

Gametogenesis in the Antarctic plunderfishes *Artedidraco lönnbergi* and *Artedidraco skottsbergi* (Pisces: Artedidraconidae) from the Ross Sea

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Abstract: The Antarctic plunderfishes *Artedidraco lönnbergi* and *A. skottsbergi* are small, bottom dwelling species inhabiting the continental shelf of the High Antarctic Zone. During cruise 97-9 of the US RV *Nathaniel Palmer* during the summer in the south-western Ross Sea, samples of both species were collected by means of bottom trawling. On the basis of macroscopic and histological analysis, we present the first data on the reproductive characteristics of these two plunderfishes, including gametogenesis, spawning period and absolute fecundity. Histologically, we found immature (stage I and II) and mature (stage V) females in both species, whereas developing females (stage III) were found only in *A. skottsbergi*. All examined male specimens of *A. skottsbergi* were in the final stage of spermatogenesis (stage III), whereas male *A. lönnbergi* were immature (stage I), mature (stage IV) and post-reproductive (stage V) individuals. In both species, spawning takes place in summer during December and January. Absolute fecundity was very low, with less than 100 and 200 oocytes in *A. lönnbergi* and *A. skottsbergi*, respectively. These data are compared with those reported in literature for other artedidraconids.

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Introduction

Within the suborder Notothenioidei, the plunderfishes (family Artedidraconidae) are predominantly small, bottom dwelling components of the Antarctic fish fauna. They are characterized by a mental barbel whose morphology is sometimes species specific (Eakin 1990, Eastman 1993). The family is endemic to the Southern Ocean and comprising four genera and 23–25 species (Eakin 1990, Balushkin & Eakin 1998). Most are widespread on the continental shelf of the High Antarctic Zone, although some of them (several species of *Pogonophryne* and *Artedidraco skottsbergi*) have been found as far north as the South Shetland and South Orkney islands (Kock 1992). Although plunderfishes have no commercial value, they play a key role in the benthic trophic web of the High Antarctic waters (Olaso *et al.* 2000).

The genus *Artedidraco* is the second most speciose group of plunderfishes, consisting of six species, two of them with a circum-Antarctic distribution (*A. lönnbergi* (Roule) and *A. skottsbergi* Lönnberg), three distributed only in East Antarctica (*A. glareobarbatus* Eastman & Eakin, *A. orianae* Regan and *A. shackletoni* Waite) and one endemic to South Georgia (*A. mirus* Lönnberg) (Eakin 1990, Eastman & Eakin 1999). Except for *A. mirus*, all other species of the genus *Artedidraco* have been recorded within the nearshore and continental shelf waters of the Ross Sea (Eastman &

Eakin 1999).

Most of studies on plunderfishes have dealt with either the morphology and function of sensory organs, like mental barbel, or with feeding habits. While the morphology of the mental barbel is a diagnostic characteristic of this group of notothenioids (Balushkin & Eakin 1998, Lombarte 1999, Eastman & Eakin 2001, Eakin *et al.* 2001), its functional significance is not understood. Its suggested use is as a lure to attract prey and/or as a somatosensory organ (Janssen *et al.* 1993, Eastman & Eakin 2001, Eastman & Lannoo 2003). Plunderfishes feed almost exclusively on moving prey such as polychaetes, using a “sit and wait” or “ambush” feeding strategies (Daniels 1982, Hubold 1992). Generally plunderfishes rely on a wide range of benthic prey, although diet composition and size of prey are considerably different and characterize each of four genera of Artedidraconidae (Wyanski & Targett 1981, Schwarzbach 1988, Olaso *et al.* 2000, Lombarte *et al.* 2003).

As far as the reproductive biology of plunderfishes is concerned, the few studies to date were carried out almost exclusively in the Weddell Sea and provided data on spawning season, egg size and fecundity (Ekau 1991, Kock & Kellermann 1991, Hubold 1992, Duhamel *et al.* 1993). Artedidraconids are generally spring or summer spawners and, relative to other notothenioids, exhibit the lowest

absolute fecundity (i.e. only a few hundred eggs per season) while producing eggs of 3–4 mm (Kock & Kellermann 1991). All these studies were carried out only on the basis of the macroscopic appearance of gonads throughout or in close proximity to the spawning season.

There are few data on reproductive biology based on histological examination of gonads and these concern primarily nototheniids (Butskaya & Faleeva 1987, Faleeva & Gerasimchuk 1990, Calvo *et al.* 1992, Rae & Calvo 1996, Eastman & DeVries 2000) and channichthyids (Macchi & Barrera-Oro 1995, Calvo *et al.* 1999, Russo *et al.* 2000, La Mesa *et al.* 2003), although there has been some recent work on harpagiferids and bathydraconids (Van der Molen 2003, Van der Molen & Matallanas 2003, 2004).

In the present study, we provide for the first time a histological description of gonads of two species of plunderfishes, *Artedidraco lönnbergi* and *A. skottsbergi*, collected in coastal waters of the western Ross Sea. These data, coupled with a macroscopic analysis of gonads, allowed us to estimate absolute fecundity and egg size at spawning, as well as to propose a maturity scale for each sex. Our results are compared with published data on other species of artedidraconids in order to provide insight into the reproductive strategy of this endemic family of Antarctic fish.

Materials and methods

The specimens of *A. skottsbergi* and *A. lönnbergi* analysed were collected during cruise 97–9 of the RV *Nathaniel B. Palmer* in the western Ross Sea, between 20 December 1997 and 8 January 1998. Fish were captured by an otter trawl at 260 m (*A. skottsbergi*) and 340 m depth (*A. lönnbergi*). Further details on sampling at sea are reported in Eastman & Hubold (1999). Specimens were identified according to Eakin (1990) and preserved in formalin aboard the vessel.

