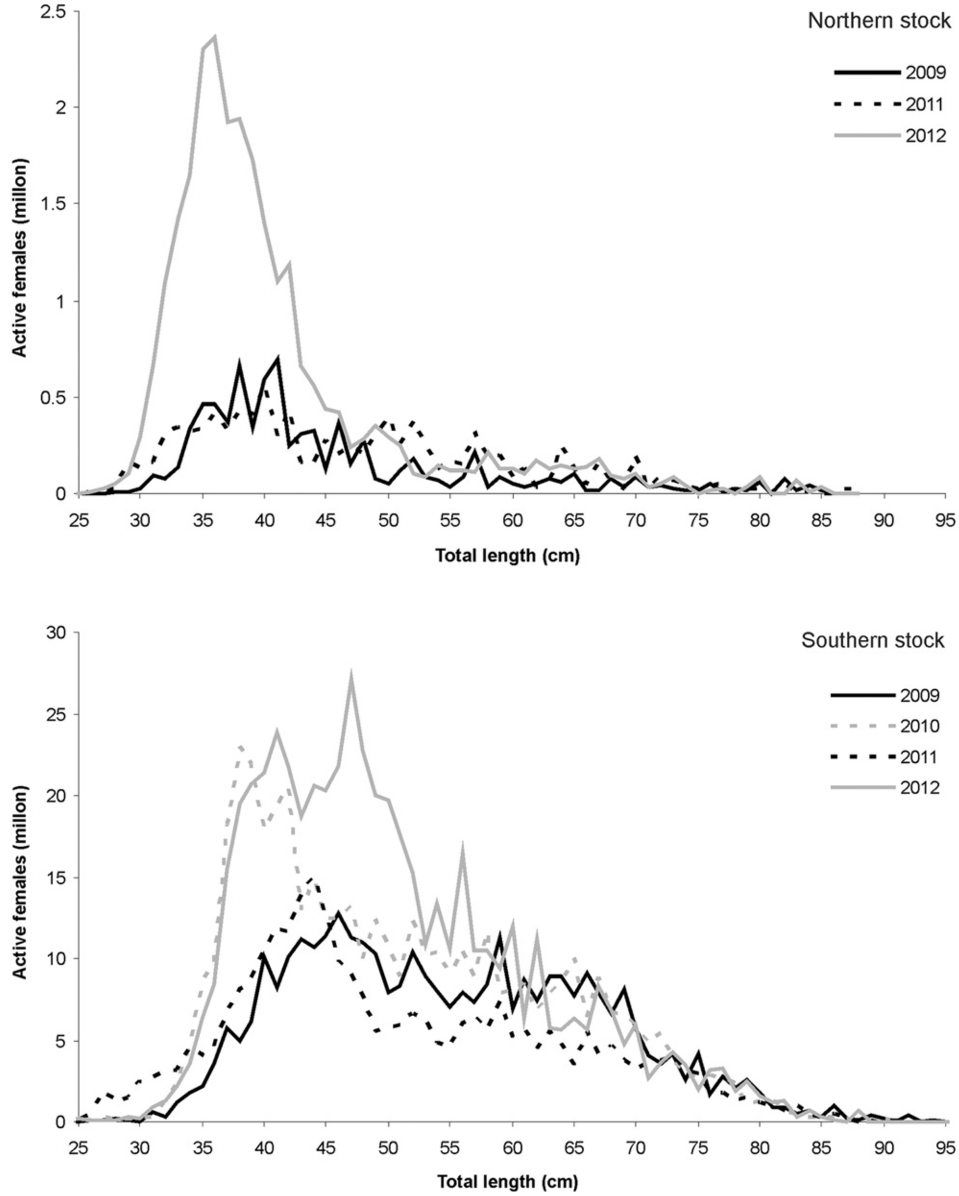

Fig. 4. Number of *M. hubbsi* active females by length class obtained for the Northern and Southern Argentine hake stocks in the main peak spawning of each group, between 2009 and 2012. Note the different scale on the *y*-axis.

model (Fig. 5A), and the relationship of BF to GW was linear (Fig. 5B). A positive power relationship was observed between BF and the HSI for both stocks (Fig. 5C), but values of the coefficient of determination were low, especially for the Northern stock, explaining about 13% of the variance. In the case of BF and Kn no significant relationships were observed.

