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Research Paper

Maternal condition, fecundity and oocyte quality of Argentine hake (*Merluccius hubbsi*) from the Northern stock

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ABSTRACT

The influence of the condition of spawning females on fecundity and oocyte quality, measured using morpho-physiological and biochemical indices, was analyzed for the Northern stock of Argentine hake (*Merluccius hubbsi*). First the relationships between morpho-physiological and biochemical indices were analyzed, and if they were influenced by female size. Samples of spawning-capable females were collected during the main reproductive peak of this stock in May 2011.

The hepatosomatic index (HSI) in *M. hubbsi* was a good indicator of lipid concentration for both the liver and muscle. HSI and the relative condition factor (Kn) were independent of female size. Muscle protein content was positively associated with maternal attributes. Relative fecundity ranged between 287 and 916 hydrated oocytes g^{-1} and showed significant positive relationships with GSI and Kn. The dry weight of hydrated oocytes (n = 100) ranged between 2.65 and 4 mg and was positively related with the HSI. The oil droplet diameter of hydrated oocytes varied between 250 and 292 µm and was also positively related with HSI, Kn, liver and muscle lipid content, suggesting that it could be a good indicator of the nutritional condition for hake females of the Northern spawning stock.

1. Introduction

The energy available to animals has to be allocated among maintenance, somatic growth, and reproduction (Callow, 1985; Sibly and Calow, 1986), and depending on their distribution has been correlated with changes in energy density of different organs (Lucas, 1996). An immature female uses assimilated energy for metabolism and growth; however, when gonadal maturation begins some of that energy is intended for oocyte development and reproductive behavior. It has been observed that energy reserves change during the spawning season (Lucas, 1996). The amount of energy allocated to growth and reproduction depends on a number of factors, some of them intrinsic (genetic, physiological), while others are environmentally driven (temperature and feeding) (Saborido-Rey and Kjesbu, 2005). Since the reproductive process imposes substantial metabolic demands on fish, regardless of gonadal development pattern (Balon, 1975; Tyler and Sumpter, 1996), those of higher condition are expected to have greater probabilities of survival and future reproductive success (Johnston et al., 2007). The term "condition" is widely used in ecological studies to refer to the state of an animal's general health, or more commonly, its energy or nutrient reserves (Peig and Green, 2009; Schulte-Hostedde et al., 2005). A high body condition (i.e., high energy or nutrient reserves) is thought to be a direct consequence of an animal's ability to acquire resources (Baker, 1989), which can then be used to meet its energetic demands. Females in poor body condition at the beginning of the spawning season could diminish their reproductive capacity, increasing their vulnerability and therefore natural mortality (Dutil and Lambert, 2000; Wootton, 1990). Maternal attributes and condition affect fish maturity (Marteinsdottir and Begg, 2002; Morgan and Lilly, 2006), fecundity and egg production (Lambert and Dutil, 2000; Marshall et al., 2006) and offspring viability (Berkeley et al., 2004; Brooks et al., 1997). In summary, maternal attributes and condition affect the stock reproductive potential, so they should be included in assessment models (Morgan, 2008).

The condition of fish can be evaluated using several criteria, ranging from simple morphometric measurements (length – weight relationship or K) to physiological (hepatosomatic-HSI index) and biochemical measurements (proximate composition, such as lipids, proteins, and other components in tissues). Another index commonly used is the gonadosomatic (GSI) which gives an idea of the fish mature state. Morphometric indices, which assume that heavier individuals of a given length are in better condition than the leanest individuals, are simple

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indicators of energy storage, and are widely used because they are constructed from simple weight and length data (Lloret et al., 2002). Although physiological condition indices, such as the liver index, estimate the energy reserves of fish more accurately than morphometric information, a more precise approach to describe fish condition is given by biochemical indices, such as lipid and protein content (Sargent and Henderson, 1986; Shulman and Love, 1999). Lipids are good indicators of energy reserves, i.e., health, because they are high in energy density (Iles, 1984), are labile (Bilinski, 1968), are a key constituent of eggs (Kaitaranta and Ackman, 1981), and are correlated with the magnitude of protein reserves (Bradford, 1993). There are fluctuations of biochemical components within the same species that could be associated with different factors: age, sex, gonadal development, migration stage, nutritional condition, spatial location, and other factors (Akpinar et al., 2009; Leonarduzzi et al., 2014; Rodrigues et al., 2013a; Rueda et al., 1997; Shearer and Swanson, 2000). Knowledge about parental stock condition could help to understand the recruitment variations observed on the natural populations (Scott et al., 1999).

Argentine hake (*Merluccius hubbsi*) is a demersal species distributed from 22° to 55° S at depths between 50 and 500 m (Cousseau and Perrotta, 2013). The Northern stock inhabits the waters of the Argentine Uruguayan Common Fishing Zone (CFZ, 34°30′–39°30′ S) up to 41° S. Besides this species, other important coastal and high seas fisheries, such as the whitemouth croaker (*Micropogonias furnieri*) and the anchovy (*Engraulis anchoita*) reproduce in this region. CFZ is also notable for its importance as a spawning and breeding area for several fish species (Militelli et al., 2013; Pájaro et al., 2011; Rodrigues et al., 2013b).

