Control of Gonad Growth, Maturation and Spawning in Teleost Fish: A Review

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Introduction

Despite their great variety of reproductive strategies, a general characteristic of most teleosts is that (where known) natural reproduction shows a long-term periodicity, even in tropical habitats (e.g. see contributions in Munro et al. 1990a). Typically, gonad development from puberty leads to fully-grown gonads by the advent of the spawning season; if conditions are appropriate, then final gonad maturation leads to the production of viable gametes during one or more breeding bouts. Subsequently, in those larger species which spawn over more than one season, the gonads regress and the individual returns to a phase where any growth is somatic. However, there is wide interspecific variability in the pattern of gonad development (Wallace and Selman 1981, de Vlaming 1983, Billard 1986, Selman and Wallace 1989).

The following recognizes two basic patterns in both sexes, although these represent the extremes of a broad spectrum. One pattern of gonad development is characterized by those species with a short, well-defined spawning season (e.g. salmonids). In both sexes, there is a synchronized development of a single cohort of gametes, which all pass as a wave through successive stages of gametogenesis to mature over a limited period; thereafter, the gonads return to the immature state until the next spawning season. This pattern of gonad development will be termed synchronous here, being comparable with the total spawner category of ecologists (e.g. Lowe-McConnell 1987).

The other extreme is typified by species which have a prolonged spawning season, during which each individual may breed several times. There is a more-or-less continuous recruitment and subsequent development of gametes in individual fish over a prolonged period before and during the reproductive period. Thus, all stages of spermatogenesis are present in males (Billard 1986); while ovaries show the presence of more than one cohort of growing oocytes (on the basis of their diameters) during much of this time. This pattern will be identified as asynchronous here; it can be compared with the ecologists' category of multiple (or batch) spawners.

Whichever pattern is exhibited, the responses of the gonads are under the control of components of the hypothalamus-pituitary axis. Section II briefly reviews recent advances in our understanding of the role of this neuroendocrine regulatory system.

In aquaculture, two contrasting types of problem can be identified in relation to the control of reproduction (Donaldson and Hunter 1983, Zohar 1989). On the one hand, captive breeding of a species may be desired but poses problems: for example, fish may not mature or spawn at all, they may be too seasonal, or else maturation may occur at inconvenient times. On the other hand, maturation may occur too readily in captivity, so that subsequent body growth is compromised and 'stunting', or even premature death, results.

There are two basic, but not necessarily mutually exclusive, approaches to solving such problems. One is by appropriate manipulations of the external environment to, for example, mimic the conditions normally found during the period of gonad development: if the correct cues are provided, then this should trigger the appropriate response. This approach is reviewed in section III. Alternatively, various technologies may be used to more directly mimic or otherwise influence one or more components of the neuroendocrine cascade of changes believed to be involved in transducing environmental cues into effects on gonad development. This approach will be reviewed in section IV.

II. Neuroendocrine regulation of reproduction

The classical regulatory control of gonad development is by way of the pituitary secretion of gonadotropic hormones (GtH). The following will review recent information on the nature of these and other pituitary hormones implicated in the regulation of gonadal development, together with how the brain regulates the secretion of these hormones, and how they in turn exert their effects on the gonads.

a. Pituitary hormones. Until recently, it was generally thought that the teleost pituitary produced only one type of glycoprotein GtH. However, there is increasing evidence that two distinct hormones, GtH I and II, are responsible for regulating gonadal development and final maturation in a variety of species (Kawauchi et al. 1989, 1991, Yu and Shen 1989, Swanson et.al. 1991, van der Kraak et al. 1992, Lin et al. 1992, Copeland and Thomas 1993, Tanaka et al. 1993). The fact that two GtH are also found in sturgeon (Moberg et al. 1991) suggests that this is the primitive condition.

Most information on the two GtH is for salmonids, where there is a switch from producing mainly GtH-I during the period of gonad growth to mainly GtH-II at the time of expected final maturation (Naito et al. 1991, 1993, Amano et al. 1993,

Saga et al. 1993). Immunohistochemical studies indicate that there are similar temporal differences in a clariid catfish (Zandbergen et al. 1993) and a poeciliid (Magliulo-Cepriano et al. 1994).

The GtH-II now generally recognised in salmonids and other species apparently corresponds to the single ('maturational') GtH of the older literature, so that most experimental studies consider only this hormone (Peter, 1993). GtH-I is a novel hormone, not to be confused with the 'vitellogenic GtH' previously described by Idler's group (since identified as the N-terminal portion of proopiomelanocortin: Idler et al. 1991). The dearth of information about the role of GtH-I represents a major lacuna in our understanding of the control of gonadal function.

There is accumulating evidence that one or more members of the 'pituitary acidophil' family of hormones - prolactin, growth hormone (GH) and somatolactin - may also play an important role in regulating gonad development in at least some teleosts. For example, circulating levels of GH are elevated during the latter portions of gonad growth in goldfish (Marchant and Peter 1986; Yu et al. 1991a) and also *Salmo salar* (Björnsson et al. 1994); this may not be the case for *Oncorhynchus mykiss* (Sumpter et al. 1991, cf. le Gac et al. 1993), where somatolactin levels are elevated during gonad development instead (Rand-Weaver et al. 1992, Rand-Weaver and Swanson 1993). Such peaks in GH levels are not associated with concommitant peaks in somatic growth (Marchant and Peter 1986, Perez-Sanchez et al. 1994).

The thyroid is an enigmatic gland: despite being diagnostic of vertebrates, it has no clearly defined role in fishes. Various reports (reviewed by Eales 1979, Leatherland 1982, 1986) suggest some role of the pituitary-thyroid axis in the modulation of gonad development in a variety of teleosts. One apparent exception may be salmonids (Cyr et al. 1988, Dickhoff et al. 1989), where it has been suggested that thyroid hormones are mainly involved in somatic growth and in switches of diet and/or habitat (Specker 1988).

Finally, there is evidence that the pituitary members of the proopiomelanocortin family (e.g. adrenocorticotropin: ACTH) may also play a role. The main evidence is for an inhibitory role: as discussed in section II.d, stress stimulates the adrenocortical tissue to produce corticosteroids through increased secretion of members of this hormone family (e.g. Pickering 1989, 1992).

b. Hypothalamic control mechanisms. The pituitary serves as a funnel by which a diversity of information integrated by the brain is converted into changes in the secretion of a limited number of signal hormones for regulation of targets in the body. Thus various populations of hypothalamic neurons, characterised by their use of different peptidergic or aminergic messengers, have been implicated in the regulation of GtH-II secretion (Fig. 1, Peter et al. 1991): there is no information available regarding the control of GtH-I secretion.

Of the known peptide modulators, the best characterized are the GtH-releasing hormones (GnRH). Different species of teleost have been reported to produce up to four different types of these peptides (Okuzawa et al. 1993, Sherwood et al. 1993), at least some of which are present in the innervation of the pituitary (Kah et al. 1993). Most experimental and applied work uses super-active analogues (e.g. Peter 1986, Peter et al. 1986, Murthy et al. 1994), where the amino acid sequence of the native GnRH have been appropriately modified to render them relatively resistant to inactivation by peptidases in the pituitary and elsewhere (Zohar et al. 1989); these may also have an increased affinity for receptors in the pituitary (Weil et al. 1992). For simplicity, the following will use 'GnRH' as an all-embracing term in considering this family of peptides together with their synthetic agonists.

As indicated in Fig. 1, there is evidence that other peptidergic neurones may contribute to the stimulatory regulation of the GtH-II cells: for example, neuropeptide Y (NPY) in salmonids and cyprinids (Breton et al. 1989, 1990, 1991, Peng et al. 1990, 1993a-c, Danger et al. 1991, Peter et al. 1991) and also cholecystokinin/gastrin (CCK/G) in goldfish (Himick et al. 1993). In the case of NPY, there is some evidence for differences in seasonal responses between salmonids and goldfish: while the secretion of GtH-II in response to this peptide increases during gonad development in goldfish (presumably as a result of positive steroid feedback: see below), NPY's control of GtH-II secretion in *O. mykiss* appears to be more subject to negative feedback from steroids (Breton et al. 1989).

The best studied of the aminergic modulatory mechanisms is the role of dopaminergic systems. Available evidence for goldfish suggests that activity in these inhibits both the activity of hypothalamic GnRH neurones and the responsiveness of GtH-II cells to GnRH, the effect being most marked in mature females (Peter et al. 1986, 1991). Thus, dopaminergic agonists block, and antagonists enhance, GnRH-induced elevations in GtH-II secretion; similar effects have been reported in a variety of other cyprinids, as well as some siluroids, an anguillid and two freshwater acanthopterygians (Peter et al. 1986, de Leeuw et al. 1986, Dufour et al. 1991, Gissis et al. 1991, also the indirect evidence of Ng et al. 1994). The existence of such an inhibitory dopaminergic control is less distinct in salmonids (Billard et al. 1984, van der Kraak et al. 1986), and is absent in those marine acanthopterygians studied (Copeland and Thomas 1989, Zohar, 1989). The effects of dopaminergic drugs, on their own, on basal GtH-II secretion rates are less clear (Kaul and Rishi 1986, Peter et al. 1986, de Leeuw et al. 1986).

