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ABSTRACT

Understanding the patterns of development of fisheries across trophic levels and their effects on ecosystems is essential for sustainable harvests. We develop an age-structured food web model to explore some of the bioeconomic causes and consequences of fishing patterns. We illustrate some of the model behaviors using a food chain ecosystem, parameterized using species found in the northwest Atlantic. We explore the effects of different relationships between profitability (defined as total profit per unit fishing effort) and trophic level of the target species on ecosystem and fishing dynamics. Across the profitability scenarios we explore, different patterns in ecosystem and fishery dynamics emerge, with greater variability and depletion in ecosystem biomass, greater variability and less yield to the fishery, and more variable profit when lower trophic level are more profitable and subject to more intense fishing pressure. For all scenarios we calculate the mean trophic level of the catch (TLC) in each year (where trends in this metric are often assumed to be an indicator of fishing patterns and ecosystem health) and compare it with the mean trophic level of the ecosystem. The relationship between the TLC and trophic level of the ecosystem varies with the way in which the fishery develops, and also with the particular species, suggesting that the TLC may not be the best indicator of ecosystem dynamics.

Introduction

Understanding patterns of development of fisheries across trophic levels (TLs) and their effects on global marine ecosystems is essential for crafting policies that ensure sustainable harvests. Much research has focused on identifying simple ecosystem indicators that summarize the status of an ecosystem that may be calculated from available data (e.g., Samhouri, Levin, and Harvey 2009). Perhaps the most well-known ecosystem indicator is the trophic level of the catch (TLC). This was first introduced by Pauly et al. (1998), who found a

dramatic decline in TLC in most marine ecosystems, and it was subsequently labeled "fishing down the food web." Fishing down the food web was interpreted by many as a sign that our global fisheries were in crisis (Essington, Beaudreau, and Wiedenmann 2006). Under this pattern, fisheries were initially developed for upper TL species, but as those species became overfished, fisheries began developing for lower TL species, in turn, depleting them. However, a number of alternative viewpoints have emerged, showing that declines in the mean TLC can occur when fisheries expand to lower TL while maintaining high catches of upper TL species (termed "fishing through the food web"; Essington, Beaudreau, and Wiedenmann 2006), or by fisheries targeting species preferentially based on their availability (Branch et al. 2010). In many regions, however, no decline (Branch et al. 2010) or even increases in the mean TLC have been observed over time (fishing up the food web; Erlandson, Rick, and Braje 2009; Litzow and Urban 2009).

The studies described above raise a number of important questions about how patterns of fishing dynamics develop and what effect such patterns have on an ecosystem. Only very recently has there been an attempt to understand some of the drivers of fishery development. Sethi, Branch, and Watson (2010) explored the relationship between the trophic level of a species and its market value. They found that profitability, not trophic level, was the primary driver of fishing, and that a species' trophic level was not a predictor of its profitability. Additionally, Wilen and Wilen (2012) showed that different profitabilities across TL can result in both fishing down and fishing up the food web.

Understanding the roles that both economics and ecological dynamics play in patterns of fishery development, and their resulting impacts on the ecosystem, is fundamental for management, but many questions remain. For example, what are the important economic and biological drivers of exploitation patterns, and how do these influence both the structure of the ecosystem and the status of the harvesting sector? What drives profitability (price, costs or abundance), and does it matter? What role does the structure of the food web (e.g., number of TLs or top-down vs. bottom-up control) have on the response of the ecosystem to fishing? How do different behavioral responses in a fishery impact stability of the system?

Empirical answers to such questions are needed, but constraints on research funds and the need to predict forward in time make ecosystem modeling an essential complement to empirical studies. Here, we develop a simple, transparent integrated economic food web model to better understand how interactions between economically driven fishing dynamics and ecosystem dynamics influence patterns of fishing across TL, and whether the mean TLC is a useful ecosystem indicator.

Methods

The model has two main components: a food web model and an economic model describing the behavior of the fishery. We first describe the population dynamics and interactions of species within the ecosystem, and then detail the dynamics governing fishing effort within the ecosystem.

Ecosystem dynamics

We describe model variables and parameters in Table 1, and equations governing population dynamics and predator–prey interactions in Table 2, such that the equations in the table are

Table 1. Description of the variables and parameters used in the model.

Variable	Description
i,j,a,t	Indices denoting species (i and j), age and year, respectively
N	Numerical abundance
B	Biomass
W	Individual mass
L	Individual length
R	Recruitment
a_R	Age of recruitment to the population
M_s	Natural mortality from consumption (starvation)
M_p	Natural mortality from predation
M_0	Baseline level of consumption mortality
V	Biomass of a species vulnerable to predation
v	Fraction of prey vulnerable to a predator (due to size selectivity)
$\widetilde{S}$	Realized spawning biomass
ψ	Fraction of biomass available to predators or fishery (i.e., not in a refuge)
d	Predator demand per unit biomass of the predator
$d_{\max}$	Maximum per unit biomass demand of the predator
$V_{0.5}$	Vulnerable biomass where $d = 0.5\, d_{\max}$
D	Predator demand
$\widetilde{D}$	Predator consumption
Θ	Condition factor (consumption/demand)
C	Target catch
$\widetilde{C}$	Realized catch
ρ	Fraction of total demand that is removed
X	Total removals (catch + predation)
F	Fishing mortality rate
Y	Total mortality rate from predators and fishery
s	Selectivity in the fishery
P	Fishery profit
p	Price per unit catch
E	Fishery effort
c	Cost per unit effort
q	Fishery catchability coefficient (biomass caught per unit effort)
τ	Effort response rate
λ	Fraction of equilibrium biomass where profitability becomes 0

denoted Eq. T2.1, T2.2, and so on. Population dynamics in our model are age-structured, and the annual numbers-at-age of a species is a function of new recruits entering the population and individuals that survive from the previous year (Eq. T2.1). Recruitment to the population follows the Beverton–Holt stock–recruit relationship (Eq. T2.2), and is a function of the effective spawning biomass, which is the sum of the mature biomass, adjusted by a condition factor (Watters et al. 2006; Eq. T2.3) related to foraging success. Parameters controlling the stock–recruit relationship are calculated following Mangel, Brodziak, and DiNardo (2010; Eq. T2.4). Maturity and fishery selectivity at age follows a logistic function (Eq. T2.5), and annual biomass-at-age (mature and immature) is the product of abundance and weight at age (Eq. T2.6). Weight-at-age is a function of length-at-age (Eq. T2.7), which we calculate from the von Bertalanffy growth equation (Eq. T2.8).