Table 3
Number of trawls, number of *Merluccius hubbsi* mature females (histologically staged), number of postovulatory follicles (day 1 POF)/to estimate the spawning frequency (days between partial spawnings) in the Northern and Southern area. POF: postovulatory follicles, PD: daily proportion of spawning females, CV: variation coefficient.

Stock	Year	Trawls	Mature females	Day 1 POF	PD	CV	Spawning frequency
Northern	2009	21	282	29	0.07	0.31	13
	2011	20	303	21	0.12	0.20	8
	2012	21	294	25	0.09	0.23	10
Southern	2009	35	708	138	0.19	0.09	5
	2010	40	824	129	0.16	0.12	6
	2011	33	565	85	0.15	0.13	7
	2012	41	859	131	0.15	0.22	7

Relative fecundity estimates for Argentine hake females from the Northern stock obtained during May 2009, 2011 and 2012 ranged between 243 and 916 hydrated oocytes g^{-1} (female weighed without ovaries), and RF for females from the Southern stock estimated during January 2009, 2010, 2011 and 2012 ranged between 86 and 1115 hydrated oocytes g^{-1}. The two-way ANOVA applied to examine the main effect of the years and stocks on RF did not show significant differences ($P > 0.05$), with mean values of 526 hydrated oocytes g^{-1} (standard deviation [SD] 142) and 530 hydrated oocytes g^{-1} (SD 185) estimated for the Northern and Southern stocks, respectively. Power significant relationship ($P < 0.01$) between RF and GW, and positive linear relationships between RF and the morphophysiological variables of TL, HSI, and Kn were obtained, but the coefficients of determination were low for all regressions, explaining in some cases 4% or 5% of the variance (Table 3). The highest determination coefficients ($r^2 = 0.11$ and 0.10 for the Northern and Southern stocks, respectively) were obtained with the relationship RF vs. HSI (Table 4).

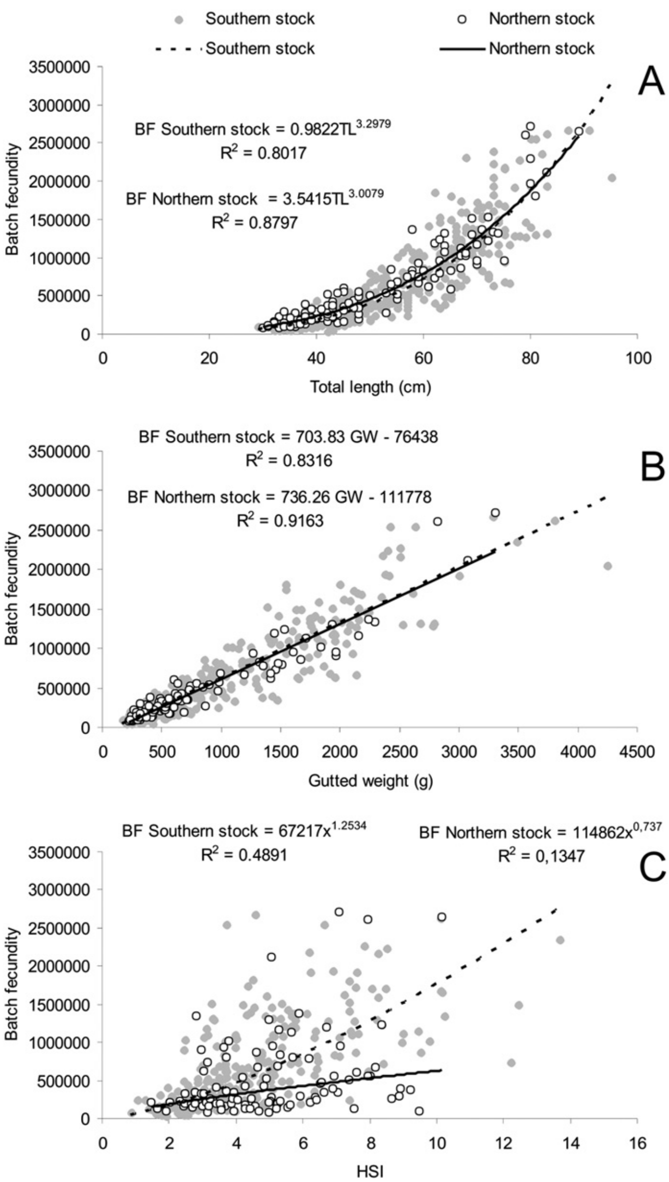

Fig. 5. Batch fecundity as a function of total length (A), gutted weight (B), and hepatosomatic index (HSI) (C), for Northern and Southern stocks of *M. hubbsi*, which were sampled during the peak spawning between 2009 and 2012.

