

Corticosteroids and Osmoregulation in Fishes

M DHARMAMBA

Department of Zoology, University of Delhi, Delhi 110 007, India

The effects of corticosteroids in the osmoregulation of fishes have been reviewed. Information on fishes other than the teleosts is scanty. 1α -hydroxycorticosterone has a role in the regulation of rectal gland function in elasmobranchs. The role of cortisol, a natural hormone of teleosts, in the adaptation of fish to freshwater (FW) and seawater (SW) environments has been considered. Cortisol, in low doses, augments Na-uptake by gills in FW fish. In SW teleosts cortisol is involved in the compensatory mechanisms at various osmoregulatory effector organs. It increases the intestinal transport of salt and water. The water movement is associated with the development of a chloride pump. At the gill it stimulates the Na outflux, the chloride cells and the $\text{Na}^+\text{-K}^+$ -dependent ATPase activity. Evidences indicate that $\text{Na}^+\text{/K}^+$ exchange component of Na outflux possibly mediated by $\text{Na}^+\text{-K}^+$ -dependent ATPase, is under the control of pituitary-interrenal system. Cortisol stimulates the mucosa to serosa permeability to water and ions in the urinary bladder. The possible role of esophagus in the osmoregulation of SW eel and its regulation by cortisol has been indicated. The transitory increase in plasma cortisol when FW eel is transferred to SW and the time course of development of compensatory mechanisms for SW habitat emphasizes the physiological significance of the effects of cortisol and suggests its importance in the migrating eel in nature.

Introduction

Hormonal control of osmoregulation in fishes is well established and the role of adrenocorticosteroids in fish hydromineral balance has been reviewed several times (Chester Jones 1957, Chester Jones et al. 1969a, 1974, Maetz 1968, 1969a, Henderson et al. 1970, Utida et al. 1972a, b, Utida & Hirano 1973). The present account shall review the salient features of the role of corticosteroids in the salt and water metabolism of fishes with reference to their effects at various osmoregulatory effector organs.

Cyclostomes

Very little is known of the interrenal tissue, its secretions and their role in the osmoregulation of cyclostomes. It is, therefore, difficult to attribute any physiological significance to the effects produced by aldosterone in the hagfish and aldosterone and cortisol in the freshwater lamprey (see Chester Jones et al. 1969a, Falkmer et al. 1974) excepting that they indicate a possible role of corticosteroids in the osmoregulation of these fishes. More investigations on morphologi-

cal, biochemical and physiological aspects of interrenals are necessary in this group.

Elasmobranchs

Information in elasmobranchs is again meagre and it has been reviewed by Chester Jones et al. (1969a). Idler and his group have shown that 1α -hydroxycorticosterone is the principal adrenocorticosteroid secreted by these fishes (Chester Jones et al. 1974). Corticosterone, aldosterone and cortisol have also been reported.

In the lip-shark (*Hemiscyllium plagiosum*), Chan et al. (1967b) did not find any effect of cortisol or deoxycorticosterone on the electrolyte composition of the intact fish but observed that these corticosteroids reduce the rate of secretion by the rectal gland of this shark. Interrenalectomy in *Raja radiata* did not result in any clear-cut changes in plasma electrolyte concentrations in spite of a 95% reduction in the plasma level of 1α -hydroxycorticosterone 24 hr after interrenalectomy (Idler & Szeplaki 1968). More recently, Holt and Idler (1975) observed that interrenalectomy of the skate, *Raja ocellata* produced a decline in the rectal gland fluid volume, a decrease in the osmolarity, sodium and chloride concentrations and an increase in the potassium concentration of the rectal gland fluid; treatment with 1α -hydroxycorticosterone or corticosterone increased the output of the rectal gland fluid in the interrenalectomized skate, a result contradictory to the findings of Chan et al. (1967b) in the intact shark. It is not known if the corticosteroid regulates the sodium transport or the water permeability in the rectal gland. Since rectal gland is known to play a role in the extrarenal excretion of salt, it would be of interest to investigate if 1α -hydroxycorticosterone functions as a salt-excreting factor in elasmobranchs as cortisol does in the seawater teleosts (see below).