Where investigated, there is evidence that other amines are generally excitatory, although their level of action (GnRH neurones vs. GtH-II cells) is unclear. Serotoninergic agonists facilitate GtH-II secretion at all stages of ovarian development in goldfish (Somoza et al. 1988, Somoza and Peter 1991, Yu et al. 1991b), but only in females with fully-developed gonads of a marine
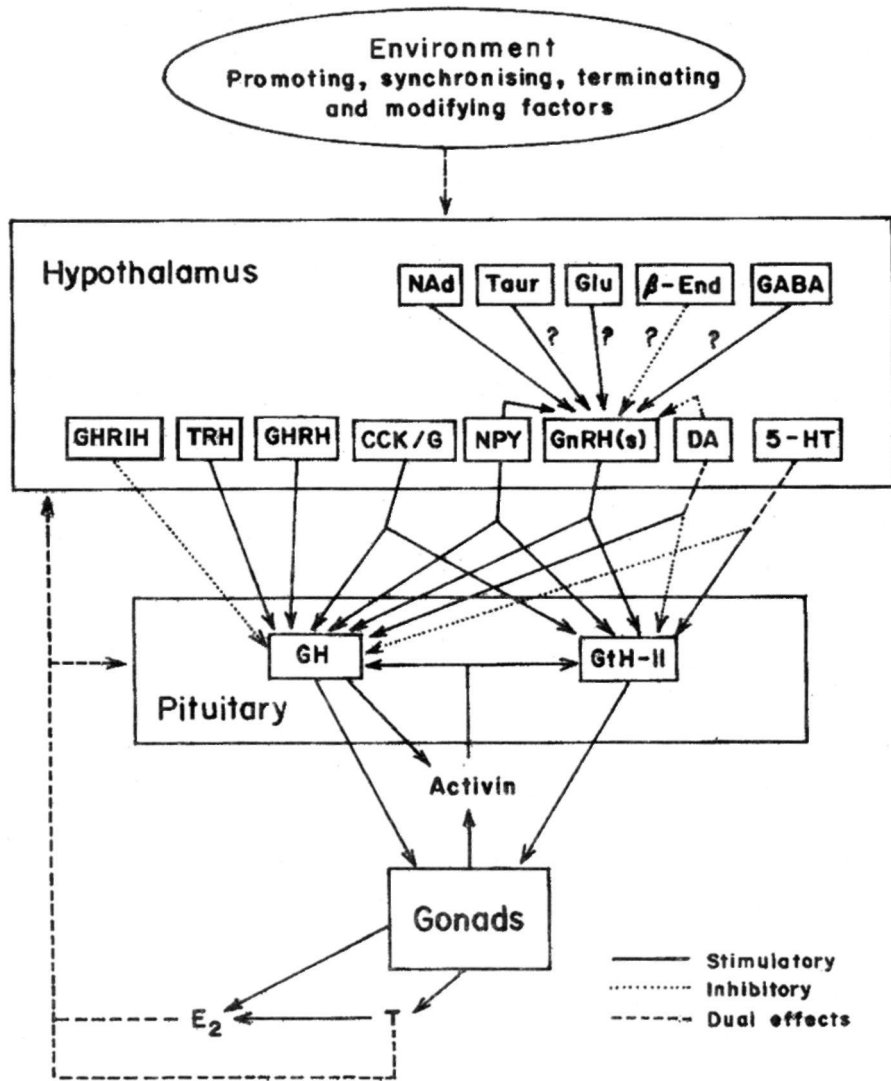
Fig. 1. Summary of the known regulatory controls of the pituitary-gonad axis, mainly based on studies in Peter's lab on goldfish (see text for details). CCK/G, cholecystildnin/gastrin; DA, dopamine; E$_2$, oestradiol; ß-End, ß-endorphin; GABA, τ-aminobutyric acid; GH, Growth hormone; GHRH, GH-releasing hormone; GHRIH, somato-statin; Glu, glutamate; GnRH(s), GtH-releasing hormone(s); GtH-II, gonadotropin II;5-HT, serotonin; NAd, noradrenaline; NPY, neuropeptide Y; T, testosterone; Taur, taurine; TRH, thyrotrophin-releasing hormone.

acanthopterygian (Khan and Thomas 1992, 1994). Noradrenergic systems are facilitatory in goldfish with regressed or early recrudescent ovaries (Chang et al. 1983, 1991, Chang and Peter 1984, Yu and Peter 1992). Where tested, serotoninergic and noradrenergic antagonists had no effect on basal GtH-II secretion (Chang et al. 1983, 1991; Chang and Peter 1984, Goos et al. 1987, Somoza et al. 1988, Khan and Thomas 1992); this suggests a modulatory, rather than a primary regulatory, role.

There is evidence that certain neuromodulatory amino acids - glutamate (acting via NMDA receptors), and more especially τ-aminobutyric acid (GABA) and taurine - may exert an excitatory influence over GtH-II secretion in goldfish, acting indirectly by way of the hypothalamus (Kah et al. 1992, 1993, Trudeau et al. 1993a, b, Sloley et al. 1992, 1994, see Fig. 1). There is also evidence for an indirect effect of NMDA agonists on GtH-II secretion in *O. mykiss* (Flett et al. 1994). Earlier studies indicated that monosodium glutamate results in local destruction of portions of the hypothalamus in goldfish, associated with a transient elevation of plasma GtH-II levels (Kah 1986). Such excitotoxic effects were not seen in the tilapia, *Oreochromis mossambicus* (Munro et al. 1990b).

Traditionally, the secretion of GH is considered to be under the dual control of growth hormone-releasing hormone and growth hormone release-inhibiting hormone (somatostatin) (Peter and Fryer 1983). However, recent studies on goldfish indicate that the range of hypothalamic controls for GH secretion has to be expanded to encompass all of those implicated in the regulation of GtH-II secretion (Fig. 1). Thus GnRH's also stimulate GH secretion (e.g. Lin et al. 1993, Murthy and Peter 1994), as do NPY (Peng et al. 1990, 1993a-c, Peter et al. 1991) and CCK/G (Himick et al. 1993). On the other hand, dopamine stimulates (Lin et al. 1993, Wong et al. 1993a, b), and noradrenaline and serotonin inhibit (Somoza and Peter 1991), GH secretion in cyprinids: effects opposite to those on GtH-II secretion (see above). In the case of dopamine, the GH cells are likely to be more sensitive than those secreting GtH-II, on the basis of the characteristics of their respective receptor-subtypes (Omeljaniuk and Peter 1989, Wong et al. 1993c).

In contrast, available data for the salmonid *O. mykiss* suggest that dopamine does not affect GH secretion (Flett et al. 1994); while there are conflicting reports regarding the efficacy of GnRH on GH secretion (le Gac et al. 1993, Flett et al. 1994).

Little is known about the control of pituitary thyroid-stimulating hormone secretion in teleosts. Evidence suggests that the predominant hypothalamic control may be inhibitory, and that somatostatin may be one component (Peter and Fryer 1983).

 c. Pituitary regulation of gonad function. Vertebrate GtH are considered to exert most of their actions indirectly, by way of gonadal steroids as transducers. Thus, there is evidence that C_{18} ('estrogenic') and C_{19} ('androgenic') steroids are mainly involved in the gonadal growth processes of females and males, respectively; and that there is a switch to the production of C_{21} ('progestagens') steroids, in response to elevated GtH-II levels, during the subsequent final maturation processes in both sexes (reviewed by Kime 1993). Fig. 2 provides a general summary of the pathways involved in teleost steroidogenesis.
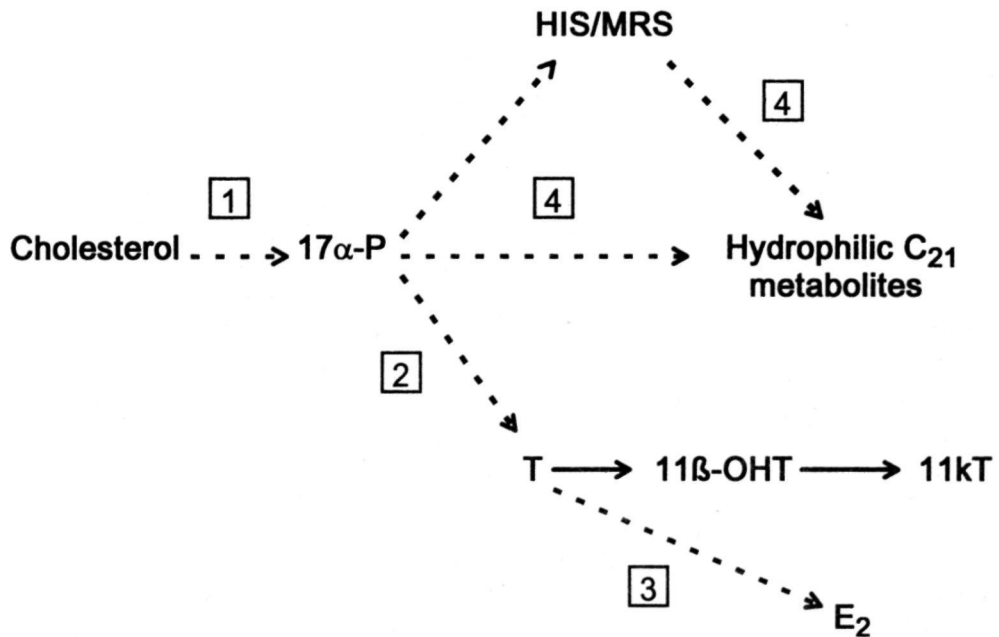

Fig. 2. Summary of the main steroids involved in the regulation of reproduction. 17α-hydroxyprogesterone (17α-P) is produced from cholesterol through a sequence of enzymes (1), and is in turn converted to testosterone (T) by another series of enzymes (2) in immature gonads. In turn, T acts as the precursor for the principal androgens - 11ß-hydroxytestosterone (11ß-OHT) and 11-ketotestosterone (11kT) - and, by aromatization (3), estrogens such as estradiol (E2). During final gonad maturation, the increased production of 17α-P leads to the synthesis of other, hydration-inducing (HIS) and maturation-resolving (MRS) C_{21} steroids; prior to this, the activity of various other enzymes instead leads to the production of inactive metabolites which, being hydrophilic, are readily excreted.

There is some evidence the two GtH may differ in their affinity for different receptor populations in the salmonid post-vitellogenic ovary, and thus possibly in their biological actions (Yan et al. 1991, 1992). Nevertheless, available evidence indicates that they have broadly similar steroidogenic activities in salmonids (reviewed by Planas et al. 1993) and cyprinids (van der Kraak et al. 1992).

Members of the pituitary acidophil family (GH, prolactin and somatolactin) may either stimulate steroidogenesis or (goldfish) potentiate it in response to GtH-II (Singh et al. 1988, van der Kraak et al. 1990, le Gac et al. 1992, 1993, Planas et al. 1992, Rubin and Specker 1992, Singh and Thomas 1993, see below). The hormone(s) involved may vary with species.

There is some evidence that thyroid hormones may promote gonadal steroidogenesis in a diversity of teleosts, including salmonids (e.g. Cyr and Eales 1988, Jana and Bhattacharya 1993, Soyano et al. 1993).

i. Males. Like gonadotropic preparations, repeated injections of both salmon GH and salmon prolactin have been found to maintain testicular weights in hypophysectomized *Fundulus heteroclitus* (Singh et al. 1988). Consistent with the notion that steroids act as transducers for pituitary hormones (Fig. 3), high doses of testosterone have also been found to maintain most or all stages of spermatogenesis in hypophysectomised teleosts (reviewed by Fostier et al. 1983, Billard 1986). Similarly, in vitro studies on goldfish indicate that testosterone is able to induce and sustain spermatogenesis (Remacle 1976, de Clercq et al. 1977). The role of androgens has been most clearly demonstrated in the eel, *Anguilla japonica,* where 11-ketotestosterone (but not the other androgens tested, or Cortisol) stimulated complete spermatogenesis in vitro (Miura et al. 1991a, b, 1992). Non-steroidal transducing elements may also play a role: there is evidence that insulin-like growth factors (IGF) stimulate spermatogonial proliferation in salmonids, although their origin and the nature of their secretory control remains to be determined (Loir and le Gac 1994). Nothing is known about any differences in the endocrine control of spermatogenesis between synchronous and asynchronous species.

