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Original Article

A novel model of predator – prey interactions reveals the sensitivity of forage fish: piscivore fishery trade-offs to ecological conditions

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Ecosystem-based fisheries management seeks to consider trade-offs among management objectives for interacting species, such as those that arise through predator – prey linkages. In particular, fisheries-targeting forage fish (small and abundant pelagic fish) might have a detrimental effect on fisheries-targeting predators that consume them. However, complexities in ecological interactions might dampen, negate, or even reverse this trade-off, because small pelagic fish can be important predators on egg stages of piscivorous fish. Further, the strength of this trade-off might depend on the extent to which piscivorous fish targeted by fisheries regulate forage species productivity. Here, we developed a novel delay-differential bioeconomic model of predator – prey and fishing dynamics to quantify how much egg predation or weak top-down control affects the strength of trade-off between forage and piscivore fisheries, and to measure how ecological interactions dictate policies that maximize steady-state profits. We parameterized the model based on ecological and economic data from the North Sea Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*). The optimal policy was very sensitive to the ecological interactions (either egg predation or weak top-down control of forage by predators) at relatively low forage prices but was less sensitive at high forage fish prices. However, the optimal equilibrium harvest rates on forage and piscivores were not substantially different from what might be derived through analyses that did not consider species interactions. Applying the optimal multispecies policy would produce substantial losses (> 25%) in profits in the piscivore fishery, and the extent of loss was sensitive to ecological scenarios. While our equilibrium analysis is informative, a dynamic analysis under similar ecological scenarios is necessary to reveal the full economic and ecological benefits of applying ecosystem-based fishery management policies to predator – prey fishery systems.

Keywords: bioeconomic modelling, ecosystem-based fisheries management, forage fish, predator – prey, trade-offs.

Introduction

There is growing need to develop tools to identify and measure trade-offs among management objectives for natural resources stemming from species interactions (Link, 2010). In fisheries, there is a potential trade-off between fisheries targeting high trophic level fish species and those targeting forage fish that may be important prey for predators (Hannesson and Herrick, 2010; Hunsicker *et al.*, 2010; Pikitch *et al.*, 2014). Because forage abundance can regulate the productivity of piscivores, it may not be possible to simultaneously maximize yield and revenue in both fisheries

(Walters *et al.*, 2005). These types of trade-offs have the potential to be pervasive because fisheries in most ecosystems target multiple trophic levels simultaneously (Essington *et al.*, 2006). Yet, predicting trade-offs is difficult in complex foodwebs (Yodzis, 2000; Essington and Munch, 2014). Direct empirical evidence relating piscivore production to forage fish abundance is often equivocal (Hannesson, 2013) partly because synoptic time series of predator productivity and prey abundance are often lacking or are too short to detect signals, or do not provide sufficient information to distinguish correlation from causation.

In the absence of direct empirical evidence relating the dependency of high trophic level fish species on the abundance of fished prey species, models are commonly used to anticipate trade-offs. These models are often used to derive generalizations about conditions in which one or both species should be fished to maximize economic benefits (May *et al.*, 1979; Ragozin and Brown, 1985; Clark, 1990), or to derive heuristics for precautionary limits on fishing mortality rate that are expected, on average, to produce acceptable ecological and economic outcomes (Smith *et al.*, 2011; Pikitch *et al.*, 2012). Less commonly, models are used to derive specific predictions about optimal allocation of fishing effort, e.g. to specifically estimate the trade off, or lost yields, due to fishing forage species (Hannesson *et al.*, 2009; Hannesson and Herrick, 2010). All models are simplifications of reality (Walters, 1986), and the simplifying assumptions made can have a substantial bearing on the model predictions (Plagányi, 2007). It is therefore important to consider trade-offs across a wide range of different models, each emphasizing a unique aspect of ecological interactions between fish predators and their prey.

Striking a balance between model complexity and tractability requires an understanding of what aspects of predator–prey interactions substantially affect the trade-off between forage and piscivore fisheries (Dickey-Collas *et al.*, 2014). Predator–prey interactions in marine ecosystems are strongly size structured (Jennings *et al.*, 2001), so that early life history stages of piscivores may compete with or be consumed by the same forage species that support energetic needs of adult stages (Köster and Möllmann, 2000; Walters and Kitchell, 2001; Bakun, 2006). For example, Minto and Worm (2012) demonstrated that small pelagic fish can reduce the survivorship of early life stages of Atlantic cod (*Gadus morhua*), a common piscivore. Egg stages of piscivorous fish may be particularly susceptible to predation by planktivorous forage fish (Köster and Möllmann, 2000). Incorporating the negative as well as the positive effect of forage fish on piscivores might dampen, or even reverse, the expected predator–prey trade-off between forage and piscivore fisheries. Additionally, interaction strengths between predators and prey can be asymmetric, whereby either the bottom-up effect of prey or the top-down effect of predators is stronger than the other (Houli *et al.*, 2013). The decoupling of predator–prey feedbacks as top-down interaction strengths become weaker dampens the trade-off between fisheries (Hannesson and Herrick, 2010; Essington and Munch, 2014), but relatively few models have directly compared the magnitude of the trade-off between alternative model configurations producing asymmetry in predator–prey interactions.

Here we aim to provide advances in understanding the sensitivity of predicted trade-offs between fisheries-targeting piscivorous fish and their prey to these ecological conditions by developing a novel generalized bioeconomic model. Our generalizable model of forage fish and piscivores allows for multiple types of complex species interactions, such as egg predation, bottom-up effects of forage fish on piscivore growth, and flexibility in the extent of top-down regulation of forage fish by piscivores. Because the models are nested, we can use this framework to quantify the extent to which egg predation by forage fish or asymmetric interaction strength changes the strength of the trade-off between fisheries. We compare optimal equilibrium harvest rates on forage and predators, and use these rates to determine when and by how much the optimal multispecies policy depends on the nature of ecological interactions, and to measure the trade-offs when the optimal multispecies solution is implemented.

