Can fish consumption rate estimates be improved by linking bioenergetics and mercury mass balance models? Application to tunas

Bridget E. Ferriss *, Timothy E. Essington

School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195, USA

ABSTRACT

We developed an approach to estimate consumption rates by applying statistical methods to coupled bioenergetics and individual-based mercury (Hg) mass balance models, applied to bigeye (*Thunnus obesus*), yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), and albacore (*Thunnus alalunga*) tunas. Direct measurement of consumption rates for these highly migratory species involves laborious and infrequent point estimates, while individual bioenergetics or contaminant-based models are biased by errors in parameter estimation due to a lack of data. We linked bioenergetics and Hg mass balance models by using consumption rate estimates produced from the former as inputs into the latter and determined whether the model could predict observed Hg-at-age. Consumption rate estimates derived from conventional bioenergetics and Hg mass balance models diverged considerably and the coupled bioenergetics-Hg mass balance model, based on default parameters, could not predict patterns of Hg accumulation. The statistical estimation approach (we found maximum likelihood estimates of metabolic expenditures related to swimming and the Hg concentration in tuna diets) generated biologically plausible daily consumption rates (yellowfin: 5.8–9%, skipjack: 4.5–6.7%, bigeye: 9.4–13% body weight for a 10 kg tuna), but failed to fit the albacore Hg data. Statistically based methods that use patterns of Hg bioaccumulation hold promise to advance our ability to estimate consumption rates, but are limited by high variance in Hg-at-size data and uncertainty in prey Hg data.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

The quantification of consumption rates is a common tool in the study of fish ecology, providing insights into the impacts of predation on prey population abundance (Essington et al., 2002), the role of fish in nutrient cycling (Schindler and Eby, 1997), contaminant bioaccumulation (Post et al., 1996), individual growth (Rice et al., 1983), fish behavior (Preisser et al., 2005), and the impact of environmental changes on growth and prey consumption (Hill and Magnuson, 1990). These types of analysis are central to understanding how fish interact with their physical and biological environment at individual and population scales, contributing to the base of knowledge required to implement marine ecosystem-based management (Link, 2002). A central challenge in estimating consumption rates of fish in natural settings is that it is not directly observable. Thus, all available approaches use some kind of observation coupled with a model to derive the consumption rate that must have occurred to produce the observed data. However, because all methods rely to some extent on models, there are limits to the precision and accuracy of these methods because of model selection and parameter uncertainty.

Bioenergetics and contaminant mass balance models are commonly used to estimate consumption rates in fishes, and both have limitations affecting their precision and accuracy (Chipps and Wahl, 2008). Bioenergetics models estimate consumption rates based on the energy required for growth, metabolism and waste. Consumption estimates derived from these models require knowledge of allometric and thermal scaling of energy expenditures (Kitchell et al., 1977) that are often only available from studies in captive settings and may not reflect levels in natural settings. Highly migratory fish, in particular, have physiological and morphological adaptations to travel large distances in search of food and suitable habitat resulting in high energy costs (Dewar and Graham, 1994) that are difficult to quantify reliably in captivity. Alternatively, contaminant mass balance models have been used to estimate fish consumption rates using mercury (Hg) (Trudel et al., 2000), cesium (Olson and Boggs, 1986), and polychlorinated biphenyls (Madenjian et al., 2000). These models balance the amount of contaminant consumed with observed growth rates, prey contaminant concentrations and changes in fish contaminant concentrations over discrete time intervals. The accuracy of these estimates depends on the assumed prey contaminant concentrations and contaminant elimination rates, both of which are difficult to measure precisely (Trudel et al.,

* Corresponding author. Tel.: +1 206 616 3698.
 E-mail address: ferriss@uw.edu (B.E. Ferriss).

2000). When applied to large, mobile fish, these and other methods of estimating consumption (e.g., stomach contents analysis and estimation of consumption to biomass ratios) produce estimates based on unknown parameter values borrowed from other species or based on regionally and temporally limited data (e.g., Menard et al., 2000). Parameter uncertainty and the resulting uncertainty in consumption rate estimates reveal a need for an alternative approach.

Advances in statistically based estimation procedures that do not presume model parameters are known with certainty have been developed and applied to consumption models to better account for uncertainty in key parameters and resulting parameter estimates. First Essington et al. (2001) explored the use of the von Bertalanffy growth function (VBGF) as a simplified bioenergetics model to estimate consumption rates from size-at-age data and applied Bayesian parameter estimation techniques to quantify the uncertainty in consumption rate estimates. Walters and Essington (2010) developed this model by statistically estimating VBGF parameters from tagging studies that account for temperature dependence and energy allocation between structural and other (somatic and gonadal) tissues. In a different context, Beaudreau and Essington (2009) developed an approach to estimate consumption rates from field studies accounting for uncertainty in gastric evacuation rates and gut residence time. Application of maximum-likelihood or Bayesian approaches to estimate consumption rates signifies an important advance because it permits explicit representation and estimation of uncertainty. However, the precision of statistical estimation can be limited by the information content of the data, correlated parameters, and parameterizing models that account for temperature dependence, seasonal activity or compensatory growth (Essington et al., 2001; Walters and Essington, 2010). The authors of these studies discuss the utility of using multiple data sets (such as size-at-age data and tagging data) as the basis for statistical estimation models to avoid sampling bias and to increase the ability to extract information from the data. In addition, while key unknown parameters could be statistically estimated, the precision of the underlying model is still reliant on the model selection and associated assumptions.

