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Authors

Essington, Timothy E
Sanchirico, James N
Baskett, Marissa L

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Economic value of ecological information in ecosystem-based natural resource management depends on exploitation history

Timothy E. Essington^{a,1}, James N. Sanchirico^{b,c}, and Marissa L. Baskett^b

^aSchool of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195; ^bDepartment of Environmental Science and Policy, University of California, Davis, CA 95616; and ^cResources for the Future, Washington, DC 20036

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Ecosystem approaches to natural resource management are seen as a way to provide better outcomes for ecosystems and for people, yet the nature and strength of interactions among ecosystem components is usually unknown. Here we characterize the economic benefits of ecological knowledge through a simple model of fisheries that target a predator (piscivore) and its prey. We solve for the management (harvest) trajectory that maximizes net present value (NPV) for different ecological interactions and initial conditions that represent different levels of exploitation history. Optimal management trajectories generally approached similar harvest levels, but the pathways toward those levels varied considerably by ecological scenario. Application of the wrong harvest trajectory, which would happen if one type of ecological interaction were assumed but in fact another were occurring, generally led to only modest reductions in NPV. However, the risks were not equal across fleets: risks of incurring large losses of NPV and missing management targets were much higher in the fishery targeting piscivores, especially when piscivores were heavily depleted. Our findings suggest that the ecosystem approach might provide the greatest benefits when used to identify system states where management performs poorly with imperfect knowledge of system linkages so that management strategies can be adopted to avoid those states.

natural resources | bioeconomic modeling | trade-offs | sustainable fisheries | risk

Natural resource management is evolving toward holistic, ecosystem-based approaches to decision making to ensure the delivery of valued ecosystem goods and services (1, 2). These approaches consider the multiple benefits that ecosystems provide, such as conservation of species, livelihoods, employment, cultural values, equity, and agency (3, 4). They also seek to improve the scientific basis for decision making by highlighting trade-offs among ecosystem services that emerge through alternative courses of management actions (5), anticipating indirect consequences of actions on valued components of these systems (6, 7) and protecting components of systems that confer resilience (8). The science underpinning these trade-offs and indirect consequences, therefore, needs to account for the complexity of multiple interacting components within and across coupled natural-social systems.

For the advocates of the ecosystem approach, the societal gains to adopting it seem clear. For instance, dynamics of harvested populations are driven by environment, habitat, and species interactions (9, 10), so it therefore follows that conventional management that does not account for such interactions is putting these systems at risk for collapse and incurring large costs to society. Although the intuition for ecosystem approaches is straightforward, the resulting gains are an empirical question, and its application inevitably involves transitional costs such as investments in science to better understand the nature and strength of complex ecological dynamics and investments of time and resources in new or modified management decision-making processes (11).

With limited management resources, a natural question to ask is: where and when are the societal gains from adopting the approach likely to be the greatest? Kellner et al. (12), for example, showed in a coral reef system that the incremental gains are greatest in cases when ecosystem approaches correct past fishery management failures and when multiple objectives (conservation and fishery management) are considered simultaneously. Although informative, Kellner et al. (12) consider a situation where the fishery manager has complete understanding of system structure. In many situations, managers are certain that interactions across the system exist, but the science is not clear on the nature or strength of the interactions (13). It also not clear whether managers need to gain complete understanding of system structure to maximize economic and ecological benefits or whether defining a safe operating space based on partial knowledge might be sufficient to achieve this goal. Finally, does information on ecological interactions primarily assist in identifying trade-offs in expected economic gains (e.g., profitability), or is it better suited to identify trade-offs in risk (the probability of severe adverse outcomes)?

In marine fisheries, a main focus of the ecosystem approach has been accounting for ecological interactions among targeted species (9, 14, 15). This focus is motivated, in part, by the recognition that fisheries in most ecosystems target both predators and their prey (16). Thus, there is a potential conflict between the desire to have ecosystems that are productive for predators or for their prey because decisions and outcomes in one fishery can influence the performance of other fisheries (9). However, calculating trade-offs

Significance

Natural resource management is evolving toward a more holistic approach that acknowledges ecological connections among species. To date, there has been no demonstration of where or when this approach provides economic benefits. Here we find only modest economic benefits from having detailed knowledge of ecological linkages between species. However, the costs of incomplete or incorrect knowledge are unevenly distributed across user groups and are greater after historical overfishing. The ecosystem approach to natural resource management might therefore provide the greatest benefit by defining safe zones where management is robust to our limited understanding of ecological systems.