In laboratory, total length (TL) was measured to the nearest mm below and total weight (TW) recorded (g) for each of the specimen caught. After a macroscopic examination of the gonads, they were weighed to 0.1 g and the maturity stage determined according to the five-point scale proposed by Everson (1977) and revised by Kock & Kellermann (1991). The gonadosomatic (GSI) index was calculated as the percentage of gonad weight to total weight. Absolute fecundity, defined as the number of ripening eggs found in the female prior to the next spawning period (Bagenal 1973), was calculated by counting all the ripe eggs found in the ovaries. Relative fecundity, i.e. the number of eggs per unit of total weight (Kartas & Quignard 1984), was also calculated. In mature females, mean size of ripe eggs was determined by measuring the maximum diameter of 20 oocytes representing as much as possible of the whole size range observed in the ovary (West 1990).

For histological analysis, gonad samples were removed

from fish and fixed in Bouin's solution for 12 h. They were then dehydrated through increasing concentrations of ethanol and embedded in paraffin. Sections 7 µm thick were cut, mounted on slides and stained with Mayer's haematoxylin-eosin and Galgano's trichrome following a standardized procedure (Beccari & Mazzi 1972). Each section was examined with a Nikon Eclipse 800 optical microscope at magnifications 40–400x. Measurements of oocytes were carried out using the Nikon software package Lucia 4.51.

On the basis of histological appearance and cell structure, ovarian follicles were classified on the basis of six development stages: I. chromatin nucleolar (immature), II. perinucleolar (immature), III. yolk vesicle or cortical alveoli formation (early maturation), IV. vitellogenic (late maturation), V. mature, VI. postovulatory follicle (post-reproductive) (Wallace & Selman 1990, West 1990). To determine the oocyte developmental pattern throughout the ovary (De Vlaming 1983), an analysis of the stage/size frequency distribution was performed by counting oocytes at different stages of maturity on five sections, taken at 1 mm intervals, for each ovary. As notothenioids, according to Wallace & Selman (1981), generally exhibit "group synchronous ovaries" (Kock & Kellermann 1991), each specimen was staged based on the most advanced stage of development observed in the ovary sections. For each stage of development, cellular and nuclear diameters (µm) were measured on 20 oocytes and the nucleoplasmic index (NP) was calculated as follows: $NP = V_n / (V_c - V_n)^{-1}$, where V_n is the nuclear volume and V_c is the cellular volume.

In males, the spermatogenic activity was assessed by the evaluation of different types of gametocytes (i.e. from spermatogonia to spermatozoa) in the seminiferous lobules of each testis. The presence of spermatogonial mitoses was noted as well. Testes maturity was assessed according to a five-point scale (Billard 1986): I. immature stage (presence of spermatogonia and spermatogonial mitoses), II. early development stage (first meiotic division), III. advanced development stage (second meiotic division), IV. mature stage (presence of spermatozoa cysts), V. post-reproductive stage (presence of collapsed lobules and residual spermatozoa).

Results

Overall, the gonads of nine males and two females of *A. lönnbergi* and twelve males and three females of *A. skottsbergi* were analysed. Males and females of *A. lönnbergi* measured between 46–80 mm and 79–93 mm as TL and weighed between 0.6–3.2 g and 2.7–5.7 g, respectively. Males and females of *A. skottsbergi* measured between 84–99 mm and 56–106 mm as TL and weighed between 3.9–7.2 g and 1.0–8.1 g, respectively.

