

ORIGINAL ARTICLE

No room for dessert: A mechanistic model of prey selection in gut-limited predatory fish

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Abstract

Predatory fish structure communities through prey pursuit and consumption and, in many marine systems, the gadoids are particularly important. These predators have flexible feeding behaviours and often feed on large prey items. Digestion times of large prey are usually longer than handling times, and gut processing limits feeding rate at high prey density. Optimizing the gut content mix can therefore be an important behavioural strategy. Here, we develop a foraging model that incorporates gut processing and use the model to disentangle internal and external limitations on feeding in the omnivorous cod (*Gadus morhua*, Gadidae). We extend the traditional definition of prey profitability to consider prey digestive quality, which we quantify for prey of Northeast Atlantic cod populations. We find an important role for gut limitation; within a range of ecologically relevant temperatures and prey densities, predicted feeding rates were strongly reduced compared to feeding constrained by external factors only, and the optimal diet composition under gut limitation differed from predictions from traditional foraging theory. Capelin, a main prey of Northeast Arctic cod, had the highest digestive quality of all prey across ecosystems, but the cold temperatures in the Barents Sea strongly limited feeding rate by slowing down digestion. Baltic cod fed on a higher proportion of poor-quality prey compared to the other populations, contributing to its slow growth in relation to water temperature. Gut limitation is particularly important to consider in foraging models for fish with many alternative prey species or fish occupying cold waters where digestion is slow.

KEYWORDS

foraging models, gut limitation, omnivorous fish, predator-prey interactions, prey profitability, stomach capacity

1 | INTRODUCTION

The feeding rate of most predators appears to be limited by prey encounter or digestion rather than prey handling (Giske & Salvanes, 1995; Jeschke, Kopp, & Tollrian, 2002), which was the main focus in early optimal foraging models (Charnov, 1976; Emlen, 1966; MacArthur & Pianka, 1966; Pulliam, 1974; Schoener, 1971; Werner

& Hall, 1974). If a predator frequently encounters, attacks and consumes prey at a rate that fills up its stomach, it will be forced to take a break from feeding (Van Gils et al., 2005). This sets an upper limit on predation risk for prey, and the predator can spend more time in safety, digesting. Stomach storage capacity and gut processing time

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limit foraging in taxa as diverse as ladybird beetles (*Propylea quatuordecimpunctata*, Coccinellidae; Papanikolaou, Milonas, Demiris, Papachristos, & Matsinos, 2014), prairie voles (*Microtus ochrogaster*, Cricetidae; Zynel & Wunder, 2002), oystercatchers (*Haematopus ostralegus*, Haematopodidae; Kersten & Visser, 1996) and lake trout (*Salvelinus namaycush*, Salmonidae; Jensen, Hrabik, Martell, Walters, & Kitchell, 2006). However, very few studies compare internal and external constraints on foraging even though an animal's foraging behaviour and digestive system are co-adapted and jointly underlie its feeding ecology (Whelan & Brown, 2005; Whelan & Schmidt, 2008).

Fish feeding on large prey usually spend less time feeding and more time digesting compared to fish feeding on many small prey (e.g. piscivorous vs. planktivorous fish; Breck, 1993). Therefore, gut limitation plays a larger role in the feeding process of predatory fishes. Water temperature also affects gut processing times in fish since metabolic rates are temperature-dependent (Andrade, Cruz-Neto, Abe, & Wang, 2005), leading to slower digestion in colder waters (Temming & Herrmann, 2003). How gut limitation influences prey selection has received relatively little attention in the history of foraging theory, except in models of herbivore foraging (Farnsworth & Illius, 1998; Hirakawa, 1997; Penry & Jumars, 1987; Verlinden & Wiley, 1989; Westoby, 1974). Nevertheless, many predators regularly feed to satiation (Jeschke, 2007) and benefit from selecting prey with high energy return per unit digestion time rather than handling time (Gill & Hart, 1998; Verlinden & Wiley, 1989).

Foraging models and studies of prey selection in fish tend to be tested with small fish or on the larvae of larger species, while less attention has been given to the mechanisms of prey selection in adult fish in general, and to adult marine predatory fish in particular. In the North Atlantic, data on the diets of predatory fish are especially abundant for commercially important gadoids, such as Atlantic cod, whiting (*Merlangius merlangus*, Gadidae), haddock (*Melanogrammus aeglefinus*, Gadidae) and saithe (*Pollachius virens*, Gadidae; Link & Almeida, 2000; Pinnegar, 2014). Diet data have been increasingly collected in monitoring programmes since multispecies and ecosystem considerations were introduced in fisheries management (Hunsicker et al., 2011), but these data are rarely analysed with prior theoretical expectations about how small-scale ecological processes give rise to larger-scale patterns (Horodysky, Cooke, & Brill, 2015; Persson, Leeuwen, & Roos, 2014). For example, analyses of stomach contents tell us what an individual has eaten but not the sequence of mechanisms and behavioural decisions leading to the ingestion, and it is therefore not possible to predict the diet composition under other prey mixtures or environmental circumstances than those sampled. We need foraging models and evolutionary theory to predict emergent diets from constraints, trade-offs and the environment.

Foraging has remained a central topic in ecology since the advent of optimal foraging theory, though the focus has shifted from optimality to more detailed individual- and trait-based models where motivation, personality and stochasticity affect decision-making (Railsback & Harvey, 2013). Early foraging theory was a major step forward in ecology, and its predictions still have value

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for understanding basic decisions animals make. In this paper, we present a mechanistic foraging model that explicitly incorporates gut limitation and disentangle internal and external limitations on feeding rate in fishes. We include three alternative algorithms for prey selection and compare their predicted diets with field data. Our aim is not to construct a model of the full complexity required for precise prediction of fish foraging, but to capture the essential drivers of prey selection with special attention to gut limitation. We use the commercially and ecologically important Atlantic cod as a model organism, and (a) quantify the relative profitabilities of prey in terms of energetic, behavioural and digestive properties, (b) explore how water temperature, foraging time and prey density affect feeding rate limitation, (c) predict the optimal diet composition of cod in the Barents Sea from regional prey availability with alternative models of prey selection and (d) compare the predictions to empirical data on cod stomach contents. Since the water temperature is low in the Barents Sea and cod feeds on a diversity of prey, many of which are

large, we hypothesize that cod is gut-limited and that this limitation influences prey selection. Finally, we compare prey profitability in the diets of cod in the Barents, Baltic and North seas, relating the relative proportions of high-quality prey to differences in growth rates between the populations.

2 | MATERIALS AND METHODS

2.1 | The models

The classic optimal foraging model, termed the “contingency model” by Belovsky (1984), focuses on the behavioural and external properties of foraging—the time it takes for the predator to stalk, attack, capture, manipulate and ingest prey. The contingency model predicts a predator's probability of attack given an encounter with prey from the relative energy gained per time unit by attacking it compared to ignoring it and searching for prey that is more profitable. The “digestive rate model” (Verlinden & Wiley, 1989) focuses on internal physiological aspects of prey selection. The digestive rate model treats predators as gut-limited as opposed to handling-limited, using the digestibility, or assimilable energy per unit digestion time (“digestive quality”), as a proxy for prey profitability. As opposed to the “either-or rule” of the contingency model, where a specific prey type is either selected or ignored (Schoener, 1971), the digestive rate model predicts partial preferences as the predator may fill up the remaining gut space, if any, with lower quality prey (Quaintenne, Gils, Bocher, DeKinga, & Piersma, 2010; Verlinden & Wiley, 1989). Apart from these differences, the contingency and digestive rate models are structurally similar and operate with similar assumptions (for a summary of the assumptions, see table 1 in Hirvonen & Ranta, 1996). To compare predictions from the two models, the contingency model must also include a gut constraint on foraging potential. To our knowledge, the only comparison of the contingency and digestive rate models under a gut constraint is from studies of a molluscivorous shorebird, the red knot (*Calidris canutus*, Scolopacidae; Quaintenne et al., 2010; Van Gils et al., 2005).

