Polar Biol (2006) 29: 963–970
DOI 10.1007/s00300-006-0138-1

ORIGINAL PAPER

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Gametogenesis and reproductive strategies in some species of the Antarctic fish genus *Trematomus* (Nototheniidae) from Terra Nova Bay, Ross Sea

Received: 29 November 2005 / Revised: 24 March 2006 / Accepted: 24 March 2006 / Published online: 25 April 2006

Abstract Species of the genus *Trematomus* are the most common nototheniids in the High-Antarctic Zone, and several live sympatrically on the Ross Sea continental shelf. Histological analysis of gonadal development of *T. bernacchii*, *T. hansoni* and *T. newnesi* was carried out on samples collected during the austral summer in the coastal waters of Terra Nova Bay, western Ross Sea. Gonads of both females and males of the three species were described based on macroscopic and histologic scales. Histologically, both males and females of *T. bernacchii* were in postspawning or in early maturing condition, thus indicating that they recently completed spawning. Conversely, most specimens of *T. hansoni* were in spawning condition, as evidenced by the histological appearance of gonads and by the high value of gonado-somatic index (GSI) of females between 20 and 36%. In the same period, females of *T. newnesi* had maturing ovaries, whereas males were at an early developmental stage of maturity. In all species, the testicular structure closely resembled the unrestricted spermatogonial type, although spermatogonia were more concentrated in the blind end of tubules. On the basis of the pattern of oocyte maturity observed within the ovarian lamellae, all *Trematomus* had a group synchronous ovary, as commonly reported in Antarctic fish. Furthermore, the presence of oocytes showing the commencement of yolk deposition in spent females confirms that vitellogenesis is a slow process, extending over at least 1 year. The reproductive strategies of *Trematomus* are discussed in terms of timing of the spawning season of each species as a function of the seasonal production cycle and of the interspecific relationships. The spawning activities of the three species investigated appeared to be mismatched with respect to time as well as location within the range of distribution of each.

Introduction

Among notothenioids, the Antarctic rockcods (family Nototheniidae) are by far the most common and conspicuous group of Antarctic fishes. This family is composed of 12 genera and 49 species which are distributed both on the continental shelves of the Antarctic continent and around the sub-Antarctic islands (DeWitt et al. 1990; Eastman and Eakin 2000). In particular, the genera *Notothenia* and *Lepidonotothen* are widespread in the Seasonal Pack-ice Zone, whereas the genus *Trematomus* predominates in the High-Antarctic Zone (Kock 1992).

The genus *Trematomus* is generally composed of small to medium-sized fishes including benthic (*T. bernacchii*, *T. hansoni*, *T. nicolai*, *T. pennellii*, *T. scotti* and *T. tokarevi*), epibenthic (*T. eulepidotus*, *T. lepidorhinus* and *T. loennbergii*) and semipelagic (*T. newnesi*) species (Andriashev 1970; Eastman 1993). In the Ross Sea, these species are distributed on the continental and inner shelf depressions as deep as 1,000 m and, according to depth distribution, they can be classified as shallow, intermediate and deep-water fishes (Eastman and Hubold 1999; Vacchi et al. 1991; Donnelly et al. 2004).

As far as the reproductive biology of nototheniids is concerned and, in particular, that of *Trematomus*, most data available so far have been obtained from the Weddell and Ross Seas (Dearborn 1965; Ekau 1991; Hubold 1992; Duhamel et al. 1993; Vacchi et al. 1996; Russo et al. 2000), as well as in Davis and Mawson Seas (Butskaya and Faleeva 1987; Shandikov and Faleeva 1992). In the High-Antarctic Zone, species of *Trematomus* are generally spring or summer spawners

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and produce relatively few eggs (i.e. thousands per season) at least 3.0–3.5 mm in diameter (for a review, Kock and Kellermann 1991). Due to their relatively large size, the eggs of *Trematomus* are probably benthic, as directly observed in *T. bernacchii* (Moreno 1980) and *T. eulepidotus* (Ekau 1989). In addition, *T. bernacchii* females have been observed to guard eggs deposited in sponges (Moreno 1980).

However, as often reported for other notothenioids, few studies have dealt with the histological analysis of gonads of *Trematomus* (Hureau 1970; Beniaz et al. 1980; Butskaya and Faleeva 1987; Shandikov and Faleeva 1992; Fusco et al. 1997). In the Ross Sea, detailed oocyte cytology has been investigated in *T. bernacchii*, *T. hansoni*, *T. lepidorhinus* and *T. pennellii* (Motta et al. 2005), whereas the testis structure and spermatogenic activity in *T. bernacchii* were described by Russo et al. (2000).

