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HISTOLOGICAL STUDY ON THE OVARIAN DEVELOPMENT OF MACKEREL ICEFISH (*CHAMPSOCEPHALUS GUNNARI*) FROM THE SOUTH GEORGIA ISLANDS

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Abstract

A histological analysis was carried out on ovarian development in *Champsocephalus gunnari* caught by the RV *Dr Eduardo L. Holmberg* in the South Georgia and Shag Rocks areas in February and March 1994. Six phases of oocyte development were identified, and these are similar to those described for other species. A gonad maturation scale for studies using microscopes (microscopical scale) was elaborated and adapted to correspond with the macroscopic (i.e., unaided visual observation) scale commonly used. The first five stages correspond with those described macroscopically for various species of Channichthyidae. Stage six includes ovaries undergoing oocyte resorption processes, which macroscopically resemble a maturity phase but microscopically conform to a regression stage. In some cases these ovaries presented few atretic oocytes; in others a generalised regression was found, which was observed in 41% of mature fish. A high proportion of juvenile individuals (45%) was found, together with a relatively low occurrence of females that spawned or were in condition to spawn in the current season (32%).

Résumé

Il a été procédé à une analyse histologique du développement ovarien de *Champsocephalus gunnari* capturé par le navire de recherche *Dr Eduardo L. Holmberg* dans le secteur de la Géorgie du Sud et des îlots Shag en février et mars 1994. Six phases de développement des ovocytes ont été identifiées, phases similaires à celles décrites pour d'autres espèces. Une échelle de maturation des gonades a été créée pour les études au microscope (échelle microscopique). Elle a été adaptée de manière à ce qu'elle corresponde à l'échelle macroscopique (observation à l'œil nu) couramment utilisée. Les cinq premiers stades correspondent à ceux décrits par l'observation macroscopique de diverses espèces de Channichthyidae. Au sixième stade, les ovaires suivent le processus de résorption des ovocytes ce qui, par observation macroscopique, ressemble à une phase de maturité mais au microscope, correspond à un stade de régression. En certains cas, ces ovaires présentaient peu d'ovocytes atrétiques; dans d'autres cas une régression généralisée était observée et ce, dans 41% des poissons matures. La proportion observée de juvéniles était relativement élevée (45%) alors que celle de femelles qui s'étaient reproduites ou étaient en condition de reproduction était plutôt faible (32%).

Резюме

Был проведен гистологический анализ яичникового развития у особей *Champsocephalus gunnari*, выловленных судном *Dr Eduardo L. Homberg* в районах Южной Георгии и скал Шаг в период февраль-март 1994 г. Было определено шесть этапов развития ооцитов, которые подобны стадиям, определенным для других видов. Была разработана шкала определения созревания гонад, предназначенная для использования при проведении исследований с помощью микроскопов (микроскопическая шкала). Затем эта шкала была модифицирована с тем, чтобы она соответствовала широкоиспользуемой макроскопической шкале (т.е. наблюдение невооруженным глазом). Первые

пять стадий соответствуют макроскопическим, описанным для различных видов семейства Channichthyidae. Стадия шесть охватывает ооциты, подвергающиеся процессам ресорбции, которые макроскопически похожи на стадию созревания, но микроскопически соответствуют стадии регрессии. В некоторых случаях в этих яичниках встречалось мало атретических ооцитов, в то время как в других обнаружена обобщенная регрессия, что наблюдалось в 41% половозрелых рыб. Наблюдалось большое количество молоди (45%), а также относительно низкое количество отнерестившихся самок или самок в состоянии отнереститься в текущий сезон (32%).

Resumen

Se hizo un análisis histológico del desarrollo ovárico en ejemplares de *Champsocephalus gunnari* capturados por el BI *Dr Eduardo L. Holmberg* en las zonas de Georgia del Sur y de las Rocas Cormorán durante febrero y marzo de 1994. Se identificaron seis etapas de desarrollo oocitario, y éstas son similares a las descritas para otras especies. Se elaboró una escala de madurez gonadal para medir maduración de las gónadas usando microscopios, y se la adaptó para que corresponda a la escala macroscópica (es decir, observación visual solamente) comúnmente usada. Las primeras cinco etapas corresponden a aquellas descritas macroscópicamente para varias especies de Channichthyidae. La sexta etapa incluye ovarios en proceso de reabsorción oocitaria, lo que macroscópicamente parece ser una etapa de maduración pero microscópicamente corresponde a una etapa de regresión. En algunos casos los ovarios exhibieron escasos oocitos atrésicos; en otros se encontró una regresión generalizada, como se observó en un 41% de los peces adultos. Se encontró una alta proporción de ejemplares juveniles o inmaduros (45%), junto a una incidencia relativamente baja de hembras que desovaron o que estaban en condición de desovar en la temporada actual (32%).

Keywords: fish, reproduction, histology, Channichthyidae, South Georgia, Antarctica, CCAMLR

INTRODUCTION

Antarctic fish have developed a series of strategies to facilitate their adaptation to the environment. In reproduction, some common characteristics are a prolonged gametogenesis, delayed maturation, large yolky eggs and low fecundity (Andriashev, 1987; North and White, 1987). In many fish species these strategies are complemented by complex reproductive behaviours, such as nest guarding (North and White, 1987; Kock, 1989).

One representative of Antarctic ichthyofauna, the mackerel icefish (*Champsocephalus gunnari*), has been one of the commercially important species of interest to CCAMLR. Together with other biological and oceanographic information (e.g., diet composition, physical-chemical parameters), knowledge of the reproductive aspects of this species is useful for interpreting abundance/biomass estimates obtained from assessment work. For example, Everson *et al.* (1991) indicated that the reproductive success of this species at South Georgia could be closely related to the availability of krill, its main food source. This suggestion is based on the generalised oocyte resorption process found in a high proportion of individuals caught in summer 1991 and the concurrent scarcity of krill in the area (Everson *et al.*, 1991).

