

1 Appendix A

2 *Acoustic disturbance*

3 Based on a meta-analysis of sound exposure experiments [1], we summarize known effects of
4 anthropogenic noise for fish in Table S1. Subsequently, we identify, based on documented
5 responses of fish to changes in physiology or behaviour, potential direct consequences for
6 individual-level processes in the model (energy expenditure, food intake, mortality and
7 reproductive output; Table S1). It should be noted that, while many acoustic disturbances are of
8 an impulsive nature (seismic surveys, pile driving), our choice of 'potential effects' relate to
9 regular exposure to such pulses, not the effects of individual pulses. We give a broad overview
10 of how acoustic disturbances may affect individual-level processes (Table S1) to motivate the
11 link between acoustic disturbances and changes in individual level processes.

12 Across different fish species, anthropogenic noise has been shown to increase stress and affect
13 foraging behaviour, movement behaviour and the auditory system [1]. Stress has been linked to
14 increased energy expenditure, decreased food intake, increased mortality and decreased
15 reproductive output (Table S1). Changes in foraging behaviour may result in increased energy
16 expenditure or lower food intake, while short-term consequences for mortality or reproductive
17 output seem unlikely (Table S1). Changes in movement behaviour may lead to increased energy
18 expenditure (Table S1) but have not been documented to affect food intake or reproductive
19 output. Changes in the auditory system of fish may lead to decreased food intake, increased
20 mortality and decreased reproduction (for example, through the negative consequences of
21 elevated hearing thresholds; Table S1). Although it has often been argued that displacement
22 from foraging areas and spawning grounds affects fish [2], these effects play on a larger scale
23 than the experiments reviewed by Cox et al. [1] and we did not include this link in our table. Yet,
24 we do analyse the effect of reduced reproductive output on the population growth rate based on
25 another link in the table. In summary, anthropogenic noise could eventually lead to increased
26 energy expenditure, reduced food intake, increased mortality and reduced reproductive output
27 for individual cod (Table S1).

28 *Model formulation*

29 The body mass of an individual is assumed to consist of structural mass x (muscles and bones),
30 reserves y_r (lipids and fat) and gonads y_g . Total individual body mass w is hence given by:

31
$$w = x + y_r + y_g.$$

32 The mass-length relationship equals:

33
$$x = \frac{\gamma l^\delta}{(1 + q_j)},$$

34 which relates the structural mass x to the condition parameter q_j and the length l with scaling
35 parameters γ and δ .

36 Food ingestion follows a Holling type-II functional response. Unlike van Leeuwen et al. [3], we do
37 not explicitly consider multiple food resources. Instead, the food ingestion rate $I(l)$ is defined as
38 the ratio between the feeding level $F(l)$ and the time the individual needs to digest a unit mass
39 of food $G(l)$ (the inverse $1/G(l)$ equals an individual's maximum feeding rate):

40
$$I(l) = \frac{1}{G(l)} (1 - \psi_I) F(l).$$

41 The feeding level $F(l)$ is assumed constant in time, but body size-dependent (figure S1B). Food
42 ingestion decreases proportionally with acoustic foraging disturbance multiplier ψ_I . Digestion
43 time scales with length as:

44
$$G(l) = \varepsilon l^\theta,$$

45 with scaling constant ε and exponent θ .

46 The net-energy $N(l, w)$ equals:

47
$$N(l, w) = \sigma I(l) - (1 + \psi_T) T(w).$$

48 Ingested food is assimilated to energy with efficiency σ . The energy is then first used to cover the
 49 energy expenditure for metabolic maintenance. The standard metabolic maintenance
 50 requirements are represented by term $T(w)$. The energy expenditure increases proportionally
 51 with the acoustic disturbance energy expenditure multiplier ψ_T relative to the standard
 52 metabolic maintenance requirements. The standard metabolic requirements depend on the total
 53 body weight, including both structural and reversible mass:

$$54 \quad T(w) = \alpha w^\beta,$$

55 with scaling constant α and exponent β .