In the western Ross Sea, the coastal fish fauna of Terra Nova Bay is largely dominated by species of genus *Trematomus*, both in terms of abundance and biomass (Vacchi et al. 1991). In particular, *T. bernacchi* and *T. hansoni* are overwhelmingly the most common benthic nototheniids, whereas the water column is dominated by the semipelagic species *T. newnesi*. Although these species are largely sympatric in Terra Nova Bay, the feeding overlap between them is generally low, as interspecific competition is reduced by taking either different prey or different amounts of the same prey (Vacchi et al. 1994; La Mesa et al. 1997). In addition, at the intraspecific level, a high degree of feeding plasticity has been recently observed in *T. newnesi* in response to different environmental conditions (La Mesa et al. 2000). Thus, it is appropriate to compare the reproductive characteristics of these species, with the aim of testing the existence of different strategies in situations where spatial or food overlap is high (both benthic species) or low (benthic vs pelagic species).

In the present study, we report on the histological analysis of gonads of *T. bernacchii*, *T. hansoni* and *T. newnesi* collected in coastal water of Terra Nova Bay during the austral summer. Coupling the histological analysis with macroscopic data available in the literature, we reconstruct the reproductive features of each species, testing the hypothesis of a common strategy to avoid inter-and intraspecific competition in the investigated area.

Materials and methods

Fish samples were collected off Terra Nova Bay between 8th January and 13th February 2002 during the XVII Italian Antarctic Expedition. Fish were caught in shallow waters down to 100 m depth near the Italian Base (74°41′42″S, 164°07′23″E) by means of trammel and gill nets. For each fish caught, total length (TL) was recorded to the nearest millimetre below and sex and stage of gonad maturity determined macroscopically according to the five-point scale of Everson (1977) and Kock and Kellermann (1991). Similarly, total weight (g) and gonad weight (0.1 g) were also recorded from each specimen. The reproductive effort was evaluated in terms of gonado-somatic index (GSI), calculated as the percentage of gonad to total weight. 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 the histological analysis, whole or portions of gonads were selected from each male and female, respectively, and fixed in Bouin's solution for 12 h. The samples were then dehydrated in ethanol and embedded in paraffin. Thin sections (7 μm) were obtained from each sample, mounted on slides and stained with Mayer's haematoxylin–eosin and Galgano's trichrome following a standard procedure (Beccari and Mazzi 1972). Each section was examined with a Nikon Eclipse 800 optical microscope at magnifications of 40–400 ×. Measurements of oocytes were carried out using the Nikon software package Lucia 4.51.

On the basis of histological appearance, ovarian follicles were classified according to six development stages: (I) chromatin nucleolar; (II) perinucleolar; (III) cortical alveoli formation; (IV) vitellogenic; (V) mature; (VI) postovulatory follicle (Wallace and Selman 1990; West 1990). To estimate the ovarian activity, an analysis of the stage/size frequency distribution was performed for each ovary by counting oocytes at different stages of maturity on five sections taken at 1 mm intervals. As notothenioids generally exhibit group synchronous ovaries sensu Wallace and Selman (1981) Everson 1984; Kock and Kellermann 1991), each specimen was staged on the basis of 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 nucleoplasmic indices (NP) were 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 on the basis of the different types of gametocytes, i.e. from spermatogonia to spermatozoa, in the seminiferous lobules of each testis. The presence of spermatogonial mitoses was recorded as well. Testis maturity was evaluated according to a five-point scale (Billard 1986): (1) immature stage (the presence of spermatogonia and spermatogonial mitoses); (2) early development stage (first meiotic division); (3) advanced development stage (second meiotic division); (4) mature stage (the presence of spermatozoa cysts); (5) postreproductive stage (the presence of collapsed lobules and residual spermatozoa).

Linking macroscopic and histologic stages of maturity, males and females of *Trematomus* were staged as summarized in Tables 1 and 2. Note that macroscopic and histologic stages of development are numbered with Roman and Arabic numerals, respectively.

