

ARTICLE

A first assessment of atresia in the Chilean jack mackerel *Trachurus murphyi* (Teleostei, Carangidae) from the South-eastern Pacific Ocean

Primera evaluación de la Atresia en el jurel *Trachurus murphyi* (Teleostei, Carangidae) en el Pacífico sureste

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Resumen. El jurel, *Trachurus murphyi* sustenta una importante pesquería en el Pacífico sureste la que ha declinado considerablemente en el tiempo. *T. murphyi* tiene un desarrollo ovárico asincrónico con desoves oceánicos (septiembre a enero). A pesar de la importancia económica de este recurso, se desconocen aspectos críticos de su biología, como las características y la dinámica de la atresia, que pueden afectar el rendimiento reproductivo. Hembras de *T. murphyi* capturadas en distintas estaciones de desove fueron analizadas para describir los patrones de prevalencia e intensidad de atresia. Se realizaron modelos lineales generales (GLM) usando prevalencia e intensidad de atresia como variables de respuesta e índice gonadosomático, factor de condición, temperatura de la superficie del mar, folículos postovulatorios y mes/año como variables predictoras. La fecundidad parcial y la fecundidad relativa se compararon entre hembras con atresia, hembras con folículos postovulatorios y hembras no atrésicas. Las etapas de atresia identificadas fueron alfa, beta y gamma. El GLM mostró que las variaciones en la prevalencia e intensidad de la atresia fueron explicadas por todas las variables, excepto el factor de condición para la prevalencia y el índice gonadosomático para la intensidad de atresia. De acuerdo con estos resultados, la dinámica de alfa y beta atresia pueden considerarse un potencial proxy para cualquier interrupción de la temporada de desove. La fecundidad parcial y la fecundidad relativa fueron más bajas en comparación con otros *Trachurus* spp. En esta especie, se hace una primera evaluación que compara la fecundidad entre hembras con y sin atresia.

Palabras clave: Atresia, factor de condición, fecundidad, estación de desove, *Trachurus*

Abstract. The Chilean jack mackerel *Trachurus murphyi* support an important fishery in the South-eastern Pacific Ocean and has declined considerably over time. *T. murphyi* have asynchronous ovarian development with an oceanic spawning (September to January). Despite the economic importance of this resource critical issue such as characteristics and dynamics of atresia, which affect the reproductive output, are unknown. Females of *T. murphyi* caught in different spawning seasons were analysed to describe patterns of prevalence and intensity of atresia. General linear models (GLM) were performed by using prevalence and intensity atresia as response variables and gonadosomatic index, condition factor, sea surface temperature, postovulatory follicles and month/year as explanatory variables. The batch fecundity and relative fecundity were compared between females showing atresia, postovulatory follicles and non-atretic females. The stages of atresia identified were alpha, beta and gamma. The GLM showed that variations in the prevalence and intensity of atresia were explained for all variables, except condition factor for prevalence, and gonadosomatic index for intensity of atresia. According to our results, the dynamic of alpha and beta atresia could be considered a potential proxy for any disruption of spawning season. The batch fecundity and relative fecundity were lowest compared with other *Trachurus* spp. This is the first assessment comparing fecundity between atretic and not atretic females for this species.

Key words: Atresia, condition factor, fecundity, spawning season, *Trachurus*

INTRODUCTION

In the South-eastern Pacific Ocean (SEP), industrial fisheries for the highly migratory Chilean jack mackerel *Trachurus murphyi* Nichols, 1920. The main fishery includes the coast off Peru and Chile, extending from the central coast of Chile to the South-west Pacific Ocean, reaching the coast around New Zealand and Tasmania has been described (Serra 1991, Cárdenas *et*

al. 2009, Vásquez *et al.* 2013). The peak in the catch was achieved in the 1990s, (*ca.*, 4,600,000 tons) after which the catch for all fleets steadily decreased and for 2019 the South Pacific Regional Fisheries Management Organisation recommended a limit of capture of 591,000 tons (SUBPESCA 2018). The main reason explaining this situation was the strong fishing mortality and potentially unfavourable environmental conditions (Dragon *et al.* 2018).

In the SEP, Chilean jack mackerel conform a single large population (Poulin *et al.* 2004, Cárdenas *et al.* 2009) that can be found in three different habitats (Arcos *et al.* 2001) according to its life history: a) nursery ground area, b) coastal feeding area and c) a large, main oceanic spawning area off central Chile (Bertrand *et al.* 2004, Cubillos *et al.* 2008, Vásquez *et al.* 2013). Interestingly, otolith chemistry indicates that all adult Chilean jack mackerel come from the same oceanic spawning area (Ashford *et al.* 2011). Recently, Parada *et al.* (2017) indicated the presence of a potential new spawning and nursery ground area associated with the seamount region in the Challenger break and the East Pacific ridge (32°S-39°S and 105°-126°W).

