

Reproductive cycle of the sub-Antarctic nototheniid *Patagonotothen cornucola* (Nototheniidae) in the Argentine Patagonian Shelf

Ciclo reproductivo del nototénido subantártico *Patagonotothen cornucola* (Nototheniidae) en la costa de la Patagonia Argentina

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Resumen.- La familia Nototheniidae es la más numerosa entre los nototénidos y, a pesar de ser principalmente Antárticos, están muy bien representados en aguas patagónicas. Desde la Antártida hasta las aguas de Sudamérica, han adoptado una gran variedad de estrategias reproductivas. Los peces antárticos suelen tener un ciclo reproductivo bienal mientras que en aguas sub-antárticas los nototénidos pueden reproducirse anualmente o bianualmente. En la zona intermareal de la Patagonia central, el pez más abundante es *Patagonotothen cornucola* y, a pesar de esto, hay poca información sobre su biología. Por esto, el objetivo principal de este trabajo fue estudiar su ciclo reproductivo en la zona intermareal rocosa usando métodos histológicos y morfológicos. Las muestras fueron recolectadas mensualmente en dos sitios intermareales en el Golfo San Jorge, y se calculó el factor de condición, índices hepatosomáticos y gonadosomáticos y se realizaron cortes histológicos de las gónadas que fueron teñidas con tricrómico de un tiempo para determinar los estadios gonadales, además se estimó la fecundidad potencial y relativa. Se determinó que machos y hembras maduran sincrónicamente alcanzando los valores máximos de índices gonadosomáticos entre julio y agosto. En las hembras el índice hepatosomático aumenta simultáneamente con el gonadosomático mientras que en machos se mantiene constante durante todo el ciclo. Se concluye que *P. cornucola* tiene un ciclo reproductivo anual y que el desove ocurre en el invierno. La fecundidad potencial máxima fue de 27.095 oocitos en una hembra de 11,7 cm y se incrementa con la talla.

Palabras clave: *Patagonotothen cornucola*, reproducción, Patagonia, Nototénidos

Abstract.- Nototheniidae is the most numerous family of notothenioids and, although they are mainly Antarctic, they are also well represented in Patagonian waters. In both Antarctic and sub-Antarctic waters, they adopt a wide variety of reproductive strategies. In Antarctic waters they usually have a biennial reproductive cycle, whereas in sub-Antarctic ones, they reproduce annually or biannually. In the intertidal zone of central Patagonia the most abundant nototheniid fish is *Patagonotothen cornucola* and, despite this, there is little information about their biology. The aim of this work was to study its reproductive cycle in a rocky intertidal coast of Argentine Patagonia by means of histological and morphological analyses. Samples were collected monthly at two intertidal sites in the San Jorge Gulf. Condition factor, gonadosomatic and hepatosomatic indexes were calculated and thin sections of gonads were stained with one-step trichrome to determine gonadal stages. Relative and potential fecundity were also estimated. Males and females mature synchronously and reach maximum gonadosomatic index between July and August. In females the hepatosomatic index increases synchronously with gonadosomatic index, while in males it remains constant throughout the cycle. It is concluded that *P. cornucola* has an annual reproductive cycle and that spawning occurs in winter. Maximum potential fecundity is approximately 27,095 oocytes in a 11,7 cm female and it increases with size.

Key words: *Patagonotothen cornucola*, reproduction, Patagonia, nototheniids

INTRODUCTION

The suborder Notothenioidei is a large group of fishes, comprising eight families, distributed mainly in the cold waters of the Antarctica as well as in temperate sub-Antarctic waters. Among notothenioids, the family Nototheniidae is the most numerous, with 12 genera and about 49 species (Eastman & Eakin 2021). On the coast of Argentine Patagonia,

notothenioids are represented by the family Bovichtidae with two genera, *Bovichtus* and *Cottopeca*, the monotypic family Eginopidae with the species *Eginops maclovinus*, and the family Nototheniidae, with one species of the genera *Dissostichus*, *Paranotothenia* and *Lepidonotothen*, two species of the genus *Notothenia*, and eleven species of the genus *Patagonotothen* (Menni *et al.* 1984, López *et al.* 1996).



In Patagonia, some species like *Bovichtus chilensis* and *Notothenia angustata* are benthic and live in rocky reefs (Menni & Gosztonyi 1982, Torres *et al.* 2006), whereas others such as *Eleginops maclovinus* is benthic-pelagic fish living along the coast (Gosztonyi 1974, Sánchez & Prenski 1996, Ceballos *et al.* 2012). Other species like *Patagonotothen ramsayi* and *Dissostichus eleginoides* are abundant in deeper waters (Martínez & Wöhler 2010, Bovcon *et al.* 2013) and are benthic-pelagic. Some of these species grow in intertidal habitats protected under rocks or in rockpools until they migrate to the definitive areas where adults live (Hidalgo *et al.* 2007). In the intertidal zone, they coexist with other representatives such as *Patagonotothen cornucola* and *P. sima* (Gosztonyi & Lopez-Arbarello 2000, Hidalgo *et al.* 2007).