Table 1 Scale of gonadal maturity of *Trematomus* females from Terra Nova Bay

Macroscopic stage of maturity	Histological appearance
1. Immature	–
2. Developing	Some oogonia, previtellogenic oocytes of different size (stage I, II and III)
3. Maturing	Previtellogenic oocytes of different size and few oocytes starting vitellogenesis (early stage IV)
4. Mature	Mature hydrated oocytes free in the ovarian lumen (stage V), as well as previtellogenic and vitellogenic oocytes; some atretic oocytes also present
5. Spent	Postovulatory follicles and a reserve stock of previtellogenic (stages I, II and III) and vitellogenic (IV) oocytes; some atretic oocytes

Table 2 Scale of gonadal maturity of *Trematomus* males from Terra Nova Bay

Macroscopic stage of maturity	Histological appearance
1. Immature	Cysts of spermatogonia with evidence of mitoses filling the entire lobule (stage I)
2. Developing	Seminiferous lobules with cysts of meiotic spermatocytes I and II (stage II)
3. Developed	–
4. Ripe	Few cysts of interstitial spermatogonia, cysts of spermatozoa starting to fill the lobule lumina (stage IV)
5. Spent	Residual spermatozoa in the lumen of some lobules (stage V)

Results

The pattern of relative frequency distribution of oocytes at different stages of development were evaluated separately for maturing and spent females of *T. bernacchii*, for mature and spent females of *T. hansoni* and for maturing females of *T. newnesi*, as summarized in Fig. 1.

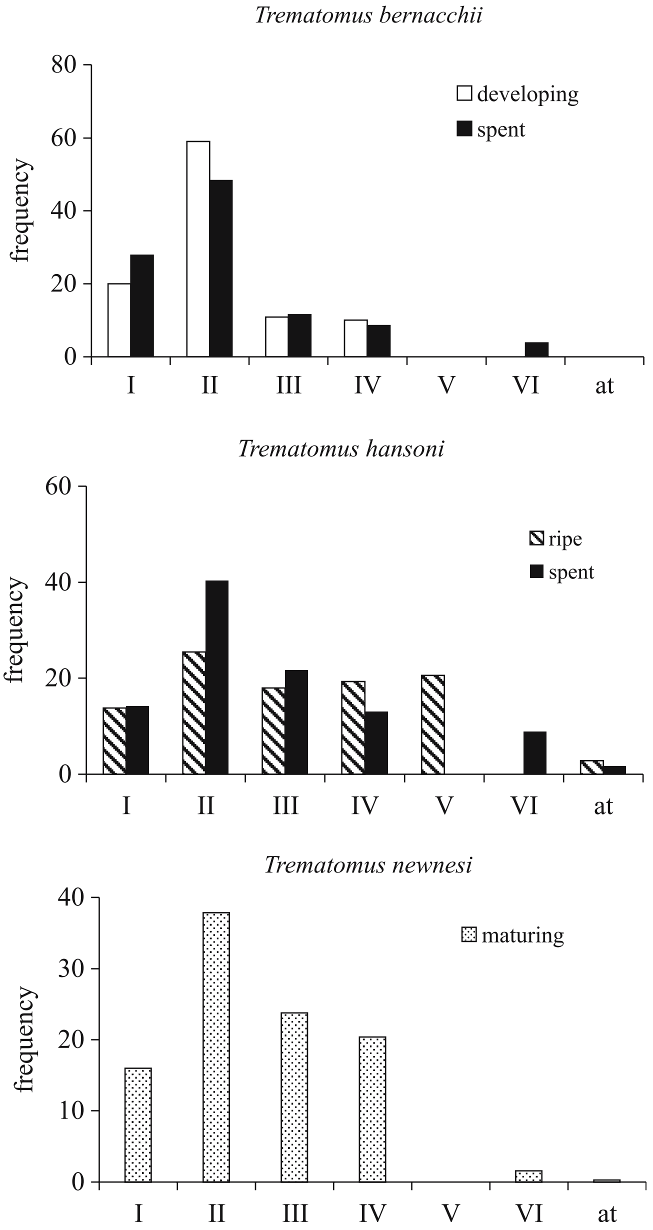

Fig. 1 Relative frequency distribution of oocytes at different histological stages of development. *I* Chromatin-nucleolar, *II* perinucleolar, *III* cortical alveoli formation, *IV* vitellogenic, *V* mature, *VI* postovulatory follicle, *at* atretic oocytes

Trematomus bernacchii

Overall, 27 females ranging between 195 and 340 mm in TL and 84.2–494.7 g in weight and 8 males ranging between 173 and 230 mm in TL and 66.2–145.3 g in weight were analysed.

From the histological analysis, we determined mean cellular and nuclear sizes and the NP of each oocyte stage of development as summarized in Table 3. During oogenesis both the cellular and nuclear sizes increase, although cell size does so at a greater rate, hence NP decreases.

Most females (18) were spent, showing ovaries with resorbing postovulatory follicles, oocytes in the first developmental stages (i.e. chromatin nucleolar, perinucleolar and cortical alveoli stages) and oocytes in early vitellogenesis (stage IV) (Fig. 2a). In these specimens, gonad weight ranged from 0.6 to 14.4 g, accounting for a GSI between 0.7 and 3.1% (mean 2.3%).

