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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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4137, DK-2800 Kgs. Lyngby, Denmark: mvd@aqua.dtu.dk 1 ABSTRACT: In ecological sciences, animal diets are often simplified to "resources" or "caloric quantities". 2 3 However, in the present study, we investigated the optimal foraging strategy of Atlantic cod (Gadus morhua) when both macro- and micro-nutritional requirements are accounted for. Proteins cannot 4 be synthesized from fatty acids, so the proteins for gonad development must come from other 5 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 Denmark and Sweden. The model predicted that energy acquired from dietary protein should be 10 twice that acquired from lipids, with a small increase in the lipid requirements when gonads are 11 growing. The model also predicted that the "energy sparing effect of lipids" made it beneficial to 12 engage in risky foraging activity to supplement a lean diet with a little bit of fat. When we 13 constructed the model to also optimize ARA uptake, the cod consumed relatively more ARA-rich 14 crabs in the months prior to spawning, despite the otherwise poor energetic value of this prey. In 15 support of the model predictions, field observations indicated that lipid stores reached a peak 16 shortly after the arrival of the lipid-rich migrating herring and the fatty acid signal of these herring 17 were evident in the liver of nearly all cod. Three month later, only half of the cod contained the 18 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.

- 22
- 23
- 24 KEY WORDS:

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Arachidonic acid; boom and bust; food quality; *Gadus morhua*; *Clupea harengus*; *Carcinus 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 to health, growth, and reproduction, but less is known about how animals achieve this in the wild. 30 In ecological sciences, animal diets are often simplified to "resources" or "caloric quantities" (e.g. 31 Emlen 1966; MacArthur and Pianka 1966; Charnov 1976), where lipids are often in focus because 32 of their high energy density (e.g., Lawson et al. 1998). Lipid tissue can be virtually free of water 33 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 tissue during growth. The disciplines of animal husbandry and human nutrition are therefore to a 36 37 lesser extent concerned with caloric quantities, and instead emphasize the relative proportions of the different macronutrients, where proteins and lipids jointly characterize diet quality, and the 38 39 inhibitory consequences of micronutrient deficiencies are carefully studied and accounted for. In contrast to what is known about husbandry and human wellbeing (Southgate et al. 1991; 40 Kestemont et al. 1996), the ecological and evolutionary implications of the qualitative aspects of 41 food are largely unknown, although recent studies (mainly from insects) have indicated that some 42 animals are in fact capable of modulating feeding strategies to fulfil both macro- and micro-43 nutritional needs (Cruz-Rivera and Hay 2000; Simpson and Raubenheimer 2000; Jensen et al. 2012; 44 Ravenscraft and Bogg 2016). However, it is reasonable to hypothesize that diet choices have 45 46 evolved as foraging preferences in all wild animals that actively seek food, including changes following from shifts in nutritional requirements related to ontogeny. This was first theoretically 47

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).

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

90

#### 92 METHODS

## 93

#### 94 Bioenergetic optimization model

95 It is challenging to document and interpret dynamic changes in internal stores of metabolites over time in the wild. We therefore constructed a bioenergetic model as a basis for refining hypotheses 96 and aiding interpretation of relevant field and laboratory data. The model assumes that foraging 97 behavior has evolved as an adaptation whereby prey are selected for their specific nutrient 98 99 composition to fulfill the requirements of growth and reproduction. The basics of the bioenergetics model is the same as used in Holt and Jørgensen (2014), which is built on the Wisconsin framework 100 (Hanson et al. 1997) and parameterized for Atlantic cod Gadus morhua. The model book-keeps 101 102 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 McNamara 1999; Clark and Mangel 2000). This allows for identification of the optimal foraging 104 105 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 (2014) for details and describe here the model's main characteristics and how it has been modified 107 108 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 to some degree lipids (Kjesbu 1989; Kjesbu et al. 1991). (2) The energetic cost of digesting proteins 111 is higher than for lipids as more bioenergetic conversions are necessary (Kieffer et al. 1998). (3) 112