Patagonotothen cornucola Richardson, 1844 is one of the most abundant intertidal fishes of central Patagonia. This species is a typical benthic fish that lives under rocks, among algae or in tidal pools. It is distributed in the southern American cone, including the Falkland Islands (Lloris & Rucabado 1991). The feeding habits of this species are well known throughout much of its distribution (Moreno & Jara 1984, Hidalgo *et al.* 2007, Hüne & Vega 2016, Marcinkevicius *et al.* 2021), but there are no data about its reproductive cycle.

It is well known that Antarctic nototheniids have a biennial sexual cycle and that the season in which they spawn depends on latitude. Those living in the seasonal-pack ice zone

spawn in autumn and winter, while those living in the high Antarctic zone spawn in spring and summer (Duhamel *et al.* 1993, La Mesa *et al.* 2006). In the Beagle Channel, at the southernmost tip of South America, *Patagonotothen tessellata* has a biannual sexual cycle and spawns in July and February (Rae & Calvo 1995a, b), *Paranotothenia magellanica* has an annual cycle with winter spawning (Rae 1991), and *Harpagifer bispinis* has an annual cycle and spawns from mid-July through August (Llompart *et al.* 2020).

The aim of the present study was to provide first and original data on the reproductive cycle of *P. cornucola* in an intertidal rocky shore, using histological and morphological techniques.

MATERIALS AND METHODS

STUDY SITE

The study was carried out in two sites of an intertidal rocky coast of the San Jorge Gulf (central Patagonia), 12 km apart: "El Pique" in the north (45°43'06"S-67°20'38"W) and "Playa Km 8" in the south (45°48'47"S-67°24'46"W) (Fig. 1). Both sites are broad rocky platforms with shallow tide pools, scattered free rocks and channels that connecting them to open waters.

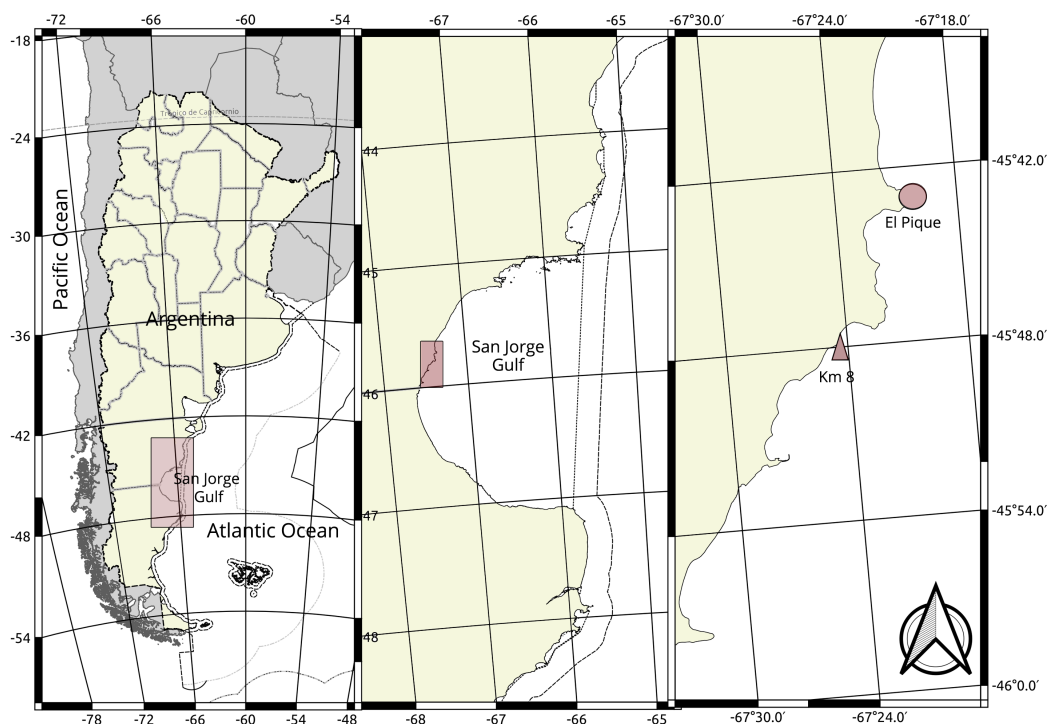


Figure 1. Sampling sites at "El Pique" and "Playa Km 8" beaches in the San Jorge Gulf, Chubut, Argentina / Sitios de muestreo en las playas "El Pique" y "Playa Km 8" del Golfo San Jorge, Chubut, Argentina

