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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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In ecological sciences, animal diets are often simplified to 'resources' or 'caloric quantities'. 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 be synthesized from fatty acids, so the proteins for gonad development must come from other dietary sources. In addition, micronutrients are required in smaller quantities. For example, for cod, arachidonic acid (ARA) acts as a micronutrient precursor for prostaglandins, which is important for reproduction. We formulated a dynamic state-dependent model to make predictions about optimal 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 twice that acquired from lipids, with a small increase in the lipid requirements when gonads are growing. The model also predicted that the 'energy sparing effect of lipids' made it beneficial to engage in risky foraging activity to supplement a lean diet with a little bit of fat. When we constructed the model to also optimize ARA uptake, the cod consumed relatively more ARA-rich crabs in the months prior to spawning, despite the otherwise poor energetic value of this prey. In support of the model predictions, field observations indicated that lipid stores reached a peak shortly after the arrival of the lipid-rich migrating herring and the fatty acid signal of these herring were evident in the liver of nearly all cod. Three month later, only half of the cod contained the herring-derived fatty acid signal, supporting the predicted shift in prey type prior to spawning. From these model predictions and field observations, we conclude that, also in the wild, nutritional requirements can be at least as important as pure energy acquisition.

Keywords: arachidonic acid, boom and bust, *Carcinus maenas*, *Clupea harengus*, food quality, forage fish, *Gadus morhua*, lipids, macro-nutrients, micro-nutrients, nutritional quality, protein

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Introduction

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. In ecological sciences, animal diets are often simplified to 'resources' or 'caloric quantities' (Emlen 1966, MacArthur and Pianka 1966, Charnov 1976), where lipids are often in focus because of their high energy density (Lawson et al. 1998). Lipid tissue can be virtually free of water and can store ten times as much energy per mass compared to glycogen or protein, but while lipids (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 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 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, Kestemont et al. 1996), the ecological and evolutionary implications of the qualitative aspects of food are largely unknown, although recent studies (mainly from insects) have indicated that some animals are in fact capable of modulating feeding strategies to fulfil both macro- and micro-nutritional needs (Cruz-Rivera and Hay 2000, Simpson and Raubenheimer 2000, Jensen et al. 2012, Ravenscraft and Boggs 2016). However, it is reasonable to hypothesize that diet choices have 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 pointed out by Pulliam (1975), who modelled foragers that maximize caloric intake given dietary requirements for micronutrients. Later Simpson et al. (2004) demonstrated this by constructing a theoretical fitness landscape over nutrient space and proposed how needs for multiple nutrients can be assessed experimentally. More recently, Schmitt et al. (2016) demonstrated how elephant carrying capacity is better estimated when micronutrients and diet breadth is accounted for.

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

In this paper, we modeled the optimal foraging strategy of Atlantic cod *Gadus morhua* and compared with physiological and behavioral observations. We formulated a dynamic state-dependent model that accounts for macro- and micro-nutritional requirements while identifying the optimal combination of diet choice and foraging activity across seasons in a 'boom and bust' situation (Jackson 2008). We applied the model to a particularly telling case in the narrow Øresund Strait between Denmark and Sweden, at the entrance to the Baltic Sea, allowing us to compare model predictions with various sources of observational data, such as intra-annual trends in lipid reserves and prey composition inferred by fatty acid trophic markers (FATM) (Dalsgaard et al. 2003, van Deurs et al. 2016).

In the Øresund Strait, adult herring *Clupea harengus* (belonging to the Western Baltic spring spawning herring stock) stop in late summer on their migration from the feeding grounds in the 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 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 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-dwelling fish and smaller local clupeids (Ljungberg 2013, van Deurs et al. 2016, Funk et al. 2021). Such a benthic diet generally has more protein (and ARA from shore crabs), but less lipids than the migrating herring. There is thus seasonality in both food availability and nutrient composition, which likely has implications for cod physiology, behavior and optimal diet composition.

Methods

Bioenergetic optimization model

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 and aiding interpretation of relevant field and laboratory data. The model assumes that foraging behavior has evolved as an adaptation whereby prey are selected for their specific nutrient 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 (Hanson et al. 1997) and parameterized for Atlantic cod *Gadus morhua*. The model book-keeps how energy flows from ingestion and digestion through to various metabolic purposes. 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 behavior (foraging activity and habitat choice) under the assumptions that increased foraging 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 for this analysis. Figure 1 shows an overview of the model.