Author contributions: T.E.E., J.N.S., and M.L.B. designed research, performed research, and wrote the paper.

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Data deposition: All code and model outputs are available at <https://github.com/tessington/PNAS-EBFM>.

¹To whom correspondence should be addressed. Email: essing@uw.edu.

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is difficult due to the complexity of potential interactions between high- and low-trophic level species in marine ecosystems. For example, small pelagic fish are commonly important prey for piscivorous fish when the latter are large but are also predators on early life history stages (eggs and larvae) of piscivorous fish (17, 18) or competitors on juvenile stages of piscivores (19). Collectively, these interactions can reduce piscivore reproductive success and potentially drive phase shifts between piscivore-dominated and prey fish-dominated states (20). The implication is that management targets, such as population densities and catches, need to incorporate the chance of these phase shifts between states (21). However, the strengths of ecological interactions that underlie the potential for such shifts are difficult to precisely measure.

Here we seek to identify where and when ecosystem based management is likely to lead to the largest economic gains and to articulate the nature of these gains. Specifically, we ask how economically optimal management decisions in a multispecies fishery depend on the type of species interactions and population status and how the economic value from ecosystem-based management depends on correct knowledge of the species interactions. To this end, we consider a series of alternative, nested economic-ecological models that differ in terms of complexity of predator-prey interactions of a common piscivore and prey fishery system and determine the optimal harvest trajectories. We solve optimal trajectories, the series of harvest rates that maximize long-term economic profits from the fishery (net present value), from a set of initial conditions for each of the fish stocks. This highlights how the economic value of including additional ecological information depends on the current state of the system, which itself reflects the history of management. In this way, we identify the conditions under which knowledge of ecological conditions provides the most benefits.

Model and Results

We use a recently developed economic-ecological model of piscivore-prey interactions described in ref. 22 parameterized to resemble Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*) in the North Sea. This ensured that our findings were founded on ecologically and economically plausible parameters. We explore alternative scenarios to expose generalities via sensitivity analyses.

As detailed in *Materials and Methods*, this model follows the linked biomass abundance dynamics of the two focal species as they depend on growth, mortality, harvest, time-lagged recruitment, and the array of species interactions described in the next paragraph. This delay difference population dynamic model is ideally suited for our analysis. First, the unique formulation reduces the number of state variables in the system while being consistent with more complex age-size structured models. This feature is critical to enable the calculation of optimal economic-ecological management trajectories of fishing mortality rates over time. Second, the model can flexibly capture distinct types of ecological interactions allowing us to evaluate optimal dynamics under a series of four nested ecological models. In addition to the base model parameterization described in the *Materials and Methods* and *Supporting Information*, we also conducted sensitivity analyses to ensure that our findings were robust across a wider range of parameterizations. These analyses addressed discount rates, price differences between piscivore and prey, and the strength of the predator-prey linkage between the two species.

Models are nested such that each subsequent model adds one additional ecological interaction to the model that precedes it. The first model ("independent") is one in which prey and piscivores are independent of each other (Fig. 1A). The second model incorporates a predation interaction between adult piscivores and prey ("+predation"). In this model, fishing prey always reduces piscivore productivity (Fig. 1B). The third model adds consumption of piscivore eggs by prey species ("+egg predation"). In this model, the effect of fishing prey on equilibrium piscivore

abundance varies depending on fishing level on piscivore (22). When piscivores are abundant, increasing fishing on prey lowers piscivore abundance, but when piscivores are depleted, fishing prey increases piscivore abundance (Fig. 1C). The fourth model makes the same assumptions as the third but includes a saturating functional response of prey consuming piscivore eggs, which creates depensatory recruitment at low piscivore spawning abundance ("+depensation"). In this case, there is always a nonstable equilibrium point below which the piscivore reproduction cannot replace adults (Fig. 1D). Thus, the nature of ecological interaction and system state governs the magnitude and direction of interaction strength between predators and prey.

