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ROLES OF PROLACTIN IN SALMONIDS

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Since the pioneer finding by Pickford and Phillips (1959) that hypophysectomized *Fundulus heteroclitus* require prolactin (PRL) for survival in freshwater, PRL has been recognized as the principal freshwater-adapting hormone. Numerous studies have confirmed the osmoregulatory effects of this hormone at the branchial, renal, intestinal, bladder, and integumentary levels (see recent reviews: Loretz and Bern, 1982; Hirano *et al.*, 1987). However, as pointed out by Bern (1975), "no accurate generalization regarding prolactin dependency for freshwater survival will apply to the Teleostei as a group." This would particularly apply to salmonids for which hypophysectomy only induces a slight decrease of plasma ion levels in fresh water (Komourdjian and Idler, 1977; Björnsson and Hansson, 1983) leading one to question the osmoregulatory role of PRL in these fish.

Another well known characteristic of PRL is its wide spectrum of actions in vertebrates (Clarke and Bern, 1980; Hirano, 1986). However, in salmonids, most of the studies on PRL are related to its osmoregulatory role and no information is available on actions of this hormone on other physiological processes, such as reproduction, growth or metabolism. Isolation of pure hormone from pituitaries (Kawauchi *et al.*, 1983; Prunet and Houdebine, 1984) allowed the recent development of specific radioimmunoassays for salmonid PRL (Hirano *et al.*, 1985; Prunet *et al.*, 1985) and investigations on its biological role. Recent data presented in this paper will emphasize actions of PRL on osmoregulation, stress and reproduction.

PROLACTIN AND STRESS

Measurements of plasma PRL levels during particular physiological situations need, for interpretation, to avoid any bias due to stress conditions, which can be easily observed in salmonids (Schreck, 1982). While response of the pituitary-interrenal axis to stress has been widely studied in fish, little if any information is available on PRL. However this hormone has been shown to respond to stress in various mammalian species (Riegle and Meites, 1976; Raud *et al.*, 1971; Du Ruisseau *et al.*, 1979). Recently, Avella *et al.* (1989b) investigated the effects of chronic stress on PRL in juvenile coho salmon. Five to twelve hours after application of continuous confinement stress, an increase of plasma PRL levels was observed in freshwater adapted fish and two days after, PRL levels returned to control values. In seawater adapted salmon, application of the same stress during one day induced a similar increase of PRL levels although values were lower and significantly different from control only at 24 hours. Measurement of cortisol levels in these experiments showed that PRL always increased several hours after cortisol and the PRL peaks were of a shorter duration than cortisol peaks, arguing against a direct stimulation of PRL by cortisol. Moreover, Young and Prunet (unpublished data) did not observe any change of plasma PRL levels after cortisol treatment in juvenile coho salmon. Further studies are needed to characterize the mediator(s) involved in PRL response to stress.

What is the function of elevated PRL during chronic stress? As chronic stress is associated with disruption of hydromineral balance both in fresh water (FW) and seawater (SW) (Eddy, 1981; Redding and Schneck, 1983; Avella *et al.*, 1989a,b), PRL may have an osmoregulatory function during severe stress. However, lack of knowledge of the exact osmoregulatory role of this hormone in salmonids does not allow us to be more conclusive. In any case, the PRL response to stress must be considered when designing studies on PRL in salmonids.

PROLACTIN AND OSMOREGULATION

Information on the osmoregulatory role of PRL in salmonids may derive from studies of plasma PRL levels in fish facing various osmotic situations. In rainbow trout transferred from FW to SW, PRL levels decreased whereas the converse transfer induced an increase (Prunet *et al.*, 1985). Similar data were obtained in other salmonid species—chum salmon (Hasegawa *et al.*, 1987), Atlantic salmon (Prunet and Boeuf, 1985; Prunet *et al.*, 1989; Potts *et al.*, 1989) and coho salmon (Avella *et al.*, 1989a). Preadaptation to SW life, which develops during smoltification, is also associated with a decrease of plasma PRL levels which coincides with maximum hypoosmoregulatory ability of both coho and Atlantic salmon (Prunet *et al.*, 1989; Young *et al.*, 1989). This was further confirmed in a study of parr and smolt from the same Atlantic salmon population, indicating that such decrease of PRL level is characteristic of fish undergoing parr-smolt transformation (Prunet and Boeuf, 1989). The above results suggest both elevated

PRL functiona in FW adaptation and that depressed PRL levels may be important for development of SW osmoregulatory mechanisms.