Chilean jack mackerel can spawn throughout their whole distribution (Taylor 2002, Gerlotto *et al.* 2012), and the time extension of the spawning period varied between area and years (Perea *et al.* 2013). For the main oceanic spawning area from central coast of Chile (32°S-38°S, 80°W-92°W) the spawning period extends from September to January when mature fish begin the annual migration from the feeding area to the oceanic spawning area; that extends more than 1,800 km off the coast (Cubillos *et al.* 2008, Leal *et al.* 2013).

Like other *Trachurus* species, *T. murphyi* present asynchronous ovarian development (Leal *et al.* 2013). George (1995) suggests an indeterminate fecundity for *T. murphyi* based in the frequency of oocytes size distribution, length of the spawning season as well presence of atresia. A generalized prevalence of atresia and resorption of mature oocytes at the end of the spawning season has been described for fishes with indeterminate fecundity (West 1990). Accordingly, fecundity estimates should be made using the most advances development oocytes (hydrated oocytes) instead the vitellogenic oocytes (Saborido-Rey & Kjesbu 2005). For *T. murphyi*, is not easy to find females harbouring hydrated oocytes during the spawning season (George 1995, Leal *et al.* 2013), consequently vitellogenic oocytes could be counted, and in this case, atresia must be quantified (Saborido-Rey & Kjesbu 2005). Atresia is

a normal process of oocyte renewal (Kurita *et al.* 2003, Lowerre-Barbieri *et al.* 2011), which increases at the cessation of spawning when all remaining vitellogenic oocytes are resorbed (Saborido-Rey & Kjesbu 2005).

In mature females, atresia can occur at any time during the reproductive cycle. Sometime, females delay its reproduction, inclusive for one year, increasing the prevalence and intensity of atretic oocytes. In highly migratory species, such as *T. murphyi*, it is expected that during the spawning period, some females will have atretic oocytes due to potential energy loss during annual migration. As atresia can have strong consequences in recruitment, the knowledge of the spatio-temporal dynamics of this process is important to assign the status of female in the spawning stock during spawning season. Atresia can have direct effect on the number of eggs that females can produce. Like other reproductive traits, atresia depends on the female's physiological conditions (*e.g.*, age, length, condition) and environmental factors (*e.g.*, temperature). Therefore, the main objectives were (1) to describe the phases of atresia in *T. murphyi* caught during the post-migration spawning period in order to evaluate the spawning history, (2) to determine the prevalence and intensity of atresia in different spawning periods and its relation with physiological conditions and environmental factors and (3) to determine the impact of atresia in the fecundity.

MATERIALS AND METHODS

ETHICAL STATEMENT

Ethical approval was not required for this study, due all specimens were collected as part of research cruises that are performed for the evaluation of spawning biomass (DEPM) in the Chilean jack mackerel, *Trachurus murphyi* from oceanic spawning area off central Chile (Table 1). Fish arrived dead at fishing port. No samples were collected by the authors; permission was granted to use biological database and gonads of all fish.

Table 1. Cruises performed for the evaluation of spawning biomass (DEPM) in the Chilean jack mackerel, *Trachurus murphyi* from oceanic spawning area off central Chile between 2004 and 2014 / Cruceros realizados para evaluar biomasa desovante (MPDH) en el jurel, *Trachurus murphyi* desde el área de desove en Chile central entre el 2004 y 2014

	Cruise					
	2004	2005	2006	2012-2013	2013	2014
S	S1	S2	S3	S4	S5	S6
Months by S	Nov	Nov	Nov	Dec/Jan	Dec	Nov/Dec
Lat (°S)	32°20'-38°00'	34°20'-38°40'	33°14'-38°50'	32°12'-36°30' 34°57'-35°18'	29°53'-35°40'	32°33'-36°30' 32°41'-38°00'
Long (°W)	75°41'-91°51'	76°50'-87°54'	71°01'-91°46'	71°59'-88°40' 73°47'-74°08'	71°50'-76°50'	74°25'-85°48' 72°12'-86°57'
SST (°C)	15.0-19.0	14.5-17.5	13-17	15-17/13-13.5	13-14.4	15.5-16.4/13.9-15.1
FL (cm)	32(23-58)	32(25-49)	36(27-55)	34(23-48)/30(25-36)	36(27-64)	37(29-47)/37(24-49)
BW (g)	115-1850	200-1110	240-1800	165-1270/180-525	250-3090	330-1200/125-1300
n	988	596	727	287/139	431	162/320

S= spawning season, Lat= latitude, Long= longitude, SST= sea surface temperature, FL= fork length, BW= body weight, n= number of females

SAMPLE COLLECTION

Mature females ($n=3,650$) were sampled along the spawning area off central Chile (30° - 39° S; 71° - 88° W), according to the methodology described by Sepúlveda *et al.* (2009). Briefly, for each successful trawl a set of females were selected at random. Females caught were longer than 23 cm fork length. Fork length (FL, cm) and body weight (BW, g) were measured and gonad tissue samples were collected on board. Besides, sea surface temperature (SST) was recorded at each trawl.

Gonads were processed for histology using standard protocols. The ovaries were fixed in 10% neutral buffered formaldehyde at board of fishing vessels. In the laboratory a cross-section of tissue was sampled from the middle parts of the ovary. Each sample was embedded in paraffin, sectioned transversely with a thickness of 5 μ m and stained with haematoxylin and eosin (H+E). The histological methodology was followed Brown-Peterson *et al.* (2011) and applied for Leal *et al.* (2013) to describe and characterize the reproductive maturity phases for this species.