For each ecological scenario, we find the optimal management trajectory of fishing rates (the instantaneous fishing mortality over time, hereafter called harvest trajectory) directed at piscivores and prey to maximize the net present value of total economic returns from fishing (Eq. 2). We constrained the solution so that the biomass of each species reached management targets at a future date T . The targets roughly correspond to levels that would maximize sustainable yield of each species in the absence of ecological interactions. To capture how past fishing history effects the dynamic solutions and economic returns of ecosystem-based management, we solved for the trajectories from four starting conditions, each representing a combination of piscivore and prey being at relatively high or low abundance (*Materials and Methods*).

In all scenarios the harvest trajectories consisted of a transient period characterized by changes in fishing rates, unique for each starting case, and a stable period where the fishing rates and population levels were relatively unchanged [and were essentially identical across starting positions because these rates approximate the steady-state levels due to the "turnpike" nature of the optimal solutions (see, e.g., refs. 23 and 24)]. We address each separately, beginning with the steady-state fishing rates, defined here as fishing rates in year 20. Generally, compared with the three models with species interactions, the year 20 fishing rates in the independent model had markedly lower piscivore and higher prey fishing intensity (Fig. 2). The lower piscivore fishing rate in this scenario is largely due to the absence of a compensatory increase in prey abundance that would otherwise enhance piscivore productivity following piscivore depletion. The higher

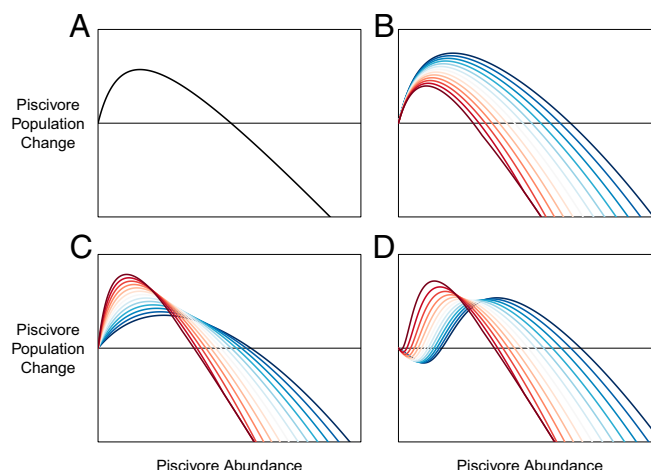


Fig. 1. Piscivore net productivity (rate of change) as a function of piscivore abundance for each nested ecological scenario: (A) independent, (B) +predation, (C) +egg predation, and (D) +depensatory egg predation. Each line depicts a different fishing level on prey, where blue is no fishing and red is heavy fishing. Lines are calculated by setting prey abundance to equilibrium levels given each piscivore abundance. Horizontal line indicates where net productivity equals 0 so equilibrium abundance is the intersection between the curve and the horizontal line.

prey fishing rate is due to two factors. (i) Without predation, prey are more productive, so they can withstand higher fishing rates. (ii) There is no benefit in having lower fishing on prey to enhance piscivore productivity. Across the other scenarios, the steady-state fishing rates that maximize NPV are generally similar. The three sensitivity analyses (*Supporting Information*) provided additional support to the finding that the three ecological scenarios that include predation generally have similar steady-state fishing rates.

In comparison, the harvest trajectories, especially on piscivores, were markedly different across the ecological scenarios and starting conditions (Fig. 3). In general, the optimal harvest trajectories on prey followed intuition derived from standard bioeconomic models that do not include species interactions (Fig. 2). Specifically, these models generally predict that if a population is above (below) the steady-state level, then optimal fishing rates start high (low) and monotonically decrease (increase) to move the population toward the steady-state level (24, 25) (biomass trajectories are provided in Fig. S1). In contrast, this intuition fails for piscivores. For example, in the case when piscivores were initially low and prey were high in the +egg predation scenario (Fig. 3C and Fig. S1), there was an initial moderate fishing rate which declined to 0 and remained there for approximately three periods, before monotonically increasing thereafter. This unique optimal path occurs even though the initial piscivore level was below its steady-state level. The initial high fishing rate reflects the fact that adult piscivores did not initially generate many offspring because of egg predation, so there was little reproductive benefit in maintaining adults until after prey became depleted. A similar pattern also occurred when both piscivore and prey were at high abundance (Fig. 2A), suggesting that it is high prey abundance that drives this outcome. Optimal harvest trajectories were nearly identical in the discount rate and price differential sensitivity analysis and only slightly modified in the enhanced predator–prey linkage analysis (*Supporting Information* and Figs. S2 and S3).

