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1 Bioenergetic modelling of the marine phase of Atlantic salmon (*Salmo salar* L.)

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3

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11

## 12 **Abstract**

13 A bioenergetic model of marine-phase, wild Atlantic salmon was constructed to investigate the  
14 potential effects on post-smolt growth of predicted changes in oceanic conditions. Short-term  
15 estimates of growth in weight were similar to measurements in captivity and simulated growth  
16 varied with water temperature and swimming speed as expected. Longer-term estimates of  
17 growth in length were less than that achieved by wild salmon, particularly with constant  
18 swimming assumed. The model was sensitive to parameters relating to maximum daily food  
19 consumption, respiration and the relationships between body energy content, length and weight.  
20 Some of the sensitive parameters were based on substantive information on Atlantic salmon and  
21 their realistic ranges are likely to be much narrower than those tested. However, other parameter  
22 values were based on scant data, farmed Atlantic salmon or other salmonid species, and are  
23 therefore less certain and indicate where future empirical research should be focussed.

24

25 **Keywords:** Atlantic salmon, post-smolt, marine phase, growth, temperature, climate change,  
26 marine ecology, mathematical models

27

## 28 **1. Introduction**

29 Populations of Atlantic salmon (*Salmo salar* L.) have declined considerably across the species'  
30 range on both sides of the North Atlantic Ocean since the 1970s (Jonsson and Jonsson, 2004).

31 While in some populations, there may be causal factors during the freshwater phase of the life

32 cycle, there are indications of a widespread increase in mortality during the marine phase not  
33 attributable to directed fishing (Hawkins, 2000). In most of the well-studied stocks, there has  
34 been a 30-year trend of increasing marine mortality in salmon that mature after two or more  
35 winters in the sea. Among salmon that mature after only one winter at sea ('grilse'), there  
36 appears to have been a sudden increase in marine mortality in the late 1980s, which has persisted  
37 subsequently (Potter and Crozier, 2000). Assuming that marine predation on salmon is highest  
38 when post-smolts are small (Peterson and Wroblewski, 1984; Griffiths and Harrod, 2007), it  
39 seems likely that such significant variation in survival is linked to changes in the nature or  
40 intensity of processes operating in the first few weeks after emigration from rivers to the sea.  
41 There is mounting evidence that marine mortality of salmon is inversely related to growth rate  
42 during the early marine phase and that growth is strongly related to sea temperatures experienced  
43 by the fish in that period (Friedland et al., 2005; Peyronnet et al., 2007; McCarthy et al., 2008;  
44 Todd et al., 2008).

45

46 It is not clear whether the influence of temperature on historical variation in post-smolt growth  
47 rate is predominantly a direct effect on salmon physiology or an indirect effect related to ocean  
48 currents or prey availability (Hawkins, 2000). Temperature certainly has a direct effect on  
49 metabolic processes (Brett and Groves, 1979), but Beaugrand and Reid (2003) have detected  
50 significant correlations among indices of climate variability, zooplankton abundance and an  
51 index of salmon abundance.

52

53 An understanding of how salmon survival may be affected by future changes in oceanic  
54 conditions is required to inform management decisions on how best to conserve Atlantic salmon  
55 stocks (Solomon et al., 2003). One approach to this is bioenergetic modelling, in which the  
56 energy available for somatic growth is estimated from the balance of energy gained from feeding  
57 against that lost through egestion, excretion, standard and active metabolism, and reproduction  
58 (Brett and Groves, 1979). Combined with a model of how the oceanic ecosystem may respond to  
59 climatic changes, this provides a tool for investigating the consequences of future climate  
60 scenarios for salmon stocks, as has been done for sockeye salmon (*Oncorhynchus nerka*) in the  
61 north Pacific Ocean (Rand et al., 1997). There have been numerous published bioenergetic  
62 models of salmonids, including wild juvenile Atlantic salmon in fresh water (Broekhusien et al.,  
63 1994; Elliott and Hurley, 1997; Forseth et al., 2001; Jones et al., 2002; Gurney et al., 2003).  
64 Empirical models of growth in relation to temperature, ration and body size have been  
65 constructed for marine-phase Atlantic salmon in aquaculture (Austreng et al., 1987; Cho and

66 Bureau, 1998), but there are no published bioenergetic models of the marine phase of wild *S.*  
67 *salar*.

68

69 The aim of the present study was to construct and test an individual-based model (Grimm et al.,  
70 1999) of growth in marine-phase Atlantic salmon, using existing information on temperature and  
71 body size dependencies of consumption and energy losses. Owing to the limited information on  
72 some aspects of the energy metabolism of marine-phase Atlantic salmon, it has been necessary to  
73 use parameters estimated for closely-related species or freshwater stages of *S. salar* for some  
74 functions. The sensitivity of the model to variation in uncertain parameters has therefore been  
75 investigated to indicate where future empirical research effort should be directed. The present  
76 model is not spatially explicit (i.e. does not include a representation of varying geographical  
77 location), but we have previously reported a model for simulating trajectories of migrating  
78 Atlantic salmon (Booker et al., 2008). Coupling these approaches with a climate-driven  
79 ecosystem model of the North Atlantic Ocean (e.g. Palmer and Totterdell, 2001) will allow  
80 spatially explicit modelling of marine-phase growth.

81

## 82 **2. Methods**

### 83 *2.1. Model description*

84 The model consisted of a system of equations, described below, for calculating daily energy gain  
85 and loss from food consumption, egestion, excretion and respiratory losses under different  
86 conditions of body size, water temperature, day length, swimming speed and prey availability.  
87 Growth was then calculated from the net energy gain. Since the model was not spatially explicit,  
88 spatial aspects, such as water temperature, day length and prey density were held constant for  
89 each run of the model. The initial salmon body length was taken as 0.125 m as a typical value for  
90 wild smolts (Shearer, 1992; although variation in this value was investigated) and initial weight  
91 was calculated from a weight-length relationship derived from unpublished data on smolts from  
92 British rivers (I. Russell, G. W. Smith, pers. comm.).

#### 93 *2.1.1. Prey encounter and capture*

94 Analysis of stomach contents indicates that salmon prey on a wide variety of invertebrates and  
95 fish during their marine phase (Jacobsen and Hansen, 2000). In estuarine and nearshore waters,  
96 post-smolts take terrestrial insects and other arthropods, such as intertidal amphipods (Hansen

97 and Quinn, 1998; Sturlaugsson, 2000). As post-smolts move further offshore, marine prey  
 98 species become more prevalent and mainly comprise planktonic crustaceans, such as decapod  
 99 larvae, copepods, amphipods and euphausiids, and larval fish (Sturlaugsson, 2000; Andreassen et  
 100 al., 2001; Haugland et al., 2006). At oceanic feeding grounds and during the spawning migration,  
 101 small pelagic fish, such as capelin, sandeels, myctophids and clupeoids, dominate the diet by  
 102 weight, although in the north-east Atlantic, planktonic crustaceans also constitute a considerable  
 103 proportion of the diet (Hislop and Shelton, 1993; Holst et al., 1993; Jacobsen and Hansen, 2000,  
 104 2001). Prey items span a wide range of sizes and energy densities. It has been suggested that  
 105 salmon are opportunistic feeders, implying a lack of selectivity, although there is some evidence  
 106 of preference with respect to prey species (Andreassen et al., 2001; Jacobsen and Hansen, 2001)  
 107 and prey size (Holst et al., 1996; Jacobsen and Hansen, 2001).

108  
 109 Available prey was modelled as a uniformly distributed constant total biomass per unit volume  
 110 of sea water, divided proportionally into seven categories for simplicity (Table 1). Average  
 111 individual mass of prey obtained from published weight-length relationships were used to  
 112 calculate numerical abundance of each prey category from its biomass. Published values of  
 113 energy density were used to calculate the energy content of prey items in each category (Table  
 114 1).

115  
 116 Salmon were assumed to encounter each category of prey,  $i$ , within a cylindrical volume of  
 117 water,  $V_i$  ( $\text{m}^3$ ), defined by swimming speed,  $u$  ( $\text{m s}^{-1}$ ), the duration of the model time step (1 d)  
 118 and the salmon's reaction distance – the distance within which they may attack encountered prey  
 119 items, which can vary by prey category:

$$120 \quad V_i = 8.64 \times 10^4 u \pi d_i^2$$

121 The reaction distance,  $d_i$  (m), of salmon of length  $L_s$  (m) to prey of length  $L_i$  (m, Table 1) was  
 122 calculated using a function given by Hughes and Dill (1990):

$$123 \quad d_i = 120 L_i (1 - e^{(-20 L_s)})$$

124 This function indicates that for a given prey length, salmon length has little influence on  
 125 detection distance when salmon length is  $>0.1$  m, as is the case for most post-smolts (Shearer,  
 126 1992).

127

128 Following Keeley and Grant (2001), after Wankowski (1979), the range of prey sizes that could  
 129 be taken was set to  $0.012 L_s$  to  $0.105 L_s$ . It was assumed that prey width was the limiting  
 130 dimension and width-length ratios were set for each prey category. The range of prey sizes  
 131 acceptable to salmon of particular sizes was used to calculate the proportion of each prey  
 132 category available.

133

134 To calculate the number of prey items potentially eaten within a model time step, a form of the  
 135 Holling type 2 disc equation (Holling, 1959) was applied, assuming that no more than one prey  
 136 item can be consumed at a time, salmon can not search for prey while capturing and ingesting  
 137 ('handling') a prey item and the salmon may not consume every prey item that it encounters. The  
 138 time spent searching for prey,  $t_s$  (s), was given by:

$$139 \quad t_s = \frac{t_f}{1 + \left( \sum_{i=1}^{i_{\max}} \rho_i V_i a_i h_i \right)}$$

140 where  $t_f$  is the time available for feeding (set to 12 h per day in seconds),  $i_{\max}$  is the number of  
 141 prey classes,  $\rho_i$  is the density of prey class  $i$  ( $\text{m}^{-3}$ ),  $a_i$  is the attack rate on prey class  $i$  (proportion  
 142 of encountered prey items taken) and  $h_i$  is the handling time for prey class  $i$  (s). The potential  
 143 number of prey items of class  $i$  eaten per time step,  $n_i$ , was given by:

$$144 \quad n_i = t_s a_i \rho_i V_i$$

145 and the total weight of prey class  $i$  potentially consumed per time step,  $W_i$  (g), given unlimited  
 146 stomach size was:

$$147 \quad W_i = n_i \bar{w}_i$$

148 where  $\bar{w}_i$  is the average individual weight in prey class  $i$  (g). The mean energy density of prey  
 149 consumed,  $\bar{E}$  ( $\text{J g}^{-1}$ ), was given by:

$$150 \quad \bar{E} = \frac{\sum_{i=1}^{i_{\max}} (W_i E_i)}{\sum_{i=1}^{i_{\max}} W_i}$$

151 where  $E_i$  is the energy density of prey class  $i$  ( $\text{J g}^{-1}$ ).