Most studies of mackerel icefish reproduction have been limited to macroscopic descriptions of the maturation cycle and to estimations of parameters used in fisheries biology, such as length at first maturity and fecundity (Silyanova, 1981; Lisovenko and Zakharov, 1988; Kock, 1989; Duhamel, 1994). For this species, the histology of reproduction has been studied only partially (Everson *et al.*, 1991).

In this paper we present a histological analysis of *C. gunnari* ovaries with the aim of describing the oocyte development stages and elaborating a gonad maturation scale for studies using microscopes (microscopical scale). Also, the oocyte resorption process, termed 'atresia', is described and its level of occurrence in the sample is analysed.

MATERIAL AND METHODS

Gonads were removed from *C. gunnari* taken in catches made in 12 bottom trawls on the shelves around South Georgia and Shag Rocks

during the RV *Dr Eduardo L. Holmberg* survey in March 1994 (Marschoff *et al.*, 1994) (Table 1). A total of 130 ovaries were collected for histological examination; the weight of these ovaries ranged from 0.5 to 120 g. Total length (cm) and weight (g) of the fish were also recorded. The length and weight ranges were 16 to 49 cm and 20 to 1 050 g respectively. The age groups of the specimens ranged from two to five years, estimated from the age/length key presented in Barrera-Oro *et al.* (1994a). The ovaries were first fixed on board in 10% neutral buffered formalin. At the laboratory, they were dehydrated in alcohol and then embedded in paraffin wax. Sections 4 to 5 µm thick were obtained and stained using Mayer's haematoxylin and eosin procedure (Allen, 1993). The descriptions were made with a Leitz Dialux optic microscope at magnifications ranging from 40x to 400x.

RESULTS AND DISCUSSION

Oocyte Development Stages

Stages of oocyte development similar to those described for some Antarctic species of Nototheniidae (Silyanova, 1981; Butzkaya and Faleeva, 1987; Hourigan and Radtke, 1989) were identified and described (Table 2). The classification used was compared to that presented in Forberg (1982) and Mayer *et al.* (1988).

The following six stages of oocyte development were identified.

Primary Growth Phase

Stage I (previtellogenesis): diameter less than 50 µm and nucleus-to-cytoplasm ratio (n/c) of about 0.72. Cytoplasm is strongly basophilic, spherical nucleus (germinal vesicle) with several nucleoli located in its peripheral zone (Figure 1A).

Secondary Growth Phase

Stage II (early primary vitellogenesis): at the start of vitellogenesis the oocytes increase in size (50 to 120 µm); this is accompanied by a diminution of the n/c ratio (0.45). A small number of yolk vesicles appear in the cytoplasm, initially in the outer cortex; some oocytes exhibit a unique large vacuole beside the cytoplasmic membrane (oolema) (Figures 1A and 1B).

Table 1: Sampling stations, length and weight data for *C. gunnari*. 'N' is the number of specimens examined.

Station	Latitude (S)	Longitude (W)	N	Length(cm)		Weight(g)	
				Range	Mean	Range	Mean
46	55°07'00''	35°39'54''	7	25-29	26.1	80-110	96.4
51	53°57'00''	37°04'54''	7	17-33	21.3	20-160	50.7
53	53°56'54''	37°05'12''	12	21-25	22.6	50-100	64.7
54	53°57'06''	37°04'36''	31	16-25	21.4	20-80	54.2
55	53°57'06''	37°04'42''	9	16-23	20.6	20-70	47.8
57	53°56'54''	37°04'48''	5	18-22	19.6	20-60	40.0
59	54°59'18''	35°06'06''	7	23-49	30.9	70-1050	252.9
60	54°10'42''	37°57'54''	11	24-35	28.8	75-220	122.8
61	54°10'48''	37°57'42''	15	22-33	28.1	55-170	118.7
62	54°10'36''	37°58'00''	7	22-31	27.7	57-160	122.3
63	54°10'42''	37°57'36''	12	24-33	28.4	75-200	123.7
65	53°26'54''	42°21'54''	7	26-28	27.4	90-120	107.9

Table 2: Oocyte development stages for *C. gunnari* and corresponding classification used by other authors.

This Study	Forberg (1982); Mayer *et al.* (1988)
Primary growth phase:	
Previtellogenic oocyte (I)	Chromatin nucleolus stage Chromatin perinucleolus stage
Secondary growth phase:	
Early primary vitellogenesis (II)	Yolk vesicle stage I
Advanced primary vitellogenesis (III)	Yolk vesicle stage II
Early secondary vitellogenesis (IV)	Primary yolk stage
Advanced secondary vitellogenesis (V)	Secondary yolk stage
Total maturation (VI)	Tertiary yolk stage

Stage III (advanced primary vitellogenesis): the oocytes' diameters range between 200 and 400 μm, the n/c ratio is about 0.36. In this maturity phase the number and size of the yolk vesicles increase significantly (Figure 2A). A thin acellular membrane of eosinophilic material, the zona radiata, becomes visible around the periphery of the oocyte. The follicular elements, which are comprised of a granulosa cell stratum surrounded by the follicle theca, are readily observed at this stage.

Stage IV (early secondary vitellogenesis): the oocytes' diameters range between 450 and 500 μm, the n/c ratio is 0.20. The secondary vitellogenesis starts with the accumulation of strongly eosinophilic yolk globules in the inner cortex. Thus, two zones are distinguished in the cytoplasm: the external, with great accumulation of yolk vesicles and the internal, with abundant yolk globules (Figure 2B). The nucleus contains numerous small round peripheral nucleoli. The zona radiata has increased in thickness (about 12 μm) and now has a striated appearance.

Stage V (secondary advanced vitellogenesis): the size of the yolky oocytes increases significantly (600 to 1 000 μm), the n/c ratio diminishes to the minimum value (about 0.16). The cytoplasm is strongly eosinophilic with numerous yolk globules merged (Figure 3A). The yolk vesicles are on the periphery, in contact with the oolema. The zona radiata increases in thickness (20 μm), showing its characteristic transversal strias. The nucleus becomes irregular in shape, due to the accumulation of yolk globules in the cytoplasm. The granulosa cells increase in thickness (12 μm) until they are cylindrical and show the nucleus strongly basophilic (Figure 3B).

