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Macroscopic and histological analyses of gonads during the spawning season of *Chionodraco hamatus* (Pisces, Channichthyidae) off Terra Nova Bay, Ross Sea, Southern Ocean

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Abstract A macroscopic and histological analysis of gonads was carried out during the spawning season of the high-Antarctic channichthyid *Chionodraco hamatus* in the western Ross Sea. Samples were collected between December and February during several years in the coastal waters of Terra Nova Bay. Gonad maturity stages were described for males and females according to macroscopic and histological scales. Using multi-year data, the estimated length at first spawning of females was about 35 cm TL, very similar to that obtained indirectly for males. Similar to many other high-Antarctic fish, *C. hamatus* is a summer spawner. The greater part of the stock was indeed in spawning condition between December and February, although a large proportion of females large enough to spawn probably did not spawn in that season. The present data confirm that *C. hamatus*, as is typical for Antarctic fish, probably spawns a single batch of oocytes once a year. In addition, vitellogenesis is a slow process that extends over at least 1 year. Discrepancies between the macroscopic and histological appearance of gonads were found. These were associated mainly with spent and resting females (maturity stages 5 and 2, respectively). This study demonstrates the importance of histological analysis of gonads in order to confirm the results of the macroscopic analyses routinely carried out in studies of reproductive biology. This is of particular importance in determining size at maturity and spawning stock biomass, for assessment purposes.

Introduction

One of the most interesting components of the suborder Notothenioidei is the family Channichthyidae, which is composed almost completely of species endemic to the Antarctic region. The lack of haemoglobin in the blood, which characterises these fishes, has probably played a key role in determining their distribution within the cold and highly oxygenated waters of the Antarctic, where metabolic requirements dependent on temperature are low (Eastman 1993). Consequently, several studies on these species have focussed on their blood physiology, as well as on the structure and function of antifreeze components (Kunzmann 1989, 1991; Wells et al. 1990; Egginton 1996; Wöhrmann 1996, 1997).

Several studies have dealt with aspects of the reproduction of channichthyids. These studies include annual cycles of gonad development, fecundity, egg size and gonadosomatic index (GSI). However, the literature is largely restricted to information on the few species of commercial interest, such as *Chaenocephalus aceratus*, *Champocephalus gunnari* and *Pseudochaenichthys georgianus* from South Georgia, South Orkneys, South Shetlands and Kerguelen Islands (Permitin 1973; Kock 1979, 1981, 1990; Sosinski 1981; Duhamel 1987; Lisovenko and Zakharov 1987; Lisovenko 1988; Everson et al. 1996, 2000; Sosinski and Trella 2002). Some reviews have also summarised data on the reproduction of notothenioids, indicating a prolonged gametogenesis, low fecundity and large yolky eggs as common characteristics (Everson 1984; North and White 1987; Kock and Kellermann 1991; Duhamel et al. 1993; Christiansen et al. 1998).

The only studies that have reported histological data on gonad development of channichthyids are on *Champocephalus gunnari* (Everson et al. 1991; Macchi and Barrera-Oro 1995), *Champocephalus esox* (Calvo et al. 1999) and *Neopagetopsis ionah* (Lisovenko and Trunov 1988).

The channichthyid *Chionodraco hamatus* (Lönnerberg 1905) is a common icefish within the cold waters of the

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high-Antarctic Zone. Indeed, this species shows a circumantarctic distribution, although it is mainly recorded on the continental shelf of East Antarctica down to 600 m depth (Iwami and Kock 1990). Off Terra Nova Bay, as well as in the Ross Sea, *Chionodraco hamatus* is by far the most abundant and eurybathic icefish, both in terms of biomass and frequency of occurrence (Eastman and Hubold 1999; Vacchi et al. 1999).

