



Review

Body composition in fishes: body size matters



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ABSTRACT

Fish proximate body composition is of great interest in aquaculture because it affects fish appetite, growth and the efficiency of food utilization. Proximate body composition also affects other aspects of fish biology and ecology, including reproduction, survival, and energy value to predators. Two very strong relationships among body components are revealed by taking into account fish body size in terms of water mass. There is a very strong relationship between water mass and protein mass, with the amount of water per unit protein decreasing in larger fish. The strength of this relationship and its presence in a variety of fish species suggest a physiological or biochemical cause. Similarly, there is a very strong relationship between water mass and ash mass, with the amount of water per unit ash decreasing in larger fish. These two strong relationships enable fish body composition to be predicted from wet weight and percent water. Calculated water mass is used to predict mass of protein and ash, then lipid mass is found by subtraction of water, protein, and ash from body mass. Results from this approach suggest that there is virtually no functional relationship between body lipid and body water. Fish energy density can be calculated from proximate composition. These relationships should be useful in studying fish bioenergetics and other aspects of fish growth.

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1. Introduction

Fish body composition affects many aspects of fish biology and ecology, and is of special interest in aquaculture because it influences fish appetite, growth and the efficiency of food utilization. Differences in body composition, especially lipid content, are associated with differences in fish appetite (Bull and Metcalfe, 1997; Jobling and Miglavs, 1993), growth (Brett et al., 1969; Broekhuizen et al., 1994; Cui and

Wooton, 1988; Elliott, 1976; Gerking, 1955; Shearer et al., 1997), reproduction (Cargnelli and Gross, 1997; Henderson and Wong, 1998; Thorpe et al., 1998), and survival (Gardiner and Geddes, 1980; Sogard and Olla, 2000; Thompson et al., 1991).

Fish body composition determines the energy density of fish (Brett and Groves, 1979). Energy density can be calculated from body composition using standard energy values for protein and lipid (Brett and Groves, 1979; Craig et al., 1978; Paine, 1971). Fish energy density – and how it changes over the period of interest – needs to be specified to properly simulate fish growth in bioenergetic models (Canale and Breck, 2013; Hartman and Brandt, 1995). Hatchery biologists are interested in influencing lipid content of reared fish to insure adequate survival while preventing early maturation at small body size (Silverstein et al., 1999). Wildlife biologists are interested in the energy value of

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fish because of the potential importance for growth and reproduction of piscivorous mammals and birds (Benoit-Bird, 2004; Lawson et al., 1998; Van Pelt et al., 1997).

Fish proximate body composition is commonly categorized as water, protein, lipid, and ash (Elliott, 1976; Paine, 1971). Some carbohydrate is present, but the amount in fish is generally such a small percentage of wet mass that it is typically assumed to be negligible (<0.14%; Brett and Groves, 1979; Craig, 1977; Craig et al., 1978). In this paper I will make the common assumption that carbohydrate is negligible.

Fish proximate body composition is commonly reported as percent wet mass or percent dry mass in order to account for size differences among individual fish. In mammals and birds, very strong relationships have been observed among the fat-free components of body mass (protein, water, and ash), and the protein:water relationships are size-dependent (de Greef et al., 1992; Eits et al., 2002; Moulton, 1923; Rivera-Torres et al., 2011). If there were analogous relationships in fish so that the proportions of protein, water and ash changed as fish increased in size, then accounting for the influence of body size would help clarify patterns in fish body composition.

The purpose of this paper is to describe some very general and very strong patterns in proximate body composition with fish size, to demonstrate how body composition and energy density can be estimated from the mass of water, and to describe some implications for bioenergetics modeling of fish growth.

## 2. Methods

To assess the influence of fish body size on proximate composition, data are needed that span a wide range in both body size and in proximate composition, especially in lipid levels. Data sources were selected that included either a 10-fold or more range in wet weight or extended the weight range for a particular species. Data sources were selected that contained information on body mass as well as values for water, protein, lipid and ash. Some sources also had information on fish length and measured energy density (kJ/g). Data were obtained from published articles, Master's theses and doctoral dissertations. Body composition data described in the report by Rottiers and Tucker (1982) were obtained from D. O'Connor and C. Madenjian (U.S. Geological Survey, Biological Resources Division, Great Lakes Science Center, personal communication).

