POTENTIAL APPLICATION OF BIOENERGETICS MODELS TO HABITAT MODELING AND IMPORTANCE OF APPROPRIATE METABOLIC RATE ESTIMATES WITH SPECIAL CONSIDERATION FOR ATLANTIC SALMON

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ABSTRACT

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Reliable fish habitat models are required for fisheries management and habitat restoration. Recent studies suggested the bioenergetics modeling approach, which uses the net energy gain to describe habitat quality, as powerful tool. However, the reliability of predictions of bioenergetics models is strongly dependent on the accuracy of the input variables. Here, we give an overview of the potential application of bioenergetics models to fish habitat modeling and of the different bioenergetics components, especially focusing on the standard metabolism of Atlantic salmon (*Salmo salar* L.). In a literature review, 30 studies with estimates or models on the standard metabolism of Atlantic salmon of different age stages, origins, and under a variety of environmental conditions were identified.

RÉSUMÉ

Enders, E.C., and Scruton, D.A. 2006. Potential application of bioenergetics models to habitat modeling and importance of appropriate metabolic rate estimates with special consideration for Atlantic salmon. Can. Tech. Rep. Fish. Aquat. Sci. 2641: v + 40 p.

Les modèles d'habitat de poisson fiables sont requis pour une gestion de la pêche et une conservation de l'habitat efficace. Les études récentes ont suggéré que l'approche de la modélisation bioénergétique, qui utilise le gain d'énergétique net afin d'écrire la qualité d'habitat, comme l'outil puissant. Cependant, la fiabilité de prédictions des modèles bioénergétiques est fortement reliée à la précision des variables d'entrée. Ici, nous donnons un compte rendu sur l'application potentielle des modèles bioénergétiques afin de modéliser l'habitat de poisson et sur les composantes bioénergétiques, en focussant sur le métabolisme standard de saumon atlantique (*Salmo salar* L.). Dans une revue de littérature, 30 études avec des estimations ou des modèles de métabolisme standard de saumon atlantique, à des stades de développement différents, à des origines différentes et à des conditions écologiques diverses, ont été identifiées.

BIOENERGETICS MODELS

Bioenergetics studies the partitioning of energy by living organisms applying thermodynamic principles to organisms and biological systems. The basic principle of bioenergetics is that all energy acquired through food ingestion is deposited as new body tissue, used in metabolic processes or ultimately lost as waste in faeces and excretion. Thus, bioenergetics provides a framework for the study of relationships between feeding rates or growth rates of organism subjected to different environmental conditions. The first fundamental study on the energy budget of fish was pioneered by Ivlev (1939). His work written in Russian was unfortunately never translated. In 1956, Winberg published an extensive review on fish energetics. Due to increased attention of fisheries management and the aquaculture industry in fish bioenergetics, there has been considerable research interest in bioenergetics studies over the last few decades. Several multi-authored books and reviews have been published that provide a detailed introduction into the principles and methodologies of fish energetics (Hoar and Randall 1969; Gerking 1978; Tytler and Calow 1985; Wootton 1990; Jobling 1994).

Bioenergetics models have been used to quantify consumption, growth, and activity rates of fish populations under specified environmental conditions and to predict the carrying capacity of ecosystems (Kitchell et al. 1977; Stewart et al. 1983; Rice and Cochran 1984; Brandt et al. 1992; Boisclair and Rasmussen 1996). A computerized fish bioenergetics model, also referred to as the 'Wisconsin bioenergetics model' developed by Hewett and Johnson (1992), led to a wide application of the bioenergetics approach. Bioenergetics models for almost 40 fish species are readily available in the current version of the *Fish bioenergetics model 3.0* (Hanson et al. 1997). The model provides researchers with a powerful tool to assess food consumption, growth, or reproduction of fish. A major advantage of bioenergetics modeling is that it provides an easy and less labor-intensive approach to estimate food consumption or production than to directly measure it in the field. However, it is important to be aware that the accuracy of predictions generated by bioenergetics models is dependent on the validity of the input coefficients and possible errors in the estimation of the coefficients affect directly the accuracy of the model output (Ney 1993).

APPLICATION OF BIOENERGETICS MODELS TO HABITAT MODELING

Fausch (1984) proposed that bioenergetics models could also be applied to habitat management and restoration by estimating the expected net energy gain in relation to habitat as a means to describe habitat quality. Net energy gain (NEG) is used as the link between habitat use and fitness of fish, based on the assumption that measures of net energy intake can be translated into measures of fitness (Ware 1982). For good fitness, an organism must maintain balance between the energy it gains from its microhabitat and the energy it requires for growth, metabolism, and losses (Fausch 1984). Numerous researchers have suggested that NEG is a promising approach to define fish habitat quality (Fausch 1984; Hughes 1992; Hill and Grossman 1993; Hayes et al. 2000; Sabo et al. 1996; Van Winkle et al. 1998; Vehanen et al. 2000).

Bioenergetics approach may therefore provide a better link between habitat models and biological mechanisms than conventional models based on habitat preferences related to the three abiotic habitat variables water depth, substrate, and flow velocity. The approach takes into account both the effect of biotic variables such as inter- and intra-specific competition and risk of predation and the effect of abiotic variables, such as water temperature, which play a role in determining fish physiology and energetics. The bioenergetics approach therefore provides information on the mechanisms underlying observed growth and production and therefore can contribute to a more definitive understanding of the determinants underlying correlates of fish abundance. Furthermore, the bioenergetics modeling approach may theoretically be more transferable among river systems than conventional habitat models (Guensch et al. 2001). Additionally, advances in computing power and potential for increased spatial data collection will make spatially explicit modeling efforts more practical (Harding et al. 1998). Numerous authors have attempted to use bioenergetics modeling to predict habitat selection (e.g., Hill and Grossman 1993; Hughes 1992; Hayes et al. 2000) or habitat suitability (Baker and Coon 1997; Braaten et al. 1997). Bioenergetics models have been shown to accurately predict microhabitat choice by a variety of drift-feeding fishes, e.g. Arctic grayling *Thymallus arcticus* (Hughes 1992), rosyside dace *Clinostomus funduloides* and rainbow trout *Oncorhnychus. mykiss* (Hill and Grossman 1993), Atlantic salmon *Salmo salar* (Nislow et al. 1999, 2000), brown trout *Salmo trutta* and mountain whitefish *Prosopium williamsoni* (Guensch et al. 2001).

Bioenergetics models were predominately applied to predict habitat choice and growth primarily at microhabitat scales. However, Hughes (1998) extended the bioenergetics model for stream-dwelling fish to predict reach and whole stream size distributions of salmonids. The bioenergetics approach may also be applied to predict fish growth. Hayes et al. (2000) demonstrated that the bioenergetics approach may generate accurate lifetime growth trajectories for brown trout. Similarly, using a bioenergetics model for juvenile Atlantic salmon, Nislow et al. (2000) demonstrated that bioenergetics modeling provide a realistic prediction for growth rate in different river habitats. Finally, Rosenfeld and Boss (2001) generated predictions of NEG for juvenile cutthroat trout that were consistent with observed patterns of growth in pool and riffle habitats.

The purpose of the present report is to give a general overview on the basic principals and input variables of bioenergetics model. Furthermore, we analyse the limitations and assumptions of bioenergetics models.

BASIC PRINCIPLES OF BIOENERGETICS MODELS

The study of fish bioenergetics involves the partitioning of ingested energy into the major physiological components of the energy budget equation. In its simplest form the equation can be represented as:

(1.1) $$E(in) = E(P) + E(out)$$

where E (in) is the energy ingested as food, E (P) represents energy retained as production and E (out) are energy losses.

The equation is usually expanded to the form:

$$C = P + R + F + U \quad (1.2)$$

where consumption C is the energy of food consumed, production P the energy for somatic and gonadal growth, respiration R the energy lost in form of heat produced during the metabolism, F is the energy lost in the faeces, and U is the energy lost in the excretory products, particularly nitrogenous products such as ammonium and urea (Wootton 1990).

The respiration R can be further divided in standard metabolism (SMR), activity metabolism (R_A), and metabolism related to digestion named specific dynamic action (SDA) after Rubner (1893):

$$R = SMR + R_A + SDA \quad (1.3)$$

Bioenergetics modeling requires estimations of all components of the energy budget. A variety of calorimetric and respirometric methods can be used to estimate the components, however it is not technically feasible to estimate all components simultaneously; therefore input coefficients are often modeled. As previously mentioned, an inappropriate assumption could have strong influence on the accuracy of the prediction generated by bioenergetics models (Ney 1993).

Physiological rates like consumption, production, and respiration rate are dependent on several biotic and abiotic factors e.g. body mass, water temperature, dissolved oxygen concentration, salinity, pH, reproductive cycle, food availability, inter- and intra-specific competition, and predation. The majority of biological traits, including physiological rates, are size dependent. The relationship between body mass and biological variables can be described by a potential model:

$$f(M) = a \cdot M^{b} \quad (1.4)$$

The mass exponent b increases usually allometrically with increasing body mass M (Fig. 1).

