A Review on Fish Reproduction with Special Reference to Temperature Anomalies

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Introduction

There is a great variety of reproductive styles in fish. Most fish reproduce sexually, but some are parthenogenetic. Sex differentiation in some species may be influenced by environmental factors, such as temperature or social status (Shapiro 1984). In other species, sex changes occur in adult fish such as redband parrotfish (*Sparisoma aurofrenatum*) due to social interaction. Strategies for the protection of progeny range from oviparity to placental viviparity, viviparity being uncommon in teleosts (2.5% of the species) but the normal reproductive mode in chondrichthyes (Wourms *et al.* 1988). The number of spawning occasions varies. For example, Pacific salmons are semelparous, whereas most other fish are able to spawn recurrently. Most species of fish spawn once a year in a demarcated period, but others such as tench (*Tinca tinca*) are batch-spawners, spawning recurrently in a season. The variation in age and size at maturity is immense with sizes ranging from 8 mm in the guppy *Trimmaton* spp. to 15 m in the whale shark (*Rhincodon typus*) (Wootton 1992). Spawning activities take place in a wide variety of environmental circumstances, reflecting regional environmental characteristics.

Reproductive processes, exhibiting endogenous rhythms, are set in train by environmental cues (*zeitgebers*) such as annual astronomical cycles and water temperatures (Baggerman 1990). The adaptive significance of this timing is obvious because of the paramount importance of optimal environmental conditions for survival of the progeny. Variation in timing may account for most of the variations observed in year-class strength in many species.

Water temperatures affect the reproductive process in a number of ways, and may also have adverse effects. Because of the deleterious effects on fish reproduction caused by the water temperature anomalies of cooling water discharges, or as may be expected in the future by sudden drastic climatic changes, there is need for a survey of current knowledge about this aspect of fish reproduction. The fish adaptation possibilities under strong anthropogenic stress differ between species, which influences their relative abundance and survival. The reproduction system is particularly sensitive to change and may respond with alterations to the sex cycle, reflected in peculiarities of sex cell development and functioning.

An overview of the gametogenesis (gonadal development)

Gonadal differentiation in fish is a complex and labile process and starts early in the development process e.g. at the larval stage in species like yellow perch (*Perca flavescens*) (e.g. Malison *et al.* 1986). Stimuli of internal or external origin affect the brain by modifying the activities of specific neurohormones and neurotransmitters in order to regulate the secretion rates of gonadotropin-releasing hormone (GnRH) and dopamine from the hypothalamus (reviewed by Redding & Patiño 1993; fig 1). The release of pituitary gonadotropin (GtH) is under dual hypothalamic control; secretion is stimulated by GnRH and inhibited by dopamine. Other neurohormones may also directly affect the release of GtH. At the end of the hypothalamic–pituitary–gonadal axis, GtH stimulates gametogenesis and steroiodogenesis by the testis or ovary. This multihormonal control of GtH secretion implies that its regulation can be very precise. Within the gonads, germ cells produce gametes, and somatic cells support, feed and regulate the development of germ cells. In most species of fish, gonoducts transport the gametes to locations where fertilization takes place.

The undifferentiated period.

The number of primary sex cells (gonium, gonocytes) and the development of sexual and gonadal differentiation varies greatly between fish species (Persov 1966, 1975, Meznin 1978, Volodin & Grechanov 1985, Talikina 1995a, b). In salmonids, the primary sex cells are quite big before mitotic divisions begins (gonium diameter up to 30µ, nucleus up to 16µ). At a certain stage in development, the nuclei are polymorphic, depending on the physiological status of the sex cells (Sakun 1964). The intensity of gonium divisions rapidly multiplies the number of sex cells. For example, in pike-perch (*Stizostedion lucioperca*) the number of primary sex cells increases to 20 000 within 7 months, while in *Oncorhynchus gorbuscka* numbers rise to 3000 within 39 days (Persov 1959, 1966, 1975).

Gonad Differentiation.

Sex differentiation coincides with premeiotic phenomena, when the nucleus is in a phase of generative activity (Raven 1964). Anatomic differentiation (gonadogenesis) is indicated by the appearance of connective tissue and germinate epithelium, i.e. an increase in the number of epithelium and sex cells (Persov 1966). The temporal division between anatomical and cytological differentiation varies between fish species and three major groups can be identified (Meznin 1978, Volodin & Grecanov 1985, Talikina 1995a, b):

1. Anatomical differentiation precedes sexual differentiation. Both sexes will be differentiated simultaneously.
2. Anatomical differentiation does not necessarily occur prior to cytological differentiation. At first, all gonads are unisexual and sex changes will only take place later on in certain fish (e.g. *Oncorhynchus gorbuscka*).
3. Cytological and anatomical differentiation are simultaneous phenomena (e.g. Atlantic salmon, *Salmo salar*).

After cytological differentiation, the gonium starts to develop male or female characteristics (fig. 2). The next stage of gametogenesis is a complicated process – the change of oogonia and spermatogonia into mature sex cells. During this period, the development of nuclei and cytoplasmic structures takes place, and the oogonia and spermatogonia acquire sex-related physiological and morphological features.

Spermatogenesis

Spermatogenesis is the formation of male sex cells in the testis (e.g. Sakun & Buckaja 1963, Raven 1964, Glazarian & Belousov 1983, Koselev 1984, Ivanov 1956, Makeeva & Emelianova 1989). The testis contains haploid germ cells in synchronous or variable stages of development. In addition, somatic cells, such as Sertoli and Leydig cells, support and regulate spermatogenesis. The Sertoli cells are closely associated with the germ cells, which they physically support and feed. Leydig cells are found in the connective tissue surrounding the Sertoli-germ cell units, primarily producing sex steroids. The teleostean testis has a paired structure and is usually gonochoristic (unisexual), though sometimes hermaphroditism does occur. Within the testis, the organisation is either lobular or tubular (Nagahama 1983). During spermatogenesis the cells reduce in size; primary spermatogonia are the biggest cells and spermatozoa the smallest.

Characteristic cytological changes during spermatogenesis include mitotic proliferation of spermatogonial stem cells (fig 3a; from Sakun & Buckaja 1963). After several divisions, a group of small spermatogonia appears, enclosed within a membrane (cyst). The cysts are located in the male gonad channels (central lumen). The number of cells within the cysts depends on the intensity of mitotic division, which is species-specific. These cells form primary spermatocytes. The first meiotic division, i.e. the process of chromosome reduction (from diploid to haploid), converts the primary spermatocytes secondary spermatocytes (fig 3b; from Sakun & Buckaja 1963). At the end of this stage, the spermatocytes enlarge. The primary spermatocytes divide twice and form into secondary spermatocytes, in which the second meiotic division starts. After the second meiotic division, these change into spermatids. Step by step, the spermatids will develop into spermatozoa. Changes in nucleus and cytoplasm occur; in the cytoplasm characteristic spermatozoid structures form – an acrosomic apparatus and components of the neck and tail. A flagellum develops and the spermatids separate from their supportive tissue (Sertoli cells) and become spermatozoa. It is during this phase of development that the spermatozoa acquire their species characteristic differences in shape (Lagler *et al*. 1977). When the mature spermatozoa have formed the membrane of the cyst breaks and they spread into the male gonad channels (fig 3c; from Sakun & Buckaja 1963). These channels normally lead to efferent ducts, ending in the urogenital opening. In every cyst the cells are at the same stage of spermatogenesis, but cysts in the same gonad may be at different developmental stages, depending on the type of spawning (fig 3d; from Sakun & Buckaja 1963).

Classification system of spermatogenesis

Spermatogenesis passes through several developmental stages, and these have been divided into six stages (e.g. Sakun & Buckaja 1963):

I stage – the occurrence of only large spermatogonia in the testis, i.e. the immature stage.

II stage – intensive reproduction of spermatogonia.

III stage –rapid enlargement of the testis volume. Sex cells are at all stages of spermatogenesis. Spermatides and spermatozoa are formed at the end of this stage.

IV stage – the end of the spermatogenesis process. Some gonad channels are filled up with mature spermatozoa, in others, the spermatogenesis continues.

V stage – the spread of mature spermatozoa.

VI stage – resorption of remaining spermatozoa.

Characteristics of spermatogenesis in perch and roach

Perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) spawn in early spring, but male spermatogenesis patterns are different (fig 4). In perch, an intensive spermatogenetic process starts already in August and ends later in the autumn. The gonads rest during winter at maturation stage IV. In roach, however, the male gonads rest during winter at maturation stage II–III. The spermatogenesis resumes in spring, ending shortly before spawning. In May–June, after the resorption process is completed, the regeneration of male gonads starts with a new wave of spermatogenesis (stage II).

Oogenesis

Oogenesis is the process of egg development in ovaries. The structure of a mature ovarian follicle is similar in most fish species (fig 5). The developing oocyte in the centre of the follicle has an acellular layer, zona radiata. A sublayer of granulosa cells surrounds this zona. The oocyte and the granulosa cells are interconnected by pore canals (microvilli) through the zona radiata, probably allowing nutrients and metabolic messengers to pass (reviewed by Redding and Patiño 1993). The outer follicle layer consists of theca cells, separated from the granulosa cell layer by a basement membrane. Oogenesis basically proceeds in three steps: reproduction, growth, maturation. According to the classic characterization of female reproductive development, these steps are divided into four periods:

I. Reproduction –first oogonial period

The oogonium becomes an oocyte (ovum) at the first meiotic division during maturation (The completion of the second meiotic division is triggered by the fertilization of the egg). After several mitotic divisions, the oogonia start growing and become oocytes. The ovary lobes are formed.

II. Growth – cytoplasmic period

This growth period is called cytoplasmic (synonyms: protoplasmic, previtellogenesis). At first, the oocytes grow slowly, whereas processes in the nucleus (known as premeiotic phenomena) go faster and 1–2 nucleoli develop within the nucleus. The nucleus form is circular, and the number of nucleoli may total 30 or more. Thereafter, the synthesis of cytoplasm starts, and the diameter of the oocytes increases substantially. In larger oocytes, yolk granules are produced, originating from the Golgi complex and mitochondria. The formation of an endogenous membrane also begins, i.e. the zona radiata. Step by step, follicle and connective tissue layers appear. The oocyte acquires two layers of follicle cells during the cytoplasmic period, which can go on for quite a long time, sometimes several years, before the fish becomes sexually mature.

III. The vitellogenetic period

During this period vacuolation of the oocytes and a yolk and fat accumulation process is taking place. Circulating vitellogenin is absorbed by the oocytes, changes to yolk granules and is deposited. The yolk material consists of protein, fats, lipids and some carbohydrates. The Golgi apparatus participates in the formation of the yolk structure. Vitellogenin is produced by the liver in response to estradiol (eg. Matsuyama *et al.* 1991), which, in turn, is secreted by the ovarian follicle cells in response to GtH action (Nagahama 1983). During this process, the weight of the gonads increases significantly. In many species of fish the vacuolation process goes from the periphery to the centre of the oocyte, occupying larger and larger parts of the cytoplasm. At the start, the yolk granules are in the unvacuolated zone, but they gradually fill up the whole cytoplasm, pushing the vacuoles to the periphery of oocyte. The vacuoles fuse into larger cortical alveoli. The vacuoles contain proteins, neutral and acid mucopolysaccharides. By the end of this period the oocytes will have reached their maximal size.

Together with yolk accumulation, the membranes are transformed, a process which stops at the end of this period. This process includes endogenous formation

of primary membrane(s) within the oocytes, (i.e. zona radiata) and exogenous formation of the secondary membranes of the follicular epithelium. In some species (acipenseiridals), the zona radiata is divided into an external and an internal layer. In fish species producing "sticky" eggs, mainly cyprinids, there is an external villous layer, which helps the eggs attach themselves to the spawning substrate. In some species, (perch, sheat-fish (*Silurus glanis*)), a jelly-like membrane forms between the zona radiata and the follicular cell layers, leading to the formation of an egg-strand at spawning.

At the end of the vitellogenetic period, the micropyles form. These are funnel-shaped channels through the zona radiata, covered by enlarged follicle cells. Acipenseirid eggs have 6–11 micropyles, cyprinids and percids only one.

