The reproductive biology of two epibenthic species of Antarctic nototheniid fish of the genus *Trematomus*

MARIO LA MESA1*, VINCENZO CAPUTO2 and JOSEPH T. EASTMAN3

1ISMAR-CNR, Istituto di Scienze Marine, Sede di Ancona, Largo Fiera della Pesca, 60125 Ancona, Italy
2Istituto di Biologia e Genetica, Università Politecnica delle Marche, Via Ranieiri 65, 60131 Ancona, Italy
3Department of Biomedical Sciences, College of Osteopathic Medicine, Ohio University, Athens, OH 45701-2979, USA

*mlamesa@ismar.cnr.it*

**Abstract:** *Trematomus eulepidotus* and *T. loennbergii* are two of the most common epibenthic fish in the waters of the High Antarctic continental shelf. Since the reproductive biology of these species has not been studied in the Ross Sea, we provide a macroscopic and histological analysis of the reproductive effort and gonadal development in both sexes. Most samples were collected during benthic trawl surveys in the south-western Ross Sea in the 1996 and 1997 summer seasons. The aim of the study was to define the reproductive characteristics of these two sympatric species and to examine the hypothesis that different reproductive strategies mitigate interspecific competition. We found that, in common with most Antarctic notothenioids, both species possess a suite of similar reproductive strategies including delayed sexual maturity, prolonged gametogenesis, group-synchronous oocyte maturation, a single spawning event per year and iteroparity. Both species show a comparable reproductive effort in terms of potential fecundity with between 2000 and 20 000 eggs per female per season. Nevertheless, the two species exhibited a considerable difference in the timing of the breeding season, spawning in summer (*T. eulepidotus*) and in autumn (*T. loennbergii*). This gives rise to a mismatch in the time of appearance of larvae in the environment and probably leads to reduced competition.

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**Key words:** gametogenesis, reproductive strategies, Ross Sea, sexual maturity

**Introduction**

In number of species, abundance and ecological diversity, fish of the genus *Trematomus* dominate the fauna of the High Antarctic shelf (DeWitt 1971, Kock 1992, Hureau 1994). *Trematomus* is composed of 11 species encompassing benthic, epibenthic and semipelagic lifestyles (Andriashev 1970, Eastman 1993). Their radiation filled a wide range of habitats on the shelf and was probably the result of pelagization, an evolutionary trend whereby lineages originating from benthic ancestors have repeatedly evolved to live or at least feed in the water column (Klingenberg & Ekau 1996). In ecomorphological analyses, *Trematomus eulepidotus, T. lepidorhinus* and *T. loennbergii* cluster as epibenthic species (Ekau 1988, 1991, Klingenberg & Ekau 1996), living on or in close proximity to the bottom as documented by underwater photography and video (Ekau & Gutt 1991, Gutt & Ekau 1996). These species share similar body morphology, characterized by a streamlined appearance, moderate activity levels, absence of substrate contact adaptations and lower percentage weights in seawater than most other nototheniids (Eastman 1993, Wohrmann 1998). The most recent phylogenetic analysis of *Trematomus*, including 10 of 11 species, indicates that the genus is monophyletic and that *T. lepidorhinus* and *T. loennbergii* are sister species (Sanchez et al. 2007). However *T. eulepidotus* is external to these species by several nodes and thus the epibenthic lifestyle was not attained by common ancestry, and the ecomorphological index of Ekau (1988, 1991) does not reflect phylogeny but rather similar life styles that were independently acquired (Sanchez et al. 2007).

Although the epibenthic species share a suite of morphological characters, they differ in diet, depth distribution and relative abundance. Dietary data indicate that *T. eulepidotus* is a zooplanktivore, preying primarily on euphausiids, hyperiids, copepods and pteropods, but occasionally on other crustaceans, polychaetes, chaetognaths and fish (Permitin & Tarverdieva 1978, Targett 1981, Schwarzbach 1988, Roshchin 1991, Pakhomov 1997, Brenner et al. 2001). Conversely, *T. loennbergii* feeds mostly on benthic species, usually associated with the substrate, including polychaetes, isopods, decapods, amphipods, bivalves and fishes (Eastman 1985, Schwarzbach 1988, La Mesa et al. 1997).