All other females were in developing or maturing stage of development. Developing females (six specimens) were characterized by ovaries filled with previtellogenic oocytes of different size (chromatin nucleolar, perinucleolar and cortical alveoli stages) and their GSI ranged from 0.5 to 1.9% (mean 1.1%). Maturing females had ovaries of increasing size (gonad weight range 1.7–7.3 g) with previtellogenic oocytes and a small portion of oocytes in early vitellogenesis (first inclusions of

Table 3 Morphometric data for oocytes in different stages of development in *Trematomus* (mean value ± standard error)

Stage of maturity	*Trematomus bernacchii*			*Trematomus hansoni*			*Trematomus newnesi*		
	Cellular size (μm)	Nuclear size (μm)	NP	Cellular size (μm)	Nuclear size (μm)	NP	Cellular size (μm)	Nuclear size (μm)	NP
I	64 ± 3	30 ± 2	0.11	65 ± 3	30 ± 3	0.11	46 ± 3	25 ± 3	0.19
II	235 ± 8	99 ± 4	0.08	196 ± 11	94 ± 4	0.12	184 ± 6	87 ± 3	0.12
III	494 ± 4	170 ± 8	0.04	740 ± 18	177 ± 6	0.01	442 ± 19	147 ± 5	0.04
IV	1,010 ± 16	300 ± 17	0.02	800 ± 34	244 ± 26	0.03	1,052 ± 19	–	–
V				2,685 ± 327	–	–			

See text for histological characteristics of each stage of maturity
NP Nucleo-plasmic index

yolk granules, early stage IV) (Fig. 2b). Their GSI was between 1.9 and 2.5% (mean 2.2%).

Of the eight males investigated, five were small immature specimens, showing testes uniformly containing spermatogonial cysts with some evidence of mitotic activity. Gonad weight of these specimens was between 0.1 and 0.2 g and the GSI range was between 0.1 and 0.3% (mean 0.2%). Two specimens were spent, as evidenced by the presence of collapsed lobules and residual spermatozoa in some lobule lumina (Fig. 2c). In addition, the cortical region of the testes contained spermatogonia I and II as well as spermatogonial mitoses. Gonad weight of these specimens was between 0.4 and 0.6 g and GSI was between 0.3 and 0.5%. Only one fish appeared to be in developing stage, with evidence of first meiotic division in some spermatogonia (gonad weight 0.6 g, GSI 0.4%).

Trematomus hansoni

The available sample of *T. hansoni* was composed of 20 females ranging between 267 and 355 mm in TL and 197.8–684.0 g in weight and only 2 males of 206–225 mm TL and 102.3–135.1 g.

Mean cellular and nuclear sizes and the NP of each oocyte stage of development are reported in Table 3. It is worth noting the large size of mature oocytes (stage V), which attain a maximum diameter of about 3.8 mm just before ovulation.

Most females (13) were mature and close to ovulation, with gonads almost completely filling the abdominal cavity. These ovaries were made up of large and hydrated mature oocytes (stage V) (Fig. 3a) and of the late vitellogenic stage (IV), as well as a batch of previtellogenic oocytes (stage I, II and III) probably constituting the reserve stock for the next spawning season. Some atretic oocytes were also observed. Gonad weight of these specimens was very high (between 79.1 and 190 g), accounting for a GSI between 20.1 and 36.5% (mean 25.4%). All other females were in late spent condition, as evidenced by the presence of large postovulatory follicles and oocytes in the first developmental stages (chromatin nucleolar, perinucleolar and cortical alveoli) and early vitellogenic stage (IV) (Fig. 3b). In these cases, gonad weight ranged between 3.3 and 21.5 g and the GSI between 1.7 and 4.6% (mean 3.3%).

The two males examined were both ripe and at the end of the spermatogenic process, with testes characterized by a massive confluence of cysts of spermatozoa which started to fill the lobule lumina (Fig. 3c). Gonad weight and GSI were similar in the two specimens (0.2–0–3 g and 0.2%, respectively).

Trematomus newnesi

Overall, the gonads of 12 females ranging in size between 185 and 224 mm in TL and 56.6–120.6 g in weight and of 23 males ranging between 185 and 227 mm TL and 65.8–131.3 g were histologically analysed.