The different optimal harvest pathways beg the question: what is the economic and biological implications of assuming one set of interactions when in fact another one is driving the system? To explore this question, we calculated the economic loss, in terms of percentage reduction in NPV, of applying the incorrect optimal harvest pathway for each combination of true and assumed ecological interaction and each starting condition. We find that in general, the loss of NPV from assuming the wrong interaction was generally small (<10%), but the frequency of moderate (>10%) losses depended on the fishing history (Fig. 4). If piscivores were initially depleted by fishing, 5 of the 24 possible combinations of true/assumed led to roughly 10–15% reductions in NPV, regardless of prey fishing history. In contrast, if

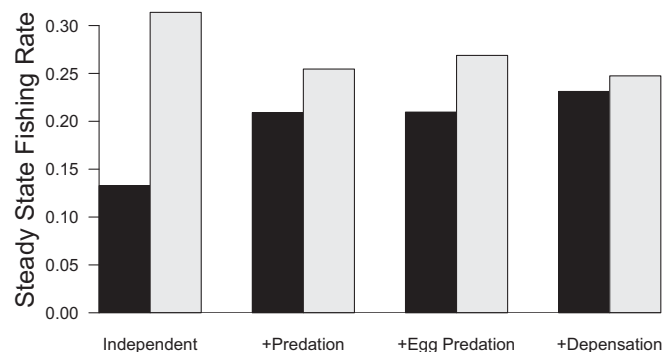


Fig. 2. Year 20 fishing rates (y^{-1}) on piscivores (black) and prey (gray) across the four nested scenarios.

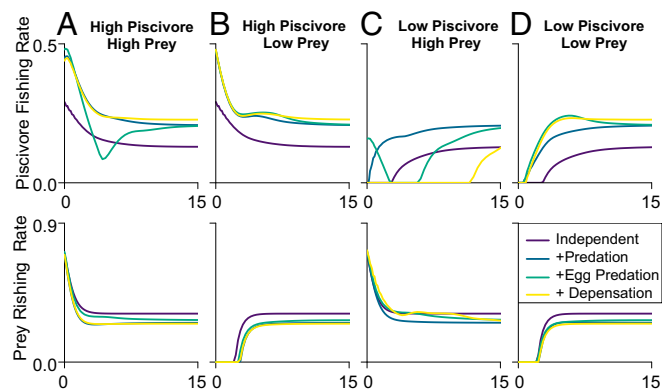


Fig. 3. Initial optimal harvest trajectories on piscivores (*Upper*) and prey (*Lower*) for four starting conditions (panels) and ecological scenarios (colors). Each starting condition represents a different exploitation history (A–D), where high abundance follows from low historical fishing rates and vice versa. x axis denotes time. Biomass trajectories are illustrated in Fig. S1.

piscivores were subjected to low fishing rates and were therefore initially abundant before management, only two combinations of true/assumed led to >10% reduction, and none had reductions of 15% or greater.

Although these reductions in total fishery-wide NPV were generally modest, the costs of applying the incorrect trajectory were unequal between the piscivore and prey fisheries, and the cost of incorrectly specifying the ecological interactions increased when piscivores were initially depleted. Namely, the piscivore fishery had the most severe outcomes from incorrect model specification (Fig. S4), where the costs of being incorrect ranged from +18% (a benefit) to –300% (a cost). A reduction in NPV greater than 100% is possible because NPV can be negative when profits per time step are negative, especially in the early time steps. In comparison, costs of being incorrect in the prey fishery ranged from +15% to –20% (Fig. S5). Thus, the benefits and costs of ecosystem-based approaches where predator–prey interactions link distinct human uses may be more strongly felt at the level of the individual fishery rather than at the aggregate level, highlighting the potential political–economic issues that arise in its implementation.

In summary, in aggregate the loss of NPV is modest, but within fisheries the loss can be considerable, a finding supported through our three sensitivity analysis runs (Figs. S6 and S7). In fact, only extremely high levels of diet linkage between piscivore and prey caused substantive losses in aggregated NPV (as much as 50% loss), and losses were still highest in the piscivore fishery.