To date, data on the reproduction of this species have been reported from several sites around the Antarctic continent, such as the Ross and Mawson Seas (Vacchi et al. 1996), the Davis Sea (Shandikov and Faleeva 1992) and the Weddell Sea (Ekau 1991; Duhamel et al. 1993). Nevertheless, almost all of these studies were based on the macroscopic analyses of the gonads. Indeed, the reproductive potential of fish species is often studied by analysing macroscopic gonadal appearance (i.e. the cyclic modifications in size and pigmentation of ovaries and testes occurring during gametogenesis). The five-point maturity scale commonly used to determine the gonad stage of nototheniids and channichthyids (Everson 1977; Cielniaszek and Parkes 1989; Kock and Kellermann 1991) is based on such macroscopic characteristics.

From a histological study of the gonads of the channichthyid *Champocephalus gunnari*, Macchi and Barrera-Oro (1995) found some inconsistencies between the macroscopic appearance of ovaries and, hence, stage of maturity and microscopic pattern (stage of development of gametes). In addition, without histological examination, non-spawning adult fish of *Champocephalus gunnari* are indistinguishable from those in the adolescent phase (i.e. stage 2 of maturity) (Everson 1994). Since estimates of some parameters used in fisheries biology, such as length at sexual maturity/first spawning and fecundity, are only based on the macroscopic stage of maturity, this is likely to provide incorrect data and, consequently, could lead to the mismanagement of the fishery.

In this paper, we present both macroscopic and histological analysis of gonads of *Chionodraco hamatus*, in order to compare the two different approaches used to determine the stage of maturity of fish. Furthermore, length at first spawning was calculated using multi-year data, and the results are discussed in terms of the reproductive effort of the spawning population.

Materials and methods

Macroscopic analysis

Samples of *Chionodraco hamatus* were collected during several research surveys carried out in the coastal waters of Terra Nova Bay, Ross Sea. Sampling data from all surveys are summarised in Table 1. Fish were caught by means of trammel and gill nets. Further details on sampling activities of each survey have been reported by Vacchi et al. (1999). For each fish caught, total length (TL) was measured to the nearest millimetre below, and maturity stage was determined according to the five-point scale of Kock and Kellermann (1991). Total weight (g) and gonad weight (0.1 g) were

Table 1 Summary of sampling data of *Chionodraco hamatus* for each survey

Year	Period	No. of hauls	No. of fish
1987/1988	Jan/Feb	61	165
1990/1991	Dec/Feb	90	154
1997/1998	Jan/Feb	18	43
2001/2002	Jan/Feb	34	43

also recorded, and the GSI was calculated as the percentage of gonad to total weight. Based on the stage of maturity of the gonads, the proportion of specimens within each centimetre size class that had gonads in stages 3–5 was calculated. The length at first spawning (L50), representing the length at which 50% of the population was mature (i.e. stage 3–5), was determined by fitting the logistic equation (Ni and Sandeman 1984)

$$p = [1 + e^{-(\alpha + \beta TL)}]^{-1}$$

to the proportion of fish in each size class, where p is the estimated proportion in a size class, TL is the total length (mm) and α and β are coefficients. Unfortunately, the very low number of immature specimens (i.e. in stage 1 of maturity) in our samples did not allow us to estimate the length at sexual maturity as well.

Histological analysis

Fish samples were collected off Terra Nova Bay during the austral summer 2001–2002 (XVII Italian Antarctic Expedition). Fish samples were caught by means of trammel and gill nets set down to 100 m depth. A full set of data (see above) was preliminarily recorded from each fish. Some fish were kept alive in aquaria with running aerated seawater at temperatures ranging between -2 and 0°C .

Due to the uniform structure of the ovary of *Chionodraco hamatus* females, a portion of gonad was cut and fixed in Bouin's solution for 12 h. They were then dehydrated in ethanol and embedded in paraffin. Sections ($6\ \mu\text{m}$ thick) were stained with Mayer's haematoxylin-eosin and Galgano's trichrome and prepared for histological examination (Beccari and Mazzi 1972). Ovarian follicles were classified according to five development stages (I, chromatin nucleolar stage; II, perinucleolar stage; III, yolk vesicle stage; IV, vitellogenic or yolk stage; V, mature stage) (Wallace and Selman 1981; West 1990). For each stage of development, cellular and nuclear diameters of 20 oocytes were measured (μm) and the nucleo-plasmatic index (NPI) was calculated.