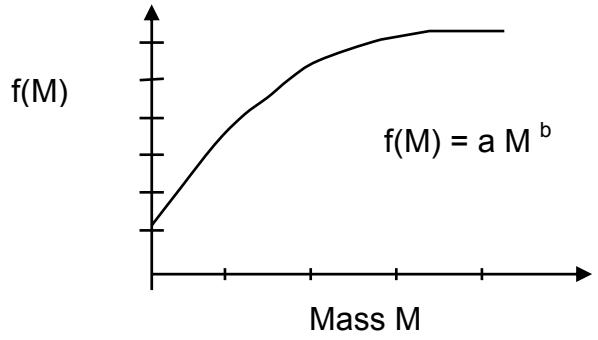

Figure 1. Allometric relationship between fish body mass M and physiological rates like food consumption, production, and respiration (after Brett and Groves 1979).

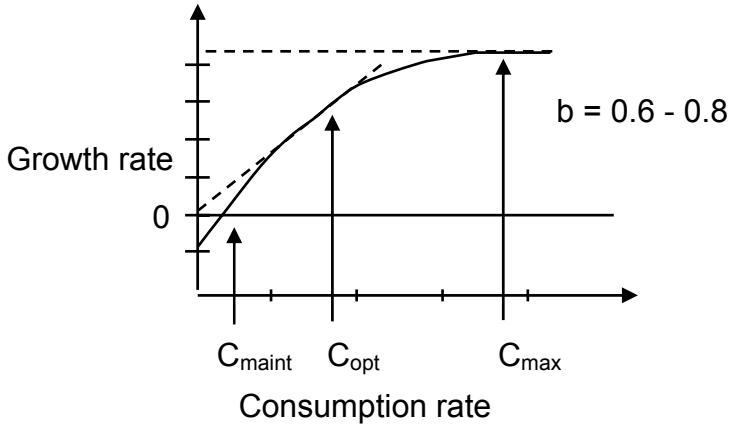

Figure 2. Relationship between food consumption rate and growth rate. The growth-ration curve illustrates maintenance C_{maint}, optimum C_{opt}, and maximum C_{max} consumption rates (after Jobling 1993).

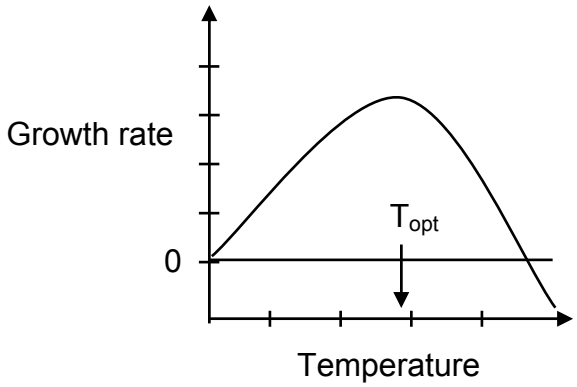

Figure 3. Relationship between water temperature and growth rate (after Brett and Groves 1979).

Water temperature has also a major influence on physiological rates. The relationship between water temperature and physiological rates is described by an exponential model:

$$f(T) = e^{c \cdot T} \quad (1.5)$$

The temperature coefficient c ranges usually between 0.05 - 0.1, which corresponds to Q_{10} values of 1.7 - 2.7 (Jobling 1993).

FOOD CONSUMPTION AND GROWTH RATE

Ingested energy that is neither lost as heat in metabolism nor as faecal or excretory products, is available for growth, which could be either somatic or reproductive. Growth is defined as an increase of the energy content in the fish body. It is usually measured as mass gain which implies the assumption that the tissue composition of fish is constant over time and that changes in body mass will exclusively reflect changes in the energy content of the body. However, body composition may not be constant and the relative proportion of protein, lipids, carbohydrates, and water may change over time.

The relationship between food consumption and growth rate is curvilinear (Fig. 2). At zero consumption the fish is starving and loses body mass. Growth rate increases rapidly, crosses the point of zero growth at the maintenance ratio. With increasing levels of food consumption, growth rate increases less rapidly and reaches the point of maximum growth at the optimal consumption rate. It then plateaus at the maximal consumption rate (Jobling 1993). For the majority of fish species the maximum consumption rate has been observed to scale in proportion to body mass raised to the power 0.6-0.8 (Jobling 1993).

In addition, water temperature has a major effect on the amount of food consumed. When fish are given access to unlimited food supply, an increase in water temperature leads initially to increased consumption rates. Food consumption peaks at species-specific optimal water temperature before it declines as water temperature approaches the upper thermal tolerance limit of the species (Fig. 3).

The most comprehensive field study on food consumption and growth rate of fish was undertaken by Elliott (1975a, 1975b, 1975c, 1975d, 1976a, 1976b, 1976c, 1993). He analyzed for more than 25 years food consumption and growth rate in relation to body mass, water temperature, and other environmental variables of brown trout *Salmo trutta*.

METABOLIC RATE

Losses due to metabolic demands usually constitute a large proportion of the energy budget of a fish. These energy costs can be partitioned into the minimal costs required for maintaining basic body function, those associated with activity and those related to the digestion, absorption, and processing of food. While this partitioning is straight forward from a theoretically point of view, it is very complicated to separate the different metabolic components in experiments. This has led to a lack of consistency in the use of the terms defined by different authors, and no universally acceptable set of definitions has yet been presented.

The terminology of the different metabolic components and methodologies used to estimate metabolic rates are presented in Section 2. In general, fish metabolism is strongly influenced by variables such as body mass (Brett 1964), water temperature (Liao 1971), salinity (Rao 1967), feeding rate (Brett and Groves 1979), activity (Brett 1962) and different stress factors such as handling or sudden temperature changes (Peterson and Anderson 1969).

FAECES AND EXCRETION

The non-digestible fraction of the diet, along with sloughed intestinal epithelial cells, mucus, catabolized digestive enzymes, and bacteria constitute the main components of faeces. Energy losses as nitrogenous excretory products, mostly ammonium and urea, come from two sources:

(1) Endogenous nitrogen excretion is produced by the catabolism of protein in energy-yielding respiration. In fish, protein is the usual substrate for respiration.

(2) Exogenous nitrogen excretion is related to feeding. It results from the loss of excess protein or during the adjustment of the balance of amino acids.

The excretion of ammonium and urea takes primarily place over the gills (Jobling 1994). The excretion rate U is dependent on body mass M:

$$f(U) = a \cdot M^{b} \qquad (1.6)$$

The proportion of energy ingested and lost as ammonium or urea excretion decreases as the food consumption rate increases, but increases with water temperature (Elliott 1976a). These effects are opposite to those on the proportion of energy lost as faeces. Faeces may also include some nitrogenous wastes, therefore it is expedient to combine the losses through faeces and nitrogenous excretion. Assimilation efficiency can be calculated as:

$$\text{Assimilation efficiency} = 100 \cdot (C - (F + U)) \cdot C^{-1} \qquad (1.7)$$

where consumption C is the energy of food consumed, F is the energy lost in the faeces, and U is the energy lost in the excretory products (Wootton 1990). Assimilation efficiency changes little over a wide range of water temperatures and ration size because of the opposite effects of these two variables on faecal and nitrogenous excretion (Elliott 1976a). The assimilation efficiency may range between 70-75% as suggested by Elliott (1976a) for brown trout feeding on *Gammarus*.

Fish faeces compromise not only undigested food but also mucus, dead cells of the gut walls, enzymes, and bacteria from the intestine endogene flora, therefore the increased amount of faeces may lead to an underestimation of the actual assimilation efficiency (Jobling 1994). Furthermore, due to leaching processes, the accuracy of faecal estimates is often poor as the suspended and soluble fraction may easily be lost (Elliott 1976a).

MODEL LIMITATIONS AND ASSUMPTIONS

The simple equation of Winberg (eq. 1.2) only utilized four input coefficients, however, the more complex computerized bioenergetics models developed by James Kitchell and his students at the University of Wisconsin-Madison (often refereed to as the Wisconsin model), taking into account body mass and water temperature dependencies, may require between 10-30 coefficients (Hanson et al. 1997). Due to the difficulty to obtain all needed input coefficients for the bioenergetics model, the five following assumptions are frequently applied in bioenergetics modeling:

1. Extrapolation of allometric functions
   The relation between body mass and variables like food consumption and standard metabolism are described by an allometric function. The coefficients and exponents of the allometric function are often derived from laboratory experiments using juveniles, but estimates are extrapolated to adult life stages.

2. Unjustified “species borrowing”
   In order to obtain input values coefficients and exponents are often borrowed from other well-studied species (Beauchamp et al. 1989). A recent study on Pacific salmonids has however demonstrated that models derived from even closely related Pacific salmonids did not accurately predict the metabolic rates of a given Pacific salmon species, indicating that the practice of ‘‘species borrowing’’ should be avoided whenever possible in assessing metabolic rates (Trudel et al. 2004).

