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Reproductive biology of the icefish *Champsocephalus esox* (Günther, 1861) (Channichthyidae)

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Abstract: *Champsocephalus esox* is the only icefish species found outside Antarctica. In a population from the Beagle Channel, the complete annual reproductive cycle has been determined. Gonad maturity stages have been established for males and females by histological analysis. Males are sexually mature from January–September with a maximum gonadosomatic index (GSI) of 3.63%. Histologically, testes are very homogeneous and the degree of maturation of the testicular cysts is similar among different tubules at the same maturation stage. Running ripe testes have mature sperm and a few spermatogoniae arranged near the blind end of the tubules. In sexually active females that are found from February–November, ovaries contain only ripe oocytes or postovulatory follicles, together with a batch of previtellogenic oocytes. During hydration, oocyte diameter reaches 2.7 mm, and oocyte dry weight increases due to material intake, the maximum GSI in ovulated ovaries is 21.89 and hepatosomatic index (HSI) decreases. These facts suggest a transfer of matter from liver to the gonads. Absolute fecundity ranges from 3303–8600 oocytes. Relative fecundity ranges from 22.5–43.5 oocytes per gram total weight. In *C. esox*, relative fecundity has a similar range to those quoted for the different *C. gunnari* populations, whilst mature oocyte diameter is small and reproductive season extended compared to the same parameters in other Channichthyidae.

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Introduction

Almost all of the species of the family Channichthyidae, commonly called icefish, are found only in the Antarctic region. The absence of haemoglobin in the blood constrains their distribution to cold waters with high oxygen content, and where their metabolic requirements, dependent on temperature, are low (Eastman 1993). *Champsocephalus esox* is the only species of this family not inhabiting Antarctic waters (Nakamura *et al.* 1986), and is confined to the Magellan Province (*sensu* Balech 1954).

Previous studies on reproduction in icefish have described egg size, fecundity and gonadosomatic index (GSI) (Kock 1990, Kock & Kellermann 1991, Vacchi *et al.* 1996) but gonads were rarely examined histologically.

Macchi & Barrera Oro (1995) have recently carried out a histological study of the ovarian development in *Champsocephalus gunnari* Lönnnberg but their descriptions are limited to specimens caught during February and March. Shandikov & Faleeva (1992) studied the histological characteristics of gonad development in *Chionodraco hamatus* Lönnnberg, *C. myersi* Tyler and *Neopagetopsis ionah* Nyebelin on samples taken during the summer months and finally, Pestarino *et al.* (1995) performed a short histological description in *C. hamatus*.

In Channichthyidae, fecundity is very low, a total of 35 000 oocytes was not exceeded (Permitin 1973, Kock *et al.* 1985, Kock & Kellermann 1991). Given their reproductive characteristics, it is likely that channichthyds have a limited capacity to overcome intensive fishery exploitation. Duhamel (1991) and Kock (1991) observed a reduction in both the abundance of the stocks and the total area of distribution in the populations exploited at South Georgia and the South Orkney Islands.

Champsocephalus esox is distributed around Magellanic and southern Patagonian waters (Nakamura *et al.* 1986, Miller 1993, Kock & Everson 1997). Miller (1993) suggested that this species is not commercially exploitable because it was only captured in low quantity. Furthermore, he quoted Hart (1946) who reported no capture around the Falkland Islands during winter.

In the Beagle Channel, the diet of *C. esox* population consisted of crustaceans and small nototheniids (Isla 1993). However, other biological characteristics, such as growth and reproductive biology have not yet been investigated.

The reproductive features of *C. esox* could give an insight into the reproductive adaptations of the Channichthyidae. The aims of this paper are to describe the reproductive cycle, to estimate the absolute and relative fecundity and to compare their reproductive traits with those of the other icefish.

Material and methods

Material was processed according to the regular sampling protocol applied in the research project "Bioecology of the

Beagle Channel Ichthyofaunal Resources" (Calvo *et al.* 1992).

Trammel nets were deployed at 2–5 m depth for 24 h in fixed stations near Ushuaia Bay (54°50'S, 68°20'W) on a monthly schedule. Sampled specimens were carried to the laboratory, measured (Total Length, nearest mm below) and weighed (nearest 0.1 g of total weight, TW). Gonads, liver and stomach were removed, weighed (nearest 0.01 g).

Absolute fecundity was established as total number of oocytes contained in both formalin-fixed ovaries, while relative fecundity was stated as the number of oocytes per gram of total or gutted weight. Oocyte diameter and aspect were examined in smears and oocytes were counted by the naked eye. For