Methods

Model development and rationale

Our goal was to develop the simplest possible model that enabled us to explore consequences of forage fish egg predation on piscivores, and allow for variable top-down effect of piscivores on forage fish. To this end, we required a model with a minimum of two stages for piscivores, because we needed to distinguish life history stages during which the piscivore consumes forage fish from those that are consumed by forage species. We represent the forage species as a single state variable, because we are not specifically interested in how size-structured predation affects forage species. We then applied equilibrium economic models to identify how the optimal allocation of fishing intensity on each species depends on the underlying ecological system structure. We provide a schematic representation of the model, including state variables with dynamic rate processes and feedbacks in Figure 1. A list of all parameters and parameter values are provided in Table 1.

Even this simple model that uses a few state variables requires that we make assumptions about the functional forms of birth, death, and growth processes, we use well-known and widely used functional forms, but these cannot capture all possible relationships in nature (Munch *et al.*, 2005). We use them because their properties are understood, and they allow us to focus on the sensitivity of trade-offs to a subset of highly uncertain components of ecological interactions.

We considered three model scenarios, each generated by adjusting the model parameterization: base model, egg predation, and asymmetric interaction strengths. For our base model, we included no egg predation and set the functional response parameters to generate top-down and bottom-up interactions between forage and piscivores. This produced a typical predator–prey model whereby piscivores exert some top-down control on forage fish and forage fish are always a benefit piscivores. For the egg predation scenario, we added to the base model mortality of piscivore eggs caused by forage fish predation. For the asymmetric scenario, we adjusted

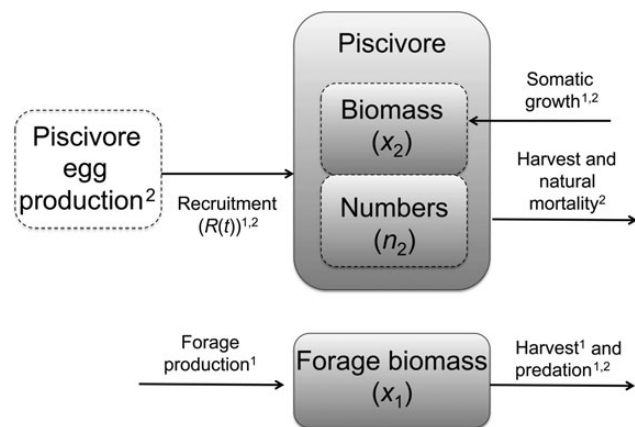


Figure 1. Schematic representation of model state variables and key rates that drive dynamics. Boxes with grey shading represent state variables explicitly represented in the model, note that piscivores are represented with two state variables, numerical (n_2) and biomass (x_2) density, while forage fish are represented with biomass (x_1) density. Each arrow depicts a rate that influences a state variable. Superscripts denote whether rate is a function of forage (1) or piscivore (2) biomass. Egg production and recruitment is modelled implicitly through a delay-differential framework.

Table 1. Summary of model parameters and state variables.

Variable	Description	Base parameters	Units
x_1	Prey biomass	State variable	mt km ⁻²
x_2	Adult piscivore biomass	State variable	mt km ⁻²
n_2	Adult piscivore number	State variable	Number km ⁻²
r	Prey maximum production rate	0.7	Year ⁻¹
K	Prey carrying capacity with no predation	10	mt km ⁻²
F_1	Fishing mortality on prey	+	Year ⁻¹
F_2	Fishing mortality on piscivore	+	Year ⁻¹
C_{\max}	Maximum feeding rate of piscivores	5.88	mt mt ⁻¹ yr ⁻¹
α_{21}	Effective search and capture of piscivore on prey	0.098	mt ⁻¹ yr ⁻¹
Y	Per-biomass consumption of other prey	1.47	mt mt ⁻¹ yr ⁻¹
γ	Predator-dependence term in functional response	+	Unitless
M_2	Natural mortality rate of piscivore	0.2	Year ⁻¹
w_r	Weight of individual recruit	0.005	mt individual ⁻¹
κ	Growth rate parameter	–	Year ⁻¹
w_∞	Asymptotic mass of piscivore	0.020	mt
θ	Assimilation efficiency of piscivore	0.65	Unitless
H	Mass consumed per unit piscivore mass	–	mt ^{1-d} yr ⁻¹
d	Allometric slope of consumption	0.75	Unitless
k	Mass-specific anabolic rate	+	Year ⁻¹
$w(a,t)$	Mass of age a piscivore at time t	–	mt
M_e	Instantaneous daily mortality rate of egg and larvae	0.2	d ⁻¹
α_e	Effective search and capture rate of prey on piscivore eggs/larvae	+	mt ⁻¹ d ⁻¹
b_e	Egg predation saturation constant	0	km ² egg ⁻¹
E_o	Egg density after spawning	–	egg ⁻¹ km ²
M'_e	Egg mortality due to other causes	+	d ⁻¹
f	Piscivore fecundity	685 × 10 ⁶	egg mt ⁻¹
s	Maximum survival rate from larvae to age-1	6.1E–4	ind egg ⁻¹ yr ⁻¹
b	Density dependence in survival from larvae to age-1	2.93E–7	ind ⁻¹
a_r	Age at maturation	4	Year
M_j	Juvenile mortality rate	0.4	Year ⁻¹
P_1	Weighted average Price of herring	\$512	\$2000 US per unit of biomass
P_2	Weighted average Price of cod	\$1191	\$2000 US per unit of biomass
c_1	Cost parameter for herring	\$511	\$2000 US per year
c_2	Cost parameter for cod	\$811	\$2000 US per year

–, values are dynamic; +, parameters was set to different values to generate scenarios.

the base model parameterization to produce weak top-down regulation of forage by the piscivore.