3. Unknown activity costs
   Winberg (1956) considered activity to be a simple integer multiple of two times the standard metabolism. Kitchell et al. (1977) suggested a multiplier of three. Recent studies have however showed that fish activity may vary from 3- to 22-fold (Tang et al. 2000), indicating that a fixed multiplier may lead to potential inaccuracy in

the prediction of bioenergetics models. Despite the obvious potential inaccuracy, the approach of using a fixed multiplier is still commonly used.

4. Inadequate estimation of external variables
   Bioenergetics models do not free users from the obligation of field sampling to obtain representative data. All external variables may be subject to errors that could render model outputs inaccurate.

5. Laboratory experiments
   Many of the techniques used to evaluate physiological coefficients and exponents for bioenergetics modeling are based on laboratory experiments and thus their relevance to fish in the wild is unknown. Fish behavior and performance exhibited in the laboratory may be artificial and not truly representative for field conditions (Hansen et al. 1993; Ney 1993).

In conclusion, it can be concluded that model uncertainties and coefficient variability are high. Generally, little considerations are given to limitations of bioenergetics model predictions and models often lack confidence limits (Schaeffer et al. 1999; Bajer et al. 2003). Furthermore, true validation of bioenergetics models is difficult as estimates derived from the laboratory or from the field are based themselves on assumptions. A comparison between model and field or laboratory data must therefore be seen as corroboration rather than a validation. Even corroborations are rare in the literature (but see Beauchamp et al. 1989; Madenjian et al. 2004), probably because exhaustive and thus expensive field studies must be conducted to obtain the necessary data. Bioenergetics models are nonetheless a powerful tool for predicting fish consumption, production, activity, and habitat quality if valid input values are available. Therefore, bioenergetics habitat models may offer a promising mechanistic approach to predict habitat suitability and habitat-specific growth rates on the basis of food intake and swimming costs (Rosenfeld 2003). However, for stream-dwelling fish one of the main limitations of present bioenergetics models relate to uncertainties in the capture efficiency of drifting food particles and in how fluctuations in flow velocity effect the swimming costs of fish (Boisclair 2001). The credibility of the bioenergetics approach will continue to be compromised if erroneous input values are used (Hansen et al. 1993; Trudel et al. 2004).

METABOLISM

TERMINOLOGY OF METABOLIC LEVELS: BASAL, STANDARD, ROUTINE, ACTIVITY METABOLISM, AND SPECIFIC DYNAMIC ACTION

Basal metabolism is the minimum rate of energy expenditure to keep an organism alive (Brett and Groves 1979) and considerable documentation exists on the basal metabolism for homeotherms (Kleiber 1947; Blaxter 1989). Basal metabolism (BMR) of homeotherms is usually measured for unfed but not starved individuals after sleep while resting in a warm environment. In fish, the metabolic rate is generally estimated by determining oxygen consumption in a respirometer. The first attempt to measure the

metabolic rate of fishes was done in closed system respirometer (Ege and Krogh 1914; Fry 1947). This method only enabled the determination of oxygen consumption rates over long periods of time. As most fish routinely showed slight activity over these time periods, it was impossible to completely exclude metabolic costs due to locomotor activity from the measured metabolic rate (Krogh 1916). Therefore, Krogh (1914), for fish, replaced the term basal metabolism by *standard metabolism* (SMR). SMR was considered as the metabolic rate of a fish in relative rest, making as few swimming movements as possible (also referred to as *resting metabolism*). In addition, fish was supposed to be unfed but not starving.

Since fish frequently exhibit spontaneous activity, the measured metabolic rate was often influenced by locomotor activity. For this reason Fry (1957) defined *routine metabolism* (RMR) as the metabolism of a resting, unfed, but not starving fish which shows frequent spontaneous activity. The increased oxygen consumption rates due to spontaneous activity were included in the estimation of routine metabolism (Beamish and Mookherjii 1964).

Activity metabolism R_A refers to the amount of energy fish use for swimming (migration, predation, and escape). Uniform swimming modes of fish are generally classified in three categories: *Sustained, prolonged,* and *burst swimming* (Brett 1964; Hammer 1995). These categories do not only reflect fish behavior but also biochemical processes that provide fuel for the different swimming categories:

(1) *Sustained or cruising speed* is defined as the speed fish can maintain for at least 200 min. The locomotor activity is exclusively powered by aerobic metabolism in red musculature.

(2) P*rolonged speed* fish may maintain for intermediate time periods (1-200 min). It is thought to be mainly aerobically powered by the use of red musculature.

(3) *Burst speed* can not be maintained for longer than several seconds (15-30 s, depending on the author). Burst swimming is fuelled by anaerobic metabolism using white musculature.

Swimming at uniform speeds, however, may comprise only a small fraction of the daily fish activity pattern in natural flow environments. Thus, it is desirable to equally obtain estimates on the energetic costs of different *spontaneous activity* patterns. Several studies have demonstrated that the energetic costs for sustained swimming at constant speeds and directions, as determined in swimming experiments (Brett 1964; Beamish 1978; Schurmann and Steffensen 1994), may be considerable lower than the energetic costs for spontaneous activity such as accelerations and turns (Smit 1965; Koch and Wieser 1983; Wieser et al. 1988; Krohn and Boisclair 1994). The divergence is due to differences in the biochemical mechanism underlying the different swimming modes or activity pattern.

When fish digest food, the metabolic rate increases because processes associated with digestion involve energy expenditure. This was first noticed by Rubner (1894) who defined it as *specific dynamic action* (SDA). Respiration reaches a peak within a few hours after feeding and then decreases slowly to the level before food intake. Ingestion, digestion, and post-digestive processes can impose a significant metabolic cost. Energy expenditure for SDA is influenced by fish body size, water temperature, food ration, and diet composition (Tandler and Beamish 1979). Jobling (1981) pointed out that energy expended for SDA may reach 15% of the energy content of the food digested. SDA usually decreases with increasing body size for a given food intake because SDA is a surface dependent process and thus follows an allometric relationship.

METHODS USED TO ESTIMATE METABOLIC RATES

In general, respirometry experiments are used to analyze metabolic rates in fish and in these experiments, oxygen consumption rate is estimated using oxygen depletion over time. Obtained oxygen consumption rates may further be converted using an oxycalorific coefficient, which is the energetic equivalent of oxygen consumption. For fish, generally an oxycalorific coefficient of 13·59 $kJ \cdot g^{-1}$ is applied (Jobling 1994).

Closed systems were the first approach to measure metabolism (Ege and Krogh 1914; Fry 1947). The disadvantage of closed systems is that the method only enabled estimations of oxygen consumption rate over relatively long time periods (several hours). During these prolonged periods, oxygen concentration declined whereas excretory products increased within the respirometer, which may potentially lead to additional stress to the fish. Stress generally leads to an increase in the oxygen consumption of fish. The first experimental respirometers were of a simple tank design (Ege and Krogh 1914; Fry 1947), in 1960s two types of tunnel respirometers were developed by Blazka et al. (1960) and Brett (1964), and these are now widely used (Fig. 4).

Spoor (1946) developed a *flow-through respirometer* system, which avoided both the decline of oxygen concentration and the accumulation excretory products. Spoor (1946) however reported a time lag between increase in activity and the attendant increase in oxygen consumption. The duration of the lag and the magnitude of the estimated response are dependent on the flow rate through the system and the volume of the respirometer (Steffensen 1989). Estimated oxygen consumption rates must therefore be corrected for the time lag associated with flow-through respirometry systems according to formula given by Niimi (1978).

Measuring oxygen consumption in closed or flow-through respirometers over long time periods permits measurements of routine metabolism. Fry (1971) however stated that determination of standard metabolic rate of fish needs to be accompanied by a measure of fish activity. Forstner and Wieser (1990) also recommended that estimates of fish metabolism should be accompanied with monitoring the locomotory activity of fish. The new approach to overcome the problems due to the inference of fish activity

was the development of *intermittent flow* respirometry (Forstner 1983; Steffensen 1989). Intermittent-flow respirometry avoids the disadvantages of both closed and flow-through respirometers (Fig. 5). In these systems, the water flow through the respirometer chamber is closed for regular time intervals, interspersed by intervals in which the respirometer chamber is flushed with aerated ambient water. Several studies successfully applied intermittent-flow respirometry which allowed metabolic rate to be estimated over very short time periods of 3 to 10 min (Forstner 1983; Steffensen et al. 1984, Kaufmann et al. 1989; Herrmann and Enders 2000). Due to the high temporal resolution of the measuring intervals, it is possible to distinguish between metabolic rates that are affected or unaffected by spontaneous activity. Simultaneous video recordings allow further examination as to whether increased metabolic rates resulted from fish activity. Herrmann and Enders (2000) proposed a standardized procedure to exclude increased metabolic rates due to locomotory activity by extracting the lowest metabolic rates for estimation of standard metabolism. This method of data extraction of the lowest observed metabolic rates, not influenced by spontaneous activity, has been successfully applied in several studies (Panten 1995; Enders and Herrmann 2003; Hölker 2003).