56 To assess the population growth rate, we consider a situation with ample food availability. The
 57 net-energy is always taken to be positive and we do not consider starvation conditions.

58 A proportion k of the net-energy is invested in growth in structural mass; the remaining
 59 proportion $1 - k$ of the net-energy is invested in reversible and gonad mass (see below). The
 60 proportion k is defined as:

$$61 \quad k(l, x, y_r, y_g) = \begin{cases} \frac{1}{q(l) + 1}, & \frac{y_r + y_g}{x} > q(l) \\ \frac{1}{q(l) + 1} \left(\frac{y_r + y_g}{q(l)x} \right)^2, & \text{otherwise.} \end{cases}$$

$$62 \quad q(l) = \begin{cases} q_j, & l < l_m; \\ q_a, & \text{otherwise.} \end{cases}$$

63 The proportion k depends on the ratio between the reversible ($y_r + y_g$) and structural (x) mass.

64 The proportion k targets for a constant ratio $q(l)$ between reversible and structural mass (note

65 that $k = 1/(q(l) + 1)$ when $y_r + y_g = q(l)x$). When the actual ratio between reversible and

66 structural mass drops below the target condition level $q(l)$, $k(l, x, y_r, y_g)$ decreases with a

67 decrease in the ratio between the reversible and structural mass. This slows down growth in

68 structural mass and favours restoring reserve mass to reach the target condition. The value of

69 $q(l)$ depends on the size of the individual, it is equal to q_j before, and equal to q_a after they have

70 become sexually mature. Sexual maturity is reached when an individual reaches the size at
 71 maturation l_m . Since $q_j < q_a$, adults accumulate more reserves than juveniles, a surplus they
 72 allocate to reproduction.

73 For each individual, mortality is a sum of background mortality μ_0 , size-dependent background
 74 mortality D_s , and, fisheries D_v mortality, resulting in the following equation for the per capita
 75 mortality rate:

$$76 \quad D(l) = (1 + \psi_D)\mu_0 + D_s(l) + D_v(l).$$

77 The term $\psi_D \mu_0$, background mortality multiplied by acoustic disturbance mortality multiplier
 78 ψ_D , represents the increase in mortality due to acoustic disturbance. The size-dependent
 79 background mortality $D_s(l)$ decreases exponentially with body size:

$$80 \quad D_s(l) = \mu_s e^{-\left(\frac{l}{l_s}\right)^\delta},$$

81 with mortality constant μ_s and characteristic size l_s . Fisheries mortality $D_v(l)$ depends on body
 82 size following a double sigmoid function (see Figure S1C):

$$83 \quad D_v(l) = \mu_v \left(X(l, l_v, l_{vh}) - (1 - \rho) X(l, l_{vd}, l_{vdh}) \right),$$

84 in which $X(l, l_1, l_2)$ is defined as:

$$85 \quad X(l, l_1, l_2) = \begin{cases} 0.0, & nx \leq 0.0 \\ \frac{1}{6} nx^3, & 0.0 < nx \leq 1.0 \\ \left(-\frac{3}{2} nx + \frac{3}{2} nx^2 - \frac{1}{3} nx^3 + 0.5\right), & 1.0 < nx \leq 2.0 \\ \left(\frac{9}{2} nx - \frac{3}{2} nx^2 + \frac{1}{6} nx^3 - 3.5\right), & 2.0 < nx \leq 3.0 \\ 1.0, & \text{otherwise} \end{cases} \quad \text{with } nx = 1.5 \frac{(l - l_1)}{(l_2 - l_1)}.$$

86 The fisheries mortality depends on mortality constant μ_v , the average fisheries retention in the
 87 largest size classes' ρ and sigmoid function $X(l, l_1, l_2)$. The sigmoid function depends on the
 88 body length l , the length at the start l_1 and at 50% l_2 of the s-shaped part of the function. For the
 89 increasing part of $D_v(l)$, the sigmoid is defined by the length at the start (l_v) and at 50% (l_{vh}) of

90 fisheries retention. For the decreasing part of $D_v(l)$, the sigmoid depends on the length at the
 91 start (l_{vd}) and at 50% (l_{vdh}) of the fisheries mortality decline (Figure S1C).