Here, we consider the diet of an omnivorous predatory fish from both the contingency model and the digestive rate model, while explicitly considering the time it takes for food to pass through the gut. We compare the growth rate for a predator selecting prey based on the external handling time and prey search time (contingency model) and one that also takes the digestive quality of the diet into consideration (digestive rate model). Although the contingency model is based on external ecology, prey must still pass through the gut, which is why this model may yield a suboptimal diet if prey items differ in their energy density or digestibility. We also compare predictions from the contingency and digestive rate models to a non-selective model with gut limitation to get the diet under the null assumption of indiscriminate feeding, in proportion to prey encounter rate. Below, we present the central parameters of the models, an overview of the study system and a technical model description with code (Supporting Information).

2.2 | Search rate

In the models, search rate β_i (volume per unit time) for prey i depends on the prey-specific radius at which the predator can detect the prey, R_i , the angle of the visual search field, θ , and the average (long-term sustainable) swimming speed of the predator, \bar{v} (Equation 1, Huse & Fiksen, 2010):

$$\beta_i = \pi(R_i \sin \theta)^2 \bar{v} \quad (1)$$

The visual range R_i depends on several factors related to predator vision, prey size and ambient light conditions (Meager, Moberg, Strand, & Utne-Palm, 2010), but for simplicity, we use fixed values of R_i for each potential prey throughout the daily foraging time (Table 1).

2.3 | Capture, handling and digestion

Two parameters characterize the behaviour of predator and prey during an attack: capture probability and handling time. These parameters are often assumed to depend on relative prey and predator lengths (e.g. in fish larvae, Deslauriers, Rosburg, & Chipps, 2017; Hoyle & Keast, 1987; Miller, Crowder, Rice, & Marschall, 1988). Here, we assume capture probability c_i for adult fish scales with relative prey and predator lengths as it does in fish larvae (L_i = prey length, L_p = predator length, Equation 2). However, faster prey are usually better at escaping, so we also include relative swimming speeds of prey and predator (v_i , v_p ; see Supporting Information) in the capture probability submodel (Figure 1a):

$$c_i = \left(1 - \frac{L_i v_i}{L_p v_p}\right)^3 \quad (2)$$

This captures some of the known variation in swimming ability for prey of similar size (e.g. the maximum swimming speed of herring is twice that of a similarly sized capelin; Behrens, Præbel, & Steffensen, 2006; Brawn, 1960).

Handling time is the search time lost to the predator from the moment it decides to attack a prey until search for other prey can be resumed (e.g. Hughes, 1979). We set the minimum handling time to 0.05 min (3 s) since cod must turn and slow down to capture even the smallest prey, and assume that handling time increases cubically (e.g. Scharf, Buckel, Juanes, & Conover, 1998) with relative lengths and swimming speeds of prey and predator up to a maximum time of 5 min each for the length-dependent and speed-dependent components of the equation (Figure 1b; Equation 3). This gives reasonable handling times compared to those actually measured for juvenile cod (Arnott, 1996; Arnott & Pihl, 2000; Ellis & Gibson, 1997):

$$h_i = 0.05 + 5(L_i/L_p)^3 + 5(v_i/v_p)^3 \quad (3)$$

The digestive rate of prey in grams per day (24 hr) is estimated from a modified exponential gut evacuation model developed for Atlantic cod, where the digestive rate depends on a prey-specific

TABLE 1 Main parameters used in the models, including units and source

Symbol	Description	Unit	Source
a_i	Density of prey i	ind/m ³ or ind/m ² (benthic prey)	Averages from field data
β_i	Search rate for prey i	m ³ /min	Equation 1
c_i	Capture probability of prey i	dimensionless	Equation 2
D_{tot}	Total mass of prey digested during a foraging cycle	g/day	Equation 5, modified from Temming and Herrmann (2003)
e_i	Prey-specific energy content	kJ/g wet weight	From the literature ^a
\hat{e}	Average prey-specific energy content weighted by the mass of each prey in the stomach at the end of a foraging cycle, δ_i	kJ/g wet weight	Equation 5 (replacing ρ_i with e_i)
h_i	External handling time for one prey i (time from detection to ingestion)	min/ind	Equation 3
I	Total ingestion rate in the contingency model	kJ/min	Equation 6
j	The least profitable prey species in the contingency model		See Modelling feeding and digestion
L_i	Body length of prey species i	cm	Averages from field data
L_p	Body length of the predator	cm	Average for 7-year-old cod from field data
m_p	Mass of the predator	g	Average for 7-year-old cod from field data
n	The least profitable prey included in the contingency model diet		See Modelling feeding and digestion
P_i	Profitability of prey i in the contingency model: $P_i = c_i \frac{e_i}{h_i}$	kJ/min	Schoener (1971), Visser and Fiksen (2013)
Q_i	Digestive quality of prey i in the digestive rate model; $Q_i = \frac{e_i}{d_i}$, where d_i is the digestion time for one prey i derived from the single-species version of Equation 5	kJ/min	Modified from Verlinden and Wiley (1989)
R_i	Detection radius for prey i	m	Set to 0.25 m for small pelagic and demersal prey, 0.5 m for larger demersal prey and 2 m for pelagic/mesopelagic fish prey
T	Water temperature	°C	Averages from field data
v_i	Max swimming speed of prey i	m/min	From the literature ^b
v_p	Burst swimming speed of the predator	m/min	Reidy, Kerr, and Nelson (2000)
ρ_i	Prey-specific evacuation parameter	g ^{0.5} /hr	Temming and Herrmann (2003), Andersen (2012)
$\hat{\rho}$	Average prey-specific evacuation parameter weighted by the mass of each prey in the stomach at the end of a foraging cycle, δ_i	g ^{0.5} /hr	Equation 4
δ_i	Mass of prey i in the stomach at the end of a foraging cycle	g	Equations 1 and 6
$\hat{\delta}_{\text{tot}}$	Total mass of prey in the stomach at the end of a foraging cycle	g	Equations 1 and 6
θ	Angle of the visual field	radians	$\pi/5$ (30°), Fiksen, Aksnes, Flyum, and Giske (2002), Huse and Fiksen (2010)

^aBogstad and Mehl (1997), dos Santos and Jobling (1995), Harvey, Pleuthner, Lessard, Bernhardt, and Shaw (2012), Holdway and Beamish (1984), Jangaard (1974), Kaiser, Andrew, Hughes, and Gibson (1992), Mårtensson, Gotaas, Norddy, and Blix (1996), Temming and Herrmann (2003).

^bArnott, Neil, and Ansell (1998), Arnott, Neil, & Ansell, 1999), Beamish (1966), Behrens et al. (2006), Brawn (1960), Breen, Dyson, O'Neill, Jones, and Haigh (2004), Finke, Pörtner, Lee, and Webber (1996), Ignatyev (1996) Kaiser, Gibson, Gibson, and Hughes (1992), Videler and Wardle (1991).

evacuation constant (ρ_i), the mass of the predator (m_p), water temperature (T) and the mass of prey consumed δ_i (Temming & Herrmann, 2003; Figure 1c). We turn the evacuation rate into a single digestion

rate for the whole gut contents instead of calculating it separately for each prey species (following the reasoning of Andersen & Beyer, 2005; see also Supporting Information), using the mean evacuation

