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Some aspects of the biology of feeding and growth in fish

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The biology of fish, and in particular the biology of growth and reproduction, has been the subject of vast study for many decades. In recent years, 4000–5000 original research papers have been published annually in over 400 journals covering all aspects of fish biology (Cvancara, 1992). A number of recently published books review fish nutrition (Halver, 1989; Steffens, 1989; Wilson, 1991); bioenergetics, feeding biology and growth (Hoar *et al.* 1979; Tytler & Calow, 1985; Weatherley & Gill, 1987); ecology and ecophysiology (Wooton, 1990; Rankin & Jensen, 1993), and the chemical composition of fish (Love, 1980).

The research effort devoted to fish is not surprising given that fish species (about 22 000 had been described by the mid-1980s) constitute almost half the total number of recognized extant vertebrate species (Nelson, 1984). Teleosts are by far the most abundant (in number of species) and diversified group of all the vertebrates. About 21 000 species placed in thirty-five orders, 409 families, and 3876 genera represent approximately 96% of all extant fishes. About 39% of fish species occur exclusively or mainly in freshwater lakes and rivers that cover only 1% of the Earth's surface and accounts for less than 0·01% of its water. Fish exhibit an enormous diversity in their behaviour, morphology and physiology adaptations, in the habitats they occupy, and in their sources of nutrition.

A further impetus to research relates to the management and conservation of wild fish stocks, and to the development of aquaculture. Fish and fish products such as fish meal, are major sources of nutrition for both humans and farm animals. On a global basis, in 1989, the human consumption of fish represented about 30% of the estimated total consumption of meat which was 51·6 kg/person per year (New, 1991). Fish provides a good dietary source of high-quality protein, while the lipids found in fish, especially the *n*-3 polyunsaturated fatty acids such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), may be effective in the prevention and treatment of a number of human diseases. A knowledge of fish biology, and the principal factors which determine growth and body composition, is important when considering the role of fish as a source of nutrition. The objective of the present paper is to provide a brief introduction to the biology and physiology of growth in fish.

THE NATURE OF GROWTH IN FISH

The generalized growth pattern in fish is different from that found in higher vertebrates. In mammals and birds, subject to individual variability, there is a characteristic rate of growth and ontogeny for each species and a characteristic adult size, which normally coincides with sexual maturation (Asdell, 1946). In contrast, organismic growth in fish is demonstrably plastic in nature. Growth in fish is essentially indeterminate, to the extent that it is difficult to establish the ultimate maximum body size of individuals of a particular species. Fish appear to continue growing for as long as they live. Various ecological and evolutionary theories to account for the difference in growth pattern and intraspecific growth variation between fish and higher vertebrates are discussed by Weatherley & Gill (1987).

The final adult body size so characteristic of sexual maturity in higher vertebrates is not usually observed in fish. In fish, maturity appears to depend on the attainment of a critical body size; the age at which this critical size is reached will depend on somatic growth rate. In Arctic charr (*Salvelinus alpinus*) for example, wild populations of fish typically mature at an age of 4–7 years, but under farming conditions, charr normally mature at an age of 1–3 years (Jobling & Baardvik, 1991). Policansky (1983) concluded that fish generally mature at the earliest age at which they are developmentally able to do so. A positive correlation between growth rate and age of maturity has been shown for almost every salmonid species (Thorpe, 1986), and this may depend on the trophic opportunities at critical times of the year when they are sensitive to the triggering of the maturation process. In salmonids, initiation of maturation is known to be regulated via photostimulation of their gonadotrophic hormone systems (Bromage *et al.* 1992). This occurs in nature during spring when daylength is increasing, but the reproductive cycle can be manipulated by artificially controlling the photoperiod.

Despite the indeterminate nature of growth in fish, it is clear that fish, as in most if not all animals, have genetically-determined maximal growth rates and body size to which they tend. Fishes range in size from one of the smallest so-far described, the goby (*Trimmatom nanus*) of the Chagos Archipelago, where mature females reach only 8–10 mm in length, to the giant whale shark (*Rhincodon typus*), which attains a length estimated to reach about 18 m (Nelson, 1984).

METABOLISM IN FISH AND HIGHER VERTEBRATES

Fish are amongst the most efficient of animals in converting food into body tissue. The daily energy requirement for maintenance in thermally acclimated fish at near their optimum temperature (for growth) ranges from 40 to 100 kJ/kg body weight$^{0.75–0.85}$ (Jobling, 1985; Steffens, 1989). This energy requirement is about 10–20% that of homeotherms of the same body weight. The dietary protein intake required per unit body-weight gain in fish does not differ greatly from that of other terrestrial vertebrates. However, the energy required per unit protein gain is between 2- and 20-fold lower in fish than in chickens, pigs and cattle (Smith *et al.* 1978).

There are several factors which contribute to the low energy requirement of fish. First, the metabolic costs of locomotion are generally considerably lower than those in land animals, and fish do not need the large antigravitational muscles of land animals. Second, unlike mammals and birds, fish are poikilotherms and do not expend metabolic energy in thermoregulation. Finally, the excretion of nitrogenous waste products resulting from

protein catabolism is an energy-costly process in terrestrial animals. NH_3, derived principally from the deamination and transamination of amino acids, is toxic in its un-ionized form and must be rapidly excreted or converted to a less toxic form. Mammals and birds convert NH_3 to urea or uric acid at considerable energy cost. Teleost fish are ammoniotelic, but they excrete approximately 60–90% of their waste N as NH_3/NH_4^+ by passive diffusion down a concentration gradient through the gills into the water, with little or no energy cost (Randall & Wright, 1987). Consequently, fish derive more metabolizable energy from catabolism of proteins than do terrestrial animals. Although all the enzymes of the ornithine–urea cycle have been detected in teleost tissues, it is generally believed that this metabolic pathway does not function significantly in this group of fishes (Cowey & Walton, 1989). This contrasts with the situation in marine elasmobranch fish, where high levels of synthesized urea in tissues and blood (typically 350–450 mmol/l) play an important role in water balance by maintaining the intra- and extracellular fluids approximately isosmotic with sea water (Holmes & Donaldson, 1969).

