ROLE OF HORMONES IN REGULATION OF THE OXIDATIVE METABOLISM IN FISH

BY

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THESIS SUBMITTED IN FULFILMENT OF THE REQUIREMENT OF THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY
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Abstract

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The survival of organisms solely depends on the supply of energy needed for a large number of physiological and metabolic functions. Energy is produced by the oxidation of assimilated food. During the process of oxidation, oxygen is consumed and energy is released and stored in the form of ATP. There is a direct correlation between the rate of oxygen consumption and the energy production. Now it is a well established fact that the rate of oxygen consumption is not merely an index of activity or energy production, but also a standard of overall measure of metabolic processes.

The rate of respiration is influenced by both external (temperature, photoperiod, feeding status, etc.) and internal (hormones, etc.) factors. In nature, vertebrates are exposed to an ever-changing environment. In order to cope up with varying energy demands in relation to the environment and activity, vertebrates have developed a complex neuroendocrine mechanism for regulating energy metabolism to ensure successful survival and reproduction. In homeotherms, the energy metabolism is regulated mainly by the thyroid hormones. However, the calorigenic action of these hormones in poikilotherms has been found to be temperature-dependent, and they do not stimulate the respiratory rate at low ambient temperature. Moreover, there is a complete lack of information on the involvement of iodinated tyrosine derivatives like monoiodotyrosine (MIT) and diiodotyrosine (DIT) in regulation of the oxidative metabolism. Recent studies strongly suggest that the energy metabolism of reptiles and amphibians during winter is controlled mainly by gonadal and adrenal hormones. However, there is a scarcity of information on the role of these hormones in the energy

metabolism of any species of fish. Earlier reports on the calorigenic effect of thyroid hormones in fishes are contradictory. Most of the reports were based on the observations made on the whole body oxygen consumption monitored under controlled conditions. It is important to mention that the placement of a fish in close chamber of respirometers may adversely affect the respiratory rate, and different tissues might not be responding in a similar way to the hormonal treatments. Therefore, measurement of the respiratory rate of tissues seems to be a better parameter for monitoring the calorigenic effect of hormones.

Earlier studies indicate a possible involvement of gonadal steroids and adrenal hormones in regulation of the respiratory rate of fish, but there is practically no information on the regulatory role of thyroidal, adrenal and gonadal hormones in regulation of tissue respiration at natural high and low ambient temperature/under natural climatic conditions. There is also a lack of information on annual/seasonal variations in the rate of respiration of vital tissues of a fish. Since fish differs from amphibians and reptiles in respect of habit and habitat, it may have a different hormonal mechanism for regulation of energy metabolism. Thus, keeping in view the lack of information, the phylogenic position and the economic importance of the fish, it was thought worthwhile to undertake a comprehensive study on the role of various metabolic hormones in the regulation of the tissue respiration in an air breathing fish, male *Clarias batrachus* maintained under natural climatic conditions.

The present dissertation has been divided into six chapters. The abstract of the chapters with findings has been given in the following sections.

Chapter-I : Materials and Methods

This chapter deals with the details of materials and methods used in this Ph.D. dissertation. It incorporates description of the experimental animals, mode of treatments, collection of tissues, methodology for measuring the rate of oxygen consumption and statistical techniques used for analysing the data.

For all experiments adult male *Clarias batrachus* (body weight 70-80 g) were purchased locally during the first week of each month. The fishes were maintained in the earthen pots and acclimatized at least for 15 days in the laboratory under natural climatic conditions at Shillong (Latitude 25°30'N, Longitude 91°52'E, Altitude 1450 ASL, minimum water temperature 4°C and maximum water temperature 22°C). During the acclimatization, the fishes were fed daily with minced earth-worms *ad libitum*. Water was changed frequently to avoid infections.

Hormonal Treatments

Hormonal treatments were given both *in vivo* and *in vitro* conditions. A brief description on the mode of treatments is given below:

In vivo experiments were conducted during both winter (November to March) and summer/rainy (April to October) seasons. After acclimatization, fishes were divided into different groups (four in each group) for different types of treatments. The desired dose of a hormone was injected intra-muscularly on the lateral side of the dorsal fin for four days. The details of doses of hormones and duration of treatments are given in the experimental protocols of the respective chapters. Water temperature was recorded daily at 10.30 am during the experiments.

Collection of Tissues

At the end of four days of a treatment, fishes were decapitated, the tissues (liver, muscle, kidney and brain) rapidly removed, rinsed in ice-cold fish buffer- saline and stored in a refrigerator (-10°C). The rate of tissue respiration was measured within 15 days. When the tissues were stored in the refrigerator, no significant alteration was found in the rate of tissue respiration upto one month.

In vitro effects of the selected hormones on the rate of tissue respiration were studied during both winter and summer/rainy seasons. Four adult male fishes were first weighed and decapitated. The tissues (liver, muscle, kidney and brain) were quickly removed separately, rinsed in ice-cold fish buffer-saline. The tissues were used to study the *in vitro* effect of hormones within 15 days. For *in vitro* treatments, the tissues were blotted, weighed and homogenized in a loose fitting glass homogenizer in ice-cold fish buffer-saline solution (pH 7.4). One ml of homogenate was added to 3.9 ml of fish buffer saline and incubated with 0.1 ml of hormone (having the desired concentration).

MIT, DIT, L-T_3, L-T_4, testosterone, and melatonin treated tissue homogenate were pre-incubated at 4°C for one hour prior to the measurement of the rate of oxygen consumption. This incubation was felt necessary to allow the binding of these hormones to the tissues. The homogenates treated with catecholamines and corticosteroids were incubated only for 15 minutes in the incubation chamber of the oxygen electrode at 25°C before the measurement of oxygen consumption.

Chemicals

Hormones, antagonist and inhibitors used in the experiments were purchased from Sigma Chemical Company, U.S.A. General chemicals were purchased from

BDH. Cyproterone acetate was a gifted from Prof. Dr. M.F. ElEtreby, Berlin.

Measurement of Tissue Respiration

The rate of oxygen consumption of each tissue (liver, muscle, kidney and brain) was measured with the help of an oxygen electrode (Digital Oxygen System, Model 10, Rank Brothers Ltd., England). The system is composed of an incubation chamber of plexi glass (with Ag^+ as anode and platinum as cathode) and a control panel (with knobs to regulate sensitivity, polarizing voltage and speed of the magnetic bar). A thermostatically controlled water circulator is used for circulating water in the incubation chamber of oxygen electrode. For measuring the rate of respiration, polarizing voltage was kept at 0.6V and fish buffer-saline (pH 7.4) was used as the polarizing medium.

For the measurement of tissue respiration, the tissue were first blotted, weighed and homogenized in a loose-fitting all-glass homogenizer (Remi Homogenizer, Remi equipments, Bombay) in ice-cold fish buffer-saline (9:1) solution (pH 7.4). The rate of oxygen consumption of tissue homogenates were measured at 25°C by circulating water at 25°C in water jacket of the incubation chamber using the thermostatic water circulator.

For measuring the rate of respiration of tissues from *in vivo* experiments, 1 ml of homogenate was added to 4 ml of fish buffer saline solution and placed into the incubation chamber of the oxygen electrode. The homogenate were incubated in the chamber for 15-20 minutes before recording the readings. Reading were recorded at an interval of 5 minutes for half an hour. The rate of tissue respiration was expressed as µl O_2/mg wet tissue/h.

Statistical Analysis

Data were analysed statistically with the help of student's t-test and regression analysis (Snedecor, 1961). A $P<0.05$ was considered to be significant.

The above mentioned standard procedures were followed in all the experiments incorporated in this thesis.

Chapter-II

Study of Annual Variations in the Oxidative Metabolism of male *Clarias batrachus* with special reference to Temperature, Photoperiods and Feeding Status

This chapter deals with the study of monthly variations in the rate of oxygen consumption of vital tissues (liver, muscle, kidney and brain). This chapter also deals with the effects of simulated temperature, photoperiod and feeding/fasting on the rate of tissue respiration. The major findings and conclusions based on the experiments included in this chapter are listed below:

1. All the four tissues (liver, muscle, kidney and brain) exhibited an annual rhythm in the rate of oxygen consumption.
2. Liver, muscle and kidney tissues showed similar annual patterns in their rate of oxygen consumption, while the annual pattern of brain respiration was different during winter months.
3. Liver, muscle and kidney tissues exhibited a positive correlation with the natural water temperature.
4. Brain tissue respiration did not show any significant difference in its average rate of oxygen uptake during winter and summer/rainy month.

Further, there was no significant correlation between the brain tissue respiration and the natural water temperature.

5. The rate of muscle tissue respiration was found always to be the lowest and that of the brain to be the highest. The respiratory rate of liver was always higher than that of the kidney tissue.
6. The average rate of oxygen consumption of the liver, muscle and kidney tissues was found to be significantly higher during summer/rainy months as compared to that of winter months.
5. Within the tolerance range, the rate of respiration of liver and muscle tissues linearly increased with the increase in the simulated water temperature. Both tissues show a strong positive correlation with the simulated temperature.
6. Brain and kidney tissue respiration significantly increased with the increase in simulated temperature upto 25° C, thereafter, it sharply decreased with further increase in temperature. Both tissues exhibited a negative correlation with the increase of temperature above 25° C.
7. The liver, muscle and brain tissues respiration exhibited a negative correlation with increasing daylength, while kidney tissues oxygen uptake showed no significant correlation with daylength.
8. All the four tissues (liver, muscle, kidney and brain) showed a positive correlation with the duration of feeding. The respiratory rate of all the tissues except brain significantly decreased after 10 days of fasting.
9. Liver and muscle tissues indicated a negative correlation with the duration of fasting. Kidney respiration exhibited positive correlation with the duration of fasting, which might be associated with the increased active transport rate and removal of the nitrogenous waste product by the kidney. Brain tissue respiratory rate did not exhibit any significant correlation with the duration of fasting.

On the basis of these findings, it may be concluded that the energy demand of different tissues varies with seasons, and seems to be related with the seasonal changes in physical and reproductive activities of the fish. The respiratory rate of liver and muscle tissues seem to be directly affected by the change in temperature, daylength and feeding status. Kidney respiration of the fish seems to be independent of the changes in daylength, however, it increases with the duration of fasting. Brain tissue respiration does not seem to be adversely affected by temperature and fasting. Brain might be possessing a self-regulating mechanism for ensuring the successful survival of the fish during the stressful conditions of winter.

Chapter-III

Role of Thyroid Hormones in Regulation of the Oxidative Metabolism in Male *Clarias batrachus*

This chapter deals with the *in vivo* and *in vitro* effects of mono- iodotyrosine (MIT), diiodotyrosine (DIT), L-triiodothyronine (T_3), L-thyroxine (T_4) and propyl thiouracil (PTU) on the rate of oxygen consumption of tissues during winter and summer/rainy months. This chapter also contains data of experiments pertaining to mechanism of action of iodotyrosines (MIT and DIT) and L-T_3. The major findings of this chapter are as follows :

1. *In vivo* administration of L-T_3 and L-T_4 did not stimulate fish tissue respiration during winter months. However, both L-T_3 and L-T_4 significantly stimulated the respiratory rate of all the tissues during summer/rainy months.

2. *In vitro* treatment of L-T_3 and L-T_4 stimulated only brain tissue respiration during winter, but significantly increased the respiratory rate of all the tissues during summer/rainy months.
3. *In vivo* administration of MIT significantly increased the respiratory rate of muscle and brain tissues during winter and only of muscle tissue during summer/rainy months. However, *in vitro* treatment of MIT significantly increased the respiratory rate of all the tissues during winter and only of liver and muscle during summer/rainy months.
4. *In vivo* and *in vitro* administration of DIT significantly stimulated the respiratory rate of all the tissues irrespective of seasons. It seems that DIT is more important than MIT in stimulating of the oxidative metabolism in this fish.
5. *In vivo* administration of MIT and DIT stimulated the fish tissue respiration in a dose-dependent manner.
6. *In vivo* administration of PTU significantly decreased the respiratory rate of liver, muscle and kidney tissues irrespective of water temperature. while brain tissue respiration was inhibited by PTU at high temperature.
7. PTU significantly decreased the rate of tissue respiration during both summer/ rainy and winter seasons. During summer PTU-induced decrease in tissue respiration was reversed significantly by L-T_3 and L-T_4.
8. The decreased tissue respiration after PTU treatment during winter seems to suggest that the indogenous thyroid hormones are involved in the oxidative metabolism of the fish at low temperature.
9. Treatment of the tissue homogenates with ouabain and actinomycin-D separately, significantly decreased the respiratory rate of liver, muscle and kidney tissues.
10. Both ouabain and actinomycin-D significantly, but not completely, inhibited the stimulatory effect of L-T_3 suggesting that L-T_3 stimulated

tissue respiration via transcription process as well as by increasing the activity of Na^+- K^+- ATPase.

11. The significant inhibition of the stimulatory effect of MIT and DIT on respiration seem to suggest that, similar to L-T_3, MIT and DIT also stimulated tissue respiration through DNA-dependent RNA synthesis and Na^+- K^+- ATPase.

These findings clearly indicate that L-T_3 and L-T_4 are ineffective in stimulating tissue respiration of the fish during winter. MIT and DIT seem to be actively involved in the regulation of tissue respiratory rate irrespective of the water temperature. The indigenous thyroid hormones are involved in the regulation of tissue respiration of the fish also during the winter months. The iodotyrosines and the iodothyronines seem to produce their calorigenic effect in tissue respiration by stimulating the activity of mitochondrial enzymes, Na^+-K^+-ATPase and the transcription process. MIT and DIT seem to produce their stimulatory effect through a similar pathways like that of T_3 and T_4. The temperature-independent calorigenic action of MIT (tissue-dependent) and DIT indicates that these hormones might be the initial regulators of the oxidative metabolism and their calorigenic role might have been replaced by T_3 and T_4 during the course of evolution.

Chapter-IV

Role of Testicular Hormones in Regulation of the Oxidative Metabolism in male *Clarias batrachus*

This chapter deals with *in vivo* and *in vitro* effects of testosterone and cyproterone acetate (a blocker of androgen receptors) on the rate of tissue respiration

during winter and summer/rainy months. It also contains data of experiments conducted to find out the mechanism of action of testosterone. The major findings of the experiments included in this chapter are mentioned below :

1. Testosterone significantly stimulated the respiratory rate of all the tissues irrespective of temperature and seasons.
2. Testicular hormones seem to be directly involved in regulation of the oxidative metabolism of the fish.
3. Cyproterone acetate always inhibited the respiratory rate of liver, muscle and kidney tissues.
4. Administration of actinomycin-D or cyproterone acetate significantly, but not completely, blocked the stimulatory effect of testosterone on the rate of tissue oxygen uptake.
5. Testicular hormones increased the respiratory rate of the tissues by stimulating the transcription process (genomic pathway) via androgen receptors and the enzyme Na^{+}-K^{+}-ATPase (extra-nuclear/non-genomic pathway).

Therefore, on the basis of the present findings, it may be concluded that the testicular hormones play an important and direct role in the regulation of the oxidative metabolism of the fish due to their temperature-independent metabolic action. These hormones might be more important than thyroid hormones, particularly T_3 and T_4, in ensuring the energy production for successful survival of the fish during the cold winter season.

Chapter-V

Role of Catecholamines and Corticosteroids in Regulation of the Oxidative Metabolism in male *Clarias batrachus*

This chapter deals with the experimental studies on *in vivo* and *in vitro* effects of adrenal hormones (epinephrine, norepinephrine, corticosterone, cortisol, and cortisone) and metapyrone (an inhibitor of corticosteroid biosynthesis) on the rate of tissue respiration. It also deals with the experiments conducted to study the synergistic effects of thyroid hormones and catecholamines, and the mechanism of action of catecholamines. The findings of these experiments are mentioned below :

1. Catecholamines (epinephrine and norepinephrine) invariably stimulated the respiratory rate of all the tissues (liver, muscle, kidney and brain) in the fish irrespective of mode of treatments (*in vivo*/*in vitro*), water temperature and seasons.
2. The degree of stimulation by epinephrine and norepinephrine is higher during winter as compared to that of summer/rainy months.
3. Epinephrine is more potent than norepinephrine in stimulating the rate of muscle tissue oxygen uptake, while norepinephrine is more potent than epinephrine in stimulating liver tissue respiration.
4. The stimulatory effects of the catecholamines during winter was significantly potentiated by L-T_3 and L-T_4. However, during summer/rainy months the catecholamines and the thyroid hormones produced a synergistic effect on the rate of tissue respiration in both *in vivo* and *in vitro* treatments.

5. Both α- and β-adrenergic receptors are involved in the calorigenic action of catecholamines in the fish. The α- and β-adrenergic receptors of the tissue exhibited a cross-reactivity for different agonists.
6. The degree of involvement of α- and β-adrenergic receptors in the calorigenic action of catecholamines varies with tissues and season.
7. *In vivo* and *in vitro* administration of corticosteroids invariably stimulated the respiratory rate of all the tissues irrespective of water temperature and seasons, except cortisone which did not stimulate brain tissue oxygen uptake in *in vitro* experiments during summer.
8. The degree of stimulation of tissue respiration by corticosteroids was comparatively higher during winter as compared to that during summer/ rainy seasons.
9. The administration of metapyrone significantly decreased the oxygen uptake of the tissues (liver, muscle, kidney and brain). However, administration of the corticoids reversed the adverse effect of metapyrone on tissue respiration.

It, thus, seems that the catecholamines and the corticosteroid hormones are very important for the regulation of tissues respiration of the fish, *Clarias batrachus*. Since the production of these hormones is increased during stress and under emergency situations, they might be acting as the emergency hormones for the regulation of the energy metabolism to ensure successful survival under adverse climatic conditions. The potentiation of the calorigenic action of the catecholamines by the thyroid hormones during winter suggests an important but indirect role of endogenous thyroid hormones in the regulation of the oxidative metabolism of the fish. Both α- and β-adrenergic receptors are employed in the calorigenic action of the catecholamines in the fish, *Clarias batrachus*, and might be using cAMP, Ca^{++}, IP_3 etc. as the second messengers.

Chapter-VI

Effects of Melatonin on the Oxidative Metabolism in Male *Clarias batrachus*

This chapter incorporates the data of *in vivo* and *in vitro* experiments conducted to study the effects of melatonin on the rate of tissue respiration during winter and summer/rainy months. The findings of these experiments are listed below:

1. Melatonin invariably stimulated the respiratory rate of all the tissues (liver, muscle, kidney and brain) irrespective of water temperature and seasons.
2. The *in vitro* effect of melatonin on the tissue metabolic rate seems to suggest that melatonin has a direct effect at tissue level in stimulating the oxidative metabolism in the fish.
3. Melatonin stimulated tissue respiration in a dose-dependent manner.

On the basis of these findings, it may be concluded that melatonin has a capability to stimulate the tissue respiration of the fish directly. Since short daylengths and low temperature have been reported to increase melatonin production in several vertebrates, the observed involvement of melatonin in the oxidative metabolism of the fish might be helpful as an additional hormone in maintaining the minimum metabolic rate during winter to ensure the survival of the fish. The degree of stimulation of the respiratory rate seems to depend on the tissue and the daylengths.

CONCLUSIONS

On the basis of the major findings of the present Ph.D. dissertation, it can be concluded that the vital tissues of the fish *Clarias batrachus* exhibit an annual rhythm of variation in their rate of respiration. The tissue metabolic rate in the fish seems to be regulated by a complex set of external factors (like temperature, photoperiod, availability of food etc.) and internal factors (hormones). The thyroidal, adrenal, testicular and pineal hormones seem to play a major role in the regulation of the fish tissues respiration. The relative involvement and role of different endocrine glands and their hormones vary with tissues and seasons of the year. The exogenous L-T_3 and L-T_4 produce a temperature-dependent effect in fish tissue respiration, however, the endogenous thyroid hormones stimulate the oxidative metabolism indirectly by potentiating the calorigenic action of catecholamines. MIT and DIT are calorigenic in the fish irrespective of the ambient temperature, and, therefore, might be playing an important role in the regulation of the oxidative metabolism of the fish. Further, the involvement of the iodotyrosines might be of evolutionary significance. The catecholamines and corticosteroid hormones, which are produced in response to non-specific stress and under emergency conditions, produce a temperature-independent calorigenic effect in the fish and seem to act as emergency hormones for the oxidative metabolism of *Clarias batrachus*. The testicular hormones also seem to be directly involved in the regulation of fish energy metabolism, particularly at low ambient temperature. The involvement of the testicular hormones in the oxidative metabolism might be a mechanism to ensure higher metabolic rate required for successful reproduction in case of a sudden decline in the ambient temperature during breeding season and/or for survival during winter months. In addition to these hormones, melatonin also seems to be capable in stimulating the metabolic rate of the fish. This might be helping to meet the energy demand particularly during winter when temperature is low and daylength is short which favour melatonin

production. The testicular and thyroid hormones seem to stimulate tissue respiration via nuclear pathway as well as via the enzyme Na^+-K^+-ATPase. NE and EP seem to act via both α-and β-adrenergic pathways. However, the mode of action of melatonin remains to be established.

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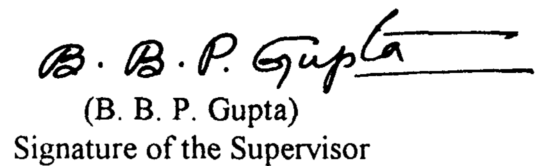
I hereby certify that the thesis entitled ***"Role of Hormones in Regulation of the Oxidative Metabolism in Fish"*** by Mr. D.S. Lynshiang for the Degree of Doctor of Philosophy of the North-Eastern Hill University, Shillong (Meghalaya) embodies the record of original investigation carried out by him under my supervision. He has been duly registered and the thesis presented is worthy of being considered for the award of the Ph. D. degree. This work has not been submitted for any degree of any University.



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PREFACE

Survival of vertebrate solely depends on the supply of energy needed for a large number of physiological and metabolic functions. In biological systems, energy is produced by oxidation of digested food. The entire process of energy production is termed as energy metabolism or oxidative metabolism. During the process of oxidation, oxygen is consumed and energy is released. There is a direct correlation between the rate of oxygen consumption and energy production. Now it is well established that the rate of oxygen consumption is not merely an index of activity or energy generation but is also a standard of overall measure of metabolic processes.

The rate of respiration is influenced by both climatic (temperature, photoperiod, feeding, etc.) and internal (hormones) factors. Hormones play a major role in regulation of the oxidative metabolism. The vertebrates are exposed to an ever changing environment (both external and internal). In order to cope up with varying energy demands in relation to the environment and physical activity, vertebrates have developed a complex neuroendocrine mechanism for regulating energy metabolism to ensure successful survival and reproduction. Homeotherms and poikilotherms seem to differ from each other in respect of hormonal regulation of respiration. In homeotherms, the energy metabolism is regulated mainly by thyroid hormones. However, the calorigenic action of these hormones has been found to be temperature-dependent in poikilothermic vertebrates. Since thyroid hormones do not stimulate respiratory rate of fish, amphibian and reptiles exposed to low temperature (below 20°C), they can not ensure energy supply and hence survival of the poikilotherms at low ambient temperature, especially during winter season. Recent studies strongly suggest that the energy metabolism of reptiles and amphibians during winter is

controlled mainly by gonadal steroids and adrenal hormones. However, there is scarcity of information on the role of these hormones in the energy metabolism of fish. A large body of information suggests that thyroid hormones are calorigenically ineffective in fish exposed to low temperature. Most of the earlier reports are based on observations made on whole body oxygen consumption monitored under controlled conditions. Placement of fish in a closed chamber respirometer may adversely affect the respiratory rate. Moreover, different tissues might not be responding to hormones in a similar way. Therefore, measurement of the respiratory rate of tissues seems to be a better parameter for monitoring calorigenic action of hormones of the thyroid and other endocrine glands. However, there are only few reports regarding the effects of thyroid hormones on the rate of fish tissue respiration. Further, earlier studies indicate a possible involvement of gonadal steroids and adrenal hormones in regulation of the respiratory rate of fish. But there is practically no information on regulatory role of adrenal and gonadal hormones in the regulation of tissue respiration of high (at or above 20°C) and low (below 20°) temperature under natural climatic conditions. There is also lack of information on the annual variations in the rate of respiration of vital tissues of a fish. Since fish differs significantly from amphibians and reptiles in respect of habit and habitat, it may have a different hormonal mechanism for regulation of energy metabolism. Therefore, keeping in view the lack of information and the phylogenic and economic importance of the fish, it was thought worthwhile to undertake a comprehensive study of the role of various metabolic hormones in the regulation of tissue respiration (oxidative metabolism) of the air breathing fish, *Clarias batrachus* maintained under natural climatic conditions.

The present dissertation has been divided into six chapters. The details of the chapters are given in the following sections.

Chapter - 1 : Materials and Methods

This chapter deals with the details of materials and methods used for this Ph.D. dissertation. It incorporates description of the experimental animals, mode of treatments, isolation of tissues, methodology used for measuring the rate of oxygen consumption and statistical techniques used for analysing the data.

Chapter - 2 : Study of Annual Variation in the oxidative metabolism of Male *Clarias batrachus* with Special Reference to Temperature, Photoperiods and Feeding status

This chapter deals with the study of monthly variations in the rate of oxygen consumption of vital tissues (liver, muscle, kidney and brain). This chapter also deals with the effects of simulated temperature, photoperiod and feeding/fasting on the rate of tissue respiration.

Chapter - 3 : Role of Thyroid Hormones in Regulation of the Oxidative Metabolism in Male *Clarias batrachus*

This chapter deals with the *In vivo* and *In vitro* effects of mono- iodotyrosine (MIT), di-iodotyrosine (DIT), L-tri-iodothyronine (T_3), L-thyroxine (T_4) and propyl thiouracil (PTU) on the rate of oxygen consumption of tissues during winter and summer/rainy months. This chapter also contains data of experiments pertaining to mechanism of action of iodotyrosines (MIT and DIT) and L-T_3.

Chapter - 4 : Role of Testicular Hormones in Regulation of the Oxidative Metabolism in Male *Clarias batrachus*

This chapter deals with *in vivo* and *in vitro* effects of testosterone and cyproterone acetate (a blocker of androgen receptors) on the rate of tissue respiration during winter and summer/rainy months. It also contains data of experiments conducted to find out the mechanism of action of testosterone.

Chapter - 5 : Role of catecholamines and corticosteroids in Regulation of the Oxidative Metabolism in Male *Clarias batrachus*

This chapter deals with the experimental studies on *in vivo* and *in vitro* effects of adrenal hormones (epinephrine, norepinephrine, corticosterone, cortisol, and cortisone) and metapyrone (an inhibitor of corticosteroid biosynthesis) on the rate of tissue respiration. It also deals with the experiments conducted to study the synergistic effects of thyroid hormones and catecholamines, and the mechanism of action of catecholamines.

Chapter - 6 : Effects of Melatonin on the oxidative metabolism in Male *Clarias batrachus*

This chapter incorporates the data of *in vivo* and *in vitro* experiments conducted to study effects of melatonin on the rate of tissue respiration during winter and summer/rainy months.

Findings of the present study suggest that in addition to T_3 and T_4, MIT and DIT are also involved in regulation of the oxidative metabolism of *male Clarias batrachus*. Since the calorigenic effect of MIT and DIT seems to be temperature-

independent, they might be playing an important role in calorigenesis during winter and at lower temperatures. Further, as in amphibians and reptiles, testicular hormones, adrenal hormones and melatonin also seem to be directly involved in the regulation of respiration of this fish. The present findings seem to provide, for the first time, a complete picture of hormonal regulation of tissue respiration in a fish and to contribute significantly to our knowledge regarding evolution of hormonal regulation of the oxidative metabolism in poikilothermic vertebrates.

INTRODUCTION

The oxidative metabolism is an intricate process which was evolved for efficient oxidation of food substrates and production of energy. The energy released ruing oxidation is used for thermoregulation and is also stored as high energy bond of ATP which is utilized for various energy-dependent processes. The oxidative metabolism is influenced by both internal and external factors. The internal factors include sex, age, feeding status, neurotransmitters and hormones. The external factors include temperature, photoperiod, rainfall, seasons, humidity, availability and type of food etc. Animals rarely live under a constant environmental conditions. They face marked diurnal and seasonal oscillations which alter physical activity and the metabolic rate (Prosser, 1955, 1969; Aschoff and Pohl, 1970). Amongst the internal factors, hormones play a major role in the regulation of energy metabolisms. A large number of hormones secreted by several endocrine glands (e.g., gonads, thyroid, pineal, adrenals, pancreas, pituitary etc.) have been reported to be actively involved in regulation of the oxidative metabolism of vertebrates (Padgaonkar and Rangnekar, 1974; Nedergard and Linberg, 1979; Idler and Fruscott, 1980; Danforth and Burger, 1981; Thapliyal, 1980; Barre and Rouenet, 1983; Matty and Love, 1983; Thapliyal and Gupta, 1983; Nelson *et al.*, 1984; Binkley, 1988; Gupta and Thapliyal, 1991). Amongst the external factors, temperature, photoperiods and seasons have been found to play an important role in the energy metabolism of vertebrates (Ballinger *et al.*, 1969; Prosser, 1973; Bartholomew, 1977; Albert, 1988; Bjonsson *et al.*, 1989, 1994; Swanson, 1991; Basco *et al.*, 1996). These external and internal factors, jointly and/or separately, are directly or indirectly responsible for variations in the oxidative metabolism of vertebrates.

It is important to mention that the oxidative metabolism is studied in term of the metabolic rate (the rate of oxygen consumption). The metabolic rate is a reflection

of over all catabolic energy transformation within the body. Due to this reason, the oxidative metabolism has been termed as the "fire of life" (Kleiber, 1961). The energetic transformations are essential for all biological activities starting from molecular and biochemical levels to processes of great evolutionary significance like growth/development, maturation, reproduction etc. The amount of energy produced is directly proportional to the amount of oxygen consumed. Thus, the rate of oxygen consumption acts as an index of the metabolic rate. It seems that the degree of involvement of the internal and external factors depends upon the phylogenic position of vertebrates. A critical summary of the vailable information regarding the role of various climatic factors and hormones in the oxidative metabolism of different groups of vertebrates is given below.

Seasonal cycles of animal behaviour and physiology are influenced by changes in daylengths (Dark *et al.*, 1983; Farner, 1985). It is reported that photoperiod acts as the most reliable parameter for seasonal cueing in the temperate zone lizard, *Lacerta viridis* where it influences body temperature (Tb) selection (Rismiller and Heldmaier, 1982, 1987, 1988). Since it is very difficult to delineate effects of photoperiod and photoperiod-associated alteration in ambient temperature under natural conditions, it seem that the natural variations in joint effects of photoperiod and ambient temperature provide information for seasonal acclimation involving both behavioural and physiological adjustments (Rismiller and Heldmaier, 1982, 1988). Thus, seasonal changes in photoperiod and temperature can alter the metabolic rate of vertebrates (Hutchinson, 1971; Hutchinson and Kohl, 1971; Saarela and Vakkuri, 1982). In *Varanus scalaris*, the standard metabolic rate (SMR) and resting metabolic rate (RMR) were found to change with seasons, and were significantly higher in wet season, though there were no differences in maximal oxygen consumption between seasons (Christian *et al.*, 1996). The metabolic effects of photoperiods (Long or short

daylengths) might be mediated by the pineal gland. In response to alteration in photoperiod, the pineal gland sends metabolic signals by releasing its hormone, melatonin (Axelrod, 1974; Cagnacci *et al.*, 1993). Changes in daylength have been found to play a prominent role in the synchronization of bodily functions. In *Salmo salar* long photoperiod (15L/9D) increased the activity of Na^{+}-K^{+}-ATPase, where as short photoperiod (9L/15D) depressed the activity of this enzyme (McCormick *et al.*, 1995). The metabolic rate of pigeons decreased under short daylength (Basco *et al.*, 1996). However, in Djungarian hamster short daylength increased the nonshivering thermogenesis (Heldmeier *et al.*, 1982; Puchalski *et al.*, 1983; Wiesinger *et al.*, 1989). Short day and low temperature in red back voles induced an increase in basal metabolic rate and nonshivering thermogenesis (Lynch, 1973; Feist and Rosmann, 1976; Wickler, 1980; Feist and Morison, 1981; Haim, 1982). It has also been reported that short daylength and low temperature (8L/16D, 5°C) increased the resting metabolic rate (RMR), nonshivering thermogenesis (NST), liver cytochrome oxidase activity and brown adipose tissue (Li-Qing *et al.*, 1995), while short daylength and high temperature had no effect on nonshivering thermogenesis (NST) (Ballinger et al., 1969; Chaffee and Allen, 1973) and basal metabolic rate (BMR) of the voles (Hoffman, 1979).

Temperature is another well known environmental factor which affects most of the physiological processes, particularly in the poikilothermic vertebrates. It has profound influence on different aspects of reproduction, hormonal regulation of development of gonadal activity, timing of ovulation/spawning, etc (Bohra and Nazi, 1984; Saidapur, 1989). Changes in environmental temperature directly cause alterations in activities and metabolic rate of ectotherms. This thermal dependence has both advantage sand disadvantage for poikilothermic vertebrates (Somera and Hochachka, 1971). At low body temperature, activity, synthetic as well as energy

extraction capacities and energy expenditure are greatly reduced resulting in great energy economy (Baranska and Wlodawer, 1969; Bennett and Nagy, 1977). Increased body temperature of poikilotherms has direct effects on biological processes and greatly accelerates the cellular reaction rate (Dean, 1969; Young etal., 1979; Cossin and Bowler, 1987; Anderson and Pandey, 1990). Within the thermal tolerance range, teleosts have been reported to increase or decrease oxygen uptake according to fluctuations in temperature (Fry, 1971). Studies in *Sebasticus marmoratus* indicates that the rate of oxygen consumption increases with temperature up to 23°C. However, above 23°C the rate of oxygen consumption decreased with increase in temperature (Kia *et al.*, 1996). Studies on isolated hepatocytes of rainbow trout, *Oncorhynchus mykiss* suggest that increasing incubation temperature stimulate protein synthesis and oxygen consumption (Panevis and Houlihan, 1992). Further, experimental studies on *Sockeye salmon* indicate that the maximum oxygen uptake in response to temperature is 4-8 times higher than the resting metabolic rate. The oxygen uptake increases as temperature rises up to 15°C above which there is less variation in respiratory rate with further increase in temperature (Brett, 1964). In the goldfish it was found that over the range of 5°C-35°C, the standard metabolism increased to its highest value at about 30°C. The SMR was maintained constant or decreased slightly at temperature higher than 35°C (Fry and Hart, 1948; Veronica, 1973). It seem that the energy requirement of the species increase with the water-temperature. However, *Salvelinus fontinalis* seems to be exception where the rate of oxygen consumption was not affected by acclimation temperature (Schwarzbaum *et al.*, 1992). A study in the catfish, *Ichtalurus punctatus* showed an increase in cell size and enzyme activity when acclimatised at 10°C (Kent *et al.*, 1988). A critical analysis of the above mentioned information seems to suggest that the nature of effect of temperature on the metabolic rate varies from species to species.

The role of temperature in reptiles has been reported to vary with tissues and species. Low temperature in *Calotes versicolor* increased brain tissue respiration (Das and Patnaik, 1979; Sharan, 1983). In *Uromastyx microelpris* (Zari, 1991) and *Uromastyx philbyi* (Zari, 1996), the SMR was significantly increased at 20°C-25°C. The whole body oxygen consumption of *Iquanas* increased at 35°C and the metabolic rate of *Anolis gundlachi* decreased at 30°C (Rogowitz, 1966). However, studies on *Thamnophis_sirtalis* suggest that change in acclimation temperature from 23°C-33°C and 33°C-23°C has no effect on brain tissue respiration (Bennet and Dawson,1976).

Unlike in poikilotherms, the body temperature of homeotherms does not decrease or increase with the environmental temperature, while their metabolic rate is influenced by the ambient temperature. Exposure of chicks to low temperature results in increased rate of whole body oxygen consumption (Freeman, 1964, 1967; Drent and Klassen, 1989). Generally, the metabolic rate of birds has been reported to increase during the winter months and decrease during the late spring (West, 1965; Pohl and West, 1973; Hohtola, 1982; Hohtola and Stevens, 1986; Connor, 1995). It has also been reported that there is onset of shivering in pigeons and green finches when they are exposed to low temperature (Saarela *et al.*, 1995).

Mammals exposed to low temperature show an increase in non-shivering thermogenesis (NST) Freinkel and Lewis, 1975; Tomasi and Mitchel, 1976). However, low temperature has been reported to inhibit electron transport in the respiratory chain in the ground squirrel (Gehnrich and Aprille, 1988) and to decrease the activity of liver mitochondrial enzymes of hibernating mammal (Pechowich and Wang, 1984, 1987; Gehnrich and Aprille, 1986, 1988). When rats were transferred from a high (23°C) to a low (6°C) temperature, their metabolic rate was found to be increased (Kuroshima *et al.*, 1967; Lynch, 1973). Similarly, pig was found to increase its whole body oxygen

consumption when exposed 10°C (Feist and Rosenmann, 1976). Seasonal increase in maximum metabolism and non-shivering thermogenesis during winter have been reported in many wild rodents (Wickler, 1980; Haim, 1982). Further, it has also been reported that cold acclimation increased thermogenesis in new born of non-hibernating rodents. A number of lower mammalian species show a significant increase in their RMR during cold acclimation (LeBlanc and Valliere, 1967; Gordon *et al.*, 1968). Dryer *et al.* (1970) have reported that high temperature significantly decreased the rate of oxidation of succinate and free fatty acids in mammals. In general, the warm-blooded animals (birds and mammals) can tolerate only a narrow range of environmental temperature. In mammals the body temperature is maintained between 36°C and 38°C and in birds between 39°C and 42°C (Prosser, 1973). With the increasing temperature, the body temperature of homeotherms has been reported to increase by 2-3°C above the normal body temperature after which (after few hours) they come back to normal. Once the ambient temperature exceeds the body temperature, homeotherms resort to evaporative cooling and decrease BMR in order to maintain a constant body temperature (Prosser, 1973).

Availability of food is another major external factor which regulates energy metabolism in most of the vertebrates. The standard metabolic rate (SMR) of the Brook trout has been reported to decrease after fasting for three days and the decreased SMR remained constant for 8-10 days (Beamish, 1964). Re-feeding increased the metabolic rate in rats (Defrutors *et al.*, 1991) and the cat-fish (Machado *et al.*, 1988). It has also been reported that in *Barilius bendelisis*, fasting for 90 days led to a decrease in protein and lipid content (Alliot *et al.*, 1984; Charel *et al.*, 1992; Bahuguna and Rawat, 1994). Fasting in golden perch has been reported to result in decreased heat Somatic Index (Collin and Anderson, 1995). Further, it has also been reported that the plasma glucose level of fasted rainbow trout were significantly lower

as compared to the fed fish (Farbridge *et al.*, 1992; Castellini and Ria, 1992; Vijayan and Moon, 1992; Reddy and Leatherland, 1995). Starvation in *Cyprinus carpio* leads to a decrease in lipid, glycogen, protein and RNA contents (Kuruvilla *et al.*, 1993). The average rate of oxygen consumption in *Perca fluviatelis* has been reported to decrease during starvation (Mehner and Wieser, 1994). Similarly, food deprivation has been reported to decrease the metabolic rate of reptiles (Galton, 1980; Sievert *et al.*, 1988; Seymour and Seely, 1996). Feeding of lizards with thread mill worms reportedly increases the rate of whole body oxygen consumption (Christian *et al.*, 1996).

Feeding in Penguin, *Eudyptula minor* has been found to increase the metabolic rate (Costa and Kooyman, 1984; Baudinette *et al.*, 1986), while fasting in *Tengmalm ovol* decreases the body temperature (Groscolas, 1990; Hohtola *et al.*, 1994). Further, the meal has been reported to increase thermogenesis in brown adipose tissue of hamster (Locke *et al.*, 1982) and the rate of whole body oxygen consumption of dogs (Astrup *et al.*, 1985). Dietary restriction caused a reduction in the activity of the enzyme cytochrome oxidase in mice and reduced serum T_3 level in rats (Glass *et al.*, 1978; Ross, 1969; Richard *et al.*, 1980). Further, it also diminished the metabolic rate of rats (Reichlin, 1957; Harris *et al.*, 1978; Kaplan and Utinger, 1978; Kaplan, 1979; Rondeel *et al.*, 1992). Feeding in the musk rat, *Ondatra zibethicus* increased resting metabolic rate (McArthur and Campbell, 1994), and basal metabolic rate of mice (Speakman and Queenie, 1996). Rats fed on protein diet had been reported to increase their thermogenesis (Hillgartner *et al.*, 1987). Fasting for 72 hr has been shown to reduce RMR of rats. However, refeeding leads to an increased rate of oxygen consumption (Rothwell *et al.*, 1982b).

These reports clearly suggest that the metabolic rate of vertebrates are, directly or indirectly, influenced by the changes in the external factors like, daylength,

temperature, availability of food, etc. The effect of daylength on the oxidative metabolism can not be dissociated from that of temperature due to the fact that the increased daylength is always associated with high environmental temperature. However, effects of daylength or seasons vary from species to species. In poikilotherms, short daylength and temperature seem to decrease the metabolic rate, while in homeotherms low temperature induces thermogenesis and increased metabolic rate. Further, unlike in poikilotherms, where high temperature increases enzyme activity and metabolic rate, in homeotherms high temperature above the body temperature generally decreases the metabolic activity. It seem that availability of food stimulates oxidative metabolism in both poikilotherms and homeotherms. While food deprivation leads to a decrease in the physiological activity and metabolic rate of all vertebrates. However, the rate of reduction in metabolic rate varies from species to species, length of fasting and food consumption.

A careful analysis of the available literature also suggests that unlike in higher vertebrates, there is limited information on effects of external factors on the oxidative/energy metabolism of Poikilotherms in general and of fish in particular.

Hormonal Regulation of the Oxidative Metabolism

The neuroendocrine system act as a link between the environment and the vertebrates. It plays a major role in adaptation of vertebrates against ever changing environment. In general, the changes in environment alter the synthesis, release and metabolism of the hormones. In addition to their direct effect, environmental factors also alter the metabolic rate by altering the production of the metabolic hormones.

Moreover, hormones seem to influence the rate of the oxidative metabolism independent of the changes in environmental factors. Due to these reasons, attempts have been made to investigate the role of various hormones in regulation of the oxidative metabolism of vertebrates. A critical review of the available information on hormonal regulation in the oxidative metabolism in different vertebrates groups is given below.

Hormonal regulation of the oxidative metabolism in mammals

The role of hormones in regulation of the oxidative metabolism of mammals is well studied. A summary of the available information on effects of hormones on the oxidative metabolism of mammals has been mentioned in Table-I. The energy metabolism of mammals seems to be regulated primarily by thyroid hormones (Tata *et al*., 1963; LeBlanc, 1972; De-Groot and Stanburg, 1975; Turner and Bagnara, 1976; Oppenheimer, 1979; Ellison and Skinner, 1990; Soboll,1993). Magnus-Levy (1895) for the first time reported that hypothyroidism decreased and hyptethyroidism increased the rate of oxygen consumption in man. Further, thyroidectomy reportedly decreased and administration of thyroid hormones reversed the effect of thyroidectomy (Hsieh and Carlson, 1957; Triandafillou, 1982). Thus, thyroid hormones seem to be essential for defence against cold, specially in the hypothyroid animals (Fregly *et al*., 1973). However, high doze of thyroxine produced uncoupling of oxidation and phosphorylation with depressed phosphorylation, a catabolic action with decreased oxygen uptake (Tata, 1964). It has also been reported that thyroid hormones' thermogenic action change the morphology and physiology of mitochondria (Hoch, 1977; Shear, 1980). Edelman (1979) reported that the metabolic rate of all tissues except brain of the adult mammals is responsive to thyroid hormones. Unlike in adults, the brain of neonatal rats reportedly responds to L-T_3 administration by increasing its

rate of oxygen consumption (Reiss and Wyatt, 1956; Ranjan *et al.*, 1982). However, contradictory reports suggest that the brain mitochondrial a-glycerophosphate (a-GPD) and cytolic malic enzyme (the biochemical indices of thyroid function) do not respond to the administration of thyroid hormones both in adult and neonatal rat brain (Shapiro *et al.*, 1966).

It is important to mention that in most of the earlier studies only L-T_3 and/or L-T_4 were assessed for their calorigenic action. However, only few attempts have been made to investigate the role of other secretions of thyroid gland, particularly of low molecules thyroid hormone like mono-iodothyrosine (MIT), di-iodotyrosine (DIT), mono-iodothyronine (T_1) and di-iodothyronine (T_2) (Jorgensen, 1978). Recently T_2 has been reported to increase the activities of mitochondrial enzymes in rat liver (Goglia *et al.*, 1994) and also to stimulate oxygen consumption in human mono-nuclear blood cells (Kvetny, 1992). Further, combined administration of L-T_3 and T_2 in hypothyroid rats induced a significant increase in the liver cytochrome oxidase activity and restore mitochondrial protein content (Lanni *et al.*, 1992). T_2 is reportedly produced *in_vivo* by the action of iodothyronine deiodinase on L-T_3. Further, it has a short term effect on the oxidative metabolism and is more potent than L-T_3 in stimulating the metabolic rate (Horst *et al.*, 1989; O'Reilly and Murphy, 1992). Ingestion of one gram of T_1 significantly increased prolactin (PRL) in both men and women (Tan *et al.*, 1991). It, thus, seems that both T_1 and T_2 act as hormones and are capable of stimulating the oxidative metabolism of mammals. Though MIT and DIT have also been reported to be present in the blood (Norman and Litwack, 1978; Gorbman et *al.*, 1983; Martin, 1985), there is practically no information on the biological significance of these molecules in mammals.

The ability of thyroid hormones to stimulate oxygen consumption has been attributed to their capability to stimulate mitochondrial or ribosomal protein synthesis (Tata, 1966; DeNayer, 1987; Soboll, 1993). Administration of desiccated thyroid increased the respiratory rate of liver, muscle, and kidney of rats and other mammals (Rohrer, 1924; Mayer and Meshan, 1959; Kadenbach, 1966; Brown, 1966; Pegg and William-Ashman, 1968; Oppenheimer, 1969; Edelman *et al.*, 1970; Katyare *et al.*, 1977; Sterling, 1979; Tata, 1980; Muller and Seitz, 1981, 1984; Seitz *et al.*, 1985). It has also been reported that administration of thyroid hormones increase the activity of cytochrome oxidase and a-GPDH activity (Maley, 1957; Lee *et al.*, 1959; Lee and Lardy, 1965; Oppenheimer, 1975; Sterling, 1977; Dillman *et al.*, 1977; Shambaugh, 1978; Somojen *et al.*, 1981). Administration of thiouracil reduced the plasma thyroid concentration (Greer *et al.*, 1968). While PTU decreased, T_2 increased liver respiration in rat. Further, combined treatment of PTU and T_2 has been found to increase the liver oxygen consumption (O'Reilly and Myrphy, 1992).

Thyroid hormone receptors have been identified in the nucleus, mitochondria and cytoplasm of the target cells (Oppenheimer *et al.*, 1975; Oppenheimer, 1979; Tata, 1980). However, Esmail-Beigi and Edelman (1970, 1971, 1977) and Nunez (1985) suggested that large portion of L-T_3-induced increase in the rate of oxygen consumption of tissue slices was due to stimulation of Na^+-K^+-ATPase which hydrolyses adenosine triphosphatase (ATP) membrane. The hydrolysis of ATP to ADP results in decreased P/O ratio. The decline in P/O ratio stimulates mitochondrial respiration resulting in increased cellular oxygen uptake. In the intact animals, however, the involvement of Na^+-K^+-ATPase in L-T_3-induced increment in oxygen consumption may not be as high as *in vitro* treated tissue slices (Ismail-Beigi and Edelman, 1971 and Edelman and Ismail-Beigi, 1974). Tobin *et al.* (1973) reported that thyroid hormones do not increase oxygen uptake of rat liver slices by an effect on the

Na^+-K^+-ATPase activity, but rather suggested that the rate of respiration in the normal liver slices might be controlled by the availability of oxidizable substrates that thyroid hormones may provide by altering the cellular intermediary metabolism. Administration of ouabain decreased whole body and muscle oxygen consumption (Alber, 1972). However, combined treatment of ouabain and L-T_4 led to an increase in oxygen uptake (Biron *et al.*, 1979).

It has also been reported that thyroid hormone receptors are present in the nucleus both in the presence and absence of the hormones (Spindler *et al.*, 1975). These receptors have a higher affinity for L-T_3 than for L-T_4 (Oppenheimer, 1974). The regulation of transcription through binding of nuclear receptors is frequently considered to be the initiation of most of the cellular action of thryroid hormones (Oppenheimer, 1979; Bres and Eales, 1988). The effect of thyroid hormones on protein synthesis can be blocked by the administration of actinomycin-D and chloramphenicol (Lee *et al.*, 1959; Tata, 1963; Dillman *et al.*, 1977; Gorbman *et al.*, 1983).

Thyroxine has also been reported to be de-iodinated to 3,3',5'-tri-iodothyronine which is termed as reverse T_3 (rT_3). This hormone has been found in man, rats, sheep, lambs and other mammals (Wray *et al.*, 1980; Vybiral *et al.*, 1985). In rats, rT_3 seems to be involved in the regulation of basal metabolic rate and counteracts the calorigenic action of adrenaline (Vybiral *et al.*, 1985). It has also been reported that rT_3 inhibited the calorigenic effect of L-T_3 in lambs (Lynch *et al.*, 1979, 1985) and regulated de-iodination of L-T_4 to L-T_3 (Obregon *et al.*, 1986). Starvation has been reported to decrease L-T_3 receptors (Oppenheimer, 1979) and to increase the formation of rT_3 (Schussler and Orlando, 1978). It has also been suggested that in fasting mammals the synthesis of thyroid hormones and thyroid receptors decreases,

but the production of rT_3 increases which might be responsible for the low metabolic rate (Abdel-Fattah *et al.*, 1990).

Although gonadal steroid hormones play a major role in the regulation of reproduction in mammals, they have also been found to influence erythropoiesis and oxidative metabolism of male accessory sex organs (Barron and Hugin, 1944; Bern, 1953; Krantz and Goldwasser, 1965; James et al., 1971; Naets, 1971; Gordon et al., 1973; Datta, 1975). Administration of β-estradiol in the hypothyroid rat reportedly decreased the BMR (Sherwood, 1941). It has also been reported that castration in mammals decreased the BMR while administration of testosterone reversed the effect of castration (Barron and Huggin, 1944; Laszlo Dux *et al.*, 1979). Further, castration decreased and administration of testosterone increased the cytochrome oxidase activity in rat liver (Mayer and McShan, 1959; Pegg *et al.*, 1968; Koenig *et al.*, 1980). Testosterone decreased the respiratory rate of liver tissue in *Funambulus pennanti* (Dommeu, 1983). Administration of testosterone in rat increased the oxygen consumption of the hypothalamus (Aquillar *et al.*, 1972).

The action of the gonadal hormones on the target cell is mediated through their specific receptors (Jensen and Desomber, 1972). Androgens are transported largely in a protein-bound state to the target tissues where they dissociate from the carrier proteins, diffuse into the target cells and bind to the receptors in the cytosol or the nucleus (Simental *et al.*, 1991; Thakur, 1978). Androgen binding induces a conformational change in the receptor that facilitates receptor's translocation from cytoplasm to the nucleus, dimerization of the hormone-receptor complex (Charmain *et al.*, 1995) and conversion of the inactive receptor into its active DNA binding state (Colvard and Wilson, 1987; Crino *et al.*, 1987). Furthermore, the androgen receptor protein and mRNA response to androgens varies with tissues (Shan *et al.*, 1990;

Krongard *et al.*, 1991). Once the androgens bind to the receptors, they are then translocated as steroid-receptor (S-R) complex into the cell nucleus (O'Malley *et al.*, 1975; Charmain *et al.*, 1995). Recently it has been found that both the free and occupied androgen receptors are localized in the nucleus (Mendelson, 1992; Thakur, 1978). The homodimers of S-R complexes bind to the hormone responsive elements (HREs) of the DNA (Palvimo *et al.*, 1993; Wong *et al.*, 1993). The binding of the hormone-bound receptor to its HRE alters the rate of transcription of the target gene, probably through interactions with other components of the transcription complex near the transcription initiation site of the gene (Beato, 1989; Archer *et al.*, 1991; Adler *et al.*, 1991; Ho *et al.*, 1993). Administration of cyproterone acetate(CA) has been reported to inhibit testosterone action on the target cells by blocking androgen receptors (Neumann *et al.*, 1966; Walsh and Koreman, 1970).