Fishing pressure plays an important role removing larger and older individuals from the spawning stock with the consequent effect on reproductive potential. *Merluccius hubbsi* of the Northern stock has experienced a drastic decrease in biomass as a consequence of overexploitation since the 1990s (Aubone et al., 2000; Irusta and D'Atri, 2013). Besides the decrease in abundance, changes have been recorded in length and age structure It was observed that individuals smaller than 35 cm of total length (TL) are the most frequently found in commercial captures (Irusta and D'Atri, 2013), being size at maturity 26.8 cm TL for hake males and 29.3 cm TL for females (Rodrigues and Macchi, 2010). This scenario clearly indicates a negative trend in the population composition of this stock, which could lead to the disappearance of larger individuals (Aubone et al., 2000).

This stock shows a protracted spawning season during fall and winter, with the main peak in May, mostly north of 38°30′S. Argentine hake is a batch spawner with indeterminate annual fecundity (Macchi et al., 2004); for this type of reproductive strategy, the number of spawning events would be affected by the nutritional quality of the food, temperature, and other environmental factors (Wootton, 1990). This fact and the negative trend in the population composition may have consequences on the reproductive potential of the Northern hake stock. As was reported for this species, egg production is influenced by age and size composition of the population (Macchi et al., 2004; Rodrigues et al., 2015). As occurs in the Southern hake stock, larger females have a longer spawning season (Macchi et al., 2004), oocyte dry weight increases with female size (Macchi et al., 2006), and the oil droplet diameter in hydrated oocytes also increases with female size (Macchi et al., 2013).

Since reproductive potential is the starting point in the recruitment process (Solemdal, 1997), it is essential to establish how the nutritional condition of spawners affects its ability to produce offspring. Consequently, the goal of this research was to analyze the relationship among condition of spawning females, estimated from morpho-physiological and biochemical indices, and fecundity and oocyte quality, determined from the dry weight, diameter and oil droplet diameter of hydrated oocytes during the main reproductive peak of the Northern hake stock. To achieve this objective the following relationships were analyzed: (1) Morpho-physiological versus biochemical indices; to check if the simple condition indices reflect the nutritional status, (2) Maternal condition indices versus females attributes, to check for influence with size (3) Maternal condition indices versus fecundity and oocyte quality.

2. Materials and methods

Samples of *M. hubbsi* females (n = 41) were obtained in the Argentine Uruguayan Common Fishing Zone (CFZ) during a research survey conducted by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) during the reproductive peak of the Northern Argentine hake stock in May 2011 (Fig. 1). Argentine hake specimens were captured at depths between 50 and 300 m using a bottom trawl with a mouth width of approximately 20 m, a height of about 4 m, and with a 20 mm mesh size at the inner lining of the codend.

For this study, only spawning capable females were selected, i.e., those that had ovaries with hydrated oocytes, corresponding to stage 3 of a visual maturity key of five stages: (1) immature, (2) developing, (3) spawning capable, (4) regressing, and (5) regenerating (Macchi and Pájaro, 2003; Brown-Peterson et al., 2011). For each specimen, the following measurements were recorded: total length (TL) in centimeters, gutted weight (GW), liver weight, and gonad weight in grams. Due to hake exhibit a high growth rate, indeterminate fecundity, and a protracted spawning season, a short sampling period was chosen to minimize the energy expenditure of adults due to reproduction.

One ovary per specimen was preserved in 10% formalin for histological processing in the laboratory, which consisted of dehydration in ethyl alcohol, clearing in xylene, and embedded in paraffin. Sections were cut at approximately 5 μm and stained with Harris' hematoxylin, followed by eosin counterstain. Histological staging of ovaries was based on the stage of oocyte development (Wallace and Selman, 1981), the postovulatory follicles (POF), and atresia occurrence (Hunter and Goldberg, 1980), following the classification described for the Southern stock of Argentine hake (Macchi et al., 2004).

Gonadosomatic index (GSI) and the condition indices, hepatosomatic (HSI) and relative condition factor (Kn), were calculated for all sampled females. The 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). Gonadosomatic and