SAMPLING AND ANALYSIS METHODS

Sampling was performed monthly from June 2008 to January 2011. A total of 1,214 fishes were collected (Table 1). Specimens were collected by hand under rocks and processed in the laboratory. The total length (TL) of each fish was recorded to the nearest mm. Sex was determined macroscopically by observing the gonads, which were preserved in 10% formalin solution. Eviscerated weight (EW), liver weight (LW) and formalized gonadal weight (GW) were determined with a precision of 0.01 g.

For histological analyses, 435 specimens (176 males and 259 females) were selected from June 2008 to November 2010 (Table 1). Gonads were refixed in Bouin's solution (Kristoffersson & Pekkarinen 1975) and stored in 70% ethanol. They were then dehydrated in ethanol and butanol, and embedded in paraffin. Sections between 5 µm and 7 µm were cut and stained with the one-step trichrome procedure (Gabe 1968).

Following the terminology proposed by Brown-Peterson *et al.* (2011), gonads were histologically classified into four stages: developing, spawning, regressing and regenerating. The gonadosomatic index (GI), calculated as $GI = (GW/EW) \cdot 100$, was considered a proxy indicator of energy invested in reproduction. The hepatosomatic index (HI), calculated as $HI = (LW/EW) \cdot 100$, was considered as a proxy for the energy reserve stored in the liver. Finally, Fulton's condition of factor (K), calculated as $K = (EW/TL^3) \cdot 100$, was considered as a proxy for energy stored in muscle. Gonadal reproductive phases, GI, HI and K were plotted against month, and data from both sites were pooled (Muñoz *et al.* 2010, Hajji *et al.* 2013).

Potential fecundity was estimated gravimetrically with fixed ovarian samples from 73 specimens (Murua *et al.* 2003, Witthames *et al.* 2009). The anterior, middle and posterior sections of each ovary were sampled, weighed to the precision of 0.1 mg and the number of oocytes counted. Only vitellogenic oocytes were used to estimate fecundity. Potential fecundity was calculated as the ratio of ovary weight to sample weight multiplied by the number of oocytes in the sample. Relationships of potential fecundity with TL and EW were assessed by simple linear regression (Sokal & Rohlf 1995). Relative fecundity was calculated as potential fecundity divided by EW.

Sex ratio was tested using the "prop.test" function of the "stats" package of the R software (R Core Team 2020) in RStudio (2020).

Table 1. Distribution of *Patagonotothen cornucola* samples by month and year of sampling in the San Jorge Gulf intertidal / Distribución de las muestras de *Patagonotothen cornucola* por mes y año de recolecta en el intermareal del Golfo San Jorge

	2008		2009		2010		2011	
	N	H	N	H	N	H	N	H
January	-	-	18	10	30	-	26	-
February	-	-	20		64	40	-	-
March	-	-	49	13	54	27	-	-
April	-	-	63	13	30	20	-	-
May	-	-	66	29	64	22	-	-
June	15	4	65	45	60	6	-	-
July	25	5	64	29	31	-	-	-
August	20		64	28	30	-	-	-
September	27	14	55	35	59	-	-	-
October	25	-	53	34	28	-	-	-
November	16	6	11	16	46	31	-	-
December	22	8	-	-	14	-	-	-

N: number of specimens collected by month

H: number of specimens used in histological analyses by month

RESULTS

Out of a total of 1,214 fish sampled, 526 were females and 688 males. The TL of females varied between 5.1 and 13.2 cm, whereas the EW varied between 1.56 and 30.07 g. The TL of males varied between 4.4 and 13.2 cm and the EW varied between 1.25 and 34.89 g. The overall sex ratio (male:female) was 1.3:1 (*i.e.*, significantly different from the expected ratio of 1:1) ($X^2 = 21.352$, $df = 1$, $P < 0.0001$).

In females, the plot of GI against month showed an annual reproductive cycle with one reproductive event (Fig. 2). GI remained low from September to May, when it started to increase until August. Spawning occurred between July and August. HI had approximately the same cycle as GI. Maximum HI values were observed in June, shortly before GI reached its maximum values. Although K it did not show a great annual variation, values decreased in June, before spawning.

In males, the GI plot against month also showed an annual reproductive cycle with one reproductive event (Fig. 3). Corresponding to what was observed in females, GI remained low between September and May, reaching the maximum value in August. HI and K showed no variation during the year.