Final maturation in males is associated with testicular hydration (often incorrectly referred to as 'spermiation': see Baynes and Scott 1985, Grier 1993), where secretion of fluid into the lumen of the testes leads to increased milt volumes with a decrease in the concentration of sperm. This is associated with elevated GtH-II levels; GH may also play a role (le Gac et al. 1992, 1993). These hormones stimulate the production of a hydration-inducing steroid (HIS, Fig. 3), responsible for seminal thinning and priming sperm motility (through increasing the pH of the semen). HIS include 17α,20ß-dihydroxy-4-pregnen-3-one (17α,20ß-P) in salmonids (Ueda et al. 1984, Sakai et al. 1989, Miura et al. 1992) and anguillids (Miura et al. 1991b); and its epimer, 17α,20α-P , in cyprinids (Barry et al. 1990a). However, it should be noted that GtH-II also has direct (apparently steroid-independent) actions on salmonid

testicular duct epithelium, to stimulate ion pumps which may thus contribute to hydration (Marshall et al. 1993).

Evidence for salmonids (Ueda etal. 1985), anguillids (Miura et al. 1991b) and cyprinids (Asahina et al. 1990, 1993, Barry et al., 1990a, b) indicates that the HIS is produced by a 20-dehydrogenase present in the spermatozoa (although these may not be the only testicular source of this enzyme: Loir 1988, Sakai et al. 1989, Miura et al. 1991b, Vizziano et al. 1991). Normally, the production of HIS appears to be limited by the presence of other enzymes, in somatic cells, which generate inactive metabolites (Fig. 2). However, an increase in the pool of 17α-P produced by the somatic cells, as a result of the elevated GtH-II levels, saturates both the biosynthetic pathway towards androgen biosynthesis and the shunt systems producing inactive metabolites (Abdullah and Kime, 1994); as a consequence, excess 17α-P leaks out into the lumen of the testes to become available to the 20-dehydrogenase present in the spermatozoa (Barry et al. 1990a, b, Fig. 3). Subsequently, the availability of 17α-P is further increased by HIS switching off the enzymes associated with androgen production (Barry et al., 1990a, b).

ii. Females. The main portion of ovarian growth is mediated by estrogens in response to gonadotrophic stimulation; GH also appears to be involved (Singh et al. 1988). Estrogens are important for the hepatic production of the yolk-precursor vitellogenin (reviewed by Mommsen and Walsh 1988, Selman and Wallace 1989) and precursors of the egg-envelope or 'chorion' (Larsson et al. 1994, Murata et al. 1994, Oppen-Berntsen et al. 1994). There is evidence that other hormones may have a facilitatory or permissive action on the liver during vitellogenesis. Thus hypophysectomy attenuates the hepatic vitellogenic response to exogenous estradiol in male *Oreochromis mossambicus* (Munro et al. unpubl.), and blocks it in anguillids (Burzawa-Gerard and Dumas-Vidal 1991); experiments on the latter implicate GH and/or prolactin (Kwon and Mugiya 1994), recalling the importance of GH in reptiles (Ho 1986, Callard et al. 1990). Thyroid hormones may also play a role in some species: whilst tri-iodothyronine (T_3) was found to have no effect on oestradiol-induced production of vitellogenin by salmonid hepatocytes in vitro (Kwon et al. 1993), T_3 and/or thyroxine have been found to enhance oestradiol-induced hepatic vitellogenesis in vivo in goldfish and some, but not all, of a variety of small tropical teleosts (Munro et al. in prep.).

Uptake of vitellogenin is mediated by specific receptors in the oocyte membrane (Stifani et al. 1990, Chan et al. 1991, le Menn and Rodriguez 1991, Tyler and Lancaster 1993, Lancaster and Tyler 1994). The process is dependent on pituitary hormones, although their role is not known: whilst both GtH may be involved in goldfish (van der Kraak et al. 1992), only GtH-I appears to be implicated (during the first portion of ovarian growth) in salmonids (Tyler et al. 1991). Insulin and thyroxine have also been reported to stimulate vitellogenin uptake in salmonids

(Nagahama et al. 1993), as has the N-terminal portion of proopiomelanocortin in these and other teleosts (Idler et al. 1991).
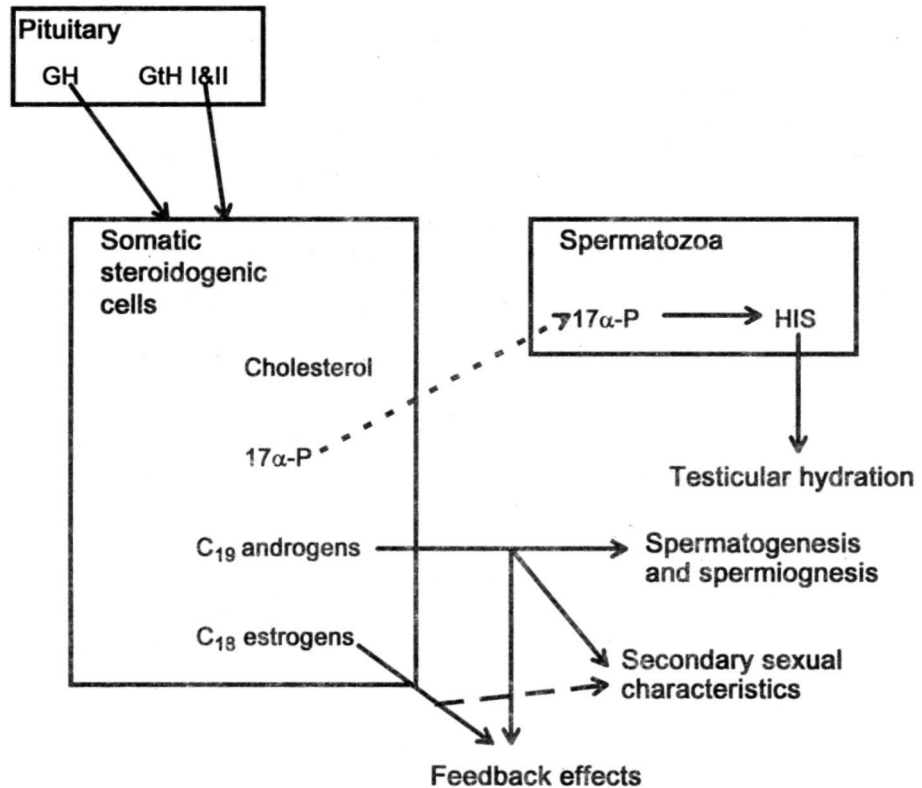

Fig. 3. Summary of the known endocrine controls of reproductive development in male teleosts. Somatic testicular cells - Leydig and possibly Sertoli cells - are responsible for producing the androgens and estrogens (see Fig. 2) involved in most aspects of reproductive development. Testicular hydration results when increased production of the precursor 17α-P leads to spill-over which can be converted by enzymes in the sperm to the HIS.

Having completed vitellogenesis, a female is ready to undergo final oocyte maturation and ovulation (FOM-O) as a prelude to imminent mating. FOM-O occurs in mature females as a result of a GtH-II surge (reviewed by Goetz 1983, Aida 1988, Kime 1993), which is usually triggered by specific environmental stimuli (see section III.c); GH may also play a role (le Gac et al. 1993). The result of a GtH-II surge is to stimulate two more-or-less distinct sets of processes (Goetz 1983): final oocyte maturation (FOM) and the discharge of the oocyte from the follicle (ovulation).

FOM includes the migration of the oocyte nucleus (germinal vesicle) to the future animal pole, and then its breakdown for the resumption of meiosis. There is generally also oocyte hydration, especially in marine fish with pelagic eggs, mediated in part by active uptake of monovalent cations, and probably also by yolk proteolysis in some species (Greeley et al. 1986, 1991, McPherson et al. 1989, Selman and Wallace 1989, LaFleur and Thomas 1991, Thorsen and Fyhn 1991, Wallace et al. 1992).

In turn, the processes associated with FOM can be divided into two stages. The first of these is steroid-independent (e.g. Kobayashi et al. 1988, Zhu et al. 1989, Patiño and Thomas 1990a, Kagawa et al. 1994a), although it may be facilitated by testosterone (e.g. Patiño and Thomas 1990a, Truscott et al. 1992); whilst the second stage is mediated by certain C_{21} steroids, termed here maturation-resolving steroids (MRS: the growing evidence for a two-phase effect of GtH-II on FOM, with the first being steroid-independent, would seem to render the traditional term 'maturation-inducing steroid' inappropriate).

During the first stage, GtH-II initiates germinal vesicle migration towards the periphery of the oocyte, together with RNA and protein synthesis (e.g. Nagahama 1987, Patiño and Thomas 1990a, Kagawa et al. 1994a, King et al. 1994); the latter may include the production of membrane receptors for MRS in the oocytes of some species (e.g. Kobayashi et al. 1988, Zhu et al. 1989, Patiño and Thomas 1990c, Thomas and Patiño 1991), although such receptors may already be present in others (Yoshikuni et al. 1993b, Selman et al. 1994). There may also be an increase in levels of enzymes required for the synthesis of the MRS by the follicle wall, at least in salmonids (Nagahama 1987, Nagahama and Yamashita 1989, Nagahama et al. 1993).

Having completed the first stage and thus attained maturational competence (Patiño and Thomas 1990a), the MRS produced by the follicle in response to continuing elevated GtH-II levels is responsible for initiating a second suite of effects, associated with germinal vesicle breakdown and completion of the first and most of the second meiotic division (Nagahama et al. 1993). The best characterized MRS are 17α,20ß-P in salmonids (Nagahama 1987) and 17α,20ß,21-tri-hydroxy-4-pregnen-3-one (17α,20ß,21-P; 20ß-dihydro-11-deoxy-cortisol) in sciaenids (Thomas and Tran, 1989, Patiño and Thomas 1990b, c). These and similar C_{21} steroids have been proposed to be the MRS in other species also, with some suggestion that more than one MRS may be involved in certain species (reviewed by Kime 1993, see also, for example, Truscott et al. 1992, Petrino et al. 1993, Yoshikuni et al. 1993, King et al. 1994a, b, Selman et al. 1994).