In the case of males, whole testes were removed and fixed in Bouin's fluid. After dehydration in ethanol, paraffin sections were prepared as previously described for females. Spermatogenic activity was assessed by evaluating the different types of gametocytes (from spermatogonia to spermatozoa) in the seminiferous lobules of each testis. Presence of spermatogonial mitoses was also recorded.

All sections were observed with a Leica Diaplan photomicroscope. Measurements of the various gametocyte stages were performed with the Nikon videoanalysis package.

Results

Macroscopic data

To determine the length at first spawning (L50), data from the three surveys were pooled together. Overall, stage of gonad maturity and GSI were collected from 126 females and 236 males, size range 323–438 mm TL and 300–400 mm TL, respectively.

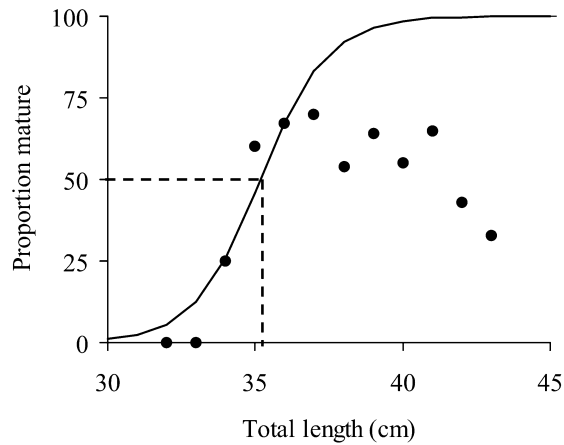


Fig. 1 Logistic curve fitted to the proportion of mature females of *Chionodraco hamatus* (maturity stages 3–5) in relation to fish size. Dashed line indicates the length at first spawning estimate (L50)

By fitting the logistic equation to the available data, the estimated length at first spawning of females was 35.2 cm TL (asymptotic standard error = 0.3165, CV = 0.009, $r^2 = 0.89$) (Fig. 1). However, this value (as well as the curve) was obtained considering only size classes up to 370 mm TL. Taking into account all size classes, the curve would have been stretched to the right with a very poor fit, resulting in unrealistically high estimates of L50. Indeed, Fig. 1 shows that from a body size of 370 mm TL upwards, a large proportion of fish were probably not coming into spawning condition, but were in the resting stage (stage 2). Unfortunately, it was not possible to fit a logistic curve to data for males, as the sample comprised only large fish (greater than 300 mm TL).

The pattern of gonad maturation of *Chionodraco hamatus* during the summer season (December/February), according to the macroscopic scale of maturity (Kock and Kellermann 1991), is summarised in Tables 2 and 3. Considering gravid females (stage 4), as well as spent females (stage 5), approximately 58% of the whole female sampled population was in spawning condition or had already spawned during the season. The very low value of the GSI observed in maturing virgin or resting females (stage 2) compared with that of gravid females (see Table 2), suggested that this part of the population would not spawn in the current season.

Table 2 Macroscopic pattern of gonad maturation of *Chionodraco hamatus* females at Terra Nova Bay between December and February [N number of specimens; GSI gonado-somatic index (%)]

Maturity stage	N	GSI (mean \pm SD)
1. Immature	1	0.5
2. Maturing virgin or resting	52	1.1 \pm 0.4
3. Developing		
4. Gravid	66	22.5 \pm 6.9
5. Spent	7	1.9 \pm 1.1

Table 3 Macroscopic pattern of gonad maturation of *Chionodraco hamatus* males at Terra Nova Bay between December and February [N number of specimens; GSI gonado-somatic index (%)]

Maturity stage	N	GSI (mean \pm SD)
1. Immature	8	0.1 \pm 0.05
2. Developing or resting	4	0.6 \pm 0.2
3. Developed	28	1.3 \pm 0.4
4. Ripe	194	1.8 \pm 0.5
5. Spent	2	0.8 \pm 0.5

A similar pattern was also found in males, as much as 83% of the whole sampled population being in spawning condition (Table 3).

