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Published in:
Oikos

Link to article, DOI:
[10.1111/oik.08739](https://doi.org/10.1111/oik.08739)

Publication date:
2022

Document Version
Peer reviewed version

[Link back to DTU Orbit](#)

Citation (APA):
van Deurs, M., Persson, A., Nilsson, A., & Jørgensen, C. (2022). Fish resist temptation from junk food: State-dependent diet choice in reproductive Atlantic cod (*Gadus morhua*) facing seasonal fluxes of lipid-rich prey. *Oikos*, 22(7), Article e08739. <https://doi.org/10.1111/oik.08739>

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TITLE:

Fish resist temptation from junk food: State-dependent diet choice in reproductive Atlantic cod (*Gadus morhua*) facing seasonal fluxes of lipid-rich prey

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1 ABSTRACT:

2 In ecological sciences, animal diets are often simplified to “resources” or “caloric quantities”.

3 However, in the present study, we investigated the optimal foraging strategy of Atlantic cod (*Gadus*
4 *morhua*) when both macro- and micro-nutritional requirements are accounted for. Proteins cannot
5 be synthesized from fatty acids, so the proteins for gonad development must come from other
6 dietary sources. In addition, micronutrients are required in smaller quantities. For example, for cod,
7 arachidonic acid (ARA) acts as a micronutrient precursor for prostaglandins, which is important for
8 reproduction. We formulated a dynamic state-dependent model to make predictions about optimal
9 diet choice and foraging behavior. We applied the model to a case study in the strait between
10 Denmark and Sweden. The model predicted that energy acquired from dietary protein should be
11 twice that acquired from lipids, with a small increase in the lipid requirements when gonads are
12 growing. The model also predicted that the “energy sparing effect of lipids” made it beneficial to
13 engage in risky foraging activity to supplement a lean diet with a little bit of fat. When we
14 constructed the model to also optimize ARA uptake, the cod consumed relatively more ARA-rich
15 crabs in the months prior to spawning, despite the otherwise poor energetic value of this prey. In
16 support of the model predictions, field observations indicated that lipid stores reached a peak
17 shortly after the arrival of the lipid-rich migrating herring and the fatty acid signal of these herring
18 were evident in the liver of nearly all cod. Three month later, only half of the cod contained the
19 herring-derived fatty acid signal, supporting the predicted shift in prey type prior to spawning. From
20 these model predictions and field observations, we conclude that, also in the wild, nutritional
21 requirements can be at least as important as pure energy acquisition.

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24 KEY WORDS:

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25 Arachidonic acid; boom and bust; food quality; *Gadus morhua*; *Clupea harengus*; *Carcinus*
26 *maenas*; nutritional quality; protein; lipids; forage fish; macro-nutrients; micro-nutrients

27

28 INTRODUCTION

29 It is well known from public health and animal husbandry that a nutritious and balanced diet is key
30 to health, growth, and reproduction, but less is known about how animals achieve this in the wild.

31 In ecological sciences, animal diets are often simplified to “resources” or “caloric quantities” (e.g.
32 Emlen 1966; MacArthur and Pianka 1966; Charnov 1976), where lipids are often in focus because
33 of their high energy density (e.g., Lawson et al. 1998). Lipid tissue can be virtually free of water
34 and can store ten times as much energy per mass compared to glycogen or protein, but while lipids
35 (and carbohydrates) are great energy carriers they lack the amino acids required to synthesize new
36 tissue during growth. The disciplines of animal husbandry and human nutrition are therefore to a
37 lesser extent concerned with caloric quantities, and instead emphasize the relative proportions of the
38 different macronutrients, where proteins and lipids jointly characterize diet quality, and the
39 inhibitory consequences of micronutrient deficiencies are carefully studied and accounted for.

40 In contrast to what is known about husbandry and human wellbeing (Southgate et al. 1991;
41 Kestemont et al. 1996), the ecological and evolutionary implications of the qualitative aspects of
42 food are largely unknown, although recent studies (mainly from insects) have indicated that some
43 animals are in fact capable of modulating feeding strategies to fulfil both macro- and micro-
44 nutritional needs (Cruz-Rivera and Hay 2000; Simpson and Raubenheimer 2000; Jensen et al. 2012;
45 Ravenscraft and Bogg 2016). However, it is reasonable to hypothesize that diet choices have
46 evolved as foraging preferences in all wild animals that actively seek food, including changes
47 following from shifts in nutritional requirements related to ontogeny. This was first theoretically

48 pointed out by Pulliam (1975), who modelled foragers that maximize caloric intake given dietary
49 requirements for micronutrients. Later Simpson et al. (2004) demonstrated this by constructing a
50 theoretical fitness landscape over nutrient space and proposed how needs for multiple nutrients can
51 be assessed experimentally. More recently, Schmitt et al. (2016) demonstrated how elephant
52 carrying capacity is better estimated when micro-nutrients and diet breadth is accounted for.

53 A reproductive female cod can spawn a total volume of eggs that exceeds her own body volume.
54 While a lot of this volume is water provided for osmoregulation during the pelagic egg stage,
55 typically 20% of a female's pre-spawning body volume is highly specialized gonadal mass
56 dominated by proteins, and at spawning further proteins are mobilized from her muscle tissue
57 (Kjesbu et al. 1996). While lipids are great for fueling energy, cod lack the ability to synthesize
58 proteins from fatty acids, so the proteins for gonad development must come from other dietary
59 sources, often intermediary stored as muscle tissue. Macronutrients are only one side of a well-
60 balanced diet. Essential micronutrients are required in smaller quantities to facilitate and underpin a
61 range of physiological functions. Some fatty acids can for instance serve as precursors for signaling
62 molecules, but fish may lack the ability to biosynthesize these fatty acids. For cod, this is the case
63 for arachidonic acid (ARA), which acts as a precursor for prostaglandins and therefore plays an
64 essential role in the late phase of gonad maturation and ovulation (Røjbek et al. 2014). A particular
65 effect of this fatty acid is that it increases the survival of spawned eggs and larvae, at least during
66 the first 8 days post-hatching (Røjbek et al. 2014), giving rise to the hypothesis that ARA
67 concentration have a direct fitness consequence to which females may have evolved specific
68 foraging strategies.

69 In this paper, we modeled the optimal foraging strategy of Atlantic cod (*Gadus morhua*) and
70 compared with physiological and behavioral observations. We formulated a dynamic state-
71 dependent model that accounts for macro- and micro-nutritional requirements while identifying the

72 optimal combination of diet choice and foraging activity across seasons in a “boom and bust”
73 situation (Jackson 2008). We applied the model to a particularly telling case in the narrow Øresund
74 Strait between Denmark and Sweden, at the entrance to the Baltic Sea, allowing us to compare
75 model predictions with various sources of observational data, such as intra-annual trends in lipid
76 reserves and prey composition inferred by fatty acid trophic markers (FATM) (Dalsgaard et al.
77 2003; van Deurs et al. 2016).