152 2.1.2. *Maximum daily consumption*

153 Maximum daily consumption,  $C_{\max}$  ( $\text{g g}^{-1} \text{d}^{-1}$ ), was calculated as dry mass of prey per unit dry  
 154 mass of salmon by a Thornton-Lessem function (Thornton and Lessem, 1978), using the weight  
 155 exponent of Beauchamp et al. (1989) and fitted to  $C_{\max}$  estimates for post-smolt *S. salar* at  
 156 different temperatures (Handeland et al., 2003; Jørgensen and Jobling, 1994; Damsgård. and  
 157 Arnesen, 1998; Toften et al., 2003; Stead et al., 1996; Koskela et al., 1997). Iterative non-linear  
 158 fitting procedures (Wilkinson et al., 1992) failed to converge, so the function was fitted by eye  
 159 (Table 2).

160

161  $C_{\max}$  was converted to maximum wet weight of prey that could be consumed daily,  $W_{\text{cmax}}$ , using  
 162 published values of prey species water content (Table 1), water content of salmon from the  
 163 formula of Johansen et al. (2001), and the body weight of the salmon. Achieved daily  
 164 consumption,  $W_c$  (g), was taken as the lesser of  $W_{\text{cmax}}$  and  $\sum_{i=1}^{i_{\max}} W_i$ . Daily ingested energy,  $I$  (J),  
 165 was the product of  $W_c$  and  $\bar{E}$ . Where  $W_c$  was constrained to be  $W_{\text{cmax}}$ , the number of prey items  
 166 eaten was recalculated.

167 2.1.3. *Egestion, excretion and specific dynamic action*

168 The proportion of ingested energy lost in the faeces,  $P_f$ , was calculated in relation to water  
 169 temperature,  $T$  ( $^{\circ}\text{C}$ ), and consumption as a proportion of maximum consumption from:

170 
$$P_f = F_a T^{F_{b1}} e^{F_{b2} \frac{W_c}{W_{\text{cmax}}}}$$

171 where  $F_a$ ,  $F_{b1}$  and  $F_{b2}$  are the constant, temperature coefficient and consumption coefficient,  
 172 respectively, derived for brown trout, *Salmo trutta* (Elliott, 1976b; Table 3). The proportion of  
 173 energy lost by excretion was calculated with the same form of relationship using the parameters  
 174  $U_a$ ,  $U_{b1}$  and  $U_{b2}$ , respectively (Table 3).

175

176 Specific dynamic action, the additional heat liberated after feeding, can be represented as a  
 177 constant proportion ( $P_{\text{SDA}}$ ) of metabolizable energy (i.e. energy ingested minus energy lost  
 178 through egestion and excretion) independent of temperature or ration size (Brett and Groves,  
 179 1979). A value of 17% of metabolizable energy was adopted (Nimi and Beamish, 1974).



## 180 2.1.4. Respiration

181 A function relating rate of oxygen consumption ( $M_{O_2}$ ) to body weight, swimming speed and  
 182 temperature derived from measurements of farmed adult Atlantic salmon by Grøttum and Sigholt  
 183 (1998) was found to produce unrealistic values for small fish and higher swimming speeds.  
 184 Another function was derived from relationships given by Brett and Glass (1973) for standard  
 185 and active rates of oxygen consumption in sockeye salmon (*Oncorhynchus nerka*) as functions of  
 186 body weight at different temperatures. ‘Active’ measurements were made at the maximum  
 187 swimming speed sustained for 1 h (termed the ‘critical’ swimming speed,  $U_{crit}$ ). Brett and Glass  
 188 (1973) also gave temperature-specific relationships between  $U_{crit}$  and body length. Values of  $M_{O_2}$   
 189 at intermediate swimming speeds were obtained by interpolating between the standard and active  
 190 values for the appropriate body weight, temperature and  $U_{crit}$  (Brett and Glass, 1973). In this  
 191 way, an array of predicted oxygen consumption rates was generated for a range of weights (10,  
 192 50, 100, 700 and 2000 g), temperatures (5, 15, 20 °C) and swimming speeds (body lengths per  
 193 second,  $bl\ s^{-1}$ ) as a proportion (0.2, 0.4, 0.6, 0.8, 1.0) of  $U_{crit}$ . The weight and temperature  
 194 increments chosen reflected the conditions under which the relationships of Brett and Glass  
 195 (1973) had been obtained. Length was calculated from the weight-length relationship given by  
 196 Brett and Glass (1973). A relationship between rate of oxygen consumption and the independent  
 197 variables was estimated by multiple regression and found to be of the form:

$$198 \quad M_{O_2} = 3.021 \times 10^{-2} W^{(-0.0068T + 0.0902U)} 1.1017^T 1.6803^U 0.9778^{TU}$$

199 where,  $M_{O_2}$  is rate of oxygen consumption ( $mg\ O_2\ g^{-1}\ h^{-1}$ ),  $W$  is weight (g),  $T$  is temperature (°C),  
 200 and  $U$  is swimming speed ( $bl\ s^{-1}$ ). The multiple regression was highly significant ( $F_{5,69}=429.89$ ,  
 201  $p<0.0001$ ,  $r^2=0.967$ ), with significant interactions between the effects of weight and temperature,  
 202 weight and swimming speed, and temperature and swimming speed. The Grøttum and Sigholt  
 203 (1998) model assumed the effects of these variables were independent.

204  
 205 Comparison of oxygen consumption rates predicted by this function with literature values is not  
 206 straightforward, owing to the considerable variation in methodology and conditions in published  
 207 studies and, in some cases, a lack of information on swimming speed. Nevertheless, oxygen  
 208 consumption rates predicted by this function were strongly correlated with values reported for *S.*  
 209 *salar* at a range of life stages, body sizes, water temperatures and swimming speeds (Withey and  
 210 Saunders, 1973; Higgins, 1985; Lucas et al., 1993; Lucas, 1994; Maxime, 2002).

211

212 The mass of oxygen consumed (mg) was converted to an energy equivalent (J) with an  
 213 oxycalorific coefficient of 13.563 J mg<sup>-1</sup> (Elliott and Davison, 1975).

214

215 Modelled salmon were assumed to swim at a constant relative speed while migrating  
 216 ('cruising'), but swam at maximum speed to capture specified prey items ('burst' swimming).  
 217 Respiration was calculated separately for the proportion of the time that salmon were burst  
 218 swimming and cruising. Each time a mobile prey item of type  $i$  was attacked (determined by  
 219 prey encounter and attack rates), the salmon was assumed to travel at burst speed for a distance  
 220 equating to the radius of half of the capture area,  $(0.5 d_i^2)^{1/2}$ . It was assumed that burst swimming  
 221 was required to capture prey in the 'small fish', 'large fish' and 'squid' categories.

222

223 Burst swimming speed ( $u_{burst}$ , m s<sup>-1</sup>) of salmon was calculated in relation to temperature ( $T$ , °C)  
 224 and body length ( $L_s$ , m) from:

$$225 \quad u_{burst} = (0.121 T + 5.4525) L_s^{(-0.0074T+0.7009)}$$

226 which was derived from equations fitted by Turnpenny et al. (2001) to values reported by  
 227 Wardle (1975).

### 228 2.1.5. Growth

229 Assimilated energy ( $A$ , J) that was not lost in respiration was assumed to be partitioned into  
 230 reserves ( $Y$ ), such as lipids, which may be mobilized to meet metabolic requirements during  
 231 starvation, and structure ( $S$ ), which determines body length and can not be mobilized. Following  
 232 Broekhusien et al. (1994) and Jones et al. (2002), the rate of change in reserves was equal to net  
 233 assimilation rate ( $A$ ) minus losses in respiration ( $R$ ) and the rate of energy commitment to  
 234 structural tissues:

$$235 \quad \frac{dY}{dt} = A - R - \frac{dS}{dt}$$

236 The rate of commitment to structure was a variable proportion ( $\kappa$ ) of the rate of assimilation:

$$237 \quad \frac{dS}{dt} = \kappa A$$

238  $\kappa$  was scaled to ensure that (so far as was possible) the ratio ( $\lambda$ ) of reserves to structure did not  
 239 fall below a 'defended level' ( $\lambda_{def}$ ) (Jones et al., 2002).  $\kappa$  was interpolated between zero (since

240 structural energy should not be lost) and a specified maximum value ( $\kappa_{\max}$ ) when the  
 241 reserve/structure ratio lay within a specified range ( $\lambda_{\text{switch}}$ ) above the defended level:

$$242 \quad \kappa = \frac{\kappa_{\max} (\lambda - \lambda_{\text{def}})}{\lambda_{\text{switch}}}, \quad \lambda_{\text{def}} \leq \lambda < (\lambda_{\text{def}} + \lambda_{\text{switch}})$$

243 When  $\lambda$  was below  $\lambda_{\text{def}}$ , all assimilated energy was allocated to reserves ( $\kappa = 1$ ). When  $\lambda$  was  
 244 above  $\lambda_{\text{def}} + \lambda_{\text{switch}}$ , the proportion  $1 - \kappa_{\max}$  of assimilated energy was allocated to reserves.  
 245 Parameter values for the calculation of  $\kappa$  are given in Table 4.

246

247 Structural and reserve energy content at the start of the next time step were calculated from:

$$248 \quad S_{(t+1)} = S_t + \frac{dS}{dt}$$

$$249 \quad Y_{(t+1)} = Y_t + \frac{dY}{dt}$$

250 Salmon length in the next time step,  $L_{s(t+1)}$ , was given by:

$$251 \quad L_{s(t+1)} = L_0 S^\alpha$$

252 where  $L_0$  and  $\alpha$  are parameters derived from a re-arrangement of a function relating body energy  
 253 content to length and weight (Elliott, 1976a; Table 4), applying an estimate of the proportion of  
 254 body energy content that can not be mobilized during starvation (28.8%, Jonsson et al., 1997)  
 255 and substituting for weight with a rearranged weight-length relationship (Broekhuizen et al.,  
 256 1994).

257

258 Body weight in the next time step,  $W_{s(t+1)}$ , was given by:

$$259 \quad W_{s(t+1)} = W_0 L_{s(t+1)}^\beta (Y_{(t+1)} + S_{(t+1)})^\gamma$$

260 where  $W_0$ ,  $\beta$  and  $\gamma$  are parameters derived from a rearrangement of Elliott's (1976a) empirical  
 261 relationship for total energy as a function of length and wet weight of brown trout, *S. trutta*  
 262 (Table 4). Thus, body length depended only on structural energy content, whereas body weight  
 263 depended on length and total energy content (Jones et al., 2002). Body weight could reduce, but  
 264 length could not.