92 The individual life history is a mix of continuous and discrete time processes that operate within
 93 each year. The individual-level functions for feeding, energy allocation and mortality lead to a set
 94 of ODEs that describe the continuous-time changes of the individual throughout its life. The age
 95 a , structural mass x , length l and survival probability s change continuously with time τ as:

$$96 \quad \frac{da}{d\tau} = 1.0,$$

$$97 \quad \frac{dx}{d\tau} = \kappa N,$$

$$98 \quad \frac{dl}{d\tau} = \frac{dx}{d\tau} / \frac{dx}{dl} = kN \frac{l}{\delta x},$$

$$99 \quad \frac{ds}{d\tau} = -D(l)s.$$

100 The dynamics of the reversible mass of reserves y_r and gonads y_g depend on the time of the year
 101 and the sexual maturity of the individual. During the first period, with length τ_r , of each year, the
 102 energy invested in reversible and gonad mass is stored in the reserves only and the gonads
 103 remain empty. Within each year n with length Y , these dynamics during the intervals $(nY) \leq \tau <$
 104 $(nY + \tau_r)$ are hence described by:

$$106 \quad \frac{dy_r}{d\tau} = (1 - k) \eta$$

$$107 \quad \frac{dy_g}{d\tau} = 0.0.$$

105

108 At day τ_r within each year (that is, at all time-points $q_n = (nY + \tau_r)$), the individual decides
 109 whether it will spawn at the end of the year. This decision depends on the reserve mass in
 110 relation to the target body condition:

$$111 \quad y_g(q_n^+) = \begin{cases} 0.0, & y_r(q_n^-) \leq q_j x(q_n^-) \\ y_r(q_n^-) - q_j x(q_n^-), & y_r(q_n^-) > q_j x(q_n^-) \end{cases}$$

$$y_r(\varrho_n^+) = \begin{cases} y_r(\varrho_n^-), & y_r(\varrho_n^-) \leq q_j x(\varrho_n^-) \\ q_j x(\varrho_n^-), & y_r(\varrho_n^-) > q_j x(\varrho_n^-) \end{cases}$$

113 If the ratio of reserves over structural mass is smaller than or equal to q_j , the individual will not
 114 spawn because any investment in reproduction would lower the body condition below the
 115 target condition q_j . In this case, all variables stay the same. On the other hand, if the ratio of
 116 reserves over structural mass is larger than q_j , the individual will spawn. In this case, the
 117 surplus of reserve mass, in excess of the target body condition q_j , is transferred to the gonads.
 118 All other variables stay the same.

119 Depending on the decisions about spawning at time points ϱ_n , the dynamics that occur
 120 subsequently until the end of the year, during intervals $(nY + \tau_r) \leq \tau < (nY + Y)$, are:

121 for years without spawning:

$$122 \quad \frac{dy_r}{d\tau} = (1 - k)N,$$

$$123 \quad \frac{dy_g}{d\tau} = 0.0,$$

124 for years with spawning:

$$125 \quad \frac{dy_r}{d\tau} = \begin{cases} (1 - k)N, & l < l_m, \\ 0.0, & l \geq l_m, \end{cases}$$

$$126 \quad \frac{dy_g}{d\tau} = \begin{cases} 0.0, & l < l_m, \\ (1 - k)N, & l \geq l_m. \end{cases}$$

127 If no spawning occurs, energy invested in reversible mass is stored in reserves by all individuals.
 128 In years with spawning, energy invested in reversible mass is stored in the gonads by
 129 individuals with a length larger than l_m . while energy invested in reversible mass is stored in
 130 the reserves by immature individuals, with length smaller than l_m .