78 In the Øresund Strait, adult herring (*Clupea harengus*) (belonging to the Western Baltic spring
79 spawning herring stock) stop in late summer on their migration from the feeding grounds in the
80 eastern North Sea and remain in Øresund in great numbers until winter, when they continue
81 migration towards spawning grounds in the Western Baltic Sea (van Deurs and Ramkær 2007). The
82 cod feasts on these seasonally available herring, which are rich in lipids and contain significant
83 amounts of protein and therefore could be perceived ideal building material for gonads, except that
84 herring is almost void of ARA (van Deurs et al. 2016). For the remainder of the year, a staple in the
85 cod diet is shore crabs (*Carcinus maenas*) and to some extent other invertebrates, lean bottom-
86 dwelling fish, and smaller local clupeids (Ljungberg 2013; van Deurs et al. 2016; Funk et al. 2021).
87 Such a benthic diet generally has more protein (and ARA from shore crabs), but less lipids than the
88 migrating herring. There is thus seasonality in both food availability and nutrient composition,
89 which likely has implications for cod physiology, behavior, and optimal diet composition.

90

91

92 METHODS

93

94 **Bioenergetic optimization model**

95 It is challenging to document and interpret dynamic changes in internal stores of metabolites over
96 time in the wild. We therefore constructed a bioenergetic model as a basis for refining hypotheses
97 and aiding interpretation of relevant field and laboratory data. The model assumes that foraging
98 behavior has evolved as an adaptation whereby prey are selected for their specific nutrient
99 composition to fulfill the requirements of growth and reproduction. The basics of the bioenergetics
100 model is the same as used in Holt and Jørgensen (2014), which is built on the Wisconsin framework
101 (Hanson et al. 1997) and parameterized for Atlantic cod *Gadus morhua*. The model book-keeps
102 how energy flows from ingestion and digestion through to various metabolic purposes.
103 Numerically, the model is embedded into a dynamic programming framework (Houston and
104 McNamara 1999; Clark and Mangel 2000). This allows for identification of the optimal foraging
105 behavior (foraging activity and habitat choice) under the assumptions that increased foraging
106 activity incurs reduced survival through risk-taking behaviors. We refer to Holt and Jørgensen
107 (2014) for details and describe here the model's main characteristics and how it has been modified
108 for this analysis. Figure 1 shows an overview of the model.

109 Four key processes were identified in the literature and incorporated into the model: (1) Somatic
110 growth requires protein as building blocks, whereas gonad growth relies mainly on protein, but also
111 to some degree lipids (Kjesbu 1989; Kjesbu et al. 1991). (2) The energetic cost of digesting proteins
112 is higher than for lipids as more bioenergetic conversions are necessary (Kieffer et al. 1998). (3)
113 Metabolic processes are fueled more by lipids than by proteins, as long as lipids are available in the

114 diet or from lipid stores, also known as the “protein sparing effect of lipids” (Bromley 1980). (4)
115 Dietary arachidonic acid (ARA) improves egg quality and offspring survival (Røjbek et al. 2014).
116 We considered a female cod of 55 cm body length (L) and a lean Fulton’s condition factor of 0.85,
117 which corresponds to a somatic body weight (W_{somatic}) of 1414 g (i.e. the weight of a lean cod
118 without lipid stores and gonads and calculated as $W_{\text{somatic}} = 0.0085 \times L^3$). In the model, final gonad
119 size and composition is fixed. The cod is tasked with developing gonads corresponding to 20% of
120 W_{somatic} (i.e., ~280g) and with a protein content of 70% by the time of spawning in February
121 (Kjesbu 1989; Kjesbu et al. 1991; Hüsey 2011). ARA content in the gonads is considered to be
122 beneficial for fitness through its effect on egg and larval survival. Key to this model is how it keeps
123 track of the diet differences and differential usage of proteins versus lipids, and accounts for ARA
124 as an important micronutrient (Table 1). Survival emerges from a series of risk components that
125 vary with the cod’s habitat choice and foraging activity (through exposure to predators), its total
126 metabolic energy use (as escaping a predator is harder when exhausted), and the size of its energy
127 stores (proteins and lipids) and gonads (as fatter cod are less agile and enduring swimmers). The
128 model simulates one year in weekly time steps and maximizes the expected number of surviving
129 cod larvae.

130 Foraging activity φ is a behavioral trait that is optimized in the model. Through foraging,
131 individuals acquire a resource intake H [$\text{J} \cdot \text{week}^{-1}$]:

132 $H = \varphi \cdot B_{\text{SMR}}(W_{\text{somatic}}, T_{\text{std}})$ (Eq. 1)

133 where B_{SMR} is the standard metabolic rate (see Table 2), here calculated using a standard
134 temperature of $T_{\text{std}} = 10^\circ\text{C}$. The variable φ thus quantifies foraging activity in units of standard
135 metabolic rate of a lean fish and can easily be compared across body sizes.

136 Importantly, the model accounts for how the resource intake is split between nutrients n and keeps
137 track of these throughout acquisition and use. Thus,

138 $H_n = H \cdot c_{h,n}$ (Eq. 2a)

139 where H_n is intake [$\text{J} \cdot \text{week}^{-1}$] of nutrient type n , where $n = \text{proteins}$ or $n = \text{lipids}$, and $c_{h,n}$ is the
140 proportion of the energy sourced from habitat h , where $h = \text{benthic}$ or $h = \text{pelagic}$, that is of nutrient
141 type n (see Table 1 for habitat properties). We only consider lipids and proteins, so in this model
142 $H = \sum_n H_n = H_{\text{proteins}} + H_{\text{lipids}}$. A fraction of the lipid intake consists of ARA, which is book-
143 kept separately [$\text{J} \cdot \text{week}^{-1}$]:

144 $H_{\text{ARA}} = H_{\text{lipids}} \cdot c_{h,\text{ARA}}$ (Eq. 2b)

145 The type of nutrient has consequences for digestibility D (Table 1) and thus stomach evacuation
146 rate E and digestion costs B_{SDA} (detailed in Table 2). The nutrients are also stored in different parts
147 of the body, and they are differentially utilized for various purposes. Accounting for the various

148 types of metabolic expenditures and how lipids can be selectively used to cover purely energetic
149 needs, the net intake N available for growth and reproduction [J week^{-1}] of the two nutrients are:

$$150 \quad N_{\text{proteins}} = H_{\text{proteins}} - B \cdot (1 - c_{\text{lipiduse}}) \quad (\text{Eq. 3a})$$

$$151 \quad N_{\text{lipids}} = H_{\text{lipids}} - B \cdot c_{\text{lipiduse}} \quad (\text{Eq. 3b})$$

152 Here $B = B_{\text{SMR}} + B_{\phi} + B_{\text{SDA}} + B_{\Delta G}$ is the total metabolic cost, composed of standard metabolic
153 rate, cost of foraging, cost of digestion (or specific dynamic action), and gonad biosynthesis costs,
154 respectively, all with unit [J week^{-1}] (see Table 2 for details of each). The factor at the end,
155 $c_{\text{lipiduse}}=0.6$, defines the proportion of these energetic costs that are covered by lipids, the rest by
156 proteins, in line with the protein-sparing effect of lipids (Bromley 1980).