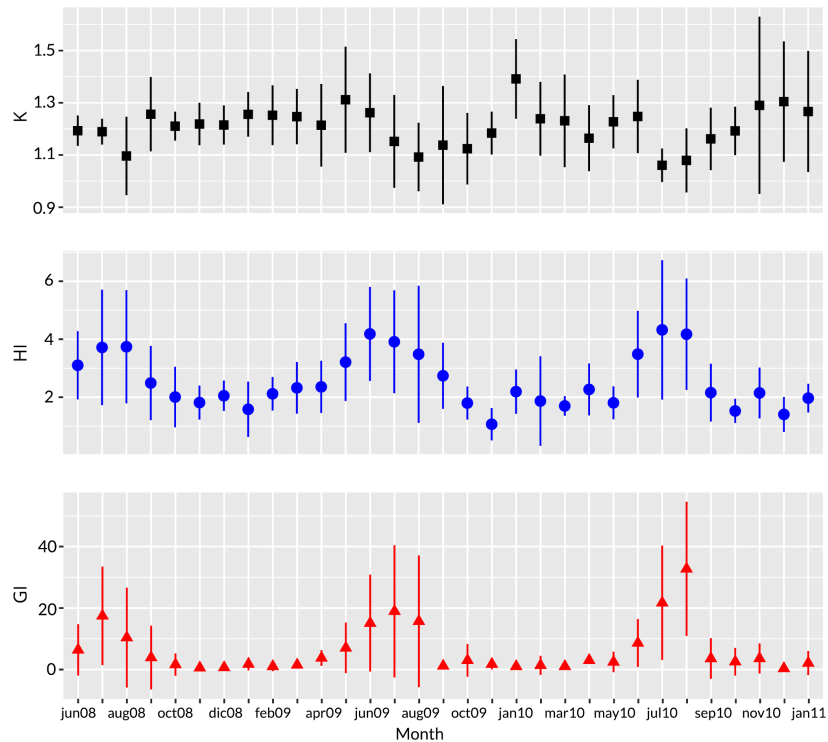


Figure 2. Monthly variation of gonadosomatic index (GI), hepatosomatic index (HI) and Fulton's condition factor (K) for *P. cornucola* females / Variación mensual del índice gonadosomático (GI), índice hepatosomático (HI) y el factor de condición de Fulton (K) para hembras de *P. cornucola*

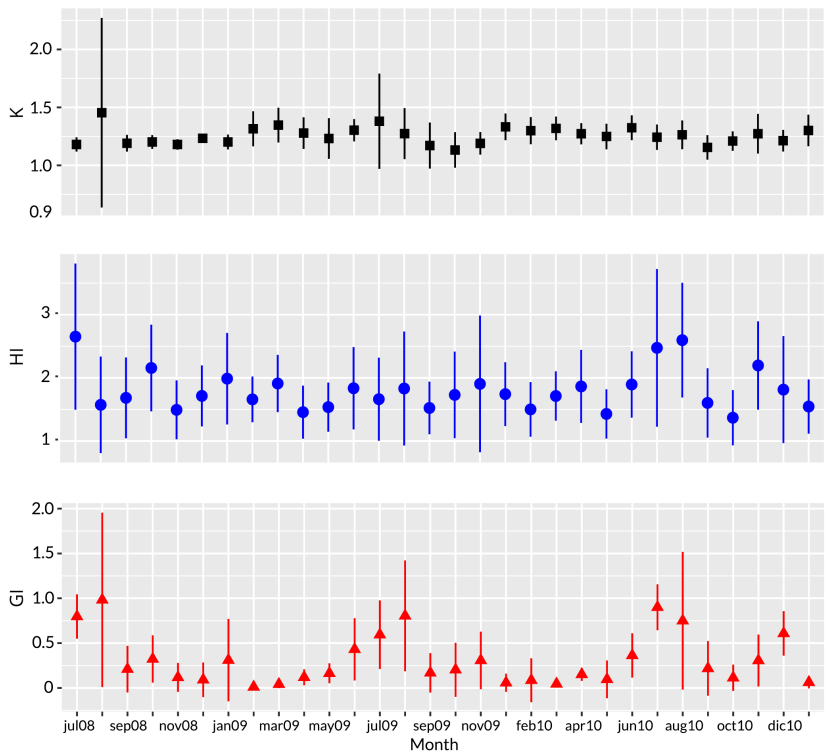


Figure 3. Monthly variation of gonadosomatic index (GI), hepatosomatic index (HI) and Fulton's condition factor (K) for *P. cornucola* males / Variación mensual del índice gonadosomático (GI), índice hepatosomático (HI) y el factor de condición de Fulton (K) para machos de *P. cornucola*

Histological analysis confirmed the results of the annual GI cycle. Maximum abundance of vitellogenic oocytes 3 (Vit3) was observed in July, while the presence of oocytes in germinal vesicle migration phase (GVM) was observed in July and August (Figs. 4A and 5). This indicates that oocytes were ready to spawn. In September, most oocytes were in the cortical alveoli (CA) phase, indicating that spawning had been completed. Maximum frequency of testis in spawning capable phase (SC) was observed in July and August, whereas that of testis in regressing phase (Rss) was observed in September and October (Figs. 4B and 6). This observation is consistent with the maturation phases of females and confirms that spawning occurs between July and August.

