The error associated with the prediction of digestible protein contents of fish diets from tabulated values

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ABSTRACT: Numerous species available for culture, and lengthy, tedious and demanding digestibility experiments necessitate the use of tabulated values to calculate the apparent digestible nutrient contents of compound fish diets. The error associated with the above practice was evaluated in the present study with the use of apparent protein digestibility coefficients (APDCs) and dietary crude protein (CP) contents obtained in independent studies on fish nutrition. Prediction of APDCs of 21 compound diets evaluated in 18 studies with rainbow trout (*Oncorhynchus mykiss*), by using APDCs of 27 individual feed ingredients determined for this fish species, presented a mean prediction error (MPE) of 0.0489 between observed and predicted values. However, the above APDCs resulted in an overestimation of 7.86% (MPE = 0.0899) for APDCs of compound diets (n = 15) tested with 7 species other than rainbow trout. The CP contents of the above compound diets were overestimated with MPE's of 0.3029 and 0.3200 for rainbow trout and other species, respectively, when using CP contents of individual feed ingredients as predictors. This eliminates the use of tabulated values to calculate apparent digestible protein contents of compound fish diets, except if databases are regularly updated with CP values for feed ingredients used.

Keywords: fish diets; protein; digestibility coefficients; prediction

Data on nutrient digestibility is often applied in the formulation of fish diets to maximise feed efficiency and decrease environmental pollution due to undigested feed. An aquatic environment and the unique biological features of the animal caused digestibility studies with fish to be more complicated, lengthy, tedious and prone to error than with terrestrial animals (Cho et al., 1982). The above, together with cultivation of numerous fish species that differ in digestive capacity, result in the frequent use of tabulated digestibility values in fish feed formulation.

The main assumption in the use of digestibility values is that digestibility coefficients determined for individual feed ingredients are additive in compound diets, suggesting the absence of interactions among ingredients and no influence due to dietary inclusion level. However, the validation of additivity for apparent digestible contents of energy, protein, amino acids and lipid is based on few studies (Cho et al., 1982; Wilson and Poe, 1985; Watanabe et al., 1996; Lupatsch et al., 1997; Allan et al., 1999; Tibbets et al., 2006) with finfish. Furthermore, digestibility coefficients for individual feed ingredients are influenced by numerous factors other than species, related to the rearing environment, ingredient history, and digestibility technique (National Research Council, 1993; Glencross et al., 2007). The latter includes, among others, acclimatisation period, indigestible marker used, faeces collection

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method, leaching of nutrients from feed and faeces, assay diet, and equation to calculate the digestibility coefficient.

Digestibility coefficients (energy, protein, lipid, carbohydrates) for several feed ingredients evaluated with rainbow trout (*Oncorhynchus mykiss*) have been tabulated by the National Research Council (1981) from studies conducted before 1980. However, a majority of the above values were obtained from the study of Smith et al. (1980), who used an aquatic modification of metabolism chambers developed for terrestrial animals that allowed separate collection of gills, urine and faecal excretions. This method, which has been successful only with rainbow trout, is open to criticism. Fish are immobilised and force-fed, which might cause stress that hampers the effective utilisation of feed (National Research Council, 1993).

A study was conducted to evaluate the accuracy of the prediction of apparent protein digestibility of compound fish diets with the use of values obtained for individual feed ingredients in independent studies. Although amino acids, rather than total protein, should be the primary consideration of nutritionists in the formulating of fish diets (Sales, 2008), insufficient suitable values hampered an evaluation of amino acid digestibility values.

MATERIAL AND METHODS

Description of datasets

Crude protein (CP) contents and apparent protein digestibility coefficients (APDCs) of feed ingredients commonly used in the formulation of diets for rainbow trout were collected from studies as presented in Tab1e 1.