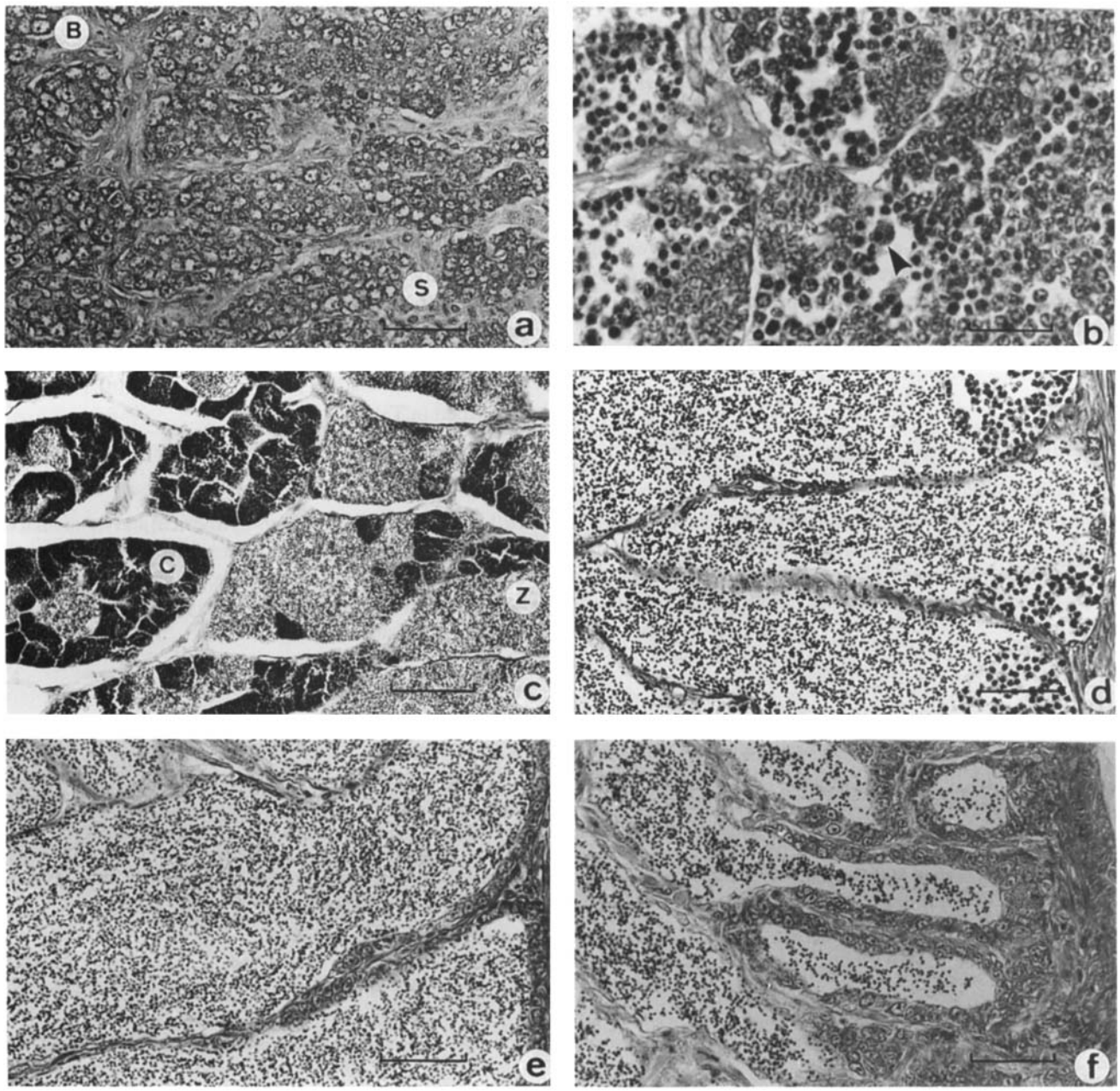

Fig. 1. a. Proliferation stage. Big spermatogoniae (B) at the bottom of the tubules, in the right side small spermatogoniae (S) in one or two layers. Bar = 250 μm. **b.** Advanced Maturation stage. Several cysts contain different kinds of male cells. Phagocytary cells (Arrow). Bar = 400 μm. **c.** Advanced Maturation Stage. Left side with spermatocyte cysts (C), in the right side spermatozoa (Z) free in the tubules near the ducts. Bar = 100 μm. **d.** Advanced Maturation Stage. In the late development, the spermatocyte cysts are confined to the bottom of the tubules. Spermatozoa are free in the tubular lumen. Bar = 250 μm. **e.** Total Maturation. Isolated spermatogoniae at the bottom of tubules, filled with free spermatozoa. Bar = 250 μm. **f.** Post Evacuation. Tubule walls are thick, spermatogoniae are organised in layers. Free spermatozoa are scarce. Bar = 250 μm.

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each mature ovary, several aliquots of a hundred formalin fixed oocytes were washed with fresh water, oven dried at 70°C to a constant weight and then weighed to the nearest 0.1 mg.

The remaining gonads were macroscopically described and fixed in 10% formaldehyde or Bouin's fluid that improves histological appearance. Then, testis and immature ovaries were embedded in paraffin wax following the standard procedures. Mature ovaries were washed in chloroform and methyl benzoate and afterwards embedded in celloidin-paraffin wax. This process improves the consistency of the material when there is abundant yolk. Sections 5–7 mm thick were cut and then stained with Erlich's haematoxylin-eosin and Gomori's trichrome stain.

GSI was calculated as the percentage of gonad weight to total weight ± standard deviation (s d). HSI was calculated as the percentage of liver weight to total weight. Relationships among different stages were analysed using one-factor Anova and the respective comparisons were performed by Tukey test (Zar 1984).

