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METHODS

Linking economic and ecological models for a marine ecosystem

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Abstract

Increasingly, economists and ecologists have begun to recognize the value to public policy of combining information and results from each discipline into multidisciplinary studies. Here, we present a methodological approach that links economic and ecological analyses. We develop an economic–ecological model by merging an input–output model of a coastal economy with a model of a marine food web. We describe distinct linear system sub-models of the economy and the ecosystem, and we develop a method for linking the two. Our method extends the work of earlier researchers by incorporating an ecosystem matrix into resource multipliers, and by showing how these multipliers may be calculated. We present a numerical example for the New England region using coastal economic and marine ecological data from the region for a restricted set of industry sectors and food web trophic levels. We calculate resource multipliers for the example, and we simulate the economic impacts of changes in primary production in the ecosystem on final demands for fishery products. The results illustrate the effects of incorporating the impacts of habitat destruction and ecosystem structure on resource multipliers. Our approach can be extended to incorporate the full range of sectors in the economy and trophic levels in a linked ecosystem.

Keywords: Input–output; Resource multiplier; Coastal economy; Marine ecosystem; Fisheries

1. Introduction

Marine ecologists have begun to argue for a more rational approach to ecosystem science, one that incorporates an understanding of the economic implications of alternative ecosystem states (cf. Ayensu et al., 1999; Sherman and Duda, 1999). This argument reflects a deep understanding that ecosystem conservation depends upon political decisions, and political decisions, in turn, are influenced by their potential economic consequences.

Various US laws and regulations require an assessment of the economic impacts associated with proposed regulatory changes (e.g. fisheries management measures) on related communities (Hoagland, 2001). For example, amendments to the Magnuson–Stevens Fishery Conservation and

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Management Act in 1996 [P.L. 104-297] require that fishery management plans now include a "fishery impact statement" to assess, specify, and describe the likely effects of resource conservation and management measures on participants in fisheries and on fishing communities.

In this paper, we develop a formal way of responding to this call by analyzing the economic links between a coastal economy and a marine ecosystem. Specifically, we develop an economic–ecological model by merging an input–output model of a coastal economy with a linear model of a marine food web. We illustrate the model with a numerical example for the New England region using economic and ecological data from the region.

This type of analysis is based on the seminal work conducted by Isard et al. (1968) more than 30 years ago. It makes sense to revisit this approach because of the emergence of an improved input–output framework (Minnesota IMPLAN Group, 1997) and the development of marine ecosystem models for New England (Sissenwine et al., 1984). Given these developments, creating an integrated economic–ecological model may improve public policy decisions by clarifying the ramifications of fishery management actions or other types of conservation measures on society and nature.

A linear systems model that links economic and ecological subsystems can be used to answer a variety of policy-relevant research questions. For example, a change in final demand for the output of a particular industry can be traced back to determine its impact on the structure of the ecosystem. On the other hand, a change in the structure of the ecosystem can be followed through to determine its "economic impact"[1]. Because there may be more than one feasible ecosystem state, the economic impacts of alternative states might be compared. As an example, the depletion of an important groundfish stock may result in adverse consequences for those industries that supply the commercial fishing industry.

Except for the early work of Isard et al. (1968), there are few studies that link an ecological model to an input–output model[2]. Hite and Laurent (1972) suggest an adaptation of the Isard et al. approach in the special case where the energy transfer coefficients are unknown. Economic input–output models have been developed for the northeast coastal economy (Jin et al., 2000; Hoagland et al., 2000) and marine food web models have been developed for the Georges Bank ecosystem (Sissenwine et al., 1984; Jones, 1984; Cohen et al., 1979). We are unaware, however, of any published attempt to link an economic input–output model to a marine food web model for a marine ecosystem. Establishing such a link is the focus of this research.

2. Comparison of input-output to other ecological-economic models

Existing ecological–economic models may be categorized into three groups. The first group can be characterized by its focus on only a few species and markets. The "bioeconomic" approach to link ecological and economic models has been explored by Clark (1976) and others since the mid-1970s. Its strengths lie in revealing economically optimal levels of yield and the net benefits of the implementation of alternative management measures. In some circumstances, the bioeconomic approach also can be used to determine the optimal dynamic path to a steady state. Because it often involves the use of nonlinear dynamic models of production and species growth and interactions, the bioeconomic approach is difficult to apply to a large number of species or markets.

The second group of studies has focused on integrating complex environmental and economic system models. Bockstael et al. (1995) describe a comprehensive approach for ecological–economic modeling and ecosystem valuation for the Patuxent River drainage basin in Maryland. These authors argue that two salient features of ecologi-

[1] Economic impacts can be expressed in several useful ways, including impacts on employment, income, tax revenues, etc.

[2] The model of Isard et al. examines a marine ecosystem: Plymouth and Duxbury Bays in Massachusetts.

cal models, dynamics and spatial disaggregation, are important for modeling the economy as well. The two types of models often differ, however, in terms of time step, geographic scale, and level of aggregation. In Bockstael et al.'s analysis, the two types of models are developed in parallel and at their own levels of specificity. The two types of models exchange information on their respective ecological and economic elements. For example, specific environmental and natural resource parameters may be calculated by the ecological model and then used as input parameters for the economic model.

In order to analyze systems with a large number of interacting elements, such as industries and consumers in an economy or species in an ecosystem, economists and ecologists have explored the use of the third group of models: linear models. A model of this type can be represented as a system of linear equations, and the principles of linear algebra can be used to solve for the values of interest, such as industry output or species biomass. Where nonlinear relationships exist among the elements, the model can be viewed as a localized linear approximation. Such models typically are used to examine systems in equilibrium.

A linear economic "input–output" model answers the following question: given a specified shift in the level of final demands for economic goods and services, how do the levels of output from each of the industrial sectors of the economy change? The model is useful because it provides a map of the links between industrial sectors. The scale of these links can be summarized by one or more of a family of measures known as "multipliers".

Input–output models have been widely used in regional economic impact analyses (Loomis, 1993). A small number of studies have examined the economic impact of fisheries and marine-related activities in New England (Briggs et al., 1982; Grigalunas and Ascari, 1982; Andrews and Rossi, 1986; Steinback, 1999).

The major advantage of the input–output model is its explicit inclusion of all the links across industrial sectors. For example, suppose a fisheries management option requires a reduction in the number of fishing vessels in a fleet. To capture the full effect of this reduction, we need to quantify the economic importance of the industry to the economy of the region. Fisheries contribute to employment and to household incomes. Port buildings and equipment also provide a basis for tax revenues that support local and state government programs. In addition, as purchasers of inputs, the fishing industry supports a number of other industries such as boat-building and repair. When all the links within the economy are considered, income and employment generated by the fishing industry have ripple effects on the overall income and employment of the region.

Since the late 1960s, input–output models have been extended to incorporate links to environmental or natural resource sectors. Most of them have been concerned with the effects of pollution from one or more industrial sectors on the output of other sectors (e.g. Ayres and Kneese, 1969; Leontief, 1970; Førsund and Strøm, 1976; Lee, 1981; Perrings, 1987). In a recent study, Xie (2000) described the concept and application of an environmentally extended social accounting matrix for environmental policy analysis[3].