265

## 266 2.2. Simulations

267 To test the sensitivity of the bioenergetic algorithms to variation in their parameters, the model  
268 was run with each parameter varied individually between -50% and +50% of the default values  
269 (in 25% increments), with combinations of a range of constant sea surface temperatures (2–18°C,  
270 by 2°C) and constant swimming speeds (0.5–2.5 bl s<sup>-1</sup>, by 0.25 bl s<sup>-1</sup>). Cotterell and Wardle  
271 (2004) measured a maximum sustainable swimming speed of 2.99 bl s<sup>-1</sup> for 0.3-m post-smolt  
272 Atlantic salmon at 10°C. Within simulations, available prey density and feeding time were held  
273 constant, but variation in these parameters was also investigated between simulations. Other  
274 spatial aspects of the model, such as directionality of migration, ocean currents and migratory  
275 responses to ocean currents were disregarded. The effects of simple behavioural options in the  
276 model were also tested: ‘burst’ swimming to capture prey, optimising cruising speed (using a  
277 constant swimming speed that maximised daily energy gain) and optimising daily cruising  
278 duration (salmon swam at a defined speed until maximum daily consumption had been achieved  
279 and at a defined minimum speed, 0.05 m s<sup>-1</sup>, for the rest of that day).

280

281 Simulated growth under these constant conditions was represented by the length attained after  
282 15.5 months: the average duration of the marine phase for a one-sea-winter salmon emigrating  
283 from its home river in early May and returning in mid-August typical of British rivers  
284 (unpublished data: FRS, CEFAS). The effect of changes in parameter values has been  
285 summarised by the difference in final salmon length between that obtained with a 25% increase  
286 in the default parameter value and that obtained with a 25% decrease, expressed as a percentage  
287 of the final length obtained with the default parameter value.

288

289 To compare growth in weight indicated by the model with published measurements of post-smolt  
290 growth rate in captivity (progeny of wild parents), simulations were run with fish of the same  
291 size and at the same temperature as the empirical studies, with prey attributes set to resemble an  
292 excess of the commercially available feed pellets used (moisture content 5%, energy density  
293 24 MJ kg<sup>-1</sup>, density 1.59 × 10<sup>3</sup> kg m<sup>-3</sup>). The conditions in two empirical studies were modelled:  
294 fish length 0.18 m and weight 61 g simulated over a period of 30 d at 4.3°C, 9.4°C or 14.3°C  
295 (Handeland et al., 1999); and fish length 0.37 m and weight 528 g simulated over a period of  
296 84 d at 9°C (Thodesen et al., 1999). Swimming speeds in the published studies were not  
297 reported, so simulations were run with speeds of 0.5 bl s<sup>-1</sup> and 1.0 bl s<sup>-1</sup>, which were thought  
298 likely to encompass the average values. Specific growth rate (SGR) was calculated as  $(\ln W_2 -$

299 In  $W_1)/\Delta t$ , where  $W_1$  and  $W_2$  are the simulated body weights (g) at the start and end of a period  
 300 of  $\Delta t$  days (Handeland et al., 1999). Thermal-unit growth coefficient (TGC) was calculated as  
 301  $(W_2^{1/3} - W_1^{1/3})/T\Delta t$  (Thodesen et al., 1999), where  $T$  is the temperature ( $^{\circ}\text{C}$ ).

### 302 **3. Results**

303 With the default bioenergetic parameter values, growth varied with sea surface temperature and  
 304 swimming speed (Fig. 1). At any given temperature, final length was greater at lower swimming  
 305 speeds, but the effect of swimming speed was less at lower temperatures. At any given  
 306 swimming speed, final length increased with temperature to a maximum at 14–16 $^{\circ}\text{C}$  and  
 307 declined slightly at 18 $^{\circ}\text{C}$ . The effect of temperature on growth was less at higher swimming  
 308 speeds. The maximum final length with default parameter values was 0.44 m (at a temperature of  
 309 14 $^{\circ}\text{C}$  and a swimming speed of 0.5 bl  $\text{s}^{-1}$ ).

310

311 Simulated growth was most sensitive to certain of the parameters directly affecting energy intake  
 312 (parameters of the function for maximum daily consumption, prey energy density, relative dry  
 313 weight proportions of salmon and prey), energy expenditure (some of the respiration parameters,  
 314 burst speed parameters) and the parameters of the length-structure relationship (Table 5, 6).

315 Certain parameters, mostly powers, led to zero energy reserves ('bioenergetic death') with a 25%  
 316 change from the default value: these were the initial weight-length power, maximum  
 317 consumption parameter  $C_{\text{TL}}$ , respiration-temperature coefficient, respiration-temperature-speed  
 318 coefficient, length-structure power and weight-energy power.

319

320 Changes in certain other parameters had a marked effect (>10%) on final length without causing  
 321 simulated energy reserves to fall to zero (Table 5, 6). In relation to energy intake, for example,  
 322 growth was positively related to the maximum consumption scale,  $C_A$  (Fig. 2a), consumption-  
 323 weight power,  $C_B$  (Fig. 2b), the prey energy density (Fig. 2c) and the salmon dry weight  
 324 constant,  $DW_a$  (Fig. 2d), and was negatively related to the prey dry weight ratio (Fig. 2e). These  
 325 effects increased with temperature and decreased with swimming speed. Sensitivity to some  
 326 other parameters was negatively correlated with temperature and swimming speed (e.g.  
 327 consumption parameter  $C_Q$ , Fig. 2f). Parameters associated with prey encounter rate and  
 328 ingestion, such as minimum edible prey size, prey density and reaction distance had less  
 329 influence on growth (Table 5, 6). At higher temperatures (Table 5) and slower swimming speeds

330 (Table 6), simulated growth was greater with larger maximum edible prey sizes. Available  
331 feeding time and prey item handling time had no effect within the range of values tested.

332

333 In relation to energy loss, growth was sensitive to parameters of the respiration function (Fig.  
334 3a), with the effects being greater at higher temperatures and swimming speeds. Growth was also  
335 sensitive to the burst speed constant (negatively, Fig. 3b) and the burst speed-length-temperature  
336 constant (positively, Fig. 3c). Growth was moderately sensitive to parameters of the egestion  
337 (Fig. 3d) and excretion functions (Table 5, 6).

338

339 In relation to the functions for determining length and weight from assimilated energy, in  
340 addition to the high sensitivity to changes in the length-structure power and the weight-energy  
341 power mentioned above, growth was sensitive to the length-structure scale (Fig. 4a) and, to a  
342 lesser extent, to the maximum proportion of assimilated energy committed to structure ( $\kappa_{\max}$ , Fig.  
343 4b), these effects being positively related to temperature and negatively related to swimming  
344 speed. Growth was comparatively insensitive to the defended reserve ratio ( $\lambda_{\text{def}}$ ) and, at a  
345 swimming speed of  $1 \text{ bl s}^{-1}$ , the weight-length-energy scale ( $W_0$ ) and the weight-length power ( $\beta$ ,  
346 except at low temperatures). At  $10^\circ\text{C}$ , the influence of the last two parameters varied negatively  
347 and positively, respectively, with swimming speed (Table 6). The allocation switch width  
348 ( $\lambda_{\text{switch}}$ ) had no effect within the range of values tested.

349

350 For most parameters to which growth showed marked sensitivity, the differences in final length  
351 varied monotonically with temperature and swimming speed over the range of values tested.  
352 However, with certain parameters, there was an inflection in sensitivity within the tested range of  
353 temperatures, including the maximum consumption parameter  $C_{\text{TO}}$ , (Fig. 5), the burst speed-  
354 length-temperature constant,  $\kappa_{\max}$  and the length-structure scale.

355

356 The implementation of burst swimming to catch nektonic prey items caused a slight reduction in  
357 growth, particularly at combinations of high temperatures and low cruising speed (i.e. conditions  
358 of maximum growth; Fig. 6). Optimising daily cruising duration resulted in growth being higher  
359 and largely independent of cruising speed, particularly when compared with higher continuous  
360 cruising speeds (Fig. 7). The percentage improvement in growth over that at given continuous  
361 cruising speeds was almost constant across the temperature range, except at higher speeds, when  
362 the improvement in growth increased over the lowest temperatures (Fig. 8). Optimising cruising

363 speed produced almost identical results, since salmon encountered sufficient prey items to  
364 achieve their maximum daily consumption even at the minimum speed.

365

366 With prey attributes set to resemble commercial pelleted feed and initial body weight of 61 g  
367 (Handeland et al., 2003), modelled values of SGR at swimming speeds of  $0.5 \text{ bl s}^{-1}$  and  $1.0 \text{ bl s}^{-1}$   
368 bracketed the published empirical value for  $4.3 \text{ }^{\circ}\text{C}$ , but was slightly less than the published  
369 values at higher temperatures (Table 7). The modelled TGC for a fish of 528 g at  $9.0 \text{ }^{\circ}\text{C}$   
370 swimming at  $0.5 \text{ bl s}^{-1}$  was close to the published value (Table 7).

#### 371 **4. Discussion**

372 The maximum salmon length attained over a simulated 15.5-month period with the default  
373 parameters (0.44 m) was somewhat smaller than the typical size of one-sea-winter salmon in UK  
374 rivers (e.g. mean length of 0.66 m in the Chester Dee, CEFAS, unpublished data). The constancy  
375 of temperature, prey density, swimming speed and available feeding time in the non-spatial  
376 simulation was not intended to represent the seasonally varying conditions experienced by real  
377 salmon (although some of the simulated values may reflect annual averages in the ocean), so the  
378 absolute values of the final lengths attained can not be expected to be realistic. In particular,  
379 salmon are unlikely to swim continuously at a constant speed for 24 hours per day over  
380 prolonged periods, but there is, as yet, little information on swimming speeds during marine  
381 migration and at oceanic feeding grounds. Ultrasonic tracking of post-smolts in the early stages  
382 of marine migration has indicated rapid movement during both day and night, with speeds over  
383 the ground of  $0.1$  to  $>0.5 \text{ m s}^{-1}$  and a strong tidal component to speed and direction (Holm et al.,  
384 2003). However, tagged post-smolts recaptured in the Faroe-Shetland Channel 38–56 days after  
385 release from their home rivers in Ireland had been displaced at speeds of  $0.2$ – $0.3 \text{ m s}^{-1}$  – slower  
386 than the Slope Current in which they were found (Holst et al., 2000). Observations of farmed  
387 salmon in sea cages have shown a variety of sustained swimming speeds and diel patterns of  
388 speed, ranging from minimum speeds of  $<0.5 \text{ bl s}^{-1}$  to maximum daily values of  $1.0$ – $1.5 \text{ bl s}^{-1}$   
389 (Sutterlin et al., 1979; Kadri et al., 1991; Juell and Westerberg, 1993; Smith et al., 1993; Andrew  
390 et al., 2002). In the present model, modifying the behaviour of simulated salmon to optimise  
391 swimming speed, or to swim at minimum speed after the maximum daily consumption had been  
392 achieved, led to more realistic growth rates, particularly when higher swimming speeds would  
393 otherwise have applied. Comparison of modelled rates of growth in weight over shorter periods  
394 with available published values for progeny of wild parents indicated good agreement under

395 some conditions and underestimates in others (Thodesen et al., 1999; Handeland et al., 2003).  
396 Without knowing the swimming speeds in the empirical studies it is not possible to account for  
397 the differences.

