A Functional Response Model Fit to Empirical Consumption Data

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Abstract

The anticipated empirical consumption level of a target (prey) species by its predators is an important variable when implementing the *constant biomass escapement* strategy in fisheries management. For a single predator, the projection of empirical consumption will depend, among others, on projected distribution in space–time of the predator, degree of predator overlap with prey, and considerations of fluctuating environmental variables (e.g., temperature) that may affect the consumption rate. Hence, the projected empirical consumption is usually uncertain, as it involves the integration of uncertain space-time data and high-throughput models and sub-models. The inclusion of such modeling frameworks into an overall assessment model is usually non-trivial.

The goal of this paper is to approximate estimates of the empirical consumption rate of capelin by cod in the Barents Sea, using an analytical functional response (FR) model. The empirical consumption rate is estimated by integrating projected space-time (biotic and abiotic) data with a cod stomach evacuation model. We consider the time series of empirical consumption rates as observation data, and use an optimization procedure to estimate parameters of the FR model. We assess the model performance by the degree to which derived uncertainty envelopes encompass the input data, and evaluate its prediction ability using data that were excluded in the parameter estimation process.

Our results show that the FR model provides good approximations to estimates of empirical consumption. A major advantage of the FR modeling framework is that it facilitates

hypothesis testing, uncertainty quantification, and seamless integration of the FR model into an overall stock assessment model for capelin.

1 Introduction

Including considerations of species interactions when assessing the state of fish stocks is a key step towards implementing ecosystem-based fisheries management. This is because predator-prey interactions determine the dynamics of fish populations through alterations in prey (and predator) behavior, distribution, and density (Edgar et al., 2019; Baum and Worm, 2009; Romare and Hansson, 2003; Swain et al., 2015). Such considerations are especially important for forage species (see example species in, for example, Skern-Mauritzen et al., 2016; Tyrrell et al., 2011) since they are often exploited commercially, in addition to being key preys for species at higher trophic levels in the ecosystem. One way of dealing with predation mortality in stock assessment models is to include this as part of the total natural mortality (which includes mortality due to disease, competition, cannibalism, old age) of the species. Explicit considerations of predation mortality within the assessment model has also been reported by several authors including Gislason and Helgason (1985); Hollowed et al. (2000); Bogstad et al. (1997) and Jurado-Molina et al. (2005).

The *constant biomass escapement* is a fisheries management strategy that aims at preventing stock collapse by ensuring that the spawning stock biomass is above a predetermined threshold value that is deemed prerequisite for recruitment success. The harvestable biomass is thus the total biomass, less the sum of the escapement biomass and the anticipated consumption by predators. This is the strategy adopted in the management of e.g., the capelin stocks in the Barents Sea (Gjøsæter et al., 2015), and in Icelandic waters (Gudmundsdottir and Vilhjálmsson, 2002). Escapement strategies are also used in the North Sea, in the single species management of sandeels and Norway pout (Kempf, 2010). For short-lived species (characteristic of forage species), an escapement strategy is believed to be an optimal harvest strategy (Holden and Conrad, 2015). Success of the escapement strategy, however, is premised on good estimates of the predation mortality.

Stomach content data provide direct observations of predator-prey interactions and the diet composition of predators in the wild (Eriksen et al., 2020; Bogstad et al., 2000; Planque et al., 2014). Examination of individual stomach content, however, only gives a snapshot of the recent individual predator diet. Gastric evacuation rates may be influenced by meal size, body weight, dietary content of prey, and temperature (Jobling et al., 1977; Jobling, 1987), while overall consumption may be influenced by factors, such as relationship between prey and predator abundance and their overlap probabilities in space-time (Carroll et al., 2019). It is challenging when multiple prey items are present in the predator stomach, since the detection probability of an individual prey is influenced by their digestion rate (Kulatska, 2019). A modeling approach to estimating consumption involves using models that combine quantity of prey in guts, prey digestion rates, and sea temperature, to calculate predator daily rations (see Bromley, 1994; He and Wurtsbaugh, 1993). The total amount of prey consumed

by the overall predator population is then upscaled by the abundance of the predators (Bailey and Duffy-Anderson, 2009).

The elaborate estimation procedure of integrating models, prey/predator population abundance indices and stomach content analysis over space-time can involve several uncertain parameters and data of different scales and uncertainty levels. Furthermore, this consumption estimation procedure using diet data and evacuation models is costly, time-consuming, and difficult to directly integrate into a stock assessment model (See discussion in Liao et al., 2005). In practice (see e.g., Gjøsæter et al., 2002; ICES, 2023), the estimated empirical consumption rates serve as input in estimation of parameters for a secondary consumption model that is integrated into the assessment and management decision procedures. This secondary model may also require additional assumptions and levels of uncertainty, whose effect on the assessment and management procedures is non-trivial.

This paper investigates a viable alternative approach, which involves the use of classical functional response (FR) functions to approximate empirically calculated consumption rates, and total consumption. We investigate how temperature effects may be included in the analytical functional response equation, and whether this improves model fit to empirical estimates. We investigate this using data from the Barents Sea capelin stock. Our choice of this stock is influenced by several factors. It is a short-lived forage species that has been subjected to several episodic recruitment failures, although it is one of few stocks identified by Skern-Mauritzen et al. (2016) that includes predation by cod in short-term projections of stock size.

It is important to note that our approach corresponds to what has been termed a *reductionist* strategy: the FR model is fitted directly to empirical consumption estimates, rather than being embedded within a full predator–prey dynamical model (Koen-Alonso et al., 2021). As such, the quality of the approximation depends both on the ability of the FR structure to represent underlying processes, and on the accuracy of the empirical estimates themselves, which are produced through a sequence of modeling and analytical steps with their own assumptions and limitations (see Appendix A). The interpretation of our results should therefore be understood as an approximation to these empirical estimates, not as a correction for possible biases in the empirical estimation process.

The rest of the manuscript is organized in the following way: Section 2 gives a brief background to the capelin stock; its role in the Barents Sea ecosystem in terms of predator-prey relationships. Section 3 presents the current method for calculating empirical consumption of capelin by cod, considered as the main predator of capelin. Section 4 presents a brief discussion of FR models and a rationale for our choice of FR model, while Section 5 gives an overview of all data sources, and their role in estimating the empirical consumption rate. We present the procedure for estimating the FR model parameters and a description of other numerical experiments in Section 6. Results from the fitted FR model are presented in Section 7, followed by a brief discussion and conclusion in Section 8.

2 The Capelin-Cod Interaction

The Barents Sea ecosystem is characterized by a relatively simple food web in terms of dominant feeding links. The food web is characterized as being waist-wasp, i.e., controlled by intermediate trophic interactions (Ciannelli et al., 2005; Yaragina and Dolgov, 2009; Fauchald

et al., 2011). The intermediate interactions are linked to stocks of three economically important species: Northeast Atlantic cod (*Gadus morhua*, hereafter cod), the Barents Sea capelin (*Mallotus villosus*, hereafter capelin) and the Norwegian spring-spawning herring (*Clupea harengus*, hereafter herring) (Dvoretsky and Dvoretsky, 2015). The most dominant pelagic species, capelin, exerts a top-down effect on its prey (zooplankton) (Skjoldal et al., 2022), and bottom-up effect on its main predators, mainly cod (Bogstad and Gjøsæter, 2001).

Although cod is a generalist predator, its diet composition shifted in the late 1960s to include a higher proportion of capelin. This change is believed to be associated with the collapse of the Norwegian spring-spawning herring in the Barents Sea (Orlova et al., 2006; Lees et al., 2006; Johannesen et al., 2012; Fall et al., 2021). In the following years, the cod-capelin interaction remained very strong, exhibiting semi-cyclic patterns that are reflective of changes in capelin stock size (Hylen, 2002; Durant et al., 2014; Holt et al., 2019) and environmental conditions (Orlova et al., 2006; Kjesbu et al., 2014; Fall, 2019). Cod feeding patterns on capelin also vary with seasonal changes in the Barents Sea. In the winter periods, cod consumes more capelin as higher capelin densities are found, in connection with the spawning migration (Bogstad and Gjøsæter, 2001; Fall et al., 2018; Holt et al., 2019). Since the capelin stock is managed using an escapement strategy, quantifying the consumption of capelin by cod is crucial not only for understanding the predator-prey population dynamics but also for informing the harvest control rule (HCR) (Gjøsæter et al., 2002; Ciannelli et al., 2005; Hjermann et al., 2010; Durant et al., 2014).