In the above studies fish size ranged from 3.6 (Watanabe and Pongmaneerat, 1991) to 266 g (Glencross et al., 2005). All studies kept fish in fresh water, with water temperature varying from 12 (Watanabe and Pongmaneerat, 1991) to 22°C (Glencross et al., 2005). Two to five replicates were used in individual studies to determine digestibility. Four studies (Sugiura et al., 1998; Cheng and Hardy, 2002, 2003a,b) used yttrium oxide as indigestible marker, acid-insoluble ash was used in the study of Bureau et al. (1999), whereas all other studies utilized chromic oxide. Methods other than a settling column (Cho et al., 1982) to collect faeces were stripping (Cheng and Hardy, 2003a; Glencross et al., 2005) and the St. Pee system (Gomes et al., 1995; Kaushik et al., 1995). The latter technique is based on the filtering of drainage water from fish tanks through metallic screens that separate faeces from water as they move linearly (Choubert et al., 1982). Except for the studies of Watanabe and Pongmaneerat (1991), Pongmaneerat and Watanabe (1993), and Yamamoto et al. (1997, 1998), which used single protein diets with direct calculation of APDCs, studies replaced 30% of a reference diet with the feed ingredient. In the latter the relative contribution of the nutrient from the reference diet and the test ingredient to the combined diet in calculation of digestibility, as described by Forster (1999), was applied by Sugiura et al. (1998), Bureau et al. (1999) and Glencross et al. (2005). Crude protein content was determined by Cheng and Hardy (2002, 2003a,b) and Glencross et al. (2005) according to the Dumas method (Ebeling, 1968), with the Kjeldahl technique (AOAC, 1990) used in other studies.

Eighteen studies (Cho et al., 1974, 1976; Pongmaneerat and Watanabe, 1992; Watanabe et al., 1993; Oliva-Teles et al., 1994; Akiyama et al., 1995; Bjerkeng et al., 1997; Refstie et al., 1997, 2000; Lanari et al., 1998; Barrias and Oliva-Teles, 2000; Green et al., 2002a,b; Sørensen et al., 2002; Yamamoto et al., 2002; Cheng et al., 2003; Romarheim et al., 2006; Barrows et al., 2007) were identified that tested diets, which contained combinations of similar ingredients like those presented in Table 1, for protein digestibility with rainbow trout. Ingredients were compared based on the type of processing, CP content, and geographical region where the study was conducted. Fish size in the above studies varied from 3 (Watanabe et al., 1993) to 500 g (Sørensen et al., 2002), and water temperature from 7 (Refstie et al., 2000) to 16.8°C (Yamamoto et al., 2002). In the study of Romarheim et al. (2006) fish were reared in sea water. Chromic oxide, yttrium oxide and ytterbium oxide were used as indigestible markers, faeces were collected by a settling column, the St. Pee system or stripping, and CP contents determined according to either the Dumas or Kjeldal method. In order to decrease bias in results, values were limited to one diet per study, except for the studies of Pongmaneerat and Watanabe (1992) (2 diets) and Oliva-Teles et al. (1994) (3 diets), where diets included different ingredients. Selection of diets per study was done according to the maximum number of ingredients included in diets, equal distribution of ingredients

Table 1. Digestibility coefficients of individual feed ingredients for rainbow trout

Ingredients	International feed number	Crude protein (g/kg dry matter)	Apparent protein digestibility coefficient (%)	Reference
Barley	4-00-549	190.9	95.50	Cheng and Hardy (2002)
Blood meal, whole blood, spray-dried		884.0	97.00	Bureau et al. (1999)
Fishmeal, anchovy	5-01-985	737.0	93.70	Sugiura et al. (1998)
Fishmeal, brown, included at 31% in a single protein diet		676.4	89.20	Watanabe and Pongmaneerat (1991)
Fishmeal, brown, included at 46% in a single protein diet		676.4	89.80	Watanabe and Pongmaneerat (1991)
Fishmeal, herring	5-02-000	736.0	94.60	Sugiura et al. (1998)
Fishmeal, white, included at 15% in a single protein diet		672.6	91.80	Watanabe and Pongmaneerat (1991)
Maize gluten	5-28-242	723.0	97.30	Sugiura et al. (1998)
Malt protein flour, included at 67% in a single protein diet		514.0	85.50	Yamamoto et al. (1997)
Meat meal, included at 15% in a single protein diet		796.5	89.70	Watanabe and Pongmaneerat (1991)
Meat and bone meal, included at 20% in a single protein diet		523.2	70.90	Watanabe and Pongmaneerat (1991)
Soybean meal, defatted, included at 23% in a single protein diet		461.6	91.20	Pongmaneerat and Watanabe (1993)
Soybean meal, defatted, included at 44% in a single protein diet		461.6	94.10	Pongmaneerat and Watanabe (1993)
Soybean meal, dehulled, defatted		480.0	92.80	Kaushik et al. (1995)
Soybean meal, dehulled, solvent extracted, 48% CP	5-04-612	532.0	90.10	Sugiura et al. (1998)
Soybean meal, dehulled, solvent extracted, heat treated		518.0	92.10	Glencross et al. (2005)
Soybean meal, defatted, extruded, included at 74% in a single protein diet		472.0	96.90	Yamamoto et al. (1998)
Soybean, full-fat, raw		449.1	88.00	Cheng and Hardy (2003a)
Soybean, full-fat, extruded		444.1	97.20	Cheng and Hardy (2003a)
Soybean, full-fat, toasted, micronized		383.0	96.30	Gomes et al. (1995)
Wheat	4-05-268	181.7	98.90	Cheng and Hardy (2002)
Wheat, whole		191.4	95.60	Cheng and Hardy (2003b)
Wheat, whole, extruded		128.9	90.20	Cheng and Hardy (2003b)
Wheat, toasted, micronized		139.0	81.80	Gomes et al. (1995)
Wheat flour	4-05-199	155.0	100.00	Sugiura et al. (1998)
Wheat gluten	5-05-221	850.0	100.00	Sugiura et al. (1998)
Wheat middlings	4-05-205	205.0	90.70	Sugiura et al. (1998)