398

399 Under the default bioenergetic parameters, the optimal temperature for growth was 14–16 °C.  
400 This optimum arises from the different temperature dependencies of maximum daily  
401 consumption, which peaks at 17–18 °C, and respiration, which increases exponentially with  
402 temperature. From rather sparse data on Norwegian farmed strains of Atlantic salmon post-  
403 smolts, Handeland et al. (2003) estimated that the optimum temperature for growth was 13 °C. A  
404 wild strain grew faster at 14 °C (the maximum temperature tested) than at 9 °C or 4 °C  
405 (Handeland et al., 2003). Koskela et al. (1997) estimated an optimum temperature for growth in  
406 large juvenile Baltic salmon (*Salmo salar*, 16–29 cm total length) of 16 °C.

407

408 Simulated growth declined with increasing swimming speed, due to the additional energy used in  
409 active metabolism. Empirical studies have produced mixed results about the effects of exercise  
410 on growth rate in Atlantic salmon (Davison, 1997). In some studies, growth rate was higher  
411 under moderate exercise regimes (Totland et al., 1987; Jørgensen and Jobling, 1993), owing to  
412 greater appetite, utilisation of feed (Jørgensen and Jobling, 1993) and perhaps release of growth  
413 hormones (Barrett and McKeown, 1988). However, these results are difficult to interpret in the  
414 present context, because the low swimming speeds in these studies involved holding salmon  
415 together in still or slow-flowing water, leading to greater stress from agonistic activity, which  
416 may have depressed appetite and increased the metabolic rate.

417

418 Output from the model was very sensitive to the values of certain parameters, so it is important  
419 to consider their likely range of values. For some of these parameters, a 25% change may have  
420 resulted in unrealistic values. For example, the initial weight-length power was varied to  
421 extremes of 2.3 and 3.8, whereas the 95% confidence limit of this parameter derived from over  
422 6500 measurements of Atlantic salmon from the British Isles (CEFAS and FRS, unpublished  
423 data) was 3.02 to 3.03 (analysis in present study). Over a range of 2.8 to 3.2 (i.e. -7% to +7%),  
424 there was little effect on final length.

425

426 The length-structure power, weight-energy power and weight-length power were derived from a  
427 combination of information from Atlantic salmon (weight-length relationship and maximum  
428 energy loss during starvation) and brown trout (*Salmo trutta*; a function relating body energy



429 density to length and weight). There may therefore be greater uncertainty about the value of  
430 these parameters and, given their importance to the model, an energy-length-weight relationship  
431 derived for post-smolt Atlantic salmon would be helpful, but difficult to obtain for wild fish.

432

433 Output from the present model was also very sensitive to maximum consumption parameter  $C_{TL}$ ,  
434 which contributes to defining the temperature dependence of daily food consumption at higher  
435 temperatures. In the Thonton-Lessem function for maximum daily consumption, four of the  
436 parameters define temperatures at which consumption is certain proportions of the maximum  
437 (Table 2). Paradoxical results may be obtained if these temperatures are out of sequence, as may  
438 have occurred by varying one of them independently of the others. Other parameters of the  
439 maximum daily consumption function also had a strong influence on the output. The parameters  
440 were fit to data on Atlantic salmon fed on fish meal pellets under controlled conditions, but there  
441 are few data for post-smolts below 8 °C and above 14 °C. There is therefore scope for studying  
442 food consumption of wild post-smolts fed on natural prey over a range of temperatures, although  
443 it is not easy to keep wild fish healthy in captivity or to supply natural prey.

444

445 Not surprisingly, simulated growth was sensitive to certain other parameters directly affecting  
446 energy intake: prey energy density and the relative dry weight proportions of salmon and prey.  
447 The relative dry matter contents of salmon and prey are important because maximum  
448 consumption is calculated first on the basis of dry weight of prey per unit dry weight of salmon.  
449 The wet weight of prey is then calculated from the ratio of the proportions of dry weight in prey  
450 and salmon. Water content of salmon and prey species is variable, but the values chosen are  
451 thought to represent average conditions. Prey energy density varies seasonally and spatially  
452 among and within species, but again, the values chosen were considered to be representative.

453

454 Parameters associated with prey encounter rate and ingestion, such as minimum edible prey size,  
455 prey density, reaction distance, available feeding time and prey item handling time had little  
456 influence on growth within the range of values tested. Under most conditions tested, simulated  
457 salmon were able to achieve their maximum daily consumption. However, in the North Atlantic  
458 Ocean, prey density and available feeding time will vary by more than the plus or minus 50%  
459 differences tested here. The influence of prey abundance and distribution can be investigated by  
460 coupling bioenergetic, migration and ecosystem models.

461

462 Values of the parameters in the respiration function had a strong negative influence on simulated  
463 growth, particularly the respiration-temperature coefficient and the respiration-temperature-  
464 speed coefficient, which both led to bioenergetic death when increased by 25%. However, all of  
465 the respiration parameters had important effects on simulated growth, which is not surprising,  
466 given that respiration is the major energy loss. The respiration function was derived from  
467 relationships given by Brett and Glass (1973) for standard and active rates of oxygen  
468 consumption in sockeye salmon (*Oncorhynchus nerka*). Although the predictions from this  
469 function compared reasonably well with the limited available measurements of Atlantic salmon,  
470 it would be worthwhile to conduct a detailed study of metabolic rate in marine-phase Atlantic  
471 salmon in relation to body size, temperature and swimming speed, so that respiratory losses can  
472 be modelled more reliably.

473

474 Level of activity is one of the most uncertain aspects of bioenergetic modelling of salmon during  
475 the marine phase. There is a pressing need to extend empirical studies of swimming activity from  
476 estuarine and coastal waters to offshore areas during both migration and non-migratory periods  
477 in oceanic feeding grounds. In the meantime, spatially explicit modelling provides insights into  
478 the consequences of different migratory behaviours (Booker et al., 2008).

479

## 480 **5. Conclusions**

481 An individual-based bioenergetic model has been developed to estimate variation in marine  
482 growth, and indirectly survival, of Atlantic salmon in relation to smolt body size, sea water  
483 temperature, prey availability and swimming activity. Short-term estimates of growth in weight  
484 were similar to empirical measurements made in captivity; longer-term estimates of growth in  
485 length were more difficult to assess, owing to uncertainty about the oceanic conditions  
486 experienced by wild salmon and their patterns of swimming activity. The non-spatial model is  
487 sensitive to certain physiological parameters for which there is limited information available for  
488 wild, marine-phase *Salmo salar* and this highlights areas for future empirical research. When  
489 coupled with an ecosystem model of the North Atlantic Ocean, the present bioenergetic model  
490 will allow the effects of future changes in oceanic conditions on the growth and survival of  
491 Atlantic salmon to be investigated.

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499

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729 Research Board of Canada 30, 1898–1900.

730 **Figure legends**

731 Figure 1 Contours of final salmon length (m) as a function of sea surface temperature and  
732 swimming speed with default bioenergetic parameter values.

733

734 Figure 2 Contours of final salmon length (m) as a function of sea surface temperature and the  
735 value of certain parameters of the growth model: (a) maximum consumption scale (constant),  
736  $C_A$ ; (b) maximum consumption-weight exponent,  $C_B$ ; (c) prey energy density; (d) salmon dry  
737 weight proportion scale,  $DW_a$ ; (e) proportional dry matter content of prey; (f) maximum  
738 consumption parameter  $C_Q$  – the low temperature ( $^{\circ}\text{C}$ ) at which maximum daily consumption is  
739 a defined proportion (default 0.25) of the value at the optimum temperature (Hewett and  
740 Johnson, 1987). Swimming speed  $1 \text{ bl s}^{-1}$  in all cases.

741

742 Figure 3 Contours of final salmon length (m) as a function of sea surface temperature and the  
743 value of certain parameters of the growth model: (a) respiration scale; (b) burst speed constant;  
744 (c) burst speed-length-temperature constant; (d) egestion scale (a proportion). Swimming speed  
745  $1 \text{ bl s}^{-1}$  in all cases. Crosses indicate combinations of parameters under which energy reserves  
746 reached zero during the simulation.

747

748 Figure 4 Contours of final salmon length (m) as a function of sea surface temperature and the  
749 value of certain parameters of the growth model: (a) length-structure scale; (b) maximum  
750 proportion of assimilated energy committed to structure,  $\kappa_{\text{max}}$ . Swimming speed  $1 \text{ bl s}^{-1}$  in all  
751 cases. Crosses indicate combinations of parameters under which energy reserves reached zero  
752 during the simulation.

753

754 Figure 5 Contours of final salmon length (m) as a function of sea surface temperature and value  
755 of the maximum consumption parameter  $C_{TO}$ , at a swimming speed of  $1 \text{ bl s}^{-1}$ .  $C_{TO}$  is the  
756 temperature ( $^{\circ}\text{C}$ ) below the optimum temperature at which maximum daily consumption is 0.98  
757 of the value at the optimum (Hewett and Johnson, 1987).

758

759 Figure 6 Final salmon length (m) as a function of sea surface temperature and swimming speed  
760 with (black contours) or without (grey contours) burst swimming to capture nektonic prey items.

761

762 Figure 7 Final salmon length (m) as a function of sea surface temperature and swimming speed  
763 with (black contours) or without (grey contours) optimising the duration of cruise swimming by  
764 swimming at a specified minimum speed after maximum daily consumption had been achieved.

765

766 Figure 8 Contours of the percentage increase in final length achieved by optimising the duration  
767 of cruise swimming, as a function of sea surface temperature and the swimming speed.

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773 **Table legends**

774 Table 1. Attributes of prey categories.

775

776 Table 2. Parameter values for the Thornton-Lessem function fitted to maximum daily  
777 consumption estimates for post-smolt *Salmo salar* (symbols after Hewett and Johnson, 1987).

778

779 Table 3. Parameter values for the function relating the proportion of ingested energy lost through  
780 egestion or nitrogenous excretion as a function of water temperature and consumption as a  
781 proportion of the maximum daily consumption.

782

783 Table 4. Parameter values of functions for allocation of assimilated energy to reserves or  
784 structure, calculation of length from structure and calculation of weight from length and reserves.

785

786 Table 5. Sensitivity of simulation results to variation in the model parameters at different sea  
787 surface temperatures and a swimming speed of  $1 \text{ bl s}^{-1}$ . Difference in final salmon length  
788 between that obtained with a 25% increase in the default parameter value and that obtained with  
789 a 25% decrease, expressed as a percentage of the final length obtained with the default parameter  
790 value. Asterisks indicate cases in which the simulated salmon reached zero energy reserves  
791 (bioenergetic 'death') during simulations with altered parameter values.