The proportion of gravid females and ripe males (stage 4) throughout the sampling period is reported in Figs. 2 and 3, respectively. For females, the spawning peak was in December, because the proportion of gravid specimens quickly decreased in January and February. This trend was common to all size groups. Conversely, the proportion of ripe males did not show any significant change throughout the period, although a shift towards

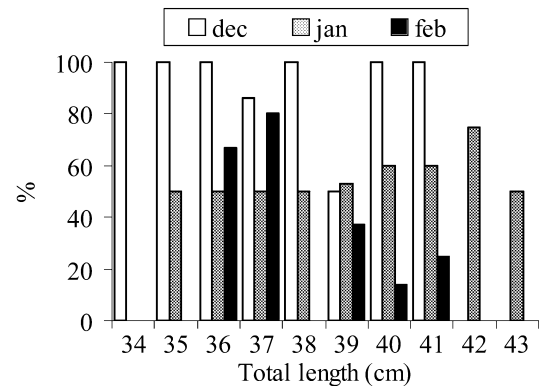


Fig. 2 Proportion of gravid females of *Chionodraco hamatus* in relation to fish size throughout the sampling period from all surveys

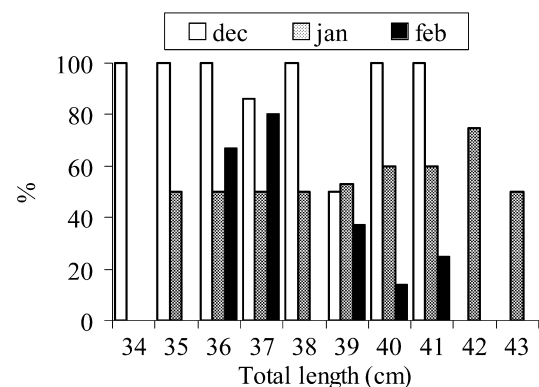


Fig. 3 Proportion of ripe males of *Chionodraco hamatus* in relation to fish size throughout the sampling period from all surveys

Table 4 Morphometric data of oocytes in different stages of development (mean values) (*NPI* nucleo-plasmatic index)

Stage	Cellular diameter (µm)	Nuclear diameter (µm)	NPI
Perinucleolar (II)	91	53	59.5
Yolk vesicle (III)	521	212	40.8
Vitellogenic (IV)	705	208	29.6
Ripe (V)	4500		

larger ripe specimens appeared to occur from December to February.

Histological data

Overall, the gonads of 27 females ranging in size from 325 to 450 mm TL and 288 to 732 g were analysed histologically. Mean cellular and maximum nuclear diameters, as well as the NPI, for each oocyte stage of development are summarised in Table 4.

Twelve females were mature and close to ovulation, with ovaries made up of oocytes in three different stage of development, namely perinuclear (stage II), yolk vesicle (stage III) and mature oocytes (stage V). In these females, gonad weight ranged from 61 to 241 g, accounting for a GSI between 16.7 and 38.7% (mean 23.7%, standard deviation 6.4).

All other specimens (15) were in post-spawning condition, as highlighted by the presence of large post-ovulatory follicles (maximum diameter = 1,195 µm, $n=20$) with numerous apoptotic cells in their wall

(Fig. 4A), and by resorption of ripe oocytes, in which the zona radiata had become thicker and fragmented while the yolk formed compact granules (Fig. 4D). In these females, other than clusters of small perinuclear oocytes (stage II, Fig. 5A), ovaries also contained a considerable proportion of larger oocytes with yolk vesicles (stage III, Fig. 5B, C) in the cytoplasm or in early vitellogenesis (first inclusions of yolk granules, early stage IV, Fig. 5B–D). Their gonad weight ranged between 1.9 and 13.4 g, with GSI values between 0.6 and 2.7% (mean 1.2%, standard deviation 0.5).