Catecholamines also seem to be very important as calorigenic hormones in mammals. Large doses of epinephrine and norepinephrine reduce oxygen consumption transiently and then increase the metabolic rate significantly in mammalian species (Muller and Krake, 1963; Elis, 1965; Brodie *et al.*, 1966; Rothwell and Stock, 1982; Ellison and Skinner, 1990; MeDevit and Speakman, 1996). Adrenaline secretion is supposed to be the last defensive mechanism against cold and other kinds of stress (Cannon, 1928; Evonak and Hannon, 1963; Joel, 1975; Foster *et al.*, 1980). It has also been documented that in mammals with intact sympathetic enervation, noradrenaline infusion increases blood flow in brown fat adipose tissues of new-born rabbit (Haim and Hull, 1966; Hardman and Hull, 1970) and in rats (Foster *et al.*, 1980; Hirata, 1982). The role of the sympathetic catecholaminergic nervous system in the control of heat production has largely been documented with reference to non-shivering thermogenesis (Cockburn *et al.*, 1967; Himms-Hagen, 1967). Allison and Skinner (1990) suggested that norepi-nephrine induces non-shivering thermogenesis in pouch

mice, *Saccostomus canipetris*. Cold acclimation leads to a large enhancement in calorigenic response to administered catecholamines (Egdahl and Richards, 1956; Hsieh and Carlson, 1957; Heroux *et al.*, 1969; Jansky *et al.*, 1969; LeBlanc and Villamaire, 1970; Allison and Skinner, 1990). The intravenous infusion of catecholamines produces a much larger calorigenic response than does the intra-muscular or subcutaneous administration, and the elevated oxygen uptake is maintain during the infusion (Depocas, 1958). Similarly, injections of norepinephrine or isoproteronol (a β-adrenergic agonist) significantly enhanced the calorigenic processes (LeBlanc and Pouliot, 1964; LeBlanc *et al.*, 1972). Activation of thermogenesis in rat has been shown to be mediated by the sympathetic nervous system via the release of noradrenaline which stimulates thermogenesis mainly in the brown adipocytes (Bukowicki *et al.*, 1980). Brown adipose tissues is known to have a rich sympathetic enervation and to undergo hypertrophy and hyperplasia in response to the chronically enhanced sympathetic activity following cold acclimation (Bernard *et al.*, 1980). As much as 40% of energy intake of rats might be spent for thermogenesis of brown adipose tissue (Himms-Hagen, 1984). It has also been reported that production of heat or fat oxidation seem to be mediated by sympathetic nervous system (Hull and Segal, 1965; Hartman and Hull, 1970; Williamson *et al.*, 1970). In mammals, cold acclimation increased activities of α-GPDH, LDH and CoA in brown fat in bats (Barnard *et al.*, 1970). Adrenaline has also been reported to promote glycogenolysis in liver and muscle leading to hyperglycaemia, increased oxygen consumption and heat production (Frieden and Lipner, 1971). It has been demonstrated that norepinephrine elevates cGMP in vas-deferens and cerebral tissues (Schultz *et al.*, 1973; Ferren-dalli *et al.*, 1975). Adrenaline has also been reported to increase the rate of oxygen consumption in a dose-dependent manner in dogs and rats (Heidi, 1956). In addition to its calorigenic action, epinephrine also influences erythropoiosis (Lowy *et al.*, 1960; Karantz and Goldwasser, 1965; Naets, 1971).

Catecholamines stimulate tissue oxygen uptake through α- and β-adrenergic receptors. The calorigenic action of catecholamines via β-adrenergic receptors is mediated through a cAMP-dependent mechanism, while the action via α-adrenergic receptors is mediated through a Ca^{++}-dependent mechanism (Wickberg, 1979; Szillart, 1981). In mammalian brown adipose tissue (BAT), catecholamines have been reported to stimulate about 80% of respiration through the β-adrenergic receptors and 20% via the α-adrenergic component (Mohell *et al.*, 1983). It has also been reported that the α-adrenergic stimulation of respiration leads to plasma membrane depolarisation (Nedergard and Lindberg, 1982) and increase in Na^+ permeability (Fink and Williams, 1976). The resulting increases in Na^+ concentration may lead to extrusion of Ca^{++} from mitochondria and possibly to an increased level of Ca^{++} in the cytosol (Nedergard, 1981). This increase in Ca^{++} concentration may perhaps lead to an increased turnover of phosphatidylinositol (Garcia-Sainz *et al.*, 1980). Thus, an increase in Na^+-entry and observed changes in K^+ equilibrium (Nedergard, 1981) would result in an increased activity of plasma membrane bound Na^+-K^+-ATPase which may lead to a need of ATP synthesis followed by increased respiration (Horowitz, 1972).

The Calorigenic effect of norepinephrine is potentiated by thyroid hormones (LeBlanc and Villemaire, 1970). In the hibernating ground squirrel, *Spermophilus richardsoni*, the inhibition of mitochondrial respiration has been found to be associated with decreased activity of the enzyme phospholipase-A_2 (Demeneix and Henderson, 1978a; Florant *et al.*, 1982). Further, thyroid hormones reportedly attenuate the activity of the sympathetic nervous system (Axelrod, 1975). It, thus, seems that thyroid hormones stimulate metabolic rate directly and indirectly by potentiating the calorigenic action of catecholamines. Heidi (1956) suggested that thyroxine and adrenaline influence consecutive rate limiting reactions in the metabolic cycle,

thyroxine acting at later stage than adrenaline. Thyroxine increases metabolism by partially uncoupling oxidation and phosphorylation resulting in inefficient storage of energy as ATP and also by increasing the availability of substrates which acts as a rate limiting factor. Thus, thyroxin and adrenaline may have a synergistic action on the oxidative metabolism where adrenaline increases the rate of production of substrate and thyroxine increases its oxidation. In the absence of thyroxine the rate of oxidation is limited by utilization of high energy phosphate and cannot be increased by an increase in substrate (Dutoit, 1952). Thyroxine doubled the effectiveness of 40 mg of adrenaline and prolongation of adrenaline action (Heidi, 1956). Klein *et al.* (1984) reported that L-T_3 infusion over 10 days enhanced the norepinephrine-induced stimulation of oxygen consumption of adipose tissue in the ovine foetus. It has also been reported that catecholamines stimulated uptake of free fatty acids during lipid synthesis is dependent on thyroid hormones. Administration of T_4 or T_3 to the hypothyroid mammals immediately restores the free fatty acid response to epinephrine. The available reports suggest that the thyroid hormones modulate the lipolytic activity of catecholamines (Wrutnaik and Cabello, 1986), and affect non-shivering thermogenesis of mammals also through the lipolytic activity of catecholarmines (Andrew *et al.*, 1979; Klein *et al.*, 1984).

Hormones secreted from adrenal cortex are also involved in the regulation of the rate of oxygen consumption in mammals. A single injection of hydrocortisone results in a marked increase in oxygen uptake by rat liver homogenate (Goetsch and McDonald, 1962). Further, corticosterone treatment has also been reported to increase the metabolic rate of rat liver and ATP production (Bottoms and Goetsch, 1968). However, the effectiveness of glucocorticoids in oxidative metabolism of mammals depends on tissues studied and on the length of hormonal treatment (Goetsch and McDonald, 1962). A single injection of predinisolone and hydrocortisone was found to

increase oxygen consumption in liver, while chronic treatment, however, produced opposite effects (Goetsch and McDonald, 1959, 1962). *In vitro* treatment with hydrocortisone inhibited oxygen uptake in rat liver mitochondria. Further, administration of cortisol and cortisone produced an anabolic action in liver and skeletal muscle. The adrenocorticoids have been reported to increase blood glucose level due to gluconogenesis followed by deposition of glycogen in the liver (Exton and Park, 1972; Gorbman *et al.*, 1983).

At the cellular level, most known effects of glucocorticoids are mediated by an intracellular protein (>4 KDa), the glucocorticoid receptor (GR) (Evans, 1988). The receptors are believed to be constantly shuttling bidirectionally between cytosol and the nucleus (Pratt, 1993; Madan and DeFrances, 1993). Glucocorticoids being lipophilic are able to cross the cells membrane readily to interact with the cytoplasmic receptors (GRs). The ligand binding to GR induces a conformational change in the GR molecule resulting in the dissociation of the hsp-complex (Tuss and Beato, 1993; McEwan *et al.*, 1994; Tsai and O'Malley, 1994; Hutchin *et al.*, 1993; Hu *et al.*, 1994), hyperphosphorytlation of GR (Orti *et al.*, 1992; Bodwell *et al.*, 1993) and finally translocation of the ligand-bound GR to the nucleus (Picard and Yamamoto, 1987; Akner *et al.*, 1994).

At the nuclear level, the ligand-bound receptor homodimer binds to the glucocorticoid response elements (GREs) in the promoter region of the glucorticoid-responsive genes. When bound to the GRE, the GR homodimer interacts with components of the basic transcription machinery, either directly by physical contact or by protein-protein interaction (Yang-Yen *et al.*, 1990; Lucibello *et al.*, 1990; Schüle *et al.*, 1990).

Schutz *et al.* (1973) have reported interaction between the transactivation domain of glucocorticoid receptor (GR) and basic transcription factor, TFIIB (Tuss and Beato, 1993; Tsai and O'Malley, 1994; Beato *et al.*, 1995), or indirectly via bridging factor SRC-1 (Onate *et al.*, 1995). This interaction is sufficient to stabilize the preinitiation complex on the promoter and thus enhances transcription by RNA polymerase II (Tsai and O'Malley, 1994). Further, binding of the GR homodimer to the GRE can induce a re-arrangement of the chromatin structure in the respective promoter region, thus allowing other transcription factors to bind to the previously inaccessible DNA (Bresnick *et al.*, 1990; Tuss *et al.*, 1992; Truss *et_al.*, 1995). Many effects of glucocorticoids are achieved by inhibition rather than by activation of target genes (e.g., negative transcriptional regulation of immune genes, collagenase and the interleukin-z genes) (Paliogianni *et al.*, 1993; Karin *et al.*, 1993; Pfahl, 1993; Heck *et al.*, 1994; Saatcioglu *et al.*, 1994; Helmberg *et al.*, 1995). These genes are positively regulated by activating protein-1 (AP-1), a transcription factor composed of dimers of the transcription factors (TFs) c-Jun and c-Fos protein (Ransone and Verma, 1990; Angel and Karin, 1991). The activity of these TFs is activated by growth factors. (Karin, 1995). AP-1 TFs bind to specific target sequences within the responsive promoters (Lee *et al.*, 1987). Deletion of these AP-1 binding sites abrogates both AP-1-mediated stimulation and GR-mediated repression of gene transcription even though GR itself does not bind to AP-1 site (Jonat *et al.*, 1990; Yang-Yen *et al.*, 1990). Cortisol increases the amount of mRNA that direct the synthesis of a specially inducible hepatic enzyme (Tryptophan oxidase) in rat liver. Corticosteroids elevate blood glucose level by their action on carbohydrate metabolism (Chester Jones *et al.*, 1976). Divakaran and Friedman (1976) suggested that these hormones have a direct effect at the nucleus and stimulate transcriptional process.

There are few indications that melatonin influences metabolic rate of mammals directly by increasing the behavioural thermoregulation as well as the non-shivering thermogenesis (Heldmaier *et al.*, 1981; Hall and Lynch, 1985; Heldmaier and Lynch, 1986; McElroy and Wade, 1986). It has also been reported that melatonin influences metabolic rate indirectly by affecting thyroid activity (Lewinsky *et al.*, 1987). Both food intake and body mass of garden dormouse has been reported to increase with the duration of the night. It, thus, seems that the energy metabolism of this mammal is affected by melatonin (Le-Gouic *et al.*, 1996). It has also been reported that the maximum resting metabolic rate of *Serinus caneria* increased on average by 5% during treatment with melatonin (Pohl, 1996), while high doses of serotonin was found to increase cerebral metabolic rate (Freo, 1996). These reports strongly suggest that melatonin is involved in the regulation of energy metabolism of mammals, particularly during winter months when day length is short (favourable for increased melatonin synthesis) and temperature is low. The pineal gland, through it cyclic secretion of melatonin, transmits signals concerning photoperiod to a central neuroendocrine network that controls circadian and seasonal rhythm in all vertebrates (Deguchi and Axelrod, 1972; Haldar, 1977; Reiter, 1981; Dark *et al.*, 1983; Binkley, 1988; Wingfield, 1988; Wingfield *et al.*, 1993). It has been reported that melatonin mediates the effects of daylength on both daily and seasonal behavioural and physiological events in vertebrates (Nelson *et al.*, 1987; Smale *et al.*, 1988; Armstrong and Redman, 1993; Goldman and Nelson, 1993). The physiological adjustments under short daylength, like non-shivering thermogenesis and reproduction in Djungarian hamster is reportedly mediated by the pineal hormone, melatonin (Hoffmann, 1973; Heldmaier and Steinlechner, 1981; Buchberger *et al.*, 1983; Darrow and Goldman, 1985; Heldmaier and Lynch, 1986, 1989; Deacon and Arendt, 1994).

Hormonal regulation of the oxidative metabolism in birds

The involvement of thyroid hormones in regulation of the oxidative metabolism in birds has been reported by several workers (Table-II). It has been found that thyroidectomy decreases and administration of L-thyroxine or L-triiodothyronine increases the rate of oxygen uptake of goose (Lee and Lee, 1937), chicken (Winchester, 1939; Raheja and Snedecor, 1971), pigeons (Marvin and Smith, 1943), fowl (Gorbman, 1963; Snedecor *et al.*, 1972), *Couturnix couturnix japonica* (Konecka and Majeska, 1980), *Lonchura punctulata* (Thapliyal *et al.*, 1977, 1981; Thapliyal and Sharan, 1980) and *Emberiza bruniceps* (Thapliyal and Gupta, 1983a). Thryroidectomy has been reported to inhibit the liver, muscle and kidney tissue oxygen uptake of *Emberiza bruniceps* (Thapliyal and Gupta, 1983a). However, the effect of thyroidectomy seems to be dependent on the time of the day (Thapliyal *et al.*, 1981). There is a direct relationship between the production of L-T_3 and level of food intake in chickens (Sharp and Klandorf, 1985). Administration of thyroxine reportedly increased the metabolic rate and cytochrome oxidase activity of skeletal muscle, heart, liver and kidney tissues (De-Groot *et al.*, 1975, Kamal *et al.*, 1990; Bishop *et al.*, 1995). However, there is a complete lack of information on the role of mono-iodotyrosine (MIT), di-iodotyrosine (DIT), mono-iodothyronine (T_1) and di-iodothyronine (T_2) in oxidative metabolism of birds. There is also scarcity of information on the involvement of r-T_3 in the oxidative metabolism of birds. There are reports that, as in mammals, r-T_3 has a hypometabolic action and inhibits the metabolic rate in birds (Abdel-Fattah *et al.*, 1990). It has also been reported that r-T_3 formation is increased in chickens during fasting (Sechman *et al.*, 1989). These findings perhaps suggest the involvement of r-T_3 in conservation of energy during starvation by competing for L-T_3 receptors (Chopra, 1977).

There are only few reports on the role of gonadal hormones in the energy metabolism in birds (Assenmecher, 1973). It has been reported that testosterone increased the liver tissue respiration in birds (Balnave, 1968; Pearce and Balnave, 1974). The treatment of thyroxine and testosterone, separately or in combination, has been reported to stimulate the respiratory rate of liver, skeletal muscle and kidney tissue of *Lonchura punctulata* (Thapliyal *et al.*, 1982). Testosterone has also been found to increase the whole body oxygen consumption of this species (Chandola and Thapliyal, 1973). There are reports that castration in Japanese quail *Coturnix coturnix* decreased and testosterone administration increased the rate of oxygen consumption of the Japanese quail (Hanssler and Prinzinger, 1979) and *Emberiza bruniceps* (Thapliyal *et al.*, 1983b). However, administration of testosterone to the castrated quail had no effect on the rate of oxygen uptake (Feuerbacher and Prinzinger, 1981).

Unlike in mammals, there is scarcity of information on the calorigenic role of adrenal hormones in birds (Table-II). Earlier reports indicate that both adrenaline and noradrenaline have no calorigenic effect in pigeon and black headed gull, *Larus ridibunduz* (Palonkangas *et al.*, 1971). However, administration of epinephrine in *Gallus domesticus* has been reported to induce 30 per cent increase in the rate of oxygen consumption (Freeman, 1966). On the contrary, in the earlier experiments, neither winter acclimated pigeons nor cold acclimated chickens showed any metabolic response to catecholamines (Chaffee and Robert, 1971). The first metabolic response to intra-venous injections of epinephrine and norepinephrine was shown in the king penguin where these hormones had a hypertensive effect associated with increased metabolic rate (DeSantis *et al.*, 1975). Glucocorticoids have been reported to cause hyperglycemia and glycogen deposition in birds (Snedecor *et al.*, 1963). Further, corticosterone has been found to increase the metabolic rate in passerine birds (Bottom *et al.*, 1991).

There is practically no information on the calorigenic role of melatonin in birds. There are few indirect indications that melatonin might be involved in avian thermoregulation (John and George, 1984, 1986; George and John, 1986; Heldmaier *et al.*, 1989), certain metabolic adjustments (John and George, 1976) and endocrine functions (Mckeown *et al.*, 1975; John and George, 1986). Melatonin has been found to have a lipid mobilizing effect in pigeons when injected in scotophase but not in photophase (Barfus and Ellis, 1971; John and George, 1976; Binkley, 1981). Further, it may also be mentioned that exogenous melatonin increases body weight, energy uptake, and plasma levels of triiodothyronine and thyroxine in the growing chicken (Cogburn and Harrison, 1980; Osei *et al.*, 1989). It has been found that pinealectomy significantly increases nocturnal oxygen consumption and rectal temperature due to modification of circadian rhythm of metabolic rate and food intake in adult hens (Pietras, 1996).

Hormonal regulation of the oxidative metabolism in reptiles

Hormonal regulation of the oxidative metabolism in reptiles is undoubtedly well documented (Table-III). Earlier reports showed that thyroid feeding in *Emys* and exogenous administration of L-T_4 in *Anolis carolinensis* had no effect on the oxidative metabolism (Drexler and Von-Issenkutz, 1935; Maher and Levedahl, 1959). However, later on it was reported that the seasonal cycle of the reptilian thyroid is dependent on environmental temperature (Lynn, 1970; John-Alder, 1988), and that changes in temperature of the environment may even interfere with the response of the reptilian tissues to exogenous thyroid hormones (Thapliyal and Chandola, 1973). A critical analysis of the available literature suggests that neither thyroidectomy nor thyroid hormones has any effect on the rate of respiration in reptiles at low temperature (below 20°C) (Maher and Levedahl, 1959; Maher, 1961, 1965; Coulson and Harnandez, 1964;

Wong *et al.*, 1975; Chiu, 1982; Chiu *et al.*, 1983; Thapliyal and Gupta, 1984). However, at high temperature (20°C and above) thyroidectomy decrease both *in vivo* and *in vitro*, and administration of L-T_4 and L-T_3 increased the rate of respiration in *Anolis carolinensis* (Maher and Levedahl, 1959), *Lacerta muralis* (Maher, 1961), *Eumes faciatus* (Maher, 1965), *Sceloporus cyanogenys* (Wilhoft, 1966), *Calotes versicolor* (Chandola *et al.*, 1973, 1974), *Natrix piscator* (Thapliyal *et al.*, 1975), *Calotes versicolor* (Oommen, 1981; Sharan, 1983; Gupta and Thapliyal, 1985), *Hemidactylus bowringii* (Wong *et al.*, 1975), *Hemidactylus flaviviridis* (Kumar, 1976; Thapliyal, 1980), *Chelodina longicollis* (Hulbert and William, 1988), *Ptays mucosus* (Kar *et al.*, 1989). It has been reported that administration of thyroxine causes a significant rise in the metabolic rate of reptiles irrespective of prior thyroidal status of the animals (Dodd *et al.*, 1960; Wilholf, 1966; Benett and Dawson, 1976; Thapliyal, 1980; John-Alder, 1983, 1990; Thapliyal and Gupta, 1983; Chandola and Kar, 1990). Thyroid hormones have also been reported to increase the metabolic rate of liver, skeletal muscle, kidney and brain of reptiles at higher temperature (Maher, 1964; Wilhoft, 1966; Lynn, 1970; Turner and Tipton, 1972; Chandola *et al.*, 1973; Thapliyal *et al.*, 1975; Oommen, 1976; Gupta and Thapliyal, 1985; Peter and Oommen, 1987, 1989; Joos and John, 1990). However, the responsiveness of tissues to thyroid hormones seems to vary with species and seasons of the year (Thapliyal and Gupta, 1983a). Thyroid hormones reportedly stimulate activities of mitochondrial enzymes like cytochrome oxidase and succinic dehydrogenase (SDH) (Plisetskaya *et al.*, 1983; Oommen and Sreedeviamma, 1988; John-Alder, 1990a). However, both MIT and DIT, though present in the blood, had no effect on the energy metabolism of reptiles (Wong and Chiu, 1974).

Administration of Thiourea in *Sceloporus cyanogenys* was found to suppress the rate of oxygen uptake of the whole body and also of liver, kidney and brain tissues(Wilhoft, 1966; Turner and Tipton, 1972b). Similarly, administration of

Ouabain (inhibitor of Na^+-K^+-ATPase) in *Calotes versicolor* decreased the liver and skeletal muscle respiratory rate (Thapliyal, 1980).

There are reports that gonadal hormones, besides their involvement in reproductive function, also influence the rate of the whole body oxygen consumption in a number of reptiles (Gorbman, 1963; Thapliyal *et al.*, 1975a; Oommen, 1980; Gupta, 1982; Thapliyal and Gupta, 1984; Gupta and Thapliyal, 1985; Al-Sadoon and El-Banna, 1986). Gonadal steroids have been found to stimulate the respiratory rate of tissues and suppress the thryoidectomy-induced decline in oxygen uptake (Thapliyal *et al.*, 1973; Kumar *et al.*, 1974; Thapliyal *et al.*, 1974a; Thapliyal *et al.*, 1975; Gupta and Thapliyal, 1985). It has also been reported that testosterone-induced increase in oxygen uptake could be the direct effect on mitochondrial respiration or on some energy consuming steps in the intermediary metabolism (Gupta and Thapliyal, 1991). Further, gonadectomy/ castration was found to decrease the rate of whole body and tissues oxygen uptake, and the administration of gonadal hormones reversed the decrease in tissue respiration in castrated reptiles (Thapliyal *et al.*, 1975d; Gupta and Thapliyal, 1985; Al-Sadoon *et al.*, 1990). Castration has also been reported to decrease the liver mitochondrial cytochrome oxidase activity in *Calotes versicolor* and the treatment with testosterone restored the enzyme activity (Wahal *et al.*, 1977; Oommen and Sreedeviamma, 1988). In *Natrix piscator*, orchidectomy reduced serum glucose level and administration of testosterone increased it significantly (Thapliyal *et al.*, 1974). Further, orchidectomy reportedly inhibits the respiratory rate of liver, and muscle, while treatment with testosterone reversed the ill-effects of orchiedectomy (Chandola *et al.*, 1973b; Thapliyal *et al.*, 1974c; Oommen, 1976).

In vivo administration of testosterone in *Calotes versicolor* significantly increased tissues' respiration both at high (30°C) and low (15°C) temperature

(Oommen, 1976; Thapliyal and Gupta, 1984; Gupta and Thapliyal, 1985). Further, it has also been reported that under natural condition of temperature variation, male hormone increased metabolic rate of kidney irrespective of the seasons (Gupta, 1982, 1987; Gupta and Thapliyal, 1985). However, *in vitro* treatment of testosterone at low (15°C) temperature, inhibited skeletal muscle oxygen uptake and had no effect on liver tissue respiration (Oommen, 1985). Testosterone in male and estradiol in female *Chalcide ocelletus* at 15°C increased the whole body oxygen consumption. However, in this lizard increase in the ambient temperature decreased the tissue sensitivity to the gonadal steroids (Al-Sadoon *et al.*, 1986). In a number of reptiles, the combined treatment of L-T_4 and testosterone has been reported to increase the rate of oxygen uptake and erythropoiesis (Gorbman, 1963; Gordon *et al.*, 1973; Kaur and Thapliyal, 1975; Datta, 1975; Thapliyal and Gupta, 1983a; Pati and Thapliyal, 1984). Administration of actinomycin-D decreased the whole body oxygen uptake, while testosterone reversed its inhibitory effect (Oommen, 1980).

Adrenal hormones have been proposed to act as emergency hormones in regulation of the oxidative metabolism of reptiles (Gupta and Thapliyal, 1983a; Gupta and Thapliyal, 1991). Under the natural condition, adrenaline was reported to stimulate oxygen consumption of *Calotes versicolor* during all the seasons (Gupta, 1982; Gupta and Thapliyal, 1982). Catecholamines have also been found to reverse the effect of thyroidectomy on the oxidative metabolism in reptiles (Gupta and Thapliyal, 1983a; Thapliyal and Gupta, 1984). Administration of adrenaline and noradrenaline were found to increase significantly the rate of whole body oxygen uptake and also the respiratory rate of liver, muscle, kidney and brain tissues (Mehendale and Padgaonkar, 1977; Gupta and Thapliyal, 1983b; Thapliyal and Gupta, 1984; Gupta and Thapliyal, 1985, 1991). Administration of catecholamines in *Alligator missisipiens* transiently inhibited resting metabolic rate (RMR) (for 2 hours) and then increased it significantly

(Coulson and Hernandez, 1986). Ronald *et al.* (1986) have reported that catecholamines inhibited the metabolic rate of the alligator for the first 45-125 mins followed by an increase after 3 hours. The ability of catecholamines to promote glycogenolysis in reptiles is well documented. Adrenaline has been reported to increase the total plasma cholesterol and also that of liver of *Natrix piscator* (Thapliyal and Kaur, 1976) while thyroidectomy decreased it (Thapliyal *et al.*, 1973; Gupta *et al.*, 1975).

Administration of corticosterone to the *Calotes versicolor* stimulated the respiratory rate of liver and skeletal muscle (Gupta and Thapliyal, 1983). The administration of corticosterone at low temperature (15°C) had no effect on the respiratory rate of the whole body or the isolated tissues (liver, muscle, kidney); but increased brain tissue respiration. However, when administered at higher temperature (30°C), corticosterone induced an increase in the respiratory rate of skeletal muscle and brain tissue. Administration of corticosterone in thyroidectomized lizards increased the kidney tissue respiration (Gupta and Thapliyal, 1983a). Corticosterone was found to stimulate kidney respiratory rate during pre-hibernation phase (15°C), but it had no effect either on the rate of whole body oxygen consumption or on liver, muscle and brain tissue metabolic rate. However corticosterone administration to the thyroidectomized lizard during this phase induced a significant increase in skeletal muscle respiration, but inhibited kidney oxygen uptake (Thapliyal and Gupta, 1984). It has also been reported that administration of corticosterone increases the activity of glucose-6-phosphatase and induces hyperglycemia in *Calotes versicolor.* While low dose of hydrocortisone decreased, high dose increased the activity of the enzyme cytochrome oxidase (Prasannakumar and Oommen, 1988; Jacob and Oommen, 1992). It, thus, seems that corticoids, depending on seasons, types of tissues and presence or

absence of thyroid hormones, may inhibit, stimulate or have no effect on the rate of tissue respiration (Gupta and Thapliyal, 1983a).

There is practically no information regarding involvement of melatonin in regulation of the oxidative metabolism of reptiles. However, few reports indicate that the pineal complex might be involved in the process of thermoregulation of the lizard *Anolis carolinensis* (Hutchinson and Koch, 1974), *S. magister* (Engbretson and Hutchinson, 1976; Ralph *et al.*, 1979; Bartholomew, 1982), *Crotaphylus collaris* (Firth *et al.*, 1988). It has also been reported that pinealectomy decreased the body temperature of the lizard *Sceloporus occidentalis* (Stebbin, 1960). However, parietalectomy in *Anolis carolinensis* reportedly increased body temperature (Roth and Ralph, 1976). It has been found that short photoperiod and administration of melatonin decreased the body temperature in *Lacerta viridis* (Rismiller and Heldmaier, 1982, 1985, 1987 and 1988). It, thus, seems that the pineal complex is directly or indirectly involved in the process of thermoregulation (and hence in the oxidative metabolism) of reptiles. However, the mechanisms through which the pineal complex and/or melatonin influence the oxidative metabolism of reptiles remain largely unknown.

Hormonal regulation of the oxidative metabolism in amphibians

Amphibians are the ectothermic vertebrates which possess the characters of both terrestrial and aquatic vertebrates. Due to both aquatic and terrestrial habit, their body temperature is liable to frequent changes according to ambient temperature. It is important to mention that alteration in body temperature leads to changes in the rate of hormonal synthesis as well as in other physiological functions (Harri and Hedenstam, 1972). Attempts have been made to investigate the role of hormones in regulation of

the oxidative metabolism in amphibians (Table-IV). A large number of reports suggest that the thyroid gland plays an important role in the energy metabolism of amphibians (Jankowsky, 1960; Ashley and Frieden, 1972; Dent, 1988; Galton, 1988). A critical review of available literature reveals that depending on the experimental conditions and species, thyroid hormones have been reported to increase, decrease or have no effect on the oxidative metabolism of amphibians (Gupta and Thapliyal, 1991). Thyroid hormones had no effect on the respiratory rate of skeletal muscle and heart of frogs and toads (Taylor and Barker, 1967), standard metabolic rate of tadpoles (Etkin, 1934; Fletcher and Myant, 1959; Funkhouser and Mill, 1969), and on the rate of whole body oxygen consumption of *Rana esculenta* (Henschel and Stauber, 1935), *Rana pipiens* (Galton and Ignbar, 1962), Toad *Scaphopus sp.* (Packard and Packard, 1975), and *Rana tigerina* (Brucker and Cohen, 1976). Thyroidectomy has been reported to decrease and thyroxine to increase the rate of oxygen uptake in *Triturus sp.* (Taylor, 1939), *Rana temporaria* (Jankowsky, 1960) and isolated tissues of toads (Donoso, 1960; Thornburn and Matty, 1964). In most of the earlier cited studies, there was no mention of ambient temperature. Thyroid hormones have been reported to increase the rate of oxygen consumption only at higher temperatures (20°C and above) but they have no effect on the metabolic rate at lower temperatures (below 20°C) (Maher, 1967; McNabb, 1969; Meints and Carver, 1973; Packard and Packard, 1974, 1975; Chiu and Tong, 1979; Suzuki, 1985; Deka-Borah, 1989; Sutharam and Oommen, 1989; Gupta and Chakrabarty, 1990; Gupta and Deka-Borah, 1995, Gupta and Mahanta, 1997). Further, thyroid hormones stimulated a number of mitochondria oxidative enzymes like cytochrome oxidase (cox), L-glucose phosphate dehydrogenase (L-GPDH), Cytosolic and mitochondrial malate dechydrogenase (MDH) in a number of tissues (skeletal muscle, liver, kidney, etc.) of amphibians (Pesetsky, 1965; Lagerspetz *et al.*, 1974; Brucker and Cohen, 1976; Lagerspetz, 1977; Goto *et al.*, 1982; Sutharam *et al.*, 1990). In *Bufo melanostictus* maintained at natural temperature

thyroid hormones stimulated tissues respiration during summer (14°C-25°C) but not during the winter (5°C-20°C) (Deka-Borah, 1989). *In vivo* administration of L-T_3 and L-T_4 did not stimulate the rate of oxygen consumption of liver and skeletal muscle of *Rana limnocharis* maintained at natural low temperature either during winter (16°C) or during summer (21°C) (Gupta and Chakrabarty, 1990). *In vivo* administration of thyroxine has been reported to stimulate oxygen uptake of *Bufo woodhousii* and *Rana pipiens* at ecretic (preferred) temperature (Maher, 1967; McNabb, 1969), of isolated tissue of *Scaphiopus bombifrons* at 25°C (Packard and Packard, 1974), and of skin of *Rana pipiens* tadpole (Barch, 1954). A single dose of L-T_3 and L-T_4 did not stimulate liver and skeletal muscle tissue respiration of *Rana cyanophlyctis* during winter, but significantly increased the respiratory rate of the tissues during summer after 6 and 12 hours (Gupta and Mahanta, 1997).

Administration of propyl thiouracil (PTU) has been reported to decrease the liver tissue respiration of *Gegenophis carnosus* (Sutharam *et al.*, 1990). *In vivo* treatment of PTU in *Rana limnocharis* and *Rana cyanophlyctis* has been reported to significantly decrease the respiratory rate of liver, muscle and kidney of these species both during winter and summer (Gupta and Mahanta, 1997). Thus, a decrease in tissue oxygen uptake, might be due to an inhibitory effect of PTU on the synthesis and release of endogenous thyroid hormone which leads to a decline in tissue respiration.

There is a lack of information on the mechanism of action of thyroid hormones in amphibians. Unlike in mammals and birds, there is scarcity of information on the synergistic action of thyroid hormones and catecholamines in the regulation of respiration in amphibians (Gupta and Thapliyal, 1991). Administration of propyl thiouracil (PTU) reduced the metabolic action of both epinephrine and norepinephrine in both the species. This suggests that the endogenous thryroid hormones might be

involved in the potentiation of the calorigenic action of catecholamines (Mahanta, 1994).

Unlike in reptiles, there is scarcity of information on the involvement of gonadal hormones in the energy metabolism of amphibians. Recent reports suggest that testicular hormones might also be involved in regulation of the oxidative metabolism of amphibian species (Gupta and Chakrabarty, 1990; Gupta and Thapliyal, 1991; Gupta and Deka-Borah, 1995; Gupta and Mahanta, 1997). Administration of testosterone in *Rana limnocharis* and *Rana cyanophlyctis* was found to increase the respiratory rate of liver, skeletal muscle and kidney tissues of both the species irrespective of seasons and temperature (Gupta and Mahanta, 1997). Further, the administration of estrogen in *Xenopus laevis* has also been reported to increase the whole body oxygen consumption (Follet and Redshaw, 1968). Administration of either estradiol or testosterone in *Bufo melanostictus* significantly increased the respiratory rate of liver and skeletal muscle (Deka-Borah, 1989; Gupta and Deka-Borah, 1995). Testosterone has also been reported to be involved in the regulation of the oxidative metabolism of an apodan, *Gegenophis carnosus* (Sutharam *et al.*, 1991) and in the intermediary metabolism of the frog, *Rana esculenta* (Sinha, 1982).

A critical review of the available information indicates that testosterone is actively involved in regulation of the oxidative metabolism of amphibians irrespective of temperature and seasons. However, there is scarcity of information regarding the effects of castration or anti-androgenic drugs on the amphibian respiration. Similarly, there is no information on the mechanism of action of testosterone in the energy metabolism of poikilothermic vertebrates (Gupta and Thapliyal, 1991). Recent studies on frogs indicate that administration of cyproterone acetate (an androgen receptor blocker) inhibits liver and muscle tissue respiration and administration of testosterone

in the presence of cyproterone acetate does not stimulate the oxygen uptake of these tissues (Gupta and Mahanta, 1997). Further, pre-incubation of the liver and muscle tissue homogenates with Actinomycin-D, cyclohexamide (inhibitors of transcription) and ouabain(an inhibitor of Na^{+}-K^{+}-ATPase) completely blocked testosterone-induced stimulation of the respiratory rate of the amphibian tissues (Mahanta, 1994). The ineffectiveness of testosterone in stimulating respiratory rate of tissues in the presence of Actinomycin-D and Cyclohexamide indicates that the hormone stimulates the rate of oxidative metabolism of stimulating the process of transcription (Mahanta, 1994). Blocking of the calorigenic action of testosterone by ouabain indicated involvement of Na^{+}-K^{+}-ATPase in testosterone-induced increase in tissue respiration.

Information on the role of catecholoamines in regulation of the oxidative metabolism in amphibians is limited. The available reports suggest that both norepinephrine and epinephrine stimulate the rate of oxygen uptake in *Rana pipiens* (Ahlgren, 1925), *Rana temporaria* (Harri and Hadenstam, 1972; Gist, 1978), *Rana catesbeiana* (Herman, 1977), *Ambystoma maxicanum* (Janssen *et al.*, 1983), *Rana limnocharis* and *Rana cyanophlyctis* (Gupta and Chakrabarty, 1990; Gupta and Mahanta, 1997). Adrenaline has also been reported to stimulate the activities of several enzymes such as lactase dehydrogenase (LDH), succinate dehydrogenase (SDH), Cytosolic and mitochondrial malate dehydrogenase (MDH), L-Glucose phosphate dehydrogenase (L-GPDH) and cytochrome oxidase (COX) in an apodan, *Gegenophis carnosus* (Danforth *et al.*, 1962; Josekumar and Oommen, 1988). Both adrenaline and noradrenaline stimulated the rate of whole body oxygen consumption irrespective of seasons and temperature in *Rana temporaria* (Harri and Hadestam, 1972), and the respiratory rate of tissues (liver, muscle, and kidney) of *Rana limnocharis* and *Rana cyanophlyctis* (Gupta and Mahanta, 1997). Catecholamines have also been reported to be involved in the regulation of the intermediary metabolism in *Rana catesbeiana*,

Xenopus laevis and *Ambystoma maxicanum* (Herman, 1977; Janssens and Griggs, 1984; Janssens *et al*., 1986) and *Rana pipiens* (Janssens *et al*., 1983).

There is a lack of information regarding the mechanism of action of catecholamines in amphibians. Recently, it has been reported that propyl thiouracil (PTU) significantly inhibits the stimulatory effect of epinephrine and norepinephrine on the metabolic rate of liver and kidney tissues of *Rana limnocharis* and *Rana cyanophlyctis* (Gupta and Mahanta, 1997).

In vitro treatment of tissues (liver/muscle) with phenylephrine (an alpha-adrenergic agonist) or isoproterenol (a beta-adrenergic agonist) significantly increased the rate of oxygen uptake of liver and muscle in *Rana limnocharis* and *Rana cyanophlyctis*. However, administration of prazosin (an alpha-adrenergic antagonist) significantly inhibited the phenylephrine's stimulatory effect on muscle tissues of both the species. The pre-treatment of the tissue homogenates with propranolol (a beta-adrenergic antagonist) significantly reduced the stimulatory effect of isoproterenol only in liver of *Rana limnocharis* and muscle of *Rana cyanophlyctis* (Mahanta, 1994). The combined treatment of both prazosin and propranolol significantly inhibited the stimulatory effect of both phenylephrine and isoproterenol. Further, it was found that prazosin had no effect on epinephrine-induced increase in liver tissue respiration, but inhibited the stimulatory effect of norepinephrine in muscle tissues. Propranolol significantly inhibited the calorigenic effect of norepinephrine in liver and muscle tissues. Combined treatment of propranolol and prazosin was found to completely inhibit the calorigenic effect of both epinephrine and noepinephrine in liver and muscle tissues. These findings indicate that catecholamines stimulate tissue respiration in amphibians through both alpha and beta-adrenergic receptors (Mahanta, 1994; Mahanta and Gupta, 1998).

There is scarcity of information on the calorigenic role of corticosteroids in amphibians. Corticosterone has also been reported to increase the whole body oxygen consumption of *Bufo japonicus* (Jolivet-Jaudet and Ishi, 1985) and tissue respiration in *Bufo melanostictus* (Deka-Borah, 1989; Gupta and Deka-Borah, 1995), *Rana limnocharis* and *Rana cyanophlyctis* (Gupta and Chakrabarty, 1988; Gupta and Mahanta, 1997). Administration of corticosterone has been reported to increase activities of oxidative enzymes lactate dehydrogenase (LDH), succinic dehydrogenase (SDH), cytochrome oxidase (COX) and Catalase in an apodan, *Gegenophis carnosus* (Josekumar and Oommen, 1988). Corticosterone has also been reported to influence the metabolic reactions and to increase the activities of the enzymes malate dehydrogenase (MDH) and glucose-6-phosphate dehydro-genase (G-6-PDH) (Hanke, 1990).

Administration of glucocorticoids have been reported to induce hyperglycemia and glycogenesis in some amphibian species (Hanke and Neumann, 1972; Woody and Jaffe, 1985). Corticosterone has also been reported to enhance conversion of thyroxine to a more potent tri-iodothyronine in tadpole/toad larvae (Galton, 1990; Hayes and Wu, 1995). It also increases binding of T_3 to its receptors in bull-frog tail fins (Suzuki and Kikuyama, 1983). Thus corticosteroids might be involved directly or indirectly via thyroid hormone and/or their receptors in the regulation of amphibian respiration. However, the mode of calorigenic action of the corticosteroids in amphibians still remains unknown.

In addition to the hormones of thyroid, gonads and adrenal gland, melatonin also seems to be involved in the energy metabolism of amphibians. Parietalectomy in frog, *Rana temporaria* at different temperature has been reported to be inconsistent

(Kashbohm, 1967; Chugunov and Kispoev, 1969). Melatonin reportedly antagonized the action of thyroxine (T_4) in promoting regression of tadpole tail tip, and also depressed the secretion of thyroxine (Wright *et al.*, 1991, 1996). Recently, it has been reported that *in vivo* administration of melatonin significantly increased the respiratory rate of liver, muscle and kidney tissues of *Rana limnocharis* and *Rana cyanophlyctes* in a dose-dependent manner. Whether melatonin is involved directly in the regulation of oxidative metabolism or indirectly by potentiating the calorigenic role of other calorigenic hormones (like thyroid hormones, catecholamines etc.) and/or mobilization of substrates (free fatty acids, triacyl glycerols etc.) remains to be established.

Hormonal regulation of oxidative metabolism in fish

As in mammals, thyroid hormones exert effects on embryonic development, maturation of central nervous system and activities of several metabolic enzymes in fish (Van-der Kraak and Eales, 1980). Dury and Eales (1968) pointed out that thyroid activity, judged by histology, might be activated, depressed or remain unchanged with respect to temperature variation. However, unlike in other poikilotherms, there was no reliable evidence that thyroid hormones in physiological doses could affect oxygen consumption in fish till seventies (Chester-Jones *et al.*, 1974). Reports regarding the role of thyroid hormones in oxygen consumption of teleostean fishes were found to be contradictory (Table-V). Several investigators using either thyroid stimulants or depressant claimed that such treatments had no significant effects on the rate of oxygen uptake in *Lebistes reticulatus* (Drexler and Von-Issekutz, 1935; Smith and Everest, 1943); *Opsanus tau* (Root and Etkin, 1937; Etkin *et al.*, 1940; Hessler and Meyer, 1942; Chavin and Rossmoore, 1956; Hoar, 1958), *Rhodeus amatus* (Punt and Jungbloed, 1945), *Salmo gairdneri* (Baraduc, 1963), *Clarias batrachus* at 16°C

(Gupta, 1988). It has also been reported that thyroidectomy did not alter the rate of oxygen uptake in *Scylluin canicula* (Matty, 1954), *Salmo gairdneri* (Fromm and Reineke, 1957) , Parrot fish (Pickford *et al.*, 1957), and *Lebistes reticulatus* (Sage, 1965). Administration of thiourea had no effect on the rate of whole body oxygen uptake in *Fundulus heterolitus* (Mathew and Smith, 1947). Notwithstanding these reports, other investigators have reported that thyroidectomy decreased the rate of oxygen consumption in *Pseudoscarus guacamaia* (Matty, 1957), *Umbralimi sp.* (Hanson and Stanley, 1970), *Aquiden latiformes* (Ruhland, 1971). Similarly, treatment with thiourea or thiouracil inhibited the rate of oxygen uptake in *Compostoma anomalom* (Osborn, 1951), *Salmo salar* (Zaks and Zamkova, 1952), *Mugil auratus* (Leray *et al.*, 1969), Carps (Gobos *et al.*, 1973), *Heteroneustes fossilis* (Pandey and Munshi, 1976), *Cyprinus carpio* (Sharad *et al.*, 1980), *Anabas testudineus* (Peter and Oommen, 1989); and *Lebistes reticulatus.* Administration of thyroxine reversed the respiratory depression induced by thiourea (Sage, 1965). Several investigators have reported that thyroid hormones increased the rate of whole body oxygen uptake in *Carassius auratus* (Muller, 1953; Thornburn and Matty, 1963), *cyprinus carpio* (Haarman, 1936; Gobos *et al.*, 1973; *Bathustoma sp.* (Smith and Mathew, 1948), *Squalus sukloi* (Pritchard and Gorbman, 1960), *Protopterus sp.* (Mohsen and Godet, 1960), *Ophiocephalus punctatus* (Madanmohanrao, 1961), *Oreonectus erezardi* (Zarrow *et al.*, 1964); *Salmo trutta* (Massey and Smith, 1968), *Heteroneustes fossilis* (Pandey and Munshi, 1976), *Anabas testudineus* (Peter and Oommen, 1987). Further, di-iodothyronine (T_2) and L-T_3 have been reported to increase the metabolic rate of *Amia calva* and *Salvelinus namaycush* (Ballantyne *et al.*, 1992), and *Sarotherodon mossambica* at 25°C (Sunitha Devi *et al.*, 1993).

Prolonged administration of low dose of thyroxine has been reported to increase specific activities of oxidative enzymes in several species of teleosts (Massey

and Smith, 1968), *Mugil auratus* (Leray *et al.*, 1970); *Sarotherodon mossambica* (Shivakumar and Jayaraman, 1984), *Channa punctatus* (Begum *et al.*, 1984), *Anabas testudineus* (Peter and Oommen, 1987; Jameela and Oommen, 1988; Peter and Oommen, 1989). It has also been reported that di-iodothyronine (T_2) is more potent than L-T_3 in stimulating the state-3 oxidation of pyruvate in liver mitochondria, while L-T_3 in more potent than T_2 in stimulating state-3 oxidation of pyruvate in muscle mitochondria (Leary *et al.*, 1996). Further, T_2 was found to be more potent than L-T_3 in stimulating state-4 pyruvate oxidation of both red muscle and liver mitochondria, and had no effect on the liver mitochondrial pyruvate oxidation. However, the state-4 rates for glutamate oxidation was elevated only by L-T_3 in both red muscle and liver mitochondria (Leary *et al.*, 1996).

Thyroxine and its analogs, depending on the dose and temperature, have been reported to produce both anabolic and catabolic effects in fish species (Plisetskaya *et al.*, 1983). A direct involvement of thyroxine in carbohydrate metabolism of fish have been proposed by Hochacka (1962). Administration of thyroid hormones caused hyperglycemia in *Cyprinus carpio* (Murat and Serfaty, 1970). *In vivo* treatment of eels and trouts with L-T_3 showed a decrease in liver glycogen content (Farbridge and Leatherland, 1989), while in catfish it produced a tissue-dependent effect (Singh, 1979).

Houlihan *et al.* (1988) have reported that protein synthesis is associated with increased oxygen consumption. A study on isolated hepatocytes from rainbow trout indicated that energy costs for protein synthesis were inversely related to the rate at which proteins were synthesized (Pannevis and Houlihan, 1992) and protein synthesis accounted for 31 per cent of the total oxygen consumption (Houlihan *et al.*, 1993).

Unlike in reptiles and amphibians, there is scarcity of information on the role of gonadal hormones in energy metabolism of fish (Gupta and Thapliyal, 1991). It has been reported that in some of the fishes, hypophysectomy resulted in decreased metabolic rate, presumably due to decreased level of gonadal hormones (Hanson and Stanley, 1970; Johanson and Gomery, 1973). Few of the available reports indicate that the administration of testosterone in *Gairdinus guppi* and *Rhodneus sp*., feeding of ram testis in *Carassius auratus*; and injection of estradiol in *Perca sp*. was found to increase the metabolic rate of the animals (Raffy and Fountain, 1930; Stanley and Tescher, 1931; Mann, 1939). Treatment with testosterone or stilbesterol induced an increase in the rate of oxygen uptake of goldfish *Carassius auratus* (Hoar, 1958) and *Clarias batrachus* (Gupta, 1988). It has also been reported that *in vivo* and *in vitro* administration of testosterone and 17ß-estradiol in a teleost *Anabas testudineus* increased activities of a number of the hepatic oxidative enzymes (Peter and Oommen, 1989b,d).

Gonadal hormones are known to play a major role in reproduction, development and growth of the teleost fishes (Hessler and Mayer, 1942; Higg *et al*., 1982; Matty, 1985). It has been reported that testosterone induced an increase in the activity of the enzymes needed for the conversion of L-T_4 to a more active hormone L-T_3 (MacLatchy and Eales, 1988). Administration of 80 mg/fish/day of 17 ß-estradiol or 800 mg/fish/day of testosterone increased the hepatic glycogen content. Treatment with estradiol increased the lipid content of liver but has no effect on the muscle content of lipids, proteins and free amino-acids. Both testosterone and estradiol increased the activities of various hepatic enzymes (Wiegand and Peter, 1980; Dasmahapatra and Medda, 1982; Bun Ng *et al*., 1984). Administration of low dose of 17 ß-Estradiol increased serum contents of protein, lipid, glycogen as well as activities of hepatic enzymes, while high dose (800 mg) produced an inhibitory effects on

pituitary and other metabolic hormones (Bun Ng *et al.*, 1985). These reports suggest that gonadal steroids might be involved in the regulation of the oxidative metabolism of fish as reported in amphibians and reptiles.

There is limited information available on the role of catecholamines in the energy metabolism of fishes. As in mammals (Frieden and Lipner), reptiles (Thapliyal and Gupta, 1984), and amphibians (Gupta and Deka-Borah, 1995; Gupta and Mahanta, 1997), there are reports that catecholamines significantly increased the metabolic rate in lampreys (Bentley and Follet, 1965); teleosts (Hoar and Randall, 1969; Busacker and Charin, 1977), *Anguilla angilla* (Larson, 1973); *Clarias batrachus* (Gupta, 1988), *Salmo gairdneri* (Richard *et al.*, 1990; Ferrel *et al.*, 1991). Adrenaline has also been reported to significantly increase the activities of respiratory enzymes like cytochrome oxidase (COX), Succinic dehydrogenase (SDH), α-glucose phosphate-dehydrogenase (α-GPDH), ATPase, malate dehydrogenase (MDH), lactate dehydrogenase (LDH). These reports seem to suggest that catecholamines produce their stimulatory effect on the oxidative metabolism of fish by acting both at cytosolic and mitochondrial levels (Ignatius and Oommen, 1987). Adrenaline has been reported to have inhibitory effects on the metabolic rate of *Girella nigricans* (Smith and Mathew, 1942); *Tilapia mossambica* (Banerjee and Joshi, 1981) and *Sarotherodon mossambica* (Akbarsha, 1984). The reported inhibitory effect of adrenaline in some of the fish species might be possible due to several reasons like very high dose of the hormone, induction of anaerobic respiration, depression of the respiratory rate due to stress caused due to enclosure in the respirometers etc. So far no attempt has been made to study the in vitro and in vivo effects of catecholamines on the rate of respiration of vital tissues of any fish species. There is also scarcity of information on the mechanism of action of catecholamines in fish and their synergistic effects with

other metabolic hormones like thyroid hormones in regulation of the oxidative metabolism (Gupta and Thapliyal, 1991).

In addition to their influence on the oxidative metabolism, catecholamines have also been reported to influence the hepatic carbohydrate metabolism in fishes (Sherwin and Sacca, 1984; Janssens *et al.*, 1986; Janssens and Lowrey, 1987). Catecholamines reportedly activated both glycogenolysis and glucaneogenesis in carps (Mazeaud, 1964; Janssens and Lowrey, 1987); goldfish (Young and Chavin, 1965; Birnbaun *et al.*, 1976), eels (Butler, 1968; Larson, 1973), catfish (Ottolenghi *et al.*, 1985), rainbow trout (Morata *et al.*, 1982; Mommsen *et al.*, 1988), rockfish hepatocytes (Danutal and Mommsen, 1990) and norepinephrine is more potent than epinephrine (Danutal and Mommsen, 1990). Low dose of adrenaline treatment increased total liver protein and elevated activity of glucose-6-phosphatase, while high dose of 16 mg produced an inhibitory effect and it also decreased liver glycogen content in a time-dependent manner (Jameela and Oommen, 1988). *In vitro* administration of norepinephrine has been reported to increase the release of fatty acids and glycerol from the triglycerol in Coho salmon (*Oncorhynchus kisutch*) liver (Sheridan, 1987). Epinephrine is potentially more active than norepinephrine in increasing plasma fatty acid level in eel (Lasson, 1973). However, norepinephrine induced rapid lipolysis, while epinephrine had no significant lipolytic effect in the rainbow trout, *Salmo gairdneri* (Taskima and Cahill, 1965; Perrier *et al.*, 1972) and the Carp, *Cyprinus carpio* (Farkas, 1967, 1968).

Corticoids are known to play a major role in the osmoregulation and regulation of electrolytes in fresh water teleosts (Laragh and Sealey, 1973). Administration of cortisol has been reported to increase the rate of oxygen consumption in *Anguilla japonica* (Chan and Woo, 1978b; Foster and Moon, 1986; Bismal and Specker, 1991). Similarly, corticosterone reportedly stimulates the liver and skeletal muscle oxygen

uptake (Gupta, 1988). *In vivo* and *in vitro* injection of cortisol in fresh water *Fundulus* increased the activity of Na^+-K^+-ATPase and chloride cells' numbers (Pickford *et al.*, 1970; Madsen, 1990; McCormick and Bern, 1989; Bismal and Specker, 1991; McCormick *et al.*, 1995). It has also been reported that glucocorticoid treatment in *Anabas testudineus* increased the activity of glucose-6-phosphatase (Smith *et al.*, 1985).