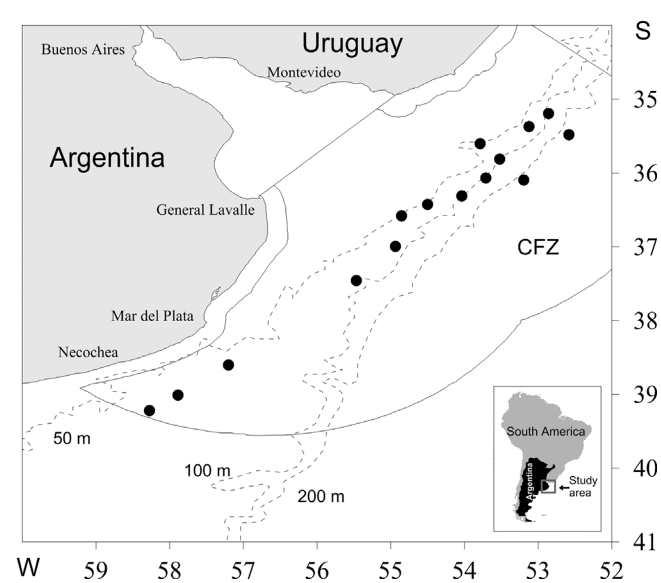

Fig. 1. Spatial distribution of demersal trawl stations in the spawning area of *M. hubbsi* in the Argentine-Uruguayan Common Fishing Zone (CFZ) during May 2011.

condition indices (HSI, Kn) were defined by the following equations:

$$GSI = \frac{Gonad\ weight}{Gutted\ weight} \times 100 \quad HSI = \frac{Liver\ weight}{Gutted\ weight} \times 100 \quad Kn = \frac{Gutted\ weight}{0,017 * LT^{2,75}} \times 100$$

The muscle (fillet without skin), one gonad (ovary), and liver were dissected from each specimen sampled and preserved in a frozen state at −22 °C, stored in vacuum-sealed plastic bags until their analysis in the laboratory. These tissues were analyzed for lipids and protein content (content refers to percentage of wet weight tissue). To determine lipid content, sub-samples from frozen samples of different weights were taken according to each tissue type: muscle (10–20 g), gonads (5–10 g), and liver (3–5 g). This component was extracted by the Bligh and Dyer method modified by Undeland et al. (1998), and was gravimetrically quantified by the Herbes and Allen (1983) method. Protein content was determined from frozen tissue (1 g) using bovine serum albumin (BSA) concentrated at 1 mg/ml as a standard and following the protocol of Lowry et al. (1951). Carbohydrate content was not measured because that component is generally low in marine species and its contribution to total energy content is close to zero (Anthony et al., 2000).

To determine the number and quality of oocytes to be released by spawning capable females, the following variables were estimated: relative fecundity, dry weight, and oil droplet diameter of the hydrated oocytes. Relative fecundity (RF: number of hydrated oocytes per gram of ovary-free body weight) was used instead of batch fecundity (BF: number of oocytes released per spawning) because the latter is related to female size (total length and gutted weight) and may bias other relationships. Relative fecundity was estimated gravimetrically with the hydrated oocyte method on fixed ovarian samples (Hunter et al., 1985), using only ovaries showing no evidence of recent spawning (i.e., no new POFs, n = 38). To estimate RF, batch fecundity was first determined. Three pieces of ovary of approximately 0.1 g each one were sampled from the anterior, middle and posterior sections of each gonad; each was weighed (± 0.1 mg) and the number of hydrated oocytes counted. BF was the product of the mean number of hydrated oocytes per unit of ovarian weight and total ovarian weight. Finally, RF was calculated as the BF divided by female weight, excluding the ovary weight.

To obtain the dry weight of hydrated oocytes (DW), a sample of 100 oocytes was removed from each gonad (n = 41); 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. DW was considered an index of egg quality for the spawning hake 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 were aware that this procedure to determine oocyte dry weight is biased due to losses during storage in formaldehyde (Hislop and Bell, 1987), it was the only option for ovaries preserved at sea and the best available for our application. Oocyte and oil droplet diameters of hydrated ovaries (n = 30) were measured to the nearest 0.01 μm. The oil droplet diameter (ODD) was measured because the oocyte diameter (OD) may be influenced by the degree of hydration. The ODD is possibly associated with egg quality, because it functions as an energy source for larvae (Rodgveller et al., 2012; Wiegand, 1996). The rest of the hydrated ovaries collected (n = 11) were not used because the oocytes were in bad condition as a consequence of long-term preservation in formalin solution.

Generalized linear models (GLM) were performed to evaluate the relation between maternal attributes, condition index (HSI, GSI and Kn) and proximal compositions (lipid and protein content in liver, gonad and muscle) with the dependent variables (relative fecundity, oocyte dry weight, oocyte diameter and oil droplet diameter). Due to overdispersion in relative fecundity data, the models employingthis variable had a log link function and a binomial negative error structure. In all other cases the models had an identity link function and a Gaussian error structure. All the variables analyzed were modeled as continuous variables. Due to the correlation among covariates, we evaluated the multicollinearity between different covariates by calculating the variance inflation factor (VIF). Residual plots were evaluated for violations of model assumptions. Each model fit was analyzed regarding the level of deviance explained by the pseudo r^2 values (Swartzman et al., 1992). This pseudo coefficient of determination was calculated as the deviance in the model containing only the intercept minus the deviance after adding all factors, divided by the null deviance of the model containing only the intercept. All statistical analyses were conducted with the statistical software R, vers. 3.2.3 (R Core Team, 2015).