3.4. Oocyte dry weight

The dry weight (DW) of 100 hydrated oocytes estimated from spawning females of the Northern stock collected during May 2009, 2011 and 2012 showed no significant differences among years ($P > 0.05$). DW ranged from 2.3 to 4.05 mg, with a mean value of 3.08 mg (SD 0.37). In case of DW of females from the Southern stock there were differences between January 2012 and the other years analyzed ($P < 0.01$). In 2012, DW ranged between 2.25 and 3.87 mg with a mean value of 3.0 mg (SD 0.29), being significantly higher than the values obtained for January 2009, 2010 and 2011 all together (from 1.8 to 3.95 mg with a mean value of 2.84 mg [SD 0.35)]). It was determined that the oocyte dry weight of females from the Northern stock was significantly higher than that of females from the Southern group for the same size range (31–83 cm), excluding from this analysis data from January 2012 ($P < 0.0001$).

There were a weak but positive relationship between DW and all morphophysiological variables considered during this study: TL, GW, HSI, and Kn, except between DW and Kn from females of the Northern stock (Table 5).

3.5. Egg production

The egg production values estimated for the main peak spawning of the Northern hake stock in May 2009, 2011 and 2012 were 9×10^{12}, 19×10^{12} and 22×10^{12} respectively. In 2009 production was much lower than in the following years, but this difference would be related to the size structure of active females, since the production depended almost exclusively of younger females, smaller than 50 cm TL (Fig. 6A). During 2011, a high proportion of the egg production depended on spawners larger than 50 cm TL (Fig. 6A). In May 2012 a greater production of young adult females (<50 cm TL) was recorded, but it was also observed a second peak between 65 and 70 cm TL (Fig. 6A).

The egg production values estimated for the Southern stock of Argentine hake in January 2009, 2010 and 2012 were 1295×10^{12}, 1073×10^{12} and 1208×10^{12} eggs respectively, while in January 2011 the production was lower (692×10^{12}). Even so, the Southern stock generates an average egg production between 1 and 2 orders of magnitude higher than the Northern hake stock during the peak spawning. Fig. 6 shows that egg production of the Southern stock during all years analyzed depended mostly on females larger than 50 cm TL. In general during January 2011 and 2012 the levels of production by length class were similar in the size range 45–76 cm TL, but in 2010 a slight increase between the size classes 61 cm and 69 cm TL was observed. During 2009, the contribution to the reproductive potential of the largest females was even higher (Fig. 6B).

4. Discussion

The western continental shelf of South America, where the Argentine hake is distributed, has a relatively narrow (70 km) eastern side (22°S Cabo Frio, Brazil) and it gets progressively wider southward (55°S Burdwood Bank, Argentina), where it reaches a maximum width which is close to 850 km. This wide submarine terrace is the most notable bathymetric characteristic of South America and constitutes the largest continental shelf within the southern hemisphere (Bisbal, 1995). These differences in the shelf bathymetry are certainly

Table 4
Results of the regression analyses between relative fecundity (RF) and the variables: total length (TL), gutted weight (GW), relative condition factor (Kn), and hepatosomatic index (HSI), for the Northern and Southern stock of *M. hubbsi*, which were sampled during spawning peak between 2009 and 2012. r^2: coefficient of determination; a and b: equation parameters, *n*: sample size, *P*: *P*-value of the relationship.

