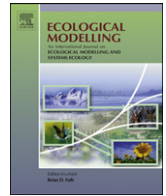




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NEATS: A Network Economics Approach to Trophic Systems[☆]

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ABSTRACT

The main principle of the economic approach to a trophic system we propose here lies in assuming that there is a transfer of food along a path between a prey and a predator if, for the predator, the benefits are greater than costs of predation on this path. Conversely, if the costs exceed the benefits, there are no flows. This trade-off, considered all along the food chains of an ecosystem, together with ecological processes (assimilation, somatic maintenance) results in a model coupling mass balance equations (biological constraints) and complementarity principles (Walras' law). Here is the core of the Network Economics Approach to Trophic Systems (NEATS).

We illustrate with simple examples of ecosystems how these principles result in algebraic equations which can be analyzed mathematically and solved numerically. We show, in a more sophisticated example of an input/output trophic network, that they result in "affine variational inequalities", whose solutions can be estimated. We make explicit how the approach can be applied to address ecological questions, concerning differences of productivity, causes of biological diversity, or the nature of controls in marine ecosystems.

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1. Introduction

The idea of equilibrium and its relation to the "Balance of Nature" are central in theoretical ecology (Egerton, 1973; Cuddington, 2001). Defining an ecosystem, using an analogy with the "environment within" an organism, implies that there is some persistence or "homeostasis" in the dynamics of a part of nature; one cannot speak of an ecosystem when dealing about evanescent dynamics. At the same time, however, ecosystems must be treated as complex changing entities.

It happens that the power and the fragility of the idea of ecological equilibrium are due to their resonance in other scientific fields, such as mathematics or economics. There are at least three very different concepts of ecological equilibrium. First, equilibrium is related to conservation laws such as in physical sciences: a quantity (population number, species number, energy, biomass) is conserved, or transformed in a deterministic way, through ecological processes (predation, assimilation, individual growth, spawning, dispersal). It has been the objective of many ecologists to find such conservations laws not only in the biological processes, but also in the ecological data themselves, for example in population

data (Egerton, 1973). Second, ecological equilibrium is based on the mathematical formulation of a dynamical system, that is on differential equations, and the subsequent study of its dynamics, mainly the description of its steady states or more generally its attractors, or attracting basins (Scheffer and Carpenter, 2003). In that case, ecological equilibrium is directly related to the mathematical stability of ecosystems. According to a long tradition from Lotka, Volterra, Odum, to Holling, this is the purpose of many ecological models to address the coupling of balance-based and dynamical concepts of equilibrium. Now ecologists assimilate balance of nature and mathematical equilibrium, although background principles of both concepts may be considered irreducible (Cuddington, 2001). A third definition of equilibrium issued from economic theory has been applied to ecological systems. It is based on a complementarity principle, whose simplest expression is Walras' law (Fig. 1): there is an economic exchange between two agents when supply price equals demand price; if there is a surplus of supply price on demand price, there is no exchange; there are no other alternatives. The above complementarity principle is used, for example, in the optimal foraging theory (MacArthur and Pianka, 1966): as a predator in a patchy environment seeks to forage where searching and predation costs are lower, there is a tendency to a balance between energy costs and energy gain. Due to these different approaches, the concept of ecological equilibrium is widely debated (Pimm, 1979; De Angelis and Waterhouse, 1987); the hypothesis of intermediate disturbance (Townsend et al., 1997), which relates biological diversity to the lack of equilibrium states in ecological systems, is a remarkable illustration of the theoretical issues of this debate.

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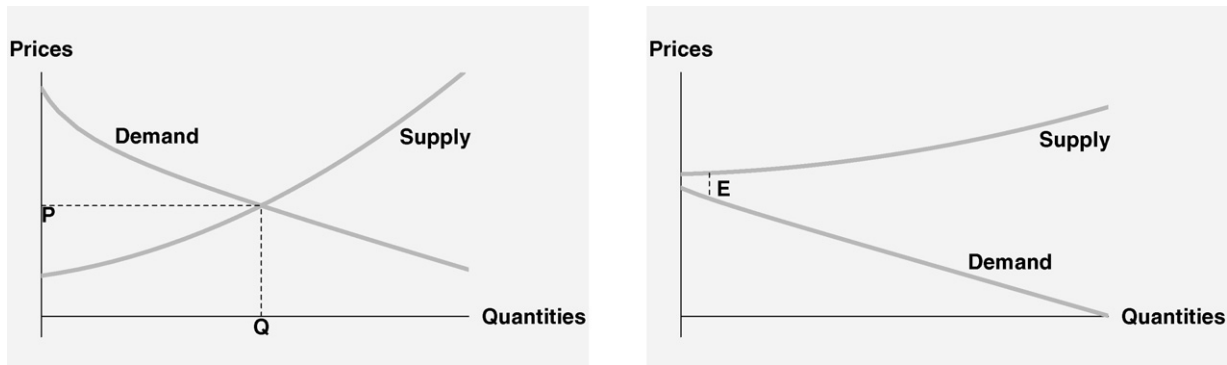


Fig. 1. Walras' law. Demand price decreases and supply price increases with exchanged quantities. There is an economic exchange between both agents when supply price equals demand price. If there is a surplus of supply price on demand price, there is no exchange. The remaining alternative is not relevant to economics, since it would imply a null supply price for non-null quantities. Thus, either the flow is positive, either the surplus is positive, and only one between flow and surplus is non-null. Equilibrium is at the intersection of supply and demand curves. Thus, at equilibrium, we have, either $Q > 0, E = 0$ (left) or $Q = 0, E > 0$ (right) where Q is exchanged volume and E is excess of supply price on demand price. This alternative is called a “complementarity equation”.

This paper is in the continuity of a continuous exchange between economics and ecology to explore ecological equilibrium (Odum, 1971; Hannon et al., 1991), which has been reviewed by Hannon (1997). In this regard the importance of recent works, which propose to analyze the “general equilibrium” of ecosystems (Tschirhart, 2000; Finnoff and Tschirhart, 2003) by merging the input/output approach and the economic equilibrium approach must be underlined. Here we propose a Network Economics Approach to Trophic Systems (NEATS), which, in a simple way, allows representing the economics of ecosystems, and we show how it addresses classical questions of bio-economics or theoretical ecology, such as the food-web structure, the role of cannibalism, the impact of intra-specific competition on biological diversity, and the structure of controls in trophic webs. It is based on a trade-off for predators between costs and benefits of predation that is density dependent, while avoiding a restrictive definition of costs and benefits.

Our approach is relevant to Network Economics (Nagurney, 1993) whose principle lays in the coupling of constraints equations (such as balance equations) and complementarity equations; one may relate this to the coupling of Ohm's law and Kirchhoff's law in an electric circuit. There are many applications of Network Economics (Nagurney, 1993) to very different research fields, such as economics, transportation, structural dynamics, migration, supply chain planning, etc. In recent years, there has been an important development of mathematical tools that allow defining and calculating equilibriums in networks systems. Main tools are the “variational inequality” (Nagurney, 1993), and the “complementarity problems” (Facchinei and Pang, 2003), which allow combining the ingredients of economic equilibrium, i.e., balance relationships and complementarity.

In a network model of a food web, nodes or compartments correspond to species (or functional groups of species) and links correspond to food flows between species. At each node, occurs a mass balance equation. On each link, occurs a complementarity principle.

The paper is organized as follows. We formulate in mathematical terms the principles of NEATS. We examine with several simple examples of trophic networks how NEATS allows revisiting some classical problems of ecological theory such as optimal foraging or cannibalism. We formulate a more realistic model of a marine ecosystem and prove that it has an equilibrium and that this equilibrium is computable. We apply NEATS (1) to analyze productivity differences in upwelling ecosystems, (2) to revisit the issue of the species coexistence, and (3) to

explore shifting dynamics of the pelagic ecosystem of the Chilean coast.

2. Principles of NEATS

2.1. Background

2.1.1. Mass balance equations

NEATS uses a conventional mass balance equation which expresses the equality, inside a compartment of (1) the production of new biomass (assimilation), and (2) the loss of biomass, due to predation, other mortality and somatic maintenance. We will use the following formulation. Species or functional groups of species of the trophic network are denoted i . Biomass of species i is denoted B_i . Flows, i.e. the amount of biomass of species i preyed upon by species j are denoted X_{ij} . We denote P_i the assimilated biomass. We assume $P_i = \gamma_i \sum_j X_{ji}$ where γ_i is the trophic assimilation efficiency. For autotroph species, $P_i = \gamma_i E_i$ where E_i is the inflow (energy and nutrients). A part of the loss of biomass corresponds to the biomass consumed by other species: $Q_i = \sum_j X_{ij}$. Other losses R_i , corresponding to somatic maintenance, are assumed to be proportional to biomass: $R_i = \mu_i B_i$. Then, considering that $E_i \neq 0$ and $X_{ij} = 0$ for autotroph species i , that $X_{ij} = 0$ for top predator species and fisheries j , the mass balance equations of a marine ecosystem is

$$\gamma_i(E_i + \sum_j X_{ji}) = \mu_i B_i + \sum_j X_{ij}$$

Rearranging this equation, we obtain:

$$B_i = \frac{\gamma_i(E_i + \sum_j X_{ji}) - \sum_j X_{ij}}{\mu_i} \quad (1)$$

This relationship implies constraints for trophic flows, which must not result in negative values for biomass of prey species. Given trophic parameters γ_i, E_i , a combination of flows (X_{ij}) must be such that, for all $i, j, X_{ij} \geq 0$ and, for all $i, B_i \geq 0$.