IV Maturation

This period, which ends oogenesis, starts with a polarization of the oocytes and ends with ovulation, which in vertebrates takes place in the metaphase of the second meiotic division. The nucleus begins to migrate to the animal pole, and the nucleus membrane disintegrates. During this migration, the number of nucleoli decrease, and they concentrate in the centre of the nucleus. Parallel changes in the follicle membrane also take place. The water uptake of the oocytes increases their diameter and they reach their final sizes. The yolk granules usually lose their crystal structure, although this is not the case with cyprinids.

The final maturation of the oocytes is controlled by GtH, triggering the production of oocyte maturation-inducing substances (MIS) such as hydroxylated progestins from the theca cells (reviewed in Redding & Patiño 1993). This steroid is then modified by the granulosa cells. The MIS pass through the zona radiata and induce the maturation of the oocytes. It should also be noted that gap junctions in the zona radiata seem to be hormonally-regulated, controlling the transfer of MIS to the oocyte. As in most vertebrates, ovulation of the mature fish oocytes is induced by a drastic increase in plasma GtH (surge). The mature oocyte is thus expelled from its follicle. Proteolytic enzymes from the follicle cells facilitate the rupture of the follicle and the release of the oocyte is also helped by the contraction of specialised theca cells.

The ovaries are attached to the body cavity on either side of the dorsal mesentery, with some exceptions in lampreys and teleosts (Nagahama 1983). Ovaries are usually paired structures, although in certain fish such as perch, only one is developed. Oviducts occur in most teleosts, but are lost secondarily during development in, for example, salmonids (Hoar 1969). Three main types of ovary anatomy can be identified:

1) Ovary without opening (salmonids, acipenseirids)
2) Ovary with the opening on the back (cyprinids)
3) Ovary with the opening in the centre (percids)

Ovarian development can be either synchronous, group synchronous, or asynchronous (Gorbman 1983). In monocycle fish, such as Pacific salmons and freshwater eels (*Anguilla* spp.), all oocytes develop simultaneously (synchronic development) and the fish spawn just once in a lifetime (semelparity). In

polycycle fish there are wide variations in sex cell development as well as spawning times, duration and frequency according to which polycyclic fish can be divided into the following groups:

a) Group synchronous fish, in which two or more generations of oocytes at different developmental stages co-exist. The group synchronous fishes are thus able to spawn recurrently after completion of the ovary cycle. The annual spawning takes place on a single occasion – early in the spring (roach, perch, pike (*Esox lucius*), pike-perch, rainbow trout (*Oncorhynchus mykiss*) or in autumn (whitefish (*Coregonus* spp.), salmon, vendace (*Coregonus albula*).

b) Asynchronous fish contain oocytes at all stages of maturity, which allows for continuous ovulation as in tench and gudgeon (*Gobio gobio*) (Kestemont 1987). Spawning occur intermittently (batch-spawning), mainly in summer (rudd (*Scardinius erythrophtalmus*), tench, ruff (*Gymnocephalus cernuus*), bleak (*Alburnus alburnus),* sticklebacks, crusian carp (*Carassius carassius*).

c) Species exhibiting single or intermittent spawning, depending on the environmental conditions. Spawning occurs in late spring or in summer (bream (*Abramis brama*), silver bream (*Blicca bjoerkna*), vimba (*Vimba vimba*)).

d) Continous development of oocytes with spawning more or less all year round (mainly tropical fish).

Classification system of oogenesis

The development from oogonium to mature oocyte passes through different stages. There are several opinions about how to classify these maturation stages (Mejen 1927, 1939, Trusov 1947, Kazanskii 1949, Sakun & Buckaja 1963, Koselev 1984, Makeeva & Emelianova 1989), as well as how detailed this classification should be. However, six-stage system as put forward by some researchers is likely to be the most relevant in terms of describing and analysing the effects of water temperature on female fish as presented in this review.

Stage I – Oogonia and early meiosis. This stage is of very short duration, i.e. the first few months after hatching. It is characterized by the development of oogonia (diameter (d) about 10µ) and oocytes (d≈20–35µ) in early meiosis.

Stage II –Cytoplasmic growth. The diameter of the oocytes increases. This stage may last for several years in juvenile fish before sexual maturation is reached, but for group synchronous mature fish it only lasts for 1–2 months between spawning and the start of the next oocyte growth period.

Stage III –Vitellogenesis. The main period of oocyte growth is characterized by a large increase in gonad weight and oocyte diameter. The vacuolation of the cytoplasm and the accumulation of yolk granules begins. At the end of this stage, the oocyte is filled with trophic substances and the membranes are fully developed. The oocytes attain their final size.

Stage IV – Maturation. The nucleus moves to the animal pole, the nucleus membrane disintegrates, the second meiotic division begins and the egg is finally ready for ovulation.

Stage V – Ovulation. The duration of this stage depends on the type of spawning (it is much longer for batch-spawning fish).

Stage VI –Post-spawning. Resorption, e.g. of empty follicles, takes place. This stage lasts for about 1–1.5 months.

Oocyte development in roach and perch

Examples of oocyte development in cyprinids and percids are given for roach and perch, two of the most common species in European inland waters and in the Baltic Sea, with similar gonad development rhythms (Mejen 1939, Trusov 1947). We will briefly present the gametogenesis from oogonium to matured oocyte, following the different development periods and stages. The histological material was prepared using the Romeis method (1954). These pictures have not been published before, and were taken through a Zeiss microscope system. The fish were sampled in the Baltic Sea at the Swedish coast and in inland waters of Lithuania.

The annual cycles of gonad growth in roach and perch are very similar. Stage I – the oogonium period – only lasts for the first few months after hatching, followed by oocyte growth into stage II – the cytoplasmic growth period (Fig 6a & 7a). During this period, the diameter of the roach oocyte increases to 210–260µ and the GSI-values rise (gonadosomatic index) to about 2%. In perch, oocytes reach 140–170µ in diameter and GSI is about 0.5%. Oogenesis can be arrested at this stage for 3–4 years before the fish reach sexual maturity.

The period of vitellogenesis (stage III) is initiated in late summer (August) and its early stage ends in autumn (October) (fig 6b & 7b). The gonadal development then continues throughout winter until spawning occurs the following spring (Le Cren 1951, Craig 1977, Papageoriou 1977). The diameter of the oocytes increases as well as the GSI. In roach, the oocyte diameter increases to 800–900µ, and GSI to about 6–8%, and in perch to 500–600µ and 5–7%, respectively. The late period of vitellogenesis between November and April includes vacuolation of the cytoplasm, accumulation of yolk granules – in perch fat droplets also form (fig 6c & 7c) – and the oocytes reach their final size (in roach: d≈900–1200µ). Small granules of glycogen appear between the yolk granules at the end of late vitellogenesis in roach oocytes. The egg membrane also forms: in roach, the membrane width is about 30µ and is made from zona radiata, villous and follicle layers (fig 6d), while in perch the width of the egg membrane is over 100µ, and is made from zona radiata, jelly (which forms the greater part of the membrane), and the follicle layer (fig 7d).

The vitellogenesis ends and the female gonad passes into a short maturation period (stage IV) before spawning (Fig 6e & 7e). The nucleus moves to the animal pole and disintegrates; the second meiotic division starts and finally the egg is ready for ovulation (April–May). In roach, yolk homogenization does not occur, only a fusion of nucleus granules into larger ones, while in perch large fat droplets form surrounded by homogenized yolk (fig 7f). Ovulation happens quickly, in perch it takes only a few minutes as all the eggs are spawned at one time as a single egg-strand. After spawning (stage VI), only empty follicles are left together with oogonia and oocytes in the cytoplasmic stage. At the post-spawning stage, resorption takes place over a period of 1–1.5

months (April–June) and the gonads are defined as being in stage II (Fig 6f & 7g). Females, which do not recover from spawning, may rest during the next gonadal cycle. Their gonads will then stay in stage II through winter, and transition to stage III will not then be possible before the end of the next summer.

The timing of reproduction

The endogenous rhythm of fish reproduction is synchronized by environmental cues, *zeitgebers*, in particular water temperature and photoperiod, in order to ensure that the progeny hatch when the chances of optimal conditions for growth and survival are highest (eg. Lam 1983, Baggerman 1985, 1990, Munro 1990, Van Der Kraak & Pankhurst 1996). The environmental impact on the endocrinological regulation of reproduction is obviously very complex; the combined effects of photoperiod and water temperature vary not only between species but also during the gametogenesis (eg. Billard & Breton 1981). Photoperiod and temperature presumably affect both GtH secretion and the responsiveness of target organs to hormonal stimulation. Synergetic and/or compensatory effects of temperature and photoperiod have been shown for a number of species of fish (e.g. Seymour 1981, Razani *et al*. 1987, Baggerman 1990, Fraile *et al*. 1994). The reproductive cycle of temperate teleosts follow three different patterns according to the time of year when gametogenesis occurs (Billard *et al*. 1981), although there are wide variations in gonadal growth in temperate fish species, due to environmental factors:

Group I – gametogenesis is fully induced in summer and autumn during decreasing photoperiod and temperature in autumn (salmonids).

Group II – gametogenesis begins in summer or autumn, but stops during the cold season and is completed in spring (cyprinids, percids, pleuronectides).

Group III – gametogenesis occurs with increasing temperature and photoperiod (tench).

In the Japanese sardine *(Sardinops melanostictus*), ovarian recrudescence is encouraged by decreasing temperatures in March (Matsuyama *et al.* 1991). In gudgeon, the oocytes have a group synchronous distribution at the beginning of recrudescence, whereas the end of vitellogenesis, distribution is completely asynchronous (Kestemont 1990). There can be marked differences between the sexes; in pike, testicular growth is completed in late summer, whereas ovarian growth continues over winter till spawning in spring (Medford & Mackay 1978, Diana & Mackay 1979).

In the three-spined stickleback (*Gasterosteus aculeatus*), the ovarian cycle has two stages (reviewed in Baggerman 1990). After the previtellogenetic stage, vacuolation begins in late summer or autumn, i.e. endogenous formation of yolk substances in the oocytes. After a period of quiescence, vitellogenesis is normally resumed during spring, characterized by a sharp increase in egg diameter and yolk deposition. As the three-spined stickleback is a batch-spawner, the ovaries always contain oocytes at different developmental stages during the spawning season. Baggerman (1990) has shown that the initiation of the second stage of vitellogenesis has to be stimulated by increasing photoperiod; i.e. there is a photoreactive threshold in three-spined stickleback when

the fish either become fully mature or do not respond at all. Manipulations with long photoperiods may cause gonadal recrudescence even in autumn. Temperature has been observed to have a synergetic effect in that initiation was facilitated by increasing temperature, although a raised temperature regime alone could not initiate gonadal growth. However, besides these two external factors which are important for synchronizing gonadal development, it was also discovered that the oocyte development of the three-spined stickleback is governed by an endogenous rhythm, and that vitellogenesis is strongly dependent on photoperiod. Initiation of the second stage of vitellogenesis is related to a reduction in the photoperiod from 16 hrs. in early autumn to fewer than 8 hrs. at the end of January. It could also be concluded that this "measurement" of daylength is related to a daily endogenous rhythm of photosensivity. The actual length of the photoperiod did not matter, but what was shown to be important was the time of day when "sunset" occurred.

The environmental control of the final maturation differs from the control of gonadal recrudescence (reviewed by Hontela & Stacey 1990). The critical event in both processes is an enhanced level of plasma GtH, the latter stimulating steroid synthesis, initiating follicular rupture. Even though the gametogenesis progresses over the year, final gamete maturation will not occur as a consequence of the completion of gonadal growth. For example, in cyprinids there needs to be a rise in temperature in order to attain the ovulation state, whereas in salmonids, although vitellogenesis and spermatogenesis occur in summer, spawning is promoted by the decreasing temperatures and photoperiod of autumn (Billard *et al.* 1978, Smith 1978, Breton *et al.* 1980, Worthington *et al.* 1982, Jafri 1987, 1989, Kestemont 1990). In the cyprinid *Notemigonus crysoleucas*, de Vlaming (1975) noticed that both temperature and photoperiod have to increase for the completion of gonadal development, whereas the ovaries regressed, if there was just an increase in temperature. Jafri (1989) observed in roach that exposure to a short photoperiod during the spawning season inhibited spawning and led to gonadal regression, whereas similar treatment during summer stimulated vitellogenesis in the ovary. Exposure to warm water temperatures during the pre-spawning period reduced the gonadosomatic index in both sexes and caused *atresia* in the ovary.