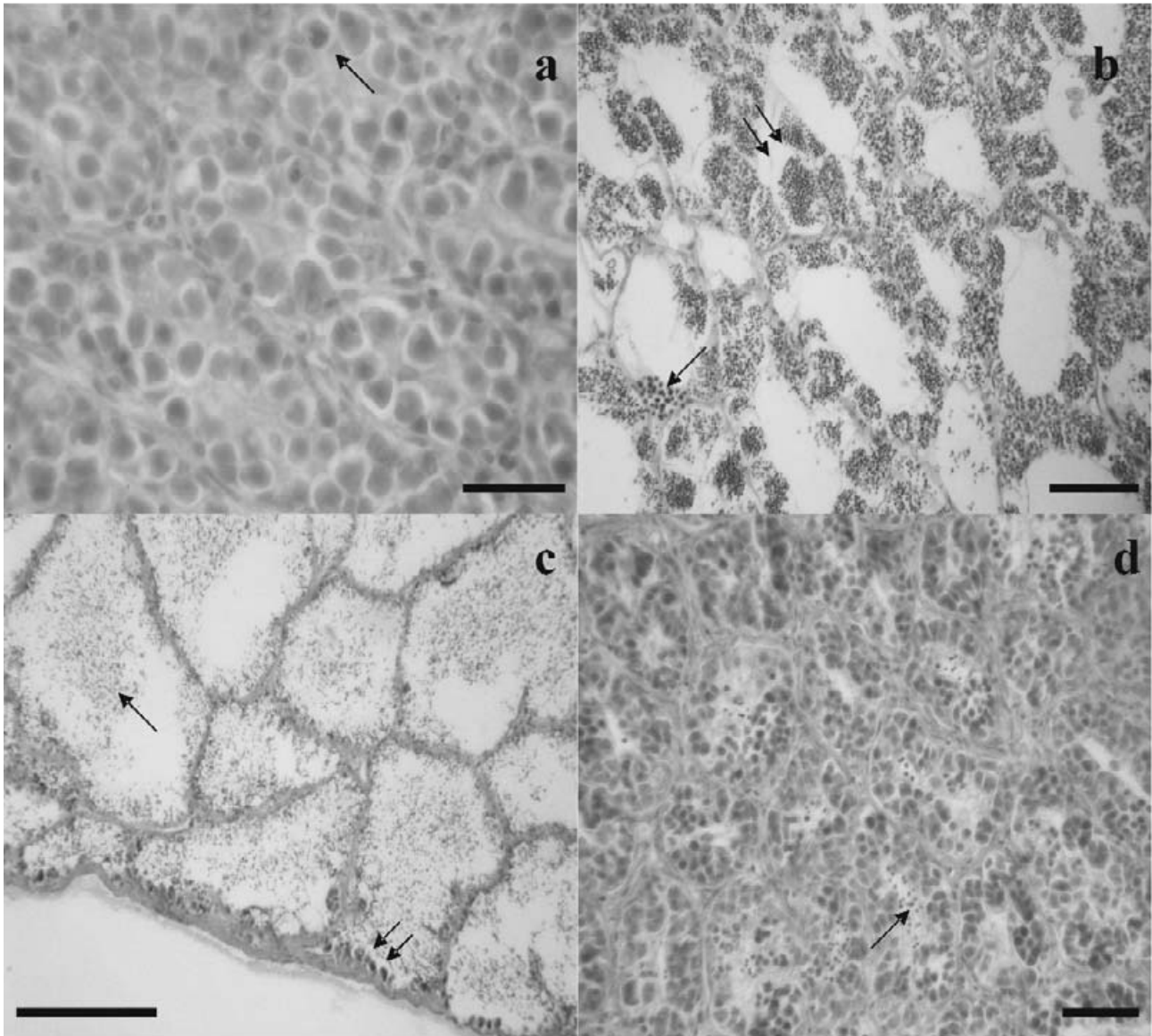


Fig. 1. Cross sections of testis at different stages of development. **a.** *Artedidraco lönnbergi*, immature stage (I), showing lobules filled with cysts of spermatogonia, with evidence of spermatogonial mitoses (arrow); scale bar = 70 μm . **b.** *A. skottsbergi*, advanced development stage (III), with cysts of spermatocytes II (arrow) and spermatids (double arrows); scale bar = 100 μm . **c.** *A. lönnbergi*, mature stage (IV), showing lumina of lobules filled with free spermatozoa (arrow), as well as some interstitial spermatogonia (double arrows); scale bar = 90 μm . **d.** *A. lönnbergi*, post-reproductive stage (V), with lobules collapsed and few residual spermatozoa in lumina of lobules (arrow); scale bar = 40 μm .

Reproductive effort

Reproductive effort was evaluated in terms of GSI, fecundity and egg size (Kamler 1992).

Histologically, all males of *A. skottsbergi* (12) were in advanced development (stage III), with a mean GSI of 1.0% (range 0.2–1.7). Two females were mature (stage V) and close to ovulation, with a mean GSI of 7.3% (range 6.7–7.8), whereas another one was immature (stage II) with a GSI of 0.1%. The total and relative fecundity of mature females ranged between 110–183 oocytes and 17.2–22.6

oocytes/g TW, respectively. Mean size of ripe eggs in both mature females was 2.1 mm (range 1.9–2.2 mm).

In *A. lönnbergi*, a high proportion of males (seven) were small immature fish (stage I), and their testes too small to be weighed. Of the two other males, one was mature (stage IV) with a GSI of 1.6%, and another one was in a post-reproductive condition (stage V), with a GSI of 0.5%. Out of two females studied, one was in early maturation (stage III). The other one was mature (stage V), with a GSI of 13.1%. Total and relative fecundity of this specimen was 89 oocytes and 15.6 oocytes/g TW, respectively, with a mean