Model description

The forage fish (biomass x_1) follow logistic growth at a rate r and with carrying capacity K in the absence of fishing and predation. They experience fishing at a rate $F_1(t)$. They experience predation by piscivores (biomass x_1) given a type II (saturating) functional response with maximum mass-specific consumption rate C_{\max} (mt mt⁻¹ yr⁻¹) and piscivore attack rate α_{21} (year⁻¹). The piscivores also consume other prey at a rate Y (mt/mt/yr), and the functional response can be parameterized to allow for predator dependence via the parameter γ . The forage fish biomass dynamics are then

$$\frac{dx_1}{dt} = \frac{rx_1(t)}{K}(K - x_1(t)) - F_1(t)x_1(t) - \frac{C_{\max}\alpha_{21}x_2(t)^{1+\gamma}x_1(t)}{C_{\max} + \alpha_{21}x_1(t)x_2(t)^\gamma + Y} \tag{1}$$

Note that we adopted the predator-dependence formulation of Hassell and Varley (1969) such that $\gamma = -1$ implies ratio dependence and that the fraction of forage fish consumed becomes insensitive to changes in piscivore density. When $\gamma = 0$, the functional response is a standard type II functional response, and values of γ between -1 and

0 give intermediate predator dependence (Essington and Hansson, 2004). To generate our asymmetric interaction strength scenario, we set $\gamma = -0.75$. For the base and egg predation scenarios, $\gamma = 0$.

The piscivore component of the model tracks adult piscivores in terms of numbers (n_2) and in biomass (x_2). Piscivore numbers (n_2) depend on recruitment rate into the adult stage, $R(t)$ (numbers yr⁻¹), and natural and fishing mortality rates, M_2 and F_2 (year⁻¹). Individuals recruit to the adult stage at age a_r (i.e. individuals become mature at age a_r), and recruitment rate is a function of spawning biomass (and forage biomass in the egg predation scenario) at time-step $t - a_r$, thereby introducing a delay to account for the period of growth and maturation. Piscivore biomass depends on the weight of new recruits (w_r), and the growth rate of adults described by asymptotic weight, $w_\infty(t)$, a metabolic rate parameter (κ), as derived from a delay-differential model (Quinn and Deriso, 1999).

Under these assumptions, the delay-differential equations for piscivore abundance and biomass are

$$\frac{dn_2(t)}{dt} = R(t) - (M_2 + F_2)n_2(t), \tag{2a}$$

$$\frac{dx_2(t)}{dt} = w_rR(t) + \kappa w_\infty(t)n_2(t) - (M_2 + F_2 + \kappa)x_2(t). \tag{2b}$$

We need to relate the parameter $w_\infty(t)$ to the functional response of piscivores so that growth is responsive to changes in consumption

rate. From Equation (1), we know that total consumption rate of the adult portion of the piscivore population equals

$$\frac{dC(t)}{dt} = \frac{C_{\max}x_2(\alpha_{21}x_1(t)x_2^\gamma(t) + Y)}{C_{\max} + (\alpha_{21}x_1(t)x_2^\gamma(t) + Y)} \quad (3)$$

We presume that growth is the difference between assimilated consumption and metabolic and reproductive costs, which is accounted for using a generalized von Bertalanffy model, which is a simple energetic-based model that relates consumption rates to growth (Essington et al., 2001):

$$\frac{dw(t)}{dt} = \theta H(t)w(t)^d - kw(t), \quad (4)$$

where individual consumption rate is equal to $H(t)w(t)^d$, θ is the assimilation efficiency, and k is the mass-specific metabolic expenditures and reproductive losses. Consumption rates dictate the von Bertalanffy asymptotic weight parameter, $w_\infty(t)$ in the following manner (Essington et al., 2001):

$$w_\infty(t) = \left(\frac{\theta H(t)}{k}\right)^{1/(1-d)} \quad (5)$$

Thus, $H(t)$ (individual mass-specific consumption rate for a fish with mass = 1 mt) fluctuates according to $dC(t)/dt$. Essentially, we need to compute the integral of $H(t)n(a)w(a)^d$ over all ages a . This is approximated by using a constant reference body size, w_{ref} such that the integral is calculated as

$$\int_{a_r}^{\infty} Hn(a, t)w(a, t)^d da = Hx_2(t) \int_{a_r}^{\infty} w(a, t)^{d-1} da \approx Hx_2(t)w_{\text{ref}}^d. \quad (6)$$

We then set the right-hand side equal to $dC(t)/dt$ to solve for $H(t)$:

$$H(t) = \frac{C_{\max}\alpha_{21}x_1(t)x_2(t)^\gamma}{w_{\text{ref}}^{1-d}(C_{\max} + \alpha_{21}x_1(t)x_2(t)^\gamma + Y)}. \quad (7)$$

Note that the delay-differential model presumes an approximation to the growth equation:

$$\frac{dw(t)}{dt} = \kappa(w_\infty(t) - w(t)), \quad (8)$$

where $w_\infty(t)$ has the same meaning as defined above, but κ is not readily calculated from bioenergetics processes that govern growth. However, numerical simulations indicated that setting $\kappa = \exp(-k)(1 - d)$ provided a good approximation to the von Bertalanffy growth equation for adult fish.