In salmonids, plasma GtH rises several days before ovulation and due to high post-ovulatory viability, spawning can take place successfully more than a week after ovulation. On the other hand, the complete maturation cycle in cyprinids, from the GtH surge to the oviposition, must take place within 24 hrs (Hontela & Stacey 1990). This release of GtH is stimulated in female goldfish (*Carassius auratus*) by an increase in temperature but also by the presence of aquatic vegetation. Thus, the females never ovulate in captivity in water below 15 °C in the absence of vegetation, but do so at 12 °C, if vegetation is present. Furthermore, an intriguing synchronization has been shown between the ovulation process of the female and the mobilisation of male milt production and male spawning behaviour. This is mediated by waterborne pheromones, affecting the male olfactory system. The GtH surge in females at dawn leads to a production of progesterones, which are released in part into the surrounding water. The steroid has a stimulatory effect on the male, leading to an immediate GtH surge in the males too. During the night ovulation and milt production is completed. Some 10 hrs. following this GtH surge in the female, ovarian

prostaglandins are produced which stimulate the sexual behaviour of the female. This substance or others related to this process are also released into the water, synchronising the male spawning behaviour with that of the female at dusk.

The impact of energy status on reproduction

The temporal displacement between optimal conditions for feeding and for the development of eggs and larvae is commonplace in most temperate teleosts (e.g. MacKinnon 1972), although to a lesser extent in batch-spawning fish such as tench and three-spined stickleback (Wootton 1979). This constraint on reproduction leads to a temporal partitioning of energy resources, seen most clearly in long-distance migratory fish such as salmonids and freshwater eels. The effects of a food shortage on gonadal development depends on when in the gonadal cycle the shortage occurs and may ultimately lead to arrested gametogenesis (Johnston *et al.* 1987, Rowe *et al.* 1991) or even to gonadal regression (reviewed in Wootton 1979).

After spawning in spring, cyprinids such as roach, store fat in muscle tissue, the liver and the mesentery until August (Pęczalska 1968, Mackay & Mann 1969, Vyatchanina 1971, Hellawell 1972, Bryuzgin 1974, Penczak *et al.* 1977, Shikhshabekov 1974, Lyagina 1972, Billard *et al.* 1978, Jafri 1990). The fastest gonadal growth is in September, when somatic growth slows down and fat concentrations diminish, due to the gonadal growth. The mesenteric fat is used up first and thereafter the fat stores in the liver and the muscle tissues. The fat content in females is reduced more than in males because of the higher energy demands of oogenesis.

The annual cycle of gonadal growth in perch is, as described above, similar to that of roach (Le Cren 1951, Craig 1977, Papageoriou 1977); female gonadal growth starts in late summer and continues through the winter until spawning the following spring, whereas although the testis also starts to grow in late summer, it will have already reached its maximal size in autumn (fig 4). Body condition also increases from a minimum after spawning to a maximum in autumn, when in both sexes it decreases once again. In another spring-spawning fish, pike, the ovaries grow throughout the winter without any apparent decrease in energy reserves until March (Medford & Mackay 1978). As the energy needs of the female are much greater than those of the male, it has been suggested that the female has a higher feeding rate during winter. Energy losses could, however, be detected just before spawning on final maturation of the ovary. The liver seems to be the main energy store in both sexes, as the female liver decreased sharply in size before spawning and the male during spawning. Selective depletion of energy reserves has also been observed in three-spined stickleback (Allen & Wootton 1982).

Thus, fat content or its ratio, as well as temperature in particular, (e.g. Volodin 1980, Billard *et al.* 1981, Korsgaard *et al.* 1986, Vondracek *et al.* 1988, Hutchings & Myers 1994), is a governing factor of gonadal growth, fecundity and egg size (Billard *et al.* 1978, 1981, Wootton 1979, Davies *et al.* 1986, Worthington *et al.* 1982, Vondracek *et al.* 1988). Fecundity, egg size, quality and viability have been observed to be related to fish growth, condition and fat content in roach, as the oocytes can be resorbed (*atresia*), if the nutritional status deteriorates (Mackay & Mann 1969, Bryuzgin 1974, Lyagina 1972, 1975, Penczak *et al.*

1977, Kuznetsov & Khalitov 1978, Burrough & Kennedy 1979, Spivak *et al.* 1979, Backiel & Zawisza 1988). There is support for the theory of density-dependent fecundity, i.e. food-limited fecundity, in roach (Mackay & Mann 1969, Burrough & Kennedy 1979), bream (Lammens 1982), and pike (Craig & Kipling 1983). A shortage of food has also been observed to reduce fecundity in fish such as plaice (*Pleuronectes platessa),* and the salmonids (reviewed in Billard *et al.* 1981).

However, impact of energy status on reproduction is not restricted to seasonal influences, leading to annual variations in fecundity and maturation rate. Gonadal development starts already at the larval stage and it has been shown that by varying the environmental conditions during the embryogenesis, subsequent development may be affected, leading to differences in sex ratio and gonadal developmental rate (Volodin & Grechanov 1985). In recent years, the importance of age or rather, size, for successful reproduction has been recognized (e.g. Hutchings & Myers 1993). The combined effects of higher fecundity, the probable higher fertility of the spawn, and longer spawning periods of older individuals, in Atlantic cod (*Gadus morhua*) are considered to be of the utmost significance for stock recruitment. It is likely that this increased fertility of older and larger individuals is linked to a improved energy levels. However, increased size might also be a hindrance to continued reproduction (Dutil 1986); the spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*) declined with size because of the energy constraints in larger fish.

An integrated model of life-history and physiology

A physiological model has been put forward to show the hormonal control of maturation in Atlantic salmon (*Salmo salar*) (Rowe *et al.* 1991, Thorpe 1994). This model suggests that maturation in fish is environmentally regulated by two mechanisms; the size of the fat stores which depend on water temperature and food supply, and the photoperiod which allows the release of the inhibitor of the maturation process for only a short period of time during the annual light-cycle, i.e. the so-called “maturation window”. The model is based on the assumption of a positive feedback loop by which oestrogens are produced by aromatization of androgens in the mesenteric fat stores during spring (fig 8). Hence, the maturation of fish can be seen as a step-wise process, which only moves on from one step to the next if the physiological status of the fish allows it to do so. The advantages of such a control mechanism, which is ultimately related to external factors, is obvious. The maturation process will stop when the prospects of successful reproduction and survival of both the adult fish and its progeny are jeopardised by energy constraints.

It should also be noted that this model departs from the model predicting reaction norms for age and size at maturity under different growth and demographic conditions, presented by Stearns and Koella (1986). According to this latter model, the organism reacts according to the growth rate it experiences, following a specific trajectory of age and size at maturity. However, experimental (Vondracek *et al.* 1988, Maffe 1992) as well as field studies (Sandström *et al.* 1995, Svedäng *et al.* 1996) have found that plasticity in these traits cannot be predicted by growth rate alone, because variations in growth rates under different environmental conditions lead to different life-history solutions, which, in turn, cannot be attributed to genetic variability. The former model (Rowe *et al.*

1991, Thorpe 1994), with its incorporation of a plausible physiological control mechanism, allows the fish to time its reproduction in accordance with its energy status, irrespective of its age or size. Furthermore it suggests that genetic variability in age and size at maturity corresponds to differences in threshold levels in the rate of fat acquisition, hormone secretion, responsiveness of target organs to hormonal stimulation and so on, thereby allowing a population to evolve adaptive physiological responses under predictable environmental conditions by balancing mortality risks against the advantages of early reproduction. This kind of life-history solution could in a game-theoretic context be regarded as a conditional strategy (Maynard Smith 1982), i.e. modes of fish reproduction are ”opportunistic”, i.e. include the costs of hazardous environmental variability, rather than optimal resource allocation strategies (c.f. Stearns & Koella 1986).

Effects of raised temperatures on fish reproduction

Water temperature has a very marked effect on the physiological and biochemical processes in fish, and a raised temperature regime has complex effects on fish reproductive, nerve and endocrine systems. Increased temperature affects fat synthesis, metabolism, and the endocrine system which results in the failure of the generative process (Shatunovskij 1988). Effects of cooling water discharge on gametogenesis have been observed in cyprinids (Cragg-Hine 1970, Bray 1971, Wilkońska 1977, Detollenaere & Micha 1980, Mattheeuws *et al*. 1981, Długosz 1983b, Horoszewicz 1983, Morawska 1984, Gajdůšek *et al.* 1987, Lapina 1988, Jankovič 1990, Lukšienė & Sandström 1994), percids (Długosz 1983a, Lukšienė *et al*. manuscript) and in pike (Lukšienė *et al*. manuscript). Gametogenesis has been observed to be accelerated by cooling water discharges, especially in females (Bray 1971, Astrauskas & Rachunas 1975, Detollenaere & Micha 1980, Mattheeuws *et al.* 1981, Długosz 1983a,b, Lukšienė *et al.* manuscript). That fish may take advantage of thermal discharges has also been observed in yellow perch which select temperatures in the field close to their requirements for gametogenesis (Ross & Siniff 1982). Spawning of roach was observed to take place about two months earlier in an English river with an elevated water temperature regime: eventually the fish were able to spawn twice in a season because of the faster development of the ovaries (Bray 1971). It was also reported that many of the early spawning females were only partly fulfilling the spawning and that many eggs were resorbed.

Lukšienė and Sandström (1994) and Lukšienė *et al.* (manuscript) observed serious gonadal malfunctions in female roach, perch and pike exposed to cooling water discharges during winter (fig 9a). The histological analysis revealed high frequencies of egg resorption (fig 9b), and the gonads developed arhythmically; the level of oogenesis deviated both within and between individuals (fig 9c & d). The oocyte resorption occurred mainly during stage III. In addition, eggs with two or more nuclei, hermaphroditism, and some other anomalies were observed (fig 9e & f). The temporal division of the gonadal development differed between heated and unheated areas in both roach and perch. In a normal thermal regime, the vitellogenesis period lasted about one month longer, and the spawning generally started in May, whereas in heated areas spawning occurred earlier in April–May (fig 4). It should be noted that early vitellogenesis started in August irrespective of thermal regime, indicating that this event in the maturation cycle is governed by the light-cycle.

Similar disturbances in female roach gonadal development, such as significant differences between individuals in oocyte development, were also observed in a Polish cooling water lake, although no disturbances were observed in male roach (Długosz 1983b). In a detailed study of bream in a cooling reservoir in Lithuania, it was concluded that the enhanced temperature regime resulted in increased oocyte growth asynchronicity (fig 9c), and degenerative processes in the gonads as well as smaller egg size and reduced fertility (Gajdůšek *et al.* 1987). However, it should also be pointed out that similar gonadal damages in roach such as asynchronous development, atresia and hermaphroditism, have been observed in natural areas of the Baltic Sea, considered to be linked to infections of a microsporidian parasite (Wiklund *et al.* 1996). Large fish were much more affected than small fish, corresponding to the observations at Swedish nuclear power plants. That gonadal impairements are generally caused by parasites is, however, not likely, since reproductive malfunctions have been observed in cooling water reservoirs both in the sea and in fresh waters and in different species, and since parasitic infections have been seldom recorded in histological analyses. Furthermore, damaged reproductive organs have been noted to recover from one year to the next when the cooling water exposure has ceased (see below).

Changes in the reproductive system can thus be detected at different levels of organization: cell, tissue, organ, organism and population (Shmalgauzen 1982, Shvarc 1980, Akimova & Ruban 1996):

Cell level: divisions of oocytes during the cytoplasmatic period (amitosis; deformation of oocytes in the trophoplasmatic stage; fig 9a).

Tissue level: increase of asynchrony during the trophoplasmatic period; partial spawning (fig 9b), increased number of blood vessels in gonads, total or partial degeneration of oocytes during both the cyto- and trophoplasmatic periods (fig 9c).

Organ level: occurrence of hermaphrodite individuals (fig 9e), unbalance of season and level of sex cell development.

Organism level: Reproductive rates, fertility of sex cells and GSI-values decrease due to a high level of degenerative processes (fig 9c & d).