The significance of potential differences in FL and BW between spawning periods was analysed using Kruskal-Wallis test. Differences between immature and mature females for FL and BW were analysed using Mann-Whitney test. Gonadosomatic index (GSI) that indicate the tendency of the degree of gonadic maturity in its reproductive cycle, were recorder for each specimen. GSI was calculated as $GSI = (GW/BW) \times 100$ (Zimmermann 1997); where GW is gonad weight (g). Condition factor (K) was calculated as an overall measure of robustness of the fish in relation to reproductive maturity phases. K was estimated as $K = (BW/FL^3) \times 100$ (Zimmermann 1997). The mean values of GSI and K , obtained for the different maturity stages during each sampled period, were compared using the Kruskal-Wallis tests. Potential relationships between GSI and K for the total samples were analysed with Spearman's correlation coefficient. The presence and age of postovulatory follicles (POFs) were identified according to Hunter & Goldberg (1980) and Hunter & Macewicz (1985). The POFs were classified into three age classes: day 0= new POF, indicating that the females spawned approximately 24 hours prior; day 1= spawning occurred between 24 and 48 h ago; and day 2= old POF in which spawning occurred more than 48 hours before being caught.

The prevalence of atresia (PA) was defined as the number of fish containing ovaries with at least one phase of atretic oocytes relative to the number of all individuals examined, expressed as a percentage (Ganias *et al.* 2008). The presence/absence of atresia was modelled using a generalized linear model (GLM) with a binomial error

distribution for the response variable and a logit link function (Ganias *et al.* 2008). Prior to selection of variables to be included in the GLM for presence/absence of atresia, Spearman's correlations were performed to detect collinearity between the quantitative variables (FL, K , GSI and SST). The explored explanatory variables were FL, K , GSI, POF, SST and month/year (MY). Three models were performed. The first model included as response variable all atresia phases identified (alpha, beta and gamma) and their combinations, the second model included only A-atresia, and the third model included only B-atresia. The selection of the best models was checked with Akaike's Information Criterion (AIC) and Deviance (D^2). Additionally, the Receiver Operating Characteristic (ROC) curve was used to evaluate the sensitivity and specificity of the models.

For females with alpha-atresia, the intensity of atresia (IA) was calculated as the number of alpha-atretic oocytes divided by the total number of vitellogenic oocytes (alpha-atresia + non-atretic follicles) following Nunes *et al.* (2011). Simple counting from histological sections was used as a proxy of intensity of atresia (Ganias *et al.* 2008, Nunes *et al.* 2011). The IA was evaluated using a generalized linear model (GLM) with a normal distribution for the response variable and a log link function. The explanatory variables included in the model were FL, K , SST and MY.

Batch fecundity (BF) was estimated via gravimetric methods on hydrated females (Hunter & Macewicz 1985b) in order to compare contribution of hydrated eggs in spawning seasons showing atresia or POF. Three female stages were identified: females non-atretic oocytes ($n=71$), females with atretic oocytes ($n=41$) and females with presence of POF ($n=66$). Batch fecundity (BF), defined as the number of oocytes released per spawning event, was determined as the number of hydrated oocytes in actively spawning ovaries. Two pieces of ovary were removed from the middle parts of the gonad and weighed (approx. 0.2 g), and hydrated oocytes were counted. These hydrated females were caught during the spawning period S6 (November and December to 2014). Relative batch fecundity (RF), defined as the number of hydrated oocytes per gram of body weight, was determined by dividing BF by BW. Significance differences in BF and RF amongst three female stages were evaluated using Kruskal-Wallis tests and the Dunn *a posteriori* test. In this case, effects of the explicatory variables FL, K and female stages for BF and RF were tested with a generalized linear model (GLM) with a Poisson distribution for the response variable and a log link function. GLM analysis and ROC curve were performed in R Software (R Core Team 2016).

RESULTS

REPRODUCTION AND CONDITION

Fork length (FL) for the whole sample ranged from 23 cm to 64 cm (mean 34.1 cm \pm 5.2), while the body weight (BW) ranged from 115 g to 3,090 g (mean 481 \pm 234). Significant differences were found for FL ($H=946.63$, $P < 0.001$) and BW ($H=1156.76$, $P < 0.001$) between month/year, with the females caught in January 2013 being the smallest ones (Table 1). Also, immature females ($n=43$) showed differences from matures females ($n=3607$) for FL ($U=15288.5$, $P < 0.0001$) and BW ($U=18830$, $P < 0.0001$).

Immature females and developing females were observed at low frequency during several seasons spawning (Fig. 1). Conversely, potentially spawning capable females (range: 2-81%) and actively spawning females (range: 8-18%) were recorded in all samples except January

2013, increasing the proportion of regressing (61%) and regenerating (17%) females (Fig. 1). The absence of females in the actively spawning reproductive phase and the high frequency of advanced maturity phases (regressing and regenerating) indicated that the long spawning period ended by January.