Predator–prey dynamics control the reproductive success and mortality in our model. To determine the effects of consumption on a population (both predator and prey), we determine the total biomass consumed, which is a function of the demand of the predator, and the abundance and vulnerability of the prey to that predator. We model the demand of a predator (in weight) as a saturating function of prey abundance; this function can either be a Holling's Type II or III response (Holling 1959) depending on the exponent in Eq. T2.9. Predator demand saturates at a maximum value, which we calculate using the consumption

Table 2. Equations governing the ecosystem and fishery dynamics in the model.

Equation	Description
Abundance, biomass, and life history	
1 $$N(i, a, t+1) = \begin{cases} R(i, t+1) & a = a_R(i) \\ N(i, a-1, t)e^{-M_T(i, a-1, t) - s(i, a-1)F(i, t)} & a > a_R(i) \end{cases}$$	Numerical abundance-at-age
2 $$R(i, t) = \frac{\tilde{S}(i, t - a_R(i))}{\alpha(i) + \beta(i)\,\tilde{S}(i, t - a_R(i))}$$	Recruitment to the population
3 $$\tilde{S}(i, t) = \sum_a m(i, a)B(i, a, t)\,\Theta(i, a, t)^{\gamma(i)}$$	"Realized" spawning biomass
4 $$\alpha(i) = \frac{S_0(i)(1 - h(i))}{4h(i)R_0(i)}$$ $$\beta(i) = \frac{5h(i) - 1}{4h(i)R_0(i)}$$	Stock–recruit parameters, calculated from the steepness parameter, and the unfished biomass and unfished recruitment
5 $$m(i, a) = \left(1 + e^{\frac{a_{m,50\%}(i) - a}{\chi_m}}\right)^{-1}$$ $$s(i, a) = \left(1 + e^{\frac{a_{s,50\%}(i) - a}{\chi_s}}\right)^{-1}$$	Maturity-at-age (m) and selectivity-at-age in the fishery (s; both proportions)
6 $$B(i, a, t) = N(i, a, t)W(i, a)$$	Biomass-at-age
7 $$W(i, a) = b_1 L(i, a)^{b_2}$$	Weight-at-age
8 $$L(i, a) = L_\infty(i)\left(1 - e^{-k(a - a_0(i))}\right)$$	Length-at-age
Removals: consumption and fishing	
9 $$d(j, a, t) = \frac{d_{max}(j)V(j, a, t)^{\theta(j)}}{V_{0.5}(j, a) + V(j, a, t)^{\theta(j)}}$$	Demand of the *j*th predator at age *a* and time *t*
10 $$\frac{Q(j)}{B(j)} = 3.06\,W_\infty(j)^{-0.202}T^{0.612}A(j)^{0.516}3.53^{H(j)}$$	Consumption (*Q*) to biomass (*B*) ratio calculated based on asymptotic ($W\infty$) temperature (*T*), aspect ratio of the caudal fin (*A*), and whether the species is a herbivore (*H* = 1) or not (*H* = 0).

Table 2. (*Continued*)

	Equation	Description
11	$$d_{max}(j) = \zeta \frac{Q(j)}{B(j)}$$	Maximum demand per-unit-biomass
12	$$v(i, a_i, j, a_j) = \begin{cases} 0 & L(i, a_i) > \varphi(j)L(j, a_j) \\ 1 & L(i, a_i) \leq \varphi(j)L(j, a_j) \end{cases}$$	Length-based proportion vulnerable to predation
13	$$V(i, a_i, j, a_j, t) = \psi(i)\, v(i, a_i, j, a_j)\, B(i, a, t)$$	Age-specific biomass of prey i vulnerable to predator j
14	$$V(j, a_j, t) = \sum_{i \neq j} \sum_a V(i, a_i, j, a_j, t)$$	Total prey biomass (of all species and age classes) vulnerable to the predator
15	$$V_{0.5}(j, a_j) = \upsilon(j) \sum_{i \neq j} \sum_a V(i, a_i, j, a_j, t=0)$$	Biomass where prey vulnerability is half the maximum
16	$$D(i, a_i, j, t) = \sum_{a(i)} d(i, a_i, j, a_j, t)B(j, a_j, t)$$	Demand of prey per unit biomass of the predator
17	$$D(i, a_i, j, t) = \sum_{a(i)} d(i, a_i, j, a_j, t)B(j, a_j, t)$$	Total biomass demand of prey by a predator
18	$$\rho(i, a_i, t) = min\left(\frac{\psi(i)B(i, a, t)}{\sum_{j \neq i}D(i, a_i, j, t) + C(i, a_i, t)} ,\; 1 \right)$$	Fraction of available biomass that is consumed or removed by the fishery
19	$$\tilde{C}(i, a_i, t) = \rho(i, a_i, t)C(i, a_i, t)$$	Realized annual catch at age
20	$$\tilde{D}(i, a_i, j, a_j, t) = \rho(i, a_i, t)D(i, a_i, j, a_j, t)$$	Total biomass of prey species i consumed by predator j
21	$$X(i, a_i, t) = \tilde{C}(i, a_i, t) + \sum_{j \neq i} \sum_{a_j} \tilde{D}(i, a_i, j, a_j, t)$$	Total removals of a given species (catch + biomass consumed)