Interestingly, some gravid females kept alive in aquaria released their eggs in captivity. Some of these were sacrificed 1 week after ovulation, and their ovaries showed small and convoluted post-ovulatory follicles (maximum diameter = 505 µm, $n=20$), but still with an evident lumen (Fig. 4B). In other females, which were sacrificed 2 weeks after ovulation, the follicles (maximum diameter = 303 µm, $n=20$) were even smaller and without a lumen (Fig. 4C).

As reported for other channichthyids (Calvo et al. 1999), the testes of this species have a cystic lobular pattern associated with the unrestricted spermatogonial type (Grier et al. 1980), with spermatogonia distributed along the tubules, although more concentrated in their blind end. Histological data on spermatogenesis were obtained from 16 males ranging between 310 and 375 mm TL and 224 and 417 g. With reference to spermatogenic activity, almost all males (12) were at the peak of the spermatogenic process, with a massive confluence of spermatozoal cysts towards the lobule lumina, filling them (Fig. 6A, B). Their gonads weighed

Fig. 4A–D Cross-sections of the ovary of *Chionodraco hamatus* after spawning. **A** After recent ovulation, showing large post-ovulatory follicles (double arrows) and stage III oocytes (single arrow); scale bar = 150 µm; inset shows an apoptotic cell in the post-ovulatory follicle wall, scale bar = 5 µm. **B** One week after ovulation, showing post-ovulatory follicles (double arrows) and stage III oocytes (single arrow); scale bar = 150 µm. **C** Two weeks after ovulation, showing post-ovulatory follicles in resorption (double arrows) and stage III oocytes (single arrow); scale bar = 150 µm. **D** Atretic oocyte (single arrow) in a post-spawning ovary; scale bar = 150 µm

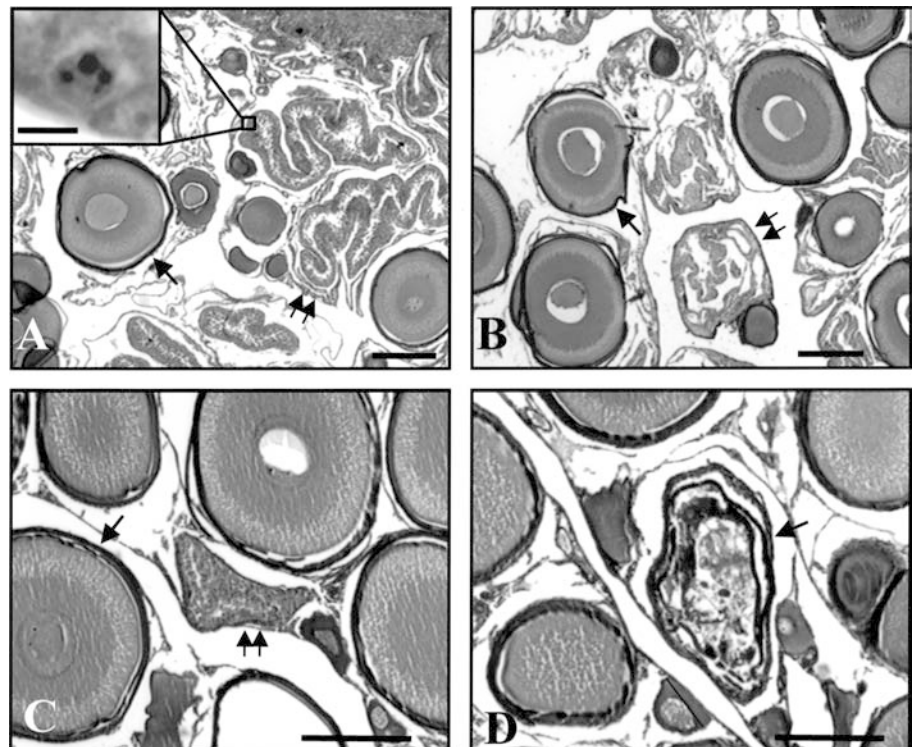


Fig. 5 **A** A “nest” of stage II oocytes; scale bar = 30 μm . **B** Cross-section of an ovary showing stage III (double arrows) and stage IV oocytes (single arrow); scale bar = 200 μm . **C** Detail of a stage III oocyte (arrow indicates the yolk vesicles in the cytoplasm); scale bar = 150 μm . **D** Detail of an early stage IV oocyte (double arrows indicate the yolk granules in the cytoplasm); scale bar = 100 μm

