

Environmental effects on feed utilization

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Abstract

Both external and internal factors affect the response of fish to variations in dietary quantity and quality. An attempt is made to review major, recent studies on the series of intermediate steps (intake, digestion, metabolism, excretion and retention) involved in the global response of fish to environmental changes. Among these external factors, greater attention is however devoted to those that are the most important natural effectors within the aquatic environment: temperature, ambient oxygen and salinity. The changes brought about by a change in temperature at different levels of nutrient utilization have been studied to a great extent in the recent past. As temperature affects in the first instance, the voluntary food intake, a discussion on current nutrient requirement data should preferably be dealt with in absolute terms. While critical levels of oxygen below which growth is hindered are sufficiently defined for many species, precise data on the direct effects of oxygen deficiency on nutrient utilization are still fragmentary. With regard to salinity, a distinction between stenohaline and euryhaline species and a knowledge of the physiological mechanisms corresponding to their life cycles are required before attempting comparative analyses. Within euryhaline species, best performances are noted at salinities isotonic to the internal medium. Despite accumulating evidence on the effects of cyclical phenomena, the chronobiological approach to fish culture remains practically unexplored.

Introduction

Some recent reviews deal with the effects of abiotic factors on growth (Brett 1979) and other physiological functions (Ali 1980). Fry (1971) classified these abiotic factors into four main categories: controlling, limiting, masking or directive factors inasmuch as they affect growth and/or other metabolic functions in different ways. In most of these works, greater emphasis was placed on the interaction between ration size and an environmental variable such as temperature as it affected growth (Elliott 1982). The present paper discusses the effects of some these factors

(temperature, salinity and oxygen availability) on several of the intermediate steps involved in nutrient utilization which contribute to the eventual modifications in terms of growth. The choice of these three factors as the most important effectors of the aquatic environment is due to the predominant roles they play in poikilothermy, osmoregulation or energy metabolism.

Effects of temperature

Water temperature is considered to be the major environmental factor that controls food utilization at all levels and all stages of fish growth. Temperature

affects maturation, gonadal development, early growth, food intake, maintenance requirements, metabolic rates, the whole enzyme machinery, membrane functions and so on. The effects of temperature have been considered both in terms of acute, temporal changes during the course of acclimation to a new temperature and in terms of homeostatic compensations or adaptational compromises to a changed environment (Smith 1976). In most teleosts, the optimal temperature for maximum growth appears to be thus more or less correlated with the specific final preferendum in a thermal gradient (McCauley and Casselman 1981). However, the fishes' responses in terms of food intake or growth also would differ depending on whether they were grown under constant or fluctuating, cyclic temperatures (Hokanson *et al.* 1977; Cox and Coutant 1980).

Early development

Temperature affects the utilization of endogenous reserves during ontogenesis of teleosts (Heming 1982; Heming *et al.* 1982; Kamler and Kato 1983). As embryonic development is greatly affected by temperature, the duration of early development of almost all teleosts is commonly expressed in terms of degree days or thermal units. High rearing temperatures reduce the efficiency of yolk utilization in both fresh water and marine species (Jager *et al.* 1981; Heming 1982; Kamler and Kato 1983; Quantz 1985). Utilization of endogenous nitrogen reserves during early ontogenesis of the common carp is variably affected by temperature depending upon the stage of development, with the Q_{10} values varying between 2.3 and 3.5 (Kaushik *et al.* 1982). In chinook salmon, maximum tissue or alevin weights varied inversely with temperature (Heming *et al.* 1982). According to these authors, temperature and the timing of initial food presentation interact to create optimum zones of feeding and biomass increase. In a majority of species, the metabolic rate of embryos at hatching is directly correlated with temperature. The influence of temperature appears to be greater than that of initial body size (Dabrowski *et al.* 1984) and is likely to affect the nutritional requirements of larvae.

Intake and requirements

Voluntary food intake is one of the variables most affected by temperature. Weight-specific food intake decreases with size of fish, and increases with temperature (Elliott 1982). Although it is well-recognized that the adjustment of voluntary food intake is to meet the energy requirements, relatively little data on the nutritional requirements in relation to water temperature are currently available.