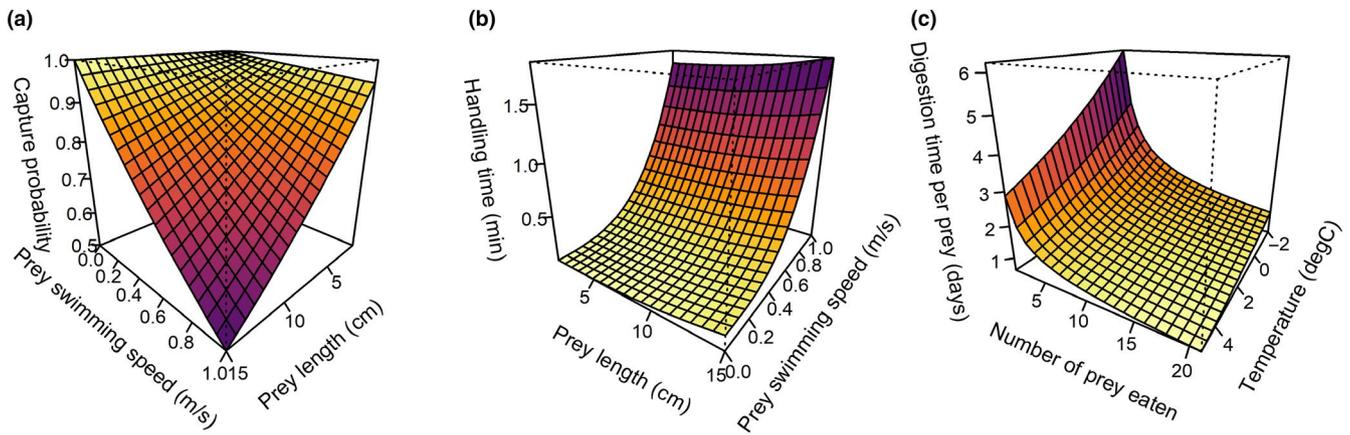


FIGURE 1 Submodels of (a) capture probability (Equation 2), (b) handling time (Equation 3) and (c) digestion time (derived from Equation 5). The values range from yellow (favourable for the predator) to purple (favourable for the prey). Capture probabilities and handling times were calculated from the full range of predator–prey lengths and swimming speeds used in our application of the model for Barents Sea cod. Digestion times were calculated for capelin prey at -2 to 5°C using Equation 5 with masses corresponding to 1–21 prey individuals, where 21 is the maximum number that fits in the stomach of our model predator. [Colour figure can be viewed at wileyonlinelibrary.com]

parameter ($\hat{\rho}$) of the consumed prey types weighted by the mass of each prey type in the gut (Equation 4):

$$\hat{\rho} = \frac{\sum_{i=1}^j \rho_i \delta_i}{\sum_{i=1}^j \delta_i} \quad (4)$$

The digestion rate D_{tot} then becomes:

$$D_{\text{tot}} = 24 \hat{\rho} m_p^{0.305} e^{0.117} \delta_{\text{tot}}^{0.5} \quad (5)$$

where δ_{tot} is the total mass of prey in the stomach at the end of the daily feeding period (see below).

2.4 | Prey profitability and digestive quality

In the contingency model, prey profitability P_i is the energy ingested from prey i per unit handling time (Schoener, 1971). Here, we also weigh it by capture probability (Visser & Fiksen, 2013), implicitly assuming that the predator is familiar with the expected capture probability of different prey items given an attack. In the digestive rate model, prey digestive quality Q_i is defined in terms of energy assimilated per unit digestion time; prey that yields higher energy return per unit digestion time has a higher quality. We define Q_i based on the digestive rate of a gut full of each prey, and let the prey profitability measure for our digestive rate model be $\min(P_i, Q_i)$; that is, we explicitly evaluate profitability in terms of both external and internal handling and assume that the lowest of the two is limiting (Jeschke et al., 2002) and governs prey selection. Prey profitability and digestive quality are thus defined independent of prey density.

2.5 | Modelling feeding and digestion

In the contingency model, prey are ranked by profitability, P_i . Starting with a diet containing only the most profitable prey type (ranked as prey 1), the energy intake rate I (kJ/min) is calculated from Holling's

disc equation, given search rate β_1 , capture probability c_1 , handling time h_1 and prey density a_1 :

$$I = \sum_{i=1}^n (c_i e_i a_i \beta_i) / \left(1 + \sum_{i=1}^n h_i a_i \beta_i \right) \quad (6)$$

To find the optimal diet, we add prey sequentially from the profitability ranking and calculate I for each new addition. The least profitable prey type that should be included in the diet (n) appears when adding prey $n + 1$ to the diet reduces I from only including prey 1 to n . This occurs when the search time lost is more valuable than the handling time of prey $n + 1$.

In the digestive rate model, we first evaluate whether the predator can fill its gut with the highest quality prey, $\min(P_1, Q_1)$, given a limited daily feeding period, the estimated search rate (Equation 1) and prey density. If the gut can be filled with the best prey, the predator should select this prey only and ignore all others to maximize energy assimilation. If the gut cannot be filled with the best prey, the predator should also pursue other prey it encounters, in descending order of digestive quality.

In the non-selective model, the predator feeds in proportion to the encounter rate, under the constraints of daily foraging time, gut volume and digestive capacity. This implies a possibility for suboptimal use of both foraging time, that is spending time handling prey with low energy return on handling time, and gut processing, by feeding on prey that give low energy return on the digestion time. Non-selective feeding may nevertheless be the most profitable when prey density is limiting (Giske & Salvanes, 1995; Schoener, 1971).

Finally, we find the scope for growth ΔB (kJ/day), which is the energy left after sustaining respiration H and specific dynamic action S , the energy cost of digestion (Hansson et al., 1996; Strand & Huse, 2007):

$$\Delta B = C - H - S - F - U \quad (7)$$

Here, C is the consumption, that is the total prey mass digested from Equation 5 converted to energy using the weighted mean energy content of the consumed prey species (as in Equation 4), and F and U are energy losses from egestion and excretion, respectively (values taken from table 2 in Strand & Huse, 2007). The total energy used for respiration H includes a term for mass-, temperature- and activity-dependent metabolic rate (see Strand & Huse, 2007), and here, we calculate this term for a 3.5-kg fish (see the next section) with an average swimming speed of 0.5 m/s (Arnold, Walker, Emerson, & Holford, 1994) in an ambient temperature of 1.5°C.

2.6 | Diet selection case-study: Northeast Arctic cod

Next, we use the prey field and stomach data of cod in the Barents Sea, also called Northeast Arctic cod, to make a real-world application of these models. With a stock size of approximately 3 million tonnes (ICES, 2018), Northeast Arctic cod has a strong influence on the structure and function of the Barents Sea ecosystem, in particular through predation on the planktivorous fish capelin (*Mallotus villosus*, Osmeridae; Link, Bogstad, Sparholt, & Lilly, 2009). Although cod is one of the few commercially important fish species whose behaviour is well studied (Meager, Fernö, & Skjæraasen, 2017), the bulk of knowledge on feeding behaviour comes from studies on larval and juvenile cod (e.g. Kristiansen, Jørgensen, Lough, Vikebø, & Fiksen, 2009; Meager, Solbakken, Utne-Palm, & Oen, 2005; Munk, 1995), and the mechanisms of prey selection in adults remain largely unexplored (but see van Deurs et al., 2016).

We parameterize the models to resemble conditions experienced by cod during the late summer feeding season (August–October). We use a 7-year-old cod as our model predator, the approximate age at 50% maturity for the Northeast Arctic cod population (ICES, 2018). Cod of this size is omnivorous, mainly feeding on fish but also on invertebrates such as pandalids, hyperiids and euphasiids (Dolgov, Bogstad, Johannesen, & Skern-Mauritzen, 2011). We calculate average, depth-integrated prey densities and bottom water temperatures from samples taken during the Joint Barents Sea Ecosystem Survey, including one year with low (0.3 million tonnes, 2005) and one with high (3.6 million tonnes, 2012) capelin population biomass (details on the calculations and averaged prey density and temperature data are found in Supporting Information; raw data are not shared). This Norwegian–Russian survey (Figure 2) collects synoptic data on several trophic levels between August and October each year, using bottom and pelagic trawls, CTD casts, acoustics and other gear (Michalsen et al., 2011). Stomach samples are taken from cod caught in standard bottom trawl hauls, where in each haul, one individual cod from each 5-cm-length group is randomly chosen for sampling of age, mass, maturity stage and stomach contents. Stomach samples are frozen on-board the ship, and weighed and identified to the lowest possible taxonomic level in the laboratory (for further details on the stomach sampling protocol, see Dolgov et al., 2007). We restrict the data to the central-northern Barents Sea—the main overlap area between cod and capelin (Fall, Ciannelli,