Table 1
Minimum (min) and maximum (max) values of the maternal attributes and morpho-physiological indices analyzed for 41 females of *Merluccius hubbsi*, Northern stock sampled during 2011.

	Min	Max
Total length (cm)	33	83
Gutted weight (g)	221	3076
Liver weight (g)	4	150
Ovary weight (g)	7	518
GSI	3.17	41.25
HSI	1.35	8.32
Kn	0.87	1.15

3. Results

Sampled females covered a wide range of sizes. The minimum and maximum values estimated for all maternal attributes and morpho-physiological indices analyzed are listed in Table 1.

Biochemical indices, lipids and proteins exhibited large variations for the three tissues sampled. Lipid content in the muscle ranged from 0.48 to 6.61% with a mean value of 3.41%; these values were duplicated in the gonads (3.28–12.70%, mean value of 6.49%). On the other hand, lipids were the most abundant constituent of the liver, with percentages of tissue composition between 5.37 and 46.41% and an average close to 29% (Table 2). Analyzing the coefficient of variation (CV) estimated for the three tissues, lipid content in the muscle was the most variable component (Table 2). Compared to lipids, proteins were the main constituents in the muscle and gonads. The mean protein content values were 20.46%, 11.52% and 18.19% in the muscle, gonads, and liver, respectively. In the muscle, the CV was very low (Table 2).

3.1. Relationship between morpho-physiological and biochemical indices

The relationships between condition morpho-physiological (Kn and HSI) and biochemical indices (lipid and protein content of the muscle, gonads and liver) were analyzed. The results indicate that both HSI and Kn were positively correlated with muscle and liver lipids, and liver proteins (Table 3). The relationships with HSI had the highest coefficients of determination. No statistical relationship was found between the condition morpho-physiological indices and gonad lipid content, neither between these indices and proteins content in muscle and gonad.

Table 2
Range and mean values of lipids and proteins (% wet weight tissue) for the muscle, gonads, and liver of spawning capable females of *M. hubbsi* during the reproductive peak. CV: coefficient of variation.

	Lipid			Protein		
	Range	Mean	CV	Range	Mean	CV
Muscle	0.48–6.61	3.41	0.52	17.66–23.48	20.46	0.07
Gonad	3.28–12.70	6.49	0.27	8.73–18.72	11.52	0.24
Liver	5.37–46.45	28.89	0.43	11.02–23.83	18.19	0.18

Table 3
Results of significant linear regression analyses between biochemical indices (lipids and proteins) for each tissue (muscle, gonads, and liver) and the morpho-physiological indices (HSI and K) for 41 females of *M. hubbsi*, Northern stock. r^2: coefficient of determination; a and b: equation parameters; *p*: *p*-value of the relationship.

		HSI				Kn			
		r^2	a	b	*p*	r^2	a	b	*p*
Lipid	Muscle	0.65	0.65	0.16	**< 0.001**	0.37	15.81	12.47	**< 0.001**
	Gonad	0.04	0.15	5.72	0.23	0.08	7.12	0.66	0.08
	Liver	0.72	4.81	4,80	**< 0.001**	0.39	113.65	85.22	**< 0.001**
Protein	Muscle	0.04	0.13	19.80	0.21	0.00	0.61	19.84	0.88
	Gonad	0.01	−0.14	12.24	0.47	0.01	4.14	7.36	0.52
	Liver	0.31	0.82	14.10	**< 0.001**	0.26	24.23	6.13	**< 0.001**

3.2. Relationship between maternal condition indices and females attributes

Total length and gutted weight of females showed no significant relationships with the morpho-physiological indices (Kn and HSI), i.e., there was no relationship between these variables during maximal gonadal development of the ovaries (Fig. 2). In contrast, a significant positive relationship was observed between GSI and the condition indices HSI and Kn, although the coefficients of determination were low (Fig. 3).

The analysis of maternal attributes and biochemical components showed that total length and gutted weight of spawning capable females showed a significant positive relationship with muscle protein content but had low coefficients of determination. The GSI showed a positive relationship with lipid content in the muscle and liver, and protein content in the liver, but this index showed a negative relationship with proteins in the gonads (Table 4).

3.3. Relationship between maternal attributes, condition indices, proximal composition and the number and quality of hydrated oocytes

This section shows the results of generalized linear models GLM. Those that contain maternal attributes and condition indices, the total length was not included to avoid multicollinearity.