It is important to recognize that input–output analysis is theoretically consistent with the kind of welfare analysis represented by a neoclassical growth model. This is because the coefficients of an input–output model are derived from complete income and product accounts for an economy, which include net national product (NNP) (Miller and Blair, 1985). Weitzman (1976) has shown that NNP is the maximum welfare attainable along a competitive trajectory for an economy. Weitzman's treatment of NNP has been extended by Solow (1986) to include exhaustible resources, and by Hartwick (1990) and Maler (1991) who consider renewable resources and pollution. The Hartwick–Maler–Solow–Weitzman framework forms the theoretical foundation for natural re-

[3] In many integrated economic–ecological models, natural resource inputs and pollutants are expressed in physical units, while economic exchanges are expressed in monetary units (Isard et al., 1968; Leontief, 1970; Xie, 2000). Weale (1991) has constructed environmental multipliers from a system of physical resource accounting. For an excellent discussion of the issue of non-commensurate measures (i.e. economic vs. physical), see Hannon (2001).

source and environmental accounting (Hrubovcak et al., 2000)[4]. Notwithstanding this consistency with macroeconomic welfare theory, it is clearly understood among economists that the input–output model is not designed to guide resource allocations, since the framework does not fully capture consumer surplus gains or losses.

A marine food web model specifies the trophic relationships among groups of species in an ecosystem. A food web usually is organized hierarchically into trophic levels, and groups of species at one trophic level typically consume individuals of species at a lower level (or sometimes at the same level). One potential use of a marine food web is to discern how much of the sun's energy results in commercially exploitable fishery resources (Steele, 1965). Analogous to the technical coefficients of the input–output model, in a food web, "energy transfer coefficients" represent the fraction of the total biomass of a species group supplied by prey species groups[5]. Thus, given levels of biomass for groups of species at a specific trophic level, the biomass levels of species at other trophic levels can be determined[6].

Where there exists some overlap between the elements of an input–output model and a food web model, the two systems may be linked and solved simultaneously. The most natural overlap occurs through the harvest of one or more species from an ecosystem. Other interactions may occur through the negative effects of pollution on elements of the food web (toxic waste, nutrient induced eutrophication). Alternatively, in some circumstances, increased levels of macronutrient inputs, such as nitrogen from agricultural runoff, might enhance primary productivity up to some threshold.

3. Methods

We follow a framework developed initially by Daly (1968) and Isard (1968). A concise description of this type of model can be found in Miller and Blair (1985) and Hannon (2001).

3.1. Basic structure of economic–ecological model

Suppose that there are n industry sectors in the economic system and m components in the ecosystem. Following Daly (1968) and Isard (1968), we present key components of an economic–ecological model in a partitioned matrix of size $(n+m)\times(n+m)$:

$$\begin{bmatrix} \mathbf{A} & \mathbf{E} \\ \mathbf{G} & \mathbf{B} \end{bmatrix} \tag{1}$$

where $\mathbf{A}$ is a $n\times n$ matrix representing an economy that describes flows between economic sectors (i.e. matrix of economic exchanges); $\mathbf{B}$ is a $m\times m$ matrix describing flows within the ecosystem (i.e. matrix of ecological exchanges); $\mathbf{G}$ is a $m\times n$ matrix describing flows from the ecosystem to the economic sectors (i.e. matrix of ecological to economic exchanges); and $\mathbf{E}$ is a $n\times m$ matrix describing flows from the economic sectors to the ecosystem (i.e. matrix of economic to ecological exchanges).

There are two general types of links between the ecosystem and the economic system. The first link (**G**) captures the supply of marine ecosystem resources, goods, and services to a coastal economy (e.g. fish stocks as inputs to the fish harvesting industry), and the second (**E**) describes the impacts of economic activities on the ecosystem (e.g. marine pollution or destruction of habitat).

[4] Many integrated economic–environmental analyses have been conducted in the area of "green accounting" (Lange, 1998). Issues and progress in developing resource and environmental accounting have been summarized in Nordhaus and Kokkenlenberg (1999). See also Hannon (2001). Hrubovcak et al. (2000) present a theoretical framework for environmental accounting in the agricultural sector. Tai et al. (2000) developed a simple procedure for valuing fisheries depreciation in natural resource accounting.

[5] Note that not all of the biomass at a lower trophic level can be converted into biomass at a higher level. Some of the consumed biomass from lower trophic levels is dissipated through metabolism and as waste products. A rule of thumb in marine food webs is that only 10% of the biomass from a lower trophic level is converted into biomass at a higher level (Steele, 2001).

[6] Typically, we start with an estimate of primary production or the biomass of phytoplankton at the lowest trophic level. Food webs may also incorporate "export" and "detritus" elements, which may be considered analogous to components of an input–output model's final demand sector.

3.2. Economic system

A static Leontief input–output model of an economy is a system of linear equations:

$$(\mathbf{I}-\mathbf{A})\mathbf{X}=\mathbf{Y} \tag{2}$$

where $\mathbf{I}$ is the $n \times n$ identity matrix; $\mathbf{A}$ is a $n \times n$ technical coefficient matrix; $\mathbf{X}$ is a $n \times 1$ column vector denoting output; and $\mathbf{Y}$ is a $n \times 1$ column vector denoting final demand. The idea behind the model is that the output of any industry (x_i, an element of $\mathbf{X}$) is needed as an input in many other industries, or even in that industry itself. Therefore, the level of x_i will depend on the input requirements of all the n industries as well as on final demand (Chiang, 1974).

The elements of $\mathbf{A}$, a_{ij}, are dimensionless technical coefficients defined as

$$a_{ij} = \frac{z_{ij}}{x_j} \tag{3}$$

where z_{ij} is the monetary value of the flow from sector i to sector j ($/year); and x_j is the total output of sector j ($/year).

The matrix $(\mathbf{I}-\mathbf{A})$ is called the technology matrix. If the technology matrix is not singular, the impact of changes in final demand ($\mathbf{Y}$) on output ($\mathbf{X}$) can be estimated as

$$\mathbf{X}=(\mathbf{I}-\mathbf{A})^{-1}\mathbf{Y} \tag{4}$$

where $(\mathbf{I}-\mathbf{A})^{-1}$ is called the Leontief inverse. For a comparative static analysis, the partial derivative gives us the matrix of multipliers

$$\frac{\partial \mathbf{X}}{\partial \mathbf{Y}}=(\mathbf{I}-\mathbf{A})^{-1} \tag{5}$$

It measures the direct and indirect effects on industry output ($\mathbf{X}$) associated with one dollar's increase in final demand ($\mathbf{Y}$).

For empirical analysis, an input–output table (transactions table) includes all processing sectors (industries), final demand (including consumer/household purchases, private investment, government purchases, and exports), and a payments sector (value added including labor cost, capital cost, taxes, rental payments, and profit). Total industry outlays equal the value of total industry outputs. Outlays are payments made by firms for inputs and for other purposes in the payments sector. Inputs are purchased locally (within the region) or imported from outside the region[7]. Outputs are goods or services produced by the industry. They can be consumed directly by households and others as final demand within the region, or sold to other industries as intermediate demand.