In teleosts, excretion of NH_3 is dependent largely on the dietary N intake, but temperature and the weight of the fish are also contributing factors. For rainbow trout (*Oncorhynchus mykiss*), Paulson (1980) described the average NH_3 excretion rate over 20–24 h following the ingestion of a single meal of known total N content by:

$$E = 13.274k^{7\cdot677(R)\ +\ 0\cdot016(T)} \cdot W^{0\cdot616},$$

where, E is NH_3 excretion rate (μg/h), k is 10, R is N intake (g/d), T is temperature (°), and W is live fish weight (g).
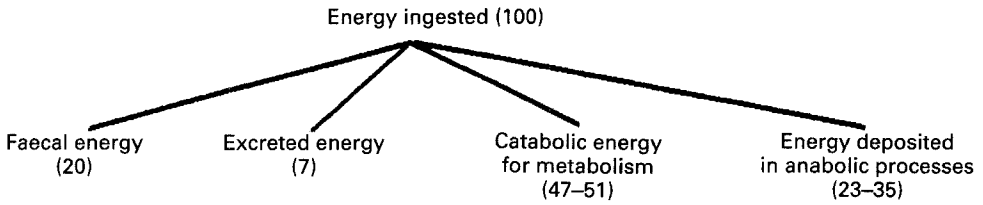
In salmonids, NH_3 excretion typically peaks between 4 and 8 h following a meal at temperatures of about 10–15°. The timing of this peak is directly related to temperature, reflecting temperature-dependent digestion processes such as gut evacuation rates (Fänge & Groves, 1979; Smith, 1989). Endogenous N excretion derived from the turnover of tissue proteins ranges from 30 to 300 mg N/kg per d, depending on species, fish size, temperature, and previous nutritional history.

ENERGY BUDGETS IN FISH

Fishery biologists have long recognized the value of analysing growth in fish in terms of rates of energy intake, energy transformations and losses, and the partitioning of energetic resources within the animal. A bioenergetics approach has been central to much of our understanding of the biology of fish, and provides a convenient framework within which to examine the major environmental and physiological factors determining growth in fish (Brett, 1979; Brett & Groves, 1979; Tytler & Calow, 1985; Jobling, 1993). Energy budgets have been compiled for various fish species despite the many potential sources of error. Aquatic animals do not lend themselves easily to such studies, and there are considerable technical difficulties in accurately measuring food intake, in quantifying excretory products, standardizing activity levels, and estimating energy losses resulting from metabolic processes (Brafield, 1985).

The basic energy budget states that all energy acquired through ingestion of nutrients, is ultimately lost as wastes in faeces or via urinary and branchial excretion, catabolized for basal or standard metabolism (the terminology used to describe metabolic processes in fish are somewhat different from that conventionally used for higher vertebrates; these

Carnivorous fishes

Energy ingested (100)

Faecal energy (20)   Excreted energy (7)   Catabolic energy for metabolism (47–51)   Energy deposited in anabolic processes (23–35)

Herbivorous fishes

Energy ingested (100)

Faecal energy (41)   Excreted energy (2)   Catabolic energy for metabolism (37)   Energy deposited in anabolic processes (20)
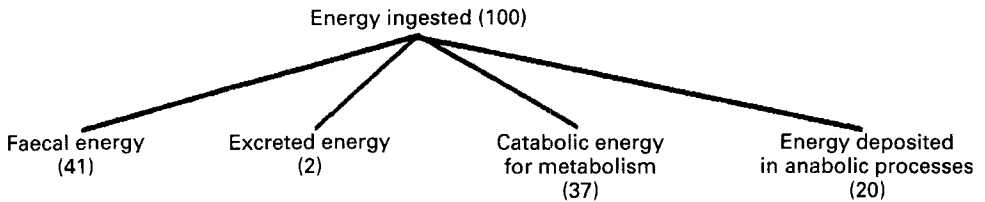
Fig. 1. Partitioning of energy in carnivorous and herbivorous fish (after Brett & Groves, 1979).

terms are discussed in detail by Jobling (1993)), feeding metabolism, locomotor activity, and tissue repair not accounted for in biomass gain, or deposited via anabolic processes as new body tissue (somatic and reproductive, plus tissues and tissue products lost, eg, mucus). Following an extensive review of the published literature, Brett & Groves (1979) derived generalized energy budgets (Fig. 1) for young, growing fish, where food supply is not limiting. Some general trends illustrated in Fig. 1 include lower assimilation efficiency (higher value for faecal energy) in herbivores, relatively small energy losses in nitrogenous excretion, and higher values for heat loss (catabolic energy) relative to energy stored in growth (energy deposited), both somatic and reproductive. In terms of the energy budget, Jobling (1993) considered reproductive and somatic growth to be competitive demands for finite resources.

GROWTH MODELS

Various models have been proposed, based on either theoretical considerations of bioenergetics or on empirical studies, to describe the growth process in fish in numerical terms, and to quantify the influence of biotic and abiotic factors on growth (Ricker, 1979). In situations where food is not limited in quality or quantity, the two factors having the greatest influence on growth in fish are temperature and fish size (Corey *et al.* 1983).