Cho and Slinger (1980) showed that the maintenance energy requirements of rainbow trout increased with increasing temperatures. In several species of fish, the routine metabolic rate increases with temperature but only within a limited range of temperatures (Caulton 1977, 1978; Ott *et al.* 1980). Caulton *et al.* (1977) distinguished three phases in the relation between oxygen uptake rates of tilapia and water temperature with different Q_{10} value at each range of temperature to which the fish were acclimatized. Differences between cyclic and constant temperatures are also noticed with respect to standard or routine metabolic rates (Dulthie and Houlihan 1982; Vondracek *et al.* 1982).

As regards the protein requirements for growth, the early works on chinook salmon (Delong *et al.* 1958) showed some temperature dependency. Later works (Possompes 1973; Slinger *et al.* 1977; Cho and Slinger 1978) on rainbow trout did not confirm such an increase in protein requirements with the rise in temperature. The assumption that the greater absolute need of the trout for protein at higher temperatures are satisfied through increased intakes of even low protein diets (NRC 1981) can only be strengthened if available data are recalculated in absolute terms, as unit protein need per unit weight gain, for instance.

Digestion and absorption

At the digestive level, the rates of transit of food-stuffs through the digestive compartments, digestibility of major nutrients, the activities of digestive enzymes are all affected by water temperature to which the fishes are adapted. Both compensatory and non-compensatory mechanisms

are involved as regards the digestive enzymes. Hofer (1979b) showed that under natural conditions, proteolytic and amylolytic activities in the roach (*Rutilus rutilus*) and the rudd (*Scardinius erythrophthalmus*) were correlated with the seasonal temperature cycles. In rudd, the amylolytic activity was more dependent on season than on temperature (Hofer 1979a). Specific activities of trypsin and chymotrypsin were the same at 10 and 15°C in rainbow trout (McLeese and Stevens 1982), whereas in brook trout, perfect thermal compensation for the specific activity of pepsin was evidenced (Owen and Wiggs 1971). Acclimation to higher temperatures increases the absorption (Wedemeyer 1973; Groot *et al.* 1983) and metabolism (Yamawaki 1983) of carbohydrates as well.

Gastric evacuation and transit rates increase with increasing water temperatures in most teleosts (Fange and Grove 1979). Fauconneau *et al.* (1983) analyzed the effects of a rise in temperature from 10 to 18°C, on the fractional evacuation rates from different compartments within the digestive tract of rainbow trout. From their data, it would appear that a rise in temperature would lead to an increase in transit rates in all compartments and that adaptation to a new temperature regimen would take place within 7 days of transfer. Such increased transit rates and the consequent decrease in duration of contact between nutrients and the digestive enzymes or absorptive surfaces in the digestive tract do not, however, seem to affect the digestibility of major nutrients. On the contrary, Choubert *et al.* (1982), working under identical conditions, showed that digestibilities of protein, energy and dry matter were improved at 18°C. An increase in food intake and in rates of digestion and absorption would offset any disadvantage resulting from an accelerated transit of nutrients through the digestive tract consequent to the increase in temperature. This is also exemplified by the results of Kaushik (1981) on nitrogen and energy budgets in rainbow trout. The beneficial effects of a rise in temperature on overall nitrogen or energy retention were more attributable to the increased food intake rather than to any significant improvement at either digestive or metabolic levels. The nitrogen or energy losses (fecal,

branchial and urinary), relative to intake were practically the same at 10 and at 18°C.

Intermediary metabolism

Of the many enzymes of the intermediary metabolism, only a few have been subjected to detailed studies with respect to thermal acclimation of fish. The overall aspartate aminotransferase (EC 2.6.1.1) levels in trout liver increases with increasing temperature (Jurss 1979). In carp, seasonal effects have been found to be superimposed on the effects of temperature (Lacombe 1973). Specific activities of both aspartate and alanine (EC 2.6.1.2) aminotransferases decreased when carp at natural temperatures of 7, 15 and 20°C underwent a rapid rise of 8°C; when carp at summer water temperature of 25°C was acclimated to 33°C, the specific activities increased. Of the several enzymes involved in ammonio- and ureogenesis in trout, only arginase (EC 3.5.3.1) showed perfect thermal compensation to a rise in temperature (Vellas *et al.* 1982). Other enzymes like glutamate dehydrogenase (EC 1.4.1.3), glutaminase (EC 3.5.1.2) and uricase (EC 1.7.3.3) showed an increase in activity immediately after transfer and remained unchanged.