131 Spawning occurs at the end of each year at day Y , at the time points $\zeta_n = (nY + Y)$:

$$132 \quad B = (1 - \psi_B) \frac{\sigma_r y_g(\zeta_n^-)}{m(l_b)},$$

140
$$R_0(\zeta_n^+) = R_0(\zeta_n^-) + B s(\zeta_n^-),$$

141
$$y_g(\zeta_n^+) = 0.0.$$

133 The number of offspring B that an individual produces depends on the mass of the gonads, the
134 mass $m(l_b)$ at the size of birth l_b and the gonad-to-offspring conversion efficiency σ_r . The
135 number of offspring produced decreases proportionally with the reproductive failure multiplier
136 ψ_B due to acoustic disturbance. To calculate the lifetime reproductive output R_0 , the number of
137 offspring B is multiplied by the survival probability of the individual and added to the offspring
138 the individual has produced so far. The gonadal mass is set to zero. All other variables do not
139 change.

142 The initial state of an individual in the model is defined at the moment at which the individual
143 starts feeding actively. At this moment, the individual age is a_b and body size is l_b . Its survival
144 probability up to that moment depends on the mortality in the egg and larval phase μ_e . The
145 individuals reserves contain a portion of the total mass such that, while the gonads are empty,
146 the ratio between reversible and structural mass is equal to the target ratio q_j . This results in the
147 following state of the model variables for newborns:

149
$$a(0) = a_b,$$

150
$$x(0) = \frac{1}{(1 + q_j)} m(l_b),$$

151
$$l(0) = l_b,$$

152
$$s(0) = e^{-\mu_e a_b},$$

153
$$h(0) = 0.0,$$

154
$$y_r(0) = \frac{q_j}{(1 + q_j)} m(l_b),$$

155
$$y_g(0) = 0.0.$$

148

156 *Feeding level functions*

157 For the intermediate and low feeding-levels, we assume sigmoid function:

158

$$F = f_1 + f_2 X(l, l_1, l_2).$$

159

The feeding-level starts at level f_1 and gradually shifts following function X with length to $f_1 +$

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f_2 . The shift starts at l_1 and at length l_2 the shift is halfway. With $l_1 = 0.39$ cm and $l_2 = 30$ cm,

161

we define the intermediate feeding level function as $F_{int} = 0.7 + 0.25 X(l, 0.39, 30)$ and the low

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feeding level function as $F_{low} = 0.55 + 0.35 X(l, 0.39, 30)$ (Figure S1B).

163

Model parameters

164

Parameters and their values are listed in Table S2. The parameter values used by van Leeuwen

165

et al. [3] are based on Baltic Sea cod. To represent Atlantic cod in the North Sea, we adjust the

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length at maturation (l_m), adult target condition (q_a) and the size-dependent functions for

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fisheries retention, energy expenditure for metabolic maintenance, and digestion time (Figure

168

S1A-C). The derivation of these parameter values is described below. Otherwise, we use the

169

parameter values as given in van Leeuwen et al. [3].

170

The metabolic rate and the digestion time are temperature dependent. The average annual

171

North Sea SST is ~ 10 °C [4]. Assuming the sea bottom is about 2 degrees colder, we use 8 °C for

172

the derivation of the size-dependent metabolic rate and the digestion time. The metabolic rate is

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derived from oxygen consumption of cod reared in light at 8 °C [5]. We convert dry-to-wet body-

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mass with conversion factor 5 [see data in 5], oxygen to grams energy using an oxy-calorific

175

coefficient of $13.6 \text{ kJ} \cdot \text{g}^{-1} \text{ O}_2$ [6] and energy-to-wet-weight ratio of 7 kJ/g [7]. To compress

176

annual activity into $Y = 250$ days (Table S2), we rescale the metabolic rate parameters to $\beta =$

