

APPENDIX 1. CONTRASTING CONSUMPTION APPROACHES: A CALL FOR PARSIMONY

There are multiple approaches to estimating fish consumption, including: percent body weight (%BW), daily ration, consumption to biomass ratios (C/B or Q/B), caudal fin ratios, evacuation rate models, functional response models, and bioenergetics models.

The %BW method calculates the amount of food eaten per unit biomass per unit time, requiring body weight (W) and stomach weight (S):

$$\%BW = \frac{S}{W} \quad \text{EQ B1.1}$$

This approach assumes what is found (on average) in stomachs represents population level consumption for any period of time. Data required are average body weight and stomach contents. This metric is more often a diagnostic back-calculated from other methods.

The daily ration approach is from Bajkov (1935) and similarly calculates the amount of food consumed (C) per capita per day, requiring stomach weight (S):

$$C = S \cdot \left(\frac{24}{n}\right) \quad \text{EQ B1.2}$$

where n is the number of hours to evacuate a stomach. This approach assumes that what is found (on average) in stomachs is linearly evacuated. Data required are mean stomach contents. It too can be a diagnostic back-calculated from other methods.

The caudal fin-aspect ratio method (Palomares and Pauly 1989) assumes that body shape of fish roughly approximates a fish's activity and can be captured by the caudal fin. The aspect ratio of the caudal fin:

$$A = \frac{h^2}{s} \quad \text{EQ B1.3}$$

uses the height (h) and surface area (s) of the fin and assumes that the aspect ratio is loosely related to consumption (or more specifically, Q/B or C/B ratios). This approach is admittedly best suited for tuna-like fishes.

The consumption to biomass (C/B or Q/B) ratios are basically literature values that are taken from consumption estimates, mostly 1940s and 1950s lab physiology studies (cf. references in Link et al. 2006). The caudal fin aspect ratio (general body plan; Palomares and Pauly 1989) or lab based evacuation/consumption study results are then reapplied to biomass estimates to come up with these ratio estimates. Values from similar species are often used as a proxy for species without direct measurements. This approach assumes constancy across a wide range of factors and produces unitless ratios applied to population level biomass, not abundance. This approach can also be a diagnostic back-calculated from other methods.

To estimate per capita consumption in a bit more specified manner, the gastric evacuation rate method is one approach (Eggers 1977, Elliott and Persson 1978). There are several approaches used for estimating consumption, but this approach was chosen as it was not overly simplistic (as compared to % body weight; Bajkov 1935) or overly complex (as compared to highly parameterized bioenergetics models; Kitchell et al. 1977). This approach is modified from Bajkov (1935) but explicitly accounts for temperature. Additionally, there has been copious experience using these models (e.g., Bromley 1991, dos Santos and Jobling 1988, 1991, 1992, 1995, Gerking 1994, Hansson et al. 1996, Jobling 1981, 1986, 1988, Jobling et al. 1994, Mehl

and Sunnana 1991, Ponomarenko et al. 1978, Rindorf and Lewy 2004, Stefánsson and Pálsson 1997, Teschner et al. 2010, Teming and Andersen 1994, Temming and Herrmann 2003, Tyler 1970, Ursin et al. 1985, Waiwood and Majkowski 1984, Winger and Walsh 2001), particularly in the northeast shelf large marine ecosystem (NES LME) region (Durbin et al. 1983, Ursin et al. 1985, Pennington 1985, Overholtz et al. 1991, 2000, 2008, Tsou and Collie 2001a, 2001b, Link and Garrison 2002b, Link et al. 2002b, 2006, NEFSC 2007a, 2007b, 2010a, 2010b, 2011, Overholtz and Link 2007, Tyrrell et al. 2007, Link and Sosebee 2008, Link and Idoine 2009, Moustahfid et al. 2009a, 2009b, Deroba et al. 2010, DFO 2010). The main form is:

$$\frac{dS_i}{dt} = C_i e^S \quad \text{EQ B1.4}$$

where different assumptions about e^S yield subtly different formulae. In one of the more common forms, using the evacuation rate model to calculate consumption requires two variables and two to three parameters. The per capita consumption rate, C_i is calculated as:

$$C_i = 24 \cdot E_i \cdot \bar{S}_i^\gamma \quad \text{EQ B1.5}$$

where 24 is the number of hours in a day and the evacuation rate E_i is:

$$E_i = \alpha e^{\beta T} \quad \text{EQ B1.6}$$

and is formulated such that estimates of mean stomach contents (S_i) and ambient temperature (T) are the only data required. The parameters α and β are set as values that can be chosen from the literature (e.g., Durbin et al. 1983, Tsou and Collie 2001a, 2001b, Overholtz 2000) or estimated experimentally (Bromley 1991, dos Santos and Jobling 1988, 1991, 1992, 1995, Jobling 1988, Temming and Anderson 1994, Temming and Herrmann 2003). The parameter γ is a shape function and is almost always set to 1 (Gerking 1994). The approach models evacuation (of stomach contents) rate by assuming non-linear evacuation, constant consumption, and that consumption equals what was evacuated.

Functional response models fit relationships between predator and prey populations (Holling 1959a, Yodzis 1994). This approach requires abundance of predator (P), prey (N_i), and alternate prey (N_k); foraging times (F), search times (f), and growth rates (r) of prey; capture rate (C) and handling times (h) of a particular prey k by a particular predator:

$$\frac{dN}{dT} = rN - FP \quad \text{EQ B1.7}$$

or

$$\frac{dN}{dt} = rN \cdot \left(1 - \frac{N}{K}\right) - FP \quad \text{EQ B1.8}$$

where,

$$F = \alpha N \quad \text{EQ B1.9}$$

or

$$F = fF \cdot \left(\frac{C}{1 + \sum h_k C_k}\right) \quad \text{EQ B1.10}$$

This approach assumes one of three standard “Types” of responses (I, II, or III; Holling 1959a, Moustahfid 2010), although other relationships have been described that explicitly address heterogeneity of predator and prey distributions (see Cosner et al. 1999) and variation in satiation effects (Jeschke et al. 2002). This approach generally assumes that predation rate

depends upon prey and predator densities. Usually this method emphasizes a two species predator-prey pairing.

Bioenergetic models, aka the Wisconsin model (Kitchell et al. 1977; modified from Winberg 1956), model the full physiology of an (average) individual fish with a mass balance constraint. This approach requires detailed knowledge of basal metabolic rates (M), growth (G), and waste (W) to estimate consumption (C):

$$C = P + M + W \quad \text{EQ B1.11}$$

where

$$P = G + \textit{Repro} \quad \text{EQ B1.12}$$

and

$$M = \textit{Resp} + \textit{MA} + \textit{SDA} \quad \text{EQ B1.13}$$

and

$$W = F + U \quad \text{EQ B1.14}$$

with production (P) comprised of somatic growth (G) and reproduction (Repro, or gonad production), metabolism comprised of respiration (Resp), metabolic activity (MA, or active metabolism), and specific dynamic action (SDA, or the “cost” of digestion), and waste comprised of feces (F, or egestion) and urea (U, or excretion) needing to be measured, accounted for, or assumed.

The bioenergetics approach models the amount of food that is required to support other activities and is usually based on a laboratory experiment for estimates. The main assumption is that inputs equal outputs. Data required are probably the most extensive for any consumption estimating approach, often required detailed measurements of fish inhabiting respirometers.