Because the true state of nature is likely unknown, we provide an initial step toward formalizing how alternative decisions stemming from this limited knowledge might produce trade-offs. Trade-offs might exist in two dimensions: each choice of harvest trajectory could pose trade-offs in expected NPV and risk of missing management targets across fisheries. To evaluate these, we assumed for simplicity that each state of nature is equally likely to be true and calculated the expected NPV for each fishery (piscivore, prey) under each choice of harvest trajectory. We measured risk as the average extent to which population biomass targets were missed [i.e., $\text{risk} = -E(\min(0, \Delta B_{i,j}))$ where $\Delta B_{i,j}$ is the percent difference between final and target biomass for species j under all possible i states of nature (26)]. Risk in terms of stock status is consistent with the manner in which fisheries are currently managed, for instance, in the US, where federal legislation requires that stocks be managed to achieve targets and avoid limits.

The magnitude of trade-offs, which is likely inversely related to the ease of decision making, varies depending on the initial condition of the fisheries (Fig. 5). In most cases, there is at least one harvest trajectory that poses small risks in both fisheries

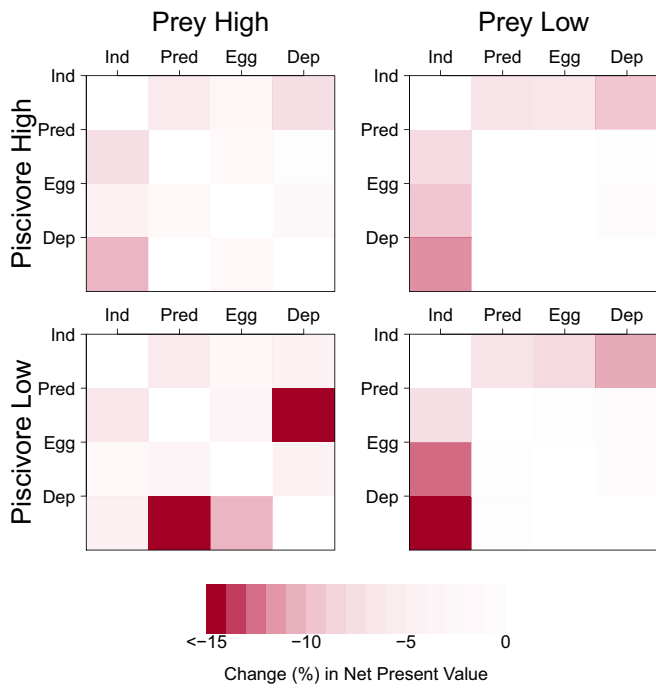


Fig. 4. Percent loss in net present value (NPV) when the optimal harvest trajectory based on one ecological scenario is applied to other ecological scenarios. In each panel, the rows depict the true state of nature, and the columns are the assumed interaction. Each panel represents a different initial condition expressed in terms of initial abundance of piscivores and prey. Ind refers to the independent scenario, Pred refers to the +predation scenario, Egg refers to the +egg predation scenario, and Dep refers to the +depensation scenario.

while performing similarly well in terms of NPV. For instance, in the cases where piscivores are initially high (Fig. 5, *Upper Left*), only the independent scenario has substantial risk (here of missing the prey management target), whereas the +pred and +egg harvest trajectories carry little risk and perform equivalently in terms of NPV within each of the two fisheries. In comparison, the case when piscivores are initially low and prey are high (Fig. 5, *Lower Left*) carries trade-offs between NPV in the prey fishery and risk in the piscivore fishery. In this case, all management choices except the +dep harvest trajectory induce large risks of missing management target in the piscivore fishery. However, this management strategy performs by far the worst for the prey fishery (10% reduction in NPV). Thus, in this case, there is a stark trade-off between taking actions to prevent the collapse of one population (and preserve any attendant ecological and economic benefits that it provides) and economic performance of the fishery in aggregate.

Discussion

Here we explored the cost of applying resource management decisions when there is ambiguity about ecological interactions. On one hand, our results are reassuring to managers because we find that management performance, as measured by aggregate economic value, was commonly robust to uncertainty regarding the nature of ecological interactions. Although the specific harvest pathways varied considerably, the lost net present value from applying the incorrect harvest pathway was minimal compared with other sources of error that are likely in fisheries, e.g., implementation error and observation error. Indeed, borrowing on the concept of pretty good yield (27), we find that application of harvest pathways can produce pretty good value in fisheries, even when the underlying species interactions are not known precisely.