Four key processes were identified in the literature and incorporated into the model: 1) somatic 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 is higher than for lipids as more bioenergetic conversions are necessary (Kieffer et al. 1998). 3) Metabolic processes are
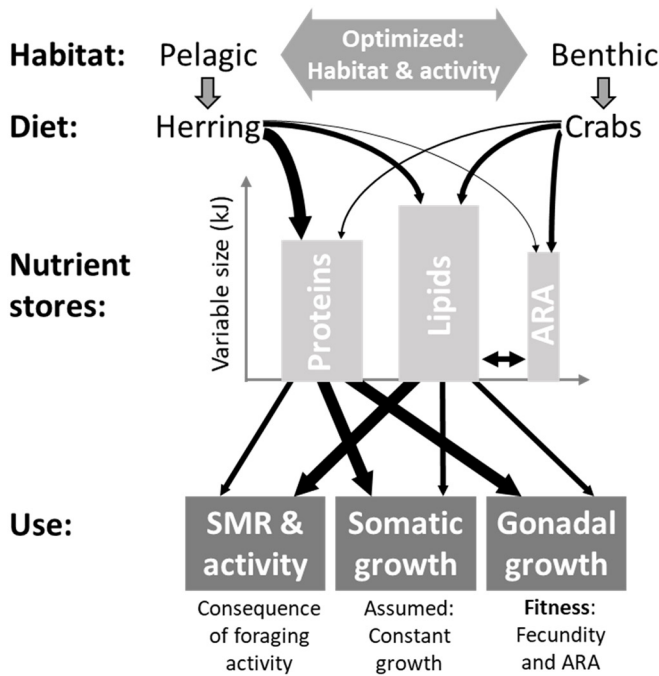

Figure 1. Overview of the diet choice model from habitat choice through physiological flows through to consequences for fitness. The two habitats differ in terms of the dominant prey and their nutrient composition, which through digestion fills (curved arrows) internal nutrient stores of the cod. These stores in turn fuel metabolism, growth and reproduction (grey boxes), which differ in their nutrient requirements. Metabolism can rely more heavily on lipids. Somatic growth requires abundant proteins. Gonadal growth requires abundant proteins, plus that arachidonic acid (ARA) increases offspring survival greatly. A key challenge is how ARA cannot be selectively stored or utilized, but is mixed with other lipids when used, so that a high ARA content is beneficial when gonads grow most intensely. The model is run in weekly time steps.

fueled more by lipids than by proteins, as long as lipids are available in the diet or from lipid stores, also known as the 'protein sparing effect of lipids' (Bromley 1980). 4) Dietary arachidonic acid (ARA) improves egg quality and offspring survival (Røjbek et al. 2014).

We considered a female cod of 55 cm body length (L) and a lean Fulton's condition factor of 0.85, which corresponds to a somatic body weight (W_{somatic}) of 1414 g (i.e. the weight of a lean cod without lipid stores and gonads and calculated as $W_{\text{somatic}} = 0.0085 \times L^3$). In the model, final gonad size and composition is fixed. The cod is tasked with developing gonads corresponding to 20% of W_{somatic} (i.e. ~280 g) and with a protein content of 70% by the time of spawning in February (Kjesbu 1989, Kjesbu et al. 1991, Hüssy 2011). ARA content in the gonads is considered to be beneficial for fitness through its effect on egg and larval survival. Key to this model is how it keeps track of the diet differences and differential usage of proteins versus lipids, and accounts for ARA as an important micronutrient (Table 1). Survival emerges from a series of risk components that vary with the cod's habitat choice and foraging activity (through exposure to predators), its total metabolic energy use (as escaping a predator is harder when exhausted), and the size of its energy stores (proteins and lipids) and gonads (as fatter cod are less agile and enduring swimmers). The model simulates one year in weekly time steps and maximizes the expected number of surviving cod larvae.