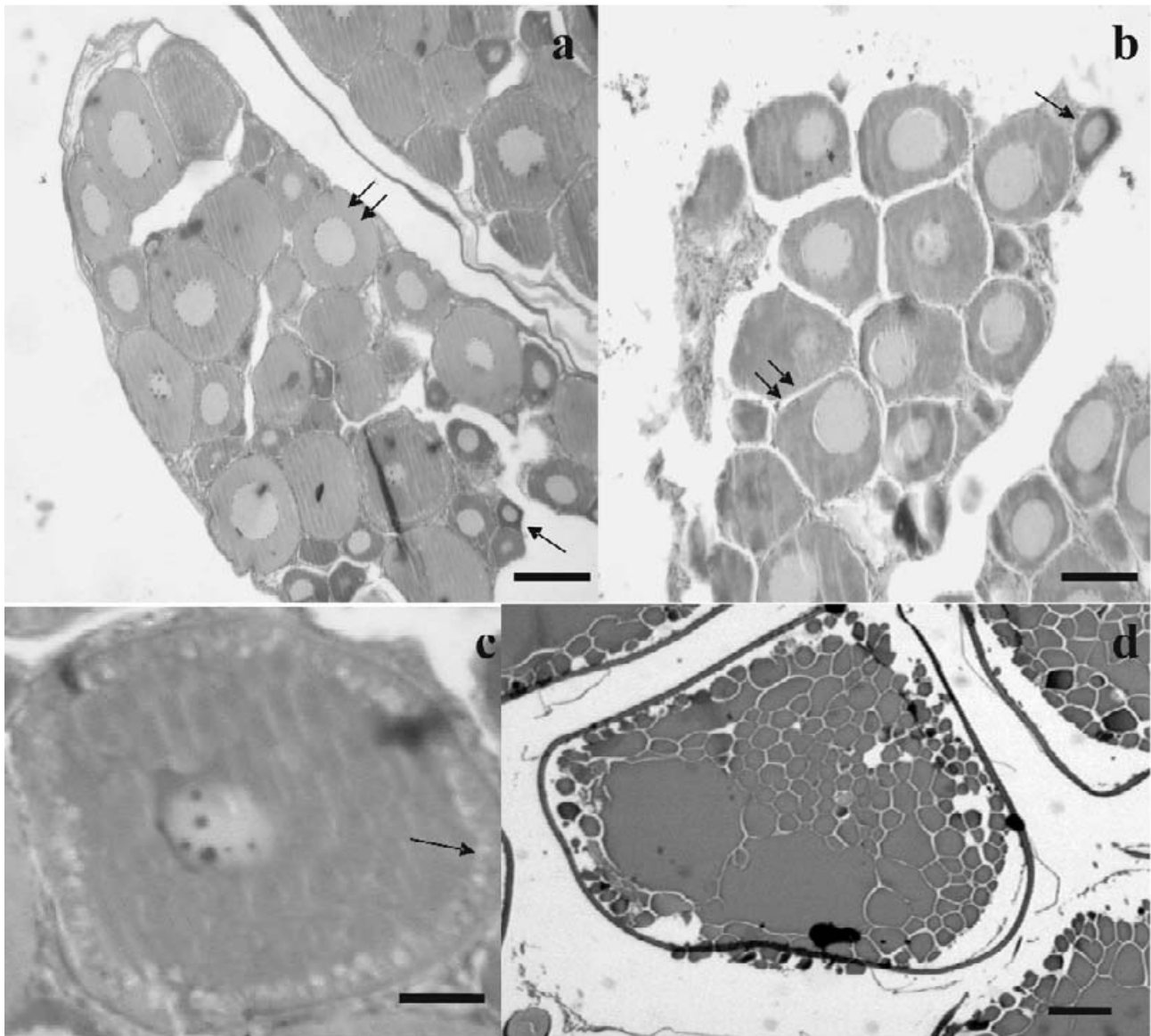


Fig. 2. Cross sections of ovary with oocytes at different stage of development. **a.** *Artedidraco lönnbergi*, chromatin nucleolar stage (I), showing oocytes with basophilic cytoplasm and a large nucleus (arrow), and perinucleolar stage (II), with oocytes slightly stained and characterized by several nucleoli at the periphery of nucleus (double arrows); scale bar = 150 μ m. **b.** *A. skottsbergi*, description as in **a**; scale bar = 60 μ m. **c.** *A. lönnbergi*, cortical alveoli stage (III), showing a single oocyte characterized by chromophobic vesicles (i.e. the cortical alveoli) in the region adjacent to the plasmatic membrane (arrow); scale bar = 40 μ m. **d.** *A. skottsbergi*, mature stage (V), with large oocytes completely filled by yolk granules coalescing in plates of various size; scale bar = 250 μ m.

Table I. Morphometric data for oocytes in different stages of development in *Artedidraco skottsbergi* (above) and *A. lönnbergi* (below) (mean value \pm standard error). NP = nucleo-plasmic index.

Stage	Cellular diameter (μ m)	Nuclear diameter (μ m)	NP
Chromatin nucleolar (I)	56.1 \pm 3.5	34.8 \pm 2.5	0.32
Perinucleolar (II)	135.5 \pm 12.8	60.2 \pm 2.2	0.09
Mature (V)	2075 \pm 17.0		
Chromatin nucleolar (I)	42.0 \pm 2.5	22.6 \pm 2.7	0.23
Perinucleolar (II)	123.3 \pm 7.2	59.4 \pm 3.8	0.13
Yolk vesicle (III)	311.3 \pm 12.4	116.1 \pm 7.5	0.06
Mature (V)	2720 \pm 24.9		

size of ripe eggs of 2.7 mm (range 2.6–2.8 mm).

Testicular structure and spermatogenesis

In both species, the paired testes are located dorsally in the body cavity near the kidneys and are fused in close to the anal opening. Each testis is covered by a thick wall composed of connective tissue fibres and muscular tissue, the *tunica albuginea*. As reported in other notothenioids (Calvo *et al.* 1999), the testes of *A. lönnbergi* and *A. skottsbergi* have a cystic lobular pattern, with long and

finger-like lobules. Based on the terminology of Grier *et al.* (1980), the internal structure of testes in both species is of the “unrestricted spermatogonial” type which is typical of Perciformes, characterized by a random distribution of spermatogonia along the entire length of the lobules.

Histological observation of testes allowed characterization of four of the five stages of gonad development or spermatogenesis, each described below.

- Immature stage (I): in this stage, lobules consist of several cysts densely filled with spermatogonia, with some evidence of spermatogonial mitoses (Fig. 1a). Small and fusiform Leydig cells are located around each cyst of spermatogonia. Inner lumina of lobules are occupied by cysts of spermatogonia.
- Advanced development stage (III): in this stage, testes are in active spermatogenesis, with the seminiferous lobules filled with cysts of meiotic spermatocytes II, with a deeply stained cytoplasm, and spermatids (Fig. 1b).
- Mature stage (IV): testes are composed of lobules with very thin walls and broad lumina filled with either free spermatozoa or spermatozoal cysts (Fig. 1c). In this stage, there are some cysts of staminal spermatogonia at the periphery of seminiferous lobules (interstitial spermatogonia).
- Post-reproductive stage (V): this stage is characterized by the presence of residual spermatozoa in lumina (Fig. 1d). Lobules are collapsed, and their structure will be regenerated by the interstitial spermatogonia.

Ovarian structure and oogenesis

According to Hoar (1969), the paired ovary of *A. lönnbergi* and *A. skottsbergi* can be classified as cystovaries. They are located in the dorsomedial region of the body cavity, with a sub-cylindrical shape. Their caudal ends open into a short oviduct, and the ovarian lamellae lie transverse to the major axis of ovary from the ovarian wall to the small central lumen. The ovarian wall is composed of a peritoneal epithelium and two layers of smooth muscular tissue, the outer with longitudinal fibres and the inner with circular fibres.