On the other hand, our results raise concerns. That is, when one species (here piscivore) becomes depleted, the costs of

applying the wrong model increase considerably and produce trade-offs in expected returns and risks across the fisheries. The presence of a depensatory tipping point amplifies this effect, whereby population collapse is likely if management does not take specific steps to avoid it. Furthermore, the optimal fishing rates on the prey species required to recover depleted piscivores in this case are prohibited under the current US fisheries statutes and also far exceed rates being advocated for forage fish around the world (14, 28). In other words, managers would likely have to apply suboptimal pathways to balance the legal and political considerations associated with ecosystem-based management, which could incur significant costs to both fisheries.

Given that the true state of nature is rarely known with a high degree of confidence (29), an ecosystem-based management strategy might simply aim to maintain piscivore abundance at levels where annual fishing regulations pose smallest cost or risk. Indeed, high-profile natural resource collapses, such as the northern cod, are characterized by scientific uncertainty, conflicts among stakeholders, and high exploitation rates (30). More broadly, ecosystem-based decision making might therefore benefit ecosystems and fisheries by exploring key structural uncertainties to identify high-cost/risk and low-cost/risk states and implement management measures intended to maintain the system in a neighborhood of the desired states (31).

The ecosystem approach to natural resource management might therefore have a bigger and more justifiable role in setting safe zones with thresholds instead of defining management strategies to meet specific population targets. The idea of safe zones is often applied with attention given to ecological benefits (31), yet our model illustrates an additional benefit to setting management safe zones, where decisions are potentially easier because trade-offs between risks and reward are more equitable across stakeholders. Shifting the focus away from targets to safe zones would require a new paradigm for fishery management around the world where the goals are to attain and sustain target stock levels (e.g., biomass that produces maximum sustainable catch). Safe zones are consistent with the concept of maintaining resilience in a system (8, 21, 32), by applying heuristics that are simple, are easily understood, and achieve satisfactory outcomes (33), and acknowledge upfront the difficulties of prediction in the face of ecological complexity.

This approach might be useful in resolving conflict among fisheries, such as that currently occurring in the US mid-Atlantic region. Presently, there is conflict between commercial fisheries

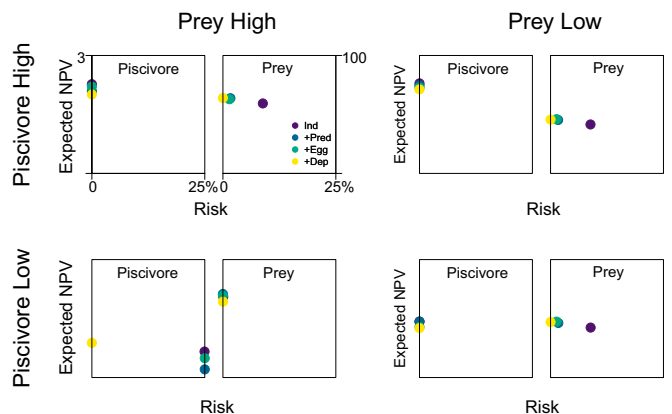


Fig. 5. Expected NPV (year 2000 US dollars per square kilometer) and risk of missing management target for each assumed harvest trajectory. For each panel pair, the left-hand panel illustrates NPV vs. risk for the piscivore fishery, and the right-hand panel illustrates NPV vs. risk for the prey fishery. Each panel pair represents a different starting condition, as in Fig. 4. Colors denote harvest trajectory. Axis scaling is identical across panel pairs as is denoted in *Upper Left*.

targeting Atlantic menhaden (*Brevoortia tyrannus*) and recreational fisheries targeting striped bass (*Morone saxatilis*), where the latter group has advocated for changes to the menhaden harvest rules, whereas the former has successfully lobbied to maintain the status quo. Recently, scientific uncertainty has been used to defer taking action away from the status quo, largely because it is not possible to precisely predict effects of menhaden fishing on striped bass fishing opportunities (34). Rather than delaying action in the hopes of future scientific precision, a safe zone approach could identify high-risk states, and alternative management strategies can be tested for their ability to avoid those states.

