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Annual variations of gonadotropin content and ovarian development of feral female catfish, *Silurus asotus*, in central China

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Synopsis

The Japanese catfish *Silurus asotus* is widely distributed throughout the freshwaters reservoirs, lakes and rivers of China, Korea and Japan, and is a commercially valuable aquaculture fish in some regions of China and Japan. We studied seasonal variations of gonadotropin (GtH) content of the plasma and pituitary as well as ovarian development. Plasma GtH titres increase in April in the Pearl River and in May in the Liao River in central China. Annual cycles of plasma GtH levels in both rivers are the same, with a gradual decrease after ovulation with the lowest values observed in September (in the Liao River) or October (in the Pearl River). Plasma GtH levels increase gradually in the early stages of ovarian development, with the highest values observed during the late stages of development, and with the lowest GtH titres observed during ovarian regression in both rivers. GtH content of the pituitary remained very high through the spawning period, with the highest titres observed in March in the Liao River, and in July in the Pearl River. As with plasma GtH, the lowest concentrations of pituitary GtH were observed during stages when the ovary was regressed. We analyzed the relationships between plasma and pituitary GtH and reproductive conditions, such as gonadosomatic index (GSI), hepatosomatic index (HSI), oocyte diameter (OD) and oocyte weight (OW). The results indicate that annual changes of GtH content of the plasma and pituitary paralleled GSI, OD and OW, but were negatively correlated with HSI in feral female catfish.

Introduction

The elucidation of physiological mechanisms of regulating reproductive cycle in teleosts requires a basic understanding of the gonadal and hormonal changes during the reproductive cycle. In many teleost species, ovulation is associated with a surge of gonadotropin (GtH) secretion triggering ovulation of a large number of oocytes, perhaps the entire oocyte population (Peter 1981, Peter et al. 1991). Frequently, appropriate environmental conditions cannot be provided under culture conditions, making artificial regulation of reproduction necessary. As a basis for understanding the reproductive physiology, it is necessary to know the cyclical events taking place under natural conditions to further investigate the rhythm of GtH secretion. It is necessary to study the natural reproductive cycle to know what strategies to use to regulate follicular development, and the optimize our approach to induce ovulation and spawning.

Studies on the relationship between gonadal development and hormone have been conducted in several commercially important species, including rainbow trout, *Oncorhynchus mykiss* (Whitenead et al. 1978), common carp, *Cyprinus carpio* (Yaron & Levavi-Zermonsky 1986), African catfish, *Clarias gariepinus* (Van Oordt et al. 1987), sea bass, *Dicentrarchus labrax*, and striped bass, *Morone saxatilis* (Prat et al. 1990). Studies on the relationship between gonadosomatic index (GSI) and hepatosomatic index (HSI) and the reproductive cycle have been conducted in the mouthbrooding cichlid, *Oreochromis niloticus* (Tacon et al. 1996), red drum, *Sciaenops ocellatus* (Craig et al. 2000), anglerfish, *Lophius litulon* (Michio et al. 2001), yellowtail kingfish, *Seriola lalandi lalandi* (Poortenaar et al. 2001), and Korean spotted sea bass, *Lateolabrax maculatus* (Lee & Yang 2002). The relationships among oocyte diameter (OD) and oocyte weight (OW) and the reproductive cycle have been studied in walleye, *Stizostedion vitreum* (Malison et al. 1994) and channel catfish, *Ictalurus punctatus* (Pacoli et al. 1990), among others.