The TL of the specimens used to determine fecundity ranged between 6.5 cm and 11.7 cm, whereas their EW ranged between 3.42 g and 18.68 g. Potential fecundity ranged between 1,826 to 27,095 oocytes per female and relative fecundity ranged between 260.4 and 2,651.7 oocytes per gram of EW. The variation of potential fecundity with TL ($AdjR^2=0.39$) and EW ($AdjR^2=0.42$) is shown in Figure 7A and B. In both cases, an increase in potential fecundity was observed with increasing size.

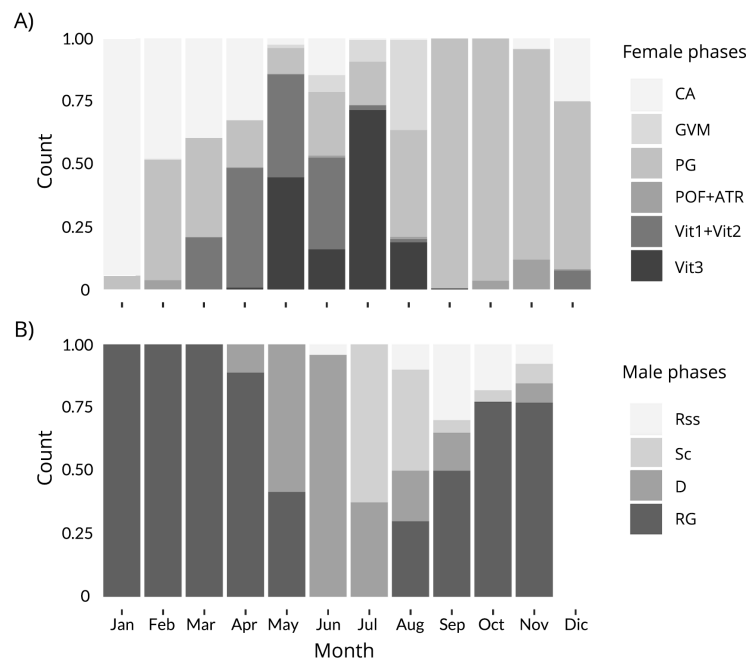


Figure 4. Monthly variation of gonadal phases during reproductive cycle of *P. cornuicola*. A) Female phases. B) Male phases. ATR: atretic oocyte, CA: oocyte in cortical alveolar phase, D: development stage, GVM: oocyte in germinal vesicle migration phase, PG: oocyte in primary growth phase, POF: post-ovulatory follicle, RG: regenerating stage, Rss: regression stage, Sc: spawning capable stage, Vit1: oocyte in primary vitellogenic, Vit2: oocyte in secondary vitellogenic, Vit3: oocyte in tertiary vitellogenic / Variación mensual de las fases gonadales durante el ciclo reproductivo de *P. cornuicola*. A) Fases de hembras. B) Fases de machos. ATR: oocito atrésico, CA: oocito en fase cortical alveolar, D: fase de desarrollo, GVM: oocito en fase de migración de la vesícula germinal, PG: oocito en fase de crecimiento primario, POF: folículo post ovulatorio, RG: fase de regeneración, Rss: fase de regresión, Sc: fase de preparados para el desove, Vit1: oocito en vitelogénesis primaria, Vit2: oocito en vitelogénesis secundaria, Vit3: oocito en vitelogénesis terciaria