Population level: Spawning frequency decreases due to disturbances in metabolism and degenerative processes. Both individual and population reproduction rates are harmed.

This breakdown by organizational level can help us to understand more precisely the mechanisms behind the changes in the reproductive system, and the possible consequences of damage at both organism and population levels.

Histological studies are comparatively laborious and time-consuming. However, as visual observations could be validated by cross-examination with histo-pathological analyses (Lukšienė *et al.* manuscript), it was possible to diagnose gonadal malfunctions visually, thereby increasing considerably the number of observations that could be made. Female gonads from Baltic roach, perch and pike, collected both from natural and elevated temperature regimes were

examined. The study showed that in 30–60% of the gonads of all species had suffered damage during gametogenesis in a raised water temperature regime. The major deviations from normal development that were observed consisted of resorption of the oocytes (fig 9b). To evaluate the reproductive performance of those fish eventually maturing and finally spawning, perch egg-strands were sampled from waters with normal and elevated temperature regimes (Sandström *et al*. manuscript). The egg-strands were incubated *in situ* as well as transferred indoors, closely following the embryonic development. It was found that even if there were no indications of inhibited gametogenesis, and the fish had spawned in an appropriate manner, the quality of the egg-strands from those areas with an elevated temperature regime was inferior as they disintegrated quickly and all eggs died shortly afterwards in the field as well as in the laboratory. This hazardous effect of temperature on fish reproduction has serious implications, because maturing fish are attracted to those areas where water temperature is too high for normal gonadal development. In other words, the studied fish have no behavioural defense mechanism to help them avoid winter temperatures that are too high for normal gonadal development. Similar reproductive failures have been discovered in Lake Erie coho salmon (*Oncorhynchus kitsutch)* (Flett *et al*. 1996). It has been suggested that low survival rates of coho salmon embryos was due to delayed oocyte maturation and over-ripening, which could have been caused by warm water exposure during the period of late ovarian maturation.

Furthermore, in Lithuanian cooling water reservoirs, changes in fish species composition and distribution have coincided with new temperature regimes (Astrauskas *et al*. 1997). Some species have practically vanished (smelt), others have adapted to the new living conditions (bleak, vendace), whereas pike, showing degenerative processes in gonads under maximal thermal load (in up to 22% of the population), have started to avoid the warm water zone, and as a consequence the percentage of fish with damaged gonads has decreased in recent years (Lukšienė 1983, Astrauskas & Virbickas 1984). In other species such as perch and roach, their abundance has not been affected in spite of high numbers of damaged sex cells and/or the arrest of maturation after spawning, leading to reduced spawning frequency. Reduced reproductive performance in adults, however, can be offset against the generally positive effects of young fish growth and survival at higher temperatures, for example, and explains why these populations have survived.

It is well-known, that in some bony fish hermaphroditism and sex changes are normal phenomena (as is the case with sparids and serranids; Suvorov 1948, Okada 1965a,b). Hermaphroditism has been documented at very low levels of frequency in several fish species in natural water bodies (e.g. Salechova 1965, Hilge &Conrad 1975, Hlarek & Norden 1977, Sloof & Klootwijk-Vandijk 1982), although the frequency of potential hermaphrodites has been recorded as being as high as 8% in maturing ruff in the Gulf of Finland (Buckaja 1976). The occurrence of hermaphroditism indicates serious disruption to gonadogenesis. It has been shown that sex reversals can be induced experimentally by the manipulation of temperature, light and feeding regimes (e.g. Chernishova 1960, Anpilova 1965, Buckaja 1980, Berg & Hurk 1983).

The recovery of the reproductive systems has been monitored by lowering temperature experimentally (Lukšienė *et al.* manuscript). In the Biotest basin at Forsmark on the Swedish east coast, an enclosed area which has had an elevated temperature regime for about sixteen years, the cooling water influence was stopped for a period of almost two years in 1995–1996. At the end of this two year period it was noticeable that the levels of abnormal female gonads were back at the levels for the reference areas. This observation strongly supports the hypothesis that the damage to the reproductive organs is related to immediate effects of the raised temperature regime on gametogenesis, and that individuals' reproductive organs can recover from one year to the next.

Conclusions

The adverse effects on fish reproduction caused by raised water temperature such as in cooling water discharges (Lukšienė and Sandström 1994) may be related to two unconnected phenomena. Firstly, the elevated temperature regime during the winter period may deplete the fat stores by increasing the metabolism at a time of the year when feeding opportunities are scarce. This situation may harm the female production of gametes more than the male and may eventually lead to regression of the ovaries as was observed in roach. Secondly, the water temperature anomalies may interfere with the hormonal regulation of gametogenesis. The combination of these two effects of an elevated temperature regime could, in theory, lead to regression of gonads as well as other types of gonadal malfunctions. However, no evidence of temperature effects on hormonal function has ever been reported (see Van Der Kraak & Pankhurst 1996 for a review). Besides the adverse effects on fish exposed to high temperatures in cooling water discharges, which may have serious implications due to the aggregation of fish to these discharge areas, global warming can also be expected to have some effect on fish reproduction, but at the moment it is not possible to predict what these effects might be.

References

Allen, J.R.M. & Wootton, R.J. 1982. Effect of food on the growth of carcase, liver and ovary in female *Gasterosteus aculeatus* L. J. Fish Biol. **21**, 537–547.

Anpilova, V.I. 1965. Sex reversal in baunti whitefish *Coregonus lavaretus* Baunti Muchamedjarov caused by ecological situation. J. Ichthyology **5**, 207–210. (In Russian).

Akimova, N.V. & Ruban, T.I. 1996. Systematization of reproductive disturbances in *Acipenseridae* during anthropogenic influence. On Ichthyology **36**, 65–80. (In Russian).

Astrauskas, A.S. & Rachunas, L.A. 1975. Hydrobiological condition in the reservoir–cooler of the Lithuanian state regional electric power station. Gidrobiologicheskii Zurnal **1**, 19–27. (In Russian with English summary).

Astrauskas, A.S. & Virbickas, J. 1984. Species composition and spatial distribution. Thermal power generation and environment. Functioning of populations and communities of aquatic animals in the cooling pond of the Lithuanian central steam power station. **4**, 72–78. Mokslas, Vilnius. (In Russian with English summary).

Astrauskas, A., Bernotas, E., & Didrikas, T. 1997. Ignalina Nuclear Power Plant (NPP) effluents impact on fish. Ekologija, **1** (in press).

Backiel, T. & Zawisza, J. 1988. Variations of fecundity of roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) in Polish lakes. Pol. Arch. Hydrobiol. **35**, 205–225.

Baggerman, B. 1985. The role of biological rhythms in the photoperiodic regulation of seasonal breeding in the stickleback *Gasterosteus aculeatus* L. Netherlands J. Zool. **35**, 14–31.

Baggerman, B. 1990. Sticklebacks. In: Reproductive seasonality in teleosts: environmental influences, pp. 79–107. A.D. Munro, Scott, A.P. & Lam, T.J. (eds). CRC Press, Boca Raton, Fl.

Berg. B. & Hurk, R. 1983. Oocytes in the testis of threespined stickleback, *Gasterosteus aculeatus*. Copeia **1**, 259–261.

Billard, R. & Breton, B. 1981. Le cycle reproducteur chez les poissons téléosteens. Cah. Lab. Hydrobiol, Montereau **12**, 43–56.

Billard, R., Breton, B., Fostier, A., Jalabert, B. & Weil, C. 1978. Endocrine control of the teleost reproductive cycle and its relation to external factors: salmonid and cyprinid models. In: Comparative Endocrinology, pp. 37–48. P.J. Gaillard & H.H. Boers (eds). International symposium on comparative endocrinology **8**.

Billard, R., Bry, C. & Gillet, C. 1981. Stress, environment and reproduction in teleost fish. In : Stress and fish, pp. 185–208. A.D. Pickering (ed). Academic Press, London.

Bray, E.S. 1971. Observations on the reproductive cycle of the roach (*Rutilus rutilus*) with particular reference to the effects of heated effluents, pp. 93–99. Proc. 5th Br. Coarse Fish Conf.

Breton, B., Horoszewicz, L., Bieniarz, K. & Epler, P. 1980. Temperature and reproduction in tench: Effect of a rise in the annual temperature regime on gonadotropin level, gametogenesis and spawning. II. The female. Reprod. Nutr. Dévelop. **20**, 1011–1024.

Bryuzgin, V.L. 1974. The relationship of condition, fatness, fecundity and weight of gonads in fish. Hydrobiol. J. **10**, 76–80.

Buckaja, N.A. 1976. About mass intersexuality of ruff (*Acerina cernua* (L.)) in eastern part of the Finnish Gulf. On Ichthyology **16**, 812–821. (In Russian).

Buckaja, N.A. 1980. Role of temperature and photoperiod in sexual cycle of ruff (*Acerina cernua*). J. Ichthyology **20**, 849–858. (In Russian).

Burrough, R.J. & Kennedy, C.R. 1979. The occurrence and natural alleviation of stunting in a population of roach, *Rutilus rutilus* (L.). J. Fish Biol. **15**, 93–109.

Chernishova, V.M. 1960. Reaction of fish sex glands on changed ecological conditions. Thesis of third meeting of embryologists of Soviet Union, pp. 181–182. Moscow State University. (In Russian).

Cragg–Hine, D. 1970. The growth of *Rutilus rutilus* (L.) and bronze bream *Abramis brama* (L.) in the effluent channel of Peterborough Power Station. Central electricity research laboratories, UK. 9 p.

Craig, J.F. 1977. The body composition of adult perch, *Perca fluviatilis* in Windermere, with reference to seasonal changes and reproduction. J. Anim. Ecol. **46**, 617–632.

Craig, J.F. & Kipling, C. 1983. Reproduction effort versus the environment; case histories of Windermere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. J. Fish Biol. **22**,713–727.

Davies, P.R., Hanyu, I., Furukawa, K. & Nomura, M. 1986. Effect of temperature and photoperiod on sexual maturation and spawning of the common carp. III. Induction of spawning by manipulating photoperiod and temperature. Aquaculture **52**, 137–144.

Detollenaere, A. & Micha, J.–C. 1980. Effects de rejets thermiques d'une centrale nucléaire sur les poissons de la Meuse. In: Technical consultation on allocation of fishery resources, pp. 138–145. J.H. Grover (ed). Vichy.

Diana, S.D. & Mackay, W.C. 1979. Timing and magnitude of energy deposition and loss in the body, liver, and gonads of northern pike (*Esox lucius*). J. Fish. Res. Bd Can. **36**, 481–487.

Długosz, M. 1983a. A histological picture of pike-perch (*Stizostedion lucioperca* L.) gonads from heated waters of Lake Gos awskie. Rocz. Nauk Rolnic. **100**, 29–43.

Długosz, M. 1983b. Development of gonads in roach (*Rutilus rutilus* L.) originating from heated Gos awskie lake. Rocz. Nauk Rolnic. **100**, 73–90.

Dutil, J.-D. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). Copeia **4,** 945–955.

Flett, P.A., Munkittrick, K.R., Van der Kraak, G. & Leatherland, J.F. 1996. Overripening as the cause of low survival to hatch in Lake Erie coho salmon (*Oncorhynchus kisutch*) embryos. Can. J. Zool. **74**, 851–857.

Fraile, B., Sáez, F.J., Vicentini, C.A., González, A., de Miguel, M.P. & Paniagua, R. 1994. Effects of temperature and photoperiod on the *Gambusia affinis holbrooki* testis during the spermatogenesis period. Copeia **1**, 216–221.

Gajdůšek, J., Astrauskas, A., Virbickas, J., Lukšienė, D. & Misjunene, D. 1987. The ecology of the bream in the cooling reservoir of a Lithuanian thermal power station. Acta Sc. Nat. Brno. **21**, 1–36.

Glazarian, K.T. & Belousov, L.B. 1983. Biology of individual development of animal. Moscow. p. 287. (In Russian.)

Gorbman, A. 1983. Reproduction in cyclostome fishes and its regulation. In: Fish physiology IXA, pp. 1–29. W.S. Hoar & D.J. Randall (eds). Academic Press. New York.

Hoar, W.S. 1969. Reproduction. In: Fish physiology III, pp. 1–72. W.S. Hoar & D.J. Randall (eds). Academic Press, New York.