To model recruitment, we presume that individuals proceed through distinct early life history stanzas: egg, larval to age-1, and age-1 to maturity, each with unique mortality rates. We introduce the possibility of forage species regulating piscivores via egg predation by implicitly modelling survivorship through these stages. We assume density-independent mortality (due to predation and other causes) during the egg stage, a combination of density-independent and density-dependent mortality in the post larval stage–age-1 stage, and density-independent mortality thereafter. This assumption is supported by empirical and theoretical evidence about the

importance of juvenile-stage density dependence (Myers and Cadigan, 1993; Walters and Juanes, 1993; Walters and Korman, 1999). Total egg production ($E_o(t)$) is the product of mass-specific fecundity f times biomass density $x_2(t)$. The number of eggs that survive is equal to $E_o(t)\exp(-M_e(t)T_e)$, where $M_e(t)$ is mortality rate during the egg stage and T_e is the duration of the egg stage. Mortality rate can be decomposed as two components, the portion due to predation by forage species and the portion due to other causes. We specify a type II functional response relationship between egg consumption and initial egg density, so that the total mortality rate of eggs equals

$$M_e(t) = \frac{\alpha_e x_1(t)}{1 + b_e E_o(t)} + M'_e, \quad (9)$$

where M'_e is the portion of mortality unrelated to forage abundance, and α_e and β_e are parameters of the functional response. High values of b_e can introduce compensatory production dynamics and multiple steady states (Richardson et al., 2011), but because here we only examine equilibrium conditions we set $b_e = 0$. When a_e is set to 0, there is no egg predation mortality, so that all mortality is due to other causes. In our model comparison, we introduced egg predation by specifying the maximum fraction of egg mortality (p_e) that is due to forage species when forage species are at 50% of their carrying capacity. For our egg predation scenario, we set $p_e = 0.25$, i.e. forage species can account for a maximum of 50% of piscivore egg mortality, when $x_1 = K$. The α_e term in Equation (9) equals $(1 - p_e)/(0.5K)$. In the base and asymmetric interaction strength scenarios, there is no egg predation, so $p_e = 0$.

We assume an asymptotic function to describe the number of post-egg-stage individuals that survive to age-1, and presume density-independent mortality thereafter at a rate equal to M_j . Thus, recruitment (in numbers) equals

$$R(t) = \frac{sf x_2(t - a_r)\exp[-M_e(t - a_r)T_e]}{1 + bf x_2(t - a_r)\exp[-M_e(t - a_r)T_e]} \exp[-M_j(a - 1)], \quad (10)$$

where a_r is age at maturation, s is the maximum survival rate from post-egg stage to age-1, and b dictates density dependence in survivorship during the larvae to juvenile stanza.

Economic model

Because the contribution of the paper is to develop a generalized model of predatory–prey systems that nests multiple interactions within one model, we choose to represent the economic portion of the bioeconomic model with as simple a model of fishing profits as possible while still providing a realistic description of fishery systems. Total profits for each fishery (piscivore and prey) are the difference between catch value and the costs required to obtain that level of catch (Clark, 1990). We assume a regulator that is knowledgeable, and understands population dynamics and whose objective is to maximize fishing profits in each fishery by choosing equilibrium fishing mortality rates (Wilens, 2000). Specifically, the problem the regulator solves is:

$$\max_{F_1, F_2} \sum_{i=1}^2 P_i(F_i, x_i) - C_i(F_i), \quad (11)$$

subject to the population dynamic delay-differential equations [Equations (1) and (2)]. The variable $P_i(F_i, x_i)$ is the revenue

function of forage ($i = 1$) and piscivore ($i = 2$), and $C_i(F_i)$ is the cost function with respect to fishing mortality. Revenues are a function of the catch rate and respective fish prices, where $P_i(0, x_i) = 0$ and $P_i(F_i, 0) = 0$. Following Quass *et al.* (2012), the revenue function is $P_i(F_i, x_i) = p_i(1 - e^{-F_i})x_i$, where p_i is the price of fish, and F_i is the fishing mortality. We assume prices are exogenous for herring (Bjørndal and Lindroos, 2004) and for cod (Quass *et al.*, 2012).

We model total costs increasing with fishing mortality and that there are no fixed costs ($C(0) = 0$). Specifically, we employ $C_i(F_i) = c_i F_i$, where c_i is the marginal (and average) cost per unit of fishing mortality. The combination of our revenue and cost functions implies that the cost of harvesting a unit of biomass increases as the stock size decreases. Whether this relationship holds for a schooling species, such as herring, is an empirical question that depends on the combination of the costs of finding the stocks then once found the cost of harvesting the school. Once the school is found, we would expect harvesting costs to be independent of the stock size (Quass *et al.*, 2012). Our representation, however, is acceptable if finding the school is more difficult at lower stock sizes, which is likely the case in the limit unless, for example, the stocks are obligate to the same locations each year. Profit functions with similar characteristics have been used for herring fisheries (e.g. Bjørndal and Conrad, 1987; Bjørndal and Lindroos, 2004; Nostbakken, 2008) and for cod fisheries (e.g. Kronbak, 2005; Quass *et al.*, 2012).

Parameterization

We do not intend this model for precise prediction of trade-offs for any specific fishery system. Rather, we seek to derive generalizations about the relative effect of each dynamic explored on forage–piscivore trade-offs, but use a specific case study to derive parameters ensures that the values used are ecologically and economically plausible. To that end, we used as our primary source of parameters the cod and herring stocks in the North Sea. We chose these species and ecosystem because there is rich ecological and economic data, and cod and herring commonly co-occur in a wide range of ecosystems in the Pacific and Atlantic Ocean (although different species in each ocean basin). We then conduct sensitivity analyses on the ecological scenarios and the prices of herring and cod to enhance generality.