The Japanese catfish, *Silurus asotus,* is widely distributed throughout freshwater lakes, reservoirs, rivers of China, Korea and Japan, and is a commercially valuable aquaculture fish in some regions of China and Japan. In Japan, the influences of spawning and season on fatty acid composition and content of ovarian and liver tissue (Shiraia et al. 2001), and the endocrine regulation of final oocyte maturation and ovulation in feral and cultured Japanese catfish have been investigated (Miwa et al. 2000). In China, studies on the reproductive and endocrine physiology of the catfish have received attention due to a decrease of natural stocks in recent years (Wei & Huang 1997, Wen et al. 2000). The aquaculture industry culturing this catfish is dependent on induced spawning by injection of human chorionic gonadotropin (HCG) and [D-Ala^{6}, Pro^{9}Net]-luteinizing hormone-releasing hormone analogs (GnRHa) (Pan et al. 1992, Liu et al. 1998). However, the effects of induced ovulation and spawning as well as egg production varied greatly among individuals. Therefore, it is desirable to study endocrine physiology of the feral female catfish, particularly regarding seasonal changes of GtH secretion in an attempt to develop a reliable method to induce ovulation in aquacultural catfish. In the present study, we investigated seasonal changes of GtH levels in the plasma and pituitary and how they relate to GSI, HSI, OD, OW in feral female catfish. Very little information is known about variations in pituitary and plasma GtH levels during the reproductive cycle of feral female catfish.

Materials and methods

Collection of feral female catfish

We captured adult female catfish (135 fish) from the Liao River (North River) in January, March, May, July, September and November in 2000, and from the Pearl River (Guangzhou, Guangdong Province, central China) in January, March, April, June, July, October in 1999. Prior to the experiments fish were held indoors for 5–7 days in recirculating 250-l aquaria under natural photoperiod. The body length (BL, the length between the snout and the base of the caudal fin) and body weight (BW) and the numbers of Japanese catfish from both river systems are shown in Table 1.

Determination of the stages of gonadal development and GSI, HSI, OD, OW

In fish from the Liao River, we classified ovaries from feral female catfish as either early vitellogenic

Table 1. Seasonal BL and BW of feral female Japanese catfish in the Pearl River (in 1999) and the Liao River (in 2000).

Month	Liao River			Pearl River		
	BL (cm)	BW (g)	n (fish)	BL (cm)	BW (g)	n (fish)
January	31.2 ± 1.3	241.5 ± 5.8	11	30.3 ± 4.2	237.8 ± 2.8	12
March	34.6 ± 3.8	342.8 ± 6.2	13	33.8 ± 4.7	251.2 ± 4.6	13
April				32.6 ± 3.3	240.9 ± 5.2	14
May	36.3 ± 7.8	437.8 ± 8.8	15			
June				34.2 ± 7.4	330.9 ± 4.6	9
July	34.8 ± 5.4	300.9 ± 9.8	10	31.9 ± 4.8	328.8 ± 5.9	8
September	29.6 ± 6.6	280.8 ± 3.6	9			
October				32.0 ± 5.1	318.9 ± 4.9	10
November	31.9 ± 3.9	320.9 ± 6.7	11			
Total			69			66

Each value represents the mean value ± SD.

(November to January), or late vitellogenic (February to April), or mature and ovulating (May to July), or regressed (August to October). The stages of ovarian development and oocyte phase have been described by Wei & Huang (1997) and Wen et al. (1998). In the Pearl River, the stages of ovarian development are delayed by 1 month relative to catfish from the Liao River. GSI = [(ovary weight)/(BW − ovary weight)] × 100, HSI = [(liver weight)/(BW − liver weight)] × 100, OD (mm) is calculated from the mean maximum diameter of 50 oocytes, and OW (mg) is calculated from the mean dry weight of 100 oocytes.

Sampling the blood and pituitary and determination of GtH

We sampled blood by puncturing the caudal vasculature with a 25-guage 1.3-cm needle attached to a 1.2-ml disposable syringe. We allowed blood samples to clot on ice for several hours, and then separated the serum by centrifugation (15 000 rpm) for 5–7 min and stored at −25°C. After dissecting the skull, we removed the pituitary gland (PG) and stored it at −25°C for measurement of GtH contents. We determined GtH levels of plasma and pituitary extract by radioimmunoassay (RIA) using an antiserum against the −β subunit of carp GtH (cGtHβ). We used cGtH for the assay standard and tracer (^{125}I). The assay protocol followed that previously described by Peter et al. (1984) except for the use of cGtHβ antiserum at a final dilution of 1 : 200 000. Serial dilutions of plasma and pituitary extract from *S. asotus* resulted in an excellent parallelism with the cGtH standard curves (data not shown).