Hellawell, J.M. 1972. The growth, reproduction and food of the roach *Rutilus rutilus* (L.), of the River Lugg, Herefordshire. J. Fish Biol. **4**, 469–486.

Hilge, V. & Conrad, C. 1975. Zum Laichvermogen eines hermaphroditen Karpfens (*Cyprius carpio*). Arch. Fischereiwiss. **26**, 49–51.

Hlarek, R.R. & Norden, C.R. 1977. Two hermaphroditic fresh-water alewives from Southern Lake Michigan. Prog. Fish Cult. **39**, 104–105.

Hontela, A. & Stacey, N.E. 1990. Cyprinidae. In: Reproductive seasonality in teleosts: environmental influences, pp. 53–77. A.D. Munro, Scott, A.P. & Lam, T.J. (eds). CRC Press, Boca Raton, Fl.

Horoszewicz, L. 1983. Reproductive rhythm in tench, *Tinca tinca* (L.), in fluctuating temperatures. Aquaculture **32**, 79–92.

Hutchings, J.A. & Myers, R.A. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquatic Sci. **50**, 2468–2474.

Hutchings, J.A. & Myers, R.A. 1994. Timing of cod reproduction – interannual variability and the influence of temperature. J. Mar. Ecol. Prog. Ser. **108**, 21–31.

Ivanov, M.F. 1956. Walls of fish eggs, their comparative morphology and ecological significance. News of Leningrad University **21**, 79–90. (In Russian).

Jafri, S.I.H. 1987. Incidental breeding of roach (*Rutilus rutilus*) in an aquarium. Progr. Fish-Cult. **49**, 237–238.

Jafri, S.I.H. 1989. The effects of photoperiod and temperature manipulation on reproduction in the roach *Rutilus rutilus* (L.) (Teleostei). Pak. J. Zool. **21**, 289–299.

Jafri, S.I.H. 1990. Gametogenesis in roach *Rutilus rutilus* (L.) (Cyprinidae: Teleostei). Pak. J. Zool. **22**, 361–377.

Janković, D.V. 1990. Effects of warm wastewaters from thermal power stations on ecosystems of the Sava and the Velika Morava, tributaries of the Danube. Wat. Sci. Tech. **22**, 155–160.

Johnston, C.E., Gray, R.W., McLennan, A. & Paterson, A. 1987. Effects of photoperiod, temperature, and diet on the reconditioning response, blood chemistry, and gonad maturation of Atlantic salmon kelts (*Salmo salar*) held in freshwater. Canadian Journal of Fisheries and Aquatic Sciences **44**, 702–711.

Kazanskii, B. N. 1949. The function of the hypophysis and the ovary in intermittent spawning fishes. Reports from the Laboratory of Fish Breeding Principles **2**, 64–120. (In Russian).

Kestemont, P. 1987. The reproductive cycle of the gudgeon, *Gobio gobio* L. Part 1. J. Appl. Ichthyol **3**, 145–157. (In French with English summary).

Kestemont, P. 1990. Dynamic aspects of ovogenesis in an asynchronous fish, the gudgeon, *Gobio gobio* L. (Teleostei, Cyprinidae), under controlled temperature and photoperiod conditions. Aquat. Living Resour. **3**, 61–74.

Korsgaard, B., Mommsen, T.P & Saunders, R.L. 1986. The effect of temperature on the vitellogenic response in Atlantic salmon post smolts (*Salmo salar*). Gen. Comp. Endocrinol. **62**, 193–201.

Koselev, B.V. 1984. Ecology of fish reproduction. Nauka, Moscow. (In Russian).

Kuznetsov, V.A. & Khalitov, N.Kh. 1978. Alterations in the fecundity and egg quality of the roach, *Rutilus rutilus* in connection with different feeding conditions. J. Ichthyology **18**, 74–83.

Lagler, K.F., Bardach, J.E. Miller R.R. & May Passino, D.R. 1977. Reproduction, pp. 268–310. In: Ichthyology. John Wiley & Sons, New York.

Lam, T.J. 1983. Environmental influences on gonadal activity in fish. In: Fish physiology IXB, pp. 65–116. W.S. Hoar & D.J. Randall (eds). Academic Press, New York.

Lammens, E.H.R.R. 1982. Growth, condition and gonad development of bream (*Abramis brama* L.) in relation to its feeding conditions in Tjeukemeer. Hydrobiol. **95**, 311–320.

Lapina, N.N. 1988. The biology of the bleak (*Alburnus alburnus* (L.)) from Kopor cape in the Gulf of Finland. Biological sciences (Zoology) **5**, 47–51. (In Russian with English summary).

Le Cren, E.D. 1951.The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol. **20**, 201–219.

Lukšienė, D. 1983. Peculiarities of reproduction of fish in cooling water reservoir of LCPP. Thesis for a candidate degree, p. 188. Vilnius. (In Russian).

Lukšienė, D. & Sandström, O. 1994. Reproductive disturbance in a roach (*Rutilus rutilus*) population affected by cooling water discharge. J. Fish Biol. **45**, 613–625.

Lukšienė, D., Sandström, O. & Andersson, J. The influence of high temperatures on the gametogenesis of female fish (manuscript).

Lyagina, T.N. 1972. The seasonal dynamics of the biological characteristics of the roach (*Rutilus rutilus* (L.)) under conditions of varying food availability. J. Ichthyology **12**, 210–226.

Lyagina, T.N. 1975. Connection of egg weight with biological indices of female roach, *Rutilus rutilus*, with different abundance of food. J. Ichthyology **15**, 652–663.

Mackay, I. & Mann, R.K.H. 1969. Fecundity of two cyprinid fishes in the River Thames, Reading, England. J. Fish. Res. Bd Can. **26**, 2795–2805.

MacKinnon, J.C. 1972. Summer storage of energy and its use for winter metabolism and gonad maturation in American plaice (*Hippoglossoides platessoides*). J. Fish. Res. Bd. Canada **29**, 1749–1759.

Maffe, G.K. 1992. Plasticity of life-history characters in Eastern mosquitofish (*Gambusia holbrooki*: Poeciliidae) in response to thermal stress. Copeia **1,** 94–102.

Makeeva, A.P. & Emelianova, N.T. 1989. Periods of oogenesis in cyprinid fish species. On Ichthyology **29**, 931–943. (In Russian).

Malison, J.A., Kayes, T.B., Best, C.D. & Amundson, C.H. 1986. Sexual differentiation and use of hormones to control sex in yellow perch (*Perca flavescens*). Can. J. Fish. Aquatic Sci. **43**, 26–35.

Mattheeuws, A., Genin, M., Detollenaere, A. & Micha, J.-C. 1981. Etude de la reproduction du gardon (*Rutilus rutilus*) et des effets d'une élévation provoquée de la température en Meuse sur cette reproduction. Hydrobiologia **85**, 271–282.

Matsuyama, M., Adachi, S., Nagahama, Y., Kitajima, C. & Matsuura, S. 1991. Annual reproductive cycle of the captive female Japanese sardine *Sardinops melanostictus:* relationship to ovarian development and serum levels of gonadal steriod hormones. Mar. Biol. **108**, 21–29.

Maynard Smith, J. 1982. Evolution and the theory of games. 224 p. Cambridge University Press, Cambridge.

Medford, B.A. & Mackay, W.C. 1978. Protein and lipid content of gonads, liver, and muscle of Northern pike (*Esox lucius*) in relation to gonad growth. J. Fish. Res. Bd Can. **35**, 213–219.

Mejen, V. A. 1927. Observations of annual changes in the ovary of perch (*Perca fluviatilis* L.). Russian Zoological Magazine **1**, 75–113. (In Russian).

Mejen, V.A. 1939. On yearly cycle of changes in the ovary of bone fish. News of Academy of Sciences of USSR, Series Biol. **3**, 389–420. (In Russian).

Meznin, F.I. 1978. The development of gonads in early ontogenesis of perch *Perca fluviatilis* L. J. Ichthyology **18**, 84–100. (In Russian).

Morawska, B. 1984. The effect of water temperature elevation on incipient and cumulative fecundity of batch-spawning tench, *Tinca tinca* (L.). Aquaculture **42**, 273–288.

Munro, A.D. 1990. General introduction. In: Reproductive seasonality in teleosts: environmental influences, pp. 1–11. A.D. Munro, Scott, A.P. & Lam, T.J. (eds). CRC Press, Boca Raton, Fl.

Nagahama, Y. 1983. The functional morphology of teleost gonads. In: Fish physiology IXA, pp. 223–275. W.S. Hoar, D.J. Randall & E.M. Donaldson (eds). Academic Press, New York.

Okada, Yo K. 1965a. Bisexuality in sparid fishes. I. Origin of bisexual gonads in *Mylio macrocephalus*. Proc. Japan. Acad. **41**, 294–299.

Okada, Yo K. 1965b. Bisexuality in sparid fishes. II. Sex segregation in *Mylio macrocephalus*. Proc. Japan. Acad. **41**, 300–304.

Papageorgiou, N.K. 1977. Fecundity and reproduction of perch (*Perca fluviatilis* L.) in Lake Agios Vasilios, Greece. Freshw. Biol. **7**, 559–565.

Pęczalska, A. 1968. Development and reproduction of roach (*Rutilus rutilus* L.) in the Szczecin firth. Pol. Arch. Hydrobiol. **2**, 103–120.

Penczak, T., Zalewski, M., Molinski, M. & Gajos, M. 1977. The ecology of roach, *Rutilus rutilus* (L.), in the barbel region of the polluted Pilica River. IV. Elements of production and food consumption. Ekol. Polska **25**, 241–255.

Persov, G.M. 1959. Age and growth and gonadal status in sterlet in the gonadal differentiation period. In: Biological principles of fishery, pp.56–63. Tomsk University. (In Russian.).

Persov, G. M. 1966. Early period of gametogenesis in anadromous salmon. Reproduction and acclimation of salmonids in Barents and White Sea, pp.7–44. Nauka, Moscow–Leningrad. (In Russian).

Persov, G.M. 1975. Differentiation of sex in fish, p. 148. Nauka, Moscow–Leningrad. (In Russian.)

Razani, H., Hanyu, I. & Aida, K. 1987. Critical daylength and temperature level for photoperiodism in gonadal maturation of goldfish. Exp. Biol. **47**, 89–94.

Redding, J.M. & Patiño, R. 1993. Reproductive physiology. In: The physiology of fishes, pp. 503–534. D.H. Evans (ed). CRC Press, Boca Raton, Fl.

Romeis, B. 1954. Technique of microscoping. Inostrannoja Literatura, Moscow. (In Russian).

Ross, M.J. & Siniff, D.B. 1982. Temperatures selected in a power plant thermal effluent by adult yellow perch (*Perca flavescens*) in winter. Can. J. Fish. Aquatic Sci. **39**, 346–349.

Raven, Chr. P. 1964. Oogenesis. Moscow (In Russian.)

Rowe, D.K., Thorpe, J.E. & Shanks, A.M. 1991. Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. Can. J. Fish. Aquatic Sci. **48**, 405–413.

Sakun, O.F. 1964. Sex cells amitosis and conditions of its origin in fish. Problems of contemporary embryology, pp. 295–297. Ed. Moscow State University Moscow. (In Russian.)

Sakun, O.F. & Buckaja, N.A. 1963. The evaluation of stages of maturation and study of sexual cycles of fish, p. 36. Moscow. (In Russian.)

Salechova, L.P. 1965. Sexual structure of sea crusian carp (*Diploduo annularis* L.) population in relation to pecularities in the oogenesis. On Ichthyology **2**, 378–380. (In Russian).

Sandström, O., Neuman, E. & Thoresson, G. 1995. Effects of temperature on life history variables in perch. J. Fish Biol. **47**, 652–670.

Sandström, O., Abrahamsson, I., Andersson, J. & Vetemaa, M. Temperature effects on spawning and egg development in European perch, *Perca fluviatilis*. (Manuscript).

Shmalgauzen, I.I. 1982. Organism as a unit in individual and historical development, p. 228. Nauka. (In Russian).

Shatunovskij, M.I. 1988. About physiological-biochemical indicators of fish conditions in cooling water reservoirs of energy objects. Methods of bioindication of environment in NPP regions, pp. 97–100. Nauka. (In Russian).