The small sample of females (five) available for the study allowed histological description of four of the six stages of ovarian development or oogenesis, as given below. Mean values for cellular and nuclear diameters and NP are summarized in Table I.

- Chromatin nucleolar stage (I): oocytes are small (between 34–52 μm and 48–67 μm in *A. lönnbergi* and *A. skottsbergi*, respectively) with a very basophilic cytoplasm and a central and rounded nucleus occupying most of the cell (Fig. 2a & b). Several nucleoli are randomly distributed within the nucleus.

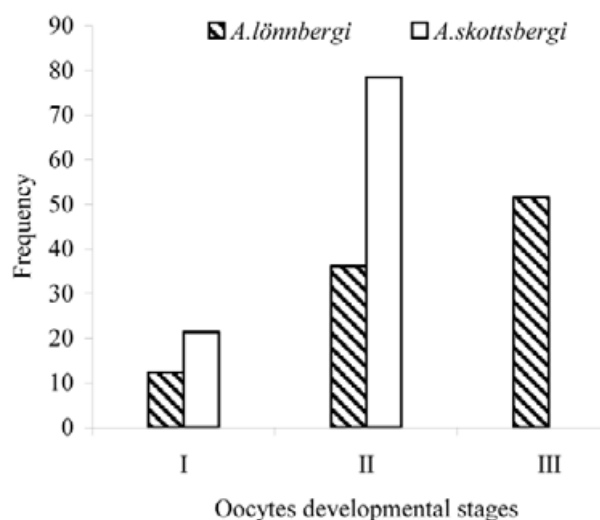


Fig. 3. Frequency distribution of oocytes in different stage of development. I = chromatin-nucleolar stage, II = perinucleolar stage, III = cortical alveoli formation stage.

At this early stage of development, the nucleoplasmic index (NP) is 0.23 in *A. lönnbergi* and 0.32 in *A. skottsbergi*.

- Perinucleolar stage (II): in this stage, oocytes are basophilic, with cytoplasm slightly stained with haematoxylin, and their size ranges between 90–158 μm and 109–180 μm in *A. lönnbergi* and *A. skottsbergi*, respectively. The nucleus is still spherical and is characterized by a large number of peripherally located nucleoli (Fig. 2a & b). NP is decreasing with respect to the previous stage, ranging between 0.13 (*A. lönnbergi*) and 0.09 (*A. skottsbergi*).
- Yolk vesicle or cortical alveoli formation stage (III): oocytes in this stage start to increase considerably in size, reaching 266–363 μm in *A. lönnbergi* (Fig. 2c). Their cytoplasm is slightly stained and contains chromophobic vesicles in the region adjacent to the plasma membrane. These vesicles, the cortical alveoli, gradually increase in size and number and move towards the centre of the cytoplasm. The nucleus shows the same pattern and morphology of the previous stage, but its relative volume with respect to the cytoplasmic volume is slightly lower (NP of 0.06).
- Mature stage (V): at this stage oocytes reach more than 2000 μm in both species and fill completely the ovary. The nucleus is completely disintegrated and the yolk granules coalesce to form yolk plates (Fig. 2d). The zona radiata is very thick, measuring on average 48 μm . A few previtellogenic oocytes at different stage of development are also present in the ovary. They measure from 177 μm to 480 μm in *A. skottsbergi* and from 134 μm to 554 μm in *A. lönnbergi*, clearly forming two batches of eggs with the large yolked eggs

Table II. Scale of gonadal maturity for *A. lönnbergi* and *A. skottsbergi*.

Macroscopic stage of maturity	Macroscopic features	Histological features
Females		
1. Immature	ovaries very small, no oocytes visible to the naked eye	clusters of oogonia, few basophilic oocytes at chromatin nucleolar and perinucleolar stages (I and II)
2. Developing	ovaries still small, with a granular appearance	some oogonia, few basophilic oocytes at stage I and II and dominance of yolk vesicle oocytes (stage III)
3. Maturing	-	-
4. Mature (gravid)	ovaries large, filling the body cavity, with large oocytes clearly visible	a few previtellogenic oocytes, mature hydrated oocytes free in the ovarian lumen (stage V)
5. Spent	-	-
Males		
1. Immature	testes very small, visible as thin stripes close to the vertebral column	cysts of spermatogonia filling the entire lobule (stage I)
2. Developing	-	-
3. Developed	testes of larger size and convoluted	seminiferous lobules with cysts of spermatocytes II, presence of spermatids (stage III)
4. Mature	testes large, milt produced under pressure	few cysts of interstitial spermatogonia, dominance of spermatozoa free into the lumen of lobules (stage IV)
5. Spent	testes shrunk and flaccid	few interstitial spermatogonia, residual spermatozoa in the lumen of lobules (stage V)

described above.

The frequency distribution of the oocyte developmental stages, based on an immature female of *A. skottsbergi* (stage II or perinucleolar) and an early maturing female of *A. lönnbergi* (stage III or yolk vesicle), is summarized in Fig. 3. Note that the most advanced stage of development observed in both females represents the most frequent stage as well.

Gonad maturity scales

As shown in Table II, we used histological observations of testes and ovaries and macroscopic appearance of gonads to construct a maturity scale for males and females of both species of *Artedidraco*.