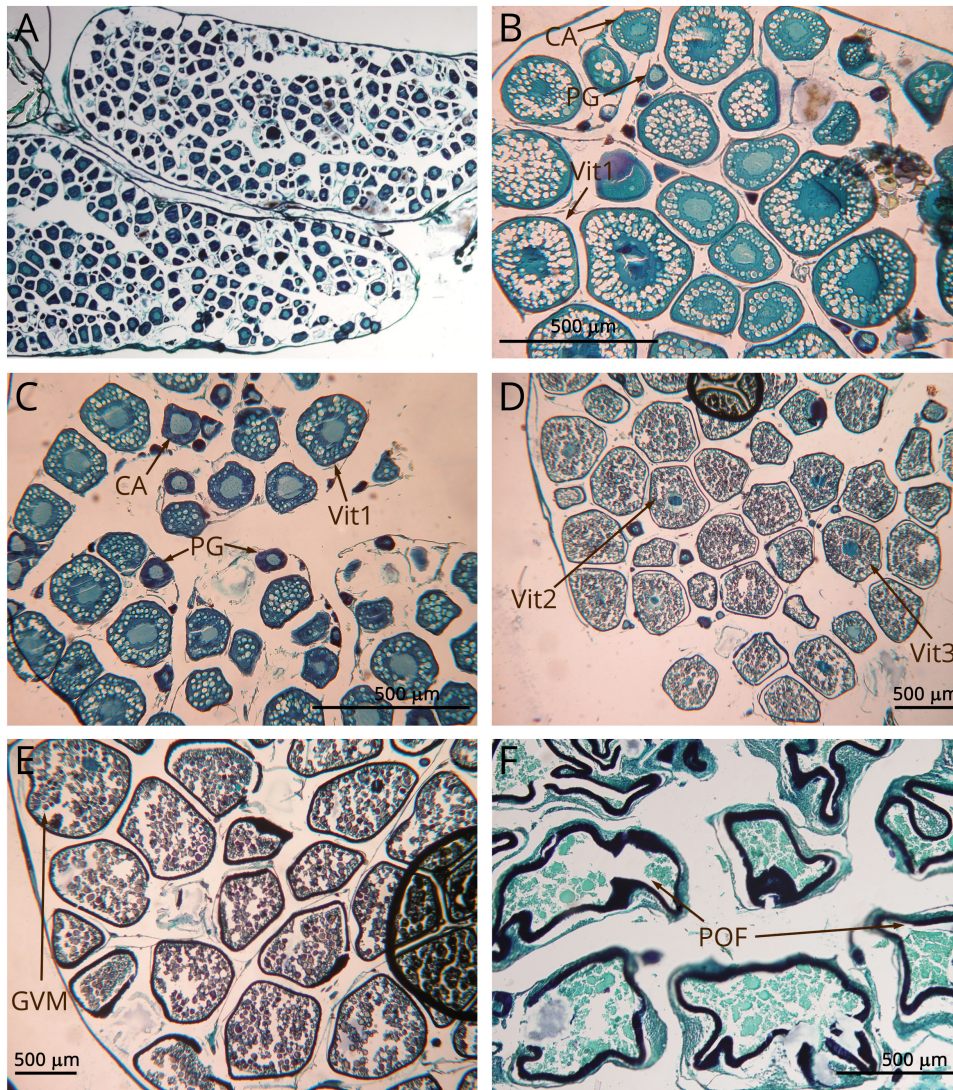


Figure 5. Photomicrograph showing the stages of ovary development in *P. cornucola*. A) Overall view of a regenerating ovary, B-C) ovary in early development stage, D) ovary in advanced development stage, E) ovary in spawning capable stage, F) ovary in regressing stage. CA: oocyte in cortical alveolar phase, GVM: oocyte in germinal vesicle migration phase, PG: oocyte in primary growth phase, POF: post-ovulatory follicle, Vit1: oocyte in primary vitellogenic, Vit2: oocyte in secondary vitellogenic, Vit3: oocyte in tertiary vitellogenic / Microfotografía mostrando los estadios de desarrollo del ovario en *P. cornucola*. A) Vista general de un ovario en regeneración, B-C) ovario en estadio de desarrollo temprano, D) ovario en estadio de desarrollo avanzado, E) ovario en estadio preparado para desovar, F) ovario en estadio de regresión. CA: oocito en fase cortical alveolar, GVM: oocito en fase de migración de la vesícula germinal, PG: oocito en fase de crecimiento primario, POF: folículo post ovulatorio, Vit1: oocito en vitelogénesis primaria, Vit2: oocito en vitelogénesis secundaria, Vit3: oocito en vitelogénesis terciaria

