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Dynamics of protein and lipid intake regulation of rainbow trout studied with a wide lipid range of encapsulated diets and self-feeders

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ABSTRACT

Feed intake in fish is examined extensively but there is not much information about the dynamics of regulation i.e. how fish react to different diets, and how these reactions change, over a longer period of time. The present study was designed to evaluate the dynamics of food intake regulation in rainbow trout over a very wide range of dietary protein and lipid levels; from a very low lipid level (5%) to an extremely high level (55%). The study was conducted with three subsequent 40-day blocks of 20 fish and the intake dynamics of the lipid effect were studied by splitting the 40-day experimental period to shorter periods of 10 days. Depending on a diet the rainbow trout were more willing to ingest larger surpluses of both protein and lipid during the periods 0–10, 10–20 and 20–30 days if compared with the anticipated nutritional intake target of rainbow trout. A strong regulatory response against high lipid intake was seen during the last period (days 30–40) leading not only to a decrease in lipid intake but much more drastic decrease in protein intake. Thus, a significant nonlinear interaction between time and dietary protein and lipid was found indicating that the effect of protein and lipid was dynamic.

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1. Introduction

Fish like all animals need several different nutrients to satisfy their needs for energy and essential structure molecules. Thus, for maintaining body functions and growth they ought to feed macro- and micronutrients in right proportions with adequate digestible energy content. This is the basic task of functional feed intake regulation.

It is widely shown that feed intake in fish is strongly regulated by the dietary energy level [1–5]. This energy-dependent regulatory system appears to have some limits, since it has been showed that fishes' ability to compensate for lower digestible energy content of diets by increased feed intake failed when dietary cellulose content exceeded 40–50% [6]. In addition, energy intake is not the only regulatory factor in feed intake of fish. It has been shown that fish can regulate feed intake more extensively, as completing the macronutrient intake from different food sources [7,8] and possibly avoiding imbalanced food, as seen in fish selecting proper dietary mineral or amino acid concentrations under a choice situation [9]. Consequently, it seems that fish are capable of regulating the food intake in diverse ways, and this regulation is based on the composition of the available diet or diets.

Dietary lipid is an extensively examined macronutrient in fish food. Its effects as energy and essential fatty acids source are well known [10] and using lipid as the main energy source in the diet has some benefits in fish farming as protein sparing effect and improved growth [11–14]. However, high lipid content in diet can also have some undesired effects on growth, such as increased visceral fat which leads to high body fat content and suppression of feed intake [15–18]. Thus, it seems that lipid effect on feed intake can be dynamic depending on both the dietary lipid level and the duration of feeding on a particular diet.

The present study was designed to evaluate the capacity of rainbow trout to regulate food intake in relation to different digestible lipid levels over a wide range; from a very low lipid level (5%) to a high level (55%), in the presence of a constant amount of good quality dietary protein. Self-feeding of gelatine encapsulated diets was used to provide accurate individual feed intake data for analysis of the dynamics of food intake regulation over a longer period of time.

2. Materials and methods

2.1. Diets

Rainbow trout (*Oncorhynchus mykiss*) were fed encapsulated diets formulated to contain different lipid levels. The diets consisted of only protein and lipid and provided 5 to 55% dietary lipid. Carbohydrates were not added because no dietary requirement for carbohydrates has been demonstrated for carnivorous fish [19]. The diets were packed to pharmacological gelatine capsules, thus there was no difference in taste, smell or texture between the diets. Empty weight of a gelatine capsule was ca. 95 mg (size #0). In order to have a constant protein content independent of the lipid level and to keep the proportion of

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Table 1
Per capsule compositions of the encapsulated diets

Diet	d5	d20	d40	d55
Total lipid, mg	16	84	221	386
Total protein, mg	294	294	294	294
Added lipid, mg	0	68	205	370
Dietary lipid level, %	5	20	40	55
Basal mix, mg[a]	231	231	231	231
Gelatine, mg[b]	95	95	95	95
Dry matter, mg	326	394	531	696
Gross energy, kJ[c]	7.68	10.33	15.68	22.11

[a] Fish meal 200 mg (8% lipid level), amino acids 15 mg (isoleucine, lysine, methionine, phenylalanine), vitamin premix 9 mg, mineral premix 7 mg.
[b] From the capsule, no gelatine was added.
[c] Calculated with values 39 kJ/g lipid and 24 kJ/g protein.

dietary gelatine less than 1/3 of the dietary protein, 200 mg good quality fish meal with 8% lipid (Raiso Ltd, Finland) was added to each capsule. In addition, to balance the amino acid profile of the dietary protein (according to Ref. [20]) and to meet the vitamin and mineral requirements of rainbow trout [19] certain amino acids, vitamins and minerals were added to fish meal. This basal mix (fish meal, amino acids, vitamins and minerals) made up a total of 230 mg per capsule. The lipid levels of the diets were then adjusted by adding 0, 68, 205 or 370 mg fish oil to the capsules (Table 1). Encapsulated diets were made by filling gelatine capsules with the help of a semi-automatic capsule-filling machine (Fenton, Belgium). First, the basal mix was added to the capsule. Then the additional fish oil, amount depending on the targeted dietary lipid level, was measured with a pipette on the basal mix and the capsule was closed. Gelatine capsules have been shown to disintegrate in the stomach of rainbow trout in less than 20 min [21] so the volume of the capsule in the stomach collapses relatively quickly to that of its contents.