As summarized in Table 3, the trend of cellular and nuclear sizes and the NP of each oocyte stage of development closely resemble that observed in *T. bernacchii*. Most females (11) of this species were maturing, with ovaries consisting of a few postovulatory follicles largely reabsorbed and evidence of advanced vitellogenetic activity (i.e. the presence of late stage IV oocytes) (Fig. 4a). At this stage, oocytes in all first developmental stages (I, II and III) are abundant, as observed in other *Trematomus* species examined. Gonad weight of these specimens was between 2.3 and 7.8 g and the GSI range was between 4.1 and 6.9% (mean 5.4%). Only one specimen was a developing female, showing ovaries with only previtellogenic oocytes (stage I, II and III) (Fig. 4b).

Except for a small fish that was immature (185 mm TL, 65.9 g), all males were in a developing stage with testes characterized by seminiferous lobules filled with cysts of meiotic spermatocytes I and II (Fig. 4c). The weight of testes ranged between 0.2 and 0.7 g, accounting for a GSI of 0.2–0.5% (mean 0.3%).

Discussion

From a histological perspective, the characteristics of the gametogenic processes observed in *Trematomus* are very similar to those described in other nototheniids

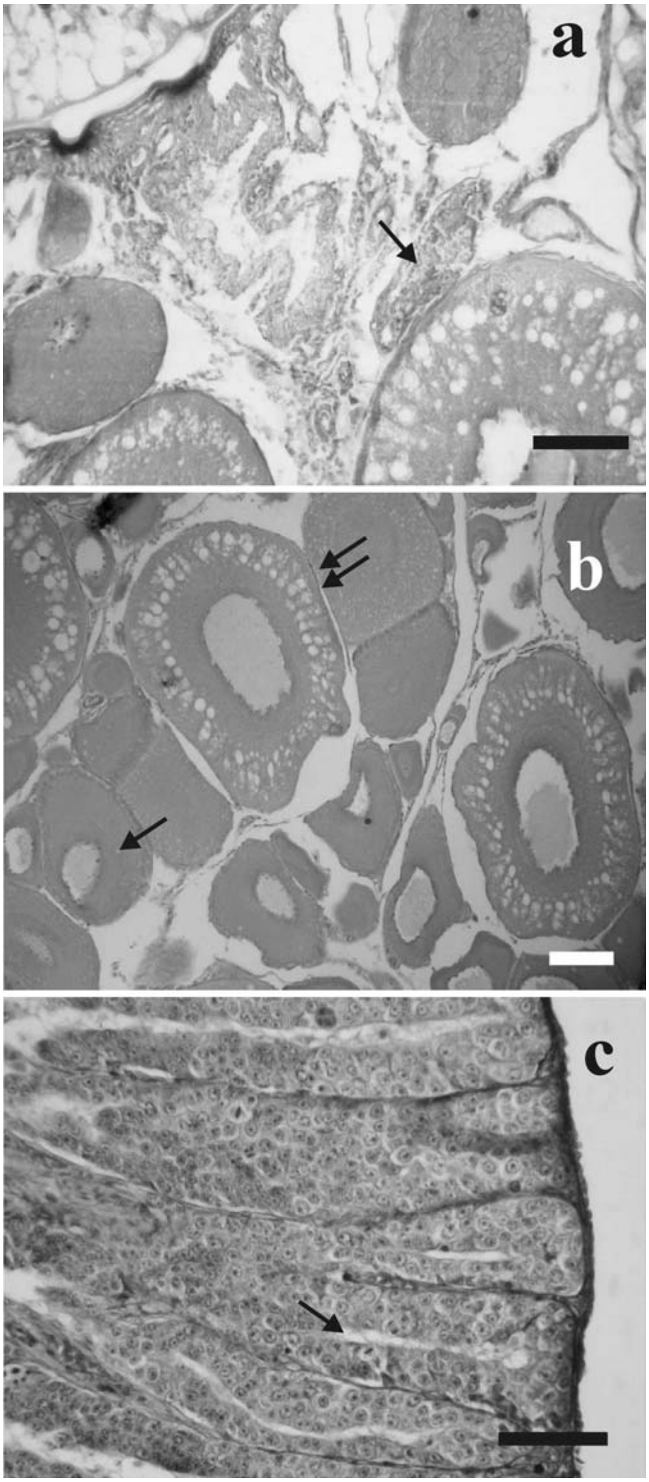

Fig. 2 Photomicrographs of histological sections of gonads of *T. bernacchii* sampled in Terra Nova Bay. **a** Spent female, showing postovulatory follicles in resorption (*arrow*) and oocytes in the first developmental stages, *scale bar* 100 µm; **b** maturing female, showing previtellogenic oocytes (*arrow*) as well as early vitellogenic oocytes (*double arrows*), *scale bar* 100 µm; **c** spent male, with lobules collapsed and few residual spermatozoa in lobules lumina (*arrow*); *scale bar* 100 µm

(Andriashev et al. 1979; Silyanova 1981; Butskaya and Faleeva 1987; Faleeva and Gerasimchuk 1990; Rae and Calvo 1996; Eastman and DeVries 2000; Russo et al. 2000).