within diets, and significance levels among APDCs obtained from diets within studies.

To evaluate the possible use of APDCs obtained with rainbow trout in other fish species, studies including similar feed ingredients like those presented in Table 1 in compound diets, and conducted with African catfish (*Clarias gariepinus*) (Ali and Jauncey, 2004), Atlantic cod (*Gadus morhua*) (Albrektsen et al., 2006; Toppe et al., 2006), Atlantic halibut (*Hippoglossus hippoglossus*) (Grisdale-Helland and Helland, 1998), Atlantic salmon (*Salmo salar*) (Aksness, 1995; Refstie et al., 1998, 1999, 2000, 2001; Storebakken et al., 1998; Bjerkeng et al., 1999), common carp (*Cyprinus carpio*) (Pongmaneerat et al., 1993), European sea bass (*Dicentrarchus labrax*) (Boujard et al., 2004; Kaushik et al., 2004) and Nile tilapia (*Oreochromis niloticus*) (Köprücü and Özdemir, 2005) were selected. Stripping was used in eight studies to collect faeces, whereas siphoning was used by Ali and Jauncey (2004) and dissection by Albrektsen et al. (2006). A mean value for the APDC was used in the study of Storebakken et al. (1998), who compared different faecal collection techniques (stripping, sieving, dissection), without any significant differences found among methods. Similarly like for rainbow trout, values were reduced to one diet per study. Limited values prevented the reduction of values to a maximum of two values per fish species and author, thus Atlantic salmon occurred in seven studies.

Calculations and statistical analysis

Predicted values for compound diets were calculated from relative proportions of feed ingredients multiplied by either APDCs (%) or CP contents (g/kg dry matter) of corresponding individual feed ingredients presented in Table 1. Despite the absence of information on moisture status of diets in some studies, values were converted to a dry matter basis if presented as wet weight.

Simple linear regression analysis to evaluate the relation between predicted (y) and observed (x) values was performed with the use of the software STATISTICA (data analysis software system, Version 7.1; StatSoft, Tulsa, OK, USA), as described by Sales (2008). With linear regression the coefficient of determination (R^2) illustrates how well the regression line represents the data, whereas the root mean square error (*RMSE*) indicates the magnitude of variation.

Mean square prediction error (MSPE) analysis, as described by Sales (2009), was included to identify the error of predicted relative to observed values (Theil, 1966):

$$\text{MSPE} = \sum_{i=1}^{n} (O_i - P_i)^2/n$$

where:

n = the number of experimental observations

O_i, P_i = the observed and predicted values, respectively

The mean prediction error (MPE) was calculated by presenting the root MSPE ($\sqrt{\text{MSPE}}$), which can be expressed in the same units as the output, as a fraction of the observed mean ($\bar{O}$):

$$\text{MPE} = \frac{\sqrt{\text{MSPE}}}{O}$$

The MSPE was divided into: (1) error in central tendency (ECT) or mean bias, (2) error due to regression (ER) or line bias, and (3) error due to disturbance (ED) or random bias:

$$\text{ECT} = (\bar{X}_P - \bar{X}_O)^2$$

$$\text{ER} = (s_P - r \times s_O)^2$$

$$\text{ED} = ((1 - r^2) \times s_O)^2$$

where:

$\bar{X}_P$, $\bar{X}_O$ = the mean predicted and observed values, respectively

s_P, s_O = the standard deviations of the predicted and observed values, respectively

r = the correlation coefficient between predicted and observed values

RESULTS AND DISCUSSION

Apparent protein digestibility coefficients

Feed ingredients are identified in National Research Council feed tables by a five-digit international feed number, preceded by a feed class number, with numbers assigned successively as new feed names are created. However, these numbers are seldom reported in studies on fish nutrition, especially in studies conducted in countries outside the United States of America, as illustrated in Table 1.

Considerable variations in both CP contents and APDCs are indicated in Table 1 for similar feed ingredients of different origin and subjected to differ-

ent processing methods, such as fishmeal, soybean meal and wheat. In fish- and soybean meals differences between the lowest and the highest CP contents were over 60 g/kg dry matter, whereas APDCs in soybean meals and wheat differed with around 7 percentage units. According to Sales (2008) the range of APDCs obtained in numerous studies with fish species varied from 56.00 to 99.00% for fishmeals, and 49.70 to 99.40% for soybean meals/flours, indicating that feed ingredients selected in the present study were in the upper limits.

Values of 100% for apparent protein digestibility, as presented for wheat flour and wheat gluten (Table 1), are a common phenomenon in studies evaluating feed ingredient digestibility with fish species. Furthermore, the assumption that digestibility coefficients will be between 0 and 100% is often not true. This could be attributed to, among others, analytical errors for markers or nutrients, poor mixing of the marker, non-representative samples of diets or faeces, interaction (associative effects) among feed ingredients (Glencross et al., 2007), and differential leaching of some nutrients within ingredients that is not accommodated by equations used for calculation (Allan et al., 2000; Sales and Britz, 2002).

Table 1 demonstrated an increase in APDCs for brown fishmeal (Watanabe and Pongmaneerat, 1991) and defatted soybean meal (Pongmaneerat and Watanabe, 1993) with an increase in the inclusion level of the protein source. This is in accordance with the linear relationship between dietary CP and apparent digestible protein contents in fish diets presented by Sales (2008). The former authors related these differences to the possible influence of metabolic faecal nitrogen. Metabolic faecal nitrogen is more correlated with dry feed intake than dietary protein content, with the result that the proportion of metabolic faecal nitrogen in faeces from fish fed low protein diets will be higher than for fish fed high protein diets. Furthermore, protein quality improves and the content of carbohydrates decreases with an increased dietary protein content, resulting in an increase in protein digestibility (Austreng and Refstie, 1978). However, it should be emphasized that the above findings have been obtained for diets with a single ingredient as the only source of dietary protein.

Across individual feed ingredients (Table 1), grains (barley, wheat), characterised by a low CP content relatively to other feed ingredients, do not follow in general a decrease in the APDC when evaluated by the reference substitution method. Their low CP content would however result in little contribution to the apparent digestible protein content of a compound diet. Lower APDCs for rainbow trout have been found at lower inclusion levels of fishmeal (Aksness et al., 1996) and lupin varieties with a lower CP content (Glencross et al., 2003), when applying the reference diet substitution method. Similar differences have been detected (Allan and Booth, 2004) with canola meal substituted at either 30 or 50% in reference diets for Australian silver perch (*Bidyanus bidyanus*). However, Appleford and Anderson (1997) reported a non-significant decrease in APDCs of soybean meal for common carp with an increase (10 to 40%) in replacement level, attributed to the possible influence of protease inhibitors in soybean meal. Similarly, decreased APDCs at higher inclusion levels have been found with feather meal, field beans and field peas evaluated with rainbow trout (Pfeffer et al., 1995), and