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 ( $W_{\text{somatic}}$ ) 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	$W_{\text{somatic}}$ (i.e., ~280g) and with a protein content of 70% by the time of spawning in February
121	(Kjesbu 1989; Kjesbu et al. 1991; Hüssy 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  $\varphi$  is a behavioral trait that is optimized in the model. Through foraging,

131 individuals acquire a resource intake H [J·week<sup>-1</sup>]:

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

- 133 where  $B_{\text{SMR}}$  is the standard metabolic rate (see Table 2), here calculated using a standard
- temperature of  $T_{\rm std} = 10^{\circ}$ C. The variable  $\varphi$  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  $H_n = H \cdot c_{h,n} \tag{Eq. 2a}$
- 139 where  $H_n$  is intake [J·week<sup>-1</sup>] of nutrient type *n*, where *n* = proteins or *n* = lipids, and  $c_{h,n}$  is the
- 140 proportion of the energy sourced from habitat h, where h = benthic or h = 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  $[J week^{-1}]$ :
- 144  $H_{ARA} = H_{lipids} \cdot c_{h,ARA}$  (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

types of metabolic expenditures and how lipids can be selectively used to cover purely energetic needs, the net intake N available for growth and reproduction [J week<sup>-1</sup>] of the two nutrients are:

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

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

Here  $B = B_{SMR} + B_{\phi} + B_{SDA} + B_{\Delta G}$  is the total metabolic cost, composed of standard metabolic 152 rate, cost of foraging, cost of digestion (or specific dynamic action), and gonad biosynthesis costs, 153 respectively, all with unit [J week<sup>-1</sup>] (see Table 2 for details of each). The factor at the end, 154 155 clipiduse=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 prepare for spawning, accordingly a few simplifications were made. Since fish are indeterminate 158 growers, we forced the model with a background protein uptake (from foraging) to sustain a 0.5% 159

weight increase per week. This is mainly to avoid an unrealistic outcome where foraging activity is driven solely by the need to grow gonads. This also means that somatic growth is assumed to be constant and not influenced by foraging decisions. In addition, we made the simplification that 40% of final gonad weight is generated the last two weeks before spawning, while the rest is laid down at a constant rate for the 25 weeks prior to that. Consumed and digested proteins and lipids that are not metabolized or used for growth end up in protein and lipid stores. From one time step (week) to the next, protein stores  $S_{\text{proteins}}$  and lipid stores  $S_{\text{lipids}}$  change as:

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

168	where $\Delta W_t$ and $\Delta G_t$ are the somatic and gonadal growth [g], respectively, during timestep <i>t</i> , 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

cormorants (MacKenzie et al. 2002; Östman et al. 2013) and cod as large as 55 cm (as used in the 176 177 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 and metabolic use have consequences for risk taking and expected survival. Following the cod 179 180 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 escapement speeds (see Table 2 for details). Very low condition could also have negative effect on 183 escapement speed due to critically reduced muscle mass. This may have been relevant if modeling 184 185 cod in the Eastern Baltic Sea (Neuenfeldt et al. 2020). However, in the present case, avoiding

bulkiness was considered a more important driver of model dynamics. Total mortality rate [year<sup>-1</sup>]