Cortisol is generally considered to be a metabolic hormone in fish, and several studies have implicated the hormone in the regulation of hepatic intermediary metabolism (Freeman and Idler, 1973; Chan and Woo, 1978; Lidman *et al.*, 1979; Leach and Taylor, 1982; 1985; Foster and Moon, 1986; Reid and Perry, 1991; Vijayan and Leatherland, 1989 and 1992a; Vijayan *et al.*, 1991, 1993). Administration of hydrocortisone in *Salmo gairdneri* and *Oncorhynchus tshawystecha* showed a protein catabolic action in the parietal muscle (Robertson *et al.*, 1963; Guyton, 1981). In teleosts, cortisol appears to produce hyperglycaemia and maintain liver glycogen (Bentley and Follet, 1965; Butler, 1968, 1969; Truscott, 1980; Vijayan *et al.*, 1993). Administration of hydrocortisone in *Anabas testudineus* induced an increase in the liver glycogen, protein and glucose-6-phos-phatase activity, but inhibited the acid phosphatase in a time-dependent manner (Jameela and Oommen, 1988).

After a comparison of the above mentioned information regarding the role of hormones in the regulation of the oxidative metabolism of different groups of vertebrates, it becomes obvious that there is scarcity of information on the regulatory role of different hormones in the energy metabolism of fish species. It is now clear that most of the earlier experiments designed to evaluate the calorigenic action of hormones in fishes were not conducted under well-defined conditions of climatic factors using physiological doses of hormones. Further, steps were not taken to measure the rate of

whole body oxygen consumption under stress-free conditions which can be obtained by measuring the rate of respiration of vital tissues. Moreover, the studies were fragmentary and incomplete in relation to the range of the hormones, temperature, doses etc. There is also practically no information on the calorigenic role of gonadal hormones and melatonin in any species of fish. Similarly, the role of corticosteroid hormones and catecholamines is not well studied in fish. Further, the role of thyroid hormones, particularly of MIT and DIT, remains to be established at the tissue level. Keeping in view the lack of a comprehensive study of hormonal regulation of the oxidative metabolism in fish, we decided to study in detail the role of different hormones (especially those which play important role in calorigenesis of reptiles and amphibians) in the regulation of the oxidative metabolism at tissue level in a fish species with special reference to the natural climatic conditions. The study included in this thesis is an attempt to unravel a complete picture of the endocrine regulation of fish respiration.

Tables

Table-I

Effects of Hormones on the Oxidative Metabolism in Mammals

Animal/Species	Treatments	Responses	Reference
Rat	T_3,T_4	I(L, SM, K)	Rohrer, 1924
	Thx	D (WB)	
Dog	Castr	D (WB)	Barron & Huggin ,1944
Rat	EP, NE	I (WB)	Morin,1946
Rat	T_4 + EP	I (L)	Heidi, 1956
Neonatal rat	T_3	I (BR)	Reiss & Wyatt, 1956
	T	I (WB)	
Rat	T_3, T_4	I(L,COX)	Maley, 1957
Rat	Thx	D (WB)	Barker, 1957
Rat	NE (LT)	I(MR)	Hsieh & Carlson, 1957
	Thx + T4	I (WB)	
Rat	EP (LT)	I(MR)	Depocas, 1958
Rat	Thyroid fed	I(L, α-GPDH)	Lee *et al.*, 1959
Rat	T	I(K)	Mayer & Mcshan, 1959
	Castr	D(COX)	
	Castr + T	I(COX)	
Mammal	T_4 + EP, NE	I (WB)	Pitt-Rivers & Tata, 1959
Mammal	EP + NE	I (WB)	Karlberg *et al.*, 1962
Rat	Cortisol	I(L)	Goetsch & McDonald, 1962
Rat	T_3	I (BMR)	Tata *et al.*, 1963
	Act-D	D(BMR)	
Mammal	EP + NE (high dose)	D (WB)	Muller & Krake, 1963
Mammal	T_4	I (WB)	Tata, 1964
Rat	Isoproterenol	I (WB)	LeBlanc *et al.*, 1964
Rat	EP + NE (high dose)	D (WB)	Ellis, 1965
Mammal	T_3	I (WB)	Roodyn *et al.*, 1965
Rat	T_3, T_4	I(COX, GPDH)	Lee & Lardy, 1965
Rat	T_3, T_4	I(COX, L,SM,K)	Kadenbach, 1966
Rat	EP + NE	I(MR)	Brodie *et al.*, 1966
Male rat	T_3	I (WB)	Tata & Windnell, 1966
Rat	T_4	I(SM)	Brown, 1966
Rat	T_3	NR(BR)	Shapiro & Percin, 1966

Animal/Species	Treatments	Responses	Reference
Rat	Castr	D(COX)	Pegg & Ashman, 1968
	Castr + T	I(COX)	
Rat	T_3, T_4	I (WB)	Hoch, 1968
Rat	Cortico	I(L)	Bottom & Goetsch, 1968
Rat	T	I(K)	Pegg & Ashman, 1968
Rat	Adx	D(Na^+-K^+-ATPase)	Jorgensen, 1968
Rat	T_3, T_4	I(L,SM, K,H)	Oppenheimer, 1969
		NR(BR)	
Rat	T_4	I(MR)	Tata, 1970
Rat	T_3	I(L)	Edelman *et al.*, 1970
Rat (Mitochondria)	T_3, T_4	I(WB)	Gordon *et al.*, 1973
Rat	T_4	I(L)	Hassinen *et al.*, 1971
			Medvedeva, 1971
Rat	Isoproteronol	I(WB)	LeBlanc *et al.*, 1972
Rat	Ouabain	D(WB)	Alber, 1972
Rat	T_3	I(α-GPDH, COX)	Oppenheimer, 1975
Mammal	Corticosteroid	I(L)	Bentley, 1976
Mammal	T_3, T_4	I(MR)	Turner & Bagnara, 1976
Rat	T_3	I(L.COX)	Sterling, 1977
Rat	α-Aminitin	D(GPDH)	Dillman *et al.*, 1977
Rat	T_3, T_4	I(L)	Katyare *et al.*, 1977
Rat	T_3, T_4	I(α-GPDH)	Shambaugh, 1978
Hamster	NE	I (WB)	Nedergard & Lindberg,1979
Rat	Ouabain	D(SM)	Biron *et al.*, 1979
	Ouabain + T_4	I(SM)	
Neonatal rat	T_4	I(BR)	Oppenheimer, 1979
Newborn lamb	T_4	I (WB)	Andrew *et al.*, 1979
Rat	T_3, T_4	I(L)	Tata, 1980
Rat	Castr	D(K-COX)	Koening *et al.*,1980
	Castr + T	I(K-COX)	
Rat	T_3,T_4	I(α-GPDH)	Bernal & DeGroot, 1980
Newborn rabbit (in vitro)	T_4	I(L)	Klein *et al.*, 1981
Rat	T_3	I(L)	Muller & Sutz, 1981
Rat	T_3	I(α-GPDH)	Somjen *et al.*, 1981

Animal/Species	Treatments	Responses	Reference
Newborn rabbit	T_3	NR(L)	Klein *et al.*, 1981
		I(Na^+-K^+-ATPase)L	
	Ouabain	D(L)	
	T_3 + NE	I(L)	
Rat	NE	I(RMR)	Rothwell & Stock, 1982
	Fed, PROP	D(WB)	
Neonatal rat	T_3	I(BR)	Rajan & Katyare, 1982
Rat	NE	I(RMR)	Rothwell & Stock, 1982
Rat	Act-D + Chlo	D (WB)	Gorbman *et al.*, 1983
Mammal	EP, NE	I (WB)	Landsberg & Young, 1983
Funambulus pennantri	T	D(L)	Oommen, 1983b
Lamb	T_4 + NE	I (WB)	Klein *et al.*, 1984
Mammal	T_3	I (WB)	Nelson *et al.*, 1984
Mammal	T_3, T_4	I(L)	Muller & Seitz, 1984
Lamb	T_3	I (WB)	Lynch *et al.*, 1985
Newborn lamb	T_3,T_4 + EP	I (WB)	Wrutniak *et al.*, 1985
Rat	EP	I (WB)	Smith *et al.*, 1985
Rat	T_3	I(L)	Seitz *et al.*, 1985
Rat	T_3	I (WB)	
Mammal	T_3	I(L)	DeNayer, 1987
Rat	T_2	I(L)	Horst *et al.*, 1989
Saccostomus campetris	NE	I(RMR)	Ellison & Skinner, 1990
Rat (blood cells)	T_2	I(COX)	Kvetny ,1992
Rat	PTU	D(L)	O'Reilly & Murphy, 1992
	T_2	I(L)	
	PTU + T_2	I(L)	
	Cyclo + T_2	I(L)	
Rat	T_2	I(COX)	Lanni *et al.*, 1992
Rat	T_2	I(L)	Lanni *et al.*, 1994a,b
Mammal	T_3	I(L)	Soboll, 1993a
Rat	T_2	I(COX)	Goglia *et al.*, 1994
Microtus agretis	NE	I(BMR, NST)	McDevit & Speakman,1996
Rat	Serotonin	I(CMR)	Freo, 1996
Rat	T_4	I (WB)	Bandyopadhyay & Bhattacharya, 1996

Animal/Species	Treatments	Responses	Reference
Rat	T_2	I(COX) SM	Lombardi *et al.*, 1997
Rat	Ouabain	D(Na^+-K^+-ATPase) SM	Dorup & Clausen, 1997
	Dexamethasone	I (Na^+-K^+- ATPase)	

Abbreviations : Act-D = actinomycin-D; Adx = adrenalectomy; BMR = basal metabolic rate; BR = brain respiration; CA = cyproterone acetate; Castr = castration; Chlo = choramphenicol; CMR = circadian metabolic rate; Cortico = corticosterone; COX = cytochrome oxidase; Cyclo = cyclohexamide; D = decrease; DIT = diiodo-L-tyrosine; E_2 = estradiol; EP = epinephrine/adrenaline; Gnx = gonadectomy; G-6-Pase = glucose-6-phosphatase; α-GPDH = α-glycerophosphate dehydrogenase; H = hibernation phase; Hpx = hypophysectomy; I = increase; K= kidney respiration; L = liver respiration; LT = low temperature; MDH = malatae dehydrogenase; MIT = monoiodo-L-tyrosine; MR = metabolic rate; NE = norepine-phrine/noradrenaline; NR = no response; NST = non-shivering thermogenesis; Orch = orchidectomy; Ovx = ovariectomy; PRA = prazosin; Pre-H = pre-hibernation phase; PROP = propranolol; PTU = propyl thiouracil; Px = pinealectomy; Radio-Thx = radio-thyroidectomy; RMR = resting metabolic rate; SDH = succinate dehydrogenase; SM = skeletal muscle respiration; SMR = standard metabolic rate; T_2 = diiodo-L-thyronine; T_3 = triiodo-L-thyronine; T_4 = L-thyroxine; T = testosterone; Thx = thyroidectomy; TU = Thiourea; WB = whole body oxygen consumption;

Animal/Species	Treatments	Responses	Reference
Emberize bruniceps	Thx	D(WB,L, SM)	Thapliyal *et al.*, 1983a
		NR(K)	
	Thx+T_4	I(WB,L)	
		NR(K,SM)	
Emberize bruniceps	Thx	D (WB)	Thapliyal *et al.*, 1983b
	T	I (WB)	
Lonchura punctulata	Castr	I(SM)	Oommen, 1983a
	T	D(SM)	
		NR(L)	
Chicken	T_3	I (WB)	Sharp & Klandorf, 1985
Chicken	T_3	I(BMR)	Kamal *et al.*, 1990
Passerine birds	Cortico	I(MR)	Butlemer *et al.*, 1991
Duck	Thyroid fed	I(RMR)	Bishop *et al.*, 1995
(*Aythya faligula*)	T_4	I(RMR)	
		I(COX)	
		I(SM)	
Hens	Px	I(WB)	Pietras, 1996
(*Serinus caneria*)	Melatonin	I(MR)	Pohl, 1996

Abbreviations : As mentioned in Table - I.

Table-II

Effects of Hormones on the Oxidative Metabolism in Birds

Animal/Species	Treatments	Responses	Reference
Columbia livia	Thyroprotein	I (WB)	Sierens & Noyon, 1926
Columbia livia	Thx	D (WB)	Haarman, 1936
& Chicken	T_4	I(L,H,SM)	
Goose	Thx	D (WB)	Lee & Lee, 1937
Chicken	Thx	D (WB)	Winchester, 1939
Pigeon	Thx	D (WB)	Marvin & Smith, 1943
Chicken	Thx	D (WB)	Mallen *et al.*, 1962
Fowl	Thx	D (WB)	Gorbman, 1963
	T_4	I (WB)	
Spotted munia	T_4	I(L,SM)	Gorbman, 1963
Chicken	EP (LT)	NR (WB)	Chaffee & Robert, 1971
Black headed gull	EP + NE	NR (WB)	Palonkangas *et al.*, 1971
Spotted munia	T	I (WB)	Chandola & Thapliyal, 1973
	T_4	I (WB)	
Pullets	T	I(L)	Pearce & Balnave, 1974
King Penguin	EP, NE	I(MR)	De Santis *et al.*, 1975
Bird	T_4	I(H,SM, K,L)	DeGroot & Stanbury, 1975
Bird	Cortico	I(L)	Bantley, 1976
Spotted munia	Thx	D(L,3 & 21 month)	Thapliyal *et al.*, 1977
	T_4	I(SM,21 month)	
	Thx + T_4	I(L,3 & 21 month)	
Japanese Quail	Castr	D (WB)	Hanssler *et al.*, 1979
	T	I (WB)	
Lonchura punetulata	T_4	I (WB)	Thapliyal, 1980
Lonchura punctulata	Thx	D/NR/I	Thapliyal *et al.*, 1981a
	Thx + T_4	I (WB)	
Japanese quail	Castr	D (WB)	Feuerbacher & Prinzinger, 1981
	Castr + T	NR (WB)	
Lonchura punctulate	T_4	I(SM,K)	Thapliyal *et al.*, 1982
	T_4 + T	I(L,SM,K)	
	T	I(L)	
Lonchura punctulata	Thx	D (WB)	Thapliyal & Gupta, 1983
	T_4	I(L,SM)	

Table-III

Effects of Hormones on the Oxidative Metabolism in Reptiles

Animal/Species	Treatments	Responses	Reference
Emys	Thyroid fed	NR (WB)	Drexler & van Issekutz, 1935
Anolis carolinenis	25°C Thx	NR (WB)	Maher & Levedahl, 1959
	T_4	NR (WB)	
	32°C Thx	D (WB)	
	T_4	I (WB)	
Lacerta muralis	30°C Thx	D (WB)	Maher, 1961
	T_4	I (WB)	
	20°C T_4	NR (WB)	
Lizards	T	I(WB)	Gorbman, 1963
Aligator 28°C	Thyroid powder	NR (WB)	Coulson & Hernandez, 1964
	Pituitary powder	I (WB)	
Eumeces obsoletus	30°C T_4	I(L,BR)	Maher, 1964
		NR(SM)	
Eumeces fasciatus	30°C T_4	I (WB)	Maher, 1965
	Thx	D (WB)	
	20°C T_4,Thx	NR (WB)	
Sceloporus cyanogenys	T_4	I(WB,L, K,BR)	Wilhoft, 1966a
	Thiourea	D(WB,L, K,BR)	
	32°C T_4	I (WB)	
	Thx	D (WB)	
	16°C T_4	NR (WB)	
Calotes versicolor	30°C T_3, T_4	I(L,SM)	Lynn, 1970
Natrix rhombitera	32°C T_4	I(L)	Turner & Tipton, 1972a
	Thiourea	D(L)	
	15°C T_4,Thx	NR(L)	
Calotes versicolor	30°C Thx	D(WB,L,SM)	Chandola & Thapliyal, 1973a
	T_4	I(WB,L, SM)	
Calotes versicolor	30°C T_4,T	I(L,SM)	Chandola & Thapliyal, 1973b
(in vitro)	Thx,Orch	D(L,SM)	
Calotes versicolor	Thx	D(WB,L, SM)	Thapliyal & Chandola, 1973
	Thx+T	I(WB,L, SM)	
Natrix piscator	30°C T_4,T	I(L,SM)	Kumar *et al.*, 1974
	Thx	D(L,SM)	
	Thx+T_4	I(L,SM)	
	Thx+T	I(L,SM)	
	Thx+T_4+T	I(L,SM)	

Animal/Species	Treatments	Responses	Reference
Calotes versicolor	30°C T_4,T	I(L,SM)	Chandola *et al*., 1974a
	Thx	D(L,SM)	
Hemidactylus flaviviridis	30°C T	I(L)	Chandola *et al*., 1974b
		NR(SM)	
	Orch	D(L,SM)	
	Orch + T	I(L,SM)	
Lizards	MIT & DIT	NR (WB)	Wong & Chiu, 1974
Calotes versicolor and *Natrix piscator*	30°C Thx	D(L,SM)	Thapliyal *et al*., 1974a
	Thx + T	I(L,SM)	
Natrix piscator	30°C T (5mg)	I(L)	Thapliyal *et al*., 1974b
		NR(SM)	
	T (10mg)	I(L,SM)	
	Orch	D(L,SM)	
	Orch + T	I(L,SM)	
Hemidactylus bowringii	30°C Thx	D(L)	Wong *et al*., 1975
	Thx + T_4	I(L)	
	20°C T_4	NR	
Natrix piscator	30°C Thx	D(L,SM)	Thapliyal *et al*., 1975d
	T_4	I(L,SM)	
	T	I(L,SM)	
	Thx+T_4	I(L,SM)	
	Thx+T	I(L,SM)	
	T_4+T	I(L,SM)	
Natrix piscator	Te	I (WB)	Thapliyal *et al*., 1975e
Natrix piscator	Castr	D(L,SM,K)	Thapliyal *et al*., 1975d
	Castr+T	I(L,SM,K)	
Lizards	T_4	I(WB)	Benett & Dawson, 1976
Calotes versicolor	Castr	D(L.COX)	Wahal *et al*., 1977
	Castr+TP	I(L.COX)	
Calotes versicolor	Spring T_4	I(L,SM)	Thapliyal, 1980a
	Summer Thx	D(L,SM)	
	Fall T_4	NR(L,SM)	
		Winter Thx	NR(L,SM)
	Ouabain	D(L,SM)	
H. flaviviridis	Thx	D(WB,L,SM)	Thapliyal, 1980b
	T_4	I(WB,L,SM)	
Calotes versicolor	T_4	NR(WB)	Thapliyal, 1980c
		I(L after 1 hr)	
		I(SM after 3 hr)	

Animal/Species	Treatments	Responses	Reference
Lizards	30°C Act-D	D (L)	Oommen, 1980
	T	I (L)	
	Act-D + T	I (L)	
Calotes versicolor	Ouabain	I(BR)	Das *et al.*, 1980
Calotes versicolor	30°C Thx	D(L,SM)	Oommen, 1981
	T_3, T_4	I (L,SM)	
Lizards	T_4	I (WB)	Chiu, 1981
Dipsosaurus dorsalis	T_4	I(SMR)	John-Alder, 1982
Calotes versicolor	Thx	D(WB,L,SM)	Gupta, 1982
	EP	I(WB,L,SM, K,BR)	
	T	I (WB,L,K)	
Ptyas korros Ecretic temp	T_4	NR	Chiu, 1982
	Thx	NR	Chiu *et al.*, 1983
	Thx + T_4	NR	
Dipsosaurus dorsalis	T_4	I(SMR)	John-Alder, 1983
Calotes versicolor	T_4	I(COX)	Plisetskaya *et al.*, 1983
Calotes versicolor	30°C T_4	I(WB)	Thapliyal *et al.*, 1983
Calotes versicolor	T_4	I(L after 1& 2 hr)	Sharan, 1983
		I(SM after 2,3&24 hr)	
	Thx	D(L after 1,2,24,48, 168 hr)	
		D(SM after 1,3,6,12,24,48,168 hr)	
	Thx + T_4	I(L after 2,3& 24 hr)	
		I(SM after 6 & 24 hr)	
Calotes versicolor	15°C T_4	NR(WB,L,SM,K,BR) (Pre-H)	Thapliyal & Gupta, 1984
	T	I(WB,L,K)	
		NR((SM,BR)	
	EP	I(WB,L, K,BR)	
		NR(SM)	
	Cortico	I(K)	
		NR(WB,L, SM,BR)	
	Thx+T_4	NR(WB,L,SM,K,BR)	
	Thx+T	I(SM,K)	
		NR(WB,L,BR)	
	Thx+EP	I(WB,SM,K,BR)	
		NR(L)	
	Thx+Cortico	I(SM)	
		D(K)	
		NR(WB,L,BR)	

Animal/Species	Treatments	Responses	Reference
Calotes versicolor	30°C Thx	D(WB,L, SM,K,BR)	Gupta & Thapliyal, 1985a
	T_4	I (WB,L,SM,K,BR)	
	15°C T	I (L,SM)	
Calotes versicolor	EP, NE	I (L,SM,K,BR)	Gupta & Thapliyal, 1985b
Calotes versicolor	30°C T	I(SM,L)	Oommen, 1985
(*in vitro*)	15°C T	D(SM), NR(L)	
Calotes versicolor	EP+NE	I(WB,L, SM)	Gupta & Thapliyal, 1985c
	Thx	D(WB,L,SM)	
	Thx+EP	I(WB,L,SM)	
	Thx+NE	I(WB,L,SM)	
Calotes versicolor	30°C T_4	I(WB,L, SM,K)	Gupta & Thapliyal, 1985d
	Mar-Nov	I(BR)	
	Mar-Apr, Jul-Aug, T	I(WB,L)	
	Jan, T	I(SM,K)	
	Jan, Thx	D(WB,L,SM,K,BR)	
Chalcide ocellatus	15°C T_4	I (WB)	Al-Sadoon & El-banna, 1986
Alligator	EP + NE	D(45-125 min) I(after 3 hr)	Caulson & Hernandez, 1986
Calotes versicolor	T_3, T_4	I(L)	Peter & Oommen, 1987
Calotes versicolor	Hydrocortisone	I(COX)	Prasannakumar & Oommen, 1988
Snake	T_4	NR	Chiu & Woo, 1988
Chelodina longicollis	Thx	D(WB)	Hulbert and William, 1988
	Thx+T_4	I(WB)	
Calotes versicolor	30°C Thx	D(COX)	Oommen and Sreedeviamma, 1988
	T_3, T_4	I(COX)	
	T	I(COX)	
Sceloporus undulatus	T_4	I(SMR)	John-Alder, 1989
Ptays mucosus	Thx	D(WB,L,SM)	Kar *et al.*, 1989
C. versicolor	T_3, T_4	I(L)	Peter and Oommen, 1989
Chalcide ocellatus	Castr, Ovx	D(WB)	Al-Sadoon *et al.*, 1990
	Castr +T	I(WB)	
	Ovx+E_2	I(WB)	
	Ovx + T	NR(WB)	
	Castr + E_2	NR(WB)	
Sceloporus undilatus	T_4	I(SMR)	John Alder, 1990a
	30°C T_4	I(WB)	Chandola & Kar, 1990

Animal/Species	Treatments	Responses	Reference
Calotes versicolor	EP, NE	I(WB)	Gupta & Thapliyal, 1991
	25°c T_3, T_4	I(WB)	
Calotes versicolor	Hydrocortisone	I(COX)	Jacob and Ooommen, 1992

Abbreviations : As mentioned in Table - I.

Table-IV

Effects of Hormones on the Oxidative Metabolism in Amphibians

Animal/Species	Treatments	Responses	Reference
Frogs	EP	I(SM)	Ahlgren, 1925
Amphibian tadpoles	T_4, T_3	NR(SMR)	Etkin, 1934
Rana esculanta	T_4	NR	Henschel & Stanber, 1935
Triturus sp	Thx	D(WB)	Taylor, 1939
	T_4	I(WB)	,
Rana pipiens	T_4	I(WB)	Warren, 1940
Rana pipiens (tadpole skin)	T_4	I(WB)	Barch, 1954-55
Tadpoles	T_3, T_4	NR(SMR)	Fletcher & Mayant, 1959
Toads	Th	NR(K,H, SM)	Donoso, 1960
	T_4	I(K,H) NR(L,SM)	
Rana pipiens	T_4	NR(WB)	Galton & Ingber, 1962
(Tadpole)	T_4	I(L)	Bennett *et al.*, 1962
Bufo Sp.	T_3, T_4	I (WB)	Matty and Green, 1963
Rana pipiens	EP, NE	I (WB)	Watlington *et al.*, 1965
Bufo woodhousii	20°C T_4	I (WB)	Maher, 1967
	5,10,15° C T_4	NR	
Rana pipiens	20& 25°C T_4	I (WB)	
	10 & 15°C T_4	NR	
Anuran sp.	T_4	NR(SM,H)	Taylor & Barker, 1967
Xenopus laevis	Estrogen	I(MR)	Follet & Redshaw, 1968
Rana pipiens	T_4(30°C)	I (WB)	McNabb, 1969
Tadpole	T_4	NR	Funkhouser & Mill, 1969
Rana temporaria	EP, NE	I(MR)	Harri & Hadenstam, 1972
Toad	Ouabain	D(lens)	Lefevre, 1973
Scaphiopus Sp.	T_4	D (WB)	Packard & Packard, 1973
R. pipiens cornbifrous	25°C T_3	I (WB)	Meints & Carver, 1973
Rana pipiens	T_4(25°C)	I(L)	Packard *et al.*, 1974
Rana temporaria	T_3, T_4	I(COX, L,SM,R)	Lagersptez *et al.*, 1974
Rana trigrina	T_4(15°C)	NR	Brucker & Cohen, 1976a
	T_4(25°C)	I(COX)	
Rana catesbeiana	T_4	I(COX)	Brucker & Cohen, 1976b
Rana pipiens	EP	I (WB)	Farrar & Frye, 1977

Animal/Species	Treatments	Responses	Reference
Rana temporaria	T_4	I(COX : L, K)	Lagerspetz, 1977
Rana temporaria	EP	I (WB)	Gist, 1978
Rana tigrina	T_4(25°C)	I(WB)	Chiu & Torg, 1979
	T_4(15°C)	NR	
Rana catesbeiana	T_4	I(COX)	Goto *et al.*, 1982
A. maxicanum	EP	I (WB)	Janssens *et al.*, 1983
Bufo japonicus	Cortico	I (WB)	Jolivet-Jau & Ishi, 1985
Rana tigrina	15°C T_4	NR	Peter & Oommen, 1987
	25°C T_4	I (WB)	
Rana tigrina	15°C T_4	NR	Oommen & Sreederiamma, 1988
	25°C T_4	I (WB)	
G. carnosus	EP	I(COX)	Josekumar & Oommen, 1988b
G. carnosus	Cortico	I(COX)	Josekumar *et al.*, 1988a
Bufo melanostictus	Cortico	I(L,SM)	Gupta & Deka-borah, 1989
	T_3, T_4(5-20°C)	NR(L,SM)	
	T_3, T_4(14-25°C)	I(L,SM)	
G. carnosus	T_3, T_4(28-30°C)	I(COX)	Sutharam & Oommen, 1989
Axolotle & *Rana temporaria*	E_2	I (WB)	Hanke, 1990
	28°C-37°C, T & E_2	D (WB)	
	Cortico	I(G6P)	
Rana limnocharis	EP,NE, T	I(L,SM)	Gupta & Chakravarty, 1990
	T_3, T_4(15°C)	NR(L,SM)	
	T_3, T_4(25°C)	I(L,SM)	
G. carnosus	T_3, T_4	I(COX)	Sutharam *et al.*, 1990
	PTU	D(L)	
Bufo melanostictus	Estradiol	I(L,SM)	Gupta & Thapliyal, 1991
G. carnosus	Androgens	I (WB)	Sutharam *et al.*, 1991
Bufo melanostictus	EP, NE	I(L,SM)	Gupta & Deka-borah, 1995
	5-16°C T_3, T_4	NR(L,SM)	
	Cortico	I(L,SM)	
	16-26°C T_3,T_4	I(L,SM)	
	Cortico	I(L,SM)	
	26°C E_2	I(L,SM)	
	Cortico	I(L,SM)	
	EP	I(L,SM)	
	NE	I(L,SM)	
R. limnocharis &	7-15°C T_3, T_4	NR(L,SM)	Gupta & Mahanta, 1997

Animal/Species	Treatments	Responses	Reference
R. cysnophlyctis	T_3	I(K)	
	PTU	D(L,SM,K)	
	T	I(L,SM,K)	
	CA	D(L,SM,K)	
R. limnocharis &	12-21°C T_3,T_4	I(K)	
R. cysnophlyctis	PTU	D(L,SM,K)	Gupta & Mahanta, 1997
	T	I(L,SM,K)	
	CA	D(L,SM,K)	
	EP	I(L,SM,K)	
R. limnocharis &	8°C EP,NE	I(L,SM,K)	Gupta & Mahanta, 1997
	21°C EP,NE	I(L,SM,K)	
R. cyanophlyctis	8°C & 21°C Cortico	I(L,SM,K)	
	8°C & 21°C Cortisol	NR(L,SM,K)	
R. cyanophlictis &	ISO, PHE	I(L,SM)	Mahanta & Gupta, 1998
R. limnocharis	ISO+PHE	I(L,SM)	
	PHE+PRA+PROP	D(L,SM)	
	ISO+PRA+PROP	D(L,SM)	

Abbreviations : As mentioned in Table - I.

Table-V

Effects of Hormones on the Oxidative Metabolism in Fishes

Animal/Species	Treatments	Responses	Reference
Gairdinus guppyi	Male hormone	I (WB)	Raffy & Fontaine, 1930
Carassius auratus	Ram testes fed	I (WB)	Stanley & Tescher, 1931
Lebistes reticulatus	T_4	NR	Drexler & Von-Issekutz, 1935
Cyprinus carpio	T_4	I (WB)	Haarman, 1936
Opsanus tau	T_4	NR	Root & Etkin, 1937
Goldfish	Thyroid fed	NR	Etkin *et al.*, 1940
Goldfish	T_4	NR	Hesler & Meyer, 1942
	T	I (WB)	
Girella nigricans	EP	D (WB)	Smith & Mathew, 1942
Lebistes reticulatus	T_4	NR	Smith & Everest, 1943
Carassius auratus & *Rhodeus amatus*	T_4	NR	Punt & Jungbloed, 1945
Fundulus heterolitus	Thiourea	NR	Mathew & Smith, 1947
Bathustoma sp. Parrot fish	Thyroid fed & L-T_4 injected	I (WB)	Smith & Mathew, 1948
Compostoma anomalom	Thiouracil	D (WB)	Osborn, 1951
Salmo salar	Immersion in Thiourea	D (WB)	Zaks & Zamkova, 1952
Carassius auratus	T_4	I (large animal) NR (small animal)	Muller, 1953
Scyllium canicula	Thx	NR (WB) (16.2,17.5)°C	Matty, 1954
Carassius auratus	T_4	NR	Chavin & Rossmoore, 1956
Salmo gairdneri	Radio-Thx	NR	Fromm & Reineke, 1957
Pseudoscarus gaucamaia	Thx	D (WB)	Matty, 1957
Carassius auratus	T & Stilbesterol	I (WB)	Hoar, 1958
	20°C T_4	NR	
Squalus suckloi	T_3, T_4	I(WB)	Pritchard & Gorbman, 1960
Protopterus sp.	T_4	I (WB)	Mohsen & Godet, 1960
Ophiocephalus punctatus	T_4 (fed)	I (WB)	Madanmohanrao, 1961
Brook trout	T_3	I(L)	Hochachka, 1962
Salmo gairdneri	T_4	NR	Baraduc, 1963
Fish	T_4	I(COX)	Grief *et al.*, 1964
Oreonectus evezardi	T_4	I (WB)	Zarrow *et al.*, 1964

Animal/Species	Treatments	Responses	Reference
Lampreys	EP	I (WB)	Bentley & Follet, 1965
Lebistes reticulatus	Thiourea	D (WB)	Sage, 1965
	T_4	NR	
	Thiourea + T_4	I (WB)	
	Thx	NR	
Lebistes reticulatus	Thiourea	D (WB)	Sage, 1968
	Thiourea + T_4	D (WB)	
Samlo trutta	T_4	I (WB)	Massey & Smith, 1968
Teleosts	EP	I (WB)	Hoar & Randall, 1969
Mugil auratus	PTU	D (WB)	Leray *et al.*, 1969
Anguilla rostrata	Cortisol	I(SM)	Butler, 1969
Umbralimi sp.	Hpx	D (WB)	Hanson & Stanley, 1970
Mugil auratus	T_4	I(COX)	Leray *et al.*, 1970
Teleost fish	T_4	I (WB)	Singh, 1970
Aquiden latiformes	Radio-Thx	D (WB)	Ruhland, 1971
Carassius auratus	Hpx	D (WB)	Johanson & Gomery, 1973
Salma gairdneri	Cortico	I(L)	Freeman & Idler, 1973
Carp sp.	Thiourea	D (WB)	Gabos *et al.*, 1973
	T_4	I (WB)	
Anguilla anguilla	EP, NE	I(MR)	Larson, 1973
H. fossilis	Thiouracil	D(WB)	Pandey & Munshi, 1976
	T_3, T_4	I(WB)	
Aquilla japonica	Cortisol	I (WB)	Chan & Woo, 1978
	Cortisol + T_3	I (WB)	
Teleost sp.	T_4	I (WB)	Donaldson *et al.*, 1979
Tilapia mossambica	EP	D(MR)	Banerjee & Joshi, 1981
Carp sp. & Tilapia	T_3,T_4	I(L,SM)	Matty *et al.*, 1982
	T_3,T_4	I(L,SM)	
	Act-D	D(L,SM)	
Epinephelus akaara	T	I(L)	Bun *et al.*, 1984
S. mossambica	T_4	I(COX)	Shivakumar & Jayaraman, 1984
	EP	D (WB)	Akbarsha, 1984
Channa punctatus	T_4	I(SDH)	Begum *et al.*, 1984
Aquilla rostrata	Cortisol	I(SM)	Foster & Moon, 1986
Anabas testudineus	EP	I(COX,SDH	Ignatius & Oommen, 1987
		I(MDH, α-GPDH)	
Anabas testudineus	T_3	I(WB)	Peter & Oommen, 1987
		I(COX)	
Anabas testudineus	EP	I(COX)	Jameela & Ooommen, 1988

Animal/Species	Treatments	Responses	Reference
Clarisa batrachus	16°C T_3, T_4	NR(L,SM)	Gupta, 1988
	T	I(L,SM)	
	Cortico	I(L,SM)	
	EP	I(L,SM)	
Anabas testudineus	Thiouracil	D (WB)	Peter & Oommen, 1989a
	T_4	I(COX)	Peter & Oommen, 1989b
Anabas testudineus	PTU	D(L)	Peter & Oommen (1989c)
Anabas testudineus	Glucocorticoid	I(COX)	Ignatius *et al.*, 1990
Samlo gairdneri	EP, NE	I(WB)	Richard *et al.*, 1990
Salmo salar	Cortisol	I(Na^+- K^+-ATPase)	Bismal *et al.*, 1991
Rainbow trout	EP	I(H)	Ferrel *et al.*, 1991
Amia calva &	T_2	I(L)	Ballantyne *et al.*, 1992
Salvelinus namaycush	T_3	I(SM)	
S. mossambica	25°C,T_4	I(WB,L)	Sunitha Devi *et al.*, 1993
	Cortisol	I(L)	Vijayan *et al.*, 1993
Carassius auratus	T_2, T_3	I(L)	Leary *et al.*, 1996
Serinus caneria	Serotonin	I(Br)	Freo, 1996
Anabas testudineus	Thiouracil	D(G-6-Pase & Na^+-K^+-ATPase)	Nair & Oommen, 1997
	PTU + T_4	I(G-6-Pase, Na^+-K^+-ATPase)	

Abbreviations : As mentioned in Table - I.

Chapter-I

MATERIALS AND METHODS

Introduction

Fishes are aquatic vertebrates that differ in many aspects of habits and habitats compared to the terrestrial vertebrates. During the course of evolution, they developed a special mechanism by which they could extract dissolved oxygen from water through their gills. The air breathing in fish is a common phenomenon, which can be found among a wide range of freshwater as well as marine species (Graham, 1976; Sayer and Davenport, 1991). The freshwater air breathing fishes supplement their aquatic respiration primarily by utilising atmospheric oxygen (O_2) and release carbon dioxide (CO_2) aquatically (Johenson, 1970). However, marine air breathing fish species emerge out of water completely and are able to exchange O_2 as well as CO_2 in air (Graham, 1976; Bridges, 1988, 1993a, 1993b).

The bodily functions of fish are directly or indirectly subjected to fluctuations in the environment. Changes in the environment lead to continuous adjustment in the physiological and morphological characteristics of the fish (Adolph, 1964; Dill *et al.*, 1964). Fish body temperature is more or less parallel to the environment temperature, and increases/decreases with the rise/fall of the surrounding temperature. This change in body temperature has a pervasive effects on the biological processes, greatly accelerating reaction rates with increasing temperature (Cossins and Bowler, 1987). Unlike mammals and birds, fishes must cope with the effects of extreme and varying body temperature on their activity and behaviour. Fluctuations in environment exert a regulatory influence on the oxidative metabolism and the metabolic rate.

The rate of oxygen consumption by the fish is the standard measurement of its metabolic activity which is influenced by a number of external and internal factors (Fry, 1971). Many workers, using teleosts, have tried to explore the calorigenic action of various hormones, but the results have been contradictory. Most of the investigations in this respect were restricted to water breathing species in which only whole body oxygen consumption was monitored. It is important to mention that the confinement of the fish in the chambers of the respirometer or containers exposes the animal to stress which leads to altered behaviour, activity and resultant changes in the rate of whole body oxygen consumption might not be a true reflection of the calorigenic effect of the hormone treatment. In majority of earlier studies, either water temperature was not monitored or the experiments were conducted at simulated temperature without looking into or referring the importance of natural temperature/seasons. Therefore, we decided to conduct all experiments on the Indian air-breathing fish, *Clarias batrachus* maintained under natural climatic condition and to monitor the rate of tissue respiration.

Clarias batrachus : *Clarias batrachus* is a teleost which is widely distributed all over India (expect at high altitude). In nature it usually lives in shallow rivers, ponds and muddy places, and survives even in water with low O_2 content. It exhibits a bimodal (aquatic and atmospheric) breathing habits, and often comes to the surface of water to engulf atmospheric air.

Clarias batrachus breeds during monsoon (Lehri, 1967, 1968; Thakur, 1978). The gonadal activity undergoes a cyclic change (both in morphology and histology) with the change in season so that spawning will take place in the most propitious time of the year ensuring maximum survival and faster growth of the young ones. The gonadal activity slowly increases during the months of January and February at

23.3°N. It then becomes fully active from March-April and spawning occurs from June to October. Then gonads become inactive again in November-December. However, at 26.1°N, the gonadal activity increases from January to April, and becomes fully active during the month of May and June, followed by spawning during the months of July and August. Then again the gonads slowly become inactive during September to December. This cyclic change in the gonadal activity is possibly cued by the external factors (e.g. water temperature, photoperiod etc.). It has been suggested that pituitary gland through the cyclic synthesis and release of gonadotropins regulates the cyclic activity of gonads resulting in synchronised gonadal maturation and spawning (Baker, 1938). *Clarias batrachus* is commonly used for fish farming under various conditions.

For this dissertation, adult male *Clarias batrachus* (body weight : 70-80 g; body length : 18-22 cm) were purchased locally during the first week of each month. Fishes were maintained in the earthen pots and acclimatized at least for 15 days in the laboratory under natural climatic conditions at Shillong (Latitude 25.30°N, Longitude 91.52°E; Altitude 1450 ASL; Minimum water temperature 4°C and maximum water temperature 22°C). During the acclimatization, the fishes were fed daily with minced earthworms *ad libitum*. Water was changed frequently to avoid infections.

Hormonal Treatments : Hormonal treatments were given both *in vivo* and *in vitro* conditions. A brief description on the mode of treatments are given below :

***In vivo* Experiments** : The *in vivo* experiments were conducted during both winter and summer/rainy seasons. After acclimatization, fishes were divided into different groups (four in each group) for different types of treatments. The desired dose of hormone was injected intra-muscularly on the lateral sides of the dorsal fin. The details of doses of hormones, and duration of treatments are given in the respective chapters. Water temperature were recorded daily at 10.30 a.m. Twenty-four hours after the last

injection, fishes were decapitated, the tissues (liver, muscle, kidney and brain) rapidly removed, rinsed in ice-cold fish buffer saline and stored in the ice-chamber (-8°C to -10°C) of a refrigerator. The rate of tissue respiration was measured within 15 days. When tissue were stored in the refrigerator, no significant alteration was found in the rate of tissue respiration upto one month.

***In vitro* Experiments** : *In vitro* effects of the selected hormones on the rate of tissue respiration were also conducted during both winter and summer/rainy seasons. Four adult male fishes were first weighed, and then decapitated. The tissues (liver, muscle, kidney and brain) were quickly removed separately, rinsed in ice-cold fish buffer saline and stored in a freezer as mentioned earlier. The tissues were used to study the *in vitro* effects of hormones within 15 days. For *in vitro* treatments, the tissues were blotted, weighed and homogenized in a loose fitting all glass homogenizer in ice-cold fish buffer saline solution (pH 7.4). One ml of homogenate was added to 3.9 ml of fish buffer saline and incubated with 0.1 ml of hormone solution having the desired concentration.

The tissue homogenates treated with mono-iodotyrosine (MIT), di-iodotyrosine (DIT), L-T_3, L-T_4, testosterone, and melatonin were pre-incubated at 4°C for one hour prior to the measurement of the rate of oxygen consumption. This incubation was necessary to allow the binding of these hormones to the tissues. The homogenates treated with catecholamines and corticosteroids were incubated only for 15 minutes in the incubation chamber of the oxygen electrode at 25°C before the measurement of the rate of tissue oxygen consumption. Readings were taken at an interval of 5 minutes for half an hour when the oxygen consumption was found to be linear. The rate of tissue oxygen consumption was expressed as µl O_2/ mg wet tissue / h.

Chemicals : Hormones, antagonist and inhibitors used in the experiments were purchased from Sigma Chemical Company, USA General chemicals were purchased from BDH. Cyproterone acetate was gifted by Prof. Dr. M.F. ElEtreby, Berlin.

Measurement of Tissue Respiration

The rate of oxygen consumption of each tissue (liver, muscle, kidney and brain) was measured with the help of an oxygen electrode (Digital Oxygen System, Model 10; Rank Brothers Ltd., England). The system is composed of an incubation chamber of plexi glass (with Ag^+ as anode and platinum as cathode) and a control panel (with Knobs to regulate sensitivity, polarizing voltage and speed of the magnetic bar). A thermostatically controlled water circulator is used for circulating water in the incubation chamber of oxygen electrode. For measuring the rate of respiration, polarizing voltage was kept at 0.6V. Fish buffer saline (pH 7.4) was used as the polarizing medium.

For the measurement of tissue respiration, the tissue were first blotted, weighed and homogenized in a loose fitting all-glass homogenizer (Remi Homogenizer, Remi equipments, Bombay(in ice-cold fish buffer saline (9:1) solution (pH 7.4). The rate of oxygen consumption of tissue homogenates were measured at 25°C by circulating water at 25°C in water jacket of the incubation chamber using the thermostatic water circulator.

For measuring the rate of respiration of tissues from *in vivo* experiments, 1 ml of homogenate was added to 4 ml of fish buffer saline solution and placed into the incubation chamber of the oxygen electrode. The homogenate were incubated in the chamber for 15-20 minutes before recording the readings. Reading were recorded at an

interval of 5 minutes for half an hour. The rate of tissue respiration was expressed as $\mu l\ O_2$ / mg wet weight tissue/hr.

Statistical Analysis : The data were analysed statistically with the help of student t-test and regression analysis (Snedecor, 1961). A $P<0.05$ was considered as significant.

The above mentioned standard procedures were followed in all the experiments incorporated in this thesis.

Chapter-II

STUDY OF ANNUAL VARIATIONS IN THE OXIDATIVE METABOLISM OF MALE *Clarias batrachus* WITH SPECIAL REFERENCE TO TEMPERATURE, PHOTOPERIODS AND FEEDING STATUS

Seasonal climatic changes are commonly faced by most of the species in nature. Animals have developed adaptive strategies to overcome extremes of climatic factors and to synchronise their reproductive activity so that breeding phase coincides with the most favourable period of the year when conditions for survival of their offsprings is optimal (Vivien-Roels, 1985). The environmental cycles of photoperiod, temperature, and rainfall provide predictive information and are used by many species as indicators of seasons. Further, seasonal changes in temperature and photoperiod have been reported to influence the activity of the neuroendocrine system of fish (Tomasso *et al.*, 1981; Fu *et al.*, 1990; Khan and Joy, 1990a, b; Lamer *et al.*, 1992) which ultimately regulate activities of various endocrine glands (Verma *et al.*, 1996). Seasonal alterations in the environmental factors reportedly regulate the annual variations in the concentrations of circulating hormones as well as the responsiveness of tissues to these hormones in sevaral vertebrates (Jallageas and Assenmacher; 1972; Young et al., 1979; Litch et al., 1983; Eales, 1985; Crim *et al.*, 1989; Khan and Joy, 1990a; Guerrero *et al.*, 1990; Manikam and Joy, 1990; Saligaut *et al.*, 1992a,b; Trudeau *et al.*, 1993a,b; McCormic *et al.*, 1995; Verma *et al.*, 1996). Increasing temperature has been reported to accelerate the synthesis and turnover of hormones and to increase the physical activity and metabolic rate of fish (Beamish, 1964; Swift, 1964; Pandey and Munshi, 1976; Taurog, 1978; Patra *et al.*, 1983; Suzuki, 1985; Leloup *et al.*, 1985; Sinha *et al.*, 1988; Nayak, 1991). However, in some studies it has been reported that temperature had no effect either on the synthesis of hormones or on the rate of oxygen

consumption in fish (Shaklee *et al.*, 1977; Perrier *et al.*, 1979; Eales *et al.*, 1980; Kent *et al.*, 1988; Schwarzbaum *et al.*, 1992).

Seasonal changes in temperature have also been reported to change the activity of various enzymes of energy-yielding pathways in a number of tissues (Shaklee *et al.*, 1977; Lind, 1992; William *et al.*, 1977). Long daylengths reportedly increased the activity of Na^{+}-K^{+}-ATPase as well as gonadal activity and gametogenesis (Bullough, 1939, 1940; Vanden, 1946). However, in Salmonid fish short daylength has been reported to accelerate the maturation and activity of gonads (Billard *et al.*, 1978; Amano *et al.*, 1994). Keeping in view the cyclic changes in climatic factors, hormones and reproductive activity; attempts have been made to study the rate of energy metabolism/oxidative metabolism of fish with special reference to climatic changes/seasons.

Seasonal fluctuation in temperature and photoperiod greatly affect the availability of food in nature which might have a direct effect on the behaviour, physical activity and physiological function in general and on the energy metabolism of the animal in particular. However, there is scarcity of information on the effect of feeding/fasting on the rate of oxygen consumption at the tissue level. Feeding has been reported to increase and fasting to decrease the whole body oxygen consumption and also the activity of cytochrome oxidase (COX) in vertebrates (Love, 1958; Ross, 1969; Weindruch *et al.*, 1980; Costa and Kooyman, 1984; Baudinette *et al.*, 1986; MacArthur and Campbell, 1994; Secor and Diamond, 1995; Seymour and Seely, 1996; Lane *et al.*, 1996). However, dietary restriction have been reported to have no effect on brain mitochondrial activity (Ross, 1969; Rajwade *et al.* 1975; Ooka *et al.*, 1978; Richard *et al.*, 1980).

Most of the earlier reports are based on studies of the whole body oxygen consumption of fish species which are totally dependent on oxygen dissolved in water.

But practically there is no information on the annual variation in energy metabolism of any fish species either at whole body or at tissue level. In fish, seasonal changes in the environment have been reported to alter the erythrocytes' osmotic fragility (Siddal *et al.*, 1995) and membrane fluidity of the cells (Chapman, 1967; Simensky, 1974; Hazel *et al.*, 1992; Roy, 1993; William *et al.*, 1994). So far no attempt have been made to study the metabolic changes at individual tissue level. The measurement of whole body oxygen consumption may provide ambiguous results, since due to the placement of a fish in the chamber of a respirometer fish might be exposed to stressful conditions. Therefore, the whole body oxygen uptake might not reflect the actual metabolic rate of the fish. Therefore, it was thought worthwhile to investigate the seasonal variation in energy metabolism of different vital tissues (liver, muscle, kidney, brain) of an Indian air breathing fish *Clarias batrachus* with special reference to natural and simulated temperature, photoperiods and feeding status. The findings of the present study indicate that the rate of tissue respiration is influenced by seasons, climatic factors and feeding status.

Materials and Methods

Annual variation in tissues respiration

For the study of the annual variations in tissue metabolic rate, fishes were purchased locally in the third week of every month, acclimatized under natural climatic conditions, and scarified on the 15th day of the following month. During acclimatization, the fishes were fed with minced earthworm *ad libitum*. Water temperature was recorded every day at 10 a.m. throughout the acclimatization period. Fish were decapitated between 10 a.m. and 10.30 a.m., tissues (liver, muscle, kidney and brain) were quickly removed, rinsed in ice-cold fish buffer-saline solution and

stored in a refrigerator at -6°C to -8°C for measurement of tissue respiration. For detailed information on acclimatization, please refer to Chapter-1.

Effects of simulated temperature on the rate of tissues respiration

For this purpose, experiments were conducted during the month of February. Fishes were purchased from the local market and acclimatized for 15 days. Then the fishes were divided into four groups of 10 fishes each, kept in containers having a capacity of 10 litre water. One group was kept at room/natural temperature. The remaining groups 2, 3 and 4 were kept under simulated temperature at 15°C±1°C; 25°C±1°C, and 35°C±1°C respectively in BOD incubators. These groups were exposed to 12L/12D photoperiod. The photoperiod was controlled by an electric timer-device. During the experiment, fishes were fed with minced earthworms *ad libitum*. After 30 days the fishes of all the four groups were decapitated between 10 a.m. to 10.30 a.m., tissues (liver, muscle, kidney and brain) were quickly removed, rinsed in ice-cold fish buffer-saline (pH 7.4) and stored in a refrigerator at -6° to -8°C for the measurement of the rate of tissue respiration.

Effect of simulated photoperiod on tissue respiration

For this study, fishes were purchased from the local market during the month of January, and acclimatized in the laboratory for 15 days. Then the fishes were divided into four groups of eight fishes each and maintained in plastic cages of 10 litre capacity. One group was kept at room/natural daylength and room temperature. The other three groups 2, 3 and 4 were kept at simulated photoperiod of 9L/15D, 12L/12D and 15L/9D, respectively in BOD incubators with a constant temperature of 25°C. During the course of study, fishes were fed with minced earthworms *ad libitum*. After

maintaining the fishes under above mentioned simulated photoperiod and temperature for 30 days, the fishes were decapitated and tissues (liver, muscle, kidney and brain) were quickly removed, rinsed in ice-cold fish buffer-saline (pH 7.4) and stored in a refrigerator at -6°C to -8°C for the measurement of the rate of tissue respiration.

Effect of Feed/Fasting on the Rate of Tissue Respiration

For the study of tissue respiration in relation to feeding or fasting, fishes were purchased from local market and acclimatized for 15 days under natural climatic conditions as mentioned in Chapter-I. During acclimatization, the fishes were provided with minced earthworms *ad libitum*. After acclimatization, on the 16th day fishes were divided into two groups of 20 fishes each. One group was provided with minced earthworms *ad libitum* and the other group was totally deprived of food. The water temperature was recorded every day at 10 a.m. After 5 days, 10 days, and 15 days of feeding and fasting of both the groups, 4 fishes from each group were randomly selected, decapitated and tissues (liver, muscle, kidney and brain) were quickly removed, rinsed in ice-cold fish buffer-saline (pH 7.4) and stored in a refrigerator at -6°C to -8°C for measurement of the rate of tissue respiration.

Measurement of tissue respiration

The rate of oxygen consumption of the tissues collected in the above experiments was measured with the help of oxygen electrode following the methodology discussed in Chapter-I : Materials and Methods.

Results

Annual variations in the rate of tissue respiration

The data are presented in Tables 1:1 & 1:2; Figs. 1:1 & 1:2. All the four tissues exhibited seasonal variations in the rate of respiration. The rate of respiration of the brain tissue was found always to be higher and that of muscle tissue to be lower than that of other tissues. The rate of liver tissue respiration was higher than that of kidney and muscle but lower than the rate of brain tissue respiration. Similarly, the rate of oxygen uptake of kidney was higher than that of muscle but lower than the rate of liver and brain respiration (Table 1:1; Fig. 1:1).

The pattern of seasonal variation in the respiratory rate of the tissues was found to be more or less similar except brain respiration. The respiratory rate of liver, muscle and kidney was found to be minimum during winter months (December-March). However, the rate of brain tissue respiration was found to be higher during winter months. The brain respiration reached to a maximum during the month of November and the high respiratory rate was maintained upto the month of January. Thereafter, the brain respiratory rate declined sharply during the month of February reaching to a minimum during the month of March. However, during the month of April, there was a significant increase in brain tissue respiration which reached again to a significantly higher level during the month of May which was maintained at increased level upto the month of August. Then it decreased significantly during the month of September followed by a significant increase during the month of October.

The respiratory rates of liver, muscle and kidney tissues were found to be low during the month of December to March with insignificant monthly fluctuations. However, the respiratory rate of the tissues increased significantly during the month of April reaching to a peak value during the month of May. The increased rates of

respiration of these three tissues were maintained during the month of June to September with insignificant monthly fluctuations. Unlike the brain respiration, the respiratory rate of these tissues gradually decreased during the month of November to December reaching to a minimum during the month of January (Table 1.1, Fig. 1.1).