The epibenthic species of *Trematomus* have a circum-Antarctic distribution and occur sympathetically in the large shelf areas of the Weddell and Ross seas (DeWitt et al. 1990). They exhibit reasonably disjunct depth distributions, with *T. eulepidotus* most common in shallow water, *T. loennbergii* in deep water, and *T. lepidorhinus* ranging from shallow to moderately deep water (Lannoo & Eastman 2000). Specific depth ranges for these three
species in the Ross Sea are 130–344 m, 663–1191 m and 130–663 m, respectively (Eastman & Hubold 1999, Lannoo & Eastman 2000). One species is usually more abundant than the others, perhaps because of these depth preferences (Eastman 1993). In the Weddell and Ross seas, for example, *T. eulepidotus* is the dominant epibenthic fish in shallower depths, whereas in deeper waters it is replaced by *T. loennbergii* (Ekau 1990, Hubold 1992, Eastman & Hubold 1999, Vacchi et al. 1999a, Donnelly et al. 2004). Although the three species share the shelf habitat, they have different feeding strategies and depth preferences that overcome or partially mitigate interspecific competition.

Different reproductive strategies, consisting principally of a temporal mismatch in the spawning period (La Mesa et al. 2006), also reduces interspecific competition among sympatric species of *Trematomus* in the Ross Sea. For example, the benthic species *T. bernacchii* and *T. hansonii* spawn, respectively, between October–December and January–February, whereas the semipelagic *T. newnesi* spawns between March–April (Dearborn 1965, Shust 1987, Vacchi et al. 1996, La Mesa et al. 2006). Most information on the reproductive biology of epibenthic species of *Trematomus* is from specimens collected in the Weddell Sea, and analyses have been based exclusively on macroscopic examination of gonads (Ekau 1991, Duhamel et al. 1993). These species have not been studied in the Ross Sea. Therefore, employing both macroscopic and histologic approaches, we: 1) investigate features of the reproductive biology of *T. eulepidotus* and *T. loennbergii*

from the south-western Ross Sea, and 2) compare our findings with the literature to examine the hypothesis that these species employ a common reproductive strategy to avoid interspecific competition.

**Materials and methods**

Samples of *T. loennbergii* were collected during cruises 96-6 and 97-9 of the RV Nathaniel B. Palmer in the south-western Ross Sea. Fish were caught at five stations between 663 and 1191 m depth (Fig. 1). Most specimens of *T. eulepidotus* were collected during cruise 97-9 near Beaufort Island at about 250 m depth (Fig. 1). All fish were caught by an otter trawl towed at 2–3 knots for 30–60 minutes (Eastman & Hubold 1999). A few additional samples of *T. eulepidotus* were obtained off Terra Nova Bay between 8 January and 13 February 2002, during the XVII Italian Antarctic Expedition. Fish were caught at several stations located near the Italian station (74°41′42″S, 164°07′23″E), by trammel and gill nets set down to 100 m depth. Overall data on available fish samples are summarized in Table I.

In the laboratory, each specimen was measured for total length (TL, mm) and weighed (TW, g). After dissection, sex and stage of maturity were assessed on the basis of macroscopic appearance of gonads, according to the five point scale of maturity for nototheniid fish (Everson 1977, Kock & Kellermann 1991). After this procedure, the gonads were removed and weighed on an analytical balance with an accuracy of 0.01 g (Wg, g) and then stored in 70% alcohol.

As a measure of reproductive effort and stage of gonad maturity, the gonadosomatic index was calculated as the percentage of gonad to total body weight (GSI = 100 × Wg/TW) (Crim & Glebe 1990). To determine fish fecundity, all mature females (i.e. in stage 4 of macroscopic scale) were selected and their gonads processed as follows. A preliminary microscopic analysis indicated that the ovaries of these specimens exhibited a group-synchronous development, as two main cohorts of oocytes were easily distinguished by size (Wallace & Selman 1981, West 1990). As a consequence, the gravimetric method was used to estimate fecundity (Murua et al. 2003). According to this method, three subsamples of known weight (generally about 1 g each with an accuracy of 0.001 g) were sampled from three different parts of the ovary and the number of ripe oocytes counted under a stereomicroscope at low magnification. Hence, potential or absolute fecundity (F) was estimated applying the

