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TONIN Perrine

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Economic exploitation and dynamics of marine food webs

Influence of the price and body-size of the exploited fish

Abstract

Commercially exploited fish species are part of complex interaction webs, though most of the studies leading to fishery management only focus on small ecosystems. Moreover, traditional resource economics is almost entirely built on the concept of logistically growing resources. This view ignores that the fish standing stock size feeds back to its own carrying capacity through density-mediated indirect interactions. To study the declining productivity of fisheries and understand how human exploitation impacts ecosystem function, we modeled marine food webs using consumer-resource body-size ratios and non-linearities in feeding behavior. We started with the study of a simple food chain with economic exploitation of the top species, and then scaled up to more complex food webs with multiple exploited species.

Our results highlight a major difference between expectations based on the logistically growing populations and the less simplistic and more realistic, Allometric Trophic Network models: fishery exploitation at the optimum rate predicted by the logistic model results in the extirpation of a similarly parameterized species in our models. Regarding fish body size, our results suggest that the frequent effect of reduced fish body-size due to economic exploitation shifts systems from those optimized by more profitable fishing with less effort to those optimized by less profitable fishing with more effort. We also found more subtle results including "hydra" effects whereby fish standing stock and profit are counter-intuitively optimized simultaneously, and two categories of attractors. The initial conditions determine which attractor the system finds itself in. When effort is allowed to be determined by market mechanisms, one category of attractors can lead to extirpation of the fishes while the other category allows sustainable fisheries.

Résumé

Les poissons exploités commercialement font partie intégrante de réseaux écologiques complexes, bien que la plupart des études sur le management des pêcheries s'appuient sur de plus petits écosystèmes. En outre, l'économie des ressources naturelles se base presque intégralement sur le concept de la croissance logistique. Ce modèle ignore le fait que la taille des stocks de poisson exerce une rétroaction sur sa propre capacité de charge, via des interactions indirectes densité-dépendantes. Afin d'étudier le déclin de la productivité des pêcheries et de comprendre l'impact humain sur ces services éco-systémiques, nous avons modélisé des réseaux trophiques marins en utilisant des relations allométriques entre ressources et consommateurs, ainsi que des comportements de prédation non-linéaires. Après avoir étudié une petite chaîne alimentaire avec exploitation économique du superprédateur, nous avons augmenté en complexité jusqu'à la pêche de plusieurs espèces au sein de gros réseaux trophiques.

Nos résultats ont révélé une différence majeure entre le modèle à croissance logistique et notre modèle Allometric Trophic Network, plus complexe et aussi plus réaliste. Une pêcherie dont l'exploitation est optimisée selon le modèle logistique induit la disparition de l'espèce pêchée dans nos modèles. En ce qui concerne la taille du poisson, nos résultats suggèrent que l'effet fréquemment observé de la diminution de la taille liée à l'exploitation économique fait passer d'un optimisation avec une pêche très rentable et un effort faible, à une pêche moins rentable et un effort plus important. Nous avons aussi mis en évidence des phénomènes plus subtils, dont l'effet "hydre" qui permet d'optimiser simultanément le stock de poisson et le profit, ainsi que deux catégories d'attracteurs pour lesquels les conditions initiales permettent de choisir dans quel bassin d'attraction le système va se placer. Lorsque l'effort est déterminé par des mécanismes économiques, l'une des catégories d'attracteurs peut conduire à la disparition des espèces tandis que l'autre permet une pêche durable.

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Chapter 1

Introduction

We lack basic information on the dynamics of social-ecological systems and the relationships of ecosystem services to human well-being. (Carpenter *et al.* 2009)

The great challenges to ecosystems, which provide services critical for human life on Earth, are increasingly well recognized. Climate change, biodiversity loss and habitat degradation due to human activity are chief among these challenges (Rockstrom *et al.* 2009). Some immediate and dramatic results of these perturbations are the loss of species native to ecosystems (Hughes *et al.* 1997), the invasion of ecosystems by species alien to them (Williamson 1996) and the declining productivity of fisheries (Worm *et al.* 2009). How such changes impact the composition and productivity of ecosystems, leading to further losses of biodiversity and human welfare as well as changes in ecosystem function, are much less well understood (Carpenter *et al.* 2009). Humans and ecosystems clearly form complex highly interdependent systems, but we poorly understand how this interdependence plays out in the context of rampant global change (Liu *et al.* 2007). NSF's Advisory Committee on Environmental Research and Education (2010) emphasized that NSF's Strategic Plan 2006-2011 directive "to strengthen our understanding of the links between human behavior and natural processes" is "not progressing at the rate required by the magnitude and urgency of the environmental challenges that face this nation and all societies."

Juxtaposed against this need for knowledge of coupled human-natural systems is a rapidly expanding understanding of ecological networks describing the structure and function of biodiversity within natural systems (Pascual & Dunne 2006). It is only within the last several years that the central stabilizing forces of consumer-resource body-size ratios (Brose *et al.* 2006, Otto *et al.* 2007), non-linearities in feeding behavior (Williams & Martinez 2004, Gross *et al.* 2009), and network architecture (Martinez *et al.* 2006, Otto *et al.* 2007, Gross *et al.* 2009) have been discovered. This in turn has allowed simulations of complex ecological networks to be applied to understanding human impacts including species loss (Brose *et al.* 2005, Berlow *et al.* 2009) and invasion (Romanuk *et al.* 2009) combined with issues such as nutrient pollution (Brose *et al.* 2005).

Such applications focus on the symptoms of human impacts on ecological systems without addressing the mechanisms of human behavior behind these impacts. Probably the most powerful of such mechanisms are economic, especially when the impact concerns the extraction of biomass for financial gain including industries such as forestry, biofuels and fisheries. Recent work on human impacts on ecosystems have begun to shift attention from ecological to economic aspects of these systems. For example, a widely accepted hypothesis is that fisheries are serially depleted moving down the food web from exploiting species at higher trophic levels before pro-

ceding to exploiting lower trophic level species. The recent creation of a global database on fish landings and prices (Sumaila *et al.* 2007) enabled researchers to replace that hypothesis with harvest pressure being primarily driven by the difference between revenues and extraction costs i.e., profits (Sethi *et al.* 2010). As these researchers have suggested: "for successful fisheries management, it will be necessary to move beyond the symptoms of fishing and to take into account drivers of harvest pressure." (Sethi *et al.* 2010).

Within this context, our study performs foundational research on ecological and economic aspects of ecosystems. Previous foundations are almost entirely built on the concept of logistically growing resources such as species populations. This model of growth asserts a constant carrying capacity that constrains the intrinsic growth rate of a populations depending how close the population is to its carrying capacity. While much current theory uses the logistic model for species such as plants at the base of ecological networks, most species at higher trophic levels such as fishes are currently modeled by making their capacity for growth depend on food resources which vary in time as opposed to logistic populations with constant carrying capacity. Furthermore, newer dynamic models of species populations scale up to complex networks that more realistically model natural ecosystems. However, resource economists have yet to embrace these new models of resources partly due to their newness, to the field inertia and partly due to the non-linearity of these models which prevents a complete and rigorous mathematical analysis.

I conducted my internship with an interdisciplinary ecologist who pioneered the new ecological approach through complex networks. We initiated this research building a simple model, amenable to a complete analysis: a bio-economic three-species "food chain" model that incorporates recent advances in ecology concerning body-size ratios and feeding non-linearities. Then we scaled up to more complex food webs, less amenable to thorough analysis yet still informed by insights from the simpler one. While the food chain models included economic exploitation - managed through quotas or market driven - of only one species, the food web models include economic exploitation of multiple species. Ecosystem services, usually difficult to quantify and communicate, are measured in terms of economic effort and revenue, notoriously easier to quantify in terms of profit and employment respectively.

Chapter 2

Three species food chain

2.1 Methods

2.1.1 Model structure

We analyzed a 3-species food chain consisting of an autotroph grazed by an herbivore which is eaten by a carnivore. We subjected this system to one of three basic scenarios: 1) no economic exploitation (pristine scenario), 2) fixed exploitation effort (managed scenario), first with fixed prices, then with three models of price as a function of the harvest and 3) variable exploitation effort of the top species that increases with fishery profit and decreases with fishery loss (market driven scenario), for prices either fixed or as a linear function of the harvest. Following Brose *et al.* (2006), the dynamics of species biomass densities is governed by consumer-resource equations where the growth rates are based on species metabolic rates which are size-dependent: small animals have high metabolic rates while large animals have a relatively slow metabolism. This Allometric Trophic Network model (ATN) was synthesized with Conrad's (1999) governing equation that model changes in economic exploitation effort as a function of cost of effort and price of biomass extracted:

$$
\begin{cases}
\dot{B_B} = r(1 - \dfrac{B_B}{K})B_B - x_I y_{IB} B_I \dfrac{F_{IB}}{e_{IB}} & (2.1) \\[2ex]
\dot{B_I} = -x_I B_I + x_I y_{IB} B_I F_{IB} - x_T y_{TI} B_T \dfrac{F_{TI}}{e_{TI}} & (2.2) \\[2ex]
\dot{B_T} = -x_T B_T + x_T y_{TI} B_T F_{TI} - q B_T E & (2.3)
\end{cases}
$$

$$
F_{ij} = \frac{B_j^h}{B_0^h + B_j^h} \tag{2.4}
$$

Eq. 2.1 describes the changes in the biomass density of the population of the autotroph (B_B), whereas eq. 2.2 and 2.3 describe the changes in the biomass densities of the herbivore (B_I) and carnivore (B_T). In these equations, r is the mass-specific maximum growth rate of the basal species, K is its carrying capacity, x_i is species i's metabolic rate, y_{ij} is the maximum consumption rate of consumer i when consuming species j, relative to its metabolic rate, e_{ij} is the assimilation efficiency of consumer i when consuming species j. The functional response, F_{ij}, describes the realized fraction of species i's maximum rate of consuming species j. We used a weak Holling-type III functional response (eq. 2.4., Williams & Martinez 2004, Brose *et al.* 2006). In the economic exploitation model (eq. 2.5), q is the catchability coefficient (expressing the biomass per volume extracted from population i per unit effort) and E_i is the exploitation effort directed at the population of the carnivore ($E_B = 0$, $E_I = 0$ according to scenarios, see

"Parameterization and sensitivity analysis"), e.g. the number of fishing boats operating. Their multiplication gives the fraction of population exploited.

The variable exploitation scenario similar to an open access fishing regime is modeled as (Conrad 1999):

$$\dot{E} = \mu(pqB_T - c_o)E \tag{2.5}$$

where E is fishing effort for the top species, p is the price per unit catch, q is the "catchability coefficient", B_T is the biomass density of the top species, c_o is the cost per unit effort, and μ is the economic flexibility which describes how fast the effort changes based on profit or loss. As long as the fishery is at least partially open ($\mu > 0$), E increases if the difference between income (pqB_TE) and cost (Ec_o) is positive indicating profit and decreases when negative indicating loss. Allowing E to vary allows the fishery to seek its bioeconomic equilibrium that occurs when its income equals its costs.