Qualitative changes

As regards the body composition of fish, no definite pattern emerges since variations in the proximate composition of fish in relation to temperature seem to be species-specific. On the contrary, a definite interaction between diet quality and temperature exists as was demonstrated by Atherton and Aitken (1970).

Protein synthesis rates have been found to be affected by temperature with Q_{10} values ranging from 2 to 20 depending on the species, tissues or the temperature ranges (Haschemeyer *et al.* 1979; Smith *et al.* 1980; Fauconneau 1984). Drawing on data obtained by Kaushik (1981) and Fauconneau and Arnal (1985), it can be shown that an increase in temperature increases intake, protein synthesis

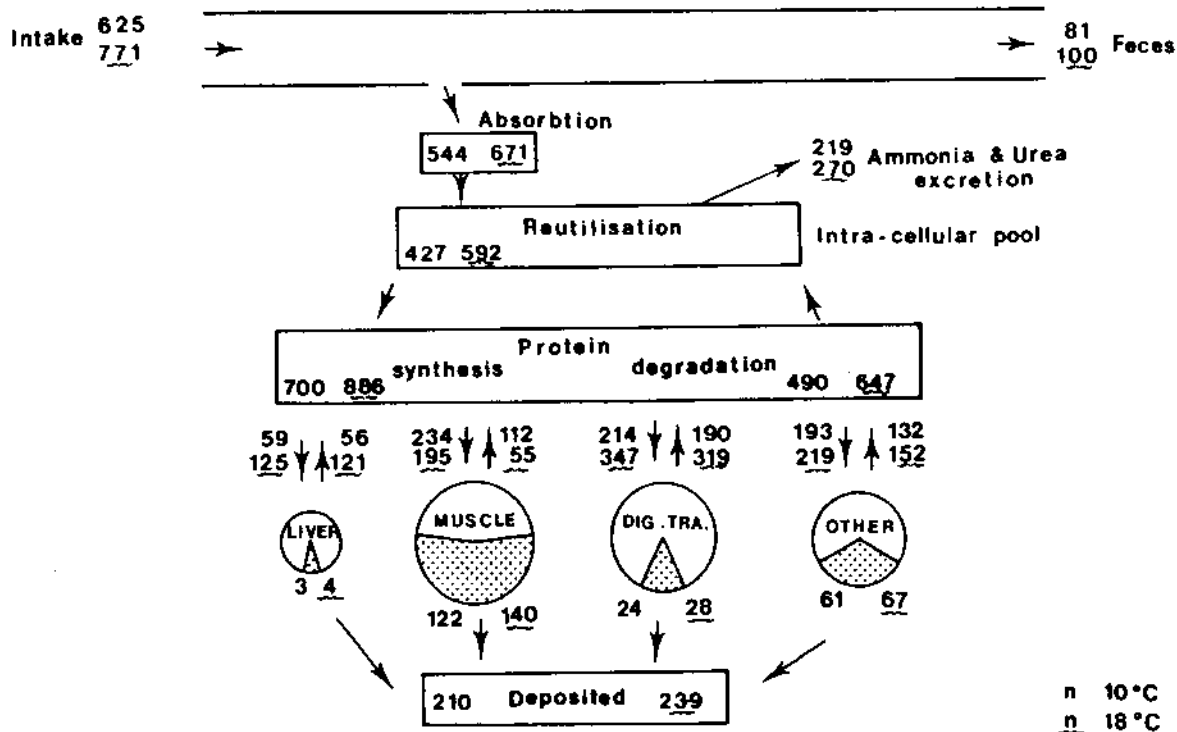


Fig. 1. Effect of rise in temperature from 10 to 18° on protein metabolism in rainbow trout of 100 g BW (units: mg Protein/100 g BW/day).

and breakdown and also re-utilization at the intra-cellular level (Fig. 1). The relative weights of different organs or tissues in rainbow trout were also affected by water temperature (Fauconneau and Arnal 1985). In warm-acclimated trout (18°C), the relative sizes of liver and the digestive tract decreased. As these organs have high rates of protein turnover, which are again affected by the temperature, it should be possible to divert protein deposition towards edible tissues through manipulations of temperature.