As with males, there is evidence that the GtH-II surge is associated with increased production of 17α-P by the follicle, and that the increased availability of the latter affects the profile of C_{21} steroids produced in cyprinids (Kime and Abdullah 1994, Kime et al. 1994). Thus, with low levels of 17α-P substrate, any C_{21}

derivatives produced are inactive polar metabolites; as substrate availability is increased, the enzymes responsible for producing these metabolites become saturated (due to their low capacity), thereby allowing production of the relevant MRS in sufficient quantities for biological activity (Kime 1992, Kime and Abdullah 1994). The enzymes responsible for the production of inactive C_{21} metabolites may thus serve to sharpen the MRS response to elevations in GtH-II, as well as restricting the locus of action to follicles undergoing FOM-O in species with asynchronous ovaries (Kime 1990, Petrino et al. 1993). Furthermore (as with HIS in the male), the initial rise in MRS production may, in turn, switch off androgen and oestrogen production by the follicle; this would further increase the availability of 17α-P and, consequently, MRS production (Kanamori et al. 1988).

There is in vitro evidence that various other C_{21} steroids, including those which are generally labelled as corticosteroids, may play some modulatory role during FOM-O (e.g. Jalabert 1976, Goetz 1983, Jalabert and Fostier 1984a, b); these steroids may be produced by the ovary itself (reviewed by Kime 1993). Available evidence indicates that, whatever their source, physiological levels of Cortisol may also be capable of acting as an MRS in at least some species (e.g. Patiño and Thomas 1990b, c). Moreover, the adrenocortical tissue is also responsive to GtH-II stimulation in salmonids (Schreck et al. 1989), and produces significant amounts of 17a,206-P in mature fish of both sexes (Sangalang and Freeman 1988). As an extension of such observations, adrenocortical secretions (possibly in response to stimulation by GtH-II rather than ACTH) have been implicated as the main control of FOM in the Indian catfish, *Heteropneustes fossilis* (Sundararaj and Goswami 1977); this contrasts with African *Clarias* catfish, where the ovary is apparently the source of MRS (Schoonen et al. 1989).

In many teleosts, a peak in testosterone occurs before or during the onset of FOM-O, in association with decreasing oestradiol levels (e.g. Aida 1988, Tamaru et al. 1991, Marte and Lam 1992, Kime 1993, Malison et al. 1994); this is apparently the result of a decrease in aromatase activity in salmonids (Nagahama et al. 1993). In species with asynchronous ovaries, this testosterone peak is often followed by a rise in oestradiol levels during the latter portions of FOM-O; the latter is presumably produced by smaller, still-growing follicles in response to the rising GtH-II levels (e.g. Kobayashi et al. 1987, Aida 1988, Zairin et al. 1992). The functional significance of the testosterone peak in the interregnum between the completion of vitellogenesis and FOM-O is not clear. As noted by Kime (1993), it is to be expected that estrogen production (and thus hepatic vitellogenesis) should fall off as soon as possible (at least in species with synchronous ovaries), to minimise the costs associated with producing excess vitellogenin over and above that required for oocyte growth. Hence a switch to androgen production may merely reflect the continuing need for steroidal feedback to modulate GtH-II secretion, and thus possibly prevent 'spontaneous' FOM-O in most teleosts (see below). Moreover, this feedback by testosterone may play a role in priming the pituitary for generating a

GtH-II surge in response to relevant environmental cues (e.g. Kobayashi et al. 1987, 1988, 1989, Trudeau et al. 1993c, see below). In addition (or alternatively), androgens may act within the ovaries themselves to regulate oocyte responsiveness (e.g. Jalabert and Fostier 1984a, b, Goswami et al. 1985, Patiño and Thomas 1990a, b, see above): this contrasts with that oestrogens inhibit (premature) FOM in salmonids (Jalabert 1975), but not in those asynchronous species studied (e.g. Pankhurst and Stacey 1985, Kobayashi et al. 1987, Matsuyama et al. 1988, 1990a, Patiño and Thomas 1990b).

Hormones other than steroids may play a role in regulating FOM-O. For example, the thyroid hormone tri-iodothyronine (T_3) is effective on its own in inducing in vitro FOM-O in carp, as well as enhancing the response to the candidate MRS (Epler and Bienarz, 1983). Similarly, insulin may increase the effectiveness of C_{21} steroids in inducing FOM in goldfish (Lessman 1985): it is not clear whether this action is the result of increased MRS production. In a sparid, insulin and IGF have direct actions on oocytes to induce FOM; lower dosages of these peptides were ineffective on their own, but they acted synergistically with the putative (but itself ineffective?) MRS (Kagawa et al. 1994b).

The second process associated with FOM-O, ovulation, is mediated by prostaglandins of the F series; available evidence (Fig. 4) indicates that these may be produced by the adjoining epithelium lining the oviducal lumen; this is in response to the MRS in some species, whereas there is evidence for a direct effect of GtH-II in others (Goetz 1983). These prostaglandins induce contractions of the follicle wall, together with other actions to facilitate oocyte expulsion into the ovarian lumen (Goetz 1983, Goetz et al. 1989, Berndtson et al. 1989). They also serve as signals to the brain in oviparous species, where they induce spawning behavior in the presence of a male (Stacey and Goetz 1982); presumably, this is to ensure that the ova can be fertilised as soon as possible after ovulation, to minimize the risk of their over-ripening (see section III.c).

d.   **Feedback control of pituitary activity.**   In contrast to maturing salmonids (reviewed by Peter 1983), recent studies suggest that steroidal negative feedback at the level of the hypothalamus or pituitary (cf. testes) may be normally of little significance in cyprinids (Kobayashi and Stacey 1990, Trudeau et al. 1991a, b, 1993c, d).

In addition to the traditional concept of negative feedback (which could be mediated by dopaminergic systems in cyprinids: Trudeau et al. 1993e), a positive feedback by estrogens and aromatizable androgens has also been described for teleosts, with two basic types recognisable on the basis of available information. In salmonids of both sexes (e.g. Crim and Evans 1983, Magri et al. 1985, Goos et al. 1986, Amano et al. 1994a) and female anguillids (Dufour et al. 1988, 1989, Quérat et al. 1991), these steroids stimulate the synthesis, and possibly the release (in the

long-term), of GtH-II in juveniles; where known, there is no increase in GtH-I synthesis, in contrast to natural puberty (Dickhoff and Swanson 1990, Amano et al. 1994b).   There also may be an increase in GnRH synthesis in male salmonids (Amano et al. 1994a) and female anguillids (Dufour et al. 1993).
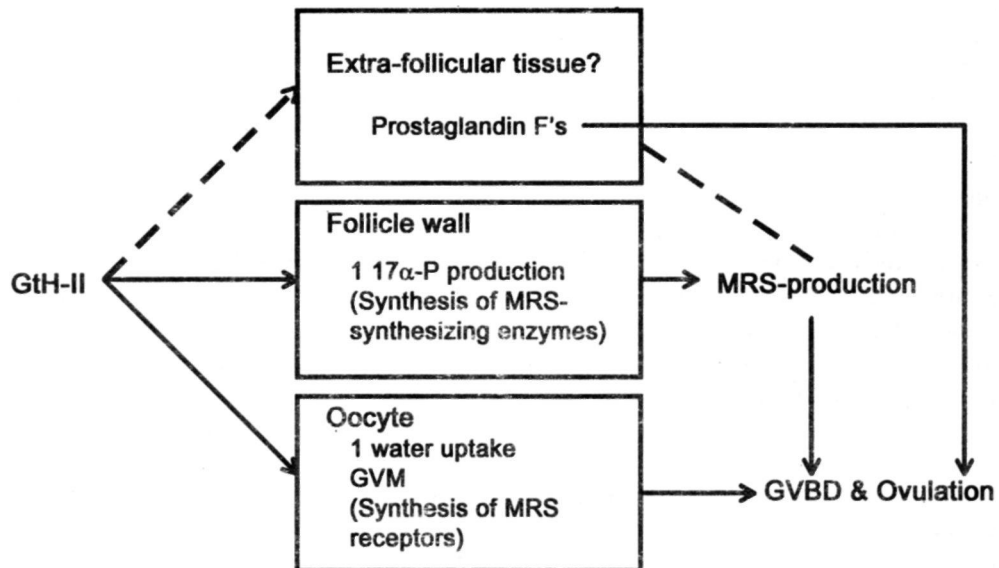

Fig. 4   Summary of known endocrine controls of the processes associated with final oocyte maturation and ovulation (see text for details); dotted lines indicate uncertain (species-variable?) actions.   GVBD, germinal vesicle breakdown; GVM, germinal vesicle migration; MRS, maturation-resolving steroid; 17α-P, 17α-hydroxyprogesterone.

Another type of positive feedback by aromatizable androgens, in particular, has been described in goldfish and some related species: these do not affect GtH-II synthesis, but promote the secretory response of GtH-II cells to GnRH and NPY (Kobayashi and Stacey 1990, Trudeau et al. 1991a, b, 1993a-e), with evidence for theopposite in the case of CCK/G (Himick et al. 1993).   These actions may be mediated in part at the level of the hypothalamus, through effects on several systems: for example, the activation of GABAergic and taurinergic systems (Kah et al. 1992, Trudeau et al. 1992, 1993a, b), as well as through enhanced synthesis of NPY (Peng et al. 1994), together with an increased sensitivity of GnRH neurones to this peptide (Peng et al. 1993b, c).

Perhaps reflecting the overlap in hypothalamic controls of GtH-II and GH in cyprinids, there is also evidence for a positive feedback of oestrogens on GH cell activity in goldfish: both basal circulating levels of GH and the secretory response of the GH cells to GnRH and NPY are increased by sex steroids, although that to dopamine is reduced (Trudeau et al. 1992, Peng et al. 1993b, Wong et al. 1993b). There is also evidence that oestradiol stimulates GH cell activity in the cichlids, *Aequidens pulcher* (Munro unpubl.) and *Oreoehromis mossambicus* (Poh et al. in prep.). Again, the salmonid *O. mykiss* appears to be an exception, since oestradiol is reported to depress GH secretion (le Gac et al. 1993, Björnsson et al. 1994).

Apart from the feedback of steroids, there is evidence for a gonadal positive feedback by a dimeric peptide, activin, on both GtH-II and GH secretion in goldfish (Ge and Peter 1994a, b). Furthermore, activin is also produced by the GH cells; presumably it acts in a paracrine fashion to stimulate the secretion of both GtH-II and GH in goldfish (Fig. 1, Ge and Peter 1994a, b).

ID. Reproductive control through manipulations of the external environment

a.   General.   From the onset of puberty or gonad recrudescence, a reproductive cycle comprises three main transitions, with each generally occurring at a predetermined time of year: (i) gonad growth, (ii) one or more spawning episodes and then (iii) gonad regression (section I).   While there may be an underlying endogenous rhythmicity regulating some or all of these transitions, synchrony with the environment is achieved by tracking particular external factors ('cues').   In the following, we briefly consider how this is accomplished in wild populations, and thus how the relevant cues may be used to manipulate captive populations under controlled conditions.

b. Gonad growth. Under natural conditions, this is initiated and maintained by relatively general environmental changes (e.g. daylength and/or temperature at higher latitudes); the variables used constitute the predictive or promoting cues of Munro (1990a, Munro and Lam 1990). Promoting cues presumably act by way of the activation of GnRH neurons (Amano et al. 1994b), at least.   Different sets of promoting cues may be involved for initiating different stages of ovarian development, but the evidence is not clear (Munro and Lam 1990).