Analysis of results and statistical analysis

All data are expressed as mean values ±SD. We used Duncan's multiple range test to compare the changes of GtH or GSI or HSI or OD or OW.

Results

Seasonal variations of plasma GtH contents and their correlation to the stages of ovary development

In feral female catfish of the Liao River, annual plasma GtH levels fluctuated greatly. GtH levels of the plasma begin to increase from January and peaked in May (8.1 ± 0.92 ng ml^{-1}), then decreased gradually from May to July, with the lowest values in September (0.9 ± 0.32 ng ml^{-1}) (Figure 1A). With respect to ovarian development, plasma GtH levels increased gradually during early ovarian development (November to January, stage III), with the highest values from February to April (stage IV) and in mature ovary from May to July (stage V). The lowest GtH were observed coincident with the regressed ovary from August to October (stage VI) (Figure 1B).

In the Pearl River, annual GtH levels in plasma also fluctuated greatly. Plasma GtH levels began to increase in March and peaked in April (10.0 ± 1.31 ng ml^{-1}), Relating high GtH levels remained from June to July (spawning period in Pearl River) and with the lowest values in October (0.32 ± 0.19 ng ml^{-1}) (Figure 2A). The GtH levels in plasma increased significantly in early ovarian development (November to January, stage III), with the highest values from February to April (stage IV) and during maturation

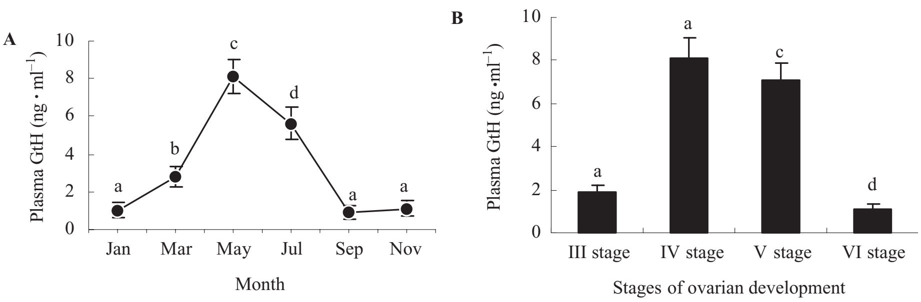

Figure 1. The seasonal changes of the plasma GtH levels (A) and stages of ovarian development (B) in feral female catfish in the Liao River. Each value represents the mean ± SD, the significant difference are identified by the different low case letters ($p < 0.05$ by Duncan's multiple range test).

(May to July, stage V). The lowest GtH values were observed coincident with the stage of sexually regressed ovary from August to October (stage VI) (Figure 2B).

Seasonal variations of pituitary GtH contents and relationship to ovarian development

In the Liao River, pituitary GtH content increased from January and peaked from March to July, with the highest value in March (14.3 ± 1.48 μg mg^{-1}) and the lowest value in September (5.0 ± 0.99 μg mg^{-1}) (Figure 3A). During the early stages of ovarian development (November to January, stage III), the mean GtH content of the pituitary is 8.0 ± 0.56 μg mg^{-1}, and peak value occurred in stage IV from February to April (the mean value is 10 ± 1.34 μg mg^{-1}). Higher levels of pituitary GtH remains through the spawning period from May to July (stage V). The lowest mean pituitary GtH was 5.6 ± 0.49 μg mg^{-1} in stage VI of ovarian development from August to October (Figure 3B).

In Pearl River, pituitary GtH increased from January and reached to the highest value in June (12.8 ± 2.17 μg mg^{-1}) and July (13.3 ± 2.12 μg mg^{-1}), and with the lowest value in October (5.36 ± 1.22 μg mg^{-1}) (Figure 4A). Mean pituitary GtH content was 8.7 ± 0.84 μg mg^{-1} in the early stage of ovary development (November to January, stage III), with the highest levels in stage V from May to July (the mean value is 12.3 ± 1.7 μg mg^{-1}). The lowest mean pituitary GtH was 5.3 ± 0.64 μg mg^{-1} in stage VI of ovary from August to October (Figure 4B).