Stage VI (oocytes in total maturation): the size of these elements increases significantly, to about 2 500 μm in diameter. The nucleus breaks and the yolk globules tend to coalesce to form a slightly eosinophilic amorphous mass (Figure 4A). The oocyte rapidly increases in volume due to hydration. Oil droplets are not observed, suggesting that the eggs of the species could be demersal. This was also reported for other channichthyids (North and White, 1987; Kock, 1989). The follicle epithelium thins and stretches due to the rapid increase in cell volume. The zona radiata increases in thickness and two zones are observed: the internal, with transversal strias, are thicker (70 μm) and strongly eosinophilic; the external are thinner (8 μm) and slightly eosinophilic (Figure 4B). After spawning, the zona radiata will constitute the chorion of the egg, which in C. *gunnari* is highly rigid.

Post-ovulatory Follicles (POF)

The POF consisted of irregularly-shaped structures composed of cylindrical follicle cells and an underlying connective tissue theca arranged in convoluted strings. The lumen characteristically contained eosinophilic granules and follicle cells in degradation (Figure 5A).

After spawning, these structures are absorbed, showing different stages of degeneration (Figure 5B).

Oocyte Resorption Processes

Although atresia processes in fish are commonly associated with the post-reproductive phase, they can occasionally affect the oocytes during maturity, in their different development stages (Hunter and Macewicz, 1985).

Before complete resorption, the atretic oocytes pass through several phases. These start with the degradation of the nucleus, followed by the dilution of the yolk and the fragmentation of the zona radiata. The follicle cells proliferate, invade the oocyte through the broken zona radiata and digest the yolk by active phagocytosis (Figure 6A).

Oocyte resorption processes were observed in C. *gunnari* in the post-reproductive phase as well as during pre-reproductive phases. In the first case, atresia occurs in remnant oocytes, after spawning; in the second, elements in maturation are affected. Resorption in the pre-reproductive phase can be found in few oocytes or is presented as a generalised phenomenon. In general, for those gonads with few yolky components in resorption, the rest of the elements showed signs of alteration (nuclear degradation, rupture of the zona radiata and vitellus coalescence) (Figure 6B). Thus, these ovaries were considered the starting phase of a generalised atresia and were included in the group of gonads in regression.

The phenomenon of atresia in ovaries of C. *gunnari* has already been reported by Everson *et al.* (1991), who indicated the macroscopical resemblance of this condition to a normal stage 2.

Ovarian Maturity Scale

A six-stage microscopical ovarian maturity scale was elaborated on the basis of oocyte development phases, the POF and the processes of atresia described above. The first five stages corresponded with those described macroscopically for different species of Channichthyidae (Cielniaszek and Parkes, 1989; Kock and Kellermann, 1991). Stage 6 includes ovaries in oocyte resorption processes, which macroscopically resemble a maturity phase but microscopically conform to a regression stage.

The main histological features of the development stages are described in Table 3. Oocytes in early secondary vitellogenesis (Table 3, stage 4) are not present in stages of advanced maturity and total maturity (Table 2, stages 3 and 4). This indicates that no immature elements are incorporated into the cohort of yolky oocytes that will be evacuated during the current spawning season. This was previously observed by Everson (1970), Everson *et al.* (1991) and Kock and Kellermann (1991), who suggest that pre-vitellogenic elements and oocytes in primary growth conform to the reserve 'stock' for the following spawning season. This is characteristic for species which spawn all eggs of one generation simultaneously, as was thought to be the case for *C. gunnari* (Permitin, 1973).

Percentage Composition of Maturity Stages

The number of specimens examined per station is not large enough to allow a statistical analysis of the spatial distribution of maturity stages expressed as percentages.

45.4% of the total sample was comprised of smaller-sized immature fish (stage 1) and fish in the stage of early maturation (stage 2). Stage 3 specimens comprised 25.4%, represented by specimens in advanced maturation that were capable of spawning in the current season. Individuals in stages of total maturation (4) and post-spawning (5) occurred in low numbers (2.3% and 4.6% respectively). 22.3% of ovaries were in regression stage (6), but this percentage may be underestimated due to the high number of juvenile individuals represented (stages 1 and 2). Considering mature fish alone, 40.8% exhibited ovaries in pre-productive regression.

As has already been stated, only ovaries with yolky oocytes can reach the stage of total maturity during the current spawning season. Therefore, *C. gunnari* specimens were grouped into two categories: 1994 spawners and the non-spawner population. Within the first category only ovaries in advanced, total, and post-spawning maturity stages were included, constituting 32.3% of the samples. Thus, a high proportion (67.7%) of the sampled population will not spawn in the current season, because it is composed of juvenile individuals or those with ovaries in the pre-reproductive regression stage. However, these data should be treated with caution because of the relatively low number of individuals in the samples and the high degree of size variability observed between stations.

Information on the feeding status of this stock of *C. gunnari*, derived from diet analyses of fish caught during the surveys of RV *Dr Eduardo L. Holmberg* and MV *Cordella*, indicated a low abundance of krill around South Georgia during the 1993/94 summer (Barrera-Oro *et al.*, 1994b;

Table 3: Maturation scale used for ovaries of *C. gunnari*.

Maturity Stage	General Histological Features
1. Immature	Compact ovigerous lamellas, with oocytes I and II
2. Early maturation	Oocytes I, II and III elements starting secondary vitellogenesis (IV)
3. Advanced maturation	Oocytes I, II, III and V
4. Total maturation	Oocytes I, II, III and VI
5. Post-spawning	Lax ovigerous lamellas, with oocytes I, II and III. Residual components V in resorption and post-ovulatory follicles
6. Pre-reproductive regression	Compact ovigerous lamellas, with oocytes I and II. Yolky elements (V) in different resorption phases

Kock *et al.*, 1994). This and the results of the present study seem to accord with the suggestion of Everson *et al.* (1991), which establishes a strong relation between the reproductive success of this species in a particular spawning season and the availability of krill, its main food source.

CONCLUSIONS

Six stages of oocyte development were identified and described; these are similar to those described for some Antarctic species of Nototheniidae.