Results

The testis

In *C. esox*, paired testes are fused at the level of the anal opening and are located in the dorsal portion of the visceral cavity close to the kidneys. The testes are white in colour, and their brightness varies according to the degree of maturation. In transverse section, the testes vary from circular to heart-shaped.

Externally, the testis is covered by a thick and consistent *tunica albuginea* constituted by numerous connective fibres and muscular cells. Blood vessels with a wide lumen are present in all histological images.

In cross section (Fig. 1), two different zones can be distinguished:

a) The central region, where testes are in contact, with wide spaces corresponding to the main ducts covered by cubic epithelial cells, and

b) a denser peripheral region where spermatogenesis occurs and where connective walls are conspicuous and separate each spermatic tubule.

Tubules are radially orientated, slightly oblique to the caudal region. Each maturation stage has a defined microscopic image and is determined by the most abundant cell type of the male germinal line. In post-evacuation specimens, the epithelial cells that cover the duct increase in thickness, contain vacuolae in its apical extreme and seem to be actively phagocytizing the residual spermatozoa. Connective and muscular fibres become very conspicuous as both intertubular and external walls increase in thickness. Reproductive condition of males is described in Table I.

The ovary

In this species, ovaries are sub-cylindrical and somewhat short in relation to the size of the specimens. During maturation there are changes in ovarian volume, (especially in the diameter) and in colour (changing from white to yellowish and translucent at Total Maturation).

Table I. Description of gonad maturity stages for male icefish *Champsocephalus esox*.

Maturation stage	Cellular type and diameters	Abundance	Location	Mean GSI Range Sample size
Proliferation (Fig. 1a)	large SPG under cellular division 10–12 μm small SPG, 5–7 μm	less abundant more abundant	isolated or in cluster near to the blind end of the tubule towards the centre of the testis forming one or two layers	0.17 0.07–0.79 24
Maturation	small SPG, 5–7 μm SPC, 3.5 μm	regular, decreasing in number regular, increasing in number and become dominant	close to the testis wall starts close to the duct, and extends to the periphery	0.58 0.1–1.12 19
Advanced Maturation (Fig. 1b)	SPG (on cellular division) SPC (on cellular division) SPD SPZ, 1–1.5 μm	regular to scarce dominant type scarce variable	maturation wave goes from centre to the periphery of the testis (Fig. 1c & d)	2 0.87–3.63 12
Total Maturation	SPG SPC SPZ	scarce scarce dominant	close to the blind end of the tubule (Fig. 1e) attached to the tubule walls filling the tubules	2.01 0.7–3.22 6
Post Evacuation (Fig. 1f)	SPG SPZ	scarce moderate	blind end of the tubule Disorderly in the tubule lumen	0.53 0.21–0.7 3

SPG = spermatogonia; SPC = spermatocyte; SPD = spermatid, SPZ = spermatozoa

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The ovarian wall is composed of a peritoneal epithelium and strong muscular layers, which varies in thickness according to the ovarian content. The ovarian lamellae are scarce and are placed transversally to the major ovarian axis from the walls to the lumen. Their unions with the wall are formed by a significant number of muscular and connective fibres. Wide zones filled with blood plasma are frequently observed in the germinal crest between the oocytes.

Major microscopic characteristics distinguishing oocyte development and sexual maturation stages are described in Table IIa and Table IIb, respectively.

Atresia processes

Atresia could occur by autolysis or phagocytizing activity.

Autolysis, with non-intrusion of phagocytic cells was observed in basophilic oocytes larger than 120–150 μm as well as in the vesicular yolk oocytes of about 200 μm and in some oocytes with globular yolk. Cytoplasm becomes intensively basophilic, the nucleus becomes deformed and the chorion fragmented.

Phagocytizing activity was only observed in oocytes containing globular yolk. Numerous follicular cells pass

Table IIa. Microscopic characteristics for the determination of the maturity stages in the ovaries of *Champsocephalus esox.*

Germ Cells	Nucleus	Cytoplasm	Thecal cells	Follicular cells	Chorion
Oogoniae	5–15 μm. One conspicuous nucleolus.	< 20 μm	none	none	none
Previtellogenic oocyte (Fig. 2a)	lampbrush chromosomes and several peripheral nucleoli. 10–50 μm	20–150 μm and basophile	1 layer	none	none
Vesicular yolk oocyte	lampbrush chromosomes and several peripheral nucleoli. 50–120 μm	120–400 μm. Acidophilic yolk vesicles with centripetal growth	1 layer	5–7 μm height	5 μm thick
Globular yolk oocyte (Fig. 2b)	100–150 μm Irregular contour with about fifteen peripheral nucleoli	300–350 μm. Beginning the deposition of PAS positive and acidophilic globules of 25 μm. 500–700 μm. Filled with yolk globules of 50 μm	v. thin	3–5 μm height	5–30 μm thick with transversal and tangential striations
Hyalinized oocyte (Fig. 2c)	Nucleus is displaced to the periphery	Yolk coalescence starts at 700 and ends at 2700 μm in diameter. Peripheral basophilic ring surrounded by yolk vesicles.	v. thin	5 μm height	25–30μm thick