Photoperiod has been identified as the promoting cue in some temperate species: for example, salmonids (reviewed by Bromage et al. 1990, Scott 1990), sticklebacks (reviewed by Baggerman 1990), and certain marine teleosts (reviewed by Bye 1990). Where known, changes in relative daylength act by entrainment of an internal circannual clock for gonad growth. Thus, photoperiod regimes can be used to influence the onset and rate of gonad development (as assessed by spawning time)

in salmonids (e.g. Pohl-Branscheid and Holz 1990, Davies et al. 1991, Randall et al. 1991, Duston and Saunders 1992, Johnston et al. 1992, Beacham and Murray 1993, Beacham et al. 1994, Gillet 1994), the European sea-bass (*Dicentrarchus labrax:* Zanuy et al. 1991, Carrillo et al. 1989, 1991) and certain marine flatfish (*Scophthalmns maximus* - Bye 1990, *Hippoglossus hippoglossoides* - Smith et al. 1991).

Alternatively, various other temperate fresh- and brackishwater teleosts appear to be less dependent on photoperiod: temperature also plays a role. This appears to be the case for many temperate cyprinids (reviewed by Hanyu et al. 1983, Razani et al. 1989, Hontela and Stacey 1990, Munro and Lam 1990, Aida et al., 1991), cyprinodonts (e.g. Lin et al. 1989, Taylor 1990), oryziids (Awaji and Hanyu 1989) and mugilids (Kelley et al. 1991). There is a suggestion of intraspecific latitudinal variability in the role of particular cues (Lin et al. 1989, Awaji and Hanyu 1989), and generally no clear evidence for any underlying circannual rhythmicity. However, there is evidence for an endogenous component in some Japanese cyprinids (Munro and Lam 1990), best known for some species of bitterling (Shimizu and Hanyu 1993, Shimizu et al. 1994).

For tropical teleosts, the limited information available on possible promoting cues is largely restricted to freshwater species; endogenous rhythms may form an important underlying control mechanism in large species without parental care (Munro, 1990b). Amongst abiotic factors, temperature has been identified as the main variable entraining the circannual clocks in a population of an Indian catfish, *Heteropneustes fossilis,* towards the northern extreme (30° N) of its range; photoperiod may also play a less important role (Sundararaj and Vasal 1976, see also Munro 1990b). Changes in conductivity (presumed to indicate flooding) have been implicated in two groups of electroceptive teleosts (Kirschbaum 1979, 1984, 1987); however, there is little evidence that this is a relevant cue in a number of other small species (Munro and Lam 1990, Ng and Munro 1994, and in prep.).

c. **Final gonad maturation.** In some species, this is presumed to occur spontaneously: for example, salmonids (Scott 1990). However, in the majority of species, there is evidence that various external cues are used by mature individuals in order to ensure that final maturation occurs shortly before the anticipated arrival of suitable spawning conditions; these synchronising cues are generally more specific and 'local' than are the promoting cues responsible for regulating gonad growth (Munro 1990a, Munro and Lam 1990). Presumably, synchronizing cues induce a GtH-II surge through increased activity of GnRH neurons, together with an inhibition of dopaminergic activity in some teleosts at least (see section II.b). This more precise timing is important in view of evidence for most teleosts studied to date (with the exception of salmonids, clupeids and some pleuronectids) that the oocytes, in particular, are short-lived once they have been ovulated (Billard 1986, Billard et al. 1986). Thus 'over-ripening' generally leads to a rapid decrease in viability after ovulation (Howell and Scott 1989, Formacion et al. 1993); although this may be

delayed by treatment with progestagens (Formacion et al. 1995), it implies that spawning should generally occur as soon as possible after FOM-O.

The role of synchronising cues is best-documented for female goldfish, where FOM-O can be induced by either an elevation in temperature (e.g. from 12 to 20 °C) or the introduction of plants as a spawning substrate; a male is not necessary (Stacey et al. 1979). In *Cyprinus carpio,* rising temperatures and the presence of a male may be important (Davies et al. 1986, Lin et al. 1986, Aida 1988). These cues presumably mimic the onset of flooding in spring, when natural spawning occurs over freshly-inundated areas of vegetation (Horváth 1985). Irrespective of the time of application of the synchronising cue, ovulation always occurs during the expected night in both species, so that spawning occurs around the anticipated dawn (Stacey et al. 1979, Aida 1988). If females of either species are maintained under constant warm temperatures, they undergo a series of spontaneous ovulations, which are synchronised in the case of groups of female goldfish (Davies and Hanyu 1986, Kobayashi et al. 1988).

Another example where adequate temperatures and the provision of a suitable spawning site stimulate natural breeding is the Murray cod (*Macullochella peeli*)*,* an Australian freshwater serranid which spawns at the end of the dry season. Pairs lay eggs in a suitable cavity, and then guard them, once temperatures exceed 20 °C. The onset of spawning can apparently be accelerated by providing iron drums, laid on their sides, as spawning sites: if part of the side of the drum is above water, exposed to the sun, the the water inside warms up faster and pairs will consequently spawn earlier (Cadwallader et al. 1979).

Many large species of tropical fish breed only during flooding, when suitable spawning sites are created; it has been suggested that compounds leached from inundated, previously dry soils serve as synchronizing cues but, if so, then their chemical nature has yet to be confirmed (reviewed by Munro 1990b). This would explain one technique for stimulating natural FOM-O and spawning of large tropical cyprinids and catfish: ponds are left to dry in the sun for a period, and then filled with water, after which the mature broodstock are introduced (e.g. Knud-Hansen et al. 1990, reviewed by Munro 1990b). Various Australian freshwater fishes can also be induced to spawn by this technique, provided that temperatures also show a rapid sustained rise to above a critical threshold (Lake 1967). A combination of short-term reduction in water level with concurrent transient increase in temperature has been used to induce pond-spawning in *Lates calcarifer;* the changes may mimic a tidal cycle (Kungvankij and Suthemechaikul 1986).

Social factors may also play a role (reviewed by Munro 1990a, b). In the case of cyprinids, in particular, there is evidence that hormones associated with FOM-O (C_{21} steroids and prostaglandins: section II.c) and their metabolites also serve as pheromones to enhance male reproductive performance, in terms of both

testicular hydration (and thus the quantity and quality of the milt) and behavioral arousal (reviewed by Stacey et al. 1994). Similarly, male pheromones may also contribute to sexual synchronization by promoting FOM-O in some species (reviewed by van den Hurk and Resink 1992, Stacey et al. 1994). Another possibility, intrasexual pheromonal communication, is suggested by a report that hormonally-induced FOM-O of as few as 10-20% of female Chinese carp broodstock in a pond results in the rest of females also undergoing FOM-O (Lin 1982); a similar effect has been reported for male carp (Billard 1989).

d. Gonad regression. While the end of the natural spawning season may be signalled by withdrawal of promoting cues, there is little evidence that this is important for most of the few species which have been studied. Instead, gonad regression may occur spontaneously through an internal clock, especially in those species where the environment also entrains a circannual clock for gonad growth (e.g. Sundararaj and Vasal 1976, see Munro 1990b).

Alternatively, regression may occur as a result of other 'terminating' cues which signal the end of suitable breeding conditions (reviewed by Munro 1990a, Munro and Lam 1990). For example, high temperatures cause gonad regression in an estuarine goby, *Gillichthys mirabilis;* at lower temperatures, fish can apparently remain continuously mature (de Vlaming 1972a, b). Similarly, changes in photoperiod and/or temperature have been identified as terminating factors in temperate cyprinids (e.g. Razani et al. 1989, Aida et al. 1991).

There is evidence for endogenous termination of reproductive activity (as assessed by spontaneous ovulations) in female *C. carpio* maintained under constant warm temperatures for a prolonged period; however (as in the wild) the gonads do not regress. Instead, reproductive activity can be restored by temporary cooling (Davies and Hanyu 1986).

e. The role of modifying factors. The time of onset of each of the above gonadal transitions, and the rate of their subsequent development, is influenced by various modifying factors. Thus, these affect the otherwise 'reflex' responses to promoting, synchronizing, and terminating cues (Munro 1990a).

For example, the day-night cycle acts as a modifying factor to determine the precise timing of the GtH-II surge, and thus FOM-O, in response to sychronizing cues in cyprinids (Aida 1988, see above) and other teleosts. The lunar cycle also plays an important role in a variety of species (Munro 1990b, Robertson et al. 1990, Taylor 1990); available information for one species of estuarine cyprinodont suggests that lunar rhythms may be entrained by counting numbers of days, and also by artificial cycles of dim moonlight (Taylor 1991).

Similarly, food availability (and thus body-size and growth rate) exerts an influence on when immature fish can enter puberty and, for species which can spawn more than once in a season, the number of broods of eggs produced (Wootton 1982, 1985). However, it should be noted that size is not an absolute determinant of when puberty can occur: age also plays a role, at least in small (short-lived) species (Stearns and Crandall 1984).

In salmonids, body size has been shown to determine whether an individual can enter puberty upon exposure to an otherwise stimulatory photoperiod (e.g. McCormick and Naiman 1984, Crandell and Gall 1993a, b). Also, experimental and other evidence indicates that increased food availability and the resultant faster growth rates (especially during a temporal 'window', in late spring, at higher latitudes) are associated with an increased proportion of precociously-maturing male salmonids (e.g. Rowe and Thorpe 1990a, b, Rowe et al. 1991, Berglund 1992, Simpson 1992, Clarke and Blackburn 1994). Likewise, the food supply to females during the first portion of ovarian growth period may influence final fecundity (Washburn et al. 1990, Bromage and Jones 1991).