2.1.2. Complementarity equations

Let us denote F_{ij} the costs for a predator j to feed on one unit of biomass of prey i , which corresponds to the difference between advantages and inconveniences. Costs values are opposite to suitability of predation. According to optimal foraging theory both are usually expressed in energy terms (MacArthur and Pianka,

1966) and resulting complementarity principle is equivalent to the marginal value theorem (Charnov, 1976). Transfer of food along path ij appears as a trade-off between the energy that a predator needs for preying upon a prey and the energy gained by its ingestion. This energy gained is different according to the prey. It can be related to some relative preferences due to, e.g. swimming behavior, aggregation patterns, biomass assimilation, taste, distance between distribution areas and to prey density.

In the present version of NEATS, costs are assumed to depend linearly on the biomass of both prey and predator: they are assessed as the sum of (1) a constant term, ϕ_{ij} , which is related to the distance between distribution areas of prey i and predator species j ; it is also related to difficulties of handling and ingestion; (2) a negative linear term, $-\kappa_i B_i$, expressing the easiness of predation due to the abundance of prey B_i ; (3) a positive linear term, $\lambda_j B_j$, expressing intra-specific competition of predator species j ; this process is sometimes termed “predator interference” and can be formalized in different ways, see for example Arditì and Ginzburg (1989). These assumptions ignore several other factors such as the relationship between distribution areas and prey abundance. However, it is the simplest way to represent density dependence effects on predation costs. Summarizing these assumptions, the predation costs between a prey i and a predator j are assumed, in this version of NEATS, to be given by

$$F_{ij} = \phi_{ij} - \kappa_i B_i + \lambda_j B_j \quad (2)$$

Then, equilibrium is due to the following mechanism: (1) if $F_{ij} > 0$, prey is not accessible enough; flows X_{ij} decrease; biomass of prey B_i increases; F_{ij} costs decrease. (2) if $F_{ij} < 0$, there are many accessible prey; flows X_{ij} increase, B_i decreases, costs F_{ij} increase. The system moves towards a situation where either $X_{ij} > 0$ and $F_{ij} = 0$, or $F_{ij} > 0$ and $X_{ij} = 0$. If there are flows from i to j , there is an economic balance between advantage and inconveniences of predation. If there is no flow, this is because the costs of predation are greater than the advantages for the corresponding predator. It is clear that these assumptions imply that there is a threshold of prey biomass under which there is no predation; this is thus an expression of foraging arena theory (Walters et al., 2000): a part of prey biomass is not accessible simply because, at low density, it is too costly for predators. The model only examines equilibrium situations but does not represent situations in which a predator consumes its prey until extinction for example.

This encompasses the mathematical definition of network equilibrium. We denote K the set of admissible flows $X = \{X_{ij}\}$ which satisfy the constraints $X_{ij} \geq 0$ and $B_i \geq 0$, where B_i is given by Eq. (1). Let $X^* = \{X_{ij}^*\} \in K$ and $F^* = \{F_{ij}^*\}$ the associated predation costs. Then X^* is an equilibrium if it is a solution of the complementarity equations: for all i and j , one has $X_{ij}^* > 0$ and $F_{ij}^* = 0$, or $F_{ij}^* > 0$ and $X_{ij}^* = 0$.

2.2. Network equilibrium of simple trophic networks

Let us illustrate how to apply NEATS to some very simple and typical trophic networks (Fig. 2).

2.2.1. Prey–predator

First, we consider the simplest ecological system (Fig. 2A) with a prey population i with biomass B_i , a predator population j with biomass B_j and the trophic flow X_{ij} from i to j . Mass balance equations are (1) $\gamma_i E_i = X_{ij} + \mu_i B_i$ and (2) $\gamma_j X_{ij} = \mu_j B_j$. To simplify expression of results, we assume that there is no intra-specific competition: $F_{ij} = \phi_{ij} - \kappa_i B_i$. Then, adding complementarity equations $\phi_{ij} - \kappa_i B_i = 0$ when flows $X_{ij} > 0$, one obtains a linear system, whose

solution is

$$B_i = \frac{\phi_{ij}}{\kappa_i}$$

$$B_j = \frac{\gamma_j (\gamma_i \kappa_i E_i - \phi_{ij} \mu_i)}{\kappa_i \mu_j}$$

$$X_{ij} = \frac{\gamma_i \kappa_i E_i - \phi_{ij} \mu_i}{\kappa_i}$$

There is no flow ($X_{ij} = 0$) when $\gamma_i \kappa_i E_i < \mu_i \phi_{ij}$. In this case, $B_i = \gamma_i E_i / \mu_i$. A minimal level of abundance is defined for prey in such a way that if there is not enough prey, there is no predation flow, and thus no predator. With this principle, we can represent an ecosystem in which some environment factor, such as climate, affects accessibility parameters and, due to the above rule, provokes sudden switches in the ecosystem dynamics.

2.2.2. A short food chain

Secondly, we consider a short food chain (Fig. 2B) with a primary producer i and its biomass B_i , a foraging species j and its biomass B_j , a top predator species k and its biomass B_k , the trophic flow X_{ij} from i to j , the trophic flow X_{jk} from j to k . Mass balance equations, together with complementarity equations (still assuming no intra-specific competition), when there are positive flows ($X_{ij} > 0$, $X_{jk} > 0$) become a linear system with five unknowns and five equations:

$$\gamma_i E_i = X_{ij} + \mu_i B_i$$

$$\gamma_j X_{ij} = X_{jk} + \mu_j B_j$$

$$\gamma_k X_{jk} = \mu_k B_k$$

$$\kappa_i B_i = \phi_{ij}$$

$$\kappa_j B_j = \phi_{jk}$$

Solving this system, we obtain the following expressions for biomass and flows:

$$B_i = \frac{\phi_{ij}}{\kappa_i}$$

$$B_j = \frac{\phi_{jk}}{\kappa_j}$$

$$B_k = \frac{\gamma_k \gamma_j \gamma_i E_i}{\mu_k} - \frac{\gamma_j \gamma_k \mu_i \phi_{ij}}{\kappa_i \mu_k} - \frac{\gamma_k \mu_j \phi_{jk}}{\mu_k \kappa_j}$$

$$X_{ij} = \gamma_i E_i - \frac{\mu_i \phi_{ij}}{\kappa_i}$$

$$X_{jk} = \gamma_j \gamma_i E_i - \frac{\gamma_j \mu_i \phi_{ij}}{\kappa_i} - \frac{\mu_j \phi_{jk}}{\kappa_j}$$

All these quantities must be positive, which implies algebraic conditions upon coefficients. The last equations allow to study the impact of any change of a given parameter on the structure of the network. For example, an increasing energy inflow E_i has an impact only on top predator biomass B_k (third line of previous equation), not on B_i (first line) and B_j (second line). This is in conformity with conventional modeling approaches, which have shown, that without intra-specific interference, an increase of primary production has an impact on upper trophic levels, not on intermediate trophic levels (Ginzburg and Akçakaya, 1992).

2.2.3. Cannibalism

In the same way, we consider a very simple network model of an ecosystem, where cannibalism is possible (Fig. 2C). It gives the following mass balance equations: (1) $\gamma_i E_i = X_{ij} + \mu_i B_i$ and (2) $\gamma_j (X_{ij} + X_{jj}) = X_{jj} + \mu_j B_j$. Similarly as before, if flows X_{ij} and X_{jj} are positive, adding complementarity equations $F_{ij} = 0$ and $F_{jj} = 0$

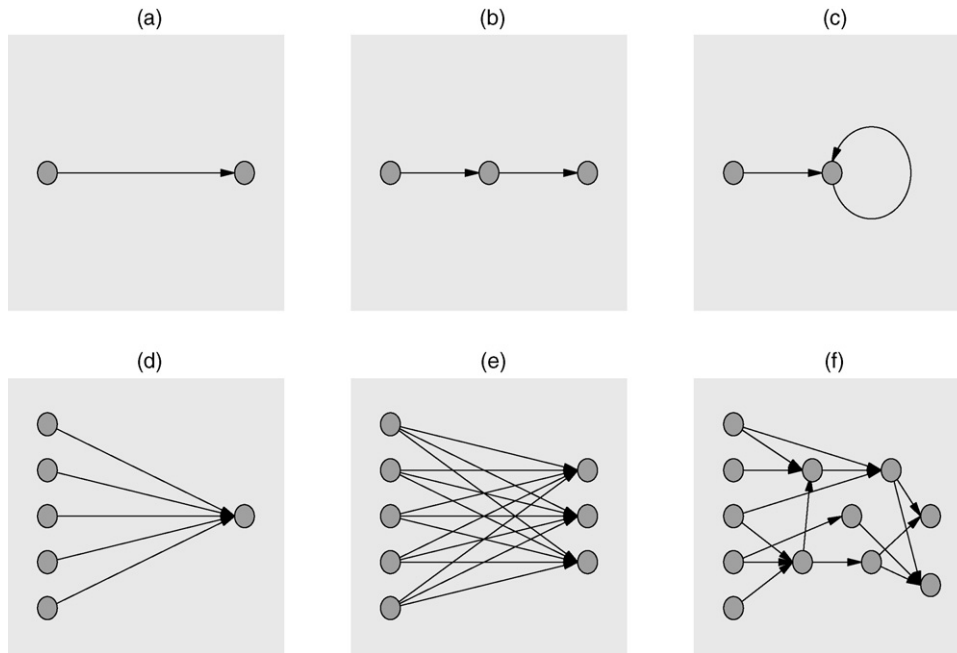


Fig. 2. Building blocks: (A) a prey–predator relationship; (B) a simple food chain; (C) cannibalism; (D) a generalist predator; (E) a simple food web; (F) a bi layer network.

results in a linear system, whose solution is

$$\begin{aligned}
 B_i &= \frac{\phi_{ij}\kappa_i}{\kappa_j} \\
 X_{ij} &= \gamma_i E_i - \mu_i \phi_{ij} \kappa_i \\
 X_{jj} &= \frac{1}{1 - \gamma_j} (\gamma_i \gamma_j E_i - \frac{\gamma_j \mu_i \phi_{ij}}{\kappa_i} - \frac{\mu_j \phi_{jj}}{\kappa_j})
 \end{aligned}$$