The most frequently used numerical description of growth is the instantaneous or specific growth rate (SGR):

$$\text{SGR (\%/d)} = \frac{\ln W_1 - \ln W_0}{t} \times 100,$$

where W_0 and W_1 are the initial and final weights respectively and t is time (d).
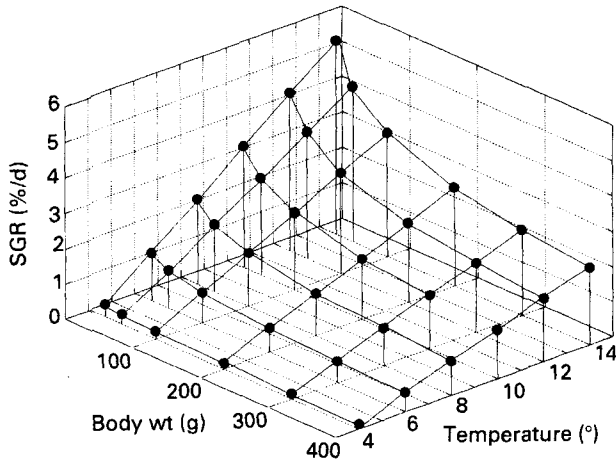
Fig. 2. A representation of the relationships between water temperature, body weight and specific growth rate (SGR; %/d) based on the empirically derived algorithm developed for brown trout (*Salmo trutta*) by Jensen (1985). For details, see below.

Cho (1992) commented that use of the natural logarithm in the calculation of SGR underestimates the weight gain in the period of measurement, and overestimates predicted body weights at the end of the period over which SGR has been determined. Cho (1992) proposed the use of a thermal unit growth coefficient (TGC) to quantify and predict the growth potential of a given species and stock of fish in relation to diet, husbandry, fish size, and temperature:

$$\text{TGC} = (W_1^{0.333} - W_0^{0.333})/(\text{mean daily temperature (°)} \times t).$$

Estimated final body weight (EBW) can be calculated as:

$$\text{EBW } (W_1) = (W_0^{0.333} + (\text{TGC} \times \text{mean daily temperature (°)} \times t))^3,$$

where W_0 and W_1 are the initial and final weights respectively and t is time (d).

Empirically-derived growth patterns and rates for fish of a given species, diet, and rearing conditions are frequently used as the basis for calculating the daily ration of salmonids in aquaculture (Corey *et al.* 1983; Austreng *et al.* 1987; Cho, 1992).

BIOTIC AND ABIOTIC INTERACTIONS

The inter-relationships between temperature, body size and growth rate have been described for various fish species, both in wild and captive populations. Jensen (1985) for example, derived algorithms to describe these relationships for Arctic charr and brown trout (*Salmo trutta*) living in a reservoir in Norway:

trout: $\ln \text{SGR} = \ln (13\cdot8 (-0\cdot3474 + 0\cdot1053T)) -0\cdot325 \ln W$,
charr: $\ln \text{SGR} = \ln (12\cdot6 (-0\cdot0815 + 0\cdot0917T)) -0\cdot325 \ln W$,

where T is temperature (°) and W is live body weight (g). For most fish species so far studied, when food supply is not limiting, specific growth rate has been found to increase with increasing temperature, while for any given temperature, SGR decreases with increasing body weight (Fig. 2). In temperate regions, gains in weight typically show a
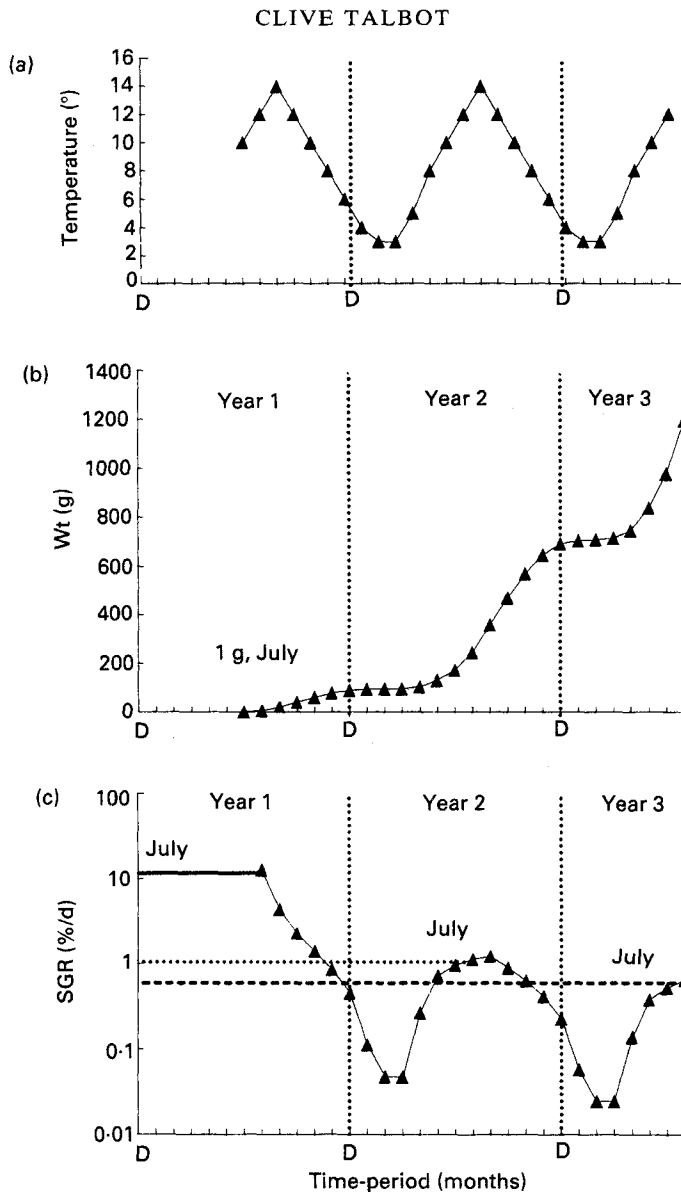
Fig. 3. Representation of the gain in weight (b), and specific growth rate (SGR; %/d) (c), of a typical salmonid over a 24-month period, based on the empirically derived algorithm developed for brown trout (*Salmo trutta*) by Jensen (1985), for a given hypothetical annual temperature cycle (a). D, December. Note log scale on the ordinate of 2c.

distinct seasonal pattern. Weight increases rapidly during the summer and autumn months, but little growth occurs during the winter period (Fig. 3). Specific growth rate varies directly with temperature over the annual cycle, but for any given temperature in successive years, SGR falls as a function of increasing body weight (Fig. 3(c)). The smooth growth curves generated by such iterative models are unlikely to be seen in nature due to many factors which include the effects of circannual photoperiod cycles, food supply, and reproduction.