Teleosts

Teleost fishes are known to maintain their internal osmolarity fairly constant (between 250 and 350 mosm/L) irrespective of their external environment ranging from fresh water (ca. 5 mosm/L) to sea water (ca. 1100 mosm/L). The regulation of a constant *milieu intérieur* becomes more important in certain euryhaline fishes which encounter both fresh water (FW) and sea water (SW) environments in their life-history. Endocrines are known to play a role in the osmoregulatory processes of teleosts. The role of corticosteroids in FW and SW osmoregulation shall be considered here. A perusal of literature would indicate that studies have been mostly restricted to the three euryhaline eel species, namely, *Anguilla anguilla* (European eel), *Anguilla japonica* (Japanese eel) and *Anguilla rostrata* (American eel). It has been unequivocally established that cortisol is the major corticosteroid secreted by the teleost interrenals along with smaller amounts of cortisone, 11-deoxycorticosterone and corticosterone while aldosterone, a major mineralocorticoid in the tetrapods has not been recorded except in a very few species and only in trace quantities (Chester Jones et al. 1969a, 1974). Various experimental approaches have clearly delineated the presence of a pituitary-interrenal axis in several species of teleosts (Maetz 1969a). Therefore, the effects of ACTH shall also be considered among the actions of corticosteroids.

Freshwater osmoregulation

In fresh water, teleosts are hyper-osmotic to their environment and consequently face an osmotic influx of water, mostly through the gills. In order to eliminate the excess water the kidney of the FW teleost excretes an abundant quantity of dilute urine. A loss of sodium (Na) and chloride (Cl) ions occurs through the urine besides the passive loss of

these ions through the gills. To compensate this loss, gills actively uptake these monovalent ions from the environment. The gut seems to play a minimal role in FW osmoregulation as the fish drinks very little in this medium. Hormonal factors are known to mediate these compensatory mechanisms.

Chester Jones et al. (1964) performed the first interrenalectomy in the European eel whose discrete morphology of the interrenals facilitated this surgical operation. Interrenalectomy of the FW eel caused a decrease in the uptake of Na by the gills resulting in a net Na loss reflected by the reduction of plasma Na, and it also caused an increase in the tissue water content (Chester Jones et al. 1965, 1996). A low dose of cortisol (2 mg/kg) injected into interrenalectomized eel increased the net uptake of Na (Chester Jones et al. 1966). Interrenalectomy of the eel also resulted in a reduction in the urine output and an increase in the urine Na concentration but without renal Na loss, and cortisol treatment restored the urine output and urine electrolyte concentrations to normal levels (Rankin et al. 1967, Chan et al. 1969).

Hypophysectomy of fish in FW caused a similar effect of reducing the plasma Na in *A. anguilla* (Olivereau and Chartier-Baraduc 1966, Olivereau & Olivereau 1970) and in several other species (Ball 1969a,b, Lam 1972). The effects of cortisol or ACTH on the plasma electrolytes in hypophysectomized fish are equivocal. Cortisol treatment further reduced the plasma Na in *A. anguilla* Lemoine & Olivereau 1974), but had no effect in *A. rostrata* (Butler & Carmichael 1972) and *Tilapia mossambica* (Dharmamba 1970). Similarly, ACTH had no effect in elevating the plasma Na in the hypophysectomized *Poecilia latipinna* (Ball & Ensor 1967), *Carassius auratus* (Lahlou & Sawyer 1961), *Fundulus kansea* (Stanley & Fleming 1967) and *T. mossambica* (Dharmamba

1970). However, Chan et al. (1968) have observed that cortisol or ACTH partially elevated the plasma Na in the hypophysectomized *A. anguilla* in FW.