The Gonadosomatic index (GSI) showed significant differences between the reproductive maturity phases ($H=1414.91$, $P < 0.05$); high values (GSI > 5) were observed in females showing the actively spawning phase. Immature females ($n=43$) showed the lowest GSI values (GSI < 1.0) when compared with regressing and regenerating females (Fig. 2). Condition factor (K) ranged from 0.43 to 1.92 (mean 1.12 \pm 0.13), but three females showed $K > 2.0$ (data not included) in all spawning periods analysed (Fig. 2). Additionally, K varied between the reproductive phases ($H=47.97$, $P < 0.05$), although K for immature females did

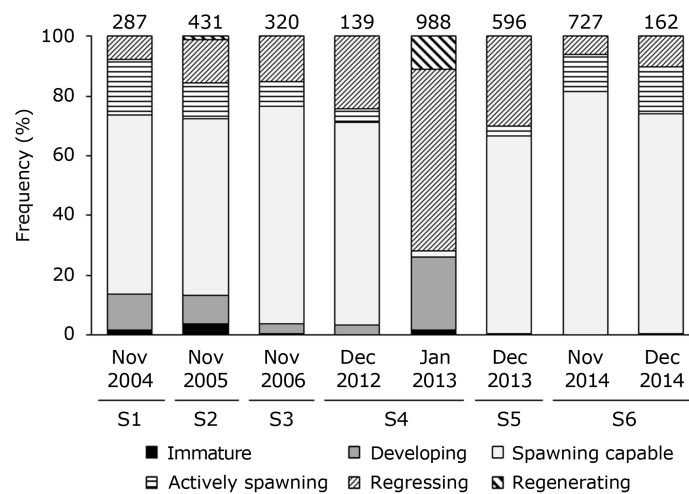


Figure 1. Frequency distribution (%) of reproductive phase of female *Trachurus murphyi* for months and spawning seasons (S). Numbers of specimens examined per month are indicated in parenthesis / Distribución de frecuencia (%) de las fases reproductivas en hembras de *Trachurus murphyi* por meses y estaciones de desove (S). Número de especímenes examinados por mes son indicados entre paréntesis

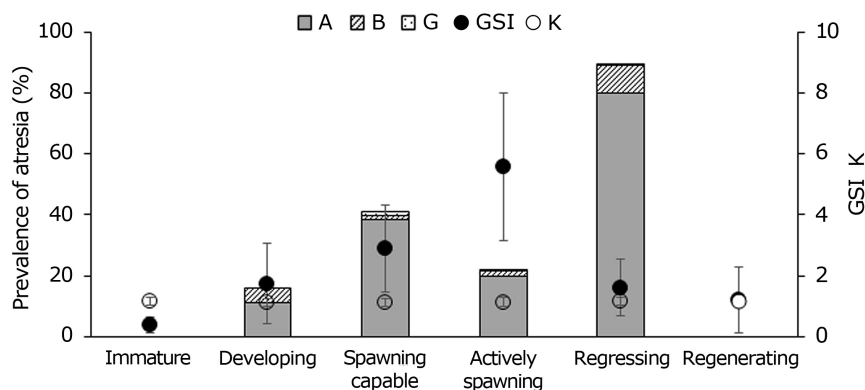


Figure 2. Gonadosomatic Index (GSI), condition factor (K) and prevalence of atresia (%) for reproductive phase. A= Alpha-atresia, B= Beta-atresia, G= Gamma-atresia / Índice Gonadosomático (GSI) factor de condición (K) y prevalencia de atresia por fase reproductiva. A= Alpha-atresia, B= Beta-atresia, G= Gamma-atresia

not show differences from mature females ($U=72,788.5, P=0.48$). Considering the whole sample, GSI was negative (but marginally) correlated with K ($\rho=-0.053, P<0.001$).

ATRESIA MORPHOLOGY

Three main sequential stages of atresia were observed: Alpha (A), Beta (B) and Gamma (G) (Fig. 3). For A-atresia three morphological stages were identified: initial (A1), intermediate (A2) and advanced (A3) (Fig. 3b, c, d). During A-atresia, follicular diameter diminished gradually. The first signal for A1-atresia was an internal, non-smooth zona radiata, which subsequently showed a small fragmentation (Fig. 3b). Some oocytes may show thickening of zona radiata before their fragmentation. Additionally, the disintegration of the nucleus is evident from dark basophilic staining. At this stage, the oocyte retains its shape and sometimes looks like a healthy oocyte.

In A2-atresia, the disintegration and fragmentation of the zona radiata were evident and broke up into irregularly shaped segments; also, unstained vacuoles were apparent inside the ooplasm (Fig. 3c). For the A3-atresia phase, the follicle had the appearance of beta-atresia, but few yolk globule follicles were evident when compared with the other stages (Fig. 3d). A decreased prevalence was evident for the three A-atresia sub-stages from the initial stage to the advanced one, 67% in A1-atresia (initial), 52% in A2-atresia (intermediate) and 24% in A3-atresia (advanced). These sub-stages of A-atresia can also co-occur, where the combination of sub-stages A1-atresia and A2-atresia was the most prevalent (PA=38%). B-atresia was characterized by the presence of many empty vacuoles and some blood vessels (Fig. 3e). The G-atresia was characterized by yellow-brown granular pigments inside the granulosa cells (Fig. 3f).