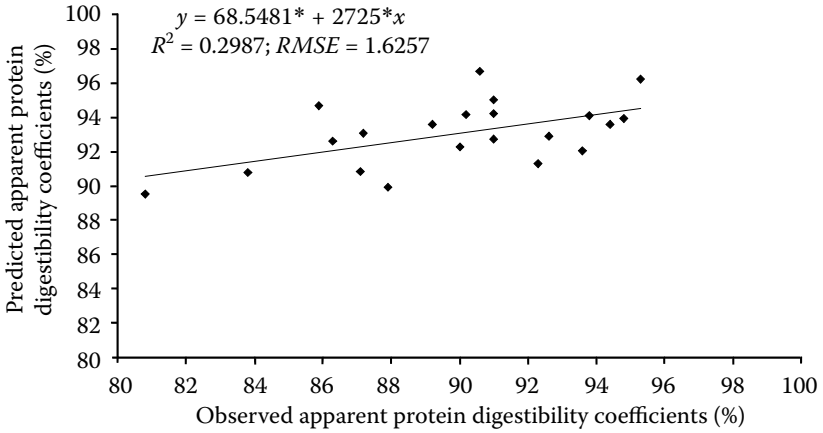

Figure 1. Linear relationship between predicted and observed apparent protein digestibility coefficients evaluated with rainbow trout (n = 21, 18 studies)
*different ($P < 0.05$) from 0 for intercept and 1 for slope

leaf meal with blue tilapia (*Oreochromis aureus*) (De Silva et al., 1990). In contrast, Da Silva and Oliva-Teles (1998) found no statistical differences in APDCs of various feed ingredients (fishmeal, fish protein concentrate, soybean meal, blood meal, meat meal) included at either 15 or 30% in test diets when evaluated with European sea bass, whereas fishmeal (Kim et al., 2006) and soybean meal (Kim et al., 2007) included at levels of 10–40% in a reference diet presented similar results with haddock (*Melanogrammus aeglefinus*). In addition, the inclusion level had no influence on APDCs of raw and extruded soybean meal (Allan and Booth, 2004) and meat meal products evaluated with Australian silver perch (Stone et al., 2000), or meat and poultry meals for Australian snapper (*Pagrus auratus*) (Booth et al., 2005). It seems that in addition to feeding habits and digestive physiology of fish, digestibility might also be influenced by the chemical composition of the reference diet and test feed ingredients (Kim et al., 2006).

Accuracy of predicted apparent protein digestibility values of diets for rainbow trout

The linear relationship between observed and predicted APDCs of compound diets for rainbow trout is characterised by an intercept and slope that differed significantly from 0 and 1, respectively, and an R^2-value of less than 0.3000 (Figure 1).

However, with empirical validation there is no interest to predict a value from an observation, eliminating the main purpose of linear regression, and rendering the R^2-value meaningless. The fitted line is irrelevant to validation, and is simply the best summary of a straight line relationship among the samples of points provided by pairs of predictions and observations. With a significant regression achieved with any cloud of points with a tendency to avoid two opposite corners, regression is not sensitive enough to quantify the quality of the line, once past the conventional thresholds of P = 0.05, 0.01 or 0.001. Furthermore, a low scattering of points caused lower standard errors and higher computed values of the t-statistic used for the null hypothesis tests for the intercept and slope, resulting in values that are likely to be significant from 0 and 1, respectively (Mitchell, 1997). A further contributing factor to the poor performance of linear regression in the present study could be the narrow ranges of ob-

Table 2. Mean prediction errors (MPEs) and decomposition of mean square prediction errors (MSPEs) between predicted and observed protein values

	n	$\sqrt{\text{MSPE}}$ (g/kg dry matter)	MPE	Bias[a]	Proportion of MSPE		
					error in central tendency	error due to regression	error due to disturbance
Rainbow trout							
Digestibility coefficients (%)	21	4.3965	0.0489	3.1105	0.5005	0.0016	0.4978
Crude protein (g/kg dry matter)	21	133.4583	0.3029	115.7102	0.7517	0.1325	0.1158
Other fish species							
Digestibility coefficients (%)	15	7.8694	0.0899	6.6443	0.7129	0.0097	0.2775
Crude protein (g/kg dry matter)	15	144.1430	0.3200	134.9719	0.8768	0.0303	0.0930