Here we explore whether it is possible to derive more precise and biologically realistic consumption rates that also robustly predict patterns of Hg-at-size. Specifically, we hypothesize that key parameters governing growth and Hg dynamics might be estimable from patterns of Hg-at-size data alone by jointly considering growth processes that give rise to bioaccumulation in an integrated framework. We first compare bioenergetics and Hg based consumption estimates, and explore why they give divergent estimates by directly linking them in an integrated model. We then apply statistical estimation procedures whereby two highly uncertain parameters (the minimum swim speed multiplier and the slope of the relationship between Hg in tuna diets to tuna weight) are estimated directly by fitting the integrated model to Hg-at-size data. The key step in linking these models is to recognize that bioenergetics models produce an estimated consumption rate-at-size, while the contaminant models relate changes in Hg-at-size to consumption rate and growth. Thus, the models can be coupled by using the consumption rate from bioenergetics models as an input into Hg mass balance models, generating predictions of Hg-at-size which can then be fit to observed data on Hg-at-size in a maximum likelihood framework. We apply this estimation method to yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), albacore (*Thunnus alalunga*), and bigeye (*Thunnus obesus*) tunas as they are highly mobile, apex predators that support some of the world's largest fisheries. Bioenergetics parameters and consumption rates are poorly understood in these tunas as they are not directly observable in the wild, and are challenging to study in captivity. Improved estimates of consumption rates and bioenergetics parameters will contribute to our understanding of how these species interact with their ecosystems and to the sustainable management of fisheries on these tunas and their prey.

2. Methods

We approach this problem in three steps. First, we estimated mass-specific consumption rates for yellowfin, skipjack, albacore, and bigeye tunas generated from bioenergetics and Hg mass balance models separately, using standard methods (best available data in the literature) for deriving model parameters. Second, we coupled the models by incorporating the consumption rate produced by the bioenergetics model into the Hg mass balance model allowing us to predict Hg-at-size. Third, we evaluated whether key parameters could be estimated using the integrated model by fitting the model to data on Hg and body size for four species of tunas (Fig. 1). Key equations and parameter values are described in Sections 2.1–2.3 and the remaining equations and parameters are listed in Tables A.5–A.7 of the appendix.

2.1. Bioenergetics models

We applied bioenergetics models to yellowfin, skipjack, albacore, and bigeye tuna following the framework of Olson and Boggs (1986) as modified and parameterized (with the exception of bigeye tuna) by Essington et al. (2002) and Essington (2003) (Eq. (1), Tables A.5 and A.7):

$$\kappa = \frac{\text{SMR} + \text{AMR} + G + \text{REP}}{A} \tag{1}$$

where daily consumption rate (κ: $\text{J g}^{-1}\,\text{d}^{-1}$) is related to the energetic costs of standard (SMR) and active (AMR) respiration ($\text{J g}^{-1}\,\text{d}^{-1}$), growth ($G$: $\text{J g}^{-1}\,\text{d}^{-1}$), and costs of reproduction (REP: $\text{J g}^{-1}\,\text{d}^{-1}$). We used the albacore and skipjack mass-based metabolic rates summarized by Korsmeyer and Dewar (2001), avoiding the additional assumptions involved in calculating SMR and AMR separately (Essington, 2003). Assimilation efficiency (A: 0.675; Essington et al., 2002) is the proportion of consumed energy available to the fish after accounting for fecal losses, excretion, and specific dynamic action. We followed the method of Essington et al. (2002) and Essington (2003) to calculate the average swimming speed (the main component of active respiration) by linearly interpolating minimum swimming speed across size classes (Magnuson, 1973) and multiplying the speed-at-size by the ratio of actual swim speeds to minimum swim speeds (skipjack: 1.1 and albacore: 1.75; Essington, 2003, yellowfin: 1.3; Essington et al., 2002). The ratio of actual to minimum swim speeds were calculated using tagging data, requirements for hydrodynamic lift, and other assumptions specified in Essington et al. (2002) and Essington (2003). We refer to this parameter as the minimum swim speed multiplier in the rest of this study. Daily energy intake (J d^{-1}) (i.e. consumption rate) was converted into grams per day by dividing energy intake by the mean energy density (J g^{-1}: Table 1) of the size-specific composite diet (Table A.8).

Because there was no previously published bigeye tuna model, we created a novel model using parameter values for yellowfin tuna modified to reflect differences in growth, reproduction and body temperature (Table A.7). Length-at-age was based on the von-Bertalanffy parameter estimates provided by Schaeffer and Fuller (2006), used in the eastern Pacific bigeye stock assessment (Aires-da-Silva and Maunder, 2009). We selected this model as it provided the most realistic sizes at older age classes. We calculated the proportion of mature individuals at length x (Y_x) using the Richards function (Schaeffer et al., 2005). The calculations determining the mature proportion of the population were based on female tuna.