Discussion

In evaluating data on the reproductive biology on Antarctic fish published to date, several common features emerge: prolonged gametogenesis (which in females generally lasts

more than one year), one spawning event per year, low fecundity and large egg size at maturity. Furthermore, most species produce demersal eggs that give rise to larvae with a long pelagic phase (Kock & Kellermann 1991). With regard to latitudinal distribution across the Southern Ocean, there are different pictures of the reproductive characteristics of fish living in the Seasonal Pack Ice Zone and those living in the High Antarctic Zone. In nototheniids, for example, total and relative fecundity generally decrease and egg size increases towards higher latitudes. In addition, the species of the Seasonal Pack Ice Zone are generally autumn or winter spawners, whereas in the High Antarctic Zone most species spawn in spring or summer (Kock & Kellermann 1991).

As typical elements of the fish fauna living in the High Antarctic Zone, artedidraconids clearly exhibit all the common characteristics mentioned above. In particular, within the genus *Artedidraco* (see Table III), all species spawn in summer in the Weddell Sea and in the Ross Sea, except for *A. shackletoni* that spawns in spring. Hence, there are no differences in spawning time between different sites. Total and relative fecundity are at the lower end of scale for

Table III. Reproductive characteristics of mature females in the genus *Artedidraco* from the High Antarctic Zone.

Species	Fish length (mm)	GSI	Egg size (mm)	Spawning period	Total fecundity	Relative fecundity	Site	Source
<i>A. lönnbergi</i>	112	-	3.7	summer	136	16.2	Weddell Sea	1
	93	13.1	2.6–2.8	summer	89	15.6	Ross Sea	5
<i>A. oriana</i>	132–155	-	0.7–1.6	summer	206–361	-	Weddell Sea	4
<i>A. shackletoni</i>	-	15.5–16.3	2.5–3.2	spring	170–310	8.6–16.1	Weddell Sea	2
<i>A. skottsbergi</i>	85	-	3.3	summer	73	-	Weddell Sea	1
	-	-	3.0	-	-	-	Ross Sea	3
	100–106	6.7–7.8	1.9–2.2	summer	110–183	17.2–22.6	Ross Sea	5

Data source: 1. Duhamel *et al.* 1993, 2. Ekau 1991, 3. Lisovenko 1987, 4. Van der Molen 2003, 5. present data.

Antarctic fish, with only few hundred of eggs per spawning event and less than 20 eggs per gram of total weight, respectively. Egg size, generally inversely related to fecundity, differs substantially among the species of *Arteididraco*, ranging from less than 1 mm in *A. orianae* to 3.7 mm in *A. lönnbergi*. In addition, *A. lönnbergi* and *A. skottsbergi* apparently produce larger eggs in the Weddell Sea than in the Ross Sea (Table III). Considering egg size and fecundity, artedidraconids can be placed between channichthyids, which exhibit very large eggs and low fecundity, and nototheniids, which produce small eggs and have high fecundity (Ekau 1991, Kock & Kellermann 1991).

As a consequence of the relatively large egg size and low fecundity, several authors have suggested the possibility of parental care within the genus *Arteididraco* (Ekau 1991, Kock & Kellermann 1991, Duhamel *et al.* 1993). Indeed, a positive relationship between egg size and the extent of parental care in fish has been frequently reported (Kolm & Ahnesjö 2005). In the Southern Ocean, egg guarding and nesting behaviour are known for several species of the related genus *Harpagifer*, such as *H. antarcticus* Nybelin, *H. bispinis* Schneider and *H. spinosus* Hureau *et al.* (Daniels 1978, White & Burren 1992, Van der Molen & Matallanas 2004), which occupy an ecological niche in the Seasonal Pack Ice Zone similar to that of *Arteididraco* in the High Antarctic Zone (Duhamel *et al.* 1993). Hence, coupling this hypothesis with data on reproductive effort, in *Arteididraco* a tendency towards a K-strategy in the production of few large eggs possibly guarded by parents can be hypothesized. This would increase the probability of survival against predators and reduce egg dispersal over unsuitable habitat (Kolm & Ahnesjö 2005). Circumstantial evidence in support of the hypothesis of parental care in *Arteididraco* is the probable production of demersal eggs, as suggested by the absence of oil droplets in mature oocytes, a fundamental step in the evolution of parental care in fish (Potts 1984).

Because there is a considerable increase in egg diameter after fertilization and an increase in volume by a factor of 1.5–2.4 (Kock & Kellermann 1991), hydrated oocytes of *Arteididraco* attain a maximum final size of approximately 1.3–4.9 mm. Unfortunately no data are available on the incubation period of eggs of artedidraconids. However, considering that in the Weddell Sea *A. lönnbergi* and *A. skottsbergi* larvae hatch in spring (i.e. October–November) (Kellermann 1990, Kock & Kellermann 1991), an overwintering period of egg incubation of at least five to six months can be suggested.

From a histological point of view, testes of *A. lönnbergi* and *A. skottsbergi* have spermatogonia randomly distributed along the lobules, a pattern typical for the order Perciformes, defined as the “unrestricted spermatogonial” type by Grier (1981). This structure has been also described in other notothenioid fish, such as *Patagonotothen*

tessellata Richardson (Rae & Calvo 1996), *Chionodraco hamatus* Lönnberg (La Mesa *et al.* 2003) and *Champocephalus esox* (Günther) (Calvo *et al.* 1999).

Females of *A. lönnbergi* and *A. skottsbergi* exhibit the most common type of gonad observed in teleosts, namely a cystovary (Hoar 1969). Histologically, mature ovaries contain two well defined batches of oocytes, that can be easily separated and distinguished morphologically. There is a batch of yolked oocytes about 2.0–2.5 mm that will be completely spawned in the current season, and a second batch of small previtellogenic oocytes at several stages of development (i.e. chromatin nucleolar, perinucleolar and cortical alveoli stages measuring from 0.1–0.5 mm). The latter represent the reserve stock for the next spawning season. Thus, according to Wallace & Selman (1981), both species of *Arteididraco* have a group synchronous ovary, which is a common feature among Antarctic fish (Kock & Kellermann 1991).