In both the fixed effort and variable exploitation scenarios, we considered variable p as three different functions of catch ($Y = qE_iB_i$) to model the influence of variable supply and demand on p (**Conrad**):

- linear: $p = a(1 - bY)$
- isoelastic: $p = aY^{-b}$
- non-linear and non-isoelastic: $p = \dfrac{a}{1 + bY}$

In all models, b quantifies the sensitiviy of the price to the harvest. In the linear model, a is the maximum p which only reached when $Y = 0$ and p decreases as Y increases until $Y \geq 1/b$ when $p = 0$. With the isoelastic model, $p \to \infty$ when $Y \to 0$ and $p \to 0$ when $Y \to \infty$. The third model is non-linear as is the isoelastic model but prevents p from approaching ∞ or zero.

2.1.2 Parameterization and sensitivity analysis

We used the above model to explore three basic scenarios for the food chain; 1) "pristine" with no exploitation, 2) "managed" with fixed exploitation rate, and 3) "market driven" with variable exploitation. Within each scenario, we explored the effects of varying fish body size by varying the fishes metabolic rate x_T. Within the exploitation scenarios, we also explored the effects of fixed and variable prices p using 3 prices models described above.

Table 2.1 describes the values and units of the ecological parameters which are either chosen to represent realistic values for aquatic communities (K, r, M, e_I) or are based on earlier studies on allometric food web dynamics (y, e_T, Yodzis & Innes 1992, Brose *et al.* 2006). The value of y was slightly modified to fit aquatic communities better (Boit *et al.* in prep.). In the scenario lacking exploitation, the values of K and r are varied instead of being assigned as given in Table 2.1. If unspecified, collections of initial biomass densities were chosen from a uniform distribution in the ranges $B_B =$5-500, $B_I =$2-200, $B_T =$1-100 $\mu gC/L$. Extraction costs are fixed ($c_o = 1$) so that the price is seen as compared to the costs.

In 1) the pristine scenario, we explored how the metabolic rates of the herbivore and the carnivore affected the biomass density of the carnivore. In preliminary model runs we tested the range 0.02-0.2 d^{-1} for both the herbivore and the carnivore which are plausible values for the size range of zooplankton and fish (de Castro, in prep.). Since varying x_T in the range 0.08-0.2 d^{-1} had little effect on final biomass densities, we only present results for varying x_I in the range of 0.02-0.2 d^{-1} and x_T from 0.02-0.08 d^{-1}. We also varied the values of K and r in the range of 200-900 $\mu gC/L$ and 0.3-2.1 d^{-1}, resp., at the same time.

In 2) the managed scenario, we set catchability to 1% and varied effort between $E = 1 - 100$. The metabolic rate of the herbivore, x_I was set to 0.15 and x_T was varied among 0.02, 0.04, and 0.08. We analyzed biomasses and drew a comparison with a one-species logistic-growth

Table 2.1: Ecological parameterization

Name	Description	Unit	value	Reference
K	Carrying capacity of basal species	$\mu gC/L$	450	
r	Basal species growth rate	d^{-1}	1.1	Boit *et al.* in prep.
y_{ij}	Maximum grazing rate of consumer i relative to its metabolic rate	d^{-1}	10	Boit *et al.* in prep.
e_{ij}	Assimilation efficiency for carnivores / herbivores	-	0.85 / 0.66	0.85: Yodzis & Innes 1992; 0.66: Nielsen & Olsen 1989
B_0	Half-saturation density of j when consumed by i	$\mu gC/L$	80	Muck & Lampert 1984
h	Hill exponent	-	1.2	Williams & Martinez 2004

List of ecological parameters and their description. The parameters not listed were varied across the simulations (see Methods).

model, whose carrying capacity K was estimated as top species biomasswithout extraction, and whose intrinsic growth rate was $r = x(y-1)$, which corresponds to $F = 1$. We then analyzed profit using our four price scenarios, fixed and variable, each time for extraction costs negligible and non-negligible compared to the price (resp. $p > 10$ and $p \simeq 1$, with $c_o = 1$). For variable price scenarios, we explored the influence of the price sensitivity to rarity with different values of b coefficient: between 0 and 1 for linear prices, 0 and 10 for isoelastic prices and between 0 and 5 for non-linear and non-isoelastic prices.

In 3) the market driven scenario, we allowed the effort to change based on profit. With the fixed price model, there was a threshold for the initial conditions over which the whole resource was depleted. We studied the influence of the economic and biological factors on this threshold. Then we varied μ, q, p and x_T while keeping the other parameters constant at their values in Table 2.1 and the initial conditions so that the top species cannot be depleted. In each simulation, we varied μ between 0.01 and 0.3, q between 0.005 and 0.02, x_T among 0.02, 0.04, 0.08 and p between 1 and 200. The relative range of price tested is much wider than that of the other parameters as price is the least constrained by physical factors and is, therefore, hugely variable. Initial effort was set as in the constant effort scenario above. For each set of parameters, we ran 40 simulations and took the means and the standard deviations of biomasses and effort over these simulations.

With the variable price scenario, we only studied the linear model because it prevents the price to reach the infinity when the harvest reaches zero. Thus, it cannot describe the luxury economies for which it is always possible to find someone ready to pay more than the increasing extraction costs (Courchamp *et al.* 2006), but rather describes common fishing ecnomies. We first looked at the behavior of the biomasses and the effort over time and highlighted multiple attractors (equilibria and limit cycles). Then we quickly studied the influence of the initial effort and the initial top species biomass on the reached equilibrium. Finally, we varied the maximum price a between 0.5 and 100, the price sensitivity b among 0.01, 0.05, 0.1, 0.5, and the top species metabolic rate x_T among 0.02, 0.04, 0.08. The other parameters were set to $\mu = 0.3$, $q = 0.01$, $x_I = 0.15$. The initial conditions for the basal and intermediate species biomasses were randomly chosen. The initial top species biomass was chosen between 1 and 600 $\mu gC/L$ and the initial effort 1 and 100, to be sure to see, when relevant, the multi-equilibria for the whole range of realistic values. For each set of parameters values and effort/top species initial conditions, we ran 10 simulations and took the mean over these simulations. We analyzed the equilibrium effort and top species biomass to see the influence of body-size, price sensitivity and maximum price.

We conducted 30000 simulations, each lasting 5000 times steps for each of the scenarios, but

the last one, among all the various parameters choices. For the variable effort and linear price scenario, each simulation was conducted over 2000 time steps for equilibrium and permanent regimes were achieved quicker. Our analyses focused on the overall dynamics arising and the means of specific variables (biomass density, profit) during the last 400 of the 5000 (or 2000 for the last scenario) time steps. Previous analyses of similar models demonstrated that 1000 time steps are sufficient for the transients to disappear (Brose *et al.* 2006, Berlow *et al.* 2009). Among our simulations, no large, slow oscillations emerged which might have motivated analyses of more than the last 400 steps.

All simulations were performed in Matlab version 6.5 and 7.10 using solver ode45 for ODEs with the default settings, as after a preliminary tolerance test we concluded that it is not necessary to adjust the relative error tolerance or maximum step size.

2.2 Results

2.2.1 The pristine scenario

Without exploitation, the highest biomass on the third trophic level is supported if the ratio x_T/x_I is around 0.2 (results not shown). The plant and the herbivore biomasses are independent of the metabolic rate of the top predator, which only affects its own biomass density. An implication is that the relationship between the ratio of top species / mesoconsumer metabolic rates we see in our set-up is independent of the number of trophic levels in the chain, as it is not a consequence of cascading effects in the food chain.

Fisheries might decrease the body mass of the exploited fish with up to a factor of 3 (Chapman & Kramer 1999). This corresponds to a top-intermediate species metabolic rate ratio of 0.27. This shifts the system into a parameter range where the biomass density of the top species is decreased by 75%. The biomass density of the top species nonlinearly changes with the ratio of metabolic rates in the relevant parameter range, so changing the body size of fish has disproportionately large effects on its biomass density.

The growth rate of the primary producer and its carrying capacity did not have a substantial influence on the biomass densities at the end of the simulations within the parameter range $0.3 < r < 2.1d^{-1}$, $200 < K < 900\mu gC/L$. The system showed stable equilibrium dynamics for all ranges of parameters.

2.2.2 The managed scenario

2.2.2.1 Analysis of the biomasses

The shape of the relationship between the fraction of biomass harvested and the biomass density of the three populations is the same for all three levels of metabolic rates (x_T) tested (Fig. 2.1). Very low fraction harvested results in a slight decrease in the population density and the system tends towards an equilibrium as without exploitation (dynamic regime 1). In the range of slightly higher exploitation rates, the biomasses of all three species reach a limit cycle and the means of carnivore and herbivore biomass densities are higher than their levels at zero exploitation rates (regime 2). Further increasing the harvested fraction results in more complex permanent oscillations and a decrease of the mean population densities of the carnivore but the herbivore density still increases (regime 3). For slightly higher extraction rates, the biomasses reach equilibria and all the species biomasses decrease (regime 4). Finally, at even higher exploitation rates the exploited top species goes extinct and the two other species reach a 2D equilibrium (regime 5). For all regimes, the autotroph species density always decreases when the harvested fraction of the carnivore increases.
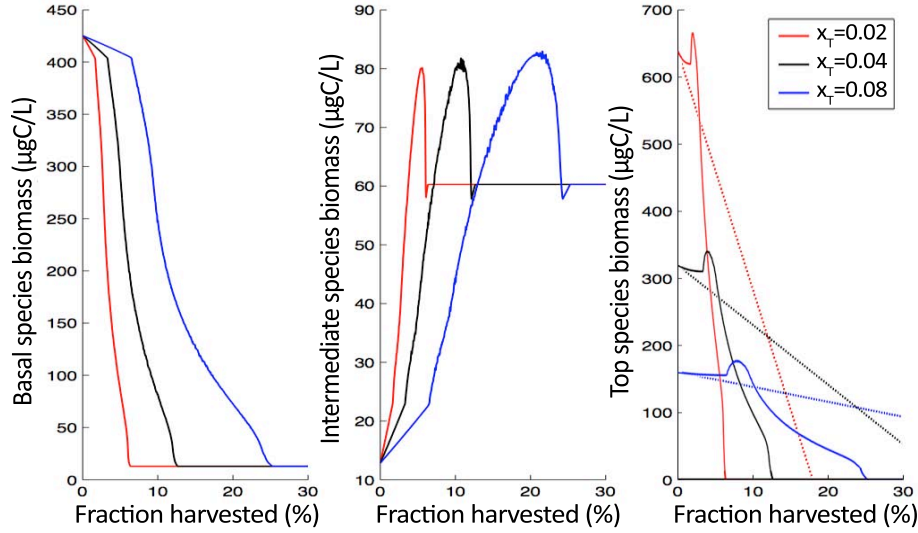
Figure 2.1: Biomasses for the three species in the constant effort scenario, in function of the fraction of the extracted rate of top species biomass, for our three species model where the top species is extracted (solid line) and in the case of a one-species with logistic growth model (dotted line). Parameters are set as in Table 2.1, with $x_I = 0.15$ and $x_T = 0.02$ (red line), 0.04 (black line) & 0.08 (blue line). We calculated the equilibrium / average biomasses over the last 400 of 5000 time steps. The irregularities of the solid curves are due to the fact that we calculated the mean values of the biomasses over a time period of 400 time steps which is not a multiple of the period of the permanent oscillations.