[a]predicted – observed

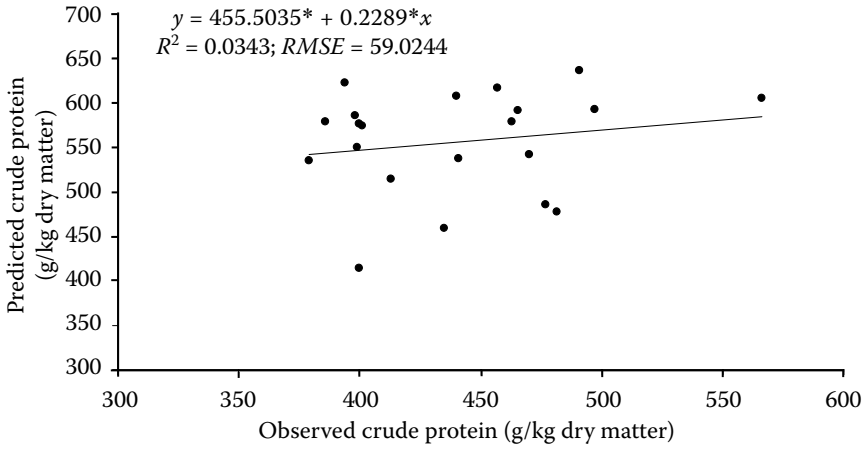

Figure 2. Linear relationship between predicted and observed crude protein content (g/kg dry matter) in compound diets for rainbow trout (n = 21, 18 studies)
*different (P < 0.05) from 0 for intercept and 1 for slope

served values. Although the relationships between observed and predicted values are graphically represented in the text below, discussions are mainly restricted to results from MPE analysis.

In contrast to linear regression, deviations, calculated as prediction minus observation, give direct information on the failure of the model to simulate the system exactly (Mitchell, 1997). These deviations are incorporated in mean square prediction error analysis, which is frequently used in animal nutrition for the validation of models (see Sales, 2009). An MPE of 0.0489 indicated an overprediction of 4.40% of observed values when tabulated APDCs for individual feeds were used to calculate coefficients for compound diets (Table 2). The MSPE was caused by a consistent overestimation of observed values by predicted values (ECT), and a failure to predict the pattern of fluctuations across observed values (ED).

Speculation about the possibility of non-additivity among feed ingredients causing overestimations of observed values would be unjustified in the present study, considering the diverse origin of feed ingredients. Non-additivity due to associative effects among dietary ingredients, a common phenomenon in terrestrial herbivore nutrition and also found with some aquatic species (see Sales and Britz, 2002), caused a higher or lower digestibility value in a mixture of ingredients than the mean digestibility of the individual feed ingredients composing the mixture. Furthermore, with 0.6000 arbitrarily set as an acceptable MPE, APDCs used for individual feed ingredients (Table 1) could be reduced by 7.52 percentage units, or increased by 1.37 percentages units (with values not exceeding 100% for the latter). This indicates a degree of insensitivity of APDCs to change, and could find application in practical feed formulation for compound fish diets.

However, the use of CP contents of individual feed ingredients (Table 1) to calculate the CP contents of compound diets (Figure 2) resulted in an MPE of over 0.3000 (Table 2), with most (>75%) of the MSPE attributed to a consistent overestimation of observed values (ECT). This eliminates the prediction of apparent digestible protein content (CP content × APDC) of compound diets from

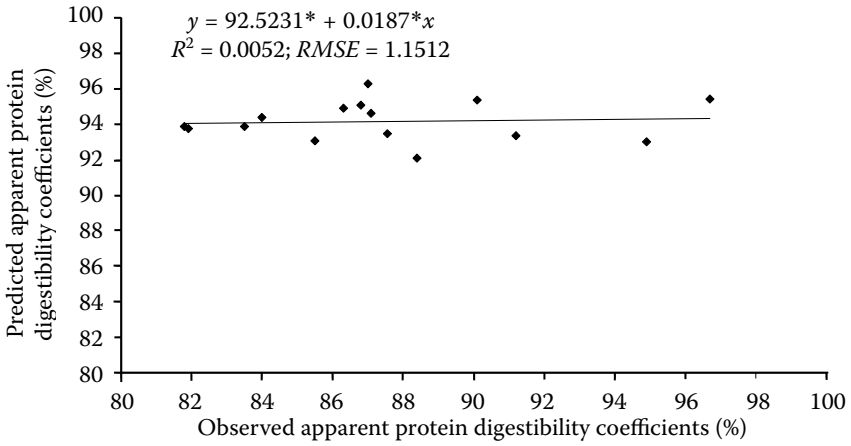

Figure 3. Linear relationship between predicted and observed apparent protein digestibility coefficients evaluated with different fish species (n = 15, 7 species, 15 studies)
*different (P < 0.05) from 0 for intercept and 1 for slope