<table>
<thead>
<tr>
<th>Cruise</th>
<th>Date</th>
<th><em>T. loennbergii</em></th>
<th><em>T. eulepidotus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>96/6</td>
<td>8 Jan</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>97/9</td>
<td>20–28 Dec</td>
<td>37</td>
<td>42</td>
</tr>
<tr>
<td>2002</td>
<td>8 Jan–13 Feb</td>
<td>12</td>
<td></td>
</tr>
</tbody>
</table>

**Table I. Number of fish samples available for the study.**

![Diagram of the south-western Ross Sea, showing sampling locations for *Trematomus eulepidotus* (crosses) and *T. loennbergii* (dots). Dotted line represents the 500 m isobath.](image-url)
following relationship (Kock 1989, Murua et al. 2003):

\[ F = \frac{W_g \left( \sum o_i / w_i \right)}{n} \]

where \( W_g \) is gonad weight, \( o_i \) is the number of ripe oocytes in the ith subsample, \( w_i \) is the weight of ith subsample and \( n \) is the number of subsamples. A chi-square test revealed no significant differences (\( P > 0.05 \)) for numbers of ripe oocytes per gram (\( o_i/w_i \)) among different parts of the ovary.

The relative fecundity (\( F_r \)) was calculated as number of oocytes per gram of total body weight (TW). The relationship between fish size and absolute/relative fecundity was investigated applying linear regression analysis (Kartas & Quignard 1984). Finally, in each mature female, the mean size of ripe oocytes was assessed by measuring the maximum diameter of 10 oocytes taken randomly from the subsamples used to estimate fecundity.

Based on the stage of macroscopic maturity of gonads, the proportion of individuals in stages 3–5 for each centimetre size class was recorded. The length at first spawning \( (L_{m50}) \), representing the length at which 50% of the population was mature (namely at stage 3–5, Kock 1989), was determined by fitting a logistic equation to the proportion of fish in each size class (Ni & Sandeman 1984):

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

where \( p \) is the estimated proportion in a size class, \( TL \) is the total length (mm) and \( \alpha \) and \( \beta \) are coefficients. The values of coefficients were obtained by linearizing the equation through log-transformation of both terms:

\[ \log p/1-p = \alpha + \beta TL \]

Hence, the length at first spawning \( (L_{m50}) \) was estimated as the negative ratio of coefficients, \(-\alpha/\beta\), by substituting \( p = 0.5 \) in the linear equation. Unfortunately, the few immature specimens available in our sample did not allow estimation of the length at sexual maturity (Kock 1989).

As far as the histological analysis is concerned, whole or subsamples of gonads were removed from each specimen and fixed in Bouin’s solution for 12 hours. The samples were subsequently dehydrated in ethanol and embedded in paraffin. A series of cross-sections 10 \( \mu m \) thick were obtained from each sample, mounted on slides and stained with Mayer’s haematoxylin-eosin following standard procedure (Beccari & Mazzi 1972). Sections were examined with a Nikon Eclipse 800 optical microscope at magnifications of 40–400x. Measurements of oocytes were made using the Nikon software package Lucia 4.51.

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 & Selman 1990, West 1990).

The relative frequency of oocytes at different histological maturity stage was obtained pooling fish in the same stage.
of macroscopic maturity. In addition, the size frequency distribution of oocytes was determined for each of the histological maturity stages described.

As females exhibit group synchronous ovaries (see above), 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 ($\mu m$) were measured on 20 oocytes (if not otherwise indicated) and nucleoplasmic indices (NP) were calculated as follows:

$$NP = \frac{V_n(V_c-V_n)^{-1}}{}$$

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 (from spermatogonia to spermatozoa) in the seminiferous lobules of each testis, and also the presence of spermatogonial mitoses. Maturity of testes was evaluated 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). Note that macroscopic and histologic stages of development are numbered with Roman and Arabic numerals, respectively.

**Fig. 4.** Plot of gonadosomatic index (GSI) in relation to fish size and stage of gonad maturity for *Trematomus loennbergii* a. females, and b. males.