157 The problem we focused on is how to acquire the optimal level and composition of nutrients to
158 prepare for spawning, accordingly a few simplifications were made. Since fish are indeterminate
159 growers, we forced the model with a background protein uptake (from foraging) to sustain a 0.5%
160 weight increase per week. This is mainly to avoid an unrealistic outcome where foraging activity is
161 driven solely by the need to grow gonads. This also means that somatic growth is assumed to be
162 constant and not influenced by foraging decisions. In addition, we made the simplification that 40%
163 of final gonad weight is generated the last two weeks before spawning, while the rest is laid down at
164 a constant rate for the 25 weeks prior to that. Consumed and digested proteins and lipids that are not
165 metabolized or used for growth end up in protein and lipid stores. From one time step (week) to the
166 next, protein stores S_{proteins} and lipid stores S_{lipids} change as:

$$167 \quad S_{n,t+1} = S_{n,t} + N_n - \Delta W_t \cdot c_{W,n} - \Delta G_t \cdot c_{G,n} \quad (\text{Eq. 4})$$

168 where ΔW_t and ΔG_t are the somatic and gonadal growth [g], respectively, during timestep t , while
169 the different coefficients c are the required amounts of protein and lipid synthesized into one gram

170 of new tissue. Again, n refers to nutrient type and is either ‘proteins’ or ‘lipids’. If stores become
171 negative, it is assumed that the model fish dies. In cod, nearly all lipids are stored in the liver, which
172 constitutes up to 10% of the total weight of the fish and has a fat content of 40-80% depending on
173 environmental factors and season (Holdway and Beamish 1984; Marshall et al. 1999), while
174 proteins are stored as increased white muscle mass.

175 Predators going after mature cod in the present study area are practically limited to seals and
176 cormorants (MacKenzie et al. 2002; Östman et al. 2013) and cod as large as 55 cm (as used in the
177 model presented here) are almost exclusively predated by seals. However, these predators can be
178 plentiful, posing a considerable threat to the individual cod. The model accounts for how foraging
179 and metabolic use have consequences for risk taking and expected survival. Following the cod
180 model in Holt and Jørgensen (2014), also this model assumes that risk is higher for smaller fish,
181 when foraging behavior is intense, when metabolic rate is near the limit for aerobic respiration, and
182 when total body weight is high relative to body length because that increases drag and lowers
183 escapement speeds (see Table 2 for details). Very low condition could also have negative effect on
184 escapement speed due to critically reduced muscle mass. This may have been relevant if modeling
185 cod in the Eastern Baltic Sea (Neuenfeldt et al. 2020). However, in the present case, avoiding

186 bulkiness was considered a more important driver of model dynamics. Total mortality rate [year⁻¹]

187 is thus

$$188 \quad M = M_{\text{fixed}} + M_{\text{foraging}} + M_{\text{respiration}} + M_{\text{condition}} + F \quad (\text{Eq. 5})$$

189 and survival per week is $S = e^{-M/52}$. In the present study, we used a background mortality (M_{fixed})

190 of 0.02 year⁻¹ and a fishing mortality (F) of zero, although, some sports angling and small scale

191 commercial fishing (no trawling only sporadic gill net fishing) takes place in the area.

192 In line with the surprisingly strong effect of ARA on survival of cod eggs and larvae documented

193 by Røjbek et al. (2014), we assume that the fitness of the individual female is either proportional to

194 ARA content in the gonads at time of spawning (ARA effect on) or independent of it (ARA effect

195 off). We assume that the cod have no capacity to prioritize ARA over other fatty acids, so the ARA

196 content of the gonads reflects the ARA concentration in the cod's lipid stores at the time of

197 transferring lipids to the gonads (a little bit every week and more towards the end). Further, the cod

198 cannot selectively retain ARA, so when lipids are used for metabolic purposes, ARA is also used in

199 proportion to its current concentration in the lipid stores (as indicated in Figure 1). The model then

200 optimizes habitat choice and foraging intensity throughout the year prior to spawning by

201 maximizing expected survival multiplied with the ARA effect when it was included.

202 The model was parameterized to mimic the situation for cod in the Øresund Strait between

203 Denmark and Sweden, where adult cod feed predominantly on shore crab and herring (van Deurs et

204 al. 2016). We focus on adult female cod and their choice of feeding in a pelagic habitat with fat

205 herring versus a benthic habitat with shore crabs and lean fish. The fraction of the lipid pool

206 consisting of ARA is much higher in shore crabs compared to herring (van Deurs et al. 2016). Shore

207 crab was available all year in the model, whereas fat herring was available in low abundance until

208 September (we will refer to this as the background herring level) and in high abundance from

209 September until spawning commences in February (Hüssy 2011) (the Western Baltic spring
210 spawning herring overwinter in Øresund). To explicitly investigate how prey quality affected prey
211 choice, the energy intake acquired per unit foraging activity was the same for crab and herring from
212 September and onward (but remember that foraging activity is a dynamic behavior optimized by the
213 model so it could vary depending on motivation and utility). Food was available all year, except that
214 it was assumed that no feeding takes place around spawning time (Fordham and Trippel 1999).
215 Parameters and key equations are listed in Tables 1 and 2. The MATLAB® code is available as an
216 online appendix.

217

218 **Field observations and fatty acid markers**

219 Seasonal patterns predicted by the model were compared to seasonal dynamics in the hepatosomatic
220 index (HSI; here calculated as the weight of the liver divided by $W_{somatic}$ and then multiplied by
221 100%) of cod caught in the Øresund Strait from 2014-2016. These cod ranged from 50 to 80 cm and
222 cod from 50 cm and up are supposedly capable of preying on the migratory herring. For further
223 details see van Deurs et al. (2016). The liver content of two fatty acid trophic markers (FATM)
224 (20:1n-9 + 22:1n-11) and ARA (22:4n-6; in this case also used as a FATM) in cod from November
225 and late January ($n = 12$ and 15 , respectively) were analyzed to allow FATM-based estimates of the
226 prey composition ingested by cod in the months prior to the sampling dates. Further details about
227 fatty acid extraction and the specific fatty acids selected for the FATM analysis can be found in van
228 Deurs et al. (2016). The following equations were formulated to mechanistically derive the

229 expected FATM liver levels (ρ [area % of total lipid pool]) for a range of hypothetical prey ratios
230 (R):

$$231 \quad \rho = \frac{(R\beta_1\alpha_1 + \beta_2\alpha_2)}{(R\beta_1 + \beta_2)} \cdot 100 \quad (\text{Eq. 6})$$

232 In the present case we solved the equation for different diet ratios between herring and shore crab
233 (i.e. $R = \text{herring[g]}/\text{crab[g]}$) and we estimated ρ for 20:1n-9+22:1n-11 and ARA, separately. The
234 parameters α_1 and α_2 are ρ of fish that have been feeding exclusively on either prey type 1 or prey
235 type 2 (in this case herring or shore crab, respectively). The parameters β_1 and β_2 are the lipid
236 proportion of prey type 1 and 2, respectively (i.e. the weight of the total lipid pool in the prey
237 divided by the weight of the prey). The equation assumes the following: (1) only two prey types
238 dominate the diet; (2) selected FATMs differ between prey types; and (3) selected FATMs are
239 stored in the liver and used in a non-selective manner. Parameter values were derived from figure 4
240 and 6 in van Deurs et al. (2016) ($\alpha_1=0.005$, $\alpha_2=0.03$, $\beta_1=0.2$, $\beta_2=0.03$).