187 is thus

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

and survival per week is  $S = e^{-M/52}$ . In the present study, we used a background mortality ( $M_{\text{fixed}}$ ) of 0.02 year<sup>-1</sup> and a fishing mortality (F) of zero, although, some sports angling and small scale 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 by Røjbek et al. (2014), we assume that the fitness of the individual female is either proportional to 193 ARA content in the gonads at time of spawning (ARA effect on) or independent of it (ARA effect 194 195 off). We assume that the cod have no capacity to prioritize ARA over other fatty acids, so the ARA content of the gonads reflects the ARA concentration in the cod's lipid stores at the time of 196 197 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 optimizes habitat choice and foraging intensity throughout the year prior to spawning by 200 maximizing expected survival multiplied with the ARA effect when it was included. 201 202 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 herring versus a benthic habitat with shore crabs and lean fish. The fraction of the lipid pool 205 206 consisting of ARA is much higher in shore crabs compared to herring (van Deurs et al. 2016). Shore crab was available all year in the model, whereas fat herring was available in low abundance until 207 208 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 $^{\otimes}$ 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 index (HSI; here calculated as the weight of the liver divided by  $W_{\text{somatic}}$  and then multiplied by 220 100%) of cod caught in the Øresund Strait from 2014-2016. These cod ranged from 50 to 80 cm and 221 cod from 50 cm and up are supposedly capable of preying on the migratory herring. For further 222 details see van Deurs et al. (2016). The liver content of two fatty acid trophic markers (FATM) 223 (20:1n-9 + 22:1n-11) and ARA (22:4n-6; in this case also used as a FATM) in cod from November 224 225 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 fatty acid extraction and the specific fatty acids selected for the FATM analysis can be found in van 227 Deurs et al. (2016). The following equations were formulated to mechanistically derive the 228

expected FATM liver levels ( $\rho$  [area % of total lipid pool]) for a range of hypothetical prey ratios

230 (*R*):

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

In the present case we solved the equation for different diet ratios between herring and shore crab 232 233 (i.e. R = herring[g]/crab[g]) and we estimated  $\rho$  for 20:1n-9+22:1n-11 and ARA, separately. The 234 parameters  $\alpha_1$  and  $\alpha_2$  are  $\rho$  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  $\beta_1$  and  $\beta_2$  are the lipid proportion of prey type 1 and 2, respectively (i.e. the weight of the total lipid pool in the prey 236 divided by the weight of the prey). The equation assumes the following: (1) only two prey types 237 dominate the diet; (2) selected FATMs differ between prey types; and (3) selected FATMs are 238 stored in the liver and used in a non-selective manner. Parameter values were derived from figure 4 239 240 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

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

exclusively on the lipid-rich herring (i.e. high lipid-protein ratio) is temporary, and already after six 250 251 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 interestingly the results supported the model prediction (Fig. 2c). More than 90% of the livers from 255 cod >50 cm sampled in November suggested that cod had been feeding mainly on the migrating 256 257 herring since their arrival. In contrast, in late January, only half of the cod sampled could be recognized as herring eaters, whereas the other half carried a different FATM signal, indicating that 258 259 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 time the herring arrive, foraging activity decreases, indicating that moderate foraging activity for 263 264 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

spawning (Fig. 2a). It should here be noted that consumption rates in the model never exceeded 2/3
of maximum consumption, confirming that energy acquisition was regulated by the emergent
optimal behavior.

In order to investigate whether the predicted patterns in feeding behavior and internal condition were context specific, we manipulated timing, quantity, and nutritional quality of the herring overabundance in the model as an ecological sensitivity analysis (Fig. 3). In all scenarios, cod were predicted to have an annual period of reserve rebuilding (lipid stores increased) and a period of 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. $M_{\text{foraging}}$ 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 lipids and proteins, but also based on its current ARA content, which directly affects survival of the 287 288 eggs produced. Because ARA constitutes a relatively high proportion of the lipids in shore crabs, the model predicted that cod should partially trade off the physiological benefits of lipids (i.e. the 289 protein sparing effect of lipids and the higher conversion efficiency) for the improved egg survival 290 due to a higher ARA content, by feeding to a lesser extent on herring and more on shore crab (Fig. 291 292 3).