A decline in SGR with increasing body weight is typical for many species of fish (Jobling, 1993), and can be described by an allometric function:

$$SGR = a.W^b,$$

where b is the weight exponent and a is the growth rate for a fish of 1 g body weight. For a number of salmonid species, the weight exponent is close to -0.35 (Jobling, 1993) when the fish are feeding at maximal rates. This relationship derives partly from the relatively lower body weight-dependent scaling factor for maximum ingestion rates (exponent approximately 0.75), compared with that for the maintenance requirement, where the average weight exponent appears close to 0.86 (Jobling, 1993). Hormonal factors are also likely to be important (Matty & Lone, 1985); however, little is known about the endogenous hormonal control of growth in fish (Sumpter, 1992).

Temperature exerts a major influence on weight-specific rates of both energy intake and energy requirement. Given access to an unlimited food supply, the increase in SGR with increasing temperature for thermally-acclimated fish of a given weight reflects both increasing appetite and food consumption rates, and biochemical reaction rates (metabolic rates increase 1.65–2.7-fold depending on the species, for every $10°$ rise in temperature), within the thermal tolerance range of the fish (Brett & Groves, 1979; Jobling, 1993). Appetite will peak at some temperature approaching the upper thermal tolerance limit of the species, but will fall precipitously towards both extremes of the tolerated temperature range. The regulatory mechanisms underlying the relationships between growth rate and temperature are largely unknown, but these are likely to be related to the hormonal modulation of metabolic processes (Sumpter, 1992).

The limits of temperature tolerance and the effects of temperature on growth are not fixed, and many fish species demonstrate metabolic and biochemical adaptations to different temperature regimens (Johnson, 1993). Fish in winter may be active at temperatures which are lethal to fish acclimated to summer temperatures and *vice versa* (Brett, 1956). A number of studies report adaptive changes in cell membrane fluidity in response to thermal acclimation. This may involve changes in the fatty acid composition of structural lipids; however, the exact mechanism of homeoviscous adaptation is unclear, and some non-lipid components of cell membranes might be involved (Dey & Farkas, 1992). Polar and tropical stenothermal fishes tolerate temperatures ranging between -2 and $15°$, and 18 and $36°$ respectively, while temperate eurythermal fishes tolerate temperatures ranging from approximately 2 to $28°$.

In addition to temperature, the annual photoperiod cycle is a major synchronizing cue for the seasonal cycles of growth depicted in Fig. 3, as well as many seasonal physiological processes such as reproduction and the parr–smolt transformation in anadromous salmonids (Hoar, 1988). The thermal optimum for growth may also be influenced by photoperiod. Woiwode & Adelman (1991) found that hybrid bass (*Morone* sp.) exhibited a higher temperature optimum for growth on increasing daylengths compared with decreasing daylengths. For a given temperature, specific growth rate in juvenile Atlantic salmon can be several-fold higher during times of the year when daylength is increasing than rates found when daylength is decreasing (Higgins & Talbot, 1985). These photoperiod-related annual cycles in growth rate, which have been observed to occur also under conditions of constant temperature (Hogman, 1968; Pálsson *et al.* 1992), are under endocrine control via the pineal–pituitary axis (Sumpter, 1992).

The interactions between fish weight and temperature appear to hold true only in the

most general sense, and apply only under conditions of unlimited food supply. Major differences exist within any species at different life-history stages. For example, populations of sibling juvenile Atlantic salmon typically develop a bimodal length-frequency distribution during their first year (Thorpe, 1977). Under identical environmental conditions, upper-growth-mode fish show a greater appetite and consume a higher weight-specific daily ration compared with lower-growth-mode fish, with fish in each growth mode exhibiting a characteristic temperature-dependent daily food intake rate (Higgins & Talbot, 1985). As in higher vertebrates, appetite in fish is under multifactorial control involving metabolic, neurophysiological and hormonal mechanisms (Fänge & Groves, 1979; Fletcher, 1984; Smith, 1989).

Reproduction can exert a pronounced effect on the biology, body composition and somatic growth in fish. Several fish species are *semelparous*, such as the Pacific salmonids (*Oncorhynchus* sp.) which spawn once and then die. Obligate semelparous fishes may become anorexic during the later stages of maturation, and demonstrate a marked degree of emaciation and irreversible degenerative changes (Talbot *et al.* 1986). The majority of species, however, are *iteroparous* and spawn several times in a season, e.g. the three-spined stickleback, *Gasterosteus aculeatus*, or, as in the brown trout (*Salmo trutta*), as a single spawning in successive years. Reproductive growth may occur to the detriment of somatic growth depending on food supply and intake, and food supply may influence reproductive growth through its effects on egg size, gamete quality or fecundity (Wooton, 1985; Bromage *et al.* 1992). Fish of many species show distinct patterns of somatic growth (Jobling & Baardvik, 1991), and depletion and repletion of body protein and lipid in relation to the reproductive cycle and available food supply (Love, 1980; Black & Love, 1986; Storebakken *et al.* 1991). Wooton (1985) concludes that the energy cost of the annual reproductive effort of fishes amounts to approximately 10% of the energy content of the food consumed over a breeding season, irrespective of the life-history strategy.

Clearly, the diet composition and nutrient digestibility exert a considerable effect on growth, as do dissolved O_2 levels, salinity, locomotor activity, and health status. All these factors, singly or in combination, can affect the food intake of fish and the efficiency of conversion of the ingested nutrients into biomass gain. Brett (1979) invoked four categories of biotic and abiotic factors which govern growth in fish, i.e. controlling, limiting, masking, and directive, and he described many of the principal interactions between them. Dissolved O_2 levels are an example of a growth-limiting factor. In rainbow trout, appetite and growth decline rapidly when the O_2 concentration falls below 6 mg/l, and conversion efficiency falls at levels below 7 mg/l (Pedersen, 1987). Of course, wild fish are not entirely captive to their environment, and they may migrate within the water column or elsewhere to areas which provide optimum conditions, and minimize the risks of adverse environments (Coutant, 1985).