**Fig. 5.** Photomicrographs of histological sections of *Trematomus eulepidotus* ovarian tissue. a. Maturing virgin female, with ovaries filled mainly with oocytes at cortical alveoli formation stage. Presence in the ovarian stroma of several previtellogenic oocytes, respectively, at chromatin nucleolar (arrow) and perinucleolar (arrowhead) stages. b. Gravid female, oocyte in late vitellogenesis, with cytoplasm completely filled by yolk granules. c. Late vitellogenic oocyte, in which yolk granules are fused together giving the characteristic transparency. d. Atretic oocyte (arrow), with chorion convoluted and invaded by granulosa cells. Scale bars 250 $\mu m$ in all photos.
Overall, 23 females ranging between 182–306 mm TL and 47–327 g TW and 31 males ranging between 182–271 mm TL and 40–208 g TW were analysed. Applying the chi-square test for goodness of fit, the sex ratio was not significantly different from unity ($\chi^2 = 1.18$, df = 1, $P > 0.1$). On the basis of the macroscopic appearance of gonads, 10 females between 182–240 mm TL were considered to be maturing virgins (stage 2), with a GSI range between 0.2–1.4%. All other females (13 specimens) were gravid (stage 4), attaining a GSI between 11.0–19.4%. As for males, 13 specimens were relatively small (182–210 mm TL) and immature (stage 1), with a GSI range of 0.03–0.1%. All other males (18 specimens) were ripe (stage 4), exhibiting a GSI range between 1.9–3.6%. In plots relating GSI to fish size, both sexes showed an obvious gap between different stages of gonad maturity (Fig. 2a & b).

The length at first spawning ($L_{so50}$) of $T$. eulepidotus estimated by fitting the logistic function to the length-at-maturity data was, respectively, 210 mm TL in males and 240 mm TL in females. The absolute fecundity ($F$), estimated from 13 females ranging from 244 mm TL to 306 mm TL, varied between 3550–10736 eggs per individual (mean ± SE, 6637 ± 535) (Fig. 3). A positive relationship was found between $F$ and fish size, as fecundity increased significantly with increasing length of females ($F = 19331.5 + 94.4$ TL, $n = 13$, $r^2 = 0.76$). Relative fecundity ($F_r$) in $T$. eulepidotus ranged between 24.3 and 35.3 eggs/g (mean ± SE, 30.8 ± 0.9) (Fig. 3), with little relationship with fish size.

Size of mature oocytes, as measured in gravid females (stage 4) ranged widely between 1.9 mm and 2.7 mm (mean size 2.0–2.5 mm). However, on the basis of size distribution, mature oocytes were easily distinguished from all other previtellogenic oocytes dispersed within the ovarian stroma (see below), since there were few and they were of considerably smaller size (0.2–0.6 mm).

A total of 37 specimens were studied, with 27 females ranging between 117–326 mm TL and 7–278 g TW and 10 males ranging between 162–237 mm TL and 23–88 g TW. The sex ratio differed significantly from unity ($\chi^2 = 7.81$, df = 1, $P < 0.005$). On the basis of the macroscopic gonad maturity scale, 14 females between 117–235 mm TL were immature (stage 1), with a GSI range of 0.29–0.56%. All other females (18 specimens) were ripe (stage 4), exhibiting a GSI range between 1.9–3.6%. In plots relating GSI to fish size, both sexes showed an obvious gap between different stages of gonad maturity (Fig. 2a & b).

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the stages of gonad maturity. The length at first spawning ($L_{m50}$) in females, estimated by fitting the logistic function to the length-at-maturity data, was $c. 26$ cm TL. The lack of males in advanced stage of maturity (only one in stage 3) did not allow evaluation of $L_{m50}$. Similarly, the absence of mature females did not enable us to determine the total and relative fecundity for this species as well. Indeed, when an ovary is sampled too early in the season (i.e. not in mature females), it may not be sufficiently developed to allow the identification of all oocytes destined to be spawned, providing a biased estimate of fecundity (Murua et al. 2003).

**Histological analysis**

**Trematomus eulepidotus**

Histology revealed that females encompassed two development stages. Gonads of small fish (180–240 mm TL) were made up of oocytes in three stages of development, chromatin nucleolar (stage I), perinucleolar (stage II) and cortical alveoli formation (stage III).
(Fig. 5a). With maturation, cellular size increased progressively, while the nucleoplasmic ratio decreased (Table II). All other females had relatively large ovaries, filled with oocytes in late vitellogenesis (stage IV–V) and few oocytes in the previtellogenic and endogenous vitellogenic stages (II and III respectively). The cytoplasm of large yolked oocytes was completely filled by yolk granules (Fig. 5b), which in some cases were fused giving these oocytes their characteristic transparency (Fig. 5c). Occasionally, yolked oocytes underwent resorption through atretic processes (Fig. 5d). No postovulatory follicles were recorded at this stage. The size-frequency distribution of oocytes in different stages of histological maturity was markedly discontinuous (Fig. 6), confirming the presence of group-synchronous ovaries in this species.