Solving this linear system, provides the condition on parameters that allows cannibalism:

$$\gamma_i \gamma_j E_i - \frac{\gamma_j \mu_i \phi_{ij}}{\kappa_i} - \frac{\mu_j \phi_{jj}}{\kappa_j} \geq 0$$

That is: $\phi_{jj} \geq \phi^0$, where

$$\phi^0 = \frac{\kappa_j \gamma_i \gamma_j E_i}{\mu_j} - \frac{\kappa_j \gamma_j \mu_i \phi_{ij}}{\mu_j \kappa_i}$$

2.2.4. Foraging

Finally, we consider an ecosystem (Fig. 2D) with several prey populations $i \in I$, their biomass B_i , one predator population j , its biomass B_j , and the trophic flows X_{ij} between i and j . Mass balance equations are (1) $\gamma_i E_i = X_{ij} + \mu_i B_i$ for all i , and (2) $\gamma_j \sum_i X_{ij} = \mu_j B_j$. Then, if all flows are > 0 , complementarity equations (still assuming no intra-specific competition) results in a linear system, whose solutions are

$$\begin{aligned}
 B_i &= \frac{\phi_{ij}}{\kappa_i} \\
 X_{ij} &= \gamma_i E_i - \frac{\mu_i \phi_{ij}}{\kappa_i} \\
 B_j &= \sum_i \left(\frac{\gamma_j \gamma_i E_i}{\mu_j} - \frac{\gamma_j \mu_i \phi_{ij}}{\mu_j \kappa_i} \right)
 \end{aligned}$$

Optimal foraging theory (MacArthur and Pianka, 1966) is based on a detailed examination of the energy costs of predation for search, capture and ingestion. Assuming economic principles, it allows studying relationships between spatial structures (a patchy environment) and population dynamics. With NEATS, we get a simple, if rough formalism of this theory and some subsequent ones

such as that of the marginal value theorem (Charnov, 1976) or the ideal free distribution theory (Fretwell and Lucas, 1970).

2.3. Network equilibrium of input/output food webs

The previous examples are solvable algebraically, due to the equality of the number of equations and unknowns, and the few number of situations to observe when constraints are not satisfied. This approach becomes impossible for more complex systems: we would have to examine 2^n situations for a system with n compartments; and it is supposed that the general complementarity problem belongs to the class of NP-problems (not computable in polynomial time). However, the theory of Network Economics (Nagurney, 1993) shows that in a much larger class of systems, there are solutions and they are computable. We will show this in the case of a more general biological system with several linked compartments (Fig. 2F). We restrict the problem to “input/output” oriented systems (loopless digraphs), i.e. the network is “oriented” between an input part and an output part. There are no loops, for example no cannibalism.

Recall that predation costs on a path ij are given by $F_{ij} = \phi_{ij} - \kappa_i B_i + \lambda_j B_j$. This model includes a compartment fisheries which is considered using exactly the same formalism as for species compartments. Similar to a top predator compartment, it has a cost function, “somatic maintenance” and “mortality” coefficients. We use the same unit, biomass, also for fisheries by considering rates of exchanges between biomass and money. Interpretation of coefficients is quite easy: inflow $I_k = \sum_j X_{jk}$ is the biomass caught by the fishery; K_k is the amount of capital owned by the fishery, that is proportional to its fishing capacity (expressed in biomass currency); $p_k I_k$ is the income of fishery; $c_k K_k$ is the capital costs of fishery. One has still the balance relationship $p_k I_k = c_k K_k$. We assimilate then $\gamma_k = p_k$, the efficiency coefficient of the fishery and $\mu_k = c_k$ the mortality rate of the fishery.

Mass balance equations are as before, for all compartments, including fisheries:

$$\gamma_i (E_i + \sum_j X_{ji}) = \mu_i B_i + \sum_j X_{ij}$$

And complementarity equations are

$$\begin{aligned} X_{ij} > 0 &\Rightarrow \phi_{ij} - \kappa_i B_i + \lambda_j B_j = 0 \\ X_{ij} = 0 &\Rightarrow \phi_{ij} - \kappa_i B_i + \lambda_j B_j \geq 0 \end{aligned}$$

We consider the set K of admissible flows defined in Section 2.1.2. The equilibrium solution of the trophic network corresponds to the solutions of an “affine variational inequality” (Nagurney, 1993) that is simply expressed in terms of the problem parameters. This is due to the following propositions (see Appendix A.1 for references and proofs).

Proposition 1. *The set of admissible flows K is a polyhedron in the set of flows. Moreover K is compact (closed and bounded).*

Proposition 2. *To $X = (X_{ij}) \in K$ we associate B_i according to formula 1 and F_{ij} according to formula 2. We put $F(X) = (F_{ij})$. Then $X \rightarrow F(X)$ is a linear function.*

Proposition 3. *A vector of flows X^* is an equilibrium state if and only if it satisfies the “affine variational inequality”: $S = F(X^*)(X - X^*) \geq 0$ for all $X \in K$, where S is the scalar product $S = \sum_{ij} F_{ij}(X^*)(X_{ij} - X_{ij}^*)$.*

Proposition 4. *Solution set of the above “affine variational inequality” is not empty.*

Proposition 5. *In order to get an unique solution, it is sufficient that, for all species $\gamma_i \kappa_i = \lambda_i$.*

These propositions allow us to compute equilibriums using “projection” algorithms (Nagurney, 1993), or Newton-like methods (Facchinei and Pang, 2003). The last theorem allows us to define a “strong” equilibrium. Considering that there are few differences between trophic efficiencies, strong equilibrium characterizes ecosystems in which intra-specific competition decreases with accessibility.

3. Using NEATS

3.1. Productivity of upwelling systems

We apply the model of a short food chain presented in Section 2.2.2 to the comparisons of upwelling ecosystems in the Humboldt and Benguela currents. The main characteristic of these highly productive and variable ecosystems is the dominance of small pelagic fish (anchovies and sardines). Two opposite situations are observed (Fig. 3); in the Humboldt ecosystem, primary production is relatively moderate and pelagic fish are very abundant; in the Benguela ecosystem, primary production is very high meanwhile pelagic fish are much less abundant. These differences are puzzling (Mackas et al., 2006). The results of Section 2.2.2 suggest that an important factor to be taken into account is food accessibility to explain the disparity in relative ecosystem productivity. Thus plankton accessibility is low in the Benguela and high in the Humboldt (which can be related to hydrodynamic activity); pelagic fish accessibility is low in the Benguela, medium in the Humboldt (which remains an open question); while nutrient input is high in the Benguela and medium in the Humboldt (which is observed). This type of coupling

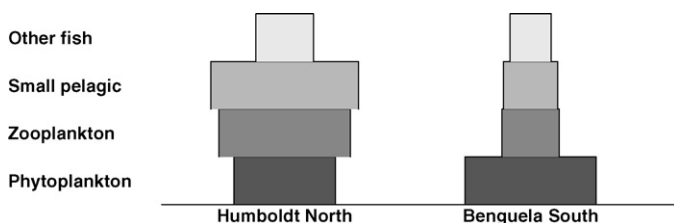


Fig. 3. Schematic representations of the differences of biomass in two important upwelling ecosystems. From estimation and models by L. Shannon and J. Tam.

represents an illustration of a now conventional theory of ocean productivity (Bakun, 1996).

3.2. Competition and diversity

Considering a bi-layered network (Fig. 2E) may allow addressing in an original way the question of the coexistence of species. With only two trophic levels, mass balance equations are: $\gamma_i E_i = \sum_j X_{ij} + \mu_i B_i$ for prey species, $\gamma_j \sum_i X_{ij} = \mu_j B_j$ for predator species, which results in some simplification of the equations (Appendix A.2). We build a simulation experiment in which, equilibrium is computed for an ecosystem comprised of 8 prey species and 50 predator species, with increasing values of the predator density dependence parameter λ_j . It is set up as follows. For fixed values of a parameter of the intra-specific competition, $\Lambda = 0, 0.02, 0.04, 0.06, 0.08, 0.1$, we repeat many times the sequence: (1) randomly choose the intra-specific parameter $\lambda_j \in [\Lambda, 2\Lambda]$; (2) randomly choose other parameters $E_i \in [1000, 2000]$, $\gamma_i \in [1, 2]$, $\mu_i \in [0.5, 1]$, $\gamma_j \in [0.1, 0.2]$, $\mu_j \in [0.2, 0.4]$, $\phi_{ij} \in [0.1, 0.3]$, $\kappa_i \in [0.1, 0.2]$, $\phi_{ij} \in [0.1, 0.3]$; (3) compute the resulting equilibrium, get the number of each species N_i and its proportion $p_i = N_i/N$, with $N = \sum_i N_i$. Then we observe how resulting diversity indices such as: S the number of predator species with positive abundance $N_i > 0$, the Shannon index $H = -\sum_i p_i \log(p_i)$, the Simpson index $1/\sum_i p_i^2$, depend on the parameter of intra-specific competition.

The results are given in Fig. 4. We observe that without any intra-specific competition, ($\Lambda = 0$) the number of predator species is equal to the number of prey. This is Gause’s principle in its crude form. For each prey, the most efficient of its predators survives: this latter puts the biomass of prey at a level which renders them inaccessible to other predators. In a very robust manner, we observe an increase of biodiversity related to the level of intra-specific competition: as in the mathematical studies of Lotka Volterra equations, the main factor explaining diversity of predators is the intra-specific competition. However, while the conventional theory predicts that particular relationships between inter- and intra-specific competition allow the coexistence of several competitors, our model suggests that very low levels of intra-specific competition are sufficient to allow coexistence of several competitors. This is not surprising from a mathematical point of view: in the present modeling approach, intra-specific competition is a limiting factor for the biomass of a given predator, and thus when production of prey is abundant, the most efficient predator leaves some available food for other predators.