GROWTH–RATION RELATIONSHIPS

The growth–ration relationship, together with its derived conversion efficiency equivalents, is fundamental to understanding the action of biotic and abiotic factors, including nutrition, on growth in fish. The growth–ration relationship typical of salmonids in culture or experimental situations when fed on nutritionally-complete diets is illustrated in Fig. 4.
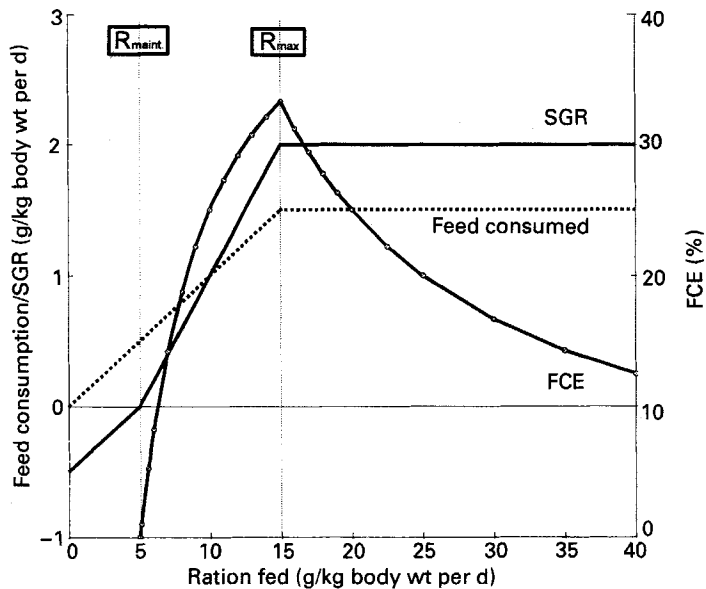
Fig. 4. Theoretical relationships between the ration fed to individual fish or whole populations, the ration actually consumed, and gross feed conversion efficiency (FCE) based on assumptions for specific growth rate (SGR; %/d), maintenance ration (R_{maint}) and maximum feed consumption (R_{max}).

Fish, like all animals, lose weight when their nutrient intake rate falls below that required for maintenance. As food availability increases, the quantity consumed will increase, resulting in a more-or-less linear increase in growth up to the point of maximum voluntary food intake. The mathematical relationship between food intake and growth rate determines that gross food conversion efficiency increases from zero in fish fed at the level required to satisfy their maintenance requirement, to some maximum value which is attained at the maximum consumption rate. The maintenance ration or requirement and maximum ration may vary independently; however, under normal circumstances both variables will vary directly in some loose relationship; low food intake resulting in reduced metabolic and substrate turnover rates (Millward, 1989), and possibly some energy-conserving behavioural changes, which will reduce the maintenance requirement, and *vice versa*.

Smith (1989) comments that in most terrestrial animals studied maximum growth efficiency occurs at maximum food intake, but that this is not the case in fish. The growth–ration relationship for fish frequently shows the features of a sine curve (e.g. Brett *et al.* 1969) in which growth rates initially increase with increasing ration, but a distinct plateau, or even an inflection downwards, is observed at the highest feeding rates employed. Various explanations have been offered to account for this, and for the apparent difference between fish and higher vertebrates. These include decreasing digestion efficiency at high rations (Elliott, 1976) and disproportionately higher metabolic costs of capturing, digesting, and metabolizing larger meals. Undoubtedly, part of the reason for the shape of these growth–ration curves in fish results from discrepancies between the ration dispensed and the actual ration consumed, where the

proportion of uneaten food increases with increasing daily ration. Tacon & Cowey (1985) demonstrated an almost linear relationship (approximately 7·5 g protein/kg body weight per 1% increase in SGR) between protein requirement and growth for twenty species of fish. In contrast to studies of terrestrial animals, it is often very difficult in practice to determine the food consumption of individual fish or of whole populations. A number of authors have critically reviewed the methodologies used in fish research with regard to feeding and growth studies (Talbot, 1985; Jobling, 1993), and in quantifying nutrient requirements (Tacon & Cowey, 1985; Cowey, 1992).

Baker (1984) concluded that growth responses to dietary supplements result from the combined effects of both stimulation of food intake and improved metabolic efficiency. Actual food consumption is seldom quantified directly in the majority of published studies related to the effect of environmental factors on growth and the nutritional requirements of fish. Minor differences in food consumption rates between different treatments may result in potentially large differences in growth and food conversion efficiency (FCE), and this will influence the conclusions drawn from empirical studies.

For example, various studies have demonstrated the beneficial effect of high-energy diets on growth and food conversion efficiency in fish (for review, see Steffens, 1989; Cho, 1992). This response is usually attributed to the dietary non-protein energy sources 'sparing' dietary protein to be utilized for anabolism rather than being metabolized as an energy substrate. Cho & Woodward (1989) concluded that optimum growth rate and FCE is obtained in rainbow trout with diets having digestible protein (DP): digestible energy (DE) values of 22–24 g DP/MJ DE and a minimum dietary DE value of 15–17 MJ/kg. Furthermore, since it is generally accepted that weight-specific food consumption in fish is inversely related to the energy content of the diet, a lower daily ration of high-energy diets compared with low-energy diets is often recommended in aquaculture (Cho, 1992). There is, however, little direct evidence that voluntary food consumption in fish is regulated to maintain a constant energy intake or, indeed, that energy requirement remains constant when fish are fed on diets differing in DE and DP:DE values, and growing at different rates.

