### Dynamics and Equilibria of Ecological Predator-Prey Networks as Nature's Supply Chains

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I would like to thank Professor Adam Rose for organizing the Memorial Sessions at this Conference in honor of Professor Walter Isard.

#### Some Reflections on Professor Walter Isard

I last saw Professor Walter Isard at the RSAI North American meetings held in Brooklyn, NY, November 18-22, 2008 and, on April 1, 2009, at Cornell University.

I was so pleasantly surprised when, at age 90, he came to my presentation at Cornell two years ago.

#### Some Reflections on Professor Walter Isard



Because of Professor Isard's incredible intellect, energy and stamina, plus his networking and organizational skills, he created the interdisciplinary, scholarly community of regional science that now spans the globe.

*His leadership and vision gave us courage to break disciplinary boundaries.* 

Through regional science, we have had intellectual and (travel) experiences we never could have imagined as students.



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**Ecological Predator-Prey Networks** 

The intellectual legacy of Isard that I, in particular, appreciate was his:

- Emphasis on conceptualization and theory;
- Appreciation and use of appropriate mathematical and computational methodologies, and
- ► Understanding of the *importance of a system perspective*.

#### WALTER ISARD ecologic-economic analysis for regional development

CHARLES L. CHOGUILL • JOHN KISSIN RICHARD H. SEYFARTH • RICHARD TATLOCK with the assistance of NETH E. BASSETT • JOHN G. FURTADO • RONALD M. IZUMITA

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From the first paragraph of the Preface of Isard's 1989 book:

The combination of the two words *Ecologic* and *Economic* in the title of this book, is an unusual one. It is set forth, nevertheless, as a true combination, in the sense of a synthesis and of analyses of two systems within the world of actuality. Throughout this book, we stress the need for this synthesis. We constantly assert that no longer can regional development and regional planning be treated in their traditionally narrow contexts. Emphasis on the strict economics of such development and planning, with only passing consideration of physical environment and design, let alone of social, political, and other cultural factors, can no longer be tolerated.

This presentation is in his memory and is based on the paper, "Dynamics and Equilibria of Ecological Predator-Prey Networks as Nature's Supply Chains," A. Nagurney and L. S. Nagurney, *Transportation Research E* **48** (2012): pp 89-99.

#### Outline of Presentation

- Background and Motivation
- The Dynamic Predator-Prey Network Model
- Predator-Prey Networks, Spatial Price, and Supply Chain Network Equilibrium Problems
- An Algorithm
- An Application
- Summary and Suggestions for Future Research

#### Background and Motivation

Equilibrium is a central concept in numerous disciplines from economics and regional science to operations research / management science and even in ecology and biology. In ecology, equilibrium is in concert with the "balance of nature," in that, since an ecosystem is a dynamical system, we can expect there to be some persistence or homeostasis in the system (Egerton (1973), Cuddington (2001), and Mullon, Shin, and Cury (2009)).

Equilibrium serves as a valuable paradigm that assists in the evaluation of the state of a complex system.

Equilibrium, as a concept, implies that there is more than a single decision-maker or agent, who, typically, seeks to optimize, subject to the underlying resource constraints.

Hence, the formulation, analysis, and solution of such problems may be challenging.

Notable methodologies that have been developed over the past several decades that have been successfully applied to the analysis and computation of solutions to a plethora of equilibrium problems include variational inequality theory and the accompanying theory of projected dynamical systems (cf. Nagurney (1999) and Nagurney and Zhang (1996) and the references therein). We utilize the theory of variational inequalities for the formulation, analysis, and solution of both centralized and decentralized network problems.

**Definition: The Variational Inequality Problem** The finite-dimensional variational inequality problem,  $VI(F, \mathcal{K})$ , is to determine a vector  $X^* \in \mathcal{K}$ , such that:

$$\langle F(X^*)^T, X - X^* \rangle \geq 0, \quad \forall X \in \mathcal{K},$$

where F is a given continuous function from  $\mathcal{K}$  to  $\mathbb{R}^N$ ,  $\mathcal{K}$  is a given closed convex set, and  $\langle \cdot, \cdot \rangle$  denotes the inner product in  $\mathbb{R}^N$ .