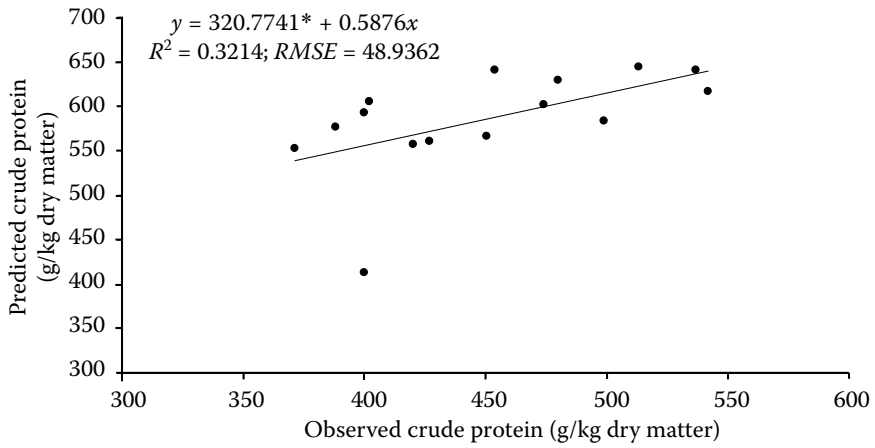

Figure 4. Linear relationship between predicted and observed crude protein content (g/kg dry matter) in compound diets for different fish species (n = 15, 7 species, 15 studies)
*different (P < 0.05) from 0 for intercept and 1 for slope

tabulated values. An MPE of 0.3404 and overprediction of 135.1942 g/kg dry matter was obtained for this measurement with current results. Sales (2008) presented a linear regression equation ($y = -10.0731 + 0.8942x$) to predict apparent digestible protein (y; g/kg dry matter) from CP contents (x; g/kg dry matter) for individual feed ingredients across a wide range of fish species, feed ingredients, feed types, nutrient levels, life stages and rearing conditions. This equation facilitates different digestibilities at variable CP contents, and takes endogenous losses into account. However, due to the use of several studies included in the present study in the computing of this equation (Sales, 2008), it could not be evaluated in the current study.

Accuracy of predicted apparent protein digestibility values of diets for other fish species

The use of APDCs for individual feed ingredients established with rainbow trout (Table 1) to predict APDCs of compound diets for other fish species (Figure 3) resulted in an MPE of almost 0.0900 (Table 2). This put a restriction on the safe use of APDCs established with a specific fish species in other species.

Predicted CP contents (Table 2) presented a similar MPE, with a higher overestimation ($\sqrt{\text{MSPE}}$) than found with rainbow trout above. Although the fish factor (APDCs) was not taken into consideration in this calculation and the results were expected to be similar, differences, both in linear regression equations (Figures 3 and 4) and MPE analysis (Table 2), showed that differences existed among similar feed ingredients between the two datasets.

CONCLUSIONS

This study presents evidence that, based on prediction error analysis between predicted and observed values, the APDC of a compound fish diet can be predicted with a high degree of accuracy from APDCs determined for individual feed ingredients in independent studies. Furthermore, a certain degree of flexibility of the latter gave an acceptable level of accuracy. However, it seemed that the above procedure was to some extent specific for fish species, and generalisation across species would not be recommended. Furthermore, it should be accentuated that only high quality, commonly used feed ingredients were included in the present study. A lack of suitable values, mainly caused by an incomplete description of products in studies, eliminated the evaluation of non-conventional feed ingredients that might present low digestibility values.

Contrary to APDCs, the use of corresponding CP contents of feed ingredients to calculate the CP content of compound diets gave erroneous results, and prevented the prediction of apparent digestible protein contents from tabulated values. This accentuates the well-known variability in CP content of similar feed ingredients, influenced by numerous factors, such as geographical origin and processing. Regular evaluation of the chemical composition of feed ingredients included in feed composition tables is of utmost importance. Furthermore, this cannot be restricted to feed ingredients specific to a certain region, seen the regular distribution of feed ingredients worldwide. Although this might be a logical fact, it is often ignored by feed formulators. The present study contributes by quantifying the error associated with not taking the above into account.

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