When the average rate of tissue respiration was calculated for winter (November to February) and summer/rainy months (March to October), it was found that the average respiratory rate of brain did not vary significantly during winter and summer/rainy months (Table 1:2; Fig. 1:2). However, the average respiratory rate of liver, muscle and kidney tissues was found to be significantly higher during summer/rainy months as compared to that of winter months (Table 1:2; Fig. 1:2).

Effects of simulated temperature on the rate of tissues respiration

The data are presented in Table 1:3; Fig. 1:3. The respiratory rate of the tissues was influenced differently by simulated temperatures (Table 1:3; Fig. 1:3). While the rate of liver and muscle tissues exhibited linear increase with the increasing temperature, the respiratory rate of kidney and brain tissues increased significantly upto 25°C and decreased significantly at 35°C as compared to the respiratory rate both at 15°C and 25°C.

When the data were analysed with the help of regression analysis, the nature of correlation between the respiratory rate and the simulated temperature was found to be different for different tissue. While the respiratory rate of liver and muscle exhibited a very strong positive correlation with temperature ($r = +0.99$ and $+0.97$ for liver and muscle, respectively). However, the respiratory rate of kidney and brain exhibited an insignificant negative correlation with temperature ($r = -0.25$ and -0.35 for kidney and brain, respectively).

Effects of simulated photoperiods on the rate of tissues respiration

The data are presented in Table 1:4; Fig.1:4. The respiratory rate of the tissues was influenced significantly by the photoperiods. The respiratory rate of brain, liver and muscle tissues was found to be maximum in the fishes maintained at 9L/15D photoperiod (temperature : 25°C). The respiratory rate of all the tissues (except kidney) taken from the fishes maintained at 12L/12D and 15L/9D (temperature 25°C) was found to be significantly lower as compared to the group maintained at 9L/15D. However, there was no difference between the respiratory rate of tissues from the fishes exposed to 15L/9D and 12L/12D photoperiods. A very strong negative correlation was found between the lengths of photoperiods and the respiratory rate of liver (r=-0.94), muscle (r=-0.99) and brain (r=-0.72). There was no significant correlation between the rate of kidney respiration and photoperiod (r=0.38).

Effects of feeding/fasting on the rate of tissue respiration

The data are presented in Table 1:5; Fig.1:5. The respiratory rate of the tissues of the fed and fasted groups was measured after 5 days, 10 days and 15 days. It was found that there was no significant effect of fasting on the rate of tissue respiration on the 5th day. However, the respiratory rate of liver, muscle and kidney tissues decreased significantly after 10 days of fasting as compared to the fed group. The rate of oxygen consumption of liver and muscle tissue was found to be significantly lower and that of kidney to be higher after 15 days of fasting as compared to the fed control group. There was no significant difference between the respiratory rate of brain tissues of fed and fasted groups. Regression analysis of the data showed a strong negative correlation between the duration of fasting and respiratory rate of liver (r = -0.99) and muscle (r = -0.95). A significant positive correlation was found between the kidney

respiratory rate and the duration of fasting (r = +0.64). No significant correlation was found between the rate of brain tissue respiration and the length of fasting (r = 0.13).

Discussion

All the tissues (liver, muscle, kidney and brain) exhibited seasonal variation in their rate of respiration (Table 1:1; Fig.1:1). During winter, the respiratory rate of liver, muscle and kidney were found to be minimum. This finding suggest that the physical activity of the fish at low temperature is decreased leading to a decreased energy demand. Further, during winter the collective influence of various environmental factors reportedly suppress activities of various endocrine glands of vertebrates to the minimum (Bullough, 1940; Van-den, 1946; Singh, 1968; Thapliyal and Chandola, 1973; Kashinathan and Basu, 1973; Assenmachar, 1973; Haldar, 1977; Ooka *et al.*, 1978; Thapliyal, 1980; Randeel *et al.*, 1992; Shi *et al.*, 1993; Wingfield *et al.*, 1996). In mammals, low temperature and short daylengths have been reported to inhibit the activity of respiratory enzymes like succinate dehydrogenase (SDH) and co-enzyme-Q (Lerner *et al.*, 1972; Fedotcheva *et al.*, 1985; Hackenbrook *et al.*, 1986), and also reduced electron transport in the respiratory chain (Gehnrich and Aprille, 1986, 1988). A similar mechanism might also be responsible for the decreased metabolic rate of the tissues in the fish *Clarias batrachus* exposed to low temperature during winter months. Thus, reduced activity, inhibition of growth (Beamish, 1964a; McCormick *et al.*, 1995) and low rate of protein synthesis during winter (Houlihan *et al.*, 1988; Pannevis and Houlihan,1992; Houlihan *et al.*, 1993) appear to decrease energy demand and might be responsible for low rate of oxygen consumption of the tissues during winter months as compared to summer/rainy months.

The respiratory rate of the brain tissue was found to be maximum during the winter months (Table 1:1; Fig.1:1) as reported in other poikilotherms (Das and Patnaik, 1979; Sharan *et al.*, 1981; Gupta and Thapliyal, 1986; Zari, 1996). The increased brain respiratory rate during winter might be due to increased synthesis and release of neurotransmitters for better systemic co-ordination at low temperature (Leoduc, 1961; Baldwin and Hochachka, 1970; Baldwin, 1971; Thapliyal and Sharan, 1980; Khan and Joy, 1990; Manickam and Joy, 1990; Senthikumaran and Joy, 1995). Thus, the increased metabolic rate of the brain might be helpful in ensuring survival of the fish at low water temperature during winter months. Towards the end of the winter season (February, March), liver, muscle and kidney tissues did not show significant variation in oxygen uptake despite an increase in the water temperature (Fig. 1:1). It, thus, seems that temperature alone failed in increasing the metabolic rate of tissues when the daylength was still below the required duration to activate the neuro-endocrine system necessary to increase the metabolic rate. Brain tissue respiration showed a sharp drop in March and September. This might be signalling the end of the unfavourable and beginning of the favourable climatic conditions while the decline in the brain respiratory rate during September seems to signal the end of the breeding phase as well as favourable conditions, and the onset of the cold/unfavourable conditions. The altered brain respiration might influence the metabolic rate of other vital tissues to conserve energy for the ensuing winter season.

The respiratory rate of all the tissues increased significantly during the month of April. The respiratory rate of muscle and kidney reached to peaks in June and July respectively; while liver and brain tissues oxygen uptake exhibited a peak during the month of June. Thereafter, the high metabolic rate of all the tissues was maintained upto September. The increased oxygen uptake of the tissues during the month of April to September, might be due to increased energy demand of the fish for various activities related to reproduction. It has been reported in teleosts that the gonadal

developments are induced by the collective influence of daylengths and temperature variation (Crim, 1982). Long daylengths activate the hypothalamo- hypophysial gonadal axis (Vanden, 1946; Ferner *et al.*, 1973; Reiter, 1978; Kupawade and Saidapur, 1986; Saidapur, 1983) and increased levels of testicular hormones (Church, 1960; Warner, 1969; Ralph, 1983; Bohra and Nazi, 1984; Duellman and Trueb, 1986; Saidapur, 1989). Further, availability of food and increased temperature and daylength have been reported to increase thyroid hormone production (Assenmacher, 1973; Jobin *et al.*, 1973; Danforth *et al.*, 1975; smith, 1982; Rothwell *et al.*, 1982a; Dawson, 1984; Nicholls *et al.*, 1988; McCormick *et al.*, 1995; Wingfield *et al.*, 1996) and also increased the release of catecholamines (both epinephrine and nor-epinephrine) during the breeding season (Donoso and Sagura, 1965; Manickam and Joy, 1989; Senthilkumaran and Joy, 1995). It, thus, seems that increased daylength, temperature and availability of food, stimulated the production of gonadal steroids, thyroid hormones and catecholamines during breeding season. The respiratory rate of fish and other poikilotherms has been reported to be stimulated by testicular steroids (Hoar, 1958; Gorbman, 1963; Chandola *et al.*, 1973; Thapliyal *et al.*, 1975; Oommen, 1976; Gupta, 1988; Peter and Oommen, 1989b,d; Gupta and Chakrabarty, 1990; Gupta and Mahanta, 1997); thyroid hormones (Pandey and Munshi, 1976; Thapliyal, 1980; Matty, 1985; Gupta and Thapliyal, 1985; Oommen and Sreedeviamma, 1988; Gupta and Thapliyal, 1991) and catecholamines (Larson, 1973; Gupta, 1988; Gupta and Thapliyal, 1991; Gupta and Mahanta, 1997). Therefore, the increased production of these metabolic hormones during summer/rainy months might be responsible for the increased metabolic rate of the tissues.

The Changes in ambient temperature have been reported to influence the metabolic rate of vertebrates (Smith, 1930; Bishop, 1952; Bishop and Gordon, 1967; Beamish, 1970; Fry, 1971; Cossin and Bowler, 1978; Pough, 1980; Hochachka and Somero, 1984). In the present study (Table 2:2; Fig.2:2), the oxygen uptake of both

liver and muscle tissues showed a positive correlation with the increasing temperature. There are reports that increase in temperature stimulates and decrease in temperature inhibits synthesis and release of metabolic hormones, e.g. thyroid hormones and catecholamines (Chiu *et al.*, 1973; Taurog, 1978; Suzuki, 1985; Leloup and De-Luze, 1985; Schmidt *et al.*, 1985; Burton et al., 1985, 1987; Eales and Brown, 1993; Senthilkumaran *et al.*, 1995). The temperature- induced increase in the level of these hormones might be responsible for increased mobilisation and oxidation of substrates to meet high energy demand associated with increased level of physical activity and protein synthesis (Butler and Turner, 1988; Hillman and Withers, 1987; Buckel *et al.*, 1995; Franklin *et al.*, 1995; Martinez *et al.*, 1996; Kia *et al.*, 1996; Hanel *et al.*, 1996).

The respiratory rate of the brain tissue showed a negative correlation with increase in water temperature (Table 2:2; Fig. 2:2). The decreased respiratory rate of brain and kidney tissues at 35°C seems to suggest that at temperature above 25°C these tissues tend to adjust their metabolic rate by altering enzyme activity leading to a low metabolic rate and decreased oxygen uptake (Hochachka and Hyne, 1962; Frankel and Ferrante, 1966; Nemoto and Frankel, 1970; Fernandes *et al.*, 1995). Present findings seem to suggest that the metabolic rate of somatic tissues of *Clarias batrachus* is significantly influenced by water temperature.

Daylength is known to play a variable role in enhancing or inhibiting release of various hormones in vertebrates (Figala *et al.*, 1973; Osei, 1981; Sharp *et al.*, 1984; Rees *et al.*, 1983; Nicholls *et al.*, 1988; Guerrero *et al.*, 1990; Saligaut *et al.*, 1992; Jile *et al.*, 1992; Wingfield *et al.*, 1996) and enzymes activities (Robert *et al.*, 1964; McCormick *et al.*, 1995). In the present study, it was found that the respiratory rate of liver, muscle and brain tissues showed a negative correlation with the increase in photoperiod while kidney respiratory rate was not significantly correlated with photoperiod (Table 2:3; Fig. 2:3). *Clarias batrachus* is nocturnal in habit with

increased physical activity during the dark phase/night and lowered activity during the light phase/day. Therefore, the inverse correlation between the activity of the fish and the daylength might be responsible for a negative correlation between respiration and daylength. Short daylengths have been reported to stimulate neurones of central nervous system (Amano *et al.*, 1995), activity of liver oxidative enzymes (Robert *et al.*, 1964), concentration of circulating corticosterone (Osei, 1981; Rees *et al.*, 1983) and secretion of melatonin (Figala *et al.*, 1973). It is important to mention that catecholamines, corticoids and melatonin stimulate tissue respiration in amphibians and reptiles (Gupta, 1988; Deka-Borah, 1989; Hanke, 1990; Gupta and Chakrabarty, 1990; Gupta and Deka-Borah, 1995; Gupta and Mahanta, 1997). Therefore, there is a possibility that short daylengths/photoperiods might be increasing the respiratory rate of tissues in *Clarias batrachus* by increasing levels of these hormones resulting in increased mobilization of precursor molecules and their oxidation (Smale *et al.*, 1988). Thus, present findings suggest that alteration in daylength/photoperiod might be influencing the rate of oxygen consumption mainly by altering the levels of hormones and physical activity of the fish *Clarias batrachus*.

The regular supply of food significantly increased the metabolic rate of all the tissues and a positive correlation was found between the duration of feeding and the respiratory rate of the tissues (Table 2:4; Fig. 2:4). This finding is similar to the effect of feeding on respiratory rate recorded in other vertebrates (Costa and Kooyman, 1984; Baudinett *et al.*, 1986; MacArthur and Campbell, 1994; Christian *et al.*, 1996; Speakman *et al.*, 1996; Seymour and Seely, 1996). Food intake reportedly increase the synthesis and release of metabolic hormones which accelerate the enzyme activity leading to increased rate of mobilization/oxidation of substrates as well as protein synthesis for growth and activity of the fish (Danforth *et al.*, 1975; Klandorf *et al.*, 1981; Eales, 1988; Danforth and Burger, 1989; Mehner and Wieser, 1994; Zamal and Ollevier, 1995). Therefore, it seems that feeding might have stimulated tissues'

respiration by providing nutrients/substrates and also by stimulating the release of metabolic hormones. Fasting had a significant adverse effect on the respiratory rate of liver and muscle tissues (Table 2:4; Fig. 2:4). While there was a negative correlation between duration of fasting and the respiratory rate of liver and muscle, kidney tissue showed a positive correlation with the duration of fasting. However, brain tissue respiration was not affected by starvation. The decline in oxygen uptake of liver and muscle tissues from the fasted groups might be due to reduced supply of substrates for oxidation, reduced protein synthesis and decreased physical activity of the fish, *Clarias batrachus*. In other vertebrates, fasting has been reported to decrease thyroid activity followed by low conversion of T_4 to T_3 and reduction in thyroid hormones receptors (Burman *et al.*, 1977; Carupbell *et al.*, 1977; DeGroot *et al.*, 1977; Higgs and Eales, 1977; Harris *et al.*, 1978; Schussler and Orlando, 1978; Oppenheimer, 1979; Gatten, 1980; Leatherland, 1981; Burger et al., 1981; Connor *et al.*, 1985; Sievert *et al.*, 1988; Blake *et al.*, 1991; Oommen and Matty, 1991; Rondeel *et al.*, 1992; Shi *et al.*, 1993; Van Haasteren *et al.*, 1995, 1996).

It is important to mention that increased thyroid activity, higher conversion of T_4 to T_3 and increased number of thyroid receptors stimulate activity of many oxidative enzymes and metabolic rate (Pickford *et al.*, 1970; Laragh and Sealey, 1973; Oppenheimer, 1979). It, thus, seem that fasting-induced decrease in the respiratory rate of the fish tissues might also be due to decreased levels of thyroid hormones and/or their receptors. Fasting has been reported to increase the circulating level of corticoids (Ballamy, 1968b; Rees *et al.*, 1983; Jolivet-Jaudet and Ishii, 1985; Bobek et al., 1986; Reddy and Leatherland, 1995; van Haasteren *et al.*, 1996). Further, cortico-steroids have been reported to be calorigenic in reptiles and amphibians (Thapliyal and Gupta, 1983; Gupta and Deka-Borah, 1995; Gupta and Mahanta, 1997). Increased level of cortocosterone during fasting has been reported to stimulate protein catabolism in fish (Ball *et al.*, 1966; Loughna and Goldspink, 1984; Robin *et al.*, 1987;

Pastoureaud, 1991). Therefore, there is a possibility that the increased oxygen uptake of the kidney during fasting was due to the stimulatory effect of corticosterone for rapid removal of waste products and other harmful metabolites resulting from protein catabolism. Starvation had no significant effect on brain mitochondrial respiration in mice (Weindruch *et al.*, 1980). In the present study also, fasting did not affect brain respiratory rate significantly (Table 2:4; Fig. 2:4 Thus, the brain respiration in fish is not adversely affected by unavailability of food (fasting). This might be a mechanism for ensuring survival of the fish during fasting or at low caloric intake.

On the basis of the present findings, we conclude that the annual changes in the metabolic rate of the fish tissues are affected directly or indirectly by temperature, daylength/photoperiod and availability of food. Low temperature and short daylength of winter leads to scarcity of food decreased activity of the neuroendocrine axis followed by decreased activity and reduced oxygen uptake. High temperature and long daylengths/photoperiods during summer/rainy months at Shillong seem to increase the availability of food, physical activity, development of gonads, synthesis and release of metabolic hormones in the fish. All these factors seem to be jointly responsible for an increased rate of oxygen consumption of the fish tissues during summer/rainy months. The respiratory rate of liver and muscle tissues are significantly influenced by the changes in water/ambient temperature, daylength/photoperiod and feeding status. Kidney respiration seems to be predominantly affected by temperature and not by daylengths. However, brain tissue respiration does not seem to be adversely affected by low ambient temperature and unavailability of food. The brain respiratory rate seems to be inversely related to photoperiod. It, thus, seem that, as reported in reptiles (Gupta and Thapliyal, 1986), brain has a self-regulated energy metabolism to ensure survival of the fish under adverse condition during cold winter months. Further, it seems that the energy metabolism of different tissues of the fish respond differently to the changes in the environmental factors. The seasonality in the metabolic rate of the

vital tissues seems to be programmed/cued by these cycling factors in such a way so that each tissue performs its function optimally in order to ensure the survival of the fish during adverse conditions and successful breeding during the most favourable months/season of the year.

Table 2: I- Study of seasonal variation in the rate of tissue respiration of male *Clarias batrachus*.

Months	Rate of Tissue Respiration (μl O_2/mg wet tissue/h)			
	Liver	Muscle	Kidney	Brain
November	3.11±0.11[a]	2.08±0.05[a]	2.76±0.03	5.39± 0.08[c]
December	2.85±0.05	1.76±0.09[a]	2.56±0.08	5.07± 0.07[a]
January	2.69±0.06	0.89±0.08[c]	2.53±0.05	5.01±0.04
February	2.82±0.17	1.25±0.07[a]	2.47±0.13	3.31±0.15[c]
March	2.47±0.03	1.06±0.11	2.08±0.09[a]	2.82±0.12[a]
April	3.82±0.09[c]	2.66±0.03[c]	3.46±0.16[c]	4.62±0.06[c]
May	4.78±0.14[b]	3.11±0.17[b]	3.78±0.07	5.26±0.09[b]
June	4.97±0.05	3.03±0.08	3.85±0.08	5.23±0.05
July	4.81±0.12	2.86±0.02[a]	4.01±0.03	5.07±0.10
August	4.72±0.10	2.82±0.14	3.76±0.16	5.17±0.09
September	4.49±0.16	2.56±0.12	3.95±0.09	4.17±0.03[c]
October	3.59±0.08[b]	2.44±0.10	3.18±0.18[b]	4.43±0.06[b]

All values are expressed as mean ± standard error; N = 4.

[a, b, c] Differ from the value of preceeding month : $P < 0.05$, 0.01 and 0.001, respectively.

Table 2.2 - Comparison of the rate of tissue respiration of male *Clarias batrachus* during winter and summer seasons/months (based on Table 1).

Months	Rate of Tissue Respiration (μl O_2/mg wet tissue/h)			
	Liver	Muscle	Kidney	Brain
Summer (March-October)	4.21±0.40	2.57±0.30	3.51±0.30	4.59±0.39
Winter (November-February)	2.87±0.08[a]	1.50±0.23[a]	2.58±0.05[a]	4.69±0.41

All values are expressed as mean ± standard error (S.E.).

[a] Differs from the respective value of summer : $P<0.05$.

Table 2:3 - Effects of simulated temperatures on the rate of tissue respiration of male *Clarias batrachus* at a constatnt photoperiod (12L/12D).

Temperature	Rate of Tissue Respiration (µl O_2/mg wet tissue/h)			
	Liver	Muscle	Kidney	Brain
Room Temperature (10° C; 10.44L/13.10D)	2.69±0.12	0.99±0.11	2.50±0.10	5.01±0.08
15° C	3.46±0.05[a]	2.89±0.07[b]	5.17±0.05[b]	5.91±0.10[a]
25° C	6.64±0.17[b,d]	4.85±0.09[b,d]	6.97±0.15[b,d]	7.16±0.18[b,c]
35° C	8.67±0.19[b,d,e]	5.78±0.08[b,d,e]	4.53±0.07[b,c,f]	3.53±0.07[b,d,f]
Correlation Coefficient (r)	+0.99	+0.97	NS	-0.64

All values are expressed as mean ± standard error (S.E.); N = 4.

[a, b] Differ from the value at room temperature : P<0.01 and 0.001, respectively.

[c, d] Differ from the value at 15°C : P<0.01 and 0.001, respectively.

[e, f] Differ from the value at 25°C : P<0.01 and 0.001, respectively.

Table 2:4 - Effects of simulated photoperiod on the rate of tissue respiration of male *Clarias batrachus* at a constant temperature (Av. water temp. : 25° C).

Photoperiod	Rate of Tissue Respiration (μl O_2/mg wet tissue/h)			
	Liver	Muscle	Kidney	Brain
9L/15D	7.19±0.12[b]	5.36±0.10[a]	6.97±0.05	7.80±0.09[b]
12L/12D	6.68±0.05	4.94±0.07	6.80±0.09	6.90±0.14
15L/9D	6.55±0.06[e]	4.69±0.16[d]	7.06±0.04[a]	7.13±0.07[e]
Corr. Coeff.(r)	-0.94	-0.99	NS	-0.72

All values are expressed as mean ± standard error (S.E.); N = 4.

[a, b] Differ from 12L/12D : P<0.05 and 0.01, respectively.
[d, e] Differ from 9L/15D : P<0.05 and 0.01, respectively.

Table 2:5 - Effects of feeding and fasting on the rate of tissue respiration in male *Clarias batrachus* during summer (Av. water temp. : 22° C).

Duration	Status	Rate of Tissue Respiration (μl O_2/mg wet tissue/h)			
		Liver	Muscle	Kidney	Brain
'0' Day		4.78±0.14	3.11±0.17	3.79±0.07	5.26±0.09
5 Days	Fed	4.94±0.03	3.21±0.04	3.75±0.02	5.29±0.05
	Fasted	5.01±0.09	3.31±0.05	3.85±0.06	5.39±0.04
10 Days	Fed	5.14±0.04[a]	3.56±0.03[a]	4.04±0.07[a]	5.36±0.03
	Fasted	4.85±0.05[d]	3.18±0.07[d]	3.47±0.05[b,c]	5.59±0.07[a,c]
15 Days	Fed	5.23±0.02[a]	3.59±0.04[a]	4.14±0.05[b]	5.46±0.07
	Fasted	4.72±0.03[e]	3.08±0.08[d]	4.17±0.06[b]	5.39±0.09
Corr. Coeff(r)	Fed vs duration	+0.97	+0.89	+0.96	+0.99
	Fasted vs duration	-0.99	-0.99	+0.46	NS

All values are expressed as mean ± standard error; N = 4.

[a, b] Differ from the respective value of '0' day control : $P<0.05$ and 0.01, respectively.

[c, d, e] Differ from the respective value of fed group : $P<0.05$, 0.01 and 0.001, respectively.

Figure 2:1- Study of seasonal variation in the rate of tissue respiration of male *Clarias batrachus*.

All values are expressed as mean ± standard error; N = 4.

[a, b, c] Differ from the value of preceeding month : $P< 0.05$, 0.01 and 0.001, respectively.

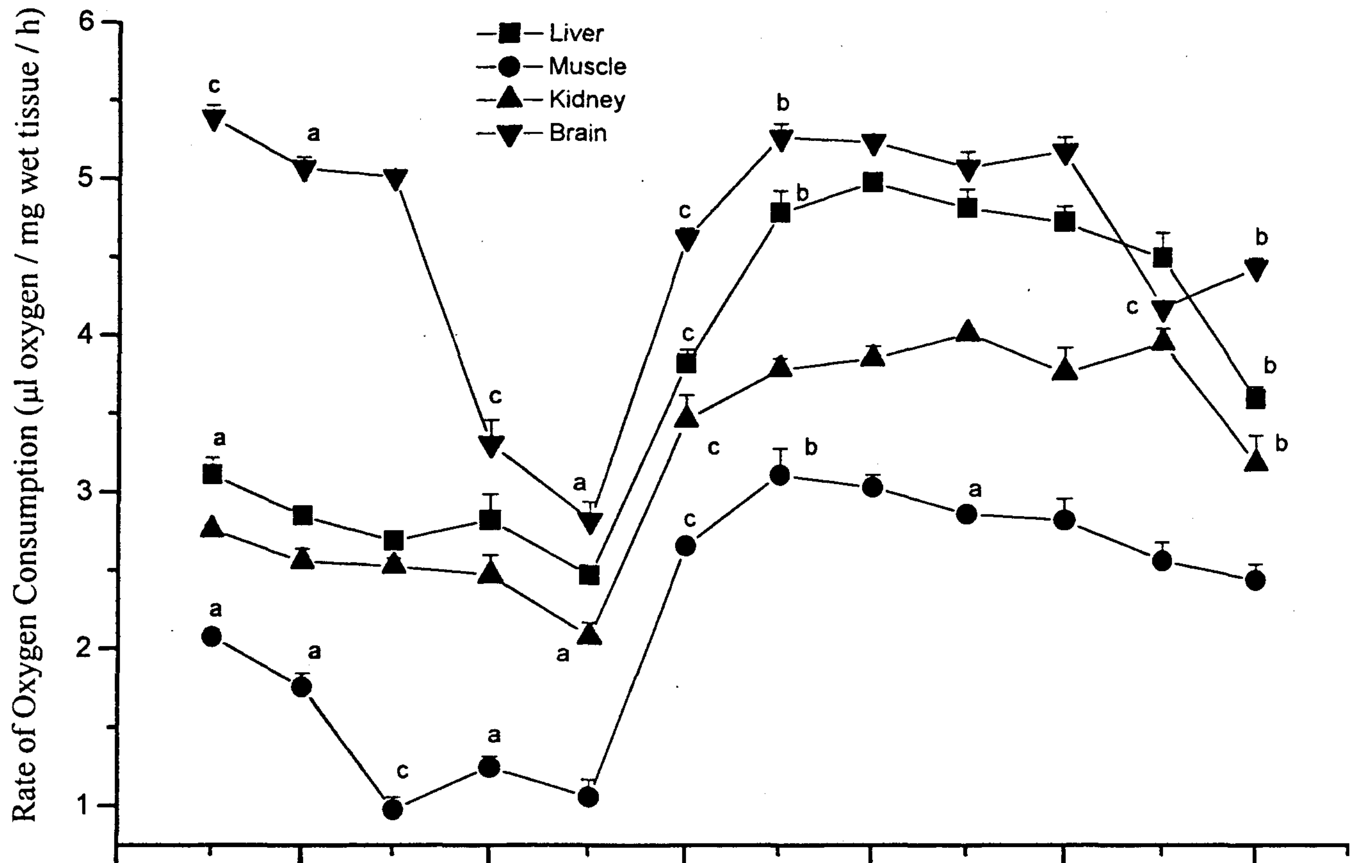

Rate of Oxygen Consumption (µl oxygen / mg wet tissue / h)
Liver
Muscle
Kidney
Brain
Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct
Water Temp (°C) 14 11.5 9.6 13 16 21 22 21 20 20 20 18
Av. Daylength (h) 11 10 10 11 12 12 13 13 13 13 12 11
Min. 05 37 44 17 06 54 23 43 35 23 04 32

Figure 2:2 - Comparison of the rate of tissue respiration of male *Clarias batrachus* during winter and summer seasons/months (based on Table 1).

All values are expressed as mean ± standard error (S.E.).

[a] Differs from the respective value of summer : $P<0.05$.

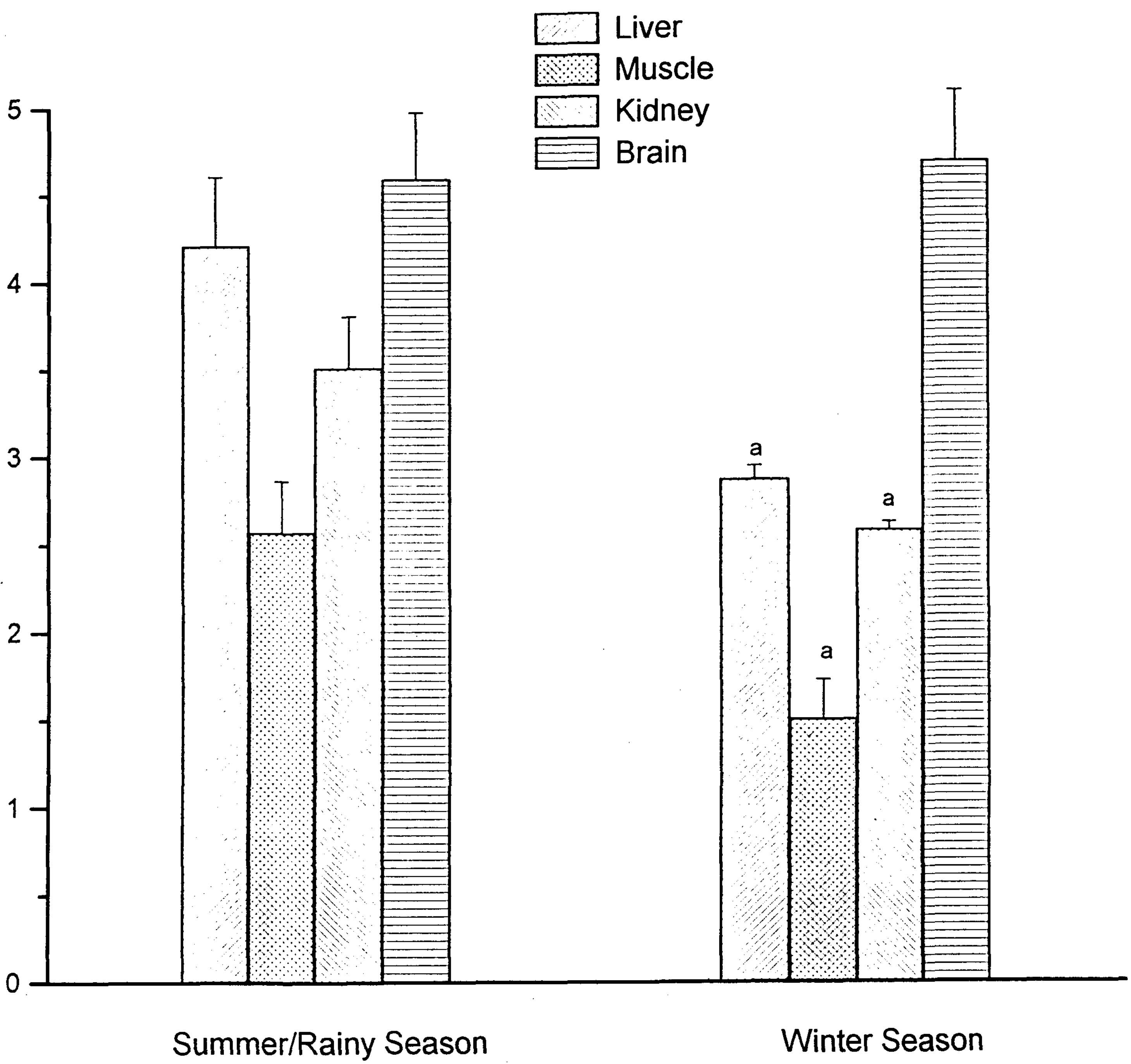

Liver
Muscle
Kidney
Brain
Rate of Oxygen Consumption (μl O2/mg wet tissue/h)
0
1
2
3
4
5
a
a
a
Summer/Rainy Season
Winter Season

Figure 2:3 - Effects of simulated temperatures on the rate of tissue respiration of male *Clarias batrachus* at a constatnt photoperiod (12L/12D).

All values are expressed as mean ± standard error (S.E.); N = 4.

[a, b] Differ from the value at room temperature : $P<0.01$ and 0.001, respectively.

[c, d] Differ from the value at 15°C : $P<0.01$ and 0.001, respectively.

[e, f] Differ from the value at 25°C : $P<0.01$ and 0.001, respectively.

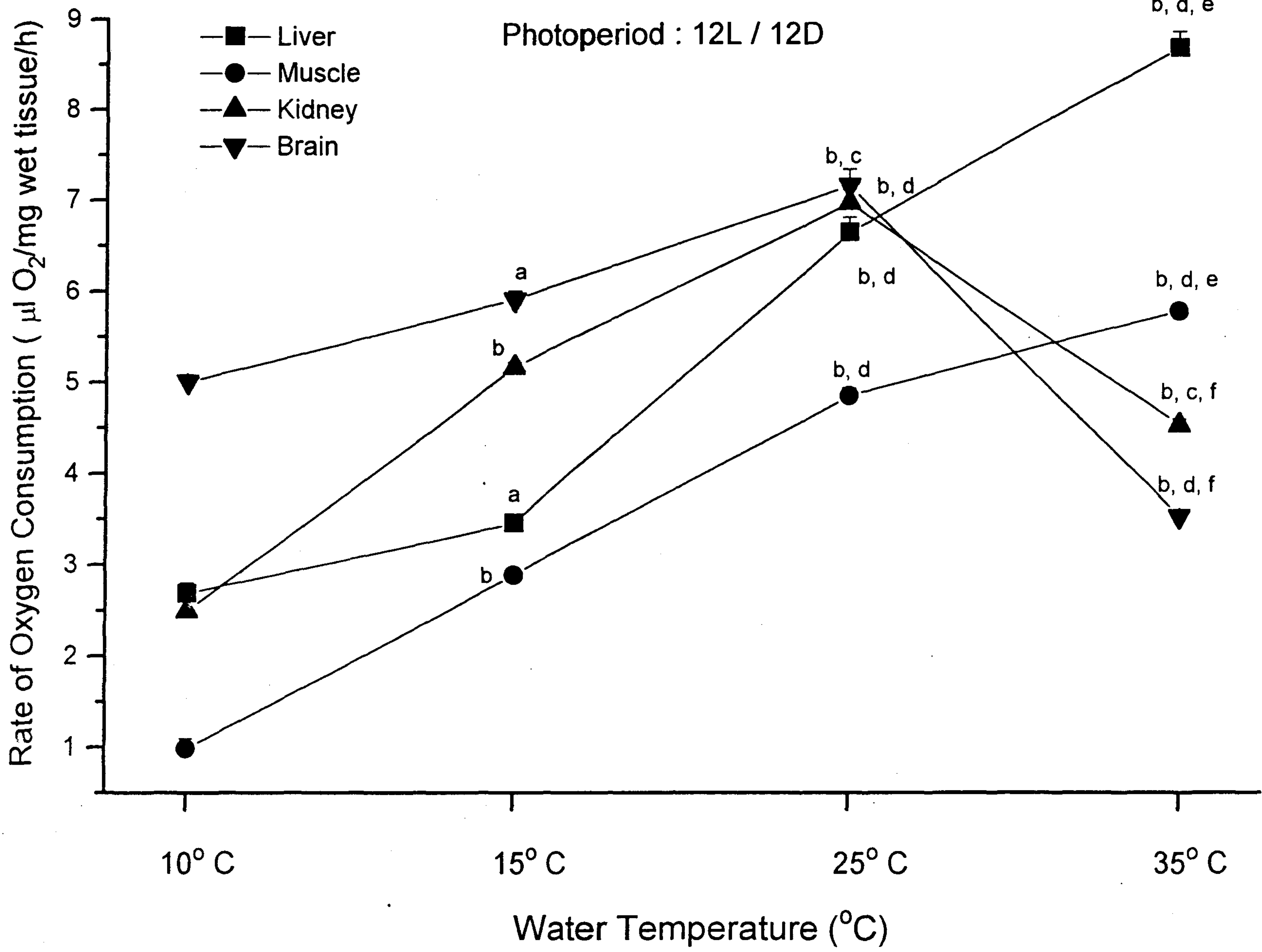

Photoperiod : 12L / 12D
Liver
Muscle
Kidney
Brain
Rate of Oxygen Consumption (µl O2/mg wet tissue/h)
1
2
3
4
5
6
7
8
9
a
b
a
b
b, c
b, d
b, d
b, d
b, d, e
b, d, e
b, c, f
b, d, f
10° C
15° C
25° C
35° C
Water Temperature (°C)

Figure 2:4 - Effects of simulated photoperiod on the rate of tissue respiration of male *Clarias batrachus* at a constant temperature (Av. water temp. : 25° C).

All values are expressed as mean ± standard error (S.E.); N = 4.

[a, b] Differ from 12L/12D : $P<0.05$ and 0.01, respectively.

[d, e] Differ from 9L/15D : $P<0.05$ and 0.01, respectively.

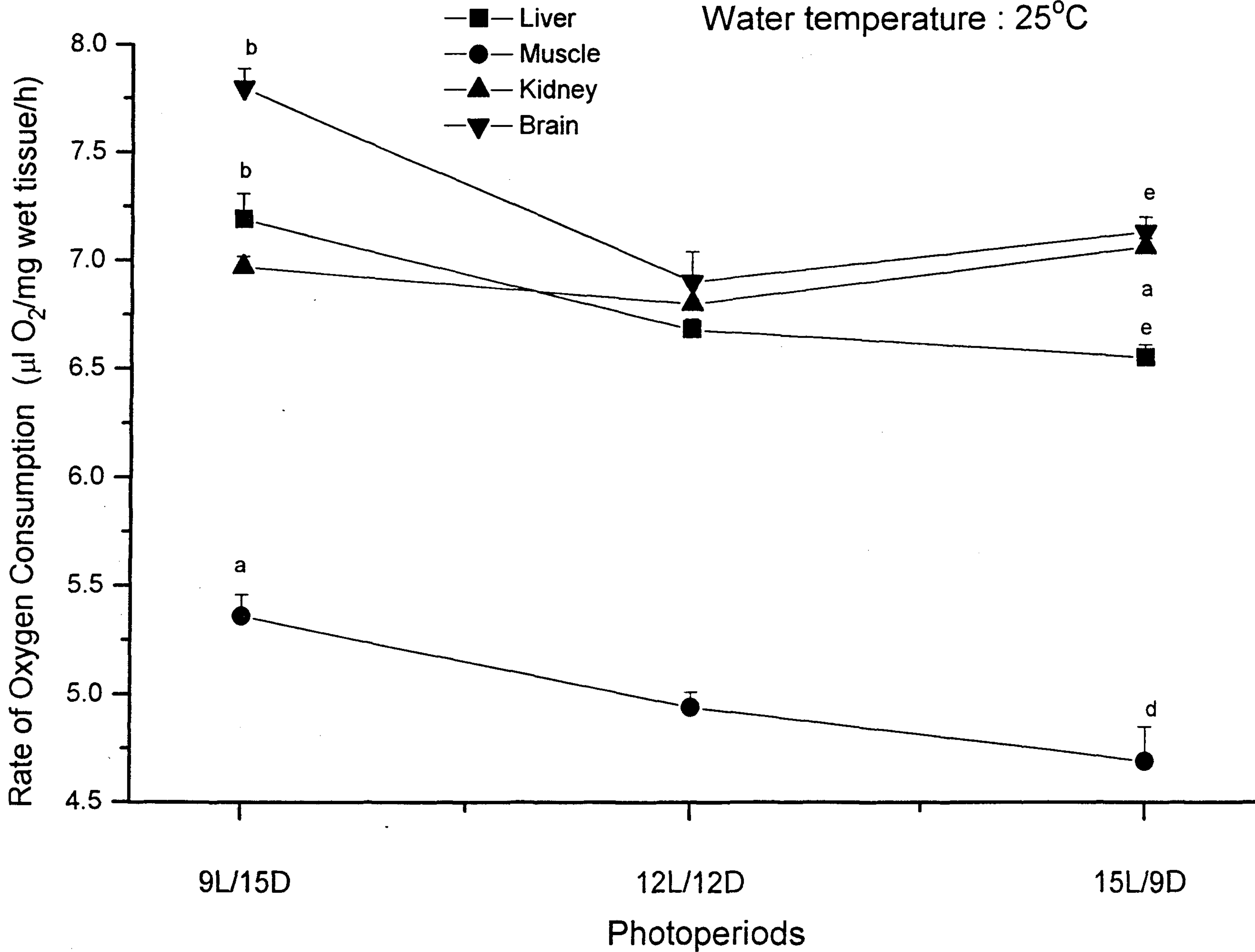
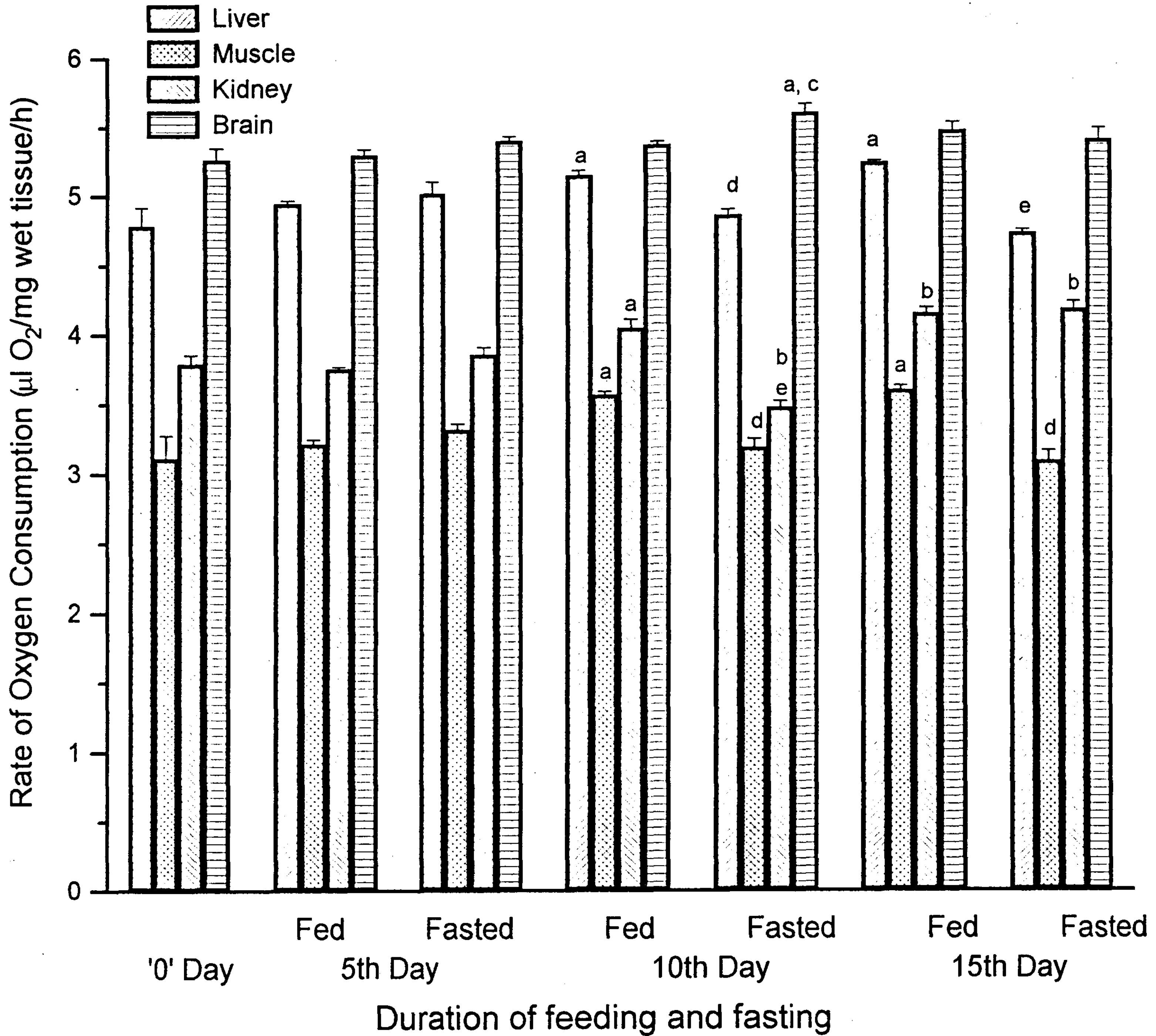

Liver
Muscle
Kidney
Brain
Water temperature : 25°C
Rate of Oxygen Consumption (µl O2/mg wet tissue/h)
8.0
7.5
7.0
6.5
6.0
5.5
5.0
4.5
b
b
e
a
e
a
d
9L/15D
12L/12D
15L/9D
Photoperiods

Figure 2:5 - Effects of feeding and fasting on the rate of tissue respiration in male *Clarias batrachus* during summer (Av. water temp. : 22° C).

All values are expressed as mean ± standard error; N = 4.

[a, b] Differ from the respective value of '0' day control : P<0.05 and 0.01, respectively.

[c, d, e] Differ from the respective value of fed group : P<0.05, 0.01 and 0.001, respectively.



Liver
Muscle
Kidney
Brain
Rate of Oxygen Consumption (µl O2/mg wet tissue/h)
0
1
2
3
4
5
6
a
a
a
d
d
b
e
a, c
a
a
b
e
d
b
Fed
Fasted
Fed
Fasted
Fed
Fasted
'0' Day
5th Day
10th Day
15th Day
Duration of feeding and fasting

Chapter - III

ROLE OF THYROID HORMONES IN REGULATION OF THE OXIDATIVE METABOLISM IN MALE *Clarias batrachus*

The calorigenic role of the thyroid hormones in homeotherms is well established (Lee and Lee, 1937; Baraduc, 1954; Barker and Klitgaard, 1962; Gorbman, 1963; Barrington, 1964; Roodyn *et al.*, 1965; Woeber *et al.*, 1970; DeGroot and Stanburg, 1975; Oppenheimer, 1975; Sterling, 1979; Thapliyal, 1980; Muller and Seizt, 1981; Marzoev *et al.*, 1983; Nelson *et al.*, 1984; Gapp, 1987; Bishop *et al.*, 1995). Thyroidectomy reportedly decreased and thyroid hormones increased the respiratory rate of whole body and tissues of mammals (Haarman, 1936; Pitt-Rivers and Tata, 1959; Barrington, 1964; Bentley, 1976; Oppenheimer, 1979; Ingbar, 1985). However, thyroid hormones are reported to be calorigenic in poikilotherms only at high temperature, i.e. above 20°C (Maher, 1961, 1965; Wilhoft, 1966a; Turner and Tipton, 1972b; Walker, 1973; Wong *et al.*, 1975; Packard and Packard, 1975; Kumar, 1976; Oommen, 1976; Chiu and Tong, 1979; Eales, 1979; Thapliyal, 1980; Rosenkilde, 1981; Thapliyal and Gupta, 1984; Eales, 1985; Gupta and Thapliyal, 1985; Peter and Oommen, 1987; Galton, 1988; Oommen and Sreedeviamma, 1988; Deka-Borah, 1989; Eales, 1990; Gupta and Chakrabarty, 1990; Gupta and Thapliyal, 1991; Gupta and Deka-Borah, 1995; Gupta and Mahanta, 1997). Unlike in other poikilotherms, the calorigenic role of thyroid hormones in fishes seems to be contradictory. Some workers have reported that neither chemical thyroidectomy nor administration of thyroid hormones had any significant effect on the rate of oxygen consumption in fishes (Drexler and Issekutz, 1935; Root and Etkin, 1937; Etkin *et al.*, 1940; Hasler and Mayer, 1942; Smith and Everest, 1943; Root and Etkin, 1947;

Fromn and Reineke, 1957; Matty, 1957; Hoar, 1958; Baraduc, 1963; Sage, 1965). However, an equally good number of workers have reported that thiouracil treatment decreased and thyroid hormones increased oxygen uptake in a number if fish species (Osborn, 1951; Zaks and Zankova, 1952; Muller, 1953; Chavin and Rosmoore, 1956; Hopper, 1959; Kinnear, 1960; Pritchard and Gorbman, 1960; Mohsen and Godet, 1960; Madanmohanrao, 1961; Thornborn *et al.*, 1963; Zarrow *et al.*, 1964, Sage, 1965; Massey *et al.*, 1968; Lerey *et al.*, 1969; Ruhland, 1971; Rangneker *et al.*, 1971; Chiu *et al.*, 1972; Gabos *et al.*, 1973; Pandey and Munshi, 1976; Turner *et al.*, 1977; Donaldson *et al.*, 1979; Matty, 1985a; Sharad *et al.*, 1980; Matty, 1985; Peter and Oommen, 1987; 1989a, Nair and Oommen, 1997). Thyroxine has been reported to inhibit the rate of oxygen uptake in one study (Sage, 1968). In mammals, di-iodothyronine (T_2) has been reported to stimulate mitochondrial oxidative enzymes in liver (Horst *et al.*, 1989; Kretny, 1992; Reilly 1992; Horst *et al.*, 1992; Lanni *et al.*, 1992, 1994a; Goglia *et al.*, 1994), and also stimulated state-3 and state-4 oxidation in liver and muscle of fish, respectively (Leary *et al.*, 1996). However, there is a complete lack of information on the calorigenic role of low molecular weight iodinated tyrosine derivatives like mono-iodotyrosine (MIT) and di-iodotyrosine (DIT) which are reportedly present in the blood circulation of vertebrates (Wong and Chiu, 1974; Gorbman *et al.*, 1983; Martin, 1985; Suzuki, 1985; Norman and Litwack, 1987).

Earlier reports regarding the role of thyroid hormones in regulation of fish respiration were mainly based only on the measurement of the whole body oxygen consumption for which fishes were kept in a chamber of respirometers and probably subjected to non-specific stress. As a result, the rate of oxygen consumption might not be the true reflection of the actual metabolic rate of fishes. Further, water temperature was not considered in most of the earlier experiments. The whole body oxygen consumption does not reflect the metabolic rate of individual tissues. But so far no attempt has been made to study in detail the role of thyroid hormones in the regulation

of oxygen consumption at the tissue level with special reference to the water temperature (Gupta and Thapliyal, 1991). There is also lack of information on the mechanism of action of thyroid hormones in fishes. Therefore, keeping in view the phylogenic position, economic importance of fish and lack of information based on well planned experiments, it was thought worthwhile to investigate in detail the role of thyroid hormones including iodinated tyrosine derivatives (MIT and DIT) in the regulation of tissue respiration and their mode of action in the fish, *Clarias batrachus*. For this purpose, both *in vivo* and *in vitro* experiments were conducted on male *Clarias batrachus* acclimatized at natural climatic conditions of temperature and photoperiod during both winter and summer/rainy months. Findings of the present study suggest that the calorigenic role of L-T_3 and L-T_4 are temperature-dependent, while the stimulatory effect of MIT and DIT on fish respiration seems to be temperature-independent.

Materials and Methods

Adult male *Clarias batrachus* (body weight: 70-80 gm; Length: 18-22 cm) were purchased from a local supplier. For *in vivo* and *in vitro* experiments, fishes were kept in a container and acclimatized under natural climatic conditions at least for 15 days before treatments during both winter (November-March) and summer/rainy months (April-October). For other details please see Chapter-1. The experiments were conducted as per the details of the experimental protocol as follows.

Experimental Protocol

Expt. No.	Treatment	In vivo/ In vitro	Month (Temp.)	Dose	Duration of Treatment
(A)	Saline	In vitro	Jan		
	MIT		(9.6°C)	1 μM	
	DIT		July	1 μM	
	L-T_3		(20°C)	1 μM	
	L-T_4			1 μM	
(B)	Saline	In vivo	Jan		4 days
	MIT		(9.6°C)	2 μg/fish/day	4 days
	DIT		Sept	2 μg/fish/day	4 days
	L-T_3		(20°C)	2 μg/fish/day	4 days
	L-T_4			2 μg/fish/day	4 days
(C)	Saline	In vivo	May		4 days
	PTU		(22°C)	1 μg/gm/day	4 days
	L-T_3			2 μg/f/day	4 days
	L-T_4			2 μg/f/day	4 days
	PTU + L-T_3			1 μg/g+2 μg/f/day	4 days
	PTU + L-T_4			1 μg/g+2 μg/f/day	4 days
(D)	Saline	In vivo	March		4 days
	PTU		(10±1°C)	1 μg/gm/day	4 days
(E)	Saline	In vivo	December		4 days
	MIT		(11.5°C)	2 μg/f/day	4 days
				4 μg/f/day	4 days
				8 μg/f/day	4 days

Expt. No.	Treatment	In vivo/ In vitro	Month (Temp.)	Dose	Duration of Treatment
	DIT			2 μg/f/day	4 days
				4 μg/f/day	4 days
				8 μg/f/day	4 days
(F)	Saline	In vitro	July		
	L-T_3		(21°C)	1 μM	
	Ouabain			2 μM	
	Act-D			2 μM	
	Ouabain + L-T_3			2 μM+1 μM	
	Act-D + L-T_3			2 μM+1 μM	
(G)	Saline	In vitro	Aug.		
	Ouabain		(20°C)	2 μM	
	Act-D			2 μM	
	MIT			1 μM	
	DIT			1 μM	
	Ouabain+MIT			2 μM+1 μM	
	Ouabain + DIT			2 μM+1 μM	
	Act-D + MIT			2 μM+1 μM	
	ACT-D + DIT			2 μM+1 μM	

Results

In vivo effect of L-T_3, L-T_4, MIT and DIT on the rate of tissues respiration :

The data are presented in Tables-3:1, 3:2, 3:3, 3:4; Figs. 3:1, 3:2, 3:3, 3:4. *In vivo* administration of L-T_3 and L-T_4 did not increase respiratory rate of any of the tissues during winter (Table 3:1; Fig. 3:1). However, both L-T_3 and L-T_4 significantly stimulated the respiratory rate of all the tissues (liver, muscle, kidney and brain) during summer/rainy months (Table 3:2, Fig. 3:2). Administration of mono-iodo-L-tyrosine (MIT) significantly increased the respiratory rate of muscle and brain tissues during winter and only of muscle during summer/rainy months (Tables 3:1&3:2; Figs. 3:1 & 3:2). Di-iodo-L-tyrosine (DIT) administration significantly increased the rate of oxygen uptake of all the tissues during both winter and summer/rainy months (Tables 3:1 & 3:2; Figs. 3:1 & 3:2). Further, MIT and DIT increased the rate of tissues respiration in a dose-dependent manner (Tables 3:3 & 3:4; Figs. 3:3 & 3:4).