Table IIb. Description of gonad maturity stages for female icefish *Champsocephalus esox.*

Ovarian stages	Histological features	Muscular tunica	GSI s d sample size
Proliferation	cluster of oogonia, few basophilic and vesicular oocytes	30–50 μm thick	0.41 0.13 2
Early maturation (Fig. 2a)	Oogonia; basophilic and dominance of yolk vesicles oocytes	50–110 μm thick	0.72 0.37 15
Advanced maturation (Fig. 2b)	Basophilic yolk vesicle and dominance of globular yolk oocytes	100 μm thick	1.66 0.99 13
Total maturation (Fig. 2c)	Few basophilic and dominance of hyalinized oocytes	25 μm thick	9.75 5.12 12
Ovulated (Fig. 2d)	Few oogonia, basophilic oocytes and post-ovulatory follicles into retracted germinal crest. Free hydrated oocytes (1000–2700 μm) into the ovarian lumen	25 μm thick	14.9 8.1 5
Post spawning maturation	Basophilic, vesicular and globular yolk oocytes. Residual ovulated oocytes larger than 1000 μm and post-ovulatory follicles under different degree of resorption	100–220 μm thick	0.69 0.03 7

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through the chorion and invade the oocyte cytoplasm (Fig. 2e). After this the remaining yolk is resorbed inside the atretic body (Fig. 2f), while some zones of the follicular layer remain complete. The intrusion of phagocytic cells also occurs in the remaining mature oocytes which had been already ovulated. The chorion remains somewhat complete but the cytoplasm undergoes vacuolisation and liquefaction.

Seasonality of the reproductive cycle

Fish were captured throughout the year with the maximum caught from January to March (n = 121) and many fewer during the remaining months (n = 46). Sexual active specimens (*males*: Advanced and Total Maturation stages and *females*: Total Maturation, Ovulated and Post-spawning stages) were