3 Quantifying Empirical Consumption of Capelin

The current calculation of empirical consumption is based on the model developed by Bogstad and Mehl (1997). This approach integrates data from stomach content analysis, temperature, and cod weight into a gastric evacuation model derived from laboratory experiments (see Santos and Jobling, 1992; dos Santos and Jobling, 1995). The model calculates the biomass of capelin consumed per cod per unit time. However, other methodologies for estimating the empirical consumption of capelin exist, each yielding slightly different results due to variations in their underlying assumptions and data integration techniques (see summary by Johannesen et al., 2006). For comprehensive details on the equations and computational methodologies of the discussed models, refer to the Appendix A.

A significant drawback of the current approach to incorporating results from complex consumption modeling frameworks into stock projection models is the potential for errors and uncertainties from individual sub-models to propagate and intensify throughout the system. This can reduce the reliability of the overall stock projections, especially when each sub-model is highly sensitive to its initial conditions or input parameters. Additionally, quantifying the overall uncertainty in stock projections becomes particularly challenging, as it requires integrating the compounded uncertainties from multiple sub-models, making it difficult to assess the true level of risk or confidence in the projection outcomes.

This paper aims to develop an analytical FR model to approximate the empirical consumption per cod model described in Bogstad and Mehl (1997). Creating such an analytical function offers several advantages. It simplifies the complex calculations involved, making assessments faster and more accessible to understand. Additionally, an analytical function highlights the key factors driving cod consumption of capelin, enabling easier parameter

estimation and scenario analysis. Simplified models are more straightforward to communicate to stakeholders and improve the robustness and replicability of findings. However, it should be noted that, the performance and accuracy of this analytical approach are inherently dependent on the empirical estimates it seeks to approximate. These estimates are themselves model-based, relying on assumptions about stomach evacuation dynamics, predator distribution, equilibrium between consumption and evacuation, and parameter transferability from laboratory to field conditions (see Appendix A). Consequently, any biases or uncertainties in the empirical model may propagate into the functional response fit. A mismatch between FR predictions and empirical estimates may therefore reflect limitations of the FR model, shortcomings in the empirical estimates, or most realistically a combination of both.

4 Functional Response Fit to Empirical Consumption

The functional response is a mathematical modeling framework that describes the density-dependent (average) consumption rate (Holling, 1959a) of a predator, during encounter with prey species (see e.g., Jeschke et al., 2002, for an overview). There are in general, three types of functional response models - type I, II, and III. The type I and II responses show, respectively, linear and hyperbolic increase, while the type III response exhibits a sigmoidal increase with prey density (Holling, 1959b).

In fisheries science and ecology, the two most common models are the types II and III functional responses (Skalski and Gilliam, 2001). If we define the *per capita* comsumption rate, F, as depending on B number of prey, such that,

$$F(B) = \frac{aB^\lambda}{1 + ahB^\lambda} \tag{1}$$

then the type-II and III FR (Holling, 1959b,a; Abrams and Ginzburg, 2000) are defined respectively by $\lambda = 1$ and 2. The parameter a is attack rate, and h is the handling time per prey item, influencing how the consumption rate saturates as prey density increases. Note that the handling time may also be defined as relating to the time taken to eat and digest a prey item (Jeschke et al., 2002). Observe that (1) defines a prey-dependent FR, since F is a function of prey density alone. An alternative to the prey-dependent formulation are predator-dependent models, which recognize that predation rates depend on both prey and predator densities (see e.g., Hassell and Varley, 1969; DeAngelis et al., 1975; Arditi and Akçakaya, 1990).

In addition to a prey- and predator-dependent FR, this paper also investigates a ratio dependent (prey$B$-to-predator$P$) Holling FR (RDFR) (see Abrams and Ginzburg, 2000; Arditi and Akçakaya, 1990; Hassell and Varley, 1969), given by (2), where the predation rate, C, depends on the ratio of prey-to-predator abundance, rather than on the absolute numbers of either, or both species.

$$C(x, a, h) = \frac{aP^{-x}B}{1 + ahP^{-x}B} \tag{2}$$

where a and h are defined as previously. The attraction with this choice of FR is that several version of Holling-type FR models can be derived as special cases. For instance, by setting $x = 0$, C becomes a prey-dependent, Type-II FR (see Holling, 1959a). As pointed out by

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Haque (2009), ratio-dependent FR models continue to gain acceptance (among theoretical and experimental ecologists) as a more suitable description of predator-prey interactions under condition of intense predation pressure. By fitting the empirically calculated consumption rate to the RDFR, we approximate the capelin-cod functional response as reflected in the available empirical estimates.

4.1 Incorporating the Effect of Temperature

The literature reports effects of temperature on the parameters a, h, and the integrated effect on the consumption rate for both terrestrial and aquatic species (see Haubrock et al., 2020; Mofu et al., 2019; South and Dick, 2017; Thompson, 1978). The general picture (e.g., Thompson, 1978; Haubrock et al., 2020) is that the attack rate tends to increase, while the handling time usually declines, with increasing temperature. This general trend might differ across ontogeny (as pointed out by Haubrock et al., 2020, for geckos), perhaps reflecting the priorities (growth, maturation, or body maintenance) at individual life stages of the predator.

The effect of temperature on the attack rate is introduced by defining a as a function of temperature (T in °C) and a set of real-valued variables, following Sentis et al. (2012). Specifically, $a(T)$ was defined using a function with a non-zero local support in the interval $T_0 \leq T \leq T_l$, where T_0 and T_l are lower and upper threshold temperatures:

$$a(T, b_a) = b_a(T - T_0)(T_l - T)^{\epsilon_a}, \tag{3}$$

where b_a scales the magnitude of the attack and ϵ_a is a parameter that controls the curvature of the temperature response.

In this manuscript, we neglect the temperature dependence of handling time and treat h as a constant b_h. Thus, in our baseline model, attack rate is temperature-dependent following (3), while handling time is held constant.

5 Data Sources and Pre-processing

The data, covering a 17-year period (2001-2017), is taken from the database of the annual Winter Surveys carried out by the Norwegian Institute of Marine Research and PINRO (the Polar branch of the Russian Federal Research Institute of Fisheries and Oceanography), and the annual reports of the ICES Arctic Fisheries Working Group (AFWG). Specifically, for the empirical consumption calculations, stomach content data for cod are derived from the relevant geographical regions (Fig .1) and season (February - March). The total area of the Norwegian demersal fish survey in the winter consists of six regions (A, B, C, D, E, and S; Mehl et al., 2013). However, in computation of empirical consumption, the data are aggregated into three areas, I (A+B), II (C+D), and III (E+S), which define a natural division of the Barents Sea into one northern and two southern parts. These combinations of regions reflect, to a certain degree, the changes in the geographical distribution of abiotic and biotic components of the ecosystem (Bogstad and Mehl, 1997). The R code (R Core Team, 2017) for computational reproducibility of cod consumption of capelin by combined regions, season and year can be found at github (https://github.com/NatoyaJourdain/BarentsSeaCod_EmpiricalConsumption.git). Figure 2 shows plots for calculated empirical
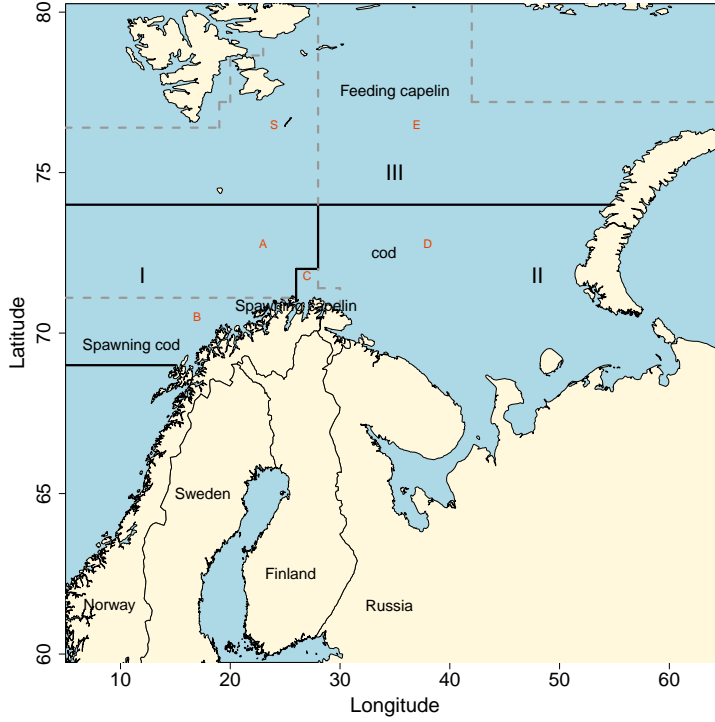
Fig. 1 Geographical distribution of cod and capelin and region division used in the consumption calculation (Bogstad et al., 1997; Mehl et al., 2013).
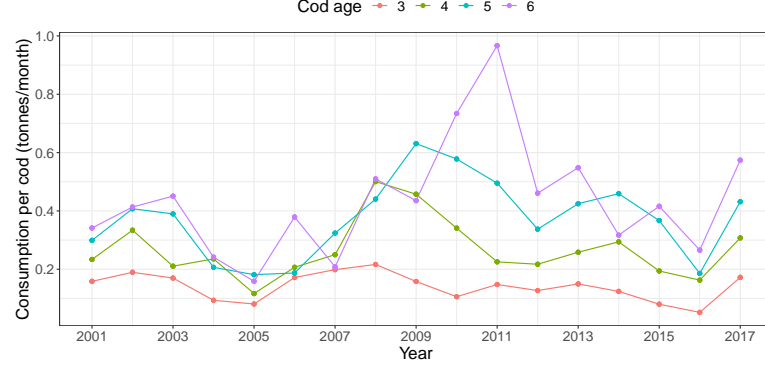
consumption of capelin by ages 3–6 cod, alongside the corresponding average temperature trends for various areas.