Foraging activity φ is a behavioral trait that is optimized in the model. Through foraging, individuals acquire a resource intake H (J week⁻¹):

$$H = \varphi \times B_{\text{SMR}}\left(W_{\text{somatic}}, T_{\text{std}}\right) \tag{1}$$

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

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

$$H_n = H \times c_{h,n} \tag{2a}$$

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

$$H_{\text{ARA}} = H_{\text{lipids}} \times c_{h,\text{ARA}} \tag{2b}$$

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

	Habitat h	
Property	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, $c_{h,\text{ARA}}$	0.5%	7%
Digestibility d_h (–)	−0.168	−0.403

The type of nutrient has consequences for digestibility D (Table 1) and thus stomach evacuation rate E and digestion costs B_{SDA} (detailed in Table 2). The nutrients are also stored in different parts 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^{-1}) of the two nutrients are:

$$N_{\text{proteins}} = H_{\text{proteins}} - B \times \left(1 - c_{\text{lipiduse}}\right) \tag{3a}$$

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})	$E_h = D_h \times L^{1.3} \exp\left(0.083 T_h \rho_h^{-0.085}\right) \sqrt{W_{\text{gut}}}$	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})	$B_{\text{SMR}} = \exp\left(23.9 - \dfrac{5020}{T + 273.15}\right) \times W_{\text{somatic}}^{0.75}$	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})	$B_\varphi = 0.15 \times H$	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})	$B_{\text{SDA}} = H_{\text{proteins}} \times c_{\text{SDA,proteins}} + H_{\text{lipids}} \times c_{\text{SDA,lipids}}$	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})	$B_{\Delta G} = \Delta G \times c_{\text{G,biosynthesis}}$	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})	$A = \left[218 \times T^{(-0.015T+1.062)} + 380\right] \times W_{\text{somatic}}^{0.75}$	Adapted from Claireaux et al. (2000)
10a	Foraging-related mortality (year^{-1})	$M_{\text{foraging}} = 0.015 \times \varphi^2$	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})	$M_{\text{respiration}} = 0.20 \times \left(\dfrac{B_\varphi}{A}\right)^3$	Mortality rate when total metabolic rate approaches total aerobic capacity. From Holt and Jørgensen (2014).
10c	Mortality due to bulky shape (year^{-1})	$M_{\text{condition}} = 0.05 \times \left(\dfrac{100 \times W_{\text{actual}}}{L^3}\right)^3$	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).

$$N_{\text{lipids}} = H_{\text{lipids}} - B \times c_{\text{lipiduse}} \qquad (3b)$$

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

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 growers, we forced the model with a background protein uptake (from foraging) to sustain a 0.5% 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_{proteins} and lipid stores S_{lipids} change as:

$$S_{n,t+1} = S_{n,t} + N_n - \Delta W_t \times c_{W,n} - \Delta G_t \times c_{G,n} \qquad (4)$$

where ΔW_t and ΔG_t are the somatic and gonadal growth (g), respectively, during timestep t, while the different coefficients c are the required amounts of protein and lipid synthesized into one gram of new tissue. Again, n refers to nutrient type and is either 'proteins' or 'lipids'. If stores become negative, it is assumed that the model fish dies. In cod, nearly all lipids are stored in the liver, which constitutes up to 10% of the total weight of the fish and has a fat content of 40–80% depending on environmental factors and season (Holdway and Beamish 1984, Marshall et al. 1999), while proteins are stored as increased white muscle mass.

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 model presented here) are almost exclusively predated by seals. However, these predators can be 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 model in Holt and Jørgensen (2014), also this model assumes that risk is higher for smaller fish, when foraging behavior is intense, when metabolic rate is near the limit for aerobic respiration, and 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 escapement speed due to critically reduced muscle mass. This may have been relevant if modeling 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^{-1}) is thus

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

and survival per week is $S = e^{-M/52}$. In the present study, we used a background mortality (M_{fixed}) of 0.02 year^{-1} 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.

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 ARA content in the gonads at time of spawning (ARA effect on) or independent of it (ARA effect 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 transferring lipids to the gonads (a little bit every week and more towards the end). Further, the cod cannot selectively retain ARA, so when lipids are used for metabolic purposes, ARA is also used in proportion to its current concentration in the lipid stores (as indicated in Fig. 1). The model then optimizes habitat choice and foraging intensity throughout the year prior to spawning by maximizing expected survival multiplied with the ARA effect when it was included.