Relative fecundity (RF) ranged from 287 to 916 hydrated oocytes per female gram (ovary-free), with a mean value of 532 ± 144 hydrated oocytes. Results from the generalized linear model showed that

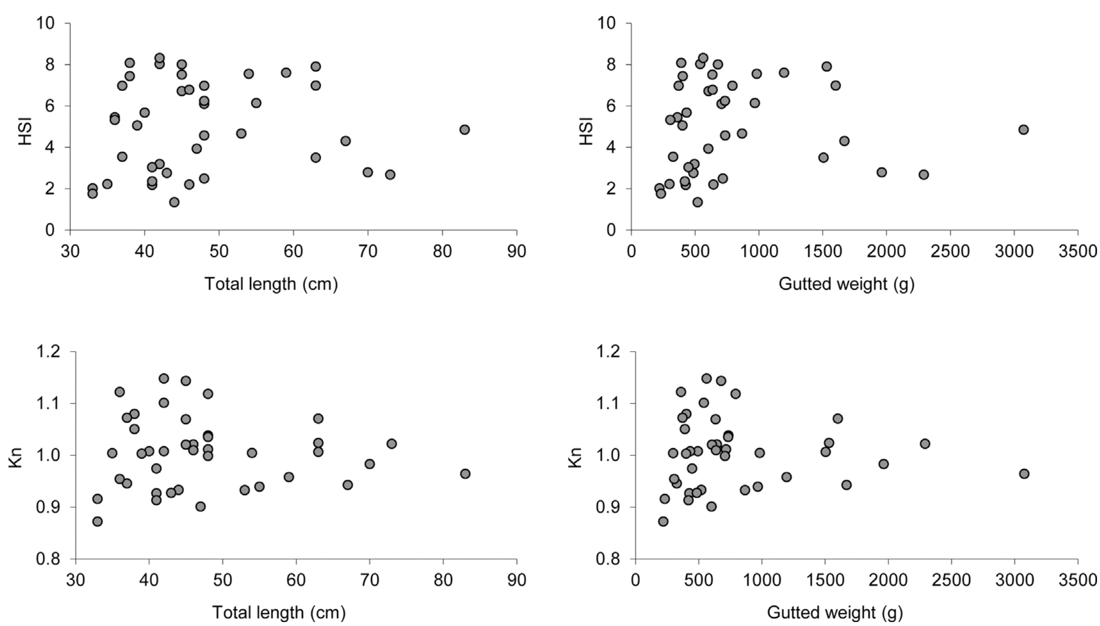

Fig. 2. Maternal attributes (total length and gutted weight) in relation to morpho-physiological indices (HSI and Kn).

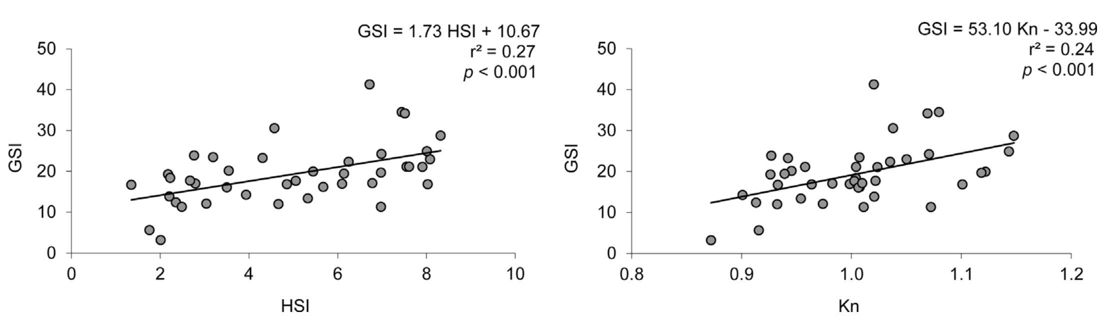

Fig. 3. Morpho-physiological indices (HSI and Kn) versus GSI (index that relates the gonadal size to the individual weight).

Table 4
Results of significant linear regression analyses between biochemical indices (lipids and proteins) for each tissue (muscle, gonads, and liver) and the maternal attributes (total length, gutted weight), and gonadosomatic index (GSI) for the Northern stock of *M. hubbsi*. r^2: coefficient of determination; a and b: equation parameters; *p*: *p*-value of the relationship.

		Total length				Gutted weight				GSI			
		r^2	a	b	*p*	r^2	a	b	*p*	r^2	a	b	*p*
Lipid	Muscle	0.002	−0.006	3.72	0.79	0.005	< 0.001	3.57	0.67	0.243	0.119	1.12	**0.001**
	Gonad	0.003	−0.008	6.87	0.74	0.000	< 0.001	6.45	0.93	0.056	−0.056	7.57	0.14
	Liver	0.030	−0.187	37.83	0.27	0.037	−0.004	32.02	0.23	0.157	0.669	15.95	**0.01**
Protein	Muscle	0.318	0.070	17.12	< **0.001**	0.282	0.001	19.45	< **0.001**	0.015	0.025	19.98	0.43
	Gonad	0.029	−0.040	13.43	0.29	0.008	< 0.001	11.84	0.57	0.184	−0.159	14.58	< **0.01**
	Liver	0.005	0.019	17.28	0.67	0.002	< 0.001	18.03	0.81	0.168	0.168	14.72	< **0.01**

GSI and Kn influenced positive and significantly the RF Northern stock of Argentine hake (Table 5 Model 1). This model explained 69% of RF variability, being the deviance value of Kn very low with respect to GSI. In case of biochemical components only muscle lipids showed positive significant relationships of RF (pseudo $r^2 = 0.21$, Table 5 Model 2).