A second approach to estimate standard metabolism is to use forced swimming experiments and extrapolate the swimming speed-oxygen consumption relationship back to zero swimming speed (Brett 1962; Beamish 1978). Brett and Groves (1979) assumed that the metabolic rate determined in this way is close to the standard metabolic rate. The extrapolation method is generally accepted to provide reliable SMR estimates, and several studies successfully demonstrated that estimates obtained from the extrapolation method and the direct measurement of SMR both provide accurate SMR values (Brill 1987; Leonard et al. 1999; Reidy et al. 2000), however the extrapolation method has been criticized because estimated metabolic rates, derived using this approach, are not determined experimentally (Smit 1965; Forstner and Wieser 1990). Forstner and Wieser (1990) also suggested the extrapolation approach may estimate higher metabolic rates because fish exhibit increased spontaneous activity at low flow velocities. Bushnell et al. (1994) similarly showed, in a comparative study on standard metabolism of Atlantic cod *Gadus morhua* that estimates from forced swimming experiments resulted in higher SMR estimates than determined without flow.

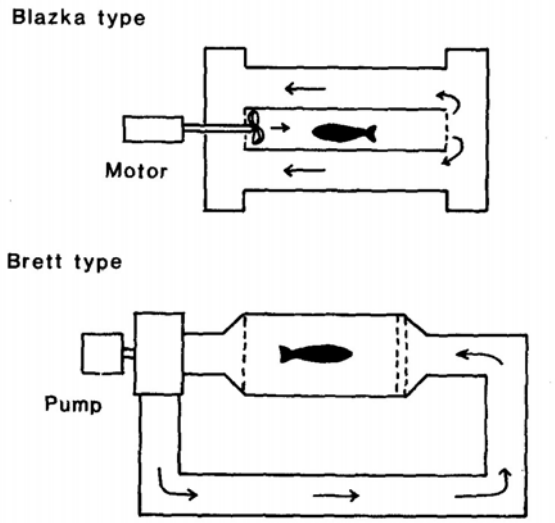

Figure 4. Schematic diagrams of a Blazka-type and a Brett-type respirometer used to study the effects of swimming activity on the metabolic rate in fishes.

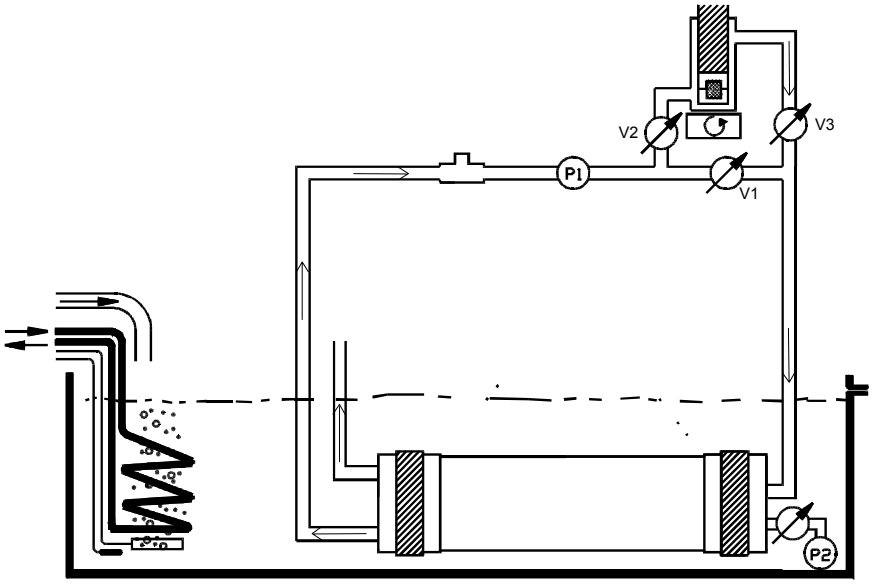

Figure 5. Experimental setup of an intermittent flow respirometer used to estimate the standard metabolism (valve V 1-3). Water is continuously pumped by pump P1 to the oxygen sensor. In intermittent intervals of 5 min the respirometer is flushed using a submerged water pump P2.

The authors assumed that higher SMR estimates from forced swimming experiments may be related to stress to the fish and by uncontrolled appearance of spontaneous activity at low flow velocities in a tunnel respirometer.

A third attempt to exclude activity costs from SMR estimates involved an experiment by Brill (1979) who paralyzed tunas using a neuromuscular blocking agent. He therefore prevented all swimming movements to estimate SMR of a continuously swimming pelagic fish species that, under natural conditions, never rests. Brill (1979) determined a mass exponent of 0.50 to 0.57 for *Thunnus albacares*, *Euthynnus affinis* and *Katsuwonus pelamis* which did not show any activity in the respirometer chamber. Using a similar method, Benetti et al. (1995) reported a mass exponent of 0.38 for dolphin fish *Coryphaena hippurus*. Alternatively, Gooding et al. (1981) extrapolated SMR from the swimming speed-oxygen consumption relationship and described a mass exponent of 1.19 for *Katsuwonus pelamis* and of 1.18 for *Thunnus alalunga.* Obviously, the mass exponent increases with the degree of activity involved. Dewar and Graham (1994), by extrapolating the swimming speed-metabolic rate relationship back to zero swimming speed, obtained estimates of SMR of *Thunnus albacares* hat were identical to SMR of paralyzed fish measured by Brill (1987).

Finally, starvation experiments are another promising approach to evaluate the standard metaboic rate of fish (Karås 1990). This approach however assumes that the effect of spontaneous activity during the experiments is negligible and Kerr (1982) demonstrated that starved fish reduce their activity.

ACTIVITY METABOLISM

Laboratory experiments

Converting fish movements to activity costs requires relationships between characteristics of movements and energy expenditures. The relationships are generally developed using respirometry experiments performed in laboratories. Activity metabolism is often measured using forced swimming experiments where fish swim against a uniform flow velocity (Brett 1964). Brett (1962, 1964, 1965) investigated the energetic requirements for swimming at various levels of the sustained capacity in sockeye salmon *Oncorhynchus nerka*. For this purpose, he constructed a tunnel respirometer, which allowed water to flow at precise velocities, with minimal wall effects or irregular flow patterns. In a series of experiments, he determined the oxygen consumption rate for a wide range of body sizes, water temperatures, and flow velocities for sockeye salmon (Fig. 6). Generally SMR scales with a mass exponent of less than unity, implying that larger fish consume less oxygen per gram of body mass than smaller fish, whereas R_A usually scales with a mass exponent greater than unity (>1), implying that larger fish have higher oxygen consumption rates related to activity per gram of body mass than smaller fish. Consequently, metabolic scope generally increases with body mass (Armstrong et al. 1992; Goolish 1991).

As swimming at a sustained speed comprises only a small part of activity patterns of fish, it is also desirable to obtain quantitative measurements of the energetic costs of different activity patterns such as accelerations, turns, or direction changes. These patterns are generally referred to as spontaneous activity. Experiments were carried out to define the energetic costs of spontaneous activity by means of mechanical activity recorders (Spoor 1946), heat loss sensors (Kausch 1968), or photocells (Smit 1965). Recent experiments estimated spontaneous activity, in terms of energy expenditures, by simultaneously measuring fish activity with a video monitoring system coupled to a respirometer (Krohn and Boisclair 1994; Tang and Boisclair 1995; Enders and Herrmann 2003). In this approach, fish swim freely in the respirometer without any flow.

Comparison of the results obtained by those two methods revealed that metabolic costs for sustained swimming at constant speeds, determined in forced swimming experiments, were significantly lower than the energetic costs for spontaneous activity. Spontaneous activity was found to be 3- to 22-times more expensive for same fish mass, temperature, and average swimming speed than forced swimming (Tang et al. 2000). The difference between forced swimming and spontaneous activity has been attributed to the costs of performing accelerations and turns which are not considered during forced swimming (Forstner and Wieser 1990; Boisclair and Sirois 1993; Enders and Hermann 2003).The increased costs of spontaneous activity in comparison to forced swimming lie in the use of different muscles. Fish swimming at uniform speed utilize their red muscles (aerobic metabolism) whereas, for more complicated movements such as acceleration, turns, or, strong bends, they use their white muscles, and therefore anaerobic metabolism, which is energetically less efficient and consequently more expensive (Goolish and Adelman 1987).

The quantification of energetic costs related to activity may also be directly estimated. This approach requires both knowledge of the amount and the intensity of fish movement and determination of the costs per unit movement, which are not easy to obtain. Activity metabolism is therefore often calculated as the difference between the energy consumed minus the energy used for production, SMR, SDA, and energetic losses in excretory products.