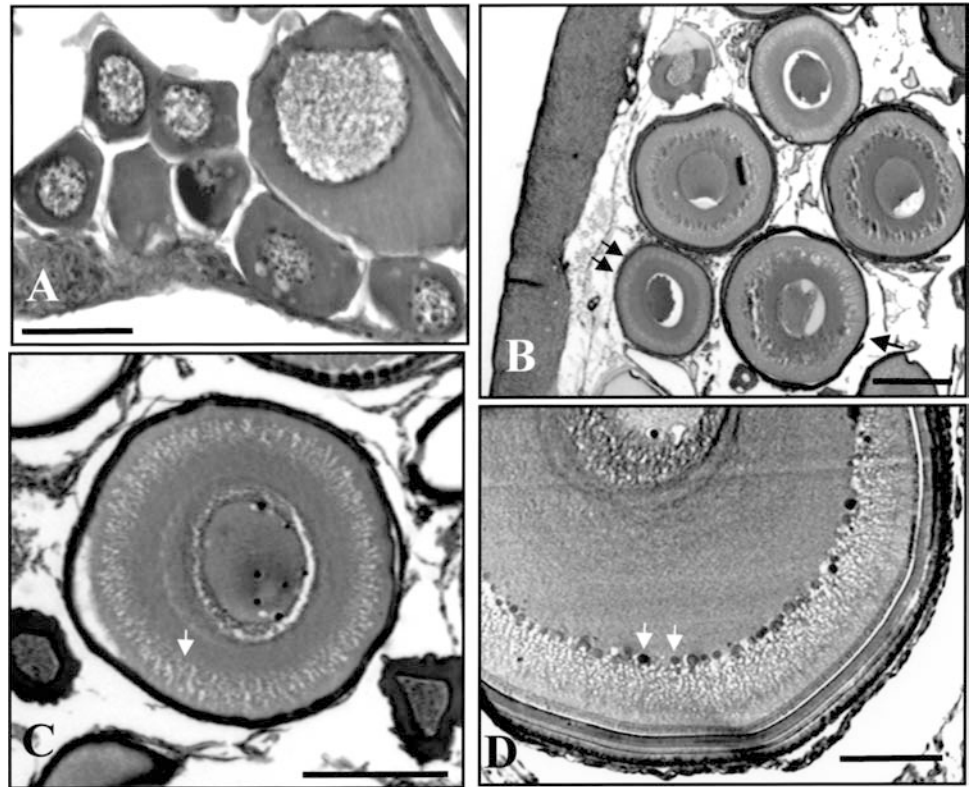
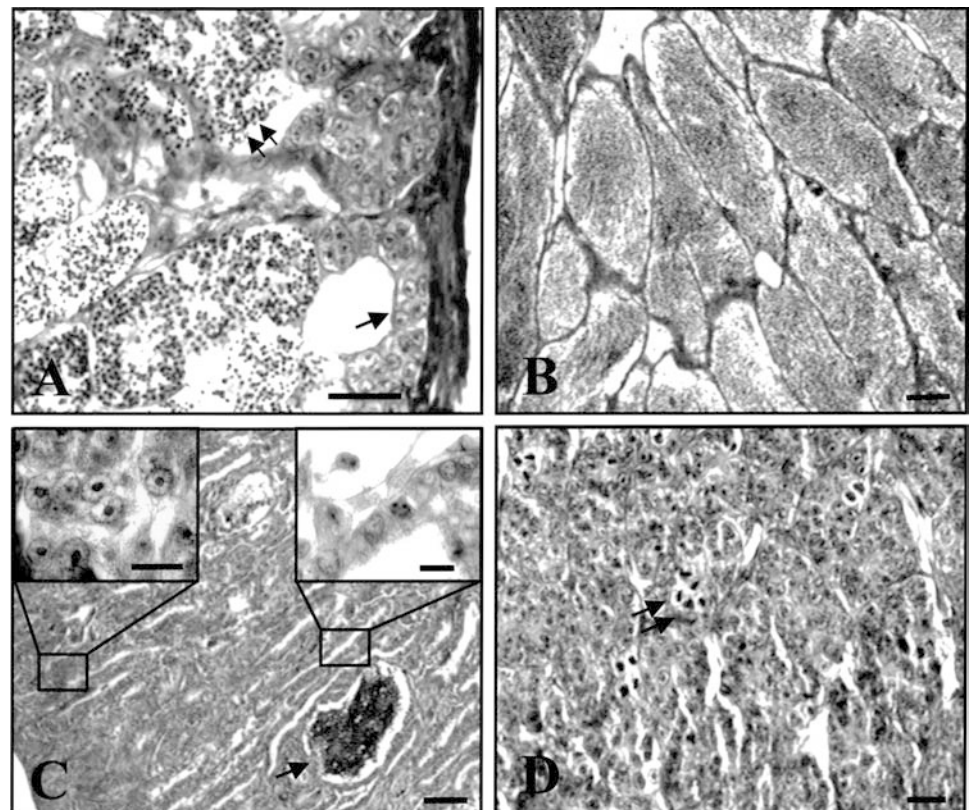