Seymour, E.A. 1981. The effects of powdered carp pituitary on ovarian development, ovarian ascorbic acid and ovulation in *Carassius carassius* L. exposed to various photoperiod and temperature regimes. J. Fish Biol. **19,** 675–682.

Shapiro, D.Y. 1984. Sex reversal and sociodemographic processes in coral reef fishes. In: Fish reproduction: Strategies and tactics, pp. 13–33. G.W. Pott & R.J. Wootton (eds). Academic Press, London..

Shikhshabekov, M.M. 1974. Features of the sexual cycle of some semi-diadromous fishes in the lower reaches of the Terek. J. Ichthyology **14**, 79–88.

Shvarc, S.S. 1980. Ecological regulations of evolution. 280 p. Nauka. (In Russian).

Sloof, W. & Klootwijk-Vandijk, E. 1982. Hermaphroditism in the bream. J. Fish Deseases **5**, 79–81.

Smith, R.J.F. 1978. Seasonal changes in the histology of the gonads and dorsal skin of the fathead minnow, *Pimephales promelas*. Can. J. Zool. **56**, 2103–2109.

Spivak, E.G., Pinus, G.N. & Sentishcheva, S.V. 1979. The age composition of the spawning population and the characteristics of the spawners size-age structure and fecundity of the roach, *Rutilus rutilus* spawning in Kakhovska reservoir. J. Ichthyology **19**, 75–80.

Stearns, S.C. & Koella, J.C. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution **40**, 893–913.

Svedäng, H., Neuman, E. & Wickström, H. 1996. Maturation patterns in female European eel: age and size at the silver eel stage. J. Fish Biol. **48**, 342–351.

Suvorov, E.K. 1948. Bases of Ichthyology. 580 p. Soviet Nauka. (In Russian).

Talikina, M.G. 1995a. Sex differentiation and gonad development in the first life-time years of bream *Abramis brama* in Rybinsk water reservoir. J. Ichthyology **35**, 114–119. (In Russian).

Talikina, M.G. 1995b. Growth and early gametogenesis in roach of two ecological forms under experimental impacts. Problems of rational use of bioresources of water reservoirs, p. 226. Kiev.

Thorpe, J.E. 1994. Reproductive strategies in Atlantic salmon, *Salmo salar* L. Aqua. Fish. Manage. **25**, 77–87.

Trusov, V.Z. 1947. Histological analysis of called the stage IV of maturation of ovary in pike-perch. Reports from the Laboratory of Fish Breading Principles **1**, 155–167. (In Russian).

Van Der Kraak, G. & N. W Pankhurst. 1996. Temperature effects on the reproductive performance of fish. In: Global Warming: Implications for Freshwater and Marine Fish. G. McDonald & C. M. Wood (Eds.). Cambridge University Press, Cambridge (in press).

de Vlaming, V.L. 1975. Effects of photoperiod and temperature on gonadal activity in the cyprinid teleost, *Notemigonus crysoleucas*. Biol. Bull. **148**, 402–415.

Volodin, V.M. 1980. The effect of temperature on resoption in practically mature eggs and the development of the next generation of oocytes in the Blue bream *Abramis ballerus* (L.), from Rybinsk reservoir. J. Ichthyology **25**, 639–646.

Volodin, V.M. & Grechanov, I.G. 1985. Effect of temperature on gonadal development and sex ratio in the progeny of a pair of White bream *Blicca Bjoerkna*. J. Ichthyology **25**, 52–59.

Vondracek, B., Wurtsbaugh, W.A., & Cech, J. Jr. 1988. Growth and reproduction of the mosquitofish, *Gambusia affinis*, in relation to temperature and ration level: consequences for life history. Env. Biol. Fish. **21**, 45–57.

Vyatchanina, L.A. 1971. Dynamics of fat accumulation in the roach (*Rutilus rutilus*) of Kremenchug reservoir as a function of maturation of the gonads. Hydrobiol. J. **7**, 80–84.

Wiklund, T. Luonasheimo, L., Lom, J. & Bylund, G. 1996. Gonadal impairment in roach *Rutilus rutilus* from Finnish coastal areas of the northern Baltic Sea. Dis. Aquat. Org. **26**, 163–171.

Wilkońska, H. 1977. Growth of roach (*Rutilus rutilus* L.,) in heated Liche skie lake. Rocz. Nauk Rolnic. ser H. **97**, 74–87.

Wootton, R.J. 1979. Energy costs of egg-production and environmental determinants of fecundity in teleost fishes. Symp. zool. Soc. Lond. **44**, 133–159.

Wootton, R.J. 1992. Constraints in the evolution of fish life histories. Netherlands Jour. Zool. **42**, 291–303.

Wourms, J.P., Grove, B.D. & Lombardi, J. 1988. The maternal-embryonic relationship in viviparous fishes. In: Fish physiology XIB, pp. 1–134. W.S. Hoar & D.J. Randall (eds). Academic Press, London.

Worthington, A.D., Macfarlane, N.A.A. & Easton, K.W. 1982. Controlled reproduction in the roach (*Rutilus rutilus* L.). In: Proceedings of the International symposium on reproductive physiology of fish, pp. 220–223. C.J.J. Richter & H.J.Th. Goos (eds). Wageningen, The Netherlands.

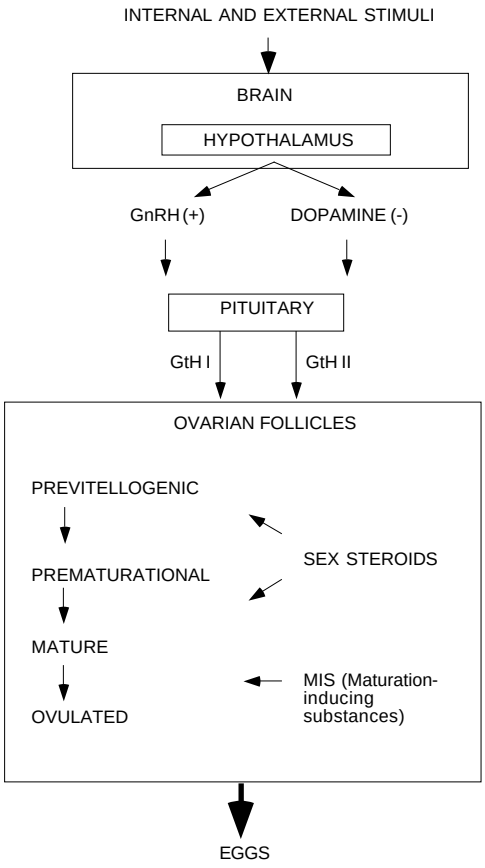

Figure 1. *A schematic view of the hypothalamic-pituitary–gonadal axis. The release of pituitary gonadotropin (GtH) is under dual hypothalamic control; secretion is stimulated by GnRH and inhibited by dopamine. Other neurohormones may also directly affect the release of GtH. At the end of the hypothalamic–pituitary–gonadal axis, GtH stimulates gametogenesis and steroiodogenesis by the testis or ovary. (Modified from Van Der Kraak & Pankhurst 1996).*

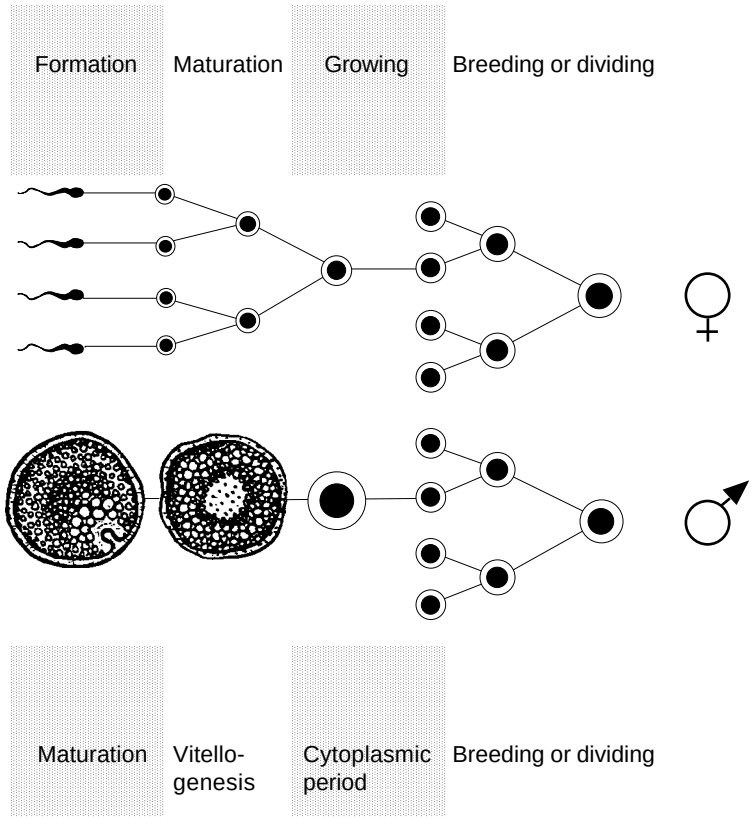

Figure 2*. A generalized figure of female and male gametogenesis.*

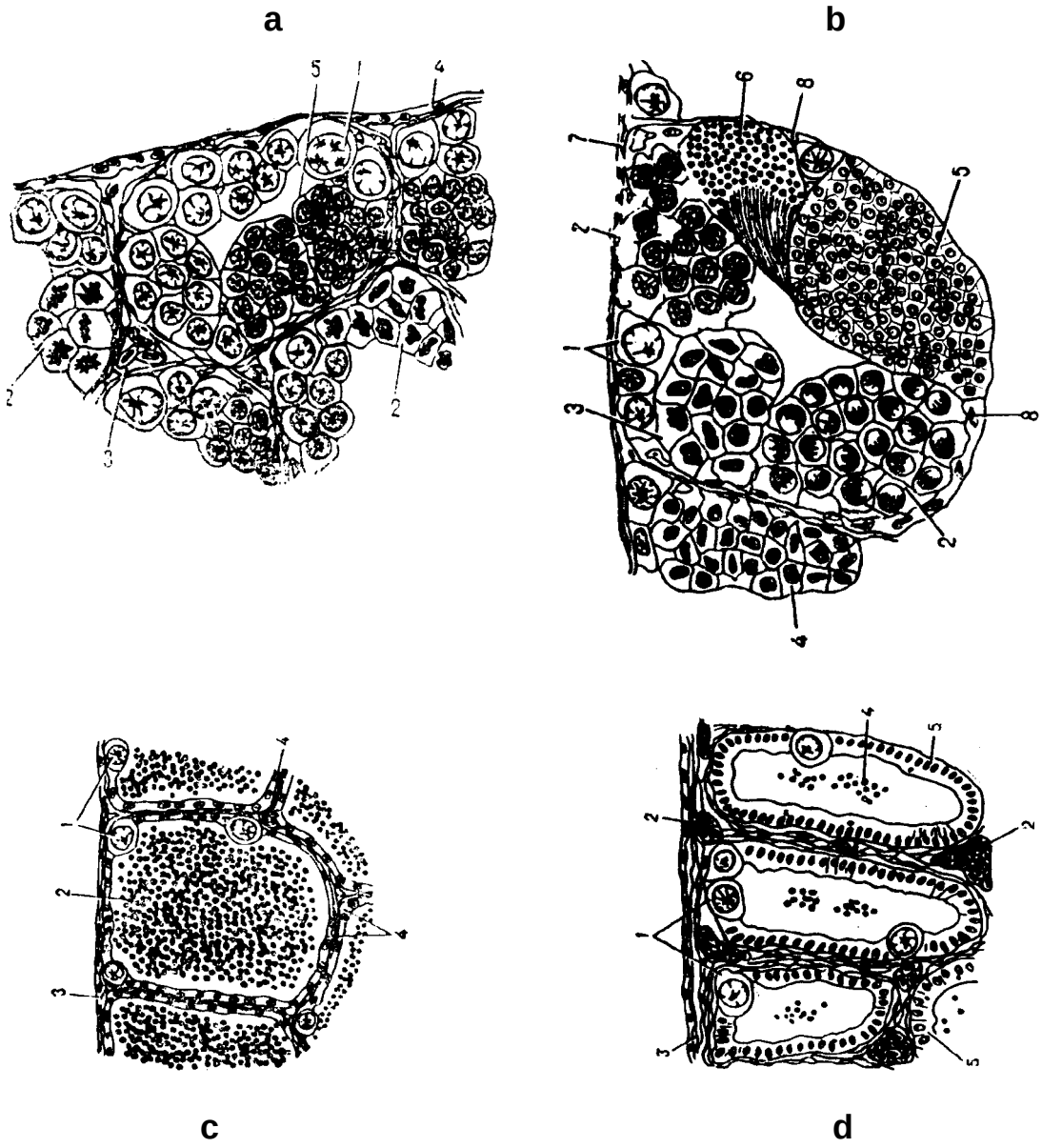

Figure 3. *A generalized figure of spermatogenesis. a) Testes at stage II. (1. Primary spermatogones 2. Dividing spermatogones 3. Blood-vessels with erythrocytes 4. The membrane of the testis.) b) Testes at stage III. (1. Spermatogones 2. Cysts with primary spermatocytes 3. Cysts with dividing primary spermatocytes 4. Cysts with dividing secondary spermatocytes 5. Cysts with spermatides 6. Cysts with formed spermatozoa 7. The opening of the testis 8. The follicular epithelium). c) Testes at stage IV. (1. Spermatogonium 2. Spermatozoa 3. Opening of testis 4. The follicular epithelium). d) Testes at stage VI. (1. Spermatogonia 2. Blood-vessel with erythrocytes 3. Opening of testis 4. The remaining spermatozoa 5. The follicular epithelium).*