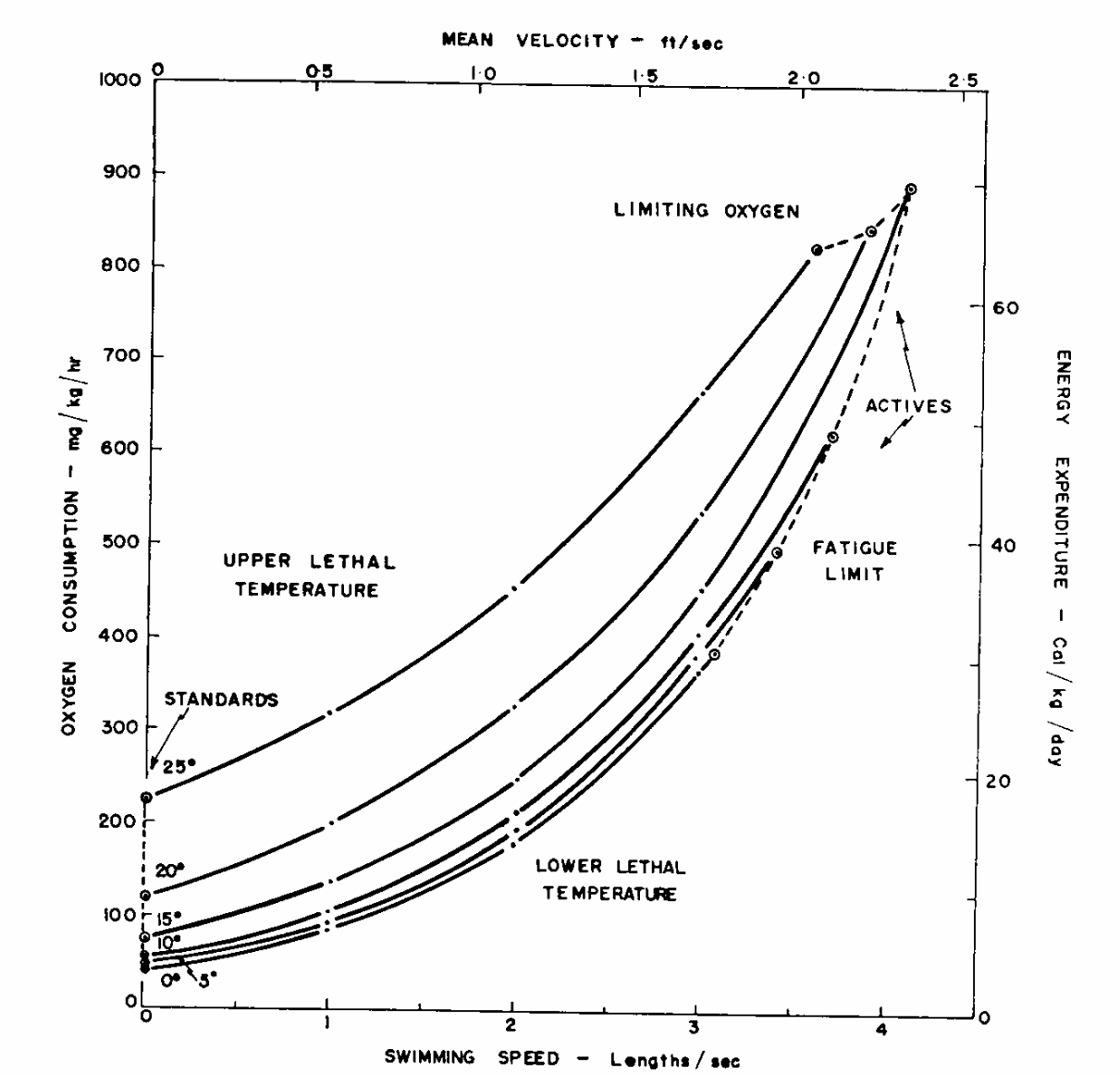

Figure 6. General relation between swimming speed and metabolic rate for yearling sockeye salmon in air-saturated freshwater (from Brett 1964).

Field activity

Several methods have been developed to quantify fish movements in the field including: mark-recapture experiments with data storage chips (Arnold et al. 1991), tracking of fish schools with 'split beam sonar' (Pedersen 1996), or single fish tracking with ultrasonic transmitters (Diana 1980) to assess tracks of individuals or populations. Fish movement in the field may also be estimated using an index related to movement such as heart rate telemetry (ECG) (Armstrong 1986, 1998), axial muscle electromyogram telemetry (EMG) (Briggs and Post 1997; Cooke et al. 2004), opercular activity (De Jager et al. 1976), or by underwater observation with e.g. the stereocinematographic method (Ménard 1991; Boisclair 1992). These methodologies may result in quite different outcomes. Priede and Young (1977), for example, measured heart beat frequency for brown trout and found an activity metabolic rate of 1.5-times the standard metabolism, while Briggs and Post (1997), measuring electromyograms, found the activity factor to be 2, and Boisclair and Sirois (1993) estimated an activity factor of 1.6- to -3.8-times the SMR in enclosure experiments.

Heart beat frequency, as an activity indicator, is compromised by the fact there is not always a direct relationship between heart rate and swimming activity as heart rate may be influenced by other variables. Therefore, cardiac output transmitters that measure simultaneously heart rate and blood volume are used in recent studies because fish may vary both variables in response to stress and energetic demands (Gamperl and Farrell 2004). Similar problems occur using electromyograms as activity indicator as activity estimates may be erroneous due to occurrences of different swim *modi* that are based on red or white muscles which are associated with different metabolic pathways (Weatherley and Gill 1987). Similarly, opercular activity may become independent from fish activity (De Jager et al. 1976). For example, fast swimming fish species can ventilate water over the gill by opening the mouth while swimming with velocity 'ram ventilation'. This behavior has the advantage that no energy is needed for the gill ventilation but ventilation rate becomes independent from activity.

Activity metabolism has been argued to be the most important factor influencing the energy turnover in fish (Brett and Groves 1979) and it may not only represent a large but also variable proportion of fish energy budget (Boisclair and Sirois 1993). The accurate determination of the size and variability of activity metabolism is therefore of particular relevance to the appropriate prediction of the net energy gain under given environmental conditions.

MASS EXPONENT B OF THE METABOLIC RATE FUNCTION

Much attention has been paid to the allometric scaling of metabolic rate with body mass because estimation of the allometric exponent of metabolic rate is particularly relevant for bioenergetics modeling. Winberg (1956) first published an average value for the mass exponent b of 0.81 for fish metabolism and included in his analysis data from many fish species. Similar composite values for the mass exponent b were reported from several authors: e.g. Glass (1969) stated an exponent b of 0.88, De Jager et al.

(1976) 0.83, Brett and Groves (1979) 0.86 and Kerr (1982) 0.82. Metabolic rates in these investigations corresponded to routine metabolism because oxygen consumption rates were determined over long time intervals, which implied that the measurements were influenced by spontaneous activity. Although the effect of spontaneous activity on SMR estimates is known, a mass exponent b of ~ 0.8 for the standard metabolism is still frequently assumed in bioenergetics models (Kitchell et al. 1977; Krohn et al. 1997).

The influence of activity apparently leads to higher estimates of the metabolic rate and the effect of activity is lower for smaller fish, which leads to an increase of the mass exponent with the degree of activity. Relatively low mass exponents were also described in a number of investigations for flatfish with b values ranging from 0.5 to 0.7 (Edwards 1971, Duthie 1982). Panten (1995) demonstrated a mass exponent b of 0.60 for the 'sit-and-wait' predator sea scorpion *Myoxocephalus scorpio* using the technique of intermitted flow respirometry. Benthic species generally lie on the bottom over longer periods and show only occasionally spontaneous activity and, due to this behavior, estimates of the mass exponent b of benthic species may be considered standard metabolism, independent of the methodology applied. The decreasing effect of excluding activity on b, regardless if it is derived by anesthetic, data extraction, or behavior, appears to be a general inter- and intra-specific phenomenon. A new critical evaluation of the allometric scaling of metabolism of fish may therefore result in b values lower than 0.81 and 0.86, as reported by Winberg (1956) and Brett and Groves (1979), respectively. In Atlantic salmon, considerable intra-specific variation has been observed, with mass exponents of fasted fish ranging from 0.67 to 0.84 (Kazakov and Khalyapina 1981, Grøttum and Sigholt 1998).

The reasons for the negative allometric relationship between oxygen consumption and body mass are still not completely understood. Sarrus and Rameaux (1838) suggested that the metabolic rate of warm-blooded animals should vary with the body surface rather than with body mass. Rubner (1893) published a set of measurements which provided the first reliable empirical foundation for the 'surface rule' of the metabolic rate. The mass exponent b was considered as 2/3 (0.66). Kleiber (1947) established that, for mammalian species ranging in size from mouse to elephant, the mass exponent b is approximately ¾ (0.75) rather than 2/3 (0.66). Heusner (1982) called into question the whole concept of Kleiber, claiming it to be a statistical artifact, a contention that was immediately challenged by Feldman and McMahon (1983).

One of the reasons for the negative allometry may lie in the fact that the size of organs with a high metabolic rate increase disproportionally with body mass. The empirical exponent b of 0.81 published by Winberg (1956) was considerably higher than the Rubner (1893) exponent of 0.66. Neither Winberg nor other authors could give a conclusive explanation for this discrepancy. Recent utilization of the intermittent flow technology in the respirometric experiments however explained that the overestimation resulted from the influence of activity, as routine metabolism influenced by activity rather than standard metabolism was measured.