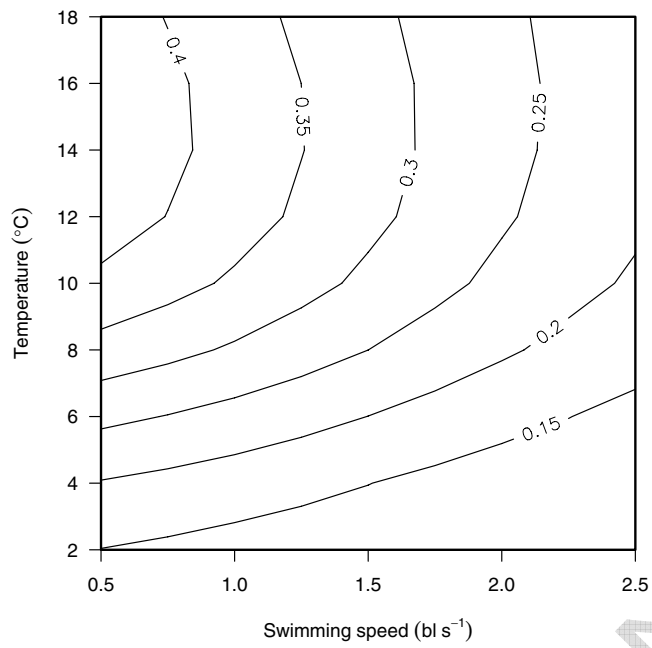
792

793 Table 6. Sensitivity of simulation results to variation in the model parameters at different  
794 swimming speeds and a sea surface temperature of  $10^{\circ}\text{C}$ . Difference in final salmon length  
795 between that obtained with a 25% increase in the default parameter value and that obtained with  
796 a 25% decrease, expressed as a percentage of the final length obtained with the default parameter  
797 value. Asterisks indicate cases in which the simulated salmon reached zero energy reserves  
798 (bioenergetic 'death') during simulations with altered parameter values.

799

800 Table 7. Comparison of simulated and published values of specific growth rate (SGR) and  
801 thermal-unit growth coefficient (TGC) under different conditions of initial body weight,  
802 temperature and swimming speed.

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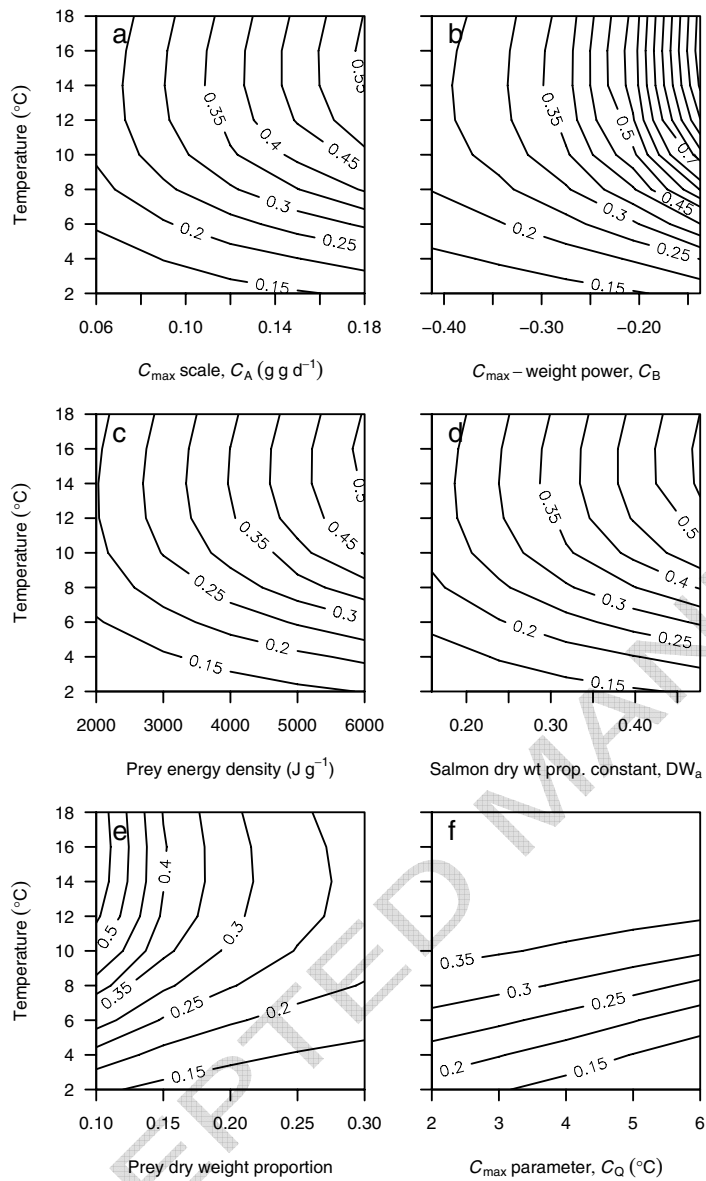


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806 Fig 1

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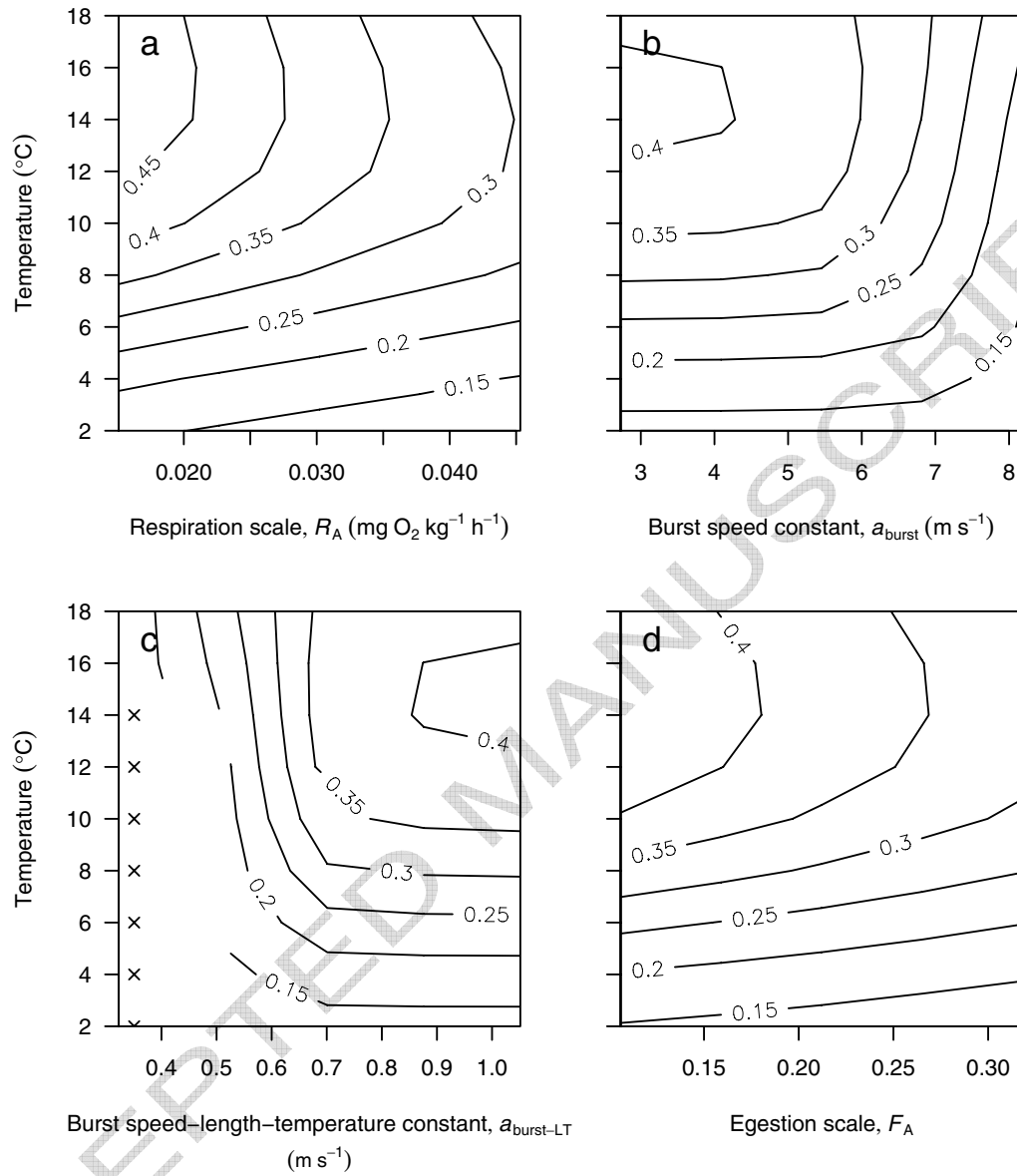


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810 Fig 2

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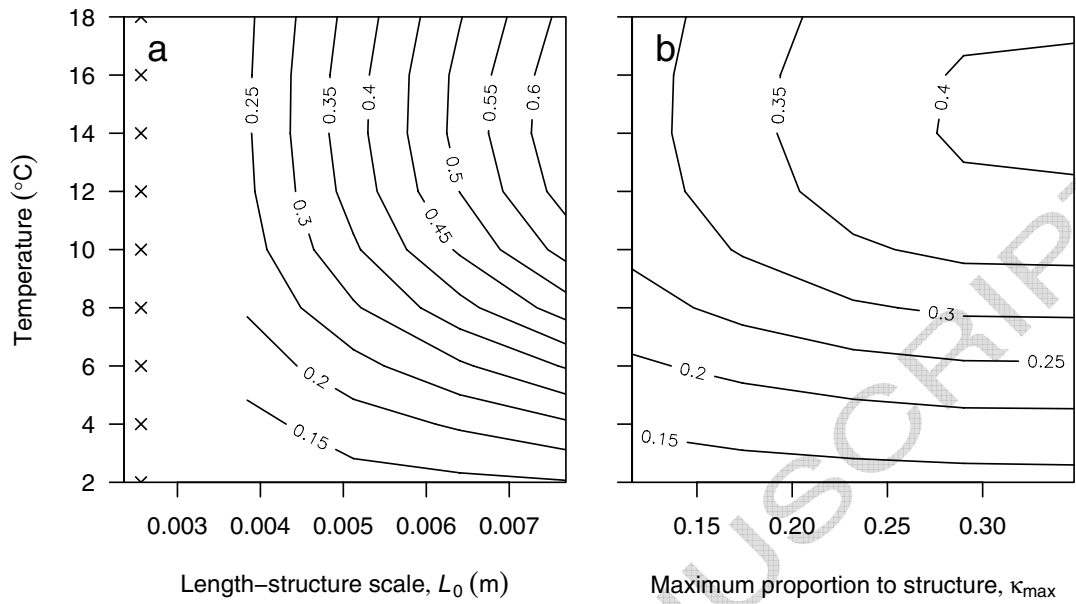
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814 Fig 3