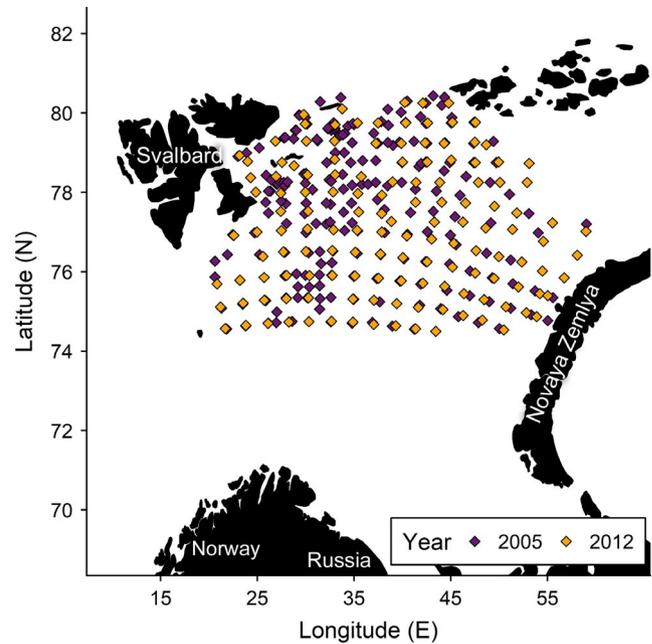


FIGURE 2 The sampling stations used for calculating average prey densities were restricted to the main areas of cod–capelin overlap in the Barents Sea (20–60°E and 74–80°N). Stations were selected from a year with low capelin abundance (2005) and one with high capelin abundance (2012). Each station involves pelagic and bottom trawling and a CTD probe to measure water temperature throughout the water column. Acoustic registrations were performed continuously along predetermined transects between the stations [Colour figure can be viewed at wileyonlinelibrary.com]

Skaret, & Johannesen, 2018; Figure 2)—and pick the 12 most important prey species/groups found in cod stomachs as potential prey in our models. Individual prey energy content and swimming speeds are obtained from the literature (Table 1). It is important to note that the scale at which the data are sampled (trawling: approximately 2-km-long hauls and 65 km interstation distance, acoustics: aggregated over approximately 2 km, continuous recordings) is large compared to the scale of the individual foraging process and that we consider average, homogeneously distributed prey densities only.

To compare the model runs with data collected in the autumn period, we set the daily foraging time to 8 hr, reflecting the number of daylight hours in early October. For a visual predator, seasonal and daily light cycles can have a large influence on the ability to find and catch prey (Meager et al., 2010). In our model, we consider the foraging hours equal in terms of light, while under natural conditions, there will be a gradient in light levels throughout the day, gradually affecting the visual range of predators and prey (Aksnes & Utne, 1997).

2.7 | Model output and comparison

The models are run over time until the gut reaches steady state (stomach fullness converging). Then, we explore the specific patterns of prey intake that emerge from the rates at which the predator can find, ingest and digest prey. We explore effects of prey density

on diet composition and scope for growth and the combined effect of temperature and prey density on encounter versus gut limitation and finally compare the modelled diet with observed stomach contents from 7-year-old cod. For this, we use the wet mass of the 12 prey groups in each individual cod stomach. In cases where the stomach contents were identified to a lower taxonomic level than the selected prey groups, the masses for prey types belonging to that group were summarized. All modelling was done in R version 3.5.0 for Windows (R Core Team, 2019).

2.8 | Comparing prey profitability and diet composition across ecosystems

We also quantify the profitability of cod prey in two other ecosystems, the Baltic Sea and the North Sea. Prey species are selected based on Pachur and Horbowy (2013), who studied the diet of cod sampled outside the Polish coast in the Baltic Sea in February and November 2006–2007, and Hüsey, Andersen, and Pedersen (2016), who studied the diet of cod sampled in the north-eastern North Sea in August 2009–2011. Information about prey energy content, swimming speed, digestibility, etc., is collected from the literature (Supporting Information), and prey profitability P_i and digestive quality Q_i are calculated as described above. We use a water temperature of 12°C for the North Sea (mean of the range 7–17°C in the study area; Hüsey et al., 2016). As temperature was not reported in the Baltic Sea study, we use 7°C, the average annual bottom temperature in the southern Baltic Sea (Rak & Wiczorek, 2012). To be consistent, we show results for a 70-cm cod in all three systems. However, the length-at-age and age-at-maturity differ between the ecosystems (Köster, Trippel, & Tomkiewicz, 2013), and a more representative adult size from the Baltic Sea is 40 cm, which we use to select prey species and to present diet composition based on Pachur and Horbowy (2013). Prey profitability is also calculated for a single temperature (6°C) across systems, in order to facilitate comparison. In this calculation, swimming speeds of cod and prey from the North and Barents seas are adjusted (down and up, respectively) to reflect the temperature change. Finally, to compare the relative proportions of prey of different quality in observed Barents, Baltic and North Sea cod diets, prey are divided into four groups based on the temperature-standardized values of Q_i , using the 15%, 50% and 85% quantiles as breakpoints.

3 | RESULTS

3.1 | Profitability of Barents Sea prey from handling and digestion

The average bottom water temperature at the sampled locations in the Barents Sea was 1.5°C in the low-capelin year and 1.7°C in the high-capelin year. Based on the gut evacuation model (Equation 5), a stomach full of a single prey type takes several days to digest at these temperatures, ranging from 3 days for amphipods (*Themisto* sp., Hyperiididae) to 11 days for shrimp (*Pandalus borealis*, Pandalidae) at

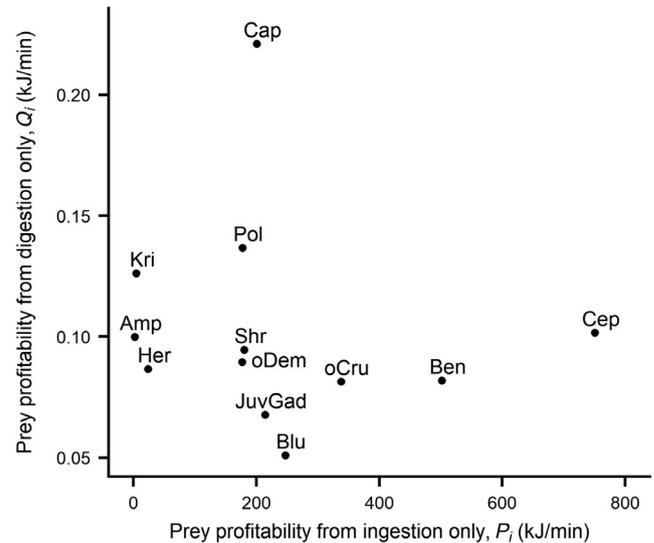


FIGURE 3 Prey profitability from ingestion only (P_i) versus prey profitability from digestion only (Q_i , prey digestive quality). P_i is the energy gain per unit external handling time (kJ/min), weighted by capture probability. Q_i is the energy gain per unit digestion time (kJ/min). Prey species are indicated with abbreviations: Cap = capelin; Pol = polar cod; Kri = krill; Amp = amphipods; Her = herring (*Clupea harengus*, Clupeidae); Shr = shrimp; oDem = other demersal fish; JuvGad = juvenile gadoids (cod and haddock); Blu = blue whiting (*Micromesistius poutassou*, Gadidae); oCru = other crustaceans

1.5°C (6 days for capelin). Consequently, digestion times for all prey were much longer than the theoretical time cod needed to capture any of its prey given an encounter. Prey profitability from digestive quality Q_i was therefore always lower than profitability from ingestion only P_i (Figure 3), and prey profitability for the digestive rate model was therefore always Q_i . Capelin gave the highest energy return per unit digestion time, followed by polar cod (*Boreogadus saida*, Gadidae) and krill (*Thysanoessa* sp. and *Meganctiphanes norvegica*, Euphausiidae), while cephalopods (mainly *Gonatus fabricii*, Gonatidae, and *Rossia palpebrosa*, Sepiolidae) gave the highest energy return per unit handling time, followed by benthic invertebrates (a diverse group of polychaetes and other invertebrates, excluding crustaceans).

3.2 | Diet composition versus capelin density

The prey selection during one day, starting from an empty gut (Figure 4), and steady-state diet composition were sensitive to capelin density in all models. Capelin, polar cod, krill and amphipods dominated the prey community, and this was reflected in the predicted diet at stable state (see *Diet breadth in data compared to models for the Barents Sea*). The proportions of capelin in the contingency model and non-selective model diets were lower than in the digestive rate model, but cod could still fill up its gut with other prey, mainly polar cod (Figure 4). In the absence of capelin, all models predicted increased feeding on polar cod, while the non-selective model also predicted increased feeding on krill. Due to the optimization criterion of maximizing energy assimilation, the digestive rate model predicted feeding on capelin at lower capelin density than the other models.