(*Continued on next page*)

Table 2. (*Continued*)

Equation	Description
22 $$\widetilde{D}(j, a_j, t) = \sum_{j \neq i} \sum_{a_j} \widetilde{D}(i, a_i, j, a_j, t)$$	Total biomass of all prey consumed by the jth predator
23 $$D_{max}(j, a_j, t) = d_{max}(j)B(j, a_j, t)$$	Maximum biomass of prey that could be consumed by a predator age class
24 $$\Theta(j, a_j, t) = \frac{\widetilde{D}(j, a_j, t)}{D_{max}(j, a_j, t)}$$	Condition factor relating to observed maximum potential consumption by a predator

Mortality

Equation	Description
25 $$M_T(i, a_i, t) = M_S(i, a_i, t) + M_p(i, a_i, t)$$	Total natural mortality
26 $$M_S(j, a_j, t) = \frac{M}{\Theta(j, a_j, t)^{\varepsilon}}$$	Starvation-based mortality
27 $$X(i, a_i, t) = \frac{Y(i, a_i, t)}{Y(i, a_i, t) + M_S(i, a_i, t)} B(i, a_i, t) \left(1 - e^{(-Y(i, a_i, t) - M_S(i, a_i, t))}\right)$$	Total deaths in biomass (catch + natural deaths). *Y* is the combined mortality rate from predation and fishing
28 $$F(i, a_i, t) = Y(i, a_i t) \frac{\widetilde{C}(i, a_i, t)}{X(i, a_i, t)}$$ $$M_P(i, a_i t) = Y(i, a_i t) \frac{\sum_{j \neq i} \sum_{a_j} \widetilde{D}(i, a_i, j, a_j, t)}{X(i, a_i, t)}$$	Fishing and predation-based natural mortality rate (*F* and M_P, respectively)

Fishery dynamics

Equation	Description
29 $$C(i, a_i, t) = q(i)E(i, t)\psi(i)s(i, a_i)B(i, a_i, t)$$	Target catch in weight
30 $$P(i, t) = p(i) \sum_a C(i, a_i, t) - c(i)E(i, t)$$	Annual profit fishing on species *i*
31 $$E(i, t + 1) = E(i, t) + \tau(i) \frac{P(i, t)}{E(i, t)}$$	Annual effort fishing on species *i* when effort cannot move across species (or TL)

(*Continued on next page*)

Table 2. (*Continued*)

Equation	Description
32 $$E(i, t+1) = E(i, t) + \tau(i)\frac{P(i, t)}{E(i, t)} + \sum_{i \neq j}\left[\tau(i)\left(\frac{P(i, t)}{E(i, t)} - \frac{P(j, t)}{E(j, t)}\right)\right]$$	Annual effort when fishing effort can move across species
33 $$p(i) = \frac{P(i, t_{eq})}{E(i, t_{eq})}\left[q(i)B(i, t_{eq})(1 - \lambda(i))\right]^{-1}$$	Price per-unit-biomass of the catch
34 $$c(i) = p(i)q(i)B(i, t_{eq})\lambda(i)$$	Cost per-unit-effort in the fishery
Ecosytem metrics 35 $$TLC(t) = \sum_i TL(i)\frac{C(i, t)}{\sum_i C(i, t)}$$	Mean trophic level of the catch
36 $$TLE(t) = \sum_i TL(i)\frac{B(i, t)}{\sum_i B(i, t)}$$	Mean trophic level of the ecosystem

to biomass ratio of a predator (Palomares and Pauly 1989; Eq. T2.10). We calculate maximum predator demand per-unit-biomass by assuming it is some multiple (≥ 1) of the estimated ratio of consumption to biomass (Eq. T2.11).

Predator demand saturates with the total biomass of prey that is vulnerable to the predator. Vulnerability of a prey species is a function of the size selectivity of the predator (Eq. T2.12), and the total biomass of the prey not in a refuge (Eq. T2.13). The total biomass of all prey species vulnerable to the predator is the sum of the vulnerable biomasses of all prey species consumed by the predator (Eqs. T2.14 and T2.15). We assume that the predator consumes prey in proportion to the vulnerable biomass. The demand for a particular prey species per-unit-biomass of predator is the product of the proportion of the prey in the total pool of vulnerable biomass and the total demand of the predator (Eq. T2.16). The rate at which predator demand saturates in response to prey abundance is controlled by $V_{0.5}$ (Eq. T2.9), defined as the vulnerable biomass where predator demand is half of the maximum. To estimate $V_{0.5}$, we first compute the unfished population biomass-at-age for each species using the specified unfished recruitment and an assumed natural mortality rate estimated using Hoenig's (1983) relationship between natural mortality and maximum age. Given an estimate of equilibrium size for each species we can calculate the biomass vulnerable to a particular predator using Eq. T2.14, and assume that $V_{0.5}$ is some fraction (≤ 1) of the total vulnerable biomass. We studied the sensitivity of the results to variation in this fraction to confirm that qualitative results did not change. Total predator demand (in weight) is

therefore the sum of the product of the per-unit biomass demand and the biomass of the predator (Eq. T2.17).

We model demand at the species level because it is possible that in a given year there is not enough biomass available to meet the needs of the predators and the fishery, since both occur simultaneously throughout the year. We therefore calculate an adjustment factor to scale the total potential removals (target catch + predator demand) in cases where they exceed the available prey biomass (Eq. T2.18). Both fishery catch and predator demand are adjusted equally (Eqs. T2.19 and T2.20). For example, if the total biomass available to both predators and the fishery is 80% of the potential removals (target catch + demand; Eq. T2.21), then both the achieved predator removal and fishery catch are 80% of the target. The consumption by a predator is the sum of the consumption across all species consumed (Eq. T2.22), and the ratio of this consumption to the maximum amount possible (where we calculate maximum consumption with Eq. T2.23) is used as a measure of the condition of the predator (Eq. T2.24).