The maximum of top species biomass is not achieved for a zero harvest: regime 2 shows an increase of its density as a response of an increase of its mortality (hydra effect, Abrams 2009). Because a higher exploitation rate on the carnivore involves a lower grazing pressure on the herbivore, this allows the mesoconsumer population to increase and consequently increases the top species growth rate more than what is needed just to counterbalance the higher exploitation rate. For higher fraction of harvested biomass (regime 3), the herbivore still proliferates thanks to the grazing pressure decline, but this supplement of food for the top species does not increase anymore its growth rate enough to counterbalance the loss due to extraction. The hydra effect occurs then for the mesoconsumer, for the same reasons as previously with the top species. There is no hydra effect for the basal species because its nutrient amount is fixed through its logistic growth behavior. In our model, hydra effect occurs only when the system reaches permanent oscillations, that allow the functional responses to oscillate alternatively over a significant range. Such a behavior allows the top species biomass to reach very high values, so that its mean over time is higher than without harvesting.

The threshold exploitation rates where a change occurs in the dynamic regime depends on the metabolic rate of the top species. Under the oscillating biomass regimes (2-3), at a given exploitation rate, the mean biomass density of the herbivore decreases when x_T increases. Because the grazing pressure on the mesoconsumer is higher when x_T is higher, a higher exploitation rate is needed to counterbalance it. Therefore, the range of exploitation rates where the hydra effect occurs is also higher. So with big harvested fish (i.e. low x_T), the hydra effect occurs for small exploitation rates and the top species is very sensitive to an increased effort (Fig. 2.1). With smaller carnivore fish, the hydra effect occurs for higher fraction of biomass harvested and the biomass density of the top species is less sensitive to increasing harvest (Fig. 2.1).

We compared the top species biomass of our model to the theoretical biomass of an isolated species following a logistic growth function (Fig. 2.1, dotted line). Before the hydra effect occurs, for low harvested fraction of biomass, the one species logistic growth model slightly underestimates the equilibrium biomass, but the most important difference is in the maximum fraction harvested before the species goes extinct: at the exploitation rate for which the harvested
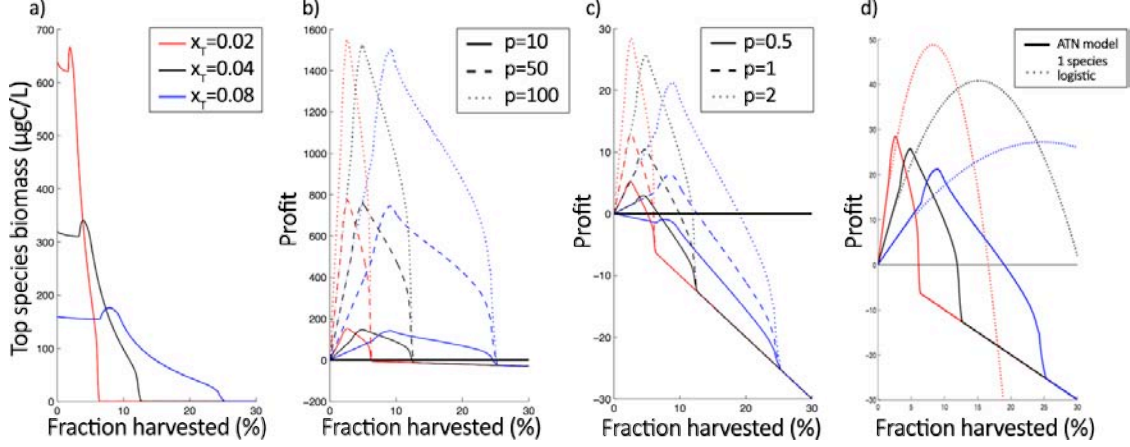
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Figure 2.2: Top species biomass (a) and profit in function of the percentage of top species harvested, in the constant effort scenario, for 3 metabolic rates and fixed prices when extraction costs are negligible (b) and when they are not (c). Parameters are set as in Table 2.1, with $x_I = 0.15$ and $x_T = 0.02$ (red line), 0.04 (black line) & 0.08 (blue line). We calculated the equilibrium / average biomasse and profit over the last 400 of 5000 time steps. Panel d) draws the comparison between the profit when p=2, for our ATN model (solid line) and the one species with logistic gowth model (dotted line).

species is depleted in our three species model, the biomass of the isolated species with logistic growth is about 2/3 of its maximal value. So the harvested species is much more sensitive to a change of the exploitation rate than what could be assumed from a simpler model.

2.2.2.2 Analysis of the profit

The shape of the relationship between the fraction of biomass harvested and the profit of the fishery is similar for all three levels of metabolic rates tested (Fig. 2.2), whatever price model we choose. So we analyzed the influence of body size only for the fixed price scenario. For variable price models, results are shown only for the intermediate body-size $x_T = 0.04$.

Fixed price scenario

Increasing the fraction harvested initially results in increasing profit of the fishery (Fig. 2.2). However, further increasing the fraction harvested results in decreasing profit due to the decrease or collapse of the fish stock. A notable feature is the maximum sustainable profit which occurs when the harvested fish biomass is maximal.

For very high prices ($p \gg c_o$ Fig. 2.2.b.), the range of profitability is about ten times wider for small fishes and the optimum profit is almost the same for the three metabolic rates. So harvesting small fishes allows a high profit and a wider range of profitability. When the price about equals the cost of effort (Fig. 2.2.c.), maximal profit is higher for big fishes than for small ones. However, the fishery becomes unprofitable at a lower exploitation rate. The range of profitability is no more than twice bigger for small fishes than for big ones. So fisheries have to choose between high profit with big fishes or high employment with small fishes.

The most important difference between the results from our ATN model and those from the isolated species with logistic growth model (Fig. 2.2.d.) is that when the profit should be maximal according to the simple one species logistic growth model, the harvested species has already been wiped out according to our model. The simpler model also overestimates the maximum profit to make with such a fisheries, and an increase of the metabolic rate decreases more the maximum profit within the simpler model than within the ATN model.
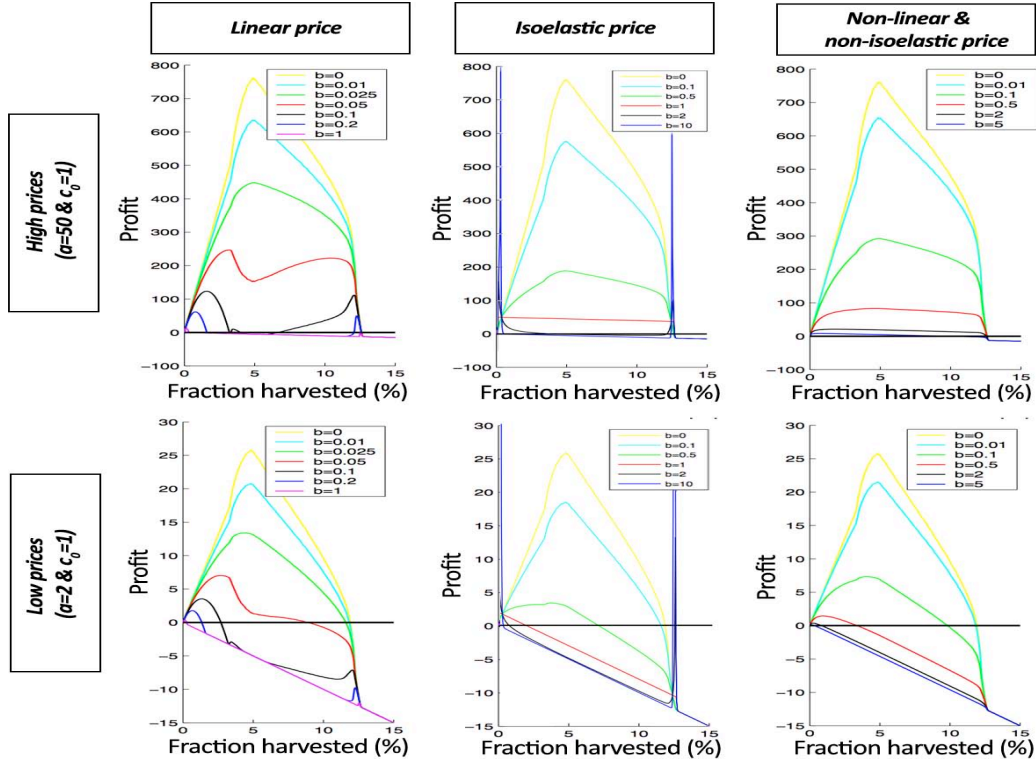
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Figure 2.3: Profit as a function of the harvested fraction of top species biomass, in the managed fisheries scenario, with $x_I = 0.15$ and $x_T = 0.04$, and for the three variable price models: linear (left column), isoelastic (middle column) and non-linear & non-isoelastic (right column). We analyzed two cases: when extraction costs are negligible compared to the price ($a = 50$ & $c_o = 1$, first row), and when they are not ($a = 2$ & $c_o = 1$, second row). We studied the influence of b, the price sensitivity on rarity within each price model. Parameters are set as in Table 2.1. We calculated the equilibrium / average profit over the last 400 of 5000 time steps.

Variable price scenarios

In the linear price scenario (Fig. 2.3, left column) and for a low sensitivity of price ($b \leq 0.025$) profit is just reduced compared to fixed price scenario. For a higher sensitivity ($b > 0.05$), the profit curve shows two peaks, either for a very low effort or for a top species on the verge of extinction. With very high prices (Fig. 2.3, first row where $a \gg c_o$), both peaks are profitable. When the price about equals the cost of effort (Fig. 2.3, second row where $a \simeq c_o$), only the first peak is profitable, favorizing low employment rather than much endangered species. The strange shape of the profit, when $b = 0.1$ and the exploitation rate is between 3% and 5%, is due to the permanent oscillations of the top species biomass around the value for which price reaches zero.

In the isoelastic price scenario (Fig. 2.3, middle column), the profit behavior is similar to the one with linear price model. However, two major differences appear: for $b = 1$ the profit is linear and equals to $(a - c_o E)$, and for $b > 1$, the profit peaks reach the infinity.

In the non-linear and non-isoelastic price scenario (Fig. 2.3, right column) and for a low sensitivity of price ($b \leq 0.1$) profit is just reduced compared to fixed price scenario. For a high sensitivity ($b \geq 0.5$), there are no peaks anymore, but just an almost linear profit $\sim (a/b - c_o E)$. For negligible extraction costs (Fig. 2.3, first row where $a \gg c_o$), fishing is then always profitable. With non-negligible extraction costs (Fig. 2.3, second row where $a \simeq c_o$), only low employment is profitable.

The three variable price models give almost the same results on the whole. For low and medium sensitivities of price to rarity, the maximum is reach when top species biomass is max-

imal. To sum up, with a high sensitivity of price to rarity, negligible costs lead to two peaks of profitability (low employment or endangered top species) for all price models but the last one. Non-negligible costs, however, lead to only one peak of profitability (when effort is very low) with all price models. Moreover, it seems that the linear model, though simple, encompasses the overall results, as well as the more complex isoelastic model, and if costs are not negligible, as well as the most realistic non-linear/non-isoelastic model. This is why we decided to later limit the study of variable effort and price scenario to the linear price model. Nevertheless, more differences should be expected between the three price models in the open access scenario, because there is a feedback of the price on the biomasses, which does not occur when the effort is fixed.