Ecological model

Several ecological parameter values were held constant across alternative model scenarios (Table 1). We fit the Beverton–Holt stock–recruitment relationship to the age-1 recruitment and spawning biomass estimates generated by stock assessments for North Sea cod, extracted from the RAM legacy database (Ricard *et al.*, 2011). The Beverton–Holt parameters s and b were estimated by assuming 97% mortality during egg stages ($M_e = 0.2 \text{ d}^{-1}$, $T_e = 20 \text{ d}$) (Heessen and Rijnsdorp, 1989; Rijnsdorp and Jawarski, 1990). Mass-specific fecundity (f) was based on 685 eggs g^{-1} for mature females, so that $f = 342.5 \text{ eggs g}^{-1}$ of x_2 . We set C_{\max} equal to 5.88, which is the estimated annual maximum consumption ($\text{g g}^{-1} \text{ yr}^{-1}$) of a 10 kg cod at optimal temperature (Hansson *et al.*, 1996). We specified an initializing consumption rate equal to a fraction p of that value when forage are at one-half of their carrying capacity. We set p equal to 0.25 based on Schindler and Eby (1997). From these assumptions, we calculated H from the initializing consumption rate, and use that to estimate the k that produced the assumed w_∞ value. We also specified the fraction of piscivore diets that consists of forage when forage are at one-half of their

carrying capacity and piscivore density equals 1 mt km^{-2} . This fraction was set to 0.25, which is higher than that reported by Mackinson and Daskalov (2007), but is consistent with projections based on body size produced by Engelhard *et al.* (2013), where herring is $> 30\%$ pelagic fish consumed by cod, and large cod ($> 0.5 \text{ kg}$) consumes 75% pelagic fish. The parameters Y and α_{21} were calculated from these inputs, based on Equation (3). We set $d = 0.75$ (Essington *et al.*, 2001), $\theta = 0.65$, and $w_\infty = 20 \text{ kg}$ when prey is at one-half of carrying capacity. Finally, we set $w_t = 5 \text{ kg}$, $r = 0.7 \text{ year}^{-1}$, and $K = 10 \text{ mt km}^{-2}$. Juvenile mortality (M_j) was assumed to be 0.8, adult mortality (M_a) was 0.2.

Economic model

North Sea fish prices are weighted prices where the annual weights are the share of the total catch between the nations harvesting cod and herring in and around the North Sea, which includes United Kingdom, the Netherlands, Belgium, Sweden, Russia, Germany, Poland, and Denmark. The data are from the Sea Around Us Project (<http://www.seaaroundus.org/>). One potential bias with our price series is that our data contain Atlantic cod and Atlantic herring catches outside of the North Sea and are also omitting catches by other countries in the North Sea (e.g. France). To address these issues, we use sensitivity analysis to explore a range of prices for cod and herring.

Weighted prices (WP) were calculated as follows:

$$WP_i = \sum_j \tau_{i,j} P_{i,p}, \tag{12}$$

$$\tau_{i,j} = \frac{\text{catch}_{i,j}}{\sum_j \text{catch}_{i,j}},$$

where $i = \{\text{herring, cod}\}$ and $j = \{\text{United Kingdom, the Netherlands, Belgium, Sweden, Russia, Germany, Poland, Denmark}\}$. In the main set of analysis, we use the average weighted price over the sample from 1974 to 1990, which are \$1191.25 (\$2000 US) for cod and \$511.56 (\$2000 US) for herring, to be consistent with the range of data we consider for estimation of the cost parameter.

To calibrate the relative magnitude of the cost parameters, we assume that profits are approximately equal to zero ($WP_{i,t}(1 - e^{-F_{i,t}})x_{i,t} - c_{i,t}F_{i,t} = 0$) and solve for the $c_{i,t}$ such that this condition is met in each year of our sample. We choose the period 1974–1990 for our main analysis, because it is the period most likely to satisfy that profits/rents are equal to zero over that time, as the fisheries were operating under regulated open-access conditions (Symes, 1997). The data for the stock size are spawning stock biomass for cod and total biomass for herring to be consistent with our model formulation and ecological parameterization (ICES, 2014). The median (mean) of c_i for herring is \$511 (\$553.70) (\$2000 US) and the median (mean) for cod is \$811 (\$967) (\$2000 US). Our base case uses the median but we use the range of our costs for sensitivity analysis.

Results

The predicted effect of forage fisheries on piscivore fisheries varied markedly across the ecological scenarios (Figure 2). The base model predicted the largest reduction in piscivore fishery profits with increasing fishing on forage species, because the fishing-induced depletion of forage fish population lowered the productivity of the piscivore. The maximum profit in the piscivore fishery was reduced by more than one-half when forage fishing increased

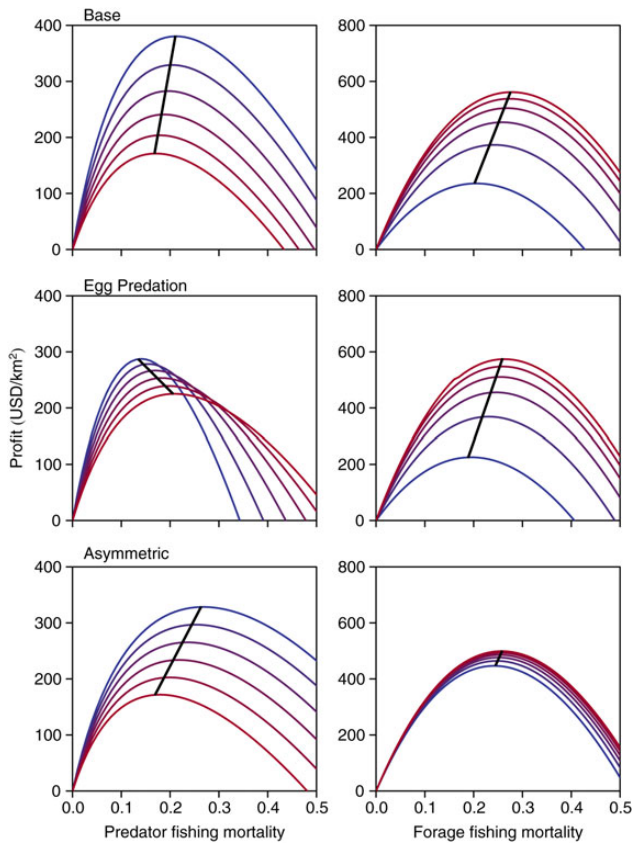


Figure 2. Profit vs. fishing mortality for piscivores (left) and forage (right) under alternative ecological scenarios. On the piscivore figures, lines depict alternative fishing rates on forage species (ranging from $F = 0$, blue, to $F = 0.5$, red, in increments of 0.1), while for the forage figures line depict alternative fishing rates on piscivore species (same ranges of F). Each row is a different ecological model: base, egg predation, and asymmetric interaction strengths. Black lines connect optimal fishing mortality rates and profits to aid comparison.

from 0 to 0.5 year⁻¹. The fishing mortality that maximized profits in the piscivore fishery declined slightly with increasing forage fishing.