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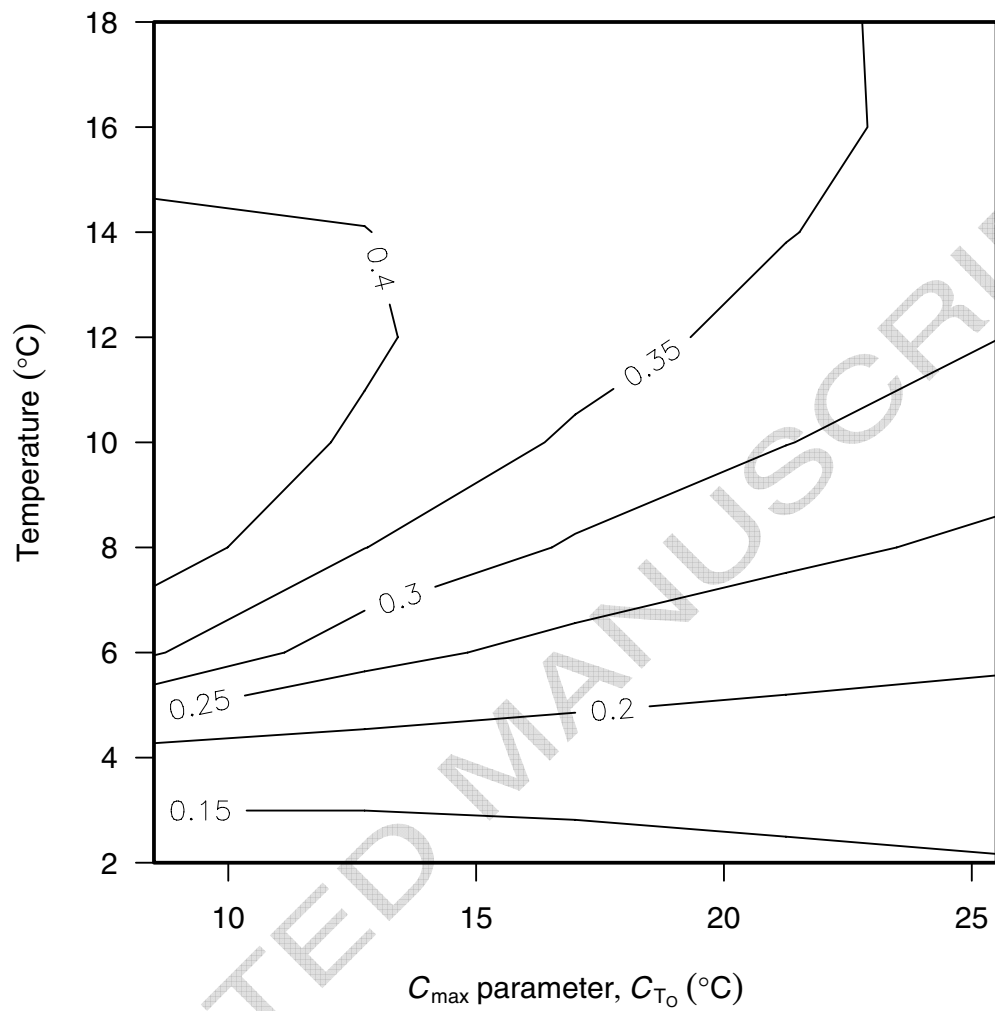


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818 Fig 4

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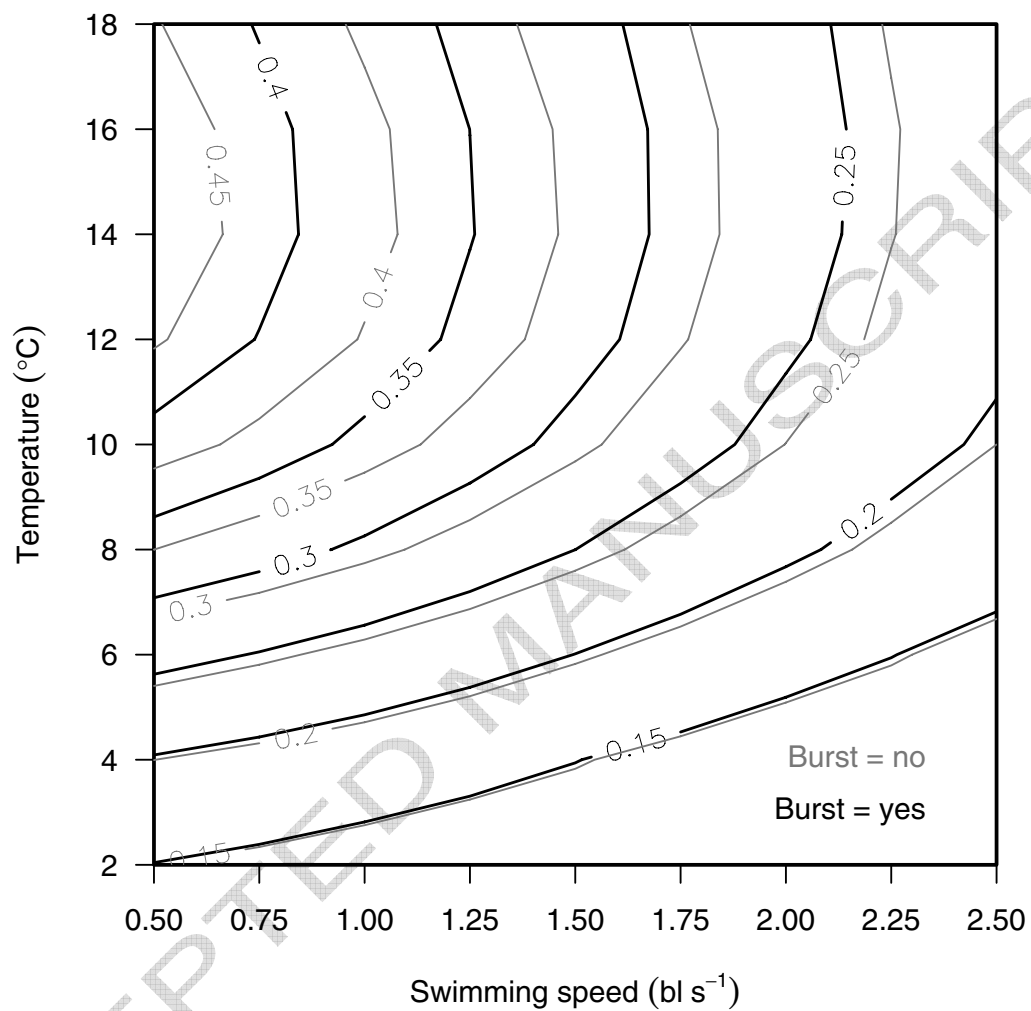
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822 Fig 5

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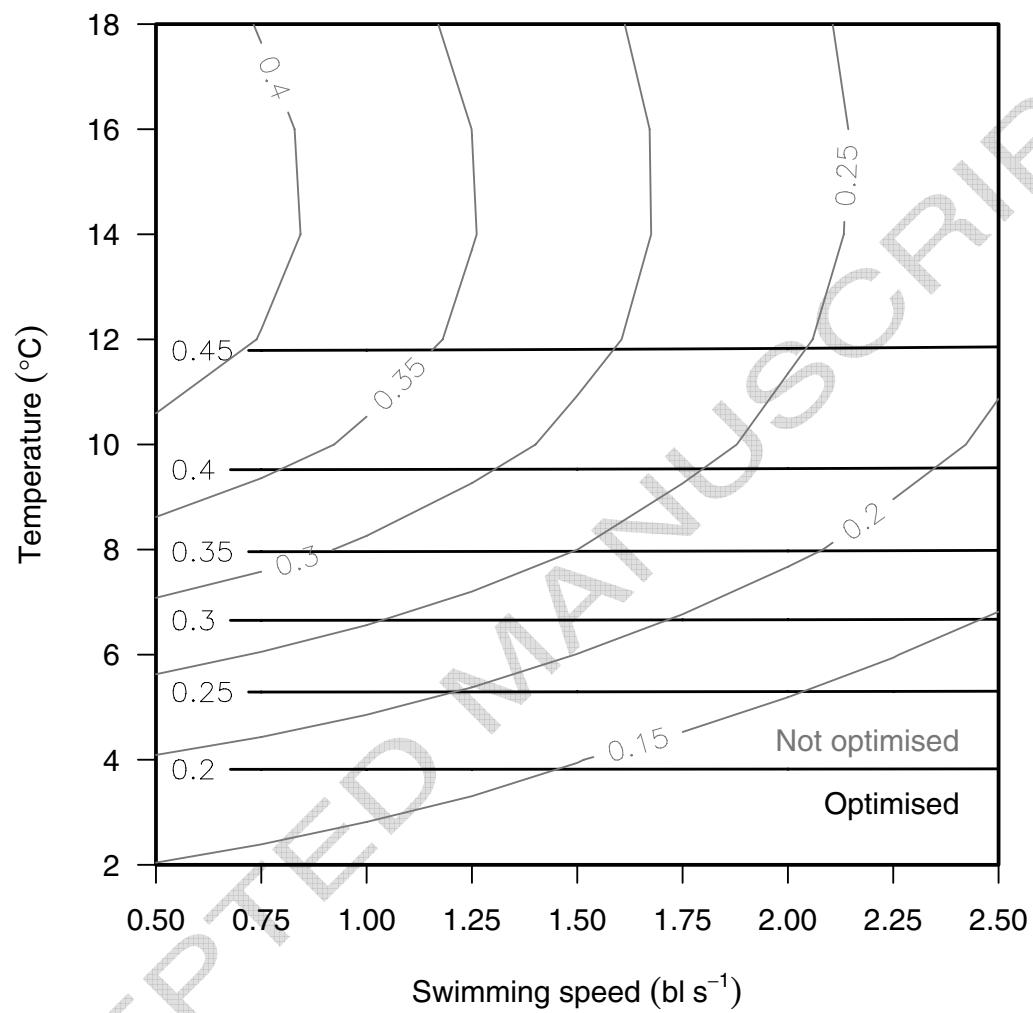
824 Fig 6