STANDARD METABOLIC RATE OF ATLANTIC SALMON

Standard metabolic rate of salmonids is strongly influenced by body mass, water temperature, salinity, and stress factors such as handling or sudden temperature changes (Brett 1964; Peterson and Anderson 1969; Beamish 1978). Additionally, physiological processes such as smoltification (Maxime et al. 1989; Wiggs et al. 1989) and sexual maturation (Beamish 1964a) may increase the standard metabolic rate. Numerous studies on the standard metabolic rate of Atlantic salmon have been conducted to examine the effects of these variables on the standard metabolic rate at different life stages. Currently, despite the large number of studies on this species, a comprehensive model predicting standard metabolic rates over a wide range of life stages and environmental conditions is still lacking. The absence of a model specifically developed for Atlantic salmon that allows prediction of standard metabolic rates over a wide range of environmental conditions had led to the fact that standard metabolic rate estimates have been borrowed from closely related species. As previously mentioned, Trudel et al. (2004) suggested that borrowing standard metabolic rates from other species should be avoided because standard metabolic rates derived even from closely related species may not accurately predict the standard metabolic rate of the targeted species.

The aim of the present review is therefore to synthesize existing data on the standard metabolic rate of Atlantic salmon to ultimately develop a comprehensive standard metabolic rate model. A total of 36 studies on the metabolic rate of Atlantic salmon were identified by literature search using the reference research engine *Aquatic Sciences and Fisheries Abstracts (ASFA), Web of Science* and *Fishbase*. The methodological approach used to estimate metabolic rates, the origin and life stage of fish used in the experiments, and the effects of independent variables such as body mass and water temperature on the metabolic rate are summarized and discussed.

EXPERIMENTAL APPROACH

All studies, except one that used the direct calorimetry approach, estimated standard metabolic rate with the indirect respirometry approach. Three different experimental setups were applied in the respirometry studies: 31.4% of the studies used closed systems, 51.4% flow-through systems, and 17.1% intermittent flow systems. Fish of different origins were used in the experiments. The majority of the experiments were conducted with hatchery fish (63.9 %). Only 8.3% of the studies used wild fish. 13.9% of the studies were interested in the metabolic rate of domesticated fish from the Norwegian National Breeding and 8.3% of the studies analyzed the metabolic rate of growth-enhanced transgenic Atlantic salmon. In two studies the fish origin was not specified.

EFFECTS OF BODY MASS AND WATER TEMPERATURE ON THE STANDARD METABOLIC RATE OF DIFFERENT LIFE STAGES OF ATLANTIC SALMON

Fertilized egg and larvae

The first study on the metabolic rate of Atlantic salmon goes back to Lindroth (1942) who analyzed the oxygen consumption rate of different life stages of Atlantic salmon. He observed that fertilized eggs had very low oxygen consumption of 1.9 $mg \cdot kg^{-1} \cdot h^{-1}$ at 4 °C (Fig. 7). Larval fish of a body mass of 0.15 g had slightly increased oxygen consumption of 35.7 $mg \cdot kg^{-1} \cdot h^{-1}$ at 4 °C. In comparison, oxygen consumption rates of Atlantic salmon parr ranged between 119 and 257 $mg \cdot kg^{-1} \cdot h^{-1}$ at 20 °C.

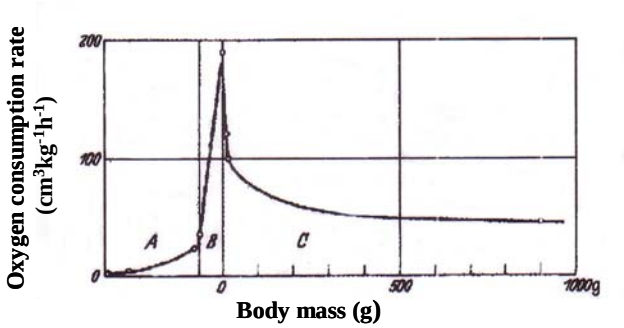

Figure 7. Standard metabolic rate of different life stages of Atlantic salmon at 10 °C. A. Fertilized egg, B. Larvae with yolk sac, C. Atlantic salmon fry and parr (Lindroth 1942). The oxygen consumption rate of the adult stage was obtained from Van Dam (1938) on a 900 g rainbow trout *Oncorhnychus mykiss*.

Fry and parr

Using the calorimetry approach, Smith et al. (1978) estimated heat production which corresponds to SMR of unfed Atlantic salmon fry weighing 1 to 4 g at water temperatures ranging from 3 to 18 °C. Standard metabolic rate increased linearly with water temperature over the temperature range tested:

$$(3.1) \qquad SMR = 0.66 + 0.0339 \cdot T \qquad (r^2 = 0.97,\ p < 0.05)$$

where SMR is standard metabolic rate in $kcal \cdot kg^{-1} \cdot h^{-1}$ and T is water temperature in ºC. Interestingly, standard metabolic rate did not follow an exponential line as described by Krogh (1914) and Winberg (1956).

Power (1959) analyzed SMR of Atlantic salmon parr living on the northern limit of their natural distribution (Ungava, Québec, Canada) over a temperature range from 4 to 16 ºC. Mean body mass ± S.D. of the studied parr was 42.5 ± 11.2 g. At 10 ºC, SMR of a 40 g parr from the Arctic environment was 0.061 ml $O_2 \cdot g^{-1} \cdot h^{-1}$, significantly lower than SMR of a parr from the temperate environment obtained by Lindroth (1942) at same body mass and water temperature.

Higgins (1985) measured SMR separately for the upper (UMG) and the lower modal group (LMG) of juvenile Atlantic salmon (after Thorpe 1977). At water temperature of 7.5 ºC, UMG fish with a body mass ranging from 4.6 to 67.5 g had significantly higher SMR in comparison to LMG fish with a body mass ranging from 2.0 to 30.3 g.

(3.2) UMG: $SMR = 0.0268 \cdot M^{1.1168}$ ($n = 29$, $p < 0.001$)
(3.3) LMG: $SMR = 0.0477 \cdot M^{0.7554}$ ($n = 25$, $p < 0.001$)

where SMR is standard metabolic rate in mg $O_2 \cdot animal^{-1} \cdot h^{-1}$ and M is body mass in g.

Dabrowski (1986), using a circular tube respirometer chamber, measured the metabolic rate in relation to swimming speed using the positive light (optomotor) reaction of juvenile salmonids. Extrapolation of the metabolic rate to swimming speed relationship to zero swimming speed allowed the estimation of SMR. For Atlantic salmon fry of 136 mg, SMR was 0.47 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ at 22 ºC.

Wright (1991) published two relationships between body mass and SMR for fast (corresponds to the upper modal group UMG) and slow (corresponds to the lower modal group LMG) growing Atlantic salmon parr. Fish were tested at 10 ºC.

(3.4) UMG: $SMR = 0.04080 \cdot M^{1.138}$ ($n = 6$, $r^2 = 0.73$, $p = 0.1$)
(3.5) LMG: $SMR = 0.04036 \cdot M^{0.975}$ ($n = 6$, $r^2 = 0.89$, $p < 0.01$)

where SMR is standard metabolic rate in mg $O_2 \cdot l^{-1} \cdot h^{-1}$ and M is body mass in g.

Wright et al. (2001) developed two relationships between body mass and SMR of Atlantic salmon parr at 5 and 15 ºC, respectively. Fish body mass ranged from 2.98-7.85 g.

(3.6) 5 ºC: $SMR = 0.126 \cdot M^{0.733}$ ($n = 8$, $r^2 = 0.574$, $p < 0.2$)
(3.7) 15 ºC: $SMR = 0.349 \cdot M^{0.607}$ ($n = 8$, $r^2 = 0.742$, $p < 0.05$)

where SMR is standard metabolic rate in mg $O_2 \cdot animal^{-1} \cdot h^{-1}$ and M is body mass in g.

Extensive research on SMR of juvenile Atlantic salmon has been conducted by the research group of Dr. Metcalfe at University of Glasgow, Scotland. The group published several SMR models for juvenile Atlantic salmon:

(1) SMR of fry of body mass from 0.12-0.31 g at a water temperature of 11.7 ºC ranged from 0.089-0.277 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ (Metcalfe et al. 1995). SMR increased linearly with body mass:

(3.8) $SMR = 0.08995 \cdot M + 0.0120$ ($n = 176$, $r^2 = 0.20$, $p < 0.001$)

where SMR is standard metabolic rate in ml $O_2 \cdot g^{-1} \cdot h^{-1}$ and M is body mass in g.

(2) O'Connor et al. (2000) observed that SMR increased linearly with body mass for fry (1.3-4.5 g) at 10 ºC:

(3.9) $\ln SMR = 0.53 \cdot \ln M - 2.14$ ($n = 57$, $r^2 = 0.19$, $p < 0.001$)

where SMR is standard metabolic rate in ml $O_2 \cdot h^{-1}$ and M is body mass in g.