The model was parameterized to mimic the situation for cod in the Øresund Strait between Denmark and Sweden, where adult cod feed predominantly on shore crab and herring (van Deurs et 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 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 September (we will refer to this as the background herring level) and in high abundance from September until spawning commences in February (Hüssy 2011) (the Western Baltic spring spawning herring overwinter in Øresund). To explicitly investigate how prey quality affected prey choice, the energy intake acquired per unit foraging activity was the same for crab and herring from September and onward (but remember that foraging activity is a dynamic behavior optimized by the model so it could vary depending on motivation and utility). Food was available all year, except that it was assumed that no feeding takes place around spawning time (Fordham and Trippel 1999). Parameters and key equations are listed in Table 1 and 2. The MATLAB code is available as Supplementary information.

Field observations and fatty acid markers

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 $W_{somatic}$ and then multiplied by 100%) of cod caught in the Øresund Strait from 2014 to 2016. These cod ranged from 50 to 80 cm and cod from 50 cm and up are supposedly capable of preying on the migratory herring. For further details see van Deurs et al. (2016). The liver content of two fatty acid trophic markers (FATM) (20:1n-9 + 22:1n-11) and ARA (22:4n-6; in this case also used as a FATM) in cod from November and late January (n = 12 and 15, respectively) were analyzed to allow FATM-based estimates of the 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 Deurs et al. (2016). The following equations were formulated to mechanistically derive the expected FATM liver levels (ρ [area % of total lipid pool]) for a range of hypothetical prey ratios (R):

$$\rho = \frac{\left(R\beta_1\alpha_1 + \beta_2\alpha_2 \right)}{\left(R\beta_1 + \beta_2 \right)} \times 100 \qquad (6)$$

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

Results

Seasonal dynamics of lipid reserves predicted by the model mimicked the field observations, both in terms of timing and maximum reserve levels (Fig. 2a–b). For example, the predicted maximum lipid store matches observed liver weights in November, assuming that ~70% of the liver weight consists of lipids (Lie et al. 1986). As illustrated in Fig. 2b, herring arrives in September and stay 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 weeks it becomes optimal to feed mainly on lean shore crabs (i.e. low lipid–protein ratio), switching only occasionally to herring. This feeding behavior emerges from the model despite

a constant and high availability of herring from September and until spawning in February–March. In order to test 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 cod > 50 cm sampled in November suggested that cod had been feeding mainly on the migrating 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 a large proportion of the prey ingested since November comprised shore crab or other prey types with a FATM composition similar to that of shore crabs.

Another noteworthy pattern emerging from the model is that maximum feeding activity (and 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 nine weeks (six weeks in September/October and another three weeks spread out over the following 3–4 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 enlarged and the maximum occurring earlier if time between arrival of migrating herring and spawning increased (i.e. early arrival of migrating herring), and in particular if the herring overabundance was more transient (i.e. brief residence time). Cod who had access to an overabundance of herring earlier and for a longer time-period were the least active and therefore also suffered from the lowest mortality. Reducing the lipid content of the herring or removing the overabundance from September and onward (i.e. no arrival of migrating herring), resulted in a marked reduction in cod survival probability, stemming from an increased foraging activity leading to increased mortality (i.e. $M_{foraging}$ increased).