177

0.9124 and $\alpha = 0.022$ (Figure S1A). The digestion time G is derived from data of maximum

178

growth in body mass in Atlantic cod, fed ad lib in captivity [8]. For a situation with maximum

179

feeding, the growth in body mass equals the weight increase (N) in the model; $N = \sigma \frac{1}{G} - T$. We

180

derive digestion time scaling parameters $\varepsilon = 270.651$ and $\theta = -2.389$ from the growth rate

181

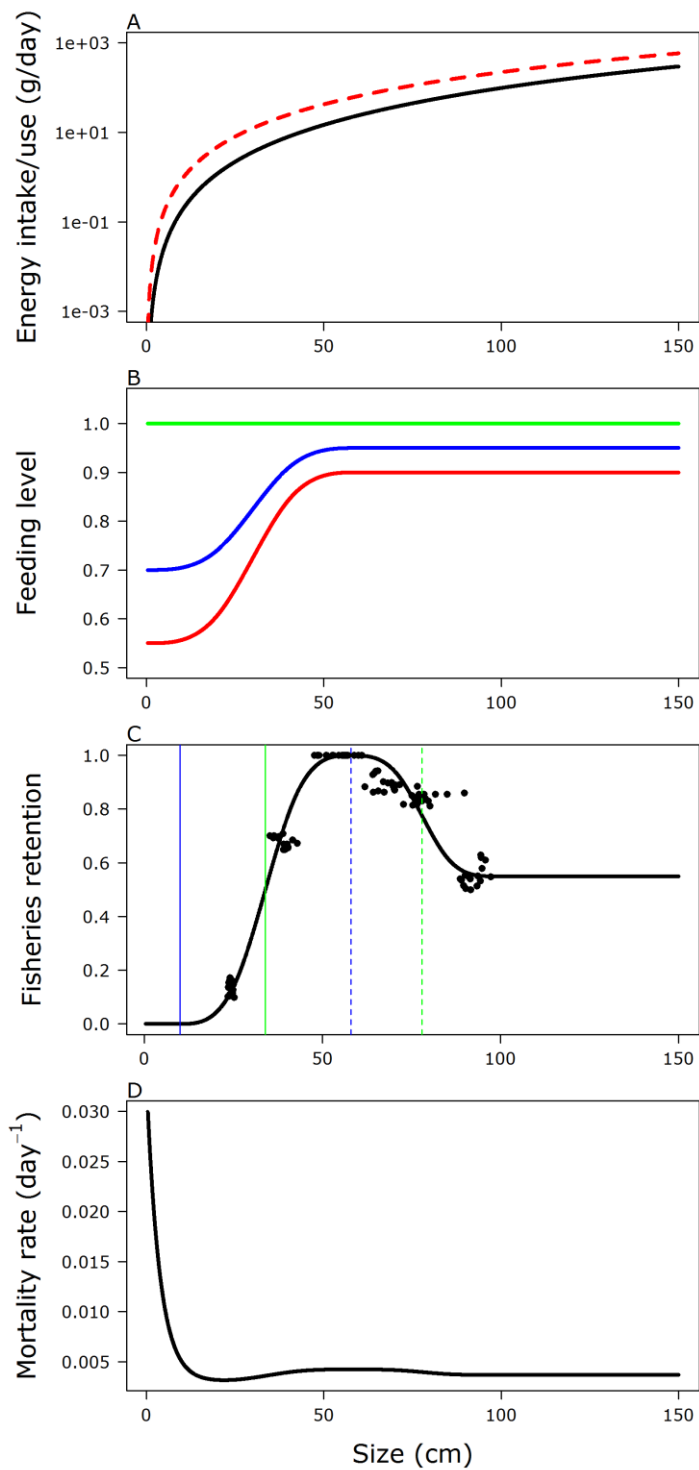
between $l = 0.39 - 150$ cm at 8 °C, using a year with length $Y = 250$ days, $\sigma = 0.6$ (Table S2)

182

and the metabolic rate above (Table S2, Figure 1B).