241

242

243 RESULTS

244

245 Seasonal dynamics of lipid reserves predicted by the model mimicked the field observations, both
246 in terms of timing and maximum reserve levels (Fig. 2ab). For example, the predicted maximum
247 lipid store matches observed liver weights in November, assuming that ~70% of the liver weight
248 consists of lipids (Lie et al. 1986). As illustrated in Figure 2b, herring arrives in September and stay
249 plentiful for at least four months. However, the model predicted that the advantage of feeding

250 exclusively on the lipid-rich herring (i.e. high lipid-protein ratio) is temporary, and already after six
251 weeks it becomes optimal to feed mainly on lean shore crabs (i.e. low lipid-protein ratio), switching
252 only occasionally to herring. This feeding behavior emerges from the model despite a constant and
253 high availability of herring from September and until spawning in February-March. In order to test
254 the realism of this prediction, we conducted fatty acid trophic marker analysis (FATM) and
255 interestingly the results supported the model prediction (Fig. 2c). More than 90% of the livers from
256 cod >50 cm sampled in November suggested that cod had been feeding mainly on the migrating
257 herring since their arrival. In contrast, in late January, only half of the cod sampled could be
258 recognized as herring eaters, whereas the other half carried a different FATM signal, indicating that
259 a large proportion of the prey ingested since November comprised shore crab or other prey types
260 with a FATM composition similar to that of shore crabs.

261 Another noteworthy pattern emerging from the model is that maximum feeding activity (and
262 thereby also risk taking) takes place prior to the arrival of the migrating herring (Fig. 2a). By the
263 time the herring arrive, foraging activity decreases, indicating that moderate foraging activity for
264 nine weeks (6 weeks in September/October and another 3 weeks spread out over the following 3-4
265 months) is sufficient to accumulate enough lipids in the liver to complete gonad maturation and
266 spawning (Fig. 2a). It should here be noted that consumption rates in the model never exceeded 2/3
267 of maximum consumption, confirming that energy acquisition was regulated by the emergent
268 optimal behavior.

269 In order to investigate whether the predicted patterns in feeding behavior and internal condition
270 were context specific, we manipulated timing, quantity, and nutritional quality of the herring
271 overabundance in the model as an ecological sensitivity analysis (Fig. 3). In all scenarios, cod were
272 predicted to have an annual period of reserve rebuilding (lipid stores increased) and a period of
273 reserve utilization (lipid stores decreased). However, the model predicted that the liver would be

274 enlarged and the maximum occurring earlier if time between arrival of migrating herring and
275 spawning increased (i.e. early arrival of migrating herring), and in particular if the herring
276 overabundance was more transient (i.e. brief residence time). Cod who had access to an
277 overabundance of herring earlier and for a longer time-period were the least active and therefore
278 also suffered from the lowest mortality. Reducing the lipid content of the herring or removing the
279 overabundance from September and onward (i.e. no arrival of migrating herring), resulted in a
280 marked reduction in cod survival probability, stemming from an increased foraging activity leading
281 to increased mortality (i.e. M_{foraging} increased).

282 Since the main source of ARA was the shore crabs and not the herring, ARA uptake increased when
283 the overabundance of herring was either completely removed (i.e. no arrival of migrating herring)
284 or if the residence time of the migrating herring was brief. However, all model simulations
285 described so far assume that cod possess no information about the ARA content of available prey
286 types. In the last model run, we therefore allowed the cod to optimize the intake of not only dietary
287 lipids and proteins, but also based on its current ARA content, which directly affects survival of the
288 eggs produced. Because ARA constitutes a relatively high proportion of the lipids in shore crabs,
289 the model predicted that cod should partially trade off the physiological benefits of lipids (i.e. the
290 protein sparing effect of lipids and the higher conversion efficiency) for the improved egg survival
291 due to a higher ARA content, by feeding to a lesser extent on herring and more on shore crab (Fig.
292 3).

293 Prior to the arrival of migrating herring, the model predicts that a balanced diet was maintained by
294 feeding mainly on shore crab, but mixed with a bit of herring consumed at reduced foraging activity
295 (Fig. 2a). This indicates that a diet consisting of shore crab alone results in a lipid deficit, which
296 translates to a high survival cost per unit of energy acquired through foraging (i.e. M_{foraging}
297 increased). This incentivized the cod to consume from the low background herring availability in

298 the model (i.e. lower energy gain per unit time invested in foraging, but higher energy gain per unit
299 of survival loss). Lastly, optimal dietary lipid:protein ratio (quantified in terms of energy content,
300 not mass) was identified by employing the model with equal access to shore crab and herring
301 throughout the year. The optimal lipid:protein ratio was found to be somewhere between 0.5 and
302 0.7, increasing from 0.5 in spring to 0.7 in August, where it remained until spawning (Fig. 4a).
303 Switching off the “protein sparing effect of lipids” in the model resulted in a ~15% decline in the
304 optimal lipid-protein ratio, indicating the importance of this physiological mechanism in the model
305 (Fig. 4b).

306 A sensitivity analysis on 13 parameters and model assumptions showed that changing a single
307 parameters in the model by $\pm 20\%$ had only minor effects on the 7 model outputs assessed (Table
308 3). Only 18% of the 13 \times 7 recalculated model outputs changed $> 5\%$ and only 8% changed more
309 than 10%. Most of the larger changes to model output were expected. For example, changing
310 foraging mortality influenced survival and changing fish size influenced lipid stores, protein stores,
311 and prey consumption. Most noteworthy, was the relatively large effect on a wider range of model
312 outputs that resulted from changing the proportion of protein in gonads and the energetic cost of
313 digesting protein.

314

315

316 DISCUSSION

317 Seasonal overabundance of prey and predation hotspots are probably common phenomena in the
318 wild (Cotte and Simard 2005; Temming et al. 2007). One of the most widespread examples of such
319 “boom and bust” (Jackson 2008) dynamics in food webs comes with the relatively small
320 zooplanktivorous fish species occupying the pelagic zone (often referred to as forage fishes or small

321 pelagics). It is through those species that the main flow of energy from secondary producers to
322 larger fish, birds, and mammals pass (Cury et al. 2000; Alder et al. 2008). However, while they are
323 extremely abundant and often rich in energy, they are typically also migratory and display distinct
324 seasonal patterns in abundance and nutritional quality (Hislop et al. 1991; van Deurs et al. 2011;
325 Slotte and Fiksen 2000; Behrens et al. 2006), leading to a phenology where predators are presented
326 with the opportunity to feast on an overabundance of lipid-rich forage fish for a limited period of
327 time every year. The present study is to our knowledge the first to consider nutritional requirements
328 in relation to marine boom and bust dynamics.