3.3. Ecological inputs to economic sectors

One link between the ecosystem and the economic system involves the supply of ecosystem resources, goods, and services to the economy, such as fish stocks as inputs to the fish harvesting industry. This link is captured in the $m \times n$ $\mathbf{G}$ matrix. Each column of $\mathbf{G}$ corresponds to an industry sector, while each row represents an ecological component (e.g. an ecological commodity).

An element of $\mathbf{G}$, g_{ij}, is an "ecological commodity input coefficient", defined as

$$g_{ij} = \frac{q_{ij}}{x_j} \tag{6}$$

where q_{ij} is the amount of ecological commodity i used in industry sector j (tons/year); and x_j is the total output of industry sector j ($/year). For example, g_{ij} is the quantity of fish species i harvested in the production of a dollar's worth of fishing industry j's output. The units of g_{ij} are tons/$.

With $\mathbf{G}$ and Equation (4), the direct and indirect ecological effects of increasing final demand may be calculated as

$$\mathbf{S}=\mathbf{G}\mathbf{X}=\mathbf{G}(\mathbf{I}-\mathbf{A})^{-1}\mathbf{Y} \tag{7}$$

where $\mathbf{S}$ is an $m \times 1$ vector of total ecological commodity inputs to the economic system. An element of $\mathbf{S}$, s_i is the total amount of ecological commodity i consumed by the economic system.

[7] For accurate estimations of regional economic impacts, one must carefully separate the local portion from the imported portion in every purchase/payment.

For example, s_i is the total utilization of fish species i in all industry sectors.

We now have a resource multiplier

$$\frac{\partial \mathbf{S}}{\partial \mathbf{Y}} = \mathbf{G}(\mathbf{I}-\mathbf{A})^{-1} \quad (8)$$

It measures the direct and indirect effects on natural resources (**S**) of one dollar's increase in final demand (**Y**). This formulation was developed by Hite and Laurent (1972), and has been used in many other analyses (see Miller and Blair, 1985; Weale, 1991).

In order to facilitate the examination of resource impacts, we partition **S** into two components: an $m \times 1$ vector **W** denoting the biomass available for consumption by the economy from each ecosystem trophic level[8] and an $m \times m$ matrix **K** with $k_{ij} = 0$ or 1, where 0 represents unharvested species or trophic levels and 1 represents harvested ecosystem components[9]. If the ecosystem has enough resource stocks to meet demand for inputs to the economy, then

$$\mathbf{KW} = \mathbf{S} = \mathbf{G}(\mathbf{I}-\mathbf{A})^{-1}\mathbf{Y} \quad (9)$$

3.4. Impacts of economic outputs on the ecosystem

In addition to harvesting resources from the ecosystem, the economy may influence the ecosystem. This link is captured in the matrix **E**[10]. **E** is $n \times m$, each row corresponds to an industry sector and each column denotes an ecological component.

An element of **E**, e_{ij}, is the "environmental impact coefficient", defined as

$$e_{ij} = \frac{f_{ij}}{x_i} \quad (10)$$

where f_{ij} is the amount of ecological commodity j affected by the output from industry sector i (tons/year), and x_i is the output of industry sector i ($/year). Thus, e_{ij} is the amount of ecological commodity j affected per dollar's worth of output from industry sector i. e_{ij} is measured in units of tons/$. In general, the impacts of economic activities on the ecosystem may be either negative or positive. For example, e_{ij} is negative when an ecological commodity is damaged and positive if the commodity is enhanced.

Let **D** be an $m \times 1$ vector of total environmental impacts; an element of **D**, d_i, represents the total impact of all industry sectors on ecological component i. Each element d_i has a negative value if the economy has a damaging effect on the component. With **E** and **X**, we have

$$\mathbf{D}' = \mathbf{X}'\mathbf{E} \quad (11)$$

Because the impact of economic activities on the ecosystem (**D**) alters ecological stocks, the available resource stocks to the economic system now are equal to the original resource consumed by the economy (**W**) plus the impacts: **W**+**D**. Modifying Equation (9), we have

$$\mathbf{K}(\mathbf{W}+\mathbf{D}) = \mathbf{S} = \mathbf{G}(\mathbf{I}-\mathbf{A})^{-1}\mathbf{Y} \quad (12)$$

Substituting Equations (4) and (11) into (12) and rearranging terms we have

$$\mathbf{KW} = (\mathbf{G}-\mathbf{KE}')(\mathbf{I}-\mathbf{A})^{-1}\mathbf{Y} \quad (13)$$

This result suggests that when the economy affects the ecosystem, the ecosystem needs to provide enough resource stocks to support the economy as described in **G** and, in addition, to offset the impacts of the economy on the stocks as described in **E**. In this case, the resource multiplier for harvested species becomes

$$\frac{\partial \mathbf{KW}}{\partial \mathbf{Y}} = (\mathbf{G}-\mathbf{KE}')(\mathbf{I}-\mathbf{A})^{-1} \quad (14)$$

The resource multiplier captures both the direct and indirect effects of one dollar's increase in final demand on the resource stocks. A comparison of (8) and (14) indicates that while Equation (8)

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[8] At this point, we do not necessarily consider the total biomass in each component of the ecosystem.

[9] **K** is necessary because **G** and **S** have non-zero values for harvested resources, while **W** has non-zero values for all components.

[10] According to Miller and Blair (1985), **E** describes flows from the economic sectors to the ecosystem. For example, pollutants are generated in the economic system and flow to the ecosystem. We do not account for pollutants in the **B** matrix (the ecosystem). We use **E** to capture the impacts of pollution on the ecosystem.

captures the first link (**G**) between the economic system and the ecosystem, Equation (14) combines the effects of the two links (**G** and **E**). The result is analogous to the model developed by Hite and Laurent (1972) for their analysis of coastal zone planning decisions.

3.5. Ecosystem

B describes flows within the ecosystem. The complementarities between economic input–output models and ecological food web models have been recognized for more than three decades, but cases in which the models have been linked are rare (Isard et al., 1968; Leschine and Smith, 1978). It is not clear why linked models have not been fully explored. One reason may be that food webs models are complex, and fully specified food web models are rare.

As noted, we consider a marine food web with m components. Let c_i be energy (carbon or biomass) flux through the ith component ($i = 1, \ldots, m$). The units of c are kcal/m^2 per year[11]. A typical linear formulation of a marine food web model is described by Steele (2001) as follows

$$\frac{c_i}{\varepsilon_i} = \sum_j \beta_{ij} c_j + \theta_i, \quad i = 1, \ldots, m \tag{15}$$

where ε_i is the ecological (or transfer) efficiency, β_{ij} is the fraction of c_j consumed by c_i, and θ_i is a constant rate of external input to c_i. In this formulation, c_i is the energy flow available to higher trophic levels, and j denotes components in the trophic levels lower than the ith component's trophic level (or the same trophic level). Thus, Equation (15) describes how energy flows from j to i and onto the next (higher) trophic level.