(3) McCarthy (2000) developed four different relationships between body mass and SMR for different stages of juvenile Atlantic salmon at a water temperature of 12.9 ºC. He distinguished between fry, surviving fry, and parr separated in upper (UMG) and lower (LMG) modal group (after Thorpe 1977).

(3.10) Fry: $\log SMR = 0.803 \cdot \log M - 0.304$ ($n = 39$, $r^2 = 0.255$, $p = 0.001$)
(3.11) Surviving fry: $\log SMR = 0.802 \cdot \log M - 3.02$ ($n = 28$, $r^2 = 0.196$, $p = 0.05$)
(3.12) UMG: $\log SMR = 0.792 \cdot \log M - 0.846$ ($n = 17$, $r^2 = 0.773$, $p = 0.001$)
(3.13) LMG: $\log SMR = 0.710 \cdot \log M - 0.832$ ($n = 11$, $r^2 = 0.761$, $p = 0.001$)

where SMR is standard metabolic rate in µmol $O_2 \cdot h^{-1}$ and M is body mass in g. Atlantic salmon parr from the upper modal group had significantly higher SMR as individuals from the lower modal group.

(4) For Atlantic salmon fry of a mean ± S.E. body mass of 0.44 ± 0.03 g at a water temperature of 9 ºC, Cutts et al. (2002a) developed the following SMR model:

(3.14) $\ln SMR = 0.71 \cdot \ln M - 2.85$ ($F_{1, 63} = 16.83$, $p < 0.0001$)

where SMR is standard metabolic rate in ml $O_2 \cdot h^{-1}$ and M is body mass in g.

(5) Using a wider range of body mass of juvenile Atlantic salmon ranging from 1.04-8.99 g at a water temperature of 9 ºC, Cutts et al. (2002b) published the following relationship between body mass (M, g) and SMR (ml $O_2 \cdot h^{-1}$):

(3.15) $\ln SMR = 0.85 \cdot \ln M - 1.91$ ($n = 63$, $r^2 = 0.58$, $p < 0.0001$)

Herbert et al. (2001) showed for juvenile Atlantic salmon treated with growth hormone (GH) in their food supply that GH did not affect SMR of these fish (mean body mass 9.2 g). SMR was not significantly different for fish treated with GH (n = 7, 129 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$, S.D. 12.5) and for untreated fish (n = 7, 124 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$, S.D. 23.2) at a water temperature of 14 ºC.

Finstad et al. (2004) estimated SMR for juvenile Atlantic salmon under winter conditions. SMR at 1 ºC was on average 6.6 $J \cdot g^{-1} \cdot d^{-1}$ under simulated ice cover and 9.4 $J \cdot g^{-1} \cdot d^{-1}$ under natural day length without ice cover for fish of a mean body mass of 16.1-18.6 g.

Smolt

Several comparative studies have been conducted on SMR of Atlantic salmon parr and smolt. Most of these studies focused on a single water temperature. Baraduc and Fontaine (1955), for example demonstrated a 30% increase in the mass specific SMR of smolts in comparison to parr at 8 ºC. The authors suggested a possible link between metabolic rate and hormone production in smolts.

Higgins (1985) similarly observed a significant increase in the mass specific SMR of smolt in comparison to parr at 7.5 ºC and developed a SMR model for smolt of a body mass range from 7.0-66.4 g.

$$\text{SMR} = 0.00129 \cdot M^{1.2641} \qquad (n = 14,\ p < 0.001) \tag{3.16}$$

where SMR is standard metabolic rate in mg $O_2 \cdot \text{animal}^{-1} \cdot h^{-1}$ and M is body mass in g.

Two studies analyzed the effect of spring warming on smolts. Firstly, Power (1959) measured the SMR of smolts living on the northern limit of their natural distribution (Ungava, Quebec, Canada) over a temperature from 4-16 ºC. He observed that smolt have a lower mass specific SMR than parr below 13.5 ºC, but a higher above this temperature. Power (1959) suggested that these observed differences might be due to higher metabolic sensitivity of smolt to temperature changes than parr. He developed the following SMR model for smolts of a mean body mass of 80 g:

$$\log \text{SMR} = 0.06123 \cdot T + 2.1087 \qquad (n = 20,\ p = 0.001) \tag{3.17}$$

where SMR is standard metabolic rate in ml $O_2 \cdot g^{-1} \cdot h^{-1}$ and M is body mass in g.

Maxime et al. (1989) studied SMR of parr and smolts in parallel during their growth period in freshwater while exposed to seasonal changes in both water temperature and photoperiod. They demonstrated that the mass specific SMR of smolt is 50% higher than in parr over the tested temperature range of 8.3-18.0 ºC.

Maxime (2002) subsequently confirmed that pre-smolts had 52% lower SMR than smolts. She also investigated the effects of seawater transfer on SMR through the process of smoltification. The effect of a sudden transfer to seawater on SMR was investigated at different combinations of developmental stage, body mass, and water temperature. The abrupt transfer from fresh- to seawater changed SMR in different ways depending on the developmental stage and the corresponding adaptability to seawater. Pre-smolts had a 17% decrease in SMR whereas smolts had up to a 14% increase in SMR.

The higher mass specific SMR of smolt in comparison to parr may be due to endocrine activity during smoltification. Smolts have an increased respiratory enzyme activity and increased cell concentration of mitochondria (Blake et al. 1984) which is related to an increase of thyroid hormone levels (Hoar 1976, Boeuf et al. 1989). The

decrease in SMR observed by Maxime (2002) for pre-smolt after seawater transfer may be caused by physiological disturbances due to ionic disequilibrium whereas the increase in SMR for smolts, i.e. once smoltification is completed, are due to adaptations to increased salinity such as increased osmoregulation, ventilation, and protein turnover (Maxime 2002).

Withey and Saunders (1973) observed that smolts subjected to a reciprocal photoperiod regime (decreasing day length from early March and increasing day length from late June) had significantly lower SMR than those fish under natural light conditions. SMR ± S.E. was 85.7 ± 8.9 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ for smolts held under natural conditions (n = 9, mean body mass = 194.2 ± 16.0 g) and 111.2 ± 5.4 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ for smolts held under the reciprocal photoperiod regime (n = 11, mean body mass = 226.5 ± 14.3 g). The reduced SMR is consistent with reduced voluntary feeding and growth rates and food conversion efficiencies in similarly treated fish indicating a general metabolic suppression. The reciprocal photoperiod regime may have lead to shift in the salmon physiology to winter conditions. Beamish (1964b) observed similar seasonal differences in SMR for other salmonid species such as brook charr *Salvelinus fontinalis* and brown trout *Salmo trutta* where SMR was observed to be lower during winter and spring than during summer and autumn.

Adult

Only the studies of Lucas et al. (1993) and Lucas (1994) use experimental set-ups and designs to estimate SMR of adult Atlantic salmon. Lucas et al. (1993) used a large annular respirometer for measuring the anaerobic metabolic rate of cultured adult Atlantic salmon in seawater. SMR was estimated (i) by extrapolating the swimming speed to metabolic rate relation back to zero swimming speed and (ii) from experiments at zero activity and reduced ambient light levels. Experiments were conducted with a school of eight salmon (mean body mass ± S.D. 1979 ± 366 g) at a water temperature of 11 ºC. SMR values ranged from 52 to 255 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$. SMR of adult Atlantic salmon was substantially higher than predicted by extrapolation of the swimming speed to metabolic rate relation.

Lucas (1994) measured SMR of cultured adult Atlantic salmon in freshwater at two water temperatures of 4 and 10 ºC. Standard metabolic rate (SMR ± S.D.) at 4 ºC was 36.7 ± 8.4 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ for fish of a mean body mass (± S.D.) of 1804 ± 404 g while at 10 ºC, the SMR was 72.8 ± 11.9 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ for fish 2045 ± 385 g. There were no significant differences between male and female fish.

Several studies provide data on the routine metabolic rate of adult Atlantic salmon. For example, Kazakov and Khalyapina (1981) analyzed the metabolic rate of wild male and female Atlantic salmon captured during their spawning period in freshwater. Metabolic rate was measured only one hour after fish capture. The obtained metabolic rates are therefore likely to overestimate SMR due to stress of capture and experimental handling. Two-sea-winter males of mean body mass of 2.7 kg had a

metabolic rate of 182 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ while two-sea-winter females, with mean body mass of 5.9 kg, had a metabolic rate of 153 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$. Kazakov and Khalyapina (1981) developed the following model for adult Atlantic salmon of a body range from 1.6-13.2 kg:

$$RMR = 0.1408 \cdot M^{0.84} \quad (3.18)$$

where RMR is metabolic rate in ml $O_2 \cdot h^{-1}$ and M is body mass in g. Water temperature during the experiments was not given.

Bergheim et al. (1991) measured the oxygen consumption rate (MO_2) from adult cultured Atlantic salmon in seawater. During the experiments, fish were on a regular feeding regime and were swimming at a low flow velocity of approximately 0.5 $BL \cdot s^{-1}$ (BL = body length). The oxygen consumption rate ranged between 108-288 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ for fish of a body mass ranging from 1018-2100 g. Water temperature between experiments varied from 6.8-7.5ºC.