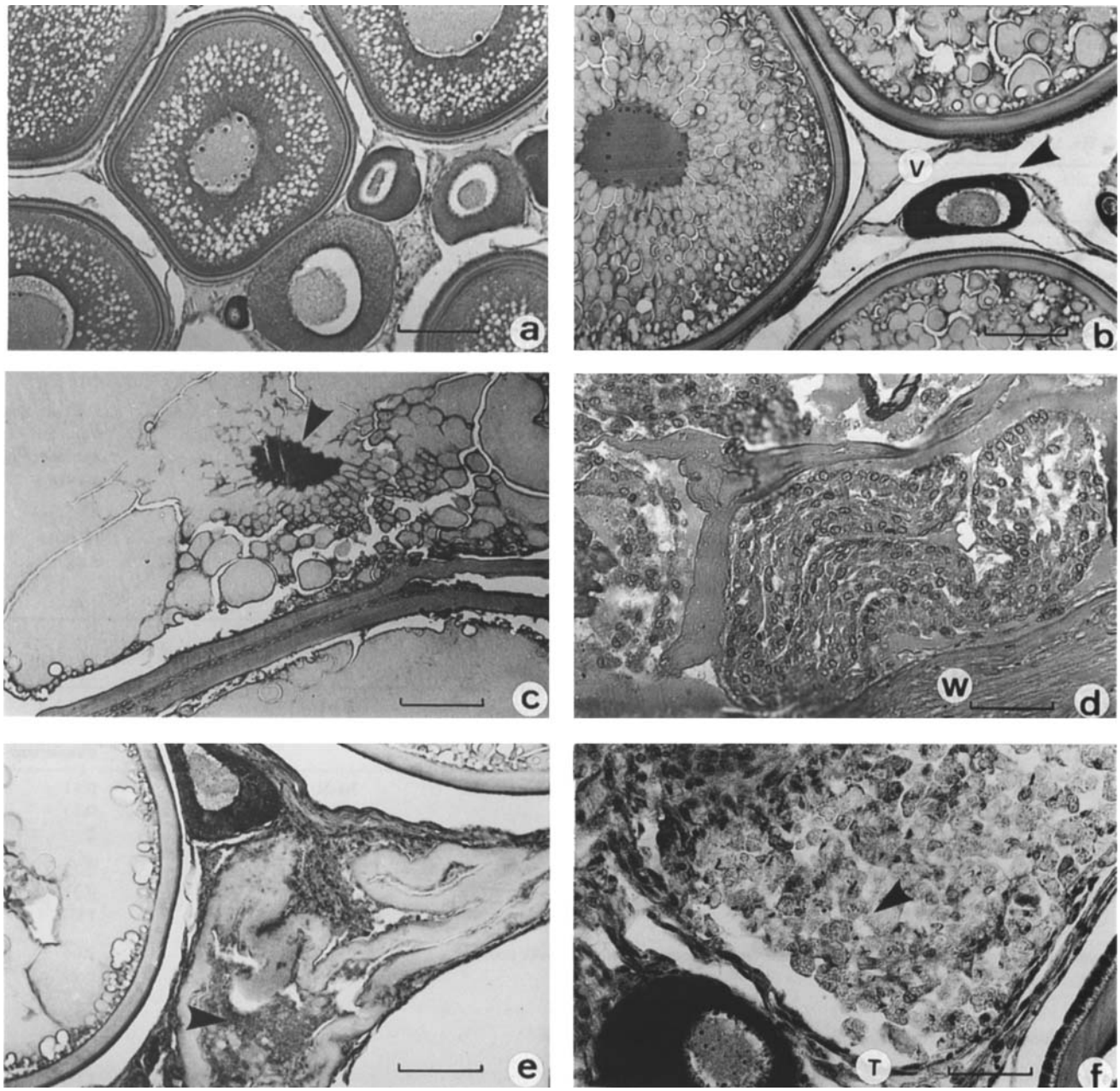

Fig. 2. a. Early maturation. Previtellogenic and yolk vesicular oocytes. Bar = 100 μm. **b.** Advanced Maturation. Globular yolk oocytes with a peripheral ring of vesicular yolk. Basophilic previtellogenic oocytes (arrow). Large blood vessel (V). Bar = 100 μm. **c.** Total Maturation. Coalescence of yolk globules and oocyte nucleus displacement (arrow). Bar = 100 μm. **d.** Post spawning. Post ovulatory follicle in a retracted ovarian crest, near ovarian wall (W). Bar = 250 μm. **e.** Atretic process in a yolked oocyte. Chorion contorted and invaded by granulosa cells (arrow). Bar = 100 μm. **f.** Corpora atretica with granular phagocytic cells (arrow) and remains of globular yolk. Thecal layer (T). Bar = 250 μm.

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found from December to October, with maximum abundance during late March–August (Fig. 3). From January to early March, the samples were mainly composed of males in Proliferation and Maturation stages and by females in Proliferation and Early Maturation stages. Only a few females were in Massive Atresia stage.

Gonadosomatic and hepatosomatic index variation

In *C. esox* males, HSI (mean: 1.97; s d: 1.33) reach a maximum of 3.06. Its variation was not correlated with gonadal maturation stages, or to GSI ($P > 0.05$). In contrast, females HSI was positive correlated to both. It can be seen (Fig. 4), that females undergoing a pre-maturation period had GSI values lower than 2%, which correspond to HSI values lower than 4%. On the other hand, specimens in Total Maturation showed GSI values higher than 10%, while HSI reached a maximum value of 5%. Finally, GSI tended to increase while HSI decreased to values closed to 5% during the Ovulated stage. Tukey test for comparison showed significant differences in HSI between Total Maturation stage, previous stages, i.e. from Proliferation to Advanced Maturation; and Post Evacuation stage ($P < 0.05$). However, Total Maturation and Ovulated stages showed similar HSI ($P > 0.05$).

In relation to GSI, the statistical comparison showed no significant variation between Total Maturation and Ovulated stages ($P > 0.05$). Nevertheless, these were different to the remaining stages ($P < 0.05$).

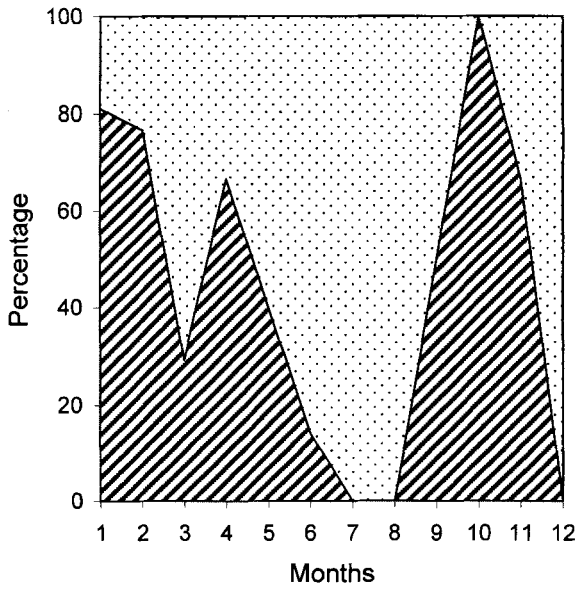

Fig. 3. Temporal distribution of gonad stages of males ($n = 59$) and females ($n = 58$). Dotted area corresponds to Advanced and Total Maturation stages, and Total Maturation; Ovulated and Post-spawning for male and females, respectively. Hatched area corresponds to remaining stages.

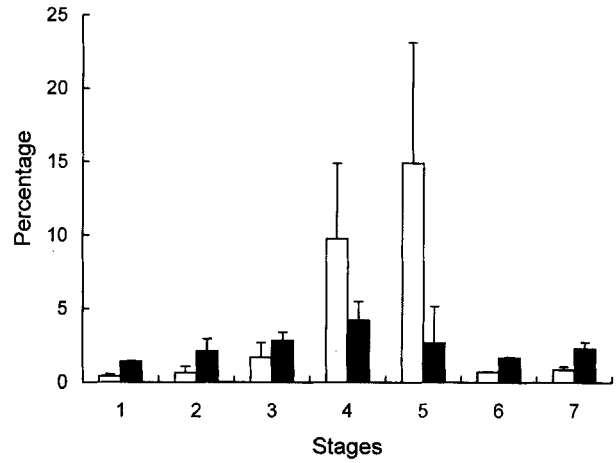

Fig. 4. Relationship between average hepatosomatic index (HSI, solid bars) and average gonadosomatic index (GSI, open bars) in each female gonadal stage. 1. Proliferation ($n = 4$), 2. Early Maturation ($n = 18$), 3. Advanced Maturation ($n = 14$). 4. Total Maturation ($n = 13$). 5. Ovulated ($n = 7$). 6. Post-spawning Maturation ($n = 4$), 7. Massive Atresia and Phagocytic Atresia ($n = 7$). Vertical lines - standard deviation.