We have also examined FW trout exposed to artificial media containing various external calcium and sodium levels, which induce important osmoregulatory changes, especially at the level of the gills (Laurent *et al.*, 1985; Perry and Wood, 1985; Avella *et al.*, 1987). After transfer to FW with different Ca^{++} but normal Na^+ levels (FW + 10 mM Ca^{++} or deionized water-DW - + 2.6 mM Na^+) plasma PRL levels remained unchanged (Prunet, unpublished), suggesting that PRL is not involved in Ca^{++} regulation in rainbow trout as suggested by Flik and Perry (1989). However transfer to artificial water without Na^+ (DW or DW + 1 mM Ca^{++}) induced a decrease of PRL levels which was more pronounced in the presence of Ca^{++} (Prunet, unpublished). Adaptation to such an environment is usually associated with increase of branchial Na^+ influx and Na^+ , K^+ -ATPase activity together with proliferation of chloride cells on gill secondary lamellae (Avella *et al.*, 1987).

These last results and those obtained in the SW transfer experiments lead us to raise the possibility of an inhibitory effect of PRL on gill Na^+ , K^+ -ATPase activity and on development of gill chloride cells as already suggested in other fish by Pickford *et al.* (1970) and Foskett *et al.* (1982). This hypothesis was tested both in SW-adapted rainbow trout and FW Atlantic salmon smolt showing high gill Na^+ , K^+ -ATPase activity. Ovine PRL treatment (cholesterol implant during two weeks) induced only a slight increase of plasma osmotic pressure in rainbow trout and did not impair SW adaptability of salmon smolt (Prunet and Boeuf, unpublished data). Moreover no significant changes in gill Na^+ , K^+ -ATPase activity was observed after oPRL treatment in both experiments. These results suggest that, in salmonids, PRL may not be involved in the control of active salt extrusion at the gills. Moreover, in a recent study on sodium balance in adult Atlantic salmon, Potts *et al.* (1989) showed that Na^+ uptake is fully activated immediately following transfer from SW to FW whereas plasma PRL levels only increased eight hours after transfer. It therefore seems unlikely that PRL could be involved in the control of active Na^+ uptake during adaptation to FW. Thus, in salmonids, PRL may not be involved in control of active Na^+ transport at the gills. Rather, PRL may control epithelial permeability as suggested by numerous studies (see reviews: Clark and Bern, 1980; Loretz and Bern, 1982; Hirano, 1986). More knowledge on the osmoregulatory role of PRL is still needed before any conclusion can be drawn.

PROLACTIN AND REPRODUCTION

Studies of reproductive effects of PRL were initiated by monthly measurements of plasma PRL during the reproductive cycle of female rainbow trout. Although no significant changes were observed between June and January (ovulation period), an increase in PRL occurred one month after ovulation, and the hormone

remained elevated at least until May (Prunet, B Th Björnsson and C. Haux, unpublished). The seasonal study was further refined by weekly sampling around ovulation. During the 17α hydroxy 20β dihydroprogesterone (17-20-P) peak, PRL remained low but increased four weeks after ovulation and later when 17-20-P levels had decreased to low levels. Possible feed-back effects of steroid on pituitary PRL were also investigated: only 17α hydroxyprogesterone treatment (1 or 10 mg/kg) was able to induce a significant decrease of PRL levels in immature rainbow trout whereas both testosterone and estradiol- 17β were ineffective.

Possible reproductive effects of PRL were further confirmed by *in vitro* studies of ovarian steroidogenesis. Salmon PRL potentiated GtH stimulation of estradiol or 17-20-P production by incubated ovarian follicles from rainbow trout (Fostier and Prunet, unpublished data). Similar effects of PRL on female steroidogenesis have been reported in other fish species (Singh *et al.*, 1988; Tan *et al.*, 1988).

These data substantiate a role for PRL in fish reproduction. Although preliminary, these results indicate that PRL-steroid relationship may be the converse in salmonids to what is observed in mammals: *in vivo* progesterone treatment decreases plasma PRL levels, and PRL, when active, stimulated steroidogenesis in females. The function of PRL in reproduction needs to be examined in detail, especially during the early phase of female reproductive cycle, where significant estradiol production has been demonstrated (De Mones *et al.*, 1989).

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