Data for the tilapia, *Oreochromis niloticus* also indicate that protein load (and hence growth rate) influences the onset of puberty. This occurs when females exceed a certain critical weight (Gunasekera et al. 1995). This contrasts with some other studies on various tilapias, where the phenomenon of stunting has been correlated with a combination of good feeding conditions and crowding (Iles 1973, Noakes and Balon 1982, de Silva and Amarasinghe 1989), or experimentally attributed to poor nutrition (Mironowa 1978). Experimental and other data for a variety of other teleosts suggest that food availability (or, more specifically, the amount of dietary protein) is an important determinant of gonad development and maintained reproductive activity, with evidence for effects on egg-size and/or fecundity (e.g. de Vlaming 1971, Hunter and Macewicz 1984, Hislop et al. 1978, Wallace and Selman 1978, Wee and Tuan 1987, Hay and Brett 1988, Hay et al. 1988, Lin et al. 1989, de Silva and Radampola 1989, Rosenblum et al. 1991, Rajasilta 1992, Simpson 1992, Kjesbu 1994). Some of these studies indicate that food availability may be important at only some stages of the reproductive cycle. Thus, fat reserves accumulated during previous seasonal food abundance may be important in natural populations of many tropical freshwater species (reviewed by Munro 1990b):

Within the normal range, temperature influences the rate of gonad development in those species where photoperiod has been identified as the promoting cue (e.g. Billard 1986, Bromage and Cumaranatunga 1987, Davies and Bromage 1991, Mackay and Lazier 1993); presumably, this is basically a Q_{10} effect. On the other hand, elevated temperatures act to delay the endogenously-regulated onset of ovarian regression at the end of the normal spawning season of *H.fossilis* (Sundararaj and Vasal 1976).

Extremes of temperature constitute one form of 'stress', and can block gonad development (Gerking 1980, Billard 1986). Other stressors, such as capture and handling (Lam 1982, Carragher and Pankhurst 1991, Wallace et al. 1993), various forms of pollution (natural or otherwise; including lack of oxygen) (e.g. Pickering 1989, Donaldson 1990, Thomas 1990, Kime 1995), and confinement in too small an enclosure (possibly *Chanos chanos:* Marte et al. 1988a) have been found to inhibit gonad development or to cause gonad regression in mature fish (see also Lin et al. 1989). Both acute and chronic stress reduce androgen levels in male salmonids, and decrease hepatic oestrogen receptors in females (reviewed by Pickering 1989).

The effects of stress may be mediated in part by increased secretion of Cortisol to above normal (resting) levels, as part of a long-term coping response. Thus, artificially elevated levels of Cortisol, typical of those seen during stress, have generally been found to be detrimental to reproductive function. Most evidence is available for salmonids, where chronic elevations in plasma Cortisol levels inhibit gonad growth: GtH-II secretion is suppressed, and the responsiveness of the gonads and liver (to GtH-II and estradiol respectively) is reduced (Carragher et al. 1989, Carragher and Sumpter 1990, Pottinger et al. 1991). Cortisol also depresses levels of sex steroids in both sexes of tilapia (*Oreochromis mossambicus*) (Foo and Lam 1993a, b); rates of ovarian growth were also reduced by exogenous Cortisol (Foo and Lam 1993b), although other studies failed to demonstrate any effect on induced hepatic vitellogenin production in males (Munro et al. unpubl.). The situation in other teleosts is less clear: for example, a synergistic interaction of Cortisol with oestrogens during ovarian growth has been proposed in the case of the Indian catfish *Heteropneustes fossilis* (Sundararaj et al. 1982), where Cortisol could play a role in the mobilization of body reserves for vitellogenesis.

IV. Reproductive control through manipulations of the internal environment

Where the relevant promoting and/or synchronising cues are either unknown or impractical to simulate, attempts have been made to mimic the internal signals that such cues are believed to activate in order to exert their gonadal effects (despite the risk of higher mortalities among broodstock: Bry et al. 1989). The following section aims to summarize some of the approaches which have been successfully applied to achieve this end.

It is important to note that, even if no attempt is made to supply the appropriate promoting and/or synchronizing cues, the previous section implies that holding conditions should be optimised. Thus consideration should be given to potential modifying factors so that, for example, nutrition is optimized and stress minimized.

On the other hand, reproduction may be undesirable: for example, somatic growth is sacrificed for gonad growth with the onset of puberty or gonad recrudescence (reflected in the fact that the gonads may be up to 20-30% of body weight in mature fish). An extreme example is pond populations of tilapia, which show the phenomenon of 'stunting': they mature at a much smaller size than they do in large water bodies, and thereafter essentially stop growing.

a.   Methodological approaches. The traditional approach has been to administer various treatments in aqueous vehicles: saline for GnRH and gonadotropic preparations and an acid/anti-oxidant vehicle (with sonication) for monoaminergic drugs. Dimethylsulphoxide has also been used for the latter, to overcome problems of solubility. These protocols lead to a transient large rise in the agent injected, the brief nature of which may limit the efficacy of the treatment. While the use of superactive analogues of GnRH (section II.b) and of steroids (e.g. 17α-methyltestosterone, 17α-MT) may prolong the period of treatment by retarding metabolic clearance, the duration of the increase is only modest with these vehicles.

To overcome this problem, various slow-release techniques can be used to increase the duration of treatment with GnRH or steroids (Crim 1985). However, there may be the problem of using too high a dose of GnRH (e.g. Garcia 1989): depending to some extent on the GnRH used, prolonged exposure may lead to a loss of pituitary responsiveness due to de-sensitization (Habibi 1991a, b, Lin et al. 1994). The most commonly-used slow-release technique is the intraperitoneal or intramuscular implantation of pelletised preparations, which are of two basic types: those in silastic or synthetic polymers, and those in cholesterol-based mixtures with various binding agents to regulate the rate of release (Lee et al. 1986a, Crim et al. 1988, Sherwood et al. 1988, Garcia 1989, Zohar et al. 1990).

As an alternative to pellet-implantation (which is relatively stressful, and not readily applicable to small fish), sustained release from liquid injection boluses has been used. Vehicles used include vegetable oils for steroids (Shehadeh et al. 1973a); and emulsions of aqueous solutions of peptides with Freund's complete (Aida et al., 1978) or incomplete adjuvants (Ng et al. 1994 and in prep.). A variant on the latter is the injection of saline suspensions of micro-encapsulated GnRH (Breton et al. 1990, Zohar et al. 1990, Lee et al. 1993).

Alternatively, steroids (Weber and Lee 1985, Lee and Weber 1986) and GnRH (Thomas and Boyd 1989) may be administered in the diet; whilst relatively large amounts of drug are required, this approach minimises handling stress. The latter consideration does not apply for a variant on this approach, where GnRH and other drugs are administered by direct intubation into the gut (Solar et al. 1990, Sukumasavin et al. 1992). Trials have also shown that steroids (e.g. Kobayashi et al. 1987) and GnRH (Sherwood and Harvey 1986) can be effectively administered by immersion, although no studies are forthcoming. In the case of GnRH, this approach

is limited by fish size (i.e. bath volumes); however, uptake can also be achieved by applying a solution of GnRH in dimethylsulphoxide to the air-exposed gills under anaesthesia (Sherwood and Harvey 1986).

b. Stimulation of gonad growth. As summarized in section II.c (Fig. 3), androgens might be expected to induce testicular development and promote spermatogenesis; and to delay gonad regression at the end of the spawning season or after exposure to inhospitable conditions. However, where androgens have been reported to be effective in stimulating testes growth (salmonids - e.g. Crim and Evans 1983, *Mugil cephalus* - Shehadeh et al. 1973a, Weber and Lee 1985, Lee and Weber 1986, Lee et al. 1992, a poeciliid - Schreibman et al. 1986), it would seem likely that they are also acting at least partly through positive feedback on the hypothalamo-hypophysial axis. The same appears to apply for female *Anguilla japonica,* where testosterone implants on their own can induce full gonad development (Lin et al. 1991).

As noted in section II.d, positive steroidal feedback is usually only partial. Thus, steroids may mainly stimulate the synthesis of GtH-II, with or without that of GnRH (salmonids, *Anguilla anguilla*)*;* or they may sensitize the GnRH - GtH-II axis (temperate cyprinids). The concurrent use of a slow-release preparation of GnRH is thus generally used to ensure that GtH-II secretion is also stimulated; this procedure has been found to induce testicular development in salmonids (e.g. Crim and Evans, 1983), *C. chanos* (Marte et al. 1988a) and the tropical cyprinid Labeo bicolor (Mok et al. 1994). Treatment with a slow-release preparation of GnRH on its own had no detectable effect (e.g. Crim and Evans 1983, Mok et al. 1994).

Stimulation of ovarian development using a slow-release combination of androgen and GnRH appears to be less consistent. Thus it is generally ineffective in salmonids (e.g. Crim and Evans 1983) and *L. bicolor* (Mok et al. 1994). However, implantation of GnRH in combination with testosterone accelerated ovarian development in *M. cephalus* and allowed multiple spawnings, whereas GnRH with 17α-MT was inhibitory (Tamaru et al. 1989). Conversely, implantation of GnRH in combination with testosterone (Marte et al. 1988a) appears to be less effective than that with 17α-MT (Lee et al. 1986b, c) in female *C. chanos,* although it is difficult to make direct comparisons between the two studies (Marte et al. 1988a). Again, treatment with a slow-release preparation of GnRH on its own is generally relatively ineffective (e.g. Lee et al. 1986b, c).

The relative inefficacy of treatment with GnRH and androgens in females may reflect a role for other regulatory controls of GtH-II (and/or GtH-I?) secretion. For example, while repeated injections of estradiol and GnRH only stimulated GtH-II synthesis in female *Anguilla anguilla,* a combined treatment of oestradiol and GnRH with the dopamine antagonist pimozide also stimulated the release of GtH-II and ovarian growth (Dufour et al. 1988, 1991). This suggests that dopaminergic

inhibition (perhaps activated by steroid negative feedback: section III.d) may normally act as a brake in this species (cf. *A. japonica,* above).

Clomiphene citrate and other anti-estrogens are generally assumed to act by blocking steroid negative feedback in teleosts. However, this assumption has to be re-evaluated in the light of recent findings in goldfish (section II.d; Trudeau et al 1991a, 1993c): thus, clomiphene may even be oestrogenic with positive feedback effects. Whatever its mode of action, clomiphene has been reported to accelerate ovarian development in *C. carpio* (Kumar and Chandrasekhar 1980). Trials using this drug, with or without a slow-release preparation of GnRH, were ineffective in another cyprinid, *L. bicolor,* however, clomiphene on its own was neither vitellogenic nor able to block estradiol-induced vitellogenesis, raising question: about its efficacy at the dosage used (Mok et al. 1994).

c. Final gonad maturation. For induced spawning, the main problem has been to achieve FOM-O. Thus, the following will concentrate mainly on the female; however, mention will be made in passing of methods to promote testicular hydration in cases where milt yields are low.

The first protocols for inducing final gonad maturation aimed to mimic an endogenous GtH-II surge by injections of a homologous or heterologous gonadotropic preparation in saline, either as a crude pituitary extract or as a more-or-less purified teleost or mammalian gonadotropin (e.g. Lam 1982, 1985). The procedure developed using gonadotropic preparations will be described first, after which more recent alternatives using other forms of treatment will be briefly reviewed.