Seasonal variations in GSI and HSI and their relationship to the reproductive cycle of catfish

In the Liao River, GSIs of female catfish in the late stages of ovarian recrudescence began to increase

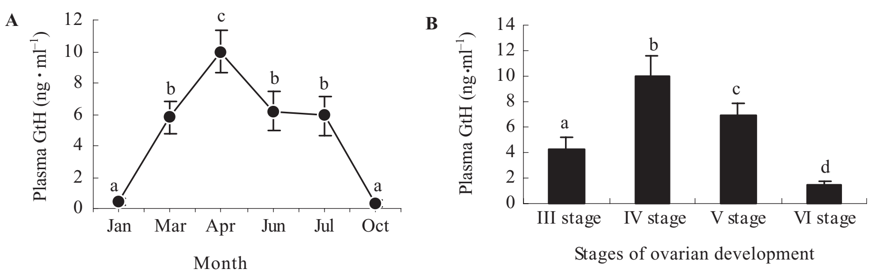

Figure 2. The seasonal changes of the plasma GtH levels (A) and stages of ovarian development (B) in feral female catfish in the Pearl River. Each value represents the mean ± SD, significant difference are identified by the different lower case letters ($p < 0.05$ by Duncan's multiple range test).

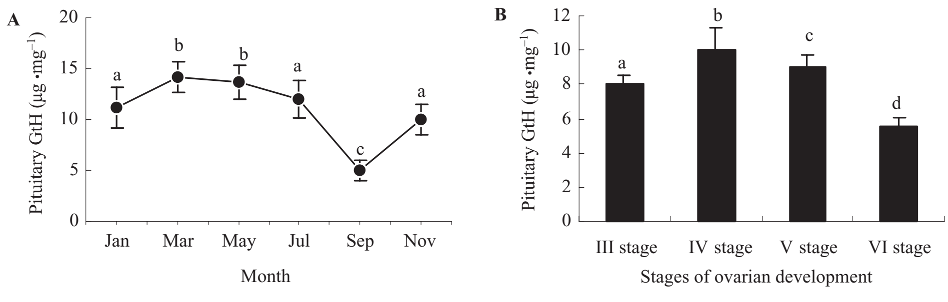

Figure 3. The seasonal changes in the pituitary GtH levels (A) and stages of ovarian development (B) in feral female catfish in the Liao River. Each value represents the mean ± SD, significant difference are indicated by the different lower case letters ($p < 0.05$ by Duncan's multiple range test).

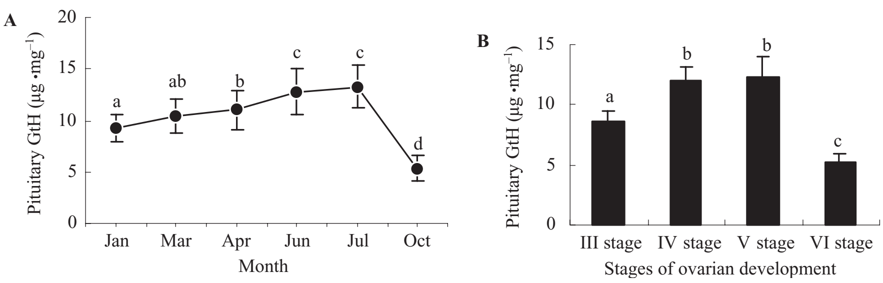

Figure 4. The seasonal changes in the pituitary GtH levels (A) and stages of ovarian development (B) in feral female catfish in the Pearl River. Each value represents the mean ± SD, significant difference are indicated by the different lower case letters ($p < 0.05$ by Duncan's multiple range test).