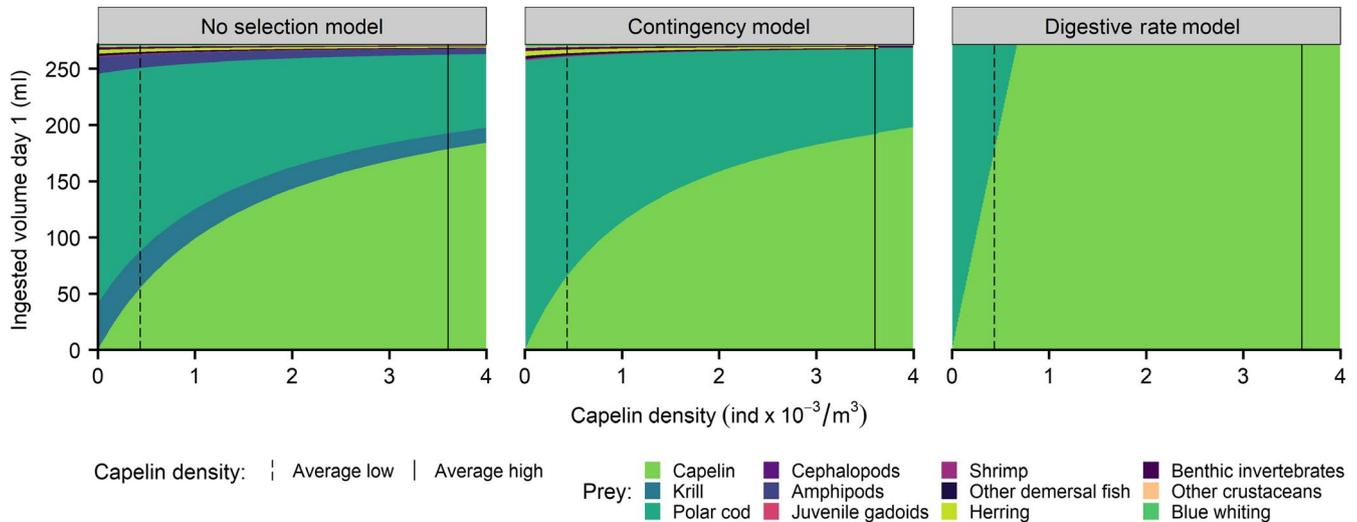


FIGURE 4 Predicted diet composition of cod from different prey selection models for increasing capelin densities. The upper limit on the y-axis represents the total gut volume of the model predator. The figure shows feeding during one day (8 daylight hours) and illustrates the immediate response to increasing capelin density starting with an empty gut. Dashed and solid vertical lines represent average capelin densities in a year with low and high capelin abundance, respectively. All three models include explicit calculations of gut processing time as a function of cod mass, prey mass, prey digestibility and temperature. [Colour figure can be viewed at wileyonlinelibrary.com]

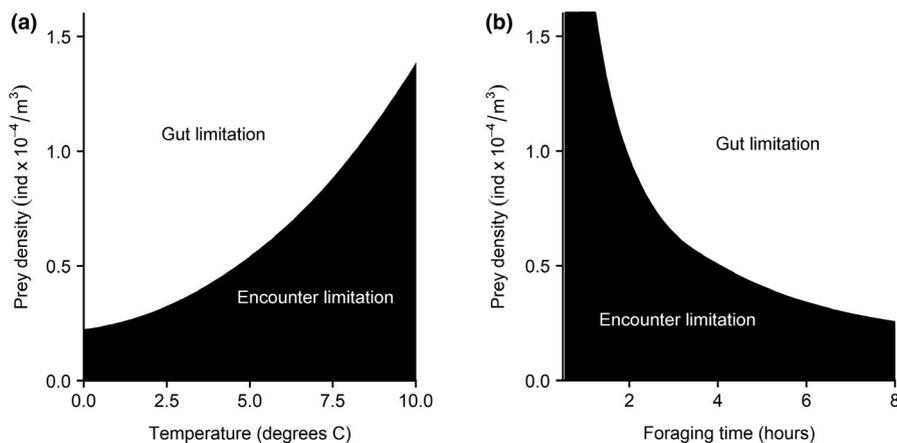


FIGURE 5 Prey density, water temperature and foraging time all influence feeding rate limitation. The black fields indicate encounter-limited feeding; that is, the encounter rate with prey determines the feeding rate. The white fields indicate gut-limited feeding; that is, the predator is released from behavioural time constraints and gut processing time determines the feeding rate. The figures show effects of (a) temperature and prey density and (b) foraging time and prey density on feeding rate limitation when feeding on a single prey type (capelin). For comparison, the capelin density used in the model (average low) was 4.4×10^{-4} individuals/m³. The figures result from running any of our models (contingency model, non-selective model, digestive rate model) with a range of prey densities, temperatures and foraging times relevant to our study system

3.3 | Feeding constraints differ with environment and prey density

In our model, the prey density at which the predator becomes encounter-limited increases with temperature as the digestive rate increases (Figure 5a), but the prey densities at the intersection between the two limitations were much lower than the average low capelin density at ecologically relevant temperatures (cf. Figure 4). The temperature had to be raised to an unrealistic 18 degrees for the digestive rate to match the feeding rate with capelin evenly spread out over the Barents Sea.

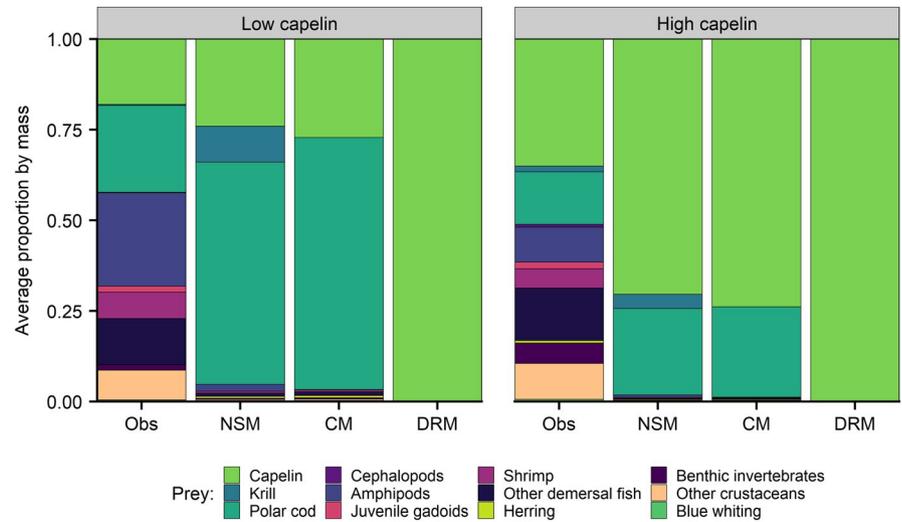
The Barents Sea has a strong seasonal light cycle, ranging from the extremes of midnight sun to polar night. As the available

foraging time decreases, whether due to seasonal changes in light or because the predator is occupied with other activities, a gut-limited predator (i.e. digestion times of prey » handling times) will eventually become encounter-limited if prey density remains constant (Figure 5b).

3.4 | Diet breadth in data compared to models for the Barents Sea

Out of 198 sampled stomachs in the low-capelin year, 6.6% (13) were empty, while in the high-capelin year, 26 out of 425 stomachs (6.1%) were empty. Compared to observations, all models predicted

FIGURE 6 Average diet composition of 7-year-old cod with non-empty stomachs sampled in the northern Barents Sea (“Obs”) in a year with low capelin density (left panel, $n = 185$) and one with high capelin density (right panel, $n = 399$), and steady-state diet composition predicted from the models using average prey densities and bottom temperature data from the same years. CM: contingency model; DRM: digestive rate model; NSM: non-selective model. [Colour figure can be viewed at wileyonlinelibrary.com]



narrower diet breadths and/or lower proportions of prey other than capelin, krill and polar cod (Figure 6). The average proportion of capelin in the diet at low capelin abundance was reasonably well predicted by all models except the digestive rate model (Figure 6, left panel). At high capelin abundance, the modelled proportion of capelin was higher than the average observed, while polar cod was important both in the observed diet and in the non-selective and contingency model predictions (Figure 6, right panel).