329

330 **Model predictions of prey choice dynamics in the default “boom and bust” scenario:**

331

332 Previous studies have linked the condition of Atlantic cod (*Gadus morhua*) and cod stock
333 productivity with periodic availability of lipid-rich forage fish (e.g. Marshall et al. 1999; Eero et al.
334 2012; Rose and O'Driscoll 2002). The annual peak in HSI of cod range from 4 to 10% in the wild
335 (e.g. Schwalme and Chouinard 1999; Lloret and Rätz 2000; Skjæraasen et al. 2009), although
336 higher values have been reported in aquaculture studies (Lie et al. 1986). HSI higher than 9% is
337 considered abnormal (Jobling 1988). By combining detailed bioenergetics modeling with optimal
338 foraging theory, we here found that nutritional imbalances are likely to arise if cod only maximize
339 expected energy acquisition rather than paying attention also to the differential physiological
340 functioning of protein and lipids. The seasonal patterns in behavior and physiological state
341 emerging from our model aligned well with observational data. Both model and data indicated that
342 lipid stores reached a peak after the arrival of migrating herring and the size of the modeled lipid
343 stores matched the observations remarkably well. Hence, the model clearly suggested that the

344 observed increase in lipid stores was initiated by the arrival of herring followed by six weeks where
345 the cod chose to feed solely on the herring. After this period the cod shifted back to shore crab as
346 the main prey, despite an overabundance of herring that lasted for several months. This indicates
347 that the cod in our model only exploited the overabundance of herring moderately and for a limited
348 period of time, and thereafter favored prey with a relatively higher content of protein rather than
349 maximizing energy (lipid) intake. This diet shift away from herring prior to spawning may not
350 apply to cod in general. Michalsen et al. (2008) analyzed stomachs from two cod stocks in Lofoten
351 area during the spawning period and found that some fish fed on the herring even when they were in
352 a spawning state.

353 Before the herring period, when lipids stores had not yet been built, cod in the model constantly
354 needed to supplement a crab diet with small amounts of herring from the low background herring
355 availability. By doing so, they could reduce their exposure to predators per unit of energy acquired,
356 and this effect was markedly stronger when the model allowed the cod to preferentially utilize lipids
357 for energetic metabolic demands while saving proteins for growth of somatic and gonadal tissue.
358 However, it should be noted that the mortality associated with foraging in the present model was a
359 simplification compared to Strand and Huse (2007), where mortality rate was explicitly modeled as
360 a function of water column position and light levels. Building such mechanisms into the present
361 model may have reduced the profitability of preying on herring in the pelagic zone.

362

363 **Fatty acids trophic markers as indicators of prey choice dynamics in the field:**

364

365 The apparent indication of a shift from herring to shore crab when lipid stores are rebuilt matches
366 well with the observations made using fatty acid trophic markers (FATMs). All cod livers sampled

367 in November were low in ARA and rich in herring-related FATMs, 20:1(n-9) and 22:1(n-11),
368 presumably acquired from calanoid copepods and euphausiids on the herring feeding grounds 500-
369 800 km away in the North Sea (Ackman et al. 1970; Falk-Petersen et al. 2009). In contrast, 50% of
370 the cod livers from three months later did not possess the herring-derived FATM signal, indicating
371 that these fish stopped feeding on the migrating herring a couple of months prior to capture. Instead,
372 the FATM profiles of these fish mimicked that of the much leaner shore crab.

373

374 **The effect of manipulating the characteristics of the “boom and bust” situation:**

375

376 Manipulating timing, quantity, and nutritional quality of the herring overabundance in the model
377 did not change the general picture of a single annual peak in lipid stores followed by a period of
378 reserve depletion toward spawning. In contrast, maximum lipid stores and the date at which this
379 maximum was reached changed according to the environmental forcing implemented in the model.
380 Contexts resulting in an early peak in stored lipids also yielded a higher maximum level. Cod
381 accumulated lipids even when the herring overabundance was left out of the model. However, in

382 such a situation a marked decrease in survival probability was observed, as compensatory foraging
383 activity was required to account for the reduced availability of fat prey.

384

385 **The potential role of dietary ARA for prey choice dynamics in the model:**

386

387 ARA is a precursor for eicosanoids, such as prostaglandins (that play a role in the late phase of
388 gonad maturation and ovulation). In a controlled experiment, increasing dietary ARA for female
389 cod from 1 to 4 mg g⁻¹ resulted in a doubling of the number of eggs produced and increased larval
390 survival, at least during the first 8 days (Røjbek et al. 2014). The relative amount of ARA in crab
391 lipids is much higher than in the herring lipids. Therefore, when we re-constructed the model to also
392 optimize ARA levels in the cod gonads, the cod were still predicted to accumulate lipid stores
393 (although to a slightly lesser degree), but also to consume relatively more crabs in the months prior
394 to spawning. It is, however, important to say that an underlying model assumption was that number
395 of viable larvae is a robust measure of fitness. While the highest daily rates of natural mortality
396 takes place among eggs and early larvae (Bogstad et al. 2016), the total mortality of eggs and larvae
397 may still be lower than that of the much longer juvenile phase. We can therefore not be certain that
398 number of surviving larvae is a suitable fitness proxy.

399

400 **The optimal diet:**

401

402 Another general pattern emerging from the model was the ratio between herring and shore crab in
403 the diet, which was nearly invariable between environmental contexts. However, when lipid content
404 of the herring was reduced, herring in the diet increased, illustrating how the cod optimizes its
405 foraging strategy to meet nutritional requirements. We used the model to predict that the optimal
406 diet is one where energy from lipids divided by the energy from proteins (i.e. the lipid:protein ratio
407 quantified by energy content in Joules) lies somewhere between 0.5 and 0.7. This is remarkably
408 close to what growth studies have shown to be the optimal ratio for growing cod, namely ~0.5
409 (recalculated from Grisdale-Helland et al. 2008). In comparison, the lipid:protein ratio of shore crab
410 is ~0.4 and that of fat herring is ~2.3. Hence, neither of the two prey types qualifies as an optimal
411 diet. The lipid:protein ratio of the migratory herring is far above the optimum and the ratio of crabs
412 slightly below, explaining why the model predicted that cod in the model supplemented a crab diet
413 with small amounts of lipid-rich herring also before the migratory herring arrives. During the period
414 of herring overabundance, lipid reserves fill up where after cod forage mainly on shore crabs, with
415 the metabolic lipid requirements being supplied by the reserves. The model furthermore predicted
416 that an individual preparing for spawning by growing gonads should benefit from a higher
417 lipid:protein ratio than an individual prioritizing somatic growth.