In the histological sections mature oocytes attain a large size, about 2 500 µm in diameter. They show a well-developed chorion and an absence of oil-droplets, which is typical of demersal eggs.

Those oocytes that are not yolky during the pre-reproductive period will not be released in the current spawning season, thus conforming to the notion of a reserve 'stock'.

Oocyte resorption processes were observed during ovarian maturation. In some cases the ovaries presented few atretic oocytes; in others a generalised regression was found.

The percentage composition of the ovarian maturation stages showed in the total sample a high incidence of juveniles (45%) and a relatively low occurrence of females that spawned or were ready to spawn in the current season (32%). Likewise, a high proportion of mature fish exhibited ovaries in the pre-reproductive regression stage (41%).

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REFERENCES

Allen, T.C. 1993. Haematoxylin and eosin. In: Prophet, E.B., B. Mills, J.B. Arrington and M.D. Sobin (Eds). *Laboratory Methods in Histotechnology*. American Registry of Pathology, Washington, D.C. 53-58.

Andriashev, A.P. 1987. A general review of the Antarctic bottom fish fauna. In: Kullander, S.O. and B. Fernholm (Eds). *Proceedings of the V Congress of the European Ichthyological Society, 1985*. Stockholm, Sweden: 357-372.

Barrera-Oro, E.R., E.R. Marschoff and R.J. Casaux. 1994a. Age/length key for *Champsocephalus gunnari* from Subarea 48.3, RV *Dr Eduardo L. Holmberg* survey, February/March 1994. Document *WG-FSA-94/11*. CCAMLR, Hobart, Australia: 10 pp.

Barrera-Oro, E.R., R.J. Casaux and A. Roux. 1994b. Diet composition of *Champsocephalus gunnari* in Subarea 48.3, RV *Dr Eduardo L. Holmberg* survey, February/March 1994. Document *WG-FSA-94/27*. CCAMLR, Hobart, Australia: 17 pp.

Butzkaya, N.A. and T.I. Faleeva. 1987. Seasonal changes in the gonads and fecundity of Antarctic fishes *Trematomus bernachii*, *Trematomus hansoni* and *Pagothenia borchgrevinki*. *Journal of Ichthyology*, 27: 27-36.

Cielniaszek, Z. and G.B. Parkes. 1989. Proposed maturity scale for icefish (Channichthyidae). Document *WG-FSA-89/7*. CCAMLR, Hobart, Australia: 2 pp.

Duhamel, G. 1994. New data on spawning, hatching and growth of the Kerguelen Islands *Champsocephalus gunnari* shelf stock. *CCAMLR Science* (this volume).

Everson, I. 1970. Reproduction in *Notothenia neglecta* Nybelin. *Br. Antarct. Surv. Bull.*, 23: 81-92.

Everson, I., K.-H. Kock, S. Campbell, G. Parkes, Z. Cielniaszek and J. Szlakowski. 1991. Reproduction in the mackerel icefish, *Champsocephalus gunnari*, at South Georgia. Document *WG-FSA-91/7*. CCAMLR, Hobart, Australia: 12 pp.

Forberg, K.G. 1982. A histological study of development of oocytes in capelin, *Mallotus villosus* (Müller). *J. Fish Biol.*, 20: 143-154.

Hourigan, T.F. and R.L. Radtke. 1989. Reproduction of the Antarctic fish *Nototheniops nudifrons*. *Marine Biology*, 100: 277-283.

Hunter, J.R. and B.J. Macewicz. 1985. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. *Fish. Bull. US*, 83(2): 119-136.

Kock, K.-H. 1989. Reproduction in fish around Elephant Island. *Archiv. für Fischereiwissenshcaft*, 39: 171-210.

Kock, K.-H. and A. Kellermann. 1991. Reproduction in Antarctic notothenioid fish (Review). *Antarctic Science*, 3(2): 125-150.

Kock, K.-H., I. Everson, L. Allcock, G. Parkes, U. Harm, C. Goss, H. Daly, Z. Cielniaszek and J. Szlakowski. 1994. The diet composition and feeding intensity of mackerel icefish (*Champsocephalus gunnari*) at South Georgia in January/February 1994. Document *WG-FSA-94/15*. CCAMLR, Hobart, Australia: 24 pp.

Lisovenko, L.A. and G.P. Zakharov. 1988. On fecundity of 'pike glassfish' *Champsocephalus gunnari* off South Georgia. *Journal of Ichthyology*, 27: 131-134.

Marschoff, E.R., B. Prenski, B. Gonzalez, C. Remaggi and C. Balestrini. 1994. Preliminary results of the *Dr Eduardo L. Holmberg* 1994 cruise to Subareas 48.3 and 48.2. Document *WG-FSA-94/29*. CCAMLR, Hobart, Australia: 70 pp.

Mayer, I., S.E. Shackley and J.S. Ryland. 1988. Aspects of the reproductive biology of the Bass, *Dicentrarchus labrax* L.I. An histochemical study of oocyte development. *J. Fish Biol.*, 33: 609-622.

North, A.W. and M.G. White. 1987. Reproductive strategies of Antarctic fish. In: Kullander, S.O. and B. Fernholm (Eds). *Proceedings of the Vth Congress of European Ichthyological Society, 1985, Stockholm, Sweden, 1985*: 381-390.

Permitin, Y. 1973. Fecundity and reproductive biology of icefish (Channichthyidae) fish of the family Muraenolepidae and dragonfish (Bathydraconidae) of the Scotia Sea (Antarctica). *Journal of Ichthyology*, 13(2): 204-215.

Silyanova, Z.S. 1981. Oogenesis and maturity stages of fish family Nototheniidae. *Voprosy Ikhtiologii*, V21 (4): 684-694.