Additional data on some of the other 25 species of artedidraconids are needed to provide a more comprehensive picture of the biology of these poorly known fish, that compose a major element of high latitude fish species diversity.

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References

- BALUSHKIN, A. & EAKIN, R.R. 1998. A new toad plunderfish *Pogonophryne fusca* sp. nova (Fam. Artedidraconidae: Notothenioidei) with notes on species composition and species groups in the genus *Pogonophryne* Regan. *Journal of Ichthyology*, **38**, 575–579.
- BAGENAL, T.B. 1973. Fish fecundity and its relations with stock recruitment. *Journal du conseil permanent International pour l'Exploration de la Mer*, **164**, 186–198.
- BECCARI, N. & MAZZI, V. 1972. *Manuale di tecnica microscopica*. Milano: Vallardi, 366 pp.
- BILLARD, R. 1986. Spermatogenesis and spermatology of some teleost fish species. *Reproduction Nutrition Development*, **26**, 877–920.
- BUTSKAYA, N.A. & FALEEVA, T.I. 1987. Seasonal changes in gonads and fecundity of Antarctic fishes *Trematomus bernacchii* Boulenger, *Trematomus hansonii* Boulenger and *Pagothenia borchgrevinkii* (Boulenger). *Journal of Ichthyology*, **27**, 27–36.
- CALVO, J., MORRICONI, E. & RAE, G.A. 1999. Reproductive biology of the icefish *Champocephalus esox* (Günther, 1861) (Channichthyidae). *Antarctic Science*, **11**, 140–149.
- CALVO, J., MORRICONI, E., RAE, G.A. & SAN ROMAN, N.A. 1992. Evidence of protandry in a subantarctic nototheniid, *Eleginops maclovinus* (Cuv. & Val., 1830) from the Beagle Channel, Argentina. *Journal of Fish Biology*, **40**, 157–164.
- DANIELS, R.A. 1978. Nesting behaviour of *Harpagifer bispinis* in Arthur Harbour, Antarctic Peninsula. *Journal of Fish Biology*, **12**, 465–474.