	Northern stock				Southern stock			
RF vs.	TL	GW	Kn	HSI	TL	GW	Kn	HSI
Relationship	Linear	Power	Linear	Linear	Linear	Power	Linear	Linear
r^2	0.04	0.08	0.07	0.11	0.05	0.09	0.04	0.10
a	1.91	0.11	460.56	24.41	3.04	0.16	398.16	28.39
b	430.74	236.38	51.74	392.24	363.40	162.64	128.08	404.69
n	140	99	99	99	371	279	279	279
P	<0.05	<0.01	<0.05	<0.001	<0.001	<0.001	<0.001	<0.001

Table 5
Results of the regression analyses between oocyte dry weight (DW) and the variables: total length (TL), gutted weight (GW), hepatosomatic index (HSI) and relative condition factor (Kn) for both stocks of *M. hubbsi*. Samples were taken in May 2009, 2011 and 2012 for the Northern stock, and in January 2009, 2010 and 2011 for Southern stock. r^2: coefficient of determination; a and b: equation parameters, *n*: sample size, *P*: *P*-value of the relationship.

	Northern stock				Southern stock			
DW vs.	TL	GW	Kn	HSI	TL	GW	Kn	HSI
Relationship	Power	Power	Linear	Linear	Power	Power	Linear	Linear
r^2	0.12	0.12	0.03	0.12	0.13	0.17	0.05	0.12
a	0.15	0.06	0.76	0.06	0.18	0.07	0.82	0.08
b	1.68	2.15	2.33	2.80	1.36	1.71	2.01	2.49
n	154	100	100	100	230	181	181	181
P	<0.001	<0.01	0.07	<0.001	<0.001	<0.001	<0.01	<0.001

reflected in the dimensions of the reproductive area of each Argentine hake stock, since, as it has been demonstrated in this study, spawning females of both stocks are generally concentrated in waters between 50 and 100 m depths. The main reproductive area estimated for the Northern stock was significantly smaller than the one obtained for the Southern group (23,770 km^2 and 52,460 km^2, respectively). The first one was located between 35° and 38 °S and the second one between 43°30′ and 46°S. Despite the spatial and seasonal differences in reproduction of both hake groups, it has been observed that some of the physical characteristics of the environment during the spawning are similar in both stocks (Macchi et al., 2010; Rodrigues and Macchi, 2010). These authors have reported that the main spawning schools of hakes from