At the individual level, the proportion of capelin in the observed diet was highly variable, especially in the high-capelin year (Figure 7a). In both years, some individuals had no capelin in their stomachs, and others had capelin only, though the latter was rare in the low-capelin year (Figure 7a). The models predicted high, but reasonable, values of gut fullness compared to observations (mass prey in stomachs weighted by cod mass; Figure 7b), and the non-selective model and contingency model predicted somewhat higher gut fullness in the high-capelin year. Conversely, in the data, there was a tendency towards lower gut fullness in the high-capelin year (Figure 7b).

3.5 | Prey profitability and diet composition in Northeast Atlantic cod populations

At ecosystem-specific temperature, North Sea prey generally had higher digestive quality Q_i than prey from the Baltic and Barents seas (Figure 8a). Apart from Baltic sprat (*Sprattus sprattus*, Clupeidae), which had a quality comparable to North Sea prey, Baltic and Barents Sea prey had a similar range of Q_i despite the higher temperature in the Baltic Sea. The prey profitability from ingestion P_i had a similar range for North and Barents Sea prey, while prey from the Baltic Sea had very low P_i values, lacking the easier-to-catch fish prey of the Barents Sea and the relatively energy-dense benthic prey of the North and Barents seas. With temperature-standardized values for Q_i , capelin had much higher quality than any other prey (Figure 8b).

High-quality prey made up equivalent proportions of cod diets in the Barents and Baltic seas, while North Sea cod had a much lower proportion of high-quality prey in their diet (Figure 9). However,

almost 30% of the Baltic cod diet was low-quality prey compared to none in the North Sea diet and less than 1% in the Barents Sea diet.

4 | DISCUSSION

Atlantic cod live in a wide range of habitats in the Northeast Atlantic. At the extremes, we find habitats in the North Sea, heavily exploited, and at the upper limit of cod's temperature range, in the Baltic Sea, where oxygen deficiency and low salinity pose challenges to cod recruitment, and in the Barents Sea, where cold-water habitats undergo rapid change at the frontier of climate change. Our results show that prey digestive quality also differs much within and between these ecosystems, contributing to the different growth rates observed among the populations.

Cod in the Barents and North seas have a similar length-at-maturity (70 cm), but Barents cod need around seven years to grow this large compared to three years in North Sea cod (Köster et al., 2013) despite a higher proportion of high-quality prey in their diet. For Barents cod, we conclude that internal limitations on feeding are stronger than external limitations down to very low prey densities due to the low water temperatures. Interestingly, it is a prey from the Barents system—the capelin—that has the highest quality of all prey when quality is considered at the same temperature across systems. This suggests that Barents Sea cod would grow even slower if this prey was absent from the region.

North Sea cod lives in the warmest waters and has the highest growth rate of the three populations. If prey densities in the North Sea are equivalent to those in the Barents Sea, it is possible that the feeding rate of cod in the warmest parts of the North Sea is limited by prey encounter instead of gut processing. Temperature is an important influence on cod growth (Drinkwater, 2005), but in addition, the overall quality of North Sea prey seems to be relatively high, lacking prey in the “low quality” category. Our results suggest that sandeel and Norway pout are the highest quality prey in the North Sea. Cod feeding relatively more on Norway pout had higher growth rates than cod feeding on other prey, but surprisingly, individuals

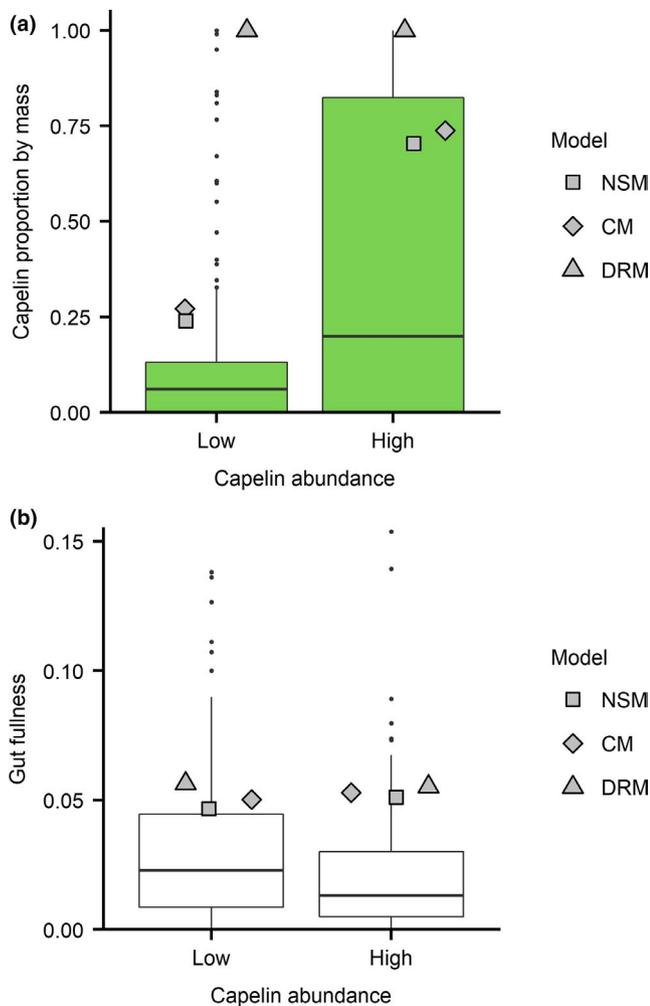


FIGURE 7 (a) Observed proportion of capelin in the diet of individual 7-year-old cod (cf. average proportion in Figure 6), versus predicted proportion of capelin in the diet at steady state for models (symbols, corresponding to Figure 6, CM: contingency model; DRM: digestive rate model; NSM: non-selective model). (b) Observed versus modelled gut fullness. Models: mass of stomach contents at steady state weighted by cod mass. Observations: mass of stomach contents weighted by cod mass for all sampled cod of age 7 (excluding empty stomachs). The number of daylight hours at the time of sampling was minimum that used in the models (8 hr), and the models were run with the average mass of sampled cod, average bottom temperature and average prey densities measured in the respective year. The model symbols are jittered horizontally for illustrative purposes [Colour figure can be viewed at wileyonlinelibrary.com]

feeding relatively more on sandeel had lower growth rates (Hüssy et al., 2016). This could be related to a lagged response to poor sandeel recruitment (Hüssy et al., 2016). Alternatively, the high-energy sandeel lack other nutrients that are essential for growth in larger cod; growth of young North Sea cod was positively correlated with the biomass of sandeel, whereas growth of older cod (>2 years) was positively correlated with the biomass of demersal fish prey (Rindorf, Jensen, & Schrum, 2008).

Like North Sea cod, Baltic cod matures at around three years of age but at a much smaller length of 40 cm (Köster et al., 2013).

Temperature alone cannot explain this difference, as an important contributing factor is the low levels of dissolved oxygen in many areas of the Baltic, which stunts growth (Chabot & Dutil, 1999). We also find that this population feeds on a higher proportion of poor-quality prey compared to North and Barents Sea cod. An important prey in the Baltic is the isopod *Saduria entomon*. While *S. entomon* has low quality based on its energy content in relation to digestion time, it occurs in very high densities in some areas of the Baltic (Haahtela, 1990). It also contains essential fatty acids that can be complimentary to the fatty acid composition of higher quality prey, such as sprat and herring (Karlson et al., 2019; see also van Deurs et al., 2016). In the past 20 years, Baltic cod condition has declined. This has been linked to increased hypoxia in deep areas, resulting in *S. entomon* moving away from the cod habitat (Karlson et al., 2019). In addition, the encounter rate between cod and suitably sized pelagic prey has declined due to shifts in trophic control in the system (Gårdmark et al., 2015), while competition and predation from grey seals (*Halichoerus grypus*, Phocidae) have increased with increasing seal abundance (Karlson et al., 2019). In this situation, it is likely that cod will be forced to feed increasingly on low-quality prey, further reducing condition and growth.