Successful induction of FOM-O requires the use of suitably gravid females, selected on the basis of external criteria (e.g. Lam 1982, Weil et al. 1986) or oocyte diameters and other criteria (based on ovarian biopsies: e.g. Lam 1982, Tamaru et al. 1988). The standard protocol for many species is to administer a gonadotropic preparation as two injections (priming and resolving) in saline, 3 - 24 hours apart (e.g. Lam 1982, 1985, Zohar 1989); if necessary, at the same time as females recieve their second dose, a single injection can be given to males to induce seminal thinning (e.g. Lam 1982, Donaldson and Hunter 1983, Weil et al. 1986, Zohar 1989). The time until ovulation depends on the initial size of the oocytes (e.g. Ayson 1991). The physiological basis for the need for two separate injections in females is presumably that the priming injection is responsible for the initial 'direct' effects of GtH-II on FOM (i.e. germinal vesicle migration, etc.), while the resolving injection is mainly associated with MRS production (and its resultant mediation of subsequent events during FOM) and ovulation (section II.c). Thus, the resolving injection should be given at a time when the maturing oocyte has become sensitive to the MRS: during germinal vesicle migration to the animal pole (Canario and Scott 1990a, Patiño and Thomas 1990a, b), or soon after this has been completed (Kuo and Nash 1975, Weil

et al. 1986). The interval between the two injections is not standard, with differences both between and within species (e.g. Patiño and Thomas 1990a); it is also affected by temperature and other factors. Where necessary, the timing can be optimized by biopsies after the first injection, although the problem of stress must be borne in mind.

However, there are potential drawbacks associated with the use of gonadotropic preparations: for example, the lack of standardization of crude extracts, the lack or expense of suitable purified gonadotropins, and the expense and/or ineffectiveness of heterologous gonadotropins (Lam 1982, 1985, Donaldson and Hunter 1983, Weil et al. 1986, Lee et al. 1988, Billard 1989, Zohar 1989). Thus, attention has been directed towards inducing a surge of endogenous GtH-II. Typically, this has been through the use of GnRH, with or without other relevant treatments', the latter generally involve a dopamine antagonist such as pimozide, domperidone (which has the advantage that it may not cross the blood-brain barrier, and so may act only on the pituitary) or metoclopramide (advantageous because of its ready solubility in saline). Thus, a GnRH analogue (with or without a dopamine antagonist) is substituted for one or both injections of a gonadotropic preparation in the above protocol (e.g. Peter et al. 1988, Zohar, 1989), with evidence that GnRH may be more economical (Lee et al. 1988, Fermin 1991). The time between priming and resolving injections is the same as gonadotropic preparations; when both injections include GnRH, the first dose also potentiates the pituitary's secretory response to the second (Peter 1986, Habibi and Peter 1991, Lin et al. 1994). Where there is a problem of milt quality or quantity in males, they may be given an injection of the same preparation at the same time as the females receive the resolving dose.

In contrast to the foregoing generalization, only one saline-based injection of either a gonadotropic preparation or GnRH (+ a dopamine antagonist) has proved sufficient to induce FOM-O in various species of siluroid catfish (Ros et al. 1984, de Leeuw et al. 1985a, b, Richter et al. 1987, Thalathiah et al. 1988, Ngamvongchong et al. 1988, Zheng et al. 1988, Zairin et al. 1992, Alok et al. 1993). Similarly, a single injection of a gonadotropic preparation was generally effective in the Australian percichthyid *Macquaria ambigua* (Rowland 1983), the ostariophysan *C. chanos* (Marte et al. 1988b), and the anabantoid *Colisa lalia* (Ng et al. 1994 and in prep.); and a single injection of a GnRH sufficed in an Indian carp (*Cirrhina mrigala:* Kaul and Rishi 1986), a clupeomorph (Kreiberg et al. 1987) and *C. chanos* (Marte et al. 1988b). Similarly, a single injection of a GnRH together with a dopaminergic antagonist induced FOM-O in in several species of Chinese carps (e.g. Peter et al. 1988) and common carp (*Cyprinus carpio*) (Drori et al. 1994). Where documented, this increased responsiveness was generally seen in individuals where germinal vesicle migration and other aspects of early FOM have already occured: thus the oocytes were already naturally primed, and thus maturationally competent (Rowland 1983, Drori et al. 1994, cf. Ng et al, 1994). A similar explanation may apply to those studies on other teleosts which report that only a single injection is necessary for

those female broodstock where the oocytes are already of a sufficient size (e.g. *M. cephalus,* Shehadeh et al. 1973b, *C. chanos,* Tamaru et al. 1988): this parameter may at least partly reflect a contribution from oocyte hydration (section II.c).

On its own, the use of a maturation-resolving steroid (MRS) might be expected to be relatively ineffective: even if oocytes have completed the initial stages of FOM and are thus maturationally competent, the MRS appears to be relatively ineffective as an ovulatory agent (Goetz 1983). One exception is the catfish *C. gariepinus,* where one or two injections of 17a-P sufficed for completion of full FOM-O, associated with plasma 17α,20ß-P levels (Richter et al. 1987). However, in some other species, the MRS (or even 11-oxy- or 11-deoxycorticosteroids) may be substituted for the resolving dose of a gonadotropic preparation or GnRH, if the timing is correct (e.g. Lam 1982, 1985, Donaldson and Hunter 1983; Weil et al. 1986, Zohar 1989, Patiño and Thomas 1990a, b). It is not clear whether this reflects an intrinsic ability of the MRS to also induce ovulation, or whether the latter process is the result of a delayed response to the priming (non-MRS) injection. In passing, it should be noted that a knowledge of the precise nature of the MRS may be unnecessary. First, compounds normally classified as corticosteroids may be used instead. Secondly, recent evidence that the availability of precursor (17α-P) for MRS- (and also HIS-) production may be the limiting factor (see section II.c) suggests that 17α-P could be given instead, as a cheaper alternative; the results of experiments with the catfish *C. gariepinus* are consistent with this (Richter et al. 1987).

Other studies have indicated that more prolonged exposure to a gonadotropic preparation or a GnRH may be required for FOM-O. For example, slow-release preparations of GnRH (in Freund's incomplete adjuvant) are required to induce FOM-O in the anabantoid *Colisa lalia* (latency 28 h). This may be through the need for stimulation of endogenous GtH-II synthesis: a single injection of a mammalian gonadotrophin resulted in ovulation (latency ≈ 18 h), whereas two injections of either GnRH in saline or homologous pituitary extracts (< 4 pituitaries/fish) at varying intervals (6 - 24 h) were ineffective (Ng et al. 1994 and in prep.).

There is evidence that oocytes must exceed a certain threshold size in order to be able to undergo FOM-O; where female broodstock are found by biopsy to have oocytes which are too small, multiple injections or, preferably, the use of slow-release preparations of GnRH have been found necessary to bring these above threshold and thus undergo FOM-O (e.g. Tamaru et al. 1988). This has been most studied in salmonids, where implants of GnRH (e.g. Crim et al. 1986, Zohar et al. 1990), or injections of GnRH in saline (e.g. Breton et al. 1990, Mylonas et al. 1992, Taranger et al. 1992) or in a micro-encapsulated form (Breton et al. 1990, Zohar et al. 1990), have been used to accelerate and synchronize the protracted final phases of ovarian growth and maturation.

A third situation where more sustained exposure is required is illustrated by *Lates calcarifer,* which normally spawns over several successive days at a particular phase of the moon. This can be induced by GnRH given either as multiple daily injections or as a single sustained-release implant; implants have also been used to induce spawning bouts at other phases of the lunar cycle (Almendras et al. 1988, Garcia 1992). Similarly, daily spawning over a prolonged period can be induced in female sparids by administration of sustained-release GnRH preparations (Zohar et al. 1988). The reliability of such a prolonged response is greater than that obtained after a single aqueous injection of a gonadotropic preparation or GnRH (Zohar and Gordin 1979, Zohar et al. 1988). Nevertheless, the fact that the latter is capable of inducing more-or-less sustained daily spawning in a proportion of females suggests that a brief exposure can potentially trigger a longterm switch in the activity of the hypothalamus-pituitary-gonad axis under some circumstances, in sparids at least.

It should be noted that the use of slow-release preparations of a GnRH may not always be advantageous. Thus, various studies have reported that excessive dosages of gonadotropic preparations or GnRH may have deleterious effects, possibly through uncoupling of ovulation from the processes associated with FOM (e.g. Kuo and Nash 1975, Lam 1982, 1985, Mylonas et al. 1992). Despite this temporal dissociation, FOM may continue to completion after ovulation, at least in salmonids and a flatfish; where this occurs, it has been suggested that stripping should be delayed until the ova have matured adequately (reviewed by Howell and Scott 1989, Mylonas et al. 1992).

In section III.e, it was noted that the onset of the photophase may serve as a modifying factor for the precise timing of environmentally-induced FOM-O. Studies on responses to exogenous GnRH suggest that this may depend in part on diurnal changes in the responsiveness of the pituitary-gonad axis. Thus there is a diurnal rhythm of sensitivity to GnRH in a sciaenid, based on circulating GtH-II levels (Khan and Thomas 1994); whilst the latency until ovulation varied with time of day when GnRH was administered in the serranid *Dicentrarchus labrax* (Alvariño et al. 1992). On the other hand, the efficacy of GnRH (+ a dopamine antagonist) in inducing FOM-O shows no such diurnal variation in carp (Drori et al. 1994), although there was some evidence for such an effect in males (Billard et al. 1987).

There are several other hypothalamic factors which modulate GtH-II secretion, at least in goldfish (section II.b and Fig. 1). Yet it would appear that a possible role for these other systems in the regulation of GnRH-induced FOM-O has been tested in only one teleost, the anabantoid *C. lalia* (Ng et al. 1994 and in prep.). We have found that the response to GnRH (in Freund's incomplete adjuvant) may be enhanced not only by dopaminergic antagonists but also by α- and ß-adrenergic agonists; whilst an opioid agonist and antagonist both had an inconsistent facilitatory effect, reminiscent of the effects of opioid drugs on GtH-II secretion in goldfish (Rosenblum and Peter 1989). On the other hand, various serotoninergic agonists and

antagonists, and $GABA_A$ and $GABA_B$ agonists, had no effect (Ng and Munro in prep.). We have also been unable to induce ovulation with neuropeptide Y, whether administered in saline or adjuvant (Ng and Munro in prep.).

An alternative means of inducing an endogenous, relatively prolonged surge of GtH-II has been the use of anti-oestrogens such as clomiphene and tamoxifen (reviewed by Donaldson and Hunter 1983, Zohar 1989, Chang et al. 1992), although clomiphene was ineffective in *C. lalia* (Ng et al. in prep.). These drugs are generally assumed to act by blockade of feedback inhibition by estrogens, but this requires clarification (see Trudeau et al. 1991a, section IV.b).