The decline in plasma sodium following hypophysectomy in FW is due to a reduction in Na influx and/or an increase in Na outflux through the gills in several species investigated (see Dharmamba & Maetz 1972). Cortisol seems to increase the Na influx in the hypophysectomized *A. anguilla* (Langford 1971). Cortisol may share this action with prolactin which also seems to correct the Na influx in *F. kansae* (Ball 1969a) and increase the urine flow in hypophysectomized *F. kansae* and *C. auratus* in FW (Stanley & Fleming 1967, Lahlou & Giordan 1970). Cortisol could elevate the plasma Na to normal levels and reduce the tissue water-retention in the hypophysectomized eel in FW only when it was administered along with prolactin while prolactin alone had the ability to reduce the tissue water-retention (Chan et al. 1968) and elevate the plasma Na to normal levels in several species by preventing the Na loss mainly by decreasing the Na outflux (Ball 1969b, Dharmamba & Maetz 1972, Lam 1972). On the other hand, cortisol administration to intact fish, in high doses, may cause a Na loss in FW (Chester Jones et al. 1969) which will be deleterious to the fish in a hypotonic environment.

In general, cortisol seems to play a role in the Na uptake by the gills while in other regulatory mechanisms at the gill and the kidney, other hormonal factors, chiefly prolactin, may play a major role in the FW osmoregulation of teleosts (Maetz et al. 1964, Chester Jones et al. 1969b, Lam 1972, Johnson 1973, Pang 1977). Cortisol may also be necessary for maintaining the water movement across the intestine even in the FW fish, as cortisol restored the rate of water transport across the intestine which had been impaired by interrenalectomy in

the FW *A. anguilla* (Gaitskell & Chester Jones 1970).

Branchial Na⁺-uptake mediated by Na⁺-K⁺-dependent ATPase (Na-K-ATPase) seems to take place in FW teleosts (Maetz 1974, 1976). However, from the data available so far, it is not certain if this mechanism is under the control of pituitary-interrenal axis. Hypophysectomy reduced the Na-K-ATPase activity of gills in FW *A. rostrata* and cortisol treatment prevented this decrease (Butler & Carmichael 1972). But hypophysectomy had no effect on the branchial Na-K-ATPase activity in the FW *A. anguilla* (Milne et al. 1971). Similarly, Butler and Carmichael (1972) could not find a decrease in the Na-K-ATPase activity in interrenalectomized *A. rostrata* in FW. Need for more work in this area is indicated.

Sea water osmoregulation

Seawater teleosts being hypo-osmotic to their environment, are posed with the problem of osmotic loss of water. Compensatory mechanisms include drinking water which is absorbed by the intestine along with the salt, excretion of reduced volume of isotonic urine and extrarenal excretion of excess salt absorbed through the gut and via the gills. Consequently, the branchial Na and Cl outfluxes are much higher in SW fish than in their FW counterparts (Maetz 1976). Adaptation to SW environment takes place at various osmoregulatory organs, the gill, the gut, the kidney and perhaps, the urinary bladder. The action of cortisol is implicated in the adaptive mechanisms of these effector organs.

(i) *Intestine*

Intestinal absorption of water and salt is increased by the adaptation of eel to higher external salinity and this has been demonstrated *in vivo* in *A. anguilla* (Skadhauge & Maetz 1967) and *in vitro* in *A. japonica* (Oide 1967, Oide & Utida 1967, Utida et al. 1967). Hypo-

physectomy reduced the intestinal water flux in SW Japanese eel and prevented adaptation of the eel intestine to SW habitat, while administration of ACTH or cortisol to the hypophysectomized eel restored the water movement across the intestine (Hirano 1967, Hirano et al. 1967, Hirano & Utida 1968, Utida et al. 1972a, b). Cortisol also increased the Na and water movement across the intestine in FW *A. japonica* and in a similar fashion to that observed after the transfer of the eel from FW to SW (Hirano & Utida 1968, 1971).