2.2.3 Open access exploitation with fixed price

2.2.3.1 Initial conditions threshold to prevent depletion

With high prices ($p > 50$) and a given range of high initial top species biomass, a total resource depletion was often observed. The study of the influence of price, catchability and extraction costs on the top species initial biomass threshold, above which depletion occured, highlighted a link between the depletion threshold and the marginal initial profit (i.e. profit per unit of effort), which is:

$$\frac{\partial \Pi}{\partial E} = pqB_T - c_o \tag{2.6}$$

For an initial marginal profit above the threshold, the fishery will deplete the resource because there is so much money to make that the equivalent of gold rush occurs. The top species has no opportunity to recover and crashes down. The other economic and biological parameters, such as body-size and openness of the market, influence also the threshold.

The influences of the openness and the basal and intermediate species initial biomass are not easily understandable. However, they do not change significantly the threshold. We decided then to minimize the depletion threshold over all the observed values. The initial effort had an influence only when the system was already close to the threshold, with a carnivore biomass at $\pm 1 \mu g C/L$ around the threshold. Finally, the metabolic rate did not have any influence of the depletion threshold. Given the fact that the extraction costs were always set to $c_o = 1$, we then set the non-depletion condition to:

$$pqB_T(t = 0) < 10 \tag{2.7}$$

Thus, the price allocation is very important when a new fishing economy is created. For example, with a catchability around 1%, an initial stock of fish of $10 \mu g C/L$ (resp. $100 \mu g C/L$ and $500 \mu g C/L$) would not allow a price per unit of catch higher than 100 (resp. 10 and 2). Without fish extraction and with the body-sizes we considered, the top species biomass hardly exceeds $650 \mu g C/L$. So, in the worst case, the price should not be higher than 1.5. Thus, the system is always out of extinction risk only if extraction costs are not negligible.

2.2.3.2 Typical behavior over time - influence of body-size and price level

The top species metabolic rate and the price level have an influence on the system dynamics (Fig. 2.4). The frequency of the oscillations of the transient, and eventually of the permanent regime, increases with the top species metabolic rate because big fishes cannot eat fast and then slow down the system dynamics.
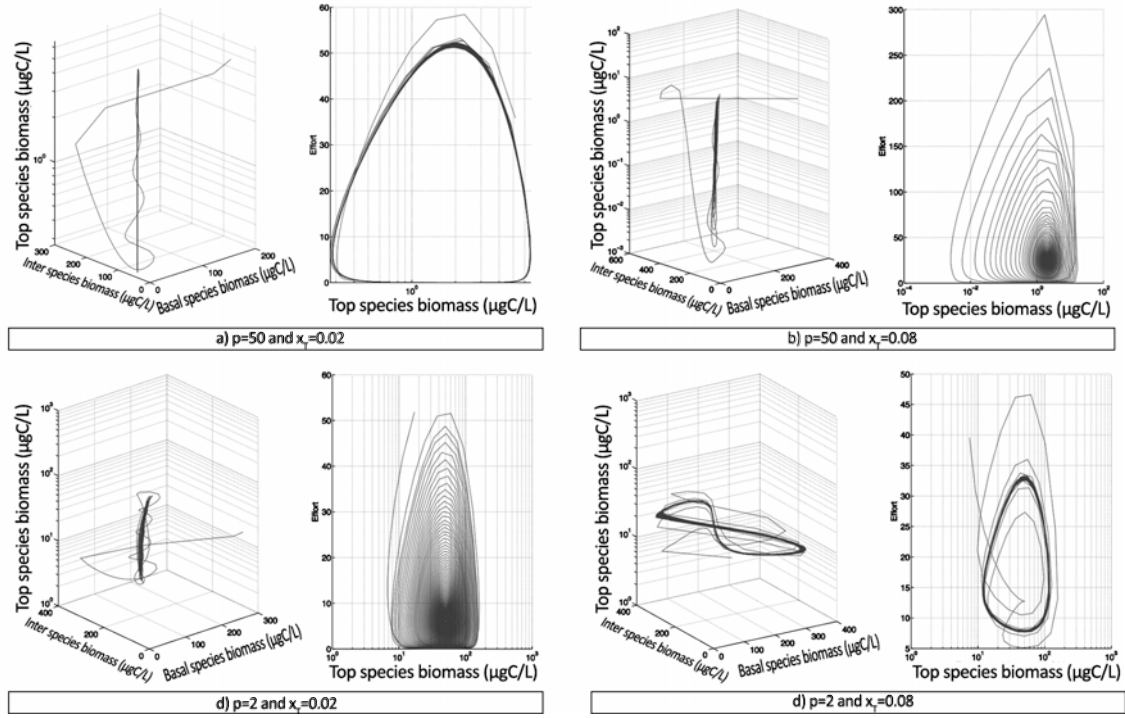
Figure 2.4: Phase diagrams over 5000 time steps of the three biomasses (3D curves), and of the effort and the top species biomass (2D curves), in the market driven scenario with fixed prices, for $\mu = 0.3$, $q = 0.01$ and $c_o = 1$. Extraction costs are either negligible ($p = 50$, a. & b.), or not ($p = 2$, c. & d.). Initial biomasses and effort were chosen randomly, taking into account the depletion threshold for the initial top species biomass. Simulations for two top species metabolic rates: x=0.02 (a.&c.) and x=0.08 (b.&d.). Parameters are set as in Table 2.1, with $x_I = 0.15$.

When price is high and top species metabolic rate low (Fig. 2.4.a.), gold rush phenomenons occur periodically, so that the resource is almost depleted and takes lots of time to recover from the periodic harvest. The mean top species biomass is always low and its fluctuations do not have a strong impact on the other two species biomasses. In this case, the systems dynamics is mainly determined by the economy: effort and top species biomass are then two coupled oscillators.

When price and x_T are high (Fig. 2.4.b.), gold rushes also occur. But x_T is high enough to have an impact on the other biomasses. In this case, economy still drives this dynamics, but the carnivore biomass is also coupled with its food biomass. The frequencies of the two groups of coupled oscillators differ. The interferences dampen the oscillations and the system reaches an equilibrium.

For low price and low x_T (Fig. 2.4.c.), the mean top species biomass is always high, since the economic condition of zero profit $B_T = c_o/pq$ is high. Gold rushes occur, though the resource is never in jeopardy. The carnivore biomass is high enough to have a strong impact on the two other biomasses. Top species biomass is then coupled with the economic effort on the one hand, and on the other hand with the autotroph and herbivore biomasses. The frequencies are different, so the oscillations are dampened and the system reaches an equilibrium.

For low price and high x_T (Fig. 2.4.d.), the carnivore mean biomass is always high and it can eat so fast that the magnitude of the biomasses oscillations are even bigger for the two other species than for the carnivore. After a short transient period, the effort and the three biomasses oscillate at the same frequency. The four state variables are then coupled and allow the system to reach a permanent oscillating regime.

2.2.3.3 Influence of economics and body-size on the mean/equilibrium values

In this scenario, we studied the influence of the openness μ, the catchability q and the price per unit of catch p, on the asymptotical average of the three biomasses and the effort (Fig. 2.5). No hydra effect was highlighted in this scenario because the effort adjusts itself to the biomass and consequently an increased biomass due to an increased mortality would only involve an even higher mortality (i.e. effort).

The harvested species biomass is always independent of its metabolic rate (Fig. 2.5.a.), whereas the others biomasses and the effort strongly depend on the top species body-size. This is due to the equilibrium condition for a top species biomass equilibrium $B_T^* = c_o/(qp)$, which is only driven by economics, and not the biology. The carnivore metabolic rate appears however in the others equilibrium equations.

As with fixed effort scenario, smaller fishes allow higher employment (Fig. 2.5.d.). However, the top species metabolic rate has a different influence on the biomasses sensitivity in this market-driven scenario. In the managed scenario, the sensitivity of the three biomasses was higher with big fishes because the top species could not eat fast enough to regenerate under the constant fishing effort. In this scenario, basal and intermediate species biomasses are more sensitive with smaller carnivores, because in this case top species biomass does not depend on its metabolic rate, but its total grazing does.

The openness has no influence on the equilibrium values. It only changes the transient frequencies and its duration (results not shown). For low values ($\mu < 0.1$), the decrease of the means and the high standard deviations are due to depletion events: the non-depletion condition (page 13) we took is not efficient anymore for such values of openness. The influence of price is very different depending on whether extraction costs are negligible or are not (Fig. 10.d.). When price and costs are of the same magnitude (p<5, co=1) the equilibrium effort increases with price until it levels off. The smaller the extracted fish, the higher the price for which the plateau is reached.

2.2.4   Open access exploitation with linear price

2.2.4.1 Typical behavior over time - existence of multiple equilibria

In this scenario, asymptotical dynamics are reached quicker than with fixed prices. As with the fixed price model, smaller top species involve higher frequencies for the transient and, if relevant, for the permanent oscillations. This is due to the ability of the top species to eat very quickly, so there is no inertia as with bigger species.

When the price sensitivity to rarity is very low ($b \simeq 0.01$, i.e. the price equals zero when the harvest is $Y = 100\mu gC/L$), the depletion of the top species can occur if a and $B_T(t = 0)$ are too high. This is very similar to the fixed price scenario (page 13): the sensitivity to rarity is too low to allow the price to decrease significantly when the harvest is high and the situation dangerously profitable. For higher sensitivity values however, depletion cannot occur because gold rushes cannot either: if effort is suddenly increasing because there is huge profit to make, the price will crash down and prevent the fisheries to harvest the whole species.

Multiple asymptotical dynamic regimes were highlighted, depending on the biological and economic parameters values and the initial conditions. As in the fixed price scenario (page 13), equilibria or limit cycles can occur. Within the linear price model, there are three possibilities for the equilibrium/averaged biomasses and effort: 1) top species depletion. This happens only for low price sensitivity, high maximum price and high initial top species biomass (see above). 2) "economic" regime, with low top species biomass ($\simeq 1\mu gC/L$) and rather high effort ($\simeq 10$). The price is almost always at its maximum and dynamics is similar to the fixed price scenario.
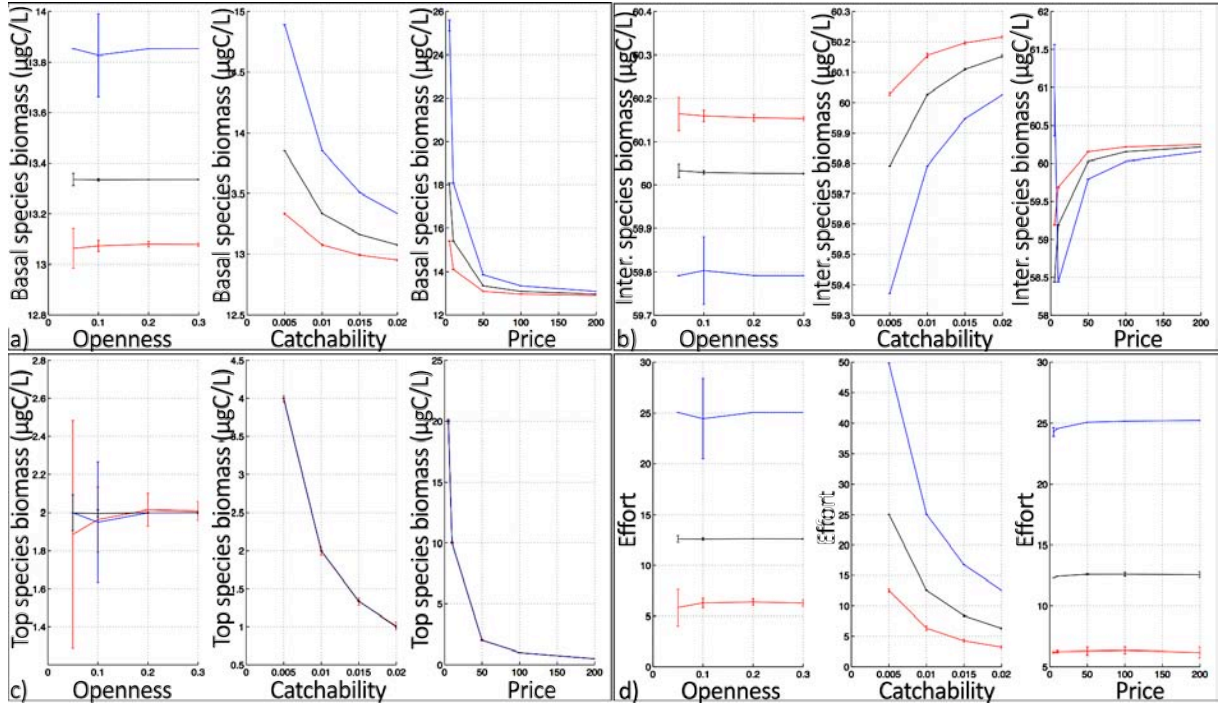
Figure 2.5: Influence of the openness μ (left panels), the catchability q (middle panels) and the price (right panels) on the average of a) basal species biomass, b) intermediate species biomass , c) top species biomass and d) effort, over the last 400 of 5000 time steps in the market driven scenario with fixed prices. Simulations for three top species metabolic rates: 0.02 (red line), 0.04 (black line) and 0.08 (blue line). Parameters are set as in Table 2.1, with $x_I = 0.15$. For each set of economic parameters, 40 simulations were run, with random initial conditions, taking into account the non-depletion condition (page 13). Means and standard deviation over theses 40 simulations are shown.