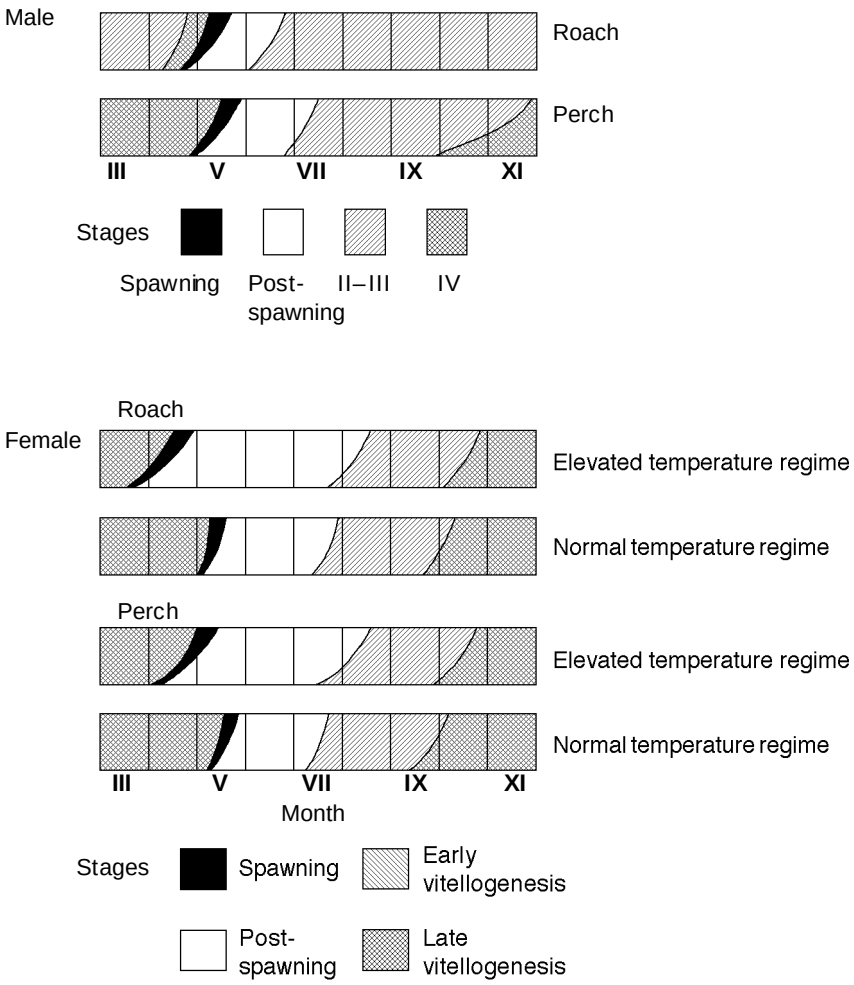

Figure 4*. The temporal division of the maturation cycle in an elevated and normal temperature regime both for female and male roach (Rutilus rutilus) and perch (Perca fluviatilis).*

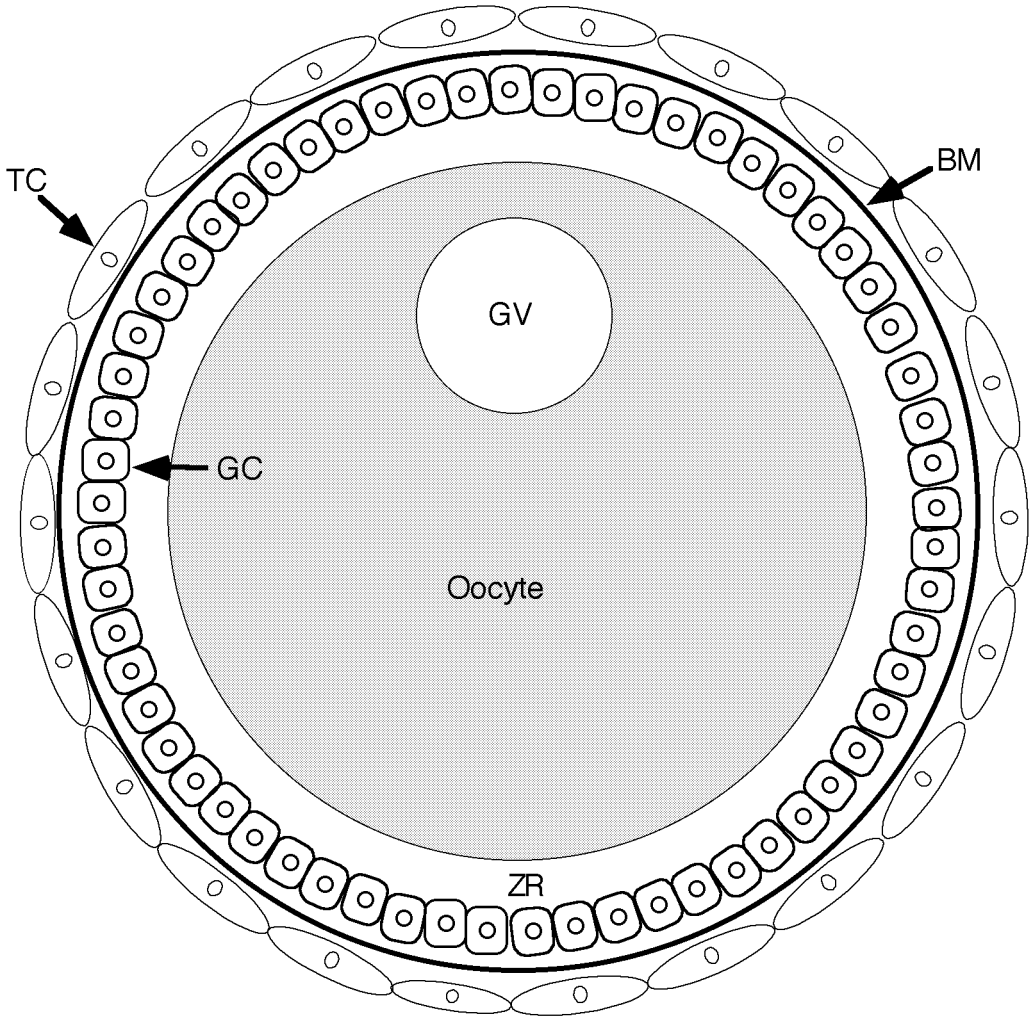

Figure 5*. A generalized figure of a full-grown, immature fish ovarian follicle (from Redding and Patiño 1993). The developing oocyte in the centre of the follicle has an acellular layer, zona radiata (ZR). A sublayer of granulosa cells (GC) surrounds this zona. The oocyte and the granulosa cells are interconnected by pore canals (microvilli) through the zona radiata, probably allowing nutrients and metabolic messengers to pass. The outer follicle layer consists of theca cells (TC), separated from the granulosa cell layer by a basement membrane (BM).*

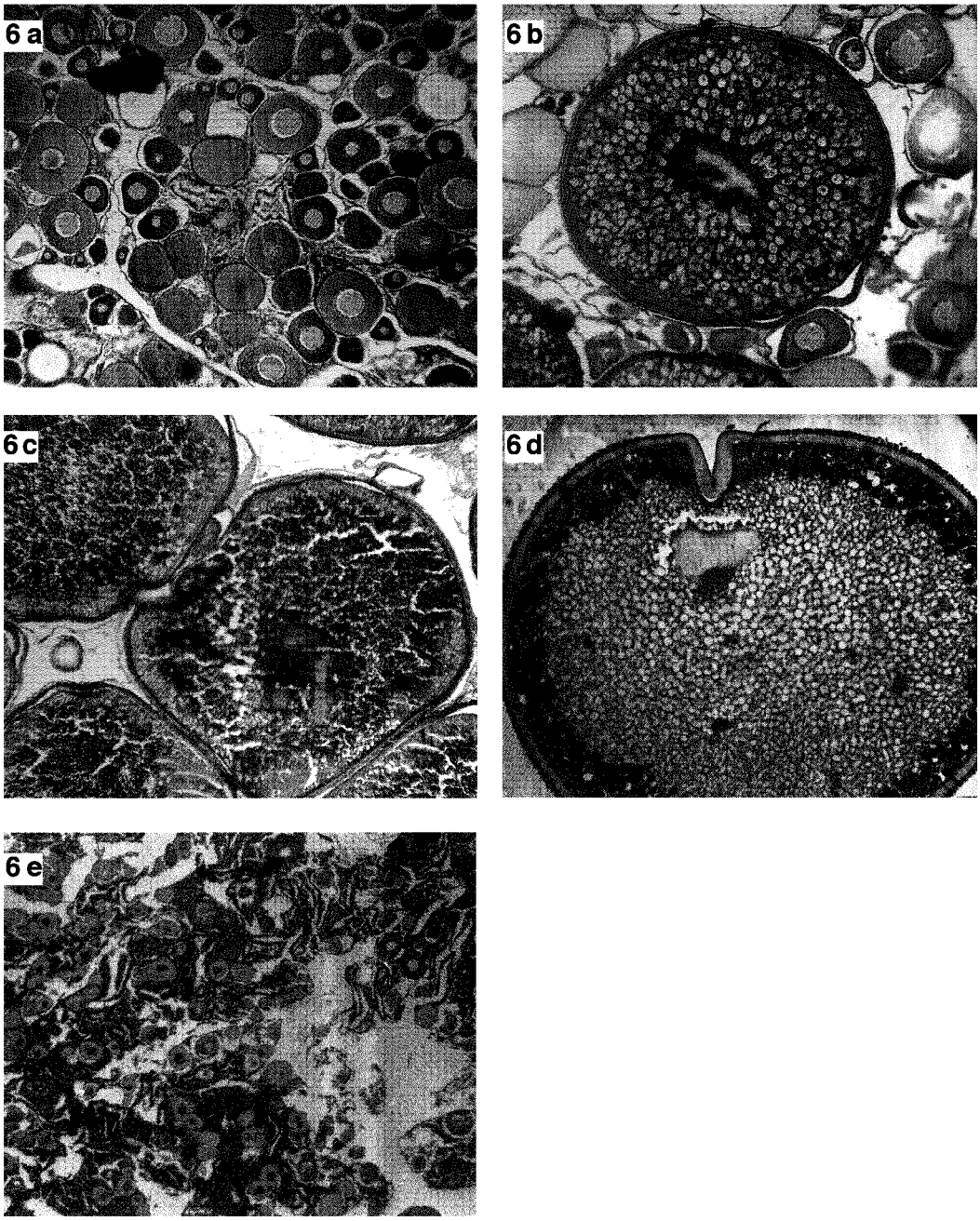

Figure 6*. The normal gonadal development in roach (Rutilus rutilus): a) stage II: The oocytes in cytoplasmic growth (June). b) stage III: The oocytes in vacuolation phase (August). c) stage IV: The oocytes are filled with trophic material (April). d) stage IV: The oocytes are mature. The nucleus is migrating to the animal pole. The micropyle is clearly seen. e) stage IV: The membran. f) stage VI: The follicles are empty after spawning and some oocytes in the cytoplasmic stage could be seen.*