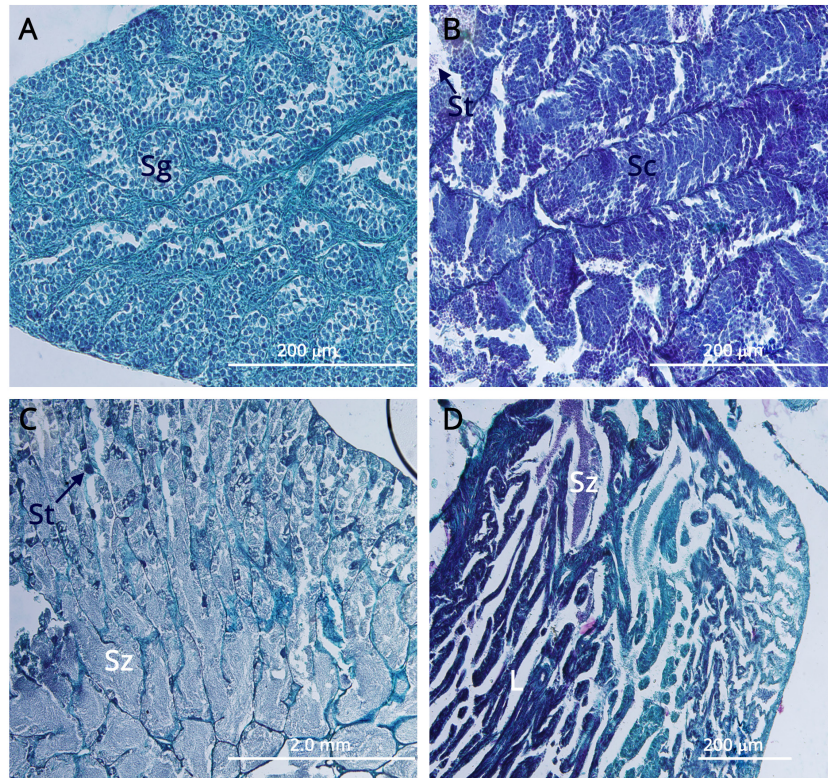


Figure 6. Photomicrograph of testicular development stages in *P. cornucola*. A) testis in regenerating stage, B) testis in developmental stage, C) testis in spawning capable stage, D) testis in regression stage. L: lumen, Sc: spermatocyte, Sg: spermatogonia, St: spermatid, Sz: spermatozoa / Microfotografía los estadios de desarrollo testicular en *P. cornucola*. A) testículo en estadio de regeneración, B) testículo en estadio de desarrollo, C) testículo en estadio preparado para desovar, D) testículo en estadio de regresión. L: lumen, Sc: espermatocito, Sg: espermatogonia, St: espermátida, Sz: espermatozoide

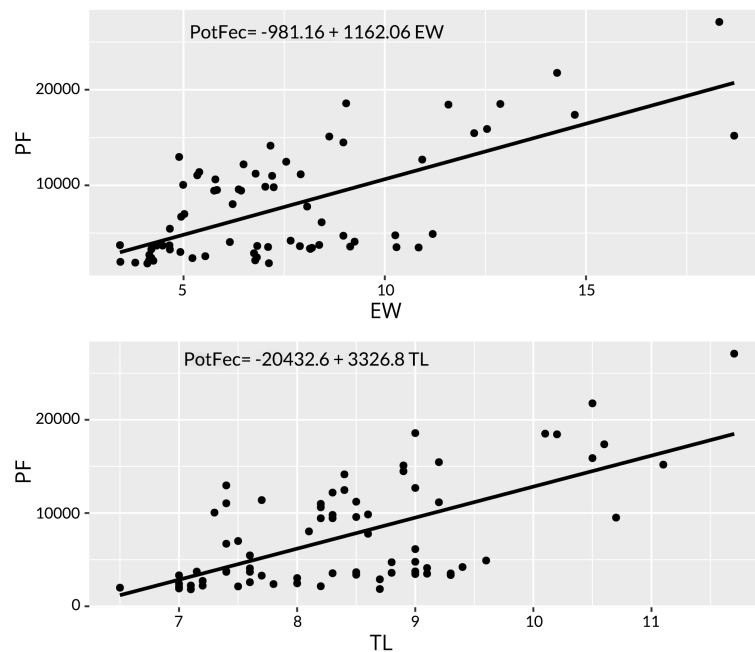


Figure 7. Regression of potential fecundity (PF) with respect to: A) eviscerated weight (EW) and B) total length (TL) in *P. cornucola* from Patagonian intertidal rocky shores / Regresión de la fecundidad potencial (PF) respecto de: A) peso eviscerado (EW) y B) longitud total (TL) en *P. cornucola* de intermareales rocosos patagónicos

DISCUSSION

This study provides the first data on the reproductive cycle of the nototheniid fish *Patagonotothen cornucola*. The gonads are like those of most teleosts: females have cystovarian-type ovaries, in which the coelom forms a closed sac, the lumen, where ovulation occurs (McMillan 2007), whereas males have unrestricted lobular-type testes, with blind lobules at their distal end, and cysts with developing germ cells distributed around them (Vizziano *et al.* 2008).