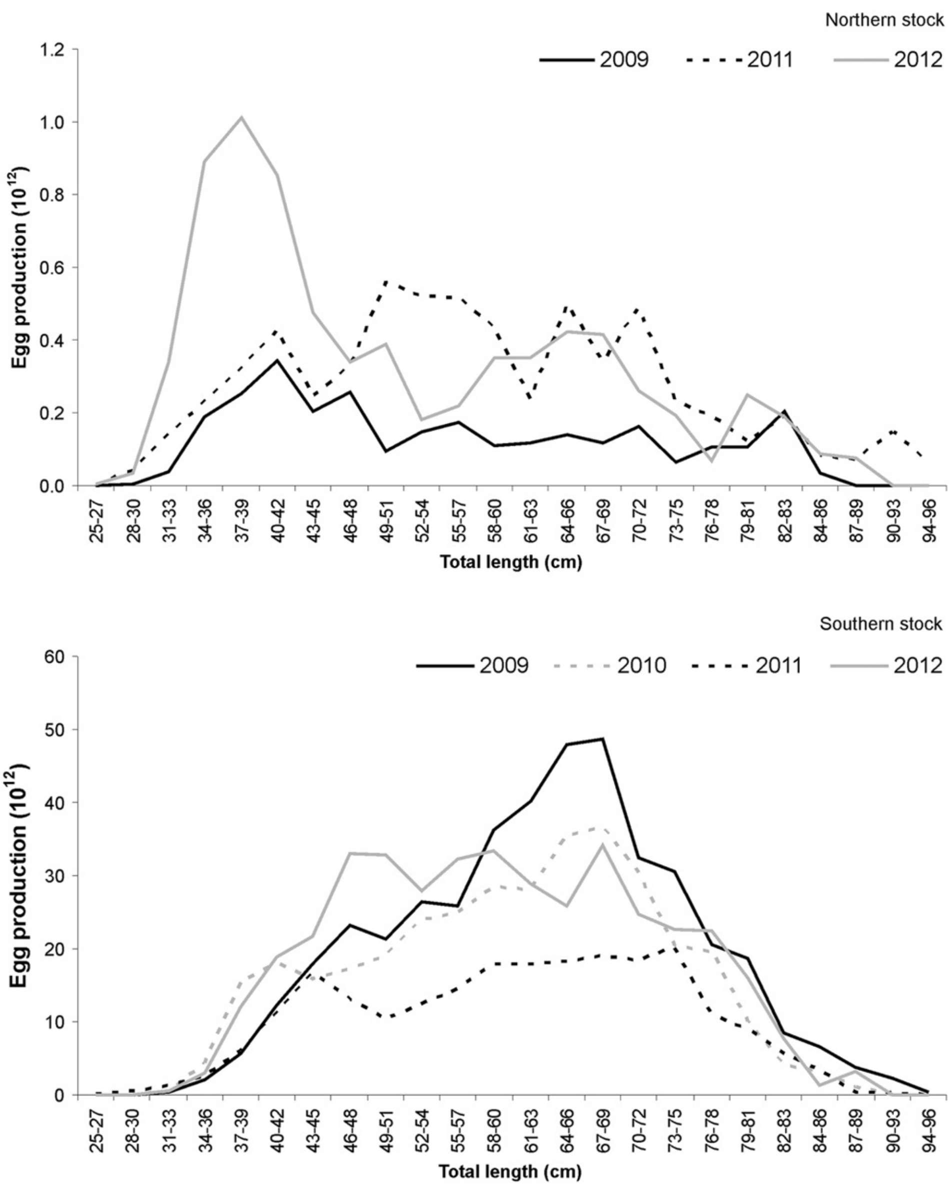

Fig. 6. Total egg production per 3 cm length class estimated for *M. hubbsi* during the main reproductive peak of the Northern and Southern hake stocks, between 2009 and 2012.

both stocks coincide from a spatial point of view with a bottom thermal front, within a range of temperatures between 9 °C and 14 °C, and salinities between 33.2 and 33.7.

The analysis of the oceanographic features in the spawning and nursery areas of fish populations is fundamental to understand the variations of the recruitment, since in most cases the success of this process is essentially based on the physical attributes that define the spawning areas and promote the egg and larvae retention (Iles and Sinclair, 1982; Sinclair, 1988; Sinclair and Iles, 1985). In the case of *M. hubbsi* from the Argentinean Sea, the main spawning areas in general are spatially coincident with the ones that show the greater concentration of larvae and postlarvae of this species. A nursery area has been recorded for the Northern stock, which covers the 50 and 100 m isobaths, southern of 37°S, and extends all the way to the 200 m isobath to the north of that latitude, where the shelf narrows (Ehrlich, 2000; Ehrlich et al., 2013). It has been reported that one of the retention mechanisms in the breeding area of the Northern stock could be the Ekman transport to the coast, present all year round but specially during winter, when the postlarvae and juveniles of hake are found (Ehrlich, 2000). Regarding the Southern stock, the reproduction occurs near a front system produced as a result of the tides dynamics, characterized by a high biological productivity (Carreto et al., 1986; Mianzan and Guerrero, 2000; Ramírez et al., 1990; Viñas and Ramírez, 1996). The spawning area, as mentioned before, coincides spatially with the greatest concentrations of larvae and postlarvae of the species (Ehrlich and Macchi, 2003), where the existence of strong retention mechanisms has also been suggested during the spawning season of the hake (Álvarez Colombo et al., 2011).

The relationship between the location of spawning females and the spatial distribution of hake schools demonstrated different patterns between the two stocks of this species. In January, during the peak reproductive activity of the Southern group, Argentine hake was concentrated in the North Patagonian area at depths below 100 m, where the main aggregations of hake in spawning stage were also observed. On the other hand, during the reproductive season of the Northern stock (May), the spawning females were also concentrated in coastal areas (close to 50 m depths), yet separated from the greater concentrations of Argentine hake, which were detected at greater depths, outside the 100 m isobath. This difference in the spatial distribution of the hake aggregations between stocks was also reflected in the abundance of active females within the spawning areas. The Patagonian stock showed values up to 30 times higher than the ones estimated for the Bonaerense group. These differences could be partly associated with the fact that the Northern group has been subjected to a more intensive commercial exploitation throughout the years in comparison to the Southern hake stock. Fishing activity in the Bonaerense region began in the 1960s by both the Argentine and Uruguayan commercial fleets. After 1973, an expansion took place toward fishing grounds in the Patagonian waters. For the second half of the 1980s, there was a decreases in the fishing activity north of 41°S caused by a decline in abundance (Giangiobbe et al., 1993), and finally, by the mid-1990s, both stocks of hake were considered overexploited. For this reason, since 1997 an extensive year-round fishing closure was established in Patagonian waters to protect Argentine hake juveniles and spawners of the Southern stock (Macchi et al., 2005; Alemany et al., 2013). These authors concluded that the permanent closed area, only established for the Patagonian region, would have a positive effect in this hake stock, increasing its abundance and rebuilding the size structure. In case of the Northern hake stock, since 1992 seasonal closures have been implemented for the preservation of juveniles (Rey et al., 1996; Bezzi and Tringali, 2003), but at present it has not been established yet a permanent closed area to protect spawners.