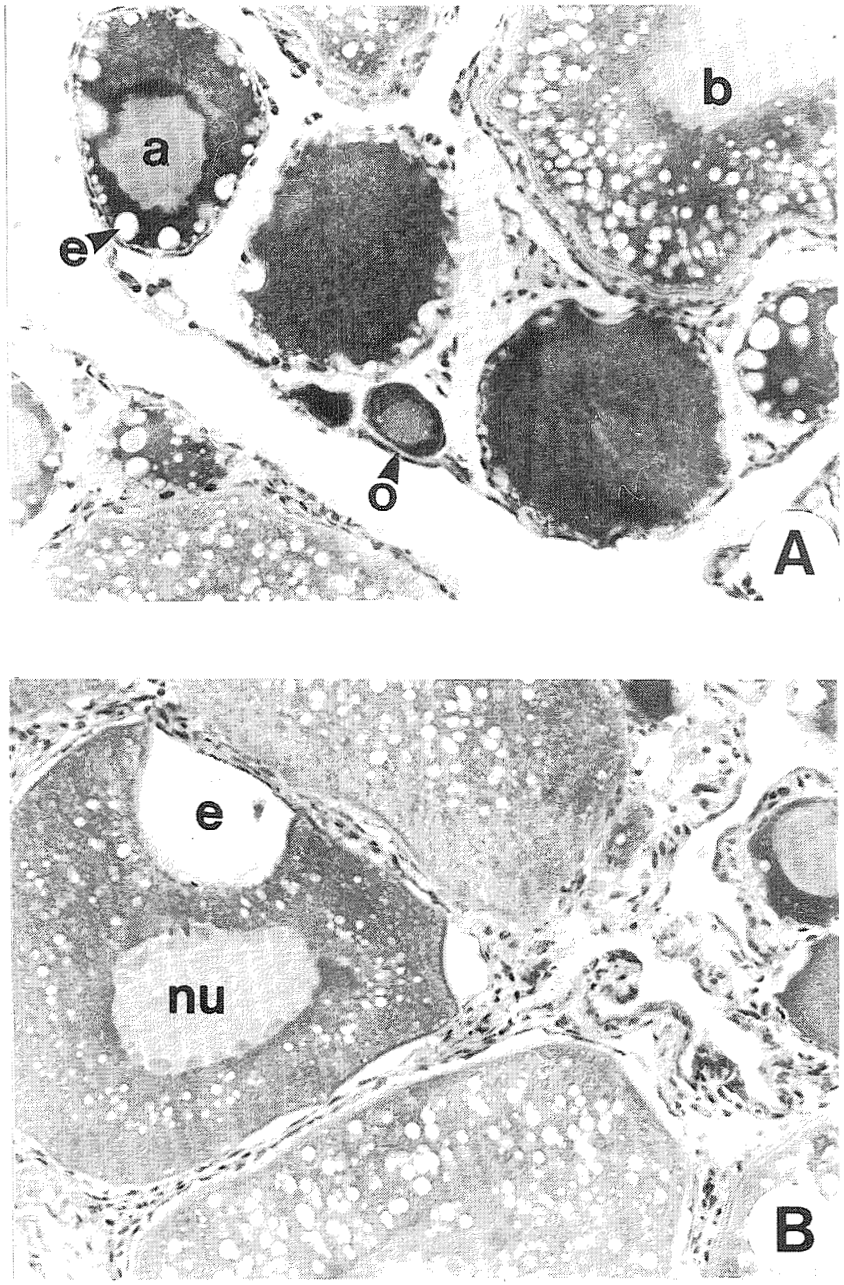

Figure 1: Ovaries of *C. gunnari* with oocytes at different developmental stages: pre-vitellogenesis oocytes (o), oocytes in early primary vitellogenesis (a) and oocytes in advanced vitellogenesis (b). B shows an oocyte in primary vitellogenesis with a large yolk vesicle in the cytoplasm (e). nu - nucleus. Magnification - 250x.