4.1 | Gut limitation and prey selection

A gut-limited predator benefits from favouring prey with high energy return (or other relevant currency) per digestion time over prey with high energy return per time spent handling prey. Prey selection based on digestive properties has been demonstrated in sticklebacks (*Gasterosteus aculeatus*, Gasterosteidae) feeding on isopods (Gill & Hart, 1998) and in shorebirds feeding on molluscs (Quaintenne et al., 2010; Varennes, Hanssen, Bonardelli, & Guillemette, 2015). Digestive limitation can also influence diet composition even without active prey selection through satiation effects on predator feeding motivation, efficiency and prey size selection (Hart & Gill, 1992; Turesson, Brönmark, & Wolf, 2006). A passive prey size selection effect can be included in our model by limiting prey intake to whole prey items, forcing the predator to turn to progressively smaller prey types as the stomach fills up.

We found that capelin is the most profitable prey in terms of energy gain per digestion time but not handling time (Figure 3) and that cod would achieve long-term energy maximization by selecting capelin over other prey (digestive rate model). Knutsen and Salvanes (1999) showed a similar change in the relative ranking of juvenile cod prey when digestion was incorporated. However, in our study the average observed proportion of capelin in Northeast Arctic cod stomachs was closer to predictions from the non-selective model, that is feeding in proportion to the environmental abundance, than the digestive rate model (Figure 6). The models also underestimated the consumption of less profitable and abundant prey. Since the diet of cod often reflects local prey availability (Meager et al., 2017), this may be an indication of opportunistic foraging, but could also imply that cod's true encounter rate with capelin is lower than predicted since the modelled stomachs were fuller than seen in the data (Figure 7b).

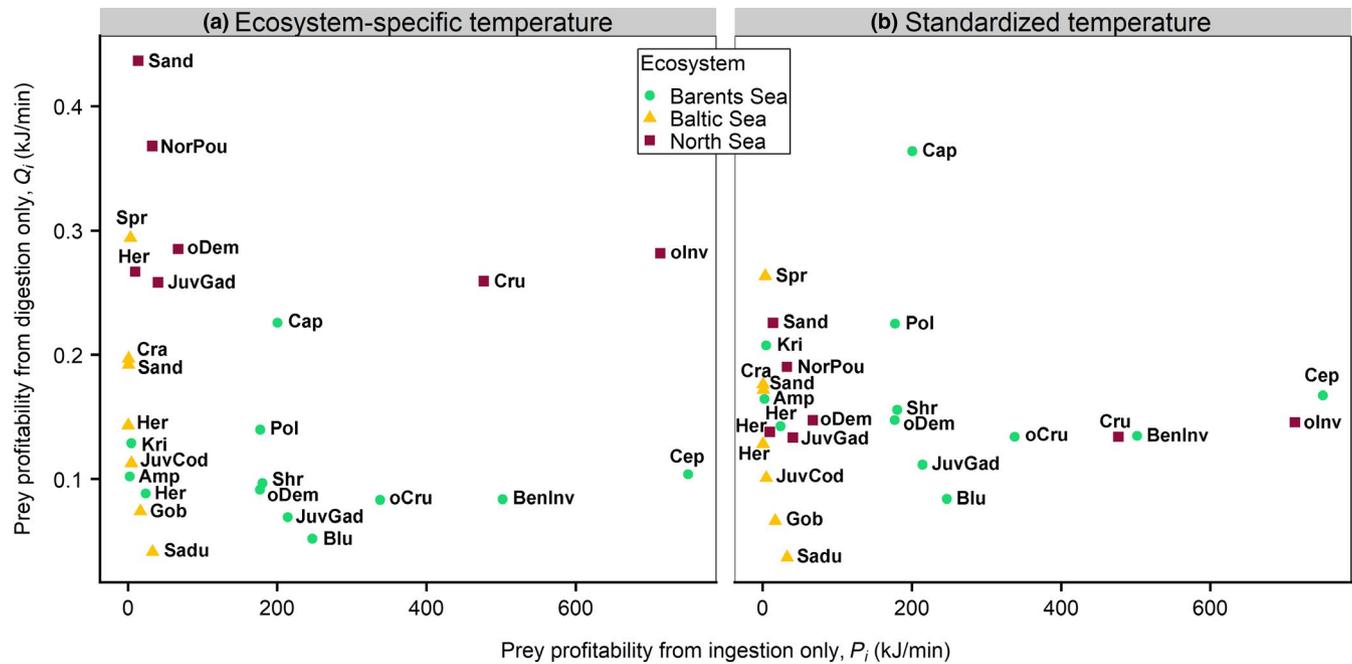


FIGURE 8 Prey profitability from ingestion only (P_i) versus prey profitability from digestion only (Q_i , prey digestive quality) for cod prey in the Barents, Baltic and North Sea ecosystems. Panel (a) shows P_i and Q_i at ecosystem-specific temperature, while panel (b) shows temperature-standardized (6°C) profitabilities. Prey species are indicated with abbreviations: Amp = amphipods; BenInv = benthic invertebrates; Blu = blue whiting; Cap = capelin; Cep = cephalopods; Cra = brown shrimp (*Crangon crangon*, Crangonidae); Cru = crustaceans; Gob = Gobiidae; Her = herring; JuvCod = juvenile cod; JuvGad = juvenile gadoids (Barents Sea: cod and haddock; North Sea: cod, haddock and whiting); Kri = krill; NorPou = Norway pout (*Trisopterus esmarkii*, Gadidae); oCru = other crustaceans; oDem = other demersal fish; oInv = other invertebrates; Pol = polar cod; Sadu = *Saduria entomon* (Chaetillidae); Sand = sandeel (*Ammodytes* sp., Ammodytidae); Shr = shrimp; Spr = sprat [Colour figure can be viewed at wileyonlinelibrary.com]

Overestimation of feeding is common in foraging models as they depict an idealized environment (Deslauriers et al., 2017); for example, we assume that prey are homogeneously distributed and that their distribution and abundance do not change over time. In nature, spatial and temporal heterogeneity in prey encounter rates can strongly influence feeding rates and diets (Ahrens, Walters, & Christensen, 2012; Boyd, 1996; Carroll et al., 2017). In the marine environment, prey patchiness is frequently caused by schooling or swarming (e.g. Fauchald & Erikstad, 2002), an important predator-avoidance strategy (Pitcher & Parrish, 1993). A heterogeneous prey field violates the model assumption of simultaneous search for prey (e.g. Rindorf & Gislason, 2005), making it difficult for a predator to get an overview of the available prey in the environment, which may in turn facilitate inclusion of suboptimal prey in the diet (Hansen & Beauchamp, 2014). This hypothesis is supported by the large observed variation in the proportion of capelin, a schooling fish, eaten by cod, as well as the variation in gut fullness. Strand and Huse (2007) modelled the presence of capelin as a stochastic process and found that when capelin schools were present, cod became satiated within the first hours of feeding. It is likely that heterogeneity in prey distributions results in a spatially and temporally variable landscape of encounter-limited and gut-limited feeding. This implies that the evolutionary advantage of maximizing intake rate, assimilation rate, or simply feeding indiscriminately will depend on the relative probabilities that these situations occur over time (Orlando, Brown, & Whelan, 2009).