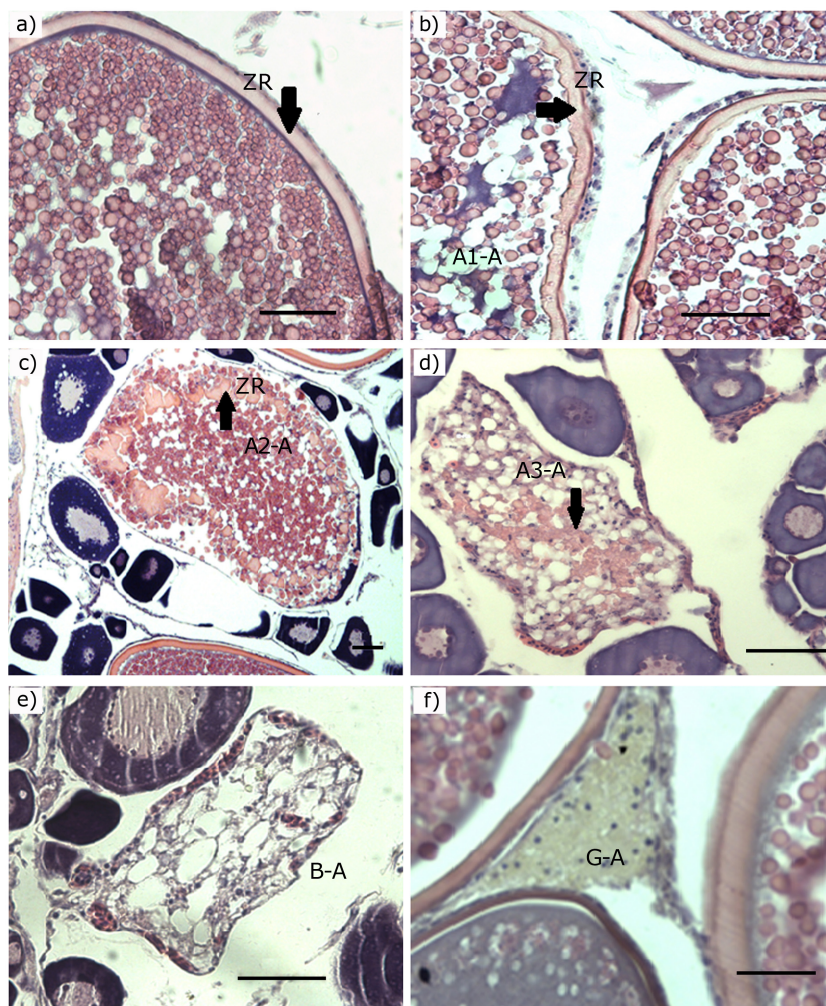


Figure 3. Atretic follicles in *Trachurus murphyi*. Histological sections were stained with haematoxylin and eosin. a) non atretic oocyte, b) A1-A= initial alpha atresia, c) A2-A= intermediate atresia oocytes, d) A3-A= advance alpha stage atresia, e) B-A= beta atresia oocyte, and f) G-A= gamma atresia. ZR= Zona radiata, black arrows. Scale bar= 50 μ m / Foliculos atrécicos en *Trachurus murphyi*. Secciones histológicas fueron teñidas con hematoxilina y eosina. a) ovocito no atrécico, b) A1-A= atresia alpha inicial, c) A2-A= atresia alpha intermedia, d) A3-A= atresia alpha avanzada, e) B-A= beta atresia, and f) G-A= gamma atresia. ZR= Zona radiata, flecha negra. Barra= 50 μ m

PREVALENCE OF ATRESIA

Overall and during all months/year were identified atretic oocytes, being Alpha (A)-atresia the most frequently stage observed (Fig. 4). For A-atresia (n= 1,485), the 39% co-occur with a combinations of Beta (B)-atresia, Gamma (G)-atresia, while with B-atresia (n= 107) the 74% of ovaries co-occurs with G-atresia (Fig. 4). Females in regenerating reproductive phases not showed atresia. Alpha-atresia was the most prevalent stage in the remaining reproductive phases, including females with hydrated oocytes that showed A-atresia and B-atresia (Fig. 2). Females in the regressing reproductive phase showed prevalence of atresia >80% due to higher co-occurrence of A-atresia and B-atresia (Fig. 2). Also, 27% of mature females recorded post ovulatory follicles (POFs) in all reproductive phases, except the regenerating phase. Thirty-two per cent of females exhibited POFs in co-occurrence with atresia, mainly A-atresia. The prevalence of POFs at age 0 was higher in females with hydrated oocytes. The frequency of B-atresia and G-atresia increased with POFs at age 1 and age 2.