As a consequence of overexploitation it has been reported that the total and reproductive biomasses of the Northern stock have decreased 77% and 85% respectively since 1986 (Irusta and D´Atri, 2013). The Southern stock of Argentine hake also showed a reduction of the biomass during these years, yet much less significant, between 10% and 20% of what it was estimated in the early 1990s (Aubone et al., 2000; Santos and Villarino, 2013). There have also been recorded changes in the structure of the ages and sizes of both stocks, with a tendency to extinction of the groups with the largest size, mainly in the Bonaerense area (Aubone et al., 2000; Irusta and D´Atri, 2013). In fact, the analysis of the size distribution of active females from 2009 to 2012 showed differences between both stocks. The Northern stock was characterized by a greater presence of active young females (<50 cm TL) regarding the Southern stock. This pattern registered at present is very different to the one observed for this stock during the 1980s (Ubal et al., 1987), thus, the evident decrease of spawning individuals of larger size could be associated with the overexploitation of this resource. In general, it has been observed that the size and age of spawners can affect the reproductive activity; the largest, and generally oldest, individuals start the spawning period earlier and have longer reproductive seasons (Trippel et al., 1997; Macchi et al., 2004), so the changes in the size structure could have consequences in the extension of the reproductive period and its synchronization with the peaks of planktonic production (Kjesbu et al., 1996).

In addition to the spawning season, some reproductive parameters such as the spawning frequency, fecundity and quality of the eggs, may show variations depending on the maternal characteristics such as the size, age or condition factor (Fitzhugh et al., 2012; Marshall et al., 2003). These parameters may change between stocks of the same species, but also within the same stock when the size or age structure changes, modifying its reproductive potential (Marshall et al., 2003). In some species it has been reported that the spawning frequency increases with the size of the individuals (Claramunt et al., 2007), while in the Southern stock of hake it has also been observed that this parameter changes during the spawning season (Macchi et al., 2004). When considering the estimations provided during the reproductive peak of both Argentine hake groups, there were no significant differences within each stock (8 to 13 days for the Northern stock and 5 to 7 days for the Southern group). However, there were noticeable differences between stocks, with lower frequency values for the Northern hake group (1 to 3 spawnings by month) in comparison with the Patagonian stock (around 5 spawnings by month). These differences are due to the low daily proportion of spawning females obtained for the Northern stock, which again could be associated to the lower abundance of active females observed during May.

Unlike the spawning frequency, partial and relative fecundity estimated during the reproductive peak of both hake groups were similar. Batch fecundity ranged between 74,244 and 2,716,655 hydrated oocytes for the Northern stock and between 40,673 and 2,674,279 hydrated oocytes for the Southern one (sizes ranging between 30–89 cm and 29–95 cm, respectively). This variable showed a positive relationship with most of the maternal characteristics analyzed (total length, gutted weight and HSI) for both stocks but it was not observed a significant relationship between batch fecundity and female condition expressed by the Kn index. The batch fecundity values estimated for the Northern stock were greater than the ones obtained during the 1980s and the 1990s (Christiansen et al., 1986; Louge, 1996) but, probably since these authors used samples collected at the end of the spawning season, when the fecundity values tend to be lower (Macchi et al., 2004). Relative fecundity estimated for both spawning groups was similar and the means were calculated in 526 (SD 142) and 530 (SD 185) oocytes per female gram (without ovaries) for Northern and Southern stocks respectively. This variable showed a significant positive relation with total length, gutted weight, the Kn and the HSI of the spawners, although the percentage of variability explained by the models was extremely lower in all cases.