Utida et al. (1972b) suggest that the increased water movement in SW eel intestine effected by cortisol is associated with the development of Cl⁻ pump. Cortisol administration to FW eel induced in the intestine a serosa negative potential, an increase in the short circuit current and an increase in the movement of salt and water, all characteristics observed in the SW adapted eel intestine. The findings that SW adaptation also increases the Na-K-ATPase activity of intestinal mucosa in the eel (Oide 1967, Jampole & Epstein 1970), cortisol increases the intestinal Na-K-ATPase activity in *Fundulus heteroclitus* (Pickford et al. 1970), and ouabain, an inhibitor of Na-K-ATPase activity seems to decrease the serosa negative potential of the SW eel intestine (Utida et al. 1972b) prompt one to speculate if the Cl⁻ pump generated in the intestine is associated with Na⁺/K⁺ exchange or active transport of Na as has been suggested for the teleost gill (Maetz 1976). Ando (1974) has demonstrated by simultaneous measurement of transepithelial potential difference (PD) and water flux that cortisol acts directly on the intestinal epithelium and increases the serosal negativity of the PD and the water permeability and suggested that tight junction and lateral intercellular space of intestinal epithelium may be one of the effective sites of cortisol action.

(ii) Gills

Gill adaptation to SW environment involves development of mechanisms to eliminate the excess salt taken in via the gut and the gills. SW-adapted fish have a higher turnover rate of Na and this rate increases with the increase in external salinity (Maetz 1970). Branchial adaptation seems to be under the influence of the pituitary-interrenal system inasmuch as hypophysectomy reduced the Na turnover rate and the Na outflux in the SW adapted *A. anguilla*, *F. heteroclitus* and *Platichthys flesus*, and administration of ACTH or cortisol restored the Na turnover rate and Na outflux to normal levels in the eel and partially in *F. heteroclitus* (Maetz et al. 1967a, b, Maetz 1969a, Langford 1971, Macfarlane & Maetz 1974). Similarly, interrenalectomy of the SW eel reduced the Na turnover rate and the Na outflux thereby increasing the plasma Na concentration, and cortisol restored these parameters to normal levels (Mayer et al. 1967, Maetz 1969). Cortisol or ACTH has also been observed to increase the Na-turnover rate in the intact eel and is thus considered as a salt-excreting factor (Mayer & Maetz 1967, Maetz 1969). Aldosterone which is not a natural hormone of the eel, has also been found to increase the Na turnover rate of the intact SW eel (Mayer & Maetz 1967).

Sea water adaptation has been shown to increase the gill Na-K-ATPase activity and in general, the enzyme activity in stenohaline marine fishes has been found to be much higher than in the FW species (Kamiya & Utida 1969, Jampol & Epstein 1970). Among the euryhaline species, Na-K-ATPase activity of gills is higher in SW-adapted fish than in FW fish (Maetz & Bornancin 1975, Dharmamba et al. 1975, Towle et al. 1977). Hypophysectomy reduced the gill Na-K-ATPase activity in SW fish and ACTH or

cortisol administration in these fish increased this enzyme activity to normal (*A. anguilla*: Milne et al. 1971, Langford 1971, *A. japonica*: Kamiya 1972, *A. rostrata*: Butler & Carmichael 1972, *F. heteroclitus*: Epstein et al. 1967, Pickford et al. 1970). Cortisol also increases the gill Na-K-ATPase activity in intact FW *A. rostrata* and *A. japonica* (Epstein et al. 1971, Doyle & Epstein 1972, Forrest et al. 1973a, Kamiya 1972) but in *A. anguilla* it did not seem to increase this enzyme activity in intact FW fish while increasing the activity in intact SW fish (Scheer & Langford 1976).