According to the classification of testes based on the morphology of their seminiferous compartments (Billard 1986), males of all *Trematomus* investigated show a cystic lobular pattern, with blind ended testicular lobules. On the basis of a further classification based on the arrangement of spermatogonia within the lobules (Grier et al. 1980), testes of *Trematomus* closely resemble the unrestricted spermatogonial type, in which spermatogonia are scattered throughout the lobules, although they are more concentrated in the distal (or blind) ends. However, the spermatogenic stage observed in adult males in summer is remarkably different in each species investigated. Adult males of *T. hansoni* appeared to be in the final stage of spermatogenesis, being ready to release sperm that completely fill the lobule lumina. Conversely, adult males of *T. bernacchii* had already spawned, as evidenced by the collapse of lumina of the lobules and the presence of a few residual spermatozoa that are destined to be phagocytosed. In *T. newnesi*, the proliferative phase of spermatogenesis was at an advanced stage and the first meiotic stage had already started.

As for the microanatomic ovarian structure, the paired gonads of all *Trematomus* species can be classified as cystovaries (sensu Hoar 1969). According to the classification of Wallace and Selman (1981), all of them are characterized by having a group synchronous ovary, which is a common feature among Antarctic fishes (Kock and Kellermann 1991). This kind of ovarian structure, represented by two or more size groups of synchronously developing oocytes, is typical in species that spawn once in each reproductive season (Wallace and Selman 1981). In maturing and gravid females of *Trematomus*, two clutches of oocytes can easily be distinguished and separated by size: one more advanced batch of vitellogenic or mature oocytes that will be completely ovulated in the current spawning season, and another batch composed of previtellogenic oocytes (i.e. in the chromatin-nucleolar, perinucleolar and cortical alveoli stages) forming the reserve-stock for the next spawning season.

The occurrence of early vitellogenic oocytes during the entire annual cycle is a common feature among other Antarctic species (Duhamel et al. 1993; Everson 1994; Kock and Kellermann 1991), and can also be assumed for adult specimens of *Trematomus*. Furthermore, the presence of previtellogenic oocytes in spent females that are destined to spawn the next year, indicates that vitellogenesis is a slow process, extending over at least 1 year. The reproductive effort spent by females throughout the period of vitellogenesis is, however, considerable, as the GSI increases about ten times from spent to gravid females (at least in *T. hansoni*). The lack