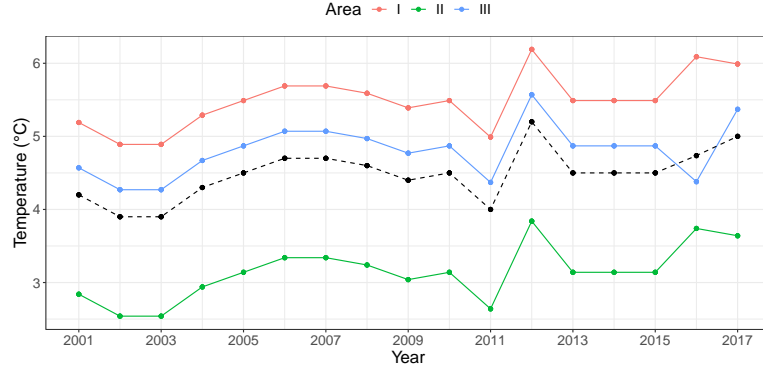# 6 Parameter Estimation and Numerical Experimental Procedures

The approach is to use data from empirically determined consumption $\tilde{C}$, to estimate a, h and x in (2), and any auxiliary parameters, such as b in (3).

We adopt the functional definition of $C_i(\boldsymbol{\theta})$, given by (2), where $\boldsymbol{\theta}$ is the parameter vector, i.e., $\boldsymbol{\theta} = \{x, b_a, b_h, \varepsilon_a\}'$, with $x \geq 0$, $b_a > 0$, $b_h > 0$ and $-1 \leq \varepsilon_a \leq 1$. Furthermore, we use the general form of a given by (3), but with an indeterminate exponent. Then for $T_{\min} \leq T \leq T_{\max}$ (known $T_{\min}$ and $T_{\max}$), (4) gives the functional response model description.

$$
\left.
\begin{aligned}
C_i(\boldsymbol{\theta}) &= \frac{a(b_a, \varepsilon_a) P_i^{-x} B_i}{1 + a(b_a, \varepsilon_a)\, h(b_h)\, P_i^{-x} B_i}, \\
a(b_a, \varepsilon_a) &= b_a (T - T_{\min})(T_{\max} - T)^{\varepsilon_a}, \\
h(b_h) &= b_h.
\end{aligned}
\right\}
\tag{4}
$$

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a. Total empirical consumption of capelin

b. Average temperature

Fig. 2 Age-specific total empirical consumption (left) and area-specific average (January-March) temperature (right). The dark, stippled temperature curve represents the average temperatures for all areas.

For *n* number of observations, the negative log-likelihood function to be minimized for the log-normal distribution is given by (5)

$$\mathcal{L}(\boldsymbol{\theta}, \sigma) = \frac{n}{2} \log(2\pi) + n \log \sigma + \sum_{i=1}^{n} \log \tilde{C}_i + \frac{1}{2\sigma^2} \sum_{i=1}^{n} \left[\log \tilde{C}_i - \log C_i(\boldsymbol{\theta}) \right]^2, \qquad (5)$$

where σ^2 is the variance of the residuals in log space. This formulation corresponds to a log-normal error structure, which guarantees strictly positive predictions of the consumption.

Ideally, the $T_{\min}$ and $T_{\max}$ should also be estimated, but due to a small number of observations we set these to 0.1°C below/above the respective minimum/maximum temperature observed in any of the areas I, II or III. We fit the model to the empirical consumption data for each age-group of cod group separately. The likelihood estimation involving (4) and (5) is implemented using template model builder, TMB (Kristensen et al., 2016).

We apply the procedure described above to two different setups. In the first setup, we use aggregated consumption data (i.e., the sum of empirical consumption for areas I, II and III), and the mean temperature of the three areas (black line in Figure 2b) as input to *a*. This

gives one model per age group (4 models). In all scenarios, we split the data in a training period (2001-2013), where the data is used to estimate the model, and a validation period (2014-2017), where we compare the model prediction to the observations.

Using the optimized parameters, we investigate the nature of the functional response surface as a function of changing temperature and prey biomass. Let Ω_T and Ω_B define, respectively, gridded intervals over T and B. The goal is to describe the surface $C(\Omega, \theta^*)$ representing $C(T, B, \theta^*)$, where $\{T, B\} \in \Omega_T \times \Omega_B$, and θ^* represents an optimized set of parameters.

We have used average temperatures (which is consistent with calculations of empirical consumption) for parameter estimation and in model validation. Given that large temperature variations may exist between areas, the use of average temperature (over aggregated areas) may highly impact model performance and prediction uncertainty. We therefore investigate an alternative approach for quantifying both estimation and prediction uncertainties for aggregated data, using the following procedure: For a large integer value $m > 0$, we generate a vector $\boldsymbol{T}$ of ordered temperature values, uniformly distributed between $T_{\min}$ and $T_{\max}$. For each $T_j(j = 1, \ldots, m)$ belonging to $\boldsymbol{T}$, we estimate a set of model parameters $\boldsymbol{\theta}_j$, and predict consumption for 2014–2017 on the basis of the estimated parameters. We use the set of m model fits to observation, and their corresponding predictions to define uncertainty envelopes for model performance and predictions. We refer to this approach as a stochastic temperature (ST) approach.

7 Modeling Results

In all scenarios, the parameter x is estimated to not be significantly different from zero. This parameter determines the influence of the predator population, P. We, therefore, set $x \equiv 0$, effectively taking cod out of equation (4). Since we only have 13 years of observations, we do not expect to get significant results for all parameters. The parameter b_a cannot be set to zero, because then $C_i \equiv 0$.

Table 1 gives parameter estimation results for Setup 1 (aggregated consumption data), while Fig. 3 shows the functional form of a for this setup. Figure 4 shows the estimation and uncertainty envelopes for the estimation (2001-2013) and validation (2014-2017) periods. The uncertainty envelope for the validation period is based on a Monte Carlo simulation that uses the variance estimate from the estimation period. Figure 5 presents the functional response surfaces for the aggregated data, derived by variability in the temperature and prey biomass.

Figure 6 gives results for the ST approach and shows the mean predictions and 95% confidence intervals of ($m =$) 200 re-sampled temperature measurements. The sampled temperature values were generated from a uniform distribution over the interval $[T_{\min} \ T_{\max}]$ of the three areas together, and the model parameters were re-estimated for each new sample.

Our findings indicate significant temporal dynamics in cod predation on capelin, heavily influenced by temperature variations. The model predictions closely align with the observed data, demonstrating robustness and reliability.