Fecundity

Absolute fecundity estimated in fishes ranging between 27 and 35 cm (TL) varied between 3303 and 8600 oocytes. Regressing oocyte number on TL showed that an expotential model would account for almost 60% of the fecundity variation (Fig. 5). Relative fecundity varies between 22.5 and 43.3 oocytes g^{-1} TW, and 27.3–51.5 oocytes g^{-1} gutted weight.

Diameter distribution of hydrated oocytes from mature ovaries showed a high variation in each specimen, which may represent considerable dispersion in oocyte volume or mass.

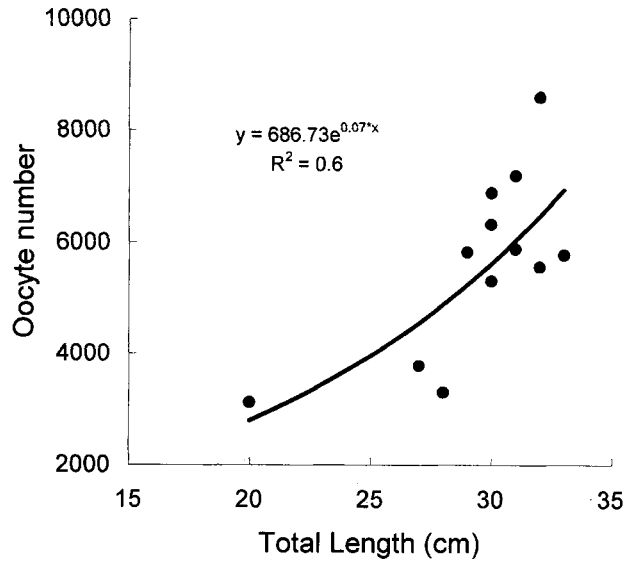

Fig. 5. Scatter plot of Total Length against absolute fecundity in mature ovaries.

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The observed maximum oocyte diameter was twice the minimum value (Fig. 6). In addition, the oocyte dry weight was positive correlated with mean oocyte diameter and GSI (Fig. 7).

Discussion

Previous research on the reproductive biology of Channichthyidae determined fecundity, oocyte diameter and spawning season but the gonad histology has never been described during a complete annual cycle (Permitin 1973, Kock 1979, Duhamel *et al.* 1993, Ekau 1991).

Microanatomical testicular structure

In teleosts, Grier *et al.* (1980) and Billard (1986) established the presence of two different types of testicular structure. In the restricted spermatogonial type, characteristic of Atheriniform, spermatogoniae are restricted to the final portion of the tubules. In the unrestricted spermatogonial type, observed in the remaining teleosts, spermatogoniae are arranged all along the tubules.

The immature testes of *C. esox* match with the unrestricted spermatogonial type. From Fig. 1 a, b & d, the "maturation wave" of germinal cells can be observed from near the deferent duct to the blind end of the tubules. During the late maturation stages, spermatogonia remain restrained to this zone. A similar arrangement is found in other subantarctic nototheniids (Calvo *et al.* 1992, Rae & Calvo 1995a, 1995b) making a difference from the general pattern described for the "unrestricted testes" teleost species. In them, spermatogonia are distributed along the tubules (Grier *et al.* 1980, Billard 1986).

After spawning, spermatogoniae begin to proliferate inwards along the tubules from the bottom and lateral walls (Fig. 1f).

Reproductive effort

In *C. esox* males, the highest GSI was 3.22%, showing one of the smallest reproductive effort described for the Channichthyidae that normally range between 6% and 8% (Kock *et al.* 1985). This situation links *C. esox*, with species exhibiting a protracted spawning season such as *Sebastolobus macrochir* (Koya *et al.* 1994), several Mediterranean and Black Sea species (Oven 1977) and *Parasilurus aristotelis* Agassiz (Iliadou & Fishelson 1995).

The efficiency of male reproduction increases with close mating; nesting or similar reproductive behaviour enhances the fertilisation rate. Billard (1986) supported the hypothesis outlined by Peters (1971) about the relationship between low male GSI and the requirement for releasing sperm near the females. Although this hypothesis cannot be tested at present, it should be considered in the analysis of the reproductive strategy of *C. esox*.

In *C. esox* females the maximum GSI was 22%. Such a value is similar to those in other Channichthyidae (Kock 1985); e.g., *Chionodraco hamatus* from Antarctic waters (Vacchi *et al.* 1996). In *C. hamatus* absolute and relative fecundity were lower (2360–4158 oocytes, 2.9–7.9 oocytes g^{-1} respectively) and the oocyte size higher (4–5 mm diameter) than in *C. esox*.