The alternative is to invest in a greater understanding of the type of ecological interaction that is occurring. Although favorable management outcomes likely will not depend on having precisely parameterized models, they will be sensitive to broad information on the type of interactions occurring and their relative strengths. In some contexts, existing data or manipulative experiments can be used to measure interaction strengths between species. However, in marine ecosystems, data time series are typically short relative to species' generation times and low-frequency environmental variation, and experiments are not feasible (35). Sampling of food habits can reveal what species consume, but they do not reveal interaction strengths (36). Depensation occurs when there is a saturating functional response of prey on piscivore eggs, yet estimating functional response in situ is notoriously difficult (37). Thus, in many cases, decisions will have to be made without knowing the strength or nature of interaction of species. We recognize that in cases of severe collapse, the value of accurate ecological information becomes high, yet this information is insufficient to ensure recovery as fully functioning governance systems and social institutions that foster trust and cooperation become essential (38, 39).

Our model necessarily made several simplifications that likely affected the severity of estimated costs of applying the wrong model. On one hand, we considered the case where the manager followed a harvest trajectory that was based on presumed optimal targets, and they did not update their management over time. In this way, our results inflate the potential costs because fishery managers would likely adjust their management decisions based on observations on the fish stock. On the other hand, other simplifying assumptions would have the opposite effect. We did not consider stochasticity both reducible and irreducible (40) and the role that this plays in evaluating the risk associated with different management strategies. Stochasticity can push the system past safe limits into zones where recovery is lengthy and costly (41). We also assumed that the initial system states were known without any error. Finally, our model does not consider management error (implementation error due to inaccurate assessments or enforcement error), which can be significant and costly when managers are slow to detect rapid changes in population status (42).

Our work further suggests that compared with management end points, management trajectories may be more sensitive to ecological context. In fisheries, there is a large and growing literature on how conventional management targets are affected by consideration of multispecies interactions (10, 43), but to our knowledge, there has been little accompanying attention to the pathway of management decisions. In our model, the harvest trajectories were especially sensitive to the egg predation by prey on piscivores, particularly when prey were initially abundant. In contrast, the steady-state exploitation rates were comparably less sensitive to the initial conditions or the ecological scenario. We therefore suggest that the application of ecosystem approaches might alter the approach to achieving management end points rather than necessarily changing the end points themselves.

This model is an application of dynamic control to a generalized case of two-species harvest. Here we used a simple general case for the benefit of computational tractability and so that the qualitative

findings and implications of the model would be generalizable to other contexts. Although this implies that the specific findings are not likely to hold for all situations, it also means that the approaches that we used are likely widely applicable. These approaches are twofold. The first is using models to evaluate the risks and likely outcomes for alternative management decisions in the presence of model uncertainty, as is central to structured decision making (44). The second is using the outcome of these exercises to develop simple and transparent management strategies that are designed to avoid high-risk states of nature while ensuring economic viability and other social goals (21). For example, the safe zone management approach could be appealing to decision makers because it seeks to avoid so-called "wicked problems," where uncertainty is high, stakeholders have widely different values that shape their preferred outcomes, and there are large costs to making the wrong management decision (45).

Materials and Methods

Ecological Model. We used the delay differential model of piscivore-prey interactions described in ref. 22. This model is ideally suited for the main aims of our present work. Namely, it can flexibly capture distinct types of ecological interactions and do so with few state variables. The latter feature is critical to enable the calculation of optimal management trajectories. In this model, prey biomass is represented as single state variable, whereas piscivores are represented as two state variables: adult abundance and adult biomass. In this way, we can account for changes in piscivore body size that results from variation in prey abundance. Moreover, we implicitly model recruitment via a density-dependent stock recruitment relationship with a time lag. The model can be parameterized to include egg predation which governs the recruitment rate. There is an implicit juvenile piscivore stage that is not directly affected by densities of the prey species. Detailed overview of the model and parameterization is given in [Supporting Information](#).