418

419 **The protein sparing effect of lipids:**

420

421 Besides the need for lipids as building blocks in egg synthesis, the “protein sparing effect of lipids”
422 included in the model was what drove the need for a lipid supplement. This mechanism is well
423 known in aquaculture, where it has been shown that metabolic energy costs are to a larger extent
424 covered by lipids than by proteins, as long as there are sufficient dietary lipids available. Hence,
425 aquaculture researchers have experimented with feed formulas that optimize this mechanism
426 without fattening the fish, to make sure the more expensive protein in the feed is retained as new
427 tissue rather than being respired. The high energy density of lipids makes it more suitable for
428 storing energy. However, as food was available year round in the model, except during spawning
429 (when they are assumed uninterested in food), storing energy was not a prerequisite for avoiding
430 starvation mortality. Hence, our study showed that moderate energy storage is still beneficial, even
431 if periods of starvation are not anticipated nor extensive migrations undertaken, as it reduces the
432 amount of protein that is metabolized and lost. This is also true for periods during which dietary
433 lipid is scarce, as it enables cod to target prey with relatively more protein and channel that towards
434 gonad maturation and growth.

435

436 **General conclusions:**

437

438 A few studies (mainly on Arthropoda) have indicated that that even animals with simple cognitive
439 systems are to some degree capable of adjusting feeding strategies to avoid micronutrient limitation
440 (e.g. Jensen et al. 2012; Ravenscraft and Bogg 2016). Furthermore, it has been proposed that also
441 variation in life histories influence the ability to regulate micro-nutritional intake. Take for example
442 Cruz-Rivera and Hay (2000) who suggested, based on amphipod experiments, that sedentary
443 species benefitted more from substituting food quantity for food quality than the more mobile

444 species. Adding to this limited line of research, we here utilized observations from a boom and bust
445 system with a dynamic bioenergetics model to disentangle key trade-offs related to food quality.
446 The model predicted, for example, that in an ideal situation, energy required from dietary protein
447 should be twice that required from dietary lipids, with a small increase in lipid requirements when
448 gonads are growing. The model also predicted that this balance is worth striving for, as the “energy
449 sparing effect of lipids” made it possible to reduce overall foraging risk. At the same time, a diet too
450 rich in lipids would interfere with growth and reproduction, and both the model and the
451 observations of fatty acid profiles indicated that cod were able to resist the temptation from junk
452 food. Hence, storing lipids when opportunities arise is a significant fitness asset, even if periods of
453 starvation are not expected to occur, but only up to a point. From this we conclude that, also in the
454 wild, paying attention to a nutritionally balanced diet is important and should replace a focus purely
455 on energy acquisition, and that evaluating the associated survival costs and benefits are necessary to
456 interpret what is the right balance between lipids and proteins.

457

458 ACKNOWLEDGEMENT

459 The research was funded by Danish council of independent research DFF-4002-00114 and the BONUS
460 INSPIRE project supported by BONUS (Art 185), funded jointly by the EU and the Swedish research council
461 Formas.

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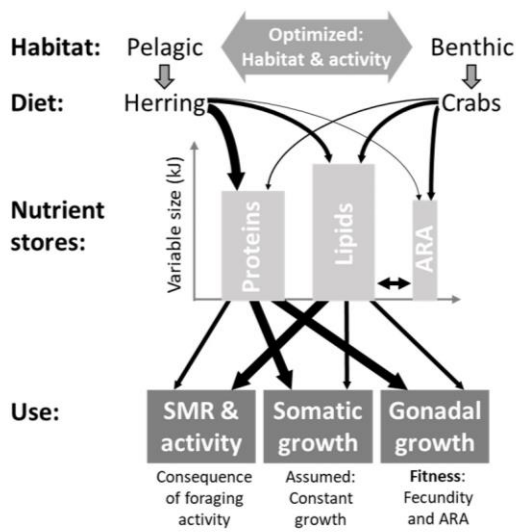
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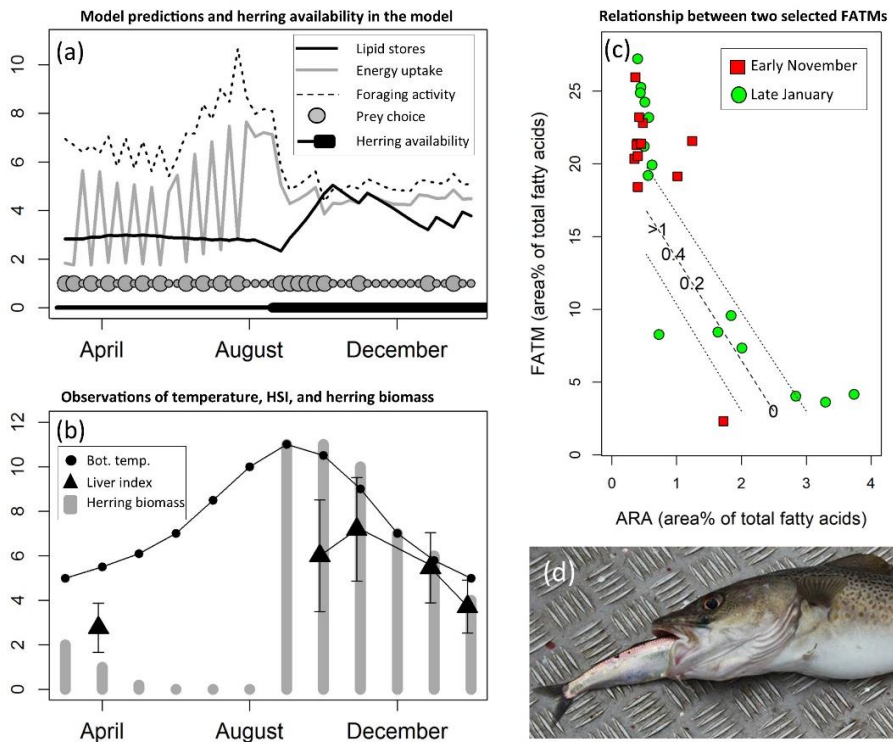
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600 Figure 1. Overview of the diet choice model from habitat choice through physiological flows
601 through to consequences for fitness. The two habitats differ in terms of the dominant prey and their
602 nutrient composition, which through digestion fills (curved arrows) internal nutrient stores of the
603 cod. These stores in turn fuel metabolism, growth, and reproduction (grey boxes), which differ in
604 their nutrient requirements. Metabolism can rely more heavily on lipids. Somatic growth requires
605 abundant proteins. Gonadal growth requires abundant proteins, plus that arachidonic acid (ARA)
606 increases offspring survival greatly. A key challenge is how ARA cannot be selectively stored or

607 utilized, but is mixed with other lipids when used, so that a high ARA content is beneficial when
608 gonads grow most intensely. The model is run in weekly time steps.

