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A general model of polyunsaturated fatty acid (PUFA) uptake, loss and transformation in freshwater fish

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ABSTRACT

Polyunsaturated fatty acids (PUFA) are crucial nutrients for fish and have been identified as globally-limited nutrients that are needed for ecosystem and human health. Greater understanding is needed into the processes influencing observed PUFA levels in fish because human demand for PUFA is increasing due to their nutritional benefits and because anthropogenic stresses threaten to reduce PUFA production. We present a general, process-based mass balance model for freshwater fish that estimates concentrations of n-3 (α-linolenic acid: ALA, eicosapentaenoic acid: EPA and docosahexaenoic acid: DHA) and n-6 (linoleic acid: LIN and arachidonic acid: ARA) PUFA from prey food items. Our model considers the processes of dietary uptake, absorption efficiency, egestion, transformation (elongation and/or desaturation) and β-oxidation. The model relies on rate constants derived from multiple regression analysis for egestion, transformation and β-oxidation based on ecological and physiological variables (i.e. body weight, diet, PUFA interactions). All regression equations had adjusted $R^2 \geq 0.47$ and p values <0.001. Application of the model to Yellow Perch (*Perca flavescens*) from the Upper Bay of Quinte, Canada provided estimates of ALA, EPA, DHA, LIN and ARA contents that were within a standard deviation of measured values without model calibration. The model showed that diet was the main source of ALA, EPA, LIN and ARA. Transformation of EPA to DHA was the dominant source of DHA. We hypothesize that within-fish transformation of precursor and the resultant product PUFA can compensate, to some extent, for dietary deficiencies in long chain PUFA in the diet of this freshwater fish.

1. Introduction

Polyunsaturated fatty acids (PUFA) play a role in mitigating cardiovascular disease (Lemaitre et al., 2003; Yokoyama et al., 2007), moderating tissue inflammation (Ruxton et al., 2004; Uauy and Valenzuela, 2000), and contributing to the development of nervous (Burdge, 1998), reproductive (Sidhu, 2003), and visual (Kim and Mendis, 2006) systems in humans and other vertebrates. The essentiality of some PUFA (i.e. α-linolenic acid and linoleic acid) stems from the inability of animals, including humans, to synthesize them de novo and/or, in the case of long-chain PUFA (LC PUFA = PUFA with 20 or more carbon atoms), at rates sufficient to maintain optimal health (Bell and Tocher, 2009).

In addition to a vital role in human health, lipids are critical components in fish nutrition as sources of energy, essential fatty acids (EFA) and sterols (Hansen et al., 2011). PUFA are crucial for fish because they affect metabolic activity, growth rates and reproduction. When available in adequate supply, EFA reduce the likelihood that fish will exhibit various pathologies (Watanabe, 1982). Additionally, PUFA are required for regulating hormonal processes (Arts and Kohler, 2009). In fish, the physiologically essential PUFA include the n-3 FA α-linolenic acid (ALA, 18:3n-3), eicosapentaenoic acid (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3) and the n-6 FA linoleic acid (LIN, 18:2n-6) and arachidonic acid (ARA, 20:4n-6) (Parrish, 2009 inter alia). Parrish (2009) also proposed that docosapentaenoic acid (DPA, 22:5n-3) is an EFA but we do not consider it further because of a lack of information.

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The low melting points of PUFA (around −50 °C) are an important factor in the maintenance of cell membrane fluidity and consequently PUFA play an important role in biochemical adaptation to cold, aquatic environments (Arts and Kohler, 2009). As noted above, fish cannot synthesize ALA or LIN at all or transform these FA de novo into EPA, DHA and ARA, respectively, at rates sufficient to maintain themselves in an optimum physiological state (Parrish, 2009). As such, ALA and LIN must be obtained largely through the diet whereas longer chain PUFA can be supplied, to some extent, by transformation (Bézard et al., 1994; Hessen and Leu, 2006; Kainz et al., 2004). These requirements for specific FA contribute to the general finding that dietary FA composition is, at least in part, reflected in fish tissues (Karalazos et al., 2011; Richard et al., 2006; Teoh et al., 2011). Thus, PUFA have been used in conjunction with other FA as biomarkers to elucidate trophic relationships (Bérge and Barnathan 2005; Gomes et al., 2010; Van Biesen and Parrish, 2005).

The importance of PUFA to human and aquatic ecosystem health led Budge et al. (2014) and Arts et al. (2001) to propose that PUFA have a limited global supply and as such, should be managed in order to ensure adequate supplies. At the same time as global demand for PUFA is increasing, their production at current rates may be threatened by several anthropogenic stressors. For example, eutrophication of freshwater systems can cause lowered production due to a shift from high PUFA quality algal communities (i.e. diatoms) to low PUFA quality algae communities (i.e. cyanobacteria) that then limit the flow of mass/energy through the food web (Brett and Müller-Navarra, 1997). Similarly, increased water temperatures associated with climate change has the potential to reduce PUFA production at the base of aquatic food webs (Fuschino et al., 2011). These competing pressures of increasing PUFA demand by human consumers and potentially reduced production due to human stressors invite a better understanding of the associated processes and emphasize the need for more effective management of PUFA supply and demand. Here we present a model that allows for exploration of these competing pressures in the context of a single fish.