<u>Geometric Interpretation of  $VI(F, \mathcal{K})$  and a Projected</u> Dynamical System (Dupuis and Nagurney, Nagurney and Zhang)

In particular,  $F(X^*)$  is "orthogonal" to the feasible set  $\mathcal{K}$  at the point  $X^*$ .



#### Associated with a VI is a Projected Dynamical System, which provides the underlying dynamics to the equilibrium.

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**Ecological Predator-Prev Networks** 

It has now been recognized that *numerous equilibrium problems* as varied as

- ▶ the classical Walrasian price equilibrium problem,
- the classical oligopoly problem,
- the portfolio optimization problem,
- and even migration problems (cf. Nagurney (2003)), which in their original formulations did not have a network structure identified, actually possess a network structure.

Also, it has been established, *through the supernetwork (cf. Nagurney and Dong (2002)) formalism* that supply chain network problems, in which decision-makers (be they manufacturers, retailers, or even consumers at demand markets) compete across a tier, but necessarily cooperate (to various degrees) between tiers, can be reformulated and solved as (transportation) network equilibrium problems. The same holds for *complex financial networks with intermediaries* (see Liu and Nagurney (2007)).

In addition, the supernetwork framework has even been applied to *the integration of social networks with supply chains* (see Cruz, Nagurney, and Wakolbinger (2006)) and *with financial networks* (cf. Nagurney, Wakolbinger, and Zhao (2006)).

Hence, it is becoming increasingly evident that seemingly disparate equilibrium problems, in a variety of disciplines, can be uniformly formulated and studied as network equilibrium problems. Such identifications allow one to:

1. graphically visualize the underlying structure of systems as networks;

2. avail oneself of existing frameworks and methodologies for analysis and computations, and

3. gain insights into the commonality of structure and behavior of disparate complex systems that underly our economies and societies.

Nevertheless, although deep connections and equivalences have been made (and continue to be discovered) between/among different systems through *the (super)network formalism, the systems, to-date, have been exclusively of a socio - technical economic variety.* 

# Here, we take on the challenge of proving the equivalence between

ecological food webs and spatial price equilibrium problems as well as supply chain network problems; thereby, providing a foundation for the unification of these disparate systems and, in a sense, the fields of economics (and regional science) closer to ecology (and biology).

### Supply Chains in Nature



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Ecological Predator-Prey Networks

#### The Dynamic Predator-Prey Network Model

#### The Dynamic Predator-Prey Network Model



Our work is inspired by the path-breaking paper of Mullon, Shin, and Cury (2009) which introduced variational inequality theory to this application domain by utilizing the network economics approach inspired by Nagurney (1999).

We consider an ecosystem in which there are m distinct types of primary prey and o distinct types of predators with n intermediate species, which are both predators of the primary prey as well as prey of the predator species.

The biomass of a species h is denoted by  $B_h$ .

 $E_h$  denotes the inflow (energy and nutrients) of species *h* with the autotroph species, that is, the primary prey, in Figure 1, having positive values of  $E_h$ , whereas all predators have  $E_h = 0$ .

The parameter  $\gamma_h$  denotes the trophic assimilation efficiency of species h and the parameter  $\mu_h$  denotes the coefficient that relates biomass to somatic maintenance.

The variable  $X_{hl}$  is the amount of biomass of species h preyed upon by species l and we are interested in determining their equilibrium values for all prey and predator species pairs (h, l) as well as the underlying dynamics of their interactions.

#### The Dynamic Predator-Prey Network Model

The prey equations that must hold for the top nodes in Figure 1 are:

$$\gamma_i E_i = \mu_i B_i + \sum_{j=1}^n X_{ij}, \quad 1, \dots, m.$$
(1)

Equation (1) states that, for each top-tiered prey species i, the assimilated biomass must be equal to its somatic maintenance plus the amount of its biomass that is preyed upon.

The predator equations, in turn, that must hold for the bottom nodes in Figure 1 are:

$$\gamma_k \sum_{j=1}^n X_{jk} = \mu_k B_k, \quad k = 1, \dots, o.$$
 (2)

Equation (2) signifies that for each bottom-tiered predator species k, its assimilated biomass is equal to its somatic maintenance (which is represented by its coefficient  $\mu_k$  times its biomass).