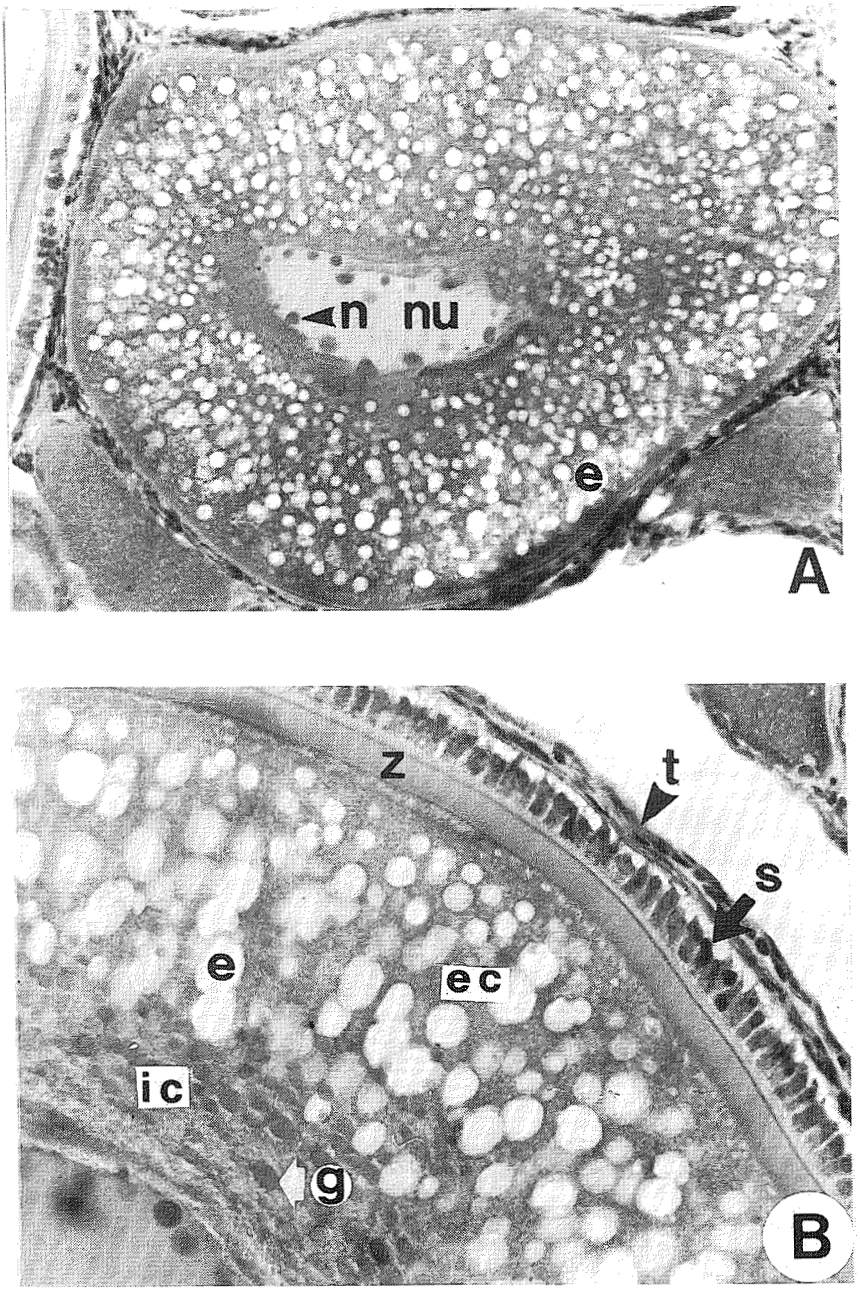

Figure 2: Oocytes in advanced primary vitellogenesis (A) and in early secondary vitellogenesis (B). nu - nucleus, n - nucleoli, ec - external cytoplasm with yolk vesicles (e), ic - internal cytoplasm with yolk globules (g), z - zona radiata, s - zona granulosa, t - follicular theca. Magnification: A - 250x, B - 400x.

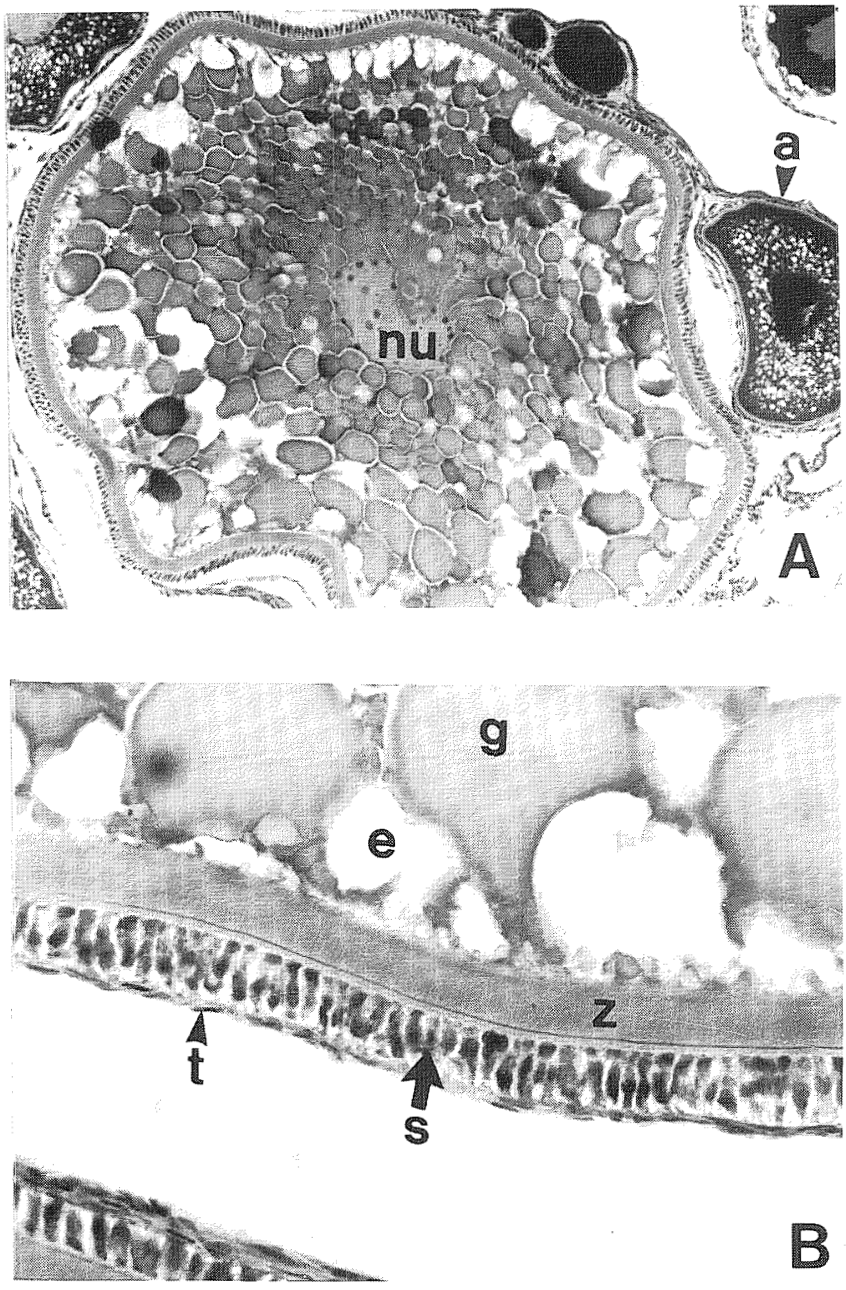

Figure 3: Oocyte in advanced secondary vitellogenesis. nu - nucleus, g - yolk globules, e - yolk vesicles, z - zona radiata, s - zona granulosa, t - follicular theca, a – oocyte in early primary vitellogenesis. Magnification: A - 100x, B - 400x.