2.2. Facilities

Rainbow trout were held singly in 20 tanks, each with a water volume of 120 l. The tanks were supplied with re-circulated freshwater at 5 l/min that passed a temperature controller and a UV-sterilizer. The tanks were subjected to a photoperiod regime of 12 h light and 12 h dark and the temperature ranged from 13 to 16 °C during the experiments.

Each tank was equipped with a computer-controlled self-feeding system that was based on an inductive sensor (modified from Ref. [22]) and a capsule feeder. A multi-threaded LabView (National Instruments) computer program (written by us) allowing feeding instances on several channels simultaneously controlled the system. All feed demands by the fish were recorded to the computer with a time stamp for later processing. Each feed demand was rewarded with one capsule but only during the light hours. During the dark phase no demands were rewarded to avoid excess waste of capsules as observed in preliminary trials. Uneaten capsules floated quickly out from the tank and were collected by a net collector and counted. Afterwards the number of uneaten capsules was subtracted from the feeding records.

2.3. Experimental arrangement

The study was conducted as a randomised block design with three subsequent ca. 40-day blocks of 20 fish. Fish were randomly distributed to three 20 fish blocks ($n = 3 \times 20$, initial mean weight in blocks 1 to 3 was 663 g, 339 g and 702 g, respectively). In addition, tanks in each block were randomly allocated to the four different encapsulated diets. All fish were acclimated to the tank system before the trials, and weighed individually at the start and the end of each experimental block.

2.4. Statistics

The individual records of capsule demands were converted to cumulative capsule intake data for each individual over the experimental period (38–41 days, see Table 2 and Fig. 1 in each experimental block). These cumulative intake curves were subjected to response surface modelling by having dietary lipid level (expressed as added lipid mg per capsule) and time as fixed effect factors and individual fish as a random effect factor (repeated measures), i.e. by using a mixed-effects model [23]. Including individual as a random level of variation allowed control for individual-to-individual variability in the data that substantially increases the statistical power of the study. The interaction between dietary lipid level and time was included in the model as it is the term describing dietary effects over time. Also, the effect of experimental block was tested in connection to this but found negligible and removed from the model. The cumulative curves were anticipated to exhibit nonlinear behaviour in relation to the fixed effects and were therefore modelled with the help of B-splines of degree 3 (e.g. [24]). The mixed-effects models were fitted with the lme4 package [25] under the R language [26]. The residuals of the models were studied to reveal any serious deviations from the assumptions, such as variance homogeneity and normally and independently distributed errors (incl. autocorrelation). There were two fish that stopped feeding totally during the trial (one on diet d5 and one on diet d55), and the data from these fish were only included to modelling up to the point when they ceased feeding. Predictions from the above-mentioned response surface model for the cumulative capsule intake in relation to time and dietary lipid level were used for inference by converting the modelled cumulative capsule intakes to dry matter, protein, lipid and energy intake. This was done by multiplying the number of capsules by their respective contents of these quantities (see Table 1). The uncertainty related to these converted intakes was estimated by Markov Chain Monte Carlo (MCMC) simulation of the fitted model parameters (e.g. [27]).

Wet weight growth data was available from 44 individual fish. Growth was expressed as relative growth index (final weight divided by initial weight) and a dose–response model in relation to dietary lipid was fitted. B-splines of degree 3 (e.g. [24]) were used in modelling to allow for nonlinearity in the response, and the model included block as a random effect.

3. Results

3.1. Dietary lipid effect on capsule intake in relation to time

Observed cumulative capsule intake on different diets during the trials, are illustrated as curves in Fig. 1. Mean values of daily capsule intake on the studied dietary lipid levels from the three successive experimental blocks are given in Table 2. Increasing dietary lipid level of capsules was associated with decreasing mean daily capsule intake (DCI). The standard deviations (S.D.) of DCI were substantial indicating that the individual day-to-day variation in feed intake was large but this was about equal on all diets.

Dietary lipid level and time interacted indicating that the effect of lipid was dynamic. The modelled response surface is represented in Fig. 2. This response surface represents the best average description of

Table 2
Mean values of daily capsule intake (DCI ± S.D.) of the three experimental blocks for each experimental diet

Block	Duration	No. of fish	Diet			
	days		d5	d20	d40	d55
1	40	4 × 5	30.53 ± 5.74	25.58 ± 5.54	20.32 ± 6.99	11.59 ± 5.46
2	38	4 × 5	32.18 ± 7.87	30.52 ± 16.39	26.22 ± 7.68	19.09 ± 7.35
3	41	4 × 5	34.74 ± 6.36	25.92 ± 6.04	17.00 ± 3.17	13.76 ± 3.95

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