Since the main source of ARA was the shore crabs and not the herring, ARA uptake increased when the overabundance of herring was either completely removed (i.e. no arrival of migrating herring) or if the residence time of the migrating herring was brief. However, all model simulations described so far assume that cod possess no information about the ARA content of available prey 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 eggs produced. Because ARA constitutes a relatively high proportion of the lipids in shore crabs, the model predicted that cod should
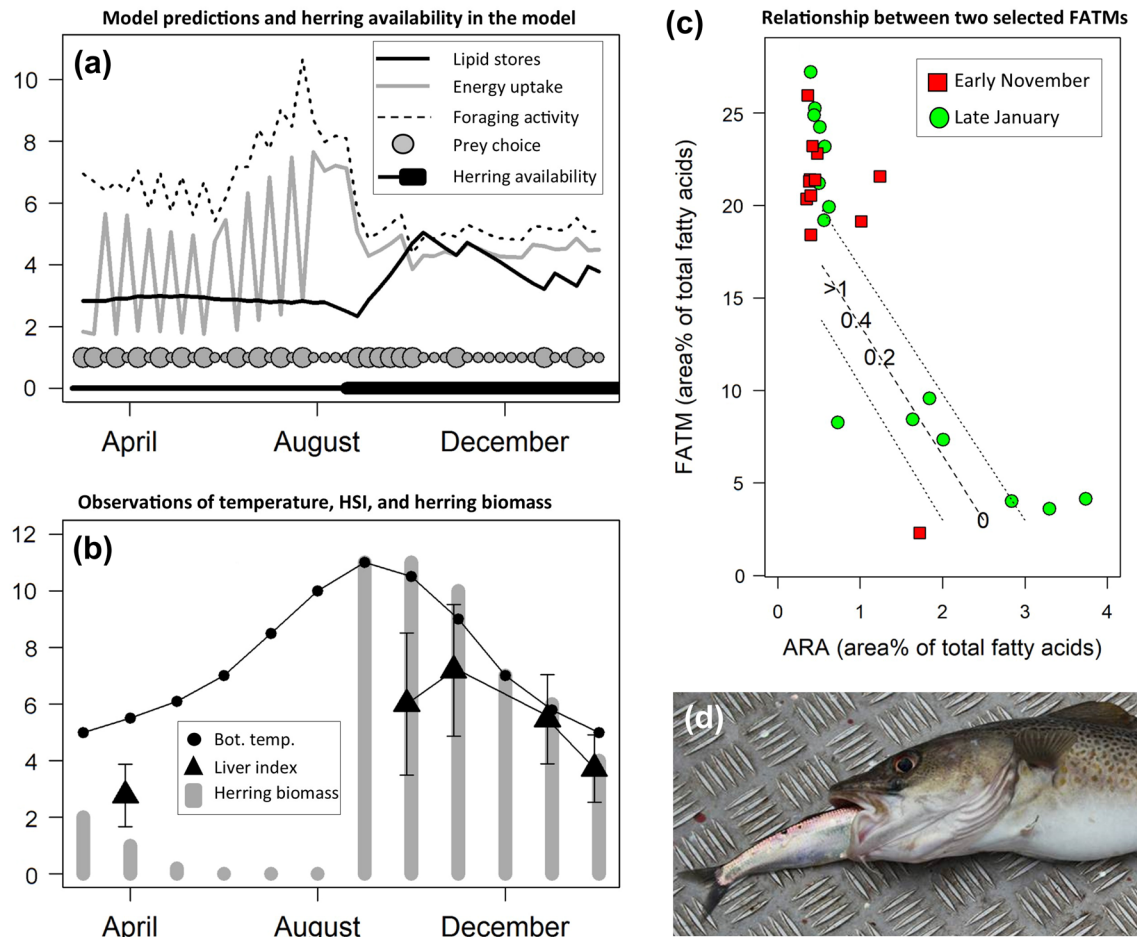
Figure 2. Relating simulated data (a) to field observations (b–c). (a) Simulated data was extracted from the default model, which represents an adult female cod *Gadus morhua* feeding on shore crab *Carcinus maenas* and herring *Clupea harengus* in the Øresund Strait. The graphs show the modeled weekly energy uptake (10^2 kJ week^{-1}) (grey line), lipid stores (lipids as a percentage of somatic body weight, $W_{somatic}$) (solid black line), foraging activity (levels from 1 to 15) (dashed black line) and prey choice (shore crab: small bubbles; herring: large bubbles). The thick horizontal line at the bottom of the plotting window indicates availability of herring in the model (i.e. the migrating herring population arrives in late summer leading to more than a tripling of the herring biomass). Reproduction takes place at the end of the simulated time period, which runs until 28th February. Energy uptake is proportional to foraging activity and therefore also predation risk (i.e. high energy uptake equals high risk). (b) Seasonal patterns in the Øresund Strait of average ($\pm$ 1 SD) HSI (hepatosomatic index; liver weight as percentage of $W_{somatic}$) (triangles), herring biomass (10^3 tons) (grey columns) (reproduced from Nielsen et al. 2001) and local bottom temperature (°C) (black dots connected by line) (adapted from Henriksson 1969). (c) Relationship between the proportions of two selected FATMs in cod livers. Colored data points are observed FATM levels in cod livers sampled in November (red squares) and January/February (green circles) (ARA on the x-axis and 20:1n-9+22:1n-11 on the y-axis [area % of total fatty acids]). Dashed lines is the predicted FATM levels (area % of total fatty acids) (ρ in Eq. 6) for a range of hypothetical mass ratios between herring and shore crab (R in Eq. 6). R are superimposed along the dashed line, allowing visual resolving of diet compositions from observed FATM levels in cod livers. Dotted lines represent $\pm$ 1 standard deviation applied to α-parameters in Eq. 1. (d) Photograph of a cod caught unintentionally while angling for herring in the Øresund Strait in October 2014.