3.3. Trophic controls and keystones in the pelagic ecosystem of the Chilean coast

In this part, NEATS is applied to the study of the coastal pelagic system of Chile based on a previous study by Neira et al. (Neira and Arancibia, 2004; Neira et al., 2004). The structure of this system is plotted in Fig. 5. All parameters needed by NEATS, collated from (Neira and Arancibia, 2004; Neira et al., 2004), are given in Table 1. Biomass B_i , energetic input E_i , trophic efficiency γ_i and other mortality parameter μ_i are classical output of mass balance models. To set accessibility parameters, intra-specific parameters and predation cost parameters, we proceed as follows. The complementarity relationship (when there is a flow $X_{ij} > 0$ then predation costs are such that $\phi_{ij} = \kappa_i B_i - \lambda_j B_j$) allows us to determine ϕ_{ij} using the estimated biomass values. More hypothetically, it has been assumed that the system is not far from its “strong” equilibrium, which is easily computable using the relationship between parameters $\gamma_i \kappa_i = \lambda_i$, meaning that accessibility and intra-specific competition are related. Finally, the accessibility parameter has been assumed lower for intermediate trophic level species (gregarious behavior).

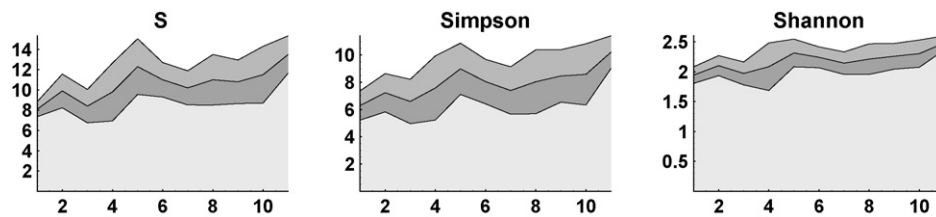


Fig. 4. Diversity values. On the x-axis, intra-specific competition parameter Δ . On the y-axis, mean values plus or minus standard deviations of S (number of species), Simpson's and Shannon's indices.

3.3.1. Analysis of controls

A sensitivity analysis of the impact of input parameters allows us to reconsider the puzzling question of trophic controls (Hairston et al., 1960; Slobodkin et al., 1967; Fretwell, 1977; Oksanen et al., 1981; Fretwell, 1987) in the context of marine ecology (Cury et al., 2000). To address this question with NEATS, equilibrium states of trophic networks have been assessed according to specific changes of predation costs.

To represent the dynamics induced by a bottom-up control, predation costs parameters ϕ_{ij} for grazers j of phytoplankton or macrobenthos i have been multiplied successively by 0.5, 0.6, 0.7, ..., 2.0. The results are presented in terms of food transfer along the food chain (Fig. 6). When the accessibility of phytoplankton is high (top), its biomass is at a medium level and the resulting competition is detrimental to demersal fish and mesopelagics. When the accessibility of phytoplankton is low (bottom), its biomass is at a higher level, the macro-zooplankton is dominant in the zooplankton community and small pelagic fish disappear. Between these situations a shift occurs in which small pelagic fish supplant zooplankton species, due to their lower intra-

specific competition. This gives an indication about the behavior of the system and its ability to represent shifting dynamics. We give in the Supplementary Material file a more complete view of the resulting dynamics. This is confirmed by Fig. 7 (left panel), which represents the evolution of biomass of all species. We may observe a shift between a regime where microzooplankton, jellies, sardine and anchovy are dominant when phytoplankton biomass is low, and a regime where macro-zooplankton, mesopelagics and demersal fish are dominant when phytoplankton biomass is high. These two alternative food chains are related to differences in the function of zooplankton species in the food web.

We have represented the top-down control hypothesis by changing predation costs parameters ϕ_{ij} for fisheries i . We multiply them successively by 0.8, 0.85, ..., 1.25. We observe in Figs. 7 and 8 (right panel) that the main characteristics of the dynamics are the consequence of the competition of fisheries with all the top predator species of the ecosystem (chondrichthyans, demersal fish I and II, pelagic fish II, large hake, sea lion and sea birds). See also the Supplementary Material file.

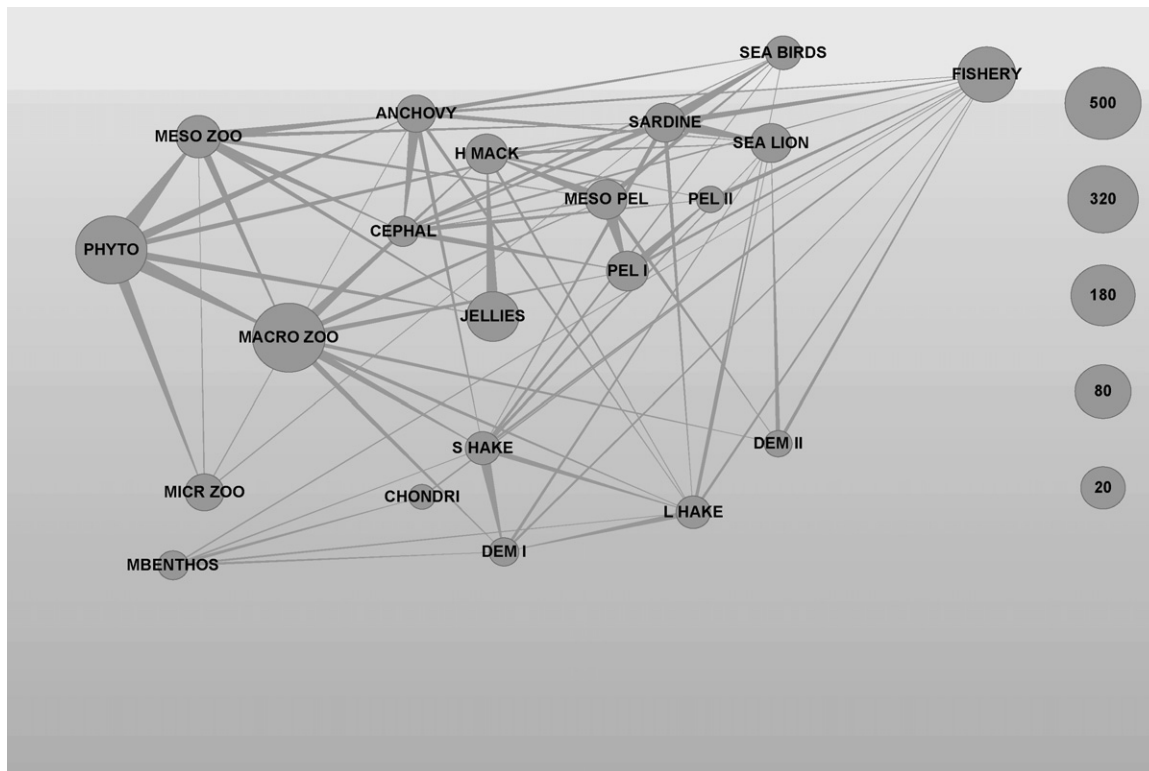


Fig. 5. Trophic flows in the pelagic ecosystem of the Chilean coast. Diameters of disks and thickness of arrows are related to biomass of corresponding compartments and trophic flows. Abbreviations are phytoplankton, PHYTO; macrobenthos, MBENTHOS; meso-zooplankton (copepods), MESO ZOO; microzooplankton, MICR ZOO; macro-zooplankton (euphausiids), MACRO ZOO; jellies (salps and jellyfishes), JELLY; cephalopods, CEPHAL; chondrichthyan, CHONDRI; small hake, S HAKE; horse mackerel, H MACK; demersal fish I (benthic feeders species), DEM I; mesopelagics, MESO PEL; pelagics I (medium-sized pelagic fish like hoki), PEL I; common sardine, SARDINE; large hake, L HAKE; pelagics II (large-sized pelagic fish like swordfish), PEL II; demersal fish II (pelagic feeders species), DEM II; sea birds (penguins, pelicans, cormorants), BIRDS.