The GLM showed that MY, SST and incidence of POF were the variables showing higher effect on PA in the three evaluated models. As FL was significantly correlated with GSI (Spearman's correlations ρ , $P < 0.001$) was excluded from the analysis. GSI were not significant for explain the presence of atresia in model 2 (Alpha-atresia) while K in all evaluated models (Table 2). In the three models, the proportion of explained variance (deviance) was low but significant. Additionally, the prediction of the models was good (ROC= 0.8) (Table 2).

Table 2. Chi-Square values of the binomial GLM model analysing the effects of sea surface temperature (SST), gonadosomatic index (GSI), condition factor (K), presence/absence of postovulatory follicles (POF) and month/year (MY) on the prevalence (presence-absence) of atresia and normal GLM for intensity of atresia in Chilean jack mackerel *Trachurus murphyi*. Model 1= all atresia stages and their combinations, model 2= only alpha atresia and model 3= only beta atresia. AIC= Akaike's Information Criterion, D²= deviance of model, AUC= area under ROC curve, n= number total females / Valores de Chi-cuadrado del modelo GLM binomial analizando el efecto de la temperatura superficial del mar (SST), índice gonadosomático (GSI), factor de condición (K), presencia/ausencia de folículos postovulatorios (POF) y meses/año (MY) sobre prevalencia (presencia-ausencia) de atresia y normal GLM para intensidad de atresia en el jurel *Trachurus murphyi*. Modelo 1= todos los estados de atresia y sus combinaciones, modelo 2= solo Alpha atresia y modelo 3= sólo beta atresia. AIC= Criterio de información de Akaike, D= Deviance del modelo, AUC= área bajo curva ROC, n= número total de hembras

	Prevalence atresia			Intensity atresia
	Model 1	Model 2	Model 3	
SST	194.67**	43.77**	63.03**	34.25**
GSI	63.29**	0.02 ^{n.s}	25.87**	0.27 ^{n.s}
K	0.31 ^{n.s}	2.58 ^{n.s}	0.37 ^{n.s}	6.79**
POF	3.50*	4.96*	8.54*	10.50**
MY	470.21**	391.94**	81.07**	422.17**
Criteria				
AIC	3509.1	2506.4	423.06	254285
D ²	17.35	15.15	30.95	
AUC	0.75	0.73	0.88	
n	3606	2881	2076	2881

^{n.s} non-significant; * 0.05>P>0.01; **P < 0.001

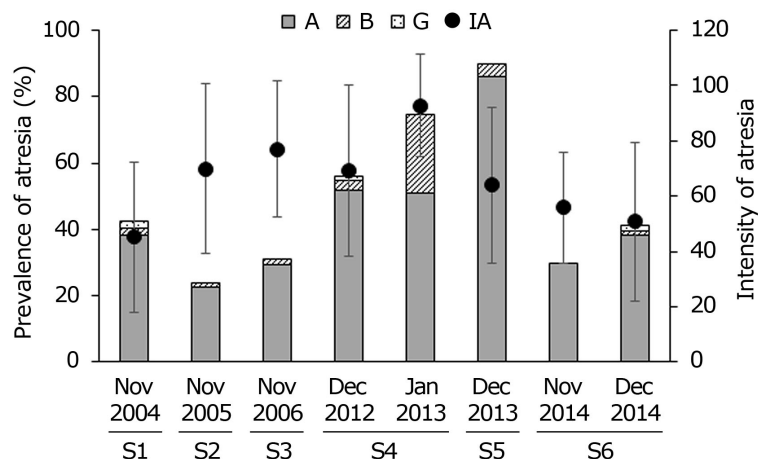


Figure 4. Prevalence of atresia (%) and intensity of atresia (IA) for months and spawning seasons (S). A= Alpha-atresia, B= Beta-atresia, G= Gamma-atresia / Prevalencia de atresia (%) e intensidad de atresia (IA) por mes y estación de desove (S). A= Alpha-atresia, B= Beta-atresia, G= Gamma-atresia

INTENSITY OF ATRESIA

Intensity of atresia (IA) was high in all spawning periods (range: 45-77%); January 2013 showed the highest value of IA (92%), confirming that this month corresponded to the end of the spawning period (Fig. 4). GLM showed that MY, SST, POF and *K* were variables that explained the IA, with MY being the most important variable (Table 2).

FECUNDITY

Batch fecundity (BF) estimated for females that no showed atresia or postovulatory follicle (POF) ranged from 6200.0 to 114566.8 hydrated oocytes (mean 35293.55 ± 23955.4), while relative fecundity (RF) ranged from 14.2 to 185.2 (mean 69.7 ± 32.8) (Fig. 5). Fork length was significantly correlated with BF and RF (Spearman's correlations ρ ; $P < 0.001$ for both). *K* was only correlated with BF ($\rho = 0.014$, $P = 0.047$) but not with RF ($\rho = 0.06$, $P = 0.37$). Both fecundities varied between stages of females: non-atretic females and females with atretic oocytes and females with POF (Fig. 5). Females showing POF showed the lowest BF (mean $28,588.3 \pm 18,542.2$) and RF (mean 54.62 ± 25.98). Females with POF showed significance difference with non-atresia females for batch fecundity (BF) ($H = 9.61$, $P = 0.008$, Dunn, $P < 0.05$) and relative fecundity (RF) ($H = 7.48$, $P = 0.02$, Dunn, $P < 0.05$). GLM showed that BF and RF were significantly explained for FL, *K* and stage of females (non-atretic, atretic and POF), being FL the most important explanatory factor (Table 3).