In vivo effects of propyl thiouracil (PTU) and thyroid hormones on the rate of tissues respiration :

The data are presented in Tables 3:5 & 3:6; Figs. 3:5 & 3:6. *In vivo* administration of propyl thiouracil (PTU) at simulated low temperature (10±1°C) during the month of March significantly decreased the respiratory rate of liver, muscle and kidney tissues; while it significantly increased the brain tissue oxygen uptake (Table 3:5; Fig. 3:5). During summer/rainy months (temperature 22°C), administration of PTU significantly decreased the respiratory rate of all the four tissues. The combined treatments of PTU either with L-T_3 or L-T_4, however, significantly inhibited the stimulatory effect of L-T_3 and L-T_4 on the rate of respiration of all the four tissues (Table 3:6; Fig. 3:6).

In vitro effects of L-T_3, MIT and DIT in the absence and presence of ouabain and actinomycin-D during summer/rainy months :

The data are presented in Tables 3:9 & 3:10; Figs. 3:9 & 3:10. *In vitro* treatment with L-T_3 during summer/rainy season significantly increased the respiratory rate of liver, muscle and kidney tissues. Administrations of ouabain and actinomycin-D significantly decreased the basal respiratory rate of all the tissues (Table 3:9; Fig. 3:9). The pre-treatment of the tissue homogenates with ouabain or actinomycin-D significantly but not completely blocked the stimulatory effect of L-T_3 on the respiratory rate of all the three tissues.

In vitro treatment of the tissue homogenates with MIT during summer/rainy season significantly increased the respiratory rate of only liver and muscle tissues. However, DIT increased significantly the respiratory rate of all the tissues during summer/rainy months (Table 3:10; Fig. 3:10). Both ouabain and actinomycin-D significantly but not completely blocked the stimulatory effect of MIT and DIT.

Discussion

In vivo and *in vitro* administration of L-T_3 and L-T_4 during winter (water temperature 9.6°±1°C) did not stimulate liver, muscle and kidney tissue respiration. These hormones, when administered *in vitro*, stimulated brain tissue oxygen uptake. During summer/rainy months (water temperature 20°C ± 1°C), both L-T_3 and L-T_4 significantly stimulated the rate of tissue respiration both *in vivo* and *in vitro* experiments (Tables 3:1, 3:2, 3:7, 3:8; Figs. 3:1, 3:2, 3:7, 3:8). These findings seem to suggest that the oxidative machinery of the tissues becomes insensitive to thyroid hormones at low temperature during winter. It might be due to the lack/insufficiency or

adverse modification of receptors of the thyroid hormones. The energy generating pathway regains its sensitivity to thyroid hormones (L-T_3 and L-T_4) during summer/rainy months. Thus, the tissues of *Clarias batrachus* seem to exhibit a rhythm of sensitivity and insensitivity to thyroid hormones over an annual time scale. The changes in the sensitivity of the metabolic machinery/pathway of the tissues might be an adaptation to conserve energy during winter and increased energy output/metabolic rate during summer/rainy months to meet the increased energy requirements for higher degree of physical and metabolic activity associated with reproduction. Low degree of binding of these hormones to the receptors, insensitivity of hormone responsive elements (HRE) of DNA to hormone receptor complex or the translation machinery, separately or jointly, might be responsible for the insensitivity of the somatic tissues to the thyroid hormones during the winter months. The non-responsiveness of brain tissue to *in vivo* treatment with L-T_3 and L-T_4 during winter months and *in vivo* stimulation of brain respiration during summer/rainy season might be due to seasonal variation in the property/function of blood-brain barrier. The increased metabolic response of tissues to L-T_3 and L-T_4 during summer/rainy months might be due to temperature-induced increase in the synthesis of thyroid hormone receptors, and/or increased sensitivity of transcription and/or translation machineries to thyroid hormones/hormone-receptor complex resulting in increased rate of oxygen consumption. In reptiles and amphibians, the sensitivity of several tissues to L-T_3 and L-T_4 changes during different seasons (Packard and Packard, 1975; May and Packer, 1976; Oommen, 1976; Thapliyal and Sharan, 1980; Thapliyal and Gupta, 1984; John-Alder, 1988; Deka-Borah, 1989; Gupta and Chakrabarty, 1990; Gupta and Thapliyal, 1991; Gupta and Deka-Borah, 1995; Gupta and Mahanta, 1997). It, thus, seems that the altered sensitivity of the oxidative machinery of tissues in poikilotherms to thyroid hormones might be of an adaptive importance for need-based efficient regulation of the energy metabolism. Further, as in other poikilothermic vertebrates (i.e., amphibians and

reptiles), the calorigenic effect of L-T_3 and L-T_4 seems to be influenced by seasonal alterations in temperature.

In vivo treatment with MIT during winter stimulated muscle and brain oxygen uptake, while it increased only muscle tissue during summer/rainy months (Tables 3:1 & 3:2; Figs. 3:1 & 3:2). Further, *in vitro* treatment with MIT stimulated the respiratory rate of all the tissues during winter and only of liver and muscle tissues during summer/rainy months (Tables 3:7 & 3:8; Figs. 3:7 & 3:8). Unlike MIT, *in vivo* and *in vitro* administration of DIT invariably stimulated the respiratory rate of all the tissues irrespective of water temperature and seasons (Tables 3:1, 3:2, 3:4, 3:7 & 3:8; Figs. 3:1, 3:2, 3:4, 3:7 & 3:8). These findings strongly suggest that both MIT and DIT are involved in the regulation of the oxidative metabolism of *Clarias batrachus*. However, the comparative importance of MIT and DIT for metabolic regulation seems to be different in the fish. The metabolic action of MIT seems to be dependent on tissues, mode of treatment, ambient temperature/seasons and other factors. However, the calorigenic effect of DIT seems to be unequivocal and independent of temperature and seasons. It, thus, seems that DIT might be more important than MIT for the oxidative metabolism in the fish, *Clarias batrachus*. It has been reported recently that administration of di-iodothyronine (T_2) in the gold fish, *Carassius auratus* and the lake-char, *Slavelinus namaycush* increased the state-3 oxidation of pyruvate in liver mitochondria and state-4 oxidation in red muscle mitochondria (Ballantyne *et al.*, 1992; Leary *et al.*, 1996). T_2 has also been reported to increase the activity of the enzyme cytochrome oxidase (COX) in mitochondria of rat liver and bovine heart (Horst *et al.*, 1989; Kvetny, 1992; Lanni *et al.*, 1992; O'Reilly and Murphy, 1992; Goglia *et al.*, 1994a,b; Lombardi *et al.*, 1997). Therefore, there is a possibility that DIT also stimulates tissue respiration in fish by stimulating mitochondrial enzymes as reported for L-T_2, L-T_3 and L-T_4 (Sterling and Mitch, 1975; Sterling et al., 1980; Muratova *et al.*, 1982; Oppenheimer, 1975; Sreedeviamma and Oommen, 1988;

Sutharam *et al.*, 1990; Soboll, 1993a; Goglia *et al.*, 1994a,b; Lanni *et al.*, 1994; Lombardi *et al.*, 1997).

It is important to mention that MIT and DIT were the first iodinated molecules associated with proteins in higher invertebrates (molluscs, annelids, echinoderms etc.) and protochordates (Gorbman, 1955; Berg *et al.*, 1959; Barrington, 1959). Later on, during the course of evolution iodothyronines (e.g., T_2, T_3 and T_4) appeared in the blood of vertebrates. Therefore, it seems that MIT and DIT were evolved first to serve as regulatory molecules (hormones) in lower animals species before the evolution of thyroid gland followed by synthesis of more effective hormones like T_3 and T_4 in vertebrates. Recent reports regarding calorigenic function of T_2 strongly suggest a gradual evolution of iodinated molecules for regulation of the oxidative metabolism to meet the increasing requirement of energy with the evolution of complex organs/systems in higher vertebrates. Thus, MIT and DIT might have been more important for the regulation of energy metabolism in lower vertebrates (Poikilotherms). During the course of evolution, these primitive iodinated molecules might have been gradually replaced functionally by more evolved iodinated molecule like T_2, T_3 and T_4. Considering the phylogenic position of fish, we suggest that the iodinated tyrosine molecules, particularly DIT, are more important than T_3 and T_4 for calorigenesis especially at low temperature of winter months when both T_3 and T_4 are caloriginically inactive (Oommen, 1976; Thapliyal and Sharan, 1980; Thapliyal and Gupta, 1984; Deka-Borah, 1989; Gupta and Chakrabarty, 1990; Gupta and Thapliyal, 1991; Gupta and Deka-Borah, 1995; Gupta and Mahanta, 1997).

In order to assess the role of indigenous thyroid hormones, we studied the effect of propyl thiouracil (a goitrogen) on the rate of tissue respiration. *In vivo* administration of propyl thiouracil (PTU) significantly suppressed the respiratory rate of liver, muscle and kidney tissues irrespective of the ambient temperature, and

administration of L-T_3 reversed the inhibitory effect of PTU. PTU inhibited brain tissue respiration only during summer/rainy months but not during winter (Tables 3:5 & 3:6; Figs. 3:5 & 3:6). It, thus, seems that the metabolic rate of brain is influenced by thyroid hormones during summer/rainy months, while during winter it might be regulated by hormones other than that of thyroid. The decreased respiratory rate following PTU treatment during summer/rainy months might be due to inhibitory effect of PTU on iodine uptake by the thyroid tissue as well as inhibition of peripheral conversion of T_4 to T_3 leading to decreased synthesis of thyroid hormones and of low availability of T_3 (Ingber, 1985; Norman and Litwack, 1987). Thus, inhibition of thyroid hormones' production and conversion of T_4 to T_3 might be responsible for the decline in the rate of tissue oxygen uptake following PTU treatment (Goswami and Rosenberg, 1978; Giudecalli, 1978; Malbon *et al.*, 1978; Ciaraldi and Marinetti, 1978; Scarpase and Abrass, 1981; Gupta and Mahanta, 1997). There are reports that administration of PTU decreased the whole body oxygen consumption in *Mugil auratus* (Leray *et al.*, 1969) and Carps (Gabos *et al.*, 1973). Further, PTU has been reported to inhibit the activity of Na^+-K^+-ATPase and mitochondrial enzymes, while administration of thyroid hormones reversed the inhibitory effect (Edelman, 1970; Ismail-Beigi *et al.*, 1977; Lin and Akera, 1978; Ciaraldi and Marinetti, 1979; Nunez, 1985; Chaudhury *et al.*, 1987; Peter and Oommen, 1988; Srabani *et al.*, 1992; Nair and Oommen, 1997). Exogenous thyroid hormones are ineffective at low temperature of winter, while PTU treatment at low temperature inhibited tissue respiration. This finding suggests that indigenous thyroid hormones are involved in the regulation of oxidative metabolism even at low temperature of winter. It has been reported that catecholamines regulate energy metabolism in mammals, reptiles and amphibians exposed to low temperature, and thyroid hormones support the metabolic rate by potentiating the calorigenic action of catecholamines (Himms-Hagen, 1975, 1976, 1983; Gupta and Thapliyal, 1982, 1983; Gupta and Mahanta, 1997). Similarly, indigenous thyroid hormones might be involved

indirectly in the energy metabolism of *Clarias batrachus* by potentiating the calorigenic action of catecholamines at low temperature of winter.

In order to know the mode of action, we studied *in vitro* effects of iodinated compounds (L-T_3, L-MIT and L-DIT) on tissues' respiration in the presence of ouabain (specific inhibitor of Na^+-K^+-ATPase) and actinomycin-D (inhibitor of transcription). As mentioned earlier (Tables 3:9 & 3:10; Figs. 3:9 & 3:10), the stimulatory effect of L-T_3, L-MIT and L-DIT was significantly reduced in tissue homogenates pre-treated either with ouabain or with actinomycin-D. These findings seem to suggest that the iodinated compounds increased tissue respiration of *Clarias batrachus* by stimulating the process of transcription as well as the activity of Na^+-K^+-ATPase enzyme. It has been reported that thyroid hormones bind to the receptors present in the nucleus and form the hormone receptor (HR) complex. Then HR-complex binds to the hormone responsive element (HRE) of DNA and stimulates transcription process and protein synthesis (Lee *et al.*, 1959; Hoch, 1962; Mitchel, 1966; Tenabe *et al.*, 1969; Tata, 1970 Singh and Eales, 1975; Dillman *et al.*, 1977; Oppenheimer, 1979;van der Kraak and Eales, 1980; Darling *et al.*, 1982; Seelig *et al.*, 1982; Gorbman *et al.*, 1983c; Nayer, 1987; Nelson *et al.*, 1987; Bres and Eales, 1988; Pannavis and Houlihans, 1992; Houlihans *et al.*, 1993; Soboll, 1993a). Thyroid hormones have also been reported to stimulate the respiratory rate by stimulating the membrane- bound enzyme Na^+-K^+-ATPase in mammals (Ismail-Beigi and Edelman, 1970; Tobin *et al.*, 1973; Ismail-Beigi *et al.*, 1977; Nunez, 1985); reptiles (Sharan, 1983), amphibians (Litch et al., 1989; Mahanta, 1994) and fish (Srabani *et al.*, 1992; McCormick and Bjornsson, 1994. Nair and Oommen, 1997). It seems that L-MIT and L-DIT also produce their calorigenic effect via DNA-dependent mRNA synthesis and Na^+-K^+-ATPase. The incomplete inhibition of the stimulatory effect of L-T_3, L-MIT and L-DIT by ouabain and actinomycin-D indicates that these iodinated tyrosine derivatives stimulated tissues respiration through more than one pathway. In addition

to its effects on transcription and Na^+-K^+-ATPase, L-T_3 has also been reported to increase tissue respiration by increasing the electron transport in the respiratory chain (Stryer, 1988; Ballantyne *et al.*, 1992; Leary *et al.*, 1996) and directly stimulating the activity of mitochondrial enzymes in mammals (DeGroot and Stanburg, 1975; Oppenheimer, 1975; Sterling *et al.*, 1980; Triandafillou *et al.*, 1982; Soboll, 1993a,b; Goglia et al., 1994a), reptiles (Sreedeviamma and Oommen, 1988), Amphibian (Lagersptez *et al.*, 1974; Brucker and Cohen, 1976; Lagersptez, 1977; Goto *et al.*, 1982; Sutharam and Oommen, 1989; Sutharam *et al.*, 1990) and fish (Leray *et al.*, 1970; Begum *et al.*, 1984; Shrivakumar and Jayaraman, 1984; Peter and Oommen, 1987, 1989; Soboll, 1993b; Leary *et al.*, 1996). Thus, inhibition of one pathway failed to abolish the stimulatory effect of thyroid compound (Sterling, 1979; Kenneth *et al.*, 1980). Further, T_2 has been reported to stimulate the pyruvate oxidation (Ballantyne *et al.*, 1992; Leary *et al.*, 1996) and to interact directly with cytochrome oxidase leading to conformational changes followed by stimulation of enzyme activity (Goglia *et al.*, 1994b; Lanni *et al.*, 1994; Lombardi *et al.*, 1997). A similar mechanism might also be employed by L-MIT and L-DIT in the stimulation of tissue respiration in the fish, *C. batrachus*. It, thus, seems that as in mammals, thyroid hormones stimulate fish tissue respiration by stimulating transcription, Na^+-K^+-ATPase, and mitochondrial enzymes.

On the bases of these findings we conclude that exogenous L-T_3 and L-T_4 are calorigenic in fish only at higher water temperature (at and above 20°C). However, the indigenous thyroid hormones seems to be involved in calorigenesis even at low temperature of winter months, while stimulatory effect of L-MIT varies with tissues, mode of treatment and season. L-DIT stimulates tissue respiration irrespective of temperature and seasons. Similar to T_2, T_3 and T_4, L-MIT and L-DIT seem to produce their calorigenic effect in *Clarias batrachus* by their action at multiple sites of the cells like membrane bound Na^+-K^+-ATPase, genes and mitochondria. Thus, in addition to

T_2, L-T_3 and L-T_4, L-MIT and L-DIT also seem to be involved in the regulation of the oxidative metabolism of *Clarias batrachus*.

Table 3:1 *In vivo* effects of thyroid hormones on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Saline (Control)	2.88±0.07	1.12±0.05	2.69±0.08	5.26±0.09
Monoiodotyrosine (MIT)	3.17±0.11	1.47±0.11[a]	2.98±0.10	5.55±0.05[a]
Diiodotyrosine (DIT)	3.27±0.03[b]	1.54±0.05[c]	3.08±0.04[b]	5.65±0.04[b]
Triiodothyronine ($L-T_3$)	2.82±0.05	1.18±0.09	2.72±0.05	5.10±0.11
Thyroxine ($L-T_4$)	2.85±0.07	0.96±0.07	2.66±0.06	5.04±0.07

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

Table 3:2 - *In vivo* effects of thyroid hormones on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 20° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Saline (Control)	4.71±0.08	2.72±0.05	4.10±0.05	4.30±0.07
Monoiodotyrosine (MIT)	4.91±0.02	2.98±0.03[b]	4.20±0.03	4.49±0.04
Diiodotyrosine (DIT)	5.26±0.05[b]	3.08±0.08[b]	4.46±0.09[a]	4.59±0.06[a]
Triiodothyronine ($L-T_3$)	5.61±0.06[c]	3.27±0.07[c]	4.65±0.05[c]	4.75±0.08[b]
Thyroxine ($L-T_4$)	5.45±0.12[b]	3.49±0.09[c]	4.84±0.07[c]	4.97±0.09[c]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

Table 3:3 - Dose-dependent in vivo effects of monoiodotyrosine (MIT) on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 11.5°C)

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Saline (Control)	2.92±0.09	1.15±0.05	2.66±0.06	5.29±0.03
2 µg MIT	3.14±0.05	1.50±0.10[a]	2.95±0.12	5.52±0.06[a]
4µg MIT	3.46±0.10[b,d]	1.92±0.08[c,d]	3.43±0.11[c,d]	5.84±0.03[c,e]
8µg MIT	3.78±0.16[b,e]	2.37±0.07[c,f,h]	3.88±0.14[c,e,g]	6.09±0.07[c,f,g]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : P < 0.05, 0.01 and 0.001, respectively.

[d, e, f] Differ from the group treated with 2 µg MIT : P < 0.05, 0.01 and 0.001, respectively.

[g, h] Differ from the group treated with 4 µg MIT : P < 0.05 and 0.01, respectively.

Table 3:4 - Dose-dependent in vivo effects of monoiodotyrosine (DIT) on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 11.5° C)

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Saline (Control)	2.92±0.09	1.15±0.05	2.66±0.06	5.29±0.03
2 µg DIT	3.40±0.11[a]	1.79±0.10[b]	3.11±0.05[b]	5.77±0.08[b]
4µg DIT	3.78±0.07[c,d]	2.24±0.09[c,d]	3.53±0.12[c,d]	6.09±0.03[c,d]
8µg DIT	4.10±0.05[c,e,h]	2.56±0.10[c,e]	3.98±0.09[c,f,g]	6.32±0.05[c,e,h]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e, f] Differ from the group treated with 2 µg DIT : $P < 0.05$, 0.01 and 0.001, respectively.

[g, h] Differ from the group treated with 4 µg DIT : P < o.o5 and 0.01, respectively.

Table 3:5 - In vivo effects of propyl thiouracil on the rate of tissue respiration in male *Clarias batrachus* at simulated low temperature (10±1°C)

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
'0' Day (16±1°C)	2.44±0.04	1.09±0.03	2.12±0.07	2.79±0.06
Saline	1.71±0.03	0.59±0.06	1.54±0.04	3.05±0.07
PTU	1.54±0.05[a]	0.26±0.04[b]	1.38±0.05[a]	3.27±0.03[a]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b] Differ from saline treated control group : $P<0.05$ and 0.01, respectively.

Table 3:6 - In vivo effects of thyroid hormones and propyl thiouracil (PTU) on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 22° C)

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Saline (Control)	4.87±0.04	3.17±0.05	3.98±0.05	5.290.05
L-T_3	5.45±0.03[c]	3.66±0.07[b]	4.59±0.05[c]	5.71±0.07[a]
L-T_4	5.55±0.10[c]	3.56±0.03[c]	4.87±0.04[c]	5.65±0.09[a]
PTU	4.43±0.07[b]	2.82±0.08[a]	3.62±0.10[a]	4.94±0.10[a]
PTU + T_3	5.20±0.03[c,f]	3.30±0.02[a,c]	4.23±0.05[a,c]	5.45±0.03[a,d]
PTU + T_4	5.23±0.05[a,g]	3.33±0.04[a,h]	4.46±0.09[b,h]	5.42±0.02[a,g]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e, f] Differ from the group treated with L-T_3 : $P < 0.05$, 0.01 and 0.001, respectively.

[g, h] Differ from the group treated with L-T_4 : $P < 0.05$ and 0.01, respectively.

Table 3:7 - *In vitro* effects of thyroid hormones on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp.: 9.6° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Control	2.69±0.06	0.89±0.08	2.53±0.05	5.01±0.04
Monoiodotyrosine (MIT)	2.95±0.05[a]	1.34±0.03[c]	2.79±0.08[a]	5.26±0.08[a]
Diiodotyrosine (DIT)	3.05±0.07[b]	1.28±0.05[b]	2.92±0.11[a]	5.45±0.07[b]
Triiodothyronine ($L\text{-}T_3$)	2.72±0.09	0.79±0.02	2.56±0.05	5.65±0.06[c]
Thyroxine ($L\text{-}T_4$)	2.63±0.12	0.75±0.07	2.60±0.09	5.87±0.05[c]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

Table 3:8 - *In vitro* effects of thyroid hormones on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 20° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Control	4.81±0.12	2.85±0.02	4.01±0.03	5.07±0.07
Monoiodotyrosine (MIT)	5.16±0.05^{a}	3.11±0.06^{b}	4.10±0.09	5.36±0.11
Diiodotyrosine (DIT)	5.36±0.07^{b}	3.37±0.09^{b}	4.43±0.07^{b}	5.48±0.05^{b}
Triiodothyronine (L-T_3)	5.52±0.04^{b}	3.53±0.07^{c}	4.68±0.12^{b}	5.61±0.06^{c}
Thyroxine (L-T_4)	5.45±0.03^{b}	3.40±0.16^{a}	4.81±0.07^{c}	5.71±0.07^{c}

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

$^{a, b, c}$ Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

Table 3:9 - In vitro effects of L-T_3 in the absence and presence of ouabain and actinomycin-D on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 21° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)		
	Liver	Muscle	Kidney
Control	4.81±0.12	2.85±0.02	4.01±0.03
L-T_3	5.52±0.04^{b}	3.53±0.05^{c}	4.67±0.12^{b}
Ouabain	4.55±0.03^{a}	2.63±0.06^{a}	3.65±0.07^{b}
Actinomycin-D	4.43±0.10^{a}	2.40±0.05^{c}	3.62±0.14^{a}
Ouabain + L-T_3	5.26±0.03^{a,c}	3.33±0.04^{b,d}	4.23±0.08^{a,d}
Actinomycin-D + L-T_3	5.13±0.04^{a,c}	3.11±0.07^{a,d}	4 20±0.05^{a,d}

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

$^{a, b, c}$ Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

$^{d, e}$ Differ from the group treated with L-T_3: $P < 0.05$ and 0.001, respectively.

Table 3:10 In vitro effects of monoiodotyrosine (MIT) and dioiodotyrosine (DIT) in the absence and presence of ouabain and actinomycin-D on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 20° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)		
	Liver	Muscle	Kidney
Control	4.71±0.10	2.82±0.014	3.75±0.16
MIT	5.20±0.07[a]	3.33±0.05[a]	4.20±0.11
DIT	5.52±0.05[c]	3.56±0.08[c]	4.55±0.03[b]
Ouabain	4.46±0.03[a]	2.47±0.02[a]	3.30±0.05[a]
Actinomycin-D	4.33±0.10[a]	2.44±0.04[a]	3.21±0.04[a]
Ouabain + MIT	5.01±0.04[a,d]	3.17±0.02[a,d]	3.91±0.03[a,d]
Ouabain + DIT	5.04±0.05[a,f]	3.33±0.05[a,c]	4.33±0.06[a,c]
Actinomycin-D + MIT	4.97±0.03[a,d]	3.17±0.03[a,d]	3.85±0.04[d]
Actinomycin-D + DIT	5.23±0.08[b,c]	3.27±0.03[a,c]	4.26±0.06[a,f]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : P < 0.05, 0.01 and 0.001, respectively.

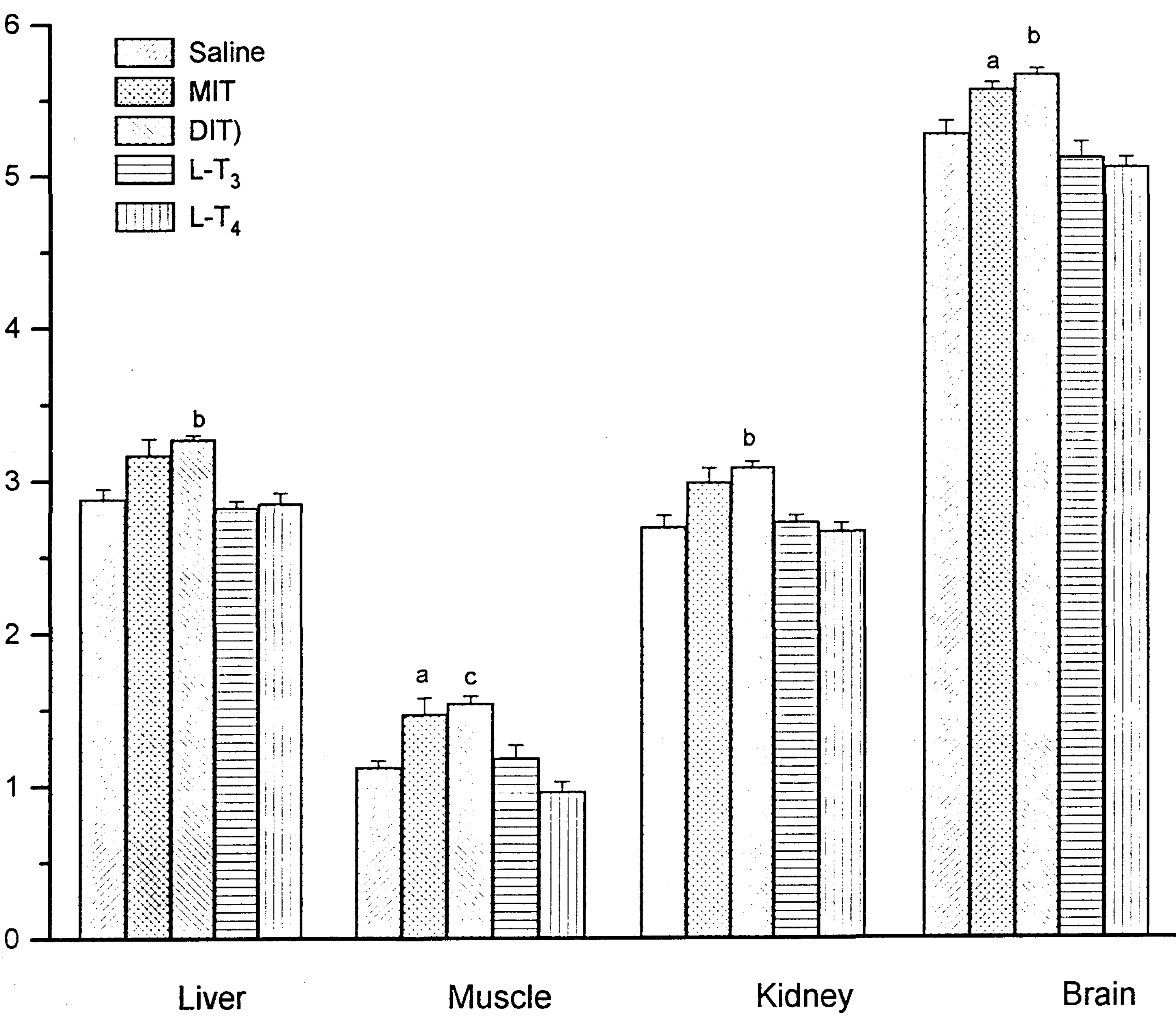
[d] Differs from the group treated with MIT : P < 0.05.

[c, f] Differ from the group treated with DIT : P < 0.05 and 0.01, respectively.

Figure 3:1- *In vivo* effects of thyroid hormones on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

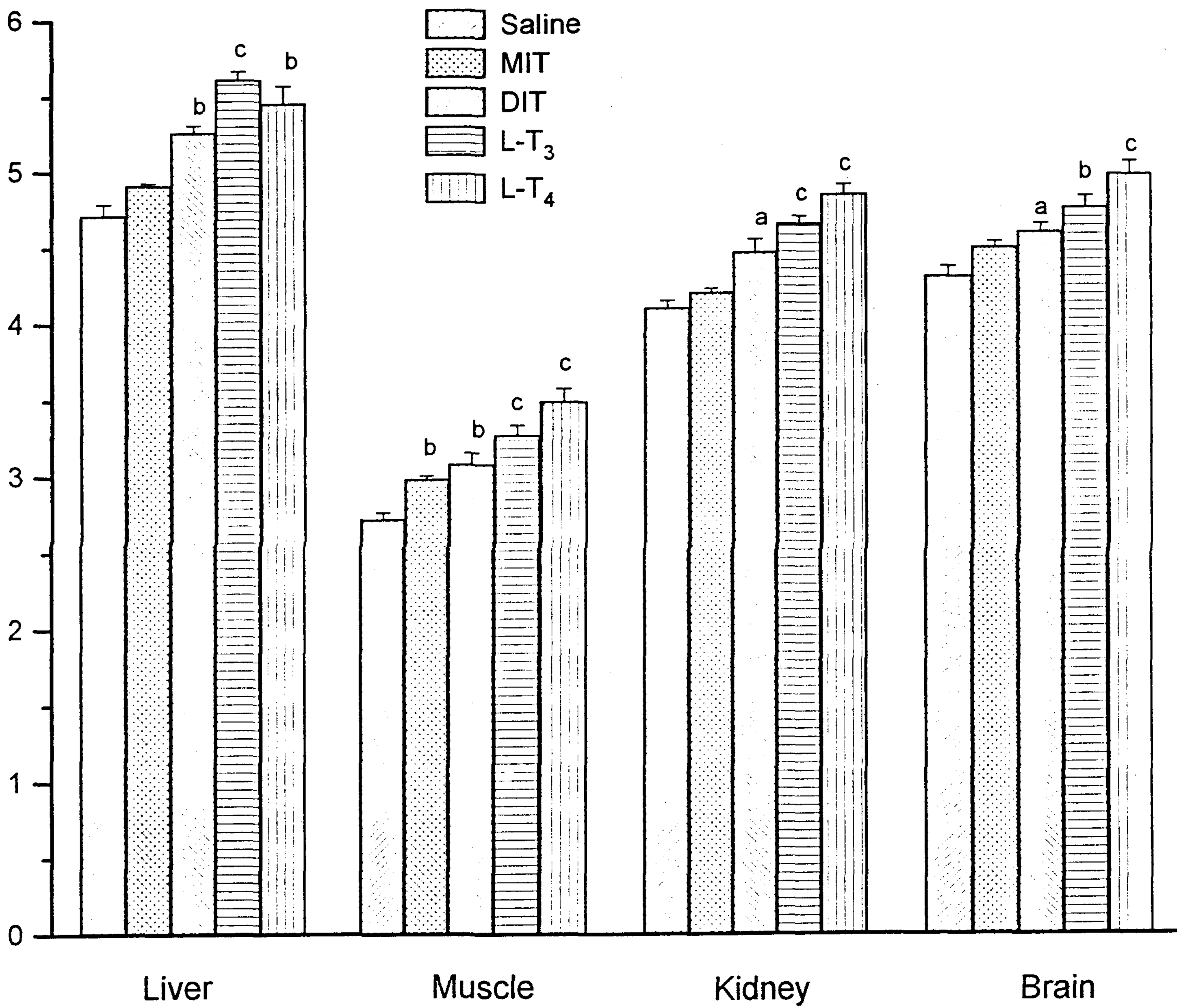


Rate of Oxygen Consumption (μl O2/mg wet tissue/h)
0
1
2
3
4
5
6
Saline
MIT
DIT)
L-T3
L-T4
b
a
c
b
a
b
Liver
Muscle
Kidney
Brain

Figure 3:2 - *In vivo* effects of thyroid hormones on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 20° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.



Rate of Oxygen Consumption (µl O2 / mg wet tissue / h)
0
1
2
3
4
5
6
Saline
MIT
DIT
L-T3
L-T4
Liver
Muscle
Kidney
Brain
a
b
c

Figure 3:3 - Dose-dependent in vivo effects of monoiodotyrosine (MIT) on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 11.5° C)

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

$^{a, b, c}$ Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

$^{d, e, f}$ Differ from the group treated with 2 μg MIT : $P < 0.05$, 0.01 and 0.001, respectively.

$^{g, h}$ Differ from the group treated with 4 μg MIT : $P < 0.05$ and 0.01, respectively.

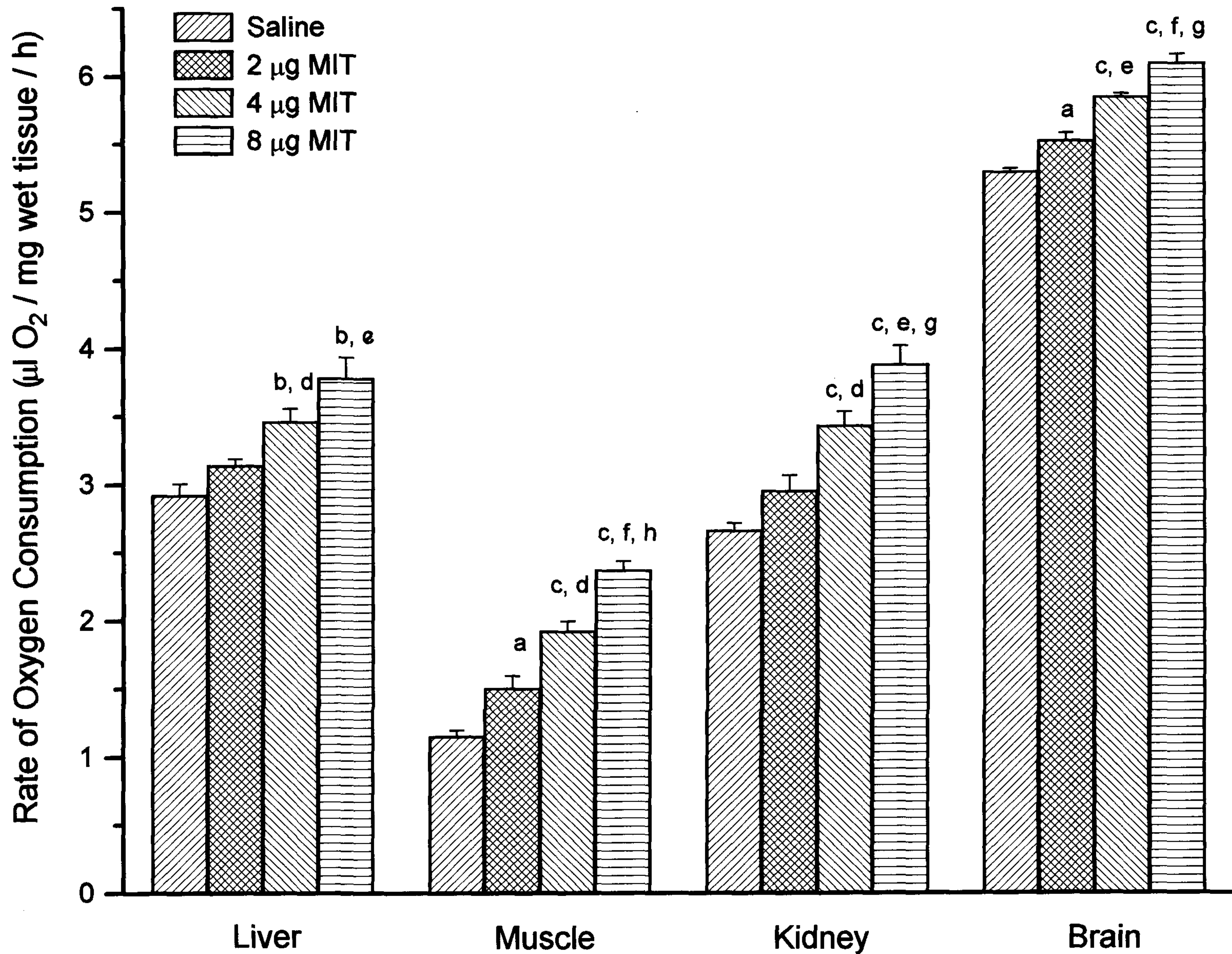

Saline
2 μg MIT
4 μg MIT
8 μg MIT
Rate of Oxygen Consumption (μl O2 / mg wet tissue / h)
0
1
2
3
4
5
6
b, d
b, e
a
c, d
c, f, h
c, d
c, e, g
a
c, e
c, f, g
Liver
Muscle
Kidney
Brain

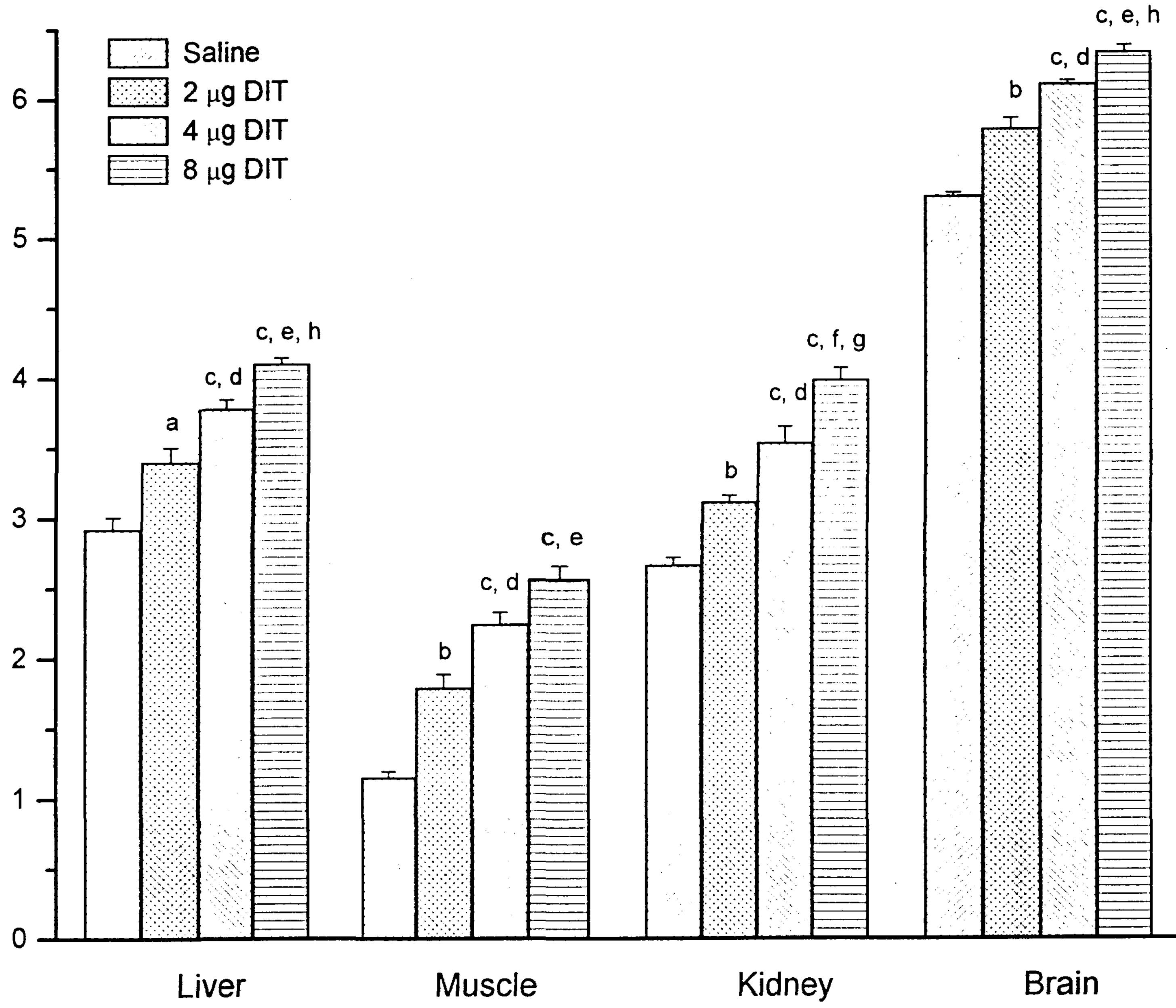
Figure 3:4 - Dose-dependent in vivo effects of monoiodotyrosine (DIT) on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 11.5° C)

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e, f] Differ from the group treated with 2 μg DIT : $P < 0.05$, 0.01 and 0.001, respectively.

[g, h] Differ from the group treated with 4 μg DIT : P < o.o5 and 0.01, respectively.

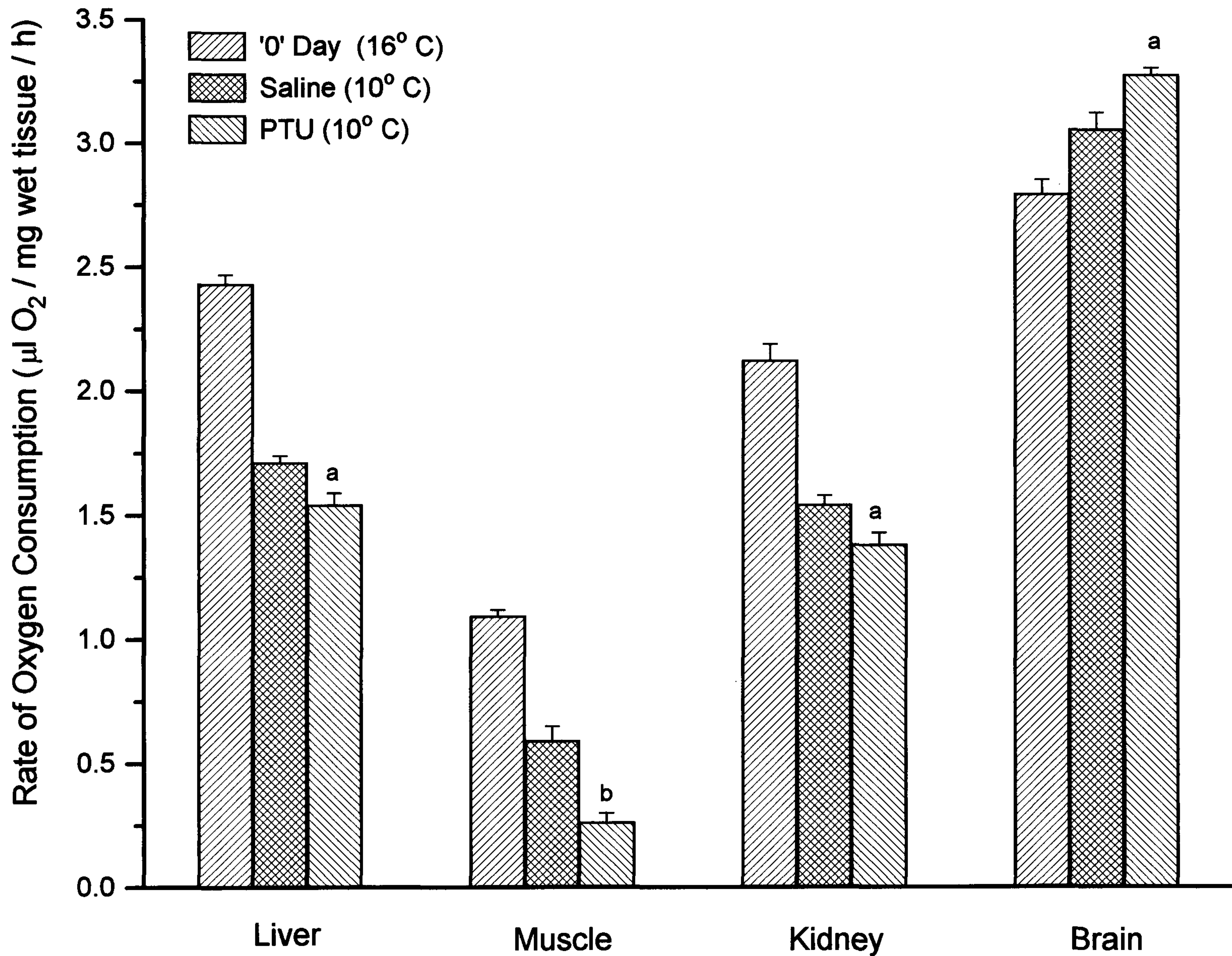


Rate of Oxygen Consumption (µl O2 / mg wet tissue / h)
Saline
2 µg DIT
4 µg DIT
8 µg DIT
0
1
2
3
4
5
6
a
c, d
c, e, h
b
c, d
c, e
b
c, d
c, f, g
b
c, d
c, e, h
Liver
Muscle
Kidney
Brain

Figure 3:5 - In vivo effects of propyl thiouracil on the rate of tissue respiration in male *Clarias batrachus* at simulated low temperature (10±1°C)

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b] Differ from saline treated control group : $P<0.05$ and 0.01, respectively.



Rate of Oxygen Consumption (μl O2 / mg wet tissue / h)
'0' Day (16° C)
Saline (10° C)
PTU (10° C)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
a
a
b
a
Liver
Muscle
Kidney
Brain

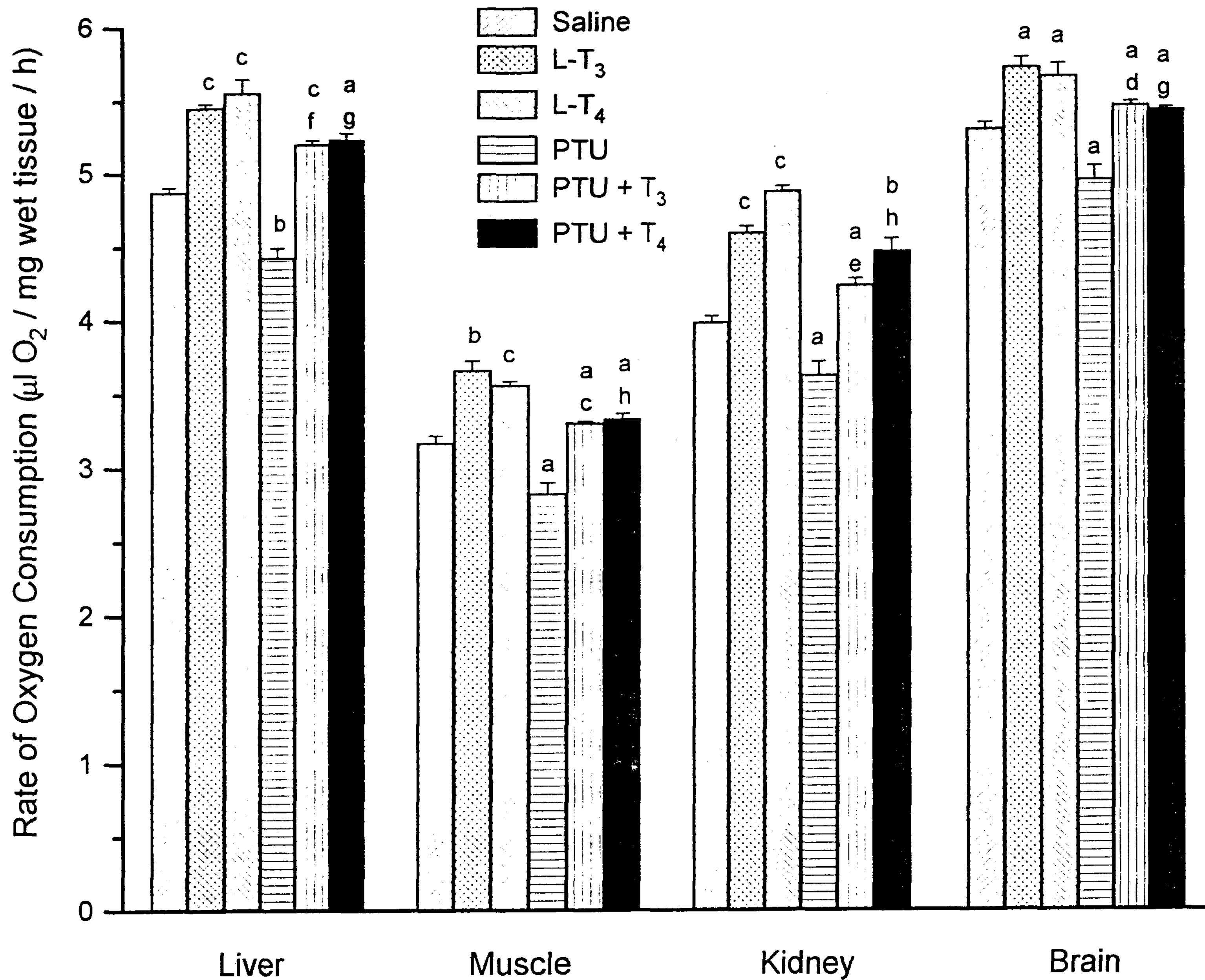
Figure 3:6 - In vivo effects of thyroid hormones and propyl thiouracil (PTU) on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 22° C)

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e, f] Differ from the group treated with $L\text{-}T_3$: $P < 0.05$, 0.01 and 0.001, respectively.

[g, h] Differ from the group treated with $L\text{-}T_4$: $P < 0.05$ and 0.01, respectively.