Egg predation weakened the effect of forage fishing on the profits in piscivore fisheries (Figure 2), because unlike in the base case, there is a benefit to piscivores from forage fishing in terms of lower egg predation. In this case, fishing forage fish lowered the profit in the piscivore fishery when there was no low piscivore fishing, while increasing the profits when there was high piscivore fishing. The net result was a smaller range of maximum piscivore profits as forage fishing was changed but the variation represented the balancing of both the positive and negative effects of the forage fishery on the piscivore fishery. For our parameter set, adding egg predation never reversed the direction of effect of forage fishing on *maximum* piscivore profits, i.e. the maximum piscivore fishery profit always declined with increasing forage fishing. Only when piscivores were heavily fished ($F_2 > 0.3$) did fishing forage species produce a benefit to piscivores (Figure 2). Also, in contrast to the base model, the piscivore fishing rate that maximized profits increased with increasing forage fishing, because of the improvement in egg survivorship that high forage fishing provided.

With asymmetric interaction strengths (top-down control of forage by piscivores was weak), the effect of forage fishing on piscivore profits was also diminished compared with the base model,

largely because the piscivore fishery profits with no forage fishing was lower in this scenario than in the base model (Figure 2). Further, the piscivore fishing rate that maximized profits was most sensitive to forage fishing intensity in this scenario, with lower optimal piscivore fishing rate with increasing forage fishing. This reduction in optimal fishing mortality is also a consequence of the weak effect of piscivore fishing on forage population. By reducing top-down control, the model predicts a dampening of an important compensatory process for the piscivores (e.g. forage release and subsequent positive effects on piscivore growth).

The three ecological scenarios were further distinguished by the way that fishing piscivores benefited forage fisheries. The base model and egg predation scenario both predicted larger benefits in the forage fishery from fishing piscivores than the asymmetric interaction scenario (Figure 2). For the base and egg predation scenario, maximum forage fishing profits increased roughly 2.5-fold as piscivore fishing increased from 0 to 0.5. The fishing mortality rate on forage species that maximized profits also increased with increasing piscivore fishing. We note, however, that piscivore fishing rates equal to 0.5 depict maximum forage fishery profits when piscivores have been virtually exterminated. In the asymmetric scenario, there are slight improvements in forage productivity with increased piscivore fishing, which is expected given that predation mortality is insensitive to piscivore abundance in this scenario.

Optimal steady-state exploitation rates

We examined the combination of piscivore and forage fishing rates that maximized the summed equilibrium profit [Equation (11)] from both fisheries as a function of forage:piscivore fish prices for each scenario. For each, there was a threshold of forage fish:piscivore prices below which any level of fishing on forage fish reduced overall profits (Figure 3). In other words, when prices are below these levels, forage fish are more valuable kept in the ocean to feed the (more valuable) piscivore species. This threshold value was greatest (0.10) in the base model, and lowest (0.067) in the egg predation model. We confirmed that this threshold was due to the benefit of forage fish for piscivore fisheries and not due to the low price of forage fish making any level of fishing unprofitable (i.e. forage fishing profits were an increasing function of forage fishing rate). Above this threshold, the optimal profits are achieved with some level of fishing on both piscivores and forage fish, where the intensity of forage fishing increased as the price of forage fish increased.

Although the optimal fishing intensity on piscivores was not as sensitive to changes in forage prices (Figure 3), there were notable differences in the trends among the scenarios. For the base and the egg predation model, the optimal piscivore fishing rate generally increased with increasing forage prices (Figure 3). In both scenarios, this policy is purposefully depleting piscivore abundance to make forage more productive. While this does not eliminate all profits from the piscivore fishery, it does reduce profits considerably and requires piscivore fishing rates that would generally be deemed excessive (over-fishing) in a single-species management system. This response was most pronounced in the egg predation model, because egg predation resulted in much lower optimal piscivore fishing levels when forage prices were low (Figure 3). These low piscivore fishing levels are needed to maintain a sufficiently high piscivore population to control prey populations and minimize egg predation.

When the predator-prey interaction strengths were asymmetric, the optimal fishing mortality rate on piscivores initially decreased with increasing forage fish price, then increased slightly. The