Effects of salinity

Depending on their natural aquatic habitat and their capacity of adaptation to different salinities, fishes can be classified into several broad categories (Brett 1979). Based on such a classification, salinities at which optimal growth rates are observed for different kinds of fish vary (Table 1). For most fresh water, euryhaline fish, this optimal

Table 1. Optimal salinity ranges for growth of different types of fish

Type*	Optimal range (ppm)	Examples of species
Fr - St	0-12	Poecilia
An - Eu	0-19	Salmonids
Ca - Eu	13-35	Mulletts
Fr/Sa - Eu	10 (0-35)	Tilapia
Sa - Eu	19-35	Paralichthys

* Classification according to Brett (1979). Fr-St, freshwater stenohaline; An-Eu, anadromous euryhaline; Ca-Eu, catadromous euryhaline; Fr/Sa-Eu, euryhaline; Sa-Eu, saltwater euryhaline.

salinity is around 10 ppt, corresponding to the intracellular osmotic concentration. This is the case for rainbow trout, tilapia and even for other anadromous migratory species, at least during their early stages (Clarke *et al.* 1982). For few marine species, optimal growth is observed at salinities in the range of 19 to 35 ppt. The effects of salinity on

other physiological and metabolic functions are also variable depending on the species and its osmoregulatory capacity.

Early development

The effects of salinity on early development have been studied in several fresh water, estuarine or marine species (Alderdice *et al.* 1979; Davenport *et al.* 1981; Jager *et al.* 1981; Lee and Menu 1981), mostly in terms of permeability of the chorionic membranes. Salinity tolerance in fresh water teleosts has been found to increase as development proceeds. In turbot, the efficiency of yolk utilization was linearly related to water salinity (Quantz 1985): at 32 ppt, the efficiency was greater (87%) than in brackish water (17 ppt, 51%).

Nutrient requirements

Currently, no data are available on protein needs of a euryhaline species at the whole range of salinities to which it can be adapted. Zeitoun *et al.* (1973, 1974) observed only slight differences in the protein requirements of rainbow trout and coho salmon at salinities of either 10 or 20 ppt. Lall and Bishop (1979) showed that protein and lipid utilization in rainbow trout adapted to fresh water and sea water differed and concluded that the protein requirement was higher in the latter. Some differences in the protein-sparing action of fats have been found in rainbow trout grown at 8 and 20 ppt (Jurss *et al.* 1985). A high protein-low fat diet was found to be more effective than a low protein-high fat diet for rainbow trout grown at 20 ppt. Best growth and feed efficiencies were noted at a salinity of 8 ppt (Jurss *et al.* 1985).

The works of Shaw *et al.* (1975) on the Atlantic salmon led to conclusions similar to those of Zeitoun *et al.* (1973, 1974) except that at salinities above 29 ppt, the maintenance needs were increased. This salinity of 29 ppt seems to be a critical level for rainbow trout beyond which significant changes within the intracellular pools occur. Free amino acids are known to take an active part in osmo-

regulation in fish (Forster and Goldstein 1976; Ahokas and Sorg 1977; Lall and Bishop 1979), and during the course of adaptation to sea water, Kaushik *et al.* (1977) found a significant increase in muscle free amino acid levels at salinities above 29 ppt.