In addition to affecting spawning output (Eq. T2.3), predator condition affects natural mortality of the predator. Total natural mortality for a species is the sum of the mortality from being eaten, and the mortality from not having enough food (i.e., starvation; Eq. T2.25). We calculate starvation-dependent mortality by scaling a baseline level of natural mortality (i.e., independent of starvation and predation) by the predator condition, such that species with a lower condition factor will have a higher natural mortality rate (Eq. T2.26). To compute the mortality from all removals (predation and the fishery), we first use the Baranov catch equation (Jennings, Kaiser, and Reynolds 2001), and numerically compute the mortality that results in the observed total removals (Eq. T2.27). We then compute the fishing and predation mortalities using this estimate of mortality, and the proportion of the total removals that are from the fishery and the predator, respectively (Eq. T2.28).

Fishing dynamics

We now introduce bioeconomically driven fishing dynamics into the system. The catch from a fishery targeting a particular species is a function of the biomass available to the fishery (which is a function of the total biomass not in a refuge and the age-specific selectivity of the fishery), the effort of the fishery, and the catchability of the species (i.e., the fraction of the population caught per unit effort of the fishery; Eq. T2.29). Based on Eq. T2.29, increases in biomass or fishing effort (or both) result in a linear increase in the catch, and vice-versa. The total profit of a fishery in a given year is the difference between the total revenue (price-per-unit-weight times total catch) and the costs (effort times cost-per-unit-effort; Eq. T2.30).

There are a number of ways to model fishing dynamics in response to species abundance and profitability. Here, we model changes in fishing effort only in response to the profit per-unit-effort of a particular fishery, and not to any management actions (i.e., unregulated fishing). We explore two ways in which effort changes: (1) only in response to the profitability of the target species (i.e., effort in a fishery is independent of other fisheries; Eq. T2.31), and (2) in response to the profitability of a particular fishery relative to the profitability of other fisheries (i.e., effort can move across fisheries targeting different species; Eq. T2.32). We call these the *separate effort* and *effort switching* models, respectively. The separate effort model is based on Wilen and Wilen (2012), and the effort switching model is a modification of the separate effort model. In the separate effort model, effort will increase as long as the fishery

is profitable, and will decrease if it becomes unprofitable. In the effort switching model, however, effort could decline for a profitable fishery if other fisheries are more profitable and some of the effort is redistributed to the more profitable fisheries.

Running the model

We use the simple food chain ecosystem with a single species at each trophic level to illustrate the ecosystem and fishing dynamics of the model. Species selected for this example are found in the Northwest Atlantic Ocean, and where possible, parameters were obtained from FishBase (Froese and Pauly 2015) or from the literature (Table 3). When parameter values were not available from these sources, we used values that resulted in a stable unfished ecosystem. This "ecosystem" is used to illustrate model dynamics, and although many parameters are based on real species, we are not suggesting that such a simple system exists.

We run the model for 200 years, with the initial population size set randomly for each species. Fishing starts in year 100 at a specified low level of effort, after each population reaches its unfished equilibrium size. We explore three different profitability scenarios for the separate effort (Eq. T2.31) and effort switching models (Eq. T2.32). The profitability scenarios explored are that initial profitability (profit/effort in the first year of fishing) (1) is equal across trophic level, (2) increases with increasing trophic level, and (3) decreases with

Table 3. Parameter values for species in the food chain ecosystem used in the model.

		Value				
Parameter	Description	Copepod (TL = 2)	Mackerel (TL = 3)	Bluefish (TL = 4)	Swordfish (T = 5)	Mako (TL = 6)
a_R	Age at recruitment	0	1	1	1	1
a_{max}	Maximum age	0	10	10	12	18
$a_{m,50\%}$	Age at 50% maturity	−1	2	2	5.2	7
ε_m	Slope of maturity function	0.1	0.5	0.5	0.5	0.5
$a_{s,50\%}$	Age at 50% selectivity	—	3	3	6	8
ε_s	Slope of selectivity function	—	0.5	0.5	0.5	0.5
L_∞	Asymptotic length (cm)	0.04	40.6	97.3	267	374
a_0	Age when length is 0	−1	−1	−1	−1.68	−1
b_1	Length–weight scalar ($\times 10^{-6}$)	7	4.6	4.5	2.7	5.2
b_2	Length–weight exponent	3	3.18	3.28	3.3	3.14
h	Stock–recruit steepness	0.85	0.62	0.8	0.88	0.6
R_0	Unfished recruitment	3×10^{18}	7.5×10^7	8.8×10^5	400	10
A	Caudal fin aspect ratio	—	3	2	8.8	4
φ	Maximum length of prey (relative to predator)	—	0.4	0.5	0.5	0.5
θ	Exponent in Eq. T2.9	1				
γ	Exponent in Eq. T2.3	1				
ε	Exponent in Eq. T2.26	1				
M_0	Baseline natural mortality rate from starvation	0.02				
ψ	Fraction of biomass available to predators/fishery	0.9				
ζ	Relates average consumption to maximum demand (Eq. T2.11)	1.2				

Notes. Species parameters were selected for copepods (*Calanus finmarchicus*); Atlantic mackerel (*Scomber scombrus*), bluefish (*Pomatomus saltatrix*), swordfish (*Xiphias gladius*), and shortfin mako (*Isurus oxyrinchus*).
Most parameter values were obtained from FishBase (Froese and Pauly 2015), although additional sources were used (Beardsley et al. 1978; Campbell et al. 2001; Joung and Hsu 2005; Kohler, Casey, and Turner 1995; Myers, Bowen, and Barrowman 1999; NEFSC 2005, 2006; O'Brien, Burnett, and Mayo 1993).
Values for unfished recruitment (R_0) were determined through iterative calibration to ensure steady predator–prey biomass dynamics, and are not reflective of estimates from stock assessment models.
Parameters at the bottom of the table with only a single value are fixed across TL.