The model simulates the dynamics of prey biomass (x_1), adult piscivore biomass (x_2), and abundance (n_2) through the following delay differential equations:

$$\frac{dx_1}{dt} = \frac{rx_1(t)}{K} (K - x_1(t)) - F_1(t)x_1(t) - x_2(t)f(x_1(t)), \quad [1a]$$

$$\frac{dx_2(t)}{dt} = w_r R(t) + \kappa w_\infty(t)n_2(t) - (M_2 + F_2 + \kappa)x_2(t), \quad [1b]$$

$$\frac{dn_2(t)}{dt} = R(t) - (M_2 + F_2)n_2(t), \quad [1c]$$

where K is prey carrying capacity in the absence of piscivores, r is maximum reproductive rate of the prey, F_i is the instantaneous fishing mortality rate on species i , $f(x_1(t))$ is a saturating functional response with a nonzero intercept to reflect feeding on other prey, w_r is the weight of piscivore recruits, κ is a metabolic rate parameter, and M_2 is the natural mortality rate of the piscivore. w_∞ is the asymptotic mass of a piscivore at time t which is a function of $f(x_1(t))$ ([Supporting Information](#)). $R(t)$ is the piscivore recruitment rate, which is a function of density of adults at lag a_r (age at maturity), and by predation rate induced by prey fish, as well as density dependent mortality and mortality due to other causes ([Supporting Information](#)). We use a saturating functional response relationship between egg consumption and initial egg density, which can create depensatory production dynamics if there is high handling time. The distinct ecological scenarios were generated by adjusting the parameterization ([Supporting Information](#)).

Economic Model and Assumptions. The basis of our economic model is the optimal control formulation first solved by ref. 46 and popularized by refs. 47 and 48. We assume a regulator that is knowledgeable and understands population dynamics and whose objective is to maximize the discounted net present value of the sum of fishing profits in each fishery by choosing fishing mortality rates over time. Specifically, the objective function of the regulator is

$$J(x_i(t), F_i(t)) = \max_{F_1(t), F_2(t)} \int_0^T e^{-\gamma t} \left[\sum_{i=1}^2 P_i(F_i(t), x_i(t)) - C_i(F_i(t)) \right] dt, \quad [2]$$

where γ is the discount rate, $J(x_i(t), F_i(t))$ is the net present value, $P_i(F_i(t), x_i)$ is the revenue function of fishery i , and $C_i(F_i(t))$ is the cost function of fishery i . These revenue and cost functions are defined in [Supporting Information](#). Total profits for each fishery (piscivore, prey) is the difference between

revenues and the costs, where the former depends on $F_i(t)$ and $x_i(t)$, whereas the latter depends on $F_i(t)$ (24).

The objective function (Eq. 2) is solved for fishing mortality rates $F_i(t)$ for each fishery, i , in each period, t , subject to the population dynamic delay differential equations (Eq. 1 a–c), initial conditions on the stocks, the constraints on the target biomass levels applied at time $T = 30$ y, and nonnegativity constraints on the stocks and controls.

The percentage loss of NPV (L) from applying the optimal harvest trajectory under ecological scenario i ($[F^*_{1,i}(t), F^*_{2,i}(t)]$ for $t = [0, T]$) to the ecological scenario j was calculated as

$$L_{i,j} = 100 \left(\frac{\text{NPV}_{ij}}{\text{NPV}_{\text{opt},j}} \right) - 100, \quad [3]$$

where $\text{NPV}_{\text{opt},j}$ is the discounted net present value obtained when the harvest trajectory that is optimal under the ecological scenario j is applied (Eq. 2).

Parameterization. We intend this model to be general but seek parameter values that are biologically and economically plausible. For that reason, we base the model parameterization loosely on the cod (piscivore) and herring (prey) fishery in the North Sea, as described by ref. 22. We assume prices are

exogenous for herring and for cod. Profit functions with similar characteristics have been used for these fisheries (see ref. 22 for supporting references). Details of the parameterization and the numerical optimization methods are found in refs. 22 and 49, respectively, and provided in [Supporting Information](#).

Initial Conditions and Target Biomass. For each ecological scenario, we calculated the optimal management trajectory for four initial conditions, each representing a combination of piscivore and prey being at relatively high or low abundance. To generate starting conditions, we set piscivore and prey to levels that correspond with equilibrium biomass for $F_1 = 0.05/0.35$ (high, low biomass) and $F_2 = 0.05/0.6 \text{ y}^{-1}$ (high, low biomass), under the +predation scenario. For the low-piscivore cases, we additionally reduced recruitment to one-half of steady-state values to represent a scenario where environmental conditions have depressed recruitment. Target biomass levels for piscivores and prey were set by finding the biomass that maximizes sustainable yield under the case when the two species were independent.

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