Prior to the arrival of migrating herring, the model predicts that a balanced diet was maintained by feeding mainly on shore crab, but mixed with a bit of herring consumed at reduced foraging activity (Fig. 2a). This indicates that a diet consisting of shore crab alone results in a lipid deficit, which translates to a high survival cost per unit of energy acquired through foraging (i.e.  $M_{\text{foraging}}$ 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 $\sim 15\%$ 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 parameters in the model by  $\pm$  20% had only minor effects on the 7 model outputs assessed (Table 307 308 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, and prey consumption. Most noteworthy, was the relatively large effect on a wider range of model 311 outputs that resulted from changing the proportion of protein in gonads and the energetic cost of 312 313 digesting protein.

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315

#### 316 DISCUSSION

- Seasonal overabundance of prey and predation hotspots are probably common phenomena in the
  wild (Cotte and Simard 2005; Temming et al. 2007). One of the most widespread examples of such
  "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	
001	
332	Previous studies have linked the condition of Atlantic cod (Gadus morhua) and cod stock
332 333	Previous studies have linked the condition of Atlantic cod ( <i>Gadus morhua</i> ) and cod stock productivity with periodic availability of lipid-rich forage fish (e.g. Marshall et al. 1999; Eero et al.
332 333 334	Previous studies have linked the condition of Atlantic cod ( <i>Gadus morhua</i> ) and cod stock productivity with periodic availability of lipid-rich forage fish (e.g. Marshall et al. 1999; Eero et al. 2012; Rose and O'Driscoll 2002). The annual peak in HSI of cod range from 4 to 10% in the wild
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332 333 334 335 336 337 338 339 340 341	Previous studies have linked the condition of Atlantic cod ( <i>Gadus morhua</i> ) and cod stock productivity with periodic availability of lipid-rich forage fish (e.g. Marshall et al. 1999; Eero et al. 2012; Rose and O'Driscoll 2002). The annual peak in HSI of cod range from 4 to 10% in the wild (e.g. Schwalme and Chouinard 1999; Lloret and Rätz 2000; Skjæraasen et al. 2009), although higher values have been reported in aquaculture studies (Lie et al. 1986). HSI higher than 9% is considered abnormal (Jobling 1988). By combining detailed bioenergetics modeling with optimal foraging theory, we here found that nutritional imbalances are likely to arise if cod only maximize expected energy acquisition rather than paying attention also to the differential physiological functioning of protein and lipids. The seasonal patterns in behavior and physiological state emerging from our model aligned well with observational data. Both model and data indicated that

343 stores matched the observations remarkably well. Hence, the model clearly suggested that the

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

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

362

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

364

The apparent indication of a shift from herring to shore crab when lipid stores are rebuilt matches 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 euphauciids 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	
575	

# 374 The effect of manipulating the characteristics of the "boom and bust" situation:

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

such a situation a marked decrease in survival probability was observed, as compensatory foraging 382 activity was required to account for the reduced availability of fat prey. 383 384 385 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 gonad maturation and ovulation). In a controlled experiment, increasing dietary ARA for female 388 cod from 1 to 4 mg g<sup>-1</sup> resulted in a doubling of the number of eggs produced and increased larval 389 390 survival, at least during the first 8 days (Røjbek et al. 2014). The relative amount of ARA in crab

lipids is much higher than in the herring lipids. Therefore, when we re-constructed the model to also 391 392 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 to spawning. It is, however, important to say that an underlying model assumption was that number 394 of viable larvae is a robust measure of fitness. While the highest daily rates of natural mortality 395 takes place among eggs and early larvae (Bogstad et al. 2016), the total mortality of eggs and larvae 396 397 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.

# 400 The optimal diet:

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 $\sim 0.5$
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.