partially trade off the physiological benefits of lipids (i.e. the protein sparing effect of lipids and the higher conversion efficiency) for the improved egg survival due to a higher ARA content, by feeding to a lesser extent on herring and more on shore crab (Fig. 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. $M_{foraging}$ increased). This incentivized the cod to consume from the low background herring availability in the model (i.e. lower energy gain per unit time invested in foraging, but higher energy gain per unit of survival loss). Lastly, optimal dietary lipid:protein ratio (quantified in terms of energy content, not mass) was identified by employing the model with equal access to shore crab and herring throughout the year. The optimal lipid:protein ratio was found to be somewhere between 0.5 and 0.7, increasing
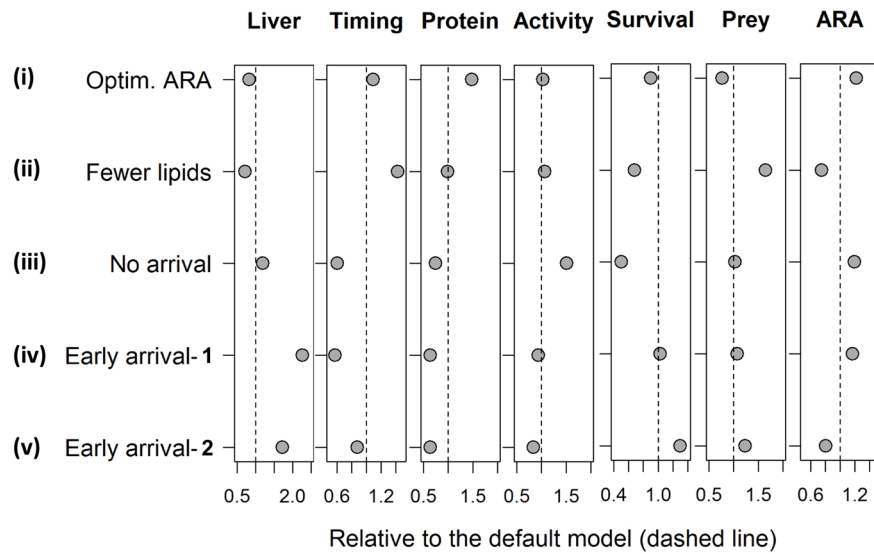
Figure 3. How timing and nutritional quality of herring arriving to the Øresund Strait in late summer affected reserve dynamics, prey choice and egg quality determined by ARA of modeled reproductive female cod. Five specific scenarios were investigated by modifying the default model. These included: (i) the hypothetical scenario where we assume that cod is 'aware' of the reproductive benefits of the high ARA levels in shore crab and optimizes prey choice accordingly (ii) fewer lipids in the herring (i.e. reduced mean size in the herring population would lead to reduced lipid concentrations (van Deurs et al. 2016) (iii) no arrival of migratory herring (only the background herring abundance also applied in the default scenario); (iv) earlier arrival by three months, but a shortened residence time (early arrival-1); and (v) earlier arrival of migrating herring by three months and no shortened residence time (early arrival-2). Results are presented relative to the default model presented in Fig. 2a, which is represented by the vertical dashed line in each plot window. In total, seven different metrics, describing the physiological and behavioral characteristics, were explored: (from left to right) maximum amount of lipids stored at any one time (liver), timing of when maximum lipid stores is achieved (timing), amount of protein stored at the end of the simulation period (protein), foraging activity (activity), survival probability (survival), preference for herring over shore crab (prey) and ARA levels at the end of the simulation period (ARA).

from 0.5 in spring to 0.7 in August, where it remained until spawning (Fig. 4a). Switching off the 'protein sparing effect of lipids' in the model resulted in a ~15% decline in the optimal lipid–protein ratio, indicating the importance of this physiological mechanism in the model (Fig. 4b).