In a recent study, (C. Talbot, unpublished results) the voluntary food intake of 500–600 g rainbow trout at 10° was measured over short periods (9 d) when the fish were fed on a range of commercially available diets of different DE and DP:DE. Food consumption was measured by the difference in dry weights of the food fed to the fish and the uneaten food collected as it was flushed out of the tanks. Expressed relative to a control diet, daily food consumption was directly related to the dietary DE content (r 0·694, $P<0·01$), and related inversely to the dietary DP:DE (r −0·863, $P<0·01$; Fig. 5(a)). Specific growth rate increased directly with increasing food intake (r 0·744, $P<0·01$), while FCE varied as a function of ration-dependent growth rate (Fig. 5(b)), in a manner similar to the theoretical relationships depicted in Fig. 4.

The reason why the trout in this study showed higher feed intake rates with the higher energy, lower DP:DE diets is not clear, nor is it known that the observed response would be maintained over longer periods of time. However, it is clear that food intake rate may be an alternative hypothesis to explain the higher growth rates frequently reported for fish fed on higher-energy diets. Furthermore, these observations demonstrate the importance of accurate determinations of actual feed consumption.

In fishes, as in higher vertebrates, marked effects of food intake rate and composition of the diet on plasma levels of known growth-promoting hormones, and on the activities
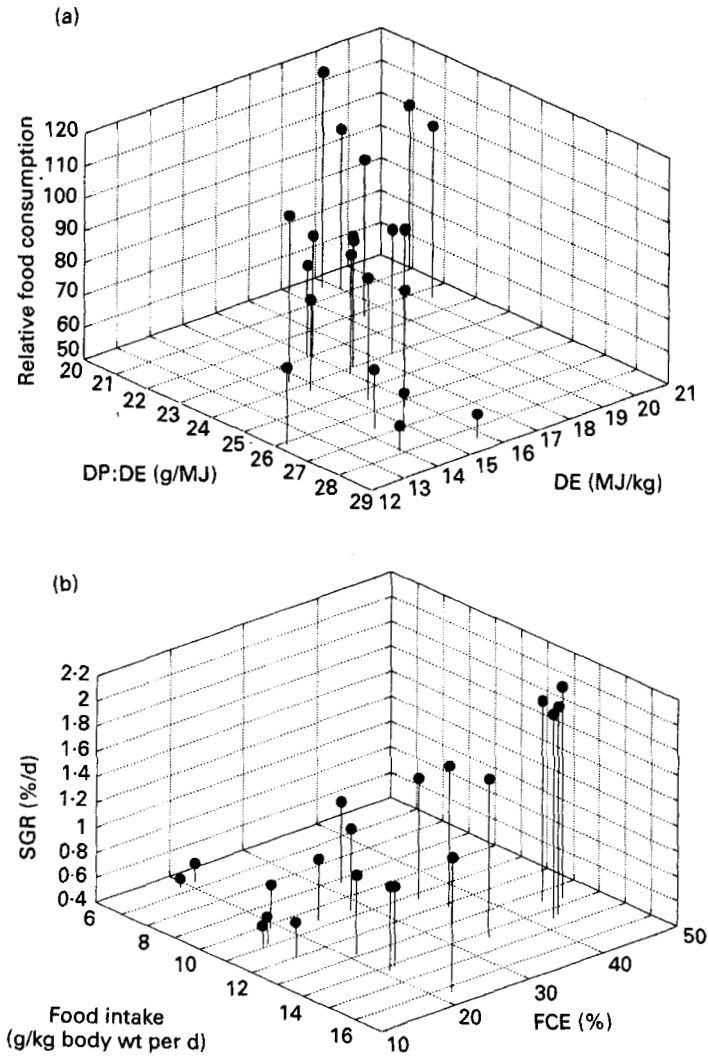
Fig. 5 (a) Voluntary food consumption by rainbow trout (*Oncorhynchus mykiss*) relative to a control diet in relation to dietary digestible energy (DE) content (MJ/kg) and dietary digestible protein (DP): DE (g DP/MJ DE). Each point represents the mean values from three replicate tanks (twenty-five trout per tank; 10°). (b) The relationship between specific growth rate (SGR; %/d), voluntary food intake (g/kg body weight/d), and the resulting gross food conversion efficiency (FCE; %). FCE was calculated as: gain in dry body weight/dry weight of food consumed. Each point represents the mean of three replicate tanks (twenty-five trout per tank; 10°). Food consumption and growth were measured over a 9 d period.

and concentrations of numerous enzymes involved in intermediary metabolism have been demonstrated (Cowey & Walton, 1989; Sundby *et al.* 1991; Sumpter, 1992). Growth-promoting hormones have been shown to affect growth not only by regulation of protein synthesis and metabolism, but also by stimulating appetite (Higgs *et al.* 1979; Gill *et al.* 1985). The relative contributions of changes in metabolic efficiency (increased

growth for the same nutrient intake) *v.* changes in appetite and food intake on growth responses in fish given different dietary treatments, has yet to be satisfactorily addressed. The X-radiography method for determining food consumption in individual fish, first described by Talbot & Higgins (1983), can be a valuable tool for quantifying food intake and feeding behaviour in fish (Jobling, 1993).

CONCLUDING REMARKS

The biology of fish is a highly complex phenomenon which is dependent on the interaction between numerous biotic and abiotic factors. The factors which determine growth are not easily studied or quantified, and these are confused by the inherently indeterminate and flexible nature of the growth process. Research into the biology of growth in fish is dominated by studies of young, actively growing animals, and much of this relates to salmonids. Almost nothing is known about the biology of the vast majority of fish species. Much of the conceptual basis for describing the growth process in fish is set in the context of bioenergetics. Feeding biology and the accurate measurement of food intake are perhaps the least well studied and quantified components of energy budgets in fish. The same can be said for nutritional studies. Developing more reliable methods for defining nutrient requirements in terms of absolute intake is likely to make an important contribution to our understanding of fish growth and physiology.