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Table 1 Model parameter estimates based on total consumption estimates for 2001-2013, and the mean temperature (of areas I, II and III) as observations.

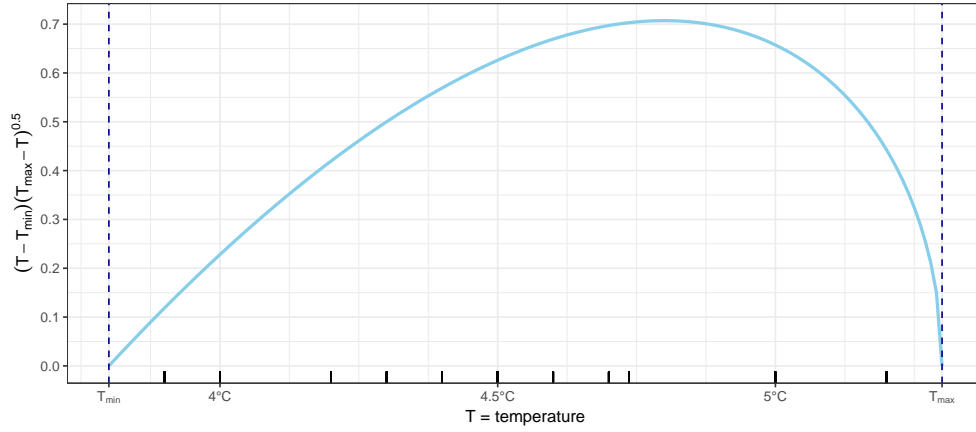| Age	Parameter	Estimate	Std.Err	Z-value	P-value	
3	b_a	0.00934	0.01710	0.55	0.58	
	b_h	6.47	0.862	7.51	0.00	***
	ϵ_a	1.00000	0.00092	1091.18	0.00	***
	σ	0.281	0.0551	5.10	0.00	***
4	b_a	0.00334	0.00151	2.21	0.03	*
	b_h	2.85	0.483	5.89	0.00	***
	ϵ_a	1.00000	0.00006	17194.95	0.00	***
	σ	0.302	0.0592	5.10	0.00	***
5	b_a	0.00284	0.00062	4.56	0.00	***
	b_h	1.70	0.239	7.10	0.00	***
	ϵ_a	1.00000	0.00001	73597.78	0.00	***
	σ	0.224	0.0439	5.10	0.00	***
6	b_a	0.00386	0.00184	2.10	0.04	*
	b_h	1.61	0.391	4.13	0.00	***
	ϵ_a	0.999	0.419	2.38	0.02	**
	σ	0.396	0.0777	5.10	0.00	***

Fig. 3 Functional form for a, with scaling $b_a = 1$. The bold tick marks along the x-axis indicate observed temperatures.

8 Discussion and Conclusions

While we recognize that alternative prey influences cod performance and capelin consumption, this study is limited by the lack of empirical data on multispecies interactions. Cod are generalist predators, but the available data focus on the dominant cod-capelin interaction, which significantly impacts capelin stock dynamics in the Barents Sea (Bogstad et al., 2000; Gjøsæter et al., 2002). Given this, we have justified using a simplified model assuming cod as the primary predator. This simplification aligns with the way empirical consumption estimates are currently derived, which already aggregate interactions into a cod–capelin focus.
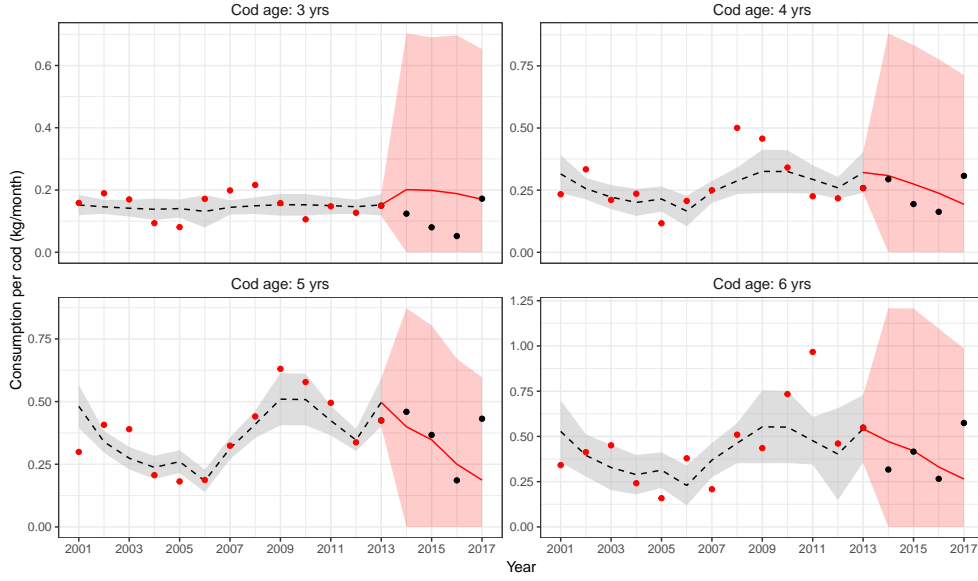
Fig. 4 Mean model estimates (stippled curves) and Monte Carlo uncertainty envelopes for estimation (2001-2013) and validation (2014-2017) periods.

In our model, the estimated effect of predator density was close to zero, meaning that the functional response mainly depended on prey density. This suggests that, with our data, we could not detect a strong effect of predator numbers on individual consumption rates. One contributing factor is that the empirical estimates we use as data were generated under assumptions that do not explicitly include predator-density effects. As a result, even when we fit a formulation that could in principle capture predator dependence, such effects may remain weak or undetectable in practice. In addition, the spatial aggregation of inputs (large-area means) can average out local predator-prey interactions, further emphasizing prey availability over predator density.

While the FR model generally captures the empirical consumption patterns, we acknowledge that some observed data points fall outside the uncertainty envelopes of our predictions. Such mismatches do not necessarily imply deficiencies in the FR formulation itself, but may instead reflect limitations of the empirical estimates, which are themselves model-derived and rest on assumptions such as equilibrium between ingestion and evacuation and fixed prey-specific evacuation parameters. During periods of low capelin availability (e.g., the mid-late 2000s collapse), these assumptions may be strained, leading to higher actual uncertainty in the empirical values. Accordingly, mismatches between FR predictions and empirical estimates such as the underestimation for ages 3-4 in collapse years could reflect (i) limits of the FR structure, (ii) deviations from assumptions underpinning the empirical estimates, or (iii) both. In this reductionist setting, such discrepancies are better interpreted as signals of years when the empirical estimation assumptions held less well, rather than solely as shortcomings of the FR.
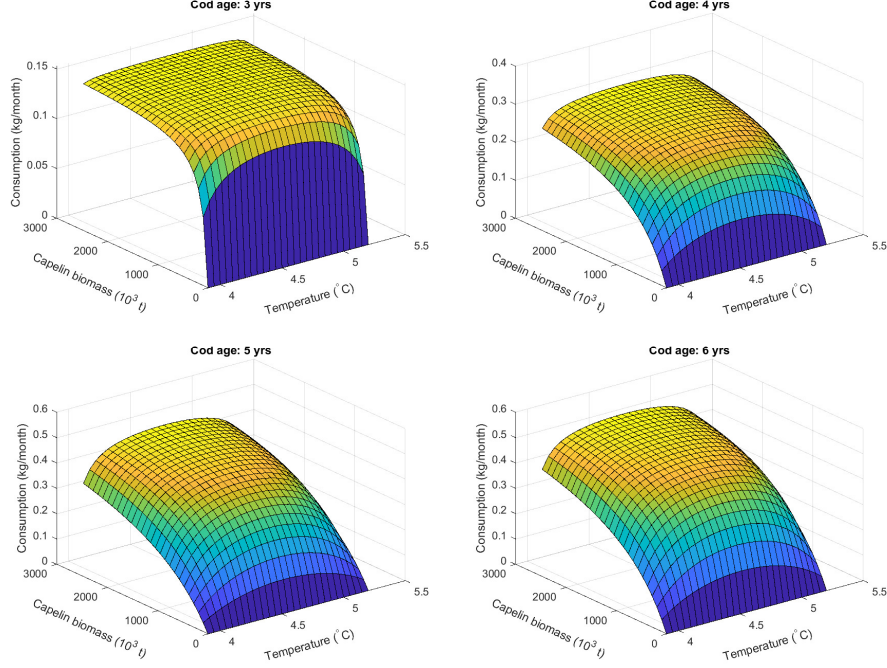
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Fig. 5 The surface $C(\Omega, \theta^*)$ using aggregated data for different ages.