In developing our **B** matrix, we modify this food web model (15) using the Leontief input–output framework. An application of the Leontief input–output model to ecosystem analysis was developed by Hannon (1973). He presented an alternative linear formulation of the food web as

$$c_i = \sum_j b_{ij} c_j + v_i, \quad i = 1, \ldots, m \tag{16}$$

where v_i is respiration, and b_{ij} is the "energy transfer coefficient" defined as

$$b_{ij} = \frac{p_{ij}}{c_j} \tag{17}$$

where p_{ij} is the flow of energy from ecosystem component i to j, and c_j is the energy flow in component j. Note that here the jth component is in a higher trophic level than the ith component's level. Thus, Equation (16) describes how energy flows from i to j and is lost (i.e. through respiration) in the process. Also, in this formulation, the ecological efficiency is not explicitly modeled and it is merged with coefficients (b_{ij}) and captured in respiration (v_i). The major difference between the two specifications is that Equation (15) describes the various prey (j) of component i, while Equation (16) depicts the predators (j) of component (i).

In matrix notation, Equation (16) can be written as

$$(\mathbf{I} - \mathbf{B})\mathbf{C} = \mathbf{V} \tag{18}$$

where **C** is a $m \times 1$ vector denoting the energy flow in each component (c_i) in the ecosystem, **V** is a $m \times 1$ vector denoting respiration, and **B** is a $m \times m$ matrix called a normalized production matrix. As noted, the unit of **C** and **V** is kcal/m^2 per year[12] and **B** is non-dimensional. As shown in Hannon (1973), this may be rewritten in a relationship similar to Equation (4)

$$\mathbf{C} = (\mathbf{I} - \mathbf{B})^{-1}\mathbf{V} \tag{19}$$

For *small* perturbations[13], we have

[11] 10 kcal = 1 g carbon = 10 g biomass.

[12] The unit can also be the amount of new biomass produced per unit of time in a given area.

[13] With a perturbation in respiration, $\Delta\mathbf{V}$, Equation (19) becomes $\mathbf{C}+\Delta\mathbf{C} = (\mathbf{I}-\mathbf{B}-\Delta\mathbf{B})^{-1}(\mathbf{V}+\Delta\mathbf{V})$ with $\Delta\mathbf{C}$ and $\Delta\mathbf{B}$ being the change in **C** and **B**, respectively. For small perturbations, $\Delta\mathbf{B} \cong \mathbf{0}$. Also, this type of perturbation is called "press perturbation" in the ecological literature (see Yodzis, 1988).

$$\frac{\partial \mathbf{C}}{\partial \mathbf{V}} = (\mathbf{I} - \mathbf{B})^{-1} \tag{20}$$

Because of its Leontief type formulation, Hannon's ecosystem model can be integrated easily into our economic–ecological model. Multiplying both sides of Equation (19) by the area of our study region (m^2), we get the relationship between energy flow and respiration at the regional level (biomass tons per year). Let **W** and **R** be the regional energy flow and respiration, respectively, and suppose that the impact of the economy on the ecosystem (**D**) and ecological commodity inputs (**S**) to the economy are also modeled explicitly together with respiration[14], Equation (19) becomes

$$\mathbf{W} = (\mathbf{I} - \mathbf{B})^{-1}(\mathbf{R} + \mathbf{S} - \mathbf{D}) \tag{21}$$

R is the new respiration vector[15], and the total regional level "respiration" is $\mathbf{R}+\mathbf{S}-\mathbf{D}$. Elements of **D** have negative values for damages. Substituting Equations (4), (7) and (11) into (21) and rearranging terms, we have

$$\mathbf{W} = (\mathbf{I} - \mathbf{B})^{-1}[\mathbf{R} + (\mathbf{G} - \mathbf{E}')(\mathbf{I} - \mathbf{A})^{-1}\mathbf{Y}] \tag{22}$$

Equation (22) describes the ecosystem (**B**) linked with the economic system through **G** and **E**. The resource multiplier is

$$\frac{\partial \mathbf{W}}{\partial \mathbf{Y}} = (\mathbf{I} - \mathbf{B})^{-1}(\mathbf{G} - \mathbf{E}')(\mathbf{I} - \mathbf{A})^{-1} \tag{23}$$

It captures the direct and indirect effects of one dollar's increase in final demand (**Y**) on the energy flow (i.e. resource stock) in each component in the ecosystem (**W**). Equation (23) suggests that the impact of final demand on ecological stocks is affected by the economic production technologies (**A**), input coefficients (**G**) (dependence of the economy on resource stocks), impact of the economy on the ecosystem (**E**), and the ecosystem itself (**B**). The above equation extends Equation (14) by capturing the interactions among the different components in the ecosystem. Thus, we can use Equation (23) to estimate the impact of changing final demands on ecological components that are not directly harvested by the economy[16].

4. An application to New England fisheries

Here we present an example to demonstrate how an economic–ecological model may be constructed. In the example, we link an input–output model for the New England coastal economy with a marine ecosystem model from Georges Bank. We focus on the important Georges Bank groundfish fishery as the link between the ecosystem and the economy. The stocks that make up the fishery, including Atlantic cod, haddock, and yellowtail flounder, are now in a state of depletion or collapse as a result of recruitment overfishing (Murawski, 1996). The depletion of these stocks is unquestionably the result of overfishing. This fishery was once the highest revenue generating fishery in the region, and it is thought to be important to the New England coastal economy. For example, in 1990, an estimate of annual economic impacts from overexploitation relative to the fishery's longterm potential yield was on the order of $350 million (MOGTF, 1990). In 1993, Edwards and Murawski (1993) estimated the economic losses to the New England groundfish fishery in terms of rents and consumer surpluses at around $140 million a year, amounting to several billion dollars in losses over decades of overfishing. Large portions of Georges Bank have now been reserved from fishing with the goal of restoring the stocks to their former levels. Because of these characteristics, this ecosystem and its associated fishery provide a relevant example to illustrate the model developed here.

[14] For a detailed discussion of relevant mass balance modeling, see Christensen et al. (2000).

[15] One could consider **R** and **V** as respiration with and without fishing, respectively.

[16] Because the economic system and the ecological system are two very different nonlinear systems, the conditions under which the two linear approximations (matrix **A** and **B**) hold may differ significantly. For example, while **A** may be valid for a certain change in **Y**, the ecosystem matrix **B** may only be valid within a much smaller range of **V**.

4.1. Matrix of economic exchanges

Using IMPLAN PRO 2.0[17], we built a county-based input–output model for the coastal New England region. Specifically, this includes coastal counties in five New England states (CT, RI, MA, NH, and ME). For simplicity in our analysis and presentation, the default 528 sectors in IMPLAN were aggregated into the following four sectors: agriculture, manufacturing, fishing, and other. In Table 1, we present the simplified economic input–output model showing the inputs from industry sectors represented by rows into the industry and final demand sectors represented by columns. The flows from sector to sector are measured in millions of dollars. A value-added (or "payments") sector typically is added as an additional row. The total output from each sector must equal the total outlays made by each sector for the model to balance. Data in Table 1 allow us to calculate the technical coefficients for the coastal New England economy. The elements of the matrix of economic exchanges (**A**) in the economic–ecological model are as follows:

$$\mathbf{A} = \begin{bmatrix} 0.035 & 0.000 & 0.001 & 0.007 \\ 0.000 & 0.001 & 0.000 & 0.001 \\ 0.107 & 0.045 & 0.201 & 0.197 \\ 0.063 & 0.019 & 0.038 & 0.175 \end{bmatrix}$$

4.2. Matrix of ecological to economic exchanges

An extension of the basic economic I–O model considers the addition of ecological sectors to represent the biological production of fish. These sectors are located in the lower-left part of the Table 2, with row labels: fish stock, zooplankton and phytoplankton. The fish stock (1.02×10^5 ton) is the sum of NMFS stock biomass of Atlantic cod and yellowtail flounder and the spawning stock biomass of haddock on George's Bank in 1998 (NMFS, 1999). These three species are the primary commercial groundfish species in the region. The fish stock sector supplies fish to the commercial fishing sector. Zooplankton and phytoplankton are not utilized directly. Note that the natural supply of fish from the ecosystem does not require outlays on the part of individual sectors (in a regulated open-access management regime, the fish bear no shadow price).

