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Effects of Nutritional Status and Environmental Factors on The Endocrine Regulation of Feeding in Freshwater Fish

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In fish, food intake is ultimately regulated by feeding centers of the brain, which receive and process information from endocrine signals from both brain and peripheral tissues such as the gastrointestinal tract. These endocrine signals induce [orexigenic, such as orexin, neuropeptide Y (NPY) and ghrelin] or inhibit [anorexigenic, such as cocaine and amphetamine regulated transcript (CART), leptin, peptide Y (PYY), cholecystokinin (CCK), proopiomelanocortin (POMC)] food intake, and maintain energy homeostasis (1, 2). Levels of energy stores, feeding status (e.g. fasting) and diet composition, as well as environmental conditions (e.g. temperature, pH, oxygen levels) influence feeding and the expression of endocrine appetite regulators.

Food quantity and quality affects feeding

Fasting induces "hunger" in fish and usually increases the expression of orexigenic hormones and decreases that of anorexigenic hormones (1, 3). However, the effects of fasting on appetite regulating hormones appear to depend on the species examined and its feeding habits, the duration of the fasting period and the tissue examined (1). For example, in Characiformes, fasting increases orexin brain expression in all species examined to date, but decreases CART brain expression in the Serrasalmidae family but not the Characidae family, and decreases gut CCK in herbivore species but not carnivores (4). In platyfish, *Xiphophorus maculatus*, fasting decreases CCK expression in both brain and intestine (5), similar to goldfish Carassius *auratus* (6) and grass carp *Hypophthalmichthys molitrix* (7) whereas in pacu *Piaractus mesopotamicus*, fasting decreases CCK in gut but not in brain (8) and in dourado *Salminus brasiliensis*, fasting has no effect on CCK in either brain or gut (9). Appetite regulators are also affected by the act of feeding and many display periprandial changes in expression, higher expression levels of orexigenic factors and anorexigenic signals occurring before and after mealtime, respectively (1, 3).

Diet composition affects food intake and the expression of appetite-regulating hormones in fish. For example, high fat diets affect brain NPY expression in goldfish (10) and NPY, CART and POMC expressions in rainbow trout *Oncorhynchus mykiss* (11). However, these changes are species-specific and depend in particular on the feeding habits. For example, in pacu, a herbivorous species, food intake and expressions of orexin, CART, CCK and leptin are not affected by replacement of fish protein with soy protein, suggesting that pacu is able to tolerate a diet rich in plant material (8). However, in dourado, a carnivorous species, food intake and the expressions of the anorexigenic hormones CCK and PYY in the intestine and in pyloric caeca decrease with increasing dietary plant protein contents (Sabioni and Volkoff, unpublished).

Environmental factors affect feeding

The influence of temperature on feeding varies depends on species and its habitat. In general, food intake increases with moderate temperature increases, and decreases when temperatures are outside the fish optimal temperature range (12, 13). In goldfish, higher temperatures increase feeding along with increases in the expressions of orexigenic hormones (brain orexin) and decreases of that of anorexigenic hormones (brain CART, and intestine YY and CCK) (14). In Atlantic salmon *Salmo salar,* temperature-induced variations in feeding have been correlated to changes in plasma concentrations of ghrelin (15) and leptin (16).

Low pH, often due to increases in CO_2, usually decreases food intake in fish, as seen in goldfish (14), fathead minnows *Pimephales promelas* (17) and Nile tilapia *Oreochromis niloticus* (18). In goldfish, this decrease in feeding is mediated by increases in the expressions of anorexigenic peptides [CART1 and CART2 in the hypothalamus and CCK and PYY in the intestine] (14). However, species-specific differences in response have been shown. For example, high CO_2 levels do not alter the behavior of silver carp *Hypophthalmichthys molitrix* (19), which might be due in part to an adaptation to low environmental oxygen conditions seen in the habitat of this species (20).

Low oxygen levels (hypoxia) usually decreases feeding (21), and this response is concomitant with changes in the expression of appetite regulators. For example, hypoxia increases hepatic leptin expression in common carp *Cyprinus carpio* (22) and zebrafish *Danio rerio* (23) and decreases in hypothalamic leptin in carp (22).

Other environmental factors such as light, turbulence, salinity, stock densities and pollutants have also been shown to affect feeding and appetite regulators [see (12, 24, 25) for review].

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