Rate of Oxygen Consumption (μl O2 / mg wet tissue / h)
Saline
L-T3
L-T4
PTU
PTU + T3
PTU + T4
Liver
Muscle
Kidney
Brain

Figure 3:7 - *In vitro* effects of thyroid hormones on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp.: 9.6° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

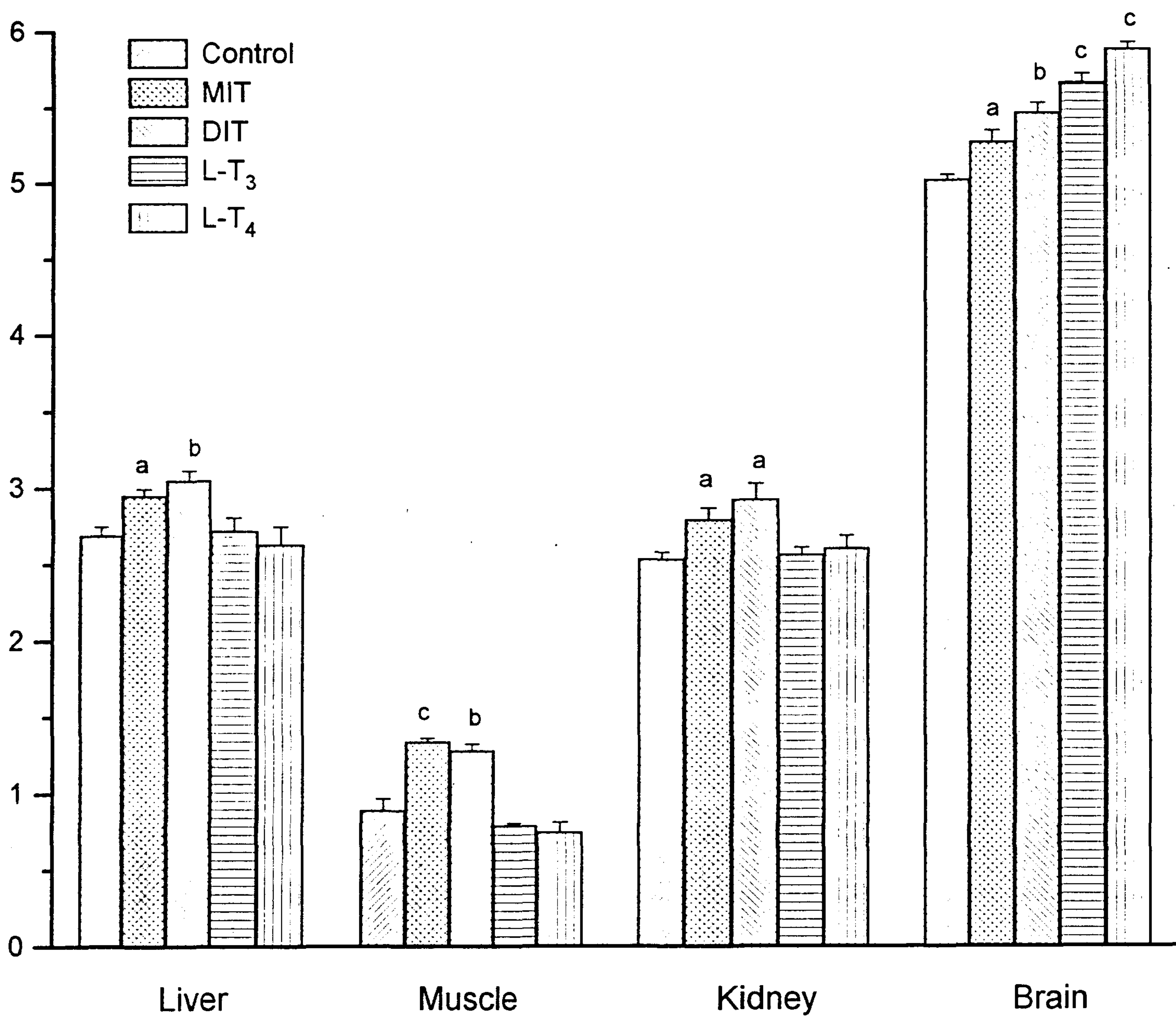

Rate of Oxygen Consumption (μl O2 / mg wet tissue / h)
0
1
2
3
4
5
6
Control
MIT
DIT
L-T3
L-T4
a
b
c
b
a
a
a
b
c
c
Liver
Muscle
Kidney
Brain

Figure 3:8 - *In vitro* effects of thyroid hormones on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 20° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

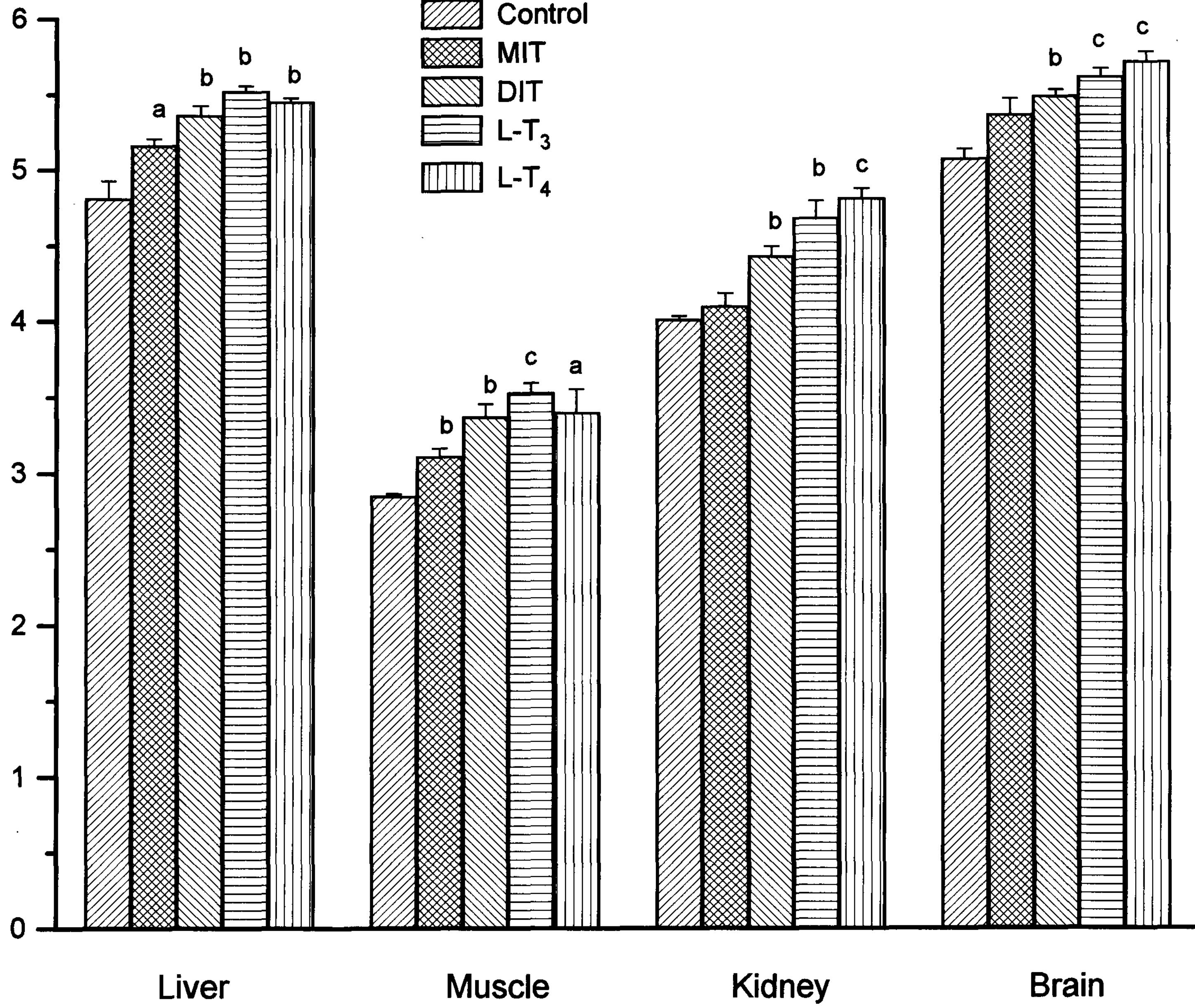
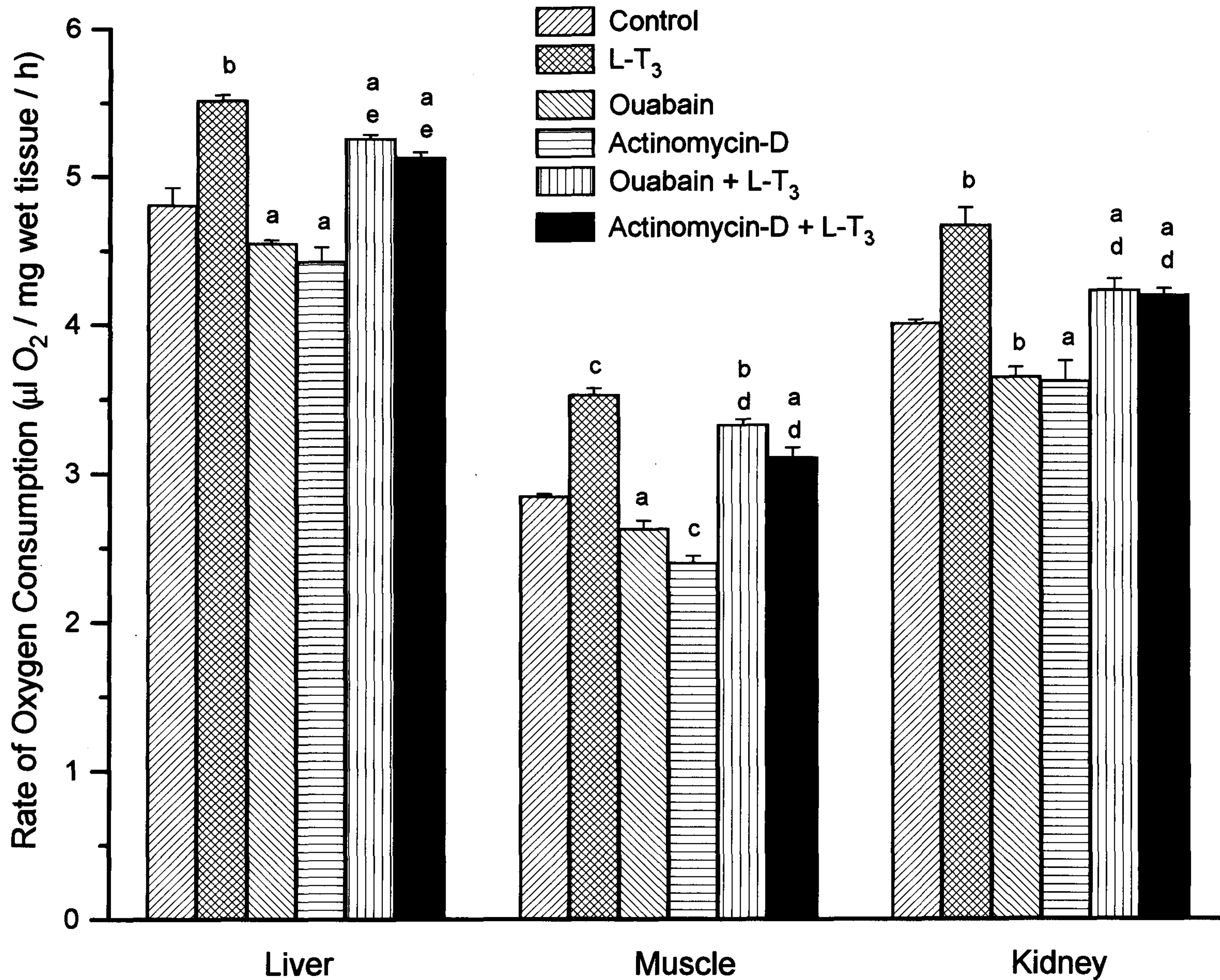

Rate of Oxygen Consumption (µl O_2 / mg wet tissue / h)
0
1
2
3
4
5
6
Control
MIT
DIT
L-T_3
L-T_4
a
b
b
b
b
b
c
a
b
b
c
b
c
c
Liver
Muscle
Kidney
Brain

Figure 3:9 - In vitro effects of L-T_3 in the absence and presence of ouabain and actinomycin-D on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 21° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e] Differ from the group treated with L-T_3: $P < 0.05$ and 0.001, respectively.



Control
L-T3
Ouabain
Actinomycin-D
Ouabain + L-T3
Actinomycin-D + L-T3
Rate of Oxygen Consumption (µl O2 / mg wet tissue / h)
0
1
2
3
4
5
6
b
a
a
a
e
a
e
c
a
c
b
d
a
d
b
b
a
a
d
a
d
Liver
Muscle
Kidney

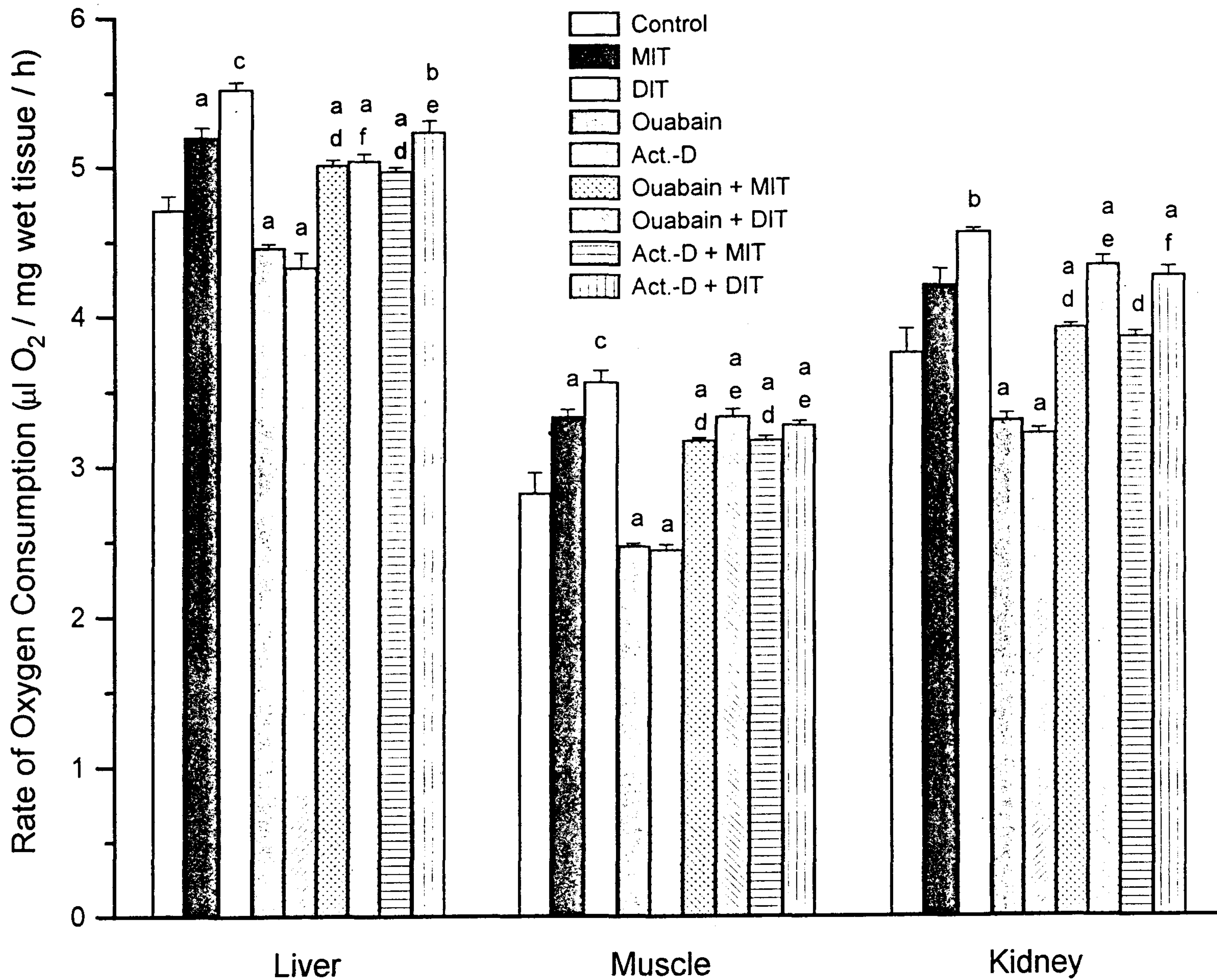
Figure 3:10 In vitro effects of monoiodotyrosine (MIT) and dioiodotyrosine (DIT) in the absence and presence of ouabain and actinomycin-D on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 20° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from saline treated controls : $P < 0.05$, 0.01 and 0.001, respectively.

[d] Differs from the group treated with MIT : $P < 0.05$.

[e, f] Differ from the group treated with DIT : $P < 0.05$ and 0.01, respectively.


Rate of Oxygen Consumption (μl O_2 / mg wet tissue / h)
6
5
4
3
2
1
0
Control
MIT
DIT
Ouabain
Act.-D
Ouabain + MIT
Ouabain + DIT
Act.-D + MIT
Act.-D + DIT
Liver
Muscle
Kidney

Chapter-IV

ROLE OF TESTICULAR HORMONES IN REGULATION OF THE OXIDATIVE METABOLISM IN MALE *Clarias batrachus*

Testicular hormones (androgens) have been generally considered as hormones for reproduction in all vertebrates. In addition to its reproductive and metabolic functions, testosterone has also been reported to influence erythropoiesis and oxidative metabolism in homeotherms (Brown *et al.*, 1966; Naets, 1971; Chester-Jones *et al.*, 1972; Pearce and Balnave, 1974; Datta, 1975; Panke *et al.*, 1978; Hanssler and Prinzinger, 1979; Thapliyal *et al.*, 1983). Similarly, in reptiles and amphibians, testosterone has been reported to have direct and temperature-independent influence on the rate of whole body oxygen consumption and tissue oxygen uptake (Follet and Red Shaw, 1968; Chandola *et al.*, 1973, 1974; Thapliyal *et al.*, 1974c, 1974b; Thapliyal, 1980, Oommen, 1980; Gupta, 1982; Thapliyal and Gupta, 1983; Gupta and Thapliyal, 1984, 1985; Oommen and Sreedeviamma, 1988; Chakrabarty, 1988; Gupta and Chakrabarty, 1990; Sutharam *et al.*, 1991; Gupta and Thapliyal, 1991; Gupta and Deka-Borah, 1995; Gupta and Mahanta, 1997). However, unlike in reptiles and amphibians, there is a scarcity of information on the calorigenic role of testicular hormones in fish. It is important to mention that in reptiles and amphibians, testicular hormones have been reported to regulate the oxidative metabolism at low temperature during winter where thyroid hormones are calorigenically ineffective (Gupta and Thapliyal, 1991; Mahanta, 1994; Gupta and Mahanta, 1997). These hormones are reportedly important for energy metabolism and survival of amphibians and reptiles at low temperature of winter months. But so far no attempt has been made to investigate in detail the role of testicular hormones in the regulation of energy metabolism of any fish species, particularly in relation to low ambient temperature where thyroid

hormones do not stimulate oxygen consumption in fish (Mann, 1939; Gupta, 1988; Gupta and Thapliyal, 1991).

Keeping in view the scarcity of information on calorigenic role of androgens in fish, the aquatic habit and habitat of fish and its phylogenic position, it was thought worthwhile to investigate in detail the calorigenic role of testicular hormones in the fish, *Clarias batrachus* maintained under natural climatic conditions during winter and summer/rainy seasons. Experiments were also conducted to find out the mode of action of testosterone using cyproterone acetate (blocker of androgen receptor) and actinomycin-D (inhibitor of transcription). The data of the present study suggest that testicular hormones play a major and direct role in the regulation of the oxidative metabolism of *Clarias batrachus*, and their calorigenic action seems to be temperature-independent. Further, *in vitro* treat-ment of testosterone seems to produce its calorigenic action via DNA-dependent mRNA synthesis.

Materials and Methods

Male *Clarias batrachus* (body weight : 70-80 g., length :18-22 cm) were purchased locally, maintained in a container with water exposed to natural climatic conditions and acclimatized at least for 15 days before the experiments. During acclimatization, fish were fed with pieces of earthworms *ad libitum*. For *in vitro* experiments, fishes were decapitated and tissues (liver, muscle, kidney and brain) were quickly removed, rinsed in ice-cold fish buffer-saline and stored in a refrigerator (for other details please see Chapter-I).

For *in vivo* experiments, after acclimatization fishes were divided into different groups (four fishes in each group). The treatment were given as per details of the following experimental protocol. Twenty-four hours after the last injection, fishes

of each group were decapitated and tissues (liver, muscle, kidney and brain) were quickly removed, rinsed in the ice-cold fish buffer-saline and stored in a refrigerator (for details please see Chapter-I). The rate of tissue respiration was measured with the help of a digital oxygen electrode following the method described in Chapter-I. The data were analysed with the help of student's 't' test (Snedecor, 1961). In vivo and in vitro experiments were performed as per the details given in the following experimental protocol.

Experimental Protocol

Expt. No.	Treatment	In vivo/ In vitro	Month (Temp.)	Dose	Duration of Treatment
(A)	Saline	In vivo	Jan		4 days
	Testosterone		(9.6°C)	2 μg/f/d	4 days
	Cyproterone acetate (CA)		Sept. (20°C)	1 μg/g	4 days
	CA+Testosterone			1 μg/g+2 μg/f/d	4 days
(B)	Control	In vitro	Jan (9.6°C)		
	Testosterone		July (20°C)	1 μM	
(C)	Control	In vitro	Sept.		
	Testosterone		(20°C)	1 μM	
	Cyproterone acetate (CA)			2 μM	
	Actinomycin-D			2 μM	
	CA+Testosterone			2 μM + 1 μM	
	Act-D+Testosterone			2 μM + 1 μM	

Results

***In vivo* effects of testosterone and cyproterone acetate (CA) on the rate of tissue respiration :**

The data are presented in Tables 4:1 & 4:2 and Figs. 4:1 & 4:2. *In vivo* administration of testosterone significantly increased the respiratory rate of liver, muscle, kidney and brain tissue both during winter and summer/rainy months (Table 4:1; Fig. 4:1). *In vivo* administration of cyproterone acetate (specific blocker of androgen receptors) significantly reduced the rate of oxygen consumption in all the tissues irrespective of seasons (Table 4:2; Fig. 4:2). When testosterone and CA were administered together, the respiratory rate of tissue was significantly decreased as compared to the tissues treated only with testosterone. However, CA did not block the stimulatory effect of testosterone completely (Table 4:2; Fig. 4:2).

***In vitro* effects of testosterone on the rate of tissue respiration**

The data are presented in Table 4:3 and Fig. 4:3. *In vitro* treatment of tissue homogenates with testosterone significantly increased the respiratory rates of liver, muscle and kidney tissues, but not of brain during winter. However, during summer/rainy months, treatment with testosterone significantly increased the rate of oxygen consumption of all the tissues (Table 4:3; Fig. 4:3).

***In vitro* effect of testosterone in the presence of cyproterone acetate (CA) and actinomycin-D**

The data are presented in Table 4:4 and Fig. 4:4. In order to assess the mechanism of action of testosterone, tissues were treated with testosterone in the

presence and absence of cyproterone acetate (specific blocker of androgen receptors) and actinomycin-D (inhibitor of transcription). Administration of testosterone significantly increased the rate of oxygen uptake of liver, muscle and kidney tissues. However, both cyproterone acetate and Actinomycin-D significantly, but not completely, blocked the stimulatory effect of testosterone on the respiratory rate of all the three tissues (Table 4:4 and Fig. 4:4).

Discussion

In vivo administration of testosterone significantly increased the respiratory rate of all the tissues during both winter and summer/rainy months (Table 4:1 and Fig. 4:1). These findings clearly suggest that testosterone is calorigenic in fish, and its stimulatory effect on the rate of tissue respiration seems to be independent of ambient temperature. Administration of cyproterone acetate always inhibited the respiratory rate of all the tissues during both winter and summer/rainy months. Cyproterone acetate blocks androgen receptors and does not allow binding of testosterone and other androgens to their receptors. A significant decrease in the rate of tissue respiration clearly indicates that indigenous testicular androgens are involved in the regulation of the metabolic rate of tissues in the fish, *C. batrachus*. As in case of *in vivo* experiments, *in vitro* treatment with testosterone also invariably stimulated the respiratory rate of liver, muscle, and kidney tissues both during winter and summer/rainy seasons. However, brain tissue respiration was stimulated by *in vitro* treatment with testosterone only during summer/rainy seasons, but not during winter (Table 4:3 and Fig. 4:3). *In vitro* stimulation of tissue respiration by testosterone strongly suggest that the hormone has a direct calorigenic effect on the tissues. Brain respiration during winter, however, seems to be indirectly regulated by testosterone. These findings seem to suggest that testicular hormones play an important role in the regulation of the oxidative metabolism of the fish. In other experiments (please see

Chapter III), we have found that the thyroid hormones could not stimulate respiratory rate of fish tissues at low temperature of the winter months. Therefore, temperature-independent and direct calorigenic action of testosterone in fish might be of great adaptational importance. Further, significant decrease in the rate of tissue respiration following cyproterone acetate treatment, especially during winter months, seems to suggest that indigenous testicular androgens might be actively involved in the regulation of the metabolic rate to ensure minimum physiological activity and survival of the fish at low temperature. The increased basal metabolic rate in some mammals has been reported to be related to the concentration of testicular hormones (Brown *et al.*, 1966). There are several reports on the stimulatory effect of testosterone and inhibitory effect of castration on the respiratory rate of reptiles (Gorbman, 1963; Chandola *et al.*, 1973; Kumar *et al.*, 1974; Chandola *et al.*, 1974; Thapliyal *et al.*, 1974a, c; Thapliyal *et al.*, 1975d; Oommen, 1976; Wahal *et al.*, 1977; Oommen, 1980; Gupta, 1982; Thapliyal and Gupta, 1984; Oommen, 1985; Oommen and Sreedeviamma, 1988; Al-Sadoon *et al.*, 1990) and amphibians (Deka-Borah, 1989; Gupta and Chakrabarty, 1990; Sutharam *et al.*, 1991; Gupta and Mahanta, 1997).

In agreement with our present findings, the calorigenic effect of testosterone has also been found to be direct and temperature-independent in amphibians (both hibernating and non-hibernating species) as well as in reptiles (Gupta and Thapliyal, 1991). It is, thus, obvious that testosterone (the major androgen), due to its direct and temperature-independent calorigenic action, plays a major role in the regulation of the oxidative metabolism in the poikilothermic vertebrates. Further, castration and CA-induced decrease in the respiratory rate of tissues in fish (present study), amphibians (Mahanta, 1994) and reptiles (Thapliyal *et al.*, 1975d; Thapliyal and Gupta, 1983; Gupta and Thapliyal, 1985a; Al-Sadoon *et al.*, 1990), particularly during winter months, suggest that testicular hormones play a leading role in the regulation of

poikilothermic energy metabolism at low temperature where thyroid hormones are generally ineffective in stimulating the metabolic rate.

Significant reduction by cyproterone acetate and actinomycin-D in the respiratory rate of liver, muscle and kidney tissues stimulated by testosterone indicates that the calorigenic effect of testosterone in tissues of *Clarias batrachus* is mediated through androgen receptors, and involves transcription processes. The calorigenic action of testosterone through androgen receptors has also been supported by *in vivo* experiment where CA significantly blocked the stimulatory effect of testosterone on tissue respiration (Table 4:4 and Fig. 4:4). In other tissues, androgens have been reported to bind to their cytoplasmic nuclear receptors and form a hormone-receptor (H-R) complex. The HR-complex, after its dimerization, binds to hormone response element (HRE) and stimulates DNA-dependent mRNA synthesis (O'Malley, 1971; Walsh and Koreman, 1973; Davier and Griffiths, 1973; Schreck, 1973; O'Malley and Means, 1974; O'Malley *et al.*, 1975; Yamamoto, 1985; Colvard and Wilson, 1987; Crino *et al.*, 1987; Shan *et al.*, 1990; Wolf *et al.*, 1993; Wong *et al.*, 1993; De vos *et al.*, 1994; Cavanaugh and Simon, 1994; Charmain *et al.*, 1995; Karin *et al.*, 1995; Onate *et al.*, 1995; Katzenellenbogen *et al.*, 1996). When androgen-induced mRNA is translated in the cytoplasm, new proteins are formed which alter the cellular functions. A similar mechanism might also be involved in the calorigenic action of testosterone in the fish. A significant but incomplete inhibition by CA and Actinomycin-D of testosterone's stimulatory effect on tissue respiration, however, indicates that testosterone increases tissue oxygen uptake through more than one mechanism and/or through non-genomic pathway(s) (Hyne *et al.*, 1978; Revelli *et al.*, 1998). Minguell and Sierralta (1975) have suggested that the effects of androgens in a particular sensitive tissue are not limited to a single biochemical parameter but might affect several pathways. It has also been reported that testosterone directly influences the activity of the respiratory enzyme cytochrome oxidase in mammals and reptiles (Meyer

and Meshan, 1959; Pegg and Ashman, 1968; Wahal *et al.*, 1977; Koenig *et al.*, 1980; Oommen and Sreedeviamma, 1988; Peter and Oommen, 1988a). Further, testosterone reportedly influences intermediary metabolism and increases Na^+-K^+-ATPase activity in mammals (Liao, 1968; Farnsworth, 1968, 1971, 1972; Pearce and Balnave, 1974). However, the question whether testicular hormones also stimulate oxygen consumption in *Clarias batrachus* via their direct action at mitochondrial oxidative enzymes, Na^+-K^+-ATPase or indirectly via intermediary metabolism, remains to be answered.

On the basis of the present findings we suggest that androgens might be initially involved in the regulation of the oxidative metabolism as well as in reproduction. However, with the evolution of homeothermy, the thyroid hormones became the major hormones responsible for the regulation of the oxidative metabolism, while testicular hormones ensured successful reproduction. Thus, calorigenic action of testicular hormones ensured both survival at low temperature and successful reproduction of cold-blooded vertebrates by removing the dependence of the metabolic rate on thyroid hormones whose synthesis and actions have been found to be temperature-dependent.

Table 4:1 - In vivo effects of testosterone on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C) and summer (Av. water temp. : 20° C)

Treatments	Rate of Tissue Oxygen Consumption (μl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
	Winter			
Saline (Control)	2.88±0.07	1.12±0.05	2.69±0.08	5.26±0.09
Testosterone	3.88±0.03[c]	1.66±0.14[a]	3.65±0.12[c]	5.68±0.05[b]
	Summer			
Saline (Control)	4.71±0.08	2.72±0.05	4.10±0.05	4.30±0.07
Testosterone	5.26±0.04[c]	3.52±0.08[c]	4.47±0.07[b]	4.59±0.09[a]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

Table 4:2 : In vivo effects of testosterone in the absence and presence of cyproterone acetate (CA) on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C) and summer (Av. water temp. : 20° C).

Treatments	Rate of Tissue Oxygen Consumption (μl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
		Winter		
Saline (Control)	2.88±0.07	1.12±0.05	2.69±0.08	5.26±0.09
Testosterone	3.88±0.03[c]	1.66±0.14[a]	3.65±0.12[b]	5.68±0.05[b]
CA	2.53±0.08[a]	0.80±0.09[a]	2.40±0.05[a]	4.94±0.07[a]
CA + Testosterone	3.24±0.09[a,f]	1.31±0.05[a,e]	3.08±0.04[b,e]	5.48±0.02[a,d]
		Summer		
Saline (Control)	4.71±0.08	2.73±0.07	4.10±0.05	4.30±0.07
Testosterone	5.26±0.04[c]	3.52±0.08[c]	4.47±0.07[b]	4.59±0.09[a]
CA	4.46±0.02[a]	2.37±0.07[a]	3.85±0.04[b]	3.98±0.06[a]
CA + Testosterone	4.97±0.05[a,e]	3.30±0.05[c,d]	4.26±0.03[a,d]	4.36±0.04[d]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e, f] Differ from the group treated with testosterone : $P < 0.05$, 0.01 and 0.001, respectively.

Table 4:3 : In vitro effects of testosterone on the rate of tissue respiration of male *Clarias batarchus* during winter (Av. water temp. : 9.6° C) and summer (Av. water temp. : 20° C)

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
		Winter		
Control	2.69±0.06	0.89±0.08	2.53±0.05	5.01±0.04
Testosterone	4.75±0.04[c]	1.63±0.05[c]	3.59±0.09[c]	4.81±0.03
		Summer		
Control	4.81±0.12	2.85±0.02	4.01±0.03	5.07±0.07
Testosterone	5.32±0.03[b]	3.75±0.05[c]	5.01±0.04[c]	5.58±0.12[a]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 anu 0.001, respectively.

Table 4:4 - In vitro effects of testosterone in the absence and presence of actinomycin-D and cyproterone acetate (CA) on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 20° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)		
	Liver	Muscle	Kidney
Control	4.81±0.12	2.85±0.02	4.01±0.03
Testosterone (T)	5.90±0.10[c]	3.75±0.05[c]	5.01±0.05[c]
Actinomycin-D	4.46±0.05[a]	2.50±0.06[b]	3.66±0.03[c]
CA	4.49±0.04[a]	2.60±0.05[b]	3.78±0.07[a]
Actinomycin-D + T	5.55±0.06[b,d]	3.33±0.04[c,e]	4.49±0.04[c,e]
CA + T	5.65±0.04[c,d]	3.53±0.07[c,d]	4.68±0.11[b,d]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e] Differ from the group treated with testosterone : $P < 0.05$and 0.001, respectively.

Figure 4:1 - In vivo effects of testosterone on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C) and summer (Av. water temp. : 20° C)

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

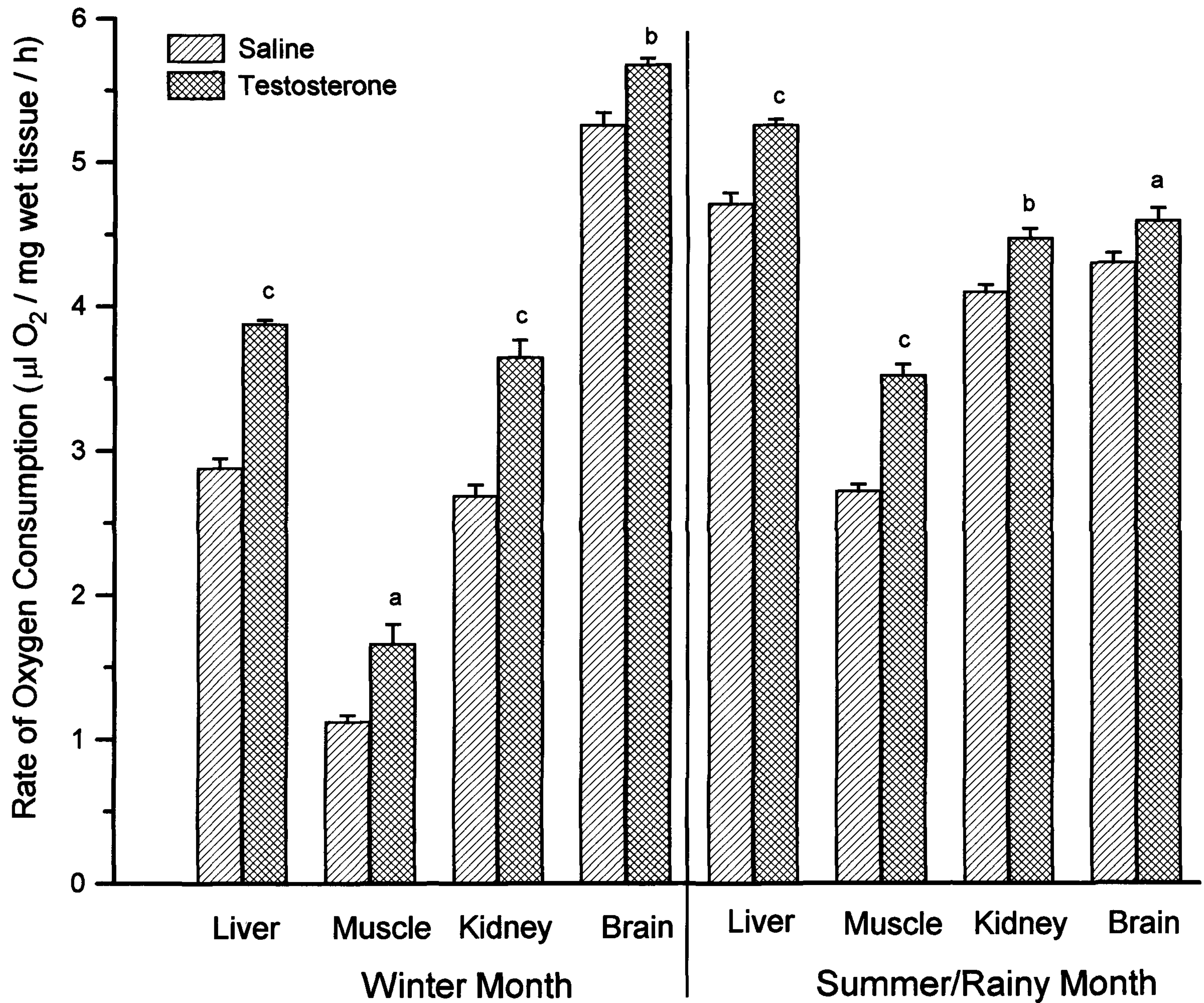
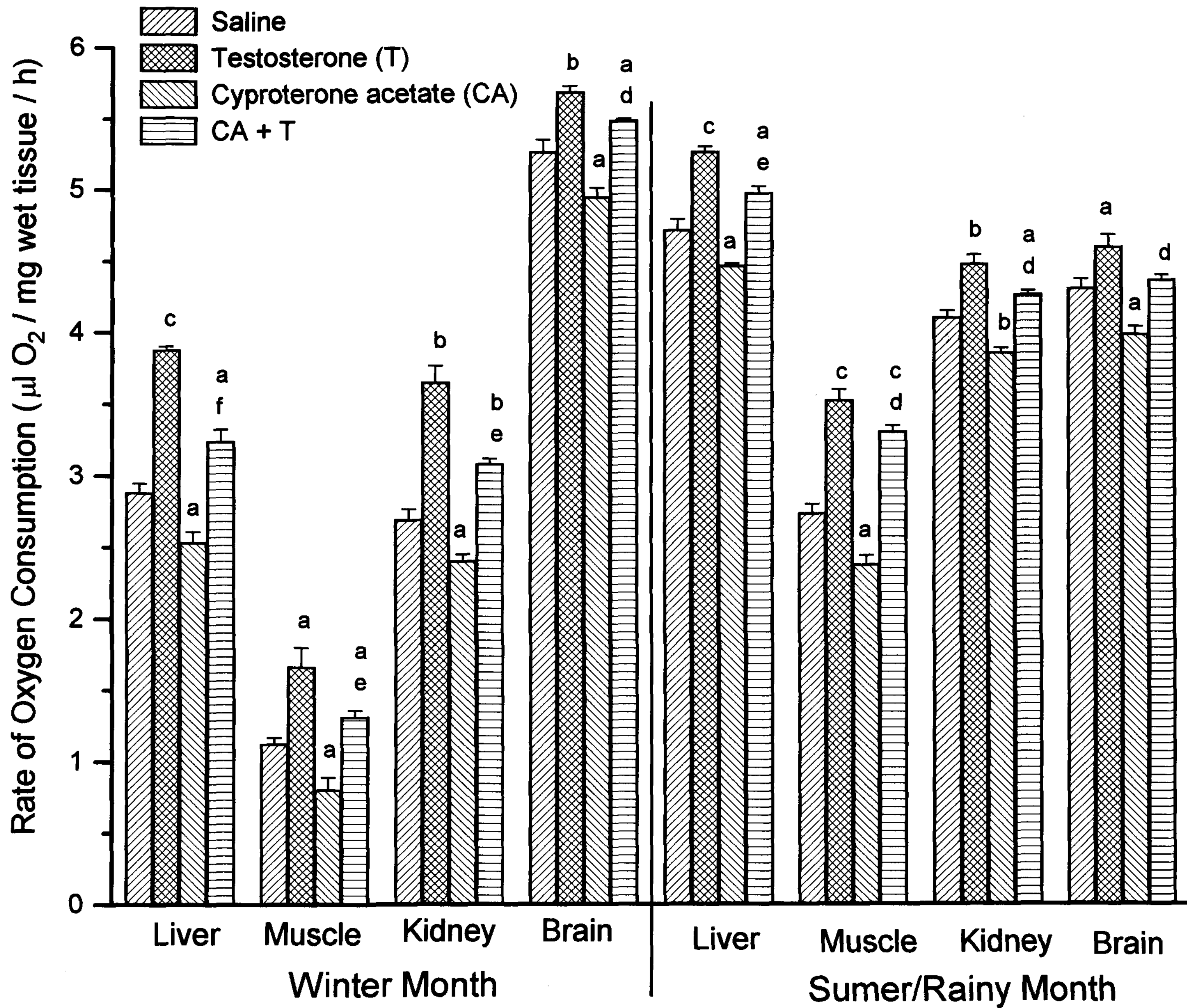

Saline
Testosterone
Rate of Oxygen Consumption (μl O2 / mg wet tissue / h)
0
1
2
3
4
5
6
c
a
c
b
c
c
b
a
Liver
Muscle
Kidney
Brain
Liver
Muscle
Kidney
Brain
Winter Month
Summer/Rainy Month

Figure 4:2 : In vivo effects of testosterone in the absence and presence of cyproterone acetate (CA) on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C) and summer (Av. water temp. : 20° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

$^{a, b, c}$ Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

$^{d, e, f}$ Differ from the group treated with testosterone : $P < 0.05$, 0.01 and 0.001, respectively.

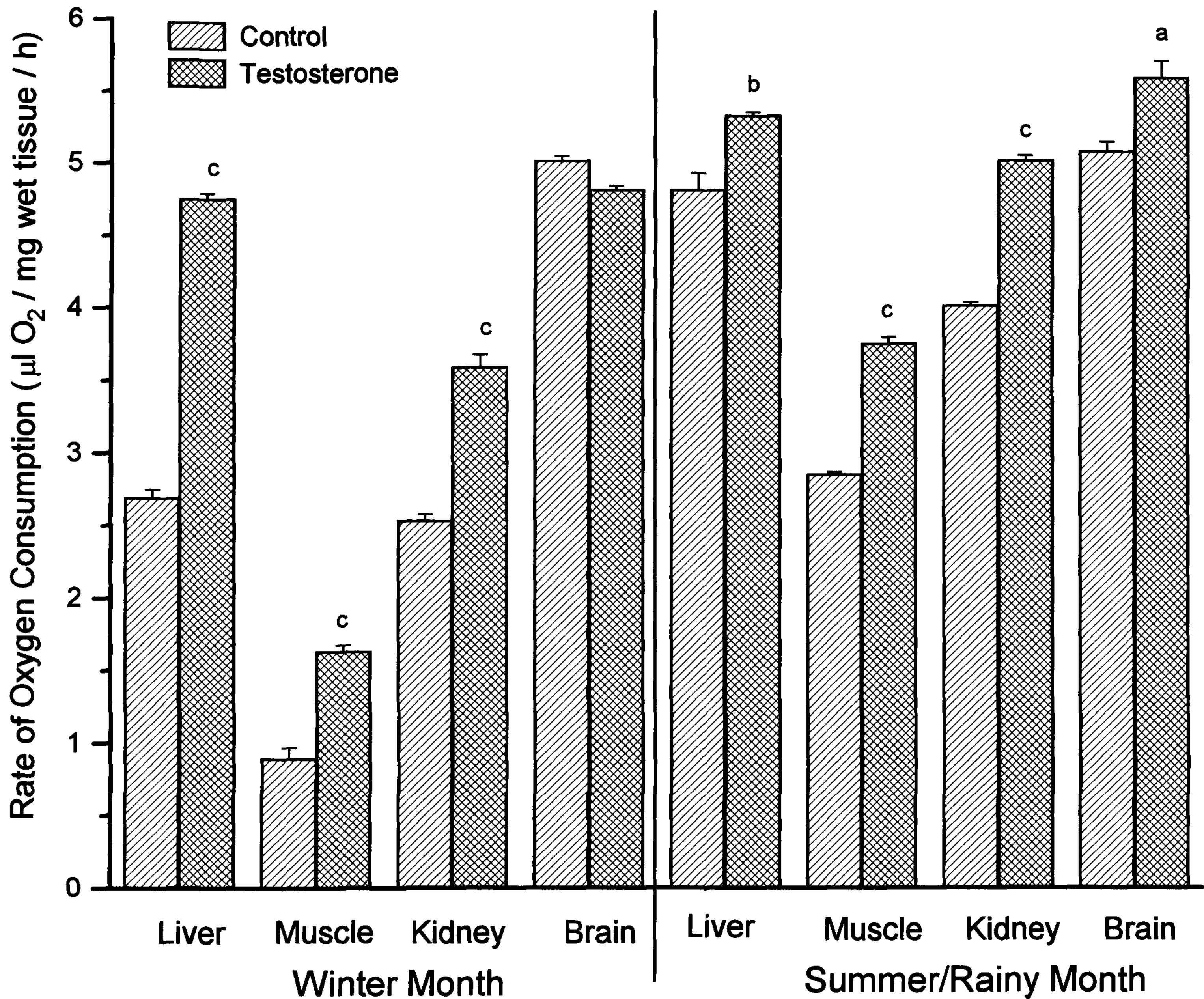


Saline
Testosterone (T)
Cyproterone acetate (CA)
CA + T
Rate of Oxygen Consumption (µl O2 / mg wet tissue / h)
0
1
2
3
4
5
6
Liver
Muscle
Kidney
Brain
Winter Month
Liver
Muscle
Kidney
Brain
Sumer/Rainy Month

Figure 4:3 - In vitro effects of testosterone on the rate of tissue respiration of male *Clarias batarchus* during winter (Av. water temp. : 9.6° C) and summer (Av. water temp. : 20° C)

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.



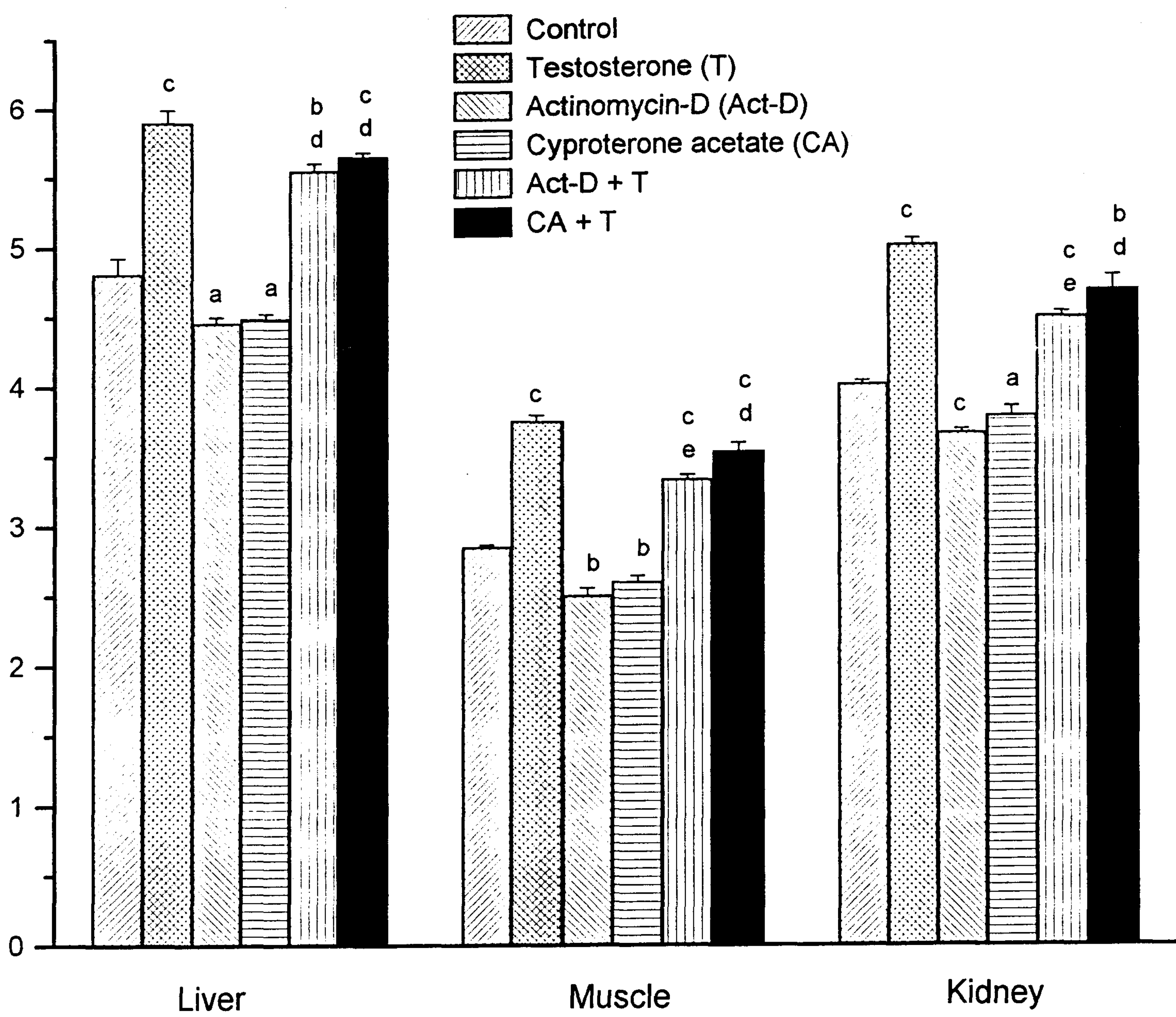
Control
Testosterone
Rate of Oxygen Consumption (µl O_2 / mg wet tissue / h)
0
1
2
3
4
5
6
c
c
c
b
c
c
a
Liver
Muscle
Kidney
Brain
Winter Month
Liver
Muscle
Kidney
Brain
Summer/Rainy Month

Figure 4:4 - In vitro effects of testosterone in the absence and presence of actinomycin-D and cyproterone acetate (CA) on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 20° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e] Differ from the group treated with testosterone : $P < 0.05$ and 0.001, respectively.


Rate of Oxygen Consumption (µl O2 / mg wet tissue / h)
0
1
2
3
4
5
6
Control
Testosterone (T)
Actinomycin-D (Act-D)
Cyproterone acetate (CA)
Act-D + T
CA + T
Liver
Muscle
Kidney

Chapter-V

ROLE OF CATECHOLAMINES AND CORTICOSTEROIDS IN REGULATION OF THE OXIDATIVE METABOLISM IN MALE *Clarias batrachus*

The adrenal gland in mammals is a discrete and compact organ. However, in teleost fishes, the catecholaminergic (CT) and corticosteroidgenic (CSG) tissues do not constitute a well defined adrenal gland. These tissues are scattered separately in the form of islets in the anterior part of the kidney. The catecholamines are produced from the CT and as a neurotransmitter from the sympathetic nerve terminals (Hillarp and Hökfett, 1953; Butler, 1973; Himms-Hagen, 1975; DeSantis *et al.*, 1975; Landberg and Young, 1985, 1992). As in mammals, the CSG tissue of the fish secrets corticoids like corticosterone, cortisol and cortisone (Baxter and Tyrrell, 1987). The catecholamines and the corticosteroids have been reported to be involved in a number of metabolic pathways of vertebrates (Gorbman *et al.*, 1983a; Christopsh *et al.*, 1996). Due to their multi-directional physiological actions, these hormones play a major role during the emergency conditions and in general adaptations against the adverse effect of a new environment (Gorbman *et al.*, 1983a; Landberg and Young, 1985, 1992; Harmaweray and Baker, 1996).

The catecholamine hormones have been reported to induce non-shivering thermogenesis in cold acclimated mammals (Hsieh and Carlson, 1957; Carlson, 1960; Himms-Hagen, 1970, 1984; Williamson *et al.*, 1970; Gale, 1973; Tenche, 1976; Horwitz, 1978, 1979; Bukowiecki *et al.*, 1980; Nedergard *et al.*, 1986; Nicholls *et al.*, 1986; Allison and Skinner, 1990; Haim and Skinner, 1991; McDevit and Speakman, 1996). These hormones have been reported to stimulate oxygen consumption in a

number of mammalian species (Himms-Hagen, 1967; Laury *et al.*, 1971; Horwitz, 1978; Sherwin and Sacca, 1984; Ellison and Skinner, 1990; McDevit and Speakman, 1996), reptiles (Gupta and Thapliyal, 1983; Thapliyal and Gupta, 1984) and amphibians (Harri and Hadenstam, 1972; Farrar and Frye, 1977; Janssens *et al.*, 1983; Gupta and Mahanta, 1997). Due to their rapid and temperature-independent calorigenic actions, catecholamines act as emergency hormones for regulation of the oxidative metabolism in the poikilothermic vertebrates (Gupta and Thapliyal, 1983; Ottolenghi *et al.*, 1985; Josekumar and Oommen, 1988; Prasannakumar and Oommen, 1988; Gupta and Chakrabarty, 1990; Gupta and Deka-Borah, 1995; Gupta and Mahanta, 1997; Mahanta and Gupta, 1998). Unlike in reptiles and amphibians, there is scarcity of information on the involvement of catecholamines in fish respiration. The available reports seem to be inconsistent and contradictory. So far no attempt has been made to study in details the calorigenic role of catecholamines in fish tissue respiration, mode of action and their synergistic metabolic action with thyroid hormones. The metabolic influence of corticosteroids on the oxidative metabolism in mammals seems to depend on tissues and the length of hormonal treatment (Goetsch and McDonald, 1962). Hydrocortisone, predinisolone and corticosterone separately increased liver oxygen uptake (Goetsch *et al.*, 1959, 1962; Goetsch and McDonald, 1962; Bottom and Goetsch, 1968). Glucocorticoid have been reported to have a direct influence on mitochondrial transcription and respiratory enzyme synthesis in mammals (McEwan *et al.*, 1994; Demonacus *et al.*, 1996). In reptiles and amphibians, the corticosteroids seem to have a direct and temperature-independent effect on the rate of tissue respiration (Gupta and Thapliyal, 1983, 1991; Gupta and Chakrabarty, 1990; Gupta and Deka-Borah, 1995; Gupta and Mahanta, 1997). They also increased the activity of oxidative enzymes in reptilian liver in a dose-dependent manner (Prasannakumar and Oommen, 1988). In amphibians also, these hormones have been reported to increase the activity of respiratory enzymes (Josekumar and Oommen, 1988; Hanke, 1990). However, unlike in other vertebrates, there is practically no information on the

calorigenic action of the corticosteroid hormones in any fish species. Therefore, keeping in view the scarcity of information on the calorigenic role of catecholamines and corticosteroids and the phylogenic position and economic importance of fish, we decided to investigate in detail the role of these hormones in regulation of the oxidative metabolism of an air breathing fish, *Clarias batrachus* maintained at natural climatic conditions during winter and summer/rainy seasons. The experiments were also conducted to know the mechanism of action of catecholamines and their synergistic action with thyroid hormones. Finding of the present study indicates that the hormones are actively involved in the regulation of the oxidative metabolism of the fish.

Materials and Methods

Adult male *Clarias batrachus* (length : 18 - 22 cm; weight :70-80 gm.) were purchased from the local market and acclimatized for 15 days under natural climatic conditions before the experiment were started (for details please see Chapter-I). *In vivo* and *in vitro* experiments were conducted during both winter and summer/rainy months as per the following experimental protocol.