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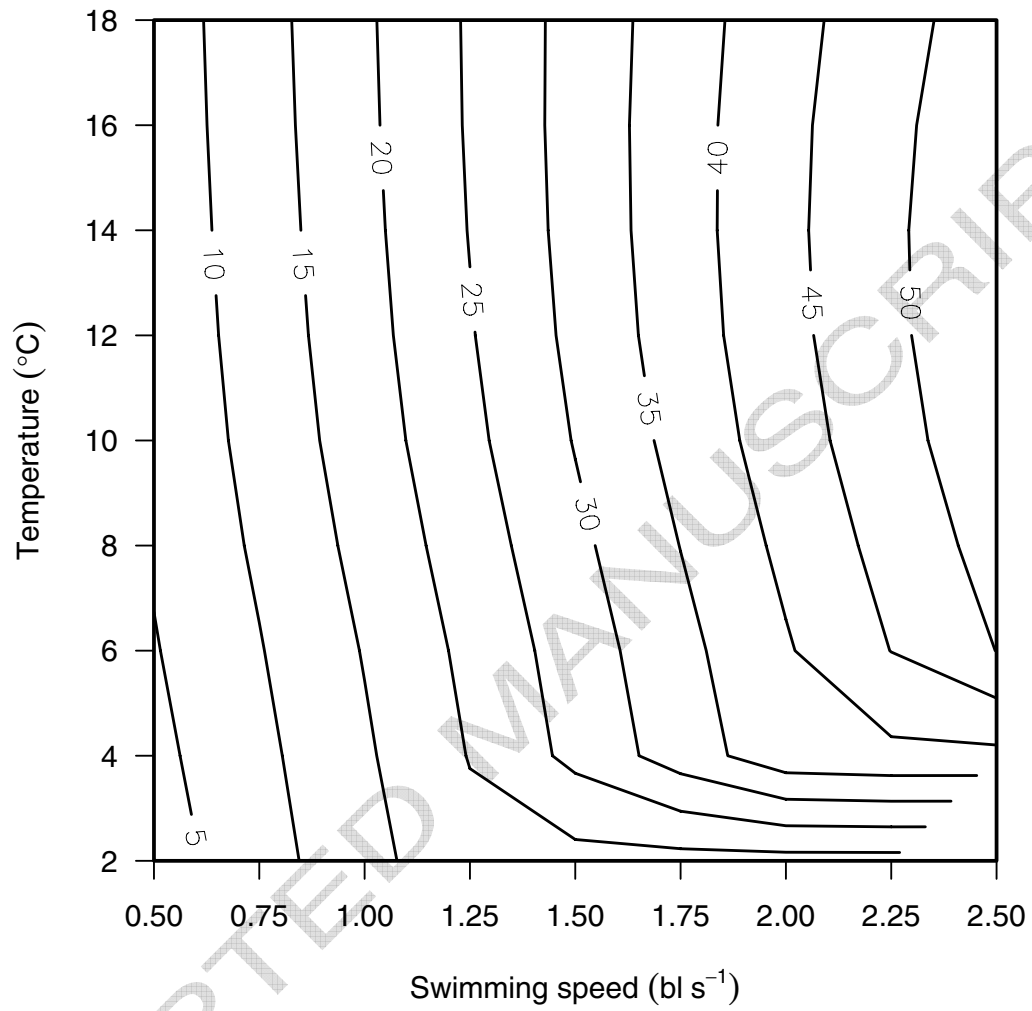
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829 Fig 7

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833 Fig 8

Table 1. Attributes of prey categories.

Prey category	1 'nauplii'	2 'small copepods'	3 'large copepods'	4 'euphausiids'	5 'small fish'	6 'larger fish'	7 'squid'
Energy density ( $\text{J g}^{-1}$ )	4000 <sup>a</sup>	5000 <sup>b</sup>	5000 <sup>b</sup>	3800 <sup>c</sup>	5000 <sup>d</sup>	6000 <sup>d</sup>	3900 <sup>d</sup>
Minimum size (m)	$2 \times 10^{-4}$ <sup>a</sup>	$5 \times 10^{-4}$ <sup>b</sup>	$1 \times 10^{-3}$ <sup>b</sup>	$2 \times 10^{-3}$ <sup>c</sup>	$2 \times 10^{-2}$ <sup>e</sup>	$6 \times 10^{-2}$ <sup>e</sup>	$2 \times 10^{-2}$ <sup>f</sup>
Maximum size (m)	$5 \times 10^{-4}$ <sup>a</sup>	$1 \times 10^{-3}$	$3.5 \times 10^{-3}$	$4 \times 10^{-2}$ <sup>c</sup>	$6 \times 10^{-2}$ <sup>e</sup>	$3 \times 10^{-1}$ <sup>e</sup>	$2 \times 10^{-1}$ <sup>f</sup>
Shape (L:W)	1.75 <sup>g</sup>	3.24 <sup>h</sup>	3.24 <sup>h</sup>	5.88 <sup>c</sup>	6.00 <sup>e</sup>	6.00 <sup>e</sup>	2.63 <sup>f,i</sup>
Weight-length constant ( $\text{g m}^{-b}$ )	$2.565$ $\times 10^4$ <sup>j</sup>	$2.565$ $\times 10^4$ <sup>j</sup>	$2.565$ $\times 10^4$ <sup>j</sup>	$1.663$ $\times 10^3$ <sup>c</sup>	$8.103$ $\times 10^3$ <sup>d</sup>	$8.103$ $\times 10^3$ <sup>d</sup>	$2.805$ $\times 10^3$ <sup>k</sup>
Weight-length power, <i>b</i>	2.919 <sup>j</sup>	2.919 <sup>j</sup>	2.919 <sup>j</sup>	2.70 <sup>c</sup>	2.98 <sup>d</sup>	2.98 <sup>d</sup>	2.4589 <sup>k</sup>
Water content (%)	80 <sup>a</sup>	80 <sup>j</sup>	80 <sup>j</sup>	80 <sup>c</sup>	78 <sup>d,l,m</sup>	74 <sup>d,l,m</sup>	80 <sup>d,m</sup>
Prey fractions <sup>n</sup>	0.58	0.27	0.15	0.3	0.25	0.1	0.15

Sources: a. Holland (1978); b. Båmstedt (1986); c. Mauchline (1980); d. Van Pelt et al. (1997); e. Wheeler (1978); f. Clarke (1966); g. Newell and Newell (1977); h. Marshall and Orr (1955); i. Hayward and Ryland (1995); j. Mauchline (1998); k. Arkhipkin and Bjørke (1999); l. Payne et al. (1999); m. Logerwell and Schaufler (2005); n. Head et al. (1999)

Table 2. Parameter values for the Thornton-Lessem function fitted to maximum daily consumption estimates for post-smolt *Salmo salar* (symbols after Hewett and Johnson, 1987).

Parameter	Value
Scale, $C_A$ ( $\text{g g}^{-1} \text{d}^{-1}$ )	0.12
Weight exponent, $C_B$	-0.275
Ascending limb lower temperature dependence, $C_{K1}$	0.25
Descending limb lower temperature dependence, $C_{K4}$	0.75
Ascending limb lower temperature, $C_Q$ , ( $^{\circ}\text{C}$ )	4
Ascending limb upper temperature, $C_{T0}$ , ( $^{\circ}\text{C}$ )	17
Descending limb lower temperature, $C_{TM}$ , ( $^{\circ}\text{C}$ )	18
Descending limb upper temperature, $C_{TL}$ , ( $^{\circ}\text{C}$ )	24

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Table 3. Parameter values for the function relating the proportion of ingested energy lost through egestion or nitrogenous excretion as a function of water temperature and consumption as a proportion of the maximum daily consumption.

Parameter	Egestion		Excretion	
Constant	$F_a$	0.212	$U_a$	0.026
Temperature	$F_{b1}$	-0.222	$U_{b1}$	0.580
Proportion of max. consumption	$F_{b2}$	0.631	$U_{b2}$	-0.299

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Table 4. Parameter values of functions for allocation of assimilated energy to reserves or structure, calculation of length from structure and calculation of weight from length and reserves.

Parameter	Value
Defended reserve ratio, $\lambda_{\text{def}}$	2.44
Allocation switch width, $\lambda_{\text{switch}}$	0.362
Maximum proportion to structure, $\kappa_{\text{max}}$	0.232
Length-structure scale, $L_0$ (m)	$3.621 \times 10^{-3}$
Length-structure power, $\alpha$	0.341
Weight-length-energy scale, $W_0$ (g)	$2.0072 \times 10^{-2}$
Weight-length power, $\beta$	0.692
Weight-energy power, $\gamma$	0.719

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Table 5. Sensitivity of simulation results to variation in the model parameters at different sea surface temperatures and a swimming speed of  $1 \text{ bl s}^{-1}$ . Difference in final salmon length between that obtained with a 25% increase in the default parameter value and that obtained with a 25% decrease, expressed as a percentage of the final length obtained with the default parameter value. Asterisks indicate cases in which the simulated salmon reached zero energy reserves (bioenergetic ‘death’) during simulations with altered parameter values.

Parameter	Sea surface temperature (°C)								
	2	4	6	8	10	12	14	16	18
Initial fish length	28.5	15.6	10.9	8.4	7.3	6.8	6.5	6.4	6.3
Initial weight-length scale	-1.7	1.5	2.1	1.9	1.8	1.7	1.7	1.6	1.6
Initial weight-length power	*	*	*	*	*	*	*	*	*
Minimum swimming speed	-3.1	-2.4	-1.9	-1.6	-1.4	-1.4	-1.4	-1.5	-1.6
Maximum swimming speed	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Minimum edible prey size	0.0	0.0	-0.1	-0.2	-0.2	-0.2	-0.2	-0.3	-0.3
Maximum edible prey size	0.1	0.2	1.1	3.3	5.9	7.4	8.0	8.0	7.4
Zooplankton density	-0.7	-1.2	-1.5	-1.4	-1.0	-0.9	-0.9	-0.9	-0.9
Zooplankton ‘lost’ to higher predators	0.0	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1
Reaction distance scale, $D_a$	-0.3	-0.7	-1.5	-2.5	-3.3	-3.6	-3.8	-3.7	-3.4
Reaction distance power, $D_b$	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Prey handling time	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maximum consumption scale, $C_A$	15.4	27.1	32.6	37.1	40.9	43.5	45.2	46.5	47.5
Maximum consumption parameter, $C_B$	15.6	28.3	40.4	53.0	63.9	70.5	74.1	76.4	77.8
Maximum consumption parameter, $C_Q$	-21.7	-30.9	-24.5	-15.5	-7.9	-3.2	-1.0	-0.2	0.1
Maximum consumption parameter, $C_{K1}$	19.4	27.1	21.5	13.6	6.9	2.8	0.9	0.1	-0.1
Maximum consumption parameter, $C_{TO}$	12.6	0.0	-21.4	-30.7	-27.3	-19.6	-12.8	-7.8	-4.7
Maximum consumption parameter, $C_{TM}$	0.0	0.1	0.2	0.3	0.6	1.2	2.0	3.5	6.0
Maximum consumption parameter, $C_{TL}$	*	*	*	*	*	*	*	66.7	0.0
Maximum consumption parameter, $C_{K4}$	0.0	-0.1	-0.1	-0.2	-0.3	-0.5	-0.7	-0.7	0.0
Prey length:width ratio	0.0	0.2	1.0	2.8	4.1	4.8	5.0	4.9	4.5
Prey dry weight ratio	-14.5	-27.7	-34.0	-39.1	-42.0	-43.9	-45.3	-46.7	-48.0
Prey energy density	11.6	26.8	33.3	38.6	41.9	43.9	45.4	46.5	47.4
Salmon dry weight constant, $DW_a$	14.7	25.6	31.4	36.2	40.1	42.8	44.5	45.7	46.7
Salmon dry weight coefficient, $DW_b$	1.8	1.5	1.1	0.8	0.7	0.7	0.7	0.7	0.7