An example is displayed on Fig. 2.6.a. red line. 3) "biological" regime, with high top species biomass ($\simeq 10^2 \mu gC/L$) and low effort ($\simeq 1$). The price is always very close to zero. In this case, the top species is so abundant in the ocean that a little effort is enough to get a very cheap fish on the market. Thus, the biology drives the dynamics. An example is showed on Fig. 2.6.a. blue line.

Simulations have shown that the "biological" regime is reached only with a high initial top species biomass and a low initial effort (results not shown). In this case, the fisheries never harvest a significant fraction of the top species biomass. Thus, the carnivore can grow peacefully. However, if the initial top species biomass is lower and/or the effort higher, the final regime will be the "economic" one (Fig. 2.6.a. red line), for which the resource is almost over-exploited, as in the fixed price scenario (page 13).

The study showed that the initial biomasses of the basal and intermediate species had a nonlinear influence on the thresholds between the multiple basins of attraction (results not shown). To free ourselves from such an effect in the following study, we launched simulations with extreme values of effort and top species biomass: $E(t = 0) \in \{1, 100\}$ and $B_T(t = 0) \in \{1, 600\} \mu gC/L$. The two other initial biomasses were randomly chosen. If only one equilibrium was highlighted, we considered that even if the other equilibria existed mathematically, they could not be seen in nature.

2.2.4.2 Influence of the metabolic rate and the price parameters

We studied the impact of the top species metabolic rate and the two price coefficients on the number and type of equilibria that can be reached within the range of reasonable initial conditions (Fig. 2.7). The regime with total depletion is observed only for very low sensitivity
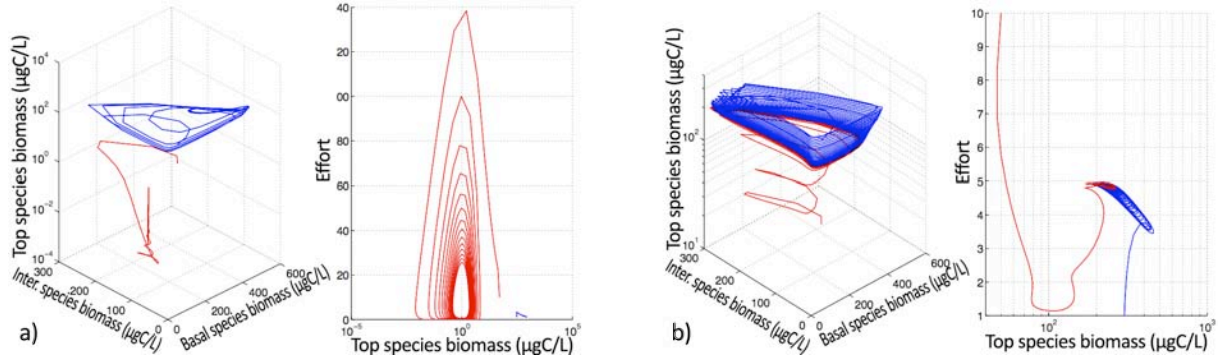
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Figure 2.6: Phase diagrams over 1000 time steps of the three biomasses (3D curves), and of the effort and the top species biomass (2D curves), in the market driven scenario with linear price. Parameters are set as in Table 2.1, with $x_I = 0.15$, $x_T = 0.02$, $\mu = 0.3$, $q = 1\%$, $c_o = 1$, $B_B(t = 0) = 100\mu gC/L$ and $B_I(t = 0) = 25\mu gC/L$. The blue lines correspond to a high initial top species biomass ($B_T(t = 0) = 300\mu gC/L$) and low initial effort ($E(t = 0) = 1$), whereas the red lines correspond to a lower initial top species biomass ($B_T(t = 0) = 50\mu gC/L$) and a higher initial effort ($E(t = 0) = 10$). The price parameters were set as follows: a) $a = 100$ & $b = 0.1$, and b) $a = 1$ & $b = 0.05$.
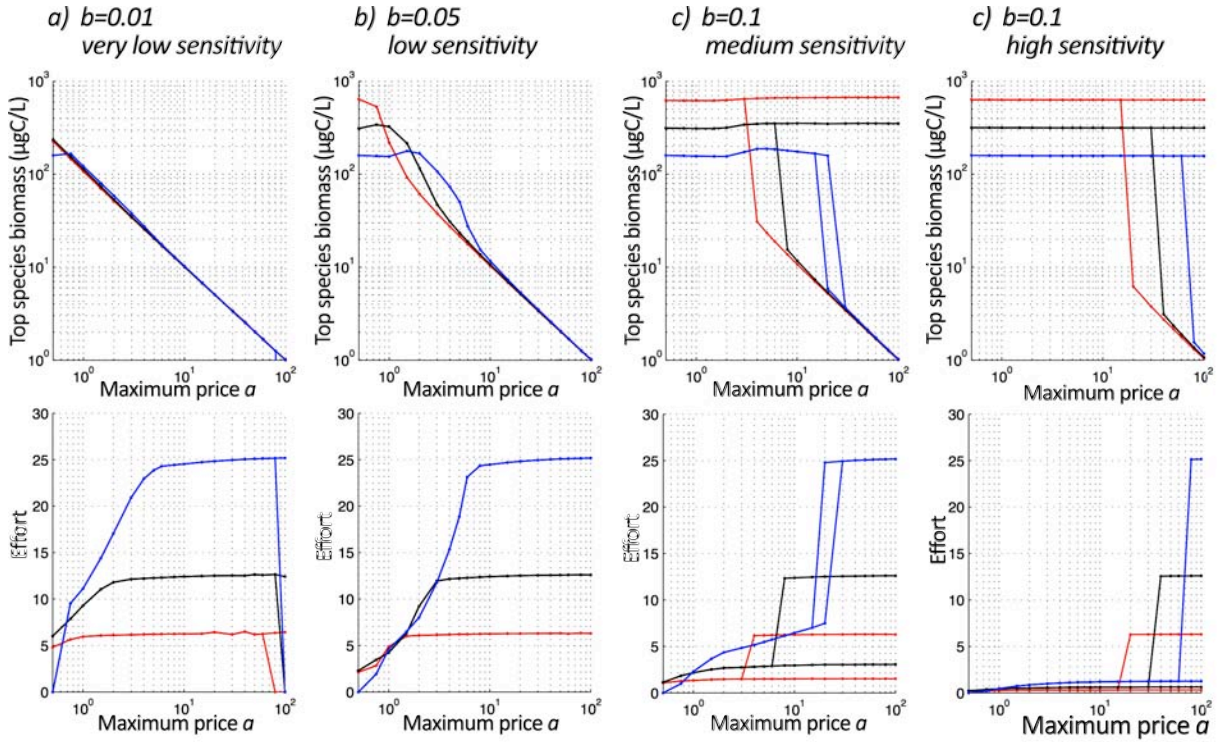

Figure 2.7: Asymptotical top species biomass (top) and effort (bottom) in the market driven scenario with linear price model as a function of the maximum price a. Top species metabolic rate was varied between $x_T = 0.02$ (red line), 0.04 (black line), 0.08 (blue line), and the sensitivity of price to rarity b among 0.01 (a), 0.05 (b), 0.1 (c), 0.5 (d). For each set of x_T, a and b values, we chose the initial effort and top species biomass among $E(t = 0) = 1$ or 100, and $B_T(t = 0) = 1$ or $600\mu gC/L$, in order to highlight, when relevant, the multiple equilibria. Basal and intermediate species initial biomasses were chosen randomly between $5 - 500\mu gC/L$ and $2 - 200\mu gC/L$. We ran 10 simulations for each set of initial conditions, then took the mean over the simulations. All the other biological parameters were set as in Table. 2.1, and the economic parameters were $\mu = 0.3$, $q = 1\%$ and $c_o = 1$.
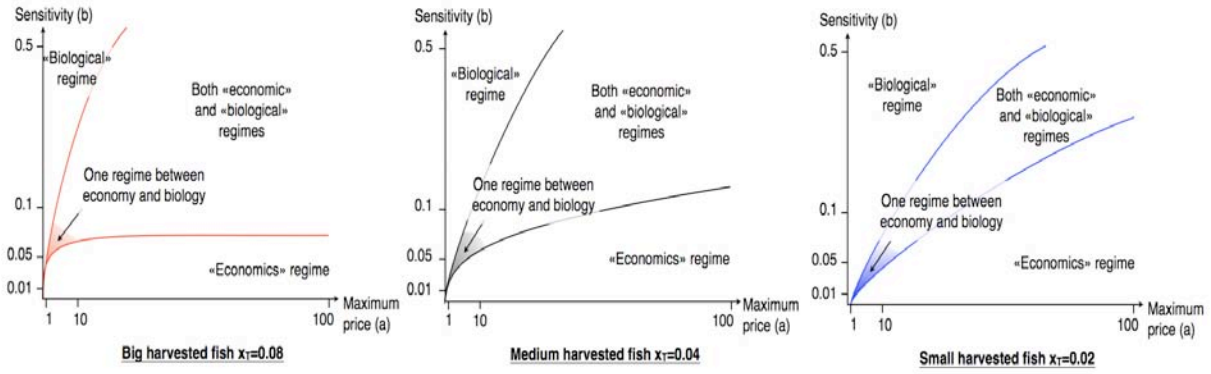
Figure 2.8: Influence of top species metabolic rate and the two price parameters on the number and nature of the asymptotical regimes in the driven market scenario with the linear price model. This diagram has been drawn from the results of Fig. 2.7.