Several FA transport and accumulation models have been proposed for humans, rats and fish. For example, Pawlosky and coworkers (2001, 2003) examined the metabolism of ALA in humans using stable isotope tracers and developed a multi-compartmental model to elucidate FA contributions to the maintenance of n-3 PUFA in plasma. Cunnane and Anderson (1997) first proposed a whole-body FA mass balance model for rats, emphasizing the importance of accumulation, transformation and β-oxidation pathways. Finally, Turchini and coworkers (2006, 2007) were the first to develop a compartmental FA mass balance method for fish, focusing on freshwater Murray Cod (*Maccullochella peelii*). Their method requires knowledge of the fish's initial and final body weight, initial and final quantitative fatty acid composition of the whole body, the total food intake, the quantitative fatty acid content of the diet, and the fatty acid digestibility of the quantitative fatty acid content of the total feces produced during the experiment. Using their mass balance method, it is possible to measure the fate of individual fatty acids with respect to transformation and β-oxidation. This method has been well received due to its simplicity and reliability. However, this method requires data that are made available through feeding trials of sufficient duration and thus cannot be applied to fish in natural environments.

We present a mechanistic, whole-body mass balance model for PUFA-specific uptake and elimination in a "generic" predatory freshwater fish. The model presented here can be used as a heuristic tool to understand the consequences of limiting individual PUFA on patterns of PUFA accumulation within a freshwater fish. Such circumstances can arise when anthropogenic stressors impact PUFA availability at the base of the food web as well as effects of changing the characteristics of the fish itself.

Our model builds on the approach previously proposed by Cunnane and Anderson (1997), Pawlosky et al. (2001, 2003), and Turchini et al. (2006, 2007). Physiological and ecological data (i.e. body weight, diet matrices and temperature) are used to predict rate constants for physiological processes, which allow application to temperate freshwater predatory fish species. This approach differs from the model of Turchini et al. (2006, 2007) that relies on laboratory measurements of PUFA in fish to calculate transformation and β-oxidation rates. Our general mass balance model for freshwater fish simultaneously examines the uptake and elimination of n-3 (ALA, EPA and DHA) and n-6 (LIN and ARA) PUFA in an individual fish consuming multiple prey species. The mass balance model simplifies the complexity of PUFA metabolism by considering the processes of dietary uptake, egestion, transformation (elongation and/or desaturation), and β-oxidation. Expressions to estimate rate constants for each of the above processes were developed using literature data and multiple regression analysis. We provide justification for the mass balance model equation and discuss the specific rate constant regression equations. We then apply the mass balance model to a single fish species, Yellow Perch (*Perca flavescens*), to illustrate the model's utility and to demonstrate how the model can provide insights into what controls observed patterns of PUFA in fish.

2. Model development

2.1. Mass balance equation

Both marine and freshwater fish PUFA profiles are affected by and reflective of their dietary PUFA (Benedito-Palos et al., 2011; Richard et al., 2006; Turchini et al., 2006). Following ingestion, a PUFA is either digested or egested (Fig. 1). Upon digestion, a PUFA may be transformed by elongation and/or desaturation to longer chain FA or β-oxidized for energy production (Fig. 1).

Chemical similarities of PUFA can lead to competitive interactions in the biochemical and physiological reactions undergone by the parent compounds, precursors and products (Sargent et al., 1999). The mass balance model presented here considers uptake, loss and interconversion of five (5) PUFA (ALA, EPA, DHA, LIN and ARA). PUFA content is expressed on a dry weight basis (i.e. mass fractions).

We express the mass balance for PUFA metabolism in a predator using the generic equation as follows:

$$\frac{dm_{i,x}}{dt} = \sum_{i,j=1}^{n} \gamma_{Gi,x} m_{j,x} k_{Aji,x} - m_{i,x}(k_{Ei,x} + k_{Oi,x}) \pm m_{Ti,xy}(k_{Ti,xy}) \qquad (1)$$

where '*m*' is the content (mg D.W.) of PUFA '*x*' and transformation product PUFA '*y*'. The form of this mass balance equation is generic – independent of any dataset or species. Five dependent mass balance equations are generated for ALA, EPA, DHA, LIN and ARA. The consumer (i.e. predator) and diet (i.e. prey) are '*i*' and '*j*', respectively. γ_G is a gut absorption coefficient (unitless). The '*k*' values are uptake/elimination rate constants (h^{-1}) and subscripts A, E and O are diet (i.e. food), egestion and β-oxidation, respectively. Subscript '*T*' is the net transformation of PUFA '*x*' through elongating and/or desaturating to PUFA '*y*'. If PUFA '*x*' transforms to PUFA '*y*', then the sign is negative as PUFA '*x*' is 'lost'. The sign is positive when PUFA '*x*' has an additional input from PUFA '*y*' that has elongated and/or desaturated to PUFA '*x*'. We assume that a transformed PUFA is subsequently available for additional elimination processes (i.e. egestion and β-oxidation).