183 Fisheries retention is defined as the ratio between the age-specific annual fisheries mortality
184 rate and the maximum fisheries mortality rate in the same year. We use data from the ICES
185 fisheries assessments between 2000-2016 [9]. Each age class is converted to a mean annual size-
186 at-age based on the mean size per age class in the years 2000-2016 of the cod IBTS-survey data
187 [10]. We use a double s-shaped function for the relationship between fisheries retention and
188 body size and fitted the curve to the data points manually (Figure S1C). Fisheries retention starts
189 at $l_v = 10$ cm and reaches 50% of its maximum at $l_{vh} = 34$ cm. From $l_{vd} = 58$ cm, fisheries
190 retention gradually decreases to the average retention in the last age class (6+ years old) $\rho =$
191 0.55 and reaches 50% of this level at $l_{vdh} = 78$ cm. Over the last ten years, the maximum
192 fisheries mortality for North Sea cod ranged between 0.35 (2016) and 0.75 (2006; [9]). We use a
193 daily mortality rate of $\frac{0.31}{Y} = 0.00124 \text{ d}^{-1}$, which is the currently advised maximum cod
194 fisheries mortality [11].

195 The typical size at maturation of Atlantic cod varies across regions; we use $l_m = 62$ cm, which is
196 the length where 50% of Atlantic cod in the North Sea are reported mature by Thorsen et al.
197 [12]. The adult target body condition is taken as $q_a = 1.2$ based on a mean 24% somatic weight
198 loss after spawning in Atlantic cod from the Gulf of St. Lawrence [13].



199

200 *Figure S1 (A) Maintenance costs (black solid line) and maximum ingestion rate $\frac{1}{G}$ (red dashed line), (B) feeding level in case*

201 *of high (green), intermediate (blue) and low (red) food availability, (C) fisheries retention data (black dots; 2000-2016, 65),*

202 *the length at the start of the increase l_v (blue solid line), at 50% of the increase l_{vh} (green solid line), at the start of the*

203 *decline l_{vd} (blue dashed line) and 50% of the decline l_{vdh} (green dashed line) of fisheries retention and fisheries retention*

204 *implemented in the model (black line) and (D) mortality rate as a function of body size implemented in the model.*

205

206 *Table S1 Potential consequences of anthropogenic noise for individual level processes. The observed effects of anthropogenic noise on fish (row names on the left) were chosen based on a*
 207 *meta-analysis of anthropogenic noise experiments with fish by Cox et al. [1]. We show an overview of potential consequences of the observed effects of anthropogenic noise for individual level*
 208 *processes (column names on top) that have been documented for fish. Colours of the cells indicate the quality of evidence (orange – documented consequences for individual level process;*
 209 *yellow – logical consequence but no consequences have been documented, or, only anecdotal studies of consequences for individual level process; blue – no short-term consequences for*
 210 *individual level process have been documented)*

Observations \ Consequences	Energy expenditure	Food intake	Mortality	Reproductive output
Stress (Higher levels of cortisol)	✓ Elevated cortisol increases the metabolic rate [14].	✓ Elevated cortisol reduces food intake [15,16].	? Stress may lead to mortality [17].	✓ Elevated cortisol decreases fertilization rate [18], and, leads to deformities in fish larvae [19].
Foraging behaviour (Decrease of foraging behavior, such as: food consumption, foraging efficiency, and discrimination error of prey items.)	✓ More energy spent to come to the same food intake [20,21].	✓ Lower food intake due to less successful foraging or less time spent foraging [22].	× No direct consequences documented.	× No direct consequences documented.
Movement behaviour (Increase of movement related behaviour, such as: adjusted swimming depth, directional changes, schooling adjustments, swimming speed.)	✓ Schooling reduces the energetic costs of movement [23] and faster swimming costs more energy [24].	× No direct consequences documented.	× No direct consequences documented.	× No direct consequences documented.
Auditory system (Changes in the auditory system, such as the hearing threshold.)	× No direct consequences documented.	? Lower prey detection.	? Lower predator detection.	? Cod uses sounds for mate finding [25].