Males were in three different stages of maturity. All specimens smaller than 210 mm TL were immature (stage I), showing testes uniformly occupied by spermatogonial cysts (Fig. 7a), with evidence of spermatogonial mitoses. All other fish showed active spermatogenesis, although they were at different stages of development. At the earlier stage, testicular lobules consisted of cysts filled with spermatocytes I and II (stage III) (Fig. 7b), whereas in more advanced stages testes had cysts of spermatozoa (Fig. 7c).

*Trematomus loennbergii*

Small females ranging from 117–235 mm TL were immature, with ovarian follicles composed only of previtellogenic oocytes (chromatin nucleolar and perinucleolar, stages I and II) (Fig. 8a). In some larger specimens, batches of oocytes had undergone endogeneous vitellogenesis (cortical alveoli or stage III), although ovaries still contained previtellogenic oocytes (Fig. 8b). All other females had ovaries with large...
Table III. Reproductive characteristics of *Trematomus eulepidotus* in the High-Antarctic Zone.

<table>
<thead>
<tr>
<th>Site</th>
<th>Size range (cm)</th>
<th>GSI</th>
<th>Egg size (mm)</th>
<th>F (eggs/fish)</th>
<th>Fr (eggs/g)</th>
<th>Spawning period</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cosmonaut Sea</td>
<td>23.0–30.0</td>
<td>16.0–31.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Feb–April</td>
<td>Roshchin 1991</td>
</tr>
<tr>
<td>Ross Sea</td>
<td>24.4–30.6</td>
<td>11.0–19.4</td>
<td>1.9–2.7</td>
<td>3550–10 736</td>
<td>24.3–35.3</td>
<td>Dec–Jan</td>
<td>present study</td>
</tr>
<tr>
<td>Scotia Sea</td>
<td>27.0–31.0</td>
<td>-</td>
<td>-</td>
<td>6043–12 854</td>
<td>22–32</td>
<td>-</td>
<td>Kock 1989</td>
</tr>
<tr>
<td>Weddell Sea</td>
<td>-</td>
<td>10.1–22.6</td>
<td>1.8–3.3</td>
<td>1400–12 300</td>
<td>12–35</td>
<td>Dec–Feb</td>
<td>Ekau 1991</td>
</tr>
<tr>
<td>Weddell Sea</td>
<td>24.0–33.7</td>
<td>11.7–19.9</td>
<td>2.1–3.3</td>
<td>2448–19 337</td>
<td>14.6–35.2</td>
<td>Feb–March</td>
<td>Duhamel et al. 1993</td>
</tr>
</tbody>
</table>

Oocytes in early exogeneous vitellogenesis (stage IV), consisting of cytoplasm filled by yolk granules and a central nucleus (Fig. 8c). At this stage of development, several previtellogenic and endogeneous vitellogenic oocytes were still present (Fig. 8c), probably forming the reserve stock for the next spawning season. This is also supported by the wide gap in cellular sizes among oocytes in different stages of development (Table II), as is also the case in *T. eulepidotus*. Finally, the relative frequency and the size frequency distribution of oocytes is provided in Fig. 9.

Most male *T. loennbergii* were immature, exhibiting testicular lobules made up of cysts of spermatogonia (Fig. 10a). All other specimens had testes at an early development stage (spermatocytes I or stage II) (Fig. 10b), except for a single fish with testicular lobules filled by germinal cells in the second meiotic division (spermatocytes II), or in the late development stage (stage III) (Fig. 10c).

**Discussion**

As is the case for most nototheniids (Everson 1984, North & White 1987, Kock & Kellermann 1991, Duhamel et al. 1993), gametogenesis in both epibenthic species investigated in the present study is a slow process, starting before the current spawning season and continuing until the next spawning season one year later. Indeed, maturing or gravid females of both *Trematomus* species are characterized by having group synchronous ovaries (*sensu* Wallace & Selman 1981), in which the more advanced batch of vitellogenic (*T. loennbergii*) or mature (*T. eulepidotus*) oocytes that will be ovulated in the current spawning season are widely separated in size from the smaller previtellogenic and endogeneous vitellogenic oocytes, which form the reserve stock for the next spawning season. As a result, spawning occurs once a year from sexual maturity onward (or iteroparity), as is generally reported in Antarctic fish (Vanella et al. 2005). On the basis of this pattern of oocyte maturation, females of both species probably release their mature eggs in a single spawning event or over a short period of time, and can be considered total spawners (Holden & Raitt 1974). This is also supported by the lack of postovulatory follicles in mature females with mature oocytes. When present, they indicate the species is a fractional spawner (Van der Molen & Matallanas 2004). As a consequence, the relatively prolonged spawning season observed in both species (see below) is mostly due to a probable size-related difference in spawning time within local population.