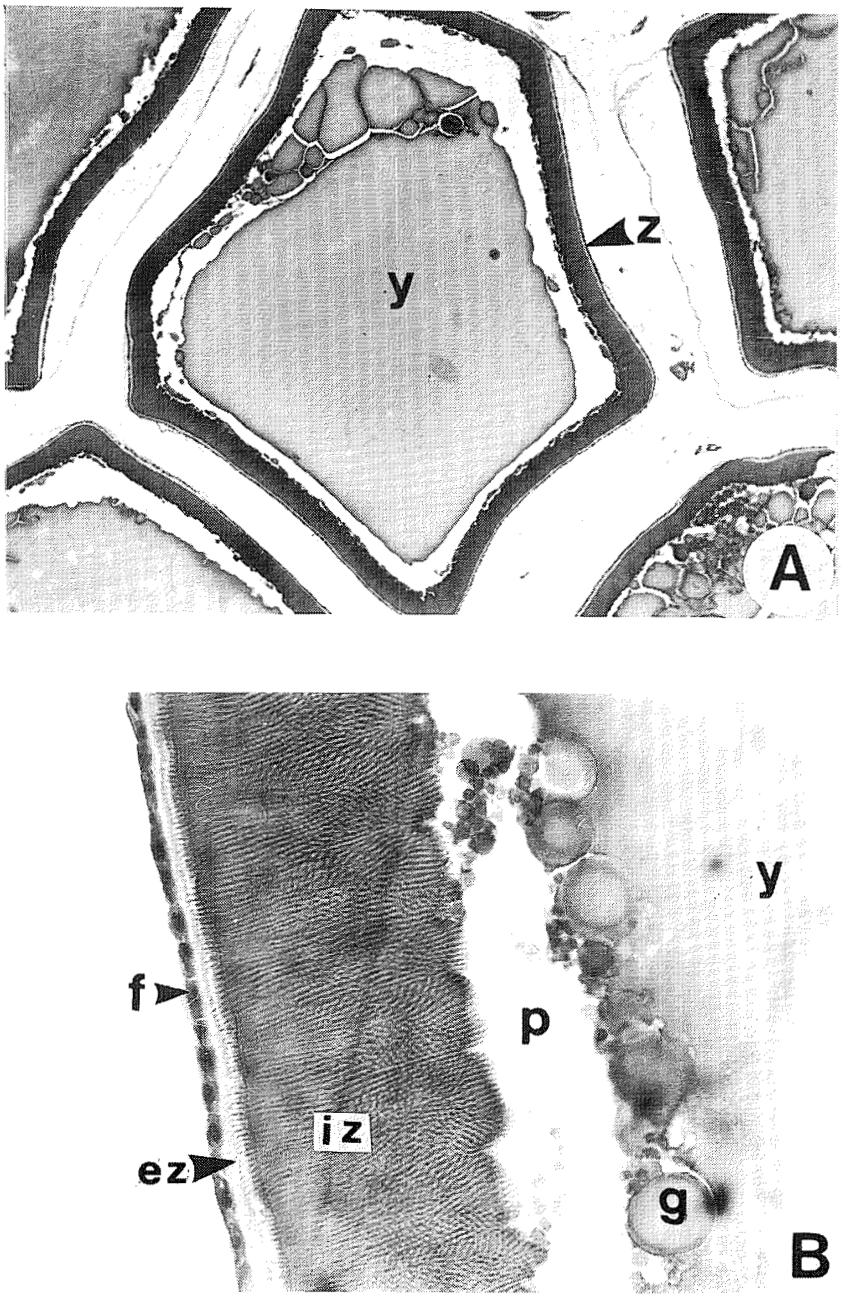

Figure 4: Oocyte at complete maturation. y - yolk, z - zona radiata, g - yolk globules, p - perivitellum space, iz - internal zona radiata, ez - external zona radiata, f - follicular cells. Magnification: A - 40x, B - 400x.