($b = 0.01$) and very high prices. The two other regimes (low biomass & high price, and high biomass & low price) actually correspond to respectively the "economics" and the "biological" ones. Depending on the top species metabolic rate x_T, the price sensitivity b and the maximum price a, only one of these regimes or both of them can be observed.

When the economics drives the dynamics, the x_T has no influence on the top species biomass, as in the fixed price scenario (page 15). Economics rules because the extracted fish density and the harvest are low enough to allow a high price, close to its maximum. The top species equilibrium biomass is then $B_T^* \sim c/(qa)$. This value is independent of the metabolic rate, and inversely proportional to the a coefficient. The effort, however, is proportional to the metabolic rate. Finally, the a coefficient has no big influence on the effort. Actually, this situation where economics rules the system dynamics is completely similar to the fixed price scenario.

When the biology drives the dynamics, the maximum price a has no effective influence on the biomass because fishes are so abundant that the systems is always close to zero price. The metabolic rate, however, plays an important role: top species biomass is inversely proportionate to its metabolic rate. Thus, the asymptotical regime is mostly determined by the harvested species metabolism. The influence of a and x_T on the asymptotical effort is as when economics is ruling. The harvest, however, is completely independent of both price parameters and top species metabolic rate, and is just proportional to the catchability.

The impact of top species metabolic rate and the two price coefficients on the nature and number of final regimes has been summarized on Fig. 2.8. On the one hand, the system reaches only the "economics" regime for low price sensitivity. The higher the maximum price, the higher the maximum allowed sensitivity. On the other hand, the system reaches only the "biological" regime when the price cannot be very high (low a values). The higher the sensitivity of price, the higher the maximum a allowed. For a and b values between to two former areas, both "economics" and "biological" regimes are possible, depending on the initial conditions (see previous section). It could then be possible to chose the final regime through the allocation of the initial effort. This area narrows when the top species metabolic rate increases. So harvesting smaller fishes might allow higher employment but reduces the range of the price parameters for which management of the fisheries is possible. Finally, for low values of a and b, only one regime can be seen, which is not completely economically oriented, nor only biologically. In this case, both the top species metabolic rate and the maximum price have an influence on the top species biomass and the effort. An example of such an asymptotical regime has been plotted on Fig. 2.6.b.

Chapter 3

Complex food webs

3.1 Methods

3.1.1 Model structure

We analyzed systems with higher complexity than with the previous 3-species food chain, to see if the phenomenons we highlighted with the simple food chain were increased or, on the contrary, lessened within food webs. We studied the impact of fishing at high trophic levels and subjected these systems to only one basic scenario: the managed one with fixed exploitation effort.

Following William & Martinez (2000, 2008), food webs were simulated using the *Original Niche Model* (ONM) which has two input parameters: the number of species S and the connectance $C = L/S^2$ (Martinez 1991), where L is the number of trophic links. In the ONM, a uniformly random "niche value" ($0 \leq n_i \leq 1$) is assigned to each species. Consumer i eats only prey species whose niche values are contained within a range r_i, whose center c_i is less than the predator's niche value n_i. The niche center c_i is randomly chosen from a uniform distribution between $r_i/2$ and $min(n_i, 1 - r_i/2)$. The niche range is calculated as follows: $r_i = xn_i$, where x is a random variable defined on $[0, 1]$ with a beta-distributed probability density function $p(x) = \beta(1 - x)^{\beta-1}$ with $\beta = 1/(2C) - 1$.

To be able to compare the food webs obtained from the ONM, we used 17 structural network properties (William & Martinez 2000, 2008, Dunne *et al.* 2002, 2008): Top, Int, Bas are the proportions of species that are respectively without predators (top), with both predators and preys (intermediate), and without preys (basal); Can, $Herb$, Omn and $Loop$ are the fractions of species that are cannibals, herbivore (only basal preys), omnivores (i.e. feeding on multiple trophic levels) and involved in loops (apart from cannibalism); $ChLen$, $ChSD$ and $ChNum$, the mean length, standard deviation of length and log number of the food chains; TL, the mean trophic level; $MaxSim$, the mean of the maximum trophic similarity of each species; $VulSD$, $GenSD$ and $LinkSD$ are the normalized standard deviations of vulnerability (number of predators), generality (number of preys) and total links; $Path$ is the mean shortest food-chain length betwenn two species and $Clust$ is the clustering coefficient (Watts & Strogatz 1998).

The population dynamics within the food webs were simulated using the same Allometric-Trophic-Network model as in Chapter 2 (page 6):

$$
\begin{cases}
\dot{B}_i = r_i(1 - \sum_{j \in autotrophs} \frac{B_j}{K})B_i - \sum_{j \in consumers} x_j y_{ji} B_j \frac{F_{ji}}{e_{ji}} & (3.1) \\[3ex]
\dot{B}_i = -x_i B_i + \sum_{j \in resources} x_i y_{ij} B_i F_{ij} - \sum_{j \in consumers} x_j y_{ji} B_j \frac{F_{ji}}{e_{ji}} - \sum_{k \in firms} q_k E_{ki} B_i & (3.2)
\end{cases}
$$

$$F_{ij} = \frac{\omega_{ij}B_j^h}{B_0^h + cB_iB_0^h + \sum_{k\in resources}\omega_{ik}B_k^h} \tag{3.3}$$

Eq. 3.1 and 3.2 decribe the changes in the biomass densities of, respectively, an autotroph and an heterotroph species. In these equations, r_i is intrinsic growth-rate of basal species i, K is the carrying capacity shared by all the basal species, x_i is i's metabolic rate ($x_{basal} = 0$, Brose *et al.* 2006), y_{ij} is the maximum consumption rate of i eating j, e_{ij} is i's assimilation efficiency when consuming j. We used a weak Holling-type III functional response (eq. 3.3). B_0 is the half-saturation density, h is the Hill exponent, c is the predator interference and ω_{ij} is i's relative inverse attack rate (i.e. i's preference towards j).

3.1.2 Parameterization and sensitivity analysis

We used the above model to explore one of the three basic scenarios from Chapter 2: the managed scenario with a fixed exploitation rate. We explored the effects of fishing only one or several species at a time, the effects of body size by adding stochasticity in the allometric allocation of metabolic rates x_i, and of the structural properties of the food webs.

Table 3.1 describes the values and units of the ecological parameters. In order to use a consistent parameterization, most of the values are from the study of lake Constance (Boit *et al.* in prep.). The food webs were simulated for $S = 30$ species and $C = 15\%$ of connectance ($S = 24$ and $C = 18\%$ in lake Constance). Basal species intrinsic growth rates were varied between 0.6 d^{-1} and 1.2 d^{-1} (Boit *et al.* in prep.) using a normal distribution with a mean of 0.6 and a standard deviation of 0.2.

Table 3.1: Ecological parameterization

Name	Description	Unit	value	Reference
S	Number of species	-	30	Boit *et al.* in prep.
C	Connectance	-	0.15	Boit *et al.* in prep.
K	Carrying capacity of basal species	$\mu gC/L$	540	Boit *et al.* in prep.
r	Basal species growth rate	d^{-1}	0.6 - 1.2	Boit *et al.* in prep.
y_{ij}	Maximum grazing rate of consumer i relative to its metabolic rate	d^{-1}	10	Boit *et al.* in prep.
e_{ij}	Assimilation efficiency for carnivores / herbivores	-	0.85 / 0.66	0.85: Yodzis & Innes 1992; 0.66: Nielsen & Olsen 1989
B_0	Half-saturation density of j when consumed by i	$\mu gC/L$	80	Muck & Lampert 1984
c	Predator interference	-	0	
ω_{ij}	Relative inverse attack rate	-	$1/\sum i' s resources$	
h	Hill exponent	-	1.2	Williams & Martinez 2004

List of ecological parameters and their description. The parameters not listed were varied across the simulations (see Methods).

For each food web, the metabolic rates of non-basal species ($x_{basal} = 0$, Brose *et al.* 2006) were calculated using species trophic levels TL_i. We used two definitions of trophic levels: on the one hand, $T1_i$ is the length of the shortest path from species i to a basal species. On the second hand, $T2 = (I - Q)^{-1} \cdot \mathbb{1}$ (Levine 1980), where Q is the weighted niche web matrix: $Q(i, j) = 1/\sum preys(i)$ if i eats j, and equals 0 if not. We took the mean over these two definitions: $TL_i = (T1 + T2)/2$. The basal species body-masses were set to unity as a reference. The body masses of predators were calculated using the average predator-prey body-mass ratios, Z: $M_i = Z_i^{TL_i - 1}$. Z was sampled from a log-normal distribution, with a distinction between fishes and invertebrates (mean=100 & SD=50 for ectotherm vertebrates, mean=10 & SD=100 for invertebrates; *Brose et al.* 2006). Species with trophic levels lower than 3 were always considered

as invertebrates, whereas a species with a trophic level greater than 3 had 60% of probability to be a fish. Finally, the metabolic rates follow negative-quarter power-law relationships with the species body masses $x_i = 0.314 M_i^{-0.24}$ for invertebrates and $x_i = 0.88 M_i^{-0.24}$ for ectotherm vertebrates (Brose *et al.* 2006).

If unspecified, collections of biomass densities were chosen from a uniform distribution in the ranges 5-500 $\mu gC/L$. Before every simulation with economic exploitation of a species, we let the system evolve without harvesting over 2000 time steps, in order to modelize the arrival of a new fishing economy in a stable ecosystem. Around 25% of the species go extinct during this first period (extinction threshold was set at 10^{-6} $\mu gC/L$), due to the instability of the initial conditions. We only selected webs for which the final networks, after 2000 time steps, were still connected. As the effort was always fixed, we set the catchability to 1% and then considered the effort as the effective percentage of extracted biomass.

We used the same procedure as with the simple three-species food chain (page 7), to see if any hydra effect would be highlighted with bigger webs. For each food web, the species to harvest were selected among the three species with the highest TL_i/x_i, in order to select big species at high trophic levels. We compared four scenarios: in the first three scenarios, only one of the three selected species was harvested. For each species, we draw a comparison with the one-species logistic-growth model. Its carrying capacity K was estimated as its biomass without exploitation, and the intrinsic growth rate calculated from the species metabolic rate: $r = x(y-1)$. In the fourth scenario, the three species were harvested simultaneously and at the same exploitation rate. The percentage of extracted biomass was varied between 0% and 100%.

We analyzed 100 food webs with a mean number of species of 25.5 (SD=2.0) and a mean connectance of 15.8% (SD=1.2%). Each time, the 17 structural properties of the web were calculated (page 19), and also the metabolic rate of the harvested species, its trophic level, whether it is a fish or an invertebrate, if it is a top, an intermediate, an hervibore and/or a cannibal species. Finally, we calculate the local structural properties of the web: vulnerability, gerenality and connectivity of the harvested species, of its preys and of its predators.

We conducted 120,000 simulations, each lasting 2000 time steps. Our analyses focused the means of the biomasses during the last 400 of the 2000 time steps, in order to make a comparison with the results from the 3-species food chain. Among our simulations, no large, slow oscillations emerged which might have motivated analyses of more than 400 time steps. All simulations were performed in Matlab version 6.5 and 7.10 using ode45 for ODEs with the default settings. The food webs were plotted with Network3D software (Yoon 2004).