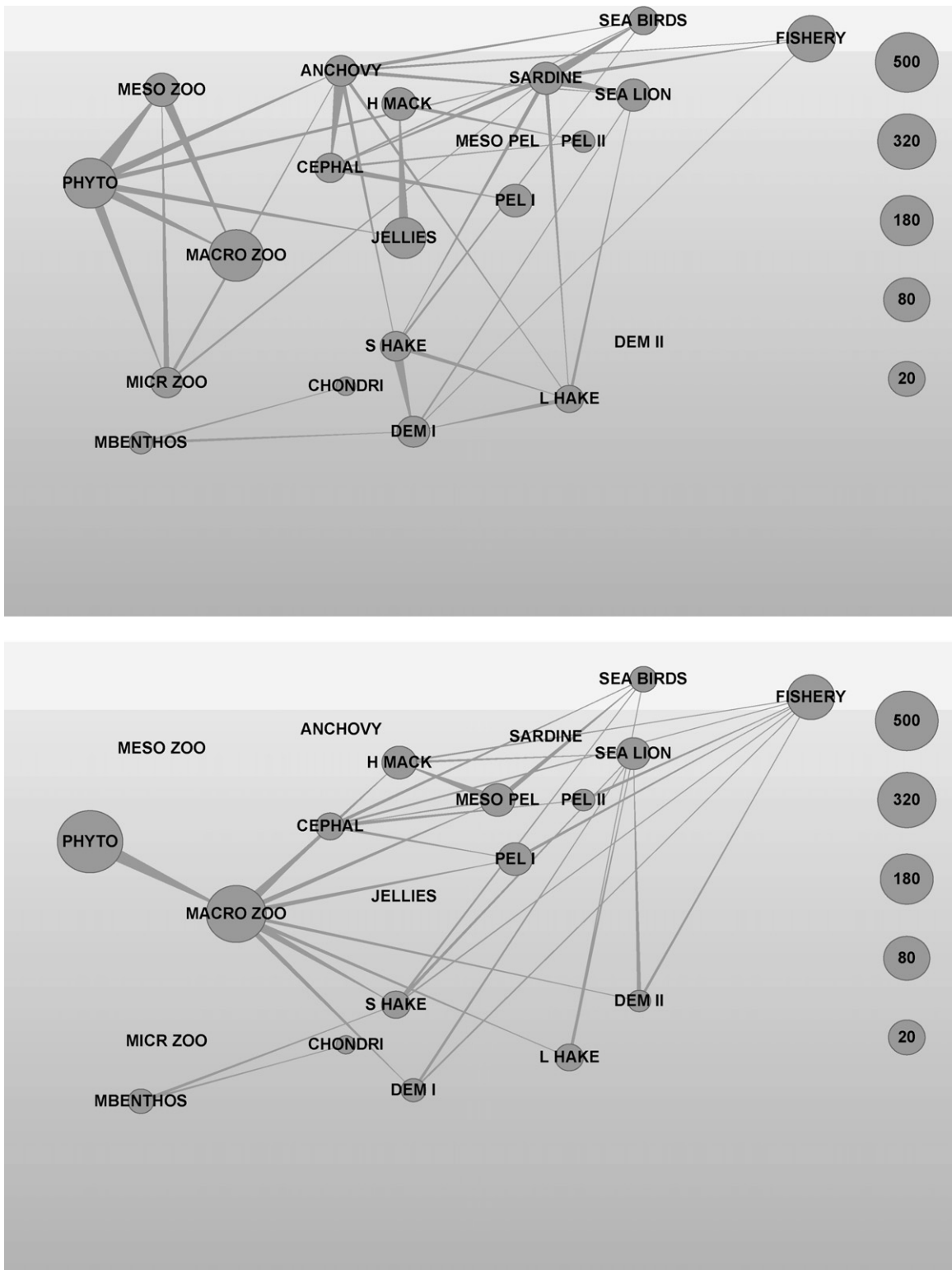


Fig. 6. Simulation of a bottom-up control. Top: high accessibility of phytoplankton and macrobenthos. Bottom: low accessibility of phytoplankton and macrobenthos.

3.3.2. Keystone species

We illustrate how this sensitivity analysis method can be applied to the analysis of keystone species in an ecosystem. For each species i , we systematically change the coefficients of predation costs: we increase ϕ_{ij} and we decrease ϕ_{ki} , for all other species j (prey of i) and k (predators of i). Then we observe the variations of biomass B_k according to the variation of B_i ; when B_i is small and $\Delta B_k / \Delta B_i$ is

important for several species k , we may consider that i is a keystone species (Power et al., 1996; Libralato et al., 2006).

We may observe how the network equilibria change according to changes of the environment of meso-zooplankton (Fig. 9, left panel). When environment is very favorable, meso-zooplankton is the only grazer of phytoplankton; it is preyed by macro-zooplankton from which starts most of the food web. There is a shift when envi-

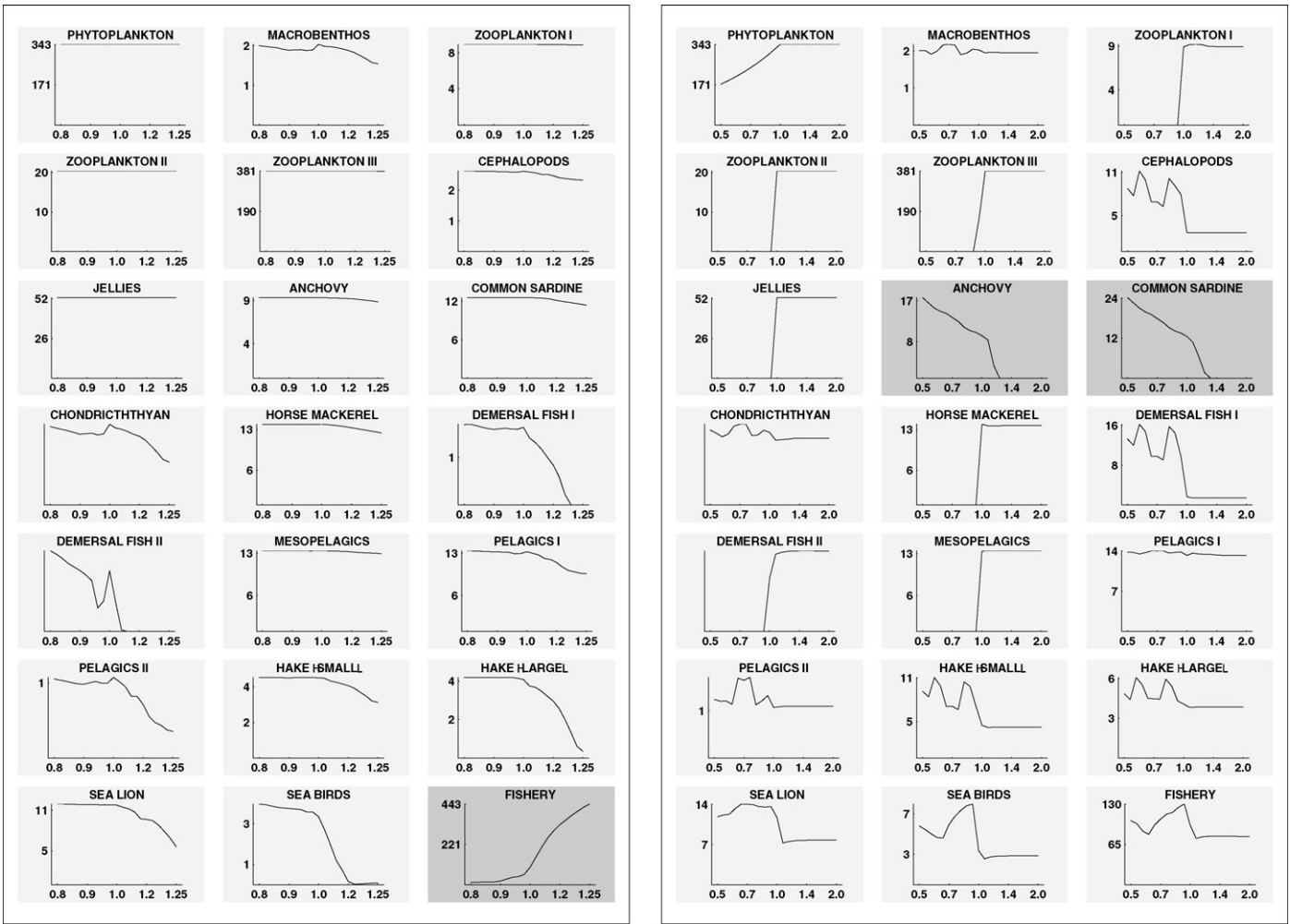


Fig. 7. For all plots: on x -axis, coefficients, 0.5, 0.7, . . . , 1.4, 2.0 or 0.8, 0.82, . . . , 1.11, 1.25; on y -axis, the biomass $B(k)$ in t/km^2 . Right panel: bottom-up control accessibility of phytoplankton and macrozoobenthos is multiplied by coefficients. Left panel: bottom-up control; fishing costs for fisheries are multiplied by coefficients.

Table 1
 Values of parameters: γ , trophic assimilation efficiency; μ , somatic maintenance coefficient; κ , accessibility; λ , intra-specific competition; E , energy input; B , reference biomass. Most of parameters values are issued from Neira et al. (2004). See Appendix A.3 for details.

Compartment	γ	μ	κ	λ	E (t/km^2)	B (t/km^2)
Phytoplankton	2.0	16.89	0.21		8000	302.50
Zooplankton I	0.5	96.87	0.23	0.11		11.62
Zooplankton II	0.29	0.04	0.20	0.05		14.09
Zooplankton III	0.41	0.01	0.26	0.10		26.35
Jellies	0.1	0.05	0.24	0.1		44.70
Macrozoobenthos	0.25	0.50	0.23		25	2.0
Anchovy	0.1	0.94	0.26	0.02		8.35
Common sardine	0.1	1.10	0.27	0.02		11.59
Mesopelagics	0.2	1.20	0.29	0.05		13.26
Horse mackerel	0.05	0.68	0.29	0.01		13.79
Hake (large)	0.11	0.13	0.25	0.02		4.28
Hake (small)	0.30	0.56	0.26	0.08		4.48
Pelagics I	0.1	0.35	0.21	0.02		13.38
Demersal fish I	0.2	0.26	0.23	0.04		1.68
Demersal fish II	0.2	0.24	0.26	0.05		0.78
Chondrichthyan	1.3	0.03	0.23	0.30		0.43
Pelagics II	0.4	0.95	0.25	0.10		0.31
Cephalopods	0.5	1.53	0.24	0.12		1.63
Sea lion	0.02	0.15		0.01		0.09
Sea birds	0.025	0.5		0.01		0.06
Fishery	0.3	0.08		0.01		12.00

ronment starts being less favorable for meso-zooplankton; then starts a competition with microzooplankton which causes a slight decline of macro-zooplankton biomass, under a threshold at which its predators (like hake) stop preying on it and disappear. With a more difficult environment for meso-zooplankton, sardine and anchovies biomass increases at a level which is sufficient to sustain the whole food chain: they become prey of hake and other predators, which due to their high intra-specific competition, prefer them to macro-zooplankton. This suggests that meso-zooplankton corresponds to the definition of a keystone species: it has a relatively low biomass, and its impact on species distant on the food chain is high; this is due to its indirect control upon macro-zooplankton.