In addition, the following equation must hold for each intermediate species:

$$\gamma_j \sum_{i=1}^m X_{ij} - \sum_{k=1}^o X_{jk} = \mu_j B_j, \quad j = 1, \dots, n,$$
 (3)

that is, the somatic maintenance of each such species is equal to its assimilated biomass minus the amount that it is preyed upon. A positive parameter  $\hat{\phi}_{hl}$  for each prey/predator pair (h, l) reflects the distance (note the spatial component) between distribution areas of prey h and predator l, with this parameter also capturing the transaction costs associated with handling and ingestion.

According to Mullon, Shin, and Cury (2009), the predation cost between each prey h and each predator I, denoted by  $F_{hI}$ , is given by:

$$F_{hl} = \hat{\phi}_{hl} - \kappa_h B_h + \lambda_l B_l, \qquad (4a)$$

where  $-\kappa_h B_h$  represents the easiness of predation due to the abundance of prey  $B_h$  and  $\lambda_I B_I$  denotes the intra-specific competition of predator species *I*. We group the species biomasses and the biomass flows intro the respective m + n + o and mn + nodimensional vectors  $B^*$  and  $X^*$ .

#### The Dynamic Predator-Prey Network Model

We now introduce the following extension.

We assume that for each (h, I) there is now a function  $\phi_{hI}$  that is a strictly increasing function of the biomass flow between h and I; that is, we assume that

$$\phi_{hl} = \phi_{hl}(X_{hl}), \quad \forall, h, l, \tag{4b}$$

where, for definiteness, we have that

$$\phi_{hl}(X_{hl}) = \eta_{hl}X_{hl} + \hat{\phi}_{hl}, \quad \forall h, l,$$
(4c)

where  $\eta_{hl} > 0$ , for all h, l. Such a function captures congestion. Consequently, the extended predation cost,  $\hat{F}_{hl}$ , that we utilize is given by:

$$\hat{F}_{hl} = \phi_{hl}(X_{hl}) - \kappa_h B_h + \lambda_l B_l, \quad \forall h, l.$$
(4d)

#### The Dynamic Predator-Prey Network Model

In view of (1), (2), (3), and (4d), we may write  $\hat{F}_{hl} = \hat{F}_{hl}(X) \equiv F_{hl}(X, B)$ ,  $\forall h, l$ . Following then Mullon, Shin, and Cury (2009), we have the following definition of the governing predator-prey equilibrium conditions:

**Definition 1: Predator-Prey Equilibrium Conditions** A biomass flow pattern  $(X^*) \in R^{mn+no}_+$  is said to be in equilibrium if the following conditions hold for each pair of prey and predators (h, l):

$$\hat{F}_{hl}(X) \begin{cases} = 0, & \text{if } X_{hl}^* > 0, \\ \ge 0, & \text{if } X_{hl}^* = 0. \end{cases}$$
(5)

The equilibrium conditions (5) reflect that, if there is a biomass flow from *h* to *I*, then there is an "economic" balance between the advantages  $(\kappa_h B_h)$  and the inconveniences of predation  $(\phi_{hl} + \lambda_l B_l)$ , with the species biomasses  $B_h$  and  $B_l$  satisfying the corresponding equations (1) - (3) for every *h* and *l*.

#### Theorem 1

A biomass flow pattern  $X^* \in R_+^{mn+no}$  is an equilibrium according to Definition 1 if and only if it satisfies the variational inequality problem: determine  $X^* \in R_+^{mn+no}$  such that

$$\sum_{h,l} \hat{F}_{hl}(X^*) \times (X_{hl} - X^*_{hl}) \ge 0, \quad \forall X \in R^{mn+no}_+, \tag{6}$$