A sensitivity analysis on 13 parameters and model assumptions showed that changing a single parameters in the model
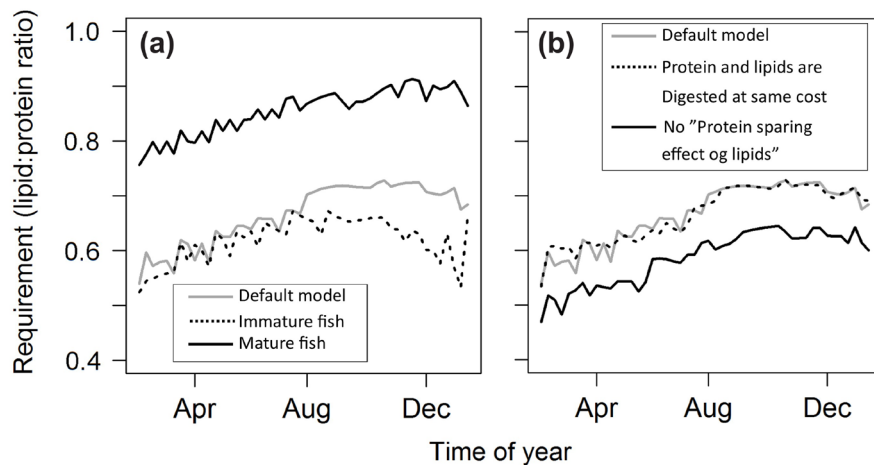

Figure 4. Model predictions of macro-nutritional requirements of dietary lipids and proteins and the sensitivity to assumptions made about the life history and physiology. Requirement is given as the lipid:protein ratio, where quantities are given in units of joules (i.e. required lipids [J] per proteins [J]). (a) Predicted requirement derived from the default model (grey line) compared to the predicted requirement of an immature fish with no gonad development (dashed line) and a mature fish growing at half the rate applied in the default model (black line). (b) Predicted nutritional requirement derived from the default model (grey line) compared to the predicted requirement from a model where the energetic cost associated with digesting lipids is the same as for proteins (instead of being higher for protein) (dashed line) and from a model where the protein sparing effect of lipids is switched off (metabolic energy is drawn from lipid and protein stores in proportion to store size, in contrast to lipids being preferentially used, if available, for metabolic energy (black line).

Table 3. Sensitivity analysis of model parameters. Numbers represent the percentage change in model estimate as a result of changing the model parameter by ± 20%. Note that the values are the average of the change observed when reducing and increasing the parameter by 20%, respectively. Model estimates are the same as in Fig. 3. Only the most imprecise model parameters (i.e. 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	$d_{h(crab)}$	2.8	1.7	0.9	3.9	1.4	1.5	0.0
Prey	digestibility herring	$d_{h(herring)}$	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prey	proportion of ARA in crab lipids	$C_{h(crab),ARA}$	0.0	0.0	0.0	0.0	18.1	0.0	0.0
Prey	proportion of ARA in herring lipids	$C_{h(herring),ARA}$	0.0	0.0	0.0	0.0	1.4	0.0	0.0

by ± 20% had only minor effects on the 7 model outputs assessed (Table 3). Only 18% of the 13 × 7 recalculated model outputs changed > 5% and only 8% changed more than 10%. Most of the larger changes to model output were expected. For example, changing 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 outputs that resulted from changing the proportion of protein in gonads and the energetic cost of digesting protein.

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 zooplanktivorous fish species occupying the pelagic zone (often referred to as forage fishes or small pelagics). It is through those species that the main flow of energy from secondary producers to larger fish, birds and mammals pass (Cury et al. 2000, Alder et al. 2008). However, while they are extremely abundant and often rich in energy, they are typically also migratory and display distinct seasonal patterns in abundance and nutritional quality (Hislop et al. 1991, Slotte and Fiksen 2000, Behrens et al. 2006, van Deurs et al. 2011), leading to a phenology where predators are presented with the opportunity to feast on an overabundance of lipid-rich forage fish for a limited period of time every year. The present study is to

our knowledge the first to consider nutritional requirements in relation to marine boom and bust dynamics.