Egestion scale, $F_a$	-10.9	-12.3	-13.4	-14.4	-15.3	-15.7	-15.8	-15.7	-15.5
Egestion-temperature coefficient, $F_{b1}$	-1.7	-3.8	-5.4	-6.7	-7.8	-8.7	-9.3	-9.7	-10.0
Egestion-consumption coefficient, $F_{b2}$	-6.9	-7.8	-8.5	-9.1	-9.7	-9.9	-10.0	-9.9	-9.8
Excretion scale, $U_a$	-0.9	-1.8	-2.7	-3.7	-4.7	-5.6	-6.3	-7.0	-7.6
Excretion-temperature coefficient, $U_{b1}$	-0.4	-1.5	-2.9	-4.5	-6.4	-8.2	-9.9	-11.5	-13.1
Excretion-consumption coefficient, $U_{b2}$	-0.3	-0.5	-0.8	-1.1	-1.4	-1.7	-1.9	-2.1	-2.3
Specific Dynamic Action proportion	-4.1	-5.7	-7.0	-8.1	-9.0	-9.7	-10.1	-10.3	-10.4
Burst speed constant	-2.7	-6.6	-13.3	-20.8	-25.9	-27.8	-27.1	-24.6	-20.9
Burst speed-temperature coefficient	-0.1	-0.4	-1.3	-2.8	-4.5	-5.8	-6.7	-7.1	-7.0
Burst speed-length-temperature constant	6.1	20.8	32.4	42.8	49.3	51.7	50.4	46.2	39.7
Burst speed-length-temperature coefficient	0.1	0.3	0.8	1.6	2.3	3.0	3.5	3.8	4.0
Respiration scale, $R_a$	-15.3	-18.3	-19.1	-20.7	-22.6	-24.3	-25.8	-27.3	-28.7
Resp.-temperature coefficient, $R_{b1}$	-23.5	-58.9	-86.1	-105.5	*	*	*	*	*
Resp.-speed coefficient, $R_{b2}$	-15.8	-29.5	-41.8	-56.4	-68.6	-76.7	-81.3	-83.6	-84.1
Resp.-weight-temperature power, $R_{b3}$	-0.8	-1.8	-3.4	-5.5	-8.2	-10.9	-13.7	-16.5	-19.3
Resp.-weight-speed power, $R_{b4}$	-5.8	-8.5	-13.8	-21.4	-28.6	-33.9	-37.4	-39.0	-38.9
Resp.-temperature-speed coefficient, $R_{b5}$	-23.9	*	*	*	*	*	*	*	*
Defended reserve ratio, $\lambda_{def}$	-0.5	-0.7	-0.7	-0.8	-0.9	-1.0	-1.0	-1.0	-1.0
Allocation switch width, $\lambda_{switch}$	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maximum proportion to structure, $\kappa_{max}$	2.5	9.8	12.8	15.1	16.9	18.0	18.4	18.3	17.8
Length-structure scale, $L_0$	10.5	41.0	51.9	60.5	66.7	70.1	71.2	70.9	69.3
Length-structure power, $\alpha$	*	*	*	*	*	*	*	*	*
Weight-length-energy scale, $W_0$	-4.0	-2.7	-0.5	0.6	1.2	1.5	1.4	1.1	0.8
Weight-length power, $\beta$	6.1	4.5	1.4	0.0	-0.7	-0.9	-0.8	-0.6	-0.3
Weight-energy power, $\gamma$	*	*	*	*	*	*	*	*	*

Table 6. Sensitivity of simulation results to variation in the model parameters at different swimming speeds and a sea surface temperature of 10°C. Difference in final salmon length between that obtained with a 25% increase in the default parameter value and that obtained with a 25% decrease, expressed as a percentage of the final length obtained with the default parameter value. Asterisks indicate cases in which the simulated salmon reached zero energy reserves (bioenergetic ‘death’) during simulations with altered parameter values.

Parameter	Swimming speed (body lengths s <sup>-1</sup> )								
	0.50	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50
Initial fish length	8.8	8.2	7.3	6.3	5.2	4.0	3.0	2.1	1.3
Initial weight-length scale	2.5	2.2	1.8	1.3	0.7	0.0	-0.8	-1.7	-2.9
Initial weight-length power	*	*	*	*	*	*	*	*	*
Minimum swimming speed	-1.4	-1.4	-1.4	-1.4	-1.4	-1.5	-1.5	-1.5	-1.5
Maximum swimming speed	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Minimum edible prey size	-0.2	-0.2	-0.2	-0.3	-0.3	-0.3	-0.2	-0.1	-0.1
Maximum edible prey size	6.7	6.4	5.9	5.1	4.1	3.1	2.1	1.4	0.8
Feeding time	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Zooplankton density	-0.9	-1.0	-1.0	-1.1	-1.4	-1.7	-1.8	-1.8	-1.7
Zooplankton ‘lost’ to higher predators	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1
Reaction distance scale, $D_a$	-3.3	-3.3	-3.3	-3.2	-3.0	-2.7	-2.4	-2.0	-1.6
Reaction distance power, $D_b$	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.2	0.2
Prey handling time	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maximum consumption scale, $C_A$	41.5	41.3	40.9	40.1	38.9	37.4	35.9	34.3	32.8
Maximum consumption parameter, $C_B$	65.9	65.3	63.9	61.5	58.0	53.8	49.1	44.4	39.9
Maximum consumption parameter, $C_Q$	-8.0	-8.0	-7.9	-7.7	-7.5	-7.2	-6.9	-6.6	-6.3
Maximum consumption parameter, $C_{K1}$	7.0	7.0	6.9	6.8	6.5	6.3	6.1	5.8	5.5
Maximum consumption parameter, $C_{TO}$	-27.8	-27.7	-27.3	-26.7	-25.9	-24.9	-23.8	-22.8	-21.7
Maximum consumption parameter, $C_{TM}$	0.7	0.6	0.6	0.6	0.6	0.6	0.6	0.5	0.5
Maximum consumption parameter, $C_{TL}$	*	*	*	*	*	*	*	*	*
Maximum consumption parameter, $C_{K4}$	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3
Prey length:width ratio	4.3	4.2	4.1	3.9	3.5	2.9	2.1	1.3	0.8
Prey dry weight ratio	-41.7	-41.9	-42.0	-41.9	-41.3	-40.0	-38.1	-36.1	-34.1
Prey energy density	41.7	41.9	41.9	41.7	41.0	39.6	37.8	35.8	33.8
Salmon dry weight constant, $DW_a$	40.7	40.6	40.1	39.3	38.0	36.5	34.9	33.2	31.5
Salmon dry weight coefficient, $DW_b$	0.7	0.7	0.7	0.7	0.8	0.8	0.8	0.9	1.1
Egestion scale, $F_a$	-15.5	-15.5	-15.3	-14.9	-14.4	-13.8	-13.2	-12.5	-11.9

Egestion-temperature coefficient, $F_{b1}$	-8.0	-7.9	-7.8	-7.7	-7.4	-7.1	-6.8	-6.4	-6.1
Egestion-consumption coefficient, $F_{b2}$	-9.9	-9.8	-9.7	-9.5	-9.1	-8.8	-8.4	-7.9	-7.5
Excretion scale, $U_a$	-4.8	-4.7	-4.7	-4.6	-4.4	-4.2	-4.0	-3.8	-3.6
Excretion-temperature coefficient, $U_{b1}$	-6.5	-6.4	-6.4	-6.2	-6.0	-5.7	-5.5	-5.2	-4.9
Excretion-consumption coefficient, $U_{b2}$	-1.4	-1.4	-1.4	-1.4	-1.3	-1.3	-1.2	-1.1	-1.1
Specific Dynamic Action proportion	-9.2	-9.1	-9.0	-8.8	-8.5	-8.2	-7.8	-7.4	-7.0
Burst speed constant	-27.3	-26.8	-25.9	-24.6	-22.7	-20.4	-17.7	-14.8	-12.0
Burst speed-temperature coefficient	-4.5	-4.5	-4.5	-4.3	-4.1	-3.7	-3.2	-2.7	-2.2
Burst speed-length-temperature constant	50.6	50.2	49.3	48.0	46.0	43.3	40.1	36.4	32.4
Burst speed-length-temperature coefficient	2.2	2.3	2.3	2.4	2.3	2.2	2.0	1.7	1.5
Respiration scale, $R_a$	-17.1	-19.8	-22.6	-25.3	-27.9	-30.0	-31.6	-32.5	-32.7
Resp.-temperature coefficient, $R_{b1}$	-104.5	*	*	*	*	*	*	*	*
Resp.-speed coefficient, $R_{b2}$	-63.2	-65.6	-68.6	-72.3	-76.7	-81.5	-86.8	-89.7	-90.6
Resp.-weight-temperature power, $R_{b3}$	-6.4	-7.3	-8.2	-8.9	-9.5	-9.8	-9.9	-9.6	-9.1
Resp.-weight-speed power, $R_{b4}$	-24.6	-26.5	-28.6	-30.6	-32.6	-34.2	-35.5	-36.1	-36.1
Resp.-temperature-speed coefficient, $R_{b5}$	*	*	*	*	*	*	*	*	*
Defended reserve ratio, $\lambda_{def}$	-1.0	-1.0	-0.9	-0.9	-0.8	-0.8	-0.7	-0.6	-0.6
Allocation switch width, $\lambda_{switch}$	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maximum proportion to structure, $\kappa_{max}$	18.4	17.7	16.9	15.9	14.7	13.4	12.1	10.9	9.7
Length-structure scale, $L_0$	71.9	69.7	66.7	63.0	58.7	53.9	49.0	44.3	39.7
Length-structure power, $\alpha$	*	*	*	*	*	*	*	*	*
Weight-length-energy scale, $W_0$	7.2	4.4	1.2	-2.0	-5.2	-8.0	-10.2	-11.7	-12.3
Weight-length power, $\beta$	-5.7	-3.4	-0.7	2.4	5.5	8.4	11.0	12.9	14.1
Weight-energy power, $\gamma$	*	*	*	*	*	*	*	*	*

Table 7. Comparison of simulated and published values of specific growth rate (SGR) and thermal-unit growth coefficient (TGC) under different conditions of initial body weight, temperature and swimming speed.

Initial weight (g)	Temperature (°C)	SGR at speed		Published value	Reference
		0.5 bl s <sup>-1</sup>	1.0 bl s <sup>-1</sup>		
61	4.3	0.342	0.225	0.274	Handeland et al. (2003)
	9.4	1.196	1.072	0.723	
	14.3	1.515	1.384	0.989	
		TGC at speed			
		0.5 bl s <sup>-1</sup>	1.0 bl s <sup>-1</sup>		
528	9.0	1.41 × 10 <sup>-3</sup>	9.57 × 10 <sup>-4</sup>	1.39 × 10 <sup>-3</sup>	Thodesen et al. (1999)

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