4.2 | Strength of gut limitation depends on foraging behaviour

How often a fish feeds also depends on its feeding strategy. Omnivorous fish, feeding on prey from different trophic levels, are more likely to have prey in their stomachs than piscivorous fish that often alternate between periods of feeding on larger and rarer prey and living off stored resources (Arrington, Winemiller, Loftus, & Akin, 2002; Vinson & Angradi, 2011). Cod diets vary ontogenetically and between populations and seasons, but a general pattern of omnivory is present in all studied populations of this species (Link et al., 2009). The short-term energy balance of fishes can be inferred from stomach contents analysis, with the frequency of empty stomachs indicating the proportion of fish having a negative energy balance at the time of capture (Arrington et al., 2002). The cod in our example, from the northern Barents Sea, had a relatively low percentage of empty stomachs (6%–7%) compared to the 26% average across 402 species of marine and freshwater fish (Vinson & Angradi, 2011). In waters off Iceland, 10%–13% of cod stomachs were empty (Stefansson & Palsson, 1997), and only three empty stomachs were found among over 2000 examined in a study off Cape Cod. Here, cod had a maintenance diet of local fish and invertebrates and fed seasonally on migrating high-energy pelagic fish (Smith, Ligenza, Almeida, & Link, 2007). In the Barents Sea, cod, haddock and saithe also feed seasonally on a migrating fish—the capelin (Bogetveit,

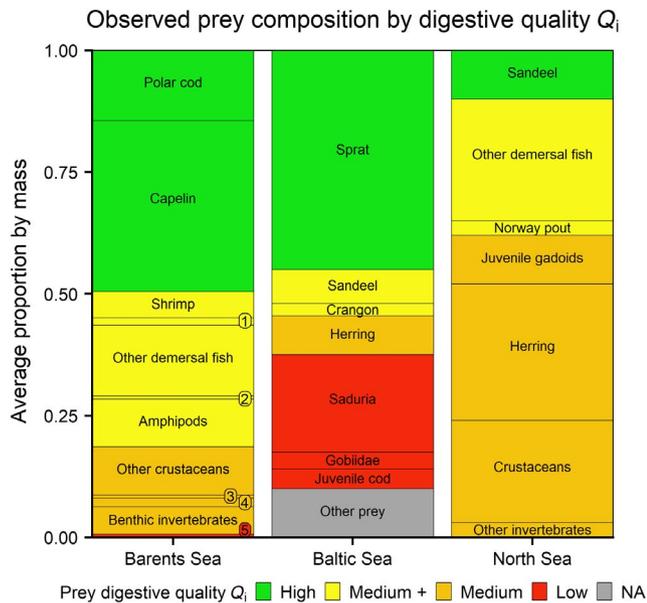


FIGURE 9 Observed average diet composition of a 70-cm cod in the Barents Sea (this study, Figure 6, high capelin abundance), a 70-cm cod in the North Sea (Hüssy et al., 2016) and a 40-cm cod in the Baltic Sea (Pachur & Horbowy, 2013). Prey are divided into four groups based on the temperature-standardized digestive quality Q_i , where “High” is assigned to prey with Q_i equal to or above the 85% quantile, “Medium +” to prey with Q_i between the 50% and 85% quantiles, “Medium” to prey with Q_i between the 15% and 50% quantiles and “Low” to prey with Q_i below the 15% quantile. Numbers in the Barents Sea column refer to 1: krill, 2: cephalopods, 3: herring, 4: blue whiting, and 5: juvenile gadoids. [Colour figure can be viewed at wileyonlinelibrary.com]

Slotte, & Johannessen, 2008). Haddock has a diet consisting of more benthic organisms than cod, while whiting and saithe are more piscivorous (Björnsson, Reynisson, Solmundsson, & Valdimarsson, 2011; Hislop, Robb, Bell, & Armstrong, 1991; Olsen et al., 2010). This was reflected in the frequency of empty stomachs in an Icelandic fjord, where whiting had the highest percentage of empty stomachs (28%–47%), followed by cod (23%–30%) and haddock (10%–23%; Jónsdóttir, 2017). Gadoids thus have dynamic feeding strategies ranging between omnivory and varying degrees of piscivory. Gut limitation seems more prominent in omnivorous than in strictly piscivorous fish, which may only experience gut limitation when they encounter schools of prey (Armstrong & Schindler, 2011; Essington, Hodgson, & Kitchell, 2000).

Foraging is constantly in a trade-off with risk of predation (Alonzo, 2002; Fiksen & Jørgensen, 2011; Giske & Salvanes, 1995). A full gut reduces escape ability during an attack (Lankford, Billerbeck, & Conover, 2001), and if possible, the predator may choose to move into safer but less profitable habitats (Swain, Benoît, & Hammill, 2015). A trade-off with predation risk was a proposed explanation for a reduced feeding probability with increasing stomach fullness observed for whiting (20–36 cm) in the North Sea (Rindorf, 2002). The reduced feeding probability was not related to absolute gut limitation, suggesting that satiation effects on gadoid feeding may be attributable to several different

mechanisms, especially in smaller individuals that experience a higher predation risk.

4.3 | Gut limitation and predator–prey interactions

Gut limitation has implications for the study of predator–prey interactions and, by extension, for multispecies management. For example, spatial ecologists are often concerned with the spatial correlation, or overlap, between predator and prey abundances as an indication of interaction strength (e.g. Hamilton et al., 2017; Kempf, Stelzenmüller, Akimova, & Floeter, 2013; Puerta et al., 2016). In this context, predator-avoidance behaviour can cause negative or no correlations between predator and prey abundances (Planque, Loots, Petitgas, Lindstrøm, & Vaz, 2011; Rose & Leggett, 1990; Sih, 2005). Here, we show another possible driver of weak spatial correlations between predator and prey abundances; if the digestive rate is much slower than the rate of ingestion, predators may reach satiation at low prey densities, thus reducing or even eliminating the need to actively track the highest prey densities (see also Horne & Schneider, 1994). This means that in order to use predator–prey spatial correlation as a proxy for potential interaction strength, it is important to understand the particular behavioural and physiological processes driving prey choice and consumption.

Temperature strongly influences metabolic rates, particularly in cold-blooded animals (Andrade et al., 2005). An ectothermic fish has a lower digestive rate in colder water, and there are several examples of fish moving to occupy temperatures that optimize their energy budget (Björnsson, 2018, and references therein). Given comparable successful meals, a fish in cold water will have to wait longer until it can feed again than a fish in warm water, translating to higher growth rate in warmer waters when food availability is not limiting and the temperature does not exceed the physiological tolerance level (Andersen, 2012; Kunz et al., 2016). Considering only the temperature effect on digestion, it is then tempting to conclude that the feeding rate of cold-water fish is more limited by gut processing than the feeding rate of warm-water fish; at low prey density, a small increase in temperature can imply a change from gut-limited to encounter-limited feeding (Figure 5a). In a warming scenario, increased digestive rate may then enable a gut-limited predator to feed more intensely on a preferred prey, potentially having a stronger impact on the prey population if the population growth rate of the prey does not increase proportionally (Pepi, Grof-Tisza, Holyoak, & Karban, 2018). However, temperature may also affect predator and prey swimming speeds, predator search and attack efficiency and overall food availability in less intuitive ways, counteracting or enhancing the effect on digestion (Bromley, 1994; Öhlund, Hedström, Norman, Hein, & Englund, 2015; Sentis, Hemptinne, & Brodeur, 2013). If predator and prey differ in their sensitivity to temperature, warming may alter the dynamics of an interaction (Dell, Pawar, Savage, & Humphries, 2014; Öhlund et al., 2015). We therefore need to know when handling or digestion is limiting for feeding rate and how temperature affects other aspects of behaviour and physiology, such as oxygen budgeting (Holt & Jørgensen, 2015) and the

overall attack rate on prey (Öhlund et al., 2015), to understand the full impact of temperature on gut limitation.

5 | CONCLUSIONS

In predatory fish, gut passage time generally limits feeding rate more than prey handling time and, at times of high prey availability, more than prey encounter rates. Even if the gut does not influence prey selection per se, the available gut space restricts the daily ration and may cause or affect temporal variability in the susceptibility of prey to predation. By combining models of prey ingestion with models of prey digestion to predict the diet of cod, we gained deeper insight into mechanisms of cod foraging. In the Barents Sea, cold temperatures slow down digestion so much that cod is gut-limited down to very low prey densities, and cod growth in this system would likely be much lower if the high-quality capelin prey, unparalleled in the other ecosystems, was not present. The fast growth of cod in the warm North Sea is supported by a variety of prey species of medium quality and cod is potentially encounter-limited in the warmest areas, while the growth of the Baltic Sea population, stunted by physiological stress, is further challenged by the relatively high contribution of low-quality prey to the diet.

Explicit modelling of foraging processes, even with highly simplified models, can elucidate mechanisms that are central for understanding how important predator-prey interactions may change under different environmental scenarios. Diet data from commercial fish populations collected during monitoring surveys provide a major, underused source of information on fish foraging and diet selection. To better analyse and translate these data into understanding of ocean ecosystems, we need to invigorate foraging theory.

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DATA AVAILABILITY STATEMENT

The averaged prey density and temperature data used as input in the models are available in Supporting Information provided with the online version of the manuscript. Raw data are not shared.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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