Model predictions of prey choice dynamics in the default 'boom and bust' scenario

Previous studies have linked the condition of Atlantic cod *Gadus morhua* and cod stock productivity with periodic availability of lipid-rich forage fish (Marshall et al. 1999, Rose and O'Driscoll 2002, Eero et al. 2012). The annual peak in HSI of cod range from 4 to 10% in the wild (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 lipid stores reached a peak after the arrival of migrating herring and the size of the modeled lipid 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 the cod chose to feed solely on the herring. After this period the cod shifted back to shore crab as the main prey, despite an overabundance of herring that lasted for several months. This

indicates that the cod in our model only exploited the over-abundance of herring moderately and for a limited period of time, and thereafter favored prey with a relatively higher content of protein rather than maximizing energy (lipid) intake. This diet shift away from herring prior to spawning may not apply to cod in general. Michalsen et al. (2008) analyzed stomachs from two cod stocks in Lofoten area during the spawning period and found that some fish fed on the herring even when they were in a spawning state.

Before the herring period, when lipids stores had not yet been built, cod in the model constantly 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, 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. 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 a function of water column position and light levels. Building such mechanisms into the present model may have reduced the profitability of preying on herring in the pelagic zone.

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

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

The effect of manipulating the characteristics of the 'boom and bust' situation

Manipulating timing, quantity and nutritional quality of the herring overabundance in the model did not change the general picture of a single annual peak in lipid stores followed by a period of reserve depletion toward spawning. In contrast, maximum lipid stores and the date at which this maximum was reached changed according to the environmental forcing implemented in the model. Contexts resulting in an early peak in stored lipids also yielded a higher maximum level. Cod 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 activity was required to account for the reduced availability of fat prey.

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

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 cod from 1 to 4 mg g^{-1} resulted in a doubling of the number of eggs produced and increased larval survival, at least during the first eight 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 optimize ARA levels in the cod gonads, the cod were still predicted to accumulate lipid stores (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 of viable larvae is a robust measure of fitness. While the highest daily rates of natural mortality takes place among eggs and early larvae (Bogstad et al. 2016), the total mortality of eggs and larvae may still be lower than that of the much longer juvenile phase. We can therefore not be certain that number of surviving larvae is a suitable fitness proxy.

The optimal diet

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

The protein sparing effect of lipids

Besides the need for lipids as building blocks in egg synthesis, the 'protein sparing effect of lipids' included in the model was what drove the need for a lipid supplement. This mechanism is well known in aquaculture, where it has been shown that metabolic energy costs are to a larger extent 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 without fattening the fish, to make sure the more expensive protein in the feed is retained as new tissue rather than being transpired. The high energy density of lipids makes it more suitable for 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 starvation mortality. Hence, our study showed that moderate energy storage is still beneficial, even 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 lipid is scarce, as it enables cod to target prey with relatively more protein and channel that towards gonad maturation and growth.

General conclusions

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 (Jensen et al. 2012, Ravenscraft and Boggs 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 species. Adding to this limited line of research, we here utilized observations from a boom and bust system with a dynamic bioenergetics model to disentangle key tradeoffs related to food quality. The model predicted, for example, that in an ideal situation, energy required from dietary protein should be twice that required from dietary lipids, with a small increase in lipid requirements when gonads are growing. The model also predicted that this balance is worth striving for, as the 'energy sparing effect of lipids' made it possible to reduce overall foraging risk. At the same time, a diet too rich in lipids would interfere with growth and reproduction, and both the model and the observations of fatty acid profiles indicated that cod were able to resist the temptation from junk food. Hence, storing lipids when opportunities arise is a significant fitness asset, even if periods of starvation are not expected to occur, but only up to a point. From this we conclude that, also in the wild, paying attention to a nutritionally balanced diet is important and should replace a focus purely on energy acquisition, and that evaluating the associated survival costs and benefits are necessary to interpret what is the right balance between lipids and proteins.

Author contributions

Mikael van Deurs: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Software (supporting). **Anders Persson**: Conceptualization (supporting); Formal analysis (supporting); Supervision (equal); Writing – review and editing (equal). **P. Anders Nilsson**: Conceptualization (supporting); Formal analysis (supporting); Supervision (equal); Writing – review and editing (equal). **Christian Jørgensen**: Conceptualization (supporting); Formal analysis (supporting); Methodology (equal); Software (lead); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sf7m0cg7n> (van Deurs et al. 2021).

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