Considering our results on length at first spawning and literature data (DeWitt et al. 1990), *T. eulepidotus* and *T. loennbergii* probably spawn for the first time relatively late in their life, i.e. at about 70–75% of their maximum length. A similar percentage was also reported for the other epibenthic species of *Trematomus*, *T. lepidorhinus* (Kock & Kellermann 1991). Such a delayed sexual maturity is a common feature in Antarctic fishes. The reproductive effort, in terms of GSI, is generally very high, reaching 20–30% in females of *T. eulepidotus* (see Table III). Thus, delayed maturity is probably the result of either the considerable energy spent during spawning or the advantage of postponing sexual maturity until achieving a size sufficiently large to feed on the most abundant food resources available in shelf waters.

The reproductive characteristics of *T. eulepidotus* are relatively well known, although most data are based only on macroscopic analysis of gonads. Most information on the reproductive biology of this species is based on specimens collected from the Weddell Sea (Lisovenko 1987, Ekau 1988, 1989, 1991, Duhamel et al. 1993) and from Davis and Mawson seas (Roshchin 1991, Shandikov & Faleeva 1992), where *T. eulepidotus* is the most common species amongst nototheniids collected both by benthic and midwater trawls. Additional data on absolute and relative fecundity of this species is from an Elephant Island population (Ekau 1989). Summarizing this data (Table III), it appears that *T. eulepidotus* spawns in the summer over an extended period lasting from December–March, and produces 2500–20 000 eggs per season depending on fish size. Interestingly, a batch of about 2000 eggs of *T. eulepidotus* were collected in the Weddell Sea on the bottom at 200 m (Ekau 1989), confirming the assumption that the eggs of *Trematomus* are demersal.

Unlike *T. eulepidotus*, knowledge of the reproductive biology of the other epibenthic *Trematomus* species is relatively scarce and restricted to the Weddell Sea (Ekau 1991, Duhamel et al. 1993). In particular, *T. loennbergii* spawns about 6000–13 000 eggs per season, whereas *T. lepidorhinus* produces 2200–20 000 eggs per season.
In general the epibenthic *Trematomus* species exhibit an overall similarity in some reproductive features, including delayed maturity, prolonged gametogenesis, group synchronous oocyte development, relatively low fecundity and a single spawning event per season. However, the reproductive strategy, in terms of spawning period, differs markedly among the species, producing a mismatch in the time of appearance of larvae in the environment. The present study and literature data indicate that *T. eulepidotus* is a summer spawner, maturing in summer between December and March (Table III), whereas *T. loennbergii* and *T. lepidorhinus* spawn, respectively, in autumn (Ekau 1991) or in winter (Kock & Kellermann 1991, Duhamel et al. 1993). Accordingly, the timing of hatching of these species, which share the same habitat as adults, shows a chronological sequence. Hatching of *T. eulepidotus* take place in May–June in the Weddell Sea (Ekau 1989, Loeb et al. 1993), when yolk sac larvae attain 10–15 mm SL. On the other hand, hatching of *T. loennbergii* could be hypothesized to occur in spring (September–October), as some postlarvae ranging from 20–23 mm SL have been caught in the Ross Sea in late December (Vacchi et al. 1999b). Finally, *T. lepidorhinus* hatches in November–December, both in the Ross Sea (Vacchi et al. 1999b) and off the Antarctic Peninsula (Kellermann 1990).

In conclusion, during the evolutionary process of pelagization, the epibenthic species of the genus *Trematomus* developed reproductive and other strategies which serve to mitigate interspecific competition. Ecologically, they differ both in feeding habits and depth preferences, factors probably linked to each other. Although they share a common process of gonadal maturation, they differ in the timing of spawning and larval hatching, consistent with avoiding food competition among the early life history stages.

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