

Table 2.1.2 (cont.)

Symbol	Parameter description	Value
Swimming Speed, U		
a _A	Intercept U (< 9 °C) (in cm/s)	3.9
a _A	Intercept U (≥ 9 °C) (in cm/s)	15.0
b _A	Coefficient U versus weight	0.13
c _A	Coefficient U versus temperature (< 9 °C)	0.149
c _A	Coefficient U versus temperature (≥ 9 °C)	0.0
Egestion and Excretion, F and E		
a _F	Proportion of consumed food egested	0.16
a _E	Proportion of consumed food excreted	0.10

a - values for age 0 and 1 herring

b - values for age 2 and older herring

2.2 Review of Clupeid biology with emphasis on energetics

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The general bioenergetics model based on the Law of Thermodynamics balances all consumed energy as follows: $G = C - R - F - U$, where G=growth, C=consumption, R=metabolism (respiration), F=egestion, and U=excretion. Consumed energy is first allocated to costs of metabolism and waste losses with the remainder available for somatic growth. Energy lost by the gametes released during spawning can also be included. Formulas and parameters provided below for the individual components in the bioenergetics model follow the terminology and symbols used in Hansen *et al.* (1997). Energy equivalent conversion factors for oxygen consumption, carbohydrates, fats, and protein can be found in Elliott and Davison (1975), with additional comments on the oxycaloric coefficient found in Brett (1985).

Consumption

Consumption (C) = $C_{\max} * P\text{-value} * f(T)$ and
 $C_{\max} = CA * W^{CB}$

Consumption (g prey·g⁻¹·d⁻¹), is generally modeled as an allometric (power) function of weight.

Maximum consumption rates are determined in laboratory experiments by feeding fish a known (by weight) *ad libitum* ration and then subtracting uneaten food after a specified time interval. For adult alewife *Alosa pseudoharengus*, the specific slope for weight dependence on maximum consumption was -0.3 (Stewart and Binkowski 1986), a value intermediate to that found in studies of larval and juvenile clupeids (De Silva and Balbontin 1974; Theilacker 1987). The specific weight-dependent slope (CB) for maximum consumption of northern anchovy *Engraulis mordax* larvae (wet weight < 0.001 g) recalculated from data in Theilacker (1987) was -0.367, while the slope for Atlantic herring (wet weight 8 – 15 g) was -0.256 (De Silva and Balbontin 1974). Rudstam (1988) used the slope and intercept derived by De Silva and Balbontin (1974) in the bioenergetics model for adult Atlantic herring *Clupea harengus* consumption. Due to a lack of data for larval and juvenile fishes, the same relations for maximum consumption of adult herring and alewives were applied to age-0 fish by Arrhenius (1998a) and Klumb *et al.* (in review), respectively.

The “P-value” in the bioenergetics model refers to the proportion of maximum consumption. This value is used to fit the bioenergetics model to observed growth or can be set constant to check resultant growth potential in varied environments.

Temperature dependence of consumption is usually modeled as simple or modified exponential functions (Hansen *et al.* 1997). For cool- and cold-water species, the temperature dependence of consumption is generally modeled using a curve proposed by Thorton and Lessem (1978), which modified the logistic equation. This function is the product of two intersecting sigmoid curves (one ascending and one descending) forming a “humped” curve across the entire temperature range inhabited by a given species.

Required parameters include the approximate temperatures for optimum consumption, and the high and low temperatures where consumption is dramatically reduced (~98%) compared to maximum consumption. Any temperatures derived from laboratory or field data showing maximum or reduced consumption levels can be used. If specific data relating consumption and temperature are lacking, the optimum of consumption is generally equated to the fish’s thermal optimum for growth (Beitinger and Magnuson 1979), and the temperatures where consumption is dramatically reduced are derived from the thermal tolerances (survival limits) of a species.