Table 4. Parameters controlling the fishery dynamics across TL (Eqs. T2.28–T2.34) for the different scenarios explored.

Variable description	Scenario	Trophic level			
		3	4	5	6
Initial fishing effort [$E(t_{eq}, i)$]	Fixed	0.50	0.50	0.50	0.50
Rate of effort change within TL	Low	0.80	0.80	0.80	0.80
	High	2.40	2.40	2.40	2.40
Rate of effort change multiplier across TL	High	0.60	0.60	0.60	0.60
	Low	0.10	0.10	0.10	0.10
	Fixed	4.00	4.00	4.00	4.00
Initial profitability [$P(t_{eq}, i)/E(t_{eq}, i)$]	Increasing	2.00	4.00	8.00	16.00
	Decreasing	16.00	8.00	4.00	2.00
	Fixed	0.010	0.010	0.010	0.010
Catchability [$q(i)$]	Increasing	0.005	0.010	0.020	0.030
	Decreasing	0.030	0.020	0.010	0.005
Profitable biomass threshold (λ)	Low	0.10	0.10	0.10	0.10
	High	0.20	0.20	0.20	0.20
Price per unit catch [$p(i)$]	Varies with each scenario	See Eq. T2.33			
Cost per unit effort [$c(i)$]	Varies with each scenario	See Eq. T2.34			

Notes. Price per-unit-catch and cost per-unit-effort also influence fishery dynamics, but they vary with the specified catchability, initial profitability, and the profitable biomass threshold (Eqs. T2.33 and T2.34).

increasing trophic level (Table 4). For each TL, we specify the initial profitability, the biomass threshold (relative to the unfished equilibrium size) where profitability goes to 0, and the fishery catchability. Based on these values, we calculate the price per-unit-catch and cost per-unit-effort for each TL using Eqs. T2.33 and T2.34, respectively. Sensitivity of these inputs was evaluated by running the model for three catchability scenarios (fixed, increasing, or decreasing with TL), two profitable biomass thresholds (fixed across TL at a low/high value; Table 4), two fishing effort response rates (low/high), and with no fishing on the lowest TL species in the model (a copepod with TL = 2; Table 3), or no fishing on the two lowest TL species (the copepod and its fish predator with a TL = 3). For each model run we compute the TLC (Eq. T2.33) and the trophic level of the ecosystem (TLE; Eq. T2.34) for all years when fishing occurs. We also calculate a number of metrics summarizing fishery (total and variability in effort, profit, and catch) and ecosystem dynamics (variability and relative depletion, defined as the ratio of total biomass in the final year to the total unfished biomass).

Results

We focus on the results across profitability and effort scenarios for the baseline model run (catchability increasing with TL, low profitable biomass threshold, and with no fishing on lowest TL), but also describe the sensitivity of results to different parameterizations in the following sections. In the baseline model run, patterns in biomass across TL varied based on both the profitability scenario and on how fishing effort responded to changes in profitability over time. Larger differences in biomass trajectories occurred across profitability scenarios for a given model of effort (e.g., compare Figure 1a–c). The different models of fishing effort generally resulted in similar biomass trajectories for a given profitability scenario (e.g., compare Figure 1b to 1e), although much greater variability in biomass was observed for the effort switching model when lower TL species were more profitable (compare Figure 1c to 1f).
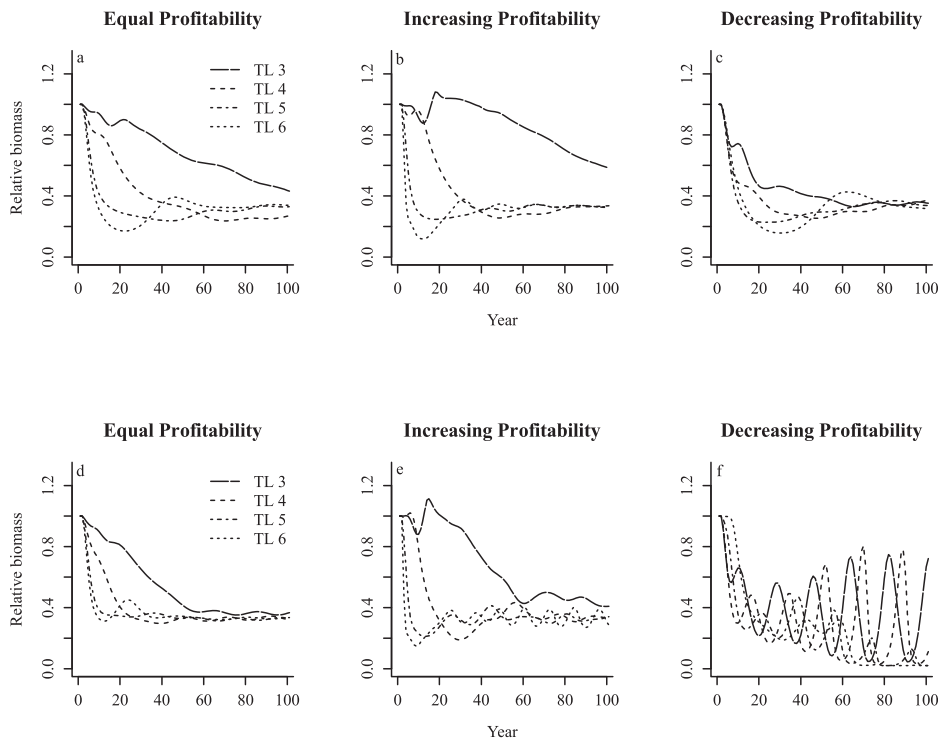
Figure 1. Trend in relative biomass by TL in the ecosystem over time as a function of initial profitability (equal, increasing, or decreasing with TL) for the runs with separate effort (a,b,c) for each TL, and where effort can move across TL (d,e,f). Results are shown by year since fishing began for the scenarios where catchability is fixed across TL and with the lower profitable biomass threshold.