Chloride cells of the gill in which evidences indicate that Na-K-ATPase is localized, are considered the sites of ionic exchanges (Maetz & Bornancin 1975). During SW adaptation the number of chloride cells increases in parallel with the gill Na-K-ATPase activity in *A. japonica* (Shirai & Utida 1970, Utida et al. 1971), *A. rostrata* (Doyle & Epstein 1972) and *A. anguilla* (Thompson & Sargent 1977). Chloride cells of the gill also seem to be under the influence of cortisol as the administration of this hormone in the American eel increased the number of chloride cells along with the specific activity of the gill Na-K-ATPase (Doyle & Epstein 1972).

Parallel increase in Na outflux and gill Na-K-ATPase activity during SW adaptation suggests that Na-K-ATPase is associated with the Na transport across the gill in SW fish. But major part of the Na outflux in SW fish seems to take place by simple diffusion favoured by a transepithelial potential gradient across the gill, and independent of a transport carrier enzyme (Potts 1976, Maetz 1976). However, there are evidences for a Na^+/K^+ exchange component of Na outflux possibly mediated by Na-K-ATPase (Maetz 1969 b, 1976, Bornancin & De Renzis 1972, Maetz & Bornancin 1975, Potts 1976). Hypophy-

sectomy inhibited the Na^+/K^+ exchange component of the Na outflux in the SW flounder (Macfarlane & Maetz 1974) and lowered the Na^+/K^+ exchange flux as well as the gill Na-K-ATPase activity in the SW European eel while cortisol treatment increased the levels of both these parameters (Langford 1971) suggesting that Na-K-ATPase mediates the Na^+/K^+ exchange component of Na outflux and that these are under the control of pituitary-interrenal axis. Fairly high levels of Na-K-ATPase in the gills of hypophysectomized SW eels, higher than that has been found in FW eels, perhaps indicate that this enzyme may not be completely under the control of pituitary-interrenal system and that the increased salt load accompanying SW adaptation may be the cause for this effect (Langford 1971, Butler & Carmichael 1972, Kamiya 1972, Maetz 1974). Or, it is possible that once the increase in the enzyme activity has been induced during SW adaptation, the pituitary-interrenal system may not be essential for the maintenance of the higher activity in SW since it has been shown that hypophysectomy of SW-adapted *A. anguilla* did not reduce the Na-K-ATPase activity while the same operation in FW eel before transfer to SW inhibited the increase of Na-K-ATPase activity, and cortisol treatment before transfer to SW increased the enzyme activity (Scheer & Langford 1976).

It is evident that cortisol is involved in the Na transport across the gill of SW fish. It seems to increase the Na outflux by (i) inducing an increase in Na-K-ATPase activity of the gill, (ii) increasing the number of chloride cells in the gill thereby increasing the number of sites of ion transport and (iii) perhaps by altering the fine structure of the chloride cells (Doyle & Epstein 1972). However, further investigations are necessary to elucidate the molecular mechanisms underlying the effects of cortisol and to study the role of cortisol in the ultrastruc-

tural modifications of chloride cells observed during SW adaptation (Sardet et al. 1978).

(iii) *Kidney and urinary bladder*

Little is known of the endocrine control of kidney function during SW adaptation. Hypophysectomy seems to inhibit the renal adjustment of reducing the urine output when the fish is transferred from FW to SW in *A. anguilla* (Chester Jones et al. 1965) and in *F. kansae* (Stanley & Fleming 1966). But it is not known if cortisol or ACTH rectifies this defect. A possible role in osmoregulation for teleost urinary bladder has been suggested and it has been demonstrated *in vitro* that hormones regulate the movements of water and ions across the urinary bladder (Utida et al. 1972b, Johnson 1973, Bern 1975). In the SW-adapted *Gillichthys mirabilis*, cortisol increased the mucosa to serosa permeability to water and salt in the urinary bladder (Doneen & Bern 1975, Doneen 1976). This action of cortisol at the urinary bladder may have an adaptive value to the fish in conservation of water in SW environment and it would be of interest to study if this effect of cortisol is extended to the kidney tubule causing reabsorption of water.