### or, equivalently, the variational inequality: determine $X^* \in R^{mn+nol}_+$ such that

$$\sum_{i=1}^{m} \sum_{j=1}^{n} \left[ \frac{\kappa_{i}}{\mu_{i}} \sum_{j=1}^{n} X_{ij}^{*} - \frac{\kappa_{i}\gamma_{i}}{\mu_{i}} E_{i} + \phi_{ij}(X_{ij}^{*}) + \lambda_{j}(\frac{\gamma_{j} \sum_{i=1}^{m} X_{ij}^{*} - \sum_{k=1}^{o} X_{jk}^{*}}{\mu_{j}}) \times [X_{ij} - X_{ij}^{*}] \right]$$

$$+ \sum_{j=1}^{n} \sum_{k=1}^{o} \left[ \frac{\kappa_{j}}{\mu_{j}} \sum_{k=1}^{o} X_{jk}^{*} - \frac{\kappa_{j}\gamma_{j}}{\mu_{j}} \sum_{i=1}^{m} X_{ij}^{*} + \phi_{jk}(X_{jk}) + \frac{\lambda_{k}\gamma_{k}}{\mu_{k}} \sum_{j=1}^{n} X_{jk}^{*} \right]$$

$$\times [X_{jk} - X_{jk}^{*}] \ge 0, \quad \forall X \in \mathbb{R}^{mn+no}_{+}.$$
(7)

**Proof:** Recall, as noted following (4d), that, for any predator-prey network, in view of equations (1) – (3), we may re-express  $B_h$  and  $B_l$  in terms of X and substitute the resultants into (4d) so that  $\hat{F}_{hl} = \hat{F}_{hl}(X), \forall h, l.$ 

The equivalence between an equilibrium solution according to Definition 1 and variational inequality (6) then follows directly from using standard arguments as in Nagurney (1999) with the feasible set consisting solely of the nonnegative orthant since the constraints (1) - (3) have been embedded into the  $\hat{F}_{hl}$  for all h, l.

With notice to Figure 1, we obtain, specifically, using (1), (3), and (2), repectively:

$$B_{i} = \frac{\gamma_{i} E_{i} - \sum_{j=1}^{n} X_{ij}}{\mu_{i}}, \quad i = 1, \dots, m;$$
(8)

$$B_{j} = \frac{\gamma_{j} \sum_{i=1}^{m} X_{ij} - \sum_{k=1}^{o} X_{jk}}{\mu_{j}}, \quad j = 1, \dots, n,$$
(9)

and

$$B_k = rac{\gamma_k \sum_{j=1}^n X_{jk}}{\mu_k}, \quad k = 1, \dots, o.$$
 (10)

#### The Dynamic Predator-Prey Network Model

Hence, with the use of (4d) and (8) – (10), we have that

$$\hat{F}_{ij}(X) = \frac{\kappa_i}{\mu_i} \sum_{j=1}^n X_{ij} - \frac{\kappa_i \gamma_i}{\mu_i} E_i + \phi_{ij}(X_{ij}) + \lambda_j (\frac{\gamma_j \sum_{i=1}^m X_{ij} - \sum_{k=1}^o X_{jk}}{\mu_j}), \forall i, j \in \mathbb{N}$$
(11)

and

$$\hat{F}_{jk}(X) = \frac{\kappa_j}{\mu_j} \sum_{k=1}^{o} X_{jk} - \frac{\kappa_j \gamma_j}{\mu_j} \sum_{i=1}^{m} X_{ij} + \phi_{jk}(X_{jk}) + \frac{\lambda_k \gamma_k}{\mu_k} \sum_{j=1}^{n} X_{jk}, \quad \forall j, k,$$
(12)

and variational inequality (7) follows.  $\Box$ 

Due to the variational inequality formulation (6) (and (7)), we may exploit the connection between the set of solutions to a variational inequality problem and the set of solutions to a projected dynamical system (cf. Dupuis and Nagurney (1993) and Nagurney and Zhang (1996a)).

In so doing, a natural dynamic adjustment process becomes:

$$\dot{X}_{hl} = \max\{0, -\hat{F}_{hl}(X)\}, \quad \forall h, l.$$
(13)

According to (8), the rate of change of biomass flow between a prey and predator pair (h, l) is in proportion to the difference between the advantage of predation and the inconvenience, as long as the biomass flow,  $X_{hl}$ , between the pair is positive; that is, if  $X_{hl} > 0$ , then

$$\dot{X}_{hl} = -\hat{F}_{hl}(X). \tag{14}$$

However, since the biomass flows must be nonnegative, we must ensure that, when  $X_{hl} = 0$ , the flow does not become negative and, therefore, (8) must hold true.