3.2   Results

We selected 200 food webs for which the system after 2000 time steps without harvesting is a fully connected network with at least 22 species. Within each web, the three biggest species with the highest metabolic rates were harvested, following the managed scenario with fixed exploitation rate.

3.2.1   The managed scenario - Harvesting only one species at a time

When the initial biomass of the species to harvest (i.e. after the stabilization of the system when $E = 0$) is lower than 10^{-3} $\mu gC/L$, the species goes extinct as soon as the effort is non-zero because even a low exploitation rate is enough to bring the biomass closer to the extinction threshold (10^{-6} $\mu gC/L$). The system has no time to recover before the threshold is crossed.
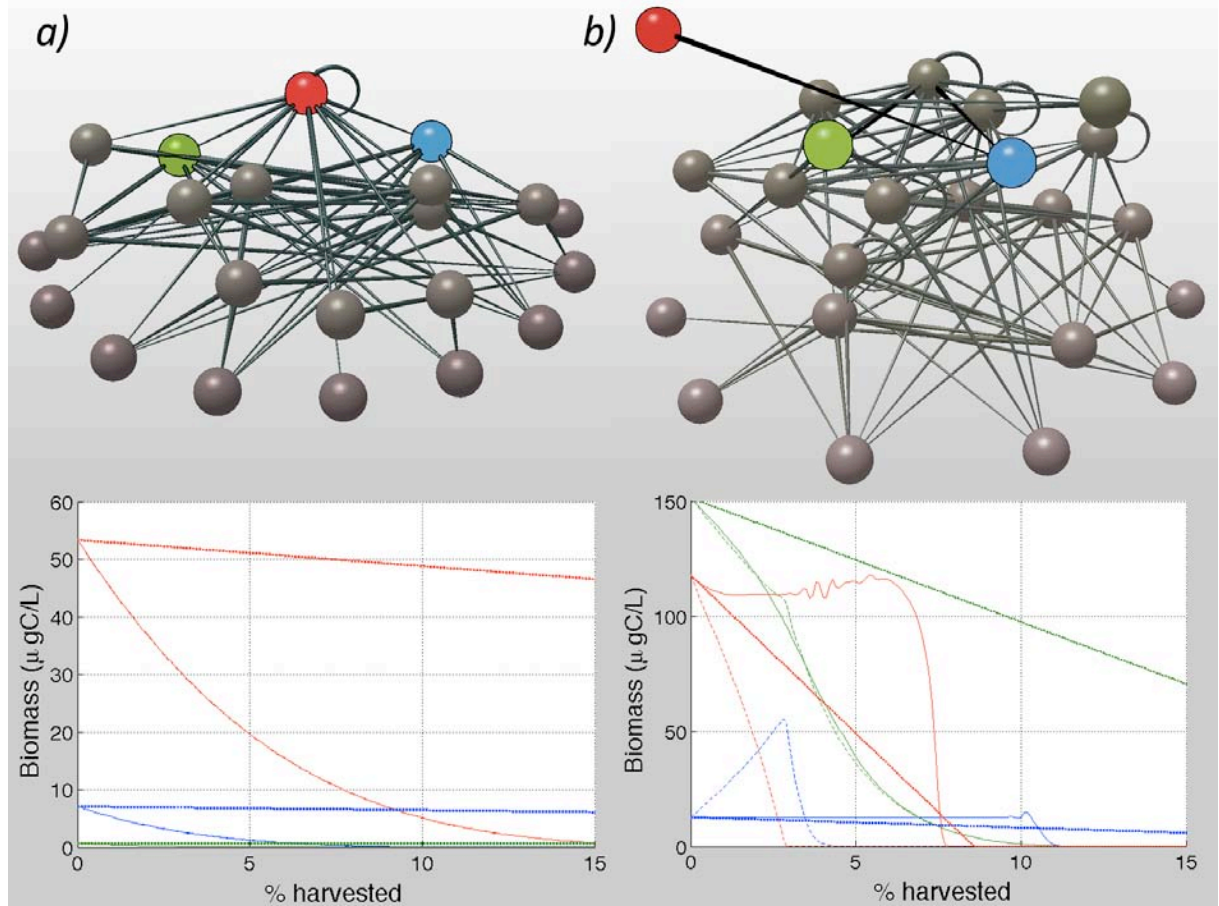
Figure 3.1: Managed scenario for two examples of foodwebs. Top: the structures of the webs are displayed in 3D using Network3D software, starting with basal species at the bottom. The height of each species corresponds to its trophic level. The three species that are harvested are highlighted in color. Bottom: biomasses as a function of the exploitation rate, when only one species at a time is fished (solid lines), when the three species are fished together (dashed lines) and when each species is modelized as an isolated species with a logistic growth function (dotted lines). The colors coincide with the 3D structure colors.

So within our model, it is impossible to create a sustainable managed economy based on the exploitation of an initial rare species. This would be the case if the species was estimated as very valuable because of its rarity in nature (Courchamp *et al.* 2006).

For most of the others harvested species that are not on the verge of extinction even when not harvesting, the shape of the relationship between the fraction of biomass harvested and the biomass density is almost always the same: the biomass strictly decreases when the effort increases, and the curve is often convex. In this case, the extinction occurs for exploitation rates lower than 20%. An example of such a behavior is displayed on Fig. 3.1.a. (solid lines).

Over the 100 analyzed food webs, there is only one for which an hydra effect has been highlighted (Fig. 3.1.b., red solid line). An analysis of the web structure showed that this network had a local food chain structure: the red species has no predators and eats only the blue species, which has only one other predator that is less abundant than the red species. When the red species is harvested, a hydra effect occurs for low exploitation rates, exactly as when fishing the carnivore of the 3-species food chain. The asymptotical regime is a limit cycle, whose mean biomass is higher than when $E = 0$, and the reason of this behavior is the same as in Chapter 2 (9). As the blue species second predator is scarce, it has a significantly smaller effect on the blue species than the red harvested one has. When the blue species is exploited, its
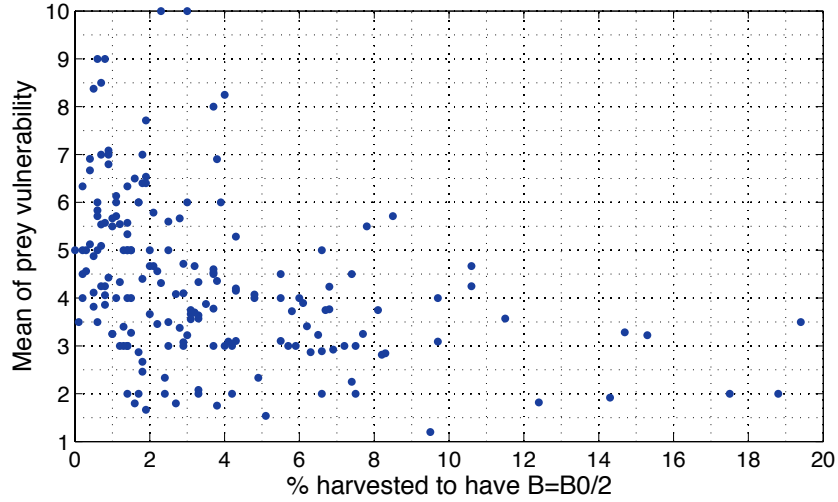
Figure 3.2: Influence of the vulnerability of the preys of the harvested species on the speed of extinction in the managed fishery scenario. The speed of extinction was estimated as the minimal fraction of biomass harvested for which the fish stock is half of its maximum value. We used the results from the 100 webs when harvesting only one species at a time.

equilibrium biomass is constant over a wide range of exploitation rates: it is the red species that actually shrinkens because of the increase in its unique resource exploitation. The total pressure from both the red species and the harvest is constant and the red species biomass decreases linearly with the exploitation rate (results not shown) until its goes extinct. Then the blue harvested species biomass suddenly goes extinct because of the high exploitation rates. Such a behavior has also been seen within the 3-species food chain, when harvesting the herbivore in presence of the carnivore (results not shown).

No other hydra effect has been highlighted because of the local structure of the web around the harvested species. Indeed, hydra effects can occur only when the local web has food chain properties, or when the preys vulnerabilities are very low (the harvested species is then their principal predator). Otherwise, the increase of the harvested species mortality would reduce the grazing pressure on the preys that would consequently increase in biomass, but then all their other predators would benefit from this increase and interfere with the harvested species.

The harvested species metabolic rate has an effect on the sensitivity of the biomass to the exploitation rate, since higher metabolic rates allow wider ranges of sustainable exploitation (i.e. without species extinction, results not shown). This is due to fact that harvested species with higher metabolic rates involve, on the whole, a higher grazing pressure on their resources. Thus, a higher exploitation rate is needed to counterbalance this high grazing pressure. This result is similar to the one for the 3-species food chain.

Their seems to be no correlation bewteen the species sensitivity to the exploitation rate and the 17 structural properties of the global webs. No effect of the local properties of the web around the harvested species has been seen either (results not shown). Only the preys vulnerability influences the species sensitivity to the exploitation rate, since low preys vulnerabilities allow wider ranges of sustainable exploitation (Fig. 3.2). If a harvested species eats very vulnerable preys, then there is competition with the other predators of its preys. With higher exploitation rates, the grazing pressure from the harvested species on the preys decreases but the exploited species cannot benefit from the ensuing increase of its preys biomasses: the other predators have already eaten the surplus.

The comparison with the one-species logistic-growth model leads to the same conclusion as with the 3-species food chain: the simpler model strongly over-estimates the biomass of the

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harvested species. When the species goes extinct according to our ATN model, its biomass is supposed to be at 85% of its maximum value according to the logistic-growth model (Fig. 3.1.a., solid & dotted lines). Thus, the harvested species is effectively more sensitive to a change in the management of the fisheries, through the exploitation quotas, than it could be assumed from the one-species with logistic growth model.

3.2.2 The managed scenario - Harvesting several species together

In this scenario, the three biggest species with the highest trophic levels were exploited together, always with the same fraction of biomass harvested. Most of the time, the shape of the relationship between the exploitation rate and the standing stock of is the same as when harvesting only the concerned species. It is the case when the species to harvest are too remote from each other in the web. It also occurs when the concerned species share some preys and/or some predators, or are even connected through a trophic link, but their trophic similarity remains low (Fig. 3.1.a., solid and dashed lines are merged). That way, the effects of fishing one species is redistributed amongst all its neighbours so that the eventual interferences between two harvested species are negligible.

Interferences were highlighted only when the initial biomasses of the concerned species were of the same range ($max(B)/min(B) < 100$), otherwise only the effect of the most abundant species can be seen. The effect of fishing three species together was different from the effect of fishing a unique species only for very specific local structure of the food webs around the harvested species.

When there is a high trophic similarity between the exploited species, the effect of harvesting might be slightly lessened. For example, in one of the studied webs, the 3 harvested species share the exact same predators and have lots of their preys in common. So exploiting the three of them helps all their resources increasing in biomass. Thus, the exploited species growth factor increases too and compensate partially the increased mortality due to harvesting. In this case, fishing several species is better than fishing only one at the same exploitation rate since the biomass is higher. Such a behavior occured for 10% of the webs.