To further explore the magnitude of such uncertainty within the FR framework, we implemented the stochastic temperature (ST) approach. By generating a distribution of temperature values within the observed range and estimating corresponding parameter sets and predictions, this method provides a broader uncertainty envelope that better reflects the underlying environmental variability. Nevertheless, some deviations remain, suggesting that localized environmental conditions and additional ecological factors not captured by the model may also contribute to the observed variability.

In general, consumption rates per year may potentially exhibit autocorrelation under conditions of environmental stability, biological cycles, lagged effects, population dynamics, and climate variability. For instance, if environmental factors influencing consumption (such as prey size and availability, and temperature) remain consistent over multiple years, or if predator-prey interactions follow cyclical patterns, consumption rates may show similar trends. Additionally, past consumption rates can impact future rates through lagged relationships. All these could lead to correlated consumption patterns.

Considering the year-to-year consumption rate as time series, the independence assumption is likely not valid. However, we do not have enough observations to estimate a correlation structure (e.g. AR(1)) for the time series. On the other hand, the assumption of independence may be arguably right, considering that collectively, the conditions that determine the rate of consumption (e.g., prey/predator abundance, species overlap, temperature, etc.) may be unique for every year. This is particularly relevant given the variability in capelin biomass dynamics, life-history trait, annual fluctuations in predator-prey overlap, and temperature distributions in the Barents Sea.
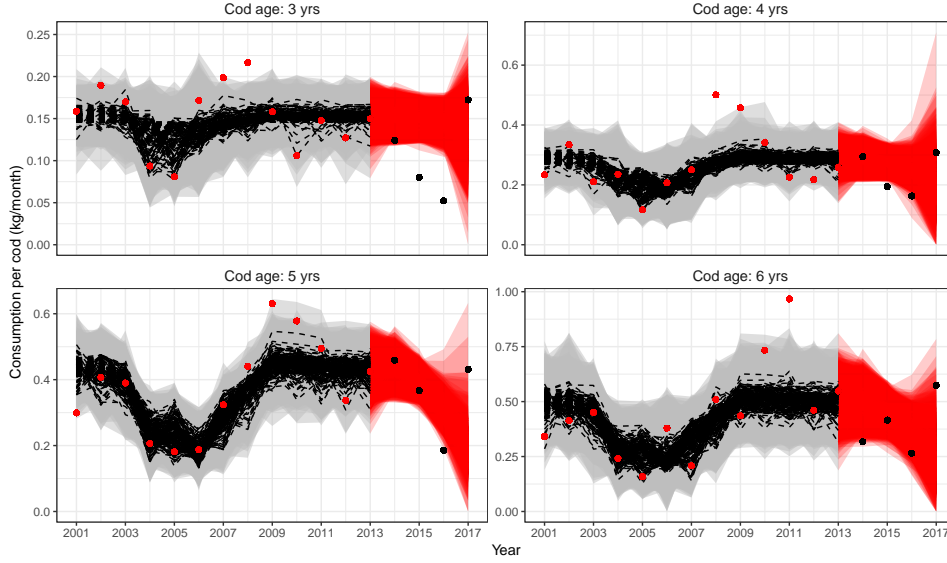
Fig. 6 Mean predictions and 95% confidence intervals of 200 re-sampled temperature measurements using a uniform distribution between the minimum and maximum temperature of the three areas. The model has been reestimated for each new sample.

Figure 5 shows surfaces of the function $C(\Omega, \theta^*)$, where C denotes cod consumption under the optimal parameter estimates θ^*. Each panel corresponds to a different age class of cod and illustrates how consumption varies jointly with capelin biomass and temperature. With handling time treated as constant in our baseline model, the temperature dependence reflects changes in the attack rate $a(T)$, while the monotone increase with prey biomass reflects the saturating functional response. Across ages, the overall level of consumption increases with body size, but the surface shapes differ: younger cod (ages 3-4) show flatter responses with respect to temperature, suggesting weaker sensitivity of consumption to $a(T)$. In contrast, older cod (ages 5-6) display more pronounced dome-shaped responses along the temperature axis, indicating stronger temperature dependence of attack rate. Thus, this figure provides a mechanistic, quantitative view of how consumption potential varies with prey abundance and temperature across age classes.

The FR model developed in this study offers a streamlined and practical approximation to the current complex empirical approaches used in capelin stock assessments. By modeling cod predation on capelin directly through a simple, with few parameters, the FR model replaces the need for multiple linked empirical models, each with their own assumptions and sources of uncertainty. This simplification makes the modeling process more transparent and less error-prone.

Additionally, uncertainty quantification becomes more straightforward, as variability can be systematically incorporated through the model structure and the stochastic temperature approach, rather than through compounded uncertainties across several empirical steps. The FR framework, when applied in this reductionist form, can support hypothesis testing about

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predator-prey interactions and environmental drivers within the boundaries of what is represented in the empirical estimates used as input. Because these estimates are based on their own set of modelling assumptions, such hypothesis tests should be interpreted within that scope. Broader ecological hypothesis testing would require embedding the FR in a population dynamics or holistic modelling framework that directly incorporates observational predator-prey dynamics.

A revised modeling framework incorporating the consumption model from this study is currently in development.

Declarations

Funding

Author contribution

M.J.: Writing and structuring the manuscript, data collection, data processing, statistical analysis, visualization, and coordinating revisions.
N.J.: Literature review, methodology support and data collection.
S.H.: Statistical analysis, visualization, and methodology support.
B.B.: Critical feedback and manuscript revisions.
S.S.: Initial drafting, research methodology, writing and structuring, and editing and proofreading.
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Appendix A Detailed Compution for Empirical Consumption of Capelin

Model basis and notation.

Following Santos and Jobling (1992); dos Santos and Jobling (1995), let $S_i(t)$ denote the stomach-content mass (g) of prey species i at time t after ingestion, and S_{i0} the initial mass of the ingested meal (g). Let W be the predator body mass (g), T temperature (°C), H_i the prey-specific half-life (h) evaluated for a meal equal to the predator body mass at 0°C, and c, β, δ constants across prey types. The general evacuation trajectory is

$$S_i(t) = S_{i0} \, \exp\left[-\ln 2 \, \left(\frac{t}{H_i \, e^{-cT} \, S_{i0}^{\beta} \, W^{-\delta}} \right)^{\kappa_i} \right], \tag{A1}$$

where κ_i is a prey-specific evacuation pattern parameter (shape exponent). The corresponding instantaneous consumption rate is

$$C_i(t) = -\frac{dS_i(t)}{dt} = \frac{\kappa_i \ln 2}{H_i} e^{cT} S_i(t) S_{i0}^{-\beta} W^\delta \left(\frac{t}{H_i e^{-cT} S_{i0}^\beta W^{-\delta}} \right)^{\kappa_i - 1}. \tag{A2}$$

For cod fed whole natural prey, setting $\kappa_i = 1$ provides a good approximation (Santos and Jobling, 1992), which simplifies (A2) considerably. In this case the evacuation is approximately exponential, and the expressions reduce to

$$S_i(t) = S_{i0} \exp\left[-\ln 2 \frac{t}{H_i e^{-cT} S_{i0}^\beta W^{-\delta}} \right], \tag{A3}$$

$$C_i(t) = -\frac{dS_i(t)}{dt} = \underbrace{\frac{\ln 2}{H_i} e^{cT}}_{F_i(T)} S_i(t) S_{i0}^{-\beta} W^\delta, \tag{A4}$$

with the temperature term defined explicitly as

$$F_i(T) = \frac{\ln 2}{H_i} e^{cT}.$$

Steady-state simplification.