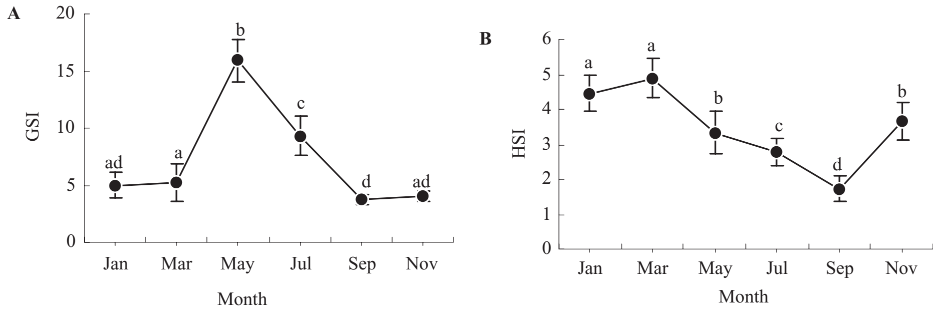

Figure 5. The seasonal changes in feral female catfish GSI (A) and HSI (B) in the Liao River. Each value represents the mean ± SD, significant difference are indicated by different lower case letters ($p < 0.05$ by Duncan's multiple range test).

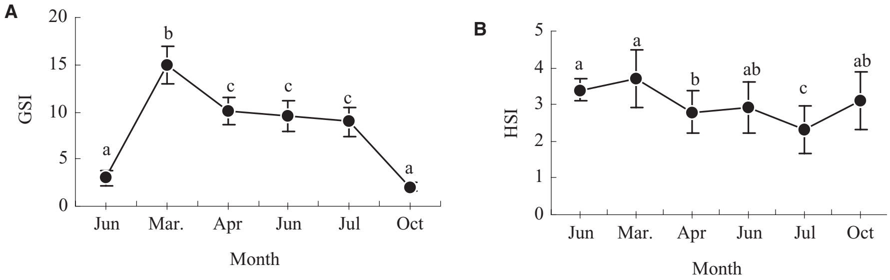

Figure 6. The seasonal changes in feral female catfish GSI (A) and HSI (B) in the Pearl River. Each value represents the mean ± SD, significant difference are indicated by the different lower case letters ($p < 0.05$ by Duncan's multiple range test).

peaking in May (15.9 ± 1.91), then gradually decreased and to reach the lowest GSI in October (3.7 ± 0.81) (Figure 5A). The highest HSIs (4.45–4.88) occurred in stage IV ovary from January to March; whereas lower HSIs were found during spawning period from May to July, and with the lowest HSI value in September (1.73 ± 0.37) (Figure 5B).

In the Pearl River, GSIs of female catfish increased until peaking in March (14.9 ± 1.97), followed by reduced GSIs from April to July with the lowest GSI (2.0 ± 0.44) in October (Figure 6A).The highest HSIs levels occurred in stage IV ovaries from January to March, while lower HSIs were found during the spawning period from May to July, and

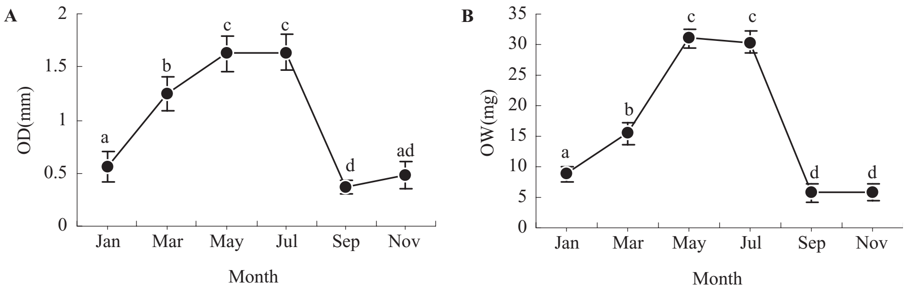

Figure 7. The seasonal changes in feral catfish ODs (A) and OWs (B) in the Liao River. Each value represents the mean ± SD, significant difference are indicated by the different lower case letters ($p < 0.05$ by Duncan's multiple range test).

with the lowest HSI value in July (2.3 ± 0.37) (Figure 6B).