Also, according to (13), if the advantage of preying on species h exceeds the inconvenience for predator I then the amount of biomass flow between h and I will increase; if, on the other hand, the inconvenience exceeds the advantage, then the biomass flow between this prey and predator pair will decrease.

If the biomass flow between a pair is reduced to zero then it stays unchanged until the next positive signal, at which it increases at a rate given by (13).

#### The Dynamic Predator-Prey Network Model

The adjustment process in vector form for all prey and predator pairs is given by (15) below, where  $\hat{F}$  is the mn + no-dimensional vector with components  $\{F_{hl}\}$ .

The pertinent ordinary differential equation (ODE) for the adjustment process of biomass flows in vector form is (see also Nagurney and Zhang (1996a)):

$$\dot{X} = \Pi_{\mathcal{K}}(X, -\hat{\mathcal{F}}(X)), \tag{15}$$

where  $\hat{F}$  is the vector with components  $\hat{F}_{hl}$ ;  $\forall h, l$ , and

$$\Pi_{\mathcal{K}}(X,v) = \lim_{\delta \to 0} \frac{(P_{\mathcal{K}}(X + \delta v) - X)}{\delta},$$
 (16)

where

$$P_{\mathcal{K}}(X) = \arg\min_{z \in \mathcal{K}} \|X - z\|.$$
(17)

Note that, in the predator-prey network model,  $K \equiv R_{+}^{mn+no}$ 

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#### The Dynamic Predator-Prey Network Model

A direct application of Theorem 2.4 in Nagurney and Zhang (1996a) yields the following result, since the feasible set K here is a convex polyhedron.

#### Theorem 2

 $X^*$  solves variational inequality (6)(equivalently, (7)), if and only  $X^*$  it is a stationary point of the ODE (15), that is,

$$0 = \Pi_{\mathcal{K}}(X^*, \hat{\mathcal{F}}(X^*)).$$
(18)

Theorem 2 establishes that the necessary and sufficient condition for a biomass flow pattern  $X^*$  to be in equilibrium in the predator-prey network is that  $X^*$  is a stationary point of the biomass flow adjustment process defined by ODE (15). For any  $X_0 \in K$  as an initial value, we associate with  $ODE(\hat{F}, K)$ an initial value problem  $IVP(\hat{F}, K, X_0)$  defined as:

$$\dot{X} = \Pi_{\mathcal{K}}(X, -\hat{F}(X)), \quad X(0) = X_0.$$
 (19)

We now investigate stability properties of the above projected dynamical system (15). We first establish that  $\hat{F}(X)$  is strictly monotone under the assumption that  $\lambda_j = \kappa_j \gamma_j$ ; j = 1, ..., n. We note that the ecologists Mullon, Shin, and Cury (2009) refer to this assumption as the strong equilibrium assumption.

**Theorem 3**  $\hat{F}(X)$  is strictly monotone, that is,

$$\sum_{h,l} \left[ \hat{F}_{hl}(X^1) - \hat{F}_{hl}(X^2) \right] \times \left[ X_{hl}^1 - X_{hl}^2 \right] > 0, \quad \forall X^1, X^2 \in K, \quad X^1 \neq X^2.$$
(20)

#### Theorem 4

Since  $\hat{F}(X)$  is strictly monotone,  $X^*$  is a strictly global monotone attractor, that is, there exists a  $\delta > 0$  such that for all  $X \in B(X^*, \delta)$ :

$$d(X,t) = \|X \cdot t - X^*\|$$
(21)

is monotonically decreasing to zero in t for all  $X \in K$ , where B(X, r) denotes the open ball with radius r and center X and  $X \cdot t$  is the solution path of the initial value problem  $IVP(\hat{F}, K, X)$  (19) that passes through X at time t = 0, that is,  $X \cdot 0 = X(0) = X$ .