Under a steady-state feeding assumption (see Bogstad and Gjøsæter, 1994), which posits equilibrium between evacuation and consumption rates, and using the standard field approximation $S_{i0} \approx \overline{S}$ with $\overline{S} = rW$ (ratio r is stomach-content/body-mass), we obtain the per-fish consumption rate ($\mathrm{g\,h^{-1}}$) for prey i:

$$C_i = \frac{S_i}{(rW)^\beta} F_i(T) W^\delta = \frac{S_i}{r^\beta W^\beta} F_i(T) W^\delta, \tag{A5}$$

where S_i is the observed stomach-content mass of prey i at sampling (i.e., dropping the explicit time index t in $S_i(t)$).

Nomenclature.

To avoid symbol conflicts, we reserve $S_i(t)$ for stomach content of prey i and use L_j for length-class indices. All quantities refer to the focal prey i unless indicated. Table A1 summarizes the symbols and definitions used in the empirical consumption calculations, particularly those appearing in Eqs. (A5)–(A9).

Table A1 Nomenclature used in the empirical consumption calculations.

Symbol	Definition
a_m	Oldest age class
$a \in \{1, 2, \ldots, a_m\}$	Age-class index
L_j	Predator length-class index
A_i	Area index, $i = 1, \ldots, N_A$
M_k	Month index in overlap window, $k = 1, \ldots, N_m$
D_{a,L_j,A_i}	Proportion of predators in age a, length class L_j, area A_i
V_{a,A_i}	Number of predators of age a in area A_i
W_{a,L_j,A_i}	Mean predator body mass (g) for age a, length L_j, area A_i
$\overline{S}^{\text{tot}}_{a,L_j,A_i}$	Mean *total* stomach content mass (all prey, g)
p_{a,L_j,A_i}	Fraction of focal prey in total stomach content (unitless)
$S_{a,L_j,A_i} \equiv p_{a,L_j,A_i}\, \overline{S}^{\text{tot}}_{a,L_j,A_i}$	Mean stomach-content mass (g) of focal prey
$T_{(M_k,A_i)}$	Area- and month-specific temperature (°C)
r	Stomach-content / body-mass ratio ($\overline{S} = rW$)
c, β, δ	Temperature, meal-size, and body-mass exponents
H_i	Half-life (h) for prey i
$F_i(T)$	Temperature term, $(\ln 2/H_i)e^{cT}$
Δt	Predator–prey overlap time (h)

From groups to per-fish and cohort consumption.

For predators of age a, length class L_j, in area A_i, combining (A5) with the group means gives the *per-fish* rate:

$$c_{a,L_j,A_i} \;=\; \frac{S_{a,L_j,A_i}}{r^\beta\, W^\beta_{a,L_j,A_i}}\, \tilde{F}_{A_i}\, W^\delta_{a,L_j,A_i}, \qquad S_{a,L_j,A_i} \;=\; p_{a,L_j,A_i}\, \overline{S}^{\text{tot}}_{a,L_j,A_i}, \tag{A6}$$

where $\tilde{F}_{A_i}$ averages the temperature term across the N_m overlap months:

$$\tilde{F}_{A_i} \;=\; \frac{\ln 2}{H_i} \cdot \frac{1}{N_m} \sum_{k=1}^{N_m} e^{\, c\, T_{(M_k,A_i)}}. \tag{A7}$$

Aggregating over length classes and scaling by abundance yields the *area-level* rate:

$$C_{a,A_i} \;=\; V_{a,A_i} \sum_j D_{a,L_j,A_i}\, c_{a,L_j,A_i}, \tag{A8}$$

and the *age-cohort* total over areas and overlap time is

$$C_a \;=\; \left(\sum_{i=1}^{N_A} C_{a,A_i} \right) \Delta t. \tag{A9}$$

Assumptions and limitations.

The following points contextualize the empirical consumption magnitudes reported here. For clarity, we group them into three categories:

(A) Experimental and parameterization constraints

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1. *Prey-specific rates:* H_i (and, when used, κ_i) are species-specific; values here pertain only to the focal prey.
2. *Lab-to-field transfer:* evacuation parameters are derived from controlled feeding of wild cod with whole prey; field behavior, activity, and stress may alter digestion.
3. *No predator-density or competition effects:* parameterization was based on individual cod experiments, without accounting for intra-specific competition or predator interference.
4. *No prey-switching dynamics:* while some experiments involved sequential feeding of different prey, explicit prey choice or switching behavior was not tested, and such mechanisms are absent from the parameter estimates.

(B) Theoretical and modeling assumptions

1. *Steady-state feeding:* Eqs. (A5)–(A6) assume ingestion $\approx$ evacuation over the window considered.
2. *Field proxy for S_{i0}:* initial meal size is replaced by observed/average stomach content ($\overline{S} = rW$); the unknown time-since-feeding introduces uncertainty.
3. *Scaling-up assumptions:* empirical consumption estimates apply laboratory-derived evacuation parameters to population-level cod–capelin interactions by combining spatial distribution, cod size, and average stomach contents; this upscaling may smooth over local non-linearities or context-dependent behaviors.

(C) Environmental constraints

1. *Temperature range and stability:* parameters were estimated for 1–14°C; predictions outside this range or under rapidly varying T are extrapolations.

Parameter values and data sources.

We use the following parameter set (values for cod consuming capelin unless noted) indicated in Table A2.

Table A2 Parameters used in Eqs. (A4)–(A7).

Symbol	Description	Value	Source
c	Temperature coefficient	0.13	Santos and Jobling (1992); dos Santos and Jobling (1995)
β	Initial meal-size exponent	0.52	Santos and Jobling (1992); dos Santos and Jobling (1995)
δ	Body-mass exponent	0.26	Santos and Jobling (1992); dos Santos and Jobling (1995)
r	Stomach-content ratio ($\overline{S} = rW$)	1.78	Bogstad and Mehl (1997)
H_i	Half-life of focal prey (h)	58.0	Santos and Jobling (1992); dos Santos and Jobling (1995)

Temperatures, stomach contents, and abundance inputs.

Let $T_{(M_k, A_i)}$ be the average temperature in area A_i during month M_k ($k = 1, \ldots, N_m$). Then $\tilde{F}_{A_i}$ is given by (A7). Group-specific means $\overline{S}^{\text{tot}}_{a,L_j,A_i}$ and fractions p_{a,L_j,A_i} are derived from stomach-content sampling; abundances V_{a,A_i} (with mortality/maturity adjustments as in the main text) and masses W_{a,L_j,A_i} are taken from the assessment inputs listed in Table A3.

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Table A3 Data sources feeding Eqs. (A6)–(A9).

Quantity	Description	Source
$\overline{S}^{\text{tot}}$	Total stomach content (all prey, g)	Winter survey (Feb–Mar); Bogstad and Mehl (1997)
p	Focal-prey stomach fraction	Winter survey (Feb–Mar); Bogstad and Mehl (1997)
T	Temperature (area–month means)	Kola transect; Bogstad and Mehl (1997)
V, W, D	Numbers, masses, and composition by age/length/area	ICES AFWG reports (years as cited in text)

Abundance and body-mass calculations.

Let m_a and F_a denote natural and fishing mortality for age a, and let p_{a,A_i} be the proportion of the age-a stock maturing in area A_i during the first quarter. Define $V_{a,A_i}^{(J)}$ as the January 1 abundance for age a in area A_i. We use simple quarter-year survival and a maturity-availability adjustment of capelin to approximate in-season abundance for two commonly used dates:

$$\underbrace{V_{a,A_i}^{(A)}}_{\text{April 1}} \approx \underbrace{V_{a,A_i}^{(J)}}_{\text{January 1}} \cdot \underbrace{\exp\!\left[-\tfrac{1}{4}\left(F_a + m_a\right)\right]}_{\text{Jan–Apr survival}} \cdot \underbrace{\left(1 - \tfrac{1}{2}p_{a,A_i}\right)}_{\text{reduced availability of maturing fish}} , \tag{A10}$$

$$\underbrace{V_{a,A_i}^{(O)}}_{\text{October 1}} \approx \underbrace{V_{a,A_i}^{(J)}}_{\text{January 1}} \cdot \underbrace{\exp\!\left[-\tfrac{3}{4}\left(F_a + m_a\right)\right]}_{\text{Jan–Oct survival}}. \tag{A11}$$