Across profitability scenarios we see declines in biomass for all fished species, with the magnitude and rate of decline varying across profitability scenarios and effort models. In general, the rate of decline is faster for the species with higher initial profitability. For the scenario when profitability is initially the same across TL, more rapid declines occur in the upper TL species (Figure 1a and e). When lower TL species are initially more profitable rapid declines occur for all TL, and greater variability and larger depletion in total ecosystem biomass occurs over the 100 year time period (Table 5). In contrast, the scenario where lower TL species are initially the least profitable results in the least variability and depletion in ecosystem biomass (Table 5).

Fishing effort for the upper TL species declines at some point in the time series while effort for the lowest TL species tends to increase or level off, albeit with fluctuations (Figure 2). When declines in fishing effort occurred for multiple TL species, the declines were generally sequential, with effort for the highest TL declining first, followed by the next highest TL, and so on. This pattern occurred across profitability scenarios, although the rate of the decline was influenced by profitability (Figure 2). Effort at a given TL fluctuated more when it could move across TL (Figure 2d, e, and f), although total fishing effort (summed across all TL) did not exhibit as much variability due to the redistribution of effort (Figure 3a). Greater variability in catch and profit also occurred in the effort switching model, particularly when lower TL species were more profitable (Figure 3b and c; Table 5).

Table 5. Estimates of different performance metrics summarizing the ecosystem and fishery dynamics.

Performance metric	Effort model	Profitability		
		Fixed	Increasing	Decreasing
Fishing effort (CV)	Separate	0.20	0.18	0.27
	Switching	0.23	0.26	0.33
Total catch ($\times 10^8$)	Separate	2.98	3.03	2.29
	Switching	2.54	2.91	2.06
Fishery catch (CV)	Separate	0.29	0.41	0.21
	Switching	0.30	0.37	0.48
Total profit ($\times 10^3$)	Separate	15.27	9.96	15.78
	Switching	9.09	6.92	6.01
Profit (CV)	Separate	0.35	0.37	1.74
	Switching	0.99	0.77	11.26
Variability in biomass of TL 3 and above (CV)	Separate	0.28	0.18	0.49
	Switching	0.41	0.32	0.56
Total biomass depletion (TL 3 and above)	Separate	0.42	0.61	0.29
	Switching	0.31	0.37	0.33

Note. Results shown are by effort model and profitability scenario for the base model run (low profitable biomass, increasing catchability with TL, and low effort response rate).

Total catch and profit (summed across TL) were higher for the separate effort model (Table 5).

The biomass and effort dynamics shown in Figures 1 and 2 resulted in different patterns in both the TLC and TLE (Figure 4). In some cases TLC declined consistently over the time
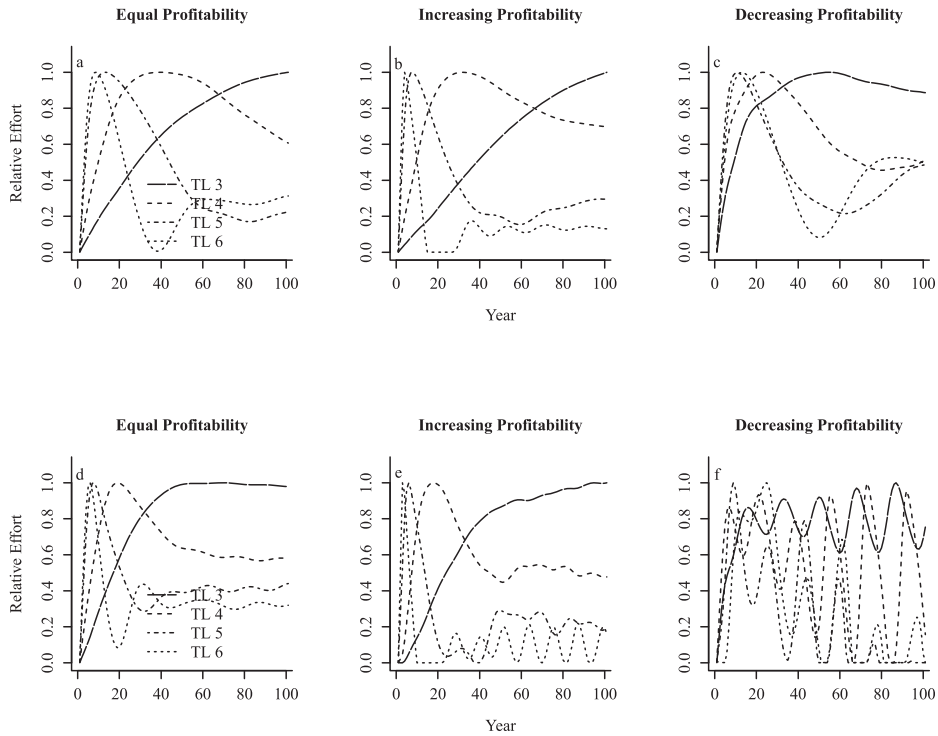