Symbol	Unit	Description	Value	Source	Derivation
Model variables					
a	[d]	Age			
x	[g]	Structural mass			
y_r	[g]	Reserves			
y_g	[g]	Gonads			
s	-	Survival probability			
R_0	-	Reproductive output			
Derived model variables					
l	[cm]	Length	$m = \gamma l^\delta$		
w	[g]	Total body mass	$w = x + y_r + y_g$		
m	[g]	Length-based mass	$m = x(1 + q_j)$		Structural mass and liver weight
Parameters					
Υ	[d]	Length of growing season	250	[3]	
τ_r	[d]	Day of spawning decision	200	[3]	
a_b	[d]	Age of first feeding	22	[3]	Atlantic cod, Norway
l_b	[cm]	Length at birth	0.39	[3]	Atlantic cod, Norway
l_s	[cm]	Characteristic length mortality	3.68	[3]	
l_m	[cm]	Maturation length	62	[12]	Length 50% mature (North Sea cod)
l_v	[cm]	Size of start fishing vulnerability	10	[9]	North Sea cod
l_{vh}	[cm]	Size of 50% fishing vulnerability	34	[9]	North Sea cod
l_{vd}	[cm]	Size of start decrease fisheries vulnerability	58	[9]	North Sea cod

l_{vdh}	[cm]	Size of %50 decrease fisheries vulnerability	78	[9]	North Sea cod
ρ	-		0.55	[9]	North Sea cod
q_j	-	Juvenile condition target	0.7	[3]	
q_a	-	Adult condition target	1.2	[13]	Atlantic cod, NW Atlantic
γ	$[(g\ cm^{-1})^\delta]$	Length-weight scaling constant	0.01	[3]	Atlantic cod, NE Atlantic
δ	-	Length-weight scaling exponent	3.0	[3]	Atlantic cod, NE Atlantic
ε	$[d\ cm^{-\theta}g^{-1}]$	Digestion time scaling constant	270.651	[5,8]	Derived from maximum growth rate, metabolic rate and $I(l)$
θ	-	Digestion time scaling exponent	-2.389	[5,8]	Derived from maximum growth rate, metabolic rate and $I(l)$
α	$[g^{1-\beta}d^{-1}g^{-1}]$	Metabolic rate scaling constant	0.022	[5]	Derived from oxygen consumption of Atlantic cod at 8 C
β	-	Metabolic rate scaling exponent	0.9124	[5]	Derived from oxygen consumption of Atlantic cod at 8 C
σ_0	-	Conversion efficiency	0.6	[3]	Across fish species
σ_r	-	Gonad-offspring conversion efficiency	0.5	[3]	Female offspring only
μ_e	$[d^{-1}]$	Egg mortality	0.03	[3]	
μ_s	$[d^{-1}]$	Size-dependent mortality constant	0.03	[3]	
μ_0	$[d^{-1}]$	Size-independent background mortality	0.003	[3]	

μ_v	[d ⁻¹]	Fishing mortality	0.00124	[11]	North Sea cod fisheries, FMSY
F_{high}			1.0		
F_{int}			0.7 + 0.25 X(L, 0.39,30)		Length dependent
F_{low}			0.55 + 0.35 X(L, 0.39,30)		Length dependent
ψ_D		Acoustic mortality multiplier	0 - 10		
ψ_B		Acoustic reproductive failure multiplier	0 - 1		
ψ_T		Acoustic energy expenditure multiplier	0 - 1		
ψ_I		Acoustic feeding failure multiplier	0 - 1		

213

214 *References used in Appendix A*

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