Metabolism/respiration

Total metabolism = Respiration + specific dynamic action (SDA)

where

Respiration (R) = RA*W^{RB} * f(T)*Activity and
f(T) = e^{RQ*T}

Metabolism of fishes is determined by measuring oxygen consumption at various temperatures over a known time period, and generally modeled as an allometric function of weight and an exponential function of temperature. Brett and Groves (1979) distinguished three types of metabolism in fishes: standard, routine and active. By definition,

standard metabolism is the minimum energy requirements needed by a fish at rest (also known as basal metabolism), and it is this metabolic state that is used in bioenergetics models. Measuring standard metabolism is difficult and requires use of anesthetized fish or fish with movements confined by small respirometers. Routine metabolism includes normal spontaneous activity, while active metabolism includes the cost for activity above the spontaneous activity level. Winberg (1956) stated that active metabolism was approximately twice standard metabolism (*i.e.* the “Winberg multiplier” of 2). However, Ware (1975) indicated active metabolism could range from 2 to 3 times standard rates. Bioenergetics models generally use allometric function parameters derived for standard metabolism multiplied by a temperature function and an activity factor to estimate total respiration costs.

Respiration (g oxygen·g⁻¹·d⁻¹) of adult fishes generally scales negatively with weight (*i.e.* negative slope), and ranges from -0.25 to -0.15 on a weight specific basis (Winberg 1956). For clupeids, slopes of the metabolism-weight relations ranged from -0.19 to -0.28 for Atlantic menhaden *Brevoortia tyrannus* (Hettler 1976), -0.215 for alewife (Stewart and Binkowski 1986), and -0.227 for Atlantic herring (De Silva and Balbontin 1974). Rudstam (1988) used -0.227 in the adult Atlantic herring bioenergetics model, and this value was also applied to age-0 herring (Kerr and Dickie 1985; Arrhenius 1998a). The slope for the metabolism-weight relation of *Maurollicus muelleri*, a mesopelagic planktivore, was -0.15 (Ikeda 1996).

The relation of respiration to weight of fishes has been found to change ontogenetically, with isometric (mass independent) relations for larvae switching to negative allometries in adults (Post and Lee 1996). However, the variability of slopes found in the review of 31 species by Post and Lee (1996) highlighted the need to derive weight-metabolism relations for the larvae of individual species. The final weight-metabolism relation derived likely depends on the range of fish sizes used. Studies of larval fishes encompassing greater than three orders of magnitude in weight documented isometric relations between metabolism and weight for Clupeidae (Klumb *et*

al., in review), Cyprinidae (Kamler 1972), and Scombridae (Giguère *et al.* 1988).

Specific dynamic action (SDA)

$$SDA = SDA*(C - F)$$

Specific dynamic action, or more appropriately termed “apparent specific dynamic action” and also known as the “heat increment”, is the energy allocated to the digestive processes of food, principally deamination of proteins but also includes energy costs of absorption, transportation and deposition of food (Beamish 1974). Oxygen consumption by fasting and fed fish in flow-through respirometers (where the fish is subjected to a known level of activity, *i.e.*, forced to swim against a known current) is required to measure SDA (Beamish and Trippel 1990). Beamish and Trippel (1990) found that SDA increased with meal size and body weight but declined with weight at fixed rations. However, in most bioenergetic models, SDA is considered a constant proportion of ingested energy with values for adult fish ranging from 10-29% (reviewed by Beamish and Trippel 1990). The SDA parameter in bioenergetics models is generally borrowed from non-related species because proper measurement requires strict laboratory experiments using specialized equipment. For adult alewife (Stewart and Binkowski 1986) and adult Atlantic herring (Rudstam 1988), SDA was assumed to be 17.5% based on data for whole *Kuhlia sandvicensis* (Muir and Niimi 1972). Arrhenius (1998a) lowered SDA to 15% for age-0 Atlantic herring. Larval clupeids have been found to assimilate food more efficiently than adults (Kiørboe *et al.* 1987). In energetic terms, Kiørboe *et al.* (1987) estimated SDA for larval Atlantic herring to be 10% of assimilated rations, and Limburg (1994) calculated the mean SDA for American shad *Alosa sapidissima* juveniles to be 13%.