Figure 2. Trend in relative fishing effort by TL in the ecosystem over time (years since fishing began) as a function of initial profitability (equal, increasing, or decreasing with TL) for the runs with separate effort (a,b,c) for each TL, and where effort can move across TL (d,e,f).
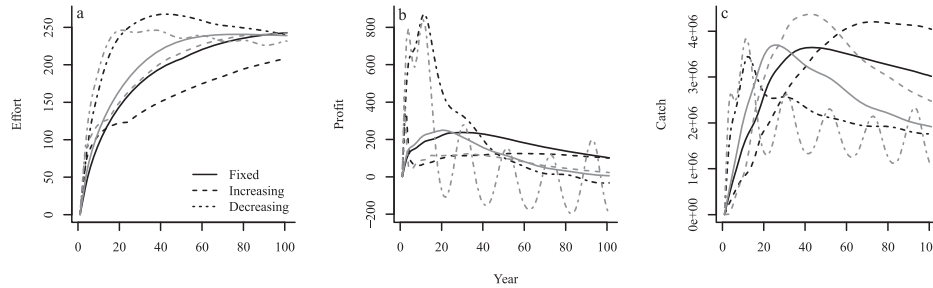
Figure 3. Annual trends in total (a) fishing effort, (b) profit, and (c) catch (summed across TL) for the different profitability scenarios and effort models (black and gray lines represent the separate effort and effort switching models, respectively).

series (Figure 4a and d), resulting in a positive correlation between TLC and TLE (Table 6). In other cases, declining TLC was associated with both declines and increases in TLE in the same time series (Figure 4c and f). Across model runs, correlations between TLC and TLE varied greatly by scenario (Table 6). Weaker correlations between TLC and TLE generally occurred for scenarios where the lower TL species were more profitable, when fishing became unprofitable at higher biomass thresholds, and when fishing effort changed at a greater rate and when it was able to switch to a different TL (Table 6). Effort switching also resulted in greater variability and depletion in ecosystem biomass, a pattern also generally observed when fishing pressure was higher on lower TL species (due to higher catchability and/or higher profitability). In contrast, reduced ecosystem biomass variability and depletion occurred when fishing was not allowed on the two lowest TL in the model, which also resulted in negative correlations between TLC and TLE across profitability scenarios (Figure 4g, h, and i; Table 6).

Discussion

The age-structured ecosystem/bioeconomic model allows us to explore the bioeconomic causes and consequences of different fishing patterns across TL. Even from the simple virtual ecosystem we explored, it is clear that trying to ascertain ecosystem dynamics using TLC is ill-advised. If a declining TLC were indicative of a sequential collapse of upper trophic level species, then we would expect to see a subsequent decline in the TLE, as the abundance of lower trophic level species would increase. Across our model simulations we found many weak relationships between TLC and TLE, and in some cases observed both decreases and increases in TLE with decreasing TLC. Branch et al. (2010) used ecosystem models, stock assessment results, and survey data to calculate TLE and also found it was often not correlated with trends in TLC. Our results indicate that the relationship between TLC and TLE varies depending on a number of factors, including how the fisheries develop, which species in the ecosystem are fished, how susceptible species at different TLs are to fishing effort, and how rapidly fishing effort changes in response to profitability. Furthermore, although declines in TLC were observed for many of the examples we explored, we also observed increases over much of the time series in some cases, a result shown in the work of Litzow and Urban (2009) and Wilen and Wilen (2012).
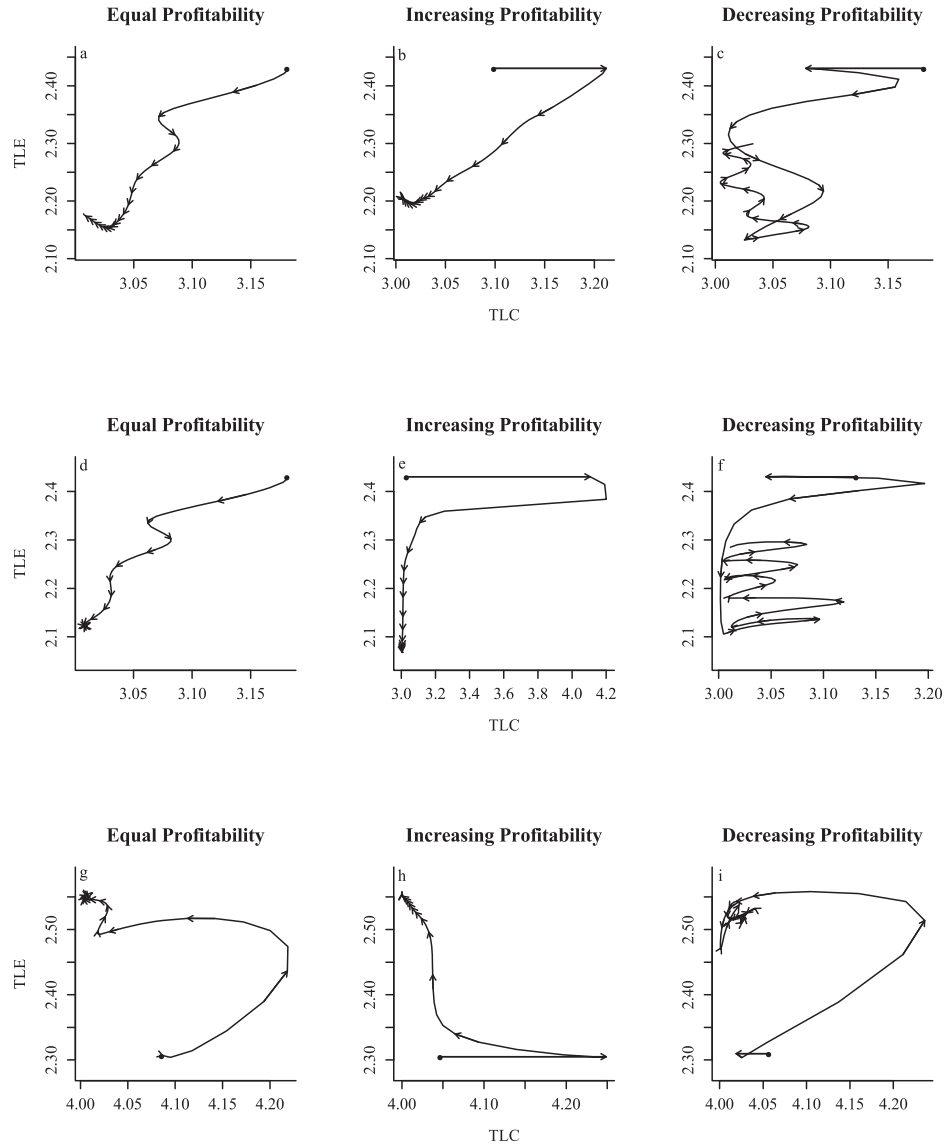
Figure 4. Relationship between TLC and TLE over time as a function of initial profitability (equal, increasing, or decreasing with TL) for the runs with separate effort (a,b,c) for each TL, where effort can move across TL (d,e,f), and with separate effort on the top three TL species (g,h,i). The dark circle represents the starting value (in year 100), and arrows indicate the direction over time.