Fivelstad and Smith (1991) similarly measured the oxygen consumption rate of cultured Atlantic salmon (200-850 g) under normal production conditions (i.e. fish were fed) in seawater. Water temperature ranged between 5-9 ºC and flow velocity in the tanks between 15-26 $cm \cdot s^{-1}$. Oxygen consumption rate increased with body mass and water temperature. Fivelstad and Smith (1991) developed the following oxygen consumption rate model for Atlantic salmon in fish culture:

$$MO_2 = 10^{-0.841} \cdot M^{-0.261} \cdot T^{1.378} \quad (n = 62, R^2 = 0.74, p < 0.05) \quad (3.19)$$

where MO_2 is oxygen consumption rate in mg $O_2 \cdot kg^{-1} \cdot min^{-1}$, M is body mass in kg and T is water temperature in ºC. Oxygen consumption rates for cultured Atlantic salmon obtained by Bergheim et al. (1991) and Fivelstad and Smith (1991) were 1.4-2.3 times higher than those of earlier models for Pacific salmon (Liao 1971; Muller-Feuga et al. 1978). These discrepancies may be partly attributed to differences in the experimental design used in the different studies (Fivelstad and Smith 1991).

Grøttum and Sigholt (1998) developed an oxygen consumption rate model for adult Atlantic salmon of the third generation of the Norwegian National Breeding Program at Sunndalsøra (Aquagen, Norway). The Sunndalsøra salmon were developed for the Norwegian fish farm industry and have been bred selectively since 1971 to attain certain characteristics such as increased growth, delayed maturity, and disease resistance (Gjedrem et al. 1991). The model was developed using oxygen consumption rates obtained for Atlantic salmon of a body mass range of 1.1-2.0 kg, at three water temperatures (5, 10, and 15 ºC) and three swimming speeds (0.5, 1.0, and 1.5 body $length \cdot s^{-1}$).

$$MO_2 = 61.6\ (\pm 6.6) \cdot M^{-0.33\ (\pm 0.11)} \cdot 1.03\ (\pm 0.10)^T \cdot 1.79\ (\pm 0.10)^U \quad (3.20)$$

where MO_2 is oxygen consumption rate in mg $O_2 \cdot kg^{-1} \cdot min^{-1}$, M is body mass in kg, T is water temperature in ºC, and U is swimming speed in body length$\cdot s^{-1}$.

TRANSGENIC ATLANTIC SALMON

Considerable effort has been made in aquaculture to optimize growth of Atlantic salmon by using optimal abiotic variables such as temperature, photoperiod, and salinity. In addition, selective breeding, manipulation of biotic variables such as ration size and food quality, and injection of growth hormones have produced significant increases in growth rate. More recently, dramatic improvements in growth rate have been achieved using molecular genetic techniques (Devlin et al. 1995). In particular, transgenic fish have been developed in which genetic material from one or more species has been transferred to another. Salmon growth hormone (GH) attached either to antifreeze protein promoter (Du et al. 1992) or to metalothionein-B promoter (Devlin et al. 1994) both have been used successfully to realize large increases in salmonid growth rate. However, rapid growth might come with some metabolic costs. Stevens et al. (1998) observed that GH enhanced transgenic Atlantic salmon have higher metabolic rates than similar sized control fish during routine culture conditions. At 12-13 °C, GH enhanced transgenic salmon grew two to three times faster than control fish throughout the study period. Under routine culture conditions, metabolic rates of transgenic juvenile and adult Atlantic salmon were 1.5- to 1.7-times higher than those of control fish (Stevens et al. 1998; Cook et al. 2000).

EFFECTS OF LIFE HISTORY AND SOCIAL STATUS ON THE STANDARD METABOLIC RATE

In species with plastic life history like Atlantic salmon, life history strategy adapted by an individual is affected by its dominance status (Metcalfe et al. 1995). Since there is a direct link between dominance and metabolism, individual SMR may determine the life history strategy of the individual (Metcalfe et al. 1995; Forseth et al. 1999). Inter-individual variation in SMR has been shown to influence the relative dominance of juvenile Atlantic salmon (Metcalfe et al. 1995; Cutts et al. 1999). Juveniles with high relative SMR (defined as residuals from the regression line. i.e. difference between observed and expected SMR) are more likely to be dominant than juveniles with lower SMR (Metcalfe et al. 1995). The study also showed that juveniles with higher SMR were more likely to be feeding first. Apparently, higher metabolic costs cause a faster depletion of the yolk reserves and therefore lead to an earlier requirement of external food resources. Similarly, Cutts et al. (1998) demonstrated that differences in SMR may contribute to differences in aggression between fry. Juveniles with higher SMR were observed to be increasingly more aggressive than juveniles with lower SMR, however, SMR had no effect on the mass specific growth rate of these fish. Individual differences in SMR remain consistent over months in juvenile Atlantic salmon (McCarthy 2000).

EFFECTS OF FOOD DEPRIVATION ON THE STANDARD METABOLIC RATE

Atlantic salmon with higher SMR will have higher energetic maintenance costs than fish with lower SMR therefore, in periods of low food abundance, they will therefore utilize food reserves faster than fish with lower SMR and consequently suffer a greater risk of food deprivation (Metcalfe et al. 1995). O'Connor et al. (2000) however demonstrated that the SMR decreases when juvenile Atlantic salmon are deprived of food resources. Thus, juvenile Atlantic salmon are able to regulate their metabolic rate downwards during periods of starvation to adapt to lower food abundance, and consequently minimize their body mass losses (Brett 1965). Jobling (1994) suggested that the reduction of SMR due to starvation may result from changes in the biochemical composition of body tissues, the relative sizes of different organs, and synthesis and turnover rates of different body tissues. The energetic maintenance costs result from the expenditures of the respiratory and circulatory system to supply body tissue with nutrients and those of cellular maintenance. A high proportion of the maintenance costs are related to protein synthesis and turnover (Houlihan et al. 1988). As fish are deprived of food, the protein synthesis is reduced leading to a decrease in the SMR. The reduction of SMR during a period of food deprivation may imply that fish can survive periods of low food abundance by lowering their maintenance costs.

EFECTS OF PHOTO PERIOD ON THE STANDARD METABOLIC RATE

Withey and Saunders (1973) demonstrated that the photoperiod affects SMR of Atlantic salmon smolt. Individuals held under reciprocal photoperiod regime (decreasing day length from early March and increasing day length from late June) had 23% lower SMR than fish held under natural light conditions. The authors suggested that the reciprocal photoperiod regime may result in a shift of the fish physiology to a winter timetable. Beamish (1964b) reported similar seasonal differences in SMR in other salmonids (brook charr *Salvelinus fontinalis* and brown tout *Salmo trutta*). SMR were significantly lower during winter and spring than during autumn. Finstad et al. (2004) similarly showed, under winter conditions, that the SMR of juvenile Atlantic salmon reared in darkness was 30% lower than the SMR of individuals reared at 6 h day light. This study also provided evidence that ice cover significantly decreased the SMR of fish directly through light induced physiological changes.

EFFECTS OF GROWTH HORMONE TREATMENT ON THE STANDARD METABOLIC RATE

Metabolic rate of Atlantic salmon increases when fish are treated with growth hormone and this has been interpreted as evidence of increase SMR due to increased anabolic activity (Seddiki et al. 1995;Seddiki et al. 1996), however changes in swimming activity and food intake were not independently analyzed. Growth Horomone (GH) treatment also induced an increase in gill (Na^+-K^+) ATPase activity in freshwater adapted fish (Seddiki et al. 1996). High levels of gill (Na^+-K^+) ATPase activity are associated with

the pre-adaptation of freshwater fish to seawater (Maxime 2002). Herbert et al. (2001) observed that growth hormone increased the metabolic rate of Atlantic salmon parr but showed that the changes were attributed to an increase in activity rather than in SMR. The authors further emphasized that any increase in SMR due to growth hormone treatment is much lower than previously suggested.

CONCLUSION

Bioenergetics models may have the potential to integrate the effects of system productivity and habitat structure. Habitat suitability models currently in use are largely based exclusively on physical variables such as substrate, water depth, and flow velocity, and therefore they do not allow predictions of fish abundance or growth as they change with increased system productivity. Bioenergetics models for drift-feeding fish conversely take into account physical habitat variables and food abundance and, as such, allow predictions on individual habitat choice and growth (Nislow et al. 2000). Bioenergetics models of Atlantic salmon are presently limited due to uncertainty related to metabolic costs of standard and activity metabolism to generate reasonable estimates of metabolic rate. The present report has identified and summarized available data in order to identify information gaps and to priorize future research. Data compiled in this report will furthermore help develop comprehensive metabolic rate models over a wide range of environmental conditions. Bioenergetics modeling has the potential to provide insight into the mechanisms underlying patterns of habitat utilization and fish production, however, whether bioenergetics will stay primarily a research tool or will successfully be applied as a management tool for habitat conservation and restoration management, remains to be seen.

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