REFERENCES

Asdell, A. (1946). Comparative chronological age in man and other animals. *Journal of Gerontology* **1**, 224–226.

Austreng, E., Storebakken, T. & Åsgård, T. (1987). Growth rate estimates for cultured Atlantic salmon and rainbow trout. *Aquaculture* **60**, 157–160.

Baker, D. H. (1984). Equalized versus *ad libitum* feeding. *Nutrition Reviews* **42**, 269–273.

Black, D. & Love, R. M. (1986). The sequential mobilisation and restoration of energy reserves in tissues of Atlantic cod during starvation and refeeding. *Journal of Comparative Physiology* **156**B, 469–479.

Brafield, A. E. (1985). Laboratory studies of energy budgets. In *Fish Energetics, New Perspectives*, pp. 257–281 [P. Tytler and P. Calow, editors]. Beckenham: Croom Helm.

Brett, J. R. (1956). Some principles in the thermal requirements of fishes. *Quarterly Review of Biology* **31**, 75–87.

Brett, J. R. (1979). Environmental factors and growth. In *Fish Physiology*, vol. 8. *Bioenergetics and Growth*, pp. 599–675 [W. S. Hoar, D. J. Randall and J. R. Brett, editors]. London: Academic Press.

Brett, J. R. & Groves, T. D. D. (1979). Physiological energetics. In *Fish Physiology*, vol. 8. *Bioenergetics and Growth*, pp. 280–352 [W. S. Hoar, D. J. Randall and J. R. Brett, editors]. London: Academic Press.

Brett, J. R., Shelbourn, J. E. & Shoop, C. T. (1969). Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Research Board of Canada* **26**, 2363–2394.

Bromage, N., Jones, J., Randall, C., Thrush, M., Davies, B., Springate, J., Duston, J. & Barker, G. (1992). Broodstock management, fecundity, egg quality and timing of egg production in the rainbow trout (*Oncorhynchus mykiss*). *Aquaculture* **100**, 141–176.

Cho, C. Y. (1992). Feeding systems for rainbow trout and other salmonids with reference to current estimates of energy and protein requirements. *Aquaculture* **100**, 107–123.

Cho, C. Y. & Woodward, B. (1989). Studies on the protein to energy ratio in diets for rainbow trout (*Salmo gairdneri*). In *Energy Metabolism of Farmed Animals. European Association of Animal Production* no. 43, pp. 37–40 [Y. van der Honing and W. H. Close, editors]. Wageningen, Netherlands: European Association of Animal Production.

Corey, P. D., Leith, D. A. & English, M. J. (1983). A growth model for coho salmon including effects of varying ration allotments and temperature. *Aquaculture* **30**, 125–143.

Coutant, C. C. (1985). Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. *Transactions of the American Fisheries Society* **114**, 31–61.

Cowey, C. B. (1992). Nutrition: estimating requirements of rainbow trout. *Aquaculture* **100**, 177–189.

Cowey, C. B. & Walton, M. J. (1989). Intermediary metabolism. In *Fish Nutrition*, 2nd ed., pp. 259–329 [J. E. Halver, editor]. London: Academic Press.

Cvancara, V. A. (1992). *Current References in Fish Research*, **17**, 1–183.

Dey, I. & Farkas, T. (1992). Temperature shifts induce adaptive changes in the physical state of carp (*Cyprinus carpio* L.) erythrocyte plasma membranes *in vitro*. *Fish Physiology and Biochemistry* **10**, 347–355.

Elliott, J. M. (1976). Energy losses in the waste products of brown trout (*Salmo trutta* L). *Journal of Animal Ecology* **45**, 561–580.

Fänge, R. & Groves, D. (1979). Digestion. In *Fish Physiology*, vol. 8. *Bioenergetics and Growth*, pp. 161–260 [W. S. Hoar, D. J. Randall and J. R. Brett, editors]. London: Academic Press.

Fletcher, D. J. (1984). The physiological control of appetite in fish. *Comparative Biochemistry and Physiology* **4**, 617–628.

Gill, J. A., Sumpter, J. P., Donaldson, E. M., Dye, H. M., Souza, L., Berg, T., Wypych, J. & Langley, K. (1985). Recombinant chicken and bovine growth hormones accelerate growth in aquacultured juvenile Pacific salmon (*Oncorhynchus kisutch*). *Bio/Technology* **3**, 643–646.

Halver, J. E. (editor) (1989). *Fish Nutrition*, 2nd ed. London: Academic Press.

Higgins, P. J. & Talbot, C. (1985). Growth and feeding in juvenile Atlantic salmon (*Salmo salar*). In *Nutrition and Feeding in Fish*, pp. 243–263 [C. B. Cowey, A. M. Mackie and J. G. Bell, editors]. London: Academic Press.

Higgs, D. A., Fagerlund, U. H. M., McBride, J. R. & Eales, J. G. (1979). Influence of orally administered L-thyroxine or 3,5,3'-triiodo-L-thyronine on growth, food consumption and food conversion of under-yearling coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Zoology* **57**, 1974–1979.

Hoar, W. S. (1988). The physiology of smolting salmonids. In *Fish Physiology*, vol. 11B, pp. 275–343 [W. S. Hoar and D. J. Randall, editors]. London: Academic Press.

Hoar, W. S., Randall, D. J. & Brett, J. R. (editors) (1979). In *Fish Physiology*, vol. 8. *Bioenergetics and Growth*. London: Academic Press.

Hogman, W. J. (1968). Annulus formation on scales of four species of coregonids reared under artificial conditions. *Journal of the Fisheries Research Board of Canada* **25**, 2111–2112.

Holmes, W. N. & Donaldson, E. M. (1969). The body compartments and the distribution of electroytes. In *Fish Physiology*, vol. 1, pp. 1–89 [W. S. Hoar and D. J. Randall, editors]. London: Academic Press.

Jensen, J. W. (1985). The potential growth of salmonids. *Aquaculture* **48**, 223–231.