According to the annual GI trend, *P. cornucola* gonads remain underweight from spring to mid-autumn and then undergo rapid growth until mid-winter, when they reach the maximum weight. This was confirmed by histological analyses, which showed that, from spring to mid-autumn, females move from the regressing (post-ovulatory follicles + atretic oocytes) and regenerating phases [primary growth oocytes (PG)] to the developing phases (PG+CA+Vit1+Vit2); and then, until mid-winter, to the SC phase (Vit3+GVM). Two groups of oocytes at different development stages were observed at the same time: one group of PG oocytes appearing throughout the year and a second group that shift to the developing phases to spawn in that season. This is clear evidence that *P. cornucola* spawn synchronously.

In the case of males, the maximum frequency of SC testes was observed in mid-winter, following the sequence of gonadal phases observed in females. This indicates that *P. cornucola* has only one reproductive period during the year and that spawning occurs in winter, between July and August. This differs from that observed in the Beagle Channel by Rae (1991), who, based on the observation of females at different stages of maturation in winter and summer, suggested that *P. cornucola* has two spawning periods in one year. However, this author did not develop a complete reproductive study. It would thus be interesting to study whether *P. cornucola* has one reproductive period per year in the north and two periods in the south of its distribution.

Results of this and previous studies allow concluding that notothenioids show different reproductive patterns. For example, in central Patagonia, *P. cornucola* has an annual oocyte maturation cycle with one yolked oocytes batch and one reserve stock of oocyte, and therefore one spawning period per year during winter. In the Beagle Channel, *P. tessellata* has a biannual oocyte maturation cycle with a batch of yolked oocyte and one reserve stock of oocyte, and therefore two spawning periods per year, one in winter and another in summer (Rae 1991, Rae & Calvo 1995a). In Antarctica, nototheniids have a biennial oocyte maturation cycle, with seasonal-pack ice species spawning in autumn/winter and high-Antarctic zone species spawning in spring/summer (Kock & Kellerman 1991).

Temperature also seems to play a very important role in the sexual cycle of nototheniids, as there is latitudinal variation in reproductive seasons related to temperature. In central Patagonia, *P. cornucola* reproduces in winter with water temperatures ranging between 8 to 11 °C (per. obs of the main author), whereas, in the Beagle Channel, *P. cornucola* has one or two reproductive periods, one in winter, with temperatures around 4.3 °C, and the other in summer, with temperatures between 9 and 11 °C (Rae & Calvo 1995a). Apparently, nototheniids do not prefer temperatures above 11 °C, so it would be interesting to study species living north of the San Jorge Gulf.

Another effect of the environmental conditions on the reproductive cycle of *P. cornucola* can be seen at the beginning and end of the SC phase: in 2008 and 2009 females reached this phase in August, whereas in 2010 they reached it in July. In contrast, in 2008 and 2009 males reached this phase in July, whereas in 2010 they reached it in August. Variability of the sexual cycle in relation to environmental conditions has also been observed in other notothenioids species, such as in *Trematomus* from Antarctic waters, which show plasticity with respect to environmental and ecological conditions that can vary geographically and temporally (La Mesa *et al.* 2006), and *P. tessellata*, in which gametogenesis occurs more rapidly in summer than in winter (Rae & Calvo 1995a).

Vitellogenin, which is involved in oocyte maturation and largely responsible for oocyte growth, is produced in the liver (McMillan 2007). The simultaneous increase in HI and GI in *P. cornucola* females and their subsequent decrease indicate that vitellogenesis is occurring. In June, just before spawning, there was a slight decrease in K. Perhaps the high energy demand in the last part of the vitellogenesis process requires an extra source of energy from somatic tissues.

In males, HI and K did not show seasonal variation as observed in GI. This is evidence of the low energy required for testicular maturation. In *P. tessellata* males from the Beagle Channel, Rae & Calvo (1995a) observed a decrease in HI during evacuation and suggested that this species uses energy stored in the liver to sustain general metabolism during nesting, a period during which males do not feed. In *P. cornucola* from San Jorge Gulf, parental care was observed during August, after spawning, but it could not determine whether it is the male or female that care of the nest or whether they feed during nesting. These issues are subject for future research.

Finally, a maximum potential fecundity (PF) of 27,095 oocytes was observed in the largest female (11.7 cm TL). As expected, the number of oocytes per female was size-dependent and increased with increasing size. These results are in agreement with those previously reported for other sub-Antarctic and Antarctic notothenioids, which showed a wide range of PFs in relation to parental fish size and latitudinal distribution. As an example, *P. tessellata* spawned 62,033 oocytes in the Beagle Channel at 24 cm TL, *Notothenia angustifrons* spawned 12,900 oocytes off the South Sandwich Islands at 17 cm TL, and *Nototheniops nudifrons* spawned 9,866 oocytes in South Georgia at 18 cm TL (Kock & Kellerman 1991, Rae & Calvo 1995b).

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