A population of *C. gunnari* at the Skif Bank, near Îles Kerguelen was studied at an equivalent size range to *C. esox*

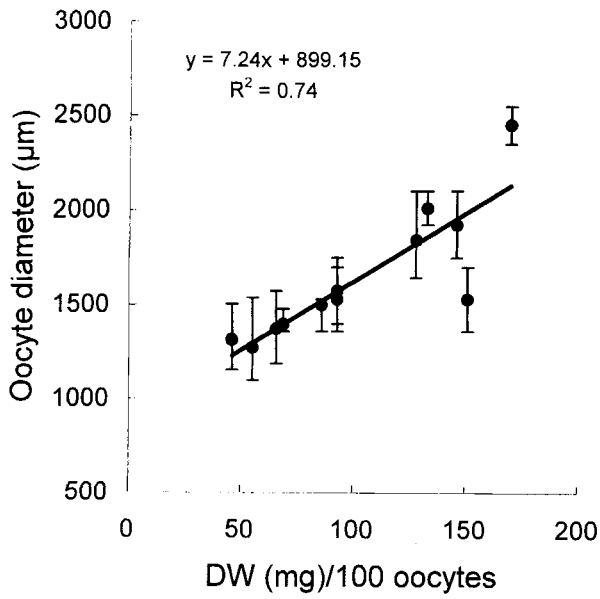

Fig. 6. Scatter plot between mean oocyte diameter of mature ovaries and dry weight of 100 mature oocytes. (Vertical lines: maximum and minimum values).

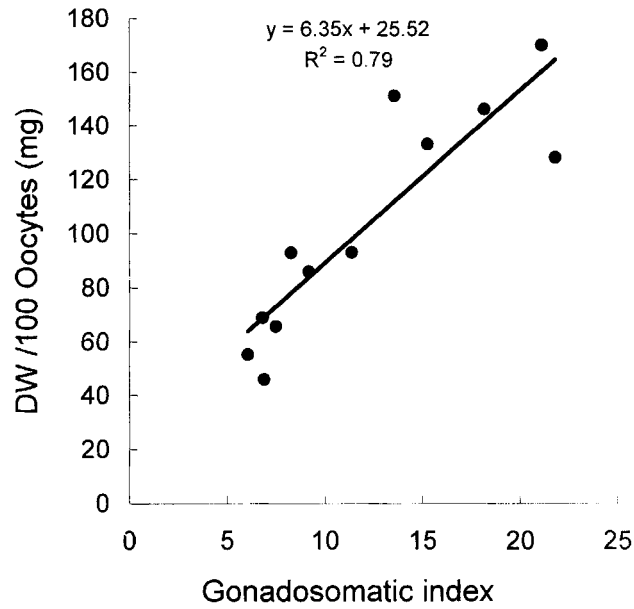

Fig. 7. Scatter plot between dry weight of 100 hydrated oocytes and GSI.

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(27 to 35 cm TL) (Duhamel 1987, quoted by Kock & Kellermann 1991). Absolute and gutted fecundity values were similar in both species. Furthermore, the other populations of *C. gunnari* and Channichthyidae species already mentioned show a wider size-range, larger mature oocyte diameter, higher absolute and gutted fecundity and constrained spawning periods (Duhamel 1995, Everson *et al.* 1996).

Annual estimation of female reproductive effort requires an assessment of the absolute fecundity and the spawning frequency each year. The most accurate method of estimation is histological analysis of the occurrence and the development of oocyte batches (Heins & Rabito 1986, Rinchard & Kestemont 1996). In *C. esox*, the significant segregation in diameter between mature and reserve oocyte batches allows an accurate absolute fecundity estimate. Thus, the risk of methodological errors such as those quoted by Kock & Kellermann (1991), is overcome. For these authors, in *C. gunnari* the variations of potential fecundity are related either to different populations or to methodological differences in egg counts.

In *C. esox,* great diameter variability was found in hydrated oocytes, with the maximum values almost the double the minimum (Fig. 6). Such a difference is not related to spawning season or to female size and it can only be explained by yolk incorporation during the hydration period, contrary to what occurs in the majority of teleosts (Hunter & Goldberg 1980).

Wallace & Selman (1985) found in *Fundulus heteroclitus* that an enormous amount of protein was incorporated into the oocyte in follicles that enlarge from 0.55 to 1.35 mm in diameter. Furthermore, the enlargement from maturation to final preovulatory size (1.85 mm) is due only to water intake. The hydration occurs within periods of 12–24 hours and causes the opaque oocytes to become translucent (Barbieri *et al.* 1994, Hunter & Goldberg 1980, Hunter & Macewicz 1980, Mellinger 1994).

Many authors have suggested that vitelline homogenisation is a particular feature in icefishes. For example, Shandikov & Faleeva (1992) reported that yolk homogenisation begins long before oocyte growth is completed. Furthermore, Kock & Kellermann (1991) based on a previous study (Kock 1979) observed that average oocyte dry weight was greatest in larger female *C. gunnari* at South Georgia and suggested that these had spawned earlier and/or tended to produce larger oocytes. This suggestion is not supported by an analysis of the relationship between oocyte diameter and dry weight for each specimen.