Jellies abundance is often considered as an indicator of the health of the ecosystem, their abundance being related to strong perturbation resulting from climate changes or over exploitation (Mills, 2001; Sommer et al., 2002; Lynam et al., 2005; Lynam et al., 2006). The present approach contributes to understanding the ecosystem effects that determine their abundance. We observe in the output of the model that Jellies (Fig. 9, right panel) have an important negative effect on zooplankton species. Their competition with the compartment demersal fish II (pelagic feeders species) is strong, but indirect; observing the structure of trophic network, the key mechanism appears to be the control of meso-zooplankton by jellies: at a given level predation by jellies puts meso-zooplankton at too low a level for being preyed on by mesopelagics and then suppresses the

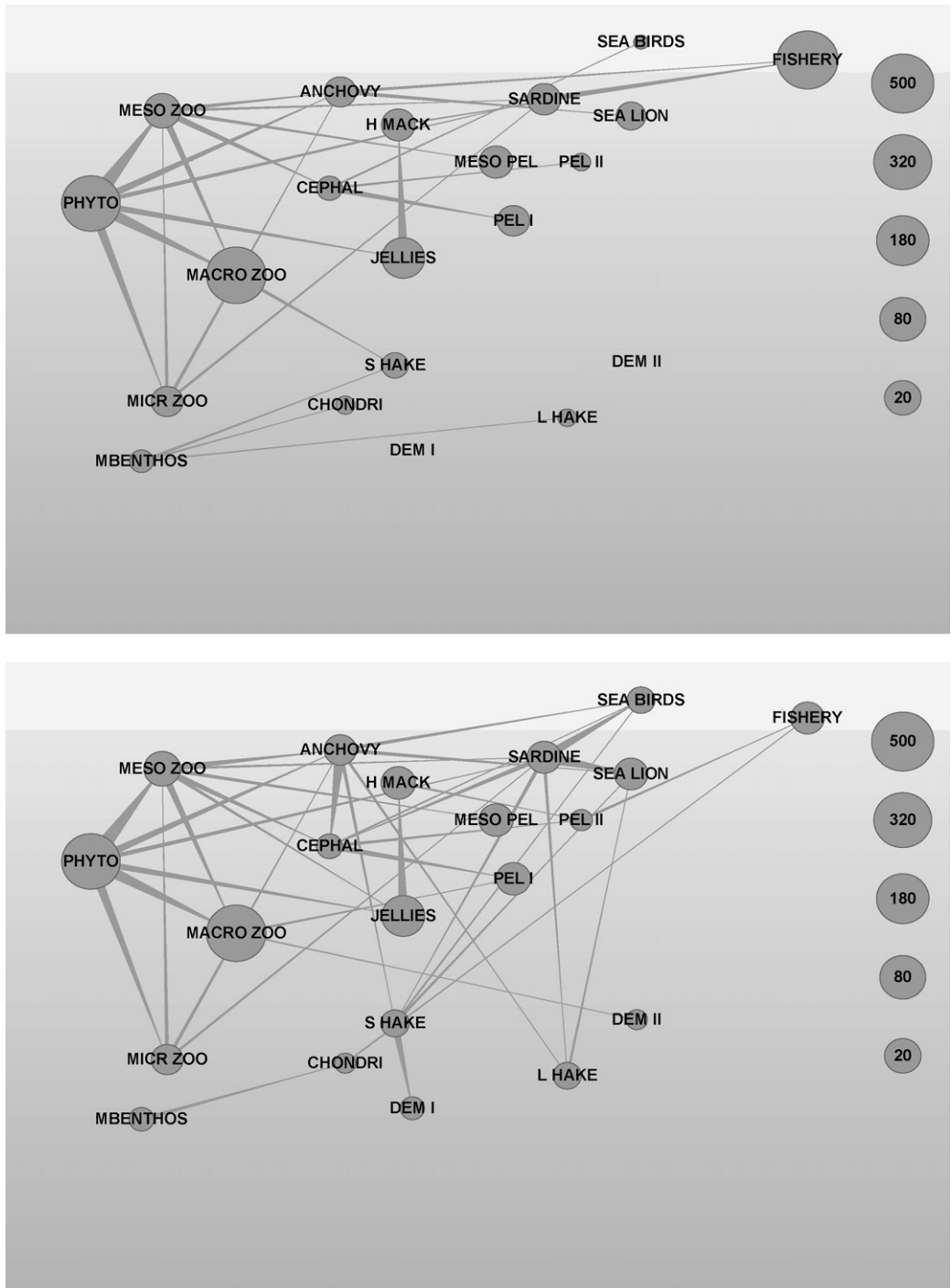


Fig. 8. Simulation of a top-down control. Top: high fishing costs. Bottom: low fishing costs.

above food chain (mainly demersal fish II) that preys on meso-zooplankton.

Observing together the effects of changing the quality of life for sardine and anchovy (Fig. 10) is an illustration of the wasp-waist control (Cury et al., 2000; Bakun, 2006; Jordan et al., 2005). Changing their environment through the change of their accessibility coefficient has a very important effect on most species. Anchovy and sardine have similar effects on almost all other species. They both have a negative top-down effect on zooplankton and a positive bottom-up effect on the upper trophic levels (demersal fish, small hake, sea birds and fishery) We can also observe their competition

and the abrupt collapses of anchovy when environment starts being favorable for sardine, and vice-versa, giving a simple representation of synchronies commonly observed in upwelling ecosystems (Schwartzlose et al., 1999).

4. Discussion

We have applied the concept of economic equilibrium to the study of trophic networks. For this study, seminal works from R. McArthur, B. Hannon, E. Charnov, and S. Tshirhart have inspired us. We have shown how the Network Economics approach of A. Nagur-

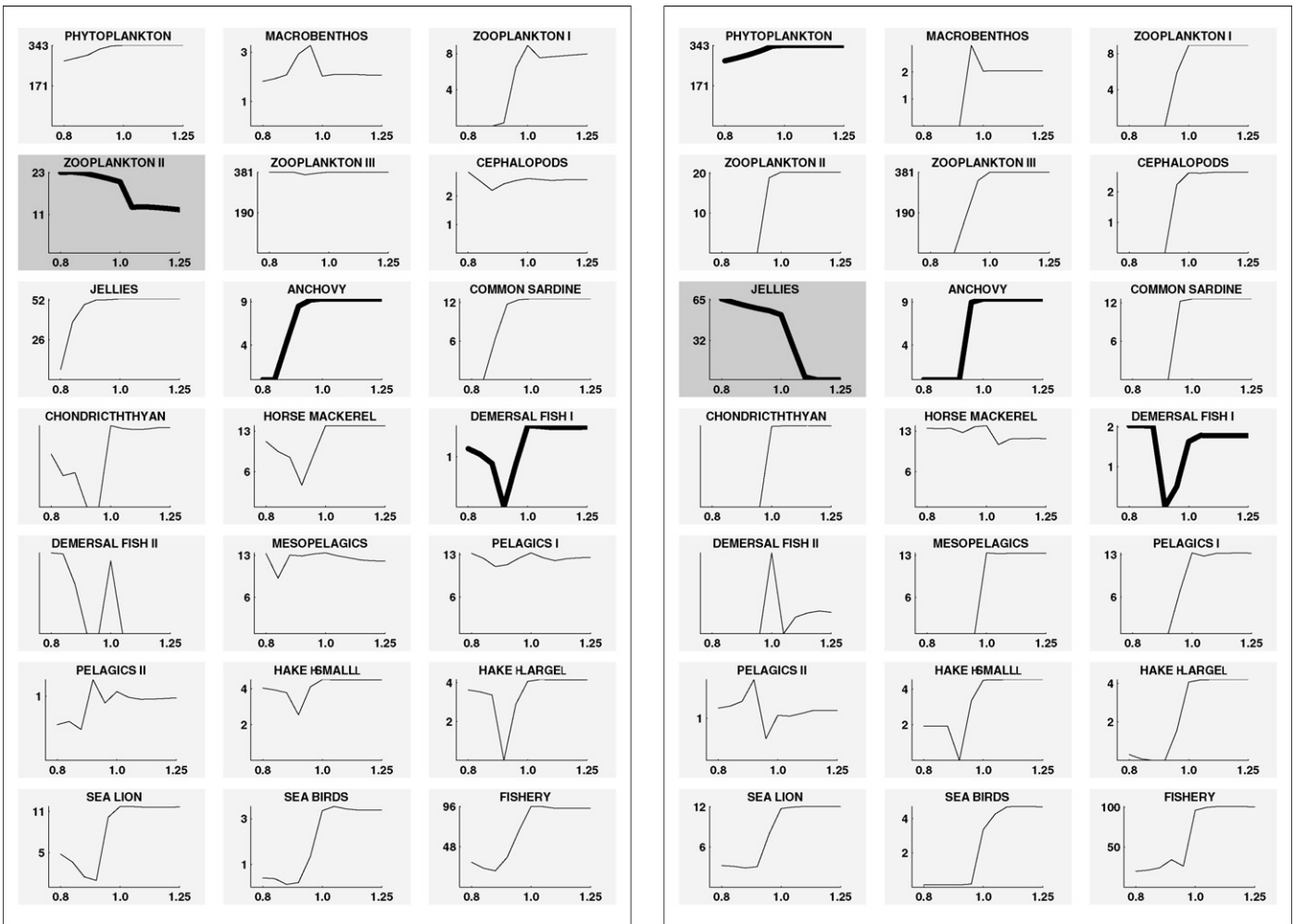


Fig. 9. Keystone species. For all plots: on x-axis, coefficients 0.8, 0.82, . . . , 1.11, 1.25; on y-axis, the biomass $B(k)$ in t/km^2 . The accessibility of tested species is multiplied by coefficients; the accessibility of its preys is divided by coefficients. Left panel: effects of changing environment of meso-zooplankton on the biomass of other species. Right panel: effects of changing environment of jellies on the biomass of other species.

ney through the variational inequality can provide an elegant way to formulate and resolve the equations defining the equilibrium. We have shown that the equilibrium of trophic networks with a reasonable number of compartments leads to a mathematical problem which is computationally tractable. Finally, we have illustrated through the example of the pelagic system of the Chilean coast how this approach provides new insights on classical problems such as the nature of controls, or the identification of keystone species.