Jobling, M. (1985). Growth. In *Fish Energetics, New Perspectives*, pp. 213–230 [P. Tytler and P. Calow, editors]. Beckenham: Croom Helm.

Jobling, M. (1993). Bioenergetics: feed intake and energy partitioning. In *Fish Ecophysiology*, pp. 1–44 [J. C. Rankin and F. B. Jensen, editors]. London: Chapman Hall.

Jobling, M. & Baardvik, B. M. (1991). Patterns of growth of maturing and immature Arctic charr, *Salvelinus alpinus*, in a hatchery population. *Aquaculture* **94**, 343–354.

Johnson, I. H. (1993). Phenotypic plasticity of fish muscle to temperature change. In *Fish Ecophysiology*, pp. 322–340 [J. C. Rankin and F. B. Jensen, editors]. London: Chapman Hall.

Love, R. M. (1980). *The Chemical Biology of Fishes*, vol. 2. London: Academic Press.

Matty, A. J. & Lone, K. P. (1985). The hormonal control of metabolism and feeding. In *Fish Energetics, New Perspectives*, pp. 185–209 [P. Tytler and P. Calow, editors]. Beckenham: Croom Helm.

Millward, D. J. (1989). The nutritional regulation of muscle growth and protein turnover. *Aquaculture* **79**, 1–28.

Nelson, J. S. (1984). *Fishes of the World*, 2nd ed. New York: John Wiley & Sons.

New, M. B. (1991). Turn of the millenium aquaculture. *World Aquaculture* **22**, 28–49.

Pálsson, J. Ö., Jobling, M. & Jørgensen, E. H. (1992). Temporal changes in daily food intake of Arctic charr, *Salvelinus alpinus* L., of different sizes monitored by radiography. *Aquaculture* **106**, 51–61.

Paulson, L. J. (1980). Models of ammonia excretion for brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*). *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 1421–1425.

Pedersen, C. L. (1987). Energy budgets for juvenile rainbow trout at various oxygen concentrations. *Aquaculture* **62**, 289–298.

Policansky, D. (1983). Size, age and demography of metamorphosis and sexual maturation in fishes. *American Zoologist* **23**, 57–63.

Randall, D. J. & Wright, P. A. (1987). Ammonia distribution and excretion in fish. *Fish Physiology and Biochemistry* **3**, 107–120.

Rankin, J. C. & Jensen, F. B. (editors) (1993). *Fish Ecophysiology*. London: Chapman Hall.

Ricker, W. E. (1979). Growth rates and models. In *Fish Physiology*, vol. 8. *Bioenergetics and Growth*, pp. 677–743 [W. S. Hoar, D. J. Randall and J. R. Brett, editors]. London: Academic Press.

Smith, L. S. (1989). Digestive functions in teleost fishes. In *Fish Nutrition*, 2nd ed., pp. 331–421 [J. E. Halver, editor]. London: Academic Press.

Smith, R. R., Rumsey, G. L. & Scott, M. L. (1978). Heat increment associated with dietary protein, fat, carbohydrate, and complete diets in salmonids: Comparative energetic efficiency. *Journal of Nutrition* **108**, 1025.

Steffens, W. (1989). *Principles of Fish Nutrition*. Chichester: Ellis Horwood.

Storebakken, T., Hung, S. S. O., Calvert, C. C. & Plisetskaya, E. M. (1991). Nutrient partitioning in rainbow trout at different feeding rates. *Aquaculture* **96**, 191–203.

Sumpter, J. P. (1992). Control of growth of rainbow trout (*Oncorhynchus mykiss*). *Aquaculture* **100**, 299–320.

Sundby, A., Eliassen, K., Blom, A. K. & Åsgård, T. (1991). Plasma insulin, glucagon, glucagon-like peptide and glucose levels in response to feeding, starvation and life long restricted feed ration in salmonids. *Fish Physiology and Biochemistry* **9**, 253–259.

Tacon, A. G. J. & Cowey, C. B. (1985). Protein and amino acid requirements. In *Fish Energetics, New Perspectives*, pp. 155–183 [P. Tytler and P. Calow, editors]. Beckenham: Croom Helm.

Talbot, C. (1985). Laboratory methods in fish feeding and nutritional studies. In *Fish Energetics, New Perspectives*, pp. 125–154 [P. Tytler and P. Calow, editors]. Beckenham: Croom Helm.

Talbot, C. & Higgins, P. J. (1983). A radiographic method for feeding studies on fish using metallic iron powder as a marker. *Journal of Fish Biology* **23**, 211–220.

Talbot, C., Preston, T. & East, B. H. (1986). Body composition of Atlantic salmon (*Salmo salar* L.) studied by neutron activation analysis. *Comparative Biochemistry and Physiology* **85A**, 445–450.

Thorpe, J. E. (1977). Bimodal distribution of length of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. *Journal of Fish Biology* **11**, 175–184.

Thorpe, J. E. (1986). Age at first maturity in Atlantic salmon, *Salmo salar* L.: freshwater period influence and conflicts with smolting. *Canadian Special Publication of Fisheries and Aquatic Sciences* **89**, 7–14.

Tytler, P. & Calow, P. (editors) (1985). In *Fish Energetics – New Perspectives*. London: Croom Helm.

Weatherley, A. H. & Gill, H. S. (1987). *The Biology of Fish Growth*. London: Academic Press.

Wilson, R. P. (1991). *Handbook of Nutrient Requirements of Finfish*. Boca Raton: CRC Press.

Woiwode, J. G. & Adelman, I. R. (1991). Effects of temperature, photoperiod and ration size on growth of hybrid striped bass × white bass. *Transactions of the American Fisheries Society* **120**, 217–229.

Wooton, R. J. (1985). Energetics of reproduction. In *Fish Energetics, New Perspectives*, pp. 231–254 [P. Tytler and P. Calow, editors]. Beckenham: Croom Helm.

Wooton, R. J. (1990). *Ecology of Teleost Fishes*. London: Chapman Hall.

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