Since we have established strict monotonicity of  $\hat{F}(X)$  the following result is immedidate from the fundamental theory of variational inequalities (cf. Nagurney (1999) and the references therein).

#### Theorem 5

The equilibrium  $X^*$  that satisfies variational inequality (6) in unique since  $\hat{F}(X)$  is strictly monotone in X.

There has been a long tradition in ecological modeling of dynamical systems, as in the classical work of Lotka-Volterra models (see also Odum (1971) and Scheffer and Carpenter (2003)).

However, our work in this paper couples not only projected dynamical systems, which can handle constraints (such as nonnegativity of biomass flows), with network structure, but also economics and biology plus logistics.

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The above models collapse to a bipartite predator-prey network model (in static and dynamic forms, respectively), if there are no intermediary species. In this special case, the network is as depicted in Figure 2 and the variational inequality simplifies to: determine  $\hat{X}^* \in R^{mo}_+$ , such that

$$\sum_{i=1}^{m} \sum_{k=1}^{o} \left[ \frac{\kappa_i}{\mu_i} \sum_{k=1}^{0} X_{ik}^* - \frac{\kappa_i}{\mu_i} \gamma_i E_i + \phi_{ik}(X_{ik}^*) + \frac{\lambda_k \gamma_k}{\mu_k} \sum_{i=1}^{m} X_{ik}^* \right]$$
$$\times [X_{ik} - X_{ik}^*] \ge 0, \quad \forall \hat{X} \in R_+^{mo},$$
ere  $\hat{X} \equiv \{\{X_{ik}\}|; i = 1, \dots, m; k = 1, \dots, o\}.$ 

#### The Dynamic Predator-Prey Network Model



Figure 2: The Bipartite Network of an Ecosystem with Prey and Predators

## In our paper, we established the relationship between the bipartite

predator-prey network model and spatial price equilibrium problems, which have served as the foundation for a plethora of applications in regional science and economics (dating from the contributions of Samuelson (1952) and Takayama and Judge (1971)) from agriculture to energy and even finance (see, e.g., Labys and Yang (1997) and Nagurney (1999)).

In addition, we proved that the predator-prey models coincide with the supply chain network equilibrium models of Nagurney, Dong, and Zhang (2002) (see also the book by Nagurney (2006)).

#### An Algorithm

Recall the Euler method which is induced by the general iterative scheme of Dupuis and Nagurney (1993), and which is designed to compute the stationary points of the projected dynamical system

$$\dot{X} = \Pi_{\mathcal{K}}(X - \hat{F}(X)),$$

or, equivalently, according to Theorem 2, to determine solutions  $X^*$  to the variational inequality problem:

$$\langle \hat{F}(X^*)^T, X - X^* \rangle \geq 0, \quad \forall X \in K,$$

where  $\langle \cdot, \cdot \rangle$  denotes the inner product in *N*-dimensional Euclidean space where here N = mn + no.

In particular, the Euler method takes, at iteration  $\tau$ , the form:

$$X_{\tau+1} = P_{\mathcal{K}}(X_{\tau} - a_{\tau}F(X_{\tau})).$$

This algorithm results in the explicit formulae for the iterative computation of the biomass flows, which are made possible because of the simplicity of the underlying feasible set K.

The expressions provide a discrete-time approximation to the dynamic trajectories associated with the continuous time evolution of the biomass flows on the links of the ecological network depicted in Figure 1.

We now discuss an application that is drawn from fisheries and which is motivated by Mullon, Shin, and Cury (2009). The ecological predator-prey network is depicted in Figure 3.

The species and their data parameters are itemized in Table 1, where note that fisheries as a predator is also included. There are 2 primary prey: the phytoplankton and the macrobenthos, 5 intermediate predator-prey species: the anchovies, the sardines, the pelagics I, the small hake, and the demersal fish I, and 3 bottom-tiered predators: the sea lions, the sea birds, and the fisheries.