Table 3. Chi- Square values of the Poisson GLM model analysing the effects of fork length (FL), condition factor (*K*), and female stage [non-atresia, atresia and postovulatory follicles (POF)] on the batch fecundity and relative fecundity for Chilean jack mackerel *Trachurus murphyi* / Valores de Chi-cuadrado del modelo GLM Poisson analizando los efectos de la longitud horquilla (FL), factor de condición (*K*) y estado de las hembras [no-atresia, atresia y con foliculos postovulatorios (POF)] en la fecundidad parcial y fecundidad relativa del jurel *Trachurus murphyi*

Explanatory variable	Fecundity	
	Batch	Relative
FL	110166**	286.99**
<i>K</i>	116188**	22.91**
Stage of females	35479**	47.3**

** $P < 0.001$

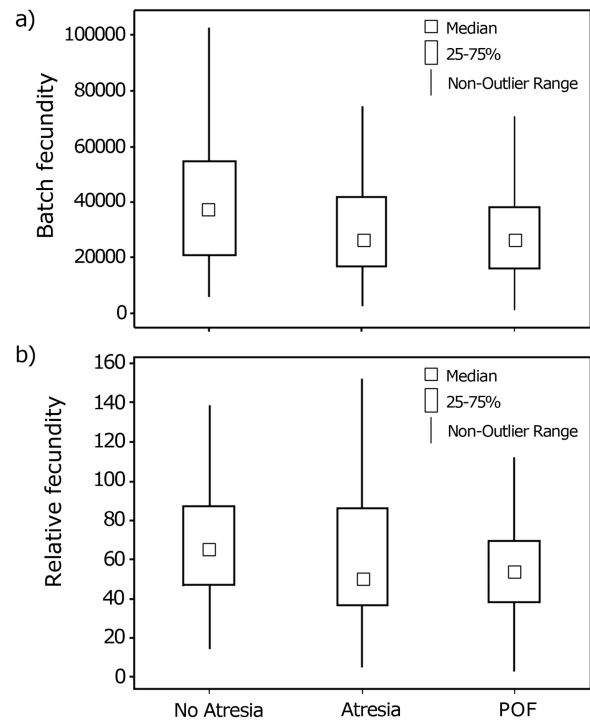


Figure 5. Relationships of batch fecundity(a) and relative fecundity (b) in relation to females stages of *Trachurus murphyi* [non-atresia, atresia and postovulatory follicle (POF)] / Relación de fecundidad parcial (a) y fecundidad relativa (b) en relación con los estados en hembras de *Trachurus murphyi* [no-atresia, atresia y foliculos postovulatorios (POF)]

DISCUSSION

Trachurus murphyi showed three mains sequential atretic stages (Alpha, Beta and Gamma), like others *Trachurus* species (Macewicz & Hunter 1993, Karlou-Riga & Economidis 1997, Gordo *et al.* 2008); being prevalence and intensity of atresia influenced by months/years of spawning seasons. *T. murphyi* has an extensive spawning season (5 months), can spawn an estimate of 5-14 batches for each reproductive period (Ruiz *et al.* 2008, Perea *et al.* 2013), and this condition can explain the co-occurrence of atresia in the different months of the spawning season analysed. Prevalence of Beta-atresia increased strongly at the end of spawning season (January); therefore, the increased proportion of this atresia could be a potential proxy to determine the length of spawning seasons, and it would allow us to detect any change in the current or future reproductive period. During December 2013, the prevalence of atresia (>80%) was higher than observed for the same month in other years, suggesting that spawning season began early this year or was shorter. The turnover

rate for the atretic oocytes in Chilean jack mackerel is unknown, but atretic follicles in fishes are thought to be short lived (Hunter & Macewicz 1985a, Kjesbu *et al.* 1991, Kurita *et al.* 2003). Turnover rates at environmental temperatures for alpha-atretic oocytes have been estimated as 7-9 days for *Engraulis mordax* Girard, 1854 at 15-16 °C but with differences between stages of atresia (Hunter & Macewicz 1985b); 4 to 7 days in Atlantic herring *Clupea harengus* Linnæus, 1758 for temperatures from 4.2 to 11 °C depending on the month of catch (Kurita *et al.* 2003); 10 days in cod *Gadus morhua* Linnæus, 1758 at 8 °C with a spawning period of 50 days (Kjesbu *et al.* 1991); and 9 days in sole *Solea solea* (Linnæus, 1758) (Witthames & Walker 1995). Understanding trends and dynamics of atretic oocytes in *T. murphyi* allows us to identify any change in the spawning period, such as a potential skipped spawning (Rideout & Tomkiewicz 2011) or previous spawning events as has been assessed for Mediterranean sardine *Sardina pilchardus* (Ganias *et al.* 2008).