- DANIELS, R.A. 1982. Feeding ecology of some fishes of the Antarctic Peninsula. *Fishery Bulletin*, **80**, 575–588.
- DE VLAMING, V. 1983. Oocyte development patterns and hormonal involvement among Teleosts. In RANKIN, J.C., PITCHER, J.J. & DUGGAN, R., eds. *Control processes in fish physiology*. London: Croom Helm, 176–199.
- DUHAMEL, G., KOCK, K.H., BALGUERIAS, E. & HUREAU, J.C. 1993. Reproduction in fish of the Weddell Sea. *Polar Biology*, **13**, 193–200.
- EAKIN, R.R. 1990. Artedidraconidae. In GON, O. & HEEMSTRA, P.C., eds. *Fishes of the Southern Ocean*. Grahamstown: J.L.B. Smith Institute of Ichthyology, 332–356.
- EAKIN, R.R., EASTMAN, J.T. & JONES, C.D. 2001. Mental barbel variation in *Pogonophryne scotti*, Regan (Pisces: Perciformes: Artedidraconidae). *Antarctic Science*, **13**, 363–370.
- EASTMAN, J.T. 1993. *Antarctic fish biology: evolution in an unique environment*. San Diego, CA: Academic Press, 322 pp.
- EASTMAN, J.T. & DEVRIES, A.L. 2000. Aspects of body size and gonadal histology in the Antarctic toothfish, *Dissostichus mawsoni*, from McMurdo Sound, Antarctica. *Polar Biology*, **23**, 189–195.
- EASTMAN, J.T. & EAKIN, R.R. 1999. Fishes of the genus *Artedidraco* (Pisces, Artedidraconidae) from the Ross Sea, Antarctica, with the description of a new species and a colour morph. *Antarctic Science*, **11**, 13–22.
- EASTMAN, J.T. & EAKIN, R.R. 2001. Mental barbel and meristic variation in the Antarctic notothenioid fish *Dolloidraco longedorsalis* (Perciformes, Artedidraconidae) from the Ross Sea. *Polar Biology*, **24**, 729–734.
- EASTMAN, J.T. & HUBOLD, G. 1999. The fish fauna of the Ross Sea. *Antarctic Science*, **11**, 293–304.
- EASTMAN, J.T. & LANNOO, M.J. 2003. Anatomy and histology of the brain and sense organs of the Antarctic plunderfish *Dolloidraco longedorsalis* (Perciformes: Nototheniidae: Artedidraconidae), with comments on the brain morphology of other artedidraconids and closely related harpagiferids. *Journal of Morphology*, **255**, 358–377.
- EKAU, W. 1991. Reproduction in high Antarctic fish. *Meeresforschung*, **33**, 159–167.
- EVERSON, I. 1977. *The living resources of the Southern Ocean*. Rome: FAO GLO/SO/77/1, 1–156.
- FALEEVA, T.I. & GERASIMCHUK, V.V. 1990. Features of reproduction in the Antarctic sidestripe, *Pleuragramma antarcticum* (Nototheniidae). *Journal of Ichthyology*, **30**, 67–79.
- GRIER, H.J. 1981. Cellular organization of the testis and spermatogenesis in fishes. *American Zoologist*, **21**, 345–357.
- GRIER, H.J., LINTON, J.R., LEATHERLAND, J.F. & DE VLAMING, V.L. 1980. Structural evidence for two different testicular types in teleost fishes. *The American Journal of Anatomy*, **159**, 331–345.
- HOAR, W.S. 1969. Reproduction. In HOAR, W.S. & RANDALL, D.J., eds. *Fish physiology*, vol. III. London: Academic Press, 1–72.
- HUBOLD, G. 1992. Ecology of Weddell Sea fishes. *Berichte zur Polarforschung*, **103**, 1–157.
- KAMLER, E. 1992. *Early life history of fish: an energetic approach*. London: Chapman & Hall, 267 pp.
- KARTAS, F. & QUIGNARD, J.P. 1984. *La fécondité des poissons téléostéens*. Paris: Masson, 121 pp.
- KELLERMANN, A. 1990. Catalogue of early life stages of Antarctic notothenioid fishes. *Berichte zur Polarforschung*, **67**, 45–136.
- KOCK, K.H. & KELLERMANN, A. 1991. Reproduction in Antarctic notothenioid fish—a review. *Antarctic Science*, **3**, 125–150.
- KOCK, K.H. 1992. *Antarctic fish and fisheries*. Cambridge: Cambridge University Press, 359 pp.
- KOLM, N. & AHNESJÖ, I. 2005. Do egg size and parental care coevolve in fishes? *Journal of Fish Biology*, **66**, 1499–1515.
- JANSSSEN, J., JONES, W. & SLATTERY, M. 1993. Locomotion and feeding responses to mechanical stimuli in *Histiodraco velifer* (Artedidraconidae). *Copeia*, **3**, 885–889.
- LA MESA, M., CAPUTO, V., RAMPÀ, R. & VACCHI, M. 2003. Macroscopic and histological analyses of gonads during the spawning season of *Chionodraco hamatus* (Pisces, Channichthyidae) off Terra Nova Bay, Ross Sea, Southern Ocean. *Polar Biology*, **26**, 621–628.
- LISOVENKO, L.A. Reproductive biology of Antarctic fish in relation to their environment. In SKARLATO, O.A., ALEKSEEV, A.P. & LIUBIMOVA, T.G., eds. *Biological resources of the Arctic and Antarctic*. Moscow: Nauka, 337–357. [In Russian].
- LOMBARTE, A. 1999. External and internal morphology of the sensory organs in Artedidraconidae, Teleostei: Nototheniidae. *Berichte zur Polarforschung*, **301**, 132–135.
- LOMBARTE, A., OLASO, I. & BOZZANO, A. 2003. Ecomorphological trends in the Artedidraconidae (Pisces: Perciformes: Nototheniidae) of the Weddell Sea. *Antarctic Science*, **15**, 211–218.
- MACCHI, G.J. & BARRERA-ORO, E. 1995. Histological study on the ovarian development of mackerel icefish (*Champsocephalus gunnari*) from the South Georgia Islands. *CCAMLR Science*, **2**, 35–49.
- OLASO, I., RAUSCHERT, M. & DE BROYER, C. 2000. Trophic ecology of the family Artedidraconidae (Pisces: Osteichthyes) and its impact on the eastern Weddell Sea benthic system. *Marine Ecology Progress Series*, **194**, 143–158.
- POTTS, G.W. 1984. Parental behaviour in temperate marine teleost with special reference to the development of nest structures. In POTTS, G.W. & WOOTTON, R.J., eds. *Fish reproduction: strategies and tactics*. London: Academic Press, 223–244.
- RAE, G.A. & CALVO, J. 1996. Histological analysis of gonadal development in *Patagonotothen tessellata* (Richardson 1845) (Nototheniidae: Pisces) from the Beagle Channel, Argentina. *Journal of Applied Ichthyology*, **12**, 31–38.
- RUSSO, A., ANGELINI, F., CAROTENUTO, R., GUARINO, F.M., FALUGI, C. & CAMPANELLA, C. 2000. Spermatogenesis in some Antarctic teleosts from the Ross Sea: histological organisation of the testis and localisation of bFGF. *Polar Biology*, **23**, 279–287.
- SCHWARZBACH, W. 1988. The demersal fish fauna of the eastern and southern Weddell Sea: geographical distribution, feeding of fishes and their trophic position in the food web. *Berichte zur Polarforschung*, **54**, 1–94.
- VAN DER MOLEN, S. 2003. *Estudio sobre la reproducción de Nototheniidae (Pisces: Perciformes) del Océano Austral*. PhD thesis, Universitat Autònoma de Barcelona, 284 pp. [Unpublished]
- VAN DER MOLEN, S. & MATALLANAS, J. 2003. Oocyte development and maturity classification of *Gerlachea australis* from the Weddell Sea, Antarctica. *Polar Biology*, **26**, 653–658.
- VAN DER MOLEN, S. & MATALLANAS, J. 2004. Reproductive biology of female Antarctic spiny plunderfish *Harpagifer spinosus* (Nototheniidae: Harpagiferidae), from Iles Crozet. *Antarctic Science*, **16**, 99–105.
- WALLACE, R.A. & SELMAN, K. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. *American Zoologist*, **21**, 325–343.
- WALLACE, R.A. & SELMAN, K. 1990. Ultrastructural aspects of oogenesis and oocyte growth in fish and amphibians. *Journal of Electron Microscopy Techniques*, **16**, 175–201.
- WEST, G. 1990. Methods of assessing ovarian development in fishes: a review. *Australian Journal of Marine & Freshwater Research*, **41**, 199–222.
- WHITE, M.G. & BURREN, P.J. 1992. Reproduction and larval growth of *Harpagifer antarcticus* Nybelin (Pisces, Nototheniidae). *Antarctic Science*, **4**, 421–430.
- WYANSKI, D.M. & TARGETT, T.E. 1981. Feeding biology of fishes in the endemic Antarctic Harpagiferidae. *Copeia*, **3**, 686–693.