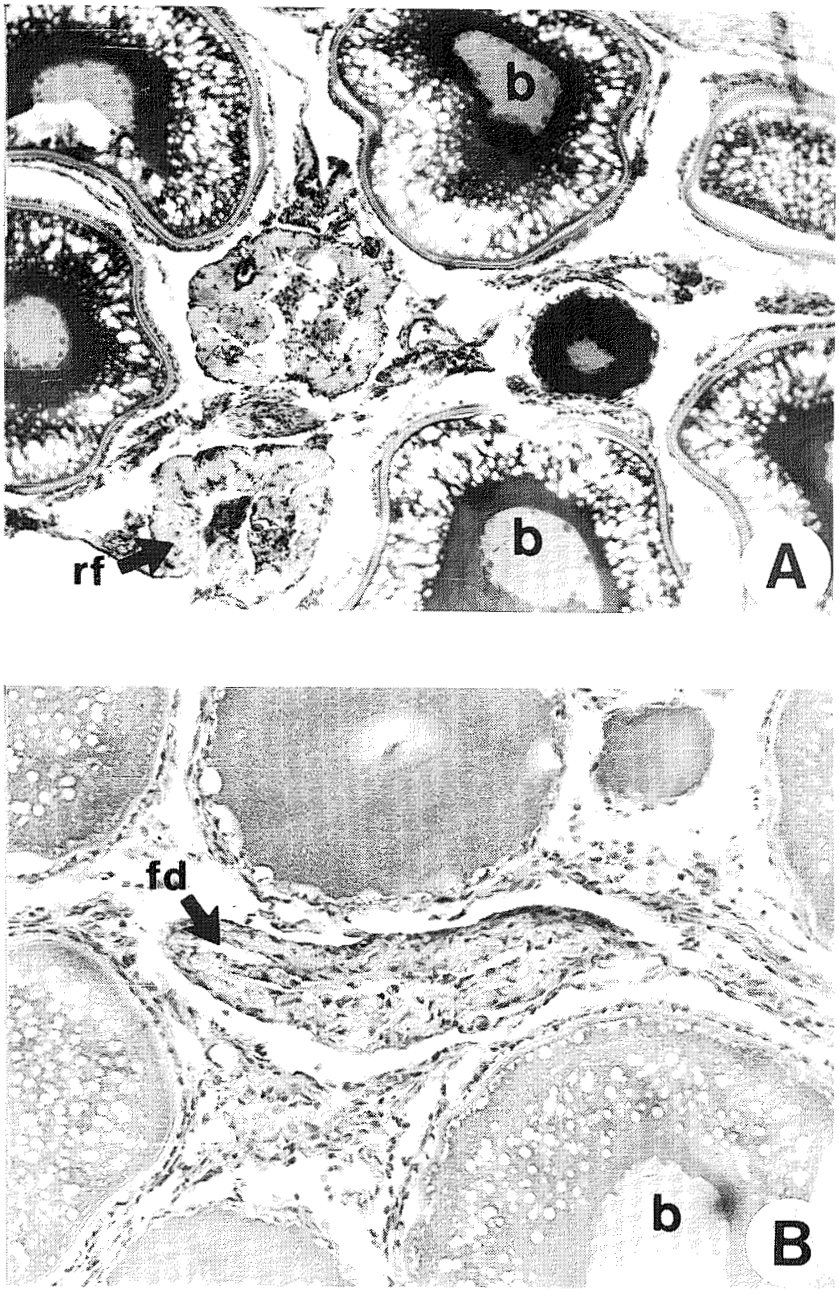

Figure 5: Ovaries of *C. gunnari* at the post-spawning stage, with oocytes in advanced primary vitellogenesis (b) and post-ovulatory follicles (POF). rf - recent POF, fd - degenerating POF. Magnification: A - 100x, B - 250x.

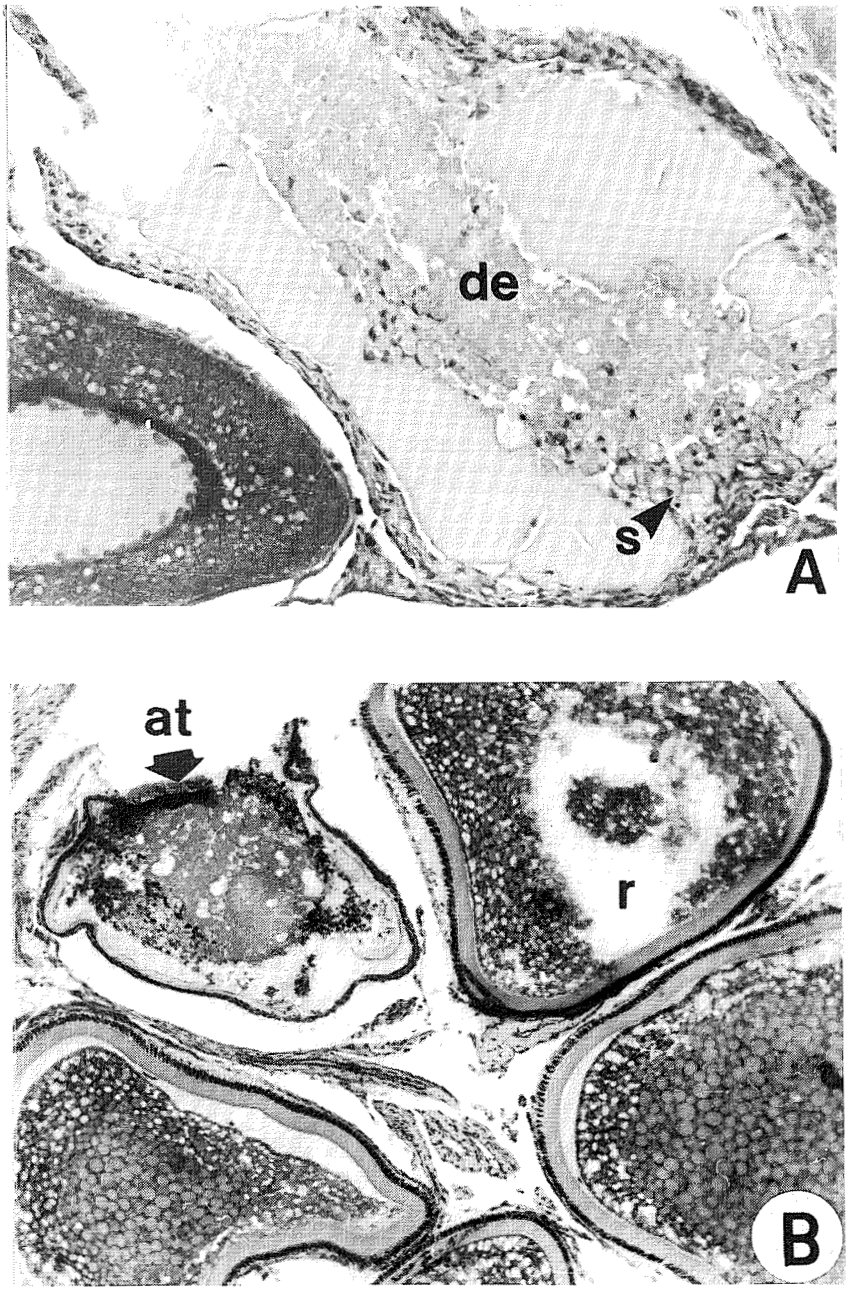

Figure 6: A - an oocytary follicle in resorption; the yolk is degenerating (de) and cells from the zona granulosa are invading the oocyte (s). Magnification - 250x.
B - an ovary with atretic oocytes (at) and oocytes at the start of resorption (r). Magnification: 100x.

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Рисунок 3: Ооцит в стадии позднего вторичного вителлогенеза. nu - ядро, g - желточные шарики, e - желточные пузырьки, z - зона-радиата, s - зона-гранулоза, t - фолликулярная тека, a - ооцит в стадии раннего первичного вителлогенеза. Увеличение: A - 100x, B - 400x.

Рисунок 4: Оооцит, достигший полного созревания. y - желток, z - зона-радиата, g - желточные шарики, p - перевителлиновое пространство, iz - внутренняя зона-радиата, ez - внешняя зона-радиата, фолликулярные клетки. Увеличение: A - 40x, B - 400x.

Рисунок 5: Яичники *C. gunnari* в посленерестовом состоянии с ооцитами в стадии позднего первичного вителлогенеза (b) и послеовуляционными фолликулами (POF). rf - недавние POF, fd - вырождающиеся POF. Увеличение: A - 100x, B - 250x.

Рисунок 6: A - фолликул ооцита в стадии ресорбции; желток вырождается (de) и клетки зоны-гранулоза вторгаются в ооцит (s). Увеличение - 250x.
B - яичник с атретическими ооцитами (at) и ооцитами в начале ресорбции (r). Увеличение - 100x.

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