T. murphyi have a reproductive strategy to disperse over their spawning oceanic area associated to SST warmer than 15-16 °C (Cubillos *et al.* 2008). According to Vasquez *et al.* (2013), the reproductive activity of *T. murphyi* is highly correlated with the Subtropical Convergence or Subtropical Front (STF), which separates relatively warm and salty tropical waters from colder and fresher Subantarctic waters (Vasquez *et al.* 2013, Parada *et al.* 2017). The results indicate that SST is an important variable explaining the presence of atresia in *T. murphyi*, and eventually SST higher or lower than the optimal temperature for spawning, could generate a mismatch between reproduction and optimal environmental conditions for progeny development (Miranda *et al.* 2013). As indicated by Hunter & Macewicz (1985a) and Witthames & Walker (1995), spawning events and atresia are temperature-dependent processes, and females can spawn or delay during migration if the temperature regime is not suitable (Ma *et al.* 1998, Haslob *et al.* 2013). For yellowtail kingfish *Seriola lalandi* Valenciennes, 1833 and *Sardina pilchardus* (Walbaum, 1793), a temperature exceeding the optimal range can cause an aborted spawning event or high prevalence of atresia, respectively (Poortenaar *et al.* 2001, Ganias 2009, Stuart & Drawbridge 2013).

In *T. murphyi*, condition factor (*K*) significantly affect the intensity but not the prevalence of atresia, suggesting that *K* is a good index for explain the intensity of atresia because a fish in bad condition will have not enough energy to develop the oocytes and consequently will have a higher intensity of atresia (Hunter & Macewicz 1985a). Cubillos & Alarcón (2010) suggested that *T. murphyi* accumulates energy reserves (autumn-winter) prior to the reproductive process (spring-summer), indicating that this species is

capital breeding. As *K* not showed differences between immature and mature female and the lowest correlation between *K* with GSI could be an evidence that *T. murphyi* is an income breeding (*i.e.*, continues to feed during migration) (Bucholtz *et al.* 2013). To confirm the dynamics of somatic energy, the trends of *K* should be evaluated during all reproductive cycle of *T. murphyi*. Besides, the relation of GSI and *K* should be complemented with the evolution of hepatosomatic index (HSI), which is a very good indicator of total energy reserves and fish condition (Zimmermann 1997, Nuñez *et al.* 2011).

In this study, high values of prevalence of atresia especially the beta-atresia, must be associated with the end of spawning season, which is consistent with an indeterminate type of fecundity (Gordo *et al.* 2008). In species with indeterminate fecundity such as *T. murphyi*, the recruitment of oocytes can continue for a long period into the spawning period if adequate food is available (Murua & Saborido-Rey 2003). Atresia might be considered an important mechanism for the adjustment of fecundity through the resorption of oocytes in unfavourable seasons (Abaunza *et al.* 2003). The batch fecundity (BF) is an important biological variable for indeterminate spawners and is used in the daily egg production method (DEPM) (Hunter & Lo 1997, Zwolinski *et al.* 2001). In this first assessment, the FL, *K*, presence or absence of atresia and POF affected BF. Fecundity of non-atretic females differed significantly from POF females, coinciding with Macewicz & Hunter (1993), who indicated that for *T. symmetricus*, the batch fecundity was lower for recently spawned females than females without evidence of a previous spawning event (POF).

Regarding the relative fecundity (RF), the results showed that *T. murphyi* recorded the lowest values (69 oocytes g⁻¹ in non-atretic females) when compared with other *Trachurus* spp., 172-250 oocytes g⁻¹ in *T. trachurus* (Karlou-Riga & Economidis 1997, Abaunza *et al.* 2003), 112 oocytes g⁻¹ *T. symmetricus* (Macewicz & Hunter 1993). The fecundity is known to vary due to nutritional conditions of the spawner (Kurita *et al.* 2003), but during the spawning season analysed (November-December 2014) *K* did not show a significant relationship with RF, suggesting that *K* is not a good proxy for RF. This result agrees with those for *Trachurus trachurus*, where *K* and lipid content are not reliable indices as proxy for fecundity (Van Damme *et al.* 2014). In *T. murphyi*, are needed further studies on seasonal dynamics of atresia through the whole maturation cycle, and thus be able to understand the trend of atresia with the body condition (*i.e.*, GSI, *K* and HSI), environmental variables (*i.e.*, temperature) and fecundity of this specie during the whole spawning season.

ACKNOWLEDGMENTS

Data obtained from projects FIP 2004-33, FIP 2005-11, FIP 2006-05, FIP 2012-10, FIP2013-31 and CBJA2014 were provided by Instituto de Investigación Pesquera (INPESCA, Chile; www.inpesca.cl). P. González-Kother thanks CONICYT N° 21130197 doctoral scholarship and CONICYT+PAI/ ATRACCION DE CAPITAL HUMANO AVANZADO DEL EXTRANJERO + Folio N°PAI80160001. M.E. Oliva was supported by MINEDUC-UA Project, code ANT 1855.

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Received 28 May 2019 and accepted 20 March 2020

Associated editor: Mauricio Landaeta D.