Seasonal variations in OD and OW and their relationship to ovarian development

In the Liao River, ODs were increased during the winter (from November to January) and increased significantly in March, with the highest OD values observed during the spawning period from May to July and the lowest OD value in September (Figure 7A). Seasonal change of OWs are correlated to ODs; the lower OW values occurred during the early stages of ovarian development (November to January) and increased significantly in March, with a higher OWs during the spawning period from May to July and the lowest OW values observed in September and November (Figure 7B).

Discussion

Dose–response competitive inhibition for cGtH and serum GtH from the *S. asotus* indicates a strong parallelism between the displacement by the standard cGtH and the GtH present in the samples. The result demonstrates that cGtH RIA is valid for Japanese catfish, indeed, which heterogenetic RIA have be used successfully for determining GtH from many fish, for example, European eel, *Anguilla anguilla* (Dufour et al. 1983), Chinese loach (Lin et al. 1986), African catfish (Goos et al. 1986) and catfish (Wen & Lin 2001). This heterologous RIA is a useful tool for reproductive endocrine studies in freshwater teleosts, in view of this specificity.

In our study, plasma GtH increased in April in the Pearl River and in May in the Liao River (Figures 1A and 2A). Annual cycles of plasma GtH levels in both rivers are similar, with GtH gradually decreasing after ovulation with the lowest values occurring in September (in Liao River) or October (in Pearl River). Plasma GtH levels increase gradually in the early stage of ovarian development, with the highest values occurring in the stages of maturation. The lowest GtH values observed in both rivers was fully in the regressed ovary stage (Figures 1B and 2B). Pituitary GtH contents retained very high levels during the spawning period, with peak values in March in the Liao River, and in July in the Pearl River (Figures 3A and 4A). The lowest GtH values observed in both systems was in the fully in regressed ovary stage (Figures 3B and 4B). The plasma and pituitary GtH cycles in Japanese catfish is similar to that of the feral African catfish (Van Oordt et al. 1987), where pituitary GtH contents pituitary reached to maximum levels during the breeding period. As in the present study, the African catfish plasma GtH surge took place at the onset of spawning and leading up to oocyte maturation and ovulation, whereas GtH content of the pituitary declined to low levels during period of gonadal regression paralleling gonadal development.

The current study examined the relationship between plasma and pituitary GtH content and GSI. The results indicate that annual changes of plasma and pituitary GtH parallel change in GSI. Pituitary GtH during early, late and maturation of ovarian development is higher in the Pearl River than in the Liao River, with the lowest value observed during ovarian regression. Recent plasma GtH increases in female catfish in the Liao River may be due to higher water temperature, and increased food availability and nutrition in the Pearl River promoting gonadal recrudescence. These results indicate that the spawning period for Japanese catfish is from May to July in the Liao River and from April to July in the Pearl River, and that most spawners are in 2–3 year old (Wei & Huang 1997, Wen et al. 2000). The single peak of plasma GtH and GSI during the annual reproductive cycle in both river systems demonstrates that the Japanese catfish utilizes a synchronous pattern of ovulation. Consequently, most eggs are retained in ovary post-ovulation (Wei & Huang 1997, Wen et al. 2000), the reasons for which are not clear.

In the Japanese catfish, the surge of plasma GtH occurring at the onset of the reproductive period and decreasing thereafter (Figures 1A and 2A) is similar to that in rainbow trout (Goetz 1983). In contrast, goldfish plasma GtH was coincident with ovulation and decreased sharply post-ovulation (Stacy et al. 1979). In some marine fishes with group synchronous or asynchronous ovarian development, the relationship between GtH secretion and gonadal development is more complex (Zohar & Mylonas 2001). A survey of the available literature suggests that the plasma and pituitary GtH profile in teleosts depends on the pattern of ovarian follicular development (Peter & Yu 1997). In general, a pre-ovulatory surge of GtH is responsible for ovulation and spawning of fishes (Lin 1996).