Rainbow trout (*Oncorhynchus mykiss*) values from Reinitz (1983) represent composite samples ranging in mean fish weight from 2.1 to 149.4 g, from six treatment groups (omitting the starvation treatment): two diets (high protein and high fat or low protein and low fat), each at three different ration levels, over 11 monthly samples. Bluegill (*Lepomis macrochirus*) values from McComish (1971) represent individual fish across a wide range of size (35–192 mm in length, 0.47–166.2 g in weight) and condition (74% to 126% in relative weight, where relative weight is wet weight expressed as a percentage of the standard weight for a given length; Blackwell et al., 2000; Murphy et al., 1991). Common carp (*Cyprinus carpio*) values from Huisman et al. (1979) represent composite samples ranging in mean fish weight from 5.37 to 953.3 g, from fish at several different ration levels and two different water temperatures (23 and 27 °C); Carvalho et al. (1997) measured water and protein (but did not report percent lipid or ash) for larval common carp from 7.8 to 82.8 mg. Lake trout (*Salvelinus namaycush*) and coho salmon (*Oncorhynchus kisutch*) values from Rottiers and Tucker (1982) represent individual fish captured in Lake Michigan, with lake trout ranging in size from 129 to 4278 g (115–910 mm) and coho salmon ranging in size from 522 to 5178 g (340–730 mm). Gunther et al. (2005) measured lake trout every four weeks from first feeding (0.22 g) to 16 weeks after first feeding (2.54 g). Neely (2006; Neely et al., 2008) did an experiment with coho salmon of two strains, each fed at two ration levels and measured fortnightly over 10 weeks, with composite samples ranging in mean fish weight from 1.9 to 23.6 g.

Because preliminary analyses indicated that starved fish had more water per unit protein than fed fish, I excluded data from experimental

treatments where fish were starved. This included treatments from experiments by Reinitz (1983) and Huisman et al. (1979). In addition, the samples of common carp from the initial conditions of Huisman et al. (1979) had much more water per unit protein than expected, suggesting that they were more similar to starved fish, so those initial samples were also excluded from this analysis.

The reported values for percent water, protein, lipid and ash generally summed to 100%, plus or minus 1%–2%. Some of this difference is due to measurement error for these various components. Some of this difference is due to ignoring carbohydrate, although this is usually much less than 1% of wet weight (Craig, 1977). I normalized the percentages so that they summed to 100%. Mass values of water, protein, lipid and ash were computed from body mass and the normalized percentages.

Linear regression was used to obtain equations for predicting protein mass and ash mass from water mass following log transformation of the variables. Because of the very strong relationships found, a fish's water mass (wet weight times fraction water) was used to predict the mass of protein and ash. Predicted values of lipid mass were then obtained by subtracting water, protein and ash from wet weight. The logarithms of predicted values of lipid mass were compared to the logarithms of observed values of lipid mass (wet weight times fraction lipid) by linear regression. An *F* test was used to evaluate the joint hypothesis that the intercept  $\beta_0 = 0$  and the slope  $\beta_1 = 1$ , following the method described by Murray (2006). The unconstrained sum of square residuals is  $SSR_u = \sum (Y - \hat{\beta}_0 - \hat{\beta}_1 \cdot X)^2$  and the constrained sum of square residuals is  $SSR_c = \sum (Y - 0 - 1 \cdot X)^2$ . The test statistic is  $F = ((SSR_c - SSR_u)/r) / (SSR_u/(n - k - 1))$ , and the critical value is  $F_{crit} = F_{r, n - k - 1}$ , where  $r = 2$  is the number of joint conditions tested (slope and intercept),  $n$  is the number of observations, and  $k = 1$  is the number of predictor variables (log lipid mass). I also computed the root-mean-square deviation (RMSD) as an additional indicator of the magnitude of error between observed and measured lipid values, somewhat similar to a standard deviation.

Many sources calculated fish energy density from proximate composition, but a few sources measured energy density by bomb calorimetry (Carvalho et al., 1997; Gunther et al., 2005; Rottiers and Tucker, 1982). Predicted values of energy density, to compare with measured values, were calculated from estimates of lipid and protein mass. A fish's total energy content (kJ) was calculated using the estimated lipid mass and energy density of fish lipid (36.2 kJ/g lipid) and estimated protein mass and energy density of protein (23.6 kJ/g protein) (Beamish et al., 1975; Brett and Groves, 1979; Paine, 1971). Dividing total energy content by wet weight gives fish energy density (kJ/g). Predicted and measured values of energy density were compared by linear regression and calculation of RMSD. The *F* test described above was used to evaluate the joint hypothesis that the intercept  $\beta_0 = 0$  and the slope  $\beta_1 = 1$ .

Analyses were conducted using the R language and environment for statistical computing (R Core Team, 2012).

## 3. Body size and body composition

A common approach to displaying body composition is to show percent lipid, percent protein, and percent ash versus percent water (Fig. 1, left panels). The purpose is to help account for size differences among individuals, with the implicit assumption that body composition does not vary with body mass. Such presentations of the data have led to the common observation that there is a negative correlation between percent lipid and percent water (Elliott, 1976; Hartman and Brandt, 1995; Iverson et al., 2002; Love, 1970; Peters et al., 2007; Plante et al., 2005; Rottiers and Tucker, 1982; Trudel et al., 2005).

A different approach to displaying fish body composition is suggested by the work of Groves (1970) (Fig. 1, right panels). Groves presented a regression equation indicating a very strong relationship between protein mass and water mass in sockeye salmon (*Oncorhynchus nerka*). Groves (1970) noted that a similar relation has been observed in mammals

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