Experimental Protocol

Expt. No.	Treatment	*In vivo*/ *in vitro*	Month (temp.)	Dose	Duration of Treatment
(A)	Control	*In vitro*	Jan (9.6°C)		
	Epinephrine		July (20°C)	1 μM	
	Norepinephrine(NE)			1 μM	
	Corticosterone			1 μM	
	Cortisol			1 μM	
	Cortisone			1 μM	

Expt. No.	Treatment	*In vivo*/ *in vitro*	Month (temp.)	Dose	Duration of Treatment
(B)	Control	*In vitro*	Jan (9.6°C)		
	T_3		July	1 μM	
	T_4		(20°C)	1 μM	
	T_3+EP			1 μM + 1 μM	
	T_3+NE			1 μM + 1 μM	
	T_4+EN			1 μM + 1 μM	
	T_4+NE			1 μM + 1 μM	
(C)	Control	*In vitro*	July (20°C)		
	Propranotol (Prop)			2 μM	
	Prozosin (Praz)			2 μM	
	Prop+ Praz			2 μM + 2 μM	
	EP			1 μM	
	NE			1 μM	
	Prop+EP			2 μM + 1 μM	
	Prop+NE			2 μM + 1 μM	
	Praz+EP			2 μM + 1 μM	
	Praz+NE			2 μM + 1 μM	
	Prop+Praz+EP			2 μM + 2 μM +1 μM	
	Prop+Praz+NE			2 μM + 2 μM +1 μM	
(D)	Saline	*In vivo*	Jan (9.6°C)		4 days
	EP		Sept (20°C)	2 μg/f/d	4 days
	NE			2 μg /f/d	4 days
	Corticosterone			2 μg /f/d	4 days
(D)	Cortisol			2 μg /f/d	4 days
	Cortisone			2 μg /f/d	4 days

Expt. No.	Treatment	In vivo/ In vitro	Month (Temp.)	Dose	Duration of Treatment
(E)	Saline	*In vivo*	Jan (9.6°C)		4 days
	T_3		Sept	2 μg /f/d	4 days
	T_4		(20°C)	2 μg /f/d	4 days
	EP			2 μg /f/d	4 days
	NE			2 μg /f/d	4 days
	T_3+EP			2 μg+2 μg /f/d	4 days
	T_3+NE			2 μg+2 μg /f/d	4 days
	T_4+EP			2 μg+2 μg /f/d	4 days
	T_4+NE			2 μg+2 μg /f/d	4 days
(F)	Saline	*In vivo*	August (21°C)		4 days
	Metapyrone(Meta)			1 μg/g/d	4 days
	Corticosterone			2 μg /f/d	4 days
	Cortisol			2 μg /f/d	4 days
	Cortisone			2 μg /f/d	4 days
	Meta+Corticosterone			1 μg/g+2 μg/f/d	4 days
	Meta+Cortisol			1 μg/g+2 μg/f/d	4 days
	Meta+Cortisone			1 μg/g+2 μg/f/d	4 days

Results

In vivo and in vitro effect of epinephrine (EP) and norepinephrine (NE)

The data are presented in Tables 5:1, 5:2, 5:3 & 5:4; Figs. 5:1, 5:2, 5:3 & 5:4. Both *in vivo* and *in vitro* administration of EP and NE increased significantly the respiratory rate of all the tissues (liver, muscle, kidney and brain) during winter as well

as during summer/rainy months. Comparatively, EP was more potent than NE in muscle, while NE was more potent than EP in stimulating liver tissue respiration. Irrespective of the mode of treatments, the degree (% increase) of stimulation of liver, muscle and kidney respiration by epinephrine and norepinephrine was higher during winter as compared to that of summer/rainy months (Tables 5:1, 5:2, 5:3, and 5:4; Figs. 5:1, 5:2, 5:3, and 5:4).

In vivo and in vitro effects of corticosteroids

The data are presented in Tables 5:1, 5:2, 5:3, 5:4 and 5:5; Figs. 5:1, 5:2, 5:3, 5:4 and 5:5. *In vivo* and *in vitro* treatments of corticosterone, cortisol and cortisone significantly increased the respiratory rate of all the four tissues (liver, muscle, kidney and brain) during both winter and summer/rainy seasons, except during summer/rainy seasons where *in vivo* administration of cortisone had no effect on the respiratory rate of the brain tissue (Table 5:2; Fig. 5:2). As in the case of catecholamines, the responses of the tissues to the corticosteroids were higher during winter as compared to that of summer/rainy seasons.

Unlike in mammals, fishes lack a well defined adrenal gland. Therefore adrenalectomy is not possible. In order to assess the role of corticoids in the oxidative metabolism of fish, metapyrone (an inhibitor of 11β-hydroxylase) was used to block the synthesis of corticoid hormones. Administration of metapyrone significantly decreased the respiratory rate of all the tissues (liver, muscle, kidney and brain) as compared to the control group. When metapyrone was administered together with the corticoids, the hormones reversed the ill-effects of metapyrone (Table 5:5; Fig. 5:5).

In vivo and in vitro effects of catecholamines and thyroid hormones

The data presented in Tables 5:6, 5:7, 5:8 and 5:9; Figs. 5:6, 5:7, 5:8 and 5:9. In order to investigate the synergistic effect of thyroid hormones on the calorigenic action of the catecholamines, *in vivo* and *in vitro* effect of NE and EP were studied in the presence and absence of L-T_3 or L-T_4 during both the seasons.

Administration of EP and NE, irrespective of the seasons and mode of treatment (*in vivo/in vitro*), significantly increased the respiratory rate of all the tissues (Tables 5:6, 5:7, 5:8 and 5:9; Figs. 5:6, 5:7, 5:8 and 5:9). Unlike EP and NE, thyroid hormones (L-T_3 and L-T_4) had no significant effect on the respiratory rate of the tissues (except brain) during the winter month (Table 5:8; Fig. 5:8). However, during summer/rainy seasons, both L-T_3 and L-T_4 significantly stimulated the respiratory rate of all the four tissues (Tables 5:7 & 5:9; Figs. 5:7 & 5:9). Though thyroid hormones (L-T_3, L-T_4) were ineffective in stimulating tissue respiration during winter, they significantly potentiated the stimulatory effect of EP and NE both under *in vivo* and *in vitro* experiments (Tables 5:6 & 5:8; Figs. 5:6 & 5:8). During summer/rainy season, when the tissue homogenates were treated either with EP or NE in combination with L-T_3 or L-T_4, the respiratory rate of the tissues were further increased significantly as compared to the rate of tissue respiration stimulated separately by EP or NE and L-T_3 or L-T_4 (Tables 5:7 & 5:9; Figs. 5:7 & 5:9). The degree of tissue response (% stimulation) to the combined treatments of EP, NE and thyroid hormones varied with tissues and seasons

In vitro effects of epinephrine (EP and norepinephrine (NE) in the absence and presence of adrenergic antagonists

The data are presented in Table 5:10 and Fig. 5:10. *In vitro* treatment with EP or NE significantly increased the respiratory rate of all the tissues during summer/rainy

months. Incubation of the tissue homogenates either with propranolol (PROP) or prazosin (PRAZ) significantly reduced the basal rate of oxygen uptake of all the tissues (liver, muscle and kidney) as compared to control. Further, tissue homogenates incubated with PROP + PRAZ further decreased the tissue respiratory rate as compared with the propranolol or prazosin treated groups. PRAZ significantly blocked the stimulatory effect of both EP and NE in all the tissues except liver where PRAZ could not inhibit the stimulatory effect of EP. Further, PROP significantly blocked the stimulatory effect of both EP and NE in all the tissues. Pre-incubation of tissue homogenates with PRAZ+PROP significantly and further blocked the stimulatory effect of the catecholamines as compared to PROP + EP and PRAZ + EP as well as PROP + NE and PRAZ + NE treated groups.

Discussion

The earlier reports on the stimulatory effect of catecholamines on the whole body oxygen consumption in fish seem to be contradictory and confusing (Smith and Mathews, 1942; Bentley, 1965; Hoar, 1969; Banerjee and Joshi, 1981; Akbarsha, 1984; Richard, 1990). There is very limited information on the calorigenic role of corticoids in fish metabolism. To the best of our knowledge, this is the first study of its kind in which the calorigenic role of catecholamines (NE and EP) and major corticosteroids (cortisol, corticosterone and cortisone) has been investigated in the respiratory rate of a number of vital tissues using both *in vivo* and *in vitro* experiments conducted under natural climatic conditions during winter and summer/rainy months. Further, this is also the first study in which the involvement of different types of adrenergic receptors with regard to the calorigenic action of catecholamines in tissues of a fish has been examined using specific agonists and antagonists of the adrenergic receptors.

In general, *in vivo* and *in vitro* administration of catecholamines and corticoids significantly stimulated the respiratory rate of all the tissues both during winter and summer/rainy months. The only exception was the brain tissue respiration which was not stimulate by cortisone during summer/rainy months (Tables 5:1 & 5:2 and Figs. 5:1 & 5:2). These findings seem to suggest that both catecholamines and corticoids are actively involved in fish tissue respiration. Further, their calorigenic action seems to be temperature independent. *In vitro* stimulation of respiratory rate of all the tissues by these hormones (Tables 5:3 and 5:4 and Fig. 5:3 and 5:4) seems to suggest that both catecholamines and corticoids stimulate the respiratory rate of fish tissues directly. Therefore, on the basis of the present findings and reports available on amphibians and reptiles it is obvious to conclude that, due to their temperature and season-independent and direct calorigenic action, the catecholamine and the corticosteroid hormones play a major role in the regulation of the energy metabolism of the fish and other poikilothermic vertebrates. Further, catecholamines and corticoids (which are secreted under stressful conditions) might be of adaptive importance for ensuring basal metabolic rate required for the survival of the fish, *Clarias batrachus*. Administration of metapyrone (inhibitor of corticoids synthesis) significantly reduced the respiratory rate of all the tissues, and combined treatment of metapyrone and corticoids reversed the inhibitory effect of metapyrone on the rate of tissue respiration (Table 5:5, Fig. 5:5). These findings also indicate that indogenous corticoids are actively involved in the regulation of tissue respiration in *Clarias batrachus*. The direct and temperature-independent calorigenic action suggests that both catecholamines and corticoids might be acting as emergency hormones for the regulation of respiration in *Clarias batrachus*. In amphibians and reptiles also these hormones have been reported to act as an emergency hormones for the regulation of the oxidative metabolism (Gupta and Thapliyal, 1982; Thapliyal and Gupta, 1983; Gupta and (Thapliyal, 1983; Gupta, 1987; Gupta and Chakrabarty, 1990; Gupta and Thapliyal, 1991; Gupta and Deka-Borah, 1995; Gupta and Mahanta, 1997). In line with our findings, it has been

reported that catecholamines and corticoids increase the liver oxygen uptake in mammals (Goetsch and Macdonald, 1962; Bottom and Goetsch, 1968; Demonacus *et al.*, 1996) and activities of enzymes and tissue respiration in poikilotherms (Pickford *et al.*, 1970; Ignatius and Oommen, 1987; Josekumar and Oommen, 1988a, b; Hanke, 1990).

Thyroid hormones (L-T_3 & L-T_4) significantly potentiated the calorigenic action of EP and NE irrespective of water-temperatures and seasons. The degree of potentiation was higher with NE as compared to EP(Tables 5:6, 5:7, 5:8 & 5:9; Figs. 5:6, 5:7, 5:.8 & 5:9). It, thus, seems that the degree of calorigenic response of the tissues to the stimulatory effect of catecholamines is influenced by thyroid hormones. There are few reports that the calorigenic response of mammalian and reptilian tissues to norepinephrine is decreased by hypothyroidism and increased by hyperthyroidism (Warren, 1940; Hsieh *et al.*, 1966; Michel and LeBlanc, 1969; Kunos, 1977; Scrapace and Abrass, 1981; Wrutniak and Cabello, 1986). Thyroid hormones have also been reported to potentiate the calorigenic action of catecholamines in mammals at low temperature (Swanson, 1956; LeBlanc and Villemaire, 1970; Louw *et al.*, 1976; Fregly *et al.*, 1979; Gupta and Thapliyal, 1982; Klein *et al.*, 1984). In the present study the exogenous thyroid hormones were found to be ineffective during winter. However, the combined treatment of thyroid hormone and catecholamines significantly increased the tissue oxygen uptake as compared to NE or EP treated groups (Tables 5:6 & 5:8; fig. 5:6 & 5:8). These findings seem to suggest that thyroid hormones are indirectly involved in the regulation of the oxidative metabolism of the fish by potentiating the stimulatory effect of catecholamines on tissue respiration at low temperature during winter.

The mechanism of action of catecholamines in mammals is well studied. NE and EP stimulate tissue respiration of mammals through α- and β-adrenergic receptors

(Robinson *et al.*, 1972). In mammalian brown adipose tissue (BAT), the catecholamines have been reported to stimulate 80 per cent of respiration through the β-adrenergic receptors and 20 per cent via the α-adrenergic receptors (Hagen and Hagen, 1964; Szillart, 1981; Mohell *et al.*, 1981, 1983). It has also been reported that the calorigenic action of NE via β-adrenergic receptors is mediated through a cAMP-dependent mechanism, while α-adrenergic receptors stimulated the hormonal response through Ca^{++}-dependent mechanism (Wikberg, 1979; Fain and Garcia-Sainz, 1980 Reid *et al.*, 1991; Perry and Reid, 1993). The α_1-adrenergic stimulation of respiration also leads to plasma-membrane depolarization and increased Na^{+}-K^{+}-ATPase activity (Horwitz and Eaton, 1975; Fink and William, 1976; Wikberg, 1979; Nedergaard and Lindberg, 1979, 1982). Pre-incubation of tissue homogenates with propranolol (PROP) or Prazosin (PRAZ) significantly reduced the stimulatory effect of NE and EP. PROP+PRAZ treatment completely blocked the stimulatory effect of both NE and EP (Table 5:10; Fig. 5:10). These findings clearly indicate the involvement of both α_1-and β_1-adrenergic receptors in regulation of the rate of tissue respiration in *Clarias batrachus*. The β_1-adrenergic receptors seem to be more important than the α_1-adrenergic receptors during summer/rainy months. Both types of the adrenergic receptors are also involved in the calorigenic action of epinephrine and norepinephrine in amphibians (Gupta and Mahanta, 1997; Mahanta and Gupta, 1998). Present findings suggest that β_1-adrenergic agonist is more effective in liver tissue and α_1-adrenergic agonist in muscle tissue. In kidney, both adrenergic receptors seems to be equally important in stimulating the rate of tissue oxygen uptake. It may be concluded that the second messengers involved in the calorigenic actions of catecholamines might be similar to that reported in mammals.

On the basis of the present findings, it may be concluded that (i) catecholamines and corticoids are directly involved in the regulation of the oxidative metabolism in fish as emergency hormones particularly at low temperature, (ii) the

calorigenic actions of EP and NE seems to be produced via both α- and β-adrenergic receptors, and (iii) thyroid hormones potentiate the calorigenic action of the catecholamines in the fish at low temperature. Catecholamines and corticoids seems to be of adaptational importance for maintaining basal metabolic rate in order to ensure survival of the fish particularly under stressful conditions of low temperature (Bostian and Nordeen, 1991). The proposed direct calorigenic action of corticoids in fish (present study), amphibians (Gupta and Mahanta, 1997) and reptiles (Gupta and Thapliyal, 1983) has been strongly supported by a recent study in which corticoids directly increased the activities of mitochondrial oxidative enzymes in mammal (Demonaccus *et al.*, 1996).

Table 5:1 - In vivo effects of adrenal hormones on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Saline (Control)	2.88±0.07	1.12±0.05	2.69±0.08	5.26±0.09
Epinephrine	4.14±0.11[c]	2.63±0.03[c]	3.69±0.05[c]	5.87±0.05[b]
Norepinephrine	4.33±0.09[c]	2.24±0.11[c]	3.78±0.07[c]	5.90±0.04[c]
Cortisol	3.88±0.16[b]	2.53±0.08[c]	4.17±0.03[c]	5.740.08[b]
Cortisone	3.53±0.12[b]	2.21±0.10[c]	3.72±0.08[c]	5.52±0.04[a]
Corticosterone	3.78±0.03[c]	2.37±0.06[c]	3.88±0.14[c]	5.61±0.07[a]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

Table 5:2 - In vivo effects of adrenal hormones on the rate of tissue respiration of male *Clarias batrachus* during summer (Av water temp. : 20° C).

Treatments	Rate of Tissue Oxygen Consumption (μl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Saline (Control)	4.71±0.08	2.72±0.05	4.10±0.05	4.30±0.07
Epinephrine	5.68±0.05[c]	3.72±0.08[c]	4.97±0.05[c]	5.04±0.07[c]
Norepinephrine	5.84±0.07[c]	3.59±0.12[c]	4.81±0.07[c]	4.91±0.14[b]
Cortisol	5.58±0.03[c]	3.85±0.10[c]	4.94±0.03[c]	4.87±0.05[c]
Cortisone	5.45±0.11[b]	3.56±0.05[c]	4.62±0.08[b]	4.33±0.09
Corticosterone	5.39±0.08[c]	3.46±0.04[c]	4.59±0.09[b]	4.68±0.03[b]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[b, c] Differ from respective controls : $P < 0.01$ and 0.001, respectively.

Table 5:3 - In vitro effects of adrenal hormones on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Control	2.69±0.06	0.89±0.08	2.53±0.05	5.01±0.04
Epinephrine	4.17±0.07[c]	2.01±0.05[c]	3.66±0.07[c]	5.81±0.09[c]
Norepinephrine	4.33±0.06[c]	1.95±0.03[c]	3.88±0.11[c]	5.84±0.06[c]
Cortisol	3.98±0.12[c]	1.44±0.07[b]	4.26±0.03[c]	5.71±0.03[c]
Cortisone	3.49±0.03[c]	1.15±0.06[a]	3.62±0.07[c]	5.32±0.07[b]
Corticosterone	3.88±0.09[c]	1.34±0.04[b]	3.94±0.09[c]	5.74±0.11[c]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

Table 5:4 - In vitro effects of adrenal hormones on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 20° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Control	4.81±0.12	2.85±0.02	4.01±0.03	5.07±0.07
Epinephrine	5.29±0.06[a]	3.85±0.06[c]	5.36±0.05[c]	5.97±0.07[c]
Norepinephrine	5.55±0.05[b]	3.46±0.04[c]	5.10±0.07[c]	5.87±0.05[c]
Cortisol	5.39±0.03[b]	3.43±0.05[c]	4.81±0.09[c]	5.77±0.08[c]
Cortisone	5.71±0.11[b]	3.55±0.08[c]	4.78±0.04[c]	5.74±0.06[c]
Corticosterone	5.45±0.07[b]	3.21±0.09[a]	3.88±0.05	5.52±0.10[a]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

Table 5:5 - In vivo effects of corticosteroids and metapyrone on the rate of tissue respiration of male Clarias batrachus during summer(Av. water temp.:21° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Saline (Control)	4.84±0.09	2.98±0.10	3.82±0.05	5.20±0.07
Corticosterone (Cort)	5.26±0.05[a]	3.53±0.07[b]	4.52±0.02[c]	5.61±0.05[b]
Cortisol	5.48±0.05[c]	3.98±0.09[c]	4.87±0.04[c]	5.81±0.03[c]
Cortisone	5.45±0.07[a]	3.62±0.05[b]	4.62±0.08[c]	4.81±0.07
Metapyrone	4.49±0.04[a]	2.50±0.07[b]	3.43±0.08[b]	4.84±0.05[b]
Cort + Metapyrone	5.10±0.02[a,d]	3.27±0.03[a,e]	4.20±0.03[c,f]	5.42±0.02[a,d]
Cortisol + Metapyrone	5.23±0.03[b,g]	3.69±0.06[c,g]	4.55±0.07[c,h,]	5.45±0.07[a,h]
Cortisone + Metapyrone	5.16±0.06[a,k]	3.33±0.04[a,k]	4.36±0.05[c,k]	4.97±0.05

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

a, b, c Differ from the saline treated control group : $P < 0.05$, 0.01 and 0.001, respectively.

d, e, f Differ from the value of group treated with corticosterone : $P < 0.05$, 0.01 and 0.001, respectively.

g, h Differ from the value of the group treated with cortisol : $P < 0.05$ and 0.01, respectively.

j, k Differ from the value of the group treated with cortisone : $P < 0.05$ and 0.01, respectively.

Table 5:6 - In vivo effects of thyroid hormones and catecholamines on the rate of tissue respiration of male *Clarias batrachus* during winter(Av. water temp.:9.6° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Saline	2.88±0.07	1.12±0.05	2.69±0.08	5.26±0.09
T_3	2.82±0.05	1.18±0.09	2.72±0.05	5.10±0.11
T_4	2.85±0.07	0.96±0.07	2.66±0.06	5.04±0.07
Epinephrine	4.14±0.11[c]	2.63±0.03[c]	3.69±0.05[c]	5.87±0.05[b]
Norepinephrine	4.33±0.09[c]	2.24±0.11[c]	3.78±0.07[c]	5.90±0.04[c]
T_3 + Epinephrine	4.49±0.04[c,d]	3.49±0.05[c,f]	4.23±0.16[c,d]	6.13±0.03[c,e]
T_3 + Norepinephrine	4.91±0.10[c,h]	2.56±0.04[c,g]	4.55±0.11[c,h]	6.22±0.07[c,h]
T_4 + Epinephrine	4.78±0.03[c,e]	2.82±0.05[c,d]	4.14±0.02[c,f]	6.29±0.10[b,e]
T_4 + Norepinephrine	5.01±0.12[c,h]	2.63±0.06[c,g]	4.71±0.20[c,h]	6.32±0.13[b,g]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

b, c Differ from the control group : $P < 0.01$ and 0.001, respectively.

d, e, f Differ from the group treated with epinephrine : $P < 0.05$, 0.01 and 0.001, respectively.

g, h Differ from the group treated with norepinephrine : $P < 0.05$ and 0.01, respectively.

Table 5:7 - In vivo effects of thyroid hormones and catecholamines on the rate of tissue respiration of male *Clarias batrachus* during summer(Av. water temp. : 20° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Saline	4.71±0.08	2.72±0.05	4.10±0.05	4.30±0.07
T_3	5.61±0.06^{c}	3.27±0.07^{c}	4.65±0.05^{c}	4.75±0.08^{b}
T_4	5.45±0.12^{b}	3.49±0.09^{c}	4.84±0.07^{c}	4.97±0.09^{b}
Epinephrine	5.68±0.05^{c}	3.72±0.08^{c}	4.97±0.05^{c}	5.04±0.07^{c}
Norepinephrine	5.84±0.07^{c}	3.59±0.12^{c}	4.81±0.07^{c}	4.91±0.14^{b}
T_3 + Epinephrine	6.03±0.04^{c,e}	4.20±0.09^{c,e}	5.74±0.09^{c,f}	5.58±0.03^{c,d}
T_3 + Norepinephrine	6.26±0.02^{c,h}	3.98±0.05^{c,g}	5.52±0.12^{c,h}	5.42±0.09^{c,g}
T_4 + Epinephrine	5.90±0.04^{c,d}	4.04±0.03^{c,d}	5.84±0.06^{c,f}	5.39±0.05^{c,e}
T_4 + Norepinephrine	6.22±0.07^{c,h}	4.36±0.04^{c,j}	5.65±0.08^{c,j}	5.45±0.10^{c,g}

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

^{b,c} Differ from the control group : $P < 0.01$ and 0.001, respectively.

^{d,e,f} Differ from the group treated with epinephrine : $P < 0.05$, 0.01 and 0.001, respectively.

^{g,h,j} Differ from the group treated with norepinephrine : $P < 0.05$, 0.01 and 0.001, respectively.

Table 5:8 - In vitro effects of thyroid hormones and catecholamines on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp.: 9.6° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Control	2.69±0.06	0.89±0.08	2.53±0.05	5.01±0.04
T_3	2.72±0.09	0.79±0.02	2.56±0.05	5.65±0.06^{c}
T_4	2.63±0.12	0.75±0.07	2.60±0.09	5.87±0.05^{c}
Epinephrine	4.17±0.07^{c}	2.01±0.05^{c}	3.66±0.07^{c}	5.81±0.09^{c}
Norepinephrine	4.33±0.06^{c}	1.95±0.03^{c}	3.88±0.11^{c}	5.84±0.06^{c}
T_3 + Epinephrine	4.71±0.05^{c,f}	2.31±0.04^{c,e}	4.14±0.15^{c,d}	6.42±0.09^{c,e}
T_3 + Norepinephrine	4.84±0.11^{c,h}	2.08±0.02^{c,g}	4.88±0.06^{c,i}	6.61±0.07^{c,i}
T_4 + Epinephrine	4.62±0.09^{c,e}	2.24±0.03^{c,e}	4.49±0.08^{c,f}	6.64±0.11^{c,e}
T_4 + Norepinephrine	4.91±0.03^{c,i}	2.31±0.07^{c,h}	4.81±0.12^{c,h}	6.80±0.14^{c,i}

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

^{c} Differs from the control group : $P < 0.001$.

^{d,e,f} Differ from the group treated with epinephrine : $P < 0.05$, 0.01 and 0.001, respectively.

^{g,h,i} Differ from the group treated with norepinephrine : $P < 0.05$, 0.01 and 0.001, respectively.

Table 5:9 - In vitro effects of thyroid hormones and catecholamines on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp.:20° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Control	4.81±0.12	2.85±0.02	4.01±0.03	5.07±0.07
T_3	5.52±0.04[b]	3.53±0.07[c]	4.68±0.12[b]	5.61±0.06[b]
T_4	5.45±0.03[b]	3.40±0.16[a]	4.81±0.07[c]	5.71±0.07[c]
Epinephrine	5.29±0.08[a]	3.85±0.06[c]	5.36±0.05[c]	5.97±0.07[c]
Norepinephrine	5.55±0.05[b]	3.46±0.04[c]	5.10±0.07[c]	5.87±0.05[c]
T_3 + Epinephrine	5.61±0.06[c,d]	4.17±0.09[c,d]	5.68±0.05[c,e]	6.29±0.10[c,d]
T_3 + Norepinephrine	5.74±0.04[c,f]	3.69±0.05[c,f]	5.42±0.05[c,g]	6.13±0.03[c,g]
T_4 + Epinephrine	5.52±0.04[b,d]	4.17±0.03[c,e]	5.55±0.02[c,d]	6.45±0.14[c,d]
T_4 + Norepinephrine	5.81±0.06[c,f]	4.36±0.10[c,h]	5.36±0.06[c,f]	6.35±0.12[c,g]

All values are expressed as Mean ± Standard Error (S.E.). N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e] Differ from the group treated with epinephrine : $P < 0.05$ and 0.01, respectively.

[f, g, h] Differ from the group treated with norepinephrine : $P < 0.05$, 0.01 and 0.001, respectively.

Table 5:10 - In vitro effects of adrenergic agonists and antagonists on the rate of tissue respiration of male Clarias batrachus during summer (Av. water temp. : 20° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)		
	Liver	Muscle	Kidney
Control	4.81±0.12	2.85±0.02	4.01±0.03
Epinephrine (EP)	5.29±0.08[a]	3.85±0.06[c]	5.36±0.05[c]
Norepinephrine (NE)	5.55±0.05[b]	3.46±0.04[c]	5.10±0.07[c]
Propranolol (PROP)	4.23±0.08[b]	2.27±0.05[c]	3.49±0.09[b]
Prazosin (PRAZ)	4.49±0.04[a]	2.44±0.08[b]	3 78±0.07[a]
PROP + PRAZ	3.59±0.06[c]	2.02±0.07[c]	3.27±0.11[c]
PROP + EP	5.01±0.04[d]	3.08±0.03[c,e]	4.87±0.10[c,d]
PRAZ + EP	5.13±0.04[a]	3.36±0.05[c,e]	5.01±0.03[c,e]
PROP + PRAZ + EP	3.82±0.12[b,e]	2.23±0.07[c,e]	3.69±0.09[a,e]
PROP + NE	5.10±0.07[a,g]	3.30±0.05[c,f]	4.91±0.02[c,f]
PRAZ + NE	5.20±0.09[a,f]	3.21±0.03[c,g]	4.87±0.04[c,f]
PROP + PRAZ + NE	3.98±0.10[b,h,m]	2.56±0.10[a,h,l]	3.88±0.08[h,m]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from the saline treated control group : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e] Differ from the value of the group treated with EP : $P < 0.01$ and 0.001, respectively.

[f, g, h] Differ from the value of the group treated with NE : $P < 0.05$, 0.01 and 0.001, respectively.

[k] Differs from PROP + EP or PRAZ + EP : $P<0.001$.

[l, m] Differ from PROP + NE or PRAZ + NE : $P<0.01$ and 0.001, respectively.

Figure 5:1 - In vivo effects of adrenal hormones on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

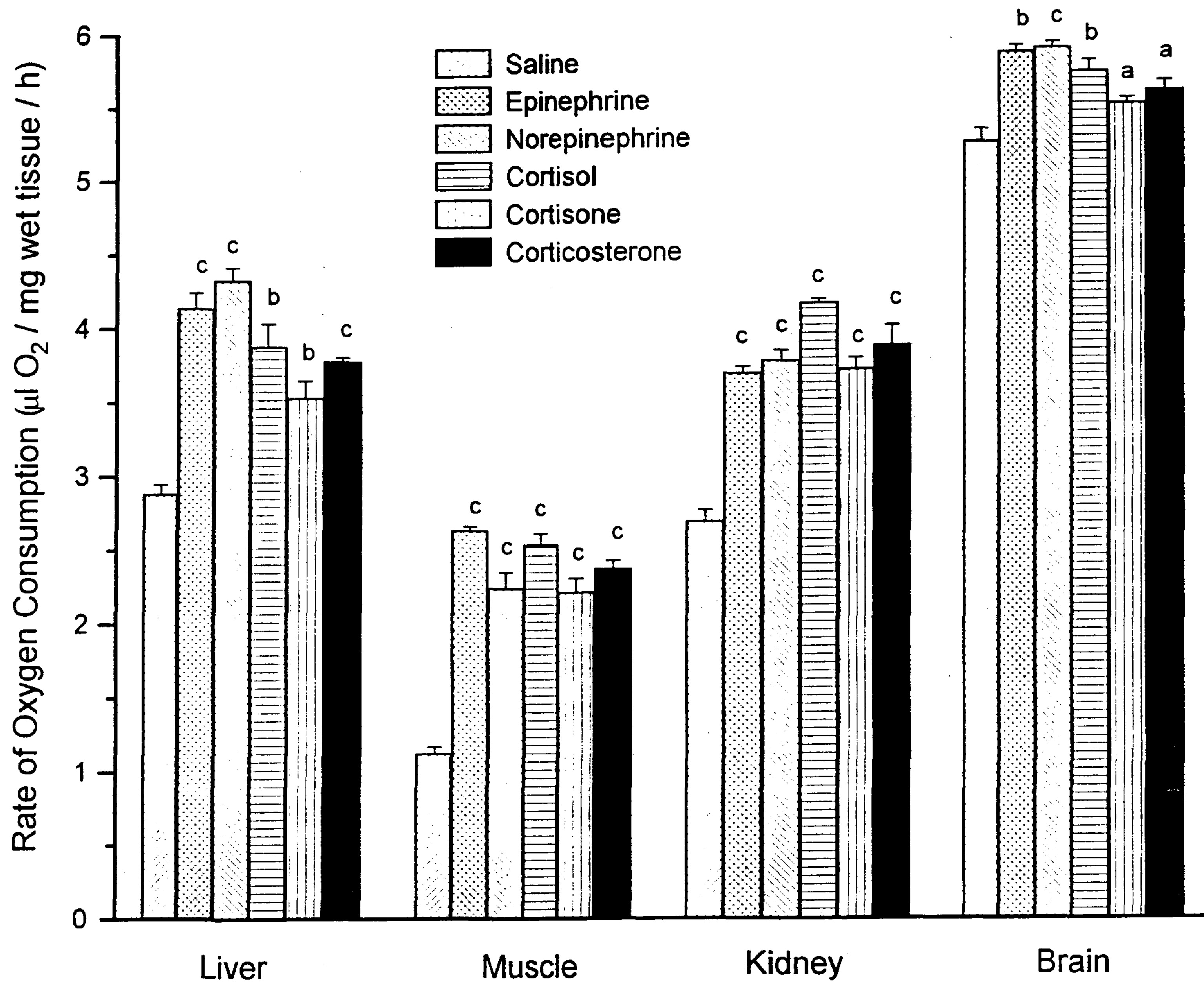
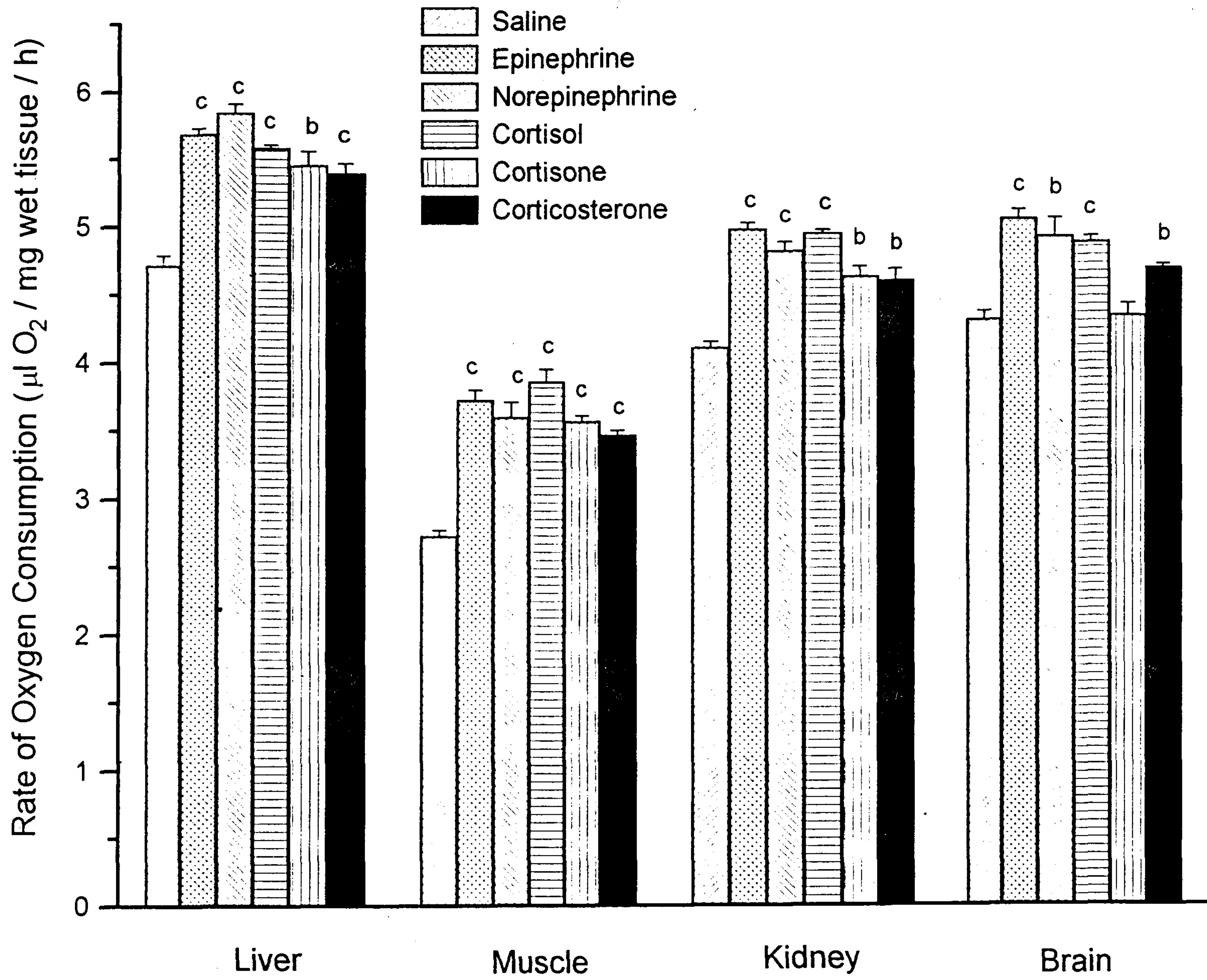

Rate of Oxygen Consumption (µl O_2 / mg wet tissue / h)
Saline
Epinephrine
Norepinephrine
Cortisol
Cortisone
Corticosterone
0
1
2
3
4
5
6
c
c
b
b
c
c
c
c
c
c
c
c
c
c
c
c
b
c
b
a
a
Liver
Muscle
Kidney
Brain

Figure 5:2 - In vivo effects of adrenal hormones on the rate of tissue respiration of male *Clarias batrachus* during summer (Av water temp. : 20° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[b, c] Differ from respective controls : $P < 0.01$ and 0.001, respectively.



Saline
Epinephrine
Norepinephrine
Cortisol
Cortisone
Corticosterone
Rate of Oxygen Consumption (μl O2 / mg wet tissue / h)
0
1
2
3
4
5
6
c
c
c
b
c
c
c
c
c
c
c
c
c
b
b
c
b
c
b
Liver
Muscle
Kidney
Brain

Figure 5:3 - In vitro effects of adrenal hormones on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

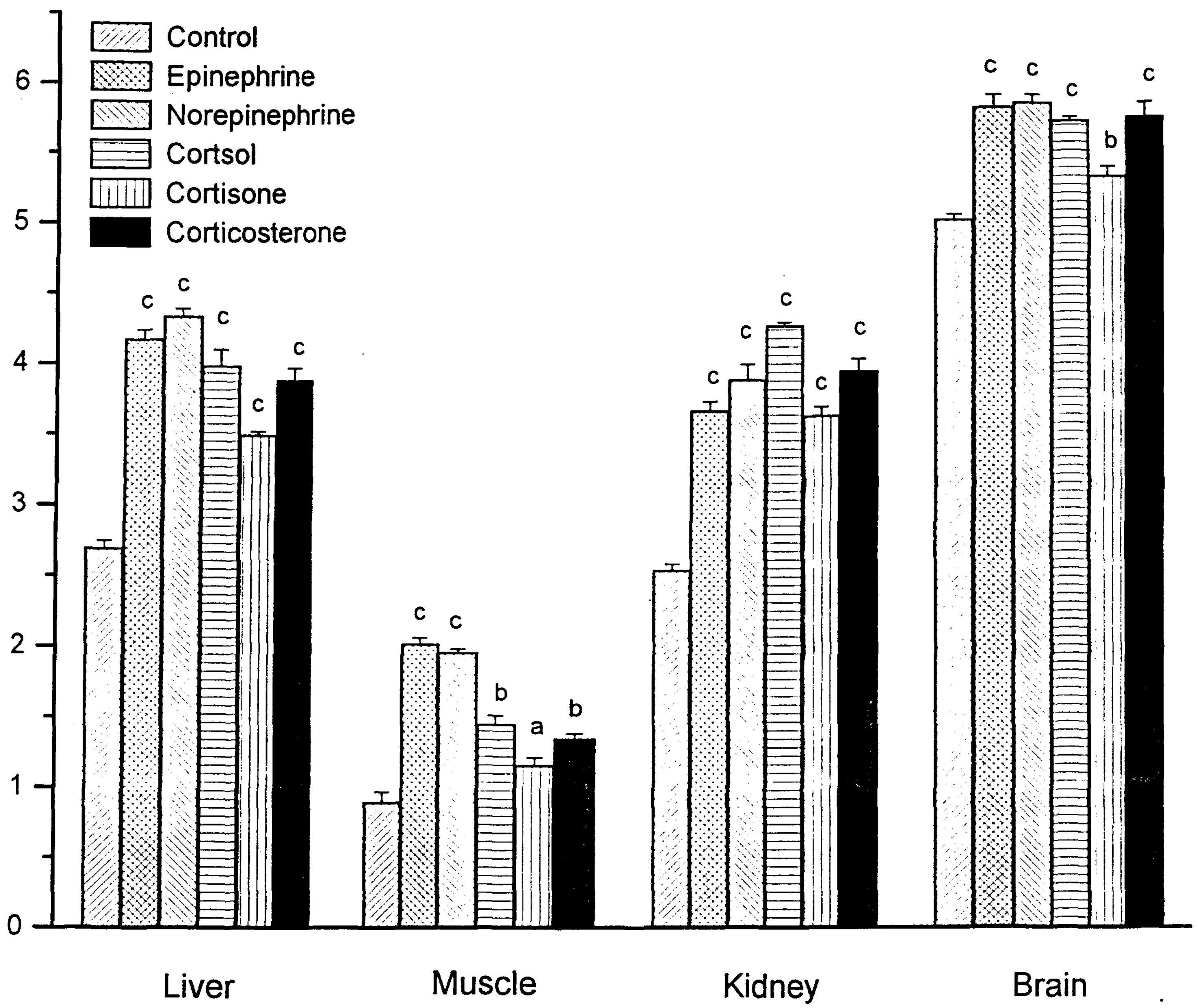

Rate of Oxygen Consumption (μl O_2 / mg wet tissue / h)
0
1
2
3
4
5
6
Control
Epinephrine
Norepinephrine
Cortsol
Cortisone
Corticosterone
Liver
Muscle
Kidney
Brain

Figure 5:4 - In vitro effects of adrenal hormones on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp. : 20° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from respective controls : $P < 0.05$, 0.01 and 0.001, respectively.

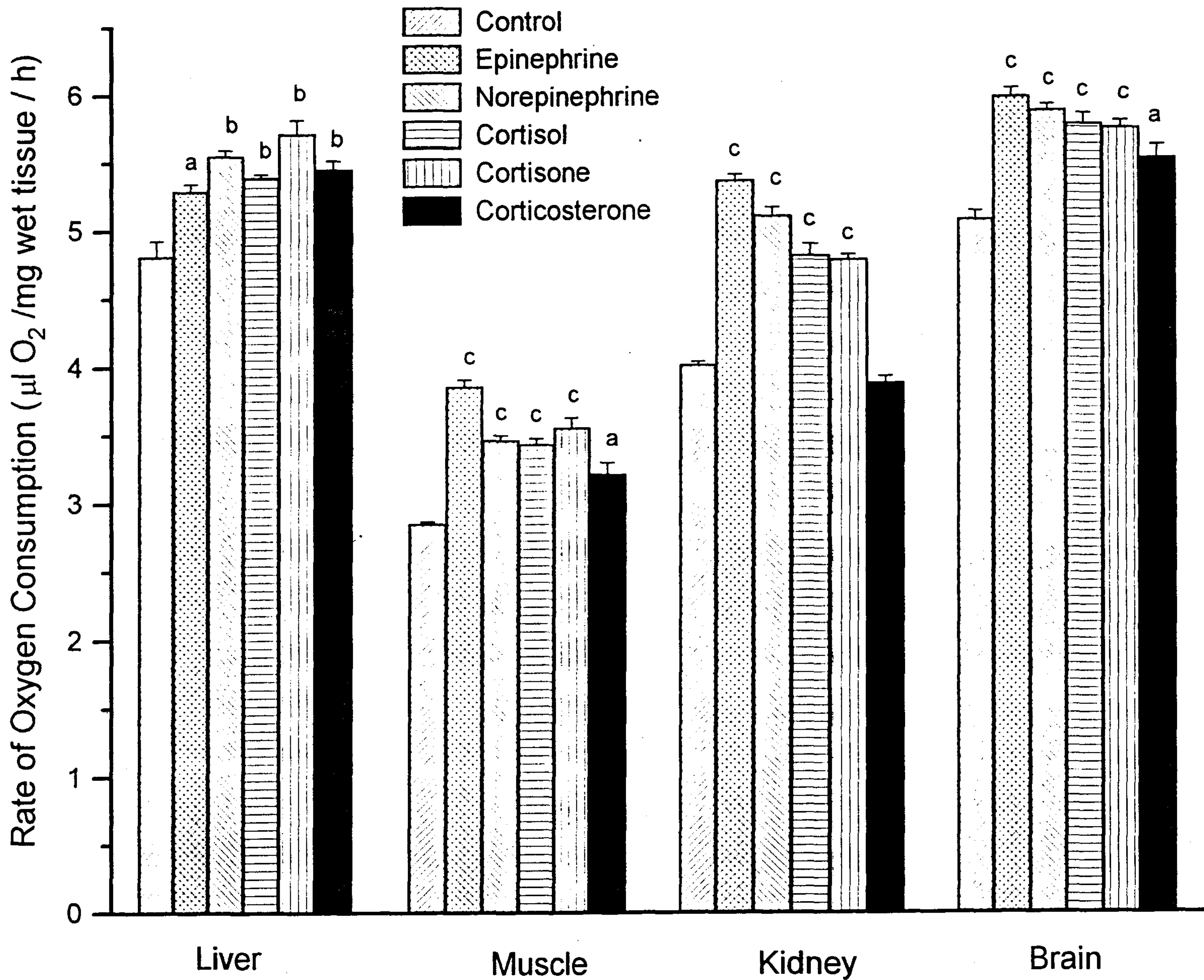

Control
Epinephrine
Norepinephrine
Cortisol
Cortisone
Corticosterone
Rate of Oxygen Consumption (μl O_2 /mg wet tissue / h)
0
1
2
3
4
5
6
a
b
b
b
b
c
c
c
c
a
c
c
c
c
c
c
c
c
a
Liver
Muscle
Kidney
Brain

Figure 5:5 - In vivo effects of corticosteroids and metapyrone on the rate of tissue respiration of male Clarias batrachus during summer(Av. water temp..20° C).

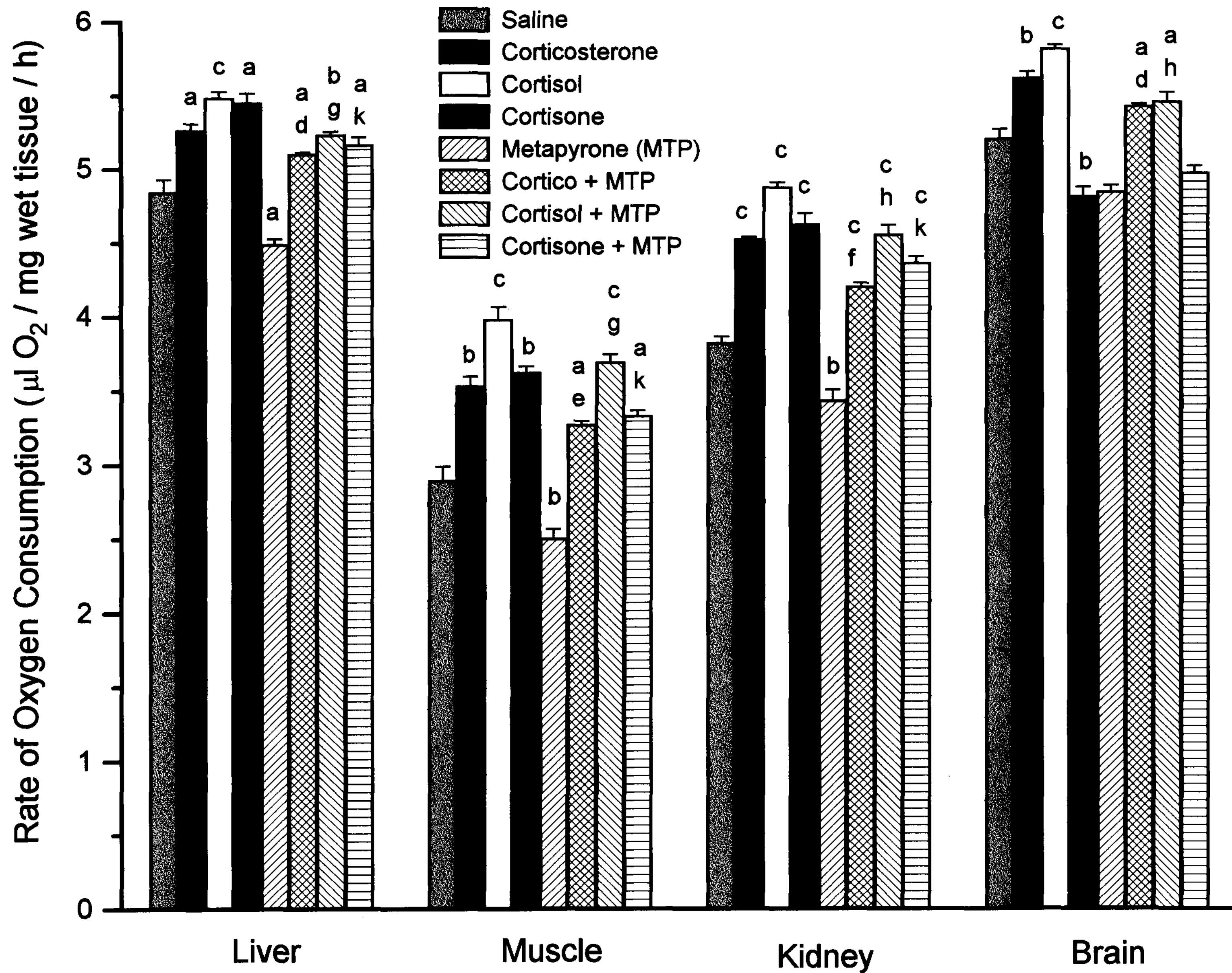
All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from the saline treated control group : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e, f] Differ from the value of group treated with corticosterone : $P < 0.05$, 0.01 and 0.001, respectively.

[g, h] Differ from the value of the group treated with cortisol : $P < 0.05$ and 0.01, respectively.

[j, k] Differ from the value of the group treated with cortisone : $P < 0.05$ and 0.01, respectively.



Rate of Oxygen Consumption (μl O_2 / mg wet tissue / h)
0
1
2
3
4
5
6
Saline
Corticosterone
Cortisol
Cortisone
Metapyrone (MTP)
Cortico + MTP
Cortisol + MTP
Cortisone + MTP
Liver
Muscle
Kidney
Brain

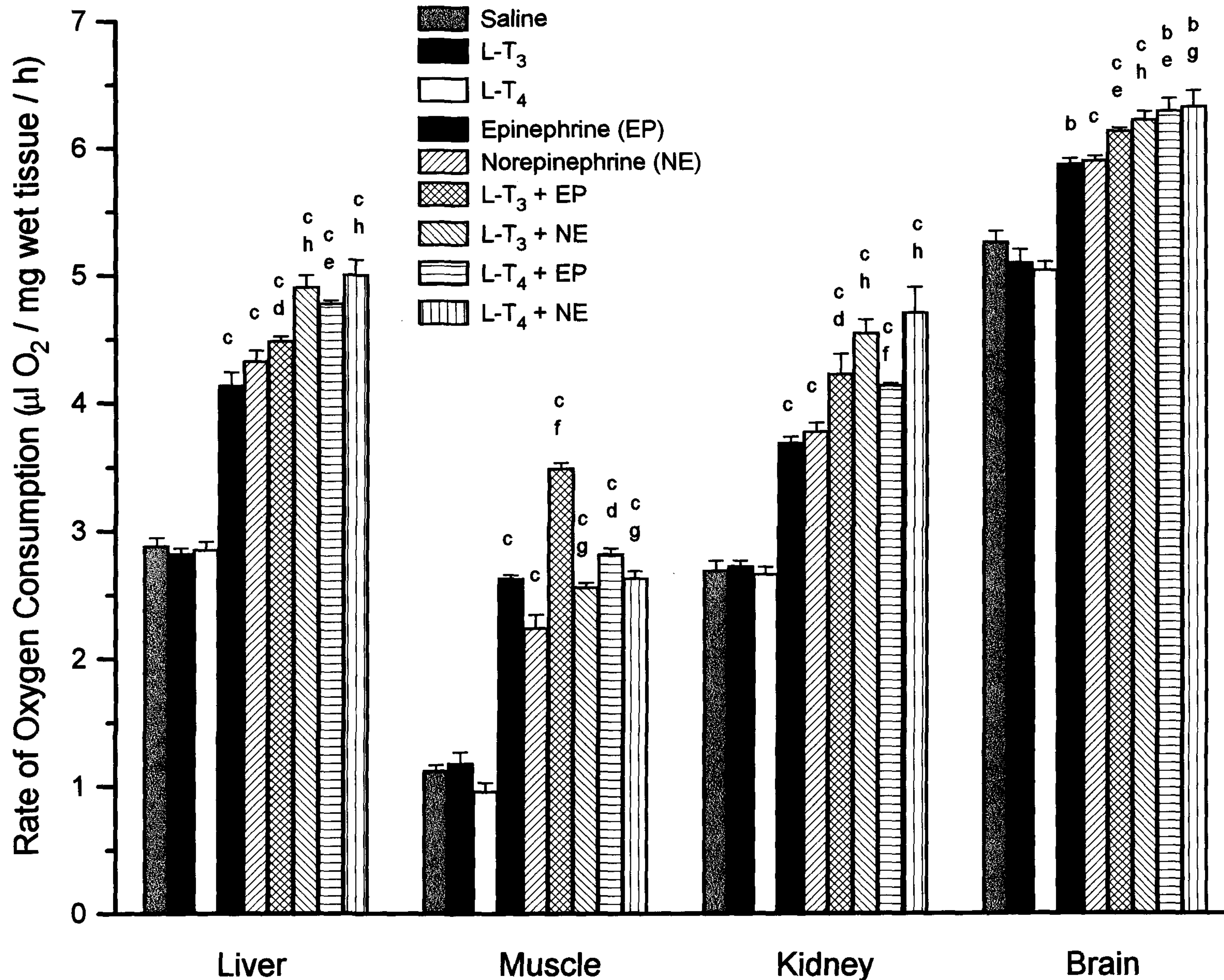
Figure 5:6 - In vivo effects of thyroid hormones and catecholamines on the rate of tissue respiration of male *Clarias batrachus* during winter(Av. water temp.:9.6° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[b, c] Differ from the control group : $P < 0.01$ and 0.001, respectively.