Finally, let $W_{a,L_j,A_i}^{(J,Y)}$ and $W_{a+1,L_j',A_i}^{(J,Y+1)}$ be mean body masses on January 1 of years Y and $Y+1$ for ages a and $a+1$ in the corresponding length classes (length classes may be re-binned year-to-year; use the mapped class L_j' for $a+1$). We linearly interpolate within the assessment year as

$$\underbrace{W_{a,L_j,A_i}^{(t)}}_{\text{at month } t \text{ in year } Y} \approx W_{a,L_j,A_i}^{(J,Y)} + f\left(W_{a+1,L_j',A_i}^{(J,Y+1)} - W_{a,L_j,A_i}^{(J,Y)}\right), \qquad f \in [0,1], \tag{A12}$$

so that

$$\underbrace{W_{a,L_j,A_i}^{(A)}}_{\text{April 1}} \approx W_{a,L_j,A_i}^{(J,Y)} + \tfrac{1}{4}\left(W_{a+1,L_j',A_i}^{(J,Y+1)} - W_{a,L_j,A_i}^{(J,Y)}\right), \tag{A13}$$

$$\underbrace{W_{a,L_j,A_i}^{(O)}}_{\text{October 1}} \approx W_{a,L_j,A_i}^{(J,Y)} + \tfrac{3}{4}\left(W_{a+1,L_j',A_i}^{(J,Y+1)} - W_{a,L_j,A_i}^{(J,Y)}\right). \tag{A14}$$

Plug $W_{a,L_j,A_i}^{(t)}$ into Eq. (A6) to compute c_{a,L_j,A_i}, and $V_{a,A_i}^{(t)}$ into Eqs. (A8) and (A9) to compute area- and cohort-level totals. This keeps the abundance and mass definitions consistent with the evacuation-based consumption formulation.

References

Arditi, R., Akçakaya, H.: Underestimation of mutual interference of predators. Oecologia **83**(3), 358–361 (1990)

Abrams, P.A., Ginzburg, L.R.: The nature of predation: prey dependent, ratio dependent or neither? Trends in Ecology & Evolution **15**(8), 337–341 (2000)

Bailey, K.M., Duffy-Anderson, J.T.: Fish predation and mortality. Elements of Physical Oceanography: A Derivative of the Encyclopedia of Ocean Sciences; Steele, JH, Thorpe, SA, Turekian, KK, Eds, 322–329 (2009)

Bogstad, B., Gjøsæter, H.: A method for estimating the consumption of capelin by cod in the Barents Sea. ICES Journal of Marine Science **51**(3), 273–280 (1994)

Bogstad, B., Gjøsæter, H.: Predation by cod (Gadus morhua) on capelin (Mallotus villosus) in the Barents Sea: implications for capelin stock assessment. Fisheries Research **53**(2), 197–209 (2001)

Bogstad, B., Haug, T., Mehl, S.: Who eats whom in the barents sea? NAMMCO Scientific Publications **2**, 98–119 (2000) https://doi.org/10.7557/3.2975

Bogstad, B., Hauge, K.H., Ulltang, Ø.: MULTSPEC–a multi-species model for fish and marine mammals in the Barents Sea. Journal of Northwest Atlantic Fishery Science **22**, 317–341 (1997)

Bogstad, B., Mehl, S.: Interactions between Atlantic cod (Gadus morhua) and its prey species in the Barents Sea. In: Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report, pp. 591–615 (1997)

Bromley, P.J.: The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. Reviews in Fish Biology and Fisheries **4**(1), 36–66 (1994)

Baum, J.K., Worm, B.: Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology **78**(4), 699–714 (2009)

Carroll, G., Holsman, K.K., Brodie, S., Thorson, J.T., Hazen, E.L., Bograd, S.J., Haltuch, M.A., Kotwicki, S., Samhouri, J., Spencer, P., *et al.*: A review of methods for quantifying spatial predator–prey overlap. Global Ecology and Biogeography **28**(11), 1561–1577 (2019)

Ciannelli, L., Hjermann, D., Lehodey, P., Ottersen, G., Duffy-Anderson, J., Stenseth, N.C.: Climate forcing, food web structure and community dynamics in pelagic marine ecosystems. In: Aquatic Food Webs: An Ecosystem Approach, pp. 143–169. Oxford University Press, Oxford, UK (2005)

Dvoretsky, A.G., Dvoretsky, V.G.: Commercial fish and shellfish in the Barents Sea: have introduced crab species affected the population trajectories of commercial fish? Reviews in Fish Biology and Fisheries **25**(2), 297–322 (2015)

DeAngelis, D.L., Goldstein, R., O'Neill, R.V.: A model for trophic interaction. Ecology **56**(4),

881–892 (1975)

Santos, J., Jobling, M.: Test of a food consumption model for the Atlantic cod. ICES Journal of Marine Science **52**(2), 209–219 (1995)

Durant, J.M., Skern-Mauritzen, M., Krasnov, Y.V., Nikolaeva, N.G., Lindstrøm, U., Dolgov, A.: Temporal dynamics of top predators interactions in the Barents Sea. PLoS One **9**(11), 110933 (2014)

Eriksen, E., Benzik, A.N., Dolgov, A.V., Skjoldal, H.R., Vihtakari, M., Johannesen, E., Prokhorova, T.A., Keulder-Stenevik, F., Prokopchuk, I., Strand, E.: Diet and trophic structure of fishes in the Barents Sea: The Norwegian-Russian program "Year of stomachs" 2015–Establishing a baseline. Progress in Oceanography **183**, 102262 (2020)

Edgar, G.J., Ward, T.J., Stuart-Smith, R.D.: Weaknesses in stock assessment modelling and management practices affect fisheries sustainability. Aquatic Conservation: Marine and Freshwater Ecosystems **29**(11), 2010–2016 (2019)

Fall, J.: Drivers of variation in the predator-prey interaction between cod and capelin in the barents sea. phdthesis, University of Bergen (2019)

Fall, J., Ciannelli, L., Skaret, G., Johannesen, E.: Seasonal dynamics of spatial distributions and overlap between Northeast Arctic cod (Gadus morhua) and capelin (Mallotus villosus) in the Barents Sea. PloS one **13**(10), 0205921 (2018)

Fall, J.J.E., Johannesen, E., Englund, G., Johansen, G.O., Fiksen, Ø.: Predator–prey overlap in three dimensions: cod benefit from capelin coming near the seafloor. Ecography **44**(5), 802–815 (2021) https://doi.org/10.1111/ecog.05473

Fauchald, P., Skov, H., Skern-Mauritzen, M., Johns, D., Tveraa, T.: Wasp-waist interactions in the North Sea ecosystem. PloS one **6**(7), 22729 (2011)

Gjøsæter, H., Bogstad, B., Tjelmeland, S.: Assessment methodology for Barents Sea capelin, Mallotus villosus (Müller). ICES Journal of Marine Science **59**(5), 1086–1095 (2002)

Gjøsæter, H., Bogstad, B., Tjelmeland, S., Subbey, S.: A retrospective evaluation of the Barents Sea capelin management advice. Marine Biology Research **11**(2), 135–143 (2015)

Gislason, H., Helgason, T.: Species interaction in assessment of fish stocks with special application to the North Sea. Dana **5**(2), 1–44 (1985)

Gudmundsdottir, A., Vilhjálmsson, H.: Predicting total allowable catches for Icelandic capelin, 1978–2001. ICES Journal of Marine Science **59**(5), 1105–1115 (2002)

Haque, M.: Ratio-dependent predator-prey models of interacting populations. Bulletin of Mathematical Biology **71**(2), 430–452 (2009)

Hjermann, D.Ø., Bogstad, B., Dingsør, G.E., Gjøsæter, H., Ottersen, G., Eikeset, A.M.,

Stenseth, N.C.: Trophic interactions affecting a key ecosystem component: a multi-stage analysis of the recruitment of the barents sea capelin. Canadian Journal of Fisheries and Aquatic Sciences **67**(9), 1363–1375 (2010) https://doi.org/10.1139/F10-064

Holt, R.E., Bogstad, B., Durant, J.M., Dolgov, A.V., Ottersen, G.: Barents Sea cod (Gadus morhua) diet composition: long-term interannual, seasonal, and ontogenetic patterns. ICES Journal of Marine Science **76**(6), 1641–1652 (2019)

Holden, M.H., Conrad, J.M.: Optimal escapement in stage-structured fisheries with environmental stochasticity. Mathematical Biosciences **269**, 76–85 (2015)