Roberts (1977) found that the endogenous nitrogen excretion (ENE) in rainbow trout was lowest at the isotonic salinity of 10 ppt and higher in both fresh water and 20 ppt salinity-adapted fish. From the works of Kaushik and Luquet (1977a), it would appear that the maintenance protein requirements of trout decrease with increasing salinity (Table 2). In fish adapted to fresh water and

Table 2. Data on the effects of salinity on requirements of selected salmonid species

	Species	Fw	10 ppt	20 ppt	Sw
<i>Growth</i>					
Protein (% diet)	RBT	35-40	40	45	-
	Coho	-	40	40-50	-
Arginine (% diet)	RBT	1.2-1.6	-	1.0	0.8
<i>Maintenance</i>					
(mgN/Kg/d)	RBT	4.6	-	-	2.1
(mgN/Kcal)	RBT	17.7	-	-	18.2

Coho, coho salmon; RBT, rainbow trout.

full-strength sea water (35 ppt), the maintenance needs were respectively 4.6 and 2.1 mgN/kg/d; protein contribution to energy expenditure was however unaffected by water salinity (18 mgN/kcal). A similar decrease in the requirement for an essential amino acid, arginine, involved among others in urea synthesis, with an increase in salinity was also shown by Kaushik (1979).

Digestibility and absorption

Digestible energy of several feedstuffs was found to be increased in sea water adapted salmonids (Lall *et al.* 1985). Absorption and transport of individual amino acids are also affected by water salinity in rainbow trout (Kaushik and Luquet 1977b;

Dabrowski and Leray, unpublished). Postprandial blood free amino acid levels increased more rapidly in fresh water trout than in those adapted to sea water. Absorption of minerals from the ambient water are also of importance in those adapted to sea water (Lall and Bishop 1979).

Enzymes of intermediary metabolism in rainbow trout plasma are most active in salinities of 10 ppt (Sauer and Haider 1979). On the other hand, in the kidney of trout, no differences in the activities of glutamate dehydrogenase (EC 1.4.1.2), alanine and aspartate aminotransferases (EC 2.6.1.2, EC 2.6.1.1), the lipogenic NADP-isocitrate dehydrogenase (EC 1.1.1.42), glucose-6-phosphate dehydrogenase (EC 1.1.1.49) and 6-phosphogluconate dehydrogenase (EC 1.1.1.43) were little affected by salinities upto 20 ppt (Jurss *et al.* 1985).

Energy and protein metabolism

Leray (pers. comm.) showed that the energy charge in rainbow trout was higher in sea water than in fresh water, indicating lesser energy demands at higher salinities. Metabolic rates of juvenile carp were also found to decrease with increasing salinities (from 0 to 11 ppt; Maceina *et al.* 1980). Adaptation to sea water led to an increase in liver protein synthesis in both rainbow trout and coho salmon (Guillaume *et al.* 1984, 1985). They suggested that gluconeogenesis and lipogenesis were decreased in sea water adapted salmonids. Similar observations can also be made with respect to marine fish. When sea bass were transferred from sea water (38 ppt) to a lower salinity (4 ppt), an increase in oxygen uptake and in the respiratory quotient were recorded (Garin 1984). Oxydative catabolism of glucose and acetate were also higher at lower salinities. From the forementioned works it appears that gluconeogenesis and protein-sparing effects are higher at lower salinities than in sea water. Further controlled experiments at wider ranges of salinities are necessary to elucidate such differences before application to practical fish culture.

Effects of ambient oxygen

The efficiency of water as a respiratory medium depends to a great extent on the solubilities of oxygen and carbon dioxide in a given body of water. This is all the more important as the concentration of oxygen in air-saturated water is about 30 times lower than that of the air and that the solubility of oxygen is further affected by water temperature and salinity. More is known on the oxygen requirements of fish as affected by these environmental factors (EIFAC 1971) than on the effects of ambient oxygen concentrations on the efficiency with which the available nutrients are utilized.

Energy metabolism

Hypoxia is known to affect blood oxygen carrying capacity with considerable temperature effects (Nikinmaa 1981). Under hypoxic conditions, severe disturbances of energy metabolism have been recorded (Kutty 1972; Jorgensen and Mustafa 1980a, b): increase in blood glucose, lactate and glycolysis. Kutty and his co-workers have shown that oxygen availability affects respiratory quotients and also the relative contributions of protein to energy needs (Kutty 1972; Kutty and Peer Mohammed 1975; Peer Mohammed 1981). Transition from an aerobic to an anaerobic metabolism has been cited as one of the main consequences of a decrease in oxygen availability and species-specific differences occur. Tolerance to hypoxic conditions is greater during early embryonic stages than in larval or post-larval stages (Davenport 1983). A progressive increase in sensitivity to decreased oxygen tensions has been recorded in almost all teleosts.