As noted in section II.c, there is also the potential for other hormones to enhance the effectiveness of a gonadotropic preparation or a GnRH in inducing final gonad maturation. Thus thyroid hormones (or more specifically tri-iodothyronine, T_3) have been found to be effective for restoring the ovulatory response of sturgeon to pituitary extracts at low temperatures (Detlaf and Davydova 1975). T_3 also enhances the ovulatory response of the salmonid *Oncorhynchus mykiss* to GnRH in saline, apparently via actions at the level of the ovaries (Sullivan et al. 1989), with some evidence for a similar effect in the anabantoid *C. lalia* treated with GnRH in adjuvant (Ng and Munro in prep.). On the other hand, T_3 was ineffective in another salmonid, *Salmo trutta,* perhaps because of the already-elevated endogenous levels of this hormone in the female broodstock (Mylonas et al. 1994).

It is generally assumed that stress of the broodstock is to be avoided when trying to induce final gonad maturation. However, the fact that corticosteroids may induce, or at least potentiate, FOM, and also the observation that the adrenocortical tissue may produce MRS in at least some species (Section II.c), suggests that this need not be a major concern (in contrast to the long-term effects on gonad growth: section III.e). In this context, it is interesting to note that stress has been reported to elevate levels of 17,20ß-P in a sparid (Carragher and Pankhurst 1991); while 'stress-induced' ovulation has been reported in skipjack tuna after capture (Kaya et al. 1982), and handling may promote spawning in siganids (Ayson 1989).

d.   Inhibiting gonad development.   Only recently have attempts been directed at achieving this through direct manipulations of the internal environment. Several such studies have aimed at inducing auto-immunity to particular components of the reproductive system. Auto-immunity to spermatozoa has been achieved by the injection of sperm suspensions (in Freund's complete adjuvant) in *O. mykiss* (Secombes et al. 1987) and *O. niloticus* (Lou et al. 1989). Whilst endogenously-produced antibodies are able to penetrate into the testicular lumen, to bind to spermatozoan membranes and thus impair their fertilization capabilities (Secombes et al. 1987), there is no evidence that this approach affects testicular development (Secombes et al. 1987). Thus, evidence suggests that this is not a promising approach if the aim is to reduce reproductive effort rather than viability.

Potentially more useful are attempts to induce auto-immunity to reproductive hormones. Initial attempts to block gonad development by immunizing salmonids against a conjugate incorporating mammalian GnRH have proved unsuccessful (Andersen et al. 1992); this may be because of the relative inappropriateness of the antigen used (Riley and Secombes 1993), and/or the briefness of exposure of the native GnRH to antibodies between its secretion and its interaction with receptors on target pituitary cells. This, together with a possible role of GnRH in the regulation of GH secretion in at least some teleosts (section II.b), suggests that alternative 'targets' (e.g. the GtH) for induced auto-immunity may be both more amenable and more specific.

The effects of monosodium glutamate (section II.b) in goldfish suggest that this might be a candidate agent for the destruction of hypothalamic areas associated with regulating pituitary activity. However, initial trials with juvenile and adult tilapia (*O. mossambicus*) proved unsuccessful in affecting reproductive status (Munro et al. 1990b).

V. General Discussion and Conclusions

On the basis of what is known about promoting cues and gonad development (section HI), the controlled timing of reproductive cycle is amenable to environmental manipulations (principally photoperiod and temperature) in temperate teleosts, but the situation appears to be less clear for tropical species. Munro (1990b) speculated that the latter may rely on a variety of different sources of environmental information (including food availability) for gonad growth, rather than just one major control cue. This may reflect the importance of modifying, rather than promoting, cues in the modulation of an endogenous 'clock' in many species. This would be consistent with a theoretical analysis of data for seasonality in temperate vs. tropical bird populations by Wingfield et al. (1992). It should be noted that there is evidence that the importance of environmental factors, including stress, may decrease with domestication (e.g. Kirschbaum 1984, Pickering 1989), so that successive generations of progeny from a pioneer captive broodstock should become easier to breed. This may have at least some genetic basis: it is possible to rapidly select for strains of *O. mykiss* which breed at different times of year, reflecting differences in responsiveness to photoperiodic information (Siitonen and Gall 1989).

While promoting and/or modifying cues may be manipulated in order to minimize reproduction, this need not translate into increased somatic growth, since conditions are likely to also be suboptimal for the latter. Moreover, once they exceed a threshold (but age-dependent?) size, environmental manipulations are unlikely to indefinitely postpone maturation in those species where cyclicity is driven by an

underlying circannual clock. Thus the development of induced auto-immune and other techniques to produce reproductive sterility would seem to be more promising.

The emerging picture from experimental neuro-endocrine studies (section II) is that there are basic differences in the control of gonadal cyclicity between salmonids and cyprinids (as exemplified by goldfish), the two 'model' groups of teleosts which have received the most attention. Thus, there are evident differences in the hypothalamic regulation of GtH-II secretion, associated with differences in the nature of steroid feedback and the role of other hormones (section II) and also the importance of environmental cues in the regulation of both gonad growth and final maturation (section III). The few data available for other teleosts hint at differences from each of these two models, at least with respect to hypothalamic control mechanisms.

The classic function of GH is the control of somatic growth; presumably, hypothalamic GHRH and GH-RIH play an as yet ill-defined role in regulating this aspect of GH function (Fig. 1). In addition, it is apparent that GH also plays a direct role in the regulation of gonadal activity (section II and Fig. 1). Thus, there is evidence for several intermeshed positive feedback inputs from the gonads which regulate both GH and GtH-II release in goldfish (Fig. 1). This suggests that gonad growth, once initiated, may be largely self-sustaining under appropriate conditions in this domesticated species. It appears likely that dopaminergic systems serve as a brake, especially to prevent spontaneous FOM-O in the absence of the appropriate synchronizing cues in those species where these cues are important.

It is interesting to note that dopamine stimulates GH secretion while inhibiting that of GtH-II and that serotonin has the opposite pattern of effects. When activated, either of these monoaminergic systems may thus serve to differentially bias the responsiveness of the GtH-II and GH cells in opposite directions in the face of common excitatory inputs (including feedback from the gonads). The physiological implications of these findings remains to be elucidated.

The significance of the numerous direct monoaminergic and peptidergic controls of secretion of GtH and GH is unclear. Given the importance of food availability and growth in determining reproductive capabilities (section III.e), it may be worth noting that both NPY and noradrenergic mechanisms are associated with increased appetite (for carbohydrate) in mammals (Blundell 1991, Leibowitz 1992), whilst members of the CCK/G family and serotonin have instead been implicated in satiety (Blundell 1991, Leibowitz 1992), with CCK/G having a similar behavioral effect in goldfish (Himick and Peter 1994).

The evidence for an apparent dual control of reproductive development by GtH and GH, at least, suggests that the use of a purified gonadotropic preparation, on its own, to replace (or supplement) any environmental manipulations may not be the

most appropriate approach. It would seem possible that treatments which include GH (e.g. pituitary extracts), or which also stimulate GH secretion (e.g. GnRH + aromatizable steroids) might be more effective in eliciting the desired response.

There is some evidence that induced spawning may be associated with poor egg-quality when this is done prior to, rather than during, the natural spawning season (Rowland 1983, Lam 1985). This may be related to the fact that oocytes have not completed the initial (presumably MRS-independent) phase of FOM prior to induced spawning (Rowland 1983, see also Goetz 1983). While hatchery-operators often claim that natural spawning results in better-quality eggs than does induced spawning, we are not aware of any controlled studies to substantiate this generalization. Nevertheless, from an applied point of view, the main considerations in evaluating techniques for inducing gonad growth and final maturation must be the quality of gametes produced, and the associated unit costs. If induced spawning does result in poor returns compared with natural spawning, then it is necessary to identify why this should be so in order to improve techniques.

If fertilizability and early development are principally affected, and there are no apparent problems with sperm quality, then one possibility is that induced spawning is associated with a retardation or disruption of the processes associated with FOM. For example, if FOM is not completed before ovulation, then stripping should be postponed until a more appropriate time (Mylonas et al. 1992. Alternatively, poor results may be the result of overripening, due to the post-ovulatory ova remaining too long in the ovarian lumen before stripping. Available evidence (section III.c) suggests that this may be mainly a problem in species which rely on specific synchronising cues (including entrained circadian cycles) to time FOM-O.

If, on the other hand, any effects on brood viability are only apparent during later development, then it may be that the oocytes have not sequestered their full complement of yolk components: progeny would thus be inadequately prepared for survival and growth. This need not be simply through having insufficient amounts of vitellogenin or its by-products: there is accumulating evidence that females may also pass thyroid and other hormones on to their eggs (reviewed by Brown and Bern 1989, Lam 1994). Such maternally-derived stores of thyroid hormones and Cortisol, at least, may play an important role in regulating the homeostasis, growth and development of the progeny before the latter have developed their own endogenous sources of these hormones (Lam 1994). Thus changes in hormones (including the GtH and sex steroids?) during the normal reproductive cycle should be interpreted not only from the point-of-view of gonad regulation in the female broodstock but also from that of the development of any progeny. This implies that offspring viability may be optimized if the yolk has been loaded with appropriate amounts of various maternal hormones during the period of oocyte growth and FOM; and raises the possibility that artificially-induced reproduction may interfere with this. The most

obvious candidates for further study would be GH, together with the IGF which it stimulates the liver to produce (circulating levels of which also show changes related to reproductive activity: e.g. Perez-Sanchez et al. 1994), since these peptides are likely to be implicated in developmental processes. This further suggests that, if there is significant uptake of maternal hormones around the time of FOM-O, pituitary extracts may be most beneficial, since these would provide other hormones for sequestration by the oocytes; however, the possibility of over-dosing the oocytes with one or more of these hormones should be borne in mind.

Similarly, the effects of stress during reproductive development have typically considered only the broodstock, emphasizing the generally deleterious effects on the latter (section III.e). However, recent evidence indicates this view is rather short-sighted. Studies on salmonids indicate that stress of broodstock, whether 'acute' (brief emersion, repeated monthly throughout the period of gonad growth) or 'chronic' (confinement for two weeks towards the end of gonad growth), has been associated with the production of less-viable offspring, although the mechanisms involved are unknown (Campbell et al. 1992, 1994). On the other hand, (presumably) moderate levels of maternal corticosteroids may be beneficial. There is evidence that these steroids accumulate in oocytes of *Lates calcarifer,* and that reserves of Cortisol may increase the survival of larvae exposed to osmotic stress (Sampath-Kumar et al. 1994).

Acknowledgments

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