Oocyte dry weight of 100 hydrated oocytes ranged between 2.65 and 4 mg, with a mean value of 3.20 ± 0.35 mg. This variable only showed a positive significant relationship with HSI, but the amount of variation explained by this model was very low (pseudo $r^2 = 0.15$, Table 5 Model 3).

The hydrated oocyte diameter (OD) ranged between 798 and 961 µm, with a mean value of 866 ± 32 µm, for females between 35 and 73 cm TL. This variable showed positive significant relationships with GSI (pseudo $r^2 = 0.29$, Table 5 Model 4). The oil droplet diameter (ODD) varied between 250 and 292 µm, with a mean value of 266 ± 10 µm, and was positive associated with both morpho-physiological indices (HSI and Kn) and the model had a pseudo $r^2 = 0.56$ (Table 5 Model 5).

The analysis of biochemical indices and oocyte quality showed significant positive relationships. Oocyte dry weight was positive related with gonads lipid and liver protein content (pseudo $r^2 = 0.27$, Table 5 Model 6). Oocyte diameter was not correlated with any of the biochemical components analyzed (Table 5 Model 7), while the oil droplet diameter showed positive significant relationships with lipid content of muscle and liver (pseudo $r^2 = 0.43$, Table 5 Model 8).

4. Discussion

Morpho-physiological indices (GSI, HSI, Kn), together with energy reserves, expressed by the chemical composition of different tissues, are key factors to consider when evaluating the stock reproductive potential (Domínguez-Petit, 2007). The development of ovarian maturity in fish mainly involves physiological and biochemical processes as a result of the massive incorporation of lipids and proteins into growing oocytes, increasing female weight in a short period of time. During the phase of peak ovarian development, many species reduce the amount of food ingested, so that the nutrients and energy necessary for ovarian growth and other functions are acquired from body reserves. Additionally, the energy reserves or condition of fishes before reproduction will influence egg and larval quality, fecundity, number of viable eggs, size of oil droplets, hatch rate, and percentage of normal larvae (Zohar et al., 1995). Other factors that affect reproductive potential are genetic pool, size/age at maturity and parental condition (Saborido-Rey et al., 2004; Scott et al., 2006). In this context, it is important to note that information on the morpho-physiological and biochemical indices of Argentine hake, and mainly the Northern stock, is scarce in the available literature.

As already mentioned, proximal composition or biochemical indices describe condition more accurately than morpho-physiological indices, since condition assessment provides insights into the energy available and how energy reserves are distributed between different tissues and biochemical components. The main energy reserves are usually lipids, those being mainly triacylglycerols, which are consumed in high-energy demanding activities, such as reproduction and migration, or in routine activities during periods of resource scarcity (Schultz and Conover, 1999). In the present study, the lipid content of hake spawning capable were similar to those reported for Patagonian hake females in the same maturation stage (Leonarduzzi, 2011). Unlike the lipid content values found in the muscle and gonads, the great variability in liver lipid content demonstrated the important dynamics of this component in the liver. These results, together with the high concentration percentage obtained, confirmed the important role of the liver in energy storage in gadoid species (Lloret et al., 2008), which are lean species, i.e., they use the liver as their main energy reservoir (FAO, 1999). Protein is an important component of muscle tissue, and more specifically, vitellogenin is responsible for oocyte growth through vitellogenesis in teleost fish (Tyler and Sumpter, 1996). The protein content of hake was relatively stable and showed little fluctuation in the muscle and liver.

In fishery science and ecological studies, condition indices are widely used to express the energy reserves stored within individual fish. Therefore, it is important to validate the link between condition indices, lipid content, and protein content in relation to body size. Our results show a significant relationship in organisms that have high values of morpho-physiological indices (HSI and Kn) and the concentration of lipids in muscle and liver, as well as the concentration of liver proteins, although in the latter case with lower coefficient of determination. This suggests that HSI and Kn are good indicators of such biochemical components, mainly the HSI, which showed the relationships with the highest coefficients of determination. Consistently, HSI has been considered a more representative indicator of nutritional status than Kn (Leonarduzzi et al., 2014; Marteinsdottir and Begg, 2002). In previous studies, HSI was the index that best reflected the concentration of lipids within the liver and muscle for Southern stock Argentine hake females (Leonarduzzi et al., 2014). Similar results were found in other species with indeterminate annual fecundity such as yellowfin tuna, *Thunnus albacares* (Zudaire et al., 2013) and in the gadoid *Trisopterus luscus* (Alonso-Fernández and Saborido-Rey, 2012). In the case of the Southern hake stock, Kn was only positively correlated with muscle proteins in ripening females, although the prediction model obtained was very low. Alonso-Fernández and Saborido-Rey (2012) found similar results for *T. luscus*.