[d, e, f] Differ from the group treated with epinephrine : $P < 0.05$, 0.01 and 0.001, respectively.

g, h Differ from the group treated with norepinephrine : $P < 0.05$ and 0.01, respectively.



Saline
L-T_3
L-T_4
Epinephrine (EP)
Norepinephrine (NE)
L-T_3 + EP
L-T_3 + NE
L-T_4 + EP
L-T_4 + NE
Rate of Oxygen Consumption (µl O_2 / mg wet tissue / h)
0
1
2
3
4
5
6
7
Liver
Muscle
Kidney
Brain

Figure 5:7 - In vivo effects of thyroid hormones and catecholamines on the rate of tissue respiration of male *Clarias batrachus* during summer(Av. water temp. : 20° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

$^{b, c}$ Differ from the control group : $P < 0.01$ and 0.001, respectively.

$^{d, e, f}$ Differ from the group treated with epinephrine : $P < 0.05$, 0.01 and 0.001, respectively.

$^{g, h, j}$ Differ from the group treated with norepinephrine : $P < 0.05$, 0.01 and 0.001, respectively.

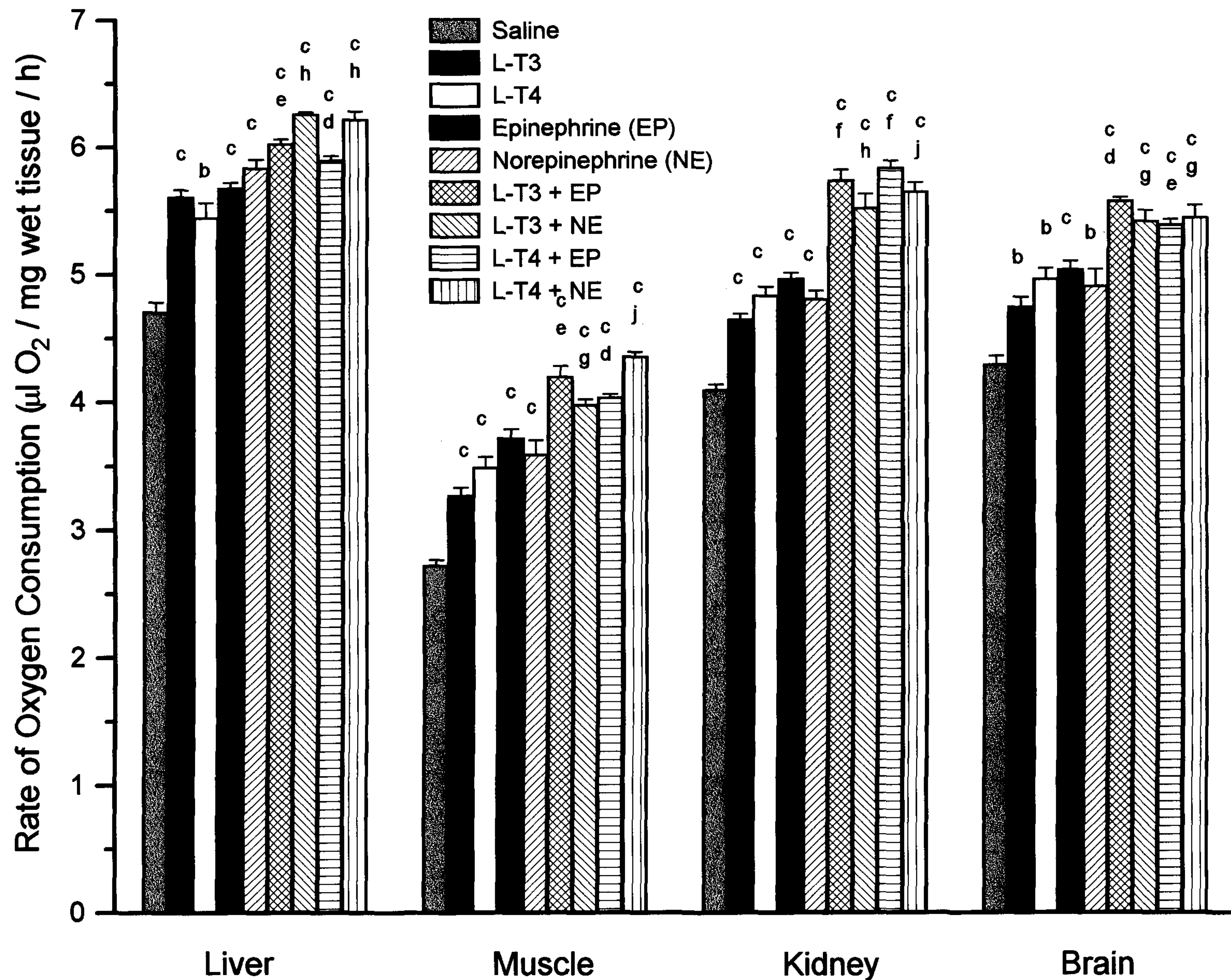

Rate of Oxygen Consumption (μl O2 / mg wet tissue / h)
Saline
L-T3
L-T4
Epinephrine (EP)
Norepinephrine (NE)
L-T3 + EP
L-T3 + NE
L-T4 + EP
L-T4 + NE
Liver
Muscle
Kidney
Brain

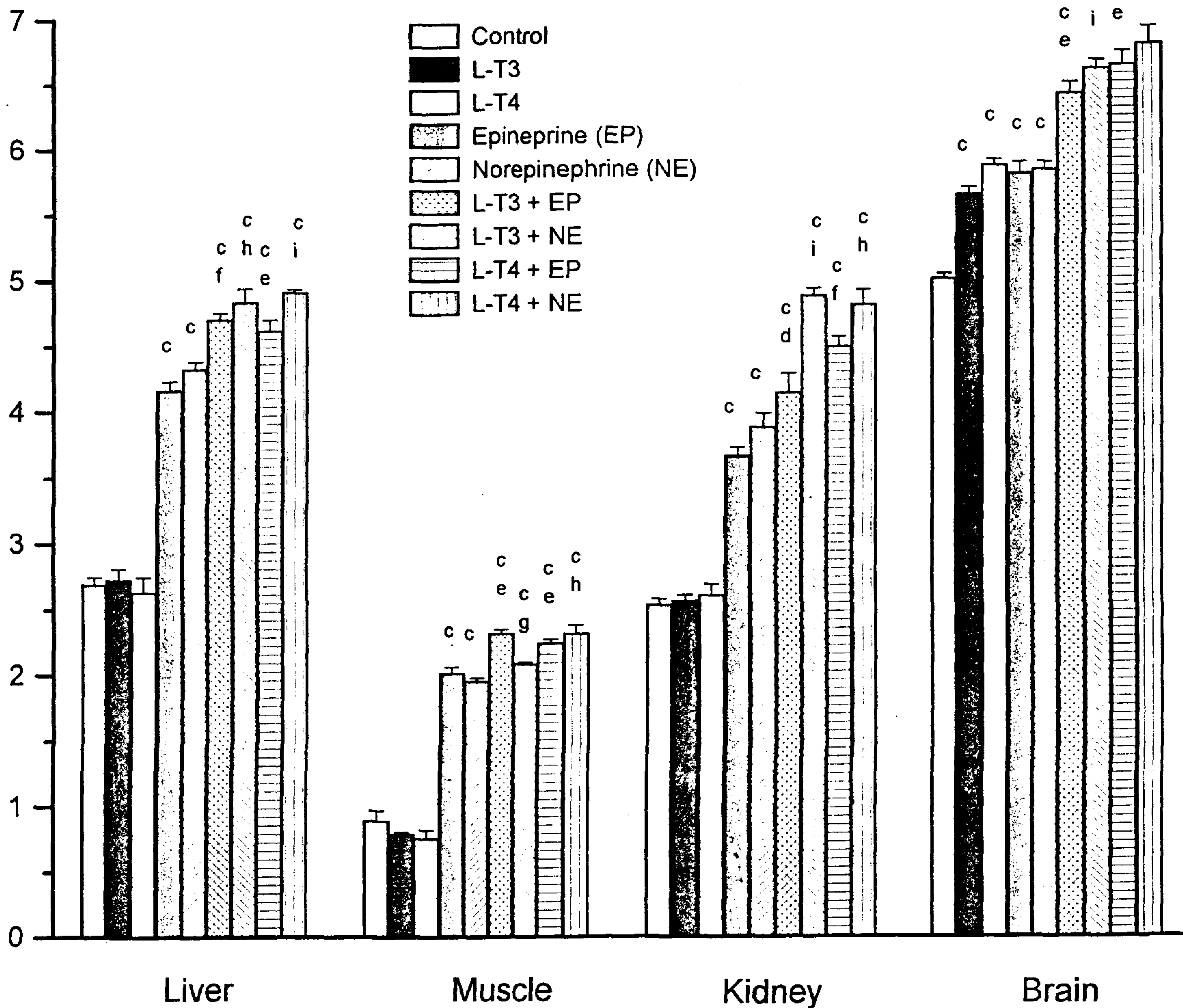
Figure 5:8 - In vitro effects of thyroid hormones and catecholamines on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp.: 9.6° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[c] Differs from the control group : $P < 0.001$.

[d, e, f] Differ from the group treated with epinephrine : $P < 0.05$, 0.01 and 0.001, respectively.

[g, h, i] Differ from the group treated with norepinephrine : $P < 0.05$, 0.01 and 0.001, respectively.



Rate of Oxygen Consumption (μl O_2 /mg wet tissue / h)
0
1
2
3
4
5
6
7
Control
L-T3
L-T4
Epineprine (EP)
Norepinephrine (NE)
L-T3 + EP
L-T3 + NE
L-T4 + EP
L-T4 + NE
Liver
Muscle
Kidney
Brain

Figure 5:9 - In vitro effects of thyroid hormones and catecholamines on the rate of tissue respiration of male *Clarias batrachus* during summer (Av. water temp.:20° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

$^{a, b, c}$ Differ from respective controls : P < 0.05, 0.01 and 0.001, respectively.

$^{d, e}$ Differ from the group treated with epinephrine : P < 0.05 and 0.01, respectively.

$^{f, g, h}$ Differ from the group treated with norepinephrine : P < 0.05, 0.01 and 0.001, respectively.

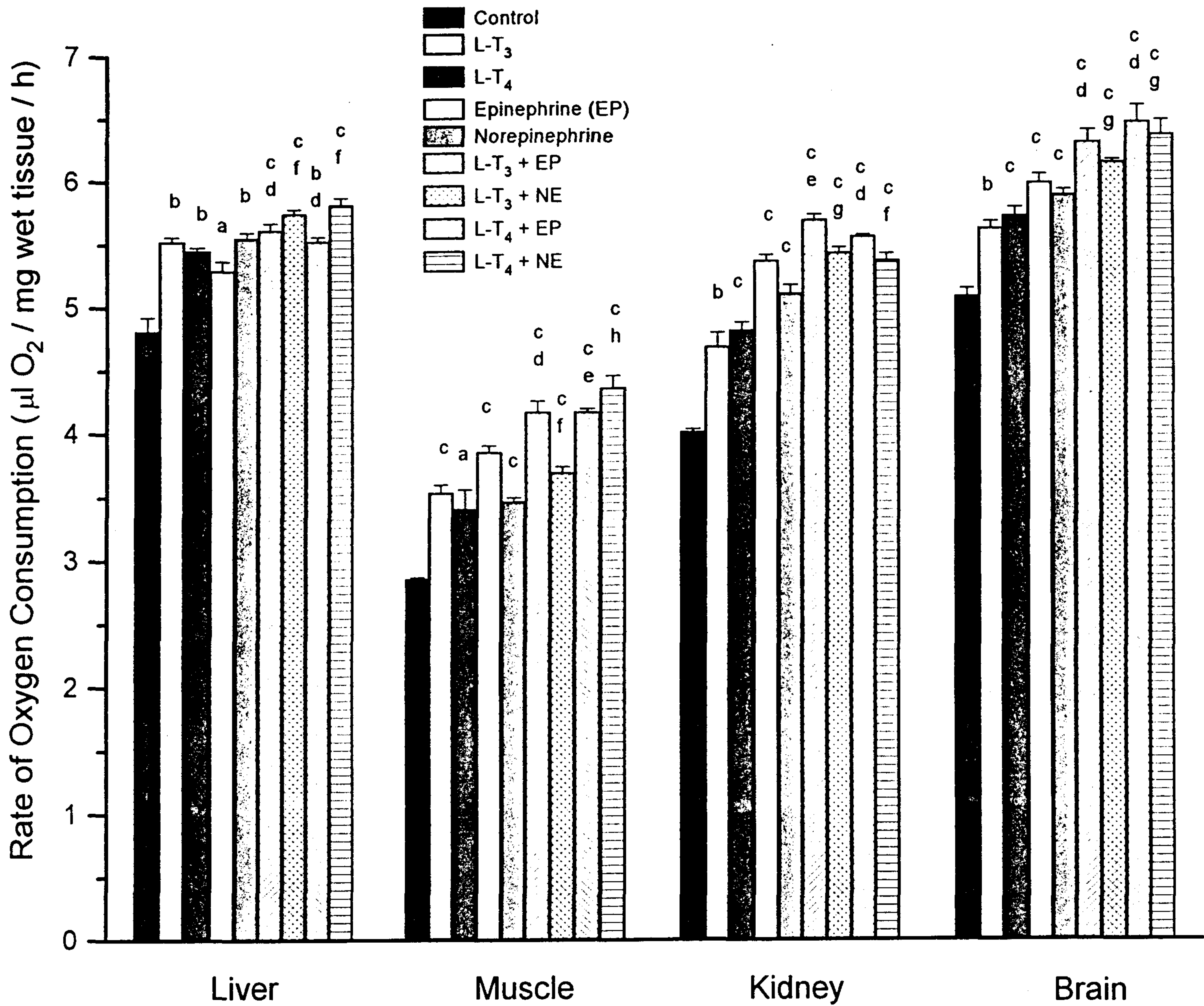

Control
L-T3
L-T4
Epinephrine (EP)
Norepinephrine
L-T3 + EP
L-T3 + NE
L-T4 + EP
L-T4 + NE
Rate of Oxygen Consumption (µl O2 / mg wet tissue / h)
0
1
2
3
4
5
6
7
Liver
Muscle
Kidney
Brain

Figure 5:10 - In vitro effects of adrenergic agonists and antagonists on the rate of tissue respiration of male Clarias batrachus during summer (Av. water temp. : 20° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

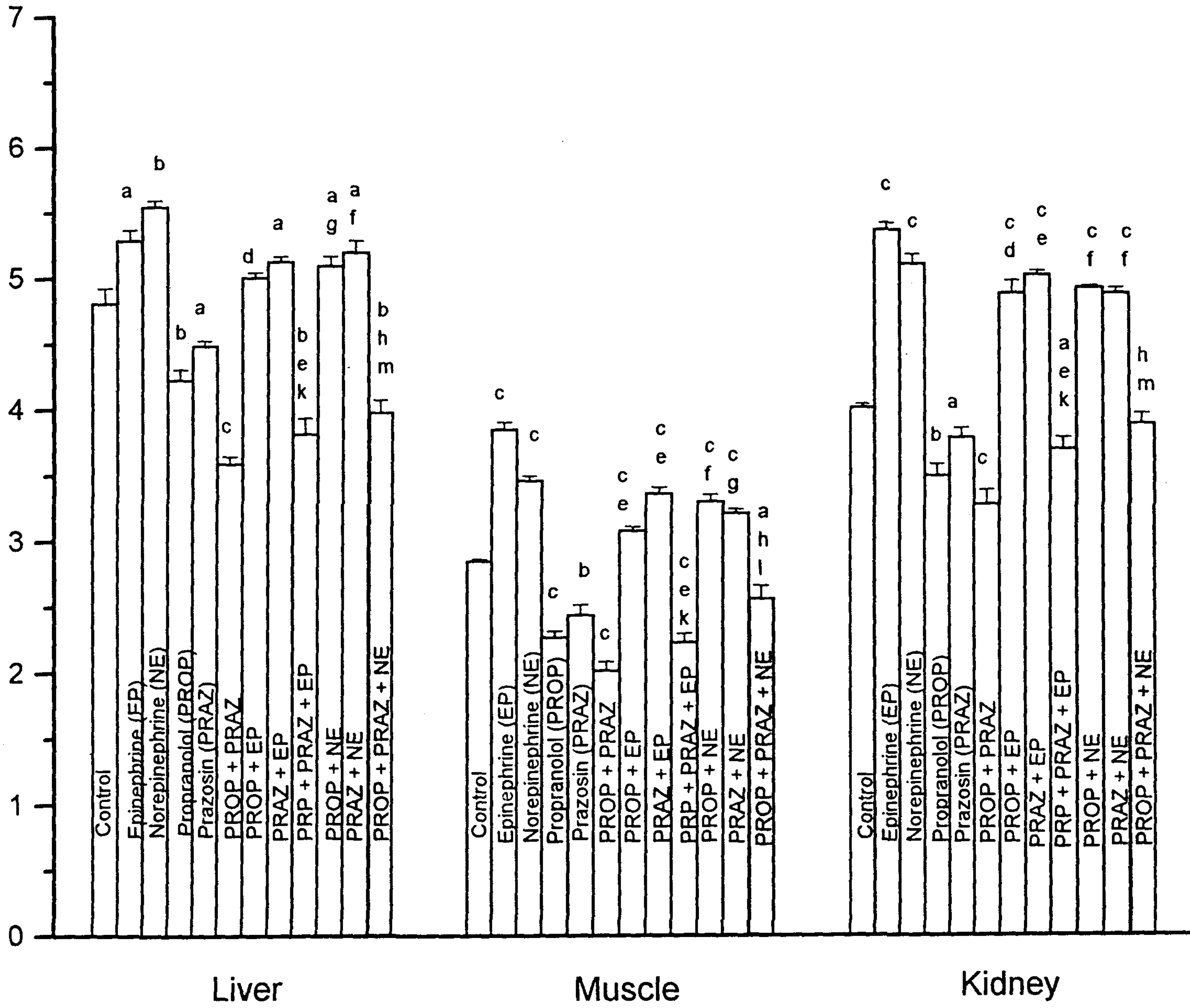
[a, b, c] Differ from the saline treated control group : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e] Differ from the value of the group treated with EP : $P < 0.01$ and 0.001, respectively.

[f, g, h] Differ from the value of the group treated with NE : $P < 0.05$, 0.01 and 0.001, respectively.

[k] Differs from PROP + EP or PRAZ + EP : $P<0.001$.

[l, m] Differ from PROP + NE or PRAZ + NE : $P<0.01$ and 0.001, respectively.



Rate of Oxygen Consumption (µl O2/ mg wet tissue / h)
0
1
2
3
4
5
6
7
Control
Epinephrine (EP)
Norepinephrine (NE)
Propranolol (PROP)
Prazosin (PRAZ)
PROP + PRAZ
PROP + EP
PRAZ + EP
PRP + PRAZ + EP
PROP + NE
PRAZ + NE
PROP + PRAZ + NE
Liver
Muscle
Kidney

Chapter VI

EFFECTS OF MELATONIN ON THE OXIDATIVE METABOLISM IN MALE *Clarias batrachus*

In fish, the pineal gland acts as a photo-neuroendocrine organ (Matty, 1985) through its cyclic secretion of melatonin. Melatonin transmits signals concerning photoperiod to the central neuroendocrine network that controls circadian and seasonal rhythms in all vertebrates (Axelrod, 1974; Reiter, 1981; Binkley, 1981). In poikilotherms, the pineal complex functions both as a phototransducer and a temperature sensor (Mendonca *et al.*, 1995). There are some reports on the involvement of pineal complex in regulation of body temperature in mammals (Heldmaier and Steinlechner, 1981, 1982a; Buchberger, *et al.*, 1983; Heldmaier and Lynch, 1986; Heldmaier *et al.*, 1989) and reptiles (Hutchinson and Koch, 1974; Bartholomew, 1982). There are few reports that melatonin produces hypothermic effects in reptiles (Rismiller and Heldmaier, 1987; Badia *et al.*, 1991). In birds, melatonin has been reported to be involved in the process of thermoregulation (John and George, 1984; John *et al.*, 1986; George and John, 1986), lipid mobilization (John and George, 1976; Ralph, 1979; Binkley, 1981; Osei *et al.*, 1989), and to increase energy metabolism (Pohl, 1996; Freo, 1996; Le-Gauic *et al.*, 1996). As in reptiles, birds and mammals, melatonin has also been found to stimulate tissue oxygen consumption in amphibians (Mahanta, 1994). However, there is a lack of information on the calorigenic function of melatonin in fish. In view of the scarcity of information and phylogenic position of fish, it was thought worthwhile to investigate the calorigenic role of melatonin in male *Clarias batrachus* maintained at natural climatic conditions during winter and summer/rainy months. The findings of the present study suggest that melatonin is capable of influencing energy metabolism of the fish.

Materials and Methods

Adult male *Clarias batrachus* (Length : 18-22 cm; Weight : 70-80 gm.) were purchased locally and acclimatized at least for 15 days under natural climatic conditions before the experiments were started. During acclimatization, fishes were fed with earthworm *ad libitum* (for details please see Chapter-I). *In vivo* and *in vitro* experiments were conducted both during winter and summer/rainy months as per the details of the experimental protocol given below:

Expermental Protocol

Expt. No.	Treatment	*In vivo*/ *In vitro*	Month (Temp.)	Dose	Duration
(A)	Saline	*In vivo*	January (9.6°C)		4 days
	Melatonin		July (20°C)	2 µg/f /d	4 days
(B)	Saline	*In vivo*	Jan (9.6°C)	1 µM	
	Melatonin		Sept	2 µg/f/d	4 days
	Melatonin		(20°C)	4 µg/f/d	4 days
	Melatonin			8 µg/f/d	4 days
(C)	Control	*In vitro*	January (9.6°C)		
	Melatonin		July (20°C)	1 µM	

Results

The data are presented in Tables 6:1, 6:2 & 6:3; Figs. 6:1, 6:2 & 6:3. Both *in vivo* and *in vitro* administration of melatonin significantly increased the rate of oxygen consumption of liver, muscle, kidney and brain tissue both during winter and summer/rainy months (Tables 6:1& 6:2; Figs. 6:1 & 6:2). Further, melatonin increased the rate of oxygen uptake in a dose-dependent manner (Table 6:3; Fig. 6:3).

Discussion

So far no attempt has been made to study the metabolic action of melatonin in fish. To the best of our knowledge, this might be the first study of its kind in which both *in vivo* and *in vitro* effects of melatonin on the respiratory rate of vital tissues of a fish has been studied. *In vivo* administration of melatonin invariably stimulated tissue respiration irrespective of water temperature and seasons (Tables 6:1& 6:2; Figs. 6:1 & 6:2). Further, melatonin increased the tissue respiratory rate in a dose-dependent manner (Table 6:3; Fig. 6:3). These findings seem to suggest that melatonin is also actively involved in the regulation of the energy metabolism of the fish. *In vitro* stimulation of fish tissue respiration by melatonin suggest a direct calorigenic action of this hormone in *Clarias batrachus*. It is important to mention that short daylengths/darkness and low temperature increase the production of melatonin in all vertebrates including fish (Barfuss and Ellis, 1971; Deguchi and Axelrod, 1972; Vivien-Roel and Arendt, 1981). It, thus, seems that the increased production of melatonin during winter might be an adaptational mechanism to support the oxidative metabolism at low water temperature. Therefore, the natural production of melatonin and its direct and temperature-independent metabolic action might be of great adaptational significance for the fish. However, the mode of action of melatonin in stimulating tissue respiration remains to be explored.

Table 6:1 - In vivo effects of melatonin on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C) and summer (20° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
		Winter		
Saline (Control)	2.88±0.07	1.12±0.05	2.69±0.08	5.26±0.09
Melatonin	3.65±0.10[c]	1.41±0.08[a]	3.27±0.03[c]	5.52±0.06[b]
		Summer		
Saline (Control)	4.71±0.08	2.72±0.05	4.10±0.05	4.30±0.07
Melatonin	5.36±0.05[c]	3.65±0.07[c]	4.75±0.08[c]	4.81±0.07[b]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from the value of saline treated control group : $P < 0.05$, 0.01 and 0.001, respectively.

Table 6:2 - In vitro effects of melatonin on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. 9.6° C) and summer (20° C).

Treatments	Rate of Tissue Oxygen Consumption (μl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
		Winter		
Control	2.69±0.06	0.89±0.08	2.53±0.05	5.01±0.04
Melatonin	3.65±0.03[c]	1.54±0.12[b]	3.21±0.07[c]	5.90±0.12[c]
		Summer		
Control	4.81±0.12	2.85±0.02	4.01±0.03	5.07±0.07
Melatonin	5.65±0.05[c]	3.98±0.04[c]	4.81±0.07[c]	5.84±0.10[c]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[b, c] Differ from the value of the control group : $P < 0.01$ and 0.001, respectively.

Table 6:3 - Dose-depenedent effects of melatonin on the rate of tissue respiration of male Clarias batrachus during winter (Av. water temp. : 9.6° C).

Treatments	Rate of Tissue Oxygen Consumption (µl Oxygen/mg /hour)			
	Liver	Muscle	Kidney	Brain
Saline (Control)	2.92±0.09	1.15±0.05	2.66±0.06	5.29±0.03
Melatonin 2 µg	3.69±0.08[c]	1.44±0.09[a]	3.24±0.07[c]	5.55±0.05[b]
Melatonin 4 µg	4.04±0.11[c,d]	1.73±0.10[b,d]	3.49±0.05[c,d]	5.87±0.11[b,d]
Melatonin 8 µg	4.65±0.05[c,f,h]	2.15±0.08[c,e,g]	3.82±0.12[c,e,g]	6.06±0.02[c,f]

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from the value of saline treated control group : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e, f] Differ from the group treated with 2 µg melatonin : $P < 0.05$, 0.01 and 0.001, respectively.

[g, h] Differ from the group treated with 4 µg melatonin : $P < 0.05$ and 0.01, respectively.

Figure 6:1 - In vivo effects of melatonin on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C) and summer (20° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from the value of saline treated control group : $P < 0.05$, 0.01 and 0.001, respectively.

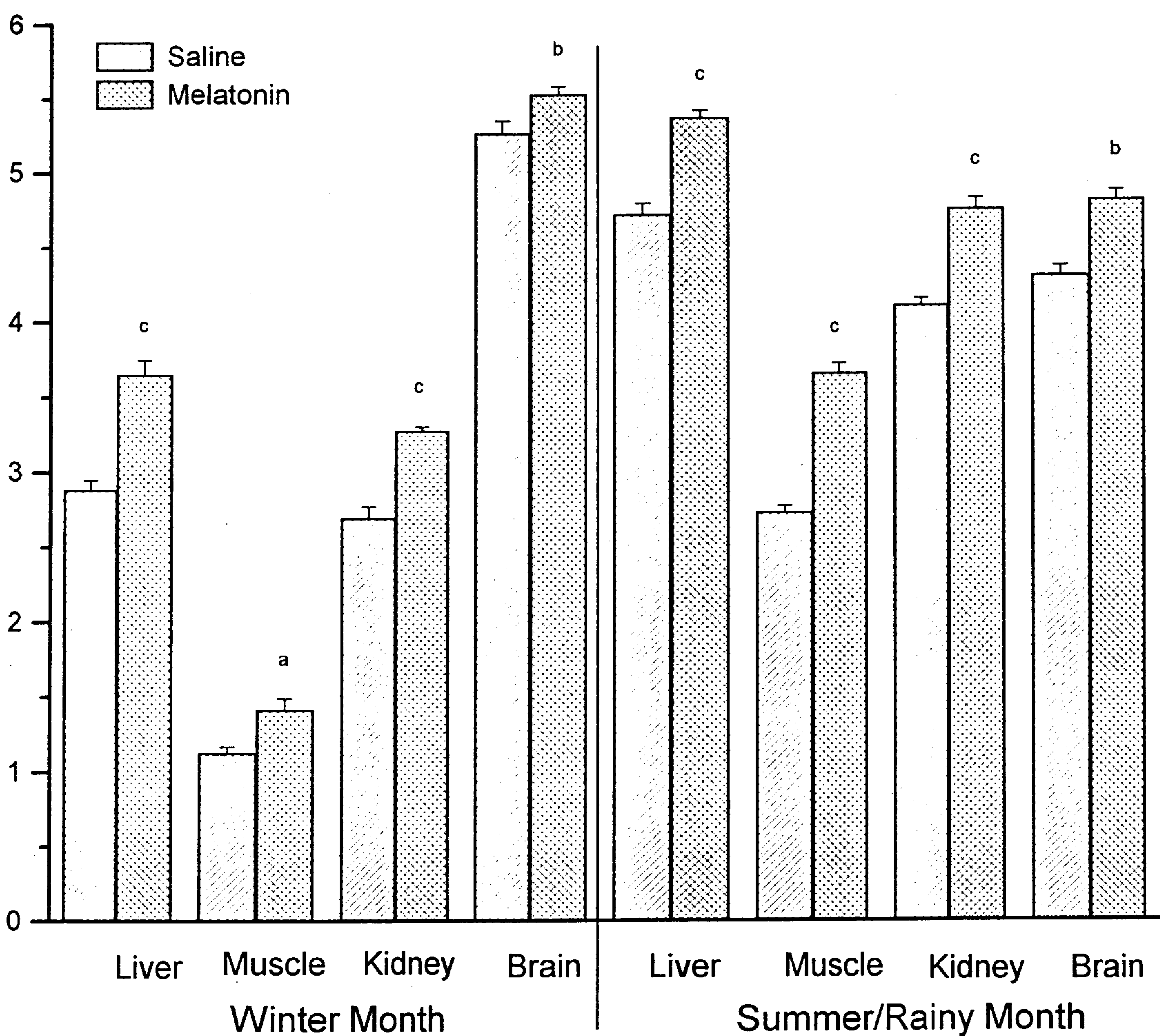

Rate of Oxygen Consumption (µl O2 / mg wet tissue / h)
Saline
Melatonin
0
1
2
3
4
5
6
a
b
c
Liver
Muscle
Kidney
Brain
Winter Month
Summer/Rainy Month

Figure 6:2 - In vitro effects of melatonin on the rate of tissue respiration of male *Clarias batrachus* during winter (Av. water temp. : 9.6° C) and summer (20° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[b, c] Differ from the value of the control group : $P < 0.01$ and 0.001, respectively.

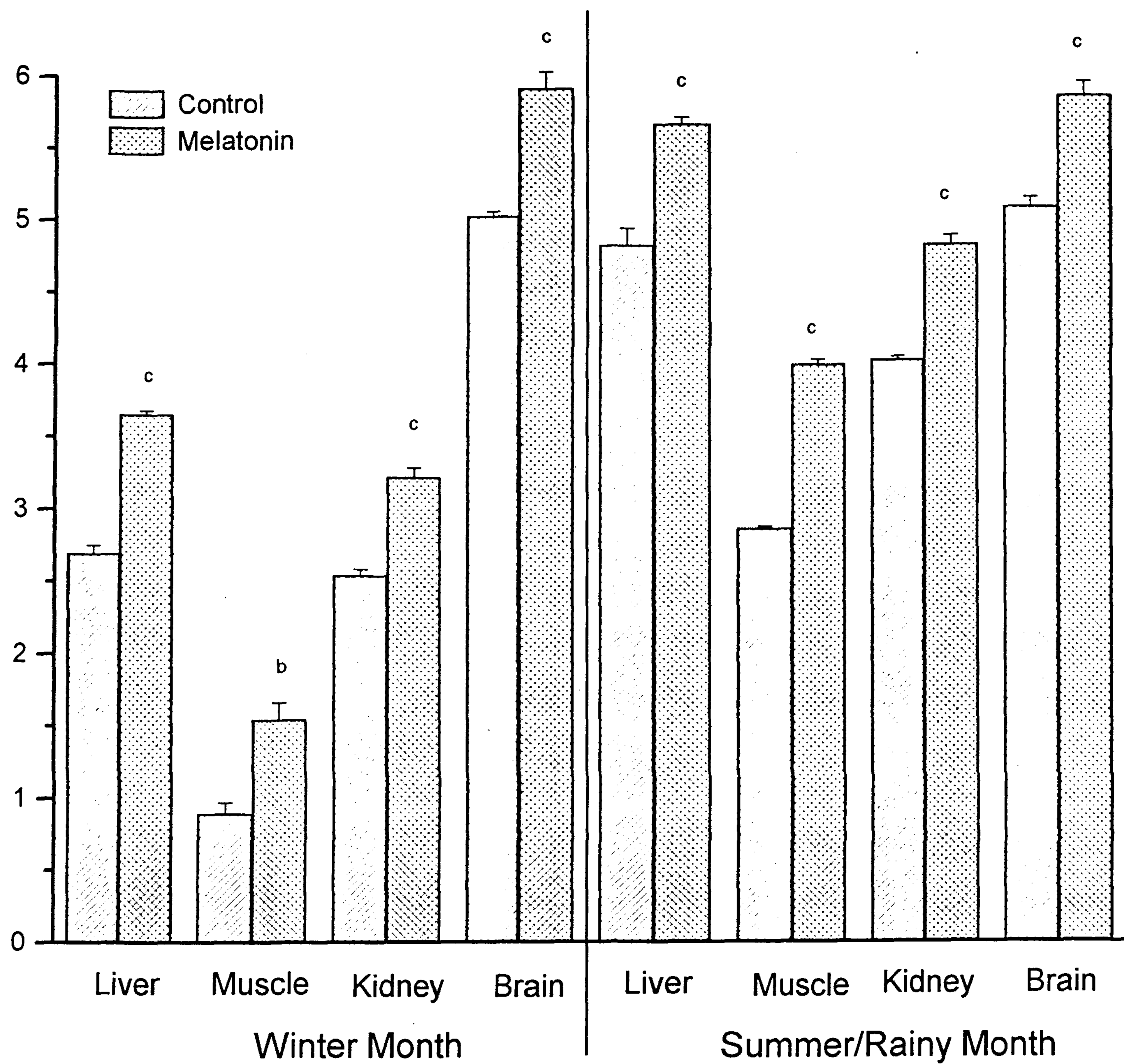

Rate of Oxygen Consumption (μl O2 / mg wet tissue / h)
0
1
2
3
4
5
6
Control
Melatonin
c
b
c
c
c
c
c
c
Liver
Muscle
Kidney
Brain
Liver
Muscle
Kidney
Brain
Winter Month
Summer/Rainy Month

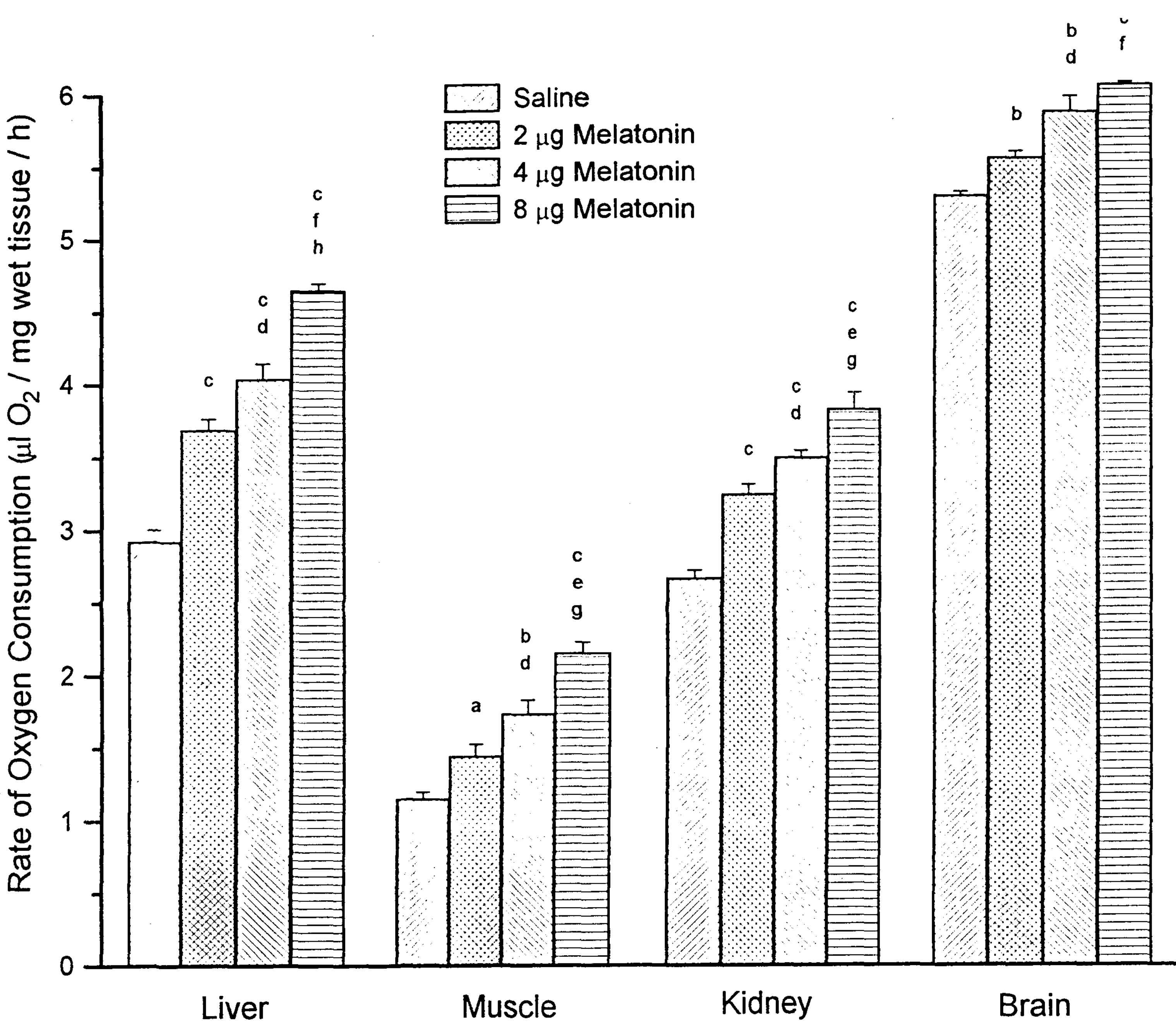
Figure 6:3 - Dose-depenedent effects of melatonin on the rate of tissue respiration of male Clarias batrachus during winter (Av. water temp. : 9.6° C).

All values are expressed as Mean ± Standard Error (S.E.); N = 4.

[a, b, c] Differ from the value of saline treated control group : $P < 0.05$, 0.01 and 0.001, respectively.

[d, e, f] Differ from the group treated with 2 µg melatonin : $P < 0.05$, 0.01 and 0.001, respectively.

[g, h] Differ from the group treated with 4 µg melatonin : $P < 0.05$ and 0.01, respectively.


Rate of Oxygen Consumption (µl O2 / mg wet tissue / h)
0
1
2
3
4
5
6
Saline
2 µg Melatonin
4 µg Melatonin
8 µg Melatonin
c
c d
c f h
a
b d
c e g
c
c d
c e g
b
b d
f
Liver
Muscle
Kidney
Brain

SUMMARY AND CONCLUSIONS

Clarias batrachus is a bimodal breathing fish commonly found all over India, except few places of high altitude. It is a nocturnal species which becomes more active during the dark phase and less active during the light phase. There is practically no information on the seasonal variations in the respiratory rate of the vital tissues (liver, muscle, kidney and brain) and the regulatory role of different climatic factors and hormones on the rate of oxygen consumption of any fish species. Experiments were planned to investigate the relative role of environmental factors and in vivo and in vitro effects of hormones of thyroid, testis, adrenal and pineal hormones during winter and summer/rainy seasons in the regulation of the oxidative metabolism of male *Clarias batrachus*. The present Ph. D. dissertation has been divided in to six chapters. A brief summary of the chapters has been given below.

Chapter-I

Materials and Methods

This chapter includes the details of the materials used, experimental conditions, methods for maintaining the fishes, for conducting the *in vivo* and *in vitro* experiments and for measurement of the rate of tissue respiration.

Chapter-II

Study of Annual Variations in the Oxidative Metabolism of male *Clarias batrachus* with special reference to Temperature, Photoperiods and Feeding Status

This chapter deals with the study of monthly variations in the rate of oxygen consumption of vital tissues (liver, muscle, kidney and brain). This chapter also deals with the effects of simulated temperature, photoperiod and feeding/fasting on the rate of tissue respiration. The major findings and conclusions based on the experiments included in this chapter are listed below:

1. All the four tissues (liver, muscle, kidney and brain) exhibited an annual rhythm in the rate of oxygen consumption.
2. Liver, muscle and kidney tissues showed similar annual patterns in their rate of oxygen consumption , while the annual pattern of brain respiration was different during winter months.
3. Liver, muscle and kidney tissues exhibited a positive correlation with the natural water temperature.
4. Brain tissue respiration did not show any significant difference in its average rate of oxygen uptake during winter and summer/rainy month. Further, there was no significant correlation between the brain tissue respiration and the natural water temperature.
5. The rate of muscle tissue respiration was found always to be the lowest and that of the brain to be the highest. The respiratory rate of liver was always higher than that of the kidney tissue.
6. The average rate of oxygen consumption of the liver, muscle and kidney tissues was found to be significantly higher during summer/rainy months as compared to that of winter months.

5. Within the tolerance range, the rate of respiration of liver and muscle tissues linearly increased with the increase in the simulated water temperature. Both tissues show a strong positive correlation with the simulated temperature.
6. Brain and kidney tissue respiration significantly increased with the increase in simulated temperature upto 25° C, thereafter, it sharply decreased with further increase in temperature. Both tissues exhibited a negative correlation with the increase of temperature above 25° C.
7. The liver, muscle and brain tissues respiration exhibited a negative correlation with increasing daylength, while kidney tissues oxygen uptake showed no significant correlation with daylength.
8. All the four tissues (liver, muscle, kidney and brain) showed a positive correlation with the duration of feeding. The respiratory rate of all the tissues except brain significantly decreased after 10 days of fasting.
9. Liver and muscle tissues indicated a negative correlation with the duration of fasting. Kidney respiration exhibited positive correlation with the duration of fasting, which seems to be associated with the increased active transport rate and removal of the nitrogenous waste product by the kidney. Brain tissue respiratory rate did not exhibit any significant correlation with the duration of fasting.

On the basis of these findings, it may be concluded that the energy demand of different tissues varies with seasons, and seems to be related with the seasonal changes in physical and reproductive activities of the fish. The respiratory rate of liver and muscle tissues seem to be directly affected by the change in temperature, daylength and feeding status. Kidney respiration of the fish seems to be independent of the changes in daylength, however, it increases with the duration of fasting. Brain tissue respiration does not seem to be adversely affected by temperature and fasting.

Brain might be possessing a self-regulating mechanism for ensuring the successful survival of the fish during the stressful conditions of winter.

Chapter-III

Role of Thyroid Hormones in Regulation of the Oxidative Metabolism in Male *Clarias batrachus*

This chapter deals with the *in vivo* and *in vitro* effects of mono- iodotyrosine (MIT), di-iodotyrosine (DIT), L-triiodothyronine (T_3), L-thyroxine (T_4) and propyl thiouracil (PTU) on the rate of oxygen consumption of tissues during winter and summer/rainy months. This chapter also contains data of experiments pertaining to mechanism of action of iodotyrosines (MIT and DIT) and L-T_3. The major findings of this chapter are as follows :

1. *In vivo* administration of L-T_3 and L-T_4 did not stimulate fish tissue respiration during winter months. However, both L-T_3 and L-T_4 significantly stimulated the respiratory rate of all the tissues during summer/rainy months.
2. *In vitro* treatment of L-T_3 and L-T_4 stimulated only brain tissue respiration during winter, but significantly increased the respiratory rate of all the tissues during summer/rainy months.
3. *In vivo* administration of MIT significantly increased the respiratory rate of muscle and brain tissues during winter and only of muscle tissue during summer/rainy months. However, *in vitro* treatment of MIT significantly increased the respiratory rate of all the tissues during winter and only of liver and muscle during summer/rainy months.

4. *In vivo* and *in vitro* administration of DIT significantly stimulated the respiratory rate of all the tissues irrespective of seasons. It seems that DIT is more important than MIT in stimulating of the oxidative metabolism in this fish.
5. In vivo administration of MIT and DIT stimulated the fish tissue respiration in a dose-dependent manner.
6. *In vivo* administration of PTU significantly decreased the respiratory rate of liver, muscle and kidney tissues irrespective of water temperature, while brain tissue respiration was inhibited by PTU at high temperature.
7. PTU significantly decreased the rate of tissue respiration during both summer/ rainy and winter seasons. During summer PTU-induced decrease in tissue respiration was reversed significantly by L-T_3 and L-T_4.
8. The decreased tissue respiration after PTU treatment during winter seems to suggest that the indigenous thyroid hormones are involved in the oxidative metabolism of the fish at low temperature.
9. Treatment of the tissue homogenates with ouabain and actinomycin-D separately, significantly decreased the respiratory rate of liver, muscle and kidney tissues.
10. Both ouabain and actinomycin-D significantly, but not completely, inhibited the stimulatory effect of L-T_3 suggesting that L-T_3 stimulated tissue respiration via transcription process as well as by increasing the activity of Na^+- K^+- ATPase.
11. The significant inhibition of the stimulatory effect of MIT and DIT on respiration seem to suggest that, similar to L-T_3, MIT and DIT also stimulated tissue respiration through DNA-dependent RNA synthesis and Na^+- K^+- ATPase.

These findings clearly indicate that L-T_3 and L-T_4 are ineffective in stimulating tissue respiration of the fish during winter. MIT and DIT seem to be actively involved

in the regulation of tissue respiratory rate irrespective of the water temperature. The indigenous thyroid hormones are involved in the regulation of tissue respiration of the fish also during the winter months. The iodotyrosines and the iodothyronines seem to produce their calorigenic effect in tissue respiration by stimulating the activity of mitochondrial enzymes, Na^+-K^+-ATPase and the transcription process. MIT and DIT seem to produce their stimulatory effect through a similar pathways like that of T_3 and T_4. The temperature-independent calorigenic action of MIT (tissue-dependent) and DIT indicate that these hormones might be the initial regulators of the oxidative metabolism and their calorigenic role might have been replaced by T_3 and T_4 during the course of evolution.

Chapter-IV

Role of Testicular Hormones in Regulation of the Oxidative Metabolism in male *Clarias batrachus*

This chapter deals with *in vivo* and *in vitro* effects of testosterone and cyproterone acetate (a blocker of androgen receptors) on the rate of tissue respiration during winter and summer/rainy months. It also contains data of experiments conducted to find out the mechanism of action of testosterone. The findings of this chapter are mentioned below :

1. Testosterone significantly stimulated the respiratory rate of all the tissues irrespective of temperature and seasons.
2. Testicular hormones seem to be directly involved in regulation of the oxidative metabolism of the fish.
3. Cyproterone acetate always inhibited the respiratory rate of liver, muscle and kidney tissues.

4. Administration of actinomycin-D or cyproterone acetate significantly, but not completely, blocked the stimulatory effect of testosterone on the rate of tissue oxygen uptake.
5. Testicular hormones increased the respiratory rate of the tissues by stimulating the transcription process (genomic pathway) via androgen receptors and the enzyme Na^{+}-K^{+}-ATPase (extra-nuclear/non-genomic pathway).

Therefore, on the basis of the present findings, it may be concluded that the testicular hormones play an important and direct role in the regulation of the oxidative metabolism of the fish due to their temperature-independent metabolic action. These hormones might be more important than thyroid hormones, particularly T_3 and T_4, in ensuring the energy production for successful survival of the fish during the cold winter season.

Chapter-V

Role of Catecholamines and Corticosteroids in Regulation of the Oxidative Metabolism in male *Clarias batrachus*

This chapter deals with the experimental studies on *in vivo* and *in vitro* effects of adrenal hormones (epinephrine, norepinephrine, corticosterone, cortisol, and cortisone) and metapyrone (an inhibitor of corticosteroid biosynthesis) on the rate of tissue respiration. It also deals with the experiments conducted to study the synergistic effects of thyroid hormones and catecholamines, and the mechanism of action of catecholamines. The findings of these experiments are as follows:

1. Catecholamines (epinephrine and norepinephrine) invariably stimulated the respiratory rate of all the tissues (liver, muscle, kidney and brain) in the fish irrespective of mode of treatments (*in vivo*/*in vitro*), water temperature and seasons.
2. The degree of stimulation by epinephrine and norepinephrine is higher during winter as compared to that of summer/rainy months.
3. Epinephrine is more potent than norepinephrine in stimulating the rate of muscle tissue oxygen uptake, while norepinephrine is more potent than epinephrine in stimulating liver tissue respiration.
4. The stimulatory effects of the catecholamines during winter was significantly potentiated by L-T_3 and L-T_4. However, during summer/rainy months the catecholamines and the thyroid hormones produced a synergistic effect on the rate of tissue respiration in both *in vivo* and *in vitro* treatments.
5. Both α- and β-adrenergic receptors are involved in the calorigenic action of catecholamines in the fish. The α- and β-adrenergic receptors of the tissue exhibited a cross-reactivity for different agonists.
6. The degree of involvement of α- and β-adrenergic receptors in the calorigenic action of catecholamines varies with tissues and season.
7. *In vivo* and *in vitro* administration of corticosteroids invariably stimulated the respiratory rate of all the tissues irrespective of water temperature and seasons, except cortisone which did not stimulate brain tissue oxygen uptake in *in vitro* experiments during summer.
8. The degree of stimulation of tissue respiration by corticosteroids was comparatively higher during winter as compared to that during summer/rainy seasons.
9. The administration of metapyrone significantly decreased the oxygen uptake of the tissues (liver, muscle, kidney and brain). However, adminis-

tration of the corticoids reversed the adverse effect of metapyrone on tissue respiration.

It, thus, seems that the catecholamines and the corticosteroid hormones are very important for the regulation of tissues respiration of the fish, *Clarias batrachus*. Since the production of these hormones is increased during stress and under emergency situations, they might be acting as the emergency hormones for the regulation of the energy metabolism to ensure successful survival under adverse climatic conditions. The potentiation of the calorigenic action of the catecholamines by the thyroid hormones during winter suggests an important but indirect role of endogenous thyroid hormones in the regulation of the oxidative metabolism of the fish. Both α- and β-adrenergic receptors are employed in the calorigenic action of the catecholamines in the fish, *Clarias batrachus*, and might be using cAMP, Ca^{++}, IP_3 etc. as the second messengers.

Chapter-VI

Effects of Melatonin on the Oxidative Metabolism in Male *Clarias batrachus*

This chapter incorporates the data of *in vivo* and *in vitro* experiments conducted to study the effects of melatonin on the rate of tissue respiration during winter and summer/rainy months. The findings of these experiments are listed below:

1. Melatonin invariably stimulated the respiratory rate of all the tissues (liver, muscle, kidney and brain) irrespective of water temperature and seasons.
2. The *in vitro* effect of melatonin on the tissue metabolic rate seems to suggest that melatonin has a direct effect at tissue level in stimulating the oxidative metabolism in the fish.

3. Melatonin stimulated tissue respiration in a dose-dependent manner.

On the basis of these findings, it may be concluded that melatonin has a capability to stimulate the tissue respiration of the fish directly. Since short daylengths and low temperature have been reported to increase melatonin production in several vertebrates, the observed involvement of melatonin in the oxidative metabolism of the fish might be helpful as an additional hormone in maintaining the minimum metabolic rate during winter to ensure the survival of the fish. The degree of stimulation of the respiratory rate seems to depend on the tissue and the daylengths.

CONCLUSIONS

On the basis of the major findings of the present Ph.D. dissertation, it can be concluded that the vital tissues of the fish *Clarias batrachus* exhibit an annual rhythm of variation in their rate of respiration. The tissue metabolic rate in the fish seems to be regulated by a complex set of external factors (like temperature, photoperiod, availability of food etc.) and internal factors (hormones). The thyroidal, adrenal, testicular and pineal hormones seem to play a major role in the regulation of the fish tissues respiration. The relative involvement and role of different endocrine glands and their hormones vary with tissues and seasons of the year. The exogenous L-T_3 and L-T_4 produce a temperature-dependent effect in fish tissue respiration, however, the endogenous thyroid hormones stimulate the oxidative metabolism indirectly by potentiating the calorigenic action of catecholamines. MIT and DIT are calorigenic in the fish irrespective of the ambient temperature, and, therefore, might be playing an important role in the regulation of the oxidative metabolism of the fish. Further, the involvement of the iodotyrosines might be of evolutionary significance. The catecholamines and corticosteroid hormones, which are produced in response to

non-specific stress and under emergency conditions, produce a temperature-independent calorigenic effect in the fish and seem to act as emergency hormones for the oxidative metabolism of *Clarias batrachus*. The testicular hormones also seem to be directly involved in the regulation of fish energy metabolism, particularly at low ambient temperature. The involvement of the testicular hormones in the oxidative metabolism might be a mechanism to ensure higher metabolic rate required for successful reproduction in case of a sudden decline in the ambient temperature during breeding season and/or for survival during winter months. In addition to these hormones, melatonin also seems to be capable in stimulating the metabolic rate of the fish. This might be helping to meet the energy demand particularly during winter when temperature is low and daylength is short which favour melatonin production. The testicular and thyroid hormones seem to stimulate tissue respiration via nuclear pathway as well as via the enzyme Na^+-K^+-ATPase. NE and EP seem to act via both α- and β-adrenergic pathways. However, the mode of action of melatonin remains to be established.

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