Activity

$$\text{Activity} = e^{RTO*VEL},$$

where $VEL = RK1*W^{RK4}$ for $T \geq RTL$
or $VEL = ACT*W^{RK4}*e^{BACT*T}$ when $T < RTL$

The energetic cost of activity is generally considered a multiple of standard metabolism. A

simple constant, *i.e.* the “activity multiplier = 2” of Winberg (1956), can be used to accord increased (aerobic) metabolic costs due to swimming. Exponential functions have been used to model activity costs of adult alewife (Stewart and Binkowski 1986) and Atlantic herring (Rudstam 1988). The exponential model is composed of three components: 1) VEL which is the weight dependence of swimming speed (cm/s), 2) the temperature (T) dependence of swimming speed (BACT), and 3) the relation of respiration to swimming speed (RTO). The parameter ACT is the intercept (cm/s) for a 1-g fish at 0°C. Swimming speed can change from temperature dependence to independence (at $T = RTL$). Swimming speeds of Atlantic herring were only dependent on weight at temperatures $> 9^\circ C$ (Rudstam 1988), and alewife swimming speeds were independent at $> 15^\circ C$. (Stewart and Binkowski 1986)

The coefficient for swimming speed dependence of metabolism (RTO) used in the adult alewife model was assumed constant ($RTO = 0.03$) and based on data in Muir and Niimi (1972). Data for Cape anchovy *E. capensis* found that coefficients before, during, and after feeding ranged from 0.01 to 0.04 (James and Probyn 1989). A coefficient relating respiration and swimming speed of 0.03 has also been reported for adult menhaden (Durbin *et al.* 1981), and the coefficient for adult coregonids was 0.02 (Dabrowski 1985). However, the coefficient relating respiration rate to swimming speed increased substantially in larval coregonids (Dabrowski 1986) and cyprinids (Kaufmann 1990); therefore, a constant relating metabolic cost to swimming speed is inappropriate for early life stages. Using an exponential activity function and a constant relating swimming speed to oxygen consumption resulted in essentially no energetic costs for the activity of YOY alewife (Klumb *et al.*, in review).

How to best model the activity costs of larval fish is uncertain since existing data from the few studies relating metabolism and swimming speeds at early life stages are equivocal. Because the slope of metabolism versus swimming speed varied with body size, Dabrowski *et al.* (1988) found active metabolic rates of coregonids to be 5 - 50 times standard metabolism. A size-effect on

the slope for the metabolism-swimming speed relation also existed for larvae of two cyprinid species (Kaufmann 1990); however, ratios of routine metabolism to standard metabolism were low (< 1.5) and essentially flat from 0.005 - 0.300 g (wet weight). In Kaufmann's (1990) study, ratios of active to routine metabolism (*i.e.*, the factorial scope) ranged from 2 - 4. These contrasting results may lie in the function chosen to describe the metabolism-swimming speed relation, *i.e.*, exponential (Dabrowski 1986; Dabrowski *et al.* 1988) or allometric (Kaufmann 1990). However, using an exponential model, Wieser and Forstner (1986) found the ratios of active to routine metabolism for larvae of three cyprinid species ranged from 1 - 4 and were independent of weight (0.01 - 0.3 g wet) and temperature (12 - 24°C). Activity rates of fishes can also vary widely with growth rate and food density (Ware 1975), while laboratory measurements of metabolism during activity may be higher than actual costs in the wild, since larvae are also passively moved by water currents. Klumb *et al.* (in review) used routine metabolism parameters without an activity multiplier in a bioenergetics model for age-0 alewife.

Clupeids have pronounced changes in activity patterns possibly due to circadian rhythms (Katz 1978; Batty 1987). Clupeids do not swim in schools during darkness (Limburg 1994). Accuracy of bioenergetic estimates of herring consumption were improved when including diel feeding cycles (Arrhenius 1998a).

Egestion

$$\text{Egestion (F)} = \text{FA} * \text{C}$$

Egestion is modeled as a constant proportion of consumption. Assimilation efficiency (in terms of energy) of adult menhaden ranged from 86 to 92% (Durbin and Durbin 1981). In the adult alewife (Stewart and Binkowski 1986) and Atlantic herring models (Rudstam 1988), egestion was assumed to be 16% of consumption.

Data for egestion processes and models are not common; most extensive studies have been done for brown trout *Salmo trutta* (Elliot 1976a, 1976b). Egestion has been found to be a function of

temperature and ration (Elliott 1976a). However, Stewart and Binkowski (1986) found small changes in estimated consumption when making the simplified assumption of egestion being a constant proportion of consumption in the bioenergetics model for alewife.