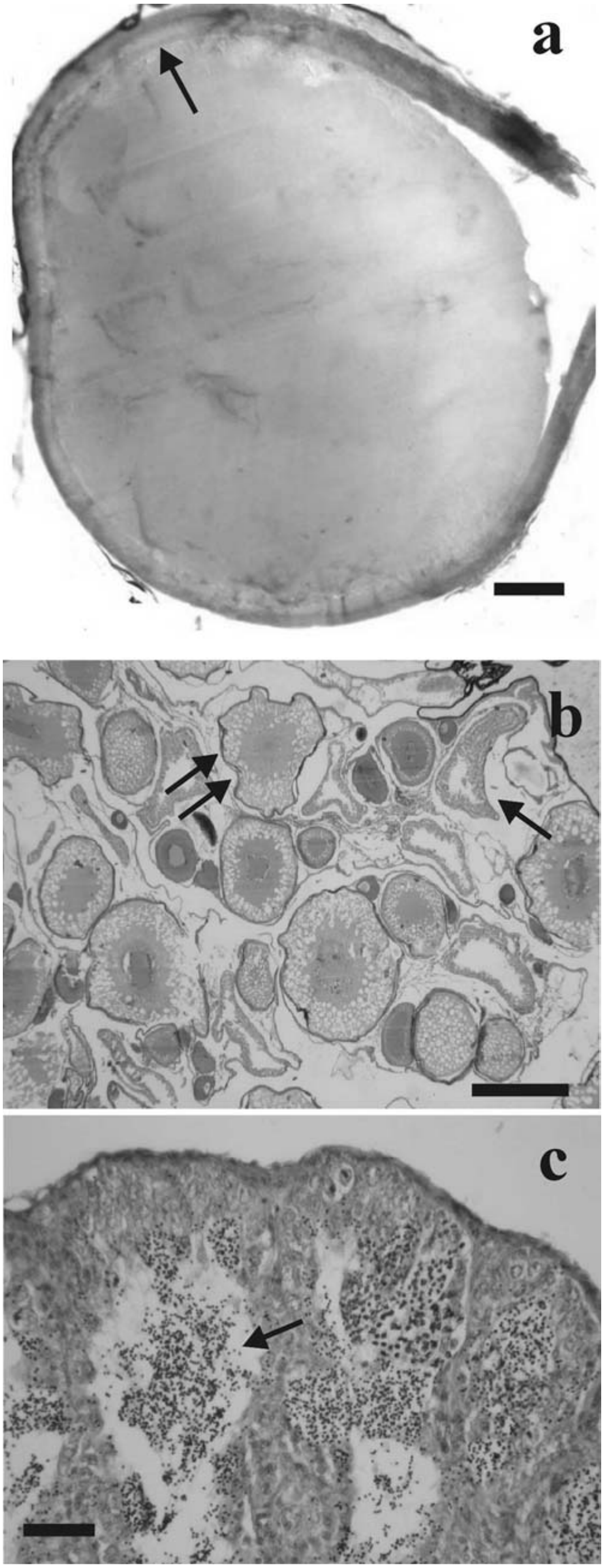

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Fig. 3 Photomicrographs of histological sections of gonads of *T. hansoni* sampled in Terra Nova Bay. **a** Mature female, a single large mature oocyte characterized by a homogeneous yolk mass and a thick zona radiata (*arrow*), *scale bar* 150 µm; **b** spent female, showing large postovulatory follicles (*arrow*) and some atretic oocytes (*double arrows*), *scale bar* 500 µm; **c** mature male, with lumina of lobules filled with free spermatozoa (*arrow*), *scale bar* 50 µm

of oil droplets and the thickness of chorion in mature oocytes of *T. hansoni* indicate that this species probably spawn demersal eggs, as directly observed in *T. bernacchii* (Moreno 1980) and reported in previous studies (Dearborn 1965; Kock and Kellermann 1991; Christiansen et al. 1998).

Taking into account the available data on reproductive biology, two main strategies have been hypothesized for Antarctic fishes: most of the species living in the Seasonal Pack-ice Zone are autumn and winter spawners, whereas a higher proportion of fish in the High-Antarctic Zone are spring and, particularly, summer spawners (North and White 1987; Kock and Kellermann 1991). However, combining present data and those reported in literature, the reproductive strategies adopted by the species investigated here seem to follow a more complex pattern.

As summarized in Table 4, considerable differences in the time of spawning can be seen both between populations of the same species living in different areas and between related species living sympatrically. For example, *T. hansoni* spawn in spring/summer in the High-Antarctic Zone (Adelie Land, Ross and Davis Seas), in summer in the Seasonal Pack-ice Zone (Antarctic

Table 4 Spawning period of the investigated species in the Southern Ocean

Species	Spawning period	Site	Source
T. bernacchii	Nov	Ant. Peninsula	Moreno (1980)
	Oct–Nov	Davis Sea	Andriashev et al. (1979), Butskaya and Faleeva (1987), Vacchi et al. (1996)
	Oct–Nov	Adelie Land	Hureau (1970)
	Nov–Dec	Ross Sea	Dearborn (1965)
T. hansoni	Feb	Ant. Peninsula	Bellisio (1966)
	Feb–Mar	South Georgia	Burchett et al. (1983), Silyanova (1981)
	Oct–Nov	Davis Sea	Butskaya and Faleeva (1987), Vacchi et al. (1996)
	Feb	Adelie Land	Hureau (1970)
	Jan–Feb	Ross Sea	Haschemeyer(1981), Vacchi et al. (1996), present data
T. newnesi	Mar–Apr	Ross Sea	Shust (1987)