The present study showed that the morpho-physiological condition indices (HSI and Kn) were not correlated with female total length and gutted weight. On the other hand, GSI was related to female condition, i.e., a positive relationship between GSI and both HSI and Kn was observed. The analysis of biochemical components showed that the lipid content of the three sampled tissues was not correlated with female length and gutted weight. This means that larger females of Argentine hake of the Northern stock do not accumulate more lipids than the smaller ones, at differences to that reported for the Southern stock (Leonarduzzi et al., 2014). Regarding protein content of the Northern hake stock, we only observed positive relationships between muscle protein, length and gutted weight of spawning females. These results indicate that larger females accumulate more proteins per weight unit

Table 5
Results of the eight generalized linear models, with the effect of gonadosomatic index (GSI), hepatosomatic index (HSI), condition factor (Kn), gutted weight (GW), muscle lipids (ML), muscle protein (MP), gonad lipid (GL), gonad protein (GP), liver lipid (LL) and liver protein (LP) on relative fecundity (RF), oocyte dry weight (ODW), oocyte diameter (OD) and oil droplet diameter (ODD) for the Northern stock of *M. hubbsi*. df = degrees of freedom.

	df	Deviance	Residual df	Residuals deviance	*p -value*
Model 1. RF = GSI + Kn + HSI + GW					
Null			37	125.07	
GSI	1	76.17	36	48.90	< **0.01**
Kn	1	5,07	35	43.82	**0.02**
HSI	1	3.53	34	40.29	0.06
GW	1	2.09	33	38.20	0.15
Model 2. RF = ML + MP + GL + GP + LL + LP					
Null			37	48.55	
ML	1	6.48	36	42.07	**0.01**
MP	1	0.68	35	41.38	0.41
GL	1	0.06	34	41.32	0.80
GP	1	0.83	33	40.49	0.36
LL	1	0.15	32	40.35	0.70
LP	1	1.99	310	38.35	0.16
Model 3. ODW = GW + HSI + GSI + Kn					
Null			38	4.75	
GW	1	0.02	37	4.72	0.67
HSI	1	0.54	36	4.19	**0.03**
GSI	1	0.13	35	4.06	0.29
Kn	1	0.02	34	4.04	0.71
Model 4. OD = GSI + Kn + HSI + GW					
Null			28	29457.29	
GSI	1	5690.53	27	23766.76	**0.01**
Kn	1	1685.43	26	22081.33	0.16
HSI	1	24.38	25	22056.95	0.87
GW	1	1043.35	24	21013.60	0.27
Model 5. ODD = GSI + Kn + HSI + GW					
Null			28	2734.49	
GSI	1	1057.16	27	1677.33	< **0.001**
Kn	1	114.13	26	1563.20	0.13
HSI	1	357.90	25	1205.30	< **0.01**
GW	1	9.14	24	1196.15	0.67
Model 6. ODW = GL + LP + LL + ML + MP + GP					
Null			38	4.75	
GL	1	0.53	37	4.21	**0.03**
LP	1	0.59	36	3.62	**0.02**
LL	1	0.04	35	3.58	0.55
ML	1	0.08	34	3.51	0.39
MP	1	0.01	33	3.49	0.72
GP	1	0.03	32	3.46	0.60
Model 7. OD = GL + LP + LL + ML + MP + GP					
Null			28	29457.29	
GL	1	1382.86	27	28074.42	0.25
LP	1	95.13	26	27979.29	0.76
LL	1	1906.91	25	26072.38	0.18
ML	1	848.80	24	25223.57	0.37
MP	1	2001.99	23	23221.58	0.17
GP	1	33.28	22	23188.30	0.86
Model 8. ODD = GL + LP + LL + ML + MP + GP					
Null			28	2734.49	
GL	1	544.66	27	2189.83	< **0.01**
LP	1	541.66	26	1648.17	< **0.01**
LL	1	65.60	25	1582.57	0.34
ML	1	5.08	24	1577.49	0.79
MP	1	0.24	23	1577.25	0.95
GP	1	17.15	22	1560.10	0.62

in their muscles which could favor the swimming capacity. In *Gadus morhua* it was observed that the swimming endurance was markedly affected by fish condition (Martínez et al., 2003).

Since female condition could have an influence on reproductive potential, its relationship with the quantity (relative fecundity) and quality of hydrated oocytes (dry weight and diameter of oocytes and oil droplets) prior to spawning was analyzed. Mean relative fecundity (RF), 532 hydrated oocytes g^{-1}, was similar to that recorded in previous years for the Northern and Southern hake stock (Macchi et al., 2010; Rodrigues and Macchi, 2010; Rodrigues et al., 2015). No tendency was observed between RF and the maternal attribute gutted weight, but a significant positive relationship was obtained between RF and the variables GSI and Kn. Moreover, RF only showed significant relationships with muscle lipid content. In the Southern hake stock, a significant relationship was observed between RF and both morpho-physiological condition indices (HSI and Kn), although they had low coefficients of determination (Macchi et al., 2013).