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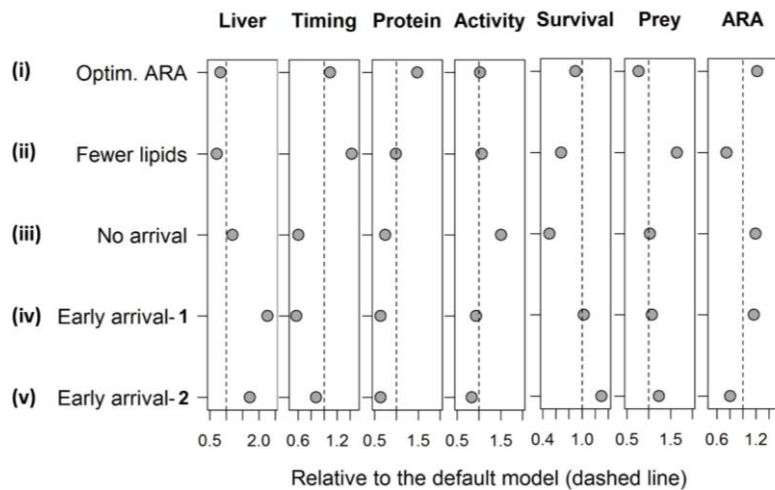
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612 Figure 2. Relating simulated data (a) to field observations (b & c). (a): Simulated data was extracted
613 from the default model, which represents an adult female cod (*Gadus morhua*) feeding on shore

614 crab (*Carcinus maenas*) and herring (*Clupea harengus*) in the Øresund Strait. The graphs show the
615 modeled weekly energy uptake [$10^2 \text{ kJ week}^{-1}$] (grey line), lipid stores [lipids as a percentage of
616 somatic body weight, W_{somatic}] (solid black line), foraging activity [levels from 1-15] (dashed black
617 line), and prey choice (shore crab: small bubbles; herring: large bubbles). The thick horizontal line
618 at the bottom of the plotting window indicates availability of herring in the model (i.e. the migrating
619 herring population arrives in late summer leading to more than a tripling of the herring biomass).
620 Reproduction takes place at the end of the simulated time period, which runs until 28th February.
621 Energy uptake is proportional to foraging activity and therefore also predation risk (i.e. high energy
622 uptake equals high risk). (b): Seasonal patterns in the Øresund Strait of average (± 1 s.d.) HSI
623 [hepatosomatic index; liver weight as percentage of W_{somatic}] (triangles), herring biomass [10^3 tons]
624 (grey columns) (reproduced from Nielsen et al. 2001), and local bottom temperature [$^{\circ}\text{C}$] (black
625 dots connected by line) (adapted from Henriksen 1969). (c): Relationship between the proportions
626 of two selected FATMs in cod livers. Colored data points are observed FATM levels in cod livers
627 sampled in November (red squares) and January/February (green circles) (ARA on the x-axis and
628 20:1n-9+22:1n-11 on the y-axis [area % of total fatty acids]). Dashed lines is the predicted FATM
629 levels [area % of total fatty acids] (ρ in eq. 6) for a range of hypothetical mass ratios between
630 herring and shore crab (R in eq. 6). R are superimposed along the dashed line, allowing visual
631 resolving of diet compositions from observed FATM levels in cod livers. Dotted lines represent ± 1
632 standard deviation applied to α -parameters in eq. 1. (d): Photograph of a cod caught unintentionally
633 while angling for herring in the Øresund Strait in October 2014.

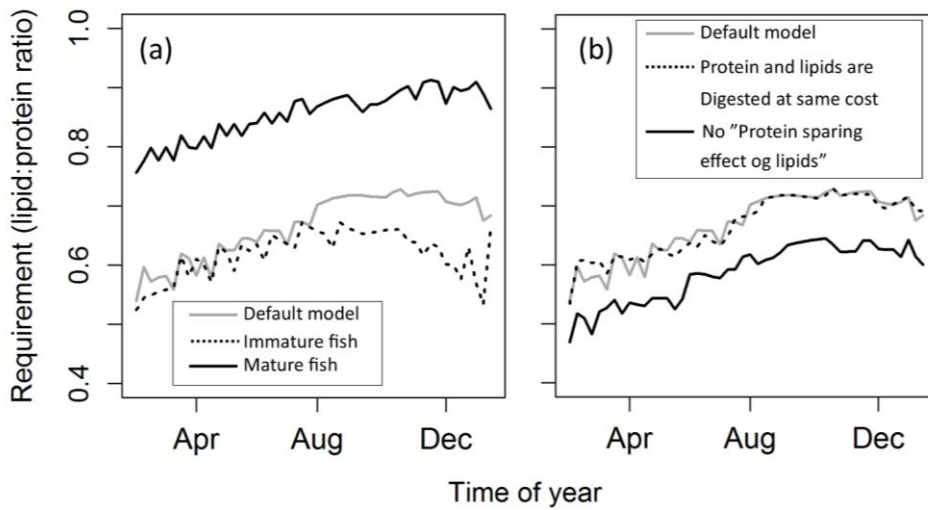


634

635 Figure 3. How timing and nutritional quality of herring arriving to the Øresund Strait in late
636 summer affected reserve dynamics, prey choice, and egg quality determined by ARA of modeled
637 reproductive female cod. Five specific scenarios were investigated by modifying the default model.
638 These included: (i) the hypothetical scenario where we assume that cod is “aware” of the
639 reproductive benefits of the high ARA levels in shore crab and optimizes prey choice accordingly
640 (ii) fewer lipids in the herring (i.e. reduced mean size in the herring population would lead to
641 reduced lipid concentrations (van Deurs et al. (2016)) (iii) no arrival of migratory herring (only the
642 background herring abundance also applied in the default scenario); (iv) earlier arrival by three
643 months, but a shortened residence time (Early arrival-1); and (v) earlier arrival of migrating herring
644 by three months and no shortened residence time (Early arrival-2). Results are presented relative to
645 the default model presented in Figure 2a, which is represented by the vertical dashed line in each
646 plot window. In total, seven different metrics, describing the physiological and behavioral
647 characteristics, were explored: (from left to right) maximum amount of lipids stored at any one time

648 (Liver), timing of when maximum lipid stores is achieved (Timing), amount of protein stored at the
649 end of the simulation period (Protein), foraging activity (Activity), survival probability (Survival),
650 preference for herring over shore crab (Prey), and ARA levels at the end of the simulation period
651 (ARA).

652



653

654 Figure 4. Model predictions of macro-nutritional requirements of dietary lipids and proteins and the
655 sensitivity to assumptions made about the life history and physiology. Requirement is given as the
656 lipid:protein ratio, where quantities are given in units of joules (i.e. required lipids[J] per
657 proteins[J]). (a): Predicted requirement derived from the default model (grey line) compared to the
658 predicted requirement of an immature fish with no gonad development (dashed line) and a mature
659 fish growing at half the rate applied in the default model (black line). (b): Predicted nutritional
660 requirement derived from the default model (grey line) compared to the predicted requirement from
661 a model where the energetic cost associated with digesting lipids is the same as for proteins (instead

662 of being higher for protein) (dashed line) and from a model where the protein sparing effect of
 663 lipids is switched off (metabolic energy is drawn from lipid and protein stores in proportion to store
 664 size, in contrast to lipids being preferentially used, if available, for metabolic energy (black line).