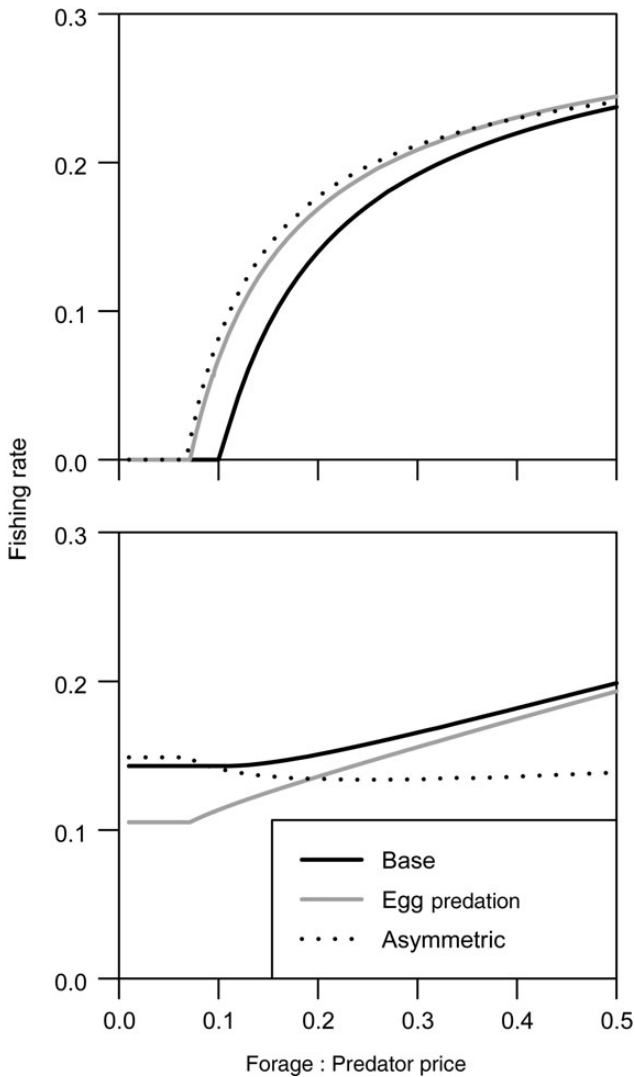


Figure 3. Optimal fishing mortality rates on forage (top) and piscivore (bottom) as a function of the ratio of prey to piscivore prices. Each line depicts a unique ecological scenario.

period of declining piscivore fishing mortality is due to the increase in forage fishing mortality and subsequent reductions in piscivore productivity. The slight increase in piscivore fishing rate at high forage prices enhanced total profits by improving forage productivity. Because top-down control was weak in this scenario, the benefit of depleting piscivores for forage fisheries was limited, which explains why the increase in piscivore fishing rates was relatively small.

We directly measured the trade-offs that are produced by the optimal policy by comparing the profits in the piscivore fishery when applying the multispecies optimal solution to the profits obtained when applying a policy that maximizes profits in the piscivore fishing only (i.e. $F_1 = 0$). As forage prices increased, the optimal policy produced substantial profit reductions in the piscivore fishery, and the extent of this reduction varied among ecological scenarios. The largest trade-off—producing >50% reduction in profits—occurred in the base model. Incorporating egg predation weakened the trade-off (Figure 4), while the asymmetric model produced effects intermediate between the base and egg predation

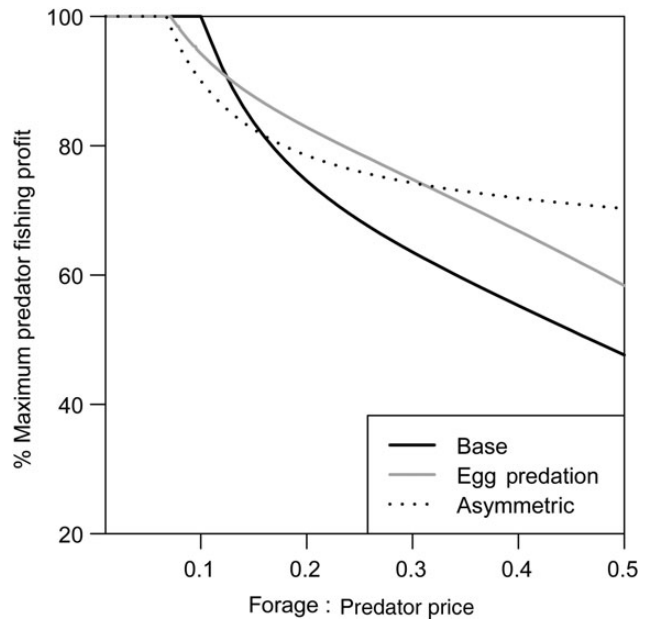


Figure 4. Realized profits in the piscivore fishery when the fishing policy that maximizes total profits is applied, expressed as percent of maximum profitability of the piscivore fishery.

model. The base case model has the highest trade-offs because here the optimal policy includes the highest fishing rates on piscivores and forage, both of which push the optimal piscivore harvest rate well above the level that would maximize harvest in the piscivore sector alone. Lost profit in the piscivore fishery is somewhat reduced in the egg predation scenario because the same increase in fishing mortality provides a marginal benefit in the form of reduced egg mortality rate. In the asymmetric model, the optimal policy does not involve as much purposeful piscivore overfishing so this result represents the lost piscivore profits produced largely via the bottom-up effect of fishing forage species.

Discussion

Here, we developed and applied a novel predator–prey bioeconomic model of fisheries to find that forage fishing diminishes potential equilibrium yields and profits in piscivore fisheries across a wide range of ecological scenarios. We find that substantial losses of catch and profits can ensue if forage species are fished too heavily, even when piscivores were generalist predators, when forage species preyed upon eggs of piscivores, and when there were asymmetric trophic interactions. The degree to which the optimal two-species solution deviated from a species-by-species approach depended on the relative prices of the two species. Despite the potential for equilibrium solutions to predict substantial trade-offs, our analyses suggest that for realistic parameter values, applying harvest rates based on individual population productivity (e.g. ignoring species interactions) would lead to harvest rates that were very close to the multispecies optimal levels.

For the models and parameterization that we explored, the optimal equilibrium multispecies fishing policy was not substantially different from policies derived by taking a single species solution. This was particularly true for the piscivore fishery, where the optimal fishing rate was not strongly dependent on the degree of fishing on the forage species. However, in a dynamic optimization

framework, where policy makers are making decisions annually based on current-year piscivore and forage abundance (Ragozin and Brown, 1985; Kellner et al., 2010), the optimal long-term discounted profits may depend more strongly on ecological scenarios. For example, the equilibrium trade-offs in the egg predation model never produced an outcome where fishing prey had a positive impact on piscivores at the optimal fishing levels. However, if forage are highly abundant and piscivores are at low abundance and their recovery is limited by recruitment, optimal policy might include a short-term increase in forage fish catch to facilitate piscivore stock recovery (Walters and Kitchell, 2001). Further model analysis that considers both distinct ecological scenarios and different starting population levels for the state variables in an optimal control framework is needed to fully judge the economic benefits of incorporating species interactions in species management.