In fishery studies, the fish stock is measured typically in biomass units (tons). As noted in Section 3.5, when analyzing an ecosystem, the energy or production flow (i.e. the amount of new biomass produced per unit of time in a given area) in the ecosystem is often used. The fish stock biomass (tons) can be converted into a production rate (tons/year) using a production to biomass (P/B) ratio. The P/B ratios differ across species (Sissenwine et al., 1984).

The stock size and total outputs in Table 2 enable us to calculate the ecological commodity input coefficients expressed in tons of biomass per million dollars. Using a P/B ratio of 0.6 (Sissenwine et al., 1984) and assuming that the amount of fish harvested (tons/year) is equal to the amount of new biomass produced (tons/year), the coefficient is 66.83 ton/million \$[18]. This is the matrix of ecological to economic exchanges (**G**):

$$\mathbf{G} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 66.83 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

[17] Development of an input–output model from primary data is a substantial undertaking. A number of ready-made regional input–output models have been developed to perform economic impact analyses (Brucker et al., 1990). The best known is a software package for personal computers, IMPLAN PRO. IMPLAN was developed at the US National Forest Service (Alward and Palmer, 1983). It is a modular input–output model that works down to the individual county level for any county in the US. The IMPLAN database consists of two major parts: (1) a national-level technology matrix and (2) estimates of sectional activity for final demand, final payments, gross output, and employment for each county. This 528-sector (based on 4-digit SIC codes), gross-domestic-based model was derived from the Commerce Department's national input–output studies. In IMPLAN, national average technology coefficients are used to develop the direct coefficients for sectors at the local level (Loomis, 1993; Minnesota IMPLAN Group, 1997).

[18] Fish stock biomass × P/B ratio/total output = $1.02 \times 10^5 \times 0.6/915.71 = 66.83$.

Table 1
Industry input–output model for the New England coastal region[a] (flows in million $)

	Agriculture	Fishing	Other	Manufacturing	Final demand	Total output
Agriculture	79.79	0.24	222.20	1066.98	921.26	2290.47
Fishing	0.00	1.08	164.97	135.41	614.25	915.71
Other	245.53	41.12	84 096.01	28 242.36	306 519.43	419 144.44
Manufacturing	144.31	17.09	15 833.33	25 023.12	102 193.01	143 210.86
Payments	1820.84	856.17	318 827.93	88 743		
Total outlays	2290.47	915.71	419 144.44	143 210.86		

[a] The simplified economic input–output model shows the inputs from industry sectors represented by rows into the industry and final demand sectors represented by columns. The flows from sector to sector are measured in millions of 1997 dollars per year. A value-added sector (or "Payments") is added as an additional row. The total output from each sector must equal the total outlays made by each sector for the model to balance.

Here **G** is 4×4 and designed to match the **E** and **B** matrices described next.

4.3. *Matrix of economic to ecological exchanges*

We turn next to the case where activities in the economy may affect the function of the ecosystem, i.e. dragging results in a decrease in fish stock. Auster and Langton (1999) find that bottom fishing reduces the complexity of seafloor habitat. A recent study by Lindholm et al. (1999) suggests that reduced habitat complexity increases predator-induced mortality of demersal cod juveniles. Results from a study by Collie et al. (1997) indicate that sites on Georges Bank that have not been disturbed by bottom fishing have higher abundance of organisms, biomass and species diversity. In their review of studies of fishing impacts to benthic communities, Auster and Langton (1999) document a range of effects to biomass and abundance of flora and fauna in a variety of geographic regions. Quantified reductions in biomass and species abundance range from 0 to 60%.

As noted above, the impact of bottom fishing on juvenile cod habitat is captured by the environmental impact coefficients in the **E** matrix (Equation (10)). To calculate the coefficient (biomass of cod/$), the biomass of cod that is reduced annually by bottom fishing must be estimated. The total biomass of juvenile cod (at year 1) on Georges Bank is estimated by multiplying the NMFS estimate of 16 million juvenile cod (at year 1) by the Sissenwine et al. (1984) estimate of 170 g for one juvenile cod (at year 1). Multiplying this total cod biomass by an estimated reduction coefficient (0–60%) will provide the biomass of juvenile cod reduced by bottom fishing per year. We employ a conservative reduction coefficient of 10%. The biomass of cod/$ reduction coefficient of trawling and dredging is calculated by dividing the reduction in juvenile cod biomass by the value of annual trawl and scallop dredge landings on Georges Bank. In 1999, the NMFS value of trawling, dredging and raking activity in New England was about $240 million[19]. Using the P/B ratio of 0.6, we have $e_{23} = -7$ ton per million $[20]. Thus, we have the matrix of economic to ecological exchanges (**E**):

$$\mathbf{E} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & -7 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

The coefficient implies that for each 1 million $ increase in output from the commercial fish harvesting sector, the natural fish stock declines by an additional 7 tons.

[19] Noting that the coefficient, $e_{23} = -7$ ton/million $, is calculated using partial damage and partial industry output (i.e. value of bottom fishing). In theory, total damage and total industry output should be used (see Equation (10)).

[20] Reduction coefficient × stock of juvenile cod × juvenile cod biomass × P/B ratio/value of bottom fishing $= 0.1 \times 16 \times 10^6 \times 0.17$ kg $\times 0.6$/\$240 million $= 0.0007$ kg/\$ $= 7$ ton/million $.

Table 2
Linked input–output and marine food web model (flows in million $; ecosystem production in tons)

	Agriculture	Fishing	Other	Manufacturing	Fish stock	Zooplankton	Phytoplankton	Final demand	Total output
Agriculture	79.79	0.24	222.20	1066.98	0	0	0	921.26	2290.47
Fishing	0.00	1.08	164.97	135.41	0	0	0	614.25	915.71
Other	245.53	41.12	84 096.01	28 242.36	0	0	0	306 519.43	419 144.44
Manufacturing	144.31	17.09	15 833.33	25 023.12	0	0	0	102 193.01	143 210.86
Fish stock	0	1.02×10^5	0	0	1.02×10^5	0	0		
Zooplankton	0	0	0	0	0	1.02×10^6	0		
Phytoplankton	0	0	0	0	0	0	1.02×10^7		
Payments	1820.84	856.17	318 827.93	88 743					
Total outlays	2290.47	915.71	419 144.44	143 210.86					

4.4. Matrix of ecological exchanges

To complete the economic–ecological system, we extend the model to include a description of the Georges Bank ecosystem. Following the framework used by Hannon (1973), we develop an input–output energy matrix that captures energy flows from the sun through producers and consumers in the ecosystem. The matrix describes energy flows (kcal/m^2 per year) between the George's Bank ecosystem components: sun, phytoplankton, zooplankton, and fish. Sissenwine et al.'s (1984) energy budget for George's Bank has been adapted to fit our framework (Table 3).