In our model the consequences of fishing from the bottom up (caused by lower trophic level species being more profitable) were generally more severe on the ecosystem (greater variability and depletion in biomass) compared to the other profitability scenarios explored. A number of concerns have been raised over the impacts of expanding lower trophic level fisheries in a number of ecosystems (Pikitch et al. 2012), and our results support the finding that intense fishing at lower TL may have undesirable ecosystem consequences.

The general behaviors of our model are the result of top-down and bottom-up controls, and the strength of each will impact the ecosystem dynamics in response to fishing (e.g.,

Table 6. Estimates of the correlation between TLC and TLE, across scenarios.

Scenario		Profitability		
		Fixed	Increasing	Decreasing
Catchability (*q*) by TL	Fixed	0.92	0.74	−0.07
	Increasing	0.91	0.44	0.52
	Decreasing	0.32	0.77	−0.12
Profitable biomass threshold	Low	0.82	0.66	0.30
	High	0.62	0.64	−0.08
Effort model	Fixed	0.79	0.78	0.26
	Switching	0.64	0.52	−0.05
Effort response rate	Low	0.72	0.65	0.11
	High	0.42	0.59	0.00
Fishing on lowest TL?	Yes	0.68	0.64	0.10
	No	−0.78	−0.73	−0.38

Note. For each scenario, the values shown are the means calculated across all other model runs. In other words, the mean for the fixed effort model with initial profitability fixed across TL was calculated as the mean across runs with different catchabilities, different profitable biomass thresholds, etc.

Estes et al. 1998; Frank et al. 2005, 2006). Bottom-up controls in the model result from the effect of consumption on spawner output (Eq. T2.3) and natural mortality (Eq. T2.25), and the strength of these effects can be easily modified by adjusting the exponents in these equations. The bottom-up controls in our model result in predator declines of the same relative magnitude in response to declines in the prey population, but the relative magnitude of predator increase is not the same in response to increases in prey. In other words, a collapsing prey population will result in a crash in the predator population, but a large surge in prey biomass results in a modest increase in predator biomass. These differential responses to changes in prey abundance result from the predator population ultimately being recruitment-limited. Increased consumption of prey reduces predator mortality and increases spawner output, but the relationship between spawner output and recruitment, and the maximum possible recruitment will depend on the input values for unfished recruitment and the recruitment steepness parameter. Having recruitment-limited populations is an important component of our model, as the factors affecting survival for prerecruits are likely very different than those for adult fish, such that it makes sense that consistent increases in the prey of adults will not result in consistent increases in the entire population of the predator.

Currently, recruitment in the model is deterministic and depends only on the spawning output of the adult population. One possible modification of the model is to have varying recruitment in response to the availability of larval prey items, as food availability is likely a primary driver of recruitment success (Cushing 1982). Recruitment could also fluctuate in response to larval predators, allowing for situations where the recovery of apex predator populations is inhibited by increases in forage fish populations that feed on the larvae/juveniles of the predator (Fauchald 2010; Walters and Kitchell 2001).

It is also possible to allow consumption to affect individual growth, such that length and weight at age vary through time. This could be accomplished by varying asymptotic length (L_∞) with consumption; see Lorenzen and Engberg (2003) and Munch et al. (2005) about how L_∞ can fluctuate in response to competition. Changes in size at age can set up interesting predator–prey dynamics due to the size selectivity of the predator. For example, Shackell et al. (2010) found that while predator biomass on the Scotian Shelf in the Northwest Atlantic has remained steady over a period of decades, declining predator body size resulted in an

exponential increase in the biomass of prey species. Fluctuating size at age may also influence population dynamics in response to fishing, as selectivity and maturity are likely size-dependent.

Modifications to fishing dynamics can be easily incorporated in the model. For example, different rates of entry and exit into the fishery could be included to mimic subsidized entry or buyback programs to reduce effort. Biomass-dependent pricing structures and nonlinear catchability in the fishery could also be incorporated, and would impact the profitability, and therefore effort, in a fishery for a heavily depleted population. We ran the model assuming the rate of change of effort in response to fishery profitability was the same across TL. Similarly, when effort can move from one TL to another, we assumed the switching rate was equal regardless of from which TL fishery the effort was coming or going. It is reasonable, however, to assume that certain fisheries may have differential changes in effort for a variety of reasons. It is also reasonable to assume that new fishing effort could be less efficient (i.e., lower catchability), at least initially. Such modifications to the fishing dynamics could easily be incorporated in our model, but were not included here because it was beyond the scope of the initial work.

The development of this model is a first step in a larger exploration of the bioeconomic causes and consequences of fishing on the ecosystem. Future work could expand on this model to explore in greater detail the specific roles that the ecosystem and the fishery play in the observed fishing patterns. Even so, our results highlight that assuming TLC is a reliable indicator of ecosystem state is unwise without additional empirical or theoretical support.

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