Fig. 6 **A** Cross-section of a testis with spermatozoa free in the seminiferous lobules (double arrows) and cysts of staminal spermatogonia in the gonad wall (single arrow); scale bar = 30 μm . **B** Seminiferous lobules filled with spermatozoa; scale bar = 100 μm . **C** Cross-section of a testis after spermiation, scale bar = 100 μm ; note staminal spermatogonia in the gonad wall (left inset) and apoptotic cells in the walls of collapsed lobules (right inset); arrow indicates residual spermatozoa in a lobule lumen; inset scale bar = 10 μm . **D** Cross-section of a testis with cysts filled with spermatogonia; double arrows indicate spermatogonial mitoses; scale bar = 20 μm



between 2.5 and 8 g, accounting for a GSI between 1 and 2.5% (mean 1.8%, standard deviation 0.5).

Three males were immature, showing testes uniformly occupied by spermatogonial cysts with evidence of spermatogonial mitoses (Fig. 6D). Gonad weight of these specimens was between 0.2 and 0.5 g, with a GSI between 0.06 and 0.2% (mean 0.13%, standard deviation 0.08).

Only one fish appeared in post-spermiation condition (gonad weight 1.2 g, GSI 0.3%), with collapsed lobules, residual spermatozoa in some lobule lumina and apoptosis of gametocytes that had not completed the spermatogenic process and of somatic cells (Fig. 6C).

Discussion

According to the available data on the reproductive biology of Antarctic fish, two main strategies have been inferred: most of the species living in the Seasonal Pack-ice Zone and around the islands north of it are autumn and winter spawners, whereas a higher proportion of fish in the high-Antarctic Zone are spring and, particularly, summer spawners (Kock and Kellermann 1991). The channichthyid *Chionodraco hamatus* is one of the most common fish of the high-Antarctic Zone, inhabiting the coastal waters around the Antarctic continent, and fits the second pattern. Previous research on the reproductive biology of *Chionodraco hamatus* indicates that this species spawns in spring (September/October) in the Mawson Sea and throughout summer (December/March) in the Ross Sea, Davis Sea and Weddell Sea (Shandikov and Faleeva 1992; Duhamel et al. 1993; Vacchi et al. 1996). As in other high-Antarctic channichthyids, *Chionodraco hamatus* females are characterised by having low fecundity, since they produce only a few thousand eggs. Also, they produce large eggs (3.5–5 mm) (Vacchi et al. 1996). The relatively small diameter of mature oocytes of *Chionodraco hamatus* reported from the Weddell Sea in spring (Ekau 1991) probably indicates that they were not fully developed, as can also be deduced by the very low GSI value (6–7%) reported in that study. Furthermore, in contrast to the results from the Davis Sea (Shandikov and Faleeva 1992), we did not find any difference in time of spawning related to size of females.