Improvements of NEATS are obviously necessary. We have to improve the formulation using more general cost functions presenting non-linearities, and more realistic representation of fisheries. We have to improve the approach itself, (1) with a more complete exploration of the set of solutions, (2) by performing statistical analysis of the solutions randomly generated with small variations of parameters, and (3) by developing a dedicated method for parameters estimations, calibration and model validation.

A simple analysis of productivity differences between upwelling ecosystems allows us to emphasize the role of accessibility costs in the predation process. Accessibility can be related to the shape of the shelf: a narrow shelf would favor encounters since it reduces the spatial extent of predators and prey distribution. Accessibility can also be related to hydrodynamic activity and the existence of mesoscale structures that could favor encounter probability (Weimerskirch et al., 2004). This should contribute to the debate about the effects of climate change on the structure of marine

ecosystems, mainly through the stratification process. It is currently assumed that global climate change will modify precipitations patterns, increase stratification and decrease in winter mixing (Young and Holt, 2007) and ultimately have an effect on plankton dynamics (Bopp et al., 2005). Our results suggest that such predicted patterns could be envisaged without any a-priori (e.g. any causal relationships).

We have shown that NEATS provides a new insight in the question of the coexistence of species; the Gause's competitive exclusion principle (Gause, 1936) states that only one predator species survives when several "similar" predator species compete for one prey species. If it is valid, why are there so many plankton species feeding on the same resource pool (Hutchinson, 1961; Elliott et al., 2001)? Why are there so many tree species in a similar tropical environment (Hubbell, 1997)? Let us remark that, according to the tradition initiated by Gause himself, most of the theoretical debate has been supported by the analysis of equilibrium states of Lotka Volterra like models (Huston, 1979; Loreau et al., 2001; Scheffer and van Nes, 2006). NEATS emphasizes the importance of intra-specific competition between predators as a factor of biological diversity. It may provide a different insight on the plankton paradox. It leads to consider that, due to some spatial heterogeneity, intra-specific competition of plankton species in the use of nutrients could be a key determinant of plankton dynamics. Going further, we may examine how this result could explain what is called the

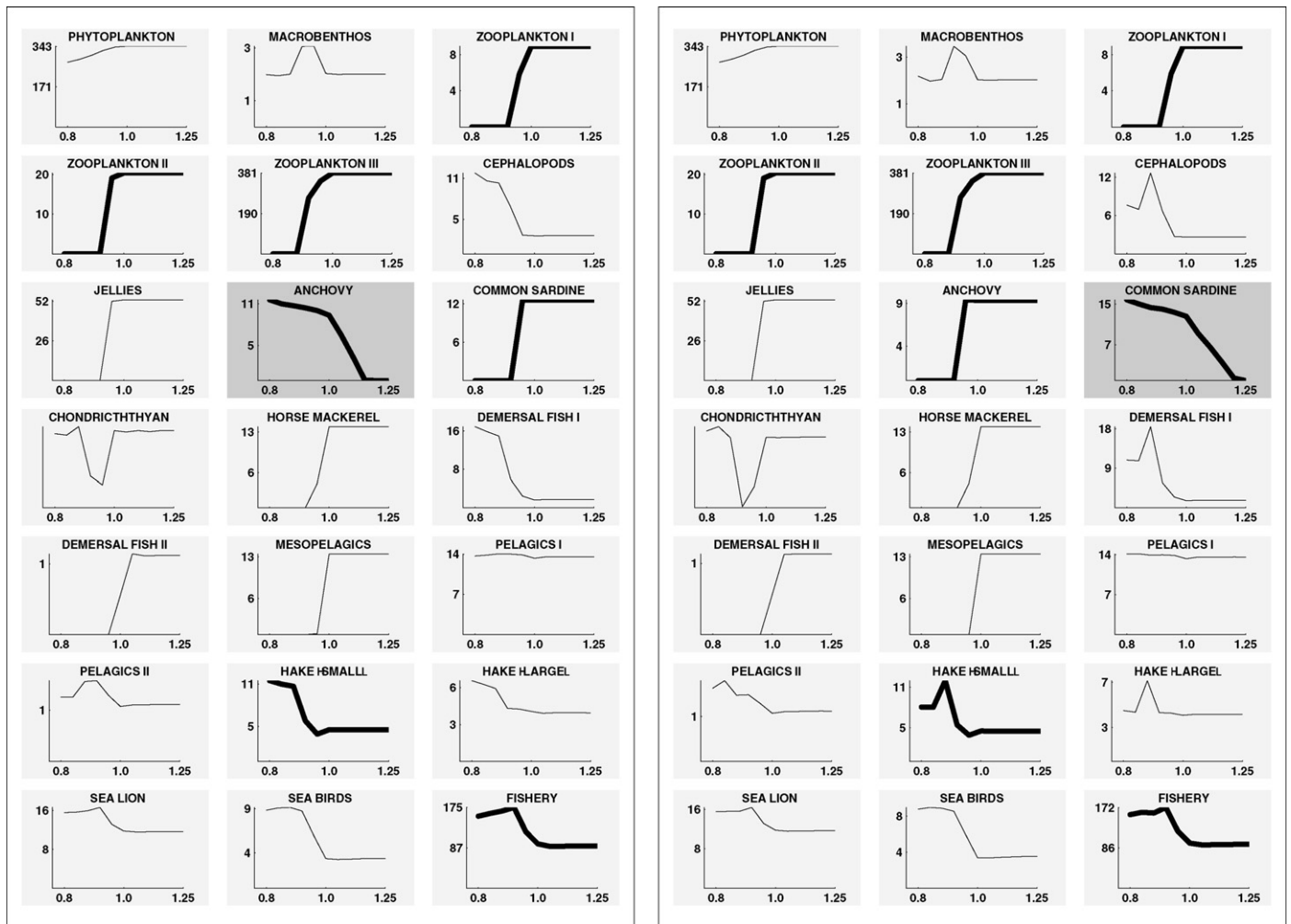


Fig. 10. Keystone species. For all plots: on x-axis, coefficients 0.8, 0.82, . . . , 1.11, 1.25; on y-axis, the biomass $B(k)$ in t/km^2 . The accessibility of tested species is multiplied by coefficients; the accessibility of its preys is divided by coefficients. Left panel: effects of changing environment of anchovy on the biomass of other species. Right panel: effects of changing environment of sardine on the biomass of other species.

wasp-waist pattern: in upwelling pelagic systems, there are few intermediate small pelagic species representing a high biomass (Bakun, 1996; Cury et al., 2000). Within our framework, we can attempt to relate these features to the propensity of pelagic fish to schooling. There have been many different ways to tackle the schooling question (Fréon and Dagorn, 2000). Here, we consider a hierarchy of prey–predator systems. At the plankton level (a common pool of resources, many plankton species): intra-specific competition may be important for plankton. At the pelagic level (many plankton species, few pelagic species): inter-specific competition between small pelagic fish may be predominant; schooling is interpreted as a limitation of intra-specific competition. At the carnivorous fish level (few small pelagic species, many carnivorous fish species): intra-specific competition may be more important. Thus, predation would be a factor of biological diversity: a predator limits the biomass of its prey. There are several predators due to intra-specific competition of predators and several prey due to differences in predation costs for predators. We have represented here the most common acceptance of the importance of top–down controls in the maintenance of biological diversity.

In the case of the Chilean coastal ecosystem, the analysis of simulations using NEATS gives an insight into the structure of a marine ecosystem, taking into account, for a predator species, the costs/advantages balance of predation, knowing that it depends on

prey abundance. The approach emphasizes the role of predation costs for a predator, the accessibility of prey, and intra-specific competition. These basic mechanisms allow us to replicate common observations of prey switching in nature.

The actual strength of NEATS consists in addressing, in a direct way, two important issues of ecological modelling. First, it allows representing discontinuous dynamics, shifts and collapses. Thus, it may in some instances appear more appropriate than conventional dynamical systems which often produce dynamical solutions that are too smooth. Secondly, it allows carrying out models of “intermediate dimensionality”. Mathematical theories are adequate to represent small dimension systems (less than 4 degrees of freedom) by dynamical system models, while very large dimension systems (millions of degrees of freedom) can be represented by tools of statistical physics. However, specificities of ecosystems imply to consider models ranging from 20 to 100 degrees of freedom, presenting discontinuous dynamics. With NEATS, we propose a model of intermediate complexity, allowing to define compartments with an adequate balance between simplicity and realism: the formalism is simple and natural, over-parameterization is avoidable, and computation is tractable. In addition, simulation results show that NEATS is able to tackle puzzling questions regarding the functioning of marine ecosystems such as the nature of their controls and the determination of keystone species.

Acknowledgements

We thank Sergio Neira, Lynne Shannon, Jorge Tam for providing us with data concerning the trophic structure of the Chilean, Peruvian and South Africa ecosystems, Pierre Fréon, Manuel Barange and anonymous referees for valuable comments and suggestions. We especially thank the students of the Summer School Dragerup 2006 for helpful remarks on a first presentation.

Appendix A

A.1. Mathematical proofs

We successively prove the following propositions:

Proposition 1. *The constrained set K is compact.*

One has $K = \{(X_{ij}) | X_{ij} \geq 0, \gamma_i(E_i + \sum_j X_{ji}) - \sum_j X_{ij} \geq 0\}$. These inequalities being linear, this defines a closed polyhedron. Let us prove that it is compact, i.e. bounded. We have $\sum_j X_{ij} \leq \gamma_i E_i$ for autotroph species and $\sum_j X_{ij} \leq \gamma_i \sum_j X_{ji}$ for other species. Thus, putting A the set of autotroph species,

$$\sum_{ij} X_{ij} \leq \sum_{i \in A} \gamma_i E_i + \sum_{i \notin A} \gamma_i \sum_j X_{ji}$$

All γ_i for $i \notin A$ are < 1 ; thus less than a value $\gamma < 1$; moreover $X_{ji} = 0$ for $i \in A$. Finally:

$$\sum_{ij} X_{ij} \leq \sum_{i \in A} \gamma_i E_i + \gamma \sum_{ij} X_{ji}$$

That is:

$$\sum_{ij} X_{ij} \leq \frac{\sum_{i \in A} \gamma_i E_i}{1 - \gamma}$$

This joined to $X_{ij} \geq 0$ implies that K is bounded; as it obviously closed, it is compact.