Regarding the spawning quality evaluated using the dry weight of the hydrated oocytes, there were no statistical differences between samples collected during the different years analyzed for the Northern stock. In the case of the Southern group, there was difference only with the samples collected in 2012, so this year was excluded from the comparison between stocks. This analysis showed significant differences between both stocks, being the average dry weight of 100 hydrated oocytes larger in the females from the Northern stock (3.08 mg) in comparison to the Southern one (2.84 mg). It has been established that the dry weight of the oocytes increases with the size of the females and the HSI, so the differences observed between the stocks, being the sizes similar, could be related to the condition of the individuals. Macchi et al. (2006) reported that the dry weight of the oocytes in *M. hubbsi* from the Patagonian region increases with the size and age of the spawners, which was later observed in *M. merluccius* from Galicia (Mehault et al., 2010). Some authors consider that larger eggs are better, since they have more quantity of yolk, which provides more energy to produce larger larvae with higher survival rates (Chambers and Waiwood, 1996; Fuiman and Werner, 2002; Hinckley, 1990; Lambert and Dutil, 2000; Marteinsdottir and Steinarsson, 1998; Nissling et al., 1998; Ouellet et al., 2001; Trippel, 1998; Wootton, 1994). Another component related to the egg quality is the oil droplet, if present, due to its role as energetic reserve during the initial development of the larvae (Rodgveller et al., 2012; Wiegand, 1996). Recently, it has been reported that in *M. hubbsi* from the Patagonian stock, the diameter of the oil droplet increases with the size of the females (Macchi et al., 2013), which strengthens the hypothesis about the existence of the maternal effect in this species.

The variation in the size structure and biomass of the spawning specimens, the fecundity and the spawning frequency determine the total egg production of the stock (Cardinale and Arrhenius, 2000; Kjesbu et al., 1996). Regarding the Northern stock of hake, the egg production estimated during May, considered the reproductive peak, ranged between 9×10^{12} and 22×10^{12} oocytes. In May 2009 it was observed the lowest production value, may be, due to the fact that it depended almost exclusively on the younger spawners (<50 cm TL), corresponding to ages between 3 and 4 years (Renzi et al., 2009). The egg production values obtained for the Southern hake stock during their reproductive peak were in average between 1 and 2 magnitude orders larger than the ones calculated for the Northern hake group. There were registered values between 692×10^{12} and 1295×10^{12} oocytes, that would correspond mainly to females larger than 50 cm TL, that is to say with ages between 4 and 8 years (Renzi et al., 2009). These values were similar to the ones reported by Macchi et al. (2004), who documented a total egg production of 855×10^{12} oocytes in January 2001, this being the most productive month for that spawning season, that depended mainly on the females between 45 and 73 cm TL.

The results found show the great difference in the reproductive potential of both stocks of Argentine hake. This difference is partly due to the great abundance of breeding specimens in the Patagonian region during the summer spawning peak, which shows a concentration strategy that could be related to the existence of a frontal system in this waters (Macchi et al., 2010). This characteristic, along with the size structure dominated by larger individuals, could cause a higher spawning frequency and egg production of the Patagonian stock. Moreover, the influence of maternal characteristics on the quality of the eggs produced suggests that the larger females (>50 cm TL) may origin larger larvae with better chances of survival. The combination of these factors, along with the productivity and the retentive characteristics showed for the North-Patagonian zone (Álvarez Colombo et al., 2011), may justify the abundance and reproductive potential of the Southern stock.

The main spawning and nursery area of the Northern hake stock does not show the same oceanographic conditions that characterize the larvae retention mechanism suggested for the Patagonian stock. This fact, along with the low values of abundance of active female obtained during May and in other months of the reproductive season (Louge, 1996; Pájaro et al., 2007; Rodrigues and Macchi, 2010), leads us to hypothesize that there may be not a pronounced spawning peak during the reproductive season of this hake stock. This feature could be an adaptive response in their spawning strategy that would avoid concentrating the main reproductive activity in a short period of time, reducing, in that way, the effect of certain high mortality events (Cushing, 1972, 1990; Mertz and Myers, 1994).

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