According to Hannon (1973), the energy transfer coefficients that describe the flow between ecosystem components are calculated by dividing each element of the input–output energy matrix by the sum of its column (see Equation (17)). This is the normalized production matrix, or matrix of ecological exchanges (**B**):

$$\mathbf{B} = \begin{bmatrix} 0 & 0.876 & 0 & 0 \\ 0 & 0.124 & 0.714 & 0 \\ 0 & 0 & 0.286 & 0 \\ 1.000 & 0 & 0 & 0 \end{bmatrix}$$

4.5. Resource multipliers

We now have data for the four exchange matrices (**A**, **G**, **E**, and **B**). The entire data matrix is summarized in Table 4. Using these data, we calculate three different sets of resource multipliers using Equations (8), (14), and (23). These resource

Table 3
Input–output energy matrix for Georges Bank[a] (kcal/m^2 per year)

	Phytoplankton	Zooplankton	Fish	Sun
Phytoplankton	0	3418	0	0
Zooplankton	0	482	69.75	0
Fish	0	0	28	0
Sun	20 810	0	0	0
Production	20 810	3900	97.75	0

[a] Values are adapted from Sissenwine et al. (1984). The sun's energy is from Hannon (1973).

Table 4
Partitioned matrix of the economic and ecological systems of Georges Bank

	Agriculture	Fishing	Other	Manufacturing	Phytoplankton	Zooplankton	Fish	Sun
Agriculture	0.0348	0.0003	0.0005	0.0075	0	0	0	0
Fishing	0.0000	0.0012	0.0004	0.0009	0	0	-7	0
Other	0.1072	0.0449	0.2006	0.1972	0	0	0	0
Manufacturing	0.0630	0.0187	0.0378	0.1747	0	0	0	0
Phytoplankton	0	0	0	0	0	0.876	0	0
Zooplankton	0	0	0	0	0	0.124	0.714	0
Fish	0	66.83	0	0	0	0	0.286	0
Sun	0	0	0	0	1.00	0	0	0

Table 5
Resource multipliers

	Agriculture	Fishing	Other	Manufacturing
Fish stock consumed by economic sector (*biomass tons/million* \$) Eq. (8): $\mathbf{G}(\mathbf{I}-\mathbf{A})^{-1}$				
Phytopankton	0	0	0	0
Zooplankton	0	0	0	0
Fish	0.0058	66.8986	0.0039	0.0821
Sun	0	0	0	0
Fish stock consumed and damaged by economic sector (*biomass tons/million* \$) Eq. (14): $(\mathbf{G}-\mathbf{KE}')(\mathbf{I}-\mathbf{A})^{-1}$				
Phytopankton	0	0	0	0
Zooplankton	0	0	0	0
Fish	0.0064	73.9058	0.0043	0.0907
Sun	0	0	0	0
Ecosystem components consumed and damaged by economic sector (*biomass tons/million* \$) Eq. (23): $(\mathbf{I}-\mathbf{B})^{-1}(\mathbf{G}-\mathbf{E}')(\mathbf{I}-\mathbf{A})^{-1}$				
Phytopankton	0.0064	73.9058	0.0043	0.0907
Zooplankton	0.0073	84.3674	0.0049	0.1035
Fish	0.0090	103.5096	0.0061	0.1270
Sun	0.0064	73.9058	0.0043	0.0907

multipliers capture the marginal impact of final demand for economic products on natural resource stocks. We consider the model without the ecosystem first. As noted, Equation (8) calculates the impact of increases in final demand on the fish stock. The equation provides a measure of the requirements from each industrial sector for additional fish stock from the ecosystem due to a 1-million \$ increase in final demand for each sector. The results suggest that an additional 66.90 tons of fish stock will be required to be "produced" by the ecosystem for a 1-million \$ increase in the final demand for fishing industry output (see top part in Table 5). If we regard the fish stock sector as a constraint to the economic system, i.e. the ecosystem is not capable of producing additional fish, then we can see how the ecosystem has an effect on the growth of the economy[21]. Importantly, because of the interrelationships of the economic system, a 1-million \$ increase in final demand for manufacture will require that the ecosystem produce an additional 0.082 tons of fish, even though the manufacturing industry may not use fish directly in its production processes.

If the damage of trawling (**E**) is considered in the resource multiplier computation (Equation (14)), the fish stock must increase from 66.90 to 73.91 tons for a 1-million \$ increase in the final demand for fishing industry output (middle part of Table 5). The increase is necessary to reflect the damage of trawling to the fish stock.

Finally, we consider the ecosystem structure (**B**), in addition to harvest (**G**) and habitat destruction (**E**), using Equation (23), the corresponding impact on the fish stock further increases from 73.91 to 103.51 tons for a 1-million $ increase in the final demand for fishing industry output. This increase is a result of balancing within the ecosystem. Since we model fishing and habitat destruction explicitly, a change in the level of fishing or habitat destruction is translated into changes in biomass flows through ecosystem components using the Leontief inverse, $(\mathbf{I}-\mathbf{B})^{-1}$ (see Equation (20)). The Leontief inverse is actually the multiplier matrix for the ecosystem that relates the rates of change in the biomass flows (or stock sizes) with respect to the exogenous fishery catch rate.

With the **B** matrix, we can calculate the impacts of final demands for outputs from different industry sectors on various components of the ecosystem. For example, the impact of final demand for fish product on phytoplankton stock and zooplankton stock is 73.91 and 84.37 tons, respectively. The last resource multiplier (Equation (23)) is very useful since it provides estimates of the economic impacts on ecosystem components that are not being consumed directly by the economy.

4.6. Resource constraints and economic production

The resource multipliers in Table 5 describe the marginal increase in necessary stock size with respect to rising final demand for economic products. Natural resource stocks are essential for economic expansion. If the final demand is moderate and the relevant stock size is large, the resource constraint is not binding. However, when the stock is low relative to economic demand, the economic production is constrained by the stock size. In other words, final demand may increase only if stock size grows[22]. Using a bioeconomic approach (Clark, 1976), Edwards and Murawski (1993) have shown that the groundfish stock size in New England associated with socially optimal management may be seven times greater than the 1989 stock size. This will, in turn, lead to growth in fish landings and associated economic benefits.

Our economic–ecological model also can be utilized to simulate the impact of changing ecological or environmental impact conditions on the economy. For simplicity, we consider only some key elements in the model and a simplified food web. In Table 2, we display the simple food web model with phytoplankton, zooplankton, and fish stock sectors, located in the lower-right part of the table[23]. In this ecological subsystem, we work with the biomass stock (instead of biomass production or fish landings) as follows. Start with a phytoplankton biomass of 1.02×10^7 tons[24]. Using the traditional marine ecological conversion ratio describing the efficiency of the conversion of biomass from one trophic level to another (i.e. 10%), these 1.02×10^7 tons of phytoplankton are converted into 1.02×10^6 tons of zooplankton. The 1.02×10^6 tons of zooplankton are converted into 1.02×10^5 tons of fish, all of which go into commercial fish harvest. With the food web, we modify the **G** matrix as[25]:

$$\mathbf{G} = \begin{bmatrix} 0 & 111 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

We use this model to determine the impacts of

[21] In a fully specified input–output model, there may be an import sector. An ecosystem constraint may then imply that additional fish would be imported, thereby relaxing the constraint on economic growth.