When there is a direct trophic link between two of the harvested species with the most abundant harvested species eating a scarce one, interferences might also occur. Fishing those two species reduces the effect of on the scarce prey because the grazing pressure on the prey decreases a lot due to the increased exploitation rate of the very abundant predator and partially compensates (or sometimes even over-compensate) its own increased exploitation rate. Such a phenomenon was highlighted for 14% of the studied webs. An example is displayed on Fig. 3.1.b. (dashed lines). This food web has a local food chain structure. The red species has no predators and eats only the blue species, which is also eaten by another, though very scarce, predator. Exploiting both the blue and the red species involves an important increase of the blue-prey biomass and a decrease of the red-predator biomass.

To sum up, there might be interferences when harvesting several species together only for very specific local structures and initial biomasses. Sometimes, it is advantageous for one species to be harvested simultaneously with other species rather than alone. It might either reduce the effect of exploitation or even sometimes lead to an over-compensation of the exploitation. Thus, it is sometimes possible to manage the fishery by chosing the number of harvested species and their exploitation rates.

Chapter 4

Discussion

As fisheries might decrease the body-masses of the exploited species with up to a factor of 3 (Chapman & Kramer 1999), we explored how the body-size affects, the fisheries potential profit, employment and standing stock. Without exploitation, there is a range of body masses of the interacting populations which maximizes their biomass density. In the context of the fisheries for the small food chain, the log_{10} body-mass ratio of the exploited predator and its prey was 0.54 in the pristine scenario, which falls within the lowest range found in nature (Brose *et al.* 2006). Fisheries shift this value to an even lower range (0.27) by decreasing the body-mass of the top species. We show that this shift results in a decreased of up to 75% of the biomass density of the top species. This effect is strongly nonlinear as a small shift in the body-mass ratio resulted in a relatively large decrease in the top species biomass. This suggests that even if the fishery stops operating in an area, the recruitment of the previously exploited populations may be hindered because of modified predator-prey body size ratios.

We drew comparisons between the logistic-growth model and the ATN model, which used the logistic model only for species at the base of ecological networks; species at higher trophic levels, such as fishes, were modeled by making their capacity for growth depend on food resources. The logistic-growth model always under-estimated the effect of fisheries in the managed scenario: the yield is supposed to be maximized when the exploitation rate equals half its intrinsic growth rate ($B = K/2$ then). For such a rate, our ATN model always involved the complete depletion of the harvested species. Besides, when the extracted species goes extinct according to our ATN model, its expected biomass from the logistic model is still at 66% of the carrying capacity within the 3-species food chain, and at 85% for the bigger webs. Thus, the more complex the studied web, the higher the under-estimation of the fisheries effects. Most of the economic studies of fisheries use logistic growth model with fixed carrying capacities. Even if some of them complicate the models using Lotka-Volterra forms of predation with maximum three species, or space fragmentation with migration between the méta-populations (May *et al.* 1979, Conrad & Smith in prep.), none of them use simultaneously non-fixed carrying capacities and non-linear functional responses in complex webs. So the conclusions that are drawn from those models about fisheries management under-estimate the effect of fisheries.

The study of the managed and market-driven scenarios wihtin the three-species food chain lead to several interesting phenomenons: hydra effects (for which the standing stock of the harvested species and the profit of the fisheries can be maximized simultaneously) were highlighted within the managed scenario. When the price was fixed or hardly elastic in the market driven scenario, a wrong initial price allocation could involve the resource depletion. When the price was more sensitive to the quantity of fish on the market, mutli-equilibria and limit cycle were highlighted with either the economy, the biology, or both of them driving the dynamics.

The main result from the managed scenario is the consequence of the hydra effect that occurs for low values of the exploitation rate: it is possible to maximize simultaneously the harvested biomass and the profit. Though no hydra effect has already been seen in nature (Abrams 2009), many theoretical studies have highlighted such a phenomenon. According to Abrams (2009), there are 3 typical cases where a hydra effect can occur: "altered population fluctuations", "temporal differences between the action of density-independent mortality and the density-dependant processes that counteract it", and when "mortality leads to more prudent resource exploitation". The hydra effects from our ATN model are due to both the first and the second case: they occurred only when a limit cycle was reached, allowing the functional responses of the harvested species and of its prey to fluctuate over a significant range, both of them being decorrelated in time. Sieber & Hilker (2011) linked the hydra effect to the existence of cycle dynamics, for example if a slow predator eats a fast prey, which is the case in our model. They also pointed out that the systems needed functional responses with a saturation effect to allow hydra effect (Holling-type II or III, but not type I or Lotka-Volterra models).

In the variable effort scenario, dynamics could be of very different kinds depending on what drove it: economy, biology are both of them. The asymptotical regimes for the harvested species biomass and the effort would then be drastically different. Thus, little changes in the economic parameterization (e.g. the price) might involve a shift from one kind of regime to another, and therefore lead to big changes in employment and fish density.

With more complex food webs, the behavior of the system in the managed fishery scenario was most of the time simpler than what could have been expected. Apart from a few special cases, the harvested species biomass monotonically decreased when the exploitation rate increased, whereas multiple regimes were highlighted for the small food chain. This idea of how more complexity might lead to more simplicity tallies with previous studies of complex food webs (Berlow *et al.* 2009). Actually, the response of the system to an increased exploitation rate depends more on the local properties of the web such as the harvested species metabolic rate and its preys vulnerability, than on the global structure of the web. Previous studies of species removal (Berlow *et al.* 2009) also showed that the effect of increased mortality spread mainly on the concerned species first neighbours, perhaps even the second neighbours, but the global repartition in biomass of the whole webs was not affected.

Contrary to the small food chain, the complex food webs never allowed any hydra effect, except for a peculiar web with a local food chain structure. We saw that when hydra effect occurred, the prey of the concerned species increased significantly. If the prey had several species, the other predators benefited from this increase, so that the subsequent increase of the harvested species? growth factor did not over-compensate the increased mortality anymore. However, fishing several species together might lessen the exploitation effect for one or all the harvested species. The multispecies fisheries might even lead to an phenomenon similar to the hydra effect: one of the harvested species benefits from the harvest of another and it over-compensates its own exploitation. These interferences between the exploitations of multiple species occurred only when the species had a high trophic similarity or when they were linked with a trophic relationship. Harvesting several species together is now common in the fisheries economy (Pauly *et al.* 1998) and especially predators and preys are more and more harvested together. Thus, our multispecies fisheries scenario is relevant to real economies.

Our analysis focused on several economic scenarios for the fisheries: managed, for which the government set fishing quotas and market-driven, for which the fishing effort increases and decreases as a function of profit and loss. Within all scenarios, we showed that higher employment was allowed for higher harvested species? metabolic rates, and consequently smaller fishes. Several

strategies may be adopted depending on the scenario.

For a managed fishery, harvesting small fishes allows higher employment and less risk of sudden extinction of the resource. If the price is fixed (or not very sensitive to the harvest) and extraction costs non-negligible, fisheries have to chose between low employment with high profit and high risk of extinction (big fishes), and high employment with lower profit and a less endangered species (small fishes). If the costs are negligible, fisheries should harvest only small fishes because they lead to the same maximum profit and higher employment. If the price is very sensitive to the harvest and the costs negligible, the fisheries can chose between two peaks of profitability: a very low employment and a safe species, or a high employment and a very endangered species. If costs aren?t negligible anymore, only the first peak is profitable.

For a market-driven fishery with fixed or not very elastic prices, the allocation of the price is critical because a too high initial marginal profit leads to the harvested species depletion. If fisheries manage to prevent the extinction, fisheries have to chose either high employment with high yield and a system in jeopardy (small fishes), or lower employment and yield but a less sensitive system (big fishes). If the price is more sensitive to the harvest, multi-equilibria are possible. One is driven by the economy and similar to the fixed price scenario. The other one is driven by the biology, with an abundant species and a very low employment. Within a range of price parameters (wider for big species), fisheries may choose the equilibrium they want.

Within a multispecies fishery, the selection of the species to harvest also determine the final equilibrium, profit and employment. Thus, with a good management of the fishery, it is possible to optimize either employment, yield, profit, biomasses or to minimize the risks of extinction. Often, fisheries may optimize several or even all of these criteria. On the contrary, a bad understanding of the system may lead to the harvested species extinction, or a much endangered species, so that a very small change in the economic strategy of the firm could have irreversible consequences.

This study of the exploitation of marine food webs was limited by the usual issue of too many dimensions that prevent a very thorough analysis. Besides, many other scenarios should be analyzed to completely understand the effects of the fisheries. We only studied the market-driven scenario for fixed and linear prices. It would be interesting to know whether the other price models strengthen or lessen the phenomenon's we highlighted, or whether they lead to completely different behaviors. For instance, the isoelastic model allows the price to reach the infinity. This fits within the necessary conditions that may involve an anthropogenic Allee effect (Courchamp *et al.* 2006).

We could also complexify the economic models, using for example discount prices (Conrad & Smith in prep.). Another relevant point is that government subsidies keep costs of fishing lower than it would be based on catchability or fuel prices (Sumaila *et al.* 2007). It would be very interesting to take this into account for further model development and analysis. We only considered variable costs of fishing. Our model should refer to constant costs, that would describe the maintenance costs of boats even when they are not in the sea, for instance. As lots of our asymptotical regimes involve big permanent oscillations similar to gold rushes, such constant costs might just induce the end of the fishery economy.

Finally, ony few simulations were performed for big webs. The driven-market scenario sould also be studied. When multiple species are harvested, it would be interesting not to set the same effort for all species, but to make the exploitation rates vary independently for each species. Moreover, all our analyses focused on the economy of only one firm. Further development of the model could consider several firms exploiting the same ecosytem. We would then start modeling systems that are both ecologically and economically complex.

Chapter 5

Conclusion

Our results illustrate a profound difference between expectations based on the extremely simplistic logistically growing populations and the less simplistic i.e., more realistic, ATN models. Under virtually all conditions, fishery exploitation at the optimum rate predicted by the logistic model results in the extirpation of a similarly parameterized species in the ATN models. Given the widespread collapse of fisheries whose management is largely based on logistic population models, our results provide a fairly robust explanation of widespread fisheries failure. Regarding fish body size, larger bodies species can lead to larger amounts of biomass exploited and profit using less effort which means that there is an especially large return on financial investment when exploiting larger bodied fishes. Maximizing profit when exploiting smaller bodies fishes has the advantage of comparatively greater effort which implies greater employment, but at a cost of decreased profit, return on investment, and yield of fish biomass. Our results suggest that the frequent effect of fishing reducing fish body size shifts systems from those optimized by more profitable fishing with less effort to those optimized by less profitable fishing with more effort.

Beyond these very general and relatively crude findings, we also found more subtle results including intriguing "hydra" effects whereby fish standing stock and profit are counter-intuitively increased by relatively small amounts of exploitation, and multiple attractors. The initial conditions determine which attractor the system finds itself in. These attractors generally fall into two categories. One is where low fish prices leads to low exploitation effort and high standing stock of fish. The other is where high fish prices lead to high exploitation effort and low standing stock of fish. When the ecosystem is unmanaged and effort is allowed to be determined by market mechanisms, the latter category can lead to extirpation of the fishes while the latter category can allow sustainable fisheries.

More generally, we found that fisheries scientists and managers should consider more realistic models in order to understand and manage fisheries. While this insight has often been repeated, few realistic models with both scientific affirmed generality and applied specificity have offered to replace the almost ubiquitously used logistic model of fished population growth. Here, we have helped show how such a realistic model can potentially provide an alternative to the logistic model. Future research will help determine whether this potential is realized.

Chapter 6

References and acknowledgements

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