Haubrock, P.J., Cuthbert, R.N., Veselỳ, L., Balzani, P., Baker, N.J., Dick, J.T., Kouba, A.: Predatory functional responses under increasing temperatures of two life stages of an invasive gecko. Scientific reports **10**(1), 1–10 (2020)

Hollowed, A.B., Ianelli, J.N., Livingston, P.A.: Including predation mortality in stock assessments: a case study for Gulf of Alaska walleye pollock. ICES Journal of Marine Science **57**(2), 279–293 (2000)

Holling, C.S.: Some characteristics of simple types of predation and parasitism. The Canadian Entomologist **91**(7), 385–398 (1959)

Holling, C.S.: The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. The Canadian Entomologist **91**(5), 293–320 (1959)

Hassell, M., Varley, G.: New inductive population model for insect parasites and its bearing on biological control. Nature **223**(5211), 1133 (1969)

He, E., Wurtsbaugh, W.A.: An empirical model of gastric evacuation rates for fish and an analysis of digestion in piscivorous brown trout. Transactions of the American Fisheries Society **122**(5), 717–730 (1993)

Hylen, A.: Fluctuations in abundance of Northeast Arctic cod during the 20th century. In: ICES Marine Science Symposia, vol. 215, pp. 543–550 (2002)

ICES: Benchmark workshop on capelin (wkcapelin). ICES Scientific Reports 5:62, ICES (2023). ICES Scientific Reports. 5:62. 282 pp. https://doi.org/10.17895/ices.pub.23260388

Jobling, M., Gwyther, D., Grove, D.: Some effects of temperature, meal size and body weight on gastric evacuation time in the dab limanda limanda (l). Journal of Fish Biology **10**(3), 291–298 (1977)

Johannesen, E., Ingvaldsen, R.B., Bogstad, B., Dalpadado, P., Eriksen, E., Gjøsæter, H., Knutsen, T., Skern-Mauritzen, M., Stiansen, J.E.: Changes in Barents Sea ecosystem state, 1970–2009: climate fluctuations, human impact, and trophic interactions. ICES Journal of Marine Science **69**(5), 880–889 (2012)

Johannesen, E., Johansen, G., Bogstad, B., Mehl, S., Tjelmeland, S., Dolgov, A.: Cod Consume Capelin– ICES AFWG WD 20. Technical report, International Council for the Exploration of the Sea (ICES) (April 2006)

Jeschke, J.M., Kopp, M., Tollrian, R.: Predator functional responses: discriminating between handling and digesting prey. Ecological Monographs **72**(1), 95–112 (2002)

Jurado-Molina, J., Livingston, P.A., Ianelli, J.N.: Incorporating predation interactions in a statistical catch-at-age model for a predator-prey system in the eastern Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences **62**(8), 1865–1873 (2005)

Jobling, M.: Influences of food particle size and dietary energy content on patterns of gastric evacuation in fish: test of a physiological model of gastric emptying. Journal of Fish Biology **30**(3), 299–314 (1987)

Koen-Alonso, M., Lindstrøm, U., Cuff, A.: Comparative modeling of cod–capelin dynamics in the newfoundland–labrador shelves and barents sea ecosystems. Frontiers in Marine Science **8**, 579946 (2021) https://doi.org/10.3389/fmars.2021.579946

Kjesbu, O.S., Bogstad, B., Devine, J.A., Gjøsæter, H., Howell, D., Ingvaldsen, R.B., Nash, R.D., Skjæraasen, J.E.: Synergies between climate and management for Atlantic cod fisheries at high latitudes. Proceedings of the National Academy of Sciences **111**(9), 3478–3483 (2014)

Kempf, A.: Ecosystem approach to fisheries in the European context–history and future challenges. Journal of Applied Ichthyology **26**, 102–109 (2010)

Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., Bell, B.M.: TMB: Automatic differentiation and Laplace approximation. Journal of Statistical Software **70**(5), 1–21 (2016) https://doi.org/10.18637/jss.v070.i05

Kulatska, N.: Baltic cod predation: mechanisms, impact on prey, implications for fisheries. phdthesis, Swedish University of Agricultural Sciences (2019)

Liao, H., Pierce, C.L., Larscheid, J.G.: An empirical model for estimating annual consumption by freshwater fish populations. North American Journal of Fisheries Management **25**(2), 525–532 (2005)

Lees, K., Pitois, S., Scott, C., Frid, C., Mackinson, S.: Characterizing regime shifts in the marine environment. Fish and fisheries **7**(2), 104–127 (2006)

Mehl, S., Aglen, A., Alexandrov, D.I., Bogstad, B., Dingsør, G.E., Gjøsæter, H., Johannesen, E., Korsbrekke, K., Murashko, P.A., Prozorkevich, D.V., Smirnov, O., Staby, A., Wenneck, T.d.L.: Fish investigations in the barents sea winter 2007-2012. Technical Report 1-2013, IMR-PINRO Joint Report Series (2013)

Mofu, L., Cuthbert, R.N., Dalu, T., Woodford, D.J., Wasserman, R.J., Dick, J.T., Weyl, O.L.:

Impacts of non-native fishes under a seasonal temperature gradient are forecasted using functional responses and abundances. NeoBiota **49**, 57 (2019)

Orlova, E., Dolgov, A., Boitsov, V., Ushakov, N., Rudneva, G.: Long-term variations in the relationships between the main components of the Barents Sea ecosystem (cod and capelin) and ecological and physiological aspects of their interactions. ICES C **3**, 24 (2006)

Planque, B., Primicerio, R., Michalsen, K., Aschan, M., Certain, G., Dalpadado, P., Gjøsæter, H., Hansen, C., Johannesen, E., Jørgensen, L.L., *et al.*: Who eats whom in the Barents Sea: a food web topology from plankton to whales: Ecological Archives E095-124. Ecology **95**(5), 1430–1430 (2014)

R Core Team: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (2017). R Foundation for Statistical Computing. https://www.R-project.org/

Romare, P., Hansson, L.-A.: A behavioral cascade: top-predator induced behavioral shifts in planktivorous fish and zooplankton. Limnology and Oceanography **48**(5), 1956–1964 (2003)

Swain, D.P., Benoît, H.P., Hammill, M.O.: Spatial distribution of fishes in a Northwest Atlantic ecosystem in relation to risk of predation by a marine mammal. Journal of Animal Ecology **84**(5), 1286–1298 (2015)

South, J., Dick, J.T.: Effects of acute and chronic temperature changes on the functional responses of the dogfish Scyliorhinus canicula (Linnaeus, 1758) towards amphipod prey Echinogammarus marinus (Leach, 1815). Environmental Biology of Fishes **100**(10), 1251–1263 (2017)

Skjoldal, H.R., Eriksen, E., Gjøsæter, H.: Size-fractioned zooplankton biomass in the barents sea: Spatial patterns and temporal variations during three decades of warming and strong fluctuations of the capelin stock (1989–2020). Progress in Oceanography **206**, 102852 (2022) https://doi.org/10.1016/j.pocean.2022.102852

Skalski, G.T., Gilliam, J.F.: Functional responses with predator interference: viable alternatives to the Holling type II model. Ecology **82**(11), 3083–3092 (2001)

Sentis, A., Hemptinne, J.-L., Brodeur, J.: Using functional response modeling to investigate the effect of temperature on predator feeding rate and energetic efficiency. Oecologia **169**(4), 1117–1125 (2012)

Santos, J.D., Jobling, M.: A model to describe gastric evacuation in cod (Gadus morhua L.) fed natural prey. ICES Journal of Marine Science **49**(2), 145–154 (1992)

Skern-Mauritzen, M., Ottersen, G., Handegard, N.O., Huse, G., Dingsør, G.E., Stenseth, N.C., Kjesbu, O.S.: Ecosystem processes are rarely included in tactical fisheries management. Fish and Fisheries **17**(1), 165–175 (2016)

Thompson, D.J.: Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, Ischnura elegans. The Journal of Animal Ecology, 757–767 (1978)

Tyrrell, M., Link, J., Moustahfid, H.: The importance of including predation in fish population models: implications for biological reference points. Fisheries Research **108**(1), 1–8 (2011)

Yaragina, N.A., Dolgov, A.V.: Ecosystem structure and resilience—a comparison between the Norwegian and the Barents Sea. Deep Sea Research Part II: Topical Studies in Oceanography **56**(21-22), 2141–2153 (2009)