[22] Here we consider demand for local products. As previously noted, the final demand can also be met by the imports.

[23] In this example, the impact of economic activities on the ecosystem is not considered. Thus, we put zeros in the upper-right part of Table 2.

[24] In practice, phytoplankton is measured in terms of primary production in gC/m^2y. Primary production = phytoplankton stock × P/B ratio. The P/B ratio for phytoplankton and zooplankton is 100 and 10 greater than that for fish, respectively. We use biomass throughout the example for simplicity.

[25] g_{12} = Fish stock biomes/total output = 1.02×10^5/915.71 = 111.39.

an increase in the primary production. Assume that the primary production (phytoplankton stock in the example) increases by 40% from 1.02×10^7 to 1.43×10^7 tons. The result is that 1.43×10^5 tons of fish are now available for the economy. Assume that the final demands for outputs from other sectors remain constant (elements y_1, y_3 and y_4 in **Y**). We explore how the increase in primary productivity affects y_2, the final demand for fish (e.g. consumption).

As noted, the current stock size in New England is low resulting from overfishing. In our economic I–O model, y_2 reflects the demand for local fish. The total demand for fish in the region is greater than y_2 and the balance is met by imports. Suppose that consumers in the region prefer local products and that additional local supply will displace an equal amount of imports.

Let y_2^* represent the new (and increased) final demand for local fish. We can calculate y_2^* using Equation (7):

$$\mathbf{S} = \begin{bmatrix} 1.43 \times 10^5 \\ 0 \\ 0 \end{bmatrix} = \mathbf{G}(\mathbf{I} - \mathbf{A})^{-1} \begin{bmatrix} 921 \\ y_2^* \\ 306\,519 \\ 102\,193 \end{bmatrix}$$

Using the values presented here, $y_2^* = \$970.3$ million, representing an increase in final demand for commercial fish products of 0.6% due to increased plankton production. Output impacts can be calculated using Equation (4):

$$\mathbf{X} = \begin{bmatrix} 1.0369 & 0.0005 & 0.0011 & 0.0096 \\ 0.0001 & 1.0012 & 0.0006 & 0.0013 \\ 0.1604 & 0.0626 & 1.2655 & 0.3039 \\ 0.0865 & 0.0255 & 0.0580 & 1.2264 \end{bmatrix} \times \begin{bmatrix} 921 \\ 970 \\ 306\,519 \\ 102\,193 \end{bmatrix} = \begin{bmatrix} 2274 \\ 1288 \\ 419\,165 \\ 143\,212 \end{bmatrix}$$

Output impacts increase for all four sectors, showing the pervasive influence of primary productivity on the expansion of the economy. Note also that, as the economy expands, employment, income, and tax revenues will increase as well.

4.7. Sensitivity analysis

Using the above procedure, a sensitivity analysis was developed with respect to the fish biomass and the efficiency coefficients. As noted, 10% has been used as the biomass conversion efficiency ratio in much of the literature. Our sensitivity analysis examines three different conversion efficiencies: 10, 15, and 20%, which correspond with oceanic, coastal, and upwelling provinces, respectively (Ryther, 1969). For a **G** matrix calculated using the fish biomass of 1.02×10^5 tons and the three efficiencies, we simulated the levels of output resulting from different levels of phytoplankton production[26]. Fig. 1 shows change in fishing industry output by phytoplankton biomass level. We find that, as the biomass increases, the industry output rises. A higher output level is associated with a higher rate of efficiency.

The ecological commodity input coefficient values in the **G** matrix are estimated using fish biomass stock values. Different stock values will lead to different **G** values, this, in turn, affects the estimates of the impacts on fish consumption associated with rising phytoplankton production. Fig. 2 depicts the effects of changing the ecological commodity input coefficients, g_{ij}, on final demand by phytoplanckton biomass level. In the simulations, the energy transfer coefficient is kept at a level of 10%, and the ecological commodity input coefficient was calculated using three different fish biomass levels (4.5×10^4, 1.02×10^5, and 1.02×10^6 tons). The fish stock value of 4.5×10^4 tons is the sum of spawning stocks of cod, haddock and yellowtail as reported in Fogarty and Murawski (1998). Since g_{ij} is positively correlated with the stock size (see Equation (6)), for a given output level, a higher stock value leads to a greater g_{ij}. In

[26] Estimates of primary production calculated using unit primary production level on Georges Bank (gC/m^{2}y) in the literature times the study area (50 000 km^2) range from about 1.5×10^{10} to 2×10^{10} tons per year. This range is probably an overestimate because production estimates are for the core of the bank rather than the entire area.

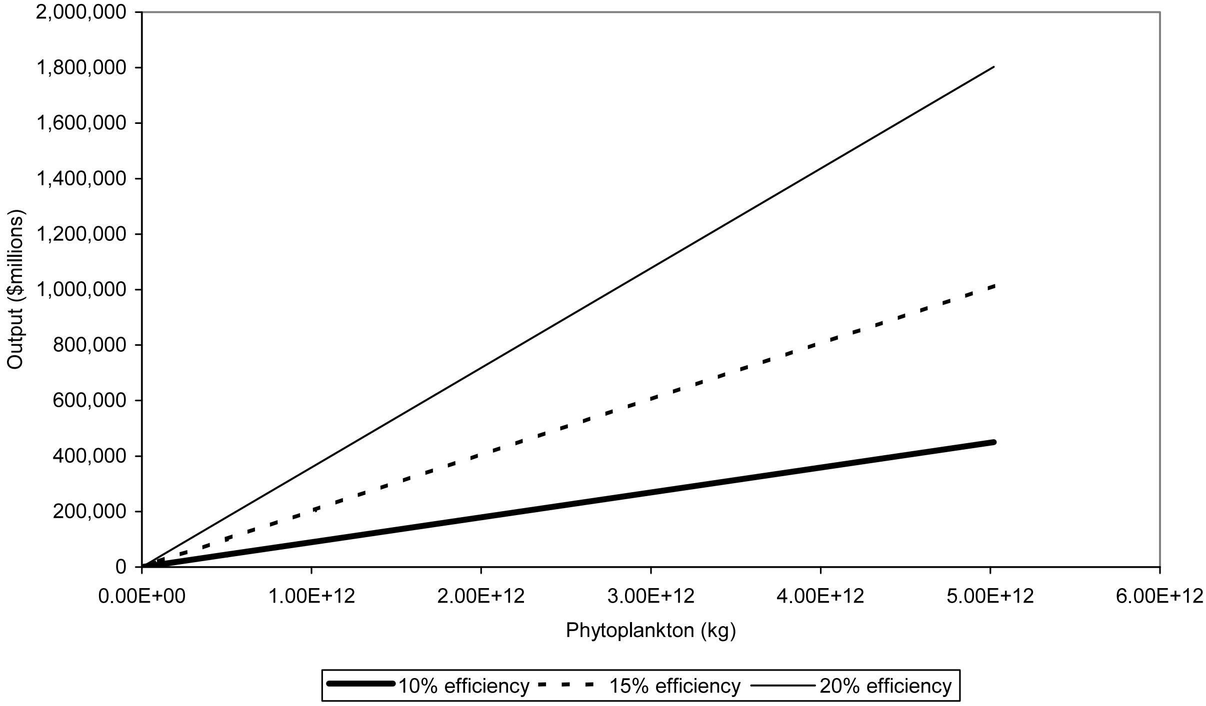

Fig. 1. Changing fishing industry output with respect to primary production. NMFS estimate of 1.02×10^8 kg fish on Georges Bank.