Protein metabolism

Protein synthesis has been found to be affected by ambient oxygen levels in *Fundulus* sp. (Jackim and Laroche 1973). A decrease in oxygen saturation from 100 to 50% led to significant changes in protein metabolism of rainbow trout grown at 15°C (Bahamondes-Rojas 1982). She showed that the

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Table 3. Effects of ambient oxygen on nitrogen utilization in rainbow trout*

	Oxygen 8	Levels (ppm) 5
Intake (% BW/d)	2.20	1.20
F.C.R.	2.00	2.60
N-excretion (% NI)	34.50	40.50
S.G.R. (%/d)	0.49	0.20
Plasma FAA (μ moles/ml)	6625	5475
Total adenylate pool (μ moles/g)	1.33	1.19
Energy charge (liver)	0.64	0.61
HSI	1.20	1.00

*Rainbow trout, 200 g initial wt; after Médale (1985)

renewal rates were decreased in plasma and in the muscle, whereas in the liver, it was increased. Médale (1985) found that trout grown at an ambient oxygen concentration of 5 mg/l, had decreased food intake, depressed growth and food conversion relative to those grown in normoxic (8 mg/l) water (Table 3). Efficiency of nitrogen utilization was also decreased.

As in the case of salinity, much work remains to be done on the effects of ambient oxygen for different life stages and species, giving more consideration to the overall energy balance, especially on the heat increment of feeding and on the preferential energy sources. Different tissues have different oxygen requirements and the effects of transitory hypoxic conditions (for instance, due to the increased oxygen demand during the post-absorptive state) on metabolic activities of specific tissues are not clearly understood.

Effects of periodic changes

Of the forementioned environmental factors, under natural conditions, temperature undergoes diel as well as seasonal changes. Among other environmental parameters, photoperiod and in some geographically limited areas, salinity are also susceptible to such periodic changes. Many of the neuroendocrine mediated physiological responses

are under control of an integrated set of environmental stimuli (Poston 1978). The main efforts in the understanding of the effects of changing environmental stimuli have been restricted to the field of endocrinology and not much is known on the repercussions at the nutritional level. With regard to salmonids, the practical advantages of controlled manipulations of the photoperiod on reproductive strategies are only too well known.

Simulation of seasonal or other photoperiods have provided variable results. Reports of reduced growth with extended exposure to light are also given for few salmonids (Phillips *et al.* 1958), whereas extension of natural photoperiod was beneficial for Atlantic salmon smolts (Saunders and Henderson 1970) and for sunfish (Gross *et al.* 1965). In coho salmon, an increasing photoperiod cycle was shown to be beneficial in terms of growth (Clarke *et al.* 1981). On the other hand, in chinook salmon, these same authors found no significant effect of photoperiod, while the temperature \times photoperiod interaction was great.

Observations are abundant on the variations in the diurnal feeding activities of various fishes under natural conditions. The effects of feeding frequencies on growth and feed utilization have been experimentally studied in several species (see Brett 1979). Kaushik (1980) found that nitrogen utilization was affected by the number and size of meals given to rainbow trout. Digestibility and transit rate of nutrients are also known to be influenced by the number of meals (Possompes 1973; Choubert *et al.* 1984).

Few works have demonstrated that circadian feeding times can influence feed consumption, growth and overall efficiency. In catfish, Sundararaj *et al.* (1982) demonstrated that maximal food intake and growth occurred when fish were fed during early dark. In goldfish and carp, similar effects of photoperiod were recorded by Noeske and Spieler (1984). The different neuroendocrine mediated environmental influences on metabolism and reproduction of salmonids and the potential interest of such environmental manipulations have been dealt with in length by Poston (1978). Diurnal, endogenous rhythms have been recorded for various endocrine functions and also in terms of

plasma metabolites (Kaushik and Oliva-Teles 1985). No doubt more systematic research is needed to fill in the gaps, such as on the possible variations in requirements, in energy utilization, and on the effects of differential distribution of protein-yielding and energy-yielding nutrients, but even with currently available knowledge, concerted efforts of physiologists and practical aquaculturists is most needed.

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