#### An Application



Figure 3: The Ecosystem for the Numerical Application

#### Table 1: Species and Their Parameters

i	species	$\gamma_i$	$\mu_i$	$\kappa_i$	$\lambda_i$	Ei
1	phytoplankton	2.00	16.89	.21	0.00	8000.00
2	macrobenthos	.25	.50	.23	0.00	25.00
3	anchovies	.1	.94	.26	.02	0.00
4	sardines	.10	1.10	.27	.02	0.00
5	pelagics I	.11	.13	.25	.02	0.00
6	small hake	.30	.56	.26	.08	0.00
7	demersal fish l	.20	.26	.23	.04	0.00
8	sea lions	.02	.15	0.00	.01	0.00
9	sea birds	.025	.50	0.00	.01	0.00
10	fisheries	.30	.08	0.00	.01	0.00

#### An Application

The  $\phi_{hl}$  functions (please refer to Figure 3 and (4c)) were given by:  $\phi_{13}(X_{13}) = .08276X_{13} + 82.76, \phi_{14}(X_{14}) = .08272X_{14} + 82.72,$   $\phi_{25}(X_{25}) = .00037X_{25} + .37, \phi_{26}(X_{26}) = .00012X_{26} + .12, \phi_{27}(X_{27}) = .00041X_{27} + .41,$   $\phi_{38}(X_{38}) = .00198X_{38} + 1.98, \phi_{39}(X_{39}) = .00198X_{39} + 1.98, \phi_{3,10}(X_{3,10}) = .00197X_{3,10} + 1.97,$   $\phi_{48}(X_{48}) = .00236X_{48} + 2.36, \phi_{49}(X_{49}) = .00236X_{49} + 2.36, \phi_{4,10}(X_{4,10}) = .00235X_{4,10} + 2.35,$   $\phi_{58}(X_{58}) = .00119X_{58} + 1.19, \phi_{59}(X_{59}) = .00119X_{59} + 1.19, \phi_{5,10}(X_{5,10}) = .00048X_{5,10} + .48,$   $\phi_{68}(X_{68}) = .0013X_{68} + 1.30, \phi_{6,10}(X_{6,10}) = .00048X_{6,10} + .48,$  $\phi_{78}(X_{78}) = .00049X_{78} + .49, \phi_{7,10}(X_{7,10}) = .00048X_{7,10} + .48.$ 

The above functions are extensions of their uncongested counterparts extracted from Mullon, Shin, and Cury (2009).

#### An Application

The equilibrium biomass flows computed by the Euler method were:

 $X_{13}^* = 4658.79, \quad X_{14}^* = 4665.89,$  $X_{25}^* = 0.00, \quad X_{26}^* = 5.48, \quad X_{27}^* = 0.00,$  $X_{38}^* = 142.13, \quad X_{39}^* = 310.22, \quad X_{310}^* = 5.10,$  $X_{48}^* = 141.53, \quad X_{49}^* = 309.56, \quad X_{4\ 10}^* = 4.46,$  $X_{58}^* = X_{59}^* = X_{510}^* = X_{68}^* = X_{610}^* = X_{78}^* = X_{710}^* = 0.00,$ with the equilibrium species biomass levels being:  $B_1^* = 395.22, \quad B_2^* = 1.54, \quad B_3^* = 8.96, \quad B_4^* = 10.03, \quad B_5^* = 0.00,$  $B_6^* = 2.93, \quad B_7^* = 0.00, \quad B_8^* = 37.82, \quad B_0^* = 30.99, \quad B_{10}^* = 35.87.$ This application demonstrates that the dynamic ecological network

framework developed in this paper can be utilized for the study of <u>ecological predator-prey networks</u>.

#### Summary, Conclusions, and Suggestions for Future Research

## Summary, Conclusions, and Suggestions for Future Research

• In this paper, we developed a new dynamic model of predator-prey interactions.

• We also established the equivalences among network systems occurring in entirely different disciplines – in ecology and biology with economics and regional science.

• In particular, we showed the *equivalence of the governing equilibrium conditions of predator-prey systems with spatial price and supply chain network equilibrium problems* through their corresponding variational inequality formulations.

• We provided both theoretical results as well as *an application to fisheries using real world data*.

• We can expect continuing research in network equilibrium models of complex food webs and in ecology in the future.

#### THANK YOU!



#### For more information, see: http://supernet.isenberg.umass.edu

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**Ecological Predator-Prey Networks**