Because forage fish can reach high abundance and are efficient planktivores (Cury, 2000), forage species have the potential to regulate piscivore recruitment via egg predation in many ecosystems. Consequently, active removal of forage fish has been suggested as a way to enhance predator species if they are in a “predation pit” (Bakun et al., 2009). In our model, fishing forage fish only had a positive effect on the piscivore fishery when piscivores were fished at rates exceeding roughly 0.3 year^{-1} . We asked what combination of other parameterizations of the model might make fishing on forage species always beneficial to piscivores, and whether these parameterizations were likely to occur in nature. Specifically, we identified levels of the initializing egg mortality fraction and piscivore diet composition that made the maximum piscivore fishery profit independent of forage fishing rate. Using our default diet composition, the portion of egg mortality due to forage species would have to be 30% when $x_1 = 0.5K$ for piscivore profits to be improved by fishing forage fish. This is a relatively high value given that this implies that roughly 60% of egg mortality would be due to predation when forage species are near their carrying capacity. Using our default egg predation fraction, the initializing piscivore diet composition would need to be less than roughly 16% (fraction of piscivore diet consisting of forage fish when $x_1 = 0.5K$) for forage fishing to benefit piscivore fishing. This diet fraction is well within plausible levels. We conclude that it is not implausible that in some circumstances forage species could have an overall net negative effect on some predator species, though it would be imprudent to enact policies assuming this effect without careful analysis and clear evidence.

The equilibrium optimal policies that maximize summed profits over both fisheries are not always practical or feasible to implement. The optimal solution when forage : piscivore prices exceed 0.2 involves purposefully overfishing piscivores, which increases forage productivity but also reduces landed value and increases costs in the piscivore fishery. Individual fishing sectors will advocate for policies that benefit their own interests, and regulations can limit fishing but can rarely require a certain level of fishing. Thus, it is unlikely that such a solution would be acceptable by all fishing sectors. Moreover, this policy might not meet legal statutes regulating fisheries policy, such as in the United States where federal legislation currently prohibits overfishing stocks except for some exemptions for mixed species fisheries (National Research Council, 2014). In reality, we expect that reasonable constraints on optimal policy, e.g. catch is never a decreasing function of fishing mortality rate, would lead to reductions in estimated optimal fishing rates of both piscivores and forage. Regardless, these constraints would not eliminate trade-offs among management objectives, because

the optimal solution will still include fishing forage species and thereby reduce the piscivore fishery profits. Thus, even though the optimal policy involves harvest rates that are similar to those expected if harvest rates are set without considering species interactions, the outcomes of those policies will create economic benefits in one sector while diminishing benefits in another. Further, so-called balanced harvesting (Garcia et al., 2012), whereby fishing spread over many species in proportional to their productivity, is likely to generate similar trade-offs that generate losses in some fishing sectors in benefits in others.

In the North Sea parameterization, both herring and cod are high value fisheries. Unlike many forage fish stocks, Atlantic herring are captured primarily for human consumption (Engelhard et al., 2013), which generates a higher price than uses for bait or fishmeal (Alder et al., 2008). Although cod are exceptionally valuable, the ratio of herring and cod prices is high, ca. 0.40. Moreover, the cost of fishing herring was estimated to be substantially less than fishing for cod, likely because herring are shallow and do not require fuel-intensive bottom trawling (Parker and Tyedmers, 2014), and because their schooling behavior allows fisheries to concentrate fishing activity on locations known to contain fish schools. Consequently, the optimal fishing rates predicted by our base model would be near $F = 0.22 \text{ year}^{-1}$ for herring and near $F = 0.26 \text{ year}^{-1}$ for cod. These estimates are similar to fishing rates that maximize single species sustainable catch (ICES, 2014). Presently, cod are fished at rates roughly double this amount (F in 2013 was 0.4 year^{-1}), while herring are fished near this level (F in 2013 = 0.2 year^{-1}) (ICES, 2014). When forage species are less valuable (e.g. used primarily for bait, as is the case in the US Gulf of Maine), the differences in optimal policies among scenarios are larger, indicating a higher sensitivity of the management decision on the ecological scenario (Figure 3).

A novel feature of our bioeconomic model is that we distinguish piscivore productivity generated via recruitment from that generated via somatic growth. This was necessary to allow us to consider consequences of egg predation on bioeconomic trade-offs in a piscivore-forage fishery system. Initial model explorations (not shown here) revealed that this model has basically different properties from other models that presume that total piscivore productivity is a linear function of total forage consumed. Most notably, we found that it was important to faithfully depict somatic growth as the differences between energy consumed and energetic requirements for metabolism (Jobling, 1994). Simpler yet common assumptions, e.g. somatic growth is a linear function of total consumption, constrains the model behavior such that there is little scope for somatic growth to contribute substantially to productivity. We conclude that development of foodweb and predator-prey models that incorporate age- or stage-structured dynamics should include thoughtful consideration of somatic growth processes to ensure that model predictions are not highly sensitive to simple representations of growth (Walters et al., 2008).

Summary

Here, we developed a simple bioeconomic model that permitted exploration of potentially important elements of piscivore-forage interactions. Although models are no substitute for direct empirical evidence on interaction strengths between species, in most contexts management policies are made without this evidence and instead rely on models. The advantage of our modelling framework is that it represents these elements through only three state variables, making it conducive to optimal control analysis. However, it does

not include complexity that arises in realistic foodwebs, where multiple trophic pathways connecting species can produce counter-intuitive trade-offs (Essington and Munch, 2014). Moreover, our model does not fully capture the size structure of predator–prey interactions (Houle *et al.*, 2013). We therefore view the framework presented here as an alternative model that can be used in concert with other models as part of a modelling ensemble (Smith *et al.*, 2011), such as individual-based models (Shin *et al.*, 2004), dynamic foodweb models (Christensen and Walters, 2004), and end-to-end ecosystem models (Fulton *et al.*, 2011).

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