The null or weak relationships between condition and biochemical indices with RF could be explained by the energy allocation strategies. In income breeder species, as hake, the food intake during the spawning season partially provides the energy needed for egg production additionally to the energy storage in the liver. Thus, environmental influence is more marked in species with indeterminate fecundity than in species with determined fecundity (Murua and Motos, 2006). In other gadoid species, e.g., cod and haddock, with a capital breeder strategy, the condition factor K significantly increased the total explained variation of fecundity (Blanchard et al., 2003). In these species, the reproduction is based on energy reserves acquired during the feeding season and they exhibit a determinate fecundity (Murua and Saborido-Rey, 2003). These strategies (capital and income breeder) are the extremes of a continuum; certain species may compensate for inadequate energy deposits with income derived from feeding (Henderson et al., 1996), like mention in *T. luscus* (Alonso-Fernández and Saborido-Rey, 2012) and *Balistes capriscus* (Lang and Fitzhugh, 2015). To determine more precisely the type of energy strategy of Argentine hake a seasonal study should be carried out.

In addition to the total number of offspring that can be produced, offspring viability is important during the first stages of life. This depends mainly on egg quality, which is associated with the amount of nutrients stored in the oocytes (Brooks et al., 1997). There are different methods and indices that can be used to estimate quality, some very simple (morphometric attributes such as the egg diameter or weight, and the oil droplet size), and others that are more complex, such as the biochemical composition of oocytes (Nocillado et al., 2000). In the Northern hake stock, the mean dry weight of the hydrated oocytes (3.20 mg) was similar to that previously reported for this stock (Rodrigues and Macchi, 2010) and for the Southern stock (Macchi and Pájaro, 2003; Macchi et al., 2010). In this study we did not observe significant relationships between dry weight and maternal attribute (GW), unlike that reported for the Southern stock (Macchi et al., 2013). This could be due to the low number of larger females analyzed in Northern stock. There was a positive relationship between mean dry weight of the hydrated oocytes and HSI, liver protein content and gonad lipid content. Macchi et al. (2013) found significant relationships among this variable and both condition indices (HSI and Kn) in the Southern hake stock.

The mean diameter of the hydrated oocytes was 866 μm, and it was not related to the biochemical indices, but, as oocyte diameter may be influenced by the cytoplasmic hydration degree, we analyzed the oil droplet size. The mean diameter of the oil droplets (266 μm) was similar to that reported for the Southern stock (Macchi et al., 2013). The oil droplet diameter did not show significant relationships with GW and GSI, but it was related to HSI, Kn and with the lipid content of muscle and liver.

The results found in relation to the oocyte quality variables allow us to conclude that oil droplet diameter is a good index of the nutritional status of Argentine hake females during the fall reproductive peak. It could be stated that larger oil droplet diameter indicate higher lipid reserves present in the females, mainly in the muscle and liver. These eggs of better quality could hatch bigger larvae with higher survival rates, which in turn could give greater recruitments (Rijnsdorp and Vingerhoed, 1994; Trippel, 1998). This result is coincident to that observed for Southern hake stock, since Leonarduzzi (2011) determined that the oocyte diameter of spawning females was a good indicator of nutritional status, and Macchi et al. (2013) reported a significant positive relationship between the size of oil droplets and egg diameter. In species bred under controlled conditions, it has been observed that the oocyte and oil droplet size are related to the type of feed supplied, as females which are better fed produce eggs and oil droplets of greater size (Lavens et al., 1999).

In most fishes, the energy intake that exceeds the cost of maintenance is used for gonadal and somatic growth (Callow, 1985), and better than average physical condition could results for example in increased fecundity. In contrast a poor condition may not allow fish to accumulate enough energy to support egg production in consecutive years (skip spawning) (Rideout et al., 2005). In our study, the low pseudo r^2 found for the relationships between the content of lipids and proteins in different tissues, and the relative fecundity could be suggesting that the Argentine hake females were in optimal nutritional condition during the study period, possibly because individuals continues feeding and incorporating energy during the spawning season (income breeder strategy). It is possible that condition estimates over a more expansive sampling period, may provide greater accuracy in determining the effect on reproductive potential. Therefore, we underline the importance to improve the study of females condition and its effects on reproductive potential, with the purpose to increase the knowledge on recruitment variability of stock.

5. Conclusions

Although the results correspond to data collected in a single year, in general, most results demonstrated that (i) condition indices were independent of female size (total length and gutted weight); (ii) GSI was positively correlated with female condition, i.e., with both HSI and Kn; (iii) HSI was significantly correlated with lipid content in the muscle and liver; (iv) relative fecundity was only correlated with the condition index Kn; (v) dry weight of hydrated oocytes was positively correlated with HSI, while the oil droplet diameter was correlated with HSI and Kn; (vi) oil droplet diameter was also correlated with liver lipid content, with a high coefficient of determination. From these results we can conclude that HSI and oil droplet diameter are the best indicators of nutritional condition of Northern stock spawning females. In addition, our results suggest that Argentine hake females were in optimal nutritional condition during the study period, possibly because they continue feeding and incorporating energy during the spawning season.

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