Focussing the attention on fish collected during the spawning season, both in terms of macroscopic and histological appearance of gonads, a series of interesting considerations about the reproductive behaviour and population dynamics of this species can be drawn.

Our results demonstrate the concurrent presence of ripe eggs, representing the current season's spawn, and oocytes in early stage of maturity (stages II and III) that represent next year's spawn in the gonads of gravid females of *Chionodraco hamatus*, a feature typical of Antarctic fish (Kock and Kellermann 1991). In addition, the presence of oocytes in early vitellogenesis (stage IV) in the post-spawning females destined to spawn the next

year, indicates vitellogenesis is a slow process, extending over at least 1 year. However, GSI, a measure of reproductive effort, increases about 10 times from post-spawning to gravid females, indicating a considerable mobilisation of resources over a short period of time.

Similar to most notothenioids (Kock and Kellermann 1991), GSI in males of *Chionodraco hamatus* is much lower than in females. However, they may mature and remain in spawning condition for a longer period (2–3 months, at least, see Fig. 3). The lack of residual spermatozoa in the testis lumen and the presence of spermatogonial mitoses in three small specimens of *Chionodraco hamatus* suggested that they were probably immature fish entering sexual maturity for the first time, rather than adult fish recovering from a recent spawning. Indeed, a partially refractory stage just after sperm release, evidenced by the absence of spermatogonial mitoses both in A and B spermatogonia, has been recently described in this species (Russo et al. 2000).

The size range of the immature males mentioned above was between 330 and 349 mm TL, consistent with the size of immature males of *Chionodraco hamatus* described by Shandikov and Faleeva (1992). Therefore, according to these data, the size at first spawning for males should be about 350 mm TL, very similar to the value obtained for females by means of the logistic equation in this study.

The relationship between the proportion of mature females and fish size, fitted by means of the logistic curve, clearly indicates that many specimens large enough to spawn probably did not spawn in the current season. According to Everson (1994), who proposed two different reproductive strategies for Antarctic fish, *Chionodraco hamatus* appeared similar to the *Champscephalus* type, in which not all adult females would spawn annually. This phenomenon was described in more detail by Macchi and Barrera-Oro (1995), who reported a large proportion of females of *Champscephalus gunnari* showing oocyte resorption processes (atresia) in pre-reproductive phases as well. Atresia in ovaries of *Champscephalus gunnari* had also been reported by Everson et al. (1991), who highlighted the macroscopical resemblance of this condition to a normal resting stage (stage 2). However, in *Chionodraco hamatus*, we only found atretic processes in post-reproductive phases, that is in ovaries with evident post-ovulatory follicles. The repeated sampling of ovaries 1 and 2 weeks from ovulation in our study, allowed us to follow the transition from spent to resting stage of maturity. Histologically, the post-ovulatory follicles of spent females, which indicate that spawning has just occurred, lasted no more than 3–4 weeks after spawning, a much shorter time than reported for some species of nototheniids (Butskaya and Faleeva 1987). Similarly, the macroscopic appearance of spent females, characterised by having shrunken flaccid ovaries with few large residual eggs, probably would not last long. This was confirmed because most females of *Chionodraco hamatus* with post-ovulatory follicles in the resorption phase, and

therefore considered to be spent, appeared macroscopically to be in the resting stage (i.e. stage 2). Furthermore, the post-ovulatory follicles are invisible macroscopically.

In conclusion, females with ovaries in both the pre-reproductive regression stage and the post-reproductive spent stage can be easily misidentified macroscopically as the resting stage of maturity. This could significantly affect the proportion of mature females judged by means of macroscopic analysis of gonads only and, consequently, the estimated length at sexual maturity or length at first spawning. Further research on the reproductive biology of Antarctic fish, based on the macroscopic analyses of gonads, should thus be supported by histological analyses of some samples.

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