419 The protein sparing effect of lipids:

Besides the need for lipids as building blocks in egg synthesis, the "protein sparing effect of lipids" 421 included in the model was what drove the need for a lipid supplement. This mechanism is well 422 423 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, aquaculture researchers have experimented with feed formulas that optimize this mechanism 425 without fattening the fish, to make sure the more expensive protein in the feed is retained as new 426 tissue rather than being transpired. The high energy density of lipids makes it more suitable for 427 428 storing energy. However, as food was available year round in the model, except during spawning (when they are assumed uninterested in food), storing energy was not a prerequisite for avoiding 429 430 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 amount of protein that is metabolized and lost. This is also true for periods during which dietary 432 433 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

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

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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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- 612 Figure 2. Relating simulated data (a) to field observations (b & c). (a): Simulated data was extracted
- 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, $W_{\text{somatic}}$ (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 ( $\pm 1$ s.d.) HSI
623	[hepatosomatic index; liver weight as percentage of $W_{\text{somatic}}$ ] (triangles), herring biomass [10 <sup>3</sup> tons]
624	(grey columns) (reproduced from Nielsen et al. 2001), and local bottom temperature [°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] ( $\rho$ 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 $\pm1$
632	standard deviation applied to $\alpha$ -parameters in eq. 1. (d): Photograph of a cod caught unintentionally
633	while angling for herring in the Øresund Strait in October 2014.















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).
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  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).

	Habitat <i>h</i>				
Property	Pelagic	Benthic			
Dominant prey	Herring	Shore crabs			
Prey presence	September until spawning	Always			
Energy density $\rho_h$ [J g <sup>-1</sup> ]	5000	2000			
Energy in the form of lipids, $c_{h,lipids}$	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 <i>d<sub>h</sub></i> [-]	-0.168	-0.403		

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

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

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

1	0b)	Mortality due to aerobic limitation [year <sup>-1</sup> ]	$M_{\rm respiration} = 0.20 \cdot \left(\frac{B_{\varphi}}{A}\right)^3$	Mortality rate when total metabolic rate approaches total aerobic capacity. From Holt and Jørgensen (2014).
1	0c)	Mortality due to bulky shape [year <sup>-1</sup> ]	$M_{\text{condition}} = 0.05 \cdot \left(\frac{100 \cdot W_{\text{actual}}}{L^3}\right)^3$	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).

680	Table 3. Sensitivi	ty analysis of mode	el parameters. Number	s represent the	percentage change in
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model estimate as a result of changing the model parameter by  $\pm 20\%$ . Note that the values are the

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.

rounded values from "qualified best guesses") were included in the sensitivity analysis.

Туре	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
	Proportion of protein in gonads								
Structural	by energy	none	6.0	7.9	0.7	6.7	4.2	1.6	6.1
	Energetic cost of digesting								
Bioenergetics	protein	$C_{\rm SDA, proteins}$	2.7	5.3	4.3	9.0	5.6	11.6	7.6
	Energetic cost of digesting								
Bioenergetics	lipids	$C_{\rm SDA, lipids}$	2.3	5.0	1.1	2.7	1.4	1.4	1.5
Mortality	Background natural mortality	M <sub>fixed</sub>	0.0	0.0	0.0	0.0	0.0	0.5	0.0
-	Mortality								
	due to aerobic	Coefficient of 0.20 in							
Mortality	limitations	$M_{ m respiration}$	0.6	3.5	0.8	1.7	1.4	4.1	1.5
Mortality	Foraging related mortality	Coefficient of 0.015 in	0.6	37	11	19	14	19.0	15
		rerroraging	0.0	5.7		1.5	1.4	15.0	1.5
	Mortality due to bulky	Coefficient of 0.05 in							
Mortality	shape	Mcondition	0.9	0.5	0.2	0.5	1.4	1.2	0.0

Prey	Digestibility crab	d <sub>h(crab)</sub>	2.8	1.7	0.9	3.9	1.4	1.5	0.0
Prey	Digestibility herring	d <sub>h(herring)</sub>	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prey	Proportion of ARA in crab lipids	Ch(crab),ARA	0.0	0.0	0.0	0.0	18.1	0.0	0.0
Prey	Proportion of ARA in herring lipids	Ch(herring),ARA	0.0	0.0	0.0	0.0	1.4	0.0	0.0