665

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668

669 **Table 1. Habitat and prey characteristics** with parameter values used in the model. Overall
 670 energy density and the percentage of energy coming from lipids and proteins respectively are
 671 rounded values derived from own laboratory analyses and calculations (conducted using the same
 672 samples as used in van Deurs et al. (2016)). Percentage of ARA is similar to what is presented in
 673 van Deurs et al. (2016). Digestibility rates are approximated from information given in Andersen
 674 (2012).

Property	Habitat h	
	Pelagic	Benthic
Dominant prey	Herring	Shore crabs
Prey presence	September until spawning	Always
Energy density ρ_h [J g^{-1}]	5000	2000
Energy in the form of lipids, $c_{h,\text{lipids}}$	70%	30%
Energy in the form of proteins, $c_{h,\text{proteins}}$	30%	70%

ARA as part of lipids, $c_{h,ARA}$	0.5%	7%
Digestibility d_h [-]	-0.168	-0.403

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677 Table 2. Additional equations for the bioenergetic model. Equation numbering continues from text to avoid ambiguity.

Eq.	Explanation	Equation	Parameters and source
7)	Max stomach evacuation rate [J week ⁻¹]	$E_h = D_h \cdot L^{1.3} \exp(0.083T_h \rho_h^{-0.085}) \sqrt{W_{\text{gut}}}$	Index h indicates habitat, D is digestibility of the typical diet in each habitat [-] and ρ [Jg ⁻¹] energy density of prey (Table 2), L [cm] is body length, W_{gut} [g] max weight of a full gut; assumed to be 10% of the somatic body weight (W_{somatic} [g]). From Andersen (2012).
8a)	Standard metabolic rate [J week ⁻¹]	$B_{\text{SMR}} = \exp\left(23.9 - \frac{5020}{T+273.15}\right) \cdot W_{\text{somatic}}^{0.75}$	Temperature T [°C] and somatic body weight W_{somatic} [g]. Modified from results in Clarke and Johnston (1999).
8b)	Energetic cost of foraging [J week ⁻¹]	$B_\phi = 0.15 \cdot H$	Set to fixed proportion of food intake H (H is defined in Eq. 2a). From Holt and Jørgensen (2014).

8c)	Energetic cost of digestion [J week ⁻¹]	$B_{\text{SDA}} = H_{\text{proteins}} \cdot c_{\text{SDA,proteins}} + H_{\text{lipids}} \cdot c_{\text{SDA,lipids}}$	Varies depending on nutrient, with $c_{\text{SDA,proteins}}=0.14$ and $c_{\text{SDA,lipids}}=0.04$. From Kieffer et al. (1998).
8d)	Energetic cost of gonad biosynthesis [J week ⁻¹]	$B_{\Delta G} = \Delta G \cdot c_{\text{G,biosynthesis}}$	Mass of new gonads grown is ΔG , $c_{\text{G,biosynthesis}}$ is the biosynthesis cost per gram of new gonad tissue (excluding the new tissue itself, which is accounted for separately).
9)	Max aerobic metabolism [J week ⁻¹]	$A = [218 \cdot T^{(-0.015T+1.062)} + 380] \cdot W_{\text{somatic}}^{0.75}$	Adapted from Claireaux et al. (2000)
10a)	Foraging-related mortality [year ⁻¹]	$M_{\text{foraging}} = 0.015 \cdot \varphi^2$	Mortality rate due to exposure to predators while foraging is modulated as a fixed proportion of the foraging activity φ squared. From Holt and Jørgensen (2014).

10b)	Mortality due to aerobic limitation [year ⁻¹]	$M_{\text{respiration}} = 0.20 \cdot \left(\frac{B_{\phi}}{A}\right)^3$	Mortality rate when total metabolic rate approaches total aerobic capacity. From Holt and Jørgensen (2014).
10c)	Mortality due to bulky shape [year ⁻¹]	$M_{\text{condition}} = 0.05 \cdot \left(\frac{100 \cdot W_{\text{actual}}}{L^3}\right)^3$	Mortality rate that accelerates as Fulton's condition factor increases. W_{actual} is the actual body weight (i.e. incl. protein stores, lipid stores, and gonads) as opposed to W_{somatic} . Adapted from formula in Holt and Jørgensen (2014).

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680 **Table 3. Sensitivity analysis of model parameters.** Numbers represent the percentage change in
 681 model estimate as a result of changing the model parameter by $\pm 20\%$. Note that the values are the
 682 average of the change observed when reducing and increasing the parameter by 20%, respectively.
 683 Model estimates are the same as in figure 3. Only the most imprecise model parameters (i.e.
 684 rounded values from “qualified best guesses”) were included in the sensitivity analysis.

Type	Description	Abbreviation	Liver	Protein	Activity	Prey	ARA	Survival	Timing
Structural	Fish Length	L	60.5	59.4	0.9	15.4	2.8	1.9	3.0
Structural	Target gonad size	none	4.8	10.8	1.7	5.4	2.8	4.9	9.1
Structural	Proportion of protein in gonads by energy	none	6.0	7.9	0.7	6.7	4.2	1.6	6.1
Bioenergetics	Energetic cost of digesting protein	$C_{SDA,proteins}$	2.7	5.3	4.3	9.0	5.6	11.6	7.6
Bioenergetics	Energetic cost of digesting lipids	$C_{SDA,lipids}$	2.3	5.0	1.1	2.7	1.4	1.4	1.5
Mortality	Background natural mortality	M_{fixed}	0.0	0.0	0.0	0.0	0.0	0.5	0.0
Mortality	Mortality due to aerobic limitations	Coefficient of 0.20 in $M_{respiration}$	0.6	3.5	0.8	1.7	1.4	4.1	1.5
Mortality	Foraging related mortality	Coefficient of 0.015 in $M_{foraging}$	0.6	3.7	1.1	1.9	1.4	19.0	1.5
Mortality	Mortality due to bulky shape	Coefficient of 0.05 in $M_{condition}$	0.9	0.5	0.2	0.5	1.4	1.2	0.0

Prey	Digestibility crab	$d_{h(\text{crab})}$	2.8	1.7	0.9	3.9	1.4	1.5	0.0
Prey	Digestibility herring	$d_{h(\text{herring})}$	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prey	Proportion of ARA in crab lipids	$C_{h(\text{crab}),\text{ARA}}$	0.0	0.0	0.0	0.0	18.1	0.0	0.0
Prey	Proportion of ARA in herring lipids	$C_{h(\text{herring}),\text{ARA}}$	0.0	0.0	0.0	0.0	1.4	0.0	0.0

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