GSI can provide a useful basic measurement of gonadal anabolism (Poortenaar et al. 2001). In feral female Japanese catfish, GSI increases in the spring as follicles enlarge and the granulosa hypertrophies, followed by a drop during spawning in April (in the Pearl River) or May (in the Liao River), with a rise in the autumn as follicles enlarge slightly (Figures 5A and 6A). Plasma GtH levels in female catfish from both river systems show a marked increase which is synchronous with the highest preovulation GSI. Peaks in plasma GtH and GSI were coincident with the onset of spawning in the Liao River in May and in the Pearl River in March (Figures 5A and 6A), whereas GtH content of pituitary remained at a very high levels during the spawning period. The highest HSIs occur pre-ovulation from January to March in both river systems, the lowest HSIs occur during the spawning period from May to July in the Liao River and from April to July in the Pearl River (Figures 5B and 6B). The annual changes in plasma GtH content parallel GSI, but are negatively correlated to HSI in female Japanese catfish. The relationship between GSI and HSI has been documented in several feral fishes.

In autumn spawning red drum, HSI peaks in spring from March to April and declines in September and October; gonadal histology demonstrates active oocyte development in July and August with liver composition varying dramatically throughout the year (Craig et al. 2000). In feral anglerfish, mean female GSI increases rapidly with ovarian development, whereas mean HSI decreases from the middle of vitellogensis until the ovaries have fully matured (Michio et al. 2001). For autumn spawning Korean spotted sea bass, GSI begins to increase in September and peaks (10.1 ± 1.8) in mid-November, with a sharply decrease in late November (Lee & Yang 2002).

It is interesting that HSIs of feral fish remain low during spawning and exhibit the same cycle in both river systems examined in this study. This could be explained in several ways. First, vitellogenin produced by the liver is transported by blood to developing oocytes which reduces HSI (Wallace et al. 1981). Seasonally, fish can utilize hepatic lipid stores for energy and depletion of hepatic lipid reserves in late spring demonstrate energetic costs of reproduction, for example, lipid metabolism in the liver and ovary is greatly influenced by spawning and season (Shiraia et al. 2001, Cejasa et al. 2003). Certain reproductive behaviors may influence vitellogenesis, for example, in mouthbrooding cichlids, changes in GSI showed that vitellogenesis was accelerated when parental care is prevented, whereas GSI of incubating females reach a plateau between days 12 and 21. These findings suggested that ovarian development was slower during the guarding phase (Tacon et al. 1996).

In Japanese catfish, ODs increase significantly from March and are concomitant with increasing OWs in the Liao River (Figure 7A and B). Both GSI and HSI in both river systems showed significant variations during the spawning season. GSI increased markedly in May (in the Liao River) and in April (in the Pearl River). These changes are correlated with increases in OD and OW, and with decreases in HSI. These data suggest that annual variations of plasma GtH content, GSI, OD, OW and HSI are related to the reproductive cycle of Japanese catfish. The same findings are also observed in other fish species. In channel catfish, only one cycle of oogenesis normally occurs each year. OD increases from September to November, remains the same until February, then increases again until maximum diameter is achieved in May (Pacoli et al. 1990). In walleye (Malison et al. 1994), OD increases rapidly from 0.2 mm in October to 1.0 mm in November, and reaches a maximum of 1.5 mm just prior to spawning. Changes in GSI parallel changes in ODs.

Our findings with Japanese catfish indicate that vitellogensis is completed by end of March and it may be possible to induce spawning 1 month prior to the normal spawning season by subjecting fish to relatively simple environment and hormonal treatments. In summary, annual variations of GtH content of the plasma and pituitary of Japanese catfish exhibit the same cycles in the Pearl and Liao Rivers, for example, the surge of plasma GtH occurs during pre-ovulation, pituitary GtH content remains at very high levels during the spawning period, and the lowest GtH values occur coincident with the regressed ovary. Annual changes in plasma and pituitary GtH parallel GSI, OD and OW, but were negatively correlated with HSI in feral female Japanese catfish.

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