The proportion of consumption egested has been found to be low in larval and juvenile clupeids (Kiørboe *et al.* 1987; Limburg 1994). Arrhenius (1998) used 16%, the value from the adult Atlantic herring (Rudstam 1988) and alewife (Stewart and Binkowski 1986) models for the proportion of assimilated ration egested by larval Atlantic herring. Both Kiørboe *et al.* (1987) and Limburg (1994) found the percentage of food egested was 10% (by mass). However, Klumpp and von Westernhagen (1996) found egestion for Atlantic herring larvae age 8 - 33 days averaged 17.6% (range 13.4 - 25.6%) of ration (*Artemia sp. nauplii*) energy content.

Based on the above three studies on larval and juvenile clupeids (Kiørboe *et al.* 1987; Limburg 1994; Klumpp and von Westernhagen 1996), Klumb *et al.* (in review) chose 0.125 as a first approximation for the proportion of consumption egested by larval and juvenile alewife.

Excretion

$$\text{Excretion (U)} = \text{UA} * (\text{C} - \text{F})$$

Excretion is modeled as a constant proportion of assimilation (consumption minus egestion). In the adult alewife (Stewart and Binkowski 1986) and Atlantic herring models (Rudstam 1988), excretion was assumed to be 10% of assimilation based on rates measured for brown trout (Elliott 1976b).

Few studies on larval fish excretion have been conducted. For three species, *Blennius pavo*, plaice *Pleuronectes platessa*, and Atlantic herring, Klumpp and von Westernhagen (1996) found the mean percent of the assimilated ration excreted was 6.0, 6.6 and 10.7%, respectively. Due to high mortality for Atlantic herring larvae in Klumpp and von Westernhagen's study, Klumb *et al.* (in review) used the average value of 7.8% for all three species as a first approximation of the

percent of assimilation excreted by larval and juvenile alewife.

Data requirements

There are four data requirements for the bioenergetics model: 1) diet (in proportions of prey types), 2) energy density of the predator fish, 3) energy density of the prey, and 4) water temperatures. The bioenergetics model is an individual based model but can incorporate populations by multiplying mean weight by population number.

Diet

Diet information was summarized by Douglas E. Hay (Pacific Biological Station, Fisheries and Oceans Canada) based on recent observations (Hay and McCarter 2001, and older literature such as Wailes 1936). Depending on the population, herring diets can be simple or complicated. The simple story is that herring eat mainly copepod eggs and nauplii as larvae, copepod adults and nauplii as juveniles and euphausiids as adults. This over-simplified story gets messy when the smaller, non-migratory marginal populations are examined because they appear to eat a wider variety of taxa. Herring feed intensely in the summer months but they also eat during winter. In all areas, winter diets, although small in relation to total annual consumption, may be more variable than summer diets. Perhaps the main point to emphasize, however, is that in southern British Columbia, most herring feed in shelf waters where the main food items are euphausiids. Atlantic herring and sprat *Sprattus sprattus* diets consisted of 70 - 73% copepods, 12 - 14% *Oikopleura*, and 9 - 12% cladocerans (De Silva 1973).

Adult clupeids feed by filtering or particulate feeding (Blaxter and Hunter 1982; Janssen 1976). Janssen (1976) found for alewives that the filter feeding mode displayed by large alewives (total lengths > 170 mm) was not size-selective, while particulate feeders (total lengths 50 - 115 mm) selected zooplankton > 1.0 mm. Transition of larvae to adult body morphology and feeding modes occurs at metamorphosis (~35 mm) after gill rakers and the upper and lower jaws become developed (Blaxter and Hunter 1982). Although

activity of clupeids may be lower at night (Katz 1978), filter feeders can still feed in darkness (Hettler 1976; Janssen and Brandt 1980; Grabe 1996).

Feeding activity of larval herring has been found to be dependent on densities of copepod nauplii (Munk and Kiorboe 1985) with success a function of prey size (Hunter and Blaxter 1982). Atlantic herring (length 25 mm) larvae were able to consume prey sizes ≥ 1.0 mm (Sherman and Honey 1971, cited in Hunter and Blaxter 1982). Foraging behavior of Atlantic herring larvae changed with prey size and was related to larval length by the equation: prey length = $0.027 \times$ larval length (Munk 1992), and attack success was directly related to relative prey size. Fiksen and Folkford (1999) included the mouth size of herring larvae, perception (visual field and reaction distance), light intensity, and the length, width and density of plankton prey when modeling encounter rates and probabilities of successful strikes.