(iv) *Esophagus*

Recently, Hirano and Mayer-Gostan (1976) have demonstrated that the esophagus of the SW *A. anguilla* is capable of selectively absorbing Na and Cl without water, thereby diluting (rather "desalting") the sea water ingested by drinking, even before it reaches the stomach and thus facilitates the function of intestine in water absorption. Hirano (1978) has indicated that cortisol may play a role in this "desalting" process of the esophagus, an interesting observation which requires investigation extended to other SW teleosts for studying the role of esophagus in osmoregulation and its endocrine control.

Although cortisol seems to play a more prominent role in the osmoregulatory mechanisms of SW fish, oddly, the circulating level of cortisol in SW eel has been found to be similar to that of FW eel; however, when an eel is transferred from FW to SW, a significant transitory increase in plasma cortisol has been observed soon after the transfer (Hirano 1969, Milne et al. 1971, Ball et al. 1971, Forrest et al. 1973b). The time course of development of the adaptive mechanisms of intestine and gill observed in the eel following transfer to SW, seems to suggest that this transient increase of plasma cortisol is critical for the SW adaptation of the fish (Hirano & Utida 1971, Forrest et al. 1973b). A latent period in the adaptation of the intestine and the gill has been observed after the increase in plasma cortisol. In *A. japonica* the plasma cortisol rises 2 hours after the transfer and the intestinal water transport increases after a lag and reaches a maximum in 48 hours (Hirano & Utida 1971) and in *A. rostrata*, the plasma cortisol increases 24 hours after the transfer, and the Na outflux gradually increases in parallel with the gill Na-K-ATPase activity, and reaches the rate of fully adapted SW fish in 9-14 days (Forrest et al. 1973b). The occurrence of a latent period is considered suggestive of the induction of some molecular or metabolic processes by cortisol, associated with the adaptive mechanisms. The delayed occurrence of the increase in Na⁺/K⁺ exchange component of Na outflux along with the branchial Na-K-ATPase activity during such sudden transfer to SW in *A. anguilla* (Bornancin & De Renzis 1972) further confirms this hypothesis. Interrenalectomy of FW *A. anguilla* before transfer to SW prolonged this lag period and also inhibited the Na outflux from reaching the rate of the eel fully adapted to SW (Mayer et al. 1967). Hypophysectomy of this eel before SW

transfer prevented the increase in the gill Na-K-ATPase activity and cortisol injection connected this impairment (Scheer & Langford 1976). Also, cortisol administration to FW *A. rostrata* before transfer to SW shortened the lag for Na outflux (Forrest et al. 1973a) and brought down the increase in plasma Na that otherwise occurred in untreated FW eel transferred to SW (Epstein et al. 1971). Thus cortisol seems to regulate the adaptive mechanisms for a SW habitat and prepare the euryhaline eel to face the osmotic stress during SW migration. The simultaneous occurrence of the transient increase in plasma cortisol and the rise in plasma Na in the sudden transfer experiments with eel (Forrest et al. 1973b) suggests that the increased level of plasma Na may be the stimulus for the higher rate of secretion of cortisol. It is also considered that while a transitory increase in plasma cortisol is necessary for initiating the induction of adaptive mechanisms in the osmoregulatory effector organs, a continued high level of plasma cortisol is not necessary for the maintenance of the adaptive mechanisms once induced (Hirano & Utida 1971). However, the similar plasma cortisol level in FW and SW eels does not eliminate the possibility of a higher secretion rate of cortisol in SW eel, but data on the turnover rates of cortisol in FW and SW fish are lacking. In the European eel the metabolic clearance rate of cortisol in SW fish seems to be twice that of FW fish while the plasma cortisol levels remain similar in both perhaps indicating a higher secretion rate in the SW eel (Leloup-Hatey 1978, personal communication).

Thus the role of cortisol as a mineralocorticoid in teleosts seems to be well established and evidences to date indicate that it is the dominant hormonal factor in the SW osmoregulation (Utida et al. 1972b, Johnson 1973).

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