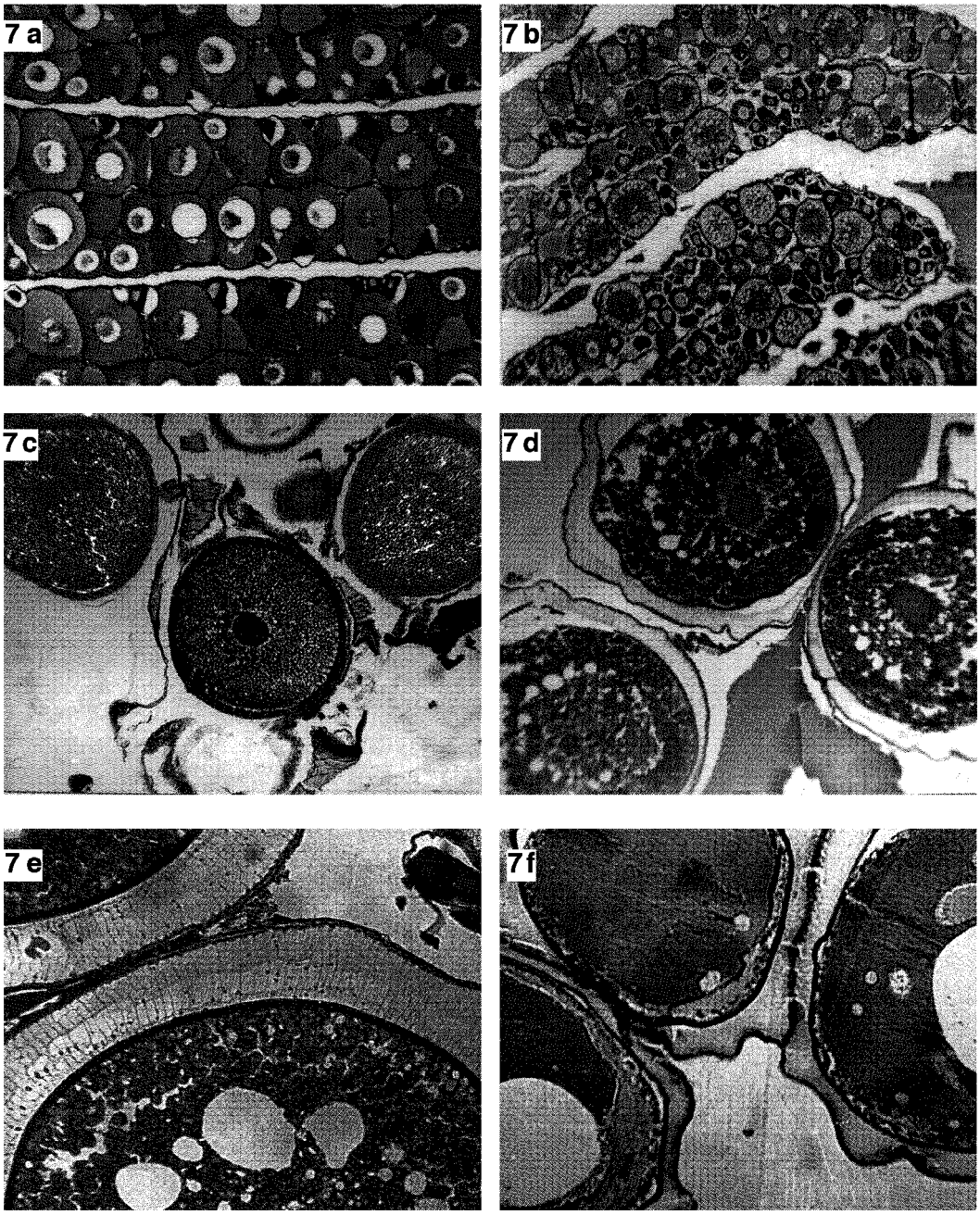

Figure 7. *The normal gonadal development in perch (Perca fluviatilis): a) stage II: The oocytes in cytoplasmic growth. b) stage III: The oocytes in vacuolation phase (August). c) stage IV: The oocytes in the stage of yolk and fat accumulation (October). d) stage IV: Formation of fat droplets. The nucleus is migrating to the animal pole (April). e) stage IV: The membrane. f) stage IV: The oocytes in the period of maturation. The yolk is homogenised. g) stage VI: The follicles are empty after spawning and some oocytes in the cytoplasmic stage could be seen.*

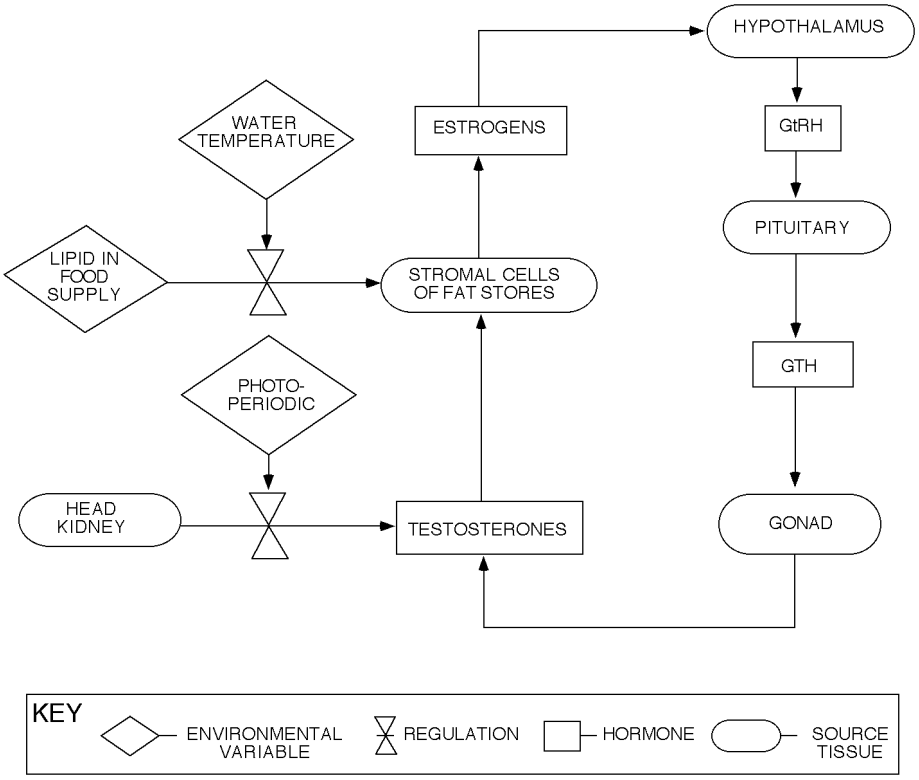

Figure 8*. A physiological model of the hormonal control of the maturation in Atlantic salmon (Salmo salar) (from Rowe et al. 1991). The model suggests that maturation in fish is environmentally regulated by two mechanisms; the size of the fat stores, depending on water temperature and food supply, and the photoperiod which allows the release of the inhibitor of the maturation process in spring. The model assumes a positive feedback loop by which oestrogens are produced by aromatization of androgens in the mesenteric fat stores during spring.*

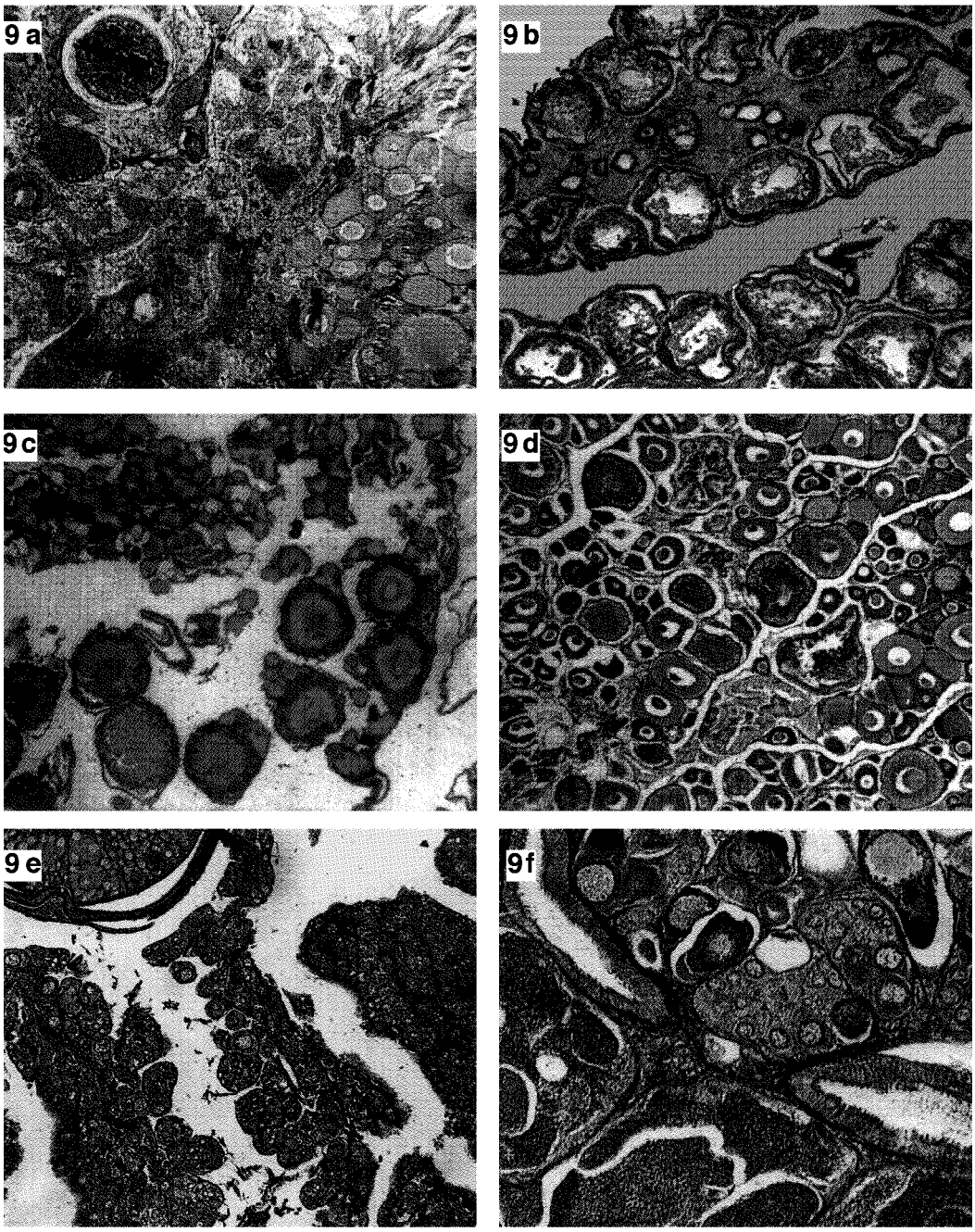

Figure 9. *Anomalies in the oogenesis in some temperate roach (Rutilus rutilus) due to raised temperature regimes: a) Total degeneration of oocytes at the trophoplasmic growth stage in October, Hamnefjärden (cooling water recipient) on the Swedish east coast b) Partial spawning: empty follicles, oocytes in cytoplasmic and trophoplasmic stages. In March, Hamnefjärden. c) Asynchronous development: oocytes are both in phases of vacuolation and yolk reservation. In October, Hamnefjärden. d) Non-seasonal maturation of sex cells: intensive reproduction of oogones, oocytes in cytoplasmic stage and also trophoplasmic stage. In April, Lake Drūkšiai, Lithuania. e) Hermaphroditism: oocytes in different degree of development at the cytoplasmic stage and ampullae with male sex cells at the end of spermatogenesis. In April, Lake Elektrènai, Lithuania. f) Oocytes with three nuclei. In May, the Biotest basin, at Forsmark on the Swedish east coast.*