Energy density of predator and prey

Energy density, also called caloric content and energy content, in bioenergetics models is used in terms of wet weight. Dry-weight data are customarily converted (approximated) to wet weight assuming dry weight is 10 - 20% of total weight. Hartman and Brandt (1995) provided many equations for estimating energy density from the percent dry weight of various marine and freshwater fish species. Assuming constant energy densities or using values that are too high or low can greatly affect bioenergetics model consumption estimates (Stewart and Binkowski 1986).

Energy density (ED) of clupeids has been found to vary seasonally, peaking in fall and declining through winter (Arrhenius and Hansson 1996; Flath and Diana 1985; Paul *et al.* 1998). Age-0 EDs are lower than older fish (Arrhenius and Hansson 1996; Flath and Diana 1985; Paul *et al.* 1998). For age-1 alewife in Lake Michigan, ED in June and July was $4520 \text{ J}\cdot\text{g}^{-1}$, increased in August and September to 4729 and 5440, respectively, then declined to 4729 in April, and 4436 by May (Flath and Diana 1985). For age-0 Atlantic herring, Arrhenius and Hansson (1996) found ED

increased from 2600 J·g⁻¹ in mid-July to 4500 J·g⁻¹ in October. The ED of age-0 Baltic Sea sprat increased from 4000 J·g⁻¹ in August to approximately 5250 J·g⁻¹ by December (Arrhenius 1998b). October ED of alewife was 5020 J·g⁻¹ (Flath and Diana 1985).

Higher energy densities were found for Pacific herring off Alaska (Paul *et al.* 1998; Foy and Paul 1999) compared to Great Lakes alewives and Baltic Sea clupeids. Age 2+ Pacific herring had EDs in fall that ranged from 9400 to 10200 J·g⁻¹ and declined over winter to 5200 to 6300 J·g⁻¹ by spring. Females had higher energy densities in both seasons than males by 200 - 400 J·g⁻¹. Age-0 herring had EDs of 5700 J·g⁻¹ in fall which declined to 4400 J·g⁻¹ by the following spring (Paul *et al.* 1998). Equations to predict ED from standard length of juveniles by month are provided in Paul and Paul (1998a). The ED for age-0 captive fasting herring declined 23 J·g⁻¹·d⁻¹ from

December to the end of January (Paul and Paul 1998b).

Energy densities of freshwater and marine invertebrates can be found in Cummins and Wuycheck (1971), while good tables of the caloric content of marine invertebrates (with references) are presented in Foy and Norcross (1999) and Foy and Paul (1999). Laurence (1976) provides energy densities for marine calanoid copepods in the Atlantic. Like fish, the energy density for invertebrates has been found to vary seasonally.

Table 2.2.1 Energy densities (jouls/gram) for main food items of Pacific herring.

Food Item	J·g ⁻¹
Copepoda	2580
Euphausiids (per gram wet weight)	5020
Fish eggs (per gram wet weight)	4520

Table 2.2.2 Existing bioenergetic models.

Reference	Comments
General models	
Winberg 1956	extensive early work but reference not that accessible
Kitchell <i>et al.</i> 1974	results of International Biological Program (IBP) workshops and first paper of the “Wisconsin” bioenergetics model – applied to bluegill sunfish (<i>Lepomis macrochirus</i>) in terms of mass balance
Elliott 1976b; 1979	general review of energetics resulting from his extensive work with brown trout (<i>Salmo trutta</i>)
Stewart <i>et al.</i> 1983	changed the Kitchell <i>et al.</i> 1974 model from mass to energy balance, for lake trout (<i>Salvelinus namaycush</i>)
Clupeid bioenergetics models	
Rudstam 1988	Adult Atlantic herring (<i>Clupea harengus</i>)
Kerr and Dickie 1985	Age-0 Atlantic herring
Arrhenius 1998	Age-0 Atlantic herring
Fiksen and Folkford 1999	Larval Atlantic herring– Individual based model, which includes metabolism, ingestion, prey encounter success, and multiple prey functional response
Stewart and Binkowski 1986	Adult alewife (<i>Alosa pseudoharengus</i>)
Hewett and Stewart 1989	Age-0 alewife: (only temperatures for the consumption component differed from the adult model)
Klumb <i>et al.</i> In review	Age-0 alewife
Durbin and Durbin 1983	Adult menhaden (<i>Brevoortia tyrannus</i>):– in terms of energy and Nitrogen