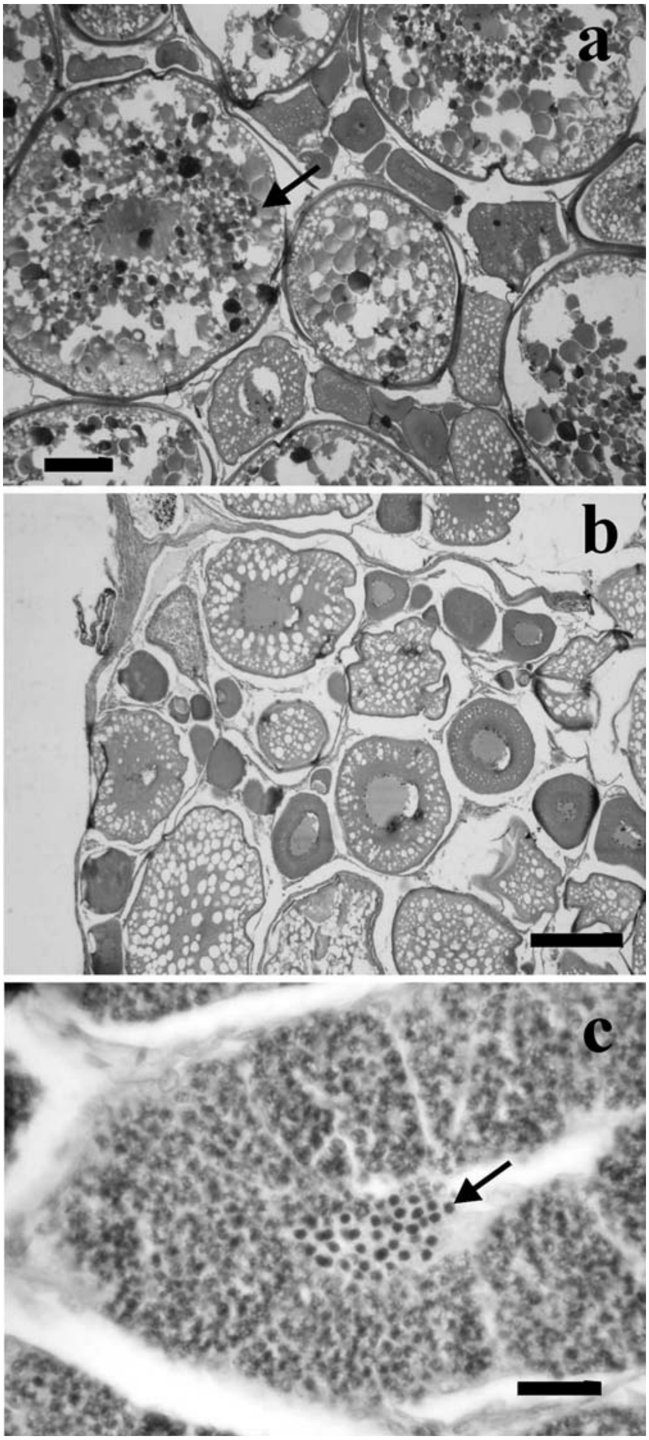

Fig. 4 Photomicrographs of histological sections of gonads of *T. newnesi* sampled in Terra Nova Bay. **a** Maturing female, showing few previtellogenic oocytes and oocytes in advanced vitellogenesis filled by yolk granules (*arrow*), *scale bar* 250 μm; **b** developing female, with a compact ovarian parenchyma comprised of previtellogenic oocytes, *scale bar* 250 μm; **c** developing male, showing seminiferous lobules containing cysts of spermatocytes I and II (*arrow*), *scale bar* 25 μm

Peninsula) and in late summer in the Ice-free Zone (South Georgia). Hence, in the absence of a simple latitudinal trend, other environmental factors such as the local seasonal production cycle or food competition seem to dictate the timing of spawning in this species. Similarly, if we consider the reproductive behaviour of related species which live sympatrically, a different pattern in the timing of spawning among them is evident.

Interestingly, the timing of spawning of *Trematomus* species in the Ross Sea seems to follow a chronological sequence. *T. bernacchii* probably spawn in late spring–early summer at the onset of the seasonal production cycle, namely between October and December (Dearborn 1965), as also supported by macroscopic and histologic data collected between January and February in Terra Nova Bay (La Mesa et al. 1997, present data). Later on, *T. hansoni* spawn between January and February, i.e. at the eighth of the summer season (Haschemeyer 1981; Vacchi et al. 1996; present data). Finally, *T. newnesi* is an autumn spawner, being mature between March and April (Shust 1987). The latter is partially supported by the relatively high GSI observed in January–February (5–6%) (Eastman and DeVries 1997; present data), assuming a steady increase of gonad weight in the later part of vitellogenesis stage.

In conclusion, the reproductive strategies in the genus *Trematomus* can be considered as opportunistic (see also Russo et al. 2000), showing a high plasticity in relation to different environmental and ecological conditions that change locally and temporally. The breeding cycles of such species, as well as being determined by the period of high production, are also probably tuned to maximize the probability of larval survival by lowering the food competition between them, thanks to a temporal mismatch in the spawning period.

Acknowledgements This work was financially supported by the PNRA (Italian National Antarctic Research Program). We are very grateful to Riccardo Rampa for his help in the editing of the figures. We are very grateful to Prof. J. T. Eastman and an anonymous referee whose comments improved the early version of manuscript greatly.

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