Kock & Kellermann (1991) explained the occurrence of heavier eggs in autumn–early winter spawner Notothenioids through the trade off between oocyte dry matter content and larval survival. In spite of this argument, *C. esox* exhibits a protracted spawning season with eggs two times lighter than, for instance, the autumn spawner *C. gunnari* at a similar length range.

The increase of liver weight before ovarian maturity and its subsequent decrease as reserves are transferred to the gonads is explained by the use of the liver as an energetic reservoir (Carnevali *et al.* 1993, Jobling 1995, Redding & Patiño 1993).

The relation between HSI and GSI shown in Fig. 4 could be explained if *Champsocephalus esox* transfers the reserve material from the liver to the ovary during the oocyte hydration stage. A similar pattern was described by Permitin (1973) in maturing specimens prior to spawning of *Pseudochaenichthys georgianus* Norman, in which HSI values ranges from 5.96–7.36%.

Ovarian maturity

It is usually assumed that in Antarctic Notothenioids, the development of mature oocytes may take more than one year, with the exception of *C. gunnari* at South Georgia (Kock & Everson 1997). The proposed general pattern is that the most advanced batch of oocytes is spawned while the previtellogenic oocytes or those undergoing yolk depositions remain in the ovary (Kock & Kellermann 1991, Everson 1994). The occurrence of early vitellogenic oocytes during the entire annual cycle is assumed as a characteristic pattern in Notothenioids (Pestarino *et al.* 1995). Macchi & Barrera Oro (1995) described the presence of both previtellogenic oocytes as well as oocytes in primary growth (with vesicular yolk) up to 400 mm diameter in maturing ovaries of *C. gunnari*.

Nevertheless, *Lepidonotothen nudifrons* Lönnnberg is the only Antarctic notothenioid that spawns twice a year, at least under laboratory conditions. Moreover, their ovaries contain a reserve batch of yolked oocytes (Hourigan & Radtke 1989).

On the contrary, subantarctic Notothenioids differ from the general Antarctic pattern. *Champsocephalus esox* showed a net segregation between the maturing batch and the reserve stock, which is formed by previtellogenic oocytes and scarce vesicular yolk oocytes (Fig. 2a & b). This pattern is shared with *Patagonotothen tessellata* Richardson, 1845 that presents winter and summer spawning seasons and their mature ovaries contain both yolked oocyte and previtellogenic reserve batches; which develop in less than six months (Rae & Calvo 1995a).

Everson (1994) proposes two different reproductive strategies for Antarctic fish:

> *Notothenia coriiceps* type, in which adult females would spawn a variable amount of oocytes in each spawning season derived from a permanent stock of yolked oocytes. The number of developing oocytes to final maturity varies according to quantity of food available,
>
> *Champsocephalus* type, in which not all the adult females would spawn annually. The number of spawning females would be negatively related to the adverse environmental conditions.

A clear segregation was observed in *C. esox* among different oocyte batches that form the ovarian stock (Fig 2b), as described in other Notothenioids (Ekau 1991, Kock & Kellermann 1991, Duhamel *et al.* 1993). This segregation is

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stressed by an atretic process that removes an important number of developing oocytes (Fig 2e & f). Within an ovary, the occurrence of both maturing oocytes and previtellogenic batch could indicate a single spawn per spawning season.

However, in some specimens ovaries contained globular yolked and residual oocytes from previous spawn that were being phagocyted. The destiny of these globular yolked oocytes could not be established and could denote another spawn or their removal by atretic process.

The presence of *C. esox* females with hyalinized oocytes from February–November and ripe males from January–September indicates an extended spawning season. This set of data suggests that, at least for the population at the Beagle Channel, this species presents significant differences from the other members of the family and from other Antarctic notothenioids. In these cases, the spawning period lasts less than four months each year and the spawn occurs at the same place (Kock 1985, North & White 1987).

Further research on the reproductive biology of subantarctic species will improve the comparative analysis between notothenioid species living at different environmental conditions.

Conclusions

1. In *Champsocephalus esox,* microanatomical testicular structure corresponds to "unrestricted spermatological type" (*sensu* Grier *et al.* 1980) and spermatogenesis is characterized by successive marked changes in the prevalence of each testicular cellular type.

2. Ovary maturation stages are defined by the dominance of a particular oocyte type. Ovulated oocyte diameter varies from 1000 to 2700 µm, absolute fecundity ranges between 3300 and 8600 and relative fecundity ranges between 22 and 43 oocyte g^{-1} TW.

3. Maximum gonadosomatic index is similar in females to those described for other channichthyids (22%), but different and lower in males (3% vs 6–8%).

4. Absolute and relative fecundity, as well as oocyte diameter values, are similar to those observed in *C. gunnari* at South Georgia, but they are lower than those found in the other populations of *C. gunnari* and other species of channichthyids.

5. As in other sympatric subantarctic notothenioids, the number of maturing eggs is restrained by autolysis of basophilic and vesicular yolk oocytes and phagocytosis of globular yolk oocytes during later maturation stages.

6. The reproductive season extends through the year with a single spawning per season.

Finally, these results provide the first information on reproductive biology for this species. However, comprehensive research is needed on the basic biology and physiological constraints, especially as this species has the most northerly distribution reported for this family.

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