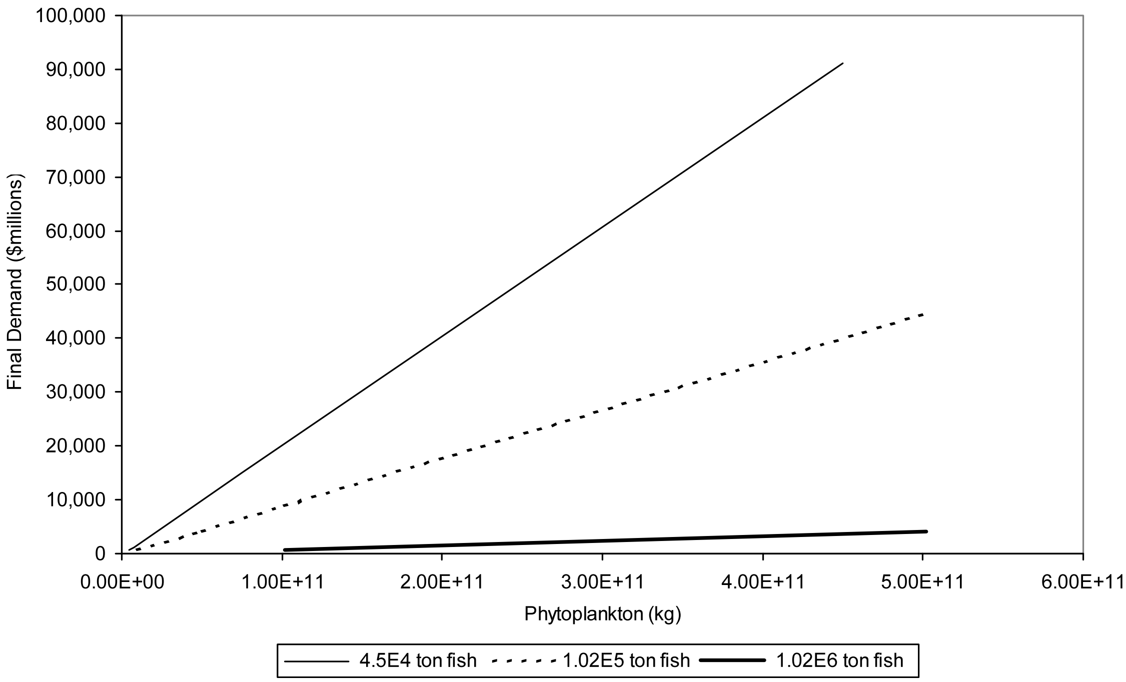

Fig. 2. Changing final demand for fish with respect to primary production.

Fig. 2, for a given level of primary production, a lower stock (lower g_{ij}) is associated with higher final demand (i.e. consumption). This is because a lower g_{ij} implies that a higher output can be generated with lower stock size.

5. Conclusions

Traditionally, economists and ecologists have tended to focus narrowly within their own specific disciplines, recognizing only at a general level the impact of their own respective objects of study on those of the other. Bodies of research have grown in each field, while the detailed nature of interconnections and feedbacks between the economy and the natural environment often have been downplayed or ignored. Increasingly, however, researchers from each discipline have begun to recognize the value to public policy of incorporating information and results from the other discipline into their analyses.

We develop a modeling approach that links the workings of an economy, which we call matrix of economic changes (**A**), to those of a related ecosystem, known as matrix of ecological exchanges (**B**). While improvements are certainly feasible in the extant models that describe such independent economic and ecological systems, our focus here is on characterizing and studying the *linkages* between the two types of systems. We link the economic and ecological systems using two matrices of coefficients. The first matrix, which we call a matrix of ecological to economic exchanges (**G**), suggests that trophic levels can be treated as analogs of the industrial sectors of an economy. In effect, each trophic level produces biomass that might be utilized as a factor in the manufacture of products by certain industries. As is common practice in commercial fisheries, these factors typically are unpriced. The second matrix, called matrix of economic to ecological exchanges (**E**), makes the external effects of industrial activities on the ecosystem more apparent. Thus, the benefits, at low levels, of macronutrient inputs or the costs of pollution can be modeled explicitly. We develop natural measures of the ecosystem impacts of changes on final economic demand (so-called "resource multipliers") that incorporate these linkages explicitly.

We illustrate the implementation of the approach with an example of a coastal economy in New England that is connected to a marine ecosystem on nearby Georges Bank, an important fishing ground. For heuristic purposes, our example employs linear economic and ecological system models[27] in which the sectors and trophic levels have been aggregated. Extensions to this approach that accommodate disaggregated sectors or trophic levels, nonlinearities, and dynamics are conceivable[28].

The case study highlights four main results of our analysis. First, the resource multipliers should be constructed to capture the full effect of ecological–economic interactions, such as fish harvesting, habitat destruction, and ecological exchanges. The resource multiplier linking the commercial fishing sector with the fish stock measures the quantity of a fish stock needed to support a marginal growth in final demand for fish product. We show that the multiplier value differs significantly in three different scenarios in which we incorporate information from following exchange matrices in succession: fish harvesting only (**G**); fishing and habitat destruction (**G** and **E**); and fishing, habitat destruction, and ecosystem interactions (**G**, **E**, and **B**).

Second, our model may be used to estimate the economic impacts on ecosystem components (e.g. zooplankton) that are not being consumed directly by the economy. The relevant multipliers are in the last resource multiplier matrix incorporating **G**, **E**, and **B** (Equation (23)) in Table 5.

[27] As described earlier, our model is static and linear, and it requires an assumption that the system is in equilibrium. In its current state of development, these characteristics arguably may limit the model's usefulness as a management tool. For our purposes, however, the model demonstrates how the different components (i.e. the exchange matrices) may interact in an ecological–economic context. The model is a useful first step (cf. Hannon, 2001).

[28] For recent developments in modeling the dynamics of a marine food web with fishing, see Walters et al. (1997) and Finnoff and Tschirhart (2003).

Third, because the model includes a link between the economy and the ecosystem, it may also be used to assess increases in economic production associated with a growth in resource stock size. We show how the increase in primary productivity in the ecosystem affects the fish consumption in the economy.

Finally, our model results are sensitive with respect to variations in some key ecological and economic parameters, such as the biomass conversion efficiency ratio and the ecological commodity input coefficient. Thus, it is important to develop accurate measures for these coefficients, which highlights the importance of further research in marine ecology and economics.

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