Proposition 2. *Let $F(X) = (F_{ij})$. Then $X \rightarrow F(X)$ is a linear function.*

We have (using that $E_j = 0$ for predator species j):

$$F_{ij} = \phi_{ij} - \kappa_i B_i + \lambda_j B_j = \phi_{ij} - \kappa_i \frac{1}{\mu_i} \left(\gamma_i \left(E_i + \sum_{j'} X_{j'i} \right) - \sum_{j'} X_{ij'} \right) + \lambda_j \frac{1}{\mu_j} \left(\gamma_j \sum_{k'} X_{k'j} - \sum_{k'} X_{jk'} \right) = \sum_{i'j'} M_{ij,i'j'} X_{i'j'} + N_{ij}$$

with

$$M_{ij,i'j'} = \frac{\kappa_i}{\mu_i} \delta_{i,i'} - \frac{\kappa_i \gamma_i}{\mu_i} \delta_{i,i'} - \frac{\lambda_j}{\mu_j} \delta_{j,i'} + \frac{\lambda_j \gamma_j}{\mu_j} \delta_{j,i'}$$

$$N_{ij} = \phi_{ij} - \frac{\kappa_i \gamma_i E_i}{\mu_i}$$

Proposition 3. *$X^* = (X_{ij}^*) \in K$ is an equilibrium if and only if $F(X^*) \cdot (X - X^*) \geq 0$ for all $X \in K$.*

Proof (Only if part). Let $X^* \in K$ an equilibrium state. Let $S = \{(ij) | X_{ij}^* = 0\}$. Then we have $F_{ij}^* = 0$ for $(ij) \notin S$ and $F_{ij}^* \geq 0$ for $(ij) \in S$. We deduce:

$$F(X^*) \cdot (X - X^*) = \sum_{(ij) \in S} F_{ij}^* (X_{ij} - X_{ij}^*) + \sum_{(ij) \notin S} F_{ij}^* (X_{ij} - X_{ij}^*) = \sum_{(ij) \in S} F_{ij}^* X_{ij} \geq 0$$

Thus, X^* is a solution of the variational inequality. \square

Proof (If part). Now, suppose that X^0 is not an equilibrium. Then, either (1) there exists $(i'j')$ such $F_{i'j'}^0 < 0$, or (2) there exists $(i'j')$ such $F_{i'j'}^0 > 0$ and $X_{i'j'}^0 > 0$.

First possibility: there exists $(i'j')$ such $F_{i'j'}^0 < 0$; as $F_{i'j'}^0 = \phi_{i'j'} - \kappa_{i'} B_{i'}$, we have $B_{i'} > 0$. Then, we consider a state X such that $X_{i'j'} = X_{i'j'}^0 + \epsilon$ and $X_{ij} = X_{ij}^0$ for $(ij) \neq (i'j')$. For ϵ small enough such a state is in K : slightly diminishing the predation of j' diminishes its biomass, but leaves it positive. And we have

$$\sum_{ij} F_{ij}^0 (X_{ij} - X_{ij}^*) = F_{i'j'}^0 (X_{i'j'} - X_{i'j'}^0) = -F_{i'j'}^0 \epsilon < 0$$

Thus variational inequality is not verified.

Second possibility: there exists $(i'j')$ such $F_{i'j'}^0 > 0$ and $X_{i'j'}^0 > 0$. We prove that this is impossible with a recurrence on the distance of j' to the way out (i.e. the top predator level). If j' is a top predator, we consider a state X such that $X_{i'j'} = -\epsilon X_{i'j'}^0$ and $X_{ij} = X_{ij}^0$ for $(ij) \neq (i'j')$. The inflow of j' is smaller, but the corresponding biomass of j' is still positive, for values of $\epsilon < 1$. Just as before it is clear that X provides a counter example to the variational inequality. Now, suppose that this part of the theorem has been proven for all links at a distance to the way out less than that of $i'j'$. We consider a state with $X_{i'j'} = \epsilon X_{i'j'}^0$ and all $X_{ij} = \epsilon X_{ij}^0$ for species $j = j'$ or species j upper than j' in the trophic chain. Then $X \in K$: for species upper than j' , inflow and outflow are multiplied by ϵ , thus biomass too; it remains positive. For species lower than j' , inflow and outflow do not change, thus biomass too. For j' , inflow remains the same, while outflow decreases, thus biomass increases and is still positive. We use the recurrence hypothesis: in the upper part, either $X_{ij}^0 = 0$, either $F_{ij}^0 = 0$, and we shows that the variational inequality is not verified

$$\begin{aligned} \sum_{ij} F_{ij}^0 (X_{ij} - X_{ij}^0) &= \sum_{ij, j \neq j'} F_{ij}^0 (X_{ij} - X_{ij}^0) + F_{i'j'}^0 (X_{i'j'} - X_{i'j'}^0) \\ &+ \sum_{ij, j > j'} F_{ij}^0 (X_{ij} - X_{ij}^0) \\ &= \sum_{ij, j \neq j'} 0 + (\epsilon - 1) F_{i'j'}^0 X_{i'j'}^0 \\ &+ \sum_{ij, j > j'} (\epsilon - 1) F_{ij}^0 X_{ij}^0 = (\epsilon - 1) F_{i'j'}^0 X_{i'j'}^0 < 0 \quad \square \end{aligned}$$

Proposition 4. *Solution set of the variational inequality is not empty.*

Proof. F is linear, hence continuous and K is compact. Then the theorem classically results from Brouwer's fixed point theorem (Nagurny, 1993, p. 14). \square

Now let us prove a theorem giving specific condition for the matrix M being definite-positive, that is such computation of equilibrium has good convergence properties.

Proposition 5. *$\sum_{ij,i'j'} M_{ij,i'j'} X_{ij} X_{i'j'} > 0$ for all X_{ij} if $\gamma_i \kappa_i = \lambda_i$ for all species i .*

Put $I_i = \sum_j X_{ji}$ and $O_i = \sum_j X_{ij}$ we have

$$\begin{aligned} \sum_{ij,i'j'} M_{ij,i'j'} X_{ij} X_{i'j'} &= \sum_i \left(\frac{\kappa_i}{\mu_i} O_i^2 + \frac{\lambda_i \gamma_i}{\mu_i} I_i^2 - \left(\frac{\kappa_i \gamma_i}{\mu_i} + \frac{\lambda_i}{\mu_i} \right) I_i O_i \right) \\ &= \sum_i \frac{1}{\mu_i} (\kappa_i O_i^2 + \lambda_i \gamma_i E_i^2 - (\kappa_i \gamma_i + \lambda_i) I_i O_i) \\ &= \sum_i \frac{1}{\mu_i} (\gamma_i I_i - O_i) (\lambda_i I_i - \kappa_i O_i) \end{aligned}$$

If $\gamma_i \kappa_i = \lambda_i$; then

$$\sum_{ij, i'j'} M_{ij, i'j'} X_{ij} X_{i'j'} = \sum_i \frac{\kappa_i}{\mu_i} (\gamma_i I_i - O_i)^2 \geq 0$$

A.2. Specific formulas for the model of competitive exclusion

In this specific case, we have

$$F_{ij} = \sum_{i'j'} M_{ij, i'j'} X_{i'j'} + N_{ij}$$

with $M_{ij, i'j'} = \delta_{ij'} \lambda_j / \mu_j + \delta_{i'i} \kappa_i / \mu_i$ and $N_{ij} = \phi_{ij} - \kappa_i \gamma_i E_i / \mu_i$. Then, we may use a classical result from variational inequality theory (Nagurney, 1993)[p. xxx]. M being obviously a symmetric matrix, one has: equilibrium is the solution of the following quadratic program: find $X \in K$ which minimizes $f(X) = (1/2)X^T M X + N^T X$. F is the gradient of f , and the derivative of F , that is matrix M is symmetric: $M_{ij, i'j'} = M_{i'j', ij}$. More over, the matrix M is semi-definite positive:

$$\begin{aligned} \sum_{ij, i'j'} M_{ij, i'j'} S_{ij} S_{i'j'} &= \sum_{ij, i'j'} \left(\delta_{ij'} \frac{\lambda_j}{\mu_j} + \delta_{i'i} \frac{\kappa_i}{\mu_i} \right) S_{ij} S_{i'j'} \\ &= \sum_j \frac{\lambda_j}{\mu_j} \left(\sum_j S_{ij} \right)^2 + \sum_i \frac{\kappa_i}{\mu_i} \left(\sum_i S_{ij} \right)^2 \geq 0 \end{aligned}$$

This monotonicity ensures the convergence of the modified projection algorithm we use (Nagurney, 1993, p. 57).

A.3. Parameterization

Table 1 has been obtained in the following way. Biomass B_i , flows X_{ij} , energetic input of autotroph species E_i , trophic assimilation efficiency γ_i , natural mortality rate μ_i are the results of a preliminary mass balance trophic model. Intra-specific competition λ_i is related to gregarious (schooling) behavior, thus at a lower value for mid trophic species (anchovies, sardines). According to the “strong equilibrium assumption”, we have $\kappa_i = \lambda_i \gamma_i$. And using the complementarity assumption, we have $\phi_{ij} = \kappa_i